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Diversity of Life History in the Genus *Porphyra*

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Abstract Species of the genus *Porphyra* have heteromorphic and biphasic life history basically. The life history of about thirty species of *Porphyra* has been observed in laboratory culture, and from these results, four basic types of life history are recognized. I. The *Porphyra tenuipedalis* type has monoecious foliose gametophytes and filamentous sporophytes. However, foliose gametophytic thalli are produced directly and successively from spherical cells on the tips of conchocelis filaments. II. The *Porphyra lacerata* type has monoecious foliose thalli bearing intermingled male and female reproductive cells on tissue. Zygotospores are therefore produced by self-fertilization at a high rate, and genetic diversity of successive generations is presumed to be low. Many species belong to this type and several different kinds of asexual reproduction occur here. III. The *Porphyra variegata* type has a monoecious foliose thallus, halved vertically into male and female parts. IV. The *Porphyra dentata* type has dioecious foliose thalli and, therefore, a high rate of cross-fertilization in zygotospores production. The four basic life histories also have some kind of asexual reproduction: archeospores, neutral spores, endospores and agamospores are produced on the foliose thallus, protoplasts from the protothallus and monospores from conchocelis. The genetic diversity of the four basic life histories and diversification of asexual reproductive modes on the genus *Porphyra* are regarded as evolutionary trends toward reproductive strategy for survival, increase in distribution and enlargement of populations.

Key words: Bangiales, life history, asexual reproductive mode, *Porphyra*, Rhodophyta, evolution, reproductive strategy.

Porphyra species, as edible seaweeds are economically important algae in Japan and in other Asian countries. The foliose thallus, used to manufacture nori-sheets, and is the male and/or female gametophyte. Three types of arrangement of male and female reproductive cells on the foliose thallus have been reported. In monoecious species, patches of male and female reproductive cells are mixed at the margins on the upper part of the foliose thallus (e. g. *Porphyra tenuipedalis* and *P. lacerata*), or the thallus is halved vertically into male and female portions (e. g. *P. variegata*). In dioecious species, male and female cells are produced different foliose thallus (e. g. *P. dentata).*

In addition, there are several kinds of asexual spores and reproductive modes in the life history of *Porphyra*, wich are important in seeding techniques for nori-farming. Archeospores (Magne, 1991), neutral spores (Hollenberg, 1958), endospores (Nelson and Knight, 1995) and agamospores (Kornmann, 1994) are produced by the foliose gametophyte thallus, and monospores (Chen *et al.*, 1970) and protoplasts from the protothallus (Cole and Conway, 1980) are produced by the filamentous sporophyte (conchocelis).

The basic life history of *Porphyra* is biphasic and heteromorphic with a haploid foliose gametophyte and diploid filamentous sporophyte (conchocelis). The author considers that three types of sexual cell arrangement are important for genetic diversification, and some kinds of asexual reproduction are important for reproductive strategy on enlargement of the population, distribution and survival of the species. Therefore, the life histories of the genus *Porphyra* were divided into four types by variation in the basic life history and arrangement of sexual reproductive cells. These are presented here, together with review of reserch on life history variation in the genus.

On the Studies of Life History in Culture

Drew (1949, 1954) established that carpospores of *Porphyra umbilicalis* give rise to filamentous thalli of *Conchocelis rosea.* Since this seminal report, the life history in culture has been documented for about thirty species of *Porphyra.* The earliest report of the complete life cycle of *P. tenera* in laboratory culture was given by Iwasaki (1961). Three types of life history were proposed by Conway *et al.* (1975), as the *P. subtumens* type, the *P. sanjuanensis* type and the *P. perforata* type, among the species of British Columbia and Washington. They described the *P. subtumens* type and *P. sanjuanensis* type as having only an asexual foliose thallus phase reproductions by archeospores (monospore) and neutral spores (aplanospores) respectively. Later, Nelson and Knight (1996) completed an asexual and sexual cycle in culture for *P. subtumens*, and Lindstrom and Cole (1990) reduced *P. sanjuanensis* to a synonym of *P. perforata* based on electrophoretic banding patterns. Therefore, only the one type on life history of *P. perforata* remained.

Notoya *et al.* (1992b, 1993a, 1993b) were proposed that the life histories of nine Japanese species were divided into three types. I. The *P. tenuipedalis* type is monoecious with mixed sexual reproductive cell on the foliose thallus, and without observable conchosporangia and conchospores; the foliose thallus develops directly from a spherical cell on the tip of the conchocelis filament. II. The *P. lacerata* type is monoecious with mixed sexual reproductive cell on the foliose thallus, and the typical biphasic and heteromorphic cycle. III. The *P. dentata* type has a dioecious foliose thallus, and the typical biphasic and heteromorphic cycle.

