Early life stage development of *Gloiopeltis furcata* (*Gigartinales, Endocladiaceae*) from northern China

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***Gloiopeltis furcata* (*Postels et Ruprecht*) *J. Agardh* is a commercial red alga with high value in nutraceuticals and pharmaceuticals. To enrich information on its life history, the early developmental process of *G. furcata* from northern China was investigated using free-hand section and microexamination methods. Early life stage development includes the formation of carpogonial branch, spermatangia, cystocarp tetrasporangia, and spores germination. Results showed that one auxiliary cell and one adjacent supporting cell constituted an ampulla. Auxiliary cell was usually near the basal part of the ampulla and generated several two to three celled carpogonial branches. One spermatangial mother cell originated in the superficial cortical cell and produced single spermatangia. After fertilization, carpogonium formed a connecting filament which fused with the auxiliary cell ultimately. Many branched gonimoblast filaments were produced from auxiliary cell and generated into carpospores. Mature cystocarps protruded on the thalli surface showing some subspherical-shaped structures. Tetrasporangium developed from the inner cortical cell generated four tetrasporangia by cruciform division. Mature tetraspores and carpospores were released, attached to the bottom of Petri dishes through the stickum within 12 h, and then divided through regular binary fission. Undergoing a month of cultivation, the spores grew up to discoid crusts with diameters ranging from 55 to 60 µm. Growth of *G. furcata* was initiated with the dome-shaped apical cell division to form the central axial structure, being the first to confirm the occurrence of apical growth of this species.**

Keywords: *Gloiopeltis furcata*, Early development, Spore germination, Discoid crust.

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Introduction

The red alga *Gloiopeltis furcata* (*Postels et Ruprecht*) *J. Agardh* belonging to *Endocladiaceae*, *Gigartinales*, is distributed widely along the coasts of China, Japan, and Korea [1]. This species has a middle to high intertidal distribution [2]. The genus *Gloiopeltis* was arranged in *Gloiosiphoniaceae* since 1928, and then was divided into *Endocladiaceae*, *Cryptonemiales* proposed by Kylin [3] for the algal material from the coast of north China. Subsequently, the family *Endocladiaceae* was reclassified under *Gigartinales* from *Cryptonemiales* [4] based on an unequivocal molecular phylogeny support as early as 1996 [5]. Given the high biological and economic value, *G. furcate* is widely used in funoran

production, silk industry, and extraction of medicinal anticarcinogenic products in recent years [6, 7]. However, most economic harvest comes from wild stock; large scale artificial seedling culture is urgently needed for a better understanding for early life stage development of the species.

On the initial stage of reproduction, studies mainly appeared in early works. Chiang [8] described the morphology of ampullae, as well as the developments of carposporangia and spermatangia in *G. tenax* (*Endocladiaceae*, *Gigartinales*); the formation process of cystocarp was also observed in *G. furcata*, generating many gonimoblast filaments during its development [3, 9, 10]. However, detailed information regarding early life development of *G. furcata* is limited, thereby restricting practical application of seedling culture techniques [8]. As the critical organization of reproductive development, auxiliary cell and its topographic position have been paid close attention to in marine red algae [11, 12, 13]. Auxiliary cells were located in the terminal and intercalary of the auxiliary cell branch in *Acrosymphyton firmum* (*Gigartinales, Rhodophyta*) [13] and *Dudresnaya lubrica* (*Gigartinales, Rhodophyta*) [11] respectively; however, they remain ambiguous or unresolved in *Gloiopeltis*. The only description in *G. tenax* revealed that the auxiliary cell was close to the basal part of ampullae. In addition, as an important vegetative character, the apical organization is widely accepted that almost all florideophytes have it, but is distinct in few species due to the finding of apical cell [14]. Other studies on the vegetative development in red algae, like *Sarcodiotheca gaudichaudii* (*Gigartinales, Rhodophyta*) [15], *Martensia elegans* (*Ceramiales, Rhodophyta*) [16], and *Veleroa setteana* (*Ceramiales, Rhodophyta*) [17], have confirmed the occurrence of apical growth; however, it is still unclear in *G. furcata*.

To our knowledge, the information on early life stage development of *G. furcata* is scattered, and no systematic research has been conducted. In the present study, we investigated the early growth development of this species from reproductive onset through to formation of discoid crusts in detail.

