GYMNOSPERMOUS WOODS WITH PRIMARY STRUCTURES FROM GONDWANA ROCKS — A REVIEW*

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SILICIFIED woods from the Gondwana series were described rather long ago. Summaries of these woods, which are mostly gymnospermous, were given by Rao (1935) and Grambast (1950). Commonly the specimens are only pieces of secondary wood and as compared to the complex wood structure of the Angiosperms, their structure is rather simple. One of the relatively outstanding features of these fossil gymnospermous wood is the arrangement of bordered pits on the radial walls of the tracheids (rarely also on tangential walls). As a rule these pits are arranged in one vertical row and are contiguous and flattened. Sometimes we find two or even more rows, then the pits are usually alternate and hexagonal. Among living conifers only the Araucariaceae show a similar arrangement of the pits. Kraus (1864) therefore, named fossil woods of that type as *Araucarioxylon*, which is only a synonym to the older name *Dadoxylon* Endlicher (1840). Some of these *Dadoxylon*, especially of Mesozoic age may be true conifers. But this is not true for the Palaeozoic. Cordaitales and other groups of Palaeozoic Gymnosperms also show the araucarian type of pitting. In the past usually the identification was based only on the characters of the secondary wood and little emphasis was given to finer but distinguishing features of the pith and primary xylem. Hence the form genus *Dadoxylon* has become a 'collecting box', for only too many fossil woods with widely different anatomical features.

It is well known that pith and primary xylem exhibit far larger differences than the secondary wood, e.g. *Mesoxylon* and its relatives, *Calamopitys*, *Mesopitys* and *Porodendron*. In 1928 Kräusel showed that it is the same with the woods from the Karoo-beds of South West Africa, which form a part of Lower Gondwana series corresponding more or less to the Permian. Since that time similar fossils have been found in South Africa, South America, India and Antarctica. It is likely that others may be discovered in Australia. They are mostly of Permian age, some perhaps slightly older or younger. Separating them from the non-committal *Dadoxylon*, new form genera were created (WALTON, 1925; KRÄUSEL, 1928 & 1956a-c; KRÄUSEL & DOLIANITI, 1958; SURANGE & MAITHY, 1961). The number of these genera has now become fairly large. We, therefore, think it most useful putting together the anatomical features on which they are founded, and to give a preliminary key for their identification.

One of the most important facts is that some forms possess, besides diploxylic leaf traces (**8**), mesarch (or even exarch) primary xylem in the stem. These centripetal elements are generally only metaxylem, but in some cases they are secondary xylem too. Rarely they form a close sheath around the pith, and it is not always that the centripetal wood has bordered pits (**19**), only the reticulate pitting is reached in that case (**15**). More frequently centripetal wood is broken up or separated into groups of tracheids. These groups may be wedge-shaped (**5**) or formed by single radial row of cells (**1**, **6**, **7**, **28**). Short tracheids of irregular form are known, like pith tracheids (**15**).

The pith itself is rather variable and may be homogeneous or heterogeneous. If homogeneous, it consists of parenchymatic cells, forming irregular vertical rows (**1**, **4**, **6**), more or less similar, rounded or polygonal in cross-section, and more or less rectangular in longitudinal section. The cell walls are

*This review was prepared during the stay of Professor Dr. R. Kräusel as a Visiting Scientist at the Birbal Sahni Institute of Palaeobotany.

usually smooth, sometimes pitted (**26**, **3**, **16**). Generally the pith is cylindrical, round or polygonal but sometimes it shows small projections (**16**, **17**, **18**). Following the secondary growth in the stem the arrangement of the pith cells too is changed. Cells degenerate and form air gaps. The gaps are sometimes of irregular shape or radially arranged (**26**). In some cases they run more or less horizontally through the pith (**8**) and at last a discoid pith is formed (**27**) as is known among the Cordaitales. But we do not think that this character is only restricted to the Cordaitales.

