

WOOD ANATOMY OF RORIDULACEAE: ECOLOGICAL AND PHYLOGENETIC IMPLICATIONS¹

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A B S T R A C T

Description of quantitative and qualitative features of root and stem wood of the two species of *Roridula*, endemics of Cape Province, Republic of South Africa, are presented because no data on secondary xylem have hitherto been published for these shrubs. Of the two species, *R. gorgonias* has wood appreciably more primitive in such respects as longer vessel elements with more numerous bars on the scalariform perforation plates. This is interpreted as correlated with the fact that *R. gorgonias* occupies maximally mesic habitats (*Sphagnum* covered covered montane seeps). *Roridula dentata* shows more specialized wood features, hypothesized to be related to greater fluctuations in water availability in its characteristic habitats. These patterns parallel ecological correlations obtained for dicotyledons as a whole. Lack of procumbent ray cells may relate to limited stem diameter in the genus if procumbent cells tend to function in radial translocation of photosynthates. Wood anatomy of *Roridula* is congruent with relationships alleged by various authors to the genus *Byblis*, and very similar secondary xylem features can be found in such "rosoid" families as Saxifragaceae (sensu lato), Hamamelidaceae, Bruniaceae, and Grubbiaceae. *Roridula* should be excluded from Droseraceae, and should probably not be placed next to Droseraceae in a phylogenetic system.

THE FAMILY Roridulaceae consists of two species, *Roridula dentata* Linnaeus and *R. gorgonias* Planchon. These are shrubs endemic to Cape Province, Republic of South Africa. Once they were thought to be insectivorous because of their viscid leaves and tentacle-like trichomes (see Bruce, 1907), but there is no evidence that insect protein is absorbed by leaves (Lloyd, 1942). At most, one might speculate that by the catching of insects on the viscid leaves, and by the ultimate fall of these leaves laden with insects to the ground, the nitrate content of the soils in which *Roridula* grows might be enhanced. The soils in which *Roridula* grows are derived from Table Mountain Sandstone, and have long been known to be highly acidic and low in nitrates (Marloth, 1925).

Both species can be said to grow in mesic pockets within the summer-dry mediterranean scrublands of Cape Province. *Roridula gorgonias* grows in seeps or marshy areas on montane slopes often cloudy in summertime. Colonies of this species were observed in the mountains above Hermanus (Carlquist 4960, RSA and other herbaria), where shrubs grow in thickets on *Sphagnum*-covered black soil. Occasional individuals of

Grubbia rosmarinifolia, also an excellent indicator of wet seeps, grow with *R. gorgonias*. *Roridula dentata* can be found on "vlakke" (flats) of the Kold Bokkeveld mountains, as at Boboskloof (Carlquist 4644, RSA and other herbaria). These sandy flats are clearly drier than the *R. gorgonias* localities in summer, but underground water is undoubtedly available from nearby streams that flow for most of the year. Thus both species of *Roridula* can be termed mesophytes, but *R. dentata* is a plant with some xeromorphic adaptations. This is, for example, suggested in the leaf anatomy. Leaves of *R. dentata* are smaller, more condensed in form, and have compact chlorenchyma with small intercellular spaces; contrasting conditions characterize leaves of *R. gorgonias* (Bruce, 1907). Because ecology proves to be closely related to wood anatomy in dicotyledons (Carlquist, 1975), the two species of *Roridula* prove suitable material for testing potential correlations.

Phylogenetically, various authors have hypothesized two placements for *Roridula*. The first of these includes *Roridula* in Droseraceae (Bentham and Hooker, 1865; Harvey, 1868; Harvey and Sonder, 1884; Phillips, 1951). This view is still current among South African botanists. The alleged insectivorous habit probably has been the overriding reason for inclusion of *Roridula* in Droseraceae by these authors. Because numerous features of floral anatomy, embryology, and wood anatomy differentiate *Roridula* from Droseraceae (sensu stricto), this placement should probably be abandoned. The second viewpoint on relation-

