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AUSTRALIAN NATURAL HISTORY

Evolution Special

AUSTRALIAN NATURAL HISTORY

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Until recently most Australian treefrogs, such as the Red-eyed Tree Frog, *Litoria chloris*, were placed in the genus *Hyla*, a group that occurs in many parts of the world. Recently Australian members of the group have been shown to differ significantly from their relatives overseas and as a result they are now recognised as a distinct Australasian genus.
Photo Hal Cogger.

One of the most curious examples of convergence (the independent evolution of similar structures in different animal groups) is that of the Australian marsupial Thylacine, *Thylacinus cynocephalus*, and a particular offshoot of the family tree of dogs, the Dingo, *Canis familiaris dingo*. Until about 3000 years ago when the Dingo first appeared in Australia, the Thylacine was common in areas of the Australian mainland as well as Tasmania. With the arrival of the Dingo on the mainland, the Thylacine began to decline and quickly became extinct. Although able to survive for millions of years as 'convergees' on different lands, the two animals probably could not coexist precisely because of their convergent similarity. Photo D. Roff (NPIAW).

EDITOR
Roland Hughes

CIRCULATION
Cathy Kerr

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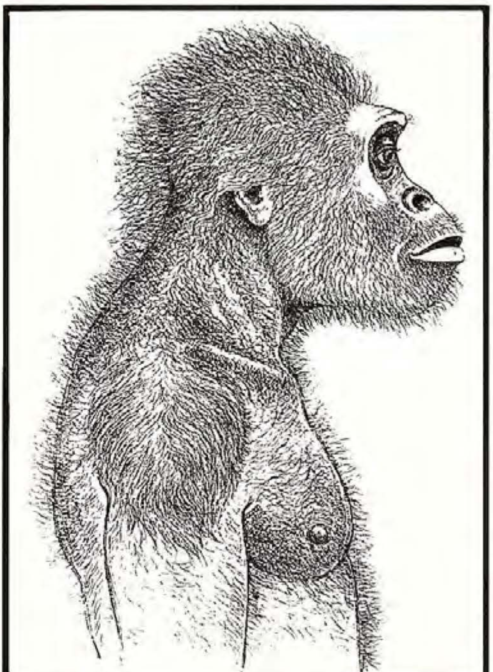


'Lucy', ***Australopithecus afarensis***, **a 3.8 million year old primate, appears to be one of the earliest known members of our own family tree. Drawing Angela Wright.**

The Perentie, *Varanus giganteus*, is found in arid Australia and is the largest of the Australian goannas, growing to a length of 2.5 metres. Goannas are found in Africa, Asia and Australia. Australia has about 70 percent of the world species as a result of an explosive radiation of the group after they reached this continent. Photo Hal Cogger.

1982 marks a very important anniversary in the history of science. It was just one hundred years ago that Charles Darwin (1809—1882), the famous English naturalist who soundly established the theory of evolution, died.

Darwin's masterly theory was published in 1859 under the title, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life,* and the entire 1,250 copies were an immediate sellout. While not being the first to come up with the idea of evolution Darwin's theory provided the mechanism by which plant and animal species change into other distinct species.

Described as "one of history's towering geniuses" and one of the "greatest heroes of man's intellectual progress", Darwin's ideas changed the course of man's thinking not only in the biological sciences, but in life generally.

Even today, evolution remains one of the most exciting and intensely debated areas of science. After 123 years, it not only still stands but is supported by more scientific discoveries, than Darwin ever would have thought possible.

This issue of Australian Natural History seeks to honour Darwin by presenting the modern view of evolution and the history of life. Each of the articles, included in this special issue, were chosen to present one of the areas that makes up the study of evolution. As the reader will soon discover the author's have done an excellent job detailing the important issues and answering the questions which intrigue us all.

December's Australian Natural History will be perfectly timed for summer as it will feature Austalia's most fearsome and misunderstood predators — sharks. Also included will be articles on cyclones and their effect on Australia, the possums of southern Australia and every school child's summer delight — cicadas.

Roland Hughes
Editor

COVER

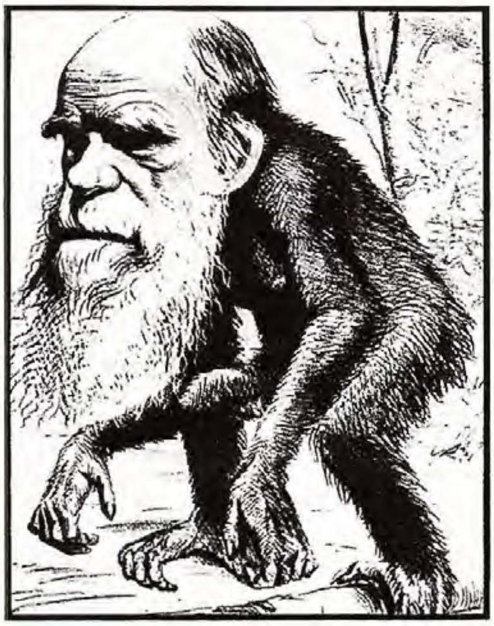
The cast of the skull of Rhodesian man, *Homo sapiens rhodesiensis*, which is dated between 40—50,000 years ago. Although the fossil human story has been rapidly unravelling in the rest of the world, new finds in Australia are putting this continent into the forefront of study on human evolution. Photo John Fields.

BACKCOVER

Charles Darwin at about 1880. After he died in 1882 at the age of 73, he was buried in Westminister Abbey. Drawing Glen Ferguson.

DARWIN, DARWINIANS AND DARWINISM

by Ronald Strahan



Although the broad evolutionary hypothesis expressed by Darwin in the *The Origin of Species* was rapidly and widely accepted, the implication that humans were related to apes was — and still is — repugnant to many. They responded by denigrating or vilifying Darwin, as in this caricature of the 1860s from the journal *Hornet*.

Charles Darwin is commonly honoured as the originator of the theory of evolution but his prime contribution was to propose a mechanism by which species could change.

Today, as 123 years ago, Darwin's theory still causes a great deal of discussion and a surprising amount of controversy. Headlines such as "Was Darwin wrong?", "Apes V Angels, Round 2", "In the beginning... there was evolution..." and "Cosmic-origin theorists on 'neo-Darwinist' hit list", leap out from the pages of our newspapers and form the basis of documentaries on radio and television.

In this article Ronald Strahan puts Darwin's ideas into perspective and discusses the events which surrounded the publication of his first book on evolution and the general reaction to it.

Ronald Strahan is a Research Fellow in the Functional Anatomy Unit, as well as the Executive Officer of the National Photographic Index of Australian Wildlife, both parts of the Australian Museum. While much of his time is spent writing and editing natural history books and co-ordinating the Index, he still keeps an interest in research on the anatomy and general biology of Australian wildlife.

The burial in Westminster Abbey of Charles Darwin, a reluctant atheist, alongside the tomb of Isaac Newton, an extremely idiosyncratic atheist, exemplifies the eclectic nationalism of the church of England — they were honoured not as Anglicans but as famous Englishmen. Few in the church had any understanding of the researches that had led to the fame of these scientists.

Just as a child is egocentric and only gradually learns to take its place in a community, so humanity as a whole has been slowly, reluctantly and incompletely jolted by a few brilliant men to recognise that the earth is not the centre of the universe and that our species is only one of its many occupants. Galileo showed that the earth is a planet and Newton explained the stability of the solar system. Lamarck provided evidence of organic evolution and Darwin provided an explanation of that process. Astronomy and biology thereby opposed some of the basic tenets of Judeo-Christianity, ideas that give comfort and status to ordinary people.

The concept of organic evolution — which emphasises that the present fauna and flora arose from earlier and different life-forms by a process of gradual diversification and that overall, complex organisms are the descendents of simpler ancestors — is as old as European history. It had been expressed by Hippocrates in the fourth century BC and by Lucretius in the first. Descartes had toyed with the idea in the seventeenth century and it was dealt with at some length by Buffon in 1760 and by Erasmus Darwin, the grandfather of Charles, in 1794. In 1809, Lamarck describ-

The Australian Cassowary, *Casuarius casuarius*, is related to the Emu and possibly also to the Ostrich and Rheas. All these flightless, running birds are confined to southern continents and may have had their origin on the supercontinent of Gondwana, which gave rise to Africa, South America and Australia. Photo Len Robinson (NPIAW).

Opposite, the Short-beaked Echidna, *Tachyglossus aculeatus*, is one of Australia's two famous monotremes — the platypus is the other. They are the most primitive mammals occurring on earth and retain in their structure and mode of reproduction some of the features that are characteristic of the oldest known fossil mammals. Today the Echidna is the most widespread of all Australia's native mammals, except for the Dingo. Photo G. Weber, the National Photographic Index of Australian Wildlife (NPIAW).

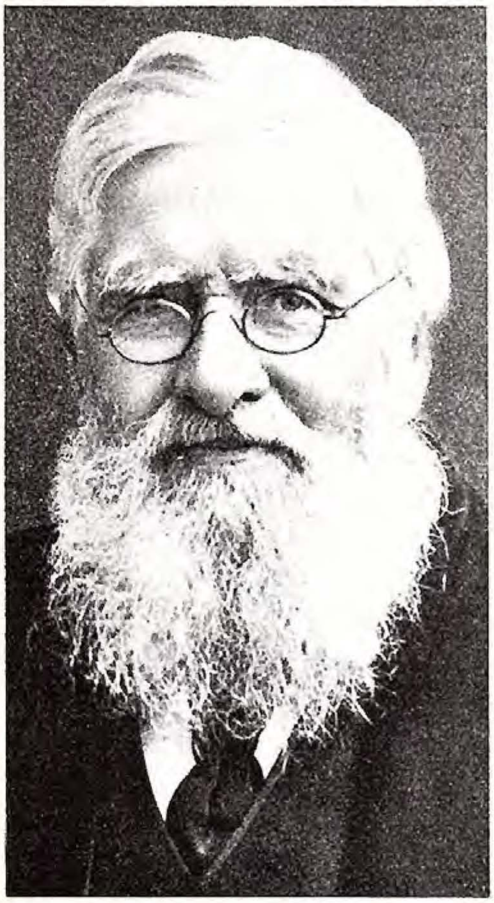
ed what he believed to be the main lines of animal evolution and proposed a mechanism for evolutionary change (which we now recognise to be incorrect).

As knowledge of living and fossil organisms expanded, it became increasingly obvious that their diversity only made sense if they were fitted into 'family trees' and, by the end of the eighteenth century, the central problem in biology was how to interpret these obvious relationships.

Evolution provided an excellent explanation but, since this was contrary to a literal interpretation of the Book of Genesis, it could not be entertained by Christians. As a result, the most brilliant biologists behaved schizophrenically, treating groups of organisms as if they were related in a family sense, but denying that species could ever change.

However, the intellectual supremacy of the Church had been successfully challenged by the successors to Galileo and that authority could again be overthrown if it could be demonstrated, or reasonably postulated, that fossil forms are directly ancestral to quite different modern forms or that species are not immutable.

Charles Darwin is commonly and incorrectly honoured as the originator of the concept of evolution but his prime contribution was to propose a mechanism by which species could change. Even in this he was not unique.



The evolution of marsupials in Australia has led to species adapted to a wide variety of ways of life. One of the most specialised is the Honey Possum, *Tarsipes rostratus*, of southwestern Australia, an animal that feeds — in competition with birds and bees — only on nectar. Photo A. G. Wells (NPIAW).

Alfred Russel Wallace, born in 1823, was a naturalist who made his living by collecting insects for sale to collectors. Like most travellers in the tropics, he had contracted malaria and, prostrated by an attack in February 1858 in the Celebes, he lay in his hammock for several days, alternating between delirium and lucidity. At one stage, he relates, "there suddenly flashed upon me the idea of the survival of the fittest". He waited impatiently for his fever to subside, then dashed off a short paper, *On the Tendency of Varieties to depart indefinitely from the Original Type*, which he sent to Darwin by the next post with the request that he submit it to the Linnean Society of London.

When Darwin received Wallace's letter four months later, he was stunned. For twenty years he had been laboriously amassing data to bolster an hypothesis that he had conceived during the voyage of HMS *Beagle* and now a naturalist of no great scientific repute had set out, in a few pages, the very essence of his arguments.

"If Wallace had my manuscript sketch written out in 1842", he complained, "he could not have written a better abstract. Even his terms stand as heads of my chapters... So all my originality, whatever it amounts to, will be smashed...".

Although the theory of evolution by natural selection is attributed to Charles Darwin, it must be recognised that Alfred Russel Wallace was the first to enunciate this in a form fit for publication. The British scientific establishment ensured that Wallace took second place to Darwin and — at least in this instance — it acted wisely. Darwin followed through the implications of the theory but Wallace was able to add nothing useful to his first brilliant insight.

Scientific ethics required that he immediately transmit Wallace's paper for publication but influential friends took the matter out of his hands and arranged for a privately-circulated abstract of Darwin's work to be communicated to the Linnean Society jointly with Wallace's manuscript (and to be printed just ahead of it) in July, 1858.

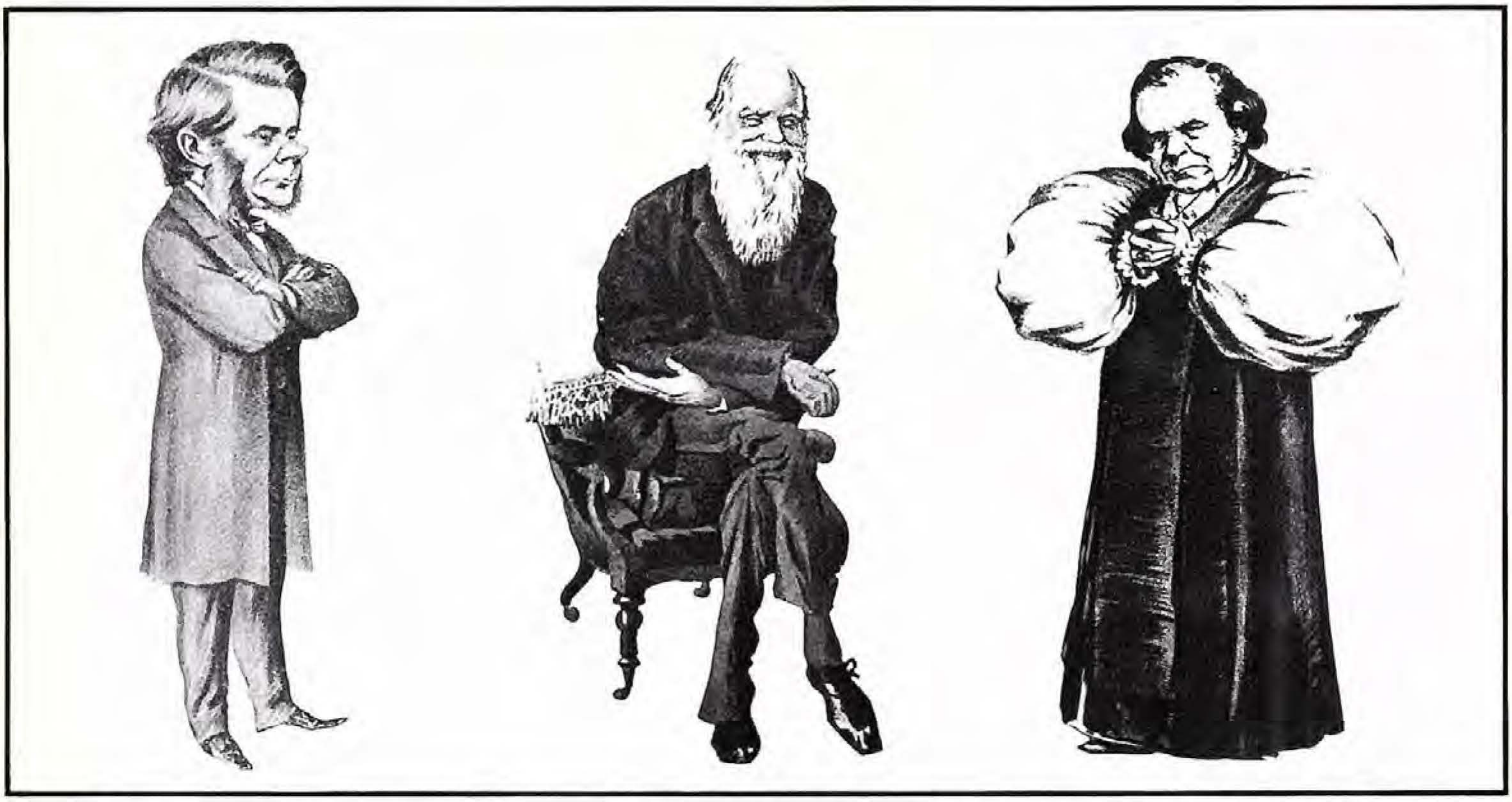
This was improper but, ever humble in the matter and referring to himself as "the moon to Darwin's sun", Wallace later suggested that honours should be shared between them in proportion to the time that each had spent on their work prior to publication, "that is to say, as twenty years is to one week".

The gist of the two remarkably similar papers can be expressed in four propositions:

1. All species produce more offspring than can possibly survive. These therefore compete for survival.
2. In each generation the weakest and least fitted to the prevailing conditions are likely to perish. The small majority of the fittest will survive as parents of the next generation.
3. If a particular variety of a species is fitter than the original type, or **parent** species, it will survive and the parent species will become extinct.
4. The surviving variety (now a new species) will itself give rise to varieties, one of which may prove to be fitter and so supplant **its** parent species, and so on.

As Wallace put it, "... we have now shown that there is a tendency in nature to the continual progression of certain classes of

Charles Darwin
Aged 31 years



In 1860, when the theory of evolution by natural selection was openly debated at a meeting of the British Association for the Advancement of Science, the shy, retiring Darwin was not present. His views were bitterly attacked by 'Soapy Sam' Wilberforce, the Bishop of Oxford and defended by Professor Thomas Huxley, 'Darwin's bulldog'. Wilberforce enquired of Huxley whether his relationship with apes was through his grandmother of his grandfather. Huxley replied that he would rather have an ape as a relative than a brilliant man who stooped to dissembling. Left, Huxley; centre, Darwin; right, Wilberforce.

varieties further and further from the original type — a progression to which there appears no reason to assign any definite limits... This progression, by minute steps in various directions, but always checked and balanced by the necessary conditions... may... be followed out so as to agree with all the phenomena presented by organised beings, their extinction and succession in past ages, and all the extraordinary modifications of form, instinct, and habits which they exhibit."

In concluding his sketch, Darwin claimed to have shown that "Each new variety or species, when found, will generally take the place of, and thus exterminate its less well-fitted parent. This I believe to be the origin of the classification and affinities of organic beings at all times: for organic beings always seem to branch and sub-branch like the limbs of a tree from a common trunk... the dead and lost branches crudely representing extinct genera and families."

From Newton's observation of a falling apple it was a great intellectual leap to the inverse-square law of gravitational attraction. The hypothesis of Darwin and Wallace involved no lesser gap between observation and theory. The available facts were merely the overproduction of offspring, the relative constancy of the numbers of any species and the existence of varieties.

What was inferred was the selective effect of the struggle for existence ('natural selection'), the breeding true of the fittest individuals (inheritance of selected characters) and the unlimited production of new varieties (genetical novelty in excess of known mutations or 'sports').

In 1859, when Darwin published his first book on evolution, *On the Origin of Species by means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life*, he brought together a mass of suggestive evidence but proved nothing. Nor (unlike Newton) was he able to propose any experiments or observations by which his theory could be tested. The discovery of a sequence of fossils demonstrating the development of varieties into species would have constituted direct proof of past evolution but Darwin believed the geographical record to be too fragmentary for such evidence to be preserved.

Why, then, was his book so well received by most leading biologists? Perhaps their response was like that of Thomas Henry Huxley who exclaimed after reading it, "How extremely stupid of me not to have thought of that!" It was a simple hypothesis that, for the first time, gave biology a unifying, materialist principle that made sense of the perceived patterns in the organisation of plants and animals. It was no longer necessary to attribute this to 'divine providence' — the existence of design need no longer imply a 'designer'.

To the churchmen who preached that the diversity and adaptations or organisms were evidence of 'divine' wisdom, Darwin was anathema. Some scientists who gave precedence to religious dogma were equally hostile. Sir Richard Owen, doyen of British comparative anatomists, was one of these who, openly and from under cover, sniped at Darwin. No account of the initial controversy over Darwinism can avoid mention of a typically British situation to which this led.

The British Association for the Advancement of Science held its meeting of 1860 in the University of Oxford and the Bishop of Oxford, Samuel Wilberforce, had let it be known that he would speak against evolution in the Biology Section. Although he knew nothing of biology, he had been coached by Owen and spoke to a crowded lecture theatre fluently, unctuously (he was known as 'Soapy Sam') and with sarcastic asides. Finally turning to T. H. Huxley, who was also on the platform, he asked him whether it was through his grandmother or his grandfather that he claimed descent from a monkey. He sat down and, when the applause and laughter had died, Huxley rose. He would not, he said, feel shame to be descended from a shambling ape, but he would be ashamed to be connected with a man such as the bishop "who used great gifts to obscure the truth". There was roar of approval from the audience and one lady fainted. Wilberforce had been convicted of a 'foul' which reverberated through the country. Huxley had acted as an English gentleman and his voice, as "Darwin's bulldog", was thereafter heard through the land.

Since 1859, evolution has remained the central theme of the biological sciences but, by the end of the nineteenth century, it became embarrassingly clear to deep-thinking biologists that Darwinism had a fatal flaw. If, as Darwin and almost every other biologist believed, the characteristics of parents are **blended** in their offspring, it would be difficult, if not impossible, for novelty to arise. Any new variation in an individual would be swamped by breeding in the next generation with individuals of the parental type — it could not persist long enough to be subject to natural selection.

Darwin himself was aware of this difficulty and the greatest criticism that can be directed against the man, so often held up as the paragon of scientific honesty and humility, is that he did not face it squarely. Instead, in successive editions of *The Origin* and other books on evolution, he diluted his theory of natural selection (based on random variation) with increasing suggestions of directed inheritance of individual adaptations, developed during the lifetime of a parent.

Such "inheritance of acquired characters" had been the basis of Lamarck's discredited theory of evolutionary change and was ferociously attacked by Darwin in his early writings. So, as he quietly slid into the same error, he warranted the criticism that "after scorning Lamarck for his shabby dress, he stole his clothes".

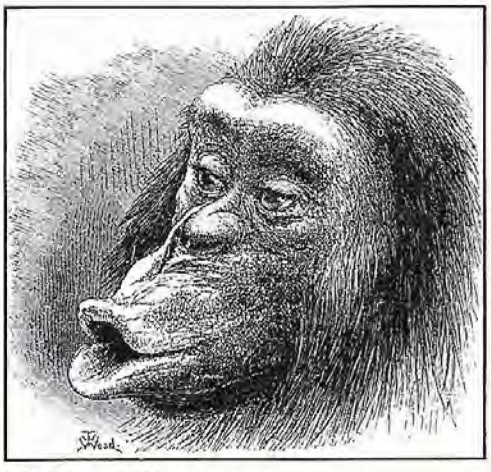
Ironically, Darwin's drift from Darwinism was quite unnecessary. The fault lay not in his theory but in his misapprehension of the nature of genetic inheritance — which we now know to be based on particulate **genes** that may interact but never blend.

This had been demonstrated by Mendel in 1865 and in the same year, Naudin showed the necessity of non-blending inheritance to the operation of natural selection. However, the significance of Naudin's work was dismissed by Darwin and, as late as 1910, Wallace rejected Mendel's discoveries as irrelevant.

In fact, the pioneering work in genetics remained generally unrecognised until the early twentieth century, when a resurgence of interest in the mechanisms of inheritance led to the discovery that genes are located on chromosomes and thus have a physical basis.

Since then, we have come to realise that genes are specific molecules (or segments of gigantic molecules) of deoxyribosenucleic acid (DNA). We have a good understanding of how they reproduce and how they exert their influences. We can designate the structure of some genes, atom by atom, and even change their structure experimentally. The basis of evolution is now abundantly clear — it is the differential survival and reproduction of the carriers of different molecules of DNA — an even more materialist explanation than was proposed by Darwin and Wallace.

The reality of natural selection has now been established in nature and it is evidenced in human activities by the rapid and predictable evolution of pesticide resistance in insects and the resistance of bacteria to antibiotics. A few examples of the evolution of varieties into species have been found among some invertebrate animals in well-preserved sedimentary rocks but the palaeontological record remains fragmentary, revealing more and more information on the general trends of evolution but still with tantalising gaps where we seek certain transitional forms.



Darwin recognised that the process of evolution involved behaviour as well as anatomy. This book, *The Expression of the Emotions in Man and Animals*, published in 1871, was the first serious contribution to the study now known as ethology. Although naive in his approach, he laid down the principle that behavioural patterns in related species are inherited (and vary) in the same way as, for example, the bones of their skeletons.

