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# **Evolvability**

## **A Unifying Concept in Evolutionary Biology?**

**Edited by: Thomas F. Hansen, David Houle, Mihaela Pavličev, Christophe Pélabon**

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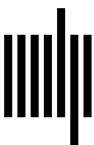
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# 15

## **Evolvability of Flowers: Macroevolutionary Indicators of Adaptive Paths of Least Resistance**

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Flowering plants are good organisms for analysis of the macroevolutionary signals of differential evolvability. The repeated evolutionary paths followed by flowering plants during their 150+ Myr history provide clues about genetic and developmental biases that yield high evolvability. Analysis of heterochronic variation suggests that evolutionary paths of low resistance (high evolvability) and much of the diversification of floral structure and function have been facilitated by heterochrony. There also appear to be links between the development and evolution of floral orientation, a feature surprisingly important in pollination. The modular independence of flowers relative to vegetative traits may enhance their evolvability, as probably do patterns of intra-floral modularity. Another good indicator of evolutionary paths of low resistance and high evolvability is the high levels of homoplasy (parallel evolution and reversals) of some traits. Parallel and convergent evolution is clearly facilitated by effective preadaptations being in place.

### **15.1 Introduction: Looking for Signals of Differential Evolvability in Flowering Plants**

Since their invasion of land some 500 million years ago (Morris et al. 2018), plants have undergone two major pulses of increasing complexity, disparity, and diversity. The first was associated with the origin of seeds in the late Devonian (ca. 350 Mybp), and the second, even larger pulse was subsequent to the origin of flowers in the early Cretaceous (or possibly late Jurassic). Thus, unlike in most animal lineages, major increases in complexity and disparity in plants occurred relatively late in their evolutionary history (Leslie et al. 2021). Flowering plants (angiosperms), the subject of this chapter, are thus characterized by this key innovation: flowers. The evolvability of floral traits will be the focus of this chapter.

My goal is to assess patterns and mechanisms of evolutionary divergence of flowering-plant populations and species in relation to potential evolutionary biases (differential evolvabilities) detected (or hinted at) within populations. Although plant evolution is not fundamentally different from animal evolution, plants provide experimental and analytical opportunities not available to most animal biologists. Plants' bodies are highly modular, with many iterative (replicated) structures on the same individual (e.g., leaves, flowers, fruits), which are basically genetically identical and usually also functionally identical. Variation among repeated units reflects ontogenetic variation, positional effects, and adaptive (e.g., sun versus shade leaves) or nonadaptive plastic responses to microenvironmental

variation (Diggle 2014). This nongenetic variation can be ecologically important, yielding direct insights into form-function relationships, as well as patterns of stabilizing and canalizing selection. Iterative plant organs also promote direct investigation into the evolutionary significance of phenotypic and genetic integration and modularity (e.g., Berg 1960; Hansen et al. 2007; Pélabon et al. 2011; see reviews in Armbruster et al. 2014; Conner and Lande 2014). Finally, most plants are easy to clone, allowing investigators to address directly environmental sources of phenotypic (co)variation (but see the cautionary notes in Schwaegerle et al. 2000; Schwaegerle 2005).

Because flowering plants are largely immobile, the majority of species employ animals to solve one or more life-history tasks, such as pollen or seed transport. Although plants have evolved a diversity of solutions to their reproductive tasks, there are recurrent themes in their evolutionary diversification, themes that suggest evolutionary “paths of least resistance” (Stebbins 1950, 497; Schluter 1996, 2000). These repeated evolutionary paths presumably reflect routes of elevated evolvability, interacting with differential fitness advantages.

Most early investigation into the evolutionary paths of least resistance in plants have focused on flower structure and related aspects of reproductive systems, a bias I continue in this chapter. However, recent molecular-genetic studies of plant evolution have explored other aspects of plant metabolism, morphology, and function (see Jaramillo and Kramer 2007; Wessinger and Heileman 2020; Julca et al. 2021; Sengupta and Heileman 2022). I will not attempt to review this research, except to acknowledge that it is beginning to yield important insights into the role of evolvability in determining divergence and convergence of organ development, structure, and function between species.

Here, I review patterns of developmental and morphological variation of flowers within and among plant populations and species. I focus on the role of developmentally based shifts and other “exaptive” transitions (*sensu* Gould and Vrba 1982; ≈ “preadaptations”; i.e., co-option of preexisting features for new functions; see Arnold 1994) and their roles in the origin of phenotypic and ecological novelty associated with the divergence of populations and species. Exaptive transitions suggest evolutionary lines of least resistance, because preadaptations often precede repeated, parallel origins of the same or similar novel feature across related lineages (“homoplasy”). Darwin (1872, 175), Simpson (1944), and Mayr (1963) suggested that when a “preadaptive” (= “preaptive,” *sensu* Gould and Vrba 1982) trait is in place, subsequent evolutionary change can happen rapidly (and presumably easily), because the basis for the change is already there (see Arnold 1994; Armbruster 1997; McLennan 2008). Thus exaptation, as a process or result, can yield important clues about evolutionary paths of low resistance.

For the purposes of this chapter, I will assume that repeated transitions in character states reflect population-level evolvability as it interacts with the transformative efficacy of selection (taken together, “evolutionary lability”), where the signal is examined at the among-population level (and above). Thus, I use variation in trait evolutionary lability in plants as a signal hinting at differential evolvability (“ease” of genetically based phenotypic change within populations), while hoping that selection is reasonably constant. This assumption seems reasonable when studying most floral evolution, because selection usually “compares” the pollination consequences of floral changes rather than the transition processes themselves. For example, selection for a new pollinator due to local extinction of an old one will be equally strong whether the needed evolutionary response

involves sepals or petals, colors or fragrances. The most likely response will be the most evolvable floral change that attracts a new pollinator. To this end, I discuss both rampant parallel evolution (homoplasy) and the mechanistic bases of such repeated transitions, as ways to gain insights into evolutionary routes of high evolvability.

