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Synorganisation without organ fusion in the flowers of *Geranium robertianum* (Geraniaceae) and its not so trivial obdiplostemony

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• *Background and Aims* Synorganisation of floral organs, an important means in angiosperm flower evolution, is mostly realized by congenital or post-genital organ fusion. Intimate synorganisation of many floral organs without fusion, as present in *Geranium robertianum*, is poorly known and needs to be studied. Obdiplostemony, the seemingly reversed position of two stamen whorls, widely distributed in core eudicots, has been the subject of much attention, but there is confusion in the literature. Obdiplostemony occurs in *Geranium* and whether and how it is involved in this synorganisation is explored here.
• *Methods* Floral development and architecture were studied with light microscopy based on microtome section series and with scanning electron microscopy.
• *Key Results* Intimate synorganisation of floral organs is effected by the formation of five separate nectar canals for the proboscis of pollinators. Each nectar canal is formed by six adjacent organs from four organ whorls. In addition, the sepals are hooked together by the formation of longitudinal ribs and grooves, and provide a firm scaffold for the canals. Obdiplostemony provides a guide rail within each canal formed by the flanks of the ante-petalous stamen filaments.
• *Conclusions* Intimate synorganisation in flowers can be realized without any fusion, and obdiplostemony may play a role in this synorganisation.

Key words: Angiosperms, diplostemony, floral architecture, floral development, floral morphology, fusion, Geraniaceae, *Geranium robertianum*, obdiplostemony, synorganisation.

INTRODUCTION

Synorganisation in flowers is commonly based on congenital and post-genital fusion of organs (Endress, 1990, 1994, 2006; Rudall and Bateman, 2002; Classen-Bockhoff and Heller, 2008; Specht and Bartlett, 2009). Cases without fusion have been much less considered (e.g. Vogel, 1969). *Geranium robertianum* is a prominent example but has never been studied in detail. Flowers of *Geranium* are also known for the occurrence of the often mentioned but poorly understood phenomenon of obdiplostemony. Whether obdiplostemony is related to floral synorganisation has not been explored.

This work has two goals. The first is to demonstrate the intricate synorganisation of the flowers of *G. robertianum* and to show how particular shapes of single organs can only be understood from the perspective of architecture and synorganisation (Endress, 2006). Although extensive congenital organ fusion is only present in the gynoecium, the flowers also have a high degree of synorganisation in the perianth and androecium. The second goal is to elucidate the phenomenon of obdiplostemony in angiosperm flowers, which is more intricate than is often expounded, and to show how both aspects, synorganisation and obdiplostemony, may be connected. Obdiplostemony has been studied in detail with floral developmental studies, and it can be understood as differential development of the sepal and petal sectors in flowers, as shown in several detailed, critical works in the 1960s (Eckardt, 1963; Leins, 1964; Rohweder, 1963, 1965, 1967, 1970; Eckert, 1966; Gut, 1966; Gelius,

1967; Klopfer, 1968, 1972, 1973; Mayr, 1969). Although an overview and discussion of obdiplostemony was provided again later by Ronse Decraene and Smets (1995), in some most recent works subtleties of obdiplostemony worked out earlier were neglected (e.g. Prenner *et al.*, 2010; Ronse De Craene, 2010). There is no need to reinvent the wheel if a more advanced model is available from almost half a century ago.

Flowers of *Geranium* are generally protandrous (Yeo, 1973; Tofts, 2004). This is also true for *G. robertianum*, although protogyny may also occur depending on environmental factors (Stäger, 1913; Wangerin, 1926; Bertin, 2001). In the male phase, at first the antesepalous anthers open, followed by the antepetalous anthers. The five stigmatic branches are at first contiguous and the receptive areas are hidden. In the female phase, the stigmatic branches expand and expose the receptive areas. The anthers fall off and only the stamen filaments remain in the flower (and keep functioning in the guidance of the pollinator proboscis to the nectaries). A shorter or longer overlap time between the male and female phase is common in *G. robertianum*. At the end of anthesis the petals abscise rapidly (Sexton *et al.*, 1983). These events in the course of anthesis should be kept in mind for a better understanding of synorganisation and elaboration of the flowers in *G. robertianum*.

MATERIALS AND METHODS

Flowering shoots of *Geranium robertianum* L. from specimens growing spontaneously in the Botanic Garden of the

University of Zurich, Switzerland (P. K. Endress 10–51 and 7224), were collected and fixed in 70 % ethanol. Flowers at different developmental stages were dehydrated, treated in osmium tetroxide, critical-point dried and sputter coated with gold for imaging by scanning electron microscopy (SEM; Hitachi S-4000, studied at 20 kV). For light microscopy, flowers were dehydrated and embedded in paraplast for microtome sectioning. Section series of 7 or 10 mm thickness were produced with a Leitz rotary microtome, stained with safranin and Astrablue, and embedded in Eukitt.

