Wood anatomy and relationships of Geissolomataceae

Sherwin Carlquist[1]

Claremont Graduate School and Rancho Santa Ana Botanic Garden,
Claremont, California 91711

CARLQUIST, S. (Claremont Grad. Sch. and Rancho Santa Ana Bot. Gard., Claremont, CA 91711). Wood anatomy and relationships of Geissolomataceae. Bull. Torrey Bot. Club 102: 128–134. 1975.—*Geissoloma marginatum*, sole species of Geissolomataceae and a shrub endemic to a restricted portion of Cape Province, South Africa, has not been described hitherto with respect to most details of wood anatomy. Quantitative and qualitative data for both aboveground and belowground stems show a strong degree of correlation between the primitive features of this wood and the mesic habitats *Geissoloma* tends to occupy. *Geissoloma* is interpreted as a relict genus; wood anatomy offers a few features suggestive of relationships. There is little similarity to Myrtales, Thymelaeaceae, Celastraceae, Oleaceae, or Salvadoraceae. Instead, close similarities to wood of Grubbiaceae, Bruniaceae, and, more distantly, certain families of Rosales and Hamamelidales can be cited.

Geissoloma marginatum (Linn.) A. Juss., sole species of the Geissolomataceae, is a shrub endemic to mid-elevation slopes of the Langeberge, a range of sandstone mountains in southwestern Cape Province, South Africa. It grows in small colonies in moist south-facing sites, often beside sandstone outcrops that provide shade, a greater degree of water retention than do unshaded places, and some protection from fires that tend to occur with frequence in the *fynbos* scrub of the Langeberge. Belowground stems tend to develop as lignotubers and are capable of sprouting after a shrub has been burned. Wood samples from both belowground and aboveground stems have been studied here.

This investigation represents a contribution toward understanding of the phylogenetic relationships of Geissolomataceae, the placement of which, discussed below, has been notably varied and can be said to be quite uncertain. To be sure, wood anatomy yields only a limited amount of information in this regard. The significance of the wood of *Geissoloma* in relation to recent concepts of wood evolution (Carlquist 1975a) is plain, however, for *Geissoloma* clearly seems a mesic relic in the largely xeromorphic scrub of Cape Province.

Materials and methods. Although I collected *Geissoloma marginatum* in several localities in the Clock Peaks above Swellendam, I have selected wood of the collection Carlquist 4518 (RSA) for study. The shrub that forms the basis for this collection had more successfully escaped fires

that burned much of the Clock Peak scrub in 1972, and provided more mature stems. The aboveground shoots were not of maximal size, only about 2 cm in diameter. Large belowground stems were available, however. Even these tend to be partially damaged by rot and fire in most of the shrubs. Wood samples were sectioned on a sliding microtome and stained with safranin. Macerations were prepared by means of Jeffrey's fluid, stained with safranin, and measured with the usual techniques.

Anatomical descriptions. The account below incorporates quantitative and qualitative data for both aboveground stems (maximal size collected), belowground portions, and a slender upper branch; these are cited in appropriate places; if not otherwise indicated, descriptions apply to wood from all portions of a plant.

