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## RECENT INVESTIGATIONS ON THE COMPARATIVE ANATOMY OF CONIFERS

UNTIL quite recently there has been an increasing tendency to regard the two important coniferous tribes which are, at the present epoch, respectively characteristic of the northern and southern hemispheres, viz., the Abietinæ and Araucarinæ, as of different origin and not nearly allied with one another. This view of their derivation is, for example, represented by Professor Seward in his monograph on the Araucarinæ<sup>1</sup> and by Professor Penhallow in his "Manual of North American Gymnosperms."<sup>2</sup> A similar opinion has even quite recently been expressed by Mr. Thomson.<sup>3</sup> While the inferences of those whose conclusions are based almost entirely on a consideration of the structure of existing representatives of the Coniferales and of their surmised ancestors from the Paleozoic, have had the marked separatist trend indicated above, of late quite another tendency has made itself felt as a consequence of the structural investigation of the Mesozoic conifers and a comparison of these with existing tribes.

An important contribution on the structure of the Jurassic woods of King Karls Land<sup>4</sup> contains an account of a ligneous species, which the author names *Cedroxylon transiens*. This species is remarkable for the fact that it at the same time manifests the ray structure of the Abietinæ and in many instances the characteristic alternating radial pitting of the tracheids, which is a feature of the wood in existing Araucarinæ. On account of the latter feature Gothan, while referring the wood to the abietineous genus *Cedroxylon* Kraus, applies the specific appellation *transiens*, to indicate that in his opinion the wood in question marks a transition from the Abietinæ to the Araucarinæ. Of the general soundness of this view there can be no question. Nearly contemporaneously Jeffrey published an account of another Mesozoic wood presenting the same structural peculiarities as *Cedroxylon transiens*, together with the added abietineous feature of the possession of short or spur shoots, re-

<sup>1</sup> "The Araucarinæ, Recent and Extinct," *Phil. Trans. Roy. Soc. London*, 1906.

<sup>2</sup> Ginn & Co., Boston, 1907.

<sup>3</sup> "The Megasporephyll of *Saxgothea* and *Microcachrys*," *Bot. Gazette*, 47, May, 1909.

<sup>4</sup> Gothan, W., "Die Fossilen Hoelzer von Koenig Karls Land," *Kung. Svensk. Vetenskap. Handlingar*, 42, No. 10.

sembling in their anatomical relations those of the living *Pinus*.<sup>5</sup> The latter author, however, differs diametrically in his point of view from Gothan, since he regards *Araucariopitys*, in spite of its numerous abietineous features, as none the less an araucarian conifer and as indicating the derivation of the Araucariæ from an abietineous ancestry rather than the reverse, as is assumed by Gothan.

Quite recently Hollick and Jeffrey have published an extensive memoir on the structural remains of the Cretaceous conifers of Staten Island,<sup>6</sup> in which they describe for the first time the anatomical organization of the branches, leaves and cones of a number of well-known Mesozoic conifers hitherto recognized from impressions alone. They reach the conclusion that the external appearance of Mesozoic conifers is in general very misleading as to their real affinities. The supposed Sequoias of the Cretaceous, for example, turn out from the internal examination of all their organs not to belong to the modern genus at all but to be closely related to those araucarian conifers, which are at present limited in their range to the southern hemisphere. The same result is reached in regard to a number of other genera, which have been connected with the living Sequoiinæ, Cupressinæ and even the Podocarpinæ. These authors further conclude that the general structure of Cretaceous conifers of araucarineous affinities is good evidence for the derivation of the Araucariinæ from a stock resembling the Abietinæ and not for the reverse mode of origin, which is universally accepted by those whose conclusions are mainly based on a structural and habitual comparison of living conifers with the gymnosperms of the Paleozoic, since the transitional forms are all clearly on the araucarian side.

Sinnott has recently described an araucarian wood, which in the former state of our knowledge would have inevitably been referred to the abietineous genus *Cedroxylon* Kraus.<sup>7</sup> From the study of the ray structure of this fossil wood and from the examination of the tracheids in connection with new criteria recently formulated, this author comes to the conclusion that his wood represents a type of the Araucariinæ, transitional towards

<sup>5</sup> Jeffrey, E. C., "*Araucariopitys*, A New Genus of Araucarians," *Bot. Gazette*, Dec., 1907.

<sup>6</sup> "Cretaceous Coniferous Remains from Kreischerville, New York," *Mem. New York Bot. Garden*, III, May, 1909.

