Phyllonomaceae

Phyllonomaceae Small in Britt., N. Amer. Fl. 22(1): 2 (1905).
Dulongiaceae J.G. Agardh (1858), nom. illeg.

V. Bittrich

Terrestrial or rarely epiphytic shrubs or small trees, completely glabrous except for the stipules. Leaves alternate, petiolate, simple, acuminate, with entire or serrate or dentate margin; stipules small, with glandular hairs on the adaxial surface, caducous. Flowers small, bisexual, green, in epiphyllous inflorescences, actinomorphic, (4)5-merous. Sepals free or very slightly connate at base, persistent; petals free, valvate, late caducous to persistent; stamens free, alternating with the petals, persistent; anthers bilobed, dehiscing by lateral slits, pollen 3-colporate; flat nectary present on top of the ovary; ovary inferior, 2(3)-carpellate, syncarpous, unilocular with protruding parietal placentae; ovules 4–14, described as bitegmic but probably unitegmic, tenuinucellate; style bifid (trifid) or free to the base, recurved, stigmas small, terete. Fruit a small 3–10-seeded berry. Seeds small, with rugose or tuberculate testa, exarillate, endosperm fleshy, containing aleuron and oil; embryo straight, very small.

A Neotropical family with a single genus of four species.

Vegetative Morphology. Most information can be found in Mori and Kallunki (1977). The Phyllonomaceae are small trees (rarely up to 15 m tall) or shrubs, often with drooping young branches. Leaves are spirally arranged, the petiole is canaliculate, the blade elliptic to narrowly ovate (or rarely obovate) with an acuminate to long acuminate tip, sometimes with a constriction between blade and acumen. The margin is variously serrate or dentate, and in some species it varies from entire to serrate in the same population or even on the same branch. The 2 stipules are small, caducous, with numerous glandular hairs on the adaxial surface (Dickinson and Sattler 1974) and enclose the unexpanded sylleptic axillary shoot. The leaves remain folded until maturity, protecting the young inflorescence inserted adaxially on the leaf blade. The lower leaves of a shoot can be sterile, all others are fertile. The inflorescence is inserted between the acumen and the middle of the leaf blade.

Vegetative Anatomy. Most data are found in the study of Dickinson and Sattler (1974) on *Phyllonoma integerrima* and in Metcalfe and Chalk (1950). The vascular bundles form an ectophloic siphonostele, and the vessels have scalariform perforations. The pericycle has a ring of fibres. Cork develops superficially. Nodal anatomy is unilacunar, giving off one trace to the leaf and two to the axillary bud, but no traces to the stipules. The leaf midrib up to the insertion of the inflorescence has a ring-like vascular bundle that may be discontinuous laterally. The bundle is enclosed by a fibre sheath with extensions to the epidermis.

Inflorescence Structure and Flower structure. The inflorescences are fascicled, sometimes pseudoumbellate, the bracts fimbriate, sometimes stipulate (Fig. 54). Stork (1956) described the inflorescences as cymose. Dickinson and Sattler (1974) and Mori and Kallunki (1977) observed considerable variation in the branching pattern. In *P. ruscifolia*, branching is highly irregular, with bracts and flowers not always closely associated, and its inflorescences were classified as irregular monochasial cymes by Mori and Kallunki (1977). In the three other species the inflorescence appears to be a cluster of one to four unbranched racemes, with rather broad bracts which enclose the bases of the pedicels. Detailed anatomical investigations of one of these species, *P. tenuidens*, however, revealed cymose branching of the

