Wood and bark anatomy of the African species of *Gnetum*

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Quantitative and qualitative data are given for the two African species of *Gnetum* (*Gnetum* section *Gnetum* subsection *Micrognemones*). These species are lianoid and lack the fibre-tracheids of *G. gnemon* but have about the same vessel element and tracheid length as in that species. Vessel diameter is related to stem age and organography. Tori are clearly present in tracheary elements of the African *Gnetum* species, a first report for the genus. In these two species, origin of the lateral meristem, which produces vascular tissue and cambia, can be traced directly and indirectly to cortical parenchyma. A second kind of meristematic action, newly reported for *Gnetum*, is produced by proliferation of axial parenchyma, fragmenting secondary xylem. Both presence of tori and site of origin of lateral meristematic activity in *Gnetum* contrast with corresponding conditions in *Welwitschia*.

ADDITIONAL KEY WORDS:—cambial variants — Gnetales — successive cambia — tori — vesturing.

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INTRODUCTION

Wood and bark anatomy of *Gnetum* has not hitherto been surveyed at the species level. The purpose of the present paper is to advance this survey, continuing a series begun with a study of *G. gnemon* (Carlquist, 1994). Wood anatomy of *Ephedra* has been surveyed at the species level (Carlquist, 1989,

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1994), and new information on Welwitschia (Carlquist & Gowans, 1995) has been presented. The reason for attempting a survey of wood and bark of Gnetales at the species level is to provide more information applicable to systematic, ecological and organographic questions. In fact, entirely new features, such as helical thickenings in vessels of Ephedra (Carlquist, 1989) and minute crystals in the intercellular spaces of parenchyma of Welwitschia (Carlquist & Gowans, 1995) have been discovered during the course of this survey of gnetalean woods. A discovery of phyletic significance in the present study is the occurrence of tori in pits of tracheary elements of the African Gnetum species. Tori have been reported to be absent in tracheary elements of Welwitschia and Gnetum (Eicke, 1957; Martens, 1971), but few Gnetum species have been studied anatomically. These discoveries demonstrate the value of comparative anatomical work, in contrast to study of selected species, which frequently form the basis for generalizations about their genera.

The selection of African species of Gnetum in the present paper as a unit to advance this series of papers has a basis in more than geography. The taxonomic subdivisions of Markgraf (1930) and their sequence within his monograph have formed the basis for this series of Gnetum papers. The sectional and subsectional names given by Markgraf must be altered so that those containing the type species (G. gnemon L.) bear the genus name (Markgraf's names are cited in parentheses below). The subdivisions recognized by Markgraf (1930) are as follows:

Section Gnetum (Sect. Gnemonomorphi)
   Subsection Gnetum (Subsect. Eugnemones)
      (two tree species of Indomalesia, G. gnemon L. and G. costatum K. Schum.).
   Subsection Micrognemones
      (G. africanum Welw. and G. buchholzianum Engl., both lianas, from Cameroons and neighbouring countries).
   Subsection Areognemones
      Six lianoid New World species, from Panama to Bolivia).
Section Cylindrostachys
      (18 species of lianas from Indomalesia and southeast Asia; subdivided into two subsections: Stititati, with seven species; and Sessiles, with 11 species).

Two more monographic studies, one on the New World species and one on the Old World lianoid species, are planned to complete the survey. A summary of wood and bark features of Gnetales will conclude the series.

Data on wood and bark of Gnetum are vital to understanding phylesis among sections, subsections, and even species. The differences in anatomy between the tree (G. gnemon) and liana species of Gnetum appear more than just those traceable to habit, and an early divergence of the genus may be reflected. In a wider context, the concepts of interrelationship between Ephedra, Gnetum and Welwitschia should involve information on wood and bark, as should concepts on relationship between Gnetales and other groups of seed plants.