Materials and Methods

Specimens were collected from middle intertidal rocks along the coast of Xiaoheishan Island (37°57′ N, 120°38′ E), Yantai, Shandong Province, China, during October, 2011 to June, 2012. Some samples for the morphological study were cultured in fresh seawater and others were preserved in 5% buffered formalin in seawater. The longitudinal and transverse sections of thalli were cut with double-edged razor blades. Free-hand sections were treated with 1% aqueous aniline blue acidified with 1% hydrochloric acid [18, 19] and made permanent if necessary by mounting in neutral resins. The whole-mount sliders, if necessary, were handled with an alcohol-xylene series (15%, 30%, 45%, 60%, 75%, 95%, and absolute alcohol; 50% absolute alcohol and 50% xylene; xylene), and then mounted in neutral resins. These procedures facilitated to clear the material so that it was easy to focus through several layers of cells to display the internal structures [20].

During the reproductive period, mature thalli collected from intertidal rocks were rinsed in filtered seawater, dried in the shade for 2-3 h and then were placed in a glass flume containing sterilized seawater to induce spore liberation. Following collection, the density of spore was adjusted to 400 spores/ml and a total of 1.5×10^3 spores were poured into each Petri dish (60 mm × 15 mm). All spores attached to Petri dishes were cultured in light and temperature controlled incubators (Zhujiang, China) under a 12:12 h of light:dark photoperiod with a light intensity of approximately 150 μmol photons/m^2·s and 16 ± 0.5°C (corresponding to the ambient surface seawater temperature at the collection site). Seawater renewed every day was filtered through fine sand and stored in the dark. The development process from spores to discoid crusts was observed every day using a

digital imaging microscope (Olympus DX43, Japan). The growth of the multicellular discoid crusts was evaluated by measuring the diameter of discoid crusts on each Petri dish. Thallus habit photographs in natural habitat were taken with a Nikon D7000 digital camera (Nikon Crop., Tokyo, Japan); photomicrographs were obtained using the Olympus microscope equipped with a DX43 digital camera (Olympus Optical Co., Tokyo, Japan), and the resulting files were converted to figures by computer software.

Results and Discussion

Thallus Habit

The general morphological characters of *G. furcata* thalli were erect and subcylindrical to cylindrical, dichotomously branched (Figure 1a). *G. furcata* was closely attached to the rocky substratum by a small discoid holdfast 4-8 mm in diameter that produce short cylindrical main axes 5-10 mm long, from which one to several fronds arose. Whole thallus, amaranthine to dark purple in appearance, 4-10 cm long and 2-4 mm across, was leathery and tensile in texture with a smooth surface. The apices of thalli were bluntly rounded or tapering (Figure 1a, 1b, 1c).

Gametophytes of *G. furcata* were dioecious, male gametophytes (Figure 1b) smaller than female gametophyte (Figure 1c) and tetrasporophyte (Figure 1d). The gametophytes were superficially similar to the tetrasporophytes during growth period; however, the latter were robust and more branched (Figure 1c). Tetrasporangia derived from tetrasporophytes were scattered into the cortex without any tubers, as well as the surface of male gametophyte, whereas cystocarps were acinose and close-grained throughout the surface of female gametophytes (Figure 1c).

Vegetative Development of Thallus

Growth of *G. furcata* from seedling was initiated by the division of a dome-shaped apical cell 15 to 20 µm in diameter (Figure 1e). The apical cell generated isodiametric axial cells which grew up to lengths of 20 µm and diameters of 8 µm and occurred only in apical or juvenile parts of fronds. A secondary cell was generated below the apical cell, and then divided further to produce few transverse pericentral cells around it (Figure 1e). Almost all pericentral cells close to axial cells continued to divide into primary cell rows, which produced dichotomously second to fifth cell rows. Fourth to fifth order cells were very common and finally constituted thallus surface as terminal cells (Figure 1f). The sizes of those cells belonging to rows diminished gradually from inside to outside. Mature thalli were hollow, retaining merely cortical cells and few layers of medullary cells (Figure 1g). However, main axes were complete since the undegenerated medulla (Figure 1h). The length of outer cortical cells of thalli varied from 6 to 12 µm, whereas pericentral cells varied from 30 to 35 µm (Figure 1f). The inner cortex consisted of 3 to 5 layers of ovoid cells; however, the superficial cells were short clubbed and perpendicular to the compact and smooth surface (Figure 1i).

