Observations on the Vascular System of the Female 'Flowers' of Coniferae¹.

BY

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With Plate XXVII.
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THESE observations were made in order to determine whether a careful study of the course and structure of the vascular bundles would throw any light upon the vexed problem as to the nature of the female 'flower' in this order. While some interesting features have been brought out, but little new light, I have found, has been thrown on the question at issue as the result of these investigations. But this is only what might be anticipated, for the anatomy alone must necessarily be utterly inadequate to solve such a profound problem as the one before us².

ARAUCARIEAE.

Araucaria Cookii, R. Br.

A single bundle leaves the central cylinder of the axis of the cone, and runs obliquely upwards through a great many

¹ From the Jodrell Laboratory, Royal Gardens, Kew.

² A general discussion, from an historical point of view, of the question of floral morphology in Coniferae will be given in a forthcoming paper, together with full references to the literature.

internodes before entering the sporangium-bearing scale. About two-thirds of the way outward in the cortex this bundle divides into two; a small bundle branches off and, turning on itself, passes slightly upwards (Fig. 1) so as to lie just above its parent-bundle, and with reversed orientation of its parts (Fig. 2). (This, therefore, is different from what occurs, according to Strasburger¹ in *A. brasiliana*, A. Rich., and *A. excelsa*, R. Br., where the bundle does not divide until it enters the scale, but agrees with his observations of what takes place in *A. Cunninghamii*, Sw.). During this transition the two bundles appear occasionally so fused with one another that the structure resembles that of a concentric bundle. The smaller bundle has about three layers of secondary xylem and is about three rows of tracheides in width: the large lower bundle has about four layers of secondary wood and is about four rows in width. There is naturally some variation in the point of branching, this taking place lower down in some cases than in others.

Immediately after this vertical branching, the lower (larger) bundle divides in the horizontal plane into three, of which the two lateral pass off somewhat to the right and left of the median one (Fig. 3). As soon as the bundles have entered the base of the scale, the upper one gives off a branch on either side, each of which *passes across* and takes up a position between the median and a lateral bundle of the lower group, so that this latter now consists of five bundles (Figs. 4 & 5). But, in some cases, only one such bundle may be given off. In other cases one of the lateral bundles of the lower group may divide, and, at the same time, a branch from the upper bundle may be given off and join the branch so formed. The upper bundle divides again into two which remain side by side (Fig. 5), and the outside bundle on each side of the lower group divides into two, of which the outermost revolves on its axis and comes to lie, with inverted orientation, on the same side as the upper bundle, so that there are now four bundles on this side and about five on the

¹ Strasburger: Die Angiospermen und die Gymnospermen; 1879.

lower side¹. In the above cases, where the two branches from the upper bundle are *intercalated between* the bundles of the lower group, the upper bundle subsequently gives off a branch, first on one side, then on the other, each of which fuses with the respective lateral bundles of the lower group. The lower bract-bundle, both before it cuts off the small upper inverted bundle, and at any time during its subsequent division, may exhibit centripetal xylem in small quantity; but this tissue is, perhaps, most frequently absent. Centripetal xylem occurs both in dorsal and ventral bundles in the stalk of the scale, as also in the region of insertion of the sporangium; the tracheides of this tissue are sometimes quite short, but often considerably elongated, and with abrupt horizontal or slightly oblique terminal walls; they have very dense, fine spiral thickenings just like those of the centrifugal xylem.

The sporangium has become imbedded in the tissues of what I regard as the seminiferous scale, and has thereby lost a portion of its individuality. This has probably taken place when the formerly orthotropous sporangium seated on the dorsal side of the scale became completely inverted, owing to intercalary growth arising below it; this change occurring in order to facilitate fertilization. When this happened, a portion of the tissues of the scale probably enwrapped it at the same time, enclosing everything except the extreme tip of the integument in the micropylar region. The tissues of the integument thus became completely fused with those of the seminiferous scale, so that no sharp line of demarcation any longer existed between them². But the limit of the integument can easily be made out; the latter consists of two thick layers: an inner whitish, and an outer yellow tissue, formed of irregular, elongated, pointed cells, intermingled like the filaments of a fungus and containing elongated nuclei. This yellow layer is separated from the tissues of the

¹ A subsequent connexion may occur between one of the two median upper bundles and one of the intermediate bundles of the lower groups.

