The Structure of the Female 'Flower' in Coniferae.

An Historical Study.

BY

W. C. WORSDELL, F.L.S.

With seven Figures in the Text.

INTRODUCTION.

THERE are few structures in plants which, to the ordinary observer, appear at first sight more simple or more easily understood than the female reproductive parts of the great order Coniferae. Yet the problem of the true morphology and structure of these organs has taxed the mental and observational resources of expert investigators for a longer period of time than, and to as great a degree as, any other botanical question of a similar nature. And still, at the present time, the nature of these organs, for the majority of botanists at any rate, remains the unsolved problem that it was at the very beginning of the century.

It is highly instructive to the modern morphological student to cast a retrospective look at the various views on the question which, for more than a century and a half, have from time to time been put forward by the botanists of France, Germany, Denmark, Sweden, Austria, Italy, America, and this country.

[Annals of Botany, Vol. XIV, No. LIII. March, 1900.]

In the following pages I shall only consider the most important and striking of the many views advanced by those authors who have expressed them in the most elaborate and authoritative manner. At the end, however, will be found a bibliography of the subject as complete as I have been able to compile, which, in any case, will be amply sufficient to afford information regarding the history of the whole subject.

The *male* reproductive organs of Coniferae are comparatively simple in structure and morphology, strangely unlike, in these respects, those of the opposite sex. But a comparison between the two cannot be instituted until some attempt has been made to unravel the structure and morphology of the female 'flowers.'

These organs are, in different genera, greatly dissimilar as regards their superficial aspect, a fact which renders all the more obscure their real nature and relationships. We have only to think of the female parts of the Pine, Cypress, Juniper, and Yew, in order to become impressed with this fact. As the various genera of the order Coniferae are manifestly more intimately allied the one to the other than any one of them is either to the Gnetaceae or the Cycads, it is obvious that it would be useless to investigate the structure and morphological nature of any one of these genera independently of all the rest; they must, on the contrary, be all considered, in this respect, interdependently, by direct comparative study of their respective parts, if we are to arrive at any worthy conclusion as to their real significance. The nature of the cone of an *Abies* cannot be considered along these lines apart from the 'berry' of a Yew or a Juniper, for parts which are obscure in their meaning in the one form are often rendered intelligible by their more easily explicable counterpart in the other, with regard to the relative positions of parts or organs, their mode of development, &c. For a full attempt at a solution of the problem it would also be requisite to institute a comparison of the Coniferae, both individually and as a whole, with the allied

orders of Gnetaceae and Cycadaceae, as also with the most nearly related fossil plants.

In the Abietineae the female organs are arranged in elongated cones, very compact and woody in character when mature. Their bulk is largely made up by large, woody scales, usually

Fig. 1. Diagram of normal 'flower' of Abietineae.
b = bract; *ss* = seminiferous scale; *sp* = sporangia;
ax¹ = primary axis of cone.

thickened and enlarged externally and known as the 'seminiferous scales,' each bearing on its upper surface at the base two inverted sporangia. The seminiferous scale is in the axil of a very much smaller bract, with which it is usually fused at the very base (Fig. 1).

In the Araucarieae there is but a single scale representing the bract, with (in *Araucaria*) an outgrowth resembling a ligule on its upper surface, and a single sporangium enclosed within

Fig. 2. Diagram of 'flower' of *Araucaria*.
b = bract; *l²* = ligule-like seminiferous scale; *sp* = sporangium. (After Eichler.)

the tissues of the scale, and situated some distance above

its base (Fig. 2). In *Agathis* there is no sign of any ligular outgrowth.

In the Cupressineae the scales are not arranged spirally in elongated cones but in whorls. Here also there is but a single woody scale, which has, however, two distinct apices or tips at its swollen anterior end. In *Juniperus* the scales composing each whorl become fleshy and fuse laterally to form a berry, so that the seeds become enclosed. Each scale in this genus has but one seed; in *Cupressus*, however, there may be very many to each scale.

In the Taxodieae the structure of the scale is the same as that in Cupressineae.

In Taxeae a single sporangium is borne at the end of a secondary axis furnished with three pairs of bracts. The sporangium is attached to no scale, but the seed or mature sporangium is enclosed by a fleshy, coloured aril.

In *Podocarpus* the anatropous ovule is fused with the bract and extends far beyond the latter, owing to its being carried up on a long stalk. It has two integuments, of which the outer is fleshy and coloured. In some species the bracts and axis are fused into a coloured, succulent whole.

The above are the principal types of structure to be met with in this order. I have simply described the structures according to their bare, superficial appearance; and will now proceed to reproduce the various views and ideas as to the significance and true interpretation of these structures.

At the outset I may state that the whole question and controversy turns on two main points: (1) the nature of the 'seminiferous scale'; and (2) that of the sporangial envelope; these two factors are intimately bound up with one another, and neither can be in any way ignored when treating of the other, if an attempt at any thorough elucidation of the problem is to be made.

HISTORICAL SKETCH.

As is naturally to be expected, the older botanists approached the question in what, to our modern notions, is

a very rough and ready manner. Their ideas about comparative morphology may often seem crude when placed in comparison with those of to-day, and as they judged primarily by outward appearances when classifying and comparing organs, it is small wonder if we find that those ideas misled them with regard to many points.

Long before the middle of the last century Linnaeus (3) had already attempted the solution of this botanical puzzle, which to-day is as much an enigmatic chaos for the majority of students as it was in his, the dawning age of botany. Linnaeus considered that the seminiferous scale of Abietineae represented a calyx; that there was no corolla; and that each ovule represented a pistil consisting of a very small ovary with simple style and stigma which became changed when ripe into a winged nut. In *Juniperus* he describes the three exterior scales of the berry as a calyx and the three interior as a corolla.

Jussieu (6), writing towards the close of the same century on the female organ of the Abietineae, mentions an outer scale bearing two pistils on its base and two glandular stigmas; and an inner scale, formed on ripening of the fruit, bearing two one-seeded, winged capsules. His deduction was that the bracts were styles from their caducous nature, and that the seminiferous scale was a bilocular ovary.

Mirbel (17, 18, 20), at the very beginning of the present century, thus describes the female organs of this order: 'The Pines, Spruces, Larches have female catkins whose flowers, hidden in cupules, are inverted so that the stigmas are directed towards the axis, and whose broad peduncles, inserted each at the base of a bract, become insensibly transformed into woody scales, covering the ripe fruits, and forming a cone or strobilus by their approximation.' Here, what the majority of botanists now call the 'integument' is for him a 'cupule,' our 'nucellus' is his 'flower,' and our 'seminiferous scale' is his 'peduncle.' Further: 'The Cypresses, the *Thuja*s, the Junipers, and *Schubertia* [*Taxodium*], have also a kind of catkin. Its axis is very short, its flowers erect, and enclosed

in cupules inserted immediately on bracts which become woody (*Cypress*, *Thuja*, *Schubertia*) or succulent (*Juniper*), and whose apices expand into a structure like a nail-head. These scales compose what some modern people call galbules.' But at a much later date (1843) he somewhat modifies this view, for he writes (of *Pinus*): 'These are assuredly the simplest flowers known; they consist of a conical nucellus contained in an open ovary.' And of *Thuja*: 'It consists simply of an ovary and a nucellus; but this flower is erect, whilst in the *Abietineae* it is inverted.'

L. C. Richard (24), in 1826, held very much the same view as Mirbel, for he says: 'In all Conifers the female flowers consist essentially of a pistil and a simple perianth or calyx.' In all Conifers, except *Taxus* and *Agathis*, he always recognizes the presence of a double scale. As regards the fruit, he writes: 'The ovary is semi-inferior, owing to its lower part being united with the calyx, which latter then necessarily takes part in the formation of the fruit to form the epicarp. The wall of the pericarp is always very thin, and so adherent to the integument of the seed that they seem to form a single membrane applied to the "amande." The fruit of Coniferae is a true caryopsis or a sort of nut, i. e. a unilocular, one-seeded, indehiscent fruit, whose pericarp is intimately fused with the integument of the seed.' In *Podocarpus* the calyx consists of an inner, bony, and an outer, fleshy portion. The aril of *Taxus* and *Phyllocladus* he describes as a special organ, an extraordinary development of the receptacle. Finally, he divides the order into two groups—the Podocarpeae, Taxeae, and *Ephedra*, possessing simple fruits; and the Cupressineae, Abietineae, and Araucarieae, possessing compound fruits. He compares the flowers of Coniferae with those of the Amentaceae.

The eminent English botanist, Robert Brown (25), emerges conspicuous from among the investigators of the first half of this century, as the first exponent¹ of the theory which now, seventy years after, is most favoured by botanists, viz. that

¹ But Ray, in 1682, held that the ovules were naked.

of *Gymnospermy*. In support of this idea, he compares the female organs of Coniferae with those of Cycads (which latter are for him evidently ovules), and with the ovules of other Phanerogamous plants. The proof lies chiefly in the resemblance between the body lying within the envelope and the nucellus of a typically-constructed ovule. The seminiferous scale is an *open carpel* bearing ovules at its base.

Schleiden (34, 36) is noted as the exponent of the view, first of all put forward in 1839, and later in his 'Grundzüge der wissenschaftlichen Botanik' in 1843, that a *placenta* is always an *axial* structure. He cites the Cupressineae and Taxineae as examples of orders with basilar ovules in which the placenta is the extremity of the axis, and the Abietineae as amongst those in which the placenta is an organ distinct from the carpellary leaves, arising later than the latter. 'In Abietineae the scale, considered by R. Brown as an open ovary, is only the axillary bud of the carpellary leaf, situated

Fig. 3. Diagram of an abnormal 'flower' of Abietinae; the seminiferous scale (ss) is split into the two first leaves of an axillary shoot; b = bract; l^2 = second pair of leaves; l^3 = third pair; ax^2 = axis of axillary bud; ax^1 = primary axis of cone.

beneath the scale, and for this latter reason only, it could not be a foliar organ, because *folium in axillâ folii* is a thing without example in the whole vegetable kingdom.'

Von Mohl (38) in 1845, in a paper dealing chiefly with the male organs of Coniferae, makes the interesting statement that in *Pinus*, &c., the bract of the female cone is greatly reduced and a leaf of a secondary axis replaces it. The same thing occurs in the vegetative shoot, where the foliage-leaf belongs to a secondary shoot and the subtending leaf is

reduced to a scale. He says also that in *Thuja*, *Cupressus*, *Juniperus*, the scales bearing the *ovules* are modified leaves of the *primary* axis, as there is no sign of any other bract, and in the vegetative shoot there is a gradual modification of the leaves from the seedling upwards.

