ANNALS OF
BOTANY
Founded 1887

PART OF A FOCUS ISSUE ON POLLINATION AND FLORAL REGULATION

Pollination syndromes and the origins of floral traits

Leandro C. S. Assis[*]

Departamento de Botânica, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais 31270-901, Brazil
[*]*For correspondence: E-mail: leandassis@gmail.com or leandroassis@ufmg.br*

- **Background** A general view in the study of pollination syndromes is that floral traits usually represent convergent floral adaptations to specific functional pollinator groups. However, the definition of convergence is elusive and contradictory in the literature. Is convergence the independent evolution of either the *same* trait or *similar* traits with the same function? A review of the concept of convergence in developmental biology and phylogenetic systematics may shed new light in studies of pollination syndromes.
- **Scope** The aims of this article are (1) to explore the notion of convergence and other concepts (analogy, homoplasy and parallelism) within the theory and practice of developmental evolution and phylogenetic systematics; (2) to modify the definitions of syndromes in order to embrace the concepts of analogy and convergence; (3) to revisit the bat pollination syndrome in the context of angiosperm phylogeny, with focus on the showy 'petaloid' organs associated with the syndrome; (4) to revisit the genetic-developmental basis of flower colour; (5) to raise evolutionary hypotheses of floral evolution associated with the bat pollination syndrome; and (6) to highlight some of the current frontiers of research on the origin and evolution of flowers and its impact on pollination syndrome studies in the 21st century.
- **Conclusions** The inclusion of the concepts of analogy and convergence within the concept of syndromes will constitute a new agenda of inquiry that integrates floral biology, phylogenetic systematics and developmental biology. Phyllostomid and pteropodid bat pollination syndrome traits in eudicots and monocots represent cases of analogous and convergent evolution. Pollination syndromes are a multivariate concept intrinsically related to the understanding of flower organogenesis and evolution. The formulation of hypotheses of pollination syndromes must consider the phylogenetic levels of universality for both plant and animal taxa, flower development, genetics, homology and evolution, and a clear definition of evolutionary concepts, including analogy, convergence, homoplasy and parallelism.

Key words: Analogy, convergence, developmental biology, flower colour, flower development, flower evolution, homoplasy, parallelism, phylogenetic systematics.

How does one 'test' the pollination syndromes? This is not obvious, which is probably one reason for the paucity of tests! As we see it, there are three steps. First, one must define what one means by the syndromes. Secondly, one must make the syndromes operational in order to test them quantitatively. Finally, one must decide what properties or predictions of the syndromes are the most important one to scrutinize.

(Ollerton *et al.*, 2009, p. 1471).

What is the ancestral pollination syndrome? How often have shifts in pollination syndrome occurred? Is there a recurring shift directionality? Are there any reversals? Are some syndromes more likely to shift than others?

(Dellinger, 2020, p. 1205)

INTRODUCTION

Pollination syndromes are suites of floral traits related to the attraction and utilization of a particular group of animal agents as pollinators, so that a correlation among multiples traits across independent evolutionary events is expected (Fenster *et al.*, 2004). Commonly recorded floral traits include flower colour and scent, flower orientation, flower size and symmetry, overall corolla shape, position of sexual organs, timing of anthesis, reward type, floral exposure from foliage, sturdiness, subtler quantitative colour differences (e.g. UV patterning), scent bouquets, and nectar composition (Raguso *et al.*, 2003; Ollerton *et al.*, 2009; Reynolds *et al.*, 2009; Rosas-Guerrero *et al.*, 2014; Dellinger, 2020). Among them, colour, reward, scent and floral shape have been used most often to justify syndrome expectations (Dellinger, 2020). The floral traits are likely to determine pollinator-mediated selection and capture differences in activity patterns, sensory attributes, dietary preferences, morphology and the behaviour of the pollinator (Fenster *et al.*, 2004; Dellinger, 2020). Current studies on pollination syndromes have identified 11 functional groups: bat, bee, beetle, bird, butterfly, carrion fly, fly, long-tongued fly, moth, non-flying mammal and wasp (Rosas-Guerrero *et al.*, 2014; Dellinger, 2020). In this way, a pollination syndrome is intrinsically associated with a functional pollinator group, which is defined as pollinators who select for an equivalent combination of floral

traits, while distinct functional groups will select for distinct trait combinations (Fenster *et al.*, 2004).

A global test of the pollination syndrome hypothesis showed that the hypothesis as classically articulated does not successfully represent the diversity of floral phenotypes or predict the pollinators of most studied plant species (Ollerton *et al.*, 2009). In contrast, Dellinger (2020), in her review of pollination syndrome studies in the 21st century, endorsed the view that pollination syndromes constitute a robust concept to accurately delimit plant–pollinator relationships at large and small scales.

Sinnott-Armstrong *et al.* (2022) reviewed the concept of syndromes, recognizing it in two primary arenas: (1) macroevolution: the independent evolution of traits onto a phylogenetic hypothesis; and (2) community ecology: species classification into distinct syndromes based on their trait combinations. In order to avoid theoretical and practical confusion, they contrasted two definitions of syndromes: (1) *Adaptive syndrome*, which has three features: (a) convergent evolution of (b) multiple traits (c) adapted to a particular driver; and (2) *Trait syndrome*, which has two of these three criteria, namely (a) convergent evolution of (b) multiple traits (Sinnott-Armstrong *et al.*, 2022, p. 4).

In the case of pollination syndromes, a general view is that floral traits usually represent convergent floral adaptations to specific functional pollinator groups (Fenster *et al.*, 2004; Schiestl and Johnson, 2013; Sobel and Streisfeld, 2013; Rosas-Guerrero *et al.*, 2014; Dellinger, 2020). Yet the definition of convergence or convergent evolution is elusive and contradictory in the literature. For instance, Fenster *et al.* (2004, p. 376) asked: 'How, then, can we reconcile this apparent paradox of diverse visitors at flowers with our observations of widespread convergence in floral traits?' According to Ollerton *et al.* (2009, p. 1471), 'Convergent evolution is a ubiquitous feature of the biosphere, as indicated by correlations between phenotype and ecology across distantly related taxa'. For Schiestl and Johnson (2013, p. 310): 'Unrelated plants pollinated by the same pollinators tend to exhibit convergence in their floral traits, including advertizing signals'. Dellinger (2020, p. 1194) said: 'Generally, pollination syndromes represent convergent floral adaptations to specific functional pollinator groups'. Although evoking floral convergence, these authors did not define categorically what convergence is. Differently, Sobel and Streisfeld (2013, p. 1; italics added) clearly stated: 'The independent evolution of the *same* trait among populations or species is known as phenotypic convergence'. By contrast, Ng and Smith (2016, p. 407; italics added) wrote: 'Phenotypic convergence, whereby distantly related species evolve *similar* traits, provides a unique opportunity to study naturally occurring evolutionary replicates'. Finally, for Sinnott-Armstrong *et al.* (2022, p. 1; italics added): 'One of the most striking and commonly studied phenomena in biology is that of convergent evolution, whereby distantly related species evolve *similar* phenotypes as adaptations to similar selective pressures'.

These elusive and contradictory definitions invite us to ask: is convergence the independent evolution of either the *same* trait or *similar* traits with the same function? The widespread use of the concept of convergence in the literature of floral biology may result in confusing comparative and evolutionary understanding. So, what is convergence indeed? The concept has been extensively revisited within the scope of both developmental evolution and phylogenetic systematics, resulting in competing and constructive interpretations (e.g. Haas and Simpson, 1946; Hennig, 1966; Patterson, 1982; Hall, 2007; Arendt and Reznick, 2008; Leander, 2008; Scotland, 2011), which will potentially shed new light on studies of pollination syndromes. Importantly, two or more structures are considered to be the *same* trait if they are phenotypically and genetically correspondent (= equivalent), whereas *similar* traits are structures that are not phenotypically correspondent, although they might be or not be genetically.

The main aim of this article is to provide a successful link among floral biology, developmental evolution and phylogenetic systematics in an attempt to guide studies of pollination syndromes. I will attempt to exemplify it through the integration of three subjects: (1) bat pollination and angiosperm phylogeny; (2) the origin and evolution of the perianth in angiosperms; and (3) flower colour as a model system for studies of plant evo-devo. In the first section, I explore the notion of convergent evolution and other concepts (analogy, homoplasy and parallelism) within the theory and practice of developmental evolution and phylogenetic systematics. Modified definitions of 'syndrome' are proposed, which embrace both analogy and convergence as distinct genetic-developmental and evolutionary phenomena. In the second section, I revisit the bat pollination syndrome in the context of angiosperm phylogeny, with focus on bat flowers. More specifically, I concentrate on the features of the showy 'petaloid' organs associated with the bat pollination syndrome. Since perianth corolla morphology is a trait traditionally considered to be associated with pollination syndromes, the third section deals with the origin and evolution of the perianth in angiosperms, showing the progress and challenges in understanding its developmental and evolutionary nature. Following this understanding, I criticize the naïve and widespread use of the terms 'corolla shape', 'corolla tube', 'open corolla', 'corolla colour' and 'petals' in studies of pollination syndromes, irrespective of theories of homology, analogy and convergence. In the fourth section, I revisit the genetic-developmental basis of flower colour and its potential impact on the discovery of analogous and convergent traits. The fifth section is a synthesis and application of the ideas presented in the previous ones, in which I raise evolutionary hypotheses of floral evolution associated with the bat pollination syndrome. I conclude by highlighting some of the current frontiers of research on the origin and evolution of flowers and its impact in pollination syndrome studies in the 21st century.

