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Taxonomy of the Genus *Symphyocladia* (Rhodophyta)

Choi, Do Sung and In Kyu Lee*[1]

Department of Science Education, Kwangju National University of Education, Kwangju 500-703, Korea; and

[1]Department of Biology, Seoul National University, Seoul 151-742, Korea

Four species of *Symphyocladia* growing along the coast of Korea were investigated in taxonomic point of view. Characters available for identification of the species were: difference in gross morphology, degree of cortication in vegetative axis, presence or absence of vegetative trichoblasts, and developmental pattern of stichidia. Vegetative structure and reproductive organs in developmental anatomy were similar among species. Branching pattern and occurrence of vegetative trichoblasts adopted for systematic criteria between Pterosiphonieae and Polysiphonieae, and between *Symphyocladia* and *Pterosiphonia* were no more confidential. The degree of congenital fusion of laterals with the parent axes was considered as only main character to distinguish *Symphyocladia* from *Pterosiphonia*.

Keywords: congenital fusion, Rhodophyta, *Symphyocladia*, taxonomy, vegetative trichoblast

The genus *Symphyocladia* was established by Falkenberg in Schmitz and Falkenberg (1897) as a member of Ceramiales, Rhodophyta, belonging to Pterosiphonieae of Polysiphonioideae, where the other genera, *Dictymenia, Pterochondria, Pterosiphonia* and *Rhodomelopsis* are included as well. The significant taxonomic characters of the genus are alternating branches, congenital fusion between main axis and laterals, pericentral cells without transverse division, and a single sporangium per segment (Hommersand, 1963).

Falkenberg (1901) mentioned that no clear fan-shaped mid-rib on the thallus and the congenital fusion between main axis and laterals up to the terminal portion were remarkable characters of the genus. Okamura (1936) realized that the degree of such fusion was rather advanced in *Pterosiphonia*. Ardré (1973) considered more significantly on an occurrence of vegetative trichoblasts in addition to congenital fusion. By a comparative study of *S. pennata* and *S. latiuscula* Choi and Lee (1987, 1991) pointed out the degree of congenital fusion varied among species as well as populations, and the occurrence of vegetative trichoblasts differed among species.

Currently the genus *Symphyocladia* includes 4 species over the world, *S. marchantioides* (Harvey) Falkenberg, the type species of the genus, *S. linearis* (Okamura) Falkenberg, *S. latiuscula* (Harvey) Yamada, and *S. pennata* Okamura (Falkenberg, 1901; Okamura, 1936; Yamada, 1941; Kraft and Wynne, 1992). Fortunately these four species occur in the coast of Korea. We therefore reinvestigate their morphotaxonomic characteristics with field and cultured materials in a phylogenetic point of view.

MATERIAL AND METHODS

Materials were collected along the coast of Korea during 1982-1992. They were fixed directly in 10% formalin seawater and transported to laboratory. Morphology and anatomy were investigated with field and cultured materials to find confidential characters. Laboratory culture was started with excised

*Corresponding author: Fax +82-2-872-6881

branch tips of carposporophyte and tetrasporophyte, using PES enriched media (Provasoli, 1966) under 8-22℃, 15 μmol photons·m^{-2}·s^{-1} and 16 : 8 (light : dark) photoperiod. The medium was changed once a week. 1N HCl was used for softening the tissue, and Olympus BH2 photomicroscope was used for microscopic observation.

RESULTS AND DISCUSSION

Key to the species of *Symphyocladia* in Korea

The taxonomic characters of the species for identification were 1) length and shape of thalli, 2) degree of cortication, 3) occurrence of vegetative trichoblasts, 4) development of tetrasporangial stichidia, etc. According to these criteria a key of the four species of *Symphyocladia* in Korea was prepared as follow:

1. Vegetative trichoblasts absent ····· 2
1. Vegetative trichoblasts present ····· 3
   2. Thallus less than 3 cm, ccorticated ····· ····· *S. pennata* Okamura
   2. Thallus up to 30 cm, corticated ····· ····· *S. linearis* (Okamura) Falkenberg
3. Thallus linear, tetrasporangia on palm-shaped stichidia ····· *S. latiuscula* (Harvey) Yamada
3. Thallus flat, tetrasporangia linear on branchlets ····· *S. marchantioides* (Harvey) Falkenberg

Habitat and phenology

The plants grew mostly on rocky substrata or were epiphytic on other algae below the mid-intertidal zone. *S. marchantioides* and *S. pennata* occurred in the subtidal zone or on other algae in tidal pool of the intertidal zone. *S. latiuscula* was in the mid to lower intertidal zone, and *S. linearis* on rocky substratum in the subtidal zone.

