PREHISTORIC AUSTRALASIA

VISIONS OF EVOLUTION AND EXTINCTION MICHAEL ARCHER, SUZANNE J. HAND JOHN LONG, TREVOR H. WORTHY AND PETER SCHOUTEN



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MICHAEL ARCHER, SUZANNE J. HAN JOHN LONG, TREVOR H. WORTHY AND PETER SCHOUTEN



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A catalogue record for this book is available from the National Library of Australia.

ISBN: 9780643108059 (hbk) ISBN: 9780643108066 (epdf) ISBN: 9780643108073 (epub)

How to cite: Archer M, Hand SJ, Long J, Worthy TH, Schouten P (2023) Prehistoric Australasia: Visions of Evolution and Extinction. CSIRO Publishing, Melbourne.

Published by:

CSIRO Publishing Private Bag 10 Clayton South VIC 3169 Australia

Telephone: +61 3 9545 8400 Email: publishing.sales@csiro.au Website: www.publish.csiro.au Sign up to our email alerts: publish.csiro.au/earlyalert

Front cover: A pair of Australian predatory theropods, Australovenator wintonensis (artwork by Peter Schouten) Back cover: (top to bottom) The Shark-toothed Dolphin, an unnamed squalodontid; mini Marsupial Lion, *Lekaneleo roskellyae*, stalking the enigmatic marsupial Yalkaparidon coheni; the carnivorous macropod Propleopus, preying on an Australian Brush-turkey (artworks by Peter Schouten) Endpapers: Tetrapod forelimbs (artwork by Peter Schouten)

Edited by Adrienne de Kretser, Righting Writing Cover, text design and typeset by Cath Pirret Design Printed in China by Leo Paper Products Ltd

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Pleistocene/Holocene

Introduction

PALAEONTOLOGISTS CAN NO MORE STOP DIGGING UP FOSSILS THAN STOP

breathing – it's an obsession! Australasian palaeontologists are particularly driven to do this because the biological histories of Australia and its smaller neighbour, Zealandia, are the least understood of all the occupied continents. Hence, every new discovery can have a huge impact on what we previously understood about the once normal inhabitants of this very unusual continent. However, while discovery of a new tooth row or skull can send palaeontologists into fits of excitement, for the general public to share in the excitement of discovery, it often takes the palaeoartist's multifaceted skills to transform the scientists' discoveries into the next best thing to flesh and blood. To produce this book, *Prehistoric Australasia: Visions of Evolution and Extinction*, many palaeontologists have worked closely for years with palaeoartist Peter Schouten to produce a unique series of panoramas, windows in time that span the last 3.6 billion years of extraordinary life of Australasia and the south-west Pacific.

A long and complicated history of becoming different

Rudyard Kipling produced a *Just So* story about how the ancestral non-hopping kangaroo became unlike all other animals after commanding its creator to 'Make me different from all the other animals by five o'clock this afternoon!' The wish was granted, giving the kangaroo powerful hopping legs just in time for it to avoid becoming a Dingo's dinner. In reality, it took a fair bit longer than a day for kangaroos and Australia's other animals to become different. In fact, it took many millions of years for this area of the world to evolve the biggest dinosaurs in the world, gigantic dromornithid birds, bizarre thingodontans, marsupial lions, spine-bristled echidnas, wombats, koalas, kangaroos, horned turtles and even gum trees. How they have changed over time is a distinctly Australasian *Just So* story, and the focus of this book.

For much of its geological history, Australia's creatures rather closely resembled those of the other continents. From at least as long ago as 3.6 billion years, the part of Earth's crust and associated inland seas that were to become Australia were often physically connected to the other continents. As a result, many kinds of life – from cyanobacteria to trilobites, lungfish, sauropod dinosaurs, megaraptors and cynodonts that thrived in Australia – belonged to groups that spanned the united lands and waterways of Earth.

About 335 million years ago, all of the continents were joined and together they formed the supercontinent Pangaea. But because continental scrums of this type have always had limited durations, Pangaea began to tear itself apart around

175 million years ago. In the crustal destruction that followed, the island continent of Australia was eventually born, separating from Antarctica first along its western edge about 100 million years ago and then finally from its eastern edge sometime between 50 million and 38 million years ago. With the severing of the continent's last ties to what was left of Pangaea, the now isolated creatures of Australia began to evolve in directions unlike those anywhere else on Earth. The origin of New Zealand is closely tied to that of Australia; until 80–60 million years ago both were part of Gondwana. Then Zealandia, the India-sized continent of which New Zealand and New Caledonia are the largest emergent parts, unzipped from Australia's eastern flank, and the world's smallest continent began its own unique 80 million years history of isolation

As this antipodean ark set out on its steady journey northward through the Indian Ocean at the breakneck pace of around 7 cm per year, global climatic cycles, alternating between greenhouse and icehouse conditions, tested, prodded and transformed the continent's biota. This tapestry of changes accumulated because Australia was no longer exchanging its land-based creatures with those of the other continents. For the last 50 million years, elephants, camels, tapirs, cats, sloths, anteaters, primates, bears, horses and many other groups were able to move back and forth between the frequently connected lands of Asia, Africa, Europe and North and South America, but none of these globally widespread groups could reach the island continents of Australia and Zealandia.

The small maps associated with the panoramas that follow provide a snapshot of how Australia's (and Zealandia's) geographic position has been changing over time.

An independent laboratory churning out evolutionary innovations

While it is true that many of this region's living and recently extinct creatures represent outcomes of independent global experiments in evolutionary history, it has also been the case that this portion of the ancient world is the first known to have developed many of the most interesting steps in the evolutionary history of life as a whole. In fact, the oldest known solid objects of any kind found on planet Earth are 4.45 billion years old zircon crystals from the Jack Hills area of Western Australia.

In terms of explosive moments in the history of life, this region of the world has produced some of the most important. Here are 35 of the region's notable world fossil records.

- 1. The first undoubted evidence for life forms on planet Earth (at least 3.5 billion years ago; however, there are controversial contenders for this title in Greenland at 3.7 billion years ago; p. 18).
- 2. The oldest undoubted cells (in the ~3.5 billion years old Apex Chert Formation from Western Australia).
- **3.** Seriously weird early organisms at 3.4 billion years ago (from the Strelley Pool Formation of Western Australia).

- **4.** Among the oldest, if not the oldest, undoubted eukaryotic cells and hence routine practice of sexual reproduction (1.5 billion years old *Tappania* from the Roper Group of the Northern Territory).
- **5.** Among the oldest evidence for Earth's earliest animals (e.g. *Myxomitodes stirlingensis*, the so-called mucous monsters at 1.2 billion years ago from the Stirling Ranges in Western Australia; or 650 million years old sponges from the Flinders Ranges in South Australia).
- **6.** Among the best-known early communities of animals (570 million years old Ediacaran vendozoans from South Australia; p. 20).
- **7.** The earliest perfectly formed eyes in predatory animals (525 million years old anomalocarids from the Emu Bay Shale, South Australia; p. 22).
- **8.** Possibly the world's first known fossil bone (495 million years old bone bits from the Gola Beds of Queensland, although this is controversial it could be arthropod cuticle).
- **9.** Evidence for the world's first forests (~400 million years old root systems from the Wee Jasper Formation of New South Wales).
- **10.** Among if not the world's first fish with bone (458 million years old *Arandaspis* from the Stairway Sandstone, Northern Territory; p. 24).
- **11.** Possibly the world's first shark, *Tantalepis* (458 million years old, known from placoid scales identical to those seen in modern sharks, from the Stairway Sandstone, Northern Territory).
- **12.** Among the world's earliest land plant communities (e.g. the 427 million years old *Baragwanathia* Flora from Victoria; p. 26).
- **13.** Among the first evidence of sexual intercourse (e.g. 385 million years old placoderm fish from Gogo, Western Australia as well as Scotland; p. 36).
- **14.** First evidence of live birth in a vertebrate (380 million years old *Mαterpiscus* from Gogo, Western Australia; p. 36).
- **15.** Among the world's first fully terrestrial, four-footed animals (340 million years old *Ossinodus* from Ducabrook, Queensland; p. 44).
- **16.** The world's biggest dinosaurs (130 million years old individual sauropod tracks 1.75 m in length on the coast north of Broome, Western Australia; p. 62).
- **17.** The longest surviving 'labyrinthodont' amphibian (*Koolasuchus* from 120 million years old sediments near Inverloch, Victoria).
- 18. The first of the world's 'modern crocodiles' (eusuchians) (*Isisfordia* from Winton in Queensland and Lightning Ridge, New South Wales at 100 million years old; p. 80).
- **19.** Among if not the world's first megaraptors (100 million years old 'Lightning Claw' from Lightning Ridge, New South Wales; p. 84).
- **20.** The world's first egg-laying monotremes (e.g. the 113 million years old *Teinolophos* from Flat Rocks, Victoria).

- **21.** The world's oldest passeriform (song) birds (55 million years old limb bones from Murgon, Queensland, are at least 20 million years older than songbirds anywhere else; p. 96).
- **22.** Among if not the world's oldest bat fossils (55 million years old *Australonycteris* from Murgon, Queensland; p. 98).
- 23. The world's only known at least partially arboreal 'drop crocs' (23-15 million years old possibly arboreal mekosuchine crocodiles from Riversleigh, Queensland; p. 138).
- **24.** The world's only 'drop bears' (actually *Nimbadon lavarackorum*, arboreal slothlike marsupials at 15 million years old from Riversleigh, Queensland; p. 140).
- **25.** Among the world's oldest known sperm cells which also have nuclei preserved inside them (17 million years old ostracod cells from Riversleigh, Queensland).
- **26.** The world's biggest birds (e.g. 8 million years old flightless dromornithid species of *Dromornis* from Alcoota in the Northern Territory and the extraordinary radiation of giant flightless ratites, the moa, from New Zealand; p. 146).
- **27.** The world's only known 'thingodontans', a whole order of mammals unique to Australia (23–15 million years old *Yalkaparidon* from Riversleigh, Queensland; p. 126).
- **28.** The world's most specialised mammalian carnivores (24 million–35 000 years old marsupial lions from many areas of Australia; pp. 124, 126, 148, 154, 170, 174, 176).
- 29. The world's largest lizard as well as the largest venomous animal known (2 million-500 000 years old *Varanus priscus* from various regions of Australia; p. 172).
- **30.** The world's largest marsupial (~2800 kg) from any continent or time, *Diprotodon optatum* (known from most of Pleistocene Australia; pp. 156, 162, 176, 190, 196).
- **31.** The world's tallest trees of any kind (Mountain Ash, *Eucalyptus regnans*, individuals of which reach 150 m in height).
- **32.** Possibly the longest-living organisms on planet Earth (e.g. King's Holly, *Lomatia tasmanicum*, individuals of which have been assessed to be up to 135 000 years old).
- **33.** The world's biggest parrot (*Heracles*, a 1 m tall 7 kg giant from the 19–16 million years old St Bathans Fauna in New Zealand, nicknamed 'Squawkzilla'; p. 136).
- **34.** The world's largest eagle anytime, anywhere (Haast's Eagle, Quaternary of New Zealand; p. 220).
- **35.** The most massive galliform bird (distantly related to chickens) ever to have evolved (*Sylviornis* from Pleistocene deposits in New Caledonia; p. 216).

Given these and other 'Guinness Book of Life's Extreme Creatures' – many of which are illustrated in the panoramas that follow – this corner of the world has clearly punched well above its weight in terms of evolving extraordinary new forms of life. Many of them went on to have huge impacts on the rest of the world.

Putting the dead to work to save the living

There is growing awareness that fossils may help us save some of today's critically endangered species. We realise that we need to learn from the past to understand the present, in order to devise better conservation strategies for the future. All around the world, as climate change begins to destabilise habitats, conservationminded palaeontologists are exploring the fossil record for clues about where threatened species might be able to be translocated to survive these changes. Often, this reveals options that might never have occurred to ecologists trying to solve the same problem. In most cases, clues are coming from Pleistocene records. This is why the critically endangered 'alpine' Takahe in New Zealand, the largest land rail in the world, was translocated out of the alpine zone to coastal islands where it had thrived during the Pleistocene – a translocation that has worked.

As this book has been coming together, some of us as palaeontologists are reaching even further back into Australia's fossil record for palaeontological clues about how we might save the critically endangered Mountain Pygmy-possum Burramys parvus. It was first named in the 1890s as a fossil recovered from a cave deposit in New South Wales before being found alive in 1966 in a ski lodge on Mount Hotham, Victoria. Ironically, this little possum is now threatened with becoming genuinely extinct as its alpine habitat is changed by climate heating. But rather than accept that this possum must become extinct, several of us have pointed out that it is the most recent member of a long chain of species in the same genus spanning at least the last 25 million years. And in every case known - B. wakefieldi from the 24 million years old Ngama Local Fauna of Lake Palankarinna in central Australia, B. brutyi from the 24-15 million years old faunal assemblages of Riversleigh in north-western Queensland, B. triradiatus from the 4.3 million years old Hamilton Local Fauna of western Victoria - these species have always lived in lowland wet forest habitats (p. 138). We suspect that at some time during the Pleistocene they followed shifting wet forest vegetation up the slopes of the Great Dividing Range then became stranded in the alpine zone when climates changed again. This is not an uncommon situation for endangered animals and plants around the world - they now occupy only marginal parts of their much larger former ranges. Based on this understanding, the Burramys Project (Fig. 1) involves construction of a lowland breeding facility in New South Wales, from where surplus individuals can be trial released into more stable cool temperate lowland wet forest habitats and monitored. If successful, similar translocation projects may be developed based on our growing knowledge about the fossil record.

A similar argument about using the fossil record to save other critically endangered species could be explored in relation to the Western Swamp Tortoise *Pseudemydura umbrina* in swamps along the western coast of Western Australia. With climate change and increasingly severe droughts, this last survivor of a highly distinctive group of turtles is headed for extinction. However, a species that is very closely related, if not the same, occurred in the middle Miocene rainforest pools in Riversleigh 15 million years ago (p. 138). Before the habitat of the living species disappears altogether, wouldn't it make sense to trial releasing a small population





into cool temperate rainforest pools in eastern Australia that lack other turtles? Eventually, as conditions in Western Australia worsen, this option may become the only one.

As knowledge about the fossil record increases, it is also providing a new tool to independently assess the degree of concern we should feel about many of the endangered animals of Australia and its close neighbours. Modern ecological studies cannot provide a deep-time perspective about how lineages have fared through time and into the present. Hence, it is sometimes hard to assess whether these lineages have been declining, increasing or staying the same through time to bring them to the situation we find them in today. To make decisions about how to best use the limited funds available for conservation programs, it would be helpful to know which seemingly endangered species should get priority attention. For example, the long-term perspective about lineage change in Platypuses suggests that for at least the last 63 million years they have been declining in diversity (one species now), geographic distribution (just the rivers systems of eastern Australia) and morphological resilience (now being toothless and hyperspecialised). Palaeontology teaches us that when the last members of

any lineage exhibit declines of this kind, even if they seem robust in their current situation they are actually in increasing danger of going extinct. A similar long-term decline in diversity and geographic area among Thylacines ('Tasmanian Tigers') – unbeknownst to the early colonists in Tasmania, many of whom persecuted them with the encouragement of the Tasmanian government of the time – ultimately led to their extinction. In contrast, although there has been a loss of many kinds of koalas over the last 25 million years and its numbers have recently declined largely because of habitat destruction, the modern Koala is far more abundant today in its forest habitat than any other koala species has ever been in the past. On this basis, palaeontologists, in contrast to some conservationists, would suggest that the Platypus is in far greater danger of extinction than the Koala.

Must all these extinct species stay extinct forever?

Most of us tend to think of the fossil record as a collection of fascinating curiosities, extinct creatures whose time in the sun has come and gone. Increasingly, however, there is interest in rethinking the 'gone' bit and it has given rise to the controversial new science of deExtinction. This involves questioning the once unarguable assumption that extinction is forever. Organisations like Revive & Restore and Geneticrescue have been stimulating scientists to think about the possibility of bringing extinct species back to life. While the introduction to *Jurassic Park* explains that the book was written to scare us into avoiding any temptation to use ancient DNA to resurrect prehistoric animals, both the book and the movie franchise that followed had exactly the opposite effect: they created intense interest in the possibility of carrying out such procedures with other extinct species.

Organisms as diverse as Siberian Mammoths, European Aurochs, North American Passenger Pigeons, Spain's Bucardos, Australia's Southern Gastric-brooding Frog and many others are now subjects of active research projects to challenge the assumption that extinction is forever. For some, such as the Mammoth Project and the Passenger Pigeon Project, this involves recovering ancient DNA from fossils and using it to transform the DNA of living relatives to produce new hybrid creatures that are physically and ecologically similar to the ones that went extinct. For others, such as the Auroch Project, research involves back-breeding to identify and resuscitate ancient genes that restore features of ancestral populations. For still others, such as the Lazarus Project focused on the Southern Gastric-brooding Frog (Fig. 2), study involves recovering whole nuclei with intact DNA from specimens of extinct species and introducing these into the enucleated egg cells of living relatives with the goal of bringing the whole of the extinct creature back to life. Even the possibility of revitalising lost dinosaurs is being explored through manipulation of the genome of the one group of dinosaurs that didn't go extinct - birds. A great deal of careful thought about risks is going into these projects. We need to assess, for example, whether the revived extinct species could be safely as well as usefully put back into ecosystems.

If deExtinction does become a reality, what other extinct Australasian species would we like to have back in the world? Certainly, the Thylacine would be a prime



Fig. 2. *Rheobatrachus silus*, the now extinct Southern Gastric-brooding Frog, shown in its original Queensland rainforest habitat. It is regurgitating its young which, remarkably, developed entirely in the adult's gut. This frog is now the focus of a deExtinction effort, the Lazarus Project, whose aim is to use nuclei from frozen tissues to bring this extraordinary, uniquely Australian species back to life.

candidate. We began recovering ancient DNA from Thylacines as early as 2000, with the ultimate goal of resurrection, and the whole mitochondrial and nuclear genomes have now been published – the 'recipe' for revitalised Thylacines. It has already been demonstrated that when some of the ancient DNA recovered from pickled Thylacine specimens is spliced into the genomes of a mouse, it works – it produces Thylacine tissues as part of hybrid embryos. Hopefully it will be only a matter of time before Thylacines are able to be returned to natural habitats in Tasmania and once again become Australia's King of Beasts. If we're successful in resurrecting Thylacines, would we consider the possibility of using ancient DNA, if it can be recovered, to try to resurrect the Thylacoleo, the magnificent lioness-sized marsupial and world's most specialised mammalian carnivore (p. 170)? How much more exciting camping trips into outback Australia would become! Projects of this kind are still a bit beyond our reach but, considering the pace at which synthetic biology is progressing, we could well have at least Thylacines back in the world by 2050.

Extinct animals are not really extinct – just paused in time

MIKE ARCHER

BUT WHAT DOES IT MEAN when we say something has become 'extinct'? To palaeontologists, whose grasp of reality focuses on the fourth dimension (time) as well as the other three (length, width and height), the idea of extinction can be complex. In the time dimension, every living cell in every organism that has ever lived on Earth is in physical contact with every other cell that has ever existed - there are challenges here to common perceptions about the nature of life. In this world view there are no gaps, and there never have been, between any of the species that have ever existed since life began on planet Earth perhaps 3.7 billion years ago. All life is a *single* time-travelling shape-changing organism, like a gigantic amoeba moving through space and time. For want of a better term, I have called it the 'Bioblob'. Among other insights provided by this view of the actual nature of life as a single time-travelling organism is the realisation that death cannot occur - it's an illusion of limited vision. Although we can understand the time dimension, we can't actually 'see' it with our eyes in the same way we see length, width and height. Hence, we perceive 'gaps' between individuals and species now and back through time despite the fact that, back along that dimension, all those parts of the Bioblob are physically interconnected parts of a single organism. And if death cannot occur, neither can extinction, at least not in the way it is conventionally conceived as an end to being alive. An 'extinct' part of the Bioblob is just a part of the organism that is not currently moving forward or

shapeshifting in space and time. But despite its pause in transformation, like the nose on your face as you walk along, it's still part of the single living organism to which it belongs.

Finally, considering the Bioblob concept, if there has only been one organism, ever, on planet Earth, what should we think of fossils given that palaeontologists treat these as parts of extinct species? In actuality, fossils are the 'dandruff' and discarded fingernails of the Bioblob, shed along the way as it moves through time and space, transforming into new forms as it adapts to changing environments and takes advantage of new opportunities. Of course, for those of us who are palaeontologists, this 'dandruff' is precious beyond words. These parts of the Bioblob that it discarded at various stages back through time are the only things that can enable us to reconstruct the Bioblob's earlier forms to understand how it has been changing over the billions of years it has been alive. Of course, fossils can only provide an extremely limited understanding about how the whole super-organism that produced these bits has been changing over the last few billion years. Most of the organism over time hasn't shed examinable bits, or if it has, these haven't vet been discovered. Further, those that have been shed are rarely preserved. Further still, those that have been preserved are in the main hidden too far below the surface for us to find them.

Moments in time when the tree of life was massively pruned

MIKE ARCHER

OVER THE LAST 500 MILLION YEARS, and no doubt many times before that, there have been at least five episodes of severe 'stunting' of growth of the branches of the Tree of Life (aka the Bioblob). We call these events 'mass extinctions'. At these times, between ~75% (e.g. the end of the Cretaceous when the Chicxulub meteorite struck the Yucatan Peninsula) and 96% (e.g. the end of the Permian) of the branches of the Bioblob stopped expanding in time and space - they become 'extinct'. The most commonly recognised five 'mass extinction' events occurred at the end of the Ordovician, end of the Devonian, end of the Permian, end of the Triassic and end of the Cretaceous.

While the causes of these five mass stunting events are often controversial (ref. 321), common explanations include climate change, volcanic events, meteorites, pollution and environmental fluctuations in elements such as selenium and nickel.

The late Pleistocene saw a similar episode of savage pruning of the Bioblob, but it was a less severe pruning than the five earlier events. Hence, it is not generally regarded as a 'mass extinction' event. There has been controversy about whether a meteor impacted Earth during or preceding these Pleistocene extinctions, but it is now generally conceded that one did in fact hit somewhere in the Northern Hemisphere, possibly correlated with an abrupt climate change interval called the Younger Dryas Event that spanned 12 900-11 600 years ago. The causes of extinction on all land masses of some of the Pleistocene megafauna (i.e. animals larger than ~44 kg

in weight) are still uncertain, despite being closest to us in time. It was often assumed that early humans must have been responsible for the extinctions, but it is becoming increasingly clear that late Pleistocene climate changes are at least an equally if not more credible common denominator of the losses around the world on all continents including Australia.

There are many thousands of bones of extinct late Pleistocene megafaunal species in Australia, and not one provides credible evidence that even a single individual megafaunal animal was killed by a human. In fact, as was the case in the Northern Hemisphere, much of Australia's extinct megafaunal species were gone before humans arrived on the continent (ref. 464). Discovery of what was reported to be a 34 000 years old skeleton of Zygomaturus trilobus at Lake Willandra, New South Wales and similar-aged megafaunal species from Cuddie Springs in New South Wales, indicate that humans and some of the extinct megafauna coexisted for at least 17 000 years. Although there is no hard evidence that humans had a significant role in the loss of any of the extinct megafaunal species, no doubt the issue will remain controversial as new evidence continues to challenge entrenched assumptions on both sides of the debate. And that evidence is coming from large investigations of sites across Australia.

Unfortunately, we humans have triggered what is now commonly regarded to be the onset of the world's Sixth Mass Extinction, with millions of animals and plants now in danger of vanishing forever. Although we could slow this unfolding process by stopping widespread habitat and climatic destruction, we don't seem to be doing enough to avoid even more horrific consequences than occurred following the end of Cretaceous mass extinction. It seems the world is in for another rough ride and possibly even our own extinction. •

Australian palaeontology: prehistoric beginnings and growing fast

Palaeontology has been practised in Australia for thousands of years, long before the arrival of Europeans. It is clear that the first palaeontologists in Australia were Indigenous Australians. Both invertebrate and vertebrate fossils have been valued by various groups of Aborigines. Some prized fossils were transported via trade routes that spanned the continent. Among people who knew the modern biota well, it is no surprise that the remains of extinct animals inspired their keen interest in fossils. But without a written record, we know far too little about the extent of these earliest investigations.

Following European settlement in the 1700s, records of research focused on the prehistoric creatures of Australia, New Guinea and New Zealand began to accumulate and influence global understanding about evolution in the Southern Hemisphere. Even Charles Darwin was profoundly impacted by the realisation that fossil deposits in Wellington Caves, New South Wales, contained extinct wombats, kangaroos and other characteristically Australian types of animals, rather than elephants, rhinoceroses and other animal types found in the fossil deposits of Europe. He considered this was clear evidence that living animals on isolated lands had descended from local ancestors – a notable departure from the creationist belief in a universal global biota that was created de nova in the Garden of Eden before being drowned and fossilised in the sediments of a global flood. The Wellington Cave fossils were a major reason why Darwin conceived his Law of Succession of Types in 1837, leading to his 1859 publication of *The Origin of Species*.

Some of Australia's colonial palaeontologists had to struggle to demonstrate their capacity to compete for attention on the global stage. For example, Gerard Krefft in the Australian Museum, despite being one of its first and most capable curators, was instructed by his anglophilic Board of Trustees to turn over the fossils he found, along with his research notes about them, to Sir Richard Owen in the Natural History Museum in London, so that Owen had the privilege of publishing the first papers about these extinct Australian animals. Although Krefft complied at first, understandably this requirement eventually frustrated him. It triggered a long and fascinating war of disagreement between Krefft and Owen about, for example, the presumed diet of the Marsupial Lion, *Thylacoleo carnifex* – Owen argued it was a carnivore and Krefft that it was a herbivore. Krefft's refusal to bow to English authority put his job in jeopardy, but it also made him one of Australia's first scientific freedom fighters. His eventual refusal to obey the Board's instructions was



Fig. 3. One of the beautiful illustrations of extinct Australian mammals from Owen's 1877 magnum opus on the Pleistocene fossil mammals of Australia. In this case, a partial skull and teeth of the marsupial lion, *Thylacoleo carnifex*.

an important step on the path that enabled Australian palaeontology to develop in its own right – even if, as it eventually turned out, Krefft was wrong and Owen right about the diet of Thylacoleo!

In addition to the centuries of palaeontological research by many local palaeontologists, international palaeontologists have also made major contributions to our understanding about the fossil record of this continent. They include palaeontologists from the University of California, Field Museum in Chicago, University of Texas, Natural History Museum in London and many others. Of particular note in relation to vertebrates, Owen's magnificent compilation of Australia's Pleistocene animals, enabled in part by the fossils begrudgingly sent to him by Krefft, stands head and shoulders above all the others. He produced the beautifully illustrated Researches on the Fossil Remains of the Extinct Mammals of Australia; with a Notice of the Extinct Marsupials of England in 1877 (Fig. 3). Similarly, he produced Memoirs of the Extinct Wingless Birds of New Zealand (1879), a compilation of 40 years of research describing the fossil birds from New Zealand.

Palaeoartistry: visionary bridge between palaeontology and the public

While palaeontologists have relatively little difficulty in comprehending the significance of most of the species they discover, sometimes based on little more than a leg bone or a tooth row, understandably the public needs more help to bridge that visualisation gap. This is why palaeoartists are so important. Translating new discoveries into whole-body reconstructions (Fig. 4) requires multifaceted skills. Rendering living animals as paintings is relatively unchallenging, as the whole animal is available to use as a model. However, to reconstruct extinct vertebrates, the artist must have more than well developed artistic skills; they must have deductive skills to work out how novel morphological features of the bones, muscle attachments and teeth translate into differences in overall shapes and behaviours. It helps if the artist also understands the nature of the ecosystems within which the animal lived,



Fig. 4. Before a palaeoartist can produce a plausible reconstruction of an extinct vertebrate such as a Marsupial Lion *Thylacoleo carnifex* (left) or an Antarctic dinosaur *Cryolophosaurus ellioti* (right), they need to work with palaeontologists to determine the approximate size and orientation of muscle masses attaching to the different elements of the skeleton. Often this understanding can be deduced by the size and shape of 'muscle scars', roughened areas where the muscles originated or inserted onto bone surfaces.

because these provide further constraints in relation to such things as plausible body markings and overall colour. For example, modern vertebrates that live in water tend to have darker upper and lighter lower colours while vertebrates that live in forests often have patchy or striped body markings that help to hide them from potential prey as well as from predators. While some palaeoartists embrace the opportunity to produce animals such as dinosaurs in glorious technicolour, arguing that some of their descendants such as birds have such colouring, others take a more conservative approach. This often leads to radically different renderings of the same animal. For most of the animals reconstructed by Peter Schouten in this book, there have been no previous full-bodied reconstructions so there will not be too many conflicts of interpretation – yet!

There will continually be new interpretations, based on new materials about the overall body shape and lifestyles of the animals being reconstructed. A classic example has been the revolution in our understanding about almost everything to do with one of the most common fossil marsupials found in the middle Miocene of Riversleigh: Nimbadon lavarackorum. When this was first discovered, all we had were a couple of tooth rows. From these it was deduced that this mammal was a new kind of herbivorous diprotodontid similar to others previously found, such as species of Ngapakaldia or Zygomaturus. It seemed probable that it was a quadrupedal leaf-eater that browsed on low vegetation growing in the understorey of the Miocene rainforests. But in the years that followed, we began to find much more of these animals, eventually including entire articulated skeletons. Karen Black began an intensive study of these skeletons and, much to everyone's surprise, concluded that just about everything we had presumed about them was wrong. The limb bones and claws indicated that rather than roaming the floor of the forest they were in fact more like sloths or sun bears in their behaviour, climbing trees and entirely capable of hanging upside down (p. 140). Further, current study of microwear on their teeth has indicated that, contrary to our earlier naïve presumptions, they weren't eating leaves; what they were eating while hanging upside down in the crowns of the rainforest trees is still under investigation. All this has added up to recognition that these were 'drop bears' in a manner of speaking - it is quite clear that now and then one of these sun bear-like marsupials would lose its grip in the trees and fall into the cave below, where we have now found the fossilised remains of more than 26 individuals from tiny juveniles to old adults.

Peter Schouten has been studying, interpreting and rendering Australia's living and fossil vertebrates for many years with consummate skills that get more stunning every year. When particularly fascinating new discoveries have been made in the Australasian fossil record (e.g. Fig. 5), Peter has produced an illustration that brings to life for the general public what it is that has so excited the palaeontologists about the new animal.

For similar reasons, many scientific journals that publish descriptions of exciting palaeontological discoveries have used Peter's art for the cover of those issues (e.g. Fig. 6).

Not uncommonly, Peter's artwork has been used to illustrate new species named in honour of individuals who have made major contributions to Australian vertebrate



Fig. 5. Peter Schouten's illustration to accompany a scientific description of *Malleodectes mirabilis*, a member of a new family of marsupials, the Malleodectidae, found in the Miocene deposits of Riversleigh that may have been specialised snail-eaters. These cat-sized carnivorous marsupials had huge, ball-peen hammer-like premolars that could only have been used for smashing hard food items such as snail shells.



Fig. 6. Reconstruction by Peter Schouten of *Obdurodon tharalkooschild* used as the cover art for the November 2013 issue of the *Journal of Vertebrate Paleontology*. Included in the cover art is an image of the first lower molar of this giant toothed Platypus and one of the fossil turtles from Riversleigh. This enormous Miocene toothed Platypus may have been more than 1 m in length and thus at least twice as long as the living Platypus.



Fig. 7. Following a long tradition of naming new species after individuals who have provided significant support for palaeontological research, this very small rainforest Marsupial Lion - illustrated by Peter Schouten - was named after Sir David Attenborough, *Microleo attenboroughi*. This cat-sized carnivore hunted in the early Miocene rainforests of Riversleigh.

palaeontology. As an example, in recognition of Sir David Attenborough's role in increasing global awareness of the fossils from the World Heritage Riversleigh area, Anna Gillespie and colleagues named a highly specialised marsupial lion after him. It was illustrated by Peter Schouten for the scientific publication (Fig. 7).

Peter's skills have long since been embraced by the rest of the world. He has reconstructed extinct and living creatures from all continents, although his primary focus has been the natural history of Australia and this region of the world. We've had the good fortune of working with Peter over many years, and the present book is one of the most comprehensive to date about this region's prehistory.

The future for discovering more about prehistory in Australasia

At a wild guess, the creatures we have focused on in this book represent less than 1% of what palaeontologists have discovered about this region's extraordinary past. At a wilder guess, all that has been discovered to date about its prehistoric menagerie probably represents less than 1/1 000 000th of 1% of the creatures that have called this place home. The challenge for future generations trying to understand more about this region's history will be to grab their hats, leave the bitumen-covered cities and start systematically searching for new fossil deposits that are out there awaiting the next generation of prehistory explorers.

Every time there's a flood, the banks and gravel bars of rivers should be examined. Whenever dams are dug in remote areas, no matter how small the hole, what's dug up should be carefully examined. When bushwalking, all non-volcanic rocks should be studied for fossil bones or tracks. Given that most fossil deposits in Australia have been found by sharp-eyed members of the public, finding new important fossil deposits is not a job that belongs only to professional palaeontologists!

The key for the beginner, whether looking for fossils or even searching for new insects, is to look for odd things in unusual places – a strange shape, curious texture or oddly coloured 'something'. In a sandstone face, for example, fossils such as bones, cones or shells are more likely to be found in ancient channel deposits revealed by discrete layers of larger pebbles. Keeping your face ~30 cm from the rock face, each object in the channel deposit should be carefully and thoughtfully examined. If an object of interest can be removed, it's important to photograph it with something to indicate the size of the object, mark the place on your map and, if possible, record GPS data for the discovery site so you know for certain the location of this exact spot. Then take the object or its photo to a palaeontologist in the nearest museum or university. If you find a skeleton in a cave, take a close-up photo on your phone (include a scale) and email it to a palaeontologist in one of Australia's museums or universities, with all the information about the location that you can relay.

Given that landowners in rural and regional areas, bushwalkers and cave explorers almost certainly outnumber palaeontologists by at least 1000 to 1, it is easy to understand why most important discoveries about our prehistoric past have been made by observant, curious and interested members of the public rather than by the palaeontologists themselves.

