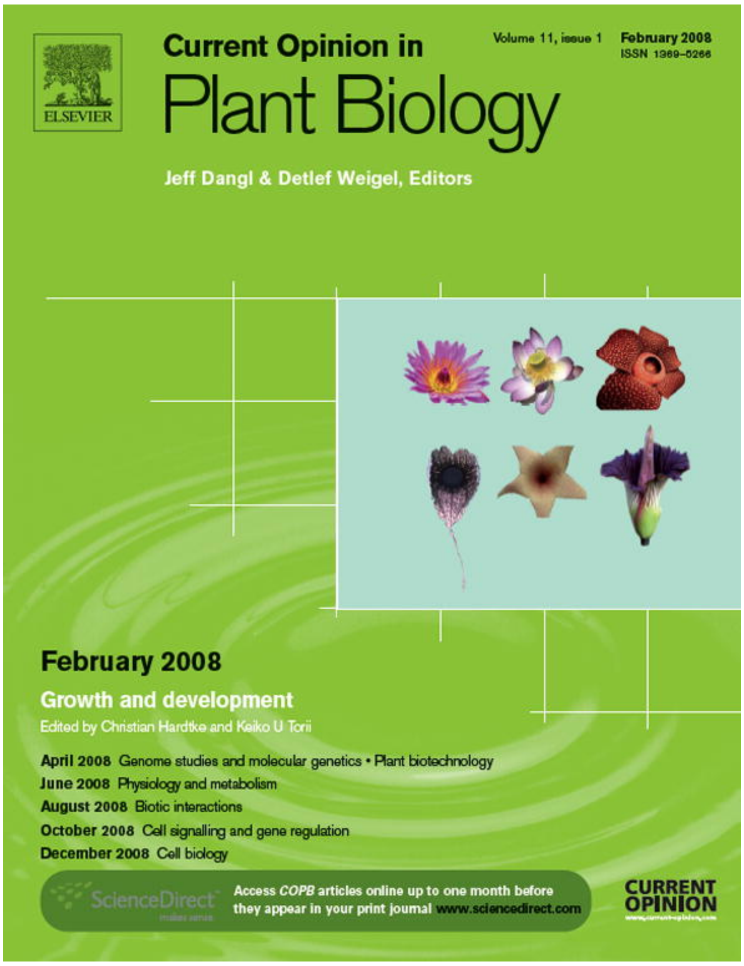
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The evolution of floral gigantism

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Flowers exhibit tremendous variation in size (>1000-fold), ranging from less than a millimeter to nearly a meter in diameter. Numerous studies have established the importance of increased floral size in species that exhibit relatively normal-sized flowers, but few studies have examined the evolution of floral size increase in species with extremely large flowers or flower-like inflorescences (collectively termed blossoms). Our review of these record-breakers indicates that blossom gigantism has evolved multiple times, and suggests that the evolutionary forces operating in these species may differ from their ordinary-sized counterparts. Surprisingly, rather than being associated with large-bodied pollinators, gigantism appears to be most common in species with small-bodied beetle or carrion-fly pollinators. Such large blossoms may be adapted to these pollinators because they help to temporarily trap animals, better facilitate thermal regulation, and allow for the mimicry of large animal carcasses. Future phylogenetic tests of these hypotheses should be conducted to determine if the transition to such pollination systems correlates with significant changes in the mode and tempo of blossom size evolution.

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Introduction

Flowers vary in size from less than a millimeter (*Wolffia*) to almost a meter (*Rafflesia*), making size one of the most variable of all floral traits. Flower size is generally assumed to be the result of a balance between pollination efficiency and the energetic cost of building floral structures. Several studies investigating flower size indicate that pollinators show higher visitation rates to larger flowers or floral displays, because they often provide greater nectar and pollen rewards. The difference in visitation rates between smaller and larger flowers can result in selection for increased floral size (e.g. [1•,2–6]).

