
Penaeaceae

Penaeaceae Guillemin, Dict. Class. Hist. Nat. 13:171 (1823).

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Shrubs or shrublets (often ericoid), varying from procumbent to ascending or erect, sympodially branching at least in the adult stage; young branches glabrous, generally with 4 ridges ending in tooth- or peg-like processes on each side of the leaf bases. Leaves decussate, simple, entire (irregularly denticulate in *Sonderothamnus*), glabrous, linear to orbicular (subterete in *Brachysiphon microphyllus*), acuminate to retuse, sessile or shortly petiolate, more or less coriaceous and sclerophyllous; stipules rudimentary, more or less colleter-like. Inflorescences highly variable, indeterminate or determinate; terminal flowers preceded by two or more pairs of decussate bracts, the lateral flowers usually by transversal prophylls. Flowers sessile or pedicellate, bisexual, actinomorphic, 4-merous, obhapplostemonous, perigynous, apetalous; sepals free, petaloid, triangular to ovate, sometimes conspicuously carnosose and reflexed at anthesis, simple-valvate or reduplicate-valvate (valvate with reflexed edges), persistent (together with hypanthium), inserted on the rim of a 5–45 mm long, campanulate or broadly to narrowly cylindrical hypanthium; colour of hypanthium and calyx varying from white to yellow, pink, crimson or red; stamens as many as and alternating with sepals, free, inserted on the rim of the hypanthium, sometimes incurved in bud, basifixed, introrse, with longitudinal dehiscence; anthers bithecate, tetrasporangiate, with an expanded connective, sometimes versatile; thecae parallel or sometimes at an angle to each other; disc structures lacking but nectar secretion by epithelial and trichomatous glands; pistil 4-carpellate, syncarpous, superior, 4-locular with a single, terete, quadrangular or 4-winged style; stigma terminal, capitate, and more or less 4-lobed or the stigmatic areas subapical and restricted to the angles formed by 4 sterile, commissural lobes or wings; locules with 2 or 4 ovules; when 2, ovules inserted more or less basally

and ascending; when 4, ovules insertion axile, 2 ascending and 2 pendant; or all 4 inserted more or less basally and ascending; ovules anatropous, bitegmic, crassinucellate. Fruit a loculicidal, smooth capsule; seeds ovoid, slightly compressed, dark brown to almost black when mature, with a glossy surface and a funicular, white elaiosome.

A family with seven genera and 23 species, endemic to the southern and south-western parts of the Cape Province of South Africa.

VEGETATIVE MORPHOLOGY. All species in this family are woody, evergreen perennials ranging from small, procumbent, much-branched shrublets to tall, erect, sparingly branched shrubs. The main stem is often thickened at its very base, sometimes forming a root-stock (ligno-tuber), as in *Brachysiphon acutus*. Branches are glabrous and have often distinct, paired ridges ending in short tips on each side of the leaf base. The leaves are opposite-decussate and often imbricate. Older branches are mostly leaf-less below, bearing numerous leaf-scars. The leaves are generally coriaceous, flat or longitudinally ridged, sometimes with thickened margins and more or less keeled abaxially. The leaf apex ranges from retuse to acuminate, bearing a tanniniferous gland (areola) in *Sonderothamnus* and sometimes in *Saltera* (Dahlgren 1968). On the leaf surface, only the midveins are distinct, sometimes poorly so, and only from the abaxial surface. The venation pattern is generally brochidodromous (Dickie and Gasson 1999). Stomata are anomocytic and the leaves are hypostomatous, amphistomatous, or sometimes intermediate. Epicuticular wax and hairs are usually absent or sparse. Stipules are minute, each divided into a row of subulate or hair-like multicellular, often reddish-brown, secretory structures (colleter-like) located in the leaf axil (Weberling 1963).