Secondary thallus branches were generated from the cortical cells of primary branches. Inner cortical cells below the developing branch began to elongate and became the medullary layer of new subordinate branch. With the growth of new branches, the medulla degenerated gradually to form the hollow structure (Figure 1g). Remaining medullary cells were colorless or yellowish refractive contents, varying from 15 to 20 µm in diameter. In addition, new branches generated some subordinate branches as well. In this way, the species *G. furcata* formed an irregularly radial shape (Figure 1c and 1d).

Growth of *G. furcata* from discoid crusts to juvenile seedlings was dependent on the division of the apical cell, but there have been no detail documents about its development. As meristematic cell, the apical cell divided into a secondary cell immediately below it. Several pericentral cells were generated by transverse or oblique divisions of the secondary cell which sequentially divided to form the axial cells. All

cells were derived from the pericentral cells by dichotomy which was one of the main development patterns for red algae [15]. The way of apical cell division in *G. furcata* closely resembled that of *Gloiosiphonia* (*Gloiosiphoniaceae, Rhodophyta*) [21, 22] and *Phycodrys* (*Delesseriaceae, Rhodophyta*) [23], thereby confirming the occurrence of apical growth in early development of the genus *Gloiopeltis*.

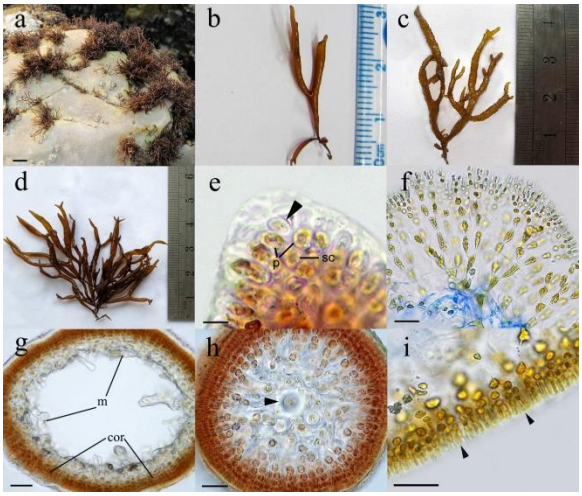

Figure 1. Habit and vegetative morphology of *Gloiopeltis furcata*. a. i*n situ* habit of *Gloiopeltis furcata* in intertidal zone, scale bar = 1 cm. b. surface view of mature male gametophyte. c. female gametophyte showing mature cystocarps on thallus surface. d. tetrasporophyte showing bushy dichotomous fronds. e. longitudinal section of the apex showing the dome-shaped apical cell (arrowhead) and few pericentral cells (p) divided from the second cell (sc), scale bar = 20 µm. f. transverse section of subcylindrical thallus showing the cortical cells (cor), remaining medulla (m) and hollow structure, scale bar = 100 µm. g. transverse section of cylindrical main axes showing central axial cells (arrowhead) and refractive medullary cells, scale bar = 50 µm. h. transverse section of thallus showing the radial cortex cells divided by pericentral cells dichotomously, scale bar = 50 µm. i. transverse section of cortex showing the short clubbed exodermis cells (arrowhead) perpendicular to thallus surface, scale bar = 20 µm.

Formation of Carpospores

Development of carpogonial branch: Carpogonial branches were produced throughout the female gametophyte, and were primarily two or three celled, orienting at different angles towards the surface with reflexed trichogynes ultimately passing through the cortex (Figure 2a). In general, 5 to 8 carpogonial branches consisted in an ampulla. The first cell below carpogonium was arched to ovoid in shape, and the second one was bigger and rounded (Figure 2b). However, the carpogonium was conical with a long and curved or twisted trichogyne. These cells of carpogonial branches were stained deeper than surrounding cortical cells and measured 18 to 20 µm long (Figure 2b). Following the second carpogonial branch cell, there was an auxiliary cell which was derived from the supporting cell (Figure 2b). The auxiliary cell was usually near the basal region of the ampulla and larger than other nearby cells. Only one auxiliary cell and one supporting cell were produced in an ampulla and were adjacent to each other (Figure 2b). In addition, the supporting cell, ovoid- or elongated-shaped with 5 to 7 µm in diameter, formed few four- to five-celled sterile filaments during the development of carpogonium (Figure 2b).

