TANICAL MEMOIRS. No. 9

21

FORM-FACTORS IN CONIFERAE

By

A. H. CHURCH, M.A.

HUMPHREY MILFORD
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CONTENTS

These notes comprise a section arranged as supplementary to the preceding Memoir (No. 8), and written out in greater detail as emphasizing the more speculative treatment of such facts of external morphology as may be readily observed without elaborate microscopic preparations, in the case of forms which are commonly available in garden-cultivation or in forestry practice; again as illustrative of the method by which such casual data may be utilized in attaining a broader view of the life-problems of this now relatively residual group of plant-organism.

BOTANIC GARDEN, OXFORD,
July 1920.

FORM-FACTORS IN CONIFERAE

During the last decades the investigation of Gymnosperms, and more particularly that of Coniferous trees, has been concerned with the detailed examination of reproductive processes and phases, as also of cytological phenomena, with a view to determining 'affinities' by the more obscure relations of the vestigial gametophytes and sexual organs.[1] Anatomy and timber-structure have been more intensively studied,[2] but the general external morphology remains very much in the state it was left at the hands of an older generation.[3] Much can, however, still be done in the observation of the more striking characters as seen with the naked eye; there being many such features which appeal to an observer in the open, though they may be less appreciated in the laboratory. Many of the older generalizations, again, are capable of revision in the light of a broader modern outlook on the general problems of ecology and biology of the vegetable kingdom as a whole.

Such broader features of growth-form cover a wide range of morphological adaptations as representing solutions of special biological problems, of a significance quite as important in the everyday life of the organism as the more minute mechanism of cell-anatomy, or of racial continuation, and may be equally archaic and vestigial in some respects, as presenting the progression of a unique and disappearing race of tree-forms.[4]

Somatic Organization, including specialization of the *space-form* of the plant, and its adaptation to subserve different functions, involves the successful utilization of a few simple *general factors* of the relation of 'stem' (*axis*) and 'leaf' (*appendage* or 'member'). This conventional standpoint is very generally accepted as a postulate for the study of subaerial vegetation, but has been deduced solely from the academic contemplation of the land-plant. Yet even these fundamental conceptions are to be traced back to submarine ancestry, as somatic adaptations for existence in a medium very distinct from that in which such plants are now found, and are to be explained as part of the inherited equipment of the race, established in response to an entirely different system of physical factors, but now ingrained as an unalterable constant feature of the organization; just as in the case of the dorsiventral human body with axis and limbs, for which an origin must be sought in the fish of ancient seas.

I. Phyllotaxis: The leaf-arrangement of Conifers is normally based on a Fibonnacci construction (ϕ ratio); i. e. the leaf-system at the growing-point shows in its first visible inception contact-curves in terms of the numbers 3, 5, 8, 13, &c. (Abietineae, Taxodineae, Araucarineae), with few minor exceptions; this spiral arrangement being remarkably constant and accurate. Relics of the pattern may be long expressed on the surface of older axes, as they are also familiar in the fruiting cones; while these primary relations of the leaf-primordia control the subsequent arrangement of the branches of the main stem.

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[1] Saxton (1913), p. 242; Seward (1919), p. 106.

[2] Penhallow (1907).

[3] Masters (1891).

[4] The most majestic productions of the vegetable kingdom are rapidly disappearing, and will never be replaced. No future scheme of forest-cultivation will even countenance a tree growing to maturity in 500–1,000 years, and persisting for 3,000–4,000. The records of an older generation are already often regarded with scepticism; cf. American data (Sargent); *Pinus Lambertiana*, 245 ft. and 18 ft. diam. (Douglas); Weymouth Pine of Eastern States (*P. Strobus*), 250 ft. and 6 ft. diam.; Sitka Spruce (1806), 300 ft. and 13 ft. diam.; *Sequoia sempervirens*, 400 ft. (Sargent); *S. gigantea*; 35 ft. diam., and 4,000 years old, giving 50,000 c. ft. of timber; Douglas Fir, 350 ft. and 16 ft. diam., *Abies grandis*, 300 ft.

The same applies to the Kauri Pine of New Zealand, recorded at 275 ft. and 22–24 ft. diam. (Kirk), with cylindrical bole 100 ft. and estimated yield of 30,000 c. ft. of timber (Hutchins). Modern forestry prefers a tree of 2 ft. diam. in 100 years.

The original pattern is to be seen most perfectly at the actual growing-apex; increased tangential extension of the members may give contact-series in lower numbers of the summation-series; just as diminished growth may imply that more contact-lines are seen (cf. *Pinus excelsa*, cone (5 : 8) in the first year, with scales broadening to (3 : 5) contact in the second season; the latter case in cones of *Araucaria brasiliensis*. In *Abies nobilis* the cone-scales, tangentially extended and flattened, retain contact-parastichies of (5 : 8); but the reflexed bract-scale laminae neatly fill rhomboidal areas of which the most obvious contact lines are (13 : 21)).

A higher ratio is also seen in the case of 'open' cones, as compared with the original pattern of the 'closed' green cone. On the adult cylindrical axis the system may remain more or less obvious; with enlarged scale-effects (*Pinus Laricio*, 5–10 years), or with the units more widely spaced (*Araucaria imbricata* for 50 years).

Owing to the relatively small size of the photosynthetic members (*microphylly*), except in *Dammara* and *Ginkgo*, as also the absence of secondary changes in size, shape, dissection of the lamina, intercalation of petioles, &c., general in 'broad-leaved' Angiosperms, the original arrangement remains particularly clear throughout the group, and is little interfered with; hence such patterns attract attention, and one asks why such constructions occur, and what they may mean. Fibonacci relations represent the mathematical solution of the problem of building a centric shoot-system, one member at a time, at successive angles of $137\frac{1}{2}°$ (very approximately), as a condition of balanced symmetry; and any ratio of the Fibonacci series closely approximates this angle. The construction was not initiated specially for land-plants, though it may have been modified and much improved in present mechanism; but is again inherited as an optimum method of older shoot-construction, probably from distant marine organism—since Fibonacci relations occur also in marine plants—unless there may be some reason for changing it.

Variations on these numbers are relatively unimportant; but the occurrence of such ratios as (3 : 4), (7 : 11), (10 : 16), which are found exceptionally at the apices of shoots, or in cones, and are open to similar secondary changes along their corresponding summation-series, suffice to indicate that the mechanism of the curve-pattern is now complex, and subject to deterioration, since no longer limited either to any accurate spacing-angle, or to strict Fibonacci numbers. Such variants are sufficiently uncommon to be regarded as anomalies in the construction-system, and the retention of Fibonacci ratios is a characteristic feature of the groups Abietineae, Taxodineae, Araucarineae, and Taxoids.

In the Cupressineae alone whorled symmetry is attained as an alternative arrangement, appearing expressed in terms of circles (*whorls*) instead of spirals, though still following the lower numbers of the Fibonacci series (2, 3), and giving whorls in alternating sequence (*dimery*, *trimery*). So strict is this feature within this group that it serves to delimit an entire series of genera. Such reduction-specialization, clearly secondary and derivative from Fibonacci-construction, may be regarded as a form of *xeromorphic adaptation*; since not only do such symmetrical constructions, by involving increased superposition, imply a diminished light-utilization, and hence less chloro-evaporation in the long run; but the lower members of the series (1, 2, 3) imply a diminished output of leaves per node, which, other things being equal, again expresses a diminished transpiration. In the special case of the decussate Cupressineae (*Thuya*, *Chamaecyparis*, *Libocedrus*) the strict symmetry of the construction in planes at right angles is utilized to extend the possibilities of shoot-construction preferably in one plane, resulting in the production of characteristic 'phyllomorphs'.

On the other hand the advantage of a symmetrical balance in any ratio of the Fibonacci series is seen in the isolation of the members of a 'false-whorl' of lateral leaders from successive members of the spiral sequence, with optimum effect at the Fibonnacci numbers themselves (3, 5, 8).

II. The Branch-system may be based on the theory of the axillary-bud, which suggests that every leaf-member may subtend a new shoot in its axil to continue the ramification of the axis; and that, conversely, no ramification takes place in these plants except by means of axillary buds. Dichotomy of the apex, and fasciation, would be regarded as a freak, or the expression of failure in normal mechanism. The origin of this mode of construction is still obscure; i. e. it also undoubtedly dates back to the sea, and normally appears in land-plants as an alternative for dichotomy of the shoot-apex (cf. *Lycopodium*); it is a fact of observation rather than a law; and hence may be assumed to represent the most generally successful method of shoot-ramification yet attained.

The phyllotaxis-construction of every axillary bud is initiated independently at its own apex; each new lateral in fact starting off in the manner of a new seedling-apex. Though certain relations of symmetry may normally obtain in some cases between the primary system and the secondary axes (cf. Phyllomorphs), there is no reason to suppose that the position of adjacent members, or any assumed pressure of the subtending leaf on the emergent bud has anything to do with the arrangement adopted.

The highest Conifers utilize the greatest number of axillary buds, and express greater complexity in such selection and differentiation. The ingenuity of the mechanism is probably centred in the fact that the axillary bud is normally in a position to be supplied with food from the subtending leaf; hence with the differentiation of the leaf-member for special functions other than that of photosynthesis, axillary ramification is at once suppressed (for want of local food-supplies). Thus bud-scales and reproductive leaves (stamens) omit axillary growths; the case of the Pine-cone may be left open for the present.

Ramification from the leaf-axils of a reduced spur-shoot is also rare (*Ginkgo, Cedrus*), but occurs normally in *Taxodium*: more than one bud from an axil does not occur in Conifers; hence such trees stripped of foliage-spurs have no power of recovery. On the other hand, *Taxus*, with few axillary buds, may produce shoots from dormant axils in profusion on clipping. Total suppression of all lateral buds whatsoever may be looked for, but would be regarded as a freak; occasional in Spruce, giving a single unbranched stem very conspicuous among associated seedlings as the 'disbudded mutant' (cf. *Helianthus*, giant-strain; *Zea*).

The greatest differentiation of axillary buds obtains in *Pinus*, in which such lateral derivatives are strictly localized, of the form (1) lateral leaders, (2) foliage-spurs, (3) staminate flowers, (4) ovulate flowers, as expressing local segregation of special morphological factors in the apices concerned. This segregation is so definite that any departure from the rule would be regarded as an anomaly; e.g. where lateral leaders or ovulate flowers replace foliage-spurs in the middle of the annual shoot (case of 'multinodal' Pine), or a foliage-spur producing juvenile leaves (*Pinus rigida*). On the other hand, in *Taxus*, vegetative buds, or ovulate shoots, arise without rule, and any foliage-leaf may subtend any type of lateral, or produce none at all; this extending even to the occasional production of ovulate flower-shoots on the staminate tree.

Types widely dissociated, as *Cedrus* and *Ginkgo*, normally utilize the axils of all the primary leaves of the main axis (except bud-scales) for the production of specialized photosynthetic spurs, with a few leaders. In others, leaders ('long shoots') are produced apparently casually from the axils of leaves at considerable distances (*Larix*), or from rhythmically selected members of the phyllotaxis-system (*Araucaria excelsa*). Staminate and ovulate flowers are similarly produced (*Picea, Abies*), the tendency being to produce them more freely at the distal end of the annual shoot, as the expression of an 'upward drift' of food-supplies to the vicinity of the growing-point and the elaborating winter-bud. Such flower-shoots may be numerous (*Picea, Abies*) or few (*Araucaria*).[1] The ultimate restriction of the lateral leaders to a cycle at the distal end of the shoot gives the case of the 'false-whorl', typical for the more precise *Pinus*-type and for *Araucaria*; less accurate in *Picea, Abies*, and multinodal Pines.

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[1] Comparison of young plants of *Picea excelsa* or *Abies pectinata* shows clearly that such restriction of laterals to the immediate vicinity of the terminal bud is an effect of enfeebled nutrition. In such ramuli with D.V. laterals two buds (right and left of the terminal) give the limiting case before complete suppression of the laterals altogether as in lower branches. Such enfeebled nutrition again is not the effect of failure in carbohydrate photosynthesis, or of effective insolation, so much as the consequence of lack of food-salts for further proteid-synthesis, and thus appears as the result of failure in the transpiration current and water-supply. A bias for the inception of such morphological phenomena as the 'false whorls' of *Pinus*, and the bilateral frond-systems of *Araucaria*, is inherent as the response to the effect of xerophytic conditions, however much such morphological factors may be subsequently specialized as constants in the generic equipment.

Araucaria, with the least differentiation of leaf-members (no bud-scales, no spurs), shows the fewest lateral leaders, with flowering shoots as the only other axillary derivatives; so far it may be regarded as a very specialized type along its own lines rather than primitive.

