
Bonnetiaceae

Bonnetiaceae (Bartl.) L. Beauvis. ex Nakai in Bull. Tokyo Sci. Mus. 22:25 (1948).

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More or less subpachycaulous small to medium-sized trees and shrubs. Leaves convolute, spiral, crowded towards apex of branches, with close, ascending lateral veins, margins serrulate, initially setulose, estipulate; petiole short or 0. Flowers single, or more or less cymose inflorescences; pedicels with 2 prophylls or several bracts; flowers bisexual, cyclic; sepals 5, unequal, free, quincuncial; petals 5, contorted, free; stamens numerous; filaments slender, free, or basally connate into 5 antepetalous bundles; anthers short, basifixed; fasciculate + or 0; ovary 3(–5)-locular, with numerous orderly arranged ovules on biseriate axile placentae; stylodia free or united into a branched or simple style; stigmas papillate. Fruits septicidal capsules with a persistent central column; seeds with scanty endosperm; embryo straight.

Three genera and about 40 species, northern South America, West Indies, Southeast Asia, West Malesia, Moluccas and New Guinea.

VEGETATIVE MORPHOLOGY AND ANATOMY. Bonnetiaceae are stout-stemmed shrubs or usually small trees with few branches. The smallest species, *Bonnetia ahogadoi*, is notable for its trailing and rooting inflorescence axis which also acts as a stolon (Fig. 10), whereas *Ploiarium alterniflorum*, a small, stilt-rooted tree, may grow up to 25 m high on swampy peat soil in Johore (Corner 1978). The terminal bud usually lacks scales, axillary buds are small, and branching appears to be sylleptic, although in *B. ahogadoi* growth of the main axis appears to be rhythmic (Steyermark 1984) and there are scales at the base of flagelliform inflorescence shoots. The leaves remain rolled up as the bud elongates, and are more or less sessile and usually have a distinct but not very prominent midrib. The plants are completely glabrous, except for tiny colleters found in the leaf axils. The leaf margin is usually minutely serrulate and only rarely entire but, in the juvenile stage, it is always provided with minute setae which fall off during leaf expansion

but persist in the tiny, revolute leaves of *Bonnetia roraimae*. *Archytaea* and *Ploiarium* have vascularised, disciform structures borne immediately inside the margin and on the lower surface of the blade and in its upper one-third. Venation is often eucamptodromous, sometimes more or less brochidodromous or parallelodromous.

The phellogen in the stem is surficial in origin, that in the root is initiated 3 or 4 layers deep in the cortex. There are brachysclereids in the stem cortex, a sheath of fibres in the pericyclic position, and groups of fibres in the secondary phloem (see also van Tieghem 1885). The heartwood is dark reddish brown and heavy. Vessel elements are solitary, of medium length, and their perforations are simple/transverse; uniseriate rays are of upright cells, and multiseriates (2–4 cells wide) consist of procumbent cells with uniseriate extensions of upright cells; axial parenchyma is scanty paratracheal, and fibres are mostly thick-walled. Xylem parenchyma forms an adaxial cap on the vessels.

Nodes are trilacunar in *Bonnetia*, unilacunar in *Archytaea* and *Ploiarium*. The separate traces are visible in leaf scars although, in taxa such as *Bonnetia ahogadoi*, traces are more or less confluent in the outer part of the cortex. *Ploiarium* has an arcuate midrib bundle, that of other taxa is more complex, the tissue on the adaxial side in particular being irregularly arranged. Vascular bundles are embedded, and the marginal setae of *Archytaea* and *Ploiarium*, but not those of *Bonnetia*, are associated with vascular tissue.

Stomata are anomocytic and an adaxial hypodermis is sometimes present. The leaf anatomy of *Bonnetia* is remarkable: the epidermis is often mucilaginous and its cells bulge and intrude between the mesophyll cells; foliar sclereids are widespread in the mesophyll; and the leaf midrib and all veins including the terminal veinlets are surrounded by an endodermis of thin-walled cells provided with Casparian strips (Maguire 1972; Dickison and Weitzman 1996; Weitzman and Stevens 1997).