Origins of cambial variants are often difficult to demonstrate and interpret decisively. Literature on successive cambia and other types of lateral meristems
in dicotyledons leads to the conclusion that clarification is necessary. Successive cambia in Gnetales have been relatively little investigated; both origin of these cambia and means for their perpetuation should be studied further. La Rivière (1916) has offered a study on origin of the lateral meristem in *Gnetum moluccense* Karst. That study does not furnish all desirable details; particular materials yield only some of the stages needed for a complete picture. Stems of the two species in the present study were in active growth, so that the origin of lateral meristem activity and of vascular strands and arcs was unusually clear. Lateral meristem activity in *Gnetum* is of interest not merely as a study in developmental anatomy, but also for phyletic reasons. Some workers have cited resemblances between *Gnetum* and *Welwitschia*, but lateral origin of new vascular tissue in *Welwitschia* is different from that in *Gnetum* (Carlquist & Gowans, 1995).

In addition, a kind of meristematic activity new for Gnetales is evident in both African *Gnetum* species. Proliferation of axial parenchyma results in fragmentation of secondary xylem.

**MATERIAL AND METHODS**

The coexistence in *Gnetum* stems of hard and soft tissue poses microtechnical problems, especially in view of the tendency of some of the hard tissues (gelatinous fibres) to shred rather than cut cleanly when sectioned. These difficulties are solved by a technique that uses ethylene diamine as a softening agent, followed by embedding in paraffin and sectioning on a rotary microtome (Carlquist, 1982). Sections were stained in a safranin-fast green combination, which proved ideal for demonstration of tori on pit membranes. For studies of crystals (Figs 3, 4), some of these sections were mounted on SEM aluminum stubs just as one would mount them on glass slides, and when dried, the paraffin was removed with xylene. SEM studies of vesturing on vessel walls and of tori on pit membranes used sections not treated with a softening agent; sectioning was done with a sliding microtome. Macerations were prepared with Jeffrey’s Fluid and stained with safranin.

The terminology of the IAWA Committee on Nomenclature (1964) has been followed. The lateral meristem activity that gives rise to successive increments of xylem and phloem is called ‘lateral meristem’ here, and is to be distinguished from the cambia within strands and arcs of vascular tissue; these are termed ‘successive cambia’. Vessel diameter was measured as lumen diameter at widest point. For the features presented in Table 1, means were derived from 25 measurements per feature (fewer in the case of multiseriate rays, which are limited in number). Vessel density figures were determined from scanning areas within the vascular increments; conjunctive tissue between the increments was not included in the areas scanned.

The collections studied are as follows: *G. africanum*, Fay 9000, Cameroons; *G. africanum*, Mezili 269, Mpalla, 10 km from Kribi on the EDEA road, Cameroons; *G. buchholzianum*, Mezili 270, 7 km from Kribi on the EDEA road, Cameroons. The Fay collection was provided with the aid of Dr Peter H. Raven, and a voucher specimen has been preserved in MO. The Mezili collections were made possible through M. Benoit Satabié, and voucher specimens have been deposited in RSA. Both *G. africanum* and *G. buchholzianum*
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Table 1. Quantitative wood features of *Gnetum*.

<table>
<thead>
<tr>
<th>Species &amp; Collection</th>
<th>1 VG</th>
<th>2 VD</th>
<th>3 VM</th>
<th>4 VL</th>
<th>5 TL</th>
<th>6 MR</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>G. africanum</em> Fay 9000</td>
<td>1.07</td>
<td>146</td>
<td>20</td>
<td>1369</td>
<td>1614</td>
<td>1501</td>
</tr>
<tr>
<td><em>G. africanum</em> Mezili 269 above ground stem</td>
<td>1.05</td>
<td>49</td>
<td>65</td>
<td>657</td>
<td>711</td>
<td>702</td>
</tr>
<tr>
<td><em>G. africanum</em> Mezili 269 underground stem</td>
<td>1.08</td>
<td>88</td>
<td>27</td>
<td>1053</td>
<td>1306</td>
<td>1617</td>
</tr>
<tr>
<td><em>G. buchholzianum</em> Mezili 270</td>
<td>1.12</td>
<td>44</td>
<td>10</td>
<td>1169</td>
<td>1169</td>
<td>536</td>
</tr>
<tr>
<td>Collections averaged</td>
<td>1.08</td>
<td>82</td>
<td>31</td>
<td>1062</td>
<td>1200</td>
<td>1090</td>
</tr>
</tbody>
</table>