CONVERGENCE AND ANALOGY, WITH MODIFIED DEFINITIONS OF 'SYNDROME'

As shown above, there are elusive and contradictory definitions of convergence in pollination syndrome studies. I suppose that such a confusion is due to the long and dynamic history of the concept itself. It is beyond the scope of this section to present an extensive review of the concept. The argumentation I will present here is based on a critical analysis provided by Scotland (2011), who recognized the problem in the definition of two important concepts in evolutionary biology: convergence and parallelism. Both concepts have been interpreted as examples

of homoplasy, although in several distinct ways. The author (Scotland, 2011, p. 217) reviewed the following interpretations:

(1) homoplastic phenotypes are structurally correspondent in parallelism but non-correspondent in convergence (Patterson, 1982);
(2) homoplastic phenotypes in closely related taxa are parallelism but in distantly related taxa are convergence (Arendt and Reznick, 2008);
(3) homoplastic phenotypes have the same ancestral character states for parallelism but different ancestral character states for convergence (Leander, 2008); and
(4) parallelism comprises homoplastic phenotypes caused by the same underlying genetics resulting from an ancestral predisposition to evolve the same character states, whereas convergent phenotypes are caused by dissimilar genetics (Haas and Simpson, 1946).

By contrast, Arendt and Reznick (2008) also proposed to abandon the concept of parallelism and only adopt convergence to the independent evolution of a given phenotype. Subsequently, Scotland (2011, p. 219) proposed a new way:

> The criteria listed … to distinguish parallelism from convergence may be unsuccessful because they treat these two ideas as mutually exclusive alternatives. But what if parallelism and convergence are not regarded as alternatives, but rather that the parallel evolution of genetic traits represents one of several possible types of explanation of phenotypic convergence. Under this model the parallel

evolution of the same genetic traits can underpin and explain some – although not all – instances of phenotypic convergence.

In this way, Scotland (2011, Fig. 3, p. 218) originally linked convergence and parallelism with phenotype and genotype, respectively. Following his proposition, convergence means the independent (convergent) evolution of the *same* phenotypic trait controlled, in part, by the independent (parallel) evolution of the *same* genetic basis. Differently, the independent evolution of *similar* phenotypic traits controlled by the same or distinct genes represents analogy (Scotland, 2011). It is expected that analogous traits are regulated by distinct genes or genetic-regulatory pathways. But it has been reported that analogous phenotypes can be underpinned by the same pre-existing genetic regulatory circuits – a phenomenon called 'deep homology' (Shubin *et al.*, 2009, p. 818). Therefore, both convergence (*sensu* Scotland, 2011) and analogy can also be explained by deep homology (= latent and process homology; Ballego-Campos *et al.*, 2023; see also de Beer, 1971; Gilbert and Bolker, 2001).

Based on this brief review, there are several ways to define convergence, a central concept that is part of the concept of 'syndrome'. I sympathize with the definitions proposed by Haas and Simpson (1946) and Scotland (2011), as they link evolution, development and genetics. More precisely, I will follow Scotland (2011) and use hereafter the following comparative concepts and their respective definitions (Fig. 1):
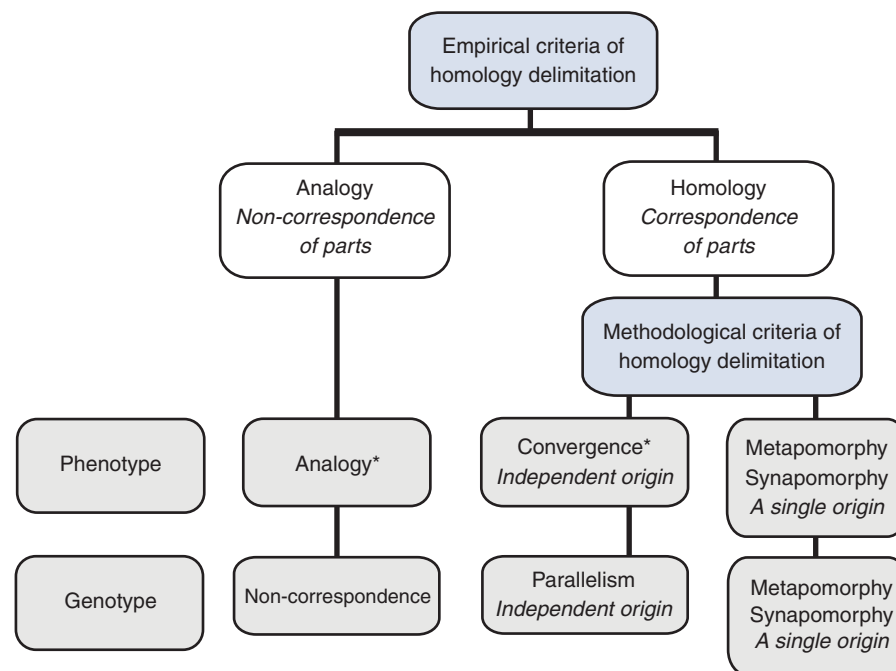

FIG. 1. The formulation of hypotheses of analogy, homoplasy (convergence and parallelism) and phylogenetic homology (synapomorphy and metapomorphy) based on empirical and methodological criteria of homology delimitation (modified from Scotland, 2011, Fig. 3, p. 218; and Ballego-Campos *et al.*, 2023, Fig. 2, p. 411). Note that the delimitation of analogy (= non-correspondence of parts) and homology (= correspondence of parts) depends on empirical criteria (genetic developmental causes, epigenetic causes, ontogeny timing, and position or topology), whereas the delimitation of phylogenetic homologies (metapomorphy and synapomorphy) and homoplasies (convergence and parallelism) depends on methodological criteria (parsimony, Bayesian and maximum likelihood analysis). Convergence and parallelism are associated with the phenotypic and genotypic levels, respectively. *Multiple hypotheses of analogy and convergence may constitute syndrome pollination traits grounded in a particular phylogenetic hypothesis.

(1) analogy: the phenomenon of independent evolution of similar phenotypes with the same function (Darwin, 1859) controlled by the same or distinct genetic regulatory basis (Shubin *et al.*, 2009; Scotland, 2011);

(2) homoplasy: the phenomenon of independent evolution of the same phenotype (convergence) and genotype (parallelism) (Scotland, 2011);

(3) convergence: the phenomenon of independent evolution of the same phenotype controlled by the same genetic regulatory basis (Scotland, 2011); and

(4) parallelism: the phenomenon of independent evolution of the same genotype (Scotland, 2011).

Since analogy and convergence constitute distinct phenomena, i.e. the independent origin of similar and the same traits, respectively, to say that all events of independent evolution are convergence (e.g. Arendt and Reznick, 2008) is inconsistent with these two distinct patterns of phenotypic development and evolution. In line with this, I propose that the definitions of syndromes be modified in order to embrace analogy and convergence:

(1) adaptive syndrome, which has three features: (a) analogous and/or convergent evolution of (b) multiple traits (c) adapted to a particular driver (modified from Sinnott-Armstrong *et al.*, 2022, p. 4).

(2) trait syndrome, which has two of these three criteria, namely that there has been (a) analogous and/or convergent evolution of (b) multiple traits (modified from Sinnott-Armstrong *et al.*, 2022, p. 4).

In addition to the concepts of 'syndrome', there is discussion in the literature about the concept of 'trait'. A recent review provided by Dawson *et al.* (2021) recognized distinct definitions of 'trait' and 'functional trait' across distinct biological areas and study systems (e.g. individual organism, taxa and biome). Yet Dawson *et al.* (2021, p. 16 441) proposed a return to the basics, endorsing a simplified version that could potentially satisfy all areas of biology, as follows:

A trait is a measurable characteristic (morphological, phenological, physiological, behavioural, or cultural) of an individual organism that is measured at either the individual or other relevant level of organization.

Such a definition contemplates the traits assessed in studies of pollination syndromes (see Dellinger, 2020) and it is adopted here.

Sinnott-Armstrong *et al.* (2022, Fig. 1, p. 5) proposed a schematic illustration of the three main features of syndromes and several approaches to deal with syndromes inquiry, including: (1) convergent evolution of traits: adequate character and taxa samples across phylogeny, an explicit 'test' for convergence, and identification of independent origin of trait combination; (2) multiple traits: sample trait space across the community and phylogeny, data collection of relevant traits, and data collection at the appropriate scale; and (3) adaptation: conducting ecological observations, experimental research, manipulation of the system, and assessment of correlated evolution with a phylogenetic hypothesis. As the pollination syndrome hypothesis depends on phylogenetic analysis, I propose that the delimitation of syndrome traits follows the logical delimitation of characters in phylogenetic systematics, including neomorphic versus transformational characters (Sereno, 2007; Assis, 2019), characters versus character states (Wagner, 2007) and organs versus attributes (DiFrisco *et al.*, 2022). In line with this, I stimulate researchers to: (1) indicate the taxonomic lineages (i.e. species and monophyletic groups) of plants and animals involved in the syndrome; (2) use and compare competing phylogenetic hypotheses and relative evidence; and (3) present clear definitions of both comparative (e.g. analogy, convergence, homoplasy and parallelism) and syndrome concepts they will adopt in their studies.