VEGETATIVE ANATOMY. As in most Myrtales, Penaeaceae have internal phloem (bicollateral bun-

¹ Largely based on the work of the late Rolf Dahlgren.

dles) and vested pits. In most wood anatomical features reviewed by van Vliet and Baas (1984), Penaeaceae stand out as rather unspecialized, compared to other members of Myrtales (Dahlgren and Van Wyk 1988). According to Carlquist and Debuhr (1977), vessels are mostly solitary and relatively uniform in the family. Vessel-elements are not notably thick-walled and have simple, bordered perforation-plates. Exceptionally wide borders were observed on perforation-plates in the roots of *Saltera sarcocolla*. Lateral walls facing other vessels or tracheids bear alternate pits; when facing rays, the pits are likewise alternate or occasionally opposite. Pit vesturing is rather conspicuous in some species such as *Brachysiphon acutus*, less so in others, such as *Penaea cneorum*. Tracheids in the form of imperforate elements with pit apertures, which are fully bordered, are common in Penaeaceae. The only exception seems to be *Endonema lateriflora*, in which the pit apertures are slightly longer than the diameter of the pit cavity. These imperforate elements would therefore qualify as fibre-tracheids. Uniseriate rays predominate over multiseriate rays in Penaeaceae as a whole. In stems, multiseriate rays are rarely more than three cells in width, and biseriate rays are by far more common than multiseriate ones, which is well in accordance with what is known from other myrtalean families. In most species, there is a predominance of upright over procumbent cells. Axial parenchyma is scanty and diffuse in distribution in the family. In all examined species, axial parenchyma strands are composed of two to four, mostly three, cells. Growth rings are generally indistinct in Penaeaceae. Crystals in the wood are relatively rare in the family. The most notable ones are found in *Brachysiphon acutus* where a few axial parenchyma cells are subdivided into a row of at least ten cuboidal, crystal-bearing cells, each of which contains numerous crystals. These crystal-liferous strands are wider than, but about as long as the tracheids. Dark-staining, amorphous deposits are present in all examined species. These may be infrequent, as in *Stylapterus fruticosus*, or abundant, as in the root-stock of *Saltera sarcocolla*. Such deposits are primarily found in the ray cells and the axial parenchyma, but in some cases spread into the vessels and even into the tracheids. The nature of these deposits has to date not been identified.

The periderm is formed by outer layers of the pericycle and is distinctly stratified (Supprian 1894), thick-walled and lignified. van Tieghem

(1893) found isodiametric, sclerotic parenchyma cells in the pith and cortex of *Penaea acutifolia*.

Leaf anatomical characters are variable and homoplasious in Penaeaceae (Dahlgren 1968; Dickie and Gasson 1999). Epidermal cells are of similar size and shape on both surfaces, mostly more or less as tall as broad. A hypodermis is absent and the mesophyll is bifacial or isobilateral; the palisade is one- or two-layered. Veins are embedded, i.e. surrounded by parenchymatous bundle sheaths. The midrib bundle is circular or slightly flattened, and surrounded by thick-walled parenchyma and often by collenchyma. Along the leaf margin, the cuticle is relatively thick and epidermal cells tend to be somewhat papillate. Druses (crystal-clusters) are found frequently in subepidermal layers and in the mesophyll (Keating 1984). Idioblasts, in the form of branched, filiform sclereids and/or branched tracheoidal cells, are common (see also Rao 1965).

INFLORESCENCES. Inflorescences vary considerably in Penaeaceae (Dahlgren 1967a, b, c, 1968, 1971). Weberling (1988) considered a thyrsoid (a thyse with terminal flower), as present in *Sonderothamnus petraeus* and *S. speciosus*, to be the basic pattern. In the majority of the taxa, the cymose, lateral paracladia (triads) are reduced to their terminal flower. The thyrsoid is thus converted to a stachyoid as, for instance, in *Saltera sarcocolla*. The inflorescences of *Brachysiphon rupestris*, *B. mundii* and *B. microphyllus* have a terminal flower whereas *B. fucatus* and *B. acutus* have indeterminate spikes, in which the apex ends in some scale-like leaves or as a dry tip respectively. In *Penaea*, the inflorescence is most often spicate. A terminal flower is, however, not uncommon in *P. mucronata*, *P. cneorum* and *P. acutifolia*. *P. dahlgrenii* is described to have a complex synflorescence, in which a terminal flower is always present (Rourke and McDonald 1989). In *Stylapterus*, the inflorescence is usually a spike-like raceme with a degenerated, dry tip. However, a terminal flower is often present in *S. fruticosus* and *S. ericifolius*. In *Glischrocolla*, the inflorescence is a compact panicle or raceme which mostly bears a terminal flower, but this may drop at an early stage. A special case in the family is the genus *Endonema*. In both species, the flowers are borne laterally on young branches which continue vegetative growth, and each flower is subtended by two or three pairs of decussate bracts.

Floral bracts are generally similar to, but often somewhat larger than foliage leaves. Prophylls