

EVOLUTIONARY HISTORY OF  
THE MONOCOT FLOWER<sup>1</sup>Margarita V. Remizova,<sup>2</sup> Dmitry D. Sokoloff,<sup>2</sup>  
and P. J. Rudall<sup>3</sup>

## ABSTRACT

This paper reviews monocot flower structure and gynoecium development and evaluates these data to clarify the evolutionary history of the monocot flower. Despite some congruence between molecular and morphological data regarding the delimitation and phylogenetic relationships of monocots, there is currently no universally accepted view on the morphology of the ancestral monocot flower, reflecting a high degree of parallelism in monocot floral evolution. We focus on two character suites that encompass the key features of monocot flowers: (1) the typical monocot groundplan of trimerous-pentacyclic flowers, and (2) a character suite related to carpel fusion, including postgenital fusion between carpels and the presence of septal nectaries. It is likely that the trimerous-pentacyclic flower represents a major synapomorphy of monocots; this flower groundplan is virtually absent from the closest relatives of monocots. Such close correlation of a particular groundplan with a phylogenetic group is analogous with the absence of the typical eudicot flower groundplan in basal eudicots, though in both instances the underlying constraints are obscure. In monocots, morphogenetic studies and analysis of character correlations lead us to favor a hypothesis that the ancestral monocot conditions were postgenital fusion between carpels and presence of septal (gynopleural) nectaries. This character-suite optimization contrasts with optimizations of individual morphological characters, which suggest that the ancestral monocot flower possessed congenitally united carpels (with no contribution of postgenital fusion) and lacked septal nectaries. Among extant early divergent monocots, flowers of *Japonolirion* Nakai (Petrosaviaceae s.l. or Japonoliriacae, Petrosaviales) appear to most closely resemble those of the ancestral monocots. A gynoecium with free carpels represents a derived condition in monocots; it evolved independently in three unrelated groups (Triuridaceae, Araceae, Alismatales), with several gains of apocarpic in Alismatales and palms. All three monocot groups that include free-carpellate species show significant variation in their individual floral groundplans.

**Key words:** Apocarpic, congenital fusion, flower evolution, monocotyledon, postgenital fusion, septal nectary, synapocry, trimerous.

Monocots form a well-supported clade that encompasses a considerable portion of angiosperm diversity. Although no single morphological character can be used to distinguish monocots from other angiosperms, they are morphologically well defined by a combination of characters, including the possession of trimerous-pentacyclic flowers. Most authors (e.g., Dahlgren et al., 1985; Takhtajan, 1987; Cronquist, 1988) have accepted monocots as a monophyletic unit derived from within a group of early divergent angiosperms (subclass Magnoliidae; sensu Takhtajan, 1987). This view is confirmed by molecular phylogenetic data (summarized in Angiosperm Phylogeny Group III, 2009). More detailed hypotheses, such as a sister-group relationship between monocots and either Nymphaeales (e.g., Schaffner, 1904; Hallier, 1905; Takhtajan, 1980, 1987) or Piperales and Chloranthaceae (see Burger, 1977; Dahlgren et al.,

1985), are not supported by recent molecular analyses. Thus, in contrast with many other plant groups, monocot boundaries have survived the molecular revolution in phylogenetics almost intact. The only exception is Hydatellaceae, a small family of tiny aquatics with highly modified reproductive structures. Although previously thought to be monocots of uncertain affinity (Hamann, 1976; Dahlgren et al., 1985), sometimes placed in Poales (Angiosperm Phylogeny Group II, 2003), Hydatellaceae are now robustly placed close to the waterlilies (Nymphaeales) among the earliest angiosperm lineages (Saarela et al., 2007). However, this interesting exception does not indicate any fundamental discord between molecular and morphological data. Traditional phylogenetic hypotheses regarding the relationships of Hydatellaceae were based on insufficient knowledge of micromorphological structure in both Nymphaeales

<sup>1</sup> We are grateful to Vladimir Chooch, Sean Graham, and Sabine von Mering for discussion, and Peter Endress and Peter Stevens for helpful reviews. Lisa Campbell and Dennis Stevenson provided material of *Hidrogalinia* and *Harpocallis* (which will be the subject of a forthcoming collaborative paper), Alexei Okolski provided material of *Triglochin*, and Margarita Bujakate supplied material of *Tofieldia*. M.V.R. and D.D.S. acknowledge support from President of Russia grant no. MD-2644.2009.4, Russian Foundation for Basic Research (RFBR) grant no. 09-04-01155, and Ministry of Education and Science of Russia (FCP "Kadry", NK-5411/P314).

<sup>2</sup> Department of Higher Plants, Faculty of Biology, Moscow State University, Moscow 119991, Russia. remizova@yahoo.com, sokoloff@yandex.ru.

<sup>3</sup> Jodrell Laboratory, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, United Kingdom. Author for correspondence: p.rudall@kew.org.

doi: 10.3417/2009142

ANN. MISSOURI BOT. GARD. 97: 617–645. PUBLISHED ON 27 DECEMBER 2010.

Volume 97, Number 4  
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carpels (e.g., Takhtajan, 2009). There are a few examples of trimerous-pentacyclic flowers among the early divergent core eudicots (see also Endress, 1996). For example, flowers of *Pterostegia* Fisch. & C. A. Mey. (Polygonaceae, Caryophyllales) and *Trihaloragis* M. L. Moody & Les (Haloragaceae, Saxifragales) are trimerous and pentacyclic (e.g., Yurtseva & Chooch, 2005; Moody & Les, 2007).

Because the trimerous-pentacyclic flower is so common in monocots, this review focuses on the exceptions. This presentation mode inevitably implies that the trimerous-pentacyclic flower represents the ancestral condition, but this implication will be discussed later. Note that this implication is not universally accepted (reviewed by Ronse de Craenc & Smets, 1995). There are three different types of deviation from the typical trimerous-pentacyclic flower arrangement in monocots. (1) Reduction of some organs can occur without altering the positions of the remaining organs. This type is often associated with synzooecium of floral organs (e.g., orchids, gingers, irises). Examples of this type are scattered across the monocot phylogenetic tree. (2) Changes can occur in flower merism, while retaining a pentacyclic isomerous construction (i.e., occurrence of the same number of organs in all whorls of a given flower). This type is surprisingly rare, and there is no obvious pattern in its distribution in monocots. For example, increased merism occurs in *Paris* L. (Trilliaceae, Liliales) and decreased merism occurs in dimorphic flowers in *Maitanthenum* F. H. Wigg. (Asparagaceae, Asparagales). (3) Finally, significant changes can occur in the groundplan, with insertion of new whorls (as in the gynoecium of *Sagittaria* L., Alismataceae, Alismatales), complete loss of whorl(s) affecting the positions of other organs (as in *Trillium apetalum* Makino, Trilliaceae, Liliales; see below), and/or loss of isometry due to multiplication of some organs (e.g., in *Pilea tenuifolia* Michx., Tofieldiaceae, Alismatales, with six stamens in the outer whorl of the androecium, all other floral whorls being trimerous). Significant groundplan changes are unequally distributed in monocots; they are common in Alismatales, Pandanales, and palms and are also present in a few scattered and species-poor groups of Liliales, some Asparagales, and Poales.

## EARLY DIVERGENT MONOCOTS

Both species of *Acorus* (Acoraceae) possess trimerous-pentacyclic flowers, with occasional exceptions in some flowers in the most distal region of the inflorescence (Buzgo & Endress, 2000). However, a trimerous-pentacyclic groundplan is remarkably rare in Alismatales. In most Araceae, flowers are highly

modified by changes in merism, loss of perianth, and/or unisexuality, although a trimerous-pentacyclic groundplan could be the ancestral condition for the family. In some perianthless Araceae, the number of carpels (*Philodendron* Schott; Mayo, 1969) or stamens (*Calla* L.; Lehmann & Sattler, 1992; Scribalo & Tomlinson, 1992) is considerably increased. The closest approach to trimerous-pentacyclic flowers occurs in some relatively species-poor order groups such as Pothoideae-Potheae and Monsteroideae-Spathiphyllaceae (Mayo et al., 1997). However, even here, merism of the perianth varies between two and three (*Pothos* L., *Spathiphyllum* Schott), tepals are sometimes united into an almost unlobed tube (*Pedicularum* M. Hotta), and the gynoecium can be monomerous or possibly pseudomonomerous (*Pothodium* Schott) (Mayo et al., 1997; Buzgo, 2001). Furthermore, in the few aroids with trimerous-pentacyclic flowers, the median outer tepal is adaxial rather than abaxial, and flower orientation with respect to the primary inflorescence axis is upside down compared with most other monocots, including *Acorus* (Buzgo, 2001).

In the alismatid family Tofieldiaceae, flowers are trimerous and pentacyclic (except in *Pilea* Michx., with increased stamen number), but they possess an additional trimerous whorl of phylloems (calculus) outside (and alternating with) the outer-whorl tepals. The calculus resembles a third perianth whorl (Remizova & Sokoloff, 2003; Remizova et al., 2006a).

Among the core alismatids, flowers are often trimerous and pentacyclic in the monospecific family Scheuchzeriaceae (Posluszny, 1983), but even here carpel number is not fixed and can reach four or six (e.g., Eber, 1934; Igersheim et al., 2001). In some populations of *Scheuchzeria palustris* L., carpel number often varies even within a single individual (Remizova & Sokoloff, pers. obs.). Other core alismatids differ from the trimerous-pentacyclic groundplan in one or several of the following features (e.g., Dahlgren et al., 1985; Posluszny & Chardon, 1993; Takhtajan, 2009; see also Singh & Sattler, 1972, 1977; Posluszny & Sattler, 1974a, b; Posluszny & Tomlinson, 1977; Posluszny et al., 1986).

1. Flower merism can be decreased, for example, to two organs per whorl in *Ruppia* L. (Ruppiceae) or one in *Triglochin scilloides* (Poir.) Mering & Kaderitf (Juncaginaceae), or increased, if we interpret flowers of *Potamogeton* L. (Potamogetonaceae) as tetramerous, though the perianth and androecium can also be interpreted as dimorphic (purely tetramerous flowers also occur within the range of variation in *Triglochin* L. species).

and Hydatellaceae. Indeed, detailed descriptions of the waterlily female gametophyte, which closely resembles that of Hydatellaceae (Friedman, 2008; Rudall et al., 2008), were published relatively recently (Winter & Shamrov, 1991a, b; Williams & Friedman, 2002; Friedman & Williams, 2003), and an earlier report of monocot-type sieve element plastids in Hydatellaceae is not supported in a new investigation (Tratt et al., 2009).

However, despite some congruence between molecular and morphological data on the delimitation and phylogenetic relationships of monocots, their floral evolution remains poorly understood. There is currently no universally accepted view on the morphology of the ancestral monocot flower, reflecting a high degree of parallelism in monocot floral evolution. Significant progress has been achieved in monocot phylogenetics since the first international monocot meeting in 1993, which included a timely and comprehensive review of monocot flowers (Endress, 1995). There are now considerable new data on flower structure and development in key groups, especially among early divergent monocots. In this paper, we review and evaluate these data to clarify the evolutionary history of the monocot flower and present a new model for floral evolution. We focus on two character suites that encompass the key features of monocot flowers: (1) the typical groundplan of trimerous-pentacyclic flowers, and (2) a character suite related to carpel fusion, including postgenital fusion between carpels and the presence of septal nectaries.