The production of a main leader from a lateral may be effected (*Pinus*) by the erection of one member (usually the strongest) of the false whorl; or several may diverge and erect more or less. In the case of *Cedrus* and *Larix*, leaders may follow on from a simple spur-growth; the less so, however, as the spur-growths are older; and similarly *Ginkgo* rarely regenerates a new leader from a spur. The case of *Araucaria excelsa* is of special interest, as a damaged terminal may regenerate a symmetrical terminal growing-point with laterals also symmetrically spaced around it.

Special *foliage-spurs*, beginning as shoot-branches with normal leaf-production (*Sequoia gigantea*), freely cut away from older branches, up to a foot in length, are more emphasized in the deciduous *Taxodium distichum*, bearing 50 leaves or more, and even branches of higher degree. By omission of internodal extension these reduce to densely tufted or clustered growths, with 30–40 leaves per season (*Larix*); reducing further to about 20 leaves per season, for many years in succession (*Cedrus*), or about 5 in the deciduous *Ginkgo*. The number reduces further, 5–3–2, in *Pinus*-types; the limit of 2 indicating the highest organization in this respect, as the limiting case of centric symmetry. The case of the single leaf (*P. monophylla*) is regarded as less satisfactory, and of the nature of a freak; but a special and equally anomalous case occurs in the 'double needle' of *Sciadopitys*, in which the entire sequence of spur-formation has been gone through, attaining a limit of 'false-whorls' of single 'bifoliar' spurs in a manner beyond even that of *Pinus*, and in a distinct alliance.

Phyllomorphs, also shed as distinct shoot-systems, may be regarded as a special case of spur-formation, on the lines of *Taxodium*, but branched to the 3rd and 4th degree (*Chamaecyparis*, *Thuya*, *Libocedrus*, *Biota*). In these last a rhythmic segregation of laterals works out a characteristic pattern, as a 'leaf-mosaic', the constants for which may vary slightly in the different forms (cf. *C. Lawsoniana*). The most interesting feature of the mosaic is possibly the modification of the general scheme in the distribution of the basal ramuli of each degree; a ramification being commonly omitted on the basiscopic side, but put in on the acroscopic flank, giving the effect of 3 (2–4) successive ramuli on the front margin (*C. Lawsoniana*, *C. Nootkatensis* 3, less commonly 2–4). Similar variations may occur in other forms, 2 (3) successive ramuli in *Libocedrus decurrens*, 3–4 *Thuya occidentalis*, 2–5 in *Thuya gigantea* with more nodal variation, but normal regular alternation in *Biota*.

III. Dorsiventrality: For want of a better term it is usual to utilize this expression, borrowed from animal morphology, to express a differentiation of upper and lower surfaces in any bilateral construction, whether of branch-nature or leaf-lamina. The dorsiventral habit in branch-organization is associated with intense insolation and the production of small foliage-members which do not irregularly shade one another. The system as a whole is orientated so that all the leaf-units may obtain a fairly equal light-exposure. As a rule, the more reduced the leaf-member the greater the demand for adjustment in the branch-system as a whole; so that the latter is treated more and more in the manner of a compound leaf. Thus *Ginkgo* with broad long-petioled foliage-leaves, more in the manner of ordinary Angiosperms, presents little branch-dorsiventrality; the extreme case of such orientation occurs in microphyllous phyllomorphic Cupressineae.

(*a*) With the differentiation of an erect leader, maintained vertically by negative geotropism, as a question of balance as well as of optimum exposure to the external medium, the available lateral space is controlled preferably by a symmetrical system of laterals which assume a more or less horizontal position, or ascend at a wide angle (over 45°) to be subsequently pulled over by their weight (*Araucaria*) in graceful curves. Such horizontal projection is also geotropically regulated, to the extent that an individual in which such control is imperfect, so that all the laterals ascend at a steep angle or vertically, is regarded as a monstrosity (fastigiate forms of *Cupressus*, *Taxus*, and Spitzfirs Spruce); or again if merely pendulous (Serpent Spruce) beyond the effect of normal drooping in a less mechanically efficient axis (leaders of Deodar, *C. Lawsoniana*, laterals of *Larix*). The free ends of laterals carried well beyond their fellows may erect (*Sequoia gigantea*, *Thuya gigantea*, *Cryptomeria*), but this in *Larix* would be regarded as a freak, as a phase of the mechanism which will reorientate a new leader if the main axis is damaged. Dwarf-forms lacking erected leaders give prostrate plants, as Meadow Spruce, dwarf Juniper, and dwarf *Pinus montana* (*P. Mughus*), and such forms may be maintained in cultivation, as by grafting.

(β) Beyond mere orientation of normally produced branch-systems, a conspicuous example of which is noted in *Cedrus*, with the spur-shoots all orientated vertically to the upper surface of the laterals, the effect may extend to the initiation of lateral ramifications of higher degree, as in *Araucaria*, in which laterals of second and third degree are formed in flanking orthostichies only of the main shoot to produce the special bilateral frond-effect (*A. excelsa*). Although this can be effected fairly satisfactorily in terms of spiral construction, the result will be much more precise when based on a preceding condition of symmetrical leaf-arrangement; and thus in Cupressineae with decussate phyllotaxis giving bilateral symmetry to begin with, the arrangement is extended to the production of laterals only from the axils of 2 series of leaves out of the 4. This sequence may be maintained for 2–3–4 degrees of ramification in the same plane of bilaterality, resulting in the familiar phyllomorphs of this section, in distinct generic forms (*Thuya*, *Libocedrus*).

(γ) A third phase of dorsiventrality is seen in the general twisting of leaf-petioles to re-orientate the foliage-units themselves with reference to incident light. Spiral systems thus present varying degrees of distortion as the members turn to the upper surface, or form two flanking series culminating in more precise *pectination* in lateral series (*Taxus*, *Taxodium*, *Sequoia sempervirens*, *Tsuga*, *Abies pectinata*); and in many cases the effect is confined to more horizontally placed laterals, while vertical shoots retain the original spiral arrangement (*Taxus*, *Sequoia sempervirens*, *Podocarpus japonica*), as a condition which has been loosely described as giving a *dimorphic* shoot-system.

(δ) A further effect may be noticed in the associated orientation of the floral shoots on dorsiventral branches, though the meaning of such response is not clear: the effect is geotropically regulated. Thus the staminate flowers erect on the upper surface of dorsiventral laterals in *Cedrus* and *Araucaria*, but turn downwards in *Larix*, *Abies*, *Pseudotsuga*, and *Taxus*. On the other hand the carpellary flowers are erected in *Cedrus*, *Araucaria*, *Larix*, and *Abies*, but are turned to the lower surface in *Taxus*. In *Biota* they are horizontally projected, as also curiously in *Cryptomeria*, and more or less inverted in *Juniperus sphaerica*.

While dorsiventrality in the leaf-lamina is structural, following from the mechanism of elaboration of a lateral leaf-primordium, however much it may be outwardly lost in fairly isodiametric needle-leaves (*Cedrus*, *Larix*, 5-needled Pines), the dorsiventrality of the branch-system is always secondary, and is superposed on a centric internal organization, apparently in response to insolation, though the mechanism may be largely controlled by geotropism. It is clear that different phases of dorsiventrality may be attained independently in different types, to varying extent, and in unequal degrees, as specific or generic constants; e.g. *Pinus* exhibits slight dorsiventrality only in primary lateral leaders; *Araucaria imbricata* and *A. excelsa* to a much greater extent in secondary and tertiary laterals as well; *Cupressus Lawsoniana* and *C. Nootkatensis* illustrate the extreme condition of phyllomorph construction; on the other hand, *Taxus* only shows dorsiventrality in the pectination of the foliage-leaves and the position of the flower shoots. Types with no specialization of dorsiventrality are less frequent. It is practically wanting in *Cryptomeria*, little in *Ginkgo*, as also in trimerous *Juniperus communis*. Loss of effective regulation may also affect one form of dorsiventrality without necessarily involving another. The fastigiate habit is apparently normal for *Biota*, giving radially orientated laterals with phyllomorphs, as in fastigiate *Cupressus Lawsoniana* (cultivated vars.); in *Taxus* the fastigiate variant also omits the pectination of the foliage-leaves, but is so rare as to be regarded as an occasional 'sport'.

IV. Strobilus Factors: A generalized shoot-construction producing sporophylls with wind-dispersed spores, compacted to a bud-formation for mutual protection from desiccation during development, is termed a *strobilus*. Among homosporous types of Pteridophyta these attained their maximum expression in fossil Lepidostrobi (Lycopodineae) of the Carboniferous; the largest known construction, apparently borne on an arboreal type, being about 18 in. long and 2 in diam. Among Cycads the staminate flowers, repeating very similar strobiloid characters, may be 2 ft. in length. The staminate flower of *Araucaria imbricata* (6 in. by 2) including about 600 sporophylls, is recognizably of the same category, and the smaller staminate constructions of other Conifers are simplified and reduced shoot-systems of the same degree and value, though no more than 5 mm. long.

Where heterospory obtains, and a zone of intermediate leaf-members is differentiated at the base of the strobilus to subserve further bud-protection during spore-maturation, the latter region becomes a '*perianth*' investment, soon restricted to a minimum series of members, as one 'cycle of contact', and the microstrobilus passes on to the condition of a more obvious *staminate flower*; other special factors of mechanism may then be added, as intercalary zones of extension and time-factors.

Though there may be now no definite evidence of the 'hermaphrodite' condition among Conifers, the primitive presentation of both micro- and mega-regions may be assumed from the evidence of the general progression of heterospory in the Pteridophyte series of Equisetaceae (fossil) and *Selaginella*; while the fact that such hermaphrodite flowers obtained among Cycadeoidea (fossil), and that a relic may be traced in the living *Welwitschia*, is sufficiently suggestive of the view that the monoecism of the modern Conifer is a phenomenon of secondary reduction, and the expression of the enfeebled nutrition of the types; just as the further progression to *dioecism* (*Taxus*, *Juniperus*) further exaggerates the separation of the two forms of spore, and in the limit may tend to increase the output of cross-fertilized seeds.

In the progressive adaptation of Conifers to conditions of more xerophytic habit (as under competition with higher grade Angiosperms), whether (1) in dry regions, tropics, or sub-tropics with hot summer, or (2) on exposed mountain slopes of northern latitudes, the staminate flowers dwindle in size; they (1) perennate in small condensed strobili naked over the dry season (*Cryptomeria*, *Cupressus*), or (2) are more securely packed within specialized perennating winter-buds. With more efficient bud-protection the perianth-region may become more definite (*Larix*), and indications of a mechanism to assist the discharge of the pollen at the time of bud-expansion in a more precise manner may be added, as following the necessities of a shorter flowering season. This may be effected by a rapid extension of all the internodes of the floral axis (*Pinus*), or by the localization of one such internodal extension between the 'perianth' and the 'stamens' (*Taxus*, *Tsuga*). In *Taxus*, especially, the perianth-members are coloured white, the innermost are the largest, and the whole series is distinctly quincuncial in the manner of a 'calyx'.

The larger strobili of the more tropical Araucarias, with no bud-scales, are so far primitive in the group; and the minute naked flowers of *Cupressus*, of only a dozen microsporophylls symmetrically placed and packed, express extreme reduction-specialization; yet the rounded sporangia of the latter type are possibly the more elementary as expressing the simplest form of a sporangial aggregate of tetrads.

The manner in which these spherical sporangia are primitively borne on the sporophyll is emphasized in the more obviously pendulous pollen-sacs of *Ginkgo*; while in the larger Araucarian flowers similar pendulous pollen-sacs are extended radially to keep pace with the greater room in the broad bud. In more advanced types a certain amount of 'fusion' with the sporophyll-stalk implies increased area for efficient absorption of food-material for the developing spores (*Cedrus*, *Pinus*); but such stamens are clearly referable to the same Araucarian model with many pollen-sacs. The terminal insertion of the pollen-sacs is again retained in *Taxus*, with 'peltate' sporophylls in the manner of *Equisetum*.

The number of pollen-sacs ranges from 8–15 (*Araucaria*), 15 *Agathis*, 5 (*Dammara*), to 3–4 (*Sequoia*, *Juniperus*, *Cupressus*), and the limiting case of 2 symmetrically paired sporangia on the bilateral leaf-lamina is widely distributed (*Pinus*, *Ginkgo*, *Sciadopitys*). It is interesting to note that no Conifer reduces to one sporangium per microsporophyll in the manner characteristic for Lycopodineae; although the latter compensated a greater wastage of spores.

