

The History and Future Prospects of Systematics of Bangiaceae, Rhodophyta

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Abstract The family Bangiaceae comprises two genera, *Bangia* Lyngbye with filamentous thalli and *Porphyra* C. Agardh with leafy thalli. The species of *Porphyra* are currently characterized by a combination of morphological characters, 1) numbers of cell layers and chloroplasts, 2) shape of blades, 3) leaf margin entire or denticulate, 4) sexuality and distribution of male and female parts, 4) division formula of antheridia and 'cystocarps' (=zygotosporangia), with supplementary information on life history and habitat preference. Additional information from molecular biology is gradually increasing. Revision of the species using morphological and molecular techniques is needed and comparison of taxa from different geographical areas is expected.

Key words: *Bangia*, Bangiaceae, *Porphyra*, Rhodophyta, systematics.

The red algal family Bangiaceae Engler includes the genera *Bangia* and *Porphyra*. They can be easily distinguished by their filamentous or leafy thalli. The genus *Bangia* was described by Lyngbye (1819), and its lectotype species for this genus is *B. fuscopurpurea* (= *B. atropurpurea*). The genus *Porphyra* was established by C. Agardh (1824) with three species, *P. laciniata*, *P. purpurea* and *P. miniata*, all of which were previously attributed to the genus *Ulva* of Linnaeus. These genera were placed in separate families by Kützinger, but later united in the same family: Bangiaceae. More than 20 species of *Porphyra* were described from European coasts as early as in nineteenth century. Then, species of *Porphyra* were described from many localities all over the world, especially from the Northern Hemisphere. Taxonomic study in the Pacific area was advanced by Kjellman (1897), who collected specimens from Japanese coasts and described 6 species, including a cultivated species: *P. tenera*. Hus (1902) introduced the character of mode of division in spermatangia and 'cystocarp (sporocarp, zygotosporangia)' in his study of the genus on the Pacific coast of North America, and he expressed the mode of division in the form of

formula (Hus's formula). In Japan, plants of *Porphyra* were used as food from ancient times and in the seventeenth century, artificial cultivation was invented. Japanese species of *Porphyra* were investigated by Ueda (1932), using "Hus's formula" in recognizing 18 species. Taxonomic study of the genus was continued by Tanaka (1952), Kurogi (1961), Fukuhara (1968) and Miura (1967, 1977). More recently, studies were undertaken in the Pacific coast of North America and other parts of the world. The number of species described is nearly 130.

Characters Used for Species Recognition in *Porphyra*

The genus *Porphyra* has rather simple morphology. Therefore, discrimination of species by morphological characters is not so easy to accomplish. The characters currently employed are as follows (Kurogi, 1972):

Number of cell layers and chloroplasts. There are three types of structure, and used for distinction of subgenera: (1) monostromatic thallus, with one chloroplast in each cell (subgenus *Porphyra*); (2) monostromatic thallus, and with two chloroplasts in each cell or partly distromatic (subgenus *Diplastidia*); (3) distromatic thallus and with

one chloroplast in each cell (subgenus *Diploderma*).

Leaf margin. Several species of the subgenus *Porphyra* have microscopic denticulation on the margin of the blade. Species of this subgenus can be divided into two groups by this character.

Shape of the blade. A characteristic shape for each species is expressed in the young stage just before spores are released. Three forms are roughly distinguishable in the shape of blade: 1) round to ovate or obovate, 2) oblong obovate to linear oblanceolate, and 3) oblong ovate to linear lanceolate. The shape of mature blade is correlated with the mode of development in the young germling. Spores germinate after settlement on the substratum to form first a uniseriate filament by successive transverse division. Then division by longitudinal walls occur at a certain stage depending on the species. A broader blade results from early longitudinal division, as early as the 3–4 cell stage. A narrower blade is caused by later longitudinal division of uniseriate germlings. Blades generally become broader upon the maturation of sexual or asexual reproductive organs. Production of monospores (neutral spores) at a certain stage of growth affects the blade shape.

