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

I. General Consideration

by

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Introduction

The thelypteroid ferns, or Thelypteridaceae, constitute a phylogenetic group of ferns, whose taxonomy still remains uncertain. This group has been variously circumscribed and classified by the fern specialists according to their own taxonomic conceptions. Considerable contributions have been made to the taxonomy of the thelypteroid ferns, yet there are debatable questions unsolved concerning the taxonomic features of this group. The purpose of the present study is to add more information concerned and to clarify the taxonomy of the thelypteroid ferns.

There are two principal themes for the taxonomic investigation of natural groups: one is the problem of circumscribing the group in question and to what groups it has natural relationship; the other is how this group should be classified and to what subdivisions each component has the natural relationship. These two themes are closely related to each other, and the investigation on one theme necessarily invite that on the other, for no taxonomic character can be evaluated without sufficient comparison with those found in both the closely and the remotely related species.

The purpose of taxonomy is to give the natural classification of the organisms. However, we can not obtain a conclusive system, because none of us have ever observed the full course of evolutionary trends of the organisms. Therefore, various supposed systems are proposed in the divergent conceptions of the evaluation of taxonomic characteristics by which the species or the species groups are distinguished and defined. When the characters are not fully recognized from the morphological point of view, the taxa are usually grouped together conventionally by a few definable characteristics, resulting in unnatural and artificial systems. It is well known that the fern classifications in the last century based only on the soral characters are wholly inappropriate from the view-point of modern taxonomy. Nevertheless, we can not safely insist that the fern classifications of the day do stand, in general, on the sound basis of the natural science. There is no system which is studied and defined

by not using the subjective judgment on the observed information. The taxonomic features must be evaluated objectively without any supposition and excessive explanation on yet unknown matters.

The thesis of taxonomy is to get the natural system of the organisms. In the old times, when little investigation had been made on this matter, the taxonomists set too much values on certain features which were applicable to define the species or the higher taxonomic categories. However, the natural relationships among the species or the species groups can only be known when the resemblances of all the characteristics are recognized among the species in question.

In order to obtain the natural system of any group, it should not be divided into subgroups by using the particular features. The classification of the organisms does not mean making certain subdivisions but making combinations of distinct groups by using the proper similarities found in their features. Individuals are united to form species which again should be grouped together into the higher taxa. The definition of these groups is made for the sake of recognition of each group by using the features in good accordance with the discriminated groups.

The evaluation of the taxonomic features should be made from the two opposite sides. One is the evaluation of characteristics, i.e. the evolutionary trends of a feature are investigated purely from the morphological point of view. In the course of this investigation, each feature should be studied separately, independent of whether a species is primitive or advanced. The other is the comparative evaluation, i.e. the variability of a feature is widely compared. In this latter method, the relationships among the closely allied species will give the solution by which features the species or the higher taxa are appropriately diagnosed. These two methods depend on each other. In the present study, I have investigated the taxonomic features on the basis of that idea.

History and Present Status of Investigation

In 1913 and 1920 CHRISTENSEN published comprehensive monographs of the American species of *Dryopteris*. Among the great contributions to the fern taxonomy made by CHRISTENSEN, his investigation in *Dryopteris* is one of the most valuable works in this field and has produced fruitful results. The modern understanding of *Dryopteris* s.lat. starts from these works.

In the first part of his monographs, CHRISTENSEN classified the tropical American species of *Dryopteris* with pinnatifid-bipinnatifid fronds into ten subgenera. Later, in the second part, he added two subgenera with bipinnate or multipartite fronds. These 12 subgenera were grouped into two higher categories; one is strictly the same as the thelypteroid in the recent treatment, the other comprising *Dryopteris* s.str. *Stigmatopteris, Ctenitis, Parapolystichum* and *Polystichopsis*. The former was diagnosed as follows:

> Lamina entire to bipinnate, very rarely tripinnate or decompound, most often bipinnatifid, more or less hairy but sparsely scaly. Hairs of different type, most often unicellular, simple or branched, never articulated; scales entire or subentire, often ciliated by simple or branched hairs or pubescent throughout. Veins free, connivent

or goniopteroid.

In fact, this is the very first recognition of the thelypteroid series of ferns, a distinct group now under consideration.

In 1938, CHRISTENSEN gave a short survey of fern classification in VERDOORN's *Manual of Pteridology*. He placed *Dryopteris* s. lat. in Dryopteridoideae of the vast family Polypodiaceae and divided this subfamily into two tribes, the second of which was Thelypterideae comprising about 15 genera related to *Thelypteris* and *Cyclosorus*. The description of these two tribes may be quoted here as follows:

> Dryopterideae. Rhizome and leaves paleaceous with often very numerous large and broad to hairlike scales, the ribs very rarely with simple, grey hairs. Leaf-stalk with 4–7 or more vascular bundles. Veins free or variously united (venatio Goniophlebii, Pleocnemiae, Sageniae, Drynariae), the free ones ending in hydathodes within the margin. Sporangia never setose.
>
> Thelypterideae. Rhizome and leaves as a rule sparsely paleaceous, rachis and veins, at least above, with simple or branched, never intestiniform hairs; leaf-stalk with 1–2 vascular bundles, veins free and generally simple or united in pairs (venatio Goniopteridis), reaching the margin. Sori mostly small, round, rarely elongated, with reniform indusia or exindusiate; sporangia often setose.

Subsequent to CHRISTENSEN, the Old World species of *Dryopteris* and its allied genera were investigated by CHING. He published a series of papers entitled *a Revision of the Chinese and Sikkim-Himalayan* Dryopteris *with Reference to Some Species from Neighbouring Regions*, from 1936 to 1938. At the end of the second part, he made, for the first two parts, a concluding remark that Thelyperideae is a distinct natural subfamily of Polypodiaceae. He took up the following features characteristic of Thelypterideae: scales on rhizome and lower part of stipe sparse and generally hairy; stipe, rachis, costa, costules and veins provided with simple or branched, pale-coloured unicellular hairs at least on upper side; adult rhizome exhibiting three or even two elongate meristeles in a transection, the stipe containing two separate broad vascular strands fused together upwards into a single gutter-shaped strand; veins generally simple, either free or united in pairs, all reaching the leaf-margin; sori mostly small, round or elongate, separated or more or less confluent at maturity, with reniform indusia or exindusiate, the sporangia with long stalks, often setose. Under this subfamily, he enumerated 13 genera.

In 1940, CHING published a new classification system of Polypodiaceae s.lat., in which he divided that family into 33 families. The seventeenth is Thelypteridaceae comprising 12 out of 13 genera mentioned above. This family is subdivided into three tribes distinguished by the difference in venation. The remaining one genus, *Sphaerostephanos*, constitutes its own family, the eighteenth.

HOLTTUM (1947 etc.) followed CHING in recognition of Thelypteridaceae, though his classification of the family into genera was fairly different from that of CHING. Moreover, HOLTTUM divided the vast Polypodiaceae in the sense of DIELS (1899), which CHING had splitted into 33 families, into only five families, Thelypteridaceae, Grammitidaceae, Polypodiaceae s. str., Dennstaedtiaceae and Adiantaceae. Thus, the comparative value of the recognition of Thelypteridaceae as a distinct family is fairly different between CHING and HOLTTUM. HOLTTUM has never given a complete list of

genera of any family, and sometimes corrected critically his own opinion without hesitation. He entertained a doubt about the current classification which overestimates the fern venation and separate *Thelypteris* from *Cyclosorus* wholly on the basis of the difference in venation. The most important fact is that he compared every characteristic minutely with each other and critically revised the classification to a comprehensive extent. As he has given no special interest to this group, there has been no detailed account of his opinion on the problems of taxonomy of this family.

COPELAND's *Genera Filicum* is one of the most important in literature concerning the fern classification. He lumped almost all species of the thelypteroid ferns into *Lastrea* and *Cyclosorus*, excluding only a few genera easy to define. Among the genera arranged in his Aspidiaceae, 10 genera were put together in a distinct group allied to *Lastrea*. COPELAND gave no diagnosis to this group of genera but some notes to each genus. All of his referrings on these genera are very useful, despite their briefness.

There are several other systems of the leptosporangiate ferns proposed in the last generation. In 1939, H. ITO distinguished the genera minutely in the first part of his revision of Dryopteridoideae in Japanese regions. Another Japanese pteridologist, TAGAWA (1959), touched briefly upon the system of ferns in his popular book written in Japanese. He followed COPELAND's *Genera Filicum* in the formal arrangement, but suggested raising the thelypteroids to a family status. Both H. ITO and TAGAWA treated only the Japanese genera, and gave no complete list of all the genera included in the thelypteroid group of ferns. In the recent florae of various regions, the classifications of the thelypteroid ferns are various: some treat them as a distinct family, some others as a subgroup of vast Polypodiaceae or the others as a single genus. Circumscription of the thelypteroid ferns is also not fixed, some genera being included in or excluded from this series of ferns.

Concerning the nomenclature of genera, MORTON (1958 etc.) insisted on arranging all the thelypteroid ferns in a single genus, *Thelypteris*. He gave no generic importance to the characteristic features now evaluated enough to discriminate the genera of ferns. This opinion will be summarised in further pages; but MORTON did not circumscribe the genus definitely nor give any suggestion concerning the relationship among the species or species groups.

Recently, I have tried to clear up the boundary of the thelypteroid series and studied some taxonomic features morphologically. In the last several years, the publications were given concerning the taxonomic evaluation of such features as the trichomes and the venation, and the reports were made on the presence of the peltate indusia and of the acrostichoid sori among the thelypteroids. Through these works, the circumscription of the thelypteroid ferns became clearer. The details on this account will be given in later pages. Several genera belonged to or were separated from the thelypteroid series. On these genera, also, the references will be made later.

In the last decade, MANTON and others made valuable contributions on the cytology of ferns. Owing to the technical difficulty, the cytotaxonomy of ferns is one of the most troublesome branches of investigations. Only the numbers of chromosomes have been reported on several species among the thelypteroids. From the distinctness

of the supposed basic numbers of chromosomes, MANTON & SLEDGE (1954) considered that the thelypteroid series of ferns is far distinct from the other members belonging to the vast genus *Dryopteris* in CHRISTENSEN's *Index Filicum*.

