Solving the **hammer orchid** puzzle

American biologist John Alcock tries to reconstruct the evolutionary steps that gave rise to the bizarre flowers of Western Australia's amazing hammer orchids.

by John Alcock

When Charles Darwin visited Western Australia in March 1836, as naturalist aboard HMS *Beagle*, he went ashore at Albany just long enough to collect some rocks and observe a corroboree. He remarked: 'I do not remember, since leaving England, having passed a more dull, uninteresting time'.

Darwin had already spent four seasick years on the *Beagle* and was eager to return to England. Perhaps the time of year also influenced his failure to appreciate his surroundings. Had he come in spring or early summer, surely he would have been impressed by the variety of flowering plants in the vicinity of Albany. A visit in September or October, instead of March, could well have produced an encounter with a hammer orchid (*Drakaea* species), which alone would have guaranteed a good report from Darwin on WA.

First 'flower'

My claim about Darwin's reaction to a hammer orchid stems partly from the fact that, when in eastern Australia, he lamented his inability to find a flying duck orchid (several species of which also flower near Albany in the spring), whose unusual flower he longed to see. Moreover, I have my own reaction to hammer orchids to draw upon.

Although my first encounter occurred some 20 years ago, I vividly recall the intense delight I felt when Andrew Brown, now the coordinator for threatened flora with the Department of Conservation and Land Management's (CALM's) Threatened Species and Communities Unit (WATSCU), steered me to a specimen not far from Albany. When he pointed to a skinny little orchid, perhaps 15 centimetres tall, growing in sandy soil, I dropped to my knees in admiration (and to get a better look at the plant).

The flower in front of me was hard to recognise as a flower of any sort. Five of its six petals and sepals were insignificant, being thinner than matchsticks and tan in colour. The remaining petal, a hinged rod projecting at right angles from the stalk, was even less flower-like. The 'rod' terminated in a strange cylinder-like object vaguely resembling the head of a hammer,

Previous page
Main The late hammer orchid (*Drakaea confluens*), is characterised by its late bloom.
Photo – Bert and Babs Wells/CALM

Above The warty hammer orchid has a hinged flower petal.
Photo – John Alcock

Right John Alcock photographing an orchid.
Photo – Andrew Brown

which to my eye actually looked more like a miniature bicycle seat. Andrew had directed me to a hammer orchid called king-in-his-carriage (*Drakaea glyptodon*). This species and my personal favourite, the even stranger warty hammer orchid (*Drakaea livida*), are reasonably common in appropriate native habitats, but, for me, they are always thrilling to find in the wild.

Anyone seeing a king-in-his-carriage, a warty hammer orchid or any of the other seven members of the genus for the first time would surely wonder about the purpose of their bizarre flowers. The conspicuous, colourful ornaments of so many run-of-the-mill plants are designed to entice an insect, bird or other animal to collect nectar or pollen. The visitor may incidentally pick up and carry some pollen to another plant, where it may be deposited on the pollen-receiving surface of that plant's flowers. When this happens, the pollen grains grow long tubes that reach down into the ovary of the plant, carrying the botanical equivalent of sperm into position to unite with egg cells, which develop into seeds that will give rise to the next generation.

Sexual allure

Hammer orchids, in contrast, produce small, inconspicuous flowers that do not offer even a drop of nectar to their visitors. And yet, as Andrew explained to me, these orchids still

Above The warty hammer orchid's labellum (modified petal or lip) resembles a female wasp.
Photo – John Alcock

Top right and right Wasp landing on a king-in-his-carriage orchid, then trying to fly away with the labellum.
Photos – Babs and Bert Wells/CALM

attract some exceedingly eager visitors. Each species of hammer orchid has a special relationship with a different wasp species. Male wasps find the extraordinary lip petal (called the labellum) of the orchid so appealing that they actually attempt to mate with it. This modified petal lures male wasps of the right species by releasing an odour—similar to that wafted into the air by sexually receptive female wasps—from dark glands on its surface. Male wasps drawn to the plant by its false sex pheromone see the labellum, which vaguely resembles the wingless females of their species. Some males then pounce upon the decoy 'female'.

