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## Balanopaceae

Balanopaceae Benth. in Benth. & Hook., Gen. Pl. 3: 341 (1880), nom. cons. ('Balanopseae').

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Dioecious small to tall evergreen trees; older bark with white, circular, prominent lenticels; hairs simple, unicellular. Leaves basically alternate, dimorphic, shoots with minute scale leaves proximally and foliage leaves distally, the latter sometimes subverticillate and restricted to the shoot tip; foliage leaves petiolate, with prominently to obscurely toothed margins; stipules a pair of minute teeth at the base of the petiole. Inflorescences usually subtended by scale leaves, less commonly by foliage leaves, in staminate plants a catkin; staminate flowers short-pedicellate and axillary to scales on the catkin axis, subtended by one or several bracts or vestigial perianth lobes, these often fewer than stamens; stamens (1-)3-6(-12), filaments short, anthers dehiscing laterally; a vestigial pistil sometimes present; pistillate plants with solitary subsessile or short-pedicellate flowers in the axils of scale leaves, with numerous densely crowded, spirally arranged deltoid "cupular" bracts subtending the naked ovary, or a terminal flower surrounded by further lateral flowers also subtended by cupular bracts; staminodes 0; gynoecium syncarpous, 2(3)-carpellate; ovary 2(3)-locular, the locules imperfectly septate at anthesis but fully septate in fruit; ovules 2 per carpel, collateral, borne axile-basally, bitegmic and intermediate between apotropous and epitropous; stylodia connate at the base and once or twice bifurcate to form ribbon-like lobes stigmatic on the adaxial surface. Fruit a yellow, orange or brown drupe with rather thin fleshy mesocarp, subtended at the base by a cup of numerous imbricate, crescent bracts; pyrenes 2-3; endosperm fleshy during fruit maturation, but crushed at maturity, and forming only a thin layer around the embryo; embryo large, green, straight.  $n = 20$  (21).

A single genus comprising nine spp., distributed across "old lands" in the S Pacific (N Queensland, New Caledonia, New Hebrides

and Fiji), and bound to forest and scrub communities; on New Caledonia growing on both serpentine and gneiss.

**VEGETATIVE MORPHOLOGY AND ANATOMY.** According to the study by Carlquist (1980), the leaves are dimorphic: prior to the fully formed leaves, scale leaves appear on each shoot. In some species (confined to New Caledonia), the foliage leaves form subverticillate clusters at the tips of the shoots only. The leaf margins are toothed to various degrees. The teeth are several cell layers thick, and the cells are filled with a dark content which is thought to be tannins. Both the scale leaves and the foliage leaves are each provided with a pair of lateral, dark-coloured stipules. Hairs are non-glandular, unicellular and early vanishing from the leaves, but persistent in the involucre bracts, which subtend the solitary female flower and fruit and form the "cupule".

*Balanops* has trilacunar nodes. For leaf anatomy, see Carlquist (1980); a notable anatomical feature is the scattered occurrence of cristarque cells in the leaves. The involucre bracts contain brachysclereids. The wood has no growth rings. The vessel elements are relatively long and possess scalariform or reticulate-scalariform perforation plates. The wood parenchyma is diffuse, and the rays are multiseriate and uniseriate, with a predominance of erect cells.

**REPRODUCTIVE STRUCTURES.** In contrast to earlier reports to the contrary, Sutter and Endress (2003) have shown that the ovary of *Balanops* is completely septate, that the ovules are weakly crassinucellate, bitegmic with a multilayered inner integument (in contrast to all previous indications), and intermediate between apotropous and epitropous, and that an obturator is not present.



Fig. 2. Balanopaceae. *Balanops sparsiflora*. A Branchlet with pistillate flowers. B Pistillate flowers enclosed by cupular bracts. C Pistillate flower. D Same, transversally sectioned. (Takhtajan 1980)

EMBRYOLOGY. Unknown.

POLLEN MORPHOLOGY. The pollen is 3–5-colpate, with colpi that show no sign of an endoaperture. The exine sculpturing consists of small spinules. The exine structure is tectate-granular to columellate. The tectum is traversed by microperforations (Erdtman 1952; Zavada and Dilcher 1986).

POLLINATION. Probably by wind.

FRUIT AND SEED. The pericarp consists mostly of thin-walled parenchyma cells, but below the epidermis two or three layers of thick-walled brachysclereids have been observed (Guillaumin 1925; Carlquist 1980). Dispersal is probably by birds (Carlquist 1980).

PHYTOCHEMISTRY. Carlquist (1980) and Sutter and Endress (2003) mention idioblasts containing dark-coloured substances, supposedly tannins, but it is unknown of which type these are. The occurrence of trivial triterpenes gives no clue for affinities (Hegnauer 1964).

AFFINITIES. The affinities of *Balanops* were dubious to early workers such as Engler (1897) and have remained so for a long time. After discussing all taxa that had been suggested as candidates for a relationship to *Balanops*, Carlquist (1980) focused on Hamamelidaceae, Myricaceae, Pittosporales sensu Thorne, and particularly Daphniphyllaceae. Takhtajan (1997) combined Balanopaceae and Daphniphyllaceae in monotypic orders in a superorder Daphniphyllanae, but in sequence analyses of the *rbcL* gene (Litt and Chase 1999; Savolainen, Fay et al. 2000; Chase et al. 2002) Balanopaceae appeared within the Malpighiales in a clade in which they are sister to Dichapetalaceae/Trigoniaceae plus Chrysobalanaceae/Euphroniaceae. In contrast, Sutter and Endress (2003) and Matthews and Endress (2008) argued that features of *Balanops* such as the unisexual flowers, the lack of a perianth, the repeatedly bifurcate stylodia and the weakly crassinucellar ovules would fit much better with a euphorbialean than the chrysobalanoid relationship. However, the multi-gene analyses of Wurdack and Davis (2009), Soltis et al. (2011) and Xi et al. (2012) provide strong support for the earlier molecular findings.

Only one genus:

*Balanops* Baill.

Fig. 2

*Balanops* Baill., *Adansonia* 10: 117 (1871); Carlquist, *Allertonia* 2: 191–246 (1980), rev.  
*Trilocularia* Schlechter (1906).

Description as for family. Nine species, for distribution see above.

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