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ON THE ANATOMY OF *DADOXYLON ARBERI* SEWARD WITH SOME REMARKS ON THE PHYLOGENETICAL TENDENCIES OF ITS TRACHEID PITS

by

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ABSTRACT

A well preserved specimen of *Dadoxylon arberi* Seward has been discovered in the Beaufort Series (Upper Karroo System) of the Empangeni district in Natal, South Africa. The species is characterized by the tracheid pits which are araucaroid in the multiseriate condition, but which are more often circular and separately arranged or appear in stellate groups. The cross field pits tend to be aligned in horizontal pairs.

Dadoxylon arberi shows a relationship with several species of the recent Araucariaceae. Its resemblance to other Gondwana woods from other Southern Hemisphere countries suggests a great uniformity in the elements of the coniferous flora of that time.

It is suggested that *Dadoxylon arberi* represents an intermediate form between the Araucariaceae and Podocarpaceae. The reduction in the seriation of the tracheid pits and a drifting thereof seems to stand in close correlation with the formation of annual rings.

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DADOXYLON ENDLICHER

Diagnosis

Annual rings present, not clear or absent; rays mostly uniseriate from 1–30 or more cells high, horizontal walls thin and smooth; radial tracheid pits uni- to multiseriate; alternate, contiguous, hexagonal; cross field with simple or bordered pits, contiguous or separate; resin tracheids sometimes present; wood parenchyma absent or weakly present (Seward, 1919; Warren, 1912).

Nomenclature

There has always been much confusion about the usage of the names *Dadoxylon* Endlicher and *Araucarioxylon* Kraus for fossil araucaroid wood. Araucaroid wood was first described by Witham (1833) and the name *Pinites* Witham was given. But the name was a homonym for the name *Pinites* Lindley and Hutton which was based on another type. Goeppert (1842) then proposed the name *Araucarites* Goeppert which was, however, preoccupied by the name *Araucarites* Presl used for a cone impression. Endlicher (1847) proposed the name *Dadoxylon* Endlicher to solve the problem. Kraus (1872), however, instituted the name *Araucarioxylon* Kraus as a synonym for *Dadoxylon*.

Both names were afterwards used with some authors using *Dadoxylon* for Paleozoic woods and *Araucarioxylon* for Mesozoic and younger woods. Gothan (1905) criticised the habit on the basis of the inaccuracy of the geological ages of some specimens and some localities. According to Gothan (1905), Grand'Eury coined the name *Cordaioxylon* Grand'Eury for the wood of the Cordaitales. Seward (1919) proposed that the names *Cor-*

daioxylon and *Araucarioxylon* should be written in brackets after *Dadoxylon* and *Araucarioxylon* in order to distinguish between the woods of the Cordaitales and araucaroid Coniferales. Gothan (1905) indicated that it is impossible to distinguish between the secondary wood of the Cordaitales and araucaroid Coniferales. This, together with the fact that the geological borders of the two taxa overlap, makes it impossible to refer a wood specimen to any of the two taxa.

According to the rule of priority the name *Dadoxylon* is the correct name and must be applied to both araucaroid Coniferales and Cordaitales woods.

DADOXYLON ARBERI SEWARD

Figures 1–8

Diagnosis

Annual rings present; rays uniseriate, sometimes biseriate in the middle; radial walls of tracheids with uni- to tri-seriate, exceptionally with tetraseriate pits, triseriate and tetraseriate pits araucaroid, biseriate pits araucaroid but more often circular, separate, or contiguous, alternate, opposite or subopposite, rows sometimes separated by a small passage, uniseriate pits circular, contiguous or separate, stellate groups often present; cross field with from 1–9 simple, circular or ovoid, separate pits which tend to build horizontal pairs; wood parenchyma absent.

