

REVIEWS

After a dozen years of progress the origin of angiosperms is still a great mystery

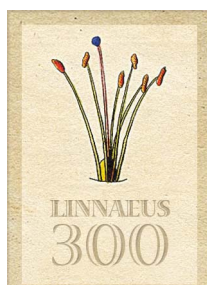
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Here we discuss recent advances surrounding the origin of angiosperms. Putatively primitive characters are now much better understood because of a vastly improved understanding of angiosperm phylogenetics, and recent discoveries of fossil flowers have provided an increasingly detailed picture of early diversity in the angiosperms. The 'anthophyte theory', the dominant concept of the 1980s and 1990s, has been eclipsed; Gnetales, previously thought to be closest to the angiosperms, are related instead to other extant gymnosperms, probably most closely to conifers. Finally, new theories of flower origins have been proposed based on gene function, duplication and loss, as well as on morphology. Further studies of genetic mechanisms that control reproductive development in seed plants provide a most promising avenue for further research, including tests of these recent theories. Identification of fossils with morphologies that convincingly place them close to angiosperms could still revolutionize understanding of angiosperm origins.

Less than a dozen years ago even the most basic questions regarding the origin of angiosperms were still disputed, including the nature of primitive flowers, what sorts of gymnosperms might have given rise to angiosperms, and the broadest outlines of the evolutionary trajectory between them. (See ref. 1 for references not cited here.) Studies of fossil flowers² showed that bisexual and unisexual flowers both occurred in the earliest fossil flower floras, so it was still possible that plants with unisexual flowers consisting of a single stamen or a single carpel (resembling extant *Ceratophyllum* or *Hedyosmum*) might reflect the ancestral angiosperm condition. Other analyses supported the directly opposite view: the overall organization of the bisexual angiosperm flower (flat structures surrounding male organs surrounding central female organs) had been inherited directly from gymnosperm ancestors. Subsequent advances, derived from new data and reinterpretations of older data, have narrowed the range of alternative explanations for origins of both flowers and angiosperms. New data have come especially from molecular phylogenetics, but also from studies of gene function, duplication and loss and from palaeobotany. The rise of evolutionary developmental biology ('evo-devo') has reinvigorated the study of plant anatomy and led to new, increasingly synthetic theories; they seek to fuse disparate fields to explain various aspects of flower origins. Formulation of detailed, testable theories combined with study of fossils and genes has the power to dispel the mystery surrounding the origin of both flowers and angiosperms.

Relationships between extant angiosperms

Relationships of relatively few groups of angiosperms are still in dispute. Furthermore, morphological and molecular phylogenetic results are now considerably more congruent than in the past. Analyses in the past five years have consistently pointed to the 'ANA' (formerly called ANITA) taxa—Amborellaceae, Nymphaeales and Austrobaileyales—as successive sister groups to the larger clades of magnoliids, eudicots and monocots (Fig. 1), although there has been some dispute over the relative positions of Amborellaceae and Nymphaeales³. A noteworthy new addition near the basal nodes of the angiosperm tree is the



Hydatellaceae, a small family of minute aquatics with small simple flowers that were previously thought to be members of the monocot order Poales. These fall as sister to Nymphaeales (Fig. 1) and extend the range of morphologies among these clades^{4,5}.

The ANA taxa, including Hydatellaceae, are each individually highly specialized. For example, *Amborella* grows in wet, forest understorey habitats in New Caledonia and is dioecious (but with vestigial organs of the opposite sex), whereas Nymphaeales with perfect flowers are all adapted to aquatic habitats.

Improvements in morphological reconstructions of primitive angiosperms can yet be expected (particularly with the application of likelihood methods that consider branch lengths in projecting character states down to the basal node¹), but the range of hypotheses now considered relevant is considerably narrower than in the past. For example, the old view of the primitive carpel as conduplicate—folded lengthways and fused at the edge—was based on magnoliid taxa now known to be relatively derived. Carpels of most ANA taxa are bucket-shaped and sealed only by a secretion³. Most importantly, several previously popular ideas can now be discarded, such as the idea that angiosperms arose from more than one 'gymnosperm' ancestor.