Despite broad interest in size increase and its importance in organismal evolution [7], we know relatively little about whether flower size evolution at the extremes of the range is governed by the same rules that act on average-sized flowers. Here we review what is known about floral size evolution in the world's largest flowers, and assess whether unique evolutionary forces are at play. We summarize the many instances of the evolution of floral gigantism and examine the ecological context under which these record-breakers appear to have arisen.

Defining gigantism

The question 'Do the same evolutionary forces act on extremely large blossoms as act on average-sized blossoms?' can only be answered once extreme size is defined (for 'blossom' definition, see Box 1). One criterion would be to consider blossom size relative to the pollinating animal. This would, however, prejudge the kinds of evolutionary forces at play, biasing our sampling at the outset. We will focus instead on lineages possessing the largest blossoms, exceeding ~30 cm in diameter. Although numerous plants have evolved extraordinarily deep tubular flowers, exceeding lengths of 30 cm, our review is focused instead on exceptional size increase in blossom diameter as perceived by the pollinator's approach *en-face* (sensu [8]). The coevolutionary arms race between deep flowers and their long-tongued sphingid moth [9–11] and nectar bat pollinators [12] has been the subject of several recent investigations (including one review), and is thus not considered here.

The evolutionary origins of gigantism

Table 1 lists 14 of the best-studied species, probably representing at least 9 independent origins of gigantism. It will perhaps not be surprising that several large-blossomed species are pollinated by large-bodied pollinators, particularly bats (e.g. *Adansonia*) and nonflying mammals (e.g. *Adansonia*, *Banksia*, and *Protea*). Additionally, some putatively sphingid moth-pollinated flowers (e.g. *Pachira*) are not just deep, but also present a large surface area to approaching pollinators. Despite these more obvious examples, however, what stands out in our survey of floral gigantism is that the most striking examples involve taxa that are pollinated by small-bodied animals such as flies and beetles.

Why has gigantism evolved?

For those giant blossoms visited by large-bodied animal pollinators with high energetic needs, for example

Box 1

- *Blossom*: rather than restrict our discussion to flowers in the morphological sense we also include flower-like inflorescences (as defined in Ref. [15]) that are composed of multiple flowers with one to many attractive floral bracts. Such inflorescences, termed *pseudanthia*, are functionally equivalent to a single flower, so long as the attractive function is similar and pollinators move around the flower-like inflorescence without flying. We would therefore assume that the same selective forces act on multiflowered aroid inflorescences, sunflower heads, or poinsettia cyathia as act on singly flowered roses, tulips, or magnolias. Although the developmental constraints probably differ between pseudanthia and individual flowers (herein referred to collectively as 'blossoms'), the selective tradeoffs affecting blossom size should be similar. Therefore, our concept of blossom gigantism also includes the large, unbranched, multiflowered inflorescence of aroids such as the titan arum (*Amorphophallus titanum*) of Sumatra, which superficially resembles a single giant flower and can reach nearly 3 m in height. However, it does not include loosely branched inflorescences, such as the talipot palm (*Corypha umbraculifera*) of India, and the century plant (*Agave americana*) of the North American desert southwest, which can reach 8 m. Their inflorescences lack attractive bracts and have flowers widely spaced enough that insect visitors would probably fly rather than crawl between them. Additional species with large columnar inflorescences are less easy to categorize. For example, *Echium*, *Lobelia*, *Puya*, and the Hawaiian Island silverswords (*Argyroxiphium*) produce large compact inflorescences, in some cases reaching several meters in height. However, these inflorescences lack subtending bracts that function in attraction, and floral visitation probably requires a non-negligible energy cost for pollinators to move from one flower to the next.
- *Pseudanthium*, a composite inflorescence consisting of multiple flowers subtended by a bract or set of attractive floral bracts, which superficially resembles a single flower.
- *Cantharophily*: pollination by beetles.
- *Sapromyophily*: pollination principally by carrion and dung-flies, but sometimes also by carrion and dung-beetles.

night-blooming flowers that are visited by nectar/pollen foraging bats, it seems reasonable to assume that blossom gigantism is driven by a combination of the need to produce and store sufficient rewards and the need to protect reproductive organs from damage caused by large pollinators. The cases that require more exploration are those involving beetle pollination (cantharophily) and carrion-fly pollination (sapromyophily; less commonly also including pollination by carrion beetles). Rather than artificially lump these, we will consider them in turn.

