

# Vegetative characters distinguishing the various groups of ferns included in *Dryopteris* of Christensen's *Index Filicum*, and other ferns of similar habit and sori

By R. E. HOLTUM

IN A SERIES of papers begining in 1907, mainly on American species, Christensen himself showed a way in which natural groups within *Dryopteris sens. lat.* of his *Index Filicum* could be distinguished, the significant diagnostic features being provided by hairs and scales on the fronds. Though he never published a formal conspectus of the whole group, he continued to develop his ideas (see Christensen 1938). Ching's series of papers on *Dryopteris* and other genera of China, published from the year 1933 onwards, carried the general investigation much further, dealing with the ferns of Asia not considered in Christensen's earlier work. Ching also used the characters (both external and internal) shown by a cross-section of the rachis, and the relation of rachis to pinna. The use of this last kind of character was developed further by me, and is most fully set forth, with some illustrations, in my book on the ferns of Malaya (1954). In trying to understand more clearly the limits of some of the genera concerned, I have been much impressed by the significance of these characters, and to clarify my thinking I have attempted a concise comparative presentation of them, as set forth at the end of the present paper. It appears to me that Ching did not pursue effectively the line of thought which he himself indicated when showing the distinction between rachis-characters of *Ctenitis* and *Dryopteris (sens. strict.)*; if he had done so, he would not have suggested that *Athyrium* and *Thelypteris* are closely related, nor that *Rumohra adiantiformis* belongs to the same genus as the *Dryopteroid* ferns which he associated with it.

I have been especially impressed by the importance of the external shape of the rachis, and the way in which this shape is modified when a pinna-rachis (or a simple pinna) is attached to it. These characters are extremely uniform in genera which, as judged by other characters, are seen to be natural ones, and I believe that all the more highly evolved genera have each a particular rachis-form. When however one looks at *Dennstaedtia*, *Hypolepis*



and related genera, which have various primitive characters and seem to be survivors of a very basic group, one finds less uniformity, and I believe that in this group one can see the beginnings of both the *Tectaria* and *Dryopteris* rachis-characters, now so strongly differentiated in these two more highly evolved genera. I believe that the limits of the genera *Dennstaedtia* and *Hypolepis* are not at present clearly defined, and that a further study of these genera, with rachis-characters (as well as other factors) in mind, may yield significant results.

There is a sharp distinction between the kind of grooved rachis shown by *Dryopteris* proper (the groove opened to admit the groove of a pinna-rachis) and on the other hand the kind of rachis which, even if it has a median groove, does not open its groove to admit a pinna-rachis groove. In ferns showing the second of these alternatives, as for example the *Thelypteroid* ferns, the main rachis and the costae of pinnae are grooved on the upper surface, but the groove of the rachis does not open to admit the groove the costa (the latter is in fact usually not grooved at its base). In *Tectaria* and *Ctenitis* there is no median groove in the upper surface of rachis or of costae of pinnae, though in *Pleocnemia* (Holttum 1951) there is a slight median groove. *Ctenitis* and *Tectaria* are characterized also by the short multicellular hairs pointed out by Christensen (he called them *Ctenitis*-hairs). But there are genera which have the rachis-form of *Dryopteris* and hairs not much different from those of *Ctenitis* (e.g. *Stenolepia* v.A.v.R.).

A quite distinct kind of rachis is found in *Davallia* and some other genera. Here the middle of the upper surface of the rachis is raised, and on either side of this raised median band, in all smaller rachises, is a slight groove, the outer edge of the groove forming a very firm narrow wing; the thickened edge of the lamina of a leaflet is decurrent on this wing, the raised midrib of the leaflet joining the side of the raised median band of the upper surface of the rachis. An almost exactly similar arrangement occurs in *Pteridrys* (Ching & C.Chr. 1934), but in rhizome this genus is very different from *Davallia*. An indication of how this arrangement of the rachis may develop in the *Tectaria* group of genera is given by *Lastreopsis* Ching (united with *Ctenitis* by Copeland; recently distinguished, with a list of species, by Miss Tindale). In *Lastreopsis* the thickened lower edge of the lamina of a leaflet is decurrent on the rachis-wing, but this wing is usually much more lateral on the rachis than in *Pteridrys*.