Anatomical features of the thelypteroid ferns is rather constant throughout the group, so little description has been given on that account. Only the fragmentary comparison has been made on some taxonomic features among the species of our series. These anatomical studies are accompanied with the taxonomic description of species, and no purely morphological comparison has yet been made concerning the thelypteroid ferns.

The thelypteroid species are, like other difficult groups of ferns, known rather obscurely in almost all regions of the world, especially in the fern rich regions. About one thousand of specific names have already been proposed among the thelypteroid series. A great number of species will be described in the future and many of the already described species will be reduced into the others. When the distribution of the species will be known more correctly, the specific taxonomy will become more scientific. Concerning the specific enumeration of the thelypteroid ferns, the results included in the CHRISTENSEN's and CHING's publications on the New World and East Asiatic species respectively, are the most comprehensive works ever published.

The fern floras of Japan and the neighbouring countries have been studied to some extent since the dawn of this century. Apart from the classical and fragmental works in the foregoing centuries by THUNBERG, HOUTTYN, HOOKER, BAKER, KUNZE, MIQUEL, FRANCHET et SAVATIER, EATON, and others, the detailed investigation of fern species in Japanese regions began from the works made by CHRIST and by MAKINO. CHRIST studied the collection of U. FAURIE and described a number of species and infraspecific taxa. MAKINO was the first Japanese taxonomist who collected the specimens by his own hands, observed them by his own eyes and described the species according to his opinion. Following MAKINO, the Japanese botanists extended their studies to the fern taxonomy. HAYATA, NAKAI, KOIDZUMI and others described many species of ferns from Japan, Korea, Ryukyu, Taiwan and Bonin. In the last generation, two fern specialists, H. ITO and TAGAWA, investigated the fern flora of Japan and the neighbouring regions and the knowledge was greatly advanced. The studies made by CHING, COPELAND, HOLTTUM, TARDIEU-BLOT, CHRISTENSEN, and others on the East Asiatic ferns greatly facilitated their investigation. The specific enumeration of the thelypteroid ferns has, therefore, almost been completely finished in our regions. Nevertheless, problems remain fragmentary. Recently, I have offered some miscelaneous nomenclatorial reports. A taxonomical review of the species seems to be useful at present on the Japanese species of the thelypteroid ferns.

In 1939, H. ITO published the first part of Dryopteridoideae in NAKAI & HONDA's *Nova Flora Japonica*, covering the area as done in the present paper. In this work, H. ITO enumerated 13 species of *Thelypteris*, 4 of *Glaphyropteris*, 5 of *Phegopteris*, 1 of *Leptogramma*, 10 of *Cyclosorus* and 4 of *Meniscium*. *Dictyocline* was excluded from his monograph. Although the generic arrangement will be discussed in the pages of classification, the number of species also increased afterwards. Many distinct species were reduced to the infraspecific taxa of some species by H. ITO, but

some of them should be kept in the specific rank.   Total 51 species are enumerated
in the present paper including several infraspecific taxa.

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classification of ferns.   I am very glad to get a chance to show my hearty thanks
to all of these persons.

The herbarium studies were carried out at several herbaria of Japan and many
specimens were kindly sent to Kyoto on loan from many herbaria.   At the head of
the specific enumeration, the herbaria on which my studies stood will be cited.   My
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their continuous encouragement, I should have been unable to accomplish this investi-
gation.

Morphology

Although the generic classification will be changed extensively in the later pages
of this paper, the discussions will be given concerning the morphology by using the
current generic names and binomials.

SPORE

In all the species of thelypteroid ferns, the spores are bilateral, usually with
distinct perispore, the trilete spores being entirely unknown.   In some species the
perispore is said to be hardly noticeable, but I have seen no species producing spores
without perispore at all.   Even when the surface of spore is entirely smooth under
the microscope, a trace of perispore is found in every case.   Colour and size of the
spores exhibit a little variation as in the case of other groups of ferns.   The surface
patterns of the thelypteroid spores are various: almost smooth, echinulate, granular,
tuberculate or reticulate.   These various figures have no close correlation with the
probable affinity of species speculated by the combination of the other taxonomic fea-

tures. Many species of *Cyclosorus* have echinulate spores and the species of *Abaco-pteris* have granular ones. Various subgroups of *Thelypteris* represent wide range of variation in the surface pattern of their spores. The features of spores will be briefly diagnosed in the pages of description. As to the variation of the thelypteroid spores, it may safely be recognized that they vary rather easily from one type to another and the parallel evolution seems to have occurred rather frequently even among the spores of such a restricted group as the thelypteroid. Therefore, positive relationships can not be established only from the morphological affinities of spores.

Although the surface pattern of spores is one of the diagnostic features to seize the thelypteroid as a whole, the spores hardly serve the purpose of distinguishing the minor groups in this series of ferns.

GAMETOPHYTE

Concerning the gametophytic generation of the thelypteroid ferns, most useful informations were given by MOMOSE in his series of papers (1937–42). Dr. MOMOSE was kind enough to show me the unpublished data observed by him and to give me various suggestions on the morphology of sexual generation. Therefore, I have not observed minutely any prothallia of the thelypteroids and the results achieved by him will be summarized below.

MOMOSE (1942) distinguishes three types in the mode of germination of fern spores: centrifugal, tangential and centripetal. Like many other higher leptosporangiate ferns, all the thelypteroid species have the spore germination of centripetal type. MOMOSE notes that in the young gametophyte developed from the spore with cen-tripetal mode of germination the following characteristic features are universally recognized: 1) the basal cell does not take further division, 2) the primary rhizoid develops laterally from lower portion of the basal cell, not stretching to the prothallial cell, 3) the basal cell projects beyond the persistent spore wall, 4) the primary rhizoid cell does not subelise but is transparent, 5) the oil bodies appearing in the germinat-ing spore are mostly transparent, 6) the basal cell contains always a little contents and is usually vacant near the base, and 7) the basal cell is almost equal to or narrower than the breadth of protonematous cells. In his 16th and 17th paper (1941), MOMOSE described and figured the prothallia of a dozen species of *Thelypteris* in the sense of CHING (1936). From the observations of these species, MOMOSE concluded that the species of *Thelypteris* represented too wide range of varieties in their char-acteristics to be diagnosed by a few common ones and suggested the difficulty in combining them in a single genus. Later in his 28th paper, MOMOSE recognized distinct subfamily Thelypteridoideae, referring to this several other species studied by himself and those already reported in various publications. His description (in Japanese) of prothallia of this subfamily reads:

Prothallia cordate, sinus deeply round, usually very deep or rarely not so, the wings usually imbricate on each other or rarely distinctly separated, the wings butterfly-shaped, crisped on margin, cells of wings usually square, basal portion of prothallia round or cuneately narrowing towards protonema: protonema 2–7-celled,

original cell cylindrical, primary rhizoid placed at basal lateral portion of the original cell. Wings glandular, setiferous or both glandular and setiferous on margin; glands clavate or simple, with a few minute chloroplasts. Rhizoid placed along midrib, pale and translucent, or pale brownish. Midrib distinct cushion from the midway to the very bottom of sinus, 5-6-cells layered. Archegonia numerous on the upper or every portion of midrib, neck cells 5-6; antheridia on midrib, round or rotundate, basal cells deeply immersed or flatt.

This subfamily is distinguished from Dryopterideae by such features as: 1) sinus deep, the wings usually imbricate on each other, 2) marginal cells sometimes elongate, projecting at margin, 3) glandular with clavate or simple glands having small chloroplasts, 4) setiferous with simple long hairs, 5) rhizoids sometimes pale-brownish, placed along midrib, 6) midrib distinctly cushion form, 7) neck of archegonia thick, with larger heads, 8) antheridia placed on midrib. In Thelypteridoideae thus circumscribed, MOMOSE included *Gymnocarpium* and *Dryoathyrium*.

In the main course of classification, MOMOSE's conclusion matches well with that of H. ITO (1939). The materials of the two authors were quite identical, for they were studied at the same laboratory. This means that the difference or similarity found in the gametophytic generation is in well accordance with that found in the sporophytes.

The following is the system proposed by MOMOSE from his investigation on the gametophytes. Here, I will enumerate the MOMOSE's figures of the thelypteroid prothallia in contrast with specific names adopted in this paper.

　　　　Subfamily Thelypteridoideae
1　*Dryoathyrium* CHING
2　*Gymnocarpium* NEWMANN
3　*Currania* COPEL.
　　　These three genera may better be transferred to the Subfamily Athyrioideae.
4　*Phegopteris* (PRESL) FÉE
　　　Phegopteris polypodioides FÉE, XVII-10 (JJB **17**: 103, figs. 19, 20)——*Thelypteris phegopteris* (L.) SLOSSON.
　　　Phegopteris bukoensis TAGAWA, XVII-12 (JJB **17**: 110, figs. 24, 25)——*Thelypteris bukoensis* (TAGAWA) CHING.
5　*Thelypteris* § *Macrothelypteris* H. ITO
　　　Thelypteris oligophlebia var. *elegans* CHING, XVII-8 (JJB **17**: 98, figs. 15, 16)——*Thelypteris torresiana* var. *calvata* (BAKER) K. IWATS.
6　*Thelypteris* § *Metathelypteris* H. ITO
　　　Thelypteris laxa (FR. et SAV.) CHING, XVII-7 (JJB **17**: 96, figs. 13, 14).
7　*Thelypteris* § *Parathelypteris* H. ITO
　　　Thelypteris glanduligera (BAKER) CHING, XVI-4 (JJB **17**: 43, figs. 7, 8).
　　　Thelypteris angustifrons (MIQUEL) CHING, XVI-5 (JJB **17**: 45, figs. 9, 10).
8　*Thelypteris* SCHMIDEL s.str.
　　　Thelypteris palustris (SALLIS.) SCHOTT, XVI-1 (JJB **17**: 35, figs. 1, 2).
　　　Thelypteris nipponica (FR. et SAV.) CHING, XVI-2 (JJB **17**: 37, figs. 3, 4).
　　　Thelypteris beddomei (BAKER) CHING, XVI-3 (JJB **17**: 40, figs. 5, 6).
9　*Glaphyropteris* PRESL sensu H. ITO
　　　Glaphyropteris falciloba H. ITO, XVI-9 (JJB **17**: 101, figs. 17, 18)——*Thelypteris*

esquirolii var. *glabrata* (CHRIST) K. IWATS.