² According to my own view as to the nature of the seminiferous scale (see *infra*), this fusion is simply that between an inner and an outer integument.

seminiferous scale by a single layer of tangentially-elongated tannin-sacs. The tissue of the scale can be clearly seen extending as a *narrow* band round the *outer side* of the sporangium, and is perceived to be continuous with the inner portion of the scale (Fig. 6). The nucellus, throughout the greater part of its length, is quite separated from the integument and easily falls out; within it is the embryo-sac filled with clear and narrow-celled endosperm (Fig. 6). The nucellus is produced into a long black beak which protrudes beyond the integument and bends upwards externally to catch the pollen. It consists of contorted, elongated cells, like those of a stigma. Both bract and seminiferous scale are traversed throughout by great numbers of irregular stone-cells.

A double system of small bundles, belonging both to the bract and the seminiferous scale, occurs in the region of the insertion of the sporangium, running below and parallel to the long axis of the latter (Fig. 6). Both systems occur throughout the sporophyll up to a short distance beyond the insertion of the sporangium. At four points, viz., right and left of the sporangium both at its base and tip, some of the bundles of the seminiferous scale fuse together into a single large bundle, having two or three layers of xylem and very conspicuous phloem; at these points they may even assume a partially *concentric* structure, xylem and phloem occurring (as seen especially in one bundle) with inverted orientation, opposite the xylem of the large bundle. The reason for the increase in size of the bundles at these four points is not quite clear. These bundles lie slightly out of the row of small bundles of the seminiferous scale, for they are situated, two just above, and two just below, the insertion of the sporangium. Two or three of the bundles of the upper system, nearest the margin, perhaps die out. *Immediately opposite* the median portion of the sporangium there is a small blank space where no bundle occurs. The bundles of the seminiferous scale are, many of them, extremely small, some being quite rudimentary, with only an element or two of xylem. The bundles of the seminiferous scale appear to have a quite regular course from

its base until just below its free tip, without bending into the sporangium anywhere; indeed, I never saw any bundles within the sporangium nor showing any tendency to enter it. The fact that the nucellus forms a continuous tissue with the seminiferous scale may obviate the necessity for bundles being set apart to pass into the sporangium, for the tissues of the latter could be as well supplied by the bundles of the scale as are any of the ordinary tissues of the latter. The fact also that the function of supplying the sporangium is distributed throughout a number of small bundles instead of two or three, will account for the fact that these small bundles of the seminiferous scale are not specially differentiated from those of the bract; they have no unusual development of centrifugal xylem and phloem, and also frequently possess centripetal xylem. The large size of the bundles at the four points above-mentioned may be due to some mechanical function which they possess.

Thus, the course of the bundles in the seminiferous scale of this plant is somewhat different from that in *A. brasiliانا*, A. Rich., as described by Van Tieghem¹ and Strasburger², and agrees more with what occurs, according to the latter author, in *A. excelsa*, R. Br. Van Tieghem is evidently in error in supposing that the sporangium has become reflexed on to the *ventral* side of the seminiferous scale, for the bundles of the latter, at least in *A. Cookii*, R. Br., run through the whole length of the organ *between the sporangium and the bract*, this fact proving beyond doubt that the sporangium is still situated on the *dorsal* side of the seminiferous scale, although slightly imbedded in the tissue of the latter. In this species there is also no sign, as above stated, of any bundles entering the sporangium, as described by Van Tieghem for *A. brasiliانا*, A. Rich.

Above the insertion of the sporangium the two large bundles at either side of the latter again divide up into a number of smaller ones, which pass further across towards

¹ Ann. d. Sc. Nat., Bot., v^e sér., tome x, 1869.

² Angiospermen und Gymnospermen, p. 92, 1879.

the dorsal side of the seminiferous scale, and lie at equal distances apart. Somewhat higher up they die out, after gradually dwindling in size, and no bundles enter the short, narrow, free tip of the seminiferous scale.

In the lamina of the *bract* there are a number of small, parallel bundles, slightly curved into an arc. Each has two or three layers of centrifugal xylem, and a large and well-developed *centripetal xylem*, consisting, as seen in transverse section, of several large angular tracheides, of which the outermost are almost or quite as large as the whole of the centrifugal xylem. Many of those on the ventral side have numerous *very small* bordered pits on their transverse walls. Transfusion-tissue occurs at the sides of the bundle, but most of the tracheides are in the ventral position. In longitudinal section the centripetal xylem consists, on the inner side, of considerably elongated tracheides which are rather broad and have very fine reticulations, amongst which small pits with narrow borders and wide openings are scattered. Further out, the tracheides become shorter and wider and lose the reticulate thickenings, retaining only the small bordered pits. The tracheides resemble those in the leaf and seminiferous scale of *A. Bidwillii*, Hook.

Araucaria Bidwillii, Hook.