Fossil flowers

The only direct evidence of early angiosperm flowers comes from fossils. Mesofossils, up to a few millimetres in size, often show exquisite three-dimensional preservation, including cell structure. Most mesozoic flowers fall within the mesofossil range. Diverse mesofossil assemblages span the late-Early to Late Cretaceous period (reviewed in ref. 6), and others extending back to the upper Jurassic are now known (E.-M. Friis, personal communication). Flowers referable to ANA angiosperms are found in the earliest mesofossil assemblages, along with flowers of Chloranthaceae, which are sister to the magnoliids in recent analyses of complete sets of genes from the plastid genome^{5,3}. Fossil pollen provides yet earlier evidence of angiosperms at roughly 136 Myr ago (Hauterivian⁶; mid-Early Cretaceous), about 10 Myr before the earliest published mesofossil floras⁷. Fossil pollen

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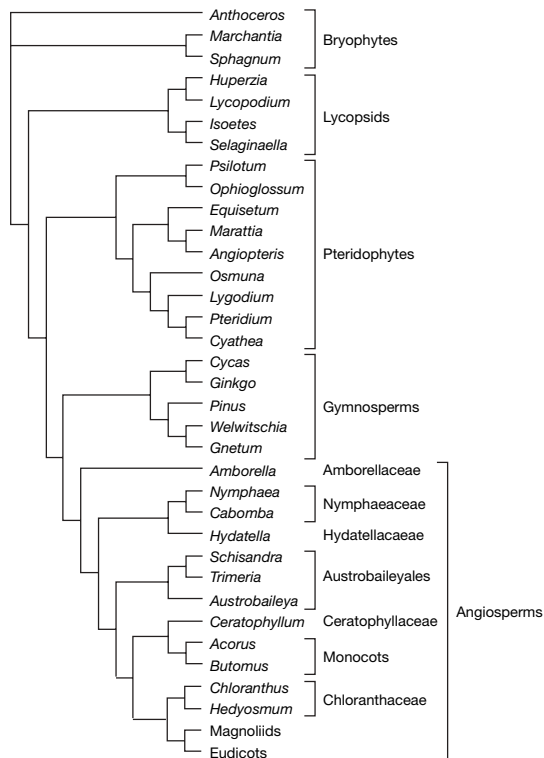


Figure 1 | The phylogenetic tree of living plant groups (based on refs 3, 51).

shows that diverse magnoliids, monocots and early eudicots had appeared by the early Aptian, about 125 Myr ago, demonstrating an early, rapid major radiation.

Molecular results have sharpened evolutionary interpretations. For example, unisexual fossil flowers similar to the extant genus *Hedyosmum* (Chloranthaceae) are among the earliest flowers known⁶. However, our knowledge that Chloranthaceae insert well above the ANA taxa clearly indicates that unisexuality in *Hedyosmum* and most probably also these fossil taxa is due to secondary reduction. The addition of Hydatellaceae as sister to Nymphaeales does not change this inference.

There are no studied fossils clearly representing stem-group angiosperms, that is, of plants related to extant angiosperms but attached below the basal node of extant angiosperms in the tree. Such fossils might provide spectacular direct evidence of morphological change along this unknown stretch of evolutionary history. *Archaeofructus*, originally thought to be a stem-group angiosperm of Jurassic age, is not; it has been re-dated as mid-Early Cretaceous, and its reproductive unit has been reinterpreted as an inflorescence, not a flower^{8,9}. Reinterpretation of *Archaeofructus* is a good example of initial morphological interpretations leading to remarkably different ideas of relationship compared with subsequent analyses.

