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A NEW SPECIES OF *DAMMAROXYLON* SCHULTZE-MOTEL, *D. NATALENSE* SP. NOV. FROM THE CRETACEOUS OF NATAL, SOUTH AFRICA*

by

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ABSTRACT

In the Cretaceous rocks of the M'hlosinga district, Zululand, Natal a new species of the form genus *Dammaroxylon* Schultze-Motel, *D. natalense* sp. nov., has been discovered. New evidence regarding the structure of the marginal ray parenchyma cells has been obtained. The conclusion is reached that *Dammaroxylon* could possibly take an intermediate phylogenetic position between the Araucariaceae and Podocarpaceae.

SYSTEMATIC PALAEOBOTANY

Class GYMNOSPERMAE

Order CONIFERALES

Family ARAUCARIACEAE

Genus *DAMMAROXYLON* **SCHULTZE-MOTEL 1966**

Type species: *Dammaroxylon africanum* Schultze-Motel

Discussion

The non-committal name *Dadoxylon* Endlicher has been used for secondary araucaroid fossil wood types since before the turn of the century. An enormous number of species has been ascribed to it. It includes woods of both the Paleozoic and the Mesozoic as well as from the Cordaitales and the Coniferales. Various authors have attempted to split the taxon, but without any success. Hence *Dadoxylon* has become a "collecting box". Kräusel and Range (1928) suggested that anatomical structural modifications in secondary wood should be looked for, on the basis of which new genera should be instituted. Border cells (=marginal ray parenchyma cells) were first observed by Greguss (1955) in recent wood and he suggested that these structures are important for. the identification of wood types. Schultze-Motel (1966) discovered border cells in araucaroid fossil wood and used it as a basis for distinguishing *Dammaroxylon* from *Dadoxylon*.

Dammaroxylon natalense sp. nov.

Plate I, Figures 1–17; Table 1

Holotype: Dept. of Botany, University of the North, Pietersburg. Slides E4a–e; Plate 1, Figures 1–17.
Locality: M'hlosinga district, Zululand, Natal.
Age: Cretaceous.

Derivation of name: The plant is named after the province of Natal in which it has been discovered.

Diagnosis

Secondary wood with annual rings; rays uniseriate, 1–7(–14) cells high; border cells undulate regularly or irregularly, shape varies from conical and tongue- to bladder-shaped, border cells double layered in some instances; radial tracheid pits constantly uniseriate, contiguous or separate, circular or horizontally slightly flattened; cross field pits 2–6(–12), circular or oval, bordered, pit apertures circular, pits aligned in horizontal pairs or rows or scattered, contiguous or separate; wood parenchyma absent.

ANATOMY OF THE FOSSIL WOOD

Cross section (Plate I, Figures 1 and 4): Annual rings are present (Figure 4). The tracheids are well preserved and are mostly circular or oval in shape (Figure 1). The radial diameter of the tracheids varies from 21–34(–46) μm, while the tangential diameter varies from 16–35(–39) μm. The tracheid walls are from 3–8(–12) μm in thickness.† There are from 4–13 rows of tracheids between each two consecutive rays. Wood parenchyma is absent.

Tangential section (Plate I, Figures 2, 6, 7, 9 and 10): The tracheid walls are smooth (devoid of pits). The rays are constantly uniseriate (Figure 2) and 1–7(–14) cells high. The shape of the ray cells is oval to rectangular. The height of these cells varies from 18–27(–36) μm while their width varies from 9–12(–18) μm. The ray cell walls measure 2–3(–5) μm in thickness. The rays are bordered above and below by border cells which vary in shape from conical (Figure 10) and tongue- (Figure 9) to bladder-shaped (Figure 6). In some instances the

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† Measurements of cell walls are that of both walls.

border cells appear on top of one another on the one side of the ray (Figure 7). The height of the border cells varies from 3–15(–30) µm.

