

inclusive or just. The precarious nature of postdoctoral contracts and the requirement for mobility between countries also go against the principles of inclusivity and diversity. Overall, I also think that we are publishing too much and reading too little. This is driven by the overuse of metrics and rankings to evaluate scientists, courses, universities, journals and so on, as well as the squeezing of our time to think, reflect and mull over. Perhaps we should introduce a maximum yearly publication quota for all researchers — quality not quantity!

### Can you tell us more about your upcoming book *Tropical Arctic*?

*Tropical Arctic* is my first foray into popular science. It is a coffee table book, full of stunning illustrations and art that encapsulate all my passions as a scientist: science–art collaboration, searching for and studying fossil plants, showing that palaeobotany and the study of fossil plants can inform our understanding of contemporary climate change and biodiversity loss, and finally public outreach. The book is illustrated and co-authored by artist Marlene Hill Donnelly and palaeobotanist Ian Glasspool, both of whom were my colleagues at the Field Museum in Chicago way back in the early 2000s. The book has been a long time in the making. It tells a story of global climate change and biodiversity loss and what Greenland's fossil plant record in particular has revealed about the mass extinction event that occurred during the transition from the Triassic to Jurassic periods in the Earth's history. A second and equally important theme throughout the book concerns the processes involved in bringing past species and landscapes to life through scientific illustrations, artistic reconstructions and dioramas. Our book explains and visually demonstrates the artistic and scientific steps that are followed to track Greenland's changing plant species and landscapes through a global climate perturbation and extinction event over 200 million years ago.

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## Quick guide Heteranthery

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**What is heteranthery?** Angiosperm flowers usually possess numerous stamens with pollen-bearing anthers supported by slender filaments. These male reproductive structures generally function to promote cross-pollination and exhibit extraordinary structural diversity among species. The stamens within a flower are usually very similar in appearance, although some species possess two, or occasionally three, structurally distinct types that often differ in reproductive function. This conspicuous morphological differentiation of stamens and anthers within a flower is referred to as heteranthery; it occurs in at least 20 families distributed among 12 orders, and has evolved numerous times. The multiple origins of heteranthery raise intriguing questions about why some plants have evolved this condition and how the different stamen types function during pollination.

Comparative studies of the diverse lineages in which heteranthery occurs indicate considerable variation in the morphological features associated with stamen differentiation, particularly in stamen position and in the size, shape, and colour of anthers (Figure 1). The most common condition involves dimorphism, in which one stamen set is short and centrally located within a flower, often with conspicuous, brightly coloured yellow anthers, and the second is displaced away from the centre of the flower on longer filaments with larger anthers that are frequently similar in colour to the petals or of a contrasting colour. The repeated evolution of these morphological patterns among different plant families strongly suggests that heteranthery is a convergent floral syndrome. Because heterantherous species are exclusively animal pollinated (most often by bees and occasionally by birds), stamen differentiation is likely to have evolved as a result of pollinator-mediated selection. Evidence to support this hypothesis comes from an examination of the traits associated with heteranthery, observations of the

pollination biology of heterantherous species, and experimental studies on the functions of the different stamen types.

### What reproductive traits are associated with heteranthery?

Several traits provide clues on how stamen differentiation functions during the pollination process. Although most animal-pollinated plants produce nectar as the main floral reward for visiting pollinators, flowers of most heterantherous species are nectarless. Instead, pollinators collect the protein-rich pollen, which they use for provisioning their nests.

In many nectarless flowers, pollen is released from anthers through a small apical pore at the tip of the anther. Visiting bees grasp the stamens and sonicate flowers using their indirect flight muscles. This causes pollen grains to bounce around inside the anthers until they are eventually ejected through the apical pore. This pollination mechanism is referred to as 'buzz pollination' and occurs widely among nectarless, bee-pollinated angiosperms and is especially common in heterantherous species.

