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Morphological Characteristics of Brown Alga *Spatoglossum crassum* Tanaka (Dictyotaceae, Dictyotales), New to Korea

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Morphological and phenological characteristics of brown alga *Spatoglossum crassum* Tanaka new to Korea were described based on the field and the indoor cultured plants. The taxonomic characteristics of the plants were agreed to those from the type locality – submerged reproductive organs in cortex, anatomical features, and absence of phaeophycean hairs on the surface. But they have rudimentary midrib on lower portion of thallus. We can observe the young plants on November, adult ones in June, and senile ones in August. This species has an annual life-cycle in the field, starting with germlings in early November. The differentiation of thallus is quite different from other species of genera in tribe Zonarieae, *e.g. Zonaria* and *Homoeostrichus*. Three different tissues, meristoderm, cortex and medulla are discerned. The outmost cortical one celled layer as a meristoderm produce cortex by unequal periclinal division. In the apical cell division, the primary inner cells are developed into 3-4 cell layered medulla of thallus. The distribution of this species extends from Korea to Shizuoka Peninsula (34°40'N) Japan, which is the type locality of this species.

Key Words: morphogenesis, morphology, phenology, *Spatoglossum crassum* Tanaka

INTRODUCTION

Genus *Spatoglossum* Kützing (1843) were established based on the *Dictyota solieri* Chauvin *ex* Montagne including three species, two of which were transferred to other genus, and *S. solierii* (Chauvin *ex* Montagne) Kützing was identified as lectogenerictype (Papenfuss 1977). They have been distinguished from others of Dictyotales by the following characteristics; polystromatic thallus, dichotomous or sub dichotomous branches, a small group of meristematic cells aligned in a line at the apex, absence of midrib on the thallus (Lindaur *et al.* 1961; Womersley 1987; Tanaka 1991). This genus is distributed world wide and 17 species have been reported from the tropical to the temperate region (Tanaka 1992). Three species, *Spatoglossum pacificum* Yendo, *S. crassum* Tanaka and *S. latum* Tanaka have been reported from the West Pacific. *S. crassum* was classified and distinguished from *S. pacificum* by having buried sporangium in the cortex and no phaeophycean hair tufts, and from *S. lactum* by thick blades and no phaeophycean hair tufts (Tanaka 1992).

Only one species, *S. pacificum* Yendo has been reported along the coast of Korea (Kang 1966; Lee and Kang 1986; Lee and Lee 1996). In this study, we make description on the biological characteristics of *S. crassum* Tanaka, based on the field and the indoor cultured plants.

MATERIALS AND METHODS

The plants from the east and south coast of Korea were used in the morphological and phenological survey (Fig. 1). The collection was done from January 1993 to March 2004. The phenological observation was made on the subtidal population of Anin by monthly observation from August 1994 to September 1995.

Collected plants were preserved in 5-10% formaldehyde-seawater for the morphological analyses. Voucher specimens were deposited in the herbarium of Kangnung National University. Some living plants were brought to laboratory and kept for indoor culture. The morphological observations were done for the plants having the height more than 15 cm and intact thallus collected on April. Microsections of thallus were made by Leica Cryocut 1800 microtome™ (Nassloch, Germany)

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and were stained with 1% aqueous aniline blue solution, and were mounted in 1-5% corn syrup for microscopic observation. Illustration was made using Camera lucida (Nikon 231412^{TM}, Japan). The structures of sporangia were described with the adult plants collected in June.

The indoor culture was initiated with the spores released by the small sliced adult thalli free from epiphytes. Culture medium was sterilized and enriched natural seawater (Provasoli 1968). Cultures were kept at 20 ± 1°C under white fluorescent light at 50-70 $\mu mol \cdot m^{-2} \cdot sec^{-1}$ and 14:10 LD photoperiod and enriched weekly.

RESULTS

Description of species

***Spatoglossum crassum* Tanaka (1991. 574, Figs 10-23)**

Description: Thalli bright brown, complanate foliaceous, epilithic, up to 30 cm in height, erect with matted rhizoidal holdfast, di(tri-)chotomous or irregularly branched, no phaeophycean hair; growth by group of apical cells in round or depressed apex; apical cells oblong, arranged in row with 20-35 cells, 50-57 μm height, 12-15 μm in width; midrib absent but rudimentary in basal portion; branches 1.5-2.0 cm broad, 300-600 μm thick, slightly tapered at base; meristoderms consisted of outmost cortical cells, oblong, 36-38 × 27-29 μm in size; cortical cells derived from unequal periclinal division of meistoderm, arranged in transverse row, oblong or polyhedral, 13-22 μm diameter; meiosporangia scattered on middle portion, submerged, subspherical or conical in surface view, elliptical to cylindrical in trans sectional view, 112 × 85 μm size; oogonia submerged in dense or paired with 3-6 cells, subspherical to elliptical in trans sectional view, 80 × 51 μm size; antheridia densely scattered with 30-40 cells, submerged or partly-submerged, cylindrical in trans sectional view, 78 × 32 μm size.

