GENETIC ARCHITECTURE OF NOVEL FLORAL ORGANS

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Flowering plants exhibit a remarkable array of morphologies due in no small part to the evolution of novelty. While flowers themselves are often considered evolutionary novelties, suites of novel traits have further evolved within flowers to produce the breadth of morphological diversity across angiosperms, including traits as dramatic as novel floral organ identities. Here, we describe and synthesize what we currently do and do not know about the evolution and genetics underlying the development of floral organs historically referred to as novel and consider how these findings impact the way we define novel organs.

Keywords: evo-devo, floral organs, morphology, novelty, organ identity.

Introduction

Flowers display varying combinations of a standard set of four organ types to produce seemingly endless variation in floral morphology. The typical floral ground plan consists of outer concentric whorls of sterile organs that enclose fertile organs: the first outermost whorl of sepals, followed inward by petals in the second whorl, then stamens in the third whorl, and carpels in the fourth innermost whorl. These "standard" organs, although consistent in whorl arrangement, vary wildly in their presence/absence, number, shape, size, texture, fusion, and color across angiosperms. Some taxa, however, have evolved novel organ types to yield five or even six distinct identities. These organs can result from the extreme modification of preexisting organs, or in other instances, new organs are thought to have evolved de novo (Ronse de Craene and Smets 2001; Chanderbali et al. 2016).

Before we can consider such novel floral organs, we should first define some critical terminology. What do we mean by a "floral organ"? Quite simply, floral organs are lateral determinate organs (i.e., modified leaves) produced by a meristem that has floral identity. It is inherently more difficult to define what we mean by "novelty," which is a notoriously debated topic across evolutionary biology (reviewed in Müller and Wagner 1991; Erwin 2015; Peterson and Müller 2016; McKenna et al. 2021; Moczek 2023). "Novel" has been used both so broadly as to make the term meaningless and so narrowly that nothing can be considered novel. For the purpose of this primer, we will employ a version of Ernst Mayr's (1960) definition of an evolutionary novelty that we are considering at the level of organ identity: a character that differs more than quantitatively from the character that gave rise to it (Mayr 1960). For instance, shifting from five to 10 stamens would not be a novelty, nor would evolving longer petals, but completely remodeling the morphology or function of a stamen so that it is no longer easily recognizable as such would be a novelty. Another related concept that is perhaps even more complex and contentious is that of homology. Fully exploring the definitions of all the hierarchical levels of homology would require a separate primer, so we would refer readers to several published reviews (Mindell and Meyer 2001; Baum and Donoghue 2002; Jaramillo and Kramer 2007) and will focus on just one relevant concept, that of process homology (see "Glossary"; Gilbert and Bolker 2001). Process homology arises because of the common inheritance of functional genetic modules, which can contribute to the development of homologous structures or, alternatively, can be co-opted to function in convergently evolved or even entirely disparate structures (Baum and Donoghue 2002; Jaramillo and Kramer 2007).

Floral development and organ identity have traditionally been characterized using development and morphology (Ronse de Craene and Smets 2001; Hufford 2003), but studying the genetics underlying development can provide further insight into the evolution and nature of novel organs. The genetic basis of floral organ identity is described by the ABC model of floral development, in which coordinated expression of homeotic MADS-box transcription factors determine organ identity: A-class genes alone code for sepals, A- and B-class genes together code for petals, B- and C-class genes together code for stamens, and C-class genes alone code for carpels (fig. 1; see "Glossary"; Irish 2017). This framework is particularly useful for comparative studies of features that directly impact organ identity rather than downstream organ elaboration and has formed the basis of much of modern floral evo-devo (Jaramillo and Kramer 2007; Kramer 2018).

