The Anatomy of some Xerophilous Species of *Cheilanthes* and *Pellaea*.

BY

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With eleven Figures in the Text.

MATERIAL.

THE species examined were all collected by Mr. A. G. Tansley either in America or in Algeria, and to him I am indebted for my material, and for his very great assistance throughout the investigation.

The plants were *Cheilanthes persica*, gathered in 1910 at Djebel Murdjadjo, Oran; *Cheilanthes Fendleri*, from Santa Catalina, California; *Ch. lanuginosa*, from Manitou, California; *Ch. gracillima*, from Crater Lake, Oregon; and *Pellaea andromedaefolia*, from Santa Catalina, California. The four last-mentioned species were all obtained in the Western United States of America in the summer of 1913.

For purposes of comparison, *Pellaea falcata*, a New Zealand mesophytic Fern, was also investigated to some extent.

EXTERNAL MORPHOLOGY AND XEROPHILOUS ADAPTATIONS IN THE LEAVES.

The fronds of all four species show well-marked xerophilous characteristics, which have been concisely expressed as follows in the 'Synopsis Filicum':

'*Cheilanthes lanuginosa*, Nuttall. Frond bipinnatifid, rachis tomentose, texture subcoriaceous; upper surface grass green, slightly tomentose; lower surface densely matted with a coat of pale brown woolly tomentum; the margin of the segment much incurved.

'*Cheilanthes persica*, Mett. (= *Ch. Szovitzii*, Fisch. & Meyer). Frond bipinnatifid, rachis scaly and tomentose, texture subcoriaceous; upper surface green, slightly tomentose; lower surface densely matted with a coat of pale brown woolly hairs; the margin of the segment much incurved.

'*Cheilanthes gracillima*, Eaton. Frond bi- or tripinnatifid, rachis slightly fibrillose, texture subcoriaceous; upper surface naked, lower densely matted with pale brown woolly tomentum; the margin of the segment much incurved.

'*Cheilanthes Fendleri*, Hk. Frond tripinnatifid, rachis densely clothed above with lanceolate acuminate entire scales; upper surface quite naked,

FIG. 1. *Cheilanthes lanuginosa*. Transverse section of leaf.

FIG. 2. Diagram of transverse section of leaf of *Pellaea andromedaefolia*.

under surface scaly only, not matted; texture subcoriaceous, margin much incurved.

'*Pellaea andromedaefolia*, Fée. Texture subcoriaceous, rachis and both surfaces naked, involucre scarcely changed from the substance of the frond, and sometimes nearly meeting edge to edge.'

LEAF ANATOMY.

In addition to these characteristics, the minute anatomy of the leaf shows in each case a reduced lacunar system, the greater or less develop-

ment of a palisade, and the localization of the stomata on the lower surface, where they are protected by the inrolled margins alone (*P. andromedae-folia*), or by inrolled margins plus a covering of scales (*Ch. Fendleri*) or hairs (the other *Cheilanthes* species). These characters are shown in the figures of transverse sections of leaves (Figs. 1, 2). The most strongly marked xerophily is shown in the *Pellaea*, which possesses a very thick cuticle on its upper surface, and has also a palisade, which in the middle of the leaf is three cells deep. The lacunar tissue is reduced, and the margins are much inrolled.

STEM ANATOMY.

The stelar anatomy of *Cheilanthes* and *Pellaea* is of interest in that each genus contains both solenostelic and dictyostelic forms, together with others that are intermediate between these types. The four species of *Cheilanthes* investigated are placed next one another in the 'Synopsis Filicum'. They are all in § *Physopteris*, and Hooker and Baker, from a study of their external morphology, must have considered them nearly related one to another. The stelar anatomy, however, is different in each species. In the investigation of this feature series of hand sections were cut, and in all except *Cheilanthes Fendleri* these were drawn, forming Figs. 3-6.

In *Ch. Fendleri* we have a true solenostele. The leaf-gaps are long but fail to overlap.

In *Ch. gracillima* (Fig. 3) the stele over the main portion of its course behaves as a simple solenostele. At certain points, apparently not in accordance with any phyllotactic rule, extra leaves are inserted in such a way that two leaves are given off almost exactly together. The result is that the two leaf-gaps are at the same level, the stele therefore at such points being dictyostelic. Such pairs of leaves are seen in sections 8-10 and 15-16 in the diagram, Fig. 3. In section 15 there is also a 'perforation' or gap not formed by the giving off of a leaf-trace. Most of the leaves are given off dorsally, but in sections 8, 25, and 32 this rule is seen not to apply.