Similarly the almost universal restriction of the pollen-sacs to the lower surface of the sporophyll appears a very distant adaptation, following the case of the Cycads, and curiously contrasting with that of the megasporangia on the upper surface (as in Lycopodineae also). As a detail of clearly subsidiary interest may be noted the change to transverse dehiscence of the pollen-sacs observed in the pendulous flowers of *Abies* and the erect flower of *Tsuga*, as probably a more recent variation.

V. The Ovulate Flower: The morphology of the ovulate flower has presented considerable difficulty. It is admittedly based on an elementary type of strobilus, of which the microstrobilus should be the parent-form; but it has been so much modified in connexion with subsequent adaptations for the production and protection of *seeds*, that the homologies are no longer obvious, and the existing ovulate flowers may have passed through a long sequence of reduction-specialization, in which useless parts have been largely eliminated. If it were not that in Cycads definite bilateral leaf-forms with marginal megasporangia still persist as actual foliaceous carpels (*Cycas*), with many stages of reduction to forms with 2 ovules borne beneath a peltate cone-scale (*Zamia*), it would be difficult to assign any carpellary significance to the members of the ovulate flowers of such types as *Pinus*.

There can be little doubt, however, that the 'bract-scale'[1] *of the Pine-flower is a vestigial carpel*; though it no longer bears the megasporangia. Nor in any Conifer can the ovules be said to be borne on a carpellary leaf, but at best are distinctly axillary or axial in origin: this being particularly obvious in the simpler constructions of the Cupressineae and Podocarps. An analogous case is seen among Lycopodineae, especially in *Selaginella*, in which, as the megasporophyll loses its photosynthetic value, the sporangium is borne in an axillary position in which it may receive food-supplies from the main shoot-system rather than from the deteriorated subtending leaf; the supply of food-material for reserve-storage to large spores being beyond the capacity of one leaf-member. This is the more emphasized when the spores germinate *in situ* to parasitic prothallia, and the same problem has to be met in Angiosperm carpels. Hence in all types with megaspores the carpels tend to dwindle as the megaspores increase in reserve-storage and future responsibilities. Such a view of the vestigial nature of the functionless carpels in Conifers is borne out by their retarded rate of production in developmental stages. Thus in *Pinus*, the limiting case in the N. Temp., the bract-scales are seen as delayed and rudimentary formations on the young cone-axis with naked apex (Dec.–March), as merely small scales which never grow enough to close over the cone-apex in a bud-formation.

There can be no objection to thus regarding the bract-scale as theoretically a megasporophyll, but it is no longer ovuliferous, and remains as a vestigial relic; in the limit merely indicative of the original phyllotaxis-scheme, and a guide to the later construction of the cone, just as, for very similar reasons, carpels may dwindle and wholly disappear (except as numerical expressions) in many higher families of Angiosperms, as their ovuliferous function is transferred to the new formation of a 'syncarpous' ovary (Cruciferae).

The progressive reduction of the functionless megasporophyll is traced in many types of the Coniferae: where most elaborate in organization it presents a terminal relic of a leaf-lamina, together with lateral lobes of suggestively 'stipular' nature, which appear to express a form of leaf-member considerably more elementary than any other appendage of the Conifer axis; as, again, possibly a vestigial relic of an archaic leaf-formation, now wholly replaced in the xerophytic foliage-system (*Abies*, *Pseudotsuga*). In the limit it appears as the merest scale-member (*Pinus*, *Cupressus*); or may be wholly lost, with the result that the ovule alone remaining appears 'terminal' (*Taxus*), as if a new 'axial' formation.

Where the original strobilus-character remains expressed, and a cone-formation with many aggregated megasporangia is retained (Pinoids), the original carpellary leaves may be retained as (1) protective to the ovules in bud-development (*Cryptomeria*, *Cupressus*), or (2) reduced to mere scales they may assist in the mechanism of pollination, and retain a more extended construction. In such case the attenuated

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[1] The term 'bract-scale' is hence objectionable, since 'bract' implies a leaf-member subtending an axillary growth of the nature of a lateral shoot. It was adopted as a concession to theories of the inflorescence nature of the Pine-cone, and is retained as a fairly established provisional convention.

laminae (' mucro') may constitute a 'pollen-collecting brush', still more or less efficient, as in *Sequoia, Pseudotsuga, Larix, Abies, Araucaria.*

In later phases, the carpellary scale (left as the bract-scale) is wholly superseded by the cone-scale,[1] and remains as the merest relic, even at the pollination-period (*Pinus, Cedrus, Picea*), to be further lost to sight in subsequent cone-development. To this extent the genera among more specialized Abietineae, in which the bract-scale is still functional in pollination, may be regarded as so far more primitive, though the special advantage in pollen-collection may be doubtful. In the higher types of the Abietineae the 'cone-scale' becomes precocious to the extent that it soon usurps the place of the carpel, and shows a similar attempt at a 'mucro' apex (*Pinus*) Probably xerophytic protection of the ovules from the effect of wind is the first essential: the attenuated points of the scales in either case may be effective in both respects as tending to reduce the velocity of the air-currents near the micropyles.

That the ovules were originally megasporangia on the upper surface of the megasporophylls may be fairly assumed: the case of restriction to a symmetrical pair in Abietineae follows the method of reduction from a marginal series in Cycads, but does not necessarily imply a similar arrangement for all the group; the sorus of many ovules (*Sequoia*) may equally tend to a limiting case of reduction to one median ovule only, associated with a median bundle for the leaf, as in Araucarineae; although, as noted, this never obtains in the case of the microsporangium.

Note. Many more or less absurd theories have been promulgated at different times,[2] which are based on the organization of the secondary adult cone-stage, and take no account of the earlier working of the floral mechanism. Thus speculations on the 'bifoliar spur' nature of the Pine-cone scale are quite futile in view of the presence of identical growths in more generalized 5-needled Pines, as also in *Cedrus*, with full type of spur, or again in *Tsuga* and *Picea*, with no spurs at all. Speculations beginning with *Pinus*, as the most complex cone of all, are of little value. To introduce ideas of 'ligules', 'arils', 'epimatia', in entire ignorance of what these words imply in actual homology, is equally vague.

Simpler views on the significance of the part played by the bract scale (*b*) and cone-scale (*c*) in floral mechanism are interesting in that they tend to mark the essential divergence of types convergent in other respects; cf. Cedrus (*c*) and Larix (*b*), with tufted spurs; *Tsuga* (*c*) and *Pseudotsuga* (*b*), *Picea* (*c*) and *Abies* (*b*).

VI. Cone-formation: The Conifer series may be sharply divided into two main sections, according as the ovulate flower retains evidence of its older strobiloid origin (Pinoids), or reduces to a limit of a single ovule (Taxoids); the latter case passing on to an association with birds for the dispersal of the seeds, while the former retains the older method of wind-dispersal with more or less 'winged' seeds. Minor irregularities in this progression, as in the small but distinct cone-construction of *Saxegothea*, or the bird-dispersed berry of some species of *Juniperus*, do not affect the main question; but are the more interesting as expressing the simultaneous approach of a new problem. In both cases reduction of ovules and seed-output appears antecedent to the necessarily comparatively recent utilization of bird-life, which serves to further emphasize a preceding xerophytic mechanism of water-storage and sclerosis.

The original cone of the Pinoid series is thus to be regarded as a secondarily adapted phyllotaxis-system of carpellary members, utilized to build a mechanism for the protection of the germinating spores, the sexual prothallia during fertilization-stages, and the ultimate growth of the embryo in the seed-stage. The significance of these events in the life-history sufficiently expresses the fundamental importance of

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[1] The term 'cone-scale' is harmless, as the growth does constitute the essential feature of the cones of higher Conifers; but 'ovuliferous scale' may introduce misconceptions. Apparently in no case can the ovules be said to be initiated on such a scale, but are always axillary to begin with; the effect of 'insertion' on the scale being due to subsequent intercalation at the base of the cone-scale as it becomes predominant in later stages of cone-formation. This is more emphasized in the case of *Abies* (sp.), in which ovules, bract-scale, and cone-scale may be conspicuously elevated on a distinct new pedicel region (*A. Veitchii, Pseudotsuga*).

[2] Coulter and Chamberlain (1910), p. 244.

[3] Worsdell (1900), *Annals of Botany*, xiv. 39.

such mechanism in a race of xerophytic arboreal organism; and the cone in its final stages of elaboration becomes, in fact, the distinctive feature of the group, playing a part in the biology of reproductive processes quite on a par with the 'ovary' specialization of the Angiosperm, and hence undoubtedly contributing to the present success of the race in maintaining a footing in the world, which otherwise has largely passed over to the domination of the Dicotyledonous 'Flowering Plant'.

Fundamentally a collection of leaf-members in a phyllotaxis system, the further organization follows the phyllotaxis-sequence, whether spiral (Fibonacci) or whorled (Cupressineae), of the photosynthetic vegetative shoots. The number of units, originally as 'indefinite' as in the microstrobilus, and possibly several hundreds (600 in *Araucaria brasiliensis*, over 200 in *Pinus Coulteri*), ranges from over 100 in most species of *Pinus*, *Picea excelsa*, *Cedrus Libani*, &c., to a few score, of which many may again be sterile at both ends of the system (*Pinus edulis*, *Sequoia*), and attains a limit of 4, 3, and 2 scales, which may alone be 'fertile' (*Callitris*, *Cupressus Nootkatensis*, 4; *Juniperus communis*, 3; *Libocedrus*, 2).

The essential departure is seen in the great increase in volume of the component units following the necessity for the protection of the enlarging prothallial stages, and a new series of growth-phenomena is required in the individual carpels. A comparably similar phenomenon obtains in the evolution of the fruiting carpel of the Angiosperm (cf. Pea-pod), and the new problems are solved along very similar lines; though subsequent to fertilization in the Angiosperm instead of before it as in *Pinus*.

If the carpellary scales are to maintain the same space-relations, and continue to subtend the same angle at the surface, an active rate of growth will be required, the greater at the periphery (*Cupressus*), to relatively massive facets. Where such growth is wanting, the scales must open out and make new contact-relations at the surface (*Araucaria imbricata*, *A. brasiliensis*). Bearing in mind the fact that the carpellary scales are themselves vestigial, and wholly decadent, the possibility of their rising to the occasion appears somewhat remote. As a fact of observation the actual cone-mechanism, in the most successful types, has been gradually transferred to a wholly new growth initiated in response to the necessity for the effective sealing of the cone. Since the new growths are thus associated with the original scales and their ovules, the same phyllotaxis-constants may be retained, and the new growths may attain the massive formation required in order to subtend the original angle, giving greatly enlarged cone-facets at the surface.

So important does their mechanism become, as the characteristic solution of this special problem, that its *precocious development* follows naturally as an inevitable consequence; and, in the limit, the secondary growth of the 'cone-scale' replaces the vestigial carpels, even in the floral mechanism of ovule-protection and pollen-collection, appearing in development as soon as the ovules themselves, and imitating by a slender pointed 'mucro' (*Pinus* only) the vestigial lamina of the original megasporophyll.

Note. In very similar fashion the secondary syncarpous ovuliferous region of an Angiosperm is precociously formed in the flowering period; the original carpels being wholly lost (cf. Cruciferae), or retained solely for pollen-collection (cf. Compositae). The essential difference between these so-called Gymnosperms and the Angiosperms, in this respect, may be traced to the fact that in the former (as in *Selaginella* and *contra* Cycads) the carpels appear to have lost the ovuliferous function before the demand for this new extension was felt, while the Angiosperm prototypes with foliaceous and ovuliferous megasporophylls more in the manner of *Cycas*, retained, at least in many cases, a capacity for the formation of a closed chamber (apocarpous or syncarpous) in varying degrees; the extreme precocity of which in floral mechanism, sealing the chamber *before* pollination, involved the elaboration of a 'stigmatic' surface. It is, again, interesting to compare the 'syncarpous' extension found in *Juniperus*, but only produced *after* initial and normal gymnospermic pollination. Thus the case of *Juniperus* illustrates one method of initiating a syncarpous ovary-chamber, giving an indehiscent fruit for bird-dispersal, without necessary progression *via* a condition of ovuliferous apocarpous carpels; a similar result being attainable by different routes ('*convergence*'). While it is

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[1] As in the case of the Angiosperm ovary and fruit, such constructions, involving the extensive utilization of basal intercalations, can be only understood by following the growth throughout the season, on a series of sectional drawings planned to the same scale.

also evident that the continued precocity in the production of protective (xerophytic) mechanism affords the clue to the evolution of the cone, as again only a phase of the same progression in land-flora, and probably contemporaneous, which initiated the Angiosperm ovary, closed before pollination even, and ultimately elaborated as a sealed chamber before the appearance of any ovules (Orchidaceae).