Beetle pollination: heat and traps

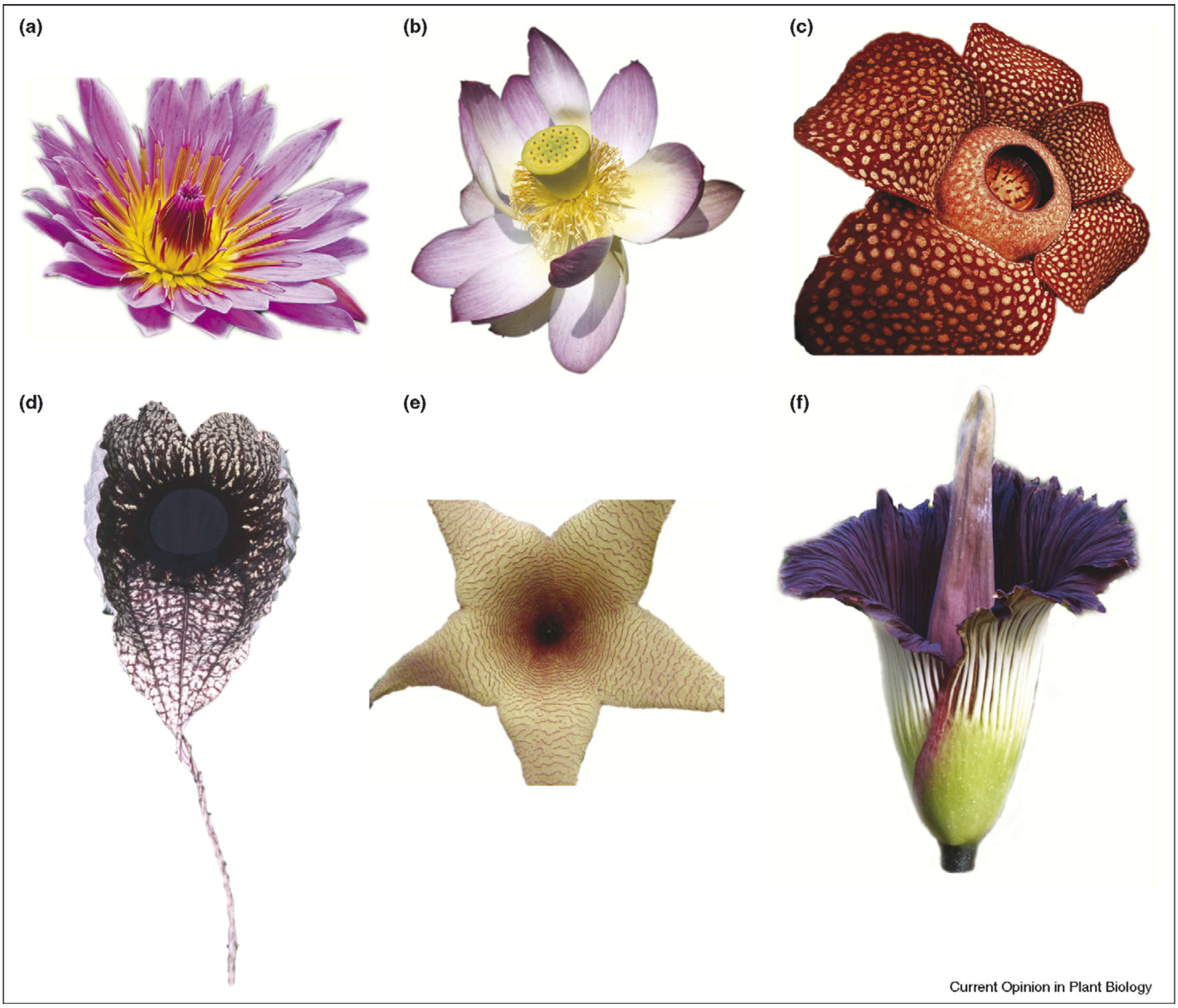
Beetle-pollinated blossoms are typically large in size, often with a broad landing area and open internal space, hence 'chamber blossoms' (Figure 1a,b) [13–15]. They are also usually night-flowering, strongly scented (fecal, fruity, musky, and nutty), pale colored (cream, pink, white, and yellow), and offer copious food rewards (pollen, stigmatic secretions, or specialized food tissues such as sterile male flowers). Beetle-pollinated blossoms have evolved as many as 34 times [13] within angiosperms, and species bearing the largest blossoms are especially common in representatives of early diverging angiosperm lineages (e.g. Nymphaeaceae and Magnoliaceae), monocots (Araceae and Cyclanthaceae), and to a lesser extent eudicots (Nelumbonaceae) [13,16]. In those species with large single flowers, the basic floral form is strikingly similar, involving many tepals surrounding a large central chamber. Indeed for many decades the eudicot *Nelumbo* (Figure 1b) was erroneously classified as a close relative of water-lilies (Nymphaeaceae, Figure 1a) based on the convergent similarities in their flowers [17]. One wonders what selective forces could explain the relatively large number of gigantic beetle-pollinated blossoms because beetles are not especially large pollinators.

