PART I INTRODUCTION TO FLORAL DIAGRAMS

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Introduction to Flower Morphology

1.1   Definition of Flowers

There is no general agreement nor any rule about how a flower should be defined. Since the end of the nineteenth century two main contrasting hypotheses have been provided and the discussion is still ongoing (reviewed in Bateman, Hilton and Rudall, 2006). The pseudanthial hypothesis accepts that flowers evolved from a branched, multiaxial structure – that is, a condensed compound inflorescence (e.g. Eichler, 1875; Eames, 1961). This means that a flower is an assemblage of separately functioning entities that became grouped together. The euanthium hypothesis states that the flower evolved from a simple uniaxial (euanthial) structure – that is, a condensed sporophyll-bearing axis with proximal microsporophylls and distal megasporophylls (e.g. Arber and Parkin, 1907). However, reconstructions of the early angiosperm flower (e.g. Sauquet et al., 2017) suffer from the absence of clear transitional forms between ancestral prototypes and angiosperms. Floral organs all have attributes of leaves, and leaf-like elements, such as stipules, leaf bases, petioles and blades, occasionally appear in flowers (e.g. Arber, 1925; Guédès, 1979). The stamen is recognized as equivalent to a microsporangiophore (an axis) or micro-sporophyll (a leaf) bearing microsporangia (the pollen sacs), while the ovary is described as a grouping of folded megasporophylls (the carpels) enclosing the megasporangia (ovules) (Endress, 2006). However, the origin of stamens is unclear, with a greater diversity of stamen structures in other seed plants (Endress, 2006). Developmental and genetic evidence supports the fertile organs of flowers to be a combination of axes and subtending leaves (at least for the ovary: e.g. Endress, 2019), reflecting a modular vegetative system of a main axis with lateral branches arising in the axil of leaves. However, not all researchers

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unanimously accept the concept of flowers evolving from a vegetative shoot. Claßen-Bockhoff (2016; see also Claßen-Bockhoff and Arndt, 2018; Claßen-Bockhoff and Frankenhaüser, 2020) pointed to the fundamental difference between flowers and shoots, including the lack of apical growth and expansion in flowers, leading to a strong differentiation from vegetative shoots.

Recent phylogenetic studies have supported the theory that flowers evolved once and that all flowers are thus homologous (the 'anthophyte hypothesis' reviewed in Bateman, Hilton and Rudall, 2006). The theory is supported by evolutionary developmental evidence that the same genes are acting on the flower and vegetative shoot, and that the flower is best interpreted as a short shoot with specialized leaves (Glover, 2007).

More specifically, a flower can be defined as a determinate structure with a generally defined number of organs (modules); it bears both staminate and pistillate parts and organs are set in four series: sepals, petals, stamens and carpels. However, several angiosperm flowers lack these defining features, and differentiation of a perianth or limits of flowers and inflorescences can be unclear. The definition of flowers implicitly refers to angiosperms, but should also include gymnosperms. The gymnosperm cone could also be described as a flower, though the organization of the cone is generally unisexual. A defining character for angiosperms is enclosure of ovules by carpels (angiospermy), separating the flowering plants from their closest relatives (gymnosperms). Despite any occurring variations, most flowers are conservative, with a well-defined ground plan (also called Bauplan) that is genetically fixed (see Smyth, 2018). Flowers are usually grouped into inflorescences that may be simple to highly complex, and are – at least in bud – often subtended by a specialized leaf, the bract, together with one or more (generally two) smaller leaves (bracteoles) placed in a lateral position. Bracts and bracteoles are absent in some species, and this can influence the position of organs in the flower. In some plant groups the limits between bracts and perianth parts are unclear. The inflated axis, called a receptacle, bears floral organs in a spiral or in whorls (or a mixture of both). The outer floral organs are sterile leaves called a perianth. When undifferentiated they are described as tepals. More often, there is differentiation into an outer whorl (calyx or sepals) and an inner whorl (corolla or petals). The androecium, or the totality of stamens, can be organized in a single series or into several whorls, with a specific position relative to the petals. The gynoecium consists of carpels bearing ovules. Carpels can be free or, more often, fused into an entity enclosing the ovules or seeds. Besides carpels and stamens, some flowers have sterile structures (staminodes or carpellodes) or other emergences of the receptacle. These are often developed as nectaries and can be conspicuous.

