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Taxonomy of the Thelypteroid Ferns, with Special Reference to the Species of Japan and Adjacent Regions

II. Circumscription of the Group

by

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The thelypteroid ferns can not be clearly circumscribed even at present, and we have several genera which are included in or excluded from this series of ferns according to the conceptions of various authors. To better understand the accurate boundary of our series, some of the recent works will be referred to here. The recent treatment of importance concerning the circumscription and relationship of the thelypteroid ferns are those given to the fern classifications by CHRISTENSEN (1938), CHING (1940), COPELAND (1947), HOLTTUM (1947 etc.) and others. In the last decade, several contributions have been made but they are fragmentary. The genera which are included in our series by some authors or excluded by the others have been studied by various botanists from the standpoint of morphology or taxonomy, but their investigations are independent from each other, little reference being made to the works by similar methods and conceptions. Therefore, a revision will be given below including all of these recent studies.

It is universally acknowledged that the thelypteroid ferns comprise such genera as *Thelypteris* (*Lastrea*), *Phegopteris*, *Glaphyropteris*, *Steiropteris*, *Cyclogramma*, *Leptogramma*, *Cyclosorus*, *Abacopteris*, *Ampelopteris*, *Stegnogramma*, *Goniopteris* and *Meniscium*. There is no question about the natural relationship of these genera. In addition to these, *Haplodictyum* and *Sphaerostephanos* are included in the thelypteroid series by most of the present day pteridologists with the exception of CHING. *Dictyocline* has also been referred to in our series, though some botanists consider this genus to be distinct from the thelypteroid series.

CHING (1940) considered that *Sphaerostephanos* constitutes its own family. He distinguished Sphaerostephanaceae from Thelypteridaceae by the various features, of which the soral characters alone are different in these two families. He describes the spores of *Sphaerostephanos* as being large, tetrahedral, without

perispore and translusent. This seems, however, to be a misobservation. The observations on *S. polycarpa* and *S. larutensis* show that their spores are bilateral, distinctly tuberculate or reticulate, and with transparent perispore. It has been mentioned under morphology that the receptacles and indusia of *Sphaerostephanos* are definitely not distinct from those of the thelypteroid ferns.

Since 1929 when COPELAND correctly identified *Dictyocline* as being an ally of the *Dryopteris* series, he has been followed by all authors with the exception of NAKAI (1933) who related it to the group of *Tectaria*. The irregular reticulate venation seen in that genus was judged to be that common in the tectarioid series of ferns. In agreement with NAKAI's treatment, CHING (1940) separated *Haplodictyum* from Thelypteridaceae and related it to the tectarioid series. On the taxonomic evaluation of venation, I have discussed in my earlier publications (1962 a, 63) and in the foregoing part of this paper. Thus, I think it would be better to include the genera discriminated only by the difference in venation, such as *Haplodictyum* and *Dictyocline* placed in the tectarioid series by CHING and NAKAI respectively, in the thelypteroid series of ferns.

I have referred two abberant species, *Dimorphopteris moniliformis* and *Aspidium boydiae*, to the thelypteroid series. The distinct features found in these two species, i. e. the strong dimorphism of the former and the round peltate indusia of the latter species, were mentioned in my earlier papers (1961, 61 a) and in the first part of the present paper. No additional account is deemed necessary to be given here to recognize the thelypteroid alliance of these two species.

The following genera should be included in the thelypteroid series as has been noted on the foregoing pages: *Thelypteris*, *Phegopteris*, *Glaphyropteris*, *Steiropteris*, *Cyclogramma*, *Leptogramma*, *Dimorphopteris*, *Cyclosorus*, *Abacopteris*, *Ampelopteris*, *Stegnogramma*, *Sphaerostephanos*, *Goniopteris* and *Meniscium*. Their relationship and classification will be fully discussed in the next part of this paper. Before going further, however, it may be well to give short notes on genera sometimes included in the thelypteroid series, and the circumscription of our group will be made clearer by these critical comments.