We broadly follow the Angiosperm Phylogeny Group classifications (e.g., Angiosperm Phylogeny Group III, 2009), which recognize 11 or 12 monocot orders, based primarily on molecular phylogenetic data (e.g., Davis et al., 2004; Chase et al., 2006; Graham et al., 2006). Specifically, the monocots consist of three informal groupings: (1) a grade of two early divergent lineages consisting of Acorales (Acoraceae, with the single genus *Acorus* L., which is sister to all other monocots) and Alismatales (Araceae, Tofieldiaceae, and 11 families of former Helobiae, here termed as the core alismatids); (2) a grade of five lilioid orders including Petrosaviales (two genera in a single family), Dioscoreales (three families), Pandanales (five families), Liliales (10 families), and Asparagales (14 families), with Dioscoreales and Pandanales pairing as sister to one another; (3) a clade of five commelinid orders consisting of Arecales (the palm family), Commelinales (five families), Dasypogonales (four genera in a single family, sometimes unplaced to order), Poales (16 families), and Zingiberales (eight families), with Commelinales and Zingiberales pairing as sister to one another.

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- There can be loss of isometry between floral whorls. For example, in *Potamogeton* (Potamogetonaceae), tepals and stamens can be interpreted as occurring in dimorphic whorls, but the carpels are unquestionably in a tetramerous whorl. In *Alisma* L., the perianth is trimerous, there are six stamens in a single whorl, and the carpel whorl is polymeric, triangular, and with sequential carpel initiation starting with three initial carpels. In many species of *Aponogeton* L. f., there are two tepals, 3 + 3 stamens, and three carpels.
- There can be an increase or decrease in the number of floral whorls. For example, there is a single perianth whorl in *Athenia* Petit (Zamiaceae), but united with Potamogetonaceae in Angiosperm Phylogeny Group III, 2009) and *Thalassia* Banks ex K. D. Koenig (Hydrocharitaceae), multiple stamen whorls in many Hydrocharitaceae and Limnocharitaceae (united with Alismataceae in Angiosperm Phylogeny Group III, 2009), a single stamen whorl in *Alisma* and *Ruppia*, and more than one carpel whorl in *Ruppia*, *Sagittaria* (Alismataceae), and *Triglochin*.
- Flowers can be unisexual (e.g., *Thalassia*, Cymodoceaceae, Zamiaceae).
- A synandrium can be present, with loss of stamen individuality (e.g., *Lipilana* J. Drumm. ex Harv. and some *Zannichellia* L. and Cymodoceaceae).

Figure 1 shows some variants of the flower groundplan in *Aponogeton*. Although *Aponogeton* typically possesses two tepals, six stamens, and three carpels, variation occurs in the number of organs of each category, illustrating the instability of the flower groundplan in the core alismatids.

## LILIoid MONOCOTS

Trimerous-pentacyclic flowers are common and probably plesiomorphic in at least four of the lilioid orders, although considerable variation occurs in the small but highly diverse order Pandanales. Petrosaviales represent a taxonomically isolated and species-poor lineage of two genera, *Japonolirion* Nakai and *Petrosavia* Becc. Cameron et al. (2003) and Angiosperm Phylogeny Group III (2009) placed both genera in Petrosaviaceae, but Takhtajan (2009) and Remizova (in press) accepted two distinct monogeneric families. Flowers of *Japonolirion* and *Petrosavia* are normally trimerous and pentacyclic, although there have been occasional records of a bicarpellate gynoecium in *Japonolirion* (Remizova et al., 2006b).

In Pandanales, loss of the typical monocot flower groundplan is so extensive that precise delimitation of

## TRIMEROUS-PENTACYClic FLOWERS

The typical monocot groundplan consists of six tepals in two alternating whorls (generally not differentiated into petals and sepals), six stamens in two alternating whorls, and three carpels (i.e., trimerous-pentacyclic flowers). Sectorial differentiation in monocot flowers was discussed in detail by Endress (1995), who noted that this arrangement is more readily achievable in trimerous than in pentamerous flowers because the sectors are broader. In many monocots, tepals and stamens inserted on the same radii are intimately linked with each other by (1) initiation as a common tepal-stamen primordium, (2) basal congenital fusion of a tepal and a stamen, (3) insertion of inner tepal-stamen complexes above the outer tepal-stamen complexes, thus affecting precise whorl alternation, or (4) functional synzooecium within a tepal-stamen complex. Endress (1995) highlighted the lack of a clear correlation between the presence or absence of common primordia and the occurrence of tepal-stamen fusion in monocots. He found that both features are homoplastic within large monocot clades and in monocots in general.

In the following review, we consider only the number and position of organs, not their shape, functional elaboration, or synzooecium. A trimerous-pentacyclic groundplan occurs in some members of all monocot orders, but with variable frequency. The widespread occurrence of trimerous-pentacyclic flowers in monocots contrasts with their virtual absence from early divergent angiosperms, magnoliids, and non-core eudicots. However, trimery itself is common among these groups, though rare in core eudicots (e.g., Kubitzki, 1987; Endress, 1996). For example, *Cabomba* Aubl. (Cabombaceae, Nymphaeales) has the same number of floral organs as typical monocot flowers (six tepals, six stamens, three carpels), but all six stamens belong to the same whorl (e.g., Tucker & Douglas, 1996; Endress, 2001; Rudall et al., 2009). Flowers of the magnolioid *Oreophea corymbosa* (Blume) Miq. (Annonaceae, Magnoliales) possess three sepals, 3 + 3 petals, 3 + 3 stamens, and three carpels (e.g., Buchheim, 1964), and differ from typical monocot flowers only in the presence of an extra perianth whorl. Some other Annonaceae possess a perianth of only three sepals and three petals (e.g., *Dennettia* Baker f.), but in all of these cases, stamens and carpels are numerous (see Kessler, 1993). Flowers of the magnolioid *Lactoris* Phil. (Lactoridaceae, Piperales) possess three petals (rather than 3 + 3 petals, 3 + 3 stamens, and three carpels (Tucker & Douglas, 1996). Some non-core eudicots, such as Menispermaceae and Lardizabalaceae (Ranunculales) have 3 + 3 sepals, 3 + 3 petals, 3 + 3 stamens, and three or 3 + 3

the inflorescence-whorl boundary is often problematic (Rudall, 2003, 2008; Rudall & Bateman, 2006). For example, if the female reproductive units of *Sarrananga* Hemsl. (Pandanales) are interpreted as flowers, they possess up to 80 carpels united to form a unilocular ovary, and the receptacle is folded in several places, so that carpels are arranged along a zigzag line. A similar carpel arrangement, with dorsoventral planes of carpels typically rotated through 90° toward the center of the flower, occurs in *Lacandonia* E. Martinez & Ramos, *Triuris* Miers, and *Peltophyllum* Gardner (Triuridaceae), recalling a comparable pattern of carpel arrangement on a folded receptacle in an asterid eudicot, *Tupidanthus* Hook. f. & Thomson, in the family Araliaceae (Hemsley, 1901; Sokoloff et al., 2007). Unisexual flowers occur in most Cyclanthaceae, Pandanales, and Triuridaceae, and organ numbers are frequently atypical for monocots in these families. The pattern of general distribution on the inflorescence is highly unusual in Cyclanthaceae, either with each female flower surrounded by four male flowers (in subfamily Carduoidaceae) or with female and male flowers united in rings (in Cyclanthoideae), with a resulting loss of flower individuality (Goebel, 1931; Harling, 1958). In the remarkable, inside-out bisexual reproductive units of *Lacandonia* (Triuridaceae), the carpels are inserted outside the stamens, and the dorsoventral carpel orientation is inverted with respect to carpel position in phylogenetically related taxa (Ambrose et al., 2000; Rudall, 2008). Flowers are at least superficially closer to the typical monocot structure in Stemonaceae and Velloziaceae. However, in Stemonaceae the perianth and androecium are either dimorphic or pentamerous, and the gynoecium is either monomerous or trimerous (Rudall et al., 2005). Within Velloziaceae, some species possess a corona of six petaloid appendages, and others show increased stamen number (Menezes & Semir, 1990; Mello-Silva, 1995; Sajo et al., 2010).

The remaining lilioid orders are relatively conservative in their floral groundplan. In Dioscoreales, deviations such as loss of one of two perianth whorls and loss of one of two stamen whorls can largely be explained by reduction. In Liliales, most of the interesting deviations from trimerous-pentacyclic flowers are found in Smilacaceae and Trilliaceae (ca. three genera that are placed within Melanthiaceae in Angiosperm Phylogeny Group III, 2009). The flowers of a few Smilacaceae possess three to 15 stamens (Takhtajan, 2009) or up to 18 stamens (Dahlgren et al., 1985) in trimerous whorls. In Trilliaceae, a highly stable organization of the vegetative shoots and highly conservative pattern of flower arrangement are associated with exceptional

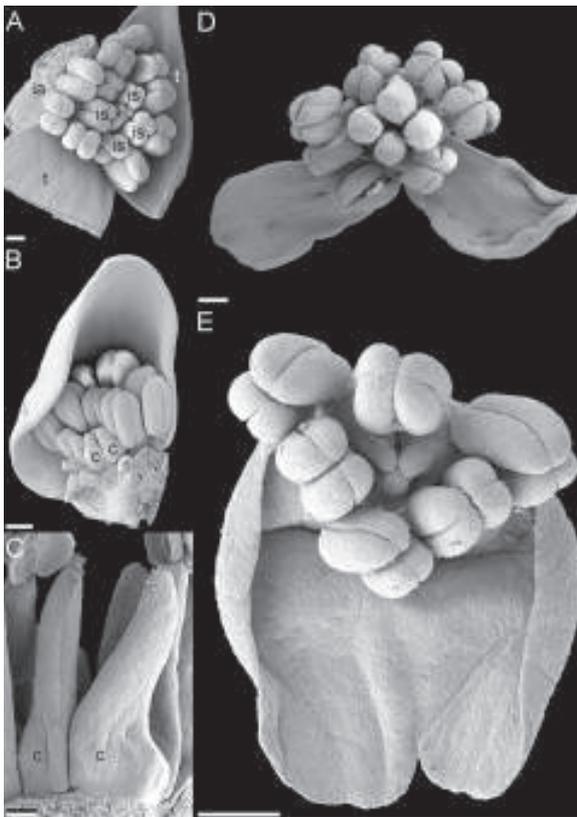


Figure 1. Flowers of *Aponogeton* L. f. (Aponogetonaceae, Alismatales) with a highly unstable floral groundplan and (almost) free carpels (SEM). A–C, *Aponogeton distachyus* L. f.—A. Flower with two tepals, 14 stamens, and four carpels. —B. Flower with single tepal. Note that some stamens have been removed. —C. Gynoecium with free plicate carpels. —D. *Aponogeton subonigatus* Schumacher & Thonn. Flower with two tepals, seven stamens, and four carpels. —E. *Aponogeton stuhlmannii* Engelm. Flower with two united tepals, six stamens, and three carpels. c, carpel; ia, inflorescence axis; is, inner-whorl stamen; t, tepal. Scale bars = 250 μm.

Hamann (1964) reproduced a floral diagram of *Rapatea paludosa* Aubl. (Rapateaceae) in which the carpels are on the same radii as the inner-whorl tepals and inner-whorl stamens, an arrangement that is fundamentally different from that of other monocots. Observations on another member of Rapateaceae, *Cephalostemon* R. H. Schomb. sp. (P. J. Rudall & M. C. Sajo, unpublished), show regular alternation of whorls. More comparative data on flowers of Rapateaceae are needed to resolve this apparent variation. Similarly, flowers of Mayacaceae were reported to be trimerous-tetracyclic, with a single stamen whorl and all whorls regularly alternating so that the carpels occupy the sites where the inner stamen whorl would be expected (T. Stützel, pers. comm., cited in Dahlgren et al., 1985: 388). However, illustrations from a recent study by Carvalho et al. (2009) confirm earlier observations (e.g., Hamann, 1964) that carpels in Mayacaceae lie on the same radii as the outer-whorl tepals, as in other monocots with trimerous flowers.

