## SUBCLASS ASTERIDAE - ASTERIDAE

The subclass Asteridae is the most highly specialized group of dicotyledonous plants. The subclass Asteridae includes the most highly developed groups of dicotyledons, characterized by many progressive features. The number of flower parts in asterids is small and always fixed (high degree of oligomerization). The corolla of its representatives is always fused-petal. In inflorescences, functional and morphological differentiation of flowers is often observed. The ovary is, as a rule, inferior, formed by two carpels. Asteridae are descended from ancient, now extinct Rosidae.

Asteridae is the largest subclass of dicotyledons, numbering about 3,500 genera and about 65,000 species.

In all probability, it has a common origin with the order Gentianales. Representatives are herbs, less often semishrubs, shrubs or trees, with alternate or less often opposite simple leaves without stipules. Vessel segments usually with simple perforation. The leaves and stems of many representatives have articulate laticifers. All of them are characterized by the presence of inulin. Flowers are usually bisexual, actinomorphic or zygomorphic, mostly 5-membered. The calyx is fused-sepals. Corolla is whith fused-petal. Stamens 5 or 2. Pollen grains of various types. Gynoecium 5-2 fruiting carpels: ovary inferior, very rarely superior or nearly superior, usually with many anatropic ovules in each socket. The ovary is unitegmal and tenuynucellate. Endosperm is cellular. Fruits are bolls, berry-like or nut-shaped. Seeds with endosperm or without endosperm.

Families: *Campanulaceae, Stylidiaceae, Goodeniaceae.*

## The family Campanulaceae

The family consists of more than 80 genera and approximately 2300 species. *Campanulaceae* grow mainly in the extratropical regions of the Old and New World, but some genera are also present in tropical countries, especially in mountainous areas. Most of the *Campanulaceae* are mesophytes, but many are hygrophytes or, on the contrary, xerophytes. There are a few aquatic plants among them. Their growth forms are very diverse.

Most *Campanulaceae* are herbs, perennial or less often annuals, erect or sometimes climbing, terrestrial or rarely aquatic or epiphytic. Some genera also include semi-shrubs and even tree-like forms, while some genera have tuberously thickened roots.

Leaves are alternate or sometimes opposite, rarely whorled, entire or dentate, lobate or rarely pinnate. Spores in phloem of leaf and stem are characteristic. In most genera, carbohydrates are deposited in the form of inulin.

Flowers are usually fairly large, in apical or more often in lateral (axillary) inflorescences, sometimes in dense heads surrounded by a involucre or in dense

spikes. Flowers are often solitary, apical or axillary, usually bisexual, very rarely unisexual, actinomorphic or more or less zygomorphic, most of them with 5 members, in most cases with 2 bracts. Calyx lobes are mostly free, usually remaining. Petals more or less fused, rarely free, almost to the base. Stamens in equal number with petals, free or more often attached to the base of corolla, to disk or less often to corolla tube; filaments free or more or less fused, usually more or less expanded at base; anthers introerose, free (and then in bud mostly glued into tube) or rather densely fused into tube. Gynoecium 5-2 peduncles, with simple or more often lobate peduncle, usually densely covered with unicellular hairs in upper part, including outer sides of stigma lobes; ovary usually inferior, but sometimes more or less semi-inferior or even superior; 2-5, rarely 6-10-locular, sometimes nearly 1-locular, usually with many ovules in each nest, most often on thick placenta. At the apex of the ovary, under the base of the stylet, there is a nectar disk, which may be cylindrical, cup-shaped, or ring-shaped.

The vast majority of *Campanulaceae* are characterized by cross-pollination, which is provided mainly by their usually very strongly pronounced protandria. Pollinators are mostly large bees and butterflies, as well as sawflies, beetles and other insects. But there are quite a few ornithophilous plants among *Campanulaceae* as well. One of the most characteristic features of the pollination mechanism in *Campanulaceae* is that pollen is delivered by a style instead of directly by the anther. This is quite unusual for flowering plants, except for representatives of the order of *Campanulaceae*.