The second main type of the pith is heterogeneous. In this we find elements of two or more different types. *Phyllocladopitys martini* Kräusel shows a central strand of very small but thick-walled cells, distinctly bordered by the outer normal parenchymatic cells, while *Taeniopitys* Kräusel and *Polyloboxylon* Maheshwari possess a distinct pith sheath of irregularly shaped or almost rectangular parenchymatic cells. Very often thick-walled sclerenchymatic cells are found in the pith. The sclerenchymatic cells may be single and isolated (**12**), in small groups (**14**) or vertical strands of varying length and arrangement (**8**). Many forms have dispersed secretory cells in the pith or short rows of secretory cells (**16**, **17**, **18**, **20**, **22**, **23**, **24**, **25**, **29**). Especially conspicuous are large secretory gaps or canals. The vertical ducts may be marginal (**26**) or distributed all over the pith (**27**, **28**, **29**). A more complicated arrangement of secretory canals is found in *Indoxylon* Maithy, where in addition to the marginal vertical canals, we have a central vertical canal, and both are connected by more or less horizontal canals (**25**).

These examples show the far-going variability of the pith and the primary xylem. They offer a solid foundation for the grouping of these woods. The two main groups are (a) woods with endarch protoxylem and no centripetal xylem and (b) woods with mesarch protoxylem and centripetal xylem. Only the former group may, at least some of the forms, represent true conifers. Woods of the second group, however, probably represent other Gymnosperms. Forms with mesarch protoxylem are:

Phyllocladopitys Krsl.
Taxopitys Krsl.
Abietopitys Krsl.
Medullopitys Krsl.
Taeniopitys Krsl.
Solenopitys Krsl.

In *Taxopitys arctica* (SHILKINA, 1960) from the Upper Carboniferous of Siberia neither the pith nor the primary structures are preserved. As such it is impossible to decide whether it really belongs to *Taxopitys*. Of *Abietopitys crassiradiata* and *A. patagonica* Archangelsky (1960) too only the secondary wood is known.

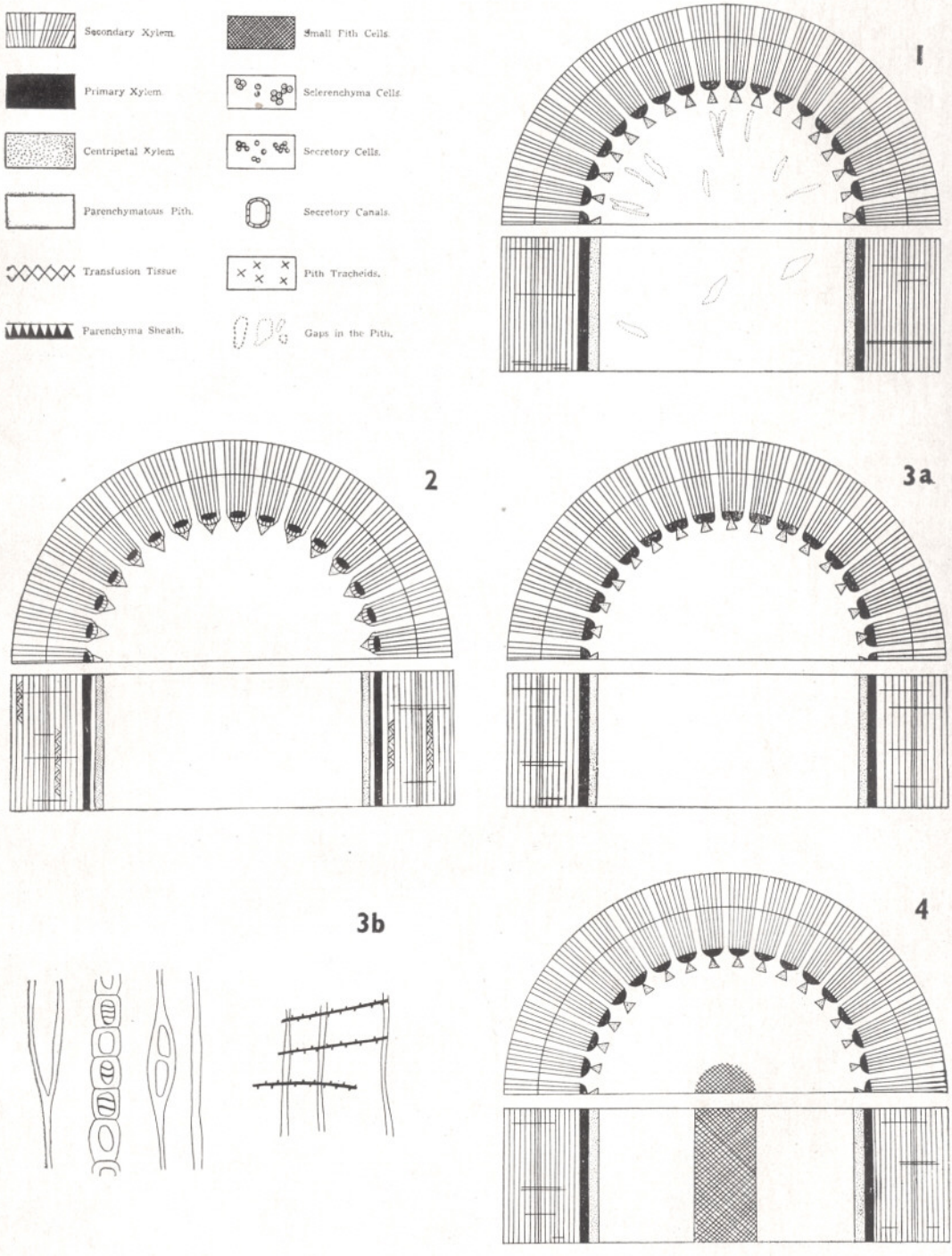
In *Dadoxylon lafoniense* Halle, *Dadoxylon indicum* Holden, and *Dadoxylon bakeri* Seward & Walton, the primary structures are said to be endarch. But there are still some doubts, and these woods need reinvestigation.