Most wind-pollinated (or self-pollinated) Poales show high diversity in floral groundplan, not always restricted to reductions of trimerous-pentacyclic flowers. Extant Typhaceae (including Sparganiaceae) have unisexual flowers with an unstable number of tepals, which are modified into hairlike structures in *Typha* L. (Müller-Doblies, 1970). Extant taxa possess from one to eight stamens and typically a single carpel, although tetralogically up to three united carpels can be found (Müller-Doblies, 1970; Dahlgren et al., 1985). Some Tertiary fossil *Sparganium* L. possessed up to 7-locular fruits (Dorofeev, 1979).

Among the graminids and restiids, which are predominantly wind-pollinated, flowers of several families (Anarthriaceae, Eriocaulaceae, Flagellariaceae, Juncaceae, Restionaceae) can be readily derived from trimerous-pentacyclic flowers by reduction of certain organs (e.g., the outer stamen whorl in Restionaceae) and transitions from trimery to dimery. There has been considerable discussion regarding the morphological interpretation of the grass flower, but flowers of most grasses can be derived from trimerous-pentacyclic flowers by reduction. Stamen number is highly variable in grasses (Gramineae or Poaceae), sometimes even within a single genus; the most common numbers are three and two, but these can be interpreted as belonging to more than one whorl (Rudall & Bateman, 2004). Some grasses possess six stamens (*Oryza* L.), and stamen multiplication has occurred in a few grass genera (e.g., *Ochlandra* Thwaites, with up to 120 stamens). The uniovulate and unicarpellar grass ovary usually bears two, but sometimes one, three, or even four stigmas (Phillipson, 1985). Highly unusual reproductive structures occur in Centrolepidaceae, a family closely related to

Restionaceae, with its center of diversity in Australia. During recent decades, the reproductive units of Centrolepidaceae have usually been understood as highly integrated pseudanthia composed of unicapellate naked female flowers and unistaminate naked male flowers (e.g., Cooke, 1998; Takhtajan, 2009). However, a recent re-examination (Sokoloff et al., 2009) supported a euanthial interpretation of these reproductive structures. Flowers of Centrolepidaceae possess one or two stamens and one to about 30 carpels. It is an open question whether phyllomes surrounding these flowers represent tepals or bracts. Multicapellate gynoecia of *Centrolepis* Labillard. are unique among angiosperm gynoecia. Carpels are arranged in a single whorl, but one side of the gynoecium is uplifted due to strong, unequal receptacle growth, so that in anthetic flowers carpels appear to be inserted in two rows along a common stalk. Some Centrolepidaceae possess polymeric gynoecia (the highest carpel number in Poales), but some other members of the family (*Aphelia* R. Br.) have a truly monomeric gynoecium, with no evidence of pseudomonomy.

In the cyperid clade, flowers are trimerous-pentacyclic in Thurniaceae and most Juncaceae. The inner stamen whorl or inner tepal whorl is occasionally lacking in Juncaceae (Dahlgren et al., 1985), but (as in Mayacaceae) the absence of the inner stamen whorl does not affect carpel position, at least in *Juncus minutulus* (Albert & Jahand) Prain (D. Sokoloff, pers. obs.). There is considerable floral diversity in Cyperaceae, which is currently subdivided into two subfamilies, Mapanioideae and Cyperoideae, that represent monophyletic sister groups (Simpson et al., 2003). Flowers of Cyperoideae could be derived from the trimerous-pentacyclic type, with floral reduction as a primary evolutionary trend (Vrijdaghs, 2006; Vrijdaghs et al., 2009). Many Cyperoideae possess bisexual flowers with three (sometimes up to six) stamens, and two or three carpels united in a unilocular ovary with a single central ovule. The bristles surrounding the flowers appear to be modified tepals; they can follow the 3 + 3 pattern (Vrijdaghs et al., 2005). In *Carex* L., which represents the most extreme case of reduction, flowers are unisexual and naked, with either two to three stamens (in male flowers) or two to three united carpels (in female flowers). In tricapellate female flowers of *Carex*, carpel orientation appears to differ from the usual condition in monocots (in which the median carpel is typically adaxial), if the bract subtending the utricle with enclosed gynoecium is interpreted as the flower-subtending bract. However, the utricle is actually the flower-subtending bract in *Carex* (reviewed in Alexeev, 1996), and therefore the median carpel is abaxial, as in other monocots.

ability in the number and arrangement of flower parts. Flowers of Trilliaceae are solitary and terminal on lateral shoots, and an involucre whorl of foliage leaves is present below each flower (e.g., Dahlgren et al., 1985; Zomlefer, 1996; Takhtajan, 2009). Merism of the involucre whorl is often the same as in the flower; the outer-whorl tepals alternate with the involucre leaves. In species of *Trillium* L. that lack a pedicel, the involucre positionally resembles a third perianth whorl. In some other species, the inner perianth members are absent, either due to suppression (*Paris tetraphylla* A. Gray, *P. incompleta* M. Bieb.) or loss (*T. apetalon*) (Takahashi, 1994; Remizowa et al., 2007a; Choob, 2008; Narita & Takahashi, 2008). In cases where the inner tepals (petals) are entirely lost (*T. apetalon*), the carpels and outer-whorl stamens develop on radii that alternate with the remaining tepals, so the orientation of the gynoecium differs from that of most other monocots. *Trillium apetalon* is taxonomically close to *T. smallii* Maxim. and is sometimes placed in synonymy with it. Within *T. smallii* s. str., there is infraspecific variation in petal number from one to three, or petals can be absent, in which case they are replaced by additional stamens, thus increasing the stamen number to nine (Chase & Chase, 1997). Within *Paris* s.l. (including *Daisya* Raf. and *Kimigasa* Taw. & Suto; see Ji et al., 2006), flower merism is typically increased (because *Paris* s.l. is monophyletic, the increased merism is a potential synapomorphy of the genus). Many *Paris* species have tetramerous flowers (e.g., *P. quadrifolia* L., *P. tetraphylla*), and *P. japonica* (Franch. & Sav.) Franch. is highly polymeric, with 7- to 10(10-12)-merous flowers (Tanura, 1998). Some species of *Paris* s.l. show an increase in the number of stamen whorls to three, four, five, or even six whorls. The species with increased stamen whorls (*P. dunniana* H. Lévl., *P. conopseoides* (Takht.) H. Li, *P. vietnamensis* (Takht.) H. Li) formed a clade in the molecular phylogenetic analysis of Ji et al. (2006), whereas a group of *Paris* species with 2-whorled stamens was paraphyletic.

Among Asparagales, several families differ from the trimerous-pentacyclic groundplan, including the most species-rich family Orchidaceae, which is sister to all other Asparagales in most analyses (e.g., Givnish et al., 2006; Graham et al., 2006). Orchid flowers are clearly derived from trimerous-pentacyclic flowers, possibly by suppression or loss of three, four, and five stamens (from both whorls) in different orchid clades (Rudall & Bateman, 2002). Some other Asparagales, such as *Pauidium* Harv. (Hypoxidaceae) and *Iridaceae*, lack one of the two stamen whorls, but the positions of the other organs, including the carpels, are the same as in more typical monocot flowers. A few Asparagales are dimereous (e.g., *Maianthemum*, Asparagaceae),

tetramerous (e.g., some *Aspidistra* Ker Gawl., Asparagaceae), or even pentamerous to heptamerous (*Neostelia* J. B. Williams, Asteliaceae; Takhtajan, 2009). Different patterns of polyandry have evolved at least three times in Asparagales (Koyan, 2007), including stamen fascicles in *Gethyllis* L. (Amaryllidaceae) and a single folded stamen whorl in *Caricallio racemosa* Ridl. (Hypoxidaceae) (Dahlgren et al., 1985; Koyan, 2007). In *A. dodocandra* (Gagnep.) Tillich, stamen number is twice the number of the perianth lobes (Tillich, 2005). Flowers of *A. locii* Arnautov & Bogner superficially resemble the inflorescences of the eudicot *Ficus* L. (Moraceae); all tepals are united to form a chamber up to 3 cm long, with a narrow opening (to 2 mm diam.), and there are 12 to 14 stamens and apparently four carpels (Bogner & Arnautov, 2004). Some Amaryllidaceae, including *Narcissus* L., possess a floral corona that is morphologically similar to the corona in Velloziaceae (Pandanales). In general, significant deviations from typical monocot flower groundplan (except losses of some stamens) are extremely rare in Asparagales.

COMMELINID MONOCOTS

Considerable floral diversity exists among the commelinid monocots, but it seems likely that trimerous-pentacyclic flowers are plesiomorphic for each of the four (or three) commelinid lineages, Arecales (palms), the sister-orders Commelinales and Zingiberales, Poales, and Dasypogonaceae (a small family of unclear affinity that is sister to Poales in some analyses, e.g., Chase et al., 2006; see also Rudall, in press). Dasypogonaceae possess trimerous-pentacyclic flowers, although these are sometimes functionally unisexual. Secondary modifications in the diverse lineage that includes the orders Commelinales and Zingiberales include losses of some organs, especially in the androecium, but apparently no organ increase. The large order Poales encompasses a basal grade of three families (Bromeliaceae, Rapateaceae, Typhaceae) and four other clades, informally termed "graminids, restiids, cyperids, and sxyrids" (Linder & Rudall, 2005). Many Poales are characterized by abiotic (usually wind) pollination (graminids, restiids, cyperids, and Typhaceae), although some members of these clades are biotically pollinated. There could have been several shifts to wind pollination in Poales, often associated with reductions in carpel and ovule number (Linder, 1998; Linder & Rudall, 2005).

Flowers are trimerous-pentacyclic in most biotically pollinated Poales (e.g., Bromeliaceae, Rapateaceae), or floral variation can be readily explained by reduction or loss of organs from ancestral trimerous-pentacyclic flowers (e.g., Eriocaulaceae, Xyridaceae).

Not all flower diversity in Cyperaceae can be explained by reduction. For example, *Evandra* R. Br. possesses up to 20 stamens and up to six carpels (Dahlgren et al., 1985). Vrijdaghs (2006) listed six other Cyperoideae with more than six stamens; for example, *Reedia spatheata* F. Muell. has more than 20 stamens and eight stigmatic branches. Some cyperids possess more than six perianth parts. For example, five of the eight tepals in *Dulichium arundinaceum* (L.) Britton correspond with five of the six tepals in *Scirpus* L.; the other three tepals in *Dulichium* Pers. are inserted at the site of the sixth, adaxial tepal of *Scirpus* (Vrijdaghs et al., 2005). In *Eriophorum* L., all tepal primordia are united into a ring meristem on which numerous hairlike perianth parts develop centripetally in several whorls (Vrijdaghs et al., 2005).

The reproductive units of Mapanioideae are often interpreted as highly specialized pseudanthia composed of several naked unistaminate male flowers, each subtended by a bract and a terminal naked female flower (e.g., Dahlgren et al., 1985; Richards et al., 2006). In some Mapanioideae, sterile bracts inserted on the main axis above the male flowers surround the female flower. An alternative interpretation is that the entire mapanioid reproductive unit is a flower, in which the structures commonly described as bracts are actually tepal homologues (e.g., Bentham, 1877; Holtum, 1948; Goetghebeur, 1998). The main problem with the latter interpretation is the presence of these putative tepals above the level of insertion of the outer stamens. However, an analogous condition occurs in the distantly related alismatid *Triglochin* (Fig. 2D), which has a similar tepal position, although in this case there are only two perianth whorls. Several authors have postulated a homology between the reproductive units of Mapanioideae and the structures that are commonly termed flowers in Cyperoideae (e.g., Bentham, 1877; Holtum, 1948). Within this concept, if mapanioid reproductive units are pseudanthia, then these so-called cyperoid flowers are also pseudanthia (e.g., Schultze-Motel, 1964; Burger, 1977), which appears unlikely (e.g., Vrijdaghs et al., 2005). Holtum (1948) suggested that the floral construction in Mapanioideae represents the primitive condition in Cyperaceae, with an unfixed number of parts. However, this interpretation also appears unlikely in a modern phylogenetic context. It remains an open question whether the reproductive units of Mapanioideae are flowers or pseudanthia (see also Alexeev, 1996). Meuse (1975) interpreted them as prefloral units, a concept that is difficult to accept in the framework of our current understanding of the phylogenetic placement of Cyperaceae.