Within populations, multivariate phenotypic covariation reflects the trajectories of ontogenetic and genetic variation. Lande (1979), Schluter (1996, 2000), Hansen and Houle (2008), and others since have argued cogently that the multivariate directions of greater genetic variation constitute the trajectories of highest evolvability, at least over the short term (see cautionary note in Hansen and Voje 2011). In turn, much of the heritable phenotypic covariation expressed in plants has an ontogenetic basis (i.e., subtle variation in the ontogenetic stage at which certain functional events occur, e.g., in flowers, the opening of petals or dehiscence of stamens). Such variation in the functional chronology in relation to the ontogenetic chronology (“heterochrony”; Gould 1977) creates heritable patterns of phenotypic covariance. We can expect, therefore, that populations, and perhaps species, will tend to diverge along these trajectories of high genetic and phenotypic variation (e.g., Haber 2016; see also Kluge and Kerfoot 1973; Johnson and Mickevitch 1977; Pierce and Mitton 1979; but cf. Sokal 1976 and Riska 1979). This view, although still contentious, is supported by some studies in plants that show population and species divergence to occur largely along the within-population phenotypic or quantitative-genetic trajectories (Armbruster 1991; Andersson 1991; Bolstad et al. 2014). This leads to the suggestion that the study of ontogenetic trajectories of covariation in flowers can reveal evolvability biases that “predict” the divergence of populations and species. The basic take-home message from this review is that plant evolution appears to proceed largely by building on preexisting states or structures or by simple changes in genetically controlled developmental mechanisms (i.e., via exaptation in the broadest sense). Preaptations define the phenotypic starting points for subsequent evolutionary paths of low genetic/developmental resistance.

## 15.2 Some Methodological Assumptions

The present review assumes that trait evolutionary lability provides some insight into trait evolvability. This relationship is not necessarily a very tight one, however, because evolutionary lability of a trait is also influenced by the efficacy of divergent or diversifying natural selection acting on the trait. Additional factors may further obscure the relationship between evolutionary lability and evolvability (e.g., variation in effective population size, influencing drift; and proximity of divergent populations, influencing gene flow). However, it is probably safe to conclude that the dominant relationship looks something like:

$$\text{Evolutionary Lability} = \text{Evolvability} * \text{Selection} \quad (15.1)$$

where  $*$  is some interactive function (e.g., multiplicative if properly scaled), and “selection” refers to transformational efficacy of divergent or diversifying selection (including effects of directionality, consistency, strength, and duration). Note that “lability” can be interpreted as a disposition (i.e., propensity or capacity) for evolutionary change in phenotype, as in the discussions of evolutionary developmental mechanisms in sections 15.3 and 15.4.

However, trait evolutionary lability can also be an observation, as when the evidence for the capacity of evolutionary change is purely macroevolutionary (i.e., drawn from the observation

of phenotypic variation among relatives and measured as phenotypic disparity). I use the term also in this sense. Homoplasy (convergence, parallelisms, or reversals in trait evolution) is a useful indicator of trait evolutionary lability in the empirical sense. Given an accurately estimated phylogeny, a high degree of homoplasy in a trait indicates high evolutionary lability, although the reverse is certainly not true (see Wake 1991; Wake et al. 2011).

### 15.3 Heterochrony: A Repeated Path of Low Evolutionary Resistance

Heterochronic variation within and across species reflects the effect on phenotype of differences in timing of various developmental events, given a sufficient degree of developmental modularity. The two main manifestations of heterochrony that emerge from species comparisons are paedomorphosis (retention of juvenile traits into sexual maturity via truncated ontogeny) and peramorphosis (exaggeration of adult traits at sexual maturity via extended ontogeny; table 15.1). Because such transitions are the result of simple changes in speed or timing of ontogenetic sequences relative to maturation, heterochronic change is a likely route of low evolutionary resistance (i.e., high evolvability), in response to selection for novel morphology and function, at least when the favored phenotype is within the domain of heterochronic possibilities.

An overlapping area of research concerns allometric/isometric transitions between species (“evolutionary allometry”). As an example, consider Gould’s (1974, 1977) presentation of allometry in and among cervine species (deer, *sensu lato*): log (mature-male antler mass) scales closely and positively (slope > 1) with log (body mass). Thus the Irish elk (*Megaloceros giganteus*) could be expected to have exceptionally large antlers by virtue of its large body size alone, although probably both have evolved in concert along a path of low resistance in response to sexual selection (Gould 1974). Evolutionary allometry usually has a heterochronic developmental basis, at least in part (see Gould 1977). The

**Table 15.1**  
Dictionary of heterochrony terms, as applied to plants (including flowers)

Phenotype term	Meaning	Process term	Process description
Paedomorphosis/ Paedomorphy	Retention of juvenile characteristics into sexual maturity via truncated ontogeny	Progenesis	Period of growth of the descendant form is stopped prematurely; advancement of sexual maturation relative to ontogeny of nonsexual structures
		Neoteny	Rate of growth is less in the descendant than in the ancestor; retardation of ontogeny of nonsexual structures relative to sexual maturation
		Post displacement	Delayed onset of growth of nonsexual structures is delayed
Peramorphosis	Exaggeration of adult traits at sexual maturity via extension of ontogenetic trajectory	Hypermorphosis	Extended ontogeny relative to timing of maturity via delayed sexual maturity (delayed offset)
		Acceleration	Extended ontogeny relative to timing of maturity by accelerated ontogeny; growth rate is increased [relative to sexual maturity] (increase in rate)
		Predisplacement	Onset of growth occurs earlier in the descendant than in the ancestor (earlier onset)

*Note:* Both paedomorphosis and peramorphosis can be produced by one or more of three processes: variation in time of termination of ontogenetic growth, variation in time of initiation of ontogenetic growth, and change in rate of ontogenetic growth relative to sexual maturity (or other temporal landmark; Alberch et al. 1979).

developmental factors that contribute to evolutionary allometry can sometimes be examined by assessing within-population allometric variation (“ontogenetic” and “static” allometries; Pélabon et al. 2013, 2014; see Armbruster 1991 for a plant example). Because both heterochronic and allometric differences between species have their origins in differing developmental trajectories, I include examples of both in this section without distinguishing between them.

### 15.3.1 Heterochronic Changes in Flowers Can Lead to Pollinator Shifts

One of the earliest well documented examples of ecologically important heterochronic change in flower morphology was presented by Guerrant (1982). He noticed that the shape of the flowers of hummingbird-pollinated *Delphinium nudicaule* in California closely resembled the buds of several bee-pollinated species of *Delphinium*. Elegant formal analyses presented a convincing case of a transition to hummingbird pollination through retention of bud-like floral shape into anthesis (i.e., floral “maturity”), which he recognized as neoteny (figure 15.1).