Type locality: Susaki, Shimoda-shi, Shizuoka Prefecture, Japan (34°40′N, 139°00′E)

Korean name: Hwangsaek-gasigumulbatangmal

Specimens examined: KNU 2010395, Gangnung Anin (Eastern coast) 25 XI 1993; KNU 2010396, Gangnung Anin (Eastern coast) 20 XII 1993; KNU 2010397, Gangnung Anin (Eastern coast) 25 XI 1994; KNU 2010398, Gangnung Anin (Eastern coast) 20 XII 1994; KNU 2010399, Gangnung Anin (Eastern coast) 20 I 1995; KNU 2010400, Gangnung Anin (Eastern coast) 28 II 1995; KNU 2010401, Gangnung Anin (Eastern coast) 14 III 1995; KNU 2010402, Gangnung Anin (Eastern coast) 15 IV 1995; KNU 2010403, Gangnung Anin (Eastern coast) 15 V 1995; KNU 2010404, Gangnung Anin (Eastern coast) 29 V 1995; KNU 2010405, Gangnung Anin (Eastern coast) 19 VI 1995; KNU 2010406, Gangnung Anin (Eastern coast) 3 VII 1995; KNU 2010407, Gangnung Anin (Eastern coast) 20 I 1996; KNU 2010408, Gangnung Anin (Eastern coast) 28 II 1996; KNU 2010409, Gangnung Anin (Eastern coast) 23 VIII 2001; KNU 2010410, Gangnung Anin (Eastern coast) 19 III 2004; KNU 2010411, Goseong-gun Gyoam (Eastern coast) 5 V 2000; KNU 2010412, Goseong-gun Ayajin (Eastern coast) 14 XI 1998; KNU 2010413, Sockcho Yeongumjeong (Eastern coast) 5 V 2000; KNU 2010414, Yangyang-gun Jeonjin (Eastern coast) 5 V 1994; KNU 2010415, Gangnung Sodol (Eastern coast) 25 XI 1993; KNU 2010416, Gangnung Jeongdongjin

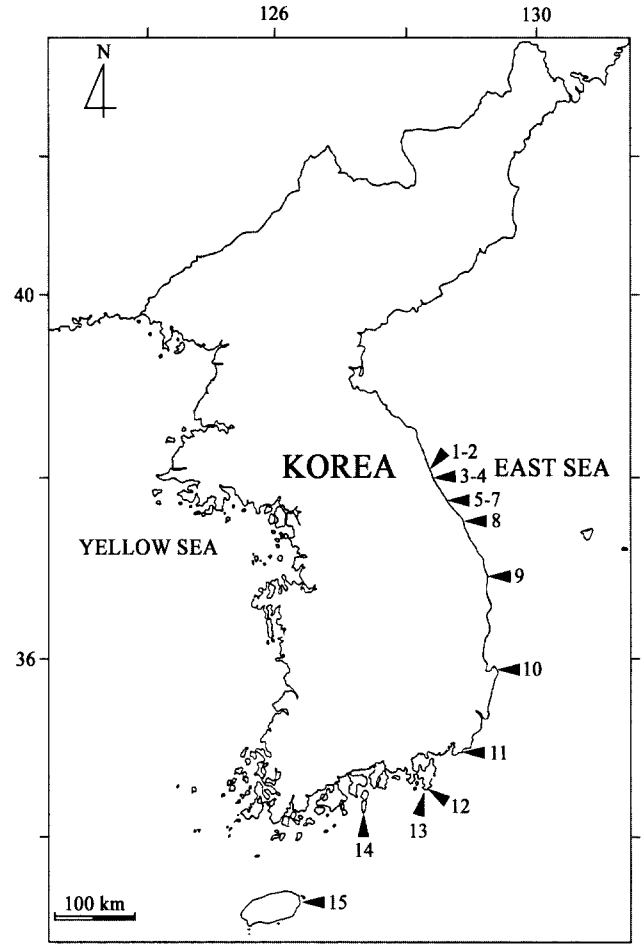

Fig. 1. A map showing the colleting sites along the coasts of Korea. 1-Goseong-gun Gyoam, 2-Ayajin, 3-Sockcho-si Yeongumjeong, 4-Yangyang-gun Jeonjin, 5-Gangnung-si Sodol, 6-Anin, 7-Jeongdongjin, 8-Samchok-si Hujin, 9-Uljin-gun Jukbyeon, 10-Guryoungpo, 11-Gijang, 12-Geoje-si Haegumgang, 13-Sobyeongdaedo, 14-Yeosu-si Dolsando, 15-Jeju Island Udo.

(Eastern coast) 23 VIII 2001; KNU 2010417, Hujin (Eastern coast) 1 III 1996; KNU 2010418, Jukbyeon (Eastern coast) 30 X 1993; KNU 2010419, Guryongpo (Eastern coast) 14 VII 1994; KNU 2010420, Gijang (Eastern coast) 1 VIII 1996; KNU 2010421, Heagumgang (Southern coast) 14 VII 2000; KNU 2010422, Sobyeongdaedo (Southern coast) 14 VII 2000; KNU 2010423, Dolsando (Southern coast) 5 VII 2001; KNU 2010424, Jeju Island Udo (Southern coast) 15 VIII 1985.