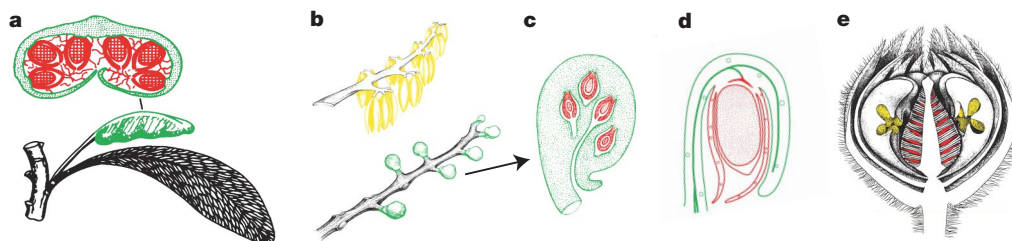


Figure 3 | Fossil gymnosperms. a, *Glossopteris* showing cupules borne on stalk above a leaf (from ref. 23). **b**, *Caytonia* male (above) and female (below) reproductive units (from ref. 11). **c**, *Caytonia* cupule (from ref. 36). **d**, Corytosperm (*Umkomasia*) cupule containing one ovule (from ref. 52). Cupule wall almost surrounds ovule, except for a slit facing the stalk.

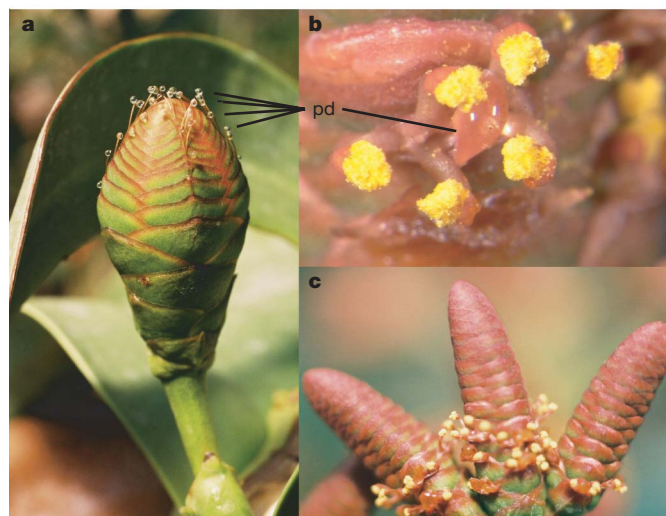


Figure 2 | *Welwitschia cones*. a, Female. **b**, Close-up of male cone, showing pollen organs and pollination droplet in between them. **c**, Male cones. pd, pollination droplet.

Evidence from phylogenetics and morphology

Living gymnosperms and angiosperms constitute the extant seed plants. The four groups of living gymnosperms are only a remnant of the substantial diversity of Palaeozoic and Mesozoic times¹⁰. In the 1980s, morphological cladistic analyses of living and fossil seed plants^{11,12} placed cycads sister to the other living taxa and identified ‘anthophytes’ as consisting of angiosperms, Gnetales (Fig. 2) and two extinct groups, Bennettitales (Fig. 3e) and *Pentoxylon*. The first three include members with reproductive units that have sterile appendages surrounding male structures with female structures in the centre, suggesting that this overall organization might be homologous in the three groups, hence much antedating origin of angiosperms. Otherwise, their reproductive structures differ markedly, but, given these relationships, morphological transformations have been proposed¹². Subsequent analyses placed Caytoniales (Fig. 3b, c), which lack this overall organization, within anthophytes as sister to angiosperms, undermining this supposed homology in overall organization¹³.

Molecular phylogenetic analyses of seed plants now indicate that living gymnosperms are monophyletic, with Gnetales related to conifers¹⁴, although this remains controversial^{16,15,16}. Palaeobotanists are increasingly willing to consider extant gymnosperm monophyly, but with varying levels of surprise and disquiet over the implications¹⁷. In the two most recent morphological analyses, placing Gnetales with conifers made trees one step longer¹⁷ or forcing extant gymnosperm monophyly cost four additional steps¹⁵, showing that the signal against extant gymnosperm monophyly is not especially strong.

e, Bennettitales (*Williamsoniella*) bisexual reproductive unit (from ref. 11); each oval pollen sac consists of several fused microsporangia. Ovules are borne among scales on the central stalk; in *Vardekloftia* each is enclosed by a cupule wall. Green, cupule wall; red, ovule; yellow, pollen organ.

