Review

Defining the limits of flowers: the challenge of distinguishing between the evolutionary products of simple versus compound strobili

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Recent phylogenetic reconstructions suggest that axially condensed flower-like structures evolved iteratively in seed plants from either simple or compound strobili. The simple-strobilus model of flower evolution, widely applied to the angiosperm flower, interprets the inflorescence as a compound strobilus. The conifer cone and the gnetalean ‘flower’ are commonly interpreted as having evolved from a compound strobilus by extreme condensation and (at least in the case of male conifer cones) elimination of some structures present in the presumed ancestral compound strobilus. These two hypotheses have profoundly different implications for reconstructing the evolution of developmental genetic mechanisms in seed plants. If different flower-like structures evolved independently, there should intuitively be little commonality of patterning genes. However, reproductive units of some early-divergent angiosperms, including the extant genus *Trithuria* (Hydatellaceae) and the extinct genus *Archaeofructus* (Archaeofructaceae), apparently combine features considered typical of flowers and inflorescences. We re-evaluate several disparate strands of comparative data to explore whether flower-like structures could have arisen by co-option of flower-expressed patterning genes into independently evolved condensed inflorescences, or *vice versa*. We discuss the evolution of the inflorescence in both gymnosperms and angiosperms, emphasising the roles of heterotopy in dictating gender expression and heterochrony in permitting internodal compression.

Keywords: angiosperm; axial condensation; bract; flower origin; heterochrony–heterotopy; inflorescence evolution

1. INTRODUCTION

The flower is one of the most charismatic of all plant structures, and the most commonly cited defining feature of flowering plants. The angiosperm flower has a relatively well-conserved structure (figure 1). Typically, organs of three or four distinct categories are arranged in concentric rings in a clear and consistent sequence: an outer region of sterile organs (the perianth) surrounds the pollen-bearing organs (stamens), which in turn surround the distal ovule-enclosing organs (carpels). Since Coen & Meyerowitz’s iconic ABC model of floral development was published in 1991, many empirical studies have been designed based on its predictions, resulting in several significant modifications of the ABC model (reviewed by Theissen *et al.* 2002; Soltis *et al.* 2007). Although new data resulting from this renaissance in floral studies have considerably improved our understanding of the dynamics of floral structure, crucial aspects of the flower remain enigmatic. Compared with the flower, the inflorescence has been relatively neglected

and hence models of inflorescence development remain relatively crude, partly because the existing inflorescence terminology is highly problematic (cf. Benlloch *et al.* 2007; Prusinkiewicz *et al.* 2007; Prenner *et al.* 2009).

Our goal in this paper is to review the physical boundaries and possible homologies of simple and compound strobili (flowers and inflorescences; table 1), defining broadly both terms and selecting examples from a wide range of seed-plant clades. Although flowers and inflorescences are normally assumed to possess strongly contrasting identities, this is by no means always the case. We make particular reference to two much-discussed early-divergent angiosperm genera in which the inflorescence–flower boundary appears ill-defined, one extant (*Trithuria*–Hydatellaceae) and one extinct (*Archaeofructus*–Archaeofructaceae). The family Hydatellaceae is phylogenetically placed close to the base of the extant angiosperms, as sister to the waterlilies (Nymphaeales; Saarela *et al.* 2007). *Archaeofructus* is a Chinese Early Cretaceous fossil genus that was initially described as a stem-group angiosperm (Sun *et al.* 2002), but was subsequently placed by other authors among early-divergent extant angiosperms (Friis *et al.* 2003). Despite representing less than 3 per cent of extant angiosperm species, the

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Figure 1. Diagram showing a terminal flower and two lateral flowers in a bracteate cymose inflorescence. bl = bracteole (prophyll), c = carpel (fourth-whorl floral organ), fsb = flower-subtending bract, p = petal (second-whorl floral organ), ped = pedicel (flower stalk), r = receptacle, se = sepal (first-whorl floral organ), st = stamen (third-whorl floral organ). Note that bracteoles could develop axillary buds and become flower-subtending bracts during the life of the individual plant. Dotted white lines indicate the (widely perceived) physical boundary of the flower, though in lateral flowers, each flower plus its associated subtending bract (or cryptic bract) together represent a single metamer (see text). In the terminal flower, no subtending bracts or prophylls are present and the pedicel is not readily distinguishable from the inflorescence axis.

early-divergent angiosperms (i.e. all extant angiosperms except monocots and eudicots) exhibit a disproportionately wide range of morphologies that may reflect the large number of extinctions inferred to have occurred among these relatively species-poor lineages. Indeed, in this respect they resemble the extant conifers. In attempts to clarify flower and inflorescence evolution, the early-divergent extant angiosperms are an essential piece of the jigsaw, because they can provide evidence from both comparative morphology and developmental genetics that allows more direct comparison with other seed plants and other angiosperms. Interpretation of their reproductive structures requires a 'bottom-up' morphological comparison with relevant fossil taxa, coupled with a 'top-down' genetic comparison with other extant angiosperms (Bateman *et al.* 2006), especially model organisms, both underpinned by a reliable phylogenetic context (figure 2).

