MEMOIRS OF THE FACULTY OF SCIENCE, KYOTO UNIVERSITY, SERIES OF BIOLOGY
Vol. VIII, pp. 85-96, March 1980

Branching Patterns of *Lycopodium cernuum* L.

By

Shigeyuki MITSUTA*

(Received September 12, 1979)

The morphology of gametophytes and sporelings of *Lycopodium cernuum* has been described rather in details: Treub (1890) made detailed anatomical studies giving a description and figures of protocorm as well as sporelings; Holloway (1910, 1915, 1916, 1919) made anatomical observation in view of ecological point; and Freeberg (1957) and Freeberg and Wetmore (1957) reported on some investigations on the experimental morphology of *L. cernuum*. Still, the branching of sporelings and young plants is not sufficiently observed as to elucidate the systematic position of this well-known species.

In the present study on the structure of *Lycopodium cernuum* observation will be made from anatomical, ontogenetical, and ecological point of view, together with a short discussion on the systematic position of this species.

Materials and Methods

Gametophytes and juvenile plants of *L. cernuum* were collected on Isl. Yakushima in Oct., 1977. Additional observations were made there and around Kyoto on the adult plants. They were observed in the field, and fixed in FAA for further observation; dried specimens were also collected after careful observation of adult plants. More detailed comparison was made mostly in the Herbarium of Kyoto University (KYO).

The steles of this plants were revealed by using pincets and needles, or by Hayata's method (Iwatsuki and Kato, 1975).

* Department of Botany, Faculty of Science, Kyoto University, Kyoto 606

Observation

Leaves and stem of juvenile plants

The gametophytes usually decay after having 6–8 prophylls on the protocorm which has numerous rhizoids at its lower part (Fig. I–1). The protocorm has its growing point at another side of the foot, and grows at first horizontally spreading prophylls alternately. Neither protocorm nor prophylls have no vascular supply as yet. When 8–10 prophylls are formed, a shifting of phyllotaxis is observed in protocorm giving prophylls to make spiral arrangement around the growth point of protocorm (Fig. I–2, 9th and 10th prophyll). The first root is formed nearly at the same time as a shifting of phyllotaxis, and grows downwards penetrating the cortical layer of the protocorm. The transformation of phyllotaxis from the alternate to the spiral arrangement is observed at the same time as a formation of vascular supply in protocorm. The main stem begins to be erected after the spiral phyllotaxis has been established. The vascular strand of the first root is directly connected with that of the main stem (Fig. I–4). The vascular strands enter into spirally arranged leaves. The vascular bundle entering into the first true leaf starts generally from the place where the stele of the stem meets with that of the root. The first root usually stops growing in its early stage by the development of the root nodules. In such a case the function of root is transferred to the second or the third root. These roots originate endogenously. At this stage the protocorm whithers and decays gradually.

The main stem continues to grow in the succeeding stages, and has spiral phyllotaxis. The first branching of the main stem is dichotomous in the lateral direction (Fig. I–5, fbr). A little later, the second branching (sbr) occurs simultaneously at both the branches of the first dichotomy. The plane of the second branching is not at the right angle but rather oblique to that of the first dichotomy. A distinct differentiation occurs at the second branches, i.e. the ventral branch is relatively stronger and straight, while the dorsal one is fine and slightly curved outwardly. This dorsal branch grows up to the first lateral branch. The second lateral branch is a smaller dorsal branch alternate to the first one. The succeeding lateral branches follow the same way and in lateral branch itself the same method is repeated, then catadromous branching established (Fig. II–1 ~ 3).