Kornmann (1994) recognized four types of life history, based on studies of *Porphyra* species from Helgoland, North Sea (Kornmann and Sahling 1991) and elsewhere, and grouped them according to thallus thickness. He proposed a new type based on the novel "agamospore" for an asexual spore produced in the presence of vestigial spermatangia and germinating to produce conchocelis of the same ploidy as the foliose phase. In some species, the life history included more than one of these types.

Four Basic Types of Life History

As shown in Fig. 1, the author has proposed four basic types of life history in the genus *Porphyra*, based on the results of previous studies on laboratory culture of about thirty five species (Tables 1–3). However, the subcycles of asexual reproduction were omitted in these diagrams.

The *P. tenuipedalis* type has a monoecious foliose thallus which develops directly from a spherical cell on the tip of the conchocelis filament. And the other three types are clearly biphasic. Different arrangements of sexual reproductive cells on the foliose thallus are observed between two types of *P. lacerata* type and *P. variegata* type. The *P. dentata* type has dioecious foliose thalli.

I. *Porphyra tenuipedalis* type (Fig. 1–I)

This type was first reported by Notoya *et al.* (1992b), and is known in only *P. tenuipedalis* (Plate I–A). Spermatangial and carpogonial patches are mixed on the foliose thallus. After fertilization, zygotospores are formed and liberated, and germinate to the filamentous thallus (conchocelis). Spherical cells are produced at the tips of the filaments, and develop directly into foliose thalli. Therefore, the spherical cells may be primitive conchosporangia or conchospores. Asexual reproduction by archeospores, neutral spores or etc. is not known in this species.

Although direct production of foliose thallus from filamentous thallus is known for four other species (*P. schizophylla* and *P. variegata*, Cole and Conway, 1980; *P. leucosticta*, Gargiulo *et al.*, 1994; *P. subtumens*, Nelson and Knight, 1996), these species also produce conchosporangia and liberate conchospores, and therefore are different from the *P. tenuipedalis* type. Krishinamurthy (1969) reported similar phenomenon in *P. cuneiformis*, but, it did not observe the complete life history.

II. *Porphyra lacerata* type (Fig. 1–II)

This classic type was described and named by Notoya *et al.* (1992b, 1993b), based on the life history of *P. lacerata* (Plate I–B), and is known in many species (Table 1). Spermat-

