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In memory of my father, Alan Peter Garnock-Jones (1915–1983), an architect who loved flowers and stereo photography, and wished he could have been a botanist; and my teacher, mentor and friend David Graham Lloyd (1937–2006).

Contents

xi Foreword by Peter Raven

xii Preface

Introduction

- **1** What is a flower?
- 4 Plant sex
- 5 Sexual systems
- **6** Why are we attracted to flowers?
- 6 A note about plant names
- **6** A note about animal names
- 8 Using the 3D viewer

100 Native Flowers of Aotearoa New Zealand

- **12** Acaena anserinifolia Piripiri
- **16** Aciphylla squarrosa Taramea
- **20** Alectryon excelsus Tītoki
- **26** Anthoxanthum redolens Kāretu
- **29** *Apodasmia similis* Oioi
- **31** Aristotelia serrata Makomako
- **36** Arthropodium cirratum Rengarenga
- **40** Ascarina lucida Hutu
- **46** Astelia banksii Wharawhara

- 50 Avicennia marina Mānawa
- **53** Beilschmiedia tawa Tawa
- **59** Bolboschoenus caldwellii Purua grass
- **63** *Brachyglottis* repanda Rangiora
- **69** *Cardamine dolichostyla* Panapana
- **73** *Carex uncinata* Kamu
- **76** Carmichaelia odorata Tarangahape
- **79** *Carpodetus serratus* Putaputawētā
- **84** *Chionochloa rubra* Haumata
- **88** Clematis forsteri Põtaetae
- **93** Clianthus maximus Ngutukākā
- **96** Coprosma grandifolia Kanono
- 99 Cordyline australis Tī kōuka
- 103 Coriaria arborea Tutu
- **107** Corokia cotoneaster Korokio
- **109** Corynocarpus laevigatus Karaka
- **113** Dianella nigra Tūrutu
- **117** *Didymocheton spectabilis* Kohekohe
- **120** Dodonaea viscosa Akeake
- **124** Dracophyllum filifolium Inanga

- **127** Entelea arborescens Whau
- **133** Epilobium billardiereanum Willowherb
- **137** Euphorbia glauca Waiū atua
- **140** Euphrasia cuneata Tūtae kiore
- **143** Exocarpos bidwillii
- **146** Freycinetia banksii Kiekie
- **152** *Fuchsia excorticata* Kōtukutuku
- **156** Fuscospora truncata Tawhairaunui
- **158** *Geniostoma ligustrifolium* Hangehange
- **162** Geranium retrorsum Matua-kūmara
- **167** Griselinia lucida Puka
- **170** Haloragis erecta Toatoa
- **173** *Hedycarya arborea* Porokaiwhiri
- **177** Hibiscus richardsonii Puarangi
- 182 Jovellana sinclairii New Zealand slipper flower
- **184** Juncus kraussii Wīwī
- **188** *Knightia excelsa* Rewarewa
- **191** Kunzea ericoides Kānuka
- **196** *Leptinella dioica* Shore cotula
- **201** Leptospermum scoparium Mānuka

- 207 Libertia ixioides Mīkoikoi
- **210** Linum monogynum Rauhuia
- **214** Lobelia physaloides Koru
- **218** *Melicope ternata* Wharangi
- **221** *Melicytus ramiflorus* Māhoe
- **225** *Metrosideros excelsa* Pōhutukawa
- 232 Microlaena avenacea Bush rice grass
- 234 Microtis unifolia Māikaika
- 239 *Muehlenbeckia astonii* Shrubby tororaro
- **243** Myoporum laetum Ngaio
- **246** Myosotis brevis
- **250** Olearia solandri
- **254** *Ourisia macrophylla* Mountain foxglove
- **258** Ozothamnus leptophyllus Tauhinu
- **261** Pachystegia rufa Marlborough rock daisy
- **264** Passiflora tetrandra Kōhia
- **268** *Peraxilla colensoi* Korukoru
- **274** *Phormium tenax* Harakeke
- **279** *Pimelea prostrata* Pinātoro