Many neobotanists and palaeobotanists use the term *inflorescence* in subtly different senses, either as groups of flowers or as compound strobili (table 1). These differences are exemplified by two important papers: Parkin's (1914) study of inflorescence evolution in angiosperms and Florin's (1951) highly influential review of gymnosperm reproductive structures. In common with the majority of authors, both Parker and Florin regarded the flower as a simple strobilus (see also Arber & Parkin 1907). Florin (1951) defined the inflorescence as a compound strobilus,

whereas Parkin (1914) restricted the term to groups of angiosperm flowers. Parkin considered clusters of strobili to be relatively rare in extant gymnosperms, occurring for example in a few cycads (e.g. male cones of *Zamia*, and both male and female cones of *Encephalartos*) and reaching by far their greatest diversity in the angiosperms. Thus, to Parkin and most later neobotanists the inflorescence is defined by its flowers (e.g. as a 'branching system consisting of flower-bearing axes'; Endress 1994, p. 469), sometimes specifically excluding the foliage leaves ('that part of the axial system of plants above the uppermost foliage leaf/pair of foliage leaves that bears flowers'; Plant Ontology Consortium 2009).

Several important 'rules' appear to govern both flower and inflorescence structure in angiosperms, giving the tantalising impression that a relatively simple developmental model would allow their deconstruction and elucidate their evolution, if we could only synthesize all the clues from the many disparate strands of evidence now available to us. Flowers and inflorescences are appropriate subjects for modelling, because they are modular and involve several interacting factors. The ABC model of flower development (Coen & Meyerowitz 1991) and the Transient model of inflorescence development (Prusinkiewicz *et al.* 2007) are designed to allow us to make predictions and draw conclusions that are otherwise not immediately obvious. However, developmental models are not designed primarily to increase our understanding

Table 1. Definitions of flowers, inflorescences and sterile leaf-like structures (bracts and bracteoles) that define their physical boundaries (cf. [Prenner et al. 2009](#)).

flower (usually interpreted as a simple strobilus)	condensed unbranched axis of restricted growth, bearing a broadly predictable number of lateral structures, including the spore-bearing organs (megasporeangia and/or microsporangia), sometimes surrounded by sterile laminar organs.
inflorescence (usually interpreted as a compound strobilus)	axial system bearing flowers (simple strobili); axis can be unbranched or branched. <i>Note:</i> a determinate inflorescence terminates in a flower, whereas in an indeterminate inflorescence the apex eventually becomes exhausted and ceases production of lateral flowers.
bract	leaf-like sterile phyllome that often (though not always) subtends a flower or lateral axis. <i>Note:</i> bracts and bracteoles are, by definition, positionally fixed with respect to either a flower or an inflorescence. Unlike fertile organs, which have other intrinsic properties, bracts and bracteoles are primarily defined by two factors: their location with respect to other parts of the reproductive complex, and the presence or absence of an axillary meristem (though the meristem may not be visible during early stages of growth). Presence of an axillary meristem is characteristic of flower-subtending bracts, whereas floral organs always lack an axillary meristem.
bracteole (prophyll)	leaf-like phyllome that typically flanks (i.e. positionally precedes, rather than subtends) a flower or lateral axis. <i>Note:</i> meristems can develop in the axils of bracteoles; for example, in a cymose inflorescence, a bracteole (prophyll) becomes a flower-subtending bract during the growth of the plant.

of evolution; in order to achieve this additional goal, they require a phylogenetic context (e.g. [Frohlich & Parker 2000](#); [Theissen et al. 2002](#); [Baum & Hileman 2006](#)). Furthermore, data from developmental genetics and comparative morphology (both neobotanical and palaeobotanical) often provide us with contrasting concepts of homology. For example, the widespread acceptance by developmental geneticists of Goethe's hypothesis that the leaf is the ground state of all floral organs (e.g. [Weigel & Meyerowitz 1994](#); [Lohman & Weigel 2002](#)) implies an underlying genetic control, but not a direct evolutionary transition. Goethe's abstract hypothesis does not necessarily require that carpels were evolutionarily derived from foliage leaves. Indeed, this interpretation is improbable, regardless of differing views expressed on seed-plant phylogeny, because most observers agree that spore-bearing organs evolved before leaves in early land plants (cf. [Arber 1937](#); [Wilson 1942](#); [Lönnig 1994](#); [Kenrick & Crane 1997](#)).

2. THE SEED-PLANT STROBILUS

(a) *Simple versus compound strobili: flowers versus inflorescences?*

Although interpretations vary, the flower is widely regarded as a simple (uniaxial) strobilus typically bearing both megasporophylls (carpels) and microsporophylls (stamens) ([table 1](#)). [Doyle \(1994, 2008\)](#) recommended use of the term 'strobilus' for specialized fertile shoots in which the axis is relatively elongated at the time of pollination, and 'flower' for relatively short shoots. The simple-strobilus interpretation is based partly on comparison of flowers of extant angiosperms with those of the extinct Bennettitales (e.g. [Arber & Parkin 1907](#); [Parkin 1923](#); [Bateman et al. 2006](#); [Doyle 2008](#); [Endress & Doyle 2009](#)). [Arber & Parkin \(1907\)](#) coined the term 'anthostrobilus' for the 'protoflowers' of bennettites and other, more hypothetical constructs that they devised, which

