Evolution of simple fronds in *Cyrtomium*—a pattern morphological study—

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光田重幸：ヤブソテツ属における単葉形成過程

The fern genus *Cyrtomium* is characterized by generally imparipinnate fronds with reticulate venation and is distinguished from *Polystichum* by these features. Among about a dozen of the species of *Cyrtomium*, the number of lateral pinnae varies between 25 as in *C. hookerianum* and 3 as in *C. caryotideum*, *C. macrophyllum*, and so on, in addition to simple-fronded *C. hemionitis*. Contrary to this, *Polystichum* is a larger genus including some 200 species generally with bipinnate fronds and free venation, although there are some species with pinnate or finely dissected fronds. From the general tendency of evolution from more dissected fronds with free venation to less dissected fronds with reticulate venation, there is general agreement to relate *Cyrtomium* as a direct descendant of *Polystichum*. According to this view, the most advanced frond-construction among the species of *Cyrtomium* should be found in the simple-fronded *C. hemionitis*.

The comparison between compound and simpler fronds has been made recently in *Doryopteris* by Tryon (1942, 1944), in *Lindsaea* by Kramer (1957), in *Anemia* by Mickel (1962), and in *Bolbitis* by Hennipman (1977). The relationship between free and reticulate venation patterns was discussed in the case of the Thelypterid ferns by Iwatsuki (1962, 1963) and in *Bolbitis* by Hennipman (1977). Various developmental stages of frond construction and venation in the juvenile plants were carefully observed by Iwatsuki (1962) and Hennipman (1977) presenting further evidence in their comparative studies.

It is intended in this paper to elucidate the process of evolution from bipinnate and free-veined fronds in *Polystichum* to simple and reticulate-veined fronds in *Cyrtomium hemionitis* through various intermediate forms represented by the species of *Cyrtomium*. Comparative observations were made on the various developmental stages of juvenile plants as well as on the various patterns exhibited by the mature plants of *Cyrtomium* in comparison with *Polystichum* and a few other genera. *Phanerophlebia* of the New World was combined with the Old World *Cyrtomium* by Copeland (1947) and *Cyrtogonellum* was generically separated from *Cyrtomium* by Ching (1938); the species belonging to these genera were also carefully observed.

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Materials and methods

Juvenile plants of the following ten species were raised from spores and cultivated in the greenhouse of Kyoto University, taking care to maintain uniform growing conditions. The materials used, the sources of the parent plants (in parentheses), and the voucher specimens of the juvenile plants are:

*Cryptomium balansae* (CHRIST) C. CHR. (Kumamoto pref. Japan) S238
*C. caryotideum* (WALL.) PR. (Kochi pref. Japan) S46, S242
*C. falcatum* (L. f.) PR. (Kyoto pref. Japan) S56
*C. fortunei* J. SM. var. fortunei (Kyoto pref. Japan) A56, S143
*C. fortunei* var. eliciosa (MAKINO) TAGAWA (Kyoto pref. Japan) A57
*C. hookeriunum* (PR.) C. CHR. (Kagoshima pref. Japan) S146, S236
*C. lonchitoides* CHRIST (Cult. in Kyoto Univ.) S136, S240
*C. macrophyllum* (MAKINO) TAGAWA var. macrophyllum (Cult. in Kyoto Univ.) S100, S321
*C. macrophyllum* var. tukusicola (TAGAWA) TAGAWA (Cult. in Kyoto Univ.) S102
*Polypodium triseriale* Sw. (Mexico) S158, S173
*Polystichum lepidocaulon* (HOOK.) J. SM. (Cult. in Kyoto Univ.) S30, S31
*P. polyphocomum* (ROEM.) PR. (Kyoto pref. Japan) S196

In addition to these materials, dried specimens were also used for the comparative studies of adult plants in the herbarium of Kyoto University (KYO).

Observation

The description of juvenile forms will be given below according to each species.