- 284 Piper excelsum Kawakawa
- **287** Pittosporum eugenioides Tarata
- **290** Plagianthus divaricatus Mākaka
- **293** *Plantago raoulii* Tūkōrehu
- **297** *Pomaderris kumeraho* Kūmarahou
- **301** Pseudowintera colorata Horopito
- **307** *Pterophylla racemosa* Kāmahi
- 310 Pterostylis alobula Greenhood orchid
- **315** Ranunculus pachyrrhizus Alpine buttercup
- **320** Rhabdothamnus solandri Taurepo
- **324** Rhopalostylis sapida Nīkau
- **327** Rubus cissoides Tātarāmoa
- **331** Rytidosperma setifolium Bristle tussock
- **335** Salicornia quinqueflora Ureure
- **338** Schefflera digitata Patē
- **341** *Scleranthus biflorus* Nāereere
- **346** *Solanum laciniatum* Poroporo
- **350** *Sophora molloyi* Kōwhai
- **354** *Spinifex sericeus* Kōwhangatara

- **358** *Tecomanthe speciosa* Akapukaea
- **361** Thelymitra longifolia Māikuku
- **365** Thyridia repens Native musk
- **368** *Triglochin striata* Arrow grass
- **372** *Veronica lyallii* Lyall's speedwell
- **376** *Veronica raoulii* Sun hebe
- **379** *Veronica stricta* Koromiko
- 386 *Viola cunninghamii* Mountain violet
- **391** Vitex lucens Pūriri
- **393** *Wahlenbergia albomarginata* Harebell
- **400** Wolffia australiana Watermeal
- **403** *Xeronema callistemon* Raupōtaranga
- **408** Zostera muelleri Nana
- 412 Afterword
- 415 Acknowledgements
- 416 Glossary
- 422 Bibliography
- 428 Index

Text Boxes

- 15 Carpels and pistils
- **24** Gender dimorphism
- **39** Delayed selfing
- **56** Blossom classes
- **66** The daisy family
- **72** Self-pollination and inbreeding
- **86** Bee pollination
- **102** Self-incompatibility

- **130** Dichogamy and herkogamy
- **151** Mammal pollination
- **176** Pollination syndromes
- **190** Secondary pollen presentation
- **205** Flower development
- 224 Scent
- **282** Butterfly and moth pollination
- **300** Apomixis

- **304** What did the first flower look like?
- **330** Wind pollination
- 344 Colour
- **353** Bird pollination
- **370** Fly pollination
- **399** Other insect pollinators

Foreword

In this charming and educational volume, Philip Garnock-Jones presents a highly original and fascinating introduction to the flowers of New Zealand. New Zealand's unusual plants evolved partly from the ancient lowland biota that drifted away from mainland Australia starting about 75 million years ago and partly from those that joined them as a result of subsequent long-distance dispersal to the mid-to-high elevations of the newly formed islands. This book highlights the plant names used by the country's Indigenous people and pays due respect to Māori classification systems and accumulated knowledge of the plants they found there. A very special feature lies in the inclusion of attractive and useful 3D illustrations of the featured flowers, which will make them easier to recognise and understand in the field.

Taken together, decades of study of these plants by New Zealand botanists has revealed a mixture of highly diverse patterns of pollination with both ancient roots and more modern evolution. These are fascinating to contemplate and to observe, and they will form the basis for continuing amateur and professional studies. One can easily imagine future scholarly dissertations dealing with some of these intricate relationships – and with equal ease, parents going out with their children to examine the magical flora that lies everywhere around them. In addition, this fine and well-reasoned book presents itself as an outstanding starting point for inquiring minds from abroad seeking to know something about the unique biology of Aotearoa, the land of the long white cloud.

—Peter Raven President Emeritus Missouri Botanical Garden, St. Louis, MO

xi

Preface

'Just living is not enough,' said the butterfly, 'one must have sunshine, freedom, and a little flower.'

– Hans Christian Andersen, *The Complete Fairy Tales*

Flowers feature in one of my sharpest early memories; I was four and a bit. On a family walk near Stafford Castle, England, the ground under the woods was a sea of bluebells. Later, after moving to New Zealand, I loved finding greenhood orchids (*Pterostylis*), puawānanga (Clematis paniculata) and shining rātā (Metrosideros *fulgens*) in the bush near home in Tawa. In university botany lab classes in the late sixties, we learnt how to analyse flowers, interpret them, and summarise their differences and similarities as floral formulas and floral diagrams. But the thing I loved most about those lab classes was looking at plants through a stereo microscope. A new world suddenly opened up: not only could flowers be magnified, they could be magnified in stereo; I could see their true shape and depth. In those botany labs, flowers became objects for scientific study as well as things of beauty. I was hooked. The stereo-microscope view of flowers continues to delight me, and now with digital macro photography it's possible to share that magic, via a simple stereo viewer (see p. 8 for instructions), in this book.