we would now view as potential stem-group angiosperms ([figure 2](#)). In particular, flowers of the Mesozoic bennettites *Cycadeoidea* and especially *Williamsoniella* apparently closely resembled those of angiosperms in their organ topology, and the close similarity of their reproductive structures makes the bennettites a probable candidate for part of the angiosperm stem group (e.g. [Harris 1944](#); [Crane 1988](#)). Admittedly, the clade containing *Williamsoniella* is probably highly derived within the bennettites ([Crane 1985, 1988](#)), and some other possible angiosperm stem-group candidates lack such readily identifiable flowers, including *Caytonia* and some of the early-divergent bennettite lineages. The female short shoot in extant *Ginkgo*, which lacks a perianth, is also widely interpreted as a simple strobilus, based mainly on comparison with the Lower Permian putative ginkgophyte *Trichopitys*, which possessed ovule-bearing sporangial trusses (simple strobili) in the axils of leaves borne spirally along an axis (e.g. [Mundry & Stützel 2004b](#)). The strobili of *Trichopitys* are sometimes regarded as simple flowers ([Florin 1949](#); [Christianson & Jernstedt 2009](#)), though the ginkgophyte affinities of *Trichopitys* have been seriously challenged by some authors (e.g. [Meyen 1987](#)).

The simple strobilus model of the flower, which readily explains the majority of angiosperm flowers, is often termed 'euanthial' or 'uniaxial' in order to distinguish it from alternative 'pseudanthial' or 'polyaxial' models (summarized by [Bateman et al. 2006](#)). Polyaxial interpretations of the flower (reviewed by [Meeuse 1972](#); [Doyle 1994](#); [Hickey & Taylor 1996](#)) are commonly dismissed as lacking evidence or being based on morphological phylogenetic inferences that are now considered by most observers as having been superseded by contrasting molecular topologies. (For example, Gnetales were formerly widely viewed as sister to angiosperms, a relationship that is a key element of the anthophyte hypothesis: see below.) However, it would be counter-productive to entirely

Figure 2. Composite trees summarizing relationships among lignophytes based on data from (a) morphology (including fossils) and (b) molecules (extant species only), modified from Rudall & Bateman (2007). The two illustrated trees conflict in several important respects, making comparison and interpretation of reproductive structures difficult. (c) Detail of tree from Doyle (2008) showing proposed relationships of *Archaeofructus* and Hydatellaceae. Names in square brackets indicate taxa known only from fossils.

dismiss polyaxial theories, because even among extant angiosperms it is sometimes possible to distinguish an evolutionary transition from a structure that is clearly an inflorescence to a structure that most observers would recognize as a true flower, implying possible multiple origins of compound structures that are indistinguishable from 'true' (simple) flowers. For example, based on comparative morphogenetic data in a relatively robust phylogenetic context, it is clear that the supposed 'flowers' of some early-divergent monocots (e.g. Zannichelliaceae and Cymodoceaceae) originated by amalgamation of two or three *bona fide* flowers, resulting in a structure that appears remarkably well integrated (Uhl 1947; Sokoloff *et al.* 2006).

(b) Interpretations of gymnosperm strobili

In this context, it is useful to briefly review the remarkably similar discussions (uniaxial versus polyaxial) that surround interpretations of reproductive structures of extant gymnosperms. One major conclusion drawn from our review is that homology interpretations of the reproductive structures of extant seed plants—including the angiosperm flower, the

gnetalean 'flower' and the conifer cone—are extremely sensitive to phylogenetic placement. Unfortunately, relationships among major clades of seed plants are by no means resolved to the satisfaction of all observers (cf. Bateman *et al.* 2006; Doyle 2006; Hilton & Bateman 2006; Mathews 2009; Rothwell *et al.* 2009). The ostensibly simple conifer cone is widely interpreted as being derived from a compound structure. Although this interpretation is based primarily on phylogenetic inference from extinct gymnosperm groups, notably cordaites (Florin 1951), it is also supported by recent ontogenetic data from *Welwitschia* and *Ephedra* (Gnetales) (Mundry & Stützel 2004a), as discussed below.

Florin (1951, p. 295) summarized the early debate on this issue with the pertinent questions: 'Does the female cone, for instance of a pine, form a simple flower (or strobilus), or is it an inflorescence (or a compound strobilus) made up of a main axis with secondary fertile dwarf shoots in the axils of bracts? In other words: do the [conifer's] 'ovuliferous scales' constitute carpels, i.e. megasporophylls, or do the 'ovuliferous scales' with their ovules represent flowers [located] in the axils of sterile bracts?' In cordaites, both male and female cone clusters are generally considered to be unequivocal examples of compound strobili (Florin 1951; Rothwell 1988; Doyle 2008; Hilton *et al.* 2009); indeed, Florin explicitly termed them inflorescences. This interpretation is significant for character optimization because in most morphological phylogenetic analyses the cordaites represent a relatively early-divergent (typically basal) branch of the lineage that includes all extant conifers and ginkgophytes. Only in a few recent studies, following reappraisal of morphological homologies, has placement of the ginkgophytes and, less commonly, of the cordaites drifted toward tentative positions a little below or a little above the point of divergence of the conifers (e.g. Doyle 2006; Hilton & Bateman 2006; Rothwell *et al.* 2009). Florin's (1951) highly influential reinterpretation of the cordait cone led him and other authors (e.g. Wilde 1944, 1975) to postulate a condensation series in female conifer cones, from the clearly compound female cones of Palaeozoic conifers to the superficially simple female cones of modern conifers. Interpretation of male conifer cones—both extinct and extant—is even more problematic. The most commonly accepted scenario involves both axial condensation and complete loss (elimination) of some lateral structures, so that male cones of some conifers are considered homologous with only the terminal parts of male cones of other conifers. Based on comparative ontogenetic data, Mundry & Mundry (2001) supported the earlier conclusions of Florin (1951) and Wilde (1944, 1975) that the apparently simple strobili of most extant conifers are evolutionarily derived from more obviously compound strobili. Thus, when viewed in a broad and palaeobotanically well-informed phylogenetic context, cones of extant conifers are widely interpreted as inflorescence homologues rather than flower homologues (figure 3), though few authors make this crucial statement sufficiently explicit.

