THE SEEDS OF ANEIMITES[1]

By DAVID WHITE

In the spring of 1900, while studying some of the collections of fossil plants from the lower Pottsville formations of the Virginian region, I was more than surprised at finding among the fossils from one locality numerous examples of a small fruit, which I had previously regarded as a new gymnospermic genus, attached by pedicels to rhachial fragments that, on account of their organic union with sterile pinnules, can not be regarded otherwise than as belonging to the fern genus commonly known as *Adiantites*. Detached specimens of these fruits had been found at a number of localities, and, on account of their external characters and their evidently deciduous habit, no question had arisen in my mind as to their seed nature. It had indeed been noticed that they were intimately associated with *Adiantites* foliage, but I was then quite unprepared to recognize them at once both as seeds and as belonging to fronds whose fern nature had hitherto been unquestioned.

At that time the sterile fragments and the correlated fruits were fully treated in my manuscript, in preparation, on the Pottsville floras, the name *Wardia* being given to the generic type of fructification. But, appreciating the gravity and the far-reaching importance of attributing seeds to a long established Paleozoic genus whose every character was pteridophytic, I postponed all special publication of the matter in the hope that further study in the course of the elaboration of the collections from hundreds of Pottsville localities would yield cumulative evidence bearing either on the internal organization of the fruits or on the structure of the fronds. The segregation as "Cycadofilices" of a number of types, principally stems and petioles, combining certain filicate and gymnospermic, particularly Cycadean, characters of structure, had already been established by Potonié,[2] and representatives of the sterile-frond genera *Sphenopteris, Neuropteris,* and *Alethopteris* had more or less definitely been referred to the group; but no type of fruit had been satisfactorily correlated with any member of that group.

[1] Published by permission of the Director of the U. S. Geological Survey.

[2] *Lehrbuch der Pflanzenpalæontologie,* 1899, p. 160.

Since the discovery of the relation of the seeds to *Adiantites,* my examinations have not only shown the generic type of fruit to be present at most of the places where *Adiantites* is found in the Pottsville formations, but they have also revealed different forms of the *Wardia* seeds in the most intimate association with four other species of the fern genus, with one of which, *Adiantites tenuifolius,* it is, again, in actual union.

Meanwhile the especial interest aroused by the correlation by Oliver and Scott,[1] on the basis of anatomical characters, of the seeds described by Williamson as *Lagenostoma* with *Lyginopteris* and, through the latter, with the *Hoeninghausii* group of Spenopterids; and the discovery by Kidston[2] of a Rhabdocarpous seed attached to the frond of *Neuropteris heterophylla,* as well as the arguments from distributional association set forth by Grand'Eury[3] make timely the presentation of the data relating to the Cycadofilic character of the hitherto unsuspected genus *Adiantites.*

Unfortunately a nomenclatorial change for *Adiantites* is at the outset necessary, the type section of the genus as proposed by Goeppert[4] being composed of species of *Ginkgo.* The name is therefore untenable in its restricted application as employed by Schimper, Stur, and others and as now generally recognized. The emended genus is indistinguishable from the American plant to which Dawson gave the name *Aneimites.* The latter name, as indicated by Etheridge,[5] is valid, as the eligible name next in priority, for the genus. Accordingly hereafter in this paper *Aneimites* will be used for *Adiantites.*

The specimens to be described were collected from a cut along the Keeney Creek branch of the Chesapeake and Ohio railway on the mountain side back of Nuttall, West Virginia. The horizon is in the Thurmond formation (lower Pottsville) about 350 feet below the Raleigh sandstone.

The plant, a new species typical of the genus *Aneimites* (*Adiantites*) may be described as follows:

ANEIMITES (WARDIA) FERTILIS n. sp.