It's time to wander through the pages of Australasia's prehistoric record, with Peter Schouten's skills to bring these creatures back to life.

Pilbara, Western Australia



HOW DID LIFE FIRST BEGIN ON EARTH? SOME

have argued, given the fact that stony meteorites all over the world have been found to contain amino acids and other organic molecules, that Earth's life may have had extraterrestrial origins. While it is probable that life abounds elsewhere in the universe, hard evidence for ancient, very simple life forms here on Earth is also abundant. Some of the most interesting comes from sedimentary rocks about 3.5 billion years old exposed in the Pilbara district of Western Australia, near a town called Marble Bar. Rocks here contain minerals that suggest they formed in hot springs where synthesis of Earth's first life may have begun. Here, there are also fossils called stromatolites, structures built by unicellular organisms called cyanobacteria. Because simple cells of this kind still occur in extreme environments in the modern

world, and in some cases still build stromatolites such as those found today in the hypersaline waters of Shark Bay, Western Australia, we know a lot about them. They can harness solar energy via photosynthesis to convert inorganic atmospheric gases into organic compounds, the chemical building blocks they need to thrive.

In this reconstruction of a scene 3.5 billion years ago, the sky appears orange rather than blue because at this time in the early history of the atmosphere it contained mostly greenhouse gases and almost no free oxygen. The shallow ocean waters were green because they were chemically different from oceans of today; altogether it was an eerie planet, but one where exciting things were happening. At the edges of the shallow ocean in a volcanically active world, hot springs were bubbling up with mineral nutrients that could have enabled



the first life to develop. In the shallow marine waters nearby, stromatolites are busily converting CO₂ into more complex organic compounds and giving back O₂ as a waste product. They were the source of the gradually accumulating mass of oxygen that eventually enabled animals, such as the vendozoans found at Ediacara in South Australia (p. 20) to evolve, thrive and diversify. Because of this fossil record in Western Australia, NASA's efforts to find evidence of former life on Mars are increasingly focused on investigating what appear to be ancient Martian spring deposits.

AGE

Archaean Eon, about 3.45-3.43 billion years ago.

LOCALITY

Pilbara, Western Australia (Dresser Formation). Possibly even older stromatolites have been reported from rocks in Greenland that are 3.7 billion years old.

ENVIRONMENT

Shallow sea adjacent to an area of land where hot springs were disgorging water and mineral nutrients from rocks below the surface. The springs would have produced pools of varying temperature where life may have begun. In the shallow ocean waters, stromatolites developed as mounds built by cyanobacteria that faced the sun. Volcanoes were active at this time, providing a constant source of nutrients.

REFERENCES 6, 100, 280

Ediacaran Hills, South Australia



APPROXIMATELY 560 MILLION YEARS AGO, THE

southern Flinders Ranges of South Australia near Brachina Gorge in the Ediacara Hills was nothing like the dusty desert landscape it is today. At that time, a shallow warm sea covered the area and in it thrived many of Earth's earliest animals. Some of these were trapped in fine silt that eventually buried them, enabling the process of fossilisation. Discovered by geologist Reg Sprigg in 1946 and now famous worldwide, the Ediacaran fossils are unique in their high diversity and excellent preservation. They represent a rare window into the appearance and lifestyles of complex multicellular animals on Earth. The time interval when these creatures lived has been formally named the Ediacaran period. The scene shown here contains feather-like sea pens (pennatulaceans) like *Charniodiscus* to the right. Like corals, these filter the water for organic matter. The little polyp-like creatures that live on each 'leaf' are akin to living coral organisms. Some of these sea pens were up to 50 cm in height and each was attached by a thick basal plate to the substrate. The thimbleshaped animal with long spikes radiating out was perhaps the world's first creature to have a supporting skeleton. Named *Coronacollina*, it was only about 1.5 cm high but its spicules extended up to 37 cm long. It likely fed like a sponge, sifting organic material form the water.

The colonial organisms in the background which are dividing into strands are Funisia, perhaps the earliest evidence of sexual reproduction in the fossil record. The fact that they budded at the same time rather than randomly suggests a mass mating event somewhat like the spawning of corals under a full moon. The giant flat worm on the bottom right is one of the largest known organisms of this age, it is the Dickinsonia rex, just over 1 m in length. It slowly moved over the sea floor either absorbing nutrients through its skin or grazing, depending on whether or not it had a mouth. Smaller Dickinsonia costata is shown in the centre of the image. Discovery of cholesterol in similaraged species of *Dickinsonia* in Russia confirms that these are in fact archaic animals because only animals have cholesterol. Other creatures depicted here include the enigmatic Tribrachidium, centre right, and Kimberella, the small elongate animal at bottom centre.

AGE

Late Ediacaran Period, about 570-540 million years ago.

LOCALITY

Ediacara Hills, Flinders Ranges, South Australia.



ENVIRONMENT

Shallow warm sea floor is the most accepted interpretation, ranging from the marine zone of fair weather wave oscillation through to distal storm wave base. A recent paper (ref. 323) suggested that some of the Ediacarans may have inhabited a cool dry soil environment, but this view has been debunked in detail (ref. 380).

REFERENCES

77, 103, 238, 323, 364, 380

Emu Bay, South Australia



LIKE ITS SLIGHTLY YOUNGER COUNTERPART THE

Burgess Shale in British Columbia, and the slightly older Chengjiang Fauna in Yunnan, China, the formation called the Emu Bay Shale is a worldclass deposit renowned for its high quality of fossil preservation. Here, not only the hard-shelled arthropods like trilobites (centre right and left) but also many kinds of soft-bodied worms and creatures of enigmatic affinity were exquisitely preserved between layers of black shale.

The top predator in this ancient ecosystem was the arthropod *Anomalocaris* (centre top) represented by two species in the fauna, the endemic A. briggsi and A. cf. canadensis, also known from the famous Burgess Shale site in Canada. A. briggsi grew to about 50 cm in length. It is seen here with a small arthropod Kangacaris, a trilobite-like form, struggling in the big predator's appendages and about to be eaten. Although A. canadensis is interpreted as a feeder on hardshelled animals like trilobites, its Australian cousin was less well equipped for hard food, and probably fed mainly on small arthropods and soft-bodied creatures. Anomalocaris had large pear-shaped eyes on stalks with about 16 000 lenses on each eye, giving it the most acute vision of any creature for this age, and equivalent to the visual acuity of a modern dragonfly. Its long feeding appendages could grasp and snatch unwary prey and lift it to its deadly circular saw-like mouth. The large trilobite in the bottom left corner is *Redlichia takooensis*, one of the commonest fossils found at Emu Bay, leaving a *Cruziania* feeding trail in its wake.

Bivalved arthropods, the earliest known prawnlike creatures, swim to the top left of the scene. *Isoxys* can be seen in the top left and *Tuzoia* a little below it. A nudibranch mollusc is seen swimming just below the centre of the scene. Although nudibranchs haven't been found at Emu Bay they are likely to exist at this time, as the first molluscs were radiating into the major groups found today.

AGE

Early Cambrian, about 514 million years ago.

LOCALITY

Emu Bay Shales, quarry on the north side of Kangaroo Island, South Australia.



ENVIRONMENT

The south-western corner of what is today Kangaroo Island was underneath a warm tropical seaway close to the ancient equator. Turbidity currents caused by tectonic activity would periodically wash animals down the shelf slopes into a deeper mini-basin on the continent's inner shelf, preserving very fine details of each fossil.

REFERENCES

105, 137, 211, 287, 288, 289, 290

Stairway Sandstone, Northern Territory ORDOVICIAN



ABOUT 465 MILLION YEARS AGO A SHALLOW

warm inland waterway called the Larapinta Sea cut Australia in half and soaked central Australia, then part of the larger Gondwana landmass. In these tropical waters lived some of the earliest known backboned animals (vertebrates), but they did not look like any of today's fishes. *Arandaspis* (the five individuals at right), named after the Aranda Indigenous peoples of the region and Greek 'aspis', meaning 'shield', is known from relatively complete impressions of its bony head shield and elongated trunk scales. It bore two small headlamp-like eyes at the front of its head and a small open mouth, lacking jaws, probably for sifting organic particles out of the sandy sea floor. Growing to about 25 cm in length, it was invested with finely sculptured bone formed in the skin (dermal bone) over its entire outer surface, but apparently lacked any ossifications inside it. It thus highlights the peculiar nature of our deep distant evolution – the first vertebrates were 'inside out' animals compared to later more advanced creatures, like us, where all the bone is deep inside the animal.

Also closely related to our ancestry are the

tiny worm-like conodonts, extinct chordates with phosphatic jaw-like structures inside the head. Some scientists place conodonts as more advanced than fishes like Arandaspis because the presence of phosphatised tissues similar to dentine is a feature that would later characterise all jawed animals. Others place conodonts a step lower on the evolutionary tree than jawless fishes because we simply don't know enough about them yet, as few are ever preserved whole. A number of them are seen here homing in on the wake of the trilobites' feeding trail. Not shown here is Porophoraspis, a close relative of Arandaspis that had a different kind of surface ornament on its bones. Scales of a tantalising possible early jawed shark-like fish, named Tantalepis, have been found in the same deposits. They are exactly like the simple placoid scales seen in many living sharks.

Giant orthocone nautiloids, squid-like creatures living inside long straight chambered shells, were clearly the top predator in this shallow marine ecosystem, some growing as large as 2 m in length. They would likely be feeding on large trilobites and other sedentary molluscs they could catch easily. Huge trilobites, some up to 75 cm in length, are represented in the fauna by their feeding trails, called Cruziania, which characterise the outcrops of the Stairway Sandstone. Trilobites feed by pushing organic-rich sediment into their backwards-facing mouths, thus leaving the distinctive trail from the scraping motion of their feeding appendages. Two examples of the little bivalve Aloconcha can be seen lying in the wake of the giant trilobites' feeding trail.

AGE

Middle Ordovician (Darriwilian), about 465 million years ago.

LOCALITY

Stairway Sandstone, Mt Watt, Mt Charlotte, central Australia.



ENVIRONMENT

Warm equatorial tropical inland sea. Australia then formed the northern edge of Gondwana.

REFERENCES

100, 339, 346, 383

Baragwanathia flora, Victoria silurian/devonian



SOME OF THE WORLD'S OLDEST WELL-PRESERVED

land plants are represented by fossils found in central Victoria near the town of Yea. They are dated at most late Silurian age, around 420 million years old. This makes *Baragwanathia* one of the most advanced land plants for its age. Fossils of *Baragwanathia* persist until early Devonian times about 395 million years ago. These include the clubmoss (lycophyte) *Baragwanathia longifolia* shown here as the central slender branching plant. It grew up to 2.5 m in length and each stem was around 5 cm in diameter. It was named in honour of the former director of the Victorian Geological Survey, William Baragwanath. It was a vascular plant with supporting tissues in the stem, each of which bore a loose spiral of short spiny leaves. It had adventitious roots that crept down from the leafy stems to anchor it to the ground. It is thought to have lived alongside rivers and marshes, where occasional floods swept the plant out to sea.

Baragwanathia was discovered and named in the mid 1930s by Isabel Cookson. An early plant species, *Cooksonia*, was later named after her. It is shown here as the clump of erect branching stems emerging from the water, each bearing terminal sporangia (to the right of the central Baragwanathia plant). Cooksonia was perhaps a little more primitive than Baragwanathia because it has a simpler type of vascular tissue supporting the stem. It grew only a few centimetres tall and lacked leaves. It belongs in the Embryophyte group which contain mosses, ferns, liverworts and their kin. Some Cooksonia stems contain holes that aided gas exchange (like leaf 'stomata') but the plant was not capable of photosynthesis. It is now known from about half a dozen different species around the world. To the left of the central Baragwanathia plant are some green weakly branching stems emerging upright from the water. These are zosterophyll plants of unknown identification. These simple branching plants have stems covered with very short spines and grew by unrolling from the tips. Other plants depicted here are known from their fossil spores in rocks of similar age in southern Australia. They allow us to reconstruct clumps of early ferns (right, centre), mosses (centre left, top) and liverworts (behind the central Baragwanathia). These are all representative of living forms found in Australia and elsewhere today.

What animals might have lived among the early plants of Victoria? Although no body fossils of animals have been found in these beds, fossils of this age associated with similar plants are known from other sites in the Northern Hemisphere. They include creatures such as tiny spider-like trigonotarbids, a few millimetres long, and early insect-like springtails that possibly fed in the leaf litter and debris of the plant undergrowth. One specimen of a fossil fish has been found in the *Baragwanathia* beds near Yea. Named Yealepis, meaning scale from Yea, it was a small shark-like fish covered in tiny scales. Because its head is unknown, its affinities to any modern fish remain a mystery.

AGE

Latest Silurian-early Devonian. First sites asserted as late Silurian, later found to be early Devonian. Later, definite Silurian *Baragwanathia* was confirmed.

LOCALITY

Wilson Creek Shale, Yea, central Victoria.



ENVIRONMENT

The fossil plants were washed out to sea and deposited in a deep marine environment. At this time the landmass was not far away, so the plants are thought to have lived in waterways close to the river mouth from where they could be swept out to sea by flood events.

REFERENCES 68, 85, 102, 138, 206

Evolution of early vertebrates



THE EVOLUTION OF VERTEBRATES HAD HUMBLE

beginnings with simple worm-like creatures whose main characteristics are the presence of a cartilaginous rod along the back, called a notochord. Top left we see an extant cephalochordate Branchiostoma (also known as Amphioxus). Second from the top is Pikaia, which lived 508 million years ago. Its fossils have been found in the Burgess Shale of British Columbia. It had W-shaped muscle bands, a dorsal notochord or stiffening rod, possible gill slits and a head with two well-developed eyes. These features are among those that make it a member of the Phylum Chordata and a likely contender as a vertebrate ancestor. Below Pikaia we see Palaeobranchiostoma, a fossil tunicate from the Permian of South Africa. Tunicates or urochordates include the modern sea-squirts (below left, sessile

adult sea squirt; right, mobile larval form). The muscular body of the larval form has been the basis for reconstructing *Paleobranchiostoma* as a chordate with fins that had the ability to swim. Its dorsal fin had several strong barbs along its leading edge. Sea squirts (bottom left) have a free-swimming larval phase that eventually settles down on the sea floor where it becomes a sessile adult that filter-feeds from the water. The presence of a well-developed pharynx with gill slits and a muscular tail places sea squirts close to the ancestry of all vertebrates, and in recent years molecular analysis of their DNA has confirmed that this is so.

The hagfish *Myxine* (top right) is perhaps the most primitive living fish, although strictly speaking most biologists do not regard it to be a true fish anymore; after all, it lacks jaws, teeth, fins and quite
a few other anatomical features seen in all modern fishes. Perhaps *Myxine* would be better regarded as an evolutionary step between urochordates and 'real' fishes.

The lampreys (right, second from top) are parasitic jawless fishes, known from many species. They have an ammocoete juvenile phase that filter-feeds in the substrate. The adult has a migratory phase in the open sea, and many species return to rivers to spawn. They all have a well-developed oral hood with keratinous horny teeth to rasp their prey and suck blood. Their gills are internally lined in pouches, unlike jawed fishes which have their gills supported on lateral bars. Fossil jawless fishes like Myllokungmingia (centre right) show the presence of a well-developed head, well-developed gill rows, and muscular tail. While their 530 million years old fossil remains from Chengjiang, China, are difficult to interpret, it is likely that they were the first true fishes, although their skeletons still lack ossified bone. Mettspriggina, recently described from the Burgess Shale, is a close contender for the first true fish because it has well-developed gill-arches supported on lateral gill bars like jawed fishes.

The conodont animal (second from bottom, right) has phosphatic bony tissues forming its feeding apparatus which looks jaw-like and contains a dentine-like layer. This is a true vertebrate characteristic, a tissue derived from neural crest cells that occur in all living animals. Complete conodont remains of Clydagnathus, dated around 330 million years old from Scotland, reveal a worm-like body with large eyes and a simple tail. Finally (bottom right) we see an early jawless fish, Arandaspis, from the 465 million years old Stairway Sandstone of central Australia, with well-developed bone covering its entire external surface. The next biggest phase in vertebrate evolution was to acquire jaws and teeth. Early shark-like scales found with Arandaspis suggest this could have taken place by the end of the Ordovician Period.

REFERENCES 97, 182, 264, 355, 359

Burrinjuck, New South Wales



THE DARK BLUE LIMESTONES AND LIMEY SHALES

outcropping in the Taemas-Wee Jasper region of New South Wales around Lake Burrinjuck were laid down in a warm shallow sea about 410-400 million years ago. Here, patches of algal reefs with interspersed colonial corals have produced the most diverse and best-preserved fauna of early fishes of this age, anywhere on the planet. The specimens are acid-prepared from the rock to reveal stunning 3-D skulls and bones that have been recently studied using micro-CT imagery to reveal the internal anatomy down to the cellular level. At least 70 species of fishes are now known. These include armoured placoderm fishes, the first vertebrates with jaws and teeth, as well as many kinds of early bony fishes. Isolated jawbones, teeth and scales of spiny acanthodians ('stem chondrichthyans') and jawless thelodonts are less common in the fauna.

The scene here shows the largest fish from this habitat, the placoderm *Cavanosteus*. It was probably a slow-swimming filter-feeder that swam like a whale shark through the warm waters of the Gondwana seaways, feeding on plankton. Below left, resting on the coral, is an acanthothoracid placoderm *Murrindalaspis* with its high median dorsal spine. Just behind it, lurking under the coral is a large lungfish *Dipnorhynchus*, which probably fed primarily on hard-shelled clams and snails. To its right are two more placoderms, these with flared spinals in front of the fins. The one on the right is the petalichthyid placoderm *Widjeaspis*. In the background an eel-like bony fish *Onychodus yassensis* darts out from the reef to catch an unwary passing placoderm.

Another fish in this fauna was Dhanguura johnstoni (centre right). The generic name means 'catfish' in the local Wiradjuri Indigenous language, while the species name honours its finder Dr Paul Johnston. Dhanguura may have reached lengths of about 2-3 m. We do not have its jaw bones so have no idea what it might have eaten. In the bottom right of the image we see a school of three ptyctodontid placoderms cruising into the scene. These are durophagous (eating 'hard' foods) fish that have powerful tooth plates for eating hardshelled prey on the reef. The body restorations shown here are based on better-known forms from the late Devonian Gogo Formation because only their tooth plates have been described from the Taemas site.

In the far distant mid-surface waters we see silhouettes of other placoderms in the centre, and some early possible ray-finned fishes (actinopterygians) to the right. We have isolated scales and bones suggesting these were present, including a skull of one form, *Ligulalepis*, a primitive kind of osteichthyan.

AGE

Early Devonian, from Pragian-Emsian, about 410-400 million years ago.

LOCALITY

Around Burrinjuck Dam, Taemas-Wee Jasper region, New South Wales.



ENVIRONMENT

Abundant marine invertebrates like shells, corals, trilobites, brachiopods and crinoids in the fish-bearing strata confirm this was largely a shallow tropical reef environment.

REFERENCES

213, 227, 386, 467, 468, 469

Georgina Basin, Queensland



THE GEOGRAPHIC REGION FROM THE CENTRAL

western Queensland border to the Canning Basin of Western Australia and down to Cobar in western New South Wales was once inhabited by the Wuttagoonaspis fauna which contained strange, armoured fishes and rare bony fishes. Wuttagoonaspis was a peculiar placoderm (named after Wuttagoona Station in New South Wales) that grew to 1 m in length. It is shown here as the largest fish (to the left of centre) with two kinds of peculiar jawless armoured fishes glancing at it from either side. Wuttagoonaspis is an enigma in the world of placoderms. It shows features of skull roof and body armour that are seen in the most diverse group of placoderms, called arthrodires, but if it belongs in this group at all it is very basal. Its remains are highly distinctive fossils characterised by linear patterns of ornamentation on the bones. Swimming away at the left of the scene is *Neeyambaspis*. The fish on the right with the long snout is the very distinctive *Pituriaspis*. Indeed, *Pituriaspis* and its cousin *Neeyambaspis* belong in a group called the Pituriaspida. When Gavin Young erected it in 1992, it was the first new class of vertebrates discovered in over 70 years. We know very little about them because they are only known from a few sandstone casts in the rocks.

In the background is a flattened placoderm typical of the early phyllolepid types, possibly one of the rare arthrodires in the fauna. Phyllolepids emerged as a common group later in the middle Devonian. This occurrence in the Georgina Basin sediments could well be the oldest known example of the group. The Wuttagoonaspis fauna is also famous for containing the oldest known members of the rhizodont fish group, which went on to become the largest bony fishes of the Palaeozoic (later forms reached 6 m in length). The Cravens Peak rhizodontid was small, about 50 cm long, and is known only from its shoulder girdle and a few odd bones. An isolated limestone layer within the succession bearing these fish fossils has yielded teeth of sharks (Maiseyodus) as well as scales of acanthodians (basal shark-like fishes) and tiny jawless fishes called thelodonts. A single jaw also shows that the eel-like onychodontids were present (Luckius).

The most fascinating thing about the *Wuttagoonaspis* fauna of Australia, known from an area of nearly 2 million km², is that it was this country's first widespread endemic vertebrate fauna. Around 30 species are now known from this fauna, the vast majority of which are placoderms. Many new specimens are being studied, so this number is bound to expand in the future.

AGE

Early-middle Devonian Boundary, about 395-390 million years ago.

LOCALITY

Craven Peak Beds, Georgina Basin, western Queensland; Dulcie Range, Northern Territory; and Cobar, New South Wales (Mulga Downs Group). Subsurface deposits containing the fauna are also known from the Canning Basin in Western Australia and Officer Basin in South Australia.



ENVIRONMENT

The lack of marine invertebrates and microfossils in the fish-bearing strata suggest this was largely a fluviatile environment, but the presence of thelodonts, common in marine deposits in the early Devonian, suggests the sediments could have been deposited close to the mouth of the river system.

REFERENCES

335, 336, 398, 466, 470

Gogo, Scene 1, Western Australia



THE GOGO FORMATION FORMED IN THE INTER-

reef basins between active reef fronts and atolls in a warm tropical sea close to the equator about 382 million years ago. The reef was built up of several kinds of algae and layered spongelike stromatoporoids with scattered corals and bryozoans. Clusters of horn-shaped rugose corals and large colonies of tabulate forms are shown here as well. Many kinds of fishes lived here, and this scene features some of the more bizarre bony fishes (Osteichthyes) as well as some of the placoderms. The perfect 3-D preservation of the Gogo fish fossils, including muscles and soft tissues in some specimens, makes it the world's best preserved and most diverse assemblage of fishes of this age. Studies on the geology of the site indicate the fishes' bodies sank into a quiet basin whose muddy seafloor lacked oxygen. Middle water layers rich in hydrogen sulphide helped preserve the animals' delicate internal structures when the fossilisation process began. Today their bodies, entombed in limestone concretions, can be found weathering out in outcrops of the Gogo Formation east of Fitzroy Crossing.

The long-shielded placoderm Holonema westolli (top left) was a bottom-feeder, probably browsing on algal oncolites with it scoop-shaped dental plates. It grew to about 1 m long and is known from several species around the world, but H. westolli from Gogo is the best preserved. Some specimens show pebbles in the gut, suggesting it either ate oncolites or ingested ballast stones to keep it on the sea floor while feeding. At the centre lower part of the scene we see the long snouted placoderm *Rolfosteus*, whose crushing tooth plates suggest it ate hard-shelled creatures like the bivalved concavicarid crustaceans that inhabited the sea floor. Its streamlined body with long tubular snout must have been useful for keeping ahead of predators in this highly diverse ecosystem.

To the bottom right we see the daggertoothed fish *Onychodus jandemarrai*, named after Jandemarra, an early Indigenous freedom fighter who lived in the region. This fish, which grew to 2 m long at Gogo but up to 4 m elsewhere, was like a killer moray eel that darted in and out of the crevices in the reef to catch unsuspecting passing prey. In this case it has seized a long snouted lungfish *Griphognathus whitei*. *Griphognathus* likely used its elongate duck-like jaws to suck up worms and other prey in the muddy sections of deeper sea floor, perhaps using its electro-sensory system at the tip of the snout. Small ray-finned fishes *Mimipiscis* swim in the top background centre as does a small arthrodire, *Compagopiscis* (top right).

AGE

Late Devonian (Frasnian), about 385-380 million years ago.

LOCALITY

Gogo and Mt Pierre Stations, east of Fitzroy Crossing, Western Australia.



ENVIRONMENT

Warm equatorial algal-stromatoporoid reef environment, 100-200 m deep in inter-reef basins where the fishes were buried. They mostly lived on and round the reef which would have been a more active habitat, quite shallow in places.

REFERENCES 8, 73, 98, 224, 225, 249

Gogo, Scene 2, Western Australia



THIS RECONSTRUCTION SHOWS VARIOUS KINDS

of placoderm fishes in the foreground with a school of ray-finned fishes *Moythomasia durgaringa*, each about 20 cm long, swimming in the top right background.

Mcnamaraspis kaprios (top left) is a 30 cm long predatory arthrodire which was proclaimed as the state fossil emblem of Western Australia in 1995, thus becoming Australia's first such emblem. Its name honours palaeontologist Ken McNamara and the species name *kaprios* (boar-like) refers to the tusks on its lower jaw. Only two specimens are known. One is in the British Museum in London and the other, a complete specimen, is on display at the Western Australian Museum.

To the bottom left we see the ptyctodontid placoderm *Materpiscus attenboroughi*, named in honour of Sir David Attenborough. It is also known as the 'mother fish' because at the time it was described its fossil remains contained the oldest known vertebrate fossil embryo, still connected to the mother by a mineralised umbilical cord. It constitutes the oldest hard evidence for live birth (viviparity) then known in any vertebrate animal and caused a stir because it meant that placoderms, once thought to be very primitive fishes, in fact had a very advanced form of mating that involved internal fertilisation. Male ptyctodontids had hook-shaped bony claspers which they inserted inside the female to transfer sperm; this was one of the earliest acts of copulation. The scene shown here hints at the imminent birth of a young pup as the tail pokes out from the mother fish's cloaca.

To the right is the strange placoderm fish Bothriolepis, which possessed bone-covered articulated pectoral fins. Its weak jaws suggest it fed by ingesting organic-rich muds from the sea floor. A close relative of Bothriolepis called Microbrachius was recently shown to possess bony claspers on the males which were fixed rigidly to the body plates on their underside. These fishes most likely mated side by side with arms interlocked.

In the centre background, below the Moythomasia shoal, is the high-spined ptyctodontid Campbellodus. Its body was covered in large overlapping scales. This one is clearly a male because of the claspers seen poking out behind its pelvic fins.

AGE

Late Devonian (Frasnian), about 385-380 million years ago.

LOCALITY

Gogo and Mt Pierre Stations, east of Fitzroy Crossing, Western Australia.



ENVIRONMENT

Warm equatorial algal-stromatoporoid reef environment, 100-200 m deep in inter-reef basins where the fishes were buried. They mostly lived on and round the reef which would have been a more active habitat, quite shallow in places.

REFERENCES 74, 218, 219, 224, 226

Canowindra, Scene 1, New South Wales



ABOUT 363 MILLION YEARS AGO IN CENTRAL

New South Wales near the small town of Canowindra a great drought occurred. It caused many fishes living in the large meandering river systems to pool together and die in the last vestiges of the water. Subsequently, layers of water-borne sands buried them, eventually creating a spectacular assemblage of fossils. The bone eventually weathered away, leaving clear impressions of their skeletons in the silty sandstone layers. In the mid 1950s a road cutting put through near Canowindra unearthed the first slab covered in fish fossils and more recent excavations by Dr Alex Ritchie, then of the Australian Museum, and his colleagues unearthed many new species of fishes from the site.

The scene here shows the pool just before all the water has dried up. It mostly comprises hundreds of examples of the antiarch placoderm fishes *Bothriolepis yeungae* and *Remigolepis walkeri*. *Bothriolepis* (pitted scale), which has long segmented pectoral fins, is one of the most common types of placoderms – about 150 species are known worldwide from both marine and freshwater deposits. *Remigolepis* (oar scale) has a single unsegmented bony arm forming its pectoral fin. It is seen here with a slightly reddish tinge, whereas *Bothriolepis* is shown as being green. These antiarchs most likely fed by ploughing into the river bottom, ingesting organic-rich muds because their mouths had very delicate weak jaws that lacked real teeth.

The lobe-finned fishes in the centre are Canowindra grossi, first described from the site in 1973 and still only known from one specimen which sits in the middle of the original 1956 slab of fishes. Canowindra grossi is named after the township and the famous German palaeontologist Walter Gross. It belongs to the tetrapodomorph fishes, which are the lineage of fishes that is closest to early land animals (tetrapods). Canowindra represents an endemic family of this group only known from East Gondwanan Devonian deposits of Australia and Antarctica. These fishes had powerful jaws and strong muscular fins and would have been strong enough to gain pole position in the centre of the remaining water supply. ●

AGE

Late Devonian (Famennian), about 363 million years ago.

LOCALITY

Near the township of Canowindra, New South Wales.



ENVIRONMENT

Fluviatile, river deposit overflow (billabong) that has dried up, leaving the fishes to die exposed. At this time Australia was further north than today, and slightly warmer with higher levels of oxygen creating lush forests near the waterways.

REFERENCES 189, 190, 215, 222, 337

Canowindra, Scene 2, New South Wales



THE ANCIENT RIVER SYSTEM NEAR CANOWINDRA

was home to a diverse community of freshwater fishes that included armoured placoderms *Bothriolepis yeungae* with its bony articulated arms (mid left centre), the arthrodire *Groenlandaspis* (bottom right) which likely fed on small worms and other creatures it could catch with its tiny needlelike teeth, and *Remigolepis walkeri* (centre right top), which may have been a bottom-feeder looking for weeds and organic-rich muds. The main predators here were the robust lobe-finned fishes called tetrapodomorphans because their skull and limb bone patterns closely resembled those of the first tetrapods, or four-legged land animals. The large *Mandageria fairfaxi*, close to 2 m long, is shown here catching an unwary lungfish *Soederbergia*, a long-snouted form also known from Greenland and North America.

Emerging from below the leaf litter (bottom left) is the small-eyed robust fish called *Gooloogongia loomesi*, an early rhizodontid. These were the giants of the early bony fish world whose later forms like *Rhizodus* would reach 6 m long in the early Carboniferous Period. *Gooloogongia* was one of the most primitive of all known rhizodontids and, together with much older fragmentary remains of the group from Antarctica, is support for a Gondwanan origin for the group. Its slender projecting lower jaw teeth and flat head shape made it an opportune lunge ambush predator that probably surprised its prey by rising up from the murky waters like a crocodile. Similar to crocs, the limbs had a rounded shoulder joint on the humerus, suggesting these large fishes were able to twist their prey in a death roll that both killed and tore them apart.

The fish swimming centre right is *Cabonnichthys*, another lobe-finned fish closely related to *Mandageria* but only half its size. Both of these fishes are members of the tristichopterid family, a group known throughout the world at this time. Recent studies, however, suggest that the Australian tristichopterids may represent an endemic Gondwana group only distantly related to those in the Northern Hemisphere. All the lobefinned fishes shown here had powerful tusks in their jaws and were clearly predators.

AGE

Late Devonian (Famennian), about 363 million years ago.

LOCALITY

Near the township of Canowindra, New South Wales.



ENVIRONMENT

Fluviatile, river deposit overflow (billabong) that has dried up, leaving the fishes to die exposed. At this time Australia was further north than today, and slightly warmer with higher levels of oxygen creating lush forests near the waterways.

REFERENCES 3, 4, 191, 192, 193, 221

Mansfield, Victoria devonian/carboniferous



HERE WE SEE THE LARGE RHIZODONTID FISH

Barameda decipiens (top centre) seizing a lungfish Delatitia breviceps (left centre) in its powerful jaws. Barameda, from an Aboriginal word meaning 'fish trap', is known from two species at Mansfield. The smaller *B. mitchelli* was one of the first of the rhizodontid group to have the skull preserved and described. It grew to about 1 m long. *B. decipiens* was the largest predator in these ancient large meandering rivers and may have reached 4 m in length. It demonstrates that rhizodonts diverged early in the tetrapodomorph group. This is borne out by the fact that the oldest and most primitive known members of the group occur in Australian and Antarctic middle Devonian deposits.

At the top right we see the sharp-spined stem shark *Gyracanthides murrayi*, which is a member of the basal shark group called acanthodians that went extinct at the end of the Palaeozoic Era. *Gyracanthides* spines are heavily ribbed and very sharp, a defence mechanism against the larger predators that shared the same rivers. A school of ray-finned fishes of the *Mansfieldiscus* variety (fish from Mansfield) are seen swimming nonchalantly away in the top right corner. These were the 'trout' of the late Devonian-early Carboniferous rivers, actively feeding on smaller fishes and invertebrates in the ancient river system.

Below is an arthrodire placoderm Groenlandaspis, which is thought to have died out at the end of the Devonian Period (359 million years ago) but is included here to highlight the uncertainty surrounding the true age of the Mansfield Basin deposits. This assemblage is enigmatic because it was thought to represents the very latest Devonian fauna of fishes, although some have argued it was early Carboniferous (about 350-330 million years ago) in age after all of the placoderms were gone. This scene takes the radical view that this fauna is latest Devonian, about 359 million years old, which is right on the Devonian/Carboniferous boundary. Much older remains of placoderms like Bothriolepis and Austrophyllolepis have been found in older fluviatile sedimentary rock outcroppings in the South Blue Range near Mansfield, first discovered by Australian geologist Edwin Sherbon Hills in the 1930s. Recent finds of teeth have revealed the presence of small fossil sharks in both the South Blue Range succession and in the Mansfield Basin red beds. These indicate possible proximity of these riverine communities to those of the open sea.

AGE

Latest Devonian-earliest Carboniferous, about 359 million years ago.

LOCALITY

Devils Plain Formation, Broken River region, Mansfield, Victoria.



ENVIRONMENT

The fish fossils at Mansfield are all found in red mudstone and sandstone deposits indicative of large meandering river settings. At this time, Australia had a warm to tropical climate, with oxygen in the atmosphere at above today's levels. Forests made of large lycopods and ferns covered the land near the waterways.