VII. Specialization of the Cone: Regarded as the product of an abbreviated phyllotaxis-system of bract-scales, subtending axillary megasporangia (1 or more), the progression of cone-factors subsequent to pollination follows a general course which is primarily the expression of xeromorphic adaptations in connexion with (1) the protection of the enclosed gametophytes from exposure and desiccation; (2) these protective adaptations are further elaborated after fertilization into the stage of the maturing seeds; and (3) they finally attain further complexity in the provision of mechanism for the separation and discharge of the seeds, as also (4) aiding their possible dispersal.

Such changes involve:—

(α) *Basal intercalation* of new extensions in the scales following the enlargement of the ovules.

(β) *Inversion of the ovules,* commonly following basal intercalation, as the micropylar end, with the sexual phases or embryos to be protected, is maintained as far from the surface as possible.

(γ) *The sealing of the cone* by extensions from the bract-scale, or by the new growth ultimately distinguished as the '*cone-scale*'.

With these may be included a feature of the non-coning Taxoids as the initiation of a new basal growth to the ovule as a 'second integument', ultimately distinguished as the '*aril*' (*Taxus*). The last point expresses the special feature of protective investment in the Taxoid series (including Podocarps); the third (γ) expresses the evolution of the characteristic *cone-scale* of the Pinoid. These secondary mechanisms have much in common; but there is no need to press homologies too far, or to obscure the relations under such expressions as 'unilateral aril', or 'epimatium', in order to bring everything under one morphological generalization. The need is the same in all; but the method of solving the problem is not necessarily identical in different phyla.

Given the theoretical axillary position of the megasporangium, and its direct axillary bundle-supply, the basal ('chalazal') end of the ovule affords a guide to the original axillary region, and to the amount of intercalated growth. The addition of new bundles at this point will be wholly secondary, as correlated with the increasing size of parts and the problems of the food- and water-supply of new regions. Such bundles may be expected to be symmetrically spaced, but once removed from the vestigial dorsiventral leaf-construction, their orientation excites no special interest.

It is interesting to note that identically similar problems occur in the case of Angiosperms; the ovary-cavity being normally extended by basal intercalary growth (cases of syncarpy and epigyny), as the ovules are also commonly inverted (anatropous), and may possess two integuments which are difficult to justify except as vestigia of some older function. New vascular bundles are again added in nucellus and testa-layers as the seeds enlarge (cf. *Helianthus* with 2 lateral V.B. from the chalaza, much as in *Podocarpus; Juglans*, *Cocos*). It is in fact difficult to avoid the conclusion that such phenomena as the inversion of the ovules, double integuments, and accessory bundle-supply of seeds, were established in Angiosperm ovules before the evolution of their characteristic ovary-chamber; that is to say, while these phyla, now classed as Angiosperms, were still in an antecedent Gymnospermic phase of reproductive mechanism, of which at this time only vague suggestions persist.

Note. (1) *Basal intercalations* to keep pace with the enlarging ovule before fertilization are analogous to the general increase of the Angiosperm ovary to keep pace with enlarging seeds after fertilization, as the necessity for the protection of the parasitic prothallia is continued and even increased. Growth takes place in three dimensions, and the cone normally increases in volume while maintaining its relative proportions; though the case of the *Pinus* apophysis (cf. *P. Pinea*) shows that such extension is not necessarily equal throughout the mass, but may present seasonal stratification.

(2) *Inversion of the ovule* is seen in its simplest phase in Podocarps, which are isolated from Taxoids by this feature. The 'erect' ovule with distal micropyle is evidently the original case; and it is difficult to say to what extent such inversion is related to the original megasporophylls, all traces of which in the Podocarps seem to have disappeared. Where erect ovules are maintained (*Cupressus*), they may be still fairly vertically orientated; but it is interesting to note cases in which the effect of inversion may be gained by a curvature of the cone-axis, as if to remove the exposed micropyles from vertical illumination or other damage: thus in *Taxus* the ovules at pollination-stage are turned to the lower side of the leafy shoots; in *Cryptomeria japonica* the ovulate flowers are projected horizontally; the same applies conspicuously to *Biota*, and inversion is fairly complete in *Juniperus sphaerica*. Partial inversion is noted in the flowering stage of *Sequoia*. Inversion has been independently established in Araucarineae and Abietineae; though in the former the ovule may remain free as in *Sequoia*, while it is characteristically fused up with the cone-scale in all Abietineae before pollination, as also with the bract-scale in the later seed-stage in *Araucaria*. Fusion of the ovule with the scale apparently follows the general principles of fusion noted in the case of the pollen-sacs with the intercalated stalk of the stamen, and subserves improved conduction and nutrition.

(3) *A second integument* ('aril') becomes typical for Podocarps and Taxoids. Only in *Ginkgo* and *Cephalotaxus* does the original integument retain simple differentiation with sarcotesta and sclerotesta; the two functions of succulence and sclerosis being again separated in testa and 'aril' of *Taxus* and *Torreya*, as also in some Podocarps. The aril is merely a basal collar-growth, very similar in organization and conception to the first integument which protected the pollenic-chamber, and apparently repeats an older growth-mechanism a second time. Its vascular supply is immaterial (cf. *Ginkgo*). There is little to be gained by pressing the homology of the cone-scale of the Abietineae with such a growth; there is no evidence whatever of this formation in the Cupressineae. It is, in fact, much more important to realize that all Taxoids must have originally possessed strobiloid cones of megasporophylls in the manner of Pinoids and Pteridophyta, than that Pinoids should have had 2 integuments in the manner of Taxoids and many Angiosperms for no particular reason that can be seen. Where the cone-construction has been lost, together with last vestigia of cone-scales and the possibility of any new extensions from such rudimentary carpels, the 'aril' appears as a simple solution of the original problem of xerophytic protection, and it is difficult to suggest a better alternative.

(4) *Sealing the Cone* (Pinoids) is based on the new application of an older mechanism; that of sealing the micropyle by a secondary growth of tissue to block the cavity over the nucellus (cf. *Pinus*). In this case a secondary growth of the integument-lips makes close contact over the nucellus-apex, and the pollen-grains are sealed in a closed and protected chamber. The methods adopted for similarly sealing the cone-scales of the entire aggregated cone constitute the most significant part of its general organization, and lead to further complications in that a mechanism must be subsequently elaborated to open it up again for purposes of seed-dispersal; again paralleled in the biology of the closing in of the Angiosperm carpel, and its dehiscence in the fruit-stage.

VIII. The Sealing of the Cone: As already indicated, it may be assumed that the biological necessity for protecting the sexual prothallia as vestigia of an older aquatic phase from the effects of exposure to air and desiccation is the factor controlling the elaboration of the more definite cone-constructions subsequent to pollination; the problem being fundamentally the same as that of the formation of the Angiosperm ovary, and the sealing is equally effective though the mechanism may be expressed in tissues of different morphological origin; the essential distinction being that in the Angiosperm-flower the elaboration of the ovary-chamber takes place early in floral development, while in the 'naked-seeded' Gymnosperm such mechanism is subsequent to pollination. On the other hand, the story of the Conifer series elegantly foreshadows the increasing precocity of this function, so that its value may be estimated; and once its significance in the life of the organism is grasped, there can be no doubt that it represents one of the most critical factors in the history of the race, determining its phyletic progression, as expressed to the present day, in the different horizons of attainment in this particular respect, which characterize the different groups of the Pinoid series. Types of the Cupressineae in which there is no true 'cone-scale' at all illustrate the primary steps:

(1) The simplest case is that seen in **Thuya gigantea**; the enlarging scales are closely adpressed, with considerable basal intercalary extension in the fertile member, taking the tips far beyond the enlarging ovules. A crested growth within the margin of each scale, on the upper surface, establishes adhesion with the next higher scale by means of closely interlocking papillose hairs (100 μ or more long). This new growth has clearly no connexion whatever with the axillary ovules, but it seals them over very effectually. The growth has no vascular supply, and hence never attains the dignity of a 'cone-scale'. It again clearly suggests the sealing mechanism of the *Pinus* ovule, as an active extension of the sub-epidermal tissue of the scale over a localized area, and in the mature cone it merely shrivels up.

(2) In **Biota** (*Thuya orientalis*) the original floral segment becomes a massive hook-like process carried up on a succulent extension of the fertile scales which completely overtops the ovules; the latter are thus quickly submerged and hidden. The margins of the adjacent scale-facets are then sealed by characteristic interlocking papillae of the epidermal cells (5 mm. cone, April). The massive new growth is supplied by a vascular bundle, taking off just above the original one, but presenting inverse orientation (with the xylem on the lower side). This bundle continues to the distal end, but curiously avoids the small sealing protuberance, extending instead into the base of the large hooked scale apex.[1] The succulent tissue contains indefinitely scattered sclerites.

(3) The same holds essentially for cones of the more generalized **Cupressus** type (*C. Macnabiana*, *C. Nootkatensis*), and close contact of the new scale-facets is similarly assured by interlocking papillae (120 μ) of surface-cells. The floral scales are more insignificant as compared with the new extension, being left as residual spinous processes on the enlarging facets; and as the sealing extension is relatively more pronounced it is supplied with vascular bundles. In these cases the inverse bundle (or branches from it, *C. Macnabiana*) passes directly to supply the new extension on the upper side of the primary one continued to the original scale. Early stages are followed in April (4 mm. cones) and June. The distribution of sclerites is particularly elegant in *C. Nootkatensis*.

(4) A variation is seen in **Juniperus**, in which the basal intercalation of the sealing growth is more emphasized, and the ovules are rapidly submerged (*J. sphaerica*, 2 mm.); the general intercalary zone continues to build the berry-like mass, and the original scales close in at the apex by interlocking papillae. In *J. communis* the basal zone of growth is so emphasized that it may be cut in transverse section as a definite ring of tissue; the ovules are carried up and appear inserted more on the sides of the new extension; so that the whole might be fairly described as 'syncarpous with basal placentation'.

(5) **Cupressus Lawsoniana** illustrates a new departure; the sealing growth on the upper surface of the extending scale is followed by a similar massive extension on the lower side. Corresponding opposed growths meet over the ovules and establish contact by interlocking papillae. It is interesting to note that the basal growth also receives a special bundle-supply (with normal orientation); and this double growth gives the ultimate effect of the so-called peltate (valvate) cone-scales, with the original carpellary unit left in the centre of the facet as a spinous projection (cf. 4 mm. cones, April, 6 mm. cones, June).

Of these variants the simple sealing-growth of the upper scale-surface or its intercalary basal extension, becomes the normal and more general solution of the problem, to be henceforward emphasized by its precocious formation. Thus in Taxodineae (cf. *Cryptomeria japonica*) a small crested growth, without V.B., is already in evidence beyond the insertion of the erect axillary ovule at the time of pollination. Subsequently this increases by basal intercalation, overlaps the enlarged ovules, and

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[1] Suggesting that the inverse character of this bundle has no necessary association phyletically with the 'cone-scale' growth.

receives a bundle-supply to form the characteristic crested 'cone-scale' region, the edges of contact being similarly sealed by interlocking papillae. The whole of the growth building the fruiting cone, by carrying up these parts and the original floral scales, is an intercalary basal extension and so far a new formation.

The crested growth attains greater prominence and elaboration in other Taxodineae (*Sequoia*, *Sciadopitys*), arising as a low ridge beyond the sorus of ovules (*Sequoia gigantea*), and ultimately presents a crenulated and frilled margin closely adherent to the scale above, following the scale contour, but more restricted to the distal region as the intercalated basal growth is more extensive; in its early formation close to the ovules suggesting precocity in production rather than a new departure beyond the condition of the Cupressineae. This is the more emphasized as considerable basal intercalation admits partial inversion of the ovules before pollination (*Sequoia*), and prepares the way for complete inversion after pollination. The characteristic construction of the Araucarineae remains at this level; and in *Dammara* the sealing growth has been termed a 'ligule' from its small dimensions, maintained into the adult cone in which it merely blocks the angle between the primary scales, and plays but a small part in the formation of the scale-facet (*Dammara*), 'fused' up in *Agathis australis*, a broad scale in *Araucaria Bidwilli*, and a mere relic in *A. imbricata*.

The continued precocity of such a formation is exhibited in simpler Abietineae (*Abies*, *Pseudotsuga*), and may be readily followed in *Larix* (April). In these forms a scale-growth of the crested *Cupressus*-type is associated with an ovule already inverted; being more massive it has a distinct bundle-supply, and appears at first sight as an extension of the chalazal end of the ovule. Extension of the scale follows rapidly after pollination, and the growth is packed to fill the interstices between the bract-scales, all chinks being filled with hairs in a manner very exceptional for Conifers. The bundle-supply of the cone-scale again shows inverse orientation (in longitudinal section appearing to be taken off from down the axis instead of from below).