The *Davallia* type of rachis is shown by *Rumohra adiantiformis* (Forst.) Ching, and this same species also has a dorsiventral



rhizome of *Davallia* type, so that a sterile plant of *R. adiantiformis* might well be identified as *Davallia*. The spores of this species also are like those of *Davallia*, not like those of *Dryopteris* and *Polystichum* (Harris 1955, pl. 7, f. 2). It seems to me therefore proved that Ching and Copeland were mistaken in associating species allied to *Dryopteris* and *Polystichum* with *Rumohra*. For these latter species, I have used the name *Polystichopsis*, but I am not at all satisfied that they form a natural group, and I believe that the matter needs further investigation. Furthermore, Mr. C. V. Morton has pointed out to me that the generic name *Polystichopsis* was first used in a different sense, and he is elsewhere proposing another name.

In the following conspectus I have not attempted to distinguish the genera of the Thelypteroid group, because I believe that more study is needed to establish clearly their distinctive characters. Everybody admits that a distinction between *Thelypteris* (or *Lastrea*) and *Cyclosorus* on the characters of free or anastomosing veins is a quite unnatural one. One could include all species in one genus, but then subgenera would need to be distinguished. For example, *Lastrea oreopteris* is surely very different from *Thelypteris palustris*, and both are very different from the group of species to which *Thelypteris brunnea* (Wall.) Ching belongs. Cytological evidence (Manton, Manton & Sledge) indicates that some species with free veins are more closely related to *Cyclosorus* than to other free-veined species, and probably such species should be united to *Cyclosorus*; but other morphological characters need to be established.

As regards the genera of the Tectaria group, it seems to me that *Ctenitopsis* Ching should be united to *Tectaria*, not to *Ctenitis* as in Copeland's *Genera Filicum*. Just as a division between *Thelypteris* and *Cyclosorus* on whether veins are free or not is unnatural, so also is a division between *Tectaria* and *Ctenitopsis*. The series of forms included in *Dryopteris dissecta* (Forst.) O. Ktze, which belong to *Ctenitopsis*, have exactly the frond-form of some species of *Tectaria*. Perhaps *Ctenitis* itself needs further subdivision, allowing some sections of it to be associated with *Tectaria*. I formerly attempted to distinguish *Heterogonium* from *Tectaria* on frond-form (I see no other practicable distinction) but now I am not sure whether this group should have generic separation. *Aspidium boryanum* Willd. (included by Copeland in *Ctenitis*) resembles *Ctenitis* rather than *Dryopteris* in external form of the rachis, but differs from both in the vascular anatomy of the stipe. I believe that this species (with some others which are closely



related to it) is nearer to *Athyrium* than to *Ctenitis*, but quite distinct from *Athyrium*, in which genus I placed it in my book on the ferns of Malaya (p. 567); in so doing I unfortunately made the mistake of referring to it specimens which are in fact *Athyrium*. Later (1959) I proposed a new generic name *Parathyrium* for *Aspidium boryanum* Willd. and its allies, but this was antedated by *Dryoathyrium* Ching (1941), based on the same type species.

In the following conspectus, *Gymnocarpium* (sensu Ching 1933) is shown as belonging to the *Dryopteris* group, not with *Thelypteris* (*Lastrea*) where Copeland placed it (1947, p. 137), and cytological evidence confirms this position. *Dryopteris phegopteris* (L.) Chr., on the other hand, belongs to the *Thelypteris* group. I believe that Copeland overlooked both hairs and rachis-characters when he wrote of these two that "their separation by reasonable generic definition is hardly possible". Similarly, I believe that the conspectus shows a clear separation between *Athyrium* and the *Thelypteris* group (on hairs, scales and rachis-characters), though both Ching and Copeland held that they were so closely allied as to be hardly separable in formal terms.