This primer in the plant sciences focuses on floral organs that have been historically considered to be novel and presents

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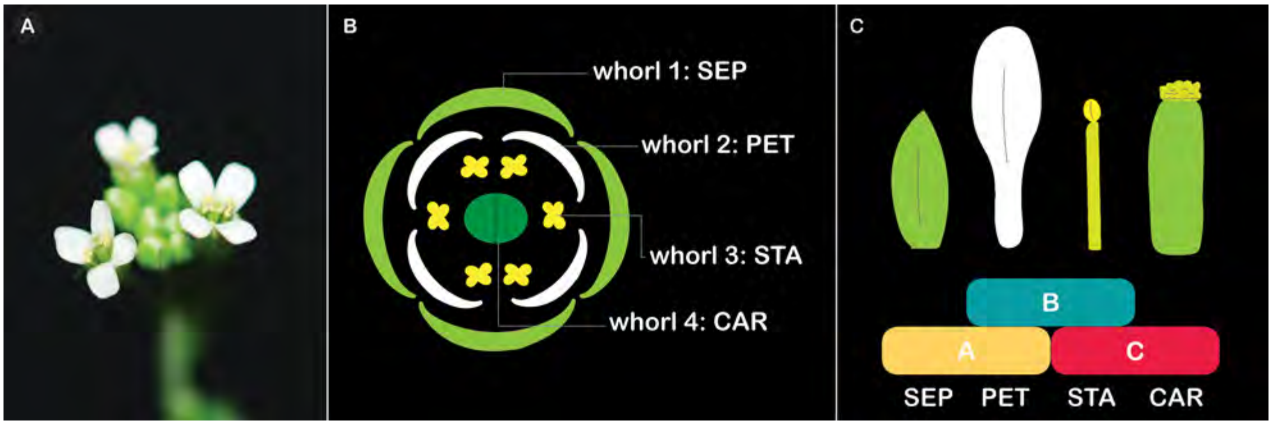

Fig. 1 *A*, Model organism *Arabidopsis thaliana* (photo: Andrea Appleton). *B*, Model organism's floral diagram. *C*, Canonical ABC model of floral organ identity. See text and "Glossary" below for more details. CAR = carpel; PET = petal; SEP = sepal; STA = stamen.

an updated interpretation of these structures based on what we have recently learned from developmental genetics. These findings raise new questions about how we should define floral organ identity and the fundamental nature of what novelty means.

Novel Organs

Novel Floral Organs through Modification of Preexisting Organs

The most commonly inferred mechanism for the origin of novel organs is for them to be derived from preexisting floral organs. Any of the four basic floral organs can give rise to novel organ identities, but we will focus on what is known about novelty derived from the perianth and the androecium.

Derived from the Perianth. *Lodicules.* Members of the Poaceae, the grass family, produce highly modified, wind-pollinated flowers that possess sterile outer floral organs that differ dramatically in appearance from typical sepals or petals, resulting in taxon-specific terminology (Kellogg 2001; Patterson et al. 2023). These novel structures are the best-understood examples of modified perianth organs from a genetic perspective.

Lodicules are sterile structures, with typically zero to two lodicules per flower, that are located within the outer protective organs, which have been considered novel as a result of their distinct morphology and uncertain evolutionary origin (fig. 2*A*; Whipple et al. 2007). Lodicules are often membranous or fleshy and swell at anthesis to assist in the opening of the flower (Whipple et al. 2007). These organs have been considered to be modified petals, modified stamens, or entirely de novo structures (Clifford 1987) because of their unique appearance and position within the flower (fig. 2*B*). Careful comparative studies of floral development and B-class gene expression in the grasses and their close relatives together with B-class function in model grasses have provided strong evidence that the lodicules represent modifications of the second-whorl petals that occur in nongrass monocots (Whipple et al. 2007; Lombardo and Yoshida 2015). The study of Whipple et al. (2007) is notable for its elegant exploration of Remane's (1952) homology criteria, which include position, special characteristics (e.g., color, texture, cell structure), and homology via intermediate evolutionary forms. In the case of lodicules and petals, they share clear correspondence

