

## WOOD ANATOMY OF GRUBBIACEAE

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### ABSTRACT

Comprehensive qualitative and quantitative data, as well as illustrations, are offered for the first time for wood anatomy of all three species of the family Grubbiaceae, as well as for infraspecific taxa. Wood anatomy is of a primitive type. Vessel elements are long with many bars per perforation plate; lateral-wall pitting is alternate on vessel-tracheid contacts, scalariform on vessel-ray contacts. Tracheids have fully bordered pits and are only a little longer—or shorter, in some cases—than the vessel elements for particular organs of each species. This latter situation is extremely rare in dicotyledons, and is difficult to explain. Rays are narrow multiseriate plus uniseriate, with procumbent cells present only in central portions of multiseriate rays. Axial parenchyma is very sparse and diffuse. A rhomboidal crystal or crystals occurs in at least some ray cells. This primitive wood is adapted to the mesic sites in which Grubbiaceae grow, although modification of foliar type also minimizes transpiration and makes mesomorphic wood patterns adaptive. Theories of relationship of Grubbiaceae are reviewed. Placement near Santalaceae has been followed by most authors, and is possible but not firmly supported by data from wood anatomy. The same is true for Ericaceae. However, wood anatomy tends to link Grubbiaceae very closely with Geissolomataceae and Bruniaceae, and to suggest a generalized “rosoid” placement for this trio of families.

### UITTREKSEL

#### DIE HOUTANATOMIE VAN GRUBBIACEAE

Omvattende kwalitatiewe en kwantitatiewe data, asook illustrasies word vir die eerste keer aangebied vir die houtanatomie van al drie spesies, en die infraspesiese taxa van die familie Grubbiaceae. Houtanatomie is van 'n primitiewe tipe. Vat-elemente is lank met baie balke per perforasieplaat; stippeling van die laterale wande is afwisselend op vat-tracheïedkontakte en leervormig op vat-straalkontakte. Die hofstippels van tracheïede het 'n volledige kraag. Tracheïede is effens langer, of in sommige gevalle korter, as die vat-elemente in dieselfde organe in elk van die spesies. Laasgenoemde toestand is uiters skaars by dikotiele en is moeilik om te verklaar. Die strale is smal multiseriaal plus uniseriaal met neerliggende selle slegs teenwoordig in die sentrale gedeeltes van multiseriale strale. Aksiale parenchiem is baie min en diffuus. 'n Rhomboidale kristalle kom in sommige van die stralselle voor. Hierdie primitiewe hout tipe pas aan by die mesiese lokaliteite waarin die Grubbiaceae groei, alhoewel modifikasies van die blaartipe, wat transpirasie tot 'n minimum beperk, dit ook moontlik maak vir mesomorfiese houtpatrone om by hierdie toestande aan te pas. 'n Oorsig van die verwantskappe van die Grubbiaceae word gegee. In die meeste gevalle dit naby die Santalaceae geplaas en, alhoewel moontlik, word dit nie sterk ondersteun deur gegewens van die houtanatomie nie. Dieselfde geld ook vir die Ericaceae. Die houtanatomie van die Grubbiaceae dui op 'n noue skakeling met die Geissolomataceae en die Bruniaceae, en suggereer ook die plasing van hierdie trio van families in die „Rosales” (sensu lato).

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## INTRODUCTION

Presentation of materials on wood anatomy of Grubbiaceae at the present time has been undertaken for several compelling reasons. First, I was able to collect material of all species in the field. Wood samples of shrubs are rarely collected, and are therefore infrequently present in wood collections. Secondly, I collected materials of roots and lignotubers, structures rarely studied by wood anatomists. Thirdly, had I not collected the wood samples myself, I would have missed understanding the ecology of these species, which proves to be very important in understanding of their woods.

Merely a few scraps of information, qualitative only, have as yet been reported for wood anatomy of Grubbiaceae, as perusal of Van Tieghem (1897), Harms (1935), and Metcalfe and Chalk (1950) shows. The account below is the first to offer complete descriptions and illustrations for wood of the family.

Because of the highly primitive nature of grubbiaceous wood, it is of particular interest for analysis. In addition, the systematic position of Grubbiaceae has been much disputed by those who have studied the family most closely (Van Tieghem, 1897; Harms, 1935; Fagerlind, 1947). Phylogenists dealing with dicotyledons as a whole are in an equally great state of disarray. Wood anatomy does, in fact, prove suggestive if not decisive in establishing the relationships of Grubbiaceae. This topic is discussed in a terminal section of the paper. In a concurrent paper (Carlquist, 1977), taxonomic considerations and ecological observations relevant to the materials below are offered.

## MATERIAL AND METHODS

For each species, sections and macerations were prepared from stems of maximal diameter and from roots. The wood of lignotubers of *Grubbia tomentosa* was also sectioned and macerated. In addition, macerations were prepared for a basal stem of *G. rosmarinifolia* subsp. *gracilis*, and for upper branches of *Grubbia rosmarinifolia* subsp. *hirsuta*, *G. rosmarinifolia* subsp. *rosmarinifolia* var. *pinifolia*, and *G. rosmarinifolia* subsp. *rosmarinifolia* var. *rosmarinifolia*. Specimens documenting these preparations are given in Table 1. Sections were prepared with a sliding microtome and stained with safranin. Macerations were obtained using Jeffrey's Fluid, followed by staining with safranin. For quantitative data, 50 measurements were secured for each feature where possible, and means obtained. Observation on crystal occurrence was made by means of polarized light.