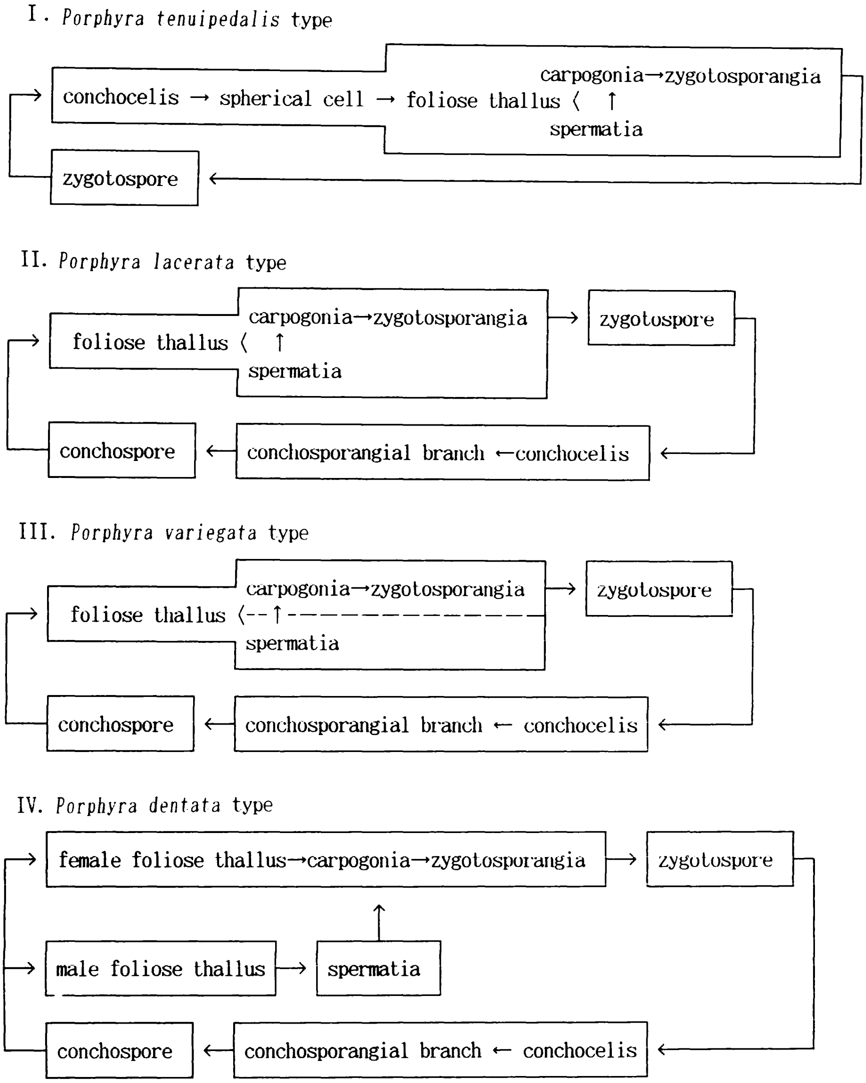

Fig. 1. Four basic types of life history in the genus *Porphyra*.

angial and carpogonial patches are mixed on the foliose thalli. After fertilization, zygotospores are formed and liberated, and germinate to produce the filamentous thallus (conchocelis). Conchosporangial branches are produced on the filamentous thalli, and liberated conchospores germinate to the foliose stage. This type is clearly a biphasic life history.

Six modes of asexual reproduction have been known in the species of this type. Archeospores, endospores, neutral spores, agamospores, monospores liberated from conchocelis, and protothallus produced directly from conchocelis are recognized (Table 1).

In this type, sexual reproductive cells or patches of male and female tissue on the foliose thallus are produced near in close proximity, sometimes microscopically intermingled, and self-fertilization probably occurs at a high frequency. Therefore, genetic diversity in zygotospores is relatively limited.

Archeospores from the foliose thallus give rise to the foliose thallus again, and sexual reproductive cells or patches are subsequently produced on this progeny. In *P. yezoensis* (Ma and Miura, 1984; Ohme *et al.*, 1986; Ohme and Miura, 1988; Tseng and Sun, 1989) and *P. torta* (Burzycki and Waaland,

Table 1. Species of the *Porphyra lacerata*-type life history and their asexual reproductive modes.

Species	Asexual spore	References
1. *P. amplissima*	neutral spore	Chen *et al.*, 1970
2. *P. carolinensis*	archeospore	Freshwater & Kapraun, 1986
	archeospore, agamospore	Kornmann, 1994
3. *P. columbina*	monospore	Avila *et al.*, 1986
4. *P. gardneri*	archeospore	Hawkes, 1977, 1978
	archeospore	Kornmann, 1994
5. *P. kinositae*	archeospore	Notoya *at al.*, 1992a
6. *P. kuniedae*	archeospore	Kurogi, 1961
	archeospore	Kornmann, 1994
7. *P. lacerata*	archeospore	Iima & Migita, 1990
	archeospore	Notoya *et al.*, 1992b, 1993b
8. *P. leucosticta*		Sidirelli-Wolff, 1992
	archeospore, protothallus	Gargiulo *et al.*, 1994
	archeospore, agamospore	Kornmann, 1994
9. *P. maculosa*	neutral spore	Hymes & Cole, 1983
10. *P. nereocystis*		Dickson & Waaland, 1985
11. *P. okamurae*	archeospore	Notoya & Kim, 1996
12. *P. perforata*		Hollenberg, 1958
(=*P. sanjuanensis)*	neutral spore	Conway *et al.*, 1975
	neutral spore	Kornmann, 1994
13. *P. rosengurtii*	archeospore, monospore	Kapraun & Luster, 1980
14. *P. seriata*		Kim & Notoya, 1996
15. *P. spiralia* var. *amplifolia*	fragmentation	Kapraun & Lemus, 1987
	agamospore	Kornmann, 1994
16. *P. suborbiculata*	archeospore	Notoya *et al.*, 1992b, 1993b
	archeospore	Matsuo *et al.*, 1994
	archeospore	Notoya & Kim, 1996
17. *P. suborbiculata* f. *latifolia*	archeospore	Notoya & Kim, 1996
18. *P. subtumens*	archeospore, protothallus	Nelson & Knight, 1996
19. *P. tanegashimensis*	archeospore	Migita & Ito, 1987
20. *P. tenera*	archeospore	Iwasaki, 1961
	archeospore	Kurogi, 1961
	archeospore	Kito, 1978
	archeospore	Kornmann, 1994
	archeospore	Notoya *et al.*, 1996
21. *P. yezoensis*	archeospree	Kurogi, 1961
	archeospore	Kito, 1978
	archeospore	Kim & Notoya, 1996
22. *P. vietnamensis*	archeospore	Lewmanomont & Chittpoolkusol, 1993
23. *Porphyra* sp.	archeospore, endospore	Nelson & Knight, 1995

