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The Trichomes of the Thelypteroid Ferns

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A good deal of problems have been remained to be settled concerning the taxonomy of the thelypteroid ferns. One of the most important features to define this group of ferns is seen in the characteristics exhibited by the trichomes: prominent setose unicellular hairs and often dorsally hairy scales. Although the trichomes are generally of great taxonomic value, no detailed investigation has been made on the trichomes so as to cover all the subgroups of thelypteroid ferns.

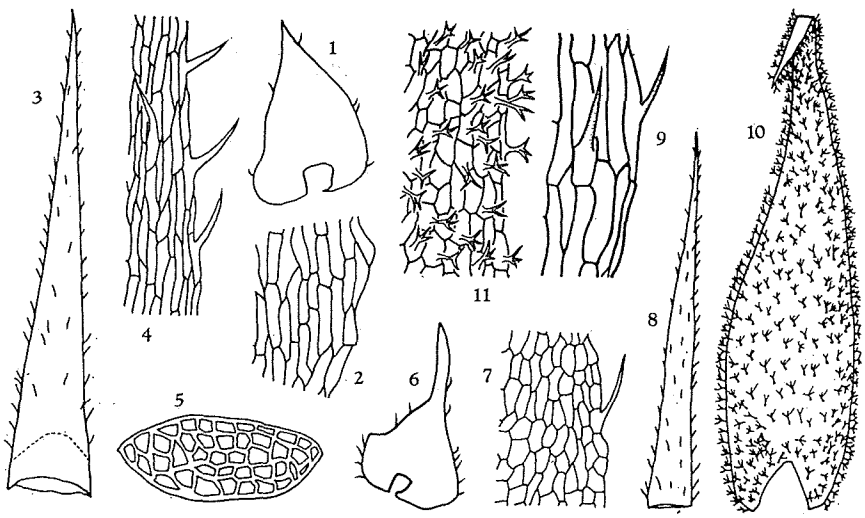
I have therefore planned in this article to revise more comprehensively the morphology and the taxonomic evaluation of the trichomes. The present study depends, however, chiefly upon the materials of the Far Eastern regions, many species from the outside of the regions having been lost to examine.

Scales

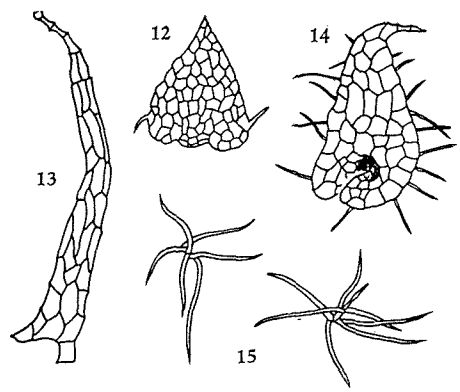
All the thelypteroid species are characterized by the presence of scales which are rather dense on rhizome and at the very base of stipes (Figs. 1–11). Several species are said to be distinct in having scaly underside of rachis, costae and costules. It seems, however, that every species has such scales also on the laminar parts, though frequently not so dense and distinct. While the fronds are young enough to be circinate, small scales are found on the axes of lamina underneath (Figs. 12–15). In most members of the thelypteroid ferns, these scales are caducous and disappear completely from the laminar parts of expanded and fully matured fronds. Therefore, the presence of such scales on laminar parts is primarily a feature common to all the species of this group, and it may be regarded as a feature only worthy of specific segregation.

Both the rhizome scales and those on the laminar parts are basifixed, never peltate in attachment[1]. The base of each scale is round in many species, but

1) HOLTTUM (1954, p. 299) has described that *Ampelopteris prolifera* has a few small peltate ciliate scales on the costae underneath. This observation may be a mis-understanding of the structure of the basifixed scales. Really, the bases of them are very deeply cordate with imbricate lobes (Fig. 14).