GENERA EXCLUDED FROM THE THELYPTEROID SERIES

Monachosorum *and the related genera.* The systematic position of *Monachosorum* has been controversial even in the last generation. BOWER (1928) is of opinion that *Monachosorum* appears to be a derivative of *Dennstaedtia*, probably along a line parallel to that of *Hypolepis*, and has its position among the Marginales as indicated by the existence of hairs and the complete absence of scales. In the next year COPELAND (1929) placed *Monachosorum* in his *Cyathea-Diacalpe* series following the original author, KUNZE, and *Ptilopteris*, a monotypic related genus, in *Cyathea-Cystopteris* series. At that time, he discussed little the characteristics of them, and distinguished these two genera without any account of the discriminative features. HAYATA described and named a number of genera

as the result of his study on the vascular structure of various ferns. Following to his own taxonomical idea, the dynamic classification, he gave much importance to the vascular structure in his generic system of ferns. He (1928, 29) made a generic distinction between *Monachosorum* and *Monachosorella* (a direct synonym of *Ptilopteris*) and related both of them to the thelypteroid members among the complex genus *Dryopteris*. Later, TAGAWA (1937) supported the opinion of BOWER, emphasizing the importance of the nature of trichomes and spores. CHRISTENSEN (1938) had the opinion that *Monachosorum* and *Monachosorella* were the members of the thelypteroid ferns, though he assigned no reason for this. CHING (1940) proposed a family Monachosoraceae comprising only two genera, *Monachosorum* and *Ptilopteris*. He held the opinion that Monachosoraceae was related to both Thelypteridaceae and the athyrioid ferns, but nothing was mentioned as to the basis of relating Monachosoraceae to each of these phyla. In his Genera Filicum (1947) COPELAND gave up his earlier opinion and inclined to consider that *Monachosorum* and *Ptilopteris* are congeneric having a relationship to the dennstaedtioid ferns. The basis of his later consideration is wholly identical with that of BOWER. HOLTTUM placed *Monachosorum* at first (1947) in his Dennstaedtioideae, stating that this genus had a creeping hairy solenostelic rhizome, a frond of the general form of the *Dennstaedtia* tribe with leaflets uneaqual at the base and grooved costae of the *Dennstaedtia-Hypolepis* type. He supplemented the same paper by a short comment of amendment to the above statement, in which he noted that the relationship of *Monachosorum* was not to *Thelypteris* in view of frond form, hairs, rachis structure and lack of scales, and suggested that *Monachosorum* might more nearly be related to *Leucostegia* than to *Dennstaedtia*. In 1948, however, HOLTTUM placed *Monachosorum* in the subfamily Dennstaedtioideae without any further comment.

As shown in the short historical sketch of the status of *Monachosorum*, this puzzling genus has gained no fixed position among the taxonomic system of ferns. I do not intend to discuss here the generic identity of *Monachosorum* and *Ptilopteris*, noting that treatment of COPELAND (1947) seems to be most referable.

Among the various taxonomic features of *Monachosorum*, those which have variously been estimated as the indicators of its position are: construction of rhizome, trichomes, rachis structure, spores and so on. The most important ground for relating *Monachosorum* to the thelypteroid ferns seems to be the construction of its rhizome: the rhizome is erect, dictyostelic, radially constructed, and sending out two leaf traces to each stipe. However, it is highly unnatural to relate a taxon with another basing only on the identity of a single character, even when it is generally accepted as one of the most fundamental characteristics. In the case of this presumption on *Monachosorum*, various contradictions arise in relation to the features other than rhizome. *Monachosorum* is characterized by having not scaly but hairy rhizome, tetrahedral spores, and the blade free from trichomes except the glandular hairs on the veins. It is clear that the genus *Monachosorum* is quite different from the thelypteroid ferns by the above-stated differences found in the respects which are the most impor-

tant indicators to circumscribe the thelypteroid ferns. Moreover, we have several examples of the group of genera, which include both the genera having the creeping and dorsiventral rhizome and those having the erect rhizome with radial construction. HOLTTUM (1949) enumerated in his Dennstaedtioideae the genus *Orthiopteris* with erect scaly root stock. Thus, the erect rhizome of *Monachosorum* is not so peculiar among the members of Dennstaedtioideae. HAYATA considered that the modern conception of natural classification was quite unsatisfactory and that no fixed classification should not be given. He called his unfixed classification as 'dynamic classification' and proposed various systems based on a single feature which was selected for reason of his own. Thus, this conception of him is completely subjective, and is entirely unscientific. Thelypteroid relationship of *Monachosorum* offered by HAYATA was founded on the ground of such opinion.