Another reproductive condition commonly associated with heteranthery is enantiostyly, a floral polymorphism in which the elongated styles of female reproductive organs (pistils) are deflected either to the right or left side of the flower. Typically, as in *Cyanella alba* (Figure 2), style deflection is accompanied by a single large stamen positioned on the opposite side of the flower. The reciprocal arrangement results in two flower types that are mirror images of one another. This form of floral asymmetry has evolved in at least ten angiosperm families. The frequent association of enantiostyly, heteranthery, the loss of nectaries and buzz pollination suggests that this syndrome of traits functions to increase the precision of cross-pollination by bees. Indeed, experimental studies of enantiostylous *Solanum rostratum* (Figure 1A), a buzz-pollinated relative of tomato, have demonstrated that sex-organ reciprocity, in association with heteranthery, functions to promote cross-pollination between left- and right-styled flowers and reduce levels of self-pollination within and between flowers on a plant.





**Figure 1. Diverse angiosperm flowers with heteranthery.**

(A) *Enantiostylous Solanum rostratum* (Solanaceae) exhibiting a large brown pollinating anther with poricidal anther dehiscence on the opposite side of the flower to the style. (B) *Melastoma malabathricum* (Melastomaceae), with cryptically coloured pollinating anthers and yellow feeding anthers. (C) *Lagerstroemia indica* (Lythraceae) with yellow feeding anthers that contain sterile pollen. (D) *Dilatris corymbosa* (Haemodoraceae), with a striking difference in the colour and size of the pollinating anthers (red) and the feeding anther (yellow). (E) *Enantiostylous Heteranthera limosa* (Pontederiaceae), with conspicuous yellow feeding anthers in front of the yellow nectar guides and a single blue pollinating anther deflected to the side of the flower. (F) *Clarkia dudleyana* (Onagraceae), with two stamen sets that disperse pollen at different times. Note the pink cryptically coloured anthers have not yet dehisced. (Panel (F) image from Kay *et al.* (2020), © The Royal Society (CC BY 4.0).)

**What is the adaptive significance of heteranthery?** Pollen grains are the agents of male gamete dispersal, and nectarless flowers therefore represent an intriguing evolutionary conundrum. The consumption of pollen by bees has the potential to reduce the number of pollen grains participating in cross-pollination, thus limiting plant reproductive fitness through male function. However, this sexual conflict has been resolved in many heterantherous species because the different stamen types within a flower are specialized for either pollinating or feeding functions. Specifically, the large and often cryptically coloured pollinating anthers deflected to the right or left side of the flower surreptitiously place pollen on either side of the bees' bodies while they actively collect pollen by buzzing the conspicuous, centrally located yellow feeding anthers (Figure 3B). This functional division of labour

is today the most widely accepted explanation for the evolution of heteranthery, but the origin of this idea has a long and venerable history going back to the 19<sup>th</sup> century when Charles Darwin and the German naturalist brothers Fritz and Hermann Müller were captivated by heterantherous flowers.

Darwin suspected that the two stamen types within a flower had different reproductive functions but he was not able to deduce what these functions were. It was not until Fritz Müller corresponded with Darwin, and he and his brother Hermann Müller wrote several papers in the journal *Nature* on various species possessing heteranthery, that the pollinating and feeding functions were first elucidated. Today, there is abundant observational and experimental evidence from species in diverse unrelated families, including Commelinaceae, Fabaceae, Lythraceae, Melastomaceae,

Pontederiaceae, Solanaceae and Tecophleaceae to support the contrasting functional roles of pollinating and feeding anthers in heterantherous flowers. Although the conspicuous feeding anthers are usually more attractive to bees and are preferentially manipulated during foraging, pollinating anthers export significantly more pollen to the stigmas of other flowers. However, not all bees are capable of mediating a division of labour between stamens: only those species that are able to buzz flowers (about half of all bees) are able to do so, with bumble bees (*Bombus*) and carpenter bees (*Xylocopa*, Figure 3B) being especially effective.

**Does stamen differentiation have other functions?** The division of labour hypothesis provides a satisfying functional explanation for the evolution and maintenance of stamen



**Figure 2.** The two flower types of enantiostylous *Cyanella alba* (Tecophilaeaceae) with right- and left-deflected styles and heteranthery.