Flowers share another characteristic besides leaves with the vegetative parts of the plant, which is the phyllotaxis or order of initiation of floral organs (see p. 00). The transition in phyllotaxis from the vegetative shoot to the flower can be gradual or abrupt and is mediated by bracts and sepals. The calyx usually continues the same spiral sequence as vegetative leaves. There is generally a disruption in the initiation sequence between sepals and petals, leading to an alternation of whorls. The stabilization of numbers and the position of floral parts relative to each other is fundamentally important in understanding and interpreting the structure of the flower.

1.1.1   *Complex versus Reduced Flowers*

The evolution of flowers is correlated with the mode of pollination. There is a marked difference between flowers with a biotic (animal) pollination syndrome and those with an abiotic (wind or water) syndrome. Animal pollination is accompanied by a series of adaptations to attract and offer rewards to specific pollinators and to protect the floral parts from damage. Differentiation of protective sepals and carpels, nectaries, showy petals and stamens are part of the arsenal leading to effective fertilization. Depending on the pollinating animal, different strategies were developed to increase the success of pollination, occasionally leading to complex flowers or inflorescences, such as an increase in the number of floral parts (especially stamens), the development of an attractive perianth and reward system, and the evolution of highly specialized spatial interactions with pollinating organisms (Proctor, Yeo and Lack, 1996). Several examples illustrate the close connection between the pollinator and the evolution of floral traits, such as the development of spurs in *Aquilegia* (Whittal and Hodges, 2007), petaloid staminodes and stamen fertility in Zingiberales (Specht et al., 2012), or the corolla length in Polemoniaceae (Rose and Sytsma, 2021). Wind or water pollination is accompanied by a syndrome of derived characters, such as smaller, unisexual flowers, loss of petals or reduction of the perianth, long styles and filaments, production of a large amount of pollen, lack of viscin in pollen and reduction in the number of ovules (e.g. Linder, 1998; Friedman and Barrett, 2008; Friedman, 2011).

Reversals in the pollination syndrome occur frequently in the angiosperms. Secondary wind-pollinated flowers evolved in all major clades with a predominance of insect pollination (e.g. *Thalictrum* in Ranunculaceae, *Poterium* in Rosaceae, *Macleaya* in Papaveraceae, some *Acer* in Sapindaceae, some *Erica* in Ericaceae, *Fraxinus* in Oleaceae, *Xanthium* in Asteraceae, *Theligonum* in Rubiaceae, *Leucadendron* in Proteaceae). Larger, predominantly wind-pollinated clades including Fagales and Poales show the occasional

reversal to insect pollination (e.g. *Castanea* in Fagaceae, most Buxaceae, *Euphorbia* in Euphorbiaceae).

Specific elaborations of petals and/or staminodes are clearly linked with pollination syndromes and are triggered by the kind of pollinators that evolved with the flowers. Secondary stamen and carpel increases are widespread, and are linked with the potential for higher pollen or ovule supply. Very often there is a close mechanical correlation between perianth and stamens, or stamens and style, in the release of pollen or the protection of the anthers. Different elaborations on the petals are also directly linked to the pollinator (e.g. the building of landing platforms, nectar containers and nectar guides: see Endress and Matthews, 2006b).

An important condition for increased complexity in flowers is the attainment of greater synorganization (Endress, 2006), allowing a concerted change and interaction of floral organs. Therefore, events such as merism change, shifts in symmetry, fusions, and stamen and carpel increases depend on a close interaction of different organs in flowers, but also on interactions within the inflorescence. Flowers are morphologically highly dynamic entities with a potential for evolution reaching far beyond our preconceived ideas of the limitations of floral evolution. This flexibility is closely linked with what is available at the organ level at a given time, as well as inherent mechanical processes controlling the development of flowers (Ronse De Craene, 2018). Subtle shifts in the timing of organ initiation or internal pressures during the floral development can cause dramatic morphological changes in the flower with consequences for pollinator interactions (see Ronse De Craene, 2016, 2018; Chinga et al., 2021; Wei and Ronse De Craene, 2020).