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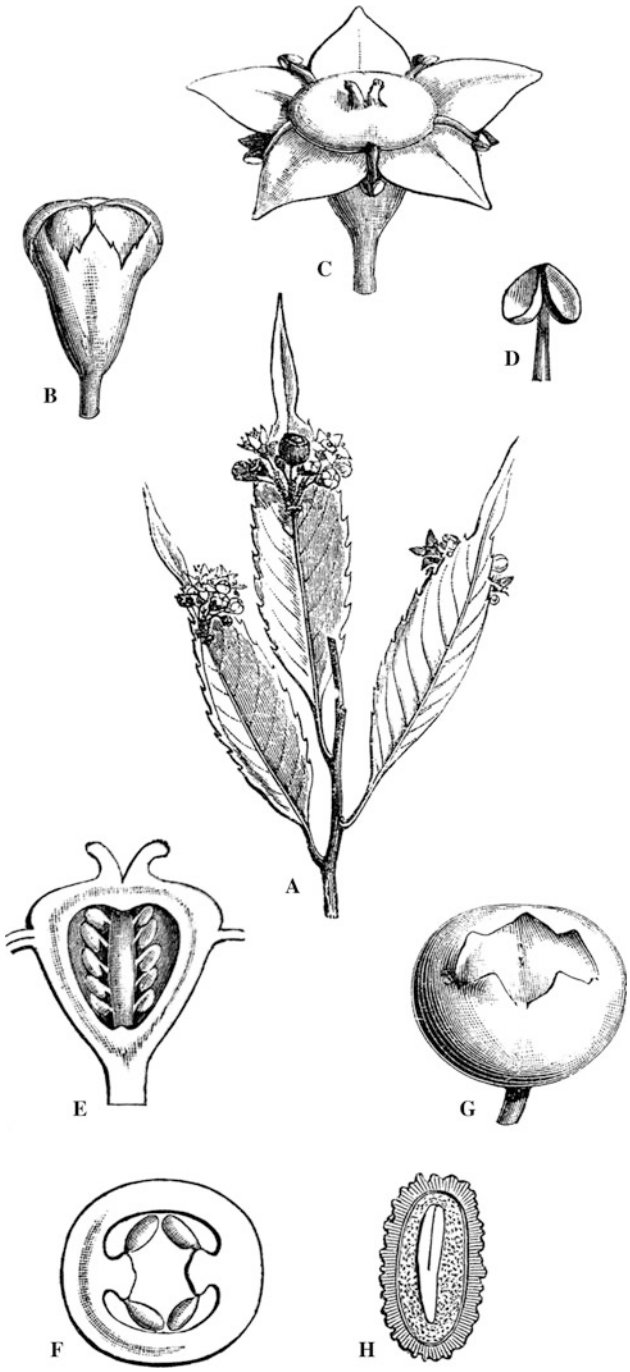

Fig. 54. Phyllonomaceae. **A–H** *Phyllonoma laticuspis*. **A** Flowering branch. **B** Flower bud. **C** Open flower. **D** Anther. **E** Ovary in longitudinal section. **F** Ovary in cross section. **G** Fruit. **H** Seed in longitudinal section. (Engler 1891, modified)

inflorescence resulting in a cincinnus, suggesting that the whole genus is characterized by monochasia (Tobe 2014) as assumed by Stork (1956). The unusual epiphyllous initiation of the inflorescences was studied in detail by Dickinson and Sattler (1974). These authors concluded that inflorescence development is truly epiphyllous as the leaves can neither be interpreted as modified branches nor do they show any evidence for "congenital" fusion with the inflorescence. Weberling (1981) maintained that the data would not exclude the possibility of recaulescence, and Weber (2004, p. 28) supported this view stating: "[. . .] the inflorescence primordium arises as a low, flat meristem extending from the leaf axil upwards. Only the distal part develops into a large meristematic head which later differentiates into bracts and flower primordia". Weber (2004) also emphasized that the epiphyllous inflorescences of *Phyllonoma* and *Helwingia* cannot be regarded as completely different, and that those of *Phyllonoma* only represent a more advanced form.

The bisexual, actinomorphic, greenish flowers show little interspecific differences (Mori and Kallunki 1977). They are small, measuring about 2–4 mm in diameter. The pedicels lack bracteoles. The sepals are free, triangular, with small multicellular glands on the margins (Tobe 2013), persistent, valvate or slightly quincuncially imbricate in bud, and the odd sepal is in an abaxial position. The petals are free, valvate in bud and spreading or reflexed at anthesis. The alternipetalous stamens are always shorter than the petals. They are first erect and become reflexed later. The globose bilobed anthers open by lateral slits. The gynoecium is syncarpous, inferior, and composed of 2(3) carpels in transversal position, with a short bifid (trifid) terminal style (or styles free to the base) and small terete stigmas. There are up to 14 horizontal campylotropous ovules originating from the protruding parietal placentae. An epigynous disk nectary with nectarostomata covers most of the ovary roof (Tobe 2013).

