Merosity in flowers: definition, origin, and taxonomic significance

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Abstract: The term merosity stands for the number of parts within whorls of floral organs, leaves, or stems. Trimery is considered to be a basic condition that arose through the cyclisation of a spiral flower. Pentamery is mostly derived from trimery by the repetitive fusion of two different whorls. Dimery is either directly derived from trimery, or through pentamery as an intermediate stage. Tetramery is linked with pentamery and should not be confused with dimery. Possible causes for a change in merosity are the reduction of the number of carpels and zygomorphy in flowers. Derivations of different merosities have important consequences for the arrangement of the androecium (the insertion of stamen whorls, their identifications, and their number). It is concluded that two main groups can be identified within the angiosperms: magnolialean and monocotyledonean taxa are mostly trimerous or dimerous; non-magnolialean dicots are mostly pentamerous or tetramerous.

By merosity (from the greek "méros") one understands the number of parts within whorls of floral organs, leaves, or stems (cf. RADFORD & al. 1974). This number can vary considerably in flowering plants, but tends to be more or less constantly distributed between different taxa; therefore some systematic significance can be attached to it. The highest frequency is five or three, but four or two are not uncommon. A "whorl" should be considered in a classical sense as a full cycle of organs that can be delimited from preceding and subsequent cycles (see ENDRESS 1992). The importance of the merosity for the configuration of flowers has mostly been overlooked in the past, but its impact has been brought to attention by EICHLER (1875 – 1878) and CEJP (1925) and more recently by DAHLGREN (1983) and KUBITZKI (1987). In a remarkable article KUBITZKI (1987) emphasised the importance of trimery in flowers and brought into focus the morphological and evolutionary relationship between different merosities. However, little is known of the origin and the relationships of the different merosities. That a characterisation of different merosities is badly needed, can be deduced from the often poor identification of specific cases. In considering the merosity of a flower all whorls have to be taken in consideration, and not only the petals or sepals. For example, dimery is all too often confused with tetramery, or all types of pentamery are considered as equivalent. Therefore, we will analyse the origin of different merosities, their nature and their evolutionary relationships in the following sections.

Material and methods

This paper is partly based on a Doctorate dissertation covering numerous species of different families (see RONSE DECRAENE 1992). For this study several floral buds of different families were analysed. Preparation for SEM and light microscopy follow the usual methods described in RONSE DECRAENE & SMETS 1991 a, b, 1992). Voucher material is kept at the Botanical Institute of the K. U. Leuven (Belgium).

Results and discussion

The origin of trimery. It is a well-known fact that trimery is common in several taxa of the *Magnoliidae* and *Hamamelidae* and is probably the primitive floral configuration for the *Liliatae* (cf. HUBER 1977, UHL & MOORE 1980, CRONQUIST 1981, DAHLGREN & CLIFFORD 1982, DAHLGREN 1983, DAHLGREN & al. 1985, KUBITZKI 1987). This led certain authors to consider the existence of a strong link between these groups, bridging the traditional separation between dicotyledons and monocotyledons (e.g., HUBER 1977, 1982). DAHLGREN (1983) and DAHLGREN & CLIFFORD (1982) accepted small trimerous flowers, such as the *Lactoridaceae*, as ancestral in several groups of the *Magnoliidae* and implied that pentamery and a spiral phyllotaxis can be derived from these. This hypothesis is emphasised by some recent cladistic and wood anatomical studies (see, e.g., CARLQUIST 1992a, b; TAYLOR & HICKEY 1992). However, such possibility was rejected by KUBITZKI (1987) on evidence that the process of floral reduction starts from a spiral flower.

The evolutionary origin of trimerous flowers has been convincingly demonstrated by ERBAR & LEINS (1981, 1983) for the *Magnoliaceae*. We refer to these papers and to LEINS & ERBAR (1991) for an understanding of the processes involved. Indeed, it is quite reasonable to believe that the ancestral flower had numerous spirally arranged organs (see also LEINS 1971; KUBITZKI 1973; EHRENDORFER 1977; TAKHTAJAN 1991; RONSE DECRAENE 1992; RONSE DECRAENE & SMETS 1987, 1992, 1993). DAHLGREN (1983: 121) also remarks that "it is not always possible to make a clear distinction between flowers with a helical (spiral) insertion of the floral parts and the trimerous spiral pseudowhorls". The transition from a continuous spiral sequence to an arrangement of trimerous whorls starts with a reduction of the number of perianth parts and their increase in size. As a result tepals become disposed in alternating whorls of three. This also induces a rearrangement of the androecium, i.e. the continuous spiral sequence of inception is fragmented and the outer stamens arise as three pairs or become inserted in the interstices of the two upper tepal whorls. In a following step the upper stamens become also rearranged in whorls of three or six, with a variable order of inception and position. Numerous examples illustrate this process (see, e.g., ENDRESS 1987; KARRER 1991; RONSE DECRAENE 1992; RONSE DECRAENE & SMETS 1990 a, b, 1993).

The derivation of trimery from a spiral arrangement is a plausible fact, which can have arisen separately several times in evolution. For example, contrary to DAHLGREN (1983), it seems unlogical to derive the complicated multistaminate flowers of *Nymphaeaceae* from trimerous *Cabombaceae*, as the other possibility is more easy to visualise. Indeed, the reduction of the floral organs along a helix can lead to trimery by small morphogenetic changes (see KUBITZKI 1987).

The origin of pentamery. Pentamery is a basic and universally widespread condition in the *Rosidae*, *Dilleniidae*, and *Asteridae*, but occurs also in the *Caryophyl-*

lidae and less frequently in the *Hamamelidae* and *Magnoliidae* of CRONQUIST (1981). A few taxa of the *Magnoliidae* have pentamerous flowers (e.g., some *Ranunculaceae*). Pentamery is practically absent from the *Liliatae*, except for a few taxa, such as *Pentastemona* (*Pentastemonaceae*; VAN STEENIS 1982, VAN HEEL 1992).

KUBITZKI (1987: 21) interpreted trimery as an evolutionary deadlock or "a morphological constraint, which offers only very limited possibilities for meristic variation with no return to pentamery or spiral anthotaxy possible". In fact KU-BITZKI believed that pentamery had arisen independently from a spiral anthotaxis and might possibly lead to a trimerous flower. In his opinion a pentamerous whorl is to be equivalent to two alternating whorls, viz. a trimerous and a dimerous. In support of this, KUBITZKI refers to earlier observations of EICHLER (1878) who mentioned that trimerous *Berberis* often have a pentamerous top-flower.

We disagree with KUBITZKI (1987: 24), who advocates the impossibility for a trend from trimery to pentamery: "A return from trimery to pentamery or tetramery seems impossible, or at least extremely rare both in monocotyledons and in dicotyledons". Why should this be so, when the constraints of floral construction make it more probable that the opposite trend happened more than once ? This can be illustrated by following examples:

The *Polygonaceae* possess both trimerous flowers, with following floral formula: P3 + 3 A6 + 3 G3 and pentamerous flowers, with floral formula: P5 A8 G3. Both conditions have been postulated to be primitive by different authors. We refer to RONSE DECRAENE & AKEROYD (1988) for a review of the question. However, the possibility that a pentamerous flower would be at the origin of a trimerous flower in *Polygonaceae* is extremely difficult to visualise for following reasons:

1. The pentamerous perianth arises in a 2/5 sequence and shows a quincuncial aestivation (Figs. 1 a, b, and 2 a). The third tepal takes an intermediate position, linking the outer (often larger) enveloping tepals with the inner. Very often, the external morphology of the outer tepals differs from the inner and this difference is also visible in the transitional tepal, which can have the texture of both or shows a dual vascular connection (Fig. 2 a, see, e.g., GEITLER 1929, VAUTIER 1949, RONSE DECRAENE & AKEROYD 1988).