Finally, the palm order Arecales exhibits considerable variation in floral organ number, arrangement, and

initiation sequence. Many palms have trimerous-pentacyclic flowers, although they are often functionally male or female, with pistillodes and staminodes, respectively (Dransfield et al., 2008). Some palm flowers have fewer organs than typical monocot flowers. For example, in *Nypa* Steck (Areaceae), female flowers have 3 + 3 tepals, no staminodes, and three carpels, and male flowers have 3 + 3 tepals, three stamens united in a syndrium, and no rudimentary gynoecium (Uhl, 1972). Some palms belonging to several unrelated groups possess polystaminate flowers with up to 950 stamens (Dransfield et al., 2008). Stamens in polymeric androecia are never arranged spirally but instead form several whorls or groups associated with the inner-whorl and outer-whorl tepals, or stamen arrangement is chaotic. Stamen development can be either centrifugal (e.g., phytelophant palms) or centripetal (e.g., Uhl & Dransfield, 1984). Sometimes carpel number is increased, although the gynoecium is always single-whorled.

Palms are unusual among monocots in that there are strong differences between the inner and outer perianth whorls, so that they could be termed "sepals and petals." In some palms, the inner and outer perianth whorls form individual sepal and petal tepals, and there is a tendency that only petals are associated with stamens (e.g., Dransfield et al., 2008; Stauffer et al., 2009). Perianth differentiation into sepals and petals is also pronounced in some other commelinids (e.g., Commelinaceae in Commelinales, Xyridaceae in Poales) and also in orchids. Stamen association with the petals occurs in some early divergent Poales (e.g., Bromeliaceae, Rapateaceae).

CARPEL FUSION

Carpels are fused in flowers of the majority of monocots, in contrast with early divergent (ANA grade, sometimes termed "ANITA grade") angiosperms and magnoliids, in which gynoecia are predominantly free-carpellate (apocarpous). The presence of fused carpels in *Acorus* (Fig. 3), the putative sister to all other monocots, and in other early divergent monocots has led some authors (e.g., Doyle & Endress, 2000; Chen et al., 2004) to postulate multiple origins of a gynoecium with free carpels in monocots. Earlier, Dahlgren et al. (1985) had also postulated that apocarp is derived in monocots, although they used a different phylogenetic framework. It is important to note that there are different views regarding the use of the term "apocarp." All authors agree that gynoecia with free carpels are apocarpous, but some follow Leinfellner (1950) and consider gynoecia in which the carpels are postgenitally united (i.e., fused at anthesis) to be structurally

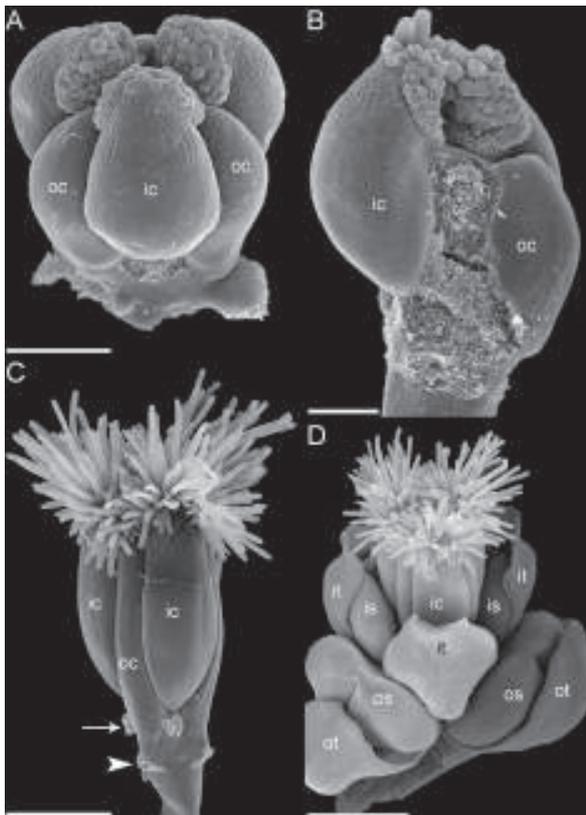


Figure 2. Gynoecium and flower morphology in *Triglochin palustris* L. (Juncaginaceae) (SEM). The gynoecium consists of three outer-whorl sterile carpels and three inner-whorl fertile carpels. All six carpels are united via the floral center. —A. Young gynoecium. —B. Young gynoecium dissected longitudinally. —C. Gynoecium at female phase of anthesis. Arrowhead indicates the level of insertion of outer-whorl stamens and tepals; arrow indicates the level of insertion of inner-whorl stamens and tepals. —D. Flower at female stage of anthesis. ic, inner-whorl fertile carpel; is, inner-whorl stamen; it, inner-whorl tepal; oc, outer-whorl sterile carpel; os, outer-whorl stamen; ot, outer-whorl tepal; re, receptacle (or possibly united ventral parts of fertile carpels). Scale bars: A = 200  $\mu$ m; B = 150  $\mu$ m; C = 600  $\mu$ m; D = 800  $\mu$ m.

(e.g., Eckardt, 1937; Philipson, 1985; Shamrov, 2009; González & Rudall, 2010) and partly because even truly monomeric gynoecia can evolve from gynoecia of several united carpels as an extreme form of meristic variation (e.g., in Centrolepidaceae; Sokoloff et al., 2009). Thus, the presence of both monomery and carpel fusion in the same group does not necessarily indicate that the presence of free carpels is an ancestral condition in the group. A similar pattern of variation (true monomery plus syncarpy, but no polymerous apocarpy) occurs in the eudicot order Caryophyllales, in which Volgin (1986) inferred that monomery evolved from syncarpy, at least within Phytolaccaceae, in the subfamily Rivinoideae. Within the monocot order Pandanales, Rudall and Bateman (2006) speculated that the monomeric gynoecium that occurs in Stemonaceae could have been derived from a gynoecium with united carpels (present in Velloziaceae) and could have given rise to the free-carpellate condition that occurs in extant Triuridaceae (see also Rudall et al., 2005). In many angiosperm groups, the conclusion that monomery represents a derived condition can be inferred from the phylogeny, but it is rare to find morphological evidence that supports an evolutionary transformation from syncarpy to true monomery (rather than pseudomonomery), as in Phytolaccaceae.

In monocots, non-monomeric free-carpellate gynoecia are restricted to the core alismatids, Triuridaceae, and some palms, notably *Nypa* and some coryphoid palms (Uhl & Moore, 1971; Uhl, 1972; Dransfield et al., 2008). Among the core alismatids (see Eber, 1934; Igersheim et al., 2001), carpels are free (or rarely weakly connate via the floral center at the very base) in most members of three clades: (1) Alismataceae–Limncharitaceae, (2) Aponogetonaceae (see Fig. 1C with *Aponogeton distachyus* L. f.), and (3) Cymodoceaceae–Potamogetonaceae–Ruppiaaceae–Zannichelliaceae (Posidoniaceae and Zosteraceae, which belong to the third clade, are monomeric or, in the case of Zosteraceae, possibly pseudomonomeric). In contrast, carpels are fused together in some other core alismatid clades: (1) Butomaceae plus Hydrocharitaceae, (2) Scheuchzeriaceae, and (3) Juncaginaceae (except the monomeric *Triglochin scilloides*). The three free-carpellate clades are intermixed with the three syncarpous clades in molecular phylogenies of Alismatales.

MODES OF CARPEL FUSION

Three modes of carpel fusion occur in monocots: congenital, postgenital, and fusion via the floral center. Both congenital and postgenital carpel fusion can co-occur during development of different parts

within the gynoecium (Fig. 4) (see also Remizowa et al., 2008). Congenital carpel fusion, the most common condition in eudicots, is present in some monocots (Fig. 5), including the basal lineage *Acorus* (Fig. 3), which also lacks septal nectaries (e.g., Rudall & Furness, 1997; Bazzo & Endress, 2000). Despite the presence of congenital fusion between carpels in *Acorus*, the putative sister to all other monocots, Remizowa et al. (2006b) concluded that postgenital fusion between carpels, which is associated with septal nectary formation, probably represents the plesiomorphic condition in monocots. Postgenital carpel fusion is common in monocots, but relatively rare among eudicots, rare among syncarpous magnoliids, and absent from early divergent (ANA grade) angiosperms, in which only some Nymphaeaceae possess united carpels, and these are congenitally fused (Endress, 2001).

Carpel fusion via the floral center, not combined with other types of fusion, is an unusual condition that is probably restricted to the core alismatids among monocots. In this condition, an internal congium is always lacking. It could be interpreted as either (1) congenital fusion of the ventral side of each carpel to an extended receptacle (i.e., a form of apocarpy), or (2) congenital fusion between the ventral sides of all carpels, although in practice it is almost impossible to confidently differentiate between these two types (see also Eber, 1934; Igersheim et al., 2001). In most Juncaginaceae, carpels are united via the floral center, but their flanks are completely free (Figs. 2, 6). Many species of *Triglochin* (Juncaginaceae) possess three outer-whorl sterile carpels plus three inner-whorl fertile carpels. Commonly, both sterile and fertile carpels are united via the floral center (Fig. 2B). However, in at least some members of the *T. bulbosa* L. complex (as defined by Kücke et al., 2010), only the fertile carpels are united while the sterile carpels remain small and free (Fig. 6). An arrangement that is probably unique to certain *Triglochin* species among monocots. Fusion via the floral center is also present in *Potamogeton crispus* L. (Potamogetonaceae), some *Aponogeton* (Aponogetonaceae), *Maundia* F. Muell. (Maundiaceae, family placement after von Mering & Kadereit, 2010), *Damasium* Mill. (Alismataceae; to a lesser degree also in other Alismataceae; Eber, 1934), and Limncharitaceae (Troll, 1932; Eber, 1934; Igersheim et al., 2001). A related (but somewhat different) condition occurs in some Hydrocharitaceae, e.g., *Ottelia* Pers. (Kaul, 1969), in which the receptacle is strongly concave and the dorsal carpel surfaces are congenitally united with the receptacle. Carpel flanks are almost free in some Hydrocharitaceae (as in *Ottelia*) but congenitally united in others (Troll, 1931; Eber, 1934; Kaul,

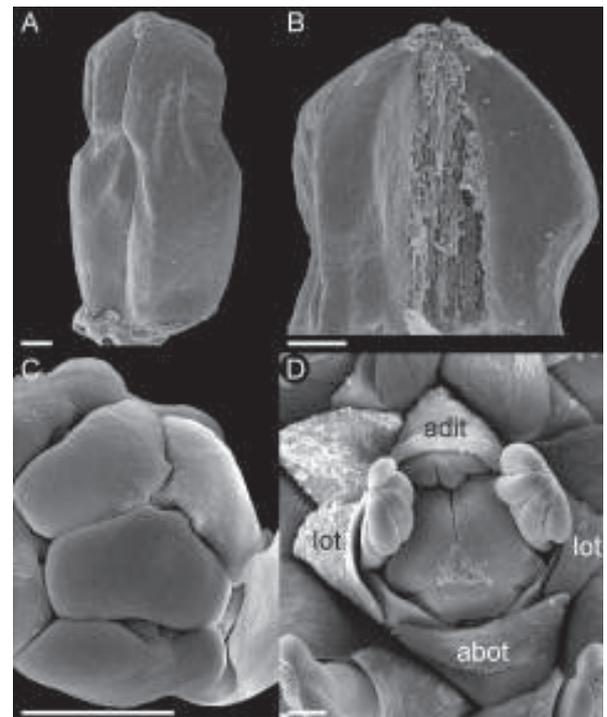


Figure 3. Gynoecium and flower of *Acorus gramineus* Sol. ex Aiton (Acoraceae) (SEM). —A. Entire gynoecium, consisting of three congenitally united carpels. —B. Upper part of a gynoecium with one carpel removed to show nonsecretory septal slits. —C. Apical view of a gynoecium. —D. Anthesis flower showing top of gynoecium with three fused carpels; only three adaxial stamens are visible, with the three abaxial stamens revealed later. abot, abaxial outer tepal; adit, adaxial inner tepal; lot, lateral outer tepal. Scale bars = 200  $\mu$ m.

apocarpous, whereas others (e.g., Takhtajan, 1966, 2009) restrict the term "apocarpy" to the condition where any type of fusion between carpels is lacking at any stage in development. Thus, in general we avoid using the term "apocarpy" without clarification, and prefer free-carpellate to apocarpous.

