Sympetaly in Apiales (Apiaceae, Araliaceae, Pittosporaceae)

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In all recent molecular sequence based analyses Apiales come out to be placed within a broadly defined group Asteridae. Within ‘euasterids II’ Apiales (Apiaceae, Araliaceae, Pittosporaceae, Aralidiaceae, as well as some former cornaceous taxa) form a monophyletic group in a position close to Asterales–Campanulales and Dipsacales. Also from a floral developmental point of view the mostly choripetalous Apiales are not out of place among these sympetalous orders: In members of Apiales (Apiaceae: Hydrocotyle; Araliaceae: Aralia, Hedera; Pittosporaceae: Sollya, Pittosporum) the corollas are initiated from a continuous ring primordium corresponding exactly to the development in Campanulales–Asterales and Dipsacales. Only in Pittosporaceae further growth of this primordium results in a weak sympetaly in adult flowers. Molecular data suggest that the subfamily Hydrocotyloideae is polyphyletic, with Hydrocotyle belonging to the lineage not placed within Apiaceae but more closely related to Araliaceae, a position fitting well with the mode of formation of the corolla.

Flowers with a corolla tube can be found in many members of the angiosperms, but are concentrated in the upper evolutionary level. The combination of the character ‘sympetaly’ with the character ‘one stamen whorl alternate with the corolla-lobes and isomerous, or stamens fewer than the corolla-lobes’ circumscribes a group which was established as the subclass ‘Asteridae’ by Takhtajan in 1964. Cronquist maintained the subclass in all his later classifications (e.g. Cronquist 1981). The group is also characterised by unitegmic and tenuinucellate ovules.

All corolla tubes were assumed to be structurally homologous and their formation has been regarded as a typical example of a ‘congenital fusion’ of adjacent organs. Ontogenetical studies, however, have shown that sympetalous corollas s. str.1 can be formed in several ways, particularly as regards the timing of their initiation. Thus a broadly used term ‘congenital fusion’ refers to rather diverse ontogenetical modes of growth.

The mode of development, in which the corolla lobes are initiated as separate primordia and become connected only later on, is called ‘late sympetaly’ (see Erbar 1991, Erbar and Leins 1996). We can find either the formation of a bridge connecting more or less abruptly the initially free petals or successive steps of a relatively slow lateral extension of the petal bases (see Figures in Erbar 1991, Erbar and Leins 1996, Leins 2000). In both cases equal growth in the petal bases and interprimordial regions results in the formation of the corolla tube s. str. Different from this mode of corolla tube formation, a corolla tube ontogenetically can be initiated extremely early, namely before the petal primordia arise. The Compositae are a good example of this mode of corolla tube inception, which is called ‘early sympetaly’: The enlargement of an initially hemispherical floral apex into a plug stage and subsequent funnel stage is due to a ring meristem (periclinal cell divisions below the dermatogen in the periphery of the floral primordium). Later on five corolla lobes arise on this ring meristem or ring primordium. The stamen primordia are initiated alternating with the petal primordia and internal to the interprimordial petal areas — the petal primordia appear to be connected by flat shoulders. Further continuous enlargement of the former ring primordium results in the corolla tube (see e.g. Figures 2–4 in Erbar 1991, Figures 80–81 in Erbar and Leins 1996, Figure 40 in Leins 2000). Early sympetaly, i.e. the occurrence of an early corolla ring primordium, is also found in all members of the Campanulales s.l. (Brunoniaceae, Calyceraceae, Campanulaceae, Goodeniaceae, Lobeliaceae, Menyanthaceae, Sphenocleaceae, Stylidiaceae) investigated until now. In these families a corolla ring primordium is formed inside or above a calyx. Apart from the Campanulales–Asterales-complex, early sympetaly seems to be present as a constant character in the Rubiales, Oleales and Dipsacales (Erbar 1991, Erbar and Leins 1996).