Extant gymnosperm monophyly moves Gnetales and cycads over many nodes compared with the shortest morphology-based trees^{15,17}, but only rarely have phylogenetics studies of morphology and DNA data agreed in plant studies, even in well-studied groups. Early morphological cladistic analyses of angiosperms underwent a radical rethinking of character homologies in the light of DNA analyses, which generated results much more in line with the DNA trees¹⁸. Interpretation of morphological homologies can radically shift if evidence of alternative relationships triggers re-examination; however, no source of phylogenetic evidence is infallible. Future studies should show whether current molecular or morphological results are erroneous.

New types of data are promising, from large-scale sequencing of nuclear genes¹⁹ to molecular fossils. Oleanane is a diagenetic product of triterpenoids found in most angiosperms. Taylor *et al.*²⁰ demonstrated oleanane associated with several Bennettitales and Permian gigantopterid fossils, but oleananes were not found in Gnetales, Palaeozoic medullosan pteridosperms or in the conifer relatives Cordaitales. Other chemical fossils are markers for Cordaitales²¹.

Monophyly of extant gymnosperms places them all equally distant from the angiosperms, which means that the lineage that eventually produced angiosperms diverged from the common ancestor with extant gymnosperms much earlier than previously thought, from among the 'pteridosperms' ('seed ferns'). Living gymnosperms show a great diversity of reproductive morphologies, and these must have resulted from numerous specializations. This makes comparison with angiosperms much more difficult.

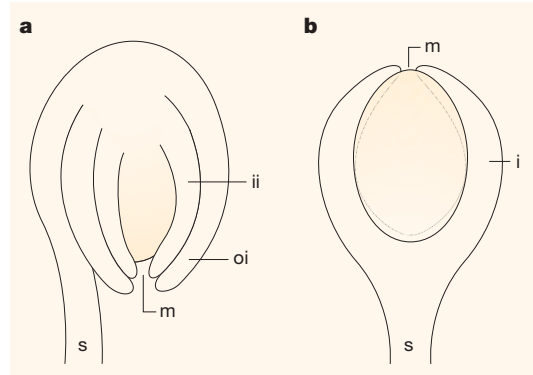
Some extinct 'gymnosperm' groups must be closely related to angiosperms. If living and fossil 'gymnosperms' are considered together, then angiosperms arose from within them, making 'gymnosperms' paraphyletic (which we indicate with quotation marks). Both Caytoniales (Fig. 3b, c) and Bennettitales (Fig. 3e), fossil 'gymnosperms' with remarkably different morphologies, have long figured in theories of angiosperm origins^{11,22} and appear as successive sister groups to angiosperms in recent studies^{15,17}. Caytoniales have cupules that could plausibly be transformed into angiosperm bitegmic ovules (see Box 1), but these are borne on slender stalks unlike carpels. The detached male structures also differ significantly from angiosperm stamens, and it is not known how either of these was borne on the plant. Some Bennettitales have bisexual reproductive units¹¹, but there is no obvious carpel precursor, and except for *Vardekloeftia*¹⁷ the ovules are not borne inside a cupule, so the source of angiosperm-type bitegmic ovules is also uncertain. Microsporophylls are highly variable, but none so far known closely resemble angiosperm stamens.

Retallack and Dilcher²³ suggested that the angiosperm carpel could be derived from structures resembling those of glossopterids (Fig. 3a), a group of Permian 'gymnosperms' that had a cupule or cupules borne on stalks above foliage leaves. Glossopterids (Fig. 3a) had one or more cupules borne on stalks above foliage leaves and have been suggested as angiosperm ancestors²³, but their early (Permian) age is problematic. Doyle¹⁷ suggested that Caytoniales may be related to glossopterids and may also have had the reproductive stalk borne above a subtending leaf. If the stalk became fused to the leaf, the resulting structure would be an ideal carpel precursor.