S. marchantioides distributes broadly in the Pacific, Atlantic and South Africa, while the other three species are endemic to the northern Pacific such as Korea, China and Japan (Grubb, 1932; Okamura, 1936; Ardré, 1973; Norris and Aken, 1985). *S. marchantioides* and *S. latiuscula* occur all the coasts of Korea, *S. pennata* in the southern coast and Dokdo Island, and *S. linearis* is found only in the eastern coast. Such a characteristic of the distribution demonstrates these species to be temperate. Especially, *S. pennata* can grow in areas over 10℃ affected by strong warm current, whereas *S. linearis* is found in areas partially affected by cold current (Kang, 1966).

The field phenology slightly differed according to species. However, the occurrence of tetrasporophytes and carposporophytes was comparatively high during the summer. They repeated *Polysiphonia* type life history, considering the occurrence of reproductive structures in the field.

The habit, phenology and distribution of the species were summarized in Table 1.

Vegetative thallus

The plants of *Symphyocladia* prostrate in early development, producing rhizoids from dorsal portion of the thallus, and erect after the growth. They become 5-25 cm, except for 1-2 cm of *S. pennata* (Fig. 1).

The species basically produce alternate branches per every segment. Such a characteristic can be observed broadly among the genera of Pterosiphonieae. However, the degree of congenital fusion of the branches to axis, which is determined by the angles of oblique division in the apical cell, differs among the genera so that it can be adopted as an important

Table 1. A comparison of ecological characteristics among four species of *Symphyocladia* in Korea

Species \ Characters	Substratum	Habitat	Distribution				Reproduction[a] in field
			East	West	South	Chejudo	
S. marchantioides	epiphytic	inter-subtidal	+	+	+	+	F, T
S. latiuscula	epiphytic/ epilithic	inter-subtidal	+	+	+	+	F, M, T
S. linealis	epilithic	subtidal	+	−	−	−	F, T
S. pennata	epiphytic	inter-subtidal	−	−	+	+	F, M, T

[a]F, Female gametophyte; M, Male gametophyte; T, Tetrasporophyte.

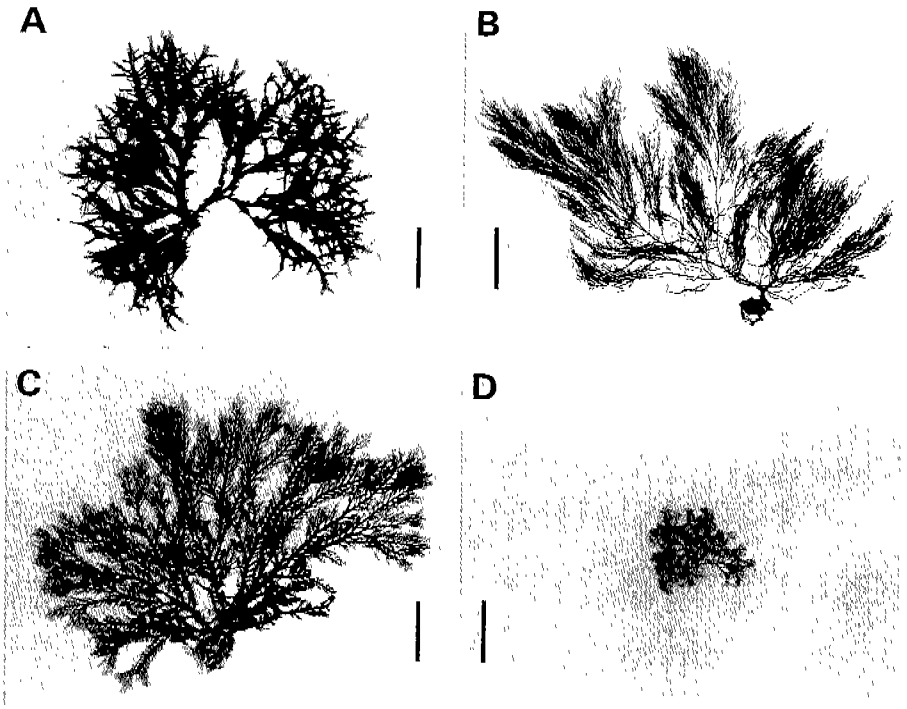

Fig. 1. Habit of thallus of *Symphyocladias* from Korea. A, *S. marchantioides* (Harvey) Falkenberg (scale bar=1 cm); B, *S. linealis* (Okamura) Falkenberg (scale bar=5 cm); C, *S. latiuscula* (Harvey) Yamada (scale bar=3 cm); D, *S. pennata* Okamura (scale bar=1 cm).