In other advanced types of the Abietineae, *Cedrus* shows the more massive cone-scale dominant at pollination, and the bract-scale so reduced and vestigial that the main bundle-supply passes direct to the cone-scale, which is sharply bent to overlap succeeding members. Ovule and bract-scale henceforward become minor structures as compared with the great development of the cone-scale region.

Similar sealing-papillae are well developed (200 μ) in patches at the margins of the cone-scales of *Sequoia gigantea* (green cone), and the scales show fine sclerites. In the simpler Abietineae sealing-papillae are often less effective; the greater part of the cone-scale surface is utilized for the formation of seed-wing areas, leaving only a narrow margin for adhesions (*Cedrus*), practically negligible in *Larix*. The same holds for cases in which the foliaceous bract-scale protrudes (*Abies*); the succulent scales of the green cones maintaining close contact by turgidity of their tissues (*A. nobilis*). On the other hand papillose areas are well developed in *Pseudotsuga*, and also behind the ends of the scales in *Picea excelsa*.

The case of *Pinus*[1] only expresses the last terms of such elaboration and precocity; the cone-scale growth appears as a protuberance at the axil of the primary bract-scale when in the most rudimentary phase (T-bud unexpanded, April); that is to say, it is now initiated simultaneously with the first modelling of the two lateral ovules. Further details are readily followed in flowering shoots of **P. sylvestris** (April–June). Flower-buds still enclosed in protective scales, cut in March, show axillary growths subtended by the feebly developed bract-scales, but with little distinction of form. By the middle of April the bract-scales are well-defined growths sharply bent upwards and overlapping, as the flower-buds begin to appear on the expanding shoot-systems; by the end of the month the axillary growths differentiate into lateral protuberances (ovules) and a median spinous protuberance (the first indication of the cone-scale). The bract-scale has a well-marked primary bundle, and the axillary growths, so far without any vascular tissue, pack the interstices of the erected bracts. As the ovules differentiate integument and micropyle, the cone-scale

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[1] Complex academic interpretations of morphology only irritate the beginner. It is better to obtain a clear idea of what actually happens in the growth of the cone and draw one's own conclusions.

portion becomes a median pointed process closely pressed against the next scale above, and ultimately just overlapping its subtending bract-scale. A new V.B. is then added to supply the median 'cone-scale mucro', and the latter develops anthocyan pigment, as does also the original bract-scale (May 15, contact-parastichies, 3 : 5).

In the pollination-stage (May 20–25) the cone-axis is only half-projected from the investment of basal scales, and the scales constituting an upper cycle (8 to 13) diverge in the manner of a distinct perianth; the lower half of the cone-system remaining enclosed and functionless, with imperfectly developed scale-stages. Only about 4 members in 5 oblique parastichy lines are functional scales (giving an average of 20–25 fertile scales per cone, and these are expanded for pollination in such a way that the cone-scale spine ('mucro') just tips the next scale above, leaving lateral apertures for the drifting in of pollen-grains on either side. The whole constitutes a very striking little crimson rosette floral-mechanism (3–4 mm. high), which is functional for barely a week at the end of May, at a time when the new annual shoot bearing the flowers is 3 in. long (to 9 on top shoots), and the foliage-needles (10 mm.) are only protruded 1–2 mm. from their silvery sheaths.

Within a week (May 30) the cones are rapidly sealed; this being effected by the active growth of succulent tissue of the cone-scale region below the mucro, which is apparently no longer required, as a distinct rounded and intercalated region, supplied directly by the new inverse bundle straight from the axis. The ovules enlarge considerably (65 μ), but are completely blocked in by the cone-scale growth. The rudimentary scales arrested at the base of the cone similarly enlarge and seal their cavities, as relics of an older organization. The V.B. supply of the cone-scale does not pass to the effete mucro-region, but supplies the growing tissue, as this becomes dominant. The bract-scale, also checked in growth, is flattened out by the enlarging cone-scale growth, soon buried in the growing mass, and henceforward lost to sight, as the ovules themselves were never exposed to view. By the end of the month (May) the cones are securely closed (6 mm. by 5); the foliage-needles projecting 2–3 mm. only. The cones may be completely deflected in another fortnight (June 15), and enlarge to 8–9 mm. by 7, showing the cone-scales closely pressed to rhomboidal facets, the mucro now relatively small; the V.B. supplying the cone-scale branches in the enlarging mass, and the bundles of spiral tracheides show end-groups of transfusion tracheides with small bordered pits (6 μ). The exposed surface-layers (2–3) of the facet become sclerosed and pitted; a layer of phellogen ultimately giving a slight cork-formation. In this condition the cones are sealed solely by the pressure of growing turgid cone-scales, to which is later added an exudation of resin filling all surface chinks; they thus perennate over the summer, green and photosynthetic throughout the mass, and also over the succeeding winter (12 mm.), growth again becoming active in the second spring.

The cones enlarge rapidly in April–May, by renewed growth of the cone-scales, these again elongating by basal intercalary extension, while the surface-facet is increased by a new 'apophysis' zone of green tissue; the umbo in turn remaining stationary and effete. In this way the cone-facets may retain their mutual contact-relations, though carried far beyond their original positions. The rapid elongation of the basal part of the scale involves the ovule-base, pulling it out in a manner which initiates the wing of the seed. The separation of this 'slip' of tissue[1] apparently follows the older abscission-line of the ovule, now extended as far as the new growth allows, and the shape of the wings to be utilized in seed-dispersal is thus outlined before any appearance of oospheres in the female prothallus (May 7). At the same time the sealing mechanism of the new apophysis-enlargement is made effective by normal interlocking of papillose epidermal cells (100 μ) over a length of 2–3 mm., leaving, as in preceding types, the enlarging ovules in free cavities of the interior. In these the ovules are protected by the overlap of about 3–5 scales, and the cone externally is divided into two distinct regions; the facets of the lower half show no definite umbo or mucro, and remain wholly sterile. Longitudinal section of the 'green' cone (June 25) shows the parallel extension of the few fertile scales, the

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[1] The recognition of the wing of the seed as a 'slip of the cone-scale' independent of the testa, as if secondarily attached to it, or 'embracing it like pincers', merely confuses the effect of the histological differentiations of cell-walls of different textures, which induce ready separation, with morphological regions.

lowest ovules being buried 10 mm. in the rounded base of the mass, now 40–50 mm. long, and the majority are 5–8 mm. beneath the surface.

Special points to note as distinct factors are :—

(1) The precocity of the mucro, its vague function and early cessation of growth.
(2) The primary sealing of the system by intercalary growth in the region below the mucro (cone-scale).
(3) The secondary sealing by apophysial facets in the second year.
(4) The parallel elongation of the cone-scales, and its relation to the extension of the seed-wings.
(5) The cones are sterilized at both ends, with an output restricted to 40–50 seeds in the region of optimum protection.

The entire cone remains soft and succulent until fertilization has been effected (June 25). Similar observations may be checked on the more elongated cones of *P. Strobus* and *P. excelsa*, in which sterilization of the basal region is less pronounced; the apophyses do not attain a peltate expansion, but are sealed by similar papillose growths.

It is now seen that *Pinus* (more particularly 2-needled forms), as the most highly specialized type, combines a number of secondary features of mechanism devoted to the same end, as:

(1) extreme limiting reduction of the original bract-scale (megasporophyll),
(2) inversion of the ovules,
(3) fusion of these to the cone-scale along one side,
(4) great extension of the sealing crest (or 'cone-scale'),
(5) the latter precociously functional in the pollination stage,
(6) with primary growth (umbo),
(7) secondary apophysis facet,
(8) sealed in close contact at the surface,
(9) the scales become wholly sclerosed and contain little vascular tissue.

The controlling factors are the necessity of a sealing mechanism, and the manner in which this is met by new growths in a basal intercalated zone, the position of which may be indicated by the original carpellary leaves even in their last phases of vestigial development.

IX. Cone-factors: The archaic strobilus-habit is traced more clearly in the case of the axes bearing microsporophylls because these are of relatively ephemeral nature; they only require bud-protection during the maturation of the pollen-grains, and this is effected by condensation of the structure and the overlap of vestigial imbricating laminae ('connective flaps'). After the discharge of the pollen they merely shrivel, dry up, and are cast off.

On the other hand the strobili of megasporophylls which become the 'cones', require to be still more efficiently protected during the stages of prothallial development, and to be supplied with large stores of food-material, as also water, from the main axis, over the period of fertilization, the development of the embryo, and the storage of reserves in the seed-stage. Where xerophytic conditions obtain the cone-structures will feel the drain of the environment possibly more than any other part of the plant; the new functions are in themselves associated with problems of economy in the water-supply to the aquatic sexual phases (seed-habit); and as the cones and their included parasitic generations living at the expense of the other tissues can only obtain water in competition with the transpiring foliage, extreme xerophytic specialization thus affords the clue to the organization of the 'adult' cone, as expressed more particularly in:

(1) Shape, (2) Size, (3) Scale-protection, (4) Succulence, (5) Woody (sclerosed) texture, and (6) as subsidiary details tending in the same direction, inversion, resin-exudation, cuticle- and cork-formations. To these may be added number of scales, ovules, and seed-output; but these last points, though significant in the individual cone-axis and the branch bearing it, are less significant in that such problems involve the further total output of cones and seeds in the entire tree.

(1) **Shape:** The original strobiloid form as a cylindrical elongated mega-strobilus is most clearly expressed in forms of *Abies* (*A. nobilis*, clothed with adpressed

bract-scales, 500), to a less extent in *Picea* (*P. Morinda*, 200 simple cone-scales), as again in the slender soft cones of 5-needled Pines (*P. Lambertiana*, 20 in., *P. excelsa*, 8–10 in.). On the other hand, the limiting case should be a sphere, as exposing minimum surface for loss by transpiration: in highly specialized *Pinus*-forms this may be very nearly approximated in *P. Pinea*, while it is more general among the simpler bract-scale cones (*Cupressus macnabiana*, *Taxodium*, *Cryptomeria*, *Cupressus Lawsoniana*, *C. pisifera*, with limiting cases in *Juniperus*: again appearing characteristically in Araucarineae, as great sub-spherical cones of *Araucaria Bidwilli*, *A. brasiliensis*, and the smaller globular cones of *A. excelsa*, *Agathis*, and *Dammara*. A telescoping effect in which a short cone is closed down with a number of thin scales is clearly exhibited in *Cedrus*.

(2) **Size** ranges from *P. Lambertiana*, 21 in. long, *P. Coulteri*, a foot long and 3 pounds in weight (dry), and spherical *Araucaria Bidwilli*, 8 in. diam., and up to 10 lb. (green), to the diminutive spherical cones of *Cupressus pisifera*, *C. Lawsoniana*, *Thuya occidentalis*, and spherical berries of *Juniperus*, 8–6 mm. diam. Other types may be arranged in intermediate sequence: the point to note being that without regarding the largest cones as necessarily primitive, the smallest are undoubtedly derivative and reduced, while depauperated cones are general in northern representatives of their respective series; cf. *P. sylvestris*, *P. montana*, and *P. Banksiana* of the *Pinus* series, *Picea sitchensis* as compared with *P. Morinda*.

(3) **Scale-protection**: The overlap of the scales of the original strobilus may be considerable (*Araucaria imbricata*); but the vestigial nature of the carpels apparently prohibits their successful utilization in imbrication: *Thuya* possibly alone presents ovules protected by the overlap of 2 bract-scales. But with the introduction of the 'cone-scale' mechanism imbrication in the sealed cone becomes effective, and the xerophytic value of the construction may be gauged by the number of scales overlapping externally to the ovules, as also by the depth of the latter below the surface. The latter may range from 1 mm. (*Tsuga canadensis*) to 2 inches (*Pinus Coulteri*), the overlap from the ends of 3 scales (*P. sylvestris*) to 6–10 in *Cedrus*. Such imbrication is again wanting in the 'valvate' *Cupressus* series, in Taxodineae as *Sequoia*, and in Araucarias as *A. Bidwilli* with more spherical cones, and in *Abies* is almost negligible.

(4) **Succulence**: In the mass of tissue thus produced, protection against desiccation follows the general lines of 'fruit'-development familiar in higher Angiosperms, and water-storage in parenchymatous tissue gives the case of the green and juicy cone; water being retained by storage of organic acids (tannins, &c.). This condition is conspicuous in the younger stages (before fertilization), and is characteristic of cones so long as they are growing. Such succulence may be specialized and utilized in post-fertilization stages (*Biota*), leading to the succulent adult cone of *Juniperus sphaerica*, and the case of the Juniper 'berry' or 'drupe'. In Taxoids similar succulence is restricted to the special growth as 'aril' of *Taxus*, *Podocarpus* (sp.), the seed-axis (*P. Totara*), or again to the sarcotesta (*Ginkgo*). In all cases equipment which is subsequently utilized in connexion with birds follows preceding special adaptations for water-storage.