Nomenclature

The name *Dadoxylon australe* Arber was proposed by Arber (1905) for an araucaroid fossil wood specimen from the *Glossopteris* flora of Australia. He was at that time, however, ignorant of the existence of the earlier homonym *Dadoxylon australe* Crie which was based on another type. To overcome the problem Seward (1917) proposed the name *D. nicolai* Seward, but the name *Araucarioxylon nicolai* Carruthers already existed and because *Dadoxylon* and *Araucarioxylon* are synonyms, the name *Dadoxylon nicolai* was illegitimate (Walton, 1925). Later on Seward (1919) proposed the name *Dadoxylon arberi* Seward, but Walton (1956), in contradiction to his earlier (Walton, 1925) reference to the illegitimacy of *D. nicolai,* used the name again. Sahni and Singh (1926) suggested that *D. bakeri* Seward and Walton (1923) shows a great resemblance to *D. arberi* and Walton (1956), although with some hesitation, made it synonymous with *D. arberi*. Sahni and Singh (1926) also pointed out that there is a great resemblance between *D. arberi* and the secondary wood of *Araucarioxylon daintreei* Chapman and concluded that the two plants are identical. Kräusel (1928), however, suggested that Sahni and Singh's specimen of *D. arberi* from the Newcastle Series in Australia differs sufficiently from the holotype of Arber to be placed into a new species. This suggestion was followed by Sahni (1933) who gave it the name *Dadoxylon kräuseli* Sahni.

Anatomy of the specimen from the Beaufort Series of the Empangeni District, Natal

Cross section (Figures 1 and 2)

The annual rings are very clear. Shearing zones occur in which the tracheids follow the typical oblique course for a short distance (Figure 2). The lumina of the tracheids in these zones are filled with a dark substance and this makes the shearing zones observable with the naked eye as dark tangential bands. The tracheids in the shearing zones are greatly deformed. According to Warren (1912) shearing zones are formed in the wider and weaker early wood tracheids in which a better circulation of water than in the narrower late wood tracheids makes them easily infiltratable by iron oxide. Great lateral pressure exerted on the wood at the time of petrification caused a shift in the alignment of the weaker zone.

The lumina of the normal tracheids in the early wood are more or less rectangular, while the radial diameter of the late wood tracheids is much smaller than that of the early wood. The diameter of the tracheids thus varies from 34–47 (–67) µm tangentially and from 18–46 (–57) µm radially. The tracheid walls are about 3 µm in thickness. There are from 2 to 8 tracheid rows between each two consecutive rays. There is no sign of wood parenchyma.

Tangential section (Section 3)

The walls of the tracheids are smooth. The rays are uniseriate except for here and there where a ray is biseriate in the middle. The height of the rays varies from 1–18 (–25) cells. The cells appear angular or oval in the middle of a ray, while the upper and lower cells are nearly circular or acute. The individual cells are from 21–28 (32) µm high and from 12–20 (–26) µm wide.

Radial section (Figures 4–8)

The radial tracheid pits show a great variety in arrangement. The pits are uni- to triseriate or they are arranged in stellate groups of 3 to 5 pits. The pits are either araucaroid or appear separate. The latter condition dominates. The uniseriate pits are circular and may stand separate (Figure 6) or appear in solid chains (middle of Figure 3). The pit aperture of the uniseriate pits tends to be obliquely oval. The biseriate pits are araucaroid (Figure 5), but more often they are circular to faintly oval, contiguous or nearly separate. The arrangement is alternate or subopposite (Figure 4). Opposite separate biseriate pits occur in combination with stellate groups (Figure 7). Two of the pits of a stellate group are opposite or subopposite with a single median pit at the top or at the bottom of the group. The pits in the stellate groups are always separate. Triseriate pits are of rare occurrence, but if so arranged they are always araucaroid. This arrangement seems to be restricted to the wider tracheids and towards the ends of the tracheids. The ends of the tracheid walls are more often transverse than oblique. The diameter of the tracheid pits varies from 7–14 µm in the tangential direction and from 7–10 µm in the longitudinal direc-

tion. The pit apertures of the uniseriate pits, as mentioned above, tend to be obliquely oval, but in the multiseriate and stellate groups the apertures are more or less horizontally oval to circular. The pit aperture, however, never reaches beyond the border of the pit (typically araucaroid).