REFERENCES

139, 180, 216, 441

Ducabrook Formation, Queensland



THE LOWER CARBONIFEROUS OF NORTHERN

Australia was a time of warm to arid climates, with large meandering rivers dominating the landscape. Lush forests fed by high oxygen levels in the atmosphere lined the waterways. These forests were probably inhabited by large arthropods such as occur elsewhere in the world at this time. Rotting vegetation and abundant insect life would have enriched the lake and river systems. These waterways were home to a variety of unusual fishes and one of the oldest well-preserved tetrapods (early amphibians) known from Australia. *Ossinodus pueri* (lower frame), meaning 'toothed bone', was one of the most primitive tetrapods of this period, and the only Carboniferous tetrapod known from Australia. Its salamander-like body was probably covered in fish-like scales. It possessed a flat broad skull that was similar in overall form to that of the late Devonian amphibian *Acanthostega* and was around 1.5 m long.

This tetrapod is accompanied by two common fishes found in the same beds. A large spined stem shark ('acanthodian') *Gyracanthides hawkinsi* (above centre) probably grew to about 60 cm in length and may have fed on plants and small invertebrates. The large rhizodontid sarcopterygian Strepsodus sp. (top right) was one of the largest bony fishes (osteichthyans) of this period, with some Scottish species possibly growing as large as 4 m. It is not clear whether the Queensland species, which was about 1 m in maximum length, is actually a species of Strepsodus or a member of a different but similar group. It is only known from fragmentary shoulder girdle bones called cleithra. These fishes were armed with long sigmoid teeth in the lower jaw and large marginal teeth on both jaws, a clear indication that they were predators. They would most likely have hunted the swift moving trout-like palaeoniscoids, early ray-finned fishes, whose remains are commonly found as isolated scales and bones in contemporaneous deposits from central Queensland.

AGE

Early Carboniferous, about 330 million years ago.

LOCALITY

Ducabrook Station, near Emerald, central south Queensland.



ENVIRONMENT

The fossils occur in a sequence representing a river delta, with bones deposited by a flood event. At the time, Australia was relatively warm with high oxygen levels giving rise to abundant land plants, mainly lycopods and ferns. Australia was at a similar latitude and orientation to its position today.

REFERENCES

194, 397, 405, 410

Blackwater Shale, Queensland



A LARGE LAKE FORMED IN SOUTH CENTRAL

Queensland about 270 million years ago. Plant material accumulated in the lake from the surrounding forests ultimately led to the formation of black coal deposits. The lake was also home to some very interesting species of extinct fishes unique to Australia. This scene is dominated by the small shark *Surcaudalus rostratus*, known from a series of nearly complete specimens from the coal deposits at Blackwater. Its generic name derives from the well-developed epicaudal or lower lobe on the tail fin, while *rostratus* refers to the welldeveloped fleshy rostrum on the head. Surcaudalus rostratus grew to about 20 cm long. Each of its teeth had three hooked cusps, a primitive condition seen in several much older Devonian sharks like *Phoebodus*, and an indication that it was a predator of other fishes. Both dorsal fins had sharp prominent spines, which suggests a possible relationship to the older *Ctenacanthus*.

Living alongside the shark were several kinds of ray-finned fishes. The most abundant of these was the deep-bodied form called *Ebenaqua ritchiei*, here seen swimming away in the top left of the panorama. The generic name is Latin for 'black water' and the species honours Dr Alex Ritchie. *Ebenaqua* had a very small mouth that lacked teeth. It most likely grazed on algae and other plants in the lake. The fishes shown in the centre being chased by the shark, and at the bottom left, represent two kinds of new unnamed rayfinned fishes whose fossils were described in an unpublished thesis. The school of fishes being hunted are a kind of urosthenid, a group of more advanced ray-fins also represented in the wellknown Jurassic Talbragar deposits of central New South Wales.

AGE

Late Permian (Wuchiapingian), about 254-259 million years ago.

LOCALITY

Rangal Coal Measures, Utah Development Corporation mine, near Blackwater, southern Queensland.



ENVIRONMENT

Australia was located closer to the South Pole at this time, close to the Antarctic Circle. Climate was cool to temperature as Gondwana emerged from the early Permian ice age. The habitat for the Blackwater deposit was a freshwater coal swamp.

REFERENCES

72, 212, 217

Blina Shale, Western Australia



TWO CHARACTERISTIC EARLY AMPHIBIANS ARE

shown here, the long snouted *Erythrobatrachus noonkanbahensis* to the left and the aptly named triangle-headed *Deltasaurus kimberleyensis* to the right. This scene is unusual in that it shows amphibians living in a marine environment, although it is possible that these tetrapods might have been swept out to sea before they were buried. The Blina Shale also contains remains of lingulid brachiopod shells, which also suggests the deposit formed in saltwater, perhaps an estuary. The outcrops of this fossil deposit occur in the Erskine Ranges between Derby and Fitzroy Crossing. They were excavated by US palaeontologist John Cosgriff after fossils were first discovered by another US expert, Dr Charles Camp, on a foraging trip to the region in the late 1960s. A partial skull of *D. kimberelyensis* is known from the Blina deposit, as well as the skull of a smaller species, *D. pustulatus*, that was recovered from deep underground in a drill core near Geraldton. The Blina species grew to about 1.25 m in length. The genus is also known from skulls found in Triassic deposits in Tasmania. Recent analysis suggests that *Deltasaurus* was a member of an endemic clade of Australian rhytidosteid amphibians in the family Derwentiidae.

Erythrobatrachus belonged to the trematosaur group of extinct labyrinthodont amphibians. Growing to about 2 m in length, it may have used its long crocodilian-like snout with many needlelike teeth to catch small fish. Living alongside it in the estuarine environment was a variety of potential fish prey, including the long snouted garlike *Saurichthys*, and medium-sized lungfish-like *Ceratodus*. The broader-headed *Deltasaurus* had more powerful jaw muscles and may well have fed on fish in the estuary, such as the ceratodontid lungfishes.

AGE

Early Triassic, about 247-251 million years ago.

LOCALITY

Blina Shale, Erskine Ranges, between Derby and Fitzroy Crossing, Western Australia.



ENVIRONMENT

A shallow marine seaway or estuary close to a large river mouth, where red sands and silts were deposited that buried the bony remains. At this time, northern Australia had a cool to temperate and relatively dry climate. Southern Australia was situated over the South Pole.

REFERENCES 86, 87, 99

Knocklofty Formation, Tasmania



TASMANIA AT THE BEGINNING OF THE AGE OF

dinosaurs was situated close to the South Pole. Cool temperate forest filled with tree ferns and seed ferns like *Dicroidium* dominated the landscape. Here we see *Tasmaniosaurus*, a primitive thecodontid reptile, in the centre of the scene, seizing a *Banksiops townrowi* amphibian out of the river. *Tasmaniosaurus* is known from a partial skeleton found in Crisp & Gunn's quarry in West Hobart in 1960 by Max Banks and John Townrow. It was about 1 m in length and was thought to be a sister taxon to proterosuchid reptiles which were basal in the tree of archosauriforms, the group that would give rise to dinosaurs, pterosaurs and crocodiles. Recent restudy of the type material revealed that it had well-developed olfactory bulbs inside the snout. One hypothesis suggests that these organs were too large for creatures inhabiting a semi-aquatic lifestyle, hence *Tasmaniosaurus* was more likely to have been a terrestrial predator.

B. townrowi was originally thought to be a species of *Blinasaurus*, a genus first described from Triassic deposits in the Kimberley region of Western Australia, but a revision of that family

indicated it was a different genus so it was given its own generic name. This creature was a typical temnospondyl amphibian about 60-80 cm in length. Its jaws were armed with sharp pointed teeth and its streamlined body shape suggests it would have been well-adapted to chase fish in the Triassic rivers that accumulated the Knocklofty Formation deposits. Potential prey would have included heavily scaled ray-finned palaeoniscoids, ceratodontid lungfishes and a coelacanth.

AGE

Early Triassic, about 240 million years ago.

LOCALITY

Knocklofty Formation, near Hobart, Tasmania.



ENVIRONMENT

Australia was situated over the South Pole in the early Triassic. Southern Australia was cool to cold, and forested.

REFERENCES

104, 107, 108, 293, 390, 407, 408

Arcadia Formation, Scene 1, Queensland



THE LONG-SNOUTED SLENDER RAY-FINNED FISH

looking somewhat gar-like, *Saurichthys* (left centre), turns away from the oncoming predators in the river. A tiny lizard-like creature called a procolophonid, sitting on a leaf whorl of a lycophyte plant, is about to be seized by the leaping salamander-like *Xenobrachyops allos*, a small chugitosaurid amphibian. First named *Brachyops* because it was thought to be closely related to that genus found in Triassic deposits in India, it was later renamed to mean 'foreign *Brachyops*' after extensive revision of its skull material demonstrated that it was quite unlike the Indian form. Its skull is 11 cm long, suggesting its total length was around 60-70 cm. It probably fed on the abundant small fishes and other vertebrates that shared this habitat.

A large capitosaurid amphibian *Parotosuchus* gunganj appears in the bottom left of the scene, sporting a broad flat skull with a long snout. This well-known amphibian occurred globally in the early Triassic. There are two species of this genus in the Rewan deposits of Queensland. *Parotosuchus gunganj* takes its name from the local Indigenous word meaning 'water dweller'. It grew to about 1.25 m in length and was probably an ambush hunter like many modern crocodiles. It had eyes close to the midline of the skull for viewing prey approaching the water's edge. Recent biomechanical studies of the skulls of *Parotosuchus* species reveal that the large palatal vacuities in the skull were important for decreasing skull weight and increasing the bite force of the jaws as they enabled more muscle mass to develop in the jaw region. The larger predatory amphibian *Acerastea wadeae*, which grew to 1.5 m, lurks menacingly in the background. ●

AGE

Early Triassic, about 240 million years ago.

LOCALITY

Arcadia Formation, Rewan Group, The Crater, near Rewan, Queensland.



ENVIRONMENT

Warm temperate climate, forests filled with tree ferns, seed ferns, regular ferns and progymnosperms. At this time northern Australia had a cool to temperate and relatively dry climate. Southern Australia was situated over the South Pole.

REFERENCES

183, 207, 395, 404, 406, 407

Arcadia Formation, Scene 2, Queensland



THE PIG-SIZED MAMMAL-LIKE REPTILE CALLED A

dicynodont is seen here coming down to drink (centre) as a predatory reptile *Kalisuchus* lunges up out of the water to take a small unwary amphibian *Arcadia myriadens. Kalisuchus* had a hooked snout with large sharp teeth. Its name derives from the Hindu goddess Kali, 'the destroyer', because the original fossil material was found as a pile of hundreds of small fragments that needed to be pieced together. *Kalisuchus* grew to about 3 m in length and was one of the largest terrestrial predators in this ancient Queensland ecosystem. The dicynodont resembles a creature called *Kannemeyeria*. These are known from South Africa where they were one of the most abundant land animals of the Triassic landscape. Dicynodonts possessed large tusks for rooting out plant material. The Australian species are only known from tusk fragments, so identification to genus is uncertain. They belong to the synapsid (mammal-like reptile) group because in terms of relationships they are closer to mammals than any other reptiles in this scene. Dicynodonts on other continents died out at the end of the Triassic but in Queensland they persisted much longer, into early Cretaceous times.

A prolacertid reptile named *Kadimakara* is seen at the left resting on the riverbank, looking a little like an early goanna. They were lizard-like hunters that preyed on smaller reptiles, fishes and amphibians in the same area. *Kadimakara* was once thought to be a close relative of the dinosaurs and a member of the relatively derived Archosauriformes, but a recent restudy of its fossil remains places it closer to the more archaic South African reptile *Prolacerta*.

AGE

Early Triassic, about 240 million years ago.

LOCALITY

Arcadia Formation, Rewan Group, The Crater, near Rewan, Queensland.



ENVIRONMENT

Warm temperate climate, forests filled with tree ferns, seed ferns, regular ferns and progymnosperms. At this time northern Australia had a cool to temperate and relatively dry climate. Southern Australia was situated over the South Pole.

REFERENCES 108, 389, 392

Hanson Formation, Antarctica



ALMOST 200 MILLION YEARS AGO, THE SOUTH

Pole was located just south of Antarctica which was the central hub of the supercontinent of Gondwana. The warm temperate climate here was favourable to forests full of ferns and cycads, and dinosaurs and mammal-like reptiles ruled the land. This assemblage of creatures was collected at an altitude of nearly 4000 m in the Transantarctic Mountains by Dr Bill Hammer and his team from Augustana College in the 1990s. It has yielded the oldest dinosaur fauna from that continent. The generic name of the predatory *Cryolophosaurus* *ellioti* (centre right) means 'frozen lizard'. The species name honours its finder, Dr David Elliot. It was a medium-sized theropod up to 6.5 m long. It is known from much of the skeleton and a near-complete skull. It bore distinctive swept-back crests above the eye ridges, possibly serving as an enhanced visual display to attract mates. *Cryolophosaurus* is regarded as a basal tetanuran, meaning it was a very primitive kind of predatory dinosaur not related to the well-known allosaurs or tyrannosaurs of the Northern Hemisphere. Its prey may well have included the 7.5 m

Glacialisaurus hammeri (centre left). This generic name means 'icy lizard' and the species name honours Bill Hammer. Glacialisaurus hammeri was a massospondylid sauropodomorphan dinosaur, one of the semi-bipedal ancestors of the gigantic, long-necked forms. It fed primarily on ferns and cycad plants. It is closely related to forms in China like Lufengosaurus. The small weasel-like creature (bottom left) is a tritylodont, a kind of advanced mammal-like reptile about 30 cm in length. It was probably omnivorous, eating worms, insects, frogs and maybe some plants. It has not yet been named because it is known from only one postcanine tooth which is indistinguishable from species of Bienotheroides from China. ●

AGE

Early Jurassic, about 195-187 million years ago.

LOCALITY

Mt Kirkpatrick, Transantarctic Ranges, about 650 km from the South Pole, Antarctica.



ENVIRONMENT

The fossil site was located between 55°S and 65°S. Here, during the early Jurassic, Antarctica was thought to have had a warm temperate climate, as shown by the abundant plants and fossil wood which indicates that large gymnosperm trees were present in the ecosystem.

REFERENCES

153, 154, 360, 362, 363

Talbragar, New South Wales



BY THE LATE JURASSIC WHEN VERY LARGE

dinosaurs were roaming the cool Australian landscape, aspects of the modern fish fauna had begun to appear in our rivers, seas and lakes. The Talbragar fish beds have yielded beautifully preserved complete specimens which show for the first time in Australian history a dominance of teleostean fishes, the group to which 99% of the modern living bony fishes belong. The scene is dominated by the presence of *Uabryichthys latus*, a large predatory macroseminonitid fish coming in from the top right, chasing a school of smaller herring-like Cavenderichthys talbragarensis. They are close relatives of a group that includes *Leptolepis koonwarri* from Victoria and *Luisella* from Argentina, a clade of fishes that were endemic to Gondwana. Below them, resting on the weedy river floor, is an elongate *Archaeomene*, looking wary at the presence of the approaching predator above it.

Madarsicus is seen at the top left. Fishes with such deep body shapes mostly fed on algae and other plants in the river system. Their large size and schooling habit protected them from most other predators. However, sharks up to 1 m long are known to have existed in these rivers and would have been the top predators in the fluvial habitat.

The floor of the river shows leaves of early conifers including branches from a species of *Wollemia*. The Wollemi Pine is a modern species of this genus that survives in the northern Blue Mountains of New South Wales and has been nicknamed the 'Pinosaur'. Fossils of many different kinds of edible insects, spiders and other small invertebrates in the Talbragar deposits indicate that there was an abundance of food items available to the fishes in these waters.

AGE

Late Jurassic, 151 million years ago.

LOCALITY

Purlawaugh Formation, Talbragar River, near Gulgong, New South Wales.



ENVIRONMENT

Australia was at a relatively high, cool temperature latitude in the mid to late Jurassic. The flora changed from an araucarian abundance to a podocarpdominated phase.

REFERENCES

36, 352, 396, 402, 403, 440

Evolution of the tetrapod forelimb



TODAY ALL LIVING LAND VERTEBRATES,

including some that have secondarily gone back into the seas, are called tetrapods, meaning they share a pattern of four limbs. Some that have secondarily gone back to life in water (e.g. whales) and others that have lost limbs (e.g. snakes) are still referred to as tetrapods because their earliest members retained the four-limbed body pattern. We call these limbs arms and legs, but they all evolved directly from the paired pectoral and pelvic limbs of fishes. This sequence shows the evolutionary stages from a primitive lobe-finned fish, a lungfish (top left) through to the human arm (extreme right). The living Queensland lungfish *Neoceratodus* (top left) shows an archipterygium, or series of bones forming the forelimb. The first bone is an adult fused humerus and radius, these two bones being separate in embryonic lungfish. The differentiation of the ulna and radius was first established in *Onychodus* (from p. 34, Gogo), well before the first tetrapodomorphan fishes evolved.

Next along to the right are series of forelimbs belonging to tetrapod-like fishes (tetrapodomorphans) all of late Devonian age (about 380-359 million years ago). The forelimb of *Sauripterus* (a rhizodontid) has a robust humerus and a well-defined ulna and radius. Third from the left is Gogonasus, from Gogo. Here the humerus is getting larger and the ulna more prominent. The next two to the right are Panderichthys (fourth from left) and Tiktaalik (fifth from left); both are elpistosteglians, which are advanced lobefinned fishes that were very close to becoming tetrapods. Both have much larger and more robust humerus-ulna-radius patterns with the appearance of bony digits in the wrist area, which were soon to descend and form the bone supporting the hand. Tiktaalik has an incipient wrist joint. In Sauripterus we see a robust broad humerus with a long entepicondylar process. This became relatively shortened in more progressive forms like Gogonasus and Panderichthys, which were more closely related to the first tetrapods. In Acanthostega this process is almost squareshaped. It is broad and flat for attachment of the lower arm muscles.

The lower series of illustrations shows the limbs of very early tetrapods. *Acanthostega* (bottom left) and *Tulerpeton* (bottom centre), both of late Devonian age, show a direct comparison of the major limb bones with that of a human arm (right). This demonstrates the continuity throughout evolution of a persistent pattern once it became established.

Digits seem to have first appeared within the fin of tetrapodamorph fishes like Panderichthys and *Tiktaalik*, although they were incorporated into the wrist area. Well-defined digits splaying out as a hand or foot first evolved in early tetrapods like Acanthostega, which had eight digits on its limbs, and Tulerpeton, whose limbs bore six digits. The oldest known tetrapods with the pentadactyl system of five fingers and toes is Pederpes from the early Carboniferous of Scotland. The human arm shows the same pattern of bones as the Devonian fish. The additional digits forming the hand were apparent in early amphibians like *Tulerpeton*, but the specialised bones of the wrist are a strictly reptilian feature that mammals inherited.

AGE

Devonian to Recent, about 380 million years ago-today.

REFERENCES 57, 75, 78, 209, 228, 356

Broome Sandstone, Western Australia CRETACEOUS



DINOSAUR TRACKS HAVE BEEN KNOWN FROM

the Broome Sandstone outcrops by the local Indigenous Bardi people for thousands of years. They believe that Marala, the Emu Man, left his footprints there along what is now called the Lurujarri Heritage Trail. In 1968 US palaeontologist Ned Colbert, working with Duncan Merrilees of the Western Australian Museum, published the first paper describing theropod trackways at Minyirr (Gantheaume Point), which they named *Megalosauropus broomensis*. These tracks were made by a medium-sized dinosaur, perhaps 4 m in length. Tony Thulborn continued investigations of these trackways and noted that some, which were 1.75 m in length, must have been made by an enormous sauropod (the one illustrated here as a probable titanosauromorph). The staggering size of these footprints indicate it was probably the largest dinosaur known from anywhere in the world. More recent investigations by Steven Salisbury and his team from the University of Queensland, working closely with local Indigenous Elders and other local volunteers, have resulted in recognition of at least 21 different kinds of dinosaur tracks - the most diverse assemblage of dinosaur trackways of this age anywhere in the world. In addition to the giant sauropod tracks noted above, others such as the ones named Oobardijama *foulksi* (little thunder, in Nyulnyulan language) represent more modest-sized animals around 12 m long. These trackways have also produced the first record of Cretaceous armoured dinosaurs (thyreophorans) like those named Garbina roeorum, a Stegosaurus-like animal up to 6 m long (shown here behind the large sauropod). Several kinds of plant-eating ornithopods left tracks here too (like the one shown centre left, in background). The largest ornithopod tracks are of Walmadanyichnus hunteri, whose footprints measure up to 80 cm. At this size, it would have been a beast slightly larger than Muttaburrasaurus from Queensland.

AGE

Early Cretaceous, Valangian-Barremian, about 140-127 million years ago.

LOCALITY

The coastal region around Broome known as the Yanijarri-Lurujarri Heritage Trail, Western Australia.



ENVIRONMENT

At this time, northern Australia would have had a cool to temperate but relatively dry climate that nevertheless supported forests filled with tree ferns, seed ferns, regular ferns and progymnosperms.

REFERENCES 79, 220, 344, 391

Strzelecki, Victoria



ALTHOUGH THE FIRST DINOSAUR BONE, A

theropod hand claw, was found in an area south of Wonthaggi, Victoria in 1904, it wasn't until the 1970s that new finds were made in the area, involving rich discoveries of seams full of fish, reptile and mammal bones. The scene here depicts some of the most spectacular early finds from the excavations at the Flat Rocks site near Inverloch. Back 120 million years ago this was a large temperate rift valley that formed as Antarctica began breaking away from Australia. In the scene we see the head of a large abelisaurid theropod, perhaps around 6 m long, attacking the 4 m newt-like labyrinthodont amphibian *Koolasuchus cleelandi*, one of the last surviving members of this gigantic amphibian clan. *Koolasuchus* lived in large rivers and captured its prey as an ambush predator, like crocodiles do today. It was named after Leslie Kool and Mike Cleeland who helped discover and excavate its remains. To the right a ceratodontid lungfish, the 1 m *Archaeoceratodus avus*, is swimming way from the violent confrontation. This fish is only known from a broken upper tooth plate and a scale. It
has been argued to be an ancestor on the line leading to the modern Queensland lungfish. The theropod head shown here was originally identified as belonging to the well-known North American dinosaur Allosaurus, based on discovery of a single ankle bone (astragalus). This was later referred to the megaraptoroid Australovenator, known from Winton in Queensland. Dinosaur experts working in South America have argued that it probably belonged to an abelisauroid dinosaur, a group of deep-headed short-armed predators known mainly from South America and Madagascar. This is quite likely to be correct, given that at this time Australia was closer to South America which at the time was an integral part of Gondwana along with Antarctica.

AGE

Early Cretaceous, Aptian stage, about 120 million years ago.

LOCALITY

The coastal shore platforms from Cape Paterson through to Inverloch, eastern Victoria.



ENVIRONMENT

At this time, southern Victoria had a cool temperate climate which supported forests filled with tree ferns, seed ferns, regular ferns and progymnosperms. Southern Australia lay within the Antarctic Circle.

REFERENCES 1, 203, 328, 330, 409

Bulldog Shale, South Australia CRETACEOUS



FOSSILISED BONES PRESERVED AS OPAL ARE

very rare. They are only found in abundance in Australia from the opal mining regions around Coober Pedy in South Australia and Lightning Ridge in New South Wales. At this time a vast sea covered inland Australia, home to a diverse range of marine life including huge clam-like molluscs, squid-like belemnites, coiled shell ammonites, many kinds of fishes, sharks and marine reptiles. In this scene we see *Umoonasaurus desmoscyllus*, a 2.5 m pliosaur (short-necked plesiosaurian), chasing a small ray-finned fish, similar to *Boreosomus* that lived in the Triassic Period in the Northern Hemisphere. *Umoonasaurus* was discovered by opal mining machinery, hence the skeleton was originally crushed into hundreds of small pieces. It was painstakingly prepared and glued together over 450 hours by Dr Paul Willis, who nicknamed it 'Eric' after the Monty Python song 'Eric the Half Bee'. This near-whole skeleton is the most complete of the known opalised skeletons found in Australia. Its skull shows the animal had well-

developed crests over the eyes and snout, likely covered by keratin extensions in life, perhaps for communication or sexual displays. Alternatively, the crests might have aided the animal in steering through the water when chasing down its fishy prey. Phylogenetic analyses show it is closely related to either the leptocleidid or polycotylid plesiosaurs. Umoonasaurus is named after the local Antakirinja language and means 'lizard from Coober Pedy region'. The species name means 'sea monster of the people', which honours the fact that the specimen - made of valuable opal - had to be bought from its owners to join the collections of the Australian Museum. This was achieved by a successful public fund-raising campaign to heighten awareness of its importance. Another skeleton of this beast, that of a juvenile, is held in the South Australian Museum.

AGE

Early Cretaceous, Aptian-Albian stages, about 115 million years ago.

LOCALITY

Coober Pedy, central South Australia.



ENVIRONMENT

The presence of ice-rafted boulders and glendonites representing ikaite, a mineral that forms only between -1°C and 6°C, in the same deposit suggest a temperature range that was seasonal, with cool to very cold winters that possibly involved surface water freezing at times.

REFERENCES

41, 110, 198, 201, 202

Otway, Scene 1, Victoria CRETACEOUS



IN THE COOL POLAR FORESTS OF SOUTHERN

Victoria 106 million years ago, a spring scene of primeval tension unfolds. The 2.5 m predator *Timimus hermani* (top left) spoils the moment when the similarly sized feathered megaraptorid dinosaur was about to pounce upon the small ornithopod *Leaellynasaura* emerging after its winter hibernation from its burrow in the riverbank. *Timimus* (named for both Tim Rich and Tim Flannery, and the species for John Herman) was at first thought to belong to one of the ostrich-like ornithomimid dinosaurs known only from Northern Hemisphere countries but some workers now assign it to the tyrannosauroid group (as depicted here), while others regard its affinities among theropods as uncertain. It is only known from its slender leg bones, two femora found within 1 m of each other. The unnamed megaraptorid shown here is based on a solitary arm bone (ulna) from the same site which has features close to those of the large *Megaraptor* from South America. These dinosaurs had elongated arms with sickle-shaped claws for grasping their prey. The two turtles depicted are forms known from reasonably well-preserved carapaces and isolated bones. *Chelycarapookus arcuatus* (bottom left, underwater) was found at a road cutting near Carapook in western Victoria. It is thought to be related to the modern long-necked turtles. *Otwayemys cunicularis* (bottom right, on land) is a cryptodire, the group containing most living tortoises and turtles. Its closest fossil relatives are from the Jurassic of China, suggesting it was a basal member of the group. ●

AGE

Early Cretaceous, Albian stage, about 106 million years ago.

LOCALITY

Eumeralla Formation outcrops and subsurface strata, Dinosaur Cove and coastal cliffs near Apollo Bay, western Victoria.



ENVIRONMENT

Cool temperate climate, forests filled with tree ferns, seed ferns, regular ferns and progymnosperms. Southern Australia lay within the Antarctic Circle.

REFERENCES

42, 95, 135, 181, 329, 361

Otway, Scene 2, Victoria CRETACEOUS



LEAELLYNASAURA AMICAGRAPHICA WAS THE FIRST

dinosaur to be formally named from Victoria, in 1989, based on discoveries from Flat Rocks and other sites near Inverloch. Its name is after Leaellyn Rich, the young daughter of palaeontologists Tom and Patricia Vickers-Rich who discovered and described the fossils, aided by a large team of volunteer helpers. Its species name honours the National Geographic Society for sponsorship of the work. This dinosaur was only about 90 cm in length. It was a basal ornithopod, the main clade of planteating dinosaurs. Because it lived in a cool climate close to the South Pole, it would have endured harsh dark winters. Its skull revealed a large margin for the eye socket and impressions of the brain showed it had enlarged optic lobes, suggesting it had large eyes with acute vision. Its teeth have fine striations perfect for slicing up ferns and other rainforest plants that were abundant in its habitat. It was a member of the basal ornithischian group, similar to hypsilophodontids. Several other genera of small plant-eating dinosaurs have been found alongside *Leaellynasaura*, comprising the commonest group of dinosaurs in this assemblage. The two possible reconstructions of *Leaellynasaura* shown here include a conventional naked one with ornithopod-like reptilian skin (above) and a version covered with hair-like feathers or quills (below). The latter is based on the fact that some theropod dinosaurs living in China at this time developed feathers or quill-like structures, as did some ornithischians like *Tuanylong*.

AGE

Early Cretaceous, Albian stage, about 106 million years ago.

LOCALITY

Coastal outcrops near Inverloch, eastern Victoria.



ENVIRONMENT

In the cool to cold temperate climate, the forests were filled with tree ferns, seed ferns, regular ferns and progymnosperms. Because southern Australia lay within the Antarctic Circle, it would have been dark for three months of the year.

REFERENCES 171, 172, 330

Toolebuc Formation, Scene 1, Queensland CRETACEOUS



CENTRAL NORTHERN QUEENSLAND WAS

covered by a vast inland sea about 100 million years ago. Some of the first and most spectacular finds from the Toolebuc Formation, the result of sediments accumulating in an expansive inland sea in the area of central northern Queensland, include the gigantic pliosaur *Kronosaurus queenslandicus*. First recognised and named from a fragment of the snout by Heber Longman of the Queensland Museum in 1924, a near-complete skeleton was retrieved in the 1930s by a Harvard University expedition in 1931. Australian museums were invited to join the expedition but were unable to participate, hence the skeleton was sent to the US and prepared over 25 years before finally going on display in Harvard University's Museum of Comparative Anatomy. Since then, many new specimens have been uncovered in the Winton-Richmond-Hughenden area of Queensland, and some are on display in the museums of these towns. The new discoveries demonstrate that a crest included at the back of the skull of the Harvard specimen was actually a mistaken plaster addition – the animals had no crest. When this was realised, for a short while the Harvard skeleton earned the nickname 'Plasterosaurus'. *Kronosaurus* is named after Cronos, the Greek Titan, who ate his children. Growing up to 11 m in length, it was the most ferocious predator in the seas around Australia at this time. Its powerful jaws sported elongated teeth up to 30 cm long. These lack carinae (distinct cutting edges) so are easily distinguished from the teeth of other giant pliosaurs like the British Liopleurodon. Stomach contents of Kronosaurus showed it preyed upon turtles and long-necked plesiosaurs like Eromangasaurus, shown here being attacked. A phylogenetic analysis shows Kronosaurus was perhaps the most specialised member of its lineage of gigantic pliosaurians.

AGE

Early Cretaceous, late Albian, about 106-103 million years ago.

LOCALITY

The region around the towns of Winton, Richmond and Hughenden in central Queensland.



ENVIRONMENT

These marine reptiles lived in a cool to temperate shallow inland sea. At this time northern Australia had a relatively dry climate.

REFERENCES

205, 229, 242, 340

Toolebuc Formation, Scene 2, Queensland CRETACEOUS



CENTRAL NORTHERN QUEENSLAND WAS

covered by a vast shallow inland sea around 100 million years ago. Ichthyosaurs like *Platypterygius longmani* shown here (centre top) were fully aquatic dolphin-like reptiles with long snouts. This oceanic fish-eating predator was Australia's only Cretaceous ichthyosaur. It is known from several complete skeletons which indicate that it grew to around 7 m in length and was armed with conical stout teeth perfectly suited for catching fish. The long-necked plesiosaur in the bottom left of the scene is *Eromangasaurus australis*, an elasmosaurid, all members of which have much longer necks than other plesiosaurians. Its long needle-like teeth suggest it hunted relatively small fish, as did the large predatory ichthyodectiform fish *Pachyrhizodus marathonesis* (seen above the plesiosaur, centre left). The saw shark *Pristiophorus tumidens* (bottom right) is lying on the sea floor. Like modern saw sharks, it would have slashed its deadly toothed rostrum into schools of fishes in order to feed on the wounded ones. It is only known from this site by its fossilised teeth. These seas were also home to a variety of ancient turtles. The little *Notochelone* costata (centre top) was about 1 m long and is represented by complete carapace fossils. It might have lived much like the Green Turtle today. *Cratochelone berneyi* (top right, background) is known from bones of the shoulder girdle. Their large size suggests that this turtle grew to about 2 m in length. Like modern turtles, they would have been omnivores feeding on fish, crabs, sponges, shellfish, jellyfishes, algae and sea grasses.

AGE

Early Cretaceous, late Albian, about 106-103 million years ago.

LOCALITY

A range of sites around the Winton-Hughenden-Richmond region of central Queensland.



ENVIRONMENT

These marine reptiles lived in a cool to temperate shallow inland sea. At this time northern Australia had a relatively dry climate.

REFERENCES

197, 198, 199, 342

Toolebuc Formation, Scene 3, Queensland CRETACEOUS



THE CARCASSES OF DINOSAURS AND

pterosaurs that inhabited the land close to the Eromanga Sea of Queensland would sometimes get swept out to sea after flooding events, becoming buried in the shallow marine sediments to become part of the Toolebuc Formation or Allaru Mudstones. Some, like the armoured ankylosaur *Kunburrasaurus ieversi* (left) are known from a nearly complete skeleton that includes well-preserved body armour and a perfectly preserved skull (this taxon was previously referred to as *Minmi*). Its name means 'shield-lizard' in the Mayi language of the local Wanumara people. At almost 3 m long, it had a well-armoured body covered by many small bony osteoderms set into its skin, and a thick bony skull. We know it fed on seeds, leaves and fungi, as evidenced by stomach contents preserved among the skeletal remains. A few vertebrae of the large, long-necked sauropod *Austrosaurus mckillopi* (right), the generic name meaning 'southern lizard', were first found in 1933 but new specimens were collected from the site on Clutha Station in 2014 by Steve Poropat and Tim Holland. It is now represented by six vertebrae and several ribs. These remains suggest it was about 4 m tall at the shoulder and up to 20 m in length. It was one of the titanosauriform sauropods, a group common in many areas of Gondwana at this time. The pterosaur Mythunga camara is seen here at the centre of the scene. The generic name is based on the local Indigenous name for the constellation Orion. *Mythunga* is represented by several bones of the skull and jaws, making it Australia's most complete pterosaur. It had a wingspan up to 4.7 m, making it Australia's largest-known flying animal. The sharp teeth of *Mythunga* suggest it fed on fish. In this scene, resting on the flank of Austrosaurus are three small Nanatius eos, a bird which was about the size of a modern blackbird. This bird is known from only a few tiny bones but is significant in being the only named bird from the age of dinosaurs in Australia.

AGE

Early Cretaceous, late Albian, about 106-103 million years ago.