In *Cheilanthes lanuginosa* (Fig. 4) the departure from solenostely is still greater, though at intervals the transverse section may be a complete ring (sections 15, 16). The leaf-traces may be given off singly (sections 4, 7, 21), in pairs (section 10), or even in threes (section 17), and the leaf-gaps of one series may remain open till the departure of the next series (section 5). The stem, as in the two species preceding, is distinctly dorsiventral, a definite cauline ventral portion of the stele persisting throughout the stem.

In *Cheilanthes persica* (Fig. 5), however, the arrangement of the leaves on the stem is radial. The leaf-gaps are also very long, so that this is the most pronouncedly dictyostelic form investigated.

A further link in this chain of variation in stelar anatomy in § *Physa-pteris* is provided by *Cheilanthes lendigera*, another species of this section which is described by Gwynne-Vaughan (2). In this, so far as the endodermis and pericycle are concerned, each leaf-gap in the stele is closed up before the next above is formed. The leaf-gap in the xylem, however, remains open until it overlaps the gap formed in the xylem by the departure of the next leaf-trace above. In this manner a small separate xylem strand

FIG. 3. *Cheilanthes gracillima*. Series of transverse sections of stem in acropetal order. In this and in Figs. 4, 5, 6, leaf-traces are represented in solid black.

is formed within the stele, which crosses over at each leaf-insertion in just the same way as does the free dorsal meristele of so many of the simpler dorsiventral dictyosteles.

In the genus *Pellaea* considerable variation in stelar anatomy also takes place. *Pellaea falcata* is a simple solenostele, and is mentioned as such by Gwynne-Vaughan, who also describes *P. rotundifolia* and *P. andromedaefolia* as examples of the simpler form of transition from solenostely

FIG. 4. *Cheilanthes lanuginosa*. Series of sections of stem in acropetal order.

FIG. 5. *Cheilanthes persica*. Series of sections in acropetal order.

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to dictyostely, viz. by overlapping of leaf-gaps formed in two rows on the dorsal surface. The *P. andromedaefolia* which I examined may perhaps have been older material than that used by Gwynne-Vaughan, for though

FIG. 6. *Pellaea andromedaefolia*. Series of sections of stem in acropetal order.

it showed a dorsiventral dictyostele, its structure was more complicated than that which he describes. The leaves come off at approximately the same level in threes or in pairs (Fig. 6). From the appearance of section 29 in my series it seems that the arrangement in threes may be produced by

the interpolation of an extra leaf at a place where primitively two are given off, an arrangement still maintained in sections 10-19.

The detailed anatomy of the stelar tissues furnished results of some interest. In none of the five xerophilous Ferns was there to be seen any protoxylem, though search was made in both transverse and longitudinal sections. In *Cheilanthes Fendleri* and *Pellaea andromedaefolia* the apical region was thoroughly examined, and it was clear in these cases that there was no special protoxylem, the tracheides to be first lignified being large scalariform elements scattered irregularly in the xylem.

There was found to be a close correlation between the stelar structure and the amount and arrangement of the wood within the stele. *Cheilanthes Fendleri* and *Ch. gracillima*, of which the former is perfectly solenostelic and the latter scarcely departs from this type, both have xylem forming

FIG. 7. *Cheilanthes Fendleri*. Transverse section of stele of stem at edge of leaf-gap. *e.ph.* = external phloem; *i.ph.* = internal phloem.

FIG. 8. Portion of transverse section of stele of stem of *Cheilanthes lanuginosa*. *i.ph.* = internal phloem; *e.ph.* = external phloem; *tr.* = tracheide; *par.* = parenchyma.

a narrow continuous band of tracheides, not broken up by parenchyma (Fig. 7). *Cheilanthes lanuginosa* is intermediate between the simple types and the large-stemmed dictyosteles. It has a wider band of wood somewhat broken up by parenchyma (Fig. 8). *Cheilanthes persica* and *Pellaea andromedaefolia* are large-stemmed dictyostelic forms with a broad band of wood, among which a good deal of parenchyma occurs (Fig. 9).