Some monocots are free-carpellate merely because they possess a single carpel, a condition termed "monomery." Monomeric species have limited significance for inferring ancestral morphology, partly because it can be difficult to distinguish between pseudomonomeric and truly monomeric gynoecia

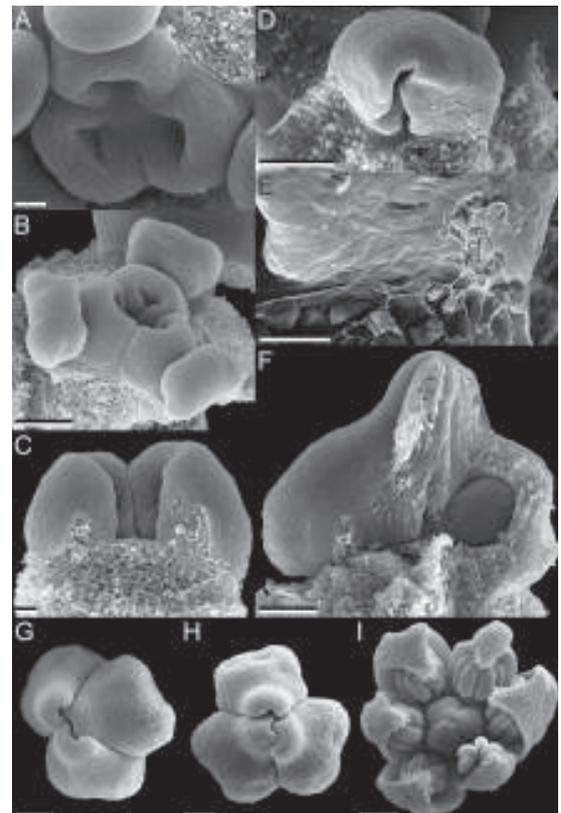


Figure 4. Gynoecium development in *Ledebouria socialis* Jessop (Asparagaceae), showing contribution of both congenital and postgenital carpel fusion (SEM). —A. Very young gynoecium with three horseshoe-shaped carpels. —B. Later stage with carpels partially united at their flanks. —C. Later stage similar to B, with one carpel removed to show areas of congenital carpel fusion. Note that postgenital carpel fusion does not occur at this stage. —D. Young gynoecium before postgenital carpel fusion, with two carpels removed. —E. Detail of D, with the region of congenital fusion between carpels enlarged. —F. Gynoecium after postgenital

1969; Igersheim et al., 2001). A concave receptacle could also contribute to formation of the outer ovary wall in other monocots, although its precise morphological identification is problematic (see below).

SEPTAL NECTARIES

Septal (gynopleural) nectaries are apparently restricted to the monocots and probably represent a key innovation of this group, although they are absent from *Acorus* (Rudall & Furness, 1997; Burgo & Endress, 2000) and therefore might be synapomorphic for a clade comprising all monocots except *Acorus*. The fact that septal nectaries are absent from some Alismatales (including Araceae) could suggest that this nectary type is synapomorphic for a clade comprising all monocots except *Acorus* and Alismatales. However, we believe that the presence of typical septal nectaries in some (though not all) genera of Tofieldiaceae supports the origin of septal nectaries below the split between Alismatales and other monocots. In this context, it is instructive that Tofieldiaceae (rather than Araceae) could represent the most basal lineage of Alismatales (S. W. Graham, pers. comm., Aug. 2010).

Typically, septal nectaries (see Fig. 7) are located between the ovary locules and disperse nectar through three narrow openings at some point on the surface of the ovary, often close to the base of the style (Daumann, 1970; Hartl & Severin, 1981; Schmid, 1985; van Heel, 1983; Simpson, 1993; Smets et al., 2000; Kocyan & Endress, 2001; Rudall, 2002; Remizowa et al., 2006b, 2008). They are sometimes termed "gynopleural nectaries" (Smets & Cresens, 1983; Smets et al., 2000) because in some taxa (e.g., *Tofieldia* Huds., Tofieldiaceae, Alismatales) they are located below the ovary locules (i.e., infralocular nectaries: Figs. 7A, B, 8A, B). In some species, a large common triadriate cavity is present at the ovary center; toward the style this cavity divides into three separate canals. This type of septal nectary is often correlated with inferior ovary formation (Daumann, 1970; Hartl & Severin, 1981; Schmid, 1985; Sajo et al., 2004).

Baum (1948), Hartl and Severin (1981), and especially van Heel (1983) achieved considerable progress in understanding the relative contributions of congenital and postgenital fusion in the development of septal nectaries. In syncarpous gynoechia with septal nectaries, carpels are always initiated by individual

primordia. The ventral sides of adjacent carpels unite postgenitally at a relatively late developmental stage. The fusion area, which defines the inner boundary of the nectary, is often very narrow. The outer boundary of the nectary is formed by the outer wall of the ovary, without postgenital fusion (Fig. 4). The outer wall develops as a tubular structure that links all the carpels, resulting in considerable deformation of the bases of the free carpel regions. Growth of the outer ovary wall extends to the level of the openings of the septal nectaries (Fig. 9A) and determines their position: the more extensive the growth of the ovary wall, the more distal are the nectary openings. Morphological interpretation of the outer ovary wall is problematic; it could represent either the congenitally fused dorsal regions of all the carpels, or a concave receptacle. In terms of morphogenesis, the development of the outer wall of a superior ovary with septal nectaries resembles the development of an inferior ovary wall except in the localization of intercalary zonal growth. In a superior ovary, tissue proliferation is confined to a ring below the periphery of the bases of the young carpels (Fig. 9A); in an inferior (or semi-inferior) ovary, this ring is thicker and extends outward to the region of the receptacle below the septal bases (Fig. 9B).

In some monocots (e.g., *Tofieldia*, cf. *T. cernua* Sm., Fig. 8), the nectaries are located below the ovary locules or in the basalmost part of the septa (Igersheim et al., 2001; Rudall, 2002; Remizowa et al., 2006b). In flowers with infralocular nectaries, the carpels often possess stipes and/or a pronounced ascidiolate zone. Carpel stipes can be obliquely inserted on a concave receptacle, giving rise to a peculiar type of internalized nectary, as seen in *Tofieldia*. In the palm *Licuala* Wurm., in addition to carpel bases, the inner surfaces of the corolla-androecium tube are also basally nectariferous (Stauffer et al., 2009). In contrast with typical septal nectaries, infralocular nectaries typically open along their outer edge if the ovary is superior. If the ovary is inferior, the nectary opens by long canal(s) extending up to the top of the ovary, as in *Heliconia* L. (Heliconiaceae, Zingiberales) (Kirchoff et al., 2009). In flowers with infralocular nectaries, the carpels remain completely free until a very late developmental stage, and carpel fusion is entirely postgenital (van Heel, 1983; Kocyan & Endress, 2001; Remizowa et al., 2006b).

fusion between carpels, cut longitudinally. The space between regions of congenital and postgenital fusion will develop into a septal nectary.—G, H. Top views of two gynoechia with different patterns of postgenital fusion between carpels in the stylar region.—I. Young flower. Note trimerous-pentacyclic groundplan.—C, E. Region of congenital fusion; pf, region of postgenital fusion. Scale bars: A, C, E, = 30 µm; B, D, F–H = 100 µm; I = 300 µm.

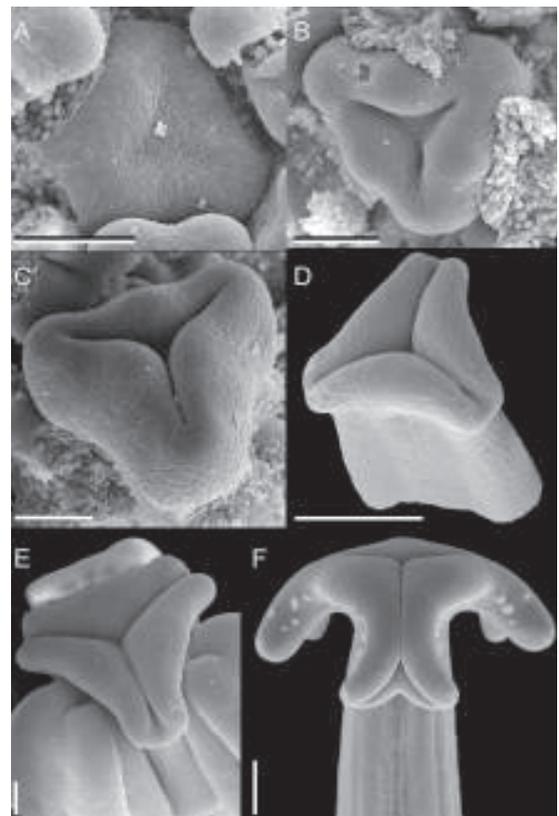


Figure 5. Gynoechium development in *Tricyrtis formosana* Baker (Liliaceae), in which carpels are almost exclusively congenitally united, and septal nectaries are absent (SEM).—A, B. Gynoechium initiation as an entire triangular meristem; carpels are congenitally united from their initiation.—C. Later developmental stage.—D–F. Stigma development and closure of gynoechium by postgenital fusion of carpel margins. Scale bars: A–C, E = 100 µm; D, F = 300 µm.

A peculiar type of infralocular nectary occurs in some core alismatids (especially Alismataceae, e.g., *Alisma*, *Damasonium*) with carpels that are almost free, and united only at their bases via the floral center (e.g., van Heel, 1983; Igersheim et al., 2001). In these species, the nectaries are confined to the lateral carpel flanks in the region of basal carpel adnation at the floral center, either level with the lowermost part of the ovary locules or just below the locules. These nectaries are open along the outer carpel edge.