HOLTTUM once compared *Monachosorum* with *Leucostegia*. At that time, he valued highly the pattern of rachis-groove, but it incurs no contradiction in including *Monachosorum* among Dennstaedtioideae. I have at present no additional datum to decide the systematic position of *Monachosorum*, and accept the opinion of BOWER and of his followers.

Acystopteris. In his *Coloured Illustrations of the Japanese Pteridophyta*, TAGAWA (1959) briefly mentioned in Japanese that *Acystopteris* resembles the thelypteroid ferns in its frond constitution and he recognized the necessity for a critical investigation on the status of this genus. Because of the presence of coarse multiseptate hairs or ctenitis-hairs, *Acystopteris* is separated from *Cystopteris*. One of the two species of this genus, *A. tenuisecta*, has been placed in various genera, but no one has actually related it to the thelypteroid series of ferns. When NAKAI established *Acystopteris*, he stood on the serious misobservation of the sori, though his resultant separation of *Acystopteris* from *Cystopteris* should be highly acceptable. The recent conception defines *Acystopteris* by the various diagnostic characters, especially by the presence of the ctenitis-hairs on the axes of fronds. TAGAWA gave much importance to the frond form and constitution of this genus and suggested its thelypteroid alliance. The minute comparison makes it clear that the genus *Acystopteris* is a member of the athyrioid ferns as indicated by such respects as trichomes, chromosome numbers, grooves on axes and so on. Thus, the detailed data concerning *Acystopteris* are not in accordance with the theme of the present paper, and so they will appear in separate paper.

Gymnocarpium *and* **Currania.** COPELAND is of opinion that the genus *Currania*, having the peculiar lamina which is sharply geniculate at the junction with stipe and deeply pinnatifid with opposite glabrous segments, is generically distinct from *Gymnocarpium*. He emphasized the phyletic independence of *Currania*, but none of the recent pteridologists would like to accept his opinion in this condition. Peculiar mode of laminar constitution found in *Currania* may

better be interpreted as to be a feature resulted from the specialization of that of *Gymnocarpium*. Although I will not go further on this problem, the two genera are considered as to be one in the following paragraphs. The generic limitation of these species was well summarized and discussed by CHING (1933).

In the midst of the last century NEWMAN established *Gymmocarpium*, a genus of three species: *G. dryopteris*, *G. robertianum* and *G. phegopteris*. These three species are similar to each other in the appearance of their frond construction, the anatomical features, the soral characteristics, the habit and geographical distribution, and so on. Both COPELAND (1929 etc.) and CHRISTENSEN (1938) followed in whole NEWMAN and related *Gymnocarpium* to the thelypteroid series. COPELAND (1947) actually included *G. dryopteris* and *G. robertianum* in his large and complex genus *Lastrea* together with *G. phegopteris*, the systematic position of the last being doubtlessly in the thelypteroid series. However, the species of *Gymnocarpium*, except for *G. phegopteris*, are different from the thelypteroid members by the several features mentioned below.

The trichomes of *Gymnocarpium* are distinct generically enough from those of the thelypteroid ferns. The scales occur only on the rhizome and at the base of stipes and are membraneous, quite glabrous and basifixed. At the base of larger costae, there are sometimes found coarse multicellular hairs, which are caducous and not found on the older fronds. The surfaces of fronds are quite glabrous in all species of the genus. In some species, there are found yellow and sessile or brown and short-stalked glands on the under surface of fronds or on the upper surface of axes.