LOCALITY

Richmond-Winton-Hughenden-Boulia region, central northern Queensland.



ENVIRONMENT

Warm, temperate climate, forests filled with tree ferns, seed ferns, regular ferns and progymnosperms. At this time northern Australia had a cool to temperate, relatively dry climate.

REFERENCES

208, 255, 257, 260, 291, 307

Winton Formation, Scene 1, Queensland



A PAIR OF PREDATORY THEROPOD DINOSAURS

Australovenator wintonensis run through warm temperate forest, trampling ferns underfoot as they hiss at each other. These dinosaurs are represented by articulated and relatively complete skeletons, the first such well-preserved theropod dinosaurs known from Australia. They were first discovered in sediments near Winton, Queensland. Recent research has led to a detailed reconstruction of their foot anatomy which has enabled estimation of the degree of pedal mobility. It is now clear that they had the ability to use the middle toe as a retractable claw on each foot, a feature found in most of the raptor group. *Australovenator*, meaning 'southern hunter', was about 2 m tall at the hip and up to 6 m in length, which is large for an Australian Cretaceous dinosaur. Apart from the few large sauropods known (featured in the next illustration), most of Australia's dinosaurs of this age, such as the hypsilophodontids, were much smaller. These smaller plant-eating dinosaurs, together with lungfishes and crocodiles that lived in the streams, could have been prey items for *Australovenator*. We know little about the lifestyle of this beast apart from what is hypothesised for other similarly sized theropods found elsewhere. Accumulations of several dromaeosaur skeletons together in the same site in the US have led to suggestions that they might have worked in packs to bring down large prey. While this may also have been the case in Australia, there is at present no evidence that this was the case. It is equally likely they were solitary hunters. Dinosaur community sizes at this time in Australia seem to have been far less dense than those in North America or Asia. The most recent phylogenetic analyses place Australovenator as a megaraptorid theropod, a group that probably originated in Australia before spreading to other regions of Gondwana. Their closest relatives include theropods from Europe and South America like Neovenator and Chilantaisaurus.

AGE

Late Cretaceous, Cenomanian Stage, about 100-94 million years ago.

LOCALITY

Winton Formation, near Winton, central Queensland.



ENVIRONMENT

While temperatures in southern Australia were very cold at this time, with polar conditions dominating, further north in Queensland was likely to have been warmer or even arid at times as suggested by the extensive red-bed deposits of sandstone and shale in the Winton Formation. Research has determined that the climate was humid with seasonal rainfall, warm to hot summers and occasional frosts in the winter (ref. 123).

REFERENCES

1, 123, 176, 259, 420, 421, 422

Winton Formation, Scene 2, Queensland



IN THE ESTUARIES, RIVERS AND BILLABONGS

that drained into the inland Eromanga Sea there lived a variety of fishes and reptiles, including the small crocodile *Isisfordia duncani*, which was just over 1 m long. The land at this time swarmed with large dinosaurs, including predatory theropods. Hence, little crocodiles like *Isisfordia* had to stay close to the water's edge to make a ready escape. No ancient relict, this was a beast well ahead of its time in that it was perhaps the earliest member of the modern crocodilians in the group Eusuchia. The perfectly preserved, uncrushed skeleton was recovered from near the town of Isisford in central northern Queensland. The species name honours lan Duncan who found the specimen. Its vertebrae exhibit a slightly convex rear face, suggesting the link to modern crocodiles which have vertebrae with strongly convex rear surfaces (the 'procoelous' condition). Its skull has the pterygoid bones incorporated into its secondary palate. These are advanced features that place it as an early member of the eusuchian group. While *Isisfordia* was only tiny, by the end of the Cretaceous the next wave of eusuchians grew to enormous sizes, some reaching nearly 10 m in length. The huge fish swimming below would have likely been too big for *Isisfordia* to tackle. It is one of the earliest members of the elopomorph group, which includes tarpons, and although not found in the exact same beds as *Isisfordia* it lived close by in the shallow marineestuarine conditions that were widespread at that time.

AGE

Late Cretaceous, Cenomanian Stage, about 100-94 million years ago.

LOCALITY

Winton Formation, near Isisford, central Queensland.



ENVIRONMENT

While temperatures in southern Australia were cold at this time, with polar conditions dominating, further north in Queensland there probably were warmer or even arid conditions at times.

REFERENCES

43, 123, 166, 176, 177, 220, 306, 308, 343

Winton Formation, Scene 3, Queensland



UNTIL RECENTLY, AUSTRALIA'S RECORD OF THE

long-necked sauropod dinosaurs from the Cretaceous Period was relatively poor. However, discovery in the early 2000s of the relatively wellpreserved sauropods from the Winton Formation has demonstrated that large sauropods, some up to 30 m long, lived in Queensland about 95 million years ago. *Diamantinasaurus matildae* (right) was discovered in 2005 as a partial arm bone (humerus) on Elderslie Station, north of Winton. Further remains of this sauropod were discovered between 2006 and 2009. Its name honours the Diamantina River and the famous song 'Waltzing Matilda', written by Banjo Paterson while staying at a cattle/ sheep station near Winton. *Diamantinasaurus* is now known from several bones including a partial skull and braincase. It was about 15–18 m long and about 2.5 m high at the hip. *Wintonotitan wattsi* (left) was discovered as partial remains in 1974 on Elderslie Station, but the partially complete skeleton now known was not recovered until excavations were completed in 2006. Its species name honours its finder, Keith Watts. It is now known from the front limbs, shoulder bones, body and tail vertebrae and part of the hip. In life, this dinosaur would have measured 16-20 m in length. The relationships of Wintonotitan are unclear but it appears to be a relatively primitive sauropod and a non-titanosaurian, in contrast to Diamantinasaurus. Subsequently a new sauropod, Savannasaurus elliotorum, was described from Winton. An analysis of the distribution of titanosaurians suggests these Australian late Cretaceous species were some of the last surviving members of a group that was once widespread across the globe during the early Cretaceous. Phylogenetic analyses suggest that Savannasaurus and Diamantinasaurus are closely related species, a little more primitive than the clade containing the lithostrotian titanosaurs - a group named because several species had solid bony plates set in the skin for protection against predators. An even larger sauropod recently found in central Queensland, named Australotitan cooperensis, may have been 6.5 m high at the hip and 30 m long. While Australotitan is the largest dinosaur known from skeletal elements, the giant footprints from Broome (p. 62) indicate that even larger dinosaurs - in fact the largest in the world - are still waiting patiently to be discovered as skeletons. A small dolichosaur (bottom right), similar to late Cretaceous species of the Northern Hemispheric genus Coniasaurus, watches carefully to avoid the heavy feet of the giant sauropods. These aquatic ophidiomorhan lizards may have been very close relatives of the gigantic marine mosasaurs.

AGE

Late Cretaceous, late Albian, about 100-94 million years ago.

LOCALITY

Winton Formation, near Winton, central Queensland.



ENVIRONMENT

While temperatures in southern Australia were cold at this time, with polar conditions dominating, further north in Queensland there probably were warmer and even arid conditions at times.

REFERENCES 123, 304, 306, 308

Lightning Ridge, New South Wales CRETACEOUS



ONE OF THE MOST FAMOUS OPAL MINING AREAS

in the world is Lightning Ridge, New South Wales, which has produced some of the world's most extraordinarily beautiful black opal gemstones. What is less widely known is that many of these gems were in fact fossils of Cretaceous animals and plants. How many unique species have been ground down over the last century to make jewellery may never be known. Fortunately, some very important fossil specimens have survived. The animals and plants represented by these specimens lived in or were washed into large freshwater lagoons at a time when much of Australia was covered by vast inland seas. Among fossils that did not get converted into gemstones are the teeth of lungfish including *Neoceratodus potkooroki*. Ferocious theropod dinosaurs such as *Rapator ornitholestoides* (the feet sloshing here through the water) would have terrorised smaller dinosaurs in the adjacent forests. An archaic egg-laying monotreme *Steropodon galmani* (floating near the surface) was a distant cousin of ornithorhychid platypuses but, because of differences in tooth and jaw morphology, has been allocated to its own unique family, the Steropodontidae. The name Steropodon comes from two Greek words meaning 'lightning tooth' in reference to the locality as well as the flash of colours in the specimen. A much weirder mammal that appears to have been a highly specialised monotreme with molar teeth that look like hotcross Easter buns was Kollikodon ritchiei (here shown crunching a mussel shell it has foraged from the bottom mud). It too has been allocated to its own family, the Kollikodontidae. Because of its bizarre tooth form, it was given the informal nickname of Hotcrossbunidon. While most of the animals and plants found in the Lightning Ridge fossil deposits were terrestrial or at least freshwater occupants, such as pinecones and turtles, occasional discoveries of plesiosaur and shark teeth indicate that the lagoon must sometimes have been in direct contact with the adjacent inland sea.

AGE

Late Cretaceous, Cenomanian, about 100 million years ago.

LOCALITY

Griman Creek Formation, Lightning Ridge, New South Wales.



ENVIRONMENT

While most of the fossils from this formation are freshwater invertebrates, the diversity of land vertebrates and plant fossils indicate that the adjacent land was almost certainly dominated by species-rich forests. Given its geographic position – more or less between the areas where the Cretaceous Winton Formation in Queensland and Eumeralla Formation in Victoria deposits accumulated – the climate may have been intermediate between those of these two areas (warm and cool respectively), and hence perhaps mild.

REFERENCES 19, 40, 119, 204, 292

Mackunda Formation, Queensland



MUTTABURRASAURUS ('THE LIZARD FROM

Muttaburra') was one of the first relatively complete large dinosaurs found in Australia, and certainly the first large plant-eating ornithopod dinosaur known from this country. It was discovered in 1963 on Muttaburra Station in the Mackunda Formation, a marine deposit in central Queensland. The discoverer, grazier David Langdon, alerted scientists at the Queensland Museum who excavated the bones. The specimen took many years to prepare using fine chisels and a range of different acids. It was finally published in 1981 by Alan Bartholomai and Ralph Molnar.

It was a bizarre-looking beast about 10 m in length, that had a strangely expanded part of the skull associated with the underlying nasal chamber. The nasal chamber might have enabled it to make unusual calls, or perhaps increased its sense of smell. It was interpreted to be an iguanodontid, a dinosaur that had a spike-thumb. Another specimen found near Dunluce, Queensland, from the slightly older Alluru Mudstone exhibits just such a structure. Other bones attributed to *Muttaburrasaurus* found in Lightning Ridge, New South Wales, suggest that more than one species might be present. The most recent analyses of its features suggest *Muttaburrasaurus* is in fact a very basal ornithopod most closely related to dinosaurs from Transylvania like *Rhabdodon*. This would suggest it may be a rhabdontomorphan rather than an iguanodontid dinosaur.

In the scene we see a young *Muttaburrasaurus* on all fours with a detail of the head of a second animal in the foreground, showing the unusual nasal swelling. The reconstructed skeleton of *Muttaburrasaurus* stands proudly in the entrance hall of the Queensland Museum in Brisbane, mounted as if standing on its hind legs. We now know, however, from trackways and biomechanical analyses, that although these dinosaurs were capable of stretching up with their arms to reach branches, they were mostly quadrupeds.

The teeth of *Muttaburrasaurus* have several strong ridges and are unusual in that they erupted all at the same time, unlike other ornithopods whose teeth erupted randomly. It was even suggested by the original authors that, although well-adapted for chewing hard ferns and conifer leaves, *Muttaburrasaurus* may have been an omnivore that scavenged carcasses from time to time.

AGE

Late Cretaceous, about 98-95 million years ago.

LOCALITY

Mackunda Formation, Muttaburra Station, east of Winton, central Queensland.



ENVIRONMENT

While temperatures in southern Australia were cold at this time, with polar conditions dominating, further north in Queensland there were probably warmer and even arid conditions at times.

REFERENCES 35, 220, 237, 256

Mangahouanga, New Zealand



IN THE CRETACEOUS SEAS AROUND WHAT WAS

to become New Zealand lived gigantic marine reptiles similar to those that ruled the world's oceans at this time. In the North Island of New Zealand, the Tahora Formation exposed by the Mangahouanga Stream, a tributary of the Te Hoe River, has produced two such reptiles. Large long-necked elasmosaurs described as *Tuarangisaurus keyesi*, family Elasmosauridae, paddle about on the surface and are being eyed by a mosasaur. These elasmosaurs were predators of smaller animals such as fish and cephalopods. However, *Moanasaurus mangahouangae*, family Mosasauridae, was the top predator in these Cretaceous oceans. It grew to about 12 m in length with a skull that was about 75 cm long. It would almost certainly have attacked elasmosaurs from time to time. Both of these species were discovered by Joan Wiffen and colleagues. Wiffen was a remarkable amateur palaeontologist who went in search of dinosaurs and, while doing so, found these huge marine reptiles. She named the first of these taxa in 1980, when she was 58 years old, and continued fieldwork in the rugged hills and rivers for the next 20 years. She carried out the fossil-bearing rocks from the site and prepared them in her backyard. Her hard work over many years has resulted in the recovery of some truly spectacular fossils and significantly expanded understanding about the distinctive Mesozoic marine reptiles of New Zealand.

AGE

Late Cretaceous (Campanian-early Maastrichtian), about 73 million years ago.

LOCALITY

Mangahouanga Stream, Hawke's Bay, New Zealand.



ENVIRONMENT

These giant sea dragons swam in nearshore waters off the coast of Zealandia when it was located in the high latitudes of about 66°S. Land was not far distant - the sediments are rich in terrestrial silts, charcoal, pollen and bones of dinosaurs. The local vegetation was evergreen temperate rainforest with Huon Pine, other podocarp conifers, southern beech and common tree ferns, indicating a mild temperate climate lacking severe frosts.

REFERENCES

174, 400, 423, 424, 425

Waipara River, New Zealand



THIS PAINTING SHOWS A SCENE IN THE LATEST

Cretaceous seas that once covered part of New Zealand. Here, well known from the South Island's Waipara River deposits, is the large mosasaur *Prognathodon waiparaensis*, which was described by S.P. Welles and D.R. Gregg in 1971 from a superb specimen now in the Canterbury Museum. This giant marine reptile must have been a fearsome sight, with a body up to 11 m long. Its 1 m jaws were lined with large conical teeth. In addition to rows of teeth on its upper and lower jaws, two rows of teeth on the roof of its mouth, all curved backwards, would have prevented prey escaping and enabled the reptile to tear off large chunks of flesh and swallow them whole. As the dominant predator of the seas at this time, it almost certainly would have preyed on elasmosaurs, turtles and large fish. Protostegid turtles were somewhat like modern leatherback turtles and were the first to show the modern body plan of marine turtles. Known from North America and Australia, they were first recorded from New Zealand by Joan Wiffen in 1981 based on eight fragmentary bones from the Mangahouanga Stream, Hawke's Bay (see p. 88). Little is known of their diet, but individuals of *Notochelone* in Australia had fragments of the mollusc *Inoceramos* in the stomach. Flying overhead is a pterosaur. Although not actually known from the Waipara River deposits, they were likely present because pterosaurs are recorded from the Mangahouanga Stream deposits a short distance away in Hawke's Bay.

AGE

Late Cretaceous, late Haumurian (Maastrichtian), about 73 million years ago.

LOCALITY

Waipara River, North Canterbury, New Zealand.



ENVIRONMENT

The late Cretaceous seas revealed by the Waipara River beds lay just offshore of Zealandia, which was a newly created land recently rifted from Gondwana. This site lay only about 100 km from the beds being deposited in Hawke's Bay just a few million years earlier.

106, 173, 412, 426

Haumuri Bluff, New Zealand



IN THIS SCENE, A LARGE TYLOSAURINE MOSASAUR,

Taniwhasaurus oweni, attacks a much smaller pliosaur. Pliosaurs had a broad body with a short neck, a short tail and four large flippers. All pliosaur remains from Haumuri Bluff are fragmentary and, although they have been referred to five species since Sir Richard Owen described *Plesiosaurus australis* from this locality in 1861, in reality few are sufficiently complete to enable confident specieslevel identification. One of the described taxa is *Polycotylus tenuis*, named by Sir James Hector in 1874. If correctly placed in this genus, which is otherwise known from North America, Russia and Australia, the Haumuri Bluff pliosaur would have had a long head at the end of its short neck. Its limbs were essentially paddles highly adapted for swimming and of little use for terrestrial locomotion. Hence, it is not surprising to find that pliosaurs almost certainly gave birth to live young, as did ichthyosaurs, which means these reptiles never had to leave the oceans.

Taniwhasaurus oweni was a large mosasaur, probably exceeding 7 m in length. Other members of the genus are known from Japan and James Ross Island, on the Antarctic Peninsula. Its generic name derives from the 'taniwha', a supernatural aquatic creature in Māori mythology. With its huge head and many large teeth, it was undoubtedly the top predator in the late Cretaceous seas in this region of the world. Given its size, it could have killed even the large pliosaurs, which themselves were major predators capable of eating large and agile prey, probably including plesiosaurs.

AGE

Late Cretaceous (Lower-Middle Campanian), about 69 million years ago.

LOCALITY

Haumuri Bluff, Kaikoura, New Zealand. This was a tremendously important site for fossil collecting in the late 19th century and a key to developing the geological timescale in New Zealand.



ENVIRONMENT

This Haumuri Bluff biota was deposited in a nearshore environment, on the Pacific margin of Gondwana towards the end of the Cretaceous period when New Zealand separated from other Gondwana fragments.

REFERENCES

70, 89, 169, 412

Tingamarra, Scene 1, Queensland



IN THE SHALLOWS OF THE TINGAMARRA SWAMP,

two crocodilians lie in wait for incautious prey. Both are species of *Kambara*, the oldest known of the extinct Australasian mekosuchine crocodilians, and grew to lengths of around 2–3 m. Tingamarra's two early Eocene *Kambara* species share a generalised crocodilian body plan, not unlike that of the modern Saltwater Crocodile *Crocodylus porosus*. Their broad flattened skulls and large size suggest they were semi-aquatic ambush predators. Each of the two species had a distinctive dentition, probably reflecting different feeding strategies. Kambara implexidens had an interlocking dentition while *K. murgonensis* had an overbite pattern. Because there is a predominance of adult- and hatchling-sized rather than intermediate-sized individuals among the fossils, the Tingamarra swamp may have been used as a nesting ground by one or both species. The relatively straight humerus and strong shoulder joint suggest that species of *Kambara* were better equipped for terrestrial locomotion (i.e. extended high walking where the body is held off the ground) and paraxial swimming (i.e. generating thrust by alternating strokes of the limbs) than are living crocodiles such as the modern Saltwater Crocodile. The Tingamarra waterbody was a low-energy freshwater lake, billabong or swamp. Intermittent bands of dolomite in the Tingamarra deposit suggest intervals of low water level that may have occasionally forced these crocodile species to come into direct contact with each other, an uncomfortable situation for most crocodilians.

Mekosuchine crocodilians were once endemic to Australia and islands in the South Pacific. They survived until the Pleistocene on mainland Australia and until the arrival of humans in Fiji, New Caledonia and Vanuatu.

AGE

Early Eocene, about 54.6 million years ago.

LOCALITY

Near Murgon, south-east Queensland.



ENVIRONMENT

This was a time of warm wet conditions, during the globally recognised Early Eocene Climatic Optimum. Australia was still tenuously connected to an ice-free Antarctica, and it to South America, with broadleaf and southern conifer forests providing corridors for dispersal across these last vestiges of Gondwana.

REFERENCES

345, 369, 370, 433

Tingamarra, Scene 2, Queensland



IN TREETOPS ARCHING OVER A QUIET BILLABONG,

the 80 cm madtsoiid snake Alamitophis tingamarra strikes at a small bird feeding its nestlings. In the process, it startles the tiny insectivorous marsupial Djarthia murgonensis foraging nearby. The nowextinct madtsoiids were constrictors found mostly in Australia, South America and Africa. Although species of Alamitophis were relatively small, some Australian madtsoiids the size of anacondas survived until the late Pleistocene – longer than anywhere else in the world. The mouse-sized marsupial *D. murgonensis* is the most primitive known member of the superorder Australidelphia, the group that includes all modern Australasian marsupials. This clade also includes the order Microbiotheria which today is represented by a single living species, *Dromiciops gliroides* from the Valdivian temperate rainforests of South America's southern Andes. Current wisdom suggests that the modern Australasian marsupial orders evolved from ancestors that dispersed from South America via Antarctica, sometime during the late Cretaceous to early Paleogene, and radiated prior to the late Oligocene. But the extremely plesiomorphic australidelphian morphology of *D. murgonensis* and the apparent absence of undoubted australidelphians from early Paleogene deposits in South America has been interpreted as evidence that they first evolved in Australasia, perhaps from a Djarthia-like ancestor. Hence, sometime after evolving in Australia from marsupials that dispersed from South America to Australia via Antarctica, at least one member of this Australian group must have migrated back to South America where they thrived and survive as D. gliroides. Tingamarra's unnamed passeriforms appear to represent a stem group that gave rise to the world's passerine songbirds. Today, passerines - which include among many other groups the wrens, lyrebirds, honeyeaters and crows - are the most diverse order of living birds. Although their phylogenetic and geographical roots remain contentious, given the fact that the Tingamarran passeriforms are the oldest known in the world, Australian origins for this group seems probable.

AGE

Early Eocene, about 54.6 million years ago.

LOCALITY

Near Murgon, south-east Queensland.



ENVIRONMENT

A forest fringing a low-energy freshwater lake, billabong or swamp. It was a period of warm wet conditions, during the Early Eocene Climatic Optimum. Australia was still tenuously connected to an ice-free Antarctica, and it to South America, with broadleaf and southern conifer forests providing corridors for two-way dispersals across these last vestiges of Gondwana.

REFERENCES

38, 58, 60, 148, 149, 347

Tingamarra, Scene 3, Queensland



AS DUSK FALLS, A 'GRACULAVID' SHOREBIRD

wades in the shallows, chasing a last meal for the day. A bat *Australonycteris clarkae* makes its first insect catch for the night and a frog *Lechriodus* casca lets fly with its first call. A soft-shelled turtle *Murgonemys braithwaitei* surfaces for air. A marsupial *Thylacotinga bartholomaii* watches from the undergrowth. The 'graculavid' is one of two or three Tingamarra species representing a grade of primitive charadriiforms that is restricted to late Cretaceous to early Eocene deposits elsewhere in the world. The generalised postcranial morphology of these birds is characteristic of several groups of early neornithine birds in both the Northern and Southern Hemispheres. *Australonycteris clarkae* is one of the world's oldest bats. It is similar to other archaic early and middle Eocene bats from both the Northern and Southern Hemispheres and represents a grade of primitive stem-bats globally extinct by the late Eocene. It navigated using echolocation, like most bats do today, and probably hunted insects over the surface of the Tingamarra lake or in the fringing vegetation. The quoll-sized omnivore *T. bartholomaii* may belong to a family otherwise known from South America and/or Antarctica and suggests a trans-Antarctic migration route between South America and Australia extending well into the early Paleogene. It probably ate fruit, seeds, soft leaves and insects. *M. braithwaitei* belongs to a group of turtles called trionychids that have flexible (soft) shells, allowing them to deform as they squeeze into small spaces chasing prey such as crayfish, frogs and small fish. Trionychids died out in Australia in the Pleistocene, around 40 000 years ago, but relatives survive in New Guinea, Asia and Africa. Lechriodus casca indicates that at least some generic differentiation among Australian frogs predates the final fragmentation of Gondwana. Its only living Australian descendant, L. fletcheri, lives around pools or streams in rainforests and wet sclerophyll forests.

AGE

Early Eocene, about 54.6 million years ago.

LOCALITY

Near Murgon, south-east Queensland.



ENVIRONMENT

A forest fringing a low-energy freshwater lake, billabong or swamp. This was a time of warm wet conditions, during the Early Eocene Climatic Optimum. Australia was still tenuously connected to an ice-free Antarctica, and it to South America, with broadleaf and southern conifer forests providing corridors for dispersal across these last vestiges of Gondwana.

REFERENCES

20, 61, 163, 357, 399, 417

Duntroon, New Zealand



SQUALODONTIDS, OR SHARK-TOOTHED

dolphins, are large, long-snouted odontocetes (echolocating toothed whales) with typically high, triangular, often multicuspid and laterally compressed teeth. They were diverse in the late Oligocene to middle Miocene and were probably specialist predators on fish and, when they could catch them, birds. They survived until the early to middle Miocene when they appear to have been replaced by relatively more modern families of toothed whales. For many years squalodontids were thought to be a family from which modern toothed whales emerged. Now, however, several families are recognised within this group. True squalodontids (Squalodontidae) include species of *Squalodon* from the North Atlantic, *Phoberodon arctirostris* from the South Atlantic and several unnamed forms including some from New Zealand and possibly '*Prosqualodon' hamiltoni* from the early Miocene of Caversham, Dunedin. In the New Zealand region, most of the extinct shark-toothed cetaceans originally thought to be squalodontids are now regarded as members of Platanistoidea (e.g. Waipatia maerewhenua), a more diverse group
that is the sister-clade of squalodontids. This broader group also contains the living platanistid Ganges River Dolphin *Platanista gangetica*. The platanistoid species illustrated here is the late Oligocene *Otekaikea marplesi* recovered from the Otekaike Limestone Formation in the Waitaki Valley of the South Island of New Zealand. It is known only from one partial skeleton that was described and named in 2014, and is one of only two species in the Waipatiidae, an extinct family of cetaceans unique to New Zealand and Australia.

AGE

Late Oligocene, 25.2 million years ago.

LOCALITY

Otekaike Limestone, Waitaki Valley, South Island, New Zealand.



ENVIRONMENT

The environment where this cetacean and many others lived was a relatively shallow mid- to inner-shelf marine ecosystem.

REFERENCES

2, 95, 127, 376, 377, 378, 379

Jan Juc Formation, Victoria



TWENTY-FIVE MILLION YEARS BEFORE TODAY'S

ocean-addicted human surfers learned to ride the waves at Bell's Beach, Victoria, ancestral baleen whales and other fascinating marine creatures cruised these same waters. The timeless energetic waves still scour the tawny yellow cliffs at the back of the beach, gouging out of them the bones and teeth of those ancient ocean-loving creatures. *Janjucetus hunderi*, one of the largest whales that left skulls and postcranial bones on the sea floor of this region, has proved to be a most fascinating cetacean because it appears to represent a 'missing link' group between ancient toothed whales (odontocetes) and the baleen whales (mysticetes). The osteology of the skull reveals that it shared key derived features with all baleen whales. However, unlike later baleen whales, it had no baleen and instead retained well-developed teeth like toothed whales. It was about the size of a large modern dolphin but, unlike all toothed whales and like most if not all baleen whales, it evidently could not echolocate. Because it had very large orbits in the skull, it probably visually located its prey, which was likely to be fish, which it savaged much as killer whales do today. The group of smaller whales shown here foraging on the ocean floor are Mammalodon colliveri. Each was about 3 m long. They appear, on the basis of skull and dental morphology, to be another member of the 'missing link' group of pre-mysticete whales that contains J. hunderi. Both are now placed in the family Mammalodontidae, this name reflecting the fact that unlike all modern cetaceans they retained relatively conventional mammal-like dentitions with incisors, canines, premolars and molars. Other vertebrates shown here include the cusk eel Ophidion granosum, a weird group of eellike fish that can burrow tail-first into the mud but spend most of their time hunting for food on the ocean floor. Heterodontus cainozoicus is a distant relative of the Port Jackson Shark in the family Heterodontidae and, like its modern counterpart, it may have been a nocturnal feeder on molluscs and echinoderms that were abundant on the ocean floor. Megalops lissa, flanking J. hunderi, was an ancestral tarpon (Megalopidae) that was an agile predator of fish in the open ocean. Gadus refertus, shown hunting near the bottom, is a predatory relative of cod fish (Gadidae) that would have eaten a wide range of foods near the bottom of this marine habitat.

AGE

Late Oligocene, about 25 million years ago.

LOCALITY

Coastal sandstone cliffs, Lorne-Queenscliff Coastal Reserve, Jan Juc, south-west of Torquay Surf Beach, Victoria.



ENVIRONMENT

Nearshore seas off the coast of south-east Australia.

REFERENCES

44, 111, 112, 186, 223

Ditjimanka Local Fauna, Scene 1, South Australia

OLIGOCENE



CENTRAL AUSTRALIA'S EPHEMERAL FRESHWATER

lake system in the Lake Eyre Basin was once home to *Australosuchus clarkae*, a 3-4 m crocodile that appears to have been a generalist aquatic predator. It probably ambushed prey that came to drink at the lake's edge. When *A. clarkae* lived, during the late Oligocene to early Miocene, these central Australian lakes may have been permanently filled with water supporting fish, turtles, platypus and even freshwater dolphins. The surrounding forests supported a diverse fauna including extinct sheep-sized ilariid marsupials, koalas, bandicoots, bats, possums of many kinds and flamingo-like paleolodids. This crocodile is known from several deposits in the Lake Eyre Basin that have produced skulls, dentaries and postcranial elements. The most common items are isolated teeth that were shed during life, and bony scutes that developed within the skin to act as defensive armour. Its teeth varied in size, shape and function along the tooth row, with some adapted for puncturing and holding prey and others with vertical ridges better suited for slicing and cutting flesh.

This crocodile was a member of the subfamily Mekosuchinae, a group endemic to the south-west Pacific region including the Australian mainland, Vanuatu, New Caledonia and Fiji. The earliest records of mekosuchines from the Australian early Eocene appear in the Tingamarra Local Fauna. Mekosuchines were common in Australia, as shown in mid to late Cenozoic fossil communities, until they became extinct sometime in the Pleistocene. However, until 3000-4000 years ago they survived on the islands of New Caledonia and Vanuatu.

AGE

Late Oligocene, about 25 million years ago.

LOCALITY

Palankarinna, Pinpa, Tarkarooloo and Ngapakaldi Lakes in the Lake Eyre Basin, South Australia.



ENVIRONMENT

In the late Oligocene, in the Palankarinna and Pinpa lakes regions of the Lake Eyre Basin, permanent freshwater lakes were surrounded by humid scrubby rainforests dominated by *Nothofagus* species. These areas became warmer and much drier in the Neogene and Quaternary and are now arid/semi-arid deserts.

REFERENCES 429, 431

Ditjimanka Local Fauna, Scene 2, South Australia

OLIGOCENE



IN THE LATE OLIGOCENE, CENTRAL AUSTRALIA

looked very different from today. The now seasonally dry Lake Eyre Basin was at that time dotted with freshwater lakes surrounded by forests dominated by *Nothofagus* (southern beech), casuarinaceans and myrtaceans. *Palaelodus pledgei*, shown flying above the lake, were tall slender birds with long legs and necks; they belonged to the extinct family Palaelodidae. These flamingo-like birds were in fact distantly related to flamingos. They were browsers that fed while swimming or standing in shallow water. In the forests lived archaic extinct marsupial ilariids (Ilariidae) and wynyardiids (Wynyardiidae), as well as the oldest known bandicoots (Peramelemorphia), koalas (Phascolarctidae) and burrowing bats (Mystacinidae). *Ilaria lawsoni* (far right) was a cow-sized quadrupedal marsupial whose selenodont teeth indicate it was a leafeater. Its postcranial remains suggest it was terrestrial with possibly some capacity for digging. Ilariids are known from the late Oligocene only and hence provide a useful marker for Australian fossil deposits of late Oligocene age. Relationships of this family to other diprotodontian marsupials are uncertain but they are at least distantly related to wombats (Vombatidae). Muramura williamsi (far left) was an extinct wynyardiid that was around the size of a dog and probably herbivorous. It is known from two articulated well-preserved skeletons. Perikoala palankarinnica (top centre), one of the oldest-known koala, is one of the extinct phascolarctids from the late Oligocene of central Australia. Bulungu muirheadae (lower far right), one of Australia's oldest-known bandicoots, is known from numerous dentaries and isolated teeth. This small insectivore or carnivore had a body mass of less than 250 g. A single tooth represents the burrowing bats (Mystacinidae) (lower right), a family that is today found only in New Zealand. All other members of this bat family appear to have been semi-terrestrial and it is likely that this central Australian species was too, feeding probably on both flying and terrestrial insects and other arthropods.

AGE

Late Oligocene, about 26 million years ago.

LOCALITY

SIAM and Tedford localities, Etadunna Formation, Lake Palankarinna, Tirari Desert, South Australia.



ENVIRONMENT

The late Oligocene scrubby rainforest forests that surrounded the waterbody that accumulated these fossils was dominated by casuarinaceans, myrtaceans and species of *Nothofagus* with araucariaceans and podocarpaceans. Sclerophyllous taxa including species of *Acacia* were also present at this time.

REFERENCES

12, 29, 151, 160, 165, 223, 276, 277, 382, 393, 437

Riversleigh, Scene 1, Queensland



ALTHOUGH THE LATE OLIGOCENE FOREST

teemed with edible creatures, it was hard for carnivores of any kind to resist trying to steal each other's kill. Here the wombat-sized marsupial lion *Wakaleo schouteni* (named in honour of the famous palaeoartist who was unaware that he was rendering his own Oligocene avatar) has decided to challenge the fox-sized thylacinid *Nimbacinus dicksoni* for access to the balbarine kangaroo that it has just killed. Given that this species of *Wakaleo* at about 23 kg was probably four times the bodyweight of *N. dicksoni* and had more formidable killing teeth, it would not have been much of a contest. The thylacinid would have had to retreat or risk becoming part of the marsupial lion's next meal.

This scene also focuses on a controversy about how some of the limestones in the Riversleigh World Heritage Area actually formed. While some clearly formed in pools in caves (replete with speleothems such as flowstones and other cave formations) and freshwater lakes (lacustrine limestones), it has been argued that some of the late Oligocene limestone may have formed in slow-moving carbonate-rich stream water that deposited limestone whenever it encountered objects like pebbles, bones or even leaves to create what are called tufa dams. As the dam walls grow, they back up more water, and bones and other objects are cemented into the accumulating layers of limestone in these trapped pools. Well-studied tufa dams of this kind occur today at points

along the Gregory River which flows through the Riversleigh World Heritage Area. This may have been how some of the late Oligocene limestones in Riversleigh originally formed, but more extensive study of these limestones is required before this hypothesis can be adequately tested.