Key: 1 (VG), mean number of vessels per group; 2 (VD), mean diameter of vessel lumen, µm; 3 (VM), mean number of vessels mm²; 4 (VL), mean length of vessel elements, µm; 5 (TL), mean length of tracheids, µm; 6 (MR), mean height of multiseriate rays, µm.

are small scandent shrubs (‘fruticulus scandens’, Markgraf, 1930). The Mezili collections were from relatively young plants; the maximal diameter of the below ground stem (probably hypocotylar in origin) of *G. africanum* was 16 mm; the above ground stem was 10 mm in diameter. The maximum diameter of the (aboveground) stem of *G. buchholzianum* was 15 mm. The collection Fay 9000 provided a stem 26 mm in diameter. Larger stems were used for study in all instances, in order to see more vascular tissue and to obtain more nearly mature patterns. Stems were preserved in formalin acetic alcohol. Anatomical differences among the specimens with respect to age and organography may be more important than differences related to taxonomic identity. In any anatomical study based on a small number of collections, anatomical differences among species must be described as tentative. There is every reason to believe, from Markgraf’s (1930) monograph, that the two African *Gnetum* species are distinguishable but not taxonomically distant from each other.

ANATOMICAL RESULTS

**Wood anatomy**

In all of the stems studied, there are two increments of vascular tissue; more xylem and phloem had been produced by the cambium of the first increment. The beginnings of a third vascular increment was visible in the stems of *G. africanum* Fay 9000. The wood of the African *Gnetum* species consists of only two tracheary element types, vessel elements and tracheids; in *G. gnemon*, fibre-tracheids are also present. Growth rings are absent, but there is some fluctuation in radial diameter of tracheids (Fig. 1).

Vessels are solitary (Fig. 1), rarely in pairs or groups of three. The number of vessels per group (Table 1, column 1) is not 1.00 because the density and diameter of vessels leads to some random contacts among vessels. *Gnetum* qualifies as a genus in which vessel grouping is minimal, relatively close to 1.00, because tracheids are present as a subsidiary conductive system. Where tracheids are abundantly present in a wood, they seem to deter grouping of vessels because the selective value of grouped vessels for
Figures 1–4. Wood sections of *Gnetum africanum*, Fay 9000. Fig. 1. Transverse section; group of axial parenchyma cells, middle right. Fig. 2. Tangential section; large multiseriate ray to right of centre. Figs 3, 4. Crystals embedded in amorphous material in ray cells from a tangential section. Fig. 3. Crystals of various sizes. Fig. 4. Crystals relatively uniform in size. Figs 1, 2, to scale above Fig. 1 (divisions = 10 μm); Figs 3, 4, scale bars = 10 μm.
conductive safety is less than the value of tracheids for insuring continuation of conduction when embolisms occur in some vessels (Carlquist, 1984).

Vessel diameter (Table 1, column 2) shows a wide range in the samples studied, although wider vessels can certainly be found in other Gnetum species (Fisher & Ewers, 1995). Vessels tend to increase in diameter with increasing stem diameter, as shown in Fig. 11, although the portion illustrated in Fig. 12 shows secondary xylem with large vessels at the centre of a stem, followed by secondary xylem with much smaller vessels. The relatively large vessel diameter of G. africanum, Fay 9000, seems related to the large size of the stem studied from that collection. Vessels are circular rather than angular in transectional outline (Figs 1, 5).

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Vessel density (Table 1, column 3) ranges from 10 to 65 vessels per mm². The latter figure is from the specimen G. africanum, Fay 9000, and may represent greater conductive capacity as a liana reaches better lighted levels of a forest.

Vessel element length (Table 1, column 4) ranges from 637 to 1369 μm. The latter figure is in the collection G. africanum, Fay 9000, which is a larger stem; tracheary element length increases as a stem increases in diameter in typically woody plants (Bailey & Tupper, 1918). The vessel element length of the African species of Gnetum is approximately the same as in G. gnemon (Carlquist, 1994) as well as other species of Gnetum.

Mean vessel wall thickness is about 5 μm in all of the collections studied (Fig. 5). Wider vessels tend to have thicker walls.

Only simple perforation plates were observed in all collections studied, even in primary xylem, which was present on radial sections. A few foraminate perforation plates were observed for G. africanum by Thompson (1916), although the majority he figured are simple.