## ANATOMICAL DESCRIPTIONS

*Grubbia rosmarinifolia* subsp. *rosmarinifolia* var. *rosmarinifolia*, Carlquist 4508 (Figs. 1-5). Diffuse porous, growth rings minimal. Vessels mostly solitary, averaging 1,14 per group in stem, 1,11 in root. Vessels per sq. mm averaging 206 in stem, 125 in root. Vessel diameter average is 37,8  $\mu$  in stem, 47,5 in root. Vessel elements with scalariform perforation plates, averaging 31,7 bars per plate

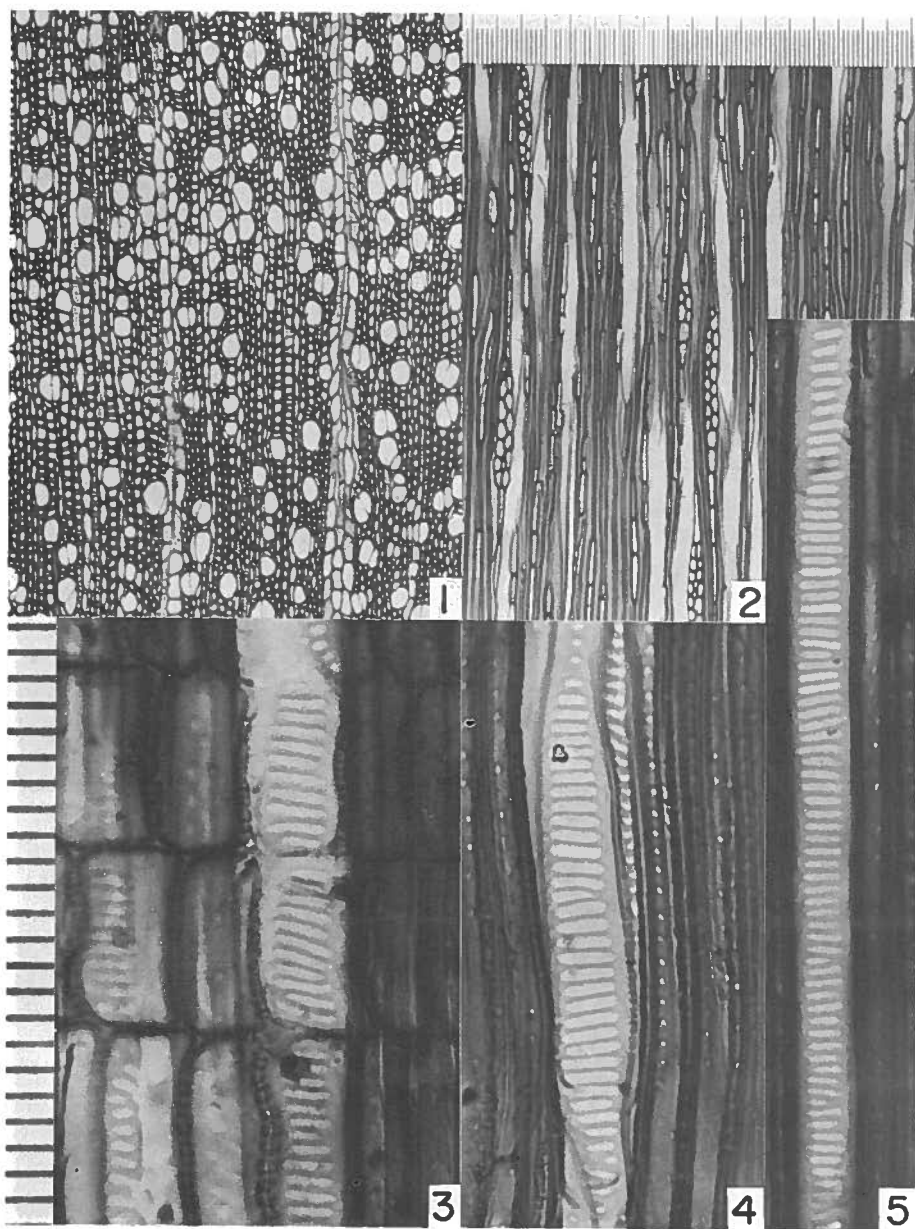


FIG. 1-5.

*Grubbia rosmarinifolia* subsp. *rosmarinifolia* (Carlquist 4508), wood sections. 1. Transsection, showing a slight fluctuation in vessel density, indicating the imperceptible growth ring activity. 2. Tangential section; multiseriate rays are narrow, few. 3-5. Portions of radial sections: 3. Ray cells, showing scalariform vessel-ray pitting. 4. A relatively short perforation plate. 5. A long perforation plate (nearly the entire length is shown). Magnification shown by photographs of a stage micrometer enlarged at the same scale as applicable photomicrographs. Fig. 1-2, enlarged according to scale above Fig. 2 (finest divisions of scale = 10  $\mu$ m). Fig. 3-5, scale to left of Fig. 3 (divisions = 10  $\mu$ m).

in stem (range: 23–43), 32,6 bars in twig (range: 13–55) and 28,2 bars in root (range: 11–47). Vessel element length averages 1 187  $\mu$  in stems, 1 183  $\mu$  in twig, and 1 176  $\mu$  in root. Lateral wall pitting of vessels scalariform to opposite facing rays, sparse, circular and alternate facing tracheids. Tracheid length averages 1 190  $\mu$  in stem, 1 155  $\mu$  in twig, and 1 220  $\mu$  in root. Tracheid wall thickness averages 2,6  $\mu$  in stem, 2,6  $\mu$  in root. Pits of tracheids have elliptical apertures shorter than the diameter of the pit cavity. Axial parenchyma very sparse, diffuse; one band seen at the single growth ring observed. Both multiseriate and uniseriate rays present; procumbent cells present only in the central portion of multiseriate rays, sheathing cells and those of the uniseriate rays square to upright. Multiseriate rays average 453  $\mu$  in height in stem, 583  $\mu$  in root; multiseriates average 2,7 cells at widest point in stem, 3,2 cells in root. Uniseriate rays average 213  $\mu$  in height in stem, 158  $\mu$  in root. Ray cells various in wall thickness, thick-walled in some ray cells of the stem. Rhomboidal crystals solitary in a very few ray cells of the stem, but also present in ray cells in root. Droplets of unidentified gummy materials in ray cell of stem and root; some massive deposits in some ray cells of stem.