Fortunately, whatever the mechanisms involved in their formation, many different kinds of limestone at Riversleigh were capable of preserving some of the most remarkable fossils ever found. In addition to bones and teeth, they include soft tissues of plants and animals, cells and, incredibly, even nuclei within those cells.

AGE

Late Oligocene, about 25 million years ago.

LOCALITY

Hiatus Site, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

There is a lack of certainty about details of the plant communities in the Riversleigh area during the late Oligocene. However, overall structure of the fauna would suggest this lowland region had large freshwater lakes surrounded by forests. The latter may have had some areas with less dense cover and been cooler than the subsequent biodiverse rainforest communities that came to dominate the Riversleigh region during the early and middle Miocene. Topographically, there were islands of much older Cambrian marine limestones and Precambrian quartzites jutting up above the trees and lakes.

REFERENCES

25, 27, 141, 142, 144, 240, 266

Pinpa Local Fauna, South Australia



LAKE PINPA IN NORTHERN SOUTH AUSTRALIA

has been a fascinating source of many weird and wonderful late Oligocene beasts, not the least of which has been the somewhat wombatlike *Mukupirna nambensis*. In 1973, the late Dick Tedford from the American Museum of Natural History put a team together to follow-up his 1971 exploration for fossils at Lake Pinpa, east of the Flinders Ranges. It was fortunate timing, as sands that normally cover the dry salt lake's surface had been blown away, thus exposing the ancient clays that had accumulated 25 million years ago in a vast freshwater lake. Animals that lived in or on the waters of this lake included three kinds of stifftailed ducks (e.g. *Pinpanetta fromensis*, bottom left) and flamingos *Phoeniconotius eyrensis* (centre left). There were also freshwater dolphins. Stranger mammals that lived in the forests surrounding this lake, such as the 100+ kg *Mukupirna nambensis*, sometimes become mired in mud near the shore or drowned and settled into the gooey clay of the ancient lake bottom, where they were transformed into articulated but jumbled and often crushed collections of bones. Those who were on that expedition (which included this book's co-author Michael Archer) found that by gently pushing slender metal rods into the dry salt lake surface - a process that seemed a bit like acupuncturing the skin of mother Earth - they could sometimes detect hard objects below. These often proved to be the bones of skeletons that were not yet exposed at the dry lake's surface. One of these was the skeleton of *M. nambensis*. It was quarried out as a large mass, secured in wrappings of plaster of Paris and transported with many other casts collected that year at Lake Pinpa to the American Museum of Natural History. The skeleton was carefully recovered from the clay-filled cast and ready for study but, sadly, Dick Tedford died before he could describe it scientifically. Years later, in 2020, the specimen was finally published by a team of palaeontologists led by Robin Beck and Julien Louys.

AGE

Late Oligocene, about 25 million years ago.

LOCALITY

Namba Formation, Lake Pinpa, north-eastern central South Australia.



ENVIRONMENT

The ancient lake was enormous and must have once extended to the ocean to the south, enabling dolphins to reach this area and adapt to freshwater. The forest surrounding the lake was filled with ringtail possums, koalas and other arboreal animals as well as creatures that lived on the forest floor such as egerniine skinks. An extinct eagle is also known from this deposit. The forest itself was probably a type of scrubby rainforest.

REFERENCES

39, 51, 125, 239, 372, 388

Ericmas Local Fauna, South Australia



Freshwater dolphins and lungfish once inhabited an extensive lake system in central Australia that covered vast areas both east and west of the Flinders Ranges. Fossils recovered from late Oligocene sediments in the Lake Frome area of the Lake Eyre Basin include specimens of an extinct group of dolphins known as eurhinodelphids. These cetaceans are recorded globally from fossil deposits in the late Oligocene to the middle Miocene, but the central Australian ones are the first known to have occupied freshwater lake environments. They may be an indication that this gigantic inland lake had a direct but perhaps ephemeral connection southwards to the Southern Ocean. Cranial fragments including toothed rostra and ectotympanics as well as vertebrae reveal that these dolphins, which were about 3–4 m long, had very long snouts. Their small peg-like teeth indicate that, like many modern dolphins, they probably ate small fish. The long snout suggests that they used it to swipe at fish, like modern swordfish do. Other aquatic vertebrates in the same deposit include ray-finned fish, chelid turtles, mekosuchine crocodiles and at least four or five lungfish species, some of which reached more than 3 m. Lungfish, which can breathe air to supplement oxygen exchange via the gills, have been well represented in both marine and freshwater Australian fossil deposits since at least the Devonian. Also from this site, a single tooth represents the extinct toothed platypus Obdurodon insignis.

AGE

Late Oligocene, about 25 million years ago.

LOCALITY

Ericmas Quarry and South Prospect Quarry, Namba Formation, Lake Namba, Frome Embayment, Lake Eyre Basin, north-eastern central South Australia.



ENVIRONMENT

At this time, the Lake Frome area was inhabited by a range of aquatic vertebrates including ray-finned fish, lungfish, chelid turtles, mekosuchine crocodiles and dolphins. The habitat surrounding the lake would have been scrubby rainforest that contained a wide range of mammals, birds and other animals.

REFERENCES

23, 125, 203, 223

Riversleigh, Scene 2, Queensland



A 4 M CROCODILE LUNGES FROM A FOREST LAKE

where a marsupial *Ngapakaldia bonythoni* and rail *Australlus disneyi* drink at the water's edge. One of four croc species in this deposit, *Baru wickeni* was a member of the subfamily Mekosuchinae which was once common in Australia and some islands in the south-west Pacific – the last mekosuchine died out only 3000–4000 years ago in New Caledonia and Vanuatu. The 'cleaverheaded croc' *B. wickeni* had a very deep box-like skull and long blade-like recurved teeth that were probably used in a slicing cleaver-like fashion to kill its prey. It has been argued that *Baru* species were semi-aquatic, ambushing prey both on land and at the water's edge. This one was almost as large as the living Saltwater Crocodile *Crocodylus porosus* of northern Australia and south-east Asia, a crocodyline crocodile. It would have taken large prey including other reptiles, birds and mammals such as the cow-sized *Ngapakaldia bonythoni*. This primitive diprotodontoid, a distant relative of living wombats and the koala, was widespread during the late Oligocene. It lived on the shores of inland lakes from central Australia in the south to Riversleigh in the north, probably feeding on leafy vegetation on the forest floor and near the water's edge. The rail *A. disneyi* may have foraged in the same areas for small animal prey as well as shoots of reeds and other soft plants. This bird was a member of the family Rallidae, one that appears to be at least distantly related to the living, globally widespread swamphens (species of *Porphyrio*).

AGE

Riversleigh Faunal Zone A, late Oligocene, about 26-23 million years ago.

LOCALITY

White Hunter Site, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

In the late Oligocene, the Riversleigh area was a limestone karst landscape covered by forest. Knowledge of the Riversleigh Faunal Zone A suggests a forest environment but one that may have been less dense than the subsequent rainforests that covered this area during the early and middle Miocene. Internally drained lakes were widespread throughout the area.

REFERENCES

46, 245, 368, 428, 448

Riversleigh, Scene 3, Queensland



BARAWERTORNIS TEDFORDI IS THE SMALLEST

known member of the Dromornithidae, a family of large to gigantic flightless birds unique to Australia. It was about the size of a cassowary. Like the Northern Cassowary, which is a member of the unrelated family Casuariidae, its powerful legs would have been capable of moving it rapidly through the undergrowth when necessary, such as when threatened by predators. Such a predator may well have been *Ekaltadeta ima* (far left), a most unusual type of kangaroo belonging to the family Hypsiprymnodontidae, the only living member of which is the Musky Rat-kangaroo Hypsiprymnodon moschatus, a small galloping (non-hopping) omnivore restricted to the tropical rainforests of north-east Queensland. *Ekaltadeta* had enormous, serrated premolars and powerful molars that indicate it specialised on animal flesh – it was a carnivorous kangaroo. *Ganawamaya couperi* (far right) was one of several very different kangaroos belonging to the archaic family Balbaridae. Like hypsiprymnodontids but unlike any modern kangaroos, it had a hallux (first toe) on the hind foot. Aspects of the hind leg suggest it would not have been as good a hopper as modern kangaroos. *Ganawamaya* were probably browsers as well as, perhaps, omnivores, a bit like modern tree kangaroos. *Onirocuscus silvicultrix*, a member of the possum family Phalangeridae, is an extinct relative of modern brushtail possums (species of *Trichosurus*) and cuscuses (species of *Phalanger* and several other genera) which live today in the forests of Australia, New Guinea and Sulawesi. *Onirocuscus* was about 2–3 kg (similar in size to a small modern brushtail possum), probably arboreal, nocturnal or at least crepuscular, and omnivorous, eating leaves and fruits but also small birds and reptiles. It would have had large eyes and a strong prehensile tail. ●

AGE

Riversleigh Faunal Zone A, late Oligocene, about 26-23 million years ago.

LOCALITY

White Hunter Site, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

Many of Riversleigh's late Oligocene local faunas (Faunal Zone A) are characterised by the high proportion of aquatic and largebodied animals compared to most of the younger Riversleigh faunal assemblages. The many large freshwater crocodiles, turtles, fish and frogs suggest that there were substantial bodies of water in the immediate area of the fossil deposits. There is no evidence for transportation of the fossils, which suggests they were relatively passively accumulated in local pools, lakes or caves with no involvement of river transport.

REFERENCES

18, 69, 81, 88, 188, 200, 279, 324

Riversleigh, Scene 4, Queensland



BADJCINUS TURNBULLI WAS A CAT-SIZED

thylacine, approximately 2.5 kg in weight, a carnivorous marsupial related to the recently (1936) extinct 'Tasmanian Tiger'. At least nine species of thylacines, all in the family Thylacinidae, are known from the Oligo-Miocene, ranging from kitten- to wolf-sized taxa. All were carnivores, with long snouts and cheek teeth characterised by oblique to longitudinal slicing blades. *Badjcinus turnbulli* is the oldest known member of this family. It is also one of the least specialised members and is close to the base of the thylacine tree. Its size suggests a diet of small vertebrates including mammals and birds such as the rail *Australlus disneyi*. Other nonpasserine groundbirds from Riversleigh include the stork *Ciconia louisebolesae*. Storks are large birds that had a global distribution. This Riversleigh species was probably similar in size to a modern white stork and thus had a 2-5 kg body mass. It was probably carnivorous, eating frogs, fish, insects, earthworms, small birds and small mammals that lived around the ponds and lakes that were abundant at this time at Riversleigh. *Namilamadeta albivenator* was a dog-sized (20 kg) quadrupedal marsupial in the family Wynyardiidae, the last member of which went extinct about 15 million years ago. Wynyardiids were distantly related to wombats and koalas among living marsupial groups. This species is known from late Oligocene and early Miocene deposits of Riversleigh. Its dentition suggests that it was a herbivore, probably feeding on leaves from shrubs and trees.

AGE

Riversleigh Faunal Zone A, late Oligocene, about 26-23 million years ago.

LOCALITY

White Hunter Site, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

The White Hunter Local Fauna is considered to have lived in a forest environment. Although it has been suggested that the main limestone that contains most of the Faunal Zone A assemblages was formed in lakes trapped by tufa dams, there is some uncertainty about how these deposits formed. This particular deposit may well have been formed in a large cave.

REFERENCES

25, 62, 268, 300, 341

Wynyard Local Fauna, Tasmania



THE EARLY MIOCENE DEPOSITS EXPOSED ALONG

the shore at Wynyard, Tasmania, have produced millions of fossils including remnants of corals and the shells of marine molluscs, brachiopods and echinoderms. Vertebrate fossils have occasionally also made an appearance. One such specimen from a locality called Fossil Bluff is the holotype of *Prosqualodon davidis*. It was originally represented by a skull (now missing) and an almost complete skeleton. There are, fortunately, casts of many of the missing elements in the Tasmanian Museum in Hobart. This marine mammal was a toothed whale in the cetacean family Squalodontidae, members of which have been called 'shark-toothed dolphins' because of the triangular shark-like form of their teeth that contrast with the usual peg-like teeth in most modern dolphins. These teeth tended to jut outwards and would probably have been visible when the mouth was closed. This squalodontid would have been about 2.3 m long and a carnivore, probably specialised for feeding on other oceanic animals like fish, squid and birds. It may even, like killer whales, have been a predator of other cetaceans.

The Fossil Bluff Sandstone is also famous for producing the first known pre-Pleistocene mammal from Australia, the enigmatic Wynyardia bassiana, which must have been washed out to sea by a coastal river. Unfortunately, when the skull and partial skeleton eroded out of the sandstone, they slid down the cliff face teeth-down. As a result, when the specimen was found sometime around 1860 at the base of the cliff, it no longer had any of its teeth. Because palaeomammalogists have traditionally relied on teeth to help them work out evolutionary relationships, when the specimen was described in 1901 as a member of a new family of marsupials, the Wynyardiidae, its interfamilial relationships were unclear. However, based on comparisons of the skull and skeletal elements, it was then thought to probably be close to phalangerid possums. Because complete wynyardiid dentitions and skulls have been found at Riversleigh, for example, we now know that wynyardiids are in fact vombatoid marsupials most closely related among living animals to wombats and koalas.

AGE

Fossil Bluff Sandstone, early Miocene, about 23 million years ago.

LOCALITY

Fossil Bluff Site, near Wynyard, Tasmania.



ENVIRONMENT

The seas just off the coast of south-eastern Australia would have been relatively warmer than they are today. Based on pollens found in the same formation, the habitat at the same time on the adjacent land would have been *Nothofagus*-gynmosperm evergreen rainforest.

REFERENCES 9, 124, 126, 223, 234

Kutjamarpu Local Fauna, South Australia



WHEN PAUL LAWSON WALKED ALONG THE

eastern edge of Lake Ngapakaldi in 1962, as a member of Reuben Stirton's expedition in search of pre-Pleistocene fossils in central Australia, he spotted pieces of fossil turtle shell lying on the surface of the dry salt-encrusted mud. In the days that followed they discovered that these had been part of an ancient streambed that they named the Wipajiri Formation, and named the site the Leaf Locality because of a fossil leaf found in shales that overlay the stream deposit. When they excavated the stream deposit, lots of other teeth and bones were found including those of a small koala *Litokoala kutjamarpensis*, an archaic wombat *Rhizophascolonus crowcrofti* and the teeth of a seriously weird animal *Ektopodon serratus* (upper left), that they concluded may have been an archaic toothed monotreme. As subsequent research demonstrated, this was the first discovery of one of the most unconventional groups of shortfaced possums, the Ektopodontidae. Its uniquely shaped molar teeth were formed by two rows of many tiny cusps that formed pseudo-lophs, a bit like the teeth of rodents but with the lophs oriented transversely rather than longitudinally. Despite subsequent discovery of teeth of many other kinds of ektopodontids in other fossil deposits, most aspects of these strange marsupials apart from their teeth and parts of the skull remain a complete mystery. They were always rare in the late Oligocene to Quaternary lowland rainforest communities in which they lived, until the last one vanished in the Pleistocene.

In 1971, palaeontologists Mike Woodburne, Bill Clemens, Mike Archer and Colin Campbell were excavating the Leaf Locality as part of another international team following up on Stirton's earlier investigations. Soon after opening the quarry, they noticed that Mike Woodburne was secretively working away at something he had found in the stream deposit. When he finally revealed his treasure, it turned out to be a spectacularly wellpreserved lower jaw of one of the first leopardsized marsupial lions. It was named Wakaleo oldfieldi (right). The generic name means 'little lion' while the species name honoured Brian Oldfield, the owner of Etadunna, the cattle station that included this region of the Tirari Desert. Did these marsupial lions hunt ektopodontids? No doubt if they found one like this foraging in the base of an epiphytic Birds Nest Fern (Asplenium sp.) for forest seeds or other things to eat, these carnivores would have been delighted to dine on such a rare but probably tasty rainforest inhabitant.

AGE

Early to middle Miocene, about 23-15 million years ago.

LOCALITY

The Leaf Locality, Wipajiri Formation (which contains a lower unit, the Basal Conglomerate, that formed in an ancient stream and an overlying clay, the Leaf Shale, that formed in a lake). This Formation is exposed on the eastern edge of Lake Ngapakaldi in the Tirari Desert of north central South Australia, between the Cooper and Warburton Rivers.



ENVIRONMENT

Many species of ringtail possums and a koala strongly suggest the presence of a forest. The immediately overlying clay beds (the Leaf Shale) contain tree leaves that have not yet been taxonomically studied. However, the fact that about 15 species from the Kutjamarpu Local Fauna also occur in the early and middle Miocene rainforest communities of Riversleigh, including *W. oldfieldi* and possibly also *E. serratus*, suggests that a vast species-rich lowland rainforest community stretched from at least what is now north-west Queensland to this area of central South Australia.

REFERENCES

16, 76, 297, 298, 302, 303, 327, 374, 436

Riversleigh, Scene 5, Queensland



ONE OF THE MOST WIDELY DISTRIBUTED AND

long-lived marsupial species was the large, perhaps sexually dimorphic diprotodontid *Neohelos tirarensis* (left). It is known from fossil deposits in Queensland, the Northern Territory and South Australia, and lived 25-15 million years ago. Body mass estimates based on partial skulls and mandibles range between 115 kg to 250 kg. It was a browser and probably fed on the leaves of shrubs and trees. *Dromornis* sp. (right) was an extinct flightless bird belonging to the family Dromornithidae that stood approximately 2.5 m tall and weighed up to 250 kg. These gigantic flightless birds appear to be most closely related to ducks and geese. The evolutionary relationships, enormous size and possibly omnivorous habits of some earned these dromornithid birds the nickname 'Demon Ducks of Doom'. Another species from this deposit with a colourful nickname is Fangaroo, an extinct species of balbarid kangaroo with the scientific name *Balbaroo fangaroo* (far right). Approximately the size of a modern Agile Wallaby, it was initially described on the basis of a partial skull in which the curved upper fanglike canine teeth are more than twice as long as the adjacent incisors. They may have used these canines for display or defence in the same way as long canines are used by herbivorous Asian mouse deer today. The extinct lyrebird from Riversleigh, *Menura tyawanoides* (middle right), is the earliest known member of its family, the Menuridae. Modern lyrebirds are among the best known and largest of Australia's songbirds, most notable for their remarkable ability to closely mimic natural and artificial sounds such as the calls of other birds or even the sound of a flushing toilet.

AGE

Riversleigh Faunal Zone B, early Miocene, about 20 million years ago.

LOCALITY

Upper Site, Godthelp Hill, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

Upper Site is one of Riversleigh's richest fossil deposits. From a limestone deposit barely 2 m³ in size, at least 60 different fossil mammal species have been recovered. It appears to represent a cave deposit in which the remains of thousands of animals accumulated in a pool on the cave floor. This was a period of warm wet conditions globally, and at Riversleigh a species-rich closed canopy forest cloaked a limestone terrain riddled with caves.

REFERENCES 52, 59, 83, 274, 278, 373, 438

Riversleigh, Scene 6, Queensland



ONE OF THE MOST ENIGMATIC PREHISTORIC

marsupials yet discovered is Yalkaparidon coheni, a small (100–250 g) marsupial known only from the late Oligocene to early Miocene forests of Riversleigh. Its highly specialised dentition has earned it the common name Thingodonta ('donta' meaning tooth in ancient Greek). It shares features with the other marsupial orders (e.g. elongate lower incisors like kangaroos and wombats, molars similar to marsupial moles, cranial morphology like bandicoots) but most of these appear to be either primitive or convergently evolved features. For this reason, it and another species in the same genus, Yalkaparidon jonesi, were placed in a separate order, Yalkaparidontia, the only Australian marsupial order to have gone extinct. There are, however, possibilities that it could turn out to be a member of an order of marsupials in South America, the Paucituberculata, a group that includes caenolestid marsupials and some of their equally distinctive extinct relatives, some of which have been found in Eocene deposits in Antarctica. Although this remains controversial, it emphasises how strange this bizarre group of

Riversleigh mammals obviously is. It was probably insectivorous, but exactly what it ate and how, remains a mystery. Its large ever-growing incisors but very reduced (zalambdodont) molars suggest food with a hard outer surface but soft insides, such as worms, caterpillars or eggs. It has been suggested that Y. coheni might have been a mammalian 'woodpecker' similar to the Striped Possum of northern Australia and New Guinea or the Aye-Aye of Madagascar, using its incisors to tear open weakened branches of trees in order to extract soft insect larvae. Predators of Thingodonta would have included the possum-sized marsupial lion Lekaneleo roskellyae. This was one of the least specialised of the marsupial lion family but was nevertheless equipped with the characteristic enlarged premolars that formed carnassial blades used in slicing through the flesh and bones of its vertebrate prey. These small marsupial lions may have been equally at home prowling among the treetops as well as on the forest floor.

AGE

Riversleigh Faunal Zone B, early Miocene, about 20 million years ago.

LOCALITY

Upper Site, Godthelp Hill, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

In the early Miocene, the Riversleigh area was covered in warm wet rainforest that cloaked the region's limestone and quartzite outcrops. There were no grasslands in Australia at this time. Caves that developed in the older limestone trapped unwary animals as they moved through the undergrowth. Pools in many of these caves enabled fine preservation of the most delicate bony structures as well as the uncrushed bodies of many different kinds of arthropods.

REFERENCES 14, 21, 37, 140, 143

Riversleigh, Scene 7, Queensland



NIMBACINUS DICKSONI WAS A SMALL FOX-SIZED

thylacine (50 cm head-tail length; upper left), a carnivorous marsupial related to the 'Tasmanian Tiger' *Thylacinus cynocephalus*. It occurs in many fossil deposits at Riversleigh and is also known from Bullock Creek in the Northern Territory. A nearly complete skeleton of this species is known from AL90 Site on the Gag Plateau at Riversleigh. It was intermediate in size and carnivorous dental specialisations between species of *Badjcinus* and *Thylacinus*. A study of bite force (mechanical performance) revealed that this small thylacinid probably occupied a broadly similar ecological niche as that of the extant Quoll *Dasyurus maculatus*. On the basis of bite force and dental morphology, it probably hunted relatively large vertebrate prey that may have exceeded its own body mass. *Emuarius gidju* (right) was a large flightless bird that lived during the late Oligocene and early Miocene. It was first known from the Leaf Locality in central Australia and is common in Riversleigh's Faunal Zones A to C. It was closely related to emus and cassowaries. Its cassowarylike skull and femur and its Emu-like lower leg and foot suggested the nickname Emuwary or Cassemu, although it is technically closer to emus and may well be an ancestral emu. It probably browsed on shrubs and grasses as well as the occasional insect and small lizard. It was shorter than the modern Emu, standing about 1.5-1.8 m tall and weighing up to about 50 kg. It had smaller eyes than the modern Emu and was not as well adapted for fast running, which reflects the fact that it lived in more densely vegetated habitats. Bellatorias sp. cf. B. frerei (left) is similar to the extant Major Skink B. frerei, one of Australia's largest skinks. An agile climber, the living species is often found around rocky outcrops in well-vegetated areas including vine scrubs, rainforests and woodlands. Like the living species, it probably ate mainly insects but also some fruit. Namilamadeta superior (bottom) is known from a near complete skull from the early Miocene Upper Site. Sheep-sized, it was slightly larger than Namilamadeta albivenator from Riversleigh's White Hunter Site. It belongs to the family Wynyardiidae, the last member of which went extinct about 15 million years ago. Wynyardiids may have been ancestral to the first diprotodontoids, all of which went extinct during or just following the late Pleistocene.

AGE

Riversleigh Faunal Zone B, early Miocene, about 20 million years ago.

LOCALITY

Upper Site, Godthelp Hill, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

The ecosystem that contributed to the Upper Site deposit was biotically highly diverse lowland rainforest. Compared with the slightly less biotically diverse ecosystems of the late Oligocene, these early Miocene forests were very wet and perhaps 1-2°C warmer. They were far more diverse than any of the rainforest communities in Australia today. However, comparable diversity today does occur in the Amazon and the lowland rainforests of Borneo.

REFERENCES 27, 184, 266, 300, 387, 449

Riversleigh, Scene 8, Queensland



AS DAY FADES, THE SHEEP-SIZED 70 KG

marsupial Silvabestius johnnilandi, one of Australia's largest arboreal mammals and an archaic member of the family Diprotodontidae, climbs a tree for the night. Here it will escape predators such as thylacines and crocodiles, and leisurely search the tree for fruits and other soft plant products. Like other extinct members of the family Diprotodontidae such as Diprotodon optatum, the last and largest member of the group, *S. johnnilandi* may well have travelled in herds. But unlike the larger diprotodontids, this herbivore's herds commonly moved upside-down in the crowns of the rainforest trees, rather like marsupial sloths or sun bears. In this highly unusual lifestyle, it was apparently similar to another even betterknown diptorodontid from the middle Miocene of Riversleigh, *Nimbadon lavarackorum* (p. 140). Also shown here foraging at dusk are several species of leaf-nosed bats. These are typically slow but very manoeuvrable fliers that catch insects by hovering and gleaning, hawking or aerial pursuit. Although some roosted in trees, most spent the day in caves. Some but not all of these ancient bats have recognisable living descendants. *Rhinonicteris tedfordi* (upper left), for example, is the oldest known ancestor of the living Orange Diamondfaced Bat of northern Australia. In contrast, the evolutionary relationships of *Xenorhinos halli* (bat shown in the foreground) remain obscure but its broad deep snout with large nasal cavities, peculiar head posture and extremely short palate suggest a unique echolocation call and foraging strategy. The larger *Riversleigha williamsi* had broad crushing teeth, tall crests on its thickened skull and only moderately inflated ear bones, suggesting it used a lower frequency call to locate prey such as heavily armoured beetles.

AGE

Riversleigh Faunal Zone B, early Miocene, about 17 million years ago.

LOCALITY

VIP and Bitesantennary Sites, Bitesantennary Valley, D Site Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

The early Miocene palaeoenvironments in the Riversleigh area appear to have been closed rainforest. Like today, the Riversleigh limestone (karst) landscape was riddled with caves that provided lairs and shelters for predators and prey, day roosts for bats, and death traps for many other animals that dropped in unexpectedly.

REFERENCES

26, 47, 156, 157, 158, 159

St Bathans, Scene 1, New Zealand



ON THE SHORES OF THE ANCIENT LAKE

Manuherikia, a few inhabitants of a lost subtropical fauna feed in the shallow margins of this huge (5600 km²) freshwater body. In terms of both diversity and number of individuals, birds dominated this aquatic ecosystem, as they do today in many areas of New Zealand. Waterfowl were particularly diverse, with nine species. Here we see the as yet unnamed progenitor of New Zealand geese (species of *Cnemiornis*, a relative of Australia's Cape Barren Goose, with three goslings. Swimming in the water is a pair of Stiff-tailed Ducks Manuherikia lacustrina, a bird about the size of a Shoveler. Like other stiff-tailed ducks, this Miocene species dove for its food. Peering into the water from its perch on a log is a heron Matuku otagoense, a bird that was about the size of a White-faced Heron but with slightly shorter legs. It and a co-occurring small fossil bittern are both the oldest and only known herons from the fossil record of Australasia. With its webbed feet, long legs and long neck, the flamingo relative Palaelodus aotearoa searches for prey in the shallow waters. Prowling around the margins of the lake is a crocodilian up to 3 m long. It may be a mekosuchine crocodile, possibly related to species known from Fiji, New Caledonia and Australia. This New Zealand species occurred further south than any of the world's other crocodilians.

AGE

Late early Miocene, about 19-16 million years ago.

LOCALITY

Map shows the continent Zealandia, emergent land at the time, and some of the modern-day coastlines.



ENVIRONMENT

A subtropical habitat containing eucalypts, casuarinas, cycads and palms surrounded the lake's margin. Farther from the lake, taller forest with up to 60 species of laurel and abundant podocarp species clothed the nearby hills. Seasonal drought affected these habitats and associated fires were relatively common.

REFERENCES

351, 454, 455, 458, 459

St Bathans, Scene 2, New Zealand



IN THE WOODLANDS BACK FROM THE EDGES OF

palaeo-Lake Manuherikia, strange yet vaguely familiar inhabitants of the lost St Bathans Fauna go about their business on the forest floor. Here foraging in the litter of eucalypt leaves we find small diplodactylid geckoes similar to those in New Zealand today. Nearby is something very much larger: an ancestral Tuatara. These are sphenodontid reptiles, sister to all lizards. Today, the last members of their order survive only in New Zealand. Competing for invertebrates with these reptiles were at least four species of burrowing bats (in the family Mystacinidae) in two genera (*Mystacina* [smaller bat] and *Vulcanops* [larger bat]). Burrowing bats survive today only in New Zealand where they spend almost as much time foraging on the ground as in the air. Although perhaps the most common bats in the St Bathans deposits, they were not the only bats in this Miocene forest. At least two other bats in two additional families were present. But there is yet another mammal in this picture (centre right, peeking out from a crevice in the log). The size of a small rodent and dubbed the 'Waddling Mouse', the relationships of this (in fact these, because there are at least two kinds) tiny terrestrial mammal remain a mystery. Discovery of these enigmatic creatures came as a major surprise because, apart from introduced species, no non-flying terrestrial mammals had been known to have existed in New Zealand. Also scurrying about on the forest floor, but cloaked in feathers, is Proapteryx micromeros, a proto-kiwi. One-third the size of the smallest living Kiwi today and perhaps surprisingly able to fly a bit, this tiny early Miocene bird evolved into the living iconic national bird of New Zealand - the Kiwi. While this proto-kiwi or its ancestor must have flown in from afar, precisely where it came from is still uncertain. Like other Kiwi, P. micromeros was an omnivore and we see it here capturing a small leiopelmatid frog. This family of frogs is at least as old as the family of Tuatara and likewise restricted to New Zealand.

AGE

Late early Miocene, about 19-16 million years ago.

LOCALITY

Early Miocene deposits along the banks of the Manuherikia River, St Bathans, Central Otago, New Zealand.



ENVIRONMENT

This seasonally dry, fire-affected woodland had much in common with those found in northern Australia today, with eucalypts, casuarinas and palms growing on the lowlands surrounding this huge lake. A large, braided river with white quartz gravel beds formed a delta where it entered the huge 5600 km² Lake Manuherikia.

REFERENCES

162, 164, 165, 195, 210, 457, 461

St Bathans, Scene 3, New Zealand



THE PALAEO-LAKE MANUHERIKIA ATTRACTED A

vast array of different species from a range of different environments in and away from the water. Low hills and floodplains around the lake supported floristically diverse forests. Parrots had diversified into at least five different species, each of which exploited aspects of the rich and varied food resources available. But these woodlands existed in a seasonally dry climate; hence, especially in the drier months, many of the animals living in the surrounding habitats had to come to the lake to drink. In the case of parrots, this was probably a daily occurrence. Here drinking on the margin of a small pool is a pair of a species of *Nelepsittacus* – small parrots that were one of at least four species of the nestorine radiation, the group which includes the familiar Kea and Kaka of today. Looking down on the smaller parrots is a strangely familiar, much larger, bird. Looking a bit like the modern Kakapo *Strigops habroptila*, we see the enormous *Heracles inexpectatus*. It was probably a member of the lineage that led
the evolution of the Kākāpō. But this giant parrot, which has earned the nickname of 'Squawkzilla', was much larger than a Kākāpō. At about 80 cm tall and perhaps up to 7 kg in weight, it is the largest parrot that has ever been found anywhere in the world. ●

AGE

Late early Miocene, about 19-16 million years ago.

LOCALITY

Deposits along the banks of the Manuherikia River, St Bathans, Central Otago, New Zealand.



ENVIRONMENT

The seasonally dry, floristically diverse woodland and forest environments around palaeo-Lake Manuherikia provided a rich food supply, from the fleshy fruits of podocarps to the nuts, cones and flowers of eucalypts, casuarinas, palms and, for carnivores, millions of incautious parrots.

REFERENCES 450, 460

Riversleigh, Scene 9, Queensland



RIVERSLEIGH'S OBDURODON DICKSONI WAS A

large platypus up to 60 cm long (head to tail). Older smaller species of *Obdurodon* are known from central Australia, and a closely related species, *Monotrematum sudamericanum* from the Paleocene of Argentina, is evidence that platypuses were once more widespread in Gondwana and not, as they are today, unique to Australia. Unlike the living Platypus, these fossil platypuses had functional cheekteeth. The welldeveloped rooted teeth of *O. dicksoni* suggest a more varied diet than that of the living Platypus, perhaps including frogs and fish as well as insect larvae, yabbies and other crustaceans. It probably made burrows in the banks of rivers and streams where it laid its eggs. *Trilophosuchus rackhami* was a small mekosuchine crocodile perhaps 1.5 m long, from the early Miocene of northern Australia. It had a short deep head, large eyes and three longitudinal ridges along its skull (hence its name). It may have been terrestrial rather than aquatic and possibly even semi-arboreal, providing evidence that Australia did in fact have 'drop crocs'. Its neck musculature suggests it held its head above its body, as do varanid lizards. It probably would have preyed on small mammals, turtles, snakes and fish. The anatomy of the back of the skull suggests that feeding might have involved rapid side-to-side, up-and-down and rotational movement of the head in order to 'roll' prey in the way the Saltwater Crocodile does today. The turtle is Pseudemydura, a close relative if not the same species as the critically endangered Western Swamp Tortoise P. umbring of Western Australia that lives in ephemeral swamps. The Riversleigh pygmy-possum Burramys brutyi is closely related to the living but critically endangered omnivorous Mountain Pygmy-possum *B. parvus* of the alpine zone in Victoria and New South Wales. The occurrence of this very similar ancestral form in a lowland rainforest environment has led to the suggestion that the living species, threatened by climate change, could be saved by translocating it into protected areas of lowland rainforest. A similar translocation strategy may be useful as a potential way to save the critically endangered Western Swamp Tortoise.

AGE

Riversleigh Faunal Zone C, middle Miocene, about 15 million years ago.

LOCALITY

Ringtail Site, Gag Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

During the middle Miocene the Riversleigh area appears to have been a mosaic of lakes, pools and caves in a karst (limestone) terrain that was cloaked by closed species-rich gallery rainforest where species diversity was much higher than that of any rainforests of modern Australia.