REVISITING THE BAT POLLINATION SYNDROME

The bat pollination syndrome classically includes 'nocturnal anthesis, drab coloration (i.e. white and green), musty smell, flowers often located on branches or tree trunks (cauliflory) or suspended on long stalks (flagelliflory), and tubular or radially symmetrical flowers, often of the "shaving brush" type, that produce relatively large amounts of hexose-rich nectar' (Fleming *et al.*, 2009, p. 1020). In more detail, Fleming *et al.* (2009, p. 1023) divided the flowers into three categories based on shape: (1) shaving brush or stamen ball with many projecting stamens (Fig. 2A); (2) bell-shaped with the corolla forming a tube (Fig. 2B); and (3) cup-shaped with an 'open corolla' (Fig. 2C). Two phylogenetically distant clades of bats are pollinators:

FIG. 2. Three categories of bat-pollinated flowers. (A) Shaving brush or stamen ball with many projecting stamens; *Abutilon regnellii* (Malvaceae) visited by *Anoura caudifer* (Phyllostomidae). (B) Bell-shaped with the corolla forming a tube; *Chelonanthus alatus* (Gentianaceae) visited by *Glossophaga soricina* (Phyllostomidae). (C) Cup-shaped with an open corolla; *Passiflora ovalis* (Passifloraceae) visited by *Anoura caudifer* (Phyllostomidae). Photograph credits: Marlies Sazima and Ivan Sazima.

(1) the New World phyllostomids, which are specialized nectar-feeders that usually visit tubular flowers produced by epiphytes and shrubs; and (2) the Old World pteropodids that visit edna shaving brush flowers produced by trees (Fleming *et al.*, 2009). According to these authors, bat pollination has been reported for about 250 genera, 67 families and 28 orders of angiosperms. Using a hypothetical phylogeny of the angiosperms (Soltis *et al.*, 2005), they estimated that bat pollination evolved independently in about 85 % of the angiosperm families, and that of the 28 orders pollinated by bats, only eight (29 %) contain taxa visited by species of the two clades of bats.

Despite enumerating different floral traits relative to phyllostomid and pteropodid pollination, Fleming *et al.* (2009) endorsed the heuristic value of the concept of bat pollination syndrome. Considering the distinct flower categories associated with these two distinct pollinator clades, it seems that rather than being restricted to a single and general concept of bat pollination syndrome (e.g. Faegri and van der Pijl, 1979), it would be more rewarding to consider two bat pollination syndromes: phyllostomid and pteropodid. However, before accepting this, it is necessary to assess if the floral traits associated with these two putative syndromes are analogous and/or convergent and adapted to a particular driver. The two bat clades seem to represent specific drivers. But what about the floral traits? The expressive independent evolution of bat pollination with an angiosperm phylogenetic hypothesis (Soltis *et al.*, 2005) may suggest that the associated floral traits also evolved independently (Fleming *et al.*, 2009). But are they analogous and/or convergent traits? Strikingly, could some of the traditional bat pollination floral traits be plesiomorphic traits, which do not satisfy the concepts of adaptive and trait syndrome? In order to infer this, it is necessary to assess the genetic-developmental and evolutionary nature of these traits. In the next sections, I will focus on the nature of the perianth and its colours.

ORIGIN AND EVOLUTION OF THE ANGIOSPERM PERIANTH

A flower may be interpreted from multiple points of view for artists, ecologists, developmental biologists and plant systematists, so leading to distinct scenarios (Assis, 2018). Usually, the most attractive flower component is the corolla. In her review of pollination syndrome, Dellinger (2020) showed that, among 244 articles recording floral traits, 52 (21.3 %) were based on the corolla. Traditionally, the corolla is defined by the set of petals, and the floral calyx by the set of sepals. The concept of petals means floral organs that are coloured or attractive, whereas sepals are generally green and dull. In addition, the corolla and the calyx constitute the inner and outer whorls of the perianth, respectively. However, these morphological characterizations are not rules, as noted by Ronse De Craene and Brockington (2013, p. 5):

the recognition of petals becomes problematic in cases where no clear distinction can be made between greenish sepals and showy petals, such as when both whorls are sepaloid (e.g. Juncaceae) or when the outer perianth whorl is petaloid and similar in appearance to the inner whorl (e.g. the 'monocotyledonous' perianth of Passifloraceae).

Furthermore, Ronse De Craene (2008, p. 302) highlighted:

The differentiation of the perianth in the core eudicots is obviously highly complex and statements about homology of petals appear to be at least 'shaky'. Petaloidy (viz. the possession of petal features such as pigmentation) is often confused with the presence of petals, as any organ such as staminodes, petals proper, sepals, or bracts can be brightly coloured and look like petals.

In terms of genetic control, there are four classes of homoeotic genes that, alone or in combination, underlie floral organ development: (1) A-function genes alone control the identity of sepals; (2) A- and B-function genes control the development of petals; (3) B- and C-function genes control the development of stamens; (4) C-function genes alone control the identity of carpels; and (5) E acts in combination with all these genes to determine organ identity (Coen and Meyerowitz, 1991; Honma and Goto, 2001). Accordingly, the genes can be expressed in different regions of the floral meristem, resulting in two petaloid floral whorls in monocotyledons and magnoliids. In terms of position, the petaloid outer whorl in monocotyledons is potentially homologous to the sepaloid outer whorl of others angiosperms, although in terms of genetic control they are not homologous. Therefore, the use of position and genetic control as criteria of homology delimitation may lead to distinct comparative hypotheses (De-Paula *et al.*, 2018; Ballego-Campos *et al.*, 2023).

In terms of evolutionary or historical derivation, the origin of the petals has been viewed from two scenarios: (2) bracteopetals and (2) andropetals (Endress, 1994; Friis *et al.*, 2006; Ronse De Craene, 2007, 2008; Ronse De Craene and Brockington, 2013). Yet a third and poorly discussed scenario is *de novo* origin (Albert *et al.*, 2002; Ronse De Craene, 2008). Traditionally, the bracteopetals occur usually in the spiral perianth and present bract-like features, including the breadth of primordia, chloroplast, three vascular traces and cellular structure (Ronse De Craene, 2008; Ronse De Craene and Brockington, 2013). Andropetals are organs with a narrow base, a single vascular trace, pigmentation of leucoplasts and chromoplasts, conical and elongated cells at the adaxial surface, and the presence of volatile oils (Ronse De Craene and Brockington, 2013). Despite these potential differences, there are practical challenges in the differentiation of bracteo- and andropetals (Ronse De Craene, 2007, 2008). With respect to the large angiosperm groups, it is hypothesized that magnoliids, monocots, Amborellales, Austrobayleiales, Nymphaeales and Illiciales present bracteopetals, whereas eudicots present andropetals (Endress, 1994; Friis *et al.*, 2006, Fig. 20, p. 283). However, Ronse De Craene (2007, 2008) and Ronse De Craene and Brockington (2013) have challenged the traditional view that most eudicots have andropetals (e.g. Endress, 1994; Friis *et al.*, 2006). According to these authors, petals in core eudicots present the same morphological features and structure as both sepals and bracts. Furthermore, changes of function in the eudicot perianth are associated with shifts in petaloidy to the other perianth whorl, or losses of the inner and outer whorls that can be secondarily compensated by the incorporation of bracts in the floral axes (Ronse De Craene, 2008). Evidence for andropetals in core eudicots include in a few taxa: (1) fusion

with the staminal tube (e.g. Molluginaceae or Caryophyllaceae); (2) the impossibility of differentiating petals from staminodes (e.g. Ranunculaceae, Dichapetalaceae, Theophrastaceae); and (3) a common stamen–petal primordium (e.g. Primulaceae, Plumbaginaceae, Rhamnaceae, Caryophyllales). Within the clade Caryophyllales, both bracteo- and andropetals may have evolved. In the case of the *Phytolacca* clade and *Portulaca* clade, the outer perianth whorl (i.e. the calyx) is coloured like petals (Ronse De Craene, 2007, 2008).

In sum, the problem of homologizing the perianth organs was clearly recognized by Ronse De Craene and Brockington (2013, p. 7; see also De-Paula *et al.*, 2018; Ballego-Campos *et al.*, 2023) as follows:

> we have explored the definition and homology of the angiosperm petal from the perspective of various criteria: topology, historical derivation, morphology, and developmental genetics. It is evident that none of these criteria, either alone or in combination, provide a unifying principle with which to homologise the petal. This is perhaps an unsurprising conclusion, because at the level of angiosperms, petals are probably non-homologous structures that have attained an analogous showy petaloid condition in order to perform a common function in the attraction of pollinators.

These theoretical and practical considerations stimulate us to raise some fundamental questions about studies of pollination syndromes. (1) How will floral homology assessment change our view of the evolution of syndromes? (2) How should we deal with the formulation of hypotheses concerning the origin and evolution of showy petaloid organs based on competing criteria of homology delimitation (e.g. topology, historical derivation, morphology and developmental genetics)? (3) Which showy petaloid organs are analogous? (4) Which ones are convergent? (5) Which phenotypic components make the showy petaloid organs? (6) Which phenotypic components are analogous syndrome traits? (7) Which ones are convergent?