In this plant the bundles of the bract and seminiferous scale *arise quite independently from the central cylinder* of the cone-axis, and at a wide vertical distance apart. Each of these bundles is a compound structure, being formed respectively of two bundles branching off from two distinct strands of the cylinder. This is well seen in tangential section of the cone. The subsequent division of the two bundles in the outer cortex appears to be the same as obtains in *A. Cookii*, R. Br. Sometimes, however, one or the other bundle appears to arise from a single strand of the cylinder.

As in *A. Cookii*, R. Br., an oval ring of bundles enters the appendage from the axis. Of these, many of those belonging

to the seminiferous scale have an *inverted collateral* or a *concentric* structure, and this structure persists right through the organ from base to tip. Many of the bundles possess a concentric structure, in which the primary phloem occupies the centre, and xylem occurs in the form of two arcs on either side, or even extends right round the phloem (Fig. 7). Often, no xylem, but phloem only, occurs on the dorsal side of the scale: often, all the xylem of the bundle is on the dorsal inverted portion and there is none on the ventral side; the phloem is on this side also sometimes absent. The dorsal portion appears to be primary, as in some bundles very small tracheides were seen situated *between* two radial rows of phloem; some parts of the xylem are, doubtless, purely secondary, the primary portion having very likely become obsolete. Some of the *concentric dorsal structures* have the xylem in the centre entirely surrounded by phloem.

Throughout the whole length of the seminiferous scale, small bundles, exhibiting the above-named structure in varying forms, occur between the sporangium and the bract, as in *A. Cookii*, R. Br.

At each end of the vascular ellipse, in the lower part of the appendage, a large bundle occupies a lateral position, thus connecting the two systems of bundles, those of the bract and those of the seminiferous scale. In one part of their course some of the bundles of the bract assume a lateral position, one or two even becoming semi-concentric (in structure like those of the seminiferous scale), but this is exceptional. The bundles of the seminiferous scale pursue a continuous course from its base, past the insertion of the sporangium, up into the free laminar portion, with the exception of the four or five small bundles situated between the sporangium and the bract, which completely die out. All this is very similar to what obtains in *A. Cookii*, R. Br., although in the present species rather more easy of observation.

In the present case also no bundles were seen to turn off and enter the sporangium. But in radial section *two strands* of phloem-like tissue were seen penetrating the basal (chalazal)

part of the sporangium, but not extending as far as the nucellus; these strands were in both cases quite unaccompanied by tracheides, although a tracheide or two was observed on the edge of the tissue of the scale as if about to enter the sporangium.

In radial section it is distinctly seen how the integument has become fused with the tissues of the seminiferous scale; but on its inner side at the micropyle it is free for a very short distance. On its outer side the narrow strip of tissue pertaining to the scale appears to be continuous with the integument to the tip.

The tracheides of all the bundles have spiral thickenings, those of the secondary elements being very close and dense; the elements are extremely narrow and elongated.

Branched sclerides, as in *A. Cookii*, R. Br., are abundant everywhere, except in the tissue surrounding the sporangium, which is devoid both of these and of tannin-sacs, but the latter occur in the outer narrow portion of the scale.

In the *free* laminar portion of the seminiferous scale the bundles almost entirely lose their concentric structure, although some are curved towards their dorsal side. In some of these bundles a small quantity of centripetal xylem occurs, which here and there is fairly well developed (Fig. 8).

Holding the theory of the *axillary bud* as the explanation of the structure of the appendage of the cone in *Araucaria*, I believe, with Celakovsky, that the 'ligule' represents the seminiferous scale which is itself the vegetatively-developed outer integument of a sporangium situated *in the anterior position* on an axillary bud. This outer integument has become almost completely fused with the subtending bract in *Araucaria*, completely so in *Agathis*. The seminiferous scale has thus in this section almost entirely lost its individuality. Is there any evidence in the structure of the vascular bundle-system for the original separation of the ventral scale or ligule as a distinct organ? In *A. brasiliiana*, A. Rich., *A. excelsa*, R. Br., *A. Cunninghami*, Sw., and *A. Cookii*, R. Br.,