The lateral wall pits of vessels have circular pit cavities about 12 μm in diameter. Pit apertures adjacent to the vessel lumen tend to be narrow and slitlike in outline (Figs 9, 10), less commonly oval. Vesturing can be seen in vessel pits of both species with light microscopy, but on the lumen side of pit apertures, a few vesutures could be observed in G. africanum (Fig. 9), but vesutures were not observed on this face in G. buchholzianum (Fig. 10). The paucity of vesutures as seen from the lumen side of pits is not surprising, because vesutures in pits of Gnetum vessels are mostly confined to pit cavities, judging from the SEM photographs of Parameswaran & Liese (1974).

Tori are clearly present on pit membranes of vessel to tracheid and tracheid to tracheid contacts in both of the African Gnetum species, although they have been figured here only for G. buchholzianum (Figs 6, 7). The tori are quite thick, as can be seen in both SEM (Fig. 6) and light microscopy (Fig. 7) preparations. Surrounding the torus is a margo with fibrillar strands (rendered indistinctly in Fig. 6). This is the first report of tori in Gnetum; they are claimed to be absent in Gnetum by Eicke (1957) and Martens (1971).

Tracheid length is given in Table 1, column 5. If the mean tracheid length for all four collections is divided by the mean vessel element length for the four, the ratio is 1.13—a notable low ratio compared to most angiosperms (Carlquist, 1975). The ratio in G. gnemon is 1.37 (Carlquist, 1994).

Tracheid wall thickness in mostly about 4 μm, sometimes a little less.
Figures 5–8. Stem sections of *Gnetum*. Fig. 5. *G. africanum*, Fay 9000. Portion of wood transverse section to show that axial parenchyma is largely diffuse; tyloses present in vessel at left. Figs 6, 7. *G. buchholzianum*, tangential sections of secondary xylem. Fig. 6. SEM photograph of a pit membrane, showing torus. Fig. 7. Light microscope photograph of adjacent tracheids, showing tori on pit membranes. Fig. 8. *G. africanum*, Fay 9000. Transverse section of secondary phloem. Figs 5, 8, to scale above Fig. 5 (divisions = 10 μm); Fig. 7, to scale above Fig. 7 (divisions = 10 μm); Fig. 6, scale bar = 10 μm.
Figures 9–12. Wood sections of *Gnetum*. Fig. 9, 10, SEM photographs of vessel walls from tangential sections. Scale bars = 10 µm. Fig. 9. *G. africanum*, Fay 9000. A few vestures are visible around the pit apertures. Fig. 10. *G. buchholzianum*. Pit apertures are slitlike, no vestures facing the lumen can be seen. Figs 11, 12. Transverse sections of *G. buchholzianum*. Fig. 11. Vessels increase in diameter as secondary growth proceeds. Fig. 12. Innermost wood of stem (below) with large vessels has been fragmented by proliferation of axial parenchyma cells. Figs 11, 12, to scale in Fig. 1.
Tracheids in the two African species are mostly smooth and fusiform as seen in macerations, but a few have papillate or even tuberculate surfaces. When sections are viewed, these surfaces prove to be intrusions into soft cells such as axial parenchyma. Tracheid to tracheid faces are relatively free from such irregularities. Tracheid to tracheid pits are circular in outline, with pit cavities about 12 μm in diameter. Pit apertures (facing lumina) are also circular in outline.

Axial parenchyma is basically diffuse in the two species (Fig. 5). There is some tendency toward lateral grouping of axial parenchyma into tangential lines of 2–4 cells (Fig. 5, upper right and lower left); this grouping is called diffuse-in-aggregates in dicotyledons and is also common in Ephedra (Carlquist, 1989, 1992). Where vessels are large and therefore intersect numerous diffuse axial parenchyma cells, a scanty vasicentric distribution could be claimed, but we believe that the contact between vessels and axial parenchyma is no more than what a random distribution of axial parenchyma cells would produce, and that this is implied in the definition of diffuse parenchyma by the IAWA Committee on Nomenclature (1964). Some patches of numerous axial parenchyma cells in groups occur (Fig. 1, right middle). Such parenchyma patches prove to be involved in parenchyma proliferation that fragments wood in some instances (e.g. Fig. 12). Axial parenchyma has thin nonlignified walls in all collections except for G. africanum, Fay 9000, which has relatively thin nonlignified walls on axial parenchyma. Axial parenchyma is typically in strands of five cells; pits between the strand cells are large in G. africanum, Fay 9000.