Both the radial and tangential walls of the ray cells are thin and smooth and are about 1,0–1,5 µm in thickness. The number of cross field pits varies from 2–4, sometimes 5, pits, but mostly there are 4 pits which are aligned in horizontal pairs (Figure 8). The pits are obliquely oval and it cannot be established whether they are simple or bordered (apparently they are bordered with wide, oblique oval apertures). The diameter of the pits (or their apertures) varies from 5–7 µm.

COMPARISON WITH RECENT WOOD TYPES

The general structure resembles that of the Araucariaceae, a family which is restricted in its geographical distribution to the Southern Hemisphere, but which has no representatives in South Africa. The absence of wood parenchyma makes *Dadoxylon arberi* more closely related to *Araucaria* Juss. than to *Agathis* Salisb. According to Greguss (1955) the horizontal alignment of the cross field pits is typical of the Araucariaceae. The number of cross field pits is more or less the same as that of *Araucaria klinkii* Lauterb., *A. rulei* F. v.M, *A. beccari* Warb., *A humboldtiensis* Buch and *A. mülleri* Brongn. and Gris. Stellate groups of tracheid pits also occur in *A. columnaris* (Forst.) Hook. as well as in *A. montana* Brongn. and Gris. (Greguss, 1955). The tracheid pit rows are also separated by a small passage in *A. columnaris*.

COMPARISON WITH OTHER GONDWANA WOOD TYPES

Several wood specimens from various Gondwana floras have been brought into connection with *Dadoxylon arberi*. In South Africa this species has been described from other localities. Arber (1910) points out that a wood specimen from the Karroo System from the Ladysmith district, Natal, only deviates from *D. arberi* in having nearly constant uniseriate pits. The variation in the arrangement of the tracheid pits is, however, a diagnostic feature of this species and this cancels out any relationship on the species level. The second species described by Warren (1912) from the Upper Karroo System shows a remarkable resemblance to *D. arberi*, especially as far as the number and arrangement of the cross field pits are concerned. The seriation of the tracheid pits of Warren's specimen is the same as in *D. arberi*, but it, however, lacks stellate groups. Interesting enough, shearing zones are also present in some of the other specimens described by Warren.

Walton (1925) described various specimens from the Karroo System of the Cape Province which he identified as *Dadoxylon arberi*. Stellate tracheid groups of pits as well as separate, uniseriate pits are quite evident in his specimen. The biseriate pits are also separated by a small passage in some instances (Walton, 1925, Plate 1, Figure 3). The tracheid pits are, however, sometimes arranged in four rows. The cross field shows up to 9 circular to elliptical apparently simple pits. Walton (1956) also described specimens of this species from the Karroo System of Malawi whose anatomical measurements and further details are more or less the same as the Empangeni specimen.

From the Upper Newcastle Series (= Lower Beaufort Series) of New South Wales, Australia, Sahni and Singh (1926) described various specimens of *Dadoxylon arberi*. Their specimens do not, however, show stellate groups. They noticed a resemblance between their specimens and the secondary wood of *Araucarioxylon daintreei* Chapman and suggested that the two names are synonyms, but that their specimens do, however, stand closer to the South African species of *D. arberi* described by Walton (1925). Sahni followed a suggestion made by Kräusel (1928) that his specimens differ sufficiently enough from both *D. arberi* and *Araucarioxylon daintreei* to be placed into a new species and renamed it *Dadoxylon kräuseli* Sahni. Walton (1956) must have been ignorant of this fact and still placed the New South Wales specimens in synonomy with *D. arberi* (his *D. nicolai*).

