On the Value for Diagnostic Purposes of Certain of the Anatomical Features of Conifer Leaves

BY

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WITH PLATES CCLVI-CCLVIII.

While the use of anatomy as an aid to the identification of plants has had many exponents, it is recognised that such a method of determination is by no means absolute, and its successful application is dependent in every case upon a correct evaluation of the anatomical features employed for the purpose. Some plant groups lend themselves more readily to this method of diagnosis than do others, and in practice it has been applied most frequently to the identification of ligneous species by their stem structure, and conifers and grasses by their leaf anatomy. That the structure of the wood of trees and shrubs often affords convincing evidence of the affinities of the plants concerned is an established fact, but it is only in recent years that the importance of this fact in relation to the solution of taxonomic problems has been appreciated by systematists, and it is now realised that errors in classification can be remedied by reference to the anatomy.¹

For identification purposes stem structure has very obvious advantages over leaf structure, for while the latter is more accessible, it is also more susceptible to the modifying influence of environmental changes, with the result that some degree of fluctuation is inevitable. This close correlation between environment and structure has been demonstrated by Larsen ² in the course of an interesting paper on the leaf structure of certain conifers, where it is clearly shown that the quality of the light to which a leaf is subjected, as well as the moisture content of the atmosphere, does have a stimulative effect upon the leaf which is reflected not infrequently in its anatomy. Larsen ⁵ observations are to some extent an amplification of the earlier work of Noack ³ on the influence of climate on the development of cuticle and the lignification of tissues in conifer needles. Incidentally, an analysis of leaf structure on these lines might prove exceedingly useful in affording

¹ S.J. Record in Tropical Woods, No. 37 (1934), 5.

J. A. Larsen in Ecology, viii (1927), 371.
F. Noack in Jahrb. für wiss. Bot. xviii (1887), 519.

a clue to the kind of environment best suited for the cultivation of various conifer species. There is no doubt that sun-leaves and shade-leaves often differ markedly in their structural details: in the amount of hypoderm developed and in the differentiation of the mesophyll; while the position of the resin ducts, which is commonly regarded as having a definite diagnostic value, has been shown to depend in some cases upon the degree of exposure of the leaf to light. It is interesting to recall in this connection that many years ago Bonnier, 2 experimenting with pine, spruce, and yew, was able to show that corresponding changes in the leaf anatomy could be induced by prolonged exposure to continuous illumination.

Notwithstanding a tendency to vary in response to the operation of external factors, the foliar organs of the Coniferae have long been utilised for taxonomic purposes, and an extensive literature bears witness to the fascination of this aspect of anatomical study. Among the pioneers in this field of research special tribute should be paid to Bertrand and Daguillon, who blazed a trail that those with a greater wealth of material and more modern methods of technique have followed in later years. Many others, such as M'Nab, Masters e and Van Tieghem, have added their quota to a general knowledge of the leaf anatomy of conifers, which an ever-widening circle of investigators is now engaged in expanding and co-ordinating. One of the latest contributions to the subject, that of Fulling on the leaf structure of species of Abies, contains a very comprehensive list of literature to date.

The chief objection to the universal employment of leaf anatomy as a deciding factor in the identification of conifers has always been this seeming instability of character, which is more apparent than real however, for usually it is the unessential features that are more affected by environmental changes, and if care be exercised in the choice of material it will be found that the usefulness of the less plastic features as specific indicators is never wholly impaired.

It is of the first importance that the relative stability of each anatomical feature should be tested at all states of growth and in every kind of environment, so that its value as a differentiating factor, or as an indicator of affinity, may be correctly assessed. By this procedure a possible source of error, arising from a mistaken belief in the con-

- F. Taubert in Mitt. Deutsch. Dendr. Gesell. No. 37 (1926), 206.
- ² G. Bonnier in Rev. gén. de Bot. vii (1895), 332.
- 3 C. E. Bertrand in Ann. Sci. Nat. Sér. 5, xx (1874), 5.
- 4 H. Daguillon in Bull. Soc. Bot. Fr. xxxv (1888), 57; Rev. gén. de Bot. ii (1890), 154.
- ⁵ W. R. M'Nab in Proc. Roy. Irish Acad. Ser. 2, ii (1875), 209, 673; and in Trans. Scott. Arbor. Soc. viii (1878), 93.
 - 6 M. T. Masters in Journ. Linn. Soc. Bot. xxvii (1891), 226.
 - ⁷ Ph. Van Tieghem in Bull. Soc. Bot. Fr. xxxviii (1891), 406.
 - 8 E. H. Fulling in Bull. Torr. Bot. Club, lxi (1934), 497.