Glossary

ABC model. A model in which coordinated expression of MADS-box transcription factors determines organ identity: A-class genes alone code for sepals, A- and B-class genes together code for petals, B- and C-class genes together code for stamens, and C-class genes alone code for carpels.
Corona. A crown-like structure present in flowers.
Floral organ. A determinate, lateral organ arising from the floral meristem.
Homology. Similarity due to shared ancestry.
Lemma. A sterile bract-like organ in the outer whorl of some Poaceae (grass) flowers, usually in tandem with a palea.
Lodicules. Usually, membranous or fleshy sterile organs in the second whorl of some Poaceae (grass) flowers.
Neofunctionalization. The evolution of novel gene function in a paralog following gene duplication.
Novelty. A character that differs more than quantitatively from the character that gave rise to it (Mayr 1960).
Palea. A sterile bract-like organ in the outer whorl of some Poaceae (grass) flowers, usually in tandem with a lemma.
Paralog. A duplicate gene copy.
Process homology. The common inheritance of functional genetic modules, which can contribute to the development of homologous structures or, alternatively, can be co-opted to function in convergently evolved or even entirely disparate structures.
Receptacle. The surface where the floral organs attach to the pedicle.
Staminode. A stamen that has evolutionarily lost its primary function of producing viable pollen.

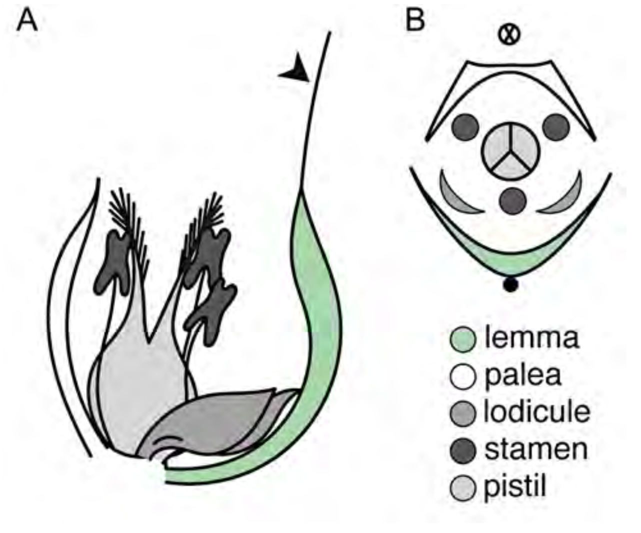

Fig. 2 Grass floral morphology. *A*, Simplified grass flower. The arrowhead denotes the awn. *B*, Grass floral diagram (modified from Patterson et al. 2023).

in position, certain traits such as sterility, and consistent dependence on B-class genes for identity. What remains to be explored is how the genetic program downstream of B-class function has diverged so dramatically in the grasses that it has given rise to an organ that, until recently, was not easily recognizable as a petal. Of course, there are other analogous examples of extreme developmental divergence downstream of canonical ABC organ identity, such as the feathery pappus of the Asteraceae, which represents modified sepals (Vijverberg et al. 2021), but the grasses are likely to hold the best chance for investigating the molecular mechanisms underlying such evolutionary phenomena.

Paleae and lemmas. Grass flowers contain one palea and one lemma, which are sterile bract-like organs that make up the outer whorl (sometimes considered the outer two whorls) of the flower (fig. 2), and three hypotheses of their homology have been proposed (Lombardo and Yoshida 2015; Patterson et al. 2023). The two structures are often examined together, with the palea always positioned inward to the lemma, but even their identities as floral organs have been questioned: early studies based on morphology hypothesized that they are a leaflike prophyll and bract, respectively, noting that in some species, they arise from the inflorescence axis rather than the floral meristem (Kellogg 2001). A second hypothesis based on developmental genetics and MADS-box gene expression suggests that both the palea and the lemma are similar to sepals of other taxa, with a note that the molecular mechanisms controlling palea and lemma development are somewhat distinct from one another (Lombardo and Yoshida 2015). Maize and rice B-class gene mutants where lodicules (=petals) are converted to paleae and lemmas support this hypothesis because of the similarity to B-class mutants in eudicots, in which petals are homeotically transformed into sepals (Lombardo and Yoshida 2015; Patterson et al. 2023). The third hypothesis of palea and lemma identity suggests that these structures are more complex than simple bracts or sepals but rather that they lie on a spectrum between these identities (Reinheimer and Kellogg 2009; Patterson et al. 2023). Of course, given the nature of process homology (Baum and Donoghue 2002), it is possible that these hypotheses are not mutually exclusive. In some grass taxa, the palea and the lemma may arise before the meristem expresses floral identity, making them technically bracts/prophylls, while in other taxa they may be true floral organs but express varying degrees of organ identity genes. This kind of developmental and evolutionary lability contributes to the difficulty in establishing firm identity interpretations across all grass lineages, and in turn, the palea and the lemma may be considered novel in some taxa (e.g., organs of hybrid identity) but not in others (e.g., simply sepals).