Growth rings nearly absent aboveground (Fig. 1), moderately pronounced in belowground wood (Fig. 3). Vessels angular in transectional view (Fig. 6), mostly solitary (1.3 per group aboveground, 1.2 belowground). Vessels per sq. mm average 26 in aboveground wood, 33 in belowground wood. Vessels average 39.8
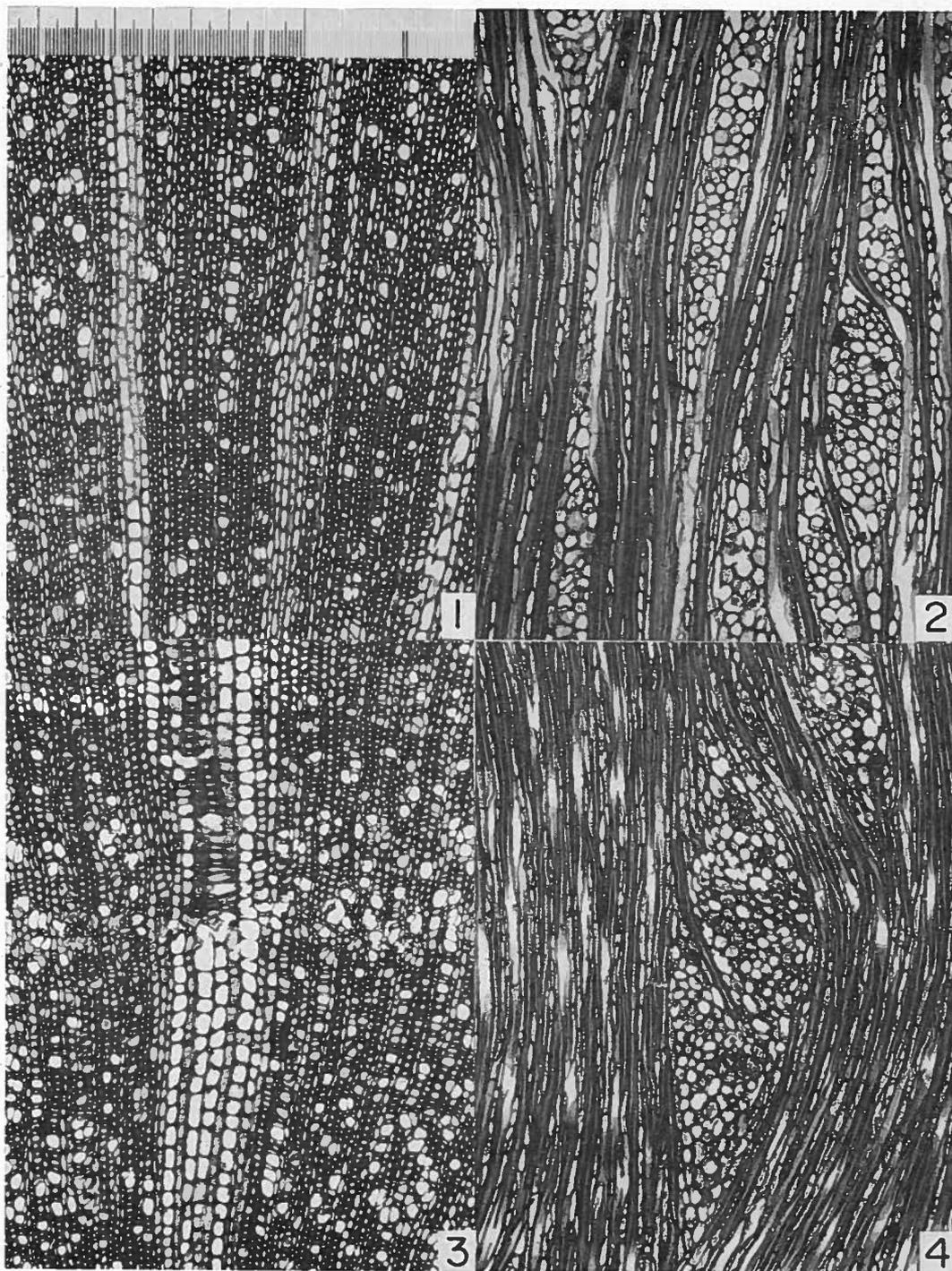
Figs. 1–4. *Geissoloma marginatum,* Carlquist 4518 (RSA), wood sections.—Fig. 1. Transection of aboveground stem.—Fig. 2. Tangential section of aboveground stem; dark deposits show in some ray cells.—Figs. 3–4. Sections from belowground stem.—Fig. 3. Transection, growth ring near center.—Fig. 4. Tangential section; note large multiseriate ray. Magnification indicated by scale above Fig. 1 in which finest divisions = 10 µm.