KEY FOR THE IDENTIFICATION OF GONDWANA FOSSIL WOODS

(Not included *Rhexoxylon* Bancroft, *Antarcticoxylon* Seward and *Dadoxylon* Nr. 2 Warren, 1912 : 350, Fig. 1c)

1. Pith homogeneous, the inner cells at most larger than the outer ones, parenchymatic. 2
– Pith heterogeneous with at least two kinds of cells. 7
2. Diameter of the pith more than 2 cm. 3
– Diameter of the pith less than 2 cm. 4
3. Cells in the cross-section polygonal to rounded, longitudinally rectangular, with radially expanded mesh-like gaps, protoxylem mesarch, centripetal xylem forming only small groups of tracheids.

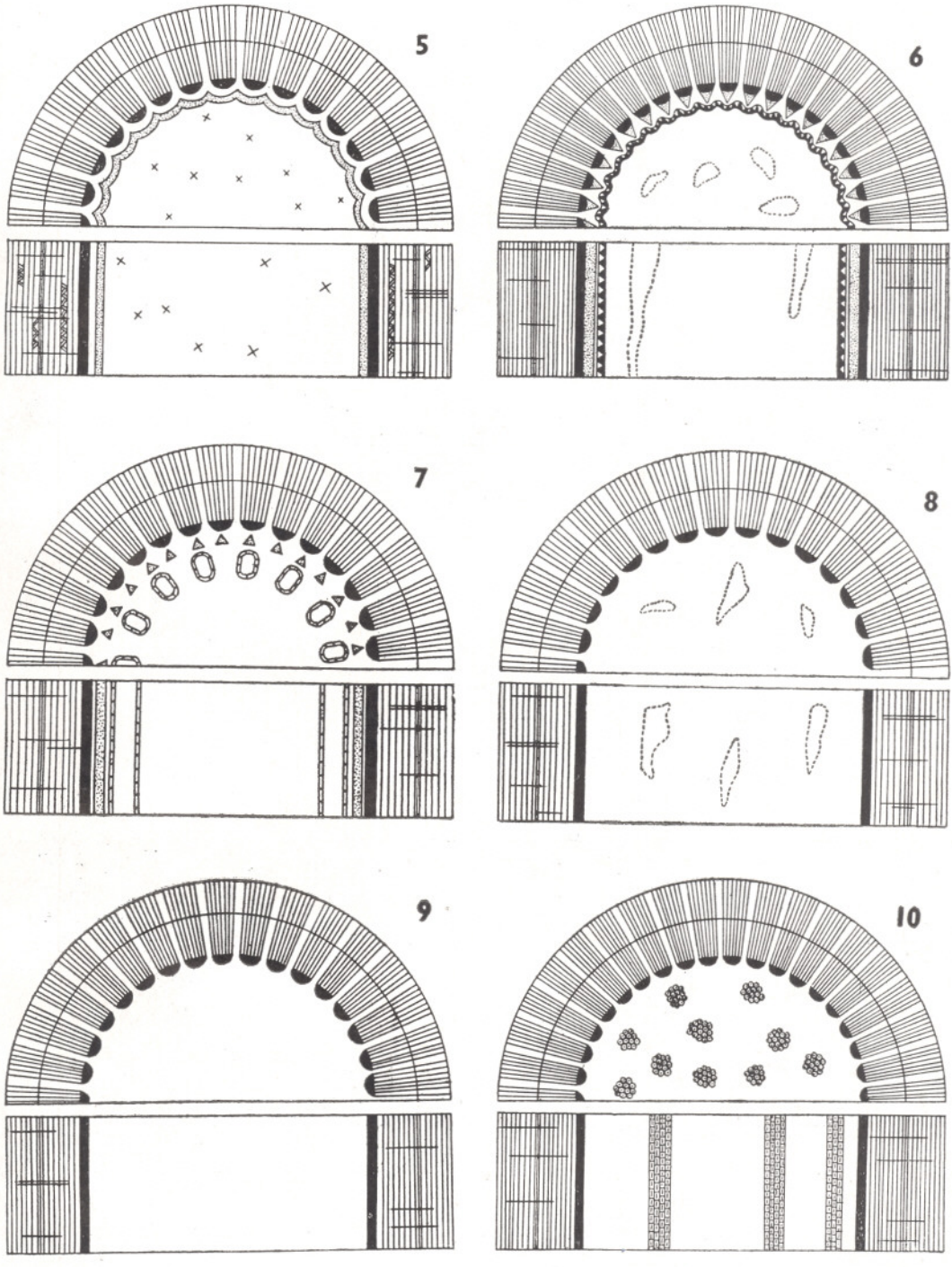
1 *Phyllocladopitys capensis* Krsl. (Text-fig. 1)