Habitat and Phenology

The plants of *S. crassum* Tanaka were collected from the coast of, Gyoam, Ayajin, Yeongumjeong, Jeonjin, Sodol, Anin, Jeongdongjin, Hujin, Uljin-gun Jukbyun, Guryoungpo, Gijang, Haegumgang, Sobyeongdaedo, Dolsando, and Jejudo Island in Korea during this study (Fig. 1). They grew in clusters on the rock at the subtidal zone ranged from 2 to 5 m in depth with less wave effect in Gangnung, Gijang and Guryoungpo, and at 10 m depth in Jejudo Island in the early August. Plants annually grew on rocks in clusters with large rhizoids.

The plants of this species could be collected every month from November to late July in Anin. The germlings were observed in late November and grew up to 7 cm height, to 15 cm in April and then grew fast to 30(-40) cm from May to early July (Figs 2A; 3A-F). They became senile thereafter. Several old plants could be found on the shadowed rocks in late July, but not after mid August.

The reproductive cycle of this species were determined by counting the plants with reproductive organs among the observed plants. All 38 plants collected on 15 May were vegetative and all 14 plants collected on 29 May 1995 had reproductive organs, sporophytes (71.4%) and gametophytes (28.6%). From 19 plants collected on 30 July 1995, the sporophytes (15.7%) and gametophytes (84.2%) were counted (Fig. 2B).

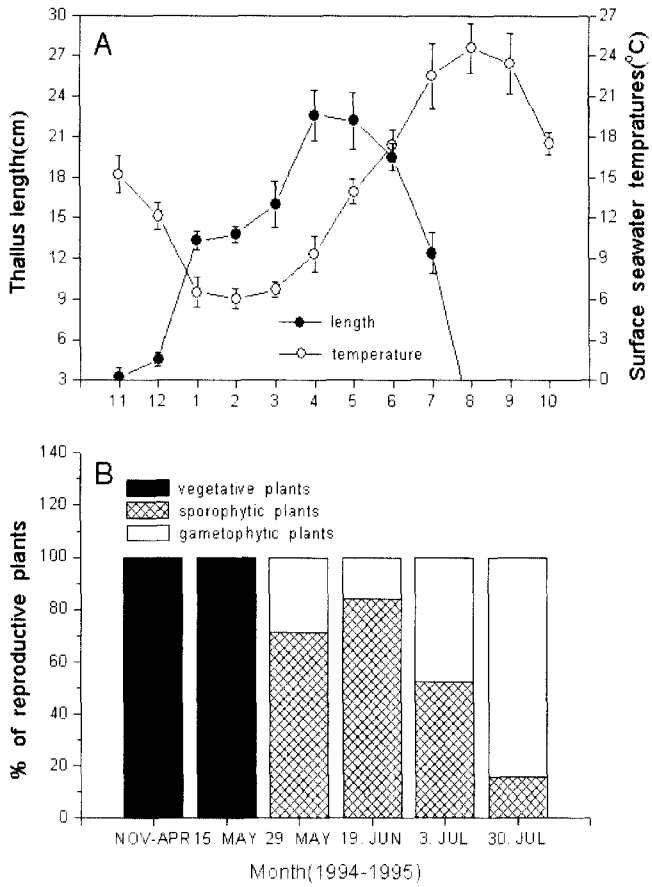

Fig. 2. Variation of thallus length and surface sea-water temperature (A), and Occurrence (%) of reproductive plants (B) of *Spatoglossum crassum* from Anin population.

Morphological Characteristics

Gross morphology of thallus: The young vegetative plants had yellow brown, adult plants dark brown and black thalli when dried. After being exposed to the air, thallus turned into greenish blue and quickly despoiled. The plants had subdichotomous or trichotomous branches and grew up to 30(-40) cm in height and 1.5-2.0 cm in width. Any phaeophycean hairs were not found on the surface of thallus. The holdfast was covered with thick rhizoidal cortication and attached to rocks. Several thalli formed on a holdfast and the cylinderical basal region had dense rhizoidal cortication. We did not find the distinct midrib on the upper part of adult thallus, but thin midrib running to 6-7 cm on the lower part. The apical portion of thallus was linguiform and forked into several parts.

Anatomical Characteristics: We define two terms of the anatomical structures of *Spatoglossum* to describe the morphogenesis of thallus as follows: Meristoderm is consisted of cells on the outmost cortical cell layer of young thallus and make periclinal division several times to result in inner cortex. The cortical cells designate cells composing inner cortex, transversely arranged in line, and having cell growth without division. Medulla is composed of longitudinal enlarged 3-4 collenchyma cell layer and located in the middle portion of thallus (Figs 4A, I, 5K).

We can describe the morphogenesis of thallus based on the longitudinal and trans sectional view of the thallus. The apical meristem is composed of 20-35(-51) rectangular cells having 55 μm in height and 14 μm in width