μm, in diameter in aboveground wood, 35.8 μm belowground. Vessel-element length averages 902 μm aboveground, 856 μm in the upper branch, and 650 μm in belowground wood. Perforation plates scalariform (Fig. 8), bars often bordered, especially at extremities (bases) of bars (Fig. 9). Number of bars per perforation plate average 23.5 in belowground wood, 18.6 in aboveground stems, and 17.2 in the upper branch. Range in number of bars observed was from 12 to 33. Lateral-wall pitting of vessels opposite or scalariform (Fig. 7) in intervascular contacts, scalariform with wide pit apertures in vessel-ray pitting. Tracheids with pit apertures the same length as diameter of pit borders (Fig. 10). Only tracheids constitute the imperforate elements of axial secondary xylem. Tracheids tend to be thick-walled (Fig. 6), averaging 4.9 μm in wall thickness in aboveground wood, 4.1 μm in belowground wood. Tracheids average 1224 μm in length in belowground wood, 902 μm in aboveground wood, and 983 μm in the upper branch. Axial parenchyma present (Fig. 5), diffuse, in strands of four or five very long cells. Multiseriate rays average 1388 μm in belowground wood, 579 μm in aboveground wood. Multiseriate rays tend to be conspicuously fewer and wider in belowground wood (Fig. 4) as compared to aboveground wood (Fig. 2). Procumbent cells are present in the central portions of multiseriate rays, with square to erect cells peripheral in rays (Fig. 5). Uniseriate rays average 341 μm in belowground wood, 188 μm in aboveground wood. Uniseriate rays more abundant in belowground wood (Fig. 4) than aboveground wood (Fig. 2). Uniseriate rays, as far as could be determined, consist of square to erect cells, with no procumbent cells. Pits among ray cells sometimes bordered (Fig. 11), especially in those ray cells that have thick walls. One or two rhomboidal crystals occur occasionally in cells of multiseriate rays of belowground wood (Fig. 12), much less frequently in multiseriate rays of aboveground wood. Numerous small crystals may be present in addition to large crystals (Fig. 12), and in a very few ray and axial parenchyma cells, numerous small crystals exclusively were observed. Only a small fraction of ray and axial parenchyma cells contain crystals. Gummy deposits which stain darkly with safranin are common in ray cells (Figs. 5, 11) in dispersed or massive form, often occluding pits in ray cells.

ADDITIONAL NOTES. Fagerlind and Dunbar (1973) illustrated bordered bars on perforation plates of *Geissoloma* by means of scanning electron microscopy. They also illustrated some perforations in vessel elements that retained pit membranes, although others do lack them. Fagerlind and Dunbar (1973) are incorrect in averring that *Geissoloma* lacks axial parenchyma. To be sure, axial parenchyma is a feature not readily observed in many dicotyledon woods, especially when it is diffuse or scarce. There is no reason for terming the tracheids of *Geissoloma* wood as fibertracheids, as Fagerlind and Dunbar do. Others who have contributed notes on a scattering of features of wood of *Geissoloma* include Van Tieghem (1893), Suprian (1894), and Metcalfe and Chalk (1950). The notes of Dahlgren and Rao (1969) are derived from those authors and offer no new data.

If one divides average vessel-element length into average tracheid (or other imperforate element) length for a given wood sample of a species, one obtains a ratio which can be used, with great reliability, as an index of primitiveness, especially where ratios are low (Carlquist, 1975a). Higher ratios are not necessarily in proportion to specialization of wood features for a given species, but they do represent various degrees of departure from primitiveness, and are indicative of increasing division of labor between the conductive and mechanical systems. In the aboveground wood of *Geissoloma*, the tracheid/vessel element ratio computed from the above data would be 1.10, which is as low as the lowest I computed in dicotyledons noted for primitiveness in wood features (Carlquist 1975a).