1987), meiosis occur in germination of conchospores. Thus, it appears that sexual differentiation or sex determination of the vegetative cell of the foliose thallus had not occurred at the germling stage of conchospore. In most species of higher Rhodophyta, meiosis and sex determination occur in the tetrasporangia at the same time. In *P. purpurea* of the *P. variegata* type, meiosis and sex determination occur at germination of the conchospore (Mitmann and van der Meer, 1994). Therefore, it is thought that *P. lacerata* type is more primitive than the species of the *P. variegata* type or *P. dentata* type. It appears that in the *P. lacerata* type the main reproductive strategy is more to increase the population, its distribution and survival, by diversification of asexual reproductive modes rather than by enhancing genetic diversity.

Table 2. Species of the *Porphyra variegata*-type life history and their asexual reproductive modes.

Species	Asexual spore	References
1. *P. miniata*	monospore	Chen *et al.*, 1970
2. *P. purpurea*		Mitman & van der Meer, 1994
3. *P. purpureo-violacea*	agmospore, archeospore	Kornmann, 1994
4. *P. umbilicalis*	neutral spore	Kornmann, 1994
5. *P. variegata*	protothallus, protoplast	Cole & Conway, 1980 Notoya & Sugawara, 1994

Table 3. Species of the *Porphyra dentata*-type life history and their asexual reproductive modes.

Species	Asexual spore	References
1. *P. angusta*	archeospore	Kurogi, 1961
2. *P. dentata*		Notoya *et al.*, 1992b, 1993b
3. *P. insolita*	neutral spore	Kornmann, 1994
4. *P. laciniata*	agamospore	Kornmann, 1994
5. *P. linearis*		Bird *et al.*, 1972
	agamospore	Kornmann & Sahling, 1991
6. *P. ochotensis*	neutral spore	Kornmann, 1994
7. *P. pseudolinearis*		Kito, 1978
8. *P. schizophylla*	protothallus, protoplast	Cole & Conway, 1980

III. *Porphyra variegata* type (Fig. 1–III)

This type was described and named by Notoya and Sugawara (1994) based on the life history of *Porphyra variegata* from Japan (Plate I–C), and is known in five species (Table. 2). Thalli again are monoecious, but with male and female tissue separated on longitudinal halves, and the life history is clearly biphasic. Asexual reproduction is known in the foliose thallus, and in the conchocelis or the agamosporogenous foliose thallus.

Mitman and van der Meer (1994) reported for the sectored foliose thallus of *P. purpurea* that meiosis and sex determination occur at germination of the conchospore. Thus, sex of the vegetative cells of the foliose thallus is determined before differentiation of the reproductive cells. This is very different from the *P. lacerata* type.

Male and female reporoductive cells part are separated clearly on longitudinal halves, and not mixed as the species of the *P. lacerata* type. The self-fertilization rate on producing of zygotospores will be smaller than mixed type of the *P. lacerata* type.

IV. *Porphyra dentata* type (Fig. 1–IV)

This type was described and named by Notoya *et al.* (1992b, 1993b) based on the life history of *Porphyra dentata* (Plate 1–D). Spermatia and carpogonia are usually produced on different thalli; however, 0.01–0.1% of thalli in the field are monoecious, and these are sectored by an almost horizontal line (Kikuchi and Notoya, 1995), and monoecious thalli also has been reported in *P. pseudolinearis* (Funano, 1961) from Japan. This is a clearly biphasic cycle, and has been reported in eight species (Table 3). Asexual reproductive spores from the foliose thallus have been reported in *P. angusta* (Kurogi, 1961), *P. insolita*, *P. ochotensis* (Kornmann, 1994) and *P. linearis* (Bird *et al.*, 1972, Kornmann and Sahling, 1991), and an asexul reproductive mode from conchocelis has been reported (Cole and Conway, 1980) (Table 3).