A few cases must be regarded as ‘transitional between early and late sympetaly’. In Apocynaceae (Asclepiadoideae), for example, five petal primordia arise on the rim of a plateau,
and the extension and connection of the petal bases coincide with the initiation of the stamen primordia. Based upon extensive ontogenetical investigations and in comparison with other characters the developmentally differentiated character states 'early' or 'late sympetaly' proved to be good markers for systematic considerations and we recognise two blocks of orders within the Asteridae and related groups (Erbar and Leins 1996). To a certain degree the two groups correspond with the presence or absence of chemical compounds, namely iridoid compounds and polyacetylenes (see Erbar 1991). A much better correlation in the bipartition of the Asteridae results, if we transpose our character states on the cladogram from Chase et al. (1993) based on rbcL sequence investigations. Our Asteridae A-block — dominated by 'late sympetaly' — corresponds nearly exactly with the asterid I-clade and our Asteridae B-block — characterised by 'early sympetaly' throughout — with the asterid II-clade (see Figures 11–12 in Leins and Erbar 1997).

In the last few years the taxon 'subclass Asteridae sensu Cronquist' has been abandoned. Due to cladistic analyses of molecular data only expanded Asteridae (in a broad sense) are regarded as monophyletic. Broadly circumscribed Asterids contain some formerly dilleniid or rosid taxa like are regarded as monophyletic. Broadly circumscribed Asteridae and their relationships to the latter two families. Traditionally Araliaceae and Apiaceae have been placed in the Apiales. Molecular data (e.g. Olmstead et al. 1992, 1993, Plunkett et al. 1996a, APG 1998, Soltis et al. 1997, 2000, Savolainen et al. 2000) also support a close relationship of Pittosporaceae to the latter two families.

**Sympetaly in Araliaceae**

In the Araliaceae the corolla is initiated as a low ring primordium which does not grow up forming a tube, so that the petals are free from each other in the adult flower (Erbar and Leins 1988). In *Hedera helix*, the initiation of the low corolla ring primordium takes place nearly simultaneously with the formation of the petal primordia (Figure 1). As in *Aralia elata* (Figure 2) the circular corolla primordium is inside the calyx. Although in *Aralia* the ring primordium is somewhat more pronounced (Figure 2e), in *Aralia* and *Hedera*, the stamen primordia originate distinctly internal to the interprimordial corolla areas (Figure 2f).²

**Sympetaly in Hydrocotyle**

The genus *Hydrocotyle*, which has no calyx, starts its floral development like the sympetalous Asteraceae with a plug stage (Figure 3a), followed by a funnel stage (Figure 3b), in which, however, in contrast to the Asteraceae, the petal primordia are already clearly visible. The five stamen primordia differentiate on the inner surface of the funnel-shaped floral apex (Figure 3c). Whereas in Asteraceae the rim of the funnel develops continuously into a corolla tube, in *Hydrocotyle* only flat shoulders remain after the inception of five stamens (Figure 3d). The adult flowers apparently are choripetalous (see Erbar and Leins 1985, Erbar 1988).

**Sympetaly in Apiaceae**

No indication of early sympetaly was seen in Saniculoideae (see Figures 1, 3–4 for *Eryngium campestre, Sanicula europaea* and *Astrantia major* in Leins and Erbar (2004)) or in Apiaceae (see Figures 5, 7 for *Foeniculum vulgare* and *Levisticum officinale* in Leins and Erbar (2004)).

**Sympetaly in Pittosporaceae**

In *Pittosporum tobira* (Erbar and Leins 1995) the petal primordia are joined laterally at the time of initiation (Figures 4a–b). Sympetaly is expressed very weakly in older flower buds (arrow in Figure 4f) or in adult flowers. Sometimes a distinct corolla tube is simulated by interlocking of the epidermal cells of the adjacent free corolla lobes, but this is unrelated to a true corolla tube whose initiation we are presently considering. In *Pittosporum* as well as in *Sollya* a true corolla tube is restricted to the very base. Nevertheless, in *Sollya fusiformis* (Erbar and Leins 1996) ‘early sympetaly’ is distinctly expressed during early development by initiation of a flat ring primordium (Figure 5a), on which five petal primordia differentiate (Figure 5b). As in *Pittosporum* (Figures 4d–e), the stamen primordia arise clearly internal to the interprimordial petal areas (Figure 5c).

