

# Gentianales (Coffees, Dogbanes, Gentians and Milkweeds)

Lena Struwe, Rutgers University, New Jersey, USA

The angiosperm order Gentianales includes the Apocynaceae (dogbanes and milkweeds), Gelsemiaceae, Gentianaceae (gentians), Loganiaceae (strychnine plants) and Rubiaceae (coffee and madder plants). They are found worldwide in most climates, but are most abundant in the tropics.

## Introduction

The angiosperm order Gentianales (subclass Asteridae) comprises five plant families: Apocynaceae (including Asclepiadaceae), Gelsemiaceae, Gentianaceae, Loganiaceae and Rubiaceae (Table 1). The families are distributed worldwide in most climates, but are most abundant in the tropics. They can be large trees, shrubs, herbs or small saprophytes. They are characterized by opposite, simple leaves usually with interpetiolar structures (stipules, lines or ridges, Figure 1). Colleters are often present at the base of the leaves or inside the calyx (Figure 2). They have showy flowers usually with 4–5 calyx and corolla lobes, and 4–5 stamens attached inside the corolla (Figure 3). Some typical phytochemicals are caffeine, toxic indole alkaloids and cardiac glycosides (e.g. strychnine, vincristine), and bitter tasting secoiridoids.

## Families Included and Morphology

Rubiaceae (coffees, gardenias and madder plants) is the largest family in the Gentianales (Table 1), and the plants have distinct interpetiolar stipules and inferior ovaries (Figures 1, 3b). This family contains mostly tropical trees and shrubs, but also herbs. Rubiaceae is the fourth largest angiosperm family.

Apocynaceae (dogbanes, frangipani and milkweeds) now includes the former family Asclepiadaceae (the milkweeds, a younger group inside the dogbanes). They have latex (milky sap), often a tuft of hairs on the seeds (Figure 4), and sometimes pollen fused in tetrads or pollinia (Figure 5b). The younger evolutionary lineages in the group have intricately formed flowers with fused corollas, stamens and/or styles with appendages (Figure 5a).

Gentianaceae (centaury and gentian) is a medium-sized family (Table 1) with several large herbaceous genera in the temperate regions. Gentians have contorted (twisted, overlapping) corolla lobes in buds (Figure 6), and have unique types of the chemicals secoiridoids and xanthones.

## Introductory article

### Article Contents

- Introduction
- Families Included and Morphology
- Economically and Horticulturally Important Species
- Ecology
- Phylogeny
- Biogeography

Loganiaceae is a smaller family (Table 1). They have imbricate (unevenly overlapping) or valvate (edge to edge) corolla lobes in buds, and sometimes produce indole alkaloids. All genera are mainly tropical. Butterfly bush (*Buddleja*) had been included in this family, but is now thought to be most closely related to the snapdragon family (Scrophulariaceae).

Gelsemiaceae (Carolina jessamine) is the smallest family (Table 1). It has heterostylous flowers and styles that are branched twice into four stigmas. Only two genera belong to this family, *Gelsemium* (North America and southeast Asia) and *Mostuea* (Africa and northeastern South America).

## Economically and Horticulturally Important Species

Many species of this order are poisonous, attractive, and have many native uses. By far, the most financially important species is coffee (*Coffea*, Rubiaceae). Another important species is *Cinchona*, the source of quinine, which is used to treat malaria. The indole alkaloids of *Strychnos* and *Catharanthus* (rosy periwinkle) are used as rat poison (strychnine) and against leukaemia (vinblastine, vincris-

**Table 1** Families of Gentianaceae; number of genera and species

Family	Genera	Species
Apocynaceae	c. 450	c. 4600
Gelsemiaceae	2	11
Gentianaceae	87	c. 1650
Loganiaceae	10	c. 400
Rubiaceae	c. 650	c. 13 000
<b>Total:</b>	c. 1200	c. 19 700

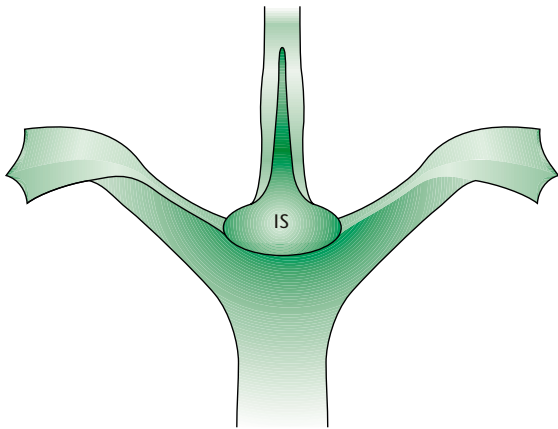


Figure 1 Stem with opposite leaves and interpetiolar stipule (IS).