Receptive female wasps contacted by a male permit their partner to carry them away to copulate elsewhere, usually on native flowering plants on which they both feed. Hammer orchid decoys that are grasped also fly away with their 'partner', but do not go far. Instead, the decoy and the male wasp travel in a narrow arc whose radius is dictated by the length of the rod between the decoy and the flexible hinge on the labellum stalk. In short order, the male wasp finds himself upside down before slamming into the pollen masses at the top of the 'column', which is the only other semi-prominent feature of the hammer orchid flower. This stalked device applies glue and one or two sacs of pollen to the back of the wasp. The presumably startled wasp then releases the pseudo-female and flies off, perhaps wondering what has happened to him. Should the male be fooled again, he will transfer pollen from the first orchid to the second, applying it to the stigma (the pollen-receiving component of the column), just below the pollen masses at the top of this structure.

Darwin would have been fascinated by this story of sexual deception. He was so fond of orchids that his first book after *On the Origin of Species* was entitled *The Various Contrivances by which Orchids are Fertilised by Insects*. In this book, he explored in great detail just how the various component parts of certain orchids help them to become pollinated. Darwin devoted himself to the mysteries of orchid pollination because, by showing that he could make adaptive sense of these intricate flowers, Darwin was demonstrating the value of his theory of natural selection. He examined orchids from all over the world, but, unfortunately, never became acquainted with a hammer orchid.

Darwinian dilemma

The very complexity of the hammer orchid's flower presents a challenge to Darwinian theory, because so many of its features seem 'designed' to interact with one particular kind of pollinator. A plant whose labellum lacked either the 'right' odour, the 'right' shape or the 'right' hinge would

seem destined to fail to reproduce, so that one might think that the orchid had to be created in its current form to be pollinated. However, evolutionary biology is founded on the premise that every living thing is the product of a long series of changes. If we applied this view to hammer orchids, we would have to solve the puzzle of figuring out what its antecedents might have looked like and how they might have managed to become pollinated.

To describe the evolution of a complex structure, such as a human eye, a bat's wing or an orchid's flower, biologists often look for clues among the relatives of the species in question. Sometimes, groups of organisms vary in the degree of complexity of an attribute, and this can be very helpful for evolutionary detective work. The stunningly complex eyes of humans are merely one example of a great array of devices for seeing. The far-less-elaborate mechanisms of vision in many other animal species help us to imagine what the precursors of human eyes might have been like—an important step in developing a hypothesis on the evolution of more complex eyes.

The comparative angle is readily available for hammer orchids, because south-western Australia has in the order of 300 species of orchids. As a North

Above Habitat of the late hammer orchid.
Photo – Andrew Brown

Left Scented sun orchid.
Photo – John Alcock

Below Lemon-scented sun orchid.
Photo – Andrew Brown

American, I experience severe orchid envy whenever I hear this figure bandied about (there are only about 30 orchid species in my home state of Arizona). In contrast, the amazingly diverse orchids of south-western Australia offer exceptional potential for comparisons that might cast light on the gradual evolution of hammer orchids.

Some WA orchids, like sun orchids (*Thelymitra* species), have lovely but not terribly unusual looking flowers. Their fairly large and colourful petals and sepals are arrayed in much the same way as those seen in tens of thousands of other flowering plants. Because this sort of arrangement is so common, and because sun orchids are genetically quite similar to hammer orchids, we can infer that a distant ancestor of hammer orchids exhibited this flower pattern.

Lip lineage

The next step surely would have involved the gradual modification of one petal into a distinctive labellum. Most WA orchids, including all spider orchids (*Caladenia* species), have a special highly modified labellum. While this group is not as closely related to hammer orchids as the sun orchids, the great variety within the spider orchids can still provide clues about how forms of the labellum may have evolved. Of special interest are the many variations in the size, distribution and colour of the glandular calli found on the labellum of different species of spider orchids. The calli provide a visual lure that attracts pollinators to the flower. In the common spider orchid (*Caladenia vulgata*), the distinctive labellum has two rows of small, pale calli that are believed to help attract pollinators, probably small bees. The abundance of this species shows that an orchid doesn't need an elaborately-deceptive labellum to become pollinated.

Other spider orchids have calli that are only slightly larger and barely more conspicuous than those of the common spider orchid. The magnificent white spider orchid (*C. longicauda*), with up to eight rows of pale purplish calli lined up on the labellum, is representative of this group. Although most populations of this species are pollinated by bees, members of one group found north of Esperance use sexual deception to attract males of a wasp species. It is likely that a small alteration in the scent produced by glands on the petals and sepals of plants in this population (now known as *C. longicauda* subsp. *rigidula*) happened to lure a few male wasps, which proved to be excellent pollinators. The odour, combined with the visual stimuli provided by the lip petal, worked well enough so that, over time, plants producing the wasp-attracting odour became the dominant form in this and other populations. This example demonstrates that even highly-imperfect female mimicry is sufficient to attract wasp pollinators, perhaps because the male wasps are extremely motivated to mate.