Branching in adult plants

The erect stem stands up on the creeping stem where the roots are occupied, and at the base of larger erect stems there are several abortive or resting lateral buds. The branching between erect and creeping stems is into two equivalent branches or in some

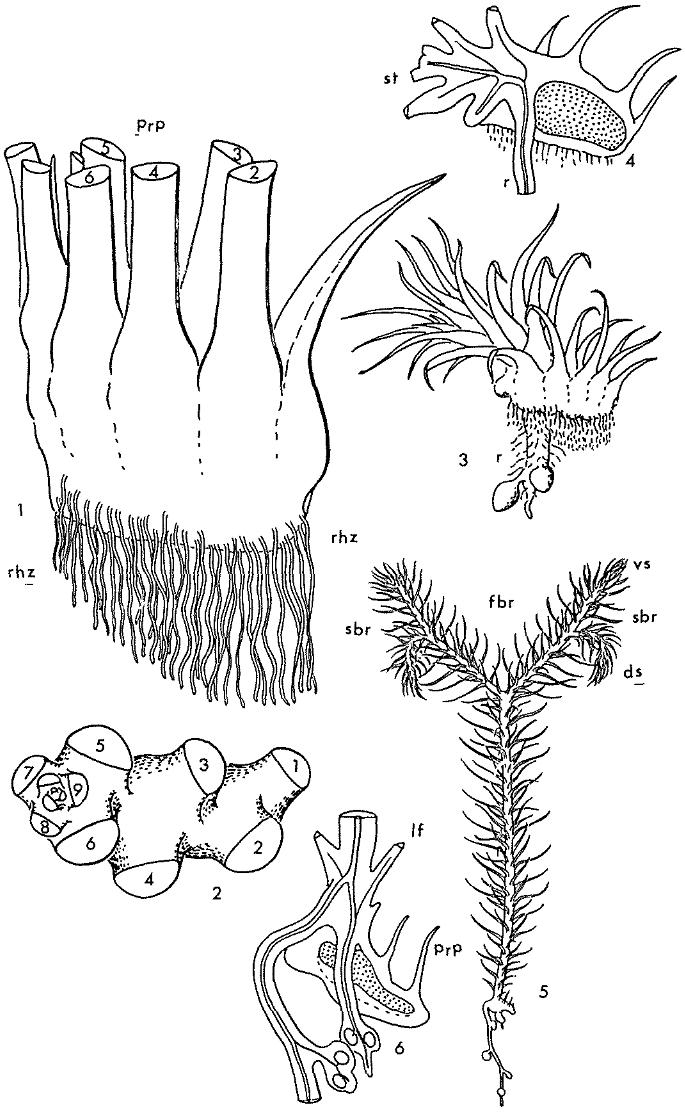

Fig. I. young plants of *Lycopodium cernuum*. 1–2: protocorm, showing arrangement of prophylls (prp). 1. side view 2. dorsal view. rhz: rhizoid. ×35. 3. very young plant with stem just formed. r: root. ×8. 4. same, longitudinal section showing vascular supplies. st: stem. ×10. 5. young plant, dorsal view. fbr: first branching, sbr: second branching, ds: dorsal branch of the stem, vs: ventral branch of the stem. ×2. 6. same, part of 5 enlarged, longitudinal section showing vascular supplies. lf: leaf 12.