10 *Lastreopsis* NAKAI nom. nud., non CHING, 1938

   Phegopteris decursive-pinnata FÉE, XVI-11 (JJB **17**: 106, figs. 21—23)——*Thelypteris decursive-pinnata* (VAN HALLE) CHING.

11 *Leptogramma* J. SMITH

   Leptogramma totta J. SMITH, III-2 (JJB **14**: 59, figs. 3, 4)——*Stegnogramma pozoi* ssp. *mollissima* (FISCH. ex KUNZE) K. IWATS.

12 *Cyclosorus* LINK

   Cyclosorus parasiticus FARWELL, VIII-1 (JJB **14**: 606, figs. 1, 2; JJB **18**: 394, figs. 1) ——*Thelypteris parasitica* (L.) K. IWATS.

   Cyclosorus acuminatus NAKAI, VIII-2 (JJB **14**: 609, figs. 3, 4)——*Thelypteris acuminata* (HOUTTYN) MORTON

13 *Meniscium* SCHREBER sensu H. ITO

   Meniscium triphyllum Sw., XIX-5 (JJB **17**: 294, figs. 9—11)——*Thelypteris triphylla* (Sw.) K. IWATS.

14 *Dictyocline* MOORE

   Dictyocline griffithii var. *pinnatifida* BEDD., XVIII-3 (JJB **17**: 151. figs. 5—8)—— *Stegnogramma griffithii* (MOORE) K. IWATS.

MOMOSE's observation is very valuable, for the characteristics of the sexual generation had been little regarded in the foregoing classification of ferns. However, the features detected in prothallia are so scanty in number and so simple in construction that any system can not be established, considering only the characteristics of gametophyte. Taking account of the informations both on the sporophytic and the gametophytic generations, the morphological features will be more correctly recognized in the comparative evaluations. Several amendment should be inevitable from the arrangement of MOMOSE and will be noted on each page of the taxa concerned.

SPOROPHYTE

Root

The roots are not particular for all the higher leptosporangiate ferns. All of the thelypteroid ferns bear the roots on all surfaces of the rhizome. As the species in question are all terrestrial, or at most growing in crevices of cliffs, the roots penetrate into soils. The roots are usually numerous and are irregularly arranged. The thickness of roots are variable according to the species and, among the related species, usually varies according to the size of rhizome. The branching occurs irregularly on the roots, not dichotomous in way. Root hairs are present throughout, very dense on the minor branches.

The root traces are produced from every portion of the meristeles of the rhizome. Internally, the roots of our species are not particular, having diarch xylem. The outer layers of cortex are sclerified, the appearance of roots being dark and dirty.

Rhizome

Almost all species of the thelypteroid series are terrestrial, a few growing in muddy crevices of rocks as in the case of *Stegnogramma gymnocarpa* ssp. *amabilis.*

The rhizomes are long creeping, short and ascending or erect by the species. The species bearing long creeping rhizome are found in some groups of *Cyclosorus* and of *Thelypteris*: the world-wide *C. gongylodus*, *T. palustris* and *Phegopteris polypodioides* are good representatives. Some species with long rhizomes bear their stipes close together or at intervals in places on rhizome: *Stegnogramma pozoi* ssp. *mollissima* is an example of species of such habit. Many species have short and ascending rhizome, which are epigenous, exposed or in humus, or subterranean. The species of *Stegnogramma*, *Goniopteris* and of some groups in *Thelypteris* and *Cyclosorus* have such habit of rhizome. Several species are distinct in having erect rhizome. The erect rhizome of *Cyclosorus papilio* is remarkable, attaining to about 1 metre high above ground. In this respect, this species is nearly a tree fern. The further notes on the habit of rhizome will be given in the pages of enumeration of species.

The thickness of rhizome are highly variable from species to species. *Thelypteris cystopteroides* is one of the examples with long creeping slender rhizome 0.4 —0.7 mm in diameter. Contrary to this, the gigantic species bear thick rhizomes, sometimes exceeding 1.5 cm in diameter: *T. esquirolii*, *T. torresiana*, *T. setigera* and others are representatives in our regions. The thickness of rhizome is not always parallel to the size of plants. Among the species of some groups, the size of rhizome varies in considerably wide range, but it is, as a matter of course, less variable within a single species.

The rhizomes are all paleate in the thelypteroid ferns. The form and size of scales, as well as their density, are highly variable according to the species. As known in many groups of the higher leptosporangiate ferns, the scales fall off from old portions of rhizome, the apices only being densely scaly. Almost all of the thelypteroid species bear the setose hairs on their rhizomes in various degrees. These hairs also are deciduous in many species.

The rhizome is radially constructed throughout the thelypteroid species. Inner construction is characterized by the inclusion of dictyostele common among the higher leptosporangiate ferns. Leaf gaps are usually larger, oblong, circumscribed by rather slender meristeles, bearing two leaf traces at each side of the base. The size and form of the leaf gaps and meristeles are different according to the species. The size of leaf gap is usually parallel to the thickness of rhizome, though that of the meristele does not correspond to the size of rhizome. Several species have well developed sclerenchymatous tissues, which form a ring in transection, enclosing almost completely the vascular bundles. In the species of such genera as *Leptogramma* and *Dictyocline*, the sclerenchymatous tissues are in full development. Many other species have the sclerenchymatous tissues dispersed in the parenchymatous tissues of rhizomes, usually surrounding the vascular cylinders.

<center>Fronds</center>

The features of adult leaves are most complex and indicate in many ways the taxonomic differences and relationships among species. CHRISTENSEN (1913) separated the thelypteroid ferns from the dryopteroid species also by the difference in frond

form: the fronds of the former group exhibiting a tendency to be oblong-lanceolate, not broadest at their bases. In recent years, HOLTTUM (1957 etc.) has emphasized the importance of taxonomic value of the grooving of frond axes. OGURA (1938) and others directed their notices to the vascular bundles in the stipes. These anatomical and organographic features should be reviewed concerning the species of the thelypteroid ferns.

Stipes. Excluding *Hypodematium* from the thelypteroid ferns, no species has the articulation at any position of stipes. The stipes are terete, usually stramineous but sometimes brownish or polished, always pubescent in various degrees and rarely paleate throughout. The length of the stipes is fairly constant to the species in relation to the dimensions of plants. In some species, the lower pinnae are extremely reduced into mere auricles. These auricles are sometimes placed just above the rhizome.

Two leaf traces run into each stipe. The cross view of each bundle represents a so-called hippocampus-form xylem. This characteristic feature is found in all of the thelypteroid species. The two hippocampus-form vascular bundles run upwards and at last, usually at the upper portion of stipes, unite with each other to form a single strand U-shaped in cross section.

Axes of Fronds. The rachises are not distinct from the upper portion of stipes in construction, colouration, hairiness and so on. In the upper portion of fronds, the rachises become always very week, usually winged on both sides and turn into a distinct or indistinct apical portion, or pinnae, of fronds. The costae and costules are almost the same as the axes of higher orders in this principal construction.

The rachises, costae, and costules are also sometimes slightly grooved on their upper surface. These grooves are usually slight and are not open at the junction with the axes of the next higher or lower order. No articulation is found at any portion of frond throughout the thelypteroid ferns. Concerning the venation, discussion will be made fairly in detail on several pages further.

On the upper portion of axes, proliferation occurs to some restricted number of species. *Ampelopteris* was revived by COPELAND (1947) distinguished from *Cyclosorus* by the distinct proliferation of frond axes. Some species of *Goniopteris* and a few of *Abacopteris* are also proliferous. This will be further discussed in the pages of *Abacopteris*.

Laminae. The outline of the fronds is, in typical forms, lanceolate, oblanceolate or at most oblong. In many species, the lowest pinnae are not the longest. Even in the case of the lowest pinnae being the longest, the basal pair, or sometimes the basal few pairs of pinnae, are more or less reflexed with the result that the blade is attenuate below in outline. These species are many in numbers among the members of *Thelypteris* and *Cyclosorus*. In some particular species, the lower pinnae are suddenly or gradually reduced even into mere auricles. This feature is distinct in certain species or species groups of *Thelypteris* or *Cyclosorus*. The fronds of such species are typically oblanceolate in outline.

There is a distinct but little known projection called aerophore occupying at the bases of costae, or even of costules, of some particular species. The species with

aerophores are those belonging to such genera as *Glaphyropteris* and *Cyclogramma*, and the groups of *Cyclosorus heterocarpus* and of *Thelypteris esquirolii*. The function of this projection is wholly unknown, though some have suggested that these are the vents of airs in young circinate fronds. There is no evidence to prove such suggestion. Although the aerophore is functionally unknown, its occurrence indicates to some extent appropriately the relationships among the species of the thelypteroid series.

Fronds of almost all species are pinnate-bipinnatifid in construction. The more compound frond construction is found only in the species of *Macrothelypteris*. Simple or pinnatifid species are known among those of *Dictyocline*, *Abacopteris* or *Goniopteris*. These differences of frond construction are found in all the groups of ferns.

The margin of segments is variously figured by the species. Even in a single species, this feature is fairly variable according to the size of the plants. As seen in the case of *Thelypteris laxa*, lobes of larger plants are deeply incised, but those of smaller plants are almost entire or very slightly crenate. Of course, the variability of this feature is very high or too slight according to the species or the species groups. The dentation and the crenation have strict relation to the vein apices: at least a single branchlet of veins is included in the ultimate lobe. The margin of laminae is usually setiferous, and in some particular species slightly cartilaginous: the latter is distinct in some species of *Abacopteris*.