The position of meiosis and sex determination, has not been reported in species of this type. Since this type is dioecious, most zygotospores are produced by cross-fertilization, and the species of this type will be the most advanced in genetic diversification among the four types of life history.

Generalized Life History of *Porphyra*

A summarized diagram of sexual and asexual modes of reproduction is shown in Fig. 2,

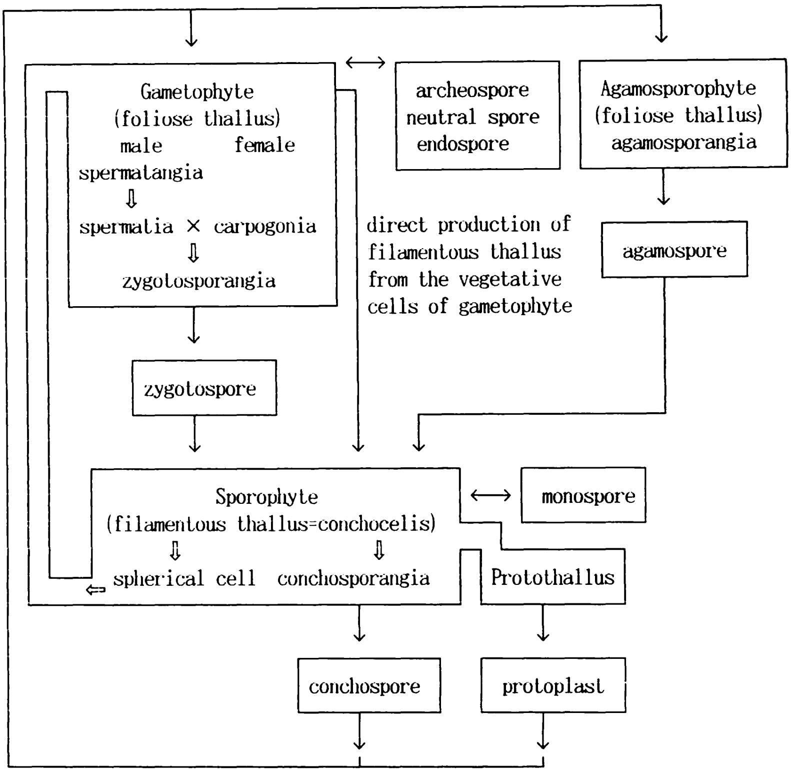

Fig. 2. A generalized life history of the genus *Porphyra*.

Table 4. Terminology of spores in the genus *Porphyra*.

Spore	References
Foliose thallus	
(Gametophyte)	
archeospore	Magne, 1991
neutral spore	Hollenberg, 1958
endospore	Nelson and Knight, 1995
agamospore	Kornmann, 1994
zygotospore	Guiry, 1990
Filamentous thallus	
(Sporophyte)	
monospore	Chen *et al.*, 1970
protoplast	Cole and Conway, 1980
conchospore	Tseng and Chang, 1954

and the terminology of spores is given in Table 4. The sexual cycle is shown at the left-hand side of Fig. 2. Spermatia and carpogonia are produced on the foliose gametophytic thallus. After fertilization, zygotospores are produced and liberated from the foliose thallus, and germinate to form the filamentous sporophytes (conchocelis). Conchosporangia are produced from these filaments, and liberated conchospores grow into the foliose gametophytic thallus. This life history occurs in all species of *Porphyra* except *P. tenuipedalis*, the species of asexual agamosporangial and neutral sporangial cycle (Kornmann, 1994). In *P. tenuipedalis*, instead of conchospores, spherical apical cells of conchocelis grow directly to foliose thallus.

Asexual reproductive modes are shown at the right-hand side of Fig. 2. The term archeospore was coined by Magne (1991) to replace "monospore", and neutral spore was proposed by Hollenberg (1958) based on the culture studies of *Porphyra perforata*. Endospores were first reported in a species from New Zealand (Nelson and Knight, 1995). These three kinds of spores are liberated from the foliose thallus, and to produce the foliose thallus again. As mentioned above, archeospores are known in many species of the *P. lacerata* type.