It is traditionally assumed that the evolution of septal nectaries was directed toward their internalization, i.e., toward their position within the septa of the gynoechium as almost closed cavities with narrow openings (Fig. 7C–E; e.g., Daumann, 1970; van Heel, 1983). This internalization hypothesis would suggest that gynoechia with infralocular nectaries are more primitive than those with typical septal nectaries. Van Heel (1983) postulated that during the course of evolutionary internalization, the secretory surfaces shifted from the carpel stipes and the base of the gynoechium toward the ovary itself, allowing a significant increase in the secretory surface, and hence potentially more nectar. Internalization of the nectaries took place via the development of a common outer ovary wall at a relatively late stage. The internalization hypothesis appears to be congruent with the relatively early divergence of some taxa with infralocular nectaries in the monocot phylogeny (e.g., *Tofieldia*, Alismataceae, *Japonalirion*). However, some aspects of this hypothesis are problematic. For example, van Heel (1983) was unable to find taxa with nectaries that could be regarded as intermediate between typical septal nectaries and infralocular nectaries. Infralocular nectaries are present in members of relatively derived monocot lineages, such as Asparagales, Poales, Araceae, Zingiberales, and Commelinales (Simpson, 1993; Kocyan & Endress, 2001; Rudall, 2002; Sajo et al., 2004; Kirchoff et al., 2009; Stauffer et al., 2009). Remizowa (2007) suggested that the location of septal nectaries in the ascidiolate or plicate zone of carpels is evolutionarily more conservative than their location relative to the fertile portion of the ovary.

Ovary position is a critical factor in evaluating the evolutionary relationships between infralocular and typical septal nectaries. In several monocot groups, species with a superior ovary and infralocular nectaries (or with septal nectaries and opening canal incurved toward the ovary base) have apparently evolved from ancestors with an inferior ovary and septal nectaries. This scenario has been proposed for Bromeliaceae, Haemodioraceae, Nartheciaceae, and Xanthorrhoeaceae (Simpson, 1993; Rudall, 2002; Sajo

et al., 2004; Remizowa et al., 2008). In these instances, change in ovary position is a key transformation responsible for the change in nectary type. Septal nectaries with relatively distal openings are adaptively less advantageous in flowers with a superior ovary because nectar is readily available to most floral visitors (Smets et al., 2000). Location of the nectary openings at the gynoechium base facilitates specialized adaptations to particular pollinators and increases the opportunities for contact between the pollinator body and the anthers and stigmas.

For obvious reasons, nectaries of any kind are absent from wind-pollinated and water-pollinated monocots. However, septal nectaries are also absent from some biotically pollinated groups and are frequently substituted by other nectary types or other pollinator rewards (e.g., moniliform hairs on stamen filaments). For example, septal nectaries are absent from all Liliales and all Orchidaceae, and in both groups some species instead possess specialized nectar-secreting regions on their tepals, sometimes in a spur (Rudall et al., 2000; Smets et al., 2000; Rudall, 2002). Perigonal nectaries, which are relatively uncommon in monocots (except Liliales), are frequently associated with epigyny (Rudall et al., 2003). Presence and absence of septal nectaries can co-occur within a single family, e.g., in Nartheciaceae (Dioscoreales), Iridaceae (Asparagales), Dasygongonaceae (unplaced in commelinids), Tofieldiaceae (Alismatales), Araceae (Araceales), Pontederiaceae, and Haemodioraceae (Commelinales).

Among other angiosperms, structures that are morphologically similar to septal nectaries have been described in some early divergent angiosperms, such as *Saruma* Oliv. (Aristolochiaceae, Piperales) and some species of *Nymphaea* L. (Nymphaeaceae, Nymphaeales) (reviewed by Igersheim & Endress, 1998). These structures are nonsecretory septal slits between the incompletely united margins of adjacent carpels (Troll, 1933; Moseley, 1961; Igersheim & Endress, 1998). An important difference from monocot gynoechia with septal nectaries is that fusion between carpels is exclusively congenital in *Nymphaea* and *Saruma*. Postgenital fusion does occur during gynoechium development of Nymphaeaceae and Aristolochiaceae, but it is restricted to the sealing of individual carpels (e.g., Endress & Igersheim, 2000) and does not contribute to fusion between carpels.

CHARACTER OPTIMIZATIONS

Among the key features of monocot flowers, only the presence of septal nectaries is restricted to monocots (Endress, 1995), none is universally present in all monocots, and a few highly unusual monocots

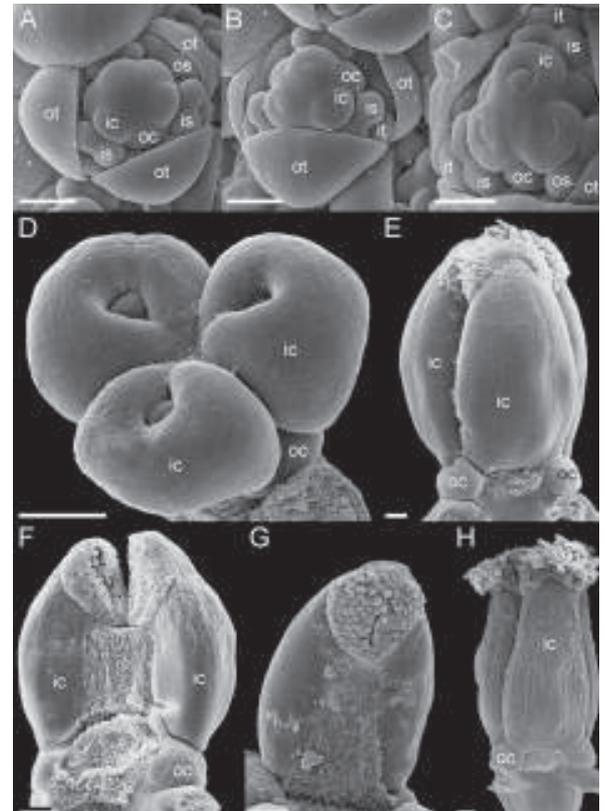


Figure 6. Gynoechium development in *Triglochin balbosa* L. s. str. (A–C) and *T. barretieri* Loisel. (D–H), two closely related species of the *T. balbosa* complex (Köcke et al., 2010) [Juncaginaceae], showing fusion via the floral center (SEM). The gynoechium consists of six carpels in two whorls. Only the inner-whorl (fertile) carpels are united via the floral center. The outer-whorl (sterile) carpels remain free from each other.—A. Carpels initiated.—B. The ascidiolate nature of the inner-whorl carpels is visible.—C. Ovules initiated.—D. Enlarged view of carpels.—E. Preanthetic gynoechium with stigmas facing each other.—F. Preanthetic gynoechium at slightly earlier stage than in E, with one inner-whorl carpel removed.—G. The inner-whorl carpel that

lack all of them. Their absence is sometimes due to drastic reduction, but other discordant examples are less readily interpretable as a consequence of reduction. Because all of the key features of monocot flowers are homoplastic, at least to some degree, it is questionable whether they represent monocot synapomorphies with subsequent reversals, or whether they evolved iteratively during the course of monocot evolution. Character mapping onto a molecular phylogenetic tree is one way to explore this question.

Mapping the presence versus absence of the "typical monocot flower groundplan" (i.e., the trimerous-pentacyclic groundplan) reveals that trimerous-pentacyclic flowers are synapomorphic to all monocots, with several subsequent reversals. However, this feature is strictly a complex character; its absence does not represent a single character state, because deviations from the "typical" groundplan differ radically. It is possible to subdivide this complex character into several characters, such as perianth merism, androecium merism, gynoecium merism, tepal number, stamen number, and carpel number. Optimizations of each of these characters would yield the result that all character states present in the "typical" monocot flower are plesiomorphic within monocots. Some of these character states, such as trimery, are shared with the outgroups, thus potentially obscuring the trimerous-pentacyclic groundplan as a key innovation of monocots.

Evaluation of carpel fusion and the presence or absence of sepal nectaries are similarly problematic. Mapping a character as "carpels fused versus free" (Fig. 10, left) would indicate that fused carpels is the ancestral character state for monocots, with at least four reversals to the free-carpellate condition (and additional reversals within Araceae-Coryphoideae; Rudall et al., in prep.). The general conclusions are not affected if "carpel fusion via the floral center" is treated as apocarpous or syncarpous, because this feature occurs only in Alismatales.

As with the floral groundplan, we regard carpel fusion as a complex character, because the character state "carpels united" incorporates gynoecia with different modes of carpel fusion (congenital and/or postgenital). However, coding congenital and postgenital carpel fusion as two separate characters, each scored as presence versus absence, suggested that congenital carpel fusion is plesiomorphic for monocots (Fig. 10, right), and that postgenital carpel fusion

(Fig. 11, left) evolved independently in many lineages. Our parsimonious optimizations also found the absence of sepal nectaries to be the plesiomorphic character state, with multiple origins of sepal nectaries in different lineages (Fig. 11, right), a hypothesis that appears difficult to accept for a character that is monocot specific. However, this optimization is highly sensitive to taxon sampling and character coding. Minor changes in tree topology and character information affect this reconstruction and make optimization of the ancestral node equivocal. For example, if the basal trichotomy in Pandanales is resolved with Velloziaceae sister to the rest of the order (Rudall & Bateman, 2006), then optimization of the ancestral monocot node changes to equivocal. Another source of inconsistency is Poales. Sepal nectaries are present in flowers of Bromeliaceae (e.g., Sajo et al., 2004) and at least some Rapateaceae (P. J. Rudall, pers. obs.), but other families of Poales lack them. If not all Rapateaceae possess sepal nectaries, the ancestral condition in Poales could be determined as "lacking sepal nectaries," depending on the distribution of this feature within Rapateaceae. In this case, even with Velloziaceae sister to the rest of Pandanales, the absence of sepal nectaries is plesiomorphic in monocots. Thus, parsimonious optimizations suggest that primitive monocot flowers were trimerous-pentacyclic, with congenitally united carpels (no contribution of postgenital fusion) and without sepal nectaries. However, in the following discussion we outline our reasons for partial rejection of this hypothesis.

CHARACTER CORRELATIONS

Some features characteristic of monocot flowers are apparently intimately linked, although the reasons for these correlations are not yet fully understood. As Endress (1995) observed, the frequent sectorial differentiation of flowers could result from their trimery, because wider gaps between organs of the same whorl allow developmental and functional links between organs of different whorls that are situated on the same radii (e.g., outer-whorl tepals and outer-whorl stamens). We suggest that the presence of only two tepal and two stamen whorls also represents a precondition for sectorial differentiation. Indeed, in flowers with more than two (or only one) tepal and/or stamen whorls (as in some magnoliids), it is spatially

was removed in F.—H. Nearly anthetic gynoecium, ic, inner-whorl fertile carpel; is, inner-whorl stamen; it, inner-whorl tepal; oc, outer-whorl sterile carpel; os, outer-whorl stamen; ot, outer-whorl tepal; re, receptacle (or perhaps the united ventral parts of outer-whorl stamens). All scale bars = 100 µm.