Radial section (Plate I, Figures 3, 5, 8 and 11–17): The tracheid pits are constantly uniseriate (Figure 3) and mainly circular, although they appear slightly flattened horizontally in some instances. The pits stand contiguous or separate. They vary from 12–17(–20) µm in height and from 15–18(–20) µm in width. The horizontal and tangential walls of the ray cells are thin and smooth (Figures 12 and 13) and measure 2–3(–5) µm in thickness. The rays are bordered above and below by border cells (Figure 16), the outer walls of which undulate regularly (Figure 11) or irregularly (Figure 5). The border cells at the top and at the bottom of the same ray may differ in height (Figure 16). A small secondary triangular cell appears in some instances on top of the border cells (Figure 8). The border cells are normally higher where they are in contact with the tracheid walls (Figures 11 and 16). The outer walls of these cells are thin. Their walls do not seem to contain any pits. Some border cells show 'septa' (Figure 17). Trabeculae occur in some of the tracheids (Figure 14). The cross fields usually show 2 to 6 pits (Figures 12, 13 and 15), but there may be as many as 12 pits per field. The pit apertures are circular (Figure 17). When less than six pits occur in a cross field, they are usually large, separate and scattered (Figure 13). When more than six pits occur in a cross field they are contiguous and aligned in horizontal rows (Figures 12 and 15). The cross field pits measure 4–6(–7) µm in diameter.

TABLE 1

The most important anatomical measurements of *Dammaroxylon natalenses* sp. nov.

TRACHEIDS	
Radial	21–34(–46) µm
Tangential	16–35(–39) µm
Wall thickness (double)	3– 8(–12) µm
Pits: height	12–17(–20) µm
width	15–18(–20) µm
RAYS	
Height (in cells)	1– 7(–14)
Height of cells	18–27(–36) µm
Width of cells	9–12(–18) µm
Wall thickness (double)	2– 3(– 5) µm
Cross field pits: number	2– 6(–12)
diameter	4– 6(– 7) µm
Border cells: height	3–15(–30) µm

Comparison with other fossil wood types

The presence of border cells identifies the specimen with *Dammaroxylon.* It differs essentially from the type species, *D. africanum* Schultze-Motel, as well as from the only other species, *D. umzambense* Schultze-Motel, to be placed in a separate species. The rays of *D. africanum* are 1–16(–20) cells high while the tracheid pits are uniseriately or biseriately arranged. The new species resembles *D. africanum* as far as the number and arrangement of the cross field pits are concerned. The type species furthermore contains wood parenchyma. Schultze-Motel's (1966) second species, *D. umzambense,* also differs from the new species in that it has a tendency to form biseriate pits while the cross field shows 1–4 pits. Wood parenchyma may also be present in this species. Both Schultze-Motel's species are from the Upper Cretaceous of the Umzamba Beds of East Pondoland. They both lack annual rings, but shearing zones are present which, according to Warren (1912), is indivative of the differentiation of the wood into early and late wood.

The new species can also be compared with *Dadoxylon jamuriense* Maheshwari H. K., an element of the Indian Glossopteris flora (Maheshwari, 1965). Maheshwari, however, only refers to the border cells of his species as a wavy wall running along the long axis of the ray cells. This species should rather be known as *Dammaroxylon jamuriense* (Maheshwari H. K.) nov. comb.

The only other wood type in which border cells are present is *Araucariocaulon breveradiatum* Lignier (1907). Although Lignier's illustration (Figure 36) clearly shows the border cells, he does not pay any attention to it in his description. Seward (1919) reproduced the same illustration, but he also did not refer to the border cells. Seward, however, described the fossil as ". . . an aberrant type the position of which is by no means clear". It is felt that this wood type should also be included under *Dammaroxylon* under the name *D. breveradiatum* (Lignier) nov. comb.