Macerations of twigs from specimens representing infraspecific taxa of *G. rosmarinifolia* provided the following data: subsp. *rosmarinifolia* var. *rosmarinifolia*, Compton 14381 (SAM): vessel elements average 821  $\mu$ m in length, 26,6 bars per perforation plate, tracheids average 884  $\mu$ m in length; *G. rosmarinifolia* subsp. *rosmarinifolia* var. *pinifolia*, Stokoe 57840 (SAM): vessel elements average 1 118  $\mu$ m in length, 32,4 bars per perforation plate, tracheids average 1 189  $\mu$ m in length; *G. rosmarinifolia* subsp. *gracilis* (basal stem or large twig), Lewis 1321 (SAM): vessel elements average 880  $\mu$ m in length, 19,9 bars per perforation plates, tracheids average 930  $\mu$ m in length; *G. rosmarinifolia* subsp. *hirsuta*, Esterhuysen 10908 (BOL): vessel elements average 1 036  $\mu$ m in length, 28,4 bars per perforation plate, tracheids average 1 158  $\mu$ m in length.

The very long perforation plates of *Grubbia rosmarinifolia* are not always perfectly scalariform; they range from virtually perfect (Fig. 4) to a condition in which one or two bars fuse (or can be described as forked), as can be seen in Fig. 5, below.

*Grubbia rourkei*, Carlquist 5115 (Fig. 6–9, 17, 18). Growth rings inconspicuous, only one seen in a stem at least 15 years old; diffuse porous. Vessels mostly solitary, averaging 1,14 per group in stem, 1,15 in root. Vessels per sq. mm. average 246 in stem, 88 in root. Vessel diameter averages 39,9  $\mu$ m in stem, 53,7  $\mu$ m in root. Vessel elements with scalariform perforation plates, averaging 26,3 bars per plate in stem (range: 16–35), 23,3 bars per plate in root (range: 16–33). Vessel element length averages 1 267  $\mu$ m in stem, 796  $\mu$ m in root. Lateral wall pitting is scalariform on vessel-ray contacts, opposite or alternate circular pits on vessel-tracheid contacts (Fig. 17). Tracheid length averages 1 239

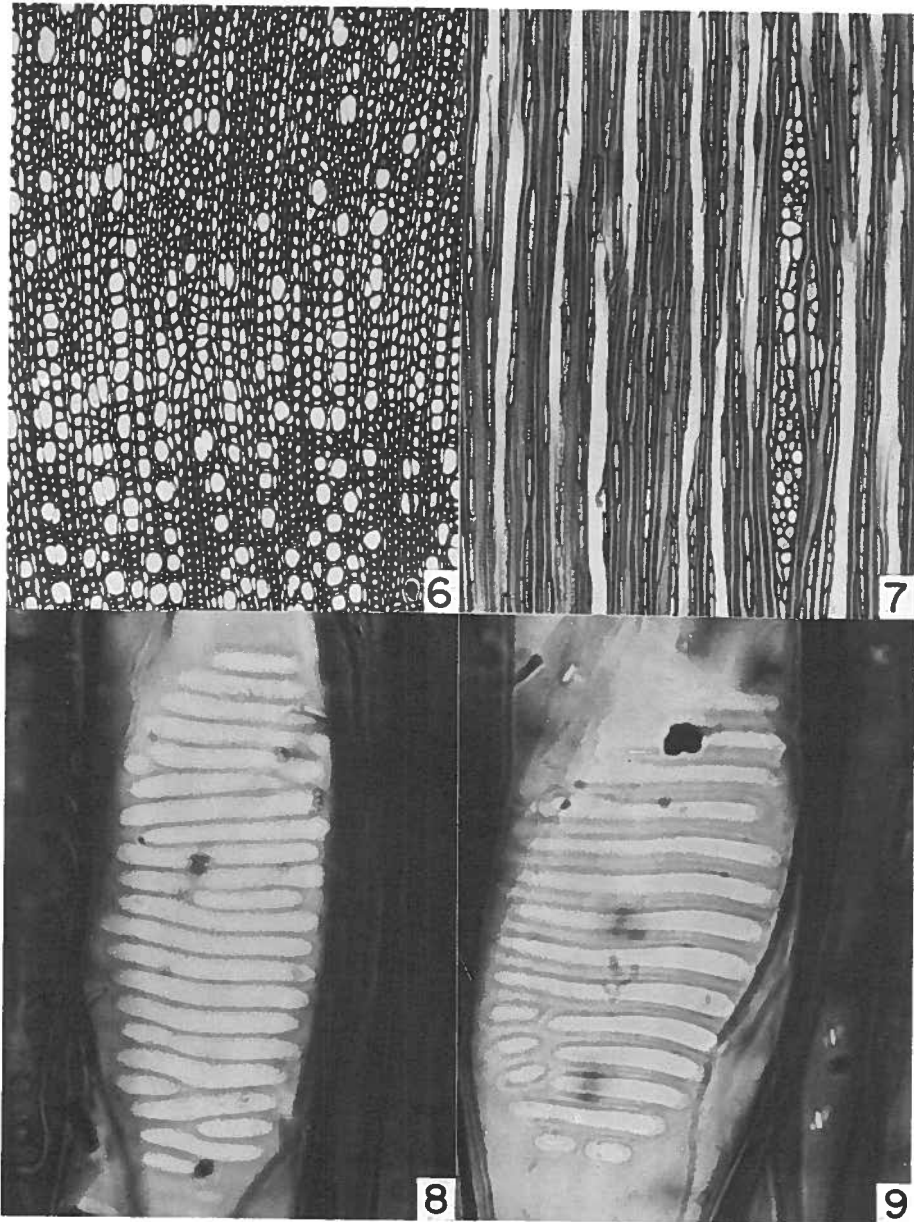


FIG. 6-9.

*Grubbia rourei* (Carlquist 5115), wood sections. 6. Transection; a growth ring, center, is visible. 7. Tangential section; multiseriate ray at right. 8. Entire perforation plate. 9. Perforation plate portion showing borders on bars; tracheid pits visible lower right. Fig. 6, 7, magnification according to scale above Fig. 2. Fig. 8, 9, magnification according to scale at right of Fig. 15.