Rao (1936) noticed the resemblance of a wood specimen from the Indian Glossopteris Flora with *Dadoxylon arberi*, but instituted the name *Dadoxylon parbeliense* Rao for it. The only real difference lies in the absence of stellate tracheid groups in Rao's specimen and Rao added: "But perhaps *D. arberi* itself has to be split up into a number of species in view of its wide distribution and the number of incompletely known woods included in it".

Nearly the same variation in tracheid pitting occurs in *Dadoxylon deccani* Shukla (1938). This specimen shows a stronger tendency towards a drifting of the tracheid pits and the rays are up to 49 cells in height. The characteristics of the cross field resembles that of *D. arberi*. A reinvestigation might prove that this specimen should be taken up into *D. arberi*.

Surange and Maithy (1962) instituted a new form genus, *Indoxylon* Surange and Maithy which is characterized by a passage separating the pit rows. This condition is here, however, much more accentuated than in *D. arberi*. *Indoxylon canalosum* Surange and Maithy resembles *D. arberi* as far as the charactersitics of the rays and the number of cross field pits are concerned. It is, however, felt that this species falls within the generic limits of *Dadoxylon*.

Dadoxylon jamudhiense Maheshwari from the Upper Permian of India only differs from *D. arberi* in having about 45 per cent of its rays biseriate. The tendency towards a drifting of the tracheid pits and the from 1–4 cross field pits, which are arranged in horizontal pairs, shows a very close relationship to *D. arberi*. The height of the rays, namely from 1–18 cells, confirms this.

The anatomical features of *Dadoxylon amparense* Sah and Jain from the Jurassic Period of Inida are similar to those

of *Dadoxylon arberi*. The only essential difference lies in the presence of resin tracheids (Sah and Jain, 1964). The same authors described *D. mandroense* which stands even more closely to *D. arberi*. The tracheid pits are uni- to triseriate and show the same variation in pattern. It also has the same number of pits in the cross fields of the late wood, while there are from 4–12 pits in the cross fields of the early wood.

Dadoxylon arberi also shows a relationship with a Gondwana wood from Brazil. This is implied by Kräusel and Dolianiti (1958) who, in a table of comparison, place *Dadoxylon roxoi* Kräusel and Dolianiti opposite *D. arberi*.

PHYLOGENETICAL CONSIDERATIONS AND CONCLUSION

Dadoxylon arberi and other Gondwana araucaroid woods exhibit a variety of arrangement of their tracheid pits. The typical araucaroid pattern in the triseriate and terraseriate pits (Walton, 1925) and to a lesser extent in the biseriate pits has been retained. There is a great tendency towards a looser arrangement of the pits in both the horizontal and vertical planes. There also exists a tendency towards a change from the alternate to the opposite arrangement. Another prominent feature is the reduction in the seriation of the pits.

The question arises whether this mixed arrangement of the tracheid pits is of any phylogenetic significance. Gothan (1907) was the first to claim that an intermediate type of pitting exists between the araucaroid and abietoid types. According to Eckhold (1921) the change from the araucaroid to the abietoid type started in the Triassic and that while the araucaroid type was declining towards the end of the Mesozoic, the abietoid made its appearance and occurred generally towards the end of that era. The change was brought about by a phylogenetic drifting ("Wandlung") of the densely packed araucaroid pits which has led to a looser arrangement. According to Eckhold the change followed two possible pathways. The one pathway is illustrated by the formation of stellate groups and the other by a reduction in seriation. *Dadoxylon brandlingii* Lindley and Hutton from as early as the Carboniferous Period shows this tendency towards a reduction in seriation and drifting of the pits — a similar condition which prevails in *D. arberi*. The opposite arrangement of the pits is considered by Henes (1959) to represent either a tendency to revert to an ancestral condition which would support Jeffrey's (1903) theory that the abietoid type is the original type, or the introduction of a new phylogenetic trend. Henes (1959) also observed a reduction in seriation, vertical drifting and formation of groups of the tracheid pits in *Eristophyton beinertianum* Zalessky, also from the Carboniferous Period, and claims that the reduction of the pits on the radial walls of the tracheids can also be observed in *Callixylon* Zalessky of the Devonian Period. Sahni and Singh (1926) also saw in the stellate groups of pits in *D. arberi* a resemblance with *Callixylon* and that the affinity between the wood types is also illustrated by the end-to-end arrangement of the tracheids.

