

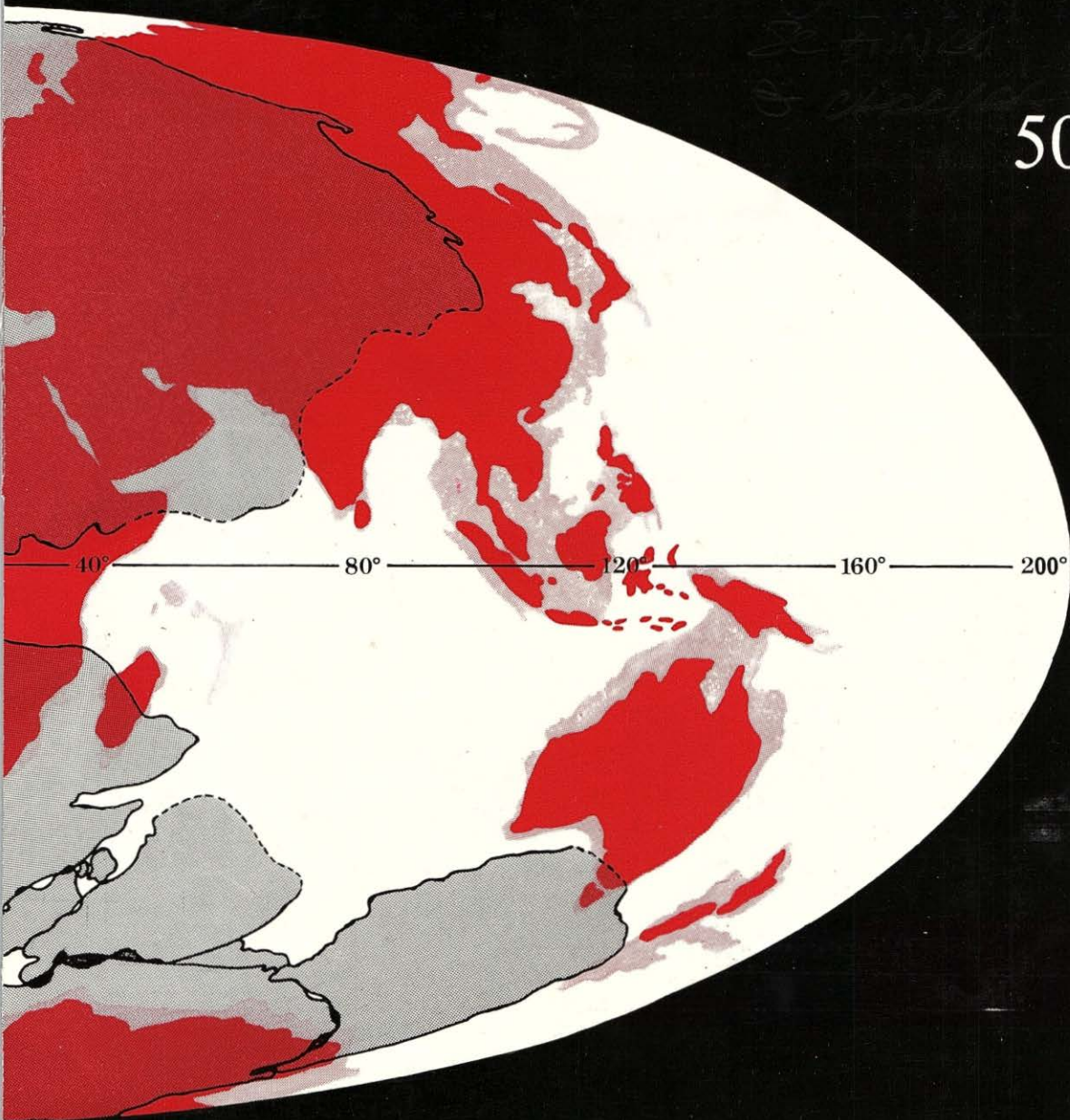
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This issue: Australia and Continental Drift

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VOL. 17, NO. 8

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This issue is devoted to the subject of continental drift, particularly as far as Australia is concerned. It contains eight extra pages.

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● FRONT COVER: The results of the last 200 million years of continental drift are depicted in this composite diagram. The distribution of the major landmasses during Triassic times is shown in black outline and fine stipple, using the present 1,000-fathom line to define the actual continental margins. The universal landmass, Pangaea, is made up of two supercontinents—Laurasia in the north and Gondwanaland in the south. The fit of the northern continents in Triassic times, as shown in the diagram, is commonly agreed on by geologists, but several versions have been proposed of the fit of the southern continents, South America, Africa, Madagascar, India, Australia, and Antarctica. That shown here is after Dietz and Holden. The distribution of the same masses today is depicted in red, with the continental shelf shown in lighter stipple.