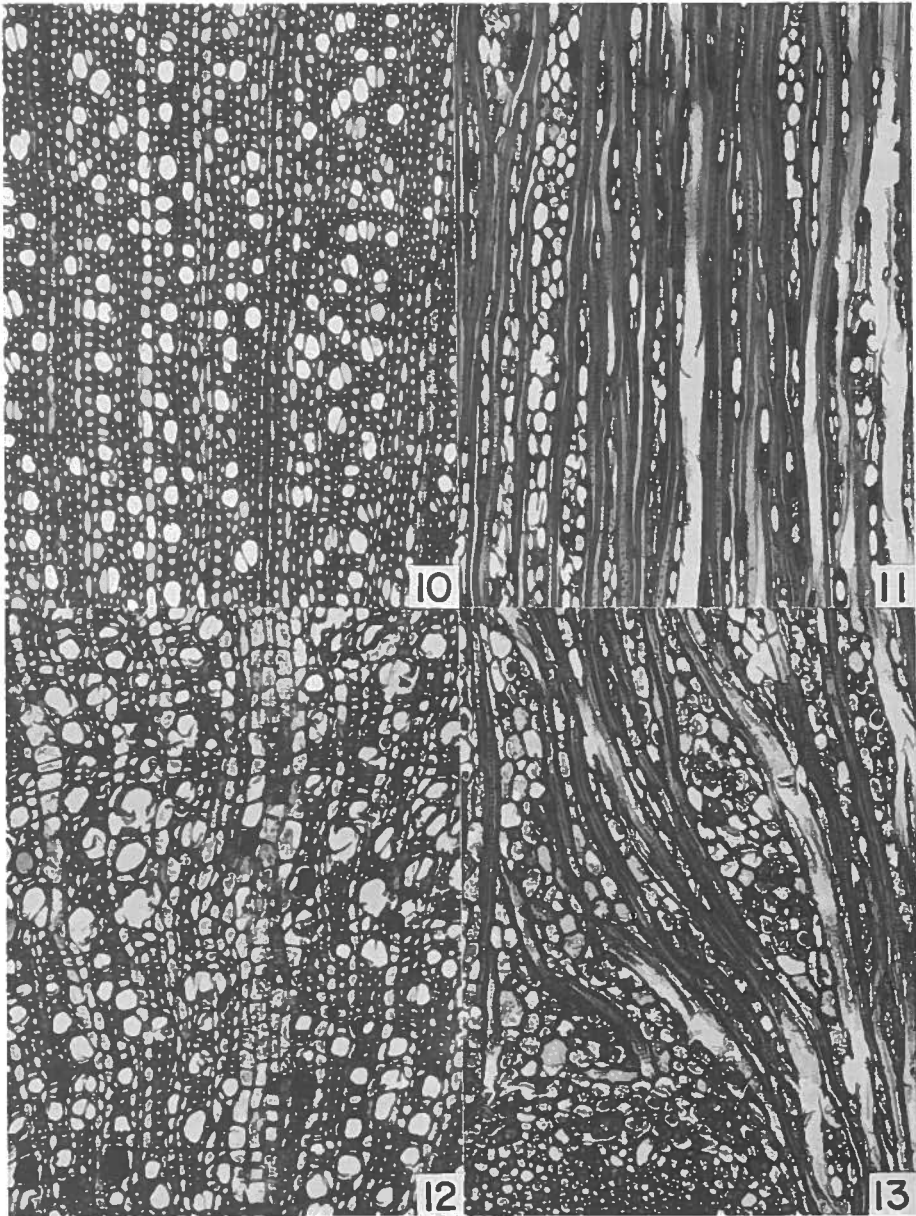


FIG. 10-13.

*Grubbia tomentosa* (Carlquist 4515), wood sections. 10-11. Sections from upright above-ground shoot. 10. Transection; no growth ring activity visible. 11. Tangential section. 12-13. Sections from root. 12. Transection. Vessels are relatively large, tracheids fewer compared to stem wood. 13. Tangential section. Rays and ray cells are larger and bulk larger in root wood as compared to that of stem. Fig. 10-13, magnifications according to scale above Fig. 2.

$\mu\text{m}$  in stem, 985  $\mu\text{m}$  in root. Tracheids have elliptical apertures shorter than the diameter of the pit cavity. Axial parenchyma very scanty, diffuse. Both multiseriate and uniseriate rays present; multiseriates have procumbent cells in centre of rays only. Multiseriate rays average 808  $\mu\text{m}$  in stem, 590  $\mu\text{m}$  in root. Multiseriate rays average 2,7 rays at widest point in stem, 2,2 cells in root. Uniseriate rays more abundant than multiseriates, averaging 455  $\mu\text{m}$  in height in stem, 329  $\mu\text{m}$  in root. Uniseriate rays composed wholly of square to procumbent cells, erect cells predominant. Ray cell walls vary in thickness; many are notably thick-walled and have borders formed on pits (Fig. 18). Rhomboidal crystals solitary in occasional ray cells in stem and root. Massive deposits and droplets of unidentified gummy materials in ray cells (Fig. 18).

Forking of bars and other minor anomalies of the scalariform perforation plates are shown in Fig. 8 and 9. The perforation plates shown there are shorter than the average, because of the difficulties in photographing long perforation plates, portions of which are usually cut away in sectioning. Bars on some perforation plates bear borders along the length of the bars (Fig. 9).