1.2   Floral Organs

1.2.1   Perianth

> *If treated in isolation, there is no character combination which could stringently prove an organ's nature as a petal or sepal.* (Endress, 1994: 26)

The perianth is the envelope of sterile leaves enclosing the fertile organs of the flower. The perianth is either differentiated into sepals and petals, or undifferentiated (perigone or tepals). In the latter case the perianth can be green (sepaloid) or pigmented (petaloid). A distinction between sepals and petals is applicable only when two different series of perianth parts are found. In cases with more than two whorls the transition between sepals and petals can be progressive with blurred limits.

In some cases there is unclear distinction between the perianth and enclosing bracts. In other cases bracts can be variably associated with the flower, often

in the form of an epicalyx (e.g. Malvaceae), or sometimes as a fused cap or calyptra (e.g. Papaveraceae, Aextoxicaceae). Bracts can be distinguished from the perianth by presence of axillary buds (never in floral organs) and differences of plastochron (transition of a decussate to spiral phyllotaxis: Buzgo, Soltis and Soltis, 2004). Endress (2003a) suggested that bracts should be considered as phyllomes with a lower complexity than tepals. However, I believe that a distinction between bracts and tepals is sometimes impossible to make, given the existence of intermediate organs and the easy incorporation of bracts in the flower. Inclusion of bracts at the base of the flower makes an originally undifferentiated perianth biseriate, as in Magnoliaceae. Some taxa have transitional organs between bracts and tepals (in German called *Höchblätter*), as in Myrothamnaceae and some Ranunculaceae. There are known cases where bracts replace sepals that have been previously lost (*Quinchamalium* in Santalaceae) or act as a secondary calyx when petals are lost (*Mirabilis* in Nyctaginaceae).

The distinction between sepals and petals is not always straightforward (for a discussion and review, see Endress, 2006; Ronse De Craene, 2007, 2008; Ronse De Craene and Brockington, 2013). While core eudicots currently have a bipartite perianth of sepals and petals, the perianth is rarely differentiated in basal angiosperms, monocots and early diverging eudicots with variable homologies. If only a single whorl of perianth parts is present, it is sometimes difficult to categorize members of this whorl as sepals or petals, because one whorl may have been lost. A distinction can be made between primary apetaly (as in basal angiosperms with tepals and no distinction between perianth parts) and secondary apetaly (apopetaly: Weberling, 1989), in cases where evidence exists that petals have been present and have been lost during evolution. Sepals are petaloid in several families or can have a mixed nature (partly green and pigmented; e.g. *Impatiens*, *Polygala*). One of the reasons for this variability is that the perianth can change function at different stages of the development of the flower. In general, the calyx tends to protect inner organs and is photosynthesizing. Later, it can become attractive for the dispersal of fruits (e.g. *Physalis* in Solanaceae). Additionally, the pigmentation of the sepals can be regulated by other factors such as variable genetic shifts (e.g. petaloid calyx of *Tulipa*: Kanno et al., 2007, and *Rhodochiton*: Landis, Barnett and Hileman, 2012), or the influence of light on the developing bud (e.g. *Nymphaea*: Wagner, Rudall and Frohlich, 2009; *Kewa*: Brockington et al., 2013). The main purpose of petals is to attract pollinators, but they can become transformed into protective organs or dispersal units (e.g. in *Coriaria*). Petals are occasionally indistinguishable from sepals in Pentapetalae, but this probably represents a derived condition (e.g. Dipentodontaceae: Byng, 2014; *Prunus*: Wang et al., 2021).