Further remarks on the nature of the border cells

Border cells were first observed by Greguss (1955) in the Araucariaceae and he described them as follows: "Marginal ray parenchyma cells: cells on the upper or lower margin of a ray, commonly different in structure from the inner ray cells and therefore important in identification." According to him these cells lack cross walls and pits, but they have a wall structure similar to that of the ray cells. They form part of the rays and are independent of the tracheid end walls. In *Ginkgo biloba* L. the end walls of the tracheids are thickened where they are in contact with the ray cells and give the impression of border cells (Greguss, 1955). Pool (1922) described border cells as intercellular spaces between the fibre tracheids and medullary rays which form "connecting frames" on the radial walls of the ray cells. Greguss (1957) also described border cells in the Podocarpaceae.

The ontogenetic origin of border cells has as yet not been investigated. Greguss (1970) states that they are "meristematic" and he describes them as ". . . probably cambial or more nearly monopleuric cambial (in) nature produced by the division of the so-called medullary ray cells proper". They should rather be interpreted as derivatives of the cambial ray initials than being cambial in nature. Also, the meristematic potentiality is limited to the ray initials and is not a characteristic of the derivatives thereof. They can rather be described as undeveloped derivatives of the ray initials. The secondary border cell may represent a derivative of a ray initial which did not develop further in the radial direction.

DISCUSSION AND CONCLUSION

Dammaroxylon seems to be limited to the Cretaceous rocks which occur along the East Coast of South Africa. The araucaroid structural pattern is exemplified by the tracheid pitting and the tendency towards horizontal alignment of the cross field pits. The ray cell walls are in the primitive, thin-walled primary stage. There are, however, indications of its abietinean affinities. This is shown by the rounded off shape of the tracheary lumen which is accompanied by a reduction in seriation of the tracheid pits.

The known species of *Dammaroxylon* can be arranged in a phylogenetical series. The most primitive of the series is *D. africanum* where the tracheid pits are typically araucaroid and always contiguous. *D. umzambense* has progressed a step farther and the tracheid pits are more often uniseriate, but still contiguous and seldom biseriate. In *D. natalense* the greatest reduction is found where the pits are constantly uniseriate. Furthermore, the series show a reduction in the number of cross field pits together with an enlargement thereof. The pits sometimes occur scattered in the field which is a deviation from the normal araucaroid pattern.

The presence of border cells in recent taxa is at this stage still problematic. The ontogenetic origin and general occurrence thereof still remain to be discovered by further investigation — especially in the Araucariaceae and Podocarpaceae. The fact that these cells have been discovered in both these taxa is indicative of a phylogenetic relationship and *Dammaroxylon* could take an intermediate position between the two taxa.

