321. MARCGRAVIA UMBELLATA

Marcgraviaceae

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Summary. *Marcgravia umbellata* (Marcgraviaceae), a native of the Lesser Antilles, is illustrated; its history, relationships, distribution, ecology and cultural requirements are discussed and a full description of the species is provided.

It is long overdue to include for the first time in this journal a member of the rather small (c. 120 spp.) but structurally and functionally very interesting, and by no means fully known, family Marcgraviaceae. This neotropical plant group, which ranges in its distribution from the tropic of cancer southwards to Peru, Bolivia, and south-eastern Brazil, has its nearest relatives in the tea family (Theaceae) and comprises mostly terrestrial and epiphytic lianas. Less commonly the plants are found as scrambling shrubs and treelets.

The species depicted here, *Marcgravia umbellata*, was the first to be described in modern botanical literature and hence is the type species of the largest genus of the family. It was named in *Species Plantarum* by Linnaeus (1753: 503) who referred to Charles Plumier's *Nova Plantarum Americanarum Genera* (1703: 7, pl. 29), which was published before the accepted starting point for plant names. Plumier described and illustrated a *Marcgravia scandens fructu radiatim posito*, but referred only to separate flowers and fruits. Since Linnaeus also described the leaf and inflorescence it seems that he had additional sources for his descriptions. In the relevant Linnean herbaria no appropriate material has been found (C. Jarvis, in litt.). So where did Linnaeus acquire this information? Plumier made the drawings himself, and the originals are kept in the Muséum d'Histoire Naturelle in Paris (Stafleu & Cowan, 1983). I have studied the relevant plate (Vol. 2: t.118) of *Marcgravia umbellata* and there the details that Linnaeus described are shown, but they were not included in Plumier's account (i.e. one inflorescence in bud and one in flower, two in fruit, and foliage characters). However, as far as we know (cf. Urban, 1920: 31, Polhill & Stearn, 1976: 324, Stafleu & Cowan, 1983: 301), Linnaeus never saw the Paris set. Later, 508 plates were copied by Claude Aubriet in 1733 and sent to Herman Boerhaave in Leiden, The Netherlands. This set became known as the *Codex Boerhaavianus* and was later acquired by Johannes Burman.

He edited plates of this *Codex* as Plumier *Plantarum Americanarum Fasciculus* . . . (1755–1760). This work contains a very instructive drawing of a flowering branch of *Marcgravia umbellata* (pl. 173, fig. 1) which was published in March 1758, after Linnaeus' *Species Plantarum*.

While Linnaeus worked in Holland in 1735–1738 for George Clifford, a botanically interested Dutch banker, he is said to have studied the *Codex Boerhaavianus* which is today housed in the University Library of Groningen. Unfortunately, I have not seen this plate but it should provide the solution to the riddle, as to how Linnaeus was able to describe perfectly the structure of the inflorescences which he had probably never seen as actual plant specimens.

According to the history of discovery and exploration of the New World, West Indian material (namely from Martinique) was the first to reach Europe. Unfortunately Linnaeus himself (1762) cited Browne (1756) and Sloane (1696), who gave the first ever reliable reference to a *Marcgravia*, under his *M. umbellata*. These references, however, are based on specimens from Jamaica, and refer to *M. brownei* belonging to another subgenus. So, Linnaeus himself laid the foundations for a long lasting confusion in the delimitation of the West Indian taxa. Mostly, the material was named *M. umbellata*, which became the 'most widely known' species of the genus although it is found only on the mountainous Lesser Antilles such as Saba, St Kitts, Montserrat, Guadeloupe, Dominica, Martinique, St Lucia, St Vincent, and Grenada. Even today cultivated plants are often labelled with this name, but do not always represent this species. The plant illustrated here by Helen Greenop grows in the Princess of Wales Conservatory and is truly the species in question.