(Plates XLVII and XLVIII)

Fronds quadripinnatifid, or quadripinnate?, spreading, a little delicate, but hardly lax, and rather dense, the divisions of the rachis

[1] *Proc. Roy. Soc.,* vol. LXXI, 1903, p. 477.
[2] *Proc. Roy. Soc.,* vol. LXXII, 1903, p. 487.
[3] *Comptes Rendus,* vol. 138, 1904, p. 607; vol. 139, p. 23.
[4] *Syst. filic. foss.,* 1836, p. 216.
[5] *Proc. Linn. Soc. N. S. W.* (2), vol. III, pp. 1301, 1302.

being slender, somewhat rigid except at the periphery of the frond, very finely striate, sparsely and obscurely punctate, rounded dorsally, shallowly canaliculate ventrally, the ultimate rachis being slightly flexuose and bordered by a very narrow wing of the decurrent lamina; penultimate pinnæ alternate or subalternate, open at or nearly at a right angle, close, usually touching or overlapping somewhat, linear or linear-lanceolate, acute or acuminate, and provided with large pinnatifid and fasciculately lobed pinnules above the ultimate pinnæ, the uppermost being sublobate or simple and narrowly cuneate; ultimate pinnæ alternate, subalternate, or sub-opposite, close, more or less open, usually rigid, overlapping a portion of their width, ovate to lanceolate or linear-lanceolate, obtuse or acute when sterile, attenuated and curviramose above when fertile. Pinnules alternate to subopposite, of greatly varying size, 3 mm.–18 mm. in length, the lobes or divisions being 1 mm.–3.5 mm. in width, narrowly cuneate, occasionally narrowly spatulate, the lateral margins slightly convex above, often slightly concave near the narrow or slightly subpedicellate base, the upper pinnules of the sterile pinnæ being very narrow and simple, becoming bifid, and bi-or tri-foliately dissected to or nearly to the base in 3–5 palmately or somewhat fasciculately radiating lobes or fully developed pinnules on an elongating axis, the apices being rounded, or truncate-rounded, more or less oblique, sometimes emarginate, the distal basal pinnule or lobe being usually noticeably broader than the other lobes or pinnules in the fascicle, while the proximal basal pinnule is often reduced in size, and more narrowly lobed; lamina very thin, decurring in an extremely narrow wing along the rachis, and minutely rugose-striate when viewed under a strong lens. Nervation very thin, but usually distinct and very slightly in dorsal relief; primary nerve strongly decurrent, forking once or twice at a wide angle in the base of the pinnule the nervilles forking once or twice at narrower or moderate angles, in passing upward, thread-like, often appearing double, nearly parallel and not very close, to the apex of the pinnule in which they often appear to slightly converge.

Fertile portions of the frond peripheral, laxly ramose at the apices and somewhat reduced as to lamina, the pinnules in the upper portions of the pinnæ becoming very small and distant, the lobes sometimes slightly thickened. Fructification (*Wardia*) small, rhomboidal, thin, deciduous, borne usually singly, but rarely doubly, in sparsely paniculate arrangement at the dilated apices of thick nervose-lineate, distantly, elongately, and faintly punctate, ramose pedicles which correspond to the greatly elongated and thickened

Explanation of Plate XLVII

Aneimites fertilis n. sp.

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Fig. 1. Fragments of primary (?) pinnæ, showing pinnules of largest proportions.

Fig. 2. Portion of the sterile frond, exhibiting typical pinnæ of the average proportions.

Figs. 2*a* and 2*b*. Pinnules enlarged to twice the natural size to show the nervation, and the details of the very thin lamina.

Fig. 3. Fragment of pinna, showing the smallest pinnules observed. The specimen is mingled with fertile fragments.

Fig. 4. Fragment of pinna with reduced pinnules, probably proximal to the fertile portions.

Fig. 4*a*. Mature and detached seed, enlarged to twice the natural size.

The originals, from Nuttall, W. Va., are in the collections of the U. S. National Museum.

2a x 2

3

4

4a x 2

2

2b x 2

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lobes of the reduced pinnules, the somewhat irregularly curved and often bifurcated pedicles constituting the uppermost divisions of the rachis. Seeds oval, rhombic, bilaterally symmetrical, the longitudinal axis averaging 4.5 mm., the transverse being 2.5 mm., rounded at the angles, slightly flatly obtuse at the apex and a little concave at the point of attachment, from which ascends on either side a narrow, striate, rather thick wing formed by a lateral dilation of the outer fibrous envelope, about .3 mm. wide at the base, gradually attaining a maximum width of .75 mm. a little below the lateral angle, narrowing somewhat abruptly above, and often difficult of observation at the apex of the fruit; outer envelope of the seed rugose by fine, irregular, longitudinal striæ, which often pass from the lateral wing to the surface of the nutlet in the compressed specimens, the seeds being also rarely traversed by numerous very obscure ribs; nutlet less distinctly rhomboidal, the lateral angles being less pronounced. Microsporangiate organs not definitely correlated.