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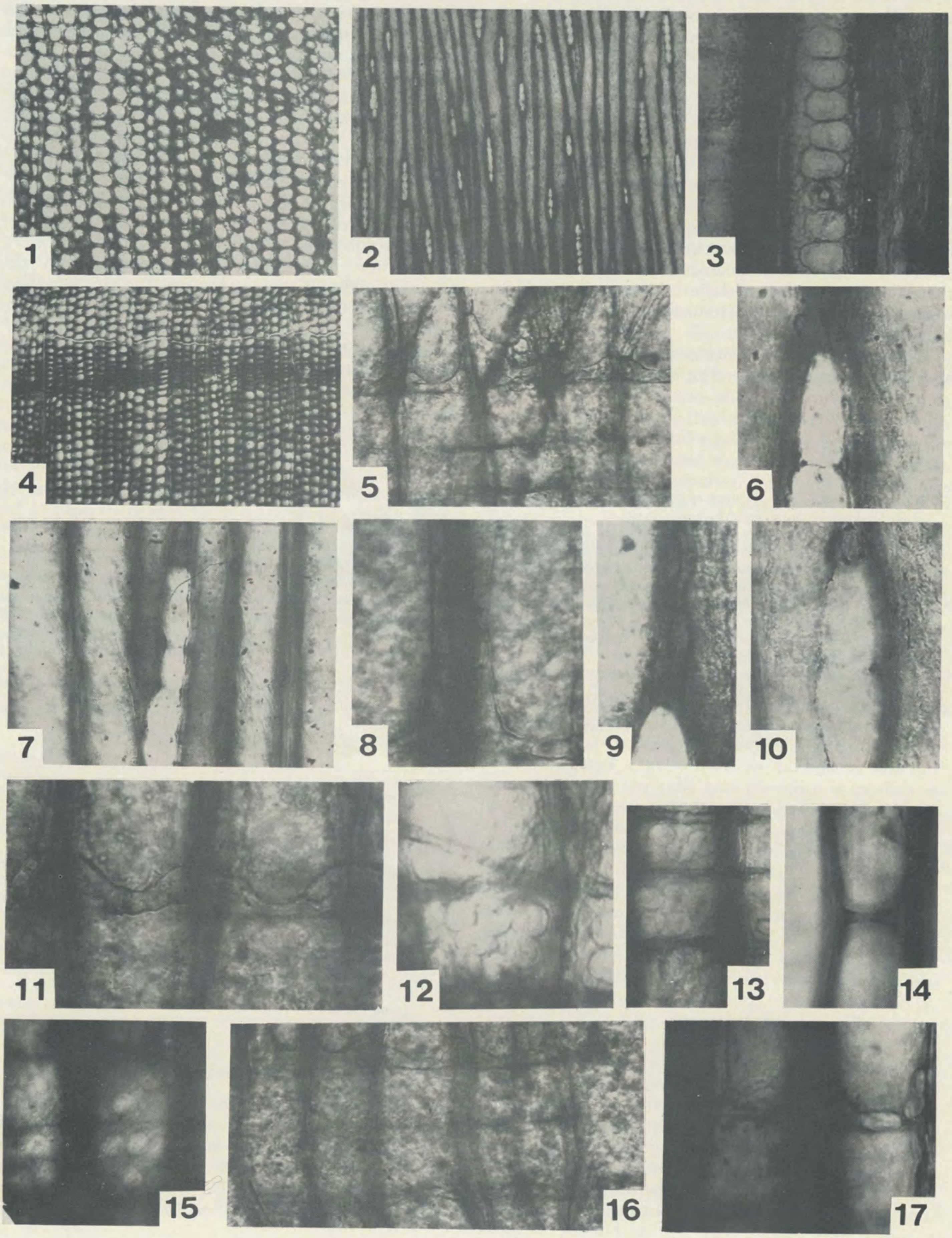
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PLATE

Figure 1. Cross section; circular tracheids; x 80.
Figure 2. Tangential section; uniseriate rays; x 80.
Figure 3. Radial section; uniseriate, contiguous, circular tracheids; x 400.
Figure 4. Cross section; early and late wood; x 40.
Figure 5. Radial section; irregularly undulating border cells; x 400.
Figure 6. Tangential section; bladder-shaped border cell; x 800.
Figure 7. Tangential section; two border cells on top of one another; x 300.
Figure 8. Radial section; secondary, triangular cell on top of border cells; x 800.
Figure 9. Tangential section; tongue-shaped border cell; x 800.
Figure 10. Tangential section; conical border cell; x 800.
Figure 11. Radial section; regularly undulating border cells; x 800.
Figure 12. Radial section; contiguous cross field pits aligned in horizontal rows; smooth end wall of ray cell; x 600.
Figure 13. Radial section; small number of separate cross field pits; smooth horizontal walls of ray cells; x 300.
Figure 14. Radial section; trabecula in tracheid; x 300.
Figure 15. Radial section; cross field pits in horizontal rows with tendency to be separate; x300.
Figure 16. Radial section; border cells on top and at bottom of ray differ in height; x 300.
Figure 17. Radial section; border cell with "septum"; cross field pits with faint circular aperture; x 500.