AN INTRODUCTION TO CONTINENTAL DRIFT

By PETER H. RAVEN

Director of the Missouri Botanical Garden, St Louis, Missouri, U.S.A.

EVER since the explorers of the late eighteenth century brought the first news of the curious plants and animals of Australasia back to Europe, people have been fascinated by their peculiarity and by their patterns of relationship with the organisms found on other continents. One of the greatest riddles of all, first discussed by the famous English botanist, Sir Joseph Dalton Hooker, in the 1840's, concerns the close similarity between some of the plants and animals of temperate Australia and New Zealand, on the one hand, and southern South America, on the other. How has it happened that these southern lands, now separated by thousands of miles of frozen Antarctic wastes, come to share so many kinds of organisms: southern beech (*Nothofagus*), Proteaceae, southern gymnosperms, marsupials, certain groups of insects—to name only a few examples.

When Alfred Wegener, a German geologist, proposed his theory of continental drift in 1915, a solution seemed to be at hand. Wegener held that Australia, South Africa, South America, and India, together with Antarctica, all formed at one time a great southern land, which he named Gondwanaland. From an original position in the south, these lands moved gradually to their present positions. Wegener based his theory upon the geological similarities between these areas, including signs of ancient continental glaciation in some, and upon similar plant fossils. He showed that some of these areas could be fitted together like pieces of a gigantic jigsaw puzzle, and considered this to be further support for his ideas.

Biologists' differing views

Biologists living in the Southern Hemisphere were much impressed by the theory of continental drift, because it appeared to explain many of the riddles of distribution they were studying. Northern



A fine specimen of a *Glossopteris* leaf from the Permian period of Antarctica. The presence of such fossils in the rocks of Australia, Africa, India, South America, and Antarctica dates from a time when these lands were joined together. It has long been taken as evidence for continental drift. [Photo: Alex Ritchie.]

Hemisphere biologists, in contrast, did not see much need for such an explanation of the distributions of organisms. Eurasia and North America are virtually in contact now, and migration between them has always been relatively simple, especially at times when the climate was less severe than it is at present. Regardless of whether or not continental drift occurred, the plants and animals of the two great northern landmasses would be expected to resemble one another.

From about 1920 to 1967, continental drift was largely discounted as an explanation for any distributional pattern involving living plants or animals. The reason is that geologists and geophysicists were unable to visualize any mechanism which would cause the continents to move in relation to one another. Further, until relatively advanced technology became available following World War II, it was impossible to prove or disprove many hypotheses about the past positions of lands and the timing of their movements. Those few biologists who thought that continental drift was a possibility considered that it took place so long ago that it could have had little or no effect on present patterns of distribution.

Plate tectonics

During the past 5 years, however, there has been a revolution in the earth sciences, one which has altered some of the fundamental principles of the field. The new theory of plate tectonics, now nearly universally accepted, states that the earth's crust is made up of a small number of rigid plates that are moving relative to one another, some at rates as high as 10 centimetres (about 4 inches) per year. These plates are 50 kilometres (about 33 miles) to 100 kilometres thick, and they include both ocean basins and continents. Earthquakes and active volcanoes occur at their margins, where moving plates jostle one another, and only rarely in the centre of the plates.

Three kinds of movements may occur at plate boundaries. As plates move apart from one another, lavas well-up, solidify, and are added to the plate on each side of the rift. The plates move apart by lateral growth owing to the addition of the lavas from the rift. Consequently, the older sea-floor, oceanic islands, continents, and continental islands are rafted to new positions. Secondly, moving plates can be thrust deep into the earth's mantle along what are called subduction zones at the site of deep ocean trenches, as along the Aleutian arc. Thirdly, plates may slide past one another along a major strike-slip fault, as in the case of the Alpine fault of New Zealand.

New ocean floor is constantly being generated along mid-ocean rises, which makes it understandable that nearly half of all the present ocean floor is of Tertiary age,

less than 65 million years old, whereas the oldest rocks, up to nearly 4,000 million years in age, are all found on the continents. As lavas well out and solidify, they are magnetized by the earth's magnetic field, which periodically reverses the direction of its polarity. Consequently, the age of lavas can now be determined quite easily, a technique which has proved powerful in determining the age of sea-floor and the past position of continents.