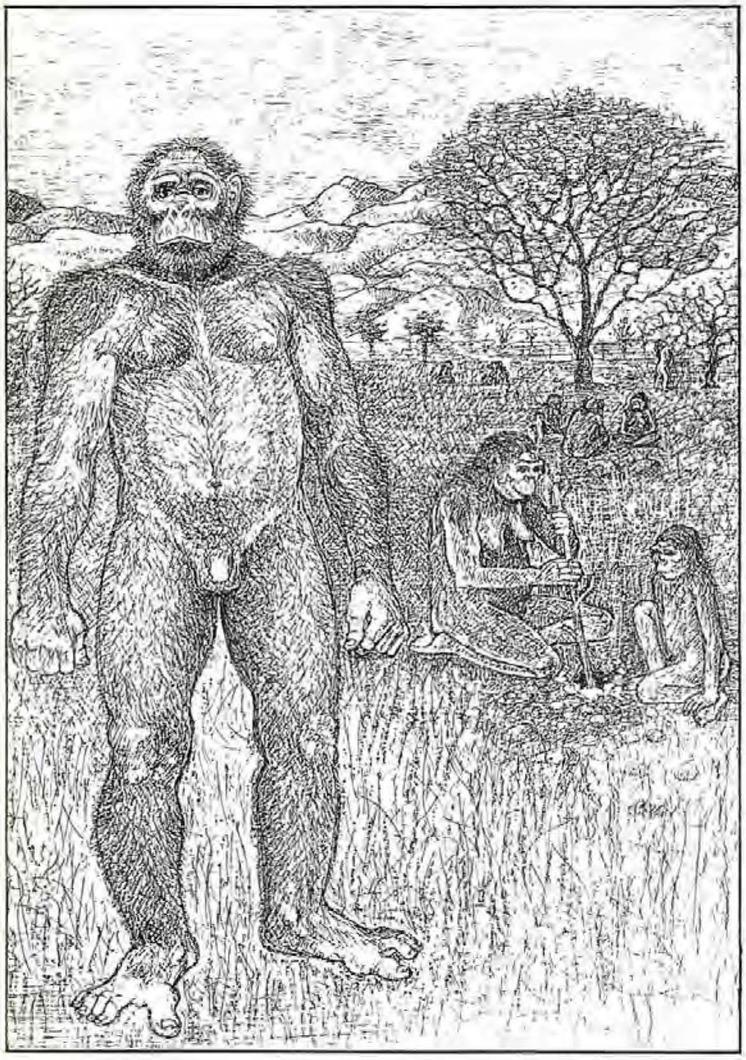
"First (and most important, as I believe), in early life both Darwin and myself became ardent beetle-hunters. Now there is certainly no group of organisms that so impresses the collector by the almost infinite number of its specific forms". In 1908 Wallace used these words to explain why he and Darwin had both independently hit upon the same idea. The illustration is from Wallace's *The Malay Archipelago*, published in 1867.

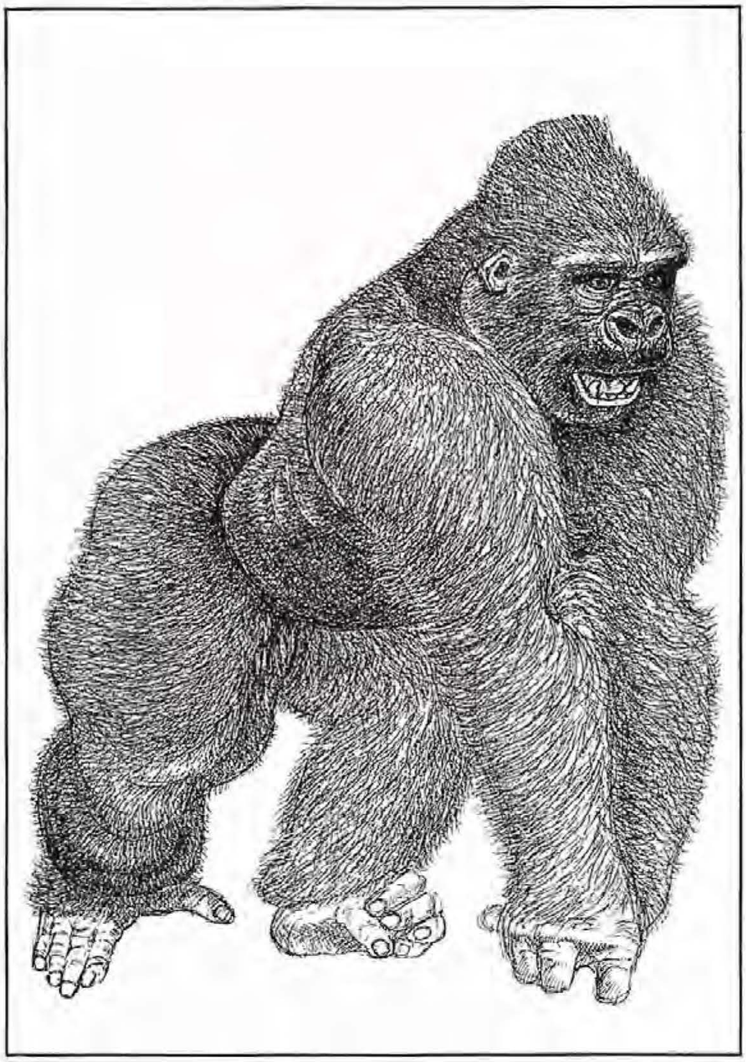
It has recently been suggested that these gaps are not fortuitous but represent periods of rapid evolution when a new group of organisms is coming into existence. This theory of 'punctuated equilibria', attractive but still not generally accepted, is one of many growing points in current evolutionary theory — now referred to as neo-Darwinism.

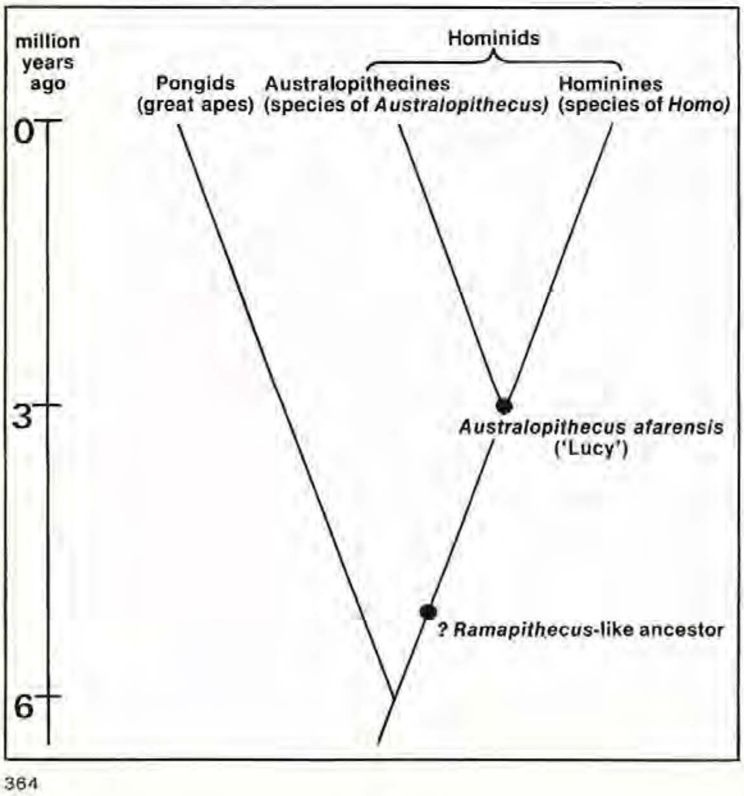
While the detailed problems of contemporary evolutionary scientists have little impact on every day life, the implications of the question rudely posed by Wilberforce remain. We are rather closely related to apes and, through the ancestors we share with them, to all animals that have ever lived. The idea that humans were especially created and that the rest of the animal and plant kingdoms were assembled by a 'creator' to serve us is untenable.

It is comforting to feel that we are at the centre of things — just as it is comfortable to be a protected infant. If we are to accept the responsibilities of maturity we must recognise that, however unique we may be as a species, we are historically and ecologically part of the whole of the life on this planet, with no externally granted licence. It is because this message is unpopular that Darwin delayed so long in publishing his work.

A hundred years after his death people are still rejecting the uncomfortable truths to which he and his successors have drawn our attention.






million years ago
Hominids
Pongids (great apes)
Australopithecines (species of *Australopithecus*)
Hominines (species of *Homo*)
0
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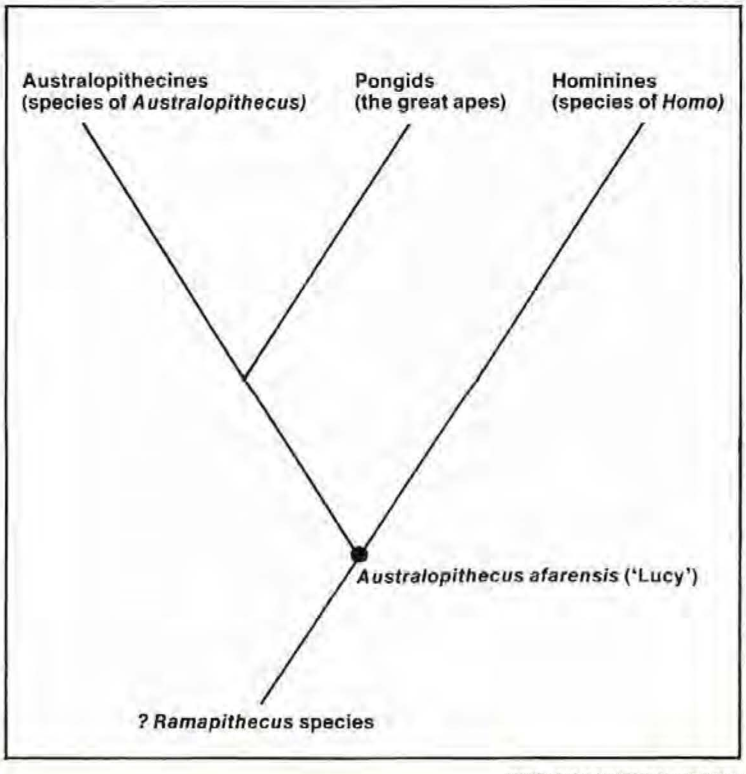
Australopithecus afarensis ('Lucy')
? Ramapithecus-like ancestor


Australopithecines (species of *Australopithecus*)
Pongids (the great apes)
Hominines (species of *Homo*)
Australopithecus afarensis ('Lucy')
? Ramapithecus species

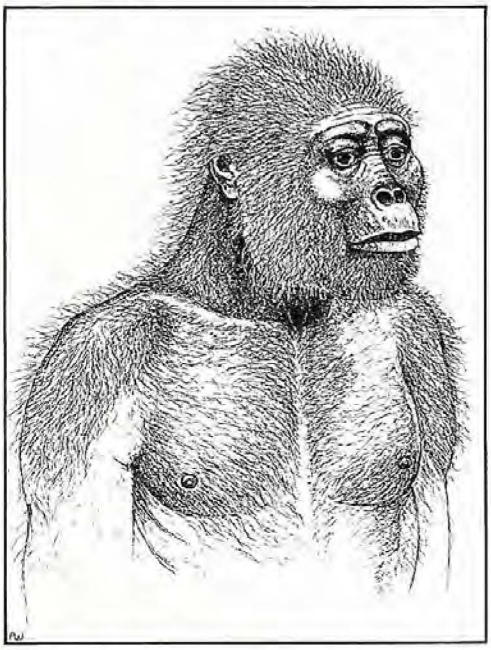
MONKEYING WITH **THE** THEORY OF EVOLUTION

by Michael Archer

Over the last few years there have been a number of significant discoveries advancing our knowledge of the origins of man. Probably none are as exciting as those recently made in Australia. These are an important contribution to the record of human evolution on this continent revealing a link between modern Australian Aboriginals and early man from Indonesia and China.

At the moment Australian biologists are concentrating on the findings of two different groups of human skeletons. One group comes from Kow Swamp in Victoria and the other from Lake Mungo in NSW. The more robust Kow Swamp 'people' are the older of the two and are thought to come from Indonesia, while the more modern Lake Mungo 'people' probably came from China. Biologists now believe the two groups of people mixed over the years and eventually became the modern Australian Aboriginal.

In this article Michael Archer tackles some of the more exciting frontiers of evolutionary research, including the history of man on earth and his development in Australia. Michael Archer, a specialist in mammal evolution, is a Museum Research Associate and Senior Lecturer in Zoology at the University of New South Wales.



'Lucy', *Australopithecus afarensis*, a 3.8 million year old primate, appears to be one of the earliest known members of our own family tree. She was just over a metre in height but, like all later members of our family tree, walked upright. Drawing Angela Wright.

Opposite, top left and right, a recent provocative suggestion has raised doubts (although only small ones) about the extinction of our rather brutish cousins, the australopithecines. Perhaps they are still with us, as the great apes. As appealing as the idea might be, it does involve an improbable reversion from the bipedal australopithecine to the quadrupedal great ape gait. Drawings Angela Wright.

Bottom left, the discovery of 'Lucy' represents a very important advance in the increasing knowledge of our own evolutionary history. 'Lucy' represents a 3—4 million year old primate that shared features of the African Ape-men, a species of *Australopithecus*, and a species of our own genus, *Homo*. Based on studies of molecular divergence, the great apes and humans diverged about 6 million years ago.

Bottom right, a diagrammatic representation of the interesting (but difficult) suggestion that great apes are the living descendents of our otherwise extinct cousins, the australopithecines.

As a decidedly egocentric species, the precise manner of our own origins has always been a source of intense curiosity. Every culture of humans has its own particular belief about the history of this event. The Christian tale, recorded in Genesis, suggests that the first human was hand-crafted out of a blob of clay and miraculously brought to life by a supernatural being. Many other cultures have equally imaginative creation beliefs and each, not surprisingly, believes theirs to be correct and the others heresay.

'Lucy' — from tiny beginnings

An increasingly well-known fossil record from Africa and elsewhere has failed to support any of the beliefs in special creation. Recently fossil bones and tracks from African sediments about 3 to 4 million years old have provided undoubted evidence for the fact that humans evolved from ancestral creatures a little over a metre in height.

The best known of these early hominids (all creatures in the family of man) has been named *Australopithecus afarensis*. Reconstructions based on a partial skeleton indicate that it represented a female (affectionately dubbed 'Lucy' when she was found) that weighed about 27 kg, was heavily muscled and strong for her size by modern human standards. She was fully bipedal (as evidenced by her skeleton and tracks from other individuals in Tanzania), long-armed, with human-like hands, ape-like wrist bones and a small brain. Her chinless jaw was large and jutted forward. The upper part of her face was small and chimplike. Overall, she looked like a small human with an ape-shaped head.

This ancestral hominid shared many of the features found in the later australopithecines (the extinct 'ape-men', all of which belong to the genus *Australopithecus)* and those found in later hominines (the lineage of hominids containing species of our own genus *Homo)* such as *Homo habilis* and *Homo erectus,* (Javan and Peking Man) and was clearly near the base of our own family tree.

The fate of the australopithecines, our more brutish cousins, has generally been assumed to have been extinction without issue, an event that left the earth to us, the only other surviving hominids.

It has recently been suggested that perhaps the great apes, including the chimpanzees and gorillas (pongids) are actually descendents of australopithecines. This could explain why recent molecular studies suggest a very close relationship between the great apes and ourselves. We can predict a comparably close genetic relationship between the otherwise extinct australopithecines and hominines based on the distinct skeletal similarities of the two groups.

The idea will probably be the subject of much debate and further investigation. Whatever the outcome of this debate, it does seem at least curious that one aspect of this theory must be the assumption that the great apes have secondarily reverted to a quadrupedal gait because we know that the australopithecines were, like us, bipedal.

Reorienting *Ramapithecus*

New Chinese finds of skulls of a species of the extinct primate genus *Ramapithecus* have provided a very curious upset of current ideas about hominid evolution.

The interpreted role of the African and European ramapithecines in human evolution has long been hotly debated. They occur in sediments as old as 15 million years and, principally because of their dental structure, were originally thought to be part of the base of the family tree of man, but representing a branch much lower on the tree than that of the more 'advanced' australopithecines. Accordingly, they were regarded as the first hominids and therefore that hominids were distinct from the great apes by at least 15 million years.

Tooth structure suggested they came out of trees to feed on the coarse grass seeds of the African savannah.

This cherished interpretation of the significance of the ramapithecines in our evolutionary history then received two challenges. The first came from a very different arena of evolutionary research — molecular biology.

Studies of the relatedness of various primates, based on antigenic properties of the blood proteins, has shown that the protein albumin of humans and that of great apes is very similar. Based on studies of rates of albumin evolution in other groups of mammals, it is even possible to estimate how much time has elapsed since the lineages of great apes and humans last shared a common ancestor. Using this 'molecular clock', it has been estimated that the last common ancestor of humans and great apes could not have lived longer ago than about 6 to 8 million years. Clearly this date was in conflict with the fossil evidence which suggested that hominids were distinct from the great apes at least as early as 15 million years ago (assuming that ramapithecines were the first hominids).

The second challenge to the established view has come from subsequent discovery of new ramapithecine fossils from Pakistan. These are better preserved than the African specimens and show a feature that casts doubt on their hominid nature. The tooth row is V-shaped rather than U-shaped like the great apes or parabola-shaped like hominids. Previously, based on the more poorly-preserved African material, the tooth row of ramapithecines was interpreted (incorrectly as later studies showed) to be parabola-shaped as it is in hominids.

The immediate consequence of these developments was that *Ramapithecus* was unceremoniously booted off the family tree of man, by many students of human evolution.

More recently, these primates have been dusted off and now may well be reinstated as early hominids. Their fall from grace was arrested by new finds from China. In lectures and popular Chinese journals, Professor Wu Rukang of the Chinese Institute of Vertebrate Palaeontology and Palaeoanthropology announced the discovery of several tremendously exciting fossil primate skulls — among them, the first nearly complete skull of a species of *Ramapithecus*. The skull shows many hominid features including weakly developed ridges on the sides of the skull, a non-ape-like lower jaw, small and narrow incisor (front) teeth, small canine teeth and thickly enamelled molar (rear) teeth. But most fascinating of all is the fact that the foramen magnum (the opening in the skull that leads the brain stem away from the head) is directly **under** the skull, a condition that indicates that this species of *Ramapithecus* normally walked upright. This normally upright posture is universal among hominids (including *Australopithecus afarensis*, but completely unknown among the great apes.

The actual date of this so far undated chinese species of *Ramapithecus* may now be the only obstacle in the way of resolving the molecular and palaeontological data. If, for instance, the chinese specimen turns out to be about 6—8 million years old, the whole business may come together.

The Chinese species of *Ramapithecus* may then have been among the first hominids and ancestral to the 4 million year old *Australopithecus afarensis* ('Lucy') and African forms like her. The question of when the great apes diverged from these early hominids could, in this context, have two alternative answers:

1. they could have evolved from a separate lineage of African *Ramapithecus*-like primates or,
2. might have been the descendents of the otherwise extinct lineages of later australopithecines.

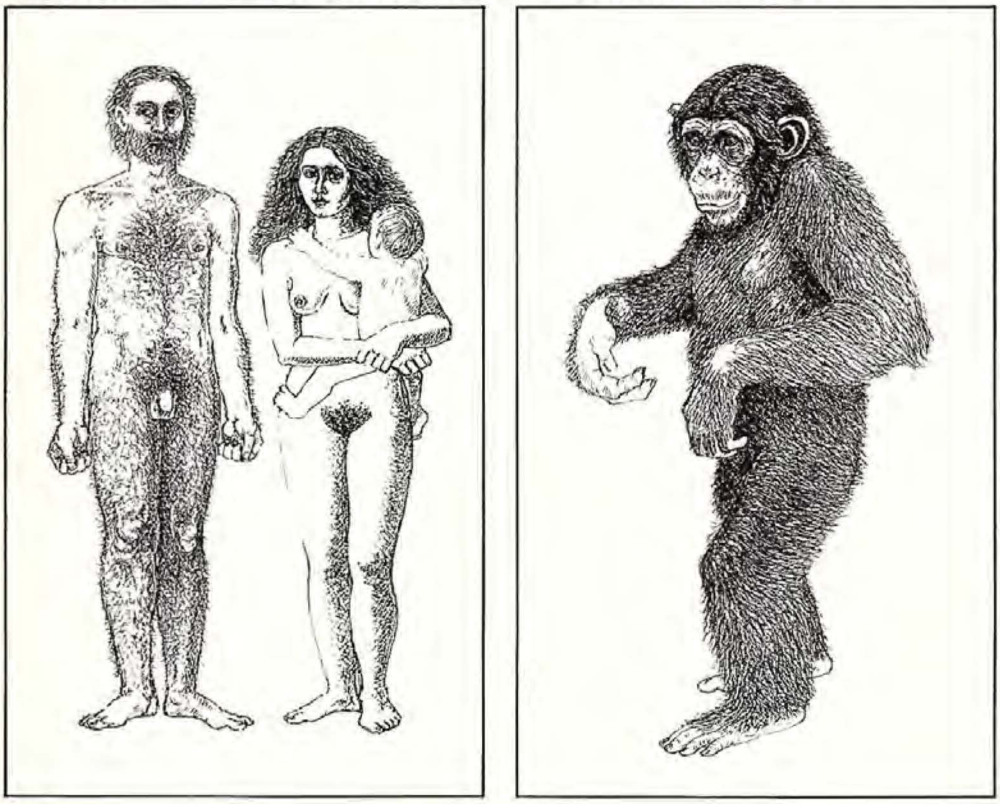
The Australian connection

The record of human evolution in Australia is being studied as intensively as that in most other continents. As elsewhere, many remarkable pieces are falling together into what is clearly a complex evolutionary tapestry.

The late Professor MacIntosh once noted that the "mark of ancient Java" was upon the Australian Aboriginals. By this he meant that some of the features of Java Man, (an eastern extension out of Africa of *Homo erectus)* could be seen in the skulls of Aboriginals. To him, this was particularly evident in some fossil skulls such as the Talgai cranium, known from the Darling Downs as early as the 1880's.

Discovery in 1967 of an assemblage of very distinctive human skeletons from near Kow Swamp, Victoria, first studied in detail by anthropologist Dr Alan Thorne, has provided much food for thought. These skeletons appear to represent a population of robust large-toothed hominids seemingly different from modern Aboriginals, and in some respects exhibiting features best represented in Java man.

The oldest dated Australian remains of a more modern type of hominid is a skeleton from Lake Mungo dated at approximately 30,000 years old. It would of course cause no problems if the more heavily built Kow Swamp skeletons were older than the more modern-looking Mungo skeleton. But this is not the case. The Kow Swamp population dates at between 9 and 14,000 years ago and overlapped in time with the more modern-



There is a lot of evidence to suggest that humans are 'neotenised' primates. Neoteny is an evolutionary process whereby the juvenile features of an ancestor are retained as adult features in its descendent. The adult human shares a great many features with juvenile rather than adult great apes, including the relatively flat face, small jaws and ventrally oriented vagina. Drawings Angela Wright.

Conventional model of Darwinian evolution

The simple model of Darwinian evolution involves four basic concepts:

1. Variation among individuals of a species.
2. The operation of a selective process (called natural selection) which acts on this variation.
3. The isolation of part of a species and its subsequent divergence from the parental population.
4. The establishment of reproductive isolation of a population and the origin of a distinct species.

Variation in individuals

A species is the sum of all individuals that are not reproductively isolated from each other. In other words, if two individuals can produce fertile offspring, they should be regarded as members of the same species.

The individuals of a species normally differ from each other in numerous behavioural and morphological features. If these differences have at least in part a genetic basis, they are inheritable variations. Examples are hair colour, ear shape, some mating behaviour and so on.

In sexually reproducing organisms, the offspring receives non-identical genetic information from its mother and father. As a result, new combinations of genetically determined features are constantly produced. New features may also result from mutations in the genetic material (chromosomes). These new combinations and mutations contribute to the differences shown by the individuals of any population.

looking hominids by at least 15,000 years.

It has been suggested by Thorne that the more *erectus*-like Kow Swamp skeletons represent the direct and little-changed descendents of the first hominids to enter Australia from the Indonesian area (perhaps as long ago as 120,000 years — although there is no clear dated evidence for hominid remains from Australia older than about 30,000 years).

The more gracile Lake Mungo hominids may represent a second, more recent immigration from eastern China. Thorne suggests that these hominids are the descendents of *Homo erectus* populations that reached China, probably about the same time that *Homo erectus* reached Java and other areas of Indonesia.

The transformation seen in Chinese fossils from the older *Homo erectus* types to the younger *Homo sapiens* types may reflect a gradual change in one large hominid gene pool that spanned Eurasia.

Early isolation in Australia of the ancestors of the Kow Swamp hominids may have enabled them to maintain more *erectus*-like features than were retained in the more rapidly changing Eurasian populations.

The fate of the Kow Swamp people is unknown but Thorne has suggested that they may have hybridized with the more modern-looking Mungo-type hominids and in so doing, blended their inheritance to become the modern Aboriginals.

Baby brains and flat faces

Before leaving the intriguing subject of human evolution, we should consider a final area of current thought — why are we so visibly unlike our otherwise nearest neighbours, the great apes, when molecular studies suggest we are very close? Put another way, in what ways and for what reasons do humans differ from all other animals?

Linnaeus, in 1758, as the first modern systematist to classify man, adroitly side stepped the problem with the cryptic definition for humans — *nosce te ipsum* — 'know thyself'. Even Darwin copped out in 1859 when it came to placing man in the web of evolution by saying "... light will be thrown on the origin of man and his history".

Certainly a lot of light has been thrown on the palaeontological origin of the family of man. But why are we, alone among primates, naked? Why do we alone have such long childhoods? Why do we have such flat faces, long lives, and so on?

Many years and philosophical treatises after Darwin's, Louis Bolk, a Dutch anatomist, came up with the theory of 'foetalization'. Although he formulated the theory in 1926, it was largely relegated to the waste-paper basket until 1977 when Steven Gould, an American palaeontologist, dusted it off and had another look at it.

In a nutshell, he suggested that most of what is unique about humans could be interpreted as the result of a process called neoteny — retention in the adult of the **juvenile** features of its ancestors. In contrast with the adults found in non-human primates, the juveniles are less hairy, have a relatively high brain weight, poorly-developed brow ridges, undeveloped cranial crests, thin skull bones, flat faces, ventrally pointing vaginas, rounded bulbous craniums, small jaws and

Natural Selection

Most organisms produce far more offspring than will survive to sexual maturity. All of the processes that determine which offspring survive to reproduce, Darwin called natural selection.

If, for example, among four kittens in a litter, one is born with slightly smaller ears than the other three, it will probably be the one too slow to detect and escape the pounce of a powerful owl. Therefore, the chances are reduced that genetic instructions for smaller ears will be passed onto the next generation.

Similarly, if some individuals in a population of kangaroos have kidneys just a bit better at retrieving water from waste fluids headed for the bladder, those individuals may be the only ones that survive the next drought.

Natural selection gradually moulds species by weeding out individuals genetically less suited to survive the demands of the environment.

Sometimes selective forces may be counteractive such that the net effect is little or no change in the individuals between generations. For example, larger male Red Kangaroos may be better able to protect their offspring from negative selective forces, such as Dingoes. Females should, therefore, preferentially mate with the male that demonstrates the greatest strength. Why then, after millions of generations of selection for larger, stronger Red Kangaroos, are Red Kangaroos not as large, or larger than horses?