Figs. 1–11. Rhizome scales.—1–2. *Thelypteris palustris.*—3–5. *T. setigera.*—6–7. *Cyclosorus gongylodus.*—8–9. *Dictyocline griffithii.*—10–11. *Goniopteris tetragona.* 1, 6 and 10, ×10; 2, 4, 5, 7, 9 and 11, ×25; 3 and 8, ×5.



Figs. 12–15. Scales of rachis and costa underneath.—12. *Thelypteris palustris.*—13. *T. quelpaertensis.*—14. *Ampelopteris prolifera.*—15. *Phegopteris bukoensis.* All×25.

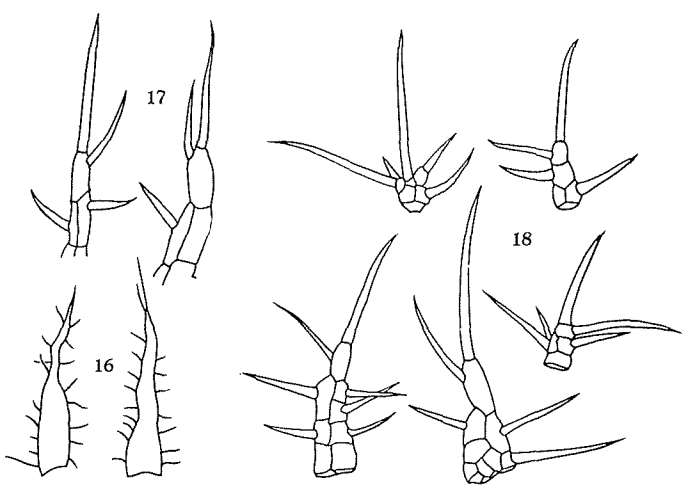
all the gradation to the cordate one is found. Forms of the rhizome scales are, to some extent, variable according to species, though mostly oblong subdeltoid to lanceolate, their apices being usually acuminate and long attenuate. In some species, the apices of scales are peculiar, as will be shown a few pages further. As the cell walls of scales are almost homogeneous throughout, neither bicoloured nor clathrate scales are found in this group of ferns. The marginal cells, having

thinner walls, are sometimes different from the inner ones, and the margin of each scale is almost entire and never lacerate.

Generally, each scale is composed of a single layer of cells. In larger scales, however, the basal portion thickens and consists of several cells, as in the case of *Thelypteris setigera* (Fig. 5). In this species, axes are prominently muricate due to the remainings of the bases of fallen scales.

The scales of thelypteroid ferns are hairy in various ways. Those of some species are almost glabrous in appearance, but marginal cells are ready to produce irregular unicellular hairs. Hairs are usually placed along the margin of scales, more often on the surfaces as well, both adaxial and abaxial, the location of hairs being constant to respective species. Density and size of hairs are, on the contrary, much variable even in a single species. The two rather artificial genera of the New World, *Goniopteris* and *Meniscium*, are distinct in having the scales with furcate or stellate unicellular hairs, which are growing on the margin or also on the surfaces (Figs. 10–11).

One of the most interesting scales is found on the various axes of *Phegopteris polypodioides* and its allies, most typically on *Phegopteris decursive-pinnata* of the Far Eastern regions. In this species, various scales are found on every axis of the plants underneath, i.e., stipe, rachis, costae, costules and veins. Those at the lower portion of stipe are lanceolate to linear lanceolate, broadest and slightly cordate at the base, acuminate and long attenuate towards the apex, up to 8 mm long, 0.5 mm broad, membraneous or very soft papyraceous, atro-brown, and setiferous on the margin, but glabrous on the surfaces. On rachis and costae, the scales become smaller in size and change in their constitution. These successive changes are illustrated in Figs. 16–18. It should be carefully



Figs. 16–18. Various forms of the scales of *Phegopteris decursive-pinnata*.—16. Rhizome scales, ×10.—17. Apical parts of rhizome scales, ×25.—18. Scales on rachis and costae underneath, ×25.

observed that, when reduced in size, the form of these scales becomes irregular. In most extreme cases, they take an appearance of 'setiferous hair'; the surfaces of scales become narrower and are equivalent to multicellular hairs bearing a setose hair to each component cell. It is very interesting that this 'setiferous hair' is quite similar in appearance to the apical portion of a larger scale of this species (Fig. 17). These 'setiferous hairs' are almost translucent, and are mixed with the needle-like unicellular hairs (Fig. 23). However, they can not be considered as a kind of hairs, but as scales reduced extremely. There is a distinct morphological gap between this 'setiferous hair' and needle-like or so-called articulated hairs.