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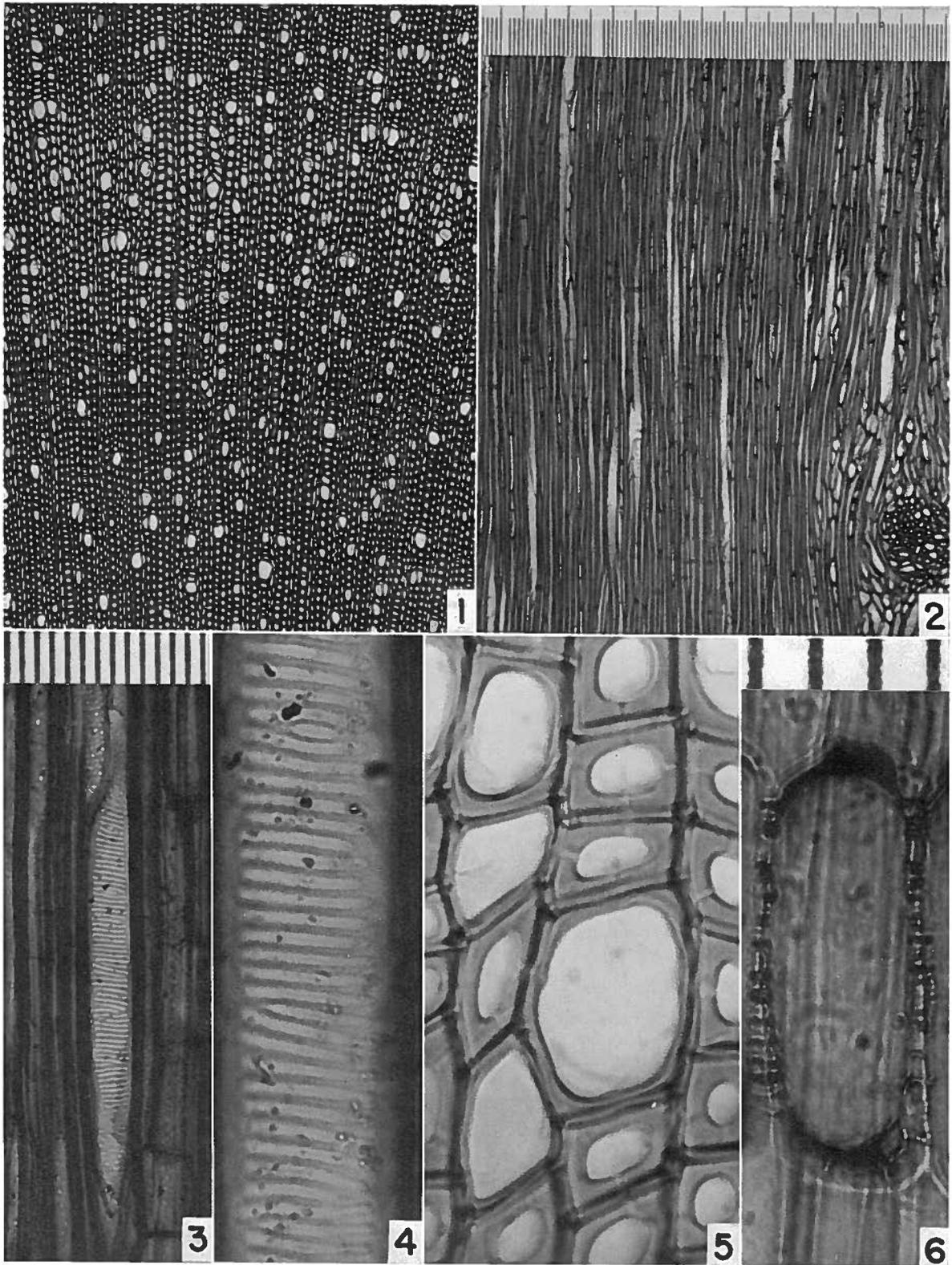