Multiseriate rays are more abundant than uniseriate rays (Fig. 2). Multiseriate rays tend to be of two distinct widths: a few rays more than 10 cells wide (Fig. 2), the remainder chiefly 2–4 cells wide. Mean height of multiseriate rays is given in Table 1, column 6. Rays are not notably tall compared with those of many lianoid or rosulan (rosette tree) dicotyledons. Ray cells are predominantly procumbent (Fig. 2), with upright sheath cells on multiseriate portions of multiseriate rays, in uniseriate tips of multiseriate rays, and in uniseriate rays. Upright cells become fewer as the stem increases in diameter, as shown by their scarcity in G. africanum, Fay 9000.

Ray cells are thin and nonlignified in all collections except in G. africanum, Mezili 269 (above ground stem), in which ray cell walls are about 4 μm in thickness, and have bordered pits on tangentially oriented walls.

Tyloses were observed in both species. They are shown in Fig. 5. Tyloses occur in only a few of the vessels in the woods studied.

Both axial and ray parenchyma cells contain deposits of amorphous yellowish material that absorbs stains readily. These deposits in the rays of G. africanum, Fay 9000, are intermixed with crystals (Figs 3, 4), and obscure the crystals in light microscope preparations. Massive deposits of the yellowish material are evident in the large vessels of central wood of G. buchholzianum (Fig. 12, below).

Crystals were observed in ray cells of G. africanum, Fay 9000, with SEM (Figs 3, 4). In some ray cells, the crystal size is diverse (Fig. 3), whereas in other cells, the crystal size is relatively uniform (Fig. 4). Crystals are always numerous and rhomboidal in shape. A few crystals were seen in tyloses, such as those of Figure 5 (crystals not visible at that magnification).
central portion of pith of *G. africanum*, Fay 9000, consists of parenchyma with thin nonlignified walls (the periphery of the pith consists of parenchyma with thin lignified walls). In cells of the central pith, numerous small crystals are present.

Pith of all collections except the one just cited is thin-walled and contains abundant starch. Cortical parenchyma and conjunctive tissue parenchyma between vascular increments is also thin walled and contains abundant starch. Starch grains are illustrated here in Figs 15–19.

**Lateral meristem activity and other cambial variants**

The first increment of vascular tissue in *Gnetum* is the product of a first cambium formed as in all vascular plants with cambial activity. The second increment of vascular tissue, however, derives from periclinal divisions of cortical cells, figured by La Riviè re (1916). This agrees with our observations in the African *Gnetum* species. This type of origin contrasts with that in *Welwitschia*, where vascular strands and arcs subsequent to the first increment are derived from phelloderm (Carquist & Gowans, 1995). The fact that phelloderm is not involved in formation of meristems or vascular tissue in African *Gnetum* species is clear because the phellogen and therefore phellem and phelloderm cells are about half the diameter of cortex or lateral meristem cells (Figs 13, 14, top). The difference in cell diameter of periderm and cells inside the periderm provides an easy way of eliminating periderm as a possible source for meristematic activity observed internal to the periderm. Lateral meristematic activity does not occur in the outer cortex cells (Fig. 13, middle), but is separated from outer cortex by several cell layers of thick walled brachysclereids that form a distinctive cylinder around the stem (Figs 13, 14, bottom).

Origin of a lateral meristem in the cortex is clearly evident in the African *Gnetum* species (Figs 13, 15, 16, 18, 19). One might well expect meristematic activity that follows the first vascular increment to originate in the cortex. The only other possible sites are phelloderm and phloem parenchyma, but neither of these are sites of origin (Figs 15–19). If origin were occurring within axial phloem parenchyma, one would find the meristem only in or at the periphery of axial phloem areas, or else these would have to be interconnected with similar divisions in phloem rays. As shown in Figures 13, 18 and 19, the lateral meristem divisions occur outside the axial phloem and outside the phloem rays. La Riviè re (1916) demonstrated that lateral meristematic activity in *G. moluccense* originates in the cortex, internal to the sclerenchyma ring, and the present study confirms this for *G. africanum* and *G. buchholzianum*.

