

# When orchids challenge an island race...

## Part 4: The tropics

In the last of four articles exploring the challenges posed to orchid systematists by studies pursued on islands, DAVID ROBERTS and RICHARD BATEMAN consider the orchid floras of tropical islands, focusing on those offshore from sub-Saharan Africa

ACCORDING TO STUESSY & ONO (1998), 'oceanic island archipelagos are profoundly interesting ecosystems in which to ask questions about evolutionary patterns and processes. Their isolation from other landmasses restricts numbers of plausible hypotheses that can be advanced to explain evolutionary events, often resulting in stronger scientific inferences. Island archipelagos may rightly be considered

one of the best places on earth to understand origins and elaborations of biological diversity.' In other words, islands generally offer simpler ecological systems than continents in which to explore evolution – a fact that was not entirely lost on Charles Darwin during his famous sojourn on the Galapagos. We might therefore hope that the genesis of tropical island orchid floras would prove to constitute a relatively tractable set of problems.

### How do islands form?

The first paper of this series reviewed several conceptual issues surrounding island floras, not least how best to define an island. We stretched beyond the obvious 'chunk of terra firma surrounded by water' to consider the considerable significance of the size of the 'chunk' and to explain that mountains and, on a smaller scale, single emergent trees can be viewed as ecological islands (albeit separated by 'fuzzier' boundaries than oceanic islands). However, we did not discuss how conventional islands are formed.

**Continental islands:** The UK is currently an island system, though only just – a mere 32km of shallow water separates Dover from Calais at present. Moreover, the British Isles were connected to continental Europe long before the advent of the Channel Tunnel, during glacial periods when sea levels dropped sufficiently to expose the bed of the English Channel. Since sea-level changes are a global phenomenon (ask any student of global warming), many islands in the Southeast Asian archipelago experienced similar shifts in their geographical status. In the Gulf of Guinea, offshore from West Africa, the island of Bioko was once joined to the mainland, or at most separated merely by a muddy puddle. The island status of such places, attached as they are to continental crust, is always tenuous.

**Tectonic rafters:** The second type of islands can be termed 'tectonic rafters'. Such islands succeeded in separating from a larger 'parental' landmass and floating away on their own tectonic plate. Some such islands have been isolated for a long time; for example, Madagascar separated from mainland Africa c140 million years ago, a little before the time when the orchid family is estimated to have



Photographs from Mascarene Islands by David Roberts



originated. Other tectonic rafters are far more recent, while yet others have still to separate. For example, the Horn of Africa is set to cross the Indian Ocean over the next 50 million years before smashing into the west coast of India, while parts of California could eventually find themselves docking with Hawaii!

**Hotspot islands:** Both continental islands and tectonic rafters already possessed well-established floras, including orchids, when they found themselves 'afloat'. In contrast, 'hotspot' islands such as Hawaii and the Galapagos are forged within the oceans from magma injected through relatively weak spots in the thin oceanic crust. These underwater volcanoes eventually break the ocean surface, but they must then

be colonised from scratch. We have been able to observe this process directly on Anak Krakatau, the modest volcano that emerged from the centre of Krakatau in 1928, following its infamous 1883 eruption. Because they begin as sterilised landscapes and have never been connected to a major landmass, such islands are relatively depauperate in orchid species. However, even the staunchest boundary to colonisation eventually proves 'leaky.'

#### How do orchids colonise islands?

The exceptional dispersability of dust-like orchid seeds in air currents over considerable distances has even allowed successful colonisation of islands such as Hawaii, some 1,000km from the nearest seed source. How-

**Above left:** *Jumellea recta* on La Réunion

**Above:** *Jumellea triquetra* on La Réunion

ever, seed dispersal is only the first step in the successful invasion of an island. The seed must fortuitously land in a suitable place to germinate, on a surface proving a compatible mycorrhizal fungal associate. The resulting seedling must then survive long enough to flower. And if that was not enough of a challenge, it has to form a relationship with a pollinator that is sufficiently competent to remove its pollinia but not so competent that it refuses to visit another compatible flower – one that has opened in the vicinity of the first and at the same moment in time. This outcome is the equivalent of acquiring the Thunderball in ➤

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the great colonisation lottery. Fortunately for orchid enthusiasts, the vastly improbable becomes probable over a geological time-scale.

**Sex outside the city: Baker's Law and reproductive assurance**

It is often stated, with some justification, that orchids are among the most specialised of all flowering plant families. Not surprisingly, therefore, they tend to evolve specialised pollination systems. Whereas many flowering plants rely on various chemical inhibition systems to prevent self-pollination and promote outcrossing (breeding with a different individual of the same species, so that the parents are likely to have modest genetic differences), most orchids are self-compatible. Rather than chemical compatibility barriers, they have evolved floral mechanisms that promote out-crossing through attracting, and influencing the behaviour of, appropriate pollinators.