character to distinguish the genera.

In *Symphyocladia* this congenital fusion always occurs over two more segments, in contrast to occur within a single segment in *Pterosiphonia* (Falkenberg, 1901). In *S. marchantioides* this angle is almost 180°, thus the divided apical cells arrange almost linearly to make the fused branches in a flat plane. In the other three species the angle is narrower and the congenital fusion occurs among 3 to 8 segments (Figs. 2A-C, 3A, B). As results, the degree of congenital fusion of these three species is intermediate between the higher *S. marchantioides* and the lower *Pterosiphonia*. As mentioned by Choi and Lee (1987), since the degree of congenital fusion varies under different environments as well as among different species in *Symphyocladia*, but constant within one in *Pterosiphonia* (Fig. 3D-F), it can be a noticeable character to distinguish *Symphyocladia* from the other genera related.

The alternate branches make the thallus plane. However, in spermatangiate plants the fertile laterals are formed in every segment and the branches become spiral (Fig. 2I). Such a spiral arrangement of speramtangiate branches can be observed in the four *Symphyocladias* as well as several species of Rhodomelaceae and Dasyaceae (Hommersand, 1963).

Scagel (1953) and Hommersand (1963) mentioned the occurrence of vegetative trichoblasts as an important diagnostic character of Pterosiphonieae and Polysiphonieae in the Rhodomelaceae. Among the species of *Symphyocladia*, *S. marchantioides* and *S. latiuscula* produce vegetative trichoblasts on determinate branches, but *S. pennata* and *S. linealis* have no such trichoblasts in their life history (Fig. 3D, F). Therefore this can not be a diagnostic character to distinguish the tribes in the family (Choi and Lee, 1991).

The first pericentral cell occurs commonly on abaxial plane in all the species of *Symphyocladia*. *S. latiuscula* and *S. marchantioides* produce 6-9 pericentral cells and *S. pennata* and *S. linearis* develop 7-8 cells. The secondary pit-connections among them can be observed. Except for *S. pennata*, the cortical cells are developed from the central cells; *S. latiuscula* develops them in 2-3 layers over all thallus except the apex, *S. marchantioides* and *S. linearis*

