Proteaceae

Proteaceae Juss., Gen. Pl.: 78 (1789).

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Perennial shrubs or trees; plants usually completely bisexual but sometimes dioecious or andromonoecious; clusters of short lateral roots ('proteoid roots') often produced. Leaves alternate or less commonly opposite or whorled, simple or pinnately to bipinnately or rarely palmately compound, entire or pinnately to tripinnately or rarely dichotomously dissected, often with marginal teeth, estipulate, petiolate or sessile; venation pinnate or occasionally parallel or palmate, or reduced to a single vein; stomates brachyparacytic or rarely laterocytic (in *Bellendena*); trichomes usually 3-celled, occasionally also glandular, rarely plants glabrous. Inflorescence simple or compound, axillary or terminal, with flowers borne laterally either singly or in pairs, rarely also with a terminal flower, racemose or raceme-like or paniculate or condensed. Flowers usually bisexual, actinomorphic or zygomorphic, hypogynous; perianth of 4 (3 in *Grevillea donaldiana* and 5 in a minority of flowers of *Eidothea hardeniana*) valvate, free or variously united tepals; stamens (3)4(5), opposite tepals, usually all fertile or sometimes 1 or more sterile; filaments partly or wholly adnate to tepals or rarely free; anthers basifixed, usually bilocular and tetrasporangiate but occasionally the lateral anthers unilocular and bisporangiate; 1–4 hypogynous glands usually present, scale-like or fleshy, free or fused into a crescentic or annular nectary; gynoecium of 1 carpel (sometimes 2, free carpels in *Grevillea banksii*); ovary superior, sessile or stipitate, with variously positioned marginal placentae; style usually distinct, often with apex functioning as a pollen presenter; stigma small or sometimes relatively large and plate-like, terminal or subterminal; ovules 1 to many, anatropous to orthotropous, bitegmic, crassinucellate. Fruit dehiscent or indehiscent, a follicle, achene, drupe or drupe-like. Seeds 1 to many, sometimes winged; endosperm present or absent at maturity.

A family comprising 80 genera and about 1,700 species, distributed mainly in the southern hemisphere, where it is almost completely restricted to Gondwanic continental blocks and fragments (Fig. 130). It is most diverse in Australia, followed by southern Africa, South America, New Caledonia, New Guinea, Malesia, South and East Asia, tropical Africa, Central America, Madagascar, New Zealand, Fiji, southern India, Sri Lanka, Vanuatu and Micronesia.

Nota bene: Statements as to apomorphy and plesiomorphy of character states are made in the context of published phylogenetic classifications and analyses, the topology of the tree shown in Fig. 131, and knowledge that the immediate outgroups to Proteaceae are, successively, Platanaceae and Nelumbonaceae.

Vegetative Morphology. Proteaceae are woody plants, ranging from almost herbaceous subshrubs to trees over 40 m tall, but mostly shrubs or small trees. They are evergreen, although alpine populations of the temperate South American *Embothrium coccineum* are facultatively deciduous. The family is probably ancestrally arborescent (Johnson and Briggs 1975). All Proteaceae, except subfam. Persoonioideae and Symphionematoideae (Lee 1978), produce proteoid roots (Dinkelaker et al. 1995 and references therein), small lateral roots of determinate growth which form dense clusters on otherwise 'ordinary' secondary roots close to the soil surface, under conditions of low phosphate availability. They are produced in seasonal flushes and remain physiologically active for only 2–3 months. They enhance nutrient uptake from the soil because their narrow diameter and densely set root hairs greatly increase the root surface area, and they exude organic acids, particularly citrate and malate, into the rhizosphere in intense bursts lasting 2–3 days, resulting in the mobilization of phosphate and possibly other nutrients. Proteoid roots probably evolved in the family's stem lineage and were secondarily lost in both Persoonioideae and Symphionematoideae.