The fruits of *Campanulaceae* are of a very diverse type. Most often the fruit is a capsule, sometimes spirally twisted, opened by apical, lateral or basal flaps or pores, or even irregularly; less often the fruit is a berry, rarely a pitted or nut-shaped. Seeds are small, usually numerous, with an erect embryo and a fleshy and usually abundant endosperm.

The largest genus in the family is the bellflower (*Campanula*), numbering up to 350 species. They are perennial herbs, less often annuals or semi-shrubs. Bellflower species occur almost everywhere (a little less than half of the species grows in Russia) in non-tropical areas of the northern hemisphere, except only for parts of the Arctic.

In the family of *Campanulaceae* many useful plants. For humans, *Campanulaceae* are primarily aesthetic value. Among them are a lot of beautiful plants, and some of them have long been included in the golden fund of ornamental horticulture. Particularly many ornamental plants among the species of the genus bellflower, some of them are widely cultivated.

Among the *Campanulaceae* there are also some edible plants. For example, bellflower Rapunculus (*Campanula rapunculus*) is used as a vegetable plant - the roots of the first year and leaves are eaten as a salad.

*Campanula rapunculus* $*Ca_{(0)}Co_{(5)}A_{(5)}G_{(\bar{2})}$

## The order Asterales

Includes only one family - *Asteraceae*.

The *Asteraceae* is the largest family of dicotyledonous plants. It includes more than 24,000 species united in about 1,200 genera. Asteraceae are found almost everywhere where higher plants can exist at all - from tundra to the equator, from seashores to alpine snows, on barren sands and on stout black soils.

Life forms: single- and perennial herbs, vines, shrubs, small trees. Leaves simple, entire or dissected, rarely compound, without stipules. Leaves are alternate, less often opposite. Many representatives have laticifiers containing latex.

Leaves are predominantly alternate. The size, shape and degree of separation of the leaf blade vary greatly, from very large, as in the Japanese butterbur (*Petasites japonicus* Siebold &Zucc. ), growing on Sakhalin, the Kuril Islands and in Japan (the lamina of its entire root bud-shaped leaf reaches 1.5 m across and the petiole 2 m long), to small, very reduced ones as in American leafless baccharis (*Baccharis aphylla* L.) with rod-shaped photosynthetic stems. In most astrophytes, leaves are characterized by one or another type of pinnate veining. However, there are leaves with strictly parallel or parallel-arc veining, as in some species of the genus Kozelia (*Scorzonera* Nutt.).

Many *Asteraceae* are characterized by pubescence. The hairs of *Asteraceae* are diverse: unicellular or multicellular, hard or soft, straight or sinuous, simple (nonbranched) or bifurcate, stellate. Dense pubescence is especially often well expressed in species which live in conditions of constant dryness or abrupt change of temperature. For example, growing in Central Asia, cotton-grass (*Lachnophyllum gossypinum* Bunge.) in its young state is covered, like absorbent cotton, with soft tangled hairs.

The vast majority of species of the family has a developed tap root. Often the root is tuberously thickened, which, for example, is characteristic of burdocks (species of *Arctium* L.). Many species of the family develop contractile (retractile) roots; in plants with a root rosette, they often ensure tight adhesion of rosettes to the ground. The woody Fitchia speciosa (*Fitchia speciosa* Hook.F.) growing on Rarotonga Island (Cook Islands) has well-defined aerial support roots. Endomycorrhiza is found in many astrophytes.

Most astrophyt *Asteraceae* are herbs, perennial or annual, which range in size from very large, like some species of sunflower, to tiny, like the medicinal dandelion (*Taraxacum officinale* Web.). But among them are also many semi-bushes and shrubs. Occur among the *Asteraceae* and trees, usually low. Many arboreal forms are characteristic of oceanic islands. As part of the genus *Scalesia* Arn. endemic to the Galapagos Islands, there are species with trunks that reach a height of over 20 m with a diameter of 25-30 cm, such as Petiolate Scalesia (*S. Pedunculata* Arn.).

Among the tree-like *Asteraceae* there are the so called rosellate trees. Their trunk does not branch or branches only slightly and has a crown of leaves like a bunch or rosette at the top. Rosemary trees in the genus *Senecio* L. reach a height of 7.5 m. Many aster plants are cushion-shaped. For example, *Haastia pulvinaris*

Hook.F., growing in the subalpine and alpine belts of New Zealand, forms cushions over 2 m in diameter and 60 cm in height.