stancy of a particular character, is eliminated. A critical analysis of the leaf structure is thus essential, involving the comparison of authenticated specimens from every possible source, and particularly of different ages, for age, as well as environment, is responsible for divergence in structural details. This is well seen in the leaves of species of Abies where the position assumed by the resin canals is relative to the age of the plant. The writer has met with this characteristic on several occasions, and it is commented upon by Viguié and Gaussen 1 in their Monograph of the genus. In the leaves of Abies Faxoniana, Abies nephrolepis, Abies sachalinensis and Abies squamata, for example, the normal position of the resin canals in adult specimens is median, whereas in young trees in cultivation, up to a certain age, the ducts are almost invariably sub-epidermal (Figs. 5, 6). This lack of conformity in the leaves of young and old trees of the same species constitutes one of the many pitfalls that beset the path of the unwary anatomist, and is a frequent source of misunderstanding when native-grown specimens are compared anatomically with their cultivated progeny. To construct a key based on anatomical features, which will cover all such contingencies, is not an easy task.

A further complication arises when a transitional stage occurs and four resin canals appear in the same leaf, one pair occupying a marginal and the other a median position (Fig. 2). Duplication of the paired resin canals is not confined, however, to species in which a change of position is possible, as well as usual, at maturity, for the phenomenon has been observed by the writer in the leaves of Douglas Firs, such as Pseudotsuga taxifolia and Pseudotsuga japonica, in which the position of the ducts is invariably sub-epidermal. It is well known that a change of position, or an increase in number, of the resin ducts in a conifer leaf is sometimes the sign of a traumatic reaction, as in the abnormal needles produced when the young shoots of Scots Pine have been injured by game-birds (Fig. 4). Such was not the case, however, with the examples quoted above, which seem to belong to the category of accidental happenings. Nevertheless, the fact that such morphological anomalies do occur occasionally serves to emphasise the unwisdom of basing conclusions on inadequate or unhealthy material, for it is not improbable that some chance abnormality may be accepted as being typical of the species, and the initial error, if undisputed, may become established as a fact. The obviously erroneous statement that the needles of Picea Maximowiczii have " a solitary canal below the midrib, as in the section Tsuga," 2 and the printed fiction that the leaves of Abies recurvata normally possess four resin canals,3 probably had their origin in some such misconception.

¹ Th. Viguié and H. Gaussen in Trav. Lab. Forest. Toulouse, tom. ii, vol. ii (1928), 35.

² M. T. Masters in Journ. Linn. Soc. Bot. xvii (1880), 549.

³ W. Patschke in Bot. Jahrb. xlviii (1913), 646, fig. 3, 3.

It sometimes happens that individuals of a species fail to develop resin canals in their leaves from one cause or another, and in such a species the diagnostic value of the canals is thereby diminished. Pinus contorta seems to possess this tendency to a marked degree, for out of 400 needles, taken at random from one particular tree, only two showed any trace of resin ducts—a single duct in each pair—while from another tree only three bifoliar spurs out of 130 selected had a complete complement of resin canals. In the variety latifoliar the percentage of needles containing the normal number of resin ducts rose to 76.

It follows from this that the examination of a single leaf is not enough, nor, for the matter of that, is a single section of a leaf sufficient, In every case a series of sections, taken at intervals from base to apex, is desirable, if not essential, since continuity of the tissues is not a constant feature of the leaves of all species. A classic example of this lack of continuity is to be found in the needles of many species of Picea, in which the resin passages take the form of an interrupted series of abbreviated ducts, and are so dispersed throughout the long axis of the leaf that it is possible to cut sections of the needles of such species as Picea glauca, Picea obovata, Picea Maximowiczii, without disclosing the presence of a single duct. This sporadic development of the resin passages, whatever its significance, would be disconcerting if it were not immaterial, for, with the possible exception of the septate canals found in the leaves of Picea brachytyla,1 these structures have little, if any, diagnostic value in the genus. Marco,2 in a paper on the needle structure of Picea pungens and Picea Engelmannii, attempts to show that the arrangement of the longitudinal series of "short" canals in these two species is such that it affords a ready means of distinguishing between them, but an examination of similar material by the writer has yielded such contradictory results, that it is believed that Marco must have based his argument on insufficient data.