Structure of the basal part. The blade attaches to the substratum by rhizoidal filaments extending downward from the cells near the base. There are substratum preferences. Certain species are epilithic and several species can grow only on a definite host plant with rhizoidal filament penetrating into the host tissue.

Thickness of the blade. Blade thickness changes according to the age. Blades are generally thinner in younger plants. In an individual, the sterile margin is thinner and the basal portion becomes thicker. Four groups of species can be recognized by the range of thickness, 1) thin, less than 40 μm , 2) medial, 40–60 μm , 3) thick, 60–80(–100) μm , and 4) very thick, more than 100 μm . Although there is intergradation among these thickness classes, thickness can be used in combination of other characters. Species of the subgenus *Diploderma* only have blades more than 100 μm thick.

Color of the blade. Although the particular tone of color for each species is difficult because of environmentally induced variation, basic color of the blade and *Conchocelis*-phase can be referred as an additional character.

Sexuality. Sexual reproduction is known for this genus, with non-motile spermatia and a carpogonium slightly modified from the vegetative cell, and ultimately the direct cell division of the fertilized carpogonium and production of zygotospores ("carpospores"). Four groups can be recognized from the sexuality, 1) monoecious individuals only, 2) dioecious (including rare and abnormal occurrence of monoecious plants), 3) androdioecious (hermaphrodite and male-only), and 4) both monoecious and dioecious plants. In bisexual individuals of monoecious and androdioecious groups, occurrence of antheridia and carpogonia is divided into three types, 1) antheridia mixed with carpogonia, 2) antheridial patches of various shape partitioned within carpogonial area, and 3) antheridial and carpogonial areas clearly separated on longitudinal halves of the thallus.

"Hus's formula." An antheridial cell divides several times and at maturity spermatia are arranged in 2 or 4 rows of 4 cells in surface view and in cross section are stacked in 4 or 8 layers, resulting in 32, 64, or 128 spermatia from one antheridial cell. The zygotosporangium ("cystocarp") is composed of 8, 16 or 32 carpospores arranged in 2 rows of 2 or 4 cells in surface view and stacked in 2 or 4 layers in cross section. These states can be expressed as 'a' and 'b' axes in surface view and the number of layers in cross section as 'c'. Formulas $32(a/4, b/2, c/4)$, $64(a/4, b/4, c/4)$, $64(a/4, b/2, c/8)$ and $128(a/4, b/4, c/8)$ are recorded for antheridia. Formulas $8(a/2, b/2, c/2)$, $16(a/2, b/2, c/4)$ and $32(a/4, b/2, c/4)$ for zygotosporangia are recognized. The combination of formulas for male and female is considered as an important species characteristic. It must be noted that the numbers in each formula represent a maximum in each species observed.

Ecological characters can be used as supplementary criteria for recognizing species. Some species grow in the intertidal zone and others are found in subtidal areas. Most spe-

cies exhibit luxuriant growth in winter, although several species appear in summer months. This phenomenon reflects photoperiodic response of spore liberation from the *Conchocelis*-stage.

Life History

Leafy thalli of *Porphyra* and filamentous thalli of *Bangia* appear in winter in the temperate zone and certain species grow in summer in the cold boreal areas. How the species persisted through unfavorable seasons for the leafy-phase, after release of carpospores, was not known for many years even when the species of *Porphyra* were brought into cultivation. Drew (1949) showed that the carpospores of *Porphyra umbilicalis* grew into filamentous germlings penetrating into shells of bivalves, resembling *Conchocelis rosea*. She did not observe spore liberation from the *Conchocelis*-phase. The complete life history was followed by Japanese phycologists, Kurogi (1953) and Ohta (1960), working independently on *Porphyra tenera*. Miura (1961) showed a different type of life history in *Porphyra tenuipedalis* wherein filaments of the *Conchocelis*-phase grew directly into leafy thalli.