Plants of this family are usually not difficult to distinguish from representatives of other families by their characteristic inflorescence, the capitule. The capitules are botryoidal inflorescences. Individual capitules are part of complex aggregate inflorescences (cymoids, panicles, racemes, spikes, heads). The base of a capitule is formed by an enlarged inflorescence bed, or common receptacle, where closely adjoining flowers are arranged. The common receptacle is surrounded on the outside by a involucre consisting of more or less strongly modified upper leaves. The main function of the involucre is to protect the flowers from adverse environmental influences. Leaflets of the involucre are arranged in one or two or several rows. The number of flowers in the capitule varies from one to several thousands. The size of capitule of wild *Asteraceae* is usually not large, varying in diameter from one to several centimeters. Only occasionally capitules are larger - up to 10-15 cm in diameter, and in cultivated annual sunflowers (*Helianthus annuus* L.) they reach the size of a large dish - up to 60 cm across. At the same time, the capitules of many wormwoods are tiny, only 2-4 mm in height and width. The common receptacle may be more or less flat (like the annual sunflower), but it may also be concave, convex, cone-shaped and other forms. Its surface is often shrunk with films, bristles or hairs. These are modified bracts, and only the hairs may be unrelated to the bracts (i.e., trichomes). The number of flowers in a capitule is also in a certain correspondence with the size of the total inflorescence. In the annual sunflower, it often exceeds a thousand, but the female inflorescences of *Ambrosia* L. contain only two flowers, and the capitule of *Echinops* L. contain only one flower.

Flowers are small, actinomorphic or zygomorphic, more often bisexual, with double perianth, with or without bracts. The calyx is modified into a pappus composed of hairs, bristles, films or completely reduced. Corolla is fused-petals and variable in shape.

Stamens, usually numbering 5, are attached to the corolla tube. Stamen filaments are loose, and anthers stick together laterally to form an anther tube, through which the style passes. The anthers are mostly elongated, longitudinally opening. Rarely, e.g., in the genus Ambrosia, anthers are loose and stamen filaments are fused. Gynoecium consists of 2 carpels with a style, which ends in 2 lobes of stigma; in sterile flowers the style is sometimes inseparable. In fruiting flowers, the lobes of the stigma protrude from the corolla and are often strongly divergent. On the inner side, the stigma's lobes are provided with a special perceptive (stigma's) tissue. Many species of the family are characterized by the presence of so-called gathering or sweeping hairs that help remove pollen from the anther tube. The location of these setae (in the form of a collar under stigma lobes or along more or less considerable length of the outer side of the lobes), their density and length vary greatly. The ovary is inferior, unilocular, at the base with one ovule (very rarely two), located on a short peduncle (funiculus). Mature seeds have no endosperm or only traces of it are found.

The brief information on the flower and related formations described above refers to the well-developed bisexual of the *Asteraceae*. However, not all species of this family have all flowers in the capitule that are bisexual and fruiting. Two other types of unisexual flowers, female (usually fruiting) and male (sterile), as well as sterile flowers, in which both androceum and gynoecium are reduced, are often found. The capitule may be unifloral (homogamous), but more often heterogamous (heterogamous). In such cases, the center of the capitule is occupied by axillary tubular flowers, while female and often brightly colored reed flowers spread out in rays along the periphery. Other combinations of flowers, different in structure and sex, can also be observed in the heterogamous capitule.

