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Cryptogams: Algae

W.F. Prud'homme van Reine and G.C. Trono Jr (Editors)

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Foreword

Many algae from freshwater and marine environments have served as food for South-East Asian people since time immemorial; indeed, the ancient Chinese pharmacopoeia, dating back to at least 4000 B.C. included certain algae for medicinal purposes as well. With burgeoning populations along all coasts of the world, an emphasis on coastal foods has become more important internationally then ever before. Algae are not only used as vegetables or for medicinal or pharmaceutical use, but are also important as producers of phycocolloids and as animal feed. This volume is therefore timely in its approach to record and reveal the nature of the algal resources, their present and past uses by indigenous people of South-East Asia and the potential for technology transfer.

While understanding the economic potential of algae is important, of equal consequence is the basic knowledge of the useful species, their nomenclature, taxonomic, ecological, life history and biogeographical data together with descriptions and illustrations. Without these data together with impressive bibliographic references, no one will adequately know enough to understand what can be expected from these plants, how to regulate their differing life cycles in order to manage them as crops rather than individual plants suitable for 'cottage gardening'. Raising them as crops would help to improve income and living standards of the rural populations of South-East Asia; such knowledge would allow the native peoples to better understand the plants of their region.

This book provides a basic understanding of the differences of these species-rich groups so that an abundance of textures, tastes and colours can be found and modified for specific purposes, from appetizers to soups, salads, entrées and desserts. The industrialized world is the biggest user of colloids extracted from many species of algae; these are principally used as stabilizers, homogenizers, thickeners, and texture and flavour enhancers, while a minor number of uses includes dental moulds, sizing, paints and a large number of decorative additions.

In separate paragraphs 70 genera, species and groups are covered, whereas general aspects of the algae are dealt with in an introductory chapter. The information presented here is the result of a collective effort of many contributors and the approach by the Prosea organization.

This volume will be very welcome and surely will establish a standard to be followed for other regions in the world.

Honolulu, August 2001

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1 Introduction

1.1 Definition and diversity of Cryptogams

1.1.1 Cryptogams

The designation 'Cryptogams' can be used for all organisms that were traditionally considered to be plants, except the *Spermatophyta* (*Gymnospermae* and *Angiospermae*). Although the term 'Cryptogams' does not cover an accepted taxon, it is still the only available terminology that can be used to include all algae, fungi, mosses, ferns and fern-allies, as well as at least some of the organisms now considered to belong to the *Bacteria*.

The Cryptogams form a rather large and very diverse commodity group, with a wide range of uses and can be found growing in many different habitats. In modern systems, *Bacteria* and *Fungi* are usually not included with the plants, although the *Fungi* are still covered by the International Code of Botanical Nomenclature. *Algae* and *Fungi* are included in this volume because they are also dealt with in the basic sources (Burkill, 1966; Heyne, 1927). The *Bacteria* have been added to make the information even more complete.

In the Prosea volume on Cryptogams the following groups will be covered (Margulis & Schwarz, 1982):

- Monera : different groups of bacteria as well as *Cyanophyta* (blue-green algae);
- Fungi : all groups, including the lichens;
- Protoctista : algal groups including *Phaeophyta* (brown algae), *Rhodophyta* (red algae) and *Chlorophyta* (green algae), as well as the fungus-like group *Chytridiomycota*;
- Plantae : mosses, clubmosses, horsetails and ferns.

Marine plants (seaweeds) are included as well as organisms growing as epiphytes in the upper branches of rain forest trees, while some other organisms grow mainly subterrestrially. A minority of the species are cultivated, either under special circumstances (fermenters for bacteria and yeasts), in gardens, plantations (mycorrhizae) or in phycoculture on rafts or lines. Very few cultivars of Cryptogams are known, usually these are ornamental plants or may be seaweeds cultivated for bulk production of phycocolloids. Most of the species of Cryptogams treated here are indigenous, although some introduced species will be included.

1.1.2 Role of Cryptogams

Because the Cryptogams do not form a real entity, it is not possible to completely summarize the commodity use for the different taxa.

Many Cryptogams are eaten in some form, often as a salad or condiment. Others have medicinal applications or form the source of vitamins, phenols, amino acids, iodine, carbohydrates, fats, antibiotic substances or even poisons. In addition, selected species are used as a laxative, vermifuge or insect repellent. Several form sugars, alcohols or colloids; there are even some timber plants or producers of fibres, dyes and tannins found among the Cryptogams. The uses of Cryptogams as feed for animals (including molluscs, shrimps, and some fish) or as a fertilizer or 'green manure' are known, as is the application of plant parts for packing and for wicker-work. Finally there are also Cryptogams that can be used as ornamental plants or as a substrate on which ornamental plants can be grown.

Cryptogams can be found in many different habitats and are often primarily used locally. In these cases they are collected for domestic use or are sold as fresh or conserved material in local markets. Only relatively few products have wider uses or are cultivated for national or international trade. These tend to be bacteria used in industrial processes; seaweeds grown for the production of colloids or for use as vegetables; edible fungi and fungi used in the production of food and drinks, and ferns and other flowerless vascular plants used as ornamentals, or (in the case of the water fern *Azolla* Lamk) as 'green manure'.

Of course collection, culture, handling and yield differ greatly, as well as the effort and capital necessary for successful production. In most cases production can be increased and improved, while sales can be increased through careful promotion and quality control of the end-product. Often the demand for Cryptogamic products is rather limited because of inadequate or lacking quality control and sudden changes in quantities offered. A stable and slowly growing demand is the best possible prospect for use as a commodity.

All representatives of the Cryptogams belong to one or more other commodity groups of the Prosea handbook, as can be seen in Table 1. These groups are listed as 'secondary uses' in the basic list of species and commodity grouping (Jansen et al., 1991).

1.1.3 Grouping of Cryptogams

The Cryptogams in Prosea volume 15 will be treated in the following subvolumes:

– 15(1) Algae	:	* blue-green algae (*Cyanophyta*) * brown algae (*Phaeophyta*) * red algae (*Rhodophyta*) * green algae (*Chlorophyta*)
– 15(2) Ferns and fern-allies	:	* ferns * clubmosses * horsetails * mosses
– 15(3) Fungi and bacteria	:	* fungi (all main groups) * lichens * bacteria

Table 1. Cryptogams arranged according to their use.

Commodity groups	Algae	Ferns	Mosses	Fungi	Bacteria	Lichens
Pulses	–	–	–	–	–	–
Edible fruits and nuts	–	–	–	–	–	–
Dye and tannin-producing plants	x			x		
Forages	x	x				
Timber trees		x				
Rattans	–	–	–	–	–	–
Bamboos	–	–	–	–	–	–
Vegetables	x	x	x	x	x	x
Plants yielding non-seed carbohydrates	(x)	x		x	x	
Cereals	–	–	–	–	–	–
Auxiliary plants	x	x				
Medicinal and poisonous plants	x	x	x	x	x	x
Spices	x			x	x	
Vegetable oils and fats		x?				
Stimulants	x			x	x	
Fibre plants		x				
Plants producing exudates	–	–	–	–	–	–
Essential-oil plants	–	–	–	–	–	–
Ornamental plants		x		x		

Note: x = used, – = not used, blank = no data.

1.1.4 Algae: definition and delimitation

The designation 'Algae' can be applied to all organisms containing the pigment chlorophyll a, except all land plants, i.e. the mosses, ferns and fern-allies and all *Spermatophyta*. Although the term 'Algae' does not cover an accepted taxon, it is still the only available term that can be used to include all of these photosynthesizing organisms.

The algae form a group containing many different taxa, with very different uses and which grow in diverse habitats. In the broadest definition of the Algae organisms that have probably secondarily lost the ability to photosynthesize and their photosynthesizing pigments may also be included. These non-photosynthesizing organisms, however, are not included in the present Prosea subvolume 15(1).

In Prosea subvolume 15(1) on Algae the following taxonomic groups will be covered (Silva et al., 1996; van den Hoek et al., 1995):

- *Cyanophyta* (= *Cyanobacteria*), with representatives of the families *Mastigocladaceae*, *Nostocaceae* and *Phormidiaceae*;
- *Phaeophyta*, with representatives of the families *Chnoosporaceae*, *Cystoseiraceae*, *Dictyotaceae*, *Sargassaceae* and *Scytosiphonaceae*;
- *Rhodophyta*, with representatives of the families *Bangiaceae*, *Bonnemaisoni-*

aceae, *Caulacanthaceae*, *Delesseriaceae*, *Galaxauraceae*, *Gelidiaceae*, *Gelidiellaceae*, *Gracilariaceae*, *Halymeniaceae*, *Hypneaceae*, *Liagoraceae*, *Rhizophyllidaceae*, *Rhodomelaceae*, *Rhodymeniaceae* and *Solieriaceae*;
- *Chlorophyta*, with representatives of the families *Caulerpaceae*, *Cladophoraceae*, *Codiaceae*, *Halimedaceae*, *Monostromataceae*, *Polyphysaceae*, *Selenastraceae*, *Siphonocladaceae*, *Ulvaceae* and *Valoniaceae*.

1.2 Role of algae

1.2.1 Macroalgae, microalgae and their importance

Economic algae are either marine macroalgae (seaweeds) or freshwater and marine microalgae. Commercially interesting microalgae are often either blue-green algae (*Cyanophyta*) or members of the unicellular green algal genera *Chlorella* Beij. and *Dunaliella* Teodor. Commercial resources of algae are often only minor components of the total standing crop of an aquatic flora. These amounts could be improved by cultivation, to the extent that amounts of material under cultivation could far exceed the natural standing stocks. It has been stated that, as a whole, seaweed resources are not greatly exploited (Michanek, 1975). Only about 3.5 million t of seaweeds are used, out of a total biomass which is probably 100 times larger (Jensen, 1993).

Macroalgae

Of the marine algae 107 genera and 493 species have some economic value; mainly macroalgae are used extensively (Tseng, 1981b). The earliest records of the occurrence of *Porphyra* C. Agardh and its food value appeared in books in China published in the years 533–544 A.D. One thousand years ago the Chinese already regarded *Porphyra* as a delicacy to be presented to the emperor annually (Tseng, 1981a). Several surveys of useful seaweeds have been published (Chapman, 1950, 1970; Hoffmann, 1938; Levring et al., 1969; Sauvageau, 1920; Tressler, 1923). In recent years lists of useful seaweeds have also been made available (Arasaki & Arasaki, 1983; Bonotto, 1979; Tokuda et al., 1987). Few lists also contain vernacular names (e.g. Calumpong & Meñez, 1997; Ganzon-Fortes, 1991; Hatta et al., 1993; Zaneveld, 1955, 1959).

Microalgae

Freshwater microalgae and marine microalgae can be grown in closed systems (including heterotrophic systems), tanks, or shallow ponds for the production of health food ('nutraceuticals'), carotenoids, proteins, fine chemicals, or for medicinal uses. Several microalgae are particularly used for the hatchery cultivation of marine molluscs and prawns (de Pauw et al., 1984; Laing & Ayala, 1990; Yúfera & Lubián, 1990). The difficulty of producing economically large quantities of microalgal feeds is currently one of the major impediments to the further development of the aquaculture industry (Apt & Behrens, 1999; Gladue & Maxey, 1994). Microalgae are a genetically very diverse group with a wide range of physiological and biochemical characteristics. They comprise a large, almost unexplored group of organisms, and thus provide a virtually untapped source of products and possibilities for commercial application (Radmer & Parker, 1994). The blue-green algae *Arthrospira (Spirulina) platensis* Gomont and *A. (S.) maxima* Setch. & N.L. Gardner are at present the richest known sources of plant protein (Jassby, 1988a). In addition, they have the highest vitamin B_{12} content of any unprocessed plant or animal and relatively high contents of β carotene (Jassby, 1988a; Mshigeni, 1982). In relation to this carotene product, however, the species of *Arthrospira* Stizenb. ex Gomont are outstripped by another genus of microalgae: *Dunaliella* (Jassby, 1988a; Moulton et al., 1987). Free-living nitrogen-fixing blue-green algae, as well as the endosymbiotic nitrogen-fixing blue-green algae growing in the *Azolla* water fern are used as fertilizers for rice fields. These algae function as a 'green manure' (Faridah Hanum & van der Maesen, 1997; Metting et al., 1988, 1990; Mshigeni, 1982).

The commercial significance of most other microalgae has been small up to the present, although many show much potential (Apt & Behrens, 1999; Radmer & Parker, 1994; Yamaguchi, 1996). The costs associated with growing and harvesting microalgae and, where necessary, extraction and purification of the product may prevent the success of many initiatives for nutritional uses from the outset (Regan, 1988). Nevertheless, the use of microalgae as sources of valuable chemicals is now established and it is assumed that the next few years will see a continued expansion of the range of commercially available microalgal products (Borowitzka, 1994).

Importance

In terms of utilization of algae, several commodities are of main interest: vegetables (direct human consumption), producers of phycocolloids, raw materials for feed and fertilizer and for medicinal or pharmaceutical use. In contrast, the extraction of soda and potash (in the 18th Century) and iodine, which was a thriving industry in the early parts of the 19th Century, is no longer of economic significance.

Algae as vegetables Specimens used as vegetables (or as material for medicinal or pharmaceutical use) are usually collected from nature (Hatta et al., 1993). This small-scale use results in offering the fresh specimens for sale at the local market. In South-East Asia especially, coastal inhabitants of the Philippines, Malaysia and Indonesia consume seaweeds. Only occasionally are freshwater macroalgae used as food (Arasaki & Arasaki, 1983).

Phycocolloids Production of phycocolloids is occasionally possible in small-scale ventures. In these cases washed-up specimens collected from the beach can be used, as well as material collected from wild populations or from cultivated stock. Those seaweeds can be sold as raw material, often washed and bleached, to be used for the home production of crude phycocolloids for the preparation of puddings and cakes, or as raw (often untreated) material for animal feed or fertilizer. Often small-scale traders buy dried seaweeds from collectors and farmers for export to other countries or to factories for phycocolloids. The cultivation of algae for phycocolloids takes place in family-owned seaweed farms or in larger complexes owned by cooperatives, exporters or factories.

Other uses Biomass from macroalgae can be prospected to provide environmentally and economically feasible alternatives to fossil fuels and can also be functional in pollution abatement (Gao & McKinley, 1994).

1.2.2 Biological and chemical products and uses

1.2.2.1 Phycocolloids

Various seaweeds are used to manufacture phycocolloids including agar, carrageenan and alginate. These water-soluble non-crystalline polysaccharides can be extracted from cell walls. They are variously designated as seaweed colloids, hydrocolloids, phycocolloids or seaweed gums. They are not found in land plants and are specific to seaweeds (Heyraud et al., 1990; Lewis et al., 1988; Tseng, 1945, 1946). However, polymers with similar properties are extracted from higher plants and all compete with pectin, gelatin and carboxymethyl cellulose (CMC) in the food additive hydrocolloid market (Bixler, 1996; Lewis et al., 1988).

Phycocolloids are extracted from red and brown algae and are included in many industrial processes. They are used to thicken aqueous solutions, to form gels or jellies of various degrees of firmness, to stabilize oil-in-water emulsions and to stabilize products such as ice-cream and whipped toppings (Guist, 1990; McHugh & Lanier, 1983). Without the phycocolloids, several biotechnological advances, many of which have the potential of being beneficial to mankind, would not have been possible (Renn, 1990). The mechanisms of gel formation differ widely for agar (heating/cooling), carrageenan (addition of monovalent ions) and alginate (addition of bivalent cations). These different properties are used in different applications in prepared food (Guist, 1990).

Phycocolloids are characterized by formation of strong and transparent gels with different viscosity, solubility and reversibility of gel formation and often by a high gel-melting temperature. Their physical behaviour (conformation of chains in solution, solubility, ion-exchange properties, gelling, viscosity) and the resulting biopolymer engineering have been described (Heyraud et al., 1990; Lewis et al., 1988; Smidsrød & Østgard, 1991). The gels usually have no acid sensitivity; they are natural and of plant origin; they have non-caloric properties, the ability to assimilate and enhance flavours and are easy to measure and use.

1.2.2.2 Agar

Agar is a hydrophyllic colloid extracted from a number of red algae, which are often collectively designated as agarophytes. Of the total global agar production in 1994, about 35% came from members of the Gelidiales (e.g. *Gelidiella* Feldmann & Hamel, *Gelidium* J.V. Lamour. and *Pterocladia* J. Agardh); most other agar came from members of the Gracilariales (e.g. *Gracilaria* Grev., including *Gracilariopsis* E.Y. Dawson) (Armisén, 1995; Armisén & Galatas, 1987; Chapman, 1970; Indergaard & Østgard, 1991; Lewis et al., 1988; Lobban & Harrison, 1994; Pérez et al., 1992).

Structure

Chemically, agars consist of a mixture of polysaccharides, viz. polymers which are chains of joint units of galactans. In agar the average sulphate content of these polymers is between 1.5 and 6%, while there are lesser quantities of

pyruvic and guluronic residues present, varying from source to source (Armisén, 1991; Cosson et al., 1995; McHugh & Lanier, 1983). The backbone structure of both agars and carrageenans is based on repeating galactose and 3,6-anhydrogalactose residues, or is formed by aragan: alternating units of D- and L-galactopyranoses (Armisén, 1991; Craigie, 1990; Knutsen et al., 1994). Another extreme backbone structure is agarose, in which all 4-linked α-L-galactose residues are in the 3,6-anhydro form. A letter code for a shorthand nomenclature system for galactan building units and sequences, using L (for L-galactose) and LA (for anhydro-L-galactose), is considered typical for agars.
The agar group (agarocolloids) differs from the highly sulphated carrageenans by having 4-linked α-L-galactose as well as D-galactose. High content of 3,6-anhydro-L-galactose and low degrees of substitution favour gelation of agar. Fractionation into a neutral good-gelling fraction lacking sulphate and other charged groups (agarose), and a residual fraction with poor gelling properties (agaropectin) is well established commercially, but the two extremes are connected to each other by many intermediates (Craigie, 1990; Pérez et al., 1992; Smidsrød & Christensen, 1991). High gel strength is usually due to the presence of longer chains of polymers in agar samples.
Ionized agarose, where molecules are highly sulphated, is dominant in some *Gracilaria*, producing a flexible and elastic gel which can not, however, meet all specifications for food grade agar (Cosson et al., 1995). Treatment of the *Gracilaria* phycocolloid with sodium hydroxide (alkaline hydrolysis), which transforms the agaroid into real agar, makes a product that meets the specifications required (Armisén, 1995). Agar in *Gracilaria* has a greater tendency to become hydrolyzed during storage, even under favourable conditions. This is not only caused by agarolytic bacteria; even if these organisms are not present, adequately dried and stored warm-water *Gracilaria* may still undergo a reduction in their agar content over a few months in storage. *Gracilaria* spp. from colder waters usually have a much greater resistance to hydrolysis but, even so, they are not as resistant to hydrolysis as agar from *Gelidium* (Armisén, 1995).

Properties

Unique properties of agar are: very strong, stable, brittle, thermo-reversible gel formation in aqueous solution, without the presence of any additives; gelation at temperatures far below the gel melting temperature (= the sol temperature: there the phycocolloid becomes liquid again); resistance to high temperatures (a 1.5% aqueous solution gels between 32 and 43°C and does not melt below 85°C); usability over a wide pH range from 5 to 8; capacity to hold large amounts of soluble solids, flavours and colours; a maximum ash content of 5% (normally maintained between 2.5–4%) (Armisén & Galatas, 1987). The difference between gel and sol temperatures is called hysteresis. This difference can be as high as 50°C and is only displayed by agar (Lewis et al., 1988). While agar is the most commonly accepted term, in French-, Spanish- and Portuguese-speaking countries it is also called 'gélose' or 'gelosa' and in Japan the dry product is called 'kanten'.

Uses

Agar (commercial code E406), insoluble in cold water but soluble in boiling water, is a major additive in the food industry because of its resistance to high temperatures (it is often used to prevent dehydration in bakery products), its rigid gel (in confectionery and canned products), its gelling properties (in marmalade production, but also to prevent meats from becoming mushy and reducing damage in transit of soft meats, permitting the reduction of fat content) and its stabilizing properties (in dairy products). Agar is also often used for viscosity control and is known for its unique application as a culture medium in bacteriology and also for orchids and vegetables. The gel is used for the preparation of medical supportives and is utilized in the manufacture of photographic films, in the print industries and to prepare mould casts for use in sculpture, archaeology and dentistry. Because gel strength varies according to the species of seaweed used as a raw material, processors often use a mixture of seaweeds. Separate uses of agarose can be grouped in the broad categories of immuno-diffusion and diffusion techniques, electrophoresis, chromatographic techniques, immobilized systems technology and special growth media (Renn, 1990). Agarose has great stability and constitutes an inert support of natural origin, modifiable by organic synthesis, with the highest known gelling power among natural colloids (Armisén, 1991; Armisén & Galatas, 1987).

1.2.2.3 Carrageenan

Carrageenans are formed in the cell walls of some red algae (carrageenophytes), including the tropical genera *Acanthophora* J.V. Lamour., *Betaphycus* Doty ex P.C. Silva, *Eucheuma* J. Agardh, *Hypnea* J.V. Lamour. and *Kappaphycus* Doty. In *Eucheuma* and *Kappaphycus*, the sporophytes and the gametophytes always contain the same type of carrageenan within each species. This differs to the situation in carrageenophytes from temperate regions, where the life-cycle phases each contain a different type of carrageenan. Although the Malay word 'agar-agar' refers to *Eucheuma*, it is now known that these yield carrageenans rather than agar-type polysaccharides.

Structure

Chemically, carrageenans are polysaccharides, their exact composition, however, varying from source to source. They all are formed by groups of linear D-galactans with varying amounts of 3,6-anhydro-D-galactose with alternating 1,4- and 1,3-linkages and variations in the amount and position of sulphate half-esters. The complex structure of carrageenan is an active field of research (Knutsen et al., 1994; Pérez et al., 1992; Stanley, 1987). Usually three or four main chemical types or 'families' of refined carrageenan are distinguished:

- Kappa carrageenan, with a rather brittle gel characterized by syneresis, a condition in which water is exuded from the gels by standing, and even more so when squeezed in a press. Originally kappa carrageenan was defined as the fraction which was precipitated by potassium chloride.
- Iota carrageenan, with a less brittle and more flexible gel, showing only little syneresis and distinct precipitation by KCl.

- Lambda carrageenan, which dissolves in cold water and does not form a gel at all when potassium or calcium salts are added, but provides increased viscosity and suspension capacity in products.
- The beta family of carrageenans, a rather new group of carrageenans found in *Betaphycus gelatinus* (Esper) Doty ex P.C. Silva, Basson & R.L. Moe (= *Eucheuma gelatinum* (Esper) J. Agardh), is competitive with certain functions of agarose in some biotechnology applications (McHugh, 1996).

The designations beta, kappa, iota and lambda carrageenan for refined carrageenans refer to certain idealized structures with quite different physical properties, although they sometimes occur in mixed structures (Craigie, 1990; Guist, 1990; Heyraud et al., 1990).

Attempts have been made to group the different disaccharide-repeating units of carrageenans into families, but that system omitted many natural complex carrageenans (Craigie, 1990; Knutsen et al., 1994). A new nomenclatural system for red algal galactans has been proposed, in which the backbone structures in the carrageenan group of polysaccharides are separated as carrageenan in its strict chemical sense and as the component carrageenose (Knutsen et al., 1994). Commercial carrageenans are available as stable sodium, potassium, or calcium salts of unstable free acids. These commercial carrageenans are most commonly mixtures of different salts.

Properties

The unique properties of carrageenan include high-quality, highly viscous, thermo-reversible gel formation; protein reactivity (especially with casein); and it can be used together with guar (*Cyamopsis tetragonoloba* (L.) Taub.) and locust bean or carob seed (*Ceratonia siliqua* L.) gums (Anonymous, 1979; Glickman, 1987; Stanley, 1987).

Uses

Carrageenans (commercial code E407; for natural grade carrageenan in Europe the code E407a is applied) are the phycocolloids with by far the widest application in food industry (Anonymous, 1998; Bixler, 1996). They are mainly used as stabilizing, thickening, suspending and gelling agents in food such as dietary and baby foods and also in canned pet-foods, syrups, fruit drink powders and frozen concentrations, milk-based products, chocolate, pasta sauce, artificial whipped toppings, imitation coffee creams and pre-cooked, packaged meats. Carrageenans are also used in non-food products: toothpaste, cosmetics, solid gel-type air fresheners and textile paints. A preferred name in the Philippines for the locally produced carrageenan is 'natural grade carrageenan' which is sometimes called 'Philippines natural grade' or 'PNG carrageenan' because of its country of origin. Other commonly used names are 'alkaline carrageenan flour' (ACF), 'alkaline-modified carrageenan' (AMC), 'alkali-modified flour' (AMF), 'alternatively refined carrageenan' (ARC), 'alkaline-treated cottonii' or 'alkali-treated cottonii' or 'alkali-treated carrageenophyte' (all as ATC), 'natural washed carrageenan' (NWC), 'processed *Eucheuma* seaweed' (PES), 'semi-refined carrageenan' (SRC)and 'seaweed flour' (SF) (Anonymous, 1998; McHugh, 1996; Neish, 1990). In a recent survey 'SRC' is used as an acronym for the total of alkali-treated chips and semi-processed powder, while 'PNG' is exclusively used for the semi-processed powder alone (Anonymous, 1998). Natural grade carrageenan is not universally accepted for classification as carrageenan, although the American Food and Drugs Administration has done so. In the European Union, however, natural grade carrageenan was mainly excluded from the arbitrary definition of carrageenan as having a maximum 2% content of acid-insoluble matter (Bixler, 1996; Luxton, 1993). In the European Union therefore it has received the official separate designation 'PES = Processed *Eucheuma* seaweed' (Anonymous, 1998; Bixler, 1996).

1.2.2.4 Alginate

Algin is often used as the name for the soluble sodium salt of alginic acid, while these and other salts and esters together are called alginates. These products are found in the cell walls of brown algae, including the tropical seaweed genera *Hormophysa* Kütz., *Hydroclathrus* Bory, *Sargassum* C. Agardh and *Turbinaria* J.V. Lamour. (Painter, 1983; Trono & Ganzon-Fortes, 1988). Most commercial alginate is produced from alginophytes occurring in temperate or even colder waters. Alginic acid itself is insoluble in water, but it swells when water is added. Alginates are also produced as microbial polysaccharides by certain bacteria (Smidsrød & Christensen, 1991).

Structure

Alginates are polysaccharides of which the exact composition varies from source to source. They form a family of linear binary copolymers containing 1,4-linked β-D-mannuronic acid (M) and its C-5-epimer α-L-guluronic acid (G). The distribution of M and G in alginate chains gives rise to three different block types, namely blocks of poly-M, blocks of poly-G and alternating blocks of the type M-G-M-G. This composition can be described in detail by using nuclear magnetic resonance (NMR) techniques (Jensen, 1995; Smidsrød & Christensen, 1991).

Gel formation or binding is an important application of alginates. A solution of 1–2% sodium alginate will stiffen to a gel by addition of calcium ions (50 mM) or other bivalent ions (Ba^{2+}, Pb^{2+}, Sr^{2+}, etc.). The bivalent ions bind the alginate chains together in a three-dimensional gel network in accordance with the 'egg box' model (Heyraud et al., 1990; Jensen, 1995). Alginate gels have various strengths, largely dependent on their content of polyguluronic acid blocks (Indergaard & Østgard, 1991). The alginate content of the warm-water seaweeds is usually somewhat lower than that in algae from other waters. In general the alginate of *Sargassum* and *Turbinaria* is of low viscosity but forms good gels. *Turbinaria* thalli usually have a higher alginic acid content (20–22% of the dry weight) than *Sargassum* (13–18%) (Pérez et al., 1992).

Properties

Unique properties of alginate are its cold-water solubility of sodium alginate, and its instantaneous calcium reactivity resulting in a highly water-retentive, non-melting, thermo-irreversible chemical gel formation.

Uses

Alginates are used as low-price viscosifiers or thickeners in a wide range of products. They are the most widely used seaweed colloids. The primary food products in which alginic acid and alginates (commercial codes E401–E405) are used include frozen desserts, where they regulate the formation of ice crystals and help to control over-run, providing a smooth, creamy body in products. Alginates prevent products from sticking to wrapping paper, especially bakery products. They are emulsifiers and stabilizers in salad dressings, meat, flavour sauces, canned food and beverages. In dessert gels alginates produce clear, firm, quick-setting gels, suitable for use with hot as well as cold water (Glicksman, 1987). In non-food industries alginates are also very often used in paint, cotton textile, plastics, vulcanite fibre, linoleum and imitation leather, waterproof products, glass-production and etching industries.

1.2.2.5 Chemical products

Several high-value fine chemicals are produced on the basis of microalgae grown in mass culture (Borowitzka & Borowitzka, 1988). The products derived from these microalgae include carotenoids, other pigments, fatty acids, sterols, vitamins and bioactive compounds (Apt & Behrens, 1999; Borowitzka, 1994).

1.2.3 Nutritional aspects

Nutritional value of marine macroalgae

Although marine macroalgae were known and prized for nutritional purposes from very early times in the Orient, most of them have rather low digestibility, containing many unfamiliar polysaccharides and minerals. It is sometimes stated that a regular intake of seaweed will help develop an intestinal bacterial flora capable of breaking down the polysaccharides, but probably the human body does not digest phycocolloids at all or only in small quantities of less than 10% (Armisén, 1991; Mori et al., 1981).

Nevertheless, major uses of seaweeds are found in human nutrition, although seaweeds can not function as a basic source for proteins or lipids, neither in man nor animals (Jensen, 1993). In the green algae, which store starch in the same way as most land plants, cell walls contain highly resistant polymers of glucose, mannose and xylose (Painter, 1983). Seaweeds are very 'filling', however, which make them good diet foods. Their soft cell walls regulate bowel action without damaging intestinal walls (Indergaard & Minsaas, 1991). In terms of amino acids, seaweed protein is similar to that of egg white and legumes (in %), while sea-vegetables are low in fats but contain considerable amounts of vitamins and minerals (Arasaki & Arasaki, 1983).

Although energy values of various seaweeds are known, these values can not be thought of as physiological energy until the digestibility, and thus bio-availability of the various compounds, has been determined (Indergaard & Minsaas, 1991; Paine & Vadas, 1969; see, however, Booth, 1964). Information about algal products, e.g. seaweed meal as fodder supplement, is mainly based on uses in Europe, while detailed reports on the use of other seaweed species are few

(Indergaard & Minsaas, 1991; Wong & Leung, 1979). Differences in the phenolic content of various algae seems vital, low contents favouring the protein digestibility of green and especially red algae at the expense of the browns.

Marine macroalgae as human food

Terrestrial vegetables are eaten because of their mineral and vitamin contents and their taste. In addition seaweeds may also bring colour, flavour, texture and chewiness, which make them delicacies (Arasaki & Arasaki, 1983; Madlener, 1977; Trono & Ganzon-Fortes, 1988). Some red algae have a reasonably high protein content. Algal phycocolloids are officially accepted as additives for human foodstuffs (Indergaard & Østgard, 1991).

The addition of seaweed meal as a source of iodine and other minerals to the diet of fast-growing children and pregnant women may be advisable even in countries with otherwise rationally balanced diets (Indergaard & Minsaas, 1991). Possibly a better means of introducing these elements into the diet might be to use seaweed meal as animal feed or as a fertilizer for the plants whose products are eventually consumed by humans.

In general, marine algae are rich in vitamins A and E. Niacin and vitamin C content are about the same in all groups of marine macroalgae. Concentrations of vitamins B_1, B_{12}, pantothenic acid, and folic and folinic acids are generally higher in the green and red algae than in brown seaweeds. Animal organs, especially liver, which are richest in vitamin B_{12}, contain a lower amount (in g dry-weight basis) of this vitamin than some of the green algae. The concentrations of algal B vitamins are, in fact, comparable to those in many common fruits and vegetables. Extraordinary amounts of vitamin A are generally found in the marine algae, occasionally much more than is present even in cod liver oil (Madlener, 1977). For tropical areas, the richest source of vitamin C from algae would be *Sargassum* spp., which are already traditionally consumed in a number of countries including Indonesia, Malaysia, the Philippines and Vietnam (Michanek, 1979; Trono & Ganzon-Fortes, 1988). Some algae from Indonesia have been screened for active substances, mainly steroids, but also carbohydrates (Harlim, 1986). 'Wild' populations of inland algae (microalgae) are only occasionally collected for use as food (Jassby, 1988a).

Marine macroalgae as feed in aquaculture

In areas where aquaculture is an important industry, seaweeds could be applied more regularly as a feed for aquatic animals. For example, *Gracilaria* can be grown in ponds with milkfish and shrimp. These animals graze on epiphytes on the *Gracilaria*, and eventually on the red alga itself if they are left in the pond for long enough or their numbers increase out of balance with the seaweed biomass (McHugh & Lanier, 1983).

Production of milkfish in fish ponds (in Indonesia: 'tambaks') is best when the bottom of the production ponds is covered by a thick mat of blue-green algae such as *Chroococcus*, *Gomphosphaeria*, *Lyngbya*, *Microcoleus*, *Oscillatoria*, *Phormidium* and *Spirulina* spp., as well as by diatoms. This algal periphyton constitutes the main food of cultured milkfish, but filamentous green algae may also be eaten (Bardach et al., 1972). The biological complex of blue-green algae, diatoms, bacteria and various animals, which is typical of well-managed milkfish ponds, is known as 'lab-lab' in the Philippines and as 'kelekap' in Indonesia (Benitez, 1984; Chong et al., 1984). Red seaweeds of the genus *Gracilaria* can also be used as food for milkfish, but the algae are unable to withstand salinities below 5‰ (Bardach et al., 1972). It is also possible to feed molluscs on these *Gracilaria* seaweeds obtained from phycoculture. When labour costs are too high to make enough profit from preparing *Gracilaria* thalli for agar production, farmers may prefer to use these algae as a direct food for molluscs, as has been the case in Taiwan (Ajisaka & Chiang, 1993).

Microalgae as human food

The blue-green alga *Arthrospira (Spirulina) platensis*, which occurs in a great variety of inland waters, is renowned as being one of the richest protein sources in the world. The alga contains significant amounts of vitamin B_{12}, other B-complex vitamins, vitamins A and E, β carotene and the essential mineral elements iron, phosphorus, magnesium, zinc and selenium (Mshigeni, 1982; Switzer, 1982; Vonshak, 1997). However, due to the production of certain toxins use of cyanobacteria as food will always entail a degree of hazard, until adequate health standards for production and marketing of cyanobacteria for single-cell protein are adopted and observed (Gorham & Carmichael, 1988).
The potential for using microalgae to combat current problems of famine and malnutrition has been reviewed. Attempts to bring small-scale microalgal production to villages for application in integrated village systems are promising (Jassby, 1988a). *Arthrospira* has little value as an energy source, but is interesting as a protein source, especially among malnourished human populations (Van Khuong, 1990). The palatability of small amounts is not the problem, but in larger quantities the strong colour, odour and taste are often not acceptable as a major food source (Jassby, 1988a).
Other freshwater algae, such as the unicellular green algae of the genus *Chlorella*, also produce a very good protein source. Its protein is especially rich in the amino acids lysine, threonine and tryptophane, which are generally poor in cereal proteins (Lee & Rosenbaum, 1987). However, *Chlorella* is not accepted as an attractive new food item. It is mainly available in health-food shops and in the form of chlorophyll pills, or added in powder form to various kinds of food products. In this form it increases significantly the level of vitamins and lipids without affecting the palatability of the food (Mshigeni, 1982). Members of *Dunaliella* are occasionally used as a protein supplement in bread (Borowitzka & Borowitzka, 1988).

Microalgae as feed in aquaculture

Most freshwater algae, as well as marine microalgae, are too small to be attractive as potential sources of human food or animal fodder, although they are indispensable as live feed in aquaculture (de Pauw et al., 1984). These feed microalgae are especially used for larvae of commercially grown crustaceans, molluscs and fish or as feed for zooplankton that in turn will be used as feed for other larval stages and juvenile fish. Several microalgae are grown for these purposes in commercial growth media (Benemann, 1992; de Pauw & Persoone, 1988; Gladue & Maxey, 1994; Shamsudin, 1992). Comparative studies of the most widely used microalgae in hatcheries worldwide have shown that their nutritional quality varies considerably (Apt & Behrens, 1999). Much of this variation can be explained by major differences in fatty acid composition, particularly with respect to the proportions of long-chain polyunsaturated fatty acids. Recent efforts have focused on the use of algal oils containing long-chain polyunsaturated fatty acids (LCPUFAs) as nutritional supplements (Apt & Behrens, 1999). The most prominent of these are the omega-3 LCPUFAs docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA). DHA is a dominant fatty acid in neurological tissue and is also abundant in heart muscle tissue and sperm cells. It is an essential nutrient during infancy. Humans are not capable of synthesizing DHA themselves. Thus, adequate supplies of DHA must be obtained from dietary sources. A number of algal groups have been identified that produce high levels of these compounds. The component EPA, however, can significantly lower growth rates of humans and animals and can also cause other developmental difficulties. Purified algal oil containing EPA is not commercially available (Apt & Behrens, 1999).

Green algae are mostly less suitable as feed, although *Chlorella* and *Dunaliella* are often used as feed for fish larvae in commercial fish farming. Several diatoms, however, are more satisfactory in many respects. Nutritional deficiencies in a diet for organisms in aquaculture can be avoided by using mixed algal diets (Volkman et al., 1989). Gross chemical and fatty acid composition of a number of tropical microalgae has been determined (Renaud & Parry, 1994; Renaud et al., 1994; Shamsudin, 1992). The greatest breakthrough in shellfish production would be the production of the right microalgae in the right quantities at the right time (Doty, 1979). Heterotrophic growth may be the solution (Apt & Behrens, 1999; Gladue & Maxey, 1994). The prospects of the green freshwater microalga *Haematococcus pluvialis* Flot. for the production of the keto-carotenoid astaxanthin, a natural food and feed colourant often used in the aquaculture industry, are promising (Borowitzka, 1994; Ding et al., 1994).

1.2.4 Medicinal and toxic aspects

Medicinal uses

The earliest information on seaweed utilization for medicinal purposes originate from the Chinese 'Materia Medica' of ShÍn-nung, dating from 2700 B.C. (Hoppe, 1979). In many areas numerous algae are used as medicaments, especially in coastal countries. They are used in folk medicine against goitre, nephritic diseases, helminths, catarrh, etc. Several algal species contain substances of pharmaceutical interest of which the active compounds are not yet characterized. In others, however, the active principle compound has been identified like a mixture of kainic and allokainic acids responsible for vermifugal properties in the red alga *Digenea simplex* (Wulfen) C. Agardh (Arasaki & Arasaki, 1983; Chapman, 1970; Michanek, 1979). Substances with anticoagulant properties, with cytotoxic activity (anticancer or antineoplastic activity), antibiotic, antifungal, antiviral or antioxidant activity are known to occur in some seaweeds, as are haemagglutinins (Chapman, 1970; Fujimoto, 1990; König, 1992; Mabugay et al., 1994; Matsukawa et al., 1997; Michanek, 1979;

Neushul, 1990; Pesando, 1990; Reichelt & Borowitzka, 1984; Santos & Guevara, 1988; Shiomi & Hori, 1990; Wong et al., 1994). Antibiotic activity is not present at all times and even samples of the same species, when collected from different localities, may give different results (Padmakumar & Ayyakkannu, 1997).

Fucoidan, a polymer of fucan sulphate, found in members of the *Phaeophyta*, contains a fairly high percentage of sulphate ester. This substance is known to have the same anticoagulant effect as heparin and a 1% aqueous solution of fucoidan obtained from a *Sargassum* sp. has shown greater antithrombic activity than the same concentration of heparin (Arasaki & Arasaki, 1983). Fucan sulphate, however, can not yet be stored satisfactorily; even deep-frozen material is not stable (Nishino & Nagumo, 1991).

The path from discovery to commercial production of a drug is long and costly (Baker, 1984). Each investigated marine organism may yield new natural products and/or new or known compounds with biological activity (König, 1992).

Compounds that are toxic for the freshwater snail *Biomphalaria glabrata* (vector for schistosomiasis) have been found in marine algae, whereas some antimalarial activity has been detected in compounds isolated from the brown algal genus *Dictyota* J.V. Lamour. and other seaweeds (König, 1992; Subramonia Thangam & Kathiresan, 1991).

Phycocolloids

The role of phycocolloids in pharmaceuticals as thickening or binding agents is similar to that in food. However, this role must be separated from their biochemical action, particularly as oligosaccharides. Only in a few instances may the phycocolloid component be considered as the active therapeutic agent (Chapman, 1979; Güven et al., 1991; Indergaard & Østgard, 1991).

Agar is used in emulsions with liquid paraffin for the treatment of constipation. The gelling power of agar is so high that it is generally used only in low concentrations. For this reason the ingested quantities are very small and its caloric contribution is negligible. Thus agar can be used in special diet food (Armisén & Galatas, 1987).

Aqueous extracts of several red algae, as well as carrageenans, have been recorded as active against retroviruses (Neushul, 1990). Some carrageenans show anticoagulant, fibrinolytic or antiaggregant activity. Such activities, however, have never been reported in alginates (Güven et al., 1991). Alginates, however, have strong ion-exchange affinities for bivalent cations (Tsytsugina et al., 1975). It has been proposed that these phycocolloids could be used to cleanse human bodies of unwanted heavy metals (Indergaard & Minsaas, 1991; Tanaka et al., 1972; Tanaka & Stara, 1979). If dairy products, cereals, fish or meat may be contaminated, the uptake of strontium especially could be prevented by the addition of alginate to food. Alginic acid has the ability to form insoluble complexes with strontium, which can pass through the intestines without being absorbed into the body. Alginates can even be used to reduce strontium already deposited in the bone and can also be used to inhibit absorption of lead, barium, cadmium and zinc (Michanek, 1979; Takana et al., 1972).

Calcium/sodium alginate is also produced as a thread in order to manufacture a woven fabric for wound healing. The threads are woven as calcium alginate

and then modified to give a mixture of sodium and calcium alginates, resulting in a product that gels on contact with the wound and one that has good haemostatic qualities. This type of fabric is available as first-aid dressings and is particularly useful in the treatment of burns (Dixon, 1986).
Alginates are also used in pharmaceutical tableting, dental impressions, bacterial cell encapsulation and enzyme immobilization (Lewis et al., 1988). The use of alginate in slow-release systems for pharmaceuticals is developing rapidly (Jensen, 1995). Combinations of agar and alginate show promising results for dental uses (Kasloff, 1990).

Iodine

A bulk use of seaweeds as a food material with obvious therapeutic benefits (nutraceuticals) is found in the brown algae which contain iodine which combats endemic goitre. Products made from *Laminaria japonica* Aresch. are widely used for such purposes in China (Michanek, 1981). Endemic goitre may also possibly be eradicated by public health information and use of seaweed food, especially in Indonesia and Malaysia (Michanek, 1979). Excess intake of iodine may, however, also produce fatal effects in both humans and animals. Goitre (thyrotoxicosis) has been demonstrated as a consequence of the high intake of kelp products by children in Japan and in adults in Australia and Finland (Liewendahl, 1972; Wheeler et al., 1982; Zuzuki, 1965).

Poisonous macroalgae

Until recently, only very few macroalgae had been recorded as more or less unwholesome, especially some *Caulerpa* spp. and *Turbinaria ornata* (Turner) J. Agardh (Russell, 1984). *Caulerpa* spp. have occasionally been mentioned as producing neurotoxins (Lemée et al., 1993; Paul & Fenical, 1986; Ribera et al., 1996; Schantz, 1970). *Turbinaria* is recorded as creating gastro- intestinal distress in humans (Russell, 1984). In comparison with the more than 1200 toxic marine organisms that were included in Russell's review of marine poisonous organisms, one must conclude that the macroalgae, as a group, are more or less non-toxic (Indergaard & Minsaas, 1991). A well-documented case where people died after eating the red alga *Gracilaria tsudai* (I.A. Abbott & I. Meneses) I.A. Abbott on Guam, however, indicates that this alga may form relatively high levels of previously undescribed toxic compounds at some stages of its life cycle (Yasumoto, 1993). The occurrence of toxic substances seems not related to the neurotoxins causing the marine food poisoning known as 'ciguatera', which is associated with toxins formed by the dinoflagellate alga *Gambierdiscus toxicus* Adachi & Fukuyo and accumulated in fish and molluscs (Stadler, 1993; Steele, 1993). The latter dinoflagellate, however, may contaminate macroalgae, to which it strongly adheres (Nakahara et al., 1996; Saint-Martin et al., 1988). Around Ambon (Indonesia) these dinoflagellates occur attached to *Sargassum*, *Turbinaria* and *Halimeda* spp. (Sidabutar, 1996).
Although it is suggested that consuming large amounts of seaweed may be a cause of human arsenic poisoning, in most algae, arsenic is in a form that is not assimilated (Norman et al., 1988; Walkiw & Douglas, 1975).

Cyanophytes

There are several blue-green algae (*Cyanobacteria*) that are known to be poisonous, especially the genus *Lyngbya* C. Agardh ex Gomont (Madlener, 1977). In the microalgae many highly toxic species occur which have not, however, been reported, as having harmful effects on macroalgal cultivation (Correales & MacLean, 1995). Most of these microalgae are not included in the present book of plant resources, except some blue-green freshwater algae that are useful because of their nitrogen-producing capacities. Not all blue-green algae are toxic, however. *Arthrospira platensis*, which is often used as food or a food supplement for humans, is completely non-toxic. A list has been published of experiments on potential therapeutic applications of *Arthrospira* (as *Spirulina* Turpin ex Gomont) as well as a review of public health aspects of microalgal products (Jassby, 1988a, 1988b). The status of microalgae as sources for pharmaceutical and other biologically active molecules has been reviewed (Borowitzka, 1995). Experiments to prepare mosquitocidal cyanobacteria provide an interesting prospect (Stevens et al., 1994).

1.2.5 Other aspects

Fertilizers and soil conditioners

Manual harvesting of beach-cast algae, mainly members of the *Phaeophyta*, has been carried out since ancient times for spreading on fields as a fertilizer and for soil conditioning, especially in maritime parts of Europe. These and other stranded algae are often the result of proliferation, due to an abundant presence of nutrients, favourable meteorological conditions and accumulation in confined areas (Morand et al., 1991). In the Philippines, in the coastal area of Ilocos Norte (north-western Luzon) the use of brown seaweeds of the genera *Hormophysa*, *Padina* Adans., *Sargassum* and *Turbinaria* as a fertilizer and soil conditioner is well documented (Fortes et al., 1993; Tungpalan, 1983). A product based on composted *Ascophyllum nodosum* (L.) Le Jol., a North Atlantic brown alga, has been used successfully in landscaping and reclamation projects. The method used to apply the soil conditioner will depend on the nature of the site. Where topsoil is available, the composted algae are mixed with the soil at a rate of 1.5 kg/m^3. However, in many cases no topsoil is available and the seaweed product must be applied to subsoils. If the site is relatively flat, the soil conditioner is worked into the top 5 cm of subsoil at a rate of 75 g/m^2, and then appropriate fertilizers and seeds are added using ordinary horticultural techniques. Often, the area to be treated includes steep slopes which are impossible to cultivate using conventional equipment and thus more liable to suffer soil loss due to run-off than flat sites. In tropical regions, heavy rains often make the problem of erosion due to run-off more acute than in the temperate zones. Spraying with a mixture containing composted *Ascophyllum*, together with clay, fertilizer, seed, a mulch (either cellulose pulp or peat) and water has given satisfactory results, even on bare rock and in tropical countries (Blunden, 1991). Processed seaweed products for crop use are of three kinds:

- meals for supplementing soil in large volumes or for blending into defined rooting media for glasshouse crops;

- powdered seaweeds; and
- liquid extracts and concentrates employed both as root dips (or soil drenches) and as foliar sprays (Menning et al., 1988, 1990).

Several crustose, calcareous red algae of the family *Corallinaceae* are used as fertilizers and soil-conditioning agents, primarily on acid soils.
The influence of microalgae on soil structure is well documented, although microalgal soil conditioners are not suited for non-irrigated soils (Metting, 1988).

Bio-fertilizers

The use of cyanobacterial bio-fertilizers, especially for growing rice, is promising (Kannaiyan et al., 1997; Venkataraman, 1994). In terms of ultimate nitrogen input in the paddy, algalization is feasible at about one-third of the cost of a chemical fertilizer. Bio-fertilization by blue-green algae can also be done indirectly by using the heterosporous floating aquatic ferns of the genus *Azolla*. Specialized leaf cavities in the water fern house the cyanobacterium *Anabaena azollae* Strasb. ex Wittr. (Faridah Hanum & van der Maesen, 1997; Metting, 1988; Metting et al., 1988, 1990). Among the known plant-cyanobacteria symbioses, only the *Azolla-Anabaena* associations have significant potential as alternative nitrogen source in agriculture, since the symbiont is capable of fixing atmospheric nitrogen at high rates. The utilization of these inexpensive bio-fertilizers has several advantages over chemical fertilizers: they make use of freely available solar energy, atmospheric nitrogen and water, thus utilizing renewable resources. In addition, they are non-polluting and, besides supplying nitrogen to crops, they also supply other nutrients such as vitamins and growth substances and improve the general fertility of the soil by improving the soil structure and increasing the organic matter. The benefits brought about by green manure such as *Azolla* are long-term, increasing grain yield during several successive crops of rice. Moreover, in low-potassium environments the application has a greater ability to accumulate potassium than does rice. Thus, when the fern decomposes, it acts indirectly as a potassium fertilizer.

Seaweed extracts

Seaweed extracts and suspensions, mainly derived from marine brown algae, are marketed for use in agriculture and horticulture. The effects of these products were traditionally explained by their content of trace elements. However, it has been shown that the amounts of trace elements form an insignificant proportion of the annual requirements of a crop. Consideration was also given to the presence of cytokinins, a diverse group of plant hormones. Results of research in this direction are not yet conclusive, although experiments in the Philippines provided good results, i.e. better growth and increased production in terrestrial crops (Fortes et al., 1993; Montaño & Tupas, 1990). There is, moreover, a sufficient body of information available to show that the use of seaweed extracts is beneficial in certain cases, even though the reasons for the benefits are not fully understood (Blunden, 1991). A survey is available of effects of commercial seaweed products on growth of plants and of cytokinins in commercial seaweed preparations (Metting et al., 1990).

Cosmetics

Several algal products are used as components of cosmetics. These include gelling substances (agar, alginates, carrageenans), algal flour and ground algae. For direct use, algal meal sachets for immersion in a bathtub are produced, as well as bath salts with algae and algal pastes to be used in thalassotherapy institutions (Arasaki & Arasaki, 1983).

Other uses

The concept of marine farms as a source of fuel was tested in the United States (Bird et al., 1990; Chynoweth et al., 1987; Flowers & Bird, 1990; Neushul, 1987; North, 1980, 1987). It is difficult, however, to attain economic profitability where energy is the only aim, although international agreements on CO_2-reduction may change this conclusion (Gao & McKinley, 1994). Some reviews suggest that microalgae show great promise for the production of 'biodiesel' liquid fuel. Others suggest that the CO_2- binding activities may be of influence on the global climate, and similarly that the large-scale cultivation of macroalgae might be used to counteract coastal eutrophication (Jensen, 1993; Norton et al., 1996). Even more success can be expected from integrated multi-use approaches, including biomass-transformation methods and use as fertilizer, resulting in products like useful chemicals, composts and biogas apart from more well-known uses as vegetables and as sources of hydrocolloids (Morand et al., 1991). Seaweeds, as well as certain microalgae, are particularly suited for the purification of nitrogen-rich domestic and urban sewage, and also for agricultural and some industrial waste effluents (de la Noüe et al., 1992; Kumaran et al., 1994; Lincoln & Earle, 1990; Oswald, 1988a; Schramm, 1991).
The accumulation and detoxification of toxic metal elements by algae also suggest promising aspects if it were to be applied to biological detoxification and control of these elements in natural waters or in industrially polluted waters (Maeda & Sakaguchi, 1990). Metal recovery in industrial applications is also feasible (Greene & Bedell, 1990).

1.2.6 Production, economic value and export

1.2.6.1 Production

Access and abundance of seaweed resources are two critical factors determining their commercial viability. Other factors determining viability include the costs of cultivation and harvesting (labour and/or equipment), drying, transportation, chemicals, water supply and environmental measures (McHugh, 1991).
The following taxa of seaweeds were cultivated in South-East Asia around 1973 (FAO, 1974): *Caulerpa racemosa* (Forsk.) J. Agardh, *Chaetomorpha antennina* (Bory) Kütz., *C. crassa* (C. Agardh) Kütz., *Cladophora* spp., *Enteromorpha compressa* (L.) Nees, *Eucheuma edule* J. Agardh (probably partly *Betaphycus gelatinus* and partly *E. serra* (J. Agardh) J. Agardh), *E. denticulatum* (Burm.f.) Collins & Herv. (as *E. spinosum* J. Agardh).
Other seaweeds have been added recently as cultivated organisms: *Caulerpa*

lentillifera J. Agardh (this is probably the correct identification of most cultivated *Caulerpa racemosa*), *Enteromorpha clathrata* (Roth) Grev., *E. intestinalis* (L.) Nees, *Gracilaria* spp., *Kappaphycus alvarezii* (Doty) Doty ex P.C. Silva, *K. striatus* (F. Schmitz) Doty ex P.C. Silva.

Until 1995 the Food and Agriculture Organization (FAO) published data on world production of all seaweeds together, thus no separation was made between data from phycoculture and from catches from natural populations. More recently these separate data have become readily available (Tables 2 and 3).

Usually FAO Fishery Statistics give seaweed quantities in metric t (wet weight). For industrial use, however, statistics are usually expressed in 'dry weight'. This is the mass of the seaweeds after it has been dried by natural means. These dried seaweeds usually contain about 20% moisture, but in *Eucheuma* and *Kappaphycus*, the main sources of carrageenan, buyers prefer 35% moisture for shipping convenience (McHugh, 1990). The fresh weight of seaweeds consists of 75–90% water. Of the remaining 'true' dry weight, about 75% is organic matter and 25% mineral ash, consisting mainly of K, Na, Mg and Ca ions (Lüning, 1993). A conversion of dry weight versus wet weight is often necessary. Red algae especially shrink considerably during drying. The prices of dried and baled red seaweeds (in dry metric t) are thus distinctly higher than

Table 2. World production of seaweeds by phycoculture (t wet weight).

	Production				
	1986	**1990–1992**	**1993–1995**	**1996**	**1997**
World					
seaweeds total	3 400 089	4 599 520	6 789 656	7 166 780	7 241 449
Phaeophyta	2 269 880	3 230 676	4 541 362	4 909 269	4 978 402
Rhodophyta	888 246	1 109 761	1 571 875	1 750 505	1 758 348
Chlorophyta	21 476	33 514	29 695	28 479	32 989
miscellaneous	221 154	314 981	647 047	478 903	472 015
freshwater Chlorophyta	667	332	317	376	305
freshwater miscellaneous	0	11	5	0	0
Indonesia					
Rhodophyta	77 462	95 000[1]	104 333v	148 000	157 000
The Philippines					
total	168 868	307 496[1]	480 438	631 387	627 105
'*Eucheuma alvarezii*'	4 627	9 244	10 426	12 903	4 533
'*Eucheuma cottonii*'	145 632	265 013	434 933	590 107	589 263
'*Eucheuma spinosum*'	8 173	15 408	13 472	8 551	8 149
Gracilaria	0	0	4	0	0
Chlorophyta (*Caulerpa*)	10 436	18 490[1]	21 606	19 826	24 890
Vietnam					
Gracilaria	1 700	3 333[1]	6 500[1]	8 500[1]	12 000[1]

[1] FAO estimate.

Sources: FAO, 1996, 1999c.

Table 3. World production from natural stocks (excluding phycoculture) of seaweeds and other aquatic plants (t wet weight).

	Total catch	Phaeo-phyta	Rhodophyta			Chloro-phyta	Miscel-laneous
			Total	Indo-nesia	Philip-pines		
1990–1992	1 133 667	737 904	213 170	11 284	1 265	23 013	159 586
1993–1995	1 101 433	716 608	176 102	8 803	1 042	22 675	185 836
1996	1 138 200	765 914	167 236	13 543	884	23 409	181 646
1997	1 193 800	784 196	168 378	15 000	494	24 517	214 756

Source: FAO, 1999a.

those for the fresh and wet product. The global prices for red algae are mainly influenced by the high prices and large amounts of *Porphyra* spp. produced in East Asia, while the high price for 'miscellaneous aquatic plants' can not be explained on the basis of the available data.

1.2.6.2 Economic value

The global value of the seaweed industry has been estimated at US$ 1 billion (10^9) and world demand for seaweeds and their products has been increasing by approximately 10% per year (Ohno & Critchley, 1993).

Calculations for phycoculture alone, however, already give a US$ 4 billion of profit/year and a turnover of more than US$ 16 billion. Total revenues for worldwide utilization of seaweeds have been calculated to be US$ 3.5 billion per year (Jensen, 1993). Phycoculture in the world uses an area of 530 000 ha, providing work and income for 250 000 family industries and almost 1 million employees, including those involved in dependent industries, repair, and maintenance (Pérez et al., 1992).

Little detailed information is available on the prices paid for seaweeds. To understand the price structure, its terminology has to be explained. For seaweed the FOB (Free On Board) price is fundamental – this is what is paid to the sellers (traders and exporters) for dried seaweed accepted on board the vessel and free to leave the port to be transported to the buyer. All costs to obtain and transport the seaweed to the vessel have to be met by the seller. The CF (Cost and Freight) price includes all costs the buyer has to meet to have the product delivered to the receiving port.

Lists are available of global prices for aquaculture products (FAO, 1996, 1999c). These are the prices of one t (wet weight) calculated from the amount produced (t) and the total value. These data are presented in Table 4.

Microalgae

Few quantitative data are available on the production of microalgae (Zhu & Lee, 1997). Microalgal production in 1991 was limited to approximately 2000 t, and was used primarily as health food and for the extraction of β carotene

Table 4. Prices of seaweeds produced by phycoculture in US$ per t (wet weight).

	1990–1992	1993–1995	1996	1997
Phaeophyta	719	666	626	620
Rhodophyta	1051	1015	803	829
Chlorophyta	608	464	382	335
miscellaneous	631	627	721	728
'Eucheuma alvarezii'	120	125	127	135
'Eucheuma cottonii'	141	92	95	84
'Eucheuma spinosum'	100	125	119	95
Gracilaria	406	422	417	408
Caulerpa	268	217	176	152

Source: FAO, 1999c.

(Benemann, 1992). In 1984 the ten largest commercial *Spirulina* farms produced just over 700 t of food-grade *Spirulina* powder, the Siam Algae Company in Thailand being the leader in terms of productivity (Jassby, 1988a). Since then other producing plants have taken over the lead position (Belay et al., 1994; Venkataraman, 1989; Vonshak, 1997). The production costs, however, are rather high (Belay et al., 1994; Vonshak, 1997).

Hydrocolloids

Of the global revenues from different food hydrocolloids, the phycocolloids accounted for 40% in 1978 (US$ 148 million of total revenues of US$ 397 million) and for 33% in 1993 (US$ 472 million of total revenues of US$ 1500 million) (Bixler, 1996; Jensen, 1993).
Globally, there are 300–350 factories in the world where raw, semi-dry algae are processed to provide the many products of algal origin that are used for innumerable aspects of modern human life (Pérez et al., 1992). For *'Eucheuma'* alone about 30 carrageenan-producing plants were active in 1987 (Neish, 1990).

Agar and agarophytes

In 1980 about 36 000 t (dry weight) agarophytes were harvested around the world, including 18 100 t from Asia (1470 t from the Philippines), and used to produce 7000 t of agar (3500 t from Asia) in the same year. Indonesia and Thailand were already known to be producing and exporting agar-bearing seaweeds, but no data were available (McHugh & Lanier, 1983; Soegiarto & Sulistijo, 1986). In 1984 150 t of agar were produced in Indonesia, probably mainly from *Gracilaria* (Armisén & Galatas, 1987), rising to 450 t in 1993 (Armisén, 1995).
By 1989 the world harvest of agarophytes had increased to 48 500 t (dry weight). Of this, less than 1000 t came from Indonesia (Luxton, 1993; McHugh, 1991). World production in 1987 was 6000 t of bacteriological grade agar (Indergaard & Østgard, 1991).

In 1990 the global production of agarophytes was 180 000 t (wet weight), resulting in a production of 11 000 t agar (Jensen, 1993).
The average price for agarophytes is higher than the price for other colloid-bearing seaweeds. Of course seaweeds which give agar with a higher gel strength, like *Gelidium*, command a better price. Often *Gelidiella* is mixed with imported *Gelidium* seaweeds in Japan, especially in lots assigned to the Philippines and to Indonesia (Armisén & Galatas, 1987). Wide fluctuations in price occur, depending on the source and the condition of the seaweed. The latter often depends on whether there are many epiphytes on the agarophytes, whether it is mixed with foreign seaweeds, and how well it has been dried and stored. It is almost impossible to store dried *Gracilaria* stocks for extended periods (Armisén, 1995).

Carrageenan and carrageenophytes

The estimated world carrageenan production in 1980 was 9200 t, including 2000 t from Asia. This correlates with 40000 and 17 900 t (dry weight) seaweeds (McHugh & Lanier, 1983). In 1989 the world harvest of carrageenophytes was 82 570 t (dry weight), of which 65 500 t was harvested in the Philippines and Indonesia (McHugh, 1991). This resulted in a production capacity in the Philippines of 9040 t of alternatively refined carrageenan and 800 t of conventionally refined carrageenan (Llana, 1990). World production of carrageenans in 1990 was 12 300 t (Pérez et al., 1992). Alternative calculations for 1990 resulted in a global production of 250 000 t (fresh weight) of carrageenophytes, to produce 15 500 t of carrageenan (Jensen, 1993). World demand in 1993 was 20 000 t of food-grade carrageenan and 5600 t of crude carrageenans or seaweed flour (Bixler, 1996), for this 80 000 and 22 000 t respectively of dried carrageenophytes were required.
The world supply scenario for carrageenan was that most of the production technology and thus manufacturing activities were in the hands of a few major manufacturers in non-tropical countries. The production of semi-refined carrageenan changed this picture completely. In 1982 the world carrageenan market size was 13 200 t, which already composed 2400 t of semi-refined carrageenan mainly produced in the Philippines. The conversion rate for 1 kg of semi-refined and refined carrageenan is 4.5 and 5.0 kg of seaweed respectively. Apart from the dried raw seaweed, products of carrageenophytes can also be exported as alkali-treated chips (Bixler, 1996; Luxton, 1993; Trono, 1994).
It is almost impossible to find accurate information about the prices paid for carrageenan. Already more than two hundred different carrageenan blends were available before 1987, tailored to meet specific applications (Stanley, 1987). Prices for food grade carrageenan in 1990–1995 were about US$ 10 per kg, while the price of semi-refined carrageenan was about 20% less (Bixler, 1996).
The yield of carrageenan in percentage of dry weight of the seaweeds varies from 14–27% in *Eucheuma gelatinum* in China to 58–65% in *Kappaphycus alvarezii* in the Philippines (Pérez et al., 1992). A 39% yield of carrageenan for conventionally dried *Kappaphycus alvarezii* has been mentioned, which can be increased to a yield of 60% after first washing the dried algae with freshwater (Bixler, 1996).

Alginates and alginophytes

The estimated world production of alginates in 1980 was 190 000 t of seaweeds, which is equivalent to 22 000 t of alginate (the amounts from Asia were only 4570 and 1950 t respectively). This global estimate excludes the production (1980) of 90 000 t of dry seaweed in China that was utilized for alginate manufacture. Only a very small portion of this large output entered the world market. Estimated world production was 180 000 t of dry alginophytes in 1989, again excluding the large amount from China (McHugh, 1991). The total world production of alginates in 1987 was estimated at 27 000 t; for 1990, however, the estimate is only 24 300 t (Indergaard & Østgard, 1991; Pérez et al., 1992).

Food

The total amount of seaweeds used as food for direct human consumption in the world was 385 000 t (dry weight) in 1980 (McHugh & Lanier, 1983). In 1989 the production of *Hizikia*, *Laminaria*, *Porphyra* and *Undaria* spp. combined was 454 800 t (dry weight) (McHugh, 1991). For 1990 it was 200 000 t (dry weight) for *Laminaria*, *Porphyra* and *Undaria* spp. together (Jensen, 1993). Except for *Porphyra*, none of these algal genera occur in South-East Asia.

1.2.6.3 Export

Dried seaweeds are often exported, especially for the production of phycocolloids. In South-East Asia these seaweeds are usually exported as raw material, although in particular the production of (semi-refined) carrageenan and salted *Caulerpa lentillifera* is growing.

Several South-East Asian countries are participating in the expansion of production of agarophytes and carrageenophytes and their associated products. Unfortunately, the logical link of production of raw material to the manufacture of agar and carrageenan, however, has often not yet been sufficiently implemented. In this way value-added benefits could be realized to the national economies of the producing countries.

Around 1980 approximately 50% of the world supply of agar was used principally in food in Asian countries. Of the 7000 t of agar produced less than 1000 t were utilized in the European Union (McHugh & Lanier, 1983). The production technology and manufacturing activities for carrageenophytes and alginophytes are in the hands of a few manufacturers only, while the farmers and collectors (especially of carrageenophytes) are poorly organized.

Between 1988 and 1990 the 1200 known applications of carrageenans increased to 4200 (Pérez et al., 1992). In 1993 the current annual demand for carrageenan was suggested to be 20 000 t, while the world capacity was then 28 000 t.

In 1980 Japan used about 20% of the world production of carrageenan, and western Europe and North America each used about 25% annually. In 1990 utilization in Japan was still about 20% of the world production, but had been to 45% in Europe and 35% in North America. However, in 1993 Japanese utilization accounted for only 8% of the world production of food grade carrageenan, while Europe still used the largest amounts (37%), followed by North

America (26%), Latin America (17%) and Australasia (13%) (Bixler, 1996). The largest production capacity for food grade carrageenan in 1993 was in Denmark (26% of the world capacity), followed by the United States (19%), France (11%), the Philippines (11%) and Chile (8%). In 1978 the latter two countries did not have any substantial carrageenan production facilities (Bixler, 1996).
The market for raw material for alginate production is not as competitive as that for other colloid-bearing seaweeds, since the major processors usually attempt to ensure supplies by buying directly from the source. The market for alginates lies principally in the textile and the food industries.
Of the microalgae produced in South-East Asia (*Arthrospira* mainly in Thailand but also in Vietnam), most is exported in the form of dried algal powder.

1.2.7 The algal industry

Indonesia

Collection and use of seaweeds are done on a local basis; the market for these products is not well-developed. An up to date inventory of Indonesian seaweeds is also lacking. Due to the importance of sea plants in the economy of Indonesia several attempts have been made to set up programmes for the comprehensive investigation of marine algae and their products (Soegiarto, 1979; Soegiarto & Sulistijo, 1986). Unfortunately, none of the proposed programmes were ever fully implemented (Eisses, 1952, 1953; Rachmat et al., 1986; Soegiarto & Sulistijo, 1986; Zaneveld, 1955, 1959). Before 1985, all seaweed production was harvested from natural stocks (Istini et al., 1998). In 1986 the total export of dried seaweeds was about 7200 t, rising to 11 423 t in 1989, and to more than 20 000 t in 1995 and 1996 (Table 5).

Marine vegetables Varieties of red, brown and green seaweeds are eaten by coastal inhabitants as a salad or as cooked vegetables (Hatta et al., 1993). At least 61 species in 27 genera of marine macroalgae are consumed as food and at least 21 species are used as herbal medicine (Istini et al., 1998).

Agarophytes Much of the final product of the agarophytes is in the form of agar strips, which are used in food preparation. In 1984, 62 t (probably dry weight) of '*Gelidium* seaweeds' from Indonesia were imported to Japan, together with 69 t of 'other agarophytes', probably mainly *Gracilaria* (Armisén & Galatas, 1987). However, *Gelidium* production (potential: 4500 t wet weight) is still only done by gathering from natural stocks (Mintardjo, 1990). Less than 1000 t (dry weight) of agarophytes are exported annually, of which in 1991 603 t of dried *Gracilaria* to Japan and 59 t of *Gelidium* to New Zealand and Italy.
In 1975 10 agar extraction companies employed 175 people and produced about 109 t agar/year. By 1993 the total number of algal extraction companies increased to 15, with a production of about 889 t agar and 980 t in 1994.
About 90% of this production was sold on domestic markets, the rest exported (McHugh, 1996). However, that is not in agreement with other published data (FAO, 1999b). Indonesia still imports agar (FAO, 1999b; Istini et al., 1998; McHugh, 1996) (Table 6). The combined capacity of the Indonesian agar production plants is 1200 t agar/year, limited by the quantity and quality of culti-

Table 5. Import and export values of dry seaweeds during the period 1995–1997 for Indonesia, Malaysia, Singapore, the Philippines and Thailand.

Country		Import			Export		
		Quantity (t)	Value (10^3 US$)	Unit price (US$/t)	Quantity (t)	Value (10^3 US$)	Unit price (US$/t)
Indonesia							
	1995	50	213	24 620	24 957	16 262	651
	1996	30	168	5 600	22 310	18 962	850
	1997	131	492	3 755	12 698	10 521	829
Malaysia							
	1995	1	1 005	1 005 000	3	320	106 666
	1996	1 263	1 540	1 219	477	727	1 524
	1997	353	2 588	7 331	1 299	597	460
Singapore							
	1995	414[1]	4 686	11 318	262[1]	1 790	6 832
	1996	874[1]	8 160	9 336	494[1]	3 274	6 627
	1997	612[1]	5 710[1]	9 330	331[1]	2 025[1]	6 117
The Philippines[2]							
	1995				28 920	39 106	1 352
	1996				26 406	41 974	1 589
	1997				n.a.	54 992	n.a.
Thailand							
	1995	298	5 932	19 906	110	1 649	14 990
	1996	477	8 364	17 535	77	1 298	16 857
	1997	383	3 697	9 653	55	797	14 491

[1] FAO estimate (1999b); [2] only carrageenophytes; n.a. = not available.
Sources: FAO, 1999a, 1999b, 1999c; Trono, 1999.

vated *Gracilaria* available. The Indonesian production levels of agar require 7200 t (dry weight) of agarophytes per year. However, only 5500 t of dried *Gracilaria* is produced by phycoculture, and thus demand exceeds the present supply (McHugh, 1996). The potential amount of agarophytes available from wild crops is estimated at 28 000 t (wet weight) (McHugh, 1996).

Carrageenophytes It was not until *Eucheuma* spp. were recognized as valuable carrageenophytes by the western carrageenan industries that large-scale export became established (Adnam & Porse, 1987; Rachmat et al., 1986; Stanley, 1987). The main species of carrageenophytes for phycoculture in Indonesia are *Eucheuma denticulatum* and *Kappaphycus alvarezii*. In the 1980s, inadequate drying and post-harvest contamination with sand resulted in poor export quality for foreign processors (Doty, 1986; Luxton, 1993; McHugh & Lanier, 1983). On the other hand, consumption by Indonesian processors and sustained de-

Table 6. Import and export values of agar during the period 1995–1997 for Indonesia and Singapore.

Country		Import			Export		
		Quantity (t)	Value (10^3 US$)	Unit price (US$/t)	Quantity (t)	Value (10^3 US$)	Unit price (US$/t)
Indonesia							
	1995	496	4711	9498	931	2942	3160
	1996	557	3783	6792	981	4974	5070
	1997	754	6640	8806	637	3327	5223
Singapore							
	1995	369	6168	16715	126	1714	13603
	1996	485	7180	14804	114	616	5404
	1997	319	4897	15351	32	369	11531

Source: FAO, 1999b.

mand by the Chinese food market for *Eucheuma denticulatum* (1500–2000 t annually) ensured a predictable base of farm production.

In 1990 between 6000 and 6500 t (dry weight) of *Eucheuma denticulatum* and between 4000 and 5000 t (dry weight) of *Kappaphycus alvarezii* were exported, to which can be added 2100 t (dry weight) of the latter species consumed by local processors (Luxton, 1993). In 1993 15 000–21 000 t (dry weight) of carrageenophytes (iota and kappa types) were exported from Indonesia for food grade carrageenan production (Bixler, 1996; McHugh, 1996). Data for 1994 give an estimated production of 26 294 t dried seaweeds, including '*Eucheuma*', *Gracilaria*, *Gelidiaceae* and others, of which 16 100 t was exported (Istini, 1998). In 1995 the dry weight production of *Eucheuma denticulatum* and *Kappaphycus alvarezii* together was estimated at 20 000 t (Trono, 1998).

In 1994 6 carrageenan-processing companies in Indonesia collectively produced 2300 t semi-refined carrageenan (SRC) and one company produced 120 t refined carrageenan (McHugh, 1996). The semi-refined carrageenan produced locally is not yet a final product, however, and has to be exported for final processing. None of this domestically produced, semi-refined carrageenan is consumed in the country itself and Indonesia must also import to meet its requirements for refined carrageenan (150–170 t annually), because its total produce is exported to Japan. For further information on carrageenophytes ('*Eucheuma*'), see Table 7.

Alginophytes Alginate has been produced by a factory in Bandung (West Java) since 1992. Production in 1992 was 300 t alginate which required 3000 t of dried *Sargassum* seaweed (Istini et al., 1998). Other data, however, estimate production at 100 t alginate per year and required 1000 t of dried *Sargassum* (McHugh, 1996). Nevertheless, Indonesian alginate imports rose from about 3700 t in 1987 to 5100 t in 1991. The estimate for 1994 was 4000 t. The main uses were in the food, brewing, pharmaceutical and textile industries (McHugh, 1996).

The farms Farming of *Eucheuma denticulatum* (market name: 'spinosum'),

Table 7. Production of carrageenophytes in Indonesia and the Philippines for the period 1990–1997.

	1990–1992	1993	1994	1995	1996	1997
Indonesia						
quantity, wet (t)	95 000[1]	110 000[1]	102 000	102 000	148 000	157 000
value (10^3 US$)	8 150	12 100	11 220	11 220	14 800	15 700
unit price (US$/t (wet))	87	110	110	110	100	100
from wild populations, wet (t)	11 284	8 395	8 438	9 575	13 543	15 000[1]
The Philippines						
quantity, wet (t)	289 664	376 379	454 708	545 407	611 561	602 215
quantity, dry (t)	38 677	47 844	50 614	58 324	117 511[2]	no data
value (quantity wet)(10^3 US$)	40 017[1]	37 384	41 984	49 158	58 716	50 910
unit price (US$/t (wet))	138	99	92	90	96	84
from wild populations, wet (t)	1 265	1 144	1 062	919	884	494

[1] FAO estimate;
[2] equivalent, calculated from produced carrageenan together with exported dry seaweed.
Sources: FAO, 1999a, 1999c.

Kappaphycus alvarezii (market name 'cottonii') and *Gracilaria* is a promising activity. In 1988 22 600 ha were identified as potentially suitable sites for seaweed culture, of which 17 700 ha was considered suitable for *Eucheuma* culture. Of these potential sites, about 900 ha are actually used for seaweed cultivation (Mintardjo, 1990). Later figures of the estimated potential exploitable area for *Eucheuma* culture, however, are approximately 9000–10 000 ha, with a production capacity of 450 000 t (dry weight) per year (Istini et al., 1998). *Gracilaria* is mainly farmed in South Sulawesi, where about 2000 farmers produce approximately 5500 t dried seaweed per year.

Microalgae PT Sun *Chlorella* Indonesia Manufacturing Company in East Java, a joint venture with Japanese companies, has 16 circular culture ponds, each capable of producing 36 t of wet *Chlorella*. The enterprise has a total production of 150 t *Chlorella* powder a year. Production started in 1995 with 6 t/year. All of the production is exported to Japan for processing and packaging.

Malaysia

Malaysia is marginally involved in the seaweed trade, although surveys have been undertaken for Malaysian seaweed resources and for species which might be potential sources of phycocolloids (Phang, 1984; Phang & Vellupillai, 1990). As yet there is no seaweed industry. The biomass of natural populations of commercial algae is unable to support harvesting for commercial extraction of phycocolloids (Phang, 1998). See also Table 5.

Marine vegetables Coastal inhabitants eat green, brown and red seaweeds, sometimes as salad, or cooked as vegetables (McHugh & Lanier, 1983). Seaweeds such as *Laminaria* ('kombu'), *Porphyra* ('nori') and *Undaria* spp. ('wakame') are imported, mainly from Japan, Korea and China.

Agarophytes In 1993 and 1994 about 6 t (dry weight) of agar from *Gracilaria* was produced by a small-scale, Thai-owned processing factory in Selangor (Peninsular Malaysia) for local consumption in jelly-type sweetmeats. In 1987 about 240 t of agar, worth US$ 2 600 000, was imported, mainly from Korea and Japan (McHugh, 1996). Since trials for *Gracilaria* cultivation were successful, and because there is a large market for domestically produced agar strip, the country seemed to be a good choice for future development of agar strip production facilities for the region (McHugh, 1996).

Carrageenophytes Jellies are also made from carrageenan extracted from *'Eucheuma'* by local coastal populations. Refined carrageenan, however, in quantities of about 150 t, with a value of US$ 1 600 000 are imported annually. These carrageenans are used in industry and this market is expected to grow at 5% per year (McHugh, 1996).

Alginophytes The domestic market for alginates in 1978 was thought to be sufficiently large to support a small alginate processor. There was, however, no information available on the extent of *Sargassum* and *Turbinaria* beds in the area, nor of the quality of any alginate extracted from them (McHugh & Lanier, 1983). Some *Sargassum* spp. from Sabah (East Malaysia), however, have a high content of guluronic acid (Wedlock et al., 1986). Alginates of these algae are supposed to form strong gels, sought after for special applications (McHugh, 1987). Recent annual import quantities of alginate for Malaysia are estimated to be 60 t (McHugh, 1996).

The farms Farming of *Gracilaria changii* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia is promising and is in an experimental stage in Peninsular Malaysia (Phang, 1998). The seaweeds are cultivated in an integrated polyculture system with shrimps (*Panaeus monodon* and *Lates calcifer*). In Sabah (East Malaysia) small-scale *Kappaphycus* culture takes place, which has resulted in the export 80 t (dry weight) of cultured *Kappaphycus alvarezii* (as *Eucheuma*) to Denmark in 1990 (Choo, 1990). More recently the crop (500–1800 t dry weight per year) is exported to the Philippines (FAO, 1999b; McHugh, 1996; Phang, 1998).

Microalgae Some microalgae are cultured to be used as feed for larval stages of organisms grown in aquaculture or for use in integrated systems for waste-water treatment (Phang, 1987; Shamsudin, 1992).

The Philippines

About 350 economically important seaweed species from the Philippines have been recognized (Trono & Ganzon-Fortes, 1988); the different uses of only 150 species of seaweeds have been reviewed (Llana, 1990; Trono, 1986, 1999; Trono & Ganzon-Fortes, 1988; Velasquez, 1953, 1972). These uses include, apart from being a source of phycocolloids or food, mainly horticultural and medicinal applications. Only 1% of the seaweed production is consumed locally as food (Llana, 1990).

Marine vegetables Over 40 species of seaweeds are gathered and directly utilized as food in the coastal areas of the Philippines. Production is seasonal and in small quantities and detailed information is lacking (Trono, 1998). There is, however, one exception: *Caulerpa racemosa* (and more recently *C. lentillifera*) has been produced in phycoculture ponds since as early as 1950. More than 400 ha of ponds are used for the cultivation of *C. lentillifera* in Mactan Island, Cebu. These algae are either sold fresh or exported as a brine-cured product to Japan. More than 20 000 t (wet weight) of these green algae are produced (FAO, 1996, 1999c). See also Table 2.

Agarophytes Of the agarophytes, mainly *Gracilaria* is available and utilized, although other algae are used as agarophytes as well (Montaño & Pagba, 1996). Domestically produced agar strips ('gulaman bars') are sold in 5 g pieces; there is a total agar production of about 30 t per year. Only relatively small amounts (less than 10 t/year) of agar are imported, mainly for applications in the biotechnology and pharmaceutical industries.
Farming of *Gracilaria* is promising (FAO, 1996, 1997) and more than a dozen species are presently grown in culture, which produced 10 t (wet weight in 1994). However, only 4 species are in commercial production: i.e. *Gracilaria heteroclada* C.F. Zhang & B.M. Xia (= *Gracilariopsis heteroclada* C.F. Zhang & B.M. Xia), *G. firma* C.F. Zhang & B.M. Xia and a still unidentified *Gracilaria* sp. are partly produced through cultivation, while *G. tenuistipitata* C.F. Zhang & B.M. Xia is produced mainly from natural stocks (Trono, 1998). The total amount of wild *Gracilaria* harvested annually is estimated at 200 t (dry weight). Apart from *Gracilaria* only *Gelidiella acerosa* is suitable for agar production, and is almost exclusively harvested through the gathering of local stocks (Trono, 1998).

Carrageenophytes The phycoculture of *Eucheuma* in the Philippines was pioneered and developed in the period 1968–1971. This greatly promoted the carrageenan industry (Anonymous, 1998; Laite & Ricohermoso, 1980; Lim & Porse, 1981; Ricohermoso & Deveau, 1979; Stanley, 1987). Annual production increased from 300 t dry wild seaweed in 1970 to 130 500 t dry weight seaweed (mainly from phycoculture) during the period 1978–1980 to 117 511 t dried carrageenophytes or an equivalent of 822 500 t wet weight in 1996 (Anonymous, 1998; McHugh & Lanier, 1983). Of the 15 000 t dry seaweed produced in the Philippines in 1980, only 700 t of carrageenans were produced in that country, and most of the seaweeds were exported as raw material. In 1990 1295 t (wet weight) of carrageenophytes were still collected from wild stocks. That amount declined to 494 t (wet weight) in 1997, as compared to 291 176 (1990) and 627 105 (1997) t (wet weight) produced by phycoculture (FAO, 1999a). Data from different sources are not always comparable, however (Dawes et al., 1990; Llana, 1990; McHugh, 1990; Trono, 1990, 1998). See also Tables 2, 5 and 7.
The principal species grown in the Philippines is *Kappaphycus alvarezii* ('cottonii'), with smaller and irregular amounts of *Eucheuma denticulatum* ('spinosum'). The seaweeds are either exported to carrageenan producers, or semi-refined carrageenan ('natural grade carrageenan') is produced locally. At present 10 different companies (mostly members of the Seaweed Industry Association of the Philippines, SIAP) export semi-refined carrageenan, while 3 export pure

carrageenan (Anonymous, 1998). In 1990 these companies provided employment for more than 10 000 people (Trono, 1998). By 1987, more than 50% of all Philippine *Eucheuma/Kappaphycus* harvests were utilized by local processors in the manufacture of carrageenan products, which then generated about 60% of the country's foreign exchange earnings. Seaweeds and their products form the third most important fishery export of the Philippines (Trono, 1999). Large quantities of semi-refined carrageenan were produced in 1995 and 1996, while 14 493 and 18 292 t respectively of semi-refined carrageenan were exported, as well as 2375 and 2252 t of refined carrageenan. The local market, however, is only small (McHugh, 1996; Trono, 1999).
In 1991 the United States Food and Drug Administration (USFDA) classified 'PNG' as carrageenan. In the European Union, however, the product is known as 'processed *Eucheuma* seaweed' (PES) and is accepted as a food additive (INS – E407a). Another designation, 'Alternatively Refined Carrageenan' (ARC) is also used (Anonymous, 1998).

Alginophytes Sargassum is mainly collected sun-dried and shipped to Japan to be used as fertilizer or in powder form as a binder of heavy metals in sewage water treatment. However, the bulk of the collected *Sargassum* biomass is presently processed into seaweed meal and utilized in the production of animal feed, whereas a part (5000 t in 1987) is still exported to Japan (Trono, 1998). The harvest of local stock is presently limited to northern Mindanao and Visayas. There is no local alginate production in the Philippines (McHugh, 1996).

The farms Over 10 000 family-owned and commercial seaweed farms were in operation around 1991, with over 170 000 people employed (Dawes et al., 1993). For 1989 the total number of 'fisher folks' directly involved in the farming of '*Eucheuma*' was about 70 000 people (Trono, 1990). In 1998 about 80 000 farmers were involved in seaweed cultivation and, in addition, more than 300 000 people engaged in activities related to the seaweed industry (Trono, 1998). In 1997 10 000–15 000 ha of seaweed farms were located in the shallow coastal waters of the Philippines (Anonymous, 1998). Farm sites are mainly centered in south-western Mindanao (Zamboanga), the Sulu Archipelago, Tawi-tawi and southern Palawan (Trono, 1998).

Microalgae There is no large-scale commercial production of microalgae. A company is promoting a novel concept for the contract growing of *Arthrospira* (*Spirulina*). The company provides training and materials such as *Spirulina* inoculum and chemicals for culture medium are sold at cost price to the contract producers. The company buys back the dried microalgae which are produced (Lee, 1997).

Singapore

The involvement of Singapore in the seaweed trade is mainly by import and export of dried seaweeds and agar (Tables 5 and 6). Nevertheless, the differences between imported and exported quantities suggest a certain amount of consumption in Singapore of both products (FAO, 1999b).

Burma (Myanmar)

Studies of the seaweed flora of Myanmar are still incomplete. Up to now 307 species of seaweeds in 122 genera have been recorded (Soe-Htun, 1998). Of these algae, experimental cultivation of *Catenella nipae* Zanardini, *Gracilaria salicornia* (as *G. crassa*) and *G. edulis* (S.G. Gmelin) P.C. Silva is being undertaken at Setse Aquaculture Research Centre, on the Tanintharyi coast.

Marine vegetables Seaweeds are not generally popular as vegetables. Nevertheless, *Catenella nipae* is available as a sea vegetable from the market in Yangon. Edible seaweeds in a dried form are sold on the domestic Burmese market, these include *Catenella*, *Enteromorpha* and *Hypnea* spp. Coastal people use *Catenella* Grev., *Gracilaria*, *Halymenia* C. Agardh, *Hypnea*, *Sargassum* and *Solieria* J. Agardh in salads (Soe-Htun, 1998).

Agarophytes There is no internal agar industry, although agar powder imported from neighbouring countries is very popular among the people. Locally farmed *Gracilaria edulis* did not attract enough demand to warrant continued production. If a local agar-processing industry could be initiated, both the domestic demand and the potential to farm *Gracilaria* are positive factors (Soe-Htun, 1998).

Carrageenophytes Carrageenan is mainly obtained from *Hypnea*, of which there is a standing stock of 1500 t (dry weight). About 25 small factories produce strips of carrageenan for the domestic market. However, this product is not very popular since people prefer imported agar powder for making jelly desserts (Soe-Htun, 1998).

Microalgae About 30 t of *Arthrospira* (*Spirulina*) are commercially harvested from volcanic lakes (Twyn Taun and others) near Butalin in Central Burma. *Spirulina* flakes are first sun-dried, then ground into fine powder and finally punched into tablets (Lee, 1997).

Thailand

The use of seaweeds is limited to only those people living in the coastal area, especially along the Gulf of Thailand and the Andaman Sea. Recent imports and exports of seaweeds are documented in Table 5.

Marine vegetables Especially *Caulerpa racemosa* and *Porphyra* are used as a vegetable. The total crop of *Porphyra* is less than 100 kg (dry weight) per year, while no data are available for *Caulerpa*. Imports in 1989 of 78 t of dried and preserved seaweeds consisted mainly of *Laminaria* ('kombu'), *Porphyra* ('nori') and *Undaria* spp. ('wakame'), which are used as food. These imports mainly came from Japan, China and Korea.

Agarophytes In 1985 production of 4233 t of seaweeds was recorded (FAO, 1995). Seaweed production data for later years are lacking (FAO, 1995, 1996, 1997). Up till 1989 about 100 t (dry weight) of seaweeds were annually exported from Thailand, including 30–50 t of *Gracilaria*, some of which was obtained from phycoculture (Saraya & Srimanobhas, 1990). Pond culture of *Gracilaria fisheri* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia (also by monoline culture) and *G. tenuistipitata* is currently successful. The combined production of *Gracilaria* from natural stocks and cultivation in ponds ranged between 50–400 t/year in Pattani Province, while data on the production from the monoline cultures in Songkhla Lake are not yet available (Lewmanomont, 1998; McHugh, 1996). Most of the material is exported. In some years, Thailand imported rather large quantities of agar (1989: 275 t) for different industrial uses and re-exported much smaller amounts (e.g. 1989: 3 t) as repacked flavour agars (Saraya & Srimanobhas, 1990).

Carrageenophytes Annual imports for carrageenan are about 1100 t/year. The large pet-food industry in Thailand uses about 780 t of semi-refined carrageenan annually, valued at US$ 2 500 000. Tuna processing, the jelly and confectionery industry and toothpaste manufacturers each use more than 100 t of imported, refined carrageenan per year. To cope with its annual demand for approximately 780 t of carrageenan, Thailand could support a semi-refined carrageenan facility if it imports the raw seaweed material from neighbouring countries or established its own *'Eucheuma'* cultivation industry (McHugh, 1996).

Alginophytes The brown seaweed *Sargassum* is the most common genus of marine algae in Thailand. When these algae are used, it is mainly for fresh consumption or as a herbal medicine. The import of 316 t of alginate for different industrial uses is documented for 1989, for 1994 the figure was 400 t, the latter with a value of US$ 4 000 000.

Microalgae The two major producers of *Arthrospira (Spirulina)* produce 150 t and 20 t *Spirulina* powder per year respectively, mainly for human consumption as health food (Lee, 1997).

Vietnam

Traditional harvesting and utilization of seaweeds by coastal people has taken place for over 100 years. Seaweeds are used for human and animal food, as traditional medicine, manure and raw materials for industry (Huynh & Nguyen, 1998).

Agarophytes In 1984 a small agar production facility existed, but production data are not available (Armisén & Galatas, 1987). The main commercial seaweeds are about 15 *Gracilaria* spp., with a total production from natural stocks of about 9300 t wet weight (= about 800 t dry weight) in 1990. These algae were harvested from the total estimated available wild biomass of 30 000 t (wet weight). At present, the main species cultivated are *G. vermiculophylla* (Ohmi) Papenf. (as *G. asiatica* C.F. Zhang & B.M. Xia), *G. tenuistipitata* and *Gracilariopsis heteroclada*. Of these gracilarioid algae, together with some *Gelidiella acerosa* (Forssk.) Feldmann & Hamel collected from natural populations, 100–300 t (dry weight) were used for agar-agar processing for foodstuffs, resulting in a production of 10 t food quality agar in 1987, 20 t in 1989 and 80–100 t in 1996 and 1997 (Huynh & Nguyen, 1998). *Gracilaria* production has become considerable, and was estimated in 1997 at 1500–2000 t (dry weight). A large part of this material is being exported to Russia, Japan and China (FAO, 1996; 1999a; Huynh & Nguyen, 1998). See also Table 2.

Carrageenophytes Both *Kappaphycus cottonii/alvarezii* and *Betaphycus gelatinus* are grown in phycoculture, each with an annual production of about 10 t (dry weight). These algae are, up to now, mainly used for food purposes. Cultivation of *K. alvarezii* started recently and is expected to become economically much more important in the coming years (Huynh & Nguyen, 1998).

Alginophytes The brown seaweed genus *Sargassum* is the largest natural seaweed resource of Vietnam. The annual production in natural *Sargassum* beds is estimated to be over 5000 t (dry weight), but the total amount harvested is only 300–500 t/year (dry weight). Annual production of alginate paste and powder from *Sargassum* is 15–20 t. These values far from satisfy the needs of the local textile industry, for which alginate has to be imported from India (Huynh & Nguyen, 1998; Van Khuong, 1990).

The farms The area used for *Gracilaria* phycoculture is around 350 ha, which is only a fraction of the potential area of more than 10 000 ha thought to be available (Van Khuong, 1990).

Microalgae In Vietnam *Arthrospira* and some diatoms in particular are cultured. Of the diatoms *Chaetoceros* sp. and *Skeletonema costatum* are grown in culture for use in shrimp hatcheries. In 1989 *Arthrospira* cultivation was executed in two factories, one of which measured 1000 m^2 in surface area. The two factories produced pellets or dried tablets to be used as nutritional supplements for women and children (Van Khuong, 1990).

No data are currently available for the use of algae or the algal industry in Papua New Guinea, Brunei or Cambodia.

1.3 Botany

Algae are all the autotrophic organisms other than plants, a group of 30 000 to 40 000 different and described living organisms (Norton et al., 1996). The total number of undescribed species, however, may exceed known ones by a factor of four to eight. For a long time algae have been considered as primitive plants without a strict tissue differentiation, but only some groups of green algae are related to the 'real' plants. The members of the informal group called 'algae' are not necessarily related. Some algae are more closely related to bacterial groups (the blue-green algae are in fact *Cyanobacteria*), while others are more closely related to some Protozoa or to fungus-like organisms than to other algal groups. Algae occur in an incredible variety of life forms, from uni-cellular species to giant kelp which may extend to more than 60 m in length. The algal body is designated as a 'thallus' or a 'frond'. In general, drawing conclusions about algae by analogy with plants, or even with other algal groups, is often fraught with potentially invalid assumptions.

Pigments

Since all algae are autotrophic, they contain chlorophylls as the main photosynthetic pigments, usually together with many accessory pigments. Due to these pigments, the algae can use light energy for photosynthesis, although several microalgae are capable of heterotrophic growth as well (Gladue & Maxey, 1994). The photosynthetic algae fix over 40% of the earth's carbon (Norton et al., 1996). All that goes into and out of an algal thallus does so by diffusion, because no roots or vascular tissue are available for transport (Doty, 1979). The highest rates of net photosynthesis under optimal environmental conditions are achieved by the sheet-like and filamentous annuals. Photosynthetic rates decrease in the more bulky growth forms of perennial algae, where many cells are set aside in the thallus for purposes of storage, translocation and stability. In some algal groups calcification of cell walls occurs, probably for protection from grazing. However, the high cost of calcification is evident from the generally low photosynthetic rates of calcified algae (Lüning, 1990).
In many cell walls of brown and red algae phycocolloids serve a structural function analogous to, but differing from, that of cellulose in land plants. Whereas land plants require a rigid structure capable of withstanding the constant pull of gravity, aquatic plants must have a more flexible structure to accommodate the varying stresses of currents and wave motion. They have adapted accordingly by hydrophilic, gelatinous, structural materials having the necessary flexibility (Lewis et al., 1988; Lobban & Harrison, 1994).

Taxonomy

Seaweeds are generally classified into four main groups, largely on the basis of their structure and pigmentation: red algae (division *Rhodophyta*), brown algae (division *Phaeophyta*), green algae (division *Chlorophyta*) and blue-green algae (division *Cyanophyta*, which is a group of the Prokaryotes). However, colour is only an approximate guide, e.g. red seaweeds show a variety of colours, from pink to purple and black. Botanists use structural features of the seaweeds as an accurate guide to classification.
Brown seaweeds are, especially in temperate regions, the most familiar, conspicuous, largest and most abundant of the seaweeds, but in number and diversity they are exceeded by the red seaweeds, of which there are 4000–6000 recognized species (McHugh & Lanier, 1983; Norton et al., 1996). Red seaweeds are usually smaller than brown seaweeds, with even some unicellular species occurring. The red seaweeds of commercial interest, however, are usually rather robust organisms. Of the green algae the majority is formed by microscopic members, but in the marine environment often multicellular representatives occur, as well as multinucleate (siphonous) thalli, in which the many nuclei are not separated by cell walls. The morphology of these green algae is very diverse, showing complicated coenocytic structures as well as plate-like or tubular thalli.
Several surveys of Philippine seaweeds have been made, including most of the economic species (Calumpong & Meñez, 1997; Trono, 1997; Trono & Ganzon-Fortes, 1988). A catalogue of the Philippine seaweeds is available (Silva et al., 1987). For Indonesia the old list of the Siboga-Expedition is still the most com-

plete survey, supplemented by a number of more regional surveys (Coppejans & Prud'homme van Reine, 1992; Verheij & Prud'homme van Reine, 1993; Weber-van Bosse, 1913–1928). There are surveys for Malaysia (Phang, 1998; Phang & Wee, 1991) and Singapore (Teo & Yee, 1983), Vietnam (Nguyen & Huynh, 1993; Pham, 1969) and Thailand (Lewmanomont et al., 1995; Lewmanomont & Ogawa, 1995). A series of papers has recently been published for Papua New Guinea (Coppejans et al., 1995a, 1995b; Millar et al., 1999).

For a broader area, e.g. the Indian Ocean, another catalogue is available (Silva et al., 1996). For freshwater algae very few recent data are available, although there is a survey of the freshwater algae of Thailand (Lewmanomont et al., 1995).

The blue-green algae are morphologically the most diverse and complicated of the Prokaryotes. Both unicellular and filamentous representatives occur, while the cells may also grow together to form colonies. Species with the potential to be used as bio-fertilizers have heterocystous filaments. *Arthrospira platensis* is an important source of protein in some inland tropical areas.

Growth and development

The numerous different algal groups show a broad variation in life cycles. In many groups there is only one major kind of life cycle present, but in other groups (e.g. in the *Phaeophyta*) several major kinds of life cycles exist, often with an alternation of generations (van der Hoek et al., 1995). These generations, known as sporophytes and gametophytes, can be isomorphic to each other or heteromorphic. In the latter case the dimensions of the thalli of the different generations may be very different and then microstages and macrostages can be distinguished. These heteromorphic generations can greatly differ in morphology and are often given separate scientific names. In several cases it has only been detected quite recently that morphologically very different algae in fact belong to a single species and are only stages or generations in the life cycle of that species.

All algae have unicellular spores and gametes, but occasionally vegetative propagules are also present in some species. Once the spores and propagules of benthic algae have been released from the parent generation, they must find a surface and stick to it. The microscopic stages of most seaweeds are inconspicuous. Resting spores or resting zygotes seldom form thick walls in marine macroalgae, while in many microalgae thick-walled resting spores and cysts are of frequent occurrence. Many seaweeds are perennial, but some opportunistic algae often occur as short-living annuals. In several seaweeds, the combined effects of temperature and photosynthesis regulate development and reproduction (Lobban & Harrison, 1994).

Productivity

Although the biomass of natural algal vegetation in tropical marine waters is not usually very impressive, the annual primary productivity can be very high. Turnover rates (total renewal of biomass) for some tropical seaweeds are 1–1.5 months, resulting in maximum values for annual primary productivity that are higher than in tropical rain forests (Harlin & Darley, 1988; Lüning, 1990).

High productivity occurs especially on coral reefs and in benthic *Sargassum* vegetations. Most nutrients there remain in a relatively closed environment with many herbivores and predators, resulting in a quick recirculation. In contrast to temperate regions, where about 90% of the seaweed biomass is thought to be decomposed and finally mineralized in detritus food chains, in tropical regions much of the seaweed biomass is consumed by grazers (Lüning, 1990). Primary productivity in the marine waters of South-East Asia is generally high, although the surrounding open oceans have much lower primary productivity values (Lembi & Waaland, 1988; Rodin et al., 1975).

1.4 Ecology

Blue-green algae and green algae, although also present in salt water, are more commonly associated with freshwater and on land (for example, on tree trunks, in soils, etc.). The largest forms of the green algae, however, occur in the sea. Red and brown algae are usually associated with marine environments, often rocky shores, although some representatives of these groups occur in freshwater. Blue-green algae are ubiquitous members of the soil microflora. Brown seaweeds are particularly abundant in cold and temperate waters and most species of commercial interest grow best in waters below 20°C, usually at or below the intertidal zone (McHugh & Lanier, 1983). Few species are found in tropical regions, of which members of the genera *Sargassum* and *Turbinaria*, however, may be locally dominant and also of commercial interest.
Red seaweeds often grow in deeper waters than the brown ones, e.g. from just above the low tide level down to more than 50 m. Many species occur in temperate to tropical waters, amongst which are several of considerable commercial interest.
Green seaweeds may become dominant in pools and in the intertidal, especially in eutrophic situations. In tropical regions, the multinucleate genera (*Caulerpa* J.V. Lamour., *Halimeda* J.V. Lamour. and others) especially form important constituents of both seagrass meadows and coral reefs.

Temperature

Temperature, and particularly water temperature, is the main abiotic factor governing the geographical distribution of seaweeds, although interactions amongst environmental variables are the rule rather than the exception. Many marine seaweeds can not survive seawater temperatures higher than 33–35°C . Some, however, can tolerate much lower seawater temperatures than occur in their own environment (Lüning, 1990). The edaphic *Cyanobacteria* generally grow and fix nitrogen optimally between 30–35°C ; thus temperature is not limiting to their growth in the tropics. Several blue-green algae are unique in the microbial world for their ability to simultaneously fix nitrogen in aerobic habitats and carbon by the oxygenic eukaryotic plant mechanism (Metting et al., 1988).

Light

Algae, being autotrophic organisms, need light to be able to survive and for that reason they can only occur in locations where at least some light will reach them. As a rule, macroalgae live attached to the seabed between the top of the intertidal zone and the maximum depth to which adequate light for growth can penetrate (Lobban & Harrison, 1994). In very transparent tropical or subtropical marine waters some algae may reach depths of around 200 m, but most of them prefer much more light and occur close to the surface of the water, often protected from strong irradiance and desiccation by canopy seaweeds that shade the understory algae. This protection is important to the survival of understory algae, including germlings of larger species (Lobban & Harrison, 1994).

Water movements

Water movements are necessary for the adequate supply of nutrients and removal of silt, detritus and excretion products from the surface of seaweeds. These water movements can increase the steepness of the diffusion gradient for all nutrients and excretion products, while both too much and too little outward-diffusion may depress growth rates (Doty, 1979). Water motion can also become excessive, resulting in the physical removal of algae from a given site.

Desiccation

Most subtidal seaweeds do not survive desiccation, but intertidal ones often exhibit a remarkable desiccation tolerance. Such algae are unable to avoid desiccation, and thus simply tolerate it and survive the related osmotic stress (Lüning, 1990).

Soil surfaces in deserts are commonly consolidated by cryptogamic communities, of which algal crusts can be important constituents. Functions of algal crusts include consolidation of the crust, mediation of infiltration and retention of water, and nitrogen input. The desert surfaces are consolidated by the combined aggregating effects of mucilaginous sheaths and the filamentous nature of dominant blue-green algae. Ensheathed blue-green algae retain water, which buffers against rapid desiccation and promotes water infiltration (Round, 1981).

Salinity

Many microalgae, and certainly all the marine ones, have a low tolerance of salinity change. Some, however, occur typically in a wide salinity range. In inland saline lakes, only few microalgal species occur and these are especially well-suited for mass culture since most of the potential contaminating and competing aerial algal spores and cysts will not be able to germinate in such extreme saline environments. Marine microalgae can also be found in an aerial environment, but they usually do not contaminate open air mass cultures in hyper-saline situations (Borowitzka & Borowitzka, 1988; Round, 1981).

Most marine macroalgae grow optimally at salinities of approximately 30‰, but there are exceptions such as *Gracilaria* spp. and the mangrove algae of the red algal genera *Bostrychia* Harv. and *Caloglossa* J. Agardh. These species often show maximum growth at much lower salinities (Lüning, 1990). In the species of the latter two genera brackish-water ecotypes may also occur; these do not tolerate high salinities (Lüning, 1990). In these euryhaline ecotypes respiration and photosynthesis decline only slightly with decreasing salinity.

Competition

Algae may experience considerable competition with other organisms, as there are other algae and phototrophic organisms (e.g. competition for space, light, carbon and nutrients), or parasites, pathogens and herbivores (Lobban & Harrison, 1994; Olson & Lubchenco, 1990). Therefore, many algae have developed toxins, digestive inhibitors, or unpalatable substances. In particular, anti-herbivore substances are often found in seaweeds; there are phenol-like substances in brown algae and halogenated substances in red algae (Lüning, 1990). Inhibiting substances might also explain the clean appearance of some brown and red algae in the field, since most epiphytic organisms are unable to settle or grow on these thalli. Most epiphytic organisms attach only superficially to the surface of their host. For this reason, some seaweeds slough their outer layers to inhibit the growth of epiphytes. Epiphytic algae decrease the growth rate of their host, increase the probability of breakage of the thalli of the host and may decrease reproductive output. Epiphytic animals may also cover large parts of the thalli of seaweeds. In epiphytic animals their larvae are chemically attracted by the preferred host alga.
Epiphytes can be removed by small herbivores which specialize in browsing on epiphytic organisms (Lüning, 1990). Most epiphytes are not specific to their host, and are not parasitic, but there are notable exceptions of specialized epiphytes and even parasitic algae.

1.5 Exploitation and cultivation

Marine agriculture has a relatively short history (approximately 250 years), especially when compared to approximately 8000–10 000 years of terrestrial agriculture. In the years 1970–1972 almost nobody would have predicted any future growth in marine agronomy and South-East Asia was barely covered in handbooks on aquaculture (Bardach et al., 1972; Doty, 1979). *Gracilaria* and other algae as food for milkfish were mentioned and the culture of *Caulerpa* in the Philippines for the fresh vegetable market was also listed. The advanced experimental culture of *Eucheuma* and *Hypnea* spp. in the Philippines was then mentioned for the first time (Bardach et al., 1972).
Traditionally, the seaweed industry has relied on the gathering of wild seaweeds to meet its raw material requirements. The accelerating pace of advances in seaweed culture techniques, however, combined with the expanding demand for seaweed products and the rising costs of operation in industrialized countries are creating forces that have potential to alter the global distribution of this industry in the foreseeable future. This in particular holds true for the seaweed colloid manufacturing sectors (McHugh & Lanier, 1983). It has been proposed that the term ‘phycoculture’ be used for farming of algae in general, and thus ‘marine phycoculture’ as the commercial farming of seaweeds (Tseng, 1981a).

1.5.1 Production systems

The natural productivity of many seaweeds is only about 1t (dry weight)/ ha/ year in nutrient-poor water, the actual productivity depending, of course, on many parameters and on the species (Wise, 1981). Productivity may, however, exceed 40 t (dry weight)/ha/year under good cultivation conditions (Morand et al., 1991).

Collection of wild resources

Harvesting techniques for wild resources of marine macroalgae vary, depending on circumstances. They can, however, be classified as follows:
- gathering of seaweeds washed to the shore;
- gathering seaweeds by cutting or uprooting them from their beds, often by scuba divers (Armisén & Galatas, 1987).

In all cases where seaweed industries expand, over-exploitation and eventual loss of local stocks are considerable risks. Thus development and commercialization of phycoculture of the exploited seaweeds is usually a necessity.
When harvesting wild populations of the microalga *Arthrospira* (*Spirulina*) several technical, ecological, and public health issues require serious evaluation before any large-scale venture can be undertaken (Jassby, 1988a).

Extensive field production of macroalgae

Seaweeds grown in open lagoons and cultivation where natural populations are supported (as in *Betaphycus gelatinus* in Hainan, China) can be considered as a form of extensive field production, although transitions to more intensive forms of cultivation frequently occur.

Intensive market gardening

For most algae that are cultivated, intensive phycoculture methods are used, for which tanks, ponds, rafts or systems of lines have to be installed and maintained. Different types of phycoculture may be characterized on the basis of the methods used (Pérez et al., 1992):
- Fragmentation by hand and growing the fragments to mature plants (vegetative propagation). This is the case in cultivation of *Caulerpa*, *Eucheuma*, *Gracilaria* and *Kappaphycus*.

  In tropical regions marine phycoculture for the production of food or of phycocolloids is either by pond culture, by fixed, off-bottom monoline methods or by floating methods, where either rafts or longlines are used. The methods to be preferred depend on the species to be cultivated and the local circumstances, as well as on the conceptual framework for marine phycoculture (Santelices, 1999). In general *Gracilaria* spp. and *Caulerpa lentillifera* are grown in ponds, while *Eucheuma*, *Kappaphycus* and several other *Gracilaria* spp. are cultured attached to monolines, rafts, longlines or off-bottom systems (Luxton, 1993). To account for and avoid the possible devastating actions of tropical storms, the areas within about 6° of the equator are considered to be the most favourable for potential seaweed cultivation sites (Doty, 1979).

Basically, a seaweed farm for *Eucheuma*, *Kappaphycus* or line-grown *Gracilaria* comprises networks of lines suspended either from mangrove stakes and then immersed a short distance below the low-tide level, or from (bamboo) rafts. Fixed bottom monoline phycoculture (constant depth farming) is an inexpensive and easy method to establish and maintain. It needs bi-filament polythene twine, either No 5 (2.5 mm) or No 6 (3.0 mm) and mangrove stakes. The 'seedlings' are inserted between the twines to start farming. A plot can be 10 m × 10 m in area (two plots of 5 m × 10 m are better), with a maximum of 32 lines, each about 32 cm apart. The lines are stretched and tied to the stakes, which are positioned approximately 5 or 10 m apart (Trono, 1990).

Material costs of the floating rafts are higher than those of off-bottom systems (Luxton, 1993). Floating raft monoline phycoculture can be used in places where the cultivated algae can be submerged in 30 cm of seawater at all times. In addition, the raft must be able to withstand the weight of the seaweeds near harvest time. Recommended material for the raft is bamboo measuring 2.5 m × 5.0 m or 5.0 m × 5.0 m. The lines are stretched within the rafts which need to be well anchored.

'Sprigs' (cuttings) of the algal seedstock are suspended from the lines. They may be pruned back when mature, with growth continuing from the remaining thalli (Lewis et al., 1988). Alternatively, farmers may harvest the whole plants and replant the farm with cuttings. The best plants from the harvest are selected and used for the next crop. The built-in mechanism of 'seed improvement' by selection is a great advantage of this practice and is not possible with the pruning method of harvesting (Trono, 1994).

- In the second group of intensive cultivation methods, parts of the culture work is undertaken indoors, where microscopic stages of the life cycle of the cultivated algae are handled (Pérez et al., 1992). These techniques are not yet commonly applied in South-East Asia (Trono, 1994). Indoor cultivation methods, however, can also be used in micro-propagation in *Eucheuma denticulatum* and *Kappaphycus alvarezii* (Dawes et al., 1993).
- In the third group of intensive phycoculture methods all actions are on land, and the cultivated algae are grown in tanks. Up to now results with seaweeds in tanks are not very promising, but cultivation of several species of microalgae can be successful and occurs, albeit not frequently, in some countries in South-East Asia.

Cultured microalgae

Unicellular freshwater algae are often grown in special facilities consisting of shallow cultivation tanks located in dry land areas with much sunshine. Blue-green algae, for direct use as agricultural fertilizer, are also grown in similar shallow cultivation tanks or ponds. When the water is allowed to evaporate in the sun, these blue-green algae form dry flakes that can be scraped off, stored in bags and be used as inoculum for rice fields after rice transplantation (Metting et al., 1988, 1990; Mshigeni, 1982).

Large-scale algal culture systems for microalgae need engineering designs of a size sufficient to produce tonnes of algae or algal products daily (Oswald, 1988b). This involves consideration of not only the application desired, but also

many other factors, such as media requirements of the species to be grown and various media inputs as a function of quality and availability for economic production. Local climatological conditions must also be taken into account, including variation in illumination, temperature, precipitation and evaporation. The following must also not be forgotten: physical properties of the design area, including slopes, drainage, water quality and quantity and the specific physical requirements for cultures, e.g. mixing, depth, residence time and power inputs needed (Oswald, 1988b). These factors, together with attainable efficiencies and productivities, harvesting and processing and the costs need to be related to the specific application to ensure success. This may be cultivation of microalgae on organic residues as the basis for production of fish and other animals or use as oxygen generators for waste oxygenation and nutrient control as well as systems for production of high-value fine chemicals or health food products (Belay et al., 1994; Borowitzka, 1992; Laing & Ayala, 1990).
Carbonation (CO_2-supply) of microalgal cultures is usually required, as well as continuous mixing in all shallow outdoor cultures (Vonshak, 1997). In some cases cultivation of freshwater algae in seawater-based culture media is feasible (Tseng & Xiang, 1993). Continuous flow mixing in shallow channelized ponds, driven by propeller or screw pumps, by air lift pumps or by paddle wheels are methods often chosen, particularly in tropical areas (Oswald, 1988b). However, not all microalgae can be grown adequately in such ponds. A fairly new development is the use of tubular photo-bioreactors (Borowitzka, 1994; Materassi, 1994; Torzillo, 1997). Another possibility is the vertical alveolar panel reactor (VAP), which can also be used in combination with open raceway ponds (Materassi, 1994; Pushparaj et al., 1997; Tredici & Chini Zittellii, 1997). A third alternative is heterotrophic growth of microalgae (Day & Tsavalos, 1996; Gladue & Maxey, 1994; Johns, 1994).

1.5.2 Domestication of algae

Seaweeds versus land plants

The difficulties involved in the domestication of seaweeds, transforming them from wild plants into crops, are many. The most fundamental is that in the farming of seaweeds one is dealing with a very different organism than in the case of farming of land plants. First of all, there is a big difference between the reproductive units of seed plants and algae. Terrestrial crops mostly reproduce by seeds which are multicellular, macroscopic and generally can be preserved by drying and eventually sown into the soil. The algae reproduce by microscopic unicellular spores and gametes which usually can not be preserved by drying or stored in any form. However, propagation using vegetative fragments is often possible in multicellular algae. The spore-liberating algae should be brought as close to the desired substrate as possible, so that the liberated spores and fertilized eggs will find the necessary place to attach and grow (Tseng, 1981a).

Tissue culture

Tissue culture is a method of propagation of sterile plants that is frequently used in terrestrial agronomy. The technique has also special problems when used in phycoculture (Polne-Fuller & Gibor, 1987). As a consequence of the aquatic habitat and unique chemical composition, seaweeds present the biotechnologist with problems which are very different from those encountered with land plants.

The aquatic habitat

Another fundamental difference between cultivation of terrestrial and phycoculture crops involves the growth media. Land crops grow on soil and in air, whereas the aquatic crop plants grow in water, usually attached to some sort of substrate. In the case of the land crop plants, the air is relatively gentle and the plant is stationary with respect to the source of light. In the case of aquatic crop plants, water is constant, but there is often vigorous motion with perpetual pounding of waves and ever-changing tidal levels. In addition, the substrates to which the algae attach must be able to withstand the continuous water motion and remain stable enough to ensure that the algae remain at a particular level where it can receive adequate light for photosynthesis. The water movements also replenish nutrients and cleanse the algae of silt, detritus and other sediments. All these and other differences naturally lead to differences in the technical methods of cultivation (Tseng, 1981a); many of the techniques have to be modified for site-specific conditions.

Marine phycoculture

Phycoculture techniques have been successfully applied to several seaweed species. The successful establishment of a large phycoculture industry in the Philippines based on seaweed had its genesis in an agar supply crisis in Japan around 1960. This eventually resulted in the collection of seaweeds in hitherto untapped areas around the world and precipitated appreciation of the fact that inadequate seaweed supplies were hindering the growth of the seaweed colloid manufacturing industry. Seaweed culture offered the best solution to raw material supply problems. Development of marine phycoculture in tropical areas especially developed as a pioneering effort in the Philippines from 1965 onwards. Farming of *Eucheuma* species required the identification of suitable sites, identifying the people who would farm and obtaining the stability of return on the investment that would keep the farmers active and industry interested in continuing use of the farm-produced material (Doty, 1979).
The phycoculture of *Gracilaria* is now well-established in several South- East Asian countries (McHugh & Lanier, 1983; Trono, 1994). Nevertheless, only species from about 15 genera of seaweeds are at present grown in marine phycoculture (Ohno & Critchley, 1993; Pérez et al., 1992). The indications are, however, that most commercially important seaweeds will be produced by phycoculture before long. In fact, this is largely already the case. Virtually all commercial brown seaweeds, as well as 63% of the commercial red seaweeds and 68% of the commercial green seaweeds are now cultivated (Ohno & Critchley, 1993). For *Eucheuma* and *Kappaphycus* it is even stated that over 95% of the crop is farmed (Lobban & Harrison, 1994). Of the total 3.9 million t (wet weight) of seaweeds used in 1991 in the seaweed industry, 2.8 million t were provided by phycoculture (Pérez et al., 1992).

Site 'fertility'

To obtain improved yields, a rational adaptation of appropriate working methods in relation to environmental factors of the area, is advocated. The importance of the site 'fertility' and the role of water require special consideration as well as an understanding of the variations in environmental factors at the site. A multi-factorial compensation hypothesis for physical control of site 'fertility' has been formulated (Doty, 1979). This takes into consideration the factors of light, water motion, water quality and temperature, in relation to algal fertility. This fertility can then be calculated in terms such as mass per unit area per unit time. Any change in one or more physical factors changes the relative position of all of the other factors when plotted in a multi-factorial figure and thus can be expected to affect the overall 'fertility' of the site. This hypothesis has merit in that it provides a conceptual explanation for the short-term, almost random changes in standing crop and production potential often found in natural habitats and it also allows controlled laboratory results to be contrasted with the variability found in the field. The concept leads to an easier understanding of the essence of marine phycoculture (Santelices, 1999).
After a site has been identified, test planting of the desired species (or, in some species, the desired cultivar) is recommended. For *Eucheuma*, *Kappaphycus* and some *Gracilaria* spp. test plots consisting of a few monolines planted with 50–100 test plants each are constructed at different strategic locations in the area. The growth of the test plants must be monitored at weekly intervals and their daily growth rates determined. Areas supporting daily growth rates of 2–5% or higher are potentially good sites. A 2–3 months long monitoring period of growth rate may be enough to start a small family farm, but for commercial farms a year-round monitoring programme is necessary, considering the possibility of problems associated with the seasonality of algal growth.

Space, labour and costs

About 530 000 ha in the world are already occupied by the existing 250 000 seaweed farms, many of which are small family enterprises, which provide employment for approximately 950 000 individuals. These developments augur well for the countries in South-East Asia with phycoculture potential in that the cultivation, harvesting and processing of seaweeds are highly labour-intensive activities (Doty, 1977). The farming of tropical algae is not a periodic activity, rather it is continuous and an alternative means of sustainable employment based on renewable resources. Incentive and free enterprise can be considered to be major factors in farm productivity (Doty, 1987). A large, successful farm could require several people for its proper operation and a smaller farm might be successful even though it may not require all the time of even one person. The cost of production of *Eucheuma* and *Kappaphycus* is much lower from family farms than from farms with paid employees (Doty, 1987; Trono, 1990). Although large and semi-intensive farms produce the highest yields, they are also the most expensive to maintain. The extensive farms derive higher net profits than the semi-intensive and intensive farms. Small farms generally obtain higher net profit, because of lower total costs (Llana, 1990).

Details of necessary investments and the costs of phycoculture of *Kappaphycus alvarezii* are readily available from the literature. These investments include the structures (poles, etc.) to fix the cultivation units, the living quarters for the farmers and the labourers, the drying house, boats, lines and nets and further miscellaneous equipment. The operating costs include mainly labour (for selecting and obtaining 'seed', planting, maintenance and weeding, harvesting, drying and washing, packing, baling and shipping) as well as some costs for materials such as polythene ties and freshwater. Overhead costs such as salaries, boat and transportation rentals, communications, representation expenses, repairs, fuel and oil also have to be taken into account. Estimates of farmer returns and future farming costs can also be calculated (Doty, 1986; Llana, 1990; McHugh, 1990).

National distribution and marketing structure

Success will not necessarily come to those who simply establish good methods of phycoculture. These efforts must be tied to the establishment and maintenance of a national distribution and marketing structure which equitably rewards and sustains seaweed collectors/farmers and ensures a necessarily more stable seaweed price and demand structure, thereby motivating investment and the production of consistent and reliable seaweed supplies (McHugh & Lanier, 1983; Trono & Ganzon-Fortes, 1988).

Culture of microalgae

The concept of mass production of microalgae was first tested around 1940 in Germany, resulting in advanced techniques for the continuous cultivation of large quantities of microalgal biomass (Burlew, 1953). Selection of promising microalgal species, strains and products requires evaluation of the cost structure of the microalgal production process, the suitability of the alga for mass culture, the value of the product, its concentration within the alga, the size of the market for the products and existing and/or future alternative sources (Borowitzka, 1992, 1994). The costs associated with growing and harvesting microalgae, extraction and purification of the products are often disappointingly high (Jassby, 1988a; Regan, 1988). The amount of free sun energy in tropical countries, however, provides interesting possibilities for cultivation of autotrophic organisms, especially when the microalgae can be grown in seawater (Tseng & Xiang, 1993).
The utilization of blue-green algae as bio-fertilizers has a long history and is inherently attractive. There is widespread interest in developing technologies for mass culture and their use with crops other than rice. A methodology for accurate, rapid estimation of standing crop or productivity of filamentous blue-green algae (*Cyanobacteria*) does not exist (Metting et al., 1988). Important physical factors influencing growth and nitrogen fixation include light, pH, temperature and cycles of wetting and drying. Soil cyanobacteria grow best under neutral to alkaline conditions. Nutrients and agro-chemicals also influence their activities and growth, in particular the availability of phosphate in the soil. The addition of lime ($CaCO_3$) to rice often stimulates the growth of blue-green algae. The effects of herbicides on growth and N_2-fixation by free-living

cyanobacteria are variable and differ widely among strains. Many components are inhibitory at high concentrations, but are stimulatory when diluted.

1.5.3 Planting material

Although algae are never really 'planted', most macroalgae need to be attached to a substrate in order to ensure survival. Cultures can be started from vegetative cuttings, spores or propagules, or by bringing young plants in from nurseries. These young plants can be seeded directly onto nets, as is usually the case with *Porphyra* cultures, or onto special nursery cord to be later attached to other substrates for further cultivation. The latter method is normally used in the phycoculture of large brown algae (kelps) in non-tropical waters (e.g. *Laminaria* spp., *Undaria* spp.), but is also used to grow *Gracilaria* sporelings. In pond cultures of *Caulerpa* and *Gracilaria* one end of a small bundle of cuttings is often buried into the mud at the bottom of the pond. When algae are to be attached to lines, this has to be done by hand. The cuttings are attached either individually or in small bundles (Trono, 1994).

In several forms of seaweed culture cuttings are used for propagation instead of spores. These cuttings, which should be prepared from healthy plants, can be broadcast in shallow pools or they can be tied to lines or nets or to dead coral branches. These substrates have to be positioned in the best possible way according to local conditions. Vegetative propagules may also be produced in well-equipped laboratories (Dawes et al., 1993).

For commercial cultivation of microalgae, sufficient amounts of fresh and healthy specimens must be added to the culture medium. Some microalgae can be preserved for many years by cryo-preservation, while cyanobacteria can be immobilized in polyurethane foam or sugar-cane waste to be used as bio- fertilizer (Day et al., 1997; Kannaiyan et al., 1997).

1.5.4 Phycoculture

Phycoculture can only be successful when cultivation methods are based on scientific research. The many differences with the agronomy of land crop plants involve various important factors and practices. Competition with other local activities may restrict the possibilities for phycoculture.

Substrate

The importance of the substrate is merely to provide a suitable attachment base for the algae. Rhizoids of algae are generally not responsible for the absorption of water or nutrients. All parts of the algae are involved in absorption as the algae are immersed in an aquatic medium.

For the seaweed farmers, however, the selection of the substrate is important from the point of view of convenience, availability, durability and economics.

The growth medium for seaweed cultivation is seawater, which contains salts that may be quite corrosive. Therefore, the substrate should be able to resist this corrosive action of the seawater, while it must also be strong enough to withstand the wave action and currents. As a result of tidal amplitude, the positioning and anchorage of the substrate should also be able to adapt to these changes. The locality where a cultivation site is established must be selected with utmost care. Thus the substrate and its positioning are of primary importance. The substrate may be natural, such as rocks and reefs, or artificial, such as ropes and wooden or bamboo structures.

Selection of locality

Other important factors in the selection of locality and position are salinity (no culture of stenohaline species near to a freshwater outlet, but euryhaline species may even need some additional freshwater), pollution (especially for species to be used as food), water movement and mobility of the bottom substrate (causing turbidity, burial of the algae or even erosion of the bottom). Water movement must be strong enough to provide the necessary minerals and gaseous exchange, but not so strong as to cause breakage and spoilage by losing pieces of the crop before harvest. In areas where strong currents occur, a retaining fence made of nylon netting (with approximately 10 cm mesh size) should be constructed on the leeward side of the farm in order to catch thalli washed away by the current. In some areas about a third of the daily harvest may consist of thalli carried out by currents (Trono, 1998).
Nitrogen normally occurs at such low concentrations in seawater that it may become the limiting nutrient. The same may be the case for phosphorus. This is especially evident in clear 'blue' waters of the tropics. In areas with upwelling, growth of most seaweeds is much better. In areas where water movement is low (with a low exchange of gas and ions), supplementation with additional nutrients may be necessary for successful phycoculture.

Spores

Algal spores are very delicate unicellular structures which can die as soon as they are removed from their medium. Therefore, it is imperative that in the 'seeding' process (i.e. the collection of spores), the substrates must be brought close enough to the seaweed fronds so that the liberated spores will have the best chance to adhere in the shortest time possible. In general, spores of seaweeds germinate only after adhering to the substrate (Tseng, 1981b). Thallus fragments used as vegetative propagules are often also designated as 'seed stocks'.