1. *Cryptomium hookeriunum* (PR.) C. CHR. (Figs. I-1-6, III-A): Prothallia grow very slowly, taking 8–12 months to mature. The first leaf is of sexual origin and shows simple dichotomous venation (1). The first pinna is made clear at the 4–5th leaves and the veins are free (3, 4). Reticulate veins begin to be formed at the 8–10th leaves and the basal acrosopic veinlet becomes included (6). Juvenile plants grow slowly, and it takes 12–15 months before the formation of the 10th leaf. Pinnae of adult leaves are narrow and usually 12-20 pairs. Areolae form single to double lines at each side of the costa, but in the latter case the outer one usually lacks included veinlets.

2. *Cryptomium balansae* (CHRIST) C. CHR. (Figs. I-7-12, III-B): Prothallia grow very slowly, taking about 12 months to mature, and gradually become short, waving ribbon-like in form. The first leaf is of sexual origin and the veins are simple dichotomous (7). The first pinna is made clear at the 4–5th leaves and the veins are free (9). Reticulate veins begin to be formed at the 7–8th leaves (12). Juvenile plants grow slowly, and it usually takes more than 12 months before the formation of the 8th leaf. Pinnae of adult leaves are lanceolate to falcate with auricles, usually 12–18 pairs. Areolae form double (rarely 3) lines at each side of the costa. The outer one also often holds included veinlets.

3. *Cryptomium lonchitoides* CHRIST (Fig. I-13–21): Prothallia are cordate and grow quickly, taking 2–3 months to mature. The first leaf is apogamous in origin, shows twice dichoto-
Fig. I. Juvenile leaves of *Crytomium* species. 1-6: *C. hookerianum*; 7-12: *C. balansae*; 13-21: *C. lonchoides*; 22-29: *C. macrophyllum* var. *macrophyllum*. See text for more details.

Mous venation as to the little prothallus (13), or somewhat monopodial as to the large one (14). Veins begin to anastomose before the formation of the first pinna (16-17). The first pinna is made clear when the areolae form 2-3 lines at each side of the mid-vein (or rachis) (18-19). Juvenile plants grow quickly, arriving at the 10th leaf within 3-4 months (21). Pinnae of adult leaves are lanceolate-oblong, usually 10-18 pairs, areolae form 3-4 lines at each side of the costa. Each areola holds single to double included veinlets.
4. *Cyrtomium macrophyllum* var. *macrophyllum* (Makino) Tagawa (Fig. I-22–29): Prothal-
lia are cordate, taking 3–4 months to mature. The first leaf is apogamous in origin and
shows twice or three times dichotomous (22), or somewhat monopodial (23), venation.
Reticulate veins are often formed from the second leaf (24), gradually adding the lines of
areolae to each side of the mid-vein while the leaves tend to remain simple (25–28).
The first pinna is formed when areolae reach 4–5 lines at each side of the mid-vein (28–29).
Juvenile plants grow rather slowly. Pinnae of adult leaves are oval to ovate, and usually
3–7 pairs. Areolae form 7–9 lines at each side of the costa. A large areola holds 3–5
included veinlets. Each included veinlet is often combined by the loop-vein.

5. *Cyrtomium macrophyllum* var. *tukusicola* (Tagawa) Tagawa: Mainly as for var. *macro-
phyllum* but differs from it in the following points: the first pinna is formed when areolae
reach 3–4 lines at each side of the mid-vein (stage 27); pinnae of adult leaves are oblong
to lanceolate-oblong, usually 6–10 pairs, and areolae form 6–7 lines at each side of the
costa.

6. *Cyrtomium caryotideum* (Wall.) Pr.: Mainly as for *C. macrophyllum* var. *macrophyllum*
but differs from it in the following points: juvenile plants grow rather quickly; each vein
tip enters into the keenly pointed serration of the juvenile leaf as well as of the adult one;
pinnae of adult leaves are auricled, and areolae form 6–7 lines at each side of the costa.