<sup>7</sup> Sinnott, E. W., "*Paracedroxylon*, A New Type of Araucarian Wood," *Rhodora*, Vol. II, Sept., 1909.

the ancestral Abietineæ, which he names *Paracedroxylon*, on account of its general resemblance to the abietineous wood genus *Cedroxylon* Kraus.

In an important though brief article on the occurrence of the "bars of Sanio" in recent and extinct coniferous woods, Miss Gerry<sup>8</sup> comes to the interesting conclusion that the presence of this structural feature, consisting of transverse bands of cellulose interposed between the radial pits of the tracheids of the wood, is characteristic of all conifers, *except the Araucarineæ*. Her results are of special significance in connection with the conclusions reached by Jeffrey and Hollick, cited above, in regard to the true affinities of the supposed Sequoias, Thuyas, etc., of the Mesozoic. On the basis of the absence of the bars of Sanio in well-preserved woods of supposed Cretaceous Sequoias, etc., she arrives at the result that these are in reality of araucarian affinities, as was inferred by the authors just mentioned, as the consequence of the combined structural study of the branches, leaves and cone-scales of the conifers in question.

The general result of all the investigations cited in the foregoing paragraphs is to show that there existed during the Mesozoic conifers, which were clearly transitional between the abietineous and araucarineous types of the present day. The predominance of the testimony moreover in favor of the Abietineæ rather than the Araucarineæ having been the older coniferous tribe is apparent. Recently Jeffrey has brought forward very definite positive evidence in favor of this view, based on the structure of Mesozoic pines.<sup>9</sup> Known structurally heretofore only as to their wood, the pines of the Cretaceous, which are not without closely allied relatives in the earlier Mesozoic, are here described in relations to the very important features of leaf structure. Among the abietineous remains the most significant because the most archaic genus is *Prepinus* Jeffrey, which has a detailed resemblance in foliar organization to certain Cordaitales of the Paleozoic, as well as the centripetally formed primary wood which is the common possession of the Pteridophyta and the lower gymnosperms. The author was moreover able to trace a complete seriation among various representatives of Cretaceous pines, in leaf organization, from the type presented by *Prepinus*, to that which characterizes contemporary species of *Pinus*. It thus appears that the abietineous line is definitely connected with the

<sup>8</sup> Gerry, Eloise, *Annals of Botany*, Vol. 24, No. 93, Jan., 1910.

<sup>9</sup> Jeffrey, E. C., "On the Structure of the Leaf in Cretaceous Pines," *Annals of Botany*, Vol. 22, No. 86, April, 1908.

Paleozoic gymnosperms, particularly with the Cordaitales, and in this respect has the strongest claim to be considered as the oldest representative of the coniferous stock.

In a recently published article, Jeffrey considers certain abietineous features, such as resin canals of the secondary wood, or the occurrence of marginal ray tracheids, which are found as abnormalities in certain species belonging to the sequoiineous and cupressineous tribes of conifers.<sup>10</sup> He reaches the conclusion that these abnormal abietineous features of the tribes in question are not indications of the derivation of the Abietineæ from them, as has been inferred by Penhallow and others, since recent structural paleobotanical investigations show that the Abietineæ are immeasurably older geologically than the sequoiineous or cupressineous tribes. The conclusion is arrived at that the resin canals or ray tracheids, which sporadically occur in the woods of *Sequoia*, *Thuja*, *Sciadopitys*, *Cunninghamia*, etc., indicate that the Sequoiineæ and Cupressineæ came off from the Abietineæ in the late Mesozoic or early Tertiary, after the latter had developed marginal ray tracheids in their wood rays.

The general result of numerous recent investigations on the anatomy of living and extinct conifers is to show that the two coniferous tribes which have to-day diametrical polar distribution are both very old, reaching back as far as the Paleozoic, that now widely separated geographically and anatomically they once flourished side by side in the northern hemisphere and were connected phylogenetically by a series of transitional forms. The preponderance of evidence moreover seems to vouch for the greater age of the Abietineæ. The more modern and cosmopolitan tribes, the Sequoiineæ, Cupressineæ, Taxineæ, and Podocarpineæ appear further to have been derived from abietineous forebears at a comparatively recent epoch. Even the Podocarpineæ of present characteristic antarctic range, appear from Miss Gerry's interesting investigations, to have come from the general abietineous stock and not from the Araucarineæ, as has been the conclusion of those who have recently investigated the microgametic structures of the araucarians and podocarps, since the latter possess bars of Sanio, which never occur in the Araucarineæ.

E. C. JEFFREY.

HARVARD UNIVERSITY.

<sup>10</sup> "Traumatic Ray-Tracheids in *Cunninghamia sinensis*," *Ann. Bot.* 22, No. 88, Oct., 1908.