Alexander Braun, the renowned German botanist, must take credit for being the first, viz. in 1853, to promulgate the view that the seminiferous scale consists of the two first leaves of a *bud axillary to the bract*, these leaves being fused by their margins (Fig. 3).

Baillon (54, 62), on three separate occasions, in important papers, advocates the ovarian theory of the ovule, making a determined stand against the opposite theory of Gymnospermy.

Fig. 4. Diagram of part of cone of Abietineae, showing the origin of the seminiferous scale (*ss*) in the axil of the bract (*b*); *ap* = apex of axis of cone. (After Ørsted.)

He bases the chief weight of his argument on the *development* of the organs concerned; he observes the seminiferous scale appearing as a papilla in the axil of the bract, just like the bud of an incipient branch (Fig. 4), and concludes therefrom that it must be of axial nature, forgetting the fact that structures may, even in their youngest stages, be already

congenitally modified, i. e. inheriting directly, without passing through the previous progressive stages, the adapted structure of the same organs in their parents. His firm conviction that the integument of the ovule is an ovarian wall is based chiefly on the fact that, in the earliest stage of development, that structure appears as two distinct papillae, which, as he thinks, must be the two carpels composing the ovary. But one fails to see exactly why this should be the interpretation, for there is variation in this respect among plants. Assuming the ovular envelope in the genus *Podocarpus* to be an ovary, we find that in one species, *P. chinensis*, Sw., it arises as a continuous ring, but in another species, *P. dactyloides*, A. Rich.,

as two papillae, so that there is just as much reason in this case for considering it an integument. The following are his main conclusions:—'The female flower is either terminal or placed in the axil of a bract or a leaf; but it is always borne by an axis and never by a bract. But the form of the axis is very variable, as is characteristic of receptacular organs. The flower, as Mirbel and Spach also thought, is not gymnospermous, but possesses an ovary of two carpels, without floral envelopes, containing an orthotropous and erect ovule on a basilar placenta. The cupule, of variable consistence and shape, surrounding this ovary, which in several genera has received the name of aril, is a late production, although it arises previous to fertilization, and is of the nature of a disk.'

Baillon will always be regarded as the champion of the developmental theory.

Caspary (53) maintained, with Braun, from the fact that he found buds in the axils of the bracts, having the two halves of the seminiferous scale as lateral appendages, that the seminiferous scale represented, in reality, the two first leaves of a vegetative bud, sometimes called 'the cotyledons of the branch' (Fig. 3), which were fused by their *anterior* or external margins. Of this view of the matter there will be more to say further on.

In 1864 the Italian botanist, Parlatore (60), gave a valuable and interesting contribution to our knowledge of the structure of the female organs in various genera. He considers the seminiferous scale to represent a shortened axis in the axil of the bract with fused and broadened leaves. The fact that it is often bifid, emarginate, notched, &c., proves its compound nature. The seminiferous scale represents the leaves of the axillary axis, which is limited to a single point at the base of the scale. In a cone of *Pinus Lemoniana* in the Chiswick Gardens, he observed the ordinary short shoots or brachyblasts, each with its two needles, springing from the axil of every alternate bract in place of the seminiferous scale. He upholds throughout the ovarian theory; the ovule being for

him always a 'flower.' In the Taxineae and Podocarpeae the 'aril' is composed, in the first case of one, in the second of two bracts of the axillary axis, which here become fleshy, and are homologues of the seminiferous scale.

In the same year (1864), Ørsted (61), a Danish botanist, produced a paper in which he describes and figures some highly interesting and instructive abnormal cones. He mentions three cases of cones, in the lower part of which the bracts had the form of foliage leaves, while higher up they assumed that of ordinary bracts, in the axil of each of which were several scales arranged as on a suppressed shoot, the two outermost of which were the largest and placed opposite each other. Still higher up, the bract gradually became reduced in size, as did the scales in number; but the outermost scales gradually increased in size, at the same time becoming connate by their margins, while rudimentary ovules appeared at the base on their dorsal side. At length the bract became reduced to its ordinary minute size, and the seminiferous scales fused into a single large broad structure, dentate or bifid at the apex. From these facts he draws the following conclusions:—

(1) 'The cone arises from the metamorphosis of a shoot, as the leafy bracts become changed into the bracts of the cone and the buds into seminiferous scales. (2) The seminiferous scales arise, like any other flower, by metamorphosis of a bud, but only two leaves of the flower are formed, viz. the two seminiferous scales which fuse together (Fig. 3). (3) That the seminiferous scales in Abietineae are open carpels with naked seeds is seen by the fact that this metamorphosis agrees entirely with misformed carpels in other plants (e.g. *Paeonia Moutan*). (4) That a leaf may represent a whole bud, and as such may be placed in the axil of another leaf' (Fig. 1). In the Larch, a malformation in just the opposite direction occurred, in which the cone was normal in structure at the base and proliferated at the top, and there resembling a vegetative shoot. The seminiferous scale was at the base at first quite normal, higher up becoming bifid; then split

into two distinct leaves; and finally representing two scales enclosing a small bud.

In *Picea alba* a cone had proliferated into a short vegetative shoot bearing a few leaves and a bud. There was an abrupt transition between this and the normal part of the cone below. The terminal bud eventually developed into a leafy branch.

From the study of the development of a cone of *Pinus montana* var. *Pumilio*, he draws the following conclusions:—
'(1) That the seminiferous scale arises in the axil of the bract just like a bud (Fig. 4), and can aptly be compared with a young bud and bract in *Bryonia dioica*, so that the development agrees with what was seen in the monstrosity. (2) The organs considered by R. Brown as ovules agree in their early origin and further development with the ovules of flowering plants in general. (3) The peculiar form of the seminiferous scale in the Pine cannot be properly understood without taking into account its growth, which extends over several years, and, after a period of rest, is once more renewed, this being connected with the slow process of fertilization.'

He then proceeds to describe the development of the cone-scale in Cupressineae and Taxodineae. At the end of the paper he draws the following general conclusions:—

'I. Both the normal development of the flowers and the various sports strengthen R. Brown's observation that the ovules are naked.

'II. The cone-scale in Abietineae is an open carpel, arising as a bud, and representing a flower. It consists (at least in *Picea* and *Larix*) of a fusion of two leaves, corresponding to the young scale-leaves of the ordinary bud. The notching at the apex of the scale is an indication of this fusion.

'III. The cone-scales in Cupressineae correspond to the bracts in Abietineae. They only rarely preserve their original form (in *Actinostrobus*); they usually undergo a transformation which does not result from a fusion of bract and carpel, but is the same change which occurs when a leaf becomes peltate. The cone-scale consists, therefore, of a single leaf.

Only in the Cupressineae verae is the scale completely peltate, in Actinostrobeae and Thuiopsidae it is incompletely so. The Cupressineae have no carpel, but the flower is represented by $12-\infty$ naked ovules, always at first attached to the axis of the cone in the axil of each scale, but which, later on, as seeds, become removed and carried up by the stalk of the scale, and in this way come to be situated on the latter.'

The name of Sachs (82), through his classical 'Lehrbuch,' first published in 1868, lends great weight to a view, then first enunciated, that the seminiferous scale in the Pineae (*Abies*, *Picea*, *Larix*, *Cedrus*, *Pinus*) is really a ventral out-growth of the subtending 'bract,' of *ligular* nature, such a structure, in fact, as we are familiar with in *Isoëtes* or *Selaginella*; so that there is in reality but one single scale instead of two, and the 'bract' is part and parcel of the carpel, bearing the ligular placenta, with inverted orientation of its vascular bundles. 'In the other Abietineae,' the seminiferous scales 'do not spring from the axils of leaves, but grow immediately out of the axis of the cone, and are therefore themselves leaves and of a carpellary nature.' This view will be further developed hereafter.

Van Tieghem (65), in the following year (1869), assumed a prominent and important rôle in the endeavour to solve the problem, by following a line of investigation different from all which had preceded him, viz. that of the evidence from the *anatomical structure*. As Baillon is the champion of the developmental method, in the same way must Van Tieghem be regarded as the champion of the anatomical method of research. His primary idea is that the seminiferous scale in all Coniferae represents the first and only leaf of an axillary branch, though he suggests the possibility of its being really two fused leaves. His view is based on the course and orientation of the vascular bundles. In the Abietineae he finds that the bundles of the bracts and seminiferous scale, as they respectively leave the central cylinder of the axis of the cone, are enclosed each in its own parenchymatous sheath, and thus represent independent

systems of bundles. The uppermost bundles divide up to form an arc with inverted orientation, i.e. with their xylem directed outwards and downwards; it is this arc which is the system belonging to the seminiferous scale, while the lower bundle, with normal orientation, belongs to the bract. One of the end-bundles of the arc sends off a strand on either side to the ovules. 'The arrangement of the bundles in an arc shows that the axillary organ is a leaf and not a branch; the outward orientation of this arc shows that this leaf is placed diametrically opposite the bract; its origin shows that this leaf belongs to the axillary branch of which it is the sole representative, i.e. of which it is the first and only appendage. The first leaf bears the ovules on its dorsal surface.

'In *Sequoia*, *Athrotaxis*, and probably also *Sciadopitys*, the foliar bundle and the upper bundles remain enclosed in the same parenchymatous sheath from the point of their insertion on the axis until near the apex, then the parenchyma separates, the two organs become isolated, and whilst the bract ends in a "languette," the first leaf of the bud continues its development, growing a short way beyond the bract. The scale is thus double.

'In the Cupressineae, *Taxodium* and *Cryptomeria*, the same structure obtains, except that the base of the seminiferous scale between the ovules and the axis is not elongated at all, and thus the ovules are situated at the very base of the scale.

'In Araucarieae, elongation only occurs below the insertion of the ovules. In these plants the scale is double, as in *Sequoia*, &c., the two sets of vascular strands being included in the same parenchymatous tissue until beyond the point of insertion of the ovules. In *Araucaria brasiliana* there are four bundles in the seminiferous scale, each set of two widely separated and orientated sideways with their xylem directed inwards; opposite the median portion of the ovule they turn outwards, and are often *concentric* in structure, with the phloem occupying the centre. In order to form the ovule, the seminiferous scale becomes reflexed towards the *ventral*

side, as is shown by the fact that its bundles enter the ovule *on the upper side* of the latter; this fact will also explain *the contact of the ovule with the bract and the parenchyma which surrounds it on its upper side*.

‘In *Dammara* the ovule has become reflexed towards the *dorsal side*.