*Cryptopus elatus*, a scentless and nectarless species from La Réunion

This confers on orchids an advantage in colonising new territory, as there is no longer an absolute need for a second compatible plant in order to generate viable seeds. Even pollinators, though undoubtedly helpful, may not be essential. In addition, the plant may be able to resort to vegetative reproduction (typically by forking of its rhizome) or to seed production without sex

**Above left:** *Angraecum cucullatum* on Mauritius  
**Above:** *Angraecum borbonicum* on La Réunion

(termed apomixis). These advantages of self-compatibility have become known as Baker's Law (Baker 1955).

As a result, we find that orchid species on tropical oceanic islands exhibit two contrasting strategies to achieve successful reproduction. Many species emulate those of tropical rain forests in producing low frequencies of viable fruits. In contrast, the second group shows much higher levels of fruiting success due to efficient self-pollination.

This approach to what is known as reproductive assurance is evident in the endemic species of *Jumellea* from the island of La Réunion in the Mascarene Island archipelago, which are pollinated by hawkmoths. In order to succeed, these have either reduced the size of their floral spurs to better fit the probosces of the moths, or they have become self-pollinating (Figs 1 and 2).

### What does reproductive assurance mean to an island orchid?

Ultimately, reproductive assurance means that the orchid passes on its genes to the next generation. However, reproductive assurance also means that characters such as floral display, scent production and method of nectar presentation are no longer selected for by the relevant pollinator(s). What is the point in having characters that are supposed to elicit pollination if no pollinator is present to appreciate them?! Thus, although the genus *Angraecum* is well known for producing a strong scent at dusk to attract hawkmoth pollinators, *A. borbonicum*, endemic to La Réunion (Figs 3 and 4), has lost its scent (Dr Thierry Paillet pers. comm).

In its putative mainland ancestor (in this context, even Madagascar constitutes a relative 'mainland'), the ability to attract an effective pollinator must outweigh the considerable energetic cost of producing the scent. But if the species becomes self-pollinating, the pollinator is eliminated from the equation and therefore scent production becomes irrelevant to the orchid's long-term well-being. Once selection has been relaxed, there is no longer pressure to purge from the population the mutations that prevent scent production. Furthermore, the energy the orchid saves by not producing a scent can usefully be reallocated elsewhere, toward higher priority objectives such as producing healthy fruit.

Could such a process help explain one of the greatest orchid-related mysteries yet to be solved: how did deception (the evolutionary loss of a pollinator reward, most commonly nectar) arise in the orchid family as an evolutionary stable strategy? (Fig 5)

There are, of course, good reasons why the majority of plants cross-pollinate. Notably, self-pollination

allows much easier perpetuation of morphological novelties that reflect genetic mutations, most of which are competitively inferior to their parents. However, competition is often lower on islands, increasing the probability that such 'hopeful monsters' will be perpetuated to form new evolutionary lineages (Bateman and DiMichele 2002).

Potential examples of such monsters from La Réunion include the endemic genus *Bonniera*, which probably evolved from an ancestor resembling *Angraecum conchoglossum* when the labellum was replaced by a less differentiated petal-like organ (Bateman and Rudall 2006). This developmental shift has also resulted



*Cynorkis* sp. nesting in recent lava flow on the rim of a volcano on La Réunion

in the loss of the spur and therefore of nectar production. Other, admittedly less dramatic, modifications are evident in several species of *Cynorkis* indigenous to the island, where the labellum has again been reduced in size to a petaloid-like organ, although in this case discrete markings have persisted (Fig 6). The morphological shifts do not appear to have hindered the evolutionary success of *Cynorkis* on La Réunion.

### A rough guide to altitudinal aspects of island hopping

Most of us associate landing on a deserted island with crawling up a beach, as archetypically portrayed by Tom Hanks in the film *Castaway*. Setting aside the fact that Hanks would dismally fail Baker's Law, since his beloved volleyball would ultimately prove to be a rather unsatisfactory reproductive partner, this image is misleading in another sense. Specifically, an orchid seed descending from air currents (or even carried on the foot of a bird) could land anywhere on the island. Relative colonisation success is of particular interest on islands such as La Réunion that reach considerable altitudes. By identifying and comparing zones of maximum species richness on islands we can explore whether orchids transfer horizontally – in other words, to a similar altitude on the island that they occupied in their original source terrain.

It is widely recognised that species richness commonly peaks at intermediate elevations. If the range of a species centres on the mid-elevation level, then the species has a greater potential to occupy more of the island, as in theory it can expand with equal ease to the top and bottom of the island. However, if the mid-point of a species' range occurs at the bottom or the top of the altitudinal range offered by the island, that species can spread within the island in only one direction – up or down, respectively. Widespread species therefore have mid-points near the centre of the elevational range, whereas localised species with a narrow altitudinal range are equally likely to be found anywhere across the elevational gradient. It follows that the greater the proportion of widespread species in a particular orchid flora, the greater the likelihood that species richness will peak

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toward the middle of the altitudinal range of the island – a phenomenon technically termed the ‘mid-domain effect’ (Colwell and Lees 2000).