REFERENCES

15, 25, 134, 275, 427, 430

Riversleigh, Scene 10, Queensland



LITOKOALA KUTJAMARPENSIS (PHASCOLARCTIDAE)

(top centre) was a small koala known from early/ middle Miocene deposits in central Australia and middle Miocene deposits in Riversleigh. It was about half the size of a modern Koala *Phascolarctos cinereus*. Almost certainly arboreal, it probably fed on a variety of tree leaves. Specialisations in the middle ear indicate that it may have used loud vocalisations similar to those of the living species. *Onirocuscus reidi* (Phalangeridae; top left) is most closely related to species of *Trichosurus*. It was almost certainly omnivorous consuming fruits, leaves, birds and eggs whenever it had the chance. *Marlu kutjamarpensis* (middle left) was a ringtail possum (Pseudocheiridae) found also in early Miocene deposits of central Australia. Its body mass has been estimated to be around 500 g. Its dentition suggests that it was a tree leaf-eater. Species of *Pildra* (bottom left) were much smaller ringtail possums (Pseudocheiridae) that may have fed on a wider range of plant foods, including lichens and mosses as well as soft leaves and blossoms. *Trichosurus dicksoni* (next to *M. kutjamarpensis*) was a brushtail possum (Phalangeridae). Like its modern rainforest counterpart, the Bobuck *T. caninus*, it was most likely an opportunistic omnivore that weighed about 1–2 kg. Species of *Cercartetus* (Burramyidae; lower right), known as pygmy-possums, are found today in a wide variety of habitats in Australia, New Guinea and Indonesia. As opportunistic omnivores they eat insects, flowers, fruit, nectar and pollen. *Macroderma godthelpi* (lower right), the carnivorous ghost bat, is related to the living Ghost Bat *M. gigas* of northern Australia. It would have used its good vision as well as echolocation to locate its prey, which would have been small mammals including other bats, small birds, lizards, snakes and insects.

Nimbadon lavarackorum is the large 70 kg treeclimbing herbivorous diprotodontid marsupial at the right. It is known from middle Miocene deposits at Riversleigh and Bullock Creek, Northern Territory. Features of its skeleton, such as the strong forelimbs, large claws and highly mobile shoulder and elbow joints, are strikingly similar to that of the living Koala, suggesting it had a similar arboreal lifestyle. However, given its much larger size, it may also have been capable of hanging upside-down when moving through or feeding in the canopies of the forest the way sloths or sun bears can do today. In terms of diet, it may have been primarily a fruit-eater but possibly also fed on soft leaves or flowers. As an arboreal fruiteater, it probably helped to disperse the seeds of the rainforest trees. It is best known from many complete skulls and mandibles and at least two complete skeletons from the AL90 Site, a cave that acted like a natural pitfall trap, catching animals that fell out of the tree canopy overhead. The known specimens of this species represent individuals ranging in age from tiny pouch young to elderly adults. This mix of individuals of all ages suggests that they moved through the treetops in family groups or mobs, much the way kangaroos do today in open country. Compared with some of the better-known members of this family such as the gigantic Diprotodon optatum, it was on the smaller end of the size range of diprotodontids. However, along with Silvabestius johnnilandi (p. 130), these were the largest marsupials that have ever lived in the forest canopies of Australia.

AGE

Riversleigh Faunal Zone C, middle Miocene, about 15 million years old.

LOCALITY

Gag Site, Gag Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

The Riversleigh area during the middle Miocene would have been a mosaic of lakes, pools and caves in a karst (limestone) environment. Palaeoecological studies suggest that the environment was dominated by species-rich rainforest.

REFERENCES

22, 48, 49, 50, 53, 54, 64, 88, 118, 155, 161, 230, 231, 278, 301, 339

Bullock Creek, Northern Territory



CROCODILES ARE A COMMON DENOMINATOR OF

most of Australia's Cenozoic palaeocommunities, and often were far more diverse in the past then they are at present. In the middle Miocene assemblages from Bullock Creek, one of the strangest forms was the crocodylid *Harpacochasma camfieldensis* which had an elongate, very toothsome mouth that made it look a bit like a living and presumably (there are controversies) unrelated Malayan False Gharial *Tomistoma schlegelii*. The diet of the False Gharial appears to include everything from fish to monkeys and even people, hence *H. camfieldensis*, while it looks like a fish-eater, may well have sampled more of the Bullock Creek biota than occurred only in the water. However, it would have been hard to pass up dining on the occasional very fleshy lungfish that were diverse in the middle Miocene waters of this area. One of these, *Neoceratodus* sp., may have been closely related to the living Queensland Lungfish *N. forsteri*. The Bullock Creek species of *Neoceratodus* coexisted with at least three other kinds of lungfish. The diversity of lungfish here suggests that the waters of this middle Miocene pool were never cold and were possibly subject to seasonal drying. Lungfish can survive shrinking deoxygenated pools by taking air into their lungs as well as by extracting oxygen from the water via their gills like other fish. In the adjacent forests, there was a wide range of animals similar to those that existed in the Riversleigh area at the same time. These included leopardsized marsupial lions, horned turtles, fox-sized thylacines, archaic kangaroos and many individuals of *Neohelos stirtoni* which was a calf-sized diprotodontid marsupial. However, there appear to have been fewer arboreal mammals in the Bullock Creek faunal assemblage than there were in the middle Miocene assemblages of Riversleigh. •

AGE

Middle Miocene, about 15 million years ago.

LOCALITY

Camfield Beds, Bullock Creek, Northern Territory. The limestone fossil deposits outcrop in a narrow belt about 50 km long near Victoria River in the Tanami Desert, Northern Territory.



ENVIRONMENT

The fossil assemblage suggests this region of the continent was beginning to become drier at the end of the middle Miocene. The thin enamel of all its mammalian herbivores suggests the vegetation was much less abrasive than it is in the same area today.

REFERENCES

52, 66, 204, 246, 273, 349, 429

Riversleigh, Scene 11, Queensland



GANBULANYI DJADJINGULI IS A QUOLL-SIZED

marsupial from the early late Miocene of Riversleigh (lower right). It shares some dental characteristics with the living Tasmanian Devil *Sarcophilus harrisii*; however, it may be a primitive dasyurid perhaps related to Riversleigh's *Barinya wangala* or belong to a separate carnivorous marsupial group. It is known only from a single upper heavily worn molar whose shape suggests this carnivore was a specialised bone-cracker. If so, it is the smallest bone-eating mammal known. *Yarala burchfieldi* (lower far right) is a tiny (mouse-sized) bandicoot representative of a family thought to be near the base of the bandicoot radiation and structurally intermediate between bandicoots and dasyurids. It would have foraged in the forest leaf litter for insects and other small animals. This archaic bandicoot does not exhibit a close relationship to any of the other known types of bandicoots. *Palorchestes annulus* (upper right), another taxon known from a single molar, is the oldest known species of this genus. Over time, *Palorchestes* species (six are known) became larger and their teeth became more high-crowned

and complex. Its youngest relative, the gigantic Pleistocene P. azael, had huge, compressed claws, powerful front limbs (adaptations to tearing bark or digging roots and tubers) and high-crowned teeth well suited to processing coarse or abrasive vegetation. To what extent features of this kind may have been present in *P. annulus* is unknown. Palorchestids are, in general, rare in the fossil record, suggesting that they were probably solitary animals. Ganguroo robustiter (upper left) is an archaic kangaroo that survived into the early late Miocene. Phylogenetic analyses using craniodental and postcranial characters suggest it belongs in the family Macropodidae, as the sister taxon to sthenurines and macropodines. Tiliqua pusilla (lower left) was a ground-dwelling insectivorous skink distantly related to the living Blue-tongued Lizard Tiligua scincoides. It is the smallest known species of the genus. The Blue-tongued Skink has a large blue tongue that it uses as a bluff-warning to potential predators.

AGE

Riversleigh Faunal Zone D, early late Miocene, about 12 million years ago.

LOCALITY

Encore Site, Gag Plateau, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

The Encore Local Fauna appears to represent a relatively more open forest palaeocommunity than those of the middle Miocene. Many of the animals in this faunal assemblage are larger than their relatives in the middle Miocene, a possible response to the beginning of drier conditions with less nutrient-rich vegetation. This is also the first time we see wombats *Warendja encorensis* that had evolved permanently growing teeth, probably an adaptation to dryness and the consequentially increasing sclerophylly of the vegetation.

REFERENCES

45, 80, 84, 267, 354, 387, 394, 462

Alcoota, Scene 1, Northern Territory



THE ALCOOTA LOCAL FAUNA PROVIDES THE BEST

opportunity to understand what Australia's land animal communities looked like in the late Miocene. While the fossil deposit appears to be missing many of the smaller creatures that must have been around at that time, bones of the larger ones occur in many thousands. One of the most common species represented is *Plaisiodon centralis* (lower left), a large (about 400 kg) diprotodontid marsupial that may have browsed on the leaves of shrubs while protecting its young from the predatory Powerful Thylacine *Thylacinus potens*. A rarer and much larger (about 700 kg) diprotodontid was the browsing *Pyramios alcootense* (centre right). Its rarity may mean that it normally lived further away, resulting in fewer individuals ending up in the deposit at Alcoota. An even rarer but smaller (about 400 kg) diprotodontid was *Alkwertatherium webborum* (lower right). In some respects, this smaller diprotodontid might have looked a bit like a giant wombat. Perhaps both of these relatively rarer species were drawn to this location during a drought due to the large body of shallow water here, where the bones

of trapped animals accumulated. Ilbandornis *lawsoni* (middle left) was one of several huge flightless, probably herbivorous birds in the family Dromornithidae that were common in the area and may have competed with diprotodontids for food. An even more awesome dromornithid known from Alcoota was Dromornis stirtoni. At more than 3 m tall and 500 kg in weight, this herbivore was the largest bird that ever existed. Hadronomas puckridgi (centre), at 1.5-2 m tall, was the largest kangaroo of its day. It may have been one of the earliest known short-faced kangaroos in the subfamily Sthenurinae, a group that went extinct in the late Pleistocene. Waiting in the water for any unwary bird or mammal was a giant mekosuchine crocodile (possibly an as yet unnamed species of Paludirex). If they got tired of waiting, crocs of this kind may well have ventured out of the water to chase down prey on the land. Very rare smaller animals have been found in this deposit, including a new kind of ringtail possum possibly related to the living Rock-haunting Ringtail Possum Petropseudes dahli of northern Australia.

AGE

Late Miocene, about 8 million years ago.

LOCALITY

Waite Formation, Alcoota, south central Northern Territory.



ENVIRONMENT

While today Alcoota is a vast area of grasslands and woodlands, in the late Miocene there would have been very little grass. However, there would have been plenty of shrubs and sparse woodlands to suit the culinary interests of the diverse large bird and mammal browsers. This was a time of drying and cooling all over the world. New Guinea, Australia's 'bumper zone', was rising as the Australian Plate crushed up against and dove under the Asian Plate, creating a significant rain shadow across Australia.

REFERENCES

51, 273, 324, 435, 465

Alcoota, Scene 2, Northern Territory



The Alcoota Local Fauna includes one of the largest carnivorous thylacinids known, the Powerful Thylacine *Thylacinus potens*. At 1.5 m in length, it was about the size and build of a modern Grey Wolf *Canis lupus*. Any of the herbivorous mammals of its day would have been wary of this predator. At Alcoota, where it was rare, or at least rarely fossilised, it would have had a bit of competition from a dog-sized marsupial lion *Wakaleo alcootaensis*. It is possible that these marsupial lions hunted more in the denser bush or even in trees, leaving open-country predation to the Powerful Thylacine. It is not clear how suited these thylacines would have been to long-distance running, and it is more likely that they were shortdistance sprinters. Rather than running down animals, they probably pounced on startled prey that failed to see them hiding in the vegetation. We can be reasonably certain that there were other kinds of carnivorous mammals at Alcoota, but for some mysterious reason local carnivores rarely ended up in this deposit. But rarity is definitely not a feature of the Alcoota fossil record for *Kolopsis torus*. This bull-like diprotodontid marsupial would have stood nearly 1 m at the shoulder and been perhaps 1.5 m long. Although distantly related to wombats (which are also curiously missing from Alcoota given that they are well known from early, middle and late Miocene deposits at Riversleigh), its teeth indicate that it had a diet of leaves that were softer than the abrasive grasses which modern wombats and kangaroos consume. Given the abundance of this diprotodontid, it is possible that it moved through this area in large herds or mobs, a strategy that would have helped to protect the more vulnerable juveniles from becoming lunch for the Powerful Thylacine. •

AGE

Late Miocene, about 8 million years ago.

LOCALITY

Waite Formation, Alcoota, south central Northern Territory. The enormously rich Alcoota fossil deposit extends laterally for 170 m. Bones and teeth are so abundant and often tightly packed in extensive bone beds that it can be difficult to excavate one fossil without breaking others that surround and overlap it.



ENVIRONMENT

The Alcoota faunal assemblage includes the greatest variety of species of diprotodontids that has ever been described, which suggests that the vegetation of the area must have been equally diverse. It is probable that during the late Miocene this area was dominantly shrublands and woodlands. Although some grasses may have been present, there is no evidence for grasslands as such in Australia until the middle Pliocene.

REFERENCES 13, 24, 272, 273, 465

Beaumaris, Victoria



MODERN WHALES FALL INTO TWO CATEGORIES:

toothed whales (e.g. the carnivorous porpoises and sperm whales) and baleen whales (e.g. the plankton-feeding right whales and humpbacks). Both groups have a long fossil history in Australia as they do in much of the rest of the world. The late Miocene *Balaena* sp. (shown here) from marine deposits at Beaumaris, Victoria, is one of the right whales (family Balaenidae). Although so far this baleen whale is only known from petrosals (bones that enclose the inner ear), these are very distinctive for the group. The non-flying fisheating penguins have an equally long fossil record, which is particularly rich in the marine deposits of the Southern Hemisphere. In Australia, their record extends from the Eocene to the present day. *Pseudaptenodytes macraei* (bottom left) is a large penguin in the family Spheniscidae represented by uniquely shaped upper arm bones (humeri) from Beaumaris. It was first described in 1970 by George Gaylord Simpson, a committed palaeomammalogist who regarded penguins as 'honorary mammals'. Among the strangest of the extinct birds from Australia, as elsewhere in the world, are the carnivorous pseudotoothed pelagornithids, such as the late Miocene Pelagornis sp. (shown flying and floating) from Beaumaris. Pelagornithids ranged in size from an albatross at the small end to giants with wingspans of 6 m. They probably used dynamic soaring to keep themselves airborne while sweeping over the sea in search of fish. Their strangest features were rows of bony projections along their jaws that looked and functioned like, but were not actually, teeth. The Beaumaris marine fossil deposit has also produced fossil whales, seals, fish and even rare land mammals. One of these is the medium-sized diprotodontid Zygomaturus gilli, which is similar to but a bit more derived than others from the Alcoota fossil deposit in the Northern Territory. The known age of the Beaumaris deposit helped to estimate the late Miocene age of the otherwise undated Alcoota deposit.

AGE

Late Miocene, about 6 million years ago.

LOCALITY

Black Rock Sandstone Formation, Beaumaris, Victoria.



ENVIRONMENT

The Beaumaris fossil assemblage accumulated in a shallow invertebrate- and vertebrate-rich sea that extended across the southern part of Victoria. Habitats on the adjacent land area probably included relatively dry sclerophyll forests and woodlands.

REFERENCES

114, 124, 244, 286, 358, 385

Awe, Papua New Guinea



SOME OF THE BIGGEST MYSTERIES OF THE

history of vertebrates of the Australasian region focus on New Guinea – when did it emerge from the sea, when was it colonised by land animals from Australia and did any that evolved in New Guinea spread back into Australia? The mid Pliocene Awe Local Fauna from the Otibanda Formation of Papua is the oldest known mammalbearing fauna from the whole island. Three of the largest vertebrates in this fauna are marsupials although these tend, on average, to be smaller than closely related forms in Australia. The largest were the diprotodontids, an extinct group that may well have had its highest diversity in the Pliocene. Some have argued that the New Guinean forms are descendants of late Miocene invaders that would have resembled species from Alcoota. Others think they were a local endemic radiation that sprung from later more derived colonists. *Kolopsis rotundus* (upper left) is similar in dental form to *K. torus* from the late Miocene Alcoota Local Fauna, part of the reason for presuming that the source for these Pliocene Awe diprotodontids may have been late Miocene forms from central Australia. The slightly smaller Kolopsoides cultridens (lower right) has very elongate upper premolar teeth, making its ancestry more of a mystery, although overall it too may well have descended from late Miocene Alcoota-type diprotodontids, in this case from something like Plaisiodon centralis. Protemnodon otibandus (upper right), a relative of larger 'giant wallabies' in the Pliocene and Pleistocene of Australia, was the largest Pliocene kangaroo known from New Guinea. It too has close relatives in Pliocene and Pleistocene deposits in Australia but there are no 'advanced' kangaroos like this in the Alcoota Local Fauna. This could be seen as support for the suggestion that there were at least two 'invasions' from Australia into New Guinea with the first (bringing in the diprotodontids) occurring during the late Miocene, and the second (bringing in species of Protemnodon) post-dating the start of the Pliocene.

AGE

Mid Pliocene, about 4-3 million years ago.

LOCALITY

Otibanda Formation, Awe, Papua New Guinea.



ENVIRONMENT

The Awe Local Fauna is not well enough known to give an unambiguous impression of the palaeoenvironment. All of the vertebrates reported so far, which, in addition to the three noted here, include rodents, a small dasyurid and a thylacinid, could be woodland or even grassland species bordering a stream. None is undoubtedly arboreal although limb bones suggest a possible tree kangaroo was present. Given the geographic and altitudinal position, it would have been at least a seasonally very well-watered palaeoenvironment.

REFERENCES

115, 120, 271, 294, 295

Chinchilla, Queensland



LEIPOA GALLINACEA IS A GIANT (4-7 KG)

malleefowl that lived in at least eastern Australia during the Pliocene and Pleistocene. Males of its smaller living relative, the Australian Malleefowl *L. ocellata*, dig depressions in the ground which they then fill up and mound over with leaf litter and sand. As the leaves rot, they give off heat which incubates the eggs. Although the males manipulate the pile to regulate the temperature, neither parent hangs around to see the young dig their own way out of the pile and race off into the bush – this is why juvenile mortality is high. The mid Pliocene *Euryzygoma dunense* was a bizarre knobble-headed large (about 2.5 m long) herbivorous diprotodontid marsupial that was probably the ancestor of the largest marsupial known, the Pleistocene *Diprotodon optatum*. The large bony processes that projected from the cheek area may have supported cheek pouches for holding food while it is being pulverised by the teeth. Alternatively, because these processes are much larger in some skulls than in others, perhaps they served as sexual signals in males because similar structures, such as horns and antlers in ungulates, are often larger in males than females. The brain was surprisingly small, only about 8 cm long in a 60 cm long skull, with most of the cranial area comprising a mass of hollow sinuses leading to descriptors like 'air head' for these large herbivorous marsupials. They had the effect of enlarging the outer surface of the skull, which increased the areas of attachment for larger muscles of mastication. The short-faced kangaroo Sthenurus notabilis (centre) was one of several Pliocene sthenurine kangaroos, a group that became far more diverse in the Pleistocene before it vanished perhaps little more than 10 000 years ago. It is likely that this kangaroo was a browser, in contrast to more 'conventional' contemporary macropodine kangaroos such as the more diverse early species of *Macropus* which were grazers. By the mid Pliocene, grasslands were spreading for the first time across much of the continent. Leaping out of a tree towards the sthenurine is a Pliocene marsupial lion, Thylacoleo crassidentatus. It was slightly smaller than it's Pleistocene descendent, T. carnifex, but just as carnivorous.

AGE

Late Pliocene, about 4-3 million years ago.

LOCALITY

Main Gully System, Chinchilla Sands, Rifle Range, Chinchilla, south-east Queensland.



ENVIRONMENT

The vertebrate fauna from Chinchilla suggests a mixed environment that included grasslands (e.g. diverse grass-consuming kangaroos, wombats and rodents), trees (tree/shrub-leaf-eating kangaroos and koalas), shrubs (possibly the diet of some of the diprotodontids) and wetlands (turtles, crocs, fishes and wading birds). It was probably slightly better-watered than the area is today.

REFERENCES

10, 51, 63, 262, 318, 326

Kanunka, Scene 1, South Australia



WHILE TODAY'S SALTWATER CROCODILE

Crocodylus porosus strikes fear in all northern Australian creatures, this 5 m mekosuchine crocodile, probably a species of *Paludirex* and possibly *P. vincenti*, may have been an even more dangerous predator if, like its smaller mekosuchine cousins, it could run down prey on land as well as leap up to grab them from the edge of the water. However, because it had an extremely broad snout, it is likely that this particular mekosuchine crocodile spent most of its time waiting in shallow water for thirsty diners to become dinner. Although the oldest Australian published record for Saltwater Crocodiles is the mid Pliocene, from the Bluff Downs Local Fauna of north-east Queensland, crocodylines did not come to dominate Australia's northern waters until all of the mekosuchine crocs had, for reasons that are unclear, become extinct. At 3 m long, 2 m tall at the shoulder and perhaps 2000 kg in weight, the Hippopotamus-like browsing *Diprotodon optatum* is far and away the largest marsupial known. As currently understood, this giant lived only during the Pleistocene, dying out probably because of climate change perhaps

35 000 years ago. Early claims that it occurred in the Pliocene were based on a few aberrant teeth of Euryzygoma dunense from Chinchilla which do, however, indicate that *E. dunense* was probably the Pliocene ancestor of this Pleistocene giant. Fossil footprints of D. optatum punched into the mud of Lake Callabonna in South Australia preserve the eerie last steps of this geographically widespread giant as it sought water from drying pools on the lake's treacherous surface of sticky mud. In the background, the small pelican Pelecanus cadimurka (whose actual age, collected from nearby Cooper Creek, is uncertain) stands beyond the reach of the crocodiles, watching for fish stranded in the shallows. Many other waterbirds, including ducks and Australia's last flamingos, occurred in the lakes and river channels of central Australia during the Pleistocene. The geological record for pelicans in Australia extends back to the late Oligocene (25 million years ago) but a little earlier elsewhere, with 30 million years old species known from fossil deposits in France. The Pleistocene in Australia served up four major droughts alternating with milder wetter interglacial periods. Every time there was a new drought, each of which was more ferocious than previous ones, many species, particularly the megafaunal animals, vanished. By the time humans arrived on the continent, most of the megafauna had already disappeared. Diprotodon optatum, however, appears to have survived alongside humans for perhaps 25 000 years until at least 35 000 years ago.

AGE

Early Pleistocene, about 2.5 million years ago.

LOCALITY

Kanunka Local Fauna, Kutjitara Formation, Lake Kanunka, Tirari Desert, South Australia.



ENVIRONMENT

The river channels in this area of central Australia were probably running through country that was similar in terms of environmental conditions to those in the area today, with arid/semi-arid shrublands and grasslands. While Australia's oldest sand dunes are only about 1 million years old, widespread grasslands were commonplace after the mid Pliocene.

REFERENCES

253, 325, 344, 432

Kanunka, Scene 2, South Australia



PROCOPTODON GOLIAH, AT 2 M TALL AND 230 KG

in weight, was the largest kangaroo known. Among its most interesting features was suppression of all but the huge fourth toe on the hind foot. In reducing the lateral toes, the species was becoming somewhat horse-like even though recent research suggests that this gigantic roo may have been a relatively poor hopper – if in fact it hopped at all. *Sthenurus stirlingi* (centre left), yet another of the diverse browsing sthenurine kangaroos all of which are extinct, at about 173 kg was one of the largest species of this genus but much smaller than *P. goliah*. Like all sthenurines, it probably had extended second and third fingers with elongate claws, useful for pulling down overhead leaf-laden branches. *Troposodon kentii* (shown bending down) was a macropodine kangaroo that belonged to a genus with controversial relationships within kangaroos in general. While originally noted to show striking similarities at the generic level to species of the living Banded Hare-wallaby *Lagostrophus fasciatus*, there were subsequent suggestions that species of *Troposodon* may represent a basal group within the subfamily Sthenurinae, which could mean that the Banded Hare-wallaby was in fact a surviving member of that subfamily. However, more recent research, while supporting the relationships between this hare-wallaby and species of Troposodon, does not support any special relationships to the sthenurines. But not all Pleistocene roos were giants; hare-wallabies like Lagorchestes sp. (bottom right), with a body length of perhaps 50 cm, was only about the size of a small dog. Like its recently extinct relative the agile Eastern Hare-wallaby L. leporides, it inhabited relatively dry country where it ate a range of ground plants. Flamingos (family Phoenicopteridae), while not part of the modern Australian biota, were once common around the shallow lakes of central Australia. Although the precise number of species and age ranges are uncertain, named Pleistocene species include the extant filter-feeding Greater Flamingo Phoenicopterus ruber (right foreground) as well as two extinct flamingos, Xenorhynchopsis tibialis (left foreground) and X. minor (background).

AGE

Early Pleistocene, about 2.5 million years ago.

LOCALITY

Kanunka Local Fauna, Kutjitara Formation, Lake Kanunka, Tirari Desert, South Australia.



ENVIRONMENT

One of the most challenging aspects of the Pleistocene in central Australia was the unpredictability of conditions, ranging from sporadically well-watered woodland savannah during 'greenhouse' intervals to arid deserts during 'icehouse' intervals. Despite this, the Kanunka Local Fauna is surprisingly diverse, suggesting that at least some of the animals and plants of the early Pleistocene may have been more environmentally resilient than their surviving descendants. Nevertheless, most Kanunka species over 44 kg in weight went entirely or regionally extinct during the Pleistocene.

REFERENCES

71, 170, 187, 318, 445

Bunyip Cave, Victoria



A RUFOUS FANTAIL RHIPIDURA RUFIFRONS

dances along the back of the Pleistocene Marsupial Tapir *Palorchestes azael* as this large herbivorous marsupial stoops to drink from a forest stream, while a modern Platypus *Ornithorhynchus anatinus* emerges from its bank-side burrow. The extinct palorchestids are often called marsupial tapirs because they have short retracted nasal bones in the skull, suggesting that they might have had a small mobile trunk like that of modern tapirs. *Palorchestes azael* was the largest of the palorchestids, with a body length of perhaps 2.5 m and some individuals weighing up to 1500 kg. Its teeth and skull morphology indicate that it may have been a browser, probably feeding on leaves, roots or tubers but also possibly the soft inner bark of trees, and perhaps even some invertebrates like insect larvae. Extensive areas on the lower jaw for the attachment of powerful jaw musculature suggest it might have had a long prehensile tongue, like those seen in living herbivores such as giraffes, for manipulating leaves and other vegetation. Powerful forelimbs and huge compressed claws may have been used to pull up shrubs, tear at the bark of trees or bring down branches to feed on foliage otherwise out of reach, while other aspects of its skeleton suggest it may have used a bipedal stance when feeding, perhaps like the ecologically similar extinct giant ground sloths of the Americas. The extraordinarily powerful forelimb was unable to be completely straightened and may have been held at about 100°. This limitation meant the animal would not have been able to reach higher than its head. Its fore and hind feet were almost certainly turned inwards, making this giant marsupial more or less pigeon-toed. None of the skeleton of the tail is known, so its length is a mystery. However, it is possible that the tail was short and solid, which would brace the animals while it was sitting on its haunches, freeing its powerful arms to do whatever they were able to do.

AGE

Pleistocene, about 1 million years ago.

LOCALITY

Bunyip Cave, Buchan Caves Reserve, eastern Victoria. One of the best-preserved specimens of this species was found there.



ENVIRONMENT

Open sclerophyll forests, probably with a grassy understorey, in many areas of eastern Australia.

REFERENCES

23, 117, 269, 270, 331

Eastern Darling Downs, Scene 1, Queensland

PLEISTOCENE



THE DIPROTODON DIPROTODON OPTATUM WAS

the first fossil mammal named from Australia, and it remains one of the best known of the Australian megafauna. The first fossils were found in the Wellington Caves, New South Wales and described in 1838 by Sir Richard Owen of the British Museum. Diprotodon is globally famous for being the largest marsupial that ever lived. With an adult size of 3.8 m long, 1.7 m at the shoulder and some 2800 kg in weight, this was a rhinocerossized mammal with pillar-like limbs, a graviportal stance and inturned feet like those of wombats and palorchestids. It was widely distributed across mainland Australia, most commonly in the relatively drier inland parts of the continent rather than the wetter fringes. It is known only from the Pleistocene and serves as a marker species for deposits of that age. Its fossils include complete skulls and skeletons, as well as hair and foot impressions. There are trackways preserved at Lake Callabonna in central Australia and one skeleton that contains the remains of saltbush in its abdomen. This giant marsupial was probably a browser, feeding on shrubs, forbs and tree leaves in Australia's open forests, woodlands and grasslands, eating daily as much as 100-150 kg of vegetation. Analyses suggest that this mega-herbivore migrated seasonally in herds or mobs in search of its preferred food, like many East African mammals do today. It co-existed with humans in Australia for at least 25 000 years. The timing and reasons for its extinction remain hotly debated. The two popular contenders are climate change or human activity, although there is no hard evidence that even a single individual was hunted by humans. Diprotodon optatum is the basis for the name of the family, Diprotodontidae. The Kookaburra Dacelo novaequineae was originally given its species name on the mistaken assumption that it had been first seen in New Guinea, where it in fact does not exist. Its generic name Dacelo is an anagram of Alcedo, the Latin word for kingfisher. It is in fact a member of the kingfisher family Alcedinidae and they do include fishes in their diet when they can catch them.

AGE

Pleistocene, 2.6 million to about 35 000 years ago.

LOCALITY

The scene depicted is based on fossils from the eastern Darling Downs, south-east Queensland. *Diprotodon optatum* is known from many sites across Australia but not from New Guinea, Tasmania, Northern Territory or south-west Western Australia.



ENVIRONMENT

Semi-arid plains, savannahs and open woodlands. During the Pleistocene, climates in Australia oscillated between dry and more equable conditions. Sea levels were periodically lower than today at times when more of the world's water was tied up as ice at the poles and high latitudes.

REFERENCES

281, 311, 313, 463, 464

Eastern Darling Downs, Scene 2, Queensland

PLEISTOCENE



OWEN'S NINJA TURTLE NINJEMYS OWENI IS A

large Pleistocene horned turtle from Queensland that had an estimated carapace (upper shell) length of 1 m and weighed around 200 kg. It resembled its larger Queensland relative, the Wyandotte Giant Horned Turtle, but the large pair of horns on its head extended to the sides rather than backwards as they tend to do in the Wyandotte species. Like other meiolaniid turtles, this meiolaniid turtle is thought to have been terrestrial and herbivorous. Meiolaniid turtles are also known from South America, where they are known from the Cretaceous to Palaeocene before they went extinct. The record in Australia isn't that old but it extends from the Eocene to the late Pleistocene and is more diverse than the South American record with species placed in several different genera. Precisely when and why the group became extinct on each of the Gondwanan continents they once occupied is not known, although they survived into the Holocene on some Australasian islands. Ninjemys oweni is shown here browsing alongside the sthenurine kangaroo Procoptodon rapha, one of many shortfaced kangaroos that co-existed with longerfaced modern kangaroos during the Pliocene and Pleistocene. They specialised on a diet of leaves from trees and shrubs, with their robust skull and shortened face thought to be related to the need for large masseter and temporalis muscles necessary to browse on tough leaves and twigs. On each foot they had a single large toe or claw, somewhat similar in appearance to a horse's hoof. On each hand they had two very long fingers with large claws that may have been used to reach over their heads to pull branches down to the point where they could bite the leaves off.

AGE

Late Pleistocene, until at least 50 000 years ago.

LOCALITY

King's Creek, Darling Downs, Queensland.



ENVIRONMENT

Streams and small rivers in this region were surrounded by sclerophyllous woodlands, scrublands and vine thickets. Grasslands may have been widespread but at a distance from the margins of the waterways.

REFERENCES

34, 131, 235, 305, 315, 318, 371, 439

Wellington Caves, Scene 1, New South Wales

PLEISTOCENE



GENYORNIS NEWTONI WAS THE LAST OF

Australia's large flightless dromornithids. Also known as mihirungs, thunder birds or even 'demon ducks of doom', these big birds are thought to be more closely related to ducks and geese than to ratites such as emus, cassowaries and ostriches. This particular dromornithid stood over 2 m tall and was very heavily built, with an estimated weight of 220–240 kg. It had small vestigial wings, and massive legs with hoof-like toes that indicate that this bird was well adapted for running. The beak was also massive and the lower jaw was unusually heavily ossified, indicating that considerable force could be used to break up its food. It appears to have been widely distributed in Australia during the Pleistocene, probably living mostly on the open plains and in open forests. Another heavyweight of this time was the bull-sized Zygomaturus trilobus, which weighed in at 500 kg or more, was 2.5 m long and stood about 1.5 m tall. This diprotodontid had prominent zygomatic arches and widely flared nasal bones. It is known from southern, eastern and south-western areas of Australia where it inhabited dry sclerophyll forests, near waterways, and fed on browse including roots and tubers. In these forests also lived Phascolarctos yorkensis, a Plio-Pleistocene koala that was about a third larger than the modern Koala P. cinereus, making it the largest arboreal marsupial of its time. During the Pleistocene, these two koala species appear to have co-existed in some areas and it remains unclear why the larger one ultimately became extinct. In the distance, short-faced kangaroos Procoptodon rapha browse on leaves from trees and shrubs, while Macropus giganteus titan, a megafaunal relative of the modern Eastern Grey Kangaroo *M. giganteus* grazes on grasses nearby. The Eastern Bearded Dragon Pogona barbata is an agamid lizard that can still be seen today in wooded parts of Australia.

AGE

Pleistocene, 2.6 million to about 11 000 years ago.

LOCALITY

Wellington Caves Reserve, Wellington, New South Wales.



ENVIRONMENT

Open sclerophyll forests and woodlands with a grassy/shrub understorey, similar to the vegetation that currently covers the hills in which the Wellington Caves occur. However, it is possible that *Zygomaturus trilobus* needed wetter terrains or even swamps which may have occurred in lower areas of the same region associated with the ancestral Bell River.