THE EVO-DEVO OF FLOWER COLOR

Colour, shape, nectar guides, scent and microscopic structures are phenotypic components of the distinct showy petaloid organs of angiosperms involved in pollination syndromes (Moyroud and Glover, 2017; Nadot and Carrive, 2021). In relation to colour, three classes of flower pigments are known: (1) anthocyanins; (2) betalains; and (3) carotenoids. Anthocyanins, broadly distributed in angiosperms, are hydrophilic pigments that belong to the well-known flavonoid biosynthetic pathway, and give rise to blue, purple and red (Grotewold, 2006; Tanaka *et al.*, 2008). They are synthesized in the cytosol and accumulate in the vacuoles (Grotewold, 2006; Tanaka *et al.*, 2008). Intermolecular copigmentation results from the interaction between anthocyanins with other non-coloured flavonoids (e.g. flavonols), so that the latter provide 'depth' to several white or cream organs (Grotewold, 2006). Biosynthetic pathways, gene expression, cellular location and vacuolar pH are responsible for colouring anthocyanin pigments (Grotewold, 2006). Betalains are also hydrophilic and nitrogen-containing compounds that accumulate in the vacuoles as glycosides, and give

rise to yellow, orange-red to violet (Grotewold, 2006; Tanaka *et al.*, 2008). In plants, they are exclusively found in the order Caryophyllales, with reversion to anthocyanins in the families Caryophyllaceae and Molluginaceae (Brockington *et al.*, 2011, 2015). Betalains and anthocyanins share part of their biosynthetic pathways and are mutually exclusive, although they may combine with carotenoids (Grotewold, 2006; Nadot and Carrive, 2021). Carotenoids are lipophilic molecules synthesized in the chromoplasts (Grotewold, 2006; Tanaka *et al.*, 2008). They are yellow, orange and orange-red, and combining with red or purple anthocyanin results in brown and bronze hues that any pigment cannot provide by itself (Grotewold, 2006). Importantly, in terms of biosynthesis, the colours or the loss of pigmentation (i.e. white and pale) resulting from these three distinct pathways are analogous to each other, even though they are visually undistinguishable (e.g. white, yellow and red). Such an understanding is a cue to the inference of colour analogy and convergence in pollination syndrome studies.

Although the biosynthetic pathways of flower pigments are well known (mostly for anthocyanins), an emerging and fascinating area is the evo-devo of flower pigmentation, which represents the genetic and molecular basis of the evolutionary transitions in flower colour (Rausher, 2008; Sobel and Streisfeld, 2013). Importantly, independent changes in the same gene, involving the same substitutions (i.e. parallelism), result in convergent phenotypes, whereas changes in distinct genes (i.e. non-correspondence) result in analogous phenotypes. Furthermore, deep homology also explains analogy (Shubin *et al.*, 2009). Flower colour changes within populations, species and clades also result from phenotypic plasticity, genetic drift, indirect selection, or as a direct target of selection via pollinator visitation, physiological features and pleiotropic consequences (Sobel and Streisfeld, 2013; Nadot and Carrive, 2021). Hence, the evo-devo of flower colour is a fundamental area of research to delimit analogous and convergent traits in pollination syndrome inquiry.

Sobel and Streisfeld (2013), for instance, substantially interested in the independent evolution of mutations (parallelism) underlying the independent evolution (convergence) of gains and losses of anthocyanin pigmentation, presented a set of studies that mapped the genetic basis involved in these evolutionary changes. They showed that different genes control the white colour of the flowers of *Petunia axillaris* (Solanaceae) (*R2R3-MYB* genes) (Quattrocchio *et al.*, 1999), *Ipomoea purpurea* (Convolvulaceae) (*R2R3-MYB* and *CHS* genes) (Habu *et al.,* 1998; Chang *et al.*, 2005) and *Parrya nudicaulis* (Brassicaceae) (*CHS* gene) and *Mimulus lewisii* (Phrymaceae) (*DFR* gene) (Wu *et al.*, 2013). Hence, the white colour is an analogy shared by these species. In line with these findings, Sobel and Streisfeld (2013) highlighted the need to continue dissecting the genetic basis of independent evolution across phylogenetic scales, including the further development and evolution of flower colour as an essential model trait in evo-devo.

Another constructive study was conducted by Ng and Smith (2016), who hypothesized the independent evolution of colour in Solanaceae via alternative biochemical pathways. The authors investigated the evolutionary patterns of red flowers underpinned by anthocyanin and carotenoid pathways using large-scale data mining and new sequence data to hypothetically reconstruct the phylogeny of 1341 species Solanaceae. For

them, all independent evolution is 'Phenotypic convergence, whereby distantly related species evolve *similar* traits' (Ng and Smith, 2016, p. 407; italics added). In this way, Ng and Smith (2016) found that red-flowered species used distinct pathways to make red as follows: (1) 12 species used exclusively anthocyanin; (2) two species exclusively carotenoids; and (3) 13 species both pigments. The character evolution reconstruction supported the utilization of anthocyanins to make red flowers at least 11 times, the utilization of carotenoids twice, and the dual use of both pigments 12 times. In turn, they delimit three levels of convergence: (1) red-anthocyanin flowers; (2) red-carotenoid flowers; and (3) red-anthocyanin-carotenoid flowers.

I see the Solanaceae problem from a different perspective. First, as previously presented, there are two scenarios of independent evolution of phenotypes: analogy and convergence. Second, in order to avoid terminological confusion, it is critical to note that what Ng and Smith (2016) called 'convergence' I call 'analogy' in the present article. In line with this, the independent evolution of red flowers in Solanaceae may represent cases of analogy (i.e. *similar* phenotypes controlled by the same or different genotypes) and convergence (the *same* phenotypes controlled by the same genotypes). In other words, red flowers exclusively originating from distinct (anthocyanin or carotenoid) pathways are phenotypically and genetically analogous to each other, whereas red flowers resulting from the same biosynthetic pathway may be analogous or convergent depending on the genetic regulatory basis (e.g. Sobel and Streisfeld, 2013). Because of the lack of information at the genetic-molecular level, the hypothesis of analogous and convergent evolution of red-anthocyanin flowers in Solanaceae cannot be effectively supported. The same is true for red-carotenoid flowers. Indeed, Ng and Smith (2016) concluded that increasing knowledge of the biochemistry and function of plant pigment pathways will provide a great opportunity for identifying the genetic-molecular changes underpinning red flower evolution across Solanaceae and testing for pleiotropic effects of colour transitions.

BAT POLLINATION SYNDROME AND ANGIOSPERM PHYLOGENY

Based on the points previously discussed and on a list of plant families pollinated by bats (Fleming *et al.*, 2009, pp. 1026–1027), I present in Table 1 the showy petaloid organs relative to bat pollination and their putative evolutionary derivations, i.e. from either bracts or stamens. Some theoretical and practical points are important. First, showy petaloid organs means they are coloured and attractive. Hence, it is necessary to note that both organ and colour constitute distinct phenotypic elements of character statements. Organ is a neomorphic character with two states (absent versus present), whereas colour is the variable (or an attribute) of a transformational character including two or more states (Sereno, 2007; Wagner, 2007; Di-Frisco *et al.*, 2022). Variables or attributes are essentially dependent on the organ or body part – 'there is no colored phenotype without a body part to have that color' (DiFrisco *et al.*, 2022, p. 8). Yet the same organ or body part in two or more organisms may have distinct states (e.g. blue, red, white) of a variable or attribute. By contrast, neomorphic characters (e.g. organs) are separable from each other, and they can be or not be developmentally

individualized (DiFrisco *et al.*, 2022). In this way, analogous, homologous and convergent organs might present analogous, homologous or convergent colours (or other attributes), depending on the evolution of the genetic-developmental regulatory systems and biosynthetic pathways (carotenoid, anthocyanin and betalain) underlying flower colour, and the angiospermic phylogenetic levels of analysis as well. Second, despite the practical challenges of distinguishing bracteo- and andropetals, as well as establishing homology relationships of the perianth organs (Ronse De Craene and Brockington, 2013; De-Paula *et al.*, 2018; Ballego-Campos *et al.*, 2023), I endorse that all these fundamentally comparative problems are constructive in formulating and refreshing pollination syndrome hypotheses. Hence, the origins of the floral organs presented in Table 1 must be continuously assessed through new evidence. Third, distinct organs have been usually called 'corolla' (or 'petals'), and such an essentialist interpretation of the corolla as a pollination syndrome trait, irrespective of theories of homology, analogy and convergence, is challenged here. Moreover, in order to satisfy the concepts of syndrome (modified from Sinnott-Armstrong *et al.*, 2022), pollination syndrome studies need to be critically supported by comparative and phylogenetic analyses in terms of competing evolutionary hypotheses of relationship and floral character evolution (cf. Assis, 2018), as well as underlying criteria of homology delimitation (cf. Scotland, 2011; Ronse De Craene and Brockington, 2013; De-Paula *et al.*, 2018; Ballego-Campos *et al.*, 2023).

With respect to bat pollination, the organs constituting what the authors (e.g. Fenster *et al.*, 2004, p. 376; Fleming *et al.*, 2009, p. 1023; Moyroud and Glover, 2017, p. 350; Dellinger, 2020, p. 1201) have usually called 'corolla' correspond to analogous and convergent organs, depending on the phylogenetic level of inquiry. In monocots (Fleming *et al.*, 2009, Fig. 3, p. 1021), they correspond to both outer and inner perianth whorls putatively derived from bracts, although in Cannaceae and Zingiberaceae they are elements of the androecium itself. In eudicots (Fleming *et al.*, 2009, Fig. 4, p. 1022), they represent the inner perianth whorl putatively derived from bracts and stamens, although in Nyctaginaceae and Proteaceae they are the outer bract-derived perianth whorl. In Cactaceae, they are putatively bract-derived and spirally arranged. Additionally, the floral tube in some monocots and asterids usually constitutes the hypanthium (i.e. the tube formed by the fusion of distinct floral whorls; Ronse De Craene, 2010), which is developmentally analogous in both clades (Ronse De Craene and Brockington, 2013) (Table 1). Therefore, considering the distinct historical, topological and developmental origins of both showy petaloid organs and floral tubes, hypotheses of bat pollination syndrome are associated with the analogous evolution of organs in monocots (Fig. 3A, B) and eudicots (Fig. 3C, D). Yet it is still necessary to assess if the variables or attributes of attraction (e.g. colour and scent) found in these organs evolved through analogous or convergent evolution (see below).