Secondary Xylem.
Primary Xylem.
Centripetal Xylem.
Parenchymatous Pith.
Transfusion Tissue.
Parenchyma Sheath.
Small Pith Cells.
Sclerenchyma Cells.
Secretory Cells.
Secretory Canals.
Pith Tracheids.
Gaps in the Pith.
1
2
3a
3b
4

TEXT-FIGS. 1-4

– No larger meshy gaps, protoxylem endarch.
2a. *Dadoxylon kraeuseli* Sahni
b. *Dadoxylon jamuriense* Maheshwari (MS)
(Text-fig. 8)

4. Protoxylem endarch. 5
– Protoxylem mesarch. 6
5. Cell walls pitted, pits coarse, simple.
3 *Dadoxylon porosum* Krsl.
(Text-fig. 9)
– Cell walls not pitted.
4 *Dadoxylon rangei* Krsl.
(Text-fig. 9)
6. Centripetal wood wedge-shaped.
5 *Taxopitys africana* Krsl.
(Text-fig. 2)
– Centripetal wood splitted into single rows of cells.
6 *Abietopitys perforata* Krsl.
(Text-figs. 3a, b)
7. Pith cells parenchymatic, of different size, single large cells dispersed throughout the pith, in the middle very small, thick-walled cells forming a distinct central strand.
7 *Phyllocladopitys martini* Krsl.
(Text-fig. 4)
– Besides the normal parenchymatic cells other elements present in the pith. 8
8. Pith with sclerenchymatic cells. 9
– Pith with secretory organs or tracheids. 15
9. Sclerenchymatic cells forming longitudinal strands. 10
– Sclerenchymatic cells dispersed or in small groups. 12
10. Strands dispersed all over the large pith.
8 *Medullopitys sclerotica* (Goth.) Krsl.
(Text-fig. 10)
– Strands only in the outermost part of the pith, mostly in front of the wood wedges. 11
11. Strands very short (less than 10 mm.) protoxylem endarch.
9 *Kaokoxylon reuningi* Krsl.
(Text-fig. 11)
– Strands much longer.
10 *Kaokoxylon sclerosum* (Walton) Krsl.
(Text-fig. 12)
12. Sclerenchymatic cells forming irregular longitudinal rows.
11 *Parataxopitys americana* (Milanez & Dolianiti) Barbosa
(Text-fig. 13)
– Sclerenchymatic cells not in longitudinal rows, groups spherical to lenticular. 13
13. Besides the groups dispersed single isodiametric sclerenchymatic cells, their walls heavily pitted.
12 *Kaokoxylon zalesskyi* (Sahni) Maheshwari (MS)
(Text-fig. 14)
– All sclerenchymatic cells in groups. 14
14. Pith octagonal, sclerenchymatic groups sometimes connected by thin bridges of sclerenchymatic cells.
13 *Dadoxylon farleyense* Walkom



TEXT-FIGS. 5-10

– Diameter of pith only few mm., pentagonal, sclerenchymatic groups not connected.