Friedman and Floyd²⁴ proposed a theory about the angiosperm female gametophyte that uses the idea of developmental modules to account for arrangements and fates of nuclei, including those that participate in double fertilization to make zygote and endosperm (food store). They suggested that the basic module consists of four nuclei, one of which moves to the centre of the initially coenocytic gametophyte to fuse with the second sperm forming the endosperm nucleus. In the module near the micropyle, where the pollen tube enters, the other three nuclei organize the two synergids and the egg cell that fuses with a sperm, making the zygote. Most angiosperms have a second module that also sends a nucleus to the centre of the gametophyte, so fusion generates the standard,

Box 1 | Ovules and cupules

In both gymnosperms and angiosperms, seeds develop from ovules. Ovules consist of a stalk that bears the nucellus (megasporangium) at its tip, with one or two covering layers (integuments) that grow from the stalk and almost completely cover the nucellus (Box 1 Figure). Only a small opening (micropyle) through the integuments allows access to the nucellus, in which the megagametophyte and egg(s) form.



Box 1 Figure | Diagrammatic ovules. a, Angiosperm ovule. b, Gymnosperm ovule. i, integument (covering); ii, inner integument; m, micropyle (opening); oi, outer integument; s, stalk. (From ref. 38.)

Gymnosperm ovules have a single integument (unitegmic) with the micropyle positioned opposite the stalk (although modified bracts in Gnetales have been called additional integuments). Most angiosperms, including all ANA taxa, have two integuments (bitegmic; reduced to one in some derived groups), and the ovule is commonly bent over, positioning the micropyle close to the stalk. The second integument is not simply a reiteration of the first; the two clearly have different attributes²², which poses questions about the origin of the second (outer) integument.

Some fossil gymnosperms bear ovules inside an enclosing structure (cupule wall; Fig. 3) that is derived from a single modified leaf or part of a leaf. In Caytoniales and Corystospermales, ovules are almost completely enclosed, except for a small opening near the stalk of the cupule. If the cupule has only a single gymnosperm-style ovule inside it (as in some corystosperms; Fig. 3d), the whole structure resembles an angiosperm ovule, with the cupule wall comparable to the outer integument of a bitegmic angiosperm ovule and the single integument of the gymnosperm ovule comparable to the inner integument of the angiosperm ovule²². Glossopteridales also have cupules, although they usually do not tightly enclose the numerous ovules (Fig. 3a).

It is not clear whether cupules of all Mesozoic gymnosperms are homologous or whether there were multiple origins of cupules. They differ in the dorsiventrality of the cupule wall: in corystosperms the outer surface is comparable to the upper side of a leaf⁵² (adaxial surface), on the basis of the arrangement of vascular tissues, whereas probably in Caytoniales and certainly in glossopterids (and in the poorly known *Petriellaea*) it is comparable to the lower side (abaxial surface). Some angiosperms develop vascular tissue in the outer integument, with an orientation suggesting that the outer surface is morphologically abaxial, pointing to Caytoniales or Glossopteridales as possible angiosperm antecedents³⁷.

triploid endosperm nucleus. There is much variation on this basic pattern, but most of this diversity is explicable by changing the numbers of modules. Nymphaeaceae have only one module, which could be the ancestral condition, especially because *Amborella* has a unique system.

Some unreasonable theories posit multiple origins of angiosperms from 'gymnosperm' ancestors^{25,26}. Angiosperms have many shared derived characters^{11,12}, and it is most unlikely that such complex features, arising independently, would fail to show differences that reveal their independent origins. All molecular and morphological analyses support angiosperm monophyly.

MADS genes

MADS-box transcription factors are important for flower origins because they specify the major floral organs and because their expression zones typically correspond to their zones of action, so expression studies are useful for inferring function. According to the classic 'ABC' model (in *Arabidopsis* terminology), sepals are specified by the 'A' gene *Ap1* (and the non-MADS *AP2*), petals by the 'A' in combination with the two 'B' genes *PI* and *AP3*, stamens by the 'B' genes and the 'C' gene *AG* and carpels by *AG* alone. *SEPALLATA* (*SEP*) or 'E' genes are now known to be required for all four organ types, and the 'D' genes have been proposed as specifying ovules. Expression of the A, B, C and E MADS genes is upregulated by *LEAFY*, a non-MADS transcription factor.