2. Trimerous polygonaceous flowers, such as *Rheum*, have their stamens arranged in an outer whorl of three paired stamens opposite the outer tepals, and an inner of three stamens opposite the inner tepals. The pentamerous flowers of *Polygonaceae* (e.g., *Polygonum, Fallopia, Persicaria, Coccoloba*: Figs. 1 a, b, 2 a) often have eight stamens, arranged in two connected whorls. Four outer stamens correspond to two of the three pairs of *Rheum*; two stamens tend to have an intermediate position and two stand opposite the two inner tepals. The two inner and one intermediate stamens alternate with the three carpels. The stamens also emerge successively: the first four stamens arise simultaneously as pairs opposite the outer tepals; the intermediate stamens opposite the third tepal arise successively and at two different levels, indicating a composite nature of this whorl (Fig. 1 a, b). One must postulate a dédoublement or the extra insertion of a stamen and a tepal to reach a trimerous condition with nine stamens.

It is possible to construct complete morphoclines between the floral diagrams of different taxa of the *Polygonaceae* in correlation with frequent switches in merosity (see RONSE DECRAENE & SMETS 1993). Further reductive trends can be easily
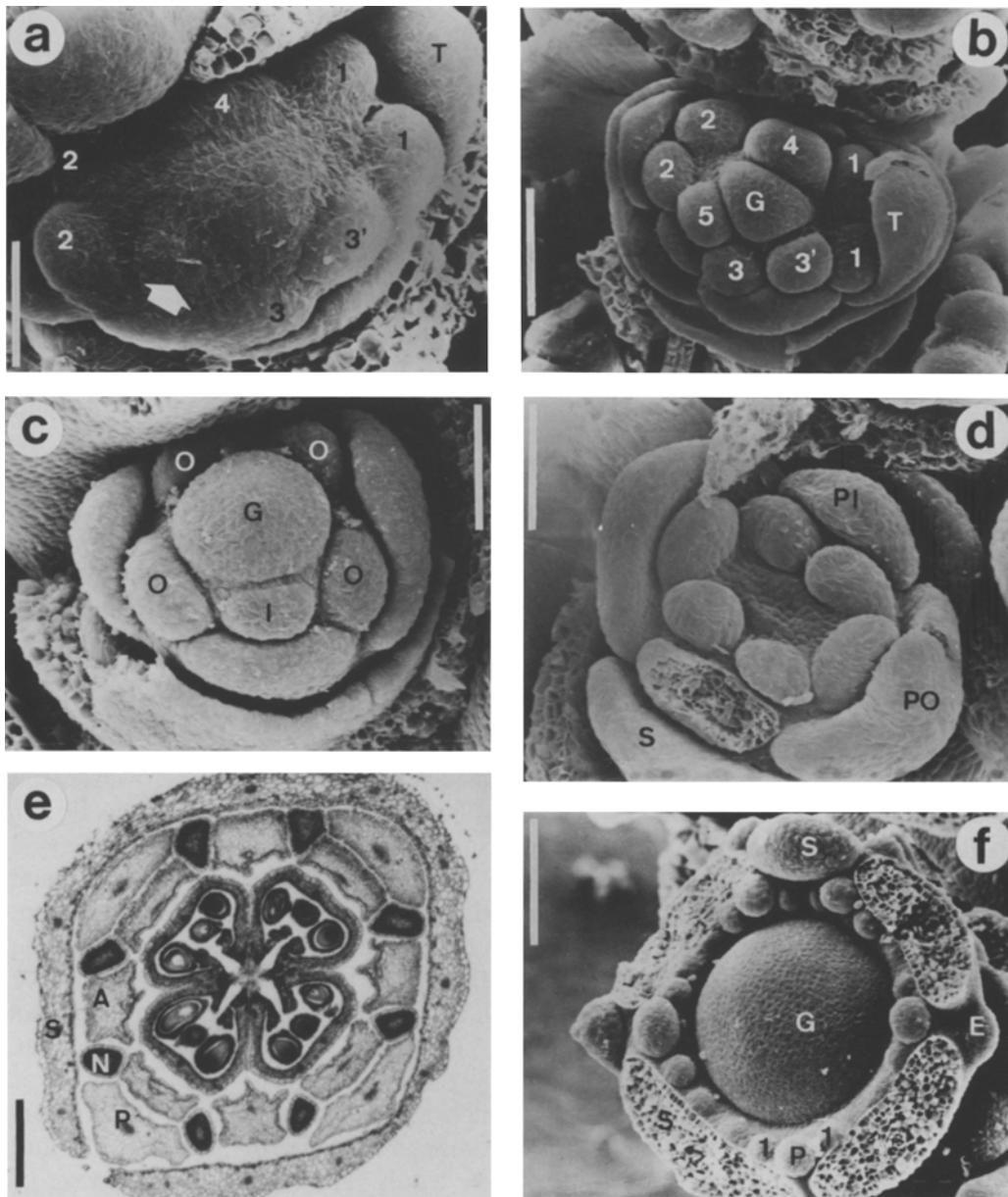
Fig. 1. *a, b Persicaria amplexicaulis* (*Polygonaceae*): successive stages of the floral development. *a* Sequential initiation of tepals (T) and associated stamens. Note the unequal position of the transitional stamens (3,3′); arrow points to stamen arising opposite the fifth tepal. Bar: 50 μm. *b* Later stage of development with the gynoecium (G) clearly visible. Note the paired arrangement of the outer stamens (1,2), the transitional outer stamen (3) and the three inner stamens alternating with the trimerous gynoecium (3′,4,5). Bar: 50 μm. *c Persicaria virginiana* (*Polygonaceae*): dimerous flower. Note the outer stamen pairs (O) and single inner (I) stamen; the posterior inner tepal is not visible (G: gynoecial dome). Bar: 50 μm. *d Corydalis lutea* (*Fumariaceae*): dimerous flower with three alternating whorls of perianth parts, an outer whorl of four stamens and an inner whorl of two stamens (S: sepal; PO: outer petal; PI: inner petal). Bar: 100 μm. *e Francoa sonchifolia* (*Francoaceae*): transverse section of a typically tetramerous flower with a diplostemonous androecium (A) and stub-like nectaries (N). Bar: 500 μm. *f Geum urbanum* (*Rosaceae*): flower bud with initiation of a low ringwall with first stamens (1) on each side of a petal (P). Note the process of transition of pentamery to tetramery by the reduction in size of a sector (S: sepal; E: epicalyx primordium). Bar: 100 μm

followed between different octomerous species and may ultimately lead to a secondary trimerous arrangement (but with only a single tepal whorl) as in *Koenigia* (Ronse Decraene 1989). In considering a polygonaceous flower with floral formula P3 + 3 A3 + 3 G3 as ancestral for the family, Dahlgren (1983) makes a preliminary mistake, firstly because he has to postulate a dédoublement for explaining the existence of flowers with nine or eight stamens and secondly, because he considers this floral formula as the base of an evolutionary trend to pentamerous flowers with five stamens (P5 A5 G3). As for the *Polygonaceae* the pentamerous flowers are best derived from trimerous flowers in the *Ranunculaceae* (cf. Salisbury 1919, Dahlgren 1983). Here the position of the outer stamen pairs (nectar-leaves or petals) has the same importance for understanding the switch in merosity, which results from the fusion of two tepals.

Two separate evolutionary steps must be postulated for the derivation of pentamery from trimery when two tepal whorls are considered (Figs. 4, 5, 6):

1. **Fusion of a perianth member of the outer whorl with one of the inner whorl** (usually parts 3 and 6 of the spiral sequence); this can be visualised on the basis of vascular anatomy or occasional transitions: e.g., *Polygonaceae* (see above, Geitler 1929, Ronse Decraene & Akeroyd 1988, Ronse Decraene 1989); *Papaveraceae* (Ronse Decraene & Smets 1990 b); *Ranunculaceae* (Salisbury 1919).

2. **The reduction (loss) of one of the perianth parts.** Several pentamerous taxa are known to have three highly developed outer and two smaller inner sepals or two smaller outer and three larger inner sepals (e.g., *Molluginaceae, Dipterocarpaceae, Ancistrocladaceae, Polygonaceae*). This may of course also be related to some ecological requirements.

An essential difference must be made between the origin of pentamerous flowers with a single whorl of tepals and those with a calyx and corolla. Reductive trends will be different for both floral constructions as we will show below.