Fig. 1-6. *Roridula gorgonias*, Carlquist 4960 (RSA), stem wood sections. 1. Transection; growth rings are absent. 2. Tangential section; a primary ray in the process of fragmentation during secondary growth is at lower right. 3. Portion of radial section, showing an entire scalariform perforation plate. 4. A perforation plate from a radial section at higher magnification. 5. Portion of a transection: to the left, above and below the vessel ele-

ships of *Roridula* can be categorized as a "rosoid" hypothesis. In this connection, one must note that Bentham and Hooker (1865), although they included *Roridula* in Droseraceae, place Droseraceae among what may be termed rosoid families, so a sharp contrast between the two viewpoints cannot be made. Marloth (1925) and Diels (1930) place *Roridula* in its own family, Roridulaceae, and group it with such families as Bruniaceae, Hamamelidaceae, and Crassulaceae. This general treatment, in modification, has been followed by Hutchinson (1959), who includes *Roridula* with *Byblis* in Byblidaceae, and places Byblidaceae within an order, Pittosporales. Hutchinson's Pittosporales includes also Pittosporaceae, Tremandraceae, Stegnospermaceae, and Vivianiaceae. The latter two families should probably be excluded from Pittosporales. Wettstein (1935) included Roridulaceae in Rosales. Cronquist (1968) includes *Roridula* in Byblidaceae, a family which he places within Rosales. Thorne (1968), like Hutchinson, recognizes an order, Pittosporales, but with considerable modification. Thorne's Pittosporales falls into three suborders: Daphniphyllineae (Daphniphyllaceae), Pittosporineae (Pittosporaceae, Byblidaceae, and Tremandraceae), and Brunineae (Roridulaceae, Bruniaceae, Geissolomataceae, Grubbiaceae, Myrothamnaceae, and Hydrostachyaceae). Thus the treatments cited could all be said to favor a rosoid affinity for *Roridula*, with differing rosters of allied families. The data on wood anatomy are not sufficient to indicate whether *Roridula* and *Byblis* should each be segregated in monogeneric families, although I am inclined toward that segregation.

MATERIALS AND METHODS—Wood samples of both stem and root wood were collected from the largest specimens available of both species, and dried. Wood sections and macerations of both stems and roots were prepared according to the usual techniques and stained in safranin. Measurements were obtained for quantitative features, and means based on 50 measurements per feature. In the anatomical descriptions that follow, details apply to both stem and root wood unless otherwise stated.

ANATOMICAL DESCRIPTIONS—*Roridula gorgonias* (Carlquist 4960, RSA and other herbaria): Growth rings indistinct or absent (Fig. 1). Vessels tending to be angular in transectional view (Fig. 5), averaging 82.9 per sq. mm of transection. Vessels mostly solitary, averaging 1.1 per

group. Average vessel diameter 38.8 μm in stems. Average vessel-element length 978 μm in stems, 987 μm in roots. Perforation plates long scalariform (Fig. 3) with inconspicuous borders on bars (Fig. 4), averaging 48.6 bars per plate (range: 37–83) in stems, 45.4 (range: 11–102) in roots. Bars only rarely forked (Fig. 4) or otherwise deviating from a purely scalariform pattern. Lateral walls of vessels with scalariform or opposite, but much more frequently alternate pitting. Tracheids moderately thick walled (Fig. 5), averaging 3.8 μm in wall thickness. Pits of tracheids fully bordered, apertures elliptical. Tracheids averaging 935 μm long in stems, 958 μm in roots. Walls of vessels and tracheids tending to appear somewhat gelatinous by virtue of shrinkage patterns in a few places. Axial parenchyma sparse, diffuse (Fig. 5), consisting of strands of about three very long cells as seen in radial section. Rays mostly uniseriate (Fig. 2), biseriate rays very scarce (a few multiseriate rays present by virtue of breaking up of primary rays (Fig. 2, lower right)). Uniseriate rays averaging 203 μm in height, biseriate rays 572 μm , in stem wood. Ray cells exclusively upright. A few ray cells thick walled (Fig. 6), some of these walls with bordered pits, but most ray cells with thin lignified walls bearing simple pits. Gummy deposits present in some ray cells (Fig. 6). No crystals observed.