The phloem of these forms is remarkable for the absence of differentiation into protophloem and metaphloem. The total number of sieve-tubes is in no case very large. These elements are narrow and arranged in a single line on each side of the xylem ring. The whole of the phloem in these Ferns may fairly be said to correspond with the protophloem of mesophytic species, the slow growth necessitated by a xerophilous habitat rendering unnecessary those facilities for active translocation which would be given by large metaphloem elements.

There was, however, in all five species, just as great a development of phloem and endodermis on the inside of the stele as on the outside, contrasting in this respect with the reduced types of stele described by Jeffrey (5) in some species of *Antrophyum* and *Vittaria*. But at the leaf-gap the phloem was found to be absent in every case, so that there was no continuity of internal and external phloem (Fig. 7). In fact, in the gap xylem and endodermis are constantly separated by only two or three layers of parenchyma. Even *Pellaea falcata* shows reduction of the phloem in the leaf-gap, though its stele has no other reduced characters.

PETIOLES.

The anatomy of the petiole was carefully investigated in each species. The petiolar stele forms a single strand in every case, lying surrounded by a sclerenchymatous cortex, which can be fairly easily separated, leaving

FIG. 9. Portion of transverse section of *Pellaea andromedaefolia*. *i.ph.* = internal phloem; *e.ph.* = external phloem; *tr.* = tracheide; *par.* = parenchyma.

FIG. 10. Transverse section of xylem of stele of *Cheilanthes Fendleri* petiole. *px.* = protoxylem.

only the central trace. The stelar strand thus obtained was embedded and microtomed. By cutting at 10μ and keeping every tenth section, I obtained a series of sections at 100μ intervals, from the base upwards. At the very base in each species there is a simple adaxially curved anarch leaf-trace, but the changes in structure found on following the petiolar strand upwards vary considerably, so that for each species it is best to have a separate description. Diagrams of the various stages are given in Fig. 11.

Cheilanthes Fendleri. The anarch C-shaped strand soon develops three protoxylems, all of which are endarch. The metaxylem immediately exterior to the median protoxylem dies out at a higher level, but the two portions of the stele thus left separate (except for the median protoxylem connexion) soon rejoin. This junction, however, is effected in such a way that our protoxylem is now in an exarch position. This protoxylem next

becomes completely detached and runs through the major portion of the petiole as a single separate group (Fig. 10). At a higher level, a little below the insertion of the first pinna, it splits into three or four smaller protoxylem groups, though the pinna trace is given off entirely from the lateral portions of the stele. The other two protoxylems become rather broader in the higher regions of the petiole, but otherwise they remain unchanged throughout. All three protoxylems were seen in longitudinal section to consist of spiral and annular elements, while the main mass of the tracheides has scalariform thickening.

Ch. lanuginosa. The series in this species is very easily derived from that in *Ch. Fendleri*. Three protoxylems appear simultaneously just above the base, but at this point the centre of the trace is so narrow that the median protoxylem occupies the whole thickness of the stele. The stele next shows a definite separation into two masses joined only by the protoxylem. As in *Ch. Fendleri*, these two masses rejoin and the median protoxylem, now exarch, soon becomes separated from the main stele. This stage is reached more quickly than in the former species, and there is the important difference that the median protoxylem does not persist. It is found for some distance as a line of thickening among the parenchyma (diagram 5 in the *Ch. lanuginosa* series, Fig. 11), but in the higher regions of the petiole no trace of it can be recognized.

Ch. gracillima. In this small plant the two lateral protoxylems, occupying an endarch position, are the only ones ever definitely organized. There is no trace of a median splitting, and only a slight and transitory indication (in the presence of somewhat smaller elements at the position shown by the dots in diagram 3) of a median protoxylem. True protoxylem elements, however, are not present, but this condition is clearly only slightly removed from that represented by diagram 5 in the *Ch. Fendleri* series. The higher regions of the petiole in *Ch. gracillima* show no further change in the number or position of the protoxylem groups.

Ch. persica. In petiolar structure this species is rather different from the American forms, but this is only what one would expect from the divergences in the stem anatomy, and from the totally dissimilar geographical distribution. The petiolar stele has the shape, in transverse section, of an obtuse-angled isosceles triangle, the base of which shows a slight adaxial curve. At each angle a protoxylem gradually becomes distinct as we examine the series of sections from the base upwards, and, once established, this structure continues throughout the length of the petiole. This type is probably related to that of *Ch. Fendleri*, being modified from some structure similar to that shown in diagram 5 of the *Ch. Fendleri* series. The loss of the two lateral hooks would easily give the type with the three protoxylem angles.