The answer probably involves other selective forces acting against very large individuals, perhaps because their food requirements are too high or, as larger and heavier young, they rupture their mother's pouch!

Or perhaps while the larger aggressive males are occupied in ritualised wrestling matches or rippling muscles at each other to impress the watching females, the smaller, less-aggressive males manage to sneak up behind the females and insert their own genetic contribution into the future, so to speak. Photo Hans & Judy Beste (NPIAW).

teeth, ventrally positioned foramen magnum (exit from the skull for the brain stem) and the strong forward alligned and nonopposable big toe.

All of these juvenile features are lost or profoundly changed in non-human primates as they become adults. Humans, on the other hand, retain these features as sexually mature adults. It is as if humans were primates whose general bodily developmental 'clock' has been slowed down and, as it were, overrun by relatively rapid sexual development. This slowing down is also evidenced in the correspondingly lengthened childhood and long life span of humans. All of these neotenic features may be the result of relatively simple changes in the genetically programmed rate of development.

In fact, it is even probable that the enormous (relative to other primates) size of the adult human brain is in large part the result of the prolonged period of brain growth at the more rapid foetal rate. In some primates the brain may increase by 60% in size after birth. In humans it more than quadruples in size after birth.

But why bother? Some of the features must be disadvantageous, such as the reduced body hair, reduced tooth and jaw size and prolonged period of dependence of the juvenile on the adult. The answer may be that the worth of one particularly beneficial neotenic feature offsets any disadvantages inherent in the rest. That feature? The increased **capacity** to learn.

Cultural inheritance

Ancestral humans, with their prolonged period of brain growth at the rapid foetal rate, may have been better able to learn to assimilate the kind of wisdom that is not instinctual. Today, we call this non-genetic wisdom our cultural inheritance. The ability to pass on to succeeding generations this rapidly increasing store of knowledge may have given our ancestors an edge in the battle for survival.

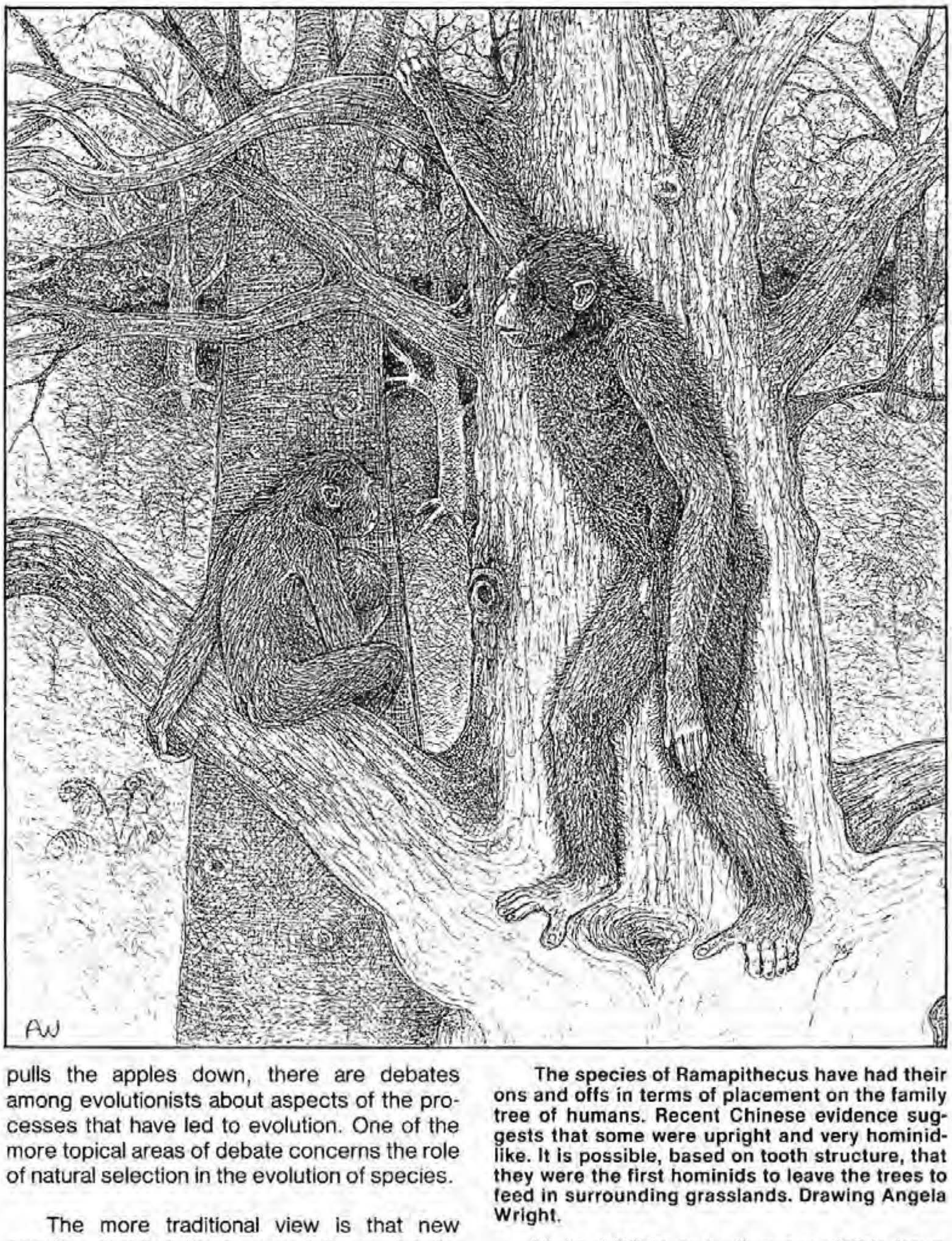
With the increase in **capacity** to pass on, through teaching, the accumulating knowledge of generations of experience, the ancestral humans became an experiment unique in evolutionary history. Through the process of neoteny, we alone have magnificently transcended the limitations of instinct that burden the rest of the animal kingdom.

Now, for each successive generation of imprintable juveniles, we have an enormous and ever increasing body of knowledge to pass on. In the long run, that may well have been a magnificent trade-off for our nakedness and the need to push our helpless larvae around in prams.

Evolution is, like apples falling from trees, a fact. Yet, like the debates about the technical nature of the force of gravity that pulls the apples down, there are debates among evolutionists about aspects of the processes that have led to evolution. One of the more topical areas of debate concerns the role of natural selection in the evolution of species.

The more traditional view is that new species develop from ancestral species by isolation of part of a population. These gradually evolve and diverge from the ancestral species because natural selection in the isolated area will be different from that in the ancestral area, reflecting the different environmental constraints or opportunities. Eventually, the evolutionary divergence caused by natural selection is so great that the isolated descendent and ancestral populations can no longer interbreed even if they eventually come back into contact. This is the allopatric ('in another place') speciation model. Natural selection is clearly a vital part of this model.

A number of geneticists and paleontologists have not been happy with this model as an explanation for all (or even most) speciation events. They suggest that speciation events may not require geographic isolation or even the driving force of natural selection.



The species of Ramapithecus have had their ons and offs in terms of placement on the family tree of humans. Recent Chinese evidence suggests that some were upright and very hominidlike. It is possible, based on tooth structure, that they were the first hominids to leave the trees to feed in surrounding grasslands. Drawing Angela Wright.

Michael White and other geneticists have presented a large body of data to demonstrate that many speciation events occur because of rapid changes in the chromosome number and the shape of organisms. These changes may occur in a single generation such as happens in the case of polyploidy where there is a rapid change in chromosome number in an individual within a population. Such a change renders it incapable of mating successfully with its nonpolyploid neighbours. This model of speciation, involving rapid chromosomal change, is often referred to as the theory of chromosomal speciation. It might not require any greater geographic isolation than that which normally occurs between adjacent populations (or demes) of the same species.

The most curious aspect of this kind of speciation event, as Steven Gould clearly points out, is that the new species does not arise as a consequence of natural selection. In fact, natural selection may have nothing to do with chromosomal speciation events because they can occur randomly, the simple result of chance. Accordingly, this sort of speciation is non-adaptive — meaning it is not a response to selection for adaptive traits.

It strikes me as curious that some cases of human infertility could be unrecognised cases of chromosomal speciation events. If a chance mutation in chromosomal structure occurred in one individual, that individual might very well prove to be reproductively incompatible with other non-mutated ('normal') individuals. But suppose two of these reproductively 'infertile' people with the same chromosomal abberation reproduced successfully with each other. In effect, they would represent a new species of humans that had developed within the range of their ancestors.

The odds against perpetuation of a new chromosomal species are, however, large unless the offspring do find other comparably mutated individuals or, as happens commonly in non-humans, the young back-cross with the parents or cross with each other.

Pursuing the concept of alternative views on the role of natural selection in evolution, means other cherished notions are also receiving a critical rethink. For example, if chromosomal speciation is the normal mode of speciation, what is the evolutionary significance of racially or regionally different populations?

Traditionally these were often named as distinct subspecies (such as *Homo sapiens sapiens*, modern humans; *Homo sapiens neanderthalensis*, 'Neanderthal Man') and interpreted to represent developing species steadily diverging from one another under the influence of natural selection.

Now, however, some geneticists view these regionally different populations of a species as nothing more than the result of a sort of fine-tuning (although led by natural selection) to adapt to the particular environment in which the population of the species exists. They suggest that these gradual fine-tuning differences are not steps along the way to ultimate speciation. If speciation events are chromosomal, they can occur at any time, in any population of the species without regard to its particular accumulation of finely-tuned distinctions.

So what role does natural selection have in these newer models of evolution if not at the level of the evolution of new species? Probably two main roles.

In the first place, if a new chromosomally distinct species develops within the range of its ancestral species, the two species will suddenly be in competition with each other for the resources they both used as a single species.

Isolation and divergence


Western Whipbird. Photo L. A. Moore (NPIAW).


Eastern Whipbird. Photo E. Hosking (NPIAW).

The forces of natural selection and a process called genetic drift (insignificant changes that occur and accumulate because they do not affect fitness or survival value) gradually change species through time.

In large populations, this type of change tends to be slow because individuals with unusual genetic variations or combinations are rare compared with those that have more standard variations. Therefore, there is a much greater probability that the genetically 'odd' individuals will mate with the more numerous 'normal' individuals and thereby reduce (by genetic blending) the chances of the 'odd' genetic instructions becoming normal.

Each individual possesses only a limited sample of the variation present in the whole species and is bound to have a number of 'odd' features among the thousands it exhibits. As a result, new populations begun by a few individuals may rapidly diverge from the more stable less rapidly evolving parental populations. This is because the offspring of 'odd' parents in small populations will be more likely to inbreed or backcross with their parents and more readily increase the frequency of 'odd' individuals. Eventually in these situations, 'odd' may become normal.

An example of how isolation may have led to divergence involves the interpreted recent history of the Australian Whipbirds Geographical or climatic disruption of the populations of a single widespread ancestral species resulted in the isolation of an eastern and a south-western population. Subsequently, the different selective forces in the two areas gradually caused the two isolated populations to diverge. As a result the accumulating differences finally led to reproductive isolation.

When this situation develops, natural selection, if it is rapid enough, will be able to fine-tune both species into forms that differ sufficiently from each other to enable them to coexist. Natural selection might, for example, result in one finch becoming larger than another otherwise identically-shaped but reproductively isolated finch in order that it can more efficiently use larger foods than those normally used by the smaller finch. The smaller finch would presumably also be fine-tuned to make more efficient use of the smaller range of foods. This sort of evolution is called character displacement.

In this way, natural selection may transform two similar but already reproductively isolated species in ways sufficient to enable them to coexist. If natural selection fails to do this, competition will probably result in one of the two species becoming extinct.

This may be the second role of natural selection in the chromosomal speciation model of evolution — species selection and trends in evolution. If speciation events are a constant chance occurrence within species, and competition between some of these cannot be adequately reduced, natural selection will weed out the less fit of the 'suddenly' produced species, just as in the more traditional view of natural selection it weeds out the less fit forms within species. In this way, through time, selection of species by extinction of competitors will result in evolutionary trends that should be recognisable in the fossil record.

This is a most curious twist of the usual conception of the manner in which natural selection works. Traditionally, natural selection has been visualised as the driving force that selects adaptive genetic traits and, in so doing, ultimately produces, by reproductive isolation, a new species. In its newer role considered here, it may act on previously isolated species that were suddenly produced by non-adaptive processes.

Life's patterns through time

As the role of natural selection in evolution undergoes reassessment, the historical record of the evolutionary process is also under intense scrutiny. In particular, paleontologists are asking whether the fossil record provides evidence for the way in which species change through time.

This arena of research is the one most often misquoted or misinterpreted by creationists. This is unfortunate because the debate involved is not about the reality of evolution, but rather about the most common mode of evolution.

Two seemingly different modes of evolution are interpretable from the fossil record.

They have come to be known as phyletic gradualism (steady, constant change) on the one hand and punctuated equilibria (rapid shifts alternating with long periods of little change) on the other.

The palaeontologists Niles Eldridge and Stephen Gould, principal proponents of the punctuated equilibrium model, have suggested that perhaps the fossil record's gaps should be interpreted as evidence that species do not normally change into new species gradually. Rather, they suggest a four-stage life history for most species and that the stages are not of equal duration.

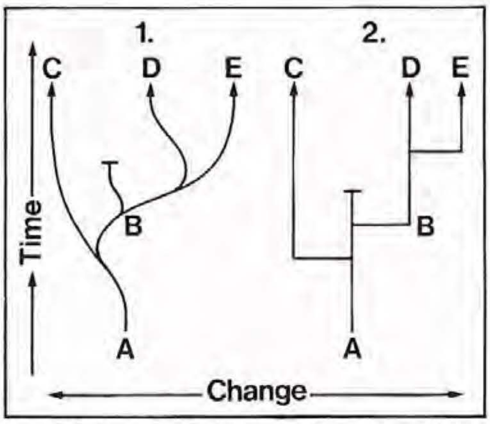
Working from a model of sudden speciation (an example is the chromosomal changes that are not directed by natural selection), the first stage in the life history of a species would be its sudden appearance. The second stage would be a very rapid shift (geologically speaking that is) in shape. Although this shift might take 5 to 50 thousand years, it would appear as a very rapid event in the geological record. Presumably this shift would be the adjustment period of character displacement led by natural selection to reduce competition with the ancestral species. The third stage would be a long period, say 3 to 5 million years of relatively little change during which any change in the shape of a species merely mirrored any slight changes in the environment. This third stage is called the period of stasis. The fourth stage would be the species extinction. Extinction could either come about by the death of all individuals without leaving any offspring or (again working within the model of rapid non-adaptive speciation) the sudden birth of a better-adapted daughter species.

There are apparent examples of the punctuated equilibrium mode of evolution in the fossil record, particularly in sequences of some invertebrates such as trilobites and gastropods and the fossil record of numerous groups of mammals.

The other and more traditional gradualist model predicts that species should change steadily through time because these changes are additive and the ultimate basis for the appearance of a new species.

Although there are some examples of phyletic gradualism in the fossil record, they are not common. Often cited examples are the evolving sequences of marine ammonites, early primates (our own order) and the microscopic foraminifera.

The main question being asked now is whether the seeming rarity of examples of phyletic gradualism are, as Darwin originally believed, the result of the incomplete fossil record or, as Eldridge and Gould suggest, an indication that phyletic gradualism has not been the main mode of evolution.



Debates about how new species originate have resulted in two evolutionary hypotheses. One of these, called phylogenetic gradualism (Fig. 1), involves a slow and steady genetic differentiation that eventually leads to reproductive isolation. The other, called punctuated equilibrium (Fig. 2), involves sudden reproductive isolation, then rapid change followed by a long period of little change. Examples of both are known.

Unravelling the web of life's past

Not surprisingly, it has been generally accepted that, where possible, the fossil record itself should be the ultimate arbitrater in debates about the phylogenetic history of life.

Many palaeontologists still defend this point of view, but some do not. They wisely point out that some 'primitive' groups can survive long after they have given rise to more 'specialised' groups.

But if the antiquity of a creature is not always a reliable guide to interpreting its relative primitiveness, how can we unravel the threads of descent that link all creatures, living and extinct?

There are many ways. Some of them, such as studies of the antigenic properties of blood proteins, the ways in which DNA molecules of different animals are capable of recombining, the comparison of the structure of enzymes, the structure of mitochondrial DNA and so on give a good indication of the relationships between species tested, and an estimate of the time elapsed since they last shared a common ancestor.

But what good are these molecular tools in unravelling the phylogenetic relationships of fossils? Until very recently, the answer to that question was a shrug. The only way the significance of the fossils could be interpreted was through the gross shape of teeth, bones or other preserved hard parts.

New techniques have once again pushed the impossible over the border into the land of the possible. Samples of the protein albumin have been found in the frozen skin of the extinct mammoth from Siberia and from the dried museum skin of a Thylacine (the extinct 'Tasmanian Tiger'). Tests of this albumin revealed not only that it is still intact but that it can be used to indicate the evolutionary relationships of these two long extinct creatures.

Extensions of studies of this kind using 'fossil' molecules are producing some very exciting results. For example, it has recently been found that protein fibres called collagen may be sealed inside the dense matrix of bone and survive intact for millions of years. Antigenic study of these fossil fibres gives reasonable estimates of the relationships of the extinct animal to living potential relatives.

It is interesting to consider a possible (although extremely remote) extension of this sort of work with the preserved proteins of extinct species. Genetic engineering has come a long way. It should now be possible to determine the sequence of amino acids in fossil proteins. These must indirectly reflect the sequence of amino acids in part of the extinct creature's DNA. How much of this sort of information would the genetic engineers of the future need to enable production of a blueprint for a do-it-yourself, real live sabretoothed tiger? The mind boggles.

As the understanding of the phylogenetic history of life grows, and scientists more fully understand the historical interrelationships of all creatures, so some scientists have become dissatisfied with the common methods for portraying this information.

The first formal attempts at comprehensive classification of living creatures did not reflect evolution.

God's creative whims

Carolus Linnaeus, in 1758, distinguished the kinds of organisms known to him at the time and placed them in a simple heirarchical classification presumably based on overall similarity. He thought like most naturalists of his day, that the only order underlying the diversity of life was God's creative whims.

Today, most classification is the formal presentation of biologists' interpretation of the order underlying the diversity of life. If this order is assumed to be evolutionary history, the classification should ideally express understanding of evolutionary history. Most scientists use a heirarchical system of taxonomic catagories that involves placing any descendent group at a level subordinate to that of its ancestral group. For example, if mammals have been determined to have evolved from a particular group of reptiles, they should be classified at a taxonomic level that is lower than, and subordinate to, that for the particular group of reptiles that was the ancestral group.

Until very recently, this sort of logic has not been the basis for most classifications, even those which have been constructed by evolutionists. For example, most text books recognise at least five equal-ranked classes as subgroups of the Phylum Vertebrata:

Class 1. Pisces (fish)
Class 2. Amphibia (frogs etc)
Class 3. Reptilia (dinosaurs, snakes etc)
Class 4. Aves (birds)
Class 5. Mammalia (mammals)

This is despite the fact that the fossil record clearly indicates that each of these 'classes' is in fact descended from a subgroup within one of the preceeding 'classes'. For example, birds evolved from dinosaurs (a subgroup of reptiles) and mammals from the mammal-like reptiles (another subgroup of reptiles). Birds and mammals should not, therefore, be classified at the same level as reptiles as a whole.

Although it might not seem like the sort of debate that would cause much fur to fly, a lot of fur has already flown. The defenders of the evolutionary heirarchical system are known as the cladists and their single most important objective is clarification of the branching sequences in the history of evolution. Expression of the interpreted branching sequence of life, in classification, results in a progressively more finely divided heirarchy of nested sets.

The defenders of the more traditional approaches to classification consider that classifications should reflect, by scaling up the rank of classification, the diversity and/or antiquity of groups. Therefore birds are classified at the same level (class) as reptiles, even though they are descendents of a subgroup of reptiles, simply because they are as diverse today as living reptiles.

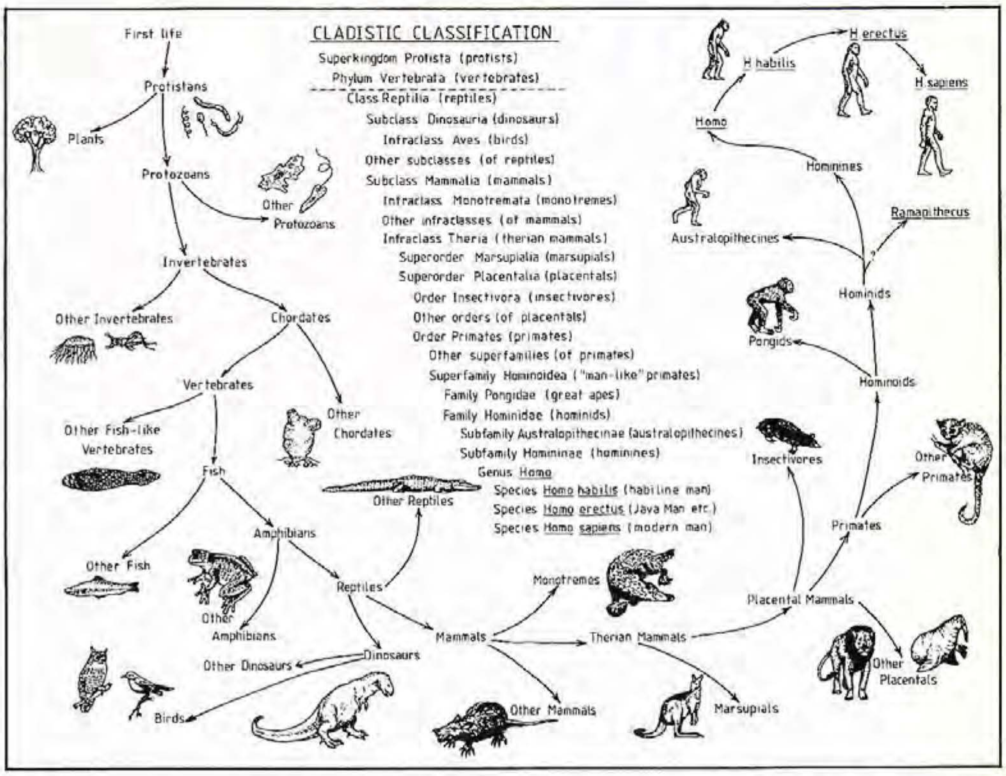
This more traditional sort of classification involves much subjective assessment and a sense of art. The result sometimes fails to reflect the growing understanding of phylogeny and this seems a pity.

Links in the chain of life

It is certainly true that there are gaps in the historical record of life, some of them quite large, despite centuries of palaeontological research. Yet it is also true that the fossil record is overflowing with creatures that form structural links between other kinds of organisms.

With time, despite a grossly incomplete geological record, palaeontology is steadily filling in gaps. In 1859, there were hundreds of thousands of gaps (some of them unrealised because the 'edges' of the gaps were unknown) that today have been filled in by 'linking' fossils — at all systematic levels.

At the most trivial level, each of us represents an undeniable 'link' between our parental genotypes and those of our offspring. At a less trivial level (species) the extinct geographically widespread *Homo erectus* was structurally intermediate between modern humans, *Homo sapiens,* and the older habiline man of Africa, *Homo habilis*.



Some evolutionists trying to express their understanding of the history of life (for example the simplified evolutionary flow diagram) are producing a rather different kind of classification — a cladistic classification. It expresses evolutionary descent as nested hierarchical sets. In this type of classification, birds are dinosaurs because they descended from a subgroup of dinosaurs. Similarly, modern humans represent a very specialised subgroup of protozoans. (For the present purpose of illustration, the phylogenetic tree shown mainly follows the events leading to the evolution of humans. The resulting cladistic classification concerns itself only with the part of the reptile radiation that led to modern humans). Chart by Jenny Hunt.

At a much less trivial level (subfamilies), the recently discovered 3.8 million year old 'Lucy', *Australopithecus afarensis,* represents a 'link' between the previously known African austalopithecines and habiline man.

At a still more fundamental level (orders), the late Cretaceous species of *Purgatorius* from North America, contemporaries of the last dinosaurs, represent a 'link' between the earliest known placental order, the Insectivora, and the later primates, our own order.

With each passing year of palaeontological discoveries, more missing parts of the evolutionary tree are found. Sometimes it is difficult to place them into an established evolutionary framework. This is most commonly the case when the group involved is poorly known, as occurs with some of the fossil invertebrates (the species of some little-known groups of arthropods or coelenterates).

However, for groups with a rich fossil record, the phylogenetic relationships of newly discovered species are commonly much more obvious. This is the case for many groups of vertebrates, and even for some groups of invertebrates (examples include trilobites, ammonites, brachiopods).

'Missing links' between higher systematic levels of organisation are often the centre of controversy between creationists and evolutionists. The creationist does not accept evidence for evolution (particularly at the higher levels such as between classes) and therefore must either ignore the fossils or attempt to trivialise any of the features that provide for the more open-minded, overwhelming evidence for evolutionary transition.

The whole concept of "missing links' is fugitive and trivial. 'Missing links' are only missing until they are found. Once found (for example *Homo erectus* between *Homo habilis and Homo sapiens),* they cannot, by definition, be 'missing links'.

Similarly, if we lacked knowledge of all reptiles, their absence would constitute a major 'missing link' between the structure of the simplest terrestrial quadrupeds, the amphibians, and the birds and mammals. But we do have knowledge of reptiles. Therefore they constitute a 'found missing link.'

To declare, as creationists are inclined to do, that the fossil record does not provide such 'links', is, therefore, utter nonsense.

For further evidence, we might consider a rather significant 'moment' in the unfolding history of the evolution of mammals.

The lower jaw of all living mammals known, from platypuses to people, articulates with the skull via a contact between the dentary bone (in the lower jaw) and squamosal bone (in the skull).

Further, there are three sound-conducting bones in the inner ear of all mammals known, the malleus ('hammer'), incus ('anvil') and stapes ('stirrup').

In reptiles, the lower jaw articulates with the skull via the articular (lower jaw) and quadrate (skull) bones. The reptilian dentary and squamosal bones do not contact.