Derived from the Androecium. *Staminodes*. Stamens, collectively termed the androecium, are extremely evolutionarily labile floral organs and serve as the precursors for multiple novel features (Kong and Becker 2021). Staminodes are simply stamens that have evolutionarily lost their primary function of producing viable pollen, and their ontogeny and classification are well established (Walker-Larsen and Harder 2000; Ronse de Craene and Smets 2001). The presence of staminodes is relatively common, occurring in at least one species in 32.5% of families across every major clade of angiosperms (Walker-Larsen and Harder 2000). Although some are retained as vestigial rudiments of stamens, others have evolved an exceptional array of forms in response to selection for alternative functions ranging from pollinator attraction to deception and protection (Walker-Larsen and Harder 2001; Appleton and Schenk 2021). Staminodes are generally found in one of three androecial configurations associated with the following distinct floral architectures: (1) flowers that contain a whorl that consists of fertile stamens as well as one or more staminodes, which occurs most frequently in flowers that have undergone the evolutionary transition from actinomorphy to zygomorphy; (2) flowers that contain a whorl (or whorls) that consists wholly of staminodes because of their loss of all stamen function in the context of unisexuality (for a recent review, see Feng et al. 2020); and (3) flowers that contain one or more full whorls of staminodes in addition to retaining a full whorl (or whorls) of functional stamens (Walker-Larsen and Harder 2000, 2001; Schenk and Appleton 2023). A debatable fourth configuration is that which occurs in early-diverging angiosperm flowers with spiral architecture, where chimeric but often sterile organs form a gradient from stamen to petal identity and from stamen to carpel identity. These sterile organs often appear to be a by-product of spiral phyllotaxy combined with a gradient of organ identity gene expression (Kim et al. 2005).

The genetic underpinnings of staminodes have been studied in several taxa. A natural starting point in determining the identity of novel organs is to examine the expression of MADS-box transcription factors. Staminodes, as derivatives of stamens, likely express B- and C-class genes, but there are up to six major clades of MADS-box transcription factors that can contribute to floral organ identity (Litt and Kramer 2010), and the precise changes to the stamen developmental program that produce staminodes appear to differ between taxa and staminode type. Perhaps the most thoroughly studied example is *Antirrhinum* (Plantaginaceae), which is bilaterally symmetrical with four stamens and a single type I staminode (fig. 3*A*, 3*A*′; Almeida et al. 1997; Luo et al. 1999). In *Antirrhinum*, MADS-box gene expression does not differ between the stamens and the staminode. Acting in parallel to the ABC program, *CYCLOIDEA* (*CYC*), a gene controlling

Fig. 3 Flowers containing well-studied staminodes. *A*, *Antirrhinum majus*, type I staminode (photo: Sabina Bajracharya). *A′*, *Antirrhinum majus* dissected (photo: P. Huijser). *B*, *Canna indica* (photo: Andrea Appleton). *C*, *Delosperma* sp., type III staminodes (photo: Didier Descouens). *D*, *Aquilegia* Kirigami, type III staminodes (photo: Colin Teo). Arrows indicate staminodes, except in *B*, where the arrow points to the fertile anther. The remainder of the petaloid organs are, in fact, staminodes in this flower. O = ovary.

bilateral symmetry, functions additively with B- and C-class genes to transform the dorsalmost stamen into a staminode (Luo et al. 1999).