One can see the initials of a vascular strand derived from lateral meristem activity in Figure 15 and one at a slightly later stage in Figure 16. These strands originate within radial files of lateral meristem zone four or five cells in radial length. The narrow cells being formed, cells which will become xylem, phloem, and cambium, are not formed within the outermost cells of a file, but within cells internal to those outermost cells. This leaves a potentially meristematic cell layer outside the phloem, and not a cell layer derived from the phloem. This meristematic cell layer remains potentially a
Figure 13–16. Transverse sections of outer stem of Gnetum. Figs 13, 14. *G. buchholzianum*. Fig. 13 Periderm above; lateral meristem zone, centre, includes maturing vascular tissue. Fig. 14. Periderm, above; outer cortex, centre; and brachysclereids and gelatinous fibres, below. Figs 15, 16. *G. africanum*, Mezili 269, underground stem. Lateral meristem zone with beginning of vascular strand differentiation. Fig. 16. Portion adjacent to that shown in Fig. 15; a more advanced stage of vascular strand differentiation is present. Fig. 13, to scale of Fig. 1; Figs 14–16, to scale of Fig. 5.
Figures 17–20. Transverse sections of stems of *Gnetum*. Fig. 17. *G. buchholzianum*. Lateral meristem zone; a vascular strand has differentiated, right. Figs 18, 19. *G. africnanum*, Mezli 269, above ground stem. Fig. 18. Section orientated with outside of stem above; brachysclereids above; phloem fibres below; lateral meristem zone; centre. Fig. 19. Section orientated with outside of stem at left. Lateral meristem extends from top to bottom, outside gelatinous phloem fibres (upper right). Fig. 20. *G. africnanum*, Fay 9000. Transverse section (periderm at top, cambium at bottom) to show an older stem portion in which cortical parenchyma is largely crushed. Figs 17–19, to scale of Fig. 5; Fig. 20, to scale of Fig. 1.
site for origin of future vascular tissue. Although divisions in ray areas are difficult to trace because they are less active than those in fascicular areas, a cell layer also appears to be left outside the ray cells produced by divisions from a meristematic cell.

Figures 17 and 18 show that the lateral meristem occurs outside the phloem: there are crushed phloem cells between the lateral meristem and the periphery of the phloem as demarcated by phloem fibres in Figure 18: In other places on the sections of *G. africanum* and *G. buchholzianum*, an even greater separation between outermost phloem and lateral meristem is observed. At any rate, the origin of vascular tissues and successive cambia associated with them does not normally occur within phloem parenchyma, but within cortex or, if cortex is not present, the parenchyma cell layer left externally after vascular tissues are subdivided from files of lateral meristem cells. The action of the lateral meristem is not continuous, but intermittent: divisions would precede origin of vascular tissue, but would not occur if origin of new vascular tissue is not imminent.

Destruction of cortex and the parenchyma cell layer left by the lateral meristem by fracturing of bark or other injury may make another site of origin of new vascular tissue necessary. Such a situation is shown in Figure 20, in which no parenchyma appears to be available for lateral meristematic activity. In this case, axial phloem parenchyma and phloem ray parenchyma might be sites for lateral meristem origin, and such parenchyma is visible in Figure 20. The stems in the present study were too young to detect such possible origins of lateral meristem, and study of older stems (or roots) of lianoid *Gnetum* species is needed.

Another type of meristematic activity, proliferation of axial parenchyma, was observed in both *G. africanum* and *G. buchholzianum*. The site of origin of such activity appears to be strands of axial parenchyma within a fascicular area such as that shown at right, middle of Figure 1. The xylem containing large vessels (Fig. 12, below) was one of several fragments in the centre of a stem of *G. buchholzianum* split apart by proliferation of axial parenchyma. In *G. africanum*, Fay 9000, a parenchyma zone such as that shown in Figure 1 was observed to fracture a secondary xylem area farther out in the stem into several portions.