(5) **Sclerosis**: Extensive lignification also follows as a normal xerophytic condition in ultimate stages of seed-habit, and the majority of cones harden, often quite suddenly, as they cease growth (cf. *Pinus*, immediately after fertilization). In this country such hardening follows the onset of the hot season (about midsummer), when perennation over summer desiccation normally begins. Cones are commonly judged as 'hard' or 'soft' according to the amount of sclerosis in general parenchyma, stone-cells and sclerites, rather than in xylem tissues. Extreme cases occur in the more massive cones of *P. Pinea*, *P. Coulteri*, among Cupressineae in *C. macrocarpa*; less-sclerosed forms (*Picea*, *Abies*, *Pseudotsuga*, *Larix*, 5-needled Pines) are thus regarded as less extremely modified, and so far probably more primitive in this respect. The most highly organized cones as xerophytic structures are Pines with massive cone-scales and spinous apophysis, comparing favourably in such special protective mechanism with any other sclerosed 'fruiting' structures in the vegetable kingdom. (Cf. *Nipa* cone.)

(6) **Inversion**: The primary position is that of a flower erected for pollination by wind-borne pollen, utilizing the primary negative geotropism of a vegetative axis,

unless there may be some reason to the contrary. Inversion implies an intentional growth-curvature, apart from the pendulous effect of weight; and its result is undoubtedly that of further protection of the cone-structures from desiccation of direct insolation. The more advanced types invert immediately after pollination (*Pinus* (sp.), *Picea*, *Pseudotsuga*), yet others (*Cedrus*, *Larix*, *Abies*, *Thuya*) retain and even emphasize the primary vertical position. The mechanism of such inversion implies the possibility of a growth-intercalation in the cone-stalk; and where sufficient extension is lacking, the growing cone may be involved in the curvature, leading to effects of asymmetry in the adult structure, with increased growth of the members on the outer convex side, often extremely conspicuous (*P. insignis*, *P. Coulteri*, and to a less extent in *P. sylvestris*).

(7) Cork is commonly formed on the exposed surface of the umbo only (*Pinus*); while resin-exudation appears between the individual scales of the first-year cone (*Pinus sylvestris*), effectively sealing all chinks; in others (*P. excelsa*) resin streams over the entire surface of green cones, and may drip like stalactites from the ends; excessive exudation, as icing on the erect cone of *Abies magnifica*.

X. Mechanism of Seed-discharge and Dispersal:

The greater the perfection of the mechanism for sealing the cone as a xerophytic construction protecting the developing seeds, the more important also becomes the necessity of providing a converse mechanism for opening it again, and liberating the seeds. These again require to be abstricted, or some alternative method of detachment must be provided. As a matter of fact it is obvious that the opening of the Pine-cone and the dispersal of its winged seeds by the agency of the wind constitute such an elaborate provision, the factors of which require to be analysed; while alternative methods and constructions may be contrasted in the scale of efficiency, as in the common example of the chances of bird-dispersal in *Taxus* and *Juniperus*.

With the original failure of the megaspore to be discharged from the megasporangium which initiates the 'seed-habit', the necessity for dispersal implies that separation or abscission must be passed on to some other structure enclosing the megaspore and its contents; as (1) the megasporangium (*ovule*), (2) the leaf bearing it (*carpel*), (3) the axis bearing the carpel (*flower*), (4) some other more distant connexion (as the entire *inflorescence*). In order of priority and phyletic probability the abscission of the ovule with its dormant embryo, as the *seed*, represents the first and simplest solution of the problem. It may be hence assumed that the seeds of Conifers were primarily abstricted, and separated from the parent-plant to germinate elsewhere; whether by the simple separation of the ovules directly, as in Taxoids and *Ginkgo* (or Cycads with foliaceous carpels), or again in the case of the closed Pinoid cones. In the latter it is evident that a secondary opening mechanism must be also provided, before the seeds can escape, as again that such dehiscence must be primitive; and any minor examples of indehiscence are to be regarded as the expression of failure in the original mechanism. In both cases the utilization of some external locomotor agency will be advantageous from the standpoint of conveyance to a distance; whether in the elementary form of effective air-currents, or in more elaborate association with the wings of birds.

The simplest case of ovule abscission is confined to Taxoids, since closed cone-structures have been so far lost, and the 'naked' ovules alone remain. The secondary and necessarily comparatively late evolution of bird-association can only utilize structures already in existence from the standpoint of xerophytic protection by means of succulent (aqueous) tissue, or sclerosed stone-cells: the biological adaptations running closely parallel with 'berry' and 'drupe'-formation among Angiosperms. In *Ginkgo* and *Cephalotaxus* the differentiation of a sclerotesta and sarcotesta may show additional effects in coloration (by residual carotin or anthocyan pigmentation), more or less storage of sugar on 'ripening', as a state of incipient decay, and the parallel differentiation of succulent aril and sclerosed testa follows closely similar mechanism in *Taxus*, *Torreya*, and species of *Podocarpus*. In default of bird-visitation, abscission of the ovule follows normally in course of time, and all grades of specialization in such mechanism may be observed (cf. the thin leathery green aril of *Torreya californica* with the case of *Taxus baccata* taken with avidity as soon as ripe in November).

In the Pinoid series arrangements for opening the sealed cone are provided for in the simplest manner by the mere shrinkage of the tissues on death and desiccation, and the abstricted ovules merely fall out to be drifted by the action of the wind. Such an elementary state of affairs persists in Cupressineae (*Thuya*, *Libocedrus*); additional gape of the scales being provided for by greater sclerosis on the inner side, or less peripherally; such cones once completely dried do not again recover closed volume on being wetted (*Cupressus*, *Thuya*). With greater succulence and less sclerosis (*Biota*) shrivelling of the cone is more pronounced, and this is still more complete in *Juniperus sphaerica* with practically no sclerosed tissue at all. Cones of the Taxodineae remain at the same level of attainment; the scales shrink, often considerably (*Cryptomeria*), but do not recover full volume, or completely close on wetting: the seeds retain a narrow point of attachment and fall out of the cone as it dries (*Sequoia*).

In all these cases with closely adpressed scales in condensed cone-formation, the seeds grow to fill narrow chinks in the interior, sending out laminate regions of the testa, as more or less 'wing'-like lateral extensions on both edges of the compressed seed (*Cupressus*, *Thuya*, *Sequoia*). In the more succulent forms (*Biota*, *Juniperus*) such extensions are conspicuously wanting, but all such wing-formation parallels the general case of simple winged seeds and enclosed fruits of Angiosperms (cf. *Betula*). Further elaboration is noted in the case of the Araucarineae; the single median seed of *Agathis* similarly sends out bilateral extensions of the testa, but only one side normally develops considerably, attaining an effective unilateral 'spinning' wing. In addition to this the scales are separated from the cone-axis. The latter phenomenon may be included as secondary shedding of the megasporophyll; in *Araucaria* this replaces the abscission of the ovules; the latter being so fused up with the scale that it comes away in one piece with included seed. In *A. imbricata* and *A. Bidwilli* the great size of the seed prevents much distant dispersal by gentle wind-currents, nor do such scales show any adaptation for spinning movements. The spinning of *Agathis* is so far an independent evolution of the mechanism from bilateral testa-extensions; and though giving a possible limiting velocity of 2½ ft. per sec. is by no means so neatly adjusted as in the case of the Abietineae; early stages of similar unilaterality may be noticed in the seeds of *Libocedrus decurrens*. Similar shedding of the scales from the cone-axis obtains in some Abietineae, where the bract-scale and cone-scale fall away in one piece (*Abies*, *Cedrus*, *Pseudolarix*), and though wholly wanting in *Picea*, *Tsuga*, and *Pseudotsuga*, may be sporadic in a few forms of *Pinus* (*P. Pinea*, *P. palustris*), possibly as a retention of older mechanism.

In all these Abietineae, also, more perfect cone-opening becomes the rule; this mechanism being also transferred to the 'cone-scale' growth, repeating the same sequence of shrinkage and divergence of the scales, in accordance with the distribution of sclerosed tissue, and with the same result that cones with less sclerosis shrink more, and do not completely recover volume or completely close on wetting (*Pinus excelsa*, *P. Strobus*). Opening and closing movements in response to hygrometric changes are more pronounced in *Picea*, *Tsuga*, *Larix*, *Pseudotsuga*; but the more massive sclerosed cones of the Pine series show the greatest advance; divergence of the scales being often associated with strong deflecting curvatures in the hooked apophyses (*P. Coulteri*, *P. Sabiniana*, *P. Gerardiana*).

With the great development of the cone-scale growth in the Abietineae, often appearing in section as an outgrowth of the base of the massive inverted and fused ovule, new possibilities of wing-development are opened up, as the abscission-line of the fused ovule cuts a new path along the cone-scale surface to extend along the intercalated region as a secondary slip of 'wing'-material. From the preceding restriction of the ovules to 2 per scale, symmetrically placed, it follows that the area of the free cone-scale surface may be equally divided between the 2 seeds, giving each a unilateral wing, the length and breadth of which are controlled by the growth-capacity of the cone-scale. An effective spinning wing is thus attained in a wholly secondary manner, which compares in efficiency with the spinning wing of any other fruits or seeds of Angiosperms; the effect being intensified by the sclerosed texture of the tissue, as correlated with the weight and pointed apex of the seed. Length of wing, as giving the radius of the spinning circle, strength of the anterior margin, and weight of the seed, are important factors, resulting (*Pinus sylvestris*) in the attainment of a limiting velocity of 2·4 to 3 ft. per sec. after a drop of only 3 ft. or so from the cone. Range for the seeds of the same tree may be considerable, according to variations in length and width of wing; average measurements suggest as normal:—*Pinus excelsa*, 3 ft. per sec.; *Picea Morinda*, 2·9; *Cedrus Libani*, 2·7; *P. austriaca*, 2·3; the general approximation of different genera being very close. With such a limiting velocity it is clear that, given air-currents deflected from the surface of the ground with a vertical component of 2 miles an hour, the seeds would not fall at all, but might be indefinitely drifted or whirled upwards. Such generalizations apply to other winged seeds and fruits of Angiosperms, but no case gives more efficient or more uniform results for the material and mechanism. It may be added that *Cedrus*, with wing broadened distally in correlation with the broad cone-scale lamina, presents no apparent advantage. Seeds without endosperm, being lighter, are less efficient. The 2 seeds of one scale spin in opposite directions; the edge nearer the middle of the scale is 'anterior' in spinning.

Failure of the cone to 'open' again may follow from (1) excessive and uniform sclerosis in xerophytic types (*P. muricata*, *P. clausa*), or from lack of sclerosis (*P. Cembra*) and insufficient differentiation. Similarly, the wing-mechanism of the seed may fail as the seeds become too massive by thick sclerosed testa and bulky endosperm (*P. Pinea*, *P. edulis*, *P. Cembra*).

The third case of the abscission of the cone as a whole follows normally in response to xerophytic demands for the elimination of structures wasting water-supply; and spent cones are dropped (*Pinus* (sp.), *Picea*) though not in the deciduous *Larix*. Many of the more massive cones are not abstricted, apparently owing to difficulties in such cladoptosis (*P. insignis*); and this is emphasized in the case of the non-opening *P. clausa*, &c. In *P. sylvestris*, grown under favourable conditions, cones may remain on for several years, but some are shed at every dry spell throughout the summer. Analogy of the case of the microstrobilus suggests that there is no reason for regarding the persistence of the cone as a primitive feature, much less its non-dehiscence, or the absence of spinning wings; these last factors are common to all the older races of the Abietineae without exception, as a part of their fundamental equipment, probably dating far back to the common ancestors of this entire sub-group. (Shaw, 1914.)

The fourth case of the abscission of a structure even beyond the floral axis (as an inflorescence-region) does not arise. Even in *Taxus* the abscission of the seed leaves the basal part of the reduced parent-shoot. Hypotheses regarding the Pine-cone itself as an *inflorescence* lead nowhere, and have no convincing foundation. (Worsdell, 1900.)

