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Early development patterns and morphogenesis of blades in four species of *Porphyra* (Bangiales, Rhodophyta)

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Abstract Pigment mutants were used as genetic markers to study the early development and morphogenesis of blades in four species of *Porphyra*. In *Porphyra haitanensis*, *P. yezoensis*, and *P. oligospermatangia*, the first two divisions are transverse during conchospore germination, yielding four cells arranged in a line. These species are representative of linear development pattern in *Porphyra*. Resulting in blades with color sectors vertically arranged. In *P. katadai* var. *hemiphylla*, the first division is transverse and the upper cell divides vertically forming two side-by-side cells, and its blades are derived mostly from the upper cell showing a bilateral development pattern with two lateral parts of different colors. In this type of germination, most or the entire blade is derived from the upper cells. Some fronds of *P. katadai* var. *hemiphylla* developed in linear pattern. In addition, 9.3% of the conchospore germlings of linear development were produced at 10°C, 15.3% at 15°C, and 38.0% at 20°C for conchospore germlings of *P. katadai* var. *hemiphylla*. More linear development occurred at higher temperatures. The results revealed general trends of early developmental patterns and morphogenesis of blades within the genus of *Porphyra*. Developmental patterns and morphogenesis of blades are under the influence of temperatures.

Keywords Blade · Development · Morphogenesis · *Porphyra* · Temperature

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Introduction

Studies on the development of *Porphyra* blades with fronds, tissues, cells, and protoplast culture have drawn much attention in the past decades. These studies have called attention to various processes of development and differentiation in the genus, in which environmental factors play a role (Drew 1954; Polne-Fuller and Gibor 1984; Zheng 1984; Araki et al. 1987; Dai and Bao 1988; Hannach and Waaland 1989; Ruangchuay and Notoya 2003).

Pigment mutants of *Porphyra* are also important in studies of development and genetics (Miura 1976, 1977; Kobara et al. 1976; Migita and Fujita 1983; Niwa et al. 1993; Yan et al. 2000, 2005; Shin 2003a, b). Mutations have been used as genetic markers in investigating the bewildering positions of meiosis (Miura and Kunifuji 1980; Ohme et al. 1986; Mitman and van der Meer 1994; Yan and Aruga 2000; Xu et al. 2002; Wang et al. 2008) and in depicting the ontogenesis of the *Porphyra* blade (Ohme and Miura 1988; Mitman and van der Meer 1994; Yan et al. 2005).

Ohme and Miura (1988) analyzed the conchospore germination of *Porphyra yezoensis* with pigment mutants. They indicated that the blade derived from four meiotic cells, arranged inline in frond similar to that in *Neurospora* (Stadler 1956; Howe 1956; Stadler and Towe 1962). Yan et

al. (2005) reported the same in *Porphyra haitanensis*. In 1994, Mitman and van der Meer described another blade development pattern in *P. purpurea*. In the first division, the conchospore splits into an upper cell and a lower cell. In the second, the upper cell divides vertically into two daughter cells side-by-side, and the bottom cell splits into two cells in the horizontal direction. Under normal conditions, the frond then forms with two zygomorphic parts from the two vertically divided upper cells (Mitman and van der Meer 1994). Although these prior studies suggest that the early developmental pattern of conchospore germination decides the formations of blades of two *Porphyra* species, the details of morphogenesis remain unclear.

Similar to *P. purpurea*, the natural fronds of most *P. katadai* var. *hemiphylla* manifest a bilateral division into male and female halves. Tang and Fei (1999) and Tang et al. (2004) observed that the second cell division of conchospore could either be vertical or horizontal. In the horizontal case, the frond would develop in a linear pattern whose morphogenesis is similar to that of *P. yezoensis*, while in the vertical case, two distinct male and female parts occur in one blade. Why the two patterns coexist in one species of *Porphyra* has thus became an interesting topic.

Certainly, environment factors must play a role in the development pattern. In this study, conchospore division in *P. oligospermatangia*, *P. yezoensis*, *P. haitanensis*, and *P. katadai* var. *hemiphylla*, as well as the effect of temperature on the development of *P. katadai* var. *hemiphylla* blades, has been observed with the use of pigment mutants as markers.

Materials and methods

Four species of *Porphyra* from China were used. The blades of *P. oligospermatangia* (no. O-9404) were collected from a natural population in Qingdao (36.04 N, 120.19 E), Shandong, China in 1994; those of *P. haitanensis* (no. H-3001) were from a farming population in Xiangshan (29.48 N, 121.8 0E), Zhejiang of China in 2003; those of *P. yezoensis* (no. Y-5003) were from a farming population in Nantong (32.01 N, 120.86 E), Jiangsu, China in 2005; and those of *P. katadai* var. *hemiphylla* (K-5004) were collected from a wild population in Qingdao (36.04 N, 120.19 E), Shandong, China in 2005.