In the reptile middle ear, there is only one bone, the columella.

Clearly, these are two fundamentally different sorts of construction. Clearly, that is, if there were no fossil record. From deposits of Triassic age, at a time just before mammals began their first evolutionary radiation, have come dozens of skulls representing a group called the "mammal-like reptiles'.

The South American representatives of this group include forms that, while a delight to evolutionists, are the stuff of indigestion for creationists. In general construction, these animals shared many reptilian as well as mammalian features.

Most curious among these features is their jaw articulation. Like any reptile, there was an articular-quadrate articulation. But unlike other reptiles and like mammals, there was also a dentary-squamosal jaw articulation. The lower jaw was hinged by both sets of bones.

In later mammal-like reptiles, the articular and quadrate bones underwent reduction and the dentary-squamosal articulation enlarged.

Reproductive isolation

Western Grey Kangaroo,
Photo A. Robertson (NPIAW)

Eastern Grey Kangaroo
Photo H & J Beste, (NPIAW)

Isolating mechanisms separating populations of a single species can of course be non-biological — such as a desert developed between areas of forest-dwelling species, or a rising seaway that separates one population on an island.

Darwin's and most modern biologists' model of speciation (the allopatric speciation model) commonly begins with geographic isolation of this kind. But geographic separation does not mean that isolated populations are different species. For speciation to occur, reproductive isolating mechanisms must have developed.

There are many kinds of reproductive isolating mechanisms. They may be behavioural, as occurs when a slightly changed courtship display or mating call of one individual no longer elicits a welcome in another. Or it may be chemical where odour hormones (pheremones) of one individual are sufficiently changed so that they no longer alert a potential partner to the presence of a willing mate. It may be physical as happens when the changed genitalia of one individual no longer fit those of the potential mate or genetic, when despite a willingness to mate, the sex cells of individuals of the two populations fail to form a functional zygote. It can also be developmental so individuals of one population become sexually mature at a slightly different time than the individuals of another population.

Hybrids are the products of matings between genetically different kinds of organisms. There are many degrees of hybrid fertility representing all degrees of development of genetic isolating mechanisms.

The individuals of most distinctly different grades of organisms (such as cats and dogs) are incapable of forming hybrids at all, let alone fertile hybrids. However, Swamp Wallabies, *Wallabia bicolor*, and Agile Wallabies, *Macropus agilis*, can produce hybrids following matings in zoos, although they are evidently sterile. Horses, *Equus caballus*, and Asses, *Equus assinus*, can produce hybrids, but only some of these are fertile. Western Australian Bush Rats, *Rattus fuscipes*, and eastern Australian Bush Rats, formerly *Rattus greyi*, produce fertile offspring and are therefore now regarded as a single species, *Rattus fuscipes*, despite the fact that they occur on opposite sides of the continent and are rather distinct. Presumably their geographic isolation was a relatively recent event.

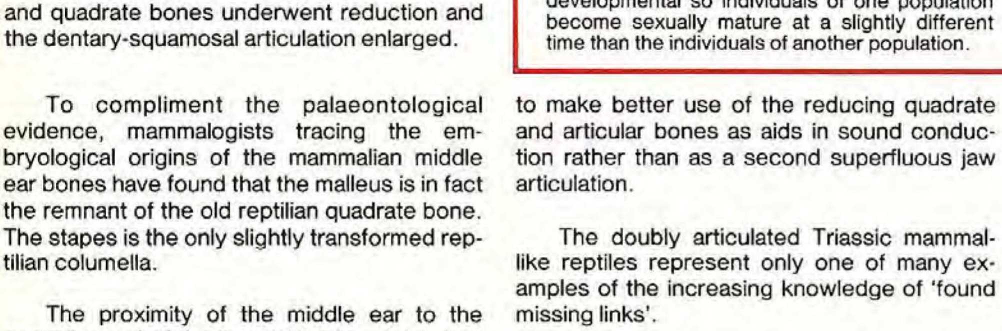
Darwin's model of gradual reproductive isolation would predict that in the course of divergence, isolated populations would progressively be capable of producing fewer fertile hybrids and eventually none at all. At this point, gradual speciation of the kind Darwin envisaged would be complete.

To compliment the palaeontological evidence, mammalogists tracing the embryological origins of the mammalian middle ear bones have found that the malleus is in fact the remnant of the old reptilian quadrate bone. The stapes is the only slightly transformed reptilian columella.

The proximity of the middle ear to the posterior end of the jaw evidently provided an evolutionary opportunity for the early mammals to make better use of the reducing quadrate and articular bones as aids in sound conduction rather than as a second superfluous jaw articulation.

The doubly articulated Triassic mammal-like reptiles represent only one of many examples of the increasing knowledge of 'found missing links'.

As each link falls into place the chain of evolution becomes more difficult to deny and another facet is added to the jewel of evolution.



Extinct links in evolution, the historical evidence for transmutation, are well-known. All living reptiles have a quadrate-articular bone joint (shown in a light tone) that hinges the lower jaw to the skull. In contrast, all living mammals have a dentary (black)-squamosal (dark tone) bone joint serving the same purpose. Extinct mammal-like reptiles include forms (for example the species of *Probainognathus*) that have a functional reptilian jaw joint (articular-quadrate) as well as an adjacent and functional mammalian jaw joint (dentary-squamosal). In the subsequent course of evolution, the steadily reducing two bones of the reptilian jaw joint ended up in the middle ear as the 'hammer' (or malleus) and 'anvil' (or incus) bones. Drawing by Jenny Hunt.

A LION IN POSSUM'S CLOTHING

by Michael Archer

Australia's mammals are world famous, both for their distinctive appearance and the fact that they include two of the most ancient living mammal groups — the primitive monotremes and the marsupials. Today Australia has more mammal families (16) than any other continent. There are 180 marsupials (kangaroos, possums, etc), three monotremes (two echidnas and one platypus) and seven families of native, placental mammals (bats, rats, the Dingo, etc).

The reason for this diversity has been Australia's isolation for over 45 million years from any other continent. Although the fossil record shows that mammals lived in other parts of the world up to 200 million years ago, the earliest evidence of mammals here is 15 million years. So the history of the proliferation of Australia's marsupials and monotremes is not known.

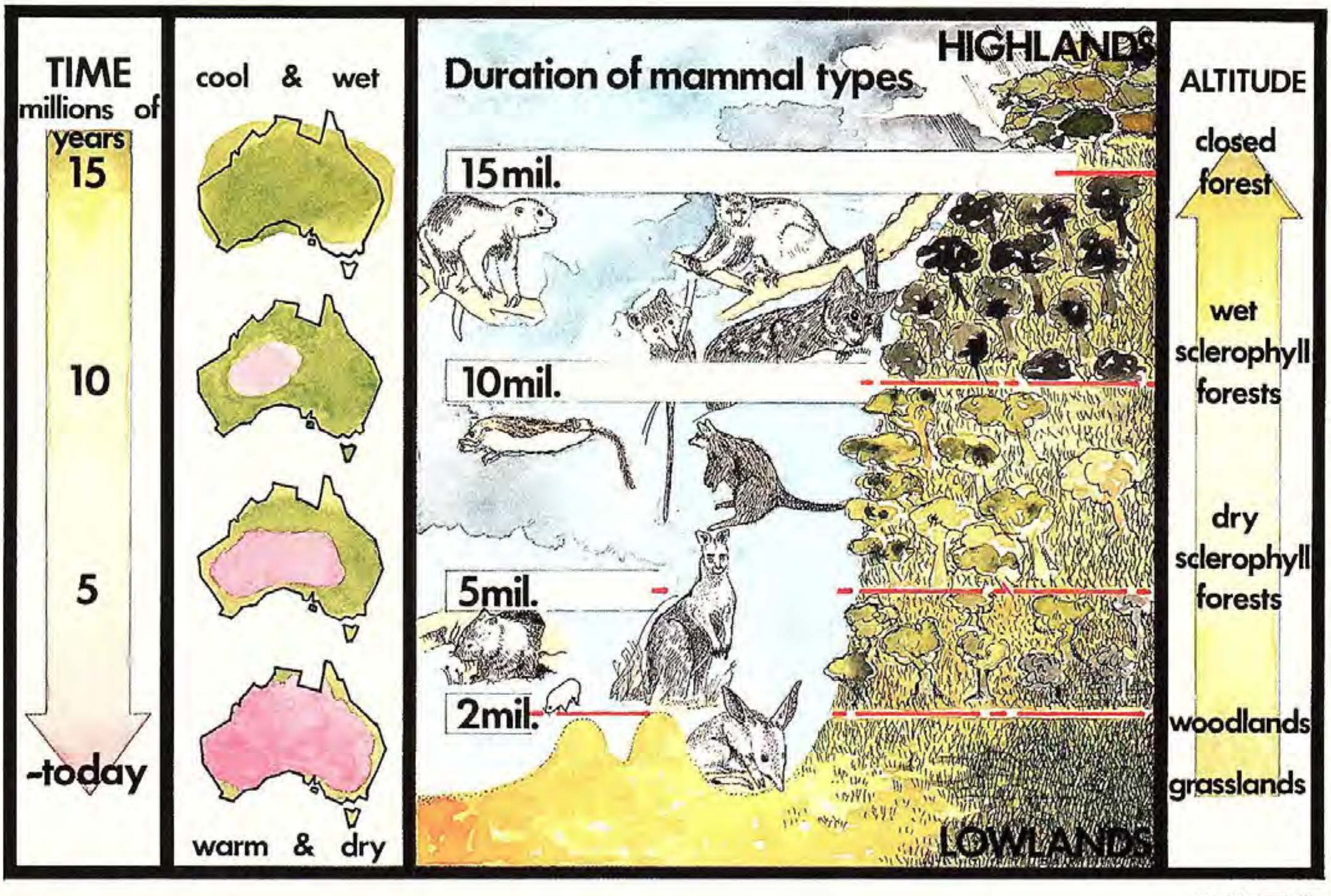
In this article on Australian mammal evolution, Michael Archer presents a history of the early research done on our mammals and a picture of how the continent looked and what type of animals roamed around it, 15 million years ago. Michael Archer, as well as being the scientific officer on the Museum's award-winning mammal gallery, is also the author of *Mammals in Australia,* published by the Museum.

1859 was a most exciting year for biology as Charles Darwin, after 23 years of thorough research, published *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life.*

In that same year, in a letter to the famous geologist Charles Lyell, Darwin said that the thing that "... first turned my mind on the origin of species" was the earlier realisation that fossil forms from any given region of the world tended to resemble the living forms of that region which replaced them. In 1837 he called this observation the law of succession of types.

Australia was catalytic in the development of Darwin's law of succession of types. Although he first noted the relationship between extinct and living forms during his travels in South America, it was probably not until he arrived in Australia in 1836 that the penny really dropped.

Here he made the acquaintance of Major



GLENN FERGUSON

Many factors influenced the evolution and distribution of Australia's mammals. Australia's continental drying out began 15 million years ago and meant the extermination of rainforest mammals from central Australia. However, the simultaneous rise of the New Guinea and north eastern Australian highlands preserved a cool rainforest habitat for these otherwise doomed types of mammals. As a result, walking up the side of a tall New Guinea mountain is rather like a walk back in time. Drawing Glenn Ferguson.

Thomas L. Mitchell, the Surveyor General of the Colony of New South Wales. Mitchell told him the exciting news of the discovery in 1830 of fossil bones in the caves near Wellington, New South Wales. These Wellington bones had been passed from one curious European naturalist to another for six years prior to Darwin's arrival in Australia. Most had agreed that they represented a curious mixture of extinct as well as still living kinds of animals and they were struck as much by the similarity of the extinct to the living forms as they were by the differences between the two.

In 1833 Lyell summarised the general opinion about these Wellington bones saying "The remains found most abundantly are those of the kangaroo. Amongst others, those of the wombat, *Dasyurus,* koala, *Phalangista* have been recognised. The greater part of them belong to existing, but several to extinct, species ... These facts are full of interest; for they prove that the peculiar type of organisation that now characterises the marsupial tribes has prevailed from a remote period in Australia ...".

This interpretation of the Wellington Caves bones evidently had a profound affect on Darwin. It was clear evidence, and the best so far available to him, for his law of succession of types. At the time of his visit to Australia, he was only 25 and intellectually facile. As Darwin later said to Lyell, his realisation of the law of succession of types, which he formulated in 1837 following his trip to Australia, was the turning point that led him to the theory of evolution.

Chewing over the first bones

As far as Darwin was concerned, the Wellington fossils probably held little intrinsic interest. Fortunately, there were many other biologists who were intently interested.

Richard Owen

Gerard Krefft

Although there seems to be some doubt about which European first discovered the Wellington Caves, there is no doubt that the local Aboriginals knew about them long before they were named by Europeans. They were known as the 'Mulwang' Caves by the local Aboriginals, who apparently feared them because *Koppa,* the 'Spirit of the Caves' lived in them. If there was a spirit, it left only bones for the first intrepid European explorers to find.

The first finding of these influential bones is usually attributed to George Ranken, a very respected colonist and magistrate from Bathurst, New South Wales. He evidently let himself down a precipitous descent by rope fixed to what appeared to be a projecting point of solid rock. According to the Reverend Dr John D. Lang, who wrote about the finding in 1831, the projection broke "... in consequence of the weight attached to it ..." and "... it was ascertained to be a large thigh bone, I conceive, of some quadruped much larger than the ox, or buffalo, and probably of the Irish Elk, the rhinoceros, or elephant".

Lang was a staunch creationist, a believer in the 'biblical deluge' and supporter of Buckland's views. Curiously, when the fossil bones were shown to the local Aboriginals" ... in the absence of persons trained in comparative anatomy ..." they nevertheless identified them much more appropriately as "Bail that belongit to Kangaroo" and "Bail that belongit to emu".

The subsequent determination of these bones (and others collected later) by European anatomists, such as Hunterian Museum Conservator William Clift and Professor Robert Jameson, as mostly species of living marsupial genera as well as a few of extinct kinds, paved the way for Darwin's formulation of the law of succession of types.

This keen early European interest in the significance of Australia's zoological antiquities also served to whet the appetite for more.

The famous British anatomist Professor Richard Owen, a man who curiously was to become one of Darwin's arch antagonists and never entirely relinquished his belief in 'creation', devoted almost half a century to the study of Australia's extinct mammals.

From 1834 to 1884 he solicited and described extensive collections from the Wellington Caves, the Darling Downs, Victoria and other Australian sites without once setting foot in Australia. Through the Colonial Secretary, he successfully persuaded the New South Wales Parliament to finance (to the tune of £200) expeditions to discover fossil

The uniquely Australian history of mammal evolution started about 45 million years ago with the separation of Australia from Antarctica. Presumably it had aboard at least an ancestral monotreme and probably a few early marsupials. Drawing Colin Stahel.

bones and send them onto him for examination. Money was also provided to help finance the illustrations for his *Researches on the fossil remains of the extinct mammals of Australia,* a monumental work finally published in 1877. This half century of Owen was a most fascinating and vigorous period of growth for Australian palaeontology.

Owen's open and stubborn antagonism to Darwin's ideas, however, eventually placed him at odds with most of his colleagues in Europe and probably to some extent frustrated the development of evolutionary thinking in Australia.

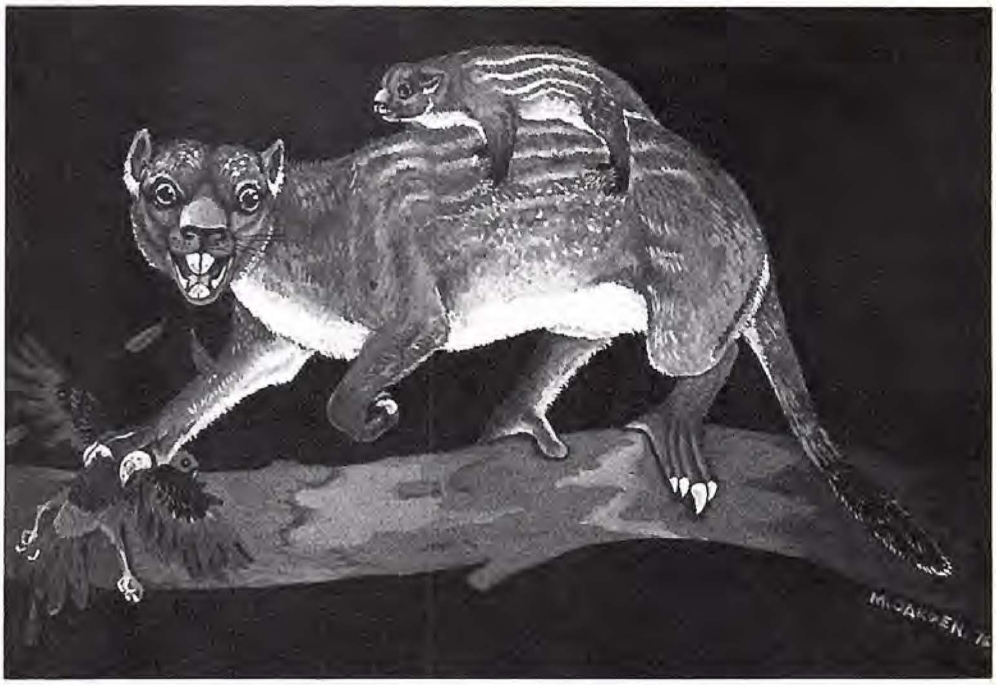
Presumably because he was a creationist, Owen rarely speculated about the evolutionary history of marsupial families. The idea, for example, that kangaroos might have evolved from possums or some other group would not have occurred to him. Thomas Huxley said (in a letter to William Macleay on 9 November, 1851) that ".... Owen is an able man, but to my mind not so great as he thinks himself. He can only work in the concrete from bone to bone, in abstract reasoning he becomes lost".

Whatever Owen's limitations may have been, few palaeontologists have contributed as much to the structural interpretation of the creatures of a whole continent as he so enthusiastically did for Australia.

Fortunately, as Owen gradually fell from grace in European scientific circles as Darwinism prevailed, a few scientists in Australia, less imbued with the idea of 'creation' than Owen, also began to devote themselves to the pleasures of palaeontology. Most notable among them was Gerard Krefft. A head-strong German immigrant to the Victorian goldfields in 1852, who became acting curator of the Australian Museum in 1861, Krefft was directed by the New South Wales Parliament to continue the search for more bones.

Perhaps unavoidably, these two stubborn anatomists, at opposite ends of the world, eventually came into scientific conflict. Where Owen bitterly fought Darwin's ideas, Krefft was one of the few in Australia to readily accept them. Although at first Krefft seemed to willingly make his own drawings, casts and specimens available to Owen for study, this quickly changed when the two fell out entirely over interpretation of the life style of one of the most fantastic of the extinct Wellington caves creatures, the Marsupial Lion, *Thylacoleo carnifex*.

It is appropriate in this historical peek at early Australian palaeontology to give brief consideration to the history of interpretation of the Marsupial Lion. This is because early controversy over interpretation of this animal in large part led for the first time to a willingness by Australian palaeontologists to openly challenge the conclusions of their English mentors.



The extinct Marsupial Lion was evidently an incredibly efficient leopard-sized arboreal carnivore. After its extinction, probably less than 30,000 years ago, possums and Aborigines alike must have passed easier nights. Debate about its culinary preferences went on for almost 150 years and marked the beginnings of an unwillingness by some Australian palaeontologists to unhesitatingly accept the scientific conclusions of the English palaeontologist Sir Richard Owen. Drawing Margaret Oakden.

Controversy flared because this bizarre creature from the caves, unlike the kangaroos and dasyures it was found with, did not fall clearly into any particular modern mould.

Owen's first look at bits of this beast from the Wellington Caves, left him very puzzled. Although he presented illustrations of teeth of the animal in Mitchell's "Three expeditions..." in 1838, he did not comment on them. After more material was sent to him, he eventually concluded 21 years later that this animal was "... one of the fellest and most destructive of predatory beasts."

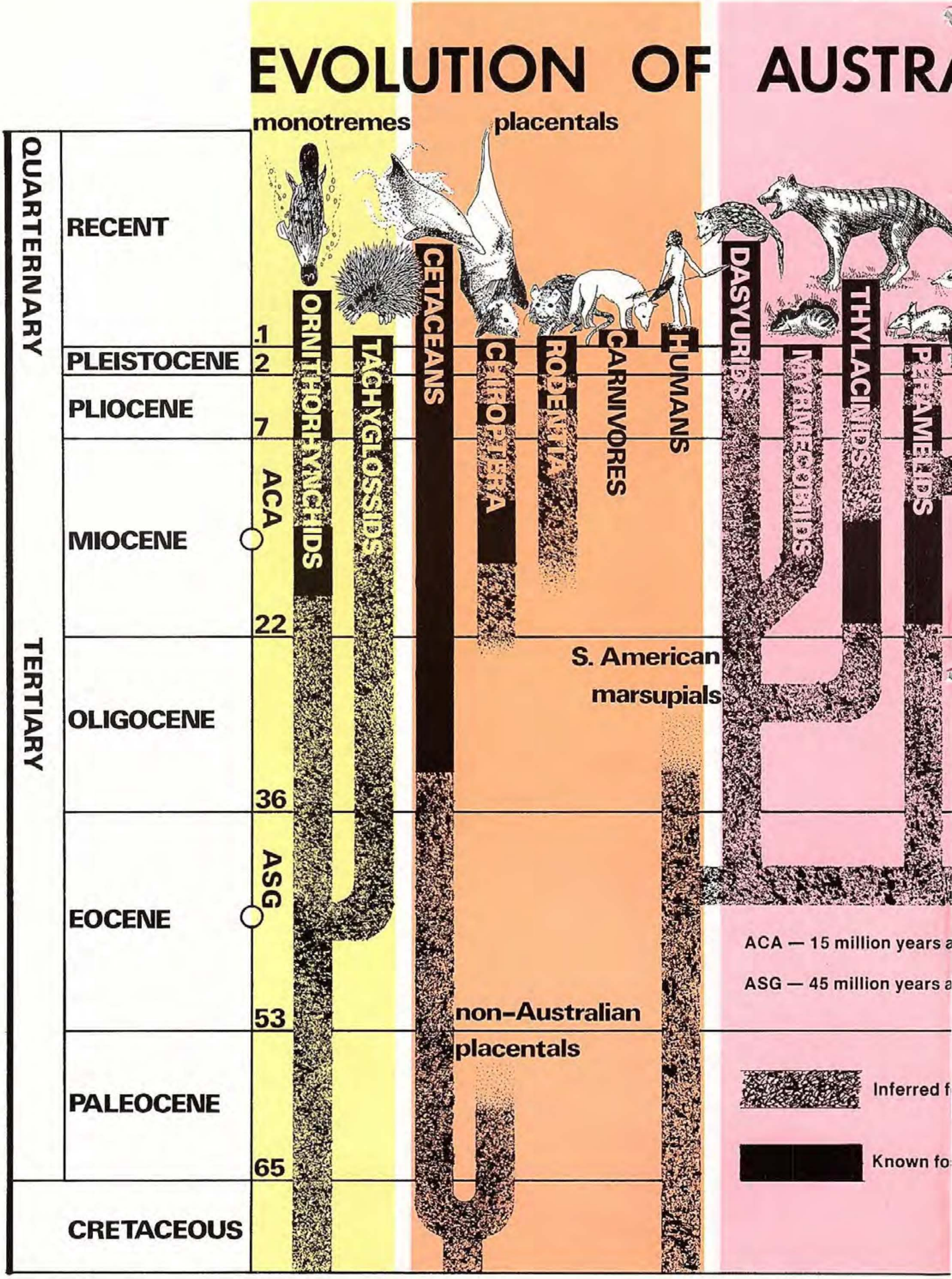
Although Krefft provided many of the specimens upon which Owen's convictions were based, **he** did not see in this extinct creature the look of a carnivore. Instead, Krefft believed it to be a gigantic rat-kangaroo and later a "... lion in phalanger hide".

At first in letters to Owen, and later in publications, he tried ineffectually to convince Owen of what he perceived as errors in the predatory beast model. Krefft even took the conflict to Darwin who in a letter dated 17 July, 1872 responded sympathetically that "It is lamentable that Professor Owen should show so little consideration for the judgement of other naturalists, and should adhere in so biggotted a manner to whatever he has said. This is a great evil as it makes one doubtful on other points about which he has written." Owen reacted equally caustically in a letter four years later to W. B. Clarke about Krefft that "As to that unfortunate man, who seems to have tried to smash all evidence of Thylacoleo in the cave exploration, a compassionate silence is one's best return."