‘Finally, it may happen that the upper bundles, instead of developing, as in the three preceding cases, sometimes both above and below the ovules, sometimes only above, or only below, are scarcely prolonged either above or below. Then the leaf is terminated by the ovule or ovules, which arise from the transformation of its entire lamina, and this leaf is sessile, or at least its petiole is exceedingly short; the ovule represents in itself the first leaf of the axillary branch almost entirely, in other words, the carpel, while retaining in its vascular system the origin, orientation, and structure proper to it, is reduced to its ovular portion,’ as in *Podocarpus*, where the first leaf of the branch is folded on its dorsal surface to form an anatropous ovule, and in *Phyllocladus* and *Pterosphaera*, and some species of *Dacrydium*, where the leaf having remained straight, produces an erect, orthotropous ovule. In these plants the ovular leaf is completely independent of the bract. In other species of *Dacrydium*, *Saxegothea*, and *Microcachrys*, the bundles of the bract and ovular leaf are contained within the same parenchymatous sheath, for a third or half of its length, as a result of which the ovule is only partially inverted. In the *Taxineae* *the two upper bundles*, which in the other groups supply the seminiferous scale, here divide up to form a circle or cylinder, and pass into *a developed axillary shoot of secondary order* bearing several bracts, some of which, or only one, bear in their axil a shoot of the third order, which either is only represented by its first leaf, or forms bracts, in the axil of some of which axillary shoots of the fourth order are developed. In *Cephalotaxus* the female bud (primary shoot) forms in the axil of a leaf a shoot of secondary order bearing three or four pairs of bracts, all of which are usually fertile. Each of these

receives its own bundle, and two upper bundles which become inverted, and pass each to one of the two ovules, which represent the bilobed first leaf of the axillary shoot. In *Taxus*, the female bud (primary shoot) forms in the axil of one of its leaves a secondary shoot bearing three pairs of bracts, of which the sixth is alone fertile. These bracts are arranged with a divergence of one-fourth or one-half, and are falsely decussate and arranged as if for the commencement of a two-fifths phyllotaxis. Two bundles leave the axis at the sixth and last bract, and both, becoming inversely orientated, enter the ovule, which represents the first leaf of an axillary shoot. The origin, orientation, and structure of its vascular system show that this is the true interpretation. The two opposite bundles of the wall of the ovule are *concentric*, the phloem occupying the centre.'

In *Torreya* the structure is the same, except that there are a greater number of fertile bracts, and that there is *one further stage of branching* than in *Taxus*.

In the same year Sperk (66) issued an important work on the subject of Gymnospermy. He found a hermaphrodite cone of *Larix* with male organs at the base and female at the top. He regards the ovules as ovaries. The seminiferous scale is of foliar nature. In *Cunninghamia*, sometimes the ovule, sometimes the seminiferous scale is formed first; in a proliferated cone the bract had three distinct leaves in its axil, which were the three seminiferous scales; between these latter and the bract was a long stalk thickened upwards, which perhaps represented a secondary axis. In *Taxus parvifolia* the outer ovular envelope is a continuation of the whorl of bracts below the ovule; the carpels are at first separate and distinct in a whorl, and later, by pressure of the bracts, become fused into a whole. In *T. baccata* the integument arises *from the axis*, and leaves a space between it and the nucellus. In *Cupressus lusitanica* the integuments were proliferated into leaves. In considering the case of *Cryptomeria japonica* he gives the following reasons why the inner scale cannot be a carpel:—'(1) In young cones the ovary

arises immediately in the axil of the bracts, as in other Cupressineae; later on small scale-like outgrowths appear between the ovaries and the bracts, which cannot be carpels as they appear later than the so-called ovules. (2) The ovaries are often not placed in the axils of these inner scales, but alternate with them, and are lateral. (3) The number of the ovaries is independent of the number of these scales; often more scales occur than ovaries, or vice versa. (4) In the anomalous development of the scale it may fuse with the ovary and increase the size of the latter. (5) In anomalous development of ovaries their foliar nature becomes apparent.'

He considers that abnormalities are of importance and follow a definite law.

In *Juniperus Hartwissiana* he finds certain objections to the carpellary theory of the bract. (1) There are an indefinite number of ovaries at the base of the bracts, three, five, or four; in the last case two ovaries occur in the axils of each two bracts, while the third is left empty; which shows that the presence of ovaries is not a necessary character of the bracts. (2) The ovaries often alternate with the bracts, as if continuing the whorl of three leaves upwards. The ovary first arises as four small protuberances.

These are his concluding remarks:—'(1) The development of the ovule of the so-called Gymnosperms corresponds entirely with that of the ovary, and not the ovule, of other Phanerogams, viz., (a) the so-called integument arises earlier than the nucellus; (b) as a result of this, the former arises from the receptacle and not from the nucellus, as a true integument should do; (c) it is formed of distinct carpel-leaves, which fuse sooner or later, a fact which does not occur in any integument. (2) The so-called integument arises independently, without a nucellus, and remains long separated therefrom, surrounding it loosely, and leaving often a considerable space between. (3) The simple structure of the ovary of Gymnosperms is no reason for considering the latter as an ovule. (4) The anatomical structure of the so-called integument is too complex for such an organ. (5) The

formation of a style and stigma in some Coniferae can only point to the presence of an ovary. (6) Several anomalous structures exhibit the foliar nature of the ovary. (7) The structure, form, and development of the ovary are repeated in the Loranthaceae, Amentaceae, &c. (8) The idea of R. Brown and others that the scale surrounding the flowers is an open carpel, is refuted by all my observations and investigations.'

Sperk does not himself attempt, however, to give any explanation of the seminiferous scale.

In the *Botanische Zeitung* for 1871, Von Mohl (69) first gave to the world his very interesting and important discovery concerning the 'double needle' of the Umbrella Pine, *Sciadopitys verticillata*. He showed that its origin was the same precisely as that of the seminiferous scale of the Abietineae, viz. from the two first leaves of a secondary axillary shoot, which have become fused by their inner or posterior margins; as a result of which the *ventral surface of the organ is directed outwards* (Figs. 1 and 3). The small axillary shoots or brachyblasts of the female cone of Abietineae and those of the vegetative shoot of *Sciadopitys*, abnormal in the one, but normal in the other, are therefore homologous structures, and, by the aid of the former abnormality, the eccentric orientation and structure of the 'double needle' is readily explained, though it required the acute insight of a Von Mohl to solve the riddle.

Strasburger's (70 and 85^a) view of the matter, expressed in his renowned work on the Coniferae and Gnetaceae, in 1872, is sufficiently original, not to say, at least for some of us, bizarre, and approaches more nearly to the views held by Baillon and by Schleiden, than to those of any other botanists. In the first place he maintains the ovarian theory of the ovule, a view which he afterwards abandoned in favour of Gymnospermy in his later book on Angiosperms and Gymnosperms. But the view as to the nature of the seminiferous scale knew with him no variation, at least in essentials, from beginning to end. He held this organ in the Abietineae

to be of the nature of a flattened axis bearing rudimentary leaves, or more definitely stated, a *disk*, chiefly on account of its late development compared with that of the ovules. Confronted by the abnormal appearance of the axillary shoot in the axil of the bract, accompanied by the splitting up of the seminiferous scale into two parts, which became transversely seated on the axillary shoot as its two first leaves, he regarded this metamorphosis of the seminiferous scale merely as the result of the struggle waged between two opposing forces, viz. the vegetative development of the cone and the normal formation of reproductive organs, in which the former had for the time being overbalanced the latter. The fleshy, outer envelope of *Taxus*, &c., he also regarded as possessing a discoid character.

Next are to be mentioned some most striking abnormalities in cones of *Picea excelsa*, Link, observed by both Stenzel (84) and Willkomm (86). The former, in 1876, described a cone in which in the axil of the bract a leafy bud arose, whose first two leaves were harder and browner and more erect than those of the ordinary vegetative shoot, and resembled more the seminiferous scale; they were directed somewhat towards the axis; the following pair of leaves were median, anterior and posterior (Fig. 3). No ovules were to be seen. The pair of larger first leaves were often fused with the small leaves of the bud. He concludes that 'the seminiferous scale of the Spruces consists of the first two leaves of an otherwise undeveloped branch arising in the axil of the bract, these leaves being fused by their posterior margins, and *thus having their dorsal side directed towards the axis of the cone*, and bearing each on this side an ovule. When the seminiferous scales fuse by their *anterior* margins, it is to be considered as an exceptional case, like that of Ferns with sori on the upper surface of the fronds.'

On another occasion he found, in the same plant, androgynous cones, in which the male organs usually occupied the base and the female the upper part; more rarely were the male scattered amongst the female; and still more rarely

did the male form a middle zone with female above and below. Some of the bracts bore pollen-sacs. He also possessed at this time a proliferated cone of *Picea alba*. The buds in the axils of the bracts bore, besides the two seminiferous scales fused by their posterior and gaping at their anterior margins, a posterior and an anterior scale, and one or two inner scales. In some cases the seminiferous scale was so completely fused with the anterior bud-scale as to form a single flat scale as seen from the front, but in reality its posterior margins were represented by two low ridges, visible from the inside, which did not, as in other cases, extend as far as the posterior bud-scale. As regards the characteristic projection or 'Dorn' on the seminiferous scale of *Pinus*, which Strasburger thinks is an *axis*, it may represent either the place of fusion of the posterior margins of the seminiferous scale, or the posterior bud-scale.

The same kind of sports as those in *Picea* occur also in *Tsuga Brunoniana*, Carr., a fact which, he says, lends weight to the above explanations. In the latter plant, the posterior bud-scale is often as well developed as the anterior one, so that the parts of the bud all come to be united laterally into a woody structure. The axis of the bud is often more elongated into a leafy shoot. The fact that the seminiferous scale is shown to consist of two leaves, is antagonistic to the idea that the ovule is an ovary. The fact that the ovular envelope arises at first as two distinct outgrowths which afterwards become fused, does not prove that they are part of an ovary; and, moreover, there is no stigma present.

Willkomm (86) observed in a proliferated cone of the Spruce great numbers of *buds* in the axils of the bracts of the upper portion, which differ from those in Stenzel's case in being extremely symmetrical and regular, and therefore hardly to be called 'monstrosities,' such as those of Stenzel; this is a very important factor in determining their morphological value. His conclusions as to the morphology of the seminiferous scale are precisely the same as those of Stenzel. The monstrous tubular or funnel-shaped anterior scale of

Stenzel's buds never occurs, this scale being always quite regular in shape. The posterior bud-scale is always quite rudimentary. The explanation lay probably in the fact that Stenzel's cones were, as a whole, more monstrous, while his own possessed exceptional symmetry and regularity. He believes that the seminiferous scale proceeds from an axillary shoot with two opposite leaves and bearing a terminal bud (Fig. 3). 'It is therefore a *metamorphosed brachyblast*, consisting of a *median axis and two leaves fused therewith on its anterior surface, whose original separation in P. excelsa is shown by the indentation of the apex of the seminiferous scale.*' He regards the seminiferous scale as consisting of 'two open carpels, and the ovules or seeds occurring on their dorsal side are naked.'