The origin of dimery. Kubitzki (1987) proposed an independent derivation of dimerous flowers from spiral flowers. This possibility exists in certain cases, as the cyclisation of a spiral may lead either to an arrangement of whorls with a 1/3 phyllotaxis or with a 1/2 phyllotaxis. However, the strong relationship of dimery with trimery is without doubt. Several trimerous families often have a few dimerous members, or some families are completely dimerous (e.g., *Laurus nobilis* L. in the *Lauraceae; Clematis* and *Thalictrum* in the *Ranunculaceae; Cissampelos* in the *Menispermaceae; Epimedium* in *Berberidaceae; Maianthemum* in *Liliaceae; Oxyria* and *Persicaria* sect. *Tovara* in *Polygonaceae;* most *Papaveraceae* and *Piperaceae;* all *Fumariaceae*: Fig. 1 d; the staminate flowers of *Begoniaceae* and the outer perianth of *Nymphaeaceae;* some *Annonaceae;* most *Araceae; Nepenthaceae)*. How can one understand the frequent co-occurrence of trimery and dimery in a same family or even a same species, if the origin of dimery is always different from trimery? It is not impossible that a dimerous flower evolved directly by the condensation of a spiral, but an easy switch by the loss of a sector in a trimerous flower is probably the origin of most cases of dimery. This is the most current derivation for families with both trimerous and dimerous flowers. The floral arrangement is not altered except for the loss of one sector within each whorl; this means that a flower with alternating trimerous whorls is almost equivalent with

flowers with alternating dimerous whorls. A second possibility for obtaining dimery is the transition from pentamery (with a single perianth whorl) to "pseudo-tetra-mery" (Fig. 6). Dimerous flowers have often erroneously been taken for tetra-merous. Pseudo-tetramery is in fact a dimerous condition, as is evident on onto-genetical grounds and by comparing different taxa from the same group (e.g., *Phytolaccaceae*: see RONSE DECRAENE & SMETS 1991 b; *Polygonaceae:* Fig. 1c; *Hamamelidaceae: Hamamelis; Brassicaceae:* Fig. 2b, CEJP 1925, ENDRESS 1992). In *Hamamelis*, loss of a tepal has resulted in a pseudo-tetramerous (dimerous) flower. There is no difference with the ontogeny of truly dimerous flowers, such as *Ledenbergia* (*Phytolaccaceae*) or *Macleaya* (*Papaveraceae*) (RONSE DECRAENE 1992; RONSE DECRAENE & SMETS 1990b, 1991b). Strictly dimerous flowers are found in *Buxaceae* and *Tetracentraceae*. Flower parts are arranged in fours but consist of alternating whorls of two.

The origin of tetramery. Tetramery occurs frequently in several families. It can affect single flowers of an inflorescence (e.g., the terminal flower of *Adoxa*), an occasional species (e.g., *Philadelphus coronarius* L. in the *Hydrangeaceae*) or even a whole family (e.g., *Grubbiaceae, Trapaceae, Eucryphiaceae, Lissocarpaceae, Stachyuraceae, Francoaceae*: Fig. 1 e). Tetramery is always derived from pentamery and usually concerns flowers with a calyx and corolla. Two pathways can be postulated in the derivation of tetramery from pentamery:

1. Loss of a whole floral sector (e.g., in the tetramerous *Onagraceae* or *Hydrangeaceae*). Loss of a sector may be caused by a progressive fusion of two sepals or petals and their replacement by a single organ (e.g., *Myrtaceae*: MAYR 1969; *Caesalpiniaceae:* EICHLER 1878, TUCKER 1988; *Mimosaceae*: RAMIREZ-DO-MENECH & TUCKER 1989; *Rutaceae*: LEINS 1967). RAMIREZ-DOMENECH & TUCKER (1989) demonstrated that pentamerous flowers of *Mimosa strigillosa* TORR. & GRAY (*Mimosaceae*) have two adaxial petals which arise closely together and appear smaller than the others. They explained the current tetramerous flowers as the result of fusion between adjacent petals. LEINS (1967) explained the occurrence of tetramery in *Aegle marmelos* (L.) CORREA (*Rutaceae*) as caused by the displacement of the first sepal in a median plane. As a result two intermediate sepals decrease in size or become replaced by a single sepal. Another possibility is the reduction in size of a sector of the flower, which disappears by compression (e.g., *Geum: Rosaceae*, Fig. 1 f). A classical example of this process can be visualised in the genus *Veronica* (*Scrophulariaceae*): most flowers have a tetramerous corolla and calyx, but some species possess a fifth smaller calyx lobe.

2. Loss of a posterior stamen and fusion of two posterior petals. This is the usual way to obtain tetramery in zygomorphic flowers (e.g., *Scrophu-lariaceae, Lamiaceae, Acanthaceae*: see below).

As we already stated, tetramery may easily be confused with dimery (pseudo-tetramery or pseudo-dimery). This is a current fallacy which may, indeed, lead to an erroneous interpretation of flowers and relationships of taxa. The presence of petals and an alternation of tetramerous whorls of different morphomes is frequently correlated with tetramery. On the contrary, dimerous flowers bear the same char-acteristics as trimerous flowers; they may lack "true" petals and arise in alternating whorls of two or four. One of the frequently observed characteristics of dimerous flowers is also the presence of outer stamen pairs or petals (by their sterilisation
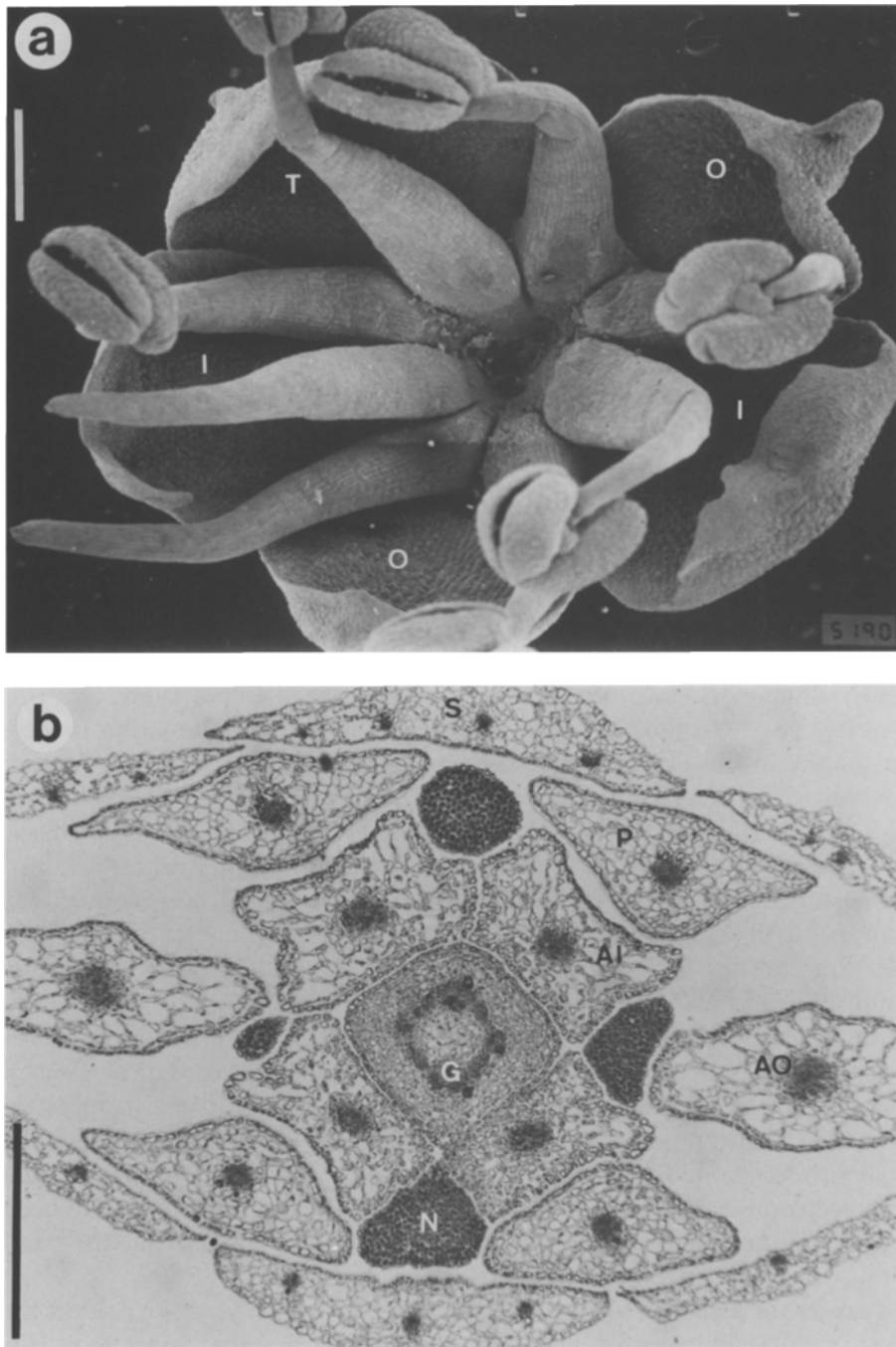
Fig. 2. *a Fallopia japonica* (*Polygonaceae*): apical view of staminate flower. Note the morphological difference between outer (O) and inner (I) tepals and the intermediate form of the transitional (T); gynoecium removed. *b Barbarea vulgaris* (*Brassicaceae*): transverse section through the flower bud. Note the dimerous floral construction with petals (P) alternating with the sepals (S), an outer whorl of two stamens (AO), and an inner whorl of four stamens (AI) (N: nectary; G: gynoecium). Bars: 500 μm