Within specific lineages, where the perianth parts are potentially the same (homologous), it is necessary to hypothesize if they evolved once (synapomorphies or metapomorphies; Assis, 2017) or multiple times (convergences). For instance, it has been hypothesized that the tubular inner perianth whorl (i.e. 'corolla tube'; Fleming *et al.*, 2009, p. 1023) (Figs 2B and 3C, D) in eudicots is an apomorphic state, whereas the open inner

TABLE 1. *Putative evolutionary origins (i.e. historical derivations) of the showy petaloid organs in bat-pollinated plant families. Bat-pollinated taxa extracted from Fleming et al. (2009, p. 1026–1027)*

Lineage	Order	Family	Showy petaloid organs or whorls of organs	Origin of outer whorl of perianth organs	Origin of inner whorl(s) of perianth organs	References
Magnoliids	Laurales	Lauraceae	Outer and inner perianth whorls (united with each other and the staminal whorls, forming a hypanthium)	Bracteal Androecial	Bracteal Androecial	Ronse de Craene and Brockington (2013) Chanderbali *et al.* (2006)
	Magnoliales	Annonaceae	Two inner perianth whorls (free from each other; and organs free from each other)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
Monocots	Arecales	Arecaceae	Outer and inner perianth whorls (free from each other; and organs of each whorl free from each other)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
	Asparagales	Agavaceae	Outer and inner perianth whorls (united with each other and the staminal whorls, forming a hypanthium)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
		Amaryllidaceae	Outer and inner perianth whorls (united with each other and the staminal whorls, forming a hypanthium)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
		Asphodelaceae	Outer and inner perianth whorls (forming or not a hypanthium)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
		Asteliaceae	Outer and inner perianth whorls (united with each other and the staminal whorls, forming a hypanthium)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
		Xanthorrhoeaceae	Outer and inner perianth whorls (free from each other; and organs of each whorl free from each other)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
	Pandanales	Pandanaceae	Bracts	N.A.	N.A.	N.A.
		Velloziaceae	Outer and inner perianth whorls (united or not with each other and the staminal whorls, forming a hypanthium)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
	Poales	Bromeliaceae	Outer and inner perianth whorls (united or not with each other and the staminal whorls, forming a hypanthium)	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
	Zingiberales	Cannaceae	Staminal whorls	N.A.	N.A.	N.A.
		Heliconiaceae	Bracts; outer and inner perianth whorls	Bracteal	Bracteal	
		Musaceae	Bracts; outer and inner perianth whorls	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
		Strelitziaceae	Outer perianth whorl	Bracteal	Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283)
Basal eudicots	Caryophyllales	Cactaceae	Outer perianth (organs free from each other)	Androecial Bracteal	N.A.	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283) Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Nyctaginaceae	Bracts; outer perianth (organs usually united with each other)	Androecial Bracteal	N.A.	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283) Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Proteales	Proteaceae	Outer perianth whorl (united with the staminal whorl, forming a hypanthium)	Bracteal	N.A.	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Santalales	Loranthaceae	Inner perianth whorl (united with the staminal whorl, forming a hypanthium)	Androecial Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)

TABLE 1. *Continued*

Lineage	Order	Family	Showy petaloid organs or whorls of organs	Origin of outer whorl of perianth organs	Origin of inner whorl(s) of perianth organs	References
Rosids	Brassicales	Capparaceae	Inner perianth whorl	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008) Ronse de Craene and Brockington (2013)
		Salvandoraceae	Inner perianth whorl	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Celastrales	Celastraceae	Inflorescence; inner perianth whorl	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Cucurbitales	Cucurbitaceae	Inner perianth whorl (organs usually united with each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Fabales	Fabaceae	Inner perianth whorl (organs free from or united with each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Geraniales	Geraniaceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Malpighiales	Caryocaraceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Chrysobalanaceae	Inflorescence; inner perianth whorl (organs free from or united with each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Clusiaceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Euphorbiaceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Passifloraceae	Inner perianth whorl (organs usually free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Rhizophoraceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Salicaceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Malvales	Malvaceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)

TABLE 1. *Continued*

Lineage	Order	Family	Showy petaloid organs or whorls of organs	Origin of outer whorl of perianth organs	Origin of inner whorl(s) of perianth organs	References
	Myrtales	Combretaceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Lythraceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Melastomataceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Myrtaceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Onagraceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Vochysiaceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Oxalydales	Elaeocarpaceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Rosales	Moraceae	Outer perianth whorl (organs free from each other)	Bracteal	N.A.	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Rhamnaceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Rosaceae	Inner perianth whorl (united with both outer perianth whorl and staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Sapindales	Anacardiaceae	Inner perianth whorl (usually united with the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Meliaceae	Inner perianth whorl (usually united with the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Sapindaceae	Inner perianth whorl (organs free from each other)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
Asterids	Apiales	Araliaceae	Inner perianth whorl (organs usually free from each other at maturity)	Bracteal	Androecial Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)

TABLE 1. *Continued*

Lineage	Order	Family	Showy petaloid organs or whorls of organs	Origin of outer whorl of perianth organs	Origin of inner whorl(s) of perianth organs	References
	Asterales	Asteraceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Campanulaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Ericales	Ericaceae	Inner perianth whorl (organs united with each other and usually with the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Marcgraviaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Polemoniaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Sapotaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Gentianales	Apocynaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Gentianaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Loganiaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Rubiaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Lamiales	Acanthaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Bignoniaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Gesneriaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial / Bracteal	Endress (1994); Friis *et al.* (2006, Fig. 20, p. 283); Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)

Table 1. *Continued*

Lineage	Order	Family	Showy petaloid organs or whorls of organs	Origin of outer whorl of perianth organs	Origin of inner whorl(s) of perianth organs	References
		Lamiaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994), Friis *et al.* (2006), Fig. 20, p. 283; Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Scrophulariaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994), Friis *et al.* (2006), Fig. 20, p. 283; Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Verbenaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994), Friis *et al.* (2006), Fig. 20, p. 283; Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
	Solanales	Boraginaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994), Friis *et al.* (2006), Fig. 20, p. 283; Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Convolvulaceae	Inner perianth whorl (organs united with each other and the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994), Friis *et al.* (2006), Fig. 20, p. 283; Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)
		Solanaceae	Inner perianth whorl (organs united with each other and usually with the staminal whorl, forming a hypanthium)	Bracteal	Androecial Bracteal	Endress (1994), Friis *et al.* (2006), Fig. 20, p. 283; Ronse de Craene (2007, 2008); Ronse de Craene and Brockington (2013)

N.A., not applicable.

perianth (i.e. 'open corolla'; Fleming *et al.*, 2009, p. 1023) whorl (Fig. 2A) is a plesiomorphic one or reversion (Ronse De Craene, 2010). In line with this, we cannot regard the open inner perianth whorl as a convergent trait (unless it is a reversion). In other words, although Fleming *et al.* (2009) relates open flowers to pteropodid pollination, such a feature cannot be considered a syndrome trait, as it is a symplesiomorphic state within the eudicots (cf. Ronse De Craene, 2010) also associated with phyllostomid and other modes of pollination (cf. Sazima *et al.*, 1999; Queiroz *et al.*, 2020). At the same time the floral tube represents an apomorphic state for the asterids (Ronse De Craene, 2010); it represents a plesiomorphic state within the clade, which is also associated with distinct modes of pollination. Indeed, bat pollination has evolved from other modes (e.g. bee, butterfly, moth and hummingbird pollination) (Fleming *et al.*, 2009 and references therein), and all of them share the floral tube as a symplesiomorphic feature within asterids. Hence, it is more appropriate to say that what evolved multiple times along the phylogeny of asterids were both flower tube shapes and colours (e.g. Acanthaceae: Tripp and Manos, 2008; Gesneriaceae: Martén-Rodríguez *et al.*, 2009; Lobeliaceae: Knox *et al.*, 2008). With respect to shaving brush flowers, they are not exclusively associated with bat pollination. In the tribe Pachycereeae (Cactaceae), for instance, bat pollination is a hypothetical ancestral mode that may have been derived from bee pollination (Wallace, 2002; Fleming *et al.*, 2009). In this case, shaving brush flowers represent a symplesiomorphic state in Cactaceae shared by bat and bee pollination. In other angiosperm groups, however, they might be analogously or convergently associated with bat pollination syndrome, but further investigation is necessary.

The occurrence of white, pale and greenish flowers in 67 families and 28 orders of angiosperms pollinated by bats (Fleming *et al.*, 2009) leads us to a constructive question: are these colours analogous or convergent syndrome traits within and among bat-pollinated angiosperm lineages? To answer this question it is necessary to investigate the biosynthetic pathways and genetic-molecular basis of the colour. However, the understanding of syndromes at the genomic level is still incipient. The vast majority of biological systems and plant–pollinator interactions have not been addressed within the scope of developmental evolution. In her review of pollination syndrome, Dellinger (2020) showed that, among 346 articles on the subject, only 20 (5.8 %) addressed syndromes in the genomic dimension (e.g. evolution of colour genes). With respect to the bat pollination syndrome, some few inferences can be made.