These features found on the trichomes of *Gymnocarpium* are sufficiently different from those of the thelypteroid ferns. In the latter group, the scales are usually hairy on margin and often on the surfaces as well, no coarse multicellular hairs are found on any portion of the fronds and setose hairs occur more or less densely on various parts of plants. *Gymnocarpium* may easily be separable from the thelypteroid series even by the indicative features of the trichomes only. Among the thelypteroid ferns, there are several species bearing apparently glabrous scales (*Thelypteris palustris*, *Cyclosorus gongylodus* and others) but they are not glabrous in strict sense as I have already noted in my earlier paper (1962). So-called ctenitis-hairs are completely absent in the thelypteroid ferns, though the seemingly articulated long hairs are found on the axes of fronds in some groups. As noted on the other pages, the most distinctive feature to diagnose the thelypteroid ferns is the presence of setose hairs usually unicellular in construction. Complete absence of these hairs on any portion of plants is the vital obstacle to combine *Gymnocarpium* directly with the thelypteroid genera.

The articulation seen on the axes is one of the distinct features of the species of *Gymnocarpium*. However, this articulation seems to be not so functional that the pinnae seldom fall off at their insertion. In this account, further discussion will be given in the paragraphs concerning *Hypodematium*. Both COPELAND (1909 etc.) and CHING (1933) pointed out the peculiar mode of insertion

of blade. In living state, the lamina is obliquely inserted to the stipe by the prominent articulation. This peculiar feature shows the generic distinctness of *Gymnocarpium* but does not indicate any actual phylogenetic relationships with any series of higher ferns. From the presence of prominent articulation, we can infer the apparent resemblance between *Gymnocarpium* and *Woodsia*, the phylogeny of the latter also obscure.

The pentagular outline of frond is the feature common to all the species of *Gymnocarpium*. This frond form seems to be one of the indications which have made up the heterogeneous grouping of NEWMAN's *Gymnocarpium*, uniting *G. dryopteris* and *Thelypteris phegopteris*. The form and size of fronds are fairly variable according to species and do not stand as the characteristics sufficient to discriminate the taxa higher than specific level, though the related species often take the appearance similar to each other. The thelypteroid species have the fronds generally oblong or oblong lanceolate in outline.

Soral character is another feature to warrant the relationship between *G. dryopteris* and *Thelypteris phegopteris*. Now, I will not go further on this account, for the presence of various soral characteristics in a single phylogenetic series is observed and discussed in other pages. MANTON (1950) and others reported the haploid chromosome number of both *G. dryopteris* and *G. robertianum* as 80. At the same time, MANTON noted that *Thelypteris phegopteris* reproduces apogamously, though the two species of *Gymnocarpium* are normal in their reproduction. These cytological data will show the existence of difference between *Gymnocarpium* and the thelypteroid ferns.

CHING (1933) related *Gymnocarpium* to the thelypteroid group in one hand and did more closely to the athyrioid in the other. He often advanced such a typological view, comparing with a phylogenetically remote group. At that time, the thelypteroid ferns are generally considered to be in the same phylogenetic group with the athyrioid ferns. Now, the thelypteroid series are clearly separated from the athyrioid group, though these two phyla are explained as two parallel ones, resembling each other in various respects. The species of *Gymnocarpium* may be placed among either of these two series of ferns, and the better choice should be the inclusion of it in the athyrioid series, together with *Woodsia* and the related groups, as seen in the nature of trichomes, the anatomical features, the chromosome numbers, and so on.

Hypodematium *and* **Lastreopsis.** Both CHING (1940 etc.) and HOLTTUM (1954) considered that *Hypodematium* and *Lastreopsis* were closely related to each other, though CHING attributed these two genera to the thelypteroid series and HOLTTUM placed them in the tectarioid group. Earlier confusion concerning their systematic position have been summarized and brought to order by these two authors. Recently LOYAL (1956, 60) made an investigation on the systematic position of *Hypodematium*. He concludes that this genus relates more closely to the athyrioid ferns than to *Dryopteris* or *Tectaria*.

Hypodematium has been related to various groups of genera because of the

particular combination of taxonomic features which are not usually seen in a single phyletic unit. The rhizome of *Hypodematium* was described and illustrated by HAYATA (1927), CHING (1935) and MEHRA & LOYAL (1956). Their observations are, however, not so detailed and precise. I have dissected several materials and revealed the vascular skeleton of the rhizome: the construction of the rhizome is typically dorsiventral, the leaf gaps being alternate in two rows on the dorsal side of stele. Both HAYATA and MEHRA & LOYAL gave schematic drawings representing three rows of leaf gaps on the dorsal side of the stele.