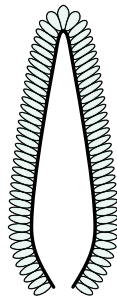


Figure 2 Colleter, multicellular gland, in cross-section, showing central glandular port and multicellular surface.

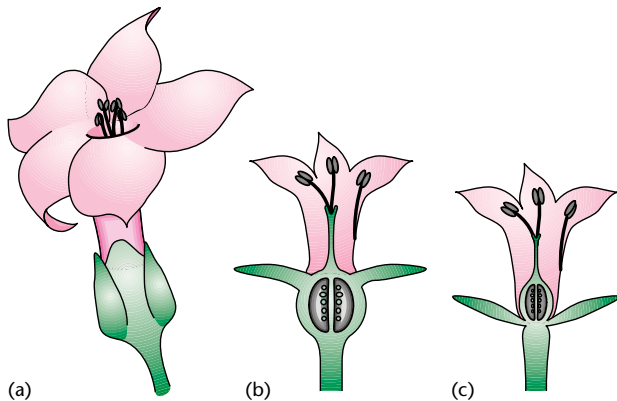


Figure 3 Flowers of Gentianales. (a) *Symbolanthus* (Gentianaceae), with basally fused calyx and trumpet-shaped fused corolla. (b) Cross-section of typical Rubiaceae flower showing inferior ovary, calyx, corolla, and stamens inserted into corolla tube. (c) Cross-section of typical Gentianaceae and Loganiaceae flower, showing superior ovary, otherwise the same as (b).

tine), respectively. *Gentiana* and relatives are used in traditional medicine worldwide in digestives, inflammation and snake-bite remedies, and as antifungal agents.

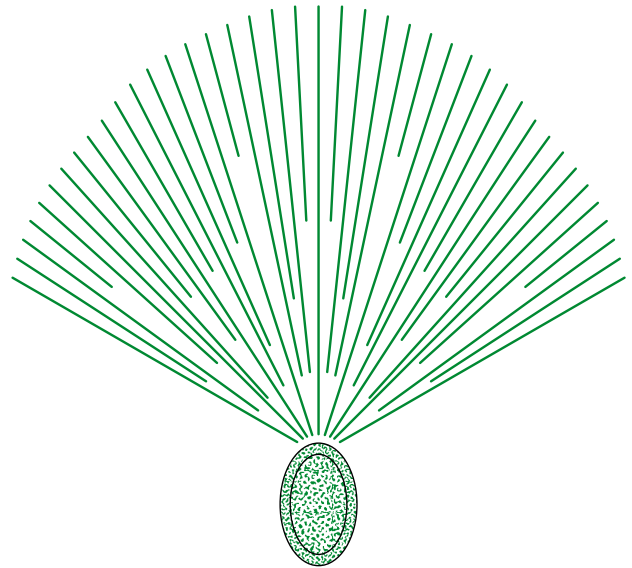


Figure 4 Seed from *Asclepias* (Apocynaceae), showing tuft of hairs on one end.

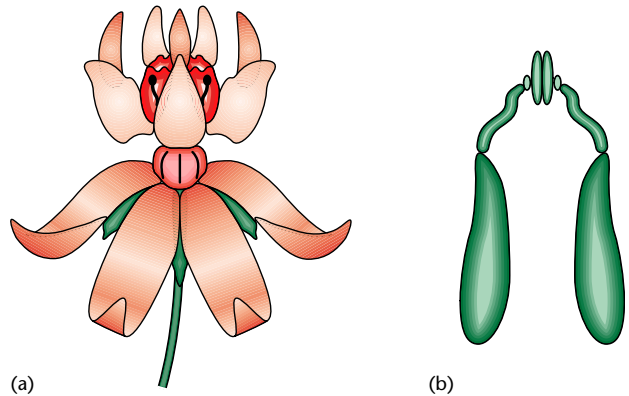
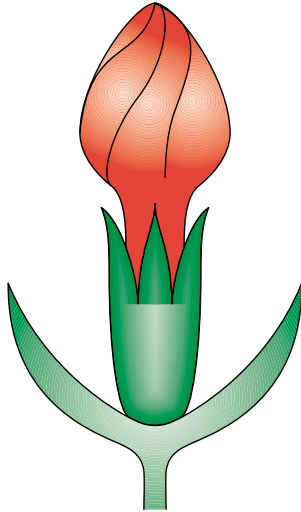


Figure 5 Flower (a) of *Asclepias* (Apocynaceae), showing intricately formed appendages on corolla, fused staminal parts around style and (b) magnified pollinia with 'handles' (called translator).