and modification, which may lead to confusion!), that become inserted in the interstices of the tepals (or sepals). In some cases both conditions are difficult to be kept apart, unless one knows more about relationships and trends of the group in question.

The confusion between tetramery and dimery has arisen largely from a wrong identification of the petals in certain groups. The *Capparales* are a typical example of this confusion, as Endress (1992: 107) states: "Indeed, perhaps in no other family of the angiosperms than the *Brassicaceae* is there such a vast and controversial literature about the formal interpretation of the floral ground plan". The flower of *Brassicaceae* has been considered by a great many authors as tetramerous and not as dimerous (see Cejp 1925, Guédès 1967, Endress 1992 for a review). For example, by comparing the petals of *Papaveraceae* with those of *Brassicaceae* one overlooked the essential difference between these two morphomes. In *Papaveraceae*, petals have a clearly tepalar (sepalar) nature and become developed as such (cf. Bersillon 1955, Sands 1973, Ronse Decraene & Smets 1990 b, Karrer 1991). In the *Brassicaceae* and some *Capparaceae*, petals are comparable with stamens in their genetic expression, anatomy, position as well as inception (Stoudt 1941, Smyth & al. 1990, Karrer 1991, Endress 1992, Fig. 2 b); they should be included as part of the androecium for a discussion of the merosity. When outer stamens are sterile, flowers "look" as tetramerous, and are often interpreted as such, as has been currently done in *Brassicaceae* (e.g., Merxmüller & Leins 1966, 1967) or *Capparaceae* (e.g., Stoudt 1941, Leins & Metzenauer 1979). Pentamerous flowers occur occasionally in the *Capparaceae*, such as *Pentadiplandra* (Merxmüller & Leins 1967, occasionally placed in *Pentadiplandraceae*: Willis 1966) or *Oceanopapaver* (Schmid & al. 1984). Merxmüller & Leins (1967) and Leins & Metzenauer (1979) derive the tetramerous calyx of *Capparis* by the loss of the third sepal and the shift of the first sepal in a pentamerous flower. However, they give no explanation for the origin of the tetramery of the petals, duly stating that the tetramery of the petals has not been caused by the splitting of two median primordia, but only by following the "Alternanzregel".

In the dimerous *Phytolaccaceae* the same process of development of the tepals as in *Capparaceae* has been observed (see Ronse Decraene & Smets 1991b). However, in this family the dimerous flower is obviously derived from an ancestral pentamery, which is current in other *Phytolaccaceae* and *Caryophyllales* as a whole. In the *Caryophyllaceae* one finds truly tetramerous flowers, which are also derived from pentamerous precursors. (e.g., *Sagina*). Similarly, pentamery may have been a preliminary condition before dimery was obtained in *Capparales*, but the basic condition must have been trimerous.

Possible causes for a change in merosity. Changes in merosity induced by the gynoecium. Switches to a higher or lower merosity may start from the perianth onwards, but also from the inner phyllomes (carpels). Several taxa have a trimerous gynoecium and a pentamerous androecium, but the trimery of the ovary often influences the merosity in the androecium, and finally in the whole flower. The majority of the dicotyledons have only three or two carpels. In flowers with an isomerous gynoecium, a reduction of the stamens within a whorl does not occur (see Ronse Decraene & Smets 1991a). A lower number of carpels is often correlated with a decrease in the number of stamens. For example, in the *Caryo-*

phyllaceae a reduced androecium tends to alternate with the carpels as "a matter of restriction of the available space on the floral apex" (STERK 1970: 493). There are two means to achieve this order: either some stamens become lost, as in *Spergularia*, where two stamens of a whorl have been lost (see also STERK 1970), or neighbouring stamens fuse laterally in pairs (e.g., *Molluginaceae*: BATENBURG & MOELIONO 1982). In *Hypericum* (*Clusiaceae*) there are usually five antepetalous stamen fascicles. In some cases the number of fascicles has become reduced to three units alternating with the three carpels (e.g., *H. olympicum* L., *H. aegypticum* L.: Fig. 3 a, b, see also LEINS 1964, HIRMER 1918). The floral anatomy and ontogeny demonstrate that four of the original five fascicles arise confluent in two pairs and in alternation with the gynoecium (Fig. 3 a, b). Their composite nature is undeniable. This fusion may extend to the remaining flower, as in *Tripetaleia* (*Ericaceae*): Five petals arise in a normal sequence, but two of them fuse postgenitally in pairs (NISHINO 1988). The androecium and gynoecium have already attained a trimerous configuration in this flower and the origin of the two trimerous stamen whorls must be sought in a similar process. RONSE DECRAENE & AKEROYD (1988) demonstrated a clear correlation between dimerous gynoecia and the loss of stamens in the *Polygonaceae*. *Persicaria* sect. *Persicaria* usually has five tepals, eight stamens and a trimerous gynoecium; they observed that the occurrence of two carpels was always related with the loss of at least one stamen. This reductive trend may ultimately affect the perianth by the loss of a transitional tepal, as in *Persicaria* sect. *Tovara* (Fig. 1 c).

The reduction of the androecium is thus an adaptation to the space intake of the gynoecium in a confined area and happens either by the fusion, or by the loss of some stamens.