**Discussion**

**Systematic position of Apiales**

From the floral developmental point of view the Apiales fit well in the early sympetalous asterid II-group where they, based on molecular data, come out as sister to the Asterales (see e.g. Plunkett et al. 1996a, Savolainen et al. 2000, Soltis et al. 2000). The connection Apiales–Asterales, however, has already been noted because of similarities in secondary chemistry (Hegnauer 1971, 1990) and in morphology (see Leins and Erbar 1987, Erbar 1988, Erbar and Leins 1988, 1995). Systematically relevant characters are:

- ethereal oils
- polyacetylenes (falcarinone type) (Hegnauer 1989, 1990, Frohne and Jensen 1992)
- anthraquinones (acetate-derived) (Jensen 1992)
- sesquiterpene lactones
- pseudanthia
- flower orientation (one petal in abaxial position)
- tendency to reduction of calyx
- isomerous androecium
- tendency to zygomorphy in peripheral flowers
- (mostly) dimerous inferior gynoecium in Araliaceae and Apiaceae, superior gynoecium in Pittosporaceae
- nectary with slits at the base of the dorsal carpel flanks (= ovary roof in inferior gynoecia)
- unitegmic ovules
- early corolla ring primordium
Systematic position of Pittosporaceae

All molecular data, e.g. Plunkett et al. 1996a, 1996b, Plunkett 2001, confirm that Apiales — that is Pittosporaceae, Araliaceae, Apiaceae, and some smaller families — form a monophyletic group in a position close to Asterales and also Dipsacales. The Apiales–Pittosporaceae clade is sister to four genera for which floral developmental data are totally lacking: Aralidium, Griselinia, Melanophylla and Torricellia (the last three formerly allied to Cornaceae).

Sometimes the superior gynoecium in Pittosporaceae has been regarded as ill-fitting the Apiales which have an inferior gynoecium (Pax 1891, Cronquist 1981, Plunkett 2001). Precise analyses reveal that the, on first glance, profound difference is not very compelling. In both families, the gynoecial primordium is formed on a flat or at most on a slightly concave floral apex (Figure 6). The intercalary growth in the floral axis (Figure 8) resulting in an inferior ovary in the Apiaceae (Figure 7c) is only a process continuing the peripheral growth after carpel initiation, and thus less important for the purposes of systematics: The inferior ovary is formed by the floral axis and the dorsal carpel flanks are not involved in this process. Due to this intercalary growth in the floral axis the nectary in Apiaceae corresponds to that in Pittosporaceae although these seem to have superficially quite a different position: In Pittosporum (Figure 7a, arrows point to nectar slits in Figure 7b) the nectary is situated at the very base of the superior ovary. In many Apiaceae it is the ovary roof of the inferior ovary that forms the nectary, the so-called stylopodium (Figure 7c, arrows point to nectar slits in Figure 7d). In both cases the nectary is formed at the dorsal base of the carpels (principle of variable proportions; Leins 1972, Leins and Erbar 1985, Erbar and Leins 1995).

Figure 1: Early corolla development in Hedera helix L. (Araliaceae). (a) Sepal inception. The sepal primordia (1–5) arise non-simultaneously in various sequences (see Leins and Erbar 2004). Within the calyx a slow ring primordium is visible. T = bract. (b–c) Five petal primordia (P) arise on a slow ring primordium. (d) Initiation of the gynoecium; the carpels (C; Se = septum) alternating with the stamens (St, removed). Sepals and petals are removed. From Erbar and Leins 1988
Figure 2: Early corolla development in Aralia elata (Miq.) Seemann (Araliaceae). (a–e) Corolla development starts with a five-humped ring primordium within the calyx (P = petal primordium, S = sepal primordium), arrow points to interprimordial region of the corolla. (f) Stamen primordia (St) arise clearly internal to the interprimordial petal areas (arrow). (a, c–f) from Erbar and Leins 1988, modified.
Systematic position of Hydrocotyle

Molecular studies suggest that Apioideae and Saniculoideae are largely monophyletic (e.g. Plunkett et al. 1996a, 1996b, 1997, Plunkett 2001). In neither subfamily was there any indication of early sympetaly, although only some species (about 25) have been investigated ontogenetically.