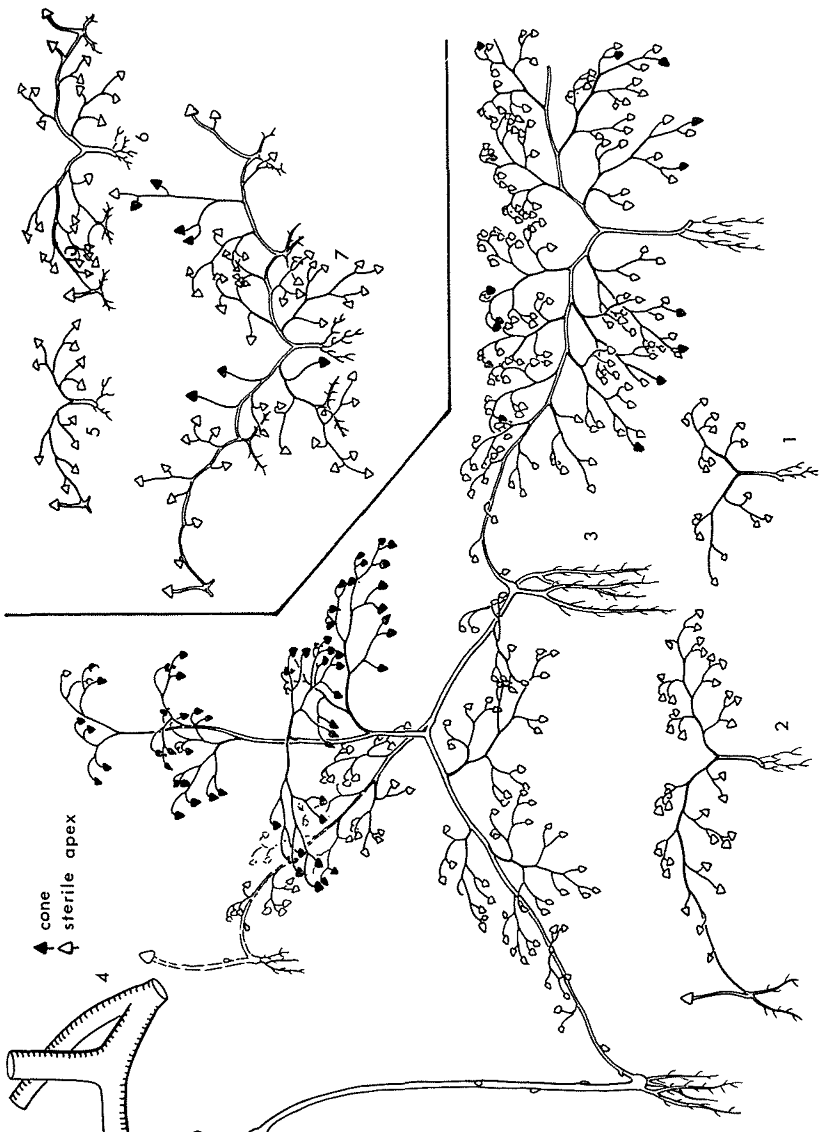

Fig. II. branching patterns of *L. cernuum*, diagramatically drawn, leaf omitted. 1–3: sunny plants in dry habitat. 1–2. young plants, 3. adult one. 4. part of 3 enlarged. 5–7: marshy plants. 5–6. juvenile plants. 7. adult one. all except 4×0.5

cases more or less modified than that (Fig. II–3, left). In case observed here branching of creeping stem is repeated by seemingly dichotomous branching and the planes of branching are perpendicular to each other (Fig. II–3, central left and 4). The roots from the creeping stem are thick and often branch dichotomously at their basal parts, and the lateral rootlets are very fine. This observation markedly contrasts with that of the roots just after the protocorm stage. They are endogenous, very fine everywhere and have monopodial branching.

Temperature and moisture seem to have an influence to the growth and morphology of *L. cernuum*. Tropical and subtropical plants of this species are sometimes nearly two metres tall, and the erect stem is thick spreading many lateral branches. Rooting is rather sparse comparing with the size of plant and each root penetrates deeply into the soil. The erect stems set numerous cones (sporangiferous clusters) (Fig. II–3). The plants in the warm- or cool-temperate region are compact or forming a mat on the ground. They root more frequently and the root spreads shallowly near the surface of the earth. The lateral branches of the creeping stems as well as erect ones set cones which are sparse, ascending to horizontal, and a few in number (Fig. II–5～7).

Erect and creeping stems

The mode of conjunction between erect and creeping stems are various according to the size and habitat of the plants. Smaller plants in cool- or warm-temperate zone are similar to the juveniles found in the tropical region in having both the erect and creeping stems resulted from nearly dichotomous branching divided in a vertical plane. Lateral branches are well developed throughout the plants (Fig. III, type A).

In larger plants, the mode of conjunction between both the erect and creeping stems is similar, but the erect stem is dominant to creeping one, and the lateral branches near rooting places are apt to be suppressed as resting buds, which are arranged alternately as in the same manner of lateral branches of creeping stem (Fig. III, type B).

The erect stem becomes to be much more dominant in larger plants in tropical or subtropical region. The common part of the erect and creeping stems are apt to stand upwards. Lateral branches are suppressed in many places except in the upper part of the erect stem. The resting buds of erect stems are arranged spirally (Fig. III, type C).