Although Čelakovský produced at this time, and a few years later, some literature on the subject, I prefer to treat his views as a whole later on, for it was not until 1897 that his maturest ideas on the whole problem were issued to the world.

Arcangeli's (90) views, published in 1880, are perhaps worth mention on account of their extraordinary nature. He considers, from the fact that the two sets of bundle-systems arise as one from the axis¹, that the bract and seminiferous scale in *Pinus*, *Cupressus*, *Thuja*, *Cryptomeria*, and *Sequoia* are really a single organ, of *axial* nature, the bract being a leaf of this branch, and the latter arising in the place of a leaf. In *Cunninghamia* 'the scale is developed chiefly with the characters of a leaf, since there is only the small upper bundle to indicate its rameal character.' In *Araucaria* the scales are true *bracts* showing no sign of a transformation into shoots, for the reason that the bundles show no sign of arranging themselves in a vascular ring, the two laterally-placed bundles which Van Tieghem considered as belonging to the upper scale being only branches passing off from the bract-bundles to the ovules. 'One must admit that the

¹ But this is, however, by no means always the case. See my former paper: 'Observations on the Vascular System of the Female "Flowers" of Coniferae.' Ann. Bot. Vol. xiii, 1899.

appendages of the cones of Coniferae may vary as regards their morphological significance,' so that the ovules may be inserted either on a leaf or a shoot. These strange branches he compares to the 'cladophylls' of *Lycopodium*, as in *L. Selago*. He rises superior to the difficulty of branches arising on the stem in place of leaves by assuming that *the leaf belongs both to the stem and to the branch in its axil*. For the axillary branch is part of the *same organ* as the leaf. He regards the ovule and pistil as being both of axial nature. The seminiferous scale, although a modified branch, is nevertheless the representative of the 'carpellary involucre' of other plants. He believes that Conifers, like Cycads and Gnetaceae, are Gymnosperms. All this appears to me, however, a rather irrational view of the whole matter.

The theory which to-day receives, perhaps, as much support from botanists as any other is that first put forward by Sachs, as we have seen, in 1868, and afterwards in 1881-2 more elaborately worked up and more definitely stated by Eichler (71, 91, 95). This theory maintains that there is but one scale, and no double scale, in Coniferae, representing a carpel or sporophyll bearing an ovule or ovules on its upper surface or on its axil; and that the so-called seminiferous scale is in all cases of the nature of a ventral outgrowth of the scale, representing a placenta or ligule, and therefore forming an integral part of the scale (Fig. 2).

In *Dammara* the bundle given off to the ovule is nothing more than an ordinary bundle leaving the carpel for the ovule: it is absent in the sterile scales, a fact which seems to show the absence of an inner scale. As regards the inverted orientation of the bundle going off to the ovule, he says: 'In all cases, where a leaf forms superficial products, which have to be provided with bundles, these last twist their elements round.' He compares other outgrowths of leaves, especially the fertile spike of *Ophioglossum*, with the ovule of *Dammara*; in all such cases the parts of the bundle are inverted. The scale is a single leaf and its appendage an ovule. It cannot be an ovary as Baillon, Parlatores, Dickson, and Sperk say,

because an ovary is the prolongation of an axis, and cannot occur on a leaf. In *Araucaria* the scale receives a *single* bundle which divides up laterally and a little above the base, sending off a few small branches to the ovule (Fig. 2), which have inverted orientation as in *Dammara*. The development, as far as is known, agrees with that of *Dammara*. The outgrowth above the ovule (Fig. 2) is a *ligular* structure, like that in *Isoëtes*, and the velum of the latter is analogous to the integument of *Araucaria*. The inner bundle-system is absent in sterile scales, as in *Dammara*. In *Cunninghamia* a single bundle enters the scale. Three bundles pass off, with inverted orientation, one to each ovule. Thus he considers that no inner scale can be present, and there is but a single leaf, and the transverse ridge is a ligule. In *Sciadopitys* there is also a single leaf with a ventral excrescence. In the Abietineae, the bract appears first in the development, then the seminiferous scale as a transverse swelling on its inner surface (Fig. 4). The bract receives a single bundle which does not further divide up. One or two bundles enter the seminiferous scale which, according to the form of the basal part of the scale, are either given off from the bract-bundle or directly from the axis of the cone; the bundle, on entering the seminiferous scale, divides up into several with inverted orientation. The seminiferous scale is thus an inner outgrowth of the bract, both together constituting a single leaf. Many think the two are quite distinct. But where they leave the axis, though only for a short distance, they are united, and the development shows one to be an outgrowth of the other. Schleiden's and Strasburger's idea that the seminiferous scale is a flattened axis or cladode, does not agree with the arrangement of the bundles, for in all cladodes the xylem is directed inwards, the bundles being either flattened together or grouped around a centre. As an objection to the views both of Van Tieghem and Von Mohl, he says that there is nothing to be seen of an axillary bud, but the seminiferous scale appears as an inner outgrowth of the bract. As an objection to Mohl's view, there is no sign of the seminiferous scale being formed of two

leaves, as, from the earliest stage onward, it appears as a single outgrowth. Neither do there occur two symmetrically-placed bundles, one belonging to each part of the scale, as in the needle of *Sciadopitys*, but, on the contrary, the single one, or the two in the base, divide up into a number, all having the same orientation. Owing to the abnormal appearance of an axillary bud and its great pressure on the seminiferous scale as a result of the compact arrangement of the scales on the cone, the bud causes the separation of the seminiferous scale into two parts, whereby it assumes the appearance of bearing them as its two first leaves.

In the Taxodineae there is a distinct ventral outgrowth, with its own bundle-system, whose parts have inverted orientation. In Cupressineae the ovules are so close to the base of the bract that they may be called axillary. Where many ovules occur in the axil they are seated on the axis of the cone for a short distance as well as on the scale (*C. sempervirens*), so that no strict distinction can be made between the ovules which are developed on the axis and those arising on the scale. They usually occupy the middle of the axil. Where two are present they occur right and left; in *Juniperus* one of these is usually absent. No differentiated ventral outgrowth is present in this order; the scale appears either quite simple or exhibits a more or less pronounced ventral swelling depressing the bract, as in *Sequoia* and *Taxodium*, and more or less clearly distinguished from it. The inverted orientation of the upper bundles is caused by the peltate thickening of the scale, and, as a natural consequence of this, the scale is at first exactly similar to the lower vegetative leaves; in the base of the scale all the bundles are arranged in a circle just as in the stalk of any peltate foliage-leaf. Although the scales cannot be said with certainty to bear the ovules, and possibly represent only bracts, they are in reality open carpels. In the Podocarpeae there is also but a single leaf. In *Microcachrys* the inner bundle-system does not even exist, which is due to the fleshiness of the carpel. It is represented in *Dacrydium* by two weak branches, with inverted

orientation. Both plants have an outer integument in the form of an arillus. In *Podocarpus dacrydioides* the ovule is inverted and fused along its whole length with the carpel. The second integument becomes fleshy like an aril, and arises later than the first integument. Just above the base of the carpel the bundle gives off two branches which terminate just above the nucellus of the ovule. The inner bundles become inverted because they arise from the inner surface of the carpel. In the remaining sections of *Podocarpus* the ovule is deeply divided from the carpel, which is overtopped by the anatropous ovule. Here the inner bundle runs up the raphe, where it divides up into several branches which bend back above the nucellus, forming a circle around it, with the xylem-ports all directed outwards. Strasburger and Van Tieghem say the 'raphe' is the inner scale, but it is not so; there are other cases in Angiosperms where the raphe is thus strongly developed. In the section *Nageia* and in several species of the section *Eupodocarpus*, the male flowers occur in a capitate inflorescence in the same position as the receptacle with ovules, so that each ovule really represents a flower subtended by a bract, and the whole receptacle is not a single flower. But in *P. Sellowii*, *P. salicifolia*, *P. Thunbergii*, &c., the receptacle corresponds to a single male flower, so that the aggregation of distinct and unfused carpels in *P. spicata* is to be considered as a single flower. In *Phyllocladus* the ovule is axillary and not borne on a carpel enclosed in an aril; the two bundles supplying it have their xylem turned towards *each other*, not towards the carpel. In *Cephalotaxus* the bundle-system is the same as in *Phyllocladus*. In *Taxus* and *Torreya* the ovular axis bearing the bracts receives two bundles with their xylems directed towards each other. An aril is present. Seeing that in these last two genera the ovules are borne on independent leafy shoots, the whole cannot be called a flower, but each ovular axis is such. The ovule is clearly of axial origin. Eichler compares the different positions of the ovule with the similar variations in position of the macrosporangium as in *Isoetes* (where it occurs on a leaf), *Selaginella* and *Lycopodium*

(in the axil), *Psilotum* and *Tmesipteris* (at the end of a short branch, and thus axial), all of which plants belong to the same circle of affinities to which Conifers are most nearly allied. The ovule is not a bud or leaf-segment, but a structure *sui generis*. A terminal ovule occurs in *Polygonum*: terminal and axillary ovules in Piperaceae, Balanophoreae, &c. Where an ovule arises from a leaf, the latter is a carpel. Seeing that in Taxodineae the leaves which function as ovule-bearing carpels are homologous with those in Cupressineae which have ovules in their axil, it follows that the latter are also carpels. The envelope of the nucellus in *Taxus* and *Torreya* is an integument, as shown by the position of the arillus in other genera in which ovules are borne on a leaf. The Araucarieae, the oldest Coniferous type, are nearly allied to Cycads. In agreement with the palaeontological sequence, the ovule in Cupressineae and certain Taxineae (the most recent types of Conifers) becomes axillary, until in *Taxus* and *Torreya* it becomes an independent flower, borne on a leafy stalk arising from the axil of a leaf.

Cycads, Coniferae, and Gnetaceae are all gymnospermous. In the latter the outermost covering of the female flower is to be considered an ovary, not quite closed and without stigmas. In *Juniperus* the carpels are closed, but there are no stigmas, and the pollen reaches the ovule directly, so that the latter is therefore gymnospermous.

The Sachs-Eichler theory of this difficult subject no doubt appeals to many owing to its great simplicity, deriving as it does the solution of the problem directly from the structures as they are presented to us to-day; its tranquillity of contemplation disturbed neither by the idea of a possible adaptive modification of these structures from others once totally different in appearance, nor by the alteration which they undergo in cases of the abnormal metamorphosis of parts: indeed, towards the latter Eichler is actively hostile, for he says—and this summarizes his general attitude in the matter—'I cannot forbear showing how forcibly the present case once more warns us that monstrosities cannot be brought to bear

on the examination of normal relations. Without those abnormalities, no one would have thought of regarding the seminiferous scale of the Abietineae as a composite organ, and we should then have been spared, or at least partially so, the complicated theories which have for so long obscured the understanding of the floral structure of one of the most important groups of plants.' Whether or not this is a sound and safe position to take up, will be seen when the most recent view of this matter is brought forward. However, both the developmental and the anatomical evidence favour it.

Velenovský (101), in 1888, described an interesting case of an abnormal Larch-cone. One axillary bud *bore ovules on the lower surface of all its leaves*. When the bud is suppressed, the two seminiferous scales *orientate themselves with regard to the axis of the cone*. In some tropical climbing *Aristolochias*, the first bract of a suppressed bud, which it covers over when young, at length increases in size and becomes *orientated with regard to the stem* which it clasps as an ochrea. The same thing was observed to occur in *Tilia grandifolia*, where the bud in the axil of the flower-bract was suppressed, so that the bract was orientated with regard to the axis in the same plane as the subtending bract, and with its upper surface directed to the latter. The double scale of a cone of Abietineae is a kind of brachyblast, and is the same morphological phenomenon as occurs in *Sciadopitys*, so that it is nothing new for this type of plant. His concluding remarks are worthy of special notice:—'The deformed cones of our *Larix* and also the Spruce-cones of Caspary, Stenzel, Willkomm, and Čelakovský, are not monstrosities in which certain parts are irregularly and haphazardly developed. We find in all stages of the scale-metamorphosis a definite law and the greatest regularity of development, so that, by retaining a right grasp of the process of development, we can *a priori* expect and, as a matter of fact, shall find, the distinct developmental forms. Such a regularity, which occurs in every normal flower, can never be an equivocal, pathological and casual phenomenon.'

Masters' (105) position was in 1884 that of Eichler, viz. that the seminiferous scale is an excrescence of the bract; this is stated in a paper on the comparative morphology of *Sciadopitys*. In this paper he makes the statement that 'the adult seed-scale of *Sciadopitys* and of Abietineae occupies the same apparent position with regard to the bract that the "needle" of *Sciadopitys* and the fascicle of "needles" of *Pinus* (with its sheath) do respectively to the true leaf.' From the consideration of an abnormality in which the 'needle' was deeply forked and from the fork sprung a short axis bearing a whorl of 'needles,' he thinks the 'needle' is of axial not of foliar nature. But this phenomenon, it seems to me, might also be interpreted as the result of the *elongation* of the otherwise suppressed or shortened axis of the brachyblast bearing the two leaves fused by their posterior margins, causing a separation of the latter, while the axis remained for part of its length *fused with one of its two leaves*, and after becoming free higher up, produced fresh leaves. In his paper of 1891, he puts forward a view of the seminiferous scale which, amongst all those which occupy our attention, has at least the distinction of being unique. I give his own words:—'Reverting to Casimir de Candolle's "Théorie de la Feuille" . . . this botanist compares the leaf to an axis, the *upper half* of whose vascular system is abortive or undeveloped, for which reason the xylem is towards the upper or inner surface, the phloem towards the lower. Apply a similar explanation to the fruit-scale, and the position of xylem and phloem becomes intelligible. According to this view the fruit-scale is an enation, either from the bract or from the axis, it is immaterial which, of the nature of a cladode or modified shoot. The *lower or outer* portion of this branch or cladode is abortive, and consequently the xylem is towards the lower or outer, the phloem towards the upper or inner surface' (Fig. 5). This view, however, appears so incongruous and incomprehensible, and offers for our contemplation a structure so anomalous, and so foreign to all other divisions of the

vegetable world, that it is not likely to find favour with many botanists.

Penzig (109), in his 'Pflanzen-Teratologie' of 1894, supports, with great enthusiasm, the position of Delpino. This latter author considers the carpels of Conifers as consisting of three parts, of which the middle part forms the bract, while the two lateral lobes bend inwards and fuse together by their margins to form the seminiferous scale, bearing the seeds (Fig. 6). When an axillary shoot appears, it separates

Fig. 5. Diagram showing the seminiferous scale *hc(ss)* and the hypothetical missing half of the cladode (*hc*); *b* = bract; *ph* = phloem; *x* = xylem; *ax¹* = primary axis of cone.

Fig. 6. Diagram of bract, showing its two basal lobes involuted and fused together to form the seminiferous scale (*ss*); *b* = bract; *sp* = sporangia.

the two fused lateral lobes of the carpel, which bend back again and assume their former lateral position. When the shoot arises at the same level as, or between, the seminiferous scale and the bract, the two lobes come to have their ventral surfaces directed towards each other. But when the axillary shoot arises *between the seminiferous scale and the axis of the cone*, the two placental lobes have their dorsal sides directed towards the axillary shoot; a fact which, says Penzig, is not explicable on the Braun theory (that the scale represents the two first leaves of the axillary shoot), but is quite easily

so on that of Delpino. That the lobes, as the metamorphosis proceeds, become more leaf-like, is only in accord with their foliar nature. When, by elongation of the axillary shoot, the two lobes are carried up by it, it appears as if they were its own appendages; but they are in reality, like the bract, members of the axis of the cone, receiving their bundles directly from it. The two medianly-placed scales of the axillary shoot are to be looked upon as its first-formed leaves, their antero-posterior position being explainable from the fact that they could not occupy the normal transverse position, for this is taken up by the placental lobes. He (Penzig) thinks the phenomenon observed by Velenovský in a Larch-cone of an axillary shoot bearing, besides the two fleshy placental lobes, five other fleshy ovule-bearing scales, speaks strongly in favour of Braun's theory. But he has previously shown how *a specific metamorphosis may be determined by adjoining organs*. In *Antirrhinum* the anterior stamens adjoining the petals in double flowers often acquire the form of the lobes of the lower lip, while the upper stamens acquire the form of the upper lip of the corolla; the two posterior stamens in Orchids, when they are actually present, acquire the form and colour of the labellum because they adjoin the latter. He attributes these cases to a wandering of the specific structural substances into the neighbouring organs. In the same way he explains the above case of the Larch; the special substances intended for the placental lobes have wandered into the axillary shoot and influenced its appendages in the same way as the lobes. The transformation of foliage-leaves into sexual organs is not uncommon in Coniferae.

Delpino's theory also enables us to understand how (as in *Araucaria brasiliana*, A. Rich, *Picea excelsa*, Link, *Tsuga canadensis*, Carr.), the seminiferous scale splits into two lobes without the appearance of an axillary shoot.

Noll (108) in 1894 examined proliferated cones of the Larch, and found the most gradual and continuous series of transitional forms between the seminiferous scale and an

axillary bud, so as to leave no doubt in his mind as to the morphological equivalence of the seminiferous scale and the two first leaves of an axillary bud. In one point his series was better than in other previously described cases: the axillary bud occupied a position *anterior to the seminiferous scale or its two component parts*, whereas in formerly described cases it occurred posteriorly thereto. The former more clearly indicates the real relationship.

Čelakovský (87, 94, 96, 103, 114) has repeatedly published his views on this subject from 1879 onwards, his latest paper having appeared in 1897. This investigator's treatment of the subject is perhaps broader and more comprehensive than that of any other botanist. He seems to leave no point of view unutilized from which a possibility of penetrating more deeply into the mysteries of this complicated problem may be found.

He is a champion of the 'axillary bud' theory, first propounded by Alex. Braun, and, taking up the abnormalities described by Stenzel and Willkomm, he thoroughly overhauls and explains them, endeavouring to show that the *continuous and gradual transitions* existing between the undivided seminiferous scale of the normal condition (Fig. 1) and the first transverse pair of foliar organs of the axillary bud, along with, in many cases, the *anterior* bud-leaf (Fig. 3), as well as the agreement, in relative position of the various appendages, between this abnormal axillary bud and an ordinary axillary vegetative bud, both go to prove this theory to be the true one.

According to Čelakovský the fact that the ventral surface of the seminiferous scale is directed towards the corresponding surface of the bract is due to the law of 'Spreitenverkehrung,' by which ligules or emergences always present their ventral surfaces to that of the leaf on which they are borne, although one would have thought that a more direct and obvious reason lay in the fact that the ovules being borne on the dorsal surface of the scale, that surface must necessarily lie uppermost in order to allow both of fertilization and the escape of the ripe seed.

He strongly criticizes the theory of the abnormalities proposed by Strasburger, who regards the transformation of the disk or flattened axis (for such he considers the seminiferous scale to be) into the two first appendages and the anterior leaf of the axillary bud as the result of the struggle carried on between two opposing forces, viz. that of the vegetative development of a bud and that of the normal formation of reproductive organs. This position Čelakovský shows to be perfectly untenable; for it is impossible for an organ belonging to one morphological category, such as an axis or disk, to become transformed into those belonging to another category, such as the foliar appendages of an axis.

Eichler's theory meets with no better fate at his hands. This author's explanation of the abnormalities was this: that the pressure exercised by the axillary bud arising between the seminiferous scale and the axis of the cone, was the agency responsible for the splitting of the scale into two parts and the wide separation of these latter into the positions which they occupy, one on either side of the axillary bud. But this theory, he says, will not hold good when it is found that the splitting of the scale frequently occurs when the axillary bud is suppressed or exceedingly reduced, and also when the latter arises on *the anterior side* of the seminiferous scale, a fact which is fatal to Eichler's placental or emergence-theory, which latter is, however, best refuted by the continuous, gradual transitions which occur in the abnormalities between the seminiferous scale and the first leaf-pair plus the anterior leaf of the axillary bud. And further, if this view of Eichler's be correct, what has become, he asks, of the first transverse leaf-pair of the bud, which should occupy the position taken up by the separated parts of the seminiferous scale?

If the view that the ovule is a *flower* be correct, he reasons, then that organ ought, occasionally, in the retrograde metamorphoses, to develop vegetatively like the seminiferous scale; which, however, it never does.

For the solution of such problems as the nature of the

seminiferous scale he regards the *development* as an unreliable factor; that this is so is shown by the circumstance that Strasburger and Eichler both rest their very different views on developmental evidence. The development of the seminiferous scale, he says, is a 'heterodox' one. Nature here takes a short cut; instead of forming a bud with two distinct lateral leaves (Fig. 3), the seminiferous scale, as we know it to-day, is developed *directly*, in its highly modified form, as an outgrowth on the bract (Figs. 1 and 4). The '*systematic-morphological comparison*' he regards as a very useful factor, but the point from which it starts must be clear and certain. Eichler started out from the Araucarineae, and Strasburger from the Taxineae, hence both from quite different points. It is also important not to compare together wrong things. *Anatomical* evidence, taken by itself, is also utterly misleading, as shown by Van Tieghem's conclusion that the seminiferous scale represents the *first leaf* of an axillary shoot, an idea clearly erroneous when we know that in all Coniferae the axillary shoot always bears a *pair* of *opposite* first leaves and never a single leaf. Čelakovský's position on this point is, therefore, this, that 'the most credible and surest method of understanding questionable metamorphosed structures, which are apt, owing to heterodox development, to be misunderstood, is the *metamorphogenesis* resting on abnormalities, the neglect and wrong estimation of which is the [third] cause of the aberrant state of morphology.'

With the usual insight which he applies to the investigation of all intricate phenomena of plant-life, the author further elucidates for us the true ulterior nature of the parts of the seminiferous scale, as also of the sporangial envelopes in the various groups of the order. And so well does he account for and explain the various structures throughout this large and diversified order that, under such skilful unravelling of the knot, this diversity becomes a unity, presenting an orderly sequence of connected forms such as had never been exhibited to us in any former treatise on the subject.

Starting out with the theory, of which he was the first

exponent, that all axial appendages primarily originated by sterilization and subdivision of the sporogonium of the lower Cryptogams, and possessed, therefore, originally a *radial*, in contradistinction to a bilateral, structure, Čelakovský believes this radial structure of the sporophyll to have been characteristic of the ancestors of the Gymnosperms or, as he calls them, the Archigymnosperms. He maintains that this radial structure has persisted to the present day, in the male sporophylls of the Gnetaceae, where the sporangia are terminal; in the female sporophylls of the Cycads, where they are marginal (this being also occasionally the case on the male side, as in *Zamia*); in the sporophylls of *Ginkgo*, as well seen in the abnormal female flower described by Fujii¹; in *Os-munda*, *Hymenophyllum*, and the Psilotaceae; and in the stamens of all Angiosperms. From the terminal, the sporangia came to assume a marginal position on the sporophyll until, when the latter in many plants became bilateral in structure, the sporangia were frequently relegated either to the dorsal or the ventral side, as in most Ferns, and the carpels of some Angiosperms.

In an early paper in 'Flora' he has shown that the integuments of an ovule have their origin in the *segments of the sporophyll*, the inner integument springing from *two* distinct segments, this latter fact thus easily accounting for the appearance of the integument of the Abietineae in its early stage as two distinct rudiments, misleading Baillon to assert so positively that this fact proved the ovular envelope in this group to be of the nature of an ovary and not of an integument.

Čelakovský urges that, throughout the entire order of Coniferae, no true carpel or female sporophyll is present, but that organ is reduced to a *single ovule* just as is also the case in the female organs of the Gnetaceae.

In the Taxaceae there are always two integuments of the normal form, enclosing the ovule. In the case of *Taxus*, and

¹ 'On the Different Views hitherto proposed regarding the Morphology of the Flowers of *Ginkgo biloba*,' 1897.

in that of *Dacrydium* and *Microcachrys* among the Podocarpeae, where the ovular integuments are distinct from each other, the ovule is spoken of as 'dichlamydeous.' In *Cephalotaxus*, *Podocarpus*, as also in Cycads, where the two integuments (consisting of the inner bony and the outer fleshy one) are intimately united, the condition is 'holochlamydeous.'

In the Araucariaceae, however (including the Abietineae, Araucarieae, and Cupressineae) the outer integument of the sporangium has assumed a *permanently vegetative* development, and is exactly comparable in this respect to the vegetatively-developed outer integument observed and described by this author in *Hesperis* and other plants. This outer integument, then, is the *seminiferous scale* or a half of it, as unlike an ordinary outer integument as it well could be, but shown to be such by the inversed orientation of its bundles, characteristic of all outer integuments (a fact first discovered by Strasburger in *Cephalotaxus*), by the fact that without it the sporangium would possess but a single integument, and thus offer an incongruous dissimilarity from the sporangium in the Taxaceae, and, not least, by the period of its development, which is always (except in *Pinus resinosa*, Soland) *subsequent* to that of the sporangium, whereas if it were a sporophyll it should be developed, naturally, before the sporangium. This dissimilarity from what obtains in the Taxaceae would again be most apparent if the seminiferous scale or its half were regarded as a sporophyll or carpel, for no such organ is found in the above-named section of the order.

As regards the homology of the sporangial envelopes with structures found amongst Vascular Cryptogams, the inner integument corresponds to the indusium of Ferns, *Isoëtes*, &c., while the outer integument is the homologue of the ligule in *Isoëtes*, *Selaginella*, &c., a view which is so far identical with that of Sachs and Eichler, who regarded the seminiferous scale as of ligular nature.

While in the Abietineae the seminiferous scale very frequently consists of the sporangial representatives of the first pair of leaves of the axillary bud fused with that of the *anterior*

leaf of the latter (this anterior leaf being twisted round through an angle of 180°), in the Araucarieae (Fig. 2), where the seminiferous scale, bearing a single ovule, is obviously not a compound but a single organ, the *scale consists solely of the anterior leaf* or its sporangial representative, the first leaf-pair of the axillary bud being entirely absent. This is the explanation of the occurrence of a single sporangium in Araucarieae. The same explanation is, in all probability, also applicable to the case of the Podocarpeae, where but a single sporangium also occurs. In the Taxodineae the seminiferous scale may frequently consist of several parts, representing the fusion of *more* than three leaves, or their sporangial representatives, of the axillary bud. Abnormalities, either in this group or in the Cupressineae, are almost unknown. But, in support of the view as to the origin of the seminiferous scale in the Taxodineae, Engelmann, in America, found a proliferated cone of *Sequoia* which clearly exhibited the compound nature of the scale, while Alex. Braun, in *Taxodium*, *Cryptomeria*, and *Glyptostrobus*, found an axillary bud replacing the scale. Although no abnormalities have ever been found to prove it, there can, nevertheless, be little doubt that in the Cupressineae, the seminiferous scale, which is almost completely fused with the bract, has the same origin as it has in the Abietineae. But a difficulty would seem to arise, owing to the presence in some species of *Cupressus* of *great numbers* of sporangia belonging to a *single* seminiferous scale, if the latter is to be interpreted as representing the fused, vegetatively-developed outer integuments of two sporangia. But the difficulty vanishes when confronted with the fact that in *Hesperis* was found a vegetatively-developed outer integument bearing *several inner integuments* or ovules, one on each vein (Fig. 7), and each corresponding to a lateral segment of the leaflet.

Fig. 7. Vegetatively-developed outer integument (*o.int.*) of *Hesperis*, showing several inner integuments (*sp*) borne on the lateral veins (after Čelakovský).

The female sporophylls of Coniferae belong to branches of a higher grade than those bearing the male sporophylls. The male sporophyll corresponds to the *bract* subtending the axillary shoot (now represented solely by the seminiferous scale), which latter bears the female sporophylls, i.e. their sporangial representatives. That this represents the real relationship is shown by those abnormalities in which the 'bracts' bear pollen-sacs on their lower surface, when the seminiferous scale, or female part of the flower, tends to disappear, and this generally in the lower part of the cone, whereas in the upper part the female parts develop in the normal way and the bracts bear no pollen-sacs. The mon-axial cones were originally hermaphrodite, like the strobili of *Selaginella*, or the flowers of most Angiosperms¹.

The real relationships, as they are regarded by the author, may be stated thus:—the *female inflorescence* of the Coniferae is equivalent to the *axillary brachyblast* of *Ginkgo*, and the main axis of Cycads. In the Taxeae the inflorescence consists of a primary axis bearing a secondary axis (the 'flower') in an axillary position; this 'flower' is unique among Conifers from the fact that, like the Cycads, it bears a number of sterile bracts in its lower portion; the sporangium has become shifted from its ordinary lateral position, into one purely *terminal* to the axis, the sporangium itself being the sole representative of the sporophyll which was the *uppermost* appendage of the axis. This 'flower' is exactly equivalent to that of *Ginkgo*.

¹ Von Mohl observed a highly interesting case in an androgynous cone of *Picea alba*, Link, which bore reduced and sterile seminiferous scales in the axils of bracts, one of which latter bore two pollen-sacs on its lower surface, while on its upper surface appeared two wing-shaped projections, one on each side at the base, but nearer the upper than the lower side, which, in mode of adherence and direction, greatly resembled sporangia, and are in fact the sporangial leaf-segments of the sporophyll. So that this would, therefore, be a hermaphrodite scale, and possibly represents what would have been the original structure of the female inflorescence when the 'bracts' bore the sporangia, and *no axillary shoots were developed*, these latter appearing later, and themselves subsequently becoming modified into the present structure. These sporangia, from their position on a sporophyll, and having no seminiferous scale attached to them, must necessarily be holochlamydeous, like the sporangium of *Cephalotaxus*, and not monochlamydeous like that of the Abietineae.

It is highly interesting, as indicating a reversion to the ancestral condition exhibited in modern Cycads, that *Torreya* has been known to produce, besides the lateral secondary axes, a 'flower' *terminal to the primary axis*. This latter fact, and the presence of the sterile bracts in the 'flowers,' clearly shows the Taxeae to be one of the very oldest groups of the order. In *Cephalotaxus* 'the normal flower consists of two lateral . . . carpels formed of ovules pure and simple, accompanied usually by a median third, but sterile, carpel. In the Podocarpeae the flower has been reduced to a *single* axial appendage, i.e. to an ovular carpel, and at the same time to an ovule actually axillary, and often carried up upon a bract.' In the Araucarieae the structure is the same (Fig. 2). In the Abietineae the seminiferous scale is 'a symphyllodial structure, consisting of three fused appendages [two in *Picea*] of an axis, of which the two lateral are fertile carpels [reduced to sporangia] fused together to form the 'crista' of the seminiferous scale, while the third median leaf—the median knob of the first rudiment—remains sterile, and either aborts or, fused with the two other fertile carpels, forms the keel and mucro (in *Pinus*).' In the Taxodineae and Cupressineae the structure is essentially the same.

The modifications which have in later times supervened amongst the Coniferae have been, firstly, the relegation of the flowers from the terminal, as in Cycads, to the axillary position, as in *Ginkgo*; secondly, the supplanting of the hermaphrodite by the diclinous condition, while finally, in some groups, the female came to belong to a different rank of branching from that of the male 'flowers'; and, thirdly, the adoption by the sporophyll, in many cases, of a bilateral instead of a radial symmetry.