Flowers are among the most familiar objects in our everyday lives, the focus in home and public gardens, and an attraction on walks and hikes. We appreciate them as ornaments and gifts, sources of perfumes and honey, and for their promise of seeds and fruits to

come. Everywhere, the mystique and charms of flowers are celebrated in culture, art and romance, but their economic and environmental values are vast and often unappreciated. New Zealand's honey exports alone bring over \$400 million to the economy; top-quality mānuka honey can retail at over \$1,000 a kilogram. We need flowers – and their pollination – for production of our food grains, fruits and spices. Familiar products - like coffee, apples, chocolate, flour, rice, beans, chilli and nutmeg - all rely on flowers. Even ryegrass and clover, the foundation of our pastoral economy, need flowers to be pollinated for the production of their seeds. A few crops, like potatoes, are propagated without flowers, but we still need their flowers for breeding new varieties. Flowers and pollination are also essential to the well-being of our natural and built environments. They contribute to both plant reproduction and dispersal, so they're essential for the maintenance of healthy ecosystems. And flowers - and the fruits and seeds they produce - feed wild insects, mammals and birds.

We're attracted to the beauty of flowers, with their seemingly infinite variety of size, shape, colour and scent, but there's so much more to appreciate if we look closely, pay attention and understand what we're seeing. How are basic structures modified to create such diversity? What is the underlying genetics? Botanists are challenged

to explain the astonishing variety of ways that flowers are pollinated. How do evolution and ecology account for it?

We can divide the land plants into seed plants and seedless plants. The seed plants in turn divide into flowering plants and cone-bearing plants. The flowering plants are the largest land-plant group by far. Nobody can say yet exactly how many species of flowering plants there are. The latest tally by Kew Gardens is 390,900, but the total is still creeping upwards because people keep finding new ones.

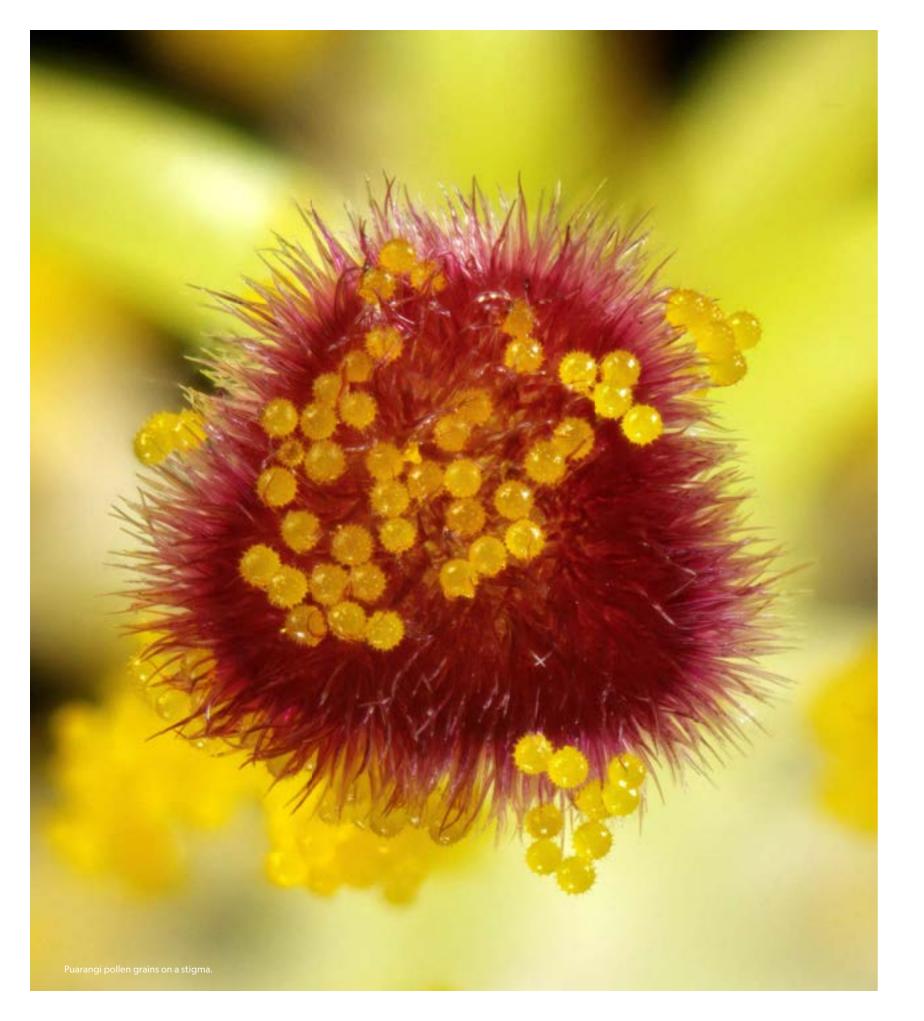
Aotearoa has at least 2,200 native species of flowering plants, but again, it's not possible to give an exact number. Their flowers have evolved here in an unusual set of conditions: the absence of long-tongued bees, and the presence of nectar-feeding birds and many pollinating flies. Eighty-five per cent of these flowers grow nowhere else on Earth. All together, this has made New Zealand a natural laboratory for studies of flower biology and flower evolution, and New Zealand botanists have contributed richly to the international flower-biology literature. University of Canterbury botanist David Lloyd (1937–2006), especially, provided ground-breaking insights into both the theory and the natural history of flower biology, often supported by observations of New Zealand flowers. Lloyd's research raised the global profile of our native flowers and encouraged numerous international botanists to study them.