The dorsiventral construction of rhizome is wholly unknown among the thelypteroid, athyrioid, dryopteroid and tectarioid ferns, except in the case of *Hypodematium*. Such a construction is known among the species of the dennstaedtioid, lomariopsidoid, polypodiaceous or grammitoid ferns or among more primitive species and others. As noted on the paragraphs of *Monachosorum*, we can find a case where both dorsiventral and radial rhizomes are found in a single phyletic group. In such cases, however, the radial construction may better be considered as being in a derived condition. Contrary to the case of *Monachosorum*, we are hardly referable that the genus *Hypodematium* is in primitive condition among one of the phyletic groups of the higher leptosporangiate groups. It seems to be explained only by such speculative alternative whether the rhizome construction has been remained in its original condition in spite of the distinct deviation of the various features of the fronds, or the dorsiventral condition of rhizome has secondarily formed as the result of adaptation to the rupicolous habit.

Concerning the morphology of stipes, a peculiar seeming articulation is found at the top of bulbiform base of each stipe. The very base of stipe swells up in a form of bulb, the surface of which only is densely covered with scales. This distinct feature was noted by CHING (1935) and others somewhat minutely. This seemingly articulated stipes do not actually fall off from that portion. The presence of such bulbiform base is the feature characteristic of the stipes. Articulation was mentioned on the paragraph of *Gymnocarpium*, but we can not regard the articulations of *Woodsia*, *Gymnocarpium* and *Hypodematium* as being of eaqual taxonomic value. In *Woodsia* articulation functions actually, and the fronds fall off from that portion. In *Gymnocarpium* actual function is not observed on the articulation, but the rachis joins obliquely to the stipe at seeming articulation. In *Hypodematium*, so-called articulation means only the demarcation between a scaly bulbiform base and a hairy terete portion of the stipe. Thus, the morphological nature and function of these 'articulations' are fairly different among these three genera. However, we can not overlook the fact that the stipes of these three genera are at any rate modified. Moreover, the bulbiform base of *Hypodematium* stipe exhibits some common conditions with the stipe base of *Dryoathyrium*, a genus of the athyrioid series.

The petiolar anatomy is one of the interesting methods to trace the phylogeny of the higher leptosporangiate ferns. From each leaf gap on the dorsal surface of rhizome of *Hypodematium*, two leaf traces of Hippocampus-type enter

into a stipe. These leaf traces unite upward into a single strand U-shaped in cross section. Such vascular construction of stipes is the characteristic feature common to all the species of the thelypteroid and the athyrioid genera. In the dryopteroid and tectarioid ferns, several leaf traces enter into a stipe. OGURA (1938) regarded that the numbers of vascular bundles in a stipe are not so important phylogenetically as the cross view and arrangement of each vascular strand. Considering the small phyla among higher leptosporangiate ferns only, however, we find that the species having two vascular bundles in a stipe are distinct from those having several leaf traces for each leaf gap. These comparative morphological result will indicate that *Hypodematium* is related not closely to the dryopteroid or tectarioid series of ferns.

The nature of trichomes found in *Hypodematium* is the most distinct feature suggesting the thelypteroid relationship of this genus. The scales are restricted to the rhizome and the bulbiform base of stipe, and are glabrous. Therefore, the scales are not identical at all with those of the thelypteroid ferns. On every portion of whole plant of *H. crenatum*, the type and most widely distributed species of the genus, there are dense setose unicellular hairs, quite the same in appearance with those of the thelypteroid members. In fact, the mature hairs of *Hypodematium* are not different from those found on the species of the thelypteroid genera. Nevertheless, we can not neglect the fact that among four species of *Hypodematium*, *H. crenatum* is, as noted above, densely setose hairy and free from glandular hairs, *H. glanduloso-pilosum* has both the setose unicellular hairs and the glandular hairs somewhat densely, and that the remaining two species, *H. fordii* and *H. cystopteroides* (non KUHN), have no setose hairs on any part of their fronds but glandular hairs on various portions of plants. Thus, the setose hairs found in the widely dispersed species are substituted by the glandular hairs in the locally specialized species. From this fact, the setose hairs of *Hypodematium* can not be considered as being completely the same hairs with those of the thelypteroid ferns. In the latter group, the setose hairs are not completely absent even in the apparently glabrous species. Therefore, the trichomes of *Hypodematium* can not stand as the determinative indicator to direct the thelypteroid relationship of this genus. Really, we are better to separate *Hypodematium* from the thelypteroid group, for the various features other than the trichomes are not in accordance with those of the latter group.