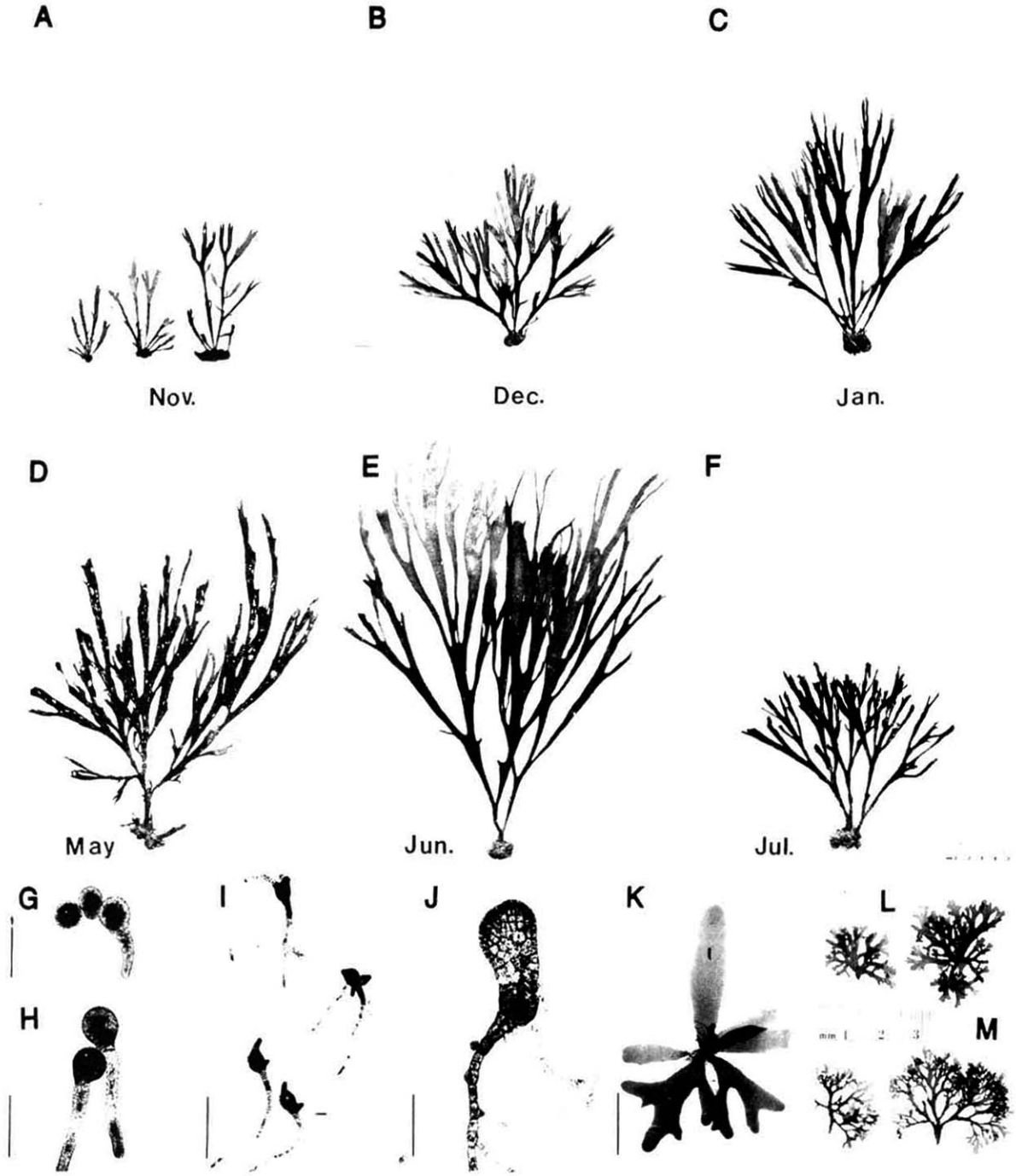

Fig. 3. Monthly variation of habits in the field, germination and indoor cultured plants of *Spatoglossum crassum*. A-B, plants on November to December in 1994; C, plant in January 1995; D-F, plants on May to July in 1995; G-H, germlings of meiospores after 4-5 days; I-K, young plant after 30-70 days; L, female plants from germling; M, male plant from germling. Scale bar: G-H, 90 μm; I-J, 350 μm; K, 2,000 μm.

(Figs 4B, 5A). Based on the longitudinal section of thallus, apical meristem cell produces subapical cell by unequal cell division (Figs 4A1, 5C), and then subapical cell continue to make periclinal division to form the two cells layer thallus around apical region to 40 cell rows from apex (Figs 4A1-A2, 4C-E). Below two cell layer thallus, cells are divided into epidermal cells, which become outmost cortical cells as meristoderm, and internal 3-4 cells, which grow to the medulla cells with irregular shape and large cell volumes (Figs A3, 4E). Meristoderm makes 11-13 times of periclinal division to produce cortex with very regular cell arrangement in the lower por-

