Shizuo Momose*: The Prothallium of Ceratopteris**

The genus Ceratopteris consists of 4 or more species of annual and aquatic or subaquatic ferns in tropics and subtropics, and also in the warm temperate region of Japan. Although the prothallium of this genus has been morphologically studied in some detail by Kay (1875), Yabe and Yasui (1913) and Mahabale (1948), and some authors have discussed the systematic position or affinity of the genus basing on the prothallium characters, no detailed diagnostic study has so far appeared. This report presents the results of a diagnostic study of prothallia of Ceratopteris thalictroides (L.) Brongn. and C. pterioides (Hook.) Hieron.

Spores of Japanese and foreign sources were used for the material of prothallium cultures of C. thalictroides. Japanese spores were collected at Ichikawa of Chiba pref., Katsushika-ku of Tokyo, Anjo of Aichi pref., and Hamamatsu of Shizuoka pref.. For the latter one I am indebted to Prof. T. Kondo of the Shizuoka University. For foreign spores, I am indebted to Botanic Gardens of the University of Kopenhagen, Johannes Gutenberg University, and Greifswald and the Palmgarden of Frankfurt am Main. For spores of C. pterioides I am indebted also to the Botanic Garden of the University of Kopenhagen. I express my gratitude to Prof. T. Kondo and the directors of those botanic gardens for the supply of spores.

Observation

1. Ceratopteris thalictroides (L.) Brongn.

The prothallium asymmetrical, irregularly heart-shaped; apex somewhat deeply cordate; lobes duplicated above the sinus; lower part of the thallus round at the dominant side and cuneately at the recessive side narrowing towards the base. The base nonfilamentous, 2-3 cells wide, embraced by the trilobed sporecoat. Wings expanded abroad, somewhat ruffled; margin irregularly wavy and adventitiously notched with antheridiate sinus; wing cells elongate, of wavy membrane; marginal cells arranging with minute intercellular notches, of con-...
vexed free side. The midrib long and narrow, running from the base to the apex, arching towards recessive side, 4-5 cells thick in the heavier distal part, rhizomate on the posterior part and arched on the anterior part. Rhizoids hyaline or slightly tanned, delicate in texture, grow on midrib from the base to the upper part. Archegonia not so many in number; the neck of archegonia small and short, bending towards posterior, consisting of 4, rarely 5, neck cell rows at the anterior side and 3, rarely 4, neck cell rows at the posterior side. Antheridia marginal and submarginal, occasionally on the surface also, embedded or subembebed, endogenous, 75-90 μ in diameter; the wall generally consisting of 3 cells.

Fig. 1. Ceratopteris thalictroides (L.) Brongn. x 17.
The description and figures 1 and 2 are based on the material of Hamamatsu, Aichi prefecture. Japanese materials of any source showed uniform prothallia. This account seems to agree in general with the illustration of Yabe and Yasui (1913) based on the wild prothallium collected at Aichi prefecture, but it does not agree in some respects with the mention of Mahabale (1948) based on the wild ones collected at the vicinity of Bombay, India.

I have also investigated some foreign materials which were supplied by some botanic gardens in Europe under the name of *C. thalictroides*. They showed uniformity in the type of prothallia, but some differences from Japanese ones. Figure 3 is based on the material of the Botanic Garden of the Johannes Gutenberg University. The differences are that 1) more regular and flabellate form of the thallus, 2) more conspicuously notched margin and 3) more abundant antheridia. This account seems rather to agree with that of Mahabale (1948).

There is, in my mind, some taxonomical difference between Japanese and "C. thalictroides" cultivated in Europe.

2. **Ceratopteris pterioides** (Hook.) Hieron.

The prothallium asymmetrical, elongate-spatulate, elongate heart-shaped, often conspicuously lobed; apex shallowly cordate; lobes duplicate above the sinus; lower part of the thallus round at the dominant side and cuneate at the recessive side narrowing towards the base. The base nonfilamentous, 2-3 cells wide, embraced by the trilobed sporal coat. Wings auriculate, narrow, ruffled; margin irregularly waving, dentately notched with antheridia at the bottom, often lobate; wing cells elongate, of wavy membrane; marginal cells arranging with minute notches, of concave free side. The midrib long and narrow, running from the base to the apex, 3-4 cells thick in the heavier distal part, rhizomate on the posterior part and archegoniate on the anterior part. Rhizoid hyaline or slightly tanned, delicate, grow on midrib from the base to the upper part. Archegonia and antheridia like those of *C. thalictroides*.

The description and figures 4 and 5 are based on the material of the Botanic Gardens of the University of Kopenhagen. I have not seen the original paper of Kny (1875) on *C. thalictroides*, but his account has often quoted in various important systematic works. Kny's figure that is quoted by Diels in Engler u. Prantl: *Die natürliche Pflanzenfamilien* I-4: 340, Fig. 178-B may be one form of *C. pterioides* (Fig. 5-A).

The prothallium of this species is distinguishable from that of *C. thalic-
troideas by 1) spatulate or elongate form of the thallus; 2) more shallowly cordate apex, 3) more clearly ruffled wings and 4) concave free side of the marginal cell. Spores of this species are also distinguishable from the preceding species by more coarsely ribbed sculpture of the surface.