RESULTS

Flowers at anthesis

The flowers are salverform with a narrow, tubular basal part and an upper part with horizontally expanded petals (Fig. 1A, B). In addition, they have a revolver architecture with five separate canals leading to five hidden nectaries at the floral base (Fig. 1C).

The five sepals have a broad base and a narrow apex with a long, terete appendage (Fig. 4A). They have three longitudinal ribs on the dorsal side, each with a vascular bundle (Fig. 2A–F). The five petals have a narrow claw at the base and an expanded blade with a rounded apex; the claw and blade are about the same length (Fig. 1B). Each claw has two longitudinal ribs on its ventral side (Figs 2B, F and 3). There is only one vascular bundle in the claw but, only higher up, in the blade, does this bundle ramify into several bundles. The longitudinal ribs of sepals and petals provide a certain stiffness to each individual organ. The sepals have a hypodermal reinforcement layer on the upper side (Fig. 2A–F), containing thickened cell walls and an oxalate druse in each cell [as common for Geraniaceae in general (Kenda, 1956)].

The ten stamens are free, but by their upright position they form a sheath around the ovary and style (Figs 2B, F, 3 and 4J). The filament is constricted at the attachment point of the anther, where the anther abscises at the end of the male phase. At anthesis the ten stamen bases are congenitally united in a short tube around the gynoecium base (Fig. 2C). The antepetalous stamens attach slightly higher up to the floral base than the antesepalous stamens in young buds

(Fig. 2A) as well as at anthesis (Fig. 2D). Below the base of each antesepalous stamen there is a nectary (Figs 1B, 2E and 4D, J). The five antesepalous stamens are longer than the five antepetalous stamens (Fig. 4J) and their anthers open earlier (Fig. 1C).

The five carpels are free only at the top, in the stigmatic region, but are congenitally united below, along the style and ovary. For most of its length, the gynoecium is symplicate; only below the placentae is it synascidiate. Each carpel has two ovules, one above the other. A compitum is present along the entire symplicate zone (Fig. 2F). In the ovary five separate strands of pollen tube transmitting tract extend to the five locules, each between the two ovules.

Floral organ synorganisation and floral architecture

The presence of the longitudinal ribs on sepals and petals becomes immediately clear when the organs are viewed in the floral architecture. As the flowers are salverform, the longitudinal ribs of both sepals and petals play a role in the tubular basal part of the flower, in which the sepals and the narrow lower part of the petals (the claws) have an upright position. The sepals have a quincuncial aestivation (also at anthesis) and the incurved margins of the outer flanks (sepals 1, 2, and one flank of sepal 3) are hooked into the groove formed by the two adjacent ribs of the adjacent inner sepal (Figs 2A–F, 3 and 4A). This results in a stable and firm architecture of the tubular basal part of the flower (Figs 1A and 4B). In addition, the longitudinal ribs of the upright lower part of the petals enhance the stability of each petal. The upper part of the petals, the blades, have a contort aestivation in bud.

As to the revolver architecture, the construction to form the five internal admissions to the five nectaries at the floral base is even more intricate. In the formation of each canal in each sepal sector no fewer than six floral organs from four floral organ whorls are involved. These six organ parts are: the median part of a sepal, the lateral parts of two adjacent petals, the lateral parts of two adjacent antepetalous stamens and an antesepalous stamen (containing the nectary below its attachment area) (Figs 2F and 3). Especially important are the two associated petals, which form the lateral boundary of the canal with their ventral longitudinal ridges, and the two