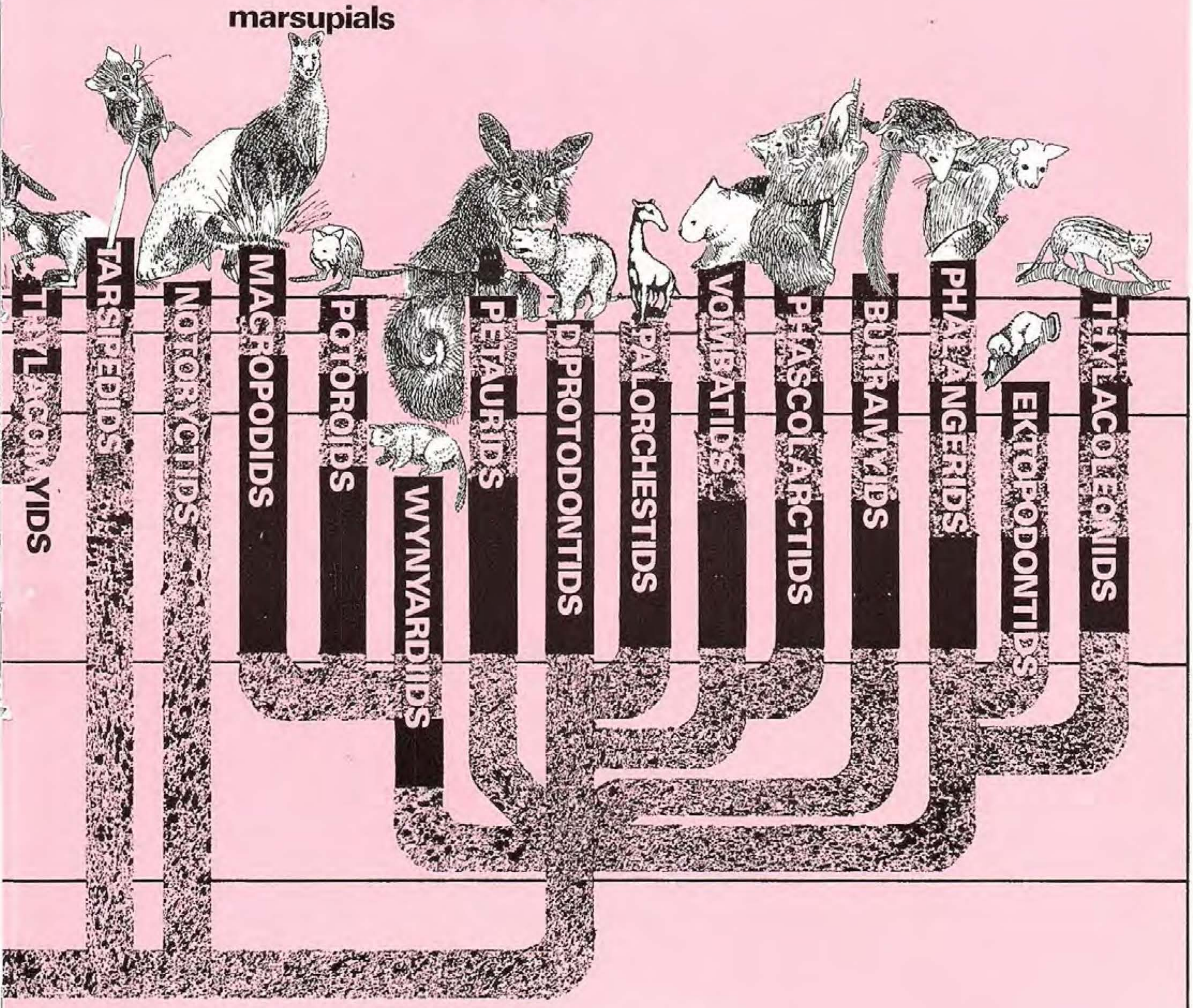
Although subsequent interpretations of this animal, based on ever more complete materials, have now swung the pendulum of scientific opinion firmly towards Owen's point of view, throughout the 150 years since its discovery, there was almost continuous debate about its lifestyle. For example, the eminant American palaeontologist Professor E. D. Cope suggested in 1882 that it fed on crocodile eggs. In 1883, the then Director of the Queensland Museum, C. W. DeVis, suggested that as an analogue of the hyaena, it fed on bones and although it "... may not have been as fell a destroyer as its name implies ... its functions, though restricted to clearing away the dead and dying from amongst the living, were no less useful. Poetry must reluctantly give place to lowlier prose."

In 1898, Scottish doctor in New South Wales, Robert Broom (later of South African ape-man fame), tackled Krefft's hypothesis of herbivory pointing out that unlike the Marsupial Lion, herbivores normally had teeth suited for grinding up plant material. Not to be outdone by Broom's pronouncement, Dr Charles Anderson, then Director of the Australian Museum, pointed out in 1929 that the teeth of the Marsupial Lion were not in fact suited for bone crushing. He went on to suggest that the peculiar combination of enormous sectorial premolars and reduced molars would nevertheless enable the animal to peel and eat the melon-like fruits of native plants or cycad seeds. With this image of the leopard-like Mar-

EVOLUTION OF AUSTR



ALIAN MAMMALS



go, approximate time of arrival of Australia in its present position near Asia.

jo, approximate time of separation of Australia from Gondwanaland.

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Glenn Ferguson

supial Lion using its bizarre teeth to peel melons, Anderson was definitely among the last to defend the idea of herbivory.

Most recently, detailed studies of tooth wear and of almost complete skeletons have, it seems, fairly well put the lid on hypotheses about herbivorous Marsupial Lions. We now know that its feet and limbs suggest it was arboreal, its hand suggests it was predatory, and details of tooth wear and jaw mechanics strongly suggest it used its enlarged lower incisors for stabbing and its enormous premolars for shearing flesh.

So, the idea of carnivority went full circle, but yet did not really arrive at the same point. Professor Owen was evidently correct in his first perceptive assessment and Krefft was evidently wrong.

But, the proof of the idea did not come from further studies and pronouncements by European anatomists. It came instead from a rapidly growing and rigorous community of Australian palaeontologists. The fiercely independent Krefft was just the beginning.

New patterns and more puzzles

Virtually all of the Australian fossil mammals involved in the feuds and debates of the last century were Pleistocene in age (less than 2 million years old). The Wellington Caves fossils may be no more than 50,000 years old. This part of Australia's fossil mammal record is a mere veneer over a very ancient record.

The Twentieth Century was excitingly ushered in when in 1900 Sir Baldwin Spencer described *Wynyardia bassiana*, a possum-like marsupial. This was the first Australian mammal to be named from a Tertiary deposit — a site older than about 2 million years. The site later proved to be about 21 million years old. As fate would have it, this early Miocene fossil is still one of the oldest known Australian mammals, give or take a few million years, and so far the only one named from any deposit older that 15 million years.

In fact, we know nothing at all about mammal evolution in Australia prior to about 23 million years ago. This state of affairs is maddening.

We know mammals had a track record in other parts of the world as early as 200 million years ago, in the late Triassic Period. We also know that Australia was part of Gondwanaland until 45 million years ago and **must** have shared groups of mammals with South America and Antartica because mammals had to enter Australia from the south **before** Australia broke free and drifted north.

So where are these older mammals in the Australian fossil record? What did the first mammalian inhabitants of our continent look like? How many different kinds were there? Which of those groups were the ancestors of Australia's living mammals? How long ago did bats (Australia's first native placental mammals) arrive on this continent? Did placental mammals arrive with the original marsupials? And so on.

Some of the kinds of Australian mammals that survived the last 15 million years of continental drying out have done so in part by gradually evolving a reduced need for free water. Some have been so successful that when rain does make one of its notoriously unpredictable appearances in central Australia, it may have a comparably unpredictable effect. Drawing Colin Stahel.

The many intriguing questions about the mammals that lived during this 180 million-year-long dark age demand answers which we as yet simply do not have. A great deal more field work must be done before the older record even begins to reveal itself.

By the earliest time for which we do have a reasonable record a fossil mammals in this continent (about 15 million years ago), most of Australia's mammals had already differentiated into the families that we see today. In other words, the oldest record we have is still much too young to reveal, by fossil intermediates, precisely how, the various families of Australian mammals are related to one another.

These are the puzzles. Yet, some facts and some patterns have also become clear over the last thirty years or so.

A mushrooming menagerie of ancient mammals

In the time prior to 1955, 29 Australian Tertiary mammals were described. Almost half of these were whales. Since 1955, a further 54 have been described, almost two thirds of the total known, and all except one were terrestrial mammals.

This very recent mushrooming of knowledge about Australia's older mammals is in large part the result of the pioneering exploratory work of Professor R. A. Stirton begun in 1953. His ground-breaking field trips into the remote outback of Australia, and those of his students and colleagues, have been a major source for much of the new material.

Although the total number of Australian Tertiary mammals so far known (83) is miserably poor by world standards, it includes representatives of kinds of mammals known from nowhere else in the world. For example, the marsupial ektopodontids, although possums in the broad sense, were also decidedly rodent-like and, perhaps significantly, vanished from the Australian record at the same time (4.5 million years ago) that placental rodents appeared.

The Marsupial Lions noted above, now accepted as carnivores, were the most specialised mammalian carnivore that ever evolved. The degree to which they reduced their molar teeth and enormously enlarged their meat-cutting third premolar has been unmatched by even the largest of the placental lions. Ongoing reconstructions of the marsupial palorchestids reveal herbivorous cow-sized creatures with short trunks, long ribbon-like tongues, slender limbs and enormous laterally compressed koala-like claws. No living creature anywhere in the world seems to serve as a suitable model for these regretably extinct marsupials.

Miraculous mountains and sand

Much of the story of Australia's extinct mammals has contributed to an understanding of the intimate relationship between the evolution of the beasts and of the land in which they live. Modern arid Australia is an atypical Australia and the majority of modern mammals regarded to be characteristic , such as the Red Kangaroo, are also decidedly atypical.

The faunas of central Australia in the middle Miocene (15 my ago) indicate a much wetter climate than occurs at present. Central Australia contained extensive forests (there are heaps of possums and koalas from the Simpson Desert, some even suggestive of rainforest), and large probably permanent inland bodies of water (flamingos, large crocodiles, tonnes of turtles) or at least perennial rivers (freshwater dolphins were even present in the Lake Frome area). The subsequent change in these faunas through time is consistent with an interpretation of progressive climatic deterioration of the kind that most other continents were suffering as the world headed towards the Ice Ages of the Pleistocene.

Range contractions are evident because cuscuses and other kinds of rainforest mammals now restricted to northeastern Queensland and New Guinea were present in central Australia in the Miocene. There was a gradual changeover among herbivores from browsing types to grazing types (an explosive radiation of grazing kangaroos occurred about five million years ago).

It is also clear that many of the forms known at present from the older forest-adapted Miocene faunas closely resemble the kinds of animals living now in the highlands of New Guinea and differ markedly from forms presently occurring in the inland of Australia. In fact, a walk up a New Guinea mountain is rather like a walk back into time.

Much of this story of Australian mammal evolution during the last 15 million years reflects the geological and climatic history of Australia. Prior to the Miocene there is little evidence for the existence of the distinct biogeographic regions found today. At that time Australia was widely covered by rainforest. Rainforest—sclerophyll—forest-types of mammals (and probably other animals) were dominant. Temperatures were evidently cool and rainfall abundant. After, or simultaneous with Australia's arrival into the Asian region (15 my ago), the New Guinea highlands began to rise and the Great Divide continued to rise. This mountain building probably created a rain shadow which, combined with Australia's loss of a major northern maritime oceanic circulation, the progressive drop in world temperatures and reduction in world precipitation, brought about a change in the vegetation across Australia.

The rainforests gave way to open forests and then to grasslands and savannah woodland. Simultaneously, the mammal (and other animal) faunas changed, possum numbers and browsers decreasing in favour of open rangeland non-arboreal forms.

By about 17,000 years ago, climatic deterioration had reached a peak with an extremely arid phase. Probably as a result of this change (and/or human arrival perhaps 40,000 years ago), the last of the giant marsupial browsers died out and the whole fauna of central Australia became the arid-adapted one familiar to us today. About the same time, many of the now characteristic desert features such as the salt lakes and sand dunes became the dominant features of inland Australia.

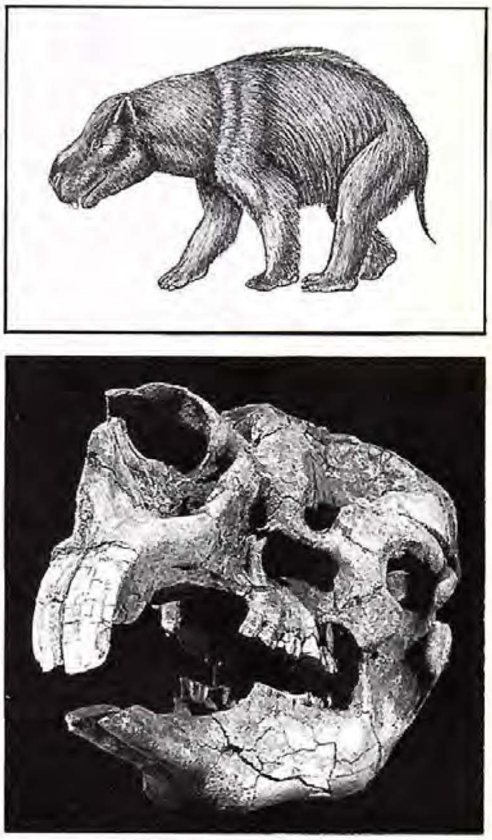
Yet, the rising of the New Guinea highlands and the Great Divide were important to Australia's mammals for another reason. In their rising and elevation into cooler altitudes, they retained the precipitation which was not available in lowland central Australia. Consequently they provided a habitat for a bunch of mammals of essentially mid-Miocene character and preserved them from the sizzling aridity that overtook central Australia — a more miraculous intervention to save the otherwise doomed inhabitants of Australia's tropical Miocene paradise would be difficult to imagine.

The condemned remnants of the pan-Australian mammal groups left in central Australia gained in other ways. We know they gained the opportunity to undergo rapid and divergent evolution to produce what is now Australia's highly distinctive arid-adapted mammals.

The future for studies of Australia's past

Certainly some stories about the development of Australia's mammals are coming together. But others have not yet begun to surface. These total-ignorance frontiers include:

1. The unknown pre-Miocene Tertiary record for Australian marsupials and bats. The recent discovery of Eocene polydolopid marsupials (extinct marsupials otherwise known only from South America) from Seymour Island in the Antarctic strongly suggests that we will one day find a most extraordinary collection of mammals in the early Tertiary record of Australia, the time crucial to an understanding of the first radiation of Australia's mammals.



The *Diprotodon* roamed Australia during the last one to two million years and may have become extinct as recently as 20,000 years ago or even later. It was the largest known marsupial and was a solidly built plant eater about the size of a large rhinoceros. Drawing Bodo Matzick, photo of *Diprotodon* skull, John Fields.

2. The totally unknown record of Australian mammals from the Mesozoic Era (older than 65 my ago). One flea from Cretaceous sediments in Victoria, said to be a mammal-biting flea, is at least suggestive that the bones of the furry victim are there waiting to be found. These Mesozoic mammals were among the last that Australia shared with the rest of the world.

Both of these Australian palaeontological 'holy grails' are the subject of continuous field work 'crusades'. These older mammals and the answers they will provide must be there. It will only be a matter of time before they are found. In the meantime, the last 20 million years of the Australian mammal story continues to unravel and amaze. This is important because as long as it continues to unravel and Australians continue to be curious about their continent's past, the fascinating work begun by Ranken, Mitchell, Owen and Krefft so long ago, still has no end in sight.

Fifteen million years ago central Australia was a tropical paradise with trees, and mammals characteristic of rainforests. As the continent began to dry out, these indicators of a lush green heart began to vanish. Drawing Colin Stahel.

REVEALING THE SECRETS OF LIFE'S HISTORY

by Alex Ritchie

Ever since 1859 and Darwin's bestseller, *The Origin of the Species,* there has been a rapid escalation in the use of fossil evidence to support the theory of evolution. Today scientists recognise two million living species of plants and animals, as well as 250,000 extinct species.

The last 14 years bear witness to some of the world's most important fossil discoveries. One of the most exciting was the discovery of skulls and skeletons of two mammal-like reptiles, a small carnivore and a large herbivore in 200 million year old rocks, 600 km from the South Pole. These animals were known for many years from rocks of the same age in the Karoo of South Africa and their appearance in Antarctica proved that the continents were once linked.

Alex Ritchie, Curator of Palaeontology at the Australian Museum, is particularly interested in the evolution of vertebrates and specialises in the earth's ancient fish.

Precambrian fossils from Ediacara, South Australia. Top, *Mawsonites,* a jellyfish and below, *Dickinsonia,* a probable annelid.
Photos Kate Lowe.

The idea that fossils represent the remains of animals and plants of the long distant past dates back to 450BC and the Greek, Herodotus. In the 15th century Leonardo described fossils and in 1669 Steno convincingly demonstrated their true nature. He showed that fossil teeth ("tongue-stones") from the rocks of Malta were almost identical to teeth of living Mediterranean sharks.

Before the 19th century fossils were widely sought after and collected but their true significance and nature was only slowly understood. Scientific landmarks such as James Hutton's discoveries in Scotland, during the late 18th century laid the foundations of modern geology. He realised that the Earth had an extremely long, complex history and had not been created in an instant as biblical tradition required. Hutton showed how geological phenomena of the present could be used as the key to the past and he saw "no vestige of a beginning, no prospect of an end." The significance of fossils as a means of relative dating of rocks was finally recognised by William Smith who used them to identify and correlate sedimentary formations over much of England.

By the early 19th century the basic pattern of the geological column and the sequence of fossil remains in it had been worked out. This was mostly done by palaeontologists who were creationists and opposed to any suggestion of evolution. They were convinced by the evidence of the fossil record, that many of the animals and plants found in the rocks represented forms no longer existing on earth. They were extinct. The older the rock formation the larger the proportion of extinct genera and species.

Various explanations were proposed. Cuvier, the leading French anatomist, suggested 'biblical flood' was only the latest of many, each sweeping away the life of a previous creation to be replaced by a new, more advanced suite of organisms. This catastrophic view became progressively less defensible as evidence accumulated — the time was ripe for a radical new interpretation which is what Darwin helped to provide.

Darwin, trained as a geologist, was familiar with the known fossil record and the problems of its interpretation. During the Beagle voyage he made many original geological and palaeontological discoveries. His strength was as a synthesiser, integrating the evidence from the fossil record with the insights he gained from living plants and animals around the world.

Rather surprisingly in *The Origin of Species* in 1859 his use of fossil evidence to support his case was curiously limited, even defensive. But if we remember the limits of palaeontological knowledge at the time this is hardly surprising. Today we probably recognise around two million living species of plants and animals and perhaps about 250,000 extinct species represented by fossils. By 1850 it is estimated that some 2000 fossil plant species and 25,000 fossil animal species had been described. Practically all of these came from western Europe and even there organised research was in its infancy. Across the Atlantic the rich fossil deposits of North America were unknown or barely scratched and Africa, South America, Asia and Australia were unexplored geologically.

In two chapters entitled *On the Imperfection of the Fossil Record* and *On the Geological Succession of Organic Beings,* Darwin discussed the fossil record. Some of the aspects which caused him most concern included:—

- estimates of the Earth's age and the

An Outstanding Achievement by an Outstanding Australian

The name of Dr George Mackaness, O.B.E., M.A., Litt. D. (Melb), D. Litt. (Syd), Hon D. Sc. (Syd), F.R.A.H.S., stands high in many fields, as educationist, historian, author. Born 1882, Dr Mackaness was in charge of the Department of English at Sydney Teachers' College from 1924 to 1946. He was the author of over 70 books and research articles and was an outstanding researcher of Australian history. His research at Sydney's Mitchell Library led him to scores of important original works which up to then had remained unpublished. This discovery inspired him with a dream. The dream was to publish privately this vast storehouse of Australian history so that others could share it with him.

So in 1935 he published the first of his AUSTRALIAN HISTORICAL MONOGRAPHS — a task he continued unabated for the next 27 years. At the end, in 1962, he had researched, edited and in many cases translated the material for 46 volumes of monographs — a stupendous feat, unrivalled in Australian publishing history. Many of the earlier monographs were published in limited editions, of only 40 copies, whilst even the later volumes were produced in editions of only a few hundred copies — so they have always been scarce, known only to specialist scholars and antiquarian book collectors.

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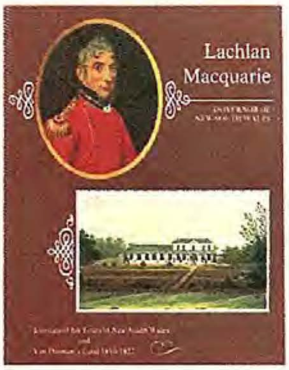

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various divisions of geological time

- the incompleteness of the fossil record
- the sudden appearance of all major groups in the fossil record and the apparent absence of Precambrian fossils
- the absence of intermediate stages between major groups
- the rates of change within and between species, and many more.

Darwin put forward various explanations to account for these deficiencies and obviously anticipated that a fuller knowledge of the record from all continents would provide many of the answers. To a large extent his expectations have been justified — in other respects we are still confronted with major gaps in our knowledge.

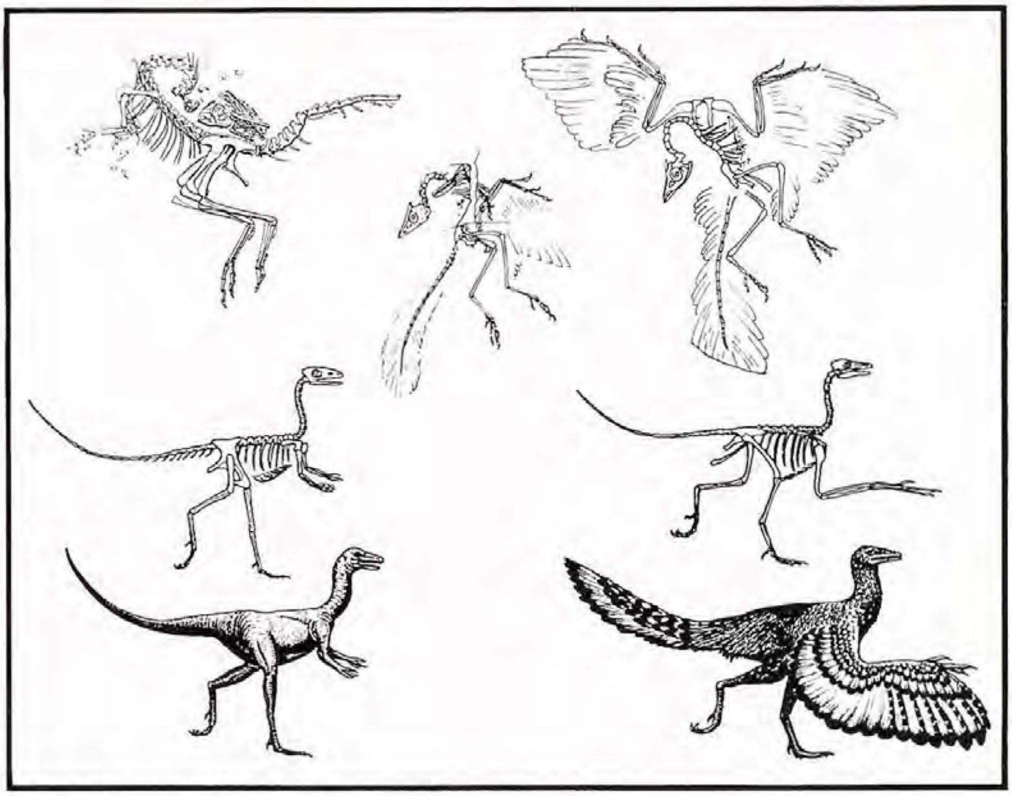
Many of Darwin's palaeontological contemporaries remained bitterly opposed to his ideas (Owen, Agassiz and others) but by the time of his death in 1882 a new generation of fossil hunters was dramatically changing the scene.

During his lifetime one of the most spectacular of the 'missing links' came to light in the form of *Archaeopteryx*, the oldest known bird from Late Jurassic rocks of Germany. Hardly a year has gone by since without major discoveries extending our knowledge of known and unknown groups of animals and plants all over the earth. Nothing has come to light since which seriously undermines Darwin's basic concept of descent by modification through natural selection operating over immense periods of geological time — and despite the protestations of creationists the time was available.

In the 19th century there was no accurate method of calculating **absolute** ages for rocks and the fossils they contained. As William Smith demonstrated, fossils are ideal for the **relative** dating of formations, based on the sequence in which genera and species appear in and disappear from, the geological column. Estimates for the age of the Earth based on cumulative thicknesses of sediment and the time required to deposit them or on the salinity of the oceans gave widely varied figures.

Physicists of Darwin's time such as W. Thomson (later Lord Kelvin) used thermodynamic calculations of the rate of crustal cooling and obtained an age of 200 million years for the Earth, far less than Darwin believed necessary for the origin and diversification of all living forms by natural means. Despite Kelvin's opposition (and reputation) Darwin stood his ground. He was vindicated long after his death when the discovery of radioactivity revealed an unsuspected source of heat within the Earth (and in the Sun) which showed Kelvin's figures to be far too conservative.

We now know from various sources, terrestrial and extra-terrestrial, that the Earth is at least 4,600 million years old, that life originated over 3,500 million years ago and that abundant remains of advanced, complex organisms, the Metazoa, first appear in rocks deposited around 600 million years ago. The same radioactivity which maintains the earth's internal heat also provides us with various methods of calculating the absolute ages for certain types of rocks, igneous and metamorphic, using the fixed decay rates of radioactive elements.



***Compsognathus* (left row), a small carnivorous theropod dinosaur and *Archaeopteryx* (right row) the oldest known bird, both from Late Jurassic rocks of southern Germany. The small *Archaeopteryx* (centre) from Eichstatt, was for several years misidentified as a *Compsognathus* until extremely faint feather impressions were detected. (After Ostrom, Wellnhofer and Halstead)**

When considering Precambrian life, Darwin remarked "if our theory be true, it is indisputable that before the lowest Cambrian stratum was deposited long periods elapsed, and during these periods the world swarmed with living creatures..... to the question why we do not find rich fossiliferous deposits belonging to these assumed earliest periods prior to the Cambrian system, I can give no satisfactory answer."

Knowledge of life older than 600 million years is still sparse but the broad outline is clear enough. The oldest single celled organisms without a nucleus (prokaryotes) come from rocks over 3000 million years old. Some formed massive layered calcareous structures, stromatolites, living examples of which occur off the coast of western Australia.

Around 2000 million years ago a more diverse microflora of tiny spheres and filaments was present, oxygen accumulated in the atmosphere and some time afterwards cells with a nucleus (eukaryotes) evolved and diversified. By 1100—900 million years ago sexual reproduction had been developed making possible genetic variation and recombination. Both processes are necessary for the progression from micro-organisms to more complex organisms, the Metazoa.

The 900 million years old Bitter Springs Formation near Alice Springs, in the Northern Territory, has produced some of the finest microfossils of this stage. Evidence of more highly developed animals, mainly impressions of soft-bodied forms and occasional trackways, comes from rare but widespread finds in rocks of the Late Precambrian, 1000—600 million years ago.

Then, quite suddenly at the beginning of Cambrian times, most of the major groups (or phyla) of animals known today, the annelids, arthropods, brachiopods, echinoderms, molluscs etc, appear in quantity and considerable diversity, indicating they had been in existence and evolving for some considerable time in the Late Precambrian. The suddenness of their appearance in the fossil record is partly explained by the almost simultaneous development of mineralised skeletal structures, in most of these lines, independently.