Discussion

From my observations, the prothallium of the genus Ceratopteris will be characterized as follows:

1. Spores are very large and globose-tetrahedral. The wall is colourless and with surface of ribbed sculpture.
2. The manner of germination of the spore shows "massive type," that is subsequent divisions at the proximal part of the spore form a mass of a few cells and produce directly a plate with the base of some cells wide.

3. The thallus is asymmetrical and variable in features. Young ones are spatulate in shape with the laterally situated meristem. Adult ones are cordate in shape with the apically situated meristem, and with ruffling and adventitiously or dentately notching wings.

4. Cells of the wings are elongate and of wavy membrane.

5. The midrib is long and narrow, running from the base to the apex, and is a thickness of 3-5 cells in the heavier part.

6. Rhizoids are hyaline or slightly tanned and delicate in texture.

7. The neck of archegonia is small and bends towards posterior and consists of 4 rarely 5 cell rows at the anterior side, and 3 rarely 4 cell rows at the posterior side.

8. Antheridia are marginal or submarginal in distribution, embedded or subembedded in condition and endogenous in formation. The wall of antheridia
consists of 3 cells in general.

Spores are comparable with those of some species of *Anemia*, *Mohria* and *Lygodium* both in the large size and in the globose-tetrahedral form. The large spore is also seen in some genera of Gymnogrammoid ferns, but spores of these ferns are tetrahedral. A characteristically ribbed sculpture of the colourless wall surface of spores is similar to those of some species of *Anemia* and *Mohria*. Such a sculpture is also found in some species of Gymnogrammoid ferns. Though Copeland states that "the ribbed spores recall those of *Orthiopteris*", the spores of *Ceratopteris* have a closer resemblance to those of some species of *Anemia* and *Mohria*.

The spore is full of abundant crystalloid reserve substance, and the plasmic contents are localized to its proximal part. As stated above, at the beginning of germination, cleavages occur at the proximal part of the spore, with subsequent divisions forming a mass of a few cells in the spore wall and then producing directly a plate of a few cells wide. As the result of proximal development the spore coat remains persistently embracing the base of the thallus. It looks like that the primary rhizoid is not produced by the first division but is produced by the later division. This manner of germination is not as ordinary in the most of true ferns, in which the spore cell firstly cuts off the primary rhizoid to the proximal side by the first division and then establishes the prothallial cell by the second division. Various manners of spore germination, in which the primary rhizoid is not produced by the first division of the spore cell, have been found in *Marsilea*, *Lygodium*, *Anemia*, *Mohria*, *Hymenophyllum* and *Grammitis*-group. The manner of spore germination of *Ceratopteris* has a probable resemblance in features to that of *Lygodium*, *Anemia* and *Mohria*, or to that of *Marsilea*.

The asymmetry of the thallus is caused by the bilaterally unequal activity of the meristem in younger stages of the plate development. Along with the development of the thallus, the meristem initiated at the lateral position of the spatulate plate changes its position to the apical and acquires the bilateral activity. Therefore the thallus soon or later develops into an asymmetrical cordate form. Such an asymmetrical thallus, is found in *Pteris*, *Onychium*, *Cheilanthes*, *Notholaena*, *Pityrogramma* and some other genera of Gymnogrammoid ferns. An extremely asymmetrical thallus, in which the meristem maintains its lateral position and continues its lateral activity throughout the life, is
characteristically found in Anemia, Mohria, Acrostichum, Anogramme and Actinopteris.

The wavy membrane of the wing cell characterizes the prothallium of some genera. I have found this feature in Lygodium, Anemia, Mohria, Cyathea (with exception of Allophila group), Dicksonia, Cibotium, Cryptogramma, Cheilanthes, Actinopteris, and some species of Adiantum.

The basal or subbasal initiation of the midrib is said to be a primitive character, and is seen in Osmunda, Anemia, Mohria, Lygodium, Cyathea, Dicksonia and others. But the thin midrib is peculiar to that of Ceratopteris. The rhizoid is like that of many of the higher ferns.

The neck of archegonia is somewhat peculiar in texture and looks like that of Lygodium. The neck that bends towards posterior is usual both in Lygodium and in Dick-

Fig. 4. Ceratopteris pteroides (Hook.) Hieron. x17.
soniaceae and Polypodiaceae sens. lat., and is said to be an advanced character.

Antheridia occur at the margin and submargin of the wings, and occasionally on the surface of the wings. This type of marginal distribution of antheridia is characteristic to *Ceratopteris*. I have found the marginal occurrence of antheridia in *Hypolepis*, *Histiopteris*, *Monachosorum*, *Cornopteris* and *A. iseanum* group of *Athyrium*. But in these ferns antheridia grow usually at the basal or lower part of the margin of wings and it seems to be

different from Ceratopteris, in which antheridia occur mainly on the upper part of the wings. The marginal distribution of antheridia of Ceratopteris may be rather related to that of the laminal distribution which is usual in Osmundaceae, Gleicheniaceae, Matoniaceae, Cheiropleuriaceae, Plagiogyriaceae, Cyatheaceae, Dicksoniaceae and Acrostichum.