*Grubbia tomentosa*, Carlquist 5010 (Fig. 10–16). Growth rings barely perceptible, diffuse porous. Vessels mostly solitary, averaging 1,10 per group in stem, 1,08 in root. Vessels per sq. mm average 139 in stem, 121 in root. Vessel diameter averages 43,2  $\mu\text{m}$  in stem, 54,0  $\mu\text{m}$  in root and 59,0  $\mu\text{m}$  in the lignotuber. Vessel elements with scalariform perforation plates, perforation plates averaging 30,8 bars per plate in a small stem, 30,0 bars in a large stem (range: 24–41), and 29,9 bars in the root (range: 21–51); number of bars averages 24 in the lignotuber, but sample too small to be conclusive. Vessel element length averages 1 014  $\mu\text{m}$  in the stem, 1 096  $\mu\text{m}$  in twig, 1 069  $\mu\text{m}$  in the root, and 755  $\mu\text{m}$  in the lignotuber. Lateral wall pitting of vessels scalariform facing rays; sparse, circular and alternate facing tracheids. Tracheid length averages 1 106  $\mu\text{m}$  in a twig, 1 139  $\mu\text{m}$  in a large stem, 1 302  $\mu\text{m}$  in the root, and 757  $\mu\text{m}$  in the lignotuber. Tracheid wall thickness averages 3,5  $\mu\text{m}$  in stem and 4,4  $\mu\text{m}$  in the root. Tracheid pits elliptical to circular, the length of the aperture shorter than the diameter of the pit cavity. Axial parenchyma very sparse, diffuse. Both multiseriate and uniseriate rays present, multiseriate rays more abundant than uniseriates (Figs. 11, 13). Multiseriate rays of the stem contain procumbent cells in the central portion of the rays, but procumbent cells are more abundant in the wide rays of the root (Fig. 13); other cells of multiseriate rays square to erect. Multiseriate rays average 1 271  $\mu\text{m}$  in height in the large stem, 731  $\mu\text{m}$  in the root. Multiseriate rays average 3,7 cells at widest point in the stem (Fig. 11), 4,0 cells in the root. Uniseriate rays average 316  $\mu\text{m}$  in height in the large stem, 273  $\mu\text{m}$  in the root; uniseriates composed of square to erect cells only. Crystals one or more per cell in many ray cells of root (Figs. 14–16), and in some ray cells of the large stem and the lignotuber. Smaller crystals also present in some cells along with the larger crystals (Figs. 14, 15).

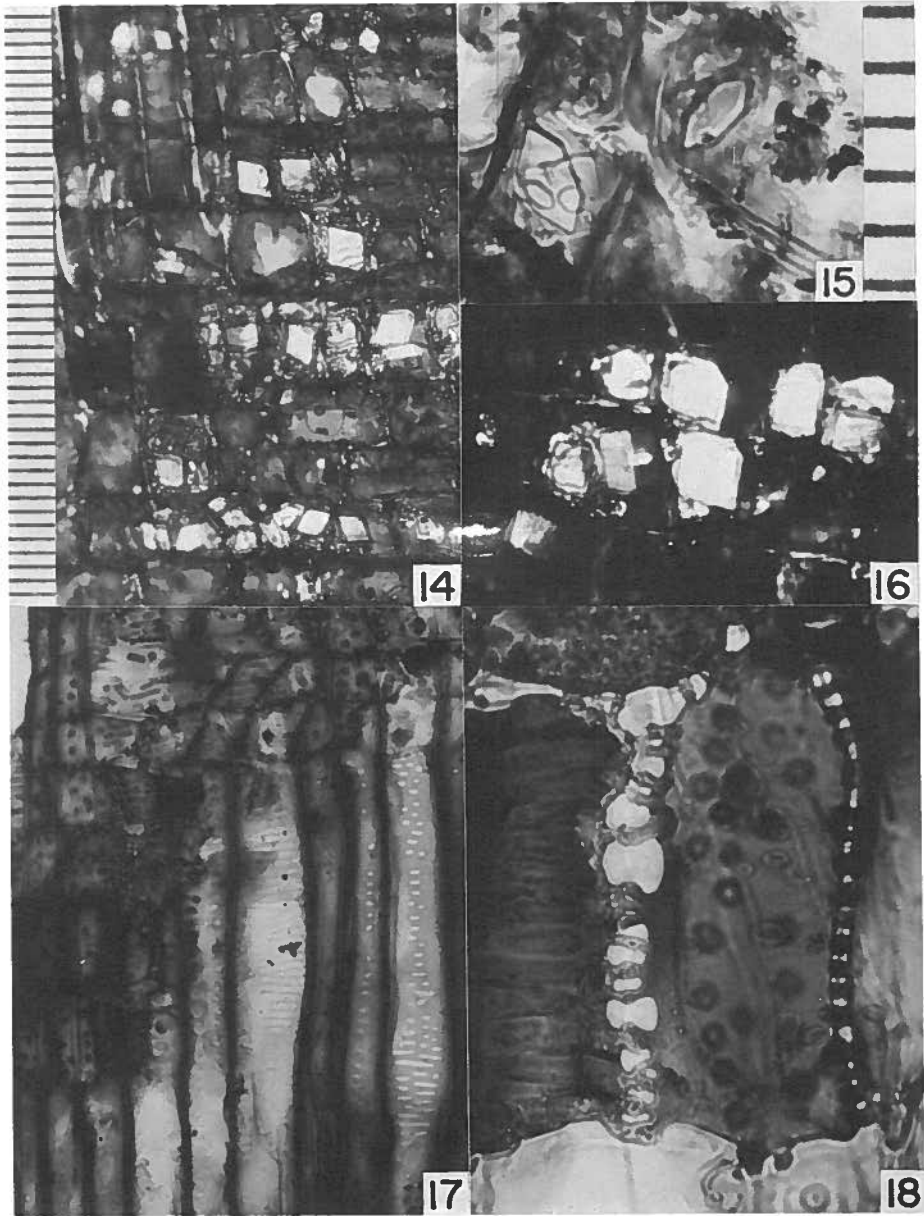


FIG. 14-18.

Details of wood histology of *Grubbia* species as seen on radial sections. 14-16. *Grubbia tomentosa* (Carlquist 4515), views of crystals in ray cells of root wood. 14. Portion of ray in partially polarized light, showing crystal density in this tissue. 15. Rhomboidal crystals of various sizes seen in non-polarized light. 16. Rhomboidal crystals of various sizes seen in fully polarized light. 17-18. *Grubbia rourkei* (Carlquist 5115). Sections from stem wood. 17. Portions of ray above and at left; vessel-ray and intervacular pitting on vessel at right. 18. Portions of ray cells to show thickened wall with bordered pits and deposits of dark-staining gummy substance. Fig. 14, 17, magnification according to scale at left of Fig. 14. Fig. 15, 16, 18, magnification according to scale at right of Fig. 15.



Dark-staining deposits of unidentified gummy materials present in ray cells of the stem (Fig. 11), root (Figs. 12, 13) and the lignotuber, and in some vessels of the root (Fig. 12).