Selection tends to favor large blossoms when pollination success increases more rapidly than the energetic tradeoffs of making a larger blossom. There could be a positive feedback mechanism that provides enhanced pollinator service as more beetles visit a single blossom. Increased blossom size could maximize the number of visiting beetles in a single flower, encouraging interactive insect behaviors that result in increased pollination and fertilization [13,18]. For example, it may be that beetles greatly favor blossoms that already have other beetles present because of the increased possibility of finding a mate. The hypothesis that larger blossoms support more beetles and results in disproportionately increased pollination and fertilization can be tested by determining the relationship between reproductive success (via seed and pollen) and the number of beetles visiting a particular sized blossom.

Another common component of beetle-pollinated blossoms is protogyny in which the female parts of the flower mature first and pollination takes place before the male parts release pollen. In these protogynous systems, cross-pollination is facilitated by holding pollinators captive in the blossom sometimes for over 24 hours, and then encouraging them to move from a blossom in the male phase to one in the female phase [16]. Such blossoms may provide chambers (or traps) where beetles are protected from predators and provided with food. Thus, larger blossoms will most probably provide better protection and more abundant food resources for trapped pollinators.

In addition to providing beetles with protection and food, a large number of these blossoms are thermogenic and provide heat as a reward [16] (Table 1). Thermogenesis in floral organs not only augments scent volatilization, but heat may also be a direct energy reward for insect visitors, allowing visiting insects to conserve energy for feeding, mating, and flight. Evidence for this idea comes from the discovery that some blossoms maintain a high, nearly constant internal temperature, despite large fluctuations in environmental temperatures — sometimes at differentials of up to 35 °C relative to ambient [19]. Furthermore,

Figure 1



Giant blossoms: flowers and flower-like inflorescences. **(a)** *Victoria amazonica* (~40 cm in diameter); **(b)** *Nelumbo nucifera* (~30 cm in diameter); **(c)** *Rafflesia arnoldii* (~1 m in diameter; photo © J Holden, with permission); **(d)** *Aristolochia grandiflora* (>1 m in median diameter, including perianth appendage); **(e)** *Stapelia gigantea* (~40 cm in diameter); **(f)** *Amorphophallus titanum* (up to 3 m in height).

it is noteworthy that the temperatures found in some thermogenic blossoms are in the same range as those preferred by active beetles [20,21••] (see also [22••] for a potentially relevant example in a bee-pollinated system).

Small blossoms with high surface-to-volume ratios are unable to retain enough heat to raise their temperature noticeably: studies in aroids have shown that maximum temperature differentials between inflorescence and ambient temperature are directly proportional to inflorescence size [23••]. Therefore, the energetics of thermoregulation in these large chambers may also be an important reason why selection may favor gigantism in beetle-pollinated blossoms.