Fig. 1. *Geranium robertianum*. Flowers at anthesis. (A) Salverform flower in the female stage, from the side. (B) Flower in the female stage, outer floral organs removed on one side (arrows point to nectaries). (C) Flower from above, with the five separate canals (arrows) that lead to the five nectaries; the anthers of the antesepalous whorl opened, those of the antepetalous whorl still closed; stigma beginning to expand. Scale bars = 1 mm.
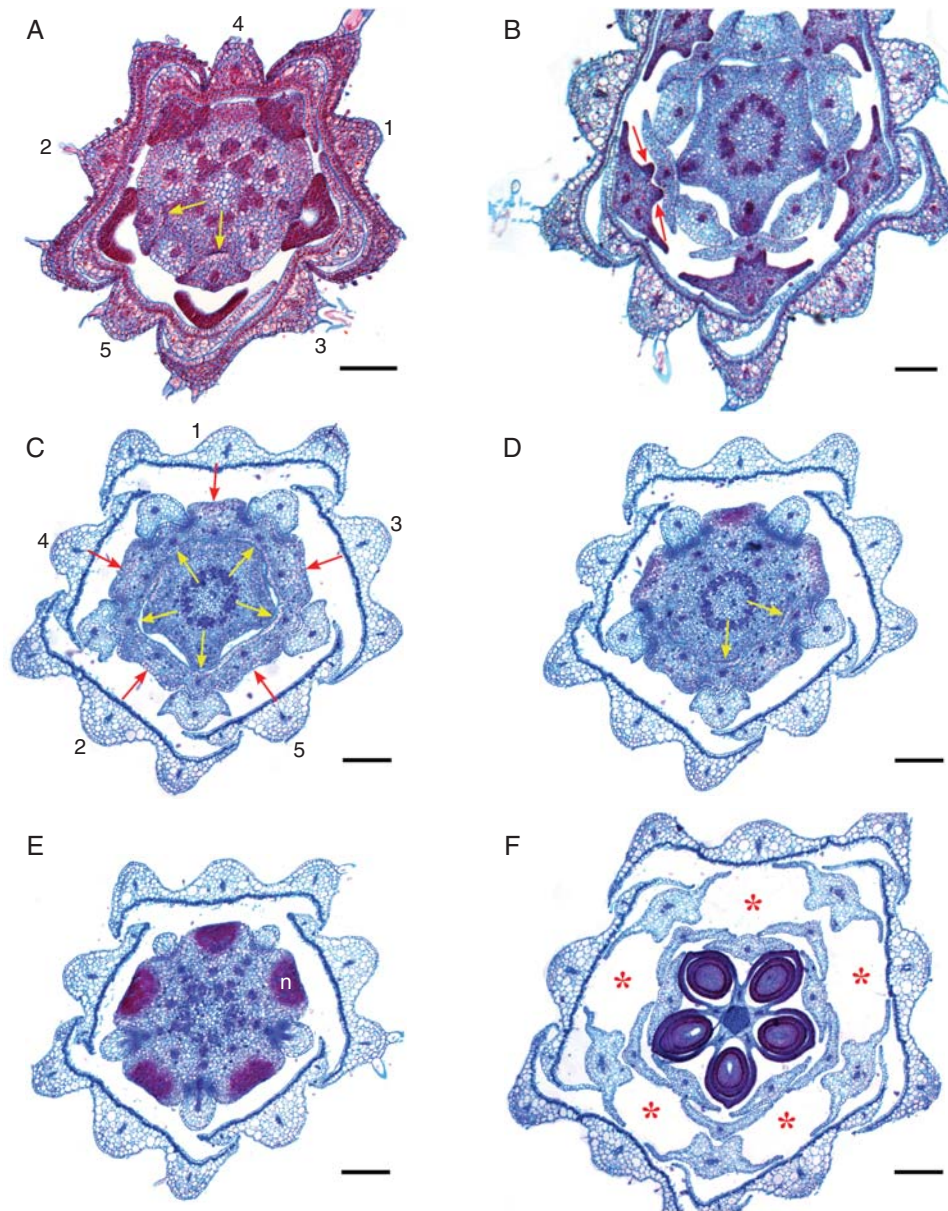
Fɪɢ. 2. *Geranium robertianum.* Transverse sections of flowers. (A) Young floral bud, level of attachment of petals and stamens; attachment of antesepalous stamens at a lower level than that of antepetalous stamens (ventral contour of two antepetalous stamens that are still free indicated by arrows); sepals numbered according to their sequence of origin. (B) Older floral bud, showing the still meristematic petals with the two ridges on the ventral side (marked with arrows in one petal). (C–E) Floral bud shortly before anthesis, at different levels, from the top down. The dark blue line on the upper surface of sepals is the hypodermal reinforcement layer. (C) Level of the short tube of congenitally united stamens; antesepalous stamens thicker than antepetalous stamens (red arrows point to outer side of antesepalous stamens, yellow arrows point to inner side of antepetalous stamens); sepals numbered according to their sequence of origin. (D) Level of attachment of antepetalous stamens (ventral contour of two antepetalous stamens indicated by arrows; compare with A). (E) Level of nectaries (n). (F) Anthetic flower; nectar canals indicated by asterisks. Ovary with compitum in the centre (five-angled dark blue area). Scale bars: (A, B) = 200 μm; (C–F) = 400 μm.

antepetalous stamens, which channel the immediate access to the nectar by their broad lateral wings by forming a guide rail (Figs 3 and 4).