14 *Kaokoxylon durum* Krsl. (Text-fig. 15)

15. Pith with dispersed plate-like groups of heavily pitted cells (pith tracheids ?), at the border passing into the centripetal xylem.

15 *Taxopitys alves-pintoi* Krsl. & Dolianiti (Text-fig. 5)

– Secretory organs in the pith. 16

16. Pith with longitudinal rows of secretory cells, those usually smaller and longer than the normal parenchymatic cells. 17

– True secretory canals present. 24

17. Pith with distinct lobes projecting into the secondary wood. 18

– Pith more or less rounded, with no such lobes. 20

18. Pith surrounded by a parenchymatous sheath.

16 *Polyloboxylon raniganjense* Maheshwari (MS) (Text-fig. 16)

– Pith not surrounded by a parenchymatous sheath. 19

19. Pith with three lobes.

17 *Trigonomyelon pedroi* (Zeiller) Walton (Text-fig. 17)

– Pith with two lobes.

18 *Lobatoxylon kaokense* Krsl. (Text-fig. 18)

20. Pith surrounded by a " specialized tissue " (cit. SEWARD & WALTON, 1923). 21

– No such tissue present. 22

21. An outer parenchymatic sheet surrounding the pith, sheet cells not pitted, protoxylem mesarch.

19 *Taeniopitys scotti* Krsl. (MS) (Text-fig. 6)

– Sheet cells pitted, protoxylem endarch.

20 *Dadoxylon indicum* Holden (Text-fig. 19)

21 *Dadoxylon bakeri* Seward & Walton

22. Pith cells often broader than high.

22 *Dadoxylon arberi* Sew. (Only S.A.Mus. 1089; WALTON 1925)

– Cells commonly higher than broader. 23

23. In the crossfield many small pits.

23 *Gondwanoxylon waltoni* Maheshwari (MS) (Text-fig. 20)

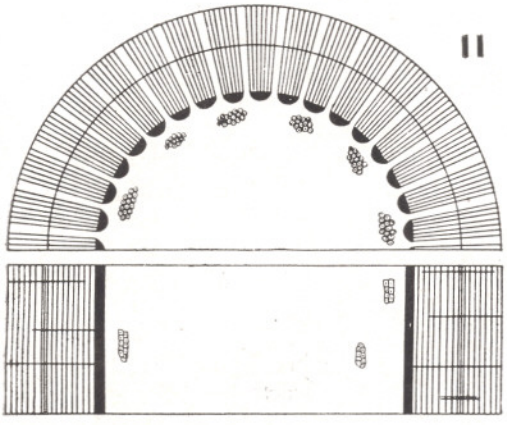
– In the crossfield 1-3 big pits.

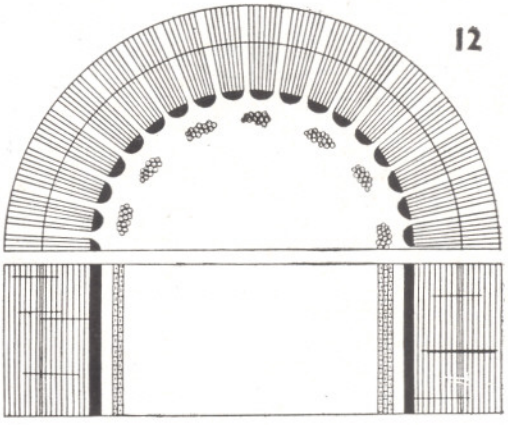
24a. *Megaporoxylon scherzi* Krsl. (Text-figs. 21a, b)