Tripp and Manos (2008) studied the evolution of pollination systems in the large genus *Ruellia* (Acanthaceae) on the basis of phylogenetic analyses, morphological ordinations, ancestral state reconstruction and character mapping reconstruction. They revealed key patterns in the direction and lability of floral characters associated with pollination. The evolutionary hypothesis is that a hummingbird ancestral syndrome switched to new pollination modes, with repeated evolution of bee- and insect-adapted species through distinct developmental means and morphological histories. In addition, bats and hawkmoths presented as specialized evolutionary dead ends. The authors (p. 1727) strikingly highlighted that 'Species that have dramatically reduced or have lost their floral pigmentation are probably evolutionary dead-ends with respect to new pollination

systems. … Once a character is lost, here, red or purple floral pigmentation, it cannot be regained'. An explanation for this pattern in *Ruellia* and other angiosperms (e.g. *Ipomoea* sect. *Mina*; Zufall and Rausher, 2004) is the irreversibility of changes in the underlying anthocyanin pathway. Possibly in line with these findings, Fleming *et al.* (2009) cited 14 examples of the evolution of bat pollination from other modes in 12 angiosperm families – Acanthaceae (Tripp and Manos, 2008), Agavaceae (Good-Avila *et al.*, 2006), Bromeliaceae (Endress 1994; Benzing, 2000), Cactaceae (Wallace, 2002), Fabaceae (Luckow and Hopkins, 1995), Gesneriaceae (Perret *et al.*, 2007; Martén-Rodríguez *et al.*, 2009), Lecythidaceae (Mori and Boeke, 1987; Mori *et al.*, 2007), Lobeliaceae (Knox *et al.*, 2008), Malvaceae (Baum *et al.*, 1998; Nyffeler and Baum, 2001), Passifloraceae (Hansen *et al.*, 2006), Polemoniaceae (Prather, 1999) and Strelitziaceae (Kress *et al.*, 1994) – but not the other way around. Yet eight of these studies were based on phylogenetic analyses, whereas the others are equivocal pending species-level phylogenetic analyses (Fleming *et al.*, 2009). By contrast, a recent study (Karimi *et al.*, 2022) in the African baobab (*Adansonia digitata*) (Malvaceae) showed hawkmoth pollination as a derived mode from bat pollination. Assessment of whether the white and pale colours are analogies and convergences within and among all these families depends on further biosynthetic and genetic-molecular analyses.

Differently across Solanaceae, rare red flowers have been identified as an evolutionary dead end derived independently from blue, purple and white, and a potential explanation is 'nonequilibrium dynamics, with selection for red flowers, or the ability to produce red pigments, arising only recently, leaving the number of taxa with this state far lower than expected' (Ng and Smith, 2016, p. 414). Interestingly, in Acanthaceae, white colour has been, otherwise, hypothesized as a dead end, explained by the irreversibility of changes in the underlying anthocyanin pathway (Tripp and Manos, 2008). The contrasting colour dead-end patterns in Acanthaceae and Solanaceae represent distinct evolutionary and genetic-developmental changes within the same anthocyanin biosynthetic pathway. Furthermore, singular pollinator mediations and pleiotropic and selective causes may explain this mosaic evolution (i.e. heterobathmy; Hennig, 1966; Rieppel, 2023) of flower colour in asterids.

Considering that betalain biosynthesis is a metapomorphy for the order Caryophyllales, in which the families Cactaceae and Nyctaginaceae are included, it is expected that the derived white and pale floral colours found in these families are analogous in relation to the white and pale colours found in the other bat-pollinated families. Because of the deep time of phylogenetic divergence between eudicots and monocots, it would be expected that they share non-correspondent genotypes controlling analogous flower colours. This expectation is grounded on the analysis of distinct genes controlling the white flower colour in eudicot species (Sobel and Streisfeld, 2013), including *Petunia axillaris* (Solanaceae) (*R2R3-MYB* genes) (Quattrocchio *et al.*, 1999), *Ipomoea purpurea* (Convolvulaceae) (*R2R3-MYB* and *CHS* genes) (Habu *et al.,* 1998; Chang *et al.*, 2005), *Parrya nudicaulis* (Brassicaceae) (*CHS* gene) and *Mimulus lewisii* (Phrymaceae) (*DFR* gene) (Wu *et al.*, 2013). Differently, Arendt and Reznick (2008) showed examples of closely related species and populations evolving similar phenotypes via distinct genes,

whereas distantly related species with similar phenotypes share the same genes. Indeed, *R2R3-MYB* genes have also been identified in monocots and some magnoliids (e.g. Muñoz-Gómez *et al.*, 2021), constituting a widespread ancestral genetic regulatory circuit across angiosperm lineages.

The bat pollination syndrome involves both analogous and convergent traits. Considering historical derivation, development and genetics it is expected that the phenotypic traits are analogous between monocots and eudicots. Yet cases of analogy and convergence can be found within these large groups. Even though 'nocturnal anthesis, drab coloration (i.e. white and green), musty smell, flowers often located on branches or tree trunks (cauliflory) or suspended on long stalks (flagelliflory), and tubular or radially symmetrical flowers, often of the "shaving brush" type, that produce relatively large amount of hexose-rich nectar' (Fleming *et al.*, 2009, p. 1020) have been traditionally classified as traits linked with the bat pollination syndrome, it is necessary to make a developmental and evolutionary analysis to hypothesize if they evolved analogously or convergently, or if they are, in some cases, symplesiomorphies shared by distinct pollination modes (e.g. the flower tube in asterids and shaving brush flowers in Cactaceae). In this article, I consider that the analogous and/or convergent traits associated with the phyllostomid syndrome include the long floral tube (Figs 2B and 3) and white, pale, greenish and yellow-greenish organs (Figs 2 and 3). The long floral tube in eudicots and monocots is analogous. Although white, pale, greenish and yellow-greenish colours evolved multiple times along angiosperm phylogeny, it is still unknown if they represent analogy or convergence, or both. Other great candidates to be bat pollination syndrome traits include nocturnal anthesis and flower placement away from foliage, which are universal or nearly so for all bat flowers (Fleming *et al.*, 2009), and sulphur-containing perfumes, commonly associated with bat pollination as well (Karimi *et al.*, 2022). Even though these features evolved multiple times, it is unknown if they are analogies or convergences. Genetic-developmental and phylogenetic analyses are necessary to clarify this. Floral traits associated with pteropodid syndrome need to be further investigated.

These considerations about bat pollination show us that generalizations about pollination syndrome traits are problematic, leading to spurious scenarios. They are more idealistic than evolutionary. On the one hand, criticisms of the theory of pollination syndrome rest on the fact that certain flowers considered especially linked to a pollination syndrome are visited by multiple functional groups. Based on their global analysis, Ollerton *et al.* (2009) stressed that they do not take their results as evidence against the independent origin of floral syndrome traits resulting from pollinator-mediated natural selection. Yet the authors proposed that thinking only in terms of selection by a single 'most effective pollinator' fails to capture the range of possibilities. In addition, these authors highlighted that the study of pollination syndromes must consider the idiosyncrasies of both geographic distribution and plant lineages. Another problem is pleiotropy and genetic linkage, which can result in the appearance of several unrelated traits evolving correlatedly (Sinnott-Armstrong *et al.*, 2022). On the other hand, some examples have reinforced the theory of pollination syndromes, so that certain authors have strongly endorsed its heuristic value (e.g. Fenster *et al.*, 2004; Fleming *et al.*, 2009; Schiestl

FIG. 3. Showy petaloid organs in monocots and eudicots. (A) Yellow inner perianth whorl; *Vriesea sazimae* (Bromeliaceae, monocot) visited by *Anoura caudifer* (Phyllostomidae). (B) Greenish outer and inner perianth whorls; *Dyckia subsecunda* (Bromeliaceae) visited by *Lonchophylla bokermanni* (Phyllostomidae). (C) Yellow-greenish inner perianth whorl; *Siphocampylus sulfureus* (Campanulaceae, eudicot) visited by *Anoura caudifer* (Phyllostomidae). (D) Greenish inner perianth whorl; *Dyssochroma viridiflorum* (Solanaceae, eudicot) visited by *Glossophaga soricina* (Phyllostomidae). Photograph credits: Marlies Sazima and Ivan Sazima.

and Johnson, 2013; Rosas-Guerrero *et al.*, 2014; Dellinger, 2020). Dellinger (2020), in her review, demonstrated that some problems, including predictive inaccuracy and visitation by multiple functional groups, have been solved by refining techniques, while others prevail. In addition, she proposed the use of sophisticated statistical tools plus the quantification of the contribution of distinct flower visitors to remedy typological–essentialist classifications. In order to avoid generalizations and oversimplifications, I propose that the formulation of hypotheses of pollination syndromes must consider (1) the phylogenetic levels of universality at both plant and animal taxonomic lineages; (2) a critical comparative analysis of character development, homology and evolution in these lineages; and (3) a clear definition of evolutionary concepts, including analogy, convergence and parallelism.

CONCLUSIONS

On the one hand, some people working with syndromes might say 'so what?' – it does not matter to a pollinator if the traits have evolved convergently or analogously. On the other hand, the distinction between analogy and convergence is a paramount issue in evolutionary and comparative biology. The inclusion of both concepts within the concept of syndrome will constitute a new agenda of inquiry that integrates floral biology, phylogenetic systematics and developmental biology. Thus, rather than solely saying that multiple traits evolved independently onto a phylogenetic scaffold, or that all independent evolution is convergence, it is necessary to assess if they evolved to the same (convergent) or similar (analogous) phenotypes. At a large phylogenetic scale, phyllostomid and pteropodid bat pollination syndrome traits in eudicots and monocots represent cases of analogous and convergent evolution. In line with this, some exciting and deep questions come to mind: (1) Are there more convergences than analogies in pollination syndromes, or vice versa? (2) Which plant lineages evolved analogies? (3) Which ones evolved convergences? (4) Did traits of a particular syndrome evolve either *de novo* or from pre-existing features? (5) Is the independent evolution of colours, shapes, nectar guides, scents and microscopic structures convergent or analogous? (6) In the case of analogous traits, do they share the same (i.e. deep homology) or distinct genetic regulatory systems? (7) Which floral organ attributes or variables evolved from phenotypic plasticity? (8) Which ones evolved from genetic changes?