Changes in merosity induced by zygomorphy. The flower of the *Asteridae* is basically "simplified" or "highly synorganised" (see ENDRESS 1990): pentamery is widespread and the number of stamens never exceeds the number of sepals or petals (see, e.g., EICHLER 1875, ROBYNS 1972, CRONQUIST 1981, WAGENITZ 1992). Within this homogenous floral plan, there is a host of variations in floral construction related to the occurrence of zygomorphy. Zygomorphy is often related with an unidirectional initiation sequence of floral morphomes. This is visible in the floral development of diplostemonous *Fabales* (see, e.g., TUCKER 1984, 1988, 1989), or haplostemonous *Scrophulariales* and *Lamiales* (see, e.g., CHATIN 1873, PAYER 1857, SATTLER 1973). Stamen initiation tends to proceed from the abaxial side of the flower to the adaxial side, in concordance with their degree of fertility. In many *Asteridae* stamens become reduced along a genetically fixed pattern. The fifth (adaxial or posterior) stamen becomes always lost first; other stamens follow only gradually. This marked trend towards a reduction of the posterior stamens is often linked with interprimordial growth between the two posterior petals (e.g., *Antirrhinum* of *Scrophulariaceae*: Fig. 3 c, d). This interprimordial growth may be expressed early in ontogeny and lead to the appearance of a single two-lobed petal (as in *Justicia* of *Acanthaceae*: RONSE DECRAENE 1992) or even a single petal with smooth apex (as in *Ajuga* of *Lamiaceae*: Fig. 3 e, f). In the process of fusion the adaxial stamen becomes gradually lost: it is sterile in *Antirrhinum* (Fig. 3 d), but absent in *Ajuga* (Fig. 3 f). A classical reduction series has been presented by EICHLER (1875) for the *Scrophulariaceae*: starting from genera as *Verbascum nigrum* L. with
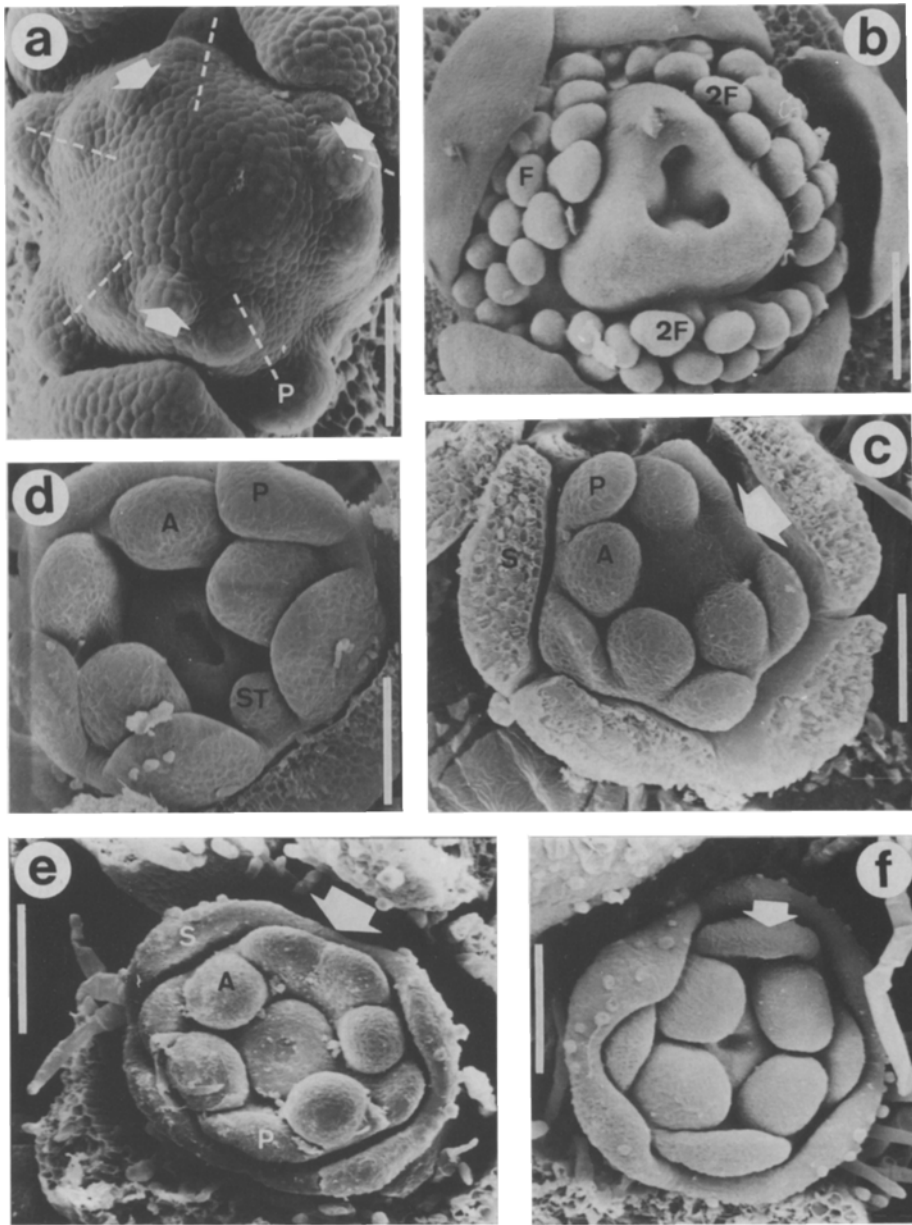
Fig. 3. *a − b Hypericum olympicum* (*Clusiaceae*). *a* Apical view of inception of three stamen fascicles (arrows) with centrifugal development of stamens; dotted lines represent the continuation of the median line of the petals. *b* Nearly mature bud. Note the alternation of the fascicles with the carpels. Two fascicles are compound (2 F) and alternate with the petals; the third (F) stands opposite a petal. *c − d Antirrhinum majus* (*Scrophulariaceae*). *c* Unidirectional initiation of four stamen primordia (A). Arrow points to interprimordial growth between two posterior petals (P). *d* Adaxial view of older bud with posterior staminode (ST) growing opposite the zone of interprimordial growth of the petals. *e − f Ajuga reptans* (*Lamiaceae*). *e* Abaxial view with initiation of the petals (P) and androecium (A). Arrow points to interprimordial growth between two posterior petals; the calyx is tetramerous. *f* Abaxial view of older bud with fifth posterior sepal. Note the complete fusion of the posterior petals (arrow) and the tetramerous arrangement of the flower. All bars: 100 μm, except *a*: 50 μm

five fertile stamens and slightly zygomorphic flowers, the posterior stamen becomes progressively reduced in some *Verbascum* or *Antirrhinum* (Fig. 3 d); in genera with only four stamens (e.g., *Linaria, Digitalis*) the adaxial stamen is completely lost. The abaxial lower pair is staminodial or completely reduced in *Gratiola* or the adaxial pair is reduced in *Ixianthes*. The lowest number of stamens in the *Scrophulariaceae* is two, as in *Veronica* or *Hebe* where only the lateral adaxial pair remains, or *Micranthemum* with two abaxial lateral stamens.

This transition of pentamery to tetramery has also been demonstrated by Armstrong (1988), who found both pentamerous and tetramerous flowers in *Torenia* (*Scrophulariaceae*). The pentamerous flowers had a smaller posterior staminode primordium, which was absent from tetramerous flowers. A similar observation was made by Sattler (1973) on *Lantana camara* L. (*Verbenaceae*). Moreover, in this species the posterior stamen may be initiated as a fully fertile stamen, as a rudiment, or may be completely suppressed. This common trend for a fusion of posterior petals and a reduction of the posterior stamen is also visible in the ontogeny of *Pedicularis* (*Scrophulariaceae*: Meier-Weniger 1977). Singh (1979) observed the initiation of adaxial petals and a stamen primordium on a common hump in *Digitalis purpurea* L. (*Scrophulariaceae*). This was followed by the rapid abortion of the stamen primordium, which is not visible at maturity.

These examples demonstrate that tetramery is a derived condition in *Asteridae* related to the zygomorphy of the flower, where successive intermediate stages are still visible among diverse taxa of the subclass. Although understated by most authors, this common reductive trend of the androecium and petals is certainly of major importance. We may suggest that the strictly tetramerous *Dipsacaceae, Caprifoliaceae, Oleaceae,* and *Plantaginaceae* are probably derived by this process as it is not excluded that some regular flowers have been derived secondarily from zygomorphic pentamerous flowers. Indeed, *Knautia* or *Dipsacus* (*Dipsacaceae*) have tetramerous flowers, but the related *Scabiosa* has zygomorphic flowers with five petals and only four stamens, as the posterior stamen is missing. Flowers of *Dipsacus sylvestris* Huds. also have larger posterior petals, suggesting that they have resulted from fusion (Roels 1993). These observations support the earlier assumption of Eichler (1875) that tetramery in many *Asteridae* is derived by the abortion of a posterior stamen and the fusion of two posterior petals, contrary to an assumption of ancestral tetramery (see Van Tieghem 1909, fide Hofmann & Göttmann 1990, for *Dipsacaceae*).

A model for the interrelationships of different merosities. There is a strong relationship between trimery, dimery and pentamery, as is clearly expressed in transitional forms of *Eschscholzia californica* Cham. (see Figs. 65, 66 in Ronse Decraene & Smets 1990 b; Fig. 7): flowers with two dimerous whorls of petals (morphologically interpreted as inner tepals: see before) are the most common in this species as in the other *Papaveraceae,* but flowers with a single pentamerous perianth or two trimerous petal whorls occur occasionally (the outer tepaline whorl or "sepal whorl" is not considered here, as it drops off early). There is no other alternative than to consider the occasional pentamery as a transitional condition between a more primitive trimery (as found in certain *Papaveraceae,* such as *Platystemon, Meconella*) and the more usual dimerous pattern. The co-occurrence of pentamerous pistillate flowers of *Begonia* and dimerous staminate flowers can only

be understood by accepting a trimerous ancestry for the genus (RONSE DECRAENE & SMETS 1990b).