In his original description of *Dryopteris bukoensis*, TAGAWA (1932, p. 89) wrote that "tota planta stellato-pilosa". These 'stellate piles' are better regarded as representing an extremely reduced form of the scales found on the rachis and costae of *Phegopteris decursive-pinnata*. As seen in Fig. 15, these are multicellular in construction, never producing plural cells from each component cell. Although there is no transition between these 'setiferous hairs' and scales bearing marginal hairs, it would be evident that the 'setiferous hairs' of *Phegopteris bukoensis* are also the scales of peculiar construction.

Unicellular Hairs

Every species belonging to the thelypteroid series has the unicellular hairs on some parts of plants. There are two kinds of such unicellular hairs: one is the setose hairs, being long needle-like and straight or hooked at the apices, and the other is furcate or stellate hairs, which stand as the diagnostic feature of the New World genera, *Goniopteris* and *Meniscium*.

The species having the furcate or stellate unicellular hairs are sometimes separated as a goniopteroid group in the series of thelypteroid ferns. COPELAND (1947, p. 153) maintained this opinion in his scheme showing a supposed phylogenetic relationship of the genera of his Aspidiaceae. *Goniopteris* is regarded by recent taxonomists as a genus confined to the New World, except only for CHING (1938, p. 259; 1940, p. 239) who considered *Hemionitis prolifera* as an Old World representative of this genus. Reviving an old genus *Ampelopteris* for this species and re-describing it, COPELAND (1947, p. 143) has stated that the rachis, costae and veins bear simple deciduous setulae. Following to him, HOLTTUM (1954, p. 299) has noted that the distinctive feature of *Goniopteris* is the presence of branched unicellular hairs on the scales of rhizome and stipes as well as on the lower surfaces of rachis and costae, but he has found no such hairs on the Malayan specimens of *Ampelopteris*. Contrariwise, CHING (1938, p. 262) has noticed in the new growth of his *Goniopteris prolifera* the presence of characteristic short stellate or forked unicellular hairs on the scaly rachis. In fact, the hairs of this kind are present in that species, though only on the edges of a vague groove on rachis above. These hairs (Fig. 27) are not needle-like but

sometimes glandular[2]. Some species of *Goniopteris*, however, have quite the same kind of furcate unicellular hairs as those found on *Ampelopteris* (e.g. *G. vivipara* and its allies). In spite of the existence of such hairs, there seems to be a considerable phylogenetic gap between *Ampelopteris* and *Goniopteris*, for, in the former genus, the furcate hairs are confined to a restricted portion and the scales are not furcate hairy but have setose and glandular hairs[3].

The long needle-like hairs are the most distinctive feature in recognizing thelypteroid ferns. They are found on various parts of plants, i.e., on rhizome, stipes, rachis, costa, costules and veins, on the margin of lobes, on the surfaces of laminar parts, on indusia and sporangia, and on the margin as well as on the surfaces of scales. Whether the setose hairs are present or absent in certain places is sometimes taken up for discriminating a species or a species group. These hairs are patent or appressed to the axes according to the parts or to the species.

The setose hairs of the thelypteroid ferns are straight or hooked at apices. Hooked hairs are found in all or some species belonging to such genera as *Phegopteris*, *Cyclogramma*, *Abacopteris* and so on. The hooked apices of these hairs are faced to various sides, showing no regular tendency of fixed direction. These hooked hairs are often mixed with straight unicellular hairs.