The sterile portions of this plant constitute an interesting type which is at once recognizable by its open pinnation, the palmate or fasciculate grouping of the divisions of the lower pinnules, and the distinctly cuneate form, deep dissection, and thin texture of the latter. The pinnules, which are usually somewhat obliquely truncate-rounded, often present a Triphyllopteroid arrangement. A marked specific peculiarity of the frond is the generally greater breadth of the distal lobe of the pinnule or of the distal pinnule in the fascicle.

The general aspect of the foliage of the species is indicated by the fragments illustrated in plate XLVII, figures 1 and 2, the pinnules of the former being of nearly the largest proportions yet found in the collections. Occasionally the pinnules are less compact and more lax, while the fragment shown in plate XLVIII, figure 2, represents the maximum proportionate broadening yet observed in the smaller pinnules. Between those of the larger ones shown in figures 1 and 2 of plate XLVII, on the one hand and the examples with very small pinnules shown in plate XLVIII, figures 1 and 3, or the smallest observed, figure 3, plate XLVII, on the other hand, the sequence is complete and irrefragible. The very small pinnules connected with the fertile portions of the frond differ only in size from the larger leaflets on the barren pinnæ. The lamina, as indicated in the enlarged details (plate XLVII, figures 2*a* and 2*b*, or plate XLVIII, figure 3*a*) is very thin, the thread-like nerves being but slightly in relief dorsally. The dorsal surface is marked by very fine striation and

occasional irregular faint lineation, and on the smaller divisions of the rachis by minute elongated punctations.

On examining the plant material from Nuttall I was more than surprised at finding specimens in which the peculiar little rhombic winged fruits (*Wardia*) usually found at other localities in association with the Pottsville *Ancimites* were not only still attached to their stalks, but in actual union with fragments of pinnæ unmistakably bearing the small reduced pinnules of the species described above. These fruits, found abundantly associated with the pinnæ of *Ancimites fertilis* at this locality, appear to present themselves in nearly all stages of development, while many detached mature examples occur scattered on the fragments of shale.

Figure 4, plate XLVIII, exhibits the lax, elongated, and ramose habit of the apical portion of the fertile pinnæ. The rachis becomes less terete and more flexuose, while forking pinnately and distantly below and more closely above. At the same time, with the disappearance of pinnules, the axes become more lax, and spread out thinner in passing upward, the distal lobes or divisions (pedicels) also becoming cuneately expanded at the apices, while revealing several thin nerve-strands, which, in the most dilated apices, give rise to a distant, dichotomous nervation, that, so far as developed, is precisely in agreement with the nervation of the sterile portions of the frond. At the distal margins of these terminal expansions are developed the fruits, usually singly, though rarely two appear on the same pedicel, in which case one is commonly immature or abortive. The more dilated apices, which retain a broader foliar lamina and more distinct nervation, seem at most not to bear more than minute and undeveloped or abortive fruits. Several imperfectly preserved fruits are seen in the specimen figured, while a number of scarred apices mark the points of detachment of other mature specimens.

The characters both of pedicels and of seeds are better shown in a more simply divided example, illustrated in figures 5 and 5*a*, plate XLVIII. This specimen shows well two of the broader, nervose, apical dilations which are seen to be shallowly and broadly digitately lobate. The lobes are always thickened and concavo-convex, and frequently seem to contain a small scar or pit. They are, perhaps, to be regarded as abortive, though it is possible that they may be sporophytic. They are strongly suggestive of a developmental stage of a sporangial type found in association with an undescribed species of *Ancimites* from the base of the Pottsville near Pocahontas, Virginia. Evidently they are less altered from the ordinary foliate type.

At the base of the nearly fully developed seed on the left in the

Explanation of Plate XLVIII

Aneimites fertilis with seeds, *Wardia fertilis* n. sp.

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Fig. 1. Fragment of frond, showing small, narrow form of pinnules.

Fig. 2. Example with proportionately broad, though small pinnules.

Fig. 3. Portion of pinna, probably from fertile part of the frond.

Fig. 3*a*. Detail showing characters of the small pinnule and the obscurely lineate and elongately punctate rachis, enlarged to twice the natural size.