**Figure 15.1**

Adaptation to hummingbird pollination in *Delphinium* flowers (see Guerrant 1982 for details). (A) Mature, orange-red flower of hummingbird-pollinated *Delphinium nudicaule*. (B) Floral bud of bee-pollinated *Delphinium glaucum*. (C) Three mature, receptive flowers of *D. glaucum*, one with pollinating bumble bee obtaining nectar. Note the striking shape similarity between the mature *D. nudicaule* flower and the bud of *D. glaucum*. Photos by W. S. Armbruster.

Heterochronic shifts in floral development have led to changes in the length of nectar spurs (outgrowth of the perianth, with nectar at the distal end) in other taxa. These morphological changes have occurred in concert with ecological changes in principal pollinators or evolutionary changes in pollinator morphology (usually proboscis length). The ecological and evolutionary significance of changes in nectar-spur length was examined in detail by Darwin (1862) and has been investigated extensively in subsequent years (e.g., Nilsson 1998; Maad 2000; Whittall and Hodges 2007; Sletvold and Ågren 2010, Boberg et al. 2014). Changes in spur length may reflect plant-pollinator coevolution (Darwin 1862; Wallace 1867), adaptive responses to shifts in pollinator species mediating selection (Whittall and Hodges 2007), or a combination of the two (Boberg et al. 2014). The development of spurs and increases in their lengths reflect localized cell proliferation and/or cell elongation over developmental time (see Wessinger and Hileman 2020, fig. 3). Thus, evolutionary increases in spur length can easily occur via peramorphosis. The ease of the transition from spurless flowers to shallowly and deeply spurred flowers is demonstrated by the large number of independent origins of spurred flowers in multiple families (e.g., Balsaminaceae, Geraniaceae, Orchidaceae, Plantaginaceae, Ranunculaceae, Scrophulariaceae, Tropaeolaceae).

In the case of spurs in *Aquilegia* (Ranunculaceae), there appears to be a trend toward increasing spur length in North American species, mediated by cell elongation late in development (Puzey et al. 2012); this is associated with sequential shifts to pollinators with longer tongues (Whittall and Hodges 2007). However, in tropical *Angraecum* and related angreoid orchids, there is molecular-phylogenetic evidence suggesting evolution of shorter spurs in some lineages as well as longer spurs in other lineages (Andriananjamanantsoa et al. 2016). Similarly, in many temperate terrestrial orchids, the evolutionary trend seems to be from longer to shorter spurs via paedomorphosis (Box et al. 2008; Box and Glover 2010). Differences in spur length in *Diascia* spp. (Scrophulariaceae) also appear to reflect adaptation to different *Rediviva* bee pollinators (Melittidae) of different leg lengths (Steiner and Whitehead 1990, 1991; Melin et al. 2021), but increasing spur length appears not to have influenced the degree of specialization (Hollens et al. 2017). Thus, changes in spur length leading to shifts in pollinators at the species level appear to be both evolutionarily labile and reversible, as would be expected for a highly evolvable trait, with change mediated by heterochrony.

Much like spurs, floral tubes (elongated bases of fused corollas and/or calyces, usually with nectar secreted at the bottom) range from short to long, and, when narrow, limiting reward access to only those animals with long-enough tongues. Transitions between tube lengths probably also have a heterochronic basis, with the evolution to shorter tubes usually reflecting paedomorphosis and evolution to longer tubes usually reflecting peramorphosis. For example, Ezcurra and de Azkue (1989) suggested that peramorphosis via accelerated corolla development is the best explanation for the evolutionary transition to elongated floral tubes associated with a shift from bee pollination to sphingid moth pollination in *Ruellia* (Acanthaceae).

An example of paedomorphosis leading to specialization in which animals can access a pollen reward is seen in a clade of *Dalechampia* vines (Euphorbiaceae) in Madagascar. All *Dalechampia* species have unisexual flowers united into hermaphroditic inflorescences, which function, in nearly all cases, as single blossoms (i.e., pollination units, or “pseudanthia”). In the basal-most species in Madagascar (i.e., resembling African ances-

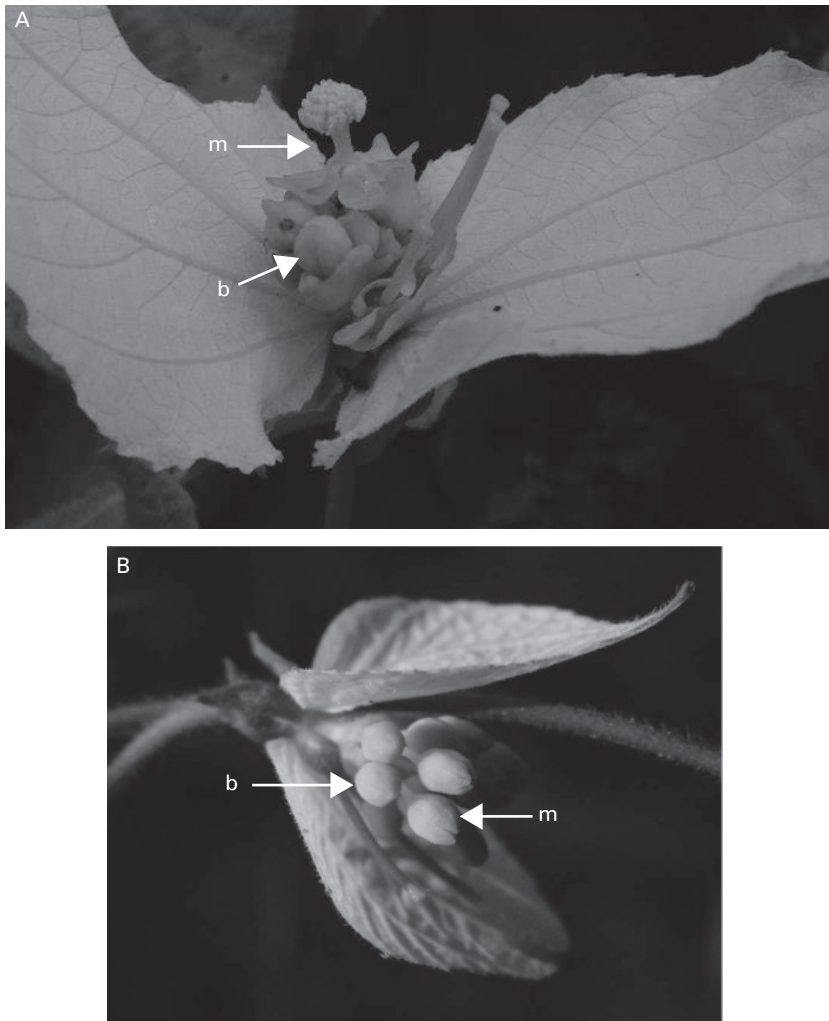
tors), the staminate flowers open fully, and pollen is eaten or collected by pollinating beetles, flies, or bees. However, in one or more clades of derived species, the staminate flowers retain two “juvenile” characteristics into anthesis (time of flower maturation): (1) the sepals fail to split and reflex, so that the flower remains in the spherical shape of a bud, although of “adult” size and with mature pollen; and (2) the receptacle to which the stamens are attached fails to elongate because of “suppressed” cell elongation, and thus the stamens remain enclosed by the sepals. At the time of stamen dehiscence, the margins of the sepals are separated by narrow cracks near the calyx apex; otherwise, the flowers look like enlarged floral buds (figure 15.2). A consequence of this arrangement is that the pollen is largely protected from being eaten by pollinivores (e.g., flies and beetles) or collected by bees unable to buzz their thoracic muscles (e.g., honey bees). Thus, paedomorphic members of this clade of *Dalechampia* have shifted from generalist pollination by beetles, flies, and/or pollen-collecting bees (Armbruster and Baldwin 1998) to more specialized pollination by only those bees, including *Xylocopa*, *Amegilla*, and *Nomia*, that can “buzz-pollinate” by vibrating their thoracic muscles at high frequencies (Armbruster et al. 2013; Plebani et al. 2015; see review in Vallejo-Marín 2019).