The origin of the perianth was discussed in several textbooks and papers, with various interpretations for the origin of petals: either from stamens, from bracts, from both structures, or as something totally new with different mechanisms leading to the differentiation of the perianth (for recent reviews, see Irish, 2009; Ronse De Craene and Brockington, 2013; Glover et al., 2015; Monniaux and Vandenbussche, 2018). In general, recent evidence from morphological and evo-devo studies suggests that petals in the majority of angiosperms are derived from bract-like structures and are homologous to the sepals in the flower. Contrary to a general assumption, cases where petals are unequivocally derived from stamens are rare in the angiosperms. Petals are inserted between outer bract-like organs and inner stamens and undergo influences from both sides. In extreme cases petals can take over stamen characteristics so as to become confused with stamen-derived structures. This is caused by a delayed initiation of the petals, leading to their absorption in stamen tissue and a stronger influence of genes affecting stamens. Morphologically this results in petals resembling staminodes (small insertion base, single vascular bundle, bilobed lamina, etc.) and may be the reason for the persistent belief that petals represent transformed stamens (see Ronse De Craene and Brockington, 2013; Wei and Ronse De Craene, 2019). In several groups, petals have variously evolved by insertion of bracts in the confines of the flower and their differentiation into two functional whorls. An undifferentiated perianth was reconstructed as ancestral for the angiosperms in recent phylogenetic studies (Soltis et al., 2005; Sauquet et al., 2017). In basal angiosperms, attraction and protection are combined with pigmentation of the entire perianth. A differentiated perianth has evolved independently several times, at least once at the base of Pentapetalae (Ronse De Craene, 2008; Litt and Kramer, 2010).

The presence of a perianth (as well as surrounding organs, such as bracts) has a stabilizing effect on the flower in causing pressure and regulating the phyllotaxis, merism and symmetry (Ronse De Craene, 2018). Loss or reduction of the perianth is generally associated with a breakdown of a regular floral arrangement (e.g. *Achlys* in Berberidaceae: Endress, 1989; *Euptelea*: Ren et al., 2007; *Theligonum*: Rutishauser et al., 1998).

Undifferentiated Perianth (Tepals or Perigone)

An undifferentiated perianth tends to be concentrated in the basal angiosperms and monocots, and is usually associated with spiral or trimerous flowers. A distinction needs to be made between a primary undifferentiated and a secondary undifferentiated perianth. In the first case, tepals have evolved from bracts that became associated with reproductive organs and have acquired

secondary functions of protection and attraction of pollinators. This kind of perianth is usually spiral with a gradual differentiation from outer bract-like to inner petaloid tepals (e.g. Austrobaileyaceae, Calycanthaceae). Alternatively, two trimerous perianth whorls of several monocots are undifferentiated and petaloid. However, the switch between sepals and petals can be easy in these cases (Ronse De Craene, 2007). A secondarily undifferentiated perianth arises by loss of either the calyx (e.g. Santalaceae, Apiaceae) or the corolla (e.g. *Geissos* in Cunoniaceae, *Rodgersia* in Saxifragaceae) and should be referred to as a reduction.

Calyx

Sepals have a spiral initiation sequence with rapid growth, a broad base, three vascular traces and an acuminate (pointed) tip. The homology of sepals with leaves is based on similar anatomy as well as on several characteristics such as the presence of stipules and stomata. Sepals are often compared with the petiole of a leaf due to their broad shape and the occasional presence of a small appendage or a dorsal crest (Arber, 1925; Guédès, 1979). On the contrary, petals often arise nearly simultaneously and have a delayed growth. They have a narrow base with only a single vascular trace and the tip is bifid or emarginated. Characteristics are more closely comparable to stamens than to leaves (Ronse De Craene, 2007).

Sepals can be fused together (gamosepaly). This fusion is often congenital (see p. 41) at their margins, leaving free calyx teeth. Sepals are more often persistent than caducous; very often, they increase in size after pollination and function in fruit dispersal. Reduction of sepals or their transformation into small scales or bristles is occasionally found in some families (e.g. in Asteraceae, Caprifoliaceae). The calyx may also vanish completely (e.g. in Santalaceae), leaving a single petal whorl combining attraction with protection of the flower.

Corolla

The corolla, or petals, represent the inner perianth whorl of the flower and are usually pigmented (petaloid). The number of petal whorls can be high, as in Annonaceae or Berberidaceae (up to four whorls). Petals can sometimes be highly distinctive, with a claw (a narrow base, compared with a broadened base in sepals), or they can be indistinct from sepals.