Fig. 4. Fertile apical portions of pinnæ, with seeds above and reduced pinnules below.

Fig. 5. Similar fragment with forking, thin pedicels, dilated at the apices.

Fig. 5*a*. One of the pedicels showing a seed and one of the foliate expansions, possibly representing an early stage in the development of the polleniferous organs, enlarged to twice the natural size.

Fig. 6. Seed still attached to the pedicel.

Fig. 6*a*. The same enlarged to twice the natural size to show the collapse of the apex, and the presence of the basal scales or possibly undeveloped ovules.

Fig. 7. Detached mature seeds, one of which is so preserved as to show the outline of the nutlet, and a broken edge of the outer envelope.

Fig. 7*a*. One of the seeds showing (exaggerated) the boundary of the nutlet, and the minute dimples at the angles of the wing, enlarged to twice the natural size.

Fig. 8. Pedicels with young and immature seeds.

Fig. 9. Similar example showing undeveloped and perhaps abortive fruits.

Fig. 10. Seeds obliquely compressed so as to foreshorten the nutlet and reveal the continuity of the wing.

Fig. 10*a*. The same, enlarged to twice the natural size to show the apex of the seed, which, in the diagonally flattened specimen, appears to be papillate.

Fig. 11. Fragment of pinna in which the apices are developed as young seeds.

Fig. 11*a*. The same, enlarged to twice the natural size to show the characters of the young fruits as well as of the pinnules.

Fig. 12. Apical fragments with delicate dichotomous, spiral, lineate appendages, thickened at the tips, possibly representing the microspore-bearing organs of the plant.

Fig. 12*a*. Portion of the same enlarged to twice the natural size to show some of the spiral appendages which are dense at the apices.

Fig. 13. Apex of a pedicel showing scars, probably those of the attachment of the spiral appendages shown in Figure 12. See similar development at the left of the latter figure.

The portion at the left in Figure 13 is shown enlarged to twice the natural size, and is cited as "*a*" in the text, p. 328.

Fig. 14. Pedicel, from which the seeds have fallen, showing obscure scars of detachment.

The originals, from Nuttall, W. Va., are in the collections of the United States National Museum.

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cited figure vestiges of small scales or undeveloped ovules may be noted. This feature, which is often to be observed, is also shown more clearly in the isolated specimen drawn in figures 6 and 6*a*, plate XLVIII. Both of these seeds show indistinct traces of a very slight collapse at the apex, a condition which may be construed as evidence of a pollenic chamber.

In the example just referred to a slight depression or dimple is noticed in the lamina of the wing just at the lateral angle. This character, which is visible in most of the seeds, I construe as possibly indicative of the presence of glands at those points. Figure 5*a* illustrates the vascular lineation of the outer envelope which is continuous from the portion over the nutlet across to the lateral dilation which forms the wing. The outline of the nutlet is rarely revealed by the tearing away of the marginal portion, but is frequently well shown, especially in the lower portions, by the circumstances of preservation, as illustrated by two proximate, mature, and detached seeds shown on the rock in figures 7 and 7*a*. The outer envelope is probably much thinner near the apex of the fruit, and in most cases is hardly distinguishable as a border near the top. The point of detachment, as shown in the figure last mentioned, is uniform in practically all the numerous isolated mature fruits and is evidently accomplished by the development of separative tissue at the base of the mature seed.

In a number of instances the arrangement of the fruits is more crowded, the seeds being borne close above the dichotomy of the pedicel, as suggested in figure 10; and this compactness sometimes lends an aspect of several seeds at the apex of a single pedicel. Fruits that are immature or about half-grown are seen in the fragments, figures 8 and 9. In these specimens a number of the seeds appear to be either imperfect or abortive. The aspect of the single or double fruit accompanied by rudiments, or possibly undeveloped ovules, at the apex of the pedicel is suggestive of the fruits of *Ginkgo*. The marginal wing is quite inconspicuous at this stage of the development of the seed. To the laxity and tenuity of the basal portions of the pedicels, as seen in figure 9, is due the generally detached and fragmentary condition of the specimens and the difficulty of exposing them so as to show a direct connection with the foliate portions of the pinnæ. The example seen in figures 10 and 10*a* is obliquely compressed so as to show the outer envelope completely surrounding the nutlet. In another example, a fragment (figure 11) from the border of the foliate portion of the pinna, a pedicel is developed at the apex of a small lateral pinna, the closely lineate sur-

face of the crushed and immature fruits being precisely in agreement with that of the seeds in figures 4 and 9.