Development of floral architecture and the advent of obdiplostemony

Between the initiation of the five sepals and five petals there is a long plastochron, and the sepals broaden and thicken

considerably so that the remaining floral apex becomes five-angled (Fig. 4E). The petals and antepetalous stamens arise in the five angles of the floral apex and the antesepalous stamens between the angles. Soon after their initiation, the development of the petals and antepetalous stamens is delayed compared with sepals and antesepalous stamens, in particular that of the petals (Fig. 4F–I). The attachment areas of both petals and antepetalous stamens are narrow and thin (Fig. 4G, H). As a consequence, the dorsal side of the
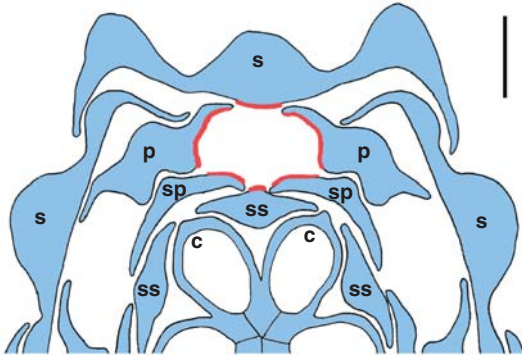
Fig. 3. *Geranium robertianum*. Transverse section of a flower at anthesis; schematic drawing (corresponding to Fig. 2F). Participation of six organs in the formation of one canal is marked with red lines. c, carpel; p, petal; s, sepal; sp, antepetalous stamen; ss, antesepalous stamen. Scale bar = 200 μm.

antepetalous stamens is slightly more inside than that of the antesepalous stamens, as expected from the second stamen whorl, but the ventral side is more outside than that of the antesepalous stamens (Fig. 2C). In addition, the attachment of the antepetalous stamens to the floral base is not further outside than that of the antesepalous stamens in early development. Only later, when they form a guide rail towards each of the nectaries, do the antepetalous stamens appear more outside (Fig. 2B, F). This change can be well visualized in SEM micrographs that show petals and stamens from the outside. At an early stage the dorsal side of the antepetalous stamens is more inside than that of the antesepalous stamens and it is narrower (Fig. 4G, H). Later the antepetalous stamens develop a wing on both sides at the base behind the the adjacent antesepalous stamens so that they now become more outside (Fig. 4I). At both these stages the petals are still minute due to their extreme delay in early development. Then the wings of the epipetalous stamens broaden conspicuously to form the guide rail for the proboscis of pollinators (Fig. 4J). At this stage the petals have surpassed the stamens in length. The stage shown in Fig. 4C seen from above shows the five outwardly curved smaller antepetalous stamens and also the five young carpels formed in the five petal sectors, where there is more space than in the sepal sectors, because the organs remain so small at the beginning of development.

DISCUSSION

Many *Geranium* species have flat, open, plate-like flowers, which display a more simple architecture than the salverform flowers of *G. robertianum* and which may therefore seem more primitive at first sight. For instance, in *G. molle* and *G. phaeum* with open, plate-like flowers, the petals are clawless and they do not have longitudinal ridges (personal observation). However, most species of the basal sub-clade of the genus, subgenus *Robertium* (which includes *G. robertianum*) (Fiz *et al.*, 2008), have salverform flowers (Yeo, 1973, 2001), including *G. macrorrhizum*, which is sister to the remainder of subgenus *Robertium*. Pollinators of *G. robertianum* are, for example, long-tongued syrphids and bumble-bees (Tofts, 2004). Salverform flowers with sunken nectaries are also present in other genera

of Geraniaceae [probably all species of *Pelargonium* and part of *Erodium* and *Monsonia* (Albers and Van der Walt, 2007)]. Thus the salverform floral architecture of *G. robertianum* may be basal in the genus and the more open, plate-like architecture of other species may be derived. However, this needs more detailed morphological studies in *Erodium* and *Monsonia* and subsequent evolutionary evaluation at the family level. In the *Geranium* species with open, plate-like flowers nectar is reached by pollinators from the centre between the attachment regions of each of two adjacent petals. The nectaries are below the attachment point of the petals in the sectors between the petals, which was first noted by Sprengel (1793) and Delpino (1873/1874), and was nicely visualized for *G. sylvaticum* by Nilsson (1984). Thus they are also revolver flowers, but the five pathways for the proboscis of the pollinators are less architecturally complex than in *G. robertianum*. Two longitudinal ridges on petal claws are also present in the salverform flowers of some Caryophyllaceae (Rohweder, 1967; Leins *et al.*, 2001). These ridges are perhaps primarily a means to reinforce the single petals in this floral architecture. In *Geranium* they are secondarily also involved in the formation of the nectar canals.

Diplostemony and obdiplostemony

Diplostemony, the presence of two alternating isomerous stamen whorls following the isomerous perianth whorl(s) is common in monocots and eudicots, especially in rosids and Saxifragales (Ronse Decraene and Smets, 1995). They are also present in Caryophyllales and a few basal asterids (Ericales). Ronse Decraene *et al.* (1998) regarded Caryophyllales with two isomerous stamen whorls not as diplostemonous but as 'pseudodiplostemonous', because the stamens arise in a spiral sequence (see also Lyndon, 1978) and because this pattern may have originated via a different evolutionary pathway. However, this argument does not hold because in rosids and Saxifragales the stamens of a whorl also do not always arise synchronously [e.g. Saxifragaceae (Soltis and Hufford, 2002)]. Distribution of diplostemony in eudicots indicates that it evolved several times and it would not be practical to use a separate term for each origination.