there appears to be no sufficient evidence for such a former state of things, the bundle-system in these plants arising as a single unit from the central cylinder of the axis, and seemingly supplying a single appendicular organ. In *A. Bidwillii*, Hook., however, there is undoubted evidence forthcoming, for in this plant, as we have seen, there are two distinct sets of vascular strands arising at separated points in the central cylinder of the axis, one of which exhibits inverted orientation of its parts. This, assuredly, would not be likely to happen if the appendicular organ which they supply represented a single scale. Any anatomist would say that the uppermost of these two systems of bundles belonged to some organ axillary to the bract which the lower bundle-system supplied. This I hold to be the case, the axis of the axillary bud being suppressed, and the latter reduced to a single leaflet, representing the vegetative outer integument of the sporangium, the cylinder of bundles which originally supplied this now obsolete axis has also become reduced to an arc of bundles such as commonly constitutes the bundle-system of a leaf. And Van Tieghem is thus far right in the views he put forward. In *all* species of *Araucaria*, however, the two bundle-systems become, either in the cortex of the axis or subsequently in the stalk of the appendage, more or less intermixed, as we have seen. In the majority of species the two systems appear to exist as a unit at *their first origin from the central cylinder*. This state of things seems to indicate an adaptive modification of the structure of long standing.

As regards the structure of the ventral portion of the appendage, the occurrence of *concentric* bundles seems to show that *Araucaria* is an ancient type of plant, and approaches the Cycads in this respect, for in the sporophylls of these latter concentric bundles are very frequent. The structure of the bundles in the free ligular portion of the appendage clearly proves that this organ is of *foliar* nature, and refutes the opinion of Strasburger that it represents the terminal portion of the axillary *axial* organ.

ABIETINEAE.

Pinus sylvestris, L.

In the female cone of this plant, four bundles leave the central cylinder of the axis of the cone: a lower one with normal orientation, an upper one with inverted orientation (which arises by fusion of two bundles springing right and left from distinct strands of the cylinder), and two lateral ones orientated sideways (Fig. 9). These all pass through the cortex and enter the base of the appendage, *without undergoing further division or alteration in position*. The lower bundle enters the small bract which is adnate for a short distance to the much larger seminiferous scale. The three other bundles enter the latter, the two lateral moving up so as to form a single row with the upper bundle (Fig. 10); by subsequent division a considerable number of bundles is formed. The plant differs from *Araucaria* in the fact that four bundles, instead of two, leave the cylinder of the axis, the bundles which supply the seminiferous scale and bract respectively *thus arising independently from the cylinder of the axis*, and no connexions occurring between the two systems during their course through the cortex. But in *Araucaria Bidwillii*, Hook., as we have seen, the two systems also arise independently from the central cylinder of the axis, and they appear to preserve their independence during their subsequent course far more than is the case in *A. Cookii*, R. Br.; *A. Bidwillii*, Hook., however, would appear to be an exception to the general rule prevailing in that genus. The direct explanation of the structure in *Pinus sylvestris*, L., lies in the fact of the more complete separation of the bract and seminiferous scale than is the case in *Araucaria*, the almost complete fusion in the latter of the two foliar organs having occasioned a similar fusion between the two otherwise distinct vascular systems, and the latter fact not necessarily implying that the appendage in *Araucaria* is really a single organ.

A single bundle with normal orientation, leaves the cylinder

of the axis, in the basal part of the cone, to supply the *sterile* seminiferous scale. It is much larger than the lower bundle of the four which supplies the bract of the fertile scale. On entering, or immediately before entering, the common stalk of the two organs, this bundle divides into two, of which the upper bundle supplies the sterile seminiferous scale, and subsequently divides up into several bundles. It will be seen that here a complete fusion of the two bundle-systems prevails, offering a wide difference from what obtains in the fertile part of the cone. But this is probably due to the loss of individuality of the system belonging to the seminiferous scale arising from the complete loss of function of the latter; hence the more economical plan for the plant would be to unite, as far as possible, the two systems into one. Except at the base of the cone, the tracheides of the cylinder have dense, fine, spiral thickenings; this is an interesting fact, as this character is otherwise only met with, as a general one, in vegetative organs, in the *older* types, like the *Taxineae*.

In the lamina of the seminiferous scale of *P. excelsa*, Wall., many of the bundles exhibit a partially concentric structure, such as is frequently found in ovular *integuments* (Fig. 11).

PODOCARPEAE.

Microcachrys tetragona, Hook.

This plant, belonging to the Podocarpeae, possesses beautiful rosy-red sporangium-bearing appendages, which are extremely succulent in character and terete in shape. Each fructification resembles in appearance a small mulberry.

Celakovsky's view, which appears to me the most tenable of all, of the structure of the female 'flower' of the Podocarpeae is this: that the sporangium is the sole representative, as in all Conifers, of the sporophyll or carpel pertaining to a completely suppressed axillary bud; that this sporangium has become carried up, for a longer or shorter distance, on to the subtending bract; and that the outer integument is

present in a normal form and not, as in the *Abietineae*, vegetatively developed into the seminiferous scale. There is nothing in the following anatomical investigation to render this view anything but quite probably true.