All the blades were dried without direct sunshine and transferred to the lab shortly. The reproductive sectors of the blade of each species were isolated and cultured in seawater (salinity 26.2‰) to produce free-living conchocelis. The conchocelis used in this study are deposited at the State Germplasm Bank for *Porphyra* in the Marine Fisheries Institute of Jiangsu, China.

Mutagenesis

About 1 g of free-living conchocelis from one blade of each species of *Porphyra* was kept in seawater (salinity 32.7‰) for 30 min and then transferred to 50 μg mL^{-1} *N*-methyl-*N*′-nitro-*N*-nitrosoguanidine (dissolved in sterilized seawater, salinity 26.2‰) for 60 min at 20°C. The conchocelis were collected by no. 200 mesh after being treated and washed in flowing seawater for 3 min.

The conchocelis stages of each species were separately cultured in 500 mL Erlenmeyer flasks and remained in the dark for the first 3 days. Culture seawater (salinity 26.2‰) was renewed once a day.

Culture

On the fourth day of culture, free-living conchocelis were chopped in the length of 100–200 μm and sprinkled on the shell with 1,000 segments cm^{-2} in density. The shell-boring conchocelis were cultivated in Provasoli-enriched seawater (Provasoli 1966) in 25×40-cm plastic tanks. The culture media were changed once every 3 days. Development of the conchocelis was observed weekly under a microscope. Suitable temperatures and light for culturing the shell-boring conchocelis varied with different developmental stages (Table 1).

Once conchospore formation was commonly observed under a microscope, the shell-boring conchocelis were transferred into a device with running seawater (salinity, 26.2‰) at 5°C lower than the culture temperature of mature conchocelis. Seawater was changed once a day. Seven days later, conchospores were released. Glass slides with conchospores were cultivated in seawater under 12:12 h LD photoperiod, photon fluence at 70–80 μmol photons m^{-2} s^{-1}. *P. yezoensis* was cultured at 18–20°C, *P. haitanensis* at 21–23°C, and *P. oligospermatangia* and *P. katadai* var. *hemiphylla* at 10–15°C.

Table 1 Culture conditions for different species and growth stages of conchocelis

Species	Culture temperatures of conchocelis		
	Growth[a] (°C)	Development[b] (°C)	Maturity[c] (°C)
P. yezoensis	20±2	24±1	23±1
P. haitanensis	21±1	27±1	23±1
P. oligospermatangia	19±1	25±1	20±1
P. katadai var. *hemiphylla*	19±1	25±1	20±1

[a] Photoperiod 14:10 h LD, 50–60 μmol photons m^{-2} s^{-1}

[b] Photoperiod 12:12 h LD, 50–60 μmol photons m^{-2} s^{-1}

[c] Photoperiod 10:14 h LD, 50 μmol photons m^{-2} s^{-1}

Temperature induction experiments with *P. katadai*

Nine glass slides with conchospores of *P. katadai* var. *hemiphylla* with a density of 30–50 individuals per vision scope (10×10 visual field under the microscope) were collected on a certain day, three pieces per group. They were cultivated at 10°C, 15°C, and 20°C (12:12 h LD photoperiod at 70–80 μmol photons m^{-2} s^{-1}), and after 3 days, conchospore germination was observed.

Observation

Conchospore germination and the growth of pigment mutants were examined and photographed under a Nikon E800 microscope. The germinations of 150 conchospores of *P. katadai* var. *hemiphylla* cultured at 10°C, 15°C, and 20°C were calculated, respectively.

Results

Conchospore germination of the four species

Observations on successive stages of conchospore germination were carried out by using pigment mutants as markers. Mutations appeared during the first two cell divisions of the germinating conchospores. During the first division, the conchospores of *P. oligospermatangia* divided into an upper cell and a lower cell. During the second, the two new cells split again in the same fashion. In other words, two horizontal divisions occurred in the conchospores of *P. oligospermatangia*, yielding four cells arranged in a line (1–4 in Fig. 1). A similar developmental pattern was observed during the conchospore germination of *P. yezoensis* and *P. haitanensis* (5 and 6 in Fig. 1).

In *P. katadai* var. *hemiphylla*, the elongate conchospores divided transversely forming an upper cell and a lower cell in a horizontal direction. A subsequent transverse division resulted in four cells. Then, the uppermost cell of the four-cell filament divided longitudinally.