Gene phylogenetics shows that each major MADS subgroup extends back to the base of extant angiosperms. There have been many duplication events within these clades, some probably reflecting whole-genome duplications, such as at the base of eudicots¹⁹.

Several pairs of major MADS clades result from duplications below extant angiosperms, such as the *PI* and *AP3* clades, and also the *AG* clade and the putative 'D' gene clade. The most closely related gymnosperm genes are sister(s) to these clade pairs.

Classical 'A' function may be limited to relatives of *Arabidopsis*, whereas in other plants 'A' function may not be separable from the other major role of the 'A' genes in helping to specify apices as floral²⁷. Lack of a unique sepal-specifying system is consistent with the suggestion that in the original flower the perianth may have been composed entirely of petals²⁸.

Understanding the specification of ovules would be especially important but remains problematic. Overexpression of a *Petunia* 'D' gene in *Petunia* generates ectopic ovules on sepals and petals, but overexpression of the *Arabidopsis* orthologue in *Arabidopsis* does little. It is unclear whether ovule function versus stamen + carpel function characterized the 'D' versus 'C' clades from their initial divergence. Kramer *et al.*²⁹ concluded that they do, but Zahn *et al.*³⁰ produced contradictory evidence. Specification of ovules and their components is highly complex³¹, and there may be differences between taxa.

In ANA angiosperms, 'B' (and to some degree 'C') MADS genes show much broader messenger RNA expression than in eudicots, which has led to the 'fading borders' model of floral organ specification^{19,32}. This posits an activity gradient of floral genes that determine organ identity, resulting in a gradient in organ morphology from the outside to the centre, in contrast to flowers of most eudicots, which have sharply distinguished organs. Many ANA grade flowers have variable numbers of floral organs often arranged spirally (instead of in whorls), suggesting less developmental homeostasis than in eudicots or monocots^{1,19,32}. Perhaps lower developmental homeostasis implies simpler systems for specifying floral organs in these plants



Figure 4 | Steps in the mostly male theory. **a**, Gymnosperm with separately borne microsporophylls (male; left) and cupules (female; right). **b**, Cupules have moved ectopically onto some microsporophylls. **c**, Microsporophylls bearing cupules are transforming into carpels and cupules into angiosperm-style ovules (from ref. 38).

that are more appropriate for comparison with gymnosperms than are systems of other angiosperms.

In gymnosperms, 'B' gene homologues are primarily expressed in developing male structures, resembling their role in angiosperm stamens. Homologues of the 'C' + 'D' clade are expressed in both male and female structures (including ovules), also suggesting broad conservation in their roles. These apparently conserved functions allow theories of flower origin based on these genes^{33–35}.

Theories based on evo-devo analysis

The 'mostly male' theory^{1,36–38} was triggered by studies of the *LEAFY* gene. It has two paralogues in gymnosperms but only one in angiosperms, in which it helps specify the flower. Data from pine suggested that the two gymnosperm paralogues may specify male versus female cones. Angiosperms have lost the latter copy, suggesting that the flower may be derived mostly from the male reproductive unit. At the extreme, the minimal female structure (for example a cupule) might have moved onto the male structure ectopically, creating the antecedent for the carpel bearing angiosperm-type ovules (Fig. 4).