At higher temperature, the foliose gametophyte liberates archeospores successively

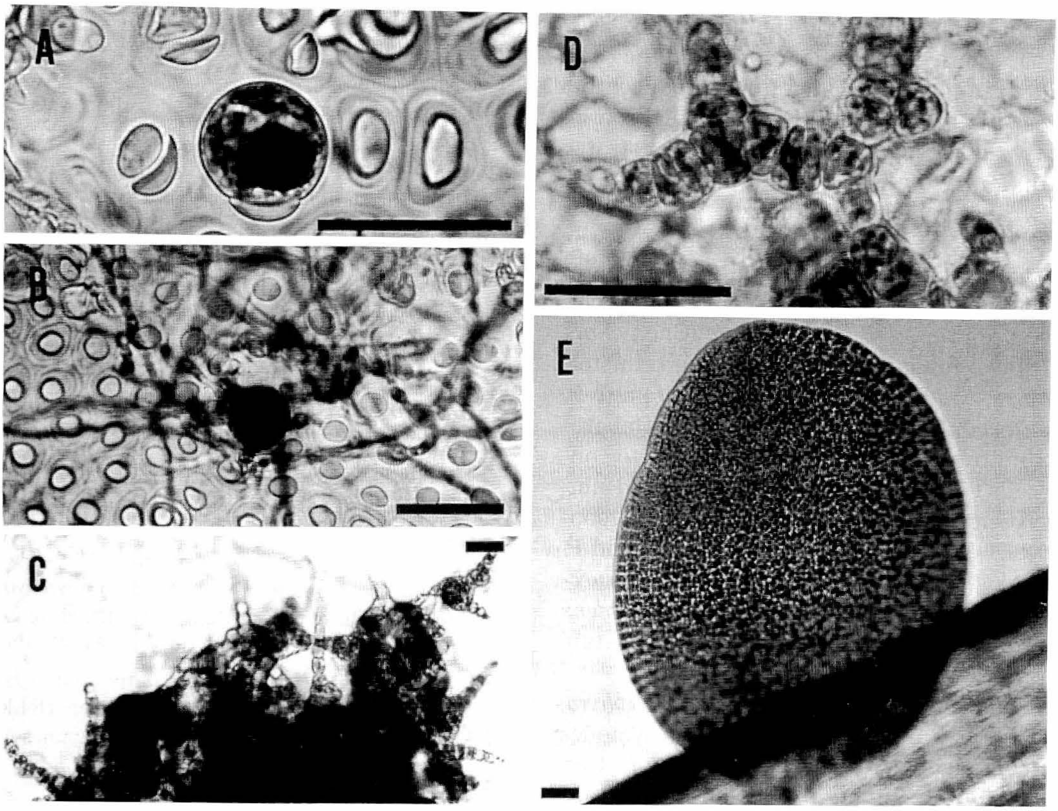

Fig. 3. Direct production of conchocelis from the vegetative cells of the foliose thallus in *Porphyra okamurae*. **A**, A pigmented cell surviving in tissue cultured about four months without change of medium, at 20℃ and 20 μmol $m^{-2}s^{-1}$. **B**, Filamentous thalli produced from a surviving vegetative cell (centre) one month after transfer to fresh culture medium and aeration. **C** and **D**, Conchosporangia, formed two weeks later. **E**, Foliose thallus, from germination of a liberated conchospore. Scale bars, 20 μm.

without producing sexual reproductive cells. However, at lower (optimum) temperatures, sexual reproductive cells are produced (Matsuo *et al.*, 1994; Notoya and Kim, 1996). Similar observations were reported in tissue culture of *Porphyra* spp. (Notoya, 1995, 1996). Therefore, these phenomena suggest that sexual or asexual propagation is related to environmental conditions, and is a survival strategy to increase the population.

Kornmann (1994) proposed the term "agamospore" for spores produced by gametophytic thalli with vestigial spermatangia (agamosporophyte), and the agamospores grow to conchocelis. The conchocelis produces conchosporangia, which in turn liberate conchospores.

Recently, the author discovered another asexual reproductive mode from the undivided vegetative cells of the gametophytic foliose thallus. Although, agamospores produced by cleavage process similar to that of zygotospores, the cells are undivided. Conchocelis is produced directly from undivided the vegetative cells of gametophyte, and produces functional conchospores. That reproduce foliose thallus (Fig. 3).