*Cornopteris* Nakai was based on a species like *Diplazium* and *Athyrium* in rachis-characters but lacking an indusium. *Hemionitis opaca* Don (in *Dryopteris* in the original *Index Filicum* of Christensen, transferred later to *Diplazium* by Christ) is very closely related to the type species of *Cornopteris*, and other species have been noted by Ching. Madame Tardieu-Blot however has added to the genus *Cornopteris* some of the species of the alliance of *Aspidium boryanum* Willd. (1956, 1958); the distinction between true *Cornopteris* and these species is shown in the present conspectus.

The genus *Hypodematium* has abundant needle-like unicellular hairs on its fronds, resembling in this the *Thelypteroid* ferns. Its scales however are quite different from those of *Thelypteris*, and I do not think that *Hypodematium* is of the *Thelypteris* alliance; on the other hand, I am not sure that it really belongs with the *Tectaria* group of genera.

Rhizome not dorsiventral (leaves and roots equally all round);  
wing of pinna-rachis, if present, thin like the lamina, except  
in *Pteridrys* and *Lastreopsis*

Main rachis lacking a median groove on upper surface; or if  
grooved, the groove not open to admit grooves of pinna-  
rachises; rachis sometimes winged, the wing joining the  
edge of the lamina of leaflets, not the edge of the costa of a  
leaflet



Hairs on upper surface of rachis multiseptate, usually very short; scales lacking superficial hairs or glands

Several separate vascular bundles throughout the stipe

**Tectaria group**

A tooth present at the base of each sinus between lobes of the lamina

Veins free; vascular bundles in stipe in a simple ring

*Pteridrys*

Veins anastomosing; vascular bundles in more complex arrangement

*Pleocnemia*

*Arcypteris*

No tooth present in sinus between two lobes of lamina

Basal basisopic vein of a vein-group springing directly from the costa, not from the costule which bears the other veins of the group; or veins much anastomosing

*Tectaria*

(incl. *Ctenitopsis*)

Basal basisopic vein of a vein-group springing from the costule; veins always free

Indusium peltate; hairs on rachis few, mainly near junction of rachis and pinnae on upper surface

*Dryopolystichum*

Indusium reniform; hairs many throughout rachis

Decurrent wing of lamina not thickened

*Ctenitis*

Decurrent wing of lamina thickened

*Lastreopsis*

One U-shaped bundle in the stipe (2 bundles near base)

*Dryoathyrium*

Hairs on upper surface of rachis unicellular, more or less needle-like; two vascular bundles in base of stipe, uniting upwards to one of U-shape

Scales lacking superficial hairs or glands, confined to swollen bases of stipes

*Hypodematium*

Scales bearing superficial glands or hairs, not confined to base of stipe which is not swollen

**Thelypteris group**

Main rachis with median groove in upper surface, this groove open to admit grooves of pinna-rachises; raised edge of a pinna-rachis groove joined to side of pinnule-costa groove, edge of pinnule-lamina decurrent on pinna-rachis as a lateral wing



Multicellular hairs, of a kind quite different from scales, lacking; groove of rachis quite smooth within

**Dryopteris-group**

Several vascular bundles in stipe

*Dryopteris*

*Polystichum*

"*Polystichopsis*"

Two vascular bundles in stipe

*Gymnocarpium*

Multicellular hairs, quite different from scales, often present; groove of rachis papillate within; some sori elongate and asymmetric or unilateral; two vascular bundles at base of stipe

**Athyrium group**

Sori indusiate

*Athyrium*

Sori not indusiate

*Cornopteris*

Rhizome dorsiventral (roots from lower surface, leaves from upper surface); pinna-rachis bearing a firm wing, edge of lamina thickened at base and decurrent on the rachis-wing; midrib of pinna raised, not grooved

**Rumohra** (*s. str.*)

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