In the largest form of this species 1.5–2 metres tall, the creeping stems seem to be accessary branches of the erect stems, and have no root. The common part of both branches stands straightly upwards, continues to erect stem directly. Lateral branches are almost perfectly suppressed everywhere except in the upper part of the erect stems. These suppressed branches become very weak resting buds, or disappear (Fig. III, type D). In the latter case lower resting buds near rooting place sometimes develop

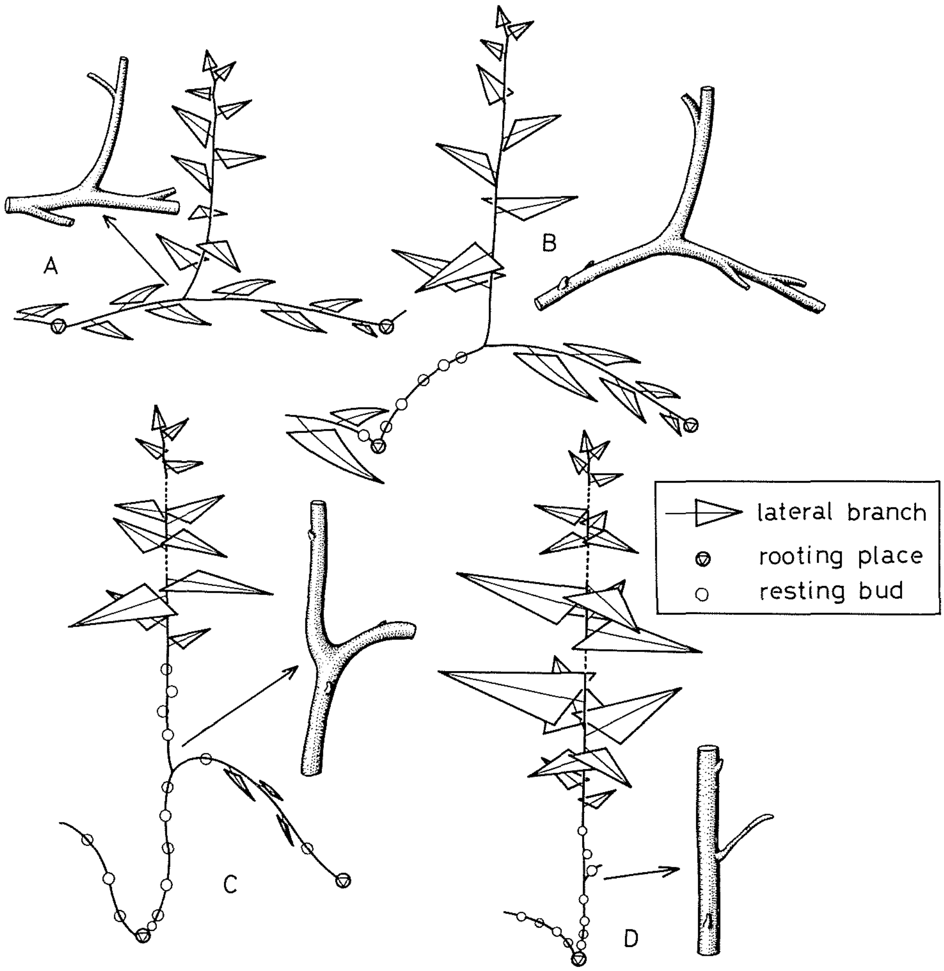

Fig. III. shema of branching of *L. cernuum*, showing four types. see text for details.

as the substitution of the primary creeping stem, which is quite accessary here, after the erect stem is well differentiated.

Variations are sometimes observed throughout these stages as mentioned above. The most common variation is that creeping stem is divided nearly into the dichotomous ones in horizontal plane soon after it departed from the basal part of erect stem. In this case, both branches of creeping stem have their first lateral branches often on the same side (Fig. IV). Another common variation is that creeping stem is divided into two branches in horizontal plane, sometimes dichotomous, often not, before it produces erect and creeping stems in vertical plane (Fig. II–4).