Development of conchospore germlings

Each of the initial four cells of *P. yezoensis*, *P. oligospermatangia*, and *P. haitanensis* divided and formed two-, three-, or four-sector chimeric germlings (7–9 in Fig. 1). Each patch was derived from only one of the first four cells, and no germling had more than four sectors.

In the case of all three species, most of the basal cells stopped dividing and developed into a rhizoid after the first two divisions of conchospores, while the upper cells of the "four-cell" germlings divided and formed the dominant part of the blades (10 and 11 in Fig. 1). One of the cells in four-cell germlings perished, stopped dividing, or grew slowly. As a result, tissues derived from the other cells occupied the whole blade or most of the whole blade.

In the case of *P. katadai* var. *hemiphylla*, the basal cells normally stopped dividing after the first division of conchospores, while the two upper cells developed constantly. Generally, the blades are derived from the upper two cells and formed two sectors, one beside the other. The bilateral development of germinating conchospores often formed a zygomorphic frond (12–14 in Fig. 1).

In *P. katadai* var. *hemiphylla*, one of the two upper cells divided more slowly than another, which resulted in blades of different sizes (15 and 16 in Fig. 1).

Some conchospores in *P. katadai* var. *hemiphylla* divided horizontally. The early cells formed a line and then developed into linear chimeric germlings (17–19 in Fig. 1), which is similar to the development of *P. yezoensis*.

Effect of temperature on development of germlings

Temperature affected the developmental patterns of conchospore germination in *P. katadai* var. *hemiphylla*. The conchospores were cultured at three different temperatures, and the proportion and type of early developed germlings varied with temperature. For each temperature group, 150 individuals were examined. At 10°C, germlings with bilateral development were dominant (about 90.7%), with linear ones amounting to only 9.3%. At 15°C, more horizontally split germlings were born in the second division, with linear ones amounting to 15.3%. At 20°C, however, 38.0% of the germlings developed linearly (Table 2).

Discussion

Two early developmental patterns

Cytological observations of germinating conchospores with the aid of pigment mutants as genetic markers showed that *Porphyra* blades develop in a special order in the early stage. Horizontal division took place in the conchospore germination of *P. oligospermatangia*, *P. haitanensis*, and *P. yezoensis* and formed linearly arranged germlings. The results are consistent with former research on the genetic tetrad and development of conchospore germlings by Ohme and Miura (1988) and Yan et al. (2005), in which the linear development of conchospore germlings of *P. yezoensis* and *P. haitanensis* was described. These three *Porphyra* species thus all develop with a linear pattern.

During the normal development of *P. katadai* var. *hemiphylla*, the first upper cell vertically split into two cells, one beside the other. Accordingly, the early develop-