The corolla can be highly elaborate by development of ventral appendages, fimbriate margins or extended tips. Petals are often trilobed, with a protruding middle lobe (e.g. Saxifragaceae, Sapotaceae) or extensive lateral lobes

(e.g. Elaeocarpaceae). Bilobed petals can be formed by reduction of the central lobe (Endress and Matthews, 2006b).

In some families, petals are highly elaborate in relation to specific pollination mechanisms. For example, Byttnerioideae (Malvaceae) have petals as inverted spoons, with a hood-like base and an extended apex. More examples are given by Endress and Matthews (2006b), who suggested a correlation between the smaller size or reduction of petals and elaborations on the petal surface. However, petal reduction or loss is linked with other factors, such as a shift of attraction to the sepals and the development of a hypanthium (Ronse De Craene, 2008). Fusion of petals (sympetaly) is a frequent phenomenon in angiosperms that occurs independently or is closely linked with the evolution of the androecium. Petal tubes appear to regulate access to flowers by a variable extent of development.

The nature and origin of petals remains a contentious subject, with uncertainty about the homology of petals (bracteopetals or andropetals), especially in Pentapetalae (Endress, 2006; Ronse De Craene and Brockington, 2013; Monniaux and Vandenbussche, 2018). However, floral developmental evidence tends to demonstrate that petals are influenced by neighbouring organs during their development. A delayed petal development can lead to them being overtaken by the stamens and their absorption in the meristematic tissue of the androecium (stamen-petal primordia: p. 54). As a result petals will resemble stamens (narrow base, single vasculature) and might even be confused with staminodial structures (Ronse De Craene, Clinckemaillie and Smets, 1993; Ronse De Craene and Bull-Hereñu, 2016; Wei and Ronse De Craene, 2019). Rapidly developing petals will often continue the spiral sequence of sepals and bear more resemblance to bracteopetals (e.g. Paeoniaceae, Clusiaceae, Pentaphyllaceae).

1.2.2   *Androecium*

The androecium consists of stamens, which make up the male part of the flower. Stamens are relatively uniform. They mostly consist of four pollen sacs arranged in two lateral thecae grouped in an anther that is linked by a connective to a filament. The orientation of anthers can be inward (introrse), lateral (latrorse) or outward (extrorse). Stamens can be basally connected into a tube (e.g. Meliaceae, Malvaceae), or connected with the petals in a common stamen-petal tube (e.g. Caricaceae, Rubiaceae). Anthers may become laterally connivent or fuse postgenitally (e.g. Asteraceae, Balsaminaceae). The number and position of stamens appear to be the most variable in the flower compared to other floral organs, but this variation is never randomized and is relatively

conservative in angiosperms. Therefore, stamen position represents one of the most significant characters in flower phylogeny (see Ronse De Craene and Smets, 1987, 1996a, 1998a). Flowers with more than two stamen whorls are rare and largely restricted to basal angiosperms and some basal monocots. In other instances they are the result of a secondary increase (see p. 00: e.g. Rosaceae).