Marcgravia umbellata shows, like all other members of the genus, a heterophylly similar to the one we know from the European ivy (*Hedera helix*). The small-leaved vegetative branches develop small rootlets and climb up tree trunks. Later, lateral branches become pendulous and develop larger, differently shaped leaves. The latter have glands on the lower surface, often in a specific pattern, which secrete a sweet liquid (at least at early developmental stages), and hence represent extrafloral nectaries. This feature is characteristic of all members of the family, but the other genera do not display heterophylly. I have observed activity involving nectar secretion only at the shoot-tips of a *Norantea guianensis* in Singapore Botanical

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Garden (cultivated outside its natural range) where this sweetish liquid was being collected by ants. I assume this to be a kind of symbiosis where the ants protect the still soft, developing leaves from predatory enemies. Mature leaves of Marcgraviaceae are often rich in stone-cells (sclereids). Of course, these phenomena of animal–plant interactions must be studied thoroughly in their natural habitats.

Finally, the shoots form umbel-like inflorescences at their apices. These pseudo-umbels are in fact very strongly contracted racemes, with the basal flowers normally developed and the apical ones remaining sterile; but the bracteoles of the sterile buds grow immensely, fuse with the petiole, and form a tubular nectary. Like the other leaves of the generative phase in *Marcgravia* these bracteoles also have hypophyllous glands. Here, in these pitcher-shaped nectaries, a sweet liquid collects and fills them, attracting animals. The petals are fused together to form a calyptrate cap which is shed at anthesis from the multistaminate flower. It was these structural peculiarities of the floral parts that initially attracted the attention of naturalists. Belt (1874) was the first to report hummingbirds visiting *Marcgravia nepenthoides* in Nicaragua, and Bryant (1905) observed hummingbirds attracted by the nectaries of a *Marcgravia umbellata* on Dominica. Soon the inflorescence of *Marcgravia* became a classical example of adaptation to bird-pollination. Taken their structure, this seems quite logical: the hummingbirds, while hovering and probing with their beaks into the nectaries, dust their wings or foreheads with the pollen of the fertile flowers above and in that way cross-pollinate the flowers.

It is strange that only very few *Marcgravia* species have brightly coloured floral parts (e.g. yellow, orange, red) which is usually associated with the syndrome of ornithophily (bird-pollination). The majority of species (including *M. umbellata*) have greenish-brown nectaries, pedicels and corolla caps. Only the stamens form a contrast with their whitish-yellow colours. Additionally, observations in greenhouses revealed that anthesis starts in the evening and often lasts only one night (Dressler, pers. obs. of *M. umbellata* and *M. polyantha*). By the morning hours the stamens have already been shed. This leads to the assumption that these species are adapted rather to night-active pollinators like bats. In the meantime some sporadic field observations have been carried out which seem to corroborate this theory. Sazima & Sazima (1980) published an

article (with photo!) on bat-pollination of *M. comosa* (syn. *M. myriostigma*) in Brazil and in Costa Rica phyllostomid bats and also oppossums were observed visiting the flowers of several *Marcgravia* species (Tschapka, pers. comm., 1997). Bailey (1922) had already expressed his doubts about the exclusive ornithophily and obligatory cross-pollination of *Marcgravia*. He had found a species in the then British Guyana to be night-flowering and with a strong self-pollinating tendency, and another species was observed, which (although flowering during daytime) was strongly self-pollinated, shedding most of the stamens together with the corolla cap.