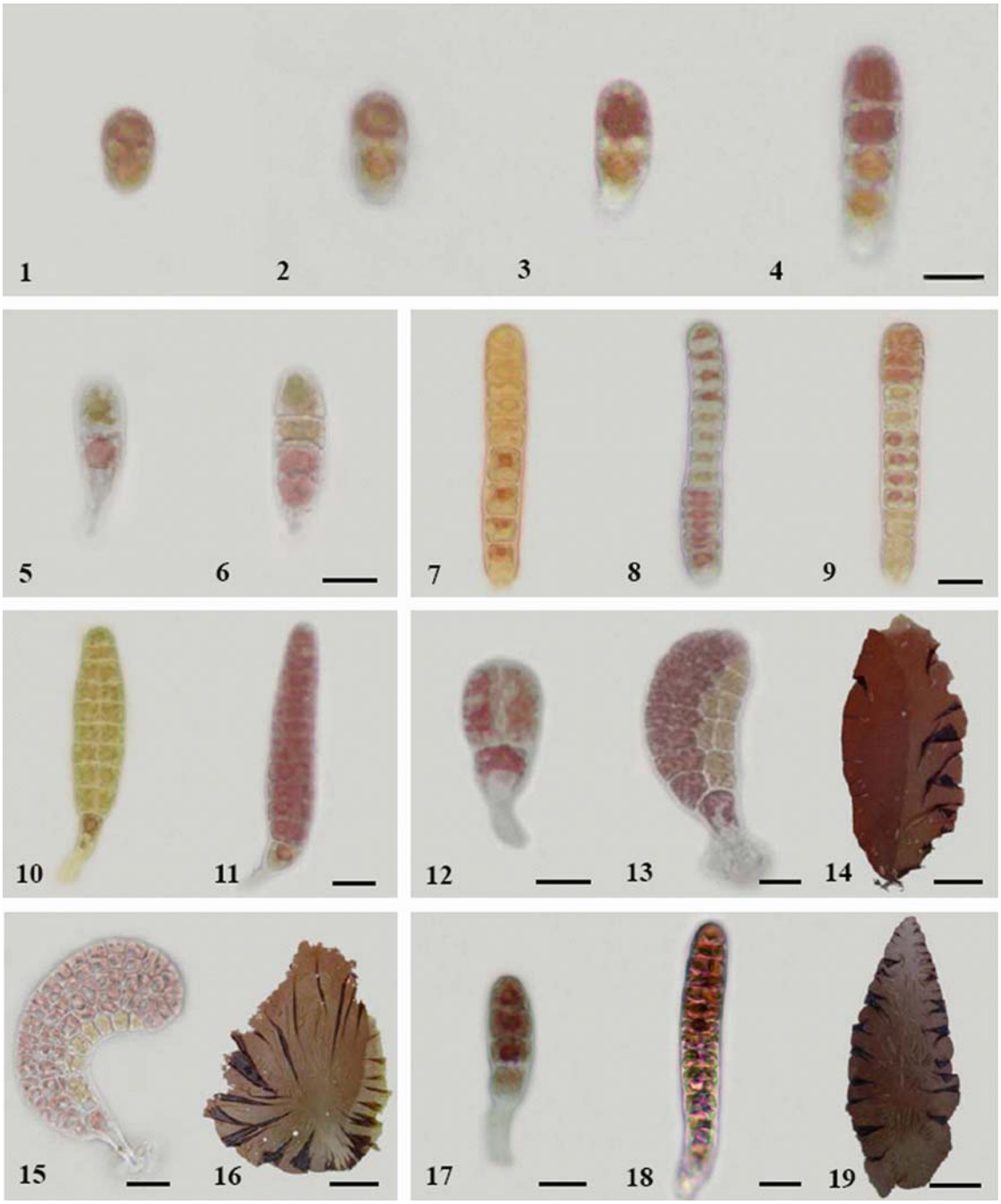

Fig. 1 *1–4* The first two divisions of germinating conchospores in *P. oligospermatangia*. *1* Conchospore germination 2 days after the spores were attached to glass slides. *2* Four hours after the first division. *3* Eight hours after the first division. *4* The second division 3 days after the attachment of conchospores. *Scale bar*=20 μm. *5*, *6* The first two divisions of germinating conchospores in *P. haitanensis*. *5* Two-cell conchospore germling. *6* Four-cell conchospore germling. *Scale bar*=20 μm. *7* Two-sector chimeric germling of *P. yezoensis. Scale bar*=20 μm. *8* Three-sector chimeric germling of *P. yezoensis. Scale bar*=20 μm. *9* Four-sector chimeric germling of *P. yezoensis. Scale bar*= 20 μm. *10* The basal cell of a conchospore germling of *P. yezoensis* with further division stopped. *Scale bar*=20 μm. *11* The basal cell of a conchospore germling of *P. haitanensis* with further division stopped. *Scale bar*=20 μm. *12–14* The mature blade of *P. katadai* var. *hemiphylla* in early divisions I. *12* Conchospores split first into an upper and a lower cell, then followed by a vertical division of the upper cell into two right-and-left cells. *13* Basal cells ceased further division, and the two upper cells developed constantly after germination. *14* The mature blades derived mostly from the upper two cells and formed two color sectors, one beside the other. *Scale bar*=20 μm in *12–13*, and 5 cm in *14*. *15*, *16* A mature blade of *P. katadai* var. *hemiphylla* in early divisions II. *15* The cell at the right of the two upper cells divided slowly. *16* The blade with different-sized parts. *Scale bar*=20 μm in 15 and 5 cm in 16. *17–19* The mature blade of *P. katadai* var. *hemiphylla* in early divisions III. *17* Four cells arranged in a line after the first two divisions of the conchospore. *18* A linear chimeric germling. *19* The mature blade of linear development. *Scale bar*=20 μm in *17–18* and 5 cm in *19*

Table 2 Development of *P. katadai* var. *hemiphylla* in different temperatures

Groups (°C)	Tests	Linear[a]	Ratio (%)	Bilateral[b]	Ratio (%)
10	150	14	9.3	136	90.7
15	150	23	15.3	127	84.7
20	150	57	38.0	93	62.0

[a] Linear development individuals

[b] Bilateral development individuals

ment gave rise to a characteristic tetrad in subsequent cell divisions. This is consistent with the findings of Tang et al. (2004) and similar to that of *P. purpurea* (Mitman and van der Meer 1994). Both species manifest bilateral development in the initial cell divisions of the conchospores.