7. *Cyrtomium fortunei* J. Sm. var. *fortunei* (Fig. II-1, 2): Mainly as for *C. lonchitoides*
but differs from it in the following points: the first pinna is formed when areolae form a
single (rarely double) line at each side of the mid-vein (1) (In a rare case, almost all the
areolae are lacking included veinlets (2)); pinnae of adult leaves are lanceolate and usually
15–25 pairs; areolae are small, forming 3–4 lines at each side of the costa, and each areola
holds single (sometimes double) included veinlets.

the first pinna is formed when areolae make double (rarely three) lines at each side of the
mid-vein. Pinnae of adult leaves are lanceolate-oblong and usually 7–15 pairs. Areolae
form 5–6 lines at each side of the costa; each one holds 2–3 included veinlets. Loop-
veins are sometimes observed.

9. *Cyrtomium falcatum* (L. f.) Pr. (Fig. II-3, 4): Mainly as for *C. lonchitoides* but differs
from it in the following points: pinnae of adult leaves are broadly falcate to lanceolate-
oblong and usually 7–15 pairs; areolae form 5–6 lines at each side of the costa; included
veinlets are 2–3 in each areola; loop-veins are sometimes observed.

10. *Cyrtomium nephrolepioides* (Christ) Cop. f. *nephrolepioides* (Fig. III-D right and central
below): Observations are of adult leaves only. Pinnae are lanceolate-oblong and
usually 8–18 pairs. Areolae are small, forming 2–3 lines at each side of the costa, and
each one includes single or double free veinlets. Loop-veins hardly observed.

11. *Cyrtomium nephrolepioides* f. *grossum* (Christ) Chino (Fig. III-D left and central above):
Observations are of adult leaves only. Pinnae are ovate to oval and usually 2–5 pairs.
Fig. II. Juvenile leaves of *Cytomium* species and other genera. 1–2: *C. fortunei* var. *fortuneii*; 3–4: *C. falcatum*; 5–9: *Polystichum polybrepharum*; 10–17: *P. lepidocaulon*; 18–25: *Polypodium triseriale*. See text for more details.

Areolae are small, forming 4–5 lines at each side of the costa, and each one holds single or double included veinlets. Loop-veins are sometimes observed.

12. *Cytomium hemionitis* Christ (Fig. III-E): Observations are of adult leaves only. The fronds are simple and the areolae are large, forming 7–8 lines at each side of the mid-
Fig. III. Adult leaves of *Cystopteris*, *Polystichum* and *Phanerophlebia*. A: *Cystopteris hookeriana*; B: C. *balansae*; C: *Polystichum lepidocaulon*; D: *Cystopteris nephrolepioides*; E: C. *heminitis*; F: *Phanerophlebia remotispora*. See text for more details.

vein. Each areola holds 2–5 included veinlets. Loop-veins are complex and customarily observed. (This species is sometimes combined with *C. nephrolepioides f. grossum*).

13. *Polystichum polybrepharum* (Roem.) Pr. (Fig. II-5-9): Prothallia are cordate and take 3–4 months to mature. The first leaf is of sexual origin showing twice to three times dichotomous venation, or somewhat monopodial in the large prothallus (5). The first pinna begins to be formed at the 2nd to 3rd leaves (6) and is made clear at the 5th leaf (7, 8). The 8th leaf is a simply pinnate frond (9) and from the 9th, later fronds gradually change to be bipinnate as seen in adult leaves. Juvenile plants grow quickly. Pinnae of adult leaves are 20–25 pairs; veins are free at all ages.
14. *Polystichum lepidocaulon* (Hook.) J. Sm. (Figs. II-10-17, III-C): Prothallia grow slowly, are short ribbon-like in form and take 8–12 months to mature. The first leaf is of sexual origin and usually shows twice to three times dichotomous venation (10). The leaves are simple during the 2nd to about the 6th, while lateral veins sufficiently increase in number (11–15). The first pinna begins to be formed at about the 7th (16), and is made clear at about the 9th (17). Juvenile plants grow slowly. Pinnae of adult leaves are lanceolate with auricles and usually 10–15 pairs. Veins are free, but rarely combined in some places.

15. *Polypodium triseriale* Sw. (Fig. II-18–25): The prothallia are cordate and take 4–6 months to mature. The first leaf is of sexual origin and broadly lanceolate to spatulate with simple veins (18). The leaves are simple from the 2nd to about the 8th, while lateral veins sufficiently increase in number (19–24). Veins anastomose similarly to those seen in *Cyrtogonium* (23–24). Vein-tip is swelling. The first pinna begins to be formed at about the 10th leaf, appearing cut away from the lower-most part of the frond (25). Pinnae of adult leaves are lanceolate and usually 7–15 pairs. The areolae contain a single included veinlet and form 3–4 lines at each side of the costa.