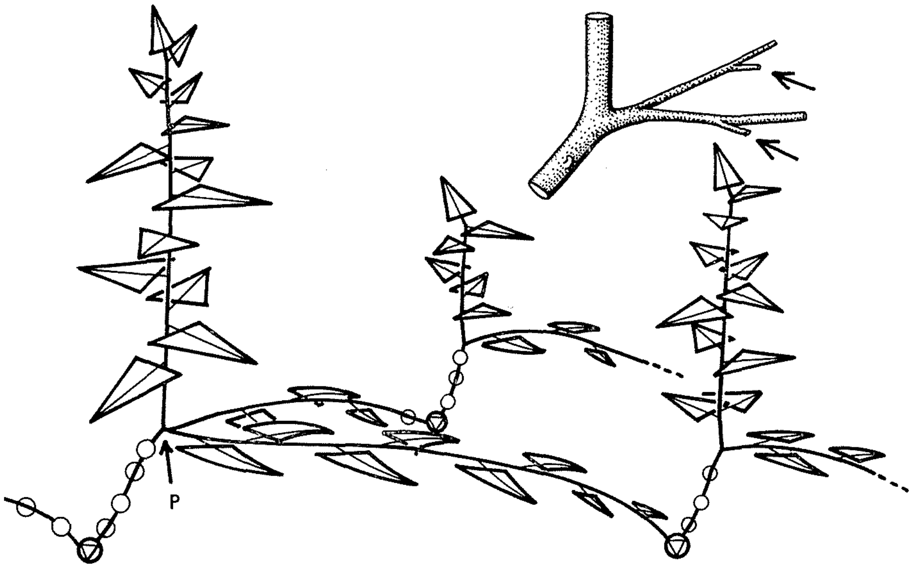

Fig. IV. variation of branching, schematically drwan, and P enlarged. arrows show lateral branches.

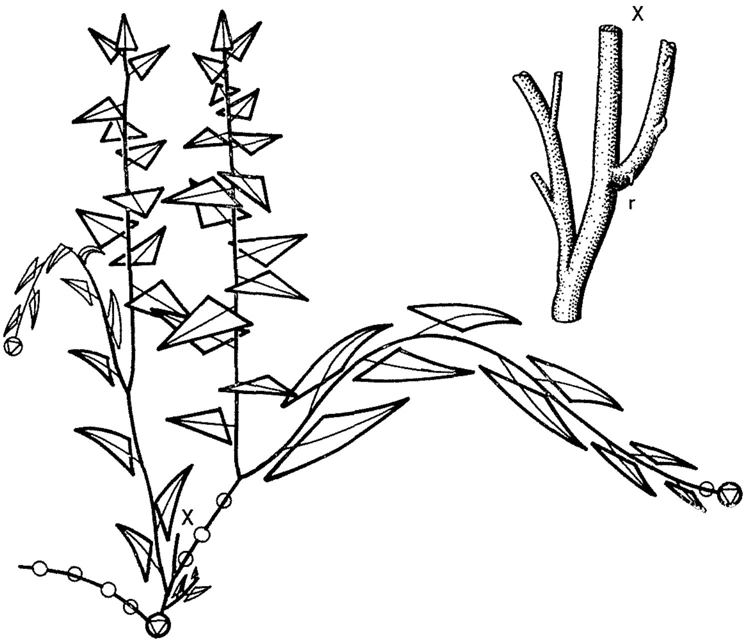

Fig. V. Two lateral sprouts of large plant, after cutting of primary erect stem at X, and partly enlarged. r: rooting.

If the apex of erect stem is injured at the early stage of differentiation in type C or D, the resting buds near rooting place begin to develop, giving one or a pair of sprouts, which show type A or type B observed above in the mode of conjunction between erect and creeping stems (Fig. V). In case that lower part of the plant is buried soon after the apex of erect stem is injured, resting buds near rooting place also begin to develop as new offshoots, which have secondary (sr1, sr2) and additional rootings (ar1, ar2, ar3). Weak lateral branch is sometimes seen at the basal part of these new offshoots (Fig. VI). If the apex of creeping stem is damaged after the erect stem was differentiated, the terminal one or two lateral branches are substituted for primary apex (Fig. VII).