**Flowers of four types:**

**1. tubular** *$Ca_{(0)}Co_{(5)}A_{(5)}G_{(\bar{2})}$

**2. lingual** $\uparrow Ca_{(0)}Co_{(5)}A_{(5)}G_{(\bar{2})}$

**3. false-lingual** $\uparrow Ca_0Co_{(0+3)}A_0G_{(\bar{2})}$

**4. funnel-shaped** $\uparrow Ca_0Co_{(5)}A_0G_0$

The flowers of the *Asteraceae* are usually small and may differ greatly from each other in appearance, but they all arose from flowers of a single type of structure. They have a double perianth, but the calyx is most often modified into a pappus consisting of varying numbers of bristles, hairs or membranes. Sometimes the calyx is completely reduced. Corolla is always fused-petal, but very variable in shape. It is very often actinomorphic, tubular, with a five-lobed, rarely four-lobed or dentate bend. Flowers with this kind of corolla are called tubular. The marginal flowers in the capitules of many asters are of the zygomorphic type. Their corolla is a whole plate fused of 3 petals, indicated by either three small teeth on its apex or three longitudinal veins. Such flowers are called false-lingual flowers. They usually have no developed stamens and are functionally female. Falsely-lingual flowers evolved from tubular flowers; flowers with a bilabiate corolla, preserved in some tropical asterids, are considered a transitional type. The biological reason for the appearance of such flowers is obvious. They are intended to attract insects-pollinators by their bright contrasting coloration and large size.

The peculiar marginal flowers of cornflower (*Centaurea* L.), called funnel-shaped, perform a similar signal function. They are sterile, usually enlarged in size, and the number of teeth of their brightly colored corolla varies from 6 to 9.

The fruit of the *Asteraceae* is the achene. It is a one-seeded unopened fruit with a more or less dense leathery and usually not thick pericarp, which usually separates from the seed. Only in very rare cases, as in species of the neotropical genus *Wulffia*, the seed has a juicy pericarp.

There are two subfamilies in the family *Asteraceae*, depending on the combination of flowers in the capitules:

1. the *Asteroideae* or *Tubuliflorae*
2. the *Lactucoideae* or *Liguliflorae*

*Asteraceae* with tubular flowers are usually subdivided into a particular subfamily, the *Asteroideae* or *Tubuliflorae*. In representatives of the subfamily *Asteroideae*, the capitule always contain tubular flowers. They may make up the whole capitule, or be in combination with false lingual or funnel-shaped flowers.

Another subfamily, *Lactucoideae* or *Liguliflorae*, is characterized only by reed flowers, less often by bilabiate flowers. The corolla of lingual flowers is abruptly irregular and formed by petals fused into a single plate. Often, five teeth or five veins are visible at the tip of the corolla plate, indicating the number of merged petals. Lingual flowers arose from regular tubular flowers. There are many transitional forms between these major ones.

*Asteraceae* have inulin (not starch, as in most other dicotyledons) as the main stored carbohydrate.

The overwhelming majority of astrophytes are insect-pollinated plants.

Relatively few astrophytes, such as the species of the genus *Xanthium* L., have protogynia. Anemophilia is not uncommon. It is regarded as a secondary phenomenon and is characteristic of plants of wide open spaces, such as species of wormwood (*Artemisia* L.); their capitules are usually small, unsightly, collected in complex common inflorescences. In some *Asteraceae*, the flowers are cleistogamous.

In addition to the normal sexual process in *Asteraceae*, apomixis is often observed, especially among representatives of the subfamily Lactucoideae, such as the genus Dandelion (*Taraxacum* Web.).

The number of fruits is large in many cases. Fruits are usually small and weigh negligible. Seeds are often no more than 5 mm long and 1 mm wide. Very often the seed fruits are provided with hairs, bristles, papillae and so on.

Among the *Asteraceae*, there are also representatives belonging to the tumbleweed life form. They are characteristic of plants inhabiting open (treeless) spaces, such as steppes. An example of them is cornflower (*Centaurea diffusa* L.), growing in open places, mainly in the south of the European part and in the Caucasus. Another example is *Asteriscus pygmaeus* Mill. It is an annual common from the Sahara to Belugistan and has hygroscopic involucre leaves. After the seeds mature, these leaves close and the plant may remain in this state for 8-10 months. Seed dispersal associated with the opening of the involucre occurs in wet weather, which contributes to their successful germination.

Among biological peculiarities of *Asteraceae* seeds, we should mention heterocarpy or heterocarpy, observed in many species of this family. Heterocarpy of *Calendula officinalis* L., widely known for the shape of its curved seeds called "marigolds", is well expressed. Claw-shaped, rook-shaped, and ring-shaped seeds, as well as transitional forms between them, can be found in calendula in one capitule.