**Discussion**

As is shown in *Polypodium triseriale*, reticulate venation of the *Cyrtogonium*-type seems to be formed independently in the course of evolution. Neotropical *Phanerophlebia* (Fig. III-F) is characterized mainly by the narrower areolae and the customary absence of included veinlets. As is shown in the juvenile leaf of *C. fortunei* var. *fortunei* (Fig. II-2), it might be presumed that the venation of the *Cyrtogonium*-type has been derived from the venation of the *Phanerophlebia*-type, though this does not necessarily mean that these two genera have evolved through a single phyletic course. It is true that in the Old World *Cyrtogonellum*, venation shows both the *Cyrtogonium*-type (in the fertile frond) and the *Phanerophlebia*-type (in the sterile one), but *Cyrtogonellum* is also characterized by the presence of articulation at the base of the terminal leaflet as well as of the lateral pinnae. This terminal leaflet is the substitution of a lateral pinna for the suppressed true terminal leaflet. This phenomenon cannot be seen in either *Cyrtogonium* or *Phanerophlebia*, so it would be best to treat these three taxa as different from each other from a viewpoint of frond constitutions.

There are four types of development in the leaves of *Cyrtogonium* and *Polystichum*. They are:

1. *Polystichum polybrepharum* type (*P. polybrepharum*): The first leaf is of sexual origin, juvenile leaves are finely dissected from the early stages and veins are free throughout all ages. The pinnae simply result from lateral lobes. The fronds of adult plants are bipinnate.

2. *Polystichum lepidocaulon* type (*P. lepidocaulon*): The first leaf is of sexual origin,
juvenile leaves are simple and almost entire at the early stage, and the pinnae are apparently cut away from the lower-most part of the frond. The veins are customarily free. The fronds of adult plants are pinnate.

3. *Cyrtomium hookerianum* type (*C. hookerianum* and *C. balansae*): The first leaf is of sexual origin. Juvenile leaves are finely dissected at the early stage and pinnae simply result from lateral lobes. The veins anastomose after pinnae establishment. The fronds of adult plants are pinnate.

4. *Cyrtomium falcatum* type (*C. falcatum, C. fortunei, C. lonchitoides, C. cryptotideum* and *C. macrophyllum*): The first leaf is of apogamous origin. The juvenile leaves are simple, slightly dissected to sub-entire and the pinnae are apparently cut away from the lower-most part of the frond. The veins anastomose before pinnae establishment. The fronds of adult plants are pinnate.

According to my observations, type 1 seems to be generally applicable to *Polystichum* with bipinnate fronds. *Polystichum* contains such apogamous species with bipinnate fronds as *P. tsus-simense* and *P. kiusiuense*. In these cases, the leaf is finely dissected from the first to the adult condition, though the first leaf usually shows monopodial venation. The first leaf of the sexual type is apparently omitted. This might be related to the storage of carbohydrates in the embryo.

In *Polystichum lepidocaule* (type 2), which is sometimes compared with *Cyrtomium*, especially with *C. hookerianum* or *C. balansae*, reticulate veins are sometimes formed as apparently causal accidents after the pinnae are established. In this respect, this species differs distinctly from the apogamous species of *Cyrtomium* such as *C. lonchitoides*. The resemblance of the frond-shape in the adult plants between *P. lepidocaule* and *C. hookerianum* or *C. balansae* results from the different formational process of juvenile leaves. *P. lepidocaule* is distinct from the species of *Cyrtomium* in various features including the nearly peltate scales on the surface of the fronds.