Figure 3. Putatively homologous structures in seed plants, based on simple-strobilus hypothesis of flower origin. (a) Female cordaite cone, (b) female conifer cone, (c) female 'flower' of *Ephedra* and (d) angiosperm inflorescence.

Another long-debated question is whether the angiosperm flower is homologous with the flower-like structures of the three disparate extant genera of Gnetales (*Ephedra*, *Gnetum* and *Welwitschia*), which also possess axes that generate sterile phyllomes enclosing fertile organs (Crane 1988; Mundry & Stützel 2004a). Recent molecular phylogenies (reviewed by Burleigh & Mathews 2004; Mathews 2009) that place a monophyletic Gnetales either embedded within extant conifers as sister to Pinaceae (gnepine hypothesis) or as sister to all extant conifers (gnetifer hypothesis) have led to extensive re-evaluation of earlier angiosperm-centred interpretations of gnetalean reproductive structures. Based on a comparative ontogenetic study, Mundry & Stützel (2004a) concluded that the 'flowers' of *Ephedra* and *Welwitschia* are actually highly reduced clusters of a few cones (probably two or three in extant taxa); if so, they represent compound strobili derived by reduction and loss of subtending bracts from an ancestor hypothesized to broadly resemble a member of the extinct cordaites. Mundry & Stützel (2004a) proposed that cordaites, conifers and Gnetales originated from an extinct common ancestor that possessed simple sporangio-phores, each bearing a terminal cluster of female sporangia. Their suggestion of a close relationship between a group containing *Ephedra* and the cordaites echoes that of Eames (1952), who considered *Ephedra* to be a highly divergent surviving remnant of the cordaite lineage, though the *Ephedra* cone is relatively condensed and simplified. An alternative placement of Gnetales close to bennettites, based on tentative fossil plant reconstructions, also merits further consideration and is consistent with the angiosperm hypothesis (cf. Friis *et al.* 2009; Rothwell *et al.* 2009).

3. SIMPLE AND COMPOUND STROBILI IN EARLY-DIVERGENT ANGIOSPERMS

(a) *Hydatellaceae: a new model organism among early-divergent angiosperms?*

More recent uniaxial versus polyaxial debates surround the early-divergent angiosperms Hydatellaceae (extant) and Archaeofractaceae (extinct). Hydatellaceae are a predominantly Australasian family consisting of a single genus (*Trithuria*) of tiny aquatic plants (Sokoloff *et al.* 2008a) in which the reproductive units (RUs) resemble flowers except that the stamens are distal to the carpels (inside-out structure: Rudall *et al.* 2007, 2009a,b). Coupled with the phylogenetic placement of Hydatellaceae close to the base of the angiosperms (Saarela *et al.* 2007), their ready availability and annual life history make them potentially the most useful genetic model organisms among early-divergent angiosperms, a goal that we are actively pursuing via extensive morphological characterizations (Rudall *et al.* 2007, 2008, 2009a,b; Remizowa *et al.* 2008; Sokoloff *et al.* 2008a,b, 2009) and studies of gene expression and molecular-developmental genetics (Rudall *et al.* 2009a,b; P. J. Rudall, A. Hay, G. Prenner & C. A. Prychid 2009, unpublished work).

RUs of *Trithuria* are often interpreted as inflorescences (e.g. Hamaan 1998; Endress & Doyle 2009), at least initially based on their former taxonomic placement in the monocot order Poales, because they superficially resemble the condensed inflorescences of some Poales (e.g. Eriocaulaceae). However, *Trithuria* RUs could equally be interpreted as flowers, which they resemble in several respects: apart from their condensed flower-like presentation (figure 4), there are strong developmental similarities between the bract-like phyllomes of *Trithuria* and the perianth of other Nymphaeales (Rudall *et al.* 2007) and the arrangement of flowers/RUs on the shoot is very similar (Sokoloff *et al.* 2009). Furthermore,

Figure 4. Reproductive unit of *Trithuria submersa* (Hydatellaceae), showing carpels surrounding a single central stamen. At this stage, the anther (just starting to dehisce) is extended above the tips of the surrounding stigmatic hairs. an = anther, fil = filament, p = bract-like phyllome, st = stigmatic hair (scale bar, 0.5 mm).