It is worth mentioning here that thermogenesis in phylogenetically diverse groups is tied to a burst in cyanide-resistant respiration via the alternative oxidase pathway, for example in Araceae, Nelumbonaceae, and Nymphaeaceae [24–26]. However, the way in which thermogenesis is triggered appears to vary. For example, while salicylic acid is the most likely trigger to heat production in Araceae [27], this is not the case in the distantly related Nymphaeaceae [28].

Table 1

The evolution of floral gigantism

Species	Size	Nearest phylogenetic relatives	Thermogenesis	Pollinators	Single flower (Flwr), inflorescence (Infl)
Annonaceae					
Sapranthus palanga [1,2]	Up to 15 cm long	See [3]. *Sapranthus* bears large flowers and is sister to the small-flowered *Tridimeris* (with tepals only 4–6 mm long)	Not known	Beetles (Tenebrionidae, Nitidulidae, and Scarabaeidae), homopterans (Cicadellidae), and bees (*Trigona*)	Flwr
Araceae					
Amorphophallus titanum [4,5]	Up to 3 m in height	See [6]	Yes	Beetles: *Diamesus*	Infl
Dracunculus vulgaris [7]	Up to 1 m in length		Yes	Beetles (Dermestidae, Staphylinidae) and flies	Infl
Philodendron selloum [8–12]	Up to 30 cm in height	See [13]	Yes	Beetles: *Erioscelis*	Infl
Philodendron solimoesense [14]	22–32 cm in height	See [13]	Yes	Beetles: *Cyclocephala colasi*	Infl
Aristolochiaceae					
Aristolochia grandiflora [15,16]	>1 m in median diameter, including perianth appendage	See [17,18]	Not known	Flies: Mainly Phoridae (but also Muscidae and Calliphoridae)	Flwr
Asclepiadaceae					
Stapelia gigantea [19]	Up to 40 cm in diameter	See [20]	Not known	Flies: *Calliphora* sp. (Calliphoridae) and *Musca domestica*	Flwr
Cactaceae					
Cereus peruvianus	Up to 20 cm in diameter	See [21]	Not known	Sphingid moths: *Agrius cingulatus*, *Manduca rustica*	Flwr
Magnoliaceae					
Magnolia macrophylla [22]	Up to 42 cm in diameter	See [23]	Not known	Various beetles, occasional hymenopterans, and moths	Flwr
Malvaceae					
Adansonia grandidieri [24,25]	Up to 23 cm in diameter	See [26]	Not known	Lemurs	Flwr
Adansonia digitata [24,25]	Up to 27 cm in diameter	See [26]	Not known	Fruit bats	Flwr
Nelumbonaceae					
Nelumbo nucifera [27,28]	Up to 30 cm in diameter	See [29]	Yes	Beetles (*Chaliognathus*) and bees	Flwr
Nymphaeaceae					
Victoria amazonica [30,31]	Up to 40 cm in diameter	See [32,33]	Yes	Scarab beetles (*Cyclocephala hardyi*)	Flwr
Orchidaceae					
Phragmipedium grande [31,34]	Petals more than 30 cm long	See [35]	Not known	Probably flies	Flwr
Proteaceae					
Banksia grandis [36]	Up to 10–12 cm in diameter and 40 cm in length	See [37]	Not known	Birds and marsupials	Infl.
Rafflesiaceae					
Rafflesia spp. [38,39]	Up to 1 m in diameter	See [40–43]	Yes, *R. tuan-mudae*	Female calliphorid flies	Flwr
Rafflesia kerrii [39]	70 cm	See [40–43]	Not known	Flies: *Chrysomya villeneuvei*, *C. rufifacies*, *Lucilia porphyrina*, and *Hypopygiopsis tumrasvini*	Flwr

Table 1 (*Continued*)