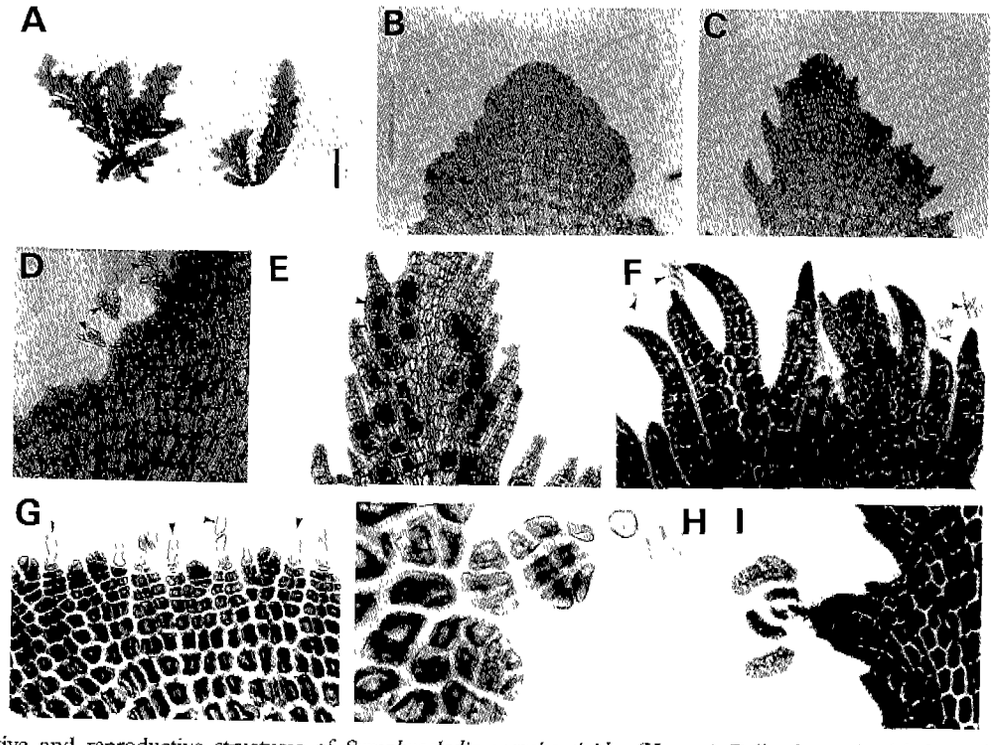

Fig. 2. Vegetative and reproductive structures of *Symphyocladia marchantioides* (Harvey) Falkenberg. A, dried specimen with soft and membranaceous thallus habit (scale bar= 1 cm); B, apex of vegetative thallus with round margin (100×); C, apex of tetrasporophytic thallus with dentate margin (100×); D, vegetative trichoblasts (arrows) in thallus (200×); E, tetrasporophyte with mature tetrasporangia (100×); F, mature sporophyte with vegetative trichoblasts (arrowheads) (200×); G, reproductive trichoblasts (arrowheads) in female plant (200×); H, young procarp (400×); I, mature spermatangial stichidia (200×).

produce them mid to lower portion of the thallus after the growth (Fig. 3C). This character is helpful to discern the species in the genus.

The vegetative characters among the species of *Symphyocladia* are summarized in Table 2.

Reproduction

The development of reproductive structures among species of *Symphyocladia* is basically same as that of the Rhodomelaceae (Ardré, 1973; Choi and Lee, 1991).

The spermatangial branches develop on monosiphonous fertile trichoblast of determinate growth, which is produced one in every segment on terminal portion of the branches (Fig. 2G). The fertile trichoblasts divide the initial cell of the pericentral cell from every segment, which produces 2-3 spermatangial mother cells. The spermatangia are enveloped by hyaline mucilage membrane. The fertile trichoblast grows no more after the development of spermatangia (Fig. 2I).

The procarps are developed from the last pericentral cell in a segment of the fertile trichoblast, and the pericentral cell becomes of the supporting cell (Fig. 2H). The procarp consists of the supporting cell, the carpogonial branch and the fertile cell groups. The supporting cell also becomes of the auxiliary mother cell. The carpogonial branch is 4 celled. The trichogyne develops when the carpogonial branch becomes 3 celled. After the fertilization the trichogyne shrinks and disappears, while the supporting cell cuts off the auxiliary cell, which coalesces with carpogonial branch. The pericarp begins to develop before the fertilization. Parsons (1980) mentioned a formation of connecting cell during the fusion of carpogonial branch to auxiliary cell in *Brongniartella* of the Rhodomelaceae. However, we could not observe such a connecting cell in *Symphyocladia*. The trichoblasts from axial cells observed in procarp stage were fallen soon after the fertilization.