The colouration of fronds are usually green to yellow green. Species of *Stegnogramma* s.lat. have a tendency to turn easily brownish in dried condition. Some species of *Abacopteris* or of the goniopteroid ferns are distinct in changing their fronds reddish when dried. Such colouration is usually specific. Both laminar surfaces are in general pubescent, but sometimes glabrous, verrucose, glandular or opaque. Texture of fronds varies from membranaceous to papyraceous according to the species.

The laminar parts are constructed with the typical parenchymatous tissues. Epidermal tissues are as those known commonly among the higher leptosporangiate ferns. The only particular tissue in lamina is the callous membrane developed at the bottom of sinus. Concerning the nature of this membrane, discussion will be made with reference to the venation.

Discussion. The vascular construction in the stipe is a characteristic feature common to all the species of the thelypteroid ferns. Ogura (1938 etc.) showed his scheme on the supposed phylogenetic development of the vascular construction in the stipe. He considered that the number of the vascular strands was phylogenetically of secondary importance. The shape of xylem in cross section of stipe is stable in the known phylogenetic groups. Among the higher leptosporangiate ferns, however, the numbers of leaf-traces are also constant according to the large assembly of the supposed natural groups. In the thelypteroid and athyroid ferns the stipe contains two vascular bundles including hippocampus-form xylem. In the asplenioid two bundles unite upward to form X-shaped xylem, and in the tectarioid and the dryopteroid several bundles with elliptic xylem run throughout the stipe. Thus, this secondary important feature is sufficiently stable as to define the higher groups of

genera. The anatomical features of stipes show that the thelypteroid ferns are not closely related to the asplenioid ferns. The alliance may better be found in the athyroid, the tectarioid or the dryopteroid ferns. In some other groups of ferns, the construction of the stipe is modified by the presence of articulation. Complete absence of articulation at any portion of fronds may indicate the primitiveness of the stelar construction of our ferns.

The athyroid ferns have resemblance to the thelypteroid in various respects. The resemblance between these two series of ferns is distinct in the stelar construction of axes. Contrary to this, the features apparent on the surface of fronds are different between the two. The trichomes are distinct as noted in the pages of that problem. The groove of the thelypteroid species is usually obscure and is not open at the junction. On the other hand, the athyroid ferns have distinct rachis-groove, which is open to admit the groove of a branch of higher order. Grooves of this current-type are common to the species of the athyroid ferns, though there are exceptions like *Dryoathyrium*. Thus the difference in the nature of groove on the axes of fronds is rather apparent, though it stands as a good indicator in some groups to separate the genera and the species groups.

In many groups of ferns, the proliferation occurs independent of the other features. COPELAND (1947) discriminated *Ampelopteris* generically from *Cyclosorus*, though he included *Abacopteris* in the latter. *Abacopteris liukiuensis* is another species distinct in the gemmiferous axiles of pinnae. In fact, the nominal species produces young plants on the rachis, though not so frequent as in *Ampelopteris*. Therefore, the generic separation of *Ampelopteris* in the sense of COPELAND is inappropriate, even when the soral characters are taken into account. Several species of *Goniopteris* are also proliferous, and *Ampelopteris* is well referable to that genus in the natures of trichomes and others.

I (1963) have stated with some stress on the morphological stability of the construction of frond apices throughout the genus *Stegnogramma* in the emended sense. Among the species of *Cyclosorus*, some have distinct apical pinna and the others bear no such pinna. The figure of the frond apices is in the thelypteroid series variable by the species, and that feature is not worthy of diagnosing any species groups except *Stegnogramma*, though it is somewhat constant within a species.

The lower pinnae distinctly reduce in some particular groups of the thelypteroid series. There are some examples of species groups in which a few members are distinct with reduced lower pinnae but ones closely related to them bear no such pinnae having the lowest pinnae not or only slightly shortened. The followings are such species groups: *Cyclogramma*, *Sphaerostephanos*, *Steiropteris*, some species groups of *Cyclosorus*, and so on. Nevertheless, the occurrence of such reduced lower pinnae seems to suggest to some extent the relationships among the species or the species groups.

The outline of the frond may easily be considered as a feature greatly variable. If this were right, there should be found more various frond forms in such a large assembly as the thelypteroid ferns. However, as noted on the pages of description and as appropriately stated by CHRISTENSEN and others, almost all species belonging

to our series bear the fronds oblong or oblanceolate in their outline. In spite of the fact that such stability is known to our species, this characteristic feature should not be evaluated as that to trace natural relationships among the species. We can only apply the difference of frond form to the discrimination in the specific rank.

<div align="center">Venation</div>

Venation has long been considered as the most important feature in the classification of the thelypteroid ferns. The large and compound genera, *Thelypteris* and *Cyclosorus*, are discriminated by the difference in venation only: the former having free and the latter reticulate venation. In his system of fern classification, CHING (1940) established three tribes in the family Thelypteridaceae, distinguishing one from another by the sole difference in venation: Thelypterideae with free venation, Goniopterideae with goniopteridoid or meniscioid venation, and Dictyoclineae with irregular anastomosis of veins. Distinguishing *Cyclosorus* from *Thelypteris* by the difference in venation, HOLTTUM (1947 etc) doubted the distinctness of these two genera, though he did not succeed to get any sufficient classification of the thelypteroid ferns.

Since the time of PRESL and FÉE, venation has been estimated as one of the most important features to define genera and genus groups of higher leptosporangiate ferns. This may be attributed to the fact that the venation is distinguished practically into two groups: whether it is free or reticulated. However, there is no general rule that the easily definable characteristics indicate necessarily the natural relationships between the species or the species groups. Like all other features in plants, the venation should be critically revised under the light of the comparative morphology and of the modern taxonomy. I have recently (1962) published a short essay on the problems of the venation of the thelypteroid ferns, in which the recent classification of this group of ferns is criticized to some extent.

Free Venation. Many of the current genera have the free venation and are included in Thelypterideae. They are *Thelypteris, Leptogramma, Cyclogramma, Phegopteris, Glaphyropteris, Steiropteris,* and others.

In the thelypteroid ferns generally, the veins are principally pinnate in the ultimate segments or pinnules. The veinlets of a pinnate vein group are both simple or once forked, but not in three-forks or more. The above difference in the mode of venation is usually distinct, but there are exceptions to this general tendency. In some species, veinlets are usually forked, but often, especially in smaller segments, all simple. These exceptions are, however, safely regarded as the reduction of forked veinlets. It may be evidenced by the fact that generally the forks of veinlets occur in some restricted groups of species, though there are also the exceptions to this tendency. I have once (1960) noted on the bifurcation of the veinlets of *Thelypteris gracilescens* and the allied species. In this case, the simple veinlets are naturally considered as those reduced from the forked ones. Contrary to this, the forks of the veinlets occur rather frequently in broader pinnae of *Stegnogramma pozoi* ssp. *mollissima*.

In many species the veinlets reach to the very margin of lobe, but in some others

they stop at a short distance from the margin. This latter case is peculiar to some species groups and may be considered as an important feature. Some species groups are sufficiently circumscribed by this feature as noted in the section of classification.

The termination of the basal veinlets is interesting. In many free-veined species, the basal veinlets run to the margin above the sinus. However, the basal veinlets run, in some particular species, to the callous membrane at the sinus bottom: they are the members of *Cyclogramma*, the group of *Thelypteris erubescens* and others. The venation of these species seems to be only a little different from the simple goniopteroid venation.

Goniopteroid or Meniscioid Venation. The genera in the recent usage with nominal venation are *Cyclosorus*, *Sphaerostephanos*, *Stegnogramma*, *Abacopteris*, *Ampelopteris*, *Goniopteris*, *Meniscium*, *Dimorphopteris*, and others. In the species of these genera, the opposite veinlets of adjacent groups join together to form excurrent veinlets. In the simplest case of this venation pattern, as in *Cyclosorus extensus* or in *Stegnogramma leptogrammoides*, some fronds have the goniopteroid venation and the others almost free venation. In the simple goniopteroid venation, sori are placed both on the conjugating and on the free veinlets, sometimes extending the sori, when naked, also to the excurrent veinlets.

The species with relatively broad pinnae, as those of *Abacopteris* or *Meniscium*, are characteristic in having the venation of meniscioid type. The conjugating veinlets increase in number, and the broader become the pinnae, the more entire is the margin. At the sinus between the obsolete lobes of slightly crenate or subentire pinnae, the callous membrane becomes obscure. In the typical meniscioid venation, the excurrent veinlets do reach to the next arching veinlet. In this venation, the two sori on an arching veinlet, when they are exindusiate, fuse together to form a crescent fused sori.

The goniopteroid or meniscioid venation is peculiar in its strict regularity of construction. In the course of developmental stages of an individual, the venation changes from free to goniopteroid: in early stages of development the venation is quite free, the basal veinlets running to the margin above the sinus bottom; in the next stage the anterior basal veinlets run to the sinus bottom; and in the succeeding stages the venation becomes of regularly goniopteroid. Thus, the regularity of the goniopteroid venation is intrinsic, supported by the orderly development.

Pleocnemioid Venation. The venation of *Dictyocline* is peculiar in the thelypteroid ferns. The main veins (costules) become faint towards their apices. Between these main veins, numerous areoles are formed without any definite arrangement. There are regularly no included veinlets. Costal areoles are usually one between each main veins. In well developed ample fronds, however, the accessary areoles and free included veins are occasionally found in the costal areoles. Thus, the accessary areoles and the free included veinlets occur freely, when laminar surfaces afford room.