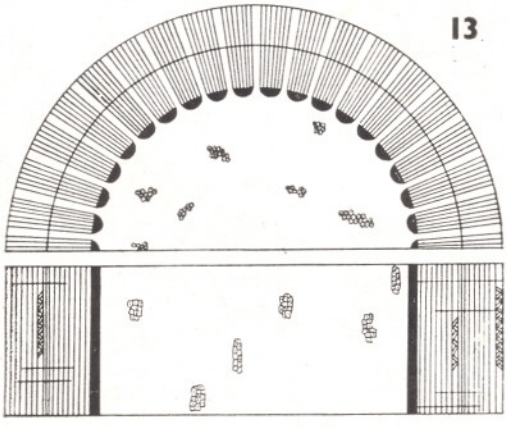
b. *Megaporoxylon zeilleri* Krsl. (Text-figs. 21a, c)

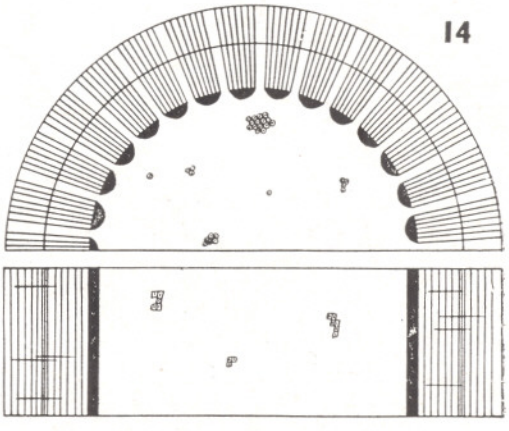
c. *Megaporoxylon kaokense* Krsl. (Text-figs. 21 a, d)

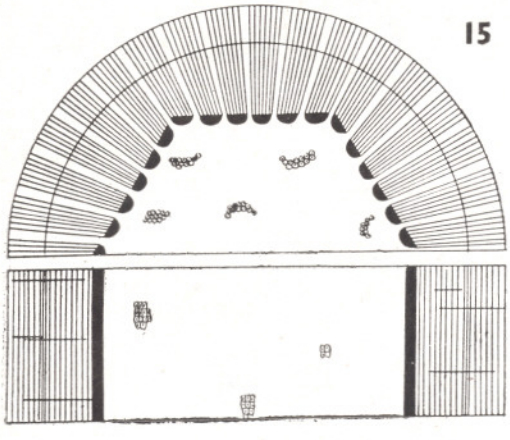
d. *Megaporoxylon kraeuseli* Maheshwari (MS) (Text-figs. 21a, e)