As in the case of *Gymnocarpium*, frond form and soral characteristics of *Hypodematium* are not so distinct to consider its systematic position. The pentagonous outline of the frond of *Hypodematium* is one of the characteristics, from which derived the systematic relationship between *Hypodematium* and *Lastreopsis*. CHING (1938) has given his opinion that *Hypodematium* relates closely to *Lastreopsis* chiefly based on the appearance of fronds. This latter genus is, however, distinctly different from the former by having the several vascular bundles in a stipe and the septate coarse hairs on the axes of fronds. Thus, we can not relate these two genera to each other only by the apparent resem-

blance of habit of plants. Similarly, it is unreasonable to refer *Hypodematium* to or separate it from a certain phylon only on the basis of its frond form and texture. Concerning the soral structure, we can not indicate safely any actual evidence of phylogenetic relationship only by that feature.

MEHRA & LOYAL (1956) reported the chromosome number of *H. crenatum* as n=41. This number shows that the cytological datum affords not the thelypteroid but the dryopteroid, tectarioid or athyrioid relationship of *Hypodematium*. *Lastreopsis* has not yet been investigated cytologically.

CHING (1938) related *Hypodematium* with *Lastreopsis*, perhaps only because of the resemblance of their frond habit. He referred *Hypodematium* to the thelypteroid series from both anatomical and morphological evidences: these evidences seem to mean the petiolar anatomy and the features of hairs, soral characters and spores. However, the genus *Lastreopsis* is different from *Hypodematium* by the characteristics found on the stelar anatomy both of stipes and rhizomes and on the nature of hairs. Then, why can that genus be considered as being a thelypteroid one? Concerning the systematic position of *Hypodematium*, HOLTTUM (1954) seems to have completely followed CHING's opinion that this genus is near to *Lastreopsis*. He appropriately placed this latter genus in the tectarioid series and added to this series the genus *Hypodematium* representing few features common with the tectarioid ferns.

Now, we know that *Hypodematium* and *Lastreopsis* should be separated distinctly by the difference seen in the stelar construction of both rhizome and stipes and in the hairs on the axes of fronds. While the latter genus may easily be referred to the tectarioid genera as fully stated by HOLTTUM (1954) and others, *Hypodematium* is one of the genera whose systematic positions are difficult to determine. I am of opinion that *Hypodematium* may be included in the athyrioid group of genera. This presumption is the same with the conclusion given by LOYAL (1960), though there are a few differences in the course of speculation. Further investigations should be made concerning the systematics of the athyrioid ferns, and, when the athyrioid series are known more precisely, the position of *Hypodematium* will be determined with better evidence.

Parapolystichum *and* **Pteridrys.** CHRISTENSEN (1938) considered with some doubts that these two were the thelypteroid genera, but he made no discussion concerning their characteristic features.

Pteridrys is doubtlessly a tectarioid genus as confirmed by the presence of coarse multiseptate hairs and of several vascular strands in a stipe. Among the pteridologists in recent, CHRISTENSEN only considered that the genus was thelypteroid, though CHING (1940), HOLTTUM (1947 etc.), COPELAND (1947 etc.) and others support the tectarioid relationship of *Pteridrys*. HOLTTUM discussed this genus most appropriately and I have little to add here to his accounts.

CHING (1940) followed CHRISTENSEN in referring *Parapolystichum* to the thelypteroid series. COPELAND (1947) included this genus in his *Ctenitis* of broad

sense. I have not studied in detail this American genus but am of opinion that *Parapolystichum* may better be referred to the tectarioid series.

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(Additional to those in Part I)

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