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Developmental specialisations in the legume family

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The legume family is astonishingly diverse; inventiveness in the form of novel organs, modified organs and additional meristems, is rife. Evolutionary changes can be inferred from the phylogenetic pattern of this diversity, but a full understanding of the origin of these 'hopeful monsters' of meristematic potential requires clear phylogenetic reconstructions and extensive, species-rich, sequence data. The task is large, but rapid progress is being made in both these areas. Here we review specialisations that have been characterised in a subset of intensively studied papilionoid legume taxa at the vanguard of developmental genetic studies.

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Introduction

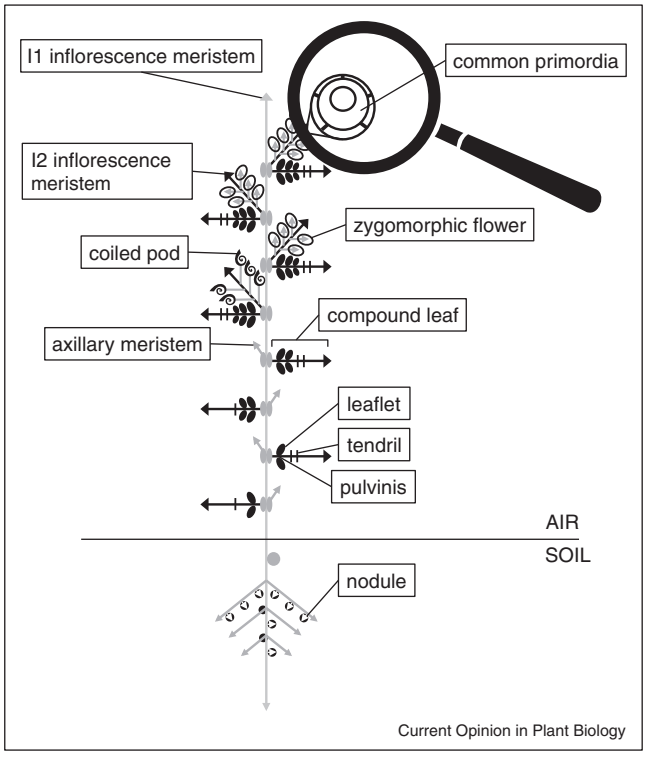
The legume family (Fabaceae, also known as Leguminosae) evolved about 60 million years ago and diversified into three subfamilies; the caesalpinioids, mimosoids, and papilionoids [1]. They make up the third largest family of flowering plants, comprising more than 700 genera and 18,000 species, with an exceptionally wide range of habits, ranging from giant forest trees to aquatic herbs [2–4]. Protein and/or oil-rich papilionoid legumes, such as soybean, peanut and chickpea account for more than one quarter of the world's primary crop production [5••] and are an essential component of low meat consumption diets. Representative genome sequences of some of these important food species have been published recently (www.comparative-legumes.org/) and many more are in the pipeline thanks to cheaper, faster sequencing technologies. This will lead to clusters of intensively sequenced species that are taxonomically closely related, so that, within these clear phylogenetic contexts, comparative genomic studies can be used to investigate genes associated with synapomorphies, characters that are shared due to common ancestry. In this review, the characters we focus on are developmental specialisations (Figure 1). Identification of the sequence variation associated with losses and secondary gains of synapomorphic specialisations provides a deep understanding of the evolution of developmental novelties.

Specialisation of inflorescence architecture

The most common type of inflorescence in legumes is a type of shoot axis known as a raceme, which includes flowering spikes, umbels and heads [6,7]. Even in mimosoid legumes, with their bottle brush or pompom-like floral clusters [8], flowers initiate acropetally on the raceme axis, after which they undergo a remarkable developmental pause until all are initiated, then, together they develop floral organs and open synchronously [6]. There is general agreement that papilionoid legume inflorescences are usually racemes, however there is disagreement on whether panicles are also common, due to differences in the definition of a panicle [6,9]. Classically defined panicles [10] are not found in legumes, while compound racemes, for example double racemes with two orders of branching, are common [7,9].

