

WOOD ANATOMY OF BYBLIDACEAE

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Byblidaceae, as recognized here, consists of two species endemic to Australia, *Byblis gigantea* and *B. liniflora*. No data on secondary xylem have hitherto been published, so a detailed description of qualitative and quantitative features is presented for *B. gigantea*; *B. liniflora* has very little secondary xylem. The wood of *B. gigantea* is unusual in having some narrow tracheid-like vessels with one or more small perforation plates. The majority of vessel elements have simple perforation plates, but scalariform perforation plates with one to three bars are frequent. All perforation plates are bordered. Tracheids have fully bordered pits; lignified ray cells have bordered pits. The simple perforation plates probably represent accelerated evolution of a structure adapted to marked seasonal fluctuation in water availability. However, the relatively primitive type of tracheids may be present because of lack of selective pressure for mechanical strength and because of the value of a conductive element resistant to development of air embolisms. Wood anatomy of *Byblis* is consistent with relationship to Roridulaceae as well as placement in orders variously recognized by phylogenists as Rosales and Pittosporales.

Introduction

The family Byblidaceae is regarded here in the strict sense, consisting only of one genus, *Byblis* Salisbury, with two species, *B. gigantea* Lindley of southwestern Australia and *B. liniflora* Salisbury of tropical northern portions of Australia. This treatment follows that of DIELS (1930). Of the two species, *B. liniflora* is a small herb with so little accumulation of secondary xylem that it has been disregarded in the present study. Plants of *B. gigantea* never attain a height exceeding 0.5 m, bear short branches near the base of the plant, and at best can be called moderately woody herbs. The main stem including cortex does not exceed approximately 1 cm in diameter. The few short branches result from survival of plants into a second or third year of growth; plants probably never exceed several years in longevity. The small amount of secondary xylem that accumulates even in the largest plants probably explains why neither SOLEREDER (1908) nor METCALFE and CHALK (1950) give information on secondary xylem for the family.

Byblis gigantea is characteristically found on white sand areas that are swampy in winter but dry in summer, and each year a proportion of the plants apparently succumbs to summer drought. The tendency for *B. gigantea* to be a rather short-lived woody herb—it could not be termed a shrub—may be related to its preference for establishment in recently burned or otherwise disturbed areas. If one searches for it in suitable white sand areas, one is not likely to find it except on burned areas, where it may occur in abundance. As growth on such an area recovers over a period of years, *B. gigantea* tends to disappear. ERICKSON (1968) gives a detailed taxonomic and distributional account of the genus. *Byblis* has attracted attention because of its allegedly insectivorous nature. This matter and other pertinent literature on the genus are reviewed by LLOYD (1942). He concludes that *Byblis* probably is not insectivorous, although BRUCE (1905) claimed posi-

tive experimental evidence and ERICKSON (1968) refers to the insectivorous habit without qualification.

With respect to wood anatomy, the marked change in water availability between winter and summer in *B. gigantea* habitats is of interest. In this respect, *Byblis* experiences a regime markedly unlike a genus often claimed to be closely allied, *Roridula*, the mesic ecology and mesomorphic wood anatomy of which have been detailed by CARLQUIST (1976).

Wood anatomy can yield only limited decisive information regarding systematic position of a group in the dicotyledons, but it tends to be more useful and reliable as an indicator of ecological preferences and phyletic level of specialization (CARLQUIST 1975). However, facts from wood anatomy can be cited both in probable negation of proposed relationships and, in some instances, in the indication of concordances between groups that can be cited as probably related because of additional features that suggest affinity. A discussion on the putative affinities of Byblidaceae and on the relevance of information from wood anatomy is given below.

Material and methods

Material collected in the field in 1967 (Carlquist 1052, RSA) was preserved in 50% formalin-acetic acid-alcohol. From the largest single plant available, a segment from the base was selected for sectioning. Sections 20 μ m thick were prepared by means of a sliding microtome and stained with a standard safranin-fast green combination. This stain combination proved helpful in discerning membranes in pits. From the same sample used for sectioning, macerations were prepared with Jeffrey's fluid and stained deeply with safranin. Quantitative and qualitative data were obtained, with averages based on 50 measures wherever possible. Maximal size of stems of *Byblis gigantea* (see above) is very limited, and reliability of quantitative data is probably lower than could be obtained in woody species because, in my experience, attainment of an adult or stable quantitative condition is not to be expected in very

small stems of an herbaceous nature. For this reason, as well as my past experiences and predictive tests on the use of statistical analysis of wood features, standard deviation and standard error were not computed. Roots of *B. gigantea* and both stems and roots on *B. liniflora* were deliberately omitted from this study because they would represent an essentially primary xylem pattern not truly comparable with secondary xylem.