TABLE 1  
Wood characteristics in *Grubbia*

| Species, portion  | Collection                  | Vessel diameter, mean, $\mu\text{m}$ | Bars per perforation plate, mean | Ratio of mean tracheid length to vessel element length | Vessel element length, mean, $\mu\text{m}$ |
|---|-----------------------------|--------------------------------------|----------------------------------|--|--|
| <i>G. r. r.</i> var. <i>rosmarinifolia</i> <sup>1</sup><br>large stem<br>root<br>twig<br>twig | Carlquist 4508 <sup>1</sup> | 37,8                                 | 31,7                             | 1,002  | 1 187                                      |
|   |                             | 47,5                                 | 28,2                             | 1,04   | 1 176                                      |
|   | R. H. Compton 13481         |                                      | 32,6                             | 0,98   | 1 182                                      |
|   |                             |                                      |                                  | 28,6   | 1,08                                       |
| <i>G. r. r.</i> var. <i>pinifolia</i><br>twig   | T.P. Stokoe 57840           |                                      | 32,4                             | 1,06   | 1 189                                      |
| <i>G. rosmarinifolia</i> subsp. <i>gracilis</i><br>stem base                                  | G.J. Lewis 1321             |                                      | 19,9                             | 1,06   | 880  |
| <i>G. rosmarinifolia</i> subsp. <i>hirsuta</i><br>twig  | E. Esterhuysen 10908        |                                      | 28,4                             | 1,12   | 1 036                                      |
| <i>G. rourkei</i><br>main stem<br>main root   | Carlquist 5115              | 39,3                                 | 26,3                             | 0,98   | 1 267                                      |
|   |                             | 53,7                                 | 23,3                             | 1,24   | 796  |
| <i>G. tomentosa</i><br>large stem<br>large root<br>lignotuber<br>twig                         | Carlquist 4515              | 43,2                                 | 30,0                             | 1,12   | 1 014                                      |
|   |                             | 54,0                                 | 30,0                             | 1,22   | 1 069                                      |
|   |                             | 49,1                                 | 24,0                             | 0,997  | 755  |
|   |                             |                                      | 30,8                             | 1,01   | 1 096                                      |

<sup>1</sup>For nomenclatural and herbarium citations, see a concurrent paper (Carlquist, 1977).

## DISCUSSION OF ANATOMICAL FEATURES

### *Growth Rings*

Despite the seasonality of the climate of Cape Province, only minor fluctuation in vessel diameter and abundance can be seen in the woods of *Grubbia* (Figs. 1, 6, 10, 12). The one pronounced growth ring observed in *G. rourkei* may have been

related to an unusually severe season. However, lack of growth rings in such mesomorphic woods is to be expected, especially considering that the habitats of all species (especially *G. rosmarinifolia*) are mesic throughout the year or have very attenuated water supply. Also, the evergreen leaves with reduced surface area, revolute margins, abaxial pubescence and varnish-like coating (notably in *G. rourkei*) suggest minimal fluctuation in transpiration.

#### Vessel Elements

As Table 1 shows, vessel elements in Grubbiaceae are relatively long compared to those of dicotyledons as a whole, although somewhat shorter than the average length in the primitive woods sampled in comparable woods (Carlquist, 1975a, p. 141), perhaps because *Grubbia* is shrubby, whereas the woods of my 1975a sample came mostly from trees. In comparing the species of *Grubbia*, one should remember that the wood samples, although of maximally large diameter for main stems and roots in their respective species, were not identical in size: the largest stem of *G. tomentosa* I could find was about 1 cm in diameter, whereas the base of the main stems of *G. rourkei* and *G. rosmarinifolia* subsp. *rosmarinifolia* var. *rosmarinifolia* I collected were about 3 cm in diameter. *Grubbia tomentosa* has smaller stems because numerous shorter-lived stems branch from the lignotuber. The somewhat shorter vessel element length reported for *G. tomentosa* (Table 1) might reflect this, because vessel element length tends to increase with age of a stem (Bailey and Tupper, 1918). The short vessel elements of the lignotuber are probably related to the contorted nature of the wood, for contorted wood tends to have shorter tracheary elements (Bailey and Tupper, 1918). The data of Table 1 tend to show that in comparing twigs with main stems there is no marked increase, and that only moderate increase in vessel element length with age occurs. The short vessel elements in roots of *G. rourkei* run counter to the general trend in dicotyledons, namely, vessel elements longer in roots compared to stems, as far as is known (Carlquist, 1975a, p. 179). Perhaps the contorted nature of roots may result in a shorter vessel element length than otherwise would be the case. However, the tendency of vessel elements to be wider in roots than in stems (Carlquist, 1975a, p. 179) does hold in Grubbiaceae.

In the book cited, I held that a low tracheid length: vessel element length ratio in a species can be regarded as a rough index of primitiveness. These ratios (Table 1) are remarkably low in Grubbiaceae. The occurrence of ratios lower than 1,00 in Grubbiaceae (twigs of *G. rosmarinifolia* subsp. *rosmarinifolia* var. *rosmarinifolia*; lignotuber of *G. tomentosa*) as well as ratios extremely close to 1,00 (Table 1) suggests that an additional factor may be operative. Such low ratios (below 1,00) have not been reported in earlier work (Bailey and Tupper, 1918; Carlquist, 1975a) on dicotyledons, although I have found ratios below 1,00 in *Myrothamnus* (Carlquist, 1976a) and certain Bruniaceae (Carlquist, unpublished data). Perhaps the vessel elements have a greater intrusive capacity in Grubbiaceae and elongate

more, compared with the length of fusiform cambial initials from which they were derived, than is typical for dicotyledons. Although vessel elements in dicotyledons at large are often thought to be about the same length as their respective parental fusiform cambial initials, at least some elongation does take place, on the average. I am hesitant to offer an explanation for the ratios at or below 1.00. That several such ratios have now been computed, both in *Grubbiaceae* and elsewhere, shows that mere sampling error is not involved. As one hypothesis, one could suggest that *Grubbia* does not have longer vessel elements than could have been predicted, but shorter tracheids. If, as hypothesized, tracheary element length is proportional to strength (Carlquist, 1975a, p. 88), the shrubby habit of *Grubbiaceae*, and especially the lignotuber of *G. tomentosa*, may be correlated with less elongate (and therefore less maximally strong) tracheids than would be the case in arboreal dicotyledons. There is, however, no truly convincing reason to advance this hypothesis at present, for shrubby and herbaceous dicotyledons do have imperforate elements longer than vessel elements in species that have been studied, with the few exceptions noted.