The term obdiplostemony was introduced by Chatin (1855) for flowers with two stamen whorls in which the antepetalous whorl is the outer instead of the antesepalous whorl and, consequently, the carpel whorl (if isomerous) alternates with the antesepalous stamen whorl. Thus there is a seeming lack of alternation between the petal whorl and the outer stamen whorl.

Broad discussions of obdiplostemony are found in Eckert (1966) and Ronse Decraene and Smets (1995). There is no need to repeat all their points. However, two aspects that were not discussed in the latter work need to be addressed. First, because the dimensions of the attachment area, i.e. the thickness and width, of the antesepalous and antepetalous stamens can be very different (this can only be seen in microtome sections, not in SEM micrographs), it is sometimes not possible to tell whether an organ is further inside than the other. This was well visualized in Leins (1964, p. 81) and Leins and Erbar (2008, fig. 21d). Further, these relative dimensions can change during development. Thus they may be different at the time of initiation, early development, late
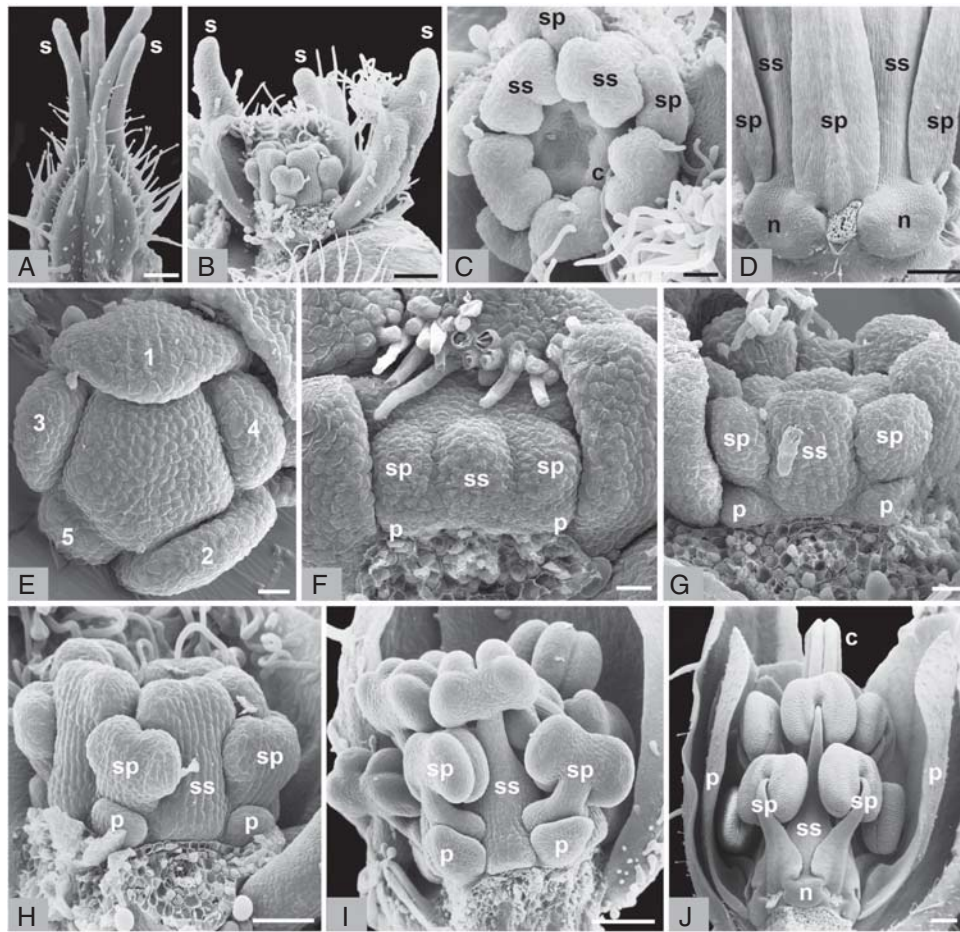
FIG. 4. *Geranium robertianum*. SEM micrographs of flowers. (A) Medium-sized floral bud from the side, showing the awn-like tips of the five sepals, and the three ridges of one of the sepals. The sepals have long secretory hairs. (B) Young floral bud from the side, with two sepals removed and the remaining three sepals spread out, showing young petals and stamens (same flower as in C and H). The size difference between the large sepals and the delayed minute petals is enormous. (C) Inner part of a flower bud from above, showing outward-directed antepetalous anthers and the antesepalous position of the young carpels (same flower as in B and H). (D) Anthetic flower, sepals and petals removed, showing two nectaries (n) and three antepetalous stamen filaments forming two guide rails leading to the two nectaries. (E) Floral bud after formation of the sepals, from above; remaining floral apex five-angled. (F–J) Floral buds at successively older stages, from the side, sepals partly removed to show petals and stamens. (F) After initiation of petals and stamens. Petals still minute, antepetalous stamens and petals forming a 'common primordium'. (G) Petals still minute, antepetalous stamens shorter, thinner and narrower than antesepalous stamens. (H) Petals still minute, antepetalous stamens directed outwards, outer contour in the attachment area more inside than that of the antesepalous stamens (same flower as in B and C). (I) Petals still minute, antepetalous stamens forming wings at the base outside the antesepalous stamens, which accentuate the obdiplostemonous appearance. (J) Petals and carpels now longer than stamens; wings of antepetalous stamens more developed. c, carpel; p, petal; s, sepal; sp, antepetalous stamen; ss, antesepalous stamen. Scale bars: (A, C, J) = 200 µm; (B, I) = 100 µm; (D, H) = 50 µm; (E, F, G) = 20 µm.