Top left Common spider orchid, a species with small pale calli (glands) on the labellum (lip).
Photo – John Alcock

Top right White spider orchid, a species with somewhat darker, but still small and dispersed, calli.
Photo – Len Stewart/Lochman Transparencies

Above Zebra orchid, a species with dark, enlarged and clumped calli that form an obvious female decoy.
Photo – John Alcock

Above Bee orchid. Note how the aggregated calli (glands) produce a female decoy.

Left Leaping spider orchid, another species with a striking female decoy.
Photos – John Alcock

Other species of *Caladenia* have larger, darker, more clumped and more conspicuous calli than those of the common spider orchid and white spider orchid. As a result, the labellum of the zebra orchid (*C. cairnsiana*), bee orchid (*C. discoidea*), leaping spider orchid (*C. macrostylis*) and others are ornamented with structures obviously similar to those exhibited by hammer orchids. In each of these cases, male wasps are tricked initially by pheromones and then by the visual stimuli of the calli into approaching the plant and grasping the female decoy on the labellum, which leads to pollination of the orchid. The existence of a whole spectrum of these types helps us to imagine how the labellum in the separate lineage of orchids, which now includes the hammer orchids, might have been gradually modified over time, eventually giving rise to a proto-hammer orchid. Step by step, diffusely distributed pale calli may have been aggregated to create a raised insect-sized mass of a size and shape more and more like that of a female wasp, with each change supplying the altered orchid in this lineage with a slightly better chance of deceiving a sex-crazed male wasp.

The lazy spider orchid (*Caladenia multiclavia*) offers a hint about what a fairly recent ancestor of the hammer orchids might have looked like. This delightful orchid has a labellum that is an obvious female decoy. A male wasp, attracted by the flower's odour, will grasp the decoy and, in attempting to carry it away to mate, induce the labellum to tilt forward on its hinged stalk, tossing the wasp into the pollen packets on the column. Although, in this species, the labellum's stalk is not elongate, all that would be required to

produce a hammer orchid-like structure would be a gradual lengthening of the stalk and a shift in the position of the hinge from the base of the stalk towards the middle. If, over time, the clumped calli were also to move closer to the front of the labellum, and if this were then to curl around to form a near cylinder, a decoy very much like that of a hammer orchid would be formed.

The existence of so many variants-on-a-theme among living orchids provides us with two important clues with which to make evolutionary sense of the hammer orchid's weird flowers. First, today's orchids show the variety of flower structures that evolutionary processes can produce. If these forms exist today, similar flowers could have existed in the past, in species ancestral to the current hammer orchids. Second, what to us are highly imperfect female decoys work well enough in some *Caladenia* species to arouse sexual responses in their pollinators. This tells us that the hammer orchids' ancestors could have been successfully pollinated without anything like the whole package of attributes possessed by modern hammer orchids. This would have set the stage for a series of additional changes over time that gradually revised the labellum in some groups, until they had taken on the form of the wonderfully strange flowers we see today.

Whenever I am fortunate enough to visit WA in spring, I make a point of travelling to some of the CALM-managed reserves on the south coast. I know that if I keep my eyes open and focused on the ground, I am likely to see orchids that Darwin never had the good fortune to see. But his ideas about evolution have greatly enhanced my own pleasure whenever I spot a spider orchid or hammer orchid. I find it satisfying to know that each species is the product of eons of change, guided by potentially understandable natural processes. We are lucky indeed to live in a world where the hammer orchids grow and where the means to decipher the history of these plants is available to us all.

Above left and above right Lazy spider orchid.
Photos – John Alcock

Left Habitat of the leaping spider orchid.
Photo – Andrew Brown

John Alcock is a professor in the School of Life Sciences at Arizona State University. He is a frequent visitor to Western Australia and has been a great admirer of Australian orchids ever since CALM's Andrew Brown kindly introduced him to these magnificent plants. His new book, *An Enthusiasm for Orchids*, will be published by Oxford University Press later this year.

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contents

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