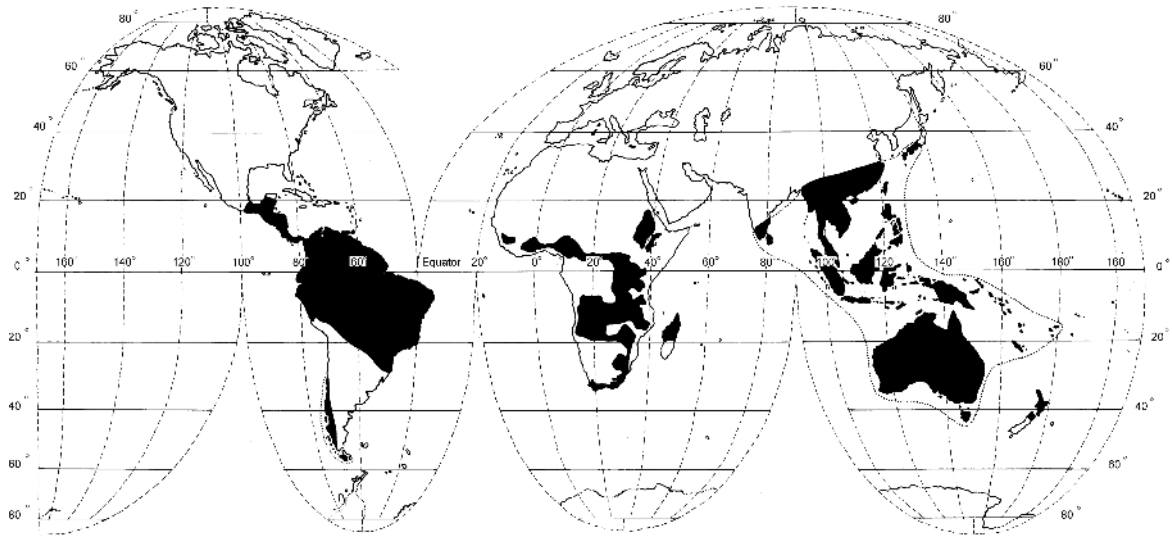

Fig. 130. Distribution of Proteaceae. (Drawn by L. Elkan)

They are not homologous with the cluster roots of Casuarinaceae, Fabaceae and Myricaceae, contrary to the assertion of Dinkelaker et al. (1995).

Leaf morphology is very variable in Proteaceae but most species have leathery leaves with brochidodromous venation. They may be compound, deeply dissected or lobed, up to a fourth order of dissection, toothed, lobed and toothed, or simple and entire. The degree to which leaf shape varies between different stages in development is a striking feature of many rainforest taxa in particular. Some species (e.g. *Alloxylon flammeum*) produce trilobed leaves as the first pair of seedling leaves, followed by a phase of simple, unlobed seedling leaves, then lobed juvenile leaves and finally, simple, unlobed leaves as adults (stages as f_0 to f_3 respectively; Johnson and Briggs 1975). In some taxa, leaves in the f_2 stage are pinnatisect (e.g. *Alloxylon pinnatum*) or compound (e.g. *Carnarvonia araliifolia*, Fig. 137B), rather than lobed. Ontogenetic variation in leaf toothing is also often overlaid over this sequence, with entire adult leaves often following toothed seedling and juvenile leaves (e.g. *Roupala montana*, Fig. 138A–D). In many other taxa, the f_0 stage is absent (e.g. *Placospermum coriaceum*, Fig. 133A, B, *Roupala montana*, Fig. 138A–D), the f_0 and f_1 stages are absent (e.g. *Stenocarpus sinuatus*) or the f_3 stage is absent (e.g. *Carnarvonia araliifolia*, Fig. 137). Other taxa produce only simple, entire leaves (e.g. *Alloxylon wickhamii*, *Persoonia*, Fig. 134, *Protea*, Fig. 136) or lobed leaves (e.g. *Bellendena montana*, Fig. 132) or pinnatisect leaves (e.g. *Symphionema montana*, Fig. 135, *Grevillea robusta*, Fig. 139). Variation in leaf form sometimes provides synapomorphies above generic level (e.g. tribe Persoonieae versus *Placospermum*, see taxonomic treatment and Weston 1994) but is more often informative at lower taxonomic levels.

The ability to resprout from a lignotuber and/or epicormic shoots following major disturbances such as fire varies even between very closely related species, but is of great ecological significance. Lignotuberous species are known in many genera of fire-prone environments, especially in Australia and Africa but also in America and New Caledonia. Sprouting from epicormic shoots is much rarer and is restricted to shrubs and trees with thick, protective bark.

Vegetative Anatomy. Proteaceous wood usually has small to medium-sized vessels, with simple perforation plates, associated with abundant axial parenchyma in curved, adaxially concave, tangential bands which span from ray to ray. The rays are commonly of two distinct kinds, large multiseriate rays and small uniseriate ones (hence, the common name 'silky oak', by comparison with the wood of *Quercus*). Libriform fibres with simple or indistinctly bordered pits form the ground mass of the wood. However, a minority of taxa have scattered large vessels, or some multiple perforation plates, or sparse parenchyma, or abaxially concave tangential bands of parenchyma, or apotra-