Times of separation

What have these new techniques told us about the past positions of the southern lands? Africa and South America separated from one another about 110 million years ago, while the approximate times of separation of the southern lands from Antarctica are as follows: Africa, 90 million years; New Zealand, 80 million years; India, 65 million years; Australia, 45 million years. South America is essentially still connected. At the time that Australia, Antarctica, and South America were still in direct contact, parts of Antarctica supported a forest of southern beech, Proteaceae, and southern gymnosperms, which now are absent there. Some modern genera of flowering plants, including the southern beech, can be recognized in the fossil record 75 million years ago. There can be little doubt, therefore, that some of the similarities between the plants and animals of Australia, New Zealand, and South America were established when these lands were in contact and more or less direct migration was possible between them.

Position of Antarctica

The position of Antarctica at the time when all of these lands were in contact is of considerable interest. In reconstructing the past position of continents, it is necessary to hold one plate fixed and move the others in relation to it. In many such calculations, Antarctica has been the plate that has been considered fixed. This is, however, biologically impossible. If Antarctica had always been in its present position, the large cold-blooded animals found there some 200 million years ago at what is now 85° south latitude could not have survived several months of cold and darkness. The forests of tree-ferns and other plants that existed in

Antarctica at the same time could not have lived under these conditions, either, nor could Antarctica have functioned as a migration route for some of the plants and animals that passed across it if it had been so far south.

Biological evidence and that derived from a study of the magnetic patterns in rocks indicate that the most likely position for Antarctica at the time when it began to separate from Australia some 45 million years ago was about 15° north of its present position. Australia and Antarctica are now separated by some 30° of latitude, with a midocean ridge, along which lavas are upwelling, located about midway between them. This Australian-Antarctic ridge seems to have remained fixed in position, with both Australia and Antarctica spreading away from it and the ridge connecting South America and Antarctica becoming distorted in the process.

There are only a few biological similarities between Africa and India and the other southern lands. This pattern is probably attributable to several factors. Africa separated from Gondwanaland before most modern kinds of plants and animals were in existence, and now all of Africa lies north of 35° south latitude. Most of the similar plants and animals of Australia, New Zealand, and South America occur at relatively high latitudes in temperate climates now found in Africa at the present day. Movement of India across the torrid tropics to its present position in the Northern Hemisphere, a dramatic shift in position that has taken place in the past 65 million years, has clearly led to the extinction in India of all south temperate plants and animals, some of which are known from the Indian fossil record.

Australia 80 million years ago

Looking in more detail now at the history of Australasia, we may begin with a reconstruction of a portion of the area about 80 million years ago (see diagram in John R. Griffiths' article, page 252). At this time, nearly all of Australia that was above water was south of the present latitude of Brisbane, about 28° south latitude. Australia and New Zealand, as well as the other lands shown in the diagram, were clothed with a more or less continuous

temperate forest that extended across Antarctica to South America. Some of the peculiar and characteristic drought-resistant vegetation of Australia may have already been evolving on pockets of infertile or shallow soil, but such vegetation types were definitely not widespread at that time.

New Zealand separated from this landmass about 80 million years ago, and has been moving slowly northwestward ever since. Its isolation has subsequently been increased by the foundering of much of the Campbell Plateau. New Zealand has always been in such a position that it has had a colder, cloudier, and rainier climate than most of Australia, and at times it has been reduced to a much smaller land area than is exposed at present. The lowland forest of New Zealand is essentially a sample of the forest that covered much of Australia 80 million years ago, changed somewhat in this long period of isolation but still remarkably similar in composition to the ancient forests of Australia. The absence of marsupials and snakes in New Zealand seems to provide a clue that they were not present in Gondwanaland before its separation, a conclusion that is consistent with the fossil record. Marsupials must have spread between South America and Australia via Antarctica, while snakes apparently reached both independently after the separation of Australia from Antarctica.

The lands that flank Australia to the east have had varying histories. New Caledonia, with a very remarkable assemblage of ancient plants and animals, clearly preserves a sort of sample of the warm temperate flora and fauna of Australia perhaps 60 to 80 million years ago. Lord Howe and Norfolk Islands, although greatly decreased in size, also contain slices of old, continental rocks and some relict plants and animals. Like New Caledonia, they have spread eastward from Australia.

Australia itself has moved northward some 15° of latitude, as we have seen, during the past 45 million years. In the process, it has moved from a fundamentally temperate climatic belt into the great subtropical zone of reduced precipitation known as the "horse latitudes". Its northward movement has been responsible for the development of widespread deserts and other arid and semi-humid areas in the centre, and for the rapid

evolution during the past 45 million years of the plants and animals characteristic of these parts of the continent. Some of their ancestors must have existed locally even earlier, but they assumed continental scope only when Australia reached the appropriate climatic zone in the course of its northward movement.

New Guinea

The northern margin of Australia now lies in the tropics. In understanding the continent's relationship to the tropics, and to Asia in general, it is important to note that New Guinea, which is part of the Australