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Vegetative and Male Reproductive Anatomy of *Laurencia intercalaris* sp. nov. (Rhodomelaceae, Rhodophyta) in Korea

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The vegetative and male reproductive anatomy of a marine alga, *Laurencia intercalaris* sp. nov. (Rhodomelaceae, Rhodophyta), is described from subtidal habitats of eastern and southern Korea. This species has terete thalli with entangled fibrous holdfasts and regularly alternate branching of ultimate branchlets, and is inseparable from *L. okamurae* Yamada on the basis of habit. Vegetative axial cells produce a trichoblast and four pericentral cells in an alternating sequence. Spermatangia are produced intercalary or subterminally from one of two laterals on suprabasal cells of trichoblasts arising from axial cells in apical pits of branchlets. The other lateral remains sterile. In this sterile lateral, budding-like regeneration occurs on older segments that are abscised. Comparison is made with other related *Laurencia* species, particularly those with terete thalli. The vegetative anatomy and the regeneration in sterile laterals of male trichoblasts, with the mode of spermatangial formation, distinguish the new species from previously described species of *Laurencia* including *L. okamurae*.

Keywords : anatomy, *Laurencia intercalaris* sp. nov., pericentral cell, spermatangium, regeneration

Laurencia Lamouroux (1813) (Rhodomelaceae, Rhodophyta) is a large, cosmopolitan genus including nearly 140 species (McDermid, 1989) in temperate to tropical waters (McDermid, 1989; Vandermeulen *et al.*, 1990; Wynne and Ballantine, 1991; Gil-Rodríguez and Haroun, 1992). Since Kang (1966), 14 species of *Laurencia* have been reported in Korea (Lee and Kang, 1986).

During the course of monographic work on this marine red algal genus and ecological work on marine algal community structure, an alga, which is superficially similar to *Laurencia okamurae* Yamada (1931), was collected from subtidal habitats of eastern and southern Korea. This alga is characterized by having terete thalli arising from entangled fibrous holdfasts, with regularly alternate branching of ultimate branchlets and is inseparable from *L. okamurae* on the basis of habit. However, vegetative and male reproductive anatomy has led to the conclusion that this Korean entity is distinct from *L. okamurae* and represents a previously undescribed species. In this paper, the vegetative and male reproductive anatomy of *Laurencia intercalaris* sp. nov. is presented, and compared to other related species.

MATERIALS AND METHODS

Data were obtained from fresh and liquid-preserved specimens collected from Cheju Island and Pohang, Korea. Plants were stored in a 10% solution of formalin/seawater. For anatomical studies plants were cleared in 5-10% NaOH in distilled water for 2-7 days. Branchlets dissected from the cleared materials were longitudinally sectioned along the central axis using a razor blade and a pith stick. Sections were mounted in pure glycerine. For permanent slides, the glycerine was exchanged with 50% aqueous corn syrup. Transverse sections of branchlets 50-200 μm or more thick were also used to observe development of vegetative axes. Observation of axial development was made on sections put re-