The sporangium is seated near the tip of the appendage, and is inverted. The other integument, or aril, is represented by a small, scale-like outgrowth occurring on the upper, distal side only of the sporangium (Fig. 12).

The axis of the cone contains several small, widely separated bundles.

In the upper part of the appendage, at the level of the insertion of the sporangium, and where the red colour is most conspicuous, there are about two layers of cells, lying below the sclerotic hypoderm, which are palisade-like in form, containing a great number of oil-globules of very varying sizes, some of which are very amorphous in shape; these are coloured red by alkannin, and dissolved by potash. Many of these cells are yellow in colour from the tannin they contain, which substance appears to stain deeply with safranin. The epidermis possesses a fairly thick cuticle. In the rest of the organ the cells are uniform throughout in shape and contents. Immediately surrounding the bundle the cells are very much smaller.

As regards the vascular structure of the appendage, there are, in spite of the assertions of Eichler and others, two distinct systems of bundles, one pertaining to the sporangium, the other to the appendage or bract. But the former is extremely minute and rudimentary. At the junction of the bract-bundle with the cylinder of the axis the small bundle pertaining to the sporangium is only represented by a few scarcely visible, non-staining, narrow tracheides with loose spiral thickenings, following the course of the bract-bundle, and either separated by a short space from, or closely approximated to, its protoxylem. While the connexion between the bract-bundle and the cylinder is very often perfectly distinct, the same was never actually observed in the case of the small bundle of the sporangium. In one case the

latter bundle was perceived in the near neighbourhood of a bundle of the cylinder and evidently situated just at the side of the latter, as the two were observed in different foci. In a transverse section of the very base of the appendage, where it is quite free from the axis, the bract-bundle (which itself is exceedingly small compared with the entire size of the appendage) and the bundle of the sporangium are both distinguished, the latter with *inverted orientation* and closely approximated to the former. This sporangium-bundle consists of a small group of *well-staining* tracheides with, possibly, rudimentary protoxylem; its phloem is absent or extremely rudimentary (Fig. 13). The bract-bundle is normal in its parts. At a higher level, the smaller sporangium-bundle increases in size and possesses a small, rudimentary phloem-group. During their upward course the two bundles are here and there mutually connected by means of some primary centrifugal tracheides which pass round the protoxylem and unite between the two bundles.

The sporangium-bundle appears, in fact, to be undergoing gradual obliteration, as shown by its appearance at the base of the appendage and in the axis. Thus, although this bundle is continuous into the sporangium, the bract-bundle in all probability performs the greater part of the conduction: hence arises the need for union of the two at various points. At the level where the smaller bundle deserts the bract-bundle to pass into the sporangium, the phloem of the former consists of but three or four insignificant cells (Fig. 14).

In the upper part of the bract, in the region of the palisade-tissue, there is a large and very broad mucilage-sac extending along the dorsal side of the bundle, and of about twice the radial width of the latter (Fig. 12). On the ventral side, between the tips of the bract and the outer integument of the sporangium, occurs a curious hump-like projection, giving a peculiar shape to the bract as seen in radial section. The laminar portion of the bract, above the insertion of the sporangium, is extremely short and rudimentary.

The bract-bundle, as far as the insertion of the sporangium,

is of the normal endarch type, with (relatively to its size) well-developed xylem and phloem, and no transfusion-tissue. In the lamina it becomes excessively reduced and insignificant, acquiring there at the same time well-marked transfusion-tissue of (usually) shortly elongated tracheides, rather unequal in size. Throughout its course the transfusion-tissue is entirely lateral in position, like that in the leaf of *Podocarpus*; in transverse section the elements are small and compactly grouped.

TAXEAE.

Taxus baccata, L.

In this plant I was unable to perceive the slightest anatomical evidence for Van Tieghem's view, that the sporangium represents the first leaf of a tertiary axis. On the contrary, Celakovsky's idea that the sporangium is *terminal* to the secondary axis bearing the bract, appears by far the most probable theory, and well supported by every character of the organs, as well as by the course of the bundles. The anatomy of the bundles of the *sterile bracts* below the sporangium is very interesting on account of the presence of well-developed *centripetal xylem*, a tissue which is (quite naturally) scarce in the bundles of the foliage-leaves (Fig. 15).

TAXODINEAE.

Sciadopitys verticillata, Sieb. & Zucc.

The sporangiferous scale of this plant consists, as in Cupressineae, of the bract and seminiferous scale very intimately united, but towards the apex the two parts are quite distinct, the latter organ extending some distance beyond the former. It is thick and fleshy and bears a great number of sporangia overlapping one another at its base, and on the upper (dorsal) surface (Fig. 16). About three bundles leave the central cylinder of the axis, two of which belong to

the seminiferous scale, and one to the bract ; the former have inverted orientation (Fig. 17).