Competition

Biotic competition with other algae, with epiphytic organisms, parasites and pathogens and with predators (herbivores) is an important factor determining the success of phycoculture. Weeding and regular pruning are necessary activities in the maintenance of every seaweed farm. If senescence of the stocks is apparent, the lines should be re-stocked with fresh 'seed'. Decreasing productivity of the stocks is an important problem in farming of tropical seaweeds (Dawes et al., 1993; Trono, 1994). Research on periphyton communities used as food in abalone culture in Pacific Canada has shown that nutrient enrichment usually does not change the competition of these periphyton communities. However, both productivity and protein concentrations increased (Austin et al., 1990). This may also be the case in pool polyculture of milkfish and *Gracilaria*, which is also mainly based on the food value of the periphyton to the fish.

Environmental effects of seaweed farming

The effects of seaweed farming on a coral reef environment are generally positive, especially when reef flats are used in areas with good tidal currents. However, the implementation of suitable legislation, as well as strict observance of the laws by the farmers are essential (Trono, 1993, 1994).

1.5.5 Crop protection

Destructive grazing by finfish, snails, sea urchins, limpets and starfish are problems in many tropical as well as temperate areas (Pringle et al., 1989). Finfish may eat large quantities of algae and a visit by a shoal can result in considerable damage. Sea urchins may almost completely destroy the vegetation of natural algal beds (Doty, 1986; Tseng, 1981b). Epiphytes can also reduce productivity.

Monocultures of seaweeds tend to be susceptible to mycoses, bacterial activity and/or viruses. Large parts of a farm can be infected, especially where plants in phycoculture are overcrowded. Literature on diseases of tropical algae is scant, except for 'ice-ice', a disease of *Eucheuma* and *Kappaphycus* (Trono, 1994). This disease is characterized as one of the 'malaises' of *Eucheuma* cultivation (Doty, 1987). It is probably not a real disease, but a symptom of poor growing conditions (Pringle et al., 1989). 'Ice-ice' can be induced by manipulation in laboratory studies, although bacteria most probably accelerate the expression of the 'disease' (Correa, 1997; Largo et al., 1995a, 1995b). In species that are only propagated vegetatively, ageing of the stocks may result in reduction of growth and productivity (Dawes et al., 1993; Pérez et al., 1992; Trono, 1994).

Successful maintenance in outdoor mass culture of microalgae requires constant feedback on the state of the culture (Belay et al., 1994; Richmond, 1988). In several microalgae, especially in *Dunaliella salina* Teodor. and some strains of *Arthrospira*, the ability of the algae to withstand high salt concentrations makes extensive open-air cultivation possible (being relatively free of competitors, pathogens and predators) (Borowitzka & Borowitzka, 1988; Tseng & Xiang, 1993).

1.6 Harvesting and post-harvest handling

Maturity indices

These differ for the various species in cultivation. Some culture methods allow *Eucheuma* plants to grow to one kg or more, while other methods allow less full-grown specimens. In addition, the optimum harvest for *Eucheuma* and *Kappaphycus* varies between different locations, depending on a number of factors including the level of loss from physical damage as thalli increase in size. A short 40–45 days growing period, with the harvesting of immature thalli of less than one kg (wet weight) is still practised in some localities, in the belief that higher yields are obtained by frequent cropping. A longer harvest interval of 50–60 days, however, produces a crop which is usually more suitable for carrageenan production (Luxton, 1993). It has been suggested that higher prices should be paid for thalli with a basal diameter greater than a given size. This may result in a better quality of the seaweeds that are offered for sale (Doty, 1986).

Harvesting

One of the advantages of phycoculture is the relative ease of harvesting and crop control. Harvest of whole plants is in some cases considered favourable to the often-used pruning methods. Over-harvesting must be avoided; this may occur frequently in the collection of wild seaweed stocks, resulting in a fluctuation of seaweed supplies. A tool to assess the best harvesting strategy for natural populations can be provided by using a simulation with the aid of a projection matrix model, which is based on studies of phenology, recruitment and mortality of the seaweed species (Ang, 1987).
Cultures of microalgae usually have a low solid content and many algal cells are very small. This means that large volumes of water have to be processed in order to extract the algal biomass. This is a major cost factor in most algal processing. The options available for harvesting include centrifugation, filtration, or flocculation (Belay et al., 1994; Borowitzka, 1994; Mohn, 1988).

Grading and drying

The need for collectors and farmers to improve post-harvest treatment (cleaning, sorting, washing, drying) is crucial to provide products with a consistently high quality (Doty, 1986; Luxton, 1993; McHugh & Lanier, 1983; Trono, 1994). The algae must be well-dried shortly after collection and as rapidly as possible. Dehydration must be sufficient to guarantee preservation of the alga, otherwise anaerobic fermentation will occur, causing high temperatures and even carbonization of the seaweeds during storage in the warehouse. In general, the moisture content is best reduced to about 20% (for *Eucheuma* and *Kappaphycus* 35%) by natural or artificial drying ('bone-dry'). Commercial seaweeds are often mixed with significant quantities of impurities such as stones, shells, sand, other seaweeds, epiphytes, as well as other products added during gathering, drying and packing (such as land weeds, leaves, wood and plastic). It is important to prevent this type of contamination of the raw material. Contact with freshwater, particularly rain, should be avoided, especially for *Eucheuma* and *Kappaphycus*. Sand causes severe problems during carrageenan extraction due to its abrasive properties (Blakemore, 1990).
The existing literature on the evaluation of seaweeds as an industrial source of phycocolloids is often confusing because the contributions generally come from scientists who often are unfamiliar with specific requirements, the different grades of phycocolloids and the analytical methods used. These evaluations usually have been made from seaweeds which are perfectly dry and clean, like herbal samples, and therefore the data have little similarity to that obtained by the manufacturers who process hundreds or thousands of tonnes of commercial seaweeds during the industrial process (Armisén & Galatas, 1987). In phycoculture the average phycocolloid yields can be improved by using more sophis-

ticated harvesting procedures (Adnam & Porse, 1987). For microalgae usually spray-drying is used (Belay et al., 1994; Switzer, 1982).

Packing, transport and storage

Large-scale seaweed processing requires that the raw material is well stabilized in order that it can be transported over long distances, at the least possible cost, and stored for long periods before use. After dehydration, the dried seaweed is compressed with a hydraulic press into bales. Obviously it is necessary to avoid wetting during transportation and/or storage (Armisén & Galatas, 1987). All storage should be in clean, cool, dry and well-ventilated places.

In some cases the problem of storage is more difficult to solve. In *Gracilaria* enzymatic hydrolysis of agar may occur spontaneously, even at a relatively low moisture content. The rates of hydrolysis are variable depending on the species, its origin and conditions. This prevents long-term storage of stocks. Agar in *Gelidium*, however, can be preserved indefinitely in seaweeds, provided they have been well-treated (Armisén, 1995; Armisén & Galatas, 1987). When the gathered seaweeds are treated with NaOH at an adequate concentration and for the correct duration, destruction of microbial contaminants takes place, perhaps also resulting in the in-activation of hydrolytic enzymes. Sterilization by gamma irradiation, however, often causes loss of gel strength characteristics (Armisén, 1995).

For *Eucheuma* and *Kappaphycus* it is known that the material is unstable and undergoes degradation during storage above a moisture content of 35%. Above 40% moisture content the carrageenan in the seaweed may not survive transportation to the factory, arriving with characteristics unsuitable for some applications. At 25–35% moisture content seaweeds are relatively stable for periods in excess of 12 months and the thalli are also flexible which is ideal for efficient baling. At 15–25% moisture content *Eucheuma* thalli are extremely stable, but are too brittle and resist compression or snap during baling. Below 15% moisture content thalli remain stable, but can cause processing problems during carrageenan extraction (Blakemore, 1990). Careful drying and good baling are essential for well-packed seaweeds and lower freight costs (McHugh, 1990).

1.7 Processing and utilization

1.7.1 Biological products

1.7.1.1 Phycocolloids

The technical requirements for the manufacture of seaweed colloids, involving production techniques and expertise of effective marketing, put up certain barriers for producers who wish to enter the trade. However, the production technology for agar and semi-refined carrageenan is not so complex, that the development of the requisite technology is beyond the resources of most countries in South-East Asia (Bixler, 1996; McHugh, 1996; McHugh & Lanier, 1983). When used in combination with other gums different forms of phycocolloids, especially agar, may behave differently in relation to gel strength (Armisén & Galatas, 1987). Due to synergism, mixtures of *Gelidium* agar with 'locust bean gum' (LBG) produce a more elastic gel; but this is not the case with *Gracilaria* agar (Armisén, 1995). Some sources of kappa carrageenan, however, show even greater synergism when mixed with LBG.

New business

When establishing a phycocolloid industry, a pilot-plant should be the first step in the evaluation of feasibility. This pre-supposes that results have been obtained from preliminary evaluations and quality control tests have been performed. Detailed knowledge of the industrial manufacturing process is essential for this evaluation, as well as knowledge of actual gel specifications required by the different markets and the practical applications of the product (Heyraud et al., 1990; Jensen, 1995). It is essential that the required seaweeds be correctly evaluated before operations start in countries or areas of potential interest. As soon as the quantities of useful algae from a part of the coast have been estimated, the quantity and quality of the colloid in the seaweeds should be evaluated in terms of its practical use. Representative sampling is very important and samples should be immediately packed in strong, waterproof, well-fastened bags. As soon as samples are received in the control laboratory, the impermeability of the polythene bags is verified and registered in the protocol. Next, aliquots need to be taken in such a way that their homogeneous composition is guaranteed, so that determinations can be made on moisture, content of pure seaweed and extraction of an aliquot part of the sample (Armisén & Galatas, 1987). It is impossible, however, to assign a general extraction method which is valid for any phycocolloid.

Tests

Gels of algal polysaccharides are generally made with 0.5–2% polymer per weight. Besides being characterized for gel and sol temperatures, these gels are tested for break force or gel strength and penetration. These parameters are measured on devices aptly called gel testers. These are machines which determine, by various means, the force necessary to break the surface of a gel (i.e. break force, expressed in g/cm^2) and the amount of deformation of the surface of the gel at break point (i.e. penetration, expressed in cm) (Lewis et al., 1988). Methods for structural analysis as well as a simple laboratory test for the determination of gel strength are available (Cosson et al., 1988; Czapke, 1979; Heyraud et al., 1990; Lewis et al., 1988).

1.7.1.2 Agar

The freeze-thaw method

The discovery (around the year 1658) of the 'freeze-thaw' extraction of agar is attributed to Japan (Booth, 1979). Agar extraction is a fairly simple process. Frozen agar gel liberates water as it thaws, profiting from the insolubility of agar in the cold (Armisén, 1995). Alternatively, synaeresis is often applied, especially in agars produced from *Gracilaria*. The term synaeresis is used in agar technology to describe the process whereby pressure is used to exclude liquid from the gel. Boiling is necessary to dissolve agar in water. The insoluble residue is usually removed by some means of filtration and the liquid, when cooled, forms a gel. Solutions with 1–1.5% agar stiffen to a firm gel when cooled to between 36–42°C and the gel will not melt below 85–90°C (Indergaard & Østgard, 1991). By alternately freezing and thawing the gel several times, the water is removed and a dried 'strip' of agar is produced. Agar is sold in strip form, but also in powder form (McHugh, 1996). Details on processing techniques and analysis of physico-chemical properties of agar are widely available (Armisén, 1995; Armisén & Galatas, 1987; McHugh & Lanier, 1983; Montaño & Pagba, 1996). Agar manufacturing has the advantage of being feasible on both small or large scales, with the corresponding capital outlay.

Gelidium and Gracilaria

Originally only *Gelidium* agar constituted what was considered genuine 'agar', assigning the term 'agaroids' to the products extracted from other seaweeds. This differentiation is no longer accepted. In 1984 approximately half of all agar produced came from members of the *Gelidiaceae*, the other half were mainly from *Gracilaria* (Armisén & Galatas, 1987). The different seaweeds used as raw material in agar production gave rise to products with differences in their behaviour. For this reason, when agar is mentioned, it is customary to indicate its original raw material as this can influence its application. To describe the product more accurately, it is usual to mention the origin of the seaweeds, since *Gracilaria* agar from one area of the world has different properties from *Gracilaria* agar from another area.

Chemical treatments

An increase in agar gel strength was obtained through improvement of the industrial process. Treatments of the seaweeds prior to extraction are very important as they will determine to a high degree the characteristics of the agar obtained. Strong alkaline conditions increase gel strength, especially in *Gracilaria* agar (Armisén & Galatas, 1987). The treatment, called sulphate alkaline hydrolysis, must be adapted to the seaweed used, to obtain as much desulphation as possible whilst avoiding the yield losses that this process can cause (Armisén & Galatas, 1987; Villanueva et al., 1997). Other corrective treatments using an alkaline solution eliminate a large quantity of foreign substances. This alkaline treatment uses sodium carbonate and is milder than the alkaline treatment with sodium hydroxide which used to improve gel strength. Pre-treatment with acetic acid, however, may also result in higher agar yields and gel strength (Roleda et al., 1997).

The gelification process in agars may be blocked by chaeotropic agents, which prevent the formation of hydrogen bonds. This reversible process occurs when urea, guanidine, potassium iodide, tannic acid or sodium thiocyanate are present. The addition of glycerol in moderate quantities avoids this effect.

The market

Agar, contrary to industrial grades of other phycocolloids, is marketed pure, without any mixture. There are different types of agar available on the world market (Montaño & Pagba, 1996; Ohno & Critchley, 1993):

- *Native and natural agar* (from *Gracilaria*) usually can not be classified as bacteriological grade agar, as there is a high content of methoxyl groups and consequently high gelling temperatures (Murano, 1995). Half of the world supply of agar is directly used in food. In Asia there is considerable household consumption of 'natural agar', mainly in traditional cooking, which is often marketed in 'strips', in bar-like 'squares' or in pill form. These are mixtures in which *Gelidium* agar dominates, but which can not be used for industrial food agar (Armisén, 1995; Armisén & Galatas, 1987).
- *Industrial agar* is sold world-wide in powder form, as pharmacological grade, biotechnological grade, bacteriological grade and purified agar. The source of these grades is mainly *Gelidium* (Armisén, 1995).
- *Food-grade industrial agar* is mainly marketed in powder form and comes mostly from *Gracilaria*. A food-grade agar should have a moisture content of less than 18%, ash content of less than 5%, gel strength greater than 750 g/cm^2 (Nikan-Sui method) and a bacterial count below 10 000 bacteria/g. Usually the lead content is specified as less than 5 ppm and arsenic less than 3 ppm (Armisén & Galatas, 1987). Food-grade agar is the least valuable of the industrial agars, because it meets neither the standards for bacteriological agar nor those for sugar-reactive agar. Demand for food-grade agar can easily decline due to replacement of the gel by other phycocolloids, especially carrageenans.
- *Bacteriological agar* (also known as 'standard agar') needs strict physical-chemical control and requires the absence of haemolytic substances and bacterial inhibitors. Nevertheless, there are no official general specifications for universal categorization as bacteriological agar (Armisén & Galatas, 1987). It must have a good transparency in sol and gel forms and a consistent gel strength from lot-to-lot. Uses in microbiology are based on special properties: a gelling temperature of 36 ± 1.5°C, a melting temperature of 87 ± 2.5°C and lack of hydrolysis by bacterial exo-enzymes. The above temperatures refer to culture media which contain 10–11 g agar/l. Requirements are a low content of oligomers and proteins (so that these can not form a source of nutrients for microorganisms), a low and regular content of electro-negative groups that could cause differences in diffusion of electro-positive molecules (e.g. antibiotics, nutrients, metabolites), freedom from toxic (bacterial inhibitors) and haemolytic substances that might interfere with normal haemolytic reactions in culture media as well as free from contamination by thermophilic spores (Armisén, 1991). Bacteriological agar, which is the highest agar grade, is prepared from *Gelidium* (and *Pterocladia*), since *Gracilaria* and *Gelidiella* give agars with gelling temperatures above 41°C.
- *Sugar-reactive agar*: gel strength, with very low sulphate content and high molecular weight, increases when sugar is added (Armisén, 1995). Sugar-reactive agar is able to form a good gel in strong sugar solutions.
- *Purified agar* is produced in much smaller quantities. This expensive agar is a bacteriological agar that could also be used in biochemistry for elec-

trophoresis or immunodiffusion. It can be considered as an agarose fore-runner, which is still being used for economic reasons (Armisén & Galatas, 1987).

Agarose

Interest in agarose resumed with the search for an electrically neutral polysaccharide suitable for use in electrophoresis and chromatography. Agarose is a derivate of high-quality agar. Its yield can be 70–80% of that of agar. The rather small market for this special product is expanding because of its current use in tissue culture and as a medium for electrophoresis. Demand is expected to remain high due to biotechnological and biochemical needs. A technique for agarose preparation using polyethylene glycol results in a product of good purity (Armisén & Galatas, 1987; Russell et al., 1964). Good commercial agarose is considered to have less than 0.35% sulphate; the pyruvate content is likewise very low (Armisén, 1991). The agar of Philippine *Gracilariopsis heteroclada* is a potential source of agarose (Hurtado-Ponce, 1994).
Modern commercial agaroses for use in biochemical separation techniques have to be chemically modified (Armisén & Galatas, 1987).

Bacteria

Some bacteria (e.g. *Cytophaga* and *Pseudomonas* spp.) can produce agar-degrading enzymes (Forro, 1987).

1.7.1.3 Carrageenan

Traditional production methods

The first mention of the use of carrageenan in the food industry is from the mid-19th Century as a fining agent in beer brewing (Booth, 1979). The traditional, refined products are made by dissolving the carrageenan out of the seaweed, filtering off the unwanted residue, precipitating the carrageenan from the extract, then separating and drying it. Before the extraction process, the seaweeds are digested with hot water under alkaline conditions to extract all of the carrageenan. The algae, however, also may be soaked in sodium, potassium or calcium chloride according to the type of gel required. In general, treatment with sodium salts results in a viscous product with low gel strength; calcium salts give an elastic gel and potash salts produce a firm gel. The solution of carrageenan is separated from the seaweed solids by filtration, or by centrifugation followed by filtration (McHugh & Lanier, 1983; Stanley, 1987).

Semi-refined carrageenan

In the Philippines 'semi-refined' carrageenan is produced from seaweeds known as *Kappaphycus alvarezii*. There are many different names and acronyms for this 'semi-refined' carrageenan. The method used was introduced in the Philippines by Japanese chemists in 1978 (Llana, 1990). Baskets full of seaweed fronds are immersed and cooked in hot, aqueous potassium hydroxide

8.5% solutions and soaked 5–6 times in freshwater to extract most of the residual alkali. In the production process most of the non-carrageenan matter in the seaweed is dissolved and removed, leaving a solid residue of cellulose and carrageenan, which is dried and milled (Stanley, 1987). The product contains some insoluble material, and thus will not yield clear gels (Neish, 1990). Material handling in the production process is greatly reduced and energy costs are lower than in the case of the full industrial process. Thus production costs are only 25–50% for that of refined carrageenan (McHugh, 1996). Therefore, the price of semi-refined carrageenan is about 50% of that of the refined product (McHugh & Lanier, 1983). With the advantages of being easier and cheaper to manufacture, it is feasible for an entrepreneur to develop the semi-refined carrageenan-processing technology on an experimental scale for a modest capital outlay, and then gradually increase the scale of operation as is done in the Philippines (Anonymous, 1998; Neish, 1990). The process is most effective when using *Kappaphycus alvarezii*, but with careful control it is also possible to treat *Eucheuma denticulatum* and its iota carrageenan. Usually, however, kappa carrageenan is the active component in semi-refined carrageenan.

Refined carrageenan

The production of refined carrageenan involves a very complex industrial process (Anonymous, 1998; Bixler, 1996; Luxton, 1993; McHugh, 1996; Neish, 1990).

Problems

The quality of carrageenan has been decreasing recently; this is thought to be the result of hybridization with native plants in the farming areas in the Philippines (Lobban & Harrison, 1994). Some bacteria, (e.g. *Pseudomonas* sp.) are capable of degrading carrageenans (Forro, 1987).

1.7.1.4 Alginate

Although alginate was already manufactured in 1881 in Scotland, the first commercial production of alginate was launched in 1929, and its use in food was patented just after 1930 (McHugh & Lanier, 1983). There is, however, only limited information available on the manufacture of sodium alginate (Lewis et al., 1988). Alginate is probably the most difficult of all the three colloids to manufacture. Chemically, its extraction is a simple process but the physical separation of insoluble cellulose from thick solutions presents formidable difficulties.

In general, alginates are manufactured in five basic operations (McHugh & Lanier, 1983):

- Removal of soluble matter by washing with water and reduction of the seaweeds to a size suitable for further processing.
- Extraction of alginate with sodium carbonate and filtration; the product may be bleached at this stage.
- Precipitation of the calcium salt by adding calcium chloride.
- Conversion of the calcium salt to alginic acid by treating it with hydrochloric acid.

- Conversion of alginic acid to its sodium salt by using a suitable alkali; the salt is then dried.

Usually the quality of *Sargassum* alginate is thought to be rather poor and not good enough to be used by the textile printing industry (McHugh & Lanier, 1983). Nevertheless, a local alginate producer in Indonesia sells about 100 t of locally produced *Sargassum* alginate to the textile industry (McHugh, 1996). Comparative research, moreover, suggests that alginate produced from Malaysian *Sargassum* is of a high quality (Fasihuddin & Siti, 1994).

Bacteria

Several bacteria, in particular *Cytophaga* spp., are capable of degrading alginates, especially under anaerobic conditions (Forro, 1987).

1.7.2 Chemical products

The potential of microalgae as a commercial source of carotenoids has been recognized for some time and extensive research and development of β carotene production using *Dunaliella salina* is underway in various parts of the world. After harvesting, the biomass must be processed to extract either glycerol or β carotene (Chen & Chi, 1981; Ruane, 1974). Microalgae are ideally suited as a source of stable isotopically labelled compounds (Apt & Behrens, 1999).

1.8 Genetic resources and breeding

For species grown in phycoculture the possibility arises for cultivation of improved seaweed strains with predictable and better yields. In the *Kappaphycus alvarezii* group several cultivars are now known. It might be possible to cross these to provide better yields, although hybridization has not yet succeeded (Trono, 1994). In *Eucheuma denticulatum* all crossing experiments have also so far failed (Pérez et al., 1992). References to tropical species are generally lacking in the literature on genetic studies in marine algae (van der Meer & Patwary, 1995). However, the presence of numerous unknown *Gracilaria* spp. in particular offers tremendous opportunities for the development of ideal seedstock strains for the agarophytes (Shen & Wu, 1995; Trono, 1994).

Genetic engineering of microalgae has provided promising results, that are not yet fully applicable (Craig et al., 1988). Highly sophisticated molecular systems are being used to include recombinant techniques especially in *Cyanobacteria* and some unicellular eukaryotic algae, but these new techniques have not yet contributed directly to a commercial product.

1.9 Prospects

There is a general tendency to deplete natural resources and algae are not an exception. To counteract this, better resource management, with closer studies of the economic interactions and information on indigenous algal species are required. Algae are able to provide sustainable raw materials that are well-suited to applications in science and technology. Such uses can contribute to the industrial transformation of countries in South-East Asia as well as to the sustainable use of the available biodiversity (Frankenberg, 1986). The role of education and training of farmers, researchers, employees and businessmen is essential to these mutual developments. Realization of the full potential of the seaweed industry must result in the provision of financial resources, incentives and proper training. Furthermore, there is a requirement for increased research into harvesting, cultivation of algae and improvement in the quality of the algal products. Finally, the absence of adequate and up-to-date international market information obstructs the trade in algae and tends to reduce profits to the producers (Pringle et al., 1989).

The long distances between the centres of phycocolloid production and its markets will become an unsustainable luxury. The phycocolloid industry must work with producers to develop refined products within the areas of seaweed production. If the processing plants can be decentralized and constructed on a smaller scale, some of the problems of disposing the waste might be solved by incorporation of both waste water and biomass residue into agricultural production (Kapraun, 1999). Discussions on the introduction of cultivars of foreign species as an alternative to depletion of natural populations of target species should be continued.

Good prospects for algal products exist, especially in the fields of fine chemicals, antibiotic substances, anticancer medicines, herbicides, vermifuges, insecticides, etc. Several algal-derived substances are very different from those that can be obtained from terrestrial organisms and therefore have different applications (Apt & Behrens, 1999). Cultivation of selected algae for production of proteins, lipids, carbohydrates, vitamins, etc. can be expected and will be augmented. Moreover, phycoculture can also be used to obtain large amounts of biomass that can be used for methanization for energy production, an option that becomes more feasible because of international agreements on CO_2-reduction (Gao & McKinley, 1994).

In recent years, developments in biotechnology have swiftly transformed laboratory discoveries into commercially useful products. Algae offer promise as direct and indirect renewable biological resources. A special application is being developed in the production of high-performance paper from seaweeds, mainly alginate fibres (Kobayashi, 1990). Promising prospects for microalgae are presented in the literature (Borowitzka, 1994; Gladue & Maxey, 1994; Lee, 1997; Radmer & Parker, 1994; Stevens et al., 1994; Vonshak, 1997).

1.9.1 Research

Phycoculture in South-East Asia is usually represented by one person in an academic department. This specialist in phycoculture must have the training of a plant physiologist, agronomist, aquatic ecologist, oceanographer or limnologist, sociologist, agricultural economist and phycologist, hopefully also with a little natural products chemistry and reasonable writing skills (Doty, 1979). There is a distinct lack of multi-disciplinary research teams in phycoculture. Problems are also encountered due to the limited availability of information about phycoculture due to both political and commercial factors and linguistic barriers (Critchley & Ohno, 1998; Ohno & Critchley, 1993; Pérez et al., 1992; Trono, 1994).

Commercial cultivation of all promising species is not yet possible, especially cultivation of several agar-producing species in the genera *Gelidiella*, *Gelidium* and *Pterocladia*. In addition, there are erratic results in the production of algae bearing iota carrageenan which still require more attention. Nevertheless, attempts to increase production from natural beds of *Gelidium*, by increasing the area of rocky substrates, farming it with ropes and rafts, and even cultivating free-floating plants in onshore tanks have met with some success (Lobban & Harrison, 1994; Melo et al., 1990).

The production of semi-refined carrageenan is promising, but may also need some adjustments (Anonymous, 1988; Bixler, 1996; Luxton, 1993).

Many new developments in biotechnology would not have been possible without phycocolloids and their derivates (Renn, 1990). Phycotechnology now constitutes a special branch of biotechnology and algae form the main focus of interest.

Main research institutions in phycology

The following main institutions in South-East Asia are involved in phycological research (usually research on seaweeds):

Indonesia

- Research and Development Center for Oceanology, PPPO-LIPI, Jakarta
- Marine Station of PPPO-LIPI, Ambon (not active at the moment)
- Agency for the Assessment and Application of Technology, Seaweed Research and Development Team, BPP Teknologi, Jakarta

Malaysia

- Institute of Advanced Studies, University of Malaya, Kuala Lumpur

The Philippines

- Marine Science Institute, University of the Philippines, Diliman, Quezon City
- Marine Laboratory, Silliman University, Dumaguete City
- Marine Biological Section, University of San Carlos, Cebu City
- Mindanao State University, Naawan
- Many universities and national organizations have phycologists in their staff, whereas industrial laboratories involved in the production of seaweed products are often active in seaweed research

Singapore

- Department of Microbiology, National University of Singapore (specialized in research on microalgae)

Thailand

- Faculty of Fisheries, Kasetsart University, Bangkok

Vietnam

- Nha Trang Institute of Materials Science, Production of Seaweeds, Nha Trang City

1.9.2 Marketing infrastructure

The marketing distribution system for seaweeds and their products in countries such as Indonesia, Malaysia and the Philippines was poorly organized in the early years of development of seaweed cultivation (Doty, 1986; McHugh & Lanier, 1983; Trono & Ganzon-Fortes, 1988). Small traders acted as middlemen to the large traders. The buyers were the exporters of the phycocolloid industry, who often established strict product specifications, upon which sales and acceptance were dependent. But exporters' purchase requirements and prices were also heavily influenced by the buying policies of foreign users. Thus, during periods of short supplies and rising prices, seaweed collection and farming was stimulated and quality requirements were lowered. The lack of stability in buyer policy induced farmers to take less care with their crops, resulting in production of inferior seaweed. This pattern of market fluctuation seemed to be more or less cyclical and applied to carrageenan-bearing seaweeds as well as the agar-bearing ones (Luxton, 1993; McHugh & Lanier, 1983). However, several of the Philippine producers, mainly making and marketing semi-refined carrageenan for human consumption, have now formed a trade association (SIAP) to represent their interests (Anonymous, 1998; Bixler, 1996). This will hopefully result in more stable prices for the seaweed farmers and improvements in the quality of raw materials.

Phycocolloids

The market for phycocolloids largely depends on relatively low prices. Agar, carrageenan and alginate may compete directly with one another in some end-use markets. Specialty gums, such as carrageenans, are sold on the basis of their functionality in specific applications. For this reason carrageenan manufacturers have to devote a substantial portion of their budget to maintaining active applications and technical marketing groups to serve the ever-changing needs of their customers. In that way the carrageenan industry tries to sustain the growth that it has enjoyed for the last 30 years. A survey of market factors (food product innovations, especially different forms of liquid diets and fat substitutes) and the successful application of carrageenan in further-processed poultry and meat has been documented (Bixler, 1996). Phycocolloids compete with gums from flowering plants, such as guar gum and locust bean gum and cheaper cellulose derivates. A variety of agar substitutes have been developed for gel media in microbiology, including alginate and polysaccharides of -nonalgal origin, such as plantgar and gellan. For a number of important food uses, however, no synthetic or other natural gums have been found that can replace phycocolloids on a cost-effective basis. This fact seems to assure the continued viability of the industry. New food applications will require gums which demonstrate pH and temperature stability, salt tolerance and cold stability; these properties are found in seaweed extracts (Guist, 1990).

Agar

The instability of the world agar market has resulted in price levels that have priced agar out of several end-use markets. A stable supply of seaweed from phycoculture would help to stabilize the price of agar. On the other hand, labour costs and manpower shortages may result in all harvested *Gracilaria* crop being used for the production of mollusc feed (Ajisaka & Chiang, 1993). Agar was used as a gelling agent in canned pet food until price rises led to its replacement by carrageenan. The agar market, however, still presents good potential for countries in South-East Asia. A global marketing approach to agar includes identification of all possible uses for agar by consumers and preparation of a good product launch (Becker & Rotman, 1990).

Carrageenan

The potential for culturing carrageenan-bearing seaweeds in countries in South-East Asia is very large. However, expansion in the number of growers has resulted already in an oversupply of certain forms of carrageenan and may lead only to the spreading of sales among a greater number of producers (at lower prices) as well as to disputes amongst the different carrageenan producers (McHugh & Lanier, 1983).

In many cases, price is not the determining factor in a buyer's choice of a seaweed colloid. Quality, and its reproducibility from one batch to another may be more important. Many buyers of seaweed colloids, satisfied with one particular brand or grade will stay with it, despite a higher price, because the risks of changing may not seem worth the savings. Thus brands already established in a market place often hold a very strongly entrenched position (McHugh & Lanier, 1983). Economic practices to encourage better-quality farmed seaweed should include bonuses or higher prices paid by industry for value-added or higher-quality seaweeds due to on-site post-purchase treatment, better drying practices and basal diameter standards for the harvested thalli, resulting in a fair partitioning of the export prices (Doty, 1986; Trono, 1990).

Biotechnology

The algal biotechnology industry needs to continue to develop more markets for algal products. Not only does this require the raising of awareness that algal products are suitable alternatives to other products, but standards of quality for algal products have to be set and the appropriate registration achieved (Borowitzka, 1994).

1.9.3 Differentiation of products

Phycocolloids

New markets for phycocolloids will be found in pharmaceutical applications such as vaccines, drug delivery, anticancer, antirhombogenic applications and antiadhesive drugs and diagnostics. The volume of phycocolloids needed for such purposes will be relatively small, but chemical purity and precisely identified structural composition will definitely be reflected in increased prices (Indergaard & Østgard, 1991). Cells entrapped in phycocolloid gels have many potential applications in biotechnology, ranging from biocatalysts in fermentation and immobilized algae for metal recovery to artificial seeds in agriculture and carrier materials for transplantation of living tissue (Jensen, 1993; Skjak-Bræk & Martinsen, 1991).

Agar

Demand is expected to increase for bacteriological agar and for agar strips for food. The high-quality agar required for bacteriological use can only be made from a limited number of seaweeds, notably *Gelidium* and *Pterocladia*. These seaweeds are in short supply and, as a result, production of bacteriological grade agar may be restricted in the future (McHugh & Lanier, 1983). However, agar from *Gracilaria* can be improved by treatment with alkali, resulting in better gel strength at the cost of lower agar yields (Armisén & Galatas, 1987). There is an urgent need, however, for the agar industries to develop studies for the promotion of agar use in food applications (Armisén, 1995).

Carrageenan

Use of carrageenan, especially semi-refined carrageenan, in further-processed poultry and meat is a proliferating market. For all carrageenan producers there is a constant need to seek new applications for these phycocolloids. They must be willing to invest in both basic carrageenan research and development and in its applications (Bixler, 1996). In the future, carrageenan may be used to produce nearly fat-free hamburgers (Lobban & Harrison, 1994). New methods for rapid screening of carrageenan composition of carrageenophytes are being developed (Vreeland et al., 1992).

Alginate

There is likely to be an increase in demand from tropical countries for alginate for use in the cotton textile printing processes. The market for industrial textile applications of alginates is, however, already covered by dominating western industries. The steady global growth of the alginate industry by some 5% annually is nevertheless expected to continue (Jensen, 1993).

Microalgae

The use of microalgae as sources of valuable chemicals is especially promising and the next few years will probably see a continued expansion of the range of commercially available microalgal products (Borowitzka, 1994; Lee, 1997; Vonshak, 1997). The development of an automated microalgal culture system in Malaysia is an attractive prospect (Ho et al., 1994).

W.F. Prud'homme van Reine

2 Alphabetical treatment of genera, species and groups

Acanthophora muscoides (L.) Bory

In: Duperrey, Voy. monde, Crypt. 4: 156 (1828).
RHODOMELACEAE
$2n$ = unknown

Synonym *Fucus muscoides* L. (1753).

Vernacular names Philippines: culot (Ilocano).

Origin and geographic distribution *A. muscoides* occurs throughout the tropics in the Atlantic Ocean (Caribbean, southern Atlantic Ocean), Indian Ocean (mainly in the western part), and Pacific Ocean (Japan, northern China, Taiwan, Melanesia). In South-East Asia it is found in northern Burma (Myanmar), Vietnam, Singapore, Indonesia (West Java), the Philippines and southern Papua New Guinea, and is always less frequent than *A. spicifera* (Vahl) Børgesen.

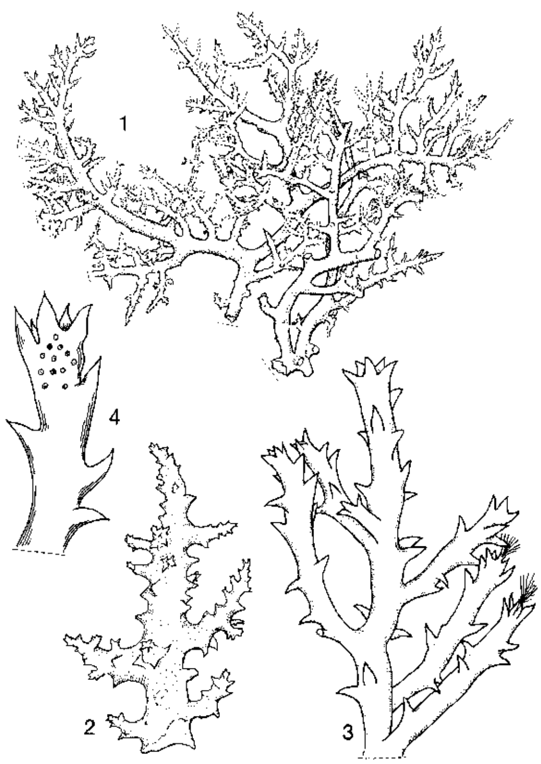
Uses In the Philippines (Ilocos Norte) *A. muscoides* is hand-collected, dried and eaten cooked with other vegetables. In Thailand and Vietnam it has been listed as a potential economic alga.

Production and international trade No statistical data are available on the production of *A. muscoides* from the wild for food or medicinal uses.

Properties In a project on plant growth hormonal activities, aqueous extracts from fresh samples of *A. muscoides* in the Philippines contain the highest auxin-like activity as well as the highest cytokinin-like activity of all seaweed extracts tested. Fresh samples of *A. muscoides* contain per g approximately: auxin 9500 μg, cytokinin 17 800 μg and gibberellin 165 μg. However, aqueous extracts of *A. muscoides* have not yet been directly tested in field bio-assays. Residues of petroleum-ether soluble fractions of methanolic extracts of this alga show rather high activity against mosquito larvae. The alga contains lambda carrageenan.

Description Thalli erect, up to 60 mm tall, cartilaginous, reddish to purple, attached by a flat, discoid holdfast. Branching alternate, branches fleshy, terete, up to 1 mm in diameter, covered with spinous outgrowths. In cross-section axial cells small, rounded, 90 μm in diameter, surrounded by 5 periaxial cells; medulla distinct, 2–3 cells thick; cortex composed of 2 layers of very small rounded cells; epidermal cells elongated, fibre-like. Life cycle diplo-haplontic and isomorphic. Tetrasporangia borne in spinous stichidial ramuli. Gametophytes dioecious; cystocarps on short branchlets, sessile, ovate to urn-shaped; spermatangial clusters disciform.

Ecology *A. muscoides* occurs on reefs, attached to sandy-coral or rocky substrates protected from strong wave action.



Acanthophora muscoides (L.) Bory – 1, habit; 2, 3, details of vegetative apical parts; 4, apical part of sporophyte with tetrasporangia.

Propagation and planting *A. muscoides* is not known in phycoculture.

Harvesting *A. muscoides* is only hand-collected from natural populations for direct local use.

Handling after harvest *A. muscoides* is sold and used fresh and/or sun-dried.

Prospects *A. muscoides* has potential for the production of fine chemicals and medical products.

Literature |1| Cordero, P.A., 1977. Studies on Philippine marine red algae. Special Publication from the Seto Marine Biological Laboratory, series IV. Seto, Wakayama Prefecture, Japan. 258 pp. |2| de Jong, Y.S.D.M., Hitipeuw, C. & Prud'homme van Reine, W.F., 1999. A taxonomic, phylogenetic and biogeographic study of the genus Acanthophora (Rhodomelaceae, Rhodophyta). Blumea 44: 217–249. |3| Laserna, E.C., Veroy, R.L., Luistro, A.H. & Cajipe, G.J.B., 1981. Extracts from some red and brown seaweeds from the Philippines. Proceedings of the Xth International Seaweed

Symposium, Göteborg, Sweden. Walter de Gruyter, Berlin, Germany. pp. 443–448. [4] Montaño, N.E. & Tupas, L.M., 1990. Plant growth hormonal activities of aqueous extracts from Philippine seaweeds. SICEN (Seaweed Information Center) Leaflet 2: 1–5. [5] Prabha Devi, Solimabi, W., D'Souza, L. & Kamat, S.Y., 1997. Toxic effects of coastal and marine plant extracts on mosquito larvae. Botanica Marina 40: 533–535.

H.P. Calumpong

Acanthophora spicifera (Vahl) Børgesen

Bot. Tidsskr. 30: 201 (1910).

RHODOMELACEAE

$2n = 64$

Synonyms *Fucus spicifera* Vahl (1802), *F. acanthophorus* J.V. Lamour. (1805), *Acanthophora thierryi* (*'thierrii'*) J.V. Lamour. (1813).

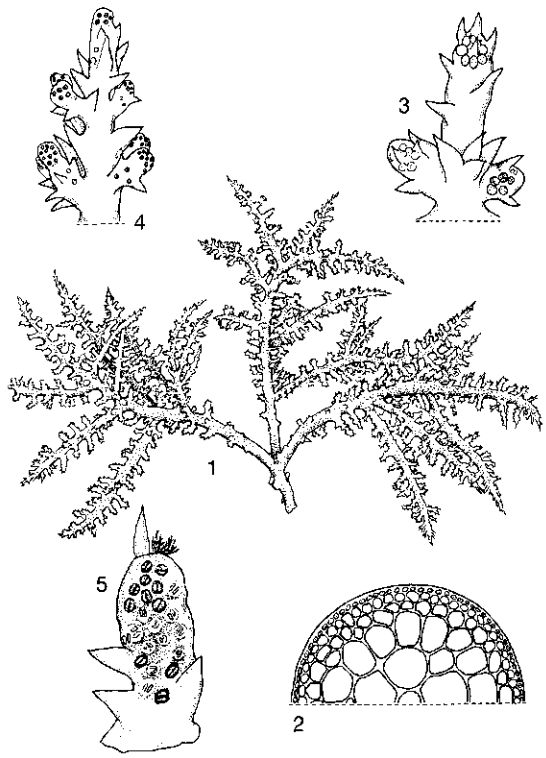
Vernacular names Philippines: culot, kulot, lagot-baye (Ilocano).

Origin and geographic distribution *A. spicifera* occurs throughout the tropics in the Atlantic Ocean (Caribbean to the Guyanas, tropical Africa), on almost all coasts of the Indian Ocean and in the western part of the Pacific Ocean (north to Japan, south to Hawaii). In South-East Asia it is widely distributed and recorded from Burma (Myanmar), Thailand (Gulf), Vietnam, Peninsular Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea, and is always more frequent than *A. muscoides* (L.) Bory.

Uses *A. spicifera* is eaten raw as a salad or cooked with other vegetables in the Philippines. In Vietnam it is a source for carrageenan processing.

Production and international trade No statistical data are available on the production of *A. spicifera* from the wild for food or medicinal uses.

Properties Extracts of *A. spicifera* show inhibitory effects on *Escherichia coli* and *Staphylococcus aureus*. Extracts in 70% aqueous ethanol show antiviral activity for several Indian strains of livestock viral diseases. The extracts show haemagglutination activity for several kinds of erythrocytes, while no such activity could be detected for *A. muscoides*. It contains lambda carrageenan, a phycocolloid of very limited occurrence. In samples of this alga (dry weight basis) 950 ppm bromine as well as 80 ppm copper have been measured. The major xanthophyll is antheraxanthin; it also contains β-carotene and b-cryptoxanthin; lutein is found in trace amounts.



Acanthophora spicifera (Vahl) Børgesen – 1, habit; 2, transverse section through axis; 3, apical part of gametophyte with cystocarps; 4, apical part of sporophyte with tetrasporangia; 5, detail of apical part of sporophyte with tetrasporangia.

Description Thalli erect, to 30 cm tall, cartilaginous, translucent, yellow-red to brown-purple, breaking easily, attached by a discoid holdfast. Branching irregular, sparse, ultimate determinate branches open, long, arcuate, bearing short branchlets rarely found on the indeterminate branches, terete, beset with spinous projections. In cross-section axial cells surrounded by 5 periaxial cells and small rounded cortical cells; epidermal cells elongated, fibre-like. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangia radially arranged at apices of stichidial branchlets. Gametophytes dioecious; cystocarps subsessile in the axils or near the bases of spine-like branchlets, globose when young, urn- to pear-shaped when mature, up to 450 μm in diameter; spermatangial clusters plate-like.

Growth and development Reproductive thalli of *A. spicifera* are generally longer than the vegetative ones, with tetrasporic thalli the longest. Both fertile and reproductive thalli occur throughout the year with the dominance of each of the three stages (tetrasporophytes, gametophytes, and vegetative) also changing within the year, although tetrasporic thalli generally dominate the population.

Ecology *A. spicifera* grows abundantly in sandy-rocky areas at the lower intertidal zone where the plants are occasionally exposed to air during very low tides, and also in the upper subtidal zone and in tide pools. It is widespread and often very common in shallow water, either in exposed situations with strong currents or in sheltered locations where it is frequently heavily epiphytized. In the Philippines, seasonal trends in the growth (length) and biomass of *A. spicifera* have been observed which seem to be enhanced by low salinity and low temperature regimes, presence of 'hard' substrate (for spore attachment) and good but not strong water movement.

Propagation and planting *A. spicifera* is not grown in phycoculture.

Harvesting *A. spicifera* is only harvested by hand from natural populations.

Yield Higher biomass production can be obtained during the rainy months from October to February (99 g dry weight/m^2 as against 51 g dry weight/m^2 for March to September).

Handling after harvest *A. spicifera* is used fresh or sun-dried for food. It is sun-dried and powdered for medical use.

Prospects *A. spicifera* shows potential for production of fine chemicals and medical products.

Literature |**1**| Buchan-Antalan, T.A. & Trono Jr, G.C., 1983. The morphology, growth and seasonality in the reproductive states of Acanthophora spicifera (Vahl) Børgesen in Bacoor Bay. Natural and Applied Science Bulletin (University of the Philippines) 35: 17–27. |**2**| Cajipe, G.J.B., Laserna, E.C., Veroy, R.L. & Luistro, A.H., 1980. On the infrared spectrum of a polysaccharide obtained by alkaline extraction of the red alga Acanthophora spicifera (Vahl) Børgesen. Botanica Marina 23: 69–70. |**3**| de Jong, Y.S.D.M., Hitipeuw, C. & Prud'homme van Reine, W.F., 1999. A taxonomic, phylogenetic and biogeographic study of the genus Acanthophora (Rhodomelaceae, Rhodophyta). Blumea 44: 217–249. |**4**| de Oliveira-Filho, E.C., 1967. On the development of tetraspores of Acanthophora spicifera (Rhodomelaceae–Rhodophyta). Botanica Marina 22: 195–206. |**5**| Laserna, E.C., Veroy, R.L., Luistro, A.H. & Cajipe, G.J.B., 1981. Extracts from some red and brown seaweeds from the Philippines. Proceedings of the Xth International Seaweed Symposium, Göteborg, Sweden. Publisher Walter de Gruyter, Berlin, Germany. pp. 443–448. |**6**| Lima Ainouz, I., Holanda Sampaio, A., Barros Benevides, N.M., Ponte Freitas, A.L., Costa F.H.F., Carvalho, M.R. & Pinheiro-Joventino, F., 1992. Agglutination of enzyme treated erythrocytes by Brazilian marine algal extracts. Botanica Marina 35: 475–479. |**7**| Premnathan, M., Chandra, K., Bajpai, S.K. & Kathiresan, K., 1992. A survey of some Indian marine plants for antiviral activity. Botanica Marina 35: 321–324.

H.P. Calumpong

Acetabularia major G. Martens

Preuss. Exped. Ost-As., Tange: 25, pl. 4, fig. 3 (1868).

POLYPHYSACEAE

$2n$ = unknown

Synonyms *Acetabularia crenulata* J.V. Lamour. var. *major* Sond. (1871), *A. denudata* Zanardini (1878), *A. gigas* Solms (1895).

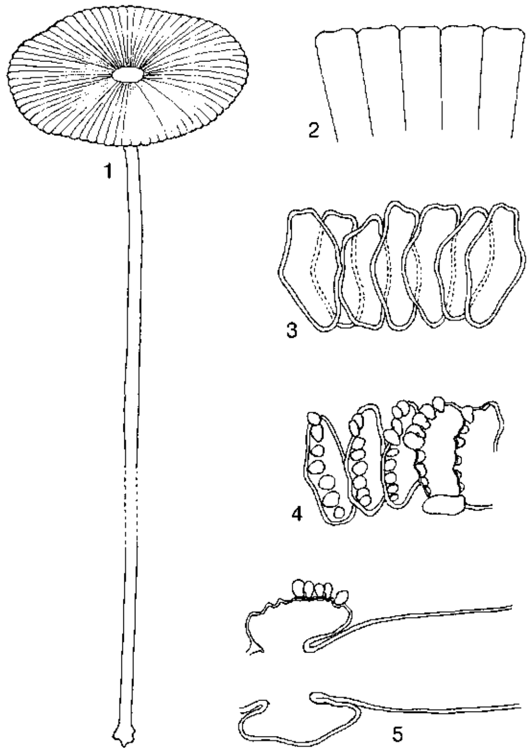
Vernacular names Mermaid's wine glass (En). Indonesia: gembur batu, keji beling, pecah beling (Javanese, Sundanese). Philippines: payong-payong.

Origin and geographic distribution *A. major* is found in the Indian Ocean from Sri Lanka and in the Pacific Ocean from Melanesia, Taiwan and islands in the Torres Strait. In South-East Asia it is known from Thailand (Gulf), Peninsular Malaysia, Indonesia (West Java, Timor, Irian Jaya) and the Philippines.

Uses *A. major* is used on the northern coast of Java as a medicine against stones in the gall-bladder, in the kidney or in the urine bladder. This is probably due to the ability of the rhizoids of the alga to secrete acids. In Indonesia (mainly West Java), *A. major* is also used as a laxative. Other *Acetabularia* spp. may also be used in the same way. Some of the unicellular, uninucleate green algae of the genus *Acetabularia* J.V. Lamour. have been used extensively for research in morphogenetics, physiology, molecular biology and cell biology.

Production and international trade *A. major* is not harvested or cultivated for commercial use. It is, however, possible to raise it in laboratory culture.

Properties $CaCO_3$ is present in *A. major* in the form of aragonite (orthorhombic). No research has yet been done on the role of this alga in destroying intestinal stones. The vegetative cell walls of *A. major* partially consist of crystalline mannan as



Acetabularia major G. Martens – 1, habit; 2, apices of rays; 3, corona inferior, front view; 4, corona superior, front view; 5, coronae in transverse section.

the skeletal component, but the gametangial cysts have cellulosic walls.

Description Thalli erect, moderately calcified, stalk slender, 2–20 cm tall, cap 10–20 mm in diameter, made up of 63–83 long slender rays, joined by calcification; tip of each ray ending in an entire, slightly emarginate or somewhat rounded margin; side walls with notches, giving them a streaky pattern. Corona superior (inside the cap) with segments 230–250 μm long, bearing (6–)8(–9) hair scars, often arranged in uniseriate rows; corona inferior (below the cap) with segments 265–280 μm long, ending in a rounded, truncate or emarginate margin. Life cycle diplontic. Gametangial cysts inside the cap rays oval, 119–129 μm × 89–109 μm, or spherical, 98–115 μm in diameter. Each cap ray containing about 100 cysts.

Growth and development The adult form of the perennial thalli of *A. major* is composed of three portions: rhizoid, stalk and cap. Following conjugation of the haploid isogametes, the zygote (50 μm) gives rise to a rhizoid, which contains a single large nucleus, and an elongating stalk which ultimately terminates its growth (after 3–4 months) by the differentiation of a species-specific cap (about 1 cm in diameter) at the tip. At maturity the cap is subdivided into many rays, each of which is functionally a gametangium. At this time the large (150 μm) nucleus divides by mitosis into thousands of secondary nuclei. The nuclei migrate through the stalk into the rays of the cap where they form cysts. The cysts are set free when the cap degenerates and ultimately give rise, after meiosis of each secondary nucleus and many mitotic divisions, to numerous motile isogametes.

Other botanical information *A. major* is the largest species in *Acetabularia*. *A. major* var. *gigas* Solms (syn. *A. gigas*) is up to 25 cm long. The cap of this variety is composed of 70–80 sporangial rays and can reach a diameter of 30 mm. The corona superior is 300–400 μm long, while each segment bears 8–10 hair scars.

Ecology *A. major* is usually solitary and grows on hard objects like dead coral on moderately wave-washed habitats near shore, on hard substrates in sheltered sand flats with seagrasses and between large seagrasses. The very large specimens of var. *gigas* have never been found in their natural habitat, but only washed ashore.

Propagation and planting *A. major* is not grown in phycoculture.

Phycoculture *A. major*, being a single-celled marine alga containing one nucleus, is capable of completing its life cycle in laboratory culture within 4–5 months, while in nature it takes at least a year.

Harvesting *A. major* is collected by hand.

Handling after harvest *A. major* can be sun-dried.

Prospects *A. major* will probably remain a traditional medicine in Java. It has to be tested for effectiveness. The thin calcareous tubes formed by this alga might be suitable for use in surgery, as a temporary substitute for skeletal elements, etc.

Literature |**1**| Berger, S. & Kaever, M.J., 1992. Dasycladales: an illustrated monograph of a fascinating algal order. Georg Thieme Verlag, Stuttgart, Germany. 247 pp. |**2**| Mariscal, R.N., 1974. Experimental marine biology. Academic Press, New York, United States. pp. 316–317. |**3**| Trono Jr, G.C. & Santiago, A.E., 1978. Notes on the genus Acetabularia (Chlorophyta) in the Philippines. Kalikasan 7(1): 77–90. |**4**| Valet, G., 1969. Contribution à l'étude de Dasycladales, 2. Cytologie et réproduction, 3. Révision systématique [Contribution to the study of Dasycladales,

2. Cytology and reproduction, 3. Systematic revision]. Nova Hedwigia 17: 551–644.

P.Y. van Aalderen-Zen

Anabaena (Bory) ex Bornet & Flahault

Révis. Nostoc. hét.: 224 (1886) [1888].
NOSTOCACEAE
Prokaryotic, thus no chromosomes

Major species and synonyms

- *Anabaena azollae* Strasb. ex Wittr., Nordst. & Lagerh., Alg. aquae dulc. exs. 28: 1340 (1896), synonyms (Drouetian): *Anabaena oscillarioides* Bory ex Bornet & Flahault (1886) [1888], *A. variabilis* status *azollae* Fjerd. (1976).
- *Anabaena flos-aquae* (L.) Bory ex Bornet & Flahault, Révis. Nostoc. hét.: 241 (1886) [1888], synonym (Drouetian): *Microcoleus vaginatus* (Vaucher) Gomont ex Gomont (1892).
- *Anabaena siamensis* Antarik., Nova Hedw. 41: 343 (1985).

Origin and geographic distribution *Anabaena* is a cosmopolitan genus and occurs primarily in freshwater, although a few species are found in marine environments. One taxon, occurring as a symbiont inside the leaves of water ferns of the genus *Azolla* Lamk, is usually considered to consist of one single species: *Anabaena azollae*. These water ferns are found in freshwater ecosystems of temperate and tropical regions throughout the world. In most of Asia the *Azolla* taxon is *Azolla pinnata* R. Br. subsp. *asiatica* Saunders & Fowler. Additional data on *Azolla* will be included in Prosea 15(2) on ferns and fern-allies.

Uses The *Azolla-Anabaena* association is used as an alternative nitrogen source in agriculture, especially in wet-rice cultivation, and is regarded by many as a 'green gold mine'. The algal symbiont is capable of fixing atmospheric nitrogen at high rates. The enzyme necessary for nitrogen fixation, nitrogenase, is oxygen-labile and is assumed to be located in the heterocysts of *Anabaena*. *Azolla* is most effective when grown as a cover crop during the fallow season of rice and incorporated as green manure into the soil. However, nitrogen is also provided when *Azolla* is grown in dual culture with wet rice. Natural or cultured growths of *Azolla* may be harvested and applied to various crops including taro (*Colocasia esculenta* (L.) Schott) and wheat (*Triticum* spp.), either by incorporating them into the soil before planting the crop or by applying them as a mulch on top of the soil around the crop plants. Often, a combination of methods of application is used.

Although the use of *Azolla* is labour intensive, as much as 100 kg N/ha can be provided to a rice crop when planted in double rows. *Azolla* is cultivated on the paddy field and, after briefly draining the field, it is incorporated into the soil at intervals during the growing season. *Azolla* can also be used as a fodder for pigs, cattle, poultry and fish. In addition, *Azolla* (and thus also *Anabaena azollae*) can be used as human food, medicine and water purifier. When the *Azolla-Anabaena* association is grown in a nitrogen-free atmosphere and/or a water medium containing nitrate, the nitrogenase in the symbiont, instead of fixing nitrogen, evolves hydrogen from the water. Hydrogen is a non-polluting high-energy fuel.

Additional nitrogen supply can also be realized by growing blue-green algae alone on suitable soils. *A. siamensis* is very suitable as a -ricefield inoculum because of its good nitrogen-fixing capacity and because its akinetes are capable of surviving long dry periods. In general, using free-living blue-green algae does not increase the rice grain yield as much as applying the *Azolla-Anabaena* association. Under less favourable conditions the latter method is, however, profitable.

A. azollae isolates, when immobilized in polyurethane foam and added to rice seedlings, significantly increase root and shoot growth, chlorophyll content, and biomass production of these rice seedlings in laboratory cultures. Experimental inoculation of rice with *A. azollae* trichomes immobilized in polyurethane foam or sugar-cane waste has resulted in higher ammonia amounts in the flood water and increased rice grain and straw yields.

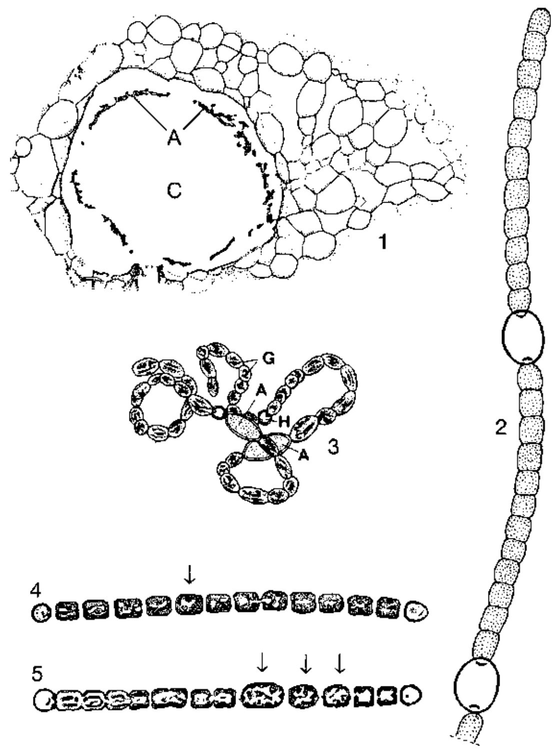
Production and international trade *Azolla* (and thus also *Anabaena azollae*) is produced on a large scale in India, Bangladesh, Indonesia (Sulawesi), Thailand, Vietnam and China.

The *Azolla-Anabaena* associations have a long history as a green manure for wet rice in the Far East. Jia Si Xue published in 540 A.D. a book 'Chih Min Tao Shu' (The art of feeding the people) describing the cultivation and use of *Azolla* in rice fields. Nevertheless, the application of *Azolla* in China did not expand markedly until 1962, since when it has been extended, first to about 1.34 million ha in 1978 then to 6.5 million ha in 1995. The use of *Azolla* in Vietnam can likewise be traced back many centuries, although in 1955 it was restricted to about 40 000 ha in the Red River delta, extending to 320 000 ha by 1965, covering about 40% of the area under rice. The association is mainly grown here during November–January in fallow, flooded fields to be used for 'spring' rice.

Properties All *Anabaena* are able to fix atmospheric nitrogen. *A. azollae*, as well as the non-symbiotic *A. variabilis* Kütz. ex Bornet & Flahault, when immobilized in polyurethane and polyvinyl foams or calcium alginate beads, release ammonia extracellularly, especially in the presence of L-methionine-D,L-sulphoximine. Different isolates differ in growth rate, biomass production and nitrogenase activity, and the immobilization usually further increases growth and ammonia excretion. Some soil *Anabaena* had positive plant growth regulator effects when extracts of these algae were administered to rice laboratory cultures. Especially the planktonic *A. flos-aquae* is notorious for producing toxic blooms in freshwater. Anatoxins released by *A. flos-aquae* and *A. circinalis* (Kütz.) Rabenh. ex Bornet & Flahault can paralyze skeletal and respiratory muscles in fish, poultry, pets, cattle and humans, in some cases resulting in death. No antidotes or treatments are currently available. Different strains of *A. flos-aquae* produce different types of toxin: anatoxin-a is a neurotoxic secondary amine alkaloid and a potent neuromuscular blocking agent, while anatoxin-a(s) is a N-hydroxyguanidine methyl phosphate ester which is a potent cholinesterase inhibitor. The (s) is added because of the promotion of salivation in these intoxications. Some *Anabaena* strains are also able to produce other toxins, like lipopolysaccharide (LPS) endotoxins in their cell envelopes, causing fevers and inflammation after bathing or showering with water containing these cyanobacterial blooms. Microcystins (cyclic hepatopeptides) cause acute liver poisoning. The latter toxin is better known as being produced by the cyanobacterium *Microcystis aeruginosa* (Kütz.) Kütz.

Description Trichomes 2.5–14 µm in diameter, unbranched, straight or coiled, not tapering, made up of 8–18 cells, with extracellular polysaccharides not accumulating as a gelatinous matrix. Cells spherical to barrel-shaped, isodiametric, or slightly shorter or longer than diameter, with constrictions at the cross-walls. Heterocysts numerous, intercalary, basal. Spores (akinetes) usually larger and more elongate than vegetative cells, single or in series between heterocysts.

- *A. azollae*. Trichomes solitary or in small groups inside cavity of leaves of *Azolla* water ferns, straight or curved, about 5 µm broad, without a visible sheath. Cells quadrangular, ellipsoidal or subglobose, 4–5.5 µm × 5–9.5 µm, greenish-blue,



Anabaena. A. azollae Strassb. ex Wittr., Nordst. & Lagerh. – 1, an oblique longitudinal section of a dorsal leaf lobe of the water fern Azolla caroliniana Willd.; the large cavity (C) containing filaments of A. azollae (A) is conspicuous in the proximal half of the lamina; 2, habit of a trichome with 2 solitary heterocysts. A. flos-aquae (L.) Bory ex Bornet & Flahault – 3, habit of trichome with akinetes (A), heterocysts (H) and gas vacuoles (G). A. siamensis Antarik. – 4, 5, habits of trichomes with terminal heterocysts and akinetes (arrows).

with granular contents. Heterocysts ellipsoidal, solitary, 6–10 µm × 7.5–11.5 µm, olive-green, occasionally lacking; usually heterocyst frequency 20–30% when actively fixing nitrogen. Spores lacking under natural conditions, observed in cultures: 6–7.5 µm × 9–13 µm, singly or in short series, usually not located near heterocyst; epispore smooth, yellowish.

- *A. flos-aquae*. Trichomes circinate, planktonic, free-floating, 4–8 µm broad, without visible sheath. Cells ellipsoidal, rarely spherical, as long as broad or longer, 6–8 µm long, mostly with gas-vacuoles. Heterocysts ellipsoidal, 4–9 µm × 6–10 µm; heterocyst frequency usually 4–8%. Spores prominently bent, convex on outside, straight on inside, 7–13 μm × 20–35(–50) μm, singly, usually located near heterocyst; epispore smooth, colourless or yellowish, often surrounded by wide gelatinous sheath.

– *A. siamensis*. Thalli mucilaginous, bright blue-green; trichomes short, single, straight, distinctly constricted at cross-walls, 30–50 μm long, without a visible sheath. Cells quadrangular to cylindrical, 2–3 μm × 2–5 μm, without gas-vacuoles. Heterocysts unipolar, spherical or subspherical, present at both ends of trichome, 2–4 μm in diameter, with a distinct yellowish smooth outer wall and hyaline yellow content. Spores (akinetes) formed in series, oval to subspherical, 5–10 μm in diameter, located away from heterocyst; epispore smooth, colourless.

Growth and development The relationship between *A. azollae* and *Azolla* is one of permanent symbiosis, i.e. the two organisms are associated in all stages of the life cycle of the fern and the association persists from one generation to the other, regardless of whether reproduction of the fern is sexual or asexual. It appears that certain bacteria present in the leaf cavities of the fern, particularly an *Arthrobacter* sp., constitute a third partner in the *Azolla-Anabaena* symbiosis. The role of the bacterium in the partnership is not yet understood.

Akinetes of *A. azollae* are present in both microsporocarps and megasporocarps of *Azolla*, but are retained to maturity only in the latter. During the development of the *Azolla* zygote the *Anabaena* akinetes germinate to produce undifferentiated, generative filaments. These become associated with the shoot apex of the developing fern sporophyte, perpetuating the symbiosis through the reproductive cycle. Growth and development of the host and the symbiont are synchronous. This is a feature that does not occur in other plant-cyanobacteria symbioses. Each apical meristem of the fern has a small colony of *Anabaena* filaments associated with it and the growth rate of the endophyte is coordinated with that of the host. These *Anabaena* filaments associated with the plant apex lack heterocysts and do not exhibit nitrogenase activity. The establishment of algal filaments in each fern leaf begins in the young leaves contiguous with the apical *Anabaena* colony and is complete by the time each leaf emerges as a distinct mature entity. The development of the cavity in the dorsal lobes of the fern leaves begins in young leaves rapidly enlarging by cellular expansion. After that the cavity becomes inoculated with *Anabaena* and as the leaf matures, the *Anabaena* filaments in the leaf cavity multiply. Then also rapid differentiation of heterocysts occurs, accompanied by a rapid increase in nitrogenase activity. Attempts have often been used to isolate *A. azollae* from its host. In many cases isolates have been obtained that are still capable of fixing nitrogen, but in all cases these cultured isolates develop different characteristics from the fresh isolates. When immobilized in polyurethane foam, isolates enhance their heterocyst frequency as well as their nitrogenase activity. It has been hypothesized that the major cyanobacterial constituent of the association is an obligate endosymbiont incapable of in-vitro growth.

In mature trichomes of *A. siamensis* a vegetative cell in the mid-region of the trichome divides itself symmetrically, giving rise to two small daughter cells which will develop into heterocysts after the trichome breaks into two at the junction of the two newly formed incipient heterocysts. Akinetes in *A. siamensis* are usually also formed in the midregion of the trichome, where a vegetative cell becomes slightly enlarged and gradually transforms into a typical akinete by synthesizing an additional wall and accumulating inner granular contents. Successively, adjoining cells can also convert, resulting in a short string of akinetes.

In clonal cultures of *A. siamensis*, molecular nitrogen as well as ammonium or nitrate could be used as a nitrogen source, resulting in a doubling time of 3.4–3.7 days. The alga grows even faster (doubling time of 2 days) when the amino acid L-glutamine is used as the sole source of nitrogen.

The light-harvesting pigments of the two partners of the symbiotic *Azolla- Anabaena* association are complementary. The endophyte accounts for 10–20% of the association's total chlorophyll and about 16% of its total protein, with phycobiliproteins (phycocyanin and phycoerythrocyanin) accounting for 4–10% of the endophyte's protein. The *Anabaena* contributes 6–10% of the total photosynthetic capability of the association and its photosynthesis is not inhibited by atmospheric oxygen.

Other botanical information Identification and classification of blue-green algae are usually heavily debated. Some morphological characters change in culture or are not expressed. The *Anabaena* species endophytic in *Azolla* might be growth forms of *A. variabilis* or some might be species of *Nostoc* Vaucher ex Bornet & Flahault or belong to *Tricornus* (Ralfs ex Bornet & Flahault) Komárek & Anagnost. Studies on fatty acid composition of the endophytes as well as immunological studies and lectin haemagglutination research suggest that these *Azolla* symbionts differ considerably from those of *Anabaena* and *Nostoc*. There has so far been no fully satisfactory demonstration of successful reestablishment of the symbiotic state with any isolate and an endophyte-free *Azolla*, though there are reports of success. Nevertheless, it will be difficult to acknowledge any of the isolates as the true endophyte until Koch's postulates have been fully demonstrated. Even the use of monoclonal antibodies has not yet solved the problem.

In the planktonic species the debate on variability is also far from reaching agreement, although database systems are being developed to help identifying the species. Because of the paired (young) intercalary heterocysts, *A. siamensis* might belong to *Anabaenopsis* Geitler.

Ecology *A. azollae* occurs exclusively as an endophyte in the free-floating *Azolla* water ferns. The endophyte in mature leaf cavities of the *Azolla* fern releases newly fixed nitrogen as ammonia, which is rapidly assimilated by the fern. Since wind and wave action, as well as other turbulence, cause fragmentation of the fern and diminish growth, *Azolla* is not found on large lakes where the waters move swiftly. It is, however, capable of luxurious growth in ponds, marshes and canals, while paddy fields form an ideal environment for *Azolla*. The association can, however, survive only a few days in a paddy field once the field is drained. Although *Azolla* can colonize waters that are nitrogen deficient, its growth can be limited by the availability of other nutrients, such as phosphorus and iron. The most important factors influencing growth and distribution of the *Azolla-Anabaena* symbiosis are light, temperature, water, mineral nutrition, pH, salinity, physical disturbance and biotic interactions. Most populations of *Azolla* have an optimal temperature range of 20–25°C. The temperature regime is difficult for farmers to manage. Direct high temperature effects mainly decrease nitrogenase activity, but are not as serious as indirect effects, the latter resulting in higher losses due to pests. When conditions are favourable, *Azolla* will grow well under full sunlight.

A. flos-aquae is a planktonic freshwater alga which uses its gas vacuoles for buoyancy regulation. *A. siamensis* occurs on most soils and in paddy fields. Because of its prominent akinetes it can easily survive long dry periods. Both the free-living *Anabaena* filaments and the endophytic ones are able to reduce N_2 under an air atmosphere and the nitrogenase is assumed to be localized in the heterocysts. *A. siamensis* is semihalotolerant and mesophilic. Its optimum growth temperature is 41°C.

Propagation and planting Cultures of *Azolla* and its symbiont must be maintained vegetatively in nurseries throughout the year to be used as inoculum since the production of a large biomass of *Azolla* from spores is slow and difficult. Just prior to the rice-growing season the fern with the symbiont must be multiplied in large quantities to be ready for field cultivation. Inoculum transport presents obstacles in regions lacking means of transport. Dried *Azolla* is logistically preferable, but its N contribution is only half that of fresh plants.

During the multiplication phase of *Azolla*, prior to the rice-growing season, the fern mats must be continually subdivided to prevent competition for light, space and nutrients. In that way a high growth rate can be maintained. The level of inoculation of fresh *Azolla* into fields is (25–) 30– 200 (–800) g/m^2, depending on growth conditions. Fronds are often fragmented to aid growth and dispersal. Usually application of phosphorus is recommended to obtain significantly higher rice grain yields. However, *Azolla pinnata* is less affected by phosphorus-deficient conditions than most other *Azolla* species.

Aquaculture Water is a fundamental requirement for successful cultivation and application of *Azolla* and its symbiont. Therefore, proper water control is essential. The *Azolla-Anabaena* association needs all the essential elements that are required by other plants as well as molybdenum and cobalt, both of which are required for atmospheric nitrogen fixation. Normally, all nutrients must be available in water throughout the period of growth of the fern. Threshold levels of P, K, Mg, and Ca required for *Azolla* growth are 0.03, 0.6, 0.5, and 0.5 mmol/l respectively; for the micronutrients Fe, Mn, Mo, and B 50, 20, 0.3, and 30 µmol/1, respectively. Phosphorus is the most important and often limiting nutrient for *Azolla* growth. Phosphorus deficiency is indicated by smaller, fragile, less vigorous plants with purple, bullet-shaped leaves, and developing very long roots. Maximum growth and atmospheric nitrogen fixation by the *Azolla- Anabaena* association requires greater P fertility than for rice alone, and this is a major barrier to applied use in many instances.

Azolla does not require any nitrogen in the culture medium, but the level of nitrogen in the water does positively affect growth and atmospheric nitrogen-fixing rates. Iron is a common limiting element, because it is an essential constituent of nitrogenase. In calcium-deficient *Azolla* the fronds become fragmented, while in potassium-deficient plants growth is stunted. *Azolla* is extremely sensitive to SO_2 pollution in the atmosphere. Ozone pollution considerably reduces nitrogen-fixation rates and heterocyst frequency in the symbiont. Exposure to atmospheric NO_2 pollution also decreases rates of growth, nitrogen fixation, heterocyst formation, and overall nitrogen cycling. The systemic fungicides Benlate (methyl-1-butyl carbamoyl-2 benzimidazole carbamate) and Vitavax (5,6-dihydro-2, methyl-1, 2-oxathiin-3-carboxanilide) stimulate ammonium production by immobilized *A. azollae* in a photobioreactor and inhibit the activity of the enzyme glutamine synthease.

Diseases and pests Some cyanophages can infect *Anabaena*, but no studies are available regarding the importance of infection in natural populations. Pathogenic fungi and free-living algae can become damaging to *Azolla*, especially during hot, humid periods. *Azolla* is subject to a number of pests, in particular insects, some of which can be disastrous to successful propagation if they are not effectively controlled. Snails are also a common pest. One of these, *Limnea natalensis*, is a schistosomiasis vector and thus of concern for public health. The use of the insecticide Vophatox 0.005% is often fatal – very few *Azolla* plants survive a treatment. There are no pests known to attack the symbionts.

Harvesting The *Anabaena* cyanobacteria are never harvested as an isolated crop. They are either included inside the *Azolla* plants or mixed with other cyanobacteria or plankton algae.

Yield A dry weight of 4.8–7.7% of the fresh material has been found for *Azolla*, containing generally 3–6% nitrogen, but it is strongly influenced by growth conditions.

Handling after harvest The harvested *Azolla* can be used immediately as green manure or can be air-dried for transport. Mixtures of soil cyanobacteria can be air-dried and used as new inoculum.

Genetic resources Several *Anabaena* species and strains but not *A. azollae* are available from algal culture collections. No systematic collection of germplasm of *Azolla* has yet been recorded. The *Azolla- Anabaena* symbiotic nitrogen-fixing complex can be studied by genetic manipulation through tissue culture using excized frond meristems of the fern which carry the cyanobiont germplasm. There has been some success in transferring *Anabaena* from one species of *Azolla* to another.

Prospects Because of the high costs of commercial N-fertilizer, the lasting concerns about environmental conservation, and the propagation of sustainable, renewable, non-polluting resources, it can be expected that both the application of *Azolla-Anabaena* associations and of suitable soil cyanobacteria will increase in the future. If no diseases and pests prevent future use of these organisms, they might become even more important as nitrogen sources for agriculture than they are at present. The popularity and the extent of their use will ultimately depend on the price of energy, which directly determines the availability and cost of inorganic N-fertilizer. Techniques to achieve a much lower phosphate requirement by the use of mutant *Azolla* plants might result in even greater popularity as a nitrogen fertilizer. However, the inability to establish free-living cultures of *Anabaena azollae* and the inability to control the induction of sporulation and germination in the field of the spores of the *Azolla* ferns are major limitations to research and applicability.
The toxic substances of some freshwater *Anabaena* might become the basis for future fine chemicals or pharmaceuticals.

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W.F. Prud'homme van Reine

Arthrospira Stizenb. ex Gomont

Monogr. Oscill.: 246 (1892) [1893].
PHORMIDIACEAE
Prokaryotic, thus no chromosomes

Major species and synonyms

- *Arthrospira fusiformis* (Woron.) Komárek & J.W.G. Lund, Algol. Stud. 58:11 (1990), synonym: *Spirulina fusiformis* Woron. (1934), Drouetian synonym: *Porphyrosiphon notarisii* (Menegh.) Kütz. ex Gomont (1892).
- *Arthrospira maxima* Setch. & N.L. Gardner, Univ. Calif. Publ. Bot. 6(14): 377–379 (1917), synonyms: *Spirulina maxima* (Setch. & N.L. Gardner) Geitler (1932) not *S. maxima* C. Bernard (1909), *S. geitleri* G. de Toni (1935), *Oscillatoria pseudoplatensis* Bourr. (1970), Drouetian synonym: *Microcoleus lyngbyaceus* (Kütz.) P. Crouan & H. Crouan ex Gomont (1892).
- *Arthrospira platensis* Gomont, Monogr. Oscill.: 247–248 (1892) [1893], synonyms: *Spirulina jenneri* (Hass.) Stizenb. var. *platensis* (Nordst.) ex Gomont (1892) [1893], *S. platensis* (Gomont) Geitler (1925), *Oscillatoria platensis* (Gomont) Bourr. (1970), Drouetian synonym: *Microcoleus lyngbyaceus* (Kütz.) P. Crouan & H. Crouan ex Gomont (1892).

The species in *Arthrospira* are often considered to be included in the genus *Spirulina* Turpin ex Gomont (1892) [1893]. *Spirulina* is, however, clearly different and phylogenically distant from *Arthrospira*.

In many papers on cultivated *Arthrospira* (often as '*Spirulina*') no species names are used. In these cases the material is usually considered to belong to *A. platensis*, although in some cases *A. maxima* material has been used.

Vernacular names In most countries generally known as 'spirulina'. Thailand: sarai kleothong.

Origin and geographic distribution *Arthrospira* is commonly found in many alkaline salt lakes in Africa and America. It is cultivated in many (mainly) tropical countries, including South-East Asia. *A. fusiformis* is the name to be used for an autochtonous species found in tropical Asia and Africa. *A. maxima* appears to be essentially confined to Central America, while *A. platensis* seems to be more widely distributed and is mainly found in Africa, but also in Asia and South America. The name *Arthrospira (Spirulina) platensis* is commonly used for almost all commercially cultivated 'Spirulina'.

Uses Early records show that dried *A. maxima* ('tecuitlatl') was consumed by natives in Mexico. In Chad a cake ('dihé') made of *A. platensis* is eaten with tomatoes, *Capsicum* peppers and various spices. About 9–13 g of this alga is consumed per meal in Chad, and it is eaten in 10–60% of the meals.

Arthrospira of food-grade quality is currently marketed (usually as '*Spirulina*') as powder or tablets with or without added calcium and/or vitamin C in the health food market ('nutraceuticals'). It can be directly used as food, mainly as substitute for green vegetables and is used especially for children. The mucoprotein cell walls of these algae are easy to digest. The food products marketed include protein powders with 10% *Arthrospira*, green coloured noodles or even chocolate bars containing *Arthrospira*. In Vietnam, the algal powder is mixed with milk and served as a nutritional supplement to treat malnourished children suffering from protein-deficiency diseases.

Several therapeutic effects have been recorded using *Arthrospira*. A cholesterol-lowering effect has been mentioned and *Arthrospira* is a potential food for persons suffering from coronary illness and obesity. Using the alga as supplement has been observed to produce hypocholesterolemic and hypoglycaemic effects, increased lactation in nursing mothers, chemoprevention and wound-healing properties. Antiviral and anti-cancer effects of *Arthrospira* and its extracts have also been found. Phycocyanin may have medical application. However, most claims have not been backed up by detailed scientific and medical research. No acute, chronic or subchronic toxicity of *Arthrospira* products has ever been detected.

Over 50% of the total production of *Arthrospira* powder is used as feed supplement. Especially in Japan *Arthrospira* is frequently incorporated as constituent of fish feed. It improves the palatability of this feed, the quality of the fish, enhances the colour of carp, and has health-promoting effects. Moreover, the mortality rate of fingerlings or post-larval stages in fish, molluscs and crustaceans can be reduced by 30–50% by adding 0.5–1.0% of *Arthrospira* to the feed. This also enhances growth of these animals. A comparable addition to fish feed can give a growth improvement of 17–25%. In Thailand and Vietnam *Arthrospira* powder is also used to feed silkworms.

Phycocyanin can be utilized as a natural pigment in the food, drug and cosmetic industries to replace the currently used synthetic pigments that are suspected of being carcinogens. The commercial product 'Lina blue-A' is used as natural food colourant for confectionery, chewing gum, -ice-cream, dairy products and soft drinks. It does not react to light, but reacts slightly to heat. Another phycocyanin product obtained from *Arthrospira*, when modified to make it non-soluble in water, can be used as colourant in cosmetics. It does not run when it comes into contact with water or sweat, and is not a skin irritant. Small quantities of phycocyanin are used as a biochemical fluorescent tracer in immunoassays, microscopy and cytometry.

The carotenoids in *Arthospira* powder can cause pigmentation when used as a dietary supplement for cultured fish and shellfish such as koi carps, red tilapia, ayu, striped jack, and several kinds of prawns.

Waste-water treatment with *Arthrospira* offers many of the same advantages as treatment with other microalgae. The efficiency of ammonia stripping and phosphate removal from effluent by *Arthrospira* cultures needs further investigation, as does the use of these cyanobacteria in palm oil effluent in Malaysia and in waste water from tapioca factories in Thailand. The latter use, however, has already been applied commercially where 30 t of animal-feed *Arthrospira* biomass is produced annually.

Immobilized microalgae, including *Arthrospira*, are already used to remove heavy metals in commercially available products.

Production and international trade Commercial production of *Arthrospira* (usually as '*Spirulina*') at present is carried out on a large scale in Mexico, Taiwan, China, Thailand, Burma (Myanmar), United States (California), Japan and India. In 1993 there were 22 '*Spirulina*' commercial plants in the world, covering about 700 ha, producing 1000 t. By 1996 there were no less than 80 *Arthrospira* producers in China alone, mainly producing for export; the local market there is still quite small.

In Thailand, the Siam Algae Co. Ltd. cultivates *Arthrospira* in an inorganic medium in a pond area of 44 000 m^2 and the products are marketed as health food, animal feed and phycocyanin products. Production reached 100 t in 1980, 125 t in 1996 and will soon reach 150 t. Neotech Food Co. Ltd., Thailand, produced 36 t *Arthrospira* powder in 1996 from an area of 50 000 m^2 (30% human consumption, 70% animal feed).

The Myanma Pharmaceutical Industries in Burma (Myanmar) is the largest production site in the world based on natural blooms. In lake Twin Taung near Butalin, located in a volcanic crater, *Arthrospira* blooms occur mainly in native ponds covering about 130 000 m^2, resulting in about 32 t sun- dried algal powder for the local market.

In Vietnam, an *Arthrospira* plant of 5000 m^2 pond area of the National Mineral Water of Vinh Hao produces about 8 t of powder for export.

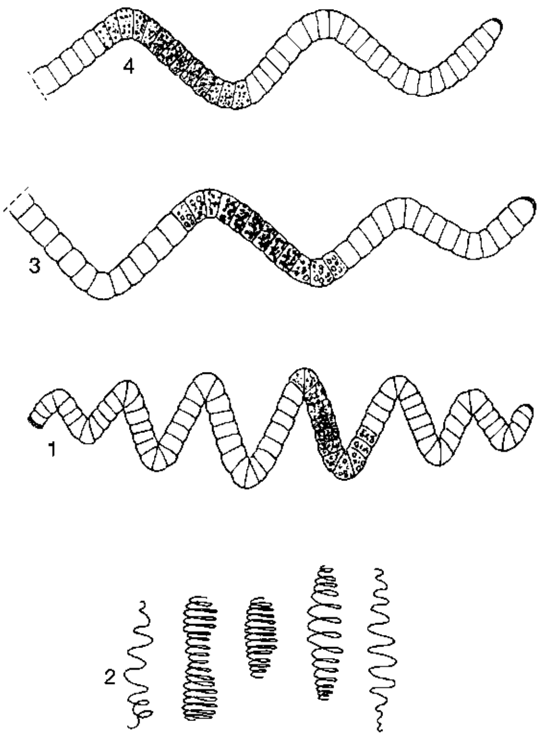
Properties *Arthrospira* contains per 100 g dry weight: water 3–8 g, protein 50–66 g, lipids 4–10(–16) g, carbohydrates 13–25 g, fibre 4–10 g and ash 6–13 g, while the amount of usable protein in poultry and seafoods is considerably higher than in *Arthrospira* powder, it falls in the same class as most other meat and dairy products. In samples not washed sufficiently with acid water to remove absorbed carbohydrates, the ash content may be as high as 25%. The energy value averages 1680 kJ per 100 g. The net protein utilization values range from 41–63%, while digestibility is 83–84%. The proteins contain many essential amino acids (in % dry weight) including isoleucine (3.5–4.1), leucine (5.4–5.8), lysine (2.9–4.0), methionine (1.4–2.2), phenylalanine (2.8–4.0), threonine (3.2–4.2), tryptophan (0.91–1.1) and valine (4.0–6.0), as well as a high number of non-essential amino acids. The biological value of these microalgal proteins, however, is limited by the low levels of sulphur-containing amino acids. The levels of these amino acids can be raised by increasing the amount of sulphate in the culture medium. The lipid fraction contains mainly hydrocarbons and terpenic alcohols, together with a low percentage of sterols. The major sterols in *A. maxima* are often clianosterol and cholesterol. The lipids contain, however, relatively high amounts of the polysaturated fatty acid 18:3 (ω-6) gamma-linolenic acid. It forms 1.0–1.2% of the *Arthrospira* dry weight and 8–32% of the total fatty acids in these algae.

The algal powder is rich in vitamins such as β carotene, biotin, cyanocobalamin, pantothenic acid, folic acid, inositol, nicotinic acid, pyridoxine, riboflavin, thiamine and tocopherol. Mineral content in mg per 100 g of the product is: calcium 100–1400, chromium 0.2–0.3, copper 0.8–1.2, iron 47–150, magnesium 140–400, manganese 0.8–5.0, phosphorus 670–900, potassium 1330–1540, selenium about 0.04, sodium 27–900 and zinc 0.2–0.3.

Pigment content in mg per 100 g dry weight is: carotenoids 290–690, chlorophyll 600–1500, and phycocyanin 14–20. Of the carotenoids (in mg per 100 *Arthrospira* powder), especially β carotene 50–140 and zeaxanthin 70–170 are interesting compounds.

Description Trichomes solitary, 200–500 μm long, with very thin sheath, free-floating or showing gliding movement, multicellular, cylindrical, helical, loosely and regularly coiled, often slightly constricted at distinct cross-walls, apices slightly tapering or not. Cells with or without gas-vacuoles; terminal cell rounded or pointed, with or without a calyptra. Heterocysts absent.

- *A. fusiformis*. Trichomes 3.4–6(–9.5) μm in diameter, not or only very slightly constricted, not or only slightly attenuate; helix very variable, up to 80 μm long, 15–50 μm wide, with end curves diminishing or widening intensely towards the ends; end cell rounded or slightly narrowed, occasionally with calyptra; all cells with regularly disposed gas-vacuoles.
- *A. maxima*. Trichomes (6–)7–9(–10) μm in diameter, not or only very slightly constricted at the cross-walls, only slightly attenuate; helix rather long, 70–80 μm long, 40–60 μm wide, with end curves shorter than middle ones; end cell rounded, or with flat calyptra; all cells with regularly disposed gas-vacuoles.
- *A. platensis*. Trichomes (4–)6–7(–8) μm in diameter, slightly constricted, attenuate, with rather short helix, 30–57 μm long, 26–36(–50) μm wide, with end curves not shorter than middle ones; last 6–7 cells narrower; end cell longer than broad, rounded, capitate, with thickened outer wall; cells with or without irregularly disposed gas-vacuoles.



Arthrospira. A. fusiformis (Woron.) Komárek & J.W.G. Lund – 1, habit of a trichome; 2, different forms of helicity. A. maxima Setch. & N.L. Gardner – 3, habit of a trichome. A. platensis Gomont – 4, habit of a trichome.

Growth and development The development of *A. platensis* follows the common pattern of many other microorganisms which undergo a simple cell division without any sexual or differentiation step. A mature trichome breaks into small pieces through the formation of specialized cells known as necridia or lysing cells. The small trichomes are further fragmented to produce gliding, short chains consisting of 2–4 cells known as hormogonia. Each hormogonium can give rise to a new trichome, increasing in length and assuming the typical helical shape as the number of cells increases through binary fission.

Apart from autotrophic growth, *A. platensis* can also, in axenic cultures, be grown under mixotrophic and heterotrophic conditions. Some studies suggest that in mixotrophic conditions the autotrophic and heterotrophic forms of growth function independently in this alga, thus without mutual interaction. Heterotrophically grown cells (on glucose) have a lower pigment content than those in the autotrophic and mixotrophic cultures. Respiration-to-photosynthesis rates measured in axenic cultures are 1% at 20°C and 4.6% at 45°C.

These rates are much lower than those recorded for outdoor cultures of *A. platensis*, where up to 34% of the biomass produced during the daylight period may be lost through respiration at night. However, the respiration rate is strongly influenced by light conditions during growth, and by light stress provoking photo-inhibition. *A platensis* cultures grown at less than the optimal temperature are more sensitive to photo-inhibition than those grown at the optimal temperature. In tropical countries, sub-optimal temperatures will occur during the early morning hours. However, lower temperatures result in decreased respiration, diminishing night loss of biomass in cultures. Nevertheless, a combination of relatively low temperatures and high light intensities may induce photo-inhibitory stress.

Exposure of cultures of *A. platensis* to high NaCl concentrations results in an immediate cessation of growth, followed by a usually somewhat slower growth rate. Photosynthesis and respiration activities both decrease markedly after exposure to high salinities. The salt-stressed cultures are very susceptible to photo-inhibition. Nevertheless, in China strains of *A. platensis* adapted to seawater are cultivated on a large scale in a seawater-based culture medium. The sand-filtered seawater is enriched with a commercial fertilizer (N:P:K = 12:12:12) and low concentrations of $NaHCO_3$ and Fe_2SO_4.

Other botanical information The taxonomy of blue-green algae in general is very complicated, and the same is true for *Arthrospira*. There is still much discussion about the separation and naming of species in this genus. *A. fusiformis* is often included in *A. maxima*. A new name was proposed, initially for the calyptrate specimens in *A. fusiformis* and later for the species name as a whole: *A. indica* T.V. Desikahary & W. Jeeji Bai. There is also much debate about the planktonic and non-planktonic nature of *A. maxima* and *A. platensis* respectively. The latter species, which forms massive water-blooms in tropical lakes, is considered to be non-planktonic by some specialists, while others think it well-founded to still consider *A. platensis* a planktonic species. The exact taxonomic position of the marine *Arthrospira* strains is also not yet clear.

Ecology *Arthrospira* grows abundantly in alkaline lakes characterized by high levels of carbonate and bicarbonate, and also in diverse habitats ranging from soils, marshes, brackish water, seawater, thermal springs and freshwaters. These algae are dominant organisms in alkaline lakes containing more than 30 g/l of salt (particularly sodium carbonate) and a pH close to 11. Optimal temperatures for growth range for different isolates from 30–42°C, varying between 30–32°C in selected temperate strains and 40–42°C in tropical ones.

Propagation and planting Zarrouk's medium is commonly used to culture *Arthrospira*. The medium contains high amounts of $NaHCO_3$ (16.8 g/l) as a carbon source and a buffer, and $NaNO_3$ (2.5 g/l) as a nitrogen source. High alkalinity is necessary for the growth of commercial *Arthrospira*, with a pH optimum of 8.3–11.0 for food growth. In outdoor pools a pH of 11.0 is growth-limiting. Usually *Arthrospira* is thought to be obligate photoautotroph and therefore unable to grow in the dark using organic carbon sources. However, it has been shown that heterotrophic growth of *A. platensis* is possible in axenic cultures. In laboratory conditions, the algae can be grown in shake flasks, aspirator bottles and photobioreactors.

Phycoculture Almost all commercial reactors for *Arthrospira* production are based on shallow raceways in which algal cultures sustained by a paddle wheel are mixed in a turbulent flow. Open raceways can be lined with concrete or formed as shallow earthen tunnels lined with PVC or some other durable plastic. In some cases, however, semi-natural lakes are used for *Arthrospira* cultivation. The size of commercial open raceway ponds for culturing *Arthrospira* ranges from 0.1–0.5 ha. Culture depth is usually maintained at 15–18 cm. In these ponds the optimal areal density of the algae must be maintained to prevent growth reduction due to self shading. This optimal areal density may also be affected by culture depth, the strain used, and the rate of mixing. Mixing (stirring) does not only enlarge the optimum density, but also prevents photo-inhibition caused by excess exposure to light of the algae staying too long in the upper and over-radiated water layers. It also lowers detrimental effects of too high oxygen concentrations in the upper layers of heavily photosynthesizing cultures. However, too high mixing and flow velocity result in fragmentation and increased coiling of the trichomes.

In an experimental plant in Thailand, the algae are mass-cultured in concrete raceway ponds (6 m × 26 m × 0.5 m) using waste water from a tapioca factory and stirred by paddle wheels. Another Thai experimental plant uses indigenous *Arthrospira* strains, mainly from north-eastern Thailand and capable of growing in brackish water. In India, in a rural location, *Arthrospira* is cultured using 2000 l tanks, agitated by manual stirring or by wheels driven by wind energy. In some cases a growth medium is used based on low-cost nutrients obtained from rural wastes such as bonemeal, urine, or the effluent of biomass digesters. In Vietnam, the medium is enriched with wastes from a fertilizer factory and the raceways are agitated by paddle wheels driven by wind energy. In order to use *Arthrospira* grown on wastewater as animal feed, it is necessary to minimize contamination of the biomass by choosing the right type of effluent to be treated. An integrated and sustainable approach is to combine the treatment of animal wastes with production of algal biomass for animal feed.

Arthrospira is also cultured in small-diameter transparent polyethylene tubes in Singapore, Italy and Israel. Other closed systems are flat plate reactors and biocoil facilities. Closed systems offer several advantages over open raceways: cultures are better protected from contaminants and can be effectively sterilized, while water loss and the ensuing increase in salinity of the medium are much reduced. They allow effective illumination due to a better surface-to-volume ratio and attainment of high biomass concentration. Because of much higher cell densities, areal volumes may be much smaller, thereby reducing harvesting costs. Finally, optimal temperatures may be established and maintained more readily in closed systems, resulting in higher output rates. All these developments still need to be tested on a large scale to evaluate whether the higher investment costs are indeed compensated by higher annual yields.

In China, most production plants are adopting a semi-closed culture system, where raceway culture ponds are covered by glass or transparent polythene sheet covering.

Diseases and pests Contamination of *Arthrospira* by other microalgae can be prevented by maintaining a high bicarbonate concentration and by keeping the dissolved organic load in the culture medium as low as possible. Development of grazers in the cultures, mainly the amoeba type, can be arrested by addition of ammonia (2 mM). Ammonia (only 1 mM) can also be used to prevent further proliferation of *Chlorella* spp. in infested *Arthrospira* cultures. Contamination by green algae is often high during early cultivation stages, when the initial density of the *Arthrospira* inoculum is low. The amount of the contamination decreases as the *Arthrospira* builds up in density. Extra-cellular products of the *Arthrospira* may have some allopathic properties, which slow down the growth rate of *Chlorella* spp. Other contaminant algae are a blue-green *Spirulina* sp. and a green unicellular alga (*Oocystis* sp.). No cyanophages attacking *Arthrospira* have been observed so far.

Harvesting *Arthrospira* can be easily removed from the medium by simple harvesting devices. The most used types of screens in filtration devices are inclining screens and vibrating screens. Inclining screens are 380–500 mesh with a filtration area of 2–4 m^2 per unit, capable of harvesting 10–18 m^3 *Arthrospira* per hour. Biomass removal efficiency is up to 95% and two consecutive units are used for harvesting up to 20 $l/m^2/h$, from which slurry (8–10% of dry weight) is produced. Vibrating screens can be arranged in double decks of screens up to 183 cm in diameter. These screens filter the same volume per unit time as the inclining ones, but require only one-third of the area and are very efficient.

In some plants in India, the biomass is harvested using two-deck gravity filters, consisting of two hemispherical cloth filters with filtration capacity of 200–670 $l/m^2/h$. This technique is labour intensive and not very efficient, but well adapted to rural cultivation systems. In Madras (India), column gravity filters have been developed; the device consists of an eight-columned unit (1.55 m tall and 28 cm in diameter) with polyester cloth (30–40 µm pore size) and can continuously treat 5–10 m^3 of culture/h. Yet another technique to remove *Arthrospira* biomass from the culture medium is vacuum filtration, a system good for small-scale production where a small pump with low energy consumption can be used.

Yield In theory at least 40 g dry weight *Arthrospira* $/m^2/d$ can be obtained from a well-mixed outdoor pond, although 15–19 $g/m^2/d$ is the maximum reached so far in open systems, and usually less than half that figure is attained in commercial production plants. Daily productivity in polythene-tube cultures ranges from 10–15 g dry weight$/m^2/d$ and productivity levels of 25–28 g dry weight$/m^2/d$ have been obtained in tubular bioreactors, while a similar areal productivity has been measured in flat plate reactors under natural illumination. In Thailand and China, however, the present productivity of *Arthrospira* in outdoor cultures is around 7–10 g dry weight$/m^2/d$.

Handling after harvest The algal slurry of *Arthrospira* (8–10% of dry weight) is rinsed in acid water (pH = 4) to remove the adsorbed carbonates. The biomass is stored at 0–20°C or frozen (−18°C) before being sent for drying. Spray-drying is the most commonly used method of drying the biomass in commercial plants, although other systems, such as surface-drying (drums or plates), freeze-drying and sonic-drying are also used. Spraying yields a product which can be easily made into pills, while drum-drying yields a product in the form of flakes. The digestibility of spray-dried products is usually higher than that of drum-dried products. For optimal preservation and storage, moisture should not exceed 3–8%. The product, when stored under vacuum in sealed drums, can be kept for up to 4 years with little change in biochemical composition or nutritional properties.

Sun-drying is considered suitable if the product is to be used for animal feed. The biomass for feed is vacuum-dried to 20% dry matter, mixed with different proportions of maize meal, and then dried in the sun. The resulting product consists of irregularly shaped pieces of *Arthrospira*/maize-meal mixture and is used as a fish feed.

In all cases a routine analysis of the chemical, physical, biochemical, and microbiological characters of the product is necessary in food-grade *Arthrospira* production, including bacteriological tests and checks for heavy metals and pesticides. Methods for chemical analysis procedures, preparation of growth media and suggested parameters for evaluation of the quality of *Arthrospira* powder are all well documented.

The consistency of biochemical composition of *Arthrospira* powder is remarkable, especially when the open nature of the production system is considered. Product quality and consistency will be even better in algae grown in closed bioreactors. The general appearance of *Arthrospira* powder should be uniform, without flakes and green to dark green, not brown. The taste ought to be mild; a bitter or salty taste may indicate insufficient washing or addition of preservatives. *Arthrospira* pills must have a smooth surface and no additional binders or coating should be used, because these may affect the digestibility of the product.

Genetic resources Many strains of *Arthrospira* are available from algal collections. Surprisingly few genetic studies have been done within *Arthrospira*. A mutant of *A. platensis* (Z19) is especially cultivated for the production of gamma-linolenic acid, while other mutants were induced for increased production of certain amino acids. A number of genes from *Arthrospira* have already been cloned and often have also been sequenced, which is a prerequisite for further genetic research.

Breeding Intensive research is being carried out to select high-yielding strains of *Arthrospira* and to improve the culture systems so that productivity can be increased. It is expected that in the near future annual production will be doubled.

Prospects Commercial production of *Arthrospira* for health food is a lucrative industry. However, due to the strict requirements that have to be fulfilled in marketing food-grade *Arthrospira* (as '*Spirulina*'), the focus has switched to the production of animal feed using agro-industrial wastes.

The main limitation of the present-day *Arthrospira* industry is the overall lack of sustainable productivity. With the increased demand for a high-quality product and a more sustainable and reliable production system for the future mass production of *Arthrospira*, development of closed systems is considered necessary. Much effort is required to further develop optimal closed photobioreactors.

Another approach is to develop technologies that are more suitable for local production of *Arthrospira* biomass in developing countries, and based on the use of conventional energy sources backed up by solar power. The operation of such a production process would be similar to that of an industrial plant, except that simpler methods would be used and more labour would be required. Plants need to be constructed using cheap local materials and inexpensive fertilizers and CO_2 sources must be used. Appropriately designed high performance solar driers would help to cut production costs.

If considerable reduction in the costs of production units can be achieved, large-scale produced microalgal biomass has the potential to become a commodity traded in large quantities and not limited to the health-food market. It can then become an inexpensive high-protein supplement for human food and animal feed.

The use of closed culture systems and further selection of seawater-adapted *Arthrospira* strains will open up the possibility of using seawater with low bicarbonate concentrations, thus saving on the cost of water and medium. Moreover, the future development of integrated systems for *Arthrospira* biomass production and wastewater cleaning looks very promising.

The fluorescent properties of phycocyanin make it well suited for very diverse future commercial applications.

The *Arthrospira*-derived gamma linolenic acid cannot yet compete with seed oil as a dietary supplement. A silica gel method being developed to fractionate gamma linolenic acid from *Arthrospira* is showing promising results.

A polymer of potential use, poly-β-hydroxybutyric acid, occurs in *A. platensis*, where it accumulates during exponential growth to 6% of the total dry weight. The product can be used as a biodegradable thermoplastic polymer.

Selected strains of *A. platensis* can be used to bring about biotransformations to obtain valuable compounds. In India the alga has been used to biotransform codeine to morphine.

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S.-M. Phang

Asparagopsis taxiformis (Delile) Trevis.

Nomencl. alg.: 45 (1845).

BONNEMAISONIACEAE

$2n$ = unknown

Synonyms *Fucus taxiformis* Delile (1829), *Asparagopsis delilei* Mont. (1841), *Falkenbergia hildebrandii* (Bornet) Falkenb. (1901).

Vernacular names Philippines: bulaklak-bato. China: haicai. Japan: kagikenori.

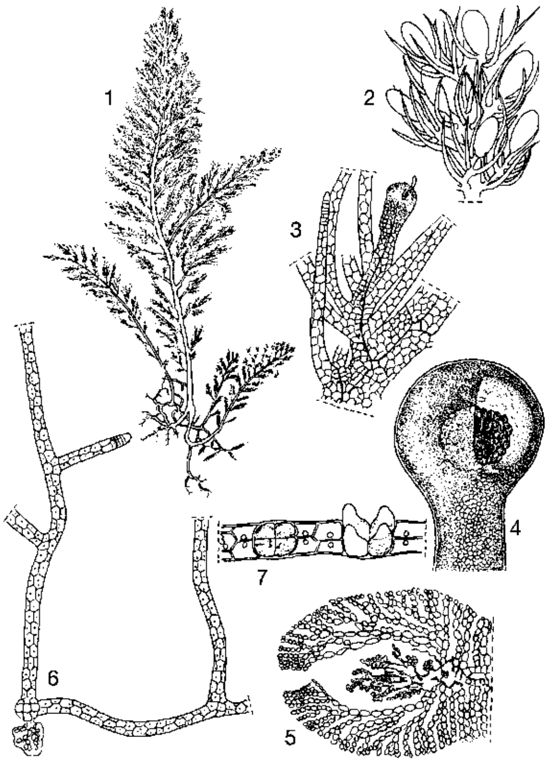
Origin and geographic distribution *A. taxiformis* is found in both the tropics and subtropics, and is common in all oceans. In South-East Asia it has been recorded in Burma (Myanmar), the eastern coast of Peninsular Malaysia, the Philippines and Papua New Guinea. Gametophytic plants are not recorded for Indonesia, although tetrasporophytes have occasionally been found there.

Uses The gametophytic plants of *A. taxiformis* are used as human food and animal fodder. The alga is considered a delicacy, with penetrating flavour and taste and fragrance of iodine which develops when allowed to stand. It is an excellent source of protein. It is used for controlling goitre. It can also be applied as fertilizer.

Production and international trade There are no known estimates of production of the gametophytic plants of *A. taxiformis*, which are used for food and medicine. In Hawaii hand-collected *A. taxiformis* is sold for prices that makes it one of the most expensive vegetables in the world.

Properties *A. taxiformis* produces unique toxins, containing the noxious compound bromoform and many derivates, as well as several halogenated acetones, haloacetaldehydes, haloalcohols, haloketones and haloacetamides. This alga is therefore not usually eaten by herbivorous fish or by sea urchins. Humans should not consume it in large quantities. It has also antibiotic and antibacterial/antimicrobial properties.

Description Gametophytic thalli with feathery or plumose erect branches, up to 13 cm tall, greenish to reddish, arising from creeping stolons attached by rhizoids to solid substrates. Erect branches with central terete axis giving rise to



Asparagopsis taxiformis (Delile) Trevis. – 1, habit of a female gametophyte; 2, detail of a male gametophyte bearing spermatangial clusters; 3, detail of a female gametophyte bearing a young fertile branch with a trichogyne; 4, detail of mature cystocarp with part of the pericarp removed; 5, detail of mature cystocarp showing section through the ostiole; 6, detail of the tetrasporophyte (also known as Falkenbergia hillebrandii (Bornet) Falkenb.); 7, tetrasporophyte detail with tetrasporangia, and tetraspores in one of the sporangia starting germination or being released.

densely arranged plumose branches at the upper 1/2 to 2/3 portion; plumose branches composed of numerous fine, delicate, branched, determinate branchlets, densely disposed around an axis; main axes consisting of a long central cell with bulbous base and two lateral axial filaments, forming the centre of the branchlets; central cell surrounded by an open space, partly filled with branched, smallcelled filaments; this open cylinder surrounded by 5–6 rows of tightly packed small, roundish cortex cells. Life cycle triphasic, diplohaplontic and heteromorphic. Gametophytes dioecious; cystocarps subspherical or ovate, bright red, borne at the apices of short branchlets, surrounded by a pericarp; spermatangia covering more or less completely the summits of special, short, clavate branchlets. Tetrasporophytes forming dense clumps or pompons of up to 5 cm in diameter, consisting of irregularly branched thin filaments, attached to other algae by multicellular haptera; filaments polysiphonous, up to 50 μm in diameter, each segment with a narrow central cell and three pericentral cells; segments about as long as they are broad. Tetrasporangia globose, one per segment, about 40 μm in diameter and tetrahedrally divided, replacing one of the pericentral cells.

Growth and development Both gametophytic and tetrasporophytic plants of *A. taxiformis* grow by means of dividing apical cells. Male and female propagational structures occur only rarely. Tetraspores in tetrasporophytes do not always divide meiotically; when they do they produce tetrasporophytes again. Fragments of tetrasporophytes often break off and can persist to form new plants.

Other botanical information Tetrasporophytes of *A. taxiformis* are known as *Falkenbergia hildebrandii*, as has been proved by culture experiments in Japan. However, these tetrasporophytes cannot be distinguished on the basis of morphological characters from *F. rufolanosa* (Harv.) F. Schmitz, which is the tetrasporophyte of the temperate species *A. armata* Harv.

Ecology Gametophytic plants of *A. taxiformis* occur on solid substrate on reefs or rocky shores exposed to moderately strong water movement. They often cover parts of upper surfaces of reefs and boulders and are not grazed by herbivores. Tetrasporophytic plants are usally entangled with other algae, both in sheltered and in exposed localities.

Propagation and planting *A. taxiformis* is not grown in phycoculture.

Harvesting *A. taxiformis* is only hand-collected from natural populations by wading or diving.

Handling after harvest *A. taxiformis* should be washed well in cold freshwater, soaked for half an hour or overnight in freshwater, then, using a wooden mallet, salted lightly and the upper branches pounded. Entire plants should be rolled into a ball. They will keep almost indefinitely without refrigeration and small quantities can be used as required.

Prospects Because of its toxic potential *A. taxiformis* may be less suitable as food but possibly is of interest as a source of fine chemicals, especially bromine-containing chemicals.

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G.C. Trono Jr

Betaphycus gelatinus (Esper) Doty ex P.C. Silva, Basson & R.L. Moe

Univ. Calif. Publ. Bot. 79: 326 (1996).
SOLIERIACEAE
$2n$ = unknown

Synonyms *Fucus gelatinus* Esper (1797), *Eucheuma gelatinum* ('gelatinae') (Esper) J. Agardh (1847), *Sphaerococcus gelatinus* (Esper) C. Agardh (1922).

Vernacular names Philippines: tamso. China: qing-zhi, shihua, shihuacai. Japan: katamen, kirinsai.

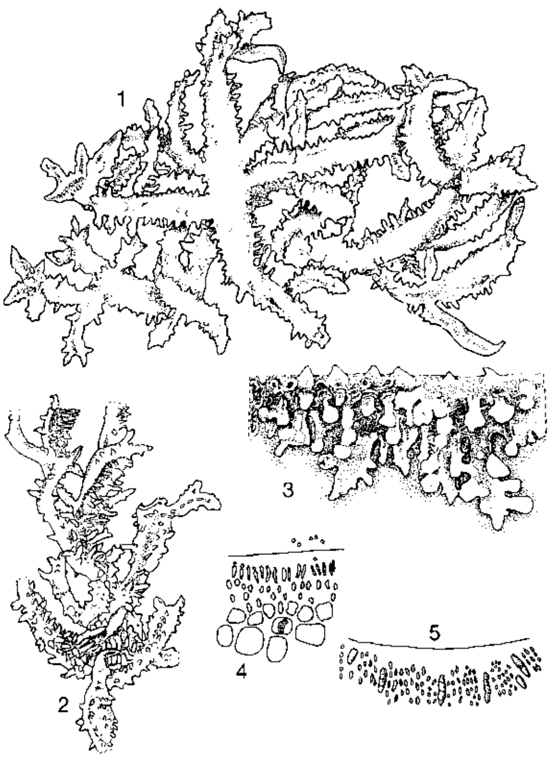
Origin and geographic distribution *B. gelatinus* is limited to the following tropical and subtropical regions in eastern Asia: eastern Indonesia, the Philippines, Vietnam, southern China and southern Japan.

Uses *B. gelatinus* has long been collected in Hainan (China) and used as a gelatinous substance in food and for wall sizing. Around 1930 the agar factory in Ningbo (Zhejiang, China) was already using this seaweed as a raw material in the manufacture of shred agar. At that time 40% of the *Betaphycus* (then as *Eucheuma*) was mixed with 60% of the agarophyte *Gelidium amansii* (J.V. Lamour.) J.V. Lamour. In recent years in China, *B. gelatinus* has also been used in salted salad, replacing *Eucheuma denticulatum* (Burm. f.) Collins & Herv. Now it is especially used to produce beta carrageenan, which is mainly applied in food. In Vietnam this alga is used for making jellies, cakes, and sweet soup. In Indonesia (Lesser Sunda Islands) it is used to prepare vegetable soup (with coconut milk), and it is also applied as a vermifuge. In Chinese herbal medicine, however, *B. gelatinus* is not used as a vermifuge but for the treatment of goitre, scrofula, cough, tonsillitis, asthma, stomach ailments, haemorrhoids and anal fistulas.

Production and international trade An annual amount of 300–400 t (dry weight) of *B. gelatinus* is produced by cultivation from a specially protected area of about 250 ha in China. This quantity was valued at US$ 450 000 in 1981. Vietnam produces 10 t dry weight of the alga. These amounts are probably entirely consumed in China and Vietnam. Production by cultivation is very limited due to the limited occurrence of coral reefs in Hainan (China). In 1984 an additional 100 t (dry weight) was marketed from wild crops in China.

Properties The thick cell walls of *B. gelatinus* are composed of D-galatan carrageenans, which are, according to some reports, principally of the beta type mixed with small quantities of the gamma and kappa types. Beta carrageenan, which lacks sulphate groups, is relatively non-ionic and quite stiff. It is used mainly in the food industry, in the making of soft sweets with a jam centre, and canned food. Other reports, however, suggest that only low percentages (6–7%) of beta carrageenan occur in *B. gelatinus*, and much higher percentages of kappa carrageenan. It is probable, however, that in these cases the studied material did not belong to *B. gelatinus*, but in fact to *B. philippinensis* Doty. This is a recently described species, and is the type species of the genus *Betaphycus* Doty ex P.C. Silva. Gel produced by (Philippine) '*B. gelatinus*' has characteristics which are similar to furcellaran, the carrageenan found in the European red algal genus *Furcellaria* Grev. In the trade *B. gelatinus* is often confused with and called '*serra*'. This results in further considerable confusion, because genuine *Eucheuma* *serra* (J. Agardh) J. Agardh produces iota carrageenan and certainly not beta and/or kappa carrageenan.

Description Thalli prostrate, entangled, attached to rocky substrate by well-developed haptera arising from crustose base and ventral side of branches, purplish-red or yellowish-green when living, leathery, pliable, irregularly branched, 10–20 cm in diameter. Branches, arising from simple, marginal proliferations, compressed, ventral surface and margins densely covered with rows of spinose branchlets, upper surface smooth, 3–5 mm broad and 1–2 mm thick. Rhizoidal filaments compacted, thick-walled, tortuose, central in medulla, often in a flattened core. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangia zonately divided, embedded in cortex region of main axes, clustered near and on determinate laterals. Cystocarps borne towards the ends of proliferations from ventral or dorsal surfaces. Spermatangia in superficial sori.



Betaphycus gelatinus (Esper) Doty ex P.C. Silva, Basson & R.L. Moe – 1, habit lower surface; 2, habit upper surface; 3, details of cystocarps growing from the lower surface of a fertile thallus with reduced spines at the near margin; 4, details of a section through a spermatangial sorus; 5, details of a section through a tetrasporangial sorus with zonate tetrasporangia.

Growth and development In culture, after broadcasting, the 'seed' thalli of *B. gelatinus* will develop a holdfast within a week, and fix themselves firmly on the coral reef. Under favourable conditions, in cultures in bays in Hainan (China), the *Betaphycus* plants may increase their weight by a factor of 5–6 in a single year, which means they can have achieved a twentyfold increase over two years.

Other botanical information *B. gelatinus* was originally included in *Eucheuma* J. Agardh section *Gelatiforma* Doty & J.N. Norris. The description of the type species of the genus *Betaphycus* (*B. philippinensis*) includes some suggestions that it contains material originally described as '*Eucheuma gelatinus*' from the Philippines, although its synonymy is not officially indicated. *B. philippinensis* has only been recorded so far from a 60 km stretch of coast near Bulusan, eastern Sorsogon Province (the Philippines) where it was collected in October and November 1987. This nomenclatural uncertainty may have resulted in different records for carrageenan types isolated from *B. gelatinus*. On the basis of data on carrageenan types of other taxa that were originally considered to belong to *Eucheuma* section *Gelatiforma*, it is clear that not all these species can be included in the new genus *Betaphycus*.

Ecology *B. gelatinus* is generally found growing in the intertidal zone, firmly attached to rocky or corally substrate at reef margins exposed to strong wave action or current. It usually forms a belt parallel to the reef margin at 0.0–0.3 m above average low-tide level, but in culture grows much better at depths of 1–3 m.

Propagation and planting *B. gelatinus* grows luxuriantly in the sea at 1–3 m depth in some bays in Hainan (China). It was first cultivated by sending divers to insert cuttings in the sublittoral reefs. In 1974 new cultivation methods were devised, which are still in use. *B. gelatinus* is farmed by means of vegetative multiplication. 'Seed' thalli should be leathery and without epiphytes. Thalli are divided into branch systems, and 1 kg of thalli may produce about 40 such systems. They are each tied to a branch of dead coral by means of rubber rings and broadcasted on a selected sea bottom at a density of about 75 000 lots per ha. Divers are then sent down to arrange them in order.

Phycoculture Healthy parts of harvested thalli of *B. gelatinus* are reserved as 'seed' stock for the next crop. The 'seed' thallus fragments are left to grow in the subtidal region.

Harvesting Harvesting of *B. gelatinus* takes place after 1–2 years of growth. Since it grows best on 1–3 m deep sea bottoms, divers must be sent down for harvesting. Each diver can collect 150–500 kg (wet weight) of the seaweed per day in floating bamboo baskets.

Yield The yield of *B. gelatinus* in Hainan is on average 1.2–1.6 t (dry weight)/ha per year.

Handling after harvest The harvested *B. gelatinus* is spread on grass and sun-dried. It should be turned at regular intervals for 3–4 days. The colour of the dried seaweed is reddish-brown and it will turn yellowish-white if washed with fresh water. The weight of the dried seaweed is about 20% of that of the fresh seaweed.
In southern China beta carrageenan is extracted from *B. gelatinus* using a relatively simple technique. The dried algal material is modified with either KC1 or NaOH prior to cooking. It is cooked for 1 h and then passed through a drum filter with a fine nylon screen. The extract is hardened in square trays of 1 m × 1 m. The gel is cut into strips which are frozen and then thawed. Then the strips are sun-dried on bamboo mats to be ready for sale.

Prospects If more beta type carrageenan were available, it would certainly have many applications. Because of taxonomic uncertainties, it is not yet certain whether South-East Asian *Betaphycus* material can be used in the same way as in China. Thus the status of the Indonesian, Philippine and Vietnamese material should be cleared without too much delay. It will then be possible to assess whether commercial cultivation of these algae outside China is feasible and profitable.

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C.K. Tseng & G.C. Trono Jr

Blue-green algae

CYANOBACTERIA, CYANOPHYCEAE, CYANOPROKARYOTA OR MYXOPHYCEAE

Prokaryotic, thus no chromosomes

Major species and synonyms

- *Anabaena* (Bory) ex Bornet & Flahault – see separate article.
- *Aphanizomenon flos-aquae* (Ralfs) ex Bornet & Flahault, Révis. Nostoc. hét.: 214 (1886) [1888], synonym (Drouetian): *Microcoleus vaginatus* Vaucher ex Gomont (1892).
- *Aphanothece stagnina* (Spreng.) A. Braun, in Rabenh., Alg. Europas exsic. 1572 (1863), synonyms: *Phylloderma sacrum* Suringar (1872), (Drouetian) *Coccochloris stagnina* Spreng. (1807).
- *Arthrospira* Stizenb. ex Gomont – see separate article.
- *Aulosira fertilissima* S.L. Ghose, J. Linn. Soc., Bot. 46: 342, pl. 31, fig. 9 (1924), synonyms: *Ghosea fertilissima* (S.L. Ghose) Cholnoky (1952), (Drouetian) *Calothrix parietina* (Nägeli) Thur. ex Bornet & Flahault (1886).
- *Brachytrichia quoyi* C. Agardh ex Bornet & Flahault – see separate article.
- *Calothrix scytonemicola* Tilden, Minn. alg. Mycophyc.: 265 (1910), synonym (Drouetian): *C. parietina* (Nägeli) Thur. ex Bornet et Flahault (1886).
- *Cylindrospermum indicum* C.B. Rao, Proc. Ind. Acad. Sci.: 169 (1936), synonym (Drouetian): *Anabaena licheniformis* Bory ex Bornet & Flahault (1886) [1888].
- *Hapalosiphon intricatus* West & G.S. West, J. Linn. Soc., Bot. 30: 271 (1894), synonym (Drouetian): *Stigonema muscicola* (Thur.) Borzí ex Bornet & Flahault (1886) [1887].
- *Lyngbya majuscula* (Dillwyn) Harv. ex Gomont, Monogr. Oscill.: 131 (1892) [1893], synonym (Drouetian): *Microcoleus lyngbyaceus* (Kütz.) P. Crouan & H. Crouan ex Gomont (1892).
- *Mastigocladus laminosus* (C. Agardh) Cohn ex Bornet & Flahault, Révis. Nostoc. hét.: 56 (1886) [1887], synonym (Drouetian): *Stigonema muscicola* (Thur.) Borzí ex Bornet & Flahault (1886) [1887].

- *Microcoleus chthonoplastes* (Mert.) Zanardini ex Gomont, Monogr. Oscill.: 353 (1892), synonym (Drouetian): *Schizothrix arenaria* (Berk.) Gomont (1892).
- *Microcystis aeruginosa* (Kütz.) Kütz., Tab. phycol. 1: 6 (1846), synonyms: *M. ichthyoblabe* Kütz. (1833), *M. flos-aquae* (Wittr.) Kirchn. ex Forti (1907), (Drouetian) *Anacystis cyanea* (Kütz.) F.E. Drouet & W.A. Daily (1952).
- *Nostoc* Vaucher ex Bornet & Flahault – see separate article.
- *Oscillatoria agardhii* Gomont, Monogr. Oscill.: 205 (1892) [1893], synonym (Drouetian): *Microcoleus vaginatus* Vaucher ex Gomont (1892).
- *Oscillatoria amphibia* C. Agardh ex Gomont, Monogr. Oscill.: 221 (1892) [1893], synonym (Drouetian): *Schizothrix calcicola* C. Agardh ex Gomont (1892).
- *Scytonema bohneri* Schmidle, Bot. Jahrb. 30: 60 (1901), synonym (Drouetian): *Stigonema muscicola* (Thur.) Borzí ex Bornet & Flahault (1886) [1887].
- *Spirulina* Turpin ex Gomont – see separate article on *Arthrospira* Stizenb. ex Gomont.
- *Tolypothrix tenuis* Kütz. ex Bornet & Flahault, Révis. Nostoc. hét.: 122 (1886) [1887], synonym (Drouetian): *Scytonema hofmannii* C. Agardh ex Bornet & Flahault (1886) [1887].
- *Trichodesmium erythraeum* Ehrenberg ex Gomont, Monogr. Oscill.: 196 (1892) [1893], synonym (Drouetian): *Oscillatoria erythraea* (Ehrenb.) Kütz. ex Gomont (1892) [1893].

Vernacular names Thailand: sarai sinum ghuan ganchiew.

Origin and geographic distribution Blue-green algae are ubiquitous, abundant in fresh and marine waters, in soil and in extreme habitats such as hot springs and land covered by ice. Some occur in symbiosis with other organisms, including fungi (lichens), ferns (*Azolla* Lamk), sponges (*Dysidea herbacea*), gymnosperms (*Cycas* L.) and angiosperms (*Gunnera* L.). They are widely distributed in the whole of South-East Asia.

Uses Several blue-green algae (especially *Nostoc* spp.) are consumed as food in China, Japan, Thailand, Malaysia, Indonesia and the Philippines. *Nostoc* spp., as well as the marine *Brachytrichia quoyi* have been used as side dishes in Japan since ancient times.

Many free-living nitrogen-fixing blue-green algae are used as algal biofertilizers for paddy fields in India, Thailand, Vietnam, the Philippines and China. 'Algalization' is a term currently used for the adjustment of introduced blue-green algae to the soil, including subsequent proliferation. A wide range of nitrogen-fixation rates has been recorded for cyanobacterial populations (diazotrophic algae) in soils and flooded fields.

The water fern *Azolla* and its algal symbiont *Anabaena azollae* Strasb. ex Wittr., Nordst. & Lagerh. are used as a green manure in wet-rice cultivation, as a feed for pigs and ducks, and in aquaculture.

Arthrospira platensis Gomont is commercially produced in many tropical countries. This alga is consumed as health food and is also used for animal feed.

Some cyanophycean microalgae have properties that make them good soil conditioners, especially in tropical and alkaline soils as well as in some deserts. They can help to improve soil structure and alter the surface tension of water. The aggregative effect of mucilaginous sheaths and the filamentous nature of many cyanobacteria help improve infiltration. They also retain water, buffer against rapid desiccation and slow down erosion.

Cyanobacteria can produce biohydrogen, which is a renewable energy production system. Generally, nitrogen-fixing blue-green algae are more efficient at producing hydrogen than other forms. To produce biohydrogen, cells of blue-green algae are immobilized on inert supporting materials such as agar, agarose, carrageenan or alginate. It is possible to produce hydrogen for about 60 days using this method. Levels of hydrogenase, nitrogenase or other oxygen sensitive enzymes will affect the efficiency of hydrogen production.

Some blue-green algae have antibiotic properties, while others can act as positive plant-growth regulators.

Production and international trade Several Asian countries such as China, India, Burma (Myanmar), Vietnam, Thailand and the Phillipines have started to popularize the practice of using algal biofertilizer. Large-scale production of algal biofertilizer for wet-rice farming is being carried out. In Thailand, the inoculum consists of *Anabaena siamensis* Antarik., *Calothrix scytonemicola*, *Cylindrospermum indicum*, *Hapalosiphon intricatus*, *Nostoc commune* Vaucher ex Bornet & Flahault, *N. muscorum* C. Agardh ex Bornet & Flahault, *Scytonema bohneri*, and *Tolypothrix tenuis*. The private sector produces between 30 000 and 60 000 t of biofertilizer annually.

Apart from cultivation of *Arthrospira* ('*Spirulina*') there is no commercial monospecific production of other blue-green algae, although farmers and governmental organizations are trying to promote the production of the water fern *Azolla* with its symbiont *Anabaena azollae* and mixed soil blue- green algae as nitrogen fixers in rice fields.

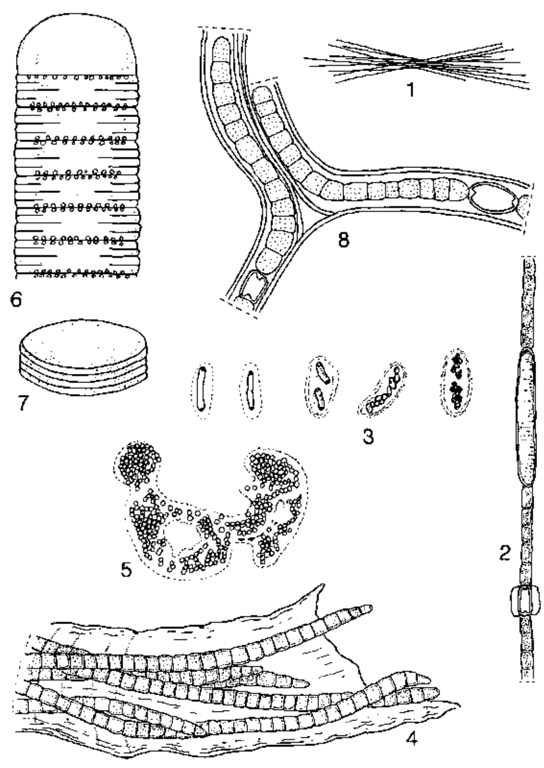
Properties Per 100 g dry weight, blue-green algal mixtures contain: protein 36–65 g, lipids 2–13 g, carbohydrates 8–20 g and nucleic acids 3–8 g. The average content of the predominant pigment phycobiliproteins is 20 g/100 g dry weight or 60 g/100 g total soluble proteins. There are three major types of phycobiliproteins: phycocyanin, allophycocyanin and phycoerythrin. The composition of phycobiliproteins in some blue-green algae varies when grown under different light qualities; this phenomenon is known as chromatic adaptation. Illumination with red light enhances the production of phycocyanin but suppresses the synthesis of phycoerythrin. The content of phycoerythrin increases when cultures are grown under green light. Other pigments in blue-green algae are chlorophyll a and carotenoids which include β-carotene (predominant), echinenone, zeaxanthin and myxoxanthophyll.