Ecological interpretations. In my 1975a account of wood anatomy in relation to ecology, I characterized a dicotyledonous wood with primitive features, such as those in the wood of *Geissoloma*, as adapted to mesic conditions. More specifically, I regarded such primitive woods as adaptive in sites where water availability is rather steady, conduction and transpiration rates presumptively slow, and where water columns of the xylem do not experience high
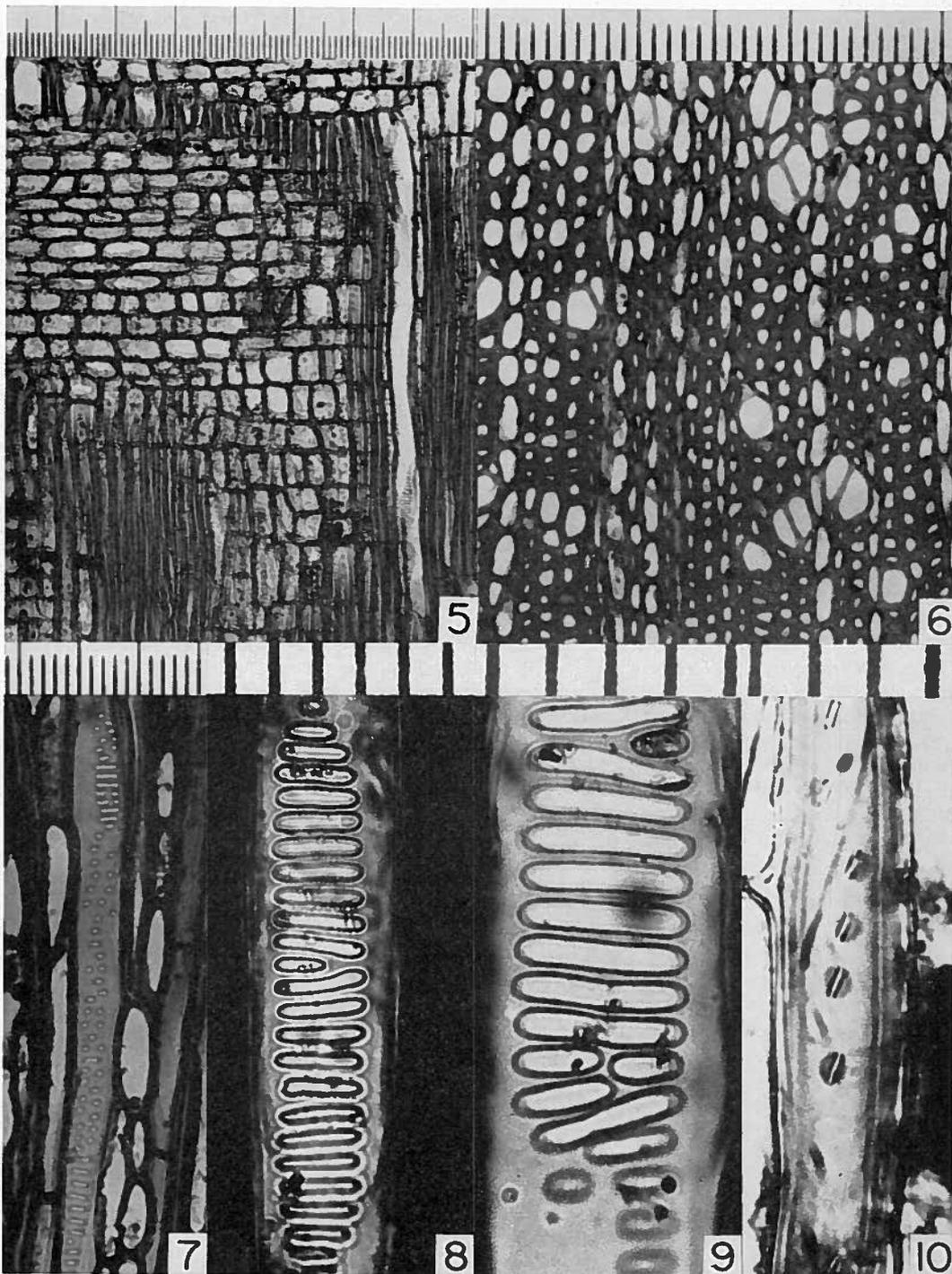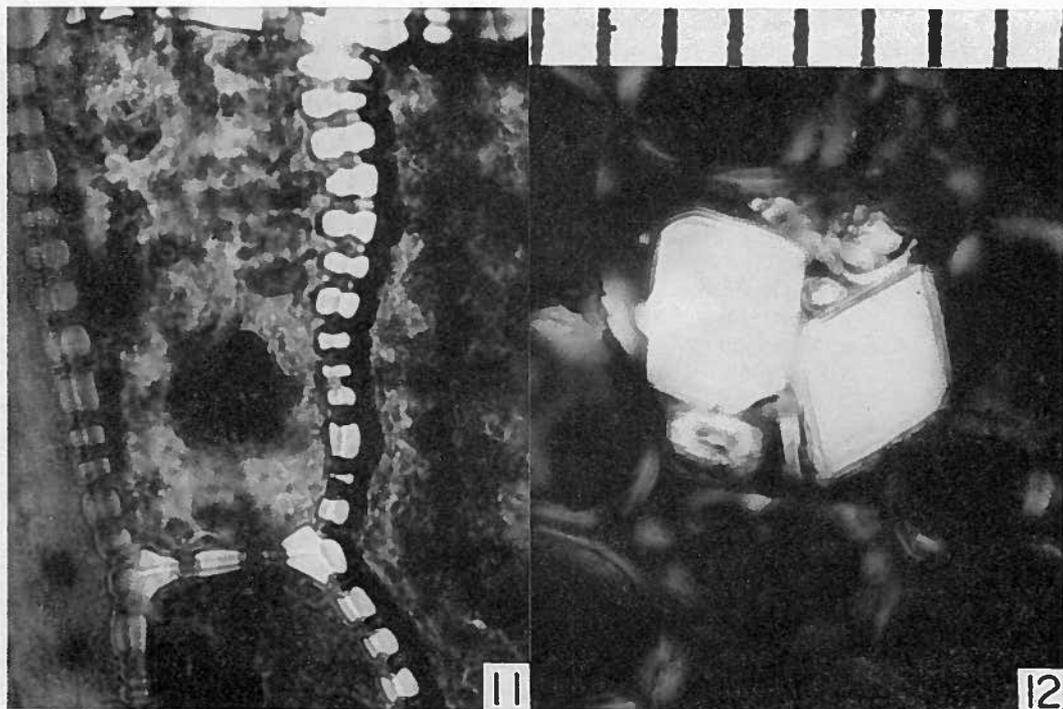
Figs. 5–10. *Geissoloma marginatum*, Carlquist 4518 (RSA), wood sections from aboveground stem. —Fig. 5. Radial section. Note shapes of ray cells; axial parenchyma strands are present to left and right of the vessel seen at right.—Fig. 6. Transection. Note thickness of tracheid walls.—Fig. 7. Vessel from tangential section showing lateral wall pitting.—Fig. 8. Perforation plate of vessel element from radial section.—Fig. 9. Portion of perforation plate showing borders on bars.—Fig. 10. Portion of a tracheid from tangential section, bordered nature of pits visible. Magnification indicated by scales above the respective figures: finest divisions = 10 μm.