Development of spermatangia: One spermatangium approximately 1 to 2 µm in diameter, ovoid-shaped, was produced only by each spermatangial mother cell which was transformed from the superficial cortical cell (Figure 2h). The spermatangia could be recognized by the deeply stained tops. Mature spermatangia were released via the disintegrated part of the thallus surface.

Development of cystocarp: When extended out through the thallus surface, the trichogyne contacted with the spermatangia. Following fertilization, the carpogonium enlarged and produced a connecting filament which crept towards the auxiliary cell and fused with it ultimately (Figure 2c). At the early stage of cystocarp development, the auxiliary cell became slightly inflated and produced the gonimoblast initial which developed towards the thallus surface (Figure 2d).

During the process of cystocarp development, many gonimoblast filaments were branched dichotomously and radially and produced from the gonimoblast initial (Figure 2d). All cells of

gonimoblast filaments, except for the gonimoblast initial, became carpospores and finally grew up to a dense mass which stained deeply (Figure 2e). Mature cystocarps, without pericarp and ostium, were scattered on the thallus surface and showed some subspherical-shaped structures with diameters varying from 250 to 300 µm (Figure 2f). Mature carpospores were spherical with diameters of about 20 µm (Figure 2g). By contrast, the unfertilized carpogonial branches gradually degenerated. During the development of gonimoblast filaments, many branched sterile filaments were generated from the supporting cell and the neighboring inner cortical cells. They grew towards the center of the thallus and their cells were spherical-shaped, 6 to 8 µm in diameters (Figure 2b and 2d).

In our study, the development of the carposporangia and spermatangia of *G. furcata* agrees with the results obtained in previous studies [3, 8, 10]. However, ampullae of *G. furcata* composed of more than one auxiliary cell, which mentioned in the study of Fan and Fan [10], was not found in the present work. In addition, the greatly enlarged auxiliary cell after being fused with the connecting filament, as described in *G. tenax* by Chiang [8], was also not observed in *G. furcata*. The branched sterile filaments were generated from the supporting cell or the adjacent inner cortical cells, and developed towards the center of the thallus. They may have the function similar to nurse cells in *Gelidiales*, which could offer nutrition to the development of carpogonium.