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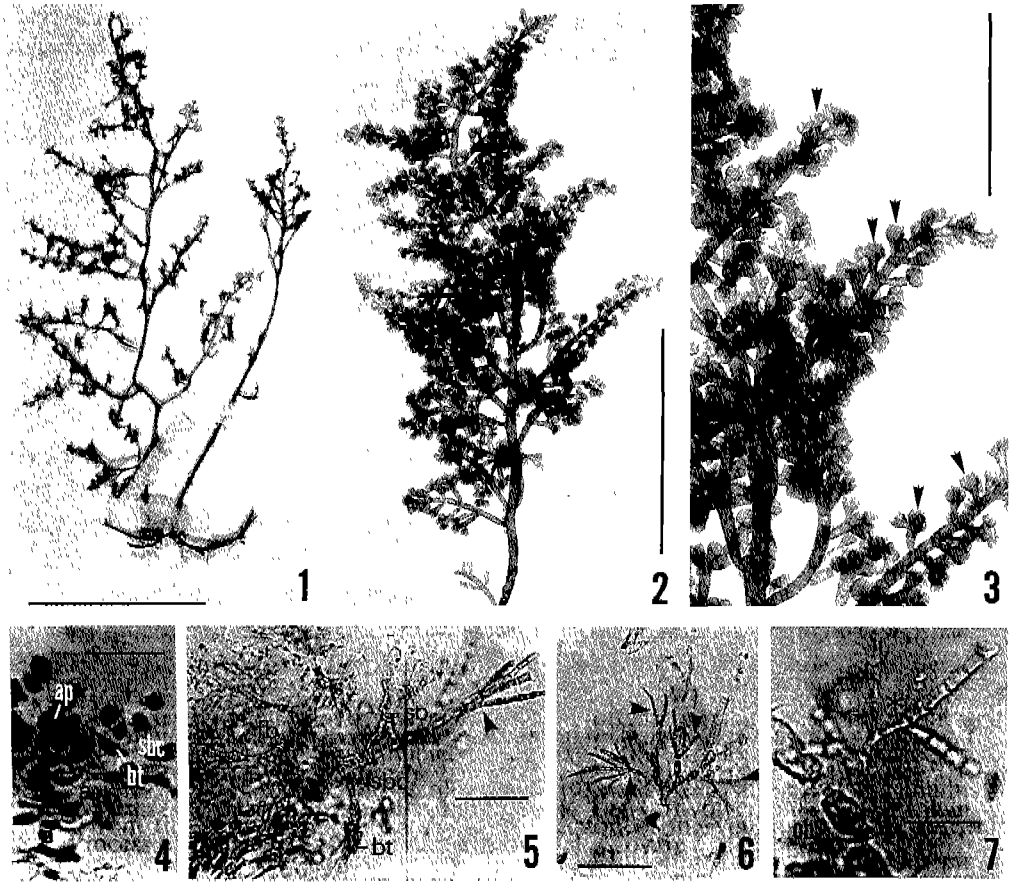
versely on a slide. This was effective for examination of the position of vegetative pericentral cells in axial segments. Squash preparations were used to observe spermatangial development. Measurements are given as length × diameter.

RESULTS

Laurencia intercalaris Nam sp. nov.

Description: Thalli ad 10 cm vel magis altum, teretes, fusci vel fulvi, carnosi aut subcartilaginei, ad substratum per ramos accessorios fibrosos aliquod affixa; axes erecti unus vel pli percurrentes, 1.0-1.2 mm in diametro, in partibus infernis saepe nudi vel sparsim ramosi; ramificatio irregulariter alterna e latusibus omnibus; cellulae epidermales prope apicem ramuli leviter procurrentes vel non procurrentes, stratum paliforme non facientes, cum fovea-connectivis inter eas; crassitudines lenticulares in parietibus cellularum medullosarum magnopere abundantes; ramuli antheridiales turbinati, 0.7-0.9 mm in diametro, cum depressionibus apicalibus cupulatis, 380-580 μm latis et usque ad 1.3 plo-2.0 plo latis quam pro-



Figs. 1-7. *Laurencia intercalaris* Nam sp. nov. Fig. 1. Herbarium mounted male holotype (N87001)(scale bar=2 cm). Fig. 2. Habit of the holotype before herbarium mounting (scale bar=3 cm). Fig. 3. Details of liquid-preserved branches with terminal cup-shaped spermatangial pits (arrowheads) from the holotype (scale bar=1 cm). Fig. 4. Young male trichoblast (arrow) in median longitudinal section (LS) through the branchlet apex (scale bar=20 μm). Fig. 5. Old male trichoblast (scale bar=40 μm). Note new sterile branch (arrowhead) on older segment abscised. Fig. 6. Sterile branch of male trichoblast with some new branches (arrowheads) produced by budding-like regeneration (scale bar=80 μm). Fig. 7. Enlargement of a new sterile branch (asterisk) regenerated from older branch (scale bar=20 μm).

Abbreviations in Figs. 1-21. a, axial cell; ap, apical cell; bt, basal cell of trichoblast; fb, fertile branch of male trichoblast; ob, old branch; p, pericentral cell; pc, primary cortical cell; pco, primary cortex; sb, sterile branch of male trichoblast; sbc, suprabasal cell of trichoblast; sco, secondary cortex; sr, rhizoidal secondary cortical cell; tb, trichoblast; ti, trichoblast initial; 1, 2, etc., formation sequence.

fundis; trichoblastus antheridialis cellula axialibus exorientes, plerumque constans ex ramis fertilibus et sterilibus, sed saepe praeter only cum segmentis fertilibus subterminalibus vel intercalaribus et ramis fertilibus limitatis ad trichoblastum sterilem; cellula terminalis 16-19×15-17 μm; ramis sterilibus per gemmationem e segmentis veteribus interdum partim regenerantes; spermatangium cum nucleo apicali, 7-10×5-7 μm; plantae femineae et tetrasporangiferae ignotae.

Thalli to 10 cm or more high, terete (Figs. 1-3), brown or yellowish brown, fleshy to subcartilaginous, somewhat soft in texture, adhering well to paper, attached to substratum by some fibrous accessory branches; one or more erect axes percurrent, 1.0-1.2 mm in diameter, paniculate outline, in the lower parts often denuded or sparsely branched; branching irregularly alternate on all sides, sometimes subopposite or subverticillate, particularly ultimate branchlets regularly alternately branched; all branches somewhat constricted at the base. Axial segments with a trichoblast and four pericentral cells; epidermal cells slightly projecting or not near the apex of branchlets, not forming a palisade layer, with secondary pit-connections between them; lenticular thickenings present in the walls of medullary cells; extensive secondary cortication usually present in older branches; spermatangial branchlets turbinate, 0.7-0.9 mm in diameter, simple or compound, with cup-shaped apical pits, 380-580 μm wide and up to 1.3-2.0 times as wide as deep; male trichoblasts arising from axial cells, consisting of fertile and sterile branches, with intercalary or subterminal fertile segments in fertile branches; fertile branches with basal sterile segment, and a large, terminal sterile cell 16-19×15-17 μm; sterile branches regenerated by budding on older segments abscised; spermatangia 7-10×5-7 μm, with apical nucleus; female and tetrasporic plants unknown.

Holotype specimen: N87001 (Fig. 1). Male; Woodo (33°31′N, 126°57′E), Cheju Island, Korea; epilithic in areas sheltered or exposed to wave action near subtidal zone; Jul. 1985; deposited in the Herbarium of Department of Marine Biology, National Fisheries University of Pusan, Korea.

Etymology: The specific epithet is derived from developmental feature of spermatangia formed intercalary from fertile branches of male trichoblasts.

Specimens examined: Isotype: Woodo, Cheju Island, Korea (?, ?. vii. 1985, N87012, N87013, N87014, N87015). Paratype: Pohang, Korea (*Nam*, 14. viii. 1993, N87016, N87017, N87018, N87019, N87021, N87022, N87023, N87024, 87025).

Korean name: Sai-seusill (nom. nov.)

Distribution: Known from Cheju Island and Pohang, Korea.

Vegetative anatomy: Apical cells, which are always sunk in apical pits of branchlets, divide slightly obliquely on three faces. The resulting wedge-shaped axial segments are arranged along a 3/8 spiral, clockwise or counterclockwise, as seen from the apex of branchlets (Fig. 8). Trichoblast initial is formed on the upper side of axial cell, and then is cut off obliquely from the axial cell. Next, four pericentral cells are formed from the axial cell in an alternating, typically rhodomelaceous sequence (Figs. 8-10).

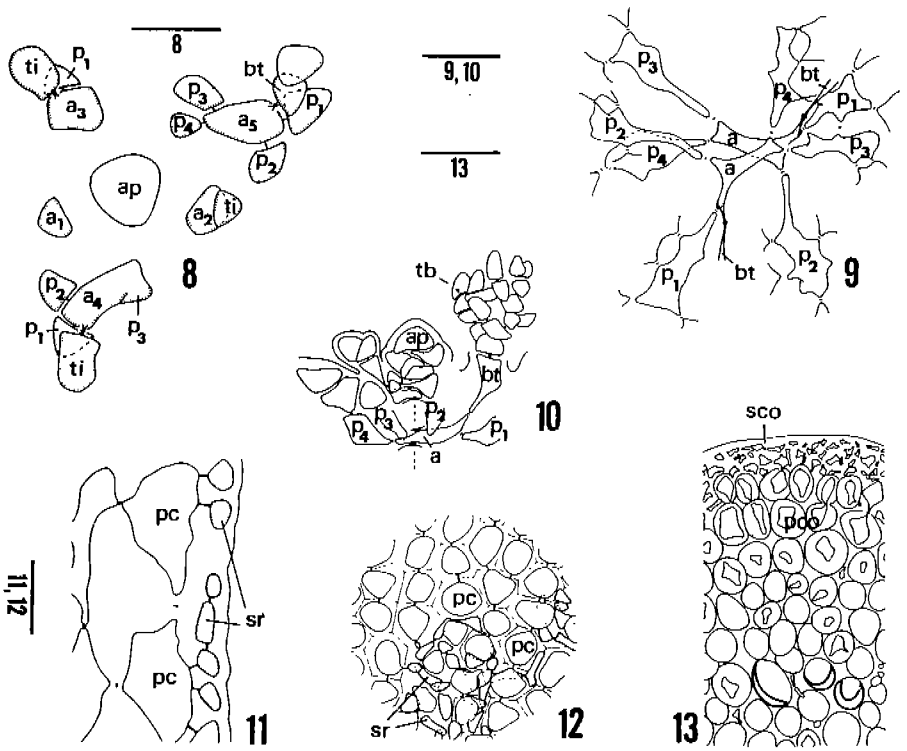
The pericentral cells produce two to four derivatives, each of which divides ternately or quaternately, giving rise to radially aligned, equal, determinate filaments. Each cell in these filaments is connected by secondary pit-connections with the adjacent cells of filaments derived from the same or successive axial segment. As a result, the cylindrical thallus with subcartilaginous texture is built up.

The deciduous trichoblasts are monopodial with dichotomous branching.

Ordinary lateral branches are produced from basal cells of the trichoblasts at regular intervals. In the newly produced branches, the spiral direction of axial segments seems to be opposite to that of parent branch. Thus, it appears that two different spiral directions occur in turn between systems of daughter and parent branches. Adventitious branchlets derived from subcortical cells usually occur on major axes.

A secondary cortex usually develops from rhizoidal filaments in the older parts of branches (Figs. 11-13). It is often extensive, giving rise to several to many layers covering the primary cortex (Fig. 13).

Epidermal cells of branchlets may or may not



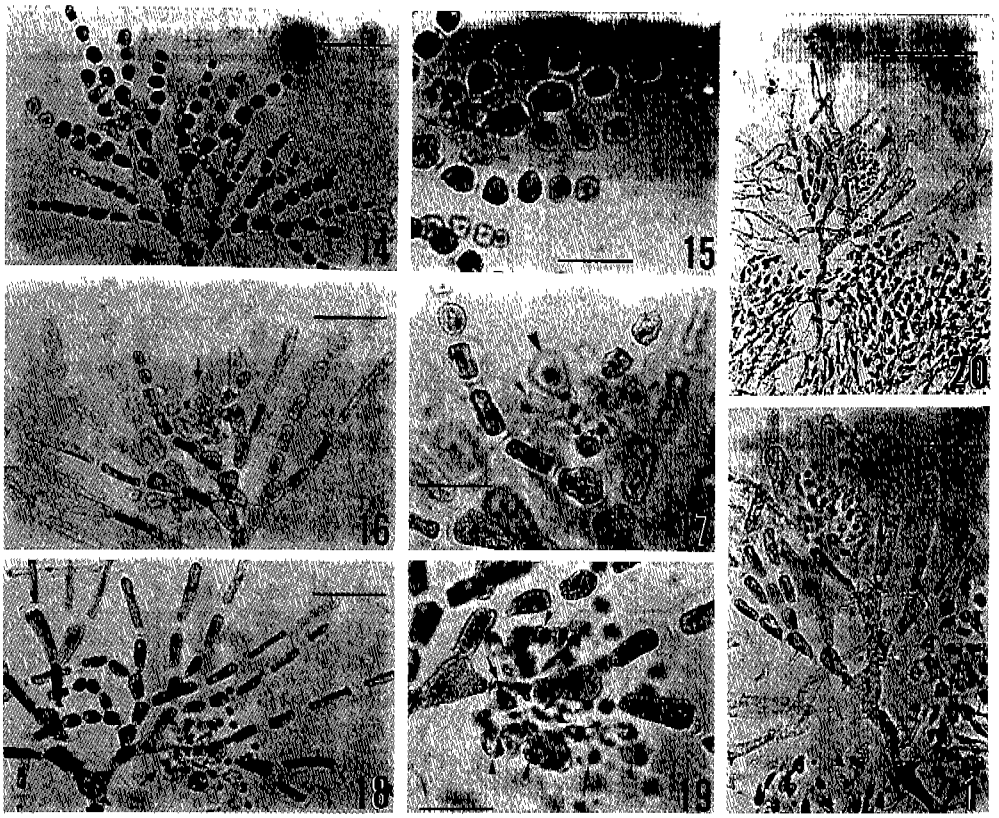
Figs. 8-13. *Laurencia intercalaris* Nam sp. nov. Fig. 8. Serial axial segments, showing the sequence of the formation of a trichoblast and four pericentral cells (scale bar=15 μm). Fig. 9. Two superimposed axial segments in TS near branchlet tip (scale bar for Figs. 9, 10=30 μm). Fig. 10. An axial segment with a trichoblast and four pericentral cells in median LS. Fig. 11. LS of older branch, showing rhizoidal secondary cortical cells on primary cortical cells (scale bar for Figs. 11, 12=60 μm). Fig. 12. Surface view of rhizoidal secondary cortical cells. Fig. 13. Lower parts of major branch with secondary cortex of several layers (scale bar=150 μm).

project slightly near branchlet apices, and are neither elongate radially nor arranged in a palisade in transverse section (TS). Secondary pit-connections are always present between them (Figs. 11, 12). Lenticular thickenings are present in the walls of medullary cells (Fig. 13). 'Corps en cerise' were not detected in the material preserved in formalin/seawater.

Male reproductive anatomy: The fertile apical pits of branchlets of male plants are considerably swollen. They develop into cup-shaped spermatangial pits, which contain numerous male trichoblasts (Fig. 3). The male trichoblasts, which have two laterals on their suprabasal cells, arise from axial cells (Figs. 4, 5). Of the two laterals, the abaxial one remains sterile, whereas the adaxial one becomes fertile. Budding-like regeneration occurs on older segments abscised in the remaining sterile lateral (Figs. 5-7). The resulting new branches have relatively small cell size and by this are readily distinguished from their parent branches (older sterile laterals) (Fig. 7). Spermatangia are formed intercalary or subterminally from axial segments of the other fertile lateral (Figs. 14-21). Occasionally, spermatangia are also produced from all axial segments of the fertile lateral except for its basal cell and terminal large vesicular cell (Fig. 5). Spermatangial mother cells are derived from pericentral cells of the axial segment, giving rise to several ovoid spermatangia. The spermatangia have a large apical nucleus (Figs. 15, 17, 19). A single spermatium is released through an apical split in the spermatangial wall. The number of spermatangial mother cells and spermatangia produced per axial segment is unclear.