Excised small pieces of tissue from juvenile foliose thalli (3–5 mm blade length) of *P. okamurae* were cultured for four months without renewed culture medium at 20℃ and 20 μmol $m^{-2}s^{-1}$. Most the vegetative cells died; however, a few cells survived, which were well-pigmented, spherical and slightly larger than the original vegetative cells (Fig. 3–A). When this tissue was cultured three weeks in fresh medium with aeration, the surviving cells produced filaments (Fig. 3–B), and the filaments produced conchosporangia (Fig. 3–C and D). Conchospores liberated from the conchosporangia germinated to reproduce the foliose thallus (Fig. 3–E). This asexual reproductive mode is considered a survival strategy under severe nutrient limitation.

Two asexual reproductive modes are known for the filamentous sporophyte (conchocelis): monospores and protoplasts from a protothallus. Monospores from conchocelis have been reported in *P. miniata* (Chen *et al.*, 1970), *P. rosengurtii* (Kapraun and Luster, 1980), *P. columbina* (Avila *et al.*, 1986) and *P. cuneiformis* (Krishnamurthy, 1969) in laboratory culture. These monospores grow to conchocelis filaments again. Protothalli and similar structures have been reported on conchocelis of four species of *P. variegata* and *P. shizophylla* (Cole and Conway, 1980), *P. leucosticta* (Garguilo *et al.*, 1994) and *P. subtumens* (Nelson and Knight, 1996). However, the fate of protothalli has not been determined.

In summary, in the life history of *Porphyra*, seven known asexual reproductive modes are connected with the basic cycle of alternating foliose gametophytic and filamentous sporophytic thalli. Therefore, it is considered that the evolutionary trend of life history in the genus *Porphyra* is genetic diversity by sexual reproduction, and enlargement of populations and enhancement of distribution and survival by diversified asexual propagation.

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アマノリ属の生活史の多様性

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アマノリ属の基本的な生活史は葉状の配偶体と糸状の胞子体との異形世代交代をすることが知られている．この属に含まれる種はこれまでに約130種が知られているが，そのうち約36種については培養によってその生活史が明らかにされている．本稿では，これまでの生活史に関する報告をレビューすると共に，培養による観察結果を基に本属の生活史について検討した．さらに，葉状配偶体に形成される雌雄生殖細胞の配置から次世代の遺伝的多様化の頻度や可能性と多様な無性的繁殖様式による個体群の増大や分布の拡大能力などから，生活史の進化の方向について考察した．すなわち基本的な4つの生活史型として，I. カイガラアマノリ型 (*P. tenuipedalis* type): 雌雄同株の葉状体と糸状の胞子体を持つが，葉状配偶体は糸状胞子体の先端に形成される球状細胞から，殻胞子嚢の形成や殻胞子 (conchospore; Tseng and Chang, 1954) が放出されることなく，直接連続的に形成される．II. ヤブレアマノリ型 (*P. lacerata* type): 雌雄同種の葉状配偶体と糸状胞子体を持ち，殻胞子嚢の形成や殻胞子の放出が見られる．葉状体上に形成される雌雄生殖細胞は比較的近くまたは混成するため，多くは自家受精によって接合胞子 (zygotospore; Guiry, 1990) が作られると考えられ，次世代の遺伝的多様性は低いとみなされるが，多様な無性生殖の様式が知られており，個体群増大や分布拡大能力は大きいとみなされる．多くの種はこの生活史型に含まれる．III. フイリタサ型 (*P. variegata* type): 雌雄生殖細胞が生中線を境に左右に形成される雌雄同種の葉状配偶体と糸状胞子体を持ち，殻胞子嚢を形成して殻胞子を放出する． IV. オニアマノリ型 (*P. dentata* type): 雌雄異株の葉状配偶体を持つ．したがって，接合胞子の多くは他家受精の結果形成されたものとみなされ，次世代は遺伝的には4生活史型のなかでは最も多様性に富むものと考えられた．以上4つの基本的な生活史型には無性的，副次的な繁殖様式として，葉状配偶体からは原胞子 (archeospore; Magne, 1990) や中性胞子 (neutral spore; Hollenberg, 1958), 内生胞子 (endospore; Nelson and Knight, 1995), 無配胞子 (agamospore; Kornmann, 1994) などが知られており，糸状体からは単胞子 (monospore; Chen *et al*., 1970), 糸状体から直接形成されるプロトタラス (protothallus; Cole and Conway, 1980) からはプロトプラスト (protoplast; Cole and Conway, 1980) が報告されている．さらに葉状体の栄養細胞が受精や分割がなされることなく直接糸状体を発達させ，この糸状体上に殻胞子嚢を形成して殻胞子を放出させ，この殻胞子は発芽して葉状配偶体となる現象を今回著者が新たに報告した．以上のことから，アマノリ属に見られる4つの基本的な生活史型における次世代への遺伝的多様化や副次的な無性的繁殖様式の多様化の方向は個体群の増大や分布の拡大などと共に生き残りの生殖戦略としての進化の流れとみなした．