On entering the seminiferous scale the two bundles branch up into a number, and spread right across the whole width of the scale (Figs. 20, 21). Branches from these bundles bend back, about two-thirds of the way up the scale, towards the place of insertion of the sporangia, but none were observed to enter these latter (Fig. 16). These bundles which supply the sporangia have a peculiar structure. They are all more or less *concentric*, most of them being incompletely so (Fig. 20) ; often several small ones are grouped together in an irregular fashion. The bundles which do not supply the sporangia are normally collateral, but some are of horse-shoe form. All possess a fair amount of *centripetal xylem*, consisting of similar tracheides to those of the abundant transfusion-tissue, viz. of angular contour and large size.

The bundle which enters the bract also branches. The larger of these bundles have *centripetal xylem* ; many rudimentary strands, consisting of xylem only, are irregularly scattered about, many of them contiguous to the mucilage-canals.

Cryptomeria japonica, D. Don.

The female cones of this plant are rounded in shape and present appendages which are clearly divided into dorsal and ventral portions, the latter, as in *Sciadopitys*, being somewhat longer than the former, and representing the 'seminiferous scale' ; it bears two elongated sporangia at its base.

Two or three bundles are given off from the central cylinder of the axis. Simultaneously one of the bundles gives off a branch, which, passing to the upper side, becomes, with its inverted orientation, the bundle of the seminiferous scale. The other bundle (when two only arise from the cylinder) branches almost at the same time, so that, eventually, four bundles enter the appendage grouped together as a small cylinder.

After entering the appendage, the two lateral bundles

divide each into two, and then into three, one or two passing towards the ventral side of the appendage so as to lie in the same plane with the bundle of the seminiferous scale, which has by this time divided into two. A very interesting fact to notice is that in the upper part of the seminiferous scale the bundles assume more or less of a *concentric* structure, and in the lower part of the appendage a concentric bundle appeared to arise quite independently of the other bundles, and ended blindly without fusing with those adjoining it; this is of great interest, as similar concentric bundles, of independent origin and course, are found in the sporophylls of the Cycads. The bract or dorsal portion of the scale eventually possesses a system of three bundles, of which two exhibit transfusion-tissue and a little centripetal xylem, while the other is completely *concentric* in structure. The only difference between this plant and *Sciadopitys*, as regards the character of the bundle-system in the scale, lies in the fact that in the former the bundles of the appendage are chiefly formed by branching of the laterally-placed bundles, in the latter of the ventrally-placed ones.

CUPRESSINEAE.

Cupressus Lawsoniana, Andr. Murr.

The bract and seminiferous scale are in this group so completely fused together that it is not easy to imagine each scale as in reality consisting of two, of which the tips only are free, that of the bract being reflexed (Fig. 21).

Three bundles leave the central cylinder of the axis; a median anterior one, and two from the lateral region of the cylinder and at a rather higher level than the first; the median bundle supplies the bract (Fig. 22).

Immediately on entering the double scale, one of the two lateral bundles (the orientation of which is at right angles to that of the bract-bundle) gives off a small branch which passes to the ventral side, assuming at the same time an

orientation the reverse of that of the bract-bundle (Figs. 23 and 24). This bundle then branches further (Fig. 25).

The two lateral bundles give off a number of branches which eventually spread round the whole contour of the double scale, the original median bundle of the three which left the cylinder of the axis remaining right in the centre of the scale (Figs. 25 and 26). Strasburger¹ suggests from this that the tissues of the seminiferous scale completely enwrap those of the bract.

There are thus a number of bundles both in the bract and the seminiferous scale. The structure of all appears to be endarch. No bundles were observed to enter the sporangia. A bundle or two also passes down into the lower reflexed lobe of the bract.

CONCLUSIONS.

Although, as was a foregone conclusion, the study of the anatomical characters of the female organs of Coniferae has failed to solve the problem of the real nature and morphology of these organs, it has, nevertheless, not been without its value, both as a means of here and there opening the way for plausible suggestions for the solution of the problem, and also as throwing some light upon the phylogenetic relationships of the order as a whole.