Roridula dentata (Carlquist 4644, RSA and other herbaria): growth rings clearly marked (Fig. 7). Vessels somewhat angular in transection, less angular than those of *R. gorgonias*, averaging 129 per sq. mm of transection in stem wood. Vessels mostly solitary, averaging 1.1 per group in stem wood, 1.02 per group in root wood. Average vessel diameter 41.0 μm in stem wood, 55.4 μm in root wood. Average vessel-element length 759 μm in stems, 767 μm in roots. Perforation plates scalariform, averaging 10.4 bars (range: 3–23) per plate in stems (Fig. 10, 11, 13), 11.9 bars (range: 6–17) in roots, but alternative types of perforation plates about equally abundant in the materials studied. Most abundant of the alternative types consist of a meshwork with rhomboidal perforations (Fig. 12). A few perforation plates scalariform, but with bars running in more than one direction (Fig. 10, left), or with alternately thin and thick bars (Fig. 14). Bars markedly (Fig. 13) or vestigially bordered. Lateral-wall pitting of vessels scalariform, opposite, or alternate, mostly alternate. Tracheids moderately thick walled, averaging 3.7 μm in wall thickness. Pits of tracheids fully bordered, apertures elliptical

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ment (center) are axial parenchyma cells. 6. Ray cell from radial section, showing thick walls. Magnifications shown by photograph of stage micrometer enlarged at same scale as applicable photographs. Fig. 1, 2, scale above Fig. 2 (finest divisions = 10 μm). Fig. 3, scale above Fig. 3 (divisions = 10 μm). Fig. 4–6, scale above Fig. 6 (divisions = 10 μm).

