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Evolutionary trends in gymnospermous wood structures during Mesozoic—Protopinaceous woods in the German Jurassic

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This paper contains the establishment for the opinion that in German Jurassic the Protopinaceae against the modern pitted (abietoid) woods are not so frequent as hitherto supposed. According to our estimations the relations between protopinaceous woods and modern pitted ones are different from those believed earlier.

Key-words—Evolution, Gymnospermic woods, Protopinaceae, Jurassic (Germany).

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सारांश

मध्यजीवी कल्प में अनावृतबीजी काष्ठ संरचनाओं में विकासीय प्रवृत्तियाँ—जर्मन जूराई कल्प में प्रोटोपाइनेसीय काष्ठ

वुल्फाँग आर० मुलर-स्टोल

यह शोध-पत्र इस मत की पुष्टी करता है कि जर्मन जुराई कल्प में प्रोटोपाइनेसी वर्तमान गर्त्त युक्त (एँबीटॉयडी) काष्ठों की तुलना में उतनी प्रचुर नहीं है जैसा कि अभी तक माना जाता था। हमारे अनुमान के अनुसार प्रोटोपाइनेसीय तथा वर्तमान गर्त्त युक्त काष्ठों के सम्बन्ध पूर्व अनुमानित तथ्यों से भिन्न हैं।

WOOD structures comparable with the secondary wood of recent Conifers essentially appear not earlier than the Cretaceous as (Kraeusel, 1949) ascertained. These younger, especially Tertiary, fossil woods may be compared, as a rule, closely to recent genera, groups of genera or families of the Conifers. The Mesozoic woods differ distinctly from younger wood forms; in general, they may be compared with recent forms at most in single characteristics but not in their total structure. Many of the Mesozoic woods may belong to the Conifers; for the most part, however, this cannot be stated with certainty. Many of these woods may have belonged to different other gymnosperms, an abundant variety of which existed during the Mesozoic.

The Mesozoic woods show a characteristic evolutionary trend. In the Triassic the ancient wood types of the Palaeozoic still prevail. The extensive collective-genus *Dadoxylon*, the tracheids of which having araucarioid pits, includes secondary wood of Conifers and other gymnosperms as well as of non-gymnosperms, while the Araucariaceae in their recent sense are not yet represented. Nevertheless, the name *Araucarioxylon* Kraus 1882 is usually considered as synonymous with *Dadoxylon* Endlicher 1847 (for discussion see Maheshwari, 1972; Lepekhina, 1972). Only since the Cretaceous it is probable and can partly be proved, that the woods of *Dadoxylon*-type belong to the Araucariaceae. From the nomenclatural point of view it is immaterial that the Palaeozoic Dadoxyla certainly are not Conifers, the younger ones, however, are probably Araucariaceae, since both groups cannot be differentiated by secondary wood alone. Primary structures of numerous Palaeozoic *Dadoxylon* of southern hemisphere, for example, those studied by Kraeusel (1956 a-c), show that they are not related to Conifers, because there is centripetal wood adjoining the path, being very wide in some of these forms.

PROTOPINACEAE IN MESOZOIC

Wood forms distinguishing in particular the Mesozoic belong to the Protopinaceae. Their tracheids show pits which represent an intermediate state between the ancient araucarioid pitting type of *Dadoxylon* and the modern abietioid pitted woods. If we concede the Protopinaceae-woods an intermediate position between the Palaeozoic *Dadoxylon* and modern woods, this is to be understood to concern the phylogeny of features and not the phylogeny of taxonomic tribes.

There has been some discussion and misunderstanding about the position of the Protopinaceae. It must be kept in mind that the Protopinaceae are not a natural group in the sense of Neobotany, but only an anatomical wood-type which may include quite different Gymnosperms. This type appears sporadically during the Triassic, reaches its great diversification in the Jurassic, and dies in the Cretaceous. Grambast (1952) reports a protopinaceous wood said to be of Early Eocene age. The question now whether the Protopinaceae are the only wood-type in Middle Mesozoic besides few representatives of araucarioid structure and certain isolated types like *Xenoxylon*. Recent investigations on extensive material of Jurassic woods have shown that beside different genera of Protopinaceae there have existed already many woods with abietioid, i.e. modern pitting of the tracheids. Those woods have not yet acquired the features of the woods of later periods. They are built up very simply throughout, and give a rather uniform impression. Their anatomical differences are as yet lesser than in the recent Gymnosperms. Only one of our samples contained resin ducts, and two showed structures like cross-tracheids along the ray borders; spiral thickening nowhere could be found. It is striking that the horizontal and tangential walls of the ray cells are never pitted. These ray structures appear in extant Gymnosperms chiefly the Araucariaceae and Podocarpaceae, with abietioid pitted tracheids sufficiently well-preserved they could be assigned to the genera *Podocarpoxylon, Phyllocladoxylon, Cupressinoxylon* and *Circoporoxylon*. Possibly there are also woods with taxodioid cross-field pitting to be considered as primitive forms of *Taxodioxylon*. Woods of these genera have existed during the German Jurassic with certainty already in greater number besides the Protopinaceae genera—*Protocupressinoxylon* Eckhold, *Protopodocarpoxylon* Eckhold, *Protophyllocladoxylon* Kraüsel and *Araucariopitys* Jeffrey. Moreover, *Protocedroxylon* Gothan and *Protopolyporoxylon* Vogellehner have been proved in German Jurassic, but they are not present in our material. The other genera of Protopinaceae, namely *Protopiceoxylon* Gothan and *Prototaxodioxylon* Vogellehner are hitherto not found in German Jurassic (Vogellehner, 1968). The driving woods, so-called "Treibhoelzer", from the Upper Lias (Jurassic), Posidonia-schists of Holzmaden, South Germany, were investigated by Vogellehner (1962). He found *Protocupressinoxylon* and *Cupresinoxylon* and for the first time in the Posidonia-schists *Protophyllocladoxylon* and *Phyllocladoxylon*; those woods are habitats for marine animals, mostly sea-lilies (*Seirocrinus subangularis*).