Until now, we haven't had an accessible and pictorial account of New Zealand flower biology drawn from the

primary research literature. *He Puāwai: A Natural History of New Zealand Flowers* is an exploration of the many different ways New Zealand native flowers work to achieve the same result: pollination. This book covers just 100 of our 2,200 native species, chosen primarily to represent, illustrate, describe and – whenever I can – explain the full range of flower phenomena – the features and functions – that are found in our flora. Here the familiar iconic flowers of kōwhai (p. 350), mānuka (p. 201) and pōhutukawa (p. 225) rub shoulders with some small and rarely noticed, but nevertheless important and interesting, flowers. There are oddities too, like the water-pollinated flowers of nana (p. 408), the minute flowers of watermeal (p. 400) and bat-pollinated blossoms of kiekie (p. 146).

At a minimum, readers can simply look at the photographs and their captions. But each flower has a story that describes its structure and explains its functions. Unfortunately, the field of flower biology is loaded with scientific terminology. While botanical terms can put up barriers for readers, they're a helpful shorthand for concepts that would otherwise need whole sentences or paragraphs. Even many botanists are unfamiliar with flower-biology jargon, so I've adopted the strategy of trying to explain things in plain language while introducing the terminology at the same time. The curious can follow this up by consulting the glossary and the text boxes scattered through the book.

xii Preface



Introduction

What is a flower?

In spite of their seemingly infinite variety, careful comparisons show that all flowers have a lot in common. Comparative biology has become one of the great enterprises of humanity. Throughout the living world, we find the same underlying forms modified for different functions; biologists call them homologous structures. Think about fingers. Horses walk and gallop on a single fingertip at the end of each leg, bats spread their membranous wings between slender elongated fingers, whales' fingertips support their flippers, and I'm typing this with my fingers on a keyboard. Eighteenth-century Swedish botanist Carl Linnaeus knew about homology, but it was Charles Darwin (1859) who explained it as a result of descent from a common ancestor, combined with natural selection of modifications that fit a structure to its function.

Just as it is with animals, plant diversity can be explained by homologous structures. Flowers share their basic structure because they are all descended from a single ancestral species of flowering plant that lived at least 135 million years ago. So in spite of all their differences, flowers are modifications on a theme. We can learn a lot by comparing them, which, as Linnaeus discovered, turns out to be very useful.

It might seem odd to assert that the so-obviously different flowers of hebes, orchids, daisies, grasses and beech trees are all structurally similar, but their differences can be understood by the modification of homologous structures. Recent research in genetics has shown that the development of equivalent parts is controlled by the same gene families in very different flowers. That's independent evidence that the traditional way botanists have interpreted, compared and analysed flowers is, in fact, correct.

Animal bodies develop all their parts in the embryo and simply grow bigger, but plants keep adding new parts all their lives. Leafy plants are modular, built of repeating similar units. The basic unit is a length of bare stem (an internode), plus a leaf, along with the potential new shoot that's hidden as a tiny bud where the leaf joins the stem. These modules are repeated, varied and rearranged to form the above-ground parts of a plant. For all its complexity, a flower can be interpreted as a very modified leafy shoot made up of many such repeated modules. A short length of stem –

the receptacle – runs through the middle of it, and all the flower parts are leaves attached to it.