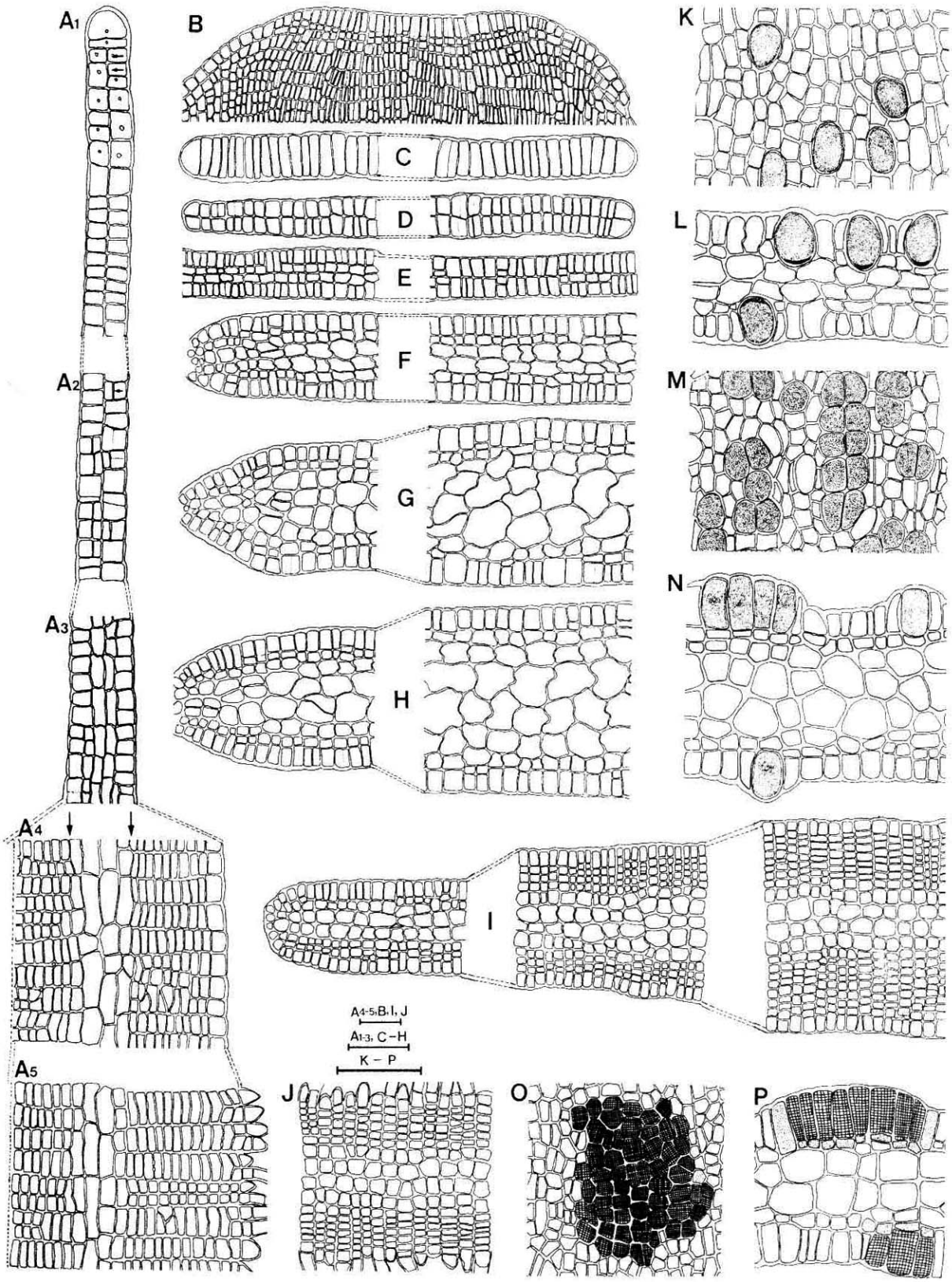

Fig. 4. Anatomical charateristics of *Spatoglossum crassum*. A1-A5, longitudinal section from apex to basal portion and showing three types of tissue, meristoderm, cortex and medulla in adult thallus; B, showing apical cell row in surface view; C-J, cross section of apical portion (C), in upper portion (D-H) from, in middle portion (H) and in lower portion (J); K, M, O, surface view of monosporangia (K), oogonial sori (M) and antheridial sori (O); L, N, P, Trans sectional view of monosporangia (L), oogonial sori (N) and antheridial sori (P). Scale bar = 100 μm.