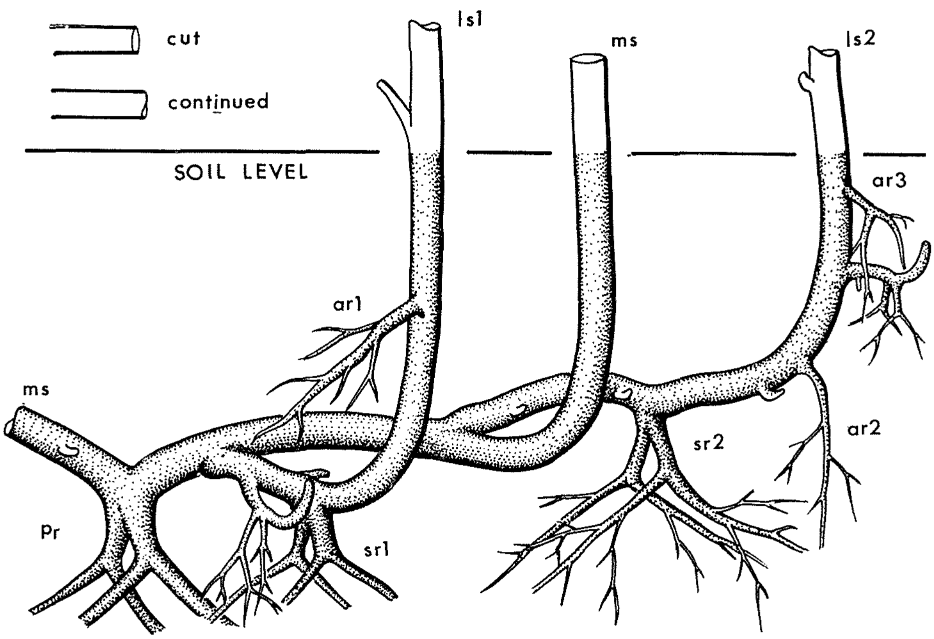

Fig. VI. basal parts of two lateral sprouts of large plant, after cutting of apical part of primary erect stem and buried in the earth. ms: main stem, ls: lateral sprouts, pr: primary rooting, sr: secondary rooting, ar: additional rooting.

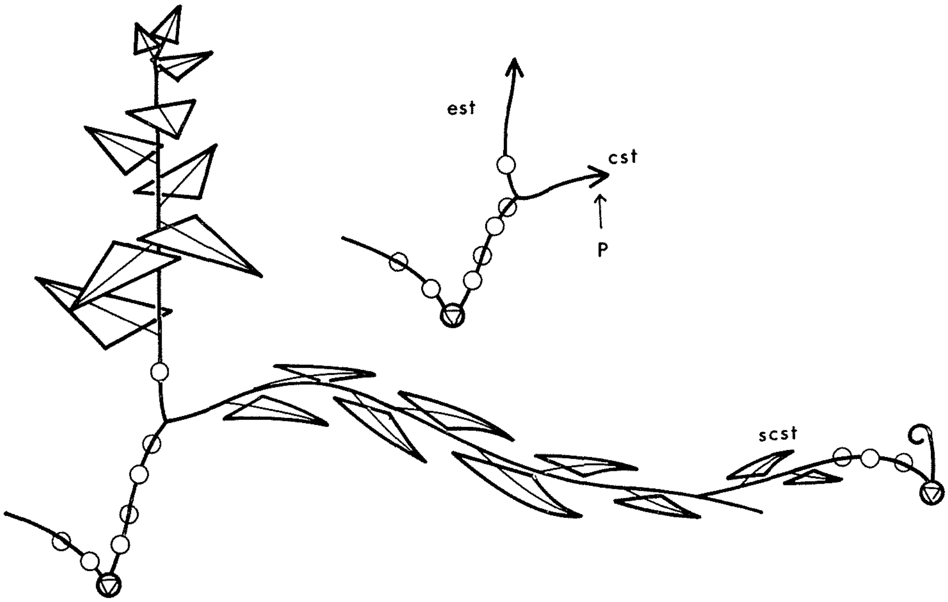

Fig. VII. substitution of creeping stem. Apex of creeping stem was cut in early stage at P. Lateral branch is substituted as secondary creeping stem. est: erect stem, cst: creeping stem, scst: secondary creeping stem.