Another common pollinator shift seen in plants is attraction and utilization of pollinators of different body sizes. In most cases, this involves developmentally based allometric/isometric shifts in flower size, with smaller, scaled-down flowers adapted to smaller pollinators and larger, scaled-up flowers adapted to larger pollinators (Armbruster 1990, 1991, 1993; cf. Marroig and Cheverud 2010). Surprisingly little work has been done on this kind of pollinator transition, perhaps because it is obvious, or perhaps because flower-size evolution is so often assumed to be correlated with changes in mating system (e.g., the “selfing syndrome;” see section 15.3.2 and Armbruster et al. 2002; Sicard and Lenhard 2011; Cutter 2019; Mazer et al. 2020). Such size shifts can be explained by changes in growth rates or duration, involving cell enlargement, proliferation, or both, and affecting some or all floral parts (Wessinger and Hileman 2020).

### 15.3.2 Heterochronic Changes Can Lead to Higher Self-Pollination Rates

The above examples notwithstanding, the vast majority of the literature on paedomorphic shifts associated with species divergence and changes in pollination systems concerns shifts from plants with large, cross-pollinating flowers to plants with smaller, self-pollinating flowers (e.g., Hill et al. 1992; Gallardo et al. 1993; Stewart and Canne-Hilliker 1998; Ehlers and Pedersen 2000; Sherry and Lord 2000; Box and Glover 2010; Li and Johnston 2010). Stebbins (1950, 1970, 1974) recognized this as the commonest evolutionary transition seen across flowering plants. There are reputed to be many hundreds of independent transitions from outcrossing to selfing and possibly dozens in the other direction (see Iqic and Busch 2013; Whitehead et al. 2018). Why is this transition so common? Although recurrent strong selection for mating-system shifts certainly cannot be ruled out as a factor, several aspects argue that the transition is highly evolvable. Response to selection for self-pollination under pollen limitation (selection for reproductive assurance) may be particularly easy, at least in species that are self-compatible, because allometric miniaturization can occur easily via early sexual maturation relative to flower-size growth. An automatic correlate of allometric floral miniaturization is reduced herkogamy (i.e., reduced *absolute* distance between anthers and stigmas in the same flower or blossom), which is associated with higher rates





**Figure 15.2**

Blossom inflorescences (pseudanthia) of two species of *Dalechampia* (Euphorbiaceae), illustrating heterochronic transition in development of the staminate (male) flowers (see Armbruster et al. 2013 for details). (A) *Dalechampia tamifolia* with “normal” development, where sepals reflex in a few seconds, and staminal column elongates in less than an hour, just prior to anther dehiscence. The pollen reward is open and available to many kinds of pollinators, including beetles. Note the vertical blossom orientation, which creates a large landing platform. (B) *Dalechampia* aff. *bernieri* with paedomorphic staminate flowers, having sepals that do not reflex and staminal columns that do not elongate. This is an adaptation for buzz pollination, where pollen is available only to those species of bees that can vibrate their thoracic muscles at the right frequency and intensity to sonicate pollen out of the cracks at the tips of the nearly closed, bud-like male flowers. Note the lateral blossom orientation. Symbols: b = staminate flower in bud; m = mature staminate flower at anthesis. Photos by W. S. Armbruster.

of self-pollination (e.g., Armbruster 1988a; Motten and Stone 2000; Armbruster et al. 2002; Opedal et al. 2017). Another consequence of floral miniaturization is, however, reduced investment in advertisements (e.g., smaller petals) and/or rewards (components of the “selfing syndrome,” as noted above), with the ecological consequence likely being reduced attraction of pollinators and thus greater dependence on autofertility. This, combined with loss of genetic diversity, has led to the view that self-fertilization in flowering plants and other organisms may be an evolutionary “dead end” or “blind alley” (Stebbins 1950, 1957; Takebayashi and Morrell 2001; Busch and Delph 2017), although there is not unanimity in this conclusion (Takebayashi and Morrell 2001; Igic and Busch 2013). The dead-end hypothesis implies a directionality to evolvability: ease of transition in one direction, but not the other (see discussion in Igic and Busch 2013).

A special case of heterochronic transitions promoting self-pollination is seen in the origin of cleistogamous flowers, which undergo self-pollination and seed maturation without the perianth (petals and/or sepals) opening. This trait is scattered across the angiosperm phylogeny, reflecting dozens of independent origins. The bud-like nature of the perianth of sexually mature cleistogamous flowers indicates that heterochrony probably played a role in each of the independent origins (Lord 1981, 1982; Minter and Lord 1983; Ezcurra and de Azkue 1989; Ezcurra 1993; Porras and Munoz 2000).