Anatomical descriptions

Growth rings are evident by virtue of fluctuation in vessel diameter and by greater abundance of vessels at the beginning of growth rings (fig. 1) and are of an apparently annual nature. Vessels are mostly solitary, averaging 1.2 per group (where vessels could be identified in transections with certainty). Mean diameter of identifiable vessels is 38 μm , but is actually less because very narrow vessels could not be distinguished from tracheids in transection and were not included in measurements. Mean vessel-element length is 144 μm (fig. 2). Lateral-wall pitting of vessels is alternate (fig. 6). Perforation plates are mostly simple, but scalariform or multiperforate perforations with one to three bars are present on end walls in all sections also (figs. 4, 5). Some end-wall perforation plates appear as one or more bordered pits only slightly larger than lateral-wall pits (fig. 6). Some tracheid-like cells must be termed vessel elements because of the presence of one or more such small perforations. Perforation plates are all bordered, including bars (figs. 4-6). Perforation plates tend to be oriented quite obliquely; few approach a horizontal position. Simple perforation plates are often narrower than the diameter of the vessel on which they occur. Mean tracheid length is 221 μm . Pits on tracheids are fully bordered, with apertures narrowly elliptical and shorter than the diameter of the pit cavity. Wall thickness of tracheids averages 3.7 μm (fig. 3). Axial parenchyma is sparse, diffuse (fig. 3), and composed of files of approximately three cells as seen in radial section. Rays are mostly biseriate or triseriate (fig. 2); the multiseriate rays average 302 μm high. Uniseriate rays are less frequent, mostly two cells high, averaging 48 μm . Some primary rays, in the process of fragmentation as secondary growth proceeds, are present and are not included in the above descriptions. Ray cell walls are mostly apparently lignified, but a few have thin apparently nonlignified cell walls. Pits on the presumably lignified ray cells have narrow borders as observed in radial sections. All ray cells (primary rays excluded) are composed of erect cells, with very few square cells; no procumbent cells were observed. No crystals or amorphous deposits were observed.

The wood of *Byblis* is unusual in having fibriform cells with one or more inconspicuous perforations. These are somewhat reminiscent of the "fibriform" vessel elements reported in Passifloraceae by WOOD-