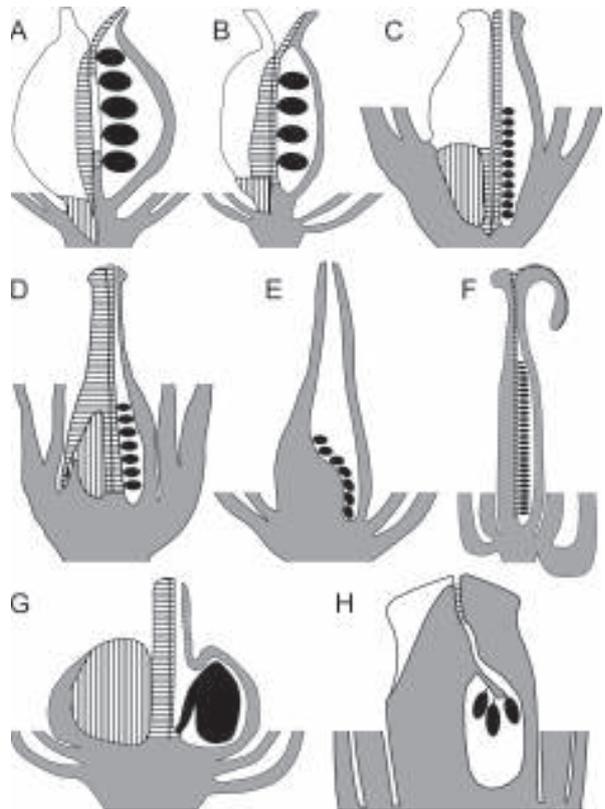


Figure 7. Diagrams of various monocot gynoecia in longitudinal section. In all sections, the locule is on the right and the septum is on the left. —A. *Tofieldia* Huds. (Tofieldiaceae). —B. *Japonolirion* Nakai (Petrosaviaceae). —C. *Petrosavia stellaris* Becc. (Petrosaviaceae). —D. *Metanarthecium* Maxim. (Nartheciaceae) (Remizowa et al., 2008). —E. *Narthecium* Huds. (Nartheciaceae). —F. *Tricyrtis* Wall. (Liliaceae). —G. *Ledebouria* Roth (Liliaceae). —H. *Acorus* L. (Acoraceae) (Buzgo & Endress, 2000). Regions of postgenital fusion are shown by horizontal hatching and sepal nectary by vertical hatching. Black, ovules; gray, other tissues.

problematic to arrange all tepals and stamens in sectorially associated pairs.

It is clear that the presence or absence of common primordia is highly homoplastic in monocots (Endress, 1995), although we do not illustrate the character optimization, due to insufficient comparative data. In fact, the presence of common primordia can be questioned in certain taxa where they have been reported (M. V. Remizowa, unpublished). For example, the presence or absence of common primordia is variable within a single species, *Tofieldia pusilla* (Michx.) Pers. (Remizowa et al., 2005). We speculate that pre-primordial patterning of the floral meristem in most monocots could include identification of sites of six tepal-stamen complexes in two whorls. At later stages, each site then divides into separate tepal and stamen sites. This sectorial model could explain both the apparent multiple homoplastic origins of common primordia and the occurrence of intermediate conditions. This hypothesis is testable by studies of gene-expression patterns in early floral meristems. However, at least the observation in the lilioid *Trillium apetalon* contradicts the sectorial model. As outlined above, *T. apetalon* lacks inner whorl perianth members, and the positions of subsequent organs, including the carpels, differ from the condition in closely related taxa, suggesting that at least in this species and its close relatives, the stamens and perianth members are patterned individually and acropetally. On the other hand, the complete absence of any visible traces of the inner-whorl stamens does not affect the gynoecium position in monocots for which we possess detailed data (e.g., Iridaceae, *Mayaca* Aubl., *Juncus minutulus*, *Scirpus*).

All three monocot groups that include some members with free carpels (Alismatales, Arcales, Pandanales) are characterized by strong variation in flower groundplan. All free-carpellate members of Alismatales and Pandanales deviate considerably from the trimerous-pentacyclic flower morphology. Within Arcales, the phylogenetically isolated free-carpellate mangrove palm *Nypa* also deviates from the typical monocot flower groundplan. Indeed, the groundplan of the male flower in *Nypa* resembles that of many Triuridaceae, another free-carpellate monocot family. Some free-carpellate Coryphoideae (Araceae) possess trimerous-pentacyclic flowers (e.g., *Tiuhirina* Mart., in tribe Cryosophileae), although flowers of *Chamaerops* L. and *Phoenix* L. are functionally unisexual, and *Phoenix* occasionally has three or nine stamens. It is significant that the diversity of the flower groundplan is very high in all three orders of Alismatales, Arcales, and Pandanales, including taxa with united carpels or a single carpel. For example, *Zombia* L. H. Bailey and

*Coccolirina* Sarg. (Araceae, tribe Cryosophileae) possess a highly reduced perianth, multistaminate androecium, and monocarpellate gynoecium (Dransfield et al., 2008).

The correlation between the stability of trimerous-pentacyclic flowers and presence of a syncarpous gynoecium in many monocots was understood in earlier studies of monocot evolution. For example, Takhtajan's (1966, 1980, 1987) evolutionary diagrams implied that monocots with conserved trimerous-pentacyclic flowers and united carpels evolved as a large clade in which lilioids represented a basal group. Takhtajan's classification placed all free-carpellate monocots and their supposed relatives with unstable and unusual flower groundplan outside this large lilioid clade and their supposed descendants. The groups not placed within Takhtajan's lilioid radiation were the core alismatids (formerly Helobiaceae), Triuridaceae, and the former Spadiciflorae or Araceae, a polyphyletic assemblage including palms, aroids, Cyclanthaceae, Pandanaceae, and Typhaceae. Takhtajan emphasized that palms could not be derived from lilioids because archaic palms possessed free carpels. Thus, Takhtajan's view was that the syncarpous gynoecium and the trimerous-pentacyclic condition stabilized simultaneously. This concept of monocot flower evolution emphasized that taxa exhibiting variant traits are relatively primitive. In contrast, the reverse paradigm, which suggests that the more common attributes reflect the primitive states in monocots, is closer to the views of Dahlgren et al. (1985) and is generally supported by parsimonious interpretation of current molecular phylogenetic topologies. Endress (1990) emphasized that stabilization of flower groundplan and syncarpy characterize floral evolution in angiosperms in general.

The concept of common as primitive implies reversals to a free-carpellate gynoecium during the course of monocot evolution (Dahlgren et al., 1985; Doyle & Endress, 2000; Chen et al., 2004). Compositum formation is considered to be a major adaptive advantage of syncarpy (Endress, 1982; Armbruster et al., 2002). An evolutionary scenario that implies a reversal to free-carpellate condition should attempt to explain why carpel fusion was lost despite its adaptive advantages. Recent evidence shows that at least some free-carpellate Alismatales (*Sagittaria potamogetifolia* Merr., Alismataceae) have a peculiar type of pollen-tube growth via the receptacle (Wang et al., 2002). This mode of pollen tube growth is functionally equivalent to internal compositum formation. A similar mode of pollen-tube growth via the receptacle has been documented in *Lacandonia* (Triuridaceae) with bisexual flowers (Márquez-Guzmán et al., 1993). In *Lacandonia*, the bisexual flowers

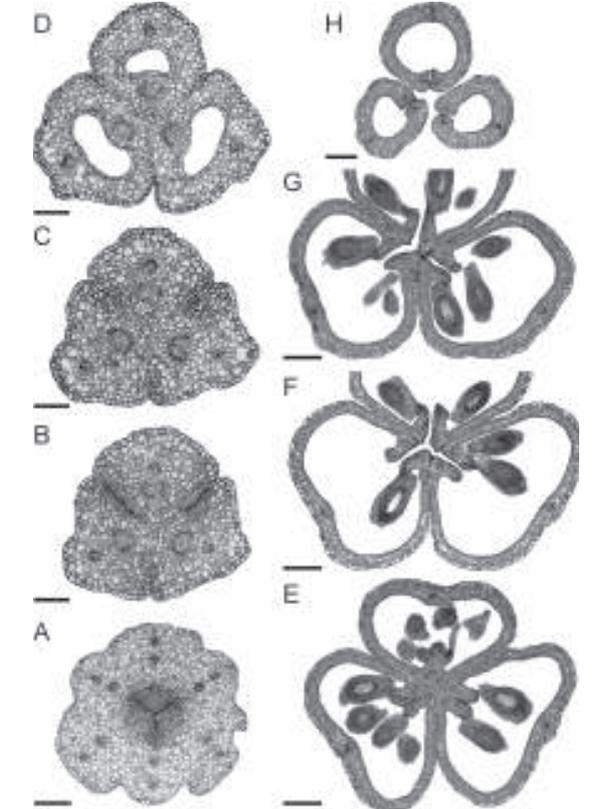


Figure 8. Gynoecium structure in *Tofieldia cernua* Sm. (Tofieldiaceae, Alismatales) in serial transverse sections of a single flower (light microscopy), showing an infra-locular, trilocular sepal nectary, and differing patterns of postgenital fusion along carpel margins and flanks in the plicate zone. —A. Central trilocular nectary at the region where the carpel stipules are inserted on the concave receptacle. Six radial pairs of vascular bundles at the periphery of the section supply six tepal-stamen pairs (not visible on other sections that show gynoecium only). —B, C. Nectary openings at the level where carpel stipules are free. —D. Postgenitally united, asciliate zones. —E–G. Postgenitally united, plicate zones through the

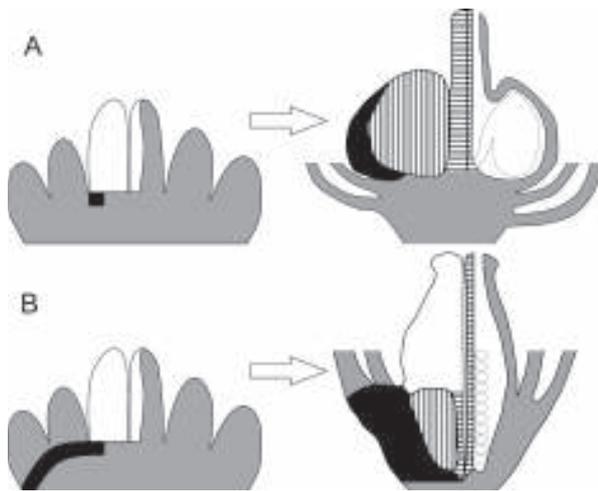


Figure 9. Contribution of intercalary zonal growth to gynoecium formation in *Ledebouria* Roth (A) and *Petrosavia* Becc. (B). In all sections, the locule is on the right and the septum is on the left. Diagrams on the right illustrate schematic longitudinal sections of anthetic flowers; they correspond to Figure 7G and C, respectively. Diagrams on the left illustrate the schematic longitudinal section of a young flower. In the left-hand diagram of *Ledebouria*, black areas indicate regions of future intercalary growth below adjacent carpels to unite them and internalize the septal nectary. In the left-hand diagram of *Petrosavia*, black areas indicate regions of future intercalary growth below and between adjacent carpels, extending to the region between adjacent carpels; this future growth will form the outer wall of the inferior part of the ovary, which internalizes the septal nectary. In right-hand diagrams of both species, black areas indicate tissues produced by intercalary growth. It is assumed that the zone of intercalary growth forms a ring of a cross section of a young flower. The region of intercalary growth is not shown on the right-hand part of each diagram, because it is impossible to draw a boundary between the product of zonal growth and the carpel wall.

are cleistogamous, and pollen germination occurs within the unopened anther. It is interesting that an internal compitum is absent in some monocots with united carpels, even from species that possess a well-developed plicate zone (e.g., *Metanarthecium* Maxim., *Nartheciacae*, *Dioscoreales*; Remizowa et al., 2008; *Japonolirion* and *Petrosavia*, *Petrosaviales*; Remizowa et al., 2006b). This is also the case in some eudicots, e.g., some *Buxaceae* (von Balhazar & Endress, 2002).

Future studies will investigate pollen-tube growth in these taxa. It is well known that septal nectary formation is correlated with postgenital or partially postgenital carpal fusion (e.g., Baum, 1948; Hartl & Severin, 1981; van Heel, 1988; Endress, 1995). When septal nectaries are absent, carpal fusion is usually completely congenital, without any contribution from postgenital fusion (e.g., van Heel, 1988; Remizowa et al., 2006b).

carpel. Note the different patterns of postgenital fusion; the gynoecium appears trilobular in E, unilobular in F, and bilobular in G. In the upper part of the gynoecium (H), carpels are free with postgenitally closed ventral slits. Scale bars: A, E–H = 200  $\mu$ m; B–D = 100  $\mu$ m.