When there is only a single whorl, stamens are either inserted opposite the sepals (haplostemony: e.g. Gentianaceae, Violaceae), or less frequently opposite the petals (obhaplostemony: e.g. Vitaceae, Primulaceae). When two stamen whorls are present, they arise separately and are often spatially separated (Figure 1.1). The number of stamens is ten in pentamerous flowers or eight in tetramerous flowers, a common pattern among rosids. Diplostemony is the condition where the outer stamen whorl is situated opposite the sepals and the inner whorl is situated opposite the petals (e.g. Coriariaceae, Burseraceae). Obdiplostemony is the opposite condition, with outer stamens opposite the petals (e.g. Geraniaceae, Saxifragaceae). The distinction between diplostemony and obdiplostemony is often the result of developmental constraints and shifts
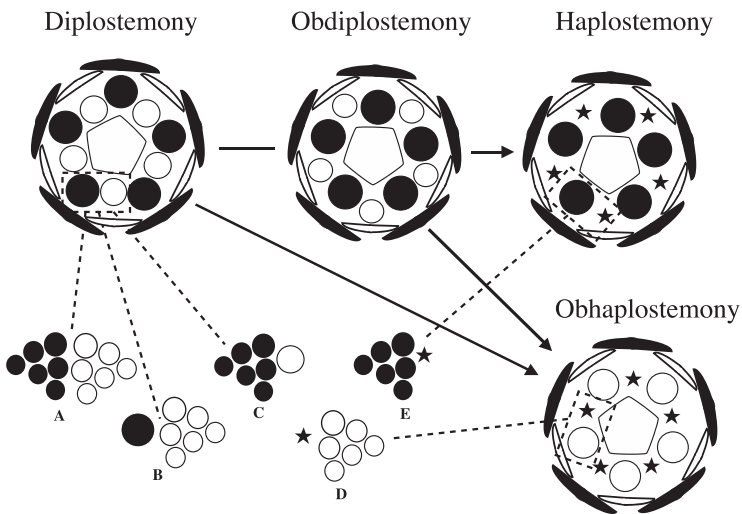

Figure 1.1 Diagram representing possible changes in the androecium of a pentamerous flower with two stamen whorls. Black dots, antesepalous stamens; white dots antepetalous stamens; asterisk, lost stamen position or staminodes. A. increase of antesepalous and antepetalous stamens; B. increase of antepetalous stamens only; C. increase of antesepalous stamens only; D. sterilization or loss of antesepalous stamens and increase of antepetalous stamens; E. sterilization or loss of antepetalous stamens and increase of antesepalous stamens

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(for a review, see Ronse De Craene and Bull-Hereñu, 2016). Obdiplostemony may be caused by the pressure of developing carpels resulting in more outward orientation and shift of the antepetalous stamens (e.g. Ericaceae, Rutaceae, Geraniaceae: Leins, 1964a; Eckert, 1966; Ronse De Craene and Smets, 1995b; Endress, 2010a). In some groups of plants, the antepetalous stamens arise before the antesepalous stamens; this inverted development is often linked with weakening or sterilization of the antesepalous stamens leading to obhaplostemony (e.g. Malvaceae, Primulaceae). The importance of obdiplostemony should not be overestimated, although it represents a stable transitional condition in the evolution of a single whorl from two stamen whorls (Ronse De Craene and Bull-Hereñu, 2016). This trend may be related to a conversion of one whorl into staminodes.

Staminodes

Staminodial structures are defined as sterile stamens. The main criterion in recognizing staminodial structures is that of position, as any emergences in the flower can arbitrarily be called staminodial (Leins and Erbar, 2010). Rarely, the presence of sterile anthers is an indication of a former function as stamens. Staminodes are widely scattered in the angiosperms (e.g. Walker-Larsen and Harder, 2000; Ronse De Craene and Smets, 2001a), and are the result of sterilization affecting a complete whorl of stamens, or a variable number of stamens within a whorl. Sterilization of stamens has evolved frequently in angiosperms – for example, it affects 72 per cent of all families of rosids (Walker-Larsen and Harder, 2000). In cases where an entire stamen whorl becomes obsolete, stamen remnants may still be identified in flowers, but they will eventually disappear and this process is irreversible. However, in many instances loss of fertility is accompanied by acquisition of novel functions not performed by stamens, such as differentiation into food bodies (*Calycanthus*), osmophores (*Austrobaileya*), building of nectar containers (e.g. Loasaceae), enhanced optical attraction (Theophrastaceae, Eupomatiaceae, Zingiberaceae), differentiation into nectaries (e.g. *Helleborus* in Ranunculaceae), or a combination of these (*Ranunculus*, *Aquilegia*). This process offers new evolutionary potential in many groups of plants. Walker-Larsen and Harder (2000) argued that sterilization of stamens within a whorl is evolutionarily reversible, such as in Lamiales, where the adaxial staminode can be restored to a fully fertile stamen by a reversal to polysymmetry. However, there is a threshold beyond which such a reversal is impossible (Ronse De Craene, 2018).