#### 15.4 Evolution and Development of Floral and Fruit Orientation

The proper functioning of most animal-pollinated flowers in pollination and seed production depends on the “correct” orientation of flowers and floral parts relative to gravity. This is because pollinator flight performance is directly constrained by the pull of gravity, which thus influences animal orientation on landing or hovering. In addition, rain usually falls from above (although not always), which might influence optimal floral orientation in wet weather (pollen viability and dispersal are generally compromised by immersion in water; Huang et al. 2002; Mao and Huang 2009). Floral orientation can also play a role in filtering pollinators, allowing specialization on the most effective pollinators (i.e., those whose visits provide the greatest increase in fitness; Fenster et al. 2009; Armbruster 2017) or better fit to those pollinators increasing fitness marginally without trade-offs (Aigner 2001). For example, pendent or semi-pendent flowers favor hummingbird pollinators by making bee visitation difficult (Gegear et al. 2017). Pendent flowers combined with viscid corolla secretions in *Proboscidea* and related Martyniaceae prevent or reduce floral entry by small nectar- or pollen-seeking insects, restricting access to large bees that are good pollinators (Armbruster, unpublished observations). While vertical (upward) floral orientation attracts sphingid moth pollination, lateral floral orientation discourages their visitation in *Zaluzianskya* (Scrophulariaceae; Campbell et al. 2016). “Correct” floral orientation is achieved developmentally by the operation of one or more of at least three distinct processes: (1) bending of the peduncle (main floral stem), (2) bending of the pedicel (secondary floral stem), or (3) twisting of the pedicel.

Below I provide examples that support the view that small developmental changes can lead to major transitions in floral orientation and pollination ecology, and hence that there is high evolvability of flower function via such simple changes. First, I build the case that floral orientation is often evolutionarily labile at the species level. I then show that this

lability can be accounted for by simple changes in development, as is reflected in the widespread occurrence of serial developmental changes in flower orientation within the “lifetime” of a flower. A third line of evidence supporting the high evolvability and ease of evolutionary change in floral orientation derives from the fact that many plants exhibit “behavioral” plasticity in floral attachment angle.

#### 15.4.1 Floral Orientation Is Evolutionarily Labile at the Species Level

The evolution and functional significance of flower attachment angle (via peduncle or pedicel bending or twisting) has been studied at the species level only to a limited extent. Most research has been on rotation of flowers through twisting of pedicels, known as resupination, particularly in orchids. A paper on the heterochronic evolution of temperate orchids showed that the 180° shift in floral orientation of *Gymnadenia austriaca* flowers, compared to relatives, was likely the result of the suppression of resupination, the last event in the developmental sequence prior to flower opening (Box et al. 2008). Similarly, *Angraecum* orchids show considerable evolutionary lability in resupination (where resupinate is the basal condition; Andriananjamanantsoa et al. 2016). The authors’ phylogenetic reconstruction shows at least 5 losses of resupination. These transitions all presumably reflect curtailment of the final stage of floral development. Adaptive loss of resupination has also been reported in lobelioids (Campanulaceae) by Ayers (1994, 1997), who noted that losses were easier than gains and that there was some degree of adaptive plasticity in degree of resupination (see below).

Variation in inflorescence and flower orientation is a dominant theme in the evolution of the tropical giant herb *Heliconia* s.l. (Heliconiaceae). The neotropical group contains 200–250 species, most of which are pollinated primarily by hummingbirds (Stiles 1975). Flowers are resupinate or non-resupinate, and inflorescences are erect or pendent. The evolution of each of these two traits is contingent on the state of the other (yielding correlated evolution; Iles et al. 2017). Resupinate flowers in erect inflorescences is the inferred basal condition; this leads to sternotribic (in this case, “under-the-chin”) pollen placement and stigma contact. The likelihood of resupination loss depends on whether the inflorescence is pendent. Loss of resupination, apparently by early termination of pedicel development, has occurred only a few times in erect-inflorescence lineages. In contrast, suppression of resupination has evolved independently in pendant-inflorescence lineages about 13 times (Iles et al. 2017). This latter combination of traits results in nototribic (in this case, “on-the-forehead”) pollen placement and stigma contact. These various developmental transitions potentially allow sympatric species of *Heliconia* to partition locations of pollen placement on pollinators, reducing loss of pollen during heterospecific visits and stigmatic clogging by heterospecific pollen.

Species-level evolution of floral orientation caused by pedicel or peduncle (inflorescence stem) bending has received less attention than that by pedicel rotation. As just described in *Heliconia* spp., bending of the peduncle during development, in combination with flower resupination or lack thereof, can result in changes in pollen placement and stigma contact across species. Evolutionary lability in floral orientation via pedicel bending was recently described in *Lonicera* by Xiang et al. (2021). Floral orientation evolved apparently in response to both the seasonal trends in the physical environment and in the main pollinator species. The authors detected 3 or 4 cases of upward-facing flowers evolving from downward-facing ancestors, and at least one reversal, in their species sample.

Species blooming early in the season tended to have downward-facing flowers, possibly facilitating heat retention and reducing pollen damage and nectar dilution by rain, while those blooming later in the season tended to have upward-facing flowers. All moth-pollinated species had upward-facing flowers, whereas the one hummingbird-pollinated species had downward-facing flowers (see also Sapir and Dudley 2013); the bee-pollinated species had either flower orientation (Xiang et al. 2021).

*Dalechampia* vines exhibit 1 or 2 origins of lateral-facing, 2 origins of pendent, and 1 origin of upward-facing inflorescences as a result of peduncle bending. In this group, lateral blossom orientation is associated with pollination by female bees collecting floral resin or pollen, pendent orientation is associated with pollination by fragrance-collecting male euglossine bees, and upward orientation is associated with pollination by beetles (see figure 15.2; Armbruster 1993; Armbruster et al. 1993; Plebani et al. 2015).

#### **15.4.2 Changes in Floral Orientation during Normal Development Suggest Floral Orientation Can Evolve Easily through Heterochrony**

In many plants, the orientation of floral buds, flowers, and fruits changes during development due to changes in the angle of the stem (pedicel or peduncle). Heterochronic changes in such developmental sequences could be an evolutionary route of low resistance, leading to evolution of novel floral orientation angle in response to changes in the pollinator environment or selection to optimize seed-dispersal mechanics during fruiting.