REFERENCES

28, 55, 92, 93, 223, 324

Wellington Caves, Scene 2, New South Wales

PLEISTOCENE



WHEN MOST OLDER AUSTRALIANS THINK OF

kangaroos, they tend to think of 'Skippy', the name of a putatively intelligent, grass-munching Eastern Grey Kangaroo Macropus giganteus that featured in an Australian television show between 1968 and 1970. Skippy's hands were often shown 'untying' knots to save someone being abused by human villains. There was one group of extinct kangaroos that would save you from harm only if they could then eat you: the carnivorous to omnivorous propleopine hypsiprymnodontid kangaroos. Earlier forms like Ekaltadeta ima from the Miocene of Riversleigh were almost certainly dominantly carnivorous. Their younger larger descendants, the Pleistocene species of Propleopus and Pliocene species of Jackmahoneya, may have been more like omnivorous bears, capable and keen to eat animals but perhaps more commonly dining on fruits, flowers or soft leaves. The most common of these was P. oscillans, which is known from several fossil deposits in the eastern states of Australia. This distant relative of the living omnivorous but much smaller Musky Rat-kangaroo Hypsiprymnodon moschatus which inhabits the rainforests of northeast Queensland may have been about 70 kg in weight, about the size of an Eastern Grey Kangaroo. But as well as having a far more catholic diet, like other propleopines it probably galloped rather than hopped - altogether a very un-Skippy-like kangaroo. The fowl dinner it is shown dining on is the Australian Brush-turkey Alectura lathami, which would have occupied the same habitat as this kangaroo and often graced its table.

AGE

Pleistocene, 2.6 million to perhaps 35 000 years ago.

LOCALITY

Although this species was never common, perhaps reflecting its role as an opportunistic carnivore in Australia's Pleistocene ecosystems, *P. oscillans* was reasonably widespread in eastern Queensland (mainly the Darling Downs), New South Wales (e.g. Wellington Caves as well as Lake Menindee), Victoria and South Australia.



ENVIRONMENT

Most of the deposits in which this species is known to occur would have accumulated in open forest or woodlands rather than closed forests.

REFERENCES

51, 92, 93, 296, 332

Wellington Caves, Scene 3, New South Wales

PLEISTOCENE



SINCE 1830, THE PLEISTOCENE MAMMALS OF

Wellington Caves have had an extremely important role in developing early understanding about the globally unique nature of Australia's ancient mammals as well as in the initial development of Darwin's realisation about the reality of evolution. After visiting South America and seeing that the ancient mammals of that land most closely resembled that continent's living types, the biblical claim about a global flood began to seem improbable. Subsequent recognition that the fossil mammals from Wellington Caves included wombats, kangaroos and possums rather than rhinoceroses, elephants and lions finally convinced Darwin that animals had evolved on each continent from pre-existing kinds unique to those lands. That said, when Sir Richard Owen first saw specimens of the animal he named *Thylacoleo carnifex*, which came to be called the Marsupial Lion, he realised it was in many ways 'lion-like', albeit a decidedly unique marsupial version that had nothing to do with placental lions other than the fact that they both were ferocious carnivores. Weighing up to 160 kg and equipped with a massive thumb claw, powerful dagger-like lower incisors, lethally sharp and enormous carnassial third premolars, and powerful arms, there were no megafaunal mammals in Australia immune to becoming this globally most specialised carnivorous mammal's dinner.

Among the millions of fossil bones and teeth jumbled together like a Christmas pudding in the reddish cave deposits exposed in the Phosphate Mine at Wellington are those of some of the largest kangaroos that have ever terrorised a leaf on this continent. Among them was the gigantic 'wallaby' Protemnodon brehus, which occurred in all states of Australia except Tasmania. While there were many other species of this genus spread between Tasmania and New Guinea, at perhaps 110 kg this was one of the largest. Like other species of the same genus, it had very long shearing premolars for cutting twigs and tough leaves. As a browser it would have spurned the rapidly expanding grasslands, preferring the leaves of shrubs and the low branches of trees, from where it would have kept a wary eye out for hungry Marsupial Lions.

AGE

Mid to late Pleistocene, about 1 million-500 000 years ago.

LOCALITY

Phosphate Mine, Wellington Caves, New South Wales.



ENVIRONMENT

The vegetation surrounding the Wellington Caves would have included sclerophyll forests, shrublands and grasslands perhaps similar to the vegetation that covers and surrounds these hills today. Depending on the particular part of the Pleistocene that hosted these animals, the overall climate of the area would have been semi-arid to Mediterranean.

REFERENCES 28, 92, 93, 170, 223

The giant lizard Megalania, eastern Australia

PLEISTOCENE



AN EASTERN GREY KANGAROO LEAPS TO ESCAPE

ambush by the world's largest known terrestrial lizard, Megalania Varanus priscus, Australia's giant extinct monitor lizard. Growing to 5.5 m long or more, and up to 500 kg in weight, this gigantic lizard was at least twice the size of its living relative, the Komodo Dragon Varanus komodoensis of Flores and nearby islands. During the Pleistocene, it was Australia's largest terrestrial carnivore. It could have taken down the largest kangaroos and probably even the rhino-sized Diprotodon Diprotodon optatum, which it would have torn to pieces using its very large claws and recurved serrated teeth. It was probably also venomous, like closely related living varanids which use a potent hemotoxin released by glands in the mouth that acts as an anticoagulant and greatly increases bleeding in wounded prey. Speculation about how living Komodo Dragons kill large prey led to the initial suggestion that bacteria in their mouths caused lethal infections after they bit the legs of the intended prey. When it was discovered that varanids have venom, that was suspected of being the way they subdued prey. But more recent studies suggest that the Komodo Dragons' primary method of killing large ungulates such as cattle is the action of their jagged teeth, which sever blood vessels in the legs and lead to death from blood loss. The Komodo Dragons only have to follow the weakening prey until it drops, unable to
defend itself. This may well be the same strategy used by Megalania to safely bring down potential gigantic meals like Diprotodon. In the Pleistocene, Megalania lived alongside smaller varanids, such as the living Perentie and Lace Monitor. But it was not the only giant lizard roaming Australia at that time – fossils from Mount Etna caves in Rockhampton, Queensland indicate that the extant Komodo Dragon also once lived and probably first evolved in Australia. Another very large monitor species is known from fossil deposits in the Lake Eyre Basin of central Australia.

AGE

Pleistocene until at least 50 000 years ago.

LOCALITY

Megalania was widely distributed but seemingly very rare across much of eastern Australia. Although skeletons are unknown, teeth, vertebrae and other bones have been found in New South Wales, South Australia, Victoria and Queensland, particularly in the Darling Downs region. It is not yet known from Tasmania, Western Australia or New Guinea.



ENVIRONMENT

During the Pleistocene, Megalania probably lived in open woodlands and grasslands across at least the eastern half of mainland Australia.

REFERENCES

101, 175, 258, 314

Thylacoleo Caves, Western Australia PLEISTOCENE



ONE OF THE MORE REMARKABLE MODERN

discoveries of Pleistocene vertebrates was reported by Gavin Prideaux and colleagues in 2007, from three closely associated cave deposits called Thylacoleo Caves, on the Western Australian Nullarbor Plain. At last count, 68 mammal species have been found including many new species; for example, eight new kangaroo species among the total of 23 recovered from the deposits. Among the new species was a giant tree kangaroo *Bohra illuminata*. As the first known skull and skeleton of an extinct member of this fascinating group of kangaroos, they exhibit features that demonstrate these were indeed arboreal kangaroos. But at around 40 kg, these tree-climbing roos were twice the size of any of the modern tree kangaroos (*Dendrolagus* sp.) living in the rainforests of New Guinea and Australia. There are also features that demonstrate older evolutionary relationships to rock wallabies (*Petrogale* sp.) some of which have been known to climb trees as well as rocky hillsides. Other kangaroos in these deposits include the very strange *Congruus kitcheneri* which had first been found in a fossil deposit in Western Australia. Other new species of Congruus in the Thylacoleo Caves deposits include one that may have had horn-like growths projecting from the skull over the orbits. Among the long list of extinct megafaunal species in these deposits is the Giant Wombat Phascolonus gigas which, if it burrowed like its modern relatives, could have been excavating tunnel systems large enough to harbour small cows. Skeletons of the extraordinary carnivorous Marsupial Lion Thylacoleo carnifex in these deposits are the best preserved of any so far found. On balance, they confirm that this was the most specialised mammalian carnivore that has evolved anywhere in the world. But they also reveal a uniquely upwardly bent tail that supported this predator as it leaned back on its haunches, thereby freeing its powerful arms to kill or dismember its prey.

AGE

Middle Pleistocene, with many of the fossils apparently accumulated 400 000-230 000 years ago.

LOCALITY

Thylacoleo Caves (Leaena's Breath Cave, Flight Star Cave, Last Tree Cave), Nullarbor Plain, Western Australia.



ENVIRONMENT

Dry, relatively open sclerophyll/woodland and shrubland environment, similar to many areas of central Australia today. Although they are not in the area now, some relatively large trees must have been present at this time to accommodate hollow-nesting parrots and two different species of giant tree kangaroos.

REFERENCES

109, 243, 318, 319, 320, 413

Naracoorte Caves, Scene 1, South Australia

PLEISTOCENE



BECAUSE OF THEIR EXTRAORDINARY RECORD OF

Pleistocene vertebrates, Naracoorte Caves were listed with Riversleigh in 1994 as a serial World Heritage property called Australian Fossil Mammal Sites (Riversleigh/Naracoorte). While Pleistocene megafaunal fossils are also known from Riversleigh, those from Naracoorte are far more diverse and better preserved. The deposits, which have been found in 26 different caves including the fossil-rich Blanche and Victoria Caves, contain many of the extinct Pleistocene vertebrate species that were once widespread throughout southern and eastern Australia. For example, the browsing Short-faced Kangaroo *Simosthenurus occidentalis* (middle right), first discovered in Mammoth Cave in Western Australia, the perhaps hippo-like diprotodontid Zygomaturus trilobus (lower right), first discovered in Tasmania, and the hypercarnivorous Sarcophilus laniarius (lower left among logs), first discovered in the Wellington Caves in New South Wales, have been found together in the Naracoorte deposits. Among the many other extinct species that have been found here are the giant long-beaked and probably worm-eating echidna Megalibgwilia ramsayi (lower middle) and the archaic wombat Warendja wakefieldi (lower left). This wombat is a late Pleistocene survivor of the earliest lineage to develop rootless teeth, an adaptation which Riversleigh's fossil taxa (e.g. W. encorensis) have demonstrated evolved over the last 15 million years in response to the increasingly abrasive vegetation of a drying Australia. Among the many other fossilised carnivores in Naracoorte's limestone treasure houses are the Thylacine Thylacinus cynocephalus (middle left), which survived on the mainland until about 4000 years ago, possibly going extinct because of competition with introduced Dingoes, and the at least partly arboreal Marsupial Lion Thylacoleo carnifex, shown here surveying from above the possible components of the day's menu, above a Diprotodon Diprotodon optatum. Although a hypercarnivore, which are normally uncommon in ecosystems, there are surprisingly high numbers of Marsupial Lion specimens in the Naracoorte Caves deposits. This may be because the scent of dead or dying animals that had fallen into the caves attracted a disproportionate number of carnivores.

AGE

Late Pleistocene, most fossils accumulated about 400 000-200 000 years ago.

LOCALITY

Naracoorte Caves, south-eastern South Australia.



ENVIRONMENT

Tall eucalypt forests with a thick understorey of hard-leaved shrubs alternating over time and space with woodlands, grasslands and swampy sedge lands. However, during most of the late Pleistocene when the Naracoorte fossils were accumulating, most of the area would have been open eucalypt woodlands.

REFERENCES

128, 232, 233, 270, 413

Naracoorte Caves, Scene 2, South Australia

PLEISTOCENE



OF ALL THE KINDS OF SNAKES KNOWN FROM

Australia, the most fascinating and mysterious are the extinct madtsoiids. Madtsoiids once thrived in South America, Africa, Madagascar, India, Australia and even some areas of southern Europe, from the late Cretaceous to late Pleistocene. However, in most areas of the world except Australia they were gone by the end of the Eocene. In Australia, they survived until the late Pleistocene. Decline of the group within Australia may have been the result of steady drying out of the continent. Madtsoiids are among the most 'primitive' snakes known, with the family falling outside all other still-surviving snake families. Because they retain many archaic skull features, they are a primary focus of research into the origin of snakes as a whole. While uncertain, it would appear that some, such as the madtsoiids from Riversleigh, were at least semi-aquatic, possibly having lifestyles similar to modern anacondas. Others such as *Wonambi naracoortensis*, which occupied drier environments in southern Australia, are more likely to have been semi-fossorial than semi-aquatic. Probably they were non-venomous constrictors, although there is no certainty about these probabilities either. *Wonambi naracoortensis* may have survived long enough to overlap in time with the first humans in Australia and it has been suggested that early sightings of this large 6 m snake, which probably had iridescent scales, might even have been the origin of the legend of the Rainbow Serpent. *Wonambi* is an Aboriginal word for a Dreamtime legend about a Rainbow Serpent.

AGE

Late Pleistocene.

LOCALITY

Naracoorte Caves, south-eastern South Australia.



ENVIRONMENT

The habitat around the Naracoorte Caves in the late Pleistocene would have been dry sclerophyll forest and woodlands.

REFERENCES

33, 263, 285, 333, 348

Texas Caves, Scene 1, Queensland PLEISTOCENE



AS CURRENTLY UNDERSTOOD, THERE ARE 12

species of extinct short-faced browsing kangaroos placed in the genus Procoptodon. They exhibited many of the morphological extremes of kangaroos, including gigantism with some species up to 2 m tall, weights of almost 250 kg and loss of all toes except the fourth toe of each hind foot. Even their hands were specialised, such that two fingers of each hand were extremely elongated, presumably adapted for grasping branches high above the reach of all other roos. They are known only from Pleistocene deposits. A series of caves near Texas. south-eastern Queensland, contain Pleistocene deposits that were excavated in a rush by the Queensland Museum in 1975 just before they went under water when the Glenlyon Dam was built on Pike Creek in 1976. A fossil-rich limestone found in

one cave known as The Joint produced, besides the first described dagger-toothed mekosuchine crocodile from Australia, a single tooth (P³) of a giant macropodid, Procoptodon texasensis (which may or may not be the same species as P. rapha). This find was extremely fortunate considering that at the time of the excavation the cave was filled with CO₂ which nearly overcame the palaeontologist (Mike Archer), who struggled to remain awake while using a hammer and chisel to gouge out blocks of the breccia. Major Mitchell's Cockatoo Lophochroa leadbeateri would have been present in the dry sclerophyll forest that surrounded The Joint as it accumulated the teeth and bones of animals that stumbled into the crevasse above.

AGE

Pleistocene, more than 292 000 years ago (precise age unknown).

LOCALITY

Texas Caves, south-east Queensland.



ENVIRONMENT

The fauna from The Joint deposit suggests that the palaeoenvironment in this region of south-eastern Queensland in the Pleistocene was dry to wet sclerophyll forest. Two species, a pademelon and bandicoot (*Thylogale* sp. and *Perameles nasuta*), however, suggest the possibility that there were patches of rainforest nearby. The presence of a mekosuchine crocodile does not necessarily indicate water, given that some of these crocodiles are regarded to have been at least in part terrestrial.

REFERENCES

11, 168, 170, 318

Texas Caves, Scene 2, Queensland PLEISTOCENE



WHEN NEWS CAME THAT THE GLENLYON DAM

was being built and that it would back up Pike Creek in south-eastern Queensland, the Texas Caves were suddenly in imminent danger of being flooded forever. Mike Archer mounted a Queensland Museum expedition to excavate as many of the fossil deposits as possible, and to survey the modern biota of the area. The fossil focus was on Russenden Cave and a fissure deposit known as The Joint. Fossils recovered from Russenden Cave included thousands of bones representing a wide range of animals, some of which had gone extinct in the region and some of which still survive. Among the extinct forms was a fascinating new species of *Antechinus* later named *A. puteus* by Steve Van Dyck; the fossil deposit in The Joint provided even more unexpected creatures. Although the precise age of these Texas Cave deposits is uncertain, some species found in The Joint deposit, such as the giant shortfaced kangaroo *Procoptodon texasensis*, indicate a Pleistocene age that has been determined to be greater than 292 000 years old. Other species found included a wombat that is probably conspecific with the Common Wombat Vombatus ursinus, a large marsupial still living in this region of Queensland. But not all the Texas Cave discoveries represented animals similar to others already known. A maxilla of a reptile that emerged from The Joint deposit was like nothing ever seen before. While it was clear that it did not represent a lizard - because the teeth were in sockets in the bone rather than attached to the sides of the bone - it nevertheless had blade-like recurved serrated teeth like those of a goanna. This was the first discovery of what eventually proved to be the highly distinctive subfamily of deep-headed semiterrestrial crocodiles, the Mekosuchinae. This one was eventually named Quinkana fortirostrum.

AGE

Pleistocene; The Joint, more than 292 000 years ago (precise age unknown); Russenden Cave, 55 000 years ago.

LOCALITY

Unnamed fossil deposits, Russenden Cave and The Joint, Texas Caves, Pike Creek area, south-east Queensland.



ENVIRONMENT

The faunas suggest the area in the region of the caves supported relatively dry sclerophyll forest with grasslands, possibly with pockets of wet sclerophyll forest and/or rainforest in adjacent areas.

REFERENCES

11, 223, 317, 401

Lord Howe Island meiolaniid turtle PLEISTOCENE/HOLOCENE



AT GROUND LEVEL, GIANT LUMBERING TURTLES

own this place. The Lord Howe Island meiolaniid *Meiolania platyceps*, with shells exceeding 1 m in length, had sheep-like horns protruding from their heads and long spiked tails ending in a large bony club. But despite their 'battle armour', these animals were no threat to other animals – they were plant-eaters. Their armour was presumably an evolutionary holdover from years and places past when their ancestors in Australia and other areas of Gondwana needed to protect themselves from a range of fearsome predators. At some point, a million or more years ago, adventurous or incautious ancestors of these Lord Howe Island turtles floated across the Tasman to land on Lord Howe Island. Presumably this proclivity for frolicking around the shores of Australia meant that many other less fortunate turtle travellers also drifted away, only to become a shark's dinner or a lump on the bottom of the ocean. The first successful immigrants to Lord Howe Island would have encountered avian denizens (terrestrial mammals do not appear to have reached Lord Howe Island) including a couple of rails, the most striking of which was the White Swamphen Porphyrio alba (left), a close relative of the Purple Swamphen P. melanotus of Australia and New Zealand. Like its relatives, these Lord Howe species would have fed on a range of plants as well as any tasty invertebrates. It is entirely possible that these omnivorous groundbirds also indulged, whenever the opportunity arose, on baby Meiolania platyceps turtles when they hatched, in the same way other rails and herons do today on islands where sea turtles breed. Abundant pigeons Columba vitiensis godmanae (top left) and parakeets Cyanoramphus novaezelandiae subflavescens (bottom right) also lived in these forests. The pigeons probably spent most of their time feeding in the forest canopy, but the parakeets would have made regular forays to the forest floor to feed on ground plants and seeds. Exactly when this turtle-dominated ecosystem collapsed on Lord Howe we do not know, but in Vanuatu some of the last meiolaniids appear to have met their end in the ovens of the first Vanuatuans about 2500 years ago.

AGE

Late Pleistocene to Holocene, about 100 000-1000 years ago.

LOCALITY

Lord Howe Island, Tasman Sea.



ENVIRONMENT

In the lowland subtropical forest that clothes the dunes at the back of what is now Ned's Beach, Kentia palms (*Howea* sp.) form thick stands and pandanus groves fill the spaces between these and the sea The calcareous sands that form the dunes near the beach appear to have been able to entomb any horned turtles that were unlucky enough to roll over or be trapped in depressions in the ground.

REFERENCES

130, 131, 133, 284, 419

Mammoth Cave, Western Australia



MAMMOTH CAVE, IN THE DENSE TALL EUCALYPT

forests south-west of Margaret River, is a most curious place. Fossil bone deposits containing at least 34 different kinds of vertebrates including the now extinct Thylacine *Thylacinus cynocephalus* were discovered there as early as 1904. Most of the animals in the deposit appear to have fallen into the cave through a now-blocked solution pipe in the roof. Possible pre-European fossil collecting in Mammoth Cave has been suggested as an explanation of the 'charms' valued by Indigenous Australians in the Kimberley area of north-western Australia. These include a third upper premolar of the hippopotamus-like diprotodontid Zygomaturus trilobus, set in spinifex gum and attached to a string made of hair. Other Kimberley charms included isolated teeth of the medium-sized sthenurine kangaroo Simosthenurus browneorum. Both species are common in the fossil deposits of Mammoth Cave but not known from northern Australia. Although trade in fossils up and down the Western Australia coast is possible, it is also possible – although perhaps less plausible – that there is an as yet undiscovered fossil deposit with these species somewhere in the Kimberley region.

One of the most intriguing fossils from Mammoth Cave, collected sometime between 1909 and 1915 by Ludwig Glauert, who was excavating by candlelight on behalf of the Western Australian Museum, was an extinct giant longbeaked echidna Murrayglossus hacketti, the largest monotreme known. Several kinds of long-beaked echidnas are known from Pleistocene fossil deposits in Australia, but today species of this genus are confined to New Guinea and adjacent islands. A recent claim that the Western Longbeaked Echidna Zaglossus bruijnii, known today only from New Guinea, survived into modern times in north-western Australia may be based on a label mix-up in the Natural History Museum in London. However, why the long-beaked echidnas like M. hacketti died out in the late Pleistocene, leaving in Australia only the common Short-beaked Echidna Tachyglossus aculeatus, is a mystery.

AGE

Late Pleistocene (precise age uncertain). Radiometric dates of items recovered from remnants of the Glauert Deposit still adhering to the cave wall have provided dates from about 55 000-44 000 years ago.

LOCALITY

Mammoth Cave, Leeuwin-Naturaliste National Park, south-western Western Australia.



ENVIRONMENT

The list of species known from the Mammoth Cave deposit, in addition to the extinct forms, includes Koalas, rock-wallabies and other modern types that still abound in forested areas of the structural kind that surrounds Mammoth Cave today. Hence, it is possible that the environment at the time this deposit accumulated may have been relatively similar to that which still occurs today.

REFERENCES 5, 17, 147, 167, 247, 248

Mowbray, Victoria



MOWBRAY SWAMP IN NORTH-WEST TASMANIA

has produced fossils of two of the most common Pleistocene marsupials that also commonly occur in continentally marginal sites around Australia: the zygomaturine diprotodontid Zygomaturus trilobus and the macropodine kangaroo Protemnodon anak. One of the two skeletons of Z. trilobus recovered from this deposit was first described by colonial palaeontologists, H.H. Scott of the Queen Victoria Museum in Launceston and C. Lord of the Tasmanian Museum in Hobart. It was a strange animal, possibly 500 kg in weight, with a wide foreshortened turned-up snout that may have supported some kind of a fleshy mobile trunk. It may have been a semi-aquatic herbivore like the Hippopotamus. It had hollow sinuses in the bones of the head that enabled the skull's outer surface to be sufficiently large for attachment of its massive chewing muscles. These 'air pockets' took up almost 25% of the total volume of the head, which is why diprotodontids exhibiting this sort of pneumatisation of their cranial bones have been called 'air heads'. *Protemnodon anak* has been described as a huge 'wallaby'. Its relationships to other kangaroos have been controversial, with recent analysis of the skulls suggesting it falls outside of all the macropodine kangaroos including the wallabies and larger species. However, recent remarkable analysis of DNA recovered from a Tasmanian specimen that was about 45 000 years old suggests that the species of Protemnodon were most closely related just to kangaroos of the genus Macropus, hence tucking in much further up the family tree. They had very elongate skulls. Their long narrow premolars and low-crowned molars suggest that they were, like the species of Zygomaturus, browsers rather than grazers. Although most of the extinct megafaunal species were gone from Tasmania before humans arrived, perhaps 45 000 years ago, it is possible that these two species were still present. Nevertheless, analysis of the bones of all extinct Tasmanian megafaunal species has revealed no evidence that humans had a role in their extinction.

AGE

Late Pleistocene, probably greater than 52 000 years ago. Efforts to date the deposit have led to the conclusion that the dates obtained are unreliable because of contamination by modern carbon sources.

LOCALITY

Mowbray Swamp, a 10 km wide deposit in the north-western corner of Tasmania, south-west of Smithton.



ENVIRONMENT

Pollen diagrams suggest the presence of forest trees, tree ferns and abundant shrubs during the approximate time when these species lived in the Mowbray Swamp area.

REFERENCES

94, 145, 146, 214, 353

Callabonna, South Australia



ONE OF THE MOST AMAZING THINGS ABOUT LAKE

Callabonna is a picture taken years ago of palaeontologist Richard Tedford squatting next to a ghostly series of enormous footprints that disappear off into the distance. They are the footprints of *Diprotodon optatum*, the largest marsupial that ever lived, and perhaps record the journey of a doomed giant searching for disappearing water during an ancient drought. If that is what happened, this individual was not struggling alone. Entombed in Callabonna's late Pleistocene clays are the skeletons of many different kinds of extinct as well as still-living animals that became mired in the treacherous muds of the drying lake. Extinct species include short-faced kangaroos (the giant *Sthenurus stirlingi* [upper left] and smaller *S.* andersoni [middle left]), cow-sized wombats *Phascolonus gigas* (upper right), the last survivor of the once diverse mirihungs or thunderbirds *Genyornis newtoni* and many other fascinating creatures. The still-surviving fish-eating Shag *Phalacrocorax melanoleucus* shown in the diorama, along with many other species that survived the sequence

of late Pleistocene extinctions, would have been part of a vast complex ecosystem when Lake Callabonna was full of water. Even today, on the rare occasions when the lake does fill with water, vast numbers of waterbirds appear within days and repopulate the arid area until the waters gradually disappear once again. Fossils in the lake's deposits were first reported in 1882. Although there have been many expeditions to collect the fossils, the most famous were those in 1893 carried out by Sir Edward C. Stirling and Amandus H.C. Zeitz of the South Australian Museum who collected some of the best skeletons known of D. optatum and G. newtoni. This led to establishment of the lake as a Fossil Reserve in 1901, one of the first in Australia. More recent expeditions, including those led by Trevor Worthy of Flinders University, have made even more extraordinary discoveries, confirming the wisdom of the 1997 decision to place Lake Callabonna on the South Australian Heritage Register.

AGE

Late Pleistocene.

LOCALITY

Although the modern dry salty Lake Callabonna in central northern South Australia is 160 km², it was probably much larger when the fossil deposits were accumulating. Most of the fossil deposits have been found near the north-eastern edge of the lake in an area that has become the Lake Callabonna Fossil Reserve. The lake surface where the fossil beds are exposed range -2 to -4 m below sea level.



ENVIRONMENT

Callitris (conifer) cones and other plant materials found in the deposit alongside the fossil bones indicate that the area evidently supported an open savannah woodland with at least some trees as well as shrubs.

REFERENCES 299, 372, 381, 415

Wyandotte Station, Queensland



AUSTRALIA WAS ONCE HOME TO A FAMILY

(Meiolaniidae) of large herbivorous terrestrial turtles characterised by having highly distinctive armoured heads and tails, adorned with horns and tail clubs. The largest of these meiolaniid turtles was the Wyandotte Giant Horned Turtle *Meiolania* sp. cf. *M. platyceps* of northern Queensland, which is estimated to have a carapace (upper shell) some 2 m long. Fossils of this giant turtle include three cow-like horn cores and a tail vertebra recovered from Pleistocene sediments along Wyandotte Creek near Greenvale. This species is distinct from the giant *Ninjemys oweni*, indicating that there were two species of giant armoured turtles living in Queensland during the late Pleistocene. The Wyandotte horned turtle was more similar to the much smaller Lord Howe Island's *Meiolania platyceps*. Apart from mainland Australia and Lord Howe Island, meiolaniid turtles once also lived in South America, New Caledonia, Vanuatu, Fiji and possibly New Zealand, suggesting that they are in fact a Gondwanan group. Their occurrence in places like Lord Howe and Vanuatu indicates that, although essentially terrestrial, they must have been able to float long distances in ocean waters, enabling them to colonise remote islands. The family is very old, possibly branching off the rest of the turtle family tree before the split between the two modern turtle lineages, the cryptodires (which pull their head straight back into the shell) and pleurodires (which fold their neck sideways under the shell). The oldest known undoubted meiolaniids in Australia come from the Eocene Rundle Shale in Queensland. The Wyandotte Giant Horned Turtle is shown here with a Bridled Nail-tail Wallaby Onychogalea fraenata, an endangered small grazing kangaroo that survives today in Queensland in small, isolated populations around Emerald. These meiolaniid bones, along with those of other living and extinct species, have been found eroding out of Pleistocene sediments over a 10 km stretch along Wyandotte Creek. Other species found here include the giant monitor lizard Megalania Varanus priscus, a madtsoiid snake (Wonambi sp.), the bizarre Marsupial Tapir Palorchestes azael, Diprotodon D. optatum and the Giant Wombat Phascolonus gigas, as well as extant species of ducks, geese, bandicoots, antechinuses, rodents and elapid snakes.

AGE

Late Pleistocene, about 43 000 years ago.

LOCALITY

Clays, sands and gravels exposed along Wyandotte Creek, northern Queensland.



ENVIRONMENT

During the late Pleistocene, this area probably would have been incised by braided streams surrounded by woodlands and grasslands.

REFERENCES

133, 136, 242, 305, 312, 371

Pureni, Papua New Guinea



VERY FEW OF AUSTRALIA'S DIPROTODONTID

marsupials were hippo- or rhino-like other than some of the largest kinds, like species of Zugomaturus and Diprotodon. As more skeletal remains of the smaller kinds turn up, there has been growing awareness that some had significantly different lifestyles. This may have been the case, for example, for Hulitherium tomasettii, a browsing zygomaturine diprotodontid from the late Pleistocene of New Guinea. Although what is known of its skull suggests some odd features such as the arched roof of the mouth, its femur is a stand-out oddity. The ball that articulates with the pelvis projects up above the shaft rather than sticking out to the side, suggesting that it had highly unusual, very extensive mobility. Its humerus similarly suggests unusually high mobility for the arm. It is possible that this rainforest browser may have been partially arboreal, like Himalayan Sun Bears or even Pandas. Despite being much larger, with an estimated weight of 75-200 kg and a body length of perhaps 2 m, in terms of lifestyle H. tomasetti may have been similar to the arboreal Miocene species of Nimbadon and Silvabestius from Riversleigh. Because its closest relationships appear to be with the equally distinctive Pleistocene New Guinean zygomaturine Maokopia ronaldi, it has been suggested that both are the products of a distinctive regional radiation that followed the arrival of the first diprotodontids into New Guinea. These first, perhaps late Miocene or early Pliocene immigrants were perhaps similar to species of Plaisiodon or Zygomaturus. The Ribbontailed Astrapia Astrapia mayeri, whose tail feathers are relatively longer than those of any other bird in the world, is a modern bird of paradise restricted to subalpine forests in the central highlands. Although not known from the Pureni fossil deposit that contains *H. tomasetti*, it may well have danced in the same tree branches that strained under the weight of this now extinct, possibly semi-arboreal marsupial.

AGE

Pleistocene, about 38 600 years old.

LOCALITY

Pureni, Southern Highlands, Papua New Guinea.



ENVIRONMENT

The Pureni deposit spans a series of habitat changes in this area from open water surrounded by forest to a grassy swamp and ultimately a cool mossy upland bog forest. Throughout the interval of deposition, the temperature was colder than the area is at present.

REFERENCES 115, 122, 223

Riversleigh, Scene 12, Queensland



TERRACE SITE IS A PLEISTOCENE RIVER DEPOSIT

that was found exposed in the banks adjacent to the modern Gregory River that runs through Riversleigh Station in north-western Queensland. The fossil deposit itself is an unconsolidated bed of gravel that was being transported by an ancestral anabranch of the Gregory. A wide range of animals that lived in the river as well as those in the woodlands along its banks ended up contributing bones to this deposit. Lumps of charcoal near the base of this deposit were used to obtain a radiocarbon date of 23 900 years ago, with a 'standard error' that meant there was a 95% probability that the actual date was between 21 200 and 28 000 years before the present. This is important, because this would be one of the youngest dates in Australia for *Diprotodon optatum* and *Palorchestes azael*. In this reconstruction, *P. azael* is shown in the water, possibly eating nutritious waterlily tubers that it has clawed up out of the river bed. But what it actually ate, and how it used its enormous, clawed forelimbs, remain controversial. The snout of a powerful 5 m crocodile *Paludirex gracilis* was also recovered from this same deposit. Agile Wallabies Macropus agilis were then and remain today one of the most common mammals found along the banks of the Gregory River. Elseua lavarackorum is a most curious member of this community. When first found, the large shells were clearly from a turtle that had not previously been scientifically described. It was named by Arthur White and Mike Archer after Jim and Sue Lavarack, the Riversleigh volunteers who found and spent many long days in the quarry carefully excavating the large carapace of this turtle. A short while later, Arthur was swimming in the nearby Lawn Hill Creek when he bumped into a strange turtle. When he caught it, to his amazement it appeared to be similar to the one they had just named on the basis of the Terrace Site specimen. Once presumed extinct, this 'Lazarus turtle' appeared to have miraculously come back to life! However, more recent research has demonstrated that the living form, which is now known as the Gulf Snapping Turtle, is in fact another new species, Elseya oneiros - making the point that we still do not know enough about Australia's living animals! Ironically, a second lesspreserved fossil turtle found in the Terrace Site deposit turns out to be the same or a very close relative of *E. oneiros*, but it wasn't given a formal name when discovered. In the background of the painting, people are shown foraging along the bank near the largest marsupial that ever lived, Diprotodon D. optatum. There is no hard evidence that these marsupials were hunted. let alone driven to extinction, by humans. What evidence there is suggests that humans and these giant marsupials overlapped for a long time before climate change triggered the extinction of these huge herbivores. Also possibly present at this time was another extinct giant of the Pleistocene, the flightless dromornithid bird Genyornis newtoni. While it may have been here, specimens were said to have been seen but not found in immediately adjacent similar riverine deposits - a challenge for future work at this important site.

AGE

Late Pleistocene, between about 28 000 and 21 000 years ago.

LOCALITY

Terrace Site, Gregory River deposits, Riversleigh World Heritage Area, north-west Queensland.



ENVIRONMENT

The Pleistocene was marked by rapid and severe changes in climate and environmental conditions. Like the rest of the world, Australia experienced extreme climatic conditions as the Arctic and Antarctic polar ice caps repeatedly grew and retreated, resulting in a constantly changing pattern of forests, grasslands and deserts because of consequent fluctuations in temperature and rainfall. Despite cyclical fluctuations, the overall trend throughout the Pleistocene was towards increased dryness.