Pellaea andromedaefolia develops three endarch protoxylem groups,

the median one of which, in the main part of the petiole, is located in the position shown in diagram 3 of the series in Fig. 8. This is a condition which perhaps shows an unfulfilled tendency towards exarchy of the central protoxylem, an end which has become realized in the species of *Cheilanthes*.

These facts admit of only one simple explanation, viz. that the base of the leaf preserves primitive characters. This is the position which has been taken up by Sinnott (7). He has pointed out that the leaf-trace of all Ferns except Osmundaceae, Ophioglossaceae, and Marattiaceae can be derived from

FIG. 11. Series of transverse sections of the xylem of the petiolar traces of the five Ferns. Each series is numbered in acropetal order. * represents in each case the structure prevalent throughout the main part of the petiole. No. 8 in the *Ch. Fendleri* series shows the arrangement just below the first pinna.

a triarch-mesarch trace, and that the nearest approach to this condition is usually found at the leaf-base. The mesarch protoxylems have in the course of evolution generally become endarch, and in very many forms all trace of mesarchy is lost, even at the leaf-base. This is the condition found at the base of the petiole of *Ch. Fendleri*, and it is only by assuming that the acropetal succession recapitulates the evolutionary succession that we can reasonably bring the peculiar petiole of *Ch. Fendleri* into line with the normal type of filicinean leaf-trace. Though it is difficult to imagine what could be the actual cause of the exarchy and detachment of the median protoxylem, it is simple, from a study of the leaf-base transition, to

derive *Ch. Fendleri* from the normal type and the other *Cheilanthes* petioles from *Ch. Fendleri*. In *Ch. lanuginosa* the series is essentially that of *Ch. Fendleri*, except that the primitive endarch condition of the median protoxylem is not represented, and that this protoxylem lasts only over a limited distance at the base of the petiole. In *Ch. gracillima* there is omission of the early stages ; there is no sign of the median splitting of the trace, of the central protoxylem there is only an indication, and even that in an exarch position. Taken alone it would be difficult to fit this Fern into the Sinnott type, but in conjunction with *Ch. lanuginosa* and *Ch. Fendleri* the connexion becomes clear.

The derivation of *Ch. persica* was mentioned when dealing with that species. In the case of *Ch. persica* especially, as also in that of the two first-mentioned species, one sees that Sinnott rather underestimated the plasticity of the Fern petiole when he spoke of the 'striking constancy' of the endarchy of the filicinean petiolar bundle. While acquiescing in his general fundamental classification and derivation of Fern leaf-traces, one sees in studying these five xerophilous Ferns that the anatomy of the leaf-base, as of the stem, may furnish a sound guide to relationships, but that it is not to single species but to groups of allied species that the test should be applied. Within quite narrow circles of affinity certain forms may slip ahead of the general evolutionary march. This holds good for the petiole of *Cheilanthes gracillima* or *Ch. persica*, which have diverged from the closely related *Ch. Fendleri*, just as for a solenostelic species occurring in a genus otherwise haplostelic (e. g. *Gleichenia pectinata*).

Another point of interest is that petiolar structure may show a secondary simplicity. Thus in *Cheilanthes Fendleri* and *Ch. lanuginosa* the ordinary transverse section of the petiole shows a single compact mass of xylem. Nearer the base we find a stage at which, but for the protoxylem forming a connexion, the xylem is split medianly into two masses. This may give place at a still lower level to a single C-shaped strand. We have seen in deriving *Ch. lanuginosa* and *Ch. gracillima* from *Ch. Fendleri* that the earlier stages may be dropped out at the base of the petiole. Such a dropping out of early stages at the base, together with a secondary simplicity at a higher level, gives the state of affairs found in many Ferns (e. g. *Onoclea sensibilis*, *Peranema*, and *Diacalpe*), where a trace, double below, unites to give a single strand at a higher level. This renders advisable a relaxation of the inflexibility of Sinnott's assertions as to the constancy of the characters of the leaf-base, but such a relaxation really adds to the strength of the theory, and disposes of the objections raised by Davie (1), who claimed that his petioles in *Peranema* and *Diacalpe* were incapable of plausible explanation on Sinnott's theory. The accumulation of this additional evidence for the theory of the primitiveness of structures found at the leaf-base, entails no necessity that one should accept all

Sinnott's corollaries to his general proposition. Especially should this be remembered before adopting Sinnott's sceptical attitude towards the theory of Tansley and Gwynne-Vaughan, 'who consider the siphonostele to have been produced by the influence of an arched trace on a protostele'.