Another example of staminode evolution in the context of zygomorphy (or asymmetry) is the family Zingiberaceae, which is notable for evolving staminodes with an array of morphologies and configurations (de Almeida et al. 2013). An extreme example of these has evolved in the well-studied genus *Canna*, in which the androecium has been generally reduced such that it contains a multipart, fused, and petaloid staminode bearing one-half of a functional anther (fig. 3*B*; Tian et al. 2018). Expression of the C-class gene *AGAMOUS* (*AG*) appears to be much higher in the fertile stamen of *Canna* than in the sterile staminode tissue (Tian et al. 2021). Consistent with restricted *AG* expression, the petaloid staminodes show upregulation of abaxial polarity identity genes that promote laminar expansion in contrast to the usually radial stamen filament (de Almeida et al. 2014). These two examples of zygomorphic staminodes—in *Antirrhinum* and *Canna*—are intriguing for a number of reasons. First, they are essentially morphological mirror images, in that *Antirrhinum* has primarily fertile stamens with one sterile stamen while the gingers have increasing degrees of sterilization, culminating in the evolution of only a partial fertile stamen in *Canna*. Second, the ABC identity pathways and *CYC* control of staminode development in *Antirrhinum* are clearly functioning in a parallel and additive manner, while in *Canna* it appears that whatever mechanism is controlling zygomorphy acts upstream of the ABC genes to affect spatial localization of *AG* expression.

Perhaps not surprisingly, differential expression of ABC MADS-box transcription factors are directly implicated in the control of type III staminode identity. For example, B- and C-class genes have been shown to be transiently expressed only in the development of petaloid staminodes in members of Aizoaceae (fig. 3*C*), which differs from the continuous expression of B- and C-class genes during fertile stamen development (Brockington et al. 2011). In addition, gene expression and functional data are available for *Aquilegia* (Ranunculaceae), which contains two whorls of papery, interlocking staminodes nested within many whorls of fertile stamens (fig. 3*D*; Meaders et al. 2020). In *Aquilegia*, neofunctionalization and differential expression of paralogs of the B-class gene *APETALA3* (*AP3*) appear to control the evolution of the staminodes, where *AP3-1* promotes staminode identity while *AP3-2* is primarily involved in stamen identity (Sharma and Kramer 2013). Although differential expression of MADS-box organ identity genes has been demonstrated in both of these taxa, Aizoaceae does not rely on gene duplication while *Aquilegia* does, consistent with their independent evolutions. Detailed comparative studies in closely related taxa, ideally with distinct conformations of staminodes, could provide greater insight into the regulatory mechanisms underlying staminode evolution and diversification.

Coronas. Coronas are loosely defined as crown-like structures in flowers. They appear to have an attractive function in most taxa, and they arise from a variety of precursor tissues, including the androecium, the corolla, the receptacle, or a combination of those tissues (Weberling 1989; Waters et al. 2013). The term "corona" has been used broadly across all major clades of angiosperms to describe structures that share few similarities beyond minor superficial appearance (Bernhard 1999; Hemingway et al. 2011; Nikolov et al. 2013; Waters et al. 2013). For example, some coronas are dramatically different in morphology from the organs in the same flower (fig. 4), while other so-called coronas appear to be only minor elaborations of typical floral organs (fig. 5). We will term examples of the first of these as type I coronas and the second as type II coronas.