If we once again consider the Mascarene Islands (Mauritius, La Réunion and Rodrigues), they lie c900km east of Madagascar. Morphological and DNA-based studies suggest that the lineages that have diversified to give the Mascarene Islands their orchid flora of c150 species originated from among the 960 species of orchids that are currently considered to occupy Madagascar. Nonetheless, the mid-domain effect explains much of the contrast in relative frequencies of endemic orchids among these islands. The similarity in altitude of Madagascar (2,876m) and La Réunion (3,069m) is reflected in the behaviour of their respective orchid floras, whereas there is a strong contrast between the distributions of comparable orchids on La Réunion (**Fig 7**) and nearby Mauritius (**Fig 8**), which rises to only 828m. These observations suggest that a species has difficulty escaping from its original altitudinal range, even when it colonises an island over three times the height of the source terrain on which it evolved (Roberts & Brummitt 2006).

In contrast, no such pattern is evident when we compare the orchid floras of the Gulf of Guinea Islands (Annobon, Sao Tomé, Príncipe and Bioko), 60–300km off the West African coast. Like the Mascarene Islands, the Gulf of Guinea archipelago evolved from a volcanic hotspot. However, the much closer proximity of the Gulf of Guinea islands to the African mainland has permitted multiple colonisation events by orchids. The effect of the proximity to major landmasses can be seen in the percentage of endemic



**7** Dramatic landscape on the high-altitude Mascarene island, La Réunion

orchid species (ie those unique to the island), which is 11 percent for Príncipe and 16 percent for Bioko, which may have been connected to the mainland during the last glacial period. In contrast, the 68 percent endemism observed in the isolated Mascarene Islands suggests that there is little movement of orchids between the islands and mainland but considerable movement among the islands.

### How do islands become enriched in species?

The most important factors determining the species richness of an island are its age, size and distance from potential sources of immigrants. Altitudinal extent and diversity of geological substrates also strongly affect the ability of the island to differentiate habitats and thereby to multiply niches that could potentially be occupied by orchids. It has also been suggested that species diversity might itself help to drive speciation



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Less dramatic landscape of the low-altitude islands of the Mascarene Islands - view from Flat island, Mauritius, of the northern off-shore islands

(Emerson and Kolm 2005).

Increasing the number of species present increases the number of likely ecological interactions, which in turn increases the number of potential niches that can then be filled by novel species – this is a classic ‘positive feedback loop’.

Such ‘niche-filling’ and subsequent speciation has been documented on La Réunion, where Thierry Pailler recently captured on film the pollination of one of the endemic species of *Angraecum*, *A. striatum*, one of three species from the endemic section *Hadangis*. It was effected not by the expected hawkmoth but rather by a bird, the white-eye. This, and two other closely related endemic species, may have evolved to fill an available niche as a result of the depauperate hawkmoth fauna of the island.

Why then are the orchid floras of islands not even more diverse? The main factor that discourages a veritable explosion of species is extinction. This can reflect the absence or precariousness of a particular habitat. For example, *Bulbophyllum variegatum*

has been extirpated from Mauritius and is declining on Réunion, where it grows epiphytically on only one species of tree – a tree that has a regrettable predilection for an unpredictable substrate, specifically recently extruded lava flows. However, extinction is typically caused by competition among species for finite resources such as nutrients or the attention of pollinators. In this context, Baker’s Law has important implications for conservation, since it implies that increased pollinator specialisation and/or self-incompatibility will predispose a species to extinction. Self-pollinating species may therefore be better suited to survive in the current changing climate due to reproductive assurance and the ability of some species to maintain a dual reproductive strategy, indulging in outcrossing when conditions permit but using self-pollination as a back-stop.

In conclusion, there is little doubt in our minds that a deep understanding of the biology of orchids is an essential prerequisite to their successful conservation. Nowhere is this statement more true than on tropical islands. ■

## REFERENCES

- Baker, HG** (1955) Reference to come
- Bateman, RM & DiMichele, WA** (2002) Generating and filtering major phenotypic novelties: neoGoldschmidtian saltation revisited. In QCB Cronk, RM Bateman and JA Hawkins (eds), *Developmental genetics and plant evolution*. Taylor & Francis, London
- Bateman, RM & Rudall, PJ** (2006) The Good, the Bad, and the Ugly: using naturally occurring terata to distinguish the possible from the impossible in orchid floral evolution. *Aliso* 22: 481–496
- Colwell, R K & Lees, D C** (2000) The mid-domain effect: geometric constraints on the geography of species richness. *Trends in Ecology and Evolution* 15: 70–76
- Emerson, BC & Kolm, N** (2005) Species diversity can drive speciation. *Nature* 434: 1015–1017
- Roberts, D L & Brummitt, NA** (2006) The influence of geometric constraints on the colonisation, speciation and range expansion of orchids. Proceedings of the 17th AETFAT Congress (Addis Ababa, Ethiopia) [in press]
- Stuessy, T F & Ono, N** (eds) (1998) *Evolution and speciation of island plants*. Cambridge University Press

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