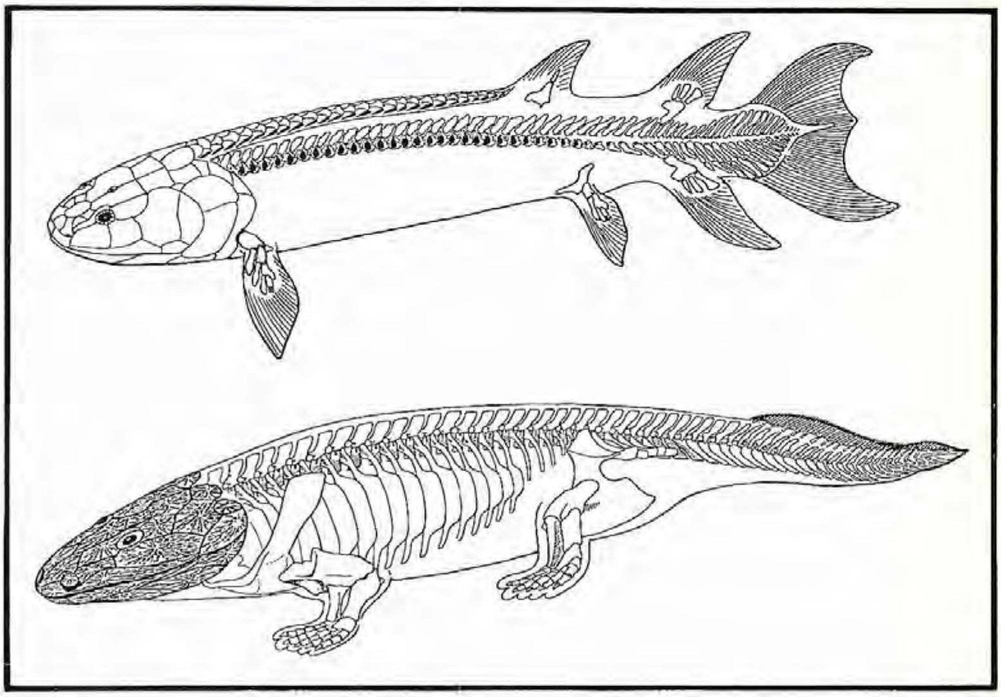
Only with the development of such hard parts did the fossil record become prolific and much more informative. But it should never be forgotten that the record is still heavily biased against the preservation of soft-bodied organisms. This can be seen in the comparison of two remarkable fossil faunas discovered this century, one from the Late Precambrian of South Australia, the other from Middle Cambrian rocks of western Canada, both of with would surely have delighted Darwin.

The Late Precambrian Ediacara fauna of South Australia, about 650 million years ago includes a wide range of soft-bodied organisms, preserved as detailed impressions in fine sandstone. Some forms are attributable to living groups, others are quite unlike anything alive today or found elsewhere in the fossil record. Most abundant are the medusoid jellyfish, circular to ovate disc-like impressions with concentric, radiating or lobed markings (such as *Mawsonites*). Also common are large, frond-like, stalked organisms (*Rangea*), tentatively assigned to the pennatulids or modern sea-pens. A small, elongate segmented animal (*Spriggina*) with a crescentic head might be an annelid, a forerunner of trilobites or an ancestor of both. Large, flattened oval animals with a central groove and radiating ridges (*Dickinsonia*) probably represent another line of annelids. One especially bizarre form (*Tribrachidium*), a circular organism with three curved, radiating ridges, is quite unlike anything known, dead or alive.

The Ediacara fauna of South Australia, although the best preserved and most diverse Precambrian fauna known, is not unique — rare remains of similar soft-bodied animals are known from 800—600 million year old rocks of Africa, North America, Europe and Asia. These tantalizing glimpses of Late Precambrian life confirm what Darwin suspected, that the evolutionary radiation of complex metazoans was well advanced in the Earth's oceans long before the first hard-shelled animals began to appear in any abundance in the Cambrian.

Early Cambrian seas supported a diverse biota of arthropods (mainly trilobites), brahiopods (mainly simpler inarticulate forms), echinoderms (several groups present but rarely found articulated), primitive molluscs, sponges, coelenterates (scyphozoans and hydrozoans but no true corals) and conodonts (extinct animals of unknown affinities with complex mineralized tooth-like parts), all forms with easily fossilised hard parts.

But it is widely recognised that the fossil record is extremely lopsided and unrepresentative — of the 30 or so animal phyla living today more than half consist of species with few or no hard parts and with virtually no known fossil record. This is why the Middle Cambrian Burgess Shale of western Canada is so important.



A crossopterygian lobe-finned fish, *Eusthenopteron*, from Canada, and the oldest known amphibian, *Ichthyostega*, from East Greenland, both found in Late Devonian rocks.

The Burgess Shale, discovered in 1909 by Charles Walcott in the Canadian Rockies, has recently been recollected, analysed and confirmed as one of the most remarkable fossil assemblages ever discovered. The fossils come from a fine-splitting black shale of Middle Cambrian age, deposited about 530 million years ago. Many deposits of the same age around the world contain abundant and well-preserved marine faunas consisting of a few genera of trilobites like *Xystridura* from near Mt. Isa in Queensland and some primitive brachiopods.

The Burgess Shale has produced an extremely rich and diverse fauna of marine organisms, preserved in exquisite detail. Of the 150 or so species identified to date (belonging to 119 genera) only about one-third had mineralised hard parts. The rest represent organisms that were largely or entirely soft-bodied. The latter include at least 30 genera of 'arthropods' and smaller numbers of 'worms', coelenterates, hemichordates, at least one chordate (the oldest known) and many other animals of unknown affinities. Most of the Burgess Shale species are only known from this locality — 10 of the 18 phyla of animals present here are unknown elsewhere.

Stratigraphic and sedimentological studies of the Burgess Shale show that this rich marine fauna lived on a muddy bottom at a depth of at least 100 metres. It is not thought that it represents an isolated or exceptional habitat. Whittington, a palaeontologist restudying the specimens, suggests that while "the preservation is a one-in-a-million chance, the fauna may well be much more representative of Cambrian faunas than those usually collected, composed only of hard parts."

The intriguing feature of the Burgess Shale fauna is that while it very effectively demonstrates the incompleteness of the normal fossil record, the forms which it does reveal do not provide us with intermediates between major groups. Even in groups which are structurally similar, the worms or the arthropods, the species present are not closely related. Indeed the diversity of arthropod-like forms is so great that it has been suggested that one phylum is not adequate to house them — various researchers on modern forms have suggested that 'arthropods' represent several phyla which have independently developed an exoskeleton and jointed legs.

Two genera in the Burgess Shale may be ancestors of later major animal groups. *Aysheaia*, an arthropod-like animal with a plumpish body and stubby conical legs, closely resembles the living onychophore, *Peripatus*. Although *Aysheaia* was marine and *Peripatus* is terrestrial, living in damp undergrowth, the resemblance is remarkable. The Middle Cambrian *Aysheaia* represents the kind of ancestor which could have given rise to myriapods and insects whose fossil record only goes back to Late Silurian or Early Devonian times.

The other likely ancestor is *Pikaia*, once considered a polychaete worm, but now thought to be the earliest known true chordate. Known from over 30 specimens in the Burgess Shale, *Pikaia* appears to show traces of a notochord, the stiffening rod from which the chordates derive their name. A regular series of narrow, V-shaped muscle blocks along the body similar to those of the primitive living chordate Amphioxus (the lancelet) and jawless fish. If correctly interpreted *Pikaia* therefore represents a major landmark in the evolution of our own phylum.

It is interesting to speculate who could have predicted, in Middle Cambrian times, that these two forms, *Aysheaia* and *Pikaia,* might one day give rise to the formidable array of insects on one hand and the spectacular diversity of fishes, amphibians, reptiles, birds and mammals on the other.

Although these and other Burgess Shale animals can be assigned to known phyla other forms are quite unlike anything known elsewhere. The aptly named *Hallucigenia* apparently walked on seven pairs of sharp, stiff, spine-like legs and bore seven flexible tentacles along its back. *Opabinia,* with a long segmented body and paired (but not jointed) appendages, had **five** eyes on the head and a long, flexible process projecting forwards. These and other bizarre forms from the Burgess Shale indicate that the Early to Middle Cambrian seas swarmed with a rich diversity of marine invertebrates many times more numerous than known Cambrian forms. Most of them were apparently evolutionary dead-ends — experiments which didn't succeed.

Startling evidence from fossils

In many other ways the fossil record provides us with evidence about events in life history about which we would otherwise know nothing. Although fossil invertebrates are much more numerous than fossil vertebrates the latter show best evidence for gradual transition, between and within groups. Scientists can deduce, from comparative anatomy, embryology, biochemistry etc, that all vertebrates have close links and that some have evolved from others but living examples are so distinct even non-biologists have no difficulty distinguishing fish, amphibians, reptiles, birds and mammals.

The fossil record, although still patchy, is extremely convincing. The order in which vertebrate groups appear in the record is as we would expect — jawless fish (500 m yrs), fish with jaws (400 m yrs), amphibians (360 m yrs), reptiles (300 m yrs), mammals (190 m yrs) and birds (150 m yrs), although some may have originated earlier than their first appearance. The best documented transitions include fish to amphibian, reptile to mammal and reptile to bird.

The oldest labyrinthodont amphibians *(Ichthyostega)* come from Late Devonian rocks of East Greenland. Undoubted footprints of a similar amphibian from south-east Australia reveal their presence here at about the same time. Few now doubt that they arose from a group of Devonian air-breathing fish, the long-extinct crossopterygians (such as *Eusthenopteron*), although the known fossil examples do not necessarily represent the direct line of descent.

Following the amphibian to reptile transition in mid-Carboniferous times the reptiles gave rise to many successful lines. One group, the synapsid or mammal-like reptiles, were extremely successful and varied in Permian and Triassic times (270—180 m yrs). Throughout this time their skeletons progressively developed features we now consider mammalian. By the end of the Triassic several different groups of synapsids were so far advanced towards a mammalian skeletal condition that it is difficult to classify some examples with reptiles or mammals (an example being *Thrinaxodon).*

The reptile to bird transition, although documented by fewer specimens, is equally convincing. The two good skeletons of *Archaeopteryx* discovered in Darwin's lifetime (the London and Berlin specimens) revealed a creature almost perfectly intermediate between birds and reptiles,. The skeleton is more reptilian than avian, with teeth, a long, bony tail, three clawed fingers in the hand etc. Only the presence of well-preserved feathers and some other features (such as a wishbone) prevent us identifying *Archaeopteryx* as a small, two-legged, carnivorous reptile.

Since Darwin's day skeletons of similar reptiles have come to light, one form *(Compsognathus)* from the same Late Jurassic formation in southern Germany as *Archaeopteryx. Compsognathus* is classified as a small, reptile-hipped (saurischian) coelurosaurian dinosaur but the resemblance between it and *Archaeopteryx* is striking. Several more specimens of *Archaeopteryx* have come to light this century.

The most intriguing is the Eichstatt specimen discovered in 1951 and initially identified as *Compsognathus!* It was not until about 10 years later that detailed examination revealed the embarrassing truth — the presence of extremely faint but undoubted feather impressions showed it to be an *Archaeopteryx.* This is despite the fact that every quarry worker in the area was on the lookout for such prize finds as *Archaeopteryx.*

The interesting question now is — when did feathers evolve and why? Many workers now believe that feathers arose in the coelurosaurian dinosaurs as a form of insulation and only later were adapted for the flight surface of bird wings. *Compsognathus* and *Archaeopteryx* were contemporaries, not ancestor and descendant. We know that the chicken came long after the egg (invented by their reptilian forerunners) and now it would appear that the feather may have come before the bird. If this were to be confirmed by fossil evidence it would provide even more elegant proof of the correctness of Darwin's great concept.

The skeleton of an extinct, horned turtle, *Meiolania platyceps,* which lived on Lord Howe Island in the Tasman Sea sometime between 100,000 and 40,000 years ago. The turtle was basically a land-living animal, and related species are known to have lived in eastern Australia in the last few million years and in South America about 50—70 million years ago. Photo John Fields.

Top, a 550 million year old trilobite, *Xystridura saint-smith,* from Middle Cambrian marine deposits on Beetle Creek, near Mt Isa, Queensland. Trilobites were abundant and varied marine arthropods whose remains are commonly found in Cambrian, Ordovician and Silurian rocks deposited between 570—400 million years ago. After this they declined in importance, becoming extinct in Permian times, around 250 million years ago. They were bottom-living or free-swimming scavengers, living on smaller organisms or decaying organic matter. Like all arthropods they had to shell their hard, outer shell periodically during growth. Most trilobite fossils consist of such cast-off shells rather than the complete animal. Photo Gregory Millen.

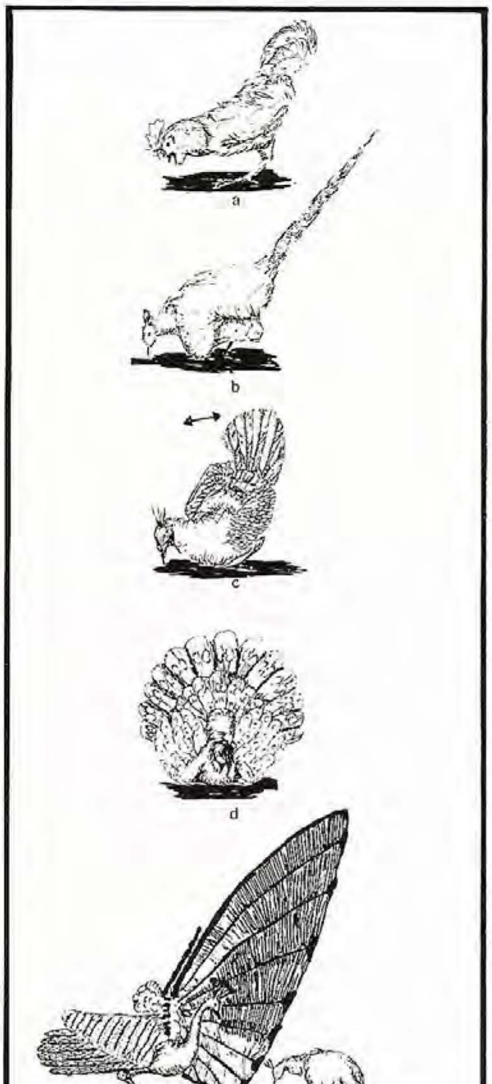
EVOLUTION AND THE ABILITY TO LEARN

When biologists study animal behaviour they deal with many different parts of a total package — social organisation, breeding behaviour, territoriality, parental behaviour etc. From this study they can build a picture of an animal's behavioural responses.

Two of the main components of an animal's behaviour are the impact of the environment and early learning experience. Biologists now believe that the ability of an animal to learn is one of the most important factors contributing to the evolution process.

Mike Cullen is Professor of Zoology at Monash University and a specialist on the social behaviour of animals. Currently he is working on the foraging behaviour of honeyeaters and the breeding biology of Little Penguins.

by Mike Cullen



Five examples of the bowing displays in game birds which biologists believe represent various ancestral stages in the evolution of the Peacock's performance to a Pea-hen. (From R. Schenkel, 1956).

It is probably no accident that the century of Darwin and the development of the theory of evolution by natural selection, was the century when naturalists in increasing numbers were discovering the world. Wallace, Bates, Thomas Henry Huxley and many others were describing the variety of animal and plant life all over the face of the earth and the depths of the sea.

On the basis of their observations, they speculated on how this variety of form and colour contributed to each creature's way of life. A sense of this amazing wealth can now be brought to every household through television. But television can do more than simply show us an animal in its natural environment. It can show how the animal behaves in its environment — hiding in ambush on a coloured flower ready to snap up any unwary insect, building a bubble nest beneath the waters of a pond, signalling to a sexual partner that is seen as a mate rather than prey, leaping from branch to distant branch while travelling through the tree tops.

When we see these natural displays we have the same feeling of wonder and astonishment as the early naturalists, followed quickly by the question — how on earth did it come to be so?

One thing scientists can be sure of is that behaviour must have changed over time — as has the structure of animals, for the two are closely entwined. But when scientists try to unravel behavioural evolution they are worse off than would be the case if they tried to understand the history of structure. Incomplete though it may be, the fossil record provides some landmarks, even signposts of evolutionary history (at least for bones and shells and other hard parts). However, there is little that we can infer about behaviour from such remains.

From fossilized limbs and pelvic girdles, scientists can tell whether some primate ancestor lived in the trees or walked upright on the ground 15 million years ago. The structure of its teeth may indicate what it ate. But questions such as how did it get food or in what kind of society did it live or what kind of language or communication system did it have, remain unanswered.

In spite of the absence of fossil evidence it is possible for biologists to say something about the evolution of some kinds of behaviour. This evidence comes from the comparison of the behaviour of species alive today.

A good starting point is the behaviour of a group of lizards of the genus *Amphibolurus,* known as rock dragons. Three rather similar looking species, *A. vadnappa, A. decresii* and *A. fionni,* live in the rocky hills of South Australia, with either one species in an area or sometimes two. But even where they overlap they remain distinct, through small structural differences which characterise them as separate species.

Dr John Gibbons, from the University of Adelaide, studied the behaviour of these lizards for a number of years in order to find out whether their behaviour was any more distinctive than their structure. From the analysis of hundreds of frames of film he found that each species evolved a distinctive species identification display which is used when an intruder is detected in a lizard's territory.

This display typically involves lowering the throat region and turning sideways to show the colour pattern on the flanks. Next, the lizard raises and coils the tail, horizontally in two of the species, vertically in the other. Then the lizard makes a series of hind leg push ups which raise and lower the rear end of the body, alternating with an odd twirling of a front leg after it is raised from the ground. Finally it makes a series of alternating downward (dips) and upward (bobs) movements of the head. This basic pattern is the same for all three species but the rhythm of the movements and their exaggeration is characteristic of each species. Interestingly, in two of the species these head movements coalesce, despite the amplitude of the movement being different. In the other species a pause is interspersed between a dip and bob. These slight differences together with those in other parts of the sequence alter the whole rhythm to create the characteristic display signature for each species.

Besides the major differences between species, John Gibbons found that there were also slight differences in the displays between populations of the same species from different localities. Although scientists do not know the reason for this, the difference in head movements between different lizards is very similar to the slight differences in structural features (limb or head size) found in animals of the same species in different populations. In these cases such variation is thought to provide the raw material for evolution.

Therefore the case of the rock dragons illustrates several features of the evolution of behaviour as it applies to communication. Scientists can recognise the same elements in the repertoire of different species even though they combine in different ways. Each species can achieve a relatively stereotyped distinctive signal based on movement and colour integration. In other animals these displays maybe combined with sound and scent signals.

While scientists do not know why one species uses one display signature rather than another it is assumed that in most cases they are probably arbitrary conventions decided by some chance event in the evolutionary past. In areas where two or more dragon species overlapped John Gibbons found that some of the display signatures showed 'character displacement' which emphasised their difference from the other species. This made them easier to recognise in places where the mistakes would be more likely to occur. Just as one might expect if natural selection favoured species recognition.

Other signals convey other kinds of information. A number of wallabies thump the ground when disturbed which acts as a signal alerting others to potential danger. In this case the signal appears to be similar in a range of species.

One of the species of rock dragon, *Amphibolurus*, uses a distinctive identification display when an intruder enters the lizard's territory. Photo Hal Cogger.

Biologists at first believed the male Peacock's display in front of the female, with raised tail and shuffling wings, was quite unique. However, studies of birds which are closely related to the Peacock found that the bird's display was a more extreme version of the exaggerated bow found in many game birds. Photo Trounson & Clampett (NPIAW).

Opposite, a White-cheeked Honeyeater, *Phylidonyris nigra*, about to feed on a flowering Banksia. The evolution of territorial behaviour has only become evident through recent studies. Photo H. & J. Beste (NPIAW).

How do such signals originate in evolution? As a group of kangaroos bound away after being disturbed one can hear the sound of each jump as the hind legs strike the ground. It appears highly likely that the signal thump originated as an exaggerated form of some preparatory leap (called a ritualised intention movement).

Similarly the threatening displays of many animals seem to be exaggerated versions of preparations to lunge or attack another. While scientists cannot be sure of this interpretation observations of all kinds of transitions between the pure attack movements and these ritualised threats make such an explanation plausible. Put more simply some displays may originate from relatively simple movements already in the repertoire of a species.

But it may not always be possible to recognise these different versions of the display. It is difficult in the case of the rock dragon's recognition display. It is even more difficult for the bizarre ceremonies which birds of paradise practise. These birds use special plumes and crests which are erected or fanned while the male calls and dances, alone or in the company of others, flying from branch to branch or sometimes in an inverted posture beneath his perch.

However even in cases where a display appears quite unlike anything in the normal repertoire of the species, comparison with related species can sometimes help show evolutionary origins. The male Peacock's display in front of the female with raised tail and shuffling wings seems quite unique — until one examines the displays of the birds most closely related to the Peacock, the pheasants and other game birds. Then scientists find that the Peacock's display before the female is just a more extreme version of an exaggerated bow which is found in many game birds where the male calls the female to partake a morsel of food he has found.

Of course it will never be possible to be certain that this is the evolutionary origin of the Peacock's display, but such speculation seems plausible especially as more is learnt about the behaviour of the Peacock and its relatives.

One interesting aspect of behavioural evolution is social organisation, especially in regard to animal's territories. The selective advantages and disadvantages which play a role in the evolution of territory behaviour have only become evident through recent findings.

Consider a honeyeater defending a flowering Banksia bush, the bird's source of

nectar (food). Chasing off intruders can be costly in terms of the total energy expended. So the problem arises how much energy should a bird invest in this type of defence to obtain access to nectar from the flowers?

Clearly the correct answer in terms of economics depends on how common territorial incursions are and how easily the intruders are repelled. But another consideration is the relative abundance of the nectar source and what alternative supplies may be available. While this seems like a complicated matter to assess, the honeyeater can make a decision on how large an area of Banksia to defend relatively quickly while the biologist takes days.

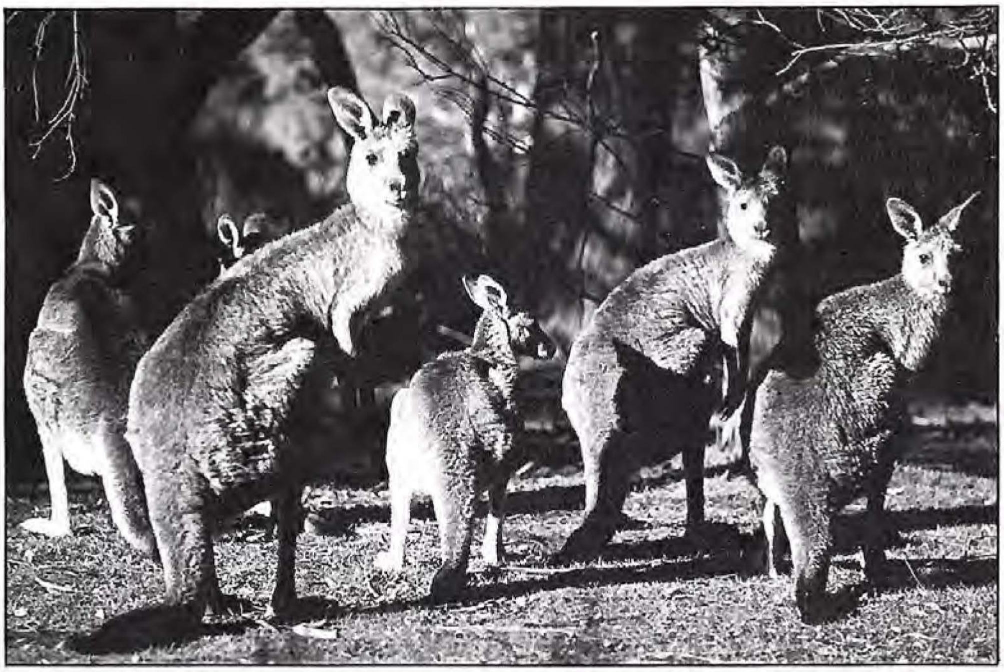
Parental behaviour raises evolutionary problems of another kind. In some mammals and most birds both the male and female share parental responsibilities whether they involve feeding, guarding the young, or defending the territory. That parents do this makes sense in Darwinian terms because, even though these duties may increase the parents' chances of being caught by a predator and decrease the amount of time they can forage for themselves, they are aiding the offspring which carry their genes and so protecting the following generations.

This is what Darwinian 'fitness' is all about. Whether one parent or both are involved seems to depend on whether both are necessary for the survival of the family.

What is surprising and in need of some additional explanation, is that in a number of species individuals other than the parents seem to join in this care of the offspring. For some reason, at present unknown, this kind of behaviour seems particularly common in Australian birds. There are probably at least 65 Australian species which are communal breeders to some extent.

White Winged Choughs for example, live in groups all the year round and nest communally. Ian Rowley, of CSIRO, studied the birds and found that the numbers of individuals varied from four to fourteen. All members of the group took part in activities associated with the nest in the breeding season. This included building as well as incubation of the eggs and feeding of the young.

If behaviour evolves and advantages an individual's own survival or that of its genes, how does it come about that other individuals help the actual parents? One answer may be that in many cases the helpers are often the offspring of a former brood. They are helping their parents to raise their half-brothers and sisters. As they share genes with these siblings, it is in the interests of their own genes to help the parents, although one would expect that they show less dedication to the task than do the actual parents since they are less related to the beneficiaries of their actions.



Biologists do not know why one animal species will use one type of display signature rather than another. This group of Eastern Grey Kangaroos, *Macropus giganteus*, will thump the ground when disturbed. This acts as a signal alerting the others to potential danger. It appears highly likely that the signal thump originated as an exaggerated form of some preparatory leap. Photo Andrew Smith (NPIAW).

This kind of 'altruism' towards kin is no more than an extension of the principles of classical Darwinian selection. In many cases of communal breeding, scientists do not know the genealogical relation of the helpers and the true parents making it uncertain at present whether 'kin selection' will account for all examples.

If behaviour does evolve according to the general Darwinian view, in the same way as that of structure then it must vary from one individual to another and this variation must be controlled, at least partly, by genes.