Taking the view that complex inflorescences are a developmental specialisation, we can ask if this complexity is regulated by iteration of the same molecular mechanism at sequential developmental time points, or by different mechanisms and whether these mechanisms are shared in other plant species. Berbel *et al.* [11••] set out to answer these questions in their study of the double raceme in *Pisum sativum*. The *Veg1* gene, encoding a MADS-box transcription factor in the euAGL79-clade, was identified as a novel genetic function that inserts a new meristem (called the I2, or secondary inflorescence, Figure 1) between the primary inflorescence axis and the flowers [11••]. This I2, a short stem terminating in a rudimentary stub, represents an additional meristem upon which novelty can arise [12•]. In *P. sativum* the identity of the I1 primary inflorescence (Figure 1) is determined by a different gene, *Determinate* [13]; its expression is restricted to the I1 by *Veg1* [11••]. Mutations of *Determinate* result in a determinate growth habit much sought after by breeders [14•]. A *Veg1*-like gene is not found in the grasses, where complex inflorescences are generated using a different set of genes [15]. Other papilionoid legumes with double racemes have a *Veg1* gene [11••], but it remains to be shown whether legumes with simple racemes have lost *Veg1* function and whether further subfunctionalisation of the *euAGL79* clade occurs in legume species with higher levels of inflorescence complexity.

Figure 1



Representation of a hypothetical papilionoid legume highlighting (in black) specialised meristems (arrowheads) and organs discussed in the text.

Novelty in flowers

Most legume flowers are pentamerous with five sepals, five petals, two whorls of five stamens each and a single carpel, but species occur with variations on this plan, featuring floral organ reduction or multiplication [2,6]. Many members of the papilionoid taxon Swartzieae, for example, are characterised by a single petal [2], while the profuse production of stamens from an innovative developmental feature, the ring meristem, is manifest in all three legume subfamilies [6]. The typical papilionoid flowers of *P. sativum*, *Medicago truncatula* and *Lotus japonicus* have ephemeral meristems known as common primordia (Figure 1) from which both petals and stamens arise [16–18]. Although the common primordia are entirely consumed by the organs arising from them, they represent an additional step in floral meristem ontogeny, echoing the structural reiteration of compound inflorescences; both remodellings of meristematic potential are 'hopeful monsters'. In *M. truncatula*, duplicated *APETALA3*-lineage genes are expressed in complementary patterns in the common primordia, petals and stamens and they interact differentially with duplicate *PISTILLATA*-lineage genes to confer petal and stamen identity [19]. Despite the absence of a motif common to other eudicots, *PISTILLATA* proteins in *P. sativum* and *M. truncatula* are fully functional in this role [20,21].

Mimosoid legumes are characterised by radially symmetrical flowers, whereas papilionoid and caesalpinioid legume flowers are usually zygomorphic (Figure 1), that is they are bilaterally symmetrical; their showy adaxial petal often stands upright and two lateral petals flank two fused keel petals when the flower opens. Like the distantly-related zygomorphic species *Antirrhinum majus*, papilionoid legumes have recruited CYCLOIDEA transcription factor family genes for the regulation of dorsal and lateral petal identity [22–25]. Functional analysis of triplicated *CYCLOIDEA* -like genes in *L. japonicus* showed that *LjCYC1* and *LjCYC2* have roles in dorsal petal patterning, while *LjCYC3* confers lateral petal identity [24,26•]. Independent genetic loci determine the asymmetry of the lateral and ventral petals [24,27], but these remain to be identified. Transcriptional profiling of individual floral organs was undertaken in *Vicia sativa* [28] and compared with gene expression in distantly-related non-zygomorphic flowers. In order to capture the particular features of this synapomorphy in papilionoid legumes, a similar approach will need to be taken on species within the same clade, for example, zygomorphic and non-zygomorphic genistoid legumes [25]. While much attention has focused on floral morphology with respect to pollinators, other factors, for example nectar composition, are also important in pollination systems [29]. Specialisation occurs in other floral organs too, such as the carpel. Legume carpels can be covered in hairs, or hairy on one side only. The former has been deduced as the ancestral state in papilionoid legumes of the tribe Fabeae, while the latter, as either abaxial or adaxial hairiness, characterises different subclades [5••].

Once fertilised, the carpel normally grows out to form the elongated seed-containing legume (or pod) that is characteristic of the entire family. A striking novelty is that some species have coiled pods (Figure 1) and this character has arisen several times independently within papilionoid legumes [2], suggesting it may have adaptive value. A study of species with coiled or uncoiled pods within the genus *Medicago* revealed a clear correlation between pod morphology and a change in the *SHATTERPROOF* gene coding sequence which affected the ability of this MADS-box transcription factor to interact with a partner [30••]. Pod coiling in *Medicago* occurs when cells at the carpel margin fail to elongate and become heavily lignified. As there is only one carpel and only one margin, inhibition of its extension results in coiling of the carpel wall tissues, which extend as usual. Coiled pods can have elaborate patterns of lignin deposition, sometimes resulting in the formation of spines, which allows seed dispersal when the pod becomes attached to the fur of passing animals. The *Medicago* clade, which contains spined and

smooth-podded species, is ideally suited to further investigation of this character.