Other than the resupination literature noted earlier in this chapter, the literature on other developmental changes in floral orientation is surprisingly scarce. In a small survey, I combined what little I could find in the literature with original observations (table 15.2). The survey shows a remarkable amount of change in floral orientation associated with development from bud, to anthesis, to fruiting. This is not surprising, because the optimal orientations of buds, receptive flowers, developing fruits, and mature or dehiscent fruits are likely to differ. Niu et al. (2016) showed, for example, that, although the optimal orientation of flowers of many plants is lateral or pendent, the optimal orientation of the fruits of those species is upright when the fruits are capsular and split open at the top. Indeed, experiments demonstrated better seed dispersal from the fruits of *Silene chungtienensis* that were in the upright position. A published survey showed that most plants with dry, partially dehiscent, “container-like” capsules had vertically oriented fruits, allowing gradual release of seeds with wind or other disturbances. A substantial proportion of these had to reorient floral/fruit structures to achieve upward-facing fruits (Niu et al. 2016; cf. table 15.2).

#### **15.4.3 “Behavioral” Plasticity of Floral Orientation Also Suggests Orientation Is Highly Evolvable**

That flowers can change their orientation “behaviorally” (i.e., exhibit rapid phenotypic plasticity in response to an external or internal stimuli) has been known at least since Darwin’s descriptions of the phenomenon (e.g., petal closure in response to cold or nightfall; Darwin, 1862, 1880). Probably the best-known floral behavior is floral heliotropism: movement in response to the sun’s position (see review in van der Kooi et al. 2019). Recent work by Yon et al. (2017) and Haverkamp et al. (2019) shows daily shifts in the orientation of flowers of *Nicotiana attenuata*: from upward by night (promoting moth pollination) to downward by day (keeping the interior of flowers cooler). In contrast, the flowers of *Eriocapitella* sp.

**Table 15.2**

Developmental changes in orientation of floral and fruit structures in a sample of flowers from field and garden surveys and the literature

Floral Orientation: Taxon	In Bud	In Flower (Anthesis)	In Fruit	Source
<i>Aquilegia vulgaris</i> L. (Ranunculaceae)	lateral?	pendent	erect	original
<i>Anisodus luridus</i> (Solanaceae)	pendent	pendent	erect	Wang et al. 2010
<i>Collinsia</i> spp. (Plantaginaceae)	lateral	lateral	erect	original
<i>Dactylorhiza fuchsii</i> , <i>Phalaenopsis amabilis</i> , <i>P. equestris</i> , (Orchidaceae) and most other orchids with lateral floral orientation and enlarged labellum	unrotated-not resupinate	rotated 90–180° to place labellum in lowermost position (resupinate)	rotated 180° (still resupinate)	original
<i>Dalechampia spathulata</i> (Scheidw.) Baill. (Euphorbiaceae)	lateral	lateral	pendent, then half-erect at dehiscence	original
<i>Diascia personata</i> Hilliard & Burt (Scrophulariaceae)	erect	lateral	erect	original
<i>Digitalis purpurea</i> L. (Plantaginaceae)	erect to lateral	half-pendent	lateral, then erect at dehiscence	original
<i>Fuchsia</i> sp. (Onagraceae)	erect to lateral	pendent	pendent	original
<i>Gymnadenia</i> spp. (Orchidaceae)	unrotated	rotated 180° (resupinate)	resupinate	Box et al. (2008)
<i>Gymnadenia austriaca</i> (Orchidaceae): apomictic	unrotated	unrotated	unrotated?	Box et al. (2008)
<i>Nemesia</i> sp. (Scrophulariaceae)	erect	lateral	erect	original
<i>Oenothera glazioviana</i> Micheli (Onagraceae)	erect	lateral	erect	original
<i>Papaver rhoeas</i> L. (papaveraceae)	pendent	generally upwards facing	erect	original
<i>Pulsatilla cernua</i>	erect	pendent	erect	Huang et al. (2002), fig. 2
<i>Salvia</i> spp. (Lamiaceae)	lateral	lateral	lateral	original
<i>Silene chungtienensis</i> (Caryophyllaceae)	—	pendent	erect	Niu et al. (2016)
<i>Stylidium</i> spp. (Stylidiaceae)	most erect	most lateral, some species facing upwards	most erect	original

Note: “Erect” is facing vertically upward; “half-erect” is facing upward at an angle between 45° and 90° (90° is vertical); “lateral” is facing sideways, horizontally (=0° ± 45°); “pendent” is hanging or facing downward; “half-pendent” is facing downward at an angle between –45° and –90° (–90° is fully pendent).

(Ranunculaceae) and many other plant species close partially and nod (face downward) at night and in inclement weather (Armbruster, unpublished observations).

Perhaps the most dramatic example of behavioral change in floral orientation is corrective floral reorientation after damage to flower-supporting structures. Many species of flowering plants have the ability to restore optimal floral orientation after mechanical injury caused by inclement weather, falling debris, or animals (Armbruster and Muchhala 2020). These corrective changes can occur through bending of peduncles (e.g., *Dactylorhiza fuchsii*), bending of pedicels (e.g., *Aconitum* and *Delphinium*), or rotation of flowers by twisting of pedicels (e.g., *Stylidium* spp.; Armbruster and Muchhala 2020).

Together these three observations (evolutionary lability, developmental sequences in orientation, and floral behavior) suggest high evolvability of floral orientation via heterochronic changes in bending or twisting of floral stems. Future research could test the prediction that lineages whose members have obvious developmental or behavioral sequences of floral reorientation also exhibit high evolutionary lability in floral orientation at the among-species level.

## 15.5 Preaptations Suggest Paths of Low Evolutionary Resistance

Another clue about evolutionary paths of low resistance comes from the study of the process of exaptation, where the existence of a preaptation appears to greatly increase the likelihood of an adaptive shift (Gould and Vrba 1982). In this view, preaptations are complex traits that coincidentally take on a second adaptive function. Thus preaptations are expected to be rare, but, arguably, evolutionarily important. As noted in section 15.1, the existence of a preaptation and its subsequent co-option into a novel adaptive function (the exaptation process) is often associated with parallel evolution at the macroevolutionary scale. In this section, I focus on several examples of apparent exaptation in plants.