I (1962) have traced the developmental changes of the venation of the *Dictyocline* in its young plants, and found that, contrary to the case of the goniopteroid or meniscioid venation, the pleocnemioid venation of *Dictyocline* developed without any
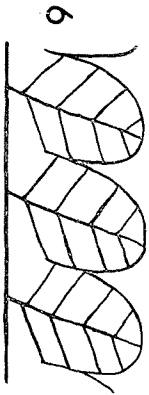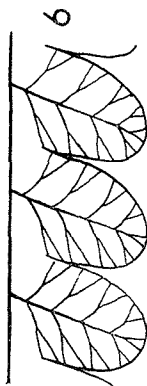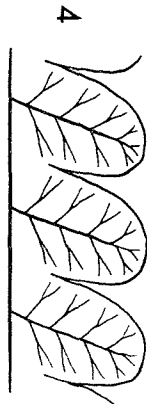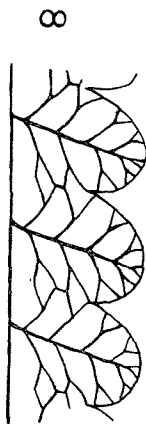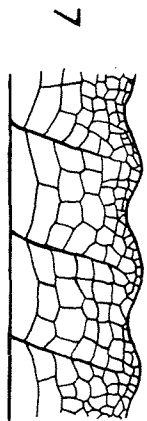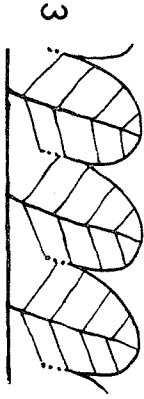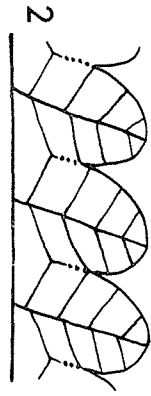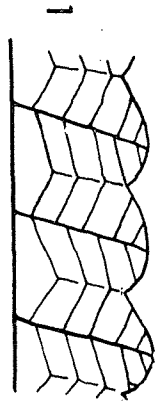
natural rule. The areoles are formed on the fronds in early developmental stage when the laminar surfaces are wide enough to allow the existense of the areoles.

Another example of the pleocnemioid venation in the thelypteroid ferns is found in *Haplodictyum*. The venation of this group represents, contrary to the case of *Dictyocline*, rather regular arrangement of areoles. The veinlets are once forked, and the outer secondary veinlets unite with the inner secondary veinlets of the next outer veinlets. The united veinlets of adjacent groups join to form rather irregular excurrent veinlets. Thus, the four rows of areoles are formed between each main veins. The sori are round and placed on the secondary veinlets, not fused to those of the neighbourings.

Sinus Membrane. The occurrence of the callous membrane at the sinus bottom is one of the features very interesting in relation to the venation. Taking an appearance like the cartilaginous membrane developing on margins of fern fronds, the sinus membrane appears, at a glance, to be quite different in construction from the laminar parts. In spite of such appearance, the sinus membrane of the thelypteroid species consists of the true leaf tissues, though the cell layers are about two-thirds time of the other portions. Because of the lacking of the chloroplasts in the constituent cells, the sinus membrane appears to be callous and colourless and is distinct from the true leaf tissues.

This peculiar membrane is present only at the bottom of sinus, usually bearing the unicellular hairs like the other parts of the margin of lobes. In the free veined species, the basal pairs of veinlets sometimes run to the callous sinus, but never join together there. The excurrent veinlets of the simplest goniopteroid venation run to and end in the sinus membrane. In the species with meniscioid venation, the lobes become obsolete, so the callous membrane is wholly wanting.

From the viewpoint of taxonomy, however, the occurrence of callous sinus seems to be a stable character. Species with sinus membrane belong to such genera as *Cyclosorus, Stegnogramma, Thelypteris, Cyclogramma* and others. On these accounts, further notes will be given in the section of classification.

Taxonomic Evaluation. The thelypteroid genera and even tribes have been separated first of all by the difference in venation, whether the veins are free or reticulate. COPELAND (1947) belonged all the free veined species of the thelypteroid ferns to a single genus *Lastrea*. HOLTTUM (1947) was more appropriate to note that there are relationships between species groups of *Thelypteris* and those of *Cyclosorus*, though he also separated these two genera for convenience. Later, MORTON (1958 etc.) lumped all the thelypteroid species into a single genus *Thelypteris*, but he noted little on the problems of the interrelationships among the constituent species. Most taxonomists pay attension to the heterogeneity of the compound genera, *Thely-*

Fig. 1. Various types of venation found in the thelypteroid series of ferns.
1) goniopteroid venation, 2) goniopteroid venation with distinct callous sinus, 3) free venation with callous sinus, 4) free venation with forked veinlets, 5) free venation with simple veinlets which do not arrive at margin of lobes, 6) free venation, 7) pleocnemioid venation, 8) haplodictyoid venation, 9) free venation with forked veinlets which arrive at margin of lobes.

pteris and *Cyclosorus*. The discrepancy of these two genera is very obscure. There are species in which the lowermost veinlets are in some cases free and in the other joining with those of the adjacent groups. *Cyclosorus extensus* and others stand as good examples. Adding to these facts, the definition of *Cyclosorus* given by CHRIST-ENSEN (1938 etc.) should be referred to here. He (1938) has diagnosed this genus as follows: veins simple and free, the basal ones running to the bottom of the sinus or more often united into an excurrent vein or two to several being united in pairs. Many species now belonged to *Thelypteris* are included in *Cyclosorus* according to the definition given above, for the species of the group of *T. falciloba* or of *T. auriculata* respond well to the definition by CHRISTENSEN.

The meniscioid venation seems to be evolved from the goniopteroid venation by the expansion of laminar surface and the deficiency of sinus. Similarly, the gonio-pteroid venation probably evolved from a free veined species by the fusion of seg-ments. The serial changes found on the developing stages of the young plants and the presence of the callous membrane at the bottom of sinus may offer sufficient evidence to the above inference. This inference suggests that the most advanced type of venation is meniscioid one as shown by such species with simple or pinnatifid fronds as *Abacopteris simplex* or *Stegnogramma dictyoclinoides*. According to this inference, the evolution of the venation may sufficiently occur in parallel on the several phylogenetic lines. When he published *Stegnogramma dictyoclinoides*, CHING (1936) stated that this was in all probability a linking species between *Stegno-gramma* and *Dictyocline* if the two genera were considered generically distinct at all. However, the pleocnemioid venation of *Dictyocline* can not be derived from the complication of goniopteroid venation. As seen in the formation of the areoles on younger plants, the irregular anastomosis of *Dictyocline* is distinct from the gonio-pteroid venation in the process of construction. Thus, the genus *Dictyocline* can not be placed on the terminal position of the series of development of venation from the simple venation having no callous sinus to the meniscioid venation. Adding to this, the venation of *Dictyocline* is distinct from that usually called pleocnemioid. In the typical pleocnemioid venation found in the tectarioid or polypodiaceous ferns, the sori are always round on the punctate receptacles. Although the construction of areoles is quite similar to those, the venation of *Dictyocline* bears no distinct re-ceptacles, having the potentiality to produce the sori on every portion.

The other example of that venation found in *Haplodictyum* is also different completely from the true pleocnemioid one. The anastomosis of the tectarioid ferns and others is quite irregular. Contrary to this, the venation of *Haplodictyum* is formed under the regular rules as described in the foregoing pages. Although I have not traced the serial changes found in the developmental stages of youger plants, little doubt is remained on that matter. Thus, we can not accept the opinion of CHING (1940) to place this genus in the series of the tectarioid genera on the basis of the seeming resemblance in the venation. Further, the venation of *Haplodictyum* is also not able to be an intermediate condition between the free venation and irregular anastomosis of *Dictyocline*. The haplodictyoid venation is a variation of goniopteroid venation: the typical goniopteroid venation is formed by the conjugation of the simple

veinlets of pinnate veins, though the haplodictyoid one is derived by the cojugation of united veinlets of the secondary veinlets of the forked veinlets of pinnately compound veins. Apparent similarity of the adult figures is sometimes resulted from the convergence of the features having the distinctly different origins.

The goniopteroid venation is a feature characteristic to the thelypteroid ferns. HOLTTUM (1948) referred to this and stated that those species with broad pinnae had developed a distinctive form of anastomosing venation otherwise only seen in some species of *Athyrium*. But he added that in *Athyrium* it is not quite identical. His treatment seems to be correct, for the anastomosis of the athyroid species like the goniopteroid venation has different construction. The excurrent veinlets of the athyroid ferns run never to the bottom of sinus, often forked near the sinus bottom. The serious change of the athyroid venation in the developmental stage is figured by NAYAR[1].

Recently, I (1963) have published a revision of the genus *Stegnogramma* s.lat., in which are included the species with venation of various types. The venation is a feature remarking the specific relationship very well, but it changes in the same manner in the various phylogenetic groups.

Reproductive Structures

All the species of the thelypteroid ferns were included in a large and heterogeneous genus *Dryopteris* by CHRISTENSEN (1905–6). The most important diagnostic feature of this *Dryopteris* was the sori with round reniform and basifixed indusia. the thelypteroid sori are, however, not always round and indusiate as shown in the following notes.

Position and Form of Sori. The sori are dorsal on the veins or the veinlets in almost all of the thelypteroid species. The receptacles are usually obsolete, though the soral characters of the thelypteroid ferns are different from those of the dryopteroid species. The receptacles of the latter are distinctly round, never being lengthened. Contrary to this, those of the former group of ferns are not round but oblong to linear, not so distinct from the other sterile portion of veinlets. The receptacle, principally not round in construction, is the characteristic of the thelypteroid ferns, whose sori are usually round but sometimes oblong to linear. In dryopteroid ferns, sori are strictly round.

The oblong or linear sori are found on the species belonging to such genera as *Phegopteris, Leptogramma, Stegnogramma* and *Sphaerostephanos*, only the last of which is indusiate with elongate indusia. In some species of *Stegnogramma* and *Dictyocline*, the sori are reticulate according to the anastomosis of the venation. The sori on the arching veinlets of the meniscioid venation are usually fused together to

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1) NAYAR, B. K., 1960. *The Gametophyte and Young Sporophyte of* Athyrium esculentum. Amer. Fern Journ. **50**: 194–203. In this paper, NAYAR illustrated appropriately the venation of this species just below the sinus bottom (fig. 27). These figures never occur in the goniopteroid venation. In this feature, the goniopteroid venation may well be referred to be specific to the thelypteroid species.

form crescent-shaped coenosori. There are some species of *Thelypteris* originally described under *Athyrium*, for their sori are oblong and bear the athyroid indusia.