Perforation plates in *G. rosmarinifolia* may seem abnormally long when wood sections are viewed (e.g., Fig. 5), but shorter ones are also present in that species (Fig. 4). In fact, as the data of Table 1 show, there is not a marked difference among the species. Borders can be seen on bars, either along the length of each bar (Fig. 9) or as vestigial borders at the ends of each perforation (Fig. 8).

Lateral wall pitting is scalariform opposite ray cells (Fig. 3, 17), but consists of sparse circular bordered pits elsewhere. The presence of scalariform pitting seems to bear a relation to the extremely low density of axial parenchyma in *Grubbia*. If axial parenchyma is scarce or absent, rays may possess the function of both vertical and lateral photosynthate translocation in wood and maximal vessel-ray contacts by means of scalariform pitting may be of selective value. This, if true, could be considered an addendum to my hypothesis about the nature of vessels in primitive wood (1975a).

If one compares vessel element length, vessel width, and number of bars per perforation plate for species and organs in Table 1, one finds all of these are roughly proportional. Shorter, wider vessel elements tend to have fewer bars per perforation plate (e.g., *G. tomentosa* lignotuber). The ranges in these features are not great within the genus. The short vessel elements, with fewer bars per perforation plate, as well as short tracheids, in *G. rosmarinifolia* subsp. *gracilis*, are probably correlated with the diminutive, almost stunted stature of plants in that subspecies.

Vessels tend to be midway between angular and round in transection (Fig. 1, 6, 10, 12), and as figures for vessels per group in the descriptions illustrate, vessels are nearly all solitary. These expressions qualify as primitive according to traditional theories of wood evolution in dicotyledons.

### Tracheids

Tracheids are not notably thick-walled in *Grubbia* (Fig. 1, 6, 10, 12) as compared to those of other primitive woods, such as that of *Illicium* (Carlquist, 1975a). Moderately thick-walled tracheids characterize the South African shrub *Geissoloma* as well (Carlquist, 1975b). All tracheids in *Grubbia* have pit apertures slit-like, but no longer than the pit cavity diameter (Fig. 9), and there is no doubt as to their identity as tracheids.

### Axial Parenchyma

Axial parenchyma is extremely scanty in woods of Grubbiaceae, although I observed it in all organs of all three species. Axial parenchyma is slightly more abundant in *G. rourkei*. The paucity of axial parenchyma in stems of *Grubbia* may be related to their relatively finite size (aerial stems rarely if ever exceed 3–4 cm in diameter). This explanation was suggested for another South African shrub, *Myrothamnus flabellifolia*, which lacks axial parenchyma and which also never becomes a large shrub (Carlquist, 1976a). Conceivably, an axial parenchyma system can be superseded by abundance of erect ray cells if a plant (or shoots from a lignotuber) are of relatively finite duration.

### Rays

Both multiseriate and uniseriate rays are present in all species. Multiseriates are wider and more abundant in *G. tomentosa* stems, roots, and especially lignotubers (Fig. 11, 13). Because of the habit of *G. tomentosa*, a higher proportion of ray tissue to mechanical tissue compared with *G. rosmarinifolia* and *G. rourkei* might be expected. The lignotubers and roots of *G. tomentosa* also have a definite storage capacity to survive burning and perhaps drought, so that greater abundance of parenchyma might be expected.

Procumbent cells are relatively infrequent in rays of all *Grubbia* species (Fig. 17). A few occur in central portions of multiseriate rays. Relative abundance of upright ray cells can be regarded as a substitute for paucity of axial parenchyma cells, as mentioned above. Uniseriate rays composed of erect to square cells, or erect cells exclusively, are relatively infrequent in dicotyledons, but occur in shrubs such as *Roridula* (Carlquist, 1976b) and may function in vertical translocation of photosynthates, as mentioned above.

Thick-walled ray cells may be found in stems in some rays of *G. tomentosa* and *G. rourkei* (Fig. 18). I have hypothesized (Carlquist, 1975a, 1975b) that thick-walled ray cells with bordered pits may represent a simple mechanism for increasing mechanical strength of a wood. This can apparently occur easily phylogenetically, and does not always occur in primitive woods.

### Crystals

Crystals are most conspicuously present in ray cells of *G. tomentosa* (Fig. 14–16). They are less common in the two other species, and very rarely seen in axial

parenchyma cells. These crystals take the form of one, sometimes more, rhomboidal crystals per cell. If more than one crystal per cell is present, one is large and the others much smaller. This was observed in *Geissoloma* (Carlquist, 1975b), and may also be observed in many Bruniaceae (Carlquist, unpublished data).

#### *Gummy Deposits*

As in *Geissoloma* and in Bruniaceae, gummy deposits, chiefly in ray cells (Fig. 11, 12, 13, 17, 18) but also, if abundant, in vessels, occur in Grubbiaceae. These deposits are least conspicuous in *G. rosmarinifolia*.

#### ECOLOGICAL INTERPRETATIONS

The habitats of the *Grubbia* species are distinctive: *G. rosmarinifolia* in montane seeps and streams; *G. rourkei* on moist slopes of Kogelberg; and *G. tomentosa* on south-facing slopes at lower elevations, in open scrub but almost invariably beside or among sandstone blocks that tend to provide pockets for moisture accumulation and retention. The lignotubers of *G. tomentosa* may also be regarded as a system moderately capable of water storage, and the pattern of numerous shoots innovated from the lignotuber provides a means of producing branches and foliage in amount appropriate to the wetness of the season. Fire and dieback from severe drought would not be fatal for *G. tomentosa*, for the lignotuber can provide new shoots indefinitely. Indeed, I suspect some individuals of *G. tomentosa* are quite old, judging from the massive size of lignotubers, which eventually fragment into several adjacent and independent portions. Deep roots in this species probably tap water well below the surface compared with the ericads, restiads, etc. with which *G. tomentosa* may be found growing. In short, *G. tomentosa* may be regarded as a plant adapted to maintenance of a mesomorphic system within a basically dry mediterranean-type climate, just as a desert annual is a mesophyte that grows only during a mesic portion of a wet year.