The former Hydrocotyloideae, however, are polyphyletic with some portions allied to the Apiaceae but others to Araliaceae (Plunkett et al. 1996a, 1996b, 1997, Plunkett 2001, Downie et al. 2001, Lowry et al. 2001). The genus
Hydrocotyle, in which the floral development was investigated, is sister to core Araliaceae. This fits as regards early corolla development (precondition for early sympetaly), although Hydrocotyle lacks a calyx.

**Outlook for further study**

Molecular data indicate that the Gentianales, Scrophulariales, Lamiales and Solanales form a monophyletic group with the...
Apiales–Campanulales–Asterales and Dipsacales on the other side. It is, however, hard to find any morphological character to support these groups. This gap can be filled by the ontogenetically differentiated character ‘formation of sympetalaly’. We can state that the character ‘ontogeny of sympetalaly’ proved to be valuable for systematic considerations. Perhaps further studies in the araliaceous Hydrocotyloids will reveal more early sympetalous genera. Another interesting field of research will be the woody Apiaceae. What is the basal floral developmental pattern?

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Notes

1 In many members of the Asteridae the stamens are attached to the corolla tube. Ontogenetical studies revealed that the two corolla parts — corolla tube s.str. and stamen–corolla tube — have to be considered independently because they are formed by two spatially and temporally separate processes. The lower part with the attached stamens, the stamen–corolla tube, results from the activity of a circular intercalary diffuse meristem below the insertion area of stamens and corolla tube s.str., thus resembling the formation of hypanthia. The timing of its initiation can vary somewhat, but in all Asteridae investigated the stamen–corolla tube is formed after the inception of the upper part of the corolla tube (see Erbar 1991).

2 The connection of the young petal primordia is hard to observe and may lie at the limits of visual detection. But the interprimordial shoulders become distinctly visible when the stamen primordia originate in front of them.

3 APG II (2003) lists 10 families (Apiaceae, Araliaceae, Aralidiaceae, Griseliniaceae, Mackinlayaceae, Melanophyllaceae, Myodocarpaceae, Pennantiaceae, Pittosporaceae, Torricelliaceae). The relationships among the small families are still unclear (APG II 2003). In addition, there are still uncertainties about the delimitation of Apiaceae and Araliaceae (Plunkett and Lowry 2001).
Figure 7: Adult gynoecia and the homologous position of the nectaries. (a–b) Pittosporum tobira (Thunb.) Aiton: (a) adult gynoecium (arrows indicate the area of the nectary at the base of the superior ovary); (b) basal part of the ovary at higher magnification showing the nectary slits indicated by arrows (a nectary tissue is probably situated only at the very base of the gynoecium; see discussion in Erbar and Leins 1995); (c) Astrantia major L. (Apiaceae). The dorsal base of the carpels has become extended to the nectar secreting ovary roof (stylopodium, arrows); (d) Ovary roof nectarium (stylopodium) of Hydrocotyle vulgaris L. with numerous nectary slits (arrows).
Figure 8: Formation of an inferior ovary due to intercalary growth in the floral axis. Longitudinal sections through flower buds of different age in *Levisticum officinale* L. (Apiaceae). To demonstrate the main directions of the cell divisions during the development (genetic) series of cells are indicated by lines in the longitudinal sections. Embryonal tissue is shaded in the sections. The process of cup formation starts already early: the direction of cell divisions changes from initially parallel to the longitudinal axis (a) to perpendicular to the longitudinal axis (b). By this the shape of the floral primordium changes from convex (a) to disciform (b). Below the rim of the disc-shaped primordium the direction of cell divisions changes to horizontal, then diverging upwards from the longitudinal axis. By this the floral receptacle becomes dish-shaped while the floral primordia are initiated (c–d). By further corresponding cell divisions, more intensive in the outer flank, as well as by differential extension growth (e–f) the receptacle becomes cup-shaped. C = carpel, P = petal, S = sepal (reduced), Sa = ovule, St = stamen. From Leins and Erbar 1985, modified.

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