Dimorphopteris is characterized by the sori in acrostichoid condition. Such condition may be derived from the expansion of the linear receptacles. The derivation of the acrostichoid sori from those having the punctate receptacle may be more troublesome comparing with the case cited above.

Indusia. Some groups of the thelypteroid series are distinct in having essentially exindusiate sori. *Phegopteris, Cyclogramma, Leptogramma, Stegnogramma, Dictyocline,* some members of *Abacopteris, Meniscium* and naturally *Dimorphopteris* are the representatives of the thelypteroid species having the naked sori. However, the species without indusia are comparatively small in number among the thelypteroid ferns. The indusiate and exindusiate species are usually fairly distinct. Among the species noted as being exindusiate by CHING (1936), *Thelypteris ornata* and *T. uliginosa* are bearing small fugaceous indusia. I have not actually examined *C. jerdonii,* the only representative with exindusiate sori in *Cyclosorus.* There is, however, only one case where the indusiate species are very closely related to the exindusiate one: this is the case of *Thelypteris erubescens* and its allies.

The thelypteroid indusia are usually round reniform, basifixed, entire or nearly so and usually hairy or glandular on the surface. The density of the hairs on indusia is highly variable even in a single species, and many infraspecific taxa recognized by the difference only in the hairiness of indusia are wholly superficial and unnatural. The indusia of many species are soft and fugaceous. Moreover, they are usually rather small in size. Thus, when the sori are fully matured, the indusia have fallen off or are buried entirely under the sporangia. As noted above, the indusia become sometimes invisible on matured fronds, and therefore the indusiate species are not rarely misjudged as to be exindusiate by the investigation only on the herbarium specimens.

There is only one exceptional case of the attachment of indusia in the thelypteroid ferns: the peltate indusia of *Aspidium boydiae.* On the systematic position of this species, I have already discussed in my earlier paper (1961). The peltate indusium was an important key character to separate *Polystichum* from *Dryopteris* in the age of *Index Filicum.* Now, the peltate indusia are found also in the thelypteroid species. The transformation between peltate and basifixed condition is an interesting theme of morphology, but we have not been able to trace the developmental stages of this peltate indusia.

Thelypteris cystopteroides and *T. grammitoides* (its synonym, *Athyrium hyalostegium*) are the thelypteroid species once belonged to the genus *Athyrium.* These dwarf species have oblong sori and the indusia of various forms. The indusia are round reniform or horse-shoe shape, but sometimes elongate at interior side along veinlets, or, in extreme cases, crescent and linear, developing only one side of veinlets, thus forming typical athyroid condition. These athyroid sori may safely be derived from the species having the oblong receptacles.

The indusia of *Sphaerostephanos* are fairly characteristic. The sori of this genus are oblong or linear, completely covered by soft membranaceous indusia in

young condition and are sausage-like in shape. Such sori as well as indusia may be considered as those of oblong sori in specialized condition. Similar condition is found on the indusia of *Diplaziopsis*, a derivative of the athyroid ferns.

The most interesting 'indusia' are found on *Phegopteris decursive-pinnata*. In this species, sori are round and no indusia are found, though a tuft of hairs occurs regularly among sporangia of a sorus. These are the tufts of several unicellular hairs which grow 3 to 7 in number clustering on receptacles. These tufts of hairs have repeatedly been described as to be true indusia: for instance in recent, H. ITO (1939), OHWI (1958), and TAGAWA (1959). However, no cells common to these hairs are found: the hairs standing separately on the receptacles, though very close together at their bases. Thus, *P. decursive-pinnata* is exindusiate in definition, for no indusial cells are found among sporangia. However, the tufts of hairs regularly growing on receptacles may be considered as the remnant of indusial hairs resulted from the strong degeneration of indusia, though there is no evidence to confirm this supposition precisely. The other species of *Phegopteris* are all exindusiate, no such hairs being found on receptacles. We shall be very fortunate if we can get any proof to direct the true nature of these tufts of hairs: whether they are the remnants of the indusial hairs or merely tufts of hairs intermingled among sporangia.

Sporangium. As in all other members of the higher leptosporangiate ferns, the sporangia are not so distinct taxonomically in the thelypteroid ferns. On oblong or linear receptacles, the sporangia gather in a cluster, developing in type of mixed sori. The sporangial feature distinct to the groups is the occurrence of setae on sporangia. Many exindusiate species have the sporangia bearing one to several setose hairs with straight or hooked apices. The sporangial hairs with hooked apices are found on such species as those belonging to *Abacopteris*, *Cyclogramma* or *Phegopteris*. However, the occurrence of such sporangial hairs are the difference found only in the discrepancy of specific rank. The case of *Thelypteris erubescens* and *T. rufostraminea* stands a good example of this: the former is an exindusiate species with naked sporangia, while the latter is a species having the setiferous sporangia and obsolete indusia.

The hairs on sporangia are often interpreted as the substitution of the indusia. Really, the sporangial hairs are always found on the exindusiate species. There are exceptions for this parallelism, and the above explanation seems to bear no scientific inevitability. The above stated *T. erubescens* and its ally may again give a good support of this objection.

Taxonomic Evaluation. Soral feature seems to have been too disregarded in recent years for the taxonomy of the species belonging to *Dryopteris* of *Index Filicum*. Although the overestimation of this characteristic as has been done by HOOKER and his students is the vital disturbance of the establishment of the natural classification, the neglect of the importance of this feature makes the other mistake in taxonomy. In the classification in this paper, the soral character is more highly evaluated by me than by any of the recent taxonomists.

As will be noted in the section of classification, the genus *Stegnogramma* s.lat. is distinguished from *Thelypteris* s.lat. by having the linear or reticulate exindusiate

sori with setiferous sporangia. Among the species of *Thelypteris* in the sense of
the present classification, there are fairly great variation among the soral characters,
including reticulate exindusiate sori as in some species of *Abacopteris*. This variation
is, however, accompanied with successive intermediate forms between the extremes,
as will be shown in the further pages in the section of classification. Contrary to
the case of *Thelypteris* s.lat., we have no intermediates in the soral construction
between *Stegnogramma* and any species of the groups of *Thelypteris*.

HOLTTUM (1948) compared the setiferous sporangia of the thelypteroid ferns with
those of the Grammitidaceae. This feature may, however, occur in parallel with
each other. Such is the characteristic feature showing no phylogenetic relation
between the far established groups.

<p style="text-align:center">Trichomes</p>

Among various taxonomic features of the thelypteroid ferns, the trichomes are
generally regarded as being of greatest value. To define the thelypteroid ferns
against the other groups, the characteristic features found in the dermal appendages
are used as one of the most easily definable and useful indicators. I have recently
published a paper treating the trichomes of the thelypteroid ferns, and discussed
rather minutely the taxonomic value of them. The essential points may better be
recapitulated here for the taxonomic discussion of this group of ferns.

The dermal appendages of the thelypteroid ferns are arranged in three kinds:
the scales, the hairs and the glands.

Scales. Every species have the scales various in their sizes and forms. When
fronds are fully expanded, scales are found only on the rhizome and at the basal
portions of stipes. However, the thelypteroid species have in general the scales on
the laminar portions in young and still circinate conditions: in some species these
laminar scales are more persistent. The density of scales are various according to spe-
cies: some species are very densely scaly as seen in the case of *Thelypteris paleata*
or *Cyclosorus crinipes*; others are not paleate at a glance, though caducous scales
occur always on some portions of plants as in the case of *Thelypteris palustris* or
Cyclosorus gongylodus. The scales are all basifixed with cuneate or deeply cordate
bases. These scales are generally composed of a single layer of cells: there are some
exceptions, especially in the larger species like *Thelypteris ornata*, having the basal
portions consisting of several layers of cells. In the species having the scales with
multilayered basal portion, the axes are prominently muricate due to the remainings
of bases of the fallen scales.

The size and form of scales are various according to species. Generally speak-
ing, the scales are ovate or subtriangular in outline with finely prolonged apices,
almost entire on the margin and usually cordate at the base. One of the most
characteristic features of the thelypteroid ferns is the hairiness of scales. In almost
all species of this series, scales bear the hairs on the margin, though sometimes the
hairs are caducous. In some species, the hairs are also found on their abaxial side,
not so rarely also on the adaxial side. The hairs on scales are unicellular and usually
setose, but sometimes they are hooked at apices or stellate as seen in the goniopteroid

species.

Some species belonging to *Phegopteris* are diagnosed to have stellate hairs. I have discussed fully on this matter with the result that the stellate hairs of some *Phegopteris* species are extremely reduced scales bearing marginal hairs.

Hairs. The hairs of the thelypteroid ferns are strongly variable. They may be distinguished into the following five forms: 1) seemingly articulated hairs, 2) straight multicellular hairs, 3) unicellular setose hairs with hooked apices, 4) unicellular setose hairs with straight apices, and 5) forked or stellate unicellular hairs. I have already discussed on these hairs in my earlier paper, comparing every forms morphologically and speculating the probable transitional steps among them.
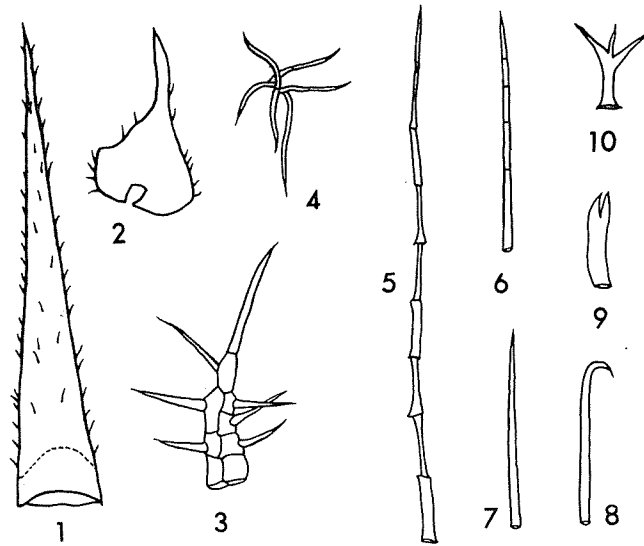

Fig. 2. Various types of trichomes found in the thelypteroid series of ferns. 1) rhizome scale with several layers of cells, 2) rhizome scale with marginal hairs, 3) scale on rachis of *Thelypteris decursive-pinnata*, 4) scale on rachis of *Thelypteris bukoensis*, 5) seemingly articulated hair, 6) multicellular hair, 7) simple setose hair with straight apex, 8) simple setose hair with hooked apex, 9) forked unicellular hair of *Goniopteris prolifera*, 10) stellate unicellular hair.