Among the shared traits of type I coronas across diverse taxa are (1) sterile elaborations, primarily of the androecium or the receptacle; (2) arising late in development, considerably after emergence of the other floral organs; and (3) expressing B- and C-class MADS-box genes (Bernhard 1999; Hemingway et al. 2011; Nikolov et al. 2013; Waters et al. 2013). However, the morphology of these coronas still differs dramatically, ranging from the trumpetlike, petaloid tube resulting from outgrowth associated with the androecium in *Narcissus* (Amaryllidaceae; fig. 4*A*) to the complex arrangement of parts described as a "series of rings, scales, or threads intervening between the petals and the

Fig. 4 Flowers containing well-studied type I coronas. *A*, *Narcissus* sp. (photo: Andrea Appleton). *B*, *Passiflora caerulea* (photo: Andrea Appleton). *C*, *Asclepias* sp., with inset showing a close-up of a flower (photos: Andrea Appleton). *D*, *Sapria himalayana* (photo: Charles Davis). Arrows indicate coronas.

stamens" (Masters 1871, p. 598) in *Passiflora* (Passifloraceae; fig. 4*B*). Members of Apocynaceae (*Asclepias*, *Matelea*, etc.; fig. 4*C*) have coronas described as elaborations originating from the androecium late in development that become secondarily fused with the corolla (Maciel Monteiro and Demarco 2017), while *Sapria* (Rafflesiaceae) has a taxon-specific structure called a diaphragm that appears to be analogous to the coronas of other taxa (fig. 4*D*; Nikolov et al. 2013). Additional taxa are likely to contain type I coronas, but we currently lack the developmental and genetic data to define them using this syndrome of traits. For instance, members of Velloziaceae possess sterile structures termed coronas that arise relatively late in development between the androecium and the corolla, but currently, no data addressing their genetic identity are published (das Gracas Sajo et al. 2010).

Type II coronas are even more diverse. For example, some members of Caryophyllaceae (*Lychnis*, *Dianthus*, *Silene*, etc.) have small outgrowths on the hinges of their petals that have been termed coronas, but these are clearly the product of simple peltate growth in the corolla (fig. 5*A*; Weberling 1989). In addition, members of the genus *Puschkinia* (Asparagaceae) are described as possessing tubular coronas, but these structures are composed of stamen filaments that have been laterally expanded and fused (fig. 5*B*; Ozudogru et al. 2022). The closely related genus *Scilla* (Asparagaceae) contains a similar structure composed of expanded but unfused stamen filaments (fig. 5*C*; Yildirim et al. 2013). Thus, we consider type II coronas to be minor elaborations of existing organs rather than distinct structures.

Perhaps not surprisingly, there are examples that are not entirely clear, such as the corona of *Jaltomata calliantha* (Solanaceae), which presents as a short ring of tissue connecting the bases of stamen filaments to hold nectar (fig. 5*D*; Kostyun et al. 2019). Kostyun et al. (2019) evaluated the homology of