This is supported by other observations: within carpels, ovules have highly variable numbers and placements, some of which must represent ectopic movement and increase in numbers. Stamens, by contrast, are highly uniform. *Arabidopsis* null mutants of *lfy* make no stamens but still form carpels, showing that *LFY* is required for male specification, but *LFY* independent genes can specify carpels. Ectopic ovules can be generated in *Petunia* by the overexpression of a single gene and in *Arabidopsis* by a different mutation, and functional ectopic ovules occur naturally on leaves of some plants of *Ginkgo* (a gymnosperm) (Fig. 5), suggesting that ectopic ovules are relatively easily produced. Liquid exuded by sterile ovules in Gnetales (Fig. 2) attracts insects to male structures, and pollination droplets on the functional female ovules also attract insects, resulting in pollination. Ectopic ovule placement in male cones in angiosperm ancestors might have conferred an immediate selective advantage by encouraging insect pollination³⁶.

Recent work on three conifers found complex patterns of expression of the two paralogues, with both being expressed at about equal levels in early female cone development, and both being expressed in early-developing male structures³⁹. This argues against any role in specifying male versus female cones. This undermines the mostly male theory, but preliminary expression data from *Welwitschia* favours the theory (E. Moyroud and M.W.F., unpublished observations), and the supporting morphological evidence remains.

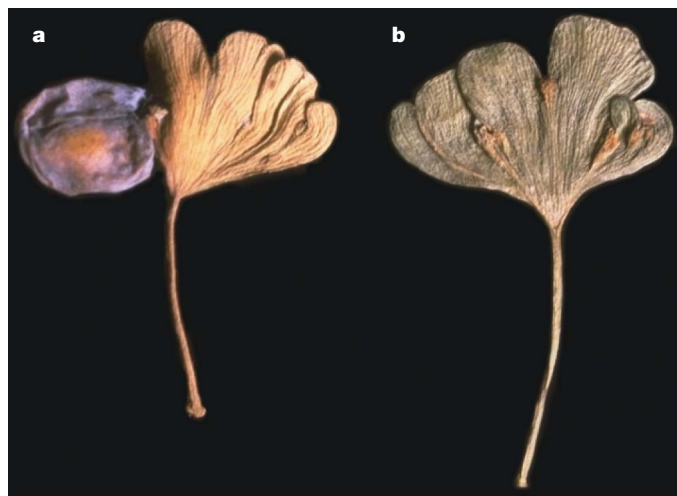


Figure 5 | *Ginkgo* leaves bearing ectopic ovules (and showing autumn colour). **a**, Leaf bearing mature seed at the base of an indentation. **b**, Leaf with many indentations that have ectopic ovules. (From ref. 37.)

An intriguing observation is the large number of mutations that can homeotically transform the outer integument of an ovule into a carpeloid structure³¹, which is consistent with the homology of both of these to a leaf. It might also suggest some ancestral structure resembling cupules borne within a cupule, but no such structure is known among fossil gymnosperms. An alternative would be the spread of some elements of cupule-wall identity from ectopic cupules onto the microsporophyll that bears them, precipitating modification of the latter into a carpel wall.

The old ‘gametoheterotopy’ theory of Meyen⁴⁰ remains relevant. It begins with the bisexual reproductive structures of Bennettitales and posits a homeotic conversion that partly imposes morphology of the pollen-bearing organs onto female structures. Some Bennettitalian microsporophylls were flattened with pollen organs on their upper (adaxial) surface. If homeotic conversion resulted in ovules borne on upper surfaces of flat microsporophyll-like structures, then the combination would serve as a carpel precursor. Bennettitales typically have a single whorl of male structures, so homeotic transformation rather than ectopic placement of ovules onto pre-existing structures would be required.

The ‘out-of-male/out-of-female’ theory of Theissen *et al.*^{33,34} centred on the origin of flower bisexuality. They noted that modern conifers sometimes make bisexual cones. Downregulation of ‘B’ gene expression in the distal portion of a male gymnosperm cone could permit the tip to become female, or upregulation of ‘B’ gene expression in basal regions of a female cone could make that region male, generating bisexual reproductive units from either male or female ancestral structures. They suggest that insect pollination could confer an immediate selective advantage, as in the mostly male theory. However, in conifers the resulting cones show normal male and female morphology in both cone regions. There is no novel morphology beyond bisexuality, so the origin of the angiosperm carpel structure is not explained.