In mainly pentamerous taxa reductions or increases in merosity are isolated phenomena and occur unfrequently (except for tetramery). Observations tend to confirm the derivations of different "merosities" by loss or fusion of floral parts or by a lateral multiplication in numerous families (see before; e.g., EICHLER 1878, LEINS 1967, MAYR 1969, SATTLER 1973, DAHLGREN & THORNE 1984, RAMIREZ-DOMENECH & TUCKER 1989). The switch from trimery to pentamery must have occurred independently and on several occasions. Important is to know at what stage this switch has occurred. Within the *Hamamelidae, Fagales* and *Juglandales* are essentially trimerous, but the *Hamamelidaceae* are often pentamerous or even dimerous. In the *Caryophyllales* a multiwhorled androecium lies at the base of the order, but in the *Polygonales* it is a two-whorled androecium, as in *Rheum* (see above). We consider the pentamerous condition in the *Caryophyllidae* and *Hamamelidae* as having a different origin from the other *Magnoliophytina*. Trimery, dimery and pentamery occur side by side in the *Polygonaceae, Papaveraceae, Begoniaceae, Hernandiaceae, Menispermaceae,* and *Ranunculaceae* and intermediates are currently found (e.g., GROSS 1913, SCHÖFFEL 1932, KUBITZKI 1969, DAHLGREN 1983, RONSE DECRAENE & AKEROYD 1988, RONSE DECRAENE 1989, RONSE DECRAENE & SMETS 1990 b).

In the reductive trend from spiral multistaminate flowers to flowers with few stamen whorls, the changes in merosity have important consequences for the androecium. Polycyclic androecia (i.e. those consisting of a high number of alternating whorls; for a review of polycycly: see RONSE DECRAENE 1992; RONSE DECRAENE & SMETS 1990 a, 1993) can be either trimerous (e.g., *Monanthotaxis: Annonaceae*), dimerous (e.g., *Eschscholzia: Papaveraceae*) or pentamerous (e.g., *Seguieria: Phytolaccaceae*).

Pentamerous polycyclic flowers differ from trimerous polycyclic flowers by the fact that they have a pronounced helical mode of inception. In trimerous flowers, stamens may be arranged in whorls of three or six, or in complex whorls of nine. The inception pattern of the androecium will be different in relation to a trimerous (or dimerous) perianth than to a pentamerous perianth. The perianth of trimerous (or dimerous) flowers is usually divided in two whorls of three (or two) with an alternation of a long and a shorter plastochron (a 1/3 or 1/2 phyllotaxis); in pentamerous flowers there is a continuous inception sequence from perianth to stamens (e.g., *Caryophyllaceae:* LYNDON 1978: a 2/5 phyllotaxis), or a sequence that is broken once (between perianth and stamens; e.g., *Nyctaginaceae:* SATTLER & PERLIN 1982, VANVINCKENROYE & al. 1993; *Polygonaceae:* GALLE 1977). This distinction becomes important when comparing the number of stamen whorls in trimerous and pentamerous flowers. Different (derived) factors may also cause a superposition of the perianth and stamens, such as the unidirectional initiation of stamens in *Basellaceae* (LACROIX & SATTLER 1988). Alternation of stamens with the pentamerous perianth is often related with a switch in phyllotaxis from a 2/5 sequence to a 3/8 sequence (i.e. a change in the divergence angle between perianth and stamens: SATTLER & PERLIN 1982, VANVINCKENROYE & al. 1993). This corresponds with a sudden change in Fibonacci numbers between different organ categories (ENDRESS 1987).

As illustrated above a pentamerous perianth is easily derived from two trimerous perianth whorls by the merging of the two alternating whorls into a single whorl (Figs. 4 − 6). This fusion of two perianth parts has important consequences for the androecium:

1. The phyllotaxis of the flower becomes transformed (a 1/3 sequence switches into a 2/5 sequence).

2. Some stamens at the point of fusion of the tepals disappear by loss or fusion.

3. The originally distinct whorls become aggregated in a series of connected whorls. The original rhythmic alternation of a long and a short plastochron (between trimerous whorls) is transformed in a more variable alternation, because the merged whorls can be variably constituted. It is more appropriate to use the term "pseudowhorl" for pentamerous flowers, because a whorl may represent an aggregation of two or more whorls. As a consequence of this, pentamerous flowers will always have a lower number of whorls than trimerous flowers (see Table 1; see also RONSE DECRAENE & SMETS 1993).

Pentamerous flowers with eight stamens occur relatively frequently. Strictly spoken, by the loss of a sector, flowers with eight stamens and five tepals are comparable to flowers with nine stamens inserted in two alternating whorls of six outer and three inner stamens, and two whorls of three tepals. Five of the eight

Table 1. A comparison between equivalent stamen positions in trimerous, pentamerous and dimerous flowers given by floral formulas. The number of stamens within each whorl can vary. The rows must be read as a sequence between different merosities; each column represents a reduction series of the androecium within a particular state of merosity

Trimerous	Pentamerous*	Dimerous
pentacycly P3 + 3 A6 + 6 + 3 + 3 + 6	tetracycly P5 A5 + 5 + **5** + 5	pentacycly P2 + 2 A4 + 4 + 2 + 2 + 4
tetracycly P3 + 3 A6 + 3 + 3 + 6	tricycly P5 A5 + **5** + 5	tetracycly P2 + 2 A4 + 2 + 2 + 4
tricycly P3 + 3 A6 + 3 + 3	dicycly P5 A5 + **5**	tricycly P2 + 2 A4 + 2 + 2
dicycly P3 + 3 A6 + 3 P3 + 3 A3 + 3	dicycly P5 A5 + 3 monocycly P5 A3 + 2	dicycly P2 + 2 A4 + 2 P2 + 2 A2 + 2
monocycly P3 + 3 A6 + 0 P3 + 3 A3 + 0	obmonocycly P5 A5 + 0 incomplete whorl P5 A3	monocycly P2 + 2A 4 + 0 P2 + 2 A2 + 0
obmonocycly P3 + 3 A0 + 3	incomplete whorl P5 A2	obmonocycly P2 + 2 A0 + 2

* Numbers in bold represent composite whorls; a whorl of 6 or 4 stamens consists of paired stamens

stamens are inserted opposite to or in the interstices of the outer perianth parts; the other three stand opposite the inner perianth parts (Figs. 1 a, 2 a).

A first series of two floral diagrams illustrates the transformation of trimery into pentamery in polycyclic flowers (Fig. 4); Fig. 4 A is based on *Monanthotaxis whytei* (Stapf) Verdc. (*Annonaceae*) whose inception has been described by Ronse Decraene & Smets (1990a). It is clear that the fusion of two tepals does not affect the position of most stamens, except for those opposite the transitional tepal (Fig. 4 B). Thus for a hypothetical androecium of 30 stamens inserted in six whorls, five stamens are lost in the process (two belonging to the group opposite the outer tepals and three opposite the inner tepals: Fig. 4 B, asterisks). Apart from the five remaining outer stamens, which are shifted to the interstices of the tepals, the remaining stamens may become conglomerated into pseudo-whorls. On the one hand the next whorl can be octomerous and consists of the original stamen pairs opposite the inner tepals (minus one) and single stamens opposite the outer tepals. The following whorl can be 7-merous and consists of pairs opposite the outer tepals (minus one) and single stamens opposite the inner tepals (minus one). The uppermost whorl may also be contracted from two trimerous whorls (minus one stamen). On the other hand, if the third and fourth whorl become amalgamated, one obtains an androecium with five pentamerous whorls. A mathematical equation can easily be made for these transitions (in this example the bold numbers represent mixed whorls):

$$\text{trimerous ancestor (30 stamens):} \quad 6 + 6 + 3 + 3 + 6 + 6$$
$$\downarrow \qquad\qquad\qquad\qquad \downarrow \;\; \downarrow \;\; \downarrow \;\; \downarrow \;\; \downarrow \;\; \downarrow$$
$$\text{pentamerous taxon (25 stamens):} \quad 5 + 5 + 3 + 2 + 5 + 5$$