It is perhaps unnecessary to call attention to the fact, which should be evident, that the value of anatomical features as specific criteria varies according to the genus. A simple illustration of this is furnished by the resin canals of the leaf, which in Picea are comparatively unmportant as differentiating factors, but in Abies and Pinnes are often exceedingly useful as aids to the identification of species. This is but one of the many aspects of the problem of relative values. In the Chinese and Formosan genus Ketelearia the conducting tissue of the leaves consists of a single vascular strand, which, together with the prominent midrib on the upper surface, provides a means of distinguishing the foliage of Ketelearia from that of most members of the

¹ M. Y. Orr in Notes, Roy. Bot. Gard. Edin. xiv (1923), 24.

² H. F. Marco in Bot. Gaz. xcii (1931), 446.

³ In the species Keteleeria Rouletti Flous, recently described in Trav. Lab. Forest. Toulouse, tom. i, vol. ii, 1936, art. xiv, the vascular strand is said to be double, as in Abies.

allied genus Abies, where a dual vascular bundle is the general rule (Figs. 6, 7). There are some notable exceptions to this rule, however, e.g. Abies magnifica, Abies nobilis, Abies Mariesii, in the leaves of which there is an undivided vascular tract similar to that found in Keteleeria.

What, then, are the particular anatomical features of conifer leaves, which, being least subject to change, are definitely of use as generic or specific indicators, and may be relied upon to provide confirmatory evidence of identity in all conditions of age and environment? In the writer's experience there are relatively few leaf characters that are entirely satisfactory from this point of view, and the features which prove most useful in providing a key to relationships that are otherwise obscure are often those of comparatively limited distribution.

First in importance in this connection may be placed the features of the epidermis. It might be supposed that of all the tissues of the leaf the epidermis, because of its position, would be the one most prone to change, but such is not always the case, and in certain genera of Coniferae its systematic importance is unquestionable. Nor is the significance of the epidermis restricted to living material alone, for Holden, writing from the angle of the palaeobotanist, states, "A comparative study of living and fossil conifers indicates that epidermal structures are of great value for accurate specific diagnosis . .", and it was the recognition of this fact that led Florin 2 to make an intensive study of the epidermis of Gymnosperm leaves—a work of inestimable value to taxonomists.

In living forms the usefulness of the epidermal tissue for diagnostic purposes depends primarily upon the possession of some peculiarity of structure, which, while consistent, is not of universal occurrence. The best examples of this are to be seen in the leaves of certain species of Larix, Juniperus and Taxus, in which the configuration of the epidermis is both unusual and unvarying. In Larix and Juniperus the distinctive appearance of this tissue is due to the presence of papillate cells on both surfaces of the leaf, while in Taxus these are replaced by less regular cuticular projections, which in almost every species are confined to the lower epidermis. It may be recalled in passing that Frimmel,3 many years ago, put forward the suggestion that the unconformities of the cuticle in Taxus, like papillae, are concerned with light-perception; but whatever physiological function these structures may subserve, their constancy is never in question, and both cuticular excrescences and papillae are indubitably of use as headmarks by which species may be known.

To illustrate this point, it is proposed to cite some examples taken from the ranks of Chinese conifers, and, for the most part, from material

¹ R. Holden in Bot. Gaz. lx (1915), 224.

² R. Florin in K. Sv. Vet. Akad. Handl. Ser. 3, x, No. 1 (1931), 1-588

F. V. Frimmel in Österr. bot. Zschr. lxi (1911), 216.

collected by the late George Forrest, particulars of which appeared in a former number of these "Notes." 1

The first of these concerns Larix Potaninii, the common larch of western China, and its Himalayan congener, Larix Griffithii. Larix Potaninii is one of the few larches possessing a papillate epidermis, the others being Larix Mastersiana, a species of local distribution in western Szechuan, Larix Kaempferi, the well-known Japanese larch, and Larix Lyallii, a native of western North America. According to Henry and Flood,² there is in Larix eurolepis, the Dunkeld Hybrid, a localised production of papillae on the leaf-midrib, which is no doubt a legacy from the female parent, Larix Kaempferi, since papillae are entirely absent from the leaves of Larix decidua, the male parent.