The hairs are not necessarily different between unicellular and multicellular ones. The thelypteroid ferns are diagnosed to have stiff unicellular hairs, but the length of hairs is not constant at all, the longer hairs having the occasional septae. The gradual transformation between the occasionally septate longer hairs and the straight multicellular hairs may safely be recognized by the presence of various intermediate conditions between the above two kinds of hairs. The seemingly articulated hairs are found on some species of *Stegnogramma,* and are ready to be considered as a specialized condition of the longer multicellular hairs as seen in *Macrothelypteris* or in

Sphaerostephanos. These seemingly articulated hairs may be morphologically distinct from the so-called *Ctenitis*-hairs or such articulated hairs. The apices of hairs are straight or hooked in various degrees. Thus, the hairs of the kinds 1)—4) in the above classification form morphologically one group and have common features to one another.

The stellate unicellular hairs are, on the contrary, fairly different from the various kinds of hairs noted above. This kind of hairs had been known only on the species of American genera, *Goniopteris* and *Meniscium,* and I noticed also on the Palaeo-tropic *Ampelopteris*. I have examined only a part of species belonging to those American species and am not certain to give a conclusive remark on the classification of these species. It seems, however, that the stellate unicellular hairs stand a good distinguishing feature of the genera cited above.

The density and localization of the hairs on the plant body of our ferns are very variable according to the portions of plants or to the species. The hairs are generally found on rhizome, stipes, and on the axes of laminar portions, i.e. on rachis, costae, costules, veins and veinlets. The laminar surfaces are also setiferous, especially on the margins. Adding to those portions, the hairs are further found on indusia, spo-rangia or even on scales. On the density of hairs, I have already discussed somewhat minutely in my earlier paper. No taxa are safely recognized only by the difference in the density of the hairs on some portions of plants.

Some species are described as to be glabrous in nature, but the thelypteroid species are all naturally hairy. So-called glabrous species, or varieties, are those having the hairs very sparsely. I have examined no specimens of the thelypteroid ferns which have no trace of setose hairs.

Glands. Many species of the thelypteroid ferns have the glands somewhere of plants. These glands are, however, various in size, form, colour, location and density according to the species. In some cases, the density and the location of the glands are variable to some extent even in a single species. The glands seem to be not the feature to give any evidence concerning the natural relationships among the species. Taxonomically, the presence of glands is useful only for the diagnosis of species or small species groups. The taxonomical meanings of the glands in each case will be noted on the pages of the enumeration of species in some pages further.

Taxonomic Evaluation. Some hold the opinion that the goniopteroid ferns are not different at all from the other members of the thelypteroid series. They propose an evidence for their opinion that the stellate unicellular hairs are not distinct enough from the other kinds of hairs found on the thelypteroid species. When the stellate multicellular hairs found on the *Phegopteris* are taken into account, the opinion cited above seems to be highly probable. Moreover, the stellate unicellular hairs of the goniopteroid ferns have occasional septae in their cells. Thus, these hairs appear to be stellate multicellular in both cases. However, we should not be misled by the apparent resemblance of some features. The stellate multicellular hairs of *Phego-pteris* are the specialized form of scales. Contrary to this, the occasionally septate stellate multicellular hairs of the goniopteroid ferns bear their septae not at the defi-nite positions and these septae are very rare. Thus, the two kinds of hairs noted

above are derived from distinctly different origins: one by the reduction of scales, the other by the deviation of unicellular hairs. Therefore, the stellate unicellular hairs of the goniopteroid ferns stand fully distinct feature and are useful for the diagnosis of this group of ferns. We can not find such hairs in the other members.

The scales with multilayered lower portion are found only on the huge species, such as *Thelypteris ornata*. This kind of scales is also known in some species of Cyatheaceae. Those huge species having such scales are characterized by their axes being prominently muricate due to the remainings of the bases of fallen scales. There has not yet been given any evidence of their morphological nature.

As the presence of the setose unicellular hairs is the characteristic feature of the thelypteroid ferns, there are some genera which are included in this group because of the presence of such hairs. *Hypodematium* is one of such genera sometimes considered as a representative of the thelypteroid series. Really, the hairs of *Hypodematium* are, at a glance, quite the same with the setose unicellular hairs of the thelypteroid ferns. Nevertheless, they can not be considered to have the same taxonomic value. When only the type species, *H. crenatum*, is known to this group, we have no evidence of the taxonomic difference of the hairs of this genus and the thelypteroid group. Now, there are known four other species in the genus *Hypodematium*. The three of the five species known to this genus bear such setose unicellular hairs somewhat densely, but the other two species, which are doubtlessly related very closely to the other three species, have no such hairs but only the glandular hairs. The glandular hairs found on three species of this genus are, on the contrary, distinct hairs which are wholly unknown among the thelypteroid species. At any rate, the setose unicellular hairs of the genus *Hypodematium* are not so constant as in the case of the thelypteroid ferns, and freely replaced by the glandular hairs by the species. Moreover, we can enumerate the other distinctions of the genus from the thelypteroid ferns as in the morphology of the rhizome and of the base of stipes, the form and lack of hairs of scales, chromosome numbers, morphology of gametophytes and so on. Therefore, the systematic postition of the genus *Hypodematium* is not among the thelypteroid series, despite of the similarity of the hairs.

CHROMOSOME

The chromosome numbers have been counted on about forty species among the thelypteroid members. The most common basic number of chromosomes found in the thelypteroid ferns is 36 in haploid condition. This number is known in all the species belonging to *Cyclosorus*, *Abacopteris*, *Leptogramma*, *Ampelopteris* and several species of *Thelypteris*. There are the other basic numbers of chromosomes in our ferns, such as 27, 29, 30, 31, 34 and 35 in haploid conditions. Apogamy is reported only for *Phegopteris polypodioides*.

As the dryopteroid and the athyroid ferns have the basic chromosome numbers of 40 or 41 in haploid conditions, the distinct counting of the thelypteroid ferns is highly valued and is taken up as to be one of the prooves to separate them in the rank of family. However, there are several basic chromosome numbers in our series

of ferns. This may be an additional evidence that the thelypteroid ferns are rather heterogeneous group of different species. MANTON (1953) suggested that the species now belonged to *Thelypteris* bearing the basic numbers 31 should be separated from the bulk of the thelypteroid. The known members of such species are *T. beddomei*, *T. auriculata*, *T. uliginosa* and *T. viridifrons*. These species are, however, quite distinct from each other and we can not combine these species into one group. If we should exclude these species from *Thelypteris* proper, they would constitute the independent groups, though the last two might be united in a single group. Thus, the chromosome numbers can suggest only the heterogeneity of the group, not the real circumscription of any group. A difference in the chromosome numbers will suggest certain taxonomic difference between the plants, but the identity in the chromosome numbers can not indicate any taxonomic identity between the plants.

For the minute classification of the thelypteroid ferns, data are as yet too scanty concerning the chromosome numbers. When more knowledges will be accumulated, this may become one of the most important indicators of the separation of groups. As known currently, however, the chromosome numbers alone are referable only to the indication of groups. No positive proof can, however, be get from the numbers of chromosomes. To analyse the specific relations, further analysis should be made on the karyotypes. It is regret that the current methods are hardly applicable to the karyotype analysis of the higher leptosporangiate ferns, for the fern chromosomes are high in number and small in size.

PANIGRAHI & MANTON (1957) made an interesting contribution to the cytotaxonomic analysis of the group of *C. parasiticus*, one of the most complex groups in the oriental tropics. Adding to the counting of chromosome numbers, they made hybridization experiment between every two species used, and obtained interesting results from that experiment. It seems, however, that the taxonomic confusions are introduced, for instance that the specific separation is impossible between *C. jaculosus* and *C. subpubescens*. On that account, further discussion will be made in the pages of these species. The results obtained will suggest that the local forms may be distinct from each other, even when real speciation is hardly established. On such intraspecific variation, further investigation should be made by using various methods.

I have made a preliminary study on the cytotaxonomy of *Abacopteris* in the Ryukyus, where four 'species' have been known. In my earlier paper on the taxonomy of this genus in 1959, I noted that *A. simplex* in the Ryukyus was considerably different from the typical form of this species found in South China. The meiotic division of the Ryukyu plants identified to this species is rather irregular in meta- and ana-phase producing a few solitary chromosomes which do not move to any pole. The spores of this species seem to be complete in their appearance, but they will not germinate in our experiments[2]. It may safely be considered that the Ryukyu plants of such habit reproduce themselves only by the vegetative method,

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2) The spores of this and the next species are sent to Dr. MOMOSE for his studies, but he also could not succeed to get any gametophyte. Cytological evidence will show the fact apparently by the irregular division of chromosomes in meiotic metaphase.

and that an individual variation is thus preserved throughout a colony. Just the same as in the species cited above, *A. insularis* is not a pure species, as the meiotic division of this species are quite irregular and no spores can actually germinate in spite of their complete appearance. This may be a natural hybrid, though no proof is yet obtained. This latter species grows abundantly in type locality, and the second place found in the island of Okinawa, about 100 km south of the type locality, is also said to be abundant in this species. The rhizome of *Abacopteris triphylla* group extend promptly, and local luxuriance of a certain species may easily be resulted by vegetative reproduction. The above stated observation is only provisional and further investigation is needed to conclude the specific relation among those species.