In *Araucaria Cookii*, R. Br., and *A. Bidwillii*, Hook., the very distinct presence in the sporangiferous appendage of the cone, of a double system of bundles, each system being independent of the other almost (or quite) from the central cylinder of the axis outward, the upper system, moreover, having its bundles orientated the reverse way to those of the lower, suggest strongly, that the appendage consists, not of one, but of two foliar organs, corresponding to the bract and the seminiferous scale in the Abietineae, which are only adnate at the very base, and whose bundles originate as

¹ Angiospermen und Gymnospermen, p. 83.

distinct systems from the central cylinder of the axis. If the ligule-like outgrowth of *Araucaria* were merely a ligule or an emergence, we should expect to find the bundles which supply it, branching off from those of the underlying organ somewhere near the insertion of the ligule, which, as we have seen, is very far from being the case.

In the Podocarpeae, again, it is supposed by many that we have to do with a single axial appendage bearing a sporangium on its upper surface. But, as I have clearly shown in *Microcachrys*, there are, as in *Araucaria*, two quite distinct systems of bundles in the appendage, with mutually inverted orientation of their parts, and which arise independently from the cylinder of the axis. Here then it appears also highly probable that we have to deal with two foliar organs, and not merely with a single one.

It is the same in this respect with *Sciadopitys*, *Cryptomeria*, and *Cupressus*. The axial appendage bearing the sporangia most clearly contains two perfectly distinct systems of bundles which arise as such from the cylinder of the axis, and have mutually inverse orientation of their parts. The two organs in the Cupressineae are so intimately fused together, being separable only at their tips, and even then in an obscure sort of way, that there is as much temptation as in the case of the Araucarieae to regard them as constituting but a single organ.

In the Taxodineae, to which we may regard *Sciadopitys* as also belonging, the compound nature of the appendage is more obvious than in the last-mentioned order, there being usually a distinct difference in size between the two organs composing it.

The Abietineae exhibit by far the best illustration of the compound nature of the axial appendage of the female cone, for in this group the two foliar organs composing it are distinct and separable except at the very base, where they are adnate to one another. The bundle-systems which supply each arise, as in the preceding case, independently from the cylinder of the axis. The whole course and

structure of the bundles of the appendages is similar to that of the bundles in the other groups.

The Taxeae differ from the other groups in the fact that the sporangia occur in a position *terminal* instead of lateral to the axis on which they are borne. The anatomy points clearly to the fact that no axial foliar appendage of any kind exists upon which the sporangia are inserted, the cylinder of the axis being directly continuous into the base of the sporangium. This latter difference, however, amounts to very little if we regard, with Celakovsky, the seminiferous scale of the other groups, as being the morphological equivalent of the outer integument of the Taxeae, which has become, with the exception of the Podocarpeae, vegetatively developed. In the Podocarpeae the relationship is precisely the same as in the Taxeae, with the exception of the axillary, instead of the terminal position of the sporangium. In this order the bundle-system belonging to the sporangium (which is, *in all the groups*, the sole representative of the sporophyll, according to the view I here adopt) becomes obvious owing to the fact that the latter gets carried, by the basal intercalary growth, on to the upper part of the bract. In the four other groups the bundle-system pertaining to the sporangia becomes very apparent owing to the vegetative development of their outer integuments which, in the form of the widely-expanded seminiferous scale, possesses a pronounced vascular tissue.

Hence, a study of the course of the vascular bundles in the female 'flowers' of this order tends towards a unification of the apparently, and from a superficial view, diverse structures which we find them exhibiting, and, although taken by itself, it will not explain their morphological significance, it will, nevertheless, greatly aid us towards some comprehension, if only a partial one, of the composition of these curious structures.

An examination into the structure of the individual bundles traversing the appendages of the cone or 'flower' affords us, as it seems to me, some clue as to the wider relationships of the plants concerned.

The bundles of the 'bract' or lowermost of the two

appendages in all the groups are in structure, as a rule, similar to those of the foliage-leaves. Sometimes they exhibit characters rather more ancient than obtain in the latter. A notable instance of this occurs in the bundles of the *sterile bracts* or *sporophylls* of the rudimentary cone of *Taxus*, where, contrary to what we know to be the case in the foliage-leaves, a large amount of *centripetal xylem* is found.

That ancestral characters should turn up in preponderating measure in those organs which are intimately associated with the most primitive parts of a plant, viz., the reproductive organs, is what one would naturally expect. Hence the mesarch structure of the bundles of the sterile bracts or sporophylls of *Taxus*. But the most ancient characters would surely be expected to be found in the actual reproductive organs themselves. In my recent paper on the sporophylls of Cycads¹ I made a special point of remarking and figuring the *concentric* structure (which I regard as *ancestral*) of many of the bundles which directly supply the megasporangia in most of the genera. While in the other parts of the sporophyll the bundles were nearly always of the collateral type of structure, *in every case* some of those which were sectioned immediately below the insertion of the sporangium², and some of those (and this is the most important point) in the *integument* of the sporangium, exhibited in unequivocal form a more or less complete *concentric* type of structure. Now, as has been described in the foregoing pages, bundles exhibiting a *concentric* type of structure occur in the seminiferous scale (the vegetatively-developed *outer integument*, according to Celakovsky's view) of *Araucaria*, *Pinus*, and *Sciadopitys*. No doubt, if further investigations had been made, they would have been found in the other genera also. The bundles exhibiting this structure are usually those in closest connexion with the sporangium, the others exhibit the ordinary collateral structure.

¹ Worsdell: 'The Vascular Structure of the Sporophylls of the Cycadaceae;' Ann. Bot. Vol. XII, 1898.

² loc. cit., Figs. 4 and 20.

The importance of this concentric structure of the bundles in the outer integument (seminiferous scale) of the megasporangium of Coniferae, as also of the mesarch structure of the bundles in their cotyledons and foliage-leaves (which I regard as a half-way stage from concentric towards endarch structure), lies in the fact of its pointing to the primitive stock of Fern-like plants, organisms to which this concentric or stelic structure of the vascular tissues is peculiar, as the source and origin of the great order of Coniferae, just as it is now all but universally admitted to be, of the allied order, Cycadaceae.

EXPLANATION OF FIGURES IN PLATE XXVII.

Illustrating Mr. Worsdell's paper on the 'flowers' of Coniferae.

The following are the abbreviations used in the lettering of the figures:—*int.*, integument; *nc.*, nucellus; *b. b.*, bundles of bract; *b. s. s.*, bundles of seminiferous scale; *s. s.*, seminiferous scale; *x.*, xylem; *ph.*, phloem; *px.*, protoxylem; *x¹.*, centripetal xylem; *x².*, centrifugal xylem; *s.*, sclereide; *b. o.*, bundle of the ovule; *b.*, bract; *o. int.*, outer integument; *ov.*, ovule; *ax.*, axis.

Figs. 1-5. *Araucaria Cookii*. Successive stages in the orientation and branching of the bundle-system from the central cylinder of the axis outward to the appendage. Diagrammatic.

Fig. 6. *Araucaria Cookii*. Diagrammatic transverse section of the appendage at the level of the sporangium, showing the two distinct bundle-systems of the bract and the seminiferous scale.

Fig. 7. *Araucaria Bidwillii*. Transverse section of a concentric bundle of the seminiferous scale. $\times 220$.

Fig. 8. *Araucaria Bidwillii*. Transverse section of a bundle in the free ligule-like portion of the seminiferous scale. $\times 285$.

Fig. 9. *Pinus sylvestris*. The four bundles leaving the central cylinder of the axis. Diagrammatic.

Fig. 10. *Pinus sylvestris*. The four bundles entering the appendage. Diagrammatic.

Fig. 11. *Pinus excelsa*. Transverse section of a bundle in the expanded laminar portion of the seminiferous scale. $\times 220$.

Fig. 12. *Microcachrys tetragona*. Radial section of the appendage of the cone, showing the insertion of the sporangium and the bundle-system. $\times 35$.

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Fig. 13. *Microcachrys tetragona*. Transverse section of the bundle-system at the base of the appendage. $\times 430$.

Fig. 14. *Microcachrys tetragona*. Transverse section of the bundle-system of the appendage at the level of insertion of the sporangium. $\times 430$.

Fig. 15. *Taxus baccata*. Transverse section of a bundle in a sterile sporophyll of the rudimentary cone. $\times 220$.

Fig. 16. *Sciadopitys verticillata*. Radial section of the appendage showing insertion of the sporangia and the bundle system. Diagrammatic.

Figs. 17, 18 and 19. *Sciadopitys verticillata*. Successive stages in the orientation and branching of the bundle-system from the central cylinder of the axis outward into the appendage. Diagrammatic.

Fig. 20. *Sciadopitys verticillata*. Transverse section of a partially concentric bundle in the seminiferous scale. $\times 430$.

Fig. 21. *Cupressus Lawsoniana*. Radial section of the appendage showing the insertion of the sporangia and the bundle-system. Diagrammatic. $\times 15$.

Figs. 22-26. *Cupressus Lawsoniana*. Successive stages in the orientation and branching of the bundle-system from the central cylinder of the axis outward into the expanded peltate portion of the appendage. Diagrammatic.

W. C. W. del.

Worsdell, Wilson Crosfield. 1899. "Observations on the vascular system of the female 'flowers' of Coniferae." *Annals of botany* 13, 527–548.

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