Embryology. Only few observations were reported by Mauritzon (1933). According to him,

the nucellus is of a transitional type, tenuinucellate but with the formation of a parietal cell, a situation today normally called weakly crassinucellar. Mauritzon also reported only one integument, while Krach (1976) considered 2 integuments as more probable (see below).

Pollen Morphology. Pollen is prolate or oblate-spheroidal, 3-colporate. The tectum is complete, the exine surface is microspinulose, granulose or smooth (Hideux and Ferguson 1976).

Karyology. Unknown.

Fruit and Seed. The fruit is a small globose or subglobose, 3–10-seeded berry. The seeds are small (up to 2.8 mm long), straight or slightly curved, their surface rugose when dry; an aril is lacking. Seed anatomy was studied in detail by Krach (1976). He described the testa as bitegmic, but with reservations as he did not observe a cuticle between the postulated integuments. Families closely related to Phyllonomaceae (cf. Soltis et al. 2011, see below) are characterized by having unitegmic ovules. According to Krach (1976), the "outer integument" is composed of several layers, with cell size diminishing continuously from the outer to the innermost layer; the "inner integument" is 2-layered. The rather large cells of the outer epidermis of the "outer integument" have thick cellulose walls and contain mucilage. The cells of the inner epidermis of the "inner integument" are filled with mucilage and tannins. The endosperm has unpitted cell walls of hemicelluloses, the cells contain aleuron and fatty oils. The embryo is straight and very small.

Dispersal. The small berries are probably bird-dispersed.

Reproductive Systems. The small nectariferous flowers suggest pollination by small insects, but observations are lacking. Nothing is known about breeding systems in the family.

Phytochemistry. Aluminium accumulation was demonstrated in four species (Hegnauer 1973).

Affinities. The family was formerly often included in the Saxifragaceae s.l. Takhtajan (1997) included it in the Hydrangeales and suggested a closer relationship with Escalloniaceae, despite pollen characters which differ from those of that family (Hideux and Ferguson 1976). Krach (1976) suggested that seed anatomical characters would point to a relationship with *Ribes* (Grossulariaceae), and Cronquist (1981) included *Phyllonoma* in the Grossulariaceae. In the APG classification (1998), the family is included in the Aquifoliales. A study of the "eudicots" (Savolainen et al. 2000) based on *rbcL* sequence data showed Phyllonomaceae and the monogeneric Helwingiaceae as sister taxa, both together forming the sister group to Aquifoliaceae. *Helwingia* Willd., formerly often included in Cornaceae or Araliaceae, occurs in Asia and is noteworthy for having, at least superficially, quite similar epiphyllous inflorescences as *Phyllonoma*, as already noted by de Candolle (1890) and studied in more detail by Dickinson and Sattler (1975) and Weber (2004). *Helwingia* species are dioecious shrubs with stipulate, alternate and serrate or dentate leaves, perianth uniseriate with 3–5, valvate, green petals, a 3–5-loculed ovary with an epigynous disk, and globose drupaceous fruits. In the angiosperm phylogeny of Soltis et al. (2011), based on sequence data of 17 genes, Helwingiaceae and Phyllonomaceae are sister taxa with 99 % BS support and Aquifoliaceae sister to these two families with BS 100 %. A clade formed of Cardiopteridaceae and Stemonuraceae is sister to the clade of the three families and all five families comprise the order Aquifoliales.

Distribution and Habitats. Species of *Phyllonoma* occur from Mexico to Peru and Bolivia in the understorey of mountain cloud forests.

Only one genus:

Phyllonoma Schultes Fig. 54

Phyllonoma Schultes in Roem. & Schultes, Syst. Veg. 6: xx (1820); Mori & Kallunki, Brittonia 29: 69–84 (1977), rev.
Dulongia Kunth (1824), nom. illeg.

Characters as for family. About four species, montane rain forests from Mexico to Bolivia.

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