REFERENCES 51, 91, 311, 418

Kelangurr Cave, Irian Jaya



WHILE THE LAST OF THE LATE CENOZOIC

diprotodontids in Australia such as Diprotodon Diprotodon optatum were 2-3 t in weight, others in New Guinea were very different. At about 100 kg, Maokopia ronaldi was a relatively small zygomaturine diprotodontid. Although it is known only from cranial remains, these suggest it was most closely related to the slightly larger Hulitherium tomasettii. Both of these late surviving New Guinean members of this family may have been semi-arboreal, like Asian Sun Bears. Alternatively, it has been suggested that they may have been more Panda-like in their behaviour as well as appearance. Until more of the skeletons of these marsupials are known, we can only begin to guess at their lifestyle, although in cranial size and shape they were clearly unlike other late Cenozoic diprotodontids. Their late survival, in spite of probable overlap with humans for at least 40 000 years, suggests their ultimate extinction may have had complex causes. Other animals recovered from this deposit include small birds, marsupials, rodents and bats, some possibly brought into the cave as prey by carnivorous owls. The only other large species found was the extinct wallaby Protemnodon hopei. This browsing kangaroo may have been the last surviving member of the genus Protemnodon, given that all others were probably extinct on the Australian mainland by 35 000 years ago. The Snow Mountains Robin Petroica archboldi shown here, which is endemic to mountains in Papua and Indonesia. occurs from about 3850-4150 m above sea level, well above the current snowline. Although not yet known to be present in the Kelangurr Cave deposit, it is possible that it co-occurred with *M*. ronaldi in the same type of high-altitude grasslands and scrub where it occurs today on Mounts Jaya and Trikora in the Snow Mountains.

AGE

Late Pleistocene, estimated to be 25 000-20 000 years ago.

LOCALITY

Kelangurr Cave in the Baliem River catchment near Kwiyawagi, central montane Irian Jaya, Indonesia.



ENVIRONMENT

The fauna suggests that these animals lived in an alpine tussock grassland and scrub habitat. Today the area around the cave is tall upper montane forest. Hence, this cave predates the loss of grasslands from this area, a transition almost certainly driven by climate change.

REFERENCES 116, 223, 236, 271

Nombe Rock Shelter, Papua New Guinea



EXCAVATIONS OF NOMBE ROCK SHELTER IN NEW

Guinea since 1964 have revealed a complex, often human-disturbed late Pleistocene record. However, the general pattern of what happened is reasonably clear. During the end of the last glacial maximum, around 25 000 years ago, there were now extinct megafaunal species such as *Protemnodon tumbuna* present in the Highlands. Most of them disappeared around 14 000 years ago, the time when glaciers began to retreat, and the highland forests gave way to alpine grasslands. Although humans were present probably as early as 60 000 years ago, there is no evidence that they hunted the extinct megafaunal species, which probably declined in response to late Pleistocene climate change in the Highlands. Nevertheless, the extinct megafaunal kangaroos at Nombe survived perhaps 15 000 years longer than their counterparts in Australia. Species of *Protemnodon* at Nombe (far right) appear not to be closely related to contemporary Australian species of this genus; rather, they were descendants of immigrants that migrated from Australia to New Guinea during the Pliocene. The Thylacine *Thylacinus cynocephalus* was present in the Nombe deposits for the entire history from more than 24 000 years ago to at least 5000 years ago, indicating that Thylacines disappeared from New Guinea about the same time they did on the Australian mainland. These disappearances may have been caused by the introduction of dogs about the same time to both areas. The living White-bibbed Fruit Dove *Ptilinopus rivoli* inhabits, among other environments in New Guinea, montane forests potentially of the kind that existed around Nombe 25 000 years ago.

AGE

Late Pleistocene, about 25 000-5000 years ago.

LOCALITY

Nombe Rock Shelter on the eastern slopes of the Highland Erimbari limestone escarpment, Simbu Province, New Guinea.



ENVIRONMENT

In late Pleistocene times, before it was naturally eroded to become a long shelter with a small cave at the rear, Nombe was a large cave with a river flowing through it. When the extinct species were alive, Nombe was close to the treeline. Smaller animals in the deposit suggest Thylacines and/ or humans brought in prey from adjacent grasslands as well as forests, but the environment around the cave itself when the extinct species were present may have been alpine rainforest.

REFERENCES 121, 223, 264, 375

South Island moa, New Zealand PLEISTOCENE/HOLOCENE



OF THE SIX GENERA AND NINE SPECIES OF

extinct moa, the most bizarre-looking has to be the Heavy-footed Moa *Pachyornis elephantopus* (shown here with two young). Just a little over 1 m high at its back and about 75 cm wide, reaching over 200 kg in weight and with its tummy nearly dragging on the ground, this moa was the most extreme of all graviportal birds known. Its name, given by Sir Richard Owen, reflects the pachydermal proportions of its tarsus. It was restricted to the lowland shrublands in the South Island and was a major component of Canterbury and eastern Otago faunas during the Holocene. It was absent in the western regions except during glacial intervals of the Pleistocene when shrublands became available in these areas. It is one of three species in the genus. The Crested Moa P. australis lived in the shrublands of the subalpine zone and the smaller Mappin's Moa P. geranoides lived in the North Island. The Heavy-footed Moa had a very stout and short bill that effectively acted like secateurs, enabling it to eat extremely fibrous plants such as flax Phormium tenax, leaves of which have been found in preserved gizzards associated with its skeletons. In the subcanopy is another of New Zealand's extinct endemic birds, the South Island Piopio Turnagra capensis. This is actually an oriole, long separated from its relatives in Australia. It had a sister species in the North Island. Both are among the ancient passerine groups of New Zealand, along with the wattle birds (Huia, kokako and saddlebacks), New Zealand

wrens and *Mohoua* species. Piopio species were omnivores, gleaning insects from leaves, eating invertebrates on the forest floor and gobbling berries when available.

AGE

Late Pleistocene to Holocene, about 100 000-750 years ago.

LOCALITY

South Island, New Zealand.



ENVIRONMENT

Lowland eastern forest with grassy glades. Forest species included giant red beech trees *Nothofagus fusca* and flax plants *P. tenax* which had strap-like leaves. A few mosses covered the forest floor. Seasonal droughts were common.

REFERENCES

322, 452, 471

South Island adzebill, New Zealand PLEISTOCENE/HOLOCENE



ONE OF THE MOST BIZARRE EXTINCT BIRDS THAT

once inhabited the New Zealand landscape was the adzebill, with a species in the North and South Islands. Adzebills, classified in their own family Aptornithidae, were large birds, standing about 75 cm tall and weighing in at about 15 kg, with a fearsomely large bill. These birds are distantly related to rails and are in the order Gruiformes. Surprisingly, DNA evidence has conclusively shown that their nearest relatives are the tiny sarothrurid rails now restricted to Africa and Madagascar. Like many gruiforms, these birds were probably omnivores although isotopic analyses of their bones suggest that they preved on vertebrates. New Zealand had lots of frogs and lizards as well as birds that were potential prey. In the scene portrayed here, the South Island adzebill Aptornis defossor has captured a large gecko Hoplodactylus duvaucelii which, growing to around 30 cm, is the largest lizard in New Zealand. It still survives in a few protected areas, mainly on islands that are rodent-free. Adzebills were entirely flightless: their wings were reduced to tiny vestigial structures, relatively little larger than the wings of kiwis. They lived in New Zealand for a long time. An ancestral form is known from the early Miocene fossil deposits near St Bathans in Otago, New Zealand. During the Holocene, the South Island adzebill was restricted to vegetation mosaics of the eastern part of the South Island. During the glacial periods, its range was far larger, including areas in the then deforested western regions. However, not long after these birds encountered humans around 750 years ago, they were extinct. This loss meant that Western naturalists never had a chance to study one of the most enigmatic components of New Zealand's avifauna.

AGE

Late Pleistocene to late Holocene, about 100 000-750 years ago.

LOCALITY

Foothills of Canterbury Plains, Geraldine, South Canterbury, New Zealand.



ENVIRONMENT

In a small forest grove on one of the low limestone hills, giant matai (*Prumnopitys taxifolia*) trees grew over 35 m tall, shading the mosses that covered the forest floor. Not far away, through a bank of shrubs, there were more open habitats dissected by gravel streams with grass-covered margins.

REFERENCES

56, 283, 384, 411, 452

Volivoli Cave, Fiji Pleistocene/holocene



THE QUIET OF A MORNING IN THE BROADLEAF

forests on the hillside are suddenly interrupted by an urgent rustle of the forest litter. A rush of movement heralds the charge out of the bushes of a 3 m crocodilian Volia athollandersoni, and with a squawk the unsuspecting Noble Megapode Megavitiornis altirostris tries to flee. Volia athollandersoni, a mekosuchine crocodile, was named after the place where this scenario played out (Volivoli Cave) and the eminent archaeologist Professor Atholl Anderson. It was undoubtedly the top predator in this land. Like other mekosuchine crocodiles, this one appears to have been more terrestrial in its lifestyle, straying far from the watery habitats favoured by most living crocodiles. It was trapped in Volivoli Cave which is up a hill, several hundred metres from the closest wetland below. It had diverse animals to prey on, with large frogs, iguanas, turtles, snakes and flightless birds including a dodo-sized pigeon and megapodes. The Noble Megapode was 75 cm tall and weighed perhaps 15 kg. It, and a giant flightless pigeon (a species of Natunaornis), were the equal largest birds in Fiji. Like its relative Sylviornis neocaledoniae in New Caledonia, this giant flightless megapode had a huge deep bill and a large head. It has been recorded in the earliest human sites in Fiji, dated at about 3000 years old, It may well have been an early casualty of human arrival in this archipelago.

AGE

Late Pleistocene-Holocene, about 20 000-3000 years ago.

LOCALITY

Volivoli Cave, Sigatoka River, Vitilevu, Fiji.



ENVIRONMENT

The broad Sigatoka River winds down the valley towards the south, draining a large part of Vitilevu's seasonally dry western region. The hills flanking the western side, a few kilometres in from the sea, are limestone and clothed in a diverse broadleaf forest. At the back of a rock shelter facing east, a dark pit drops into a void below. Here multiple animals met their death, having ventured one step too far back while sunbaking or seeking shelter from the monsoonal torrential rains. Never mind the reason, that pit, as part of the Volivoli Cave, became a rich record of intriguing animals now lost from the island of Fiji.

REFERENCES

185, 261, 443, 444, 447

Tongoleleka, Tonga HOLOCENE



THE EXTINCT IGUANA BRACHYLOPHUS GIBBONSI

sunbathes in a forest glade, while two large and brightly coloured pigeons stay in the shadows. This iguana, reaching 1.2 m long, was the largest species in its genus and the Tongan representative of a genus otherwise found then and now only in Fiji. They are assumed to have colonised these islands following long-distance dispersal from the Americas, far to the east. The pigeon, a species of *Caloenas* similar in size to the extinct *C. canacorum* of New Caledonia, was only one of many species of pigeons in the Tongan forests, but while it was not the largest - there were two larger species (Ducula shutleri and Tongoenas burleyi) - it probably had the most spectacular plumage. The sole surviving member of this genus is the Nicobar Pigeon Caloenas nicobarica found far to the west in a region stretching from the Solomons to Nicobar Islands. Extinction of large taxa like these has been a common outcome following human arrival on many of the Pacific islands. However, inadvertent introduction at the same time of the Pacific Rat Rattus exulans, which is known to predate nesting birds and eggs, into this and many other Pacific
islands may have been a significant cause of some of the extinctions that followed. Current efforts to eradicate this introduced rat from many of these islands, including those of Tonga, are based on research which shows they continue to constitute a major threat to existing birds on these islands. In the Ha'apai Group, where the birds depicted here once lived, Lapita voyagers from Fiji arrived about 2800 years ago, probably with Pacific Rats aboard. Whenever these large birds and several other extinct birds were eaten by the Lapita people, the remains ended up in the middens of the Tongoleleka Site on Lifika. Over half of the original bird species in Tonga and many other Pacific islands did not survive very long after the arrival of humans and Pacific Rats, but fortunately these enduring Polynesian middens provide a window back into time to document the species that were lost.

AGE

Holocene, about 10 000-2800 years ago.

LOCALITY

Lifika, Ha'apai Group, Tonga.



ENVIRONMENT

On the western side of a small island fringed in coconut palms, white sandy beaches are protected from the fury of the ocean by an enclosing coral reef. Passing under the coconut trees and around the pandanus groves, one quickly enters the broadleaf forest where regular rain ensures the ferns never dry out too much.

REFERENCES

309, 310, 365, 366, 367, 446

Chatham Islands, New Zealand



THE QUIET WATERS PROVIDED ABUNDANT FOOD

for a wide diversity of birds. Seals, such as the New Zealand Sea Lion *Phocarctos hookeri* and the Fur Seal *Arctocephalus forsteri* (centre right), also visited this lagoon, which is periodically open to the sea, to rest from stormy conditions at sea. Swimming on the lagoon, huge flocks of Black Swans *Cygnus atratus* browsed the vast beds of macrophytes under its surface. The swan, also found on mainland New Zealand 800 km to the west, was hunted to extinction by the first visitors before being reintroduced in the 19th century by Europeans to areas of mainland New Zealand, from whence it recolonised the Chatham Islands. It is thus a rare example of a native species that has benefited from the pastoralisation of New Zealand. Along with the swans lived many species of ducks. Perhaps the first duck to reach the Chathams was the Chatham Island Duck, formerly regarded as a distinct taxon (*Pachyanas chathamica*) on account of its large size, but now regarded to be an overgrown teal *Anas chathamica*. This larger size of an island form runs counter to the trend more often seen in insular evolution of ducks, where the island forms are smaller. Along the shore, the Chatham Island Coot *Fulica chathamensis* searches for invertebrates. Nearby, an inquisitive parrot - the recently described Chatham Island Kaka *Nestor chathamensis* - cheekily investigates a resting seal. The kaka, coot and duck are all closely related to living forms on mainland New Zealand, their differences resulting from only 1-2 million years of evolution in isolation because the islands themselves are no older than this.

AGE

Holocene, about 10 000-600 years ago.

LOCALITY

Te Whanga Lagoon, Chatham Island, New Zealand.



ENVIRONMENT

This was a large (about 15 × 5 km) shallow lagoon occupying most of the centre of Chatham Island. Regularly breached by the sea, the waters were usually somewhat salty. Large beds of sea grass grew in its shallows. To the west and south, low peat-cloaked hills surrounded the lagoon. Low forests covered the hills to the north and south of this area.

REFERENCES

251, 252, 254

North Island, Scene 1, New Zealand



PRIOR TO THE ARRIVAL OF HUMANS ABOUT

750 years ago, New Zealand was a land of birds. In the North Island, dominating this avifauna in all senses of the word were several species of moa (Dinornithiformes). Largest of all was the North Island Giant Moa Dinornis novaezealandiae (centre left), with the larger females able to reach 3 m high into the trees to browse. These giants may have weighed up to 200 kg. They lived in all habitats from the coastal dunes to the deep forests, but other smaller species, such as Mantell's or Mappin's Moa Pachyornis geranoides (background near waterfall) and Coastal Moa Euryapteryx curtus curtus (far right), were restricted to mosaics of grassland and shrubland. The dense forest was the home of the Little Bush Moa Anomalopteryx didiformis, where it browsed alongside small foraging rails such as the Snipe Rail Capellirallus

karamu (lower far left), seen here at the water's edge, while the Huia Heteralocha acutirostris gave forth melodic calls the branch overhead. Huia are famous for the fact that the sexes have differentshaped bills - that of the female is longer and more curved - and for their white-tipped tail feathers that are highly valued by Māori and Europeans alike. Along the forest margin, two large North Island Geese Cnemiornis gracilis with chicks grazed on grasses and other herbs. It was related to the Cape Barren Goose of Australia, but its lineage has been in New Zealand since at least the early Miocene about 19-16 million years ago. Many waterfowl occurred on pools developed in larger streams. Here two Scarlett's Duck Malacorhynchus scarletti alight on the pool. These are large relatives of the unique Australian Pink-eared Duck M. membranaceus and were specialist dabbling

ducks. The odd duck shown with a large pouch under its bill is the New Zealand Musk Duck *Biziura delautouri*, another endemic New Zealand species with a living relative in Australia. All of the species shown here went extinct soon after humans arrived. Factors involved in these losses probably included forest clearance and predation by both the people and the Pacific Rat *Rattus exulans* that the first arriving humans introduced to these islands. The Huia survived till European times, but European rats, stoats and hunting for its tail feathers soon led to its demise as well.

AGE

Holocene, about 10 000-600 years ago.

LOCALITY

North Island, New Zealand.



ENVIRONMENT

During the Holocene, the North Island was mostly clothed in ever-wet dense podocarphardwood forests with a dense interlocking canopy that shielded abundant mosses and ferns on the forest floor. Only on some dune areas, or along river margins and in areas recently deforested by volcanic activity, did more open habitats exist for those species that preferred shrublands and grasslands.

REFERENCES

384, 452, 456

North Island, Scene 2, New Zealand



MANY NOW-EXTINCT FLIGHTLESS BIRDS WERE

among the most conspicuous components in the environments of the North Island of New Zealand. They included one of the largest birds ever to exist, the North Island Giant Moa Dinornis novaezealandiae and some of the smallest, such as diminutive wrens. Here, the sparrow-sized North Island Stout-legged Wren Pachyplichas jagmi is dwarfed by a passing moa. The stout-legged wrens - for there is a South Island species as well, along with the Long-billed Wren Dendroscansor decurvirostris and Lyall's Wren Traversia lyalli - are famous as four of the only six known flightless passerines. Passerines, or songbirds, dominate the world's avifauna, comprising some 5300 of the approximately 10 000 known bird species, yet only on the Canary Islands in the Atlantic, where there are two species of flightless greenfinches, are there any other flightless ones. But the New Zealand wrens are famous for something else in addition to their weak or absent flying abilities - this group of five genera and seven species, members of the family Acanthisittidae, constitutes the sister group to all other songbirds on Earth. Today, New Zealand's smallest bird, the Rifleman Acanthisitta chloris, and the Rock Wren Xenicus gilviventris remain as the only living members of this family which is important for our understanding about the origins of all other passerines. It is possible that these tiny weak-flying birds have existed on Zealandia ever since that continental fragment separated from Gondwana 80-60 million years ago. However, to date the oldest known acanthisittid wren Kuiornis indicator comes from the 19-16 million years old St Bathans fauna from central Otago, New Zealand, and the oldestknown passeriform bird comes from the 55 million years old Tingamarra Local Fauna from Murgon, Queensland (p. 96).

AGE

Late Pleistocene to Holocene, about 100 000-750 years ago.

LOCALITY

North Island, New Zealand.



ENVIRONMENT

In the closed canopy forests of the North Island, where sunlight never reached the forest floor, mosses and litter covered the ground and provided habitat for abundant invertebrates. Lacking rodents before humans arrived, New Zealand evolved faunas rich in large invertebrates and a multitude of ground-dwelling flightless birds to prey on them.

REFERENCES 178, 250, 451

New Caledonia's giant megapode



ONE OF THE MOST CONSPICUOUS ANIMALS IN

the prehistoric New Caledonian landscape was undoubtedly Sylviornis neocaledoniae, a giant megapode. Megapodes are unique in the avian world for being obligate ectothermal incubators that is, they use external heat sources to incubate their eggs. Some dig holes and lay their eggs in warm soils in active volcanic landscapes, but most construct large mounds of soil and decomposing leaf litter in which the eggs are laid. The birds monitor and control the temperature in the mounds by variously increasing and decreasing the thickness of covering soil. They literally dig and scratch all day. This New Caledonian megapode was the largest of the group. It was about 1 m tall and probably weighed around 20 kg. It was very different from other megapodes and for this reason has been placed in its own family, the Sylviornithidae. It had markedly reduced wings and certainly could not fly. Moreover, its skull and especially its beak had evolved a very unmegapode-like form. The bill was deep with a large bony casque that extended back over the skull. This amazing structure is not, however, novel. A distantly related galliform, the Helmeted Curassow Pauxi pauxi of South America, sports a similar embellishment. As in this Curassow, the helmet was probably coloured and used for behavioural displays. Unfortunately, S. neocaledoniae disappeared shortly after humans arrived on New Caledonia about 3000 years ago, without leaving any clues about its natural history including what it probably ate.

AGE

Holocene, about 10 000-2800 years ago.

LOCALITY

Nepouri Peninsula, Grande Terre, New Caledonia.



ENVIRONMENT

When these species were alive, there were, as there are today, rainforests along the eastern side and dry sclerophyll forests on the western side of the peninsula. These lowland forests provided abundant litter and soil to scratch into giant mounds, and invertebrates as prey.

REFERENCES 32, 265, 304

Canterbury Plains, New Zealand



ON THE LOWLANDS OF THE CANTERBURY PLAINS,

a diverse range of habitats provided homes to the richest avifauna existing in New Zealand during the Holocene. Portrayed here, greeting each other, are a pair of the heaviest and tallest birds ever to exist in New Zealand, the South Island Giant Moa Dinornis robustus. Moas belonging to the genus Dinornis had the greatest degree of sexual size dimorphism known in birds. The females were more than twice the size of the males. Adding further to the variation in this species, we now know that their size considerably varied across the landscape. Only 100 km inland, in the hill country, mean individual size was markedly smaller and, going up-slope into the montane regions, size was further reduced such that in the high beech forests the larger female was the same size as the

smaller males of lowland Canterbury. Size variation of this kind originally led to overestimation of the number of species. This error was resolved only with the advent in recent years of ancient DNA studies. Other moas that co-existed with the species of *Dinornis* in the Canterbury forests included the specialist lowland Eastern Moa Emeus crassus and the South Island morph of the Coastal Moa Euryapteryx curtus gravis (two individuals in background). The latter was considerably larger than its North Island relative and weighed in at around 150 kg. All of these extinct moa feature prominently in Māori middens that were accumulated in the 100 years after humans first arrived in New Zealand 750 years ago, accompanied by Pacific Rats Rattus exulans. In the canopy, the Orange-wattled Crow or South Island

Kokako *Callaeas cinerea* fed on fruit and leaves. Soaring above it over the forest gaps was a giant relative of the Swamp Harrier, the extinct New Zealand Eyles' Harrier *Circus teauteensis*, on the lookout for a careless kokako or fat pigeon.

AGE

Holocene, about 10 000-750 years ago.

LOCALITY

Canterbury Plains, South Island, New Zealand.



ENVIRONMENT

In the lowlands of the Canterbury Plains, over thousands of years meandering rivers had created a mosaic of swamp forests, shrublands and grasslands. Tall podocarp trees such as Matai *Prumnopitys taxifolia* provided abundant seasonal resources of fruit and towered over understorey trees. Notable in the shrub layer were large numbers of spiny divaricating plants and other forms adapted to resist the browse of moas. These included the Lancewood *Pseudopanex crassifolius*, which had tough elongate juvenile leaves as shown near one of the moas.

REFERENCES 150, 179, 442

New Zealand giant eagle



A LARGE FEMALE HAAST'S EAGLE HIERAAETUS

moorei, formerly Harpagornis moorei, attacks a Māori man. This eagle likely was resting on a high vantage spot, either on a nearby crag or the top of a large tree, when it saw the man. Perhaps hungry in the absence of its once favoured moa prey, it risked an attack on this novel animal, possibly not understanding the risk it was taking in doing so. Reaching 13 kg in weight with a wingspan of about 3 m, this eagle was the largest in the world. It was restricted to the South Island of New Zealand where forest margins and more open habitat facilitated its hunting. There is abundant evidence of it preying on moa, with bones of Eastern Moa, Coastal Moa and even Giant Moa showing distinctive damage. Typically, this eagle landed on the back of the moa, one 30 cm wide set of claws straddling the pelvic region and the other further up the moa's trunk. The giant claws of the eagle's hind toe were capable of slicing through the feathers and skin, 5-10 cm of muscle, then the 5 mm thick bony plates of the pelvis, leaving great gashes in this bone upwards of 10 cm long. It is probable that the kidneys were then ripped apart, which would have triggered the moas to die soon after of shock . Such is the story recorded in the many moa pelvises that have been found in swamp deposits. Humans - of much smaller stature than some moas and less protected by a pelage - would certainly have been potential prey, given that the much smaller golden eagles of Eurasia can and do kill people. Haast's Eagle had a smaller ancestor, the Little Eagle Hieraaetus morphnoides of Australia, which is only a 10th the size its New Zealand descendant. Surprisingly, this ancestor appears to have colonised New Zealand perhaps only a million years ago, if the DNA evidence is to be believed, after which it must have rapidly increased in body size. Support for this origin hypothesis may well be the relatively small size of the brain of Haast's Eagle. While the occasional Māori may have met their end through struggles with this huge predator, it soon joined the moas on the long register of extinctions correlated with the arrival of Māori in New Zealand. Bones of this giant eagle are commonly found in the middens of the first Māori villages.

AGE

About 700 years ago.

LOCALITY

South Island, New Zealand.



ENVIRONMENT

The scenario pictured here might have taken place in one of the alpine valleys of the South Island or along the margins of one of the great braided rivers near the forest edge.

REFERENCES

65, 67, 152, 350, 452

Pindai Cave, New Caledonia



IN AN ANCIENT FOREST RAUCOUS WITH LIFE, A

crystal-clear stream trickles down a valley. Here, a small semi-terrestrial deep-headed crocodile *Mekosuchus inexpectatus* is cracking the shell of a *Placostylus duplex* snail it found on rocks along the edge of the stream. A giant terrestrial meiolaniid turtle waits patiently to come down to drink, while nearby a large flightless swamphen *Porphyrio kukwiedei* nervously watches the crocodile's every move. As its name records, it was a great surprise to scientists when they discovered this strange fossil crocodile on the island of Grande Terre, New Caledonia. It is now known to have been one of the last surviving members of the distinct subfamily Mekosuchinae, whose members were also known from Australia, Vanuatu, Fiji and probably New Zealand. The large horned meiolaniid turtle shares a similar distribution pattern to species of *Mekosuchus* and likewise is entirely extinct. The swamphen is a rail of the family Rallidae, a group notorious for their ability to disperse widely across water gaps, but also paradoxically for their tendency to evolve into subsequently flightless species on far-flung islands. This one belonged to the purple swamphen lineage, a group represented by flying forms that occur in lands stretching from Eastern Europe to Australia and far out into the Pacific. On New Caledonia they became huge, approaching the size of the more famous and extant New Zealand relative the Takahe *P. hochstetteri*. They thrived on Nepouri Peninsula, a small area of limestone that houses the Pindai Caves, some of which made excellent pitfall traps. All these New Caledonian animals, along with another 45 species of birds (20 of which are now extinct), had their bones preserved in these caves. The turtles, crocodiles and this swamphen became extinct shortly after humans arrived about 2800 years ago.

AGE

Holocene, about 6000-2800 years ago.

LOCALITY

Nepouri Peninsula, Grande Terre, New Caledonia.



ENVIRONMENT

Today and probably when these fossils were accumulated, the western coast of Grande Terre supports a dry sclerophyll forest on the lowlands near the coast. But around Pindai Caves on Nepouri Peninsula, the roots of broadleaved tropical trees penetrate the porous limestone, enabling this lusher vegetation to flourish.

REFERENCES

7, 30, 31, 32

South Island goose, New Zealand



ONE OF THE MOST SPECTACULAR AVIAN

inhabitants to be met by Māori upon their arrival in New Zealand were species of geese in the genus Cnemiornis. The largest was C. calcitrans from the South Island, weighing in at about 15 kg and standing over 1 m tall. These geese lived only in lowland open habitats. They were absent from closed forest environments. During the Holocene. C. calcitrans was restricted to eastern parts of the South Island where it grazed upon grasses and herbs, probably in the same way its nearest relative, the Cape Barren Goose Cereopsis novaehollandiae of Australia does today. This Australian goose creates close-cropped swards of the plants on which it feeds, and it is probable that Cnemiornis, with its squared-off bill, would have created similar mown lawns in their favoured breeding areas. The C. calcitrans lineage has been a resilient one in New Zealand, with earlier members whose bones have been found in the St Bathans fossil deposits, suggesting that it has been around since at least the early Miocene. Following the early Miocene, species of Cnemiornis became greatly modified from their Cape Barren Goose-like ancestor, including complete loss of their ability to fly. This trait may well have contributed to the downfall of the species after the arrival of Māori, within perhaps 100 years. They shared the open habitats with another endemic species, the Black Stilt Himantopus novaezelandiae. The latter breeds only in the braided riverbeds of the South Island, secreting its nest and eggs among the river stones. Although it still survives, it is highly endangered because of nest predation by introduced mammals such as the omnivorous Pacific Rat Rattus exulans that arrived with the Māori. loss of habitat and competition from the more recent colonist the Pied Stilt H. leucocephalus.

AGE

Late Holocene, about 1000 years ago.

LOCALITY

Canterbury Plains, South Island, New Zealand.



ENVIRONMENT

This was a scene typical of the edge of a river in Canterbury, where gravel-lined flood channels wound between tussock grasses. The open gravel beds provided nesting habitat for stilts and other riverine birds, such as dotterels, while the tussocks and intervening herbs provided browse for grazing geese.

REFERENCES

282, 452, 453

Acknowledgements

Mike Archer. On behalf of Sue and myself, we thank many professional colleagues who have been instrumental in helping us to reveal the fascinating deep-time history of Australia and its surrounding lands. I am very grateful in particular to my UNSW research colleagues Suzanne Hand, Karen Black, Henk Godthelp, Phil Creaser, Troy Myers, Anna Gillespie, Georgina Hickey, Stephan Williams, Ian Graham and Mike Augee. Our research at Riversleigh and Murgon has been facilitated by the Elders of the Waanyi Nation (the traditional owners of Riversleigh), Riversleigh/Lawn Hill Station, the Australian Research Council, Queensland, and Australian Museums. Oueensland Parks and Wildlife Service, Environment Australia, IUCN World Heritage Committee, UNSW Sydney, Riversleigh World Heritage Management Committee, Riversleigh Interpretive Centre, Arthur and Karen White and Riversleigh Society Inc., National Geographic Society, Mount Isa Mines, Adel's Grove, Phil Creaser's CREATE Fund, Ken and Margaret Pettit, Doug and Anne Jeanes, Elaine Clarke, Alan Bartholomai, Martin Dickson, Tim Cody, Margaret Beavis, Peter Bridge, Dick Smith, the Australian Geographic Society, Gary Johnston, Tony McGrady, Ron McCullough, the family of Alan Rackham, Michael Wentworth, John Prince, James Porter, Chris Braithwaite, Chris McInerny, Leo and Glenda Geraghty and so many others. Thanks also to my skilled co-authors on this project, Peter Schouten, Suzanne Hand, Trevor Worthy, John Long, as well as the highly professional team at CSIRO Publishing.

Suzanne Hand. On behalf of Mike and myself, a huge thankyou to the vast and growing army of extraordinary volunteers, exceptional students and brilliant researchers from across the globe who, since 1978, have given years of their lives to help interpret the fossil record at Riversleigh and Murgon. Colleagues who helped bring our research at Riversleigh to the world's attention include Sir David Attenborough, Bob Beale, Quentin Jones, Geoff Burchfield, Louise Egerton, Ross Arnett, Dorothy Dunphy, Alan Pryke, Robyn Williams, Nicky Phillips, Tony Walters, Leigh Dayton and James Woodford, to name just a few. I would also like to thank my co-authors Mike Archer, John Long and Trevor Worthy for the wonderful opportunities they have given me over many years, and to Peter Schouten for breathing new life into a hoard of our favourite fossils.

Trevor Worthy. I thank many people whose inspiration helped to reveal the fascinating world that this book examines. Principle among these were Sir Charles Fleming, John Yaldwyn, Storrs Olson, Walter Boles and David Steadman. I am grateful to numerous people that I have collaborated with, especially from New Zealand – J.A. (Sandy) Bartle, Richard Holdaway, Vanesa De Pietri, Paul Scofield, Alan Tennyson; Australia – Mike Archer, Suzanne Hand, and Aaron Camens; and the Pacific – Atholl Anderson, Christophe Sand. I thank all those landowners who enabled the exploration of fossil deposits on their land, especially Ann and Euan Johnstone, St Bathans, NZ. I also wish to thank the museums for the vital role they have in preserving specimens that underpin our research. In addition to those mentioned by John Long and Mike Archer, the Auckland Museum, Waitomo Caves Museum, the Museum of New Zealand, Canterbury Museum and Otago Museum maintain key collections that hold the fossils of the prehistoric animals herein portrayed. Importantly, I am extremely grateful to my wife Jenny Worthy who has actively indulged in and joined my passion for palaeontology to help reveal the amazing world of fossils.

John Long. I acknowledge the Gooniyandi people of the Fitzroy Crossing area on whose land we have worked over the past 38 years, and the support for research and access to collections from the Western Australian Museum, Museum Victoria, the Australian Museum, South Australian Museum and Queensland Museum. The Australian Research Council and the National Geographic Society funded many research trips. Finally, I thank many colleagues for helpful discussions over the years including Pat Vickers-Rich, Tom Rich, Gavin Young, Alex Ritchie, Sue Turner, Carol Burrow, Kate Trinajstic, Alice Clement, Tim Flannery, Steve Salisbury, Ralph Molnar, Scott Hocknull, Anne Warren, Mike Lee, Mike Archer and Suzanne Hand. My work would be impossible without the hard work of this legion of truly dedicated people.

Peter Schouten. My art would be impossible without the hard work of a legion of dedicated fossil discoverers, preparators and all the timetravelling palaeontologists who have described their finds. There are in fact too many to name, so thank you to them all! Most importantly I would like to thank my co-authors Sue Hand, Michael Archer, John Long and Trevor Worthy, not just for their contribution to this book, but also for the many decades of support, guidance and belief in my abilities. Thanks also to Briana Melideo of CSIRO Publishing for her belief in this project.

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For most of the past 300 million years, the world's continents were interlinked as the supercontinents Pangaea and then Gondwana. Around 50 million years ago, Australia tore itself free from Antarctica to become the huge, splendidly isolated island it is today. Over time, its creatures began to evolve in ways not seen anywhere else on Earth, with tree-climbing crocodiles, gigantic venomous lizards, walking omnivorous bats and flesh-eating kangaroos roaming the continent.

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