development and anthesis (Leins and Erbar, 2008, fig. 21). A second, more trivial aspect is that the position of the antepetalous stamens may seem more outside in a superficial inspection from above, because the anthers are more outside, whereas the attachment area of the stamens is not; it is at the same level or more inside (Fig. 4C, H). What is decisive, however, is the attachment area of the stamens, and not the position or direction of the anthers.

A tentative general description of the developmental establishment of obdiplostemony is as follows (see also Eckardt, 1963; Leins, 1964; Eckert, 1966; Gelius, 1967; Klopfer, 1973). In contrast to the early rapid growth and pronounced thickening of the sepals, the petals are considerably delayed and remain narrow and thin. The associated antepetalous stamens are also delayed after initiation and remain smaller compared with antesepalous stamens. Consequently, the petals and antepetalous stamens occupy less space on the remaining floral apex than sepals and antesepalous stamens. Thus although they are younger, they remain relatively further outside than the organs in the sepal sectors, and for carpel initiation there is more space in the petal sectors than in the sepal sectors. This situation may be further reinforced during further development, because the growing carpels use more space in the petal sectors. The contour of the flower (without the calyx) is not circular but pentagonal in early development, and the petals and antepetalous stamens lie in the five angles.

There is no fundamental organisational difference between diplostemony and obdiplostemony. In both cases the stamens of the two whorls are more or less in a series [sometimes all basally fused into a short tube, e.g. in Caryophyllaceae (Rohweder, 1970) and in Geraniaceae (this study)], and

those of the developmentally second whorl may be slightly more inside or slightly more outside at anthesis, even in closely related taxa, as discussed in detail for Caryophyllaceae by Rohweder (1970).

Revolver architecture and obdiplostemony

In *G. robertianum* each of the five canals for access to a nectary has a guide rail leading the insect's proboscis toward the nectar. The guide rail is formed by the flanks of two adjacent antepetalous stamens. As each nectary is situated below an antesepalous stamen, the flanks of the antepetalous stamens need to be situated outside the antesepalous stamen at the level of the guide rail at anthesis. This requirement accentuates the floral obdiplostemony.

The position of nectaries in the sepal sectors at the base of the androecium is most common in the family Geraniaceae, occurring in *Geranium*, *Erodium* and *Pelargonium* (see also Vogel, 1998). Only in *Monsonia* are the five nectaries situated in the petal sectors (personal observation). *Monsonia*, however, also deviates in that the antepetalous stamens are in double positions. Thus, the outer androecial whorl has ten instead of five stamens, which precludes a direct comparison of *Monsonia* with the other genera. Nevertheless, in *Monsonia* the antepetalous stamens also become evident after the antesepalous stamens (Klenter and Albers, 2004). They appear to be more outside than the antesepalous stamens. If only the initiation sequence is considered, there is no disruption in the alternation of stamen whorls.

In other families with obdiplostemonous flowers the position of the nectaries is not always the same. For instance, in *Oxalis* (Oxalidaceae), which also has revolver flowers, the nectaries are at the base of the antepetalous stamens (Matthews and Endress, 2002), and it is the petal margins that form two longitudinal crests producing a canal between them. Thus obdiplostemony is not necessarily linked with antepetalous nectary position.