Complex and specialised leaves

Simple leaves have been inferred to be ancestral in Angiosperms and there have been multiple gains and losses of leaf complexity. This means not all compound leaves are homologous, and neither are simple leaves, but terms have not yet been defined to reflect this. It is not clear whether the ancestral leaf form of eudicots, or within these the rosids, from which legumes arose, was simple or more complex [31•]. Maximum likelihood estimates of ancestral states suggest that among Angiosperms there is a strong bias for evolution towards simple leaves, however, within the legumes, a family characterised by compound leaves, there is no such bias, indeed evidence for the opposite trend is found [31•]. Thus the legume compound leaf (Figure 1), once acquired, tended to be retained, and provided further opportunities for developmental specialisation.

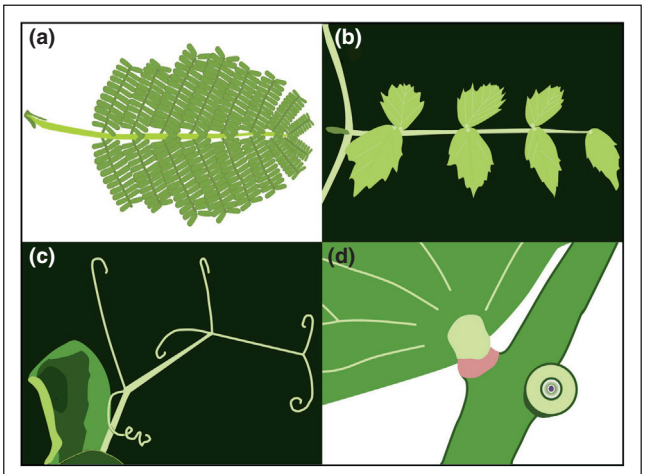
The LEAFY protein, known as Unifoliata (Uni) in *P. sativum* [32], SINGLE LEAFLET1 (SGL1) in *M. truncatula* [33,34] and PROLIFERATING FLORAL MERISTEM (PFM) in *L. japonicus* [35], is known to target many genes involved in floral patterning [36,37], but it is also proposed to have an earlier role in enabling meristem outgrowth, by inducing the transcription of genes such as *REGULATOR OF AXILLARY MERSTEMS1* [38•]. It may be through this pathway that *Uni/SGL1/PFM* generates a transient phase of indeterminacy [32] in legume compound leaves. The downstream homeodomainless KNOX transcriptional regulator FUSED COMPOUND LEAF1 has a similar role in promoting leaf complexity, as well as defining leaflet boundaries [39], while *PALMATE-LIKE PENTAFOLIATA1* (*PALM1*) repression of *Uni/SGL1/PFM* is important in ensuring that complexity is eventually curtailed [33,34]. The *PALM1* gene also regulates leaflet wax deposition and this brings a potentially serendipitous benefit to breeders: reduced wax deposition on the abaxial surface of *palm1* mutant leaves confers resistance to fungal pathogens [40••].

In the mimosoid subfamily bipinnate-leaves (Figure 2a) are common while once-pinnate-leaves (Figure 2b) are more usual in the papilionoid subfamily [2]; whether this additional complexity in mimosoids can be explained by variations in *Uni/SGL1/PFM* and *PALM1* interactions remains an open question. The compound leaves of both these taxa feature astounding leaf specialisations, such as the touch-responsiveness of leaves and of tendrils (Figure 2c). One of the genes required for tendril formation in *Pisum* and *Lathyrus* species, is *Tendril-less* (*Tl*), which is transcriptionally activated by *Uni* [41] and *Lathyroides* (*Lath*) [42•], though direct interactions have not yet been demonstrated. Sequence similarity and genetic map position suggest *Lath* is the orthologue of the *WUSCHEL-related homeobox1* (*WOX1*) transcription factor *STENOFOLIA* (*STF*), which was shown to be critical for leaflet blade development in *M. truncatula* [43]. Genes such as *JAGGED1*, recently identified in soybean [44•], are also involved in this process. In the tendrilled leaf of *P. sativum*, *Lath* appears to have acquired an additional role; not only promoting blade outgrowth in leaflets and the dorsal petal (as in *M. truncatula*) but also suppressing blade outgrowth in tendrils [42•], presumably via activation of *Tl* in the distal domain of the leaf.