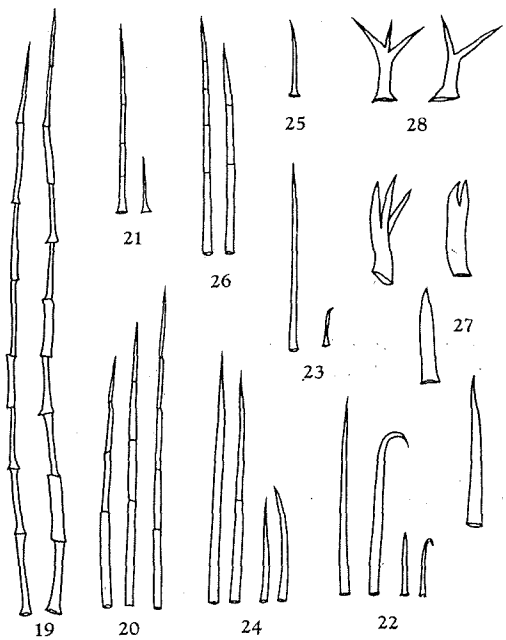
The density of these setose hairs is variable to some extent even in a single species. Infraspecific taxa have repeatedly been given to such variants based solely on the difference in hairiness. However, almost all varieties and formae thus distinguished are not distinct enough from the typical ones. So-called glabrous forms of thelypteroid species are not entirely glabrous at all, but bear some loosely growing hairs. Such are the cases found, for instance, in *Cyclosorus interruptus* and var. *hirsutus*, *C. gongylodus* and vars. *hirsutus* and *glaber*, *Abacopteris rubra* and var. *hirsuta*, *Thelypteris brunnea*[4] and vars. *hirtirachis* and *glabrata*, *Thelypteris oligophlebia* and var. *elegans*, and so on[5]. One of the most interesting example of such variabilities in hairiness is *Leptogramma mollissima* var. *pilosissima*. This variety was originally described by H. Ito and more precisely recognized by Kurata (1958, p. 41), the latter of whom stated that this variety differed from the typical one by the presence of dense long patent hairs on the laminar surfaces of fronds underneath. The common plants of *L. mollissima* bear two kinds of setose hairs, longer and shorter; the longer hairs are regularly more than 1.2 mm in length and usually found on

2) Concerning the trichomes of *Ampelopteris prolifera*, I am much indebted to Professor R. E. Holttum, who has given me valuable information about them.

3) I have examined many scales but have met only once with a marginal hair with forked apex on a rachis scale. However rather exceptional this may be, the peculiar form seems to suggest certain relation between the setose hairs and the stellate hairs.

4) This should be called *Phegopteris paludosa* (Bl.) J. Smith. *Cf.* Iwatsuki, K., 1961, Acta Phytotax. Geobot., **19**: 11.

5) These names are listed up from the enumeration given by Ching (1936b, pp. 266–347; 1938, pp. 178–262).



Figs. 19–28. Hairs.—19. Seemingly articulated hairs on the stipe of *Stegnogramma cyrtomioides*.—20. Multicellular hairs on the underside of the laminae of *Thelypteris uliginosa*.—21. Multicellular hair on the rachis (left) and unicellular hair on the upper side of veins (right) of *T. beddomei*.—22. Unicellular hairs of *T. omeiensis*.—23. Unicellular hair of *Phegopteris decursive-pinnata*.—24. Longer and shorter hairs of *Leptogramma mollissima*.—25. Unicellular hairs of *Cyclosorus dentatus*.—26. Multicellular hairs on the stipe of *Sphaerostephanos larutensis*.—27. Various hairs of *Ampelopteris prolifera*.—28. Stellate unicellular hairs of *Goniopteris tetragona*. 19–26, ×25; 27–28, ×50.

the axes of fronds only, the shorter ones less than 0.8 mm in length and dense, to a certain degree, on laminar surfaces as well as on axes of fronds. In this species, these shorter hairs are extremely variable in their density by individuals. The laminar surfaces are sometimes glabrescent but in other plants very densely hirsute with these shorter hairs. Moreover, the longer hairs are not rarely found mixed with the other hairs. Thus, the occurrence of luxuriant longer hairs results in a cob-webby appearance of var. *pilosissima*, though the density of them is also considered as a feature of great variation. The density of such setose hairs is, in fact, unreliable to distinguish taxa of the thelypteroid ferns. It may, however, be worthy of mention that in such cases as *Thelypteris japonica* and var. *glabrata* some other features are so different as to make clear the distinction of the two forms.