Peculiarities of sectorial differentiation in the two stamen whorls in early development after initiation

As in *Geranium*, in many clades with flowers with two whorls of stamens, the antepetalous stamens are shorter (mostly because of shorter filaments) or otherwise smaller than the antesepalous stamens, as shown in comparative studies in our laboratory for representatives of many orders and families, such as Cucurbitales [Anisophylleaceae, (Matthews *et al.*, 2001; Coriariaceae, Matthews and Endress, 2004)], Celastrales [Lepidobotryaceae (Matthews and Endress, 2005*a*)], Oxalidales [Connaraceae, Oxalidaceae and Tremandraceae (Matthews and Endress, 2002); Cunoniaceae (Endress and Stumpf, 1991; Matthews *et al.*, 2001; Matthews and Endress, 2002)], Malpighiales [Chrysobalanaceae *sensu lato* (stamens often in two whorls, but in groups of two or more, stamens of antepetalous groups shorter) (Matthews and Endress, 2008)], Crossosomatales [Stachyuraceae and Strasburgeriaceae (Matthews and Endress, 2005*b*)] and Sapindales [Anacardiaceae and Burseraceae (Bachelier and Endress, 2009)]. Examples of groups studied by other authors are in Saxifragales [Crassulaceae (Wassmer, 1955)], Fabales [Fabaceae (Tucker, 1987; Prenner, 2003, 2004;

McMahon and Hufford, 2005)], Malpighiales [Malpighiaceae (Anderson, 1983)], Sapindales [Rutaceae (Gut, 1966)], Brassicales [Caricaceae (Ronse Decraene and Smets, 1999*b*); see also Ronse Decraene and Smets (1995)] and Ericales [Ericaceae (Leins, 1964; Schönenberger *et al.*, 2005; Schönenberger, 2009)]. This list is by no means exhaustive. Its aim is just to show how common in a broad range of rosids (and some other eudicots) this pattern is. In a number of groups the antepetalous stamens are not only smaller but, in addition, sterile. The latter is also common in many Geraniaceae, such as *Erodium* and *Pelargonium*. In the extreme case, the antepetalous organs are lost altogether (e.g. Ronse Decraene and Smets, 1995). The reverse condition with the antepetalous stamens more developed than the antesepalous stamens is rare. It is known, for example, from Cucurbitales: Corynocarpaceae [*Corynocarpus*, only antepetalous stamens fertile, antesepalous stamens petaloid (Matthews and Endress, 2004)] and Sapindales: Burseraceae [some *Protium* species, antepetalous stamens slightly longer (Bachelier and Endress, 2009)].

As in *Geranium*, strong retardation of petals and antepetalous stamens after initiation is also present in a number of other eudicots, e.g. other Geraniales [Melianthaceae (Ronse Decraene and Smets, 1999*a*)], Saxifragales [Saxifragaceae (Soltis and Hufford, 2002)], Zygophyllales [Zygophyllaceae (Ronse Decraene and Smets, 1995)], Myrtales [Onagraceae (Mayr, 1969)] and Caryophyllales [Caryophyllaceae (Rohweder, 1967; Ronse Decraene *et al.*, 1998; Leins *et al.*, 2001)]. In some taxa the developmental delay is so strong that the petal and associated antepetalous stamen have been described as developing from a common primordium (discussion in Eckert, 1966; Ronse Decraene *et al.*, 1993).

Stamen initiation is not centrifugal in obdiplostemonous flowers

The androecium in *Geranium* is thus not centrifugal, i.e. the antepetalous stamens are not initiated before the antesepalous stamens, as erroneously stated by Frank (1876) and Schumann (1889). In *G. nodosum* the antesepalous stamens are initiated shortly before the antepetalous stamens; the antesepalous stamens develop in the upright direction, whereas the antepetalous stamens develop in a more horizontal direction (Eckert, 1966). In *G. sanguineum*, both stamen whorls are simultaneously initiated (Erbar, 1999). In *G. endressii*, the youngest stage shown by Ronse Decraene *et al.* (1993) suggests at least that the antepetalous stamens are not initiated before the antesepalous stamens. This is also true for *G. robertianum* (this study).

There are also various errors in the literature regarding obdiplostemony in other angiosperms. The two examples mentioned by Rudall (2010) as centrifugal, *Tradescantia* and *Arabidopsis*, are not clearly centrifugal. In Commelinaceae, the initiation of the stamens is not centrifugal as erroneously stated by Payer (1857) who, judging from his illustrations, apparently had not seen the earliest stages of the androecium. Centrifugality is only simulated after stamen initiation by the different direction of the stamens in the two whorls. Just as mentioned for *Geranium*, in Commelinaceae too (and other families; see Gelius, 1967) the young antesepalous stamens are more horizontally directed and the antepetalous stamens are more vertically directed (Rohweder, 1963). This is also