Individuals certainly show differences in behaviour but there can be many reasons for this. In animals such as mice and fruit flies there is plenty of evidence for behaviour differences which are due to genes. An example is the nest building of mice or the courtship activity of flies. This behaviour can be changed in the laboratory by artificial selection over several generations, or by appropriate crossing experiments. But behaviour by its very nature is more labile than the characters which geneticists usually study (for example the number of bristles or the colour of the fur). The development of many kinds of behaviour is dependent to a greater extent on the kind of environment and experience during early life.

Some behavioural characteristics vanish or change when the animal grows up in a particular environment. Even though the behaviour may depend on certain genes, there is not a close correspondence between the presence or absence of the genes and the behaviour, unless the environment is kept the same. This certainly complicates the way behaviour will evolve.

But while the environment is important there is another complication. Some animals can modify their behaviour adaptively during a lifetime in ways which resemble the much slower process of evolution. They can learn what to do and when to do it. This acquired behaviour is not transmitted to the offspring through heredity, as was supposed by the great French evolutionist Lamarck and by Darwin himself, but appears to evolve through the ability to learn.

Such adaptability can be of great value for species which have more than once-in-a-lifetime encounters, when appropriate responses are repeatedly required. It is clear that in bees and wasps a degree of learning at least in particular situations is of great importance for finding food and bringing it back to the nest. It is even more important in mammals and birds. Because of the tremendous flexibility it gives, the ability to learn is probably a much more important achievement of evolution than the development of specific behavioural responses.

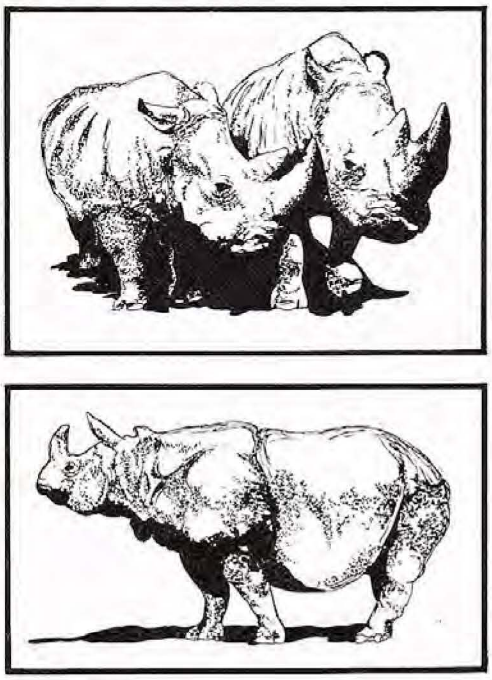
The more closely we look at behaviour the more obvious it becomes that it is just one more aspect of the total biology of the animal and that its evolution cannot be considered in isolation. Scientists may be able to speculate about the past history of behavioural evolution, but the secret lies in precisely how the behaviour of each species contributes to an individual's survival and breeding success.

GENETICS COMES TO DARWIN'S AID

Based on our present knowledge, the earth houses nearly a million animal species and well-over a quarter of a million plants. The actual numbers could well be double this! Darwin tried to explain this enormous diversity of animal and plant life without a suitable model of heredity. Now the relatively modern study of genetics has come to Darwin's aid.

Ross Crozier is Associate Professor and Lecturer in Evolution and Genetics at the University of New South Wales. His particular interest is the evolution of social behaviour, especially with our more common insects, ants, bees and wasps.

by Ross Crozier



The possession of two horns by African rhinoceroses and one by Asian ones probably does not reflect differences in selection between Africa and Asia, but rather that having one horn or two may be equivalent evolutionary strategies for these great beasts. Drawing Lois Sattler.

It is well-known that the lack of a suitable model of inheritance gravely weakened Darwin's theory of evolution. We can't blame Darwin for this. The concepts of heredity current at the time involved what is called 'blending inheritance' — when offspring always possess an average of the qualities of their parents.

The problem for Darwin's model of evolution is that the variation upon which natural selection can act, rapidly disappears under blending inheritance. In fact, if inheritance did act this way, half of the variation would be lost each generation.

With no variation there cannot be evolution. Darwin struggled unsuccessfully with the problem, suggesting an implausibly high rate of mutations to constantly replenish the supply of variation.

Gregor Mendel had already solved the problem of inheritance by the time Darwin died. It is because of Mendel's work that we know that genetic variation is not lost in the progeny of genetically-different parents, but retained, although possibly masked by dominance.

It is one of the ironies of the history of evolutionary biology that Mendel's work remained unrecognised until the start of this century.

Why was his work not accepted instantly? It appears that the then vigorous search for a mechanism for inheritance had to include an explanation for development as well. Mendel's theory cut the link solving the problem and enabled progress to be made.

Although Mendel provided the genetic background for an understanding of evolution, biologists still did not understand the fate of genetic variation in populations. While a number of people seem to have independently provided this next important part of the structure of modern evolutionary theory, we generally remember just two of them in the 'Hardy-Weinberg Principle', published simultaneously in 1908 by Hardy in England and Weinberg in Germany.

Mendel showed that genetic variability between parents is not lost in their progeny, even if it may be concealed. The Hardy-Weinberg Principle shows that a population will retain its level of genetic variability indefinitely, and that the proportions of the various genotypes present can be predicted exactly.

While mutation is vital if evolution is to occur (because it provides the necessary new genetic variation) only natural selection, of all causes of evolution, leads to adaptation. Natural selection was Darwin's big discovery (which he shared with Alfred Russell Wallace), but our view of it today differs from his.

Darwin explained natural selection as the force acting to improve adaptation — a rather imprecise definition that does not lead readily to experimentation.

Biologists now define natural selection as the occurrence of different rates of reproductive success between different genotypes.

While natural selection usually improves adaptation, this is not always the case. For example, the ability of a population to withstand sudden changes in the level of predation can be reduced by sexual selection, such as that leading to the peacock's cumbersome finery. Also, one can readily construct hypothetical examples where natural selection will favour the rise of territorial or fighting strategies which threaten a population.

Given our operational definition of natural selection, textbook examples of its role in evolution abound such as the industrial melanism phenomenon in many moth species, malaria and sickle cell hemoglobin in humans, the catastrophic evolution of insecticide resistance by many flies and drug resistance by many bacteria.

The nature of species

As with the rest of evolutionary theory, biologists' understanding of the nature of species is based on genetics and ecology. A species is a group of populations evolving separately from other species and exchanging few or no genes with them. The genetic integrity of a species is maintained by barriers to gene flow (isolating barriers). There are often a number separating any pair of species examined.

The genetics of isolating barriers has come under intensive study, although the study of genetic differences between stocks that do not normally cross is difficult!

However, it is the operation of the barriers in nature that is important evolutionarily, and they can often be overcome experimentally.

An interesting example of the genetics of isolating barriers is the Hawaiian *Drosophila* species *heteroneura* and *silvestris*, which are practically identical genetically and often occur together. Despite this, they are spectacularly different structurally and seldom interbreed in nature. The reasons are behavioural and thought to centre on the bizarre head shape differences between them — females reject the males of the other species.

The case of *D. heteroneura* and *D. silvestris* is especially significant because it is known that the spectacular head shape difference, the key to the genetic distinctness of these species, is due to differences in a few genes. No more than ten are thought to be involved. In this, as in many other cases, biologists are coming to appreciate that speciation and other evolutionary changes often involve changes in rather small numbers of genes.

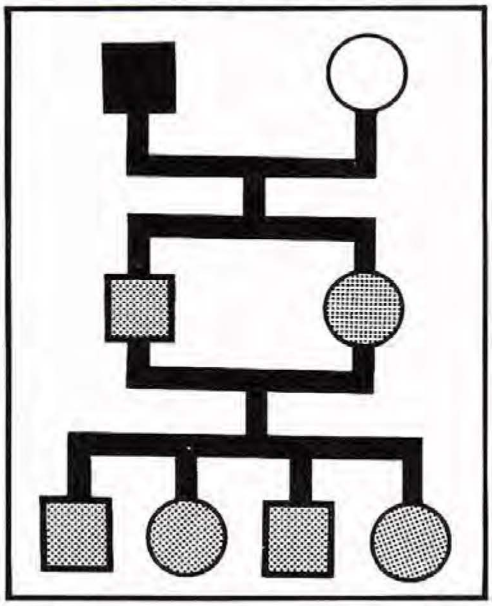
Speciation

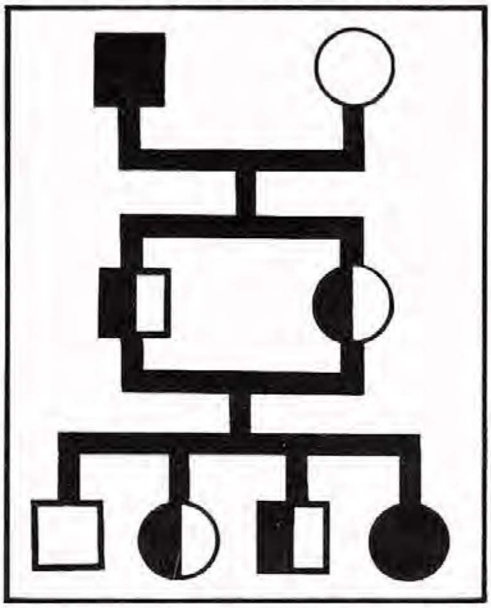
Speciation is the formation of isolating barriers, and its study, until recently, centred around theoretical models and the observation of creatures in the wild. While both these activities remain vital, they have increasingly been joined by laboratory experimentation.

Polyploidy resulting from hybridization has always been recognised as a major source of new species in plants. The pathways inferred from field studies have been extensively confirmed by successful duplication of the hypothesised events in the laboratory. A classic case is that of wheat and related cereals which now include wholly new, man-made species.

Habitat divergence is the formation of isolating barriers within a local population due to strong selection, such as caused by the introduction of a new host plant alongside the ancestral one. Because the selection required is so strong, such speciation is likely to be rare, yet it seems to have been economically important in America.

When apples were first introduced in America, the apple maggot, a native insect, fed only on hawthorn. Then it started attacking apples in one locality, and the attacks spread in succeeding years. The evidence sugests that there are now two species, one attacking hawthorn, the other apples.


Blending inheritance


Mendelian inheritance

Under blending inheritance, the generally-accepted model of heredity in Darwin's time, divergent characteristics of parents are indissolubly averaged in the progeny, whereas Mendel showed that, on the contrary, the factors producing such characteristics are preserved in the progeny and re-emerge next generation.

Significant progress in understanding evolution only came about when genetics was uncoupled from development, and the idea of single mutations producing major adaptive advances was abandoned in favour of evolution being exclusively the accumulation of very small genetic differences. Both of these shifts are to some extent now being reversed.

It has long been an axiom of genetics that you don't really have genes for specific traits — eyes, hair, teeth etc. instead all loci have the ability to affect many traits.

But it is when we consider how organs are formed during development that we appreciate how important it is to incorporate development into evolutionary thought again. Much of development consists of the establishment of concentration gradients of substances called inducers, with the various organs arising at particular points in these intersecting gradients.

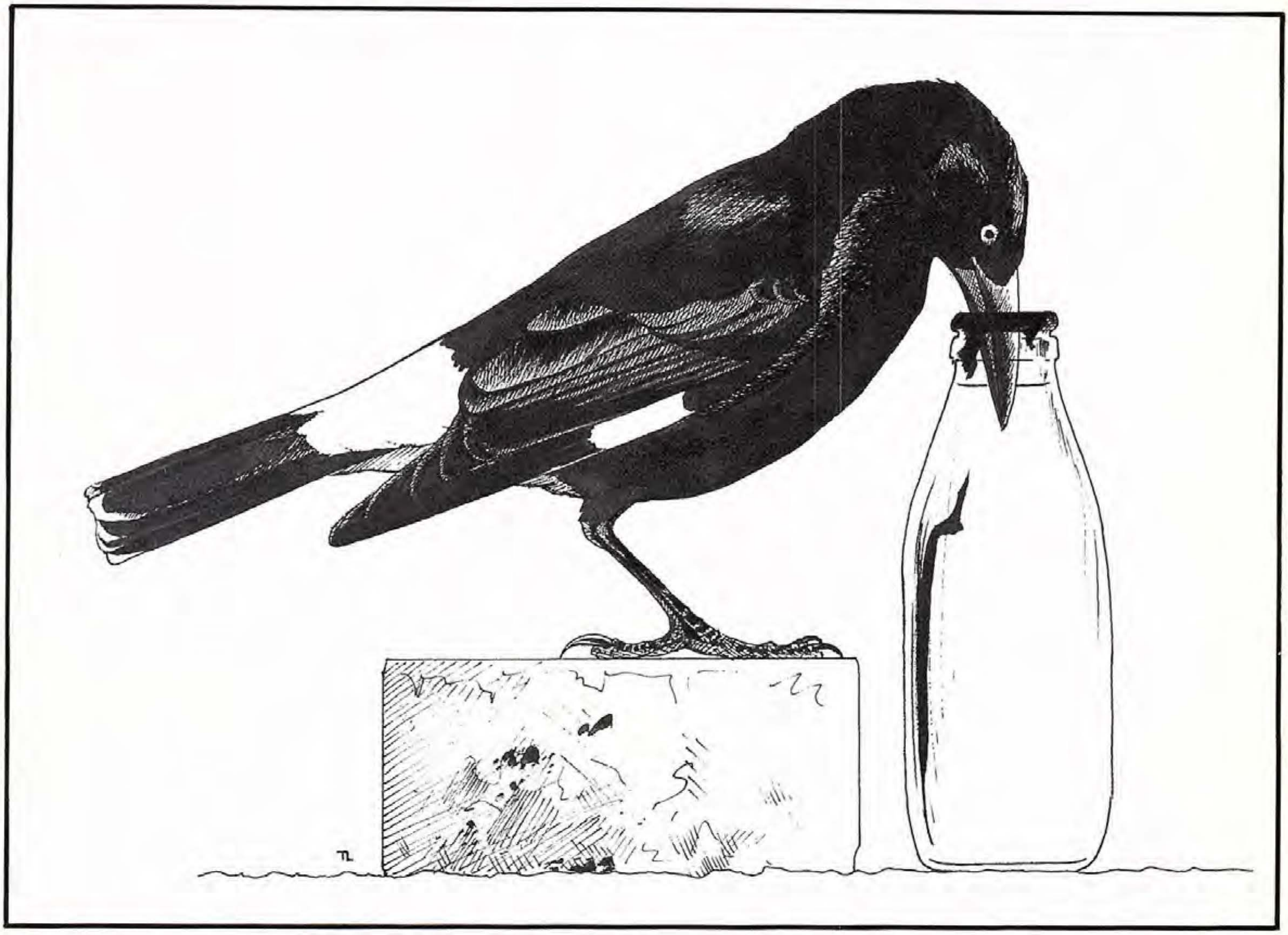
While an individual is indeed the product of its genes, they act by specifying a set of gradients, not by individually specifying individual structures. To understand this, consider the fact that you have between 10,000 and 500,000 different genes, yet your brain alone has some ten billion neurones! In terms of information theory, organisms probably contain thousands of times more bits of information than they have genes. What generates this complexity are the interactions between the genes, through the gradients they specify.

This view of evolution has a corollary: selection for one change can bring about others, because a change in growth gradients yielding one evolutionary change will often cause changes to occur in other characteristics affected by the gradient. A common observation is that relative bodily proportions change with size, for example babies have relatively larger heads than do adults.

The interaction of genes with development affects the assessment of two competing hypotheses for how high intelligence evolved in humans. The traditional view is that a hunting way of life on the African plains imposed strong selection for individuals smart enough to cooperate with each other in the competition with other groups and other species. This view faces the problem that so many human attributes, such as a love of art and music, and the ability to programme computers could scarcely have been of direct benefit to hunter-gatherers. The competing view is that our high intelligence is simply an accident, due to selection for larger body size carrying along with it an increase in brain size. Humans, then, do not differ intrinsically from apes in intelligence, but in having had a higher brain/body size ratio during evolution.

But perhaps both views of the evolution of human intelligence are right. Selection can certainly modify the growth fields, and even within a species the developmental system can be adjusted away from a simple mechanical one to accommodate size variation.

The initial shift to a high brain/body ratio may have occurred because of selection for high intelligence, and the continued response to such selection may have involved increase in size. The byproduct aspect of our nature then is not intelligence, but the culture that



Cultural inheritance in a bird — Pied Currawongs, *Strepera graculina*, learned some time ago how to open milk bottles and take the cream. This behavioural trait is passed on by imitation. Drawing Terence Lindsey.

sprang from it and from our communication skills.

Human evolution, whatever its causation, does illustrate the potential for a major adaptive change resulting from an apparently slight developmental shift.

Chimpanzees and humans differ very little genetically, about as much as particularly similar *Drosophila* species. Yet we differ profoundly from our evolutionary cousins.

While it is also true that very many examples are known of major evolutionary changes resulting from the accumulation of many small genetic changes, even small changes can have great evolutionary significance at crucial junctures during evolution. A small genetic change, perhaps altering the receptors by which an insect recognises a food-plant, could enable a population to diversify and exploit an introduced host, such as the apple in North America or Australia.

Sociobiology: post-genetic evolution?

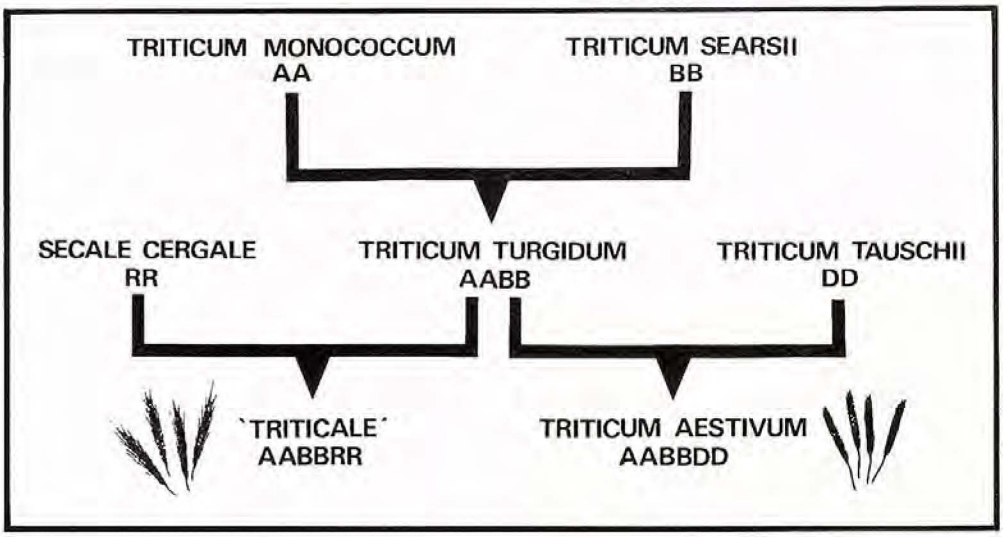
Perhaps few scientific controversies have invoked so much in the way of debate as that surrounding the formalisation of sociobiology — the study of the biological basis of social behaviour. While most sociobiologists work on non-humans, the excitement has mainly centered on human biology — the implications of the evolutionary world-view are finally influencing our views of 'humanness'.

The difficulty many see in human sociobiology is in the possibility it raises of biology controlling behaviour in a species that considers itself infinitely flexible. Not generally appreciated is the fact that such biological determination can take two forms — the partial control of behavioural variation **within** a species by underlying genetic variation, and consistent differences **between** real or imaginable species in behavioural charcteristics.

Both types of determination have long been accepted for structural traits, such as eye colour and the fact that we reasonably believe that the thick body coat of baboons compared with our own stems from innate causes and not differences in upbringing.

While instances of both types of determination are known for humans, normal humans and especially human groups, show few genetically-influenced behavioural differences that are regarded as important. Trivial ones, of course, are easy to demonstrate (think of colour vision differences and differences in the ability to taste certain bitter substances).

One of the most profound sociobiological findings is one of a greater kinship between us and other animals than previously remotely suspected. Not that our perception of ourselves has been lowered, but rather that our estimation of, for example, English blue tits and Australian currawongs has been raised through the discovery of cultural evolution in them and many other animal species. Of course, we don't mean 'culture' in the sense of appreciation of Beethoven and Dali, but rather



Some of the pathways followed during wheat evolution, as deduced by studies on living wheats and verified by laboratory replication of events. *Triticum aestivum*, or bread wheat, for example, has three sets of chromosomes, one each derived from *T. monococcum*, *T. searsii*, and *T. tauschii*. 'Triticale' is a wholly-new, man-made species involving wheat and rye chromosomes.

as the transmission of learned patterns of behaviour.

Cultural evolution, then, is the most recent subject of evolutionary study. Such an endeavour is not really a 'post-genetic' one, because the genetic makeup of any organism will predispose it to develop some patterns more than others. But cultural evolution has rules different to those of biological, or genetic, evolution. It has been termed Lamarckian, because behavioural variants acquired during life can be transmitted to progeny. But of course it is not.

Lamarckian inheritance involves the transmission of advantageous changes to offspring. Cultural inheritance differs most from genetic inheritance in that changes can be passed on infectively to large numbers of non-relatives. Cultural change can also be non-adaptive — trivial in the case of fashions, positively disadvantageous in the case of aggression or bad dietary habits.

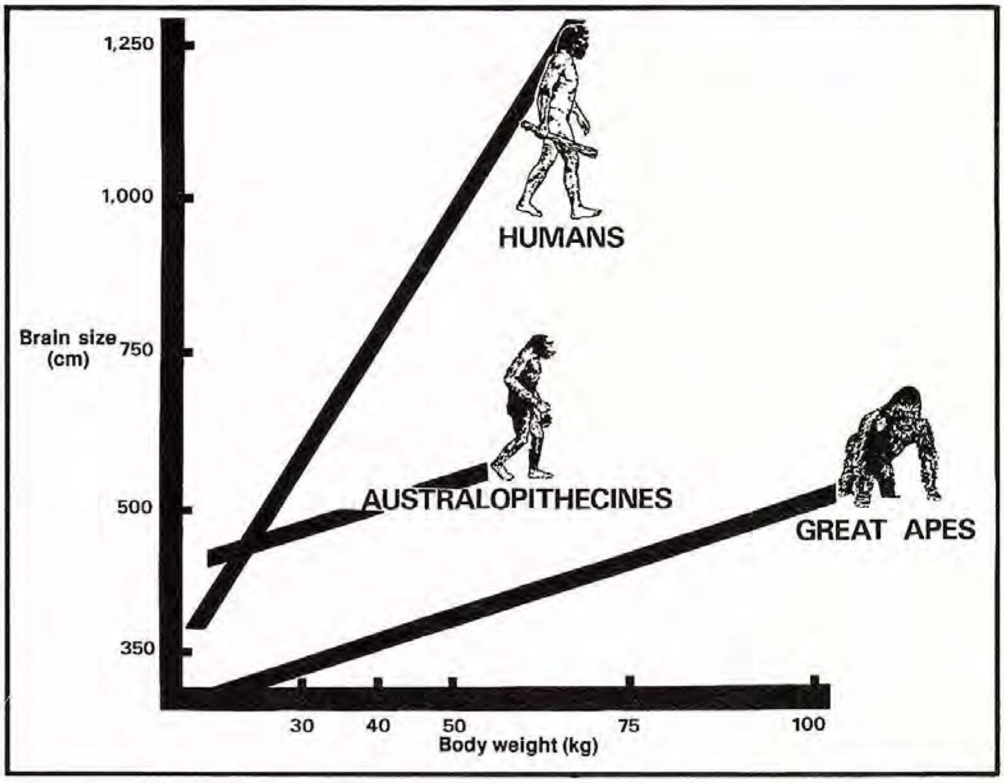
Links

Although sociobiology may seem distant from molecular genetics, links have appeared between them. In terms of adaptation, many of the recently-discovered molecular phenomena are either irrelevant or puzzling. An example is the many known 'pseudogenes' — stretches of DNA similar to active genes but themselves now apparently functionless. Pseudogenes have been suggested to be the 'rusting hulks of genes' rendered useless by mutation.

More baffling are transposons, which are genetic sequences capable of moving frequently from one place to another in the organisms DNA. But these 'jumping genes' may have functions beneficial to the whole organism, whereas there are large amounts of DNA of simple sequence that may well not.

Such 'junk DNA' has also been called selfish, because selection can have many levels, distinguishing not only between individuals, but perhaps favouring DNA sequences even if they disadvantage their carriers but are capable of multiplying themselves in the face of the error-correction machinery of the cell. If so, then such DNA would certainly be the ultimate parasite!

But what lies ahead for us? One consequence of appreciating the reality of evolution is a better understanding of some of the consequences of current trends in the way we live now.



High brain/body size ratios characterise human species in the fossil record compared with australopithecines and the living great apes. The line to humans was characterised by a shift of developmental resources towards producing the brain.

For some time, the burgeoning human population has made it and its food resources an increasingly strong selective force favouring the evolution of new strains of organisms such as insects and bacteria able to exploit such massive energy resources. Therefore the threat of pests and diseases.

We fight back with better public health measures and the chemical wizardry of drugs and pesticides. But new mutations give our competitors for the planet the ability to overcome chemicals, and the more attractive we become as a resource and the greater the evolutionary 'payoff' to living off us, the narrower becomes our margin in the race to produce new safe chemical weapons.

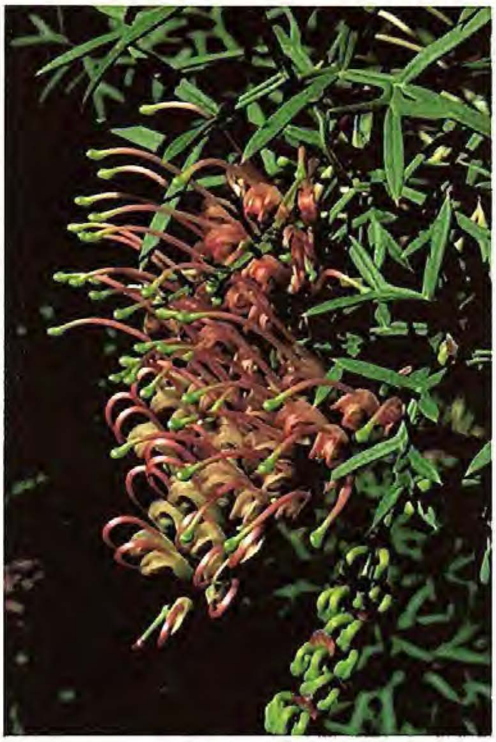
Our advances in genetic tecnology are giving us other ways to mould at least our crop plants at a faster rate than pests can evolve ways to exploit them. We can now re-shape the genetic material so that resistance factors are built-in to new crop strains, and even enable them to live in previously hostile habitats.