At the apex of the pedicel illustrated in figure 13, a portion of which is enlarged at *a*, we see some of the small scars which should perhaps be regarded as vestiges of abortive ovules, though it is possible that they may have rather to do with the development of spore-bearing organs. In other examples, like that drawn in figure 12, they are found to be associated or apparently originally connected with delicate, very narrow, dichotomous, partially coiled, lineate-nerved, laminate appendages, with slightly thickened apices. The circumstances of their occurrence, and the form of these very delicate and apparently transitory appendages, strongly suggest their function as the polleniferous organs of the plant. Additional evidence is, however, necessary before drawing conclusions in this very important matter. The scars left at the apices of the petioles after the fall of the mature seeds, as imperfectly indicated for comparison in figure 14, are at once distinguishable from those in the specimens shown in figure 13. Ordinarily, however, the abandoned pedicels are seen only in profile and show only the edges from along which their seeds were detached.

The problem of the spore-bearing organs of *Aneimites fertilis* remains to be determined by the future discovery of more conclusive material. I am strongly disposed to believe, however, that they will be found either to be connected with the appendages of the type just described or, less probably, represented by an associated, delicate, small type of *Calymmatotheca* that may possibly have been developed at the distal borders of the more dilated and distinctly venous laminæ seen at the apices of some of the pedicels, like that shown in plate XLVIII, figure 5. The arguments for *Calymmatotheca* are stronger in the case of the Pocahontas plant, already referred to, which will be fully described in the writer's monograph of the Pottsville floras. At no locality have sporangia of the genus last mentioned been found distinctly in union with any species of *Aneimites*.

SUMMARY

In the foregoing pages it has been shown that the fruits of *Aneimites* (*Adiantites* of authors) are borne singly or rarely plurally at the apices of lax, flexuose, ramose, and slightly dilated terminal extensions of the peripheral pinnæ, whose pinnules become greatly reduced in the proximate sterile portions. Each seed may be regarded as corresponding to a lobe or pinnule, whose basal stalklet is

usually much elongated. This is illustrated by the specimen shown in plate XLVIII, figure 11.

The seeds, *Wardia fertilis,* are small, oval-rhomboidal, winged fruits, obtusely rounded at the apex, and apparently consisting of an inner nutlet, probably thinly lenticular in cross-section, surrounded by a fibrous and probably somewhat fleshy outer envelope, which is laterally dilated below the angles of the nutlet to form a wing, and which is slightly denser, with larger bundles, near the base. When mature they are regularly and uniformly deciduous by cross scission of the tissue at the base of the nutlet. In the process of their development the pedicels appear to elongate somewhat, while the wing is inconspicuous in the earlier stages. They are usually accompanied, at the dilated summit of the pedicel, by smaller imperfect or abortive fruits, or scales. The evidence of an apical pore or micropylar neck is obscure, while that of a pollenic chamber rests on the occurrence of a slight collapse within the apex of the nutlet, observed in a few examples only. The slight costation noticed in some of the seeds suggests a gymnospermous type with both pollenic chamber and micropyle.

The fruits of *Aneimites* can hardly be regarded as other than true seeds, and the group of hitherto supposed ferns to which they belong is therefore to be referred to the Pteridospermæ of Oliver and Scott, the "Cycadofilices" of Potonié.

The identity and nature of the microspore-bearing organs are not yet determined; but it is highly probable that the production of pollen either has to do with branched and coiled appendages originating at the apices of some of the dilated pedicels, or that, as seems to the writer much more unlikely, it is connected with the intimately associated *Calymmatotheca* type of sporangia.[1]

To the seeds of *Aneimites* described above is given the generic name *Wardia* in honor of Professor Lester F. Ward whose comprehensive elaboration and philosophical discussions of the American Mesozoic floras are an invaluable contribution to our knowledge of the development and distribution of plant life in geological time. The type of the genus is *Wardia fertilis.*