Baum and Hileman³⁵ proposed a theory that adds mechanistic detail to the out-of-male theory. They suggested that greatly increased expression of protein encoded by a ‘C’ gene in the terminal region of a male cone could have been complexed with all the *sepallata*-encoded protein, preventing its interaction with the protein encoded by the ‘B’ gene, so switching its developmental fate to female. They also suggested that this ‘C’ protein might have repressed *WUSCHEL*, a gene required for maintenance of the apical meristem, resulting in floral determinacy.

The more explicit a theory is, the easier it is to test, so such explicit theories are especially valuable. These recent theories differ from earlier views in the crucial aspect of being testable, not only through the discovery of fossils but also by data from evo–devo studies.

The future

We certainly hope that spectacular palaeobotanical discoveries will clarify flower origins, but failing that it is evo–devo studies that will provide the most important new data, both by suggesting and testing theories of flower origin. Even simple gene-expression data may help in judging whether particular structures are homologous or not⁴¹, although such comparisons can be misleading⁴². Vestigial genes or gene expression patterns may indicate directions of evolutionary change⁴³. Gene trees analysed within organismal trees offer special power for detecting neofunctionalization as opposed to retained (plesiomorphic) gene functions⁴⁴. All of these results help to limit the range of possible theorizing, which we hope will converge on a historically accurate account of flower origins.

The comparative method applied to morphology and development fuelled the first great advances in evolutionary understanding, and similarly the comparative method applied to DNA sequences revolutionized our understanding of phylogenetic relationships between land plants. The comparative method applied to gene function and genetic controls that determine morphology will vastly

increase the power of evo–devo to explain both evolutionary mechanisms and the history of evolutionary change.

Relatively inexpensive 454 Life Sciences⁴⁵ and Solexa sequencing can detect virtually all mRNAs in a tissue, so expressed genes are known, and microarrays can measure their relative abundances. At present, in non-model organisms, gene function is often assumed to resemble that of closely related genes in model organisms, but improved reverse-genetics methods, such as VIGS (virus-induced gene silencing)⁴⁶ and TILLING (targeting induced local lesions in genomes), can downregulate genes to demonstrate function directly⁴⁷.

Phylogenetic footprinting between species identifies conserved non-coding DNA segments that probably have shared protein-binding sites that are important for regulating gene expression⁴⁸. Segments shared by distant species with similar, homologous morphologies versus segments shared among taxa with differing morphologies should reveal similarities and differences in transcription-factor-binding sites, explaining inputs to gene expression that result in various morphologies. Surface plasmon resonance and other methods can measure equilibrium and kinetics constants for protein–protein⁴⁹ and protein–DNA interactions⁵⁰ on short DNA segments and perhaps on promoters of a few thousand base pairs in length; this potentially allows measurement of regulatory outputs of the proteome and inputs to gene expression. In combination, these methods should greatly facilitate elucidation and comparison of genetic control networks in non-model organisms, vastly increasing the power of evo–devo; however, before these studies are available, phylogenetic analyses of individual gene families and expressed sequence tag/microarray studies of whole flowers and floral organs will continue to provide the most useful data, such as those of the Floral Genome Project¹⁹.

The appearance in the past decade of theories of flower origin, stimulated by developmental genetic data from modern plants, marks a major shift in attempts to solve Darwin’s ‘abominable mystery’. By building a model of the common aspects of floral developmental controls and comparing these with common elements of gymnosperm systems, we can build a picture of the genetic architecture underpinning floral structure in primitive angiosperms and test theories of how floral systems could have arisen¹⁹. This could lead to the realization that the fossils we need for understanding angiosperm origins may already be known. Incremental fossil discoveries should allow increasingly complete reconstructions of currently poorly known extinct taxa, which may then be included in phylogenetic analyses, but a palaeobotanical *deus ex machina* is possible at any time if a fossil is discovered that illustrates intermediate steps in the evolution of critical angiosperm attributes, such as the carpel with its included ovules or the angiosperm stamen with its specialized structure.

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