the inside-out structure of the *Trithuria* RU can be at least partially modified in teratological forms, producing a morphology that is closer to an orthodox flower (Rudall *et al.* 2009a,b). However, *Trithuria* RUs exhibit two features that are strikingly anomalous for flowers: the carpels develop centrifugally, and the fertile structures are 'inside-out' in *Trithuria* species with bisexual RUs; multiple carpels surround between one and three central stamens (figure 4), except in rare teratological cases that more closely resemble a true flower (Rudall *et al.* 2007, 2009a,b). Inside-out 'flowers' are otherwise known only from the monocot genus *Lacandonia* (Triuridaceae), in which the RU has been interpreted as derived either from a flower, by fasciation and/or homeosis, or from a condensed inflorescence (cf. Vergara-Silva *et al.* 2003; Rudall 2003, 2008; Rudall & Bateman 2006). Centrifugal carpel development in flowers is equally rare; the only other unequivocal example in angiosperms also belongs in Triuridaceae (including *Lacandonia*) (Rudall 2008). This remarkable positive correlation between inside-out RUs and centrifugal carpel inception in two distantly related taxa with ambiguous flower–inflorescence boundaries (Hydatellaceae and Triuridaceae) suggests the existence of a strong developmental constraint that ensures that stamens develop before the carpels.

(b) *Patterning flowers and inflorescences: predictive evidence from developmental genetics*

Despite the morphological convergence between flower-like structures derived from simple versus compound strobili, we might expect little commonality of patterning genes if they had evolved independently. Testing this prediction is hampered by imperfect understanding of the genetic bases for patterning of both flowers and inflorescences, particularly in gymnosperms, early-divergent angiosperms and even in eudicots with determinate inflorescences. Furthermore, there is considerable evidence of structural and developmental overlap between flowers (especially terminal flowers: figure 1) and inflorescences.

The floral meristem identity gene *LEAFY* (*LFY*) is implicated in both flowers and inflorescences. Schultz & Haughn (1991) suggested that *LFY* controls the development of both axillary meristem and bract, which together represent a metamer (presumed fundamental unit of evolvability). In wild-type *Arabidopsis*, only the lateral inflorescence meristems (not the flower meristems) are subtended by visible bracts; in *LFY* mutants, determinate flower meristems 'revert' to indeterminate inflorescence meristems, and bracts (or filamentous structures) are produced at most nodes (Schultz & Haughn 1991; Weigel *et al.* 1992; Long & Barton 2000). *LFY* is crucial in studies of flowers and inflorescences because it appears to play a central role in initiation of the angiosperm flower, though other factors are responsible for detailed floral patterning. In the archetypal angiosperm model organism *Arabidopsis*, which is a highly derived eudicot with indeterminate inflorescences, *LFY* acts in combination with the A-function MADS-box gene *APETALA 1* (*API*) and its redundant homologue *CAULIFLOWER* (*CAL*) to define the flower meristem (e.g. Teeri *et al.* 2006; Benlloch *et al.* 2007). In herbaceous species with characteristically indeterminate inflorescences (including *Antirrhinum* and *Arabidopsis*), homologues of *TERMINAL FLOWER1* (*TFL1*) inhibit expression of *LFY* at the apical meristem, either directly or indirectly (e.g. Parcy *et al.* 2002). Thus, formation of a terminal flower depends on the balance of expression between *TFL1*-like genes and floral meristem identity genes such as *LFY*. Differences in behaviour of these genes in different species correlate with their respective inflorescence architectures (reviewed by Benlloch *et al.* 2007). By contrast, in species with normally determinate inflorescences such as tobacco, the *TFL1*-homologue is not expressed in reproductive meristems, though other species show different patterns (Prenner *et al.* 2009).

There have been relatively few studies of *LFY* in early-divergent angiosperms. However, immunolocalization studies on the RUs of Hydatellaceae showed localization of *LFY* proteins in both RU primordia and organ primordia (Rudall *et al.* 2009a). This result demonstrates that *LFY* expression alone is insufficient to distinguish between an inflorescence and a flower, especially in cases where flower-subtending bracts are absent (as in both Hydatellaceae and *Arabidopsis*). Even the inside-out patterning of Hydatellaceae can be readily transformed in teratological forms. In *Arabidopsis*, region-specific patterning

of the flower is controlled by a combination of *LFY* and other factors such as *UNUSUAL FLORAL ORGANS (UFO)*. *LFY* is uniformly expressed in the flower meristem and activates *API*; *UFO* is expressed in a region-specific pattern in both shoot and flower meristems (Parcy *et al.* 1998). A combination of *LFY* and *UFO* (and other genes) appears to activate expression of both the B-function gene *AP3* and the C-function gene *AGAMOUS (AG)*. Thus, *UFO* patterning develops before ABC patterning, leading Parcy *et al.* (1998, p. 565) to speculate that the highly conserved concentric architecture that characterizes angiosperm flowers is achieved by ‘co-opting a meristem patterning system that evolved before flowers appeared’.

(c) Comparison of Hydatellaceae and Archaeofructus

Several authors have suggested affinities between *Trithuria* (Hydatellaceae) and the fossil genus *Archaeofructus* (Friis & Crane 2007; Rudall *et al.* 2007, 2008; Saarela *et al.* 2007; Doyle 2008). The contrasting phylogenetic placements of *Archaeofructus* have resulted partly from uncertainties caused by missing data (the genus is known from compression fossils) and partly from contrasting interpretations of its RU, which presents an interesting analogue to that of *Trithuria*. The *Archaeofructus* RU (figure 5) has been interpreted either as a perianthless bisexual flower, with carpels borne distal to paired or branched stamens on an elongated axis (Sun *et al.* 2002), or as a bractless racemose inflorescence consisting of perianthless male and female flowers, each highly reduced to only one or two organs (Friis *et al.* 2003). The latter interpretation suggested that *Archaeofructus* specimens with attenuated RUs (figure 5) are fruiting stages. The preferred interpretation of some authors is that RUs of both *Archaeofructus* and *Trithuria* represent modified inflorescences of simple flowers (e.g. Saarela *et al.* 2007; Doyle 2008; Endress & Doyle 2009). If so, they display highly contrasting morphologies: those of some species of *Archaeofructus* are elongated and lack involucral bracts, whereas those of *Trithuria* are highly condensed and possess perianth-like involucral phyllomes—a character apparently not yet scored in any published morphological phylogenetic analysis.