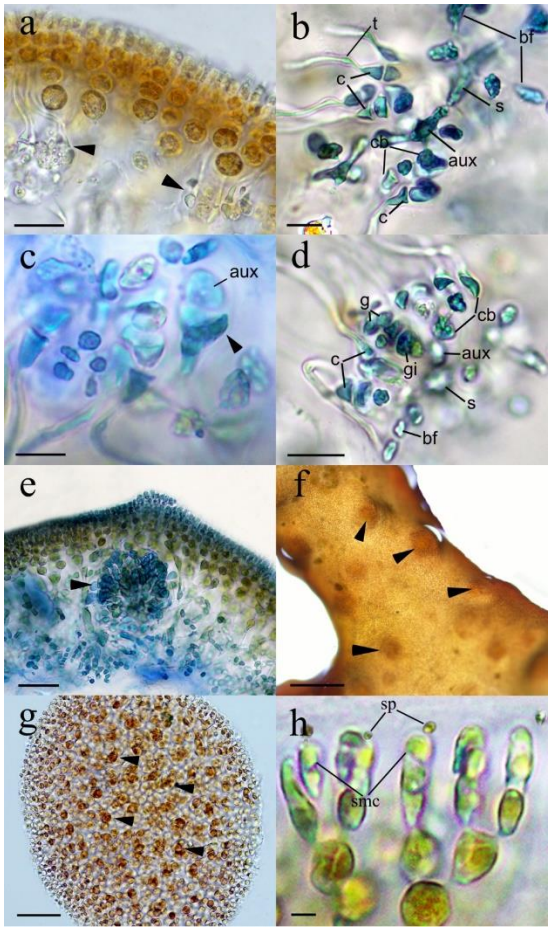

Figure 2. Reproductive anatomy of *Gloiopeltis furcata*. a. ambulla (arrowhead) consisting of 5 to 8 carpogonial branches, scale bar = 20 µm. b. early stage development of carpognial branch showing the supporting cell (s), the auxiliary cell (aux), three-celled carpogonial branches (cb), conical carpogonium (c) with a long curved trichogyne (t) and branched sterile filaments (bf), scale bar = 20 µm. c. a connecting filament (arrowhead) creeping towards the auxiliary cell (aux), scale bar = 10 µm. d. postfertilization stage showing gonimoblast initial (gi) generating some gonimoblast cells (g). Note that the supporting cell generating some branched sterile filaments (bf), scale bar = 20 µm. e. transverse section of cystocarp showing immature carpospores (arrowheads) forming a cloddy structure, scale bar = 20 µm. f. mature cystocarps (arrowhead) protruding on the surface of thallus, scale bar = 300 µm. g. transverse section of cystocarp showing several mature carpospores, scale bar = 50 µm. h. development of spermatangia (sp) from spermatagial mother cells (smc), scale bar = 10 µm.

Development of Tetrasporangia

Tetrasporangium was generated throughout the tetrasporophyte. Mature tetrasporangia were scattered merely beneath the fronds surface of the entire thallus (Figure 3a). Tetrasporangial initials were transformed from fourth to fifth cortical cells access to thallus surface and subsequently extended longitudinally to form the elongated shape (Figure 3b). Cortical cells surrounding the tetrasporangia had no obvious morphological change. The elongated-shaped tetrasporangia initials with the long axis perpendicular to thallus surface were stained deeper than the surrounding cortical cells. Subsequently, whole tetrasporangium grew transversely to form the ovoid shape (Figure 3c). Each tetrasporangium underwent successive divisions to generate four cruciformly arranged

tetrasporangia (Figure 3d). The pit connections between tetrasporangia and their surrounding cells disappeared in mature tetrasporophyte, while the margin of tetrasporangia almost reached the thallus surface. Mature tetraspores were spherical, approximately 20 µm in diameter and were being released (Figure 3e).

The family of *Endocladiaceae* mainly contains two genera *Endocladia* and *Gloiopeltis*, which are characterized by different morphological features in life history. The genus *Endocladia* had irregularly cruciately divided tetrasporangia, whereas it is cruciformly divided for *Gloiopeltis* [24].

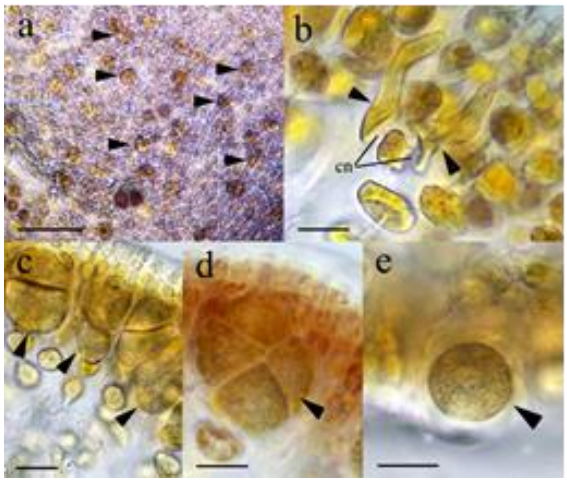

Figure 3. Tetraspores development of *Gloiopeltis furcata*. a. surface view of mature tetrasporophyte showing the tetrasporangium (arrowheads) beneath the surface, scale bar = 100 µm. b. transverse section of tetrasporophyte showing the tetraspsorangial initials (arrowheads) and the connecting pits (cn), scale bar = 20 µm. c. immature tetrasporangium (arrowhead) scattering in the inner cortex, scale bar = 20 µm. d. tetrasporangium undergoing successive divisions to generate four cruciformly arranged tetrasporangia (arrowheads), scale bar = 20 µm. e. mature tetrasporangia (arrowhead) showing a spherical shape, scale bar = 20 µm.