Four kinds of modified leaves make up the main parts of a flower, and they're always found in the same order. By convention, we list and describe them from the outside in or bottom to top. Sometimes, they're arranged as a single spiral, where sepals give way to petals, then stamens, then carpels, as in a magnolia flower. But more often, they're arranged in separate rings called whorls; all members of a whorl are attached at the same level.

Let's start with a general description of a simple flower, a native buttercup, kōpukupuku. The outermost parts of a flower are its sepals. They're often green, and they enclose and protect the rest of the flower as it develops from a bud, frequently remaining as its pistil ripens into a fruit. In a tomato, the sepals are the five green leaves where the stalk joins the fruit. In an apple, they're five papery scales at the other end of the fruit from the stalk, because in an apple, the fruit develops below the flower parts. Collectively, the sepals are known as the calyx.

Stepping further into the flower, we meet the petals. These are usually the showiest parts of the flower, the parts that attract the pollinators and, incidentally, us. In many flowers, they're large and coloured, but often delicate and usually short-lived: crumpled and red in poppies, pale and flimsy in apple blossom and fringed along their edges in carnations. Collectively, the petals form the corolla.

These two outer kinds of leaves – sepals and petals – don't play leading roles in the story of plant reproduction; they're supporting cast. Because they're broad and flat, they look much more leaf-like than the other flower parts. They're sometimes called the perianth, a Greek word meaning around the flower. The real action takes place in the flower's inner parts.

Stamens are found within the encircling perianth. They don't usually look much like leaves, except in a few flowers that are sometimes called primitive because of this. The slender stalk of a stamen – its filament – carries a blob at its tip – the anther. The anther's job is to make pollen and release it; the filament holds the anther in the right place to dust pollen onto a pollinator or to shed it into the wind. Stamens can be crowded, long and colourful, as in

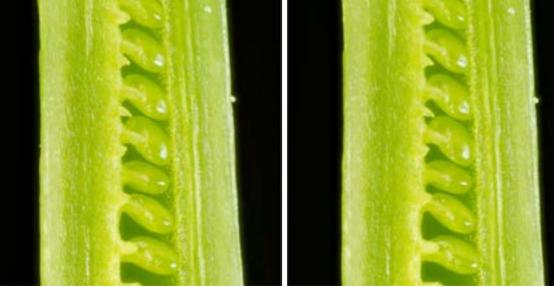
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A kõpukupuku flower (Ranunculus multiscapus) has four kinds of parts. Moving upwards from the flower-stalk, we first find five pale-green rather leaf-like sepals, here partly hidden behind the yellow petals. The sepals cover and protect all the other parts before the bud opens. Next are five larger bright-yellow petals. They're shiny, except towards their brownish bases, where a small nectary is found. Their colourful display attracts insects, and the nectar rewards them for noticing. Further in, towards the flower's centre, are about three dozen yellow stamens, each with a slender stalk - its filament - and a two-lobed head - its anther. As the flower matures. the anthers split open to release hundreds of tiny pollen grains. Finally, in the centre of the flower, is a clump of small greenish pistils, each one with a pale curved stigma at its tip and a swollen ovary at its base.



Hibiscus richardsonii pollen grains on a stigma. Pollen grain walls are tough, and in Hibiscus they're spiny. They develop from the original spore walls. Pollen grains are so distinctive in size, shape and ornamentation that species can often be identified by their pollen alone. Hibiscus pollen grains are larger than most; these are one-eighth of a millimetre in diameter.

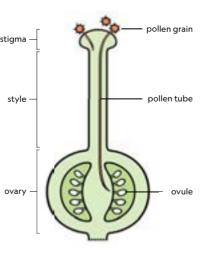


Ngutukākā (Clianthus maximus, p. 93) ovules in a row inside the long slender ovary, which has been sliced lengthwise to reveal them. Each one is six-tenths of a millimetre long and contains an embryo sac enclosed in several protecting layers of tissue, which will eventually become the outer parts of a seed.

pōhutukawa (p. 225) and Poor Knights lily flowers (p. 403), or hidden away inside the flower, as in kohekohe (p. 117) or many forget-me-not flowers (p. 246). Collectively, the stamens are called the flower's androecium (a Greek word for men's house) because they're the male parts of the flower. Linnaeus called them the flower's testicles.