Fatty acids of blue-green algae are usually shorter than 18 carbon length, with 16:0, 16:1, 18:1, 18:2 and 18:3(ϖ3) being the major constituents. Fifty percent of the total fatty acids are made up of 16:0 and 16:1.

Some genera of blue-green algae may form toxic blooms that cause the death of pets, livestock, and wild animals after ingestion of algal scum. Usually, no antidotes or treatments are available. Luckily, acute poisoning of humans has almost never been reported, because most people are repelled by the idea of eating or drinking an algal bloom. Toxic algal blooms have been recorded in freshwater areas of several Asiatic countries, but not yet in South-East Asia. The effects of ingesting toxic algal blooms vary. Transmission of neural signals may be blocked by aphanotoxins released by some strains of *Aphanizomenon flos-aquae*, while anatoxins released by some strains of *Anabaena flos-aquae* (L.) Bory ex Bornet & Flahault can paralyze skeletal and respiratory muscles or can act as an cholinesterase inhibitor. Strains of species including *Anabaena flos-aquae*, *Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, *Oscillatoria agardhii* and several others are known or suspected to produce hepatotoxins, which cause death because of liver failure. Because of the toxicity of some blue-green algal strains, commercial harvest, drying, and sale of natural blooms for use as animal feed is not recommended.

In marine environments eukaryotic microalgae are usually involved in toxic blooms, but the marine filamentous cyanophyte *Lyngbya majuscula* causes rashes (dermatitis) on the skin of susceptible swimmers.

Description Blue-green algae are prokaryotic micro-organisms characterized by a low state of cell organization. Cells lack a well-defined nucleus and cell division is by division of the protoplast. These prokaryotic algae are characterized by the absence of flagellated reproductive bodies and sexual reproduction has not yet been recorded. They are unicellular, colonial or filamentous. The unicellular blue-green algae have cells which are usu-



Blue-green algae. Aphanizomenon gracile Lemmerm. – 1, bundle of planctonic trichomes; 2, trichome with long akinete and short heterocyst. Aphanothece caldariorum P.G. Richt. – 3, stages in the formation of endospores. Microcoleus vaginatus (Vaucher) Gomont ex Gomont – 4, trichomes aggregated in a common sheath. Microcystis aeruginosa (Kütz.) Kütz. – 5, habit of a colony. Oscillatoria sp. – 6, longitudinal section of a trichome; 7, tridimensional representation of cells. Scytonema hofmannii C. Agardh ex Bornet & Flahault – 8, trichome with false branching and heterocyst.

ally spherical, cylindrical or elliptical, with or without a well-defined sheath. Examples include the genera *Aphanothece* Nägeli, *Chroococcus* Nägeli, *Gloeocapsa* Kütz. and *Microcystis* Kütz. ex Lemmerm. The simple filamentous types without heterocysts have untapered, unbranched filaments with cells arranged in a linear series (trichomes) like in the genera *Lyngbya* C. Agardh ex Gomont, *Microcoleus* Desm. ex Gomont, *Oscillatoria* Vaucher ex Gomont, *Phormidium* Kürz. ex Gomont, *Plectonema* Thuret ex Gomont and *Trichodesmium* Ehrenb. ex Gomont. In *Arthrospira* and the genuine *Spirulina*, the trichomes are helical. The term 'filament' is applied here to denote the trichome and the sheath together, although sheaths are lacking in several genera. The second group of filamentous blue-green algae has similar untapered and unbranched filaments, but produces specialized cells in the trichomes, such as heterocysts and spores. The heterocysts are the sites of nitrogen fixation. Examples of this type are *Anabaena*, *Aphanizomenon* Morren ex Bornet & Flahault, *Aulosira* Kirchn. ex Bornet & Flahault, *Cylindrospermum* Kütz. ex Bornet & Flahault, *Nodularia* Mert. ex Bornet & Flahault. and *Nostoc*. In *Anabaena*, some *Cylindrospermum* and all *Nostoc* spp. the trichomes have a beaded appearance. The heterocysts are either intercalary or terminal, adjacent to or far away from the spores. The third group of filamentous blue-green algae has false branches and untapered heterocystous filaments; typical examples include *Scytonema* C. Agardh ex Bornet & Flahault and *Tolypothrix* (Kütz.) ex Bornet & Flahault. These false branches may either be single or paired. The fourth group of filamentous blue-green algae includes forms in which filaments may or may not show false branching but are distinctly tapered, often ending in a hair. The filaments have basal and sometimes intercalary heterocysts. Examples are *Brachytrichia* Zanardini ex Bornet & Flahault, *Calothrix* C. Agardh ex Bornet & Flahault, *Gloeotrichia* J. Agardh ex Bornet & Flahault and *Rivularia* C. Agardh ex Bornet & Flahault. The fifth group of filamentous blue-green algae exhibits a complex organization. They are often differentiated into a prostrate and erect system with true branching. The cells divide predominantly in two, and sometimes, in three directions. Forms belonging to this group are *Hapalosiphon* Nägeli ex Bornet & Flahault, *Mastigocladus* Cohn ex Bornet & Flahault, *Stigonema* C. Agardh ex Bornet & Flahault and *Westiellopsis* M. Janet.

- *Aphanizomenon flos-aquae*. Trichomes planktonic, in a bundle, seldom single, straight or bent, without sheath; cells 5–6 μm × 5-15(- 60) μm, up to 10 times as long as broad in terminal portions, with gas-vacuoles; heterocysts almost cylindrical, 5–7 μm × 7–20 μm; spores cylindrical, with rounded ends, 6–8 μm × 60–80 μm, epispore smooth and hyaline.
- *Aphanothece stagnina*. Thalli free-floating, gelatinous, spherical or ellipsoidal, up to many cm in diameter, pale blue-green, dull brown or brownish; cells arranged in colonies by homogeneous mucilage, oblong, ovoid or cylindrical, 3-6.5 μm × 4.5–11 μm.
- *Aulosira fertilissima*. Thalli expanded, dark blue-green, membranous; trichomes straight or a little flexuous, parallel or densely intricate; cells (4–)6–11 μm × (5–)7--10 μm, cylindrical when young, later barrel-shaped, contents granular; sheath thick, at first gelatinous and hyaline, later firm and brown; heterocysts intercalary, oblong or elliptical, 8–9 μm × 10–14 μm; spores in series usually alternating with dead cells, generally -oblongelliptical, sometimes angular due to compression, 10–13 μm × 18–24 μm.
- *Calothrix scytonemicola*. Filaments erect, single or in small groups, lower portion attached to host, 7–8 μm broad in broadest lower portion, tapering into a narrow pointed hair, sheath not distinct; heterocysts basal, 6–8 μm in diameter, usually two in number, somewhat globose.
- *Cylindrospermum indicum*. Trichomes single, motile, with deep constrictions at the joints, 3.7 μm broad, dark blue-green; cells almost quadrate or more or less barrel-shaped, 3–4.5 μm long; heterocysts (sub)spherical, subconical, or ellipsoidal, one at each end of the trichome, 2.8–5.8 μm × 3–7.6 μm; spores ellipsoidal or cylindrical, subterminal at either end of trichome, with thick yellowish-brown outer membrane possessing a smooth outer margin, 8.8–9 μm × 15–18.5 μm without membrane, 10–12 μm × 18–22 μm with membrane.
- *Hapalosiphon intricatus*. Thalli caespitose, blue-green, floccose, thin; filaments densely interwoven, free, not coalescing laterally, 4–7 μm broad, sparsely branched; true branches irregularly lateral, often arising only on one side of filaments, false branches erect from primary prostrate filaments, most branches as broad as and similar to main filaments; sheath close to trichome, colourless, often indistinct; cells in one row, spherical to cylindrical, 1.5–3 times as long as broad; heterocysts intercalary, subquadrate to cylindrical, 3.8–5.5 μm broad; hormogonia

formed from side branches; spores spherical to ellipsoidal, rarely nearly cylindrical.

- *Lyngbya majuscula*. Thalli expanded, up to 3 cm long, dull blue-green to brown or yellowish-brown; filaments very long, curved or only slightly coiled, with colourless lamellated sheath up to 11 μm thick, often with rough exterior; trichome blue-green, brownish-green or grey-violet, single in a sheath, not constricted at cross-walls, not attenuated at the ends, 16–60(–80) μm broad; cells very sort, 2–4 μm, 5–6 times broader than long, cross-walls not granulated; end cells rotund, without calyptra.
- *Mastigocladus laminosus*. Thalli membranous to spongy, often firm, hard layered, with calcium carbonate, blackish, blue or olive-green; filaments densely entangled, 4–6(–8) μm broad, curved, when older torulose, with reverse V-shaped short branches (about 3 μm broad) arising on one side; true lateral branching as well as false branches often present; sheath distinct; cells in single series, in main filaments barrel-shaped to short cylindrical, those of side branches cylindrical; heterocysts intercalary, spherical or ellipsoidal, single or two together, up to 6.5 μm broad, thus often broader than vegetative cells.
- *Microcoleus chthonoplastes*. Filaments single or forming expanded dirty to dark green lamellated thalli, unbranched or rarely branched, coiled; sheath colourless, uneven, thick, not lamellated, gelatinizing when old; many densely aggregated trichomes together in one sheath, coiled and contorted like a rope, constricted at cross-walls, 2.5–6 μm broad, not granulated at cross-walls; cells 1–2 times as long as broad, blue-green, 3.6–10 μm long, ends of trichomes straight, mostly attenuated; end cell conical, not capitate.
- *Microcystis aeruginosa*. Colonies planktonic, when young solid, globose or slightly longer than broad, when old becoming net-like, often with attached daughter colonies; cells spherical, 3–7 μm in diameter, without individual envelope, very densely arranged in homogeneous, hyaline mucilage; cell-division in all directions; gas-vacuoles present.
- *Oscillatoria agardhii*. Thalli leathery or in the form of small bundles, free-swimming, trichomes without sheath, straight or curved, not constricted at cross-walls and at ends gradually tapering; cells mostly shorter than long, quadrate, 2.5–4 μm long, granulated at septa, with gas-vacuoles; end cells convex, bluntly conical or more or less pointed, with calyptra, seldom capitate.
- *Oscillatoria amphibia*. Trichomes single, free-swimming, without sheath, straight or coiled, not constricted at cross-walls and not tapering at ends; cells 2–3 times longer than broad, 2–3(–3.5) μm × 4–8.5 μm, with two granules at septa, pale blue-green; end cells not capitate, rounded, calyptra absent.
- *Scytonema bohneri*. Thalli filamentous, blackish-green; filaments partly creeping, partly ascending, 10–12 μm broad, false-branched; branches mostly single, generally narrow, 8–11(–19) μm in diameter, 200–300 μm long, narrower at apex, 6–7 μm in diameter; sheath colourless, 1–1.8 μm thick, homogeneous; trichomes bluish-green, single in each sheath, straight, 5–8 μm broad, not constricted and indistinctly granulated at cross-walls; hormogones terminal; cells rectangular, short at apices, in other parts 0.5–1.5 times as long as broad; heterocysts compressed, ellipsoid to rectangular, 6–8 μm × 5–16 μm, with hyaline wall.
- *Tolypothrix tenuis*. Thalli caespitose or cushion-like, blue-green or brown; repeatedly false-branched, mostly free, erect; false branches single, mostly subtending heterocysts; filaments (4–)6–17(–18) μm broad, up to 2 cm long; sheath thin, close to single trichome, at first colourless, later yellowish-brown, often lamellated; cells (4–)5–13 μm broad, quadrate or longer than broad, blue-green, slightly or not constricted at cross-walls; trichomes with apical growth; heterocysts cylindrical, rounded or discoid, 6–14 μm × 2.3–6 μm, colourless or yellowish, solitary or 2–5 in a row; hormogonia formed from tips.
- *Trichodesmium erythraeum*. Trichomes cylindrical without sheath, in free-swimming purple-red bundles, straight, parallel, constricted at cross-walls, ends gradually attenuated, 7–11(–21) μm broad; cells 0.3–1 times as long as broad, 5.4–11 μm long; apex slightly capitate, with depressed conical or convex calyptra.

Growth and development Blue-green algae reproduce vegetatively either by hormogonia, hormocysts, endospores, exospores or akinetes. Hormogonia are small pieces of trichomes with one or many uniform cells. Hormogonium formation is one of the common modes of vegetative reproduction and in some cases (e.g. *Nostocales* and *Stigonematales*) the only known mode of propagation. Endospores are small spores formed endogenously within a cell, common in certain unicellular members. Exospores are serially abstracted from the open ends of sporangia by transverse division. In some forms like *Microcystis*, the cells undergo repeated divisions so that groups of very small cells are formed in each parent cell. These are generally naked protoplasts called nanocytes. Resting spores or akinetes are very large cells with thick walls. They are formed in specific positions in relation to heterocysts and may germinate immediately, giving rise to new trichomes, while others require a resting period. They remain viable for a long time and can often withstand high temperatures and desiccation. An extensive study on blue-green algae of wet-rice fields in Orissa (India) concluded that, in starter cultures for field inoculation of nitrogen-fixing blue-green algae, the emphasis must be both on fast growth and a high nitrogen fixation potential. For that reason members of the genera *Aulosira*, *Calothrix*, *Tolypothrix* and *Westiellopsis* were preferred over the members of the genera *Anabaena*, *Cylindrospermum*, *Hapalosiphon* and *Nostoc* which occur naturally in Orissa (India). There is no reason, however, to expect that research in other areas will result in a list of similar genera of blue-green algae.

Other botanical information The taxonomy of blue-green algae is very complicated. The usage of species and genus limits varies greatly among cyanobacterial taxonomists. The earliest and most practical method used is to compare a species at hand to the morphological description that most closely fits and then designate the use of the taxon name according to the publication that has been used. The morphological phenotype of the originally described species and the species at hand may, however, be totally unrelated because of the scanty and partly unreliable morphological characters. Moreover, a large number of recently described new species have not yet been incorporated into a comprehensive identification handbook. A regrouping of cyanobacteria, almost entirely based on strains in culture, and mainly attempting to redefine or emend the generic limits within these organisms, is known as the 'Stanier' system and is based on bacteriological criteria. Species epithets were seldom employed and perhaps never will be; strain numbers replace these. However, it is likely that less than 10% of what will eventually be recognized as genera are now represented as clonal isolates in culture, and an even smaller percentage of the species. Representatives of some genera are difficult or impossible to culture. Another general regrouping and simplification of the blue-green algae taxonomy has been executed mainly by F.E. Drouet and uses the assumption that many of the described taxa represent merely phenotypic variations of the same genotype. These ecophenes are thought to represent pleomorphic responses to environmental diversity. The assumptions used in this regrouping have been made on the basis of vague and non-tested criteria, however, and thus the system is not generally accepted.

The apparent simplification represented by the 'Stanier' system is just the beginning of a complex system based on ultrastructure, physiology, biochemistry and genetics, always together with morphology. It also uses molecular data, but is not a phylogenetic classification based on nucleotide sequence data. Some rRNA nucleotide sequence comparisons have already shown that several of the genera in the 'Stanier' system are unnatural and should be re-evaluated. A natural, evolutionary classification of cyanobacteria remains far off. The present volume uses cyanobacteria (blue-green algae) names that have been characterized using morphological data. The alternative names according to the 'Drouetian' system are included for comparison. Species and genus names of blue-green algae are subject to complicated additional rules in the International Code of Botanical Nomenclature, hence the complicated authors' citations.

Ecology Blue-green algae occur in the littoral zone of marine habitats as a black encrusting film on rocks at the upper limit of the high-tide mark. The blackish algal zone consists of genera such as *Calothrix*, *Gloeocapsa*, *Nodularia*, *Phormidium* and *Rivularia*. Many species are found as epiphytes on larger algae. In salt marshes and mud flats, blue-green algae (e.g. *Microcoleus chthonoplastes*) are abundant under microaerophilic conditions; such algal flora are important in stabilizing the mud surfaces. The macroalga *Lyngbya majuscula* often blooms in coastal areas. Freshwater blooms of blue-green algae such as *Anabaena*, *Aphanizomenon*, *Gloeotrichia*, *Lyngbya*, *Microcystis* and *Oscillatoria* occur in lakes over the whole year. Some blue-green algae can grow in hot springs up to temperatures of 70–73°C. A common thermophilic blue-green alga is *Mastigocladus laminosus*. In soil habitats, blue-green algae are restricted to the upper 50 cm of the profile, although some have been found as deep as 20 m below the surface. Blue-green algae prevent erosion by binding sand and soil particles with their gelatinous sheaths. In paddy soils, up to 70% of the algal flora may consist of blue-green algae. In general, blue-green algae are only found in waters or soils with a pH > 5. *Aphanothece stagnina* forms free-floating colonies in lakes, streams and paddy fields. *Aulosira fertilissima*, *Calothrix scytonemicola*, *Hapalosiphon intricatus*, *Lyngbya majuscula*, *Oscillatoria amphibia* and *Tolypothrix tenuis* grow on submerged parts of plants and on soil in pools, ponds and paddy fields, while *Cylindrospermum indicum* moves slowly (gliding movement) over substrates in these environments. Both *Oscillatoria agardhii* and *O. amphibia* as well as *Scytonema bohneri* occur on moist soils, while *Mastigocladus laminosus* thrives in muddy locations. When these wet locations dry out, *Microcoleus chthonoplastes* takes over. *Aphanizomenon flos-aquae*, *Microcystis aeruginosa*, *Oscillatoria agardhii* and *O. amphibia* are planktonic freshwater algae, of which especially *Microcystis aeruginosa* often forms water-blooms. *Lyngbya majuscula* and *Microcoleus chthonoplastes* occur also in brackish and marine habitats. *Brachytrichia quoyi* and the nitrogen-fixing *Trichodesmium erythraeum* are strictly marine; the former is benthic, the latter typically pelagic, forming water-blooms in high seas.

Propagation and planting In India, dry flakes of a soil-based mixture containing *Aulosira*, *Anabaena*, *Nostoc*, *Plectonema*, *Scytonema* and *Tolypothrix* spp. are distributed to farmers. Farmers then culture the 'starter' in 40 m^2 ponds, producing their own inoculum for their rice fields. Superphosphate fertilizer and insecticide are added to the non-agitated ponds. Recently, there has been a shift towards using pure liquid cultures as inoculum rather than soil-based ones. In this new approach, polythene bags are used as containers, which result in more successful algalization and atmospheric nitrogen productivity in fields.

Blue-green algae can be cultured using inorganic media such as BG-11 and Bold's Basal Medium which contain NO_3^- as N-source, and HPO_4^{2-} and $H_2PO_4^-$ as P-source and as buffering agents. Basal media without combined nitrogen (e.g. Antarikanonda-medium) can be used for culturing species which fix atmospheric nitrogen. In the laboratory, the cultures are aerated with CO_2-enriched air (usually 5% v/v) or agitated by orbital shaking. Stock cultures can be maintained on agar slants (2% w/v) and placed on illuminated shelves. Illumination can be provided by fluorescent lamps (Grolux or True-lite) at an intensity of 42 µmol photon/m^2 per second in a 12:12 hours light-dark cycle or continuously.

Phycoculture Blue-green algae, when introduced into the field, are exposed to soil conditions, including chemical constituents.

Algalization is influenced by pH, temperature, light, desiccation and moisture, the presence of indigenous strains of cyanobacteria in the soil, the availability of phosphorus and the methods of N-fertilizer application. Addition of lime can be beneficial to shift the pH of acidic soils to near neutral levels. Phosphorus is often a limiting factor. Molybdenum, being a constituent of the enzymes nitrogenase and nitrate reductase, is important as well. Algalization experiments with high doses of N-fertilizer showed reduced supplementation effects of the blue-green algae. Studies on the physiology and biochemistry of N_2-fixing blue-green algae under metal stress showed that many metals (Cu, Cr, Cd, Fe, Hg, Ni, Pb, Zn) have an inhibitory effect on growth, pigment macromolecules and nitrate uptake. However, agrochemicals such as herbicides, fungicides and insecticides often stimulate cyano-bacterial growth.

It has been shown that nitrogen from cyanobacteria is directly transferred to rice plants, using up to 40% of the cyanobacterial nitrogen within 60 days.

Algalization with blue-green algae has, in general, a positive effect on grain yield. In India, field experiments showed an average yield increase of about 15%. In Thailand yields of wet rice under algalization were 10–20% higher than those without algalization. The beneficial effects of algalization are attributed to growth-promoting substances produced by the blue-green algae and/or to temporary immobilization of the nitrogen fixed by the algae, followed by a slow release after algal decomposition, permitting efficient crop nitrogen utilization. Algalization also has a positive effect on saline and sodic soils, resulting, in laboratory experiments and extrapolations, in reduction of electrical conductivity, soil pH and exchangable sodium.

Diseases and pests Grazing by ostracods, protozoa, cladocerans, copepods, mosquito larvae and molluscs can have a selective effect on the composition and mixed growth of blue-green algae, as can the action of selected cyanophages, bacteria and fungi.

Harvesting Blue-green algae are generally not harvested, except when collected as food or grown as inoculum for algalization.

Yield In Thailand, the yield of blue-green algae cultivated in culture tanks may reach 200 g dry weight/m^2 per day. In closed circulation cultures under outdoor conditions, the maximum yield obtained was 7.9 g dry weight/m^2 per day. The maximum yield obtained from cement algal ponds in Bangkok was 10–15 g dry weight/m^2 per day.

Genetic resources Although studies on genetic improvement of blue-green algae for atmospheric nitrogen fixation are frequently undertaken, the results are not yet very promising. The same holds for experiments to genetically improve hydrogen photoproduction.

Prospects As long as chemical N-fertilizers remain less expensive than the cost of producing, distributing and applying cyanobacteria inocula that do not perform consistently, the incentive for product development by the private sector will not be strong. Nevertheless, free-living species of nitrogen-fixing blue-green algae form the only option for possible use of organic N_2-fixation on non-flooded soils.

Research must focus on microbial ecology of blue-green algae in paddy soils, and screening for fast-growing species that fix nitrogen. Molecular genetics of nitrogen-fixation in blue-green algae is another area of research that needs to be intensified. Simple quantitative and qualitative methodologies to study blue-green algae in nature should be further developed to prove that algalization is an effective technology.

Phycobiliproteins from blue-green algae can be used as natural pigments in the food, drug and cosmetic industries, and as fluorescent tags in biomedical research. More blue-green algae should be screened for these pigments, and studies to optimize production of potential species should be carried out. Another promising area is the screening of blue-green algae for bioactive compounds. Neurotoxins may serve as a tool in the study of neural transmission. Moreover, research on antimicrobial compounds of blue-green algae should be intensified so that potential new drugs may be developed. In that respect research on inhibiting compounds of different strains of *Microcystis aeruginosa*, *Oscillatoria agardhii* and some other blue-green microalgae is promising. These compounds may have medical and laboratory uses. Anti-tumour activities imputable to compounds of cyanobacteria are also currently under study.

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S.-M. Phang & P. Antarikanonda

Bostrychia radicans (Mont.) Mont.

Orb., Dict. univ. hist. nat. 2: 661 (1842).

RHODOMELACEAE

$2n$ = unknown

Origin and geographic distribution *B. radicans* is widely distributed in tropical and warm temperate waters, throughout the Atlantic Ocean, the Indian Ocean and the Pacific Ocean. In South-East Asia it has been recorded in Burma (Myanmar), Thailand (all coasts), Peninsular Malaysia, Singapore, Indonesia, Brunei, the Philippines, and northern Papua New Guinea.

Uses References to the use of *B. radicans* as a food are scattered in the literature and may refer to this or other *Bostrychia* spp., but particularly to *B. tenella* (J.V. Lamour.) J. Agardh. Although *B. tenella* has been described recently as important for human consumption there are no detailed data to support this statement. Early references to both *B. radicans* and *B. tenella* (as *B. binderi* Harv.), being eaten either raw or boiled, noted that it was found intermixed with thalli of *Catenella* spp. and other algae associated with mangrove. Samples consisted mainly of *Catenella* spp., with other algae regarded as contaminants.

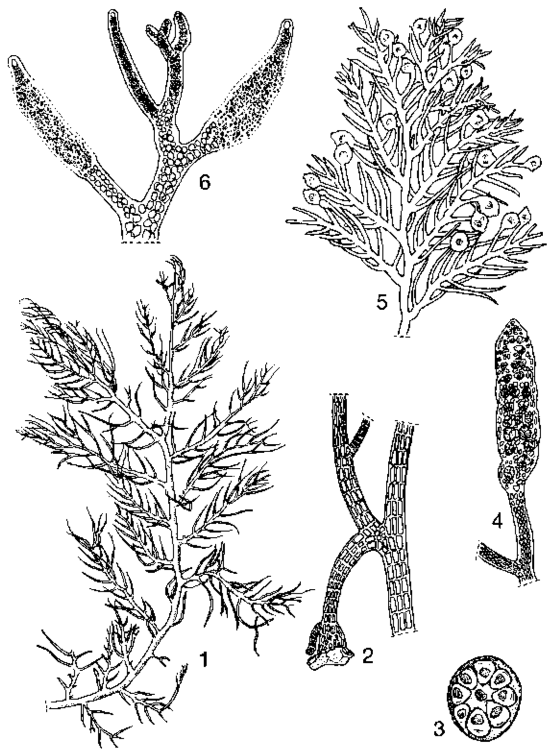
Production and international trade No data on the production of *B. radicans* are available, but quantities growing in the wild would be insufficient to allow for major harvesting.

Properties Members of the genus *Bostrychia* Harv. synthesize the sugar alcohols dulcitol and sorbitol, which act as compatible solutes (osmolites), allowing the algae to exist in regions of fluctuating and wide-ranging salinity. Although these compounds can be extracted, the process would not be commercially viable.

Description Thalli filamentous, prostrate with suberect branches, forming a low turf on the substrate, purple to brown; main axis indeterminate, 120–200 μm in diameter, up to 2 cm long, bearing determinate lateral branches 2–3 cm long with 1–2(–3) orders of alternate branching. Thalli attached by special holdfasts (cladohaptera), composed of rhizoids arising at the end of vegetative branches; main axis consisting of a polysiphonous axis with 2 tiers of pericentral cells per axial cell, (5–)7–9 pericentral cells per tier, in fertile laterals only 5 pericentrals per tier, not corticated. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangial stichidia subapical, on ultimate lateral branches, 800–1200 μm long, 120–140 μm in diameter, with 4–5 pericentral cells per tier, each forming a tetrahedrally dividing tetrasporangium of 50–80 μm in diameter and 2 cover cells. Gametophytes dioecious; cystocarps subapical, ovoid to globular, 300–500 μm long and 250–450 μm in diameter, with ostiole 35–50 μm in diameter; carpospores 100–125 μm long, 65–75 μm in diameter; spermatangial branches 200–500 μm long, 65–75 μm in diameter, with 4–5 pericentral cells per tier covered by small spermatogenous cells.

Growth and development Tetrasporophytes of *B. radicans* are much more common than gametophytes. Growth of all *Bostrychia* spp. is by division of apical cells. The pericentral cells are separated later and each *Bostrychia* species has its own characteristic further division.

Other botanical information The information on distribution, uses and properties is also largely applicable to *B. tenella* (synonym: *B. binderi*, a name that has long been considered to belong to a species that can be separated from *B. tenella*). The *B. tenella*/*binderi* complex differs clearly from *B. radicans* in its way of attachment. In *B. radicans* holdfasts (cladohaptera) are formed at the end of specialized vegetative branches, while in *B. tenella* the haptera are peripherohaptera, formed directly from peripheral and cortical cells on the ventral side of prostrate indeterminate axes.



Bostrychia radicans (Mont.) Mont. – 1, habit; 2, holdfast (cladohapteron); 3, transverse section of a branch; 4, tetrasporangial stichidium; 5, plant with cystocarps; 6, spermatangial branches.

Ecology *B. radicans* is a tropical alga associated with mangrove vegetation, where it grows on the modified roots and bases of mangrove plants. In these habitats it grows in a characteristic mixed community with other species of *Bostrychia* and with *Caloglossa* J. Agardh, *Catenella* Grev. and *Stictosiphonia* Hook.f. & Harv. This community is characteristic of mangrove habitats and is generally referred to as the *Bostrychia-Caloglossa* association. The algae of this association do not appear to be heavily grazed and the algal production is assumed to enter the food web through detrital food chains. The relative contribution of algae to the overall productivity of the mangrove community is unknown. Many fish and crustaceans feed among the mangroves and this has implications for the drainage and the so-called 'reclamation' of mangrove swamps in tropical regions, especially where there is a heavy reliance on inshore fisheries.

Propagation and planting *B. radicans* is not grown in phycoculture.

Harvesting *B. radicans* is only hand-collected from natural populations.

Handling after harvest *B. radicans* is sold either for direct consumption, or dried and then used in salads after boiling water has been poured on to it.

Genetic resources and breeding Crossing experiments with specimens from different localities but morphologically all belonging to *B. radicans* have shown that crossing barriers occur in some areas, but not in other regions.

Prospects The medical application of *B. tenella* in reducing blood cholesterol levels may also be possible for *B. radicans*.

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R.J. King

Brachytrichia quoyi (C.Agardh) ex Bornet & Flahault

Révis. Nostoc. hét.: 373 (1886).

MASTIGOCLADACEAE

Prokaryotic, thus no chromosomes

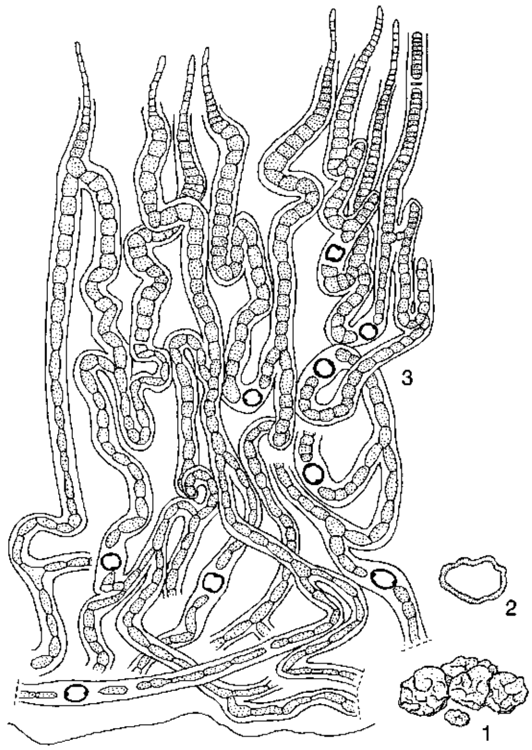
Synonyms *Nostoc quoyi* C. Agardh (1824), *Brachytrichia balani* Bornet & Flahault (1885), *B. lloydii* (P. Crouan & H. Crouan) P.C. Silva (1996).

Origin and geographic distribution *B. quoyi* occurs throughout the tropics in warm-temperate to tropical waters in the Atlantic (including the Mediterranean Sea), Indian and Pacific Oceans. In South-East Asia it is found in Burma (Myanmar), Thailand, Vietnam, Malaysia (Peninsular Malaysia, Sarawak), Singapore, Indonesia (Sulawesi, the Moluccas) and the Philippines.

Uses *B. quoyi* is eaten as a vegetable in China and Taiwan. The plants may be fried with fish and pork, or sweetened and preserved as candy.

Production and international trade Commercial cultivation of *B. quoyi* is not known to exist.

Description Thalli becoming folded and hollow



Brachytrichia quoyi (C. Agardh) ex Bornet & Flahault – 1, habit; 2, cross-section of thallus; 3, detail of thallus cross-section showing trichomes with heterocysts.

with age, forming a firm gelatinous mass, ranging from flat to spherical to irregular, and of a few mm to several cm in diameter; trichomes 4–5 μm in diameter at base, becoming broader before tapering to 1 μm at the apex; true or false branches arranged parallel or radially in the gelatinous matrix; Y-shaped branches at apices of loops. Heterocysts intercalary, spherical, oval or subglobose, up to 12 μm in diameter.

Other botanical information *B. lloydii* has recently been restored as a separate species.

Ecology *B. quoyi* grows in the upper intertidal zone, attached to rocks, wood, larger algae or seagrass leaves. It is found in areas where salinity is consistently high and the water is clear. Plants with a smooth surface are normally found on rocks exposed to direct sunlight and are deep blue-green, while those with a plicate surface generally grow immersed in tide pools and are brown.

Handling after harvest *B. quoyi* can be sun-dried after being pressed into balls and squeezed to get rid of the water.

Prospects Although there is no information on the use of *B. quoyi* as a food in South-East Asia, it may be a promising plant resource for the region. Biochemical characterization should be conducted to evaluate the nutritional value and other useful properties of *B. quoyi*.

Literature |**1**| Humm, H.J. & Wicks, S.R., 1980. Introduction and guide to the marine bluegreen algae. John Wiley and Sons, New York, United States. 194 pp. |**2**| Umezaki, I., 1961. The marine blue-green algae of Japan. Memoirs of the College of Agriculture, Kyoto University 83 (Fisheries Series No 8): 1–149. |**3**| Xia, B. & Abbott, I.A., 1987. Edible seaweeds of China and their place in the Chinese diet. Economic Botany 41(3): 341–353.

S.-M. Phang

Caloglossa leprieurii (Mont.) G. Martens

Flora 52: 234 (1869).

DELESSERIACEAE

$n = 30$, $2n =$ about 60

Synonyms *Delesseria leprieurii* Mont. (1840), *Caloglossa mnioides* Harv. ex J. Agardh (1876), *C. leprieurii* var. *hookeri* E. Post (1936).

Vernacular names China: zhegucai (as medicine).

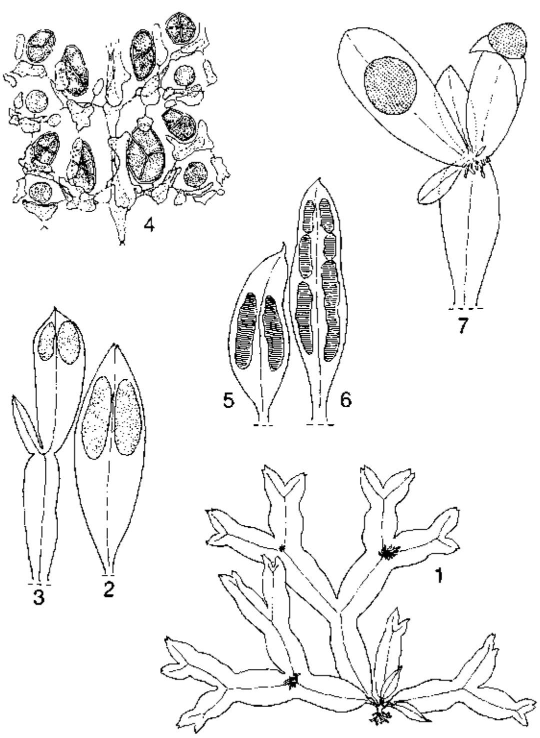
Origin and geographic distribution *C. leprieurii* is widely distributed in tropical and warm temperate waters, throughout the Atlantic, Indian and Pacific Oceans. In South-East Asia it has been recorded in Burma (Myanmar), Thailand, Peninsular Malaysia, Singapore, Indonesia, Brunei, the Philippines, and northern Papua New Guinea.

Uses References to the use of *C. leprieurii* as food (for salad and vegetable soup) are scattered in the literature and may refer to other *Caloglossa* spp. as well, particularly *C. bengalensis* (Martens) R.J. King & Puttock and *C. adhaerens* R.J. King & Puttock (as *C. adnata* sensu E. Post). In traditional Chinese medicine and also in Vietnam, *C. leprieurii* is used as a vermifuge, and was known as long ago as 1530 A.D. under the name zhegucai. In modern Chinese medicine zhegucai usually refers to another red alga, i.e. *Digenea simplex* (Wulfen) C. Agardh. In Indonesia *C. leprieurii* is used in the treatment of goitre, urinary diseases and dropsy.

Production and international trade In southern China *C. leprieurii* is sold on markets in the form of circular sheets of about 10 cm in diameter.

Properties *Caloglossa* spp. synthesize the organic osmolyte mannitol, a polyol (hexitol) unknown in other red algae. It acts as a compatible solute and as a regulator for metabolic control occurring during growth under the extremes of salinity encountered in the mangrove habitat. The compound responsible for the vermifugous properties is still unknown.

Description Thalli spreading, erect in some portions, reddish-violet, reddish-brown to pale-brown; blades strap-shaped, thin, membranous, 1–3 mm across, occasionally arising in rosettes from a stipe, alternately branched and forked at the apices, constricted, often with rhizoids at the constrictions (nodes); internodal segments elongate-ovate to linear-lanceolate, 1–4 mm long, composed of a midrib of large rectangular cells and lateral blade; secondary branches or segments - leaflike, proliferous from the forkings or midribs of blades, with small subhexagonal cells in oblique series from the midrib to the margin. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangia spherical, (23–)50–75 μm in diameter at maturity, in oblique series near upper portion of blade, with a cover cell on both blade surfaces; each sporangium forming four tetraspores. Gametophytes dioecious, rarely monoecious; procarps on ventral surface of internodes, sometimes also dorsally, at times on both surfaces; cystocarps ostiolate; spermatangial sori on blades at both sides



Caloglossa leprieurii (Mont.) G. Martens – 1, habit; 2 & 3, parts of thalli with tetrasporangial sori in 'var. hookeri'; 4, detail of tetrasporangia in a tetrasporangial sorus; 5,6, parts of thalli with spermatangial sori in 'var. hookeri'; 7, part of a cystocarpic thallus in 'var. hookeri'.

of midrib and on both surfaces of terminal and subterminal segments.

Growth and development In *C. leprieurii* growth is by a dome-shaped apical cell, which cuts off segments by transverse division. Each segment cell undergoes division into a central cell and four pericentral cells, of which the lateral ones give off oblique rows of cells that form the monostromatic wings of the thalli. Tetrasporophytes of *C. leprieurii* are much more common than gametophytes. Procarps are produced in acropetal succession by transverse pericentral cells in the terminal parts of the thalli. After fertilization of the carpogonia of the procarps, cystocarps develop formed by cortical cells of the female gametophytes.

Other botanical information Much that is reported about distribution, uses and properties of *C. leprieurii* also applies to other *Caloglossa* spp., in particular to *C. adhaerens*. In *C. leprieurii* attachment is by rhizoids that arise from scattered and isolated cells of the wings. In *C. adhaerens*, however, rhizoids are grouped together and arise from the nodes. The status of *C. leprieurii* var. *hookeri* is still under discussion. In some modern revisions this variety is not recognized, while in others it is considered morphologically and genetically distinct.

Ecology *C. leprieurii* is a tropical or warm-temperate alga often associated with mangrove vegetation, where it grows on the modified roots and bases of mangrove plants. In these habitats it occurs in a characteristic mixed community with other *Caloglossa* spp. and with red algae such as *Bostrychia* spp., *Catenella* spp. and *Stictosiphonia* spp. This community is characteristic of mangrove habitats and is generally referred to as the *Bostrychia–Caloglossa* association. The algae of this association do not appear to be heavily grazed and the algal production is assumed to enter the food web through detrital food chains. The relative contribution of algae to the overall productivity of the mangrove community is unknown. Many fish and crustaceans feed among mangroves and this has implications for the drainage and the so-called 'reclamation' of mangrove swamps, especially where there is a heavy reliance on inshore fisheries. *C. leprieurii* also occurs epilithically on fully marine coasts, but is more common in estuaries near the lower limits of salinity influence. It is also recorded in permanent freshwater habitats. Its capacity to grow in a range of salinities, and to cope with fluctuating salinities, has frequently been investigated.

Propagation and planting *C. leprieurii* is not grown in phycoculture.

Harvesting Field material of *C. leprieurii* is only hand-collected.

Handling after harvest *C. leprieurii* is collected for direct consumption or dried for medicinal use.

Prospects *Caloglossa* spp. are the only red algae producing mannitol. However, this compound is much more common in brown seaweeds and its extraction from *Caloglossa* thalli is most probably not commercially viable. If the compound responsible for the vermifugous properties can be isolated, the use of *C. leprieurii* for fine chemicals may be promising.

Literature |1| Istini, S., Zatnika, A. & Sujatmiko, W., 1998. The seaweed resources of Indonesia. In: Critchley, A.T. & Ohno, M. (Editors): Seaweed resources of the world. Japan International Cooperation Agency, Yokosuka, Japan. pp. 92–98.

|2| Karsten, U., Barrow, K.D. & King, R.J., 1998. Mannitol metabolism of the epiphytic mangrove red alga Caloglossa leprieurii (Ceramiales): a long-term field study. Phycological Research 46: 91–96. |3| Karsten, U., Barrow, K.D., West, J.A. & King, R.J., 1997. Mannitol metabolism in the intertidal mangrove red alga Caloglossa leprieurii: salinity effects on enzymatic activity. Phycologia 36: 150–156. |4| King, R.J. & Puttock, C.F., 1994. Morphology and taxonomy of Caloglossa (Delesseriaceae, Rhodophyta). Australian Systematic Botany 7: 89–124. |5| Papenfuss, G.F., 1961. The structure and reproduction of Caloglossa leprieurii. Phycologia 1: 8–31. |6| Post, E., 1936. Systematische und pflanzengeographische Notizen zur Bostrychia–Caloglossa Assoziation [Notes on the systematics and plant-geography of the Bostrychia-Caloglossa association]. Revue Algologique 9: 1–84. |7| Tjon Sie Fat, L.A., 1976. Bostrychietum, plantengeografisch onderzoek over de Bostrychia–Caloglossa-gemeenschap, de algenformatie van de mangrovebossen [Bostrychietum, a plant-geographic study on the Bostrychia-Caloglossa association, the algal formation of the mangrove forests]. MSc. Thesis, Rijksherbarium, Leiden University, The Netherlands. 115 pp.

W.F. Prud'homme van Reine

Catenella nipae Zanardini

Mem. Ist. venet. 17: 143–145, pl. 6, A (1872).

CAULACANTHACEAE

$2n$ = unknown

Synonyms *Catenella opuntia* (Gooden. & Woodw.) Grev. var. *major* J. Agardh (1876).

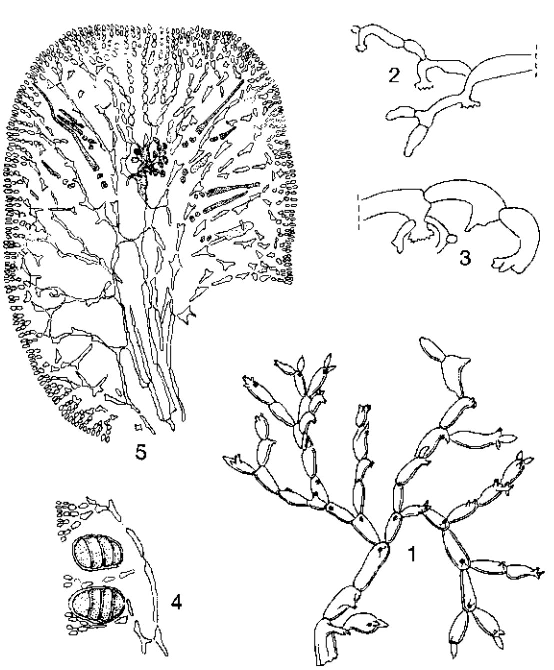
Origin and geographic distribution *C. nipae* is restricted to the Indo-Pacific region and widely distributed in South-East Asia, Australia and New Zealand. It occurs in Burma (Myanmar), Thailand, Vietnam, Peninsular Malaysia, Singapore, Indonesia, northern Borneo, Brunei, the Philippines and Papua New Guinea. It is also recorded from West Bengal (India), Bangladesh, southern China and the Ryukyu Islands in Japan.

Uses *C. nipae* is used for food and as a basis for carrageenan production, especially in Burma (Myanmar). There it is used as a salad, either fresh or after boiling water has been poured on the fresh or dried alga. Usually sesame oil and spices are used with it. For several years the 'Seaweed Technology' Company (Burma) has been producing edible seaweed sheets from a combination of *C. nipae* and *Enteromorpha* spp. (green algae). *C. nipae*, often mixed with the closely related but smaller *C. impudica* (Mont.) J. Agardh, is also commonly used as a salad in the Philippines. In Thailand it is listed as an economic alga and in Malaysia as a potential source of carrageenan. In Vietnam specimens are collected in the field, probably for food purposes.

Production and international trade It is foreseen that 1000 ha of mudflats in the Burmese mangrove swamps will be used for *Catenella* cultivation farms.

Properties The structure of cell wall galactan of *C. nipae* is under discussion. Analyses of material from samples collected in Burma (Myanmar) showed the polysaccharide to be a previously undescribed carrageenan of the β-family, designated as α carrageenan. A repeating unit of 3-0-D-galactose (= β(14)-linked D-galactose) and 4-0-3,6-anhydro-D-galactose-2-0-sulphate (= α(13)-linked 3,6-anhydro-galactose-2-sulphate) was found in these Burmese samples. However, in samples of *C. nipae* collected in Australia and the Philippines, only iota carrageenan was found, consisting of mainly galactose and 3,6-anhydrogalactose, together with minor amounts (up to 1.8 mole %) of xylose and a high sulphate ester content (about 30% of dry weight as $NaSO_3$). Only traces of glucosyl residues were detected and no mono-0-methyl-galactosyl residues. The repeating units were identified as β(14)-linked D-galactose-4-sulphate and α(13)-linked 3,6-anhydro-D-galactose-2-sulphate. The carrageenan type remains the same throughout the different reproductive phases.

Description Thalli forming decumbent patches up to 3 cm tall, dark red to purple, often bleached yellow-brown; fronds creeping below, subflabellately caespitose to erect above, composed of elongate ovoid, oblong or squarish, terete to strongly compressed segments (internodes), up to 6 mm long and about 2 mm wide, with constricted nodes; branching regular, repeatedly dichotomous or trichotomous; holdfasts (haptera) at terminal end of segments, bending down first ventrally to attach to the substrate, later becoming subterminal by subterminal growth of segments; new segments originating closely behind the haptera of the attached segments; segments internally composed of lacunose medulla of loosely interlacing and anastomosing longitudinal filaments from central axis soon becoming indistinct; filaments towards the periphery dichotomously branched, moniliform, forming a compact cortex of larger inner cells and smaller outer cells. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangia oblong,



Catenella nipae Zanardini – 1, habit; 2,3, parts of vegetative thalli with haptera; 4, detail of a section with tetrasporangia in a tetrasporangial sorus; 5, longitudinal section of an apical segment showing carpogonial branches and a fusion cell producing a gonimoblast branch on one side.

transversely zonately divided, scattered or aggregated in encircling sori below the surface of the cortex of terminal segments, 60–90(–110) μm × 40–65(–75) μm. Gametophytes monoecious in laboratory culture, with up to 8 mm long, narrow male segments and up to 1 mm long, round female segments; cystocarps ostiolate, solitary, sessile on shortened, obpyriform, subterminal segments with swollen cortex; carpospores ovoid, 45 μm × 25 μm, in chains; spermatangia small cell groups in cortical tissue, in ring-like spermatangial sori on male segments.

Growth and development Apical cells of *C. nipae* give rise to laterals on two sides, forming two periaxial cells each. Axial cells soon transform into a network of slender filaments without a distinct central axis in the segments. In laboratory culture, tetrasporelings of 3–5 mm long developed carposporophytes which became reproductive in less than 8 months. After 5 months of growth, carpospore germlings were 3–5 mm long with 2–3 segments. At that stage most had formed viable tetraporangia. The relative abundance of vegetative, tetrasporic and carposporic phases of *C. nipae* in mangrove swamps has been studied in Burma (Myanmar). The reproductive phases occur during the pre-monsoon season, after which rigorous vegetative growth of the germlings contributes to the sudden occurrence of the alga in the monsoon season. Mixed phase gametophytes have been observed in *C. nipae*, in which also zonately-divided tetrasporangia developed on the female segments of the monoecious gametophytes.

Other botanical information Although the characteristics that separate *C. nipae* from *C. impudica* are quite clear (in *C. impudica* haptera are formed from special small and narrow segments and in *C. nipae* from normal segments), much confusion occurs and often both species are mixed up. This may also be complicated by the fact that these species can occur in mixed stands. Usually, however, specimens and segments of *C. nipae* are much larger than those of *C. impudica*. For that reason *C. nipae* is probably the only species that is used for food and as a basis for carrageenan production.

Ecology *C. nipae* belongs to the so-called *Bostrychia–Caloglossa* association, characteristic of mangrove habitats, and grows on the stems and modified roots (stilt roots, pneumatophores) of mangrove plants. Records of other edible algae from this community indicate that *C. nipae* is the major species collected, the others being inadvertently included. The indirect economic importance of these algae is that they form a component of the primary production system of mangrove swamps. While nothing is yet known quantitatively, this system is nonetheless thought to be critical in maintaining inshore fish and crustacean populations.

Propagation and planting *C. nipae* is propagated by spores. Experimental cultivation of *C. nipae* has only been undertaken in Burma (Myanmar).

Phycoculture In Burma (Myanmar) bamboo sticks of 5 cm × 45 cm are used as spore collectors for *C. nipae* cultivation. The bamboo sticks are inserted to a depth of 15 cm into the mudflats of the mangrove swamps to collect the spores. Luxuriant growth of *C. nipae* was observed on the sides of the bamboo sticks after the rainy season.

Diseases and pests A gall-like outgrowth on *C. nipae* (supposed to be *C. impudica*) has been described as the parasitic red alga *Catenellocolax leeuwenii* Weber Bosse. The hemispheric and lobed parasitic plants were sterile and there are no confirmed data on their development or taxonomic status.

Harvesting *C. nipae* is harvested by hand-collection. The specially placed bamboo sticks, used for experimental cultivation of *C. nipae*, are harvested using a spoon.

Yield The yield of *C. nipae* on the planted bamboo sticks in Burma (Myanmar) was about 40–50 g (wet weight) per bamboo stake.

Handling after harvest *C. nipae* is used fresh or sun-dried for food or for carrageenan production. In Burma (Myanmar), however, carrageenan is usually mainly produced from *Hypnea* species, although *C. nipae* can also be used.

Prospects In Burma (Myanmar) about 25 small factories are now producing strips of carrageenan for the domestic market. The general Burmese public, however, is not aware whether it is carrageenan or agar and refer to both under the name 'kyaukkyaw'. Their preference is for jelly desserts that are white, hard and transparent. Due to the lack of technology for producing such quality in local strips of carrageenan, agar powder imported from neighbouring countries is much more popular and may outstrip the already declining indigenous carrageenan production in Burma (Myanmar). Production of *C. nipae* for fresh production, as well as for sun- dried directly marketed products, is still considerable in Burma (Myanmar) and is expected to continue in the future.

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R.J. King

Caulerpa J.V. Lamour.

Nouv. Bull. Sci. Soc. Philom. Paris, sér. 2, 1: 332 (1809); J. Bot. (Desvaux) 2: 141–142 (1809).

CAULERPACEAE

$2n$ = unknown

Major species and synonyms
- *Caulerpa brachypus* Harv., Proc. Amer. Acad. Arts Sci. 4: 333 (1859), synonym: *C. stahlii* Weber Bosse (1898).
- *Caulerpa cupressoides* (Vahl) C. Agardh, Syn. Alg. Scand. XXIII (1817), synonym: *Fucus cupressoides* Vahl (1802).
- *Caulerpa fergusonii* G. Murray, Trans. Linn. Soc. London, ser. 2. Bot. 3: 212 (1891).
- *Caulerpa lentillifera* J. Agardh – see separate article.
- *Caulerpa okamurae* Weber Bosse, (as *C. okamurai*) in Okamura, Bot. Mag., Tokyo 11: 5–7 (1898).
- *Caulerpa peltata* J.V. Lamour., see *C. racemosa*.
- *Caulerpa racemosa* (Forssk.) J. Agardh – see separate article.
- *Caulerpa serrulata* (Forssk.) J. Agardh, Mus. Senckenb. 2: 174 (1837), syonyms: *Fucus serrulatus* Forssk. (1775), *Caulerpa freycinetii* C. Agardh (1822).
- *Caulerpa sertularioides* (S.G. Gmelin) M. Howe, Bull. Torrey Bot. Cl. 32: 576 (1905), synonyms: *Fucus sertularioides* S.G. Gmel. (1768), *Caulerpa plumaris* Forssk. (1775).
- *Caulerpa taxifolia* (Vahl) C. Agardh – see separate article.
- *Caulerpa urvilleana* Mont., in Hombr. & Jacquinot, Voy. Pôle Sud Bot. 1: 21 (1843) (as *C. urvilliana*), synonyms: *C. serrata* Sond. (non Kütz.) (1817), *C. microdonta* J. Agardh (1872), *C. tristicha* J. Agardh (1872).

Vernacular names General: caulerpa. Indonesia: sayur laut (used for many edible algae).
- *C. serrulata*: Philippines: galgalacgac (Luzon, Ilocos).
- *C. sertularioides*: Philippines: lukay-lukay (also for *C. taxifolia*), lato (also for *C. lentillifera* and *C. racemosa*) (Visayan), salsalamagi.

Origin and geographic distribution *Cauler-*

pa is widely distributed in tropical to subtropical seas, with the greatest diversity in the tropics and on the coasts of Australia. In South-East Asia, all *Caulerpa* spp. that are listed here, except *C. okamurae*, are regularly recorded in Indonesia, the Philippines and Papua New Guinea. *C. serrulata* and *C. sertularioides* have also been recorded in Burma (Myanmar), Thailand, Vietnam, Malaysia (usually mainly from Peninsular Malaysia) and Singapore, while additional records for *C. fergusonii* are limited to Burma (Myanmar) and Malaysia only. In Vietnam also *C. brachypus* has been recorded. For *C. cupressoides* and *C. urvilleana* additional records are known from Thailand (*C. urvilleana* only from the Pacific coast). In Indonesia both species occur mainly in the eastern parts, and in Papua New Guinea at the northern coast. *C. okamurae* is often considered to be restricted to East Asia (Japan, Korea), but recently it has been recorded on the Indonesian islands of Java, Bali, Sulawesi and Halmahera.

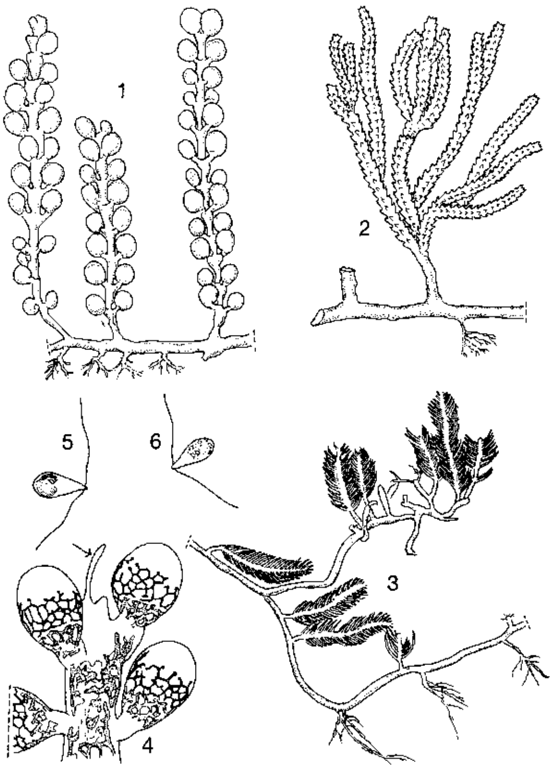
Uses Most *Caulerpa* are eaten raw or blanched as fresh salad in coastal areas of most countries in South-East Asia. Usually, after cleaning the algae, the frond parts are separated from the stolon and used for salad. For preservation, salt can be added. The frond parts can be dipped in vinegar (the Philippines: Ilocos Norte) or dressed with an all-spice sauce. In Indonesia some *Caulerpa* spp. are eaten sugar-coated, prepared as a relish, or cooked in palm sugar and soya sugar. In the Philippines *C. serrulata* and *C. sertularioides* are also stored and sold in dried form. Before being prepared as a salad the dried seaweeds are first soaked in water for a few minutes to regain succulence, then prepared in the same way as fresh fronds. Most *Caulerpa* spp. are also used as medicine to lower blood pressure or (in *C. lentillifera* and *C. racemosa*) to treat rheumatism, while *C. sertularioides* is applied to treat and prevent goitre and is listed for anti-tumour activity. Several *Caulerpa* spp. are used as ornamental in tropical marine aquaria. Some are also sold in pressed form as souvenirs.

Production and international trade Most *Caulerpa* are only used locally and are collected by hand from natural populations. For exceptions see *C. lentillifera*.

Properties *Caulerpa* may produce secondary compounds, such as caulerpin, caulerpicin, caulerpenyne and other terpenoids. Caulerpin, a dimer derivate of indole-3-acrylic acid, might serve as a growth regulator in these species. It has not been recorded from any source other than the *Caulerpales*, although it was not found in each *Caulerpa* specimen tested. Caulerpin is responsible for the peppery taste and is considered toxic for microorganisms, fish and humans. In some individuals, especially the compounds caulerpin and caulerpicin can function as mild anaesthetics and may cause dizziness, numbness of the tip of the tongue, weakening of the extremities and difficulty in breathing. These compounds can be concentrated in the bodies of specialized herbivores that feed on *Caulerpa spp.* and can thus accumulate in the food web. In *Caulerpa* these compounds are only present in fresh material, but not in air-dried specimens, although some diterpenes still can be isolated from this dried material. Haemagglutinic activity as well as antibacterial activities of extracts of fresh and dried *Caulerpa* thalli have been demonstrated. Many saturated (especially palmitic acid and stearic acid) and unsaturated fatty acids (especially myristoleic acid) are known to occur in several *Caulerpa* spp. Of the sterols, especially cholesterol is present in appreciable amounts. The presence of cytotoxic and antimitotic activity in methanol/toluene extracts of living specimens is documented for *C. prolifera* (Forssk.) J.V. Lamour., while mosquito larvicidal activity is recorded for *C. scalpelliformis* (R.Br. ex Turner) C. Agardh.
Long lists of identified minerals and other compounds are available for Philippine *Caulerpa* spp. Most of them have antibacterial and antifungal properties and several show peroxidase activity.

Description Thalli coenocytic, giant single multinucleate cells, with high degree of differentiation, generally characterized by a creeping stolon and erect fronds. Stolons rarely absent and usually bearing rhizoids, solitary, arranged in tufts or concentrated on special downwards-growing rhizophores (pillars). Fronds variable in form, simple or branched; internal septation completely absent; form of giant cell supported by numerous bars of cell wall material (trabeculae) transversing the cell lumen from wall to wall; central vacuole with lining cytoplasm full of green photosynthetic chloroplasts, colourless amyloplasts specialized for starch storage and many nuclei continuous throughout the alga; cell wall non-cellulosic, the structural component being xylan, embedded in a glucan matrix. Thalli holocarpic when fertile.

- *C. brachypus*. Plant stoloniferous; stolons ovate or terete in cross-section, 0.8–2.5 mm in diameter. Rhizoid bearing descending branches (pillars) arising from the ventral side at irregular intervals. Fronds on short and cylindrical stalks,



Caulerpa. C. fergusonii G. Murray – 1, habit. C. serrulata (Forssk.) J. Agardh – 2, habit. C. sertularioides (S.G. Gmelin) M. Howe – 3, habit. C. okamurae Weber Bosse – 4, fertile ramuli with liberation tube (arrow), female gametangial network (light grey in this figure, orange in vivo) and male gametangial network (darker in the figure, light green in vivo); 5, macrogamete, with reddish eyespot; 6, microgamete.

ligulate in form, 40–60 mm × 3–9 mm, margins with irregular teeth, 220–310 µm long and 500–800 µm wide at the base; branching of fronds irregular, branches arising from the margins or the surface of the fronds.

- *C. cupressoides*. Plant robust; stolons ovate or terete in cross-section, 1.5–3.0 mm in diameter. Descending branches (pillars) emerging from the ventral surface, ending in filiform rhizoids. Fronds on cylindrical and rather long stalks, 6–8 cm tall, axis terete or slightly compressed, 1.0–3.0 mm wide with irregular or irregular-distichous branching, bearing multiseriate or occasionally pinnate, upward curved, compressed, conical branchlets, 0.3–2.0 mm long and 0.3–0.6 mm wide at the base, with cuspidate or mucronate tips.
- *C. fergusonii*. Plant medium tall; stolons ovate in cross-section, up to 2 mm in diameter. Rhizoid bearing descending branches (pillars) 1–3 cm long, arising from ventral part at irregular distances. Fronds upright, 5–8 cm tall, with pyriform or obpyriform segments, 4–7 cm long and 3–5 mm wide, usually unbranched; segments with single or pinnate branchlets constricted at their base, rounded to clavate in form, the widest 3–6 mm in diameter.
- *C. okamurae*. Plant medium tall; stolons cylindrical, glabrous, glossy, several cm long, 1–1.5 mm in diameter. Rhizoids emitting from ventral surface at irregular distances. Fronds with cylindrical axis, as thick as the stolon, 4–12 cm tall, on cylindrical, medium to long, irregularly branched stalks and clothed more or less densely with branchlets over their whole length; branchlets mostly imbricate, sometimes distichous or opposite, and obovate, oblong, or subclavate-cylindrical in form, 2–5 mm × 1.5 mm, on short stalks, and slightly constricted at the junction.
- *C. serrulata*. Plant medium tall and robust; stolons stiff, ovate or terete in cross-section, 1.5–2.5 mm in diameter. Descending branches (pillars) terete, at irregular intervals, ending in filamentous rhizoids. Fronds flat or compressed, 4–9 cm tall, mostly twisted or curved upwards, 1.5–4.0 mm wide, irregularly or semi-dichotomously branched on short cylindrical stalks; branchlets on both margins arranged regularly, triangular, 1.5–2.5 mm × 1–1.5 mm, apex mucronate.
- *C. sertularioides*. Plant stoloniferous; stolons tubular, naked, cylindrical, 0.25–1.5 mm in diameter. Rhizoid-bearing branches (pillars) emerging from the ventral side of stolons at irregular distances. Fronds 1–12 cm tall, on cylindrical stalks 2–10 mm long and 0.3–1 mm in diameter; axis terete, 1–2 mm wide, only rarely branched; branchlets pinnately arranged, terete, curved upwardly, with uniform diameter of about 0.5 mm, not constricted at the base, with mucronate tips.
- *C. urvilleana*. Plant large and robust; stolons terete or ovoid in cross-section, 1.5–3.5 mm in diameter. Descending branches (pillars) few to many, cylindrical, with branched rhizoids at the ends. Fronds erect, 8–20 cm tall, on cylindrical stalks 2–7 mm × 1.5–2.5 mm, axis terete to compressed, 2–3.5 mm wide; branching repeatedly dichotomous or alternate; branchlets mamillate, arranged on both margins or multiseriately, 1.5–3 mm × 1 mm, apex pointed or mucronate.

Growth and development Most *Caulerpa* can be found all year round, although several are most luxuriant in shallow tide pools and lagoons during the warmest and quietest months of the year.

The life cycle is not yet completely understood. Most species are considered to be monoecious and all are holocarpic, releasing their total content in the form of microscopic, mobile, biflagellated presumed anisogametes. There are indications that all *Caulerpa* spp. have a haplontic life cycle, in which a multinucleate, coenocytic and presumably haploid gametophyte alternates with a microscopic zygote stage, but evidence concerning the ploidy of the various stages in the life cycle is incomplete. The supposed anisogametes develop inside the coenocytic thalli. Gametogenesis is a relatively inconspicuous process involving the migration of the cytoplasm into a net-like lattice of unspecialized gametangia concentrated at the terminal ends of the fronds. Migration of the cytoplasm occurs overnight, about 2 days before gamete release, resulting in transparency of the stolons. Within 12 hours before gamete release many species typically acquire a yellowish-green appearance. Light green sections of gametangia release the small microgametes, whereas brownish-orange-coloured gametangia release slightly larger macrogametes. Siphonous shedding tubes, 5–15 mm long, develop 12–36 hours prior to gamete release. Recent studies in the Caribbean Sea show that most *Caulerpa* species there release all gametes within a short period of 5–15 minutes, mainly during the annual shift from dry season to wet season. Each species seems to use a fixed and characteristic time relative to sunrise, resulting in release periods that differ for related species. In the resultant gamete clouds these gametes fuse usually rapidly, but embryogenesis of zygotes has only very occasionally been observed and is remarkably slow.

Several *Caulerpa* spp. are stenohaline and cannot grow in areas which become brackish. The long, creeping stolons produce dense upright fronds in favourable circumstances and less dense fronds in less favourable environments. In culture, near the growing tip of the stolons, tufts of downward-growing rhizoids (often on rhizophorous pillars) are formed at regular distances and, when circumstances do not change, in each individual at a constant speed. In nature, however, changing environmental conditions usually result in irregular distances between the rhizoids. Upright fronds are formed at more irregular distances and further back from the growing tip of a stolon. The growth of stolons, rhizoids and upright fronds does not differ significantly in the various *Caulerpa* spp. that have been studied in detail. The direction is controlled by gravity. In all cases the different parts of the thalli extend only at their tips or from newly formed growing points, but never intercalary. The growth rate for stolons is 2–9 mm/day in *C. prolifera* from Italy and from the Caribbean.

A specific wound response in *Caulerpa* enables the giant multinucleate thalli to cope with the cell integrity when the outer wall is damaged. As soon as damage occurs, wound plug formation is initiated, thus preventing the giant cell from losing its entire content, although in general some cytoplasm will stream out into the sea water. A new wall will be laid down behind the wound plug, sealing off the remainder of the coenocytic thallus. Wound plug formation can be induced by pressing together opposite walls of the cell, resulting in the formation of a special wall. This protective response happens often within minutes and can be used to prepare fragments for propagation. The pressure technique is commonly used in the cultivation of *Caulerpa* as ornamental plants for aquaria. After formation of these special walls, called pression walls, regeneration of the alga begins. In nature regeneration of whole plants from even small pieces often occurs and can be considered an important means of vegetative propagation. When these algae become fertile, however, normally all contents of these holocarpic coenocytes are used to produce the gametes. The empty outer walls usually degrade quickly. Depending on wave action and currents, all remnants may disappear within two hours, or shreds of the yellowish-whitish husks of emptied thalli persist for one or two more days. In aquarium practice this phenomenon is known as 'fatal bleeding' of *Caulerpa*.

Other botanical information There are more than 180 taxa (i.e. species, varieties and formae) recognizable in *Caulerpa*, of which at least 100 occur in South-East Asia. Most of these entities show high adaptability to changing environmental conditions. As a result, these entities may persist under unfavourable conditions but exhibit different morphological characters. This phenomenon is called morphological plasticity and the entities are known as ecophenes or ecads.

Ecology Sheltered and semi-protected coastal areas are the best habitats for the settlement of *Caulerpa*. The water in such areas is relatively clear, the current is not too strong and the bottom is largely soft due to sedimentation. In the tropical areas, the wide eulittoral zone has the highest species diversity of *Caulerpa*, while in the deeper zone the diversity becomes much less. In the sublittoral zone to a few metres deep, *Caulerpa* lives amongst living corals or creeping under the acropora coral canopy. *C. brachypus* lives in large colonies mixed with *C. racemosa* in the mid to lower eulittoral zone where the bottom consists of mud and sand. It occurs also in deeper water, growing solitarily on dead corals. *C. serrulata* grows on sandy bottoms and may reach 1 m in length, a greater length than it reaches on hard substrates. *C. cupressoides* and *C. urvilleana* commonly grow on loamy bottom and coexist in the seagrass meadow. A large *C. urvilleana* colony in a seagrass meadow may become 30 cm tall. The vertical distribution of *Caulerpa* is very wide. Reports indicate that *C. cupressoides*, *C. fergusonii* and *C. racemosa* are found at 20–30 m depth, *C. webbiana* Mont. even at 50 m depth, and *C. taxifolia* up to 90 m depth in the Mediterranean Sea.

The occurrence of heterotrophic assimilation by rhizoids has been suggested for several *Caulerpa* spp. For *C. taxifolia* it has been shown that endocellular bacteria in the cell lumen of rhizoids can take up inorganic phosphorous and organic carbon and nitrogen from substrata and can translocate nutrient products to the photoassimilatory organs. This rhizoid uptake of nutrients provides an explanation for the successful growth of these large coenocytic organisms in oligotrophic tropical waters.

Propagation and planting In nature *Caulerpa* may propagate in two ways: sexually and vegetatively. In culture, however, vegetative propagation is more important than sexual propagation. A small detached piece of a plant will quickly recover in a few days and grow into a small complete plant. The initiation of the sexual reproductive phase of *Caulerpa* is strongly influenced by environmental conditions and physiological stress.

Phycoculture There are no reports of any of the above mentioned *Caulerpa* spp. being commercially cultivated. Information on *Caulerpa* culture refers to *C. racemosa* and *C. lentillifera*, which have recently been successfully exploited and cultured on a large scale in the Philippines and Japan.

Diseases and pests *Caulerpa* spp. are generally not favoured for feed by grazers, although some sacoglossan opisthobranch snails are specialized feeders on these algae.

Harvesting *Caulerpa* spp. are collected by hand from wild populations and for local use only.

Handling after harvest *Caulerpa* spp. are sold and used fresh and/or sun-dried; occasionally they are preserved in salt.

Prospects The trend of increasing seaweed consumption in archipelagic countries (e.g. Indonesia and the Philippines) will provide opportunities for the development of *Caulerpa* culture to supply a fresh sea vegetable. There is also potential use for fine chemicals and medical products.

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A.M. Hatta

Caulerpa lentillifera J. Agardh

Mus. Senckenb. 2: 173 (1837).
CAULERPACEAE
$2n$ = unknown

Synonyms *Caulerpa kilneri* J. Agardh (1873), *C. longistipitata* (Weber Bosse) Sved. (1906).

Vernacular names Seagrapes, green caviar (En). Indonesia: lelato. Philippines: ararusip, arurusip (Ilocano), lato (Visayan).

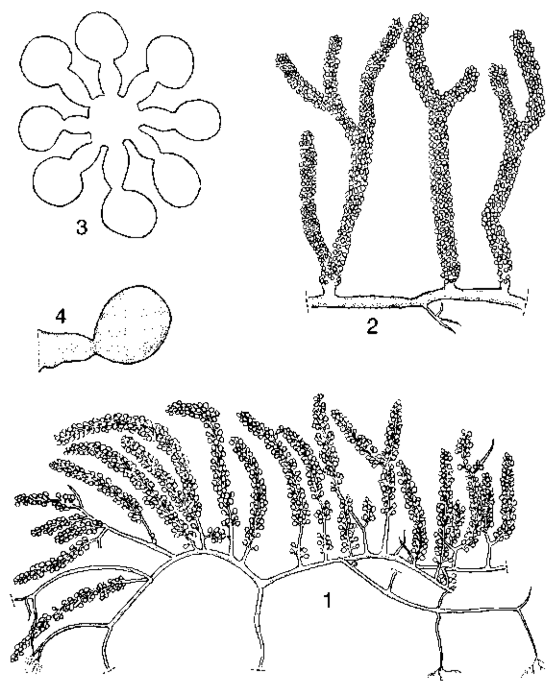
Origin and geographic distribution *C. lentillifera* is widely distributed in tropical areas of the Indian and Pacific Oceans. In South-East Asia it has been recorded in Thailand, Vietnam, Peninsular Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea.

Uses *C. lentillifera* is mainly used in a raw vegetable salad. In the Philippines it is cleaned and washed thoroughly and eaten plain or garnished with sliced tomatoes, onions, sliced green mangoes and fish sauce or the salad is dressed with sweet-sour sauce, vinegar or lemon juice, often with salt or powdered black pepper to taste. *C. lentillifera* is a favoured species due to its soft and succulent texture. Specimens packed for export can be salt-preserved. As a medicine it has antibacterial and antifungal properties and is used to lower blood pressure and to treat rheumatism.

Production and international trade *C. lentillifera* is cultivated in about 400 ha of ponds in Mactan, Cebu Province (the Philippines) and production is estimated at no less than 4000 t fresh weight per year, with more than 90% being produced during the dry months. No recent statistics on the export of fresh *Caulerpa* are available; the export of 827 t of *C. lentillifera* is registered for 1982. Commercial aquaculture in the Philippines started in the early 1950s on the island of Mactan. In Japan commercial cultivation of *C. lentillifera* started in 1986 in the tropical waters of Okinawa Province. A one-year feasibility study has shown that 12–15 t of fresh *C. lentillifera* can be produced annually in a one-hectare pond. In the Philippines, the retail price in 1995 was P20/kg. Return on investment has been calculated at 15% during the first year and double this amount for the succeeding years.

Properties *C. lentillifera* is a potential source of protein and shows haemagglutinic activity. It usually contains small quantities of terpenoids.

Description Plant stoloniferous, up to 10 cm tall; stolons branched, terete in cross-section, 1–1.5(–2) mm in diameter. Descending branches (pillars) with tufts of rhizoids arising at irregular intervals from ventral side of stolons. Fronds rather densely set, without stalks or with very short, naked lower section on the upright axis, usually less than 5 mm long and 1–2 mm in diameter, consisting of an irregularly branched or more often unbranched terete axis, completely and usually densely covered by subspherical or more or less clavate branchlets, 1–3 mm in diameter, placed on 5–8 longitudinal rows or more irregularly and imbricately placed, always supported by clearly constricted pedicels. Thalli holocarpic when fertile.



Caulerpa lentillifera J. Agardh – 1 & 2, habit; 3, detail of a cross-section of an upright frond with branchlets with globose tips and constricted pedicels; 4, detail of a branchlet.

Growth and development Sexual reproduction of *C. lentillifera* is believed to be similar to that of other *Caulerpa*, but has not yet been observed in South-East Asia. Sexual reproduction of these most probably holocarpic plants would result in empty outer walls that would disintegrate quickly.

Ecology *C. lentillifera* is generally found growing on sandy to muddy substrates on reef flats not exposed during low tides and where the water is generally calm. It may form extensive beds or meadows in exceptionally good habitats. The alga is stenohaline and cannot thrive in areas where salinity is less than 25‰. Salinities lower than 30‰ already result in a loss of crop. Growth of natural stocks in habitats where water becomes brackish during the rainy season, or those cultured in ponds, is highly seasonal.

Propagation and planting *C. lentillifera* is cultivated in the Philippines in ponds and open lagoons which are protected from strong waves. Initial stocking rate is 100 g/m² or 1000 kg/ha; the seedstock is planted on the pond bottom uniformly by burying one end of a handful of seedstock at approximately one metre intervals, using string as a guide. Broadcasting may also be used to seed the ponds. However, the seedstock is then not anchored to the bottom and may easily be carried away by waves, becoming concentrated in one part of the pond which results in patchy or uneven growth. Planting is therefore the more efficient method. When cultivated in open lagoons, the site should be shallow (0.3–0.5 m at lowest tide) with free-flowing water and the substrate must be muddy-loam. The area must first be cleared of seagrasses and other marine organisms. Branches are half-buried into the muddy substrate at 0.5 m intervals. In the wild *C. lentillifera* is highly seasonal, with peak production during the sunny dry months of the year. All year round production is, however, possible if a flow-through system is installed in the culture ponds to fully control their salinity level during the rainy season. In the ponds multiplication mainly takes place by fragmentation of thalli. Cage cultivation of *C. lentillifera* is undertaken in Okinawa (Japan). Multistage cylindrical cages are used for cultivation in the tropical waters of Yamaha Bay. Small bundles of thalli are tied to the middle of the floor of each stage of the cages, which are then hung in the sea. If the cultivation ground is too shallow for the cages to hang, mosquito nets with bundles of cut pieces tied at intervals of 0.5–1 m are laid on the bottom parallel to the currents.

The maintenance of good water quality, which can only be achieved through proper pond management, is dependent on the ponds being appropriately designed and constructed. The following are factors considered in the selection of farm sites: proximity to a source of unpolluted seawater supply, far from freshwater sources such as rivers and creeks, the level of the pond being at, or just a little above the low-tide level, protected from the direct effects of wind-driven waves which can easily erode and destroy the dikes; the substrate should be muddy-loam; very soft and deep muddy bottoms should be avoided; abandoned or non-productive fish ponds fulfilling the above criteria are preferred after some modifications. The pond should be divided into 0.5–1 ha areas. The smaller units should be laid out in such a way that a 'flow-through system' can easily be incorporated. Newly built ponds are usually acidic and require the addition of hydrated lime while old ponds usually require 0.5–1 t agricultural lime per hectare each year. The ponds are first drained to a depth of 0.3 m to facilitate planting.

Phycoculture After planting, the depth of the water should be adjusted to 0.5–0.8 m. Flooding should be done slowly, so that newly planted seedstock is not uprooted by the water currents. A practical guideline for maintaining the proper water depth in ponds, as practised by farmers, is to adjust the depth to a level so that the plants can be seen from the surface. Ideally, the pond water must be changed at least every other day to maintain adequate levels of nutrients. At the start of the growing period, however, the pond water should be changed every 3–4 days, avoiding strong currents which may dislodge the algae. The frequency of changes should be increased at about the third week.

A newly planted pond with *C. lentillifera* should be inspected after a few days and bare areas replanted to ensure uniform growth of the crop. Fertilizers may be applied when the stocks appear unhealthy, e.g. light green to yellowish. In open lagoons the *Caulerpa* plots are monitored regularly and the seaweeds and seagrasses are cropped to allow a lead-time for the *Caulerpa* to grow and successfully establish in the area.

Cages and nets require periodic cleaning. Since *C. lentillifera* is affected by salinity levels lower than 30‰, the cages should be lowered to some depth below the surface (about 0.5 m) when a decline in surface salinity is expected, such as after heavy rainfall. Other seaweeds in the ponds or nearby area compete with *C. lentillifera* for nutrients, space and light, and should be weeded out. Bleaching of *Caulerpa* spp., seen as the occurrence of white empty husks of these algae, might be the result of reproduction, as all contents are used in the production of motile reproductive cells.

Diseases and pests Bacterial contamination through domestic and industrial pollution can become problematic. Pesticides should only be applied during the seasons that no *Caulerpa* is cultured in the ponds, since otherwise the *Caulerpa* may become contaminated and unsafe to eat.

Harvesting Harvesting of *C. lentillifera* may be undertaken two months (or more) after planting, depending on the growth rate of the crop. Harvesting takes place when the bottom of the pond is uniformly covered with *Caulerpa*. About 20–25% of the original crop should be left more or less uniformly spread or spaced on the pond bottom to serve as seedstock for the next crop. Depending on the amount of seedstock left and the growth rate of the plants, the succeeding harvests may be reaped at intervals of about two weeks or longer. Harvesting is done by uprooting the plants from the mud. These are placed in a wooden dugout or banca and are washed thoroughly in clean seawater to remove the mud, silt and other dirt. Partial harvesting is also practised in open lagoon cultivation so that enough stock is left for the next crop.

Yield *C. lentillifera* harvested two months after planting is of high market quality, light grass-green, soft and succulent. Older crop, although higher in biomass, is of lower quality, tougher and with pale or colourless basal portions.

Handling after harvest Harvested *C. lentillifera* is placed in baskets or clean polythene sheets for sorting to remove any remaining dirt and other material (epiphytes), washed thoroughly in clean seawater and all excess water is allowed to drip off prior to packing.

In Japan, fresh fronds of *C. lentillifera* are packed in 100–200 g packages. These will stay fresh for about 7 days if kept chilled and moist. If refrigerated (5–10°C) in bottles or tubular polythene bags with seawater it will remain fresh for about 3 months. Brine-cured or salted and dehydrated samples, when soaked in freshwater, swell rapidly and recover their original shape within several minutes. Therefore, when distributed in ready-to-eat packets, these seaweeds and their dressing should be packed separately.

Prospects The sustained local demand for *C. lentillifera* and the growing popularity of health foods in restaurants both locally and abroad have resulted in an increasing demand for this sea vegetable. Evidence for this increasing popularity is shown by the Japanese who used to import *Caulerpa* from the Philippines. They now have developed their own farming technology for *C. lentillifera* in Okinawa to meet the high demand in Japan. Local farmers will benefit more from this industry if they are also able to produce this seaweed during the rainy season.

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G.C. Trono Jr

Caulerpa racemosa (Forssk.) J. Agardh

Lunds Univ. Årsskr., Afd. Math. Naturv. 9(8): 35–36 (1873).

CAULERPACEAE

$2n$ = unknown

Synonyms *Fucus racemosus* Forssk. (1775), *Caulerpa clavifera* (Turner) C. Agardh (1817), *Caulerpa uvifera* C. Agardh (1817).

Major varieties and synonyms

- var. *corynephora* (Mont.) Weber Bosse (1898), synonym: *Caulerpa corynephora* Mont. (1842).
- var. *laetevirens* (Mont.) Weber Bosse (1898), synonym: *Caulerpa laetevirens* Mont. (1842).
- var. *lamourouxii* (Turner) Weber Bosse (1898), synonym: *Fucus lamourouxii* Turner (1811–19).
- var. *macrophysa* (Sond. ex Kütz.) W.R. Taylor (1928), synonyms: *Chauvinia macrophysa* Sond. ex Kütz. (1857), *Caulerpa macrophysa* (Sond. ex Kütz.) G. Murray (1887), *C. clavifera* var. *macrophysa* (Sond. ex Kütz.) Sved. (1906).
- var. *peltata* (J.V. Lamour.) Eubank (1946), synonym: *Caulerpa peltata* J.V. Lamour. (1809).
- var. *racemosa*, synonyms: *Caulerpa racemosa* var. *uvifera* (C. Agardh) C. Agardh (1823), *C. racemosa* var. *clavifera* (Turner) Weber Bosse (1898).
- var. *turbinata* (J. Agardh) Eubank (1946), synonyms: *Fucus chemnitzia* Esper (1800), *C. clavifera* var. *turbinata* J. Agardh (1837), *C. racemosa* var. *chemnitzia* (Esper) Weber Bosse (1898).

Vernacular names Seagrapes (En). Indonesia: lelato (Lombok), lata (Bangka), lai-lai (South Sulawesi). Philippines: ararusip (Ilocano, general and for var. *peltata*), kulinatnat, saluysoy (for var. *peltata*).

Origin and geographic distribution *C. racemosa* is widely distributed in tropical waters and some varieties also occur in subtropical waters. It is common in South-East Asia, and has been recorded in Burma (Myanmar), Thailand, Vietnam, Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea.

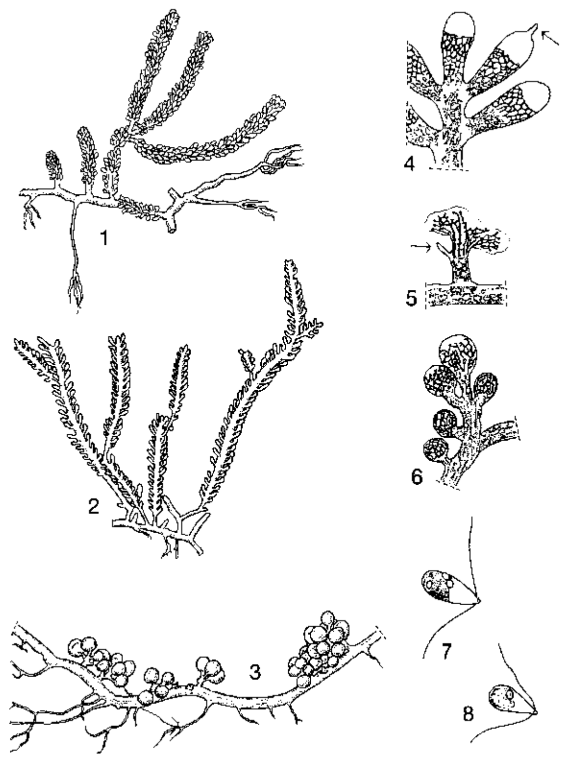
Uses In the Moluccas (eastern Indonesia) the fronds of *C. racemosa* are consumed fresh as a salad and eaten mixed with spices such as grated coconut, garlic, shallot, leaves of basil (*Ocimum basilicum* L.), salt and chilli. In Cagayan Province (the Philippines), the *C. racemosa* side dish is prepared by mixing clean fronds with salt and tomatoes or with tomatoes, onions and pepper. Var. *racemosa* and var. *peltata* in particular are used in the Philippines. These varieties are also used in Indonesia; in South Sulawesi var. *corynephora* is also much appreciated. In Thailand the varieties *corynephora* and *macrophysa* are commonly used as salad vegetables. In the Philippines *C. racemosa* is also used as fish feed and as a medicine for humans to lower blood pressure and to treat rheumatism. Antibacterial, antibiotic, antifungal and peroxidase activities are recorded.

Production and international trade *C. racemosa* is only used locally.

Properties Like other *Caulerpa*, *C. racemosa* produces secondary compounds, such as caulerpin, caulerpicin, caulerpenyne and other terpenoids. The neurotropic activity of caulerpicin is thought to be of clinical value. Both caulerpin and caulerpicin are apparently transferred along marine food chains and become concentrated in the process. In some areas this can result in toxicity to fish. *C. racemosa* is often especially rich in cholesterol and is cited as having antitubercular, haemagglutinic and hyposensitive activities.

Description Plant stoloniferous; stolons terete to ovoid in cross- section; rhizoid bearing descending branches (pillars) arising at irregular distances. Fronds mostly erect, up to 20 cm tall, crowded or rather sparse. Branching simple or irregular, not more than to third order; branchlets (assimilators) basically consisting of stalk and head of varied form (club, rounded, ovate or compressed), alternate, opposite, multiseriate or imbricate. Thalli holocarpic when fertile.

- var. *corynephora*. Fronds robust, fleshy, simple; branchlets biseriate, (sub)opposite, large distance between branchlets, -clubformed with hemispherical head; head 1–2.5 mm wide on cylindrical stalk 2–5 mm long.
- var. *laetevirens*. Fronds robust, fleshy, simple, crowded; branchlets imbricate, mostly arranged in four rows surrounding the frond's axis, clavate with hemispherical head; head 1.5–3 mm wide.
- var. *lamourouxii*. Fronds stiff, irregularly branched, compressed, on short terete stalk either entirely nude or with branchlets at one or both margins; branchlets irregularly scattered or opposite, pyriform or clavate, 1.5–3.5 mm wide on a short stalk.
- var. *macrophysa*. Plant stout, fleshy; stolons richly ramified; fronds 2–4 cm long; branchlets irregularly placed, pyriform to (sub-)spherical, always with rounded head, (2–)4 mm in diameter, on unconstricted stalk, shorter than the diameter of the branchlets.



Caulerpa racemosa (Forssk.) J. Agardh. Var. laetevirens (Mont.) Weber Bosse – 1, habit; 4, fertile branchlet with liberation tube (arrow) and gametangial network. Var. corynephora (Mont.) Weber Bosse – 2, habit. Var. racemosa – 3, habit; 6, fertile branchlets and gametangial network. Var. peltata (J.V. Lamour.) Eubank – 5, fertile branchlets with liberation tube (arrow) and gametangial network; 7, macrogamete, with reddish eye-spot; 8, microgamete.

- var. *peltata*. Plant stoloniferous, creeping, delicate to rather robust; branchlets arising directly from the stolon's surface or from short ascending axis, irregular or subopposite, peltate or depressed turbinate (shield-shaped); head 1.5–7 mm in diameter, on a relatively long cylindrical stalk.
- var. *racemosa*. Plant rather fleshy; stolons richly ramified, often with long, thin rhizophorous pillars; fronds (2–)3–4 cm long; branchlets irregularly placed to crowded, pyriform to (sub-)globose, (2–)3–4 mm long, with inflated top, head (2–)3–4 mm in diameter, on unconstricted stalk 0.5–1.5 mm long.
- var. *turbinata*. Plant stout, fleshy; stolons thick, terete, 3(–5) mm in diameter, with well-developed, short or long, branched or unbranched rhizophorous pillars; fronds generally simple, 4–8(–17) cm tall; branchlets radially or helicoidally arranged, broadly clavate, with blunt, flat or even convex head (trumpet-shaped), 4–12 mm long and 5–9 mm in diameter.

Growth and development In aquarium culture, *C. racemosa* grows relatively fast. The stolon may grow 1.1–2.0 cm per day in the first week, while the ascending fronds grow about 1 cm in the first week. In culture, propagation is mainly by fragmentation, while in nature propagation may happen by vegetative fragmentation as well as by sexual reproduction. Sexual reproduction is believed to be similar to that of other *Caulerpa*, where most of them are considered to be monoecious and holocarpic, releasing their total content in the form of microscopic, mobile, biflagellated presumed anisogametes. These gametes are usually shed from siphonous liberation tubes, 1.2–2 mm long.

Other botanical information Cross-gradient culture experiments were carried out on specimens in the *C. racemosa/peltata* complex originating from Japan. There the *laetevirens* type was formed under relatively low temperatures and high light intensities, while *peltata* type assimilators were formed under lower light intensities and low as well as high temperatures. The results were the same whether the inoculating stock was *C. racemosa* var. *peltata* or *C. racemosa* var. *laetevirens*. In nature, plants with only *peltata*-type assimilators grow on shaded rocks or in deep water, while plants with only *laetevirens*-type assimilators grow on sunny rocks in shallow water. An individual plant that extends from a shaded to a sunny habitat is often morphologically complex, showing *peltata*- as well as *laetevirens*-type assimilators on different parts of the same stolon. It has been suggested that these two different varieties should be considered as ecological growth-forms (ecophenes or ecads) of a single *Caulerpa* sp., while at least some growth-forms of *C. racemosa* var. *turbinata*, which are often mentioned as forms intermediate between var. *peltata* and var. *laetevirens*, are probably also ecads of this complex taxon. The relationship with other components of *C. racemosa* has not yet been experimentally clarified, however.

Ecology *C. racemosa* is very commonly found in shallow water less than 5 m deep. Favourable environmental conditions for most varieties consist of calm, relatively clear water with weak to medium current and loamy or sandy bottom. *C. racemosa* is also associated with mangrove forest. Very often a *C. racemosa* meadow is found in the frontier areas of mangrove forest, and it grows very well on the dead trunks of mangrove trees or covers the wooden piles of harbour bridges. Some of the varieties of *C. racemosa* (e.g. vars *lamourouxii*, *macrophysa* and *racemosa*) are tolerant of the fluctuations in salinity found in intertidal ponds. During the blooming season (in eastern Indonesia between late May–early July), *C. racemosa* grows very thick and dense and may reach a height of up to 40 cm. The varieties *racemosa* and *peltata* also occur on rocky-corally substrates exposed to strong water movement. In these habitats the stoloniferous plants may cover reef edges with closely set short fronds. Heterotrophic activity (uptake of amino acids) has been demonstrated in *C. racemosa* var. *occidentalis* from Florida, the United States.

Propagation and planting Replanting of *C. racemosa* (e.g. var. *laetevirens* and var. *macrophysa*) very often fails due to stress-accelerated reproduction. Stress may occur when *C. racemosa* is transported over long distances in polybags for more than seven hours, and directly planted afterwards. Reproduction will take place in large amounts 5–9 days after replanting. When grown in ponds small pieces of alga are planted in the sandy or muddy substrate.

Phycoculture The principal method of cultivating *C. racemosa* is by planting it in ponds. Cultivation of this alga in hanging cages gives unsatisfactory results: it grows laterally giving very long stolons and short fronds.

Diseases and pests Small *Oxynoe* and *Elysia* molluscs are often found foraging on cultivated *C. racemosa*.

Harvesting *C. racemosa* is harvested by hand from natural populations or from culture in ponds.

Handling after harvest Harvested *C. racemosa* must be washed several times with clean seawater to remove sand and attached organisms. Clean algae are placed in big plastic baskets or fine-plaited bamboo baskets, the bottom and top covered with layers of *Sargassum* seaweeds or banana leaves. The material is then transported to local markets and sold fresh.

Prospects *C. racemosa* is a promising supplementary sea vegetable, especially for coastal and island villagers. In eastern Indonesia it is regularly sold on the market, but the price is lower than that of land vegetables.

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A.M. Hatta

Caulerpa taxifolia (Vahl) C. Agardh

Syn. Alg. Scand.: 22 (1817).

CAULERPACEAE

$2n$ = unknown. However, it has been suggested that inside thalli of *C. taxifolia* two kinds of nuclei occur: small ones with three distinct chromosomes and larger ones with many chromosomes. These observations suggest that small nuclei are haploid ($n = 3$) and large nuclei polyploid.

Synonym *Fucus taxifolius* Vahl (1802).

Vernacular names Indonesia: rumput laut (general). Philippines: lukay-lukay.

Origin and geographic distribution *C. taxifolia* is widely distributed in the tropical seas of the world and is also found in some subtropical waters, e.g. in south-eastern Queensland (Australia) and in the Mediterranean Sea where it has been introduced and is considered a pest. It is common in South-East Asia, and has been recorded in Burma (Myanmar), Thailand, Vietnam, Peninsular Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea.

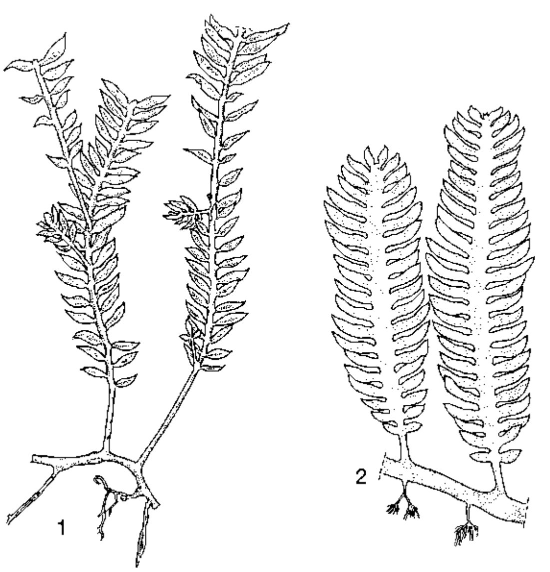
Uses *C. taxifolia* can be eaten raw in salad, but it is less in demand than *C. racemosa* (Forssk.) J. Agardh and *C. lentillifera* J. Agardh. *C. taxifolia* is frequently cultivated in aquaria for aesthetic purposes. It is also used as a medicine to lower blood pressure.

Production and international trade *C. taxifolia* is only used locally.

Properties There is much literature about the toxicity of caulerpin and other terpenoids in *C. taxifolia*, especially of the strains found in the Mediterranean Sea. It is cited as having antibacterial, antifungal, antitubercular and haemagglutinic activities.

Description Plant stoloniferous; tubular stolon 0.5–2 mm in diameter; rhizoid-bearing branches (pillars) at the lower part, at irregular intervals. Fronds 6–15 cm tall (in the Mediterranean Sea, however, giant specimens 85 cm tall have been found), often on cylindrical stalk (naked sections of the erect axis) 1–3 cm long and 0.3–1 mm in diameter; axis usually somewhat compressed, 1–2 mm wide, simple or only exceptionally irregularly branched; branchlets on very short stalks, pinnately arranged, opposite, closely approximated, mostly not overlapping, with parallel sides and slightly constricted at their bases, compressed, 3–10 mm long (3–10 times as long as broad), 0.5–1.7 mm wide and curved upwards, tapering gradually to acuminate apices, only occasionally bifurcate. Thalli holocarpic when fertile.

Growth and development Plants of *C. taxifolia* living in shallow water are susceptible to environmental change and have irregular widths and a wavy outline resulting from discontinous growth. Growth is most probably semi-perennial: no single part of the thallus persists for more than a year, but the individual persists by means of indefinite vegetative development. Growth in aquarium culture can be fast, covering all substrates within a week. It is known as an invader in the Mediterranean Sea, where it forms extensive



Caulerpa taxifolia (Vahl) C. Agardh – 1, habit; 2, detail of two short fronds.

meadows with an extremely thick cover of large fronds. Sexual reproduction is supposed to be monoecious and holocarpic, but it has been suggested that in the Mediterranean Sea only male anisogametes have been observed.

Other botanical information Morphological variation in *C. taxifolia* may appear due to differences in ecological conditions. Plants living on exposed to semi-exposed beaches have narrower, shorter and more closely packed branchlets than those living in estuaries and protected beaches. The distance between branchlets in plants living on exposed beaches is closer (sometimes even overlapping) than in the latter. Plants from deeper water (10–30 m) are often longer than those from shallow water, as are many individuals of the strains introduced in the Mediterranean Sea. In some cases specimens may develop short, wide pinnules which approach the morphology found in *C. mexicana* Sond. ex Kütz. The latter, however, is a separate species, although the mutual taxonomic difference has often been discussed.

Ecology The favoured place for *C. taxifolia* in the tropics is shallow water (1–3 m deep) on semi-protected beaches with moderate current. It grows well on both hard substrate and on a sandy bottom, and sometimes occurs as a creeping epiphytic alga on calcareous algae or on living stony corals. Its known vertical distribution reaches to a depth of 30 m, in tropical areas, and as deep as 100 m in the Mediterranean Sea. Endocellular bacteria in the cell lumen of rhizoids of *C. taxifolia* have been shown to take up inorganic phosphorus and organic carbon and nitrogen from substrates and translocate nutrient products to the photo-assimilatory organs. This rhizoid uptake of nutrients provides an explanation for the successful growth of these large coenocytic organisms in oligotrophic tropical waters as well as in oligotropic situations in the Mediterranean Sea.

Propagation and planting Propagation of *C. taxifolia* in aquaria and in the Mediterranean Sea is by vegetative fragmentation. Sexual propagation is known to take place in tropical areas, but its frequency has not yet been studied.

Phycoculture *Caulerpa* culture is generally done in ponds. *C. taxifolia* frequently coexists in *C. lentillifera* ponds, but no attempt at monoculture has been made. *C. taxifolia* often develops in marine aquaria from 'living stones' imported from tropical countries.

Diseases and pests Some sacoglossan opisthobranch snails are specialized feeders on *Caulerpa* spp. Their possible role in biological control on the invasive strain of *C. taxifolia* in the Mediterranean Sea has been discussed, but the proposed biological control actions with introduced sacoglossan mollusc species have been discouraged.

Harvesting For daily needs *C. taxifolia* is collected in the eulittoral zone at low tide. Afterwards the plants are cleaned of sand, mud and other debris. Only the fronds are consumed.

Handling after harvest *C. taxifolia* is only used fresh.

Prospects Because *C. taxifolia* is less preferred than other *Caulerpa* spp., its consumption is relatively low and its competitiveness in the market weak. The recent invasive activity of this alga in the Mediterranean Sea has generated much information. If its medicinal potential were better documented, the large biomass available in the Mediterrean Sea may become of use for public health.

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A.M. Hatta

Ceratodictyon intricatum (C. Agardh) R.E. Norris

S. Afr. J. Bot. 53: 245 (1987).
RHODYMENIACEAE
$2n$ = unknown

Synonyms *Sphaerococcus intricatus* C. Agardh (1822), *Gelidium intricatum* (C. Agardh) Kütz. (1849), *Gelidiopsis intricata* (C. Agardh) Vickers (1905).

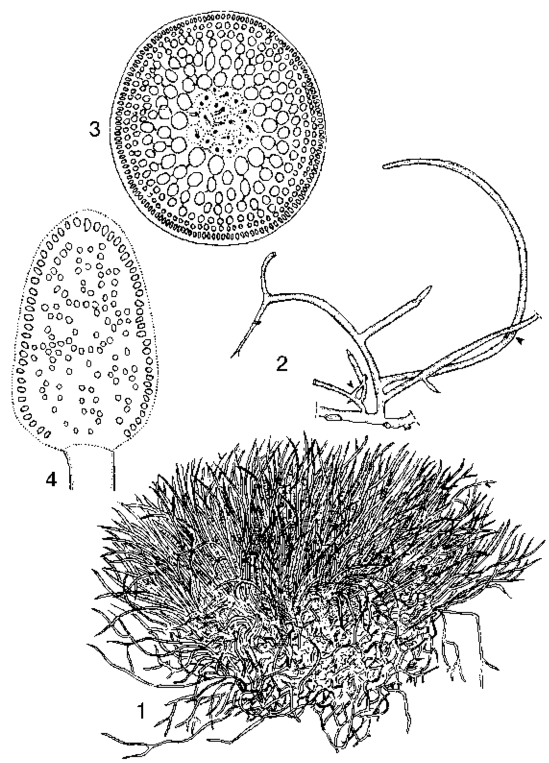
Origin and geographic distribution *C. intricatum* occurs in tropical and subtropical regions in the Indian and Pacific Oceans. Its occurrence in the Atlantic Ocean is not certain and depends on taxonomic interpretation whether or not the circumtropical *C. variabile* (J. Agardh) R.E. Norris belongs to the same species. In South-East Asia *C. intricatum* has been recorded in Burma (Myanmar), the Pacific coasts of Thailand, the Philippines, eastern Indonesia and Papua New Guinea.

Uses In the Philippines *C. intricatum* is locally used as a vegetable.

Properties *C. intricatum* contains agar.

Description Thalli from bushy, wiry clumps usually mixed with other seaweeds. Plant attached to the substrate by rhizoids, greenish to purplish-brown when fresh. Lower branches entangled, stoloniferous, connected by tenacula. Branching rather sparse, irregular and somewhat subdichotomous; upper branches erect, about 2–6 cm tall, cylindrical, 160–450 μm in diameter, tapering towards the apices; medulla composed of long and narrow cells, 7–10 μm in diameter; outer cortex cells small, 2–5 μm in diameter, inner cortex cells becoming broader, up to 20 μm in diameter, not much elongated; growth by a number of small cells, no distinct apical cell present. Tetrasporangial sori in apical, simple or compound, spatulate swollen stichidia, often on elongated unbranched terminal segments; cruciate tetrasporangia about 25 μm × 50 μm, surrounded by tissue of narrow (3 μm) filaments. Sexual organs unknown.

Other botanical information All *Ceratodictyon* spp. recorded from the area, except *C. spongiosum* Zanardini, are possibly subspecies of *C. intricatum*. The placement of *Ceradictyon* Zanardini in the family *Rhodymeniaceae* of the order Rhodymeniales supersedes earlier inclusion in the family *Gracilariaceae* of the order Gigartinales. The relationship between *Ceratodictyon* and *Gelidiopsis* F. Schmitz and their taxonomic placement is not yet solved.



Ceratodictyon intricatum (C. Agardh) R.E. Norris – 1, habit; 2, detail of vegetative part with tenacula fusing branches (arrow heads); 3, cross-section of a branch; 4, detail of a spatulate tetrasporangial stichidium.

Ecology *C. intricatum* is a common component of the algal turfs on rocky substrates in the protected portions of the reefs. It may form intricate clumps in tide pools, on rocky ledges or on top of coral colonies growing in very shallow positions or becoming emerged. These somewhat cartilaginous clumps occasionally become detached from their substrate and are washed onto the coasts.

Propagation and planting There is no known phycoculture of *C. intricatum*.

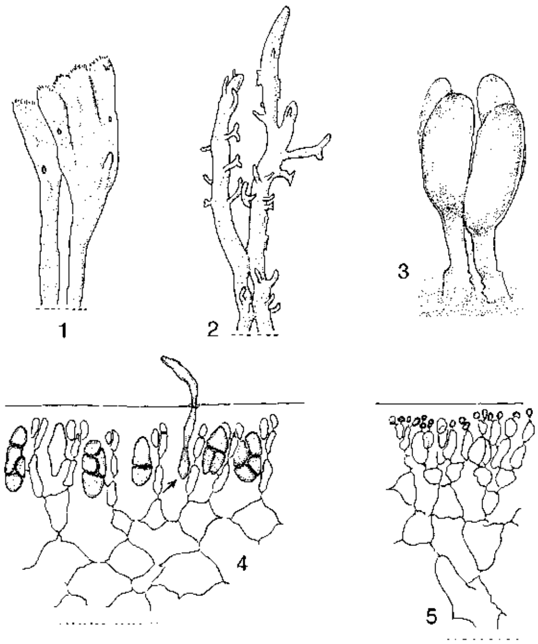
Harvesting *C. intricatum* is harvested only by hand for direct local use.

Handling after harvest *C. intricatum* is used fresh.

Prospects *C. intricatum* contains agar and might be a potential source of this substance.

Literature |1| Norris, R.E., 1987. The systematic position of Gelidiopsis and Ceratodictyon (Gigartinales, Rhodophyceae), genera new to South Africa. South African Journal of Botany 53: 239–246. |2| N'Yeurt, A.D.R., 1996. A preliminary floristic survey of the benthic marine algae of Rotuma Island. Australian Systematic Botany 9: 361–490. |3| Price, I.R. & Kraft, G.T., 1991. Reproductive development and classification of the red algal genus Ceratodictyon (Rhodymeniales, Rhodophyta). Phycologia 30: 106–116. |4| Trono Jr, G.C. & Ganzon-Fortes, E.T., 1980. An illustrated seaweed flora of Calatagan, Batangas, Philippines. Filipinas Foundation Inc. & University of the Philippines, Marine Science Center, Metro Manila, The Philippines. 114 pp.

W.F. Prud'homme van Reine



Ceratodictyon spongiosum Zanardini – 1, habit of the symbiotic association; 2, detail of the algal component, with anastomoses; 3, detail of tetrasporangial stichidia; 4, detail of a cross-secton of a tetrasporangial stichidium, with tetrasporangia and a hair; 5, detail of a cross-section of a spermatangial stichidium, with spermatangia occurring single or in small chains on cortex cells.

Ceratodictyon spongiosum Zanardini

Nuovo Giorn. Bot. Ital. 10: 37 (1878).

RHODYMENIACEAE

$2n$ = unknown

Synonyms *Marchesettia spongioides* Hauck (1882).

Origin and geographic distribution *C. spongiosum* is often common in tropical and subtropical regions in the Indian and Pacific Oceans. In South-East Asia it has been recorded in Thailand, Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea.

Uses At present *C. spongiosum* has no uses.

Properties *C. spongiosum* contains agar.

Description The symbiotic association of the sponge *Sigmadocia symbiotica* Bergquist & Tizard and the alga *C. spongiosum* forms clumps of 15–30(–70) cm in diameter and 5–15 cm tall. These associations are green-brown to purple, distinctly sponge-like, subcylindrical or compressed, hard and tough. Branching very irregular and often anastomosing, 5–10(–20)mm in diameter and with many ostioles of the sponge. Intertwining and anastomosing algal axes form a dense reticulum within the sponge cover. Specimens anchored at numerous points to solid substrates by slightly splayed but otherwise unmodified bases or lateral extensions of major axes (no expanded discs or thickened holdfasts). Algal axes terete, 100–300 (–400) μm in diameter, with a single-layered outer cortex, a pseudoparenchymatous inner cortex and a medulla of a compact core of narrow filamentous cells; distinct apical cell absent, growth by small cells in dome-shaped, multiaxial apex. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangial sori in apical, aggregated, swollen, cylindrical stichidia, about 1.5 mm long, on modified terminal algal branches projecting into sori from the tips of the branches of the symbiotic association; tetrasporangia irregularly decussate, about 10–15 μm × 20–25 μm, surrounded by tissue of narrow (3 μm) anticlinal rows of cortex cells. Gametophytes dioecious; male ones forming swollen, exerted axes superficially resembling tetrasporangial stichidia, although more mucilaginous and covered by spermatangial mother cells, each forming 1–2 distal spermatangia; female ones with dense clusters of terete to slightly flattened protruding terminal branches, simple or sparingly branched, covered by aggregates of cystocarps with often partly confluent pericarps. Mature cystocarps protuberant, about 600 μm in diameter, bluntly conical, with apical ostiole.

Growth and development The algal (*C. spongiosum*) and sponge partners reproduce completely independently of one another. It is not known when, or how, the symbiosis is established. Sponge-free algal growth has been established in laboratory culture, but the sponge partner has never been found free-living, and attempts to maintain it separately in laboratory culture have failed.

Other botanical information Other *Ceratodictyon* spp. recorded from the area, except *C. spongiosum*, are possibly subspecies of *C. intricatum* (C. Agardh) R.E. Norris. The placement of *Ceratodictyon* Zanardini in the family *Rhodymeniaceae* of the order Rhodymeniales replaces earlier inclusion in the family *Gracilariaceae* of the order Gigartinales. The relationship between *Ceratodictyon* and *Gelidiopsis* F. Schmitz and their taxonomic placement is not yet solved.

Ecology The symbiotic association of *C. spongiosum* and *Sigmadocia symbiotica* typically occurs on intertidal coral reef flats and subtidal reef slopes, but has also been recorded at greater depths (up to 100–140 m).

Propagation and planting There is no known phycoculture of *C. spongiosum*.

Prospects *C. spongiosum* may become a source of fine chemicals and pharmaceuticals, especially because sponges are known to contain many interesting biopharmaceutical compounds. Most sponges are difficult to find regularly and in suitable quantities, but because of the symbiotic association with *C. spongiosum*, *Sigmadocia symbiotica* can be easily identified and collected.

Literature |1| Cribb, A.B., 1983. Marine algae of the southern Great Barrier Reef-Rhodophyta. Australian Coral Reef Society Handbook No 2. 173 pp. + 71 plates. |2| Norris, R.E., 1987. The systematic position of Gelidiopsis and Ceratodictyon (Gigartinales, Rhodophyceae), genera new to South Africa. South African Journal of Botany 53: 239–246. |3| Price, I.R., Fricker, R.L. & Wilkinson, C.R., 1984. Ceratodictyon spongiosum (Rhodophyta), the macroalgal partner in an alga-sponge symbiosis, grown in unialgal culture. Journal of Phycology 20: 156–158. |4| Price, I.R. & Kraft, G.T., 1991. Reproductive development and classification of the red algal genus Ceratodictyon (Rhodymeniales, Rhodophyta). Phycologia 30: 106–116.

G.C. Trono Jr

Chaetomorpha Kütz.

Phycol. germ.: 203 (1845).

CLADOPHORACEAE

x = unknown; *C. antennina*, *C. linum*: $2n = 36?$, *C. aerea*: $2n = 12, 18$

Major species and synonyms

- *Chaetomorpha aerea* (Dillwyn) Kütz., Sp. alg.: 379 (1849), synonym: *Conferva aerea* Dillwyn (1806).
- *Chaetomorpha antennina* (Bory) Kütz., Bot. Ztg. 5: 166 (1847), synonyms: *Conferva antennina* Bory (1804), *Chaetomorpha media* (C. Agardh) Kütz. (1849).
- *Chaetomorpha crassa* (C. Agardh) Kütz., Phycol. germ.: 204 (1845), synonym: *Conferva crassa* C. Agardh (1824).
- *Chaetomorpha javanica* Kütz., Flora 30: 773 (1847).
- *Chaetomorpha linum* (O.F. Müll.) Kütz., Phycol. germ.: 204 (1845), synonym: *Conferva linum* O.F. Müll. (1778).

Vernacular names General: Philippines: riprípies, ririppus.

- *C. aerea*. Philippines: lumot.
- *C. crassa*. Philippines: cawat-cawat, kawat-kawat, kauat-kauat.
- *C. javanica*. Indonesia: lumut laut, sayur lompan, lumut kehur.

Origin and geographic distribution *Chaetomorpha* is widely distributed both in seas and in brackish water all over the world. In South-East Asia *C. aerea* has been recorded in Malaysia, Indonesia and the Philippines (Luzon, Negros); *C. antennina* in Burma (Myanmar), Pacific coasts of Thailand, Malaysia and the Philippines (Luzon); *C. crassa* in the same countries, where it is more common. In Thailand *C. crassa* is common on both coasts, and it occurs also in Singapore, Indonesia, in many locations in the Philippines and Papua New Guinea. *C. javanica* has been recorded in Vietnam, Sabah (Malaysia) and Java and Ambon (Indonesia). Outside the area it is only found on Christmas Island and the Maldives. *C. linum* has been recorded in Thailand, the western coast of Peninsular Malaysia, Singapore, Indonesia (not common) and the Philippines (Luzon, Visayas).

Uses *C. aerea* is used for human food and as feed for milkfish.

C. antennina is eaten as a salad in Malaysia, and also used as feed for milkfish. *C. crassa* can be used to make a gelatine-like sweetmeat. It is eaten raw as a salad in Sabah (Malaysia) and in the

Philippines. It is also used as fish bait and as feed for milkfish.

These three *Chaetomorpha* spp. form important constituents of the thick mats of mixed filamentous green and blue-green algae, covered by many periphyton algae found in fish ponds. These algal mats are known as 'lab-lab' in the Philippines, and as 'kelekap' in Indonesia. Growth of these thick algal mats is a necessary condition for successful traditional milkfish cultivation. In most cases the milkfish mainly feed on periphyton algae, by grazing the epiphytes from the hosts; only mature fish also eat the green filaments. Slow growth rates of young milkfish might be the result of inhibition of the necessary alkaline protease trypsin in milkfish by a tryptic inhibitor from a *Chaetomorpha* sp. The *Chaetomorpha* species blamed for forming this tryptic inhibitor is stated to be *C. brachygona* Harv., one of the most common filamentous algae in milkfish ponds. The filaments of the unattached species have the same dimensions as those of the attached *C. javanica*.

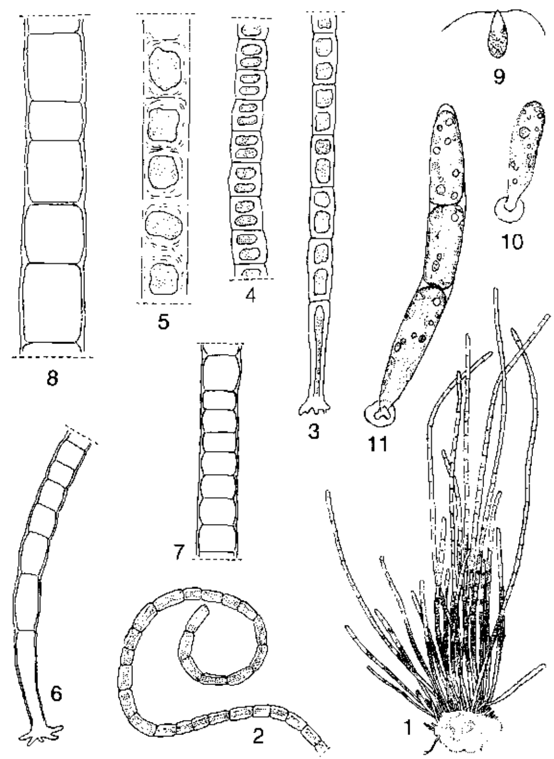
C. javanica is collected by the Chinese in Ambon (Indonesia) during the dry season (August and September). After being soaked overnight in freshwater it is boiled and eaten with bacon. In Sabah (Malaysia) it is eaten dried or boiled. *C. linum* is used in the same way as *C. aerea*.

Production and international trade In the Philippines both *C. antennina* and *C. crassa* are successfully grown in culture, usually in connection with milkfish cultivation.

Properties Seasonal variation in the soluble polysaccharide content has been demonstrated in *C. aerea*. The polysaccharides mainly consist of D-galactose, L-arabinose and D-xylose and its ester sulphates. The cell walls of *Chaetomorpha* contain 5–10% protein, especially in the outermost layers. The 'higher plant' sterol β-sitosterol is the major sterol in *C. linum*; this is peculiar because it does not occur in some organisms that are considered ancestral to higher plants. The major sterol in *C. crassa* is cholesterol. *C. antennina* contains antibacterial and antifungal compounds.

Description Plants filamentous, unbranched, unattached or attached by a cylindrical basal holdfast cell; all cells large and highly multinucleate, usually with firm lamellose walls. Life cycle haplontic or isomorphic diplo-haplontic and dioecious. Asexual quadriflagellate zoospores and sexual biflagellate isogametes formed in separate slightly enlarged cells in the filaments.

- *C. aerea*. Plant gregarious, 10–30 cm tall, light or dark green, attached by slender, subclavate basal cell with disk-like base, lobed or fimbriate at the margins; basal cell at the top, 7.5–10.5 mm long, and 2.5–4.2 times as long as the suprabasal cell, 130–150 μm in diameter; filaments slender towards the base, more than 150–300(–500) μm in diameter, stiff, the cells 1–2 mm long, slightly constricted at the septa. Zoospores in the upper cells of filaments, cask-shaped to subglobose, 600–700 μm in diameter.
- *C. antennina*. Tuft up to 7 cm tall, attached; each basal cell up to 5 mm long, about 0.1 mm in diameter, with annulate base and attached to the substrate by branched rhizoidal filaments; vegetative cells with thick striated walls, 400–600 μm long and 200–350 μm in diameter.
- *C. crassa*. Plant entangled; filaments (300–) 500–550(–700) μm in diameter, dark green; cells



Chaetomorpha. C. antennina (Bory) Kütz. – 1, habit of a tuft. C. crassa (C. Agardh) Kütz. – 2, part of a coiled filament. C. javanica Kütz. – 3, basal portion of filament; 4, middle portion showing cells dividing; 5, older, upper portion. C. aerea (Dillwyn) Kütz. – 6, basal portion of filament; 7, middle portion of filament; 8, upper portion of filament; 9, biflagellate zoid; 10, germling from biflagellate zoid, 5 days old; 11, germling 13 days old.

about as long as broad, but occasionally up to 2 mm long, with thick walls.
- *C. javanica*. Strand-like tuft, attached; each basal cell rhizoidal, clavate, about 250 μm long, 37–70 μm in diameter; upper cells 30–125 μm long, 55–100 μm in diameter, walls thick and lamellate.
- *C. linum*. Plant composed of loosely entangled, unattached filaments, yellowish-green, somewhat stiff and curled, cylindrical or the cells slightly swollen, (0.75–)1–2(–5.0) mm long, 100–375 μm in diameter.

Growth and development The unbranched filaments of *Chaetomorpha* grow quite quickly by intercalary growth. The largest upper cells, however, usually soon form spores or gametes and disintegrate rapidly. The sexual biflagellate isogametes normally fuse to form a zygote, but they can also function as zoospores and germinate to form new haploid filaments.

Other botanical information All cells of *Chaetomorpha* filaments are coenocytic, thus each compartment contains many nuclei.

Ecology *Chaetomorpha* spp. are free-living organisms as well as epiphytes and they also often grow on rocks, boulders, corals and (fragments of) shells. *C. aerea* grows attached to rocks, especially under ledges, in exposed, even surf-beaten locations. This alga is fairly resistant to environmental stress, such as high temperatures, extreme fluctuations in salinity (euryhaline) and desiccation due to lowering of water level. *C. antennina* occurs attached to rocks and shell fragments in the lower intertidal to upper subtidal areas, often in shallow rock pools and lagoons, *C. crassa* in exposed as well as sheltered conditions in intertidal and shallow subtidal areas, and is often entangled with other seaweeds or seagrasses. *C. javanica* forms tufts on rocks, walls and dead coral, while *C. linum* forms entangled masses with other macroalgae in shallow water.
Dense accumulations (mats) of *Chaetomorpha* reduce the oxygen level in water overlying sediments. This reduced condition induces the release of phosphorus from the sediments, which may result in higher productivity of algal mats in fish ponds. *Chaetomorpha* does not grow well on acidic sulphate-enriched soils.

Propagation and planting Optimal growth of *Chaetomorpha* mats in artificial fish ponds can be promoted by careful reclamation of the ponds. It is especially important to reclaim and ameliorate the acidic sulphateenriched soils in mangrove areas to avoid iron, aluminium and manganese toxicity. With proper reclamation P-fertilization might make the production of the algal mats much higher than that in less well reclaimed ponds.

Phycoculture *Chaetomorpha* is only grown as part of algal mats in milkfish cultivation.

Harvesting *Chaetomorpha* is grazed by milkfish. It is hand-collected for use as a salad.

Handling after harvest *Chaetomorpha* is mainly used fresh.

Prospects *Chaetomorpha* will probably be a lasting component of the natural algal mats in traditional fish ponds. The role of the different *Chaetomorpha* in trypsin deficiency in young milkfish has to be studied in more detail. This may result in experiments to manipulate the species composition of the natural algal mats.

Literature |**1**| Benitez, L.V., 1984. Milkfish nutrition. In: Juario, J.V., Ferraris, R.P. & Benitez, L.V. (Editors): Advances in milkfish biology and culture. Island Publishing House Inc., Metro Manila, The Philippines. pp. 133–143. |**2**| Lavery, P.S. & McComb, A.J., 1991. The nutritional ecophysiology of Chaetomorpha linum and Ulva rigida in Peel Inlet, Western Australia. Botanica Marina 34: 251–260. |**3**| Singh, V.P. & Poernomo, A.T., 1984. Acid sulfate soils and their management for brackish water fishponds. In: Juario, J.V., Ferraris, R.P. & Benitez, L.V. (Editors): Advances in milkfish biology and culture. Island Publishing House Inc., Metro Manila, The Philippines. pp. 121–132.

P.Y. van Aalderen-Zen

Chlorella Beij.

Bot. Ztg. 45: 758 (1890).
SELENASTRACEAE
x = unknown

Major species and synonyms
- *Chlorella ellipsoidea* Gerneck, Bot. Centr. 212: 250 (1907).
- *Chlorella pyrenoidosa* Chick, Proc. Roy. Soc. London, Ser. B 71: 458 (1903).
- *Chlorella vulgaris* Beij., Bot. Ztg. 45: 758 (1890), synonym: *Pleurococcus beyerinckii* Artari (1892).

Vernacular names The designation 'Chlorella' is in common use.

Origin and geographic distribution *Chlorella* is ubiquitous and found in both aquatic (freshwater, brackish and marine) and terrestrial habitats, including soil and concrete walls. It is a common contaminant of containers of water left undisturbed for long periods.

Uses In the 1950s *Chlorella* was used as a source of unconventional proteins (i.e. single cell proteins). Presently, the alga is consumed as a health food, and is used in food additives to milk products, fermented soya beans, liquors and other drinks, noodles and cakes. Some marine *Chlorella* spp. are cultured in hatcheries and several are used as aquaculture feed or feed additive, especially as larval diets for shellfish and as diets for living animal feed. *Chlorella* microalgae are often combined with other microalgae because a readily amenable species is not always nutritionally excellent. *Chlorella* extracts have been shown to stimulate biosynthesis of chlorophylls in terrestrial plants. When sprayed onto the fields, these extracts stimulate growth and rooting of fruit trees, vegetables, rice and turf grass in golf links. These extracts were approved as a growth-regulating agent by the Japanese Plant Growth Regulator Research Association in 1984.

Certain strains of *Chlorella* develop many red or orange pigments in a nitrogen-limited and/or hypersaline culture medium. This is mainly due to the accumulation of the red carotenoid pigment astaxanthin. These strains can be used as an effective feed supplement for pigmentation of cultured fish and shellfish. *Chlorella* spp. can be cultivated in combination with treatment of agro-industrial waste water.

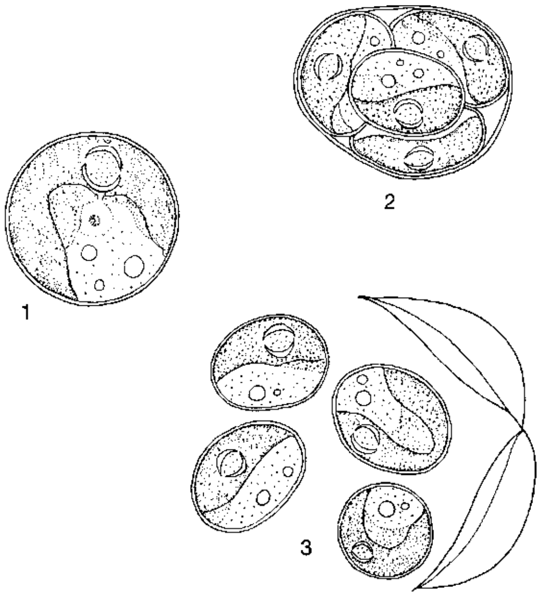
Many health-promoting effects of *Chlorella* have been suggested. These include therapeutic efficacy for gastric ulcers, wounds, constipation, leucopenia, anaemia, hypertension, diabetes, infant malnutrition and neurosis. All these effects have been validated by clinical tests and may be attributable to composite effects not only of nutritive components such as vitamins, minerals, dietary fibres and proteins, but also to a preventive action against artheriosclerosis and hypocholesterolemia by glycolipids and glycoproteins, peptides, nucleotides and related compounds. Many of the claims, however, are still not fully backed up by detailed scientific and medical research, making the claims rather controversial.