For *Archaeofructus*, Doyle (2008) found that alternative treatments in a phylogenetic analysis produced broadly similar results. Scoring its RU as an inflorescence of unisexual flowers placed *Archaeofructus* as sister to *Trithuria*, whereas scoring it as an attenuated bisexual flower placed *Archaeofructus* as sister to either *Trithuria* or to all other Nymphaeales (figure 2c). The hypothesis that the Hydatellaceae RU is a flower has not yet been tested in a published cladistic analysis, but it would be unlikely to affect these placements using existing data. The numerous differences that exist between *Archaeofructus* and *Trithuria* could merely reflect the exceptional range of morphological variation that exists among extant waterlilies; for example, leaves are simple in Hydatellaceae but dissected in *Archaeofructus* (and also in the waterlily *Cabomba*), and carpels are uniovulate in *Trithuria* but

Figure 5. Diagram of reproductive unit of the fossil genus *Archaeofructus*, based on the reconstruction by Sun *et al.* (2002). The entire reproductive unit was interpreted as a flower by Sun *et al.* (2002) but as an inflorescence (possibly an infructescence) by Friis *et al.* (2003).

multiovulate in *Archaeofructus* (and in many waterlilies). Discovery of well-preserved fossil *Archaeofructus* seeds would help to cement its possible placement in Nymphaeales, as most of the synapomorphies of this order lie in seed morphology/anatomy (Rudall *et al.* 2009b).

4. EVOLUTIONARY ORIGIN OF THE INFLORESCENCE

It is probable that the primitive inflorescence type within angiosperms is determinate, denoted by an axis that terminates in a flower. Parkin (1914) hypothesized that a solitary terminal flower is the ancestral condition in angiosperms (figure 6a), implying that the flower evolved before the inflorescence. However, he also emphasized that within the angiosperms there has been a complex pattern of structural evolution in which solitary flowers (and other inflorescence types) also evolved by reduction in multiple lineages (figure 6), thus masking the origin of the

Figure 6. Diagram of possible evolution of inflorescence based on Parkin's (1914) predictions. Flowers indicated by black spots. Number '1' denotes flower that opens first. (a, f) Solitary flowers; (b–e) cymes; (g, h) panicles; (i, j) racemes. (a) Solitary terminal flower on leafy shoot; lower leaves subtending leafy lateral axes. (b) Simple dichasium (cyme) with terminal flower and two lateral floral shoots. (c) Compound dichasium. (d) Umbellate cyme derived by internodal compression. (e) Monochasium. (f) Secondly derived solitary axillary flowers on climber (derived by reduction). (g) Panicle with terminal flower opening first. (h) Panicle with terminal flower not opening first. (i) Raceme with flowers opening acropetally; terminal flower never develops. (j) Raceme with axillary racemes produced after terminal raceme.

inflorescence. He postulated that a simple indeterminate inflorescence (raceme) was initially derived from a compound cyme (panicle) by loss of the terminal flower, perhaps via an intermediate condition in which the terminal flower was not the first to open on the multi-flowered axis (figure 6h). Stebbins (1973) also noted that there is no example in nature in which a raceme originated directly from a simple cyme, a factor that has not hitherto been considered in models of inflorescence development. These predictions of inflorescence evolution within specific angiosperm groups require urgent re-examination in a modern phylogenetic and developmental-genetic context. Parkin's argument was essentially that if the flower is plesiomorphically a condensed bisexual simple strobilus, as is widely believed, then it is by definition a terminal structure, though it should be admitted that highly reduced compound strobili could also be borne terminally on an axis.

In support of his hypothesis (here termed 'determinate-is-primitive': DIP), Parkin (1914) noted that the 'flowers' (anthostrobili) of most bennettites were lateral (axillary) structures, but he considered that a solitary terminal flower was probably the ancestral condition in this extinct group. However, it is dangerous to over-generalize the morphology of the diverse

reproductive structures of bennettites (Rothwell *et al.* 2009). Within the doubtfully monophyletic Cycadeoideaceae (Crane 1988), presentation of 'flowers' was axillary in the columnar stems of *Monanthesia* (Delevoryas 1959) and the barrel-shaped stems of *Cycadeoidea* (Delevoryas 1960). Within the Williamsoniaceae, flowers of *Wielandiella* were illustrated in dichasial clusters (Watson & Sincock 1992) and *Williamsonia* in monochasial groups (Harris 1969). Most perplexingly, the archetypal bennettite, *Williamsoniella*, has been depicted as either dichasial (Thomas 1916) or axial (Zimmermann 1959); moreover, Thomas (1916) appeared equivocal as to whether the flowers were solitary or arranged in cymose clusters. It remains unclear whether the wide range of architectures attributed to bennettites was a biological reality.