INFLORESCENCE AND FLOWERS. Inflorescences are lateral, and several species appear to have axillary flowers. However, these are probably reduced inflorescences, and the “pedicels” bear 2–several bracts along their length, sometimes very close to the calyx. The sepals of *Bonnetia*, and perhaps also *Ploiarium*, are terminated by setae very like those found on the leaf margins. The petals are predominantly white or pink. Whether or not the androecium of *Bonnetia* is fasciculate needs study; fascicles have been reported (e.g. Steyermark 1984) but their existence – at least, as evident in later bud or flower – has been questioned (Kobuski 1948; PFS, pers. obs.). It is not known if the fasciculates of *Ploiarium* secrete nectar; otherwise, there are no reports of nectar from the family (Dickison and Weitzman 1998).

POLLEN MORPHOLOGY. Pollen is 28 to almost 60 μm long, oblate-spheroidal, tricolporate with wide colpi and circular ora. Sometimes, as in *B. lancifolia*, the colpi are fused at the poles, leaving a triangular polar space. There are costal colpi in *Archytaea* and *Ploiarium*, and all taxa have costal pori. The nexine, 0.5–4 μm thick, is thicker than the sexine, which is finely reticulate (Erdtman 1952; Maguire 1972; Steyermark 1984; Sagado-Laboriau and Villar de Seoane 1992).

SEED. The seeds are quite small, and Corner (1976) suggested that the seed coat of *Ploiarium* is probably endotestal, although its development has not been studied. Exotestal cells are thin-walled and polygonal, endotestal cells are usually isodiametric, low, and with sinuous anticlinal walls, lignification is extensive and there are numerous narrow plasmodesmata. *Ploiarium alternifolium* has rather elongated endotestal cells, and the anticlinal walls of those of *Archytaea* are almost straight. There is a thin, persistent layer of endoperm surrounding the straight embryo. Although the cotyledons are generally small, those of *Bonnetia* range from 1/2–1/6 the length of the embryo. Germination is epigeal (*Ploiarium*).

PHYTOCHEMISTRY. Bonnetiaceae are rich in xanthenes with various substitution patterns, and bixanthenes and anthraquinone xanthenes have been reported from *Ploiarium* (Kubitzki et al. 1978; Bennett et al. 1990). Xanthenes are also richly diversified in Clusiaceae and Hypericaceae (Bennett and Lee 1989).

FAMILY CIRCUMSCRIPTION AND AFFINITIES. When the exudate-producing genus *Neotatea* and the anther gland-bearing genera around *Kielmeyera* and *Caraipa* are removed from Bonnetiaceae, as suggested by Weitzman and Stevens (1997), the family becomes very homogeneous. Although in the past members of the family have been included in the “intermediate” zone between Theaceae and Clusiaceae/Hypericaceae, the former are now in Ericales, and possession of xanthenes, floral morphology, testa anatomy, etc., all link Bonnetiaceae with Clusiaceae/Hypericaceae. The combination of characters of wood anatomical characters presented above sets Bonnetiaceae apart from Theaceae, with which Baretta-Kuipers (1976) compared them, and also Guttiferae and Hypericaceae.

Gene sequence analyses by Savolainen, Fay et al. (2000) and Gustafsson et al. (2002) confirm the close relationship of Bonnetiaceae with Clusiaceae/Hypericaceae. The inclusion of *Ploiarium* in Malvales (Savolainen, Fay et al. 2000) was probably due to a mistaken identification, since i.a. the distinctive seed coat anatomy of *Archytaea* is quite unlike that of Malvales. Elatinaceae have also often been considered as possibly related to Bonnetiaceae, agreeing in testa anatomy and a number of other features, but molecular data place them sister to Malpighiaceae (Davis and Chase 2004); whether or not that family is close to Bonnetiaceae, etc., is unclear.

DISTRIBUTION AND HABITATS. The two closely related, small genera *Archytaea* and *Ploiarium* are disjunct between Southeast Asia/Malesia and northern South America, whereas *Bonnetia* is restricted to continental South America, with one species on Cuba.

Archytaea prefers open habitats, often by creeks, always on nutrient-poor soil, ranging from lowland to mid-altitudes. *Bonnetia* is most speciose in the Guayana Highland and its surroundings, where 27 species are found, all but one (*B. paniculata*) of which are endemic to this region. Most of them have only a limited altitudinal range, with the majority preferring the mesothermic/submicrothermic belt (1,200–2,700 m; Huber 1988), but *Bonnetia crassa* spans a belt of 2,000 m. With increasing altitude, the bonnetias tend to be of lower stature. *Bonnetia ahogadoi* is a low shrublet growing at localized sites on peat in rock depressions of the Chimatá Massif in Venezuela