Discussion

The arrangement of prophylls is alternate on the protocorm body at least in their origin, although it is usually described as at random. This arrangement is formed by a single growing point that produces the veinless leaves (prophylls) alternately (Fig. I–1, 2). The apex of stem does not appear adventitiously among the prophylls, but the growing point of protocorms directly changes to the apex of the stem. There are a variety of processes in formation of the stems. In some cases, the growing point lies to the lower distal part of protocorm, forming apex of the true stems seemingly independent from prophylls. In other cases in which the growing point is on the upper part of the protocorm, or the protocorm transfers to the stems in early stage, the true leaves are similar to the prophylls and the stems arise independently. In *L. volubile* and *L. scariosum* which have subterranean prothallia with no protocorm stage, the early leaves have the structure of the prophylls (Chamberlain 1917).

The first root is formed endogenously at the base of the stems (Fig. II–3$\sim$6), or the first root begins to appear simultaneously with the appearance of the vascular system in protocorm. The vasculature of the first root seems to be derived directly from that of the true stems (Fig. II–6) as observed by Treub (1890).

The roots of the creeping stems are thick, exogenous in origin, and often branched dichotomously near the base, though lateral roots are fine and weak. The early roots on the juvenile stems just after the protocorm stage are, on the contrary, endogenous, fairly fine, and monopodial. The dichotomous branching of the main root occurs at later (adult) stage, when the primordium of the root appears exogenously.

Holloway (1919) discussed that among all the members of the *Inundata* and *Cernua* sections, which are nearly synonymous to *Lepidotis*, only *L. cernuum* is superb in the extent of growth, which might be derived as quite a recent adaptation to dry localities from the type of the other species of these two sections which are confined to marshy habitats and very limited in their extent of growth. As correctly pointed out by Holloway, *L. cernuum* is by no means typical for the two sections. However, the branching mode of the erect and the creeping stems of this species is similar to that of *L. inundatum* and others. In the large plants of *L. cernuum*, both the erect and the creeping stems are well differentiated, or the erect stems are much dominant, but in the small plants the differentiation of both the stems is on the way that the creeping stems are dominant. The smaller plants bear the cones on the lateral branches of the creeping stems as well as on those of the erect ones. This is not observed in any other species of the two sections concerned. In the larger plants, the resting buds are arranged spirally on the erect stems as in the case of the lateral branches. On the creeping stem they arranged alternately and the resting buds are placed on the distinct positions which are concerned with self-reproduction when the apex of the stems are damaged. This is also a particular observation on this species.

As observed in the juvenile plants of *L. cernuum*, the first branching is apparently dichotomous and the lateral branches are formed by succeedingly unequal dichotomies and monopodial branchings. Spessard (1922) reported that the first branching of *L. clavatum*, a species of *Lycopodium* s. str., is monopodial. According to my observation, however, the first branching of *L. clavatum* is also unequally dichotomous or monopodial, and typical dichotomy could not be found in any of a dozen of materials examined. Bruchman (1898) and Foster and Gifford (1974) reported that the first branching of *L. complanatum*, a species of *Diphasium*, is monopodial. Holloway (1919) noted that the young plants of *L. cernuum*, *L. laterale* and *L. ramulosum* which belong to *Lepidotis*, have always dichotomous branching at their first division. The dichotomous branching is observed for *Lepidotis* and *Huperzia*, the latter is characterized in having typical dichotomies, but is not observed for *Lycopodium* s. str. and *Diphasium*. According to Øllgaard (1979), dichotomy (in his word, isotomy) is often observed in *L. spurium* Willd., a species of *Lycopodium* s. str., but not regularly. Freeberg (1957) reported that the young sporelings of *L. complanatum*, *L. selago* and *L. cernuum* are difficult to distinguish from one another in vitro. After his observation, the first branching of the sporeling of all these three species is dichotomous.