Obviously, there are at least two early development patterns of blades in *Porphyra*, with *P. yezoensis*, *P. haitanensis*, and *P. oligospermatangia* being the three representative species of the linear development pattern and *P. katadai* var. *hemiphylla* and *P. purpurea* being representative of the bilateral pattern. Nevertheless, both of them were ordered tetrad. The four species of *Porphyra* represent general trends within the genus.

Effect of early development patterns on morphogenesis

The blades of *Porphyra* are chimeric fronds composed of four meiotic products in a single individual. Although the position and growth superiority of the initial meiotic cells might affect the morphogenesis, the formation of *Porphyra* blades is controlled mainly by early developmental patterns of the conchospore germlings.

As has been shown in many studies, meiosis occurs during the first two divisions of conchospore germination in *Porphyra* (Miura and Kunifuji 1980; Ma and Miura 1984; Burzycki and Waaland 1987; Ohme et al. 1986; Ohme and Miura 1988; Mitman and van der Meer 1994; Yan and Aruga 2000; Xu et al. 2002; Yan et al. 2007; Shimizu et al. 2008; Wang et al. 2008; Zhou et al. 2008). Observations of the early development of blades in our research and prior studies (Ohme et al. 1986; Ohme and Miura 1988; Mitman and van der Meer 1994; Yan et al. 2005) reveal that blade morphogenesis follows a pattern of four meiotic cells developing together into a chimeric frond.

Our study found that in *P. yezoensis*, *P. oligospermatangia*, and *P. haitanensis*, both the meiotic cells and frond morphogenesis develop in a linear pattern. After the second division of conchospores, nearly the whole blade of *P. katadai* var. *hemiphylla* came from the two upper cells. The blade developed in a bilateral pattern and formed a bilateral frond.

In all four species of *Porphyra*, it was regularly observed that the basal cells of "four-cell" germlings stop dividing and develop into a rhizoid cell. Interruption of further division produced chimeric fronds that lack some meiotic products (see 10 and 11 in Fig. 1). Sometimes, partial meiotic cells manifested an advantage in growth. Fast growing cells in four meiotic products broke the balance of ontogenesis and played a dominant role, while other cells had no role or a minimal role in blade morphogenesis. Accordingly, the position of meiotic cells determines the morphogenesis of the blade. This means that neither a slowly growing meiotic cell nor a basal cell plays an important part in forming the blade.

Our findings could help solve some doubts about sex determination in *Porphyra*. Mitman and van der Meer (1994) suggested that the sexually divided fronds of *P. purpurea* originated from the meiotic segregation of a pair of sex-determining alleles during early sporeling development. They also proposed that the appearance of single-sex thalli was due to the first division segregation of the sex alleles and ceasing of division of basal cells, or to the death of a meiotic cell in the tetrad. The results in our research verify their hypothesis. Furthermore, the evidence that we have found in *P. purpurea* could be used to explain the mechanism of sex determination in *P. katadai* var. *hemiphylla* and *P. haitanensis* and the species whose sex phenotype is similar to that of *P. purpurea*. For these species, they also both have monoecious and dioecious fronds.

Temperature effect on the development pattern of *P. katadai* var. *hemiphylla*

The present study demonstrates that temperature decides the proportion of two early development patterns in *P. katadai* var. *hemiphylla*. Ambient high-temperature induces more linearly developed individuals than an ambient low-temperature.

Scientists have conducted extensive research on individuals, tissues, and protoplast culture to study the blade development of *Porphyra* (Drew 1954; Kapraun and Luster 1980; Polne-Fuller and Gibor 1984; Araki et al. 1987; Dai and Bao 1988; Yan and Wang 1990). Rich evidence has been proven that points to various modes of development and expression of the species that are clearly affected by environment factors (Chen 1986, 1987; Polne-Fuller and Gibor 1987, 1990; Hannach and Waaland 1989; Notoya 1997).

Porphyra katadai var. *hemiphylla*, a cold-temperature species living between 5°C and 15°C (Tseng and Chang 1978), seems to be such a species. Wild populations of this species are distributed throughout Liaodong Peninsula and Shandong Peninsula of China where the temperature is

relatively low. Nearly all fronds of this species found in the field have monoecious blades, develop in a bilateral pattern, and are vertically divided into male and female halves with a clear line between the two halves. It is considered to be an abnormal development under relatively high temperature, though the linear pattern is noticed in the culture in the present study. The bilateral development pattern is the normal mode of conchospore germination. *P. katadai* var. *hemiphylla* is still a bilateral development species.

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