The embedded or subembedded condition of antheridia caused by the endogenous formation is most characteristic to Ceratopteris. At the formation of the antheridium, any cell of the margin or submargin near the meristem becomes antheridial initial and forms directly the antheridium of three celled wall by means of three segmentations. The antheridial initiation at the cell of meristematic margin causes the marginal notch of the wings with antheridiate sinus, and the direct formation causes the endogenous antheridium of embedded or subembedded condition. Such a mode of formation of the antheridium is never found in the other homosporous leptosporangiate ferns, but is usual in the eusporangiate ferns. In these ferns the antheridium is directly initiated from the superficial cell (of the costa in Marattiaceae), but the wall of the embedded antheridium is multicellular in constitution and is not at all like that of Ceratopteris. The antheridium of Ceratopteris seems somewhat like that of Marsilea in features. Both the marginal distribution and the embedded condition of antheridia are responsible for the peculiar and isolated appearance of the prothallium of Ceratopteris in the leptosporangiate ferns.

Since Bower (1928) regarded Ceratopteris as a relative of Cryptogramme group of the Gymnogrammoid ferns basing on the morphology of the sporophyte, most authors of the systematic works of ferns have regarded the affinity of Ceratopteris to the Gymnogrammoid ferns. Namely Christensen (1938), Ching (1940) and Holtttum (1947, '49) considered the probable affinity to the Cryptogramme group, and Copeland (1947) considered the probable affinity to the Cheilanthes group. Furthermore they have suggested that Ceratopteris probably derives from a group of the Gymnogrammoid ferns in adapting to an aquatic life and they have placed Ceratopteris in or next to the Gymnogrammoid taxa. The discussion on the phyletic origin of the Gymnogrammoid ferns, and accordingly Ceratopteris, would be well represented by the statement of Pichi-Sermolli (1959, P. 474) that "they probably derive from a schizaeoid ancestor, and represent a branch of the evolution line of the marginales, a branch with a wide perspective power which appears to be clearly, even if not closely,
related to the Schizaeales”.

The opinion of these authors that Ceratopteris has an affinity to the Gymnogrammoid ferns and derives from a schizaeoid ancestor would be acceptable in principle, because the comparison of the prothallium characters, even if there are some obviously discordant elements, shows the most probable affinity both to the Gymnogrammoid ferns and to the Schizaeoid ferns. However the suggestion that Ceratopteris derives from a group of the Gymnogrammoid ferns seems to be not justifiable for me. I imagine that Ceratopteris directly and independently derives from a schizaeoid ancestor and is an ancient fern to be placed systematically between the Schizaeoid ferns, especially Lygodium, and the Marsileoid ferns.

References


摘 や 要

ミズワラビ属の熱帯アジアの代表種 *Ceratopteris thalictroides* と、熱帯アメリカの代表種 *C. pteroides* との前葉体を記述した。日本に自生するミズワラビは *C. thalictroides* とされていて、愛知県下で得た野生種による、矢部・保井両博士の図 (1913) によく一致する。西欧諸国の植物園で、本種として栽培されているものは、おそらく熱帯アジアのどこかから移入されたものであろうが、日本産のものに限って研究に委ねよ、稲柄や細胞の構造は凹形であることがより、前葉とは明らかに区別される。*C.thalictroides*に関する Kny の研究 (1875) は、Diels が Engler 氏の Nat. Pflanzenfam. 1-4 で論議しているが、それに引用されている Fig. 178-B (p. 340) は、*C. pteroides* の 1 形 (Fig. 5-A) とよく類似する。

以上 2 種 3 系統の検討から、ミズワラビ属の前葉体は次のようによって特徴される。1）胞子は大形の球状四面体で、表面には特有の鱗模様がある。2）胞子発芽の仕方は、塊状ともいうべき独特なものである。3）葉柄は非相称で、初めへら形、成熟すれば色々の形の心臓形で、両端はヒダ緑状であり、浅い切れ込みがある。4）葉細胞は長形で、縁は波状である。5）中肋は細長く、短くから頂に至り、顕著であるが薄い。6）仮根は無色または暗かに褐色で、軟弱である。7）造芽器の頚部は短くで方方に曲り、頚細胞の数が少ない。8）造芽器は緑色、埋没生よりも内生的であり、壁は 3 細胞からなっている。これらの特徴を他のシダ群と比較すると、ミズワラビ属はフサシダ群、特にカミクサ属と、Bower のいう Gymnogrammoid ferns に深い類縁関係が見られることを示す。また、胞子の形状や発芽の仕方は、あるいは造芽器の形態から、デンジソウ群との関係も見られる。これらの所見を総合して、ミズワラビ属は Christensen (1938), Ching (1940), Copeland (1957), Holtum (1947, ’49) 氏らが書いているように、Gymnogrammoid ferns に由来しているのではなく、デンジソウ群、フサシダ群、および Gymnogrammoid ferns と同じ祖先 (schizaeoid ancestor) からそれぞれ独立して発生した自生のシダであり、分類上はデンジソウ属とカミクサ属の中間に位置すべきものと推論した。