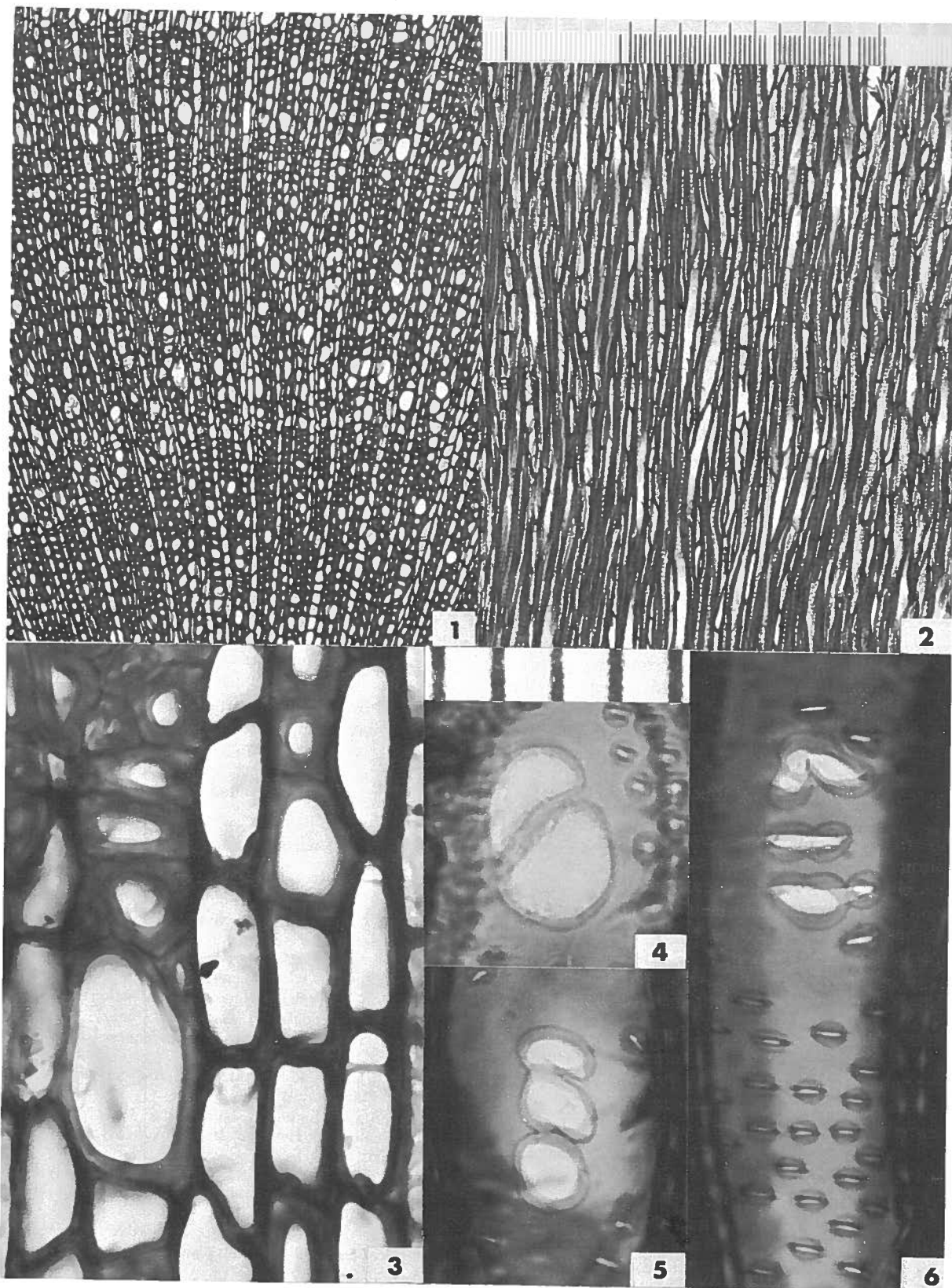
WORTH (1934, 1935). Perhaps the relatively limited amount of secondary growth is related to lowering of differentiation between tracheids and vessel elements. I do not believe that the wood of *Byblis* can be interpreted as having vascular tracheids. Vascular tracheids—a much misunderstood phenomenon—tend to occur in highly specialized woods—woods that would tend to have libriform fibers or, in the case of *Loricaria thuyoides* (CARLQUIST 1961b) or certain globose cacti (GIBSON 1973), no mechanical cells. Wood anatomists who have not studied groups in which vascular tracheids occur are often uncertain about the criteria by which vascular tracheids can be differentiated from true tracheids, criteria I have attempted to explain elsewhere (CARLQUIST 1961a, 1975). Because *Byblis* has some scalariform perforation plates and because its secondary xylem is generally rather similar to the rather primitive secondary xylem of *Roridula* (CARLQUIST 1976), vascular tracheids would not be expected. At present, vascular tracheids have been claimed only for highly specialized woods.

The nature of ray cells in *Byblis* is interesting because they are erect and only a very few are square; none is procumbent. This would constitute a ray type not included in the classification of KRIBS (1935), and it is not included in my (CARLQUIST 1961a) schematization of ray types because both uniseriate and multiseriate rays are present in the wood of *Byblis*. The presence of erect cells exclusively or predominantly characterizes some herbaceous or herblike dicotyledons (CARLQUIST 1962, 1969). I have suggested that lack of procumbent cells in such species may be related to the limited stem diameter, if procumbent cells tend to function in radial translocation of photosynthates in rays (CARLQUIST 1975, 1976). Presence of borders on the ray cells of *Byblis* is interesting; it may not be a primitive characteristic in all cases, as averred by KRIBS (1935). Bordered ray cells occur in some highly specialized dicotyledonous woods such as *Metrosideros* (SASTRAPADJA and LAMOUREUX 1969) and *Pentaphragma* (CARLQUIST 1975).