Most subsequent authors have supported the DIP hypothesis but regarded the simple cyme (figure 6b) as the probable ancestral condition (e.g. Stebbins 1973; Tucker & Grimes 1999). At least superficially, DIP appears counter-intuitive because lateral structures in vegetative axes develop acropetally (= centripetally; from the bottom upwards), so a simple indeterminate inflorescence (raceme) logically follows this developmental pattern. Within the flower itself, development is also typically acropetal, though

determinate. A residual apex occurs within flowers of some angiosperms (reviewed by Arber 1937), including some early-divergent taxa such as *Schisandra* (Tucker & Boursland 1994). This feature has sometimes been evoked as a vestigial remnant of a former indeterminate apex, but Arber (1937) noted that it could equally be interpreted as inadequately formed carpels. On the onset of flowering, vegetative growth either ceases or continues in lateral (axillary) structures (sympodial growth). On the flowering axis (inflorescence), the flower is either solitary or the terminal flower is followed basipetally by lateral structures.

The DIP hypothesis also gains some support from recent molecular phylogenies of the earliest-divergent (ANA-grade) angiosperm lineages, though this conclusion also depends on interpretation. In *Amborella*, the extant genus that is most commonly cited on molecular evidence as being sister to all other extant angiosperms, small inflorescences are borne in the axils of foliage leaves (Endress & Igersheim 2000). Although their precise structure has been variously interpreted, each inflorescence axis is terminated by a flower (Buzgo *et al.* 2004). Most Austrobaileyales possess solitary flowers, though *Trimenia* has an inflorescence with a terminal flower. However, Endress & Doyle (2009) interpreted the inflorescence in Nymphaeales as racemose (i.e. indeterminate), and hence regarded the primitive angiosperm inflorescence type as equivocal (either determinate or indeterminate). Their interpretation of Nymphaeales was due partly to inclusion of *Archaeofructus* (and interpretation of its RUs as racemose inflorescences of reduced flowers) and partly to the fact that most Nymphaeales possess solitary flowers, borne either in the axils of foliage leaves (*Cabomba*) or in the same phyllotactic spiral as the leaves (*Nymphaea*). Thus, the entire *Nymphaea* plant could in theory represent a giant raceme (Endress & Doyle 2009), though since the subtending foliage leaves are not reduced, it could equally represent a condition in which each flower is either primitively solitary or derived from a simple cyme. More work is needed on inflorescence and flower development in Nymphaeales (see also Grob *et al.* 2006).

As discussed above, genetic and morphological similarities exist between the floral primordium and the axillary shoot (e.g. Long & Barton 2000). In some angiosperm groups, considerable difficulties exist in distinguishing between terminal flowers and terminal structures composed of closely integrated uppermost lateral flowers, raising a more general question regarding the nature of the homologies between lateral flowers and bona fide terminal flowers (figure 1). The shoot is often regarded as a modular system, in which each flower plus its associated subtending bract (or cryptic bract) together represent a single metamer (unit of evolvability), though this concept is problematic in terminal flowers, which lack subtending bracts (figure 1), or in species that lack flower-subtending bracts, such as *Arabidopsis* and maize. However, in both *Arabidopsis* and maize, 'cryptic bracts' have been identified in a distinct region of cells just below each flower (Long & Barton 2000;

Baum & Day 2004). Long & Barton (2000) suggested that cryptic bracts represent an endpoint in a developmental reduction series from stem-borne leaves caused by inhibition or suppression of bract expansion by the developing flower—a hypothesis that has clear implications for inflorescence evolution. Potential support for this hypothesis comes from species in which reduction in bract size occurs toward the distal end of the main inflorescence axis (e.g. in racemes of some Brassicaceae and umbels of some Apiaceae; Weberling 1992). As a possible mechanism for bract suppression, Baum & Day (2004) speculated that either the flower meristem itself releases an inhibitory signal or there could simply be an issue of increasingly limited nutritional or hormonal availability, each developing flower in the inflorescence acting as a prioritized sink for resources.

5. KEY ROLES OF GAMOHETEROTOPY AND PAEDOMORPHIC HETEROCHRONY IN THE ORIGIN OF THE ANGIOSPERMS

Attempts to confidently identify the sister group of the angiosperms, or to reconstruct the most probable phenotypic features of the angiosperm ancestor, are confounded by two primary factors (e.g. Bateman *et al.* 2006): the many major topological conflicts evident both within and between morphological and molecular phylogenetic studies, and the limited survival of major gymnosperm lineages to the present day (compare figure 2a,b). Fortunately, some evolutionary trends in reproductive architecture are sufficiently strong that they transcend these topological ambiguities.

In a current study (R. M. Bateman, P. J. Rudall & J. Hilton 2009, unpublished work) we have identified at least four positively correlated evolutionary trends in reproductive architecture that occur iteratively in several lineages derived from the initial plexus of extinct pteridosperms, which is apparently paraphyletic but remains poorly resolved (Doyle 2006; Hilton & Bateman 2006). Most notably, we argue that the importance of increasing lateralization, determinacy and condensation of reproductive trusses via paedomorphic heterochrony has been under-estimated relative to that of the much-discussed heterotopic switch from unisexual to bisexual flowers.