Multicellular Hairs

In the thelypteroid series of ferns, there occur multicellular hairs only in such particular species as the members of the genera *Thelypteris* s. str., *Stegnogramma*, *Sphaerostephanos* and so on. These multicellular hairs are usually straight and needle-like.

The multicellular hairs found in the species of *Thelypteris* Sect. *Macrothelypteris* are quite similar to the long needle-like unicellular hairs. Contrary to these, those found on rachis (also on costae underneath though very sparsely) of *Stegnogramma cyrtomioides* resemble so-called articulated hairs in appearance. They are pale, straight, patent and needle-like[6], but the septae are brownish in colour and distinct enough. Despite this fact, it can not be presumed that they are quite identical with the articulated *Ctenitis*-hairs, which are found on the axes of ctenitoid and dryopteroid ferns. The articulated straight hairs of *Stegnogramma cyrtomioides* seem to be the hairs transformed to a considerable extent from the long needle-like hairs.

The multicellular hairs are usually restricted to the axes of fronds, especially on stipes and rachis. The density of them is usually variable to some extent.

Glands

The species having the glandular under surface of fronds are not so rare in the thelypteroid ferns. The form, size and colour of these glands are variable according to the species, but are almost constant within single species. Contrary to these, their density and location, whether they occur only on the axes of fronds underneath or also on the underside of fronds, are variable even in a single species. These glands serve a good feature to diagnose a species, sometimes a species group; CHING (1936b, pp. 246–248) treated the characteristics appropriately and distinguished ten subgroups under his *Thelypteris*.

The glandular hairs are rather rare in the species of thelypteroid ferns. Some species have such hairs on the scales or on the indusia as well as on the axes of fronds. These species are not necessarily confined to a certain species group, but are found everywhere in species groups or genera independently.

Discussion

After the separation of the thelypteroid ferns from the great assemblage of *Dryopteris* complex, made by CHRISTENSEN in his comprehensive works (1913, 1920), many suggestions have been offered concerning the phylogenetic relation-

6) CHING (1936a, p. 96) only described as "hairy throughout the rachis, hairs needle-like, spreading, multicellular". However, this species has also setose unicellular hairs on every axis of fronds.

ship of this series of ferns. Of these, HOLTTUM's opinion will be referred to, for it is based partly upon the characteristics found in the dermal appendages. He has considered that Thelypteridaceae, Cyatheaceae and Grammitidaceae are the derivatives from a Gleicheniaceae-like ancestral stock. Comparing the thelypteroid scales and hairs with those of Gleicheniaceae, he (1947, p. 131) stated that the appearance of superficial hairs on the scales of Gleicheniaceae seemed possible to be a later development. It seemed to him to be surely possible that the branched or stellate hairs of Gleicheniaceae might be reduced to a unicellular state. Later, HOLTTUM (1959, p. 44) described the superficial hairs on the stipe scales of *Cyathea latebrosa*, regarding them as an additional evidence for his inference of the relationship cited above. I have shown on the foregoing pages another resemblance of the scales between the thelypteroid ferns and Cyatheaceae: the occurrence of scales with the basal part of more than one cell layer in thickness. Among the thelypteroid species, these scales that remind us of the prickles are found only on such huge ferns as *Thelypteris setigera*, the habit of which is, to some extent, similar to that of Cyatheaceae. Nevertheless, this resemblance may be attributed to the result of a convergence of this character, for the species of *Macrothelypteris* are hardly regarded as representing an ancestral form of the thelypteroid ferns.