The structure which prevails throughout the Coniferae is found to be uniform with that prevailing in the other two groups of Gymnosperms. In the Cycads the sporophylls, with the exception of those of the female plant of *Cycas*, still retain in part their radial symmetry, while the sporangia possess a holochlamydeous or double integument. In the Gnetaceae

the male sporophylls have preserved their radial symmetry more or less completely; whilst the female are, as in Coniferae, reduced to single ovules, each with two integuments.

GENERAL SUMMARY.

In conclusion I give in brief the most important of the numerous theories relating to the nature of the 'seminiferous scale' and the 'ovule' respectively, which have been cited at greater length in the foregoing pages.

Views on the Nature of the Seminiferous Scale.

- LINNAEUS (1737, 1792): The seminiferous scale of the Abietineae is a *calyx*. In *Juniperus* the ventral tip of the scale is the *corolla*.
 JUSSIEU (1789): The bract is a style; the seminiferous scale a *bilocular ovary*.
 MIRBEL (1810-15): The seminiferous scale is a *peduncle*.
 BROWN, R. (1814-66): The seminiferous scale is an *open carpel*.
 SCHLEIDEN (1839-43), BAILLON (1860-65), STRASBURGER (1872-79), MASTERS (1891): The seminiferous scale of Abietineae is an *axis*, either in the form of a *placenta* (Schleiden), an *axillary bud* (Baillon), a *disk* or (in the Cupressineae and Podocarpeae) an *axillary bud* (Strasburger), or a *half-cladode* (Masters).
 SACHS-EICHLER (1868, 1881-82): The seminiferous scale is a *ventral outgrowth* from the open carpel, of the nature of a *placenta* or *ligule*. In the Cupressineae, Taxodineae, and Podocarpeae no differentiated ventral outgrowth exists; but the scale as a whole is an *open carpel*.
 VAN TIEGHEM (1869): The seminiferous scale is the *first and only leaf of an axillary bud*. In the Podocarpeae this leaf is represented solely by the ovule. In the Taxeae the same thing occurs on secondary shoots.
 BRAUN (1853-75), CASPARY (1860), PARLATORE (1864), ØRSTED (1864), VON MOHL (1871), STENZEL (1876), WILLKOMM (1879), ČELAKOVSKÝ (1879-97): The seminiferous scale consists of the *two first leaves (or their ovular representatives) of an axillary bud*. This view is founded chiefly on the *abnormalities*.
 DELPINO-PENZIG (1894): The seminiferous scale consists of *the two lateral lobes of the bract bent inwards and fused by their margins*.

Views on the Nature of the Sporangium.

- LINNAEUS, JUSSIEU: Pistil.
 MIRBEL, RICHARD: Complete flower, consisting of *calyx* or *cupule* (our integument), and *ovary* (our nucellus), i. e. a caryopsis or nut, whose pericarp is fused with the integument of the seed.
 BROWN, R.: Ovule. First exponent of the 'Gymnospermous' theory.
 BAILLON: Ovary. View founded on the *development*.
 PARLATORE: Ovary.

VAN TIEGHEM: Ovule.

SPERK: Ovary.

BRAUN, A.: Ovule.

STRASBURGER: Ovary (earlier view); ovule (later view).

EICHLER: Ovule.

ČELAKOVSKÝ: Ovule (representing the entire sporophyll).

It will thus be seen how various are the theories which have from time to time been put forward on this subject. It will be said by many that the problems connected with it remain still unsolved, but it seems to me that their solution depends very largely on the individual insight of each one, as to how he interprets facts placed before him. Personally, I incline strongly to the views put forth by Čelakovský, the latest author who has written upon the subject. They are views which, in their interpretation of organs, appear the least to clash with our modern morphological conceptions, and which, from their breadth of view and comprehensiveness, appeal forcibly to the scientific sense. It seems to me that the evidence accruing from the abnormalities, in which *a most gradual transition* exists between the normal seminiferous scale and the two or three first leaves of an axillary bud, is ample for the solution of the problem as to the position of the seminiferous scale between the bract and the axis (Fig. 1). I hold both with Velenovský and Čelakovský that this evidence is eminently to be relied upon, because 'in all stages of the scale-metamorphosis we find a definite law and the greatest regularity of development,' and 'such a regularity can never be an equivocal, pathological, and casual phenomenon.' This will hardly apply to the evidence derived from the anatomy or the development, which, as Čelakovský has shown, is quite untrustworthy. So that, speaking for myself, this part of the whole problem is already solved.

With regard to the vexed question of Gymnospermy which is intimately bound up with and, indeed, inseparable from that as to the nature of the seminiferous scale, the view propounded by Čelakovský is once more distinguished by its comprehensiveness of outlook, and by the fact of its suggesting a unity of morphological structure throughout,

not only the order Coniferae, but all three orders of the Gymnosperms, where before we but recognized a considerable amount of diversity. Hitherto, it has been regarded as a matter beyond all controversy that the sporangium in Coniferae possesses but a single integument; that the fleshy envelope of the Taxeae is either of the nature of a disk or *special* envelope or aril of no morphological value, as in *Taxus*, or that it represents the outer layer or layers of the single integument, as in *Cephalotaxus*, comparable to the case of the Cycads. Yet the sporangium of *Podocarpus* was, strangely enough, regarded as unique in possessing two integuments. Čelakovský's theory, however, introduces us to a plan of perfect uniformity of structure in this respect throughout the entire order. For he maintains the constant presence throughout the order of not one, but two integuments to the sporangium, thus abolishing the awkward inconsistency of the presence of such extra and unusual organs as an aril, and the unique possession by *Podocarpus* of two integuments.

There is nothing unreasonable in supposing outer integuments capable of becoming modified in the direction of vegetative development to subserve the special adaptive function of a protective covering to the sporangia. The outer integument, forming an integral part of the sporangium, would, probably, if developed as Čelakovský suggests, as a protective scale, afford greater security to that organ than would the bract, in whose axil the sporangium would lie more or less independently of the latter or, at least, not so intimately bound up with it as it is with the seminiferous scale.

In view of the comparatively one-sided nature and narrow scope of the views advanced by other writers on this subject, it appears to me probable that, in the near future, a theory of the structure of the female 'flower' in Coniferae, if not absolutely identical with, yet approximating most nearly to that which in recent years has been elaborated by Čelakovský, will occupy a paramount place in the minds of the foremost botanists of the day.

BIBLIOGRAPHY.

1. RAY : Methodus plantarum nova, 1682.
2. TOURNEFORT : Institutiones Rei Herbariae, 1719.
3. LINNAEUS : Genera Plantarum, 1737.
4. TREW, C. J. : 'Apologia et Mantissa Observationis de Cedro Libani et Cedrorum Libani Historiae,' Nova Acta Acad. Nat. Curios., iii, p. 445, 1767.
5. LAMARCK : Encyclopéd. Méthod. Bot., vol. ii, 1786.
6. JUSSIEU : Genera Plantarum, 1789.
7. GAERTNER : De Fructibus et Seminibus Plantarum, vol. ii, 1791.
8. PAVON, J. : 'Disertacion botanica sobre los generos *Tovaria*, *Actinophyllum*, *Araucaria*, y *Salmia*': Madrid, 1791.
9. LINNAEUS : Praelectiones in Ord. Naturales, p. 589, 1792.
10. HALL, R. : Elements of Botany, p. 98, 1802.
11. LAMBERT, A. B. : A Description of the Genus *Pinus*, 1803.
12. SALISBURY : Trans. Linn. Soc., vol. viii, 1807.
13. SMITH, J. E. : An Introduction to Physiological and Systematical Botany, 1807.
14. SCHKUHR : Botanisches Handbuch, vol. iii, p. 278, 1808.
15. TARGIONI-TOZZETTI, O. : Rapporto del professore di botanica T.-T. : Firenze, 1809.
16. TRISTAN : 'Mémoires sur le genre *Pinus*,' Ann. Mus. Paris, xvi, 1810.
17. MIRBEL : 'Observations sur la famille des Végétaux Conifères,' Ann. du Mus. d'Hist. Nat., tome xv, p. 473, 1810.
18. MIRBEL and SCHUBERT : Nouveau Bulletin des Sciences, vol. iii, 1812.
19. BROWN, R. : 'General Remarks on the Botany of Terra Australis,' 1814; in Miscellaneous Botanical Works, vol. i, 1866.
20. MIRBEL : 'Éléments de Physiologie Végétale et de Botanique,' Ann. des Sciences Nat., 2^{ième} sér., xx, 1815.
21. CASSEL, F. P. : Lehrbuch der natürlichen Pflanzenordnung, p. 183, 1817.
22. REES : Cyclopaedia, vol. xxvii, 1819, art. *Pinus*.
23. RICHARD, A. : Dictionnaire d'Hist. Nat., tome 4^{ième}, p. 395, 1823.
24. RICHARD, L. C. : Commentatio botanica de Coniferis et Cycadeis, 1826.
25. BROWN, R. : 'Character and Description of *Kingia*, a new genus of Plants found on the S.W. coast of New Holland, with observations on the structure of its unimpregnated ovulum and the Female Flower in Cycadeae and Coniferae,' 1827; in Miscellaneous Botanical Works, vol. i, 1866.
26. BRONGNIART, AD. : Histoire des Végétaux Fossiles, vol. i, 1828.
27. BARTLING : Ordines naturales plantarum eorumque characteres et affinitates, 1830.
28. NEES VON ESENBECK, T. F. L. : Genera Plantarum Florae Germanicae, 1835.
29. POUCHET, F. A. : Traité de Botanique, tome i, p. 320, 1835.
30. CANDOLLE, A. DE : Introduction à l'Étude de Botanique, tome ii, 1835.
31. CORDA, A. J. C. : 'Beiträge zur Lehre von der Befruchtung der Pflanzen,' pp. 599-614; Nova Acta Acad. Curios., xvii, part ii, 1835.
32. ENDLICHER : Genera Plantarum, 1836-40 (part ii, 1835).
33. DON, D. : Trans. Linn. Soc., vol. xviii, p. 163, 1839.