This observation, however, has been pointed out to be rather doubtful for the contamination of the spore of *L. cernuum* into the other two species. As observed here, the branching of *L. cernuum* is at first dichotomous, and later becomes monopodial. In this feature, this species is intermediate between *Huperzia* and *Lycopodium* s. str. or *Diphasium*. The rooting method of *L. cernuum* seems to be peculiar among *Lycopodium* species, but common method is also observed experimentally (Fig. VI).

Acknowledgements

Grateful thanks of the author are due to Mr. M. Takamiya of Hiroshima University for his kind supply of literatures. The author is also very thankful to Prof. K. Iwatsuki of Kyoto University for his linguistic check.

Summary

Structures and branching patterns of *Lycopodium cernuum* L. were observed anatomically, ontogenetically, and in ecological point of view. Prophylls are arranged alternately in origin on the protocorm body, and the growing point of protocorm directly changes to the apex of the stem. The transformation of phyllotaxis from the alternate to the spiral arrangement is observed at the same time as a formation of vascular supply in protocorm.

Modes of conjunction between both the creeping and the erect stems are various according to the size and habitat of the plants, but the creeping stems are dominant in marshy and/or smaller plants. In tallest ones, the creeping stems become to be accessary with no roots, and the role of spreading plants shifts to the resting buds which are originally comparable with lateral branches.

The early roots on the juvenile stems just after the protocorm stage are endogenous, fairly fine, and monopodial. In adult plants, on the contrary, they are thick, exogenous in origin, and often branched dichotomously near the base. Rootings are usually restricted to the tips of creeping stems, but the common method of the rooting is also observed experimentally in this species.

The first branching of sporelings of *L. cernuum* is dichotomous, though second and the later ones are not. The systematic position of this species in *Lycopodium* s. lat. was discussed on these features.

Literature Cited

Bruchman, H. 1898. Über die Prothallien und die Keimpflanzen mehrerer europäischer Lycopodien. Gotha. 119 p. 8pl.

Chamberlain, C. J. 1917. Prothallia and sporeling of three New Zealand species of *Lycopodium*. Bot. Gaz. **63**: 51–65.

Forster A. S. and E. M. Gifford, Jr. 1974. Comparative Morphology of Vascular Plants. Freeman. San Francisco

Freeberg, J. A. 1957. The apogamous development of sporelings of *Lycopodium cernuum* L., *L. complanatum* var. *flabelliforme* Fernand and *L. selago* L. *in vitro*. Phytomorph. **7**: 217–229.

——— and R. H. Wetmore 1957. Gametophyte of *Lycopodium* grown in vitro. Phytomorph. **7**: 204–217.

Holloway J. E. 1910. A comparative study of the anatomy of six New Zealand species of *Lycopodium*. Trans. New Zealand Inst. **24**: 356–370 pl. 31–34.

——— 1915. Studies in the New Zealand species of the genus *Lycopodium* I. ibid. **48**: 253–303.

——— 1916. Studies in the New Zealand species of the genus *Lycopodium* II. ibid. **49**: 80–93 2 pl.

——— 1919. Studies in the New Zealand species of the genus *Lycopodium* III. ibid. **51**: 161–216.

Iwatsuki, K. and M. Kato 1975. Stelar structure of *Asplenium unilaterale* and allied species. Kalikasan **4**: 165–174.

Spessard, E. A. 1917. Prothallia of *Lycopodium* in America. Bot. Gaz. **69**: 66–67.

——— 1922. Prothallia of *Lycopodium* in America II. Bot. Gaz. **74**: 392–413.

Treub, M. 1890a. Etudes sur les Lycopodiacées. VI. L'embryon et la placentula du *Lycopodium cernuum* L. Ann. Jard. Bot. Buitenzorg **8**: 1–14. pl. 1–5.

——— 1890b. Etudes sur les Lycopodiacées. VII. Les tubercles radiaux du *Lycopodium cernuum* L. ibid. **8**: 15–22, pl. 6–12.

——— 1890c. Etudes sur les Lycopodiacées. VIII. Consideration théoretique. ibid. **8**: 23–37.

Øllgaard, B. 1979. Studies in Lycopodiaceae II. The branching patterns and infrageneric groups of *Lycopodium* sensu lato. Amer. Fern J. 69 (2): 49–61.