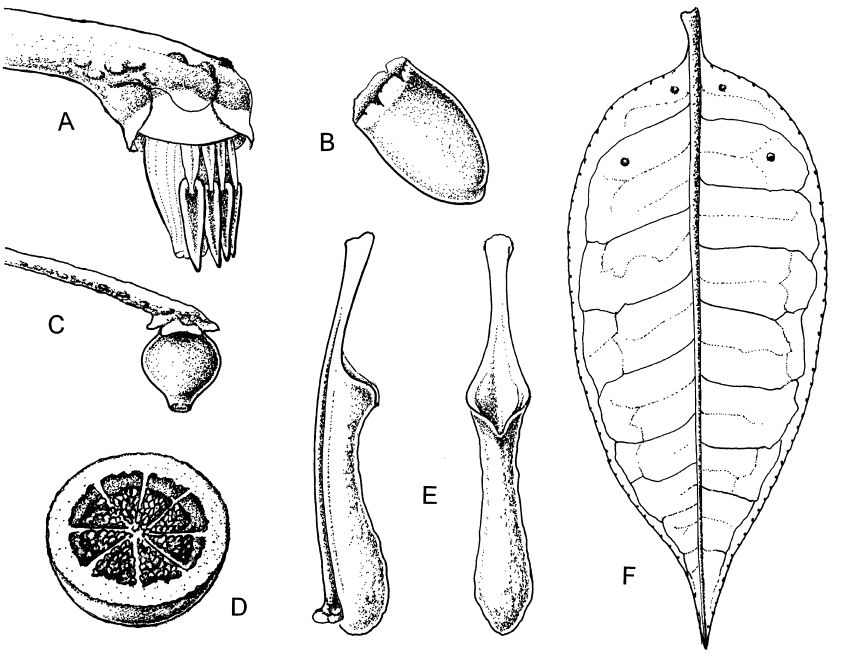
The certainly very interesting pollination biology of *Marcgravia* and the other genera is still very poorly understood and requires a great deal of further research.

Cultivation. The following information on cultivation of *Marcgravia* at Kew has been supplied by Mike Marsh, Unit Manager of the Princess of Wales Conservatory.

Marcgravia umbellata is grown in the Rainforest zone of the Conservatory, climbing up the trunk of *Cyathea fugax* from which it receives dappled shade; it has rooted on to the fern trunk but will also attach itself to walls like ivy (*Hedera helix*). Temperatures are maintained at 19°C at night and 24°C during the day; relative humidity is 70–75% and, in addition to the in-built misting system, the plant is sprayed over twice each day. A high Nitrogen foliar feed is applied once a fortnight during the active growing season. Marcgravia grows well at Kew, and propagation is achieved easily by means of cuttings, but it is rather shy-flowering.

Marcgravia umbellata L., Sp. Pl. 1: 503 (1753). Type: America calidiore. *Plumier, Nov. Pl. Amer.*: 7, pl. 29. 1703 (An Iconotype – Lectotype designated by Bedell in Howard, 1988: 303).

Description. *Liana*, fertile branches pendent, reddish- to greyish-brown, terete to angular, sometimes zig-zagged, often with rows of lenticels; lenticels tiny, to c. 1 mm long, circular to elongated, dark brown with protruding margins; young branches sometimes short bristly. *Adult leaves* petiolate, petiole 4–7(–9) mm long, 1.2–2 mm wide, semiterete, adaxially canaliculate, rarely slightly bristly; blade lanceolate to broadly elliptic, (6.3–)9–12(–13.7) cm long, (2.1–)4–5.8(–6.5) cm wide, apically acuminate, rarely obtuse with an acumen, acumen up to 2 cm long, base cuneate, rounded to obtuse, rarely truncate or cordate; margin entire to slightly crenate (marginal glands), chartaceous, midrib sulcate to canaliculate above, prominent beneath, lateral veins slightly prominent above, promi-



Marcgravia umbellata. A, flower at anthesis, some stamens removed, × 2; B, calyptrate corolla cap, × 2; C, flower during fruit development, × 1; D, cross-section of mature fruit, showing the pulpy placentae with numerous seeds, × 2; E, two nectary-bracts, × 1; F, lower leaf surface, showing the pattern of the hypophyllous glands, × 1. Drawn by Helen Greenop.