That the two theories are not so incompatible has been recently established by Salisbury (6), who has shown that narrowing of the base of the leaf-trace, found so frequently in Ferns, has no appreciable influence in checking the free supply of water to the leaf. The transpiration current being practically as great as if there were no basal narrowing of the petiolar stele, the effect of the leaf-trace on the conducting tissues of the stem, which supply the water necessary for this transpiration current, will be the effect of the full current in the main part of the petiole.

SPORE COUNTS.

All the species except *Cheilanthes persica* were bearing ripe sporangia, and counts were made of the spores per sporangium, the results being as follows:

<i>Pellaea andromedaefolia</i>	30, 31.
<i>P. falcata</i>	60, 56.
<i>Cheilanthes Fendleri</i>	53, 57.
<i>Ch. gracillima</i>	30, 31.
<i>Ch. lanuginosa</i>	32, 30.

The results show that the purely solenostelic form has in each genus more spores per sporangium than the dictyostelic species. Among the *Cheilanthes* *Ch. Fendleri* has the larger number, and this corroborates the evidence for the primitiveness of this species derived from the anatomy of the stem and petiole.

SUMMARY.

1. The xerophilous species of *Pellaea* and *Cheilanthes* show well-marked leaf adaptations. Hairs or scales on the lower surface, inrolled margins, thick cuticle, and palisade parenchyma are the chief characters observed.

2. The *Cheilanthes* species, all belonging to § *Physapteris*, show a wide range of stelar anatomy in their stems. *Ch. Fendleri* has a simple solenostele. *Ch. gracillima* has a solenostele becoming occasionally dictyostelic by the interpolation of an extra leaf, and *Ch. lanuginosa*, bearing its leaves much more closely on the stem, only rarely shows a complete ring in cross-section. These three have dorsiventral rhizomes, while *Ch. persica* has a radial dictyostele which is much more dissected than that of any of the three other species.

3. Of the genus *Pellaea*, *P. andromedaefolia* was the only xerophytic

species examined. It possesses a dorsiventral dictyostele with leaves given off approximately in pairs, though by interpolation of extra leaves these pairs are often converted into groups of three. Among other species of *Pellaea*, *P. falcata* has a typical solenostele, and Gwynne-Vaughan describes *P. rotundifolia* as a dictyostele with two dorsal ranks of leaves.

4. Parallel with the advance towards dictyostely is an increase in the thickness of the band of xylem, and in the extent to which the xylem is broken up by parenchyma. Thus *Cheilanthes Fendleri* is solenostelic, and has a narrow compact band of tracheides, while *Ch. persica* is a dictyostele with a broad band of mixed tracheides and xylem parenchyma. Intermediate between these comes *Ch. lanuginosa*.

5. There is no protoxylem in the stems of any of the five species investigated. The earliest tracheides to be organized are large and scalariform, and have no constant position in the stele.

6. The internal and external phloems are equally well developed, each consisting of a single line of small elements, corresponding in size and position with the protophloem of mesophytic Ferns. The internal and external phloems are not continuous with one another through the leaf-gaps.

7. The petioles may all be derived from a type with three endarch protoxylems such as has been described by Sinnott. This relatively primitive condition is found in *Pellaea andromedaefolia*, and at the very base of the petiole in *Cheilanthes Fendleri*. *Ch. Fendleri* at higher level shows in successive sections its median protoxylem passing through the stele, becoming exarch, and then completely detached and isolated. The other *Cheilanthes* species all show a secondary simplicity of petiolar structure in the main part of the petiole. This can be in every case derived from the *Ch. Fendleri* type, the connexion being clearest in *Ch. lanuginosa*, where the *Ch. Fendleri* peculiarities appear at the base of the petiole, but die out at higher levels.

Pellaea andromedaefolia retains its three endarch protoxylems throughout the whole length of its petiole, but the median one is situated at the end of a narrow groove, and only a short distance from the abaxial surface of the xylem mass.

8. The petiolar structure, the stem anatomy, and the greater output of spores per sporangium all point to *Ch. Fendleri* as a near approximation to an ancestral type from which *Ch. gracillima* and *Ch. lanuginosa* have been derived.

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