Systematic and ecological implications

Some early authors, such as BENTHAM and HOOKER (1865), included *Byblis* in Droseraceae, undoubtedly because of its allegedly insectivorous habit. In more recent works, *Byblis* has been excluded from Droseraceae and recognized as Byblidaceae. This seems justified because the majority of characteristics are unlike those of Droseraceae (for a discussion, see DIELS [1930]). Some authors have included *Roridula* in Byblidaceae (e.g., HUTCHINSON 1959; CRONQUIST 1968), while others retain only *Byblis* in the family (DIELS 1930; WETTSTEIN 1935; THORNE 1968; VANI-HARDEV 1972). I am following the latter treatment.

In all of the treatments in which Byblidaceae is recognized as a family, it is accorded what could be



FIGS. 1-6.—Wood sections of *Byblis gigantea* (Carlquist 1052, RSA). Fig. 1, Transverse section: growth rings are inconspicuous. Fig. 2, Tangential section: rays are composed of upright cells; most rays are biseriate. Fig. 3, Portion of transverse section: vessel at lower left; three tracheids in upper part of radial file toward right side; two axial parenchyma cells can be seen below the three tracheids. Figs. 4-6, End-wall perforation plates from radial sections: borders are visible on all perforations; fig. 4, a single bar is present; fig. 5, a perforation plate with two bars. Fig. 6, A perforation plate composed of pit-like perforations. Magnifications indicated by photographs of a stage micrometer enlarged at the same scale as applicable photographs: figs. 1, 2, scale above fig. 2 (finest divisions = 10 μ m); figs. 3-6, scale above fig. 4 (divisions = 10 μ m).

termed a rosoid or rosalean position, although various authors differ in the families they group with *Byblis*. A refinement of the rosoid grouping is represented by inclusion of *Byblis* within the order Pittosporales. HUTCHINSON (1959) recognizes within Pittosporales the families Pittosporaceae, Byblidaceae, and Tremandraceae; he also includes two families that probably should be excluded: Vivianiaceae and Stegnospermaceae. THORNE (1968) revised Pittosporales so as to include three suborders: Daphniphyllineae (Daphniphyllaceae), Pittosporineae (Pittosporaceae, Byblidaceae, Tremandraceae), and Brunineae (Roridulaceae, Bruniaceae, Geissolemataceae, Grubbiaceae, Hydrostachyaceae, and Myrothamnaceae). The Pittosporineae are Australian (with extensions by *Pittosporum* into the Pacific and Asia), whereas Brunineae are South African (with extensions into Madagascar). These placements are not entirely unprecedented. Byblidaceae follows Pittosporaceae and precedes Bruniaceae in the Englerian sequence in which DIELS's (1930) treatment appears. Byblidaceae also follows Pittosporaceae in WETTSTEIN's (1935) phylogeny and in BLACKALL's (1959) flora.

The wood anatomy of *Byblis* is consistent with a certain degree of relationship to Roridulaceae, despite the simplification of perforation plates in *Byblis*. That simplification would be expected in a plant of a habitat with strong seasonal fluctuation in water availability, for reasons discussed elsewhere (CARLQUIST 1975). However, woods with assemblages of features like those of *Byblis* may be found in other rosalean families, such as Saxifragaceae (METCALFE and CHALK 1950), and wood alone is not decisive in placement of Byblidaceae. A gen-

erally rosoid position does seem advisable on the basis of wood features, however.

Phyletic retention of tracheids, rather than evolutionary transition to mechanically stronger libriform fibers (often associated with vessels having simple perforation plates in dicotyledon woods), can be hypothesized for several reasons. The small plant size of *B. gigantea* minimizes selective value for mechanically strong cells. Tracheids are efficient conductively, particularly under conditions of water stress, because presence of membranes on pits prevents air embolisms, if they occur, from spreading throughout the xylem, whereas an air embolism in a vessel element disables an entire vertical series of vessel elements (see CARLQUIST [1975] for a discussion).

Western Australia is predominantly dry, and the only mesic portion, the extreme southwestern corner, appears to have been invaded by xeromorphic groups (CARLQUIST 1974). There might be a few exceptions to this. *Byblis* could well represent one such exception, and the presence of an appreciable number of vestigial scalariform perforation plates in its wood would be an indication. Western Australian species of *Hibbertia* have scalariform perforation plates, but the number of bars is drastically reduced in drier localities (unpublished data). Otherwise, the flora appears to consist of families and genera in which all species, as far as is known at present, have simple perforation plates characteristically.

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