PORTION OF PROTOPINACEAE IN THE JURASSIC PERIOD

Among 76 specimens of our material, usable for diagnoses, we found 5 *Dadoxylon* (6.6%), 11 *Xenoxylon* (14.5%), 24 Protopinaceae (31.6%), and 36 Abietioid pitted woods (47.3%). Therefore, the relation of protopinaceous against modern pitted woods is strongly moved against the abietioid pitted types; the relation amounts 24 to 36 specimens, i.e. 40 to 60 per cent. If the values, calculated by us, are not correct at all, because some of these woods in reality may belong to the Protopinaceae, the opinion that in German Jurassic the number of protopinaceous woods is greater than that of the modern has to be droped. This result was not to be expected as Kraeusel (1949, p. 102) calculated for the Jurassic Period in the whole world a relation of protopinaceous against modern pitted woods of 60 to 40 per cent, having considered all known findings till 1945. He pointed out that the share of Protopinaceae probably might be too small, because parts of protopinaceous woods hitherto classified to the Lower Cretaceous really may be older.

One can say that the Protopinaceae have appeared approximately at the same time as the simple structured abietioid pitted woods, or atmost a little later, as Protopinaceae is scarce in the Triassic. During the Lower Jurassic (Lias) at any rate both groups existed almost side by side. Since intermediate pitting of protopinaceous type is not rare in root-wood of recent Conifers, it could be presumed that the Protopinaceae represent samples of roots, while the modern (abietioid) pitted samples are the remains of stem-wood. However, this argument is not valid because in this case woods with intermediate pitting should be found in the Tertiary, too, but they are practically absent there. It must be stated that the Protopinaceae being a specific anatomical wood-type cannot be doubted; one must concede, however, that there need not be a featural-phylogenetic chain of tree links, namely woods with araucarioid pitted tracheids, followed by woods with intermediate pitted tracheids (Protopinaceae), and finally followed by woods with abietioid pitted tracheids (modern Conifers). The Protopinaceae

should not be considered as a necessary link in the evolutionary line, because the first abietioid pitted woods, still simply structured may have developed also directly from araucarioid pitted ancestors, because in the Triassic both wood types, i.e. protopinaceous and modern pitted woods exist side by side, like a modern pitted wood, e.g. *Podocarpoxylon triassicum* from the Keuper of Frankonia has demonstrated (Sel-Meier & Vogellehner, 1968). In the German Jurassic the Protopinaceae have their greatest extension, in the Cretaceous they declined. Therefore, woods with modern tracheids are direct descendants of araucarioid pitted forms, but only in anatomical sense. Both types, protopinaceous and modern, have their origin in the same time period. Therefore, the Protopinaceae also originated from the araucarioid stock.

Mueller-Stoll (1960) stated that the fossil with enlarged pith named *Reticulopitys suevica* from Lias of Schwaebisch Gmuend, South Germany, has a secondary wood like *Protophyllocadoxylon*; on his table 2, fig. 9 this is clearly discernible. The pores in cross-field in tangential direction are single, large, oblique-elliptical, acute on both corners, so called "Eiporen", but Schultze-Motel (1961) critisized this, because in text-fig. 1 on p. 171 the cross-field pores are round like *Circoporoxylon*, but it is only apparent because of bad preservation.

It is certain that during the Cretaceous Period the modern tracheidal pitting finally predominates, and the Protopinaceae gradually disappear. Thus the question arises: Do these woods belong to dying tribes and their particular wood structure disappeared with them, or we face a progressive evolution of the original forms whereby the secondary wood, too, has lost its ancient features? At present we can only raise this question, but cannot clearly answer it. The difficulties lie in the fact that the wood fossils are very rarely found in organic connection with other plants parts. It is usually impossible to classify them in accordance with the taxonomic system which is built up upon the structure of the reproductive organs.

While within the Protopinaceae a progressive evolution and transition to modern woods is possible and up to a certain extent probably, we also know wood types in the Mesozoic, which represent blind-ending of evolutionary lines. This concerns the genus *Xenoxylon* that existed from Triassic to Cretaceous, with maximum expansion during Jurassic, or *Circoporoxylon*, a podocarpoid wood, which appeared in Jurassic and continued beyond Cretaceous in the Tertiary. What kind of plants possessed such wood we do not know for the above mentioned reasons. *Xenoxylon* probably does not belong to true Conifers, but to some other Gymnosperms.

On the southern hemisphere wood structures developed quite differently than on the northern one, corresponding to the development of the entire gymnospermous group. The genus *Dadoxylon* (syn. *Araucarioxylon*) retained much greater importance, and contains during Cretaceous already genuine Araucariaceae. From a more extensive material of South-African Cretaceous Schultze-Motel (1966) proved that these woods show a specific anatomical feature which occurs only in some recent Araucariaceae, especially in some species of *Agathis*. There are so called "marginal cells" looking like low cell rows accompanying the ray borders.

For araucarian woods with such distinguishing features the new genus *Dammaroxylon* was established (Schultze-Motel, 1966). *Podocarpoxylon* also occupies an important share in Cretaceous Period of South Africa. We must remember that at present, too, the Podocarpaceae and Araucariaceae are specific Conifers of southern floras, a fact that became clearly obvious by the end of Mesozoic. During earlier epochs Podocarpaceae was distributed also in the northern hemisphere. These woods have more definite evidences than many dubious leaf remains. Podocarpoid woods may be traced in Central Europe with certainty back to the Jurassic.

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