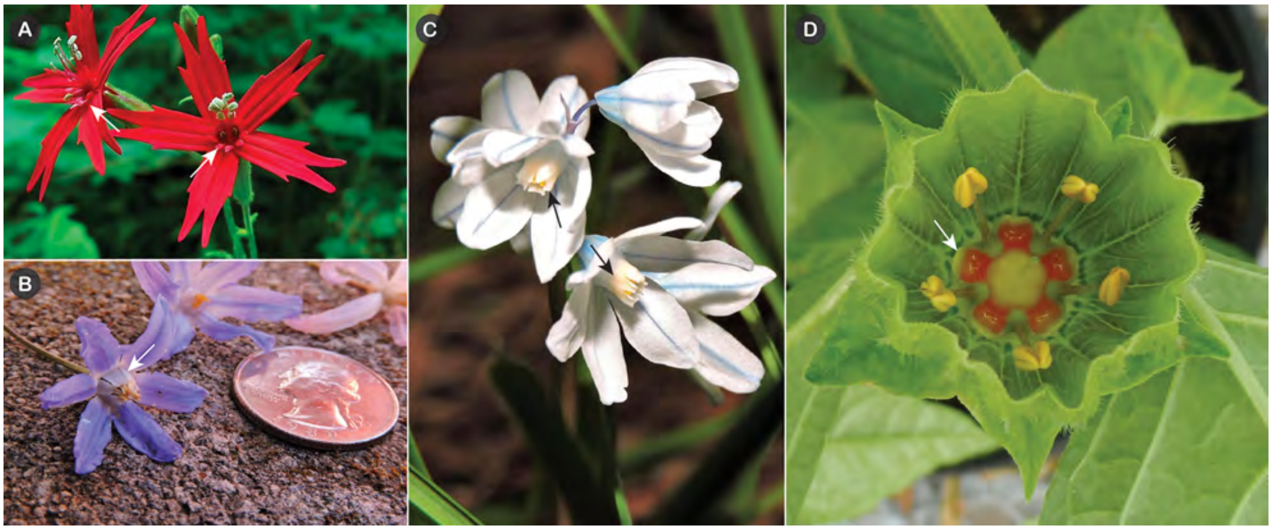

Fig. 5 Flowers containing type II (*A*–*C*) or equivocal (*D*) coronas. *A*, *Silene virginica* (photo: Jason Hollinger). *B*, *Chionodoxa sardensis* (photo: Travis Owen). *C*, *Puschkinia scilloides* (photo: Travis Owen). *D*, *Jaltomata calliantha* (photo: Indiana University Department of Biology). Arrows indicate coronas.

J. calliantha coronas using anatomical and genetic data, and they determined that these coronas have their strongest affinity with stamens, as they express B- and C-class genes and share similarities in cell type. However, their cell morphology also bears some similarity to that of petals, and the authors detected weak expression of the A-class gene *APETALA1* in the corona. So while this *Jaltomata* corona fits all the traits we defined for type I coronas, these data underscore the fact that we are still in the early days of understanding these structures.

Based on similarities across taxa that bear structures that we have termed type I coronas, we propose that all three characteristics described above are necessary for any floral structure to be considered a "true" corona. Although these characteristics appear to be shared, coronas have been independently evolved in each taxonomic group where they are present, and they are not homologous to each other. Our definition of coronas excludes type II coronas, which we consider to be simple elaborations of other preexisting organs. We also note that some coronas remain ambiguous, such as those of *Symbolanthus* (Gentianaceae), which present as a tubelike structure connecting petals and stamens (Mollina and Struwe 2008).

The traditional classification of both of these types of coronas as novel organs calls into question how we define organs: should coronas, as elaborations of preexisting organs like petals and stamens, be considered separate organs at all? In addition, we currently lack a precise understanding of how coronas initiate. Since coronas are generally late arising, meristematic genes (such as those in the KNOX family) should no longer be expressed at their origin, but are those genes being reactivated to produce new structures? Along these lines, an underexplored possibility is the role of the receptacle in generating floral structures. Zenchyzen et al. (2023) show that the androgynophore, a structure that uplifts and bears the androecium and gynoecium in *Gynandropsis* (Cleomaceae), expresses a MADS-box profile similar to that of stamen filaments and the gynophore. However, this structure is likely derived from the receptacular tissue where each organ attaches to the shoot axis, and these authors note that they do not consider the androgynophore to be a determinate lateral organ. Furthermore, it remains to be determined how the distinct morphology of coronas is established if they express the same identity code (B and C) as the stamens. It is possible that there is some temporal or spatial difference or another genetic program acting in parallel to the canonical identity program. A more precise definition of coronas, as well as more studies combining morphological, gene expression, and functional analyses, is needed to better understand their evolution and identity.

Conclusions

Flowers have evolved remarkable variation in morphology by extreme modification of their individual organs, sometimes such that the modifications have rendered the organs unrecognizable or uncategorizable. As seen with coronas, novel traits can be particularly complex and may not simply fit into the categories that botanists have previously used. In this primer, we have covered multiple potential mechanisms for generating such novelty, including the additive effect of parallel genetic pathways, the downstream divergence of canonical organ identity programs, the impact of ABC gene duplication and neofunctionalization, and a still-enigmatic potential role for elaboration of the receptacle. While these findings are intriguing, they also highlight a considerable absence of data, particularly in regard to functional studies and moving beyond standard candidate gene approaches. To truly understand how these complex, novel traits arose, we must generate more rigorous tools to study these features in nontraditional model systems.

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