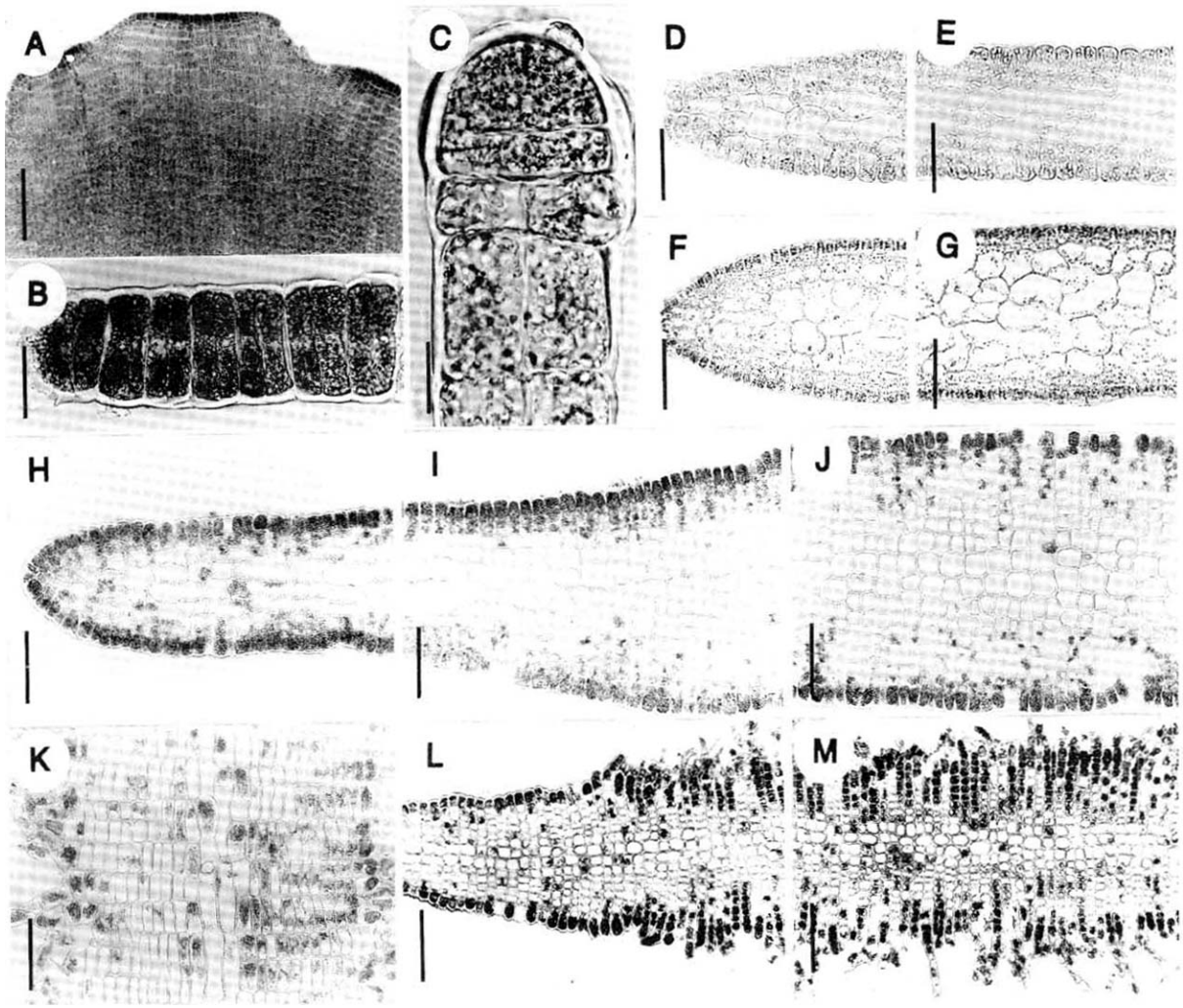

Fig. 5. Anatomical characteristics of *Spatoglossum crassum*. A, showing apical cell row in surface view; B, cross section of apical cells; C, longitudinal section of apical portion of the thallus; D-E, cross section in upper portion; F-G, cross section in middle portion; H-J, cross section in rudimentary midrib portion; K, longitudinal section of lower portion of the thallus; L-M, cross section of basal portion. Scale bar: A1-A5, 350 μm; B, 40.5 μm; C, 20 μm; others, 90 μm.

tion of thallus (Figs 4A, E-I).

In the trans sectional view, the size and arrangement of medullar cells have large variability according to the portion of thallus. The marginal part of thallus has regularly arranged small medulla cells with 29 × 47 μm in size and the central part have cell with 55 × 66 μm in size (Figs 4C-E, 5D-E). In the middle portion of thalllus, we can see the single cell layered meristoderm with cells 37 × 28 μm in size and the cortex consisted of 2-3 cells layers 20 × 28 μm in size, and 3-4 cell layered medulla with 325 μm thickness and they are spherical or multirectangular cells with 55 × 66 μm in size (Figs 4F-H, 5F-G). At the basal portion, there is an indistinct midrib, which runs from 2 to 7.5 cm from the base according to age (Fig 3A-F). The cortical width increases from the margin (3-10 cell layers) to the midrib (22-25 cell layers) (Fig. 4I). We can distinguish three kinds of tissue at the basal portion of the thallus, meristoderm, cortex consisted of regularly arranged 22-25 cells, and medullae consisted of 3-4 large irregular cells (Figs 4A4-A5, I; 5H-J). The base of thallus has rhizoidal cortex which is composed of elongated cells by outgrowth of meristoderm (Figs 4A5, J; 5K-M).

Reproductive Structures: Meiosporangium: Sporangia spread across both surfaces of thallus solely or in pairs (Figs 4K, 6A). We cannot find any sporangia on the apical, margin, and midrib of thallus. Sporangia are originated from meristordem and sometimes have a flat stalk cell (Figs 4L1, 6B-C). Most sporangia observed in this study had a monospore and some had two spores, but not four spores. Adult sporangia are imbedded in the meristoderm layer. They are conical or oval, 122 μm high and 85 μm wide, and surrounded by elongated meristo-