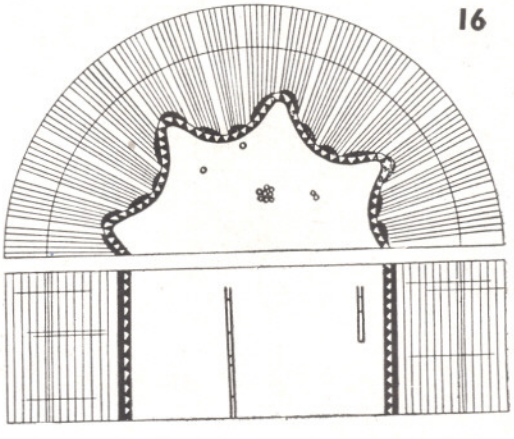




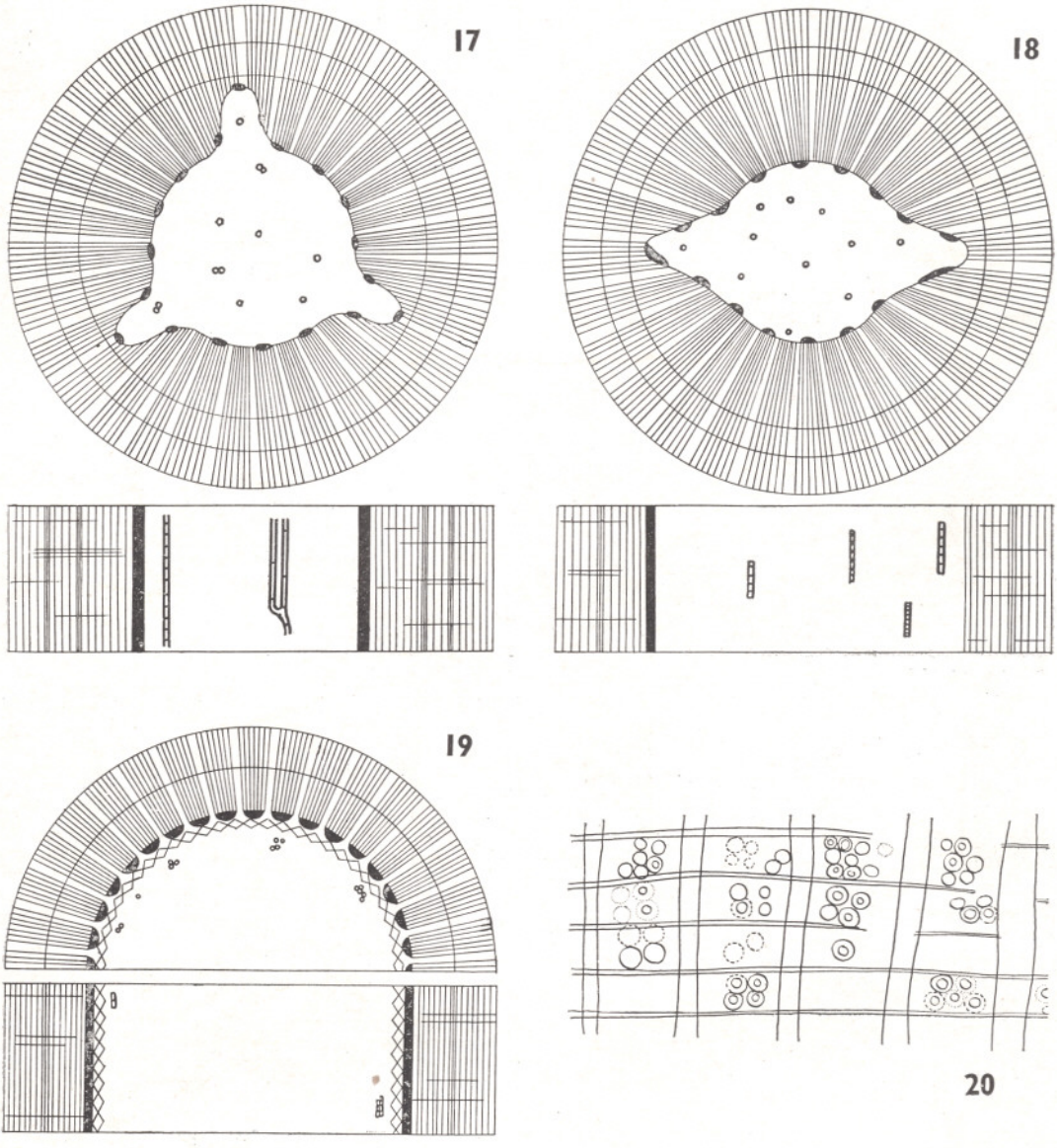








TEXT-FIGS. 11-16

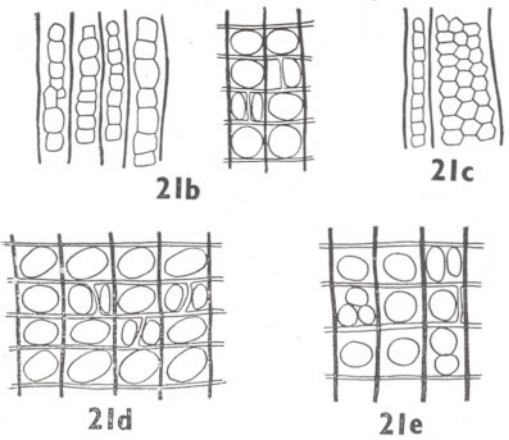


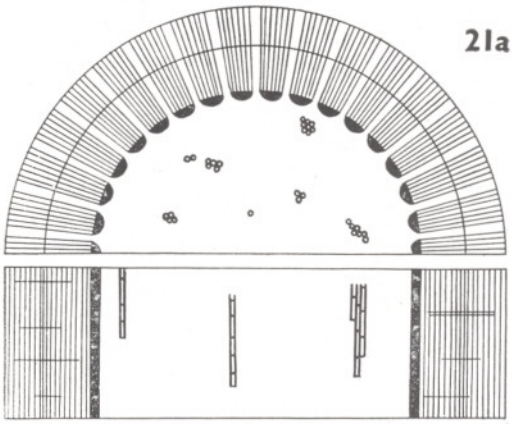
TEXT-FIGS. 17-20

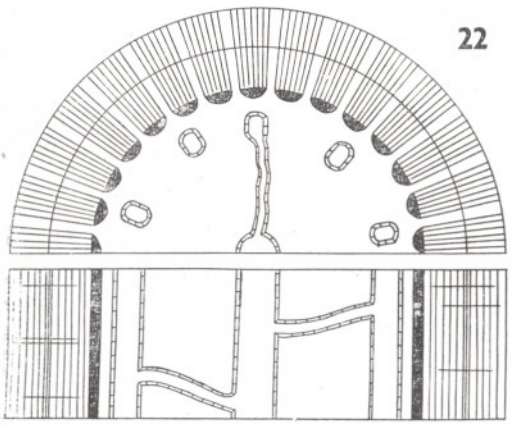
24. Secretory canals interconnected by cross canals.

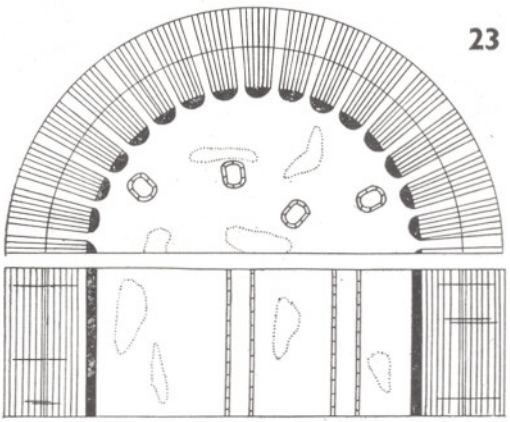
25 *Indoxylon canalosum* Surange & Maithy
(Text-fig. 22)

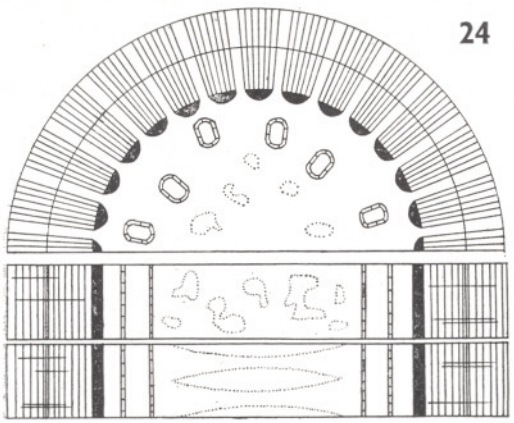
– Secretory canals not interconnected. 25
25. Pith chambered in varying degree. 26
– Pith not chambered. 27

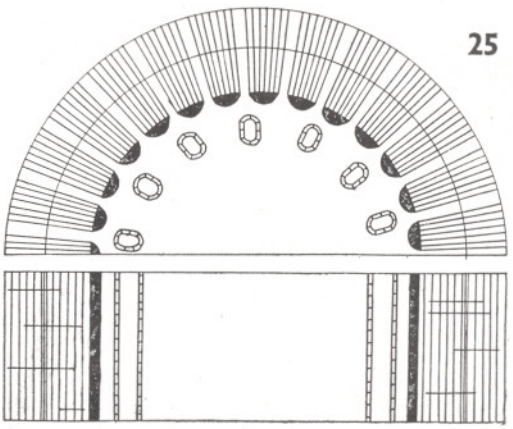












TEXT-FIGS. 21-25

26. Pith with radially arranged gaps between secretory canals.
26 *Polysolenoxylon whitei* (Maniero) Krsl. & Dolianiti (Text-fig. 23)

– Pith with horizontally arranged gaps, almost discoid.
27a. *Solenoxylon wissi* Krsl.
b. *Solenoxylon kurzi* Krsl.
c. *Solenoxylon oberholzeri* Krsl. (Text-fig. 24)

27. Protoxylem mesarch.
28 *Solenopitys paulistana* Krsl & Dolianiti (Text-fig. 7)

– Protoxylem endarch.

28. Pith cells mostly higher than broad.
29a. *Barakaroxylon jharience* (Surange & Sah) Surange & Maithy (Text-fig. 25)
b. *Barakaroxylon kraeuseli* Surange & Maithy

– Pith cells mostly broader than high.
30 *Dadoxylon lafoniense* Halle

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