Geographic Distribution and Ecology

The thelypteroid ferns are found almost in every place where the ferns are growing. Like the other groups of ferns, the thelypteroids are abundant in number of species in the tropics, the only restricted species extending both northward and southward beyond the cold temperate regions.

The regions under the specific revision of the present paper comprises a variety of geographic areas ranging from the cold temperates in Hokkaido to the tropics in Taiwan. Therefore, various distributional elements run into our regions. We find in Hokkaido and northwards only the following five species: *Thelypteris phegopteris, T. palustris, T. nipponica, T. quelpaertensis* and *Stegnogramma pozoi* ssp. *mollissima.* Of these, the first two species are known widely in the cold temperate regions of the northern hemisphere. The allied species of the third and the forth species, *T. noveborescens* and *T. oreopteris,* are known in North America and northern Eurasia respectively. The above species except the last are in Honshu and Kyushu growing only at above 1000 m elevation (*T. nipponica* is not found in Kyushu). Only the last species extends southwards to Malaysia. The first four species may be considered as the strictly northern elements, but the last one as an element of warm temperate regions extending its range even to Hokkaido.

Contrary to those cold temperate species, there are pantropic species known also in the regions now under consideration: *Cyclosorus gongylodus* and *C. dentatus* extend northwards to the southern edges of Honshu and *C. truncatus* to the Ryukyus. The species common in the tropics of the Old World are represented in our regions by such species as *Thelypteris paludosa, T. erubescens, T. torresiana, Cyclosorus subpubescens, Abacopteris triphylla* and *Goniopteris prolifera.*

Several species are endemic to some parts of our regions, i.e. *Thelypteris bukoensis, T. subaurita, T. castanea, T. cystopteroides, T. ogasawarensis, T. viridifrons, Cyclosorus kotoensis, C. ensifer, C. boninensis, Abacopteris liukiuensis, A. insularis, A. longipetiolata.* As will be noted on each species, most of the above species represent particular forms of closely related common species. Twelve species among total 51 species are comparatively high ratio of endemisms for the higher leptosporangiate ferns, though the regions are rather extensive in the present paper.

The other half of our ferns have phytogeographic relation with the fern flora of Chinese-Himalayan region or of the Philippines and Malaysian regions. Several authors carefully compared the flora of Taiwan with that of the Philippines. In recent years, Taiwan botanists made such comparison especially from the standpoint of the distribution of trees. They stated that Hunchuen (Koshun) Peninsula was the phytogeographic island distinct from the Formosa (Taiwan) proper, and that Botel Tobago (Kotosho) was related phytogeographically with Hainan and the Bonins. However, their opinion based chiefly on the counting of the numbers of the common species between the regions compared and little on the geographical and inorganic factors. The geographic distribution of Hunchuen Peninsula and the affinites among Botel Tobogo, Bonin and Hainan may well be interpreted even by the topographic and climatic points of view alone. COPELAND (1939) speculated that most of the recent ferns had their origin in Antarctica. According to his opinion, all the fern have dispersed from Antarctica northwards to the present regions. Thus, the fern flora of our regions should, by his opinion, related most closely to that of the Philippines and have parallel resemblance with that of Sino-Himalayan regions. I have once illustrated the distribution of *Cyathea* in the regions just the same as this paper. The two subgenera of that genus in those regions show the pattern quite applicable to the opinion of COPELAND. Among the ferns now under consideration, some members are found throughout Sino-Himalayan regions: *Stegnogramma griffithii, S. dictyoclinoides, Thelypteris auriculata, T. omeiensis, T. uraiensis* and *Cyclosorus papilio. Stegnogramma* s.lat. and *Cyclogramma* are as a whole typical Sino-Himalayan representatives. Contrary to these, the species common between the southern parts of our regions and continental South Asia are many in numbers: *Stegnogramma tottoides, Thelypteris angulariloba, T. beddomei, T. hattorii, T. esquirolii, Cyclosorus taiwanensis, C. acuminatus, C. parasiticus, Abacopteris simplex* and *A. aspera.* Those a little northern species, i.e. the common species between central parts of our regions and continental and southern China are: *Thelypteris decursive-pinnata, T. japonica, T. angustifrons, T. glanduligera* and *T. laxa. Stegnogramma pozoi* ssp. *mollissima* may belong to this group. These species have wide range of distribution extending towards both temperate and tropical regions. The thelypteroid species found in our regions and Malaysia but not in continental Asia are rare, represented only by two species: *Stegnogramma gymnocarpa* and *T. gracilescens.* Comparing the morphological features of these ferns, nothing is preferable to suggest that the northern species are derivatives of those of the related species found in the southern places. Therefore, the present data offers no active evidence to accept the speculation that the northern species have immigrated from the far south. No particular relationships are found between southern edge of Taiwan and Hainan or the Bonins.

As a whole, the thelypteroid species are generally found in every area where the environments allow for them to grow. However, the higher endemism indicates that the range extension is not so easy, for all the endemic species in our regions seem not to be the relics of ancient times but to be species recently established. Only one species, *Thelypteris bukoensis*, is quite distinct from all the other species and

is considered as to be a relict species, though this is one of the northern elements. The species with wide range of distribution may be rather variable, being slightly different in each locality, The cytological result obtained by PANIGRAHI & MANTON suggests that even the plants belonging to a single species are more or less different in their biological nature, the difference being less than the taxonomic recognition. The conception of species should be reinvestigated in such cases. Among the endemic species enumerated above, *Abacopteris insularis* may be hybrid as noted in the page of this species. The cytological analysis is in great need to recognize the true nature of the species.

There are distinct subgenera endemic to some particular regions. *Dimorphopteris* in Moluccas, *Cyrtomiopsis* in Hawaii and *Haplodictyum* in the Philippines are quite distinct in particular features: acrostichoid sori, peltate indusia and simple pleocnemioid venation respectively. First two are monotypic subgenera and the last consists of only two, very similar species. These species seem to be deviated and highly specialized in the above particular features to form distinct groups, but are not able to become luxuriant. Their evolution seems to be resulted in failure, and so only the restricted members are survived as relics. Contrary to these species, the members delivered to *Cyclosorus* are most flourishing one, especially in the tropical regions. There are wide ranges of variation even in a single species and are various species related closely to each other. Some of the infraspecific variants should be researched more minutely.

All of the thelypteroid species but one are terrestrial concerning the members of our regions. *Stegnogramma gymnocarpa* ssp. *amabilis* alone are growing in the muddy crevices of dry cliffs along the rivers in deep shade. The dwarfed habit of this species may be resulted from the rupicolous habitat.

The habitats of the terrestrial species are variable according to the species. Most of those ferns are growing on the floor of mountain forest where the humus are rich enough. The forests are various according to the species: northern representatives are under the deciduous broad-leaved or coniferous forests. According to the species, the humidities of their habitat are various. Some species grow along stream or on wet ground, as *Thelypteris erubescens* and *Cyclosorus truncatus*. Most of the forest dwellers are placed on deep humus. *Thelypteris phegopteris, T. bukoensis, T. nipponica* and *T. quelpaertensis* are on the humus-rich floor of the deciduous broad-leaved forests or of the coniferous forests. Those in the evergreen broad-leaved forests are many in numbers, such as *Stegnogramma griffithii, Thelypteris omeiensis, T. gracilescens, T. hattorii, Cyclosorus taiwanensis, C. subpubescens, Abacopteris simplex, A. triphylla, A. liukiuensis, A. insularis* and so on. *Stegnogramma pozoi* ssp. *mollissima* grows in a wide range of habitat. This is found on the humus-rich or sandy mountain slope under the coniferous or deciduous broad-leaved forests, on wet muddy grounds along stream in villages, on rather dry grassland, on sandy bank of river, or on humus-rich floor of the subtropical forests, usually forming a large colony by the luxuriant growth of rhizomes. *Thelypteris decursive-pinnata* and *T. esquirolii* are usually growing on the wet sandy floor of light forests, but often found near the human dwellings. The range

of the first of the two seems to be closely related to that of the villages, usually be-
ing absent in the deep mountains. *Thelypteris beddomei* and *T. cystopteroides*
are found not under the forest but on the half shaded or open grassland at edge of
the forest, generally covering fairly wide ranges. *Thelypteris uraiensis* is also
found at edge of forest, on wet muddy ground in light shade and forms no colonial
habitat. *Cyclosorus dentatus* grows in the Ryukyus on dry open bank along the
road or in light shade. At the northern edges of the ranges of this species, how-
ever, this is sometimes found on the dark wet ground at the mouth of artificial cave.
Such particular habitats are sometimes recorded at the locality in the geographical
limit of the species concerned.

The world wide *Thelypteris palustris* and *Cyclosorus gongylodus* are found
on the marsh or on wet sunny places. These species are seldom found in mountain
or under forest. The species common on grass fields in villages are *Thelypteris
japonica, T. glanduligera, T. angustifrons, T. laxa, Cyclosorus acuminatus, C.
parasiticus* and others. These species are also found on dry cleyey slope of lower
mountains, usually in light shade or in open places. The species common in the
woods by villages, *Stegnogramma pozoi* ssp. *mollissima* and *Thelypteris decur-
sive-pinnata*, are also common in villages, though these species like the habitat more
moist than that of the above members. The species growing in the sunny and dry
places are *Thelypteris subaurita, T. torresiana* and *T. viridifrons*. The first
species of them seems to be dispersed most promptly, for this is often found on the
newly formed bank or slope where even the weeds are not yet come out. This
species are not in good condition in forest or in shade. In such shady places, this
species is generally found on wet sandy ground along stream. The second species
grows on dry cleyey slope, rarely on plane field. Even in the forest, this species is
fond of sunlight and is found always at the place where the light shines in through-
out the sparse crown of trees. *Thelypteris viridifrons* is rather common on cleyey
ground near the houses even in the towns, and very rare in mountain regions.

There are many species having the colonial habitat. The species having active
growth of rhizomes easily form such formation. It is not certain how many indivi-
duals are mixed in one colony.

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