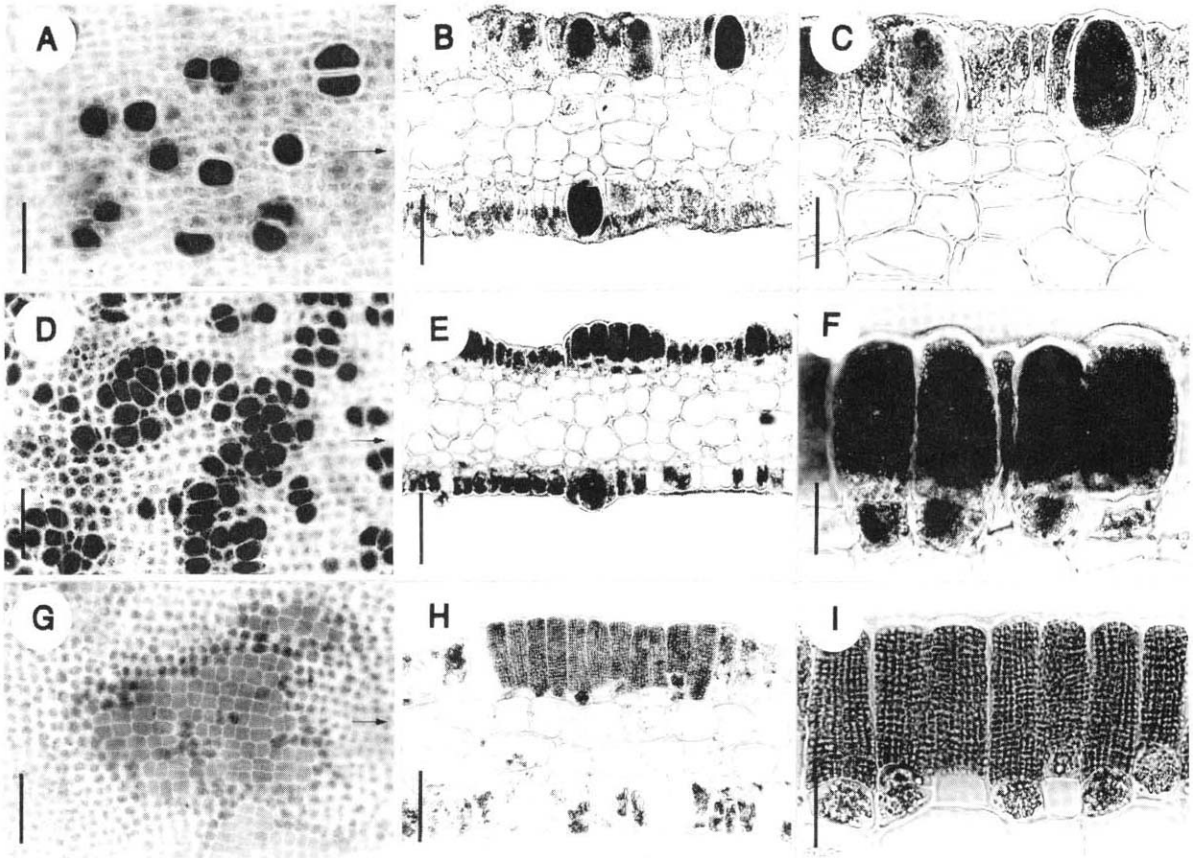

Fig. 6. Anatomical characteristics of reproductive structures in *Spatoglossum crassum*. A, meiosporangia on surface; B-C, cross section with embedded meiosporangia; D, oogonia on surface; E-F, cross section with embedded oogonia; G, antheridial sori on surface; H-I, cross section with embedded antheridial sori. Scale bar: A-B, D-E, G-H, 90 μm; C, 40.5 μm; F, I, 35 μm.

derm in transverse section view (Figs 4L, 6C).

Oogonium: Oogonia spread across both surfaces of thallus in small groups with 2-18 oogonia (Figs 4M, 6D). No oogonium is found on the apical, margin, and midrib of thallus. Oogonia are originated from meristoderm and extended above the thallus surface (Figs 4N, 6E). After elongation, meristodermal cells divide into an oogonial mother cell and a stalk cell (Figs 4N, 6F). Adult oogonia are elliptical or cylindrical, 80 μm high and 50 μm wide in transverse section view. With unaided eye, it is difficult to distinguish it from sporangium because they are very similar in appearance. However, we can distinguish them by the following characteristics. Oogonia are clustered but sporangia solitary or faired. Sporangium is larger than oogonium in size by 1.5-1.6 times. Sporangium has no stalk cell or small flat stalk cell but oogonium has a distinct rectangular stalk cell.

Antheridium: Antheridial sori also spread across both surface of thallus in groups with 10-80 of sori (Figs 4O-P, 6G-I). No antheridial sori are found on the apical, margin, and midrib of thallus. In the early developmental stage, we can find antheridial sori as irregular spot with gray color on the surface (Fig. 6G). Antheridia are developed from meristodermal cell and are buried in the meristorderm or slightly protruded above the meristorderm. After elongation, meristodermal cell divides into elongated antheridial mother cell and rectangular stalk cell. Antheridial mother cell is divided to have 117-216 loculi, containing small antherozoid 2-3 μm in width. Adult antheridia are elongated in shape, 78 μm high and 32 μm broad (Figs 4P, 6I).

Life history in indoor cultures

Indoor culture was made through spores from two sporophytes collected in the field, which had only monosporangia. We can only observe single spore or unusual 2-3 spores released from one sporangium (Fig. 3G, H). The released spores developed into germlings by bipolar development in two days and have elongated to 2-3 celled rhizoids in 4-5 days (Fig. 3G-H). They grow into 5 mm length by apical growth in 30-50 days (Fig. 3I) and make irregular dichotomous branches on basal holdfast

Table 1. Comparison of morphological characteristics of *Spatoglossum crassum* Tanaka