visible in the figures in Hardy and Stevenson (2000) and Hardy et al. (2004), but not considered by them in the discussion. In addition, the antesepalous stamens are under pressure from the sepals in bud and may therefore be slightly retarded, but only after they have been initiated. The most critical figures (fig. 1C of *Tradescantia virginiana* and fig. 3C of *T. ohioensis*) in Hardy and Stevenson (2000) show a convexity on the right flank of the floral apex, which represents the initial of an antesepalous stamen and which is the same size or even larger than the convexity of the initial of the antepetalous stamens. Although their work is otherwise excellent, an interpretation of centrifugal initiation is not convincing and needs more critical study, which – for such a seemingly unique case – would require detailed analyses of microtome section series in addition to SEM micrographs. It is sad to see the perpetuation of old misconceptions, which were convincingly shown to be wrong 40 years ago in detailed studies. There is probably no critically studied case in angiosperms with a clearly centrifugal androecium initiation in flowers with two isomerous stamen whorls: in flowers in which petals are present the antesepalous stamens are always either initiated first or both whorls appear at the same time (see Eckardt, 1963; Leins, 1964; Eckert, 1966; Gelius, 1967; Rohweder, 1967; Klopfer, 1968, 1972, 1973; Mayr, 1969). Brassicaceae (including *Arabidopsis*) are a special case because their flowers do not have isomerous stamen whorls and they are disymmetric. The entire lateral sectors are different from the median sectors in development (Endress, 1992). Initiation of petals and stamens appears to be almost simultaneous; in some taxa the lateral stamens appear before the median stamens (as expected for a flower with normal centripetal organ development), and in others this occurs the other way around, thus there is some fluctuation (Erbar and Leins, 1997). Nevertheless, in *Arabidopsis* the lateral stamens are inserted lower on the floral base than the median stamens, as expected for normal centripetal initiation (see, for example, Bowman, 1993).

A different aspect is whether obdiplostemony is present from the beginning of androecium development or arises only later. Klopfer (1973) for Saxifragales and Ronse De Craene and Smets (1999a) for *Greyia* and *Francoa* call the androecium disposition 'secondary obdiplostemony'. Probably most or all so-called obdiplostemony is developmentally secondary, as shown especially by Eckert (1966) but also in all other studies concentrating on single species. In *Geranium* it is difficult to judge whether the antepetalous stamens are really more outside than the antesepalous stamens at the beginning of development or whether they are at about the same level, because of their different size, because the antepetalous stamens form common primordia with the petals and because the floral apex is five-angled and not circular after sepal formation (fig. 5 in Ronse Decrane et al., 1993; fig. 26 in Erbar, 1999; Fig 4E in the present study).

Thus the circumscription of obdiplostemony is not so simple. A representation of the two stamen whorls in a floral diagram just in the reverse positions from diplostemony does not do justice to reality, because (*a*) the developmental sequence of the two whorls is not reversed; (*b*) the proportions of the organs of the two whorls change during development;

(*c*) the proportions are different at different topographical levels of the organs; and (*d*) they may be such that the outer surface of the antepetalous stamens is more inside and the inner surface more outside than the respective surfaces of the antesepalous stamens. A possible solution would be to draw the stamens of the antepetalous whorl with smaller sizes, as in Eichler (1878), but this also would not be completely satisfactory. All this also makes it difficult to define obdiplostemony clearly. Ironically, the clearest indicator for 'obdiplostemony' is not the position of the stamens but the position of the carpels, which are commonly antesepalous in diplostemonous flowers but antepetalous in obdiplostemonous flowers (as used, for example, by Bachelier and Endress, 2009). However, this, of course, works only in flowers with as many carpels as there are stamens in a whorl.

Conclusions

In *G. robertianum* flowers high synorganisation is effected at the morphological level by ribs and furrows in sepals and petals and at the histological level by mechanical tissue in sepals. Sepals are hooked together and form a scaffold for the other organs. These features enable a stable architecture in the absence of any fusion at the level of synorganisation in these highly elaborate revolver flowers. The emphasis of obdiplostemony, which is involved in this revolver architecture, changes during floral development. It becomes more strongly expressed in later stages based on differential growth of the different floral sectors and of the inner and outer parts of these sectors. It would be interesting to study the development and role of obdiplostemony comparatively in floral architectures of other angiosperms that are different in detail. A more detailed analysis of the evolution of the floral architecture within *Geranium* and in *G. robertianum* needs more in-depth phylogenetic research throughout the family and other families of Geraniales. At a more general level, it would be interesting to know why in many eudicots petals and antepetalous stamens are delayed in early development after initiation. Although this delay is not present in all obdiplostemonous flowers, does it reinforce the formation of obdiplostemony? Obdiplostemony is mostly or always developmentally secondary. There are no well-substantiated cases of a centrifugal stamen initiation in obdiplostemonous flowers.

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