The reciprocal arrangement of the style (S) and pollinating anthers (PA) in enantiostylous plants promotes pollination between the mirror image flowers. Note the single pollinating anther and five feeding anthers (FA).

dimorphism in most heterantherous species. However, the expression of heteranthery can vary among angiosperm lineages and there is evidence that stamen differentiation can also serve an alternative reproductive function in some taxa. For example, although heteranthery in *Clarkia* (Onagraceae) has several features in common with the more typical heterantherous species — flowers are bee pollinated and exhibit colour crypsis of one stamen whorl — *Clarkia* flowers produce nectar and the two stamen sets mature and disperse pollen at different times. Pollen is initially hidden from pollinators in the cryptically coloured, late-dehiscing stamens and only becomes available for dispersal once dehiscence is over in the early maturing stamen set. Moreover, there is no evidence that the stamen sets

specialize in pollinating and feeding functions, and pollen is transported to stigmas of other plants in similar proportions.

In *Clarkia* the gradual presentation of pollen to pollinators extends the duration of male function in flowers. What might be the advantage of such a gradual pollen-dosing strategy? Floral biologists now appreciate that the simultaneous presentation of pollen by flowers can be associated with diminishing returns to fitness through male function, due to pollen loss by pollinator grooming, and many angiosperm species have evolved floral mechanisms that limit the amount of pollen removed by individual pollinators. In *Clarkia* the temporal differentiation of pollen release between stamen types is likely to limit pollen losses via grooming and also results in more pollinators visiting flowers, resulting in greater mate diversity. Thus, according to this hypothesis, heteranthery has evolved as a consequence of intrasexual selection for male outcrossed siring success.

**What unresolved questions on heteranthery remain?** Although heteranthery occurs in numerous species of Fabaceae and Melastomaceae, its distribution among other families is scattered and within-flower stamen dimorphism in angiosperms is a rare condition. It is unclear why this should be, especially since nectarless flowers and pollen-collecting bees are not uncommon, and it is possible that developmental constraints in many lineages limit

opportunities for the evolution of within-flower stamen differentiation.

Research on a wider range of species would be valuable to determine the extent to which the pollen produced by different stamen types in heterantherous species differs in chemical composition and fertilization potential. Pollen produced by feeding anthers might be expected to have lower viability, since in many species it participates less often in the pollination process. The evidence at this stage is mixed; in most species, pollen from both stamen types is functionally similar, although differences in pollen performance and viability have been reported.

Finally, virtually nothing is known about the underlying genes and developmental pathways responsible for within-flower stamen differentiation. Comparative transcriptome analysis targeting species from diverse lineages would undoubtedly provide novel insights into the mechanisms governing this fascinating reproductive adaptation.

**Where can I find out more?**

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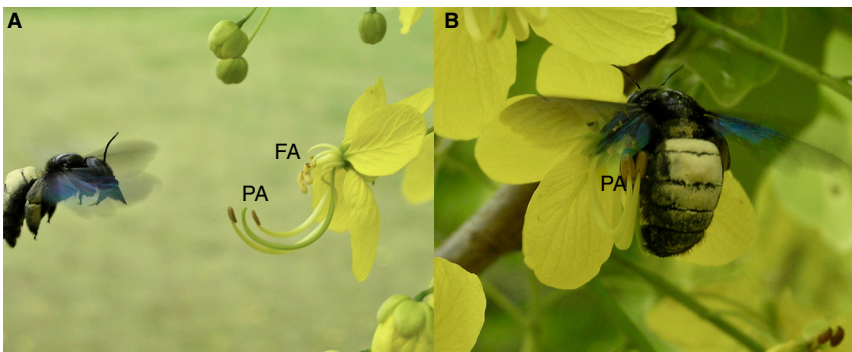
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**Figure 3.** Pollination of *Cassia fistula* (Fabaceae) flowers by a carpenter bee (*Xylocopa*). (A) Bee approaching a flower to collect pollen. (Image from Barrett (2010) © The Royal Society.) (B) Carpenter bee buzzing the feeding anthers while pollinating anthers deposit pollen on its side. PA, pollinating anthers; FA, feeding anthers.

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