Character \ Locality	Type locality	Korea
Width of blade (cm)	0.6-1.8	0.6-2.7
Thickness of blade (μm)	300-600	325-652
Number of apical cells	10-20	17-51
Size of cortical cells (μm)		
Height (H)	50-60	36-54
Width (W)	15-20	20-36
Size of medullary cells (μm)	50-80	40-70
Phaeophycean hair tufuts	Absent	Absent
Sporangium		
position	Buried	Buried or Embeded
shape	Conical	Globular
size (H × W, μm)	80-145 × 70-100	100-150 × 60-100
Oogonium		
position	Half-buried	Buried or Embeded
size (H × W, μm)	80-120 × 40-60	60-98 × 30-70
Antheridium		
position	Embeded	Buried or Embeded
size(H × W, μm)	70-80 × 20-30	54-94 × 14-56
Reference	Tanaka (1991)	This study

in 70 days (Fig. 3J-K). After six month, they grow up to 30 mm in height and have similar habit to field plants with lot of irregular branches (Fig. 3L, M). The male gametophytes were observed after 8 month growth and female gametophytes in 20 days later. The development and structures of antheridia and oogonia in indoor cultures were the same as those of the field plants in the cross sectional view. The indoor culture condition was 20°C ± 1°C, 50-70 $\mu mol \cdot m^{-2} \cdot sec^{-1}$, and 12:12 LD, which made an isomorphic life cycle consisted of sporophytes, male and female gametophytes in 11 month.

DISCUSSION

Nineteen species of genus *Spatoglossum* distribute world wide from the subtropical to the tropical regions especially in the temperate region in the Southern Hemisphere (Tanaka 1992). This report on *S. crassum* from Korea extends to temperate and cold temperature zone from the Shizuoka Peninsula (34°40'N), which is the type locality of this species.

The plants of *S. crassum* from Korea are similar to those from Japan in the morphological characteristics such as, plant height, dichotomous or subdichotomous branches, and no phaeophycean hair (Table 1). The plastid molecular sequences (unpublished data) also confirm that the plants are same species as those reported in Japan. However, Tanaka (1991) did not distinguish the midrib which was not outstanding in appearances. In this study, we can distinguish rudimentary midrib at base of thallus in the cross sectional view. Whether the plants have midrib or not is a major characteristic to distinguish genus *Dictyopteris* from genus *Spatoglossum* (Womersely 1987). It may need to examine the availability of this characteristic for criterion to distinguish between genera.

We can summarize the phenology of *S. crassum* in Gangnung as follows. Germlings observed in November grow up to adult plants with sporangia and gametangia in late May. The gametophytes are more popular than the sporophytes in late June. Most plants grow senile and distorted, but some old male plants survive on the shadowed rocks in late July. They may spend the high water temperature period from August to September as zygotic or gametophytic germlings and then may grow up to young thallus in late October or November. The seasonal growth of this species explains that the annual growth is closely related to the monthly variation of water temperature.

They start to grow in the water temperature decreasing period (at 18-15°C in October) and sustain the low growth below 10°C (in February to April) and grow fast again in the water temperature increasing period (at 15-18°C in May to July). And they become senile very fast and the upper part of thallus falls off after the water temperature become higher than 20°C (in late July). The seasonal growth pattern of *S. crassum* in Korea indicates that it is now adapted to more temperate waters. This may be supported by that they grow in the sub-tidal zone below than 2 m depth in the east coast and 10 m depth in Jejudo Island in late July with high surface water temperature.

The embeding of reproductive structures was described a major characteristic of generic type, *S. solierii* (Hamel 1939). This characteristic is also found in three species, *S. macrodontum* (Allender and Kraft 1983, Farrant and King 1989), *S. latum* (Tanaka 1992) and *S. crassum* (Tanaka 1991). But reproductive structures protrude above the meristorderm in three species, *S. schroederi* (J. Ag.) Kützing (= *S. areschougii* J. Ag.) (Vickers 1908), *S. chapmanii* Lindauer (Lindauer *et al.* 1961), and *S. pacificum* Yendo (Tanaka 1991). Moreover, the protrusion of reproductive structures can be found in most species of *Dictyopteris* including generic type, *D. polypodioides* (De Candolle) Lamouroux (= *D. membranacea* (Stack.)

Batters). The distribution and developmental pattern of sporangia or antheridia which protruded out of the cortex or are located within the cortex, are founded commonly in both *Spatoglossum* and *Dictyopteris* (Papenfuss 1977; Allender and Kraft 1983; Womersley 1987; Tanaka 1991) so that there are no reliable characters to distinguish between the two genera except for the absence of midrib or the partial prominent midrib on the old plantss of *Spatoglossum* (Lee and Bae 2002). However, the morphogenesis of midrib in the base of *S. crassum* in this study is same as those of *Dictyopteris*, suggesting instability as the generic characteristic. It may need to examine the lineage and the taxonomic status among species of both *Spatoglossum* and *Dictyopteris* based on two characteristics.

In the morphogenesis of *S. crassum*, the outmost cell layer on cortex, which originated from the apical cell, made linear and regular arranged cortical cells inward by several periclinal cell divisions in the lower portion of thallus. We call this outmost cell layer as meristoderm distinguished from cortical epidermis, which has no more division as in *Zonaria*. The thallus thickness of this species is increased by this meristoderm similar to those of Laminariales, which is different from those of *Zonaria* and *Homeostrichus* (Womersley 1987). The more characteristics of morphogenesis and molecular data will make taxonomic resolution between among species of the tribe Zonarieae.

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