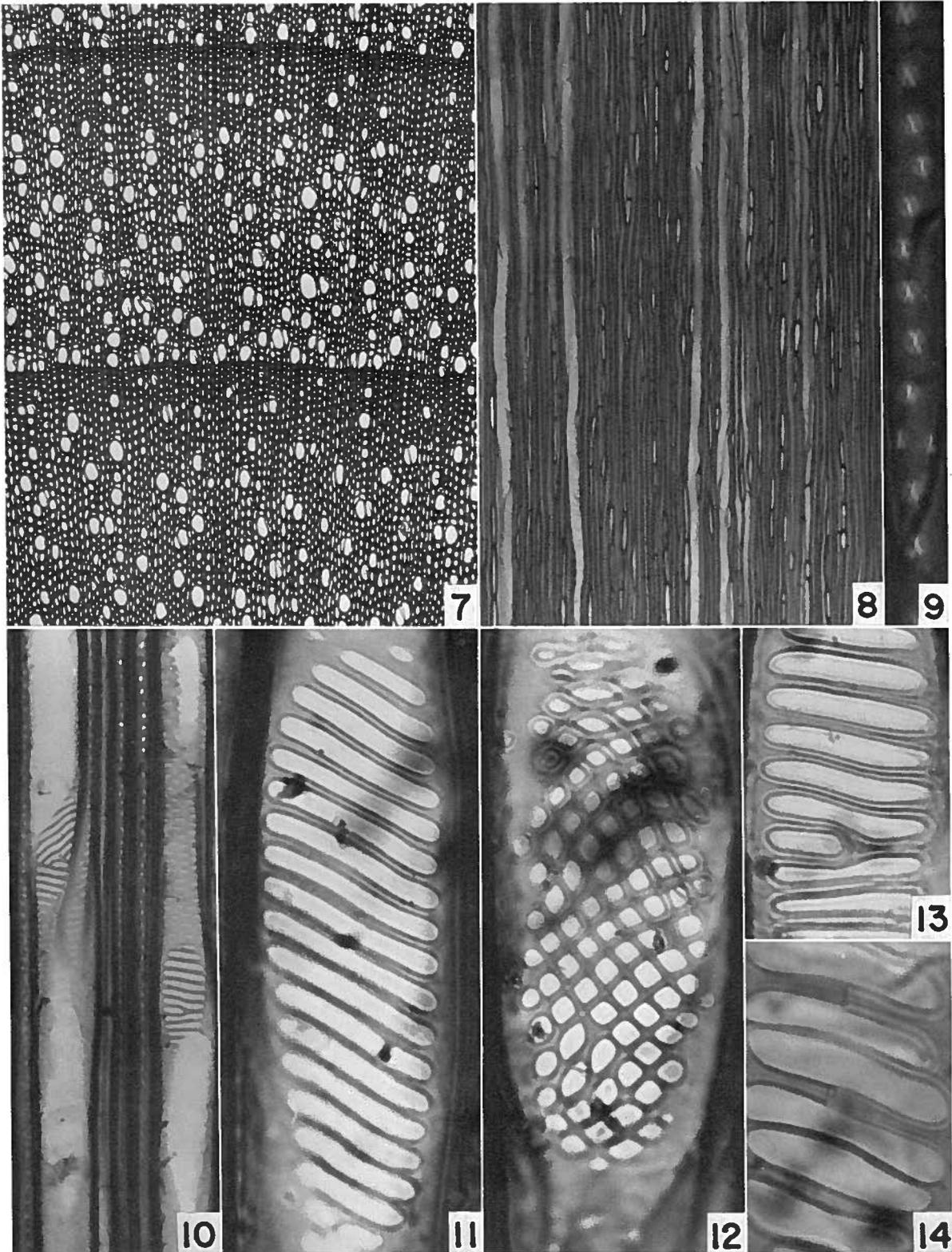


Fig. 7-14. *Roridula dentata*, Carlquist 4644 (RSA), stem wood sections. 7. Transection: growth rings conspicuous. 8. Tangential section: all rays are uniseriate. 9. Tracheid from radial section, showing borders on pits. 10. Portion of radial section, showing portions of perforation plates in two vessels.—Fig. 11-14. Perforation plates from radial sections. 11. Typical perforation plate, entire length. 12. Perforation plate with meshwork-like pat-

(Fig. 9). Tracheids averaging $904\mu\text{m}$ long in stems, $917\mu\text{m}$ in roots. Walls of vessels and tracheids tending to appear somewhat gelatinous by virtue of shrinkage patterns in a few places. Axial parenchyma sparse, diffuse, consisting of strands of about three very long cells as seen in radial section (Fig. 10, to right of vessel at left). Rays exclusively uniseriate or nearly so (Fig. 8). Rays averaging $186\mu\text{m}$ in height in stems, $128\mu\text{m}$ in roots. Ray cells consisting wholly of upright cells. Ray cell walls thin to moderately thick walled, walls lignified. Gummy deposits present in small quantities in some ray cells. No crystals observed.

Solereder (1908) mentions only a very few xylem features for *Roridula*, evidently based on primary xylem of twig material only. Solereder is incorrect in describing pits of imperforate tracheary elements as simple; perhaps he examined perimedullary fibers. Metcalfe and Chalk (1950) added no new data. The descriptions given above are thus the first accounts of secondary xylem in *Roridula*.

SIGNIFICANCE OF WOOD ANATOMY OF RORIDULA—The two species have notably primitive wood features according to generally accepted criteria (see Carlquist, 1975, for a discussion). Especially notable in this regard are the long vessel elements with scalariform perforation plates consisting of numerous bordered bars, and the presence of tracheids with fully bordered pits. The ratio between average tracheid length and average vessel-element length is low in the genus as a whole (*R. gorgonias*: stems, 1.04; roots, 1.03; *R. dentata*: stems, 1.19; roots, 1.20). According to criteria explained elsewhere (Carlquist, 1975), lowness of this ratio is a remarkably accurate index to primitiveness in woods of dicotyledons. Features of *Roridula* wood that would, according to traditional criteria, be regarded as specialized include the lack of multiseriate rays and the predominance of alternate lateral-wall pitting on vessels.