In Larix Potaninii the papillose nature of the epidermis is very apparent in transverse sections of the leaves, and it is a feature that appears to be equally characteristic of both native-grown and cultivated specimens (Fig. 8). It forms a direct contrast to the perfectly smooth epidermis of Larix Griffithii (Fig. 9), so that it is possible to distinguish between the Chinese and Sikkim larches by means of their leaf anatomy, and the importance of this when dealing with purely vegetative material of either species will be readily appreciated. It was so with much of Forrest's material of Larix Potaninii and Larix Griffithii, which, in the absence of cones, could still be identified with certainty in the dried state by the character of the leaf-epidermis. Moreover, it was the complete absence of papillae from the leaves of sterile specimens of a larch collected by Forrest on the Burma-Yunnan border in 1924 that gave the first hint of the occurrence of Larix Griffithii in that region. Confirmation of identity followed when coning specimens were secured, and the use of anatomy as a means to an end was vindicated.

In Juniperus the utility of this minor anatomical feature as a differentiating factor is practically nil, since its occurrence is restricted to two species only, and its significance here lies rather in the fact that these two junipers are so closely akin that they might be regarded as conspecific. The species in question are Juniperus recurva and Juniperus Coxii, both of which possess a characteristic papillate leaf-epidermis, which is if anything more accentuated in the latter than in the former (Fig. 10). Juniperus Coxii is a recently defined species, 3 based on a cultivated plant, grown from seed brought by Farrer and Cox from Upper Burma, where specimens similar to the type were gathered subsequently by Forrest. At the time, Forrest's material from Farrer's locality was considered to be but a form of the widely spread and variable Juniperus recurva, and the writer, while admitting that there may be grounds for varietal distinction, is searcely prepared

¹ M. Y. Orr in Notes, Roy, Bot. Gard. Edin. xviii (1933), 119.

² A. Henry and M. G. Flood in Proc. Roy. Irish Acad. xxxv, B. (1919), 55.

A. B. Jackson in The New Flora and Silva, v (1932), 31.

to concede that these are of sufficient consequence to merit specific rank. Having regard to the rarity of leaf papillae in the genus, the development of a papillate epidermis on the leaves of Juniperus recurva and Juniperus Coxii would seem to lend support to the writer's view that their specific separation is uncalled for.

In Taxus the incidence of the occurrence of a corrugated leaf-epidermis has likewise a particular significance, but it is one that is of more practical value in diagnosis, and has proved especially useful as a deciding factor in the identification of dried material of such species as Taxus Wallichiana and Taxus chinensis, which are not always clearly distinguishable in a non-living state. Taxus Wallichiana is the Himalayan Yew, and it has much in common with Taxus baccata, from which some authorities 1 do not consider it to be specifically distinct. It has been recorded from western China by Handel-Mazzetti.2 and although this extension of its range was controverted by E. H. Wilson at the time, its occurrence in the Chinese provinces of Yunnan and Szechuan has since been confirmed by the discoveries of Forrest and other collectors. Taxus chinensis, on the other hand, is closely allied to Taxus cuspidata, the Japanese Yew, of which at one time it was thought to be but a geographical variety, and evidence of this inter-relationship is plainly shown by the similar structure of their leaves. Conversely, the specific separation of the Chinese Yew from the Himalayan Yew is expressed in terms of foliar anatomy by a dissimilarity of structural detail.

In both Taxus Wallichiana and Taxus chinensis the under epidermis of the leaves is studded with prominent cuticular pegs, which, it was pointed out, is a feature not uncommon in the genus, in fact, Florin 3 states that these protuberances are invariably present in all the species to a greater or less degree. The important point to note, however, is their uneven distribution over the surface of the leaf. In Taxus chinensis the formation of cuticular pegs is limited to the region of the stomata, as in Taxus cuspidata, and in transverse sections both the margins and the midrib of the leaves present a perfectly smooth outline (Figs. 14, 15). In the leaves of Taxus Wallichiana, per contra, these projections of the cuticle are present on the midrib also, and in a transverse section they are seen extending across the median zone of the leaf in unbroken sequence (Figs. 16, 17). Thus by the simple expedient of cutting a section of a leaf it is an easy matter to determine by microscopic examination to which of these two species the leaf belongs, and so identify the specimen from which it came. The presence of cuticular teeth on the under side of the midrib in leaves of Taxus Wallichiana was noted first by Bertrand,4 who was so convinced of the stability of

¹ H. J. Elwes and A. Henry, Trees and Shrubs of Great Britain and Ireland, i (1896), 100.