According to Walton (1925) the transition from the multiseriate araucaroid to the separate and sometimes even opposite pits of *Dadoxylon arberi* supports the idea that the araucaroid type was the original type and that the abietoid type has been derived from it. The transitional wood types are all placed into the Protopinaceae by Kräusel (1919). The most primitive form genus of the Protopinaceae is *Protopodocarpoxylon* Eckhold. It resembles the Araucariaceae, but has the transitional type of tracheid pitting and is characterized by its podocarpoid cross field pits. Like the Araucariaceae the ray cell walls are thin and smooth, a feature which still prevails in all the living members of the Podocarpaceae (Greguss, 1955).

The Coniferales are only represented by their three most primitive families in the Southern Hemisphere, viz. Araucariaceae, Podocarpaceae and Cupressaceae. Only the latter two are presented in South Africa. The Podocarpaceae occur as early as the Cretaceous Period in the geological history of South Africa (Schultze-Motel, 1966). Here it is represented by the form genera *Podocarpoxylon* Gothan and *Phyllocladoxylon* Gothan. If *Dadoxylon arberi* is compared with *Podocarpoxylon umzambense* Schultze-Motel from the Upper Cretaceous Period, a great resemblance in the arrangement of the tracheid pits becomes apparent. The pits of the latter stand separate or may be contiguous in exceptional cases. Furthermore, the pits are uniseriate and are often arranged in horizontal pairs ("Zwilling-stüpfel"). Rarely stellate groups, each of which consists of three pits, occur. The typical araucaroid pattern is totally absent. In *P. angustiradiatum* Schultze-Motel from the same horizon the araucaroid pattern still prevails. Greguss (1955) considers *Podocarpoxylon* Gothan of the Triassic Period to be one of the precursors of the Podocarpaceae which, in their turn, he derives from the Araucariaceae. *Dadoxylon arberi* could thus have played an important role in the evolution of the Podocarpaceae.

It has been held by several authors in the past that there is a close correlation between tracheid size and the seriation of the pits in their walls (Henes, 1959; Bailey and Faull, 1934). The Mesozoic Coniferales more often contain annual rings than the Cordaitales. They also show a stronger tendency towards a reduction in the seriation of the tracheid pits together with a drifting thereof. Gothan (1907) noticed that the horizontal and tangential ray cell walls of *Protocedroxylon transiens* (Gothan) Eckhold (= *Cedroxylon transiens* Gothan) contain abietoid pits, while the early wood contains araucaroid pits and the late wood separate pits which are sometimes arranged in stellate groups ("Sterngruppen" of Gothan). This correlates with the observations made by Bailey (1933) in certain *Cedrus* spp. Here the abietoid type of pitting dominates by far the araucaroid in young stems, while the araucaroid and abietoid types occur mixed in old slow-growing stems. In the latter case, however, the araucaroid type is more restricted towards the wide early wood tracheids,

while the abietoid type is confined to the transitional zone between the proto- and metaxylem as well as in the narrower late wood tracheids. Bailey and Faull (1934) also demonstrated that the pits are larger and more numerous in large tracheids with thin walls and decrease in size and number as the tracheids become smaller and thick-walled in *Sequioa sempervirens*.