nent beneath; hypophyllous glands marginal, small (c. 0.5 mm long), semilunar, dark brown, 3–5 mm from the margin; basilaminar glands one per side, without perforations, mostly only visible as a dark spot, rarely well developed; laminar glands 1–2(–3), very small (0.2–0.5 mm diameter), elongated, in the lower 1/3 of the blade, close (2–4 mm) to the margin, inconspicuous with tiny perforations, sometimes only traceable as dark spots. *Sterile branches* scattered-bristly; juvenile leaves (sub)sessile, petiole if present up to 1.2 mm long, blade ovate, very variable, 1.5–4(–5.8) cm long, 1.3–3(–4.2) mm wide; apically obtuse, rarely slightly acute, basally cordate, margin entire to slightly crenate (glands), chartaceous, midrib sulcate above, prominent beneath, lateral veins prominent on both sides; marginal glands dark brown, directly along the margin with a space of 1–3 mm between; laminar glands 1(–3) per side in the lower part of the leaf, dark brown, oval, poriform, very small (0.2–0.3 mm diameter). *Inflorescence* short-bristly; pendent with (16–)18–26(–32) fertile and 4–5(–7) sterile flowers (nectaries); rachis (7–)9–12(–16) mm long, clavate (3–4 mm diameter), densely lenticelate, during fruiting enlarging and cicatricate; nectaries (in living state) greenish to rusty brown, tubulate-clavate,

terminally testiform, slightly carinate (= pedicel with numerous lenticels), subterminally hooked (sterile flower), shortly stalked, free stalk 5–6(–12) mm long, the cup 28–38(–49) mm long, 4–5.5(–8) mm diameter, the orifice strongly widened with apiculate margin, decurrent along pedicel. *Flowers* oblique to nearly rectangular on pedicels; pedicels 17–30(– 40) mm long, 1.3–2.2(–3) mm diameter, with numerous lenticels on their upper half (mostly orientated towards the nectaries); bracteoles directly subtending the inner sepals, broadly subtriangular, at most 2 × 3 mm, sometimes reduced to scales or hooks; sepals broadly ovate to broadly semicircular, rarely semilunar, spreading from the corolla, chartaceous, 2.5–3(–4) mm long, 4.5–7(–9) mm wide, unequal, margin entire to gnawed with a few (3–4) dark glandular spots; corolla cap brownish to light green, conical-ovoidal, apically slightly asymmetrically obtuse, rarely acute, 8– 10(–11) mm long, basally 4.5–6(–10) mm diameter. *Stamens* 12–20, the filaments white, linear to narrowly ovate-triangular, flattened, 2.5–4 × 0.5–1 mm, the anthers narrowly elliptical to narrowly ovate, basally cordate, 3.5–5 × 1–1.7 mm. *Ovary* turbinate, obconical, apically acuminate (style), becoming globose toward fruit development, 4.5–5 mm diameter, c. 6 mm high, smooth to longitudinally striate, locules 6–8; style 1–2 mm long, stigma crateriform to mammiform, rather large, 1.5–2.5 mm diam. *Fruit* reddish brown, globose, umbonate (style), 10–15 mm diameter, 12– 14 mm high.

[The diagnostically important characters of this species are: young branches ± densely covered with short light bristles, chartaceous leaves with clearly visible secondary venation and 1–3 laminar glands per side, shortly stalked nectaries, 2 bracteoles, sepals spreading and with marginal glandular spots, obtuse, rather stout calyptra, as well as the number of stamens (12–20) and locules (6–8).]

Distribution. Lesser Antilles: Saba, St Kitts, Montserrat, Guadeloupe, Dominica, Martinique, St Lucia, St Vincent, and Grenada.

Ecology. Lower montane to montane rain-forests, also secondarily influenced premontane rain-forest (not at the summits), at heights of 300–1000 m, most frequently 500–800 m. It grows on several soil types, but all volcanically derived, apparently requiring high humidity. Very common to occasional. Beard (1948: 62) states this species to be a typical element of climax rain-forest formations.

Uses. The species is always cited as having an antisyphilitic and diuretic effect. This certainly dates back to Descourtilz (1827: 25), hence the assignation to the true *M. umbellata* L. is questionable. More recent original references are lacking.

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