### 15.5.1 Biosynthetic Paths of Least Resistance (Biochemical Exaptation)

Biosynthetic preaptations are probably common in plants, and they most likely indicate evolutionary paths of low resistance. If a secondary compound is synthesized by a plant in a particular place for a particular purpose, it may be easily co-opted elsewhere for other purposes, given that all cells in a plant have the same genetic machinery for biosynthesis. One of the earliest suggestions of the exaptive origins of pollinator attractants was that floral-scent compounds may have originated for defense and secondarily taken on signaling and attraction roles (Pellmyr and Thien 1986). In a series of papers, my collaborators and I tested a similar idea with respect to floral resin produced by *Dalechampia* vines, finding that the resin, which today is involved in attracting pollinators in most species, retains the putative ancestral feature of being defensive against insect herbivores. Curiously, the same oxygenated triterpenoid compounds have later (in the evolution of the genus) been co-opted to again play a defensive role for both floral and nonfloral tissues (Armbruster 1997; Armbruster et al. 1997, 2009).

Another example is correlated evolution (across related species) of blossom color (petals or bracts); leaf or stem color; and in some cases, fruit color. Most of the data are anecdotal, although at least one formal analysis has been conducted. I found that the presence of anthocyanins (red, purple, or deep orange in color) in autumn leaves was a good predictor that maple (*Acer* spp.) lineages would later evolve flowers with anthocyanin-rich (red) petals. In the large sample of species studied, lineages not having red or deep orange autumn leaves never evolved red petals, and instead exhibit yellow or greenish petals, as is basal in the genus. Thus, possessing certain protective pigments in the leaves constitutes a biochemical preaptation for production and use of the same pigments in flowers to attract pollinators (Armbruster 2002). Similar vegetative-flower color correlations were seen in *Dalechampia*, *Solanum*, and *Syringa* (Armbruster 2002; see also Sobel and Streisfeld 2013; Renoult et al. 2014; Larter et al. 2018). Thus, in lineages that already produce anthocyanin pigments for protection of leaves and buds, evolutionary shifts to pollination by butterflies (e.g., pink flowers) or birds (e.g., red flowers, at least in temperate North America) may be particularly easy.

Similar evolvability arguments may hold for evolution of pigments attracting seed dispersers. For example, some strawberry lines (*Fragaria × ananassa*) have both bright-red autumn foliage and red berries, although flower petals are white. In contrast, in the hummingbird-pollinated lineage, *Fuchsia* sect. *Quelusia*, the stems and sepals are red, but the ripe fruit is blue-purple like the petals (see Berry 1989). The leathery capsules of *Euonymus europeae* are

a distinctive deep-pink when ripe (attracting birds to the arillate seeds). The autumn leaves of some varieties are the same distinctive color (at least to human eyes).

### 15.5.2 Morphological Exaptation: Leaves to Bracts

Leaves and floral bracts are serially homologous, and the homology is sometimes very close and hints at an evolutionary path of low resistance for achieving pollinator attraction or floral protection. For example, in the Southeast Asian plant *Saururus chinensis* (Saururaceae), white bracts subtending inflorescences are involved in attracting pollinators, although they are morphologically identical to leaves (Song et al. 2018). In fact, prior to floral anthesis, they are green and indistinguishable from the lower leaves (except by position). After fruit set, the bracts turn green again and look and function like leaves (Song et al. 2018). It is easy to interpret this as an evolutionary path of low resistance in the evolution of pollinator-attraction structures.

The involucrel (subtending) bracts of *Dalechampia* blossoms are a step further along a least-resistance line of evolutionary differentiation. In addition to diverging from leaves in color and function (at least during flowering), they also diverge from leaves in shape. Apparently to more tightly enclose the flowers when closed, the bracts of most species lack petioles. That this morphological transition is “easy” is suggested by occasional developmental errors, when bracts are replaced by leaf-shaped structures, or nearby leaves are replaced with bract-like structures. Another developmental link between leaves and bracts in *Dalechampia* is the correlated shape evolution of the two. Most species with 3-lobed or 3-leafleted leaves have 3-lobed involucrel bracts. Species with unlobed leaves usually have unlobed involucrel bracts. This correlation is also seen in populations of some polymorphic species (e.g., *D. heteromorpha*; Armbruster, unpublished observations).

Once *Dalechampia* bracts were evolutionarily “in place,” serial modifications down various lineages have led to greater divergence from the function of the ancestral leaf. In several independent lineages, bracts evolved the ability to open by day and close protectively by night, perhaps by modification of “sleep movements” seen in many leaves (Darwin 1880; Armbruster 1997). In many *Dalechampia*, the bract movements have evolved to synchronize blossom opening with peak activity periods of pollinators; for example, opening in late morning in *D. brownsbergensis* (Armbruster and McCormick 1990) and in late afternoon in *D. magnistipulata* (Armbruster and Webster 1979). In two independent lineages, bracts have evolved to persist into fruiting and close protectively, enveloping the developing fruits (Armbruster 1997). In both lineages they re-suffuse with chlorophyll, become cryptic, and probably contribute to the photosynthetic budget (Pélabon et al. 2015).

### 15.5.3 Morphological Exaptation: Transitions to Pollen Rewards

A common transition in flowering plants is the transition from rewarding pollinators with nectar to rewarding them with only pollen. A very conservative estimate of the number of independent transitions from nectar to pollen rewards can be obtained by counting the number of plant families identified as containing lineages with species exhibiting buzz pollination (deduced from direct observations and characteristic floral morphology). A survey in 2013 counted 65 families that probably used buzz pollination (De Luca and Vallejo-Marín 2013). This number is a gross underestimate of the total number of transitions to pollen rewards, however, because it omits taxa that have switched to pollen rewards

but not buzz pollination. Phylogenetic analysis of *Dalechampia* indicated 4 or 5 independent origins of pollen rewards in this one genus alone (Armbruster 1993; Armbruster and Baldwin 1998). At least one of these shifts, by *Dalechampia shankii*, involved so little genetic or morphological change that it and its resin-reward sister species were considered conspecific until 1988 (Armbruster 1988b; Armbruster et al. 2009).

Why is this such a common transition and a line of easy response to selection? All plants with hermaphroditic flowers have stamens (the basal condition in angiosperms), and thus have an obvious preadaptation in place for using pollen as a reward. Even when such plants have another reward, such as nectar, there may be some pollinators collecting pollen, setting the stage for a shift in importance of the pollen collectors as pollinators (i.e., exploiting a pre-existing ecological opportunity). Further response to selection for shifting to a pollen reward (e.g., dispersal beyond range of usual pollinators, as for *Dalechampia* colonizing Madagascar; see Armbruster and Baldwin 1998) is then reflected in reduction of nectar production (or, for *Dalechampia*, resin production), with concomitant energy and mineral-nutrient savings.