**Bark and phloem anatomy**

The outer surfaces of stems of both *G. africanum* and *G. buchholzianum* are covered with phellem, the cells of which are very small in diameter as seen in transection (Figs 13, 14). In the material available, no sclereids are present in phellem, so no periderm origin has taken place beneath the cylinder of bark sclereids.

The outer cortex parenchyma cells accumulate yellowish deposits that stain darkly (Figs 13, 14). Inside the outer cortical parenchyma there is a cylinder of very thick-walled brachysclereids, intermixed with a few gelatinous fibres (Fig. 13, top; Fig. 14, bottom). As the stem increases in circumference, breaks occur in the sclereid cylinder. Such breaks are evidently filled by intrusions of parenchyma cells that become sclereids, because the sclereid ring remains continuous. Such an intact sclereid cylinder has been figured in older stems
of *G. moluccense* (La Rivière, 1916) and *G. ula* Brongn. (Maheshwari & Vasil, 1961). In *G. gnemon*, the brachysclereids are distributed as nests rather than as a continuous cylinder (Carlquist, 1994).

Phloem of *G. africanum* is shown in Figure 8. Phloem fibres occur only at the top of the photograph: their secondary walls are not developed until after the sieve cells mature. By the time the fibres are mature, the sieve cells are crushed. Secondary walls of the phloem fibres are gelatinous and show layering and shrinking away from primary walls. Radial files of parenchyma cells are present in the phloem of Figure 8. These are the cells that some authors have compared to companion cells in angiosperms, but they are not sister cells of sieve tube elements as they are in angiosperms. Esau (1969) accurately described this situation and figured it for *G. gnemon*.

**CONCLUSIONS**

*Organography*

Root material was not available for study, but underground (hypocotylary) stems of *G. africanum*, Mezili 269, show some qualities like those of an upper taproot. In the underground stem, starch storage parenchyma is more abundant than in the above ground stem: the parenchyma cylinder outside of the first major vascular cylinder and inside the second cylinder is much wider than in the aboveground stem. Also, the vessels in the underground stem are much wider in diameter and fewer mm² than those of the aboveground stem. These quantitative tendencies are common in dicotyledons (Patel, 1965) as well as in *Ephedra* (Carlquist, 1989).

*Phylogeny*

In a concluding paper of this series, wood features of all Gnetales will be summarized. These features are best presented for all genera in order to assess the interrelationships of the three genera and the relationships of Gnetales to other seed plants. However, attention can be drawn here to several features of the African *Gnetum* species.

The lateral meristem of *Welwitschia* is derived from phelloderm (Carlquist & Gowans, 1995), and is thus different from that in *Gnetum*. *Welwitschia* lacks tori in pit membranes of tracheary elements (Eicke, 1957; Carlquist & Gowans, 1995), but tori are present in *Ephedra* (Eicke, 1957; Carlquist, 1989, 1992). The presence of tori in pits of tracheary elements of the African *Gnetum* species must be taken into account when comparing Gnetales with other groups of seed plants. Although tori are present in tracheary elements of a few angiosperms (Wheeler, 1983), their systematic distribution indicates that tori are apomorphic in angiosperms, whereas they are plesiomorphic in Gnetales and other gymnosperms. The torus, however, is only one of a complex of features related to the gymnospermous pit. Although gymnospermous pits are often called ‘circular’, the distinction between these pits and the scalariform pits widely thought plesiomorphic in angiosperms is more than one of shape. The circular pits of gymnosperms are large in size; the torus serves as a closure valve in case of aspiration of a gymnospermous...
tracheid, and the margo is composed of fibrils among which are relatively large pores. The circular shapes of the torus and the pit membrane of the gymnospermous pit, as well as its large size, are features related to maximizing conduction and permitting closure of the pit upon aspiration of the cell. Angiospermous tracheary elements that lack tori have membranes that uniformly contain much smaller pores; the pit membrane does not deflect upon cell aspiration, and an elongate pit membrane shape, even if it bore a torus, would not be optimally suited to closure of the pit during cell aspiration. A complex of functional differences such as these must be taken into account when comparing gymnospermous and angiospermous pits, and thus the difference between these two categories is not expressible as a change in a single character state.

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