tensions. The unusual conditions under which *Geissoloma* grows, described earlier, together with the sclerophyllous and highly cutinized nature of the leaves (Dahlgren and Rao 1969) correspond to fulfillment of these conditions. The probable low conductive rates in *Geissoloma* are underlined by the discovery by Fagerlind and Dunbar (1973) that membranes persist in some perforations of vessel-element perforation plates. *Geissoloma* seems to qualify as a relict element in the South African flora, surviving in a very few mesic pockets. Other groups in the South African flora occupying mesic sites include Bruniaceae, *Cunonia* (Cunoniaceae), *Curtisia* (Cornaceae), Grubbiaceae, Myrothamnaceae, and Roridulaceae. All of these have notably primitive woods. Mesic habitats such as those occupied by these groups have also been occupied secondarily by groups that have specialized wood, such as certain Asteraceae (*Osmitopsis*), Myrsinaceae (*Myrsine*), many Penaeaceae (*Endonema*, *Glischrocolla*, *Stylapterus*, and some spe-

cies of *Brachysiphon* and *Penaea*), as well as a scattering of the many species of *Erica* (Ericaceae) endemic to Cape Province.

The interpretation of *Geissoloma* as a relict mesic element in the South African flora is interesting because it gives us an example of how a shrub with a primitive or "inefficient" conductive system has survived in regimes other than that typical for plants with such xylem, most of which are located in wet forest (Carlquist 1975a). However, there are further implications in *Geissoloma* as a relict mesic element in the South African flora. The possibility is thereby raised that *Geissoloma* might be related to one or more of the relict families phytogeographically close to *Geissoloma*.

Phylogenetic interpretations. Obviously, any interpretation of the relationships of *Geissoloma* on the basis of wood anatomy alone is somewhat premature, because wood anatomy of some possibly

Figs. 11–12. *Geissoloma marginatum*, Carlquist 4518 (RSA), sections of ray cells.—Fig. 11. Cells from radial section of aboveground wood, showing bordered pits.—Fig. 12. Cells from tangential section of belowground wood photographed in polarized light, showing crystals. Magnification of both photographs indicated by scale above Fig. 12: divisions = 10 μm.

related families is still poorly known. However, several preliminary comments can be made by way of reviewing the great difficulties that phylogenists have experienced in assessing the relationships of *Geissoloma*. The following relationships have been claimed:

1. Penaeaceae and other Myrtales.— One can say that precedent for placement of *Geissoloma* in the order Myrtales was provided by Linnaeus (1771), who used the name *Penaea marginata* for it. Penaeaceae are now regarded as a myrtalean family (e.g., Thorne 1968). After the description of *Geissoloma* as a genus by Kunth (1830), the myrtalean placement was still followed by most early authors, as detailed by Dahlgren and Rao (1969). The similarity of *Geissoloma* to Penaeaceae is based on such superficial features as tetramery of flowers and the decussate nature of small sclerophyllous leaves. Myrtales form a very natural order—one of the most easily defined orders among dicotyledons—when properly constituted (as done by Thorne 1968). This can be strikingly demonstrated by various features of wood anatomy (for a review, see Carlquist 1975b). *Geissoloma* is clearly not myrtalean, and the extensive review of Dahlgren and Rao (1969) documents many reasons why it should not be included in that order, although it was as recently as 1951 by Phillips.

2. Thymelaeaceae.—The family Thymelaeaceae has been regarded by various authors as myrtalean, which it seems clearly not to be. Comparisons between Thymelaeaceae, Penaeaceae, and *Geissoloma* were made by Van Tieghem (1893) and Suprian (1894). Hutchinson (1926, 1959, 1967) placed Geissolomataceae in his order Thymelaeales (along with Penaeaceae). Thorne (1968) places Thymelaeaceae in Euphorbiales, a treatment that seems defensible. In any case, neither xylary features nor other aspects of morphology provide a basis for inferring any degree of close relationship between Geissolomataceae and Thymelaeaceae.

3. Celastraceae.—Baillon (1877) included *Geissoloma* in Celastraceae. A similar treatment has been essayed by Cronquist (1968), who placed Geissolomataceae in Celastrales. By contrast, Thorne (1968) placed Celastraceae in Santalales. Although primitive woods may be found in Celastraceae, and there are some resemblances between capsules of Celastraceae, and those of *Geissoloma,* the totality of features does not suggest a close link.

4. Oleaceae and Salvadoraceae.—After rejecting a placement of Geissolomataceae near Penaeaceae, Dahlgren and Rao (1969) entertain—and Dahlgren (*op. cit.*) endorses—placement of Geissolomataceae as a primitive member of a line leading to Oleaceae and Salvadoraceae. When one examines the features cited in support of this alleged relationship, one finds most of them, by virtue of being widespread throughout dicotyledons, are of no value whatever in assessing relationships. The reader who is familiar with systematic occurrence of such features as opposite leaves, hypogynous flowers, linear filaments, *Polygonum*-type embryo sacs, etc., is likely to be skeptical of Dahlgren's contention. One may note that Thorne (1968) places Oleales close to Santalales. Both orders are assemblages of dicotyledons that seem to share few critical features with Geissolomataceae.

5. Pittosporales.—Among the interesting innovations of Thorne's (1968) system is the creation of an order, Pittosporales, to include the families Daphniphyllaceae, Pittosporaceae, Byblidaceae, Tremandraceae, Roridulaceae, Bruniaceae, Geissolomataceae, Grubbiaceae, Myrothamnaceae, and Hydrostachyaceae. The novelty of Thorne's concept can be appreciated when one examines other phylogenetic treatments: these families have been distributed to various orders in amazingly disparate ways by various phylogenists. Detailed review of these treatments is not appropriate at this point. What does seem pertinent is that this assemblage of families has considerable morphological and phytogeographical unity. Also worth mention is that Thorne's Pittosporales falls in sequence (under his superorder Rosiflorae) with Rosales, which also contains many families that show considerable radiation in the southern hemisphere.

Comparisons with wood anatomy of other families. In comparing wood of Geissolomataceae with that of other families, there are two opposed perils: utilization of the numerous primitive features of wood of this species to construe relationship to families and genera with equally