Species	Size	Nearest phylogenetic relatives	Thermogenesis	Pollinators	Single flower (Flwr), inflorescence (Infl)
Rhizanthes lowii [44,45]	Up to 43 cm in diameter (including appendages)	See [40–43]	Yes	Probably flies	Flwr
Rhizanthes zippelii [45,46]	Up to 20 cm (including appendages)	See [40–43]	Yes	Female carrion flies: *Lucilia*, *Chrysomya*, and *Hypopygiopsis*	Flwr

This table presents a list of species that exhibit extreme floral gigantism (i.e. blossoms of ~30 cm or greater in diameter) as well as examples of species that produce very large, but not enormous blossoms by our criteria. We focused especially on species where pollinator data were available. Our list is not intended to be exhaustive, but instead provides a starting point to orient future phylogenetic and functional investigations of blossom size evolution. In addition, we do not wish to imply that gigantism arose exclusively in these species: it may be that this trait is shared with many of their closest large-blossomed relatives, indicating that gigantism arose earlier in the evolution of the indicated species. We have provided information on recent phylogenetic investigations that include these species, or at least their closest putative relatives, to help pinpoint the evolutionary origins of gigantism in future inquiries. Lastly, it is worth noting that gigantism may have evolved multiple times within some of these families. For example, this trait is shared by several diverse genera of Araceae, suggesting that gigantism may have arisen multiple times within the family. Such a finding would result in an overall increase in the number of times gigantism has evolved. For references see (Supplementary material).

Fly pollination: carrion mimicry

Although plant–pollinator interactions most commonly provide benefits to both parties (mutualism), many plants have evolved nonrewarding mechanisms [29]. Floral mimics, which lure pollinators through deceit, act as parasites on their pollinators. Of these, blossoms that mimic rotting animal carcasses provide the most striking instances of gigantism, and include the world's largest blossoms (Figure 1c–f): *Rafflesia arnoldii* (~1 m in diameter [30]), *Aristolochia grandiflora* (>1 m in median diameter, including perianth appendage [31]), *Stapelia gigantea* (~40 cm in diameter [32]), and *Amorphophallus titanum* (up to 3 m in height [33]). Carrion mimicry has evolved in at least 10 lineages [15,34••] and appears to be commonly associated with increased blossom size (Table 1). Although plants that mimic dung, urine, and decaying plant material can also be large, they are often smaller than carrion mimics.

Sapromyiophilous blossoms may exhibit striking olfactory, visual, and tactile similarity to the carcasses they mimic [15,29,35,36]. They are most often visited by small-bodied carrion flies and occasionally carrion beetles, which are lured into their blossoms in search of brood sites for egg-laying and food. The blossoms are deceptive, however, in that they typically do not provide suitable conditions for the growth and development of insect larvae. As with beetle pollination, sapromyiophilous blossoms typically trap pollinators using contrivances such as 'one-way hairs', 'slipways', and 'seesaw petals' [15]. Some species do produce nominal nectar rewards (e.g. *Rhizanthes* [37] and *Stapelia* [32]) that apparently function in enticement, to extend pollinator visits and/or to provide pollinators with enough energy to seek out other blossoms of the same species. However, it has been noted that nectar production in stapeliads may be more important in excrement mimics than in carrion mimics.

Sapromyiophilous blossoms commonly emit strong and fetid scents. Field and laboratory experiments have documented that carrion flies [34••,38–43] and beetles [44] possess highly acute olfactory systems, and are often initially attracted over long distances by odors. The floral volatiles that have been studied in Araceae [45,46] and *Stapelia* (Apocynaceae–Asclepiadoideae) [34••] are remarkably diverse and extremely faithful to their models in scent composition. Given that scent plays such an important role in the initial attraction of these pollinators, it is possible that large blossoms would be selectively advantageous, providing increased scent production [18,47••], and a wider odor plume [48,49]. An instructive example is *Alocasia odorata* (Araceae). In this species, which attracts visitors principally through its scent because their blossoms are visually concealed by their vegetative leaves, the number of flies attracted to blossoms is directly correlated with the size of the scent-producing appendix [50].