34. SCHLEIDEN: 'Sur la signification morphologique du placentaire,' Ann. des Sciences Nat., 2^{ième} sér., vols. xi and xii, 1839.
35. MIRBEL and SPACH: 'Notes sur l'embryogénie des *Pinus Laricio* et *sylvestris*, des *Thuja orientalis* et *occidentalis*, et du *Taxus baccata*,' Ann. des Sc. Nat., 2^{ième} sér., vols. xix and xx, 1843.
36. SCHLEIDEN: Grundzüge der wissenschaftlichen Botanik, 1843.
37. MAOUT, LE: Leçons élémentaires de Botanique, 2^{ième} partie, p. 622, 1844.
38. MOHL, VON: 'Ueber die männlichen Blüten der Coniferen,' Verm. Schriften botan. Inhalts, 1845.
39. GOTTSCHKE: 'Bemerkungen zur Inaugural-Dissertation, "De Macrozamia Preissii," auct. G. Heinzel (Breslau, 1844),' Botan. Zeitung, iii, 1845.
40. ENDLICHER: Synopsis Coniferarum, 1847.
41. LINK, H. F.: 'Revisio Abietinarum Horti Regii botanici Berolinensis,' Linnaea, Bd. xx, 1847, pp. 283-290.
42. BLUME: Rumphia, 1847.
43. CARPENTER, W. B.: Vegetable Physiology and Systematic Botany, p. 504, 1850.
44. LINDLEY: The Vegetable Kingdom, p. 226, 1853.
45. WIGAND: 'Beiträge zur Pflanzeneratologie,' Botanische Untersuchungen, 1854.
46. SCHACHT, H.: Beiträge zur Anatomie und Physiologie der Gewächse, 1854.
47. KARSTEN: 'Organographische Betrachtung der *Zamia muricata*,' Abhandl. der Königl. Akad. Berlin, pp. 193-220, 1856.
48. HENFREY, A.: An Elementary Course of Botany, p. 603, 1857.
49. AGARDH, J. G.: Theoria systematis plantarum, pp. 17-21, 1858.
50. SCHACHT, H.: Lehrbuch der Anatomie und Physiologie der Gewächse, Theil ii, 1859.
51. SCHACHT, H.: Grundriss der Anatomie und Physiologie der Gewächse, col. 507-511, 1859.
52. PAYER, J. B.: 'Rapport fait à l'Académie des Sciences sur la Fleur des Conifères,' Adansonia, i, 1860-61.
53. CASPARY, R.: 'De Abietinearum floris feminei structura morphologica,' Ann. des Sciences Nat., 4^{ième} série, vol. xiv, 1860.
54. BAILLON: 'Recherches organogéniques sur la Fleur femelle des Conifères,' Adansonia, vol. i, 1860-61.
55. BRAUN, A.: see no. 81.
56. DICKSON: 'Observations on some Bisexual Cones occurring in the Spruce Fir (*Abies excelsa*),' Edinburgh New Philosophical Journal, 1860.
57. RODET, J. A.: 'Note sur l'anatomie et sur la physiologie d'un cône de Pin,' Comptes Rendus, liii, Paris, 1861.
58. WOOD, A.: Classbook of Botany, p. 659, 1861.
59. SCHLECHTENDAHL, D. F. L.: 'Beiträge zur Kenntniss der Coniferen,' Linnaea, Bd. xxxiii, 1864-65.
60. PARLATORE: 'Studi organografici sui fiori e sui frutti delle Conifere,' Opuscula botanica, 1864.
61. ØRSTED, A. S.: 'Bidrag til Naaletroeernes Morphologi,' Videnskab. Meddelelser Nat. Foren. Kjøbenhavn, 1864. Retrogressive Metamorphosis as the normal path of development, especially with reference to the structure exhibited by Gymnospermous Flowers.

62. BAILLON: 'Nouvelles Recherches sur la Fleur femelle des Conifères,' Adanson, vols. v-vi, 1864-65.
63. FAVRE, E.: 'Recherches sur la Fleur femelle du *Podocarpus sinensis*,' Ann. des Sciences Nat., 5^{ième} sér., vol. iii, 1865.
64. DUCHARTRE, P.: Éléments de Botanique, p. 934, 1867.
65. VAN TIEGHEM: 'Anatomie comparée de la Fleur femelle des Gymnospermes,' Ann. des Sciences Nat., 5^{ième} sér., Bot., 1868-69.
66. SPERK, G.: 'Die Lehre von der Gymnospermie,' Mémoires de l'Acad. Impér. des Sciences de St.-Petersb., 7^{ième} sér., tome xiii, No. 3, 1869.
67. BRAUN, A.: 'Ueber eine Missbildung von *Podocarpus chinensis*,' Monatsber. der Akad. der Wissensch.: Berlin, 1869.
68. BRONGNIART, AD.: 'Note sur la Constitution du Cône des Conifères,' Bullet. de la Soc. Bot. de France, vol. xviii, 1871.
69. MOHL, VON: 'Morphologische Betrachtung der Blätter von *Sciadopitys*,' Bot. Zeitung, 1871.
70. STRASBURGER, E.: Die Coniferen und Gnetaceen, 1872.
71. EICHLER: 'Sind die Coniferen gymnosperm oder nicht?' Flora, 1873.
72. MAOUT, LE, and DECAISNE, J.: A General System of Botany (Mrs. Hooker's transl.), p. 739, 1873.
73. BRÜGGER, C. G.: Jahresberichte der Naturforsch.-Gesellsch. Graubündens, II. Jahrgang, 1873.
74. BENTLEY: Manual of Botany, p. 642, 1873.
75. BRAUN, A.: 'Krüppelzapfen,' Verhandl. des Botan. Vereins d. Prov. Brandenburg, p. 98, 1874.
76. THOMÉ, O. W.: Lehrbuch der Botanik, p. 213, 1874.
77. LINDLEY and MOORE: Treasury of Botany, 1874.
78. EICHLER: Blüthendiagramme, 1875.
79. BRAUN, A.: 'Abnorme Fichtenzapfen,' Flora, Nr. 26, 1875.
80. BALFOUR, J. H.: A Manual of Botany, p. 596, 1875.
81. BRAUN, A.: 'Die Frage nach der Gymnospermie der Cycadeen erläutert durch die Stellung dieser Familie im Stufengang des Gewächsreichs,' Monatsber. d. Königl. Akad. Wiss.: Berlin, 1875.
82. SACHS, J.: Text-book of Botany, Eng. ed., 1875.
83. PRANTL, K.: Lehrbuch der Botanik, p. 134, 1876.
84. STENZEL, G.: 'Beobachtungen an durchwachsenen Fichtenzapfen. Ein Beitrag zur Morphologie der Nadelhölzer,' Nova Acta, 1876.
85. BERTRAND, C. E.: 'Études sur les téguments séminaux des Gymnospermes,' Ann. des Sciences Nat., 6^{ième} sér., 1878-79.
- 85 a. STRASBURGER, E.: Die Angiospermen und die Gymnospermen, 1879.
86. WILLKOMM: 'Zur Morphologie der samentragenden Schuppe des Abietineenzapfens,' Nova Acta, 1879.
87. ČELAKOVSKÝ, LAD.: 'Zur Gymnospermie der Coniferen,' Flora, 62^{ter} Jahrg., 1879.
88. GRAY, ASA: Structural Botany, Part i, p. 270, 1879.
89. BENTHAM and HOOKER: Genera Plantarum, Part iii, p. 420, 1880.
90. ARCANGELI, M.: 'Sur la Structure de la Fleur femelle des Conifères et sur la Question de la Gymnospermie,' Congrès Internat. de Bot. et d'Hort.: Paris, 1880.

91. EICHLER : 'Ueber die weiblichen Blüthen der Coniferen,' Monatsber. d. Königl. Akad.: Berlin, 1881.
92. FIGUIER, L.: The Vegetable World, p. 334, 1882.
93. GOEBEL, K.: Grundzüge der Systematik und speciellen Pflanzenmorphologie, p. 365, 1882.
94. ČELAKOVSKÝ, LAD: 'Zur Kritik der Ansichten von der Fruchtschuppe der Abietineen,' Abhandl. d. königl. böhm. Ges. d. Wiss., 6. Folge, Band xi, 1882.
95. EICHLER : 'Ueber Bildungsabweichungen bei Fichtenzapfen,' Sitzungsber. d. königl. Akad. d. Wiss.: Berlin, 1882.
96. ČELAKOVSKÝ, LAD: 'Ueber Herrn A. W. Eichler's Entgegnung auf meine Kritik seiner Ansicht von der Fruchtschuppe der Abietineen,' Sitzungsber. d. königl. böhm. Ges. d. Wiss.: Prag, 1882-3.
97. VESQUE, J.: Traité de Botanique, p. 53, 1885.
98. MANGIN, L.: Cours élémentaire de Botanique, p. 294, 1885.
99. SCHENK: Handbuch der Botanik, Bd. iii, p. 410, 1887.
100. BOWER, F. O.: Practical Botany, p. 247, 1888.
101. VELENOVSKÝ, J.: 'Zur Deutung der Fruchtschuppe der Abietineen,' Flora, 1888.
102. HÉRAIL, J.: Traité élémentaire de Botanique, p. 412, 1889.
103. ČELAKOVSKÝ, LAD: 'Die Gymnospermen: eine morphologisch-phylogenetische Studie,' Abh. d. königl. böhm. Ges. d. Wiss., 7. Folge, Bd. iv, 1890.
104. VAN TIEGHEM: Traité de Botanique, vol. ii, p. 1461, 1891.
105. MASTERS, M. T.: 'Review of some points in the Comparative Morphology, Anatomy, and Life-History of the Coniferae,' Journ. Linn. Soc. Bot., vol. xxvii, 1891.
106. FRANK, A. B.: Lehrbuch der Botanik, 2^{ter} Band, 1893.
107. STRASBURGER, &c.: Lehrbuch der Botanik, 2^{ter} Theil, 1894.
108. NOLL: 'Der morphologische Aufbau der Abietineenzapfen,' Sitzungsber. der Niederrheinischen Ges. zu Bonn, 1894.
109. PENZIG: Pflanzen-Teratologie, 1894.
110. SCOTT: Structural Botany, vol. i, p. 268, 1895.
111. VINES, S. H.: A Students' Text-book of Botany, Part ii, p. 482, 1895.
112. GREEN, J. R.: A Manual of Botany, vol. ii, p. 178, 1896.
113. WILLIS, J. C.: A Manual and Dictionary of the Flowering Plants and Ferns, vol. ii, 1897.
114. ČELAKOVSKÝ, LAD: 'Nachtrag zu meiner Schrift über die Gymnospermen,' Botan. Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie, edited by A. Engler, 1897.
115. STRASBURGER: Das botanische Practicum, 3^{te} Auflage, 1897.

Worsdell, Wilson Crosfield. 1900. "The structure of the female 'flower' in Coniferae. An historical study." *Annals of botany* 14, 39–82.

<https://doi.org/10.1093/oxfordjournals.aob.a088771>.

View This Item Online: <https://www.biodiversitylibrary.org/item/238259>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a088771>

Permalink: <https://www.biodiversitylibrary.org/partpdf/318573>

Holding Institution

Smithsonian Libraries

Sponsored by

Biodiversity Heritage Library

Copyright & Reuse

Copyright Status: Not in copyright. The BHL knows of no copyright restrictions on this item.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.