The classical idea of pollination syndromes only links floral features with functional groups. I endorse the idea that the singular evolutionary and ecological interactions between plant and animal lineages cannot be generalized or oversimplified in this way. In order to achieve a refined evolutionary delimitation of pollination syndrome, it is important to indicate analogous and/or convergent traits, as well as specifying the taxonomic plant and animal lineages involved. Organs and their attributes or variables constitute distinct phenotypic elements. Both plant and animal lineages may present a set of known and still unknown attributes and variables that may confirm a pollination syndrome. Depending on the phylogenetic levels of universality, certain features might be syndrome traits specific to some lineages but possibly not to others. Indeed, some morphological character states may represent symplesiomorphies across certain lineages. Because of the mosaic evolution of characters across the phylogeny, pollination mode and pollination syndrome cannot be synonymous concepts. The former is a broader concept that embraces plesiomorphic and apomorphic floral characters, whereas the latter includes floral analogous and/or convergent specializations associated with specific plant–animal lineages.

Pollination syndromes are a multivariate concept (Dellinger, 2020) that relies on multi- and interdisciplinary approaches. Its understanding is intrinsically related to the understanding of flower organogenesis and evolution. Therefore, current frontiers of research on the origin and evolution of flowers will have a definite impact on pollination syndrome studies in the 21st century. Homology, analogy and convergence assessment of floral organs and their attributes continues to be a theoretical and practical challenge, regarding the distinct criteria of homology delimitation (Ronse De Craene and Brockington, 2013; Ballego-Campos *et al.*, 2023). The historical origins of the perianth from bracts or stamens have led to competing and constructive hypotheses (Ronse De Craene, 2007, 2008; Ronse De Craene and Brockington, 2013), although a *de novo* origin of the angiosperm flower has also been raised (Albert *et al.*, 2002; Ronse De Craene, 2008). The discovery of genetic-developmental programs regulating the development of bracteo- and andropetals is needed (Ronse De Craene, 2007, 2008). The understanding of serial homologies (Di-Frisco *et al.*, 2022) may explain *de novo* origins of multiple floral organs and whorls. Time of initiation, pressure of organs, alterations of the size of the floral meristems, and auxin mediation constitute critical mechanisms to understand floral organogenesis and evolution in parallel with genetics (Ronse De Craene, 2008). These physico-dynamic mechanisms associated with 3-D morphometrics (e.g. Dellinger, 2020) are critical to a realistic understanding of pollination syndromes in terms of flower ontogeny and natural selection. The analysis of the large diversity of flowers will potentially reveal new biosynthetic pathways, novel structures and genetic regulatory systems of flower colour (Tanaka *et al.*, 2008). How can fossil information contribute to pollination syndrome studies (e.g. Friis *et al.*, 2006)? The use of evolutionary pathways and cryptic markers (i.e. 'fossil fingerprints'; Sanders *et al.*, 2007, p. 719) may reveal new hypotheses of plant–pollinator adaptation and exaptation at large and small scales of geological time (e.g. colour as a plesiomorphic thermoregulatory component; and the presence of petaloid organs in the extinct Bennettitales, a potential sister group of angiosperms; Rudall, 2020). Finally, I encourage the assessment and comparison of competing hypotheses and evidence of angiosperm phylogenetic relationships (Assis, 2009, 2013, 2018), which may result in distinct hypotheses of floral evolution and pollination syndromes.

LITERATURE CITED

Albert VA, **Oppenheimer GG**, **Lindqvist V. 2002**. Pleiotropy, redundancy and the evolution of flowers. *Trends in Plant Science* **7**: 297–301.

Arendt J, **Reznick D. 2008**. Convergence and parallelism reconsidered: what have we learned about the genetics of adaptation? *Trends in Ecology and Evolution* **23**: 26–32. doi:10.1016/j.tree.2007.09.011.

Assis LCS. 2009. Coherence, correspondence, and the renaissance of morphology in phylogenetic systematics. *Cladistics* **25**: 528–544. doi:10.1111/j.1096-0031.2009.00261.x.

Assis LCS. 2013. Testing evolutionary hypotheses: from Willi Hennig to the Angiosperm Phylogeny Group. *Cladistics* **30**: 240–242. doi:10.1111/cla.12048.

Assis LCS. 2017. Patterns of character evolution in phylogenies. *Journal of Systematics and Evolution* **55**: 225–230. doi:10.1111/jse.12241.

Assis LCS. 2018. Revisiting the Darwinian shortfall in biodiversity conservation. *Biodiversity and Conservation* **27**: 2859–2875. doi:10.1007/s10531-018-1573-3.

Assis LCS. 2019. The criterion of conjunction in plant systematics and evolution. *Plant Systematics and Evolution* **305**: 925–931. doi:10.1007/s00606-019-01612-3.

Ballego-Campos I, **Bonifácio SKV**, **Assis LCS. 2023**. A unified view of homology. *Cladistics* **39**: 398–417. doi:10.1111/cla.12541.

Baum DA, **Small RL**, **Wendel JF. 1998**. Biogeography and floral evolution of baobabs (*Adansonia*, Bombacaceae) as inferred from multiple data sets. *Systematic Biology* **47**: 181–207. doi:10.1080/106351598260879.

de Beer G. 1971. *Homology, an unsolved problem*. Oxford: Oxford University Press.

Benzing DH. 2000. *Bromeliaceae: profile of an adaptive radiation*. Cambridge: Cambridge University Press.

Brockington SF, **Walker RH**, **Glover BJ**, **Soltis PS**, **Soltis DE. 2011**. Complex pigment evolution in the Caryophyllales: research review. *New Phytologist* **190**: 854–864. doi:10.1111/j.1469-8137.2011.03687.x.

Brockington SF, **Yang Y**, **Gandia-Herrero F**, *et al*. **2015**. Lineage-specific gene radiations underlie the evolution of novel betalain pigmentation in Caryophyllales. *New Phytologist* **207**: 1170–1180.

Chanderbali AS, **Kim S**, **Buzgo M**, *et al*. **2006**. Genetic footprints of stamen ancestors guide perianth evolution in *Persea* (Lauraceae). *International Journal of Plant Science* **167**: 1075–1089.

Chang SM, **Lu YQ**, **Rausher MD. 2005**. Neutral evolution of the nonbinding region of the anthocyanin regulatory gene *Ipmyb1* in *Ipomoea*. *Genetics* **170**: 1967–1978. doi:10.1534/genetics.104.034975.

Coen ES, **Meyerowitz EM. 1991**. The war of the whorls: genetic interactions controlling flower development. *Nature* **353**: 31–37. doi:10.1038/353031a0.

Darwin C. 1859. *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London: John Murray.

Dawson SK, **Carmona CP**, **González-Suárez M**, *et al*. **2021**. The traits of 'trait ecologists': an analysis of the use of trait and functional trait terminology. *Ecology and Evolution* **11**: 16434–16445.

Dellinger AS. 2020. Pollination syndromes in the 21st century: where do we stand and where may we go? *New Phytologist* **228**: 1193–1213. doi:10.1111/nph.16793.

De-Paula OC, **Assis LCS**, **Ronse De Craene LP. 2018**. Unbuttoning the ancestral flower of angiosperms. *Trends in Plant Science* **23**: 551–554.

DiFrisco J, **Love AC**, **Wagner GP. 2022**. The hierarchical basis of serial homology and evolutionary novelty. *Journal of Morphology* **284**: e21531. doi:10.1002/jmor.21531.

Endress PK. 1994. *Diversity and evolutionary biology of tropical flowers*. Cambridge: Cambridge University Press.

Faegri K, **van der Pijl L. 1979**. *The principles of pollination ecology*, 3rd edn. Oxford: Pergamon Press.

Fenster CB, **Armbruster WS**, **Wilson P**, **Dudash MR**, **Thomson JD. 2004**. Pollination syndromes and floral specialization. *Annual Review of Ecology, Evolution, and Systematics* **35**: 375–403. doi:10.1146/annurev.ecolsys.34.011802.132347.

Fleming TH, **Geiselman C**, **Kress WJ. 2009**. The evolution of bat pollination: a phylogenetic perspective. *Annals of Botany* **104**: 1017–1043. doi:10.1093/aob/mcp197.

Friis EM, **Pedersen KR**, **Crane PR. 2006**. Cretaceous angiosperm flowers: innovation and evolution in plant reproduction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **232**: 251–293. doi:10.1016/j.palaeo.2005.07.006.

Gilbert SF, **Bolker JA. 2001**. Homologies of process and modular elements of embryonic construction. *Journal of Experimental Zoology* **291**: 1–12.

Good-Avila SV, **Souza V**, **Gaut BS**, **Eguiarte LE. 2006**. Timing and rate of speciation in *Agave* (Agavaceae). *Proceedings of the National Academy of Sciences of the USA* **103**: 9124–9129.

Grotewold E. 2006. The genetics and biochemistry of floral pigments. *Annual Review of Plant Biology* **57**: 761–780. doi:10.1146/annurev.arplant.57.032905.105248.

Haas O, **Simpson GG. 1946**. Analysis of some phylogenetic terms, with attempts at redefinition. *Proceedings of the American Philosophical Society* **90**: 319–349.

Habu Y, **Hisatomi Y**, **Lida S. 1998**. Molecular characterization of the mutable flaked allele for flower variegation in the common morning glory. *Plant Journal* **16**: 371–376.

Hall BK. 2007. Homology and homoplasy: dichotomy or continuum? *Journal of Human Evolution* **52**: 473–479. doi:10.1016/j.jhevol.2006.11.010.