Production and international trade A first pilot plant of *Chlorella* mass culture was constructed in the United States, in 1951. The first commercial plant was established in Japan around 1960 and Taiwan in 1964. In 1977, there were 48 large-scale *Chlorella* factories in Asia, with a combined production of more than 1000 kg of dried alga per month. After that period, however, many plants closed down due to a glut of *Chlorella* production. In the same period a photosensitization disease affected those who ingested *Chlorella* tablets, prepared with ethanol and water from *Chlorella* biomass that had not been subjected to health treatment at the time of harvest. Most probably, chlorophyllases that remained intact induced the formation of photosensitizing pheophorbides. Heat treatment at harvest and a dry tablet-making method (without using ethanol) have solved this problem. However, a successful algal production factory for *Chlorella* powder in Peninsular Malaysia closed down in that period because of a collapsing *Chlorella* market. Today, *Chlorella*-based health food is being produced and marketed mainly by more than 70 companies in Japan under various trade names (e.g. 'Sun Chlorella' and 'Albeille d'Or').

The total quantity of *Chlorella* powder traded in Japan in 1996 was about 2000 t dry weight, which included 30 t from Indonesia and 900 t from Taiwan. In Taiwan the total production of *Chlorella* powder is about 1600 t. In eastern Java, Indonesia, a Japanese health food company has built a plant which will have a future annual production of 300 t. *Chlorella* spp. are already extensively grown in large quantities using fermentation techniques in Japan and Korea.

Properties Per 100 g edible portion (dry weight basis) *C. vulgaris* contains: protein 51–58 g, fat 14–22 g, carbohydrates 12–17 g, nucleic acids 4–5 g and ash 6–15 g. The major amino acids (% of total protein nitrogen) are glutamate (7.8%), arginine (15.8%), lysine (10.2%), alanine (7.7%), leucine (6.1%) and valine (5.5%). The dominant fatty acids (% of total fatty acids) in *C. vulgaris* are 18:1 (25%), 18:2 (29%) and 18:3 (14%). However, the fatty acid biosynthesis changes under different concentrations of KNO_3 or NH_4Cl. *Chlorella* contains chondrillasterol as well as other sterols. The chlorophyll-*a* content of *Chlorella* ranges from 0.3–2.0% (dry weight basis), and the chlorophyll *a*/*b* ratio ranges from 2–3. Total carotenoid content averages 0.2% (dry weight basis), with lutein making up 50% of the total content. Other carotenoids produced include violaxanthin, neoxanthin, α-carotene and β-carotene. Vitamin B_{12} can be isolated from *Chlorella* spp. Chemical components of the cell wall in *Chlorella* include sporopollenin (a carotenoid polymer) and sugars such as glucose, mannose and glucosamine.

Environmental conditions greatly affect the chemical composition of *Chlorella*. Fat or carbohydrate content may increase 2–3-fold at the expense of protein in some species when the cells are nitrogen-starved.



Chlorella vulgaris Beij. – 1, vegetative cell; 2, sporangium with autospores; 3, discharge of autospores.

Description Cells usually small, 2–12 μm long, either spherical (with ratio of the two axes equalling 1) or ellipsoidal (with ratio of the long axis to the shortest axis of 1.45–1.60). Chloroplasts parietal, adhering to the cell wall and covering most of the periphery, saucer-, band-, cup- or mantel-shaped. Pyrenoids common in some species. Only asexual reproduction is known.

- *C. ellipsoidea*. Cells ellipsoidal, sometimes asymmetrical; chloroplast forming a folded plate covering part of the cell wall; vegetative cells 9–9.5 μm long, 7–8 μm in diameter.
- *C. pyrenoidosa*. Similar to *C. vulgaris* but cells smaller, 3–5 μm in diameter.
- *C. vulgaris*. Cells always spherical, 4–10 μm in diameter, with cup-shaped chloroplasts; single pyrenoid occasionally present.

Growth and development Reproduction in *Chlorella* is asexual, producing 4, 8 or sometimes 16 autospores which are released by rupture or dissolution of the parental walls. Spores are not motile. Both light and temperature affect cell division; high light intensity and high temperatures are favourable.

Other botanical information The taxonomy of *Chlorella* is subject to much controversy. It is often difficult to classify *Chlorella* spp. based solely on morphology. Recently, molecular techniques have been used to sort out the taxonomic confusion, resulting in the transfer of former *Chlorella* spp. to classes other than the green algal *Trebouxiophyceae*. This classification, however, is still far from being generally implemented.

Ecology There are both mesophilic and thermophilic strains of *C. pyrenoidosa*, with temperature optima for growth ranging from 25–26°C and 38–39C, respectively. Certain freshwater *Chlorella* spp. can tolerate a salinity of 30‰.

Propagation and planting *Chlorella* grows well in most inorganic media (e.g. Bold's, Knop) using NO_3^-, NH_4^+ or urea as a nitrogen source. The cultures are bubbled with air enriched by 5% CO_2 to enhance growth. Growth and biomass production can be further enhanced by adding organic carbon sources such as glucose and acetate. Some species are capable of growing in the dark with organic carbon supplementation under heterotrophic conditions. Stock cultures can be maintained on 2% agar slants. Illumination by fluorescent lamps can be continuously or intermittently (normally 12:12 hours light-dark cycle) supplied at an intensity of 34–50 μmol photon m^{-2} s^{-1}. Micronutrients required for the growth of these green microalgae are Mn, Fe, Zn, Cu, and occasionally also Mo. These micronutrients are particularly essential for autotrophic growth, less so for heterotrophic growth.

Phycoculture Mass cultures of *Chlorella* are carried out in round (diameter 36–50 m), shallow, concrete ponds agitated by rotating arms in the centre. The Japanese *Chlorella* factory in East Java has 16 open-air ponds of 36 m in diameter. To increase the biomass yield, the cultures are supplemented with CO_2, acetic acid or glucose. These algae can also be grown in high-rate algae ponds, which consist of an open and very shallow raceway mixed by paddle wheels. These are capable of producing very high yields.

In recent years, *Chlorella* has also been grown in fermentors or in combinations of fermentors and tubular photobioreactors for continuous sequential heterotrophic/autotrophic production of biomass, and the yield attained can be 10 times higher than in open cultures. The closed systems can solve contamination problems but due to cost constraints, they are only economically feasible for the production of high-value chemicals. There is an optimum cell density in each culture for obtaining best growth yield in sunlight; above this concentration, the yield decreases due to increased respiration and limitation by light saturation.

Growth in photobioreactors was studied in several cases with different *Chlorella* spp. The effect of the inclination of flat plate reactors on productivity of outdoor cultures has been studied in Singapore for *C. pyrenoidosa*. The productivity was not much influenced, but the findings of the researchers cannot yet be generalized. Other forms of bioreactors in which *Chlorella* spp. can be grown are tubular bioreactors, which may be able to be placed in vertical 'biocoil' facilities. The cost of dry product obtained in these closed systems is usually higher than that of open air systems, although contamination problems and thus maintenance costs of the cultures are less. Costs of heterotrophically grown algal biomass, however, are usually much lower than that of autotrophic cultivation.

Diseases and pests Contamination of open air cultures of *Chlorella* by other microalgae is a general problem.

Harvesting The cultures of *Chlorella* are pumped out of the pond and undergo repeated centrifugation and washing. This is generally a costintensive stage of microalgae cultivation. The algae are concentrated 50–200-fold, giving an algal slurry of 5–15% dry weight. Combined algal production and fish culture, especially together with waste-treatment systems, are successful especially because the low capital and maintenance costs are in these cases enhanced by the elimination of harvesting problems as the algae are utilized in situ by fish.

Yield The concentration of *Chlorella* biomass in open-pond cultures ranges from 1–5 g/l, while daily productivity varies between 15–40 g/m^2, due to seasonal changes in light, temperature and salinity.

Handling after harvest The *Chlorella* slurry is dehydrated after which the algal cell walls are broken by physical disintegration and kept at low temperature. A new insect-detection immunoassay is available to assess insect contamination of the yield. The concentrates are spray-dried to produce *Chlorella* powder, which is moulded into tablets by a direct press machine.

Genetic resources Maintenance of *Chlorella* strains is very important for the future of commercial cultivation of microalgae. It is not only sufficient that the organisms be preserved, but also important that the special and unique characters of the strains be maintained, in order to ensure that the strain is genetically stable. Cryopreservation of *Chlorella* cultures allows longterm preservation of frozen algae with no significant reduction of viability for up to 22 years of storage. Recently developed recombination and transformation techniques for *Chlorella* have potential use in direct commercial application.

Prospects Research on the culture of *Chlorella* using agro-industrial wastes has been carried out in various parts of Asia. Apart from treating the wastes, the biomass generated can be used as a high-quality animal feed. Research in Malaysia showed that high biomass concentration and efficient removal of pollutants such as ammonia and phosphate as well as lowering of Chemical Oxygen Demand (COD) can be achieved by growing *C. vulgaris* in high-rate algal ponds treating rubber effluent or palm-oil mill effluent. The microalgae can also concentrate heavy metals in industrial waste water. Thus, the use of *Chlorella* to treat wastes appears to be a prospective area that deserves more intensive research in the coming years.

Literature |**1**| Huss, V.A.R., Frank, C., Hartmann, E.C., Hirmer, M., Kloboucek, A., Seidel, B.M., Wenzeler, P. & Kessler, E., 1999. Biochemical taxonomy and molecular phylogeny of the genus Chlorella sensu lato (Chlorophyta). Journal of Phycology 35: 587–598. |**2**| Kamiya, A. & Miyachi, S., 1982. General characteristics of green microalgae: Chlorella. In: Zaborsky, O.R. (Editor): CRC Handbook of biosolar resources. Vol. 1(2). CRC Press, Boca Raton, United States. pp. 25–32. |**3**| Ogbonna, J.C., Masui, H. & Tanaka, H., 1997. Sequential heterotrophic/autotrophic cultivation – An efficient method of producing Chlorella biomass for health food and animal feed. Journal of Applied Phycology 9: 359–366 |**4**| Oh-Hama, T. & Miyachi, S., 1988. Chlorella. In: Borowitzka, M.A. & Borowitzka, L.J. (Editors): Micro-algal biotechnology. University Press, Cambridge, United Kingdom. pp. 1–26. |**5**| Shihira, I. & Krauss, R.W., 1965, Chlorella: physiology and taxonomy of forty-one isolates. Port City Press, Baltimore, Maryland, United States. 92 pp. |**6**| Takeda, H., 1991. Sugar composition of the cell wall and the taxonomy of Chlorella (Chlorophyceae). Journal of Phycology 27: 224–232.

S.-M. Phang

Chnoospora J. Agardh

Övfers. Förh. Kongl. Svenska Vetensk.-Akad. 4: 7 (1847).

CHNOOSPORACEAE

x = unknown

Major species and synonyms

- *Chnoospora implexa* J. Agardh, Spec. gen. ord. alg. 1: 172 (1848).

- *Chnoospora minima* (Hering) Papenf., J. S. Afr. Bot. 22: 69 (1956), synonyms: *Fucus minimus* Hering (1841), *Chnoospora pacifica* J. Agardh (1847), *C. fastigiata* J. Agardh (1848).

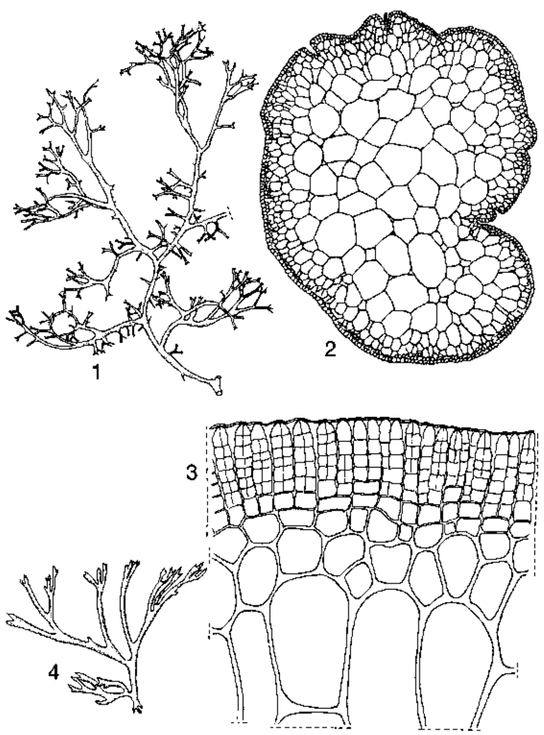
Origin and geographic distribution *Chnoospora* is widely distributed in tropical seas. In South-East Asia both species occur in Vietnam, Indonesia, the Philippines, and Papua New Guinea. Additional records for *C. minima* (as *C. pacifica*) are from Burma (Myanmar) and Malesia. Especially *C. implexa* is often abundant during the calm and warmest months.

Uses *Chnoospora* is used as human food, especially in salads.

Properties Extracts of *C. implexa* show slight antimicrobial activity against *Streptococcus* bacteria.

Description Plants of moderate size, attached by discoid holdfast, bushy; branches solid, subterete to compressed; medulla colourless, consisting of large parenchymatous cells; cells decreasing in size towards the surface; cortex of small, pigmented, angular cells, each with one chloroplast with a conspicuous pyrenoid; fertile areas often contiguous or merging, composed of numerous short, crowded, uniseriate or biseriate, filamentous plurilocular zoidangia around tufts of uniseriate, unbranched, colourless hairs in pits. Unilocular zoidangia unknown.

- *C. implexa*. Thalli erect, up to 20 cm tall, laxly branched, somewhat cushion-like, dark brown to yellowish-brown; branching irregularly alternate-dichotomous, forming wide angles (about 90°) and rounded axils; branches terete, abruptly decreasing in diameter and length from the primary axes to the terminal branchlets; the apical ones finer, distinctly bifurcate and attenuate.
- *C. minima*. Thalli erect, about 20–25 cm tall, more or less regularly dichotomously branched and not entangled, yellowish-brown; branches about 1 mm broad, subcylindrical, compressed at the joints, with numerous tufts of colourless hairs arising from superficial depressions; ultimate branchlets short with acute apices.



Chnoospora. C. implexa J. Agardh – 1, habit; 2, transverse section; 3, transverse section with gametangia. C. minima (Hering) Papenf. – 4, habit.

Growth and development The life cycle of *Chnoospora* is not yet fully understood, although it is known that the plurilocular zoidangia produce swarmers which can develop parthenogenetically into filamentous and disciform germlings. In turn these discs can form upright parenchymatous macrothalli again.

Ecology *C. implexa* occurs in the subtidal zone, attached to solid substrate on portions of reef flat just submerged at low tide which are exposed to moderate water movement. It is abundant during the summer months when it may form blooms closely associated with other species. *C. minima* occurs on intertidal rocks that are permanently wetted by wave action. In stormy seasons only small thalli and discs of this perennial alga survive, able to form new populations in quieter seasons.

Propagation and planting No phycoculture of *Chnoospora* is known.

Harvesting *Chnoospora* is only hand-collected from natural populations for direct local use.

Handling after harvest *Chnoospora* is sold and used fresh.

Prospects As long as *Chnoospora* spp. remain abundant along the coasts in the summer months they will be used as an ingredient in salad dishes.

Literature |1| Fotos, S.S., 1981. Observations on Chnoospora minima (Hering) Papenfuss (Phaeophyta, Scytosiphonales) in the field and in culture. Japanese Journal of Phycology 29: 101–108.

G.C. Trono Jr

Cladophora Kütz.

Phycol. general.: 262 (1843).
CLADOPHORACEAE
x = unknown; $2n$ = 12, 18, 24, 30

Major species and synonyms *Cladophora* is considered to be taxonomically very difficult and it has not been studied in detail for South-East Asia. Names that have frequently been recorded are *Cladophora albida* (Nees) Kütz. (1843), *C. pellucida* (Huds.) Kütz. (1843), *C. prolifera* (Roth) Kütz. (1843), *C. sericea* (Huds.) Kütz. (1843), *C. socialis* Kütz. (1849) and *C. vagabunda* (L.) Hoek (1963). These names, however, must be regarded as uncertain and preliminary and cannot be used as reliable bases for additional data.

Vernacular names Philippines: lumot, lumot jusi.

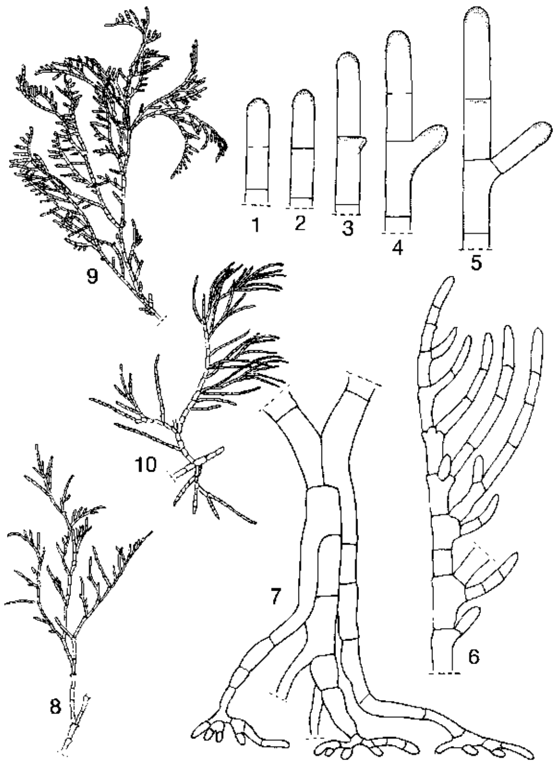
Origin and geographic distribution Approximately 150 species of *Cladophora* have been recorded worldwide. Many of these are marine algae, but several occur in freshwater. *Cladophora* is widespread over the whole globe, although it is virtually absent in polar waters.

Uses In 1974 *Cladophora* was listed as one of the few marine algae cultivated in South-East Asia. This was in relation to milkfish cultivation, where members of *Cladophora*, together with *Chaetomorpha* spp. were cultivated and fertilized to be used as feed for fish. Young milkfish and milkfish larvae mainly feed on epiphytic microalgae ('lab-lab' in Filipino and 'kelekap' in Indonesian) growing on and between the filamentous algae (see under *Chaetomorpha* spp.). Mature milkfish also eats the green filaments. *Cladophora* spp. are also used for animal feed and as a fertilizer. Some *Cladophora* spp. are known to have antibacterial and antiviral properties, whereas others have been used in Korea since the 6th century to make and strengthen paper. The algae are washed and dried until clean before they are pressed in paper processing, resulting in thin green stripes on the paper; this paper is mostly used for calligraphy.

Production and international trade There are no data available yet on the commercial use of *Cladophora*, although these algae are successfully cultured in fish ponds in the Philippines and Indonesia.

Properties *Cladophora* cell walls have a high cellulose content (up to 70%) and the cells contain almost 25% protein (dry weight basis). Some *Cladophora* spp. produce acid mucilages, which are documented as containing 20% sulphuric acid and a galactan sulphate known as cladorphorin. This compound contains acid-resistant polyuronide groups in the molecule and it is difficult to hydrolyse. Hydrolysis of *Cladophora* biomass yields arabinose, galactose, xylose, rhamnose and glucose; these sugars are present in relative molecular proportions of approximately 16:12:4:2:1. Bromine and glycine betaine are also found in *Cladophora*. *C. rupestris* (L.) Kütz., a species not yet recorded for South-East Asia, is known to contain acrylic acid which shows antibacterial activity.

Description Plants filamentous, sparingly to repeatedly branched, attached by rhizoidal extensions from the lower cells, the filaments spreading over the substratum and often giving rise to new erect shoots; growth primarily apical; chromatophores reticulate, with many pyrenoids or



Cladophora. C. vagabunda (L.) Hoek – 1–5, apical portion of thallus with pattern of apical growth and branching; 6, apical portion of thallus with developing branches; 7, base of plant, showing rhizoidal attachment. C. albida (Nees) Kütz. – 8,9, two different morphologies of apical portions of thalli. C. sericea (Huds.) Kütz. – 10, apical portion of thallus.

separate disks, and numerous nuclei in each cell. Life cycle haplontic or diplo-haplontic and isomorphic.

Growth and development Both asexual and sexual reproduction take place in *Cladophora*. Asexual zoospores arise within the vegetative cells in large numbers, and escape through a round orifice; these swarmers have four cilia. The sexual gametes arise in the same way; they have two cilia and show a red spot. The gametes conjugate in pairs (isogamy), and form a zygote which at once begins to germinate into a vegetative thallus similar to the mother plant. In some *Cladophora* spp. a chain of cells, endowed with thicker walls and denser granular contents, separates off and becomes a cyst which, after a period of rest, grows out into a new frond.

Other botanical information Recent data have made clear that *Cladophora* is of paraphyletic nature and cannot be regarded as a natural genus. Nobody, however, has yet proposed a more satisfactory classification.

Ecology *Cladophora* spp. mainly occur attached to rocky substrates, but a few can form extensive, free-floating masses in more or less stagnant, eutrophic waters, such as coastal lagoons or freshwater ponds. Usually *Cladophora* spp. occur in shallow waters, but some have been dredged from depths of up to 55 m, whereas a few of them are capable of surviving considerable fluctuations in salinity. Annual as well as perennial *Cladophora* spp. occur.

Propagation and planting Tufts or mats of *Cladophora* spp., mixed with *Chaetomorpha* spp. and many epiphytic and epipsammic microalgae are transferred to new fish ponds to promote growth of milkfish feed.

Phycoculture When necessary, commercial fertilizers are added to the tufts and mats of *Cladophora* in the fish ponds.

Harvesting *Cladophora* algae in fish ponds are mainly harvested by the fish. Thick mats can be thinned and the surplus material can be used as feed for animals or as a fertilizer.

Handling after harvest The surplus material of *Cladophora* can be used fresh as well as air-dried and cut into pieces.

Prospects *Cladophora* will be a lasting component of the natural algal mats in traditional fish ponds used for milkfish culture.

Literature |1| Ballantine, D.L., Gerwick, W.H., Velez, S.M., Alexander, E. & Guevara, P., 1987. Antibiotic activity of lipid-soluble extracts from Caribbean marine algae. Hydrobiologia 151/152: 463–469. |**2**| Benitez, L.V., 1984. Milkfish nutrition. In: Juario, J.V., Ferraris, R.P. & Benitez, L.V. (Editors): Advances in milkfish biology and culture. Island Publishing House Inc., Metro Manila, The Philippines. pp. 133–143. |**3**| Blunden, G., Gordon, S.M., McLean, W.F.H. & Guiry, M.D., 1982. The distribution of possible taxonomic significance of quaternary ammonium and other Dragendoff-positive compounds in some genera of marine algae. Botanica Marina 24: 563–567. |**4**| Van den Hoek, C., Stam, W.T. & Olsen, J.L., 1992. The Chlorophyta: systematics and phylogeny. In: Stabenau, H. (Editor): Phylogenetic changes in peroxisomes of algae. Phylogeny of Plant Peroxisomes. University of Oldenburg, Germany. pp. 330–364.

P.Y. van Aalderen-Zen

Codium Stackh.

Ner. britan.: 16, 24 (1797) [1795-1801].

CODIACEAE

x = unknown; Atlantic *C. tomentosum*: $2n = 20$

Major species and synonyms

- *Codium arabicum* Kütz., Tab. phycol. 6: 35, pl. 100. fig. 2 (1856), synonyms: *C. coronatum* Setchell (1926), *C. coronatum* var. *aggregatum* Børgesen (1940).
- *Codium bartlettii* C.K. Tseng & W.J. Gilbert, J. Wash. Acad. Sci. 32: 291–293, figs 1, 2a (1942).
- *Codium edule* P.C. Silva, in Egerod, Univ. Calif. Publ. Bot. 25: 392, Pl. 35b, fig. 18 (1952).
- *Codium geppiorum* O.C. Schmidt (as *C. geppii*), Bibl. Bot. 23 (91): 50, fig. 33 (1923), synonym: *C. divaricatum* A. Gepp & E. Gepp (1911).
- *Codium harveyi* P.C. Silva, in P.C. Silva & Womersley, Austr. J. Bot. 4: 277, fig. 11, Pl. 2 (1956).
- *Codium intricatum* Okamura, Icon. Jap. alg. 3: 74, pl. 120: figs 9–13 (1913) [1913–1915].
- *Codium ovale* Zanardini, Nuovo Giorn. Bot. Ital. 10: 37 (1878).
- *Codium papillatum* C.K. Tseng & W.J. Gilbert, J. Wash. Acad. Sci. 32: 293–295, figs 2b–d, 3 (1942).
- *Codium tenue* (Kütz.) Kütz., Tab. phycol. 6: 33, pl. 95, fig. 1 (1856), synonym: *C. tomentosum* (Huds.) Stackh. var. *tenue* Kütz. (1849). In the area covered here this is probably a misapplied name (including specimen names as *C. muelleri* Kütz.) for a yet undescribed species.
- *Codium tomentosum* (Huds.) Stackh., Ner. britan. 24, pl. 7 (1797) [1795–1801], synonyms: *Fu-*

cus tomentosus Huds. (1797), *Ulva tomentosa* (Huds.) DC. (1805). This is an often used, but misapplied name. The species of this name only occurs in Atlantic Europe and North Africa. Most records for South-East Asia probably refer to such species as *Codium bartlettii*, *C. geppiorum* and *C. 'muelleri'*. The likewise misapplied name *C. dichotomum* (Huds.) A. Gray is often cited as a synonym.

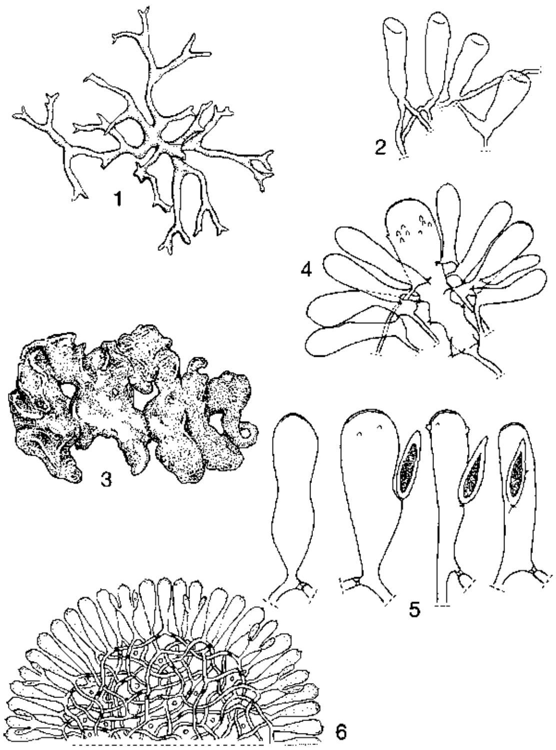
Vernacular names General: Codium. Philippines: pupuklo, pocpolo, kinkintal.
- *C. arabicum*. Vietnam: rong-nhung arab.
- *C. geppiorum*. Indonesia: donge-donge (Sulawesi). Vietnam: rong-nhung gepp.
- *C. 'muelleri'*. Philippines: popoklo (Ilocos), siling-siling, singling-singling (Visayas, Cebu).
- *C. 'tenue'*. Philippines: pupu-lo. Vietnam: rong-nhung min.
- *C. 'tomentosum'* (probably mainly *C. geppiorum*). Indonesia: susu lopek (Lombok), laur laur (Sulawesi). Philippines: ampalang. Vietnam: rong-nhung lông.

Origin and geographic distribution The 50–80 known species of *Codium* occur worldwide in tropical and warm temperate coastal waters, although a few species are known from colder waters. The distribution of the species listed (mainly in South-East Asia) is as follows: *C. arabicum* occurs in the Indian and Pacific Oceans; in South-East Asia in Burma (Myanmar), Thailand, Malaysia, Singapore, eastern Indonesia, the Philippines and the northern and southern coast of Papua New Guinea. *C. bartlettii* occurs in the Indian and Pacific Oceans; in South-East Asia in Indonesia (Sulawesi) and the Philippines. *C. edule* occurs in the Indian and Pacific Oceans; in South-East Asia in Indonesia (Sulawesi), the Philippines and the northern coast of Papua New Guinea. *C. geppiorum* occurs in the Indian and Pacific Oceans, throughout South-East Asia, and the northern coast of Papua New Guinea. *C. harveyi* occurs in Australia and New Zealand; in South-East Asia, it has been recorded in Indonesia (Sulawesi). *C. intricatum* occurs in the Pacific Ocean mainly in Japan; in South-East Asia it has been recorded in the Philippines. *C. ovale* is mainly recorded from the Indian Ocean, in the Pacific Ocean from the Marshall Islands; in South-East Asia it has been recorded in Malaysia, eastern Indonesia, the Philippines (Mindoro) and the southern coast of Papua New Guinea. *C. papillatum* was originally described from Mindoro (the Philippines), and has also been recorded in India, Kuwait and China. *C. 'tenue'* is restricted to river estuaries of South Africa. The recorded specimens from the Philippines, Indonesia and Papua New Guinea probably belong to another (not yet described) species. *C. 'tomentosum'* has been misapplied in naming specimens from Malaysia, Singapore, Indonesia and the Philippines.

Uses In South-East Asia especially *C. arabicum*, *C. bartlettii*, *C. edule*, *C. geppiorum*, *C. intricatum*, *C. 'muelleri'*, *C. ovale*, *C. papillatum*, *C. 'tenue'*, and *C. 'tomentosum'* are used, mainly in human food. *C. bartlettii*, *C. geppiorum* and *C. edule* in particular are eaten in Malaysia, Indonesia and the Philippines. They are either dried and preserved in ash or salt to be boiled in water to prepare soup or, alternatively, after washing or soaking in freshwater, the fresh or dried algae are mixed with soya bean sauce and vinegar to be eaten in salads. For the latter the algae must not be cooked or blanched, for they become soft and disintegrate quickly with heat. In Vietnam and Thailand several of these *Codium* spp. are listed as 'algae of potential use', while in the Philippines especially *C. edule* has the potential to be widely used. Other uses of *Codium* in South-East Asia are in animal feed, as an insect repellant and as a vermifuge (anthelmintic properties). In Chinese herbal medicine *Codium* powder is used as a treatment against urinary diseases and dropsy.

Properties Anthelmintic, antibacterial and antitumour properties have been recorded for *Codium*. Extracts of *Codium* spp. have shown some antibacterial activity against the growth of *Staphylococcus* and *Streptococcus* bacteria. The structural fraction of the cell walls in these algae consists of a mannan, while the amorphous matrix fraction is for the greater part arabinogalactan. In several *Codium* spp. a rich source of haemagglutinins (lectins) occurs. Some of these N-acetyl-α-D-galactosamine-binding lectins are now available commercially.

Description Mature thalli uncalcified, green, spongy, attached to the substrate by a disk or rhizoids over an extensive or limited area; unbranched (crustose, globular, foliose) or branched (repent, ascendent or erect); branching dense or lax, regularly or irregularly dichotomous or trichotomous; branches uniformly terete or (partly) compressed especially at the dichotomies; height varying from several mm in crustose species to about 1 m, in other regions even larger. Anatomically divisible into a central medulla, composed of intertwined siphonous filaments, and a single-layered cortex, composed of a surface layer of inflated photosynthetic vesicles (utricles). Dissociated fila-



Codium. C. bartlettii C.K. Tseng & W.J. Gilbert – 1, habit; 2, utricles. C. arabicum Kütz. – 3, habit; 4, cluster of utricles. C. geppiorum O.C. Schmidt – 5, utricles. Codium sp. – 6, diagrammatic cross-section of a thallus branch.

mentous stages occurring independently, forming a fibrous mat of siphonaceous, irregularly-branched filaments, often with young button-like growth of spongy differentiated thalli. Utricles in the spongy stages individual or in clusters, of various shapes and sizes, mostly clavate or cylindrical, but also capitate, obpyriform, orbiculate or wedge-shaped, with truncate, rounded, depressed, acute or mucronate apices, often bearing colourless hairs or hair scars; utricular wall mostly slightly or markedly thickened at the apices. Chloroplasts homoplastidic, without pyrenoids. Life cycle diplontic. Gametangia borne laterally on utricles, mostly oval, fusiform or elliptical, discharging anisogametes apically.

– *C. arabicum*. Thalli olive to dark green, crustose, not branched but with irregular lobes up to 10 cm long, 1–5 cm broad, tightly adhering to the substrate, becoming convoluted with age and developing orbicular, foliose excrescences 1–3 cm in diameter. Utricles in clusters; large primary utricles (sub)cylindrical to clavate, (700–)990–1120(–1300) µm long, (80–)180–230(–390) µm in diameter; hair scars common on older utricles (up to 20 per utricle); gametangia fusiform to elliptical.
– *C. bartlettii*. Thalli deep green to green-brown, erect, up to 18 cm tall, repeatedly irregularly subdichotomous-divaricately branched with very broad angles; branches terete to complanate, compressed at the dichotomies; branches adhering to each other at some points by cushion-like rhizoidal structures. Utricles individual, clavate or (sub)cylindrical, (400–)600–900(–1200) µm long, (60–)130–300(–600) µm in diameter; hairs common (1–10 per utricle); gametangia elliptical.
– *C. edule*. Thalli green to green-brown, repent, irregularly dichotomously branched; branches terete, 2–4 mm in diameter, intricate, with secondary attachments to the substrate, forming extensive mats up to 25 cm in diameter. Utricles individual, subcylindrical to clavate, (430–)700–900(–1100) µm long, (70–)130–270(–320) µm in diameter; hairs or hair scars usually present (1–10 per utricle); gametangia elliptical to ovoid.
– *C. geppiorum*. Thalli olive to dark green, repent, irregularly divaricately (sub)dichotomous; branches terete, anastomosing, about 3 mm in diameter, attached to the substrate by means of rhizoids at several places. Utricles individual, clavate, elongate obpyriform, (sub)cylindrical or orbiculate, (300–)450–620(–850) µm long, (50–)100–200(–300) µm in diameter in the widest part; hairs or hair scars 0–3(–4) per utricle; gametangia fusiform, with or without a nozzle, 1–2(–3) per utricle.
– *C. harveyi*. Thalli medium green, erect, dichotomous, up to 30 cm tall; branches terete, 3–5 mm in diameter. Utricles individual, short and irregularly swollen, 340–850 µm long, 170–600 µm in diameter, apices broadly rounded; hairs frequent; gametangia elongate-ovoid, 1–4 per utricle.
– *C. intricatum*. Thalli dark green, repent, mat-like, divaricately dichotomous, attached to the substrate by very fine rhizoids; branches short, terete, intricate. Utricles individual, cylindrical or clavate, (100–)120–540(–560) µm long, (80–)90–210(–230) µm in diameter; hairs absent; gametangia unknown.
– *C. ovale*. Thalli dark green, oval to subspherical, fully grown specimens hollow, erect, adhering to the substrate with the pointed part, up to 12–16 mm tall, 10–12 mm wide. Utricles individual,

clavate or (sub)cylindrical, (470–)600–750 (–1050) µm long, occasionally 1060–1220 µm, (155–)230–280(–400) µm in diameter; hair scars absent or occurring in one row at the apices of the utricles; gametangia elliptical to oblong.

- *C. papillatum*. Thalli green, erect, subdichotomous, up to 10 cm tall, arising from a spongy rhizoidal mass; branches of young specimens subterete and becoming complanate when old, dichotomies about 1 cm broad. Utricles individual, subcylindrical or obovoid, some with a few conical papillae, (600–)650–850(–900) µm long, 100–300 µm in diameter, apical wall thickened, 10–33 µm thick, markedly stratified and foveolate; hairs present; gametangia elliptical or ovoid.
- *C. 'tenue'*. Thalli light green, erect, up to 45 cm tall, divaricately (sub)dichotomous, interdichotomies terete, 4–6 mm in diameter, dichotomies compressed. Utricles individual, clavate, obpyriform or cylindrical, (300–)400– 600(–800) µm long, (90–)135–400(–500) µm in diameter; hairs frequently present (1–5 per utricle); gametangia elliptical or ovoid.
- *C. 'tomentosum'*. Thalli dark green, erect, 5–40 cm tall, repeatedly, regularly or irregularly dichotomous; branches terete but occasionally compressed at the dichotomies. Utricles individual, cylindrical, clavate or elongate obpyriform, (450–)600–700(–850) µm long, (80–)100–200 (–300) µm in diameter; hair scars present (1–5 per utricle); gametangia ovoid, elliptical or fusiform.

Growth and development The life cycle of *Codium* is considered to be diplontic, with a zygote developing into a diploid gametophyte; meiosis probably occurs in the gametangia. Male gametangia are yellowish, forming tiny biflagellate male gametes. The female gametangia, however, are dark green and divide into much larger biflagellate gametes, each containing many chloroplasts. *Codium* has traditionally been considered to have gametic meiosis, but the evidence for this is not yet convincing. It has not yet been possible to obtain fully grown spongy plants in culture. Growth of dissociated filamentous stages is possible in laboratory culture.

Other botanical information The *Codium* plants can be regarded as multi-nucleate unicellular organisms, although the coenocytic tubes are subdivided into compartments by rings of cell wall material (perforated cellulosic plugs). Only the gametangia are separated by real cross-walls from the rest of the thallus.

Ecology *Codium* can be epilithic, epipsammic, epiphytic or rarely even epipelic.

- *C. arabicum*. Epilithic, mainly on vertical and overhanging rock walls of reef pools in the lower intertidal zone; epiphytic on stipes of larger seaweeds and on stems of seagrasses in low intertidal or high subtidal zones of sandy lagoons.
- *C. bartlettii*. Epipsammic or epilithic, growing on subtidal coral reefs, down to 10–15 m depth.
- *C. edule*. Growing on reef flats (epilithic), in lower intertidal habitats, and in sandy tide pools (epipsammic).
- *C. geppiorum*. Epilithic on vertical and overhanging rock walls, sometimes epipsammic, in the lower intertidal and subtidal zones.
- *C. harveyi*. In the subtidal zone, down to 30 m depth.
- *C. intricatum*. In the lower parts of the intertidal and subtidal zones, mainly on rocks and overhangs, also on sandy coral substrate.
- *C. ovale*. On subtidal coral reefs or rocks (epilithic), occasionally epipsammic or on the stems of seagrasses in areas well-exposed to moderate to strong water currents. It occurs down to 10–30 m deep.
- *C. papillatum*. On lower intertidal coral reefs.
- *C. 'tenue'*. On reefs (epilithic) or on sandy substrate (epipsammic).
- *C. 'tomentosum'*. Epipsammic or epiphytic on seagrasses (epiphytic).

Propagation and planting *Codium* is not grown in phycoculture.

Harvesting *Codium* is only hand-collected from natural populations.

Handling after harvest *Codium* is sold and used fresh, sun-dried, or preserved in salt or ash.

Prospects Some of the marine algal lectins are much smaller than those derived from land plants. This characteristic alone may make the algal lectins more suitable for uses such as drug targeting, than those derived from land plants, because the smaller molecules might be expected to be less antigenic. This might result in a growing commercial interest in algal lectins, including *Codium* spp.

Literature |**1**| Pramudji, 1992. Seaweeds of the Snellius-II Expedition (East Indonesia): the genus Codium (Chlorophyta, Codiales). MSc. Thesis, Vrije Universiteit Brussel, Belgium. 60 pp. |**2**| Schmidt, O.C., 1923. Beiträge zur Kenntnis der Gattung Codium Stackh. [Contribution to the knowledge of the genus Codium Stackh.]. Bibliotheca Botanica 23 (91): 1–68. |**3**| Silva, P.C., 1952. Codium. In: Egerod, L.E. (Editor): An analysis of the siphonous Chlorophycophyta, with special reference to the Siphonacladales, Siphonales and Dasycladales of Hawaii. University of California Publications in Botany 25(5): 381–395. |4| Tseng, C. & Gilbert, W., 1942. On new algae of the genus Codium from the South China Sea. Journal Washington Academy of Sciences 32(10): 291–296. |5| Van den heede, C. & Coppejans, E., 1996. The genus Codium (Chlorophyta, Codiales) from Kenya, Tanzania (Zanzibar) and the Seychelles. Nova Hedwigia 62: 389–417. |6| Yang, M.-H., Blunden, G., Huang, F.-L. & Fletcher, R.L., 1997. Growth of a dissociated, filamentous stage of Codium species in laboratory culture. Journal of Applied Phycology 9: 1–3.

E. Coppejans, C. Van den heede &
W.F. Prud'homme van Reine

Colpomenia sinuosa (Mert. ex Roth) Derbès & Solier

In: Castagne, Suppl. Cat. pl. Marseille: 95 (1851).

SCYTOSIPHONACEAE

$2n$ = unknown

Synonyms *Ulva sinuosa* Mert. ex Roth (1806), *Asperococcus sinuosus* (Mert. ex Roth) Bory (1832), *Hydroclathrus sinuosum* (Mert. ex Roth) Zanardini (1843).

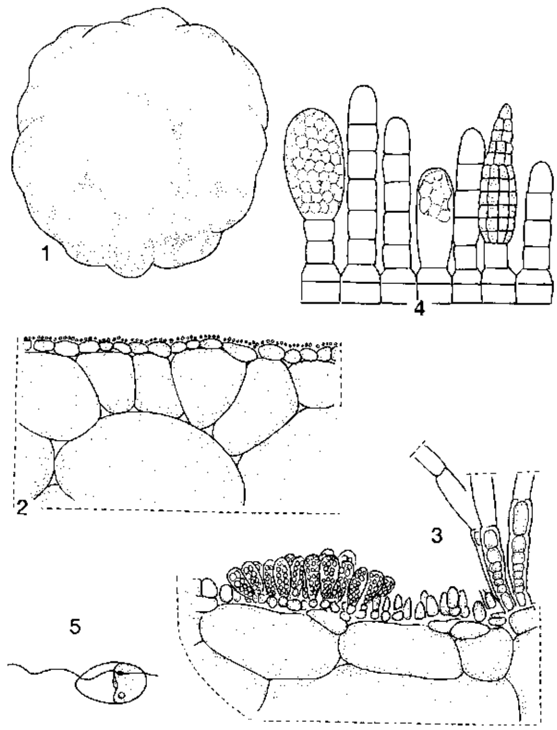
Vernacular names Philippines: tabtaba (Ilocano).

Origin and geographic distribution *C. sinuosa* is cosmopolitan in temperate, subtropical and tropical areas. In South-East Asia it is common in all countries.

Uses *C. sinuosa* is used as human food, as a raw salad vegetable or blanched and then prepared into a salad. It is also used as animal feed and a good source of phenols, vitamins, folic and folinic acids, and amino acids such as alanine, aspartic acid, glutamic acid, glutamine, glycine, serine, threonine, tyrosine and valine. It is also used as a fertilizer and as an indicator of metal pollution.

Properties The sterol composition of *C. sinuosa* is unusual for brown algae, because of its rather low level of fucosterol but high levels of 24-methylene cholesterol and cholesterol. It contains fairly low levels of alginic acid and antioxidant properties have been recorded.

Description Macrothalli yellow-brown, globular, hemispherical, hollow, smooth to irregularly convoluted, expanding with age to 5–10 cm or more in diameter; cross-section of the membrane



Colpomenia sinuosa (Mert. ex Roth) Derbès & Solier – 1, habit; 2, transverse section through thallus; 3, detail of 2, with sorus of plurilocular zoidangia and hairs; 4, diagrammatic section of a sorus with both an unilocular and a plurilocular zoidangium; 5, zoid with an eyespot.

showing cortex of 1–2 layers of small cuboidal or polygonal cells with chromatophores, about 5–8 μm in diameter; medulla with 4–6 layers of colourless cells, irregularly shaped, more or less rounded or polygonal. Plurilocular sporangia biseriate, cylindrical, about 40–50 μm long, 5–6 μm broad, aggregated on the upper surface of the thalli. Infertile hairs rare, usually longer than the sporangia.

Growth and development The life cycle of *C. sinuosa* is an alternation of heteromorphic stages, without any sign of sexuality, with saccate macrothalli forming plurilocular zoidangia only. The swarmers formed by these macrothalli germinate into pseudodiscoidal or filamentous prostrate microthalli, which measure 1–3 mm in diameter in laboratory cultures. On these prostrate microthalli both unilocular and plurilocular zoidangia can develop, depending on culture conditions. Swarmers from these plurilocular zoidangia always grow into similar prostrate microthalli again, but the zoids from unilocular zoidangia grow into small pseudodiscs that become swollen and form the saccate macrothalli again. In this life cycle no sexual stages have been discerned, which differs from the situation in the related *C. peregrina* Sauv., where zoids from plurilocular zoidangia, formed on the macrothalli, can fuse to form zygotes. Thus the plurilocular zoidangia are gametangia in *C. peregrina*. The zygotes develop into prostrate microthalli, on which both unilocular and plurilocular zoidangia can be formed. Thus, in *C. peregrina*, the saccate macrothalli can be considered to be gametophytes, and the prostrate microthalli are sporophytes. Due to parthenogenesis, however, the complete life cycle in *C. peregrina* is more complicated.

Other botanical information It is rather difficult to differentiate *C. sinuosa* from the related *C. peregrina*, which is, however, mainly a temperate alga.

Ecology *C. sinuosa* is commonly found attached to rocky substrate in intertidal areas on reef flats to shallow subtidal zones, subjected to slow to moderate water movement. Its hollow bulbous thalli are generally bigger in size in calm areas than those in wave-exposed areas. The thalli are easily removed from the substrate by strong wave action and may be transported to reef flats or to the shore as drift materials.

Propagation and planting *C. sinuosa* is not grown in phycoculture.

Prospects It can be expected that *C. sinuosa* will also be used in the future by coastal communities for food, animal feed and fertilizer. It might also become a source of pharmaceutical compounds.

Literature |**1**| Kogame, K., 1997. Life histories of Colpomenia sinuosa and Hydroclathrus clathratus (Scytosiphonaceae, Phaeophyceae) in culture. Phycological Research 45: 227–231. |**2**| Kogame, K. & Yamagishi, Y., 1997. The life history and phenology of Colpomenia peregrina (Scytosiphonaceae, Phaeophyceae) from Japan. Phycologia 36: 337–344. |**3**| Silva, P.C., Meñez, E.G. & Moe, R.L., 1987. Catalog of the marine benthic algae of the Philippines. Smithsonian Contributions to the Marine Sciences 27. 179 pp. |**4**| Trono Jr, G.C. & Ganzon-Fortes, E.T., 1988. Philippine seaweeds. Technology and Livelihood Center. National Bookstore Inc., Manila, The Philippines. 330 pp. |**5**| Stefanov, K., Bankova, V., Dimitrova–Konaklieva, St., Aldinova, R., Dimitrov, K. & Popov, S., 1996. Sterols and acylglycerols in the brown algae Colpomenia peregrina (Sauv.) Hamel and Scytosiphon lomentaria (Lyngb.) Link. Botanica Marina 39: 475–478.

G.C. Trono Jr

Dictyopteris jamaicensis W.R. Taylor

Mar. alg. east. trop. subtrop. coasts Amer.: 631, pl. 32, fig. 2 (1960).

DICTYOTACEAE

$2n$ = unknown

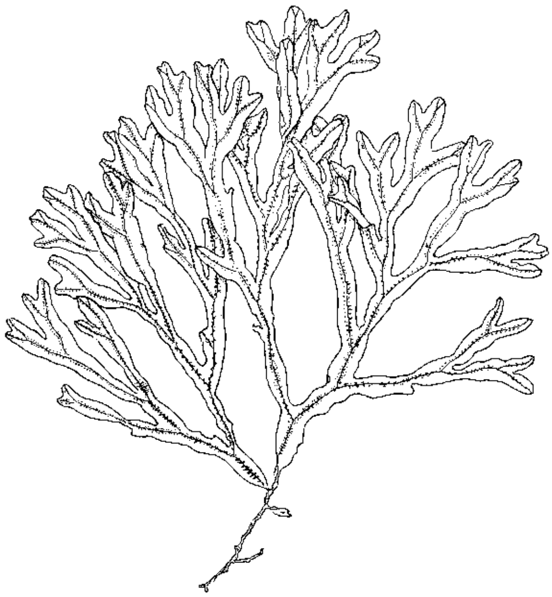
Vernacular names Philippines: laplapayag (also used for *Spathoglossum* sp.).

Origin and geographic distribution *D. jamaicensis* has been recorded in the Atlantic Ocean (Jamaica) and the Pacific Ocean (Polynesia). In South-East Asia it occurs in Indonesia (Sulawesi) and the Philippines (Luzon, Visayas).

Uses *D. jamaicensis* is used as a medicine because of its antitumor activity. It is used as food in eastern Polynesia, and this odoriferous seaweed also contains essential oils that can be used to produce products with 'sea breeze' smell.

Properties Some *Dictyopteris* spp. contain an essential oil with a 'beach odour', consisting mainly of the non-halogenated sesquiterpenes cadalene and cadinene. In other *Dictyopteris* spp. there are non-isoprenoid C_{11} compounds in the essential oil, including cycloheptadienes and dictyopterene as well as a low-viscosity alginate. *D. divaricata* (Okamura) Okamura contains 10 mg/g (dry weight) vitamin C. *D. membranacea* (Stackh.) Batters (as *D. polypodioides* (Desf.) J.V. Lamour.) is used to treat lung diseases and scrofula. *D. undulata* Holmes and *D. divaricata* have been found to be potent inhibitors of bee-venom-derived phospholipase A_2.

Description Thalli composed of subdichotomous branched straps, forming angles of less than 90°, each with a single lens-shaped apical cell. Fronds up to 12 cm tall, dark brown or yellowish-brown, attached by a well-developed holdfast. Straps 4–8 mm across, 2 cell-layers thick, narrowing at distal portion of thallus, with distinct midrib running through entire length of the straps; midrib with polyhedral quadrangular cells in surface view; lateral veins absent; tufts of hairs parallel on both sides of midrib; margin entire to minutely erose-dentate, slightly undulate. Life cycle diplo-haplontic and isomorphic. Tetrasporangia grouped in sori or scattered over the whole of the fronds, each with 4 non-motile tetraspores. Gametophytes dioecious, with oogonia and an-



Dictyopteris jamaicensis W.R. Taylor – habit.

theridia (surrounded by rows of paraphyses) grouped in sori.

Ecology *D. jamaicensis* is generally limited in distribution to rocky wave-exposed habitats such as reef crests and slopes as well as in deeper waters (33–73 m), attached to shells and coral fragments. It usually is firmly attached to hard substrates, although detached thalli may also be found among drifting seaweeds.

Propagation and planting There is no known phycoculture of *D. jamaicensis*.

Harvesting Attached and drifting specimens of *D. jamaicensis* are collected by hand.

Handling after harvest *D. jamaicensis* is mainly used fresh.

Prospects Future studies might result in additional use of *D. jamaicensis* for the production of pharmaceutical compounds. For this purpose and for further potential use as a provider of essential oils it is recommended that commercial cultivation be started.

Literature |1| Katayama, T., 1961. Chemical studies on volatile constituents of seaweed. 16. Their phylogenetic and biochemical significance. Bulletin of the Japanese Society of Scientific Fisheries 27: 75–84. |2| Moore, R.E., 1977. Volatile compounds from marine algae. Accounts of Chemical Research 10: 40–47. |3| Pickenhagen, W., Näf, F., Ohloff, G., Müller, P. & Perlberger, P.C., 1973. Thermal and photochemical rearrangements of divinylcyclopropanes to cycloheptadienes. A model for the biosynthesis of the cycloheptadiene derivatives found in a seaweed (Dictyopteris). Helvetica Chimica Acta 56: 1868–1874.

G.C. Trono Jr

Dictyosphaeria cavernosa (Forssk.) Børgesen

Revis. Forssk. alg.: 2, pl. 1, fig. 1 (1932).

SIPHONOCLADACEAE

$2n$ = unknown

Synonyms *Ulva cavernosa* Forssk. (1775), *Valonia favulosa* C. Agardh (1822), *Dictyosphaeria favulosa* (C. Agardh) Decne. ex Endl. (1843).

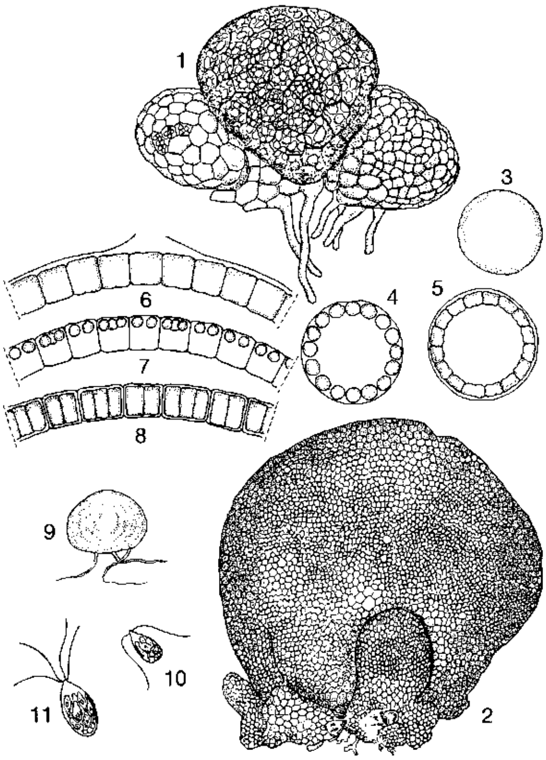
Vernacular names Australia: Green bubble weed (En).

Origin and geographic distribution *D. cavernosa* is widely spread in tropical and subtropical seas all over the world. In South-East Asia this alga is recorded in all countries except Cambodia, Vietnam and Brunei Darussalam.

Uses *D. cavernosa* is used as human food and as an antimicrobial medicine. No toxic effects to eukaryotes are known.

Description Thalli sessile, dark green, hollow, 2–5(–12) cm in diameter, nearly spherical, irregularly lobed or partly collapsed, occasionally concrescent; sometimes rupturing, irregularly saucer-shaped, and in deep water reaching a diameter of 30 cm, attached by irregularly elongated (rhizoidal) cells; thallus surface consisting of a single layer of large angular vegetative cells, 0.1–1(–4.5) mm in diameter; connecting tenacular cells numerous, 35-50 μm × 60–65 μm, lenticular, with simple or bifurcate haptera, often with fimbriate distal margins. Life cycle diplo-haplontic and isomorphic. Sporophytes with quadriflagellate zoospores; male and female gametophytes producing biflagellate isogametes.

Growth and development Isogametes of *D. cavernosa* can also develop parthenogenetically and then form new gametophytic thalli. When young, thalli form hollow spheres which rupture when mature. Isogametes fuse soon after release and the resulting zygotes settle on the substrate, germinating without any delay. Quadriflagellate zoospores, zygotes, and even unfused parthenogametes germinate in a fundamentally identical way after shedding their flagella. They first round up, forming a cell wall within 24 hours, then increase their volume and develop into spherical bodies, which produce some rhizoidal filaments. About three months after germination, segregative cell



Dictyosphaeria cavernosa (Forssk.) Børgesen – 1, habit of a young specimen; 2, habit of a mature specimen; 3, cross-section of an undivided unicellular primary vesicle (diagrammatic); 4,5, formation of secondary vesicles inside the primary vesicle (cross-sections, diagrammatic); 6, the original wall of the primary vesicle has burst; 7, spherical protoplasmatic bodies are formed; 8, tertiairy vesicles have been formed (6,7,8 diagrammatic cross-sections to show formation of tertiairy vesicles); 9, habit of unicellular germling; 10, gamete with 2 flagella and an eyespot; 11, zoospore with 4 flagella and an eyespot.

divisions take place within the unicellular germlings, which are by then 3–5 mm in diameter. First many spherical protoplasmic bodies are formed, which then develop into a layer of polygonal daughter cells that together form the monostromatic mature thalli. These are attached by rhizoidal cells formed by elongation of basal cells.

Ecology *D. cavernosa* is commonly found on rocks and reefs in the intertidal zone, where it is however often poorly developed. A little lower down on the shore it reaches full size, and it has also been recorded at depths of up to 55 m. The composition and texture of the rocky substrate greatly influence communities of this alga. It often grows on white, porous shell remains, which reflect light and have a high waterholding capacity. The alga can penetrate this substrate and then grow in semiprotected niches.

Propagation and planting Phycoculture of *D. cavernosa* is not known.

Harvesting *D. cavernosa* is harvested only by hand-collecting.

Handling after harvest *D. cavernosa* is mainly used fresh.

Prospects The use of *D. cavernosa* as human food is likely to remain limited. Its antimicrobial capacity might be developed in the future.

Literature |**1**| Enomoto, S., Hori, T. & Okuda, K., 1982. Culture studies of Dictyosphaeria (Chlorophyceae, Siphonocladales) II. Morphological analysis of segregative cell division in Dictyosphaeria cavernosa. Japanese Journal of Phycology (Sôrui) 30: 103–112. |**2**| Enomoto, S. & Okuda, K., 1981. Culture studies of Dictyosphaeria (Chlorophyceae, Siphonocladales) I. Life history and morphogenesis of Dictyosphaeria cavernosa. Japanese Journal of Phycology (Sôrui) 29: 225–236.

P.Y. van Aalderen-Zen

Dictyota J.V. Lamour.

J. Bot. (Desvaux) 2: 38 (1809).

DICTYOTACEAE

$2n = 18, 24, 32, 48$

Major species and synonyms

- *Dictyota bartayresiana* J.V. Lamour., J. Bot. (Desvaux) 2: 43 (1809), synonyms: *Dictyota bartayresii* J.V. Lamour. (1809), nom. illeg., *D. patens* J. Agardh (1882), *D. neglecta* Hörnig & Schnetter (1992), non *Dictyota bartayresiana* auct. non J.V. Lamour. sensu Vickers (1908).
- *Dictyota cervicornis* Kütz., Tab. phycol. 9: 8, pl. 17, fig. 1 (1859), synonyms: *Dictyota indica* Sond. ex Kütz. (1859), *D. pardalis* Kütz. (1859).
- *Dictyota ceylanica* Kütz., Tab. phycol. 9: 11, pl. 25, fig. 1 (1859).
- *Dictyota ciliolata* Sond. ex Kütz., Tab. phycol. 9: 12, pl. 27, fig. 1 (1859), synonyms: *Dictyota ciliata* J. Agardh (1841), *D. beccariana* Zanardini (1872).
- *Dictyota crispata* J.V. Lamour., J. Bot. (Desvaux) 2: 44 (1809), synonyms: *Dictyota bartayresiana* auct. non J.V. Lamour. sensu Vickers (1908), *D. apiculata* auct. non J. Agardh sensu Weber Bosse (1913), *D. dentata* auct. non J.V. Lamour. sensu Vannajan & Trono (1978), *D.*

mertensii auct. non (Mart.) Kütz. sensu Trono (1997).

- *Dictyota dichotoma* (Huds.) J.V. Lamour. var. *dichotoma*, J. Bot. (Desvaux) 2: 38 (1809), synonyms: *Dictyota acuta* Kütz. (1845), *D. volubilis* Kütz. (1849).
- *Dictyota dichotoma* (Huds.) J.V. Lamour. var. *intricata* (C. Agardh) Grev., Alg. brit.: 58 (1830), synonyms: *Dictyota divaricata* J.V. Lamour. (1809), *D. dichotoma* (Huds.) J.V. Lamour. var. *implexa* (Desf.) Gray (1821), *D. cirrhosa* Suhr (1839).
- *Dictyota friabilis* Setch., Univ. Calif. Publ. Bot. 12: 91–92 (1926), synonym: *Dictyota ceylanica* Kütz. var. *rotundata* Weber Bosse (1913).

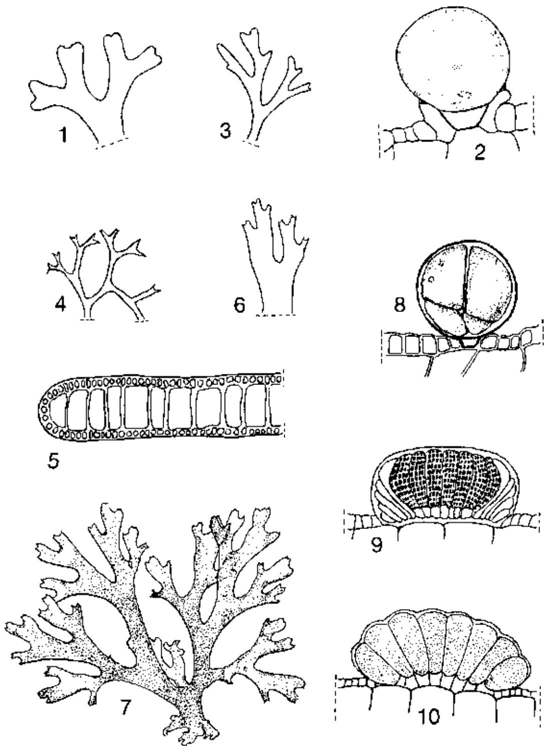
Origin and geographic distribution *Dictyota* is represented in most regions of the world, except around the poles. Species diversity is greater in the tropics than in temperate waters. The highest diversity of *Dictyota* is found in Australia. Approximately 40 different species names are recorded from the Indian Ocean, which however, can be reduced to 23 accepted species. Of those mentioned above, *D. dichotoma* is most often recorded as occurring on almost all coasts of South-East Asia, often together with its variety *intricata*. Because of taxonomic confusion, however, these distributional data (and those for *D. bartayresiana*) are not reliable. Most probably neither *D. dichotoma* var. *dichotoma* nor var. *intricata* do occur in South-East Asia.

Uses The thalli of several *Dictyota* are edible and used in Indonesia (Sulawesi), Malaysia and Thailand. In the Hawaiian Archipelago, *D. acutiloba* J. Agardh is cultivated in 'algal gardens' and sold on local markets. *Dictyota* is either eaten raw or cooked with coconut milk, pickled or preserved by smoke-drying and is very nutritious. Some *Dictyota* are known to have a somewhat bitter taste. Acetone extracts of '*Dictyota dichotoma*' in India showed synergism with a number of insecticides used to kill mosquito larvae. This synergism may be due to inhibition of some detoxifying enzymes in mosquito larvae by the algal extract. If this acetone extract can be combined with synthetic insecticides, it will result in reduced consumption of the latter, thus reducing aquatic pollution.

Properties Like most brown algae *Dictyota* contains alginic acid, an acid membrane mucilage with emulsifying, gelling and thickening properties which is very important on a world scale in a wide variety of industries. *D. bartayresiana* is known to contain a very high percentage of alginic acid: 17–18%. Unfortunately a high alginic acid content is not the only prerequisite for industrial utilization; the size and density of the crops are extremely important as well. Because of its relatively small size *Dictyota* is less attractive for commercial exploitation. The chemical composition of a *Dictyota* sp. identified as '*D. divaricata*' in the Arabian Gulf showed a very low protein content compared to similar studies of *Dictyota* spp. in different Indian Ocean localities: 1.7% of dry weight, compared to 19.8% in India. This may be due to the high salinity of the Arabian Gulf waters. *D. dichotoma* possesses a high folic acid content. Different experiments have proven that lipid-soluble extracts of several *Dictyota* possess antibiotic and antiviral substances (terpenes). The amount of these substances may vary from place to place and may depend on the season. *D. crenulata* J. Agardh was found to be active against a form of lymphocytic leukaemia and tumours. Other *Dictyota*, among which *D. dichotoma*, inhibit the growth of several human pathogenic and phytopathogenic fungi.

Description Thalli composed of dichotomously to irregularly branched straps, each with single lens-shaped apical cell; attachment by rhizoids or stolonoidal fibres. Branching by equal to unequal division of apical cell. One to several layers of large, thick-walled, medullary cells surrounded by single layer of small, pigmented cortical cells, iridescent or not – in dried specimens iridescence lost. Sori of hairs present or absent. Life cycle diplo-haplontic and isomorphic. Sporophyte forming unilocular tetrasporangia each containing 4 non-motile tetraspores; tetrasporangia grouped in sori or scattered over whole or parts of fronds. Gametophytes dioecious; oogonia and antheridia surrounded by one to several rows of paraphyses, grouped in sori.

- *D. bartayresiana*. Thalli erect, forming hemispherical tufts, 8–20 cm tall, attached by numerous patches of rhizoids, straw-coloured, never iridescent, texture somewhat crisp; individual straps up to 10–15 cm long, 5.7–7.3 mm wide, regularly dichotomously branched, branching angle 70–80°, interdichotomies short; margins smooth; surface proliferations absent; hair tufts common. Tetrasporangia scattered on both surfaces of straps, single, not surrounded by a ring of enlarged, sterile cells (involucrum). Gametangia unknown.
- *D. cervicornis*. Growth form very variable; thalli 10–15(–30) cm long, with or without well-developed base, attached by rhizoids, medium brown;



Dictyota. D. cervicornis Kütz. – 1, habit of apical portion of a thallus with truncate apices; 2, section through a young tetrasporangium with an one-celled stalk cell and an involucrum. D. friabilis Setch. – 3, habit of apical portion of a thallus with rounded apices. D. dichotoma (Huds.) J.V. Lamour. var. intricata (C. Agardh) Grev. – 4, habit of apical portion of a thallus with acute apices; 5, cross-section of a branch with one layer of large medulla cells surrounded by one layer of cortex cells. D. crispata J.V. Lamour. – 6, habit of an apical portion of a thallus with apiculate apices; 7, habit. D. bartayresiana auct. non J.V. Lamour. sensu Vickers – 8, section through a tetrasporangium with 4 tetraspores, an one-celled stalk cell and no involucrum. D. ciliolata Sond. ex Kütz. – 9, section of an antheridial sorus surrounded by paraphyses; 10, section of an oogonial sorus.

straps of whole thallus somewhat coarse, often with strongly elongated, linear interdichotomies in erect parts, average width 2.3–3.1 mm; apices truncate to rounded; branching regular dichotomous in lower and middle parts of thalli (branching angle 60–70°), apical parts typically cervicorn (branching angle 70–100°) or with recurved branches; margins smooth, sinuously curved; surface proliferations absent; hair tufts common. Tetrasporangia scattered over both surfaces of straps, not divided, mostly single, never in apical segments, surrounded by involucrum. Gametangia unknown.

– *D. ceylanica*. Growth form ascending, with very intricate appearance; thalli small, 4(–6) cm long, without conspicuous base, attached by rhizoids, medium to pale brown, blue to yellowish iridescent; straps procumbent, repent or erect, mostly filiform but extremely variable in width, (0.2–) 0.8–1.3(–5.8) mm broad; apices acute or rounded; branching mainly regularly dichotomous, branching angle broad divaricate (70–100°); margins smooth; surface proliferations absent, marginal proliferations common and obscuring the original branching pattern; hair tufts common. Tetrasporangia scattered over both surfaces of fronds, often forming a narrow, longitudinal line in the middle of the straps; sporangia rarely divided and not surrounded by involucrum. Only oogonial gametangia sori known, scattered on both surfaces of the straps, with a variable number of oogonia (12–58) per sorus.

– *D. ciliolata*. Growth form completely erect, 8–15 (–25) cm long, with conspicuous stupose holdfast giving rise to single frond of somewhat crisp texture, brown, often with broad transverse banding pattern of slightly iridescent zones alternating with non-iridescent zones; straps in whole thallus of same width, (1.5–) 3.7–9.1(–19.5) mm, width and height being highly variable between different specimens; apices regularly dichotomous or slightly irregularly dichotomous, never alternate, branching angle 35–50°; margins usually dentate, teeth slightly to prominently directed towards the apices, giving rise to marginal proliferations obscuring original branching pattern; surface proliferations absent; hair tufts common. Tetrasporangia scattered over both surfaces of fronds, sporangia without involucrum, divided sporangia frequently observed. Gametangia occasionally observed, evenly distributed over whole frond, also present in the apical segments; female gametangial sori with about 20 oogonia per sorus; male gametangial sori with about 25 oogonia per sorus, surrounded by 3–4 rows of unicellular paraphyses.

– *D. crispata*. Growth form ascending, 9–20(–30) cm long, with small prostrate base giving rise to several stiff, crisp, erect straps, harsh to the touch, brown to pale brown, not iridescent; average width between different specimens extremely variable, (1.0–)4.9–6.4(–22) mm, with anisotomous dichotomous branching, branching angle 30–70°; margins smooth; surface proliferations common to abundant, marginal proliferations absent. Tetrasporangia scattered on both surfaces of straps, single or grouped in small, longitudinal sori often placed in apical segments, involucrum present, sporangia not divided. Both oogonia and antheridia (surrounded by 2–3 rows of pigmented paraphyses) in sori evenly distributed over whole surface of straps.

- *D. dichotoma* var. *dichotoma*. Extremely polymorphic, very difficult to characterize in a single description. Thalli erect, 10–35 cm tall, sometimes spirally twisted, medium brown; main straps 4–10 mm broad, usually with rounded apices; branching regularly dichotomous; margins smooth; proliferations on surface absent; hair tufts common. Tetrasporangia scattered over whole surface, except for a narrow, sterile marginal strip. Sporangia not surrounded by involucrum. Oogonia and antheridia common in Europe.
- *D. dichotoma* var. *intricata*. Similar to var. *dichotoma* but with characteristic long and narrow (1.1–1.8 mm broad) interdichotomies, with acute apices, proliferations on surface very common, often growing into new straps of similar shape. Tetrasporangia always single, dispersed over both surfaces of fronds, absent from apical segments.
- *D. friabilis*. Growth form completely procumbent, forming dense imbricate mats (up to 20–30 cm in diameter), composed of several layers of somewhat brittle (friable) straps, resulting in typical jigsaw aspect; thalli attached by marginal bundles of rhizoids arising from all parts, medium brown, pale bluish iridescent, often with conspicuous non-iridescent longitudinal stripes. Individual thalli small (3–5 cm long), straps with typical short and broad interdichotomies, 2.5–6.4(–11.0) mm broad, branching angle 60–110°; apices rounded to obtuse; margins smooth; marginal proliferations rare, surface proliferations absent; hair tufts common. Tetrasporangia scattered on upper surface of fronds, single, absent from apical segments, not surrounded by involucrum. Gametangia unknown.

Growth and development Most *Dictyota* seem to be common all the year round in the tropical seas. Because of the frequent occurrence of tetrasporangia one would expect an equal number of sporo- and gametophytes in a population. However, gametophytes are rarely found. This leads to the assumption that in many cases no meiosis occurs in the tetrasporangia and that the diploid spores develop to new sporophytes.

Other botanical information A high morphological variability makes identification of species of *Dictyota* very difficult. There has been persistent taxonomic confusion in both *D. bartayresiana* and *D. dichotoma*. Study of the type collections of species described by J.V. Lamouroux has revealed the genuine characters of *D. bartayresiana*. It is often confused with another pantropical species, which proved to be described by Lamouroux as *D. crispata*. Both species are common in South-East Asia.

D. dichotoma, the type species of the genus, is without doubt the most frequently reported species in the genus. It has been recorded in nearly every locality where *Dictyota* spp. occur. A combination of high morphological variability and a lack of distinctive characters makes it difficult to give an accurate and concise description. It has been separated from similar species in the Atlantic Ocean by means of chromosome counts and hybridization experiments. *D. dichotona* probably does not occur at all in South-East Asia. Specimens named as *D. dichotoma* var. *dichotoma* often belong to *D. crispata*, while specimens named as *D. dichotoma* var. *intricata* often belong to *D. ceylanica* or *D. ciliolata*.

In this notoriously variable genus misidentifications are very common. Specimens from the Philippines (and possibly also records from Peninsular Malaysia), identified as *D. dentata* J.V. Lamour. and *D. mertensii* (Mart.) Kütz., most probably belong to *D. crispata*.

Ecology *Dictyota* is very common in the Indo-Malaysian region. Each species is generally found in its own specific biotope; they are most abundant in shallow lagoons, separating the fringing reef from the coast. Healthy free-floating thalli of *D. bartayresiana* often thrive well among large seagrasses.

Propagation and planting There is no phycoculture of *Dictyota*.

Harvesting *Dictyota* is harvested by hand; attached as well as drifting specimens are collected.

Handling after harvest *Dictyota* is mainly used fresh or sun-dried.

Prospects *Dictyota* is only likely to be used in a restricted way for human food. It might become important as a component of insecticides against mosquito larvae and as a provider of fine chemicals and antibiotics.

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3rd Edition. Pacific Tropical Botanical Gardens, Lawai, Hawaii. 35 pp. |2| De Clerck, O., 1999. A revision of the genus Dictyota Lamouroux (Phaeophyta) in the Indian Ocean. Thesis Universiteit Gent, Belgium. 356 pp. + 3 append. |3| De Clerck, O. & Coppejans, E., 1997. The genus Dictyota (Dictyotaceae, Phaeophyta) from Indonesia in the Herbarium Weber-van Bosse, including the description of Dictyota canaliculata spec. nov. Blumea 42: 407–420. |4| Hörnig, I., Schnetter, R. & Prud'homme van Reine, W.F., 1992. The genus Dictyota (Phaeophyceae) in the North Atlantic. I. A new generic concept and new species. Nova Hedwigia 54: 45–62. |5| Subramonia Thangam, T. & Kathiresan, K., 1991. Mosquito larvicidal activity of marine plant extracts with synthetic insecticides. Botanica Marina 34: 537–539.

O. De Clerck, E. Coppejans &
W.F. Prud'homme van Reine

Digenea simplex (Wulfen) C. Agardh

Spec. alg. 1: 389 (1822).

RHODOMELACEAE

$2n$ = unknown

Synonyms *Conferva simplex* Wulfen (1803), *Digenia wulfenii* Kütz. (1843), nom. illeg.

Vernacular names Philippines: bodo-bodo. Japan: kaininso, makuri. China: hairencao (when referring to medicine the name zhegucai is also used, but that is a misapplication of a name originally used for *Caloglossa leprieurii* (Mont.) G. Martens).

Origin and geographic distribution *D. simplex* is recorded from many localities in tropical and warm temperate areas. In South-East Asia it is only recorded from the Philippines (Luzon, Palawan), Indonesia (Tukangbesi Islands, east of Bitung, Sulawesi) and the northern coast of Papua New Guinea.

Uses *D. simplex* is mainly used as an anthelmintic medicine or vermifuge. Its use as a vermifuge was first described in Fujian Province (China) in 1530 A.D. It is the most efficient seaweed used in the treatment of *Ascaris* and *Oxyuris*, as well as whipworm (*Trichuris*) and tapeworm (*Taenia*) because it contains kainic acids. A single dose of 5–10 mg of α- kainic acid is capable of driving out *Ascaris* in adults and no unpleasant side effects have been observed. It can also be used together with santonin, where a synergetic action results in a marked increase of the ascaricidal effect. This algal compound is one of the few 'drugs from the sea' used in orthodox medicine. An extract of *D. simplex* from Asia is on the market under the names 'Helmia' and 'Digenea' for use in the treatment of worms. *D. simplex* also is a source of agar, but because of its small size and low agar content it is unlikely to gain any commercial importance.

Production and international trade The centre of collection of *D. simplex* is a very small area in the South China Sea, off the island of Pratas (= Donsha), Guandong Province (China), in an open lagoon of 16 km in diameter. About 300 t per year is produced there by some 45 divers. In addition to the Chinese production, almost the same amount of the alga used to be collected in southern Kyushu, Japan.

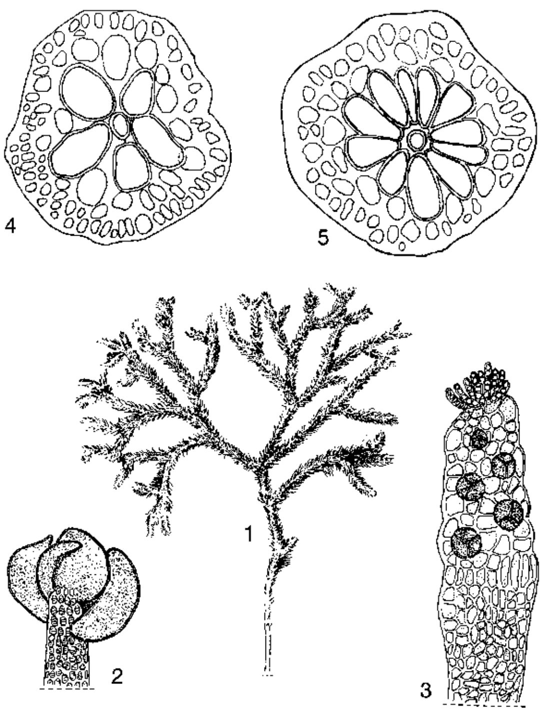
Properties *D. simplex* contains agar (10–15% of its dry weight) and kainic acids. Especially α-kainic acid is an effective anthelmintic agent, which is said to be about ten times stronger than santonin, a compound of the salt marsh plant *Artemisia maritima* L. Another anthelmintic agent from *D. simplex*, named α-allokainic acid, is only slightly anthelmintic.

Description Thalli erect, up to 10(–20) cm tall, dull brownish-red, cartilaginous, bushy, wiry below; main axes terete and heavily clothed with many radial, dichotomously branched, 3–15 mm long, stiff laterals; main axes without well-defined apical cell or polysiphonous structure. Medulla of large broadly parenchymatous cells; cortex of smaller cells; determinate lateral branchlets uncorticated, showing 6–10 pericentral cells with small deciduous trichoblasts at the apices. Life cycle diplo-haplontic and triphasic, isomorphic for tetrasporophytes and gametophytes. Tetraspores tetrahedral, in irregularly swollen, chiefly uncorticated upper parts of branchlets. Spermatangia in small ovoid disc clustered at tips of fertile branchlets; cystocarps ovoid, terminal and lateral on branchlets.

Ecology *D. simplex* is common and often abundant in the intertidal zone on rather exposed reefs and rocks. It is frequently much dwarfed and hardly more than 3–5 cm tall, but in sheltered spots it grows much larger, and is dredged to a depth of 20 m. It is a favoured support for many other algae and is commonly so heavily epiphytized that a dense colony of the dwarfed form may be completely concealed.

Propagation and planting *D. simplex* is not kept in phycoculture.

Diseases and pests *D. simplex* is usually heavily overgrown by epiphytes.



Digenea simplex (Wulfen) C. Agardh – 1, habit; 2, summit of the thallus with bent ovoid crowded spermatangial branchlets; 3, upper end of a tetrasporangial branchlet; 4,5, transverse sections of terminal branches with different numbers of pericentral cells.

Harvesting *D. simplex* is only harvested from natural populations by hand-collecting, often by divers.

Handling after harvest *D. simplex* is probably sun-dried.

Prospects Since kainic acids are now produced by the pharmaceutical industry, it is unlikely that *D. simplex* will be used for their production.

Literature |1| Blunden, G. & Gordon, S.M., 1986. Medical and pharmaceutical uses of algae. Pharmacy International 7: 287–290. |2| Michanek, G., 1979. Seaweed resources for pharmaceutical uses. In: Hoppe, H.A., Levring, T. & Tanaka, Y. (Editors): Marine algae for pharmaceutical science. Walter de Gruyter & Co., Berlin, Germany. pp. 203–235. |3| Moore, R.E., 1977. Volatile compounds from marine algae. Accounts of Chemical Research 10: 40–47. |4| Tseng, C.K. & Chang, C.F., 1984. Chinese seaweeds in herbal medicine. Proceedings of the 11th International Seaweed Symposium. Hydrobiologia 116/117: 152–154. |5| Yoo, S.E. & Kim, N.J., 1988. An efficient synthesis of the basic pyrrolidine ring for the kainoids. Tetrahedron Letters 29(18): 2195–2196.

G.C. Trono Jr

Enteromorpha Link

in Nees, Horae phys. berol.: 5 (1820).
ULVACEAE
$x = 10$

Major species and synonyms

- *Enteromorpha clathrata* (Roth) Grev., Alg. brit. 66: 181 (1830), synonym: *Conferva clathrata* Roth (1806).
- *Enteromorpha compressa* (L.) Nees, Horae phys. berol., index 2 (1820), synonyms: *Ulva compressa* L. (1753), *Enteromorpha complanata* Kütz. (1845).
- *Enteromorpha flexuosa* (Wulfen) J. Agardh, Acta Univ. Lund. 19(2): 126–128 (1883), synonyms: *Ulva flexuosa* Wulfen (1803), *Enteromorpha tubulosa* (Kütz.) Kütz. (1856).
- *Enteromorpha intestinalis* (L.) Nees, Horae phys. berol., index 2 (1820), synonym: *Ulva intestinalis* L. (1775).
- *Enteromorpha lingulata* J. Agardh, Acta Univ. Lund. 19(2): 143 (1883), synonym: *E. compressa* (L.) Nees var. *lingulata* (J. Agardh) Hauck (1884).
- *Enteromorpha linza* (L.) J. Agardh, Acta Univ. Lund. 19(2): 134 (1883), synonym: *Ulva linza* L. (1753).
- *Enteromorpha prolifera* (O.F. Müll.) J. Agardh, Acta Univ. Lund. 19(2): 129 (1883), synonym: *Ulva prolifera* O.F. Müll. (1778).

Vernacular names General: green laver (En). Indonesia: lumut benang. Philippines: lagot, lumot bitukang-manok (Tagalog), ruprupu.

- *E. clathrata*: light green aonori (En). Philippines: habol-habol.
- *E. compressa*: yellow-green aonori (En).
- *E. intestinalis*: green aonori (En).
- *E. prolifera*: dark green aonori (En).

Origin and geographic distribution *Enteromorpha* is a common genus of green algae distributed widely in South-East Asian waters.

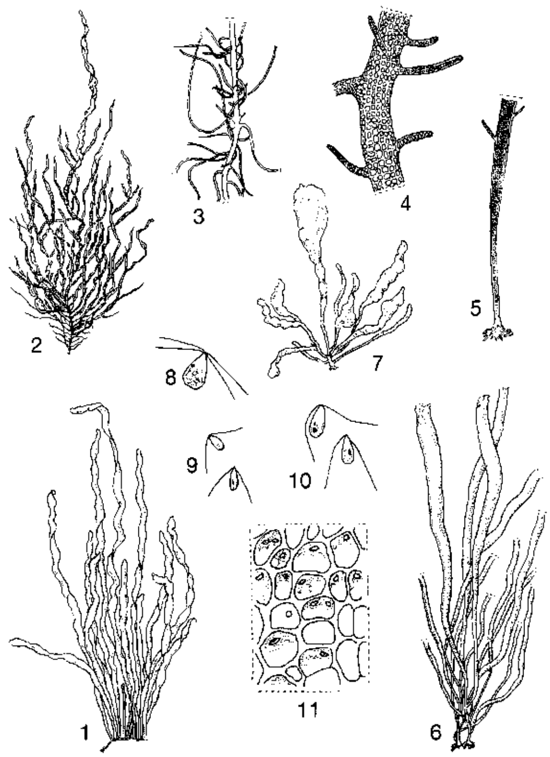
Uses *Enteromorpha* is widely used throughout the world, including Asia, for food, feed (especially for fish (milkfish) and pigs), as a fertilizer and medicine. It is also applied as fish bait. The dried and crushed fronds can be used as topping for many foods, in soups and as a coating. It is available in Japan in powdered form for similar uses or as a green colourant.

In Chinese herbal medicine *Enteromorpha* is used against goitre and scrofula, as an antipyretic, to prepare a refreshing liquid and to treat sunstroke, bronchitis, cough and asthma.
Collections from wild populations are not appreciated because these consist of thalli of different ages. The young fronds are tender and tasty, while the mature ones are cartilaginous, fibrous and somewhat bitter. When cultured, the algae can be collected in the desirable stage, based on consistency, form and colour.

Production and international trade Information on the production and international trade of *Enteromorpha* is scanty. It is collected from the wild and cultivated in small quantities for local consumption in Indonesia, Malaysia, and the Philippines. Several *Enteromorpha* spp. are recorded from 1953 on as being cultured for milkfish food in brackish water ponds in the Philippines. Here, *E. clathrata*, *E. compressa* and *E. intestinalis* are cultured for animal feed (especially milkfish) and as a source of tocopherols (vitamin E). In Tagalog the word 'lumot' is used for a large assemblage of filamentous algae found in shallow ponds, and used as natural food in milkfish cultivation together with 'lab-lab' (a mixture of mainly filamentous microalgae). *Enteromorpha* can usually be found in this assemblage, although green filamentous algae such as *Chaetomorpha* and *Cladophora* spp. are present as well.

Properties Information on the properties of *Enteromorpha* varies considerably, probably because it is not always indicated which species has been analyzed. *Enteromorpha* spp. contain (per 100 g dry weight): protein 12–15(–20) g, fat 0.3–1.5 g, carbohydrates 46–53 g, and ash 21–22.6 g. The most common lipid found is the unsaturated fatty acid sitosterol, which can help to reduce the plasma cholesterol level in cells. The carbohydrates are mostly glucides and starch. It is stated that all essential amino acids are present, together with chondrine, cysteine, D-cysteinolic acid, glutamic acid and proline. Especially data on vitamin contents are variable, indicating for 100 g *Enteromorpha* (dry weight): vit. A 500–1300 IU, vit. B1 0.04–0.6 mg, vit. B2 0.52–2.05 mg, niacine 1–6 mg, vit. C 10–43.2 mg, vit. B12 1.3 μm and folic acid 42.9 μm. Data on tocopherols (vitamin E) are not available. Minerals (mg/g dry weight) include: Ca 840–910, P 740–800, Fe 10–35, Na 530–570, and K 3200–3500.

Description Thalli inflated or tubular, crisped, contorted, or bandshaped, branched or unbranched, consisting of a single layer of cells around an open central lumen filled with water or air. Cells usually fairly uniform, except rhizoidal cells in the lower parts, irregularly arranged or more regularly in longitudinal or transverse rows. Life cycle diplo-haplontic and isomorphic. Gametophytes probably dioecious, forming two kinds of isogametes.



Enteromorpha. E. intestinalis (L.) Nees – 1, habit. E. clathrata (Roth) Grev. – 2, habit; 3, 4, details of vegetative thallus; 5, habit of the basal portion of a thallus with basal disk. E. lingulata J. Agardh – 6, habit. E. compressa (L.) Nees – 7, habit; 8, quadriflagellate meiospore; 9, male gametes; 10, female gametes; 11, surface view of thallus, cells with chloroplasts with pyrenoid.

– *E. clathrata*. Thalli 1–10(–45) cm long and 3–10 mm wide, forming light to grass-green dense mats of soft, delicate, flattened, hollow tubes, branched or unbranched, unattached or when attached with fragile stipe and small disciform holdfast. Determinate branchlets uniseriate at or near their tips, hair-like. Cells rather large, subquadrangular in surface view, 15–36 μm in diameter, fairly regularly arranged in longitudinal rows. Chloroplasts very thin or contracted, usually not obscured by starch grains. Pyrenoids 2–6 per cell.

- *E. compressa*. Thalli 1–35 cm long and 2–20 mm wide, attached by fragile stipe and small disciform holdfast, with bright to dark green bushes of tubular, strap-shaped, more or less compressed branches, not differing from the principal ones, expanded above, as well as many short, more or less filiform branchlets, intercalated between the larger ones. Branching concentrated at basal region of thalli. Cells small, rounded to irregularly polygonal in surface view, 10–15 µm in diameter, irregularly arranged or arranged in longitudinal rows. Chloroplasts parietal, with numerous large starch grains, often having a cap-like appearance. Pyrenoids 1(–2) per cell.
- *E. flexuosa*. Thalli 2–3(–60) cm long and up to 1 cm wide, usually smaller, with small disciform holdfast, forming light to yellowish-green thick tufts; individual thalli densely to sparsely branched. Branches tubular, strap-shaped to filiform, narrow in basal portions but enlarged to inflated towards their distal portions. Cells square to rectangular in surface view, 9–12 µm in diameter, regularly arranged in basal regions in longitudinal and short transversal rows, becoming irregularly arranged towards the distal regions. Chloroplast forming central transverse band, usually not obscured by starch grains. Pyrenoids 2–5 per cell.
- *E. intestinalis*. Thalli 6–20(–50) cm long, with short stipe attached by discoid holdfast, forming bright to yellowish bushes of usually unbranched, constricted and/or contorted, erect, tubular fronds, tapering below and inflated above. Cells small, polyhedral or rounded in surface view, 8–18 µm in diameter, irregularly arranged, filled with spherical to oval parietal chloroplast, often having a cap-like appearance, with numerous large starch grains. Pyrenoids 1 per cell.
- *E. lingulata*. Thalli up to 7(–15) cm long and usually not over 1–2 mm wide, attached by conspicuous basal disc, forming medium green tufts or turfs of fronds sparingly to abundantly branched in basal regions, above tubular, very slender and gradually dilated, below subsolid. Cells sharply rectangular, 9–28 µm in diameter, arranged in clear longitudinal rows. No published data available on chloroplasts, starch grains and/or pyrenoids.
- *E. linza*. Thalli up to 37 cm long and to 30 cm wide, attached by short stalk and stout disciform holdfast, with erect, strap-shaped, flat, linear to lanceolate, simple, unbranched, often gregarious, yellowish-green to medium green blades with tapering base. Blades hollow at base, in flat portions the two layers united to a membrane of a combined thickness of 35–50 µm, with a hollow margin. Cells irregular polygonal in surface view, in middle and upper regions characteristically quadrangular to rectangular or irregularly polygonal, arranged in short to long longitudinal and transverse cell rows, 10–22 µm in diameter. Chloroplast completely covering outer cell wall, usually obscured by numerous large starch grains. Pyrenoids 1(–2) per cell.
- *E. prolifera*. Thalli up to 60 cm long and 5–10 mm wide, attached by long, slender stipe with small disciform holdfast, with solitary or tufted, light yellowish-green or medium green, strap-shaped, undulating, wrinkled and lubricous fronds with a gradually narrowing base, with membrane 15–18 µm thick. Branches along the whole axis small; uniseriate branchlets mostly concentrated on the base. Cells irregularly polygonal to subangular in surface view; 8–19 µm in diameter, arranged in long to short longitudinal rows and short transverse rows. Chloroplast centrally situated, obscured by numerous starch grains. Pyrenoids 1(–2) per cell.

Growth and development Most *Enteromorpha* grow fast in natural habitats as well as in cultures. They attach to stones (epilithic), ropes or nets and also to other marine organisms. They are present throughout the year in the form of successive, short-living generations.

In fertile thalli parts degrade when their contents transform into gametes or zoospores. When these zoids are released, only the walls of the original cells remain. This release usually occurs around spring tide (lunar cycle). Biflagellate isogametes of opposite mating types fuse and the quadriflagellate zygotes stay motile during a short period only. They anchor themselves at their anterior end to solid substrates and to other algae, withdraw their flagella and secrete a cell wall. They then each divide into two cells, the basal one forming the holdfast, and the apical cell divides and redivides to produce vegetative cells of the thallus. Quadriflagellate zoospores are produced by diploid sporophytic thalli. They behave like zygotes and develop to form haploid gametophytic thalli.

When cultures of *Enteromorpha* are enriched by adding ammonium or nitrate, tissue growth is accelerated and the algae can stock nitrate in the form of dipeptides which form 3–7% of total dry weight. They can use this nitrogen source later to grow faster than the normally available nutrients should allow. The algae absorb the extra nitrogen mainly during the day, while rhodophytes usually mainly absorb nutrients during the night. *Enteromorpha* can still fix bicarbonates at pH values above 9, while many red algae cannot. *Enteromorpha* can also accumulate polyphosphates and these deposits can be easily used under conditions of phosphorus depletion.

Other botanical information Seventeen *Enteromorpha* species have been listed for the Indian Ocean, while a total of 21 species have been listed for the Pacific coast of North America and 16 species have been described from the eastern tropical and subtropical coasts of the Americas. The individual species are very difficult to distinguish. *E. compressa* and *E. intestinalis* are considered to be synonyms by several authors, although others prefer to keep them as separate species.

Ecology Several *Enteromorpha* spp. tolerate a wide range of salinity and some can even survive in almost pure fresh water. They occur often in brackish estuaries, in sandy areas with freshwater seepage and in rock pools. They are also common inhabitants of upper intertidal areas, where they attach to rocks and coral pieces exposed to air during low tide. They can also be found lying loose, especially in sheltered habitats. The cell walls of estuarine *E. intestinalis* are thinner and hence stretchier than those of marine rockpool plants of the same species, allowing the cells to swell with the influx of water in low-salinity conditions and to decrease again in the presence of waters of higher salinity.

Enteromorpha thalli can survive water temperatures of about 28°C and even higher air temperatures. They can also grow in water with high turbidity, although growth is much better under full sunlight.

Occasionally, large masses of green algae, consisting mainly of *Enteromorpha* and *Ulva* spp., wash up on the coast forming a 'green tide'. In many stressful situations (e.g. freshwater seepage, oil spills) *Enteromorpha* spp. quickly colonize the empty surfaces. Because spores and zygotes of these algae can quickly attach, germinate and grow on almost any substrate, *Enteromorpha* spp. are notorious biofouling organisms. They are difficult to control because of their tolerance to copper, a mineral often used in antifouling coatings. Their growth can, however, be prevented by using organotins as an antifouling compound. These compounds are now included into self-polishing copolymers (SPC) used extensively as paint on seagoing vessels and pleasure crafts.

Propagation and planting Mature fronds of *Enteromorpha* can be collected from natural populations and placed in small water tanks with filtered sea water. After keeping them for some time in the dark, dense spore solutions are obtained after about 30 minutes exposure to daylight. These spore solutions can be transferred to large tanks containing nets or other substrates in filtered sea water. During further dark treatment, the spores will settle on the substrates and on the following day these can be transferred to the growing areas. This method is known as 'artificial seed collection'. Another method, known as 'natural seed collection', is practised by placing suitable substrates near natural *Enteromorpha* populations during spring tides in September–October, when the sporophytes form their quadriflagellate zoospores. These substrates (usually the same nets as used for *Porphyra* cultivation in Japan and Korea) are secured in such a way that they are not exposed at low tide. The nets can be transferred to the culture grounds when juveniles are observed, usually after a few weeks. When cultivated for food production, *Enteromorpha* can best be grown on nets, either fixed by poles at shallow depths (not exposed) or in floating systems. The mixture of green algae grown as 'lumot' in milkfish ponds in the Philippines can be propagated in separate ponds as algal nurseries and later planted in fish ponds. The algae for transplant have to be transported in a moist or semi-dried state and the ponds to be planted should preferably be cleaned and drained thoroughly beforehand. Planting can be done by staking (transplanting of patches of algae by hand), sowing (broadcasting of fragments) or spreading (producing fragments by shaking bunches of algae in the fish pond water). The latter method is considered to be unsuitable for transplanting *Enteromorpha*. The ponds with algal cultures must not dry out and the water has to be changed regularly.

Protoplasts have been used successfully for propagation in laboratory culture experiments.

Phycoculture In Japan, *E. prolifera* is cultured for commercial purposes. Elsewhere, cultivation is mostly in the experimental phase, and trials are also being carried out on other *Enteromorpha* species.

Diseases and pests So far, *Enteromorpha* in culture is not vulnerable to diseases.

Harvesting When *Enteromorpha* is grown on nets, both hand-picking and machine collecting are possible. Hand-picking normally produces the highest quality product, but machine collecting is faster.

Handling after harvest The collected fronds of *Enteromorpha* are washed in freshwater and dried in the sun or in a drier. For food use the dried thalli are often lightly toasted and crushed. Fronds of the best quality are dark green and are produced under stable environmental conditions. Changes in environmental factors, especially lowering of salinity and enhanced turbidity, due to rain or human activities, result in a decrease of biomass production and quality.

Genetic resources Sterile strains of *Enteromorpha* are preferable for obtaining good quality biomass because of loss of living cells with the release of spores and gametes.

Prospects *Enteromorpha* is considered suitable for human food as well as animal feed (especially for fish). The demand for human food is expected to rise, especially in Japan.

Literature |1| FAO, 1974. A catalogue of cultivated aquatic organisms. FAO Fisheries Technical Paper No 130, FIRI/T130. Food and Agriculture Organization of the United Nations, Rome. 83 pp. |2| Ohno, M., 1993. Cultivation of the green algae Monostroma and Enteromorpha. 'Aonori'. In: Ohno, M. & Critchley, A.T. (Editors): Seaweed cultivation and marine ranching. 1st Edition. Japan International Cooperation Agency, Yokosuka, Japan. pp. 7–15. |3| Polne-Fuller, M. & Gibor, A., 1987. Tissue culture of seaweeds. In: Bird, K.T. & Benson, P.H. (Editors): Seaweed cultivation for renewable resources. Elsevier, Amsterdam, The Netherlands. pp. 219–239. |4| Rabanal, H.R. & Montalban, H.R., 1953. The growing of algae or 'lumot' in Bañgos fishponds. Fisheries Gazette 5: 3–12.

W.S. Atmadja

Eucheuma J. Agardh

Öfvers. Kongl. Svenska Vetensk.-Akad. Förhandl. 4(1): 5–17 (1847).

SOLIERIACEAE

$2n$ = possibly 20

Major species and synonyms

- *Eucheuma arnoldii* Weber Bosse, Siboga Exped. Monogr. 59d: 421 (1928), synonym: *E. cupressoideum* Weber Bosse (1928).
- *Eucheuma cottonii* Weber Bosse, see for *Kappaphycus cottonii* (Weber Bosse) Doty ex H.D. Nguyen & Q.N. Huynh in separate article on *Kappaphycus* Doty.
- *Eucheuma denticulatum* (Burm.f.) Collins & Herv., see separate article.
- *Eucheuma gelatinum* (Esper) J. Agardh ('gelatinae'), see separate article on *Betaphycus gelatinus* (Esper) Doty ex P.C. Silva, Basson & R.L. Moe.
- *Eucheuma inerme* F. Schmitz, see for *Kappaphycus inermis* (F. Schmitz) Doty ex H.D. Nguyen & Q.N. Huynh in separate article on *Kappaphycus* Doty.
- *Eucheuma serra* (J. Agardh) J. Agardh, Öfvers. Kongl. Svenska Vetensk.-Akad. Förhandl. 4(1): 16 (1847), synonym: *Sphaerococcus serra* J. Agardh (1841).
- *Eucheuma striatum* Schmitz, see separate article on *Kappaphycus striatus* (F. Schmitz) Doty ex P.C. Silva.

Vernacular names Usually the vernacular names apply to all *Eucheuma* and *Kappaphycus* spp. Indonesia: agar-agar, agar besar (common names for all *Eucheuma* and *Kappaphycus* spp.), 'spinosa' (common commercial name for all genuine *Eucheuma* spp., especially for *E. denticulatum*). Philippines: ruprupuuk (Ilocano), guso (Visayan), canot-canot (Ilocos Norte).

Origin and geographic distribution *Eucheuma* is distributed throughout the tropics. Originally *E. denticulatum* and *E. serra* probably only occurred in the Indian Ocean and in South-East Asia. In most recent times especially *E. denticulatum* has been distributed to other areas by man. *E. arnoldii* has been recorded in the Indo-Malayan Archipelago in Indonesia and the Philippines, also from northern Queensland to the southern Ryukyu Islands and Taiwan. Farming trials with *E. denticulatum* and *E. serra* carried out before 1984 failed, but nowadays the former species is cultured in many localities.

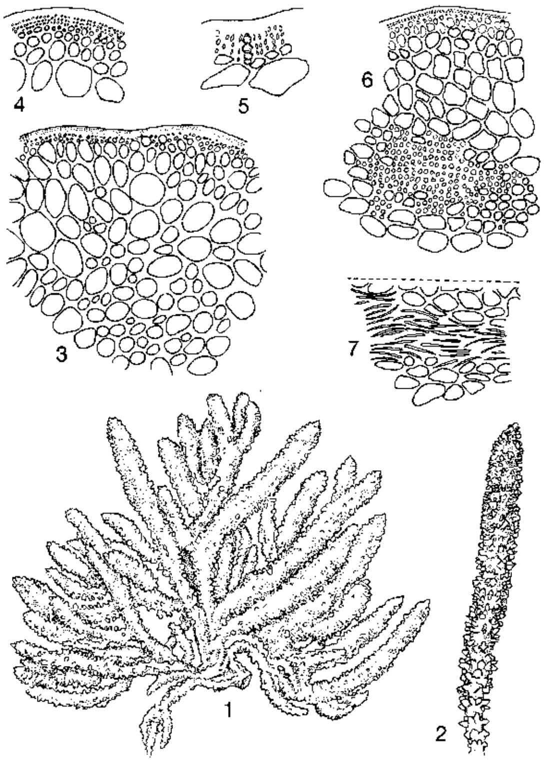
Uses Species of the *Eucheuma* sections *Eucheuma* (*E. denticulatum*, *E. serra*) and *Anaxiferae* (*E. arnoldii*) are good sources of iota carrageenan. It appears that the carrageenan from *E. denticulatum* is the most valuable to industry, since it becomes an ideal iota carrageenan upon alkali modification. It is used in industrial food and beauty aid products, in pet foods, in granulated or hydrated gel components in various formulations, or prepared as a stew mixed with vegetables. The algae are eaten fresh or blanched in boiling water and mixed with salad garnish. In Vietnam thalli of *Betaphycus* Doty ex P.C. Silva, *Eucheuma*, and *Kappaphycus* are used in traditional medicine to reduce the incidence of tumors, ulcers and headaches. They are also used as manure and fertilizer.

Production and international trade Production and trade data on '*Eucheuma*' often apply to all Eucheumoid algae (thus on *Betaphycus* and *Kappaphycus* as well), to the group of carrageenan-producing seaweeds as a whole or even to all red seaweeds together. World production (wet weight) by phycoculture of all '*Eucheuma*' together in 1986 was 160 106 t. By 1994 this figure had been 384 980 t. Of these, Indonesia produced 77 462 t in 1986 and 115 000 t in 1994 (these data also include *Gracilaria* Grev. and *Gelidiales*) (only for '*Eucheuma spinosum*' = *E. denticulatum*). The Philippines probably produced 8173 t in 1986 and in 20 190 t in 1994. Production from natural populations of *E. serra* in 1984 in the Philippines was estimated to be 60 t (dry weight).

Properties It has been established that both female gametophytes and tetrasporophytes of *E. arnoldii* contain iota carrageenan and no other carrageenans. Gel strength in carrageenan of both life stages is 280 g/cm^2. The carrageenan from cystocarpic material contains 22% 3,6-anhydro-galactose ester, while that of tetrasporic plants amounts to 23%. Cystocarpic plant carrageenan contains 32% sulphates, and tetrasporic plant carrageenan has 31%.

Carrageenan from *E. serra* has not been available for extraction and descriptive analysis. However, infrared analysis has shown spectra very similar to those of *E. denticulatum*, while molecular data (rbcL sequences) show differences with *E. denticulatum* as well as similarities with that species. Thalli of *E. serra* (from Japan) give high yields of lectins, identified as at least two different isolectins. Their quantities greatly exceed the yields from other macroalgae or other marine organisms.

Description Plants with cylindrical to flattened, erect, bushy or prostrate, fleshy to cartilaginous thalli of large size reaching over 1 kg in biomass, producing determinate spines in pairs or whorls at apex or margins and ventral surface of branches. Branches arising through spines becoming indeterminate. Secondary spines produced irregularly or uniformly over the older surfaces; branch in cross-section composed of three tissues: cortex with radiating cellular filaments of small diameter, medulla of large thick-walled cells surrounding dense central core consisting of thick-walled rhizoidal hyphae. Thalli multiaxial filamentous becoming strongly pseudo-parenchymatous. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangia zonate and embedded in the cortex. Gametophytes dioecious, with cystocarps borne near tips of branchlets; spermatangia in surface sori.



Eucheuma. E. arnoldii Weber Bosse – 1, habit; 2, portion of a branch; 3, transverse section of a thallus; 4, detail of transverse section of the cortical region of a thallus; 5, detail of transverse section of the cortical region of a thallus with a tetrasporangium. E. serra (J. Agardh) J. Agardh – 6, transverse section of a thallus; 7, detail of a longitudinal section of the medullar region of a thallus.

- *E. arnoldii*. Thalli forming thick clumps with many clavate branches with slightly acute apices, densely covered with simple or compound spinose tubercles forming verticils at distinct 'nodes' separated by 'internodes', verticils overlapping at distal portion of branches so obscuring verticillate arrangement; section of a branch revealing a medulla composed of large rounded cells interspersed with smaller ones; cortical cells very small, ovoid or elongated; central core not evident. This *Eucheuma* mimics the habit of the *Acropora* coral with which it is closely associated.
- *E. serra*. Thalli prostrate, with a disc-like holdfast with many branches arising in an irregular and circular pattern, main axes terete in basal parts, compressed to flattened in middle to apical parts, dorsal and ventral sides differing in

colour: dorsal parts milky white or milky yellow, occasionally with light red spots, ventral parts dark to light red. Sporophytes (with more terete branches and circular thorn-like protuberances) and gametophytes slightly differing in morphology: male gametophytes with mainly sagittate protuberances, female gametophytes having these also frequently on dorsal side of flattened thalli; protuberances may change into carpogonia. Medulla of axes and branches consisting of crowded rhizoid-shaped cells surrounded by a cortex of irregularly arranged thick-walled rounded cells and an outer cortex of small cells of epidermal structure.

Other botanical information The taxonomy of Eucheumoid algae has recently been reviewed. The new genera *Betaphycus* Doty ex P.C. Silva, in which several species of the section *Gelatiliforma* Doty & Norris are included, and *Kappaphycus* Doty, which was the *Eucheuma* section *Cottoniformia* Doty & Norris, have been separated from *Eucheuma* proper. Main characteristics used to distinguish the different species and genera of the Eucheumoids are the nature of the undamaged apical segment, the location of the cystocarp, the presence or absence of an axial core and the nature of the gel. Of the species that have remained in *Eucheuma*, *E. arnoldii*, which belongs to the *Eucheuma* section *Anaxiferae* Weber Bosse, has cylindrical branches producing compound spines arranged in whorls. Branches do not possess a cylindrical hyphal or rhizoidal core, cystocarps are borne on the main axes and the principal wall component is iota carrageenan. In *E. denticulatum*, which together with *E. serra*, belongs to the section *Eucheuma*, branches are cylindrical and spines are simple, regularly arranged in pairs or may form whorls. Cross-section of a branch shows a cylindrical axial core consisting of rhizoids, the cystocarps are borne on spinose laterals and the main polysaccharide component of the walls is iota carrageenan. The morphology of the *Eucheuma/Betaphycus/Kappaphycus* clade in a phylogenetic study inferred from molecular data (rbcL sequences) is well supported. Although three of the four Doty & Norris sections (and thus also the separate new genera) receive strong support, the remaining species within the genus *Eucheuma* do not form a natural group, nor does the section *Eucheuma* itself. Thus further taxonomic research is needed to elucidate the phylogeny of this group of carrageenophytes.

The use of the name *Eucheuma serra* has given rise to many problems. The type material clearly belongs to a genuine *Eucheuma* sp., containing iota carrageenan. However, it has been identified as '*Eucheuma gelatinae*' (= *Betaphycus gelatinus*), which contains beta carrageenan, and also as '*Eucheuma edule*', which might belong to the genus *Kappaphycus*.

Ecology *E. arnoldii* is commonly found growing on dead coral fragments on platforms, solid coral pavements, coral rubble, algal limestone and living coral. It is generally associated with branching coral colonies and is quite limited in its vertical distribution: at low intertidal to shallow subtidal zones about 1.25 m above the lowest tide level to about 1.2 m below mean low water. It is usually absent in habitats where conditions permit sand deposition. Its habitat is generally influenced by swift current and silt-free water and the alga is present under these conditions throughout the year.

Because of its sprawling and closely adhering habit it is often difficult to detect specimens of *E. serra*, especially when they grow mixed with turf-forming algae. It grows on rocks and corals and occurs in intertidal pools, where it can even be exposed to the air at low tide, but also at depths up to 20 m. It is especially found in locations with clear water and heavy surf or on walls of channels with rather strong currents.

Propagation and planting *Eucheuma* is largely propagated by vegetative fragmentation.

Diseases and pests One of the major diseases in cultivated *Eucheuma* is 'ice-ice' disease.

Yield Carrageenan yield in cystocarpic material of *E. arnoldii* is 53% and in tetrasporic material 47%.

Prospects On average, the world market for carrageenans has maintained a steady annual growth of 10%. In the Philippines, however, the annual growth during the period 1993–1997 has ranged between 20–30%. This high growth rate is reflected in the demand for an additional 10 000 t of dried seaweeds by the carrageenan processors. The continuing discovery of new industrial uses of carrageenan will lead to an increasing demand for supplies of raw material. Thus the prospects for farming carrageenophytes are bright. *E. arnoldii*, although presently not used in any form, is readily farmable in shallow, near-surface habitats in the vicinity of coral growth.

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Eucheuma denticulatum (Burm.f.) Collins & Herv.

Univ. Calif. Publ. Bot. 53: 106 (1917).

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Synonyms *Fucus denticulatus* Burm.f. (1768), *F. spinosus* L. (1771), *Eucheuma spinosum* J. Agardh (1847, nom. illeg.), *E. muricatum* (S.G. Gmelin) Weber Bosse (1928).

Vernacular names Usually the vernacular names are common names for all *Eucheuma* and *Kappaphycus* spp. Indonesia: agar-agar, agar besar (common names for all *Eucheuma* and *Kappaphycus* spp.), 'spinosa' (common commercial name for all genuine *Eucheuma* spp., especially for *E. denticulatum*). Philippines: ruprupuuk (Ilocano), guso (Visayan), canot-canot (Ilocos Norte). China: chilints'ai, qilinca, gilin cai.

Origin and geographic distribution *E. denticulatum* originally occurred only in the Indian Ocean (along the east coast of Africa from Natal to Djibouti, although it was probably only recently introduced into the latter country, India, Bangladesh, most island groups in the Indian Ocean, including small islands in northern Australia), in South-East Asia and in neighbouring parts of the western tropical Pacific (as far as New Caledonia). It has recently been distributed further eastward by man into the Pacific at least as far as Hawaii, Micronesia (Pohnapei) and Christmas Island in easternmost Kiribati. In South-East Asia it occurs in Peninsular Malaysia, Singapore, Indonesia (originally especially in the Moluccas), the Philippines and Vietnam. In Indonesia, farming trials with *E. denticulatum* carried out before 1984 failed, but nowadays the largest production area is around Bali.

Uses *E. denticulatum* is a source of iota carrageenan. It appears that the carrageenan from *E. denticulatum* is the most valuable to industry, since it becomes an ideal iota carrageenan upon alkali modification. It is used in industrial food and beauty aid products, in pet foods, in granulated or hydrated gel components in various formulations, or prepared as a stew mixed with vegetables. *E. denticulatum* can also be eaten fresh or blanched in boiling water and mixed with salad garnish, or made into '*Eucheuma* candy' or 'kue' by cooking in water until a gel is formed, whereafter sugar is added. It is used as garnish for other dishes such as fish. In Lombok (Indonesia) about 400 t (wet weight) of *E. denticulatum* is used annually to prepare a boiled foodstuff, wrapped in banana leaf and known as 'pencok'. In some areas it is also used as fertilizer. It can be applied in the control of heavy metal pollution by Pb and Cd, since this alga can accumulate these metals.

Production and international trade *E. denticulatum* was exported from Indonesia to China already in the 1920s, chiefly from the southern coast of Sulawesi and adjacent islands. The Philippines and Indonesia are the two main producers of *E. denticulatum*. Annual production through phycoculture in the Philippines was about 8173 t in 1986 and had risen to 20 190 t by 1994 (all wet weights). In the Philippines, *E. denticulatum* has always been more difficult to grow than *Kappaphycus alvarezii* (Doty) Doty ex P.C. Silva, while in Indonesia farming of both algae seems to be equally easy. For 1987 the total production by phycoculture of *E. denticulatum* (dry weight) for Indonesia was 4000 t and for the Philippines 2500 t, for 1990 it reached 4500 t and 2111 t, whereas for 1991 it amounted to 10 000 t and 2000 t respectively. The estimated potentially exploitable area for '*Eucheuma* culture' in Indonesia (probably including *Kappaphycus* culture as well) is 9000–10 000 ha, with a production capacity of 45 000 t/y (dry weight). This area, however, has not yet been fully exploited, resulting in a total seaweed production in Indonesia in 1994 of less than 2700 t, including harvests of *Gracilaria*, *Gelidium* and other algae.

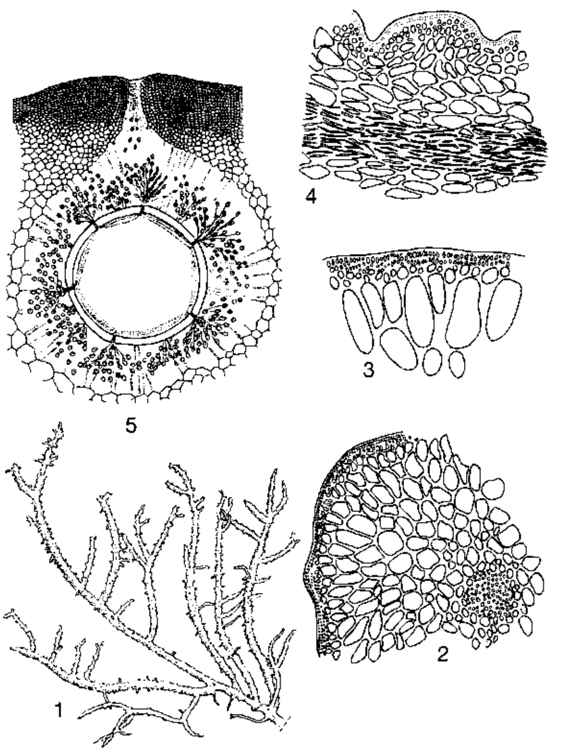
The FOB (Free on Board) selling price of *E. denticulatum* in Indonesia in the period 1986–1992 was particularly unstable, being US$ 0.32–0.43/kg in 1987. The CF (= Costs and Freight) price for dried *E. denticulatum* for Europe was in 1987 US$ 390/t and for the United States US$ 450/t. Increasing demand, particularly from the United States, and the resulting competition with European carrageenan processors for the limited resource, was the principal cause of the FOB price escalation to over US$ 1/kg in 1990. Added competition came from the growing *E. denticulatum* food market in China, for which Hong Kong buyers started activities in 1986. However, unlike the case of *Kappaphycus alvarezii* production, the increased demand for *E. denticulatum* did not result in a consistent increase in farm production. Nevertheless, prices in 1991 fell rapidly, due to a large decline in orders from foreign carrageenan processors, leaving much of the 1991 harvest unsold. Consequently, production of *E. denticulatum* in Indonesia in 1992 dropped to 1500–2000 t (dry weight), mainly for the more stable Chinese food market. Although 95% of the *E. denticulatum* crop is now farmed, in 1989 wild cropping in Indonesia was still considerable, with the largest amount, 800 t (dry weight), coming from the Aru Islands (Moluccas).

Properties Extracts of *E. denticulatum* show antitumour activity against Ehrlich carcinoma with an inhibition rate of 41.2%. *E. denticulatum* (dry weight) contains per 100 g: crude fat 0.7–1.6 g, crude protein 5.1–6.8 g, crude iodine 2.8 g, ash 15.0 g, crude fibre 5.0 g, nitrogen 0.8 g, mannitol 25.4 g. Minerals in g/100 g of dry weight: K 12.0, N 0.5, Na 4.8, Ca 0.6, Mg 0.8, P 0.1, and in ppm: Zn 13, Cu 7.5, Fe 66 and Mn 14. The sulphate content of the iota carrageenan is often 30% or higher, while the 3,6 anhydro-galactose ester content is about 27%.

E. denticulatum produces H_2O_2 under oxidative stress conditions and then also releases bromoform, diiodomethane, dibromochloromethane, perchloroethylene, chloroiodomethane, chloroform, sec-butyl iodine, methyl iodide, methyl chloroform, carbon tetrachloride, trichloroethylene and butyl iodide into its growth media. These volatile halocarbons (VHCs), of which bromoform and diiodomethane are the dominant ones, are also formed under optimal growth conditions and can be efficient in catalyzing stratospheric ozone removal.

Description Perennial plant with thalli forming low, rigid, caespitose clumps. Primary branches terete or cylindrical, bearing whorls of 1–8 mm long spinose determinate branchlets; branching at predictable intervals, forming distinct 'nodes' and 'internodes' especially towards terminal portion of branches; branchlets sometimes developing into secondary terete laterals. Cross-section of branch revealing a dense cylindrical core of thick-walled, very small rhizoidal cells at centre of medulla. Cystocarps borne near tips of lateral spines; tetrasporangia zonate, embedded in cortex; spermatangia forming surface sori.

Growth and development The growth of thalli of *E. denticulatum* is initiated by a group of apical cells. Growth rate in laboratory culture, deter-



Eucheuma denticulatum (Burm.f.) Collins & Herv. – 1, habit; 2, transverse section of a thallus; 3, detail of a transverse section of the cortical region of a thallus; 4, longitudinal section of a thallus; 5, a somewhat diagrammatic transverse section of a cystocarp.

mined by use of the respiration method, is 1–2% per day. The average daily growth rate in open air phycoculture in the Philippines is 1–5%. The optimal growth rate is about 3.5%/d, resulting in a doubling of the crop in 28 days. Daily growth in *E. denticulatum* is generally lower than in *Kappaphycus alvarezii*.

Haploid male and female gametophytes are produced from meiospores released by tetrasporophytes, suggesting a genetic determination of sexual phenotypes. It is also suggested, however, that spores from tetrasporophytes of *E. denticulatum* may form germlings that grow into sporophytes again. In cultures, cystocarpic plants are often lacking, although antheridial and tetrasporic plants can be frequently found in these cultures. However, most specimens used in phycoculture are sterile and propagate by fragmentation. Plants grown from material imported from the Philippines and in phycoculture on rafts in Djibouti waters all were fertile sporophytes, except 8 of the tested 10 000 specimens, which happened to be fertile female gametophytes.

Other botanical information The cylindrical core of rhizoidal cells distinguishes *E. denticulatum* from other *Eucheuma* spp. Several forms (cultivars) of *E. denticulatum* are farmed, amongst which green, brown and red ones. These forms retain their pigment characteristics after long-term laboratory culture, suggesting a genetic basis. The red forms are better adapted to high illumination ('sun'), the green and brown forms to lower illumination ('shade').

Ecology *E. denticulatum* is commonly found growing strongly attached to coralline gravelly-rocky or coarse sandy-rocky substrates at the intertidal to the upper (shallow) subtidal zone on the reefs exposed to moderate wave-action or strong tidal currents, where it may form thick clumps or beds. The fusion of its branches upon coming in contact with each other and its ability to form secondary holdfasts at tips of branches result in the formation of thick and strongly attached clumps or carpet-like beds which are able to withstand moderate to strong water movement. This alga has never been recorded in calm or protected habitats. Required temperatures for optimum growth rates are 24–30°C, whereas high solar energy levels are optimal. The preferred pH is 8 and salinity should be 32‰. Nitrogen levels should be 2–4 µg/l and phosphate levels 0.5–1 µg/l.

Propagation and planting *E. denticulatum* in phycoculture propagates largely through vegetative fragmentation. Laboratory grown branches, transplanted to rafts in the field in the Philippines, showed daily growth rates as high or even somewhat higher than other reported growth rates. In laboratory culture 3–5 cm long branches can be grown in inexpensive laboratory media prepared from autoclaved seawater enriched with either a commercial Philippine liquid fertilizer made from seaweed extract ('Algafer'), coconut water or soil extract.

Phycoculture *E. denticulatum* is farmed using the same methods as for *Kappaphycus alvarezii*, i.e. the fixed off-bottom mono-line, the raft-method or the floating long-line method. In Indonesia the two first mentioned culture methods for *E. denticulatum* showed no statistical significant differences, while the floating long-line method is not commonly practised in Indonesia. Polypropene rope 4 mm in diameter can also be used instead of the monofilament nylon culture lines. Generally, commercial production of *E. denticulatum* is found in areas with low tide ranges, allowing for a longer working period at a site than in areas with large tide ranges.

E. denticulatum has a greater tolerance to desiccation than *Kappaphycus alvarezii*, and thus can be farmed at sites with a longer period of tidal emergence. It can also be farmed where it is continuously submerged at relatively wave-protected sites. Productivity can be particularly high where there is freshwater run-off from land during the wet season. Such areas give poor growth of *K. alvarezii*. Conversely, off-shore flat shallow reef areas with moderate water movement are unfavourable for *E. denticulatum* farming.

Diseases and pests One of the major problems in the culture of *Eucheuma* (as well as *Kappaphycus*) is the disease 'ice-ice', which can wipe out entire crops. The early signs are slow growth, thalli becoming pale and losing their gloss, followed by white spots appearing on the branches, which finally break off at these affected spots. Entire thalli may become affected. The occurrence of ice-ice may be mainly due to adverse ecological conditions such as low light intensity, low nutrient availability, extreme water temperatures and low water movement. Whitening can also be caused by bacterial pathogens, while the high incidence of epiphytes may also affect *E. denticulatum*. Farm maintenance can be improved by removing heavy growth of epiphytes, such as *Enteromorpha* green algae. Overproduction of oxygen radicals and volatile halocarbons by the algae, which, when induced at a balanced level might protect them

against epiphytes and grazers, may cause ice-ice in *Eucheuma* monocultures.
Another problem is 'pitting' probably caused by mechanical wounding of the cortex, leading to the formation of cavities penetrating the cortex in one place and expanding into the medulla region beneath, often resulting in thallus breakage. 'Tip darkening' or 'tip discolouration' may occur when water is too cold or too warm. In most cases the affected parts decay, leading to fragmentation and losses.
Grazing by fish and invertebrates is one of the major causes of loss in biomass. The use of the floating methods (raft and long lines) has virtually eliminated the effect of benthic grazers such as sea urchins and starfish.
In some areas a shortage of available Mn, Fe, Cu and Zn may result in reduced plant resistance to physical stress in farmed *E. denticulatum*. It is suggested that destruction of seagrasses in preparing the grounds for monoculture seaweed farms may interrupt a seagrass-mediated availability of those micro-elements for cultivated algae.

Harvesting Depending on the growth rate, an *E. denticulatum* crop of 2–3 months old may be ready for harvesting. Individual plants may then weigh about 1 kg. Often complete harvesting is practised, whereby whole plants are detached from the farm support system, placed in rafted baskets or directly transferred to a boat and brought to the drying area. In some areas growing periods of 40–50 days are still practised, resulting in the harvest of immature thalli of less than 1 kg (wet weight). This is done because it is thought that higher yields are obtained by frequent cropping. A high market demand encourages early harvesting but leads to poor 'seed' selection for replanting.

Yield Depending on the quality of a crop of *E. denticulatum*, the carrageenan yield varies between 30–50% of the clean anhydrous seaweed. The carrageenan content and quality of cultured material and commercial seaweed is much influenced by post-harvest treatment.
The wet (85% moisture) to dry (35% moisture) ratio for *E. denticulatum* is 6:1 or 17%. Carrageenan yields in *E. denticulatum* are usually high (up to 67%).

Handling after harvest The harvested crop of *E. denticulatum* is cleaned of debris and other algae, and then sun-dried. The drying place is usually a platform made of bamboo slots lined with nylon netting material to prevent contamination. The crop is then spread evenly, and regularly turned to hasten drying. Drying may take 2–3 days during sunny wheather. The dried seaweeds are then packed in plastic sacks and stored under dry conditions.
Contact with freshwater, particularly rain, should be avoided, as this extends the drying time and reduces the salt content, both of which cause degradation of the seaweed or carrageenan. Washing in freshwater has no added value and in most cases reduces the quality of carrageenan. However, for the Chinese food market *E. denticulatum* material has to be rewashed in freshwater and subsequently bleached.
Inadequate drying of *E. denticulatum* and post-harvest contamination with sand result in poor quality and lower prices. If the alga contains more than 35% moisture the carrageenan is unstable and liable to degradation during storage. Above 40% moisture, the carrageenan may not survive transportation to the factory, resulting in too low percentages for some applications. Thus, *E. denticulatum* should never be stored wet. Between 25–35% moisture, the composition of the alga is relatively stable for periods of 12 months or more, and thalli are flexible enough to be baled efficiently. At lower moisture content levels thalli become too brittle, causing problems during carrageenan extraction.
To avoid degradation of the carrageenan of the harvested *E. denticulatum* material, fresh or recently dried seaweed can be immersed in a weak alkali solution to produce 'stabilized' raw material for carrageenan production. Dried material of *E. denticulatum* and *Kappaphycus alvarezii* should never be mixed, as it is then impossible to obtain suitable carrageenan quality.
The stored seaweed should be baled before transport to promote easier handling and reduction of shipping costs. Hydraulic systems for baling are preferred over screw-type balers. Some shrinkage may occur during shipment, probably mainly due to losses of moisture.
Originally, all produced '*Eucheuma*' (including cultured *Kappaphycus* as well) was exported as raw material (dried seaweed) to processors in Europe and the United States. Since 1978, however, carrageenan has been produced in the Philippines as well, with Indonesia following suit in 1988.

Genetic resources Branch, micropropagule and tissue cultures as well as clonal propagation from callus of *E. denticulatum* have been successful. However, selection for better cultivars in *E. denticulatum* has not resulted in tangible improvement.

Prospects High quality iota carrageenan is much in demand on the world market. Moreover, demand for the Chinese food market is considerable and, for the farmers, often more reliable than the unstable demand from carrageenan producers. Because of the differences in post-harvest treatment (washing in freshwater is conditional for use as food and detrimental to carrageenan quality) farmers determine which part of the crop is available for each commodity. The culture of Echeumoid algae for carrageenan production is only economically viable in areas with low labour costs. In the main production areas, productivity is now generally dropping because of diminishing daily growth rates, susceptibility to stress and 'ice-ice' disease. There is therefore a need to select new strains for genetic improvement of the stock. An additional problem is that intensive *Eucheuma* farming may have a negative ecological impact due to the production of volatile hydrocarbons.