The fourth and innermost kind of leaf is the female kind: a carpel. Carpels are often green – like regular leaves – and if you dissect them, you can sometimes see they are leaves, but leaves that are folded or rolled and joined along their edges. This way, they enclose a hollow cavity that contains one or more small rounded ovules. A complete female organ of a flower is a pistil. The simplest example of a pistil is a pea pod, a long tube containing a row of ovules; it's made up of just one carpel. You can open it out flat like a leaf. At its pointed end is a small stalk (the style) with a swollen tip (the stigma). Flowers with simple pistils can have just one pistil (e.g., kōwhai, p. 350; ngutukākā, p. 93) or many separate ones (e.g., buttercups, p. 315; porokaiwhiri, p. 173). But many other flowers have a compound pistil made up of two (e.g., Veronica spp., pp. 372–383; kāmahi, p. 307) or more (e.g., mānuka, p. 201; Viola, p. 386) carpels joined together. One of a pistil's jobs is to receive incoming pollen on its stigma. After pollination, the pollen tubes grow down the slender style -Linnaeus called it a fallopian tube – bringing sperms to fertilise the eggs inside the ovules. Fertilised eggs grow into embryos, and the ovules become seeds. We call the female parts of a flower its gynoecium – Greek for women's house. If pollination and fertilisation succeed, each pistil of a flower, whether simple (one carpel) or compound (more than one carpel) will develop into a fruit.

If flowers are all built on the same ground plan, what changes to the plan make them so different? There are a few simple modifications that produce those differences, and they're



A pistil (stigma, style and ovary) showing ovules and the male gametophyte (pollen grain and tube) at the heart of Linnaeus's system of plant classification. We can describe them as number, joining and symmetry.

The first important way flowers vary is in the number of their parts, called merism. Lilies, rushes and orchids have their flower parts in threes or in multiples of three. Many other flowers (e.g., geranium, p. 162; mānuka, p. 201; hibiscus, p. 177) have parts in fives or multiples of five. Other numbers are less common (four sepals and petals in cresses and willowherbs; two sepals and two whorls of two petals in most poppies).

Numbers of parts were paramount for Linnaeus, perhaps because they're simple to observe and they're discrete: you never find a flower with three-and-a-half petals, unless it has met with an accident. He first sorted plants into groups according to how many stamens they have: Monandria have one, Diandria two, Triandria three and so on. Within those groupings, he counted the carpels: Monogynia have one, Digynia two, Trigynia three. So the first written accounts of New Zealand plants easily classified plants never seen before by Europeans: koromiko (p. 379), with two stamens and a single pistil, was placed in Diandria Monogynia, along with familiar northern kinds of *Veronica* (in fact, the single pistil has two compartments, which is evidence it's made of two carpels joined together). Linnaeus's system was simple and brilliant, and it worked anywhere, but it has long been forgotten by botanists.

The joining of two carpels in a *Veronica* pistil is an example of the second way flowers ring the changes on their common ground plan. (For a more complete explanation of the technical differences between carpels and pistils, see box, p. 15.) Flower parts can be joined in two ways. When petals are joined to other petals edge to edge, we say they're connate, like the way ngaio (p. 243) or pūriri (p. 391) petals join together to form a tube. But when parts of one kind are joined face to face with parts of another kind, we say they're adnate: pull apart a koromiko or pūriri flower, and you'll see the stamens are adnate to the lower part of the corolla tube. Joining parts in this way allows plants to produce some fantastic shapes, like the long flower tubes of akapukaea (connate petals, p. 358) or the central column of an orchid flower (stamens adnate to the pistil, p. 361). In some flowers, all the outer parts of the flower are connate and adnate to form a compound tubular structure – the hypanthium – that surrounds the ovary and forms the outer fleshy parts of apples and cucumbers.

And lastly, there's symmetry. In bilaterally symmetrical flowers, there's a single axis of symmetry, so they have a left side and a right side (zygomorphic flowers, e.g., kōwhai, p. 350; pūriri, p. 391). In radially symmetrical flowers, there are multiple planes of symmetry (actinomorphic flowers, e.g., mānuka, p. 201; poroporo, p. 346). Perhaps the most complex flowers are the orchids, where merism, connation, adnation and symmetry combine to make weird and wonderful, even other-worldly, flowers.

P. He Puāwai 3