² H. Handel-Mazzetti in Symbolae Sinicae, vii (1929), 2.

³ R. Florin, l.c. p. 277. ⁴ C. E. Bertrand, l.c. p. 53.

this minor character that he made use of it as a distinguishing mark of this species in his key. Taxus chinensis, then an undescribed species, was unknown to Bertrand. The writer himself has made a detailed examination of all the available native material of the Himalayan Yew, collected in various localities in India by Wallich, Hooker, Lace and others, as well as specimens from China gathered by Handel-Mazzetti and Forrest, and in every case the leaves were found to possess a rugate midrib, postulating the universality of this character in the species. Similarly, when authentic specimens of Taxus chinensis, from different parts of China, were examined anatomically, these were found to be entirely devoid of any such corrugation of the cuticle on the midrib of the leaves. There are good grounds, therefore, for assuming that these two species differ consistently in this respect, and in consequence the value of this anatomical feature as a differentiating factor is considerable.

From examples such as these it will be evident that epidermal structures are not without significance when questions of identity arise, and may be employed with confidence as aids to identification in most cases. This applies equally to the more familiar epidermal structures such as stomata, although the very nature of these organs militates against the possibility of any considerable variation in constructional details. Nevertheless, structural differences do exist, and that these are definitely associated with different genera and species has been admirably demonstrated by Florin, who has shown that it is possible to utilise stomatal variations for diagnostic purposes.

Apart from their anatomical features, the distribution of the stomata on the surface of the leaf has long been regarded as being of some importance in the identification of coniferous species. Within broad lines this idea works very well in practice, for the occurrence of stomata on both sides of the leaves, and their confinement to one surface only, are characteristics which have every appearance of fixity in many species, as, for example, in Tsuga longibracteata, where the disposal of the stomata on both leaf-surfaces serves at once to distinguish this species from all its Chinese congeners. Quite a number of conifers, however, are prone to vary in this respect; it is well known, for instance, that in certain of the flat-leaved spruces, such as Picea sichensis and Picea picoensis, stomata are often present on the upper surface of their needles, in contradiction of the accepted scheme for their classification, and a similar anomaly has been observed in the case of such common Silver Firs as Abies alba and Abies Nordamamiana.

A departure from the normal arrangement of the stomata may be due to the operation of some ecological factor, or in certain circumstances it may be merely symptomatic of disease. The writer has seen a prolific development of stomata on the leaves of a plant of Abies recurvata, which was undoubtedly induced by cultural conditions.

¹ See A. P. Anderson in Bot. Gaz. xxiv (1897), 309.

Similar instances of the sporadic development of stomata come within the experience of every systematist, and it is unnecessary to labour the point that in the distribution of stomata there are fluctuations which have no relation to specific differences.

Among the other occasional features of conifer leaf-anatomy which serve as distinguishing marks are the isolated fibrous elements, often curiously misshapen, which occur sporadically in the mesophyll of certain species of Cephalotaxus, Torreya, Abies and Pseudotsuga, and are present always in the cladodes of Sciadopitys verticillata. The incidence of their occurrence in these genera is somewhat singular and is not easy to explain, but it has this virtue, that it enables the taxonomist to distinguish between species which are not unlike in external appearance. In Cephalotaxus Oliveri and Cephalotaxus Fortunei peculiarly branched fibres are common and characteristic features of the leaf-anatomy, whereas these so-called idioblasts are totally absent from the mesophyll of mature leaves of Cephalotaxus drupacea and its variety sinensis. As the latter is a frequent associate of Cebhalotaxus Fortunei in central China, and one with which it is liable to be confused, the existence of this anatomical mark of distinction is of some consequence to the systematist. In the same way it becomes an easy matter to distinguish between Torreya Fargesii and Torreya grandis when it is known that idioblasts are invariably present in the leaf mesophyll of the former, and are absent from that of the latter (Fig. 3). It is interesting to note that sclereides of a similar kind are present in the leaves of all the Asiatic species of Pseudotsuga, and it is only in the American species that these inclusions in the mesophyll have a differential value. Unbranched fibres are a characteristic feature of the leaf mesophyll of Abies firma, and are not without value as a means of distinguishing this species from Abies chensiensis at certain stages of its growth.