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G.C. Trono Jr

Ganonema farinosum (J.V. Lamour.) K.C. Fan & Yung C. Wang

Acta Phytotax. Sin. 12: 492 (1974).

LIAGORACEAE

$2n$ = unknown

Synonyms *Liagora farinosa* J.V. Lamour. (1816), *L. cheyneana* Harv. (1855).

Vernacular names Philippines: baris-baris (Ilokano).

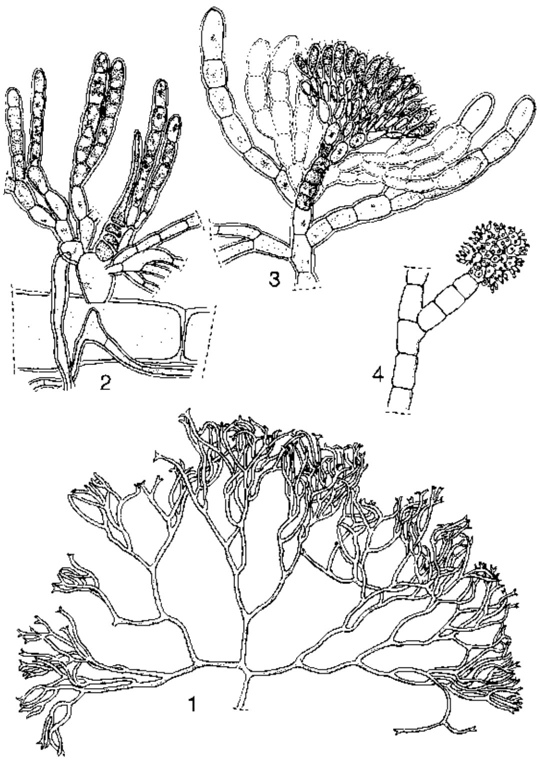
Origin and geographic distribution *G. farinosum* is widely distributed in the tropical waters of the Atlantic, Pacific and Indian Oceans. In South-East Asia it has been recorded from Thailand, Vietnam, Malaysia, Indonesia (Irian Jaya) and the Philippines.

Uses *G. farinosum* is used as human food and as a source of mucilage. In medicine, *G. farinosum* is applied as antibacterial agent and has an acetylene-containing fatty acid derivative which strongly inhibits venom PLA_2 of bees.

Production and international trade No production data are available for *G. farinosum*. Biomass is obtained from the abundant natural stocks.

Properties *G. farinosum* is not much grazed by fish (it is toxic to some of them) and has antimicrobial activity. It contains the toxic acetylene-containing lipids 4-hydroxynona-2E-en-1-a1, octadeca-5-7z–trinoic acid, octadeca-7 hydroxy-5yne-9z, 12z-dienoic acid and glyceryloctadeca-5yne-7z, 9z,12z-trinoate.

Description Thalli soft, lubricous, to about 13 cm tall, pinkish, lightly calcified, farinose, attached by small discoid holdfasts. Branching pattern basically dichotomous, with interdichotomal lengths decreasing towards terminal portions of the thallus; branches numerous, terete, about 1.5 mm in diameter, with apices forking into very short, acute, terminal branchlets. Assimilatory filaments about 445 μm long, 30 μm broad; cells



Ganonema farinosum (J.V. Lamour.) K.C. Fan & Yung C. Wang – 1, habit; 2, tuft of assimilatory filaments with rhizoidas and a 4-celled carpogonium on a medullary cell; 3, mature carposporophyte with involucre of sterile filaments; 4, spermatangial branch.

nearly moniliform throughout; cells of mature medullary filaments broad (more than 40 μm in diameter). Life cycle triphasic, diplo-haplontic and heteromorphic. Gametophytes dioecious. Antheridia borne in capitate clusters at tips of assimilatory filaments. Carpogonial branches straight to slightly curved, frequently compound; carposporophyte compact, with terminal carposporangia and little or no post-fertilization fusion of carpogonial branch cells. Tetrasporophytes only seen in laboratory culture, forming semicircular cushions (about 5 mm in diameter), *Acrochaetium*-like, filamentous, heterotrichous, with markedly ramifying creeping systems and sparsely branched erect monosiphonous parts, 14–18 μm wide, carrying scattered wide hairs on apical cells; each cell with stellate chloroplast and large pyrenoid. Tetrasporangia and monosporangia in small terminal clusters on erect filaments; tetraspores 14–16 μm in diameter, monospores 20–22 μm in diameter.

Growth and development Tetraspores of *G. farinosum* develop into *Acrochaetium*-like protonemal stages, with shorter and narrower cells than the tetrasporophytes and surrounded by mucilage of firm consistency. These protonemal stages soon grow into the gametophytic macroalgae.

Other botanical information The genus *Ganonema* K.C. Fan & Yung C. Wang was originally segregated from *Liagora* J.V. Lamour. principally on the relationship of the carpogonial branch and its location. Although this does not seem to be a consistent character, other characters are now used to retain this separation.

Ecology *G. farinosum* is found attached to rocky substrate among other algae in the subtidal and intertidal areas exposed to air during low tides.

Propagation and planting *G. farinosum* is not found in phycoculture.

Harvesting *G. farinosum* is harvested by hand-collecting only from natural populations.

Prospects *G. farinosum* is likely to continue being used as human food. Its antibacterial, antimicrobial, toxic and venom-inhibiting properties are interesting features for future pharmaceutical utilization.

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G.C. Trono Jr

Gelidiella acerosa (Forssk.) Feldmann & Hamel

Rev. gén. Bot., Paris 46: 533 (1934).
GELIDIELLACEAE
$2n = 12$

Synonyms *Gelidium rigidum* (Vahl) Grev. (1830), *Gelidiopsis rigida* (Vahl) Weber Bosse (1904).

Vernacular names Indonesia: intip-intip (Central Java), kembang karang (West Java: Banten), sangau (Lingga, Riau Archipelago). Philippines: culot (Ilocos Norte), gulaman, gayong-gayong, kulkulbot.

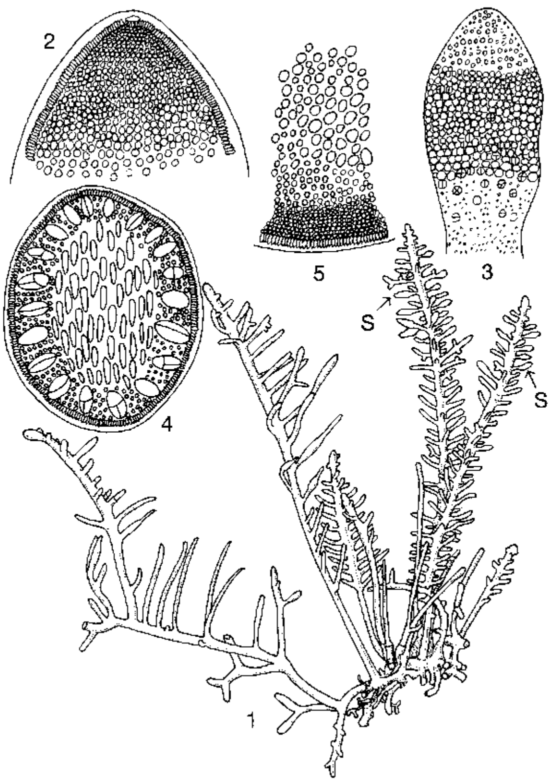
Origin and geographic distribution *G. acerosa* occurs in all tropical seas. In South-East Asia it is widely distributed in Burma (Myanmar), Thailand, Vietnam, Peninsular Malaysia, Indonesia, the Philippines and the southern coasts of Papua New Guinea.

Uses *G. acerosa* is one of the chief algae collected in Malaysia, Indonesia, the Philippines and Vietnam for the preparation of agar forming hard gellies. In Java and the Philippines, hand-collected specimens are also eaten fresh or prepared as a salad vegetable, or they are cooked and eaten mixed with rice. Collection for agar preparation and human consumption also takes place in India, China and Japan.

Production and international trade Recent representative data for *G. acerosa* are not available for South-East Asia. In India 50–300 t dry *G. acerosa* are collected each year in the south-eastern (Mandapam-Cape Comorin) and the north-western (Kathiawar Peninsula) parts. In 1976 world production of dried *Gelidium* (including *Pterocladia* and *Gelidiella*) was 5000 t. Around 1990, 350 t (dry weight) of *G. acerosa* was exported from India and China together. The only data available for the Philippines are from 1964, when a total of 200–300 t fresh *G. acerosa* was harvested. Production and international trade from South-East Asia mainly consists of sun-dried raw materials gathered from the wild. In 1977 dry *Gelidium* was valued at US$ 1000–1200 per t. Fresh or dried specimens are sold on the local markets and to traders.

Properties *G. acerosa* properties differ considerably according to locality and extraction methods. Per 100 g dry weight it contains: protein 4–18 g, fat 8–12 g, carbohydrates 9–24 g; and per 1 g dry weight also: sodium 2–38 mg, potassium 30–60 mg, calcium < 2 mg, phosphorous up to 0.035 mg. Data from the literature also differ considerably for gel strength (usually given as 'high') and sulphate content (usually given as 'low'). In India, chromium, lead and cadmium contents are high (μg/g dry weight): 1.61, 1.77 and 0.83, respectively. Antiviral activity against *Vaccinia* virus and Hepatitus-B virus (HBV) has been shown in extracts of this alga, as well as haemagglutinating activity on goat blood erythrocytes.

Description Thalli caespitose, up to 5 cm tall, several tufted, entangled, cylindrical, sometimes arcuate axes rising from decumbent, arcuate cylindrical axis, up to 650 μm in diameter, arising from creeping holdfast or stolon, up to 750 μm in diameter, attached to substrate by clusters of unicellular rhizoids. Erect axes cylindrical or very slightly compressed, up to 700 μm in diameter, sometimes gradually tapering toward the apices, usually with 1–3 orders of sparse to frequent filiform, distichously arranged opposite, subopposite or partly secund branchlets, up to 30 mm long, generally shorter apically and frequently incurved



Gelidiella acerosa (Forssk.) Feldmann & Hamel – 1, habit (S = stichidia); 2, apex (schematic); 3, stichidium with tetraspores; 4, transverse section of stichidium; 5, detail of transverse section of sterile part.

abaxially. Apical cell conspicuous, lenticular. External cortical cells anticlinally elongated in transection, up to 4 μm broad and 7 μm long. Internal cortical cells more rounded, grading into a medulla of larger elongated cells, about 30 μm in diameter, without rhizines (= hyphae). Only tetrasporic thalli common. Tetrasporangia in apical portion of modified swollen, conical branchlets (stichidia), oblong, 40–50 μm long, 20–30 μm broad, cruciately divided, sparsely and often irregularly dispersed over the branch, lower ones usually in more advanced stage of development than those near apex. Cystocarps unknown; spermatangial sori in rounded, hemispherical swellings; only occasionally observed.

Growth and development In most locations in the tropics *G. acerosa* occurs all year, with maximum occurrence and thallus size when temperatures are submaximal for the locality. In the Philippines (Ilocos Norte) it is most frequent in the dry season (November–April). After periods of maximum growth, formation of stichidia can occur and shedding of tetraspores takes place. 5000–10 000 tetraspores can be formed per g fresh weight. In India, however, reproduction is almost exclusively by vegetative propagation, while, in some populations in the Philippines, tetrasporic thalli predominate over vegetative thalli during some months of the year. Probably, maximal occurrence of tetrasporic thalli is in August, while the minimum is thought to be in the period November–February. Usually, tetrasporic plants are uncommon in *G. acerosa* from tide pools and upper intertidal habitats, while they are often common in the subtidal area. During the warmest periods, thalli begin to bleach and start dying. The mode of germination of tetraspores is of the *Gelidium* type, a type that has not been found in any red alga outside the *Gelidiales*. Sexual thalli appear to be lacking in the natural populations, although circumstantial evidence of a triphasic life cycle is provided by the haploid and diploid nuclear DNA levels obtained from plants in culture and derived from tetraspores.

Other botanical information In pre-1970 literature from India this alga is often cited as *Gelidium micropterum* Kütz. This is a misidentification; *Gelidium micropterum* also occurs in India but has no economic importance. Occasionally the name *Gelidium rigens* (C. Agardh) Grev. ex Kütz. is used for material belonging to *Gelidiella acerosa*. This is a misidentification and is probably mainly due to misspelling of the name. The correct name for *Gelidium rigens* is probably *Caulacanthus ustulatus* (Turner) Kütz., an alga that is not known to have economic value. Gelidioid algae is a designation used for all *Gelidium*-like algae, being seaweeds that are often harvested for high-quality agar production. Although quantities of commercial agar produced from other agarophytes (*Ahnfeltia* and *Gracilaria* spp.) are higher on a world-scale, the gel strength of these agars is not of the same quality as in the Gelidioid algae. Most gelidioid algae belong to the order *Gelidiales*.

The important economic species of gelidioid algae in most parts of the world belong to the genera *Gelidium* J.V. Lamour. and *Pterocladia* J. Agardh. In South-East Asia, however, the most common gelidioid agarophyte is *Gelidiella acerosa*.

Ecology *G.acerosa* occurs in the algal turf on surf-exposed and moderately wave-sheltered rocks and reefs in the eulittoral and sublittoral zone. It is also found in tide pools at higher levels on the shore and occasionally on shell fragments in shallow water. Tide pool *G. acerosa* plants are taller and bushier than intertidal and subtidal ones, but intertidal plants are better adapted to high light regimes. Usually, plants are covered with silt or occur underneath foliose seaweeds and can be characterized as 'shade adapted'. Full sunlight can be tolerated without much bleaching, but reversible photo-inhibition has been demonstrated. The alga can survive emersion and desiccation, but this results in lowering of the biomass, especially when coupled with exposure to strong sunlight. Some water movement is needed for growth, but highest water movement values in Hawaii are limiting. In the Philippines high gel strength is associated with seasonal high intensity water movement. Optimum growth in specimens from rock pools and from the shallow intertidal zone takes place in salinities of 35–40‰. It can survive short-period fluctuations of between 10–80‰. Upper intertidal plants especially tolerate low salinities (22–28‰) very well, but higher salinities (34–40‰) less well. For specimens from the northern Philippines, the optimum temperature for growth is 28°C; tetrasporic specimens show greater tolerance to temperature fluctuations than vegetative ones.

Propagation and planting Cultivation of *G. acerosa* is mainly still in an experimental stage. In India apical fragments have been grown in constant-depth plantings (attached to ropes and nets) and in constant-level plantings (attached to cement pipes and coral stones). In all cases growth was between 5–265 mg/g per day during the growth seasons. In 6 months the fragments had grown up to 7 times their original weight and the maximum population density became 129 g/m^2 wet weight. In natural populations a maximum growth of 131 g/m^2 per 6 months has been observed. Better growth and/or proliferation occurs after addition (under laboratory conditions) of 200–225 mg/l $NaNO_3$, or about 30 mg/l NaH_2PO_4, or 70–85 mg/l indole-acetic acid (IAA) or an increase in pH to 8.2–9.2.

Phycoculture In India, industrial production of agar from *G. acerosa* started around 1965. The Horizontal Single Rope Floating Raft method has had good results in India. It allows the growth and yield characters of the plants to vary according to the level at which the algae grow. This technique, however, is still not often used and harvesting is mainly done from natural stock. The growth rate in laboratory conditions has been increased by adding nitrate, phosphate, vitamins, or hormones. Although all results are promising, quantities needed differ considerably according to these experiments, as is also the case for the suitable N:P ratio. NH_4NO_3 was found to be more effective than urea, $NaNO_3$, or $(NH_4)_2SO_4$. Addition of vitamin C also promotes growth, as well as tetraspore production. Tolerance of *G. acerosa* to low salinities suggests that lowering the salinity in culture tanks could be used to eradicate other algae, such as dinoflagellates or filamentous green algae.

Diseases and pests In the northern part of the Philippines, grazing by fish and marine invertebrates has an insignificant effect on the biomass of *G. acerosa*, although in Indonesia (South Sulawesi) mono-line cultivation trials had to be interrupted because all specimens had been gnawed off by fish.

Harvesting Hand-collection during spring tides or by divers is the current method of harvesting. Mechanical collection has not been successful up to now. In the Philippines, harvest is by hand-picking at rocky shores during summer. In the northern part of the Philippines, the best harvesting period has not yet been established. One set of experiments suggested the dry season month of April, when biomass is optimal, agar extractable from the plants is of average quality, and gel qualities (gel strength, viscosity, gelling and melting temperatures, sulphate content and 3,6-anhydrogalactose or 3,6-AG percentage) are characteristically high. However, another set of experiments in the same geographic area resulted in the rainy months between July and September being selected as the best harvesting period, when yield is high and gel strength is maximal. In general the best harvest season for natural populations will be just after shedding of the tetraspores.

Yield Quantitative data on the agar contents of *G. acerosa* differ considerably, depending on the calculation methods used. Published data range between 12.6–50% (dry weight). Agar content and quality varies considerably during the seasons of the year, and this is usually associated with variations in water temperature, light intensity, photoperiod, and geography. There are also significant differences in yield and properties of agar of vegetative and tetrasporic thalli, with the highest agar yield and gel strength occurring in the vegetative thalli.

Handling after harvest *G. acerosa* to be sold fresh on the local market should be transported without delay. The harvested material is rinsed in clean sea water. If needed, the alga is bleached by repeated soaking and drying until the pigments are removed. Most specimens are sundried immediately after harvest and then sold. Dried ones used for future consumption are reconstituted to nearly fresh condition by blanching in boiling water for 2 minutes. Several different methods and procedures are used to extract the phycocolloids. In some areas in India agar is prepared by soaking sun-dried seaweed in 1% KOH solution for 12 hours, this is then washed free of alkali and boiled in water of 30–40 times its volume containing 2 ml/l acetic acid for 3–4 hours. Precipitated $CaCO_3$ is then added to achieve pH 6.5 and the product is filtered and gelled. Firm gel is sliced and frozen between −12°C and −18°C. After thawing, the shreds are soaked in 1% bleaching solution and exposed to the air (for 4 hours). Bleached shreds are washed free of chlorine with SO_2 and dried. This results in a pearl-white agar with a gel strength of 300 g/cm^2 in a 1.5% agar solution. If no freezing equipment is available agar can be flocculated by treating the filtrate with 90% industrial alcohol. The alcohol used can be redistilled. Another manufacturing method, also developed in India, involves the following steps: the dried seaweeds are subjected to cold strong acid pretreatment, followed by thorough washing with tap water, sorting out all contamination. They are given further pretreatment with hot alkali solutions. The algae are boiled at atmospheric pressure till the agar goes completely into solution. The solution is then filtered to remove insoluble impurities. The filtrate is gelled in trays and frozen for long periods. The agar is separated from the frozen water by thawing. Then the agar film is bleached with hypochlorite solutions, the residual impurities are chemically treated, the agar is sterilized and dried in hot-air ovens, then sliced into agar strips for use in the food market, or cut, ground and blended for pharmaceutical agar powder. Further chemical treatments are given to obtain pure grade agarose-rich agar. In food grade agar production *Gracilaria* spp. are mixed with *G. acerosa*.

Especially in the Philippines, many experiments have been carried out on methodologies of agar extraction in *G. acerosa*. Gamma-irradiation and pressure cooking both result in increased agar yields, but this agar is of lower quality, especially because of a decreased 3,6-AG percentage. The highest agar yield in the Philippines from *G. acerosa* (about 30%), with the highest gel strength (about 680 g/cm^2) was obtained by 0.5% acetic acid treatment for 1 hour at 16–20°C and extraction using steam pressure. The obtained agar is of bacteriological grade quality.

Prospects World demand for agar, and in particular for gelidioid agar, is higher than what the available seaweed can supply. This has often resulted in overharvesting of known seaweed populations which, in turn, has reduced subsequent harvests. As a consequence, the price of food grade agar increased out of proportion, causing a rapid decline in sales. Cycles occur every few years, discouraging the commercial producer as well as the consumer. If the future production of high quality agar is to be based on wild sources only, the fluctuating cycles will result in customers becoming discouraged by the undependable source. Thus the controlled cultivation of seaweed is essential to the future of the agar industry. If no satisfactory cultivation methods become available, hand-collecting of wild sources for the local market will remain the main way of utilizing *G. acerosa*. In all cases, a comprehensive management model, based on seasonal changes in the yield and quality of agar, should precede intensive harvesting and exploitation of these slow-growing agarophytes.

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W.F. Prud'homme van Reine,
A.M. Hatta & P. Gronier

Gelidium J.V. Lamour.

Ann. Mus. Hist. nat. (Paris) 20: 128 (1813) (= Essai Thalassioph.).

GELIDIACEAE

$x = 4–5$, $2n = 9–10$ or 20

Major species and synonyms

- *Gelidium amansii* (J.V. Lamour.) J.V. Lamour., Ann. Mus. Hist. nat. (Paris) 20: 129 (1813), synonyms: *Fucus amansii* J.V. Lamour. (1805), *Gelidium elegans* Kütz.(1868).
- *Gelidium australe* J. Agardh, Lunds Univ. Årsskrift 8(III, Mat. Nat. 6): 30 (1872).
- *Gelidium capense* (S.G. Gmelin) P.C. Silva, in

P.C. Silva, E.G. Meñez & R.L. Moe, Smithsonian Contr. Mar. Sci. 27: 26 (1987), synonyms (c.q. misapplied names): *G. versicolor* (S.G. Gmelin) J.V. Lamour. (1813), *G. cartilagineum* (L.) Gaillon (1828).
- *Gelidium crinale* (Turner) Gaillon, Dict. Sci. nat. (Cuvier) 53: 362 (1828), synonym: *Fucus crinalis* Turner (1811–1819).
- *Gelidium latifolium* Bornet ex Hauck – see separate article (as *G. spinosum*).
- *Gelidium pulchellum* (Turner) Kütz., Tab. phycol. 18: 18, Tab. 53, figs e,f (1868), synonym: *Fucus corneus* Hudson var. *pulchellus* Turner (1819).
- *Gelidium pusillum* (Stackh.) Le Jol., Liste alg. mar. Cherbourg: 139 (1863), synonyms: *Fucus pusillus* Stackh. (1795), *Acrocarpus pusillus* (Stackh.) Kütz. (1849).
- *Gelidium spinosum* (S.G. Gmelin) P.C. Silva – see separate article.

Vernacular names Indonesia: agar-agar (general), cin-cao (a Chinese term for agar jelly used in Ambon).

Origin and geographic distribution Several *Gelidium* are distributed worldwide, and are even found in cold temperate areas as far apart as the Falklands and south-western Norway. *G. amansii* is recorded in the Indian Ocean (Madagascar, Mauritius, India, Thailand, Peninsular Malaysia and Singapore) and Asian parts of the Pacific (Japan, the Philippines, Indonesia). There is, however, much discussion about the correct naming and identification of this species; especially its occurrence in the Philippines and Indonesia is challenged. Although this alga is often cited as found in South-East Asia, localities are not specified. *G. crinale* is found in all tropical and subtropical waters including those around Thailand, Malaysia, Vietnam (Nha Trang), the Philippines (Negros: Ilacan, Apo, Cebu) and Indonesia (Kai Besar, Lombok, Timor). *G. australe* and *G. pulchellum* are rather limited in distribution. The former species is well known in Australia and New Zealand. The latter has so far, in Asia, only been recorded in Burma (Myanmar), Peninsular Malaysia and Singapore, Vietnam (Nha Trang) and the Philippines (Luzon: Pangasinan, Batangas). *G. pusillum* is a name widely used for small *Gelidium* spp. occurring in temperate, subtropical and tropical waters. In South-East Asia it has been recorded in both the Indian Ocean in Burma (Myanmar), Thailand and Indonesia as well as in the South China Sea in Thailand, Malaysia, Vietnam and the Philippines. *G. capense* is possibly endemic to South Africa, although it has been often recorded (as *G. cartilagineum*) from many localities in the world, including the Philippines.

Uses In several subtropical countries especially *G. amansii* and *G. capense* (as *G. cartilagineum*) are extracted to produce high quality agar, a sulphated polysaccharide used widely in the food, pharmaceutical and cosmetic industries. Traditionally *Gelidium* is consumed as a vegetable and for making agar jelly. *Gelidium* is frequently eaten raw, but can also be steamed or cooked and mixed with spices before being served.

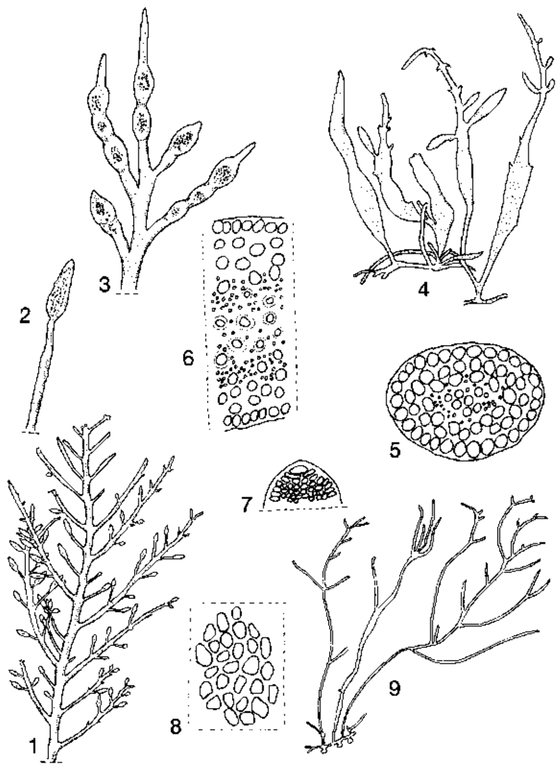
Production and international trade *Gelidium* is harvested in large quantities in subtropical waters such as in Japan, Korea, Spain, Portugal and Morocco. In the world market, the major source of agar comes from gelidioid algae (viz. the Gelidiales *Gelidiella* Feldmann & Hamel, *Gelidium* and *Pterocladia* J. Agardh) and from gracilarioid algae (Gracilariales: *Gracilaria* Grev. and *Gracilariopsis* E.Y. Dawson). Quantitative data which reflect the contribution of *Gelidium* to the agarophyte market reveal that in 1989 47% of the production of agarophytes was from Gelidiales and 53% from Gracilariales. It was stated that *Gelidium* alone accounted for 44% of all agarophyte production. In 1990 120 000 t (wet weight) of *Gelidium* were available for agar production, resulting in an estimated world production of 21 500 t (dry weight) of these dried seaweeds. Japan is currently the largest agar producer and exporter in Asia, the average agar export from this country being 713 880 t/year (1984–1986). In 1977 dry *Gelidium* had a value of US$ 1000–1200 per t. Amongst South-East Asian countries, only Indonesia and the Philippines export some *Gelidium*. However, that quantity is relatively small, i.e. 62 t from Indonesia and 3 t from the Philippines in 1984, and most probably includes *Gelidiella acerosa* (Forssk.) Feldmann & Hamel as is the case for the other data on *Gelidium* production in Indonesia. For 1989 the amount of *Gelidium* in Indonesia used for agar production was estimated at 1400 t (dry weight), while the total amount of *Gelidium* in Indonesia that year was estimated at 21 500 t (dry weight). In 1991 Indonesia probably exported a total 59 t of dried '*Gelidium*' to New Zealand and Italy.

Collection in Indonesia is spread over a wide area; the southern coast of Java yields about 30% of the total, the islands between Java and Timor about 25%, Sumatra about 15%, and the remainder comes from several areas to the North and East of Timor. The total area which could be used to produce *Gelidium* in Indonesia is 4700 ha, which would be capable of producing 4500 t (dry weight) from natural populations.

Properties The agar from gelidioid algae is better than that from other tropical agarophytes and the agarose component is dominant. The agar content in the gelidioids is usually low (19–29%). Extraction from *G. amansii* from Taiwan produces 22–36% agar and *G. capense* produces 15–20% agar. *Gelidium* contain water, fat, protein, fibre and minerals. For *G. amansii* from Japan 100 g dried algae contain: water 14–20 g, fat about 0.4 g, protein 16.1–22.5 g, fibre 10.5–13.5 g and minerals 3.5–8.5 g.

Description Plants of moderate to small size, 1–30 cm tall, with erect axis and usually laterally branched; branches firm, cylindrical or flattened, consisting of a central row of cells surrounded by pericentral cell and later paralleled by many other secondary medullary filaments; cortex cells assimilatory, short, compact, arranged in radial rows; rhizines generally present in the inner layers of the cortex or somewhat dispersed. Life cycle triphasic, haplo-diplontic, isomorphic and with dioecious gametophytes. Tetrasporangia cruciate, in sori in the cortex of tetrasporophytes. Spermatangia forming more or less extensive patches on branches of male gametophytes. Female gametophytes bearing three-celled carpogonic branches, which, after fertilization, form bilocular cystocarps with median septum embedded in the thallus.

- *G. amansii*. Plants forming dense tufts, reddish, rather rigid, cartilaginous, attached by a rhizomatous holdfast; erect thalli 10–30 cm tall, axis 0.5–2 mm wide, linear; branching pinnate or irregularly pinnate, in alternate or opposite manner, 4–5 orders, the upper portion usually with irregular ramification; branches and axes compressed at the lower part, 230–530 μm thick, and (sub)terete towards apices, with sharp and acute apices. Cross-section of branches showing a cortex of 1–4 layers of deeply pigmented small cells and a central part with rounded medullary cells; internal rhizines mainly outside the central tissue. Tetrasporangia on elongate-ovate or oblong-spatulate, claviform pedicellate branchlets. Cystocarps spherical and swollen, located beneath the apex of the branchlets.
- *G. australe*. Plants forming expanded tufts, purplish-red, attached on substrate by prostrate rhizoidal branches; erect thalli up to 8 cm tall, main axis 0.7–2 mm wide near the base, 0.4–0.7(–1) mm wide above; branching pinnate;



Gelidium. G. amansii (J.V. Lamour.) J.V. Lamour. – 1, portion of an upper branch of a tetrasporic thallus; 2, part of a terminal branch with tetrasporangia; 3, portion of an upper part of a branch of a cystocarpic thallus. G. pusillum (Stackh.) Le Jol.: var. pacificum W.R. Taylor – 4, habit; var. pusillum – 5, cross-section of an erect, terete part of a thallus; 6, cross-section of a flattened part of a thallus; 7, apex with apical cell in surface view; 8, cortical cells in surface view. G. crinale (Turner) Gaillon – 9, habit.

branches terete below and rather compressed toward the apices, not attenuate at the base, apex pointed; ultimate branchlets becoming gradually shorter on secondary axes so giving a pyramidal outline to frond. Cross-section of the axis showing rhizines profusely in inner cortex layers and rarely in the medulla. Tetrasporangia covering special clavate to tapering st· ·hidia with a short to medium stalk. Cystocarps in terminal swollen portions of branchlets.

- *G. capense*. Plants robust, bushy, up to 40 cm tall, several axes arising from a compact stoloniferous holdfast; dark brownish-red, texture tough cartilaginous. Axes several times pinnately branched, laterals opposite or alternate, not notably constricted at the base, especially when young markedly geniculate, inserted at relatively short intervals and overlapping each other. Axes compressed, up to 1.5 mm wide and about half as thick. Rhizines abundant, in younger branches in the central medulla, in older axes mainly concentrated in a subcortical layer. Tetrasporangial sori in slightly widened spatulate branch tips.

- *G. crinale*. Plants forming expanded tufts, purple to yellowish-brown, attached to substrate by widely-branching rhizome; erect thalli cartilaginous, 2–7.5 cm tall; branching irregularly alternate to pinnate; branches terete or cylindrical below, less than 300 µm in diameter, and tapering upwards towards the apices. Rhizines usually aggregated in the inner part of the cortex. Tetrasporangia in flattened and spatulate branchlets. Cystocarps in enlargements of branchlets, usually solitary.
- *G. pulchellum*. Plants forming dark red tufts, attached by clusters of branched rhizoids; erect thalli 2–10 cm tall, axes and branches terete, compressed or flat, the main branches broader than the laterals; branchlets often regularly or irregularly opposite. Tetrasporangia on flattened and elongated branchlets. Cystocarps in the central part of fusiform fertile branchlets, often with mucronate outgrowths.
- *G. pusillum*. Plants small, solitary or forming extended mats, reddish-violet, prostrate axes cylindrical, attached on substrate by small peg-like haptera; erect thalli 0.5–2.4 cm tall, terete below and flattened above, 0.5–0.8 mm wide, sparsely proliferating; branching simple or irregular; internal rhizines congested between innermost cortical cells and outermost medulla cells. Tetrasporangia irregularly arranged in spatulate terminal ramuli. Carpogonia in terminal part of branches.

Growth and development Growth of *Gelidium* in the wild has only occasionally been studied. In Indonesia, the growth of *Gelidium* in the wild seems relatively slow and heavily influenced by the season. The vegetative plants occur only in the period coinciding with the start of the rainy season. The success of vegetative growth is closely correlated with the success of their sexual reproduction and asexual propagation. The triphasic reproduction cycle of *Gelidium* is apparently similar to that of other red algae.

Ecology Species diversity in *Gelidium* is generally higher in tropical latitudes than in temperate ones. In temperate latitudes the sizes of the fronds are larger, the species are ecologically dominant and often commercially viable. Typically, *Gelidium* spp. occur on rocky substrate, often on coralline crusts, associated with rapid water movement and arranged in successive belts that can extend down to 25 m depth. The general absence of commercial crops in tropical waters has not yet been explained (Indonesia and India are exceptions). There is still no comprehensive understanding of the many roles of water movement in the biology of these algae. In tropical waters, *G. crinale* and *G. pusillum* often inhabit the rocky intertidal zone, frequently extending into the subtidal waters. *G. pusillum* can occupy substrates under various ecological conditions and occurs also on sandy and muddy stony bottoms. A mat of small *G. pusillum* is often found on the roots of mangroves. It also occurs mixed with other small algae in rock spaces in the upper tidal zone. Most *Gelidium* including *G. australe*, *G. capense* and *G. pulchellum*, however, need rather strong currents, clear water and high salinity.

Phycoculture Culture of *Gelidium* in tropical Asian countries has not been recorded, and at present all commercial crops of Gelidiales are presently from wild populations. Attempts to improve the natural production of *Gelidium* have been conducted on a small scale by spraying spores on rocks or artificial substrates, by settling spores on shells of molluscs, and by transplanting the plants. But so far the results have not been fully satisfactory and in field trials the *Gelidium* spp. are usually superseded by faster-growing seaweeds like *Ectocarpus*, *Enteromorpha* and *Ulva* spp. The same occurs with sporelings, which generally grow very slowly. These often also have to compete for space with sedentary animals, especially barnacles.

Diseases and pests *Gelidium* plants are usually regularly grazed by fish and invertebrates, and are often heavily covered by epiphytes. A genus of parasitic red algae (*Gelidiocolax* N.L. Gardner) is specialized to grow in *Gelidium* spp.

Harvesting *Gelidium* is harvested by hand, by cutting and scraping the alga from the substrate. Divers are often sent out to collect subtidal specimens. There are indications that scraping results in the destruction of creeping axes and may cause low recruitment and low regrowth. Cutting the seaweed, without damaging the holdfast, is considered to be necessary to retain harvestable populations. *Gelidium* that was washed up on the shore can also be collected, but the results are less predictable than from harvesting natural populations. Scientifically-based resource management programmes are needed to maintain maximum sustainable yields.

Yield In Indonesia in 1989 6.5% of all *Gelidium* was harvested.

Handling after harvest *Gelidium* seaweed collected for agar production must be dried as soon as possible to a moisture content of about 20%. The agar quality of dried *Gelidium* stays fairly stable during dry storage, even at tropical temperatures. To make traditional agar jelly, clean and fresh *Gelidium* is boiled in plenty of water for about an hour until all algal material has dissolved and a viscous colloid remains. Still, the colloid is sieved using fine-meshed textile. Sugar, flavouring (vanilla) and colour may be added to the colloid to improve taste. The last step is to let the colloid cool in containers at room temperature and form a firm gel. The gel is then cut into slices using metal wire, and sun-dried.

Prospects The prospects for *Gelidium* are bright, but supplies are too dependent on natural stocks. While the culture techniques for *Gelidium* remain undeveloped, it is very difficult to compete with (often cultivated) *Gracilaria* as an agar resource.

Literature |**1**| Akatsuka, I., 1986. Japanese Gelidiales (Rhodophyta), especially Gelidium. Oceanography and Marine Biology. Annual Review 24: 171–263. |**2**| Hatta, M.A. & Prud'homme van Reine, W.F., 1991. A taxonomic revision of Indonesian Gelidiales (Rhodophyta). Blumea 35: 347–380. |**3**| McHugh, D.J., 1991. Worldwide distribution of commercial resources of seaweeds including Gelidium. Hydrobiologia 221: 19–29. |**4**| McHugh, D.J., 1996. Seaweed production and markets. FAO Globefish Research Programme 48. 73 pp. |**5**| Melo, R.A., 1998. Gelidium commercial exploitation: natural resources and cultivation. Journal of Applied Phycology 10: 310–314. |**6**| Santelices, B., 1991. Production ecology of Gelidium. Hydrobiologia 221: 31–44. |**7**| Santelices, B., 1994. A reassessment of the taxonomic status of Gelidium amansii (Lamouroux) Lamouroux. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 4. pp. 35–53.

A.M. Hatta & R. Dardjat

Gelidium spinosum (S.G. Gmelin) P.C. Silva

Silva, P.C., Basson, P.W. & Moe, R.L., Univ. Calif. Publ. Bot. 79: 141–142 (1996).

GELIDIACEAE

$x = 4$–5; $2n = (9), 10$

Synonyms *Fucus spinosus* S.G. Gmelin (1768), *F. corneus* Huds. var. *attenuatus* Turner (1819), *Gelidium latifolium* Bornet ex Hauck (1883), *G. attenuatum* Thur. ex Bornet (1892).

Vernacular names Indonesia: agar-agar halus (Moluccas), kembang karang (southern coast of Central Java), kades (Garut, southern coast of West Java).

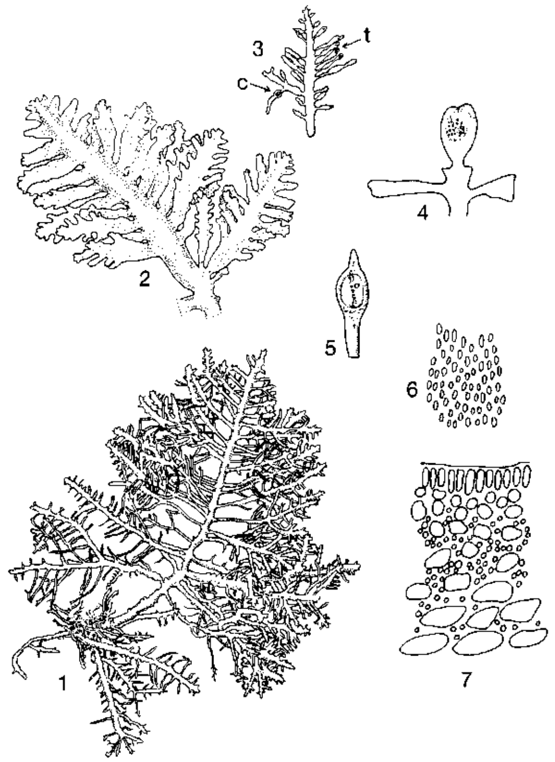
Origin and geographic distribution *G. spinosum* is widely distributed from the European North Atlantic (England) to Japan and the tropical Indo-Asian waters. In Indonesia it is found as forma *elongatum* (A.M. Hatta & Prud'homme) P.C. Silva along the southern coasts of Sumatra, Java and the Lesser Sunda Islands (Bali to Timor). It also occurs along the coast of Peninsular Malaysia.

Uses Dried *G. spinosum* is mainly sold to agar factories. In Indonesia, especially in the 1950s, this agarophyte was processed in large quantities by an agar factory in West Java. Traditional uses are as a vegetable and as raw material for making traditional agar jelly. Other raw materials used for agar include *Gelidiella acerosa* (Forssk.) Feldmann & Hamel, *Hypnea* and *Gracilaria* spp.

Production and international trade Production of *G. spinosum* in Indonesia is still dependent on natural stocks. In recent years, its contribution to the national agarophyte market has been negligible; most agarophyte materials on the market come from *Gracilaria* spp. The latter are already cultivated on a large scale, meeting national needs and also being exported.

Properties An analysis of material of *G. spinosum* from the south-western coast of Java indicated an agar content of 23.3–27.7%.

Description Plants of medium size, less than 10 cm tall, stolons relatively short and cylindrical, attached to hard substrates by peglike haptera, solitary, tufted; frond giving more or less a pyramidal outline; main axial thallus terete, compressed or almost flat, limited-growth thalli terete to slightly compressed with a single apical cell; branching opposite or bi-tetrapinnate. Cortical cells crowded, subquadrangular in cross-section; with 4–5 layers of inner cortical cells, subquadrangular to ovate, inwards gradually larger, and a



Gelidium spinosum (S.G. Gmelin) P.C. Silva f. elongatum (A.M. Hatta & Prud'homme) P.C. Silva – 1, habit; 2, portion of a vegetative terminal branch; 3, portion of a terminal branch, bearing both a cystocarp (c) and tetrasporangia (t); 4, tetrasporangial ramulus; 5, cystocarpic ramulus; 6, surface view of cortical cells; 7, cross-section of a branch.

core of medullary cells. Internal rhizines mostly concentrated between inner cortical cells, but often distributed amongst the outermost medullary cells. Tetrasporangia mostly on short spatulate terminal ramuli, rounded and irregularly arranged. Cystocarps large, protruding bulblike, on short flattened terminal ramuli.

Other botanical information The tropical form of this alga has been named *G. spinosum* forma *elongatum* (A.M. Hatta & Prud'homme) P.C. Silva (synonym: *G. latifolium* forma *elongatum* A.M. Hatta & Prud'homme).

Ecology In western Indonesia, *G. spinosum* inhabits shallow waters of the exposed coastal area typically with hard substrates, strong current and surf. It grows very well on rock-boulders in the lower eulittoral and subtidal zones where the seawater salinity is relatively high, i.e. more than 32‰.

Phycoculture *G. spinosum* is not commercially cultivated. There are two main obstacles in developing its culture: its small size and the difficulty of attaching vegetative germlings to artificial substrates.

Harvesting The traditional method of harvesting the natural stock of *G. spinosum* is by scraping the algae from the substrates. Harvesting of this agarophyte from the southern coast of Java takes place from July to December.

Prospects The characteristics of the agar of *G. spinosum* have not been seriously studied yet, but like other tropical gelidioid algae, e.g. *Gelidiella acerosa*. *G. spinosum* has good potential for being developed as agar resource, especially if phycoculture were to become feasible.

Literature |1| Hatta, A.M. & Prud'homme van Reine, W.F., 1991. A taxonomic revision of Indonesian Gelidiales (Rhodophyta). Blumea 35: 347–380.

A.M. Hatta & R. Dardjat

Gracilaria Grev.

Alg. brit.: 54 (1830).

GRACILARIACEAE

$x = 24$; *G. bursa-pastoris*, *G. coronopifolia*, *G. foliifera* (all non-Asiatic), *G. manilaensis* (Philippine): $2n$ = most probably 48; *G. 'verrucosa'* (European): $2n = 64$ (probably mis-identified *Gracilariopsis*); *G. arcuata*, *G. firma*, *G. salicornia* (from the Philippines), *G. 'verrucosa'* (European and Japanese): $x = 24$.

Nuclear genome sizes of *Gracilaria* spp. (*G. arcuata*, *G. edulis*, *G. firma* and *G. salicornia*) from the Philippines are in agreement with the assessment of $2n = 48$, except for *G. eucheumatoides*, of which the nuclear genome size comes close to that of representatives of the genus *Gracilariopsis*.

Major species and synonyms

- *Gracilaria arcuata* Zanardini, Mem. R. Ist. Venet. 7(2): 265–266, pl. V: fig. 2 (1858).
- *Gracilaria blodgettii* Harv. – see separate article.
- *Gracilaria bursa-pastoris* (S.G. Gmelin) P.C. Silva – see under *G. chouae*.
- *Gracilaria changii* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia – see separate article.
- *Gracilaria chouae* C.F. Zhang & B.M. Xia, in I.A. Abbott, Taxon. econ. seaweeds 3: 196–203, figs

9–14, 16–18, 22, 23, 25 (1992), synonyms: *G. bursa-pastoris* auct. non (S.G. Gmelin) P.C. Silva (1952, South-East and East Asian material), *G. parvispora* I.A. Abbott (1985, South-East and East Asian material).
- *Gracilaria coronopifolia* J. Agardh, Spec. gen. ord. alg. vol. 2, part 2(2): 592 (1852); probably the material recorded under this name in South-East Asia is another, yet undescribed *Gracilaria* sp.
- *Gracilaria edulis* (S.G. Gmelin) P.C. Silva – see separate article.
- *Gracilaria eucheumatoides* Harv. – see separate article.
- *Gracilaria firma* C.F. Chang & B.M. Xia – see separate article.
- *Gracilaria fisheri* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia – see separate article.
- *Gracilaria foliifera* (Forssk.) Børgesen, Revis. Forssk. algae: 7 (1932).
- *Gracilaria gigas* Harv., Proc. Amer. Acad. Arts Sci. 4: 331 (1860).
- *Gracilaria heteroclada* C.F. Zhang & B.M. Xia – see under *Gracilariopsis heteroclada* C.F. Zhang & B.M. Xia.
- *Gracilaria lemaneiformis* (Bory) Grev. – see under *Gracilariopsis lemaneiformis* (Bory) E.Y. Dawson, Acleto & Foldvik.
- *Gracilaria manilaensis* H. Yamam. & Trono, in I.A. Abbott, Taxon. econ. seaweeds 4: 95–99, figs 1–8 (1994).
- *Gracilaria salicornia* (C. Agardh) E.Y. Dawson – see separate article.
- *Gracilaria tenuistipitata* C.F. Chang & B.M. Xia – see separate article.
- *Gracilaria textorii* (Suringar) De Toni, Phyceae jap. nov.: 27 (1895), synonym: *Sphaerococcus textorii* Suringar (1867).
- *Gracilaria vermiculophylla* (Ohmi) Papenf., Phycos 5: 101 (1967), synonym: *G. asiatica* C.F. Zhang & B.M. Xia (1985), probably including *G. asiatica* var. *zhengii* C.F. Zhang & B.M. Xia (1992).
- *Gracilaria 'verrucosa'* – see separate article.

Vernacular names For all *Gracilaria* and *Gracilariopsis*: Philippines: gulaman, caocaoyan, gargararao.

Origin and geographic distribution *Gracilaria* can be found on almost all coasts of the world. It comprises probably more than 150 species, of which about 45 have been recorded from South-East Asia. For separate countries the approximate number of recorded species of *Gracilaria* is as follows: Vietnam 13, Thailand 14, Malaysia and Singapore 8, Indonesia 18, the Philippines 27 and less for Burma (Myanmar) and Papua New Guinea. In the older literature names often used are *G. verrucosa* or *G. confervoides* (L.) Grev. These names have also been used to include several *Gracilaria* spp. of more limited distribution. Of those species for which there is no separate treatment, *G. arcuata* seems to be an eastern species, not occurring in Burma (Myanmar), Thailand or Malaysia. It is difficult to summarize the distribution of *G. chouae*, *G. coronopifolia* and *G. foliifera*: due to taxonomic and nomenclatural uncertainties fully reliable data are not yet available. A species known as *G. coronopifolia*, however, is probably the most common one of the genus in the Philippines. *G. gigas* has been recorded from northern Vietnam, the Philippines (Sulu Islands) and eastern Indonesia, as well as from China and Japan. *G. manilaensis* is only known to occur in the Philippines. *G. textorii* has been recorded from many Asian countries; in South-East Asia it is listed for most countries, but not for Papua New Guinea. *G. vermiculophylla* mainly occurs in China, Japan and Korea, but has also been recorded from Vietnam.

Uses Most *Gracilaria* are used both for food and as raw material for the agar industry. Several species, especially *G. coronopifolia*, *G. edulis*, *G. eucheumatoides*, *G. firma*, *G. salicornia*, *G. tenuistipitata* and *G. vermiculophylla* (as *G. asiatica*) are often eaten raw or blanched as a vegetable (salad) or for the preparation of home-made jelly or sweet soup. Many of these algae are also used as feed for cultivated fish and invertebrates, as medicine (laxative, pulmonary complaints), as insect repellent, as fertilizer, in biogas production and for tertiary treatment of sewage. A seaweed-based pesticide and fertilizer is prepared from *Gracilaria* sp. It is very effective in preventing insect infestation, which is said to be due to the odour and taste of the crop plants sprayed with the pesticide. It is also mentioned that spraying hardens the stems and leaves of the crop plants, making them unpalatable for the insects. This might be due to the polysaccharide content of the seaweeds, which coats the plants. Additional insecticidal properties may be based on the production of hydrogen sulphide and other sulphides by anaerobic fermentation of the sulphate content of seaweed extracts. Crops sprayed with this seaweed as a fertilizer have shown increases in yield of up to 10–15%.

The world's first source of agar, from the middle of the seventeenth century, was *Gelidium* sp. from Japan. However, demand for agar exceeded the supply of these algae. Since then *Gracilaria* has played an important role in the production of this phycocolloid. The development of production processes through alkaline hydrolysis of sulphates has allowed a good quality food agar to be obtained from *Gracilaria*. The term 'agaroids' can be applied to *Gracilaria* agars produced without alkaline hydrolysis. These agaroids have greater sulphate content and much less gel strength.

Production and international trade Although several *Gracilaria* are collected and/or cultivated in the different countries of South-East Asia, in many reports only the genus name (*Gracilaria*) is provided. Data are then only available for the genus as a whole, and often include representatives of *Gracilariopsis*.

In 1991 3450 t of '*Gracilaria*' (dry weight) was harvested in Indonesia, which at the time was 13.5% of the world's *Gracilaria* production used for the agar industry. In 1993 5500 t of *Gracilaria* was farmed in Indonesia, especially in South Sulawesi (2000 farmers).

In the mid-1990s the *Gracilaria* harvest in Vietnam, mainly from cultivated stock, yielded 1500–2000 t (dry weight) per year. A large part is exported mainly to Russia, Japan and China and a smaller portion is used domestically. The total cultivated area of *Gracilaria* in Vietnam is about 1000 ha. In Malaysia only *G. changii* is cultivated on an experimental scale. In the Philippines production is mainly from natural populations, although *Gracilariopsis heteroclada* C.F. Zhang & B.M. Xia (often as *Gracilaria heteroclada* C.F. Zhang & B.M. Xia or as *Gracilariopsis bailinae* C.F. Zhang & B.M. Xia) is cultivated locally.

Gracilaria imports to Japan during the period 1984–1993 show a steady decline from over 10 000 t of dry seaweed in 1985 to about 3500 t in 1993, due to new agar production facilities in *Gracilaria*-producing countries. Exports recorded from South-East Asian countries to Japan (all dry weight) include: Indonesia 70 t (1984), 1120 t (1989) and 420–815 t/y (1990–1993), Malaysia 20 t (1989), Singapore 1 t (1993), the Philippines 1470 t (1984), 950 t (1989) and 285–850 t/y (1990–1993), Thailand 3 t(1984), and Vietnam 15 t (1984), 150 t (1987) and 60 t (1991). Cost and Freight (CF) prices for these seaweeds varied considerably between averages of 1.23–2.21 US$/t, although exports from countries in South-East Asia usually earned less, due to the greater tendency to become hydrolyzed during transport and storage.

Worldwide up to 5000 t of agar are processed annually from 25 000–30 000 t Gracilarioid algae which contain 15–20% agar on a dry weight basis. Of this, about 50% is harvested mainly from wild-growing algae in the cool-temperate waters of Chile and Argentina, and the remainder comes from cultures, mainly from fish pond culture in China, Taiwan and South-East Asia. For some years, more food grade agar has been obtained worldwide from *Gracilaria* than from any other agarophyte. In Indonesia total agar production increased from 150 t in 1984 to 450 t in 1993 and 980 t in 1994, produced in 11 agar-processing plants. In the Philippines there is a market for agar strips ('gulaman' bars), that are made by the extraction of *Gracilaria* seaweed. The actual demand is at least 30 t annually. Thailand produces about 3540 t per year of agar from locally collected *Gracilaria*. Local agar production in Vietnam, mainly from cultivated *G. tenuistipitata* and *G. vermiculophylla*, is estimated to be between 80 and 100 t/y and is mostly used for domestic purposes.

Properties Fatty acids in *Gracilaria* may have longer chains of carbon atoms then those occurring in most other seaweeds, although palmitic acid (16:0) is still the predominant saturated fatty acid also in *Gracilaria* seaweeds. *Gracilaria* agar has the advantage of greater synaeresis than *Gelidium* agar. Agar produced using properly applied synaeresis has a greater purity than that produced using the freezing-drying technique. This is due to the fact that the synaerized gel is superior to that obtained by draining the defrosted gel. Impurities remain in the dry agar in quantities directly proportional to the quantity of water remaining in the gel. These quantities of water are lower in well-synaerized gels.

Gelling temperatures of Philippine *Gracilaria* are ranging from 38–44°C, and melting temperatures from 86.6–94.6°C, while gel strength varies between 188 and 876 g/cm^2. Publications containing comparative data on worldwide agar yield and gel strength of *Gracilaria* often lack data from South-East Asia.

Most agaroids extracted directly from *Gracilaria* show a higher gelling temperature than *Gelidium* agar because of methoxylation, but also have a higher sulphate content. They also have a much lower gel strength. The higher sulphate content of Gracilarioids, however, can be greatly reduced by alkaline hydrolysis, which converts the 1-galactose-6-sulphate to 3,6-anhydro-L-galactose. In this way, the transformation of agaroid into genuine agar can be done by treating the seaweed before dissolving the polysaccharide contents.

From the chemist's point of view, seven kinds of agar from Gracilarioid algae can be recognized, and these can be separated into three major categories:

- high gel-strength agars with much non-ionic agarose,
- lesser gel-strength agars with ionic agarose,
- low gel-strength agars that have a high sulphate content.

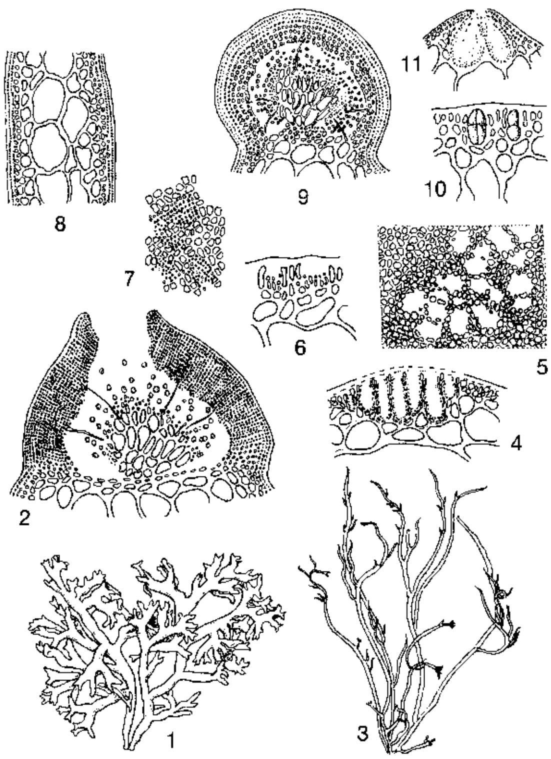
Agar of *G. arcuata* is of low quality. It produces a viscous solution that forms a soft gel (200 g/cm^2) with a high gelling point of 60°C. This *G. arcuata* agar consists of alternating 3-linked 6-0-methyl-β-D-galactopyranosyl and 4-linked 3,6-anhydro-2-0-methyl-α-L-galactopyranosyl units.

The agar melting points, gel strengths and ionic nature of the agarose are associated with the amounts of pyruvate, sulphate and methoxyl groups.

For Indonesian *G. coronopifolia*, gel strength and viscosity of the agar is lower than those for *G. edulis* and *G. fisheri*.

Aqueous extracts of *G. coronopifolia* revealed high gibberellin-like activity in laboratory bioassays, and also considerable auxin-like and cytokinin-like activity. Similar activity was measured for *G. arcuata*, while these values were much less in extracts of *G. eucheumatoides* and *G. salicornia*.

Extracts of some *Gracilaria* show antibiotic activity against a number of pathogenic bacteria and fungi.



Gracilaria. G. arcuata Zanardini – 1, habit; 2, longitudinal section of a cystocarp. G. gigas Harv. – 3, habit. G. manilaensis H. Yamam. & Trono – 4, cross-section of a thallus with deeply pot-shaped spermatangial conceptacula (Verrucosa-type); 5, detail of a surface view of a mature male thallus. G. textorii (Suringar) De Toni – 6, cross-section of shallow cup-shaped spermatangial conceptacula (Textorii-type); 7, detail of a surface view of a mature male thallus; 8, cross-section of a vegetative part of a thallus; 9, longitudinal section of a cystocarp; 10, detail of a cross-section of a tetrasporangial thallus. G. edulis (S.G. Gmelin) P.C. Silva – 11, cross-section of joint, multiple, deeply pot-shaped spermatangial conceptacles (Polycavernosa-type).

Description Plants usually bushy, arising from a small discoid base; frond cylindrical, compressed or flattened, fleshy to cartilaginous; branching dichotomous, irregular or proliferous; branches basically constricted or not. Medulla parenchymatous, consisting of large cells; cortex narrow, small-celled and assimilative. Life cycle triphasic, diplo-haplontic, isomorphic and dioecious. Tetrasporangia just below the surface of the frond. Spermatangia cut off from surface cells arranged in sori or in shallow or deeper conceptacles. Cystocarps hemispherical, with large cellular basal placenta tissue (gonimoblast) and prominent superficial pericarp composed of several layers of radiating cells; discharging through a pore.

- *G. arcuata*. Plant 6–10 cm tall, dark red; frond cylindrical, 3–4 mm wide, fleshy, robust, main axes gradually curved; branching irregularly pinnate, dichotomous or secund; branches and branchlets of almost the same diameter, attenuated towards the apex, branch bases constricted. Medullary cells 340–820 μm in diameter, cell walls 3–8 μm thick, cell transition to small cortex cells (6.7–13.5 μm × 5.5–8.8 μm) abrupt. Tetrasporangia not known. Spermatangia in deeply pot-shaped conceptacles, covering the entire inner surface of the conceptacle. Cystocarps globose, rostrate; pericarp 250–280 μm thick.
- *G. chouae*. Plant 15–20(–40) cm tall, light red, erect, solitary or caespitose, bushy, arising from

a small discoid base; frond cylindrical or slightly compressed, with fleshy texture; branching dichotomous, alternate or unilateral; branches brittle when fresh, 2–3 mm in diameter, branch bases constricted. Medullary cells 232–600 μm in diameter, cell walls 6.6–8.3 μm thick, cell transition to small cortex cells abrupt; cells of inner cortex 23–33 μm in diameter, outer cortex cells 10–17 μm × 7–10 μm. Tetrasporangia cruciate, up to 45 μm × 24 μm. Spermatangia covering the floor of depressed shallow conceptacles, 30–53 μm deep and 30–43 μm in diameter. Cystocarps conical, rounded, prominently protruding, 700–900 μm × 700– 900(–1200) μm, slightly rostrate or non-rostrate; pericarp 100–191 μm thick, cells arranged in two distinct layers.

- *G. coronopifolia*. Plant 4–20 cm tall, purplish-red to green-brown, cartilaginous to succulent, with a small discoid holdfast; frond umbrella-shaped or forming an entangled mass; axes cylindrical, not articulated; branching dichotomous and anastomosing; branches without constricted bases, 0.5–3 mm in diameter, tertiary branches often much thicker than main axes, apices often bifurcate. Medullary cells 183–470(–1000) μm in diameter, cell walls 6–9 μm thick, cell transition to small cortex cells (6.7–10.8 μm × 6.8–8 μm) gradual or abrupt. Tetrasporophytes often more robust than gametophytes. Tetrasporangia cruciate, spherical to oval, 20–23 μm × 30–40 μm. Spermatangia covering entire inner surface of deeply pot-shaped narrow-mouthed conceptacles, 33–60 μm deep. Cystocarps conspicuous, rostrate at ostiole, constricted at the base, 1000–1600 μm in diameter; pericarp 100–150 μm thick, with undifferentiated thick-walled cells.
- *G. foliifera*. Plant more than 5 cm tall, rigid; frond flattened, regularly dichotomously branched with entire margins; branches 2–15 mm wide. Tetrasporangia not known. Spermatangia in deeply pot-shaped conceptacles, covering entire inner surface of the conceptacle. Cystocarps with traversing filaments.
- *G. gigas*. Plant more than 30 cm tall, robust, coarse, cartilaginous, with disc-shaped holdfast; frond cylindrical; branching at short intervals, profusely or more scarcely irregular; branches 4–7 mm in diameter, thick, succulent, branch bases of only the long branches constricted. Medullary cells 560–1138 μm × 437–910 μm, cell walls 8–13 μm thick, cell transition to small cortex cells (5.5–13.5(–18) μm × 5.5–9.5 μm) abrupt; gland cells ovoid, 15–25 μm × 20–32 μm. Tetrasporangia cruciate, ovoid to oblong, 20–40 μm × 23–70 μm. Spermatangia covering the floor of depressed shallow conceptacles, 21–35(–40) μm deep, 26–40 μm wide. Cystocarps protruding when ripe, hemispherical, 1000–1500 μm in diameter, rostrate, slightly constricted; pericarp 100–145 μm thick, composed of somewhat compressed cells.
- *G. manilaensis*. Plant up to 60 cm or taller, purplish-red to greenish, caespitose; frond cylindrical, main axes up to 1.5 mm thick, fleshy to somewhat cartilaginous, not articulated; branching profuse, alternate or secund; branches similar to main axes, branch bases sharply constricted. Medullary cells polygonal, up to 570 μm in diameter, cell transition to small cortex cells (7.2–12.8 μm × 8.8–13.6 μm) abrupt. Tetrasporophytes often more robust than gametophytes. Tetrasporangia regularly cruciate, 35–40 μm × 24–27 μm. Spermatangia covering entire inner surface of deeply pot-shaped conceptacles, up to 71 μm deep, up to 50 μm wide. Cystocarps globose, up to 1000 μm in diameter.
- *G. textorii*. Plant 5–20 cm tall, dull or brownish-red to somewhat yellowish-red, coriaceous to membranous, caespitose; frond flattened, with cylindrical stipe, irregularly dichotomous or flabellate-cuneate below with round axillae, segments 1–2 mm wide, 500–800(–1000) μm thick, occasionally undulate, becoming slender in upper parts, margins entire or proliferous, apices blunt, bifurcate, or rather ligulate, fleshy to somewhat cartilaginous, not articulated; branching profuse, alternate or secund; branches similar to main axes, branch bases sharply constricted. Medullary cells 200–310 μm × 150–270 μm, cell transition to small outermost cortex cells (9.5–13.5(–16) μm × 6.5–11 μm) abrupt; hairs present. Tetrasporangia borne on both surfaces of almost entire frond, cruciate, 40–50 μm × 23–30 μm. Spermatangia covering the floor of shallow, cup-like conceptacles, 20–30 μm deep. Cystocarps globose, constricted at base, slightly rostrate, 1800 μm × 2000 μm.
- *G. vermiculophylla*. Plant 20–60 cm tall, purplish-brown to dark brown, occasionally greenish to yellowish; frond cylindrical, main axes 1–3 mm thick, cartilaginous, occasionally vermiform, not articulated; branching profuse, alternate or secund, with 3–4 orders of branches, last branching order tending toward slender unilateral laterals, branch bases not constricted. Medullary cells up to 400–490 μm × 270–365 μm, cell transition to small cortex cells (9–16 μm ×

4.5–6 μm) abrupt. Tetrasporangia cruciate or tetrahedral, 49–66 μm × 29–40 μm. Spermatangia covering entire inner surface of deeply pot-shaped conceptacles, up to 100–150 μm deep, up to 60–100 μm wide. Cystocarps triangular when young, becoming broader with age, slightly rostrate, constricted at base, 1500 μm × 1800 μm in greatest dimensions.

Growth and development Occasionally both tetrasporangia and gametangia are found on the same thallus in *Gracilaria*. Explanations include in situ germination of tetraspores, coalescence of spores or developing discs (formation of chimaeras), mitotic recombination, a mutation or initial failure of cell walls to form during development of tetraspores. Gametophytes and their parts may be smaller than tetrasporophytes. In general, diploids are often favoured in survival and growth rates.

Seasonal variation of biomass of wild populations of *G. manilaensis* has been studied in a coastal area in Iloilo, western Visayas (the Philippines) and compared with other algae. This alga was only frequent during three months during the dry season (November–May), occurring in quantities of 8.9–35.7 g/m^2. Growth rates of several *Gracilaria* have been measured in both an outdoor cultivation tank with flowing seawater and in an indoor closed recirculation system (aquatron). In material from Manila Bay, the Philippines (as *G. verrucosa*) maximum daily growth rates (24.4%) occurred in July at seawater temperatures of 25–26°C. At higher or lower temperatures growth was lower but still considerable. The mean daily growth rate for this alga in these outdoor tanks was 22.7 ± 0.1%, which was much higher than that for other tropical *Gracilaria*. Growth rates in the aquatron were much lower. In other experiments maximum daily growth rates for *G. manilaensis* (4.5 ± 0.4%) occurred at 25°C, while the alga grew less well at all other temperatures between 23–30°C. During cultivation experiments in the intertidal zone and in semi-enclosed ponds in the Philippines, however, daily growth rates of 1.6–5.5% were recorded for *G. manilaensis* (as *G. verrucosa*).

Other botanical information Because of the economic interest in its products, viz. phycocolloids, the study of Gracilarioid algae has spread rapidly throughout the world, resulting in numerous proposals for taxonomic and nomenclatural change. There has not yet been a monographic revision of *Gracilaria*. Its species are notably difficult in their taxonomy owing to poorly understood species limits, considerable variation in morphological features selected for classification, large number of taxa mostly studied only in a narrow geographic range and misapplication of species names due to lack of reference to type specimens. *Gracilaria* was established by Greville at which time it contained four species, while no type was designated. Schmitz lectotypified the genus with *G. confervoides* (L.) Grev., based on *Fucus confervoides* L., a later homonym of *Fucus verrucosus* Huds. Papenfuss advocated that the earliest correct name was *Fucus verrucosus* Huds. and made the combination *Gracilaria verrucosa* (Huds.) Papenf. Different lines of investigation have been followed, resulting in proposals on delimitation of taxa and in the search for new specific characters and characters that may be used to break up this large and highly variable genus into subgenera and add segregate genera. Names of genera that have been separated from *Gracilaria* include *Gracilariopsis* E.Y. Dawson, *Hydropuntia* Mont. and *Polycavernosa* C.F. Chang & B.M. Xia. In South-East Asia, however, most described differences between these genera are considered to be too technical for general acceptance, resulting in proposals to retain all species in the single genus *Gracilaria*. Nevertheless, the separation of the genera *Gracilaria* and *Gracilariopsis* is nowadays often followed, as is done in the present volume. The names *Polycavernosa* and *Hydropuntia*, however, which are full synonyms, are considered as included in the genus *Gracilaria*. On the basis of the diagnostic value of the characters of spermatangial structures, several types are established, resulting in distinguishing four subgenera:

- The *Chorda*-type, with continuously superficial spermatangia: subgenus *Gracilariella* H. Yamam. According to some authors, this subgenus includes the genus *Gracilariopsis*, although in the present volume this is considered as a separate genus.
- The *Polycavernosa*-type, with the occurrence of spermatangia in multiple cavities, borne near the periphery of the thallus: subgenus *Hydropuntia* (Mont.) C.K. Tseng & B.M. Xia.
- The *Textorii*-type, with the spermatangia forming shallow cup-shaped conceptacles: subgenus *Textoriella* H. Yamam.
- The '*Verrucosa*'-type, with the spermatangia forming deep pot-shaped conceptacles: the type subgenus *Gracilaria*.

Recent taxonomic research on type material has made it clear that the original material of *Fucus verrucosus* Huds. belongs to the separate genus *Gracilariopsis*.

The species *G. manilaensis* is similar to *G. blodgettii*, the occurrence and taxonomic position of which is still uncertain in South-East Asia. Frond length and width, as well as the number of branches of *G. blodgettii* are different, however *G. changii* is also rather similar and probably closely related to '*G. blodgettii*'. The same holds for *G. vermiculophylla*, but this species has been shown to be incompatible in reciprocal crosses.

Material identified as *G. bursa-pastoris* from Vietnam is in most cases re- identified as *Gracilariopsis heteroclada* C.F. Zhang & B.M. Xia and material identified as *G. coronopifolia* from Vietnam is often *G. edulis*.

Ecology Most *Gracilaria* grow abundantly in the intertidal zone, on rocky, sandy and muddy bottoms. These algae are often attached to small stones or shells, but also on larger rocks. Some *Gracilaria*, however, including *G. firma*, *G. tenuistipitata* and *G. vermiculophylla* can also grow abundantly when unattached in brackish pools and lagoons. These unattached algae are often especially suitable for cultivation. *G. manilaensis* occurs in sandy-muddy to coralline bottoms in shallow coves, well protected by surrounding islets and is permanently submerged. It is often associated with *Caulerpa* (green algae), such as *Caulerpa racemosa* (Forssk.) J. Agardh var. *peltata* (J.V. Lamour.) Eubank and *C. taxifolia* (Vahl) C. Agardh. It disappears at the beginning of the wet season, when heavy rainfall and storms start to occur.

Propagation and planting In *Gracilaria* phycoculture the usual method of propagation is by vegetative fragmentation, although propagation by spores has been described especially for *G. coronopifolia* and *G. chouae* (as *G. parvispora*). Thalli are chopped or split and bunches of branches or individual branches are used for planting (bottom-stocking) or broadcasting or for cultivation on ropes, either in fixed off-bottom frames, on floating long lines or on rafts. Gracilarioids usually regenerate easily when cut, a fortunate characteristic for the purpose of mass cultivation.

Selection of 'seedlings' is one of the most important factors for successful seaweed farming. Fresh, healthy and strong branches must be chosen and cut with a sharp stainless knife. Then the branches have to be washed with clean water before they are used. Stock seedlings can be maintained in a net pen or a floating cage. Initial planting for bottom monoline culture can be done on a beach or a platform near the selected site where the lines are to be placed. About 16 'seedlings' can be inserted in one 5 metre line. This operation should be done with the utmost speed, in order to prevent the algae from drying out. For pond culture cuttings are broadcast directly onto the muddy or sandy bottom of the impoundments.

Success in the farming of *Gracilaria* is highly dependent on the selection of an appropriate site. In open sea or bays the site should be protected from strong currents and wind. Areas with heavy freshwater runoff are to be avoided, but brackish water with good water flow can be used for pond culture. Ponds used for shrimp culture are usually also suitable for *Gracilaria* farming. Polyculture with shrimps, milkfish and/or crabs has been frequently mentioned to be successful. The ground should be firm and stable enough to permit easy installation of stakes. The most favourable factor in selecting a site is the availability of areas with natural *Gracilaria* stock. However, the absence of *Gracilaria* growth is not necessarily a negative sign. Before setting up a farm in a non-tested location, a test plant of 2.5 m × 2.5 m or a raft should be set up to determine the feasibility of the area chosen. When line cultures are used in areas with considerable tidal currents, the lines should be set to run parallel to these currents. These lines and their anchorage must be checked regularly and drift seaweeds that become entangled should be removed carefully.

Phycoculture *Gracilaria* cultivation can be carried out in tanks or raceways, excavated ponds with pumped water, the sea or semi-enclosed ponds and in suspended, spray, or drip culture.

Commercial phycoculture in South-East Asia is mainly done in the sea or semi-enclosed ponds.

Ponds for *Gracilaria* cultivation are usually rather small because thalli tend to be blown into concentrated areas in larger ponds. Wind-breaks perpendicular to the prevailing wind direction and short bamboo sticks (30–40 cm), anchored in the soft bottom substrate of the pond can help to prevent such concentrations. Water changes made every 2–3 days can help regulate salinity, mineral nutrient supplies and water temperature. Urea or ammonium sulphate fertilizer may be added at a rate of 3 kg/ha. Pig or chicken manure can be added in much higher quantities: 120–180 kg/ha. The pH of the water should be in the range of 7.0–8.0, preferably near 8.0. In tropical mangrove areas, where ponds are often built, the organic content of the mud used or exposed in the construction is initially high, which usually makes the pH too low. In time, the pH rises and the water quality may stabilize; only then will *Gracilaria* thrive. The depth of the pond water is usually kept at 30–40 cm, but at higher air temperatures, the pond depth may be increased to 50–60 cm.

In Vietnam especially *G. tenuistipitata* and *G. vermiculophylla* (as *G. asiatica*) are grown, mainly in brackish water lagoons and man-made ponds. They can grow in a wide range of salinities (5–22‰), but the best production is obtained within the salinity range of 15–22‰ and a temperature range of 25–28°C. In conditions of low salinity (below 10‰) and high temperatures (32–34°C) fertilizers have been shown to improve crop growth significantly. The growth of *Gracilaria* can, however, be drastically reduced or even ceased due to very low salinities during the rainy season.

Diseases and pests Contamination by agarolytic bacteria in warm water *Gracilaria* occurs easily, the most important being *Bacillus cereus*. This is, however, not the only cause of agar hydrolysis; the seaweeds' own agarolytic enzymes probably also cause enzymatic degradation. 'Ice-ice', referring to crop decay in *Eucheuma* and *Kappaphycus* spp., also occurs in Gracilarioid algae under conditions of low light, low water motion and low inorganic micronutrients.

Grazing by fish, sea urchins and molluscs can cause problems, as can sediment accumulation and epiphytes. In outdoor tank growth experiments *Gracilaria* is often heavily grazed by isopods.

Harvesting Because of the seasonal occurrence of most of the Gracilarioid agarophytes in the coastal areas of South-East Asia, continuous harvesting of natural populations of *Gracilaria* will result in a loss of productivity. Proper management of the natural stock by keeping to appropriate harvesting time, frequency and rules on quantities to be removed will improve the productivity of each species. Harvesting of natural stock should not be more than 50–75% of the available biomass, in order to allow enough 'seedlings' to regenerate for the next growing period.

Both in rope-farmed stock and in pond culture of unattached plants it is necessary to allow sufficient material for regeneration. In rope-farmed cultures this can be done by cutting thalli a few cm from the rope, in ponds by selective gathering or by special cultivation of 'seed' material.

When harvesting in ponds, 1/3–1/2 of the total biomass can be removed every 30–35 days in the best season for perennial species, and every 45 days in other months. For rope-farmed material, a growing period of 45–50 days is required for the first harvest. The individual harvested plants in rope cultivation should weigh approximately 500 g and about 100 g should be left on the line for continued growth. Successive harvesting may be done after about 35–40 days.

Yield An average yield of approximately 410 kg (wet weight) of seaweed can be expected after 45–50 days, from each 10 m × 10 m plot of line-grown *Gracilaria*, or 41 t/ha (wet weight) in pond culture. For *Gracilaria* wet to dry weight ratios vary between 8:1 and 12:1, resulting in a calculated production of about 4 t/ha (dry weight) every 45–50 days. In natural populations maximum production is probably 5t/ha/y (dry weight). Standing crops of most tropical Gracilarioid agarophytes yield up to 2 kg/m^2 of seaweed. This is considerably lower than for *Gracilaria* in temperate areas, which can reach up 7 kg/m^2. In general, a lower quality of agar (low gel strength, low 3,6-anhydro-L-galactose content, much sulphate and 4-0-methyl-L-galactose) is obtained from tropical pond-grown *Gracilaria* than from wild-growing algae.

The quality and yield of agar from natural populations of *G. manilaensis* show monthly differences. In May, when average monthly biomass is highest, the agar yield (about 20% of dry weight) is lower than in the other months (about 25% of dry weight), but gel strength is distinctly higher (about 350 g/cm^2 in May, 80–150 g/cm^2 in April and June). In May the agar gelling temperature is also higher for *G. manilaensis* than in the other months (about 42°C and 38–40°C, respectively), while the melting temperature of its agar is lower in May than during the other months (78.5°C and 80–83°C, respectively). Data on sulphate content of *G. manilaensis* from the Philippines are only available for May and June (about 16 μg/mg and 24,5 μg/mg, respectively).

The quality of the agar produced from *G. manilaensis* is similar to that of *G. changii*, but *G. manilaensis* gives a higher agar yield. In the Philippines, however, the quality of the agar produced from *Gracilariopsis heteroclada* is better. Moreover, the latter species occurs year-round whereas the *Gracilaria* spp. are seasonal in occurrence.

Handling after harvest Harvested *Gracilaria* should be cleaned on site and transported to a drying area. Before drying, the contaminants on the harvested thalli must be removed. Drying platforms with floorings made of straw or bamboo mat are best for obtaining good quality products. Rain water must be avoided. These seaweeds should never be dried directly on sand or soil. Once dried, they should be packed in bags, stored in a dry place and sold and transported as soon as possible. Bone-dry *Gracilaria* contains 18% of water. When used as a raw material for agar production all species of *Gracilaria*, unlike *Gelidium* spp., have to be processed without much delay and cannot be stored for use during years of lower availability. The agar contained in *Gracilaria* has a strong tendency to become hydrolyzed during storage, even under favourable conditions. This state of hydrolysis can totally ruin it as an industrial raw material. The agar content of *Gracilaria* from warm waters is likely to decrease within a few months, even when the algae are dried and stored under adequate conditions.

These agarophytes can be preserved for longer after collection by treating them with a sufficient concentration of NaOH at temperatures between 50 and 90°C, but marked losses in yield may occur. Sterilization by irradiation may result in loss of agar characteristics, particularly gel strength. The duration of the extraction period after 2% NaOH treatment of dried *Gracilaria* samples has considerable influence on agar yield and rheological properties of the extracted agar. Each species has an optimum length of the extraction period, during which agar with good rheological properties can be extracted. These rheological properties of agar gels are difficult to evaluate, however, especially because there is a lack of uniformity of measurement.

Genetic resources Cultures of Gracilarioids are not always stable. Different morphological strains isolated from a single *Gracilaria* plant may show differences in their agar characteristics. So far very little genetic selection in *Gracilaria* has been practised.

Prospects *Gracilaria* has now practically replaced *Gelidium* as the most important source of agar in the world. However, the short seasonal occurrence of several species (*G. changii* and *G. manilaensis* in the Philippines, *G. fisheri* in Thailand) makes these species unreliable sources of raw material for the agar industry, which requires a sufficient supply year-round. Indonesia has a growing agar market and agar-extraction industry, and demands already exceed the present supply. Research and development are needed to find the best *Gracilaria* spp. to grow. Optimum conditions for pond culture also require attention. *Gracilaria* cultivation in the Philippines and Malaysia may stimulate the development of agar strip production in the region. *Gracilaria* grown in culture in Thailand may also be used for that purpose, while part of the production of the seaweed can be exported to Indonesia.

The necessity of performing alkaline hydrolysis to obtain good quality agar for food use can cause considerable pollution in the outflows of the treatment installation. To lower the amount of waste, much research effort is being devoted to induce the transformation of 1-galactose-6-sulphate into 3,6-anhydro-L-galactose during the life of the seaweed.

Agarose is a derivate of high quality agar. Its yield can be 70–80% of that of the agar. The rather small market for this special product is expanding because of its current use in tissue culture and as a medium for electrophoresis. Demand is expected to remain high due to increased biotechnological and biochemical needs.

Gracilaria production for hydrocolloids means producing thousands of dry tonnes per year economically, in order for it to be cost competitive in the raw materials world market. *Gracilaria* farming is particularly attractive in low-labour-cost areas. Nevertheless, it is reported that most Indonesian *Gracilaria* are suitable material for agar extraction and that enough raw material is available to develop more agar extraction plants in Indonesia. Many *Gracilaria* are believed to form a potential source of methane.

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W.F. Prud'homme van Reine

Gracilaria blodgettii Harv.

Nereis bor. amer. 2: 111 (1853).

GRACILARIACEAE

$2n$ = unknown

Synonyms *Gracilaria cylindrica* Børgesen (1920).

Vernacular names Indonesia: agar-agar gros, agar-agar biru, sango sango (Sulawesi).

Origin and geographic distribution *G. blodgettii* is found along the tropical and subtropical coasts of the Atlantic Ocean (Caribbean, Florida), the Indian Ocean (Aldabra Islands, Seychelles, Mauritius, India, Sri Lanka, Andaman Islands, Australia) and the Pacific Ocean (China, Japan, Taiwan). In South-East Asia it has been recorded in Vietnam, Peninsular Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea. The type locality is Key West, Florida (United States).

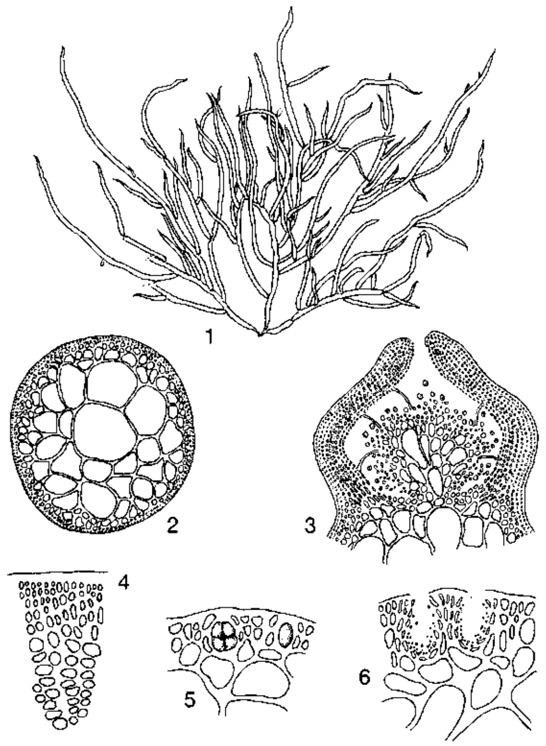
Uses The main use of *G. blodgettii* is as raw material for the agar industry. It is also consumed fresh as a vegetable (Sulawesi, Indonesia) and for making traditional jelly. In the Philippines it is used as human food, a source of agar, animal feed and fertilizer. It is used medicinally as a pectoral emollient and laxative, as well as for treating pulmonary complaints and stomach disorders.

Production and international trade There are no statistical data on the total production of *G. blodgettii* from the South-East Asian countries where it occurs. Figures from Vietnam, where this alga was recorded as forming part of the production of *Gracilaria* Grev., indicated a total production of about 8000–9300 t/y (fresh weight). Of this, 70% was *G. 'verrucosa'* (probably = *G. vermiculophylla* (Ohmi) Papenf.), 11% *G. blodgettii* (or *G. firma* C.F. Chang & B.M. Xia) and 19% other species. Other reports, from northern Vietnam, on *G. 'verrucosa'* and *G. blodgettii* state that the total production of dried *Gracilaria* in that area was about 1500 t in 1987. By 1993 production had reached 3000 t, and an area of about 2000 ha was under culture.

Data on agar production in Vietnam are conflicting. In 1963 the Ha Long canning factory in Hai Phong started agar production on a small scale, using a simple method. For this canning factory it is stated that a capacity was reached of 120 t agar per year. Some other state-owned enterprises had a production capacity of 15–20 t agar per year. In addition, about 50 families produced 3–10 kg/day each. Total production of agar-agar in 1993 was stated to be about 250 t, mainly used in the food industry for the domestic market. Other reports, however, indicate that the agar industry in Vietnam did not start until 1974 and estimate the total annual production of quality agar at 80–100 t.

Properties Gel strength of agar of *G. blodgettii* from Vietnam is 278 g/cm^2 when using alkaline treatment (2–4% NaOH) at 90–98°C for 1–2 hours. The gel strength of material from Malaysia, using non-alkaline treatment is 344 and 440 g/cm^2 for 1.5% agar solutions. The melting point of this agar is 76–88°C, and the gelling point 31–40°C. For the Philippines an agar gel strength of 963 g/cm^2 has been recorded, which is the highest for the Philippine *Gracilaria* species that have been tested so far.

Description Plant up to 10 cm tall; thalli single, erect, attached to the substrate by a discoid holdfast, with cylindrical branches reaching a width of up to 2 mm; branching pattern variable, ranging from frequently dense to sparse and from irregularly alternate to a tendency to become secund; third and higher-order branches often beset with short branchlets, 3 mm × 1 mm; branchlets spindle-shaped or obtuse; according to some descriptions, branch bases distinctly constricted. Plant in transverse section composed of two rows of small cortical cells followed inwardly by 2–3 layers of medium-sized cells; medulla consisting of large, nearly uniform cylindrical to oval very thick-walled cells (to 26 μm thick). Spermatangia organized into shallow Textorii-type spermatangial sori. Cystocarps hemispherical to globose, not constricted at the base. Transverse-section through mature cystocarps with sterile gonimoblast bearing tubular nutritive cells reaching a well-developed pericarp of 10–15 layers of cells.



Gracilaria blodgettii Harv. – 1, habit; 2, cross-section of a thallus; 3, longitudinal section of a cystocarp; 4, longitudinal section of the pericarp of a cystocarp; 5, cross-section of a tetrasporophyte with tetrasporangia; 6, cross-section of a male gametophyte with spermatangial conceptacles.

Growth and development Average daily growth rates in farm culture for *G. blodgettii* in the Philippines can be as high as 9.0%.

Other botanical information Material from Indonesia, identified as *G. cylindrica* Børgesen, has been described as the type of *Polycavernosa vanbossae* I.A. Abbott, later changed into *Gracilaria vanbossae* (I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia. However, type material of *G. cylindrica* has been excluded from *Polycavernosa vanbossae*. When the species was renamed to *G. vanbossae*, the Indonesian material was excluded as well. Specimens named as *G. blodgettii* from South-East Asia often belong either to *G. changii* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia or to *G. manilaensis* H. Yamam. & Trono, both species having branches that are markedly constricted at their bases. In some manuals *G. cylindrica* is cited as a direct synonym of *G. changii*. Material identified as *G. blodgettii* in Vietnam has often been re-identified as *G. firma*. Data for *G. blodgettii* and *G. cylindrica* are thus often also included in the data on other *Gracilaria* spp. In Harvey's original description of *G. blodgettii*, branches and branchlets are markedly constricted at their base of insertion and attenuated to an acute point; a medulla consisting of a few large thin-walled, irregularly polygonal cells and a cortex of vertically subseriate, very small, pigmented cells. This is not completely in accordance with the description given for South-East Asian material. Discussion on the correct identification and naming has therefore not yet been solved.

Ecology Plants of *G. blodgettii* are found in tide-pools or in shallow subtidal areas, attached to rocks, pieces of shells or coral fragments. In Vietnam, it is found abundantly from October to July. It is commonly cultivated in brackish water swamps along coastal areas of Hai Phong and Cat Hai island.

Propagation and planting Planting of *G. blodgettii* in pond culture in Vietnam is usually done by broadcasting. Plants are cultivated either as monoculture or polyculture with shrimp, fish and crab. Seeding density is 500–600 g/m^2. The size of monoculture ponds should be 0.5–5.0 ha, and for polyculture ponds 10–15 ha.

Phycoculture Salinity is the most important factor for growth of *G. blodgettii*. The optimal range is between 12 and 24‰. Water exchange at high and low tide should be about 30–50% and water level is maintained at 35–45 cm depth, 40–50 cm during sunny months, with a maximum level of 60 cm. The pond should be supplied with organic fertilizer such as cattle manure or poultry manure at the rate of 3–4 t/ha 3–4 times a year. In the Philippines the best conditions for growth of *G. blodgettii* (as *G. cylindrica*) are found in areas with high salinity (above 33‰), clear water, high pH (about 8.0) and a firm substrate (coralline flat).

Harvesting When a crop of *G. blodgettii* reaches over 1 kg/m^2 it can be harvested by hand or by rake and washed with pond water to remove sand, mud and dirt.

Yield Phycoculture of *G. blodgettii* in South-East Asian waters can result in the production of 3–4 t/ha/y (dry weight). The agar yield of this alga from Vietnam (after alkaline treatment) is 26.5%. Non-alkaline treatment in Malaysia resulted in agar yields of 15–26.3% and 7.6–28.8% respectively for two different localities. Highest agar contents for this alga in Malaysia were found in January and June. Periods of low salinity do not correspond to high agar yields.

Handling after harvest After washing *G. blodgettii* plants should be dried immediately to preserve quality. Dried material must be packed in bags and stored in a dry place.

Prospects The potential for increased production of *G. blodgettii* is high in some countries, especially Indonesia and Vietnam, because there are large areas of brackish water for cultivation. It is quite possible that data for *G. blodgettii* in the Philippines refer to a different species from that found in Malaysia and Vietnam. The national and world demands for agar seem to be increasing due to rapid developments in the cosmetic, pharmaceutical, food and textile industries.

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K. Lewmanomont & S.-M. Phang

Gracilaria changii (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia

Pacific Sci. 45(1): 23 (1991).

GRACILARIACEAE

$2n$ = unknown

Synonyms *Polycavernosa changii* B.M. Xia & I.A. Abbott (1987), *Hydropuntia changii* (B.M. Xia & I.A. Abbott) M.J. Wynne (1989).

Vernacular names Malaysia: sarer (known collectively with other *Gracilaria* spp.) (Malay, Kelantan). Thailand: sarai kao kwang.

Origin and geographic distribution *G. changii* seems to be restricted to southern Asia. It is widely found in Malaysia and the eastern part of Thailand. It is also recorded from Burma (Myanmar), Vietnam and the central Philippines.

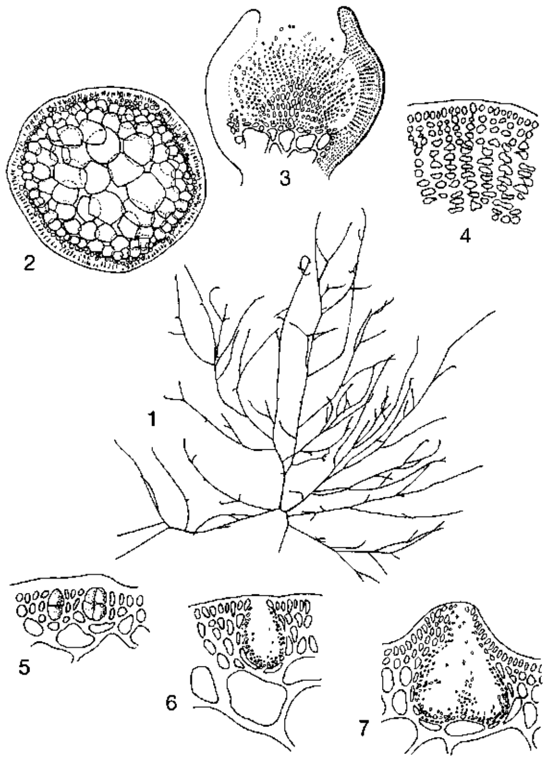
Uses Coastal communities, especially in Kelantan and Terengganu (eastern coast Peninsular Malaysia) and Selangor (western coast Peninsular Malaysia), collect *G. changii* for food. After washing, the seaweed is blanched in boiling water and served together with onions, chilli, grated coconut and lime juice, as an appetizer. In Thailand, large quantities are collected from the eastern coast of the Gulf of Thailand for food, agar extraction and abalone feed.

Production and international trade There is no known commercial cultivation of *G. changii*, but in Malaysia it is cultivated on an experimental scale.

Properties *G. changii* is an agarophyte with an agar content of 26–39% (dry weight) and an agar gel strength of 344–500 g/cm^2, when extracted after 7 days of cold alkali pretreatment with 4% NaOH and then soaked for one hour in 0.2% acetic acid. The agarose yield ranges from 13.4–16.3% while the agarose gel strength ranges from 737–950 g/cm^2. Acid and alkali pretreatment can increase the agar gel strength from 423 to 626(–650) g/cm^2 and decrease agar yield from 11 to 26%. Ash content of the agar ranges from 8.1–14.2%, while the gelling temperatures range from 32–45°C, and melting temperatures from 82–89°C.

The gel strength of *G. changii* from Thailand without pretreatment with alkali at room temperature was 714 g/m^2, with a sulphate content of 0.07%. For Philippine *G. changii* agar sulphate contents of 0.022–0.028% have been recorded. The separation of agarose directly from the seaweed gave a better yield than when its agar was used for fractionation. The gel strength of the agarose obtained ranged from 747–950 g/m^2 of a 1% gel concentration with a sulphate content from 0.17–0.4%, which is comparable to the sulphate values of commercial agarose. In conclusion, *G. changii* can be considered as producing good food-grade agar as well as agarose.

Description Thalli 6–20 cm tall, robust, purplish-brown to dark brown when dry, with one to many axes, 1.0–3.5 mm in diameter, arising from a disk-like holdfast or from a percurrent axis; branching of two to four orders, irregular, alternate or secund; branches turgid, cylindrical, 0.3–2.5 mm in diameter, abruptly constricted at the base forming a slender stipe, slightly swollen



Gracilaria changii (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia – 1, habit; 2, cross-section of a thallus; 3, longitudinal section of a cystocarp; 4, longitudinal section of the pericarp of a cystocarp; 5, cross-section of a tetrasporophyte with tetrasporangia; 6, cross-section of a male gametophyte with Verrucosa-type of spermatangial conceptacles; 7. cross-section of a male gametophyte of which the adjacent spermatangial conceptacles coalesc to form Polycavernosa-type spermatangial conceptacles.

distally, tapering towards the tip. Fronds in transverse section consisting of large rounded medullary cells (350–570 μm) with thick walls (7.5–20 μm), and 2–3 layers of small, pigmented cortical cells; transition of cells abrupt. Tetrasporangial and gametophytic plants similar in size and branching pattern. Tetrasporangia ovoid to elongate, densely scattered over frond surface, cruciately divided. Spermatangia covering the entire inner surface of conceptacles with multiple cavities or with oval to globose, solitary conceptacles. Cystocarps conical or semiglobose, up to 1.4 mm in diameter, slightly rostrate, not constricted at base; gonimoblast consisting of many small cells; basal absorbing filaments few, connecting inner and outer pericarp. Carposporangia rounded or ovoid, 18–32.5 μm in diameter; pericarp thick consisting of two kinds of tissue, the outer 5–6 rows of rounded to oval cells and the inner 7–9 rows of compressed cells.

Growth and development Recordings from the standing biomass of *G. changii* populations in two mangrove areas in Selangor, western coast of Peninsular Malaysia ranged from 58–98 g/m^2 (dry weight). In the Philippines, Iloilo (western Visayas) biomass in the dry season (January-June) ranged from 3–32.4 g/m^2. Culture trials in Selangor gave average growth rates of 1.7–3.3% per day when cultured on monofilaments in shallow mangrove ponds, 3.0–3.6% per day in shrimp ponds, and 2.5–8.4% per day in irrigation canals at the shrimp farm. In Malaysia *G. changii* is found producing carpospores and sporelings throughout the year. In Thailand, male and female gametophytic plants are found in similar proportions throughout the year but tetrasporic plants are usually in greater numbers.

Other botanical information *G. changii* has often been misidentified as *G. blodgettii* Harv. or its synonym *G. cylindrica* Børgesen, because of the similar constriction at the base of the branches at the point of insertion. This is also often the case in herbarium voucher specimens. Some data reported for *G. changii* are still confused with those on *G. blodgettii*. Some specimens also resemble *G. manilaensis* H. Yamam. & Trono.

Ecology *G. changii* grows abundantly on intertidal mudflats and attached epiphytically to mangrove tree roots, shells, pebbles, plastic debris and fish cages. It is also found on rocky-sandy substrates in water depths of 0.5–2 m, that can be exposed to strong waves during the wet season (June-October) in the Philippines. Salinity, rainfall, temperature and duration of sunshine together with nutrient levels in the water may affect the growth and development of *G. changii*. Salinity in the mangroves where much *G. changii* is found ranges 27–35‰. However the plants appear to have adapted to low salinities of 15–18‰ in culture ponds at Ban Merbok, Perak (Malaysia). *G. changii* standing biomass is higher during the warmer, drier months in Selangor (Malaysia) and this is also the case in natural populations in Iloilo (the Philippines). Better growth rates in Malaysia were exhibited by plants attached to monofilaments near the water surface than those submerged 20 cm below the water surface, in a shrimp pond and irrigation canal. Also the lower turbidity of the irrigation canal compared to the shrimp pond (Secchi disk readings of 36–43 cm in the pond versus 46–59 cm in the canal) produced better growth in the former. Light availability is therefore an important factor influencing growth.

Propagation and planting *G. changii* can be propagated vegetatively by cuttings or by tetraspores and carpospores. Average number of sporelings on raffia fibres set out amongst thalli in the mangroves in Morib (Malaysia) ranged between 7–55 per m raffia. In pond culture, monofilaments with attached thalli are best placed within the top 10 cm of the pond surface.

Phycoculture In experimental pond cultures in Malaysia, *G. changii* is cultivated in an integrated polyculture system with shrimps. When grown on monofilaments in shallow mangrove ponds, shrimp ponds and irrigation channels in the shrimp farm, maximum daily growth rates were 3.3%, 3.6% and 8.4%, respectively. In larger (0.5–1 ha) experimental ponds, 0.6–1.3 m deep, with a reduced salinity of 15–18‰ and in polyculture with the shrimps *Panaeus monodon* and *Lates calcifer*, the stock density on rafts of *G. changii* of 1–5 kg/m^2 doubles in 1 month. Best results are achieved at a stocking density of 2 kg/m^2. In pond culture, 1–2 daily water changes (up to 40% of total volume) are advisable.

Diseases and pests In integrated culture of *G. changii* with shrimps, the high nutrient content (in particular of N and P) in the ponds encourages heavy epiphytization of the thalli by other algae including *Chaetomorpha*, *Cladophora* and *Hypnea* spp. Rabbit fish are common grazers on *Gracilaria* spp.

Harvesting Plants of *G. changii* can be harvested after 1–2 months. Ponds have to be drained partially and plants are harvested manually from the floating rafts and monofilaments.

Yield The highest yield of *G. changii* obtained from a 0.5 ha pond is 8 t wet weight after one month of growth. During hot weather periods slightly higher agar yields are produced, although gel strength increases during periods of rainfall. Gelling and melting temperatures of agar of *G. changii* change little with the seasons.

Handling after harvest Harvested plants of *G. changii* should be cleaned and sun-dried on raised platforms, packed in bags and stored in a dry place.

Prospects There is a large market for agar, especially high quality agar and agarose, because of increasing use in biotechnological research. In Malaysia there is a large domestic market as shown by the imports of 189 t of agar in 1991. *G. changii* produces excellent food-grade agar and agarose, and is highly tolerant of harsh conditions and a wide range of salinities, as found in the mangroves. These characteristics make it a potentially interesting species for commercialization.

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S.-M. Phang & K. Lewmanomont

Gracilaria edulis (S.G. Gmelin) P.C. Silva

Univ. Calif. Publ. Bot. 25: 293 (1952).

GRACILARIACEAE

$2n$ = probably 48, a number found for several *Gracilaria* spp. and in agreement with the assessment of nuclear genome size for Philippine material of the present species

Synonyms *Fucus edulis* S.G. Gmelin (1768), *Polycavernosa fastigiata* C.F. Chang & B.M. Xia (1989), *Hydropuntia fastigiata* (C.F. Chang & B.M. Xia) M.J. Wynne (1989).

Vernacular names Indonesia: sayur karang, janggut monyet, bulung embulung (Java, Bali). Malaysia: agar-agar karang (Johore), sare (collectively with other *Gracilaria* spp.) (Malay, Kelantan). Philippines: gargararao (general name for all *Gracilaria* and all *Gracilariopsis* in Ilocos Province). Thailand: sarai woon.

Origin and geographic distribution *G. edulis* occurs in the Indian Ocean (East Africa, Mauritius, Laccadive Islands, India, Sri Lanka, Nicobar Islands, Andaman Islands) and in the Pacific Ocean (China, Japan, Micronesia, north-eastern Australia). In South-East Asia it is found in Burma (Myanmar), Thailand, Vietnam, Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea.

Uses *G. edulis* is collected by coastal communities for food and used either as a salad after blanching with hot water or as a source of home-prepared agar. It is also used for animal feed, as fertilizer and in waste water purification plants. In traditional medicine it is used especially for poulticing knee joints and to treat unhealthy sores.

Production and international trade A pilot seaweed farm for growing *G. edulis* in Maung Shwe Lay Gyaing in Burma (Myanmar) has ceased production by 1998 due to lack of local demand for an agar industry. The alga is now only grown in that country in small bays and inlets and in polycultures with the shrimp *Panaeus monodon* in shallow ponds.

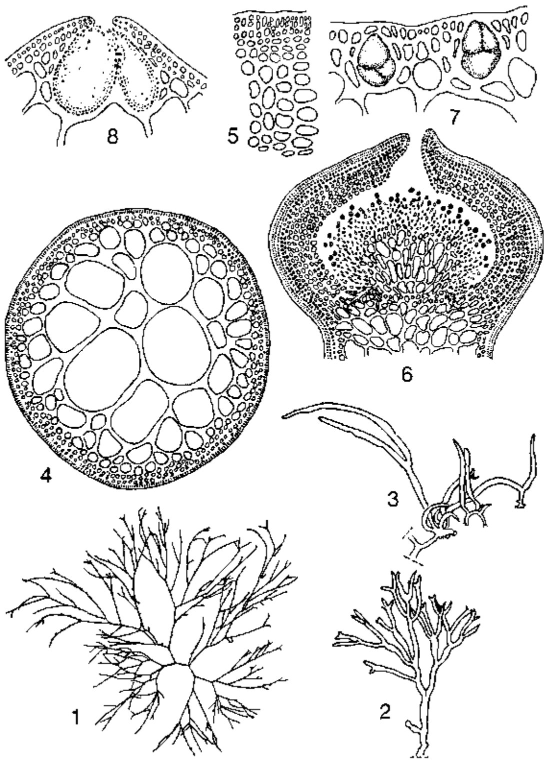
Properties *G. edulis* is an agarophyte producing an algal galactan which can be extracted in hot water and which gels at room temperature. The agar yield and quality vary depending on habitat, season, and reproductive phase. The agar gel strength ranges from 120–1100 g/cm². For the Philippines a gel strength of 890 g/cm² has been recorded. The melting and gelling temperatures range from 69.0–93.1°C and 35.0–54.0°C respectively. Alkali (3–10% NaOH) pretreatment doubles or triples the agar yield and also increases gel strength, although assessments on cultured plants do not report such an increase. Differences in NaOH concentration of between 3 and 10% for Indonesian *G. edulis* agar do not result in considerable increase of gel viscosity, but mean gelling and melting temperatures of 1.5% agar change between 45–54°C and 69–82(–85)°C respectively. For this material gel strength of 1.5% agar augments between 200–500(–900) g/cm² after pre- treatment with 3–10% NaOH, while hardness for the same material rises between 40–100(–150) g/mm² under these circumstances. Flexibility stays at low values: below 2 g/100 mm². The latter are the lowest values found for any commercial Gracilarioid agar. A sulphate value of 0.08% was found for *G. edulis* agar from Thailand that had not been pretreated with alkali. Constituents found in *G. edulis* material from India are as follows in g/100 g of dry seaweed: water 14.9, protein 7.6, fat 0.4, ash 43.4 (maximum in May), and in mg: calcium 830, phosphorus 53, iron 290, iodine 50. The energy value per 100 g dried seaweed is 1200 kJ. Per 100 g agar powder of *G. edulis* (from Sri Lanka) the following compounds are present (in g): water 18.5, ash 5.05, sulphate 2.27, sodium 2.7, potassium 1.5, calcium 0.92. Extracts of *G. edulis* (as *G. lichenoides*) show some antibiotic activity against pathogenic bacteria as well as against the protozoan *Trichomonas foetus*.

Description Thalli up to 27 cm tall, brownish-red, each arising from a discoid holdfast; branching dense and fastigiate, divaricate, dichotomous to trichotomous, up to 7 orders and with long branch intervals; branches 1–1.5 mm in diameter, cartilaginous, flexuous, with or without a constriction at their bases or with only a slight constriction, cylindrical, ending in pointed apices. Thalli in transverse section consisting of roundish thin-walled medullary cells, 100–300 μm in diameter, and 1–2 rows of small cortical cells, 5 μm in diameter, with an abrupt transition from medulla to cortex. Tetrasporangia ovoid to oblong, cruciate, 8 μm × 16 μm, scattered over surface of thalli. Spermatangia in deep, pot-like conceptacles with multiple cavities, which are arranged in groups of up to 10. Cystocarps globose, up to 2 mm, with rostrate tips and constricted at the bases; pericarp thick, consisting of 9–14 rows, cells of the outer rows oval, inner cells horizontally compressed, basal absorbing filaments robust with many branches.

Growth and development Average daily growth rates of *G. edulis* in experimental rope cultivation in the Philippines reached 9.0%, which is much higher than rates recorded for other areas.

Other botanical information Material often identified as *G. coronopifolia* J. Agardh from Vietnam turns out to be *G. edulis*.

Ecology *G. edulis* is commonly found in association with *G. changii* (B.M. Xia & I.A. Abbott) I.A.



Gracilaria edulis (S.G. Gmelin) P.C. Silva – 1, habit; 2, upper portion of branchlets; 3, rhizome-like creeping part, showing holdfasts and the bases of erect fronds; 4, cross-section of a thallus; 5, longitudinal section of a cystocarp; 6, longitudinal section of the pericarp of a cystocarp; 7, cross-section of a tetrasporophyte with tetrasporangia; 8, cross-section of a male gametophyte of which the adjacent spermatangial conceptacles coalesc to form Polycavernosa-type spermatangial conceptacles.

Abbott, C.F. Zhang & B.M. Xia. It grows abundantly on rocks, coral, mangrove roots, fish cages and on intertidal mud flats. Plants growing on fish cages have thicker primary branches and form much-branched fastigiate tufts. Entangled or loose clumps are formed on muddy substrate. In violent seas the plants readily break into pieces, which may form the starting points of new plants when they come into contact with a suitable substrate.

Propagation and planting *G. edulis* can be planted using similar techniques as those used for *G. changii*, i.e. vegetatively from cuttings or from tetraspores or carpospores. Thalli can be attached to monofilaments or rafts and cultured in ponds or the open sea. In rope culture, compact planting (5 g of plant material every 10 cm) results in higher yields than a wide planting pattern (10 g of plant material every 20 cm).

Phycoculture The most productive methods of phycoculture of *G. edulis* are on shallow reef-flat areas or in shallow tanks. Tests on Guam recorded rates of 5.4–7.6% and 4.5–5.1% growth/day respectively. In laboratory experiments growth was stimulated by adding phosphate and nitrate, but the agar yield diminished and agar quality was only slightly improved (less sulphate). In the Philippines co-farming *Eucheuma denticulatum* (Burm.f.) Collins & Herv. with *G. edulis* shows potential. The depth of water above the cultivated plants has considerable effect on the yield: maximum yield was obtained at a depth of 40–50 cm, and significantly less at depths of 0–25 cm or more than 1 m. Raft cultivation in India showed highest growth rates for plants tied to shallow ropes. Regrowth of thalli from the remaining frond bases after the first harvest is often not as good as the initial growth.

Diseases and pests Epiphytic algae like *Chaetomorpha*, *Cladophora* and *Hypnea* spp. may be found on the thalli of *G. edulis*. Especially in tank culture these epiphytes can almost totally cover the *G. edulis* plants. The epiphytes are removed by introducing grazers such as the topshell *Trochus niloticus* or the opisthobranch *Stylocheilus longicauda* or they are cleaned manually at weekly intervals. On coral reefs and in some cultures *G. edulis* is grazed by herbivorous fish. An adelphoparasite of yet unknown identity has been recorded growing on and in *G. edulis* from Manado (Sulawesi, Indonesia).

Harvesting In India it is recommended that *G. edulis* be harvested by cutting the thalli just above the base. The first harvest is done three months after planting, and further harvests are made quarterly.

Yield In north-eastern Australia the agar yield of *G. edulis*, when extracted without alkali treatment, ranges from 12.5–26.0% (dry weight). This is lower than that of most commercial Gracilarioid agarophytes, but the agar yield of alkali-treated material is within the same range as in other *Gracilaria* spp.

Handling after harvest Harvested plants of *G. edulis* should be cleaned and dried, packed in bags and stored in a dry place.

Prospects Although *G. edulis* is collected for agar extraction, the potential for commercial exploitation is limited by the low agar yield, low gel strength and low gelling temperature.

Literature |1| Gerung, G.S., Terada, R., Yamamoto, H. & Ohno, M., 1999. An adelphoparasite growing on Gracilaria edulis (Gracilariophyceae, Rhodophyta) from Manado, Indonesia. In Abbott, I.A. (Editor): Taxonomy of economic seaweeds 7. pp. 131–136. |2| Nelson, S.G., Tsutsui, R.N. & Best, B.R., 1980. A preliminary evaluation of the mariculture potential of Gracilaria (Rhodophyta) in Micronesia: growth and ammonium uptake. In: Abbott, I.A., Fostert, M.S. & Eklund, L.F. (Editors): Pacific seaweed aquaculture. California Sea Grant College Program, La Jolla, California, United States. pp. 72–79. |3| Raju, P.V. & Thomas, P.C., 1971. Experimental field cultivation of Gracilaria edulis (Gmel.) Silva. Botanica Marina 14: 71–75. |4| Rebello, J., Ohno, M., Ukeda, H. & Sawamura, M., 1997. Agar quality of commercial agarophytes from different geographical origins: 1. Physical and rheological properties. Journal of Applied Phycology 8: 517–521. |5| Thomas, P.C. & Subbaramaiah, K., 1990. Studies on the shedding of tetraspores in Gracilaria edulis (Gmel.) Silva from Mandapam Region. Phycos 29: 141–147.

S.-M. Phang, K. Lewmanomont & P. Gronier

Gracilaria eucheumatoides Harv.

Proc. Amer. Acad. Arts Sci. 4: 331 (1860). (*'eucheumioides'*)

GRACILARIACEAE

$2n$ = probably 48, although assessment of nuclear genome sizes of *G. eucheumatoides* from the Philippines suggests a size which comes close to that of representatives of the genus *Gracilariopsis* E.Y. Dawson, which probably has $2n = 64$

Vernacular names Indonesia: duyung (Bangka, Lingga). Philippines: canot-canot (Ilokano), caocaoyan, cawat-cawat.

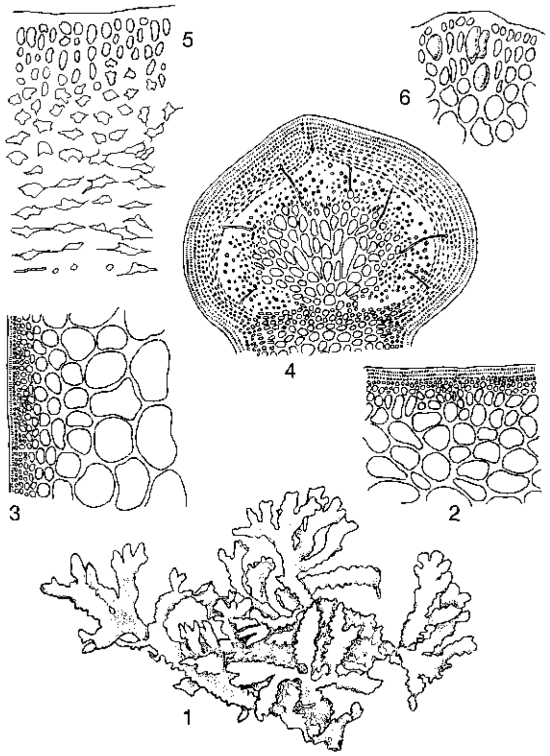
Origin and geographic distribution *G. eucheumatoides* is found along tropical and subtropical coasts in the Indian and Pacific Oceans. In South-East Asia it has been recorded from Burma (Myanmar), the eastern coast of Thailand, Vietnam, Malaysia, Indonesia, the Philippines and Papua New Guinea.

Uses *G. eucheumatoides* is used as a source of agar and as food (salad, or stew mixed with vegetables or as dessert gel). In Indonesia it is also used as a medicine to treat stomach ailments, goitre and urinary diseases. Other uses include animal feed, fish bait and insect repellent.

Production and international trade No information on the production of *G. eucheumatoides* is available. It does not lend itself to farming due to its slow growth and very strict ecological requirements. All production is from wild populations.

Properties *G. eucheumatoides* contains a good quality sugar-reactive agar, a hydrocolloid used in the food and in pharmaceutical and biotechnological industries. The general quality of agar from *G. eucheumatoides* is less than that of *G. manilaensis* H. Yamam. & Trono or *Gracilariopsis heteroclada* C.F. Zhang & B.M. Xia, but this quality can be improved to meet gel standards of the food industry by adopting an optimized alkali pretreatment in the agar extraction. Extraction methods involving alkali pretreatment (10% NaOH) at high temperatures (90°C) for 2 hours resulted in a good agar yield with a maximum gel strength of 432 ± 43 g/cm^2 for a 1.5% agar solution. Higher extraction temperatures and longer extraction times may result in even higher gel strengths, but a substantially lower yield. The alkali-treated *Gracilaria* agars contain higher 3,6-anhydrogalactose contents and lower sulphate levels. Strongest gels were obtained in July, but there is no distinct seasonal pattern for gel strength in this alga, while high agar yields are generally correlated with lower gel strength. Viscosity of the *G. eucheumatoides* agar (measured at 75°C) increases progressively from September (lowest value: 10 cP) to May (highest value: 320 cP), and thus is higher during the rainy season (May-October), while gelling and melting temperatures of the gel are generally higher during the dry season (December-March). The seasonal variations in contents of sulphate and 3,6-anhydrogalactose are generally small. The alga contains in g per 100 g dry matter: water 12.9, protein 7.9, fat 0.05, starch/sugars 58.4 and fibre 3.0.

Description Thalli greenish to purplish, cartilaginous in texture, thick and fleshy, forming loose or thick prostrate clumps, 3.4–8 cm long, attached to substrate by means of many haptera; branching irregular, dichotomous to alternate; branches flattened, irregular in width, up to 1 cm broad and with coarse, sharp teeth or short marginal spines. Medullary cells 130–132 μm in diameter, cell walls 3–6 μm thick, cell transition to cortex cells (20–30 μm to 7–13.5 μm × 4.5–9.0 μm) gradual. Gland cells elongate, 15–20 μm × 35–50 μm. Tetrasporangia cruciate, spherical, elongate in transverse section, 24–40 μm in diameter. Cystocarps globose, rarely constricted at its base, with



Gracilaria eucheumatoides Harv. – 1, habit; 2, cross section of a thallus; 3, longitudinal section of a thallus; 4, longitudinal section of a cystocarp; 5, longitudinal section of the pericarp of a cystocarp; 6, cross section of a tetrasporophyte with tetrasporangia.

pericarp 215–365 μm thick, differentiated into two layers.

Growth and development *G. eucheumatoides* is known to be very slow growing.

Ecology *G. eucheumatoides* occurs on rocks in the intertidal and subtidal zones in open sea or coral areas. It does not grow on soft substrates or in unattached populations.

Propagation and planting *G. eucheumatoides* is not grown in phycoculture.

Phycoculture There is no specific cultivation method for *G. eucheumatoides*. However, of the three methods used for other *Gracilaria* spp. the bottom-stocking method may be appropriate. This method involves the transfer of vegetative thalli, which are naturally attached to small stones and shells, to areas where an increased density is required. 10 mm mesh nylon, laced over rocks to keep thalli in place, can be used.

Harvesting Selection of the best harvesting time for *G. eucheumatoides* depends on the intentions of the collector. To obtain a maximum agar yield harvesting is done during other months of the year than for obtaining optimum gel strength. If the intention is to obtain both a maximum agar yield and an optimal gel strength, a July harvest is recommended in the northern Philippines. This suggestion, however, is based on experiments executed in a single locality only, while experiments in other localities nearby may result in different recommendations.

Yield The agar yield of *G. eucheumatoides* from samples from natural stock in the northern Philippines ranged from 20–29% (dry weight). It was lowest in March and highest in May.

Handling after harvest Harvested plants of *G. eucheumatoides* should be cleaned and dried, packed in bags and stored in a dry place.

Prospects *G. eucheumatoides* is a good source of sugar-reactive agar.

Literature |**1**| Abbott, I.A., 1992. New records and a reassessment of Gracilaria (Rhodophyta) from the Philippines. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 4. pp. 111–118. |**2**| Critchley, A.T., 1993. Gracilaria, Gracilariales, Rhodophyta: an economically important agarophyte. In: Ohno, M. & Critchley, A.T. (Editors): Seaweed cultivation and marine ranching. Japan International Cooperation Agency, Yokosuka, Japan. pp. 89–112. |**3**| Istini, S., Zatnika, A. & Sujatmiko, W., 1998. The seaweed resources of Indonesia. In: Critchley, A.T. & Ohno, M. (Editors): Seaweed resources of the world. Japan International Cooperation Agency, Yokosuka, Japan. pp. 92–98. |**4**| Villanueva, R.D., Montaño, N.E., Romero, J.B., Aliganga, A.K.A. & Enriquez, E.P., 1999. Seasonal variations in yield, gelling properties, and chemical composition of agars from Gracilaria eucheumoides and Gelidiella acerosa (Rhodophyta) from the Philippines. Botanica Marina 42: 175–182. |**5**| Villanueva, R.D., Pagba, C.V. & Montaño, N.E., 1997. Optimized agar extraction from Gracilaria eucheumoides Harvey. Botanica Marina 40: 369–372.

G.C. Trono Jr

Gracilaria firma C.F. Chang & B.M. Xia

Studia Mar. Sin. 11: 143–144, 162–163, figs 38, 39 (1976).

GRACILARIACEAE

$2n$ = probably 48, a number found for several *Gracilaria* spp. and in agreement with the assessment of nuclear genome size for Philippine material of the present species

Vernacular names Thailand: sarai woon.

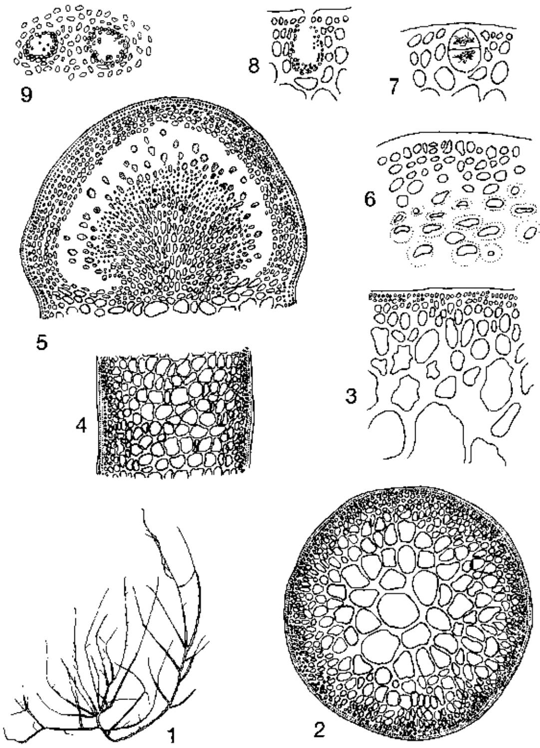
Origin and geographic distribution *G. firma* seems to have a fairly limited distribution. The type locality is Guangdong Province, China. In South-East Asia it has been recorded in eastern Thailand, Vietnam, Peninsular Malaysia and the Philippines.

Production and international trade There is some production from phycoculture of *G. firma* in the Philippines and northern Vietnam, but exact data are not available. This alga is used in commercial production in the Philippines because of the good quality of its agar.

Properties *G. firma* produces an algal galactan which can be extracted in hot water and gels at room temperature. Gel strength of agar of the non alkali-treated *G. firma* from wild populations in the Philippines is 765– 876 g/cm^2. Melting point of this agar is around 94.6°C, gelling point between 40 and 42°C. Both melting temperature and gel strength are higher than those determined for other Philippine *Gracilaria* spp.

Description Thalli erect, 4–20 cm tall, terete, caespitose or solitary, robust and rigid, arising from a disklike holdfast; branches 1–4 mm thick; branching alternate to irregularly alternate, with marked constriction at the base, either few orders of branching with long, cylindrical branches, and blunt apices with or without some furcations, or many orders of branching with short last-order branches forming clusters with acute or blunt apices. Thalli in transverse section with medulla of many layers of cells, 230–360(–500) μm in diameter, with cell walls 10–20 μm thick; cortex only 1–2 cells thick; cell transition of medulla to cortex gradual. Tetrasporangia scattered over surface of thalli, ovoid to spherical, 18–38 μm in diameter; tetraspore with conspicuously pigmented stellate central body. Spermatangial conceptacles in cavities (Verrucosa-type), 35–60 μm wide and 50–80 (–116) μm deep. Cystocarps conical or semiglobose, rostrate with or without constriction at base, 1–1.3 mm tall, 0.8–1.2 mm wide; gonimoblast filaments abundant, composed of small, dense and richly protoplasmic elongate cells; absorbing filaments scarce; pericarp 83–95 μm thick, 8–15 rows of undifferentiated cells with distinct cell walls.

Growth and development *G. firma* can be grown in outdoor cultivation tanks with flowing seawater as well as in indoor, closed-recirculating systems (aquatron). In outdoor experimental cultivation tanks in Japan with material from Thai-



Gracilaria firma C.F. Chang & B.M. Xia – 1, habit; 2, cross-section of a thallus; 3, detail of cross-section of a thallus; 4, longitudinal section of a thallus; 5, longitudinal section of a cystocarp; 6, longitudinal section of the pericarp of a cystocarp; 7, cross-section of a tetrasporophyte with tetrasporangia; 8, cross-section of a male gametophyte with spermatangial conceptacles of the Verrucosa-type; 9, surface view of a detail of a male gametophyte, showing the ostioles of the spermatangial conceptacles.

land (Trat), maximum daily growth rates (10.8%) occurred in July at seawater temperatures of 25–26°C. At lower temperatures later in the year daily growth was much lower, while at higher temperatures (27–28°C) later in the year daily growth was still considerable. The mean daily growth rate for *G. firma* in these outdoor tanks was 8.3 ± 1.5%, which was lower than for other tropical *Gracilaria* spp. Growth rates in the aquatron were much lower. Here, maximum daily growth rates for *G. firma* (0.9 ± 0.3%) occurred at 27°C, and growth took place at all temperatures between 23–33°C. The average daily growth rate for experimental outdoor rope cultivation in the Philippines was 8.7%.

Other botanical information *G. firma* closely resembles *G. blodgettii* Harv. except for the difference in transition from medulla to cortex, size of medulla cells, presence of absorbing filaments, gonimoblast and stellate chromatophore in the tetraspore. The Malaysian specimens resemble those from the Philippines in plant form, size and branching. In some manuals it is stated that the name *G. fisheri* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia is a synonym for *G. firma*. In Vietnam material of *G. firma* has previously been identified as *G. blodgettii*. However, the differences between *G. firma* and material of *G. blodgettii* from the Caribbean are listed in the original publication where *G. firma* is described.

Ecology *G. firma* is found in similar habitats to those of *G. changii* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia and *G. salicornia* (C. Agardh) E.Y. Dawson. It grows attached to shells, gravel, rock fragments in muddy areas and on fish cages, but also abundantly in its unattached form in brackish pools and lagoons.

Propagation and planting Planting of *G. firma* in pond culture is usually by broadcasting, while bushes can also be grown attached to lines.

Phycoculture *G. firma* may be cultured using vegetative methods in brackish pools and on monofilaments and rafts in open reef farming by use of methods also practised for other *Gracilaria* spp.

Diseases and pests In outdoor tank growth experiments *G. firma* is often heavily grazed by isopods.

Harvesting Wild growing populations of *G. firma* are gathered by hand.

Yield The agar yield of *G. firma* from wild populations in the Philippines after non-alkaline treatment is 13.8–20% (dry weight).

Handling after harvest Harvested plants of *G. firma* should be cleaned and dried, packed in bags and stored in a dry place.

Prospects Because of its good quality agar, *G. firma* might be cultivated commercially before long.

Literature |1| Abbott, I.A., 1988. Some species of Gracilaria and Polycavernosa from Thailand. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 2. pp. 137–150. |2| Chirapart, A. & Ohno, M., 1993. Growth in tank culture of species of Gracilaria from the Southeast Asian waters. Botanica Marina 36: 9–13. |3| Lewmanomont, K., 1994. The species of Gracilaria from Thailand. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 4. pp. 135–148. |4| Ohno, M., Terada, R. & Yamamoto, H., 1999. The species of Gracilaria from Vietnam. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 7. pp. 99–111. |5| Phang, S.-M., 1994. Some species of Gracilaria from Malaysia and Singapore. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 4. pp. 125–134. |6| Yamamoto, H., Ohno, 0. & Nguyen Huu Dinh, 1994. In vitro life histories and spermatangial types of two Gracilaria species from Vietnam, G. heteroclada and G. firma (Gracilariaceae, Rhodophyta). Japanese Journal of Phycology (Sorui) 42: 331–333.