Early Development of Carpospores and Tetraspores

Spores were released in profusion from cystocarps and tetrasporangia after 3 h in the shade condition. All spores were spherical in shape and approximately 20 µm in diameter, with a nucleus surrounded by abundance of yellowish plastids (Figure 4a). No accessories were adjacent with spores, and they sank to the bottom of Petri dishes through the action of gravity and attached to the subbottom with the stickum within 12 h.

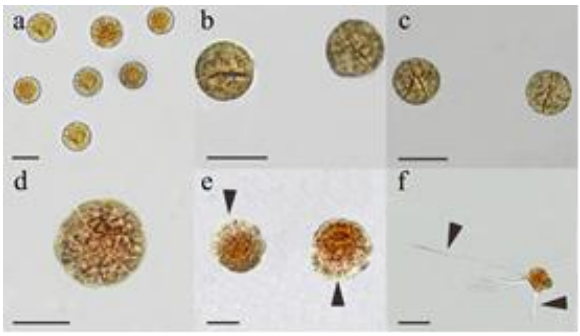

Figure 4. Spores development of *Gloiopeltis furcata*. a. spores attached to the discoid crust, scale bar = 20 µm. b. spores dividing into two cells transversely through the center, scale bar = 20 µm. c. second cell division of spores, scale bar = 20 µm. d. undergoing several divisions, the spore becomes a multicellular aggregate, scale bar = 20 µm. e. many parenchymal cells (arrowhead) were divided surrounding the multicellular, scale bar = 20 µm. f. several translucent rhizoids (arrowhead) were generated from the discoid crust, scale bar = 50 µm.

After attachment of 20 h, the first division for spores was transverse through the center, and spores developed into a two-celled stage (Figure 4b), followed by the second division perpendicularly or obliquely to the first division plane in the next 8 h (Figure 4c). More than 90% spores underwent division after 32 h attachment. The speed of division decreased with the increase of cell number. Undergoing several divisions, the spores developed into multicellular aggregates with the diameters varying from 30 to 35 µm (Figure 4d). Many parenchymal cells were divided surrounding the multicellulars at 3-4 days after attachment (Figure 4e). As a result, multicellulars increased in size and became the initial discoid crusts which varied from 35 to 40 µm in diameters and the center was obviously thicker than edges (Figure 4e). Ten days later, one to more translucent rhizoids originated from the edge of discoid crusts, about 2.5 µm in diameters and

grew up to 200 μm in length after 13 days of development (Figure 4f). By fifth days after attachment, all surviving spores in Petri dishes had almost germinated into discoid crusts. One month later, the sizes of discoid crusts expanded to approximately 55 μm; however, no other significant morphology difference was found in comparison with 15 days of discoid crusts.

The germination process of spores was influenced by various environmental factors, such as, photo flux density, desiccation, temperature and salinity [25, 26]. *G. furcata* distributes mainly in middle to high intertidal zone, and spores frequently experience relative strong photo flux density (PFD) during low tide. PFD has no significant effects on spores attachment and the formation of discoid crusts, but significantly influence the discoid crusts growth, sprouting and survival, and spores developed best under moderate intensity of PFD [26]. In addition, short-term desiccation significantly benefits discoid crusts growth. This may be because desiccation inhibits the growth of other organisms and increases the disease resistance. It has been reported that the temperature has more important effects than light. The optimum temperature ranges narrowly between 12-16°C for attachment, germination and survival of discoid crusts. Effects of salinity on the development of spores have been illustrated in *G. tenax* by Wu *et al*. [27], who reported that *Gloiopeltis* had strong tolerance ability to salinity fluctuation, which is an ecological precondition for thalli surviving and growing in the upper intertidal zone.

Conclusions

This study shows the systematic process of early development stage of *G. furcata*, and enriched the information of early life history. The species of *G. furcata* held a complex early stage development. Two or three celled carpogonial branches and an auxiliary cell were generated in the same fertile branch. Subsequently, several carpogonial branches formed an ampulla. Cystocarps protruded distinctly above the thallus surface without ostiole and pericarp. Only one spermatium was generated from a spermatangium which derived from the superficial cortical cells. Tetrasporangia divided by the tetrasporangium were arranged cruciformly and hided into the outer cortex. Spores germinated to form discoid crusts through regular binary fission.

Conflict of interest

The authors confirm that this article content has no conflicts of interest.

Acknowledgements

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