Tetrasporangia occur singly in every segment of

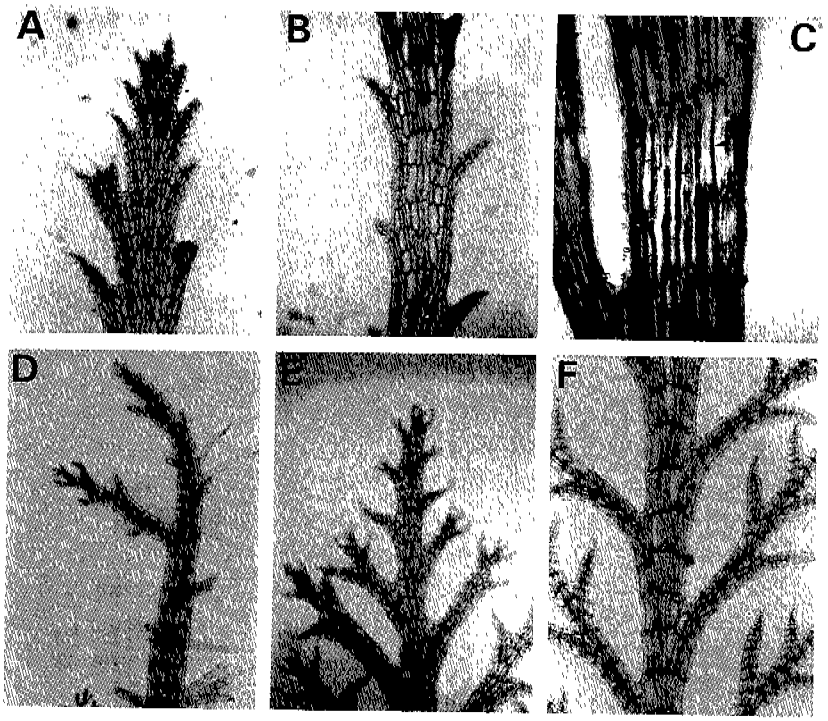

Fig. 3. Vegetative structures of *Symphyocladia linealis* (Okamura) Falkenberg (A-C) and *Pterosiphonia pennata* (C. Agardh) Falkenberg (D-F). A, B, apex and branching pattern of vegetative thallus in *S. linealis* (100×); C, surface view of corticated (arrowheads) erect axis in *S. linealis* (200×); D-F, apex and branching pattern of vegetative thallus in *P. pennata* (D, E, 100×; F, 200×). Figs. D-F, the materials from Santa Crutz, California, Febr. 1988.

Table 2. A comparison of vegetative characteristics among the species of *Symphyocladia* in Korea

Characters / Species	Thallus	Height	Cortication	Vegetative trichoblast	Congenital fusion
S. marchantioides	membranaccous	5-10	+ (in lower part)	+ axis	several axis
S. latiuscula	flabellate	5-15	+ (thoroughly)	+ segment	5-7
S. linealis	linear	10-25	+ (in lower part)	− segment	7-8
S. pennata	pinnate	1- 2	−	−	4-5 segment

the fertile branches, and are divided tetrahedrally. They are originated from one of the pericentral cells consisting of the segment. The fertile pericentral cell produces the sporangial mother cell and three different sized cover cells. In the *S. latiuscula* a palm shaped stichidium is characteristically developed by congenital fusion of the branchlets up to terminal portion, while in the other three species the lateral branches directly converted into the fertile stichidia. In *S. marchantioides*, however, the degree of congenital fusion between the branches and main axis is more, and the tetraporangia make a linear arrangement (Fig. 2C, E-F). Guiry (1978) mentioned the development and arrangement of tetrasporangia can be an important character to realize the phylogenetic relationship among red algae. In the Rhodomelaceae it is thought that the number of tetrasporangia per segment decreases in course of evolution (Hommersand, 1963). On such a view point the genus *Symphyocladia* takes evolutionary a higher position among the genera related.

Life history

Four species of *Symphyocladia* occurring in the coast of Korea exhibit basically a *Polysiphonia* type life history, considering the field and laboratory investigations. *S. latiuscula* completed a typical *Polysiphonia* type life history for about 6 months in laboratory culture. The gametophytes became 1.5-2 cm high, and the tetrasporophytes were 6-7 cm, demonstrating a typical dimorphism. This dimorphism was also confirmed in the field materials (Choi and Lee, 1991). In the *S. marchantioides* no male gametophytes were collected in the field, but the tetraspores grew to male and female plants in culture. They completed a full life history in 4 months.

S. pennata repeated basically a *Polysiphonia* type life history. However, there occurred monoecious plants and cystocarpic/tetrasporangiate mixed phases reproduction in laboratory culture (Choi and Lee, 1987). In the *S. linearis* female and tetrasporangiate plants were collected in the field, but the spores did not grow in laboratory culture and the life history was not completed during this study.

Taxonomic discussion

The genus *Symphyocladia* was first described by Falkenberg (1897) based on the species *Amansia*(?) *marchantioides* Harvey (1855) collected from New Zealand. Reinvestigating the species belonging to *Amansia, Placophora, Pollexfenia, Dictymenia* and *Rytiphloea* of the Rhodomelaceae, Falkenberg (1901) included there two more species, *S. gracilis* (Martens) Falkenberg, which was later identified as *S. linearis* (Harvey) Yamada from Iwaki, Japan, and *S. latiuscula* (Okamura) Falkenberg collected from Hakodate, Japan. After that, Okamura (1923) added a new species *S. pennata* from Japan. As a result, four species are in this genus at present.