primitive secondary xylem; and rejection of any family with relatively specialized xylary features for comparison. The families generally considered primitive in dicotyledons (see Carlquist 1961 or 1975a for a resumé) can and do represent polyphyletic retention of antique modes of dicotyledonous wood structure under mesic conditions in which such woods are adaptive. However, if numerous and compelling features other than wood anatomy link Geissolomataceae with a given family, one can add—with due caution—the primitive features to the list. In this regard, Bruniaceae and Grubbiaceae are families pertinent for comparison. Although extended accounts of wood anatomy of those families are in preparation, I can cite wood anatomy of certain species—as well as those families in their entirety—in which xylary features match those of *Geissoloma*. In fact, a survey of wood slides of Bruniaceae and Grubbiaceae shows that *Geissoloma* has no features which cannot be matched in those families. Such characteristics include presence of wide multiseriate rays in addition to uniseriate rays; crystals of the type shown in Fig. 12 in ray cells; tendency toward predominance of upright ray cells except in central portions of multiseriate rays; ray cells, where thick, with bordered pits; and dark-staining deposits in ray cells. In addition, all features of *Geissoloma* wood applicable to evolutionary level are present in Bruniaceae and Grubbiaceae: scalariform perforation plates with narrow perforations and bordered bars; opposite to scalariform lateral-wall pitting on vessels; vessels angular in transection; tracheids with pit apertures the same length as border diameter; and same length as border diameter; and diffuse axial parenchyma. *Nebelia fragarioides* (Bruniaceae) and *Grubbia tomentosa* (Grubbiaceae) have woods which, in every feature, match wood of *Geissoloma* closely enough so that if one had only a wood slide, one could assign those species to Geissolomataceae. Other Bruniaceae and Grubbiaceae share most of the features named. These astonishing similarities, together with those of floral morphology, embryology, palynology, and phytogeography (one can find all three families growing together), are very persuasive. If one cares to look in broader areas of relationship, Pittosporaceae, Daphniphyllaceae, Roridulaceae, Hamamelidaceae, Cunoni-

aceae, and woody Saxifragaceae differ from *Geissoloma* in only a few of the features named, and could be considered related to Geissolomataceae, although not as closely as Bruniaceae and Grubbiaceae. Therefore, I feel that on the basis of the preliminary findings of wood anatomy, Thorne's (1968) placement of Geissolomataceae near Bruniaceae and Grubbiaceae is justified. Woods of Celastraceae, Thymelaeaceae, Oleaceae, Salvadoraceae, and the myrtalean families are clearly different.

Literature Cited

BAILLON, H. 1877. Histoire des Plantes. Vol. 6. L. Hatchette & Co. Paris.

CARLQUIST, S. 1961. Comparative Plant Anatomy. Holt, Rinehart & Winston. New York.

————. 1975a. Ecological Strategies of Xylem Evolution. University of California Press, Berkeley, Los Angeles, and London.

————. 1975b. Wood anatomy of Onagraceae. Ann. Missouri Bot. Gard. (In press).

CRONQUIST, A. 1968. The Evolution and Classification of Flowering Plants. Houghton Mifflin. Boston.

DAHLGREN, R., and V. S. RAO. 1969. A study of the family Geissolomataceae. Bot. Notiser 122: 207–227.

FAGERLIND, F., and A. DUNBAR. 1973. Some electron microscopical methods for solving wood anatomical problems. Bot. Notiser 126: 519–533.

HUTCHINSON, J. 1926. The Families of Flowering Plants. Vol. 1. Macmillan & Co. London.

————. 1959. The Families of Flowering Plants (ed. 2). Vol. 1. The Clarendon Press. Oxford.

————. 1967. The Genera of Flowering Plants. Dicotyledones. Vol. 2. The Clarendon Press. Oxford.

KUNTH, C. S. 1830. Über die Thymeleaceen und eine neue, ihnen verwandte Pflanzenfamilien, de Peneaceen. Linnaea 5: 667–678.

LINNAEUS, C. 1771. Mantissa plantarum altera. Holmiae.

METCALFE, C. R., and L. CHALK. 1950. Anatomy of the Dicotyledons. Vol. 2. The Clarendon Press. Oxford.

PHILLIPS, E. P. 1951. The Genera of South Africa Flowering Plants. (ed. 2). Botanical Survey of South Africa Pub. 25. Pretoria.

SUPRIAN, K. 1894. Beiträge zur Kenntnis der Thymeleaceae und Peneaceae. Bot. Jahrb. 18: 316–353.

THORNE, R. F. 1968. Synopsis of a putatively phylogenetic classification of the flowering plants. Aliso 6(4): 57–66.

VAN TIEGHEM, PH. 1893. Récherches sur la structure et les affinités des Thyméleacées et des Pénéacées. Ann. Scie. Nat., Bot., 17: 185–294.