S.-M. Phang & K. Lewmanomont

Gracilaria fisheri (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia

Pacific Sci. 45 : 23 (1991).
GRACILARIACEAE
$2n$ = unknown

Synonyms *Polycavernosa fisheri* B.M. Xia & I.A. Abbott (1987), *Hydropuntia fisheri* (B.M. Xia & I.A. Abbott) M.J. Wynne (1989).

Vernacular names Thailand: sarai phom nang, sarai woon.

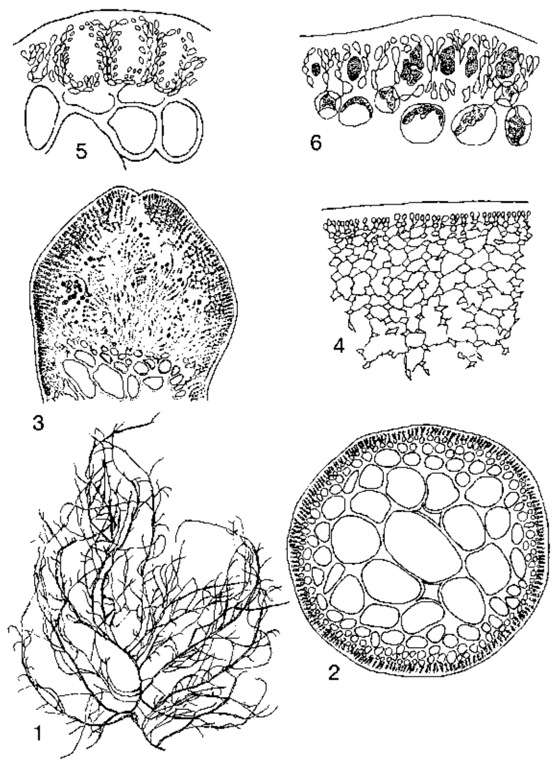
Origin and geographic distribution *G. fisheri* seems to have a fairly limited distribution. It has been recorded in Thailand (especially Songkhla Lagoon and Pattani Bay), Vietnam and Peninsular Malaysia.

Uses *G. fisheri* is the most common agarophyte in Thailand. It is sold in local markets in fresh or dry form and is eaten raw as a salad vegetable or cooked and mixed with other ingredients. The dried form is kept for sale at local markets in Thailand and nearby regions such as Kelantan (Malaysia), and exported to countries such as Japan and Taiwan for extracting agar. It is used experimentally in fresh form for abalone feed and for biological purification treatment of waste water from shrimp pond effluent.

Production and international trade Reports are available from 1956 on for Thai export of dry *Gracilaria* (*G. fisheri* and *G. tenuistipitata* C.F. Chang & B.M. Xia). Although yearly data are not available until 1975, between 20 and 200 t (dry weight) were exported annually mostly to Japan, other Asian and European countries and the United States as well. The amount fluctuates as it is harvested from natural seaweed populations. *G. fisheri* and *G. tenuistipitata* have been cultivated since 1987 using the rope-inserting method at Songkhla Lagoon and by broadcasting in pond culture near Pattani Bay. This has resulted in consistently high production from 94–135 t per year. In 1994–1995, production increased to more than 500 t per year. This may be due to effluent from intensive shrimp farming in the area, supplying nutrients. Purchase of Thai produce by Malaysians is very common, especially during Ramadan. At present, Malaysia imports dried *Gracilaria* from Thailand for a small-scale agar extraction factory in Selangor. This factory processes 70 kg of dry *Gracilaria* daily, producing 8 kg agar per day.

Properties *G. fisheri* is a good source of agar. Agar extracted by traditional methods from this alga showed gel strength of only 300–400 g/cm². However, post-extraction alkali treatment increased gel strength to 700–1000 g/cm².

Description Thalli 13–30(–45) cm tall, with many branches coming from a short stipe or from percurrent axis; branching alternate, 3–4 orders; branches cylindrical, 0.6–2.3 mm in diameter, usually less than 2 mm, constricted at their bases and tapering toward apices, often bearing short, hair-like, ultimate branches. Thalli in transverse section consisting of medullary cells, 220–620 μm in diameter, with thick layers of cortex; transition from medulla to cortex gradual. Tetrasporangia ovoid, tetraspores 20–25 μm in diameter. Spermatangia ovoid, covering the entire inner surface of single cavity conceptacle or of conceptacles with 2–3 cavities. Cystocarps conical, rostrate, unconstricted at bases, 0.3–0.7 mm × 1.0–1.3 mm; gonimoblasts consisting of many small cells; absorbing filaments lateral and upper; pericarp thick with inconspicuous cell walls and star-shaped contents. Carpospores rounded, 18–24 μm in diameter, or ovoid, 8–14 μm × 14–20 μm.



Gracilaria fisheri (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia – 1, habit of plant; 2, transection of male plant; 3, Verrucosa-type spermatangial conceptacles; 4, longitudinal section of cystocarp; 5, longitudinal section of pericarp; 6, tetrasporangia.

Growth and development Maximum growth of *G. fisheri* is related to an optimum salinity range of 20–25‰. In Thailand this usually occurs during the period January–September. During the months of the year when no harvest occurs, the seaweed subsists either as very short left-over growth or seems to disappear. In Vietnam the specimens are usually smaller than those in Thailand. After the rainy season, when environmental conditions are suitable new growth appears quickly. *G. fisheri* can be grown in outdoor cultivation tanks with flowing seawater as well as in indoor, closed-recirculating systems (aquatron). In outdoor experimental cultivation tanks in Japan, material from Thailand (Ko Yo) showed maximum daily growth rates of 14.3% in July at seawater temperatures of 25–26°C; in August, at temperatures of 27–28.4°C, daily growth was much lower, while at lower temperatures (23–25°C) daily growth was considerable. The mean daily growth rate for this alga in the outdoor tanks was 13.8 ± 0.3%. Growth rates of *G. fisheri* were much lower in the aquatron, with a maximum daily growth rate of 2.6 ± 0.7% at 25°C, which did not increase significantly at higher temperatures of 27–33°C.

Other botanical information In some manuals it is stated that the name *G. fisheri* is a synonym of *G. firma* C.F. Chang & B.M. Xia. Xia and Abbott described this alga as *Polycavernosa fisheri* from the type material purchased in a market near Kota Bahru (Kelantan), on the eastern coast of Peninsular Malaysia, which was said to have come from Pattani in Thailand.

Ecology *G. fisheri* is commonly found growing on living mollusc or empty shells (*Cerithium* sp.) and on pebbles, polythene bags and fish cages, or existing unattached to the substrate in sandy muddy areas of turbid water. It occurs abundantly together with *G. tenuistipitata* in Songkhla Lagoon and Pattani Bay. It can tolerate a wide range of salinity, from 5–40‰. In low saline conditions during the rainy season its thalli become soft and pale and deteriorate after a long period of these conditions. During summer when salinity increases the thalli become short and brittle.

Propagation and planting *G. fisheri* can be cultivated from tetraspores and carpospores. The number of carpospores produced from each cystocarp varies from about 6600 to nearly 7700 at 20 and 25‰ salinity respectively; the discharge period is 24 days. Vegetative propagation is simpler and more commonly used by local people in Thailand. Fragments of 5–10 g are prepared for either broadcasting or rope-inserting methods. Broadcast cultivation is used in Thailand in ponds at Pattani Bay and monoline culture in Songkhla Lagoon.

Phycoculture The 2 best algae for cultivation in Malaysia and Thailand are *G. fisheri* and *G. tenuistipitata*. In Thailand, *G. fisheri* is the most abundant and readily cultivated *Gracilaria* sp.

Diseases and pests In outdoor tank growth experiments *G. fisheri* is often heavily grazed by isopods.

Harvesting *G. fisheri* and *G. tenuistipitata* usually occur together and it has been shown that the presence of agar from *G. tenuistipitata* does not materially affect the gel strength of agar from *G. fisheri*. *G. fisheri* can be harvested every 6–8 weeks, yielding weights approximately 8–10 times that of the seed material. In Thailand, raking and diving are the most appropriate methods for harvesting *Gracilaria* growing at the bottom of a pond; hand-collecting is used for monoline culture as well as for alga growing in fish cages.

Yield The agar yield of *G. fisheri* from wild populations in the Philippines is (after non-alkaline treatment) 13.8–20% (dry weight). The agar content of *G. fisheri* in Thailand varies considerably, ranging from 12.9–26.7% of clean dry seaweed.

Handling after harvest Sun-drying of *G. fisheri* near collection sites is the only method used. The dry seaweed is then packed into gunny sacks and stored in the warehouse ready for sale. Grinding the seaweed after initial boiling and thoroughly pressing it after boiling is completed, or cooking under steam tend to give higher yields.

Prospects The demand for dry seaweed supplies for agar extraction is increasing. Harvest from natural populations is not enough and not constant. Without proper management the over-exploitation of *G. fisheri* will probably result in decreased yields. Research on appropriate cultivation methods is needed for the local coastal people to increase their production and income, and also to keep a constant and consistent supply of raw material.

Literature |1| Abbott, I.A., 1988. Some species of Gracilaria and Polycavernosa from Thailand. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 2. pp. 137–150. |2| Chirapart, A. & Ohno, M., 1993. Growth in tank culture of species of Gracilaria from the Southeast Asian waters. Botanica Marina 36: 9–13. |3| Lewmanomont, K., 1994. The species of Gracilaria from Thailand. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 4. pp. 135–148. |4| Ohno, M., Terada, R. & Yamamoto, H., 1999. The species of Gracilaria from Vietnam. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 7. pp. 99–111.

K. Lewmanomont & S.-M. Phang

Gracilaria salicornia (C. Agardh) E.Y. Dawson

Bull. S. Calif. Acad. Sci. 53: 4 (1954).

GRACILARIACEAE

$2n$ = possibly 48, a number found for several *Gracilaria* spp. and in agreement with the assessment of nuclear genome size for Philippine material of the present species

Synonyms *Sphaerococcus salicornia* C. Agardh (1820), *Corallopsis salicornia* (C. Agardh) Grev. (1830), *G. minor* (Sond.) Durair. (1961).

Vernacular names Indonesia: agar-agar, bulung buku, sango sango (Sulawesi). Philippines: susueldot bay bay (La Union Province, for *G. crassa*), canot-canot, lagot. Thailand: sarai kaw. Vietnam: rau cau chung vit (for *G. crassa*).

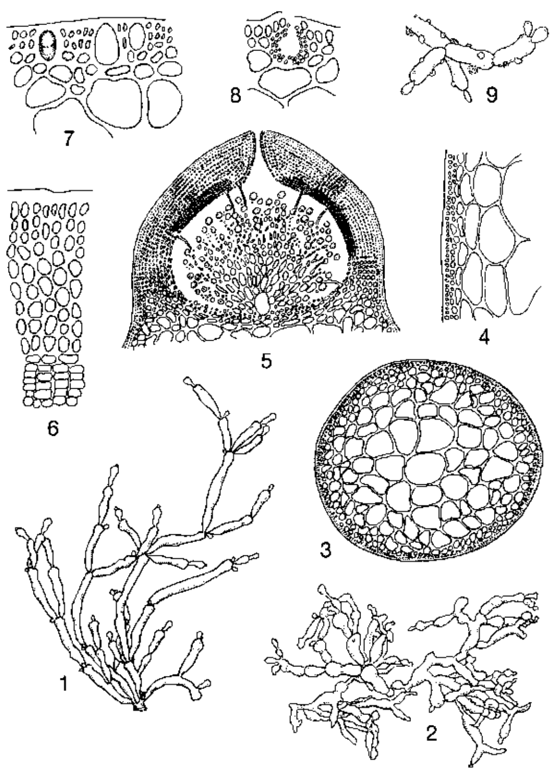
Origin and geographic distribution *G. salicornia* is found along most tropical coasts of the Indian and Pacific Oceans. In South-East Asia it occurs on the coasts of all countries.

Uses In Indonesia (Java, South Sulawesi), the Philippines, Thailand and Vietnam *G. salicornia* is collected by coastal communities and used fresh as a salad or blanched with hot water and mixed with onion, *chilli*, dried shrimp, sugar, fish sauce and lime juice. It can be used to produce home-made jelly and for agar extraction, but the gel strength is not as good as that of most other *Gracilaria* spp. It is used for abalone feed and is a food source for the green turtle. It is also applied as fertilizer, insect repellent, and in traditional medicine.

Production and international trade No commercial cultivation of *G. salicornia* is known to exist. Occasionally it is sold fresh on the local market.

Properties *G. salicornia* is an agarophyte. When collected from intertidal rocky shores in Thailand it has a low agar yield, ranging between 4.4–10.0% (dry weight). The average gel strength obtained is 345 g/cm^2. The melting and gelling temperatures range from 76–89°C and from 42–48°C respectively. It was determined that *G. crassa* gave an agar yield of 23%, a gel strength of 140 g/cm^2, and melting and gelling temperatures of 84°C and 48°C respectively. The agar contains 3.3–3.7% sulphate, 0.09–0.11% pyruvate and 26.5–35.1% 3,6-anhydrogalactose. Dried plants of *G. salicornia* from Sri Lanka contain per 100 g: water 13.7–15.5 g and ash 14.3–15.9 g (sulphate 2.4–4.2%, sodium 7.8–9.0%, potassium 11–19.3% and calcium 2.5–2.8%). The phycocolloid contains per 100 g: water 14.1–16.8 g and ash 14.3–14.5 g (sodium 3.6–5.4%, potassium 3.0–8.5% and calcium 1.9–2.6%). Data on quantities of constituents of normal *G. salicornia* and its supposed growth form '*G. crassa*' often differ.

Description Plant up to 15 cm tall, greenish-purplish to orange; all axes, branches and branchlets with more or less distinct claviform articulations; with or without main axes, regularly or irregularly branched, forming tightly entangled masses or low prostrate caespitose clumps. Fronds cylindrical, brittle and fleshy, cartilaginous and succulent when fresh. Branching irregular to dichotomous, trichotomous, tetratomous and divaricate; branches blunt, truncated or with a somewhat acute apex. Thalli with large medullary cells, 250–600(–720) μm in diameter in transverse section, with cell walls 2–15 μm thick. Transition of cells to cortex (10–15 μm × 20–30 μm in diameter) gradual or abrupt, with frequent roundish gland cells, 30–35 μm in diameter; cortex cells irregularly shaped, oblong, ovate or rounded, in 2–3 layers. Tetrasporangial and gametophytic plants similar in size and branching pattern, segments in tetrasporophytes often slightly larger. Tetrasporangia scattered over the surface of thalli, numerous, cruciately divided, sphaerical to oblong, 30–50 μm in diameter. Spermatangia covering the entire inner surface of deep pot-shaped conceptacle, 26–50 μm × 85 μm in longitudinal section. Cystocarps nearly globose, prominently protruding, usually with a distinct beak, constricted at base or not, 1–2 mm in diameter, irregularly disposed on the branches. Gonimoblast with large thin-walled central cells, connected to the pericarp by many absorbing filaments. Pericarp 180–265 μm thick, with 2 layers of tissue: elongated cells in outer layers and brick-like cells in inner layers. Carpospore globose, 23–30 μm in diameter, produced in chains.



Gracilaria salicornia (C. Agardh) E.Y. Dawson – 1, habit of a plant found in clear and relatively calm waters; 2, habit of a plant found in turbid water, exposed to moderate to strong water movement; 3, cross-section of a thallus; 4, longitudinal section of a thallus; 5, longitudinal section of a cystocarp; 6, longitudinal section of the pericarp of a cystocarp; 7, cross-section of a tetrasporophyte with tetrasporangium and large gland cells; 8, cross-section of a male gametophyte with spermatangial conceptacles of the Verrucosa-type; 9, portion of a thallus of G. salicornia with the adelphoparasite Congracilaria babae H. Yamam.

Growth and development The standing crop of *G. salicornia* on an intertidal rocky shore at Pantai Dickson, Negeri Sembilan, western coast of Peninsular Malaysia was estimated to be between 1.5–4 g/m^2 (dry weight). There are two forms of growth: one which exhibits articulations and three phases of reproduction, and the other which forms an entangled mat producing sterile or tetrasporangial plants. Spores from the mat-type of plants, when cultured under laboratory conditions, produce all stages of the life cycle, showing that the mat habit is dependent on environmental conditions like strong waves. *G. salicornia* can be grown in outdoor cultivation tanks with flowing seawater as well as in indoor closed-recirculating systems (aquatron). In outdoor experimental cultivation tanks in Japan using algal material from the Philippines (Manila Bay), maximum daily growth rates (12.7%) occurred in July at sea water temperatures of 25.2–26.2°C, although daily growth rates were still considerable at all temperatures from 23–28°C. The mean daily growth rate for these days in these outdoor tanks was 11.0 ± 0.9%, which is higher than for *G. firma* C.F. Chang & B.M. Xia, but considerably lower than for other tropical *Gracilaria* spp. Growth rates were much lower in the aquatron. Maximum daily growth rate for *G. salicornia* (0.9 ± 0.2%) occurred in the aquatron at 27°C, and the growth rate was considerably less at other temperatures of 23–33°C. When cultivated in the intertidal zone or in semi-enclosed ponds in the Philippines, daily growth rates of 1.3–2.8% have been recorded.

Other botanical information Not all specialists agree upon whether all names in the list of synonyms are conspecific. Especially *G. canaliculata* (= *G. crassa*) is often considered to be different enough to be a separate species.

Ecology *G. salicornia* grows on various substrates: rocks, gravel, shells and mangrove roots. It is usually found in protected portions of reef flats away from the impact of wave action, or in waters exposed to moderate to strong water movement, attached to small rocks or pieces of dead coral or shells, or on sandy-rocky substrate. Occasionally it is also found in shallow pools in intertidal terrigenous mudflats and between seagrasses. Temperatures exceeding 30°C are lethal to *G. salicornia*.

Phycoculture *G. salicornia* grows well in fish ponds.

Diseases and pests A commonly found parasite on *G. salicornia* is *Congracilaria babae* H. Yamam. This parasite is of the adelphoparasite type, which closely resembles the host. There are no rhizoids but the parasite connects to the host tissue by means of pit connections. Other adelphoparasites probably also occur on *G. salicornia*.

Yield The *G. salicornia* plants at Pantai Dickson (Malaysia) peaked in biomass with the return of sunny conditions after the rainy season. The agar content appeared to be negatively correlated to biomass. Biomass was positively correlated to salinity while the reverse was true for the agar content. The agar yield of dried *G. salicornia* varies widely according to the locality. Published data include 4.4–10% for Thailand, and 21.7–27.6 for the Philippines (in Ilocos Norte, however, an agar yield of 40.1% has been recorded). Outside South-East Asia an agar yield of 14–35% has been obtained from dried *G. salicornia* from Taiwan and Micronesia, and 47.2% (for *G. canaliculata*) from Hawaii.

Handling after harvest For effective extraction of agar from *G. salicornia* a strong alkaline pretreatment is advised.

Prospects The low and unpredictable agar yield and gel strength make *G. salicornia* an alga with very little potential as an agar source, and thus not a likely candidate for commercial cultivation.

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W. Moka, R. Sutijanto & P. Gronier

Gracilaria tenuistipitata C.F. Chang & B.M. Xia

Studia Mar. Sin. 11: 102–105, 161, figs 6, 7 (1976).

GRACILARIACEAE

$2n$ = unknown

Vernacular names Philippines: huganot. Thailand: sarai woon, sarai phom nang.

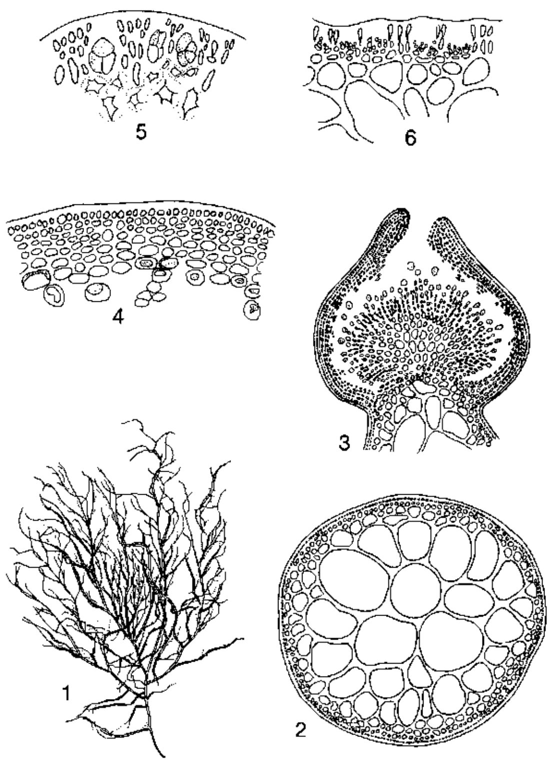
Origin and geographic distribution *G. tenuistipitata* is found in China and in South-East Asia in Indonesia, the Philippines, Thailand and Vietnam.

Uses In Thailand and Vietnam fresh *G. tenuistipitata* is commonly used as a vegetable. In both fresh and dried forms it is used in various prepared dishes. It is used for extraction of good quality agar as the gel strength is as good as that of the agar of *G. fisheri* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia. In Vietnam, the dried form is used for agar processing for local consumption. It is used as feed in shellfish culture, especially for abalone *(Haliotis diversicolor)* and as a test organism for toxicity assessment in marine and brackish environments. Other uses are as fertilizer and in traditional medicine.

Production and international trade In the Philippines *G. tenuistipitata* is mainly produced from natural stock. The quality of its agar is comparable to that of several commercially cultivated *Gracilaria* spp. Production of *G. tenuistipitata* in Thailand often occurs where *G. fisheri* is produced but it is not in itself a significant crop plant. In Vietnam, 3 *Gracilaria* species are cultivated: *G. verrucosa* (Huds.) Papenf. (synonym: *G. vermiculophylla* (Ohmi) Papenf.) (70%), *G. blodgettii* Harv. or *G. firma* C.F. Chang & B.M. Xia (18%) and *G. tenuistipitata* var. *liui* C.F. Zhang & B.M. Xia (19%). In 1987, Vietnam produced about 1500 t of dried *Gracilaria*; in 1993 the quantity reached 2800–3000 t (dry weight). This amount was used for agar processing for local consumption and some was exported to China, Russia and Japan. Other recently published data, however, assessed the cultivation area to be about 1000 ha, and annual production 1500–2000 t (dry weight). The agar extraction industry in South-East Asia using *Gracilaria* has grown. In 1987, Vietnam produced only 20 t of agar, but by 1993 this figure had risen to about 250 t. In addition to industrial-scale factories, many small-scale and family-scale ones have appeared with highly economic efficiency. However, this industry -meets local demands only, being used for confectionery and other food-based industries. Agar export from Vietnam is experiencing difficulties because of its low quality, especially low gel strength. In Taiwan *G. tenuistipitata* var. *liui* is the main taxon in cultivation. This variety grows much faster than var. *tenuistipitata*.

Properties Pretreatment with 5% alkali (NaOH) at 90°C for 3 hours in the extraction of agar gave average mean agar yield of 16.2% in *G. tenuistipitata* from the Philippines, 12.7% from Thailand and 19.7% from Vietnam. Gel strength determination using 1.5% agar was 304–473 g/cm^2 for natural agar from the Philippines and 606–726 g/cm^2 for agar after alkali treatment, and 338 g/cm^2 and 768 g/cm^2, respectively for those from Vietnam and Thailand. The agar from *G. tenuistipitata* possesses regular agarobiose- repeating units with partial methylation at the 6-position of the D-galactosyl residues.

Description Thalli filiform, 20–40 cm tall, rarely up to 1 m, arising from a small disklike holdfast, fleshy red, cartilaginous, adhering well to paper on drying; branching simple or moderately alternate near the base, with only few orders of branches; branches becoming like main axis, terete throughout, very slender and gradually tapering towards the base, above expanding to



Gracilaria tenuistipitata C.F. Chang & B.M. Xia var. liui C.F. Zhang & B.M. Xia – 1, habit; 2, cross section of a thallus; 3, longitudinal section of a cystocarp; 4, longitudinal section of the pericarp of a cystocarp; 5, cross-section of a tetrasporophyte with tetrasporangia; 6, cross-section of a male gametophyte with spermatangial conceptacles of the Textorii-type.

0.5–1.5 mm in diameter, 1–2 times branched. Medulla broad, with large thick-walled cells, 225–390 μm in diameter, cell walls 13–16 μm thick in the centre, towards the surface considerably smaller; cortex of 1–2 layers of rounded cells 10–20 μm in diameter, with cuticle 10–30 μm thick. Tetrasporangia scattered among surface layer of the frond, round in surface view, 30–33 μm in diameter, ovoid or oblong in transverse-section, 30–46 μm × 18–30 μm, cruciately divided, surrounded by modified cortical cells. Spermatangia scattered over surface of branch in small shallow, well-defined depressions 10–23 μm in diameter, separated by modified, elongated cortical cells. Cystocarps prominently protruding, 830– 950 μm tall, globose, markedly rostrate, constricted at the base. Gonimoblast composed of large parenchymatous cells, connected with pericarp by very rare nutritive filaments; pericarp 72–102 μm thick, consisting of 8–11 layers of cells, with outer cells of 1–2 layers elliptical to roundish, with obscured cell wall, with the innermost few layers of cells roundish to horizontally oval with distinct cell wall. Carpospores round or ovoid, 33–49 μm in diameter.

Growth and development In pond culture the mean annual growth rate of *G. tenuistipitata* in Taiwan is 2.4% per day, with a maximum of 3.3% per day under favourable conditions. The average daily growth rate of pond-cultivated *G. tenuistipitata* in the Philippines is 6.2%, which is lower than the daily growth rates of other Philippine *Gracilaria* species that were grown in experimental rope cultures.

Other botanical information *G. tenuistipitata* var. *liui* differs from var. *tenuistipitata*, having slender thalli bearing numerous, delicate, short to long flagelliform lateral branchlets, frequently only 0.3 mm in diameter, branching mostly from percurrent axes.

Ecology *G. tenuistipitata* var. *tenuistipitata* grows on gravel and shells in the sublittoral region of lower salinity, while var. *liui* frequently occurs naturally in fish ponds and shallow intertidal areas on muddy substrate, sometimes exposed during low tide. It can survive temperatures as high as 34°C (best growth is between 25 and 28°C), while var. *liui* can grow under salinities of 4–47‰ and thus can often be found in areas with an intrusion of freshwater. It grows best in salinities of 15–22‰. When cultivated the thalli are usually detached and without holdfasts.

Propagation and planting Propagation of *G. tenuistipitata* in cultures is usually by vegetative fragmentation. Thalli are split or individual branches broadcast in shallow ponds or grown in rectangular net cages.

Phycoculture Pond culture of *G. tenuistipitata* has been successfully practised in China, Vietnam, Thailand, Taiwan and the Philippines. This alga is considered to have potential for culture or farming in brackish water ponds due to its tolerance for a wide range of salinity and turbid waters. Of the two varieties, var. *liui* is far better than var. *tenuistipitata*, because it grows faster and is adaptable to brackish water. The ponds used for culture should be about one hectare and have a water management system. The water depth is kept at 30–70 cm and the salinity range from 15–25‰. The water should be changed once every two weeks. In the Philippines *G. tenuistipitata* and *Gracilariopsis heteroclada* C.F. Zhang & B.M. Xia (usually as *Gracilaria heteroclada* C.F. Zhang & B.M. Xia) are the most suitable algae for pond culture. The minimum water depth in the pond should be kept at 20–30 cm. If monoculture is practised, fertilization of the pond water is required. Three kg of urea is needed per hectare of pond every week, and the water should be changed once every two weeks. About 4500 kg/ha of seaweed seedlings are needed to produce 12 t. *G. tenuistipitata* was identified as a potential alga for culture or farming based on its ecological characteristics, wide availability in many areas of the country and its high yield of good-quality agar.

In Thailand, pond culture is common in Pattani Province. *G. tenuistipitata* collected from the wild is separated into small tufts or fragments and broadcast uniformly on the bottom of the pond with a muddy-sandy substrate, at a density of 500 g/m^2 of seedlings. The water is maintained at a suitable depth of about 50–70 cm. Daily water exchange by tidal flow ensures adequate nutrient supply for the seaweed and maintains the optimum water temperature in the pond.

In Vietnam and Taiwan, monoculture and polyculture in ponds with shrimp (often grassshrimp, *Panaeus monodon*), fish (often milkfish, *Chanos chanos*) and crabs (often *Scylla serrata*) have been carried out. The optimum range of salinity is 12–24‰ and the optimum temperature range is 20–30°C. Seed stock is 500–600 g/m^2. The water level is maintained at a depth of 30–45 cm, increasing to 40–50 cm during sunny months, and a maximum level of 60 cm deep. Water exchange occurs naturally at high and low tides. Addition of nitrogen is effective until a total N concentration of 4.3 μM is reached, and fertilizers significantly improve crop growth under combined conditions of low salinity (< 10‰) and high temperatures (above 32°C).

Harvesting Under optimum conditions, *G. tenuistipitata* may be harvested 2–3 months after seeding in Thailand. In Vietnam the alga is harvested by hand or by rake when the density rises above 1 kg/m^2.

Yield In Thailand yield of *G. tenuistipitata* is 1.5–2.5 kg/m^2 (wet weight) or more when harvested after 2–3 months.

Handling after harvest When used for agar production *G. tenuistipitata* has to be sun-dried, free of extraneous matter, washed in freshwater and redried before being packed for storage or transport. When sold as feed for abalone culture the fresh product can be sold directly to abalone farms, without any form of processing, thus reducing labour costs.

Chemical analyses reveal higher 3,6-anhydrogalactose and lower sulphate contents in alkali-modified agar than in natural agar. There is a considerable decrease in agar yield upon alkali treatment, but the agar quality is certainly better, with a two-fold increase in gel strength.

Prospects *G. tenuistipitata* has a good-quality agar useful for food and other specialized agar products. Its production for the agar industry for local consumption and the international market seems to have a bright future. Labour shortage, however, may result in direct selling of the fresh seaweed for feed in cultures of marine animals.

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K. Lewmanomont & S.-M. Phang

Gracilaria verrucosa (Huds.) Papenf.

Hydrobiologia 2: 195 (1950).

GRACILARIACEAE

$2n$ = most probably 48, although for European '*G. verrucosa*' a diploid number of 64 has been recorded; however, this was probably material belonging to the separate genus *Gracilariopsis* E.Y. Dawson; for all other European and Japanese material of '*G. verrucosa*', a haploid number of about 24 was established and thus is probably real *Gracilaria* material

Synonyms In Europe, material identified as belonging to '*Gracilaria verrucosa*' is partly *G. gracilis* (Stackh.) Steentoft, L.M. Irvine & Farnham, which is, however, an illegitimate name for *G. confervoides* (L.) Grev. Another part of this material belongs to *Gracilariopsis longissima* (S.G. Gmelin) Steentoft, L.M. Irvine & Farnham, which is again most probably an illegitimate name for which the correct binominal (based on the Hudson epithet) has not yet been proposed.

Vernacular names Philippines: gulaman, caocaoyan, gargararao, lagot.

Origin and geographic distribution Although records under this name appear in almost all countries of the world, *G. verrucosa* is most probably restricted to the North Atlantic Ocean. Nevertheless, it has been recorded recently in Burma (Myanmar), Vietnam, Malaysia, Indonesia and the Philippines.

Uses *Gracilaria* spp., to which this name is applied, are usually cultivated as raw material for agar production. The name is also listed as being used in traditional Chinese medicine.

Production and international trade A *Gracilaria* named as *G. verrucosa*, has been cultivated in South Sulawesi (Indonesia) since 1986 and produces monthly exports of 60–80 t dried *Gracilaria* seaweed.

Properties The agar from *G. 'verrucosa'* from Takalar, South Sulawesi (Indonesia) in a 2% agar solution and obtained without alkaline hydrolysis, is not very promising (gel strength 45 g/cm^2, gelling point 27–28°C, viscosity 51 cP). However, agar prepared using the same methods, but from *Gracilaria* material obtained from a commercial agar producer and recorded as being produced in

the same locality, gave better results (gel strength 1331 g/cm^2, gelling point 40–41°C, viscosity 75 cP). This difference may be due to differences in post-harvest handling of the raw material.
The water content of dried material is about 23.5%, while the amount of impurities (especially fine mud) can be as high as 40%, due to the high turbidity of the water in the culture ponds.

Description Plant erect, attached by a small discoid holdfast; main axes percurrent, with many orders of irregular branching; base of branches slightly constricted, the lower order branches elongate. Fronds slender, cylindrical, pale to dark brown or brownish with some yellow-green. Medulla consisting of cells 166–365 μm in diameter, with cell walls 10–30(–40) μm thick; cell transition to cortex gradual to abrupt. Spermatangia in deep, oval conceptacles. Cystocarps semiglobose, slightly or not rostrate, slightly or not constricted at bases.

Other botanical information The name *G. verrucosa* has been somewhat indiscriminately applied to terete, irregularly branched specimens of *Gracilaria*. *G. verrucosa* has been reported worldwide from temperate to tropical waters. Many records of *G. verrucosa* from outside the eastern Atlantic Ocean now are considered to be incorrect and *G. verrucosa* may be confined to the north-eastern Atlantic Ocean. Reports from outside this area require careful examination. It has often been suggested that the entity known as *G. 'verrucosa'* in many parts of the world does not belong to the same taxonomic species. Specimens previously called *G. verrucosa* from several countries have been reexamined and some of them have undergone a change of name. For example, studies on Chinese species identified as *G. verrucosa*, when compared with specimens from Weymouth, Devon (England) and from Hokkaido (Japan) resulted in the conclusion that the Chinese and Japanese specimens are similar to each other and can now be referred to as *G. vermiculophylla* (Ohmi) Papenf., which is distinctly different to the British materials.
Material collected in the Philippines and previously identified as *G. verrucosa*, was described as the new species *G. manilaensis* H. Yamam. & Trono, while specimens of *Gracilaria* from Thailand previously reported as *G. verrucosa* were re-identified as *G. fisheri* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia and *G. tenuistipitata* C.F. Chang & B.M. Xia. Therefore it seems that *G. verrucosa* is not a valid name for Asian *Gracilaria*.

Ecology There are no data available for material of *G. verrucosa* from South-East Asia.

Propagation and planting Propagation and planting for *G. verrucosa* is as for other pond-grown *Gracilaria* spp.

Harvesting Harvesting of *G. verrucosa* is as for other pond-grown *Gracilaria* spp.

Yield Agar content of *G. verrucosa* from Takalar, South Sulawesi (Indonesia) is fairly high (47.7% has been recorded).

Handling after harvest Cultivated material of *G. verrucosa* has to be thoroughly washed in running water, while much of the attached fine silt and salt crystals can be removed by vigorous shaking and beating the dried fronds before packing and sorting.

Prospects The name *G. verrucosa* should no longer be connected with *Gracilaria* spp. and their products from South-East Asia.

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K. Lewmanomont, S.-M. Phang &
W.F. Prud'homme van Reine

Gracilariopsis E.Y. Dawson

Allan Hancock Found. Publ. Occas. Pap. 7: 40 (1949).

GRACILARIACEAE

$2n$ = most probably 64

Major species and synonyms

- *Gracilariopsis heteroclada* C.F. Zhang & B.M. Xia – see separate article.
- *Gracilariopsis lemaneiformis* (Bory) E.Y. Dawson, Acleto & Foldvik – see separate article.
- *Gracilariopsis longissima* (S.G. Gmelin) Steentoft, L.M. Irvine & Farnham – see under *Gracilaria 'verrucosa'*.

Vernacular names Philippines: gulaman, caocaoyan, gargararao, lagot.

Origin and geographic distribution *Gracilariopsis* occurs in many locations but due to taxonomic and nomenclatural uncertainties, reliable general data are not yet available.

Uses Most *Gracilariopsis* are used both for food and as raw material for the agar industry. Several of these algae are also used as feed for cultivated fish and invertebrates and as medicine (as a laxative and for pulmonary complaints). Several *Gracilariopsis*, especially *G. lemaneiformis* are sources of high quality sugar-reactive agar.

Production and international trade Often no separate data for *Gracilariopsis* are available; usually these data are incorporated in information on *Gracilaria* spp.

Description Plants usually bushy, arising from a small discoid base. Fronds cylindrical; branching secund or alternate; branches basically constricted or not, fleshy to cartilaginous. Medulla parenchymatous, consisting of large cells; cortex narrow, small-celled, assimilative. Life cycle triphasic, diplo-haplontic, isomorphic and dioecious. Tetrasporangia formed in cortex. Spermatangia cut off from surface cells, arranged in continuous superficial layers. Cystocarps hemispherical, with small-celled broad-based placental tissue without nutritive filaments, with prominent superficial pericarp composed of several layers of radiating cells. Carpospores discharge through a pore.

Growth and development Shedding of tetraspores or carpospores in *Gracilariopsis* results in a remarkable increase of biomass during the months that follow. Exposure of thalli to air seems to be favourable to gamete maturation. Tetraspore formation in laboratory cultures can be induced by manipulating environmental factors such as photoperiod, photoflux density, temperature, salinity and nutrients. Laboratory-generated carposporelings can be planted out for phycoculture.

Other botanical information Because of the economic interest in its products, in particular phycocolloids, the study of Gracilarioid algae has spread rapidly throughout the world, resulting in numerous proposals for taxonomic and nomenclatural change. Names of genera that have been separated from *Gracilaria* Grev. include *Gracilariopsis*. In South-East Asia, however, most described differences between these genera are often considered to be too technical for general acceptance, resulting in proposals to retain all species in the single genus *Gracilaria*. Nevertheless, the separation of *Gracilaria* and *Gracilariopsis* is at present often followed, as is done in the present volume.

Ecology It is impossible to differentiate the ecological information found in data provided for *Gracilaria* and for *Gracilariopsis*.

Propagation and planting The usual method of propagation used in *Gracilariopsis* phycoculture is vegetative fragmentation, although methods for propagation by spores have been described. Gracilarioid algae usually regenerate easily when cut. Thalli are chopped or split and bunches of branches or individual branches are used for planting (bottom-stocking) or broadcasting or for cultivation on ropes, either in fixed off-bottom frames, on floating long lines or on rafts.

Phycoculture The methods used for *Gracilaria* cultivation can be applied to *Gracilariopsis* as well. In South-East Asia phycoculture usually takes place by broadcasting vegetative fragments in semi-enclosed ponds.

Harvesting Harvest techniques used for *Gracilariopsis* are the same as those for *Gracilaria*. Thus not more than 50–70% of the natural stock should be harvested, and also in cultivation ponds it is necessary to allow sufficient material for regeneration. Harvesting is usually done by hand.

Yield Data on *Gracilariopsis* yields are mostly included in those on Gracilarioid algae.

Handling after harvest Post-harvesting techniques are the same for both *Gracilariopsis* and *Gracilaria*. The harvested algae should be cleaned on site and transported to a drying area. Once dried, the seaweeds should be packed in bags, stored in a dry place, and sold and transported as soon as possible.

Prospects The quality of *Gracilariopsis* agar is often better than that of several *Gracilaria* spp., but a general rule cannot yet be given.

Literature |**1**| Abbott, I.A., 1995. A decade of species of Gracilaria (sensu latu). In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 5. pp. 185–195. |**2**| Kapraun, D.F., Lopez-Bautista, J., Trono, G.C. & Bird, K.T., 1996. Quantification and characterization of nuclear genomes in commercial red seaweeds (Gracilariales) from the Philippines. Journal of Applied Phycology 8: 125–130. |**3**| Tseng, C.K. & Xia, B.M., 1999. On the Gracilaria in the Western Pacific and Southeast-

ern Asia region. Botanica Marina 42: 209–217.
W.F. Prud'homme van Reine

Gracilariopsis heteroclada C.F. Zhang & B.M. Xia

Pacific Sci. 45: 22 (1991).

GRACILARIACEAE

$2n$ = most probably 64; assessment of nuclear genome sizes of Gracilarioid algae from the Philippines suggests that the size of the nuclear genome is larger for *Gracilariopsis heteroclada* than for most *Gracilaria* spp. except *Gracilaria eucheumatoides* Harv.

Synonyms *Gracilaria heteroclada* C.F. Zhang & B.M. Xia (1988), non *G. heteroclada* (Mont.) Feldmann & Feldm.-Maz. (1943), *Gracilariopsis bailinae* C.F. Zhang & B.M. Xia (1991), *Gracilaria bailinae* (C.F. Zhang & B.M. Xia) C.F. Zhang & B.M. Xia (1994, nom. inval.).

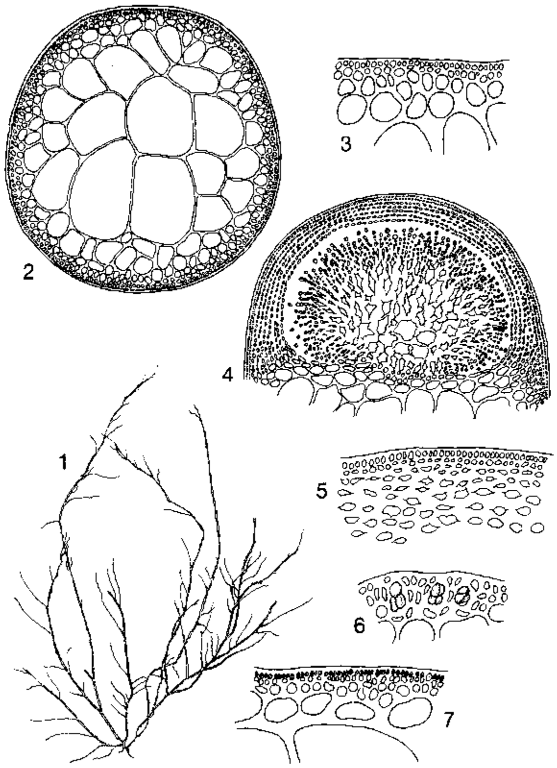
Origin and geographic distribution *G. heteroclada* seems to be restricted to southern Asia, with records from China and in South-East Asia from the Philippines and Vietnam.

Uses In the Philippines agar of *G. heteroclada* (usually as *Gracilaria heteroclada*) is produced commercially. It is strong enough to be used as industrial and bacteriological agar and thus as a potential source of agarose. In Vietnam *G. heteroclada* is eaten raw and used in cooking, for the preparation of sour vegetables, jellies, and sweet soups. In the Philippines the alga is also used for human food, animal feed, fertilizer and in traditional medicine.

Production and international trade In the Philippines and in central and southern Vietnam *G. heteroclada* (as *Gracilaria heteroclada*) is grown in cultures, which are used for commercial agar production. The total area for *G. heteroclada* in Vietnam is about 100 ha, with an annual production of 150–200 t (dry weight).

Properties Gelling temperature of the agar from *G. heteroclada* and its melting temperature have been determined as 38–46°C and 83–97°C respectively, while gel strength of this agar was assessed to be 810–905 g/cm². Thus gel strength of *G. heteroclada* is comparable to that of industrial agar, but lower than the specified gel strength of agarose (> 900 g/cm²). Seasonality in gel strength has been observed in the Philippines, with low values during the late part of the dry season (April–May, with high air temperatures) and high ones during the early part of the dry season (October–March). The source of the material in the Philippines (Manila Bay, Iloilo in western Visayas) and the quality of the pretreatment significantly influence the rheological properties of the produced agar. Except for gel strength, which on average is higher than in most Philippine *Gracilaria* spp., the other values fit within the variation of data found for the Philippine Gracilarioid algae. In Vietnam, *G. heteroclada* (as *G. bailinae*) is considered to be one of the best raw materials for agar processing, due to its high yield of high quality agar.

Description Plant usually erect, bushy, 10–50(–70) cm tall, solitary to caespitose, arising from a small discoid base. Fronds with a long, filiform, fleshy, brittle, cylindrical axis, 1–3 mm in diameter; branching with 2–4 orders of branches, irregular to almost alternate; branchlets (=



Gracilariopsis heteroclada C.F. Zhang & B.M. Xia – 1, habit; 2, cross-section of a thallus; 3, detail of a cross-section of a thallus; 4, non-median longitudinal section of a cystocarp; 5, longitudinal section of the pericarp of a cystocarp; 6, cross-section of a tetrasporophyte with tetrasporangia; 7, cross-section of a male gametophyte with spermatangial sori of the Chorda-type.

branches of the third order) short, succulent, brittle, breaking easily, spinose and non-constricted at their bases. Medullary cells 200–530 μm in diameter; cell walls 8–10 μm thick, with abrupt cell transition to small cortex cells, 7–10 μm × 4–7 μm. Tetrasporangia scattered in the cortex, ovoid or oblong, 33–36 μm × 16–26 μm in surface view, 20–30 μm × 16–26 μm in longitudinal section. Spermatangia superficial, continuously over the frond surface. Cystocarps prominently protruding or subconical, 500–780 μm × 830–1000 μm, rostrate or not, non-constricted at base; pericarp 76–100 μm thick.

Growth and development Seasonal variation in biomass of wild populations of *G. heteroclada* has been studied in coastal areas in Iloilo (the Philippines) and compared with those of two *Gracilaria* spp. (*G. changii* (B.M. Xia & I.A. Abbott) I.A. Abbott, C.F. Zhang & B.M. Xia and *G. manilaensis* H. Yamam. & Trono). In contrast to the latter two *Gracilaria*, which were only present during the dry season, the populations of *G. heteroclada* were present year-round, although its abundance and properties were not uniform during the year. *G. heteroclada* seaweed was especially abundant in Estancia (northern Iloilo) in the wet season, but more abundant in the dry season in Zarraga (mid Iloilo). The standing crop in Estancia was 13.4–119.3 g/m^2, with highest values from May to September, whereas in Zarraga it was 6.9–43 g/m^2, with highest values from November to March. In all cases the algae behaved as a perennial. Plants temporarily exposed to air usually decreased in productivity. In the rainy season *G. heteroclada* disappeared from the littoral zone. Regeneration of *G. heteroclada* after the rainy season is by vegetative fragmentation. Tetrasporangia and cystocarps occur seasonally; in Iloilo, tetrasporangia are dominant in April and May (late dry season, with high water temperatures) and cystocarps in January (after the wet season).
When cultured in outdoor tanks, the highest growth rates were reached (0.3–1.1%/d), especially at salinity levels of 15–25‰ and with addition of 0.5 mM urea. Growth in indoor tanks is always somewhat lower (maximum 0.2–0.7%/d). In biculture with milkfish, *G. heteroclada* can reach mean daily growth rates of 4.7 ± 1.6% (maximum 5.9%) in indoor laboratory culture and of 3.7 ± 0.4% (maximum 4.7%) in outdoor ponds.

Ecology *G. heteroclada* grows in muddy to sandy-muddy environments with changing and occasionally rather low salinities, where it forms almost mono-specific beds, which are sometimes exposed to air during the lowest low tides. It also occurs, however, attached to hard substrates in the intertidal region, often in a sexually reproducing form. However, in the lagoon habitats the alga is mostly found in an unattached, vegetatively reproductive state.
Usually, its biomass does not show any significant relationship with salinity (15–35‰), temperature (27–32°C), pH (7.3–8.7), turbidity (39–92%) and nitrogen (0–0.26 ppm NO_2-N and 0–0.44 ppm NH_3-N), but higher phosphate levels are positively correlated with higher biomass. *G. heteroclada* grows well in Vietnam in conditions where salinity ranges from 15–30‰ and water temperatures of 24–33°C prevail. At low salinities (< 10‰) and high water temperatures (> 34°C) growth is inhibited.

Propagation and planting In phycoculture of *G. heteroclada* in Vietnam 'seedlings' or vegetative propagules (cuttings) are normally broadcast onto the muddy or sandy bottoms of the culture ponds. In the Philippines bunches of thalli are stacked into the sandy-muddy substrate of ponds.

Phycoculture In some shrimp cultivation ponds in central Vietnam *G. heteroclada* and black tiger shrimp (*Palaemon monodon*) are cultivated in rotation in the same pond (6 months each). Both crops benefit significantly from this approach. In bi-culture with milkfish (*Chanos chanos*) in the Philippines performance of both organisms is significantly better than in monoculture.

Diseases and pests *G. heteroclada* is excessively grazed by herbivorous fish including siganids, mullets and puffers. Epiphytes such as *Cladophora* spp. were observed to cling to *Gracilariopsis* spp. The presence of these epiphytes can result in significantly lower yields of *G. heteroclada*.

Harvesting Harvesting techniques used for *Gracilaria* are also used for *G. heteroclada*, i.e. mainly hand-collecting.

Yield The biomass of *G. heteroclada* is not more than 2 kg/m^2 as expected for tropical regions. This is considerably lower than for Gracilarioid algae in temperate areas. The yield and quality of agar from natural populations of *G. heteroclada* varies considerably during the year. For areas in the Philippines the neutral (i.e. non-alkaline) agar yield is 6–23% of dry weight. In July, when agar yield is often optimal, gel strength is mostly lower than in other months. Gelling temperature and melting temperature change irregularly during the year, and the sulphate percentage especially varies throughout the year for Zarraga (Iloilo, the

Philippines) from 4.8–29.0 μg/mg.

Handling after harvest Plants of *G. heteroclada* grown in tanks kept at 26.5–31°C and salinities of 8–32‰, when treated with different concentrations of aqueous NaOH produce different agar yields. The extracted agars vary considerably in gel strength and gelling and melting temperatures. Of the statistically significant differences in gel strength, dynamic gelling and melting temperatures observed for the various treatments, both the strongest and the weakest gel were extracted after pre-treatment with 3% NaOH. The difference was in the salinity: plants grown in water with a salinity of 24‰ produced maximum gel strength, and those grown at a salinity of 32‰ produced agar with a very low gel strength. Generally, the best quality agar can be extracted after cold aqueous NaOH 4% pretreatment for 7 days.

Prospects The quality of agar of *G. heteroclada* is better than that of several *Gracilaria* spp. in South-East Asia. This together with its year-round occurrence, make *G. heteroclada* a promising seaweed for commercial purposes.

Literature |1| Alcantara, L.B., Calumpong, H.P., Martinez-Goss, M.R., Meñez, E.G. & Israel, A., 1999. Comparison of the performance of the agarophyte, Gracilariopsis bailinae, and the milkfish, Chanos chanos, in mono- and biculture. Hydrobiologia 398/399: 443–453. |2| Hurtado-Ponce, A.Q., 1994. Agar production from Gracilariopsis heteroclada (Gracilariales, Rhodophyta) grown at different salinity levels. Botanica Marina 37: 97–100. |3| Hurtado-Ponce, A.Q. & Laio, L.-M., 1998. The genus Gracilariopsis (Rhodophyta, Gracilariales) in the Philippines: morphological and taxonomic confirmations. The Philippine Scientist 35: 141–151. |4| Hurtado-Ponce, A.Q. & Pondevida, H.B., 1997. The interactive effect of some environmental factors on the growth, agar yield and quality of Gracilariopsis bailinae (Zhang et Xia) cultured in tanks. Botanica Marina 40: 217–223. |5| Luhan, Ma. R.J., 1996. Biomass and reproductive states of Gracilaria heteroclada Zhang et Xia collected from Jaro, Central Philippines. Botanica Marina 39: 207–211. |6| Pondevida, H.B., & Hurtado-Ponce, A.Q., 1996. Assessment of some agarophytes from the coastal areas of Iloilo, Philippines. I & II. Botanica Marina 39: 117–122, 123–127. |7| Rabanal, S.F., Azanza, R. & Hurtado-Ponce, A.Q., 1997. Laboratory manipulation of Gracilariopsis bailinae Zhang & Xia (Gracilariales, Rhodophyta). Botanica Marina 40: 547–556.

W.F. Prud'homme van Reine

Gracilariopsis lemaneiformis (Bory) E.Y. Dawson, Acleto & Foldvik

Beih. Nova Hedw. 13: 59 (as 'lemanaeformis') (1964).

GRACILARIACEAE

$2n$ = unknown

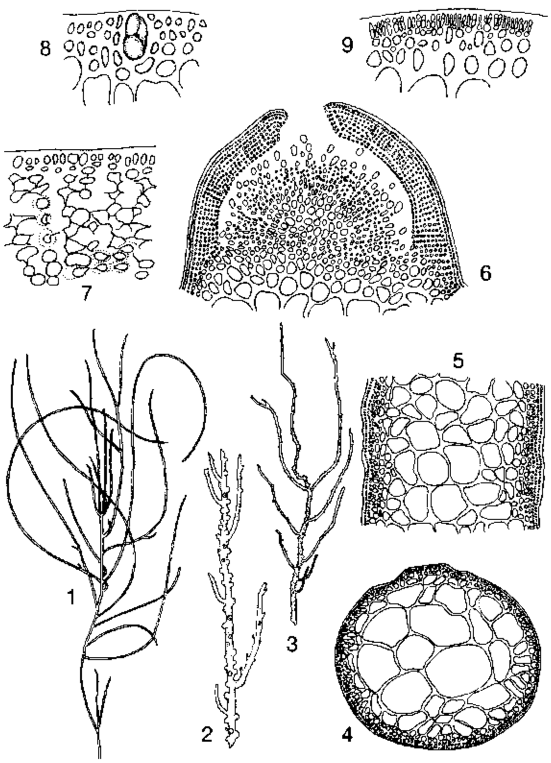
Synonyms *Gigartina lemaneiformis* Bory (1828, as 'lemanaeformis'), *Gracilaria lemaneiformis* (Bory) Grev. (1830, as 'lemanaeformis'), *Gracilariopsis sjoestedtii* (Kylin) E.Y. Dawson (1949).

Origin and geographic distribution *G. lemaneiformis* occurs in the tropical to warm-temperate parts of all oceans. In South-East Asia it has been recorded in Thailand, Vietnam, Indonesia and the Philippines.

Uses *G. lemaneiformis* is one of the useful marine red algae for agar extraction.

Properties In Japanese samples the viscosity of 1.5% agar of *G. lemaneiformis* diminished from 220–380 cP in non-alkali treated material to almost zero after alkali treatment, while mean gelling temperature (about 55°C) and mean melting temperature (about 90°C) of 1.5% agar did not change much after alkali treatment. Gel strength for non-alkali treated Japanese samples (1.5% agar) was 440–685 g/cm^2, rising to 2000–2125 g/cm^2 after 7– 10% alkali treatment. For material from Indonesia and China, both after 5% alkali treatment, gel strength values of 880 and 848–872 respectively have been recorded. Hardness (about 250 g/mm^2) of 1.5% agar of Japanese samples of *G. lemaneiformis* after alkali treatment (7–10% NaOH) is the highest of all commercial Gracilarioid agars that have been tested, while flexibility values of 2.5–9 g/100 mm^2 have been recorded for these same samples. Agar of *G. lemaneiformis* is especially interesting because it retains its gel strength with the addition of even 75 g/100 ml of sugar in a 1% agar solution, resulting in a very elastic gel. Most *Gracilaria* agars are not sugar-reactive.

Description Thalli solitary to caespitose, slender, dark green to brownish or red, up to 40 cm tall with distinct main axis and few to several long branches; branching irregular to alternate, mostly from lower portion, many thalli arising from a spreading holdfast; branches simple, cylindrical, long, filiform, slightly constricted at branch bases, 0.5–2.0 mm in diameter; branchlets 2–5, frequently occurring from a single branch apex. Fronds in transverse section consisting of medulla of large thin-walled (3–8 μm) cells, 115–700 μm in diameter, with two layers of cells in cortex; transition of



Gracilariopsis lemaneiformis (Bory) E.Y. Dawson, Acleto & Foldvik – 1, habit; 2,3, portions of apical branches; 4, cross-section of a thallus; 5, longitudinal section of a thallus; 6, longitudinal section of a cystocarp; 7, longitudinal section of the pericarp of a cystocarp; 8, cross-section of a tetrasporophyte with tetrasporangia; 9, cross-section of a male gametophyte with spermatangial sori of the Chorda-type.

cells from medulla to cortex abrupt. Tetrasporangia ovoid to ellipsoidal, embedded in slightly modified cortex of anticlinally elongated cells. Spermatangia superficial, continuously over the frond surface. Cystocarps spherical, 0.7–1 mm in diameter, with or without a short beak, constricted at the base or not, taller than diameter of bearing branch; gonimoblast of small cells, no absorbing filament; pericarp 116–182 μm thick, with undifferentiated cells.

Growth and development Plants of *G. lemaneiformis* from warm areas in South-East Asia (the Philippines, Thailand) are not as robust as those from the type locality (Peru) and other countries where surface seawater temperatures are slightly cooler. Moreover, tropical plants frequently have a percurrent, filiform axis with few to many short laterals, short-spinous to elongate. In temperate areas, the laterals may be as elongate and as thick as the axes, with few laterals of the second order, or they may be bushy plants.

Ecology *G. lemaneiformis* grows on sand or mud or in sandy-muddy areas of the intertidal zone with clear water and sheltered areas not exposed during low tide. In Thailand, it is found growing on fish cages.

Propagation and planting Methods of propagation and planting for *G. lemaneiformis* are the same as those for *Gracilaria*, thus often by broadcasting in shallow, semi-enclosed ponds, although fixed-bottom monoline cultivation as well as culture on rafts are also practised.

Phycoculture In China the floating culture method may be suitable for *G. lemaneiformis*. In Indonesia a study showed that this alga has a better potential for artificial cultivation in pond or field areas than other seaweeds.

Harvesting Harvesting techniques used for *G. lemaneiformis* are the same as those for *Gracilaria*, thus mainly hand-collecting.

Yield Agar yield for *G. lemaneiformis* varies from 20–27% of dry weight for non-alkali treated material from Japan, increasing to about 34% after treatment within 2 hours with 7–10% NaOH at 80°C. For material from Indonesia, agar yield of about 10% has been obtained after treatment with 5% NaOH.

Handling after harvest Post-harvest techniques for *G. lemaneiformis* are the same as those used for *Gracilaria*: after washing the seaweed should be dried immediately, packed in bags and stored in a dry place.

Prospects As a useful source of agar, *G. lemaneiformis* may have good prospects for phycoculture development.

Literature |**1**| Abbott, I.A., 1994. New records and a reassessment of Gracilaria (Rhodophyta) from the Philippines. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 4. pp. 111–118. |**2**| Lewmanomont, K., 1994. The species of Gracilaria from Thailand. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds 4. pp. 135–148. |**3**| Rebello, J., Ohno, M., Ukeda, H. & Sawamura, M., 1997. Agar quality of commercial agarophytes from different geographical origins: 1. Physical and rheological properties. Journal of Applied Phycology 8: 517–521.

K. Lewmanomont & S.-M. Phang

Grateloupia filicina (J.V. Lamour.) C. Agardh

Spec. alg. 1: 223 (1822).
HALYMENIACEAE
$2n$ = unknown

Synonyms *Fucus filicina* Wulfen (1791, nom. illeg.), *Delesseria filicina* J.V. Lamour. (1813).

Vernacular names Indonesia: sayur karang.

Origin and geographic distribution *G. filicina* was first recorded in Trieste (Italy). It is considered to be cosmopolitan and is widely distributed in the Atlantic, Indian and Pacific Oceans. It occurs along the entire coast of China. In South-East Asia it has been recorded for Burma (Myanmar), East Malaysia, Indonesia (Java, Sumatra, Sumba) and the Philippines.

Uses *G. filicina* is eaten as food in China and in some South-East Asian countries as a salad, in vegetable soup, as pickles and in home-made jellies. It is also a source of carrageenan and is used in medicine with anthelmintic and antibacterial properties or as a blood anticoagulant.

Production and international trade No production data are available for *G. filicina* since biomass is obtained from natural stocks.

Properties *G. filicina* contains floridosite and floridean starch (its principal reserve components), a polysaccharide known as galactan, and the steroids fucosterol and sitosterol (traces). It also contains 55.85 μM per gram dry weight of trimethylamineoxide which serves as the osmotic regulator or detoxicator of trimethylamine (TMA) substance in an organism. Reports of galactan-containing small proportions of D-L-galactose segments in what appeared to be D-D structures (carrageenan type), which might be considered hybrid molecules, have recently been confirmed in the ^{13}C Nuclear Magnetic Resonance (NMR) analysis of partial acetolysis products of galactan from related species in the genus.

Description Thalli purplish-red, gelatinous, with surface slippery, erect, linear, compressed to subcylindrical, caespitose, 15–20 cm tall, tapering to base and apex, shortly stipitate, anchored by small holdfast; branching generally pinnate, sometimes radial, branch pinnules 2–3 mm wide, commonly compressed subcylindrical. Internal structure filamentous, medulla composed of anastomosing filaments; cortex made up of anticlinal rows of cells. Life cycle triphasic, diplo-haplontic, isomorphic and dioecious. Tetrasporangia cruciate, scattered on the cortex of the frond. Antheridia in superficial patches on the cortex. Cystocarps, slightly prominent and embedded in the cortex.

Grateloupia filicina (J.V. Lamour.) C. Agardh – 1, habit; 2, cross-section of thallus with carposporophyte; 3, cross-section of thallus with tetrasporangia.

Ecology *G. filicina* grows attached firmly to dead corals and rocks on rocky, wave-exposed shores, edges of reefs or rocky walls of reef channels.

Propagation and planting *G. filicina* is not grown in phycoculture.

Phycoculture In the Philippines cultivation of *G. filicina* is still at the experimental stage and is not yet considered commercially feasible.

Harvesting *G. filicina* is collected by hand from natural populations.

Handling after harvest *G. filicina* is used fresh, blanched or air-dried.

Prospects *G. filicina* shows good prospects for development in phycoculture.

Literature |1| Nunn, J.R. & Parolis, H., 1970. Sulfated polysaccharides of Grateloupiaceae family IV. Methylation analysis of phyllymenan and desulfated phyllymenan. Carbohydrate Research 14: 145–150. |2| Llana, E.G., 1990. Status of production and utilization of seaweeds in the Philippines. FAO/NACA report on the regional workshop on the culture and utilization of seaweeds, 27–31 August, 1990. Cebu City, The Philippines. pp. 124–249. [3] Tenko, F.A. & Mino, N., 1972. The distribution of trimethylamine and trimethylamine oxide in marine algae. Proceedings of the seventh International Seaweed Symposium. University of Tokyo Press, Tokyo, Japan. pp. 506–510. [4] Usov, A.I. & Borbakadze, V.V., 1978. Polysaccharide of algae. XXVII. Partial acetolysis of the sulfated galactan from the red seaweed Grateloupia sp. Okamura Bioorganiceska Chimija Akademija Nauk SSSR 4: 1107–1115.

G.C. Trono Jr

Halimeda J.V. Lamour.

Mém. montée: 186 (1812) ('Halimedea').

HALIMEDACEAE

x = unknown

Major species and synonyms

- *Halimeda copiosa* Goreau & E.A. Graham, Bull. Mar. Sci. 17: 433, figs 1–10 (1967), synonyms: *H. opuntia* (L.) J.V. Lamour. f. *hederacea* E.S. Barton (1901), *H. opuntia* var. *hederacea* (E.S. Barton) Hillis-Col. (1959), *H. hederacea* E.S. (Barton) Colinv. (1959).
- *Halimeda cylindracea* Dec., Ess. classif. alg. calcif.: 103 (1842), synonym: *H. polydactylis* J. Agardh (1887); misapplied names: *H. incrassata* Harv. (1860), *H. incrassata* f. *monilis* E.S. Barton (1901).
- *Halimeda discoidea* Dec., Ess. classif. alg. calcif.: 102 (1842), synonyms: *H. cuneata* Hering f. *digitata* E.S. Barton (1901), *H. discoidea* var. *platyloba* Børgesen (1911), *H. discoidea* var. *intermedia* W.J. Gilbert (1947).
- *Halimeda distorta* (Yamada) Colinv., J. Phycol. 5: 33 (1968), synonym: *H. incrassata* f. *distorta* Yamada (1941).
- *Halimeda fragilis* W.R. Taylor, Pl. Bikini: 88, pl. 48, fig. 2 (1950).
- *Halimeda gigas* W.R. Taylor, Pl. Bikini: 84, pl. 44, fig. 2 (1950).
- *Halimeda gracilis* Harv. ex J.Agardh, Algern. syst.: 82 (1887), synonyms: *H. gracilis* var. *opuntioides* Børgesen (1911), *H. gracilis* f. *laxa* (E.S. Barton) E.S. Barton (1911), *H. gracilis* f. *elegans* Yamada (1941).
- *Halimeda incrassata* (J. Ellis) J.V. Lamour., Hist. polyp. corall.: 307 (1816), synonyms: *Corallina incrassata* J. Ellis (1768), *Halimeda incrassata* f. *tridentata* Duchass. ex J. Agardh (1887), *H. incrassata* f. *gracilis* Børgesen (1913).
- *Halimeda macroloba* Dec., Ess. classif. alg. calcif.: 118 (1841), synonym: *H. macroloba* var. *ecalcarea* Weber Bosse (1926).
- *Halimeda macrophysa* Askenasy, Forschungsreise Gazelle Bot., Alg.: 14, pl. 4, figs 1–4 (1888).
- *Halimeda micronesica* Yamada, Kogaku Nanyo 4: 121, fig. 15 (1941), synonyms: *H. incrassata* f. *pusilla* Barton (1901), *H. orientalis* W.J. Gilbert (1947).
- *Halimeda opuntia* (L.) J.V. Lamour., Hist. polyp. corall.: 308 (1816), synonyms: *Corallina opuntia* L. (1758), *Fucus prolifer* M. Blanco (1837), *Halimeda cordata* J. Agardh (1887).
- *Halimeda simulans* N. Howe, Bull. Torrey Bot. Cl. 34: 503–504, pl. 29 (1907), synonym: *H. incrassata* var. *simulans* Børgesen (1911).
- *Halimeda taenicola* W.R. Taylor, Pl. Bikini: 86–87, pl. 46, fig. 1 (1950).
- *Halimeda tuna* (J. Ellis & Sol.) J.V. Lamour., Hist. polyp. coral.: 309 (1816), synonyms: *Corallina tuna* J. Ellis & Sol. (1786), *Halimeda platydisca* Dec. (1842), *H. tuna* f. *albertisii* Picc. (1879).
- *Halimeda velasquezii* W.R. Taylor, Bull. Torrey Bot. Cl. 89: 176–177, figs 8–14 (1962), synonym: *H. opuntia* f. *intermedia* Yamada (1934).

Vernacular names There are many well-known *Halimeda* in Asia, but none have vernacular names.

Origin and geographic distribution Most *Halimeda* are pantropical, and many of them are widespread in South-East Asia.

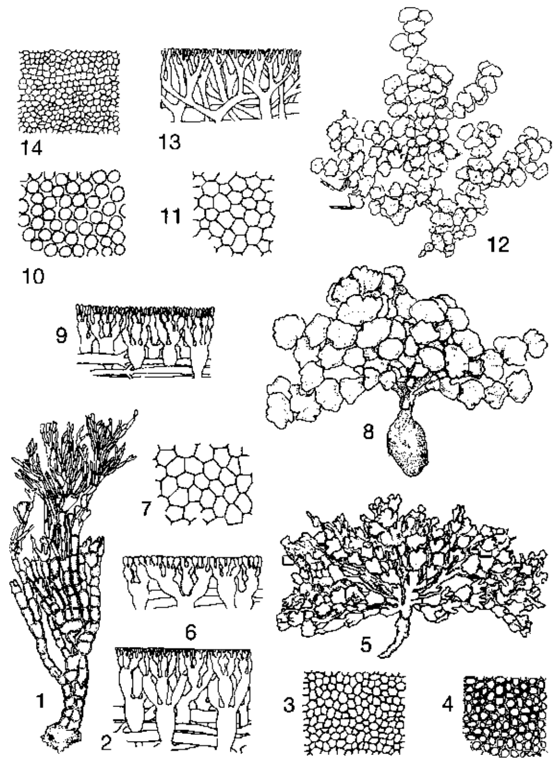
Uses *Halimeda* is used as an antibacterial medicine and against diseases caused by fungi. There are records showing that metabolites from *H. cylindracea*, *H. gigas*, *H. gracilis*, *H. incrassata*, *H. opuntia*, *H. simulans* or *H. tuna* are active against the bacteria *Bacillus subtilus* and *Staphylococcus aureus*, while *H. gracilis* is also active against the fungus *Candida albicans*. The extracts of *Halimeda* are active against P-388 lymphocytic leukaemia and Ehrlich ascites tumour systems in mice. Some *Halimeda* are used as a vermifuge. The first and possibly only published recipe for *Halimeda* as food is a 17th Century report that it makes a good dish when mixed with vinegar, salt and oil.

H. tuna is used as animal feed and often forms the food source for the green turtle. *H. macroloba* is applied as a plant growth regulator. Many *Halimeda* are used as fertilizer, especially in leached acidic soils.

Properties Extracellular deposits of aragonite (a form of $CaCo_3$) are found in *Halimeda*. The aragonitic skeletons contain about 1% $MgCO_3$ and 1.3% $SrCO_3$. *Halimeda* can thus be used as a source of carbonate. Extraction of whole thalli yields a crude fibre product containing xylose and glucose residues in a ratio of 10:1. Highly bioactive diterpenoids, including halimedatrial, have been found in many (but not all) *Halimeda* spp.

Description Plants erect, from a few mm to about 1 m long, generally bushy, often arising from a fibrous or bulbous holdfast, branched; branches with linear series of calcified segments; nodes uncalcified, flexible; segments moniliform, cylindrical or discoid, simple or lobed. Internal structure filamentous, coenocytic filaments closely parallel and indurated in the joints, loosely branched in the medulla of the segments and there laterally bearing special fascicles of branchlets, with terminal cells forming a continuous cortex; medullary filaments sometimes closed by wall thickening at forkings and at the base of the gametophores. Sexual reproduction by biflagellate gametes produced in large dark green globular to pyriform gametangia on stalks which are simple or branched, arising from node, segment or surface. The above-mentioned 16 *Halimeda* species can be divided into 3 groups:

- Plants commonly grown in sandy locations with distinct bulbous rhizoidal holdfast:
  - *H. macroloba*: segments large, 29 mm × 40 mm, subcuneate to reniform;
  - *H. simulans*: segments small, often imbricate, margins often cuneate or lobed;
  - *H. incrassata*: segments small, lower ones often partly cylindrical;
  - *H. cylindracea*: segments of the upper part of the plant cylindrical.
- Plants usually epilithic with several small holdfast areas (less than 1 cm adhering in length), each consisting of a single segment not obscured by sandy particles, laterally spreading, forming large clumps, densely branched, often heavily calcified:
  - *H. distorta*: segments 16 mm × 19 mm, often contorted;
  - *H. opuntia*: smaller segments up to 7 mm × 11 mm, often somewhat contorted;
  - *H. gracilis*: segments up to 9 mm × 15 mm, usually mainly in one plane.
- Plants usually epilithic with a single holdfast formed by a single segment not obscured by adhering sandy particles:
  - *H. micronesica*: basal segment flabellate;
  - *H. gigas*: utricles large, more than 120 μm (thus can be seen with the naked eye), segments more than 30 mm long, calcification rather light;
  - *H. macrophysa*: utricles large, more than 120 μm, segments up to 15 mm long, calcification moderate;
  - *H. copiosa*, *H. discoidea*, *H. fragilis*, *H. taenicola*, *H. tuna* and *H. velasquezii*: utricles small, segments 6–30 mm long, calcification light to heavy. Microscopical characters are to be used for distinction.



Halimeda. H. cylindracea Dec. – 1, habit; 2, sagittal section through an outer portion of about the middle of a segment to show characteristics of the cortical utricles and the extent of development of the cortex; a portion of the medulla is also included; 3, surface view of the utricles of a mature segment; 4, the same of a basal (old) segment. H. incrassata (J. Ellis) J.V. Lamour. – 5, habit; 6, sagittal section through a segment; 7, surface view of the utricles of a segment. H. macroloba Dec. – 8, habit; 9, sagittal section through a segment; 10, surface view of the utricles of a mature segment; 11, surface view of the utricles of a young segment. H. opuntia (L.) J.V. Lamour. – 12, habit; 13, sagittal section through a segment; 14, surface view of the utricles of a segment.

Growth and development Reproduction in *Halimeda* is holocarpic, thus the plants die after release of the gametangia.

Other botanical information The taxonomy of *Halimeda* is complicated and not yet solved. Most probably, specimens occurring in the Indo-Pacific region belong to species which are different from morphologically similar species in the Atlantic Ocean.

Ecology *Halimeda* algae occur from slightly below low tide to 80(–100) m depth. They occur in warm seas with temperatures of 20–25°C, and grow attached to rocks or other hard surfaces, or in sand, mud or other unconsolidated substrate. Some *Halimeda* such as *H. tuna* and *H. velasquezii* grow in regions of strong currents. *H. opuntia* sometimes covers about 90% of rock surfaces in shallow locations (0.3–0.5 m below low water level). *Halimeda* spp. are generally considered to be important reef builders, being the producers of large amounts of calcareous sand. The average mature specimen contains 8.5 g of calcium carbonate. *H. macroloba* is known to occur in brackish water as well as in the Red Sea, which has a salinity of 37–40‰.

Phycoculture Although it is possible to grow *Halimeda* in the laboratory, both in seawater or in artificial seawater, *Halimeda* has not yet been used for aquaculture.

Harvesting *Halimeda* is only hand-collected, often from material washed up along the coast.

Prospects *Halimeda*, with its antibacterial properties and calcareous contents, can be used both directly as a fertilizer and soil conditioner, especially on acid soils, or as a source of liquid extract for horticulture and agriculture.

Literature |1| Fenical, W. & Paul, V.J., 1984. Antimicrobial and cytotoxic terpenoids from tropical green algae of the family Udoteaceae. Hydrobiologia 116/117: 135–140. |2| Hillis-Colinvaux, L., 1980. Ecology and taxonomy of Halimeda: primary producer of coral reefs. Advances in Marine Biology 17: 1–327. |3| Kooistra, W.H.C.F., Calderón, M. & Hillis, L.W., 1999. Development of the extant diversity in Halimeda is linked to vicariant events. Hydrobiologia 398/399: 39–45.

P.Y. van Aalderen-Zen

Halymenia C. Agardh

Syn. alg. Scand. XIX: 19, 35 (1817).

HALYMENIACEAE

x = unknown

Major species and synonyms

- *Halymenia dilatata* Zanardini, Flora 34: 35 (1851).
- *Halymenia durvillei* Bory, Voy. monde, Crypt. 4: 180, pl. 15 (as *H. durvillaei*) (1828).
- *Halymenia formosa* Harv. ex Kutz., Tab. phycol. 16: 33, pl. 91: figs g, h (1866), synonym: *H. durvillei* Bory var. *formosa* (Harv. ex Kütz.) Weber Bosse (1921).
- *Halymenia maculata* J. Agardh, Algern. syst. 7: 12 (1885).

Vernacular names Indonesia: rumput laut, lambu argo. Philippines: gayong-gayong, lablabig, gargarnatis.

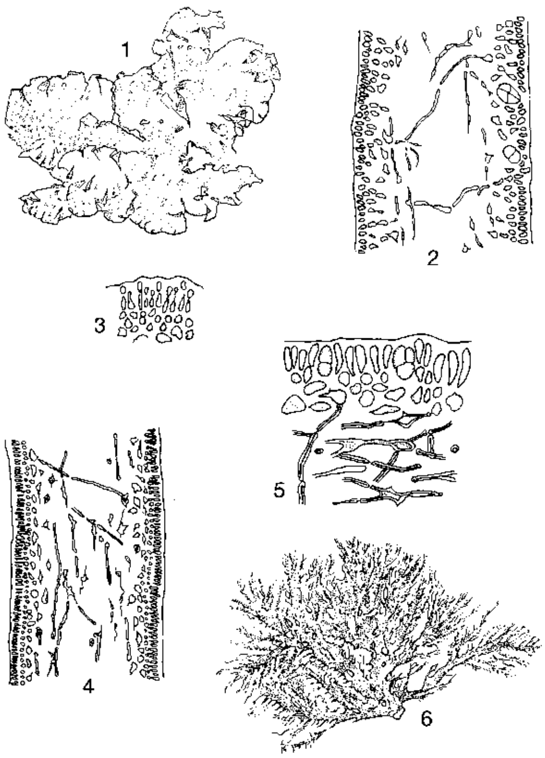
Origin and geographic distribution *Halymenia* is widespread in tropical and subtropical waters. In South-East Asia *H. dilatata*, *H. durvillei* and *H. maculata* have been reported for Indonesia, the Philippines and Thailand. *H. dilatata* also occurs in Papua New Guinea (southern coast) and *H. durvillei* also in Peninsular Malaysia, Singapore and Papua New Guinea (northern coast). *H. formosa* has been reported for Malaysia, Singapore, the Philippines and eastern Indonesia.

Uses *H. durvillei* is a known source of carrageenan. It is also used as food, especially as fresh salad. The dried form is first resoaked in water and then prepared as salad. A natural glue can be prepared from *H. durvillei*.

Production and international trade No production data are available for natural populations of *Halymenia*.

Properties The following contents of air-dried material have been determined for *H. durvillei*: crude fat (0.7% in material that was red and fresh when air-dried, 0.5% in material that was already bleached before being air-dried), crude protein (12.8% red, 11.9% bleached), iodine (6.2% red, 5.4% bleached), nitrogen (2.1% red, 1.9% bleached) and mannitol (35.5% red, 29.6% bleached). The carrageenan of *H. durvillei* is lambda carrageenan, which is the phycocolloid normally extracted from the temperate red alga *Chondrus crispus* Stackh. This phycocolloid is non- gelling and does not precipitate in KC1.

Description Plants of moderate to considerable size, foliaceous or bushy, generally of gelatinous or softly fleshy consistency; entire or variously lobed or branched. Structurally with medulla of slender filaments well separated in a soft jelly, often radiating from conspicuous ganglia-like cells; cortex of large inner cells, small outer cells, not in evident filamentous arrangement. Life cycle triphasic, diplo-haplontic, isomorphic or slightly heteromorphic. Tetrasporangia cruciately divided, scattered and immersed in the cortex. Gameto-



Halymenia. H. dilatata Zanardini – 1, habit; 2, cross section of a frond; 3, cross-section of a portion of a spermatangial sorus. H. maculata J. Agardh – 4, cross-section of a frond; 5, cross-section of a portion of a tetrasporophyte with tetrasporangia. H. durvillei Bory – 6, habit.

phytes dioecious. Cystocarps immersed with pericarp of slender filaments. Carpospores discharging through a definite pore. Spermatangia in superficial sori.

- *H. dilatata*. Thalli purplish-red with shades of green, gelatinous- membranous, 10–15 cm tall, 350–400 μm thick, attached by small scutate disc; sessile or shortly stipitate, with large transversely expanded blade, broadly oblong or irregularly lobed, 10–20(–40) cm wide, undulate-curled, simple or lobed; base reniform, subpeltate or cuneate; margin entire, crenulate, subdentate-sinuose or fimbricate with ligulate lobules. Cortex thin, with 3–5 cell layers; outermost cells shaped like rabbit ears; medullary filaments running in various directions, with highly refractive stellate cells. Tetrasporangia embedded in cortex, obovate or oblong in transverse section, 25–35 μm × 15 μm. Spermatangial sori covering the margins of the thallus. Cystocarps dot-like, deeply submerged, 200–250 μm in diameter, with ostiole.
- *H. durvillei*. Thalli large, bushy, very slippery, up to 35 cm tall, red-orange or purple, soft cartilaginous and slimy when fresh, attached to rocky substrates by discoid holdfast. Fronds flattened, with or without short stipe supporting 2–4 main axes 5–15 mm broad, about 250 μm thick, all branching pinnately-alternately 4–5 times, not in a single plane; ultimate branchlets slender, linear with acuminate tips, sometimes furcipate; margins of fronds serrate; surfaces of axis beset with few spine-like projections. Medulla containing more than half of the frond, with ganglion-like cells connecting the other medullar cells by colourless slender filaments. Outer cortex two cell layers, shaped like rabbit ears; subcortex 4–6 layers of cells. Tetrasporangia 8 μm × 20 μm. Cystocarps 250–270 μm in diameter, with inconspicuous ostiole.
- *H. formosa*. Almost identical to *H. durvillei* but fronds finely branched, very bushy, 10–20 cm tall.
- *H. maculata*. Thalli thin, membranous, purplish to greenish, 8–12 cm tall, arising in an open cluster from scutate, shortly stalked holdfast; segments irregularly proliferous; branching subdichotomous especially at distal portion of the blade; blade margin entire. Tetrasporangial thallus with 2 layers of papilla-like or irregularly shaped outer cortical cells. Medullary cells periclinally arranged fusiform filaments, 3–10 μm in diameter, without conspicuous ganglionic centres and with occasional anticlinal medullary filaments, about 10 μm in diameter, reaching from one cortex to the opposite cortex. Tetrasporangia sunk between elongated outer cortical cells acting as paraphyses, 10–20 μm × 28–31 μm, ovoid, oblong or obovate in transverse section. In cystocarpic plants only a single layer of slightly elongated cortex cells present. Spermatangia superficially borne on outer cortical cells, covering most of the surfaces. Cystocarps 96 μm × 120 μm, with several gonimolobes, surrounded by moderate number of sterile filaments.

Ecology *Halymenia* is commonly found attached to rocks in the lower intertidal to upper subtidal areas moderately exposed to wave action.

Propagation and planting *Halymenia* is not yet grown in phycoculture.

Phycoculture Research is still being done to develop a culture method suitable for commercial cultivation of *Halymenia*.

Harvesting *Halymenia* is hand-collected from natural populations.

Handling after harvest To use *H. durvillei* for the production of glue, the dried algae are cooked for two hours with water, boric acid and hydrogen peroxide. After straining through cheese cloth the extracted liquid is cooked for half an hour or until the glue acquires the proper adhesive property. Substances such as zinc oxide and *Pyrola* oil are often added.

Prospects In Japan interest in dried *Halymenia* is increasing. The present limited supply for the seaweed salad market comes mainly from natural stocks. Demand for lambda-type carrageenan from *H. durvillei* from the seaweed industry is potentially large. This carrageenan is used as a blending agent for specially formulated products. The development of farming technology for *H. durvillei* is one of the challenges for seaweed farmers in the near future.

Literature |**1**| Abbott, I.A., 1999. Notes on some species of Halymenia in the southwestern Pacific. In: Abbott, I.A. (Editor): Taxonomy of economic algae 7. pp. 163–172. |**2**| Calmorin, L.P., 1993. Glue from the red seaweed, Halymenia. SICEN (Seaweed Information Center) Newsletter 4(2): 7. |**3**| de Leon, C.A. & Domantay, J.S., 1971. Studies on some Philippine Rhodophytes and their colloidal contents. Acta Manilana, serie A, 8: 3–38. |**4**| de Leon, A.I., Eufemio, N. & Pineda, M., 1963. Chemical composition of some Philippine algae. Philippine Journal of Science 92(1): 77–87. |**5**| Kawaguchi, S. & Lewmanomont, K., 1999. Morphology and culture study of a red alga, Halymenia dilatata Zanardini, from Vietnam and Japan. In: Abbott, I.A. (Editor): Taxonomy of economic algae 7. pp. 147–161. |**6**| Llana, E.G., 1990. Status of production and utilization of seaweeds in the Philippines. FAO/NACA report on the regional workshop on the culture and utilization of seaweeds, 27–31 August, 1990. FAO, Cebu City, The Philippines. pp. 124–149. |**7**| Xia, B. & Wang, Y., 1999. Taxonomic studies on Halymenia (Halymeniaceae, Halymeniales, Rhodophyta) from China. In: Abbott, I.A. (Editor): Taxonomy of economic algae 7. pp. 173–176.

G.C. Trono Jr

Hormophysa cuneiformis (J.F. Gmelin) P.C. Silva

Smithsonian Contr. Mar. Sci. 27: 81 (1987).

CYSTOSEIRACEAE

$2n$ = unknown

Synonyms *Fucus cuneiformis* J.F. Gmelin (1792), *Cystoseira triquetra* C. Agardh (1820), *Hormophysa articulata* Kütz. (1860).

Vernacular names Indonesia: rumput laut (general name for seaweed). Malaysia: rumpair (general name for seaweed). Philippines: samô (Cebuano), aragan (Ilocano).

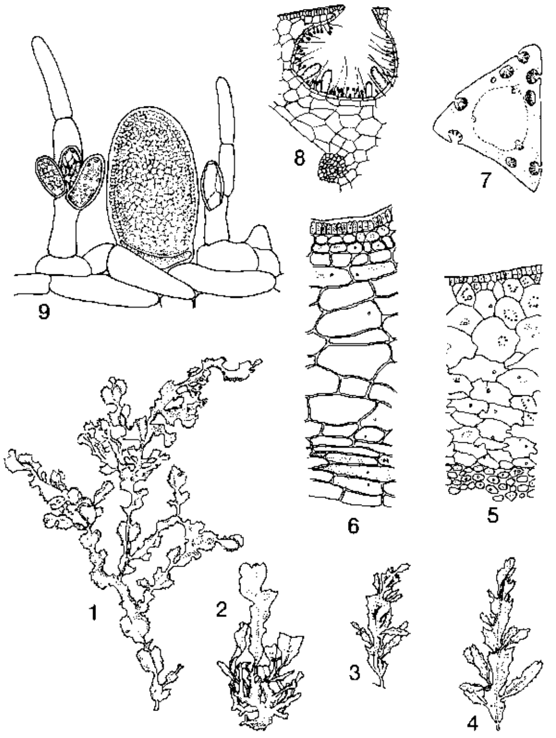
Origin and geographic distribution *H. cuneiformis* is widely distributed in the Indian Ocean, the Red Sea and the Pacific Ocean, but has not been reported in Cambodia.

Uses *H. cuneiformis* is used as animal feed, fertilizer, insect repellent, and foliar spray on crops in the Philippines. Its use in other South-East Asian countries is not well documented. It is a potential source of alginate and other natural products including phenols, carotene, chlorophyll a, chlorophyll c, fucoxanthin, tannins, laminarin and mannitol. Methanol and hexane extracts from this alga (as *H. articulata*) show antimicrobial activity especially against gram-positive bacteria, but they do not show antifungal activity.

Production and international trade *H. cuneiformis* is usually harvested from natural populations together with other large brown algae such as *Sargassum* and *Turbinaria* spp. and is mentioned under brown algae, so no specific information on its production and trade is available.

Properties For samples of *H. cuneiformis* (as *H. triquetra*) from Alabat, Quezon (the Philippines) an alginic acid yield of 41.8% (moisture-free basis) has been recorded. For material from Magnetic Island, Queensland (Australia) by following the Folin-Denis Assay, $2.3 \pm 0.1\%$ phenolic content (dry mass) was reported, while material from Qatar (Arabian Gulf) yielded 1.2% sterols, which was made up of 3.2% cholesterol, 86.7% fucosterol and 10.1% 24-methylene-cholesterol. Aqueous extracts of *H. cuneiformis* have high gibberellin-like activity when tested on rice.

Description Thalli erect, large, bushy, fleshy, up to 40 cm tall, attached to rocky substrate by discoidal holdfast from which several erect axes arise. Branches foliaceous, segmented; branching in multiple planes; segments three-ridged or triquetrous, with serrated to dentate margins, distal ones commonly with centrally disposed oblong vesicle embedded inside. Cryptostomata distinct,



Hormophysa cuneiformis (J.F. Gmelin) P.C. Silva – 1, apical portion of a thallus; 2, holdfast and basal branches; 3, branch bearing vesicles; 4, fertile branch; 5, cross-section of a triquetrous branch; 6, longitudinal section of a triquetrous branch; 7, cross-section of a branch with central vesicle and conceptacles; 8, detail of this cross-section with a bisexual conceptacle and a strand of small cells in the wall of the vesicle; 9, part of the floor of a bisexual conceptacle, showing an oogonium and two antheridial filaments.

scattered on surfaces of segments. Life cycle diplontic. Plants monoecious. Conceptacles bisexual, scattered over thallus without distinctive receptacles. Oogonia sessile, ovoid or broad based, 80–120 μm × 35–60 μm, forming a single egg; antheridia sessile or on short, branched paraphyses, elongate-ovoid, 20–30 μm × 8–12 μm. Simple paraphyses also present in the conceptacles.

Growth and development In the Philippines, *H. cuneiformis* has been collected at different months in different regions and appears to be present year-round. However, its phenology has not been examined in great detail.

Other botanical information There is thallus variation in *H. cuneiformis* between estuarine and marine forms as a result of reduced cell enlargement and cell division in the estuarine form.

Ecology *H. cuneiformis* is usually found growing with other large brown algae such as *Sargassum* spp. in shallow subtidal rocky shores exposed to moderate to strong waves. Its range of distribution, however, may be from estuarine to marine habitats. In western Australia, it has been found in an estuary with a salinity range of 45–50‰. Populations of this alga serve as a habitat for larvae of shrimps like *Penaeus semisulcatus*. However, it does not attract grazers like the sea urchins *Diadema setosum* and *Heliocidaris erythrogramma*.

Propagation and planting *H. cuneiformis* is not known to be propagated artificially nor is it used in any phycoculture in South-East Asia. However, laboratory experiments to grow the alga on rope in India suggest that it would be easy to cultivate.

Harvesting *H. cuneiformis* is not specifically targeted for harvest. Occasionally, it forms part of the harvest of other algae such as *Sargassum* spp.

Yield Results of experimental rope culture in aquaria in India indicated that stipes increased at a rate of 89 mg wet weight per day, and fronds at a rate of 333 mg wet weight per day over a period of 150 days.

Handling after harvest Samples of *H. cuneiformis* are usually harvested together with *Sargassum* spp., and air-dried. The viscosity of alginate extracted from *H. cuneiformis* increases from 77 cps (at room temperature) to 166 cps if the samples are pretreated overnight with 2% formaldehyde solution prior to extraction.

Prospects *H. cuneiformis* is usually not a dominant component of the reef. Its further development as an economic alga is not expected in the immediate future unless unusual chemicals are found and can be isolated from it.

Literature |1| Bhanderi, P.P. & Trivedi, Y.A., 1977. Rope culture of algin-yielding seaweed Hormophysa triquetra (Linnaeus) Kutzing. Botanica Marina 20: 183–185. |2| Lasema, E.C., Veroy, R.L., Luistro, A.H., Montaño, N.E. & Cajipe, G.J.B., 1982. Alginic acid from some brown seaweeds. Kalikasan 11: 51–56. |3| Papenfuss, G.F., 1967. The history, morphology and taxonomy of Hormophysa (Fucales: Cystoseiraceae). Phytomorphology 17: 42–47. |4| Tupas, L.M. & Montaño, N.E., 1987. Effects of aqueous alkaline extracts from Philippine seaweeds as a foliar spray on crops. Philippine Journal of Science 17: 29–36.

P.O. Ang

Hydroclathrus Bory

Dict. class. hist. nat. 8: 419–420 (1825).
SCYTOSIPHONACEAE
x = unknown

Major species and synonyms

- *Hydroclathrus clathratus* (C. Agardh) M. Howe, in Britton & C.F. Millsp. Bahama fl. 590 (1920), synonyms: *Encoelium clathratum* C. Agardh (1822), *Hydroclathrus cancellatus* Bory (1825).
- *Hydroclathrus tenuis* C.K. Tseng & B. Ren Lu, Chin. J. Oceanol. Limnol. 1(2): 187 (1983).

Vernacular names Philippines: lukot-lukot (Visayan), poko-poko, balbalulang (Ilokano). All names are mainly for *H. clathratus*.

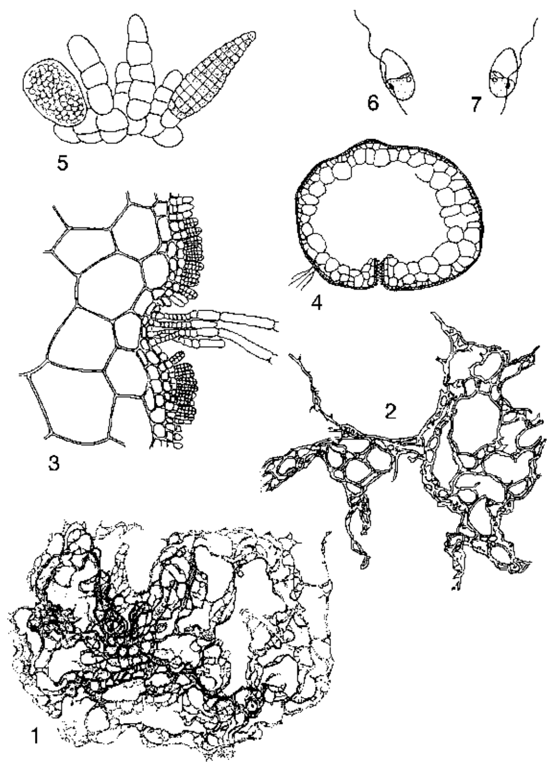
Origin and geographic distribution *H. clathratus* is the most common species and is widely distributed in most of the tropical warm waters of the world. In the South-East Asian region it is found in Burma (Myanmar), Thailand, Vietnam, Malaysia, Singapore, Indonesia, the Philippines and Papua New Guinea as well as tropical China, Japan and the western Central Pacific region. *H. tenuis* has only been recorded for the Philippines, Indonesia (Sulawesi) and the southernmost parts of China.

Uses Both *Hydroclathrus* are used in human food, in salads after blanching in hot water or as a spicy ingredient. They are also applied as fertilizer, animal fodder and insect repellent, and are a good source of alginate and iodine.

Production and international trade No production data for *Hydroclathrus* are available. It is not being cultured, the biomass being harvested from natural stocks.

Properties *Hydroclathrus* generally contains alginate. It also contains iodine (1.4%), mannitol (17.3%), a fair amount of crude protein (9.0%), crude fat (1.0%) and crude fibre (1.8%), as well as growth regulators such as auxin (8400 μ auxin activity/g seaweed when an aqueous extract is tested on oat (*Avena sativa* L.)), gibberellin and cytosin. Fucoidin is also present in small quantities as well as vitamins such as folic and folinic acids. *H. clathratus* is occasionally cited as containing harmful 'germs'. This might be related to 'curet', which are pinhead-sized poisonous crabs that breed in *Hydroclathrus* thalli. Infested thalli are reported to be deadly poisonous.

Description Round, cushion-shaped, clathrate mass when young, reticulate amorphous mass when mature; structure parenchymatous. Sporangia generally distributed over thallus surface.
– *H. clathratus*. Thalli yellow-brown, attached by rhizoids when young, vesicular or irregularly ovate, becoming hollow with many small holes; mature thalli detached from substrate, developing into well-formed network with rounded holes 0.5–2 cm in diameter, margins around holes involute. Cross-section of network about 600–900 μm thick, composed of cortex and medulla; cortical cells small, cuboidal, 5–9 μm with chromatophore; hairs grouped in shallow depressions; medullary cells colourless, large, 100–130 μm. Life cycle heteromorphic. Plurilocular zoidangia at first biseriate, scattered over surface of saccate thalli, or occurring together with unilocular zoidangia on prostrate microthalli;



Hydroclathrus. H. tenuis C.K. Tseng & B. Ren Lu – 1, habit. H. clathratus (C. Agardh) M. Howe – 2, portion of a clathrate thallus; 3, cross-section of a clathrate thallus with plurilocular zoidangia; 4, cross-section of inrolled thallus, united by rhizoids; 5, detail of a prostrate microthallus with an unilocular and a plurilocular zoidangium; 6, zoid from a plurilocular zoidangium of a clathrate thallus, with an eye-spot (dark dot) and a pyrenoid (open dot); 7, zoid from an unilocular zoidangium of a prostrate microthallus, with eye-spot and pyrenoid.

mature plurilocular zoidangia on saccate thalli often broadly based, 33.3–41.6 μm × 10.0–11.7 μm. Unilocular zoidangia sessile or shortly pedicellate, 28.6–35.7 μm in diameter.

– *H. tenuis*. Thalli yellow-brown, attached when young, vesicular, becoming hollow with perforations; mature thalli detached from substrate, developing into large reticulate network with rounded holes; reticulate thalli very thin, about 250–300 μm thick. Network consisting of cortex and medulla; cortex with small, quadrate, pigmented cells, 8–10 μm in diameter; medulla composed of several layers of large, colourless, parenchymatous cells, 70–30 μm in diameter; colourless hairs grouped in shallow depressions on surface of thalli. Plurisporangia biseriate, 22–25 μm × 6–9 μm, in groups on surface of thalli, associated with tufts of hairs.

Growth and development *Hydroclathrus* alternates between macrothalli bearing plurilocular zoidangia and prostrate microthalli bearing both plurilocular and unilocular zoidangia. In plurilocular zoidangia each of the loculi of originally biseriate zoidangia often forms 4 smaller loculi, each containing a single plurizoid. Plurilocular zoidangia on prostrate microthalli are ectocarpoid, 36–36 μm × 14–15 μm, biseriate, somewhat spindle-shaped, occasionally branched, but usually simple, without a stipe. Plurizoids from both the microthalli and the macrothalli attach and form prostrate microthalli. Many unizoids are found together in unilocular zoidangia and always on microthalli. After germination they always form macrothalli. No sexual reproduction stage is known. In experimental tests, germlings of *H. clathratus* did not grow at temperatures of 5°C and below. This explains why the alga is not found on temperate coasts.

Ecology *H. clathratus* and *H. tenuis* are very common on reef flats. Young thalli form reticulate clumps attached to coral rocks at the landward half of the reef crest and on the reef flat. The peak of abundance usually occurs during the sunny period of March–May/June when the alga forms thick blooms. The advent of the rainy season marks the start of the die-off stage of the bloom which completely disappears during the rainy months. *H. clathratus* is more abundant than *H. tenuis*.

Propagation and planting *Hydroclathrus* is not known in phycoculture.

Harvesting *Hydroclathrus* is hand-collected by local people.

Handling after harvest *Hydroclathrus* is used and sold fresh or sun-dried.

Prospects Unless commercial use of *Hydroclathrus* compounds is found, very few developmental prospects are likely in the future.

Literature |1| Kogame, K., 1997. Life histories of Colpomenia sinuosa and Hydroclathrus clathratus (Scytosiphonaceae, Phaeophyceae) in culture. Phycological Research 45: 227–231. |2| Montaño, N.E. & Tupas, L.M., 1990. Plant growth hormonal activities of aqueous extracts from Philippine seaweeds. SICEN Leaflet 2: 1–6.

G.C. Trono Jr

Hypnea J.V. Lamour.

Essai Thalassioph.: 131–132 (1813).

HYPNEACEAE

x = unknown; *H. musciformis*: $2n = 10$

Major species and synonyms

– *Hypnea boergesenii* Tak. Tanaka, Sci. Pap. Inst. Algol. Res., Fac. Sci., Hokkaido Imp. Univ. 2: 233–235, figs 6–8, pl. 53, fig. 1 (1941).
– *Hypnea cenomyce* J. Agardh, Spec. gen. ord. alg. 2 (2): 452–453 (1851) [1851–1863].
– *Hypnea charoides* J.V. Lamour., Essai Thalassioph.: 132, pl. 4 (= pl. 10), figs 1–3 (1813), synonym: *H. divaricata* auct. (1848).
– *Hypnea cornuta* (Kütz.) J. Agardh var. *stellulifera* J. Agardh, Spec. gen. ord. alg. 2(2): 449 (1851) [1851–1863], synonym: *Chondroclonium cornutum* Kütz.
– *Hypnea musciformis* (Wulfen) J.V. Lamour., Essai Thalassioph.: 131 (1813), synonym: *Fucus muscoides* Wulfen (1791).
– *Hypnea pannosa* J. Agardh, Öfvers. Förh. K. Sv. Vet. Akad. 4: 14 (1847), synonym: *H. nidulans* Setch. (1924).
– *Hypnea spinella* (C. Agardh) Kütz., Bot. Zeitung 5: 23 (1847), synonyms: *Sphaerococcus spinellus* C. Agardh (1822), *Hypnea cervicornis* J. Agardh (1851).
– *Hypnea valentiae* (Turner) Mont., in P. Webb & Berthel. Hist. nat. Iles Canaries 3, part 2, sect. 4: 161 (1841) [1839–1842], synonyms: *Fucus valentiae* Turner (1808–1809), *Hypnea hamulosa* (Turner) J.V. Lamour. (1813).

Vernacular names General: Indonesia: paris, bulong jaja (Bali). Philippines: culot, sumon-sumon.
– *H. charoides*. Philippines: anen.
– *H. spinella*. Indonesia: bulong budur (Madurese), sasangan pasir (Bawean).
– *H. valentiae*. Philippines: kulot ti pusa, samo.

Origin and geographic distribution *Hypnea* occurs in tropical seas all over the world and some species have also been recorded at higher latitudes. Several species occur regularly along the coasts of countries of South-East Asia.

Uses Most *Hypnea* can be used as a source of carrageenan. They contain the growth hormone gibberellin. Several species are used in human food as salad, mixed with rice in Thailand, Indonesia and the Philippines, but also in the form of dried noodle-like sheets or as jellies. The instant noodle-like sheets prepared from *Hypnea* are used in Burma (Myanmar) as a dietary supplement to combat goitre, inhibit the progress of hypertension, ease insomnia, prevent stomach diseases, constipation and internal parasites in digestive tracts, to stimulate greater activity and promote longevity. The dried algae are also used as medicine (in Indonesia as an anthelmintic and also antibiotic, especially antifungal, and as an antitumor compound), as fertilizer and as animal feed. However, studies on antibiotic activity of especially *H. musciformis* have resulted in contradictory results in different parts of the world. *H. musciformis* is or has been used as a commercial carrageenan source in Burma (Myanmar), Senegal, Brazil and Florida (United States). In Burma, however, many small-scale factories have been closed because of market problems: the general public in that country prefers agar powder imported from neighbouring countries to the locally produced strips of carrageenan.

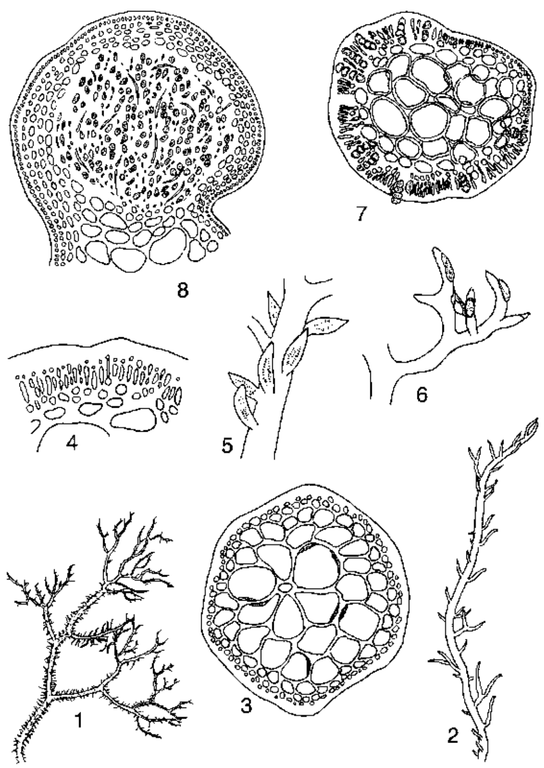
Production and international trade In South-East Asia (except Burma) hand-gathered *Hypnea* is only used for local consumption, and sold fresh or dried.

Properties *Hypnea* contains the amino acids phenylalanine, leucine, tyrosine, valine, alanine, glycine, aspartic acid, glutamic acid, serine, threonine, arginine and histidine. It also contains sulphated galactan and minerals (Ca, Fe, K, Mg, Na and smaller amounts of Cd, Cu, Mn, P, Pb and Zn). Although agar has been often cited as the prominent phycocolloid of *Hypnea*, it has repeatedly been shown that its cell walls only contain high quantities (15–48% of dry weight) of kappa carrageenan, mixed with some iota-type repeating units. In high concentrations gel strength is much better than that of standard agar and as fine as the best gelatins in the market. Gel strength (in g/cm^2) differs considerably according to species and method: *H. musciformis* 12.5–49.5, *H. spinella* (as *H. cervicornis*) 282–530 without KCl treatment and about 640 with KCl treatment, *H. valentiae* 600 when measured in a 1% phycocolloid solution treated with a 1% KCl solution. Usually, addition of an 0.1% KCl solution considerably increases gel strength in *Hypnea*.

In India rather high concentrations were measured of proteins, fat (70 mg/100 g dried *Hypnea* sp.) and vitamin C (8.6 mg/100 mg fresh *Hypnea* material) and in Pakistan fatty acids, sesquiterpene and sterol compositions have been investigated. Palmitic acid, a saturated fatty acid, was present in the largest quantities, while oleic acid was the major unsaturated fatty acid.

Description Thalli bushy, entangled, caespitose or spreading, attached to substrate by primary discoid holdfast, often creeping or descending branches with secondary holdfasts. Branches slender, terete or compressed with persistent uniaxial filament, surrounded by pericentral cells, pseudoparenchymatous cellular medulla and inner and outer cortex layer, often with spinulose branchlets. Life cycle triphasic, diplo-haplontic and isomorphic, with dioecious sexual thalli. Tetrasporangia zonate, terminal on corticating filaments, forming nemathecia on swollen parts of special short lateral branchlets; carpogonial branches three-celled, laterally on inner cortical cells. Cystocarps each enclosed in hemispherical poreless pericarp. Spermatangia cut off in chains from outermost cortical cells in slightly or inconspicuously swollen parts of terminal branchlets or proliferations or both.

- *H. boergesenii*. Thalli forming dense tufts, composed of somewhat erect branches up to 17 cm tall, brownish-green. Main branches percurrent, terete, tapering towards the apices, 410–800 μm in diameter, proliferous in upper portion, densely clothed with short, simple, acuminate lateral branchlets 300–400 μm long, or compound lateral branchlets 570–600 μm long, bifurcate or beset with short spinose projections. Axes and branches in cross-section with small central cell surrounded by 5–6 larger pericentral cells, many other large medulla cells (often with lenticular thickenings, also in walls of pericentral cells) and a rather abrupt transition to the much smaller cortex cells. Tetrasporangial sori on basal or middle parts of ultimate branchlets; tetrasporangia 50–62.5 μm × 20–25 μm. Cystocarps almost spherical, 500–600 μm in diameter, solitary or in small groups on branchlets. Spermatangia around basal part of ultimate branchlets, cut off from modified and elongate cortex cells; spermatia about 4 μm in diameter.
- *H. cenomyce*. Thalli light to reddish-brown, intricate-caespitose at upper and lower parts, forming densely entangled, cushion-like mass, 5–8



Hypnea. H. spinella (C. Agardh) Kütz. – 1, main branch with loosely and irregularly arranged branches and branchlets. H. charoides J.V. Lamour. – 2, detail of an indeterminate branch with branchlets; 5, tetrasporangial nemathecia on branchlets. H. boergesenii Tak. Tanaka – 3, cross-section of a vegetative branch: medullary cells with lenticular thickenings in their cellwalls; 4, cross-section of a spermatangial branchlet with small spermatangia formed from modified outer cortex cells. H. pannosa J. Agardh – 6, tetrasporangial nemathecia on branchlets; 7, cross-section of a tetrasporangial branchlet with tetrasporangia; 8, longitudinal section of a cystocarp with developing carpospores inside a pericarp.

cm tall, 500–1000 µm in diameter. Branching irregular in all directions; branches cylindrical, beset with numerous short and long slender spinous branchlets, often with small accessory attachment discs. Pericentral cells 4–6; lenticular thickenings in medullary cell wall absent. Tetrasporangia borne in nemathecia in lower or middle portion of ultimate branchlets, swollen. Cystocarps subcylindrical, 600–1000 µm in diameter, solitary or in small groups on branches and branchlets.

– *H. charoides*. Thalli brownish to pale red, caespitose, loosely intricate in lower parts, 10–14 cm tall. Branching alternate; branches subcylindrical, 450–600 µm in diameter, principal axes percurrent, beset with short, spinous branchlets. Transverse sections of main axes and branches not always with distinct central cell. Medulla cells (with few lenticular thickenings) not much larger than inner cortex cells, thus cell transition gradual; outer cortex cells much smaller. Tetrasporangial nemathecia on ultimate branchlets, swollen.

– *H. cornuta* var. *stellulifera*. Plant dark red to pale red, erect to caespitose, 5–16 cm tall, with or without percurrent axes. Branching freely alternate, lateral branch axes percurrent, tapering to the extremities, ultimate branchlets long or short; small stellate spinous processes of 3–6 rays, abundant, peltately attached and easily detached. Transverse-sections of axes and branches with small central cell surrounded by 4–5 much larger medullary cells and many other medullary cells, all without lenticular thickenings; cell transition to much smaller cortex cells abrupt. Tetrasporangia 50–57 µm × 21.5–28.5 µm, with small nemathecial swellings, encircling basal and middle parts of branchlets.

– *H. musciformis*. Thalli very bushy, often entangled, texture somewhat fragile, fleshy, dull purplish-red or bleached. Erect branches 10–20(–50) cm tall, about 1–2 mm in diameter; main branches dividing several times, beset by numerous, short, divaricate ultimate branchlets 1–5(–10) mm long; tips of branches often elongate, naked, usually swollen, hooked (crozier-like), bearing a row of small ultimate branchlets on abaxial side; tetrasporic branchlets usually spindle-shaped, rostrate; cystocarpic branchlets divaricate. Cystocarps swollen.

– *H. pannosa*. Thalli caespitose, greenish to purple, submerged living plants with brilliant blue iridescence; structure cartilaginous but brittle when alive, forming thick mats of intricating branches on rocky substrates. Branching irregularly, alternate-spirally to alternate-opposite, forming wide angles and rounded axils, without percurrent axis; branches terete to slightly compressed, 1.0–3.0 mm broad, dividing into short stubby spines at terminal portions of thallus. In transverse-sections of branches rather large central cell surrounded by 5–6 pericentral medullary cells and other medullary cells, all of about the same dimensions and without lenticular thickenings in cell walls; cell transition to the much smaller cortex cells rather abrupt. Tetrasporangia 30–58 μm × 12–26 μm, in saddle-shaped nemathecia at middle side of ultimate branchlets, at first on one side, later encircling the fertile part. Fertile branchlets 700–3000 μm × 400–650 μm.

- *H. spinella*. Thalli soft to subcartilagenous in texture, light red to scarlet, forming small, 1.5–3 cm tall, compact tufts on rocks, without percurrent axes. Branching irregular in all directions; branches spreading, 300–500 μm thick, smaller branches spinelike, slender ones variable in length, commonly anastomosing, proliferations usually present, not abundant. '*H. cervicornis*' is a growth form, with longer (up to 7 cm tall), less entangled and no anastomosing branches. In transverse-sections of main axes and branches, distinct central cell surrounded by 5–6 large, irregularly ovoid cells with rather thick walls (up to 5 μm thick) and lenticular thickenings; cell transition to much smaller cells rather gradual. Enlarged tetrasporangial nemathecia borne at middle or tip of determinate branchlets, 150–1500 μm × 100–200 μm; tetrasporangia 28–44 μm × 12–22 μm. Cystocarps spherical, solitary or in small groups at base of terminal branchlets, 580–1075 μm in diameter.
- *H. valentiae*. Thalli erect, up to 12 cm tall (outside South-East Asia larger, up to 50 cm tall), greenish-brown or purple, laxly alternate-spirally branched, often with distinct (percurrent) axis extending throughout entire thallus length. Branches terete, 680–2500 μm in diameter, loosely entangled at basal part, somewhat membranous in living condition; ultimate branchlets lateral, filiform, occasionally forked with acute tips, and oriented at right angles to main axis, short proliferations abundantly formed on axes and branches. In transverse-sections of main axes and branches distinct central cell surrounded by 6–8 large cells with lenticular thickenings in cell walls; cell transition to the much smaller cortex cells rather gradual. Nemathecia in the form of swollen bands, borne at middle, near base, or rarely near tip of ultimate branchlets and proliferations. Tetrasporangia 32–70 μm × 14–32 μm. Spermatangial sori 250–1500 μm × 150–450 μm; spermatia 2.5 μm in diameter. Cystocarps globose, 700–1300 μm in diameter.

Growth and development There is no reliable information on seasonality and reproduction of *Hypnea* in South-East Asia, but in India, vegetative growth of *H. musciformis* increases from October–November, reaching a maximum in February. In Hawaii *H. spinella* (as *H. cervicornis*) needs just 3 months to grow to its adult size of about 7 cm. Growth rates of about 20%/day occurred regularly in artificial culture of *H. musciformis* in warm seawater. *Hypnea* spp. have been found in the Philippines with tetraspores in December and January and with cystocarps in February. Growth rates of several *Hypnea* spp. increase considerably when nitrate is added, but only when grown in bright light. In *H. musciformis* addition of nitrate and phosphate in bright light increases growth rates but the content of phycocolloids decreases (from 44.3–27.7% in some cases).

Other botanical information *H. cenomyce* includes var. *tenuis* Weber Bosse and *H. musciformis* includes the varieties *esperi* J. Agardh and *hippuroides* (Kütz.) Weber Bosse. *H. esperi* Bory is probably different from the variety of the same name under *H. musciformis*. Recently, *H. charoides* and *H. valentiae* have been treated together as a *H. charoides-valentiae* complex because these two species cannot be differentiated. The occurrence of *H. musciformis* in South-East Asia is not well documented. In Japan most specimens formerly included under this name are now considered to belong to *H. japonica* Tan. Tanaka, because the numerous short proliferations, characteristic for *H. musciformis*, are lacking in these specimens.

Ecology Most *Hypnea* spp. grow in shallow water near the shore in areas somewhat exposed to waves and surf. *H. pannosa* grows well on rocky, slightly wave-exposed areas at or near the margin of the reef. It forms luminescent clumps when seen underwater, usually lodged between coral rocks or in depressions.

Propagation and planting *Hypnea* is not known in phycoculture, and thus is gathered from natural stocks. Cultivation of *Hypnea* from spores can be considered: both tetraspores and carpospores are potential 'seeding' material. Cultivation with vegetative fragments on lines is also possible. Mixed farming with *Eucheuma* J. Agardh has been tested. Seasonality of the *Hypnea* specimens in these mixed cultures is coincident with poor growth of the *Eucheuma* thalli.

Phycoculture In phycoculture experiments with *Hypnea*, attached thalli grow much better than free-floating ones. The differences in production between these two methods can be as large as 60–200%.

Diseases and pests In Hawaii the introduced *H. musciformis* has become a pest, and is the host of the symbiotic red alga *Hypneocolax stellaris* Børgesen, which is able to reduce the growth rate of the *Hypnea* thalli by 40% (and in laboratory cultures even by 70%). The host alga is also grazed by amphipods (Gammarids) and sea-hares (*Aplysia* spp.). Sea urchins avoid grazing on *H. cornuta*.

Harvesting The best harvest of *Hypnea* can be expected during the dry season.

Yield The carrageenan content of *Hypnea* plants can be maximized by maturing for two weeks in tanks without additional nutrients. Usually, peak levels in carrageenan occur shortly after periods of rapid growth. The phycocolloid content of *H. muscoides* in Veravalk (India) increases gradually from October–November, reaches a maximum in March, then declines, showing rapid decomposition. No data are available for South-East Asia.

Handling after harvest *Hypnea* is used fresh or dried and bleached.

Prospects The high growth rate of *Hypnea*, its high content of kappa carrageenan and the quality of its gels make *Hypnea* feature prominently as one of the most promising carrageenan sources in the tropics, coming only second to *'Eucheuma'* in commercial significance. *Hypnea* can also be used as fertilizer, as antitumor medicine as well as an antibiotic, a muscle relaxant or as a source of peptides which can agglutinate animal and human erythrocysts. The prospects of farming the seaweed commercially seem promising, although optimum phycoculture methods have to be developed for reliable future supplies.

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G.C. Trono Jr & P. Gronier

Kappaphycus Doty

In: I.A. Abbott, Taxon. econ. seaweeds 2: 171–172 (1988).

SOLIERIACEAE

x = unknown, possibly 10

Major species and synonyms

Synonym for the genus *Kappaphycus* is *Eucheuma* J. Agardh section *Cottoniformis* Doty & J.N. Norris, in: I.A. Abbott & J.N. Norris, Taxon. econ. seaweeds 1: 58–59 (1985).

- *Kappaphycus alvarezii* (Doty) Doty ex P.C. Silva – see separate article.
- *Kappaphycus cottonii* (Weber Bosse) Doty ex H.D. Nguyen & Q.N. Huynh, in: I.A. Abbott, Taxon. econ. seaweeds 5: 234 (1995), synonyms: *Eucheuma cottonii* Weber Bosse (1913), *E. okamurae* Yamada (1936).
- *Kappaphycus inermis* (F. Schmitz) Doty ex H.D. Nguyen & Q.N. Huynh, in: I.A. Abbott, Taxon. econ. seaweeds 5: 233 (1995) (as *K. inerme*), synonym: *Eucheuma inerme* F. Schmitz (1895).
- *Kappaphycus striatus* (F. Schmitz) Doty ex P.C. Silva – see separate article.

Vernacular names Indonesia: 'cottonii' (Java, Bali, Sulawesi, the common name for all *Kappaphycus* spp.), agar-agar, agar besar (both common names for *Kappaphycus* and *Eucheuma* spp.). Philippines: tamsao (northern Luzon, both for *Kappaphycus* and *Eucheuma* spp.), guso (Visayan, for species of both genera), tambalang, kanot kanot (Ilocos Norte, for species of both genera).

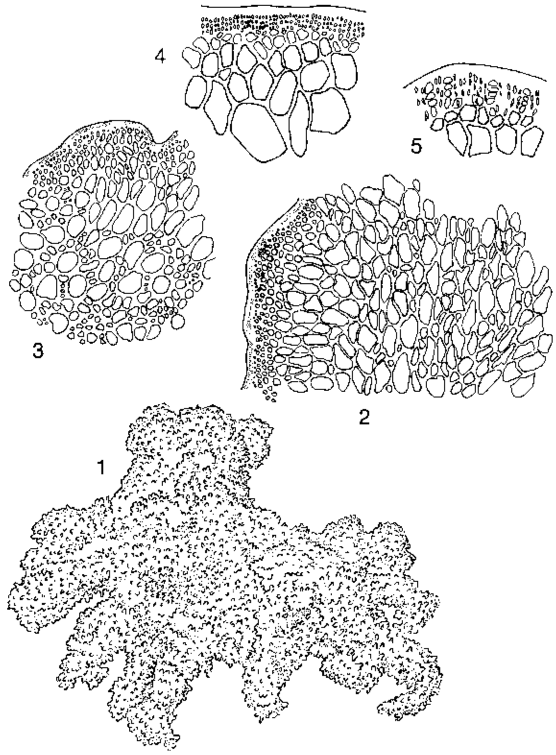
Origin and geographic distribution Originally, *Kappaphycus* only occurred in the Indian Ocean (Kenya, Tanzania, Madagascar, as well as on some small islands in the central part of that ocean), in South-East Asia and in Japan. Recently several *Kappaphycus* spp. have been distributed by humans to many other regions, including the Caribbean for cultivation trials. *K. inermis* was described from East Africa (Tanzania) and has recently been found in Vietnam.

Uses *Kappaphycus* seaweeds are generally used as a source of kappa carrageenan as indicated under *K. alvarezii*.

Production and international trade World phycoculture production for all *'Eucheuma'* spp. (including *Kappaphycus* and *Betaphycus* spp.) for 1986 was 160 106 t (all data on wet-weight basis, except for Vietnam) and by 1994 it had been risen to 384 980 t. Indonesia produced 77 462 t in 1986 and 115 000 t in 1994 (however, this also includes *Gracilaria* Grev. and Gelidiales). In the Philippines production in 1986 probably amounted to 4627 t (*'E. alvarezii'*) and 145 632 t (*'E. cottonii'*). By 1994 these figures had risen to 12 110 t and 347 300 t respectively. However, these estimates are not accurate, because the combined estimated production for Indonesia and the Philippines is higher than the given estimate for world production. Figures for Vietnam suggest that in 1995 about 10 t (dry weight) of *K. cottonii* were produced.

Properties In all cases where *Kappaphycus* was tested, both tetrasporic and cystocarpic stages consistently produced kappa carrageenan. In *K. inermis*, however, the gel strength of the kappa carrageenan is only half that of the carrageenan obtained from other *Kappaphycus* spp. In both *K. inermis* and *K. striatus* the sulphate content of the carrageenan is higher than in the other species.

Description Thalli prostrate or erect, amorphous, compressed or composed of cylindrical branches. Branching usually irregular with few to numerous coarse, blunt or spinose branchlets, occasionally arranged in rows. In cross-section, centre of medulla at or near apex of branches consisting of large, rounded cells interspersed with small, thick-walled cells forming the axial core; inner cortex and axial region in apical segments producing secondary cell structures ('thylles') extending basally as hyphae in axial region of thallus; in some species no separate central axial region visible. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangia seriate, embedded in cortex. Gametophytes dioecious; cystocarps forming hemispheres directly on main axes; spermatangia in indefinite superficial sori.



Kappaphycus cottonii (Weber Bosse) Doty ex H.D. Nguyen & Q.N. Huynh – 1, habit; 2, longitudinal section of a thallus; 3, transverse section of a thallus; 4, detail of transverse section of the cortical region of a thallus; 5, detail of transverse section of the cortical region of a thallus with tetrasporangia.

- *K. cottonii.* Thalli forming large, crust-like clumps of fused, prostrate branches, strongly attached to solid substrates by haptera arising from under surface of thallus or consisting of somewhat compressed irregular branches, attached to one another by undefined haptera forming slightly amorphous fronds; surface rough, warty, with numerous short, blunt, stubby spines or tubercles. Cross-section of thallus with medulla composed of large rounded cells without central core of rhizoidal or hyphal cells.
- *K. inermis.* Thalli erect, composed of cylindrical branches, attached by thick, fleshy, discoid holdfast forming several fronds; branching usually irregular, open, indeterminate, flexed upward, inflated. In cross-section, centre of medulla with distinct axial core, persisting to at least 10 cm in

branches less than 5 mm in diameter, consisting of large, rounded cells interspersed with small, thick-walled cells, often surrounded by rather regular border of nearly uniform medium-sized cells.

Other botanical information In the early 1970s these algae were known as *Eucheuma cottonii* (usually shortened to 'cottonii' by farmers and traders) because it was a member of the Eucheumoid algae producing 'cottonii-like' carrageenan. The genuine *Kappaphycus cottonii* was always relatively rare in commercial shipments of wild seaweed and has never been farmed. In the early stages of 'cottonii' farming, most of the material produced was what would be identified as *K. striatus*, which was used until better growing cultivars of *Kappaphycus* were generally adopted for cultivation.

The status of *K. alvarezii* as a species separate from *K. striatus* (and *K. inermis*) has been challenged on the basis of tetraspore progeny studies. It is suggested that the presence of both dichotomous and decumbent plants in the tetraspore progeny of *K. alvarezii* may represent the segregation of forms similar to ancestral parent plants, putatively of the very variable species *K. striatus*. It is not certain whether *K. inermis* and *K. striatus* are really species that differ from one another. The genera *Betaphycus* Doty ex P.C. Silva and *Kappaphycus* have recently been separated from the broad and variable complex genus *Eucheuma* J. Agardh. The species of these new genera were previously separated within sections in *Eucheuma*. In the circumscription of *Eucheuma* section *Cottoniformis* Doty & J.N. Norris (1985), *Eucheuma cottonii* is excluded. It is, however, clearly included in the circumscription of *Kappaphycus* Doty (1988).

Ecology *Kappaphycus* spp. are tropical seaweeds. They occur usually on rocks and corals in clear-water areas. *K. cottonii* grows especially on the reef edge, where it is exposed to very strong wave action. Most species are stenohaline.

Propagation and planting Only *K. alvarezii* and small amounts of *K. striatus* are used in phycoculture.

Diseases and pests The most persistent disease problem in *Kappaphycus* is 'ice-ice'. It occurs almost exclusively in phycoculture under unfavourable ecological conditions.

Harvesting In natural *Kappaphycus* populations harvesting is by hand-collecting or by collecting specimens which have drifted onto beaches.

Handling after harvest *Kappaphycus* is usually sun-dried after being collected.

Prospects If disease problems in *K. alvarezii* persist and/or become even more severe, other *Kappaphycus* spp. might become more interesting for phycoculture.

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W.F. Prud'homme van Reine

Kappaphycus alvarezii (Doty) Doty ex P.C. Silva

P.C. Silva, Basson & Moe, Univ. Calif. Publ. Bot. 79: 33 (1996).

SOLIERIACEAE

$2n = 20$

Synonyms *Eucheuma alvarezii* Doty (1985).

Vernacular names Indonesia: 'cottonii' (Java, Bali, Sulawesi, the common name for all *Kappaphycus* spp.), agar-agar, agar besar (both common names for *Kappaphycus* and *Eucheuma* spp.). Philippines: tamsao (northern Luzon, both for *Kappaphycus* and *Eucheuma* spp.), guso (Visayan, also for species of both genera), tambalang, kanot kanot (Ilocos Norte, for species of both genera).