Working in tandem with scent production is the fact that many sapromyiophilous blossoms are also thermogenic (e.g. [51–53]). Thermogenesis in floral organs in these mimics has commonly been thought to augment scent volatilization [36] and to make the blossom more closely resemble a decaying animal carcass undergoing anaerobic respiration [54]. The dragon lily (*Dracunculus vulgaris*), for example, produces meter-long inflorescences consisting of a dark purple spadix surrounded by a leathery spathe [55,56]. When the spathe opens in the morning to reveal its dark and festering, liver-colored surface, the spadix begins to produce heat, and a putrid odor that is attractive to fly pollinators. It would be interesting to know the extent to which the pulse of heat in these blossoms mimics the temperature and duration of heat production in co-occurring corpses on which the mimicry is modeled. Such coincident patterns in temperature change between mimic and model would not be surprising because the decaying carcasses of bear, deer, alligator, and pig exhibit relatively predictable and marked increases in internal temperature several days after death, when body temperatures may rise as high as ~45 °C (nearly 15 °C above ambient) [57]. Under these circumstances, larger size would probably be favored because larger blossoms maintain heat longer and more reliably [23••], and perhaps because increased heat may more accurately mimic a decaying carcass.

Visual cues are also important in carrion mimicry and probably work in concert with olfactory stimuli [41,43,44]. A larger blossom would be a more attractive target of attention, particularly in the dimly lit (and dense) rain forest understory where many of these species occur (e.g. *Amorphophallus*, the largest flowered aristolochias and Rafflesiaceae) or in the dense subtropical underbrush (e.g. *Stapelia* [32]). The color and texture of carrion mimics is also relevant: pollinators apparently cue into their dark red to brown color, which is often accentuated by the sharply contrasting white or yellow blotches on their blossoms (Figure 1c–f) [41,43]. Additionally, their tangled mat of hairs, festering pustules and darkened orifices further add to the visual and tactile sensation of the model. Finally, and perhaps most important, larger carrion may be greatly preferred as brood sites by pollinators, in which case large mimics would achieve higher visitation rates: eggs are laid at disproportionately high rates on large carcasses, presumably because females prefer large brood sites for oviposition [58–60]. This may be because larval mortality is lower on larger brood sites owing to more abundant food resources available to developing larvae. As a result, visitation rates might be greatly enhanced in carrion mimics by incremental increases in blossom size — resulting in strong directional selection for larger blossoms.

Does floral gigantism result from unique selective forces?

We have outlined a series of hypotheses that could help to explain why many of the world's largest blossoms are beetle-pollinated or carrion fly-pollinated: insect trapping, thermoregulation, scent molecule production, and the mimicry of large animal carcasses. As a first approach to testing these hypotheses, it would be valuable to conduct a rigorous statistical phylogenetic analysis to show that transitions to cantharophily or sapromyophily correlate repeatedly with dramatic increases in blossom size. Such a finding would suggest that, indeed these pollination modes favor large blossoms. Such studies should be complemented with rigorous ecological and functional investigations to evaluate whether the mode and tempo of size change in these record-breakers is fundamentally different from that in normal-sized blossoms.

Up until now, only one study has combined detailed phylogenetic information with data on flower size and sophisticated analyses of size evolution to ask whether the tempo of size evolution could be anomalous during the evolution of gigantism. Davis *et al.* [61••] examined flower size increase in Rafflesiaceae. They showed that these species, whose blossoms range in diameter from ~15 to 100 cm, evolved from tiny-blossomed ancestors within the spurge family (Euphorbiaceae), and that the rate of flower size evolution (the average change in log-size per unit time) within Rafflesiaceae was the same as that for closely related, small-flowered spurges. Strikingly, however, size evolution was estimated to have been 91 times faster on the stem lineage of Rafflesiaceae than on any other part of the phylogeny. The blossom size along this single lineage increased at a healthy rate of ~8% per million years under the most conservative estimates, whereas flower size showed negligible directional increase within Rafflesiaceae or among the spurges. Furthermore, as it is more likely that the period of accelerated size evolution was restricted to only a small portion of this lineage's 54-million year duration, the rate of increase in blossom size could have been dramatically higher.