DISCUSSION

In the western and central Pacific, the genus *Laurencia* has been separated into the subgenera (Saito, 1967, 1969; Saito and Womersley, 1974; Zhang and Xia, 1985), *Laurencia* and *Chondrophycus* Tokida et Saito (Saito, 1967), based on the presence or absence



Figs. 14-21. *Laurencia intercalaris* Nam sp. nov. Figs. 14, 18. Spermatangial development at intercalary axial segment (arrow) (scale bar for Figs. 14, 16, 18, 21=80 μm). Figs. 15, 19. Enlargement of Figs. 14 and 18 (scale bar for Figs. 15, 17, 19=40 μm). Arrows indicate axial cells and arrowheads spermatangia. Fig. 16. Spermatangial development at subterminal axial segment (arrow). Fig. 17. Enlargement of Fig. 16. Note terminal vesicular sterile cell (large arrowhead), spermatangia with apical nucleus (small arrowheads) and fertile axial cell (arrow). Figs. 20, 21. Spermatangial development (arrowhead) at a part of male trichoblast (scale bar for Fig. 20=120 μm).

of secondary pit-connections between epidermal cells and the parallel or right-angle arrangement of tetrasporangia. Taxonomic entities within the genus have been distinguished primarily by these subgeneric characters and features of habit and internal anatomy, e.g., size of thalli, branching, nature of compressed or terete thalli, shape of holdfast, presence or absence of lenticular thickenings in the medullary cell walls, and presence or absence of projections and palisade-like arrangement of epidermal cells. However, habit of *Laurencia* species is variable in many cases, and the current internal anatomy is also of limited for the genus taxonomy. Moreover, the subgeneric classification scheme of Saito (1967) needs critical revision because several species share the characters of both subgenera (McDermid, 1989; Nam, 1990; Wynne and Ballantine, 1991; Nam and Saito, 1991b; Nam and Sohn, 1994). Recently, detailed male reproductive structure and tetrasporangial development were clarified for several *Laurencia* species (Nam and Saito, 1990, 1991a, 1991b, 1994, 1995; Nam *et al.*, 1991, 1994). On this basis, several European and Californian species with potential subgeneric status were removed to the resurrected genus *Osmundea* Stackhouse, which is delimited from *Laurencia* by the production of tetrasporangia from random epidermal cells rather than from particular pericentral cells, and the production of spermatangial branches from apical and epidermal cells (filament type) rather than from trichoblasts (trichoblast type) (Nam *et al.*, 1994). Two fundamental vegetative structural types, which provide a stable basis for delimiting the subgenera *Laurencia* and *Chondrophycus*, were also characterized, one with four pericentral cells per axial segment and one with two (Nam and Saito, 1995).

Table 1. Comparison of anatomical characteristics of *Laurencia intercalaris* with other related species of *Laurencia*

Character	Species				
	L. intercalaris	*L. obtusa*	*L. nipponica*	*L. capituliformis*	*L. okamurae*
Vegetative axes	With 4P[a]	With 4P	With 4P	With 2P	With 4P
Epidermal cells					
2° pit-connections	Present	Present	Present	Absent	Present
Alignment	Npd[b]	Npd	Npd	Palisade	Npd
Projection	Absent	Absent	Absent	Absent	Absent
Lenticular thickenings	Present	Absent	Present	Absent	Present
Spermatangia					
Intercalary formation	Present	Absent	Absent	Absent	Absent
Nucleus	Apical	Apical	Central	Apical	Apical
Regeneration of SBT[c]	Present	Absent	Absent	Absent	Absent
Procarp-bearing segments	Unknown	With 5P	With 5P	With 4P	With 5P
Additional TP[d]	Unknown	Absent	Absent	Present	Absent
Position of TP	Unknown	3rd, 4th	3rd, 4th	2nd, 3rd*	3rd, 4th
Arrangement of tetrasporangia	Unknown	Parallel	Parallel	Right-angle	Parallel
References	This study	Nam *et al.*(1994)	Nam *et al.*(1991)	Nam & Saito (1995)	Nam (1990)

[a]Pericentral cells; [b]Non-palisade; [c]Sterile branches of male trichoblasts; [d]Tetrasporangial pericentral cells.
*Produced additionally.