Origin and geographic distribution *K. alvarezii* originates from the area of the Sulu Sea, Sulu Archipelago (the Philippines) and adjacent areas (easternmost Sabah, Malaysia). It has been distributed widely by humans in recent years, for example to Indonesia, Vietnam, southern China, Hawaii, Fiji, Zanzibar and southern Africa and since 1980 has largely replaced the earlier used *K. striatus* (F. Schmitz) Doty ex P.C. Silva ('elkhorn variety').

Uses *K. alvarezii* is a source of kappa carrageenan which is used as an additive in food, pharmaceutical and cosmetic products. In Indonesia it is sold in some supermarkets as sweets ('manisan agar') and it is used to prepare cakes ('kue').

Production and international trade Farmed *K. alvarezii* is commonly used in South-East Asia as raw material for domestic industries and for export. It is presently cultured in Indonesia, Malaysia, the Philippines, Vietnam and several other tropical countries. It forms the bulk (80%) of seaweed exports from the Philippines and is commercially farmed in Sulu, Tawi-Tawi, northern Bohol, Palawan and other areas in that country. The Philippines produce about 50% of all carrageenophytes in the world, and Indonesia another 25%. In Indonesia, the main production areas are in Sulawesi and Bali. In Vietnam, where *K. alvarezii* does not naturally occur, cultivation has been carried out since 1993 in offshore areas, lagoons, inlets and ponds in the central and southern parts of the country. The productivity in lagoons and inlets there reaches over 10 t (dry weight)/ha/year. It is also cultivated in Malaysia (Sempora, eastern coast of Malaysia), where the total production now is about 1800 t/year (dry weight).

Production and trade data may apply to *Kappaphycus* spp. as a whole (although in most cases *K. alvarezii* is presently by far the most important), to all Eucheumoid algae (as '*Eucheuma*'), to the carrageenan- producing seaweeds as a whole or even to all red seaweeds together. For the Philippines in 1986 production (wet weight) by phycoculture of '*Eucheuma alvarezii*' was 4627 t and in 1994 12 110 t. However, phycoculture production of *Eucheuma* '*cottonii*', which probably includes *K. alvarezii* as well was 145 632 t (1986) and 347 300 t (1994). For 1990 the total production of *K. alvarezii* (now in dry weight) by phycoculture is recorded as 46 390 for the Philippines and 11 812 t for Indonesia.

Another set of production data for *K. alvarezii* (dry weight) shows that in 1987 the Philippines produced 40 000 t and Indonesia 5000 t.

For 1991 these data are given as 60 000 t and 15 000 t, respectively. In 1992 the total production of dried *K. alvarezii* in Indonesia was estimated to be 15 200 t.

In the Philippines about 10 000 ha of reef area are now used for *Eucheuma denticulatum* (Burm.f.) Collins & Herv. and *K. alvarezii* cultures, with more than 75% devoted to *K. alvarezii*. More than 80 000 farmers are involved and about 300 000 dependents rely on seaweed farming. Amongst these are about 10 000 personnel employed by 14 companies engaged in processing, manufacture and export of *Kappaphycus* and *Eucheuma* and their carrageenans. In Indonesia, where production is only half that of the Philippines, 7 companies are engaged in processing and manufacture, and the number of farmers, dependents and employees can be expected to be half that of the Philippines. The estimated potentially exploitable area for '*Eucheuma* culture' (probably including *Kappaphycus* culture as well) in Indonesia is 9000–10 000 ha, with a production capacity of 45 000 t per year (dry weight). This area, however, has not yet been exploited optimally: total seaweed production in 1994 was less than 27 000 t, including harvests of *Gracilaria* and *Gelidium* spp. and others. A total of 21 180 t was produced by *Kappaphycus* and *Eucheuma*.

The FOB (Free On Board) selling prices of *K. alvarezii* in Indonesia were rather unstable in the period 1982–1992, being US$ 0.36/kg in 1987 with a maximum of US$ 0.74/kg in 1990, and falling back to US$ 0.30–0.40/kg in 1991. This period saw increased production in Sulawesi (Indonesia), resulting in exporters carrying large stocks and thus dropping prices. In 1993 the farm gate price for properly dried *K. alvarezii* in the Philippines was about US$ 0.27/kg. In Malaysia it was US$ 0.42–0.50/kg in 1995 and US$ 0.44 in 1998.

In 1987 CF (Costs and Freight) prices for *K. alvarezii* (dry weight) in Europe were US$ 380 /t and in the United States US$ 440 t. The *Kappaphycus* crop is partly used directly for carrageenan production, partly exported mainly to the United States, Denmark, France, Australia, Japan, Hongkong, Singapore and China. Much of the semi-refined carrageenan is exported to companies in New Zealand, United Kingdom, Germany, France, Australia and Japan.

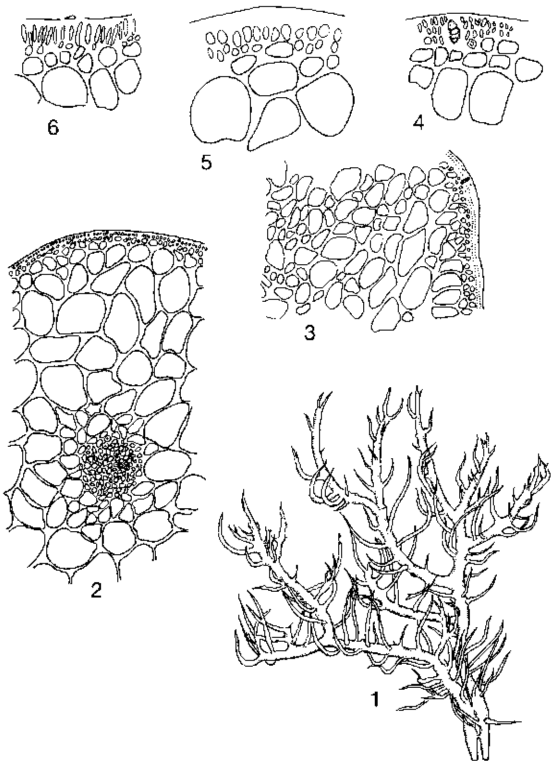
Properties *K. alvarezii* produces a nearly ideal kappa carrageenan, which is a commercially important hydrophyllic colloid with many industrial applications. The extract is a yellowish or tan to white, coarse to fine powder that is practically odourless and has a mucilaginous consistency. Often over 60% of the wall substance of this alga is kappa carrageenan. Carrageenan properties within *K. alvarezii* differ considerably in gel strength, gelling temperature, melting temperature, viscosity and sulphate content. However, both cystocarpic and tetrasporophytic plants consistently produce the same kappa carrageenan and all *Kappaphycus* spp. contain similar kappa carrageenans.

Aqueous extracts of *K. alvarezii* show high cytokinin-like activity as well as gibberellin-like activity. The mineral content (dry weight) in % is N 1.2, P 0.03, K 9.3, Ca 0.23, Mg 0.62, Na 4.0 and in ppm Cu 2.5, Fe 52, Mn 4 and Zn 16.5.

Description Thalli rigid, bush-like, axes smooth, cylindrical. Branching irregular, usually not pinnate; branches reaching surface of thalli rarely inflated above their midpoints, terete in upper parts; secondary branches usually absent. Main axis of a thallus arising from a discoid holdfast; new main axes arising from the same base very near to the primary axis or from the main axis itself below the basal primary branch. Primary cells of medulla mostly isodiametric in transection; central core of axial filaments present, especially in young tissues. Reproductive structures on or in the lateral surfaces of otherwise normal axial segments. Seriately divided tetrasporangia embedded in cortex. Gametophytes dioecious. Cystocarps swollen from the cortex; spermatangia in indefinite superficial sori.

Growth and development All stages of the triphasic life cycle have been found, which does not mean however that they all occur regularly. In culture tetrasporic plants are often lacking, while in other strains cystocarpic plants are either not found at all or only very rarely occur. The largest plant of *K. alvarezii* ever measured was more than 2 m long and weighed about 56 kg. Growth rates in the Philippines in cultures of *K. alvarezii* (% increase in fresh weight per day) vary between 1.5–5.5 and, as a yearly average 2.3% is given. A daily growth rate of about 3.5% is considered optimal, doubling the biomass in one lunar cycle of 28 days. Laboratory-grown branches transplanted to rafts in the field showed daily growth rates which are as high or even higher. In laboratory culture 3–5 cm long branches can be grown in inexpensive laboratory media prepared from autoclaved seawater enriched with either a commercial Philippine liquid fertilizer made from seaweed extract ('Algafer'), coconut water or soil extract.

In Vietnam, growth rates of 6–9%/d occur in some lagoons and inlet areas, mainly during the cool season (October–May) and even higher (10–12%/d) in areas with high nutrient concentrations. Growth rates are slightly lower, 4–6%/d, during the hot dry season (June–September) with water temperatures of 26.7–34°C. Daily growth rates are lower in raft cultures, probably mainly due to grazing by fish.



Kappaphycus alvarezii (Doty) Doty ex P.C. Silva – 1, habit; 2, transverse section of a thallus, within 1 cm from the apex; 3 & 4, transverse sections of a tetrasporic thallus; 5, detail of transverse section of the cortical region of a thallus, within 0.5 cm from the apex; 6, detail of a transverse section of spermatangia.

Other botanical information Several varieties of *K. alvarezii* have been isolated and grown in culture. The principal culture varieties are var. *alvarezii*, var. *ayakii-assii* (Doty) L.M. Liao and var. *tambalangii* (Doty) L.M. Liao. However, the formal taxonomic recognition of these 'horticultural' strains is questioned, and for the two differing varieties the designations 'Ajak-assi' and 'Tambalang' are usually used.

Apart from these varieties colour forms or morphotypes occur in the cultivated stocks of *K. alvarezii*, e.g. brown, green and red morphotypes.

However, these colour forms do not show any distinct sun or shade properties, although their growth rates and carrageenan properties differ considerably and consistently.

Ecology The natural habitat for *K. alvarezii* appears to be the reef flat area in easternmost Sabah (Malaysia) and the northern Sulu Archipelago (the Philippines). It grows on limestone rock materials in the less sandy reef flat areas. However, it grows distinctively and rapidly in a wide range of environments. Preferred sites for cultivation are reefs far from freshwater sources since this alga is stenohaline and salinities below 30‰ may adversely affect its growth. Optimal sites are reef areas with coarse, sandy to coral bottoms and characterized by moderate water movement. Winter temperatures below 18°C are unsuitable for year round cultivation of *K. alvarezii*. It can survive at low temperatures, but shows loss of photosynthetic efficiency. The alga may show negative phototropism in intense light and become prostrate and dorsiventrally flattened. This also occurs when thalli are often exposed to air, which may result in the formation of irregular 'heads'.

Propagation and planting In culture, *K. alvarezii* is propagated by vegetative cuttings. The success of farming depends primarily on the ecological characteristics of the site, and thus on the selection of the site. After a suitable site has been identified, test planting of the desired strains is recommended, followed by careful monitoring of the test plants. In general, areas where test plants double their size within 15 days can be considered suitable for cropping. Three cultivation methods are in use: the fixed off-bottom monoline method, the raft method and the hanging long-line method.

Phycoculture The most common technology for the cultivation of *K. alvarezii* in the Philippines and Indonesia is the fixed off-bottom monoline method which is cheap and easy to maintain. Wooden stakes are driven into the substrate, spaced at 1 m intervals in rows with 10 m between the rows. One end of the nylon monofilament line (180 lbs test, about 10.5 m long) is tied to a stake and tightly stretched. The other end is tied to the opposite stake in the opposite row. In Indonesia, 4 mm diameter polypropylene rope is often used for farming. Selected cuttings (50–100 g) are tied to the monoline at 25–30 cm interval using soft plastic tying materials. In culture, *K. alvarezii* is almost always observed to be sterile and without a primary basal discoid attachment. The plants are allowed to grow to 1 kg or more before they are harvested.

The raft method, in which the monolines are attached to a raft system usually made of bamboo frames, is used in deeper water and offshore locations. In some areas, plastic containers or bags filled with air or styrofoam floats are used. The raft is anchored to the bottom by means of nylon lines and is kept at a depth of 0.2–0.4 m below the surface. The application of the raft method is limited, due to the costs involved.

With the hanging long-line method the alga is brought nearer to the water surface at constant depths and kept buoyant with styrofoam float. This method can also be used in somewhat deeper water. It requires, however, higher investments than the fixed-bottom method. The operational costs are also higher in the Philippines due to the conditions, and the average production is lower. A decreased growth rate of *K. alvarezii* grown near the surface of constant-depth, was observed after the first four weeks of fast growth. The fixed off-bottom technique provides a more balanced light intensity regime and is thus more efficient for biomass production. The hanging long-line technique, however, is more effective for 'seedling' source purposes, suggesting that it is more productive to culture the seaweed for the first 30–45 days by the hanging long-line and then shift to the fixed off-bottom until the seaweed can be harvested. The average annual production in the Philippines (dry weight) is 5–6 t/ha, but may be as high as 27.9 t/ha.

In Semporna (Sabah, Malaysia) in 1997 each farm was operated by a fishing family, each having on average 20–80 lines 47 m long. Stakes were used at intervals to anchor the lines, while plastic bottles acted as floats. The lines were adjusted to 0.15 m below water level, while average salinity was 34‰ and pH 8.3. Cuttings of healthy *Kappaphycus* weighing about 0.5 kg were tied in bunches at 0.3 m intervals along the lines. The bunches were allowed to grow until fresh weights of about 7 kg had been achieved in about 45 days. In these cultures, epiphytes were removed manually from the bundles every three days.

In Vietnam, experimental intensive cultivation of *K. alvarezii* in fishponds is being carried out, often in rotation with shrimp cultivation (April–September for shrimp, October-March for algae). Growth rates of 5–6%/d can be obtained especially in the cool season (air temperatures 25–28°C, irradiance up to 50 000 lux).

Diseases and pests One of the major problems in *K. alvarezii* culture is the occurrence of 'ice-ice' disease, which can wipe out entire crops. The early signs are slow growth, thalli become pale losing their gloss, followed by roughening of the surface of the branches. White spots appear on the branches, and tissues soften and dissolve resulting in breakage. Entire thalli may become affected. The occurrence of 'ice-ice' might be due to adverse ecological conditions as well, although whitening can also be caused by bacterial pathogens. Low light intensities, low nutrient availability, extreme water temperatures and low water movement are conducive to the development of 'ice-ice'. A high incidence of epiphytes may promote 'ice-ice' as well, so removing heavy fouling growth of epiphytes such as those of the green alga *Enteromorpha* Link will diminish an outbreak of the disease.

Another constraint is 'pitting'. This refers to the formation of a cavity penetrating the cortex in one place and expanding into the medulla regions beneath, often resulting in thallus breakage and is probably caused by mechanical wounding of the cortex. 'Tip darkening' possibly related to too cold water, and 'tip discolouration' as a result of too warm water may affect *K. alvarezii* as well. In most cases, the affected parts of the alga decay, leading to fragmentation and losses.

Grazing by fish, especially rabbitfish (Siganids), by invertebrates and by green turtles are also major causes of loss in biomass. The use of the floating methods (raft and long lines) has virtually eliminated the effect of benthic grazers such as sea urchins, holothurians and starfish.

Harvesting The harvest methods used for *K. alvarezii* are: pruning branches or collecting whole plants. Plants are harvested 30–60 days after planting. In Vietnam harvesting is done every 2–3 months in the dry season and every 1.5–2 months in the cool season. In Sabah (Malaysia) the average cultivation period is 45 days and there cultivation is carried out for 8 months a year.

Yield The carrageenan content of *K. alvarezii* is about 25–70% of the salt-free dry weight. The wet (85% water) to dry (35% water) ratio is about 15%. Carrageenan content and quality of cultured material and commercial seaweed is greatly influenced by the post-harvest treatment.

Handling after harvest Fresh material of *K. alvarezii* is usually sun- dried for several days to about 35% moisture and then stored and packed for export. Drying, sorting, packing and storing should be done carefully to obtain a high quality. Mats must be used to prevent contamination. Contact with freshwater, particularly rain, should be avoided, as this extends the drying time and reduces the salt content, both of which may cause the seaweed or carrageenan to degrade. Washing in freshwater does not add value and in most cases reduces the carrageenan quality.

In Sabah (Malaysia) the moisture content of sun-dried seaweed is 32–35%, but it is common practice for farmers to sell seaweed with a higher moisture content.

For both *K. alvarezii* and *Eucheuma denticulatum* inadequate drying and post-harvest contamination with sand result in poor quality and lower prices. Above 35% moisture the algal material is unstable and undergoes degradation during storage. Above 40% moisture, the carrageenan in the seaweeds may be degraded during transportation to the factory and storage. Therefore, the alga should never be stored wet. At 25–35% moisture content, the composition of the alga is relatively stable for periods longer than 12 months, and the thalli are ideally flexible for efficient baling. At lower moisture content the thalli become too brittle and can cause processing problems during carrageenan extraction. Dried material of *K. alvarezii* and *Eucheuma denticulatum* must never be mixed, otherwise it is not possible to obtain suitable carrageenan quality. The stored seaweed must be baled before transport to make handling easier and therefore reduce shipping costs. Hydraulic systems for baling are preferred to screw-type balers. Some shrinkage may occur during shipment, probably mainly due to moisture losses. Originally, all *'Eucheuma'* produced (including cultured *Kappaphycus*) was exported as raw material (dried seaweed) to processors in Europe and the United States. From 1978 on, however, carrageenan has been produced in the Philippines in different qualities and amounts, and similar activities started in Indonesia in 1988.

Genetic resources Material of the 'Tambalang' variety of *K. alvarezii* was brought to Hawaii in 1971 from Mr Alvarez's farm in Calatagan (Batangas Province, the Philippines). The original stock came from Sitangkai (Tawi Tawi Province, the Philippines). It has prospered locally in Hawaii but has hardly spread from the sites where it was planted. The Hawaiian populations have served as a source for many of the other Pacific distributions including laboratory use in the United States (California) and Japan. It is known to have been transplanted by human endeavours and outplanted in many locations including in Indonesia. Branch, micropropagule and tissue culture, as well as clonal propagation from callus of *K. alvarezii* have been performed successfully.

Breeding A significantly better-producing variety ('Tambalang') of *K. alvarezii* was found through a selection programme involving 23 strains and species of the *'Eucheuma cottonii'* group. Another method of potential strain selection, based on tetraspore progeny within *K. alvarezii*, has recently been suggested.

Prospects The carrageenan industry is closely linked to the food processing industry. Future growth should be steady, if unspectacular. Progress may lie in achieving cost reduction in processing, and in developing more versatile and better quality-controlled products.
It is expected that the production of raw material of *K. alvarezii* in Vietnam might increase dramatically over the next few years. Moreover, for Indonesia it is calculated that the potential area for *'Eucheuma* culture' (probably including *Kappaphycus* culture as well) may be 9000–10 000 ha, with an annual production capacity of 45 000 t (dry weight).
The culture of Eucheumoid algae for carrageenan production is only economically viable due to low labour costs. In the main production areas farm productivity is dropping because of declining daily growth rates and susceptibility to stress and 'ice-ice' disease, which might be due to prolonged vegetative propagation. There is a need for selection and breeding of new strains. Cultivation of *K. alvarezii* in cages, together with carnivorous finfish, is a promising practice but still little used. Intensive *'Eucheuma'* farming may have an impact on the global climate due to the daily production of volatile hydrocarbons (VHC).

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W.S. Atmadja

Kappaphycus striatus (F. Schmitz) Doty ex P.C. Silva

P.C. Silva, Basson & Moe, Univ. Calif. Publ. Bot. 79: 334 (1996) (*'striatum'*).

SOLIERIACEAE

$2n$ = unknown, possibly 20

Synonyms *Eucheuma striatum* F. Schmitz (1895) ('striata').

Vernacular names Indonesia: agar-agar (common name for *Eucheuma* and *Kappaphycus* spp.), 'cottonii' (common name for all *Kappaphycus* spp.). Philippines: tamsao (northern Luzon, for *Eucheuma* and *Kappaphycus* spp.), guso (Visayan, also for species of both genera). Usually the commercial name 'cottonii-elkhorn' is considered to refer to *K. striatus*.

Origin and geographic distribution *K. striatus* originates from the tropical waters of the Indo-Pacific, and is found in Kenya, Tanzania, Madagascar and India in the Indian Ocean to Taiwan, the Ryukyu Islands and the Federal States of Micronesia (Belau and Pohnpei). In South-East Asia it occurs in Singapore, Indonesia, Malaysia (eastern Sabah), the Philippines and Papua New Guinea.

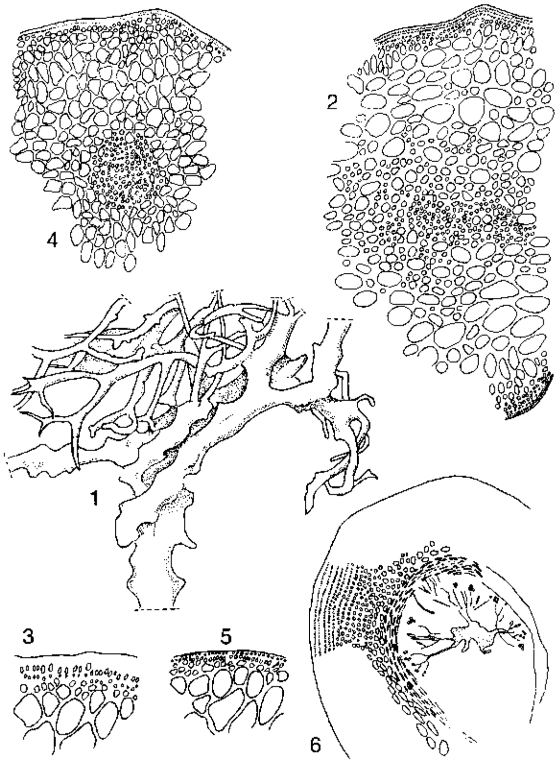
Uses Fresh *K. striatus* may be consumed as a vegetable and a sweet dessert. The alga produces kappa carrageenan which can be used as a gelling agent, thickener and stabilizer. Applications are mostly in the food, cosmetic and pharmaceutical industries. Most probably a gel prepared from this alga was used by Hesse (1939) to prepare a stable solid medium for microbiology. He applied the Malay name 'agar agar' for this gel, but the medium probably consisted of kappa carrageenan, which forms a rigid gel that will retain its form without support. The term 'agar', however, in modern phycocolloid nomenclature is applied to a different substance from different algae. Since 1980 the most commonly cultivated 'Elkhorn variety' of *K. striatus* has been replaced by the much faster growing *K. alvarezii* (Doty) Doty ex P.C. Silva.

Production and international trade In eastern Indonesia, harvesting of natural stock of *K. striatus* can produce 35–300 t dry material per year. An intensive seaweed culture may produce 4–6 t/ha per month (dry weight). In international trade, *K. striatus* contributes a much smaller amount to the world market of kappa carrageenan-producing algae than *K. alvarezii*.

Properties The kappa carrageenan of *K. striatus* possesses low quality characteristics, i.e. viscosity 83–309 cps, gelling point 20.5–30.2°C, gel strength 65–177 g/cm^2, and sulphate content 9.2–26.5%. The infra-red spectrum of this kappa carrageenan peaks at wave numbers 846 and 929/cm indicating 1–3-linked galactose-4-sulphate and 3,6-anhydrogalactose, respectively.

Description Plant erect, stiff, up to 40 cm tall, reddish, greenish or yellowish; basal thallus up to 15 mm thick, surface smooth, sometimes with small spine-like papillae. Branching irregular or irregularly dichotomous, dense at distal part with acute apices. Cross-section of branch showing 2–3 layers of cortical cells; medulla roundish, bigger than cortical cells, irregularly positioned between big and small cells; internal rhizoidal filaments usually present in a core; cystocarps bulb-like, protruding on the surface, irregularly arranged, dense.

Growth and development In eastern Indonesia, the natural stock of *K. striatus* appears at the end of the dry season (June–July), and harvesting starts from early October to early December. A daily growth rate of 4–6% is obtained when *K. striatus* is cultivated with floating bamboo rafts and plants can be harvested about 45 days after planting. In other circumstances growth rates of 1.5–5.5%/d are recorded.



Kappaphycus striatus (F. Schmitz) Doty ex P.C. Silva – 1, habit; 2, transverse section of a thick branch; 3, detail of the cortical region of 2; 4, transverse section of a thin branch; 5, detail of the cortical region of 4; 6, longitudinal section of a cystocarp.

Other botanical information The status of *K. alvarezii* as a species separate from *K. striatus* (and *K. inermis* (F. Schmitz) Doty ex H.D. Nguyen & Q.N. Huynh) has been challenged on the basis of tetraspore progeny studies. It is suggested that the presence of both dichotomous and decumbent plants in the tetraspore progeny of *K. alvarezii* may represent the segregation of forms similar to ancestral parent plants, putatively of the very variable species *K. striatus*. Nor is it certain whether *K. inermis* and *K. striatus* really are species that differ from one another.

Ecology *K. striatus* inhabits the lower eulittoral to sublittoral zones with sandy hard bottom substrates. The preferred conditions are clear water and rather fast currents. It is very often found in the lower zone of exposed seagrass meadows. Preferred salinity is above 32‰ and day temperature 25–30°C. Freshwater inflow and rain water can seriously interfere with the growth of this alga.

Propagation and planting In cultivation, vegetative thallus propagation of *K. striatus* is a rapid and economic way to produce large amounts of algal biomass. For this the thalli must be healthy, not damaged by herbivory, and not in the reproductive phase. Usually 100–150 g of young thalli is tied together in each cluster or bundle.

Phycoculture Techniques applied for commercial cultivation of *K. striatum* are very similar to those of *K. alvarezii*. Recently, especially the raft method has been applied.

Diseases and pests 'Ice-ice' is a serious disease in cultivated *K. striatus*. The most common pests are herbivorous fish, which can ruin this algal culture, while invertebrates usually cause insignificant damage.

Harvesting Methods used for harvesting *K. striatus* are very similar to those applied for *K. alvarezii*.

Yield Clean, dried *K. striatus* produces 30–88% of kappa carrageenan, depending on the age of the plant. Maximum carrageenan content is achieved at 14–21 days, or a week after its exponential growth phase. However, at that age the biomass is not yet suitable for harvest.

Handling after harvest The post-harvest handling of *K. striatus* is similar to that of *K. alvarezii*.

Prospects Although the demand in regional and international markets for kappa carrageenan-bearing algae is high, it is not anticipated that *K. striatus* will regain its once important role.

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A.M. Hatta

Laurencia J.V. Lamour.

Essai Thalassioph.: 130 (1813).

RHODOMELACEAE

x = unknown; *L. papillosa*: $2n$ = 40–52, *L. okamurae*: $2n$ = 64

Major species and synonyms

- *Laurencia botryoides* (C. Agardh) Gaillon, Résumé Thalassioph.: 363 (1828), synonyms: *Fucus botryoides* Turner (1809–1811, nom. illeg.), *Chondria botryoides* C. Agardh (1817).
- *Laurencia cartilaginea* Yamada, Univ. Calif. Publ. Bot. 16 (7): 230, fig. 0, pl. 19: fig. a (1931).
- *Laurencia composita* Yamada, Univ. Calif. Publ. Bot. 16 (7): 236, figs R, S, pl. 23 (1931).
- *Laurencia flexilis* Setch., Univ. Calif. Publ. Bot. 12: 101, pl. 19 (1926).
- *Laurencia nidifica* J. Agardh, Spec. gen. ord. alg. 3 (1): 749–750 (1852) [1852–1863], synonym: *L. obtusa* (Huds.) J.V. Lamour. var. *nana* Harv. (1834).
- *Laurencia obtusa* (Huds.) J.V. Lamour., Essai Thalassioph.: 130 (1813), synonym: *Fucus obtusus* Huds. (1778).
- *Laurencia okamurae* Yamada, Univ. Calif. Publ. Bot. 16 (7): 206, figs J, K, pl. 7 (1931, as *L. okamurai*).
- *Laurencia palisada* Yamada, Univ. Calif. Publ. Bot. 16 (7): 196, figs C, D, pl. 4, fig. a (1931).
- *Laurencia papillosa* (C. Agardh) Grev., Alg. brit.: LII (1830), synonyms: *Fucus papillosus* Forssk. (1775, nom. illeg.), *Chondria papillosa* C. Agardh (1822).
- *Laurencia parvipapillata* C.K. Tseng, Pap. Michigan Acad. Sci. 28: 204–205, pl. IV (1943).
- *Laurencia patentiramea* (Mont.) Kütz., Sp. alg.: 854 (1849), synonyms: *Chondria obtusa* (Huds.) C. Agardh var. *paniculata* C. Agardh (1822), *C. obtusa* (Huds.) C. Agardh var. *patentiramea* Mont. (1836), *Laurencia paniculata* (C. Agardh) J. Agardh (1852).
- *Laurencia similis* K.W. Nam & Y. Saito, Brit. Phycol. J. 26: 375–382 (1991).
- *Laurencia snackeyi* (Weber Bosse) Masuda, in Masuda, Y. Takahashi, K. Okamoto, Matsuo & Min. Suzuki, Eur. Journal of Phycology 32: 296 (1997), synonyms: *L. paniculata* (C. Agardh) var. *snackeyi* Weber Bosse (1923), *L. obtusa* (Huds.) J.V. Lamour. var. *snackeyi* (Weber

Bosse) Yamada (1931).
- *Laurencia tronoi* Ganz.-Fort., Kalikasan 11: 404, figs 1, 2 (1983).

Vernacular names General: Laurencia. Philippines: culot, kulot (Ilocano).
- *L. flexilis*. Philippines: culto (Ilocano).
- *L. papillosa*. Philippines: dipdipig, tartariptip, layalaya.
- *L. snackeyi*. Indonesia: sangau.

Origin and geographic distribution *Laurencia* is a common component of seaweed communities in tropical and temperate waters. In general, however, detailed knowledge is needed to identify up to species. Most species listed here have been recorded from the Philippines, where these algae are frequently studied. Records from other countries in South-East Asia are more incidental than the result of detailed research. It is possible that records for *L. botryoides* (an Australian species) and of *L. obtusa* are based on mis-identifications. Especially reportedly cosmopolitan species need critical re-evaluation.

Uses Several *Laurencia* (especially *L. cartilaginea*, *L. patentiramea* and *L. snackeyi*) are popular in areas in the Philippines and Indonesia for use in salads, in vegetable soup and as a medicine. In fact all *Laurencia* can be used for human food. Medical uses include as antibiotic (antibacterial or antifungal) and (in Indonesia for *L. snackeyi*) for treatment of stomach ailments. Occasionally, large amounts of washed-up *Laurencia* thalli are used as fertilizer.

Production and international trade There are no data available on the amount harvested for food from wild populations of *Laurencia*.

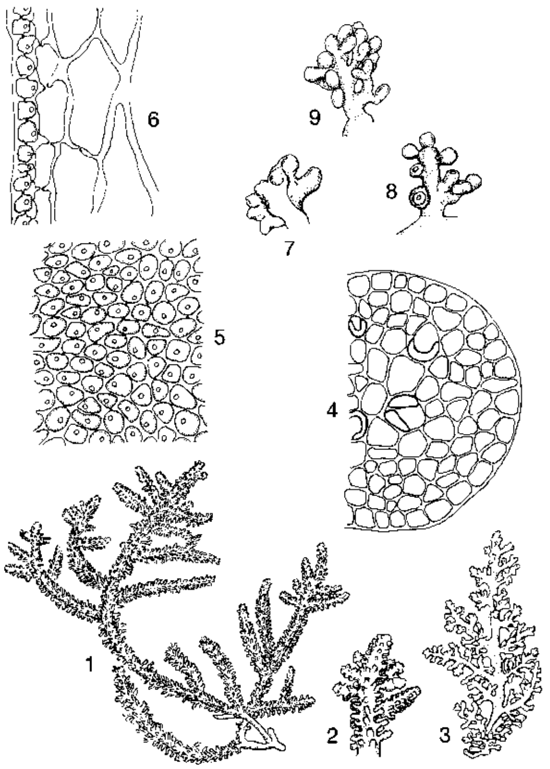
Properties Most *Laurencia* contain agar, but the quality of the phycocolloids of these algae is not yet fully known. Chemical investigations of the polysaccharide of *L. flexilis*, involving sulphate and 3,6-anhydrogalactose determinations as well as FT-IR (Fourier transform infrared spectroscopy) spectroscopic examinations, revealed an agar-type polysaccharide. Samples of *L. flexilis* from Hainan Island (China) contain 36.4% of agar (dry weight), with a gel strength of 458 g/cm^2 for the alkali-treated fraction. Detailed studies of the phycocolloid of *L. papillosa* in India suggest a relation to lambda carrageenan. However, many other researchers have suggested that the polysaccharides from cell walls of *Laurencia* should be considered as belonging to the agar group, being agarose derivates with a rather high content of alkali-stable sulphate groups and with a reduced amount of 3,6-anhydro-L-galactose residues. This has in some cases been verified by the use of agarose from the bacterium *Cytophaga*. It is obvious that different *Laurencia* produce different types of hot-water-soluble cell-wall polysaccharides.

The predominant saturated fatty acid in the lipids of *L. papillosa* is palmitic acid (16:0), while the predominant unsaturated fatty acid is linolenic acid (10.2%; 18:1).

Extracts of fresh *L. snackeyi* (as *L. obtusa*) show some antioxidant activity that might be used in the preservation of food. *Laurencia* spp., especially *L. patentiramea*, contain the phytohormones auxin, gibberellin and cytokinin, and the minerals (especially *L. papillosa*) B, Ca, Cu, Fe, I, K, Mg, Mn, N, Na, Zn, as well as chlorides and sulphates.

Many *Laurencia* contain special secondary metabolites which can be antibiotic and prevent grazing by fish and sea urchins. Despite the problems of classification and identification, the biochemical components of *Laurencia* make it biochemically one of the most studied of all algal genera. Sesquiterpenoids, diterpenoids and acetylenic non-terpenoids form the three major classes of *Laurencia*-derived compounds, often containing the halogens bromide or chlorine.

Description Thalli erect or decumbent, attached by disk or shovel-shaped holdfasts (haptera) or crustose base. Fronds fleshy, usually crisp, terete or compressed. Branches radially or pinnately divided; apices of ultimate branchlets depressed, with a tuft of usually inconspicuous, colourless hairs (trichoblasts). Central axial cells and pericentrals soon obscured by formation of other cells, thus cross-sections appearing pseudoparenchymatous; outer cortical cells in cross-section radially elongate (= palisade pattern) or nearly isodiametric and rounded to angular, with or without bright cell inclusions (cherry bodies), with or without lateral secondary pit connections; in some species surface of younger branches papillose, due to projecting outer tangential walls of cortex cells; inner cortical cells or medullary cells with or without lenticular thickenings of cell walls. Life cycle triphasic, diplo-haplontic and isomorphic. Tetrasporangia tetrahedral. Gametophytes dioecious. Spermatangia borne in stichidia on ultimate branchlets. Cystocarps conspicuous, usually nearly equal in diameter to bearing branchlet.
- *L. botryoides*. Thalli dark red to red-brown, up to 17 cm tall, firm, drying cartilaginous, pyramidal in outline. Branches usually numerous; laterals alternate, distichous, 1–1.5 mm thick, arising



Laurencia. L. papillosa (C. Agardh) Grev. – 1, habit; 2, detail of ultimate part. L. cartilaginea Yamada – 3, detail of ultimate part. L. okamurae Yamada – 4, part of a cross-section through a branchlet. L. obtusa (Huds.) J.V. Lamour. – 5, surface view of cortex cells with one cherry body in each cell and secondary pit connections; 6, longitudinal section of the same area. L. tronoi Ganz.-Fort. – 7, ultimate branchlet with cystocarps; 8, ultimate branchlet with spermatangial branchlets; 9, ultimate branchlet with tetrasporangial branchlets.

from flexuous axis, 1.5–2(–3) mm thick; axes and branches terete or slightly compressed, bearing small reproductive ramuli; ramuli first distichous, later developing on all sides forming botryoidal clusters. Outer cortical cells about 1.5 times as long as broad in cross-section, with lateral secondary pit connections, without bright cell inclusions (cherry bodies) and not projecting. Medullary cells without lenticular thickenings. Tetrasporangia ovoid, 80–100 μm in diameter, on compound branchlets comprising botryoidal clusters of very short, wart-like single ramuli, arranged in right-angled manner; spermatangial stichidia very short, in botryoidal clusters; cystocarps crowded on ramuli, sessile, globular, 0.8–1 mm in diameter, with prominent ostiole.

– *L. cartilaginea*. Thalli pink to brown, erect or caespitose, up to 9 cm tall. Main axis compressed, subcompressed or angular, cartilaginous, up to 1 mm in diameter, older portions always covered by calcareous material. Branching distichous with up to 3 orders of branching, ultimate branches terete, up to 1 mm in diameter with wart-like branchlets. Cortical cells not arranged in palisade pattern, not projecting, without cherry bodies, not connected to each other by secondary pit connections. Medullary cells with relatively thick cell walls and no lenticular thickenings. Tetrasporangiate branchlets abruptly inflated from usually long and slender bases, 0.7 mm in diameter; tetrasporangia in radial (= right-angled) arrangement; male stichidia simple, inflated, up to 1.2 mm at its widest diameter; spermatia in apex in shallow pits. No female specimens observed.

– *L. composita*. Thalli dark purple, up to 10 cm tall, soft in texture. Branches irregularly spirally arranged, long, issuing on every side of percurrent main axis, terete, 0.8–2 mm thick; branchlets simple, up to 1 cm long, alternate or subopposite, paniculate. Outer cortical cells small, connected by longitudinal secondary pit connections, with one cherry body per cell, not palisade-like, not projecting. Medullary cells with rare lenticular thickenings. Tetrasporangia in cylindrical-clavate, paniculated, or cymosely fasciculated ultimate branchlets, 120–150 μm in diameter; cystocarps ovoid, 700–900 μm × 550–740 μm, with single, wide apical ostiole; spermatangia in apical pits of ultimate branchlets.

– *L. flexilis*. Thalli purple to bleached, erect, up to 7(–13) cm tall. Main axis terete, wiry, rigid, up to 1.8 cm in diameter. Branching variable but generally radial, with up to 3 orders of branches; ultimate branches terete, simple, up to 8 mm in diameter. Cortical cells in palisade arrangement, not projecting, without cherry bodies, probably connected to each other by secondary pit connections. Medullary cells with relatively thick cell walls and no lenticular thickenings. Tetrasporangiate branches simple, up to 8 mm in diameter; tetrasporangia in a radial arrangement; male stichidia simple, rarely compound with truncate tips, up to 0.8–1 mm in its most inflated diameter; spermatia in apex in shallow pits; cystocarps globose, almost terminal up to 10 mm in diameter.

– *L. nidifica*. Thalli erect, straw-pinkish, up to 10 cm tall, with several erect axes. Axes terete, alternate-opposite or paniculately branched, texture cartilaginous but not very rigid, 1–1.5 mm thick, arising from flexuous axis, 0.5–1 mm thick. Outer cortical cells subquadrate in cross-section, with lateral secondary pit connections and bright cell inclusions (cherry bodies), not radially elongated and not projecting. Medullary cells with lenticular thickenings. Tetrasporangial arrangement parallel.

– *L. obtusa*. Thalli erect, up to 10 cm tall, deep purple, reddish, or greenish with pinkish tips, soft and fleshy in texture. Stipe short, terete, with many percurrent terete axes clothed with irregularly alternate to subverticillate branches; ultimate branchlets simple, paniculate or not, distinctly clavate, constricted at base, trichoblasts present. Outer cortical cells cuboidal to rounded in cross-section, with secondary pit connections and bright cell inclusions (cherry bodies) and not projecting. Medullary cells large, polygonal, without lenticular thickenings. Tetrasporangia arranged in parallel pattern.

– *L. okamurae*. Thalli large, robust, purplish-green to dark purple, up to 20 cm tall, fleshy to cartilaginous, not very rigid, with percurrent axes. Axes and branches terete, paniculately branched; branching alternate, opposite or verticillate. Outer cortical cells not radially elongated, with secondary longitudinal pit connections and with cherry bodies, not projecting. Medullary cells with lenticular thickenings. Tetrasporangial arrangement of the parallel type, in terminal cylindrical branchlets; spermatangia on characteristically broadened ultimate branchlets, 6.7–9.7 μm × 4.2–5.6 μm; cystocarps on lateral surface of terminal branchlets, up to 820 μm in diameter.

– *L. palisada*. Thalli 5–15 cm tall, dark red, rigidly cartilaginous, heavily to moderately clustered. Primary axes 1–3 mm thick, terete, naked below, from middle upwards bearing short, clavate-truncate branchlets. Outer cortical cells elongate in cross-section (= palisade arrangement), radial, not projecting, without secondary pit connections or cherry bodies. Medullary cells without definite arrangement, roundish, up to 23 μm. Tetrasporangia in right-angled pattern on tetrasporangial branchlets, 120–140 μm × 100–120 μm; spermatangia in cup-shaped pits on ultimate and penultimate branchlets, ellipsoidal, 9–12 μm × 6–7 μm; cystocarps laterally on ultimate branchlets, solitary or in small groups, flask-shaped, 520–800 μm × 580–800 μm, with ostiole on 100–220 μm long neck.

– *L. papillosa*. Thalli dark brown or purple, erect or partly prostrate. Main axis terete, cartilaginous, up to 1 mm in diameter; branching radial with up to 3 orders of branching; ultimate branches simple to compound, densely disposed, wart-like, generally 40–50 per 1 cm from apex, up to 1.1 mm in diameter, up to 2.8 mm long. Cortical cells in palisade arrangement, not projecting, without cherry bodies, without secondary pit connections. Medullary cells with relatively thick cell walls, with only occasional lenticular thickenings. Tetrasporangiate branches simple to compound, up to 1 mm in diameter; tetrasporangia in radial arrangement (= right-angled type); spermatangia formed in cup-shaped pits at apices of ultimate, penultimate branchlets; cystocarps globose with mamillate ostiole, up to 1 mm in diameter.

–*L. parvipapillata*. Thalli spreading, dark red to dull purple, semi-prostrate, up to 4.5 cm tall, cartilaginous. Main axes up to 800 μm thick, 2 mm wide, with subopposite short branchlets along both sides of main branches; branches usually distichous, compressed, especially near basal portion, connected to other branches by tenacula. Outer cortical cells in cross-section 20 μm in diameter, radially elongated (= palisade pattern), protruding, with sporadic secondary pit connections and bright cell inclusions (cherry bodies). Medullary cells up to 100 μm in diameter, without lenticular thickenings. Tetrasporangia arranged in right-angled pattern; tetraspores (in culture) 80–100 μm in diameter.

– *L. patentiramea*. Thalli green-red to brown-red, firm, rigid, decumbent or matted, sometimes forming cushions, attached to one another by hapteres. Main axis terete, fleshy, up to 2–3 mm in diameter; branching frequent, radial, with up to 4 orders of branching; ultimate branches terete, up to 1.8 mm in diameter, simple to compound or wart-like, closely arranged on branches. Outer cortical cells in palisade arrangement, not projecting, without cherry bodies, not connected to each other by secondary pit connections. Medullary cells with relatively thin cell walls and no lenticular thickenings. Tetrasporangiate branchlets simple to compound, with tetrasporangia in radial arrangement (= right-angled pattern); tetrasporangia 80–100 μm in diameter; spermatangia on short, branched spermatangial branchlets; cystocarps sessile, conical, 0.75–1 mm in diameter, single or with two on a branchlet.

- *L. similis*. Thalli up to 15 cm tall, pale red, cartilaginous, with 1- -2 terete, erect axes. Branching somewhat patent, irregularly alternate, subopposite, often repeatedly verticillate or subverticillate, from percurrent axis; ultimate branchlets densely covering all but lower axes, shortly cylindrical or clavate to wart-like, 0.3–0.5 mm in diameter, with truncate, swollen apices. Outer cortical cells quadrangular in cross-section, not projecting, connected by longitudinal secondary pit connections, containing two cherry bodies in each cell. Medullary cells without lenticular thickenings. Tetrasporangial branchlets cylindrical to cylindro-clavate, simple or compound, 0.4–0.6 mm in diameter, truncate, slightly swollen at the apices; tetrasporangia 100–120 μm in diameter, arranged in right-angled manner; spermatangia in cup-shaped pits on ultimate and penultimate branchlets; cystocarps on short branches, broadly ovoid, 640–800 μm × 680–840 μm.
- *L. snackeyi*. Thalli greenish-purple to red, erect, up to 22(–50) cm tall. Main percurrent axis terete, firm, fleshy, up to 3.2 mm in diameter. Branching irregularly radial, with up to 4 orders of branching; ultimate branchlets simple to compound, up to 1 mm in diameter, very fragile when dried or preserved. Outer cortical cells usually not in palisade arrangement, although occasionally radially elongated in lower portions of branches, not projecting, with one cherry body per cell, connected by longitudinal secondary pit connections. Medullary cells with relatively thin cell walls, without lenticular thickenings. Tetrasporangial branchlets simple or compound, up to 0.6 mm in diameter; tetrasporangia in parallel arrangement, 120–160 μm in diameter; male stichidia 600–800 μm in diameter; spermatangia in apex in deep pits; cystocarps broadly ovoid, 640–880 μm × 640–960 μm, laterally on branches of every order.
- *L. tronoi*. Thalli dark brown to purple, cartilaginous, with erect, decumbent branches. Branching irregular, somewhat secund or alternate; branches terete, gradually tapering towards the tips; ultimate branchlets 1.0–1.6 mm long, partly simple, cylindrical, partly bilobed, trilobed or paniculate. Outer cortical cells cuboidal, somewhat rounded to angular in cross-section, without secondary pit connections, not projecting. Medullary cells without lenticular thickenings. Tetrasporangia oval, borne on tip of tetrasporangial branchlets, arranged at right angles to axis of ultimate branchlets.

Growth and development In culture, the compressed condition of thalli of *Laurencia* persists. Tetraspores are usually formed during the whole year and tetrasporophytes dominate over gametophytes.

Other botanical information Species of *Laurencia* are notably difficult in their taxonomy and many different classifications and taxon definitions are in use. It is suggested that material from South-East Asia identified as *L. botryoides* most probably belongs to *L. cartilaginea*. It has been proposed that *L. palisada*, together with material identified as *L. intermedia* Yamada in South-East Asia belong to *L. glandulifera* (Kütz.) Kütz. For *L. tronoi* synonymy with *L. glandulifera* has also been suggested. However, in recent references, the presence of longitudinally oriented secondary pit connections in *L. glandulifera*, and parallel arrangement of its tetrasporangia exclude possible synonymy with *L. patentiramea* and *L. tronoi*.
As a result of recent research, former subgenera within *Laurencia* have been raised to generic status. Of these new genera, *Chondrophycus* (Tokida & Y. Saito) Garbary & J.T. Harper includes a number of taxa that have been described here as *Laurencia* spp.: *Chondrophycus cartilaginea* (Yamada) Garbary & J.T. Harper, *C. palisada* (Yamada) K.W. Nam, *C. papillosa* (C. Agardh) Garbary & J.T. Harper, *C. parvipapillata* (C.K. Tseng) Garbary & J.T. Harper, *C. patentiramea* (Mont.) K.W. Nam and *C. tronoi* (Ganz.-Fort.) K.W. Nam.
Many specimens in South-East Asia have been identified as *L. papillosa* although the anatomical structure is very different. In culture, it is very distinct: discoid holdfasts and very short suppressed branchlets which are densely disposed. In the field, the plants are less distinct morphologically, but are easy to differentiate from the papillose forms of *L. patentiramea by* making cross-sections and looking for cherry bodies in the cortical cells. Dried specimens are harder to differentiate, but if well rehydrated, medullary cell walls should be thicker than in *L. patentiramea*.

Ecology *Laurencia* is found attached to many substrates, including rocks, limestone, corals, sponges, seagrasses, and algae, including other *Laurencia* spp. They can be found both in the subtidal and in the intertidal zones. *Laurencia* spp. form one of the more common components of seaweed communities on reefs. In seagrass beds, especially *L. patentiramea* can form mats.
There seem to be two ecological forms of *L. papillosa*. The more common one grows on sand in the seagrass bed or on limestone in quiet waters in

the upper and lower intertidal and subtidal zones in central and southern Philippines. It has prostrate branches with very short, densely disposed papillae-like ultimate branchlets. In older branches, these ultimate branches become compound due to the initiation of branchlets but with very little elongation. This form is hard to distinguish from *L. patentiramea* unless fresh specimens are examined for the presence of cherry bodies. The other form is common in the northern Philippines, especially in the Batanes area, growing in clumps on rocks and sponges in the high-energy wave zone. The plants were heavily encrusted with the cyanobacterium *Lyngbya* and with crustose corallines.

Propagation and planting *Laurencia* is not known in commercial phycoculture.

Diseases and pests In the Caribbean, *Laurencia* is often grazed by the opistobranch sea hares (*Aplysia* spp.), which concentrate the metabolites of the algae in their digestive glands and possibly use them as a defence against predators. These sea hares cannot survive in culture without *Laurencia*.

Handling after harvest *Laurencia* algae can be used fresh or dried.

Prospects Although *Laurencia* has been much studied by biochemists, no promising chemical compounds for future commercial exploitation have been identified.

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W.F. Prud'homme van Reine

Melanamansia glomerata (C. Agardh) R.E. Norris

Taxon 44: 66 (1995).

RHODOMELACEAE

$2n$ = unknown

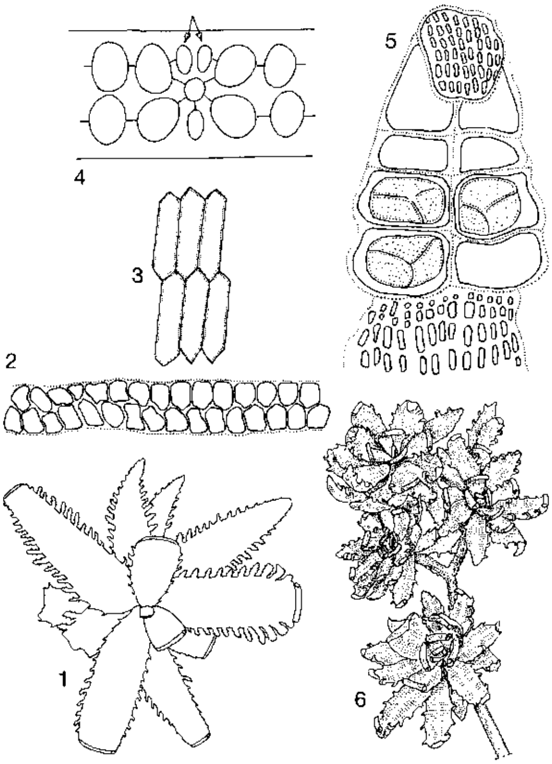
Synonyms *Amansia glomerata* C. Agardh (1822).

Origin and geographic distribution *M. glomerata* mainly occurs most probably in the Pacific Ocean: Japan, Taiwan, Hawaii, Australia (Queensland), New Caledonia, Samoa, Fiji. In South-East Asia it has been recorded in northern Burma (Myanmar), Indonesia, the Philippines and Papua New Guinea.

Uses *M. glomerata* has no economic value yet in Indonesia. In the Philippines it is cited as having some economic potential as a medicine and antibiotic. It is a food source for green turtle.

Properties *M. glomerata* contains medicinal compounds with antibiotic and antibacterial properties. This information on antibiotic potential has probably been derived from data on *Amansia multifida* J.V. Lamour. from Puerto Rico in the Caribbean.

Description Thalli pink to brownish-red, 4–6 (–15) cm tall, forming thick clumps or mats, attached to the substrate by well-developed holdfasts bearing cylindrical to slightly compressed, irregularly branched, cartilagineous axes, 0.5–0.7 mm thick. Ultimate branches in mature plants with crowded rosettes of linear-lanceolate blades with irregular serrate margins; blades up to 35 mm long, up to 7 mm broad and up to 80 μm thick,



Melanamansia glomerata (C. Agardh) R.E. Norris – 1, rosette of linear-lanceolate blades; 2, cross-section of blade showing 2 layers of cells in V-shaped transverse rows; 3, surface view of cells of a blade; 4, arrangement of pericentral cells and pseudopericentral cells (arrows) in a diagrammatic cross-section through a non-corticated part of a midrib of a blade; 5, marginal curved stichidium bearing tetrasporangia. Amansia rhodantha (Harv.) J. Agardh (from South Africa, originally described as belonging to A. glomerata C. Agardh) – 6, habit, comparable to habit of Melanamansia glomerata.

composed of 2 layers of elongated cells in V-shaped transverse rows, without cortication except at midrib; marginal teeth up to 1.3 mm long and up to 450 μm broad; central midrib present in each blade, thickly corticated, becoming narrower and disappearing towards the apex. Each central axial cell surrounded by 5 pericentral cells, with the first 2 dorsal pericentral cells each developing a smaller pseudo-pericentral cell lying adjacent to the central axial cell. Only tetrasporophytes known. Curved tetrasporangial stichidia, up to 340 μm long and up to 250 μm broad, in median portions of the blades, terminate on small, endogenous, pinnate, determinate laterals or on the marginal teeth of the blades, with 3–7 together. Tetraspores tetrahedrally divided, roundish, 80 μm × 100 μm, up to 8 per stichidium, in two longitudinal rows. Life cycle not completely known, but probably diplo-haplontic and isomorphic.

Growth and development There is a lack of information on the seasonality and reproduction of *M. glomerata*. It is not known for certain whether there are male and female plants of *M. glomerata*. The alga probably is perennial. In Indonesia, in the Spermonde Islands (South Sulawesi), Seribu Islands (Java Sea) and Bali, it grows abundantly in the dry season (August).

Other botanical information *M. glomerata* is characterized by its rosettes. However, confusion occurs with a similar species, *Amansia rhodantha* (Harv.) J. Agardh. In the latter pseudo-pericentral cells do not develop in the midribs, whereas it occurs in the western Indian Ocean, especially subtidally or in deep tide pools, and has also been cited as occurring in the Philippines. All data on *Amansia glomerata* and *A. rhodantha* in the region need careful checking. Indonesian specimens that have been identified belong clearly to *M. glomerata*.

Ecology *M. glomerata* occurs in the intertidal part of reef flats in areas moderately exposed to waves and currents. Usually the plants do not fully become exposed to air at low tide. It is also found on seaward platforms, mainly in shaded habitats. It grows on coral rubble in shallow water, forming dense carpet-like beds and is often partly covered by sand particles. It also occurs subtidally; the characteristic rosettes are less well developed there.

Propagation and planting *M. glomerata* is not grown in phycoculture.

Harvesting *M. glomerata* is collected from natural stands.

Prospects *M. glomerata* may have good prospects because world demand for chemical compounds from marine algae is increasing steadily, both for industrial purposes and for food additives.

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W.S. Atmadja & W.F. Prud'homme van Reine

Monostroma nitidum Wittr.

Förs. Monostroma: 41, pl. II, fig. 7 (1866).

MONOSTROMACEAE

$2n$ = unknown

Synonyms *Monostroma latissimum* Wittr. (1866).

Vernacular names China: jiao-mo. Japan: aonori.

Origin and geographic distribution *M. nitidum* is widely distributed in the South-East Asian region, particularly in Thailand, Vietnam and the Philippines. It is very common in China and Japan.

Uses *M. nitidum* is widely used as human food. Dried fronds are boiled with sugar, soya sauce and several chemicals, and then bottled as 'nori-jam'. Fresh *M. nitidum* is used as a vegetable in salads. Both fresh and dried *M. nitidum* are used in soups. It is also used as animal feed and as medicine (antibacterial, antitumour, lowers blood pressure, reduces blood cholesterol level).

Production and international trade Approximately 1500 t (dry weight) of *M. nitidum* are produced annually in Japan for commercial purposes. This mainly consists of what is known as *M. latissimum*, which is preferred over *M. nitidum* because of its larger fronds. No data are available on production or phycoculture of *M. nitidum* in South-East Asia, although it is often mentioned as a commercially used alga.

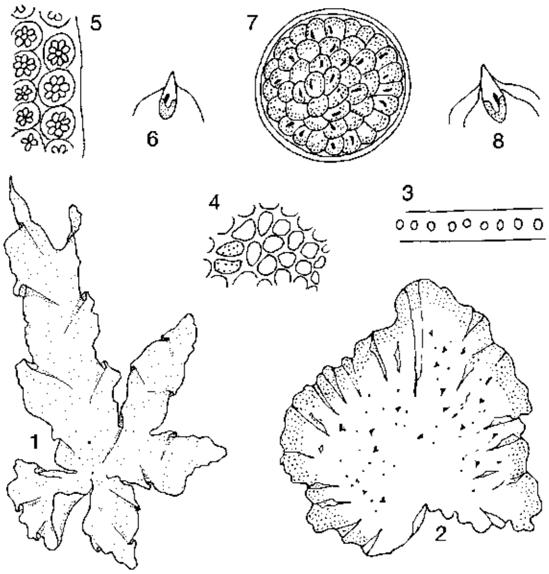
Properties Dried *M. nitidum* from Japan contains per 100 g dry weight (in g): protein 20.0, lipids 1.2, non-fibrous carbohydrates 57.2, fibrous carbohydrates 6.7, and (in mg) K 810, Na 690, Ca 690, P 200, Fe 2.5 and traces of Mn, Se and Mo. It also contains C_6-C_{12} phenols and 3,4 dihydroxyphenylethylamine dopamine.

It also contains nearly 200 mg per 100 g (dry weight basis) of a compound identified as dimethyl β-propiothetin. This compound has been found to prevent gastric ulcer in guinea pigs as well as to act as a tonic for liver function. Another compound, 3,4 dihydroxyphenylethylamine dopamine liberates dimethyl sulphide when exposed to air. Dimethyl sulphide, which emits a flavour typical of marine algae, is enzymatically formed. *M. nitidum* contains several kinds of betaine, of which β-homobetaine shows a high activity for lowering the artificially elevated level of plasma cholesterol in rats. The dialyzed residue of hot water-extractable substances from *M. nitidum* have been demonstrated to increase the life span of male mice implanted with L-1210 leukaemia cells.

Description Mature blades (gametophytes) yellowish-green, soft, lubricous, membranous, with crisped margins, 2–6(–15) cm long, one cell thick. Cells polygonal, mostly grouped in twos with slightly rounded corners, 12–15 μm in diameter (surface view). Life cycle diplo-haplontic and heteromorphic. Gametophytes dioecious; gametes 6–7 μm long, elongated, ovoid, with two identical flagella and eye-spot. Zoospores 9–10 μm long, in inconspicuous unicellular sporophytes, with four identical flagella and eye-spot.

Growth and development Gametes of *M. nitidum* fuse by isogamy, forming small and unicellular sporophytes. Zoospores germinate and form the much larger, leafy, gametophytic fronds.

Other botanical information There are not



Monostroma nitidum Wittr. – 1 & 2, habit of gametophytes; 3, cross-section of a gametophytic thallus; 4, detail of cells of a gametophytic thallus, surface view; 5, fertile cells with gametes in a gametophytic thallus; 6, gamete with two identical flagella and an eye-spot; 7, sporophyte with many spores with eye-spots; 8, zoospore with four identical flagella and an eye-spot.

many references to the conspicifity of *M. nitidum* and *M. latissimum*, and in several papers they are considered as separate species. Of these, *M. latissimum* most probably does not occur in South-East Asian waters, although it has been recorded from Palawan (the Philippines).

Ecology *M. nitidum* is found growing in brackish water habitats such as estuaries, river mouths and inner bays where it is influenced by freshwater. Thalli are attached to solid substrates. The leafy gametophytic stage appears in autumn and lasts to early summer and is thus highly seasonal in distribution.

Propagation and planting There are two methods of collecting *M. nitidum* spores: natural and artificial seeding. In the natural 'seed collection' method, zoospores are collected on culture nets submerged in selected collection grounds where natural *Monostroma* populations appear in early autumn. In recent times, poor collection techniques in Japan, render the water at the bottom of inner bays turbid, and have led to the development of artificial seeding. Here 'seed' culture begins by collecting many gametophytes during neap tides in April. The release of gametes may be induced by drying fronds overnight in the dark. A gamete solution is mixed in filtered seawater to form zygotes by isogamy. The zygotes then adhere to plastic settlement boards (20–30 cm long and 10 cm wide with both surfaces roughened on a glass-grinding machine). During summer the zygote settlement boards are maintained in large water tanks. These culture tanks are kept at room temperature and receive natural sunlight of 20–50 μmol photons/m^2/s. The seawater used for cultivation is supplemented with a solution containing nutrients and a weed killer. The cultivated zygotes (now sporophytes) gradually increase in size, reaching 50–60 μm after three months. Sporophytes are large enough by the middle of August to be allowed to mature by early September. Maturation of the sporophytes is promoted and synchronized by providing dark conditions for 2–3 weeks. Subsequently the settlement boards are transferred to smaller tanks which are exposed to a higher light intensity (100 μmol photons/m^2/s) provided by white fluorescent lamps and are used for the production of concentrated zoospore solutions. The zoospore solution is diluted in a large water tank using filtered seawater. Culture nets are then immersed in the water tank and zoospores attach themselves to them. The culture nets with attached zoospores are transferred to the cultivation grounds the following day.

Phycoculture *M. nitidum* is usually cultured in the shallow and calm areas of inner bays or river mouths where they are exposed to the influence of freshwater. One method of cultivation is the pole system, in which culture nets are supported by bamboo poles. The nets are set out horizontally at the level where the algal fronds will be exposed for about 4 hours during low tide. A second culture method is the floating system where nets are kept under the surface of the water. This allows the alga to be grown in deeper parts of the sea. During the germination of zoospores into *Monostroma* blades the seeding nets are at first spread in sets of about 5 'nursery nets' tied together. Once the fronds attain a length of 1–2 cm, individual nets are transferred to the culture ground for further growth. The growth rate usually increases in winter after transplantation.

Harvesting *M. nitidum* nets in Japan are harvested 3–4 times during the culture period. The total production is approximately 6–10 kg per net. A slight decrease in population density is observed immediately after harvesting. However, the cut fronds regenerate quickly and attain a harvestable size again after 3–4 weeks of growth.

Yield Total yield of *M. nitidum* is 300–500 g/m^2 dry weight after 3–4 harvests. The total production of nets which are harvested 3–4 times per year is higher than of nets which are harvested only once.

Handling after harvest Harvested fronds of *M. nitidum* are cleaned of contaminating organisms, washed well in seawater and freshwater, and then dried outdoors. Dryers may be used during cloudy and rainy conditions. Dried *Monostroma* is then boiled and bottled.

Prospects The increasing demand for green laver and its finished products in Japan augurs well for the *M. nitidum* industry.

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against L-1210 leukemia. Botanica Marina 25: 455–457.

G.C. Trono Jr

Nostoc Vaucher ex Bornet & Flahault

Révis. Nostoc. hét.: 181 (1886) [1888].
CYANOPHYCEAE
Prokaryotic, thus no chromosomes

Major species and synonyms

- *Nostoc commune* Vaucher ex Bornet & Flahault, Révis. Nostoc. hét.: 203 (1886) [1888], incl. var. *commune* and var. *flagelliforme* Berk. & M.A. Curtis ex Bornet & Flahault, Révis. Nostoc. hét.: 206, synonym of latter var.: *N. flagelliforme* Berk. & M.A. Curtis ex Bornet & Flahault (1886).
- *Nostoc linckia* (Roth) Bornet & Thur. ex Bornet & Flahault, Révis. Nostoc. hét.: 192 (1886) [1888], synonym (Drouetian): *Calothrix parietina* (Nägeli) Thur. ex Bornet & Flahault (1886).
- *Nostoc microscopicum* Carmich. ex Bornet & Flahault, Révis. Nostoc. hét.: 210 (1886) [1888], synonym (Drouetian): *Nostoc commune* Vaucher ex Bornet & Flahault (1886) [1888].
- *Nostoc muscorum* C. Agardh ex Bornet & Flahault, Révis. Nostoc. hét.: 200 (1886) [1888], synonym (Drouetian): *N. commune* Vaucher ex Bornet & Flahault (1886) [1888].
- *Nostoc verrucosum* Vaucher ex Bornet & Flahault, Révis. Nostoc. hét.: 216 (1886) [1888], synonym (Drouetian): *N. commune* Vaucher ex Bornet & Flahault (1886) [1888].

Vernacular names Star jelly, witches' butter, mares' eggs (En). Indonesia: jamur batu (Java). Philippines: tabtaba (= *Nostoc linckia*). China: fah-tsai or facai. Japan: ishikurage.

Origin and geographic distribution *Nostoc* has a cosmopolitan distribution. These common terrestrial and sub-aerial algae can be found in alkaline soils, especially in rice fields, and on moist rocks and cliffs. Occasionally they occur in marine waters or in brackish habitats, such as salt marshes and mangrove swamps. *Nostoc*-containing lichens can be dominant primary producers in some areas.

Uses *N. commune* is collected in moist hilly locations of the Ilocos region in the Philippines and eaten as green salad. Some other *Nostoc* spp. (*N. linckia*, *N. microscopicum*) are also collected in the same area. In Thailand *N. verrucosum* is used for food. The marine form of *N. commune*, var. *flagelliforme*, is collected for food in China, Japan and Java (Indonesia). The dried algae are cooked with noodles, vegetables and mushrooms, and served as a vegetarian dish or a soup by the Chinese. They often serve it as a New Year's dish. In paddy soils, the ability of *Nostoc* to fix atmospheric nitrogen increases the nitrogen content of those soils, and thus may increase rice yields. The blue-green algae living in the water fern *Azolla* Lamk may belong to the genus *Nostoc*, although they are usually considered to be *Anabaena* spp. *Nostoc* colonies can be a nuisance on sport turfs, as they make them very slippery.

Production and international trade Dried *N. commune* var. *flagelliforme* is exported from China to Malaysia, Singapore, Hong Kong and Taiwan, but data on international trade are not available.

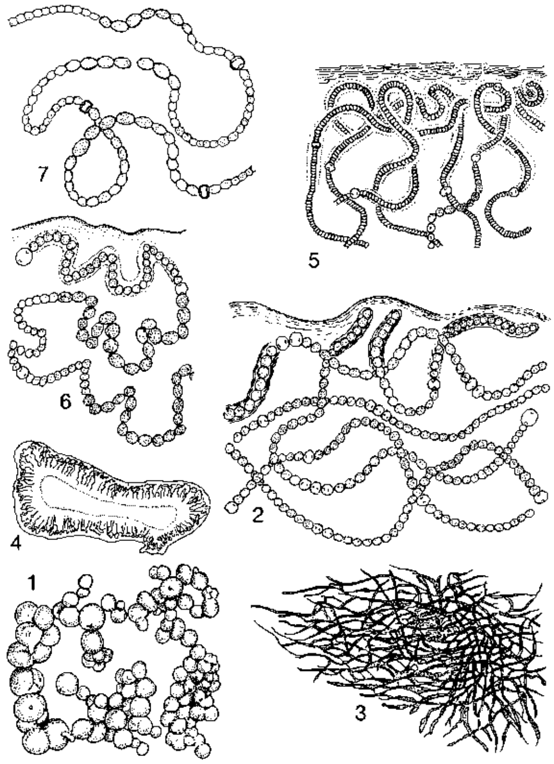
Properties Per 100 g dry weight *N. commune* contains: protein 39.9 g, lipids 5.0 g, carbohydrates 5.5–6.1 g and ash 24.3–27.5 g. The major essential amino acids (% of total protein) include leucine (6.7–9.2%), valine (7.1–9.2%), threonine (6.0–7.8%) and phenylalanine (5.5–7.2%). The dominant fatty acids (% of total fatty acids) are 16:0 (23–33%), 16:1 (10–18%), 18:1 (17–28%), 18:2 (4–18%) and 18:3 (3–28%).

Per g dry weight it contains the following pigments: phycobiliproteins 89 mg, chlorophyll a 1.8–2.7 mg and carotenoids 0.37–0.53 mg. The composition of the phycobiliproteins (% of total content) is as follows: phycocyanin (58%), allophycocyanin (25%) and phycoerythrin (19%). The carotenoids consist of β carotene (39%), zeaxanthin (10%), echinenone (17%), canthaxanthin (7%), caloxanthin (8%), nostoxanthin (7%) and myxoxanthophyll (8%).

The nitrogen fixation rate on the basis of acetylene reduction activity ranges between 567–1090 nM C_2H_4 g/h.

Phenolic extracts from *N. muscorum* have fungicidal and bactericidal properties. These inhibit mycelial development of the soil-borne phytopathogenic fungus *Cunninghamiella blakesleana*. Another species, *N. ellipsosporum* (Desm.) Rabenh. ex Bornet & Flahault, contains a bioactive compound cyanovirin. This irreversibly inactivates the HIV virus without adversely affecting the host cells. Work on this compound is being actively pursued.

Description Plants with mucilaginous, gelatinous or coriaceous thalli; thalli first globose to oblong, later globose, foliose, filiform, bullate, lobed, or warty, solid or hollow, free or attached, with periphery surrounded by firm, dense and darkly



Nostoc. N. sphaericum Vaucher ex Bornet & Flahault – 1. habit of mature thalli. N. commune Vaucher ex Bornet & Flahault – 2, detail of filaments in gelatinous thallus; var. flagelliforme Berk. & M.A. Curtis ex Bornet & Flahault – 3, habit. N. verrucosum Vaucher ex Bornet & Flahault – 4, cross-section of a gelatinous thallus; 5, details of filaments in gelatinous thallus. N. linckia (Roth) Bornet & Thur. ex Bornet & Flahault – 6, detail of filaments in gelatinous thallus. N. muscorum C. Agardh ex Bornet & Flahault – 7, detail of filament.

coloured surface layer (pellicle); filaments flexuous, curved or entangled; sheath distinct or diffluent; trichomes torulose; cells depressed, spherical, barrel-shaped or cylindrical; heterocysts intercalary; spores spherical or oblong.

- *N. commune*. Thalli firm, gelatinous, at first globose, later flattened, expanding, undulated, membranous or leathery, often perforated, up to 20 cm in diameter, blue-green, olivaceous or brown; filaments flexuous, entangled; sheath mostly only distinct at the periphery, thick, yellowish-brown, often lamellated, inside the thallus hyaline; trichomes 4.5–6 μm broad, cells short barrel-shaped or nearly spherical, mostly shorter or a little longer than broad, 5 μm long; heterocysts almost spherical, about 7 μm broad; spores very rare.
- *N. linckia*. Thalli gelatinous, attached, young stages punctiform, tuberculate or globose, when mature more or less formless, expanding, torn, varying in size, blue-green to violet or black-green to brown; filaments densely entangled, flexuous or highly coiled; sheath diffluent, colourless inside, distinct only in peripheral portion; trichomes 3.5–4 μm broad, pale green, cells short barrel-shaped; heterocysts subspherical; spores subspherical, 6–7 μm × 7–8 μm, epispore smooth.
- *N. microscopicum*. Thalli soft, but with firm outer surface, attached, spherical or ellipsoidal, usually 1 cm in diameter or smaller, first glistening, later olivaceous or brown; filaments loosely entangled; sheath more or less distinct, yellowish; trichomes 5–8 μm broad, blue-green or olive-green, cells subspherical or barrel-shaped; heterocysts nearly spherical, 7 μm broad; spores oval, 6–7 μm × 9–15 μm, olivaceous, epispore smooth.
- *N. muscorum*. Thalli gelatinous-membranous, irregularly expanded, attached by lower surface, tuberculate, 2–5 cm in diameter, dull olive or brown; filaments densely entangled; sheath only distinct at periphery, yellowish-brown; trichomes 3–4(–5) μm broad, cells short barrel-shaped to cylindrical, up to twice as long as broad; heterocysts almost spherical, 6–7 μm broad; spores rare, oblong, many in series, 4–8 μm × (7–)8–12 μm, epispore smooth, yellowish.
- *N. verrucosum*. Thalli often gregarious, at first spherical or subspherical, solid, gelatinous and firm, surface undulate or verrucose, later hollow, vesicular, soft, torn, up to 10 cm in diameter, black-green, olive-green or brown-green; filaments flexuous, densely entangled at the periphery; sheath thick, at the periphery yellowish-brown, inside the thallus hyaline and diffluent; trichomes 3–3.5 μm broad, cells short barrel-shaped, shorter than broad; heterocysts subspherical, 6 μm broad; spores oval, many in series, 5 μm × 7 μm, epispore smooth and yellowish.

Growth and development The cells of *Nostoc* divide by binary fission, which increases the length of the contorted trichomes. Reproduction is through the development of akinetes (spores) and by hormogonia (short, motile trichomes) as well as by fragmentation or budding of large colonies. Not all species form akinetes. In *N. commune* akinetes do not occur. The development of motile hormogonia forming a mature aggregate of filaments occurs entirely within a common matrix, and thus the aggregate has a fixed shape within the pellicle. This pellicle can be ruptured by the protruding hormogonia ('budding'), resulting in the formation of new colonies. The formation of motile hormogonia is promoted by red, but is blocked by green or white light. In *N. muscorum* and other *Nostoc* spp. hormogonia can form gas vesicles which probably allow the species to disperse more rapidly in flooded soils. Some strains of *Nostoc* are probably facultatively heterotrophic: in laboratory experiments many strains are able to grow on glucose, fructose, ribose, or sucrose.

Nostoc spp. are able to use various nitrogen sources, including inorganic nitrogen, amino acids, and atmospheric nitrogen. Several factors influence the rate of atmospheric nitrogen fixation. Activity increases at higher temperatures (up to 35°C) and decreases at low moisture levels. The addition of ammonia lowers nitrogen fixation rates, but the addition of nitrate probably has little effect.

Ecology Optimal temperatures for growth of *N. commune* range between 20–30°C, while optimal pH ranges between 6.5–8.5. The alga colonies can survive desiccation for months or years and recover their metabolic activity after rehydration. During desiccation, specific proteins are synthesized, fatty acid profiles and mRNA pools are altered, and nitrogenase activity is lost. The large amount of sheath material increases the resistance of the alga to desiccation and also protects it against high light intensity and grazer attack. *N. commune* var. *commune* is a freshwater variety that occurs on moist soils, rocks and in stagnant waters, including paddy fields. *N. verrucosum* occurs also on moist soils and rocks, while *N. linckia*, *N. microscopicum* and *N. muscorum* are mainly limited to moist soils only, including paddy-field soils. *N. commune* is one of the dominant algae in rice fields. The abundance of the alga is found to be significantly correlated to mean solar radiation and the amount of orthophosphate in the floodwater, but is suppressed by the addition of urea. Phosphorus and inorganic carbon generally limit productivity of *Nostoc*. Other elements related to maintenance of growth, photosynthesis or nitrogenase activity include boron (both for growth and nitrogenase synthesis), molybdenum (in nitrogenase and nitrate reductase) and vanadium (can partly substitute for molybdenum).

An important interaction of *Nostoc* with fungi is the formation of lichens. The fact that *Nostoc* can withstand repeated drying, is photosynthetic and is able to fix atmospheric nitrogen, makes it an ideal symbiont for fungi. Some *Nostoc* spp. interact symbiotically with various plants, including liverworts, hornworts, mosses, cycads, and several Angiosperms. All known *Gunnera* spp. support a *Nostoc* sp. as an endosymbiont. The *Nostoc* supplies fixed nitrogen to the host.

Propagation and planting *N. commune* can be grown in liquid or solidified inorganic medium (2% w/v agar), either BG-11 or Bold's Basal Medium. The nitrogen source can be omitted, especially if the cultures are being used for nitrogen-fixation studies. Illumination (42 μmol photon m^{-2} s^{-1}) can be provided by fluorescent lamps (Grolux or Truelite) under a 12:12 h light-dark cycle. The cultures are non-homogenous, with the filaments forming aggregates even though they are agitated by orbital shaking.

Phycoculture There is no commercial cultivation of *N. commune*. However, this is one of the species in the blue-green algal mixture cultured for use as biofertilizer in rice fields (algalization). In India, the soil-based mixture of algae is cultured in iron trays or cement tanks containing water mixed with 8–10 kg soil, 200 g superphosphate and 10 g insecticides.

Diseases and pests Some cyanophages can infect *Nostoc*, but no studies have been published regarding the importance of infection in natural populations. Insecticides such as folidol (1 ppm), parathion (7.5 ppm) or carbofuran (3% granules) are added to prevent breeding of mosquitoes and other insects in the culture basin.

Harvesting The blue-green algae for soil algalization are harvested in the form of a soil-based mixture.

Yield In the mixed cultures of blue-green algae for soil algalization each tray or tank measuring 2 m × 1 m × 0.25 m may yield up to 1.5–2 kg of algal material; however, the percentage of biomass contributed by *N. commune* is not known.

Handling after harvest After sun-drying, soil flakes containing the mixture of blue-green algae are applied in rice fields at 8–10 kg per ha, 1 week after transplanting. *N. commune* thalli collected for food are either directly sold at local markets or sun-dried before transport.

Prospects Investigations into the control of the nitrogen-fixation process in *N. commune*, especially at the molecular level, should be intensified. This includes the search for more information on the use of *Nostoc* and other blue-green algae in sustainable agricultural practices. Efforts should also focus on the selection of high-yielding strains. The potential of these algae as sources of fine chemicals, such as pigments and bioactive compounds (antibiotics and anti-HIV compounds), is worth exploring. Their demonstrated cholesterol-reducing ability suggests future use as nutraceutical. The possibility of growing these algae by immobilization for the photoproduction of gas should also be investigated.

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S.-M. Phang

Padina Adans.

Fam. Pl., part. 2: 13, 586 (1763).
DICTYOTACEAE
x = unknown

Major species and synonyms

- *Padina antillarum* (Kütz.) Picc., Alg. viagg. Vettor Pisani: 36 (1886), synonym: *P. tetrastromatica* Hauck (1887) [1886–1889].
- *Padina australis* Hauck, Hedwigia 25: 44 (1887) [1886–1889], synonym: often recorded as *P. gymnospora* (Kütz.) Sond., which is, however, probably a Caribbean species.
- *Padina boryana* Thivy, in W.R. Taylor, Pacific Sc. 20: 355–356, fig. 2 (1966), synonyms (misapplied names): *P. commersonii* Bory (1828) [1826–1829], nom. illegit.; *P. tenuis* (C. Agardh) Bory (1827); it is suggested the name *P. tenuis* Bory (1827) be considered as a newly described species, and then that name will have priority over *P. boryana* Thivy.
- *Padina minor* Yamada, Bot. Mag. (Tokyo) 39: 251–252, fig. 5 (1925).
- *Padina sanctae-crucis* Børgesen, Mar. agl. Danish W. Ind., Chloroph.: 45 (1914), synonym: *P. japonica* Yamada (1931).

Vernacular names Abanico (Sp).

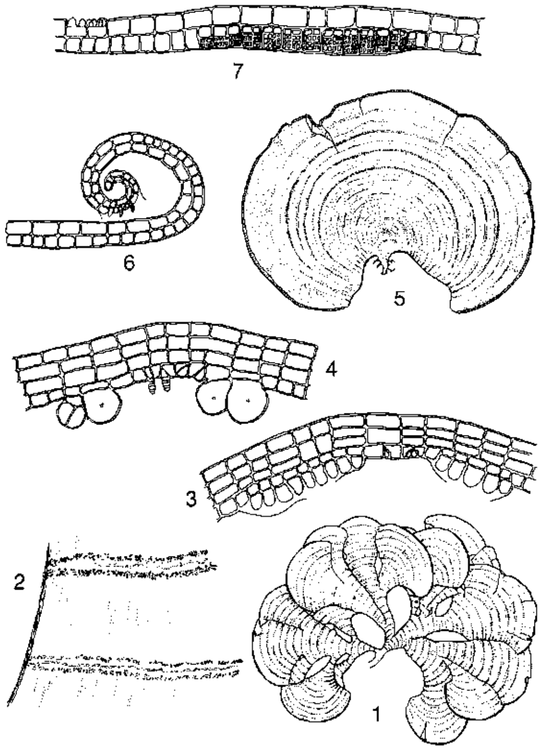
Origin and geographic distribution *Padina* occurs along all tropical and warm temperate sea coasts. In South-East Asia most *Padina* can be found on almost all coasts, although *P. antillarum* and *P. boryana* are less frequent.

Uses All *Padina* can be used as fertilizer or as a source of the phycocolloid alginate. P. *antillarum* and *P. australis* are occasionally used as human food.

Production and international trade No production data are available for *Padina*. Biomass is obtained from natural stocks.

Description Thalli flabellate, brown or whitish by a thin deposit of lime, often conspicuously zonate, attached by compacted rhizoidal holdfast; stipe often invested by rhizoids. Blades 2 to several cells thick, zonate, with zones marked by concentric rows of hairs, sometimes divided into narrow spatulate segments. Side to which blades are inrolled is called the upper surface of the blades. Life cycle diplo-haplontic and isomorphic. Gametophytes dioecious or monoecious. Reproductive cells (sporangia, gametangia) on blades scattered or in sori between hair bands.

- *P. antillarum*. Blades green-brown or yellow-brown, 5–10 cm tall, divided into few flabellate, lateral lobes, characteristically 4–6 cells thick, except at margins (2 cells thick); base rough, thicker. Calcification of blades usually conspicuous. Concentric hair lines well developed on lower surface of blade, at equal distance; faint lines in between hair lines present, especially at middle to lower portions of thallus. No '*Vaughaniella*' growth stages observed. Gametophytes dioecious, male plant generally smaller, paler and less lobed than female plant. Sporophytes generally larger, thicker, dark brown. Reproductive sori forming concentric lines on both sides of hair zones on lower blade surface. In male thallus, sori scattered in patches. Sporangia globu-



Padina. P. australis Hauck – 1, habit. P. antillarum (Kütz.) Picc. – 2, detail of lower surface of a blade with double lines of tetrasporangia aside hair lines; 3, detail of section of double indusiate sori with oogonia; 4, detail of section of double non-indusiate sori with tetrasporangia. P. sanctae-crucis Børgesen – 5, habit; 6, detail of section of circinnately inrolled margin of blade; 7, detail of section of non-indusiate antheridial sorus.

lar, 55–59 μm in diameter; mature sporangia without indusia, but indusium present in young stages. Oogonia globular, 30–35 μm in diameter, arranged in closed bands, with indusia; antheridia rectangular, about 30 μm × 30 μm, without indusia.

- *P. australis*. Thalli large, frondose, to about 15 cm tall, light brown, whitish in some portion due to slight calcification. Blades divided into several fan-shaped lobes, 2–8 cm broad, 2 cells thick throughout; blade surface divided into wide and narrow, glabrous zones by distinct concentric hair lines or filiferous zones, those on lower surface alternating with those on upper surface; narrow glabrous zones 1–2 mm wide; sterile, glabrous zones 2.5–3.0 mm wide, broader near margin. Rarely with *'Vaughaniella'* stages. Reproductive sori located at middle of narrow glabrous zone, usually on lower blade surface. Sporangia globose, without indusia, 59–85 μm in diameter. Gametophytes monoecious. Oogonia globose, 20–30 μm in diameter, rather irregularly arranged, with indusium; antheridia rectangular, 15–25 μm × 16–28 μm, without indusium.
- *P. boryana*. Blades yellow-brown, 8–10 cm tall, flabelliform, usually split into several segments, slightly encrusted with chalk on upper surface, composed of 2 layers of rectangular, thin-walled cells about 60–70 μm thick, those near base 85–90 μm thick; holdfast stupose, covered with brown hairs. *'Vaughaniella'* stages common. Concentric hair lines on blades conspicuous. Tetrasporangia forming sori, without indusium, in every glabrous zone, regularly arranged just above every hair line on lower blade surface.
- *P. minor*. Blades flabellate, yellow-brown or green-brown, light brown or whitish, 3–12 cm tall, divided into several flabellate lobes, 1–3 cm wide and 2 cells thick throughout, usually conspicuously calcified. Lower blade surface divided into concentric zones by equidistant hair lines; upper surface without hairs. *'Vaughaniella'* stages common. Reproductive sori forming concentric lines directly above each hair line. Sporangia globose, without indusia, 59–85 μm in diameter. Gametophytes dioecious. Oogonia globose, 19–31 μm in diameter, irregularly arranged, with indusium; antheridia rectangular, 13–23 μm × 17–27 μm, without indusium.
- *P. sanctae-crucis*. Blades brown to yellow-brown, 1–2 cm tall, flabelliform, often split into several segments, moderately calcified on upper surface, shortly stipitate, hairy near base, composed of two layers of rectangular, thin-walled cells, about 90–100 μm thick. *'Vaughaniella'* stages common. Hair lines conspicuous, mostly on lower surface; spaces between hair lines rather narrow, on upper surface faint hair lines discernable. Reproductive sori just above every other hair line at lower blade surface; occasionally becoming incomplete double line with additional, discontinuous sori present along lower side of hair lines. Sporangia globose, 25–35 μm in diameter, all markedly indusiate. Gametophytes dioecious. Oogonia globose, 30–40 μm in diameter, in closely packed line-forming sori, indusiate; antheridia rectangular, about 30 μm in diameter, closely packed in line-forming sori, indusiate.

Growth and development The blades of *Padina* grow by the many apical cells at the distal, curved, involute margin. In many cases an extensive, prostrate, pinnate branch system (*'Vaughaniella'*-stage) is developed from which the blades arise, attached by basal rhizoids. Flabellate branches may be produced from these branches.

Other botanical information Some authors consider *P. boryana* (often cited as *'P. tenuis'*) and *P. minor* as synonyms, but others have continued to recognize them as two separate species.

Ecology *Padina* is ubiquitous. Its different species can be found in a very wide range of habitats extending from intertidal to subtidal zones to a depth of 15–20 m in areas characterized by clear water. They can grow attached to different types of solid substrates as well as epiphytically on large seaweeds such as *Sargassum* spp. They are very abundant during the sunny months of the year.

Propagation and planting *Padina* is not known in phycoculture.

Handling after harvest *Padina* is used fresh or sun-dried.

Prospects No development prospects are expected for *Padina* in the near future.

Literature |1| Gaillard, J., 1967. Etude monographique de Padina tetrastromatica (Hauck) [Monographic study of Padina tetrastromatica (Hauck)]. Bulletin de l'Institut Fondamental d'Afrique Noire 29, série A: 447–463. |2| Gaillard, J., 1975. Padina sanctae-crucis Boergesen, Padina japonica Yamada, Padina haitensis Thivy et leurs affinités [Padina sanctae-crucis Boergesen, Padina japonica Yamada, Padina haitensis Thivy and their affinity]. Le Botaniste 57: 85–103. |3| Lewmanomont, K., 1980. Taxonomic study of the genus Padina of Thailand. In: Desikachary, T.V. & Rao, V.N.R. (Editors): Taxonomy of algae. Papers presented at the international symposium on taxonomy of algae, held at the Centre of Advanced Study in Botany, University of Madras, December 9–16, 1974. Madras, India. pp. 755–763, plates I & II. |4| Wynne, M.J., 1998. A study of Padina antillarum (Kützing) Piccone and a comparison with P. tetrastromatica Hauck (Dictyotales, Phaeophyta). Cryptogamie, Algologie 19: 271–289.

G.C. Trono Jr

Porphyra C. Agardh

Syst. alg. XXXII: 190 (1824).

BANGIACEAE

x = unknown; *P. atropurpurea*: $2n = 6$ or 8, *P. yamadae* (as *P. crispata*): $x = 3$, *P. suborbiculata*: $2n = 6$

Major species and synonyms

- *Porphyra atropurpurea* (Olivi) De Toni, Syll. alg. 4, Florideae, Sect. 1: 17 (1897), synonym: *Ulva atropurpurea* Olivi (1794).
- *Porphyra suborbiculata* Kjellm., Bih. Kongl. Svenska Vetensk.-Akad. Handlingar 23 (Afd. 2, 4): 10, pl. 1: figs 1–3; pl. 2: figs 5–9; pl. 5: figs 4–7 (1897).
- *Porphyra vietnamensis* Tak. Tanaka & P.H. Hô, Mem. Fac. Fish., Kagoshima Univ. 11: 34–36, figs 10, 11 (1962), synonym: *P. marcosii* Cordero (1976).
- *Porphyra yamadae* T. Yoshida, Phycol. Res. 45: 166 (1997), synonym: *P. crispata* Kjellm. (1897).

Vernacular names Purple laver (En). Zicai (China). Nori (Japan). Philippines: gamet (name for dried products of all *Porphyra* spp., Ilocos Province), pedazo.

- *P. vietnamensis* (as *P. marcosii*). Indonesia: huang isi, lumu lumu licin.

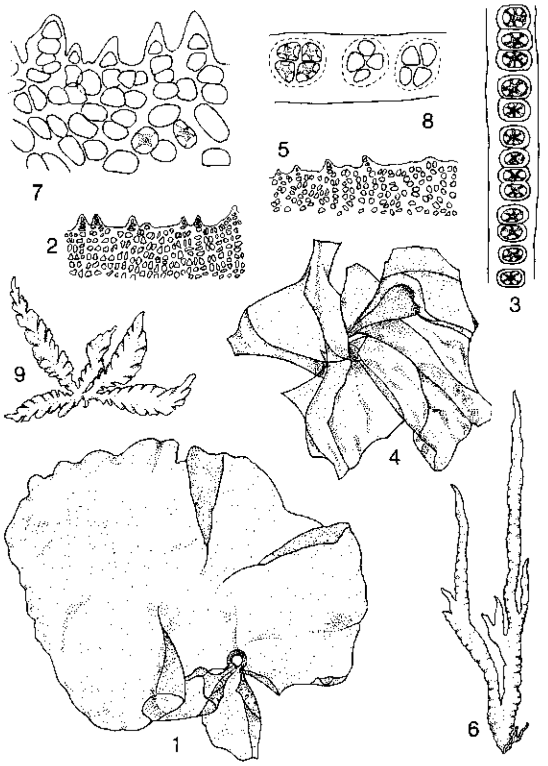
Origin and geographic distribution *Porphyra* occurs usually in non-tropical areas, although some species occur in the tropics as well. In South-East Asia *Porphyra* has been recorded from Burma (Myanmar, *P. yamadae*, as *P. crispata*), Thailand and Vietnam (both *P. vietnamensis* and *P. yamadae*, as *P. crispata*), the Philippines (Luzon, all species) and eastern Indonesia (*P. atropurpurea* and *P. vietnamensis*, as *P. marcosii*). In many countries in South-East Asia dried *Porphyra* (nori) is imported from Japan, China or Korea.

Uses The bulk of the *Porphyra* production as well as locally collected *Porphyra* is used as food in soups, sushi, and salads in Thailand, Vietnam, the Philippines and Indonesia. Several *Porphyra* spp. are also used for medical purposes, especially in Chinese herbal medicinal practice, where they are used to treat goitre and scrofula, cough, bronchitis, tonsillitis, asthma, urinary diseases and dropsy. Some *Porphyra* spp. are also applied as preventive medicine for hypertension. In northern Luzon (the Philippines) *Porphyra* ('gamet') is consistently the most popular edible seaweed. It is not generally available in southern Luzon. In Ambon (Indonesia) the locally available *P. vietnamensis* is sold at markets as dried sheets, prepared from many small thalli pressed together. In Halmahera and the Kai Islands (Indonesia) locally collected thalli are used to prepare sweetened jellies with coconut milk and the algae are also eaten in vegetable soup.

Production and international trade Although *Porphyra* cultivation is one of the most economically important food industries in Japan, Korea and China, production in South-East Asia is rather limited and usually only of local importance. There are no data available on the extent of production and international trade of *Porphyra* in South-East Asia, while the annual production of cultivated *Porphyra* in China, Japan and Korea is about 1 million t (wet weight).

In northern Luzon (the Philippines) *Porphyra* (most probably *P. suborbiculata*) is cultivated locally and the thalli are hand-picked and sold as dried sheets ('pedazo'). Dried *Porphyra* sheets are usually more expensive than other dried seaweed products. In the southern part of Thailand *P. vietnamensis* is exploited on a small scale. There, the total crop is less than 100 kg (dry weight) per year and no cultivation takes place. The slippery thalli are collected by hand in the upper littoral zone of exposed rocky coasts and reefs. In Thailand the larger thalli of *P. vietnamensis* are preferred to *P. yamadae* (as *P. crispata*); the latter is even considered to have no commercial value.

Properties Most *Porphyra* spp. have a high content of digestible protein (20–25% of wet weight) and contain many free amino acids (especially glutamic acid, glycine and alanine), which are responsible for its specific taste. Its vitamin C content is similar to that of lemons, while it is also rich in the B vitamins. *Porphyra* is an excellent source of iodine and other trace elements.



Porphyra. P. suborbiculata Kjellm. – 1, habit; 2, marginal portion of frond; 3, cross-section of vegetative frond. P. yamadae T. Yoshida – 4, habit; 5, marginal portion of frond. P. vietnamensis Tak. Tanaka & P.H. Hô – 6, habit; 7, marginal portion of frond; 8, cross-section of frond with zygotosporangia; 9, habit.

Description Foliose thalli (blades) purplish-red, round, reniform, funnel-shaped or linear, usually attached by discoid holdfast and obscure stipe with rhizoidal cells, monostromatic; cells in surface view polygonal, in cross-section elliptical to rounded containing 1 stellate chloroplast, with or without microscopic serrations along margins of blades. Life cycle diplo-haplontic and triphasic. Foliose gametophytes large, forming sori of unicellular carpogonia (zygotosporangia, zygotospores) and spermatangia (spermatia). Vegetative cells forming monospores.

- *P. atropurpurea*. Margins of leafy thalli without microscopic serrations. Although this species has been recorded as occurring and being utilized in South-East Asia, a recent reconfirmation is not available. Most probably, the name has been misapplied for one of the other *Porphyra* spp.
- *P. suborbiculata*. Foliose thalli light pink or purplish-red, round, ovate, funnel-shaped, laciniate or caespitose, 1–10 cm tall, 25–50 μm thick, with undulate or inrolled margins and microscopic serrations, entire or deeply lobed, attached at one side by discoid holdfast, 0.8–1.2 mm in diameter, with obscure stipe. Vegetative cells rounded, polygonal or angular in surface view, 20–30 μm × 12–22 μm, quadrate with rounded angles in cross-section, slightly taller than wide, 20–32(–60) μm × 20–35 μm; rhizoidal cells angular, capitate. Fertile thalli monoecious, 35–50 μm thick, deep red female areas and yellowish male ones splashed, close to margins of thalli. Usually 32 zygotospores formed from each zygotosporangium and 64–128 spermatia from each spermatangium. Monospores usually on young gametophytic thalli only.
- *P. vietnamensis*. Foliose thalli lanceolate to linear-lanceolate, basically branched, 3–27 cm × 0.3–3.6 cm, 20–32 μm thick, margins undulate, with microscopical denticulate processes, attached by small discoid holdfast. Vegetative cells angular with rounded angles in surface

view, 9–15 µm in diameter, same form in cross-section, cells 13–22 µm tall; rhizoidal cells angulate-capitate to oblong capitate. Fertile thalli monoecious, pinkish female patches at margins and apical portions of thalli, pale male areas at other margins. Usually 8 zygotospores (12–15 µm in diameter) formed from each zygotosporangium and 64 spermatia (7 µm in diameter) from each spermatangium. Monospores (18–20 µm in diameter) on young gametophytic thalli only.

– *P. yamadae*. Foliose thalli light red to black-purple, elliptical to reniform, often caespitose, 2–5 cm tall, 45–68 µm thick, margins often laciniate, with microscopic serrations, attached by discoid holdfast. Vegetative cells oblong-elliptical in surface view, longest dimensions 15–20 µm, in cross-section elliptical, half as tall as wide, (32–)55–60 µm × 20–27 µm; rhizoidal cells oblong capitate. Fertile thalli monoecious, brown-red female and yellowish male patches in separate areas along margins of thalli. Usually 32 zygotospores (8.8–14.8 µm in diameter) formed from each zygotosporangium and 128 spermatia (3–4.5 µm in diameter) from each spermatangium.

Growth and development The immobile tiny spermatia of *Porphyra*, of which many (up to 128) are formed by each spermatangial cell, attach to papilla-like protrusions of the female cells (carpogonia) which, after fertilization, become zygotosporangia forming zygotospores. These spores are liberated and, when germinating on a calcareous substrate, form the microscopic and filamentous *'Conchocelis'* stage. These filaments later form rows of spores (known as tetraspores or conchospores) which are liberated and each can germinate to form a leafy gametophyte. Cells in young gametophytes may become vegetative monospores, which may form gametophytes again. In the northern Philippines (Ilocos Norte) and in Thailand gametophytes occur in the wet season, from November to February.

Other botanical information Synonymy of *P. suborbiculata* and *P. yamadae* (as *P. crispata*) has recently been suggested. No clear differences could be observed between these taxa. Occasionally the thallus of *P. yamadae* (as *P. crispata*) is described as narrow, long, ribbon-like, up to 19–43 cm long, but probably this is a different species. The difference in form of the thalli and cells, as well as the number of spermatia formed by each spermatangium might be different enough to keep the taxa separated. The type of *P. crispata* is a green alga, hence the change of name to *P. yamadae*.

Synonymy of *P. marcosii* and *P. vietnamensis* has not yet officially been suggested. The differences in dimensions of cells, thalli and thallus form are not convincing.

Ecology The leafy gametophytes of *P. suborbiculata* in the northern Philippines and southern Thailand are usually found in the upper intertidal zone on rocky, wave-exposed shores, while the microscopic *'Conchocelis'* phase occurs in calcareous substrates such as shells of molluscs (mainly Lamellibranchiates) and barnacles. Leafy thalli of *P. vietnamensis* also grow on rocks in the upper intertidal zone, exposed to strong waves. It seems to grow best when fully exposed, moistened by spray of the breaking waves, and it can be found during the wet monsoon season. In Thailand in that season water temperature drops from 27–30°C to 24–27°C and salinity from 31–33 ‰ to (11–)18–26 ‰. The *'Conchocelis'* phase of *P. vietnamensis* grows well in shells of Lamellibranchiates.

Propagation and planting *'Conchocelis'* stages of *P. vietnamensis* can be cultured in shells at 25°C, salinity 25‰ and a light intensity of 350–500 lux for 12 h/d. At lower temperatures growth is very slow, while at 35°C the *'Conchocelis'* dies. Formation of conchosporangia occurs about 2 months after inoculation of the shells with zygotospores of *Porphyra* and is best at 30°C, and somewhat lower salinity (20‰). Each filament starts formation of conchosporangia 10 days after the temperature change and produces 10–20 conchospores after another ten days of incubation. These conchospores release 1–4 days after lowering the temperature again to 25°C and salinity to 10–15‰, and raising the light intensity to 800–1000 lux. Young leafy fronds develop best at the same temperature (24°C), somewhat higher salinities (20–25‰) and higher light intensities (1000–1200 lux). These young fronds need 40 days to grow to germlings of 1 mm tall, and a further 22–30 days to become mature and fertile.

Phycoculture Local cultivation in northern Luzon (the Philippines) of *P. suborbiculata* and/or *P. yamadae* (as *P. crispata*) is based on erecting long and branched bamboo poles, set closely together in rows along the shore. They are suitable for collecting spores from the surrounding waters. In other parts of northern Luzon and in southern Thailand the entire crop comes from natural populations and no cultivation is conducted.

Diseases and pests The list of known diseases of cultivated *Porphyra* in Japan is longer than for any other algal genus. It includes diseases caused by fungus-like protists (*Pythium porphyrae* causing red rot, and an *Olpidiopsis* sp. causing blight known as chytrid blight), bacteria (causing green spot disease or forming a filamentous bacterial felt), diatoms (forming a diatom felt) and many diseases caused by environmental conditions. In most cases the quality of dried nori sheets produced from diseased thalli is classified as inferior. Diseases also occur in the '*Conchocelis*' filaments, and at that stage of the life cycle mass cultivation is often very vulnerable to damage. Causes of '*Conchocelis*' diseases are pathogenic bacteria and fungi or fungus-like protists. Several weedy algae (especially members of the green algal genera *Monostroma* Thur., *Enteromorpha* Link, and *Ulva* L.) grow on the culture nets in between the *Porphyra* thalli. These weedy specimens can usually be killed by exposing the nets to the air for hours or even days, because the weed algae are more susceptible to desiccation than *Porphyra*. Grazing by herbivorous fish can also become a problem.

Harvesting In northern Luzon (the Philippines) and southern Thailand *Porphyra* talli are hand-picked from bamboo poles and from submerged boulders and coastal rocks.

Handling after harvest The locally produced *Porphyra* thalli in northern Luzon (the Philippines), southern Thailand and Ambon (Indonesia) are sold fresh or are prepared for the market by washing in freshwater, bleaching and sun-drying. In the Philippines this results in sheets 100–150 cm × 100 cm in size and about 5 mm thick. In Thailand and on Ambon, the dried sheets are circular and about 25 cm in diameter.

Breeding In *Porphyra* cultivation improvement is done by selecting better producing strains.

Prospects Because *Porphyra* includes the most highly domesticated marine algae, the state of understanding of its biology is quite advanced. Recent scientific advances in genetics, physiology, and biochemistry are quickly being applied in new production techniques and in the near future considerable progress is expected on the genetics of *Porphyra*. Vegetative propagation of the leafy gametophytes via protoplasts could help in eliminating the need for the expensive step of '*Conchocelis*' cultivation and will possibly bring genetic stability to the blades in cultivation.

Literature |**1**| Cordero Jr, P.A., 1976. Phycological observations II. Porphyra marcosii, a new species from the Philippines. Acta Manilana, series A, 15 (24): 14–24. |**2**| Fujita, Y., 1990. Diseases of cultivated Porphyra in Japan. In: Akatsuka, I. (Editor): Introduction to applied phycology. SPB Academic Publishing bv, The Hague, The Netherlands. pp. 177–190. |**3**| Kumar, C.A. & Panikkar, M.V.N., 1997. Indian species of Porphyra (Rhodophyceae, Bangiales). Feddes Repertorium 108: 419–423. |**4**| Lewmanomont, K. & Chittpoolkusol, O., 1993. Life cycle of Porphyra vietnamensis Tanaka & Pham-Huang Ho from Thailand. Hydrobiologia 260/261: 397–400. |**5**| Llana, E.G., 1990. Status of production and utilization of seaweeds in the Philippines. FAO/NACA report on the regional workshop on the culture and utilization of seaweeds. Cebu City, The Philippines. pp. 124–149. |**6**| Masuda, M., Ohno, M., & Trono Jr, G.C., 1991. A taxonomic assessment of Porphyra suborbiculata Kjellman, a food species from the Philippines. Japanese Journal of Phycology 39: 375–380. |**7**| Tseng, C.K. & Chang, C.F., 1984. Chinese seaweeds in herbal medicine. Hydrobiologia 116/117: 152–154.

W.F. Prud'homme van Reine

Portieria hornemannii (Lyngb.) P.C. Silva

Smithsonian Contr. Mar. Sci. 27: 39, 129 (1987).
RHIZOPHYLLIDACEAE
$2n$ = unknown

Synonyms *Desmia hornemannii* Lyngb. (1819), *Chondrococcus hornemannii* (Lyngb.) F. Schmitz (1895).

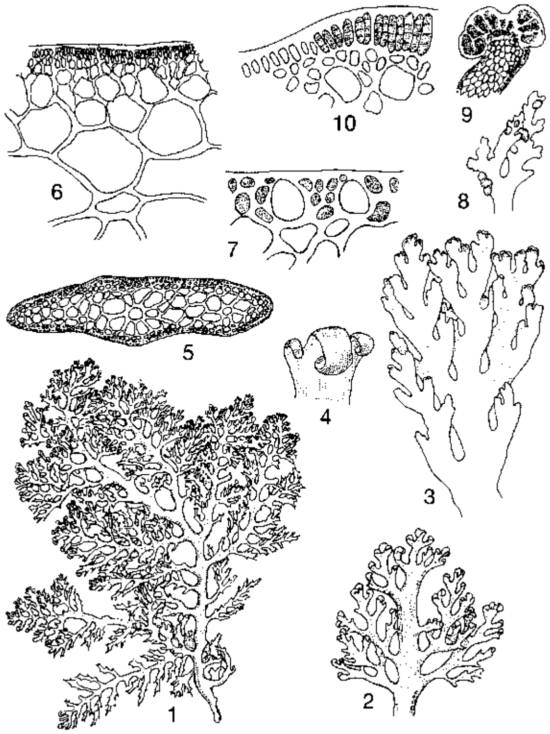
Origin and geographic distribution *P. hornemannii* is common in the tropical Indian and Pacific Oceans. In South-East Asia it has been recorded from northern Burma (Myanmar), Malaysia, Indonesia, the Philippines and Papua New Guinea.

Uses *P. hornemannii* is a source of carrageenan related to lambda carrageenan and which can be 35% of dry weight. It is also used for human food as vegetable salad.

Production and international trade There are no available estimates of production of *P. hornemannii* from the wild for food or medicinal use.

Properties *P. hornemannii* contains the terpenes chondrocole A & B (recently changed in name to apakaochtodene A & B) and the oxygenated compound chondrolactone. Especially apakaochtodene B is an effective deterrent against herbivores. A pentahalogenated monoterpene (halomon or prehalomon) from this alga shows cytotoxic activity against human tumour cells. This compound may be sequestered in gland cells distributed in the cortex of this alga and is only present in some of the samples. Most plants emit a pungent odour.

Description Thalli up to 20 cm tall, usually smaller, bright orange to red, composed of several erect, overlapping flattened branches arising from small discoid holdfasts. Branching in one plane, irregularly pinnate-alternate, in up to 5(–7) orders, forming rounded axils; diameter of primary branches not exceeding 7 mm; terminal branches at distal portion of thalli with slightly expanded curved or inrolled tips; lower lateral branchlets with simple acute teeth. Central axis in cross-section clearly visible, rather narrow, surrounded by large-celled pseudo-parenchymatous medulla and cortex of smaller cells; outer cortex in parts of thalli with many slightly larger gland cells. Two forms may coexist in the same habitat: a rigid cartilaginous form and a more flexuous, gelatinous form with finer branches. Life cycle diplo-haplontic, triphasic and isomorphic. Tetrasporangia and spermatangia in pale patches on surface of fertile thalli; cystocarps in wart-like nemathecia, mostly concentrated along thallus edges. Tetrasporangia forming solid layer without interspersed sterile cells; sporangia zonately divided, 6 μm × 45 μm. Gametophytes monoecious. Female nemathecia with semi-globose cystocarps developing several gonimolobes separated by thin sterile partitions; released carpospores globose, 9 μm in diameter. Spermatangia superficial, in pustule-like areas very similar to pale tetrasporangial patches.



Portieria hornemannii (Lyngb.) P.C. Silva – 1, habit vegetative thallus; 2 & 3, details of apical portions; 4, detail of inrolled tip; 5, cross-section of vegetative thallus; 6, detail of central axial cell, medulla and cortex; 7, detail of outer cortex with gland cells; 8, cystocarpic nemathecia; 9, longitudinal section through cystocarpic nemathecia; 10, cross-section through tetrasporangial nemathecium.

Growth and development The growth pattern of *P. hornemannii* is uniaxial. There are indications that cystocarpic thalli occur in the Philippines all year round.

Ecology The thalli of *P. hornemannii* form bright orange-red bunches strongly attached to coralline rocks at the upper subtidal zones of the reef margin or rocky shore exposed to strong wave-action, or on other algae, especially the crustose coralline *Peysonnelia* spp. Its habitat is limited to areas characterized by clear water.

Propagation and planting *P. hornemannii* is not grown in phycoculture.

Diseases and pests Aplysiid snails have been observed grazing voraciously on *P. hornemannii*.

Yield In wild *P. hornemannii* beds in the Philippines, the alga exhibits a patchy distribution, with a density of up to 2 thalli per 0.25 m^2 and an average biomass of about 1.74 g (wet weight) on such a surface. This provides an average of about 6.9 g (wet weight) potential harvest from 1 m^2.

Handling after harvest Thalli of *P. hornemannii* are sold fresh or are sun-dried.

Prospects The recorded presence of halogenated compounds in *P. hornemannii* may be worth looking into for their possible importance in medicine and in plant protection against herbivores. The available carrageenan has not yet been used for exploitation.

Literature |1| Burreson, B.J., Woolard, F.X. & Moore, R.E., 1975. Chondrocole A and B, two halogenated dimethyl hexahydrobenzofurans from the red alga Chondrococcus hornemannii (Mertens) Schmitz. Tetrahedron Letters 1975: 2155–2158. |2| Fuller, R.W., Cardellina, J.H. II., Kato, Y., Brinen, L.S., Clardy, J., Snader, K.M. & Boyd, M.R., 1992. A pentahalogenated monoterpene from the red alga Portieria hornemannii produces a novel cytotoxicity profile against a diverse panel of human tumor cell lines. Journal of Medical Chemistry 35: 3007–3011. |3| Matlock, D.B., Ginsburg, D.W. & Paul, V.J., 1999. Spatial variability in secondary metabolite production by the tropical red alga Portieria hornemannii. Hydrobiologia 398/399: 267–273. |4| Meñez, E.G., Calumpong, H.P., Newman, D.J. & West, J.A., 1996. An account of the red alga, Portieria hornemannii (Gigartinales, Rhizophyllidaceae), from the Philippines. In: Prasad, A.K.S.K., Nienow, J.A. & Rao, V.N.R. (Editors): Contributions in phycology. Volume in honour of Professor T.V. Desikachary. Beihefte Nova Hedwigia 112: 161–170. |5| Semesi, A.K. & Mshigeni, K.E., 1977. Studies on the yield and IR spectra of phycocolloids from Chondrococcus hornemannii and Sarconema filiforme from Tanzania. Botanica Marina 20: 271–276. |6| Woolard, F.A. & Moore, R.E., 1978. The structure and absolute configuration of chondralactone, a halogenated monoterpene from the red alga Chondrococcus hornemannii and a revised structure for chondrocole A. Tetrahedron Letters 1978: 2367–2370.

G.C. Trono Jr

Sargassum C. Agardh

Spec. alg. 1(1): 1 (1820).
SARGASSACEAE
x = unknown

Major species and synonyms

- *Sargassum aquifolium* (Turner) C. Agardh, Spec. alg. 1(1): 12–13 (1820), synonym: *Fucus aquifolius* Turner (1807–1808).
- *Sargassum baccularia* (Mert.) C. Agardh, Syst. alg.: 304 (1824), synonym: *Fucus baccularia* Mertens (1819).
- *Sargassum cinctum* J. Agardh, Spec. gen. ord. alg. 1: 324 (1848);
- *Sargassum crassifolium* J. Agardh, Spec. gen. ord. alg. 1: 326–327 (1848), synonym: *S. feldmannii* P.H. Hô (1967).
- *Sargassum cristaefolium* C. Agardh, Spec. alg. 1(1): 13 (1820), synonyms: *S. ilicifolium* (Turner) C. Agardh var. *duplicatum* J. Agardh (1848), *S. berberifolium* J. Agardh (1848).
- *Sargassum duplicatum* Bory, in Duperrey, Voy. monde, Cryptogamie: 127 (1828) [1826–1829].
- *Sargassum fulvellum* (Turner) C. Agardh, Spec. alg. 1(1): 34 (1820), synonym: *Fucus fulvellus* Turner (1807–1808).
- *Sargassum gracillimum* Reinbold, in Weber Bosse, Liste alg. Siboga: 172, figs 48, 49 (1913).
- *Sargassum granuliferum* C. Agardh, Spec. alg. 1(1): 31 (1820).
- *Sargassum hemiphyllum* C. Agardh, Syst. alg.: 307 (1824).
- *Sargassum ilicifolium* (Turner) C. Agardh, Spec. alg. 1(1): 11 (1820), synonym: *Fucus ilicifolius* Turner (1807–1808).
- *Sargassum kushimotense* Yendo, J. Coll. Sci., Imp. Univ. Tokyo 21(12): 73 (1907).
- *Sargassum myriocystum* J. Agardh, Spec. gen. ord. alg. 1: 314 (1848), synonym: *S. opacum* J. Agardh (1889).
- *Sargassum nigrifolium* Yendo, J. Coll. Sci., Imp. Univ. Tokyo 21(12): 127, pl. 16, figs 1–3 (1907).
- *Sargassum oligocystum* Mont., in Dum. d'Urv. Voy. Pôle Sud, Pl. cell:67–69 (1845), synonym: *S. binderi* Sond. (1848).
- *Sargassum paniculatum* J. Agardh, Spec. gen. ord. alg. 1: 315–316 (1848).
- *Sargassum polycystum* C. Agardh, Syst. alg.: 304 (1824), synonyms: *S. brevifolium* Grev. (1849), *S. pygmaeum* Kütz. (1849), *S. ambiguum* Sond. (1871).
- *Sargassum serratifolium* (C. Agardh) C. Agardh, Spec. alg. 1(1): 16 (1820), synonym: *Fucus serratifolius* C. Agardh (1815).
- *Sargassum siliquosum* J. Agardh, Spec. gen. ord. alg. 1: 316 (1848).
- *Sargassum turbinarioides* Grunov, Verh. K.-K. Zool.-Bot. Ges. Wien 65: 395 (1915) [1915–1916]. Note: Ajisaka et al. (1997) propose this name be considered a nomen dubium and that *S. turbinatifolium* C.K. Tseng & B. Ren Lu (in: Stud. Mar. Sin. 15: 9, fig. 6, pl. 7 (1979)) should be used as the correct name.

Vernacular names Indonesia: dandigum, arien wari (Ambon), agar-agar kupan (Moluccas), kakarian. Philippines: aragan (Ilocos), boto-boto, lusay-lusay.

Origin and geographic distribution *Sargassum* is a very large genus (nearly 400 species) of worldwide distribution. It does not occur in the colder seas, however. Most mentioned species listed above occur on the coasts of Indonesia, Malaysia, Singapore, Vietnam and the Philippines, fewer species have been recorded from Burma (Myanmar), Thailand and Papua New Guinea. Especially *S. crassifolium*, *S. cristaefolium*, *S. ilicifolium*, *S. oligocystum*, *S. polycystum* and *S. siliquosum* are widespread in South-East Asia. In Indonesia alone, more than 50 species of *Sargassum* have been collected.

Uses The main use of *Sargassum* is as a source of phycocolloids, in particular alginate, which is used in the textile industry in Indonesia and Vietnam. Production of alginate in the Philippines is still at the pilot stage. Many *Sargassum* are also used as food: upper parts of plants are eaten raw or cooked with coconut milk in Indonesia (Moluccas, Lombok and several other areas) and the Philippines (Ilocos Province), or as salad in Thailand and by fishing communities in Malaysia. It is also used in vegetable soup. This is especially documented for *S. aquifolium*, *S. crassifolium*, *S. granuliferum*, *S. oligocystum*, *S. polycystum* and *S. siliquosum*. Young shoots also form a common ingredient of fish dishes in northern Philippines, especially as the vegetable component of fish 'paksiw' or soups, as well as an ingredient of canned milkfish ('bangus' = *Chanos chanos*).

When used as solid fertilizer or soil conditioner, especially in Ilocos Norte (the Philippines), the seaweeds are first left to decompose in a pit for 2–3 months before use. Fresh leaves of *Gliricidia sepium* (Jacq.) Kunth ex Walp. are added to the seaweeds to hasten the decomposition process. The resulting seaweed compost is then mixed with soil and applied in crop husbandry. *Sargassum* is also used to make seaweed meal fertilizer. In Cebu (the central Philippines) commercial preparation of seaweed-based liquid fertilizers has been developed. These products are known to induce early flowering and enhance crop yield. Field bioassays by foliar spraying of aqueous extracts from *S. polycystum* in the Philippines gave an increase of 50% in fresh weight of 'petchay' (*Brassica chinensis* L.), 88% increase in total fresh weight of groundnut (*Arachis hypogaea* L.) and production of longer and heavier cobs in maize (*Zea mays* L.). *Sargassum* is also used as fertilizer/manure for the cultivation of onion (*Allium cepa* L. cv. group Common Onion), garlic (*Allium sativum* L.), chilli (*Capsicum* L.) and sweet potato (*Ipomoea batatas* (L.) Lamk) in Vietnam. In the Philippines this product is also used as a pesticide.

Sargassum is also a source for biogas production and a source of animal feed for poultry, pigs and cattle, a binder for pelletized fish feeds and is used as direct feed for cultivated abalones (*Haliotis* spp., molluscs). These seaweeds are also used as fish bait in basket traps.

Phlorotannins, which are polyphenols occurring in many brown algae including *Sargassum*, may possibly be of use as an antioxidant to prevent fish oil from becoming rancid.

In Chinese herbal medicine several *Sargassum* spp. are used to treat goitre and scrofula, as well as urinary diseases and dropsy. Some antiviral activity has been observed in some *Sargassum*, but not in the species occurring in South-East Asia. In Thailand dried *Sargassum* is used as a medicine to cure goitre and relieve fever, by boiling the seaweed with water and drinking it as tea. When used for the cure of children's fever, the algae are mixed with seagrasses, boiled, and the steam is inhaled. In the Philippines *Sargassum* spp. are also used for controlling ascariasis and for regulating the blood cholesterol level. They also show potential for normalizing blood pressure. In Indonesia these algae are used for the treatment of urinary diseases and goitre, as well as in cosmetics. An alginate factory in Indonesia produces a medical product ('Seahealth'), which is exported to China. Some *Sargassum* are also used as insect repellent.

Production and international trade At the time (17th Century) that brown algae were mainly used for burning to produce ash containing large quantities of potash and soda, *Sargassum* plants were probably cultivated in coastal zones. No data on amount or methodology are available on this early use. Although experimental *Sargassum* farms have shown that these algae can be easily grown on hard substrates in the sea, no commercial cultivation of these algae is known to exist.

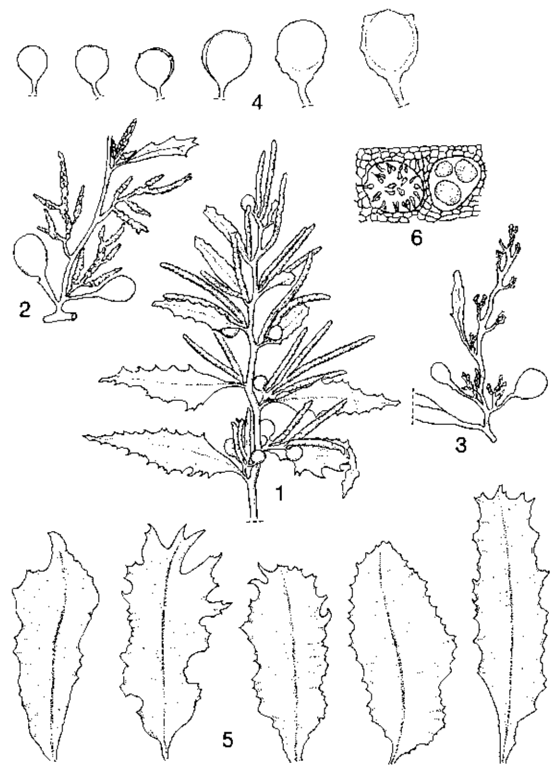
Sargassum is considered to be the largest natural seaweed resource in Vietnam. The total estimated biomass of *Sargassum* there was about 30 000 t (wet weight) in 1990, of which about 100 t (dry weight) was harvested. In 1997 harvested *Sargassum* biomass amounted to 300–500 t dry weight.

In the Philippines *S. cristaefolium*, *S. duplicatum*, *S. granuliferum*, *S. nigrifolium*, *S. polycystum*, *S. serratifolium* and *S. siliquosum* are identified as having a high level of utilization. They are all always gathered from natural stocks, mainly in areas in northern Mindanao and Visayas. In most cases they are processed into seaweed meal used in the production of animal feed, mainly for the local poultry farms. A portion of the seaweed meal is exported to Japan. In 1987 this amounted to about 4200 t. In Indonesia a factory produced 300 t of alginate in 1992, using 3000 t/y of dried *Sargassum*. Nevertheless, Indonesia still imported about 3000 t/y of alginate during that and following years, thus there is much demand for alginate.

Properties In *S. oligocystum* (as *S. binderi*) from southern Yemen the predominant unsaturated fatty acid in lipids is arachidonic acid (20:4; 12.7% of the total content of 1.3% lipid/fresh weight). This fatty acid is of particular interest because it is currently used as a precursor in the synthesis of proglandins. Dried *Sargassum* mixtures contain high amounts of potassium (up to 27% of dry weight), but relatively low levels of organic nitrogen (about 0.8%) and organic phosphorus (about 0.14%).

There is great variation in alginate yield and viscosity during growth of *Sargassum* plants, occurring between different growth stages, different species, different habitats and between seasons. In the Philippines on Negros Island highest viscosity of alginate in *S. ilicifolium* was 72.6 ± 5.4 cps and in *S. polycystum* 31.6 ± 5.1 cps. In other localities in the Philippines (Bolinao, Luzon Island) alginate from *S. oligocystum* recorded the highest viscosity (328–3270 cps), followed by *S. crassifolium* and *S. cristaefolium* (for both 200–1900 cps) and *S. polycystum* (179–1360 cps).

Description Perennial, pseudoperennial or annual, rather large seaweeds, 1(–3) m tall, consisting of a holdfast, stems and branches, leaf-like blades ('leaves'), vesicles and fruiting branchlets. Holdfast a conical disciform structure, or a larger scutate one, with or without lobes or rhizoidal outgrowths. In some cases main axes and holdfast together forming a complex rhizoidal system. Stipes or axes short or long, terete or compressed, smooth or muricate (= lumpy); the same features applying for the primary, secondary, tertiary and fourth order branches. Leaves differing in size and form, not only varying between species but also within a species, both between populations and even within individual specimens, flat, recurved, undulate, inflated, partly duplicated, or cup-forming, ranging from linear to lanceolate, ovate or spatulate, branched or unbranched and having entire, serrate, to highly dentate margins; groups of hairs sunken into surface of leaves (= cryptostomate), distributed in several different patterns, and considered to be of taxonomic importance. Vesicles often common, showing many features. Life cycle diplontic. Sexual structures are contained in modified leaves (receptacles); form and arrangement are as diverse as the vegetative features. Gametes develop in gametangia formed in cavities (conceptacles) in the surface of the receptacles. Conceptacles in dioecious species contain either male or female gametangia. In monoecious species conceptacles can be hermaphrodite with male and female gametangia in the same conceptacle, or receptacles are androgynous, containing both conceptacles with only male gametangia and conceptacles with only female gametangia. Some species are androdioecious, in which both androgynous and strictly female receptacles can occur. In each female gametangium (oogonium) only a single non-motile egg cell is formed; male gametangia (antheridia) form many small motile antherozoids.



Sargassum. S. paniculatum J. Agardh – 1, habit of portion of a fertile branch with young receptacles, leaves and vesicles; 2, detail of a portion of a fertile branch with female receptacles; 3, detail of a portion of a fertile branch with male receptacles; 4, details of vesicles; 5, leaves from different branch orders. S. alternato-pinnatum Yamada – 6, detail of a section of an androgynous receptacle with both a male and a female conceptacle.

In subgenus *Bactrophycus* J. Agardh axes are compressed, with 2 edges expanded and becoming angular; lower leaves simple, horizontally orientated; receptacles simple. The following relevant species with economic use or potential are distinguished:

- *S. fulvellum*: receptacles terete; holdfast platter-shaped.
- *S. hemiphyllum*: receptacles terete; holdfast with thin rhizoidal outgrowths; leaves hemiphyllous, without midrib.

- *S. nigrifolium*: receptacles spatulate, compressed, with dentate margins.
- *S. serratifolium*: receptacles spatulate, compressed, arranged in unbranched cluster, with smooth margins.

In subgenus *Sargassum* axes are cylindrical, compressed or flattened; leaves simple, vertical; vesicles often spherical or elliptical, often terminated by sharp tip, in uppermost part of leaves; receptacles on modified axillary branches, more or less compound, arranged in racemes, panicles or cymes. The relevant species can be distinguished by (1) leaf margins more or less duplicated or cup-shaped, (2) main branches muricate, or (3) main branches not muricate with plants dioecious and leaves either broad or (4) narrow. The following relevant species with economic use or potential are distinguished:

(1) Leaf margins more or less duplicated or cup-shaped:
- *S. crassifolium*: at leaf margins 2 rows of serration; monoecious.
- *S. cristaefolium*: at leaf margins 2 rows of serration; dioecious.
- *S. duplicatum*: leaves with cup-shaped margins; dioecious.
- *S. turbinarioides*: leaves with cup-shaped margins; monoecious.

(2) Main branches muricate:
- *S. granuliferum*: main branches slightly muricate, terete; holdfast small, conical, with rhizoids; leaves on main branches lanceolate, up to 6 cm long; leaves on fertile branches smaller; vesicles numerous.
- *S. myriocystum*: main branches distinctly muricate, terete; holdfast small, conical, with rhizoids; leaves on main branches thick, up to 5 cm long; leaves on fertile branches oblong to elliptical, much smaller.
- *S. polycystum*: main branches muricate with simple or branched protuberances (elevated cryptostomata); leaves on main branches lanceolate, thin, papyraceous, up to 6 cm × 1.5 cm; leaves on fertile branches small, lanceolate, linear or with uneven, slightly sinuous margins, up to 1 cm × 0.2 cm.