The genus *Symphyocladia* is included in the tribe Pterosiphonieae as well as *Pterosiphonia* and *Dictymenia* by the characters 1) alternate branches, 2) congenital fusion beween main axis and laterals, 3) pericentral cells without transverse division, and 4) one tetrasporangia per single segment (Okamura, 1936; Hommersand, 1963).

The tribes Pterosiphonieae and Polysiphonieae have been distinguished by the occurrence of vegetative trichoblasts and the developmental pattern of laterals to main axis; the former has no vegetative trichoblast and develops alternate-distichous branches interpositing a single no branched segment in turn, while the latter has vegetative trichoblasts and spiral branches by producing a lateral per segment (Hommersand, 1963).

In *Symphyocladia*, however, the branches are basically alternate as in the other genera of the Pterosiphonieae, but the male gametophytes produce fertile branches from every segment to make a spiral form. The occurrence of vegetative trichoblasts varies among the species; *S. latiuscula* and *S. marchantioides* bear the trichoblasts, while *S. linearis* and *S. pennata* do not produce them (Choi and Lee, 1991). Ardré (1973) mentioned the presence of vegetative trichoblasts to be a good character to distinguish *Pterosiphonia* from the other genera. However, as seen in *Symphyocladia* their occurrence is variable among species, so that it can not be a character to distinguish the genera. Since Hommersand (1963) mentioned the spiral branches were originated from the alternate, the occurrence of spiral branches in male fertile branches of *S. pennata* and *S. linealis* demonstrates them to be related more to the Pterosiphonieae, while *S. latiuscula* and *S. marchantioides*, which have no such spiral branches, are more to the Polysiphonieae.

The congenital fusion of the branches can be one of the criteria to distinguish the genera. On this the genus *Symphyocladia* can be well separated from the *Pterosiphonia* to show the fusion only in a lower basal segment of the branches, and is separated from the *Dictymenia* to bear a remarkable mid-rib. By this comparison, Okamura (1936) mentioned that *Symphyocladia* was derived from *Pterosiphonia*. Among the species of *Symphyocladia* the degree of congenital fusion exhibits that the three species, *S. linearis, S. latiuscula* and *S. pennata* can be placed in an intermediate position between *Pterosiphonia* and *S. marchantioides*. According to the investigation of *Pterosiphonia pennata* (C. Agardh) Falkenberg from Korea by Lee *et al.* (1992) and from the Northern Pacific in this paper (Fig. 3D-F), the congenital fusion of the branches occurs always less than two basal segments through the whole life history. This supports also the congenital fusion of the branches can be a good criterion to distinguish the genera of the Pte-

rosiphonieae.

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韓國產 紅藻 보라색우무屬(*Symphyocladia*) 植物의 分類

崔 秉 成 · 李 仁 圭[*1]
光州敎育大學校 科學敎育科, [1]서울大學校 生物學科

적 요

한국 연안에 생육하는 보라색우무속(*Symphyocladia*) 식물 4종을 대상으로 실내배양 및 형태분류학적 연구를 통해 식별형질들을 비교 검토하고 이들의 분류학적 타당성을 고찰하였다. 보라색우무속 식물은 전 세계에 4종이 분포하고, 종 식별형질로는 엽체의 체장 및 체형, 피층의 유무 및 발달정도, 영양모상엽의 형성 여부, 그리고 사분포자탁의 발달 양식 등이 이용된다. 생식기관의 구조 및 발달과정 그리고 수정후 발생과정은 종간에 유사하다. 본 연구를 통해 엽체의 분지양상과 영양모상엽의 형성여부는 Polysiphonieae족과 Pterosiphonieae족 그리고 본 속과 *Pterosiphonia*속의 한계 설정을 위한 식별형질로써 분류학적 의의가 없음이 확인되었고, 주축과 측지와의 연변유합 정도는 비록 본 속의 종내 변이가 관찰되기는 하지만 본 속을 *Pterosiphonia*속과 구분하는 주요 식별형질이 됨을 확인하였다.

주요어 : 홍조식물, 보라색우무속, 계통분류, 영양모상엽, 측지 연변유합

*교신저자 : Fax (02) 872-6881