Application of the hormone gibberellic acid suppresses terminal leaflet blade development and this activity is proposed to occur through increased *Uni* transcription [45]: again, upregulation of *Tl* would lead to blade suppression. Other hormones are also implicated in blade position and outgrowth, for example, reduced levels of free auxin and changes in the levels of transcription of auxin-regulated genes are seen in narrow-leafleted *stf* mutants [43] while *smooth leaf margin1* mutants have altered auxin distribution and excessive production of terminal leaflets [46]. At this point at least some of the regulators of legume leaflet versus tendril formation have been identified, but their relationships with each other are yet to be fully elucidated. Whether the leaf tendrils of climbing mimosoid legume species represent convergent evolution and whether the same physiological processes are involved in contact-induced coiling remain to be investigated. The terminal leaf tendrils of *Entada scandens* are said to be sensitive over their entire surface [47], as are *Lathyrus aphaca* tendrils, while *P. sativum* tendrils are sensitive on their abaxial surface only [48].

A novel organ, the pulvinus (Figure 2d), mediates leaf movements in some legumes and is driven by changes in turgor pressure [49]. Such responses can be rapid and reversible, whereas leaf repositioning in plants without pulvini occurs more slowly via differential growth of cells in the leaf petiole [50]. Both reversible and non-reversible mechanisms of movement may be important for the tolerance of light, temperature and water stresses. Sensitive leaves, described as seismonastic, due to the suddenness of their response to touch, have a pulvinus enabling rapid flexion from the base of the leaf or leaflet. This intriguingly radialised organ represents an intercalation of non-polarity between the flattened leaflet and the polarised leaf axis. A preliminary study has found evidence of seismonasty evolving multiple times in distinct lineages within the genus *Mimosa* [8]. One hypothesis is that the presence of a pulvinus, acting as a hinge in regular movements, such as solar tracking and day/night leaflet opening and closure, permits exaptation to seismonasty. Analysis of mutants without a pulvinus in *P. sativum*, *M. truncatula* and *L. japonicus* led to the identification of a LOB-domain transcription factor as a key component in the development of a leaflet pulvinus [51•,52•]. These legumes are all members of the 50 Ma Hologalegina clade

Figure 2



Examples of legume compound leaves and their novel leaf organs. **(a)** Bipinnate leaf, *Delonix regia*. **(b)** Once-pinnate leaf, *Cicer arietinum*. **(c)** Leaflet tendrils, *Pisum sativum*. **(d)** Pulvini, *P. sativum*. An intact leaflet pulvinis, delimited at its base by red coloured epidermal cells, is shown on the left, a section through a pulvinis on the opposite leaflet of the same leaf, as stained with toluidine blue, is shown on the right.

of papilionoid legumes [1], so this discovery naturally leads to the question of whether pulvinus formation in phylogenetically remote and distinct clades, such as the 42 Ma Mimosoid clade and the 45 Ma Millettioid clade, with pulvini at the base of their leaves as well as their leaflets, is regulated by the same process.

A novel root organ: the nodule

No discussion of developmental specialisations in legumes can ignore the novelty of nodules (Figure 1), organs that accommodate symbiotic nitrogen-fixing bacteria on underground or adventitious stem roots [3,53,54]. Nodules are not unique to legumes as indicated by their multiple independent origins in Angiosperm lineages [55], however, recent attention has focused on their evolution in legumes thanks to a new class of mutant defective in nodule identity [56••]. Maintenance of nodule identity requires suppression of root identity by the *NODULE ROOT/COCHLEATA* (*NOOT/COCH*)gene, which also has roles in leaf and floral development [56••]. In the pea *coch* mutant the most extreme leaf phenotype is the replacement of the stipules with compound structures resembling those on the rachis; reminiscent of the stipule form in *Delonix regia* [57]. The enlarged meristematic regions and supernumerary organs observed on *noot/coch* nodules, leaves and flowers suggests that long and/or short-distance stem cell pool maintenance signals are not correctly interpreted in the mutant. These broad phenotypic effects probably reflect original functions of the ancestral gene in shoot development prior to its co-option in nodule maintenance [56••]. As with many other specialised organs, in the nodule we see a clear example of evolutionary tinkering through gene recruitment.

Conclusions

It happens to be the case that most agricultural legume species are in the papilionoid subfamily, so this group is where genome sequence and genetic information is richest at present. In contrast, fascinating and potentially useful developmental specialisations are distributed throughout the legume family; the examples discussed here are but a sparse sample of the evolutionary inventiveness of this angiosperm family. Among the specialisations we have described a common feature is the intercalation of a new meristem, involving gene subfunctionalisation, which adds structural complexity. Organ sculpture into specialised shapes is another commonality, whether of leaflets, petals, or pods, members of large gene families have been co-opted to this function. New genes are driving phenotypic evolution, so it is with more extensive sequence information throughout the legume family that we can identify the newcomers and understand how they have been incorporated into existing developmental circuitries to bring about novelty.

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