Relationships—One would expect Roridulaceae to have been derived from an ancestral stock with a preponderance of primitive wood features. The near absence of multiseriate rays might be used to construe relationship to families in which some species have few multiseriate rays compared to uniseriate rays and in which at least some genera and species have an abundance of primitive wood features like those of *Roridula*. Such families would include some rosoid families such as Saxi-

fragaceae, particularly woody species), Cunoniaceae, Hamamelidaceae, Bruniaceae, Grubbiaceae, and Daphniphyllaceae (Metcalfe and Chalk, 1950, and original observations). *Byblis* has perforation plates much simplified in comparison with those of *Roridula*, but all other features of the secondary xylem are like those of *Roridula*, and specialization of the perforation plates does not rule out a relationship (Carlquist, unpublished data). The highly specialized primary xylem of Droseraceae (Bierhorst and Zamora, 1965), as well as other xylary features, would tend to support exclusion of *Roridula* from Droseraceae.

Ecological correlations—The nature of the habitat preferences of the two *Roridula* species, respectively, shows a remarkable degree of correlation with wood anatomy. *Roridula dentata*, compared to *R. gorgonias*, has shorter vessel elements with fewer bars per perforation plate, and a higher tracheid to vessel-element length ratio. These can all be considered indicative of both phyletic specialization and adaptation to a climatic regime featuring periods of increased (although probably not severe) water stress, in accordance with the hypotheses developed earlier (Carlquist, 1975). The *Sphagnum*-covered montane seeps where *R. gorgonias* grows represent the most mesic terrestrial environment possible in Cape Province, South Africa, so the existence there of a plant with a very primitive and "inefficient" conductive system is to be expected. By "inefficient" I connote relatively slow conductive rates and relatively low fluctuations in tension in xylem water columns. In addition to the specializations for *R. dentata* listed above, other xylem adaptations to somewhat drier habitats include ring porosity and a greater number of vessels per unit transection. That the differences between the species are as marked as they are is interesting, for the appreciable departure from a very primitive conducting system by one of two species within a genus suggests strong selective pressure. This parallels the fact that only an extremely small number of dicotyledons retain xylem highly primitive in most respects, a fact which I have adduced to demonstrate that survival of most dicotyledonous stocks has been accompanied by adaptations in xylem structure to sites of fluctuating water availability (Carlquist, 1975). However, *R. dentata* is not a true xerophyte, and could still be classified as mesophytic. As with Bruniaceae, Geissolomataceae, Grubbiaceae, and Myrothamnaceae, both species of *Roridula* probably represent mesopomorphic relicts that have survived in wet montane habitats of South Africa.

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tern. 13. Portion of perforation plate showing borders on bars. 14. Portion of perforation plate with alternately wide and narrow bars. Fig. 7, 8, magnification according to scale above Fig. 2. Fig. 10, magnification according to scale above Fig. 3. Fig. 9, 11–14, magnification according to scale above Fig. 6.

The presence of alternate pits on lateral vessel walls in both species of *Roridula* may seem a specialized feature not expected in a wood with so many primitive characteristics. However, alternate pits on lateral walls of vessels characterize numerous woods exceptionally primitive in most respects (e.g., *Illicium*), and scalariform lateral wall pitting is apparently present in primitive dicotyledonous wood only rarely and for reasons not completely understood yet.

The almost exclusively uniseriate rays are unusual in that they consist wholly of upright (erect) cells, and thus would not fall in any of the categories proposed by Kribs (1935). Absence of procumbent cells in rays of *Roridula* may indicate systematic relationships. However, functional correlates may be cited. Individual plants of *Roridula* are shrubs of relatively finite size. If erect ray cells represent a mechanism for vertical conduction of photosynthates in wood (Carlquist, 1975), lack of procumbent cells—which would tend to function more in radial than vertical translocation—in relatively small stems (maximal diameter of wood in *Roridula* probably does not exceed 5 cm) is understandable.

Vessel elements in roots of the *Roridula* species, respectively, are longer than those of stems. Although only scattered data are available on such comparisons in other groups, this pattern appears to occur in dicotyledons as a whole, and has been interpreted as related to lower tensions in water columns of roots as compared to stems (Carlquist, 1975).

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