A distinct difference is observed between type 3 and type 4 with regard to ontogenetical development of frond constitution. In type 3, veins anastomose after pinnae establishment, but in type 4, veins do so before pinnae establishment. This difference may result from the different developmental balance of lateral lobes, namely, the development of lateral lobes is rather remarkable in type 3, while it is very slight in type 4. It is noteworthy that a similar relationship is found between type 1 and type 3 with regard to

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*Fig. IV.* Formational process of adult leaves in *Cyrtomium* and its relatives. 1–13: Juvenile leaves. 14–20: Adult leaves (only as to 14, pinna shown). 1–8–9–14: *Polystichum polybrepharum* type (type 1); *P. polybrepharum*; 1–11–12–13–20: *Polystichum lepidocaule* type (type 2); *P. lepidocaule*; 1–8–10–15: *Cyrtomium hookerianum* type (type 3); *C. hookerianum, C. balansae*; 1–2–3–4–16–19: *Cyrtomium falcatum* type (type 4). 4–7–16: *C. fortunei* var. *fortunei*; 4–5–17: *C. fortunei* var. *clisiocola*, *C. falcatum*, *C. lonchitoides*, *C. nephrlepioides* f. *nephrlepioides*, *C. macrophyllum* var. *tukusica*, 4–5–18: *C. cryptotideum*, *C. macrophyllum* var. *macrophyllum*, *C. nephrlepioides* f. *grossum*; 4–5–6–19: *C. hemionitis*. Broken line: included veinlets; broken arrow means that this process is often omitted by the apogamous reproduction.
ontogenetical development of pinna constitution, though reticulate veins are not observed in type 1. The difference between adult pinnacles of _P. polybrephorum_ (Fig. IV-14) and that of _C. hookerianum_ or _C. balansae_ is equally comparable to the difference between juvenile leaves of _C. hookerianum_ (Fig. I-5, 6) or _C. balansae_ (Fig. I-10, 11) and that of _C. lonchitoides_ (Fig. I-17, 18).

As already stated in _C. nephrolepoides_, variations are observed in frond-forms among the plants within a single species. In this species, the number of lateral pinnacles is usually 7 to 18 for _f. nephrolepoides_, and 2 to 5 for _f. grossum_. In the former, areolae are 2 to 3 at each side of costa, and 4 to 5 in the latter. These variations are correlated with those of the breadth of the pinnacles as in the case between _C. macrophyllum_ vars. _macrophyllum_ and _tukusicolae_. _C. hemionitis_ is sometimes combined under _C. nephrolepoides_ _f. grossum_, though the frond is simple, with areolae of 7 to 8 rows at each side of the mid-vein. From these comparisons it may safely be suggested that the decrease in the number of pinnacles is correlated with the breadth of the pinna, although it is improbable to conclude here whether the evolution in the frond is from complex to simple or _vice versa_ in this species (or generally in _Clyrtomium_).

The difference between type 3 and type 4, as previously discussed, seems to be referable to the different developmental balance of lateral lobes on their ontogenetical ways. This relationship is also applicable between type 1 and type 3, so we may treat these types as three modifications of the same type. In type 4 the first leaf originates apogamously, and in types 1 and 3 it originates sexually. Type 4 may have originated from either type 3 or type 1 by the process that changed the reproductive form from sexual to apogamous. Although it may be theoretically possible that almost all the species belonging to the same genus change from apogamous to sexual, no actual evidence has been found in any of the fern genera. Summerizing the observation and discussion given above, the modification of the frond in _Clyrtomium_ may be referred to as having proceeded from a complex to a simple conditions.

Among the apogamous species of _Clyrtomium_ observed here, the following relationship is also recognized that as the rows of areolae increase when the first pinna is cut away on its ontogenetical way, the number of pinnacles decrease in adult leaves. In _C. fortunei_ var. _fortunei_, the rows of areolae are 1-(2) at each side of mid-vein and the lateral pinnacles are 12–25 pairs. In var. _clivicola_, areolae are in 2-(3) rows and the pinnacles are 7–15 pairs. In var. _clivicola_, areolae are in 2-(3) rows and the pinnacles are 7–15 pairs. In _C. macrophyllum_, the areolae are 3–4 and the pinnacles are 6–10 in var. _tukusicolae_, and the areolae are 4–5 and the pinnacles are 3–7 in var. _macrophyllum_. It is rather difficult to compare these relationships among the different species, but the general tendency of correlation between the number of pinnacles and of rows of areolae is distinct as previously noted. This correlation indicates that the evolution of frond characters seems to have proceeded along a specific line in _Clyrtomium_. The condition of simple leaf seen in _C. hemionitis_ should thus
be the ultimate condition derived from the type of *C. nephrolepidoides f. grossum*.