As compared with other Paleozoic seeds *Wardia* is perhaps most suggestive of some of the smallest species of *Cardiocarpon,* though differing from that genus by its fibro-nervose outer envelope, and the diminution of the wing in passing above the middle. It is prob-

[1] The latter hypothesis is in accord with the views of Professor Zeiller, who suggests that the pollen of *Neuropteris* may have been produced by some *Calymmatotheca. Comptes Rendus,* vol. 138, 1904, p. 663.

ably more lenticular than any of the small wingless seeds from the Coal Measures placed by authors in *Carpolithes.* As between *Lagenostoma* and *Rhabdocarpos,* the two types of seeds reported to have been definitely correlated with Cycadofilic fronds, it is evidently with the former that the closer relations probably exist, although it is difficult to determine satisfactorily the relations between seeds known chiefly by their internal structure and others known only by the external characters of the compressed specimens. The most prominent differences between *Lagenostoma,* as the latter is described by Williamson[1] or Oliver and Scott,[2] and *Wardia* are the presence of the wing, the thin and lenticular cross-section, and the absence of all traces of radial chambering near the apex, unless the faint costation is to be interpreted as due to the features of the pollenic chamber. *Wardia* has probably two distinct tests; *Lagenostoma physoides,* which has a fibrous layer, perhaps approaches more closely than do *L. ovoides* or *L. Lomaxi,* the latter of which is produced in a costate and deeply lobed cupule. Certain points of resemblance between the two genera include a degree of similarity in size and general form of the seeds, the development of the latter on pedicles, and, to some extent, a common Spenopteroid habit of the sterile fronds. Incidentally the punctation on the rachis and the pedicels of *Wardia* may be homologous with the glandiferous stalks on the pedicel and the cupule of *Lagenostoma.* On the other hand the reduced pinnules of *Aneimites fertilis* are in general form very suggestive of those of the normal *Sphenopteris elegans,* with which *Heterangium,* another Pteridospermic type, is correlated, while the narrow, ventrally sulcate, dorsally round divisions of the *Aneimites* rachis suggest the V-shaped single vascular axis of a *Heterangium* petiole.

On account of certain similarities between the sterile fronds of *Aneimites* and those of the *elegans* and *Hoeninghausii* groups of Spenopterids, together with the consideration of the points of resemblance in the seed production in *Lyginopteris,* I am disposed to regard *Wardia* as more closely related to *Lagenostoma* than to any other Cycadofilic type at present recognized. But, in the absence of knowledge of the internal organization of the rachis of *Aneimites,* and in view of the important external seed differences, the inclusion of the latter genus within the same family (Lyginodendreæ) does not at present seem warranted. However, they may, I believe, with

[1] *Trans. Roy. Soc.,* vol. CLXVII, 1877, p. 233, figs. 53–75; vol. CLXX, 1880, p. 517, figs. 61–63.

[2] *Proc. Roy. Soc.,* vol. LXXI, 1903, p. 477; vol. LXXIII, 1904, p. 4.

reasonable confidence be provisionally included within the broader scope of an order, the *Lyginodendrales*. In accordance with the classification of the supposed Cycadofilic types recently proposed by Professor Lester F. Ward,[1] this order will fall within the class Pteridospermæ,[2] and the phylum Pteridospermaphyta.

The discovery of Pteridospermic characters in *Aneimites*, in which they had not been suspected, throws serious suspicion on the sterile-frond genera, *Eremopteris*,[3] *Pseudopecopteris*, and *Triphyllopteris*, which appear to be most closely connected to *Aneimites* by the characters of their fronds, and whose fructification is wholly unrecognized.

The habitual association of *Wardia* with the foliage of *Aneimites* (*Adiantites*) at a number of localities suggests that the seeds from Altendorf figured by Stur[4] as *Rhabdocarpus conchæformis* Goepp., which resembles *Wardia* in many respects, may possibly be the fruit of one of the species, also from Altendorf, described and figured by the same author as *Adiantites antiquus* and *A. Machaneki*.

[1] *Science*, n. s., vol. xx, Aug. 26, 1904, p. 279.

[2] Oliver and Scott, *Proc. Roy. Soc.*, vol. lxxiii, 1904, p. 4.

[3] Compare *Eremopteris Cheathami* lx.

[4] *Culm-Flora*, pt. i, pl. xvii, f. 8, 9, p. 81.