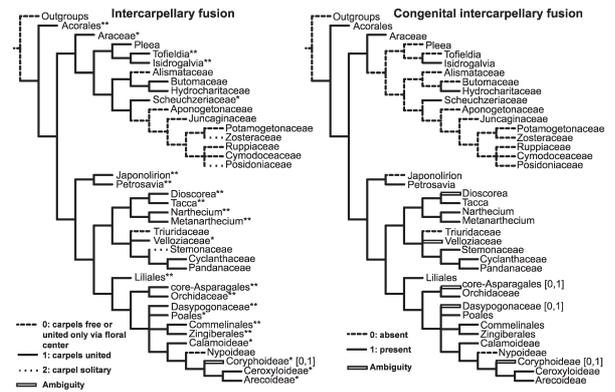


Figure 10. Maximum parsimony optimizations of features of gynoecium morphology onto a phylogenetic tree diagram of the monocots based on Angiosperm Phylogeny Group III (2009) and Stevens (2009); relationships in *Tofieldiaceae* follow Azuma and Tobe (2005). In the first tree, any type of intercarpellary fusion is considered (postgenital and/or congenital); this is congruent with Takhtajan's (2009) concept of synacry (coenacry). In the second tree, only congenital intercarpellary fusion is considered; this is congruent with Leinell's (1950) concept of synacry. Optimizations are constructed using WinClada (Nixon, 2002). Symbols on the first tree: double asterisks (\*\*) represent a single monocot flower groundplan, rarely with some organs lost, but this does not affect the positions of the remaining organs. Single asterisks (\*) represent trimerous-pentacyclic flowers that co-occur with other substantially different types of flower groundplan.

As far as we know, the only exceptions to this occur in two sister genera of *Tofieldiaceae* (Azuma & Tobe, 2007), *Isidrogavia* Ruiz & Pav. (Remizowa et al., 2005b) and *Harperocalis* McDaniel (Remizowa et al., in prep.), which differ from other *Tofieldiaceae* in the absence of septal nectaries. Carpel fusion in *Isidrogavia* and *Harperocalis* is partially postgenital, but the basal regions of the carpels are congenitally united (Remizowa et al., 2007b, in prep.), in contrast with other *Tofieldiaceae*, where congenital carpal fusion is absent (e.g., van Heel, 1988; Remizowa et al., 2006b). Thus, in this respect, *Tofieldiaceae* show the same general evolutionary tendency to replace postgenital fusion with congenital fusion as other monocot groups in which septal nectaries are lost.

However, if the septal nectaries do not meet in the center of the gynoecium (a more common condition than a single triradiate nectary), there is no obvious developmental constraint against gynoecium development exclusively by congenital fusion between carpels. For example, the gynoecium of *Ledebouria* Roth (Figs. 4, 7C), which has septal nectaries, develops through a combination of congenital and postgenital fusion between carpels, but in theory the same definitive shape and internal structure could be achieved if fusion was entirely congenital.

The reasons for the correlation between septal nectaries and postgenital carpal fusion are unclear. In *Nymphaea* and *Saruma*, septal slits occur in gynocia that lack postgenital fusion between adjacent carpels. A gynoecium with a triradiate nectary opening by three pores and carpels united above the nectary (as in *Tofieldia* or *Borya* Lahill., *Boryaceae*, *Asparagales*) cannot develop without postgenital carpal fusion.

A possible explanation of the fact that postgenital fusion is always present in gynocia with septal nectaries is that septal nectaries evolved only once, and their correlation with postgenital fusion in extant monocots is inherited from this common ancestor. This hypothesis implies multiple losses of septal nectaries. In well-investigated monocot groups, loss of septal nectaries is always associated with complete (e.g., *Nartheciacae*, *Iridaceae*) or incomplete (*Tofieldiaceae*) replacement of postgenital fusion by congenital fusion, suggesting that the presence of postgenital fusion is costly, since monocots switch to congenital

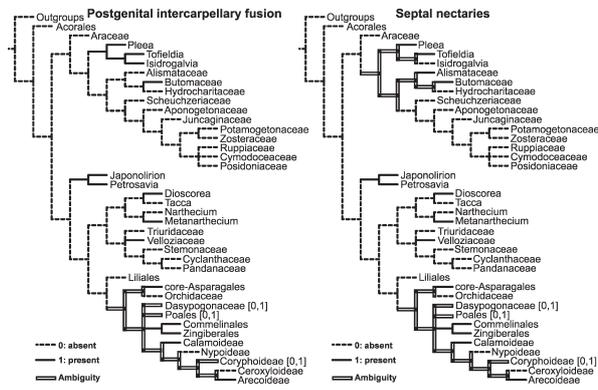


Figure 11. Maximum parsimony optimizations of features of gynoecium morphology (postgenital intercarpellary fusion and occurrence of septal nectaries) onto a phylogenetic tree of the monocots.

fusion whenever possible. Why not switch to exclusively congenital fusion in plants such as *Ledebouria*? It seems likely that the early stages of epidermal cell differentiation are similar (i.e., share developmental programs) in the region of future postgenital fusion and future septal-nectary formation. There could be a common large region of epidermal cells that later subdivides into two regions, one consisting of cells that will undergo fusion and the other that will differentiate into a nectary. Early in development, cells of these two types are often similar; before nectar production, adjacent epidermal layers in septal nectaries are in close contact with each other. This hypothesis is potentially testable through gene expression studies in epidermal cells of monocot carpels.

optimizations discussed above. Figure 12 shows another parsimonious optimization, with three character states: (0) carpels free; (1) carpels united, septal nectaries present; and (2) carpels united, septal nectaries absent. The character states are ordered to reject the transition from (2) to (1), as outlined above.

The above evidence suggests that the hypothesis that the typical condition is the primitive one is plausible for monocot flowers. Otherwise, it is difficult to rationalize a correlation between the trimerous-pentacyclic groundplan, postgenital carpal fusion, and the presence of septal nectaries in any other way than that it is inherited from a common ancestor of all monocots. It is highly unlikely that septal nectaries evolved multiple times in plants that possessed gynocia composed of exclusively congenitally united carpels, with a (partial) replacement of congenital intercarpellary fusion by postgenital intercarpellary fusion, as might be implied by parsimonious character

Placement of *Acorus* as sister to all other monocots does not necessarily require that all of its morphological features resemble ancestral states, because early divergent taxa can be highly specialized. In fact, among the extant early divergent monocots, the flower of *Japonolirion* appears closest to the hypothetical ancestral monocot flower, as outlined above. Remizowa et al. (2006b) speculated that the presence of an ascidiolate zone in the carpel, which is pronounced in many early divergent angiosperms (Endress, 2001, 2005), is a likely feature of the ancestral monocots. Our earlier observations (Remizowa et al., 2006b) suggested that carpels of *Petrosavia* are entirely nonpeltate, but detailed anatomical investigation of more extensive material has shown the presence of a short ascidiolate zone in both *Japonolirion* and *Petrosavia* (Remizowa, in press). Flowers of *Tofieldia* and *Triantha* (Nutt.) Baker (*Tofieldiaceae* sensu Takhtajan, 1997) resemble those of *Japonolirion*, but the presence of a calyx in *Tofieldiaceae* resembling a third perianth whorl (Remizowa & Sokoloff, 2003) represents a specialized feature.

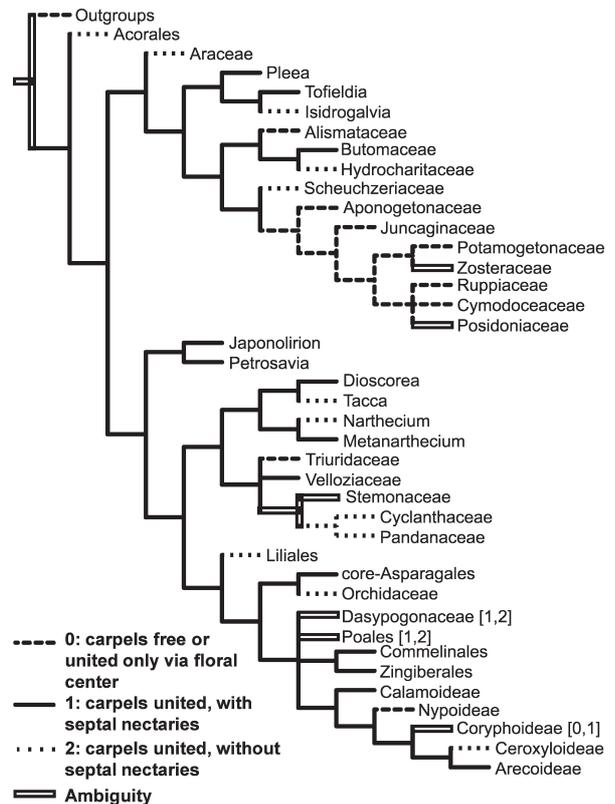


Figure 12. Maximum parsimony optimization of gynoecium morphology, understood as containing three ordered character states: (0) carpels free or united only via the floral center; (1) carpels united, with septal nectaries present; and (2) carpels united, lacking septal nectaries.

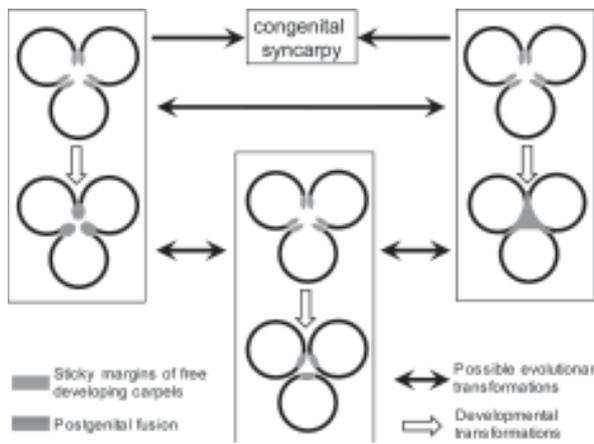


Figure 13. Possible evolutionary transformations of pathways of gynoecium development in monocots.

It is likely that the free-carpellate condition evolved several times during the course of monocot evolution, in groups where the stability of the floral developmental program was broken in various respects. A reversal to a free-carpellate condition was probably a relatively easy transformation in taxa with postgenital fusion between carpels. As Remizowa et al. (2006g) noted, the process of postgenital fusion between carpels in the ventral region closely resembles the process of postgenital closure of individual carpels in the plicate zone. We speculate that a switch from one process to the other can occur relatively easily (Fig. 13). Indeed, it can take place within a single gynoecium (Fig. 8E–H); different patterns of postgenital fusion can be seen in postgenitally united styles (Fig. 4G, H). Three other monocot groups with extensive floral variation lack polymeric apocarpy (Araceae, wind-pollinated Poales, Trillaceae), but it is significant that in these cases carpel fusion is exclusively congenital. It is possible that evolutionary transformations from postgenital congenital fusion between carpels are irreversible in monocots (Fig. 13), making a reversal to polymeric apocarpy unlikely.

Finally, it is important to note that parsimonious character optimization can be highly sensitive to tree topology, so that even minor changes in topology can result in major changes in optimization. For example, if we accept a basal placement for Tofieldiaceae (rather than Araceae) within Alismatales (S. W. Graham, pers. comm.), optimization of congenital intercarpelary fusion will not be as unambiguous as in Figure 10 (right). Instead, with ACCTRAN optimization, presence of a congenital fusion would be ancestral in monocots, whereas with DELTRAN optimization, the ancestral monocot condition would be postgenital carpel fusion. Additional sources of data, including character correlations, functional interpretations of character states, developmental constraints, and the fossil record, can provide evidence that allows amendment of parsimonious interpretation of character-state distribution along terminal groups in a phylogenetic tree, and hence introduction of novel hypotheses such as those expressed in Figures 12 and 13.

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