The setiferous sporangia of the exindusiate species of thelypteroid ferns are also compared by HOLTTUM with those of Grammitidaceae. Such a relationship may be a subject not to be concluded from the trichome analysis only.

The stellate multicellular hairs of *Phegopteris bukoensis* are, at a glance, similar to those of Gleicheniaceae. However, as seen in the successively transitional forms found in the scales of *P. decursive-pinnata*, seemingly stellate hairs of *Phegopteris* species may better be considered as the 'setiferous hairs' which are the extremely reduced forms of the scales. It seems to be sure that there is a distinct morphological difference between these 'setiferous hairs' and the branched unicellular hairs, the latter of which may be derived from the simple unicellular hairs by transformation. The forked hairs of *Ampelopteris*, mixed with simple ones, may give an evidence for this presumption.

Seemingly articulated hairs of *Stegnogramma cyrtomioides* may have directly been derived from the long needle-like multicellular hairs, which in turn are related to the setose unicellular hairs. It is somewhat difficult to recognize difference between the straight multicellular hairs and the longer needle-like unicellular hairs.

The thelypteroid trichomes consist, therefore, of scales and hairs. The scales comprise various types, from 'setiferous hairs' to those having the thickness of more than one cell layer. The hairs are the multicellular ones inclusive of the seemingly articulated hairs, and the unicellular ones which are either simple or stellate. The successive changes are not so difficult to trace among the thelypteroid species.

Summary

1. Various types of trichomes of the thelypteroid ferns are described and illustrated.

2. The scales are hairy on the margin or also on the surfaces. In some species, they are much reduced to have an appearance of 'setiferous hairs' and in other species composed of multi-layer cells at the lower portions.

3. The hairs consist of 1) seemingly articulated hairs, 2) straight multicellular hairs, 3) simple setose hairs with hooked apices, 4) simple setose hairs with straight apices, 5) forked or stellate hairs, and 6) glandular hairs.

4. Evaluations are given where there is any taxonomic availability of trichomes.

5. Comparisons are made between the thelypteroid trichomes and those of some other groups of ferns.

In closing, I wish to express my cordial thanks to Professor S. KITAMURA and Dr. M. TAGAWA for their kind supervision.

References

BOWER, F. O., 1923. The Ferns, Vol. 1. London, Cambridge Univ. Press.

CHING, R. C., 1936a. On the genera *Stegnogramma* BL. and *Leptogramma* J. SM. Sinensia, **7**: 89–112.

——— 1936b. A revision of the Chinese and Sikkim-Himalayan *Dryopteris* with reference to some species from neighbouring regions, Part 1. Bull. Fan Mem. Inst. Biol., **6**: 237–352.

——— 1938. Ditto, Part 2. Ibid., **8**: 157–268.

——— 1940. On natural classification of the family "Polypodiaceae". Sunyatsenia, **5**: 201–268.

CHRISTENSEN, C., 1913 & 1920. A monograph of the genus *Dryopteris*. Parts 1 & 2. Mém. Acad. Roy. Sci. Lett. Danem., 7me sér., **10**: 53–282 (1913), 8me sér., **6**: 1–132 (1920).

COPELAND, E. B., 1947. Genera Filicum. Waltham, Mass., Chronica Bot. Comp.

HOLTTUM, R. E., 1947. A revised classification of leptosporangiate ferns. Journ. Linn. Soc. Bot., **53**: 123–158.

——— 1954. Flora of Malaya. II. Ferns of Malaya. Singapore, Government Print. Office.

——— 1959. The scales of Cyatheaceae. Kew Bull., **1957**: 41–45.

KURATA, S., 1958. Notes on Japanese ferns, 16. Journ. Geobot. (Kanazawa), **7**: 39–43.

TAGAWA, M., 1932. Spicilegium pteridographiae Asiae orientalis I. Acta Phytotax. Geobot., **1**: 88–94.