Geographical Distribution

Nearly 130 species of *Porphyra* have been described from all over the world. Species belonging to the subgenus *Diploderma* are confined their range of distribution along the coast of Arctic Sea, North Pacific and North Atlantic. The subgenus *Diplastidia* has its distribution area restricted to northern parts of Japan and north Asia to Pacific North America. Most species of the subgenus *Porphyra* are distributed in temperate zones nearly all over the world. Nearly 30 species have been recorded from North Atlantic coasts of Europe and America. About 27 species have been described from the Pacific coast of Canada and United States, and more than 20 species were accredited to Japanese and Korean coasts. Seven species have their type localities in China and Vietnam. It is noteworthy that there are very few species common to Japan and the Pacific coast of North America. Also there is no species of subgenus *Porphyra* common to the Northern

Pacific and Atlantic Oceans. Similarly, no species is common to the Northern and Southern Hemispheres.

Recent Trends and Future Development

Species of *Porphyra* are recognized and discriminated mainly on the basis of morphological characters supplemented with ecological and physiological characters. Distinction between species is frequently very difficult unless all stages in the life history are taken into consideration. For the species under cultivation, we have much information as compared with the wild ones. Further efforts are evidently needed to obtain knowledge on each species of their characters and range of distribution. Other more sophisticated techniques are becoming available from the other fields of biology. Electrophoretic mobilities of proteins have been extensively investigated for species on the Pacific coasts of Canada (Lindstrom and Cole, 1992). Recent method in molecular systematics (e.g. DNA sequence analysis) may be widely employed in this genus for comparison of species of different geographic areas, for example, between the east and west coasts of the Pacific Ocean.

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紅藻ウシケノリ科の分類学的研究の 歴史と課題

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紅藻ウシケノリ科 Bangiaceae について、とくに日本における研究の歴史と、これからの課題に関して要

約した。

ウシケノリ科は細い糸状の体を持つウシケノリ属 *Bangia* Lyngbye 1819 と薄い葉状のアマノリ属 *Porphyra* C.Agardh 1824 の2属を含む。ウシケノリ属は少数の種を持つ。アマノリ属は世界各地から多数の種が記載され、そのうちのいくつかは日本や韓国・中国で養殖され食用に供されている。

生活史に関しては、葉状体に有性生殖で作られる“果孢子”が発芽して、石灰質の基物に穿入して *Conchocelis* と呼ばれていた糸状の孢子体になり、その体に作られる孢子(殻孢子)が葉状体となることが明らかにされた。アマノリ属は体制が比較的簡単であり、種を識別する分類形質の数は限られている。体が一層の細胞からなるか、二層であるか、および細胞あたりの葉緑体の数が1個か2個であるかの形質の組み合わせは、亜属を区分する特徴とされている。すなわち：

ヒトエアマノリ亜属 subgenus *Porphyra*: 一層細胞で1個の葉緑体を持つ。

フタツボシアマノリ亜属 subgenus *Diplastidia*: 一層細胞で2個の葉緑体を含む。

フタエアマノリ亜属 subgenus *Diploderma*: 二層細胞からなり、細胞は1個の葉緑体を持つ。

種のレベルでは、外形(線形で基部は楔形から円い体で基部は心臓形や漏斗状まで)、体の構造(体の縁辺に顕微鏡的な鋸歯を持つか全縁であるか、体の厚さなど)、雌雄性(雌雄同株、異株または同株体と雄性体、同株体と異株体)、雌雄の生殖細胞の分布、生殖細胞の分裂様式(一個の母細胞から形成される生殖細胞の数と表面から見える個数および、断面での層の数)などが重要な形質とされている。この他にもいくつかの形態的、生態的な形質を組み合わせることで種を認識している。

最近でも、世界の各地で新しい種が記載され、アマノリ属の種数は増加している。その大部分は比較的限られた地域に分布しているようで、たとえば、北半球と南半球に共通する種はないといって良く、このことは他の分類群と比較して特に顕著である。新しい種の探索とともに、既に知られている種の間関係を、分子系統学的手法も取り入れて再検討することも、これからの課題であろう。