#### 15.5.4 Morphological Exaptation: Repeated Evolution of Unisexual Flowers Based on a Simple Preadaptation

Another extremely common transition seen across the evolutionary history of flowering plants is a change in the sexual system from hermaphroditic flowers to unisexual flowers (Stebbins 1974; Thompson 1986). Transitions are estimated as, minimally, 100 (Charlesworth and Guttman 1999) and probably many more than this just for dioecy (male and female flowers on different plants) alone (Mitchell and Diggle 2005). To this we can add the many origins of monoecy (male and female flowers on the same plant). As Mitchell and Diggle (2005) point out, this is an exceptionally high level of homoplasy, through both parallelisms and convergent evolution. Evidence of convergence comes from the diversity of developmental-genetic mechanism by which stamens or styles are lost (Mitchell and Diggle 2005, e.g., their figure 7). There are, however, very few, if any, examples of the reverse transition (unisexual to hermaphroditic flowers).

A simplistic explanation for this bias (i.e., the ease of transition to unisexuality) is that it is easier to lose structures possessed than to gain structure not possessed. Thus, it seems more likely that the evolvability side of my equation (15.1) (in section 15.2) is responsible for this bias rather than the selection side. (There is no obvious selective reason to expect loss to be favored over gain.) If this evolvability bias holds true for stamens and pistils, then the presence of both sex parts in hermaphroditic flowers can be viewed as a preadaptation for the evolution of unisexual flowers, creating an evolutionary line of low resistance, as would be consistent with the large number of independent transformations from hermaphroditic to unisexual flowers.

### 15.6 Floral Modularity May Increase Evolvability

Flowers are modular units whose variation is often quasi-independent of variation in vegetative structures (Berg 1960, Armbruster et al. 1999, 2014; Hansen et al. 2007; Pélabon et al. 2011; Conner and Lande 2014;). This floral-vegetative modularity should enhance evolvability of both sets of traits in the face of conflicting selection on floral and vegetative



traits. Modular separation reduces or eliminates trade-offs otherwise manifested through pleiotropy and other integrating processes (see Hansen 2003).

Intra-floral modularity (i.e., when a flower comprises multiple variational modules) may also increase flower evolvability. This modularity may be exhibited at the between-whorl level (e.g., petals versus stamens; Armbruster and Wege 2019; Dellinger et al. 2019b), the within-whorl level (e.g., among stamens in heterantherous flowers), or at the within-organ level (e.g., anther versus anther appendage; Dellinger et al. 2019b). This level of modularity is the subject of increasing research interest, because selection on floral structures diverges if their functions differ (e.g., Ordano et al. 2008; Diggle 2014). For example, response to directional selection for larger petals better to attract the pollinators may be constrained by stabilizing selection acting on floral sexual parts so that they continue to “fit” the pollinator. This generates selection for intra-floral modularity, with variation in pollination-efficiency (sexual) structures decoupled from the variation in attraction structures (such as petals; Rosas-Guerrero et al. 2011; Armbruster and Wege 2019; Dellinger et al. 2019a, 2019b). In some cases, ovaries are decoupled from both of the above modules (Armbruster et al. 1999; Armbruster and Wege 2019).

## 15.7 Discussion and Conclusions

This review identifies properties and trends in flowering-plant evolution that indicate evolutionary lability and allow inference of elevated evolvability. Heterochrony and ontogenetic and static allometry hint at evolutionary paths of low resistance. Another clue comes from the link between developmental and behavioral variation in floral orientation and the divergence in floral orientation among species. The modularity of flowers may enhance their evolvability, both in their variational independence from vegetative traits and in the variational independence of different floral parts with different functions (see Opedal 2019). Another possible indicator of elevated trait evolvability is the rampant homoplasy such traits exhibit. Parallel and convergent evolution seems often to have been facilitated by preadaptations.

This investigation into floral-trait evolvability is based on the assumption that evolutionary lability of a trait reflects, to some extent, its evolvability. Of course, another major factor controlling evolutionary lability is the efficacy of divergent natural selection. Selection and evolvability interact along with other intrinsic and extrinsic factors, respectively, to determine evolutionary lability (see Jablonski 2017a,b, chapter 17).<sup>1</sup> Ideally, one should compare the evolutionary labilities of traits evolving under the same or similar selection regimes, so that differences in lability are more directly attributable to differences in evolvability. This goal is not easily achieved, however, and the attempts employed have often fallen short in this respect. It would have been desirable to contrast the evolutionary labilities of traits likely to exhibit heterochrony or preadaptation, for example, with those unlikely to exhibit such characteristics. The above caveat notwithstanding, it seems fair to argue that selection usually “compares” the pollination and seed-set consequences of floral changes rather than the transition processes themselves, at least if mineral-nutrient and energy demands are fairly similar.

1. References to chapter numbers in the text are to chapters in this volume.

Although a few studies show that population evolvability influences the course of population and species divergence (e.g., Bolstad et al. 2014; Holstad 2020; Opedal et al. 2023), other studies suggest instead that selection does or should overwhelm such evolvability biases at the macroevolutionary scale, at least in plants (see discussion in Bolstad et al. 2014). This may be the case in the evolution of leaf stomatal traits, where among-taxon correlations were apparently the result of selection for adaptive combinations of genetically/developmentally independent traits and not the result of any genetic or developmental factors creating an evolvability bias (Muir et al. 2021). In *Dalechampia*, some traits show among-taxon correlations that are consistent with genetic and developmental biases (e.g., involucre bract size and shape; Armbruster 1991; Hansen et al. 2003; Bolstad et al. 2014). However, other traits, such as gland-anther distance and gland-stigma distance, which influence floral fit with pollinators, show strong among-taxon correlations consistent with their functional interaction (Armbruster 1991; Armbruster et al. 2009), but they lack strong intrinsic (genetic) integration ( $r_A = 0.27 - 0.33$ ; *D. scandens*, Tulum and Tovar populations, respectively; Bolstad et al. 2014) or extrinsic (selective) integration at the within-population level (Armbruster et al., in prep.). These examples underscore the need for caution in interpreting macroevolutionary trends as always reflecting paths of high evolvability. These caveats notwithstanding, examination of macroevolutionary trends can sometimes yield important insights into patterns of differential evolutionary lability and their intrinsic (population evolvability) and extrinsic (selective) causes.

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