$$\text{a)} \; 5 + 5 + 3 + 2 + 5 + 5 \qquad\qquad \text{b)} \; 5 + 5 + 3 + 2 + 5 + 5$$
$$\downarrow \quad\;\; \downarrow \qquad\qquad\qquad\qquad\qquad \downarrow$$
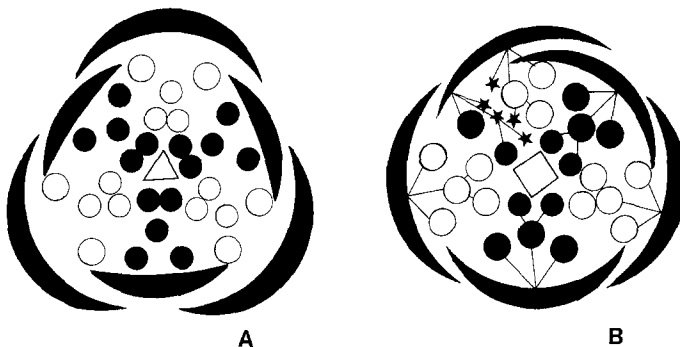$$5 + \; \mathbf{8} \; + \; \mathbf{7} \; + 5 \qquad\qquad\qquad 5 + 5 + \; \mathbf{5} \; + 5 + 5$$

Fig. 4. First diagrammatic representation of the transition of a putative trimerous flower with 30 stamens (*A*) into a pentamerous flower with 25 stamens (*B*). White dots: stamens opposite the outer tepals; black dots: stamens opposite the inner tepals; asterisks: lost stamens; triangle and square: position of the gynoecium

a) Pentamerous flowers, such as those described above, occur occasionally in some *Caryophyllales*, such as *Molluginaceae* (e.g., *Glinus lotoides* L. var. *lotoides*: HOFMANN 1973; *Phytolaccaceae* (*Seguieria longifolia* BENTH.: VOLGIN 1988). The merging of two stamen whorls (the first consisting of six and the other of three stamens) into a single whorl of eight or seven stamens respectively corresponds with a continuous helical sequence between the members of the whorl. Earlier floral diagrams of pentamerous multiwhorled *Phytolaccaceae*, as given by WALTER (1906) or FRIEDRICH (1956) have overlooked this fact in describing the androecium on a strictly positional basis.

b) The merging of two intermediate whorls into a strictly pentamerous whorl is a second possibility which gives birth to strictly alternating whorls. This possibility can be illustrated for *Aquilegia* in the *Ranunculaceae* (see, e.g., SCHÖFFEL 1932, TEPFER 1953, ENDRESS 1987).

Another model may start from a precursor with a different arrangement of paired and single stamen whorls (Fig. 5); two whorls of three members become united in a whorl of five (minus one stamen) and two whorls of six members are united in a decamerous whorl (minus two stamens). In *Ranunculus sceleratus* L. (*Ranunculaceae*) 20 stamens arise after petal initiation. Petals are considered as transformed stamens in this case ("nectar-leaves": see also SCHÖFFEL 1932, HIEPKO 1965). The order of arrangement is as follows (GUPTA & SINGH 1983): S5 P5 A5 + 10 + 5.

GUPTA & SINGH (1983) interpret the androecium as five antesepalous fascicles, which extend laterally and centripetally. We do not agree with their interpretation, as there is no ontogenetic, nor vascular evidence for complex polyandry in *Ranunculaceae*. The five stamen whorls of *Ranunculus sceleratus* (including the petals) are equivalent to seven trimerous whorls (Fig. 5 A) from which six are contracted two by two into three composite whorls (Fig. 5 B). The outer (petaline) whorl (which belongs to the androecium) is homologous with the outer stamen pairs. Thus the sequence of inception of different stamen whorls has been shifted into a lower sequence of pentamerous whorls. The following reductive scheme can be presented:
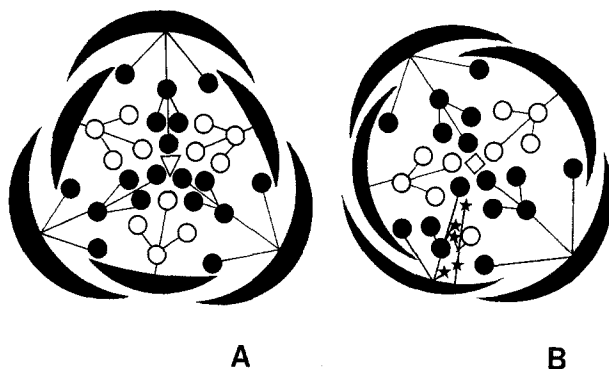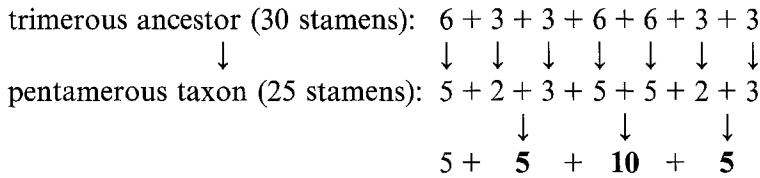

A   **B**

Fig. 5. Second diagrammatic representation of the transition of a putative trimerous flower with 30 stamens (*A*) into a pentamerous flower with 25 stamens (*B*). Black dots: stamens opposite the outer tepals; white dots: stamens opposite the inner tepals; asterisks: lost stamens; triangle and square: position of the gynoecium

trimerous ancestor (30 stamens): $6 + 3 + 3 + 6 + 6 + 3 + 3$

$\downarrow$ $\downarrow \quad \downarrow \quad \downarrow \quad \downarrow \quad \downarrow \quad \downarrow \quad \downarrow$

pentamerous taxon (25 stamens): $5 + 2 + 3 + 5 + 5 + 2 + 3$

$\downarrow \qquad \downarrow \qquad \downarrow$

$5 + \quad 5 \quad + \quad 10 \quad + \quad 5$

A third series of floral diagrams illustrates the interrelationships between the three different merosities trimery, pentamery, and dimery (Fig. 6). From a trimerous flower with four alternating stamen whorls (P3 + 3 A6 + 6 + 3 + 3: Fig. 6 A) a pentamerous flower with three whorls is easily obtained by the loss of three stamens and the merging of two tepal whorls or the loss of one tepal whorl (P5 A5 + 5 + 5: Fig. 6 B). The fusion of two other tepals (tepals three and five) or the loss of another tepal leads to a dimerous (or "pseudo-tetramerous") condition with the same number of whorls as in trimerous flowers, but with less stamens within each whorl (P2 + 2 A4 + 4 + 2 + 2: Fig. 6 C). However, in some cases dimerous flowers are probably also derived directly from trimerous flowers without the by-way of pentamery (see above). The transition from pentamery to dimery is visible in *Persicaria virginiana* (L.) Gaertn. which has been derived from a pentamerous flower with eight stamens (Fig. 1 c). A similar process must be postulated for *Hamamelis*, with four petals (stamen homologues), two successive whorls of two stamens and four staminodes (see Mione & Bogle 1990, Ronse Decraene 1992, Ronse Decraene & Smets 1993).