The various features of *Grubbia* plants seem well designed for utilization of a "primitive" or "inefficient" conductive system in which rates of flow are probably slow and in which excessively high water tensions do not develop. *Grubbia*, like *Geissoloma* (Carlquist, 1975b), *Roridula* (Carlquist, 1976b), and Bruniaceae, probably represents a relictual group, at least with respect to xylem, that has persisted in relatively mesic pockets within the otherwise rather xeromorphic flora of the Table Mountain Sandstone.

#### PHYLOGENETIC CONSIDERATIONS

The affinities hypothesized by various authors may be summarized under the following headings.

##### 1. Santalaceae and Santalales

The single perianth whorl, valvate aestivation of flowers, and inferior ovary of *Grubbia* probably provided the chief bases for this supposed relationship to which

such authors as Bartling, Bentham, and Hieronymus subscribed earlier (see Fagerlind, 1947), and which is perpetuated in the more recent systems such as those of Wettstein (1935), Hutchinson (1959), and Cronquist (1968). The wood anatomy of Grubbiaceae is not totally incongruent with that of Santalaceae because Santalaceae do have tracheids as imperforate elements and prominent crystals in axial parenchyma, but they have vessels with simple perforation plates exclusively and also have vascular tracheids (Metcalfe and Chalk, 1950). The reader who wishes information on how vascular tracheids differ from true tracheids may consult Carlquist (1961, 1975a). The degree of xylary specialization separates it markedly from Grubbiaceae, and one would perhaps be better advised to look toward groups in which the wood is not so highly different in level of specialization, rather than assume extinction of all intermediate wood types. If Grubbiaceae were related to Santalaceae, one might expect that in Africa there might be santaloids that approach Grubbiaceae either in gross morphology or in anatomy, but none appear to do so.

## 2. Ericaceae

Fagerlind (1947) presents a detailed argument for this relationship, and cites precedent in the work of Bergius, Jussieu, St. Hilaire and Hedwig. Some of these authors probably were more influenced by the ericoid appearance of herbage of *Grubbia rosmarinifolia* than by any deep-seated resemblances. Erdtman (1952) lends a degree of support to supposed ericaceous affinity on the basis of pollen. However, one must remember that neither Grubbiaceae nor Ericaceae offer any highly distinctive features in pollen grains, and have a generalized type common to many dicotyledonous families. Moreover, Erdtman's work was done prior to the advent of electron microscopy, which now offers much more precise and detailed information. Although Fagerlind cites a number of resemblances between Ericaceae and Grubbiaceae, all of the features mentioned are rather widespread in dicotyledons, and are not convincing separately or collectively. The abundance of Ericaceae in South Africa is not really phytogeographic evidence at all, for the South African ericads seem highly specialized, as evidenced by their wood, whereas ericad phylads with wood comparable in level of specialization to that of *Grubbia* are in remote localities in the northern hemisphere. The floral morphology of Ericaceae is also markedly different from that of Grubbiaceae. Fagerlind is forced to describe similarities in terms of floral diagrams rather than detailed features of histology. I do not find evidence for an Ericaceae—Grubbiaceae relationship compelling.

## 3. Hamamelidaceae

*Floral morphology, with respect to number and kinds of parts, has been* suggestive to authors who have construed a relationship between Grubbiaceae and Hamamelidaceae. The names of Decaisne, Gardner, and Sonder (see Van

Tieghem, 1897) can be cited in this regard. The wood of Hamamelidaceae offers many similarities to that of Grubbiaceae, and is to me indicative of a degree of relationship, but one more remote than the ones discussed below. Hamamelidaceae may be regarded as a "rosoid" or "rosalean" family not far removed from the familial groupings discussed below.

#### 4. *Bruniaceae*

Although Van Tieghem (1897) concluded that Grubbiaceae is allied to Bruniaceae, he has precedent in Arnott, Endlicher, Lindley, and Agardh, whereas A. de Candolle regarded Bruniaceae as a link between Santalaceae and Grubbiaceae (see Van Tieghem). One must stress that rosoids in the broad sense would include Hamamelidaceae. The concept that Grubbiaceae is allied to Bruniaceae has been most recently re-adopted by Thorne (1968), who places the South African families Bruniaceae, Geissolomataceae, Hydrostachyaceae, Myrothamnaceae, and Roridulaceae in a suborder, Brunineae, of Pittosporales. His order Pittosporales falls under a superorder, Rosiflorae, which Thorne places next to the superorder Hamamelidiflorae.

Close resemblance may be found between the woods of Grubbiaceae and Geissolomataceae, and comparison of photographs in the present paper and those in my (1975b) study of *Geissoloma* wood will reveal striking resemblances. The same applies to Bruniaceae, the woods of which I have studied, and on which I have amassed considerable qualitative and quantitative data soon to be published. I can state that in Bruniaceae a number of species match one or more of the three species of *Grubbia* so closely in wood anatomy that I might not be able to separate unlabelled slides of wood sections accurately into their respective families. I feel that more than parallelism is involved. The element of phytogeography is suggestive: Thorne's Brunineae are essentially South African (with extension into Madagascar) and all (except Hydrostachyaceae) have secondary xylem of a primitive nature. However, features other than these are persuasive, as Van Tieghem (1897) showed in a preliminary way. I hope to broaden the basis of a phylogenetic interpretation. For the present, however, I can state that resemblances in wood anatomy among Grubbiaceae, Bruniaceae, and Geissolomataceae are very close; although more features than wood anatomy are required to collate these families into ordinal groupings, the wood anatomy does at least confirm a generalized "rosoid" position of Grubbiaceae along with Geissolomataceae and Bruniaceae.

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