These relationships are schematically summarized in Figure IV.

**Note on the ecological element**: A slight difference was observed between the wild materials and the cultivated ones. For example, fronds of *C. falcatum* are often simple until 4 to 5 rows of areolae are formed at each side of mid-vein for the plants collected in exposed and dry places. Our greenhouse was kept moist and shady in order to grow such sylvan species as *C. hookerianum* and *C. balansae*, and the plants grown in such a condition are described in the above sections. *C. macrophyllum* has broad pinnae and many rows of areolae, and is usually found in wet, dense evergreen forest. *C. fortunei var. fortunei* has narrower pinnae and a few rows of areolae, and is usually found in dry, exposed places. *C. fortunei var. clivicola* has broader pinnae and more rows of areolae than var. *fortunei*, and is a sylvan variety. As a whole, the trend of simplicity in frond constitution in *Cyrtomium* does not seem to correlate with the exposed dry conditions of their habitat.

**Summary**

Comparative observations were made on the various developmental stages of juvenile plants as well as on the various patterns exhibited by the mature plants of *Cyrtomium* in comparison with *Polystichum* and a few other genera. Four different types were recognized among *Cyrtomium* and *Polystichum* species as to the developmental stages of juvenile plants. They are:

1. *Polystichum polybrepharum* type
2. *Polystichum lepidocaulon* type
3. *Cyrtomium hookerianum* type
4. *Cyrtomium falcatum* type

Among these types, it was pointed out that type 1, type 3 and type 4 are the variations of the same type from a view point of the change in activity of marginal meristems at their ontogenetical development of leaves. Among the *Cyrtomium* species, the following correlations are observed as to the leaf constitution:

1. Among the adult leaves, as the number of pinnae becomes fewer, pinnae become wider.
2. As the rows of areolae increase in number when the first pinna is cut away ontogenetically, pinnae decrease in number in adult leaves.

Based on these correlations, it was pointed out that variation in the fronds has proceeded along a specific line in *Cyrtomium*. Among *Cyrtomium* species, each simpler-fronded species also shows apogamous reproduction.

The relationships presumed from these circumstances are shown in Figure IV.

**Acknowledgement** I wish to express my thanks to Prof. K. IWATSUKI, who encouraged me to prepare this paper and willingly took the trouble to read the manuscript. Mr. M. Kido and Mr. S. TSURUSU kindly sent me several rare materials which were used extensively in this study. I am also grateful to Mr. D. E. BOUFFORD for a linguistic check.
参考文献


葉形の変化に伴う網状の変化は、ヤブソテツ属中では見られず、一連の変化は比較的様式が少ない。発展段階としての異質のものであり、それがわかった。

ヤブソテツ属の変化は、イヌデの枝葉に似ており、網状脈の型にあり、葉脈の型に違いがあり、またエゾンダ属の葉脈形成（图18-25）による変化から、両群はイヌデ属から平行的に導き出されると推定される。残りの二つは新大部の変化の影響をおぼえ、枝葉に近い形状をもち、変化は枝葉に近い脈脈をもち、枝脈形成は発展段階におけるものである。故に、ヤブソテツ属と一致するものであることが示された。

ヤブソテツ属各群の変化の比較から、以下の相関関係の傾向が指摘される。1. 成葉間で、羽片の数が減ると、枝葉は幅広くなる。2. 葉の個体発生変化において、最初の羽片が切り出される時の主脈（葉軸）に沿う網目の列が切り出される時の主脈（葉軸）に沿う網目の列が増すほど、成葉における羽片数は減少する。

これら二つの相関関係から、ヤブソテツ属については、葉の変化が異なる一連のものであることが示され、また、エゾンダ属の変化はヤブソテツ属と比べて、形態的差は少ないが、発展段階としては異質のものであることがわかった。