Many Gentianales species are cultivated for their showy flowers. Some of the most popular are the Rubiaceae and Apocynaceae genera *Allamanda*, frangipani (*Plumeria*), *Gardenia*, rosy periwinkle (*Catharanthus*), and wax flower (*Hoya*). Some Gentianaceae are also commonly cultivated (e.g. *Eustoma*, *Gentiana*) and one Gelsemiaceae, Carolina jessamine (*Gelsemium*), is grown in North America.

## Ecology

Several specialized ecological habits can be found in Gentianales, e.g. epiphytes, saprophytes without chlorophyll, and co-dependence of pollinators or symbionts and

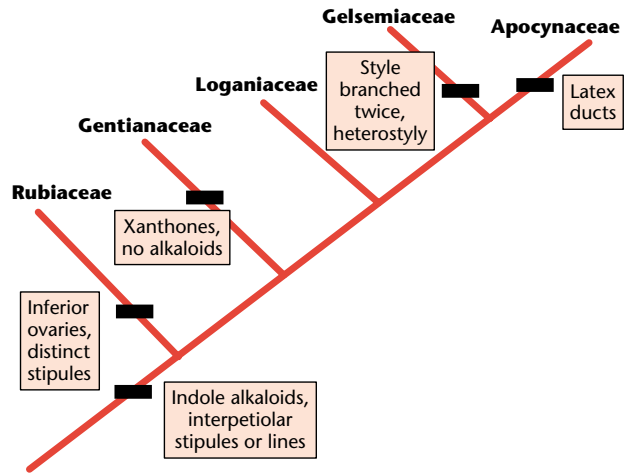


**Figure 6** Flower bud with contort corolla bud in Gentianaceae. Note calyx fused at the base and two leaves at the base of the flower.

plants. Saprophytes have evolved several times in this order and often have strongly reduced seeds and highly specialized embryological traits. Gelsemiaceae and Gentianaceae live in symbiosis with fungi (mycorrhiza). Symbioses with ants are found in, for example *Dischidia* (living in leaves, Apocynaceae), and *Hydnophytum* and *Myrmecodia* (living in stems, Rubiaceae). The poisonous milkweed (*Asclepias*, **Figure 5a**) is the host plant for the larvae of monarch butterflies, which accumulate the plant cardiac glycosides in their bodies as a protection against predators. Many flowers exhibit morphological traits specialized for a particular pollinator, such as hummingbirds, bats, hawkmoths or flies. Animal-dispersed fleshy fruits (berries, etc.) are common and have evolved independently many times from dry fruits.

## Phylogeny

The phylogeny of Gentianales has been well studied using both morphological and DNA sequence data. Rubiaceae appears to be the oldest and closest relative to the four other families (**Figure 7**). Next up in the phylogenetic family tree is Gentianaceae (including tribe Potalieae formerly in Loganiaceae). Loganiaceae is then most closely related to a group consisting of Apocynaceae and Gelsemiaceae. Apocynaceae and Gelsemiaceae (which was formerly a subgroup in Loganiaceae) are most closely related to each other. All five families are monophyletic, with Loganiaceae as the most weakly supported group.



**Figure 7** Synopsis of phylogenetic relationships in Gentianales. Characteristics for families and groups of families are noted.

## Biogeography

The biogeographic history of the Gentianales is very complex and still poorly understood. The oldest groups in Gentianaceae and Loganiaceae show geographical distributions that indicate an evolutionary origin during or before the split-up of the Gondwana supercontinent (an old, tropical origin for all families). This might suggest that the evolutionary lineages of the five different families and some of their major tribes could have been present *c.*90 million years ago (Ma). Some younger groups show relationships that suggest a northern subtropical or temperate distribution that became interrupted and restricted to smaller areas during the cooling of the Earth around 38 Ma (the break-up of the Boreotropics vegetation belt). After the formation of the Panamanian land bridge about 2–3 Ma, several genera dispersed from North America into South America. Dispersal from Asia to North America via the Bering land bridge is also known.

## Further Reading

- Backlund M, Oxelman B and Bremer B (2000) Phylogenetic relationships within the Gentianales based on *ndhF* and *rbcL* sequences, with particular reference to the Loganiaceae. *American Journal of Botany* **87**: 1029–1043.
- Endress ME, Sennblad B, Nilsson S *et al.* (1996) A phylogenetic analysis of Apocynaceae s. str. and some related taxa in Gentianales: a multidisciplinary approach. *Opera Botanica Belgica* **7**: 59–102.
- Leeuwenberg AJM (ed.) (1980) Fam. Loganiaceae. *Die natürlichen Pflanzenfamilien*. vol. 28b(1). Berlin: Duncker and Humblot. [In English.]
- Robbrecht E (1988) Tropical woody Rubiaceae. *Opera Botanica Belgica* **1**: 1–271.
- Struwe L and Albert VA (eds) (in press) *Gentianaceae – Systematics and Natural History*. Cambridge: Cambridge University Press.