Transitions of trimery to pentamery and further to dimery can run in the sequence presented on Fig. 6. However, reductive trends are manyfold for different groups, because the alternation of hexamerous and trimerous stamen whorls can be variable in trimerous flowers and because a "pseudowhorl" (in the sense of two whorls conglomerated into one) of a pentamerous flower can become transformed into a "real" whorl (in the sense of a whorl alternating with a previous whorl) by loss or fusion of some stamens; this whorl alternates with a previously initiated

A   **B**   **C**
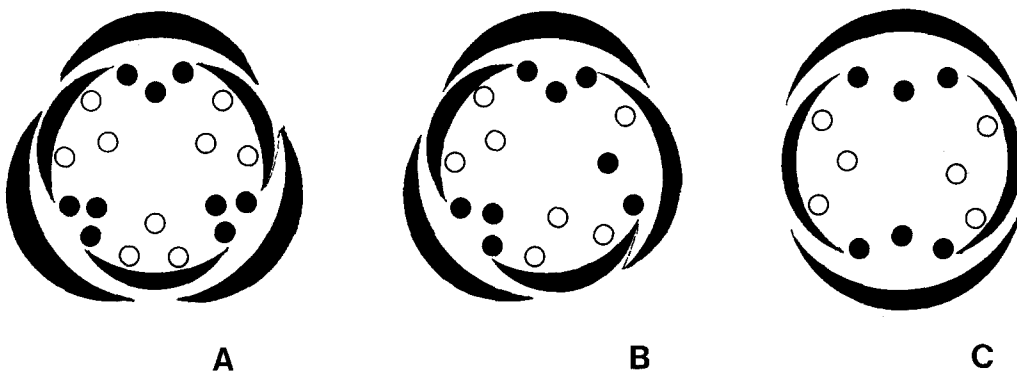
Fig. 6. Diagrammatic representation of the transitions between trimerous, pentamerous and dimerous flowers. *A* Trimerous flower with 18 stamens in four whorls. *B* Pentamerous flower with 15 stamens in three whorls. *C* Dimerous (pseudo-tetramerous) flower with 12 stamens in four whorls. Dotted lines represent fusion of two neighbouring tepals. White dots: stamens opposite the inner tepals; black dots: stamens opposite the outer tepals. See text for further explanation

pentamerous whorl and behaves as an entity, separated from another whorl by a longer plastochron. This leads to an intricate web of stamen configurations, which can only be understood by accurate observations and comparisons. In this way several reduction series can be constructed for different groups of plants.

The transition of pentamery to tetramery occurs frequently as has been discussed before. Reductions from tetramery to trimery occur less often, as in *Loranthaceae, Santalaceae, Burseraceae, Empetraceae, Scyphostegiaceae, Cneoraceae, Melasto-mataceae, Elatinaceae*, etc. Here we agree with KUBITZKI (1987: 26) that one must distinguish between two different forms of trimery, "one that originates from spiral anthotaxy and is characteristic of the magnolialean families, and one that is reached by stepwise oligomerisation via tetramerous flowers, which is characteristic of non-magnolialean dicotyledons". The origin of trimery for the latter taxa is related with a pentamerous precursor, contrary to the former. On the other hand, secondary increases by the addition of one or more sectors are not rare (e.g., *Sapotaceae:* varying from hexamerous to 18-merous, *Sempervivum* in *Crassulaceae*, heptamery in some *Symplocaceae* or *Styracaceae*).

Strictly dimerous flowers are rare in the non-magnolialean dicotyledons (e.g., *Circaea lutetiana* L. in the *Onagraceae; Clusia ovigera* PLANCH. & TRIANA in the *Clusiaceae; Gunnera manicata* LINDEN in the *Gunneraceae; Acaena buchananii* HOOK. f. in the *Rosaceae; Pimelea* in the *Thymelaeaceae*: EICHLER 1878).

Conclusions

Different aspects of the merosity of the flower have been analysed. It is clear that the merosity of flowers has an important systematic value for discussing relationships of groups of flowering plants and that the origins of trimery, dimery, pentamery and tetramery can be manyfold (Fig. 7). The figure of evolution of different merosities presented by KUBITZKI (1987: 25, Fig. 1) is too rigid, as it only accepts an independent divergence of pentamery, trimery, and dimery from a spiral phyllotaxis with a derivation of trimery from pentamery as only alternative. His presentation is clearly limited, as variations may run in different directions. Trimery (Fig. 7 B) may arise directly from a spiral flower (Fig. 7 A), but also secondarily from a pentamerous flower (Fig. 7 C) by a progressive reduction within whorls. It is clear that a secondary trimery cannot be compared with the original condition. Pentamery may also be derived from a spiral or directly from trimery, but the presence or absence of petals may have consequences for a further evolution. Pentamerous flowers without petals can easily be transformed into dimerous flowers (Fig. 7 D), because the pentamerous whorls are often compound and unstable. The presence of petals causes stability in the alternating pentamerous whorls; changes of merosity will only affect a flower sector and a tetramerous flower will be more easily obtained by loss of a sector. Similarly, trimerous flowers with stable alternating whorls of tepals (e.g., T3 + 3) will more easily be converted in dimerous flowers with a similar configuration (T2 + 2). The stability of whorls will be maintained when a tetramerous flower with sepals and petals (S4 P4) is converted into a secondary trimerous flower (with the retention of petals: S3 P3) and into a secondary dimerous flower (S2 P2).
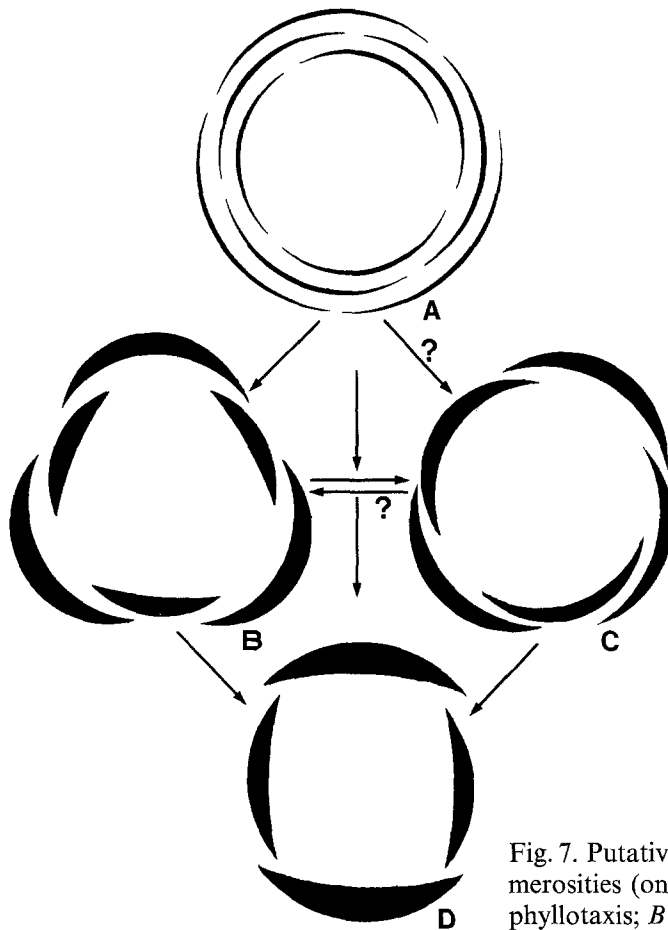
Fig. 7. Putative relationships between different merosities (only the perianth shown). *A* spiral phyllotaxis; *B* trimery; *C* pentamery; *D* dimery

An important taxonomic conclusion that imposes itself is a break between two groups of taxa in the angiosperms: on the one hand magnolialean dicotyledonous and monocotyledonous flowers (*Magnoliidae, Caryophyllidae, Liliatae,* and part of the *Hamamelidae*) are mainly trimerous, dimerous, and only rarely pentamerous or tetramerous (some *Hamamelidae, Caryophyllidae*); on the other hand, non-magnolialean dicotyledons (*Dilleniidae, Rosidae,* and *Asteridae*) are certainly basically pentamerous and become often tetramerous, while trimerous or dimerous flowers are exceptional. Important is the fact that the origin of trimery and dimery is different for these groups compared to the magnolialean taxa (see also KUBITZKI 1987). The current pentamery of *Caryophyllidae* probably has a different origin, as several characteristics link the group with *Magnoliidae* (see also RONSE DECRAENE 1992). These differences are also expressed in differences of the androecium, which are further analysed in another paper (see RONSE DECRAENE & SMETS 1993).

The present conclusions about the floral merosity make us believe that there must be an important gap between two lines of evolution in the *Magnoliophytina* (see also KUBITZKI 1973; HUBER 1977, 1982; RONSE DECRAENE & SMETS 1987, 1992). We already emphasised the existence of a gap in the androecial configurations by a distinction of two characters (oligomery and polymery; see RONSE DECRAENE & SMETS 1987). It is therefore clear that the changes in merosity of flowers are an important factor in the evolution of different groups of plants.

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