Bailey (1925) proposed that the circular type of bordered pit was not an original feature of the transitional zone between the proto- and the metaxylem, but that this type of pit had worked back into the transitional zone and even into the protoxylem which has led to the elimination of the original typical scalariform and transitional pitting of the Cordaitales. It seems that the more efficient abietoid type of pit became established in woods with annual rings and that once they became established they have shifted to the earlier stages of the ontogenetical stages.

The Araucariaceae have tracheids which are more angular in shape than the other families of the Coniferales. This is also the case in the majority of the *Dadoxylon* spp. It is only where annual rings are formed that the tracheid diameter decreases, especially in the radial direction. The lateral contact surface between the wide thin-walled tracheids is larger than that of the thick-walled tracheids with a smaller radial diameter. The relatively larger contact surface of the early wood tracheids facilitates a higher seriation or, in other words, more numerous pits. The reduction in contact surface brought about a reduction in seriation. Another factor which could have played a role in the reduction in seriation was the rounding up of the tracheids which also decreased the lateral contact surface between adjacent tracheids and has led to the pits being confined to the median part of the radial wall. The reduction in seriation consequently affected the form and structure of the bordered pits. Where the lateral transport of water and minerals took place through a larger number of pits in the araucaroid type, the same function had to be performed by a lesser number of pits. With this restriction placed on the lateral flow by the reduction in the number of pits the problem had to be overcome by an enlargement of the size of the apertures which led to the evolution of the abietoid type of bordered pit where the aperture reaches beyond the border of the pit in contrast to the smaller aperture of the araucaroid type of pit.

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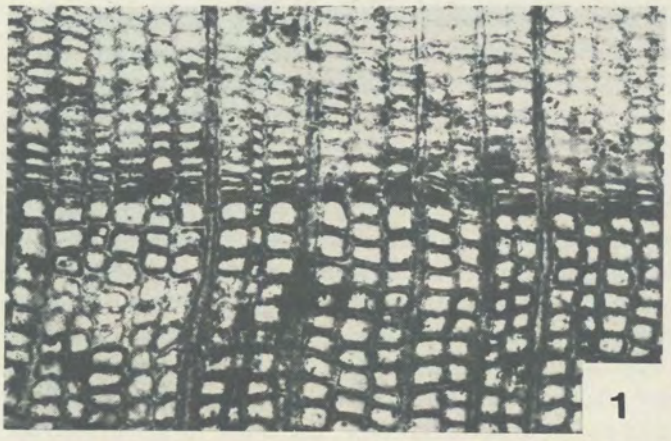
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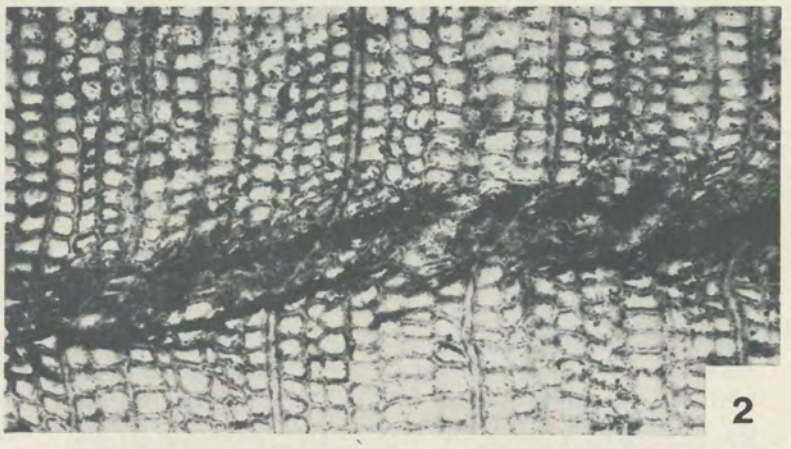
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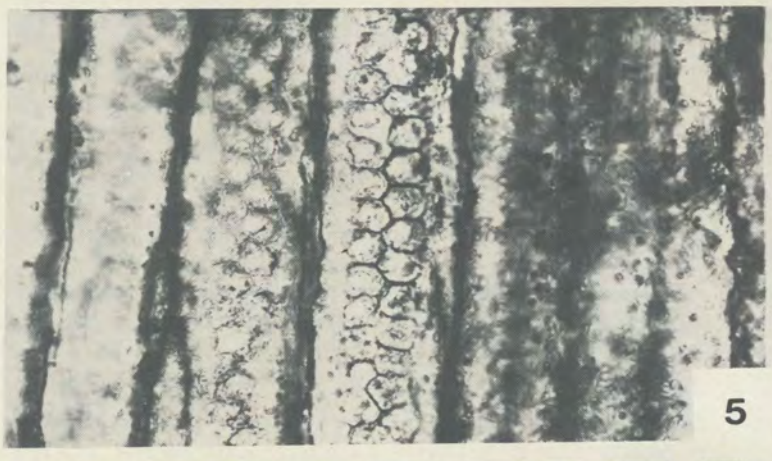
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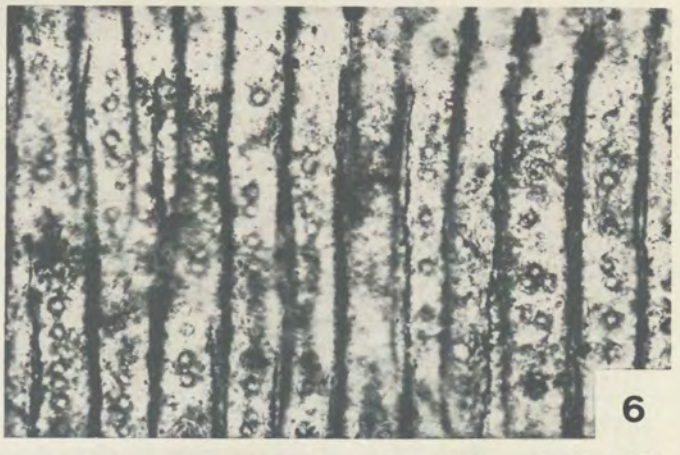