As noted by Bateman & Hilton (2009), disarticulation of fossils prevents us from being able to determine whether the earliest gymnosperms, the hydrasperman pteridosperms, were dioecious (thus resembling extant cycads, *Ginkgo* and some conifers) or monoecious (thus resembling most extant conifers). However, we can confidently state that, from the earliest pteridosperms onward (e.g. Rothwell & Scheckler 1988), individual reproductive trusses were reliably unisexual. Only one marginally hermaphrodite truss has ever been described (Long 1977a), and that was confidently interpreted as representing exceptional teratological expression of microsporangia on a fundamentally ovulate cupule (Bateman & DiMichele 2002). The obvious inference is that post-zygotic isolation mechanisms were absent from these lineages, so that a dominance of allogamy could be guaranteed

only by maintaining unisexual individuals (or perhaps bisexual individuals with strong phenological separation in the maturation of male and female trusses). With the arguable exception of some Gnetales, in which (mostly sterile) female structures are distal to fertile male structures (Endress 1996), 'male' and 'female' sporangia have been brought into close and reliable juxtaposition in only two lineages, almost certainly independently: a derived group within bennettites (e.g. Crane 1988) and the angiosperms. Both groups are considered most likely to have originated within the diverse plexus of pteridosperms *s.l.* through heterotopic expression of one gender on a truss previously of the opposite gender, such that the microsporangia surrounded the megasporangia (e.g. Long 1977b; Meyen 1988). Presumably, intrinsic sterility barriers then evolved rapidly in these novel hermaphroditic lineages.

By far the more iterative trend among seed plants is axial internodal compression, presumably achieved via increasingly precocious initiation of nodes (i.e. paedomorphic heterochrony). Compression receives less attention than bisexuality in most discussions of angiosperm origins, and those discussions that do take place tend to concentrate on the flower. However, consideration of gymnosperms suggests that condensation of the 'inflorescence' (strictly, the truss) is a more phylogenetically frequent phenomenon. The relatively open and undifferentiated trusses of early pteridosperms such as *Elkinsia* and *Moresnetia* were subsequently condensed into trusses of multiple male synangia or female cupules, each of which could in turn undergo further condensation to form megasynangia such as *Dolerotherca* and megacupules such as *Calathospermum* (reviewed by Long 1977b; Rothwell & Scheckler 1988). Even stronger developmental dominance of the reproductive axis in several other lineages led to lateralization of its many sporophylls, which experienced further condensation, allowing iterative formation of compact cones from less compact strobili *sensu* Stewart & Rothwell (1993, p. 340). A credible reduction series postulated for the cordaite–conifer lineage (Florin 1951) has benefited from subsequent reconstructions of architecturally intermediate extinct conifers (e.g. Hernandez-Castillo *et al.* 2009); similar condensation is believed to have led via strobili to cone formation in the ginkgos, cycads, pentoxyls and bennettites.

The final (and least discussed) feature that particularly interests us is that gymnosperms appear to be strongly canalized toward maintaining similar developmental programmes in 'male' and 'female' trusses. Similar ovulate and pollen-bearing inflorescence architectures are, for example, evident in the 'inflorescences' of some lyginopterids and all cordaites, ginkgos, glossopterids, caytonias and unisexual bennettites, suggesting that gender determination was under simple genetic (and/or epigenetic) control. Such developmental congruence between genders could render more straightforward the gamo-heterotopic transitions that are believed to have led to the evolution of hermaphrodite flowers in angiosperms and derived bennettites. It is easier to identify the few lineages where significant architectural divergence

occurred between male and female trusses, which is arguably evident in Cycadaceae (now recognized as the basally divergent lineage within Cycadales; e.g. Chaw *et al.* 2005) and unequivocally in extant conifers (e.g. Florin 1951).

We therefore suspect that, among the living gymnosperms, crown-group conifers represent the least suitable models for evolutionary-developmental genetic comparison with extant angiosperms; rather, they constitute a highly reproductively specialized clade that is highly divergent, both morphologically and molecularly, from the ancestor of the angiosperms. We believe that changes in the developmental-genetic systems determining the transition from vegetative to reproductive growth are more fundamental than those controlling the more detailed and canalized development of individual flowers, and evolutionarily precede the establishment of the classic ABC model of genic interactions.

6. CONCLUSIONS

The paucity of comparable genetic data and the difficulty in homologizing structures between angiosperms and gymnosperms make it problematic to construct models of seed-plant reproductive structures. Phylogenetic optimization of simple versus compound strobili in seed plants is highly sensitive to breadth of taxon sampling.

Both flower and inflorescence structure relate primarily to two factors: patterning and internode elongation. Axially condensed flower-like structures appear to have evolved iteratively in seed plants, from either simple or compound strobili. The anomalous RU of *Trithuria* (Hydatellaceae) represents a useful yardstick to evaluate flower/inflorescence evolution in early angiosperms, especially when compared with the fossil genus *Archaeofructus*. The *Trithuria* RU could be a simple strobilus that has evolutionarily 'lost' (or never achieved) typical flower-like morphology, or it could be derived from a compound strobilus in which extreme condensation of the axis has resulted in an arrangement that is both structurally and genetically close to a flower. An end-product of condensation of internodes and amalgamation between individual flowers in an inflorescence could appear as similar to a single true flower at the molecular level as it does morphologically. In either case, whether this structure should be termed a flower or an inflorescence (or even a 'non-flower'; Rudall *et al.* 2009a) remains debatable.

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