All species of Rafflesiaceae are believed to be sapromyiophilous [30,37,41,62,63], whereas few members of Euphorbiaceae exhibit this pollination system. Therefore, the study by Davis *et al.* suggests that the switch to sapromyophily occurred along the same branch as a massive increase in the rate of blossom size evolution. Although little can be inferred about evolution along the stem lineage of Rafflesiaceae, it is easy to imagine a coevolutionary arms race between deceptive flowers and their deceived pollinators analogous to that driving increases in floral depth in sphingid-pollinated flowers [10]: larger flowers being favored in response to increases in the threshold size for flies to visit a flower (or carcass) and flies being selected for ever larger size thresholds because of the negative effects of being deceived. If this is the case, the pattern of accelerated evolution in Rafflesiaceae could be repeated in other lineages switching to sapromyophily (e.g. *Aristolochia* and *Amorphophallus*), something that could (and should) be evaluated in future phylogenetic studies.

The developmental basis of gigantism

A question not answered for this, or any other system is the nature of the developmental genetic mechanisms that permit flower size to increase rapidly in certain lineages. For example, in the case of Rafflesiaceae, given the multiple origins of pseudanthial inflorescences in Euphorbiaceae [64], we should give attention to the idea, mentioned by Brown in his original description of *R. arnoldii* [65], that its blossoms might be highly modified inflorescences rather than single flowers. The numerous novel features of the reproductive morphology of Rafflesiaceae (e.g. polysporangiate anthers [66] and multiseptate ovaries with many hundreds of ovules per blossom

[67]) makes one wonder if gigantism in this group did not arise through the conglomeration of multiple floral primordia, analogous to the multiflowered inflorescences of the sympatric titan arum. Such a change in the developmental rules of blossom development might have allowed for unusually rapid size evolution by reducing dependence on rare mutations that increase flower size without disrupting floral structure. Although this would be a startling instance of developmental evolution, such a mechanism would not be general because many other gigantic blossoms (e.g. *Aristolochia*, *Magnolia*, and *Victoria*) are unquestionably single flowers.

Conclusions and future directions

Although numerous studies have established the importance of increased floral size in species with normal-sized blossoms, this is the first to summarize size increase in those with extremely large blossoms. We have suggested that a disproportionate number of examples of blossom gigantism occur in cantharophilous or sapromyiophilous species, and propose some explanations as to why these pollination modes might favor the formation of massive blossoms. Such phenomena may account for a pattern of unusually accelerated floral size evolution as appears to be the case with the origin of sapromyophily and gigantism in the world's largest flowers, Rafflesiaceae. In the future, it will be important to conduct rigorous statistical phylogenetic analyses to show that transitions to cantharophily or sapromyophily correlate repeatedly with dramatic increases in blossom size. Additionally, our hypotheses for selective forces acting on blossom size need to be tested using manipulative and correlative field experiments to examine the consequences of blossom size on plant fitness. Beyond that, there is a need for further investigation on the developmental basis of blossom size increase. It is our hope that through such research we can gain a clearer understanding of why the natural world is blessed by the existence of such imposing structures as the *Amorphophallus* inflorescence and such spectacular flowers as *Aristolochia* and *Rafflesia*.

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Appendix A. Supplementary data

Supplementary data associated with this article (i.e. the references to Table 1) can be found, in the online version, at doi:10.1016/j.pbi.2007.11.003.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

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This study of plant–pollinator interactions in a temperate grassland community established that floral visitation was strongly correlated with visual display area: species with larger diameter flowers received more visitors than small diameter ones. This is the first study to examine the importance of floral traits for pollinator attraction at the interspecific level within a community. The authors concluded that if flower size and reward were correlated, as they are within many species (e.g. Refs. [2–6]), this may account for the tremendous variation they documented in floral visitation between species.

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