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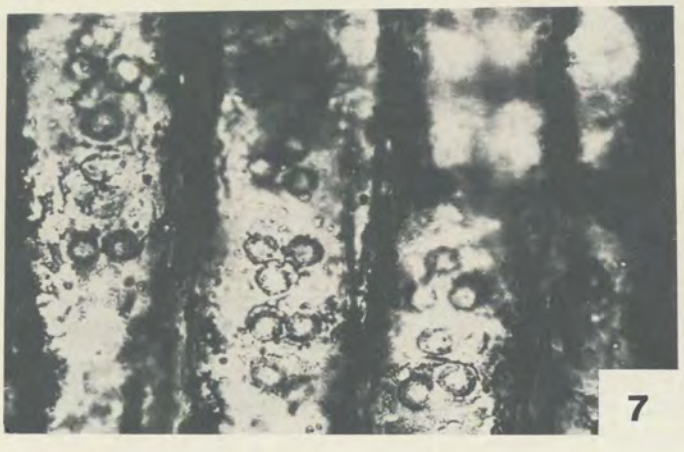

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Figure 1. Cross section; early and late wood; ×40.
Figure 2. Cross section; shearing zone; ×40.
Figure 3. Tangential section; uniseriate rays; ×40.
Figure 4. Radial section; uniseriate, contiguous, circular pits with obliquely oval apertures (at bottom); circular, subopposite pits, separated by small passage (on left hand side); ×300.
Figure 5. Radial section; biseriate, araucaroid pits; ×300.
Figure 6. Radial section; uniseriate, separate, pits; stellate group on right hand side; ×80.
Figure 7. Radial section; stellate groups; opposite pits on left hand side; ×300.
Figure 8. Radial section; obliquely oval cross field pits (or apertures) arranged in horizontal pairs; ×300.