Of course, we could do much the same for ourselves, consciously directing our own evolution and not just that of other citizens of Planet Earth. We can, in other words, choose to remake human nature ... but I doubt that, our own generation will take up this challenge!

HOW OUR FLORA DEVELOPED

by Bryan A. Barlow

To botanists and zoologists in many parts of the world, Australia's native plants and animals have certain things in common. One is the richness in species numbers which they exhibit, especially in certain groups such as marsupials, parrots, eucalypts and acacias. Another is the remarkable diversity of form which they show, apparently covering the complete spectrum of adaptation to a wide range of habitats. A third is their uniqueness, expressed in a wide range of features not found anywhere else in the world. As a result, Australian flora may seem to be a rich collection of botanical curiosities and it is natural to ask how this strange flora evolved. Where did it come from, and when? Bryan Barlow, Head of Herbarium Australiense, CSIRO, Canberra, has considered these questions in this article condensed from his essay on the origin of the Australian flora published in the first volume of the new *Flora of Australia.*



The eucalypts number 500—600 species and dominate many areas of Australia. *Eucalyptus phoenicea* is a widespread species in northern Australia.

Above, the genus Grevillea (family Proteaceae) includes about 250 species, nearly all found in Australia. *Grevillea rivularis* is found only in the Carrington Falls area of southern NSW. Photos C. Totterdell.

Strictly speaking, the 'uniqueness' of the Australian flora is a reflection of its regionality. A high proportion of its genera and most of its species occur only in Australia. However, in plants higher up the scale, this high regionality almost disappears. Almost all of the families of flowering plants which occur in Australia also occur elsewhere, and conversely almost all of the larger families of the world occur in Australia.

In this sense, then, the Australian flora is a 'unique' sample of a typical world flora. In simple terms, we can explain the origin and evolution of the Australian flora as the result of a sample of world flora undergoing a long period of evolution, in geographic isolation in Australia.

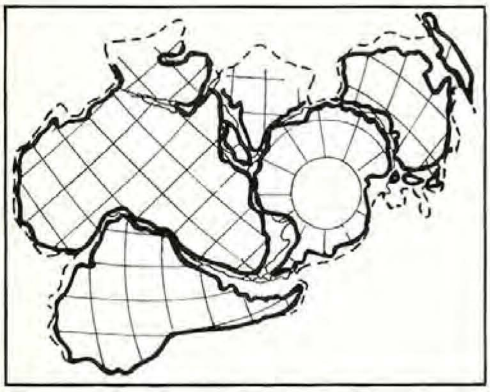
Plate theory and flora

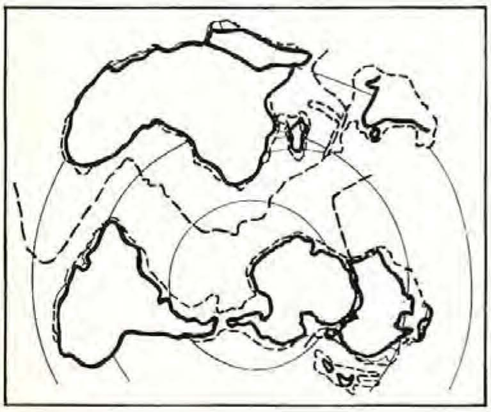
The confirmation of the theory of plate tectonics, during the last 20 years, has revolutionised our views on the evolution of the Australian flora. This theory, which now forms the basis of all palaeogeography and of most modern biogeography, is quite simple and lies very much in the realm of popular science. Its basis is the observation that earthquakes occur mostly in linear zones on the earth's surface, and that these zones enclose areas in which earthquakes do not occur. The aseismic regions of the earth's crust are called plates, and it is now known that it is the relative motion between these plates which causes deformation and earthquakes at their margins. A single plate often comprises both oceanic and continental regions, and the earth's surface is entirely covered by crustal plates in motion relative to each other.

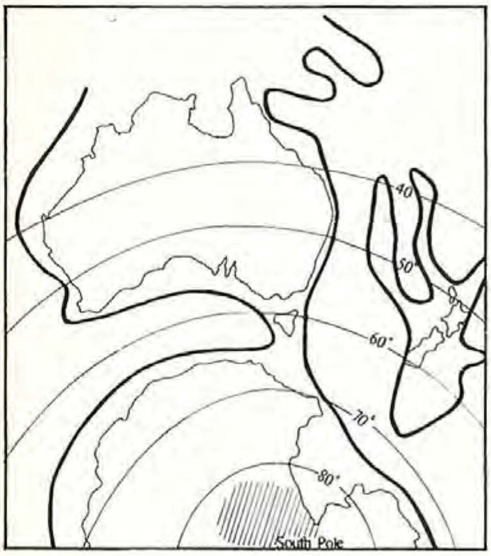
The consequence of these processes is that through geological time the relative positions of the continents have changed as their plates have moved. In particular, there is evidence that at one or more times in the past the continents have been grouped into one or two supercontinents, and that these stages have been followed by rifting and separation of entire continental masses. Complementary evidence is available from a number of sources, including matching of continental margins and mid-ocean ridges, tracing of polar wandering paths from palaeomagnetic studies, and the actual measurement of the rate of new crust formation.

The geographical history of Australia through the last 200 million years was described by Lauri Haegi, in the Flora Special Issue of Australian Natural History. About 125 million years ago (my) Australia was part of the southern supercontinent Gondwanaland. The earliest rifting resulted in the opening of the Atlantic and Indian oceans, so that Africa/Madagascar/India became separated from South America/Antarctica/Australia/New Zealand. About 80 my ago New Zealand/New Caledonia separated from Australia, but it wasn't until about 38 my ago that connections between South America, Antarctica and Australia were broken. Australia's rapid northward drift from Antarctica resulted in collision, about 15 my ago, with the Indomalayan island arcs. Meanwhile, India and Madagascar had separated from Africa, and India drifted north-east to collide with Asia about 50 my ago. In summary, then, Australia had land connections with Antarctica until 38 my ago, was then isolated for about 20 million years and subsequently has attained land connections with the south-eastern Asian region.

The biological consequences of plate tectonics obviously vary with the dispersibility of plants. For plants with high dispersibility, the positions of the continents have little effect on distribution and plate tectonics may be unimportant. Highly dispersible plant groups are well represented among coastal habitats, and a number of cosmopolitan families are common in such habitats. For groups of moderate dispersibility, changes in the proximity of drifting land masses can obviously make or break migration routes. Groups of low dispersibility, only migrate over continuous land.







Top, the position of the southern continents in Gondwanaland about 135 million years ago.

Middle, the southern continents about 60 million years ago, after the opening of the Atlantic and Indian Oceans.

Bottom, Australia and Antarctica about 45 million years ago, showing a narrow land connection between the two continents.

Worldwide flooding

At the time of maximum continental movement flooding on a world wide scale may have occurred in lowlands, causing mass extinction of plant species. When the flood waters dispersed recolonisation and adaptation would occur. Indeed there was a great spread of inland seas in the Australian region.

The effects of continental rifting would be gradual, but quite profound, with the first stage little more than a major extension of coastline as is the case with the Red Sea. However, with widening of the rift, continental climates would be moderated and changes in oceanic circulation could lead to general changes in climate. Climatic changes would also occur where a drifting block moved through different climatic zones. These processes would obviously result in massive changes in plant habitats and in adaptation, extinction and/or migration.

Similarly, collision between continental plates would evoke a gradual rather than an abrupt biological response. Ecologically, marine habitats would be destroyed and new upland or alpine habitats created, again leading to extinctions and adaptation and colonisation respectively. Exchange between the approaching floras would commence with colonisation by the more highly dispersible groups of plants while the blocks were still well apart. Competition and adaptation would occur progressively even before contact, so that a massive 'invasion' of one group of plants into the area of another might be unlikely to occur as a single event. Upon actual contact, a filtered migration along a corridor might occur, followed by general exchange across a broad front when contact became extensive. Given the time periods involved, competition could remain high throughout a collision event.

The question of the origin of the flowering plants is still unresolved, but there is no doubt that they achieved a wide distribution before the rifting of the supercontinents. Ancient fossil records suggest that they originated in western or northern Gondwanaland about 130 my ago, and reached Australia about 5 million years later. This original Gondwanan flora of Australia was therefore derived from immigration over broad fronts and probably showed a wide range of ecological adaptation from subtropical to moist temperate conditions. The ancestral Australian flora of 50 my ago existed under generally warm, moist conditions and consisted of continuous, structurally uniform, closed forest which included the southern beech, *Nothofagus*, and other plants referrable to *Araucaria, Podocarpus, Dacrydium, Anacolosa*, Cupanieae, Myrtaceae, *Nipa* and several Proteaceae.

The evolutionary history of the Australian flora has subsequently been one of differentiation from the original Gondwanan stock. The process occurred under conditions of increasing geographical isolation from the time of Australia's separation from Antarctica until its contact with the Sunda plate. There were progressive climatic changes, involving decreasing mean temperatures, increasing intensity of oceanic circulation and of atmospheric circulation, regional decreasing precipitation and increasing seasonality, which resulted in an increase in the level of habitat differentiation. The earlier pan-Australian flora therefore underwent differentiation into a spectrum of ecological associations.

The Australian element of the continent's flora emerges as a derived one rather than an ancient one. It simply comprises those components of the flora which have undergone considerable evolutionary change, under conditions of geographic isolation, to produce typically Australian plant groups with high levels of endemism. The so-called Indomalayan and Antarctic elements are now seen as comprising, at least in part, the present-day survivors of the Gondwanan flora.

Two vegetation types

The major floristic composition of the Australian vegetation was laid down over 30 my ago. It is Gondwanan in origin. It exists today as two components with a relatively strong ecological differentiation. One is the relictual component, consisting of plant groups confined to moist habitats (usually closed forests), showing little evolutionary diversification and a residual affinity with the floras of similar habitats in the other southern lands.

The other is the derived Australian component, predominantly temperate and arid-adapted, showing massive evolutionary diversification from the more unstable of the ancestral Gondawanan stocks and characterised by scleromorphy and high endemism.

The most striking aspect of the Australian sub-element is its scleromorphy. This has been described in the Flora Special Issue of Australian Natural History, by Karen Wilson. Many of the major groups of indigenous plants are characterised by relatively small, rigid leaves, short internodes and by small plant size. There is a strong representation of such types in Australian Myrtaceae, Proteaceae, Rutaceae, Epacridaceae, Mimosaceae, Fabaceae and Goodeniaceae.

It was generally assumed by earlier botanists that scleromorphy in the Australian flora represented adaptive responses to an increase in aridity, and in particular to the advent of mediterranean climate. More recently it has been identified as an evolutionary response to nutrient deficiency. Conditions favouring the evolution of scleromorphy probably developed over the last 40 million years as soils of this ancient land surface became leached of their nutrients. Scleromorphy has evolved in all situations, even in the tropics and is therefore not simply a result of the inception of mediterranean climates in temperate Australia about 25 my ago, even though scleromorphic plants are commonly found today growing under such conditions.

Our best-known member of the indigenous flora is of course *Eucalyptus*. While it is undoubtedly of ancient Australian origin, the genus does not appear in the known fossil record until about 35 my ago, and it presumably evolved while the Australian element was differentiating in seasonal, relatively dry, cooling climates. Our other well-known Australian, *Acacia*, also has a shadowy past, but probably arrived and differentiated under warm moist conditions. This genus occurs in all habitats from tropical rainforest to arid shrubland, but has achieved its greatest species diversity in the scleromorphic communities in semi-arid habitats.

Intruders from the north

The final major event in the history of the Australian flora was the collision, about 15 my ago, of the Australian plate with the Sunda and Pacific arc systems. The Sunda arc system, commonly called Sundaland is equivalent to the present Indonesian region. The collision brought together two rich floras which, until then, had been isolated from substantial direct exchange for a considerable period of time.

The so-called Australian element in the Sundaland region is highlighted by a few species in genera such as *Casuarina*, *Araucaria*, *Banksia*, *Grevillea*, *Acacia* and *Eucalyptus*. However few of the Australian groups penetrating Sundaland have extended into south-east Asia or beyond, presumably owing to the richness and stability of the northern hemisphere flora, and to the general lack of nutrient-deficient soils, to which much of the Australian flora is adapted.

Migration in the reverse direction has been more significant. New Guinea has been colonised predominantly from the Malaysian region following its elevation above sea level. Secondary exchanges from New Guinea and direct immigration from Sundaland, have contributed a significant component of the Australian flora, especially in tropical ecosystems. This is reflected in the low frequency of endemic genera in Australia's tropical zone (14 per cent) compared with that of the temperate zone (46.6 per cent).

A high proportion of the non-endemic Indomalyan plant groups in the tropical zone have only one or few species in Australia, and this can be explained as a result of relatively recent immigration into a botanically rich region in which diversification has been restricted by competition.

The elevation of mountain systems between Malaya and New Guinea has probably provided a dispersal route for cool temperate plants, and this dispersal route may have extended through eastern Australia. Long-distance dispersal between isolated highland regions has almost certainly been involved, as the Indomalyan lowlands have possibly remained continuously warm and humid. A number of typically north-temperate genera may have been dispersed to the Australian region by this route and some have apparently undergone new radiations, especially in the New Guinea highlands. Genera in Australia which may have had this history include *Veronica*, *Euphrasia*, *Poa*, *Stellaria*, *Ranunculus*, *Ajuga*, *Viola* and some Apiaceae.

The family Ranunculaceae is found worldwide but is most common in the cold and temperate regions of both hemispheres. *Ranunculus anemoneus*, has a very restricted distribution, being only known from the alpine and subalpine tracts of the Kosciusko area. *Ranunculus* species more commonly have yellow petals.

Right, about 80 percent of the world's species of *Acacia* are found in Australia. Most of the Australian species have modified leaves (phyllodes) rather than the bipinnate leaves found in overseas species. *Acacia myrtifolia* is widespread in southern Australia.
Photos C. Totterdell.

The Australian flora emerges as an amalgam of plants with diverse histories and potentials. It includes plant groups whose ancestors have been in Australia since the dawn of the age of flowering plants as well as a variety of recent colonisers. Some have only just established a foothold in Australia, while others have diversified at the expense of previous inhabitants.

Arid zone and its flora

Annually or seasonally arid lands make up more than half of Australia's area. It is clear, however, that these extensive dry regions were not present throughout the time that Australia's flora was evolving.

According to J. M. Bowler, the present expression of aridity dates from events which began about 20 my ago, as Australia drifted into lower latitudes. This drift was associated with intensification of weather systems and climatic gradients from pole to equator. Arid cycles overtook Australia from the south, building up in intensity and frequency almost to the present day.

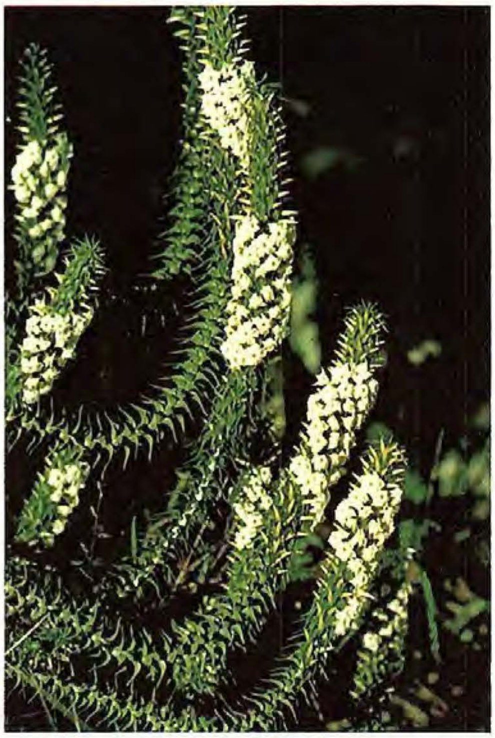
This explains why even the Australian deserts have unique features in their floras. They have evolved in isolation from other world deserts, and are lacking, for example, strong representation of succulents such as cacti or of members of the Euphorbiaceae. In a floristic analysis, N.T. Burbidge recorded 363 genera of seed plants in the eremean flora, of which 102 were endemic to it. Of the remainder, 91 genera were also represented in temperate Australia and 81 genera in the adjacent lowland tropics. The cosmopolitan element was represented by 89 genera which were further distributed throughout all regions of Australia.

The Australian arid zone flora is a young flora, which arose only after extensive arid conditions were established in relatively recent geological time. It was therefore derived by selection from the pre-existing, highly adapted, total Australian flora.

Plants with tropical lowland characteristics dominate in the northern part of the arid zone and plants apparently derived from the Australian temperate zone dominate in the southern part. The main dificulty has been in the explanation of the cosmopolitan types, including endemic genera in families such as Poaceae, Chenopodiaceae, Brassicaceae, Aizoaceae and Asteraceae, which are among the main constituents of the vegetation of all of the major world deserts. How did these colonisers cross extensive areas of unsuitable and fully occupied territory to become established in the young Australian arid zone?

The solution to the problem has generally been found in the fact that these cosmopolitan families and genera are also well represented in coastal habitats, where salinity and soil type may impose physiological conditions similar to those of deserts. Colonisation of the deserts by such groups may therefore have occurred from coastal habitats, especially in places where the arid zone extends to the coast.

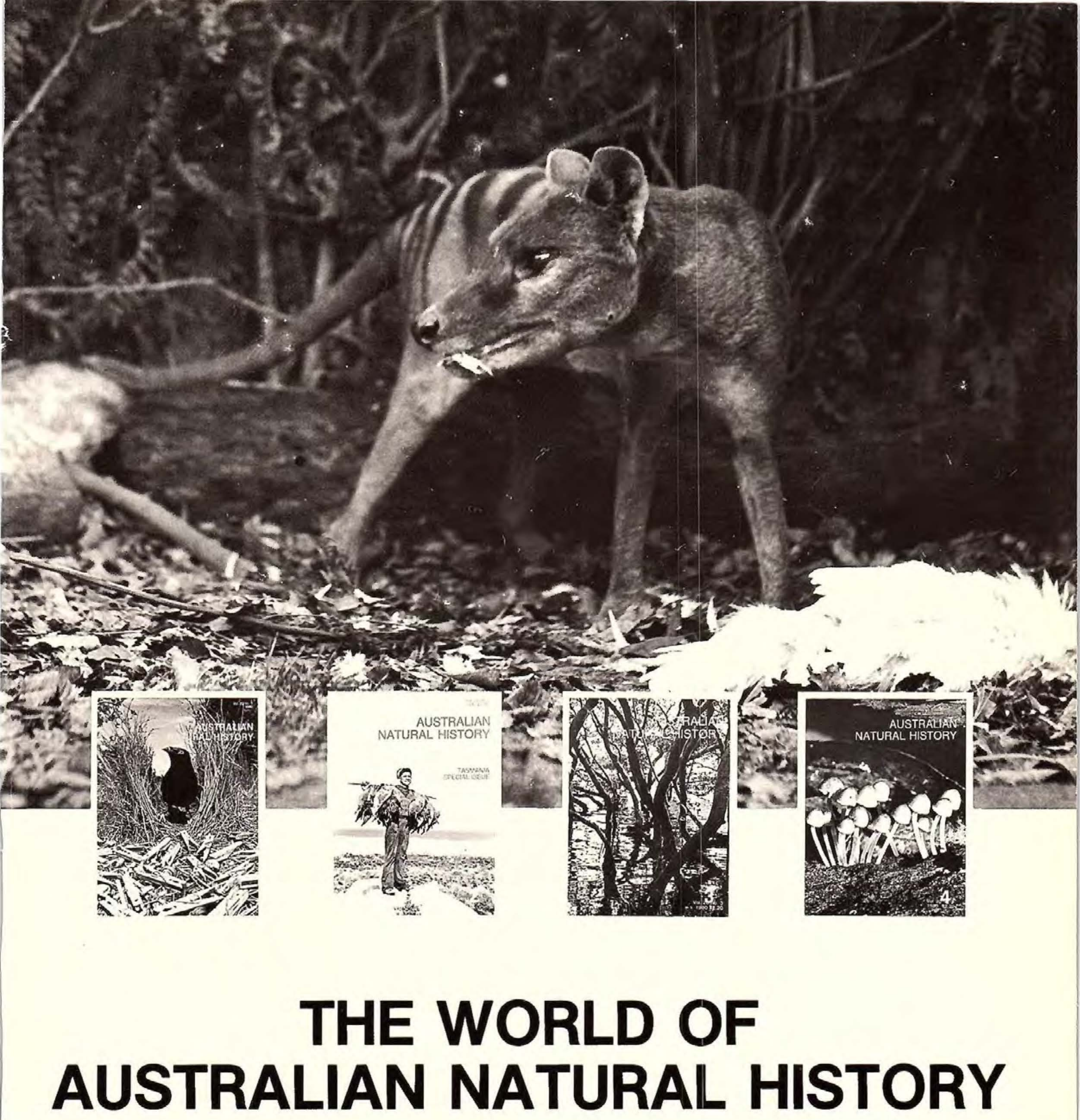
Hummock grasses dominate much of Australia's arid zone. Only a few species of eucalypts are found there, such as *Eucalyptus gamophylla,* seen here on the red sand plains south-west of Alice Springs. Photo Karen Wilson.



***Woollsia pungens* is a common sight on the NSW coast and adjoining ranges. It is a member of the family Epacridaceae which is characterised by the generally small pungent-pointed leaves with longitudinal or parallel venation. Photo C. Totterdell.**

Scleromorphy is common in Australian species. A common feature is the small tough leaves as seen in this *Melaleuca wilsonii.* Photo J. M. Baldwin.

The Australian flora of today tells the story of 100 million years of history of Australia as a southern land mass. Today it is an integrated flora, combining derivatives of the first angiosperm colonisers, persisting in habitats like those of the remote past, together with the distinctive, highly modified stocks of our open habitats and our deserts, with the relatively recent immigrants over the Indo-malayan land connection, and finally, in the last moments of the story, with the exotics introduced by man himself.



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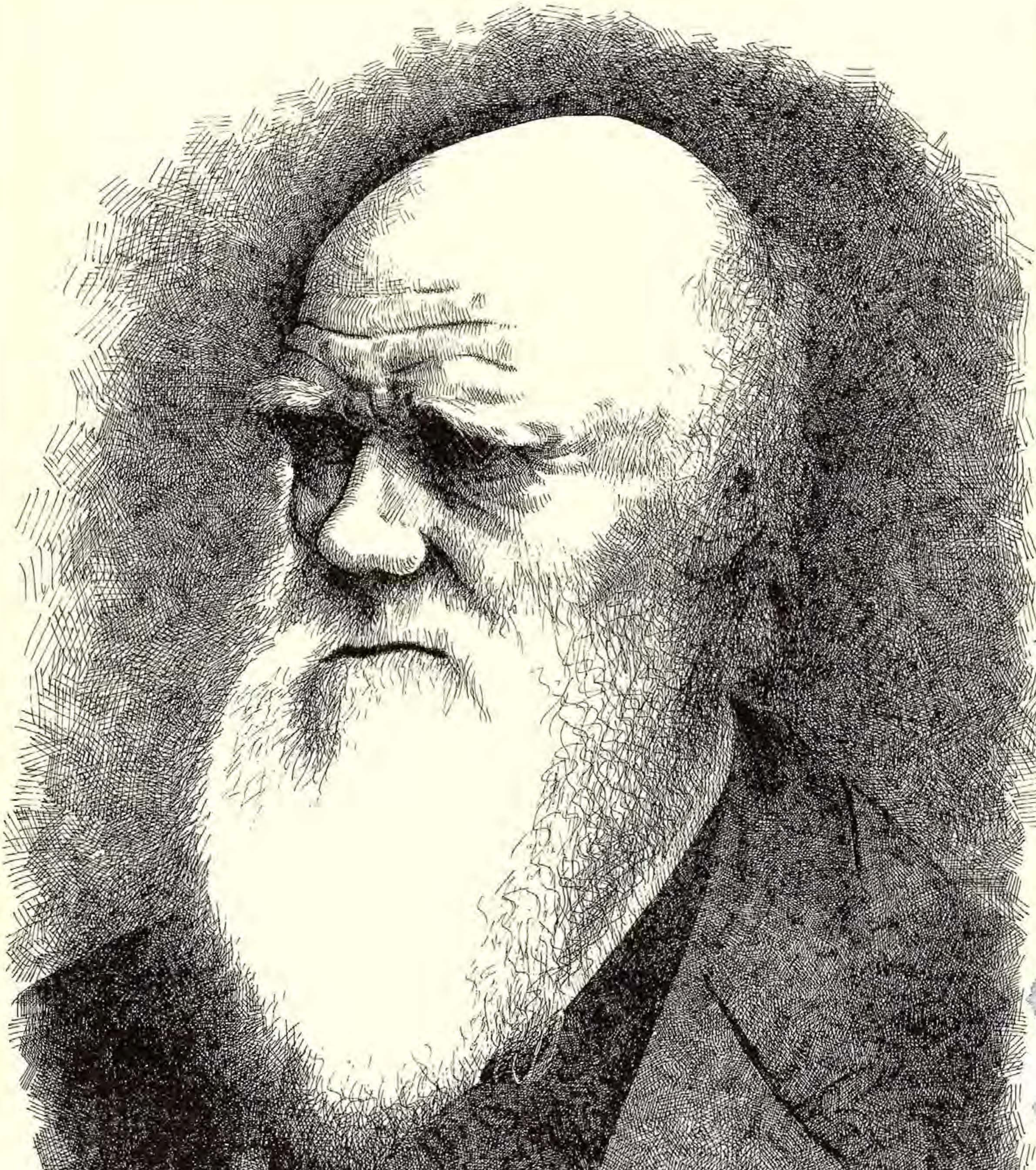
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