XI. Relation of Form-factors to Phylogeny and Classification. The preceding headings should suffice to indicate the normal trend of xeromorphic specialization as affecting the general space-form of the tree and its lateral axes, taken from the standpoint of vegetative shoot-systems (photosynthetic),and reproductive systems (flowers and cones). It is obvious that progression may take place in any type, or in any groups of types, in any one of these directions, and in any one respect, more or less independently of the others, though 'associated factors' of the same class may suggest 'family characters'. So varied are the manifestations in different degree for each factor, that it is not possible to arrange the members of the whole group in any linear series, taking all the factors into consideration together; though it may be done approximately for one factor at a time. Even then only the morphological construction has been so far considered, and a further multitude of factors similarly affect the details of the anatomical organization of stem, timber, and foliage-needles, as also the details of the sexual generation, the sexual organs, and the sexual cells. The balancing up of this consensus of factors constitutes the method of approaching the discussion of the phylogeny of the race, and the possible relationship of the different genera. The degree of success attained in this direction depends on the exact valuation of the different factors. This has been so far very vaguely done, and all suggestions as to exact classification remain wholly provisional. Three main standpoints may be taken up, as based on (1) tissue-anatomy, (2) on structural morphology, (3) on reproductive mechanism, respectively. Different criteria may have been taken by different writers, but it is sufficiently clear that all three standpoints require to be considered together, and the subject rapidly grows in complexity.

One should always remember that in nature there are no genera or species, only *individuals*; classification represents the abstract ideas of human intelligence. Plants which recognizably solve all the problems of somatic and reproductive organization in the same way, and thus appear very much the same sort of thing, are included in the same 'genus', and the *genus* becomes the historical unit of classification. Minor variants on the same methods, noticed in more detailed observation, delimit 'species', in so far as they may be constant, and such factors breeding 'true to seed'. Minor variants, or mixtures which do not breed true, give 'varieties', in different categories, which may be increased by vegetative propagation; and any apparently constant variation in a seedling (as a 'mutant') may constitute what is to all intents a new species, so far as constancy may be established. Experimental evidence is required in any given case, and this is usually wanting or imperfect in the case of tree-types; e. g. the recognition of 'hybrids' which have not been experimentally produced rests on purely hypothetical considerations. We are still doubtful as to the time required to change what is recognized at the present time as a good species into something sufficiently different to be accepted as an equally distinct form; and the time required for the isolation of a new 'generic' type is beyond human experience.

Genera which agree in wider range of main principles are grouped in *families*. Families, in which common factors of still more fundamental significance can be traced, are conceived as representing *phyla* of wider relationship. To do this it is necessary to determine the essential value of the 'factors' utilized for classification, and this varies with the knowledge and mental outlook of successive generations of 'systematists'. A broader outlook is always to be obtained by further investigation of all plant-life, and not of one group alone. Hence systematists of a single group (Monographers) are not expected to have a very wide or correct appreciation of the factors with which they deal, and there is always room for improvement in any provisional 'system'.

Such generalizations express the manner in which systematy has been built up along academic lines, as a matter of general history of the science, but other outlooks are possible. Many botanists still fail to appreciate what is meant by the individual life with which one deals in practical investigation. The individual is no longer to be regarded as an isolated unit, or a casual creation, but is the present representative of a 'race'. That is to say, the individual is not, as short-sighted chemical physiologists tend to believe, a mere physical mechanism, the creature of the external environment to which it passively responds; but it is the living presentation of a continuous line of organism, successful since living, or a 'race' leading back as the expression of continued response to very similar, but not necessarily identical, environment, in unbroken plasmatic continuity, over a period of time which, in terms of ultimate cytological history, may represent a continuous reaction and record for anything up to such an inconceivable period as two thousand million years. During this period the more fundamental reactions, as expressed in morphological units of construction, have been established as constants beyond any hope of change. No one, for example, now expects to find higher autotrophic plants expressed in any other way than in terms of nucleated plasma with chloroplasts and wall-membranes of cellulose. Even coenocytic organization is recognized as anomalous, and the rare expression of somatic deterioration, usually heterotrophic. Similarly, at a later date, the general features of stem (axis), leaf-appendages, phyllotaxis mechanism and ramification, as well as details of vascular anatomy, have been elaborated and established by such rigid natural selection that they express almost equally constant morphological factors, to which any accidental exception appears as a 'monstrosity' (cf. fasciation-effects, phylloclades of *Phyllocladus*). Even such primary factors of a land-plant may have an age of over one thousand million years behind them; and they are hence not lightly changed. It is accepted, for example, that the construction of a forest timber-tree, with minute anatomy and the attainment of the seed-habit at a horizon practically equivalent with that of *Ginkgo*, dates to the Devonian at least, or a period of probably over three hundred million years; and these factors, again, are not lightly changed. The loss of the seed-habit is practically inconceivable for higher plants (however deteriorated in Loranthaceae); and though the loss of cambium and the arboreal form is commonly expressed among Angiosperms, as organisms give 'quicker returns' in reproductive maturity, no living Gymnosperm is 'herbaceous'.

From such elementary considerations it follows that only the minor headings of systematy, expressing the smallest variations, represent the features still sufficiently plastic and open to alteration in modern lines of progression. Broader generalizations delimiting large groups cover still older features of organization now fully established, so far as one can see, for all future time. Systematy thus begins to acquire a phyletic value, and demands a phyletic consideration of the events of a remote history. Every little detail, however apparently meaningless, may have a complex story behind it, successful interpretation of which may throw an unexpected light on the life-problems of an ancient world.

In actual fossil-remains impressions of shoots and cones can be reliably traced to the Lower Cretaceous. Araucarineae were probably cosmopolitan at this epoch, and were but little different in the Palaeozoic. Pine-cones with normal apophysis and central umbo, of the highest grade of construction, and of average dimensions, occur in the Lower Cretaceous, representing a range of more than one hundred million years. Cones apparently similar to those of *Cedrus* occur in the Upper Cretaceous, as others suggestive of *Sequoia* and unmistakably Taxodinous forms are found in early Tertiary deposits of probably fifty million years ago. (Seward, 1919, p. 389.)

The environment which produced the Pine-cone, as the most complex construction of the Pinoid series, was that of ages at least antedating the Lower Cretaceous, and the extreme xeromorphic organization characteristic of the leading types of modern Gymnosperms has no necessary relation to the climate of the present day, but was settled many millions of years ago, and is not lightly changed. Thus *Larix*, though secondarily deciduous, still retains the anatomical peculiarities of the *Cedrus*-type of foliage-needle, differing only in the reduced sclerosis of identical tissue-units. The xeromorphic specialization gained at a remote geological epoch now enables the plants to survive in inferior biological stations, under pressure of competition with higher Angiosperms, but they will not change in these essential respects under the most ideal conditions of cultivation.

The fact that even generic characters may be referred to distances of fifty to a hundred million years ago implies that still wider group distinctions are much older and beyond recall. Facts of modern geographical distribution have little bearing on the inter-relations of recent types. The four conventional series of Pinoids, for example, acquire phyletic value only from purely morphological deductions, and the common ancestry of Pinoids and Taxoids remains a matter of pure speculation. The few surviving members of the Araucarineae present a coherent and isolated group of remote relationship. The Abietineae are fairly connected in the close parallelism of their cone-scale cones; the Cupressineae by their peculiar vegetative habit. On the other hand the Taxodineae remain a wholly empirical set of archaic and vestigial forms of probably very distant relationship.[1]

In determining the main lines of classification two standpoints may be illustrated, as based on:—

I. *The somatic organization of the sporophyte generation*, as expressing the mechanism of autonutrition of the successful individual life in:—
  (α) The relation of the external form to light and air-supply.
  (β) The internal organization of the photosynthetic and transpiring leaf-lamina.
  (γ) The anatomical organization of the conducting vascular tissue of the stem (including timber), which provides the supplies of ions of nitrogen and phosphorus and food-salts.

II. *The Reproductive Organization* by means of which the life of the race is continued and wastage is compensated, as expressed in:
  (α) The output of wind-borne spores (microspores only), still necessarily enormous.
  (β) The wastage of sexual cells (reduced nearly to a minimum).
  (γ) The wastage of the seed-stage in dispersal and in germination, in relation to both factors of environment and competition with other plants.

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[1] Seward (1919, p. 124); Saxton (1913, p. 253); Coulter and Chamberlain (1910, p. 303).

All such biological factors require to be analysed before the status of any genus can be regarded as satisfactorily assured. The general tendency of recent years has been to lay extreme emphasis on the details of sexual processes and the gametophyte generation; partly from an exaggerated veneration for anything sexual, and partly from the idea that the somatically deteriorated gametophyte, being the remains of an aquatic phase of reproduction, must be consequently older or more 'conservative' in its details than the giant timber-tree with the up-grade organization of dominant land-flora. Yet both generations must be equally of algal origin, and sexual processes are probably significant only so far as they relate to the phenomena of meiosis established in the sporophyte stage. Asexual reproduction is as archaic as sexual, and the advancing specializations of the photosynthetically independent forest-tree in its progression from a sea-weed are quite as likely to give a permanent racial record as may the deteriorated heterotrophic prothallia.

Also it may be noted that any race or genus may present independent progression along any of these lines at any time. No race is now likely to be wholly primitive, and all are survivors of a past age, specialized in some respect. Thus *Ginkgo*, accepted in recent years as a unique 'Link with the Past', on account of its retention of Zoïdogamic fertilization by motile antherozoids, has a shoot-system and timber anatomy of high grade, a fruit-formation as advanced as that of the Taxoid, though retaining a foliage-leaf evidently much older than the needle-form of the majority. *Araucaria* may be archaic in many respects, but there is nothing in the progression of still older groups (Pteridophyta, Cycadales) to suggest that such features have any claim to be regarded as primitive, as the multiple production of vegetative nuclei in a coenocytic male prothallus, or the germination of pollen-grains at a distance from the micropyle.

XII. Monstrosities: Though the individual plant is to be regarded not only as a living mechanism, growing under certain conditions of environment, but as the modern expression of a racial organization continuing a mechanism of response to the conditions of past ages, and thus now working by inherent rules (Heredity) established by Natural Selection, it is always subject to a certain range of error, beyond mere 'continuous variation' as an oscillation about a mean. All morphological specialization may be scheduled in definite sets of growth-factors, including factors of form and time-factors or rates of growth, and these must have some material counterpart somewhere in the organism. It is generally supposed that the chromosomes of the nuclei are the seat of such determinants; and in the production of any special growth the nuclei of the apical meristems, which remain permanently 'embryonic' and presumably contain all or a majority of such factors, segregate certain sets for this purpose; others not wanted are 'suppressed' or become 'dormant' in the so-called 'adult' phase.

In any such segregation of a set of factors required to work out a special morphological unit (a flower, leaf, special bud-construction, or any smallest detail), heredity is never absolute, and any mechanism may go wrong at any time, and in any manner: e.g. a factor may be lost or misplaced, or an entirely wrong set may be isolated. Such mistakes without rule constitute 'sports' or discontinuous variations; and where the error, to our senses, is hopeless and useless it commonly passes as a 'monstrosity' or 'freak' (Teratology). If slight and non-injurious it may be termed a 'sport'; such errors being commonly corrected in the same or another generation. If non-reversible ('mutation') the new idea is subject to natural selection, and, if a success, may conceivably initiate a new departure as a new 'species'. If a failure it only hastens the elimination of the race.

The term 'monstrosity' is thus generally applied to some phenomenon at once recognizable as anomalous; i.e. breaking the rules of observed heredity; and though often throwing a suggestive light on the grouping of factors in linked sets, such mistakes do not necessarily indicate any phyletic 'reversion' to a more primitive form (except by loss of a factor which may have been secondarily attained). Every such monstrosity requires to be studied separately for what it may be worth, knowing that from the errors of the mechanism one may possibly learn something of the causal action. The possibility of such monstrous formations or freaks becomes the greater as the mechanism (especially that of reproductive processes) grows the more complex;

hence Conifers with relatively simple floral organization show little that is conspicuously striking in teratology. (Penzig, 1894.)

Note: Since any factor may go wrong at any time, it follows that every possible case of malformation will be met with sooner or later, if only a sufficient number of individuals be examined; the more the trees are cultivated and observed, the more such irregularities are recorded. Hence there may be abundant literature dealing with *Pinus sylvestris*, *Larix europaea*, and *Picea excelsa*, but less with rarer types. Such tendency to error is again commonly increased by intensive cultivation and by 'over-feeding'; i.e. giving a plant much better conditions and more favourable food-salt supply than the race has been used to. Hence freaks, sports, and monstrosities abound in garden and nursery practice, and if curious may be retained in cultivation (cf. variegated forms, weeping forms (*pendula* vars.), dwarf forms (*nana* vars.), or fastigiate forms (vars. *fastigiata*, *virgata*), and *Retinospora* forms of *Cupressus* with juvenile leaves. (Veitch, 1900.) The more commonly observed cases may be classed as:

I. Anomalies in the mechanism of centric shoot organization, and the relation of stem and leaf.

(1) Phenomena of Fasciation include the case of growing-points with multiple centres, commonly bilaterally arranged to give banded, crested, and irregularly branched formations. Examples are general; cf. more particularly *Larix europaea*, also *P. sylvestris*, with fasciated cones; rare in *P. austriaca*, *P. Laricio*, *Picea excelsa*, *Abies pectinata*, *Juniperus communis*. Possibly the finest case on record is given by Baker (1910, p. 333) for *Araucaria Cunninghamii*, an entire tree being thus malformed.

(2) Multiple shoot-systems producing irregular masses in which internodal extension is omitted may give massive growths (up to 1–1½ ft. diameter, and attaining a weight of several pounds in *Pinus sylvestris*) bearing densely clustered leaves peripherally: these growths do not necessarily involve any outside stimulus of fungus or insect. Similar shoot-systems, as closely compacted woody masses, and buried beneath the bark, produce no leaves but consist of a mass of labyrinthine annual rings. These constitute 'burrs' or 'knauers', and may attain considerable size; they are general in all tree-forms and are occasional in Conifers; cf. *Cedrus*.

(3) Minor variations in phyllotaxis-constants are generally too inconspicuous to attract attention; but are recorded for cones of *Pinus*, *Picea*; poorly grown plants commonly give irregular constructions. A break to trimery in *Thuya* is more interesting.

(4) Irregularities in restricting the number of leaves on foliage-spurs of 2-needled Pines may apparently express a reversion to an older phase; rare in *P. sylvestris*, *P. montana*, 3 for 2; but also 3 for 5 in *P. Cembra*, and 2–3–5 on strong stump-shoots of *P. rigida*; and again 1 for 2 (*P. edulis*) as in normal *P. monophylla*.

(5) Dichotomy of the growing-point, giving twin-centres, is noticeable in the case of apparent 'twin-cones', or species with a forked apex; *P. Cembra*, *P. sylvestris*, twin-cones, also in *Larix* and *Picea excelsa*; again interesting in a dichotomous staminate flower, *Cedrus Libani*.

(6) Suppression of lateral growth-centres, if of all kinds, gives the case of the monaxial plant as the 'disbudded mutant', *Picea excelsa*, *Abies pectinata*; or in advanced Pines the case of suppression of leaders only, giving a monaxial stem with foliage spurs (*P. austriaca*).

(7) Failure in normal geotropic response and mechanism, as in dwarf and prostrate varieties: *P. sylvestris*, prostrate; *Abies pectinata*, *Picea*, with long horizontal shoots; prostrate *Cupressus sempervirens*.

Tending to negative response in laterals, giving fastigiate varieties, Spruce, *Taxus*, *Cupressus Lawsoniana*, *Taxodium distichum*.

Or tending to positive response in *pendula* vars., *Sequoia gigantea*, *Pinus Strobus*, *P. sylvestris*, *Larix*, *Picea*, *Abies*, *Cedrus Deodara*, *Thuya*, *Cupressus Lawsoniana*.

(8) *Virgata* forms ('serpent' forms): primary branches with no or few secondaries, *Pinus Laricio*, *P. sylvestris*, *Picea excelsa* (with the habit of an *Araucaria*), *Pseudotsuga Douglasii*, *Abies pectinata*, &c.

II. Anomalous segregation of lateral growths: Given 10 sorts of leaf-member and 5 types of shoot in *Pinus sylvestris*, mistakes may be excusable, and such errors may give conspicuous results, cf.:

(1) Formation of leaders instead of spurs in *Pinus* has been regarded as a relic of

'multinodal' construction, but may be merely anomalous: the monaxial Pine may be regarded as the converse case of spurs for leaders.

(2) Juvenile needles replace scales subtending spurs; general in *P. rigida, P. canariensis*, sporadic in *P. Pinea*, occasional in *P. sylvestris*.

(3) General retention of juvenile leaves in the adult stage, as in *Retinospora* forms of *Thuya* and *Cupressus*, and the heterophylly found in species of *Juniperus* and *Cupressus*. A similar sport of *Cryptomeria japonica* = *C. elegans* (Veitch).

(4) Staminate flowers for ovulate, or *vice versa*, gives the case of the dioecious tree becoming monoecious again (*Taxus*); even normally staminate trees commonly give a few fruits. Monoecious individuals also occur in *Araucaria imbricata, Juniperus virginiana, Ginkgo* (also readily grafted on).

(5) Imperfection in spur-mechanism, the apex continuing growth, either with juvenile leaves, or as a normal leafy branch in the manner of *Cedrus* and *Larix*; found following injury in *Pinus rigida*, rare in *P. sylvestris*.

(6) Ovulate flowers replacing spur-shoots, beyond the normal limiting number at the distal end of the annual shoot. Very striking examples are recorded, since conspicuous and giving massive coning regions or aggregates of cones ('cone-sickness'): cf. *Pinus halepensis* 112 cones in a mass, *P. Laricio* 47, *P. sylvestris* 227, *P. Pinaster* 60, *Picea* 107.

(7) Staminate flowers sub-terminal, *P. austriaca*; ovulate flowers terminating a main lateral instead of one of minor degree, *Sequoia gigantea*. Staminate flowers replacing scattered spurs, *Pinus Strobus*.

III. Anomalous floral constructions may suggest a return to a hermaphrodite condition, yet be wholly meaningless.

(1) Stamens in the lower region of ovulate flowers; *P. rigida*, ♂ below and ♀ above, *P. Thunbergii*; rare in *P. sylvestris, Larix, Picea, Abies, Cupressus Lawsoniana*.

(2) Cone-scale mechanism in staminate flowers, *P. Pumilio, P. rigida*; or, again, the cone-scale wholly wanting, *P. muricata*; the bract-scale exceptionally reduced, *Pseudotsuga Douglasii*, and not appearing in the adult cone.

(3) Needle-bearing spurs in the axils of cone-scales (*Pinus* sp.), used without any real grounds as suggestive of the bifoliar nature of the cone-scale.

(4) The 'proliferating' cone, the most general and striking case, in which the axis of the ovulate flower continues to grow on and produce a second cone (*Araucaria excelsa*), or, more commonly, leafy members. Where the ovulate flower normally terminates a leafy shoot, and the scales grade from leaves below, this excites the less remark (*Cryptomeria japonica*, with all transitional stages to elongated cone axes of 6 in., and occasional also in *Taxodium*). But the phenomenon may be very striking where the differentiation of bract-scale and cone-scale is once definitely established. In *Larix* such proliferating cones are particularly common, the axis continuing for several inches, and bearing foliage-needles as on the current year's, and vegetative shoots may arise in the axils of cone-scales. Such cones do not afford any direct evidence of the identity of the bract-scale with a foliage-leaf (megasporophyll), but merely indicate a mistake in the segregation of lateral appendages; just as the cone-members similarly grade from leafy members of the original leafy spur-shoot. Similar cases occur in *Picea excelsa, Tsuga canadensis, Abies pectinata, Pseudotsuga Douglasii*.

(5) Proliferation of the staminate flower to a leafy system has been recorded in *Araucaria*.

(6) Other anomalies include cases as that of *Juniperus communis*, in which, by failure of the syncarpous zone, the fruit is formed from 3 free scales. Germination of the seeds in the cone (*P. Pinea*) may follow failure in the opening mechanism.

IV. Anomalous growths induced by other organisms: Secondary growths induced in response to the stimulus of attack by insects or fungi may present mere irregularities of construction; but where structures have been already elaborated to a definite plan secondary changes may give conspicuous effects.

(1) **Witches' Brooms:** Infected shoots give increased bud-development, to characteristic bushy growths resembling the brooms of *Betula* commonly produced by the attack of a gall-mite (*Phytopus*). Distinguishing features are (1) negative geotropic effects, (2) enfeebled development of internodal extensions and of the foliage-leaves,

(3) these dwarfed systems do not flower. Such may occur in *Abies pectinata* in response to attack of the fungus *Exoascus*, also occasional in *Pinus sylvestris*.

(2) **Chermes viridis**, an Aphis, is responsible for the curious Pine-apple gall of the common Spruce (similar galls on Sitka Spruce). All the foliage-leaves of the *Picea* annual shoot are laid down in June of the preceding year, in a normal Fibonacci sequence (5 : 8), and are protected by a dense investment of bud-scales over the summer and ensuing winter. Hibernating females of *Chermes* attack the buds as soon as the hibernaculum of bud-scales loosens in spring (April), commonly unilaterally, penetrating to the apical cluster of leaf-primordia, boring the tissues, and producing a numerous progeny similarly feeding on cell-sap. In response to the primary stimulus the leaf-units more or less cease further differentiation, and reduce to mere spinous processes, while the leaf-base develops as a peltate scale in the manner of the cone-scales of Cupressineae. The axis enlarges, the intercalated leaf-base growths are forced up laterally, leaving open pockets in the leaf-axils, and the tissues fill up with large (20 μ) starch-grains.

Following the existing phyllotaxis-construction, the enlarged leaf-units present a compact cone-like aggregation; but contact-relations may be reduced to parastichies, 8 : 13, as the leaf-bases subtend a low angle. The intercalated scale-growths make rhomboidal facetted areas, to 7 mm. broad, and such a cone-like construction may include 50–70 leaf-units in spiral series, wholly centric, or on one side only of the shoot-axis; all intermediate stages may be found between complete arrest of the entire system and the affected region being unilateral, or with fully proliferating apical section. When fully grown the whole may be 40 mm. long and 16 mm. diam. (A second species [*C. Abietis*] giving pale greenish galls, $\frac{1}{2}$-in. diam. or less, on similar construction-principles, is also common, and the two forms may occur on adjacent shoots of the same Spruce.)

While these growths are taking place the larvae wander in and out of the cavities, but the edges of contact are ultimately sealed by interlocking papillae. Larvae enclosed in the gall-loculi develop pupae; those outside die off, and many pupae (to 50) may be found in one chamber. The contact-lines of the rhomboidal facets are emphasized on the axillary side of the leaf-units by papillose growths, which may be brightly coloured with anthocyan in the cell-sap. The pupa stage is attained in June, and from mid-June to July the perfect winged insects escape, often in great profusion. Starch disappears as the tissues sclerose and dry up; the loculi gape widely, opening up the cavities to the exterior, and the residual dry, dead, brown galls may persist on the shoots for 2–3 seasons.

Note. The growths once initiated are formed whether they contain imprisoned aphides or not. The opening mechanism is also provided by the plant as the new leafy shoots attain adult efficiency and drain the older portions of food and water in the hot season (end of June). The inner tissues become sclerosed and pitted, starch is depleted, and with the loss of water the tissues die. The peltate-scale effect, obvious at first on cutting a section down one of the steeper parastichy lines, is wholly lost as the pockets shrivel back and gape open.

Botanical interest centres in the fact that the shoot-system, under stimulus of attack by the parent aphis, repeats certain elementary factors of cone-formation no longer noticed in the *Picea* ovulate cone, but directly parallel with the case of *Biota* in the Cupressineae; e. g. in succulence, intercalary extension below the arrested leaf-primordium, and more especially in the sealing mechanism of papillose hairs. The loculi of the cone-formation are to all intents identical with those formed to protect the developing seeds of the Cupressoid cone. In this way vestigial factors of cone-elaboration may appear in the history of a race in response to a new stimulus, and this happy accident enables the *Chermes* larvae to obtain protection and easily taken food in early spring. Hence the second summer brood, produced at a time when there are no breaking buds on the Spruce, cannot form galls, and live exposed, or even migrate to other Conifers (*Larix* [*C. viridis*], *Pseudotsuga*, *Pinus sylvestris*); but no other Conifer produces these growths. The fact that the 'galls' induced by different species of *Chermes* are different in details as size, colour, degree of closing, indicates that the stimulus must be due to some excitant material ejected by the fundatrix, and that this may be variable, hence coming under the operation of natural selection in determining improvements in the mechanism of growth from the point of view of the insect.

(3) **Cecidomyia Taxi** of the Yew is a gall-fly (Diptera) which lays an egg in the tissues of the Yew bud-apex, inducing a more typical gall-construction. Terminal buds are commonly attacked, and the leaf-primordia having been all laid down in the previous season are not affected in number or anatomical details. But the shoots lose (1) their capacity for internodal extension, (2) the D.V. habit, while the innermost crowded leaves may be etiolated and colourless. The galls thus assume the form of close rosette or tassel-clusters of spirally arranged foliage-needles at the end of the previous season's growth (50–70), fully formed by the end of June with the shoots of the new season. Larvae perennate over the winter.

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