Hansen AK, **Gilbert LE**, **Simpson BB**, **Downie SR**, **Cervi AC**, **Jansen RK. 2006**. Phylogenetic relationships and chromosome number evolution in *Passiflora*. *Systematic Botany* **31**: 138–150. doi:10.1600/036364406775971769.

Hennig W. 1966. *Phylogenetic systematics*. Urbana: University of Illinois Press.

Honma T, **Goto K. 2001**. Complexes of MADS-box proteins are sufficient to convert leaves into floral organs. *Nature* **409**: 525–529. doi:10.1038/35054083.

Karimi N, **Saghafi S**, **Keefover-Ring K**, **Venter SM**, **Ané C**, **Baum DA. 2022**. Evidence for hawkmoth pollination in the chiropterophilous African baobab (*Adansonia digitata*). *Biotropica* **54**: 113–124.

Knox EB, **Muasya AM**, **Muchhala N. 2008**. The predominantly South American clade of Lobeliaceae. *Systematic Botany* **33**: 462–468. doi:10.1600/036364408784571590.

Kress WJ, **Schatz GE**, **Adrianifahanana M**, **Morland HS. 1994**. Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence of an archaic coevolutionary system? *American Journal of Botany* **81**: 542–551.

Leander BS. 2008. Different modes of convergent evolution reflect phylogenetic distances: a reply to Arendt and Reznick. *Trends in Ecology and Evolution* **23**: 481–482.

Luckow M, **Hopkins HCF. 1995**. A cladistic analysis of *Parkia* (Leguminosae: Mimosoideae). *American Journal of Botany* **82**: 1300–1320. doi:10.1002/j.1537-2197.1995.tb12664.x.

Martén-Rodríguez S, **Almarales-Castro A**, **Fenster CB. 2009**. Evaluation of pollination syndromes in Antillean Gesneriaceae: evidence for bat, hummingbird and generalized flowers. *Journal of Ecology* **97**: 348–359. doi:10.1111/j.1365-2745.2008.01465.x.

Mori S, **Boeke JD. 1987**. Pollination. *Memoirs of the New York Botanical Garden* **44**: 137–155.

Mori S, **Tsou C-H**, **Wu C-C**, **Cronholm B**, **Anderberg AA. 2007**. Evolution of Lecythidaceae with an emphasis on the circumscription of neotropical genera: information from combined *ndhF* and *trnL-F* sequence data. *American Journal of Botany* **94**: 289–301.

Moyroud E, **Glover BJ. 2017**. The physics of pollinator attraction. *New Phytologist* **216**: 350–354.

Muñoz-Gómez S, **Suárez-Báron H**, **Alzate JF**, **Gonzáles F**, **Pabón-Mora N. 2021**. Evolution of the subgroup 6 *R2R3-MYB* genes and their contribution to floral color in the perianth-bearing Piperales. *Frontiers in Plant Science* **12**: 633227.

Nadot S, **Carrive L. 2021**. The colourful life of flowers. *Botany Letters* **168**: 120–130.

Ng J, **Smith SD. 2016**. Widespread flower color convergence in Solanaceae via alternate biochemical pathways. *New Phytologist* **209**: 407–417.

Nyffeler R, **Baum DA. 2001**. Systematics and character evolution in *Durio* s. lat. (Malvaceae/Helicteroideae/Durioneae or Bombacaceae-Durioneae). *Organisms Diversity and Evolution* **1**: 165–178.

Ollerton J, **Alarcón R**, **Waser NM**, *et al*. **2009**. A global test of the pollination syndrome hypothesis. *Annals of Botany* **103**: 1471–1480. doi:10.1093/aob/mcp031.

Patterson C. 1982. Morphological characters and homology. In: **Joysey KA**, **Friday AE**, eds. *Problems of phylogenetic reconstruction*. London: Academic Press, 21–74.

Perret M, **Chautems A**, **Spichiger R**, **Barraclough TG**, **Savolainen V. 2007**. The geographical pattern of speciation and floral diversification in the neotropics: the tribe Sinningieae (Gesneriaceae) as a case study. *Evolution* **61**: 1641–1660. doi:10.1111/j.1558-5646.2007.00136.x.

Prather LA. 1999. The relative lability of floral vs. non-floral characters and a morphological phylogenetic analysis of *Cobaea* (Polemoniaceae). *Botanical Journal of the Linnean Society* **131**: 433–450. doi:10.1111/j.1095-8339.1999.tb01525.x.

Quattrocchio F, **Wing J**, **van der Woude K**, *et al*. **1999**. Molecular analysis of the anthocyanin2 gene of *Petunia* and its role in the evolution of flower color. *Plant Cell* **11**: 14330–11444.

Queiroz JA, **Diniz UM**, **Vásquez DP**, *et al*. **2020**. Bats and hawkmoths form mixed modules with flowering plants in a nocturnal interaction network. *Biotropica* **53**: 596–607.

Raguso RA, **Levin RA**, **Foose SE**, **Holmberg MW**, **McDade LA. 2003**. Fragrance chemistry, nocturnal rhythms and pollination 'syndromes' in *Nicotiana*. *Phytochemistry* **63**: 265–284. doi:10.1016/s0031-9422(03)00113-4.

Rausher MD. 2008. Evolutionary transitions in floral color. *International Journal of Plant Science* **169**: 7–21.

Reynolds RJ, **Westbrook MJ**, **Rohde AS**, **Cridland JM**, **Fenster CB**, **Dudash MR. 2009**. Pollinator specialization and pollination syndromes of three related North American *Silene*. *Ecology* **90**: 2077–2087. doi:10.1890/08-1141.1.

Rieppel O. 2023. 'Living fossil' and the mosaic evolution of characters. *Frontiers in Ecology and Evolution* **11**: 1119418.

Ronse De Craene LP. 2007. Are petals sterile stamens or bracts? The origin and evolution of petals in the core eudicots. *Annals of Botany* **100**: 621–630. doi:10.1093/aob/mcm076.

Ronse De Craene LP. 2008. Homology and evolution of petals in the core eudicot. *Systematic Botany* **33**: 301–325. doi:10.1600/036364408784571680.

Ronse De Craene LP. 2010. *Floral diagrams: an aid to understanding flower morphology and evolution*. Cambridge: Cambridge University Press.

Ronse De Craene LP, **Brockington SF. 2013**. Origin and evolution of petals in angiosperms. *Plant Ecology and Evolution* **146**: 5–25.

Rosas-Guerrero V, **Aguilar R**, **Martén-Rodríguez S**, *et al*. **2014**. A quantitative review of pollination syndromes: do floral traits predict effective pollinators? *Ecology Letters* **17**: 388–400. doi:10.1111/ele.12224.

Rudall PJ. 2020. Colourful cones: how did flower colour first evolve? *Journal of Experimental Botany* **71**: 759–767.

Sanders H, **Rothwell GW**, **Wyatt S. 2007**. Paleontological context for the developmental mechanisms of evolution. *International Journal of Plant Science* **168**: 719–728.

Sazima M, **Buzato S**, **Sazima I. 1999**. Bat-pollinated flower assemblages and bat visitors at two Atlantic forest sites in Brazil. *Annals of Botany* **83**: 705–712.

Schiestl FP, **Johnson SD. 2013**. Pollinator-mediated evolution of floral signals. *Trends in Plant Science* **28**: 307–315.

Scotland RW. 2011. What is parallelism? *Evolution and Development* **13**: 214–227. doi:10.1111/j.1525-142x.2011.00471.x.

Sereno P. 2007. Logical basis for morphological characters in phylogenetics. *Cladistics* **23**: 565–587.

Shubin N, **Tabin C**, **Carroll S. 2009**. Deep homology and the origins of evolutionary novelty. *Nature* **457**: 818–823. doi:10.1038/nature07891.

Sinnott-Armstrong MA, **Deanna R**, **Pretz C**, *et al*. **2022**. How to apply the study of syndromes in macroevolution and ecology. *Ecology and Evolution* **12**: e8583.

Sobel JM, **Streisfeld MA. 2013**. Flower color as a model system for studies of plant evo-devo. *Frontiers in Plant Science* **4**: 321.

Soltis DE, **Soltis PS**, **Endress PK**, **Chase MW. 2005**. *Phylogeny and evolution of angiosperms*. Sunderland: Sinauer Associates.

Tanaka Y, **Sasaki N**, **Ohmiya A. 2008**. Biosynthesis of plant pigments: anthocyanins, betalains, and carotenoids. *Plant Journal* **54**: 733–749. doi:10.1111/j.1365-313x.2008.03447.x.

Tripp EA, **Manos PS. 2008**. Is floral specialization an evolutionary dead-end? Pollination system transitions in *Ruellia* (Acanthaceae). *Evolution* **62**: 1712–1737. doi:10.1111/j.1558-5646.2008.00398.x.

Wagner GP. 2007. The developmental genetics of homology. *Nature Reviews Genetics* **8**: 473–479. doi:10.1038/nrg2099.

Wallace RS. 2002. The phylogeny and systematics of columnar cacti: an overview. In: **Fleming TH**, **Valiente-Banuet A**, eds. *Columnar cacti and their mutualists: evolution, ecology, and conservation*. Tucson: University of Arizona Press, 42–65.

Wu CA, **Streisfeld MA**, **Nutter LI**, **Cross KA. 2013**. The genetic basis of a rare flower color polymorphism in *Mimulus lewisii* provides insight into the repeatability of evolution. *PLoS One* **8**: e81173. doi:10.1371/journal.pone.0081173.

Zufall RA, **Rausher MD. 2004**. Genetic changes associated with floral adaptation restrict future evolutionary potential. *Nature* **428**: 847–850. doi:10.1038/nature02489.