Laurencia intercalaris has vegetative axes with four pericentral cells rather than two, as subgenus *Laurencia*, and has male reproductive structure of the trichoblast type. In all *Laurencia* species examined to date, spermatangia are produced from one of two laterals on suprabasal cell of trichoblasts arising from axial cells in apical pits of branchlets (Nam and Saito, 1990, 1995; Nam *et al.*, 1991, 1994). The other lateral remains sterile. *L. intercalaris* is unique within *Laurencia* in that a regeneration occurs in the sterile laterals of male trichoblasts. As described earlier, new sterile branches are produced from older segments abscised by budding-like regeneration and are readily recognizable by their smaller cell size. Regeneration in the sterile laterals may suggest that male trichoblasts need functionally sterile branches, which may protect adaxial fertile branches in opened spermatangial pits. Spermatangial development in *L. intercalaris* is also unique. It is common that spermatangia in *Laurencia* are formed from all axial segments of fertile laterals except for their basal (occasionally) and terminal segments (Nam, 1990; Nam and Saito, 1990, 1995; Nam *et al.*, 1991). However, in *L. intercalaris*, spermatangia are intercalary or subterminally produced from axial segments of the fertile laterals. The common development of spermatangia is rather unusual in this species.

In branching and habit, the new species is similar to *Laurencia obtusa* (Hudson) Lamouroux (1813), *L. nipponica*, *L. capituliformis* Yamada (1931) and *L. okamurae*. However, *L. intercalaris* is readily distinguished from these species by vegetative and male reproductive anatomy (Table 1). *L. obtusa* differs from *L. intercalaris* in lacking lenticular thickenings and in having a discoid holdfast rather than entangled fibrous holdfasts (Saito, 1967). *L. nipponica* also differs from *L. intercalaris* by having spermatangia with a central rather than an apical nucleus (Nam *et al.*, 1991). *L. capituliformis* lacks secondary pit-connections and lenticular thickenings, whereas in *L. intercalaris* these are formed. More importantly, *L. intercalaris* is distinguished from *L. capituliformis* in having four pericentral cells per vegetative axis rather than two (Table 1) (Nam and Saito, 1995). Among the four similar species, *L. okamurae*, which has entangled fibrous holdfasts, lenticular thickenings and spermatangia with an apical nucleus, appears to be most closely related to *L. intercalaris*. However, *L. intercalaris* is readily separated from *L. okamurae* by showing the regeneration in sterile laterals and the unique development of spermatangia in male trichoblasts described above.

Even though tetrasporangial arrangement is unknown, *Laurencia intercalaris* probably warrants place-

ment in the subgenus *Laurencia* rather than *Chondrophycus*, based on the presence of secondary pit-con- nections and vegetative axes with four pericentral cells.

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韓國產 海藻 新種, 사이서실(紅藻, 빨간검둥이科)의 營養體 및 雄性生殖器官의 解剖

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적 요

한국산 해조 신종, 사이서실(홍조, 빨간검둥이과)의 영양체 및 웅성생식기관의 해부가 기술된다. 본종은 소지의 규칙적인 호생분지와 함께 섬유상의 부착기에 원주상의 조체를 가지며 외형상 쌍발이서실과 구분이 불가능하다. 영양체의 축세포는 한개의 모상엽과 4개의 주심세포를 교대로 만들어낸다. 정자낭은 모상엽의 한 측지(염성지)로부터 개재적으로 또는 그것의 아정단부에서 만들어지며, 다른 한 측지(불염성지)에서는 잘려진 편절위에서 출아에 의한 재생이 일어난다. 본종과 관련있는 다른 종, 특히 원주상의 조체를 가지는 종들과 비교가 이루어진다. 정자낭의 형성방법과 함께 영양체의 해부학적 특징 및 모상엽의 불염성지에서의 재생과 관련있는 특징이 본종과 쌍발이서실을 포함하는 다른 종과의 구분의 기초가 된다.

주요어 : 해부, 사이서실, 주심세포, 정자낭, 재생

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