(3) Main branches not muricate; dioecious; leaves of primary and secondary branches and especially of fertile thalli broad, ovate, oblong, elliptical or obovate; branches terete:
- *S. baccularia*: holdfast scutate; vesicles lumpy; lower leaves up to 6 cm long.
- *S. ilicifolium*: holdfast discoid-lobed; vesicles small, marginate.
- *S. siliquosum*: holdfast scutate; vesicles smooth; lower leaves large, up to 20 cm long.

(4) Main branches not muricate; dioecious; leaves of primary and secondary branches and especially of fertile thalli narrow, linear to linear-lanceolate:
- *S. aquifolium*: branches distinctly flattened or compressed; leaves 5–6 cm × 1–1.5(–2) cm, coarsely dentated; receptacles repeatedly branched, without spiny outgrowths.
- *S. cinctum*: primary and secondary branches terete, coarse; leaves larger than 20 mm long, with denticulate margins; vesicles oblong, slightly compressed, often with apiculate tip.
- *S. gracillimum*: primary and secondary branches terete, filiform; leaves less than 20 mm long in fertile thalli; vesicles and receptacles zygocarpic, closely associated.
- *S. kushimotense*: stem terete; branches compressed; leaves about 5 cm long, less than 10x longer than wide, with sharply serrate or dentate margins, with basal part of margin entire.
- *S. oligocystum*: branches distinctly flattened or compressed; leaves up to 8 cm long, often more than 10x longer than wide, with entire or slightly dentate or undulate margins; receptacles branched, flat, shortly lobed, in dense tufts, with spiny outgrowths.
- *S. paniculatum*: primary and secondary branches terete, coarse; leaves larger than 20 mm long, with serrate margins; vesicles spherical or obovate, often with ear-like base.

Growth and development All plants of *Sargassum* are diploid and only the gametes are haploid. In the conceptacles, hiding in the receptacles, gametes are usually liberated from the gametangia and discharge through the ostiole of these conceptacles. Fertilization (oogamy) usually takes place in the sea and zygotes form a sticky wall and attach directly to all suitable substrates. In some species, however, fertilization takes place inside the conceptacles and few-celled germlings are formed that, after release and attachment, are able to grow much quicker and thus have a lead over slower growing organisms. Only zygotes and germlings that attach to suitable substrates have a chance of becoming mature plants.

In many *Sargassum* spp. fertile branches or mature degenerating branches detach or are detached from the main axes. These branches, which often have many vesicles and thus will float on the surface of the sea, form large masses of drifting algae which may eventually wash ashore or decompose in the sea.

Most *Sargassum* plants are pseudoperennials, which die back or degenerate annually, thus becoming temporarily smaller in size. In the Philippines the phenology of *Sargassum* beds in Balibago, Batangas, Luzon (beds of *S. paniculatum* and *S. siliquosum*) and Bolinao, Pangasinan, Luzon (beds of *S. crassifolium*, *S. cristaefolium*, *S. oligocystum*, *S. polycystum* and another *Sargassum* sp.) can be characterized by four phases:

- regeneration and slow growth phase in the dry season (December–May in Balibago, February-May in Bolinao) and three phases in the wet season;
- fast-growth phase (June–August in Balibago, June–September in Bolinao);
- reproductive phase (September–November and September–December respectively);
- senescence phase (November–February and December–March respectively).

These developments are more apparent in the intertidal portions of the beds than in the subtidal portions. In the intertidal area only the holdfasts, stipes and portions of the primary branches remain, while in the subtidal plants usually only the secondary laterals are lost. The species composition differs between the intertidal (mainly *S. polycystum* and *S. oligocystum*) and the subtidal (mainly *S. crassifolium* and *S. cristaefolium*), and usually the subtidal populations produce higher biomass and reach peak production 1–2 months ahead of the intertidal ones. Passing typhoons, however, may seriously disturb these general patterns.

In individual species the phenological phases are comparable to those of the *Sargassum* beds, but show considerable specific differences. During the phase of slow growth there is mainly primary growth with absence of branches of the second and higher orders; in the phase of fast growth branches of the second and higher orders are also present; in the reproductive phase receptacles are present and during senescence there is loss of vesicles, leaves and branches. In the central Philippines (Negros) *S. crassifolium* (as *S. feldmannii*), *S. cristaefolium*, *S. ilicifolium* and *S. polycystum* have been studied to obtain data on phenology and alginate yield. *S. polycystum* is present all year in low densities, but *S. ilicifolium*, although also present all year, has a distinct peak in its biomass in February, when it is reproductive, and declines (due to senescence) in April and May. In June new primary growth starts in that species. *S. cristaefolium* is present from November to April. Peak growth is in February, when the alga is reproductive, and after April no specimens were found. *S. crassifolium* first appears in November and has an explosive development in January and February, after which it becomes reproductive and reaches its peak biomass in March. In April senescence results in total decline of the population.

Other botanical information In addition to the large number of species in *Sargassum*, these algae belong to one of the anatomically and morphologically most complex genera in the Phaeophyta. All features of the leaf-like blades, stems (axes), vesicles, fruiting branches and holdfasts exhibit considerable variation in form, size, and numbers, not only between taxa, but also within a single species, both intra-individual and inter-individual. Any inspection of the literature on *Sargassum* cannot fail to demonstrate the prevailing state of uncertainty in the classification of its many species. Causes of this confusion are attributed to a number of factors including phenotypic plasticity, occurrence of different ontogenetic forms, polymorphism or over-emphasis on obvious features such as characters of the very variable blades. Moreover, hybridization and polyploidy may result in the intermixing of genomes, increases of chromosome numbers and, consequently, in the designation of myriads of varieties and forms. There is still a lot of confusion about the importance of different taxonomic traits and information on many of the taxa is greatly incomplete. This has resulted in different classifications and especially different proposals about the delimitation of species. To come to a critical revision of *Sargassum* taxonomy a wide field knowledge is needed of developmental stages and ecological variations, together with a study of the type specimens. This implies more seasonal studies, transplant experiments, interlocality studies, use of morphometrical and multivariate techniques, culture studies and application of genetic and molecular methods. Since 1985, a varying group of specialists has focused on the taxonomy of *Sargassum*, mainly those from the western Pacific Ocean and adjacent warm-water areas. In the group of species with cup-shaped or partly duplicated leaves this has already resulted in a transparent and clear classification, based on the occurrence of either monoecious or dioecious receptacles. If this distinction between monoecious and dioecious taxa is accepted, there seems to be no reason to synonymize *S. binderi* (monoecious) and *S. oligocystum* (dioecious), although thus is proposed in the most recent references and also in this volume. Their separation, however, is also supported by results of studies on alginate content and biomass in *Sargassum* in Malaysia. Populations from a single coral reef, identified as *S. binderi* and separate populations of *S. oligocystum*, differed both in phenology, viz. seasonal biomass, and in alginate content.

Ecology Many members of *Sargassum*, especially the ones in the common tropical and subtropical subgenus *Sargassum*, often dominate coral reefs and rocky shores, both in terms of biomass and species diversity. However, *Sargassum* beds also occur in the intertidal zone. Transplant studies in *Sargassum* do not suggest that there is much environmental control of morphology in these brown algae. Thus, the suggested 'environmental plasticity' in the genus has not yet been demonstrated convincingly, although shallow-water populations have generally a more compact growth form than populations occurring in deeper water. Wave action also affects the size of *Sargassum* plants, as well as the occurrence of vesicles and the distribution and morphology of the receptacles. *Sargassum* may occur in monospecific beds or in multispecies *Sargassum* beds. In both cases the *Sargassum* plants are the dominant organisms. Some species form beds in the upper intertidal zone, where the algae are totally exposed during low tide. Other species, however, occur only in the subtidal zone.

The growth stages of *Sargassum* are possibly mainly affected by tide levels, daylength, total reactive phosphorus and exposure to waves and currents, especially when related to monsoon variation.

Propagation and planting No phycoculture of *Sargassum* is known. However, harvest methods of natural crop must ensure that enough thalli are left as a source of new recruits for the next growing season. So far, tissue culture of *Sargassum* has not been successful.

Phycoculture Utilization of *Sargassum* is still only based on exploitation of natural stocks. To prevent overexploitation of these natural stocks, in Indonesia and in the Philippines efforts are being concentrated on developing the ability to culture these large brown algae.

Harvesting Harvesting of *Sargassum* does not necessarily result in the removal of individual algae from the population. Rather, harvesting its erect branches reduces the alga to its holdfast and parts of the erect axes, which can subsequently regenerate in the following growth season. Harvesting of natural stocks of *Sargassum* should be carried out by pruning the thalli near the base of the primary laterals and above the primary axis. Harvesting of erect branches does normally not damage *Sargassum* populations seriously. It may even be favourable for healthy regeneration from the remaining holdfasts and primary axes. However, harvesting can contribute to a greater mortality and to a loss of biomass resulting in reduced production of gametes, which may have an effect on recruitment. To obtain maximum biomass, *Sargassum* plants should be harvested when large and before they start to die back. Harvest in early periods of the reproductive season can result in a serious drop in population density and a very slow recovery, due to removal of the source of germlings for recruitment in the following season. Harvesting late in the reproductive season, however, gives often almost no drop in the subsequent population density, probably because many germlings would already have been released earlier. Thus, although in the Philippines (Balibago, Batangas, Luzon) the highest standing crop for *S. siliquosum* and *S. paniculatum* is available in October, it appears that November (end of the reproductive season) is a much better time to harvest these algae. For *S. crassifolium* (as *S. feldmannii*) in Negros (the central Philippines) the best time for harvest would be immediately after reproduction and before senescence. Holdfasts and a few centimetres of the stipe should be left to allow these perennial algae to regenerate.

In mixed *Sargassum* beds, annual harvest of the crop should be timed before the algae reach their peak of fertility, i.e. when approximately 50% of the plants are fertile. In intertidal beds often an intra-annual harvest is also possible. This must be done 3–4 months before the peak of fertility of the bed so that the stocks have ample time to regenerate.

When harvesting is done by 'strip cutting', meaning that strips of uncut thalli are left intact, or by random pruning leaving stands of fertile uncut thalli, enough fertile thalli are left as source of new recruits.

Yield In the Philippines (Balibago, Batangas, Luzon) harvesting *S. siliquosum* and *S. paniculatum* at the end of the reproductive season results in dry-weight yields of 21.3(–23)% alginate. Alginic acid levels range greatly, however, between and even within *Sargassum* spp.

Alginate was extracted from four dominant *Sargassum* spp. in Negros (the central Philippines) and grouped according to growth stage. In *S. crassifolium* (as *S. feldmannii*) and *S. polycystum* alginate yield was highest when the algae were in the stage of secondary growth. For *S. ilicifolium*, however, highest alginate yield was during the reproductive phase, and lowest alginate yield during secondary growth. In *S. cristaefolium* all stages were found to yield approximately the same amount. In addition, no significant differences were found between monthly alginate yield of each species in the months of occurrence, indicating that growth stage may be a more appropriate indicator of yield than month of harvest.

Among the 4 mentioned *Sargassum* spp. a higher alginate yield and higher viscosity can be obtained from *S. crassifolium* (as *S. feldmannii*) and *S. ilicifolium* than from *S. cristaefolium* and *S. polycystum*. *S. crassifolium* is the preferred species because of its rather low phenolic content and high biomass occurring during January–April. In addition, because the viscosity of its extracted alginate is not affected by age, it can be harvested any time during the growth season.

Sodium alginate yields (dry weight), obtained from 200 g fresh seaweed from Negros (the Philippines) varied for *S. crassifolium* (as *S. feldmannii*) between 1.5–3.9 g, for *S. cristaefolium* between 1.5–3.8 g, for *S. ilicifolium* between 0.7–2.8 g and for *S. polycystum* between 0.4–2.9 g. Alginate contents for Malaysian *Sargassum* (dry weight) varied between 11.9–21.9% for *S. oligocystum* and between 11.2–22.9% for '*S. binderi*'.

In mixed *Sargassum* beds in the northern Philippines (Bolinao), no significant seasonality was observed in alginate yield from either the intertidal or the subtidal populations, although subtidal samples had significantly higher yields than intertidal ones.

Handling after harvest *Sargassum* has to be washed in freshwater before drying and the dried material must be stored in airtight containers to prevent degradation of alginate which occurs when the raw material is stored for some time. Of course *Sargassum* processing first involves sorting and cleaning. Usually the dried and often also ground material is delivered by the fishermen or seaweed gatherers at 30–40% moisture content. The local processor-exporter then redries the material to 14–18% moisture content.

Prospects At present, local demand for alginate in the confectionery, pharmaceutical, textile, and even rubber industries is gradually increasing. Possibly the antioxidant activity in *Sargassum* may also be used in the future in industrial processes. In most countries in South-East Asia, however, there are no factories for the mass production of alginic acid or sodium alginate. An exception is an alginate factory in Bandung (Indonesia). The increasing local demand for both alginate production and liquid fertilizer may, however, lead to the destruction of the still abundant natural *Sargassum* beds. This implies the need for the development of a methodology for commercial phycoculture of these seaweeds before starting or enlarging alginate factories.

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W.F. Prud'homme van Reine

Scinaia hormoides Setch.

Univ. Calif. Publ. Bot. 6: 106, 125, pl. 12: figs 33–35, pl. 13: figs 36, 37 (1914).

GALAXAURACEAE

$2n$ = unknown

Vernacular names Philippines: garganatis (Ilokano, Visayan).

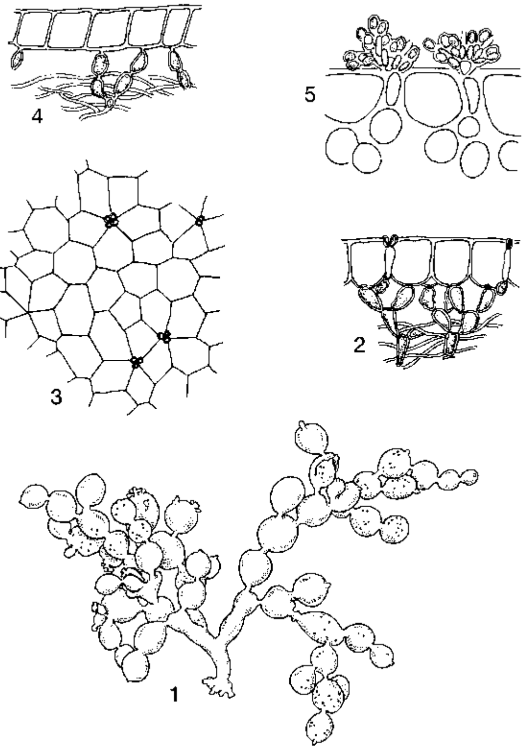
Origin and geographic distribution *S. hormoides* was originally recorded from Haleiwa, Oahu, Hawaiian Islands and is also represented in South-East Asia (Malaysia, Indonesia, the Philippines and the northern coast of Papua New Guinea). In the Pacific Ocean it is also known to occur in Japan and in Polynesia.

Uses *S. hormoides* as human food obtained from natural stocks is used. It is prepared as seaweed salad mixed with onions and tomatoes and dressed with sweet-sour sauces. It is also a good source of agar, but is not used commercially.

Production and international trade *S. hormoides* is not cultured and supply is gathered from natural stocks.

Properties *Scinaia* Bivona contains floridoside and floridean starch which are its principal carbohydrates. Mannoglycerate is also present in small quantities. Cellulose is the principal component of the cell wall. Fucosterol and sitosterol are also present.

Description Thalli up to 7 cm tall, bright red-greenish purple, attached to substrate by discoid holdfast; stipe short, not constricted, hard in texture; frond regularly dichotomously branched. Branches uniformly moniliform, composed of globular, subglobular or oblong segments, with longest segment up to 7 mm × about 5 mm. Cross-section of branch with epidermal tissues of generally colourless hexagonal to octagonal cells (utricles) on the surface, about 20 μm in diameter, mixed with few, grouped, small coloured cells; hypodermis with reddish-purple, globular or ovoid assimilatory cells. Medulla consisting of long colourless branched filaments. Life cycle probably triphasic, diplo-haplontic and heteromorphic. Tetrasporophytes probably microscopic, filamentous, branched, producing cruciately divided tetrasporangia. Gametophytes dioecious. Spermatangial stands with long, narrow spermatangial mother cells, penetrating between utricles, producing small, 4–5 times divided branches, forming hemispherical clusters of spermatangia, 250–350 μm in diameter, covering surface of male plants. Cystocarps broadly pyriform or globular, with ostiole sunken in thallus, scattered especially in middle portion of branches, surrounded by pericarp of 3–7 layers, with numerous slender gonimoblasts and carpospores released to central cavity.



Scinaia hormoides Setch. – 1, habit of a cystocarpic plant; 2, section of the outer part of a thallus, with utricles, hypodermis, medulla and groups of small coloured cells between the utricles; 3, surface view of utricles and small groups of small coloured cells; 4, section of the outer part of a thallus, with utricles, hypodermis and medulla; 5, section of a fertile male thallus with hemispherical clusters of spermatangia.

Ecology *S. hormoides* grows attached by a well-developed holdfast to solid substrates like rocks, pieces of dead corals, shells and on crevices of reef crest as well as in shallow subtidal areas characterized by clear water and moderate water movement.

Propagation and planting No phycoculture of *S. hormoides* is known.

Harvesting *S. hormoides* is only hand-collected from natural stands for direct local use.

Handling after harvest *S. hormoides* is sold and used fresh and/or sun-dried.

Prospects *S. hormoides* is suitable as edible decoration in appetizing salads.

Literature |1| Setchell, W.A., 1914. The Scinaia assemblage. University of California Publications in Botany 6(5): 79–152, pls 10–16. |2| Tazawa, N., 1975. A study of the male reproductive organ of the Florideae from Japan and its vicinity. Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido University 6(2): 95–179, pls 1–10.

G.C. Trono Jr

Tricleocarpa fragilis (L.) Huisman & R.A. Towns.

Bot. J. Linn. Soc. (London) 113: 100, table 2 (1993).

GALAXAURACEAE

$2n$ = unknown

Synonyms *Eschara fragilis* L. (1758), *Galaxaura oblongata* (J. Ellis & Sol.) J.V. Lamour. (1816), *Tricleocarpa oblongata* (J. Ellis & Sol.) Huisman & Borow. (1990).

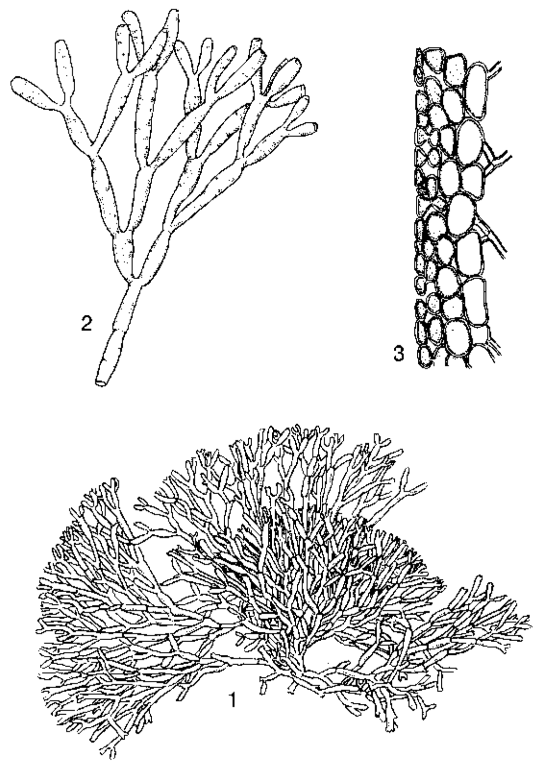
Origin and geographic distribution *T. fragilis* is widely distributed in tropical and subtropical areas. In South-East Asia it is recorded from Burma (Myanmar), Thailand, the Philippines, eastern Indonesia and the northern coasts of Papua New Guinea.

Uses *T. fragilis* is a source of sulphated polysaccharide related to carrageenan (not used commercially). It is mainly used in animal feed and as a fertilizer in leached acid soils.

Production and international trade *T. fragilis* is not used in commercial quantities and data are not available.

Properties *T. fragilis* has a high ash content, with much calcium.

Description Thalli (gametophytes) forming erect, bushy, pinkish-red clumps, up to 70 mm tall, composed of slightly calcified, terete branches. Branches regularly dichotomous and divaricately branched, forming acute angles; interdichotomal segments glabrous, cylindrical, slightly constricted and rounded at both ends, with annulate surfaces, (1–)5–8(–15) mm long, 1.5–2 mm in diameter, shortest at the apices. Cortex with 3–4 layers, innermost one inflated, colourless, grading to smaller, pigmented outer cortical cells; thallus internally composed of medulla of longitudinal filaments. Life cycle triphasic, diplo-haplontic and heteromorphic. Tetrasporophytes probably small, filamentous, branched. Gametophytes monoecious or dioecious. Cystocarps with distinct, sterile pericarp, with few sterile 3–4 celled paraphyses arising from pericarp, projecting slightly into cystocarp cavity; gonimoblast not completely lining pericarp. Carposporangia obovoid, 45–65 μm × 26–40 μm, produced terminally from gonimoblast filaments. Cystocarps spherical to slightly flattened, 400–500 μm in diameter. Spermatangia in spherical cavities formed by profuse growth of specialized branched filaments near apex of fertile plants; cavities 300–350 μm in diameter, with spermatangia 6–8 μm × 4–6 μm.



Tricleocarpa fragilis (L.) Huisman & R.A. Towns. – 1, habit; 2, detail of terminal branches; 3, cross-section of thallus with filamentous medulla and four layers of cortex cells.

Other botanical information Because the difference between *T. fragilis* and a related species, *T. cylindrica* (J. Ellis & Sol.) Huisman & Borow., is mainly based on characters of the gonimoblast morphology, synonymy of *Galaxaura dimorpha* Kjellm. (originally described from western Timor, Indonesia) has not yet been ascertained.

Ecology *T. fragilis* is commonly found attached to rocks, dead corals and shells in shallow areas, moderately exposed to wave action, where it forms large solitary clumps. Material of this alga has been dredged up in subtidal areas more than 50 m deep.

Propagation and planting No phycoculture of *T. fragilis* is known.

Harvesting *T. fragilis* is only hand-collected or collected from washed-up material.

Handling after harvest *T. fragilis* is air-dried and grounded.

Prospects There are very few development prospects for *T. fragilis*.

Literature |1| Huisman, J.M. & Borowitzka, M.A., 1990. A revision of the Australian species of Galaxaura (Rhodophyta, Galaxauraceae), with a description of Tricleocarpa gen. nov. Phycologia 29: 150–172.

G.C. Trono Jr

Turbinaria J.V. Lamour.

Fucacées in Bory Dict. class. hist. nat. 7: 71 (1825).

SARGASSACEAE

x = unknown

Major species and synonyms

- *Turbinaria conoides* (J. Agardh) Kütz., Tab. phycol. vol. 10: 24, pl. 66, fig. 2 (1860), synonym: *T. vulgaris* J. Agardh var. *conoides* J. Agardh (1848).
- *Turbinaria decurrens* Bory, in Duperrey, Voy. monde, cryptogamie: 119 (1828) [1826–1829].
- *Turbinaria luzonensis* W.R. Taylor, J. Linn. Soc. (London), Botany 58: 482, pl. 2, figs 13–17 (1964).
- *Turbinaria ornata* (Turner) J. Agardh, Spec. gen. ord. alg. 1: 266 (1848), synonym: *Fucus turbinatus* L. var. *ornatus* Turner (1807–1808).

Vernacular names General: Indonesia: rumput laut (general name for seaweed). Malaysia: rumpair (general name for seaweed). Philippines: samô (Cebuano). China: la ba zao.

- *T. ornata*. Indonesia: kakarian. Vietnam: rong loa gai.

Origin and geographic distribution *Turbinaria* is circumtropical in distribution and has been recorded from the Indo-Pacific as well as the Carribean but is more diverse in the Indo-west Pacific. *T. conoides* and *T. ornata* are probably the most widely distributed of the *Turbinaria* spp., having been found throughout South-East Asia. *T. decurrens* has a more limited distribution and has been recorded in South-East Asia from Thailand, Malaysia, Indonesia, the Philippines and Papua New Guinea. *T. luzonensis* has only been recorded from the Philippines.

Uses Various *Turbinaria* spp. are used as human food, fertilizer, pesticide and insect repellent. In Malaysia pickled specimens of *T. conoides* and *T. ornata* are used in salads. As a fertilizer or soil conditioner, a mixture of *Turbinaria* with *Sargassum*, *Hormophysa* and *Dictyota* brown algae is decomposed in a pit for 2–3 months before being used. To hasten the decomposition, fresh leaves of *Gliricidia sepium* (Jacq.) Kunth ex Walp. are added. In the Philippines, the algae are mixed and boiled with seagrasses and the steam is inhaled to serve as a cure for children's fever. In the northern Philippines, a mixture of *Turbinaria* and *Sargassum* spp. is used in vegetable gardens to keep insects away.

Production and international trade In South-East Asia, *Turbinaria* may be harvested and mixed with other large brown algae such as *Sargassum* spp. and reported as brown algae, so no specific information on their production and trade is available. There is no known phycoculture production of *Turbinaria*. In India, however, *Turbinaria* spp. are commercially harvested.

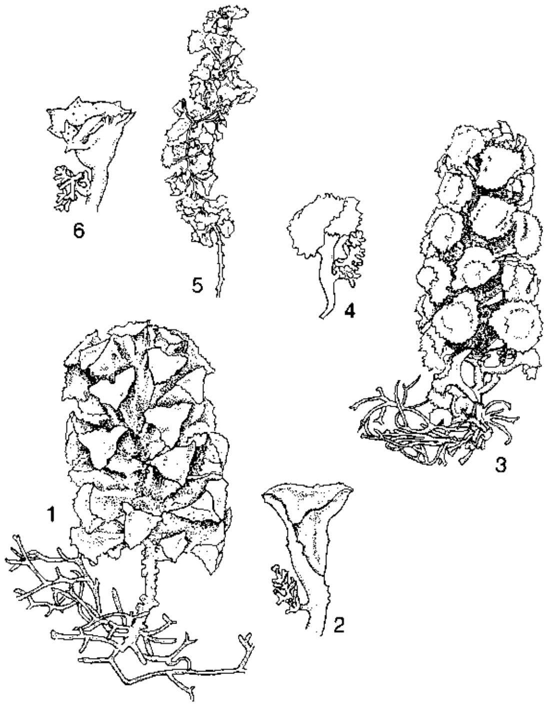
Properties *Turbinaria* contains fatty acids, tannins, phenols, alginic acid, laminarin, steroids, mannitol, minerals (including Ca, Cu, Fe, I, K, Mg, Na, Zn), phytohormones (auxin, cytokinin, gibberellin) and pigments (carotene, chlorophyll a, chlorophyll c and fucoxanthin). Cell walls of *Turbinaria* contain alginic acid, cellulose and sulphated polysaccharides. For *T. ornata* from the Philippines 46.8% alginic acid content (moisture-free basis) has been recorded. Specimens of *T. conoides* in Malaysia have an alginate content of 25.7% (dry weight), with highest values around December. Alginate and mannitol contents of *T. ornata* have been found to vary with growth and reproductive seasonality, and were highest before the reproductive period, decreasing during and after the reproductive season.

Crude extracts of *Turbinaria* have been shown to improve seed germination and seedling growth of pigeon pea (*Cajanus cajan* (L.) Millsp.) with maximum activity obtained at 1% concentration of the crude extract. Methanol and hexane extracts of *T. ornata* from Papua New Guinea exhibited positive antibacterial activity against gram-positive bacteria. Antibacterial activity was also detected in *T. conoides* from India.

Turbinaric acid, identified to be 4,8,13,17,21-pentamethyl-4,8,12,16,20-docosapentaenoic acid has been isolated from *T. ornata*. A 20-hydroxy-4,8,13,17-tetramethyl-4,8,12,16-eicosatetraenoic acid was also isolated from *T. ornata* and found to be a feeding deterrent against the herbivorous gastropod *Omphalius pfeifferi*, and a feeding inhibitor for the herbivorous green snail *Turbo marmoratus*.

Description Leaves turbinate, expanding at distal end, forming marginal blades crowned by rows of teeth. Vesicles in centre of marginal blades. Life cycle diplontic. Sexual structures contained in modified leaves (receptacles). Receptacular branches located on stalk of leaves at some distance from main axis; gametangia in cavities (conceptacles) on the surface of receptacles.

- *T. conoides*. Thalli erect, up to 1.5 m tall, attached to substrate by coarse, ramifying holdfast. Main axes terete, muricate at base; branches loose, in all directions. Leaves triangular or irregularly rounded, up to 12 mm × 9 mm in surface view, consisting of stalk, vesicle and expanded distal marginal blade crowned by short coarse teeth, sometimes cut on one side with cut extending to vesicle. Receptacular branches in clusters, 3–10 mm long, located about one-fourth distance from base of leaves.
- *T. decurrens*. Thalli erect, up to 7 cm tall, with coarse, ramifying holdfast. Leaves up to 18 mm long, often in compact, distinct rows, distally expanded to trigonous form giving an obpyramidal lateral view; distal end triangular in surface view; surface concave, with or without fine marginal teeth; centre with or without vesicle. Receptacular branches paniculate, up to 8 mm long, located at base of leaf stalk.
- *T. luzonensis*. Thalli erect, up to 10 cm tall, attached to rocks by coarse, ramifying holdfast. Main axis terete, densely covered with small, stalked leaves less than 1 cm long. Leaves expanded distally giving a triangular lateral view, in upper part of thallus with marginal blades narrowed to undulating ridge being entire or with a few teeth; terminal portion with vesicle surrounded apically by marginal blade being coarsely dentate or deeply cut. Receptacular branches racemose, less than 1 cm long, located near base of leaf stalk.
- *T. ornata*. Thalli erect, 20–30 cm tall, attached to rock by discoidal holdfast with dichotomously branched ramifying stolons tipped with adhering discs. Main branch cylindrical, with numerous branches in all directions. Leaves coarse, subpyramidal to turbinate, up to 20 mm long, 15 mm broad at distal end; distal end expanded forming rounded to triangular marginal blade surrounded by crown of short teeth; centre of blade concave, usually with vesicle encircled by row of coarse teeth. Receptacular branches racemose, located about one-third distance from base of terete leaf stalk.



Turbinaria. T. decurrens Bory – 1, habit; 2, leaf and receptacle. T. ornata (Turner) J. Agardh – 3, habit; 4, leaf and receptacle. T. conoides (J. Agardh) Kütz. – 5, portion of erect axis with leaves; 6, leaf and receptacle.

Growth and development All plants of *Turbinaria* are diploid and only the meiogametes are haploid. In bisexual conceptacles both male and female gametangia are formed. Antheridia, oogonia and paraphyses are developed from an epithelial layer in the conceptacles. In oogenesis, one of the cells lining the conceptacle cavity divides transversely, giving rise to an outer cell forming the oogonial mother cell and an inner cell that becomes the stalk-cell. The oogonial mother cell differentiates directly into the oogonium and the stalk-cell persists until the oogonium is released. Per conceptacle 6–9(–12) oogonia are produced. Phenolic bodies, polysaccharide granules and protein bodies accumulate in the cytoplasm of the oogonium during differentiation. Each released oogonium contains eight nuclei of which one will be the nucleus of the single functional egg. Antheridia are either sessile or stalked. Eggs and sperms are released about the same time and synchronous in different conceptacles. The sperms are released en masse, but the eggs remain attached to the inside of the conceptacle by means of a small stalk and are embedded in transparent mucilaginous substances. The outer wall layer of an antheridium lyses at or near the apex of the mature antheridium, discharging the sperms.

Only one phenological study on *Turbinaria* has been conducted in South-East Asia (in the Philippines) in two sites on *T. ornata* and *T. luzonensis*. Young *T. ornata* populations appeared from January to May, and *T. luzonensis* populations from March to July. Receptacular branches developed from October to December in both sites. In India, where most studies were carried out, the growth cycle of *T. conoides* commences in April, and young plants of *T. ornata* appeared in April. Reproductive plants could be found there throughout the year but peaked in November. For *T. decurrens* in India, young plants were observed in May and June, while reproductive plants were found in 11 out of 12 months of the year, peaking in the period from December to February. The standing crops of *T. ornata* in Moorea Island (French Polynesia) were the most abundant of the perennial algae, constituting 61–80% of the bulk biomass.

Ecology *Turbinaria* is commonly found on lower intertidal reef flats and shallow rocky subtidal areas exposed to moderate to strong waves and can form a distinct zone. In Pasacao, Camarines Sur, southern Luzon (the Philippines) tidal levels, temperature, and water movement seem to be the causal factors influencing the seasonality, distribution, growth and reproduction of *Turbinaria* at one station, and tidal levels, salinity, pH and water movement at another one.

T. ornata was found to stimulate slightly the growth of ciguateric dinofagellates in Mayotte Island (South-West Indian Ocean). *Turbinaria* invaded reefs on which the corrals have been killed by *Acanthaster planci* (crown-of-thorn starfish) in Moorea, French Polynesia. It appeared that *T. turbinata* was not preferred by sea urchin grazers. Various *Turbinaria* spp. form a suitable habitat for hydroids, polychaetes and dinoflagellates.

Propagation and planting *Turbinaria* spp. are not known to be propagated artificially nor used in any phycoculture in South-East Asia. There were some early attempts to culture them in India but their growth was not encouraging.

Harvesting *Turbinaria* is not specifically targeted for harvest in South-East Asia although it is commercially collected along the coast of the Gulf of Mannar (India). In South-East Asia, it may be a by-catch in the harvesting of other algae like *Sargassum* spp. For Malaysia the best time to harvest *T. conoides*, based on alginate yields, is stated to be October.

Yield A population of *T. ornata* from Tiahura Reef, Moorea Island (French Polynesia) yielded 93.8–1130.5 g/m^2 (wet weight), 3.9–13.8% of which was made up of stolons only.

Handling after harvest If harvested together with *Sargassum* spp., samples of *Turbinaria* are air-dried. It has been found that the gel strength (viscosity) of alginate extracted from *T. ornata* may increase from 10–74.5 cps (at room temperature) to 475 cps if the samples are pretreated overnight with 2% formaldehyde solution before extraction.

Prospects Although *Turbinaria* is a potential source of alginate and other chemicals, it does not usually form a substantial component of the reef and its standing crop is not large enough to support extensive harvesting. Hence, unless unusual chemicals associated with *Turbinaria* are proven to have pharmaceutical significance, large-scale harvesting or phycoculture development is unlikely in the forseeable future.

Literature |**1**| Ganzon-Fortes, E., Campos, R.R. & Udarbe, J., 1993. The use of Philippine seaweeds in agriculture. SICEN Newsletter 4(1): 2–3. |**2**| Laserna, E.C., Veroy, R.L., Luistro, A.H., Montaño, N.E. & Cajipe, G.J.B., 1982. Alginic acid from some brown seaweeds. Kalikasan 11: 51–56. |**3**| Montaño, N.E. & Tupas, L.M., 1990. Plant growth hormonal activities of aqueous extracts from Philippine seaweeds. SICEN Leaflet 2: 1–5. |**4**| Moreland, P.S., 1979. Edible seaweeds of Northern Luzon, Philippines: market prices, local taste preference, seaweed recipes, and other local uses. Philippine Journal of Science 108: 41–53. |**5**| Payri, C.E., 1984. Variations biologiques et morphologiques en fonction du milieu chez Turbinaria ornata (Turner) J. Agardh (Phéophycées) du récif de Tiahura – Ile de Moorea – Polynésie Française [Biological and morphological variations related to the environment in Turbinaria ornata (Turner) J. Agardh (Phaeophyceae) of the Tiahura reef, Moorea Island, French Polynesia]. Botanica Marina 27: 327–333. |**6**| Sokhi, G. & Vijayaraghavan, M.R., 1986. Oogonial release in Turbinaria conoides (J. Agardh) Kützing (Fucales, Sargassaceae). Aquatic Botany 24: 321–334. |**7**| Umamaheswara Rao, M. & Kalimuthu, S., 1972. Changes in mannitol and algic acid contents of Turbinaria ornata (Turner) J. Agardh in relation to growth and fruiting. Botanica Marina 15: 57–59.

P.O. Ang

Ulva L.

Sp. pl.: 1163 (1753).
ULVACEAE
x = unknown; *U. fasciata*, *U. pertusa*: $2n = 18$

Major species and synonyms
- *Ulva fasciata* Delile, Descr. Egypte, Hist. nat.: 297, pl. 58: fig. 5 (1813) [1813–1826].
- *Ulva lactuca* L., Sp. pl.: 1163 (1753).
- *Ulva latissima* auct. non L., Harv., J. Bot. (Hooker) 1: 155 (1834), synonyms: *Ulva lactuca* var. *latissima* sensu C. Krauss (1846), possibly also *U. indica* Roth (1806).
- *Ulva pertusa* Kjellm., Bih. Kongl. Svenska Vetensk.-Akad. Handl. (ser. 4) 33(1): 4–7, pl. 1, pl. 3: figs 1–8 (1897).
- *Ulva reticulata* Forssk., Fl. aegypt.-arab.: 187 (1775).

Vernacular names Sea lettuce (En). Indonesia: bulung lengas (Bali). Philippines: lumot, gamgamet, lablabig.

Origin and geographic distribution *Ulva* comprises 30 species and is widely distributed in most regions of the world. In South-East Asia all *Ulva* spp. are known to occur in Singapore, Indonesia and the Philippines, while *U. lactuca* and *U. reticulata* have been recorded from almost all countries in this region, although rarely mentioned from Papua New Guinea.

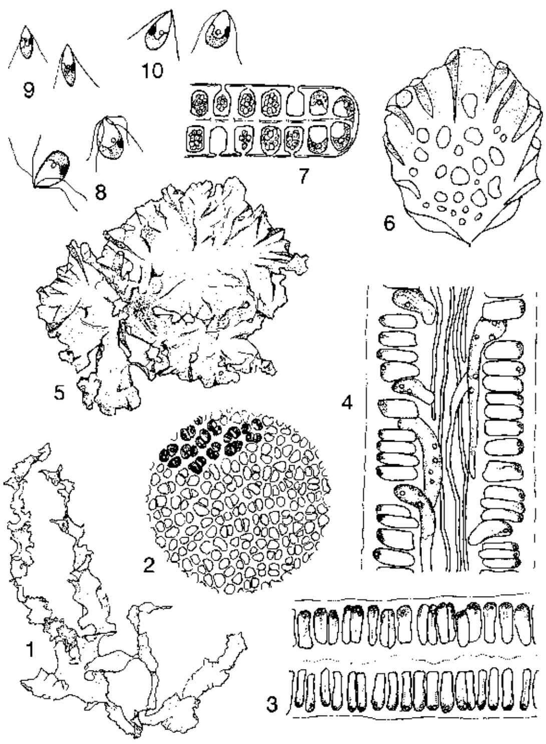
Uses *Ulva* is occasionally used in Indonesia (Bali) for animal feed. In Makassar (Sulawesi, Indonesia), however, the frequently occurring *Ulva* bloom is not used at all. In Malaysia and the Philippines these algae are used as human food (rich in vitamin E), medicine and as a vermifuge. In the Philippines they are also used as feed for fish and for stray pigs. These algae are also applied as an antimicrobial agent, an antipyretic and cooler (refreshing liquid), and for treatment of sunstroke. They are also applied as packing material to cover baskets of *Caulerpa* spp. during shipping and transport to market places and also by fish vendors to cover fish in shallow round baskets used for hawking. In coconut plantations it can be used as manure.

In Chinese herbal medicine *Ulva 'lactuca'* is known as a treatment for urinary diseases and dropsy, as well as a treatment for boils.

Production and international trade *Ulva* algae are not commercially grown. Occasionally they are collected from wild populations or washed up on beaches.

Properties *Ulva* species in general contain (in g per 100 g fresh weight): water 18.7, protein 15–26, fat 0.1–0.7, carbohydrates 46–51, fibre 2–5 and ash 16–23. They also contain vitamins B1, B2, B12, C and E. *U. fasciata* contains (in g per 100 g fresh weight): water 15.5, protein 6, fat 1.1, carbohydrates 30.2, fibre 12 and ash 35.2. Cu and Pb contents (mg/g) are 8.2 and 8.3 respectively. Ash content in *U. lactuca* is recorded as 29.1% (dry weight). The high protein level and good digestibility of the carbohydrates make them an attractive source of fish feed, while their rapid growth makes them attractive for studies on biomass production. Comparative studies on bioconversion indicate that these algae are more readily digested and give a higher methane yield than *Gracilaria* spp. In experiments done in India a lipophilic fraction of the ethanolic extract of *U. fasciata* showed significant antiviral activity against Japanese Encephalitis Virus (JEV). The active compound was identified as erythro-sphinga-4,8-dienine-N-palmitate. The same alga has been shown to contain an active significant inhibitor of Semiliki Forest Virus (SFV), as well as other active antivirus compounds.

Description Plants first subfiliform, later expanding with marginally attached or substipitate blades. Blades plane or crispate, orbicular to elongate laciniate, consisting of two cell layers separated by gelatinous cell walls thickened both internally and externally. Cells with single chromatophores with one or more pyrenoids; nuclei solitary, becoming multinucleate at cell extension of elongate holdfast. Life cycle diplo-haplontic and isomorphic. Gametes and spores are formed in undifferentiated vegetative cells.
- *U. fasciata*. Blades flat, often twisted, dark green, 5–30 cm × 1– 10 cm, attached by a small holdfast; base of blade entire, irregularly lobed or divided from base into branching linear segments; segment margins undulate, ruffled, crenulate.
- *U. lactuca*. Plants foliose, bright green or grass green; blades lanceolate to rounded, often with somewhat lobed and undulate margins, to 60 cm long or more, with glossy broad sheets, attached by a small disciform holdfast; membrane thick near base, with marginal portions somewhat thinner; cells polyhedral in surface view, arranged in linear rows.
- *U. latissima*. As in *U. lactuca*, but blades shorter than broad, much expanded at maturity.
- *U. pertusa*. Blades solitary, dark green, shiny, somewhat crisp in texture when fresh, attached by small disciform holdfast from which a thickened and decurrent base arises, commonly irreg-



Ulva. U. fasciata Delile – 1, habit; 2, surface view of cells in upper part of the blade; 3, cross-section of the upper part of a blade; 4, longitudinal section of a basal part of a thallus. U. lactuca L. – 5, habit. U. pertusa Kjellm. – 6, habit; 7, cross-section of a fertile thallus with zoosporangia or gametangia (diagrammatic); 8, quadriflagellate meiozoospores; 9. female gametes; 10, male gametes.

ularly perforated, lobed to deeply cut in segments; transverse-sections at base of blade about 165 µm thick, but much thicker immediately above the base; cells in cross-section with distinctly thickened outer walls, with cell lumen 60–65 µm long and 3–4 times its width; chloroplasts limited to inner ends of cells; sections towards middle of blade thinner, about 100 µm thick, with cell lumina 40–43 µm long, about twice as long as wide.

– *U. reticulata*. Blades flat, light to dark green, reticulate, with holes of various sizes, about 65 µm thick; in surface view cells rounded; cell lumina ovate, about 20 µm long; chloroplasts concentrated close to surface of blades.

Growth and development Gametes and spores of *Ulva* are formed in undifferentiated vegetative cells. *Ulva* is known to have an isomorphic alteration of generations with meiosis just before formation of zoospores by the sporophytic generation. Gametophytes produce biflagellate gametes and the sporophyte produces quadriflagellate zoospores. Most *Ulva* species are isogamous but some are known to be anisogamous. Sexual reproduction is through dioecious biflagellate gametes, while asexual reproduction is by quadriflagellate zoospores. In some species cells in the centre of the blade produce reproductive spores/gametes, which after release of the zoids create distinctive holes or reticulations. In other species gametes and spores are formed in cells along the margins of the blades, resulting in whitish margins when the zoids have been released. *Ulva* spp. may also multiply vegetatively by growth of fragments accidentally detached from a thallus.
Growth rates of *Ulva* decline markedly during periods of nutrient limitation and during zoospore formation. The rapid growth rate is well explained by its favourable morphology for the uptake of nutrients and use of light.

Other botanical information Most species of the genus *Ulva* are exclusively marine.

Ecology *Ulva* spp. grow in a wide range of habitats, on rocks, especially on dead coral fragments in the intertidal or subtidal zones. Their size and form vary with changes in environmental factors. They can grow luxuriantly in water enriched by organic wastes. There is even a correlation between sewage pollution in coastal waters and abundant *Ulva* growth. These algae often become a problem for seaweed farmers because as an epiphyte they grow fast on rope or even on top of cultured plants.

Propagation and planting Some *Ulva* spp. have successfully been propagated by tissue culture from fragments and protoplasts. Growth experiments in the laboratory and greenhouse cultures have resulted in selected strains for special research projects.

Phycoculture In culture experiments *Ulva* has been used to study biomass yield, biodetectors and bioaccumulators.

Harvesting Small quantities of *Ulva* are hand-collected by local people, mainly for animal feed.

Handling after harvest *Ulva* is mostly consumed fresh or sun-dried.

Breeding Culturing of *Ulva* is still in the experimental stage using natural 'seeds' or selected strains.

Prospects Future utilization of *Ulva* will be for human food and for pharmaceutical purposes, especially as antiviral agents.

Literature |1| Kamat, S.Y., Wahidulla, S., d'Souza, L., Naik, C.G., Ambiye, V., Bhakuni, D.S., Goel, A.K., Garg, H.S. & Srimal, R.C., 1992. Bioactivity of marine organisms. VI. Antiviral evaluation of marine algal extracts from the Indian coast. Botanica Marina 35: 161–164. |2| Polne-Fuller, M. & Gibor, A., 1987. Tissue culture of seaweeds. In: Bird, K.T. & Benson, P.H. (Editors): Seaweed cultivation for renewable resources. Developments in Aquaculture and Fisheries Science 16(9): 219–239. |3| Sharma, M., Garg, H.S. & Chandra, K., 1996. Erythro-sphinga-4,8-dienine-N-palmitate: an antiviral agent from the green alga Ulva fasciata. Botanica Marina 39: 213–215.

W.S. Atmadja

Valonia aegagropila C. Agardh

Spec. alg. 1(2): 429–430 (1823) [1822–1823].
VALONIACEAE
$2n$ = unknown

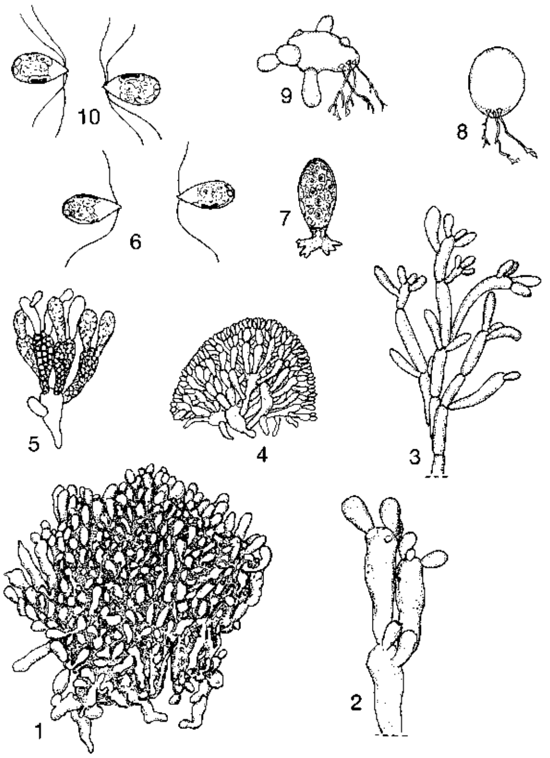
Origin and geographic distribution *V. aegagropila* is widely distributed in tropical and subtropical areas. In South-East Asia it is common in Burma (Myanmar), Thailand, Vietnam, Malaysia, Singapore, the Philippines and Papua New Guinea.

Uses *V. aegagropila* is used as human food, mainly in salads.

Properties *Valonia* C. Agardh may contain siphonoxanthin and siphonein. High concentrations of heavy metals have been recorded for rhizoids of *Valonia* spp.

Description Thalli dark green to brownish-green, coenocytic, at first attached, later often free, eventually forming masses, composed of large vesicular clavate branches, 3–13 mm × 2–4 mm. Vesicles (segments) slightly constricted at base, arranged in layers with 2–5 daughter vesicles arising from parent vesicle. Life cycle diplohaplontic and isomorphic.

Growth and development Biflagellate gametes in *V. aegagropila*, produced by transformed vesicles (gametangia) on dioecious gametophytes, fuse by isogamy. The quadriflagellate zygote soon settles and forms an isomorphic sporophyte, of which vesicles can transform into sporangia. The quadriflagellate zoospores, when released from the sporangia, settle to produce new gametophytes. Settled zygotes and zoospores first form palmate rhizoids. The large apical cell of a germling transforms into a vesicle, while the basal cell forms the primary filamentous rhizoid. From the vesicle new filamentous rhizoids as well as new vesicles arise, separated from the original vesicle by lenticular cell walls.



Valonia aegagropila C. Agardh – 1, habit; 2 & 3, portions of thallus with vesicles; 4, longitudinal section of a thallus (somewhat diagrammatic); 5, fertile gametangia; 6, biflagellate gametes with eye-spot; 7, young two-celled germling with palmate rhizoid; 8, germling with a single vesicle and several filamentous rhizoids; 9, young vesicle with filamentous rhizoids and secondary vesicles, separated from the primary vesicle by lenticular cell walls; 10, quadriflagellate zoospores with eye-spot.

Ecology *V. aegagropila* is generally found in calm and sheltered habitats such as shallow reef flats and lagoons. It is attached to rocky/solid substrate where it forms a thick crust made up of elongate clavate vesicles. Later the crust may be detached from the substrate and form one of the common components of drift, accumulated in shallow hollows on the reef flat or on shore.

Propagation and planting *V. aegagropila* is not known in phycoculture.

Harvesting *V. aegagropila* is only hand-collected.

Handling after harvest *V. aegagropila* is always used fresh. The frequently found washed up specimens have to be carefully cleaned in seawater before they can be used as food. When using freshwater to clean the alga, the vesicles may explode.

Prospects Large-scale use of *V. aegagropila* as food in the future is unlikely.

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Acronyms of organizations

- ASEAN: Association of South-East Asian Nations (Jakarta, Indonesia).
- DGIS: Directorate-General for International Cooperation of the Netherlands Ministry of Foreign Affairs (Den Haag, the Netherlands).
- FAO: Food and Agriculture Organization of the United Nations (Rome, Italy).
- FRIM: Forest Research Institute Malaysia (Kepong, Malaysia).
- IEBR: Institute of Ecology and Biological Resources (Hanoi, Vietnam).
- LIPI: Indonesian Institute of Sciences (Jakarta, Indonesia).
- NACA: Network of Aquaculture Centres in Asia-Pacific (Bangkok, Thailand).
- PCARRD: Philippine Council for Agriculture, Forestry and Natural Resources Research and Development (Los Baños, the Philippines).
- PROSEA: Plant Resources of South-East Asia (Bogor, Indonesia).
- SIAP: Seaweed Industry Association of the Philippines (Cebu City, the Philippines).
- SICEN: Seaweed Information Center (Quezon City, the Philippines).
- TISTR: Thailand Institute of Scientific and Technological Research (Bangkok, Thailand).
- UNDP: United Nations Development Programme (New York, United States).
- UNITECH: Papua New Guinea University of Technology (Lae, Papua New Guinea).
- WU (formerly WAU): Wageningen University (Wageningen, the Netherlands).

Glossary

abalone: popular name of marine gastropod mollusc of the family Haliotidae, and particularly the genus Haliotis

abaxial: on the side facing away from the axis or stem; botanically, this means on the underside of a branch or frond

acropetal: in the direction from the base toward the apex

Acropora: common genus of staghorn corals

acuminate: tapering gradually to a slender point

adelphoparasite: parasite that is closely related, phylogenetically, to the host plant; said of certain Rhodophytes

agar: a hydrophilic colloid extracted from a number of red algae and consisting of a mixture of polysaccharides, forming a strong, stable, brittle, thermo-reversible gel in aqueous solution

agaroids: non-gelling agar colloids

agarophytes: species of the Rhodophyta of which the phycocolloid agar can be produced

agarose: the neutral good-gelling fraction of agar

akinete: enlarged, highly pigmented units developed from individual vegetative cells by the accumulation of food reserves and by the thickening of cell walls including the mother cell wall; it undergoes a prolonged period of dormancy before germinating into a new plant

algalization: the process of bringing algae (mainly Cyanophytes) in the soil to promote nitrate production by these algae

alginate: polysaccharids consisting of salts and esters of alginic acid, extracted from cell walls of brown algae. Some alginates are soluble in cold water and form highly water-retentive, non-melting, thermo-irreversible, chemical gels

alginophytes: species of the Phaeophyta of which the phycocolloid alginate can be produced

aliquot: sample that is representative for the substance to be tested

allopathic: pertaining to or characteristic of allopathy (a system of therapeutics in which diseases are treated by producing a condition incompatible with or antagonistic to the condition to be cured or alleviated; also called heteropathy)

alpha carrageenan: an uncommon chemical type of refined carrageenan

alternate: a mode of branching, in which branches are placed on opposite sides of an axis, at different levels

amorphous: without significant structural organization; lacking a definite shape

amyloplast: a colourless, membraned organelle associated with the production of starch

anastomosing: plants or plant parts intermittently joining and separating or communicating by cross connections

androdioecious: on the thalli either only male gametangia occur or both male and female gametangia, occurring either mixed or with the sexes each in separate areas

androgynous: having, on the same thallus, separate areas with male and with female gametangia

angular: a form having angles

angulate: more or less angular

anisogametes: motile gametes of different sexes that differ from one another morphologically and/or behaviourally

anisogamous: relating to the union of two anisogametes

anisotomous: separated into two unequal parts (used for unequal branching)

annulate: ring-shaped or with (usually several) ring-shaped structures

anthelmintic: destructive to worms: a drug or agent that destroys worms

antheridium (plural antheridia): cell or well defined group of cells (organ) producing motile male gametes

antherozoid: male motile cell provided with flagella, and produced in antheridia; spermatozoid

anticlinal: perpendicular to the surface

antigenic: forming foreign substances which causes organisms to produce antibodies

apex (plural apices): the tip or summit of an organ

apiculate: ending abruptly in a short point

aplanospores: arrested zoospores that omit the motile stage; typically the spore wall is not fused to the wall of the vegetative cell that produced it, as in the case with an akinete

apogamy: any form of development of a diploid sporophyte from a haploid gametophyte without fertilization

appendage: a subordinate part that is appended to a major part, like laterals to a main axis

aquaculture: (commercial) culture of aquatic organisms

aquatron: apparatus to grow aquatic organisms under different and quantified environmental conditions

aragonite: one of the two forms of calcium carbonate occurring in calcified structures, forms needle-like orthorhombic crystals

arcuate: curved

articulation: a joint or a segment between successive joints

assimilator: the upright, photosynthesizing parts of some siphonaceous green algae, especially *Caulerpa* (Chlorophyta)

attenuate: gradually tapering

autospores: aplanospores that develop with the parent cell wall, as carbon copies of the parent in all respects except size; released by gelatinization of parent wall

autotrophic: applied to organisms which can synthesize organic compounds from inorganic substrates; non-parasitic

axenic culture: a 'pure' culture of an organism, containing no other organisms, not even bacteria

axil or axilla (plural axillae): the angle formed between the axis and an appendage to the axis

benthic: referring to the attached organisms of marine and aquatic environments

beta carotene: an isomere carotenoid isoprenoid polyene pigment

beta carrageenan: a form of refined carrageenan which lacks ionic sulphate groups

biflagellate: with two flagella

bifurcate: twice-forked

biseriate: arranged in two rows

blade: the flattened, expanded, foliar portion of a frond

botryoidal: like a cluster of grapes

bulbous: bulblike, with a distinct swelling at one end

bullate: blistered or puckered

caespitose: forming mats or spreading tufts

calcareous: algae with obvious calcification

calcification: deposition of calcium carbonate within cell walls or in other parts of cells

calyptra: a morphologically distinct thickening of cell wall material, often characteristically shaped, covering the apex of a trichome (Cyanophyta)

capitate: enlarged or swollen at one or both ends; shaped like a head; aggregated into a compact cluster

carpogonium (plural carpogonia): the female sex organ, consisting of a single cell (oogonium) with a drawn-out extension or process, the trichogyne (Rhodophyta)

carposporangium (plural carposporangia): single-celled structure borne on the minute, parasitic carposporophyte generation in Florideophycidae, Rhodophyta, also used for the carpospore-producing cells in gametophytes of Bangiophycidae, Rhodophyta; the reproductive products are nonmotile carpospores or zygotospores, which germinate into the tetrasporophyte generation

carpospore: a spherical uninuclear spore formed in a cystocarp, arising from the swollen tips of branched filaments resulting from the fertilization of the carpogonium (Rhodophyta)

carposporophyte: the gonimoblast filaments and the carposporangia borne on them, plus the carpogonium or the auxiliary cell producing the gonimoblast filaments, living parasitic on the gametophyte (Rhodophyta); syn. *gonimocarp*

carrageenan: a hydrophilic phycocolloid extracted from a number of red algae and consisting of a mixture of polysaccharides; forming high-quality, highly viscous, thermoreversible gels in aqueous solution

carrageenophytes: species of the Rhodophyta of which the phycocolloid carrageenan can be produced

cartilaginous: firm and elastic, not easily compressed and yet bendable

cervicorn: branching one-sided, like the horns of a deer; branching essentially dichotomous, but with one arm of each dichotomy routinely suppressed

cherry body: a spherical, bright, hyaline body found in the cortex cells of species of *Laurencia* (Rhodophyta)

chloroplast: plastids containing pigments, one of which is always chlorophyll

chromatophore: often used for a photosynthetic plastid which contains, apart from chlorophyll, also other pigments, thus then a synonym for chloroplast. The present term, however, can also be used for any cell organelle containing pigments

circinate (circinnate): coiled into a ring or partially so; rolled from the end

cladohaptera: holdfasts composed of rhizoids arising from the end of vegetative branches
clathrate: with a latticed or netlike appearance
clavate: club-shaped or thickened towards the end
claviform: club-shaped
coenocyte: a multinucleate plant body lacking partitioning crosswalls, at least in the vegetative state
coenocytic: multinucleate, but without crosswalls; composed of multinucleate cells or segments
colloid: polysaccharid substance which is able to form a gel or viscous solution
complanate: flattened, compressed
conceptacle: a superficial cavity opening to the surface, containing reproductive organs
conchosporangium (plural conchosporangia): the sporangia developed on the so-called *Conchocelis* stage of certain red algae (Bangiophycidae, Rhodophyta)
conchospores: spores formed in (or being part of) conchosporangia
conical: having the shape of a cone (cone-shaped)
contorted: twisted or bent
convolute: rolled, the margins overlapping
coriaceous: of leathery texture
corona: a crown or wreath of parts; a small crown of branch rudiments left after sterile whorls are dropped; corona superior, if above the fertile disc, and corona inferior if below (see *Acetabularia*, Chlorophyta)
cortex: the tissue of a more or less solid alga, lying beneath or including the epidermis, between this and the central tissue, the medulla or outside the medulla
cortical: belonging to or occurring in the cortex; with reference to the cortex
cortication: the secondarily formed outer covering (of cells) of a part or all of an algal thallus
crenulate: with minute rounded teeth, scallops or notches
crisp: curled
crispate: crinkled or curled
crozier-like: crooked, or hooked
cruciate: cross-shaped; referring to the red algae: a type of spore division in which the contents of a tetrasporangium are divided in two planes, at right angles to each other
crustose: crustlike in habit; an algal body growing flattened against the substrate; hard and brittle
cryopreservation: maintaining the viability of tissue or organs by storage at very low temperatures
cryptostoma (plural cryptostomata): a cavity sunken in an algal thallus but open to the surface, and bearing a bundle of phaeophycean hairs from its floor (Phaeophyta)
cryptostomate: with cryptostomata
cuboidal: approximately cubic in shape
cuneate: wedge-shaped; triangular, with the narrow end at the point of attachment
cuspidate: abruptly tipped with a sharp rigid point
cyanophage: a virus specialized to attack cyanobacteria (= blue-green algae)
cyanophyte: a cyanobacterium (= blue-green algae)
cymose: occurring in a more or less broad, flat-topped cluster, with the younger parts toward the periphery
cyst: a stage in reproduction, often a resting stage, in which a multinucleate portion of protoplasm becomes surrounded by a secreted thick enveloping membrane (Chlorophyta)
cystocarp: a gonimocarp enclosed within an envelope of tissue (pericarp)
decumbent: reclining or lying on the ground, but with the summit ascending
decussate: in alternating pairs, crossing at right angles to the next pair above or below
dentate: margin prominently toothed with the pointed teeth directed outwards
denticulate: minutely toothed
diazotrophic algae: algae that are capable to fix nitrogen
dichotomous: forked, parted by pairs
dichotomy (plural dichotomies): a paired fork of branches
dinoflagellates: a group of unicellular microalgae
dioecious: with male and female reproductive organs on separate gametophytes
diplo-haplontic: a type of life cycle with alternation of a haploid multicellular generation and a diploid multicellular generation; syn.: life cycle with alternation of generations
diploid: with two homologous sets (genomes) of chromosomes, usually written $2n$, having twice the basic chromosome number of the haploid gamete cells
diplontic: a type of life cycle in which the diploid chromosome condition is dominant, with the gametes representing the only haploid stage
disc = *disk*: a circular flat body
disciform: shaped like a disk
discoid: resembling a disk, being flat and circular
dissected: deeply divided into many slender segments
distal: situated farthest from the place of attachment
distichous: arranged in two opposite rows on either side of an axis

divaricate: extremely divergent
dorsal: pertaining to the upper or outer side (opposite to *ventral*)
dorsiventral: used of an organ with distinct front (*ventral*) and back (*dorsal*) sides
ecad: a growth form determined by ecological conditions
ecophene: see *ecad*
ectocarpoid: similar to the brown algal genus *Ectocapus* or to the family Ectocarpaceae
emarginate: notched at the tip or at the margin
endocellular: within the cell
endophyte: an organism that grows in the tissue of a living plant or alga
endophytic: growing inside an alga or a plant
endospores: minute rounded cells formed by the internal division of a parent protoplast; release of these reproductive bodies is by rupture or gelatinization of the parent cell wall (Cyanophyta)
epilithic: growing attached to a stony substrate
epipelic: growing on sand or mud
epiphyte: an alga or a plant growing on the surface of another alga or plant
epiphytic: growing on the surface of an alga or a plant
epipsammic: growing on sand grains
epispore: an external coat formed from the periplasm round the spores of certain of the higher Cryptogams or the outerside of the wall of spores of Cyanophyceae
epithelium: any distinct layer of one or more cells in thickness which bounds an internal cavity
erect: directed towards summit, not decumbent
erose: having an uneven or notched margin, as if torn
eulittoral: the zone on the shore that is alternately exposed to the air and submerged by the sea due to the tide
euryhaline: tolerant of a broad range of salinity
excrescence: an outgrowth from the surface
exospore: a spore cut off externally by a spore mother cell
eye-spot: a pigmented photoreceptor associated with motile cells
farinose: as if covered with meal
fascicle: a close cluster of parallel filaments, stems or branches
fasciculate: connected or drawn into a fascicle
fastigiate: bearing stems or branches in parallel clusters that taper to a point; when the branches are parallel and all point upward
filament: an elongated thread composed of cells attached end to end; in the blue-green algae, the living trichome plus the sheath
filamentous: threadlike
filiferous: with filamentous laterals
filiform: slender; threadlike
fimbriate: fringed
fimbricate: see *fimbriate*
flabellate: fan-shaped, dilated in a wedge-shape, sometimes plaited (folded)
flagellate: bearing flagella
flagelliform: whiplike, and usually tapering
flagellum (plural flagella): a fine, fibrate, whiplike process of protoplasm by which motile cells (often zoids) can move
flexuous: zigzag; bent alternately in opposite directions
floccose: covered with dense hairs
foliose: flat and expanded like a leaf; bearing leaf-like structures
foveolate: with small pits
frond: a flat, leaf-like, photosynthesizing part of an alga
frondose: frond-like
furcate: forked
furcipate: beset with forked structures
fusiform: spindle-shaped; tapering towards each end from a swollen centre
galactan: a polysaccharide; a polymer of galactose
gametangium (plural gametangia): a cell or a structure from or in which gametes are formed
gamete: a sexual reproductive cell, with a single set of chromosomes; a gamete usually fuses with another to form a zygote
gametophyte: a plant which is genetically constituted to produce gametes; a plant from the 'sexual' phase of alternation of generations
gametophytic: developed on or from (a part of) a gametophyte or a designation for a structure on a gametophyte or a generation formed by the gametophytes
ganglia (plural of ganglion): distinctive knots of interconnected cells, typically in the medulla of certain Rhodophytes
ganglionic: part of or arising from a ganglion
gel: semi-solid colloidal solution or jelly
gelation: the action or process of freezing; also used as a synonym of 'gelling'
gelling, gel formation, gelification, to gel: the formation of a gel from a sol; solidification; forming a gel when the solution is cooled (agar), when monovalent ions are added (carrageenan) or when bivalent cations are added (alginate)
gel temperature or gelling temperature: the temperature at which the liquid colloidal solution forms a gel

geniculate: with uncalcified or flexible joints between calcified segments
genome: the sum total of the genes contained in the nucleus or nucleoid; a complete haploid set of chromosomes as contained within the gamete and corresponding to the haploid chromosome number of the species
germling: a juvenile plant, which may or may not show its mature form
glabrous: devoid of hairs
globose: spherical or nearly so
gonimoblast: a microscopic carposporangium-producing filament growing from the carpogonium or from an auxiliary cell (Rhodophyta)
gonimocarp: the collective name for the structure formed by a group of gonimoblasts
gonimolobes: the germinal tufts of gonimoblasts
gregarious: clustered or grouped closely together
guar gum: a polysaccharid substance from the leguminous herb *Cyamopsis tetragonoloba* (L.) Taub.
gum: colloidal polysaccharid substance of plant origin
halotolerant: tolerating salt in brackish or marine environments
haploid: having a single set (genome) of chromosomes in a cell or an individual, corresponding to the chromosome number (n) in a gamete
haplontic: a type of life cycle involving a multicellular haploid gametophyte stage, alternating with a unicellular diploid zygote
hapteron (plural haptera): a branched root-like or unbranched disc-like attachment organ
helical: shaped like a helix
helicoidal: spirally twisted
hemiphyllous: with leaf-like appendages without a midrib or in which the midrib is not apparent or continuous
hemispherical: in the shape of half a sphere or globe
hermaphrodite: an individual bearing both male and female reproductive structures
heterocyst: a special cell found in some blue-green algae; it is usually glassy in appearance, and large compared with vegetative cells; nitrogen is fixed in heterocysts
heterocystous: with heterocysts (Cyanophyta)
heteromorphic: displaying two different life forms, each with a different habit or appearance
heterotrichous: the type of filamentous growth that displays both a prostrate and an erect system
heterotrophic: applied to organisms requiring complex organic compounds for their metabolic processes
holdfast: a cell or group of cells modified to act as an organ of attachment (= *hapteron*)
holocarpic: the process in which an entire plant is transformed into a gametangium
homoplastidic: possessing chloroplasts but not amyloplasts (in coenocytic green algae; opposite *heteroplastidic*)
hooked: like a slender process, curved or bent back at the tip
hormocyst: a short row of cells (hormogone) packed with food reserves and surrounded by a thick wall consisting of a common, condensed sheath (Cyanophyta)
hormogonium, hormogone (plural hormogonia): a short length of a trichome separated by the death of one or more cells, it serves in vegetative reproduction and often performs active gliding movements (Cyanophyta)
hyaline: transparent, translucent, colourless, and glassy in appearance
hydrocolloid: gel-forming polysaccharid produced from the cell-walls of waterplants, usually being seaweeds
hydrophylic: having a strong affinity for water
hypha (plural hyphae): a threadlike filament, often occurring inside a thallus
hysteresis: the difference between gel temperature and the often much higher sol temperature (in agar only)
imbricate: overlapping, like shingles on a roof
indeterminate: capable of unlimited growth
indurated: becoming firmer or harder
indusium (plural indusia): a membrane covering superficial reproductive structures
inflated: swollen
intercalary: interpolated
interdichotomal: between two successive dichotomies
interdichotomies: the distance between two successive dichotomies
internode: in a filament, the part of a cell between two end walls; the space between two joints or nodes, or points of attachment; an articulation
intertidal: occuring between high and low tide lines
intricate: entangled
involucre: sterile filamentous or pseudoparenchymatous envelope
involute: rolled or coiled inward
iota carrageenan: a form of refined carrageenan with distinct precipitation in KCl
iridescent: glowing or shining, reflecting an interplay or rainbow-like colours as when seen from different angles

isodiametric: having equal diameters; with sides of equal length
isogametes: motile gametes that are phenotypically but not genetically similar
isogamous: referring to those algae which produce isogametes
isogamy: the fusion (copulation) of isogametes
isomorphic: of like appearance; displaying two generations with similar form or appearance
kappa carrageenan: a form of refined carrageenan with a rather brittle gel characterized by syneresis
laciniate: slashed, cut into narrow lobes
lacunose: showing perforations or depressions
lambda carrageenan: a form of refined carrageenan which dissolves in cold water and does not form a gel
lamellate: made up of layers, joined together
lamellose: see *lamellate*
lanceolate: lance-shaped; much longer than broad, being widest at the middle and tapering at both ends
lateral: on or at a side; a side branch
lenticular: shaped like a double-convex lens
life cycle (also life history): the sequence of morphological and nuclear phases of an alga
ligulate: possessing an elongated, flattened, strap-shaped structure or ligule
linear: long and narrow with parallel sides
lobate: having large, rounded divisions of the margin
locule: compartment
locust bean gum or carob seed gum: a polysaccharid substance produced from the pulp around the seeds in the pods of the leguminous tree *Ceratonia siliqua* L.
lubricous: smooth; slippery
lumen: a central cavity, especially the space left in a cell after spores or gametes have escaped
lutein: a xanthophyll which is especially common in green algae
lysing cells: cells that desintegrate to encourage fragmentation of trichomes (Cyanophyta)
macroalgae: multicellular algae that can be seen by the unaided eye
macrogametes (= megagametes): the larger anisogametes of algae, presumably female
macrospores: see megaspores
macrothalli: multicellular thalli that are larger than a few cm; the largest generation in a heteromorphic life cycle
mamillate: provided with small protuberances or projections
mannan: a polysaccharid, a polymer of mannose; a hemicellulose
mannitol: a polyhydroxylalcohol derived from the hexose monosaccharide mannose; a somewhat treacle-like sweet substance
marginate: furnished with a margin of distinct character
matrix: enveloping or surrounding material; in some cases limey, and in others mucilaginous
medulla: a differentiated central core of tissue surrounded by the cortex; the pith
megasporangium (plural megasporangia): a sporangium which produces megaspores
megaspores: the larger spores of heterosporic vascular Cryptogams (opposite: *microspores*)
megasporocarp: the structure formed around a megasporangium, finally containing the single perfect megaspore (*Azolla*)
meiogametes: gametes formed by meiosis
meiosis: nuclear division in which the diploid chromosome number is reduced to half that of the parent cell to give the haploid number
meiospore: a spore formed by meiosis, bearing a single ($1n$) set of chromosomes, thus being haploid
membranous, membranaceous: thin and semi-transparent, like a fine membrane
meristem: a tissue in which the cell or cells divide frequently
mesophilic: tolerating water temperatures that are not cold nor extremely high; with optimum growth at around 25°C
microalgae: microscopic, often unicellular, algae
microgametes: the smaller and male anisogametes of algae
microsporangium (plural microsporangia): a sporangium which produces microspores
microspores: the small spores of the heterosporic vascular Cryptogams
microsporocarp: the structure in which the microsporangia are produced (*Azolla*)
microthalli: few-celled thalli, usually only a few mm long; the smallest generation in a heteromorphic life cycle
mitosis: the process of nuclear division in which the daughter cells receive the same number and identical chromosomes ($2n$) as the parent cell
mitospore: a spore formed through mitosis
mixotrophic: half heterotrophic and half autotrophic, said of growth in culture (microalgae)
moniliform: necklace-shaped, like beads on a string
monoecious: with male and female reproductive organs on the same gametophyte
monosiphonous: with a single row of cells, formed of a single tube or filament, without longitudinal walls

monosporangium (plural monosporangia): a sporangium in which only one spore is produced
monospore: a spore that is produced single by a monosporangium
monostromatic: composed of a single layer of cells
morphotype: separate growth form of an algal species, often only slightly differing from the normal habit and not genetically different
mucilage: a gelatinous substance that is similar to gum but that swells in water without dissolving and forms a slimy mass
mucilaginous: slimy, slippery
mucoprotein: glycoprotein, especially occurring in the sheaths of trichomes (Cyanophyta)
mucronate: ending abruptly in a short stiff point
multiseriate: with more than one row of cells
muricate: rough, with short and hard tubercular excrescences
nannocytes: dwarf endospores formed by cell cleavage without subsequent cell enlargement (Cyanophyta)
necridium (plural necridia): a degenerated or dead cell, sometimes known as a separation disc, which encourages fragmentation of trichomes (Cyanophyta)
nemathecium (plural nemathecia): a wart-like projection, bearing reproductive bodies (Rhodophyta)
node: the point or area of an axis where branching or leafing occurs; in a filament, the location of an end wall; a joint in a distinctly segmented axis
nucleus (plural nuclei): an organized proteid body of complex substance in the protoplasm of cells and containing the chromosomes
nutraceuticals: health food; food with therapeutic benefits
oblong: longer than broad, with the sides parallel or almost so
obovate: reverse of ovate, broader at the distal end
obpyramidal: inversely pyramid-shaped
obpyriform: inversely pear-shaped, with broader end outermost
obtuse: blunt or rounded at the end
oligotrophic: nutrient poor or with low primary production (in water bodies)
oogamy: the reproductive condition in which there is fusion of a small male gamete with a larger non-motile female gamete (egg)
oogonium (plural oogonia): a cell which is a female sexual organ, containing one or more oospheres or eggs
oosphere: a naked and nucleate mass of protoplasm, which, after coalescence with the sperm-nucleus, develops into a zygote
orbicular: flat with a more or less circular outline
organ: a part of an organism, adapted for a special vital function (gametangium, sporangium, air bladder, etc.)
organelle: a membraned subcellular and morphologically distinct unit specialized for a particular function (chloroplast, flagellum, etc.)
orifice: an opening by which spores, etc., escape
orthorhombic: having three unequal axes at right angles to each other
ostiolate: with pore-like opening
ostiole: a pore-like opening of a conceptacle or pericarp
ovate: egg-shaped in outline or in section
ovoid: a solid object which is egg-shaped (ovate in section)
ovum (plural ova): oosphere; egg
palmate: radiating fan-like or finger-like from a point
panicle: a loose, irregularly branched cluster
paniculate: growing or arranged in loose, irregularly branched clusters
papillae: soft superficial glands or protuberances, often wart-like
papillose: covered with minute nipple-like protuberances
papyraceous: papery, like paper
paraphysis (plural paraphyses): a sterile, branched or unbranched, hair- like filament borne next to a reproductive structure
parasite: an organism that lives and grows at the expense of a host organism
parietal: positioned against the inner wall of a cell
parthenogamete: a gamete which develops without pairing
parthenogenesis: a form of apogamy in which a gamete develops into the normal product of fertilization without a preceding sexual act
parthenogenetically: applied to a method of development in which a gamete germinates without fertilization
patent: spreading out
pedicel: a small stem or stalk supporting a specialized structure
pedicellate: borne on a pedicel; stalked
pelagic: living unattached in the open sea
pellicle: resembling, but no equivalent to, a firm cell wall; an outer bounding membrane
peltate: a foliar organ with its 'stalk' attaching somewhere near the centre, and away from the margin; shield-like
penultimate: next to the last
percurrent: running through the entire individual; extending through the entire length

perennial: living longer than one year
periaxial cell: *pericentral cell*
pericarp: the urn-shaped sterile envelop surrounding a gonimocarp in a cystocarp
pericentral cell: one of a ring of cells, cut off by periclinal walls from and surrounding the central (axial) cell (Rhodophyta); algae with an axial cell row and pericentral/periaxal cells are termed polysiphonous
periclinal: parallel to the surface
peripherohaptera: haptera near the circumference of a body
periphyton algae: minute algae, often microscopic, associated with but not necessarily attached to the stems or culms of larger aquatic plants, often in such masses as to be readily visible
phototrophic: applied to organisms requiring light for autotrophic metabolic processes
phototropic: applied to organisms capable to use light as their orienting stimulus
phycobiliproteins: accessory pigments which are covalently attached to polypeptides to form subunit components of proteins
phycocolloid: gels or gums produced from algal products
phycoculture: general term for farming of algae
pinnate: furnished with distichous branchlets; arranged like the plumes of a feather
pinnule: a secondary or minor part of a bipinnate, or of a pinnately compound frond
plankton: passively floating or weekly swimming minute animal and algal life of a body of water
planktonic: in plankton; living as plankton
plastid: any one of several formed organelles, double-membraned bodies in the cytoplasm of a cell; they are usually pigmented (chloroplast), but not always (amyloplast)
pleomorphic: relating to the occurrence of more than one morphologically different stage in the life cycle of a species
plumose: featherlike
plurilocular: consisting of many loculi; many-celled (Phaeophyta)
pneumatophores: special roots, used for respiration in mangroves
polygonal: with many angles
polyhedral: with many sides
polyploid: with more than two sets of chromosomes in the somatic cells, e.g. triploid (3 sets), tetraploid (4), pentaploid (5), hexaploid (6), heptaploid (7), octoploid (8), etc.
polysiphonous: consisting of a finite number of cells (pericentrals) cut off by periclinal walls from axial cells and surrounding each cell in the axial cell row
pore: small opening
pression walls: special cell walls formed when coenocytic thalli are pressed together before being fragmented; this is a protective response (*Caulerpa*)
procarp: term used to define the carpogonium and auxiliary cell(s) together, when they are members of a common branch system (Rhodophyta)
procumbent: trailing along the substrate but not secured by rhizoids, haptera, or the like
prokaryotic: organisms without nuclei and organelles in their cells
proliferation: a new part developed on a frond, and especially on a flat blade, by vegetative cell division; an outgrowth from a surface or from a margin; offshoot
propagule: a part of an algae that becomes detached and grows into a new individual; often in the form of a loosely attached and distinctively shaped branch; a reproductive portion of a frond which is not a spore
prostrate: lying flat on the substrate
protonema: a juvenile stage in the life cycle, often resembling a filament or expanded vesicle
protoplast: the living contents of a cell, including nuclear material
protuberance: projection, an extension beyond the normal surface
protuberant: projecting outward
punctiform: in the form of a point; pointed
pyrenoid: a refractile cytoplasmic body generally associated with the chloroplasts, and involved with the production or storage of starch or other reserve polysaccharides
pyriform: pear-shaped, with the broad end toward the base
quadriflagellate: provided with four flagella
raceme: a cluster of reproductive structures which mature inwardly, the youngest structures being in the centre or at the top of the cluster
racemose: arranged like a raceme
radial: along the radius; radiating; developing uniformly around a central axis
ramification: branching; the mode of arrangement of branches
ramulus (plural ramuli): a small or secondary branch; a branchlet
receptacle: the enlarged fruiting portion of a thallus, bearing sunken cavities (conceptacles in Phaeophyta)
recurved: bent or curved downward or backward
reniform: kidney-shaped
repent: creeping along the substrate

reticulate: having, or appearing as, a network
reticulum: a network
rheological properties: properties of gels in relation with flow and deformation
rhizines: filaments composed of slender, thick-walled cells which penetrate the medulla (Rhodophyta)
rhizoid: a one–to many-celled filament or cell extension, serving mainly as an organ of attachment and growing downward
rhizophore: an oblique adventitious root as in mangrove trees
rhodophyte: belonging to the Rhodophyta; red alga
rosette: a cluster of flattened thallus parts or other organs in a circular form
rostrate: beaked
ruffled: with a pronounced wavy margin
saccate: pouched; balloon-shaped
saprophytic: relating to a saprophyte, being an organism that lives on and uses dead organic material
scuba diving: diving with a self-contained underwater breathing apparatus
scutate: shaped like a shield
seagrass: marine seedplants (Angiosperms, Spermatophyta)
seaweed: macroalga that lives in the sea; marine macroalga
seaweed flour, seaweed meal: dried and milled seaweed
secund: arranged along one side only
segment: one of the divisions into which an organ may be cleft; section, joint or articulation
senescence: advancing in age
septate: with partitions or dividing walls
septum (plural septa): a partition or dividing wall
seriate: disposed in series of rows, either transverse or longitudinal
serrate: toothed like the edge of a saw, with regular pointed teeth pointing forwards
sinuose: with a deep wavy margin
siphonous: referring to a tubular, multinucleate thallus in which there are no crosswalls in the normal vegetative state
site fertility hypothesis: a method to explain the short-time, almost random changes in phycoculture in natural habitats
sol: liquid solution or suspension of a colloid
sol temperature or gel melting temperature: where the gel becomes a liquid solution again (agar)
sorbitol: a complex alcohol (hexitol); a somewhat treacle-like sweet substance
sorus (plural sori): a group or cluster of reproductive organs, appearing as superficial patches, or occurring in specialized structures (nemathecia or conceptacles)
spatulate: spoon-shaped
spermatangium (plural spermatangia): the male sex organ producing the spermatia (Rhodophyta)
spermatium (plural spermatia): the near colourless non-flagellated male gamete (Rhodophyta)
spermatozoid (= antherozoid): a flagellate male gamete, produced in an antheridium
spine: a sharp process
spinose, spinous: having spines
spinulose: with small spines
sporangium (plural sporangia): a cell or sac in which spores are produced
spore: a reproductive product, unicellular or consisting of a few cells, with or without a wall, and with or without motility. Spores are specialized for propagation and are capable, without fusion with any other cell, of growing into a new plant; spores may be the product of mitosis (mitospores) or of meiosis (meiospores)
sporeling: germling developing from a spore; very young individual
sporophyte: generation or phase of an algal life cycle, alternating with the gametophyte generation and producing meiospores
starch: a storage polysaccharide, composed of glucose residues; the photosynthetic reserve of green plants, including green algae
stellate: star-shaped
stenohaline: tolerant only for a narrow range of salinity
stichidium (plural stichidia): an inflated, often mucilaginous, specialized branch of distinctive shape, bearing several tetrasporangia (Rhodophyta)
stilt root: an oblique adventitious root as in mangrove trees
stipe: a stalk; the basal, erect, stem-like portion of a thallus
stipitate: borne on a stipe or short stalk
stolon: a horizontal runner, or stem-like organ, usually giving rise at intervals to upright organs and descending rhizoids
stoloniferous: bearing a stolon or stolons
striate: marked with fine longitudinal parallel lines, as grooves or ridges
stupose: towlike, with tufts of long hairs; felted, fibrous, matted
sub-: prefix, under or below, in compounds usually implies an approach to the condition designated, somewhat, or slightly
subclavate: somewhat club-shaped

subflabellate: somewhat like an expanded fan
sublittoral zone: benthic or bottom region of the sea, below the lowest tide level
subterrestrial: underground
suprabasal cell: the cell immediately above the basal or holdfast cell
symbiont: an individual living in symbiosis with another organism
symbiosis: the living together, in a very close association, of dissimilar organisms, with benefit to one only, or to both
synaeresis: release of interstitial water in gels, either spontaneous or through pressure
synergism: cooperative action of discrete compounds, together resulting in a greater effect
tenaculum (plural tenacula): small interconnecting pads or branchlets developed adventitiously, and specialized for attachment to a substrate or to another axis of a branched thallus. Similar to *hapteron*, but generally not basal in origin
terete: cylindrical; circular in transverse section
terrestrial: on land
tetrahedral: having or made up of four sides; also used to describe a type of cell division within a tetrasporangium when only three spores can be seen in a view
tetrasporangium (plural tetrasporangia): reproductive unicellular organs producing four haploid spores by meiosis
tetraspore: a spore formed by the division of the spore mother-cell into four parts
tetrasporelings: germlings from tetraspores
tetrasporophyte: the diploid generation that produces tetraspores by meiotic division in a tetrasporangium (Rhodophyta)
tetratomous: dividing or branching into four more or less equal parts
thallus (plural thalli): a relatively undifferentiated multicellular body that is not divided into true roots, stems and leaves; commonly used to refer to the plant body of any alga
thermophilic: growing best at high temperatures
thylakoid: a flat, disc-like vesicle, bounded on each side by plasma membranes and containing photosynthetic segments
thylle: the usually dark-coloured content of a living cell filling (part of) the lumen of a neighbouring cell by entering it through a pit connection (in *Eucheuma* and *Kappaphycus*, Rhodophyta)
tortuose: twisted or bent
torulose: cylindric, with swollen portions at intervals, somewhat moniliform
trabeculum (plural trabeculae): one of the small anastomosing projections of wall material that transverse the cytoplasm and central vacuole (only in *Caulerpa*)
translucent: permitting the passage of light, but not sight
trichoblast: a filamentous lateral outgrowth, resembling a tuft of hairs and consisting of a single row of unpigmented cells, usually much branched, borne on and derived from the surface layer of a thallus (Rhodophyta)
trichogyne: the hairlike, receptive, apical prolongation of a carpogonium (Rhodophyta), with which a spermatium fuses at the beginning of fertilization
trichome: a thread of cells without the investing sheath (Cyanophyta); any sterile filamentous outgrowth from the surface of a thallus (other algal divisions)
trichotomous: dividing or branching into three more or less equal parts
trigonous: three-angled, with plane faces
triphasic: with three phases or generations (life cycle in Rhodophyta)
triquetrous: three-sided, often with the sides channeled
truncate: appearing as if cut off at the end, flat at the top
tuberculate: covered with small excrescenses
tubular: apparently a cylindrical figure and hollow
turbinate: top-shaped or obconical
turgid: swollen, but not with air
undulate: with wavy margins
unilocular: term used for sporangia with one chamber not divided into separate compartments, but which produce numerous spores in the single cavity of the sporangium; reproductive spores are formed by meiotic division, and may be flagellated or not (Phaeophyta)
uniseriate: arranged in a single linear row of cells
unizoid: zoid formed by an unilocular zoidangium
utricle: the swollen end of a filament forming a cortical stratum at the surface; a small sac-shaped organ
vacuole: a space within the lumen of a cell filled with cell sap, it is bound by a plasma membrane, the tonoplast, and is surrounded by cytoplasm
ventral: pertaining to the lower or inner side (opposite to *dorsal*)
vermiform: worm-shaped
vermifuge: an agent expelling worms or intestinal animal parasites; an anthelmintic
verrucose: warty

verticil: a whorl, or circular arrangement of similar parts round an axis
verticillate: whorled
vesicle: a small, bladder-like sac filled with gas; a minute sac-like organelle within the cytoplasm
vesicular: like or in the form of a vesicle
xanthophyll: a photosynthetic yellow to brown assessory pigment
zoid: a flagellated reproductive cell, either gamete or spore
zoidangium (plural zoidangia): any cell in which zoids are formed
zonate: division of the contents of a tetrasporangium (Rhodophyta) by three parallel planes, so that the spores appear in a linear series; in Phaeophyta thallus with concentric markings, dividing it into zones
zooplankton: animal plankton
zoosporangium (plural zoosporangia): any cell in which zoospores are formed
zoospore: a naked, motile, non-gametic reproductive cell bearing flagella; a zoid that may be a mitospore or a meiospore
zygocarpic: when leaves, vesicles and receptacular branches are closely associated (Phaeophyceae: *Sargassum*)
zygospore: a thick-walled resistant spore resulting from the union of gametes, a thick-walled zygote
zygote: a fertilized egg; a diploid cell resulting from the union of two gametes
zygotosporangium (plural zygotosporangia): a fertilized cell which separates into many diploid spores (in *Porphyra*, Rhodophyta)
zygotospore: spore from a zygotosporangium (*Porphyra*)

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Ganonema farinosum: Trono, G.C., 1986. Philippine seaweeds. In: Guide to Philippine flora and fauna. Vol. 1. Natural Resources Management Center, Ministry of Natural Resources and University of the Philippines. Goodwill Bookstore, Manila, The Philippines. Fig. 72, p. 264 (habit); Womersley, H.B.S., 1994. The marine benthic flora of Southern Australia. Part 3A. Rhodophyta. Flora of Australia, Supplementary Series 1. Australian Biological Resources Study, Canberra, Australia. Fig. 25, p. 95 (details of carpogonium and carposporophyte); Taylor, W.R., 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Studies, Scientific Series. University of Michigan Press, Ann Arbor, Michigan, United States. Vol. 21: Plate 45, fig. 2, p. 753 (spermatangial branch). Redrawn and adapted by P. Verheij-Hayes.

Gelidiella acerosa: Westphal, E. & Jansen, P.C.M. (Editors), 1989. Plant resources of South-East Asia. A selection. Pudoc, Wageningen, The Netherlands. Fig. on p. 135. Redrawn and adapted by P. Verheij-Hayes.

Gelidium: Hatta, M.A. & Prud'homme van Reine, W.F., 1991. A taxonomic revision of Indonesian Gelidiales (Rhodophyta). Blumea 35: Fig. 8, p. 365 (details of G. pusillum var. pusillum); Santelices, B., 1988. Taxonomic studies on Chinese Gelidiales (Rhodophyta). In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 2. California Sea Grant College Program, La Jolla, United States. Fig. 3, p. 95 (cystocarpic G. amansii), Fig. 5, p. 97 (habit G. crinale), Fig. 9, p. 102 (habit G. pusillum); Santelices, B., 1994. A reassessment of the taxonomic status of Gelidium amansii (Lamouroux) Lamouroux. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 4. California Sea Grant College Program, La Jolla, United States. Fig. 6, p. 42 (tetrasporic thallus of G. amansii). Redrawn and adapted by P. Verheij-Hayes.

Gelidium spinosum: Hatta, A.M., original drawings (habit, vegetative branch); Hatta, M.A. & Prud'homme van Reine, W.F., 1991. A taxonomic revision of Indonesian Gelidiales (Rhodophyta). Blumea 35: Fig. 7, p. 362 (fertile thallus and all details). Redrawn and adapted by P. Verheij-Hayes.

Gracilaria: Chang, C.F. & Xia, B.M., 1963. Polycavernosa, a new genus of the Gracilariaceae. Studia Marina Sinica 3: Plate 1, p. 127 (spermatangia of G. edulis – named Polycavernosa fastigiata); Chang, C.F. & Xia, B.M., 1964. A comparative study of Gracilaria foliifera (Forssk.) Børgs. and Gracilaria textorii (Suring.) De Toni. Acta Botanica Sinica 12: Plate 1 (G. textorii: spermatangia, sections of cystocarp, thallus and tetrasporangia); Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Fig. 15, p. 26 (G. arcuata, habit, cystocarp), Fig. 13, p. 53 (habit G. gigas); Yamamoto, H. & Trono, G.C., 1994. Two new species of Gracilaria from the Philippines. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 4. California Sea Grant College Program, La Jolla, United States. Figs. 7 & 8, p. 98 (spermatangia of G. manilaensis). Redrawn and adapted by P. Verheij-Hayes.

Gracilaria blodgetii: Chang, J.F. & Xia, B.M., 1976. Studies on Chinese species of Gracilaria. Studia Marina Sinica 12: Fig. 28, p. 129 (habit), fig. 29, p. 130 (cross-section of thallus, sections of tetrasporophyte and male gametophyte), fig. 30, p. 131 (cystocarp, pericarp). Redrawn and adapted by P. Verheij-Hayes.

Gracilaria changii: Original drawings of the authors Phang, S.-M. & Lewmanomont, K. Redrawn and adapted by P. Verheij-Hayes.

Gracilaria edulis: Original drawings of the authors Phang, S.-M. & Lewmanomont, K. (habit, cross-section of thallus); Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Fig. 27, p. 46 (all other drawings). Redrawn and adapted by P. Verheij-Hayes.

Gracilaria eucheumatoides: Trono, G.C. & Ganzon-Fortes, E.T., 1980. An illustrated seaweed flora of Calatagan, Batangas, Philippines. University of the Philippines Marine Science Center & Filipinas Foundation, Manila, The Philippines. Fig. on p. 91 (habit); Chang, C.F. & Xia, B.M., 1976. Studies on Chinese species of Gracilaria. Studia Marina Sinica 12: Figs. 32 & 33, p. 134 (all other drawings). Redrawn and adapted by P. Verheij-Hayes.

Gracilaria firma: Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Plate 3, fig. 2, no page number (habit), fig. 30, p. 51 (all other drawings). Redrawn and adapted by P. Verheij-Hayes.

Gracilaria fisheri: Original drawing of the authors Lewmanomont, K. & Phang, S.-M. Redrawn and adapted by P. Verheij-Hayes.

Gracilaria salicornia: Trono, G.C. & Ganzon-Fortes, E.T., 1988. Philippine seaweeds. National Bookstore, Manila, The Philippines. Fig. 121, p. 172 (habits); Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Fig. 40, p. 67 (sections of thallus and tetrasporophyte), fig. 40a, p. 68 (sections of cystocarps and spermatangia); *Congracilaria babae* is in an original drawing of Phang, S.-M. & Lewmanomont, K. Redrawn and adapted by P. Verheij-Hayes.

Gracilaria tenuistipitata var. *liui*: Zhang, J. & Xia, B., 1988. On two new Gracilaria (Gigartinales, Rhodophyta) from South China. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds. Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 2. California Sea Grant College Program, La Jolla, United States. Fig. 1, p. 132 (habit), figs. 3–6, p. 133 (all other drawings). Redrawn and adapted by P. Verheij-Hayes.

Gracilariopsis heteroclada: Rabanal, S.F., Azanza, R. & Hurtado-Ponce, A.Q., 1997. Laboratory manipulation of Gracilariopsis bailinae Zhang et Xia (Gracilariales, Rhodophyta). Botanica Marina 40: fig. 13, p. 553 (habit); Zhang, J. & Xia, B., 1988. On two new Gracilaria (Gigartinales, Rhodophyta) from South China. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 2. California Sea Grant College Program, La Jolla, United States. Figs. 11, 12, 13, 15, 17, p. 135 (as Gracilaria heteroclada) (all other drawings). Redrawn and adapted by P. Verheij-Hayes.

Gracilariopsis lemaneiformis: Abbott, I.A. & Hollenberg, C.J., 1976. Marine algae of California. Stanford University Press, Stanford, California, United States. Fig. 433, p. 497 (habit, as Gracilaria sjoestedtii); Dawson, E.Y., 1949. Studies of northeast Pacific Gracilariaceae. Allan Hancock Foundation Publications, Occasional Paper 7: plate 16, p. 87 (portions of branches and longitudinal-section of thallus, as Gracilariopsis sjoestedtii), plate 17, p. 89 (spermatangia, as Gracilariopsis sjoestedtii); Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Fig. 34, p. 57 (cross-section of thallus, sections of cystocarps and tetrasporophytes, as Gracilaria lemaneiformis). Redrawn and adapted by P. Verheij-Hayes.

Grateloupia filicina: Stegenga, H., Bolton, J.J. & Anderson, R.J., 1997. Seaweeds of the South African west coast. Contributions from the Bolus Herbarium 18: Plate 95, p. 290. Redrawn and adapted by P. Verheij-Hayes.

Halimeda: Hillis-Colinvaux, L., 1980. Ecology and taxonomy of Halimeda: primary producer of coral reefs. Advances in Marine Biology 17: fig. 17, p. 38 (all surface views of utricles), fig. 20, p. 50 (all sagittal-sections); Trono, G.C. & Ganzon-Fortes, E.T., 1988. Philippine seaweeds. National Bookstore, Manila, The Philippines. Fig. 30, p. 51 (habit H. cylindracea), fig. 33, p. 55 (habit H. incrassata), fig. 34a, p. 56 (habit H. macroloba), fig. 36, p. 58 (habit H. opuntia). Redrawn and adapted by P. Verheij-Hayes.

Halymenia: Trono, G.C., 1998. Seaweeds. In: Carpenter, K.E. & Niem, V.H. (Editors): The living marine resources of the Western Central Pacific. Vol. 1. Seaweeds, corals, bivalves and gastropods. Food and Agriculture Organization of the United Nations, Rome, Italy. p. 80 (habit H. dilatata), p. 81 (habit H. durvillei); Xia, B. & Wang, Y., 1999. Taxonomic studies on Halymenia (Halymeniaceae, Halymeniales, Rhodophyta) from China. In: In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 7. California Sea Grant College Program, La Jolla, United States. Figs. 2 & 3, p. 174 (H. dilatata, cross-section of a frond, cross-section spermatangial sorus), figs. 5 & 6, p. 175 (H. maculata, cross-section frond, cross-section tetrasporophyte). Redrawn and adapted by P. Verheij-Hayes.

Hormophysa cuneiformis: Mairh, O.P. & Krishnamurthy, V., 1970. Some observations on the morphology and development of Hormophysa triquetra (C. Ag.) Kütz. Botanica Marina 13: figs. 1–11, p. 38 (holdfast, branches, sections of vegetative parts); Papenfuss, G.F., 1967. The history, morphology and taxonomy of Hormophysa (Fucales: Cystoseiraceae). Phytomorphology 17: fig. 4, p. 44 (detail of conceptacle); Trono, G.C. & Ganzon-Fortes, E.T., 1988. Philippine seaweeds. National Bookstore, Manila, The Philippines. Fig. 72B, p. 102 (apical portion of thallus); Womersley, H.B.S., 1987. The marine benthic flora of Southern Australia. Part 2. Handbook of the flora and fauna of South Australia. Adelaide, Australia. Fig. 131, p. 365 (sections of a fertile branch). Redrawn and adapted by P. Verheij-Hayes.

Hydroclathrus: Hori, T. (Editor), 1993. An illustrated atlas of the life history of algae. Vol. 2. Brown and red algae. Uchida Rokakuho Publishing Company, Tokyo, Japan. Plate 29, p. 58 (H. clathratus: cross-section clathrate thallus, prostrate microthallus, zoids); Trono, G.C. & Ganzon-Fortes, E.T., 1980. An illustrated seaweed flora of Calatagan, Batangas, Philippines. University of the Philippines Marine Science Center & Filipinas Foundation, Manila, The Philippines. Fig. on p. 45 (habit H. clathratus); Tseng, C.K., 1983. Common seaweeds of China. Science Press, Beijing, China. Plate 94, fig. 3, p. 187 (habit H. tenuis); Womersley, H.B.S., 1987. The marine benthic flora of Southern Australia. Part 2. Handbook of the flora and fauna of

South Australia. Adelaide, Australia. Fig. 110A, p. 305 (cross-section of inrolled thallus). Redrawn and adapted by P. Verheij-Hayes.

Hypnea: Xia, B. & Wang, Y., 1997. Some species in the genus Hypnea (Gigartinales, Rhodophyta) from China. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 6. California Sea Grant College Program, La Jolla, United States. Figs. 4 & 5, p. 195 (H. boergesenii), fig. 7, p. 196 (H. spinella, as H. cervicornis J. Agardh), figs. 12 & 13, p. 198 (H. charoides), figs. 36, 37 & 38, p. 203 (H. pannosa). Redrawn and adapted by P. Verheij-Hayes.

Kappaphycus alvarezii: Ganzon-Fortes, E., 1990. Taxonomy of the farmed Philippine Euchema: what's in a name? SICEN Newsletter 1(1): fig. 2, p. 3 (habit); Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Fig. 74, p. 126 (sections). Redrawn and adapted by P. Verheij-Hayes.

Kappaphycus cottonii: Trono, G.C. & Ganzon-Fortes, E.T., 1988. Philippine seaweeds. National Bookstore, Manila, The Philippines. Fig. 110A, p. 156 (habit); Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Fig. 75, p. 128 (sections). Redrawn and adapted by P. Verheij-Hayes.

Kappaphycus striatus: Weber-van Bosse, A., 1928. Liste des algues du Siboga [List of algae of Siboga]. Siboga-expeditie 59d: fig. 171, p. 424 (portion of an old branch from which new young ones develop); Xia, B. & Zhang, J., 1999. Flora algarum marinarum sinicarum, vol. 2, Rhodophyta, 5. Academiae Sinicae Edita, Beijing, China. Fig. 76, p. 129 (sections). Redrawn and adapted by P. Verheij-Hayes.

Laurencia: Ganzon-Fortes, E.T., 1982. Laurencia tronoi (Rhodophyta: Ceramiales), a new species from Calatagan, Batangas, Philippines. Kalikasan 11: Fig. 1, p. 407 (L. tronoi); Saito, Y., 1965. Morphology of the genus Laurencia of Japan. 2. Bulletin of the Faculty of Fisheries, Hokkaido University 15: Plate 5, fig. 5 (L. okamurae); Saito, Y., 1982. Morphology of British Laurencia (Rhodophyta). Phycologia 21: Fig. 7 & 8, p.301 (L. obtusa); Trono, G.C., 1986. Philippine seaweeds. In: Guide to Philippine flora and fauna. Vol. 1. Natural Resources Management Center, Ministry of Natural Resources and University of the Philippines. Goodwill Bookstore, Manila, The Philippines. Fig. 94, p. 282 (L. papillosa); Trono, G.C. & Ganzon-Fortes, E.T., 1980. An illustrated seaweed flora of Calatagan, Batangas, Philippines. University of the Philippines Marine Science Center & Filipinas Foundation, Manila, The Philippines. Fig. on p. 101 (L. cartilaginea). Redrawn and adapted by P. Verheij-Hayes.

Melanamansia glomerata: Cribb, A.B., 1983. Marine algae of the southern Great Barrier Reef – Rhodophyta. Australian Coral Reef Society Handbook No 2. Brisbane, Australia. Plate 31, fig. 1 (rosette); Norris, R.E., 1988. Structure and reproduction of Amansia and Melanamansia Gen. Nov. (Rhodophyta, Rhodomelaceae) on the southeastern African coast. Journal of Phycology 24: Fig. 2, p. 212 (diagram section of blade, habit Amansia rhodanta); N'Yeurt, A.D.R., 1996. A preliminary floristic survey of the benthic marine algae of Rotuma Island. Australian Systematic Botany 9: Fig. 185, p. 483 (stichidium), fig. 197 & 198 (details of cells). Redrawn and adapted by P. Verheij-Hayes.

Monostroma nitidum: Hori, T. (Editor), 1994. An illustrated atlas of the life history of algae. Vol. 1. Green algae. Uchida Rokakuho Publishing Company, Tokyo, Japan. Fig. 85 (habit 2, detail gametophyte, gamete, sporophyte, zoospore); Pham-Hoang Hô, 1969. Rong bien Vietnam [Marine algae of South Vietnam]. Ministry of Education and Youth, Trung-tam hoc-lieu xuat-ban. Fig. 4.2, p. 398 (habit 1, cross-section and details of vegetative gametophytic thallus). Redrawn and adapted by P. Verheij-Hayes.

Nostoc: Desikachary, T.V., 1959. Cyanophyta. ICAR Monographs on algae. Indian Council of Agricultural Research, New Delhi, India. Plate 70, fig. 1, p. 386 (N. verrucosum); Frémy, P., 1930. Les myxophycées de l'Afrique équatoriale franÁaise [The myxophyceae of French Equatorial Africa]. Archives de Botanique 3, Mémoire No 2: fig. 281, p. 341 (N. muscorum), fig. 283, p. 343 (N. commune); Frémy, P., 1934. Les cyanophycées des Côtes d'Europe [The Cyanophyta of the European coasts]. Mémoires de la Société Nationale des Sciences Naturelles et Mathématique de Cherbourg 41: plate 58 (N. linckia, N. commune var. flagelliforme), plate 59 (N. sphaericum). Redrawn and adapted by P. Verheij-Hayes.

Padina: Gaillard, J., 1967. Etude monographique de Padina tetrastromatica (Hauck) [Morphologic study of Padina tetrastromatica (Hauck)]. Bulletin de l'Institut Fondamental d'Afrique Noire 29, sér. A, (2): fig. 2, p. 450 (detail of lower surface of blade of P. tetrastromatica [= P. antillarum]), *fig.* 5, *p.* 457 (details of double sori); Gaillard, J., 1975. Padina sanctae-crucis Børgesen, Padina japonica Yamada, Padina haitensis Thivy et leurs affinités [Padina sanctae-crucis Børgesen, Padina japonica Yamada, Padina haitensis Thivy and their affinities]. Le Botaniste 57: fig. 4, p. 99 (section of margin and antheridial sorus), fig. 5, p. 100 (habit of P. sanctae-crucis [as P. japonica]); Trono, G.C. & Ganzon-Fortes, E.T., 1988. Philippine seaweeds. National Bookstore, Manila, The Philippines. Fig. 63A, p. 91 (habit P. australis). Redrawn and adapted by P. Verheij-Hayes.

Porphyra: Cordero, P.A., 1976. Phycological observations 2. Porphyra marcosii, a new species from the Philippines. Acta Manilana, ser. A, 15 (24): fig. on p. 21 (details P. vietnamensis); Cordero, P.A., 1979. Phycological observations 9. Acta Manilana, ser. A, 18: fig. 1, p. 29 (habit P. yamadae), fig. 2, p. 31, (habit P. vietnamensis), fig. 3, p. 33 (habit P. suborbiculata); Kumar, C.A. & Panikkar, M.V.N., 1997. Indian species of Porphyra (Rhodophyceae, Bangiales). Feddes Repertorium 108: fig. 2, p. 421 (habit P. vietnamensis); Tanaka, T., 1952. The systematic study of the Japanese Proptofloridеae. Memoirs of the Faculty of Fisheries, Kagoshima University 2(2): fig. 16, p. 32 (details P. suborbiculta), fig. 17, p. 35 (detail P. yamadae). Redrawn and adapted by P. Verheij-Hayes.

Portieria hornemannii: Okamura, K., 1923. Icones of Japanese algae. Vol. 4. Okamura, Tokyo, Japan. Pl. 190 (cross-sections vegetative thallus, nemathecia); Stegenga, H., Bolton, J.J. & Anderson, R.J., 1997. Seaweeds of the South African West coast. Contributions from the Bolus Herbarium 18: Plate 112, p. 319 (detail of apical portion 3, cross-section 6); Trono, G.C. & Ganzon-Fortes, E.T., 1980. An illustrated seaweed flora of Calatagan, Batangas, Philippines. University of the Philippines Marine Science Center & Filipinas Foundation, Manila, The Philippines. Fig. a & b, p. 65 (habit and detail apical portion 2). Redrawn and adapted by P. Verheij-Hayes.

Sargassum: Hori, T. (Editor), 1993. An illustrated atlas of the life history of algae. Vol. 2. Brown and red algae. Uchida Rokakuho Publishing Company, Tokyo, Japan. Fig. 77, p. 154 (section of androgynous receptacle); Trono, G.C., 1992. The genus Sargassum in the Philippines. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 3. California Sea Grant College Program, La Jolla, United States. Figs. 39–41, p. 64 (habit, vesicles, leaves); Tseng, C.K. & Lu, B.R., 1992. Studies on the malacocarpic Sargassum of China: 2. Racemosae J. Agardh. In: Abbott, I.A. (Editor): Taxonomy of economic seaweeds with reference to some Pacific and Caribbean species. Vol. 3. California Sea Grant College Program, La Jolla, United States. Fig. 27, p. 31 (details of fertile branches). Redrawn and adapted by P. Verheij-Hayes.

Scinaia hormoides: Setchell, W.A., 1914. The Scinaia assemblage. University of California Publications in Botany 6(5): Plate 12, figs. 34 & 35, p. 145 (sections outer part thallus), Plate 13, fig. 37, p. 147 (surface view thallus); Tazawa, N., 1975. A study of the male reproductive organ of the Florideae from Japan and its vicinity. Scientific Papers of the Institute of Algological Research, Faculty of Science, Hokkaido University 6(2): Fig. 5 C, p. 102 (spermatangia); Trono, G.C., 1986. Philippine seaweeds. In: Guide to Philippine flora and fauna. Vol. 1. Natural Resources Management Center, Ministry of Natural Resources and University of the Philippines. Goodwill Bookstore, Manila, The Philippines. Fig. 73, p. 264 (habit). Redrawn and adapted by P. Verheij-Hayes.

Tricleocarpa fragilis: Huisman, J.M. & Borowitzka, M.A., 1990. A revision of the Australian species of Galaxaura (Rhodophyta, Galaxauraceae), with a description of Tricleocarpa gen. nov. Phycologia 29: Fig. 47, p. 165 (cross section thallus); Trono, G.C. & Ganzon-Fortes, E.T., 1980. An illustrated seaweed flora of Calatagan, Batangas, Philippines. University of the Philippines Marine Science Center & Filipinas Foundation, Manila, The Philippines. Fig. on p. 61 (habit and terminal branches). Redrawn and adapted by P. Verheij-Hayes.

Turbinaria: Trono, G.C., 1986. Philippine seaweeds. In: Guide to Philippine flora and fauna. Vol. 1. Natural Resources Management Center, Ministry of Natural Resources and University of the Philippines. Goodwill Bookstore, Manila, The Philippines. Fig. 68, p. 260 (T. conoides), fig. 69, p. 261 (T. decurrens), fig. 70, p. 261 (T. ornata). Redrawn and adapted by P. Verheij-Hayes.

Ulva: Stegenga, H., Bolton, J.J. & Anderson, R.J., 1997. Seaweeds of the South African west coast. Contributions from the Bolus Herbarium 18: Plate 15, p. 94 (U. fasciata); Tatewaki, M., 1994. Ulva pertusa Kjellman. In: Hori, T. (Editor),

1994. An illustrated atlas of the life history of algae. Vol. 1. Green algae. Uchida Rokakuho Publishing Company, Tokyo, Japan. Plate 96, p. 194 (U. pertusa); Trono, G.C., 1986. Philippine seaweeds. In: Guide to Philippine flora and fauna. Vol. 1. Natural Resources Management Center, Ministry of Natural Resources and University of the Philippines. Goodwill Bookstore, Manila, The Philippines. Fig. 3, p. 210 (habit U. lactuca). Redrawn and adapted by P. Verheij-Hayes.

Valonia aegagropila: Enomoto, S. & Miyazato, K., 1994. Valonia aegagropila (Roth) C. Agardh. In: Hori, T. (Editor), 1994. An illustrated atlas of the life history of algae. Vol. 1. Green algae. Uchida Rokakuho Publishing Company, Tokyo, Japan. Plate 124, p. 252 (details life cycle); Taylor, W.R., 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Press, Scientific Series, Vol. 21, Ann Arbor, Michigan, United States. Plate 7, fig. 6, p. 677 (portion of thallus); Trono, G.C., 1986. Philippine seaweeds. In: Guide to Philippine flora and fauna. Vol. 1. Natural Resources Management Center, Ministry of Natural Resources and University of the Philippines. Goodwill Bookstore, Manila, The Philippines. Fig. 6, p. 213 (habit, portion of thallus). Redrawn and adapted by P. Verheij-Hayes.

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Index of vernacular plant names

Page numbers printed in bold refer to main treatment.

The Prosea Foundation
(Plant Resources of South-East Asia)

Name, location, legal status and structure

- Prosea is a Foundation under Indonesian law, with an international charter, domiciled in Bogor. It is an autonomous, non-profit, international agency, governed by a Board of Trustees. It seeks linkage with existing regional and international organizations;
- Prosea is an international programme focusing on the documentation of information on plant resources of South-East Asia;
- Prosea consists of a Network Office in Bogor (Indonesia) coordinating 6 Country Offices in South-East Asia, and a Publication Office in Wageningen (the Netherlands).

Participating institutions

- Forest Research Institute of Malaysia (FRIM), Karung Berkunci 201, Jalan FRIM, Kepong, 52109 Kuala Lumpur, Malaysia;
- Indonesian Institute of Sciences (LIPI), Sasana Widya Sarwono, Jalan Gatot Subroto 10, Jakarta 12710, Indonesia;
- Institute of Ecology and Biological Resources (IEBR), Nghia Do, Cau Giay, Hanoi, Vietnam;
- Papua New Guinea University of Technology (UNITECH), Private Mail Bag, Lae 411, Papua New Guinea;
- Philippine Council for Agriculture, Forestry and Natural Resources Research and Development (PCARRD), Los Baños, Laguna, the Philippines;
- Thailand Institute of Scientific and Technological Research (TISTR), 196 Phahonyothin Road, Chatuchak, Bangkok 10900, Thailand;
- Wageningen University (WU), Costerweg 50, 6701 BH Wageningen, the Netherlands.

Objectives

- to document and make available the existing wealth of information on the plant resources of South-East Asia for education, extension work, research and industry;
- to make operational a computerized data bank on the plant resources of South-East Asia;
- to publish the results in the form of an illustrated, multi-volume handbook in English;
- to promote the dissemination of the information gathered.

Target groups

- those professionally concerned with plant resources in South-East Asia and working in education, extension work, research and commercial production (direct users);
- those in South-East Asia depending directly on plant resources, obtaining relevant information through extension (indirect users).

Activities

- the establishment and operation of data bases;
- the publication of books;
- the sponsorship, support and organization of training courses;
- research into topics relevant to Prosea's purpose;
- the publication and dissemination of reports and the research results.

Implementation

The programme period has been tentatively divided into 4 phases:
- preliminary phase (1985–1986): publication of 'Plant Resources of South-East Asia, Proposal for a Handbook' (1986);
- preparatory phase (1987–1990): establishing cooperation with South- East Asia through internationalization, documentation, consultation and publication; reaching agreement on the scientific, organizational and financial structure of Prosea;
- implementation phase (1991–2000): compiling, editing and publishing of the handbook; making operational the computerized data bank with the texts and additional information; promoting the dissemination of the information obtained.
- Prosea beyond 2000 (Phase 2001–2005): handbook finalization; emphasis on lesser-known useful plants, and making the information services demand-driven.

Documentation

A documentation system has been developed for information storage and retrieval called Prosea Data Bank. It consists of 7 data bases:
- BASELIST: primarily a checklist of more than 6200 plant species;
- CATALOG: references to secondary literature;
- PREPHASE: references to literature from South-East Asia;
- ORGANYM: references to institutions and their research activities;
- PERSONYM: references to specialists;
- TEXTFILE: all Prosea publications and additional information;
- PHOTFILE: photographs of useful plants of South-East Asia.

Publication

The handbook in blue cover (hardbound) is distributed by Backhuys Publishers, Leiden, the Netherlands (formerly by Pudoc, Wageningen, the Netherlands). The handbook in green cover (paperback) is distributed in two price-classes: a low-price paperback, distributed by Prosea South-East Asia for all developing countries; a medium-price paperback, distributed by Backhuys Publishers, Leiden, the Netherlands, and by Prosea South-East Asia for developed countries (becoming available two years after publication of the hardbound edition). The bibliographies are distributed by Prosea South-East Asia.

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In brief, Prosea is

- an international programme, focused on plant resources of South-East Asia;
- interdisciplinary, covering the fields of agriculture, forestry, horticulture and botany;
- a research programme, making knowledge available for education and extension;
- ecologically focused on promoting plant resources for sustainable tropical land-use systems;
- committed to conservation of biodiversity;
- committed to rural development through diversification of resources and application of farmers' knowledge.

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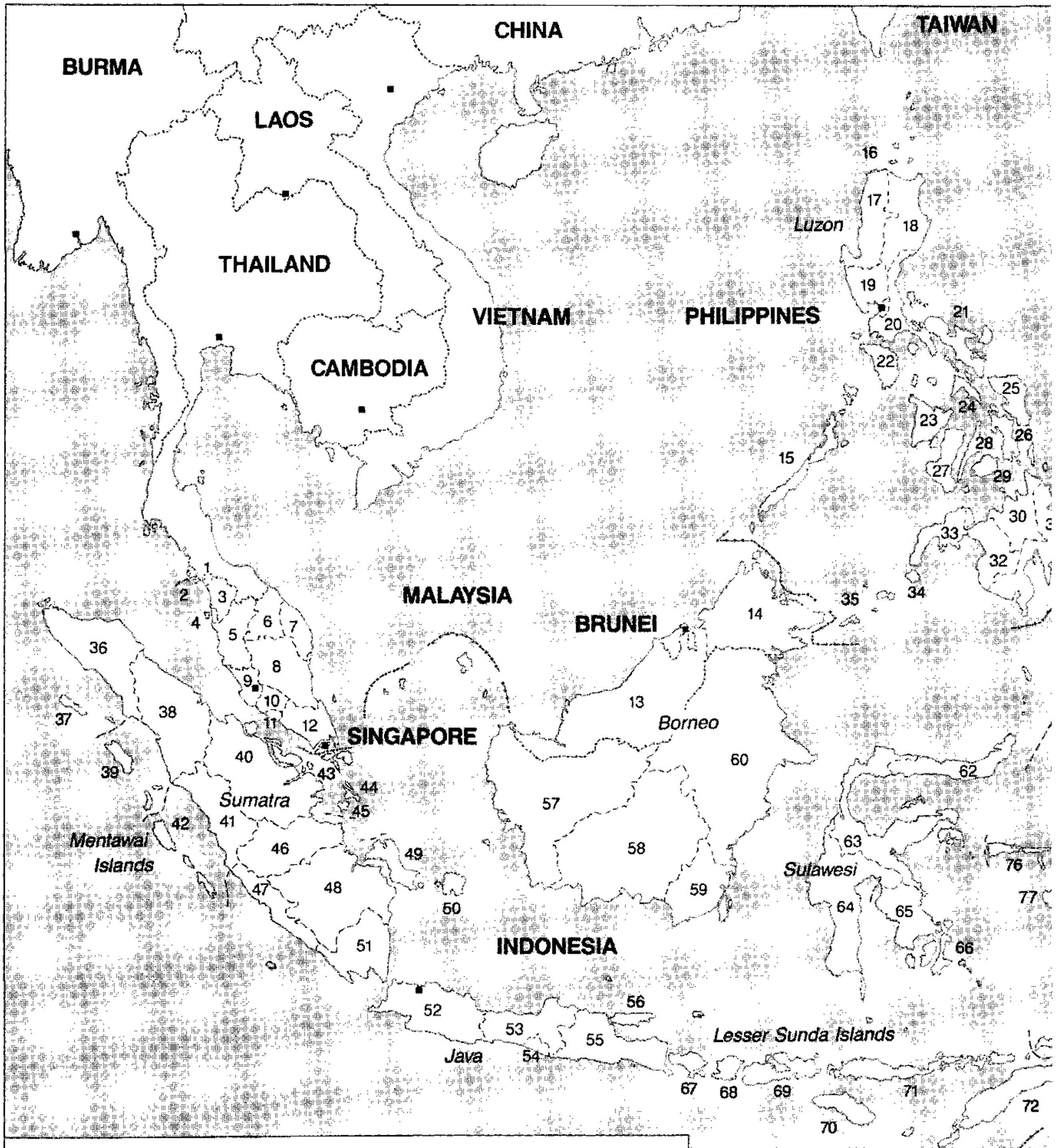
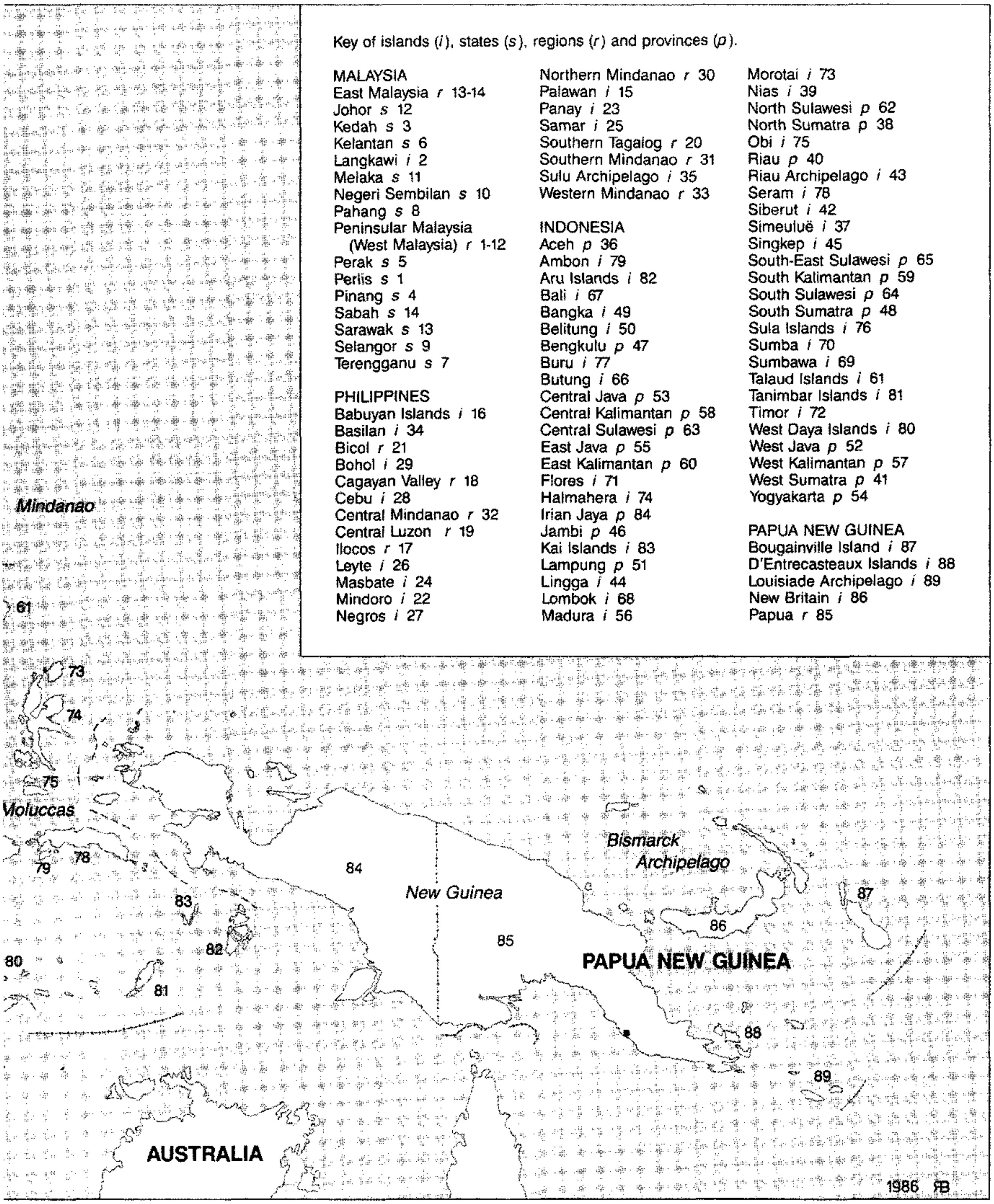


MAP OF SOUTH-EAST ASIA FOR PROSEA

Names of countries in capital letters and islands in lower case; numbers refer to the key.



Key of islands (*i*), states (*s*), regions (*r*) and provinces (*p*).

MALAYSIA
East Malaysia *r* 13-14
Johor *s* 12
Kedah *s* 3
Kelantan *s* 6
Langkawi *i* 2
Melaka *s* 11
Negeri Sembilan *s* 10
Pahang *s* 8
Peninsular Malaysia (West Malaysia) *r* 1-12
Perak *s* 5
Perlis *s* 1
Pinang *s* 4
Sabah *s* 14
Sarawak *s* 13
Selangor *s* 9
Terengganu *s* 7

PHILIPPINES
Babuyan Islands *i* 16
Basilan *i* 34
Bicol *r* 21
Bohol *i* 29
Cagayan Valley *r* 18
Cebu *i* 28
Central Mindanao *r* 32
Central Luzon *r* 19
Ilocos *r* 17
Leyte *i* 26
Masbate *i* 24
Mindoro *i* 22
Negros *i* 27
Northern Mindanao *r* 30
Palawan *i* 15
Panay *i* 23
Samar *i* 25
Southern Tagalog *r* 20
Southern Mindanao *r* 31
Sulu Archipelago *i* 35
Western Mindanao *r* 33

INDONESIA
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Bali *i* 67
Bangka *i* 49
Belitung *i* 50
Bengkulu *p* 47
Buru *i* 77
Butung *i* 66
Central Java *p* 53
Central Kalimantan *p* 58
Central Sulawesi *p* 63
East Java *p* 55
East Kalimantan *p* 60
Flores *i* 71
Halmahera *i* 74
Irian Jaya *p* 84
Jambi *p* 46
Kai Islands *i* 83
Lampung *p* 51
Lingga *i* 44
Lombok *i* 68
Madura *i* 56
Morotai *i* 73
Nias *i* 39
North Sulawesi *p* 62
North Sumatra *p* 38
Obi *i* 75
Riau *p* 40
Riau Archipelago *i* 43
Seram *i* 78
Siberut *i* 42
Simeuluë *i* 37
Singkep *i* 45
South-East Sulawesi *p* 65
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Timor *i* 72
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West Java *p* 52
West Kalimantan *p* 57
West Sumatra *p* 41
Yogyakarta *p* 54

PAPUA NEW GUINEA
Bougainville Island *i* 87
D'Entrecasteaux Islands *i* 88
Louisiade Archipelago *i* 89
New Britain *i* 86
Papua *r* 85