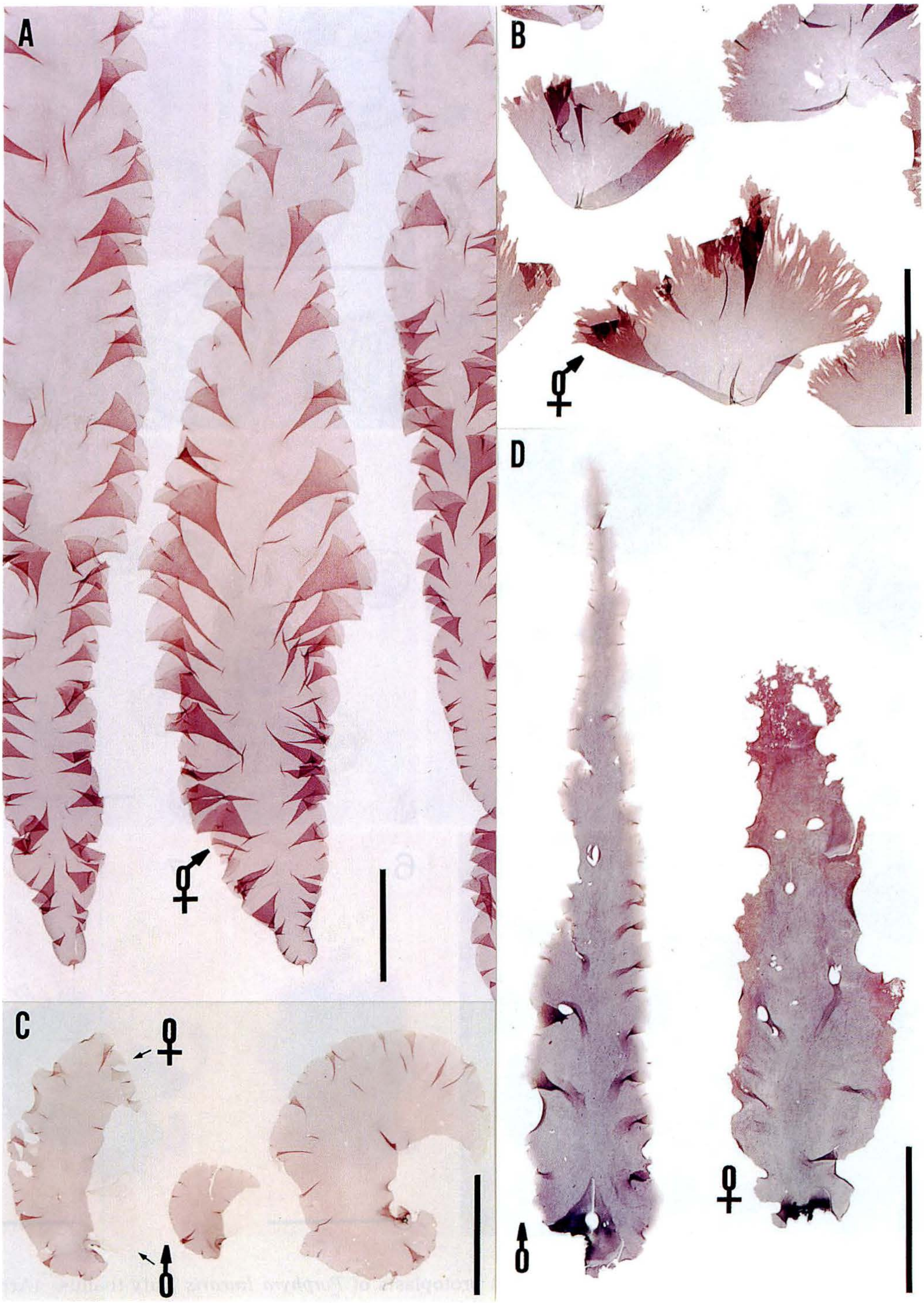

Fig. A. *Porphyra tenuipedalis* Miura. Scale bar is 3 cm for Figs. A–D.
Fig. B. *Porphyra lacerata* Miura.
Fig. C. *Porphyra variegata* (Kjellman) Kjellman.
Fig. D. *Porphyra dentata* Kjellman.