Belonging to the same category of occasional inclusions are the thickwalled elements, often with exceptionally wide lumina, which are common objects in the mesophyll of the scale-like leaves of several species of Cupressus, e.g. Goveniana, Lawsoniana, Macnabiana, and pisifera. In the genus Thuja it is rather remarkable that similar fibrous cells should be found only in the adult foliage of Thuja sutchuenensis, a little-known species from north-eastern Szechuan (Fig. 1).

Quite apart from its more minute anatomical structure, the general outline of a section of a leaf, when seen under the microscope, is sometimes illuminating, and never more so than in the case of Abies Delavayi, a Chinese species that has been the subject of endless controversy among taxonomists.

Discovered by the Abbé Delavay on the Tali range in the province of Yunnan, this remarkable Silver Fir was given specific rank by Franchet, who, in his description of the species, makes special mention

¹ A. Franchet in Journ. de Bot. xiii (1899), 255.

of the peculiar character of the foliage, which is without parallel in the genus.

In the type specimen, as in other material of this species collected subsequently by Forrest in this and other localities in Yunnan, all the leaves are excessively revolute, the margins being so completely recurved that they overlap the very prominent midrib, thus concealing the lower surface of the leaf throughout its entire length. This arrangement, as was pointed out by Franchet, makes the outline of a transverse section resemble the symbol on (Fig. 12). Prolonged immersion of the leaves of Abies Delavayi in boiling water has practically no effect upon their shape, and the tenacity with which they maintain their distinctive form would seem to imply that their revolute character is a constitutional feature of this species. From a diagnostic point of view this singularity of the foliage is important when comparison is made with the Silver Fir discovered in western Szechuan by E. H. Wilson,1 and introduced into cultivation by him under the name of Abies Delavavi. Wilson's specimens from Szechuan are precisely similar to those collected by Forrest on the Burma-Yunnan border on several occasions, but both differ from the true Abies Delavayi of Franchet in certain notable respects, so much so that Craib 2 was led to establish a new species, which he named Abies Faberi, taking Wilson's specimen from Wa-shan (No. 2089) as the type. As a natural corollary, cultivated examples of this Silver Fir, grown from seed gathered by Wilson in Szechuan, came to be known as Abies Faberi.

Among the specific characters which separate Abies Faberi from Abies Delavayi, a special point was made by Craib of the lesser degree of curvature exhibited by the leaf-margins of the former, which leads to a progressive uncovering of the lower surface as the leaves become mature. This point of difference between the species is made more apparent when transverse sections of their leaves are contrasted, for the configuration of the sections gives a definite indication of the relative amount of curvature shown by the leaf-margins in each species (Figs. II, I2). It must be made quite clear that the sections photographed were cut from leaves that had been treated, each in exactly the same way, by immersion in boiling water before sectioning, and any accentuation of the marginal curvature due to post-mortem desiccation has been eliminated. This should meet the objection raised by Wilson 3 that "in herbarium specimens this obvious character (the recurving of the leaf-margins) may be much exaggerated by careless drving." A further argument in favour of the distinctiveness of Abies Faberi and Abies Delavayi is that the contrasting features of their foliage, linked with other outstanding points of difference, are

¹ E. H. Wilson in Sargent, Pl. Wilson. ii (1914), 41.

² W. G. Craib in Notes, Roy. Bot. Gard. Edin. xi (1919), 278.

² E. H. Wilson in Journ, Arnold Arbor, vii (1926), 56.

just as apparent in specimens which have been gathered from trees growing cheek by jowl in the same locality in Western China.

Despite these facts, A. B. Jackson, in a suggested classification of the Firs of the Delawayi group, merges Abies Faberi in Abies Delawayi var. typica, this, too, with special reference to plants in cultivation. Quite apart from the marked external differences exhibited by native material of Abies Faberi and Abies Delawayi, it is very evident that plants in cultivation, raised from seed brought from Szechuan, approximate more closely in outward form and feature to Abies Faberi than to the Delavayan type, with which A. B. Jackson would associate them. Even the shape of a leaf-section from a living example of Wilson's No. 4078 would seem to preclude such a relationship as that proposed, and to favour the view that cultivated specimens of Wilson's introduction are conspecific with Abies Faberi (Fig. 13).

From the foregoing, it will be seen that in cases such as this, where the identity or relationship of a particular conifer is in doubt, the general configuration of a leaf-section, apart from its structural details, is not without significance, and may be used as evidence in reaching a decision on the point at issue.

The opinions the writer has ventured to express in this present paper are based on some considerable experience of the practical application of leaf anatomy to the identification of coniferous species, and are supported by observations on a wealth of material accumulated from various sources at home and abroad. In the context, stress has been laid on the absolute necessity of testing the constancy of each anatomical feature of a leaf before making use of it as a specific indicator, and the systematic importance of such a feature will depend not merely upon its immutability in every circumstance, but also upon the incidence of its occurrence in a genu.

While it cannot be claimed that in every case the particular structure of a conifer leaf constitutes an infallible guide to the affinity of the species to which it belongs, it will not be denied that anatomical features are often extremely useful for identification purposes, provided that their diagnostic value is based on strictly empirical grounds, and that they are employed solely in conjunction with external characters.

In conclusion, the author wishes to express his indebtedness to Miss E. R. Stott for having prepared the very excellent hand-cut sections of conifer leaves which form the subjects of the photographs illustrating this paper.

¹ A. B. Jackson in "Conifers in Cultivation" (The Report of the Conifer Conference, Nov. 1931), 244, 246. London. 1932.

EXPLANATION OF PLATES CCLVI-CCLVIII

- Fig. I.—Thuja sutchuenensis Franch. Co-type ex Herb. Mus. Paris. T.S. branch and leaves, showing thick-walled cells with wide lumina in the mesophyll.
- Fig. 2.—Abies sachalinensis Mast. Cult. Roy. Bot. Gard. Edin. T.S. leaf with four resin canals.
- Fig. 3.—Torreya Fargesii Franch. Co-type ex Herb. Mus. Paris. T.S. leaf, showing stellate idioblasts in the mesophyll.
- Fig. 4.—Pinus sylvestris Linn. T.S. abnormal leaf from young shoot injured by blackcock, showing variable position of the resin canals, and the formation of a third vascular bundle.
- Fig. 5.— Abies squamata Mast. T.S. leaf of native specimen, Wilson No. 4079, from Szechuan, with median resin canals.
- Fig. 6.— Abies squamata Mast. T.S. leaf of cultivated young tree, grown from seed, Wilson No. 4079, with marginal resin canals.
- Fig. 7.— Keteleeria Davidiana Beiss. T.S. leaf of native specimen, Forrest No. 21042, from Yunnan, showing undivided vascular strand, and prominent midrib on upper surface.

Fig. 8.—Larix Potaninii Bat. T.S. leaf of native specimen, Rock No. 3404. from Yunnan, showing papillose epidermis.

- Fig. 9.—Larix Griffithii Hook. f. T.S. leaf of native specimen, Forrest No. 27543, from Burma, showing the smooth upper epidermis characteristic of this species.
- Fig. 10.— Juniperus Coxii A. B. Jackson. Co-type, Exbury, Hants. T.S. leaf showing papillate epidermis on both surfaces.
- Fig. 11.— Abies Faberi Craib. T.S. leaf of native specimen, Forrest No. 19388, from Tali range, Yunnan, showing slight recurving of the margins.
- Fig. 12.— Abies Delavayi Franch. T.S. leaf of native specimen, Forrest No. 4606, from Tali range, Yunnan, showing the strongly recurved margins characteristic of this species.
- Fig. 13.— Abies Faberi Craib. T.S. leaf of cultivated tree, grown from Szechuan seed, Wilson No. 4078, showing absence of curvature.
- Fig. 14.—Taxus cuspidata Sieb. et Zucc. T.S. leaf of cultivated shrub, showing absence of cuticular pegs from the midrib on under side.
- Fig. 15.—Taxus chinensis Rehd. T.S. leaf from native specimen, Forrest No. 15053, from Yunnan, showing median zone completely devoid of cuticular pegs.
- Fig. 16.—Taxus Wallichiana Zucc. T.S. leaf of native specimen, Wall. Cat. 6054a, from Himalayas, showing cuticular teeth on midrib below, and presence of cells with resinous contents in mesophyll.
- Fig. 17.—Taxus Wallichiana Zucc. T.S. leaf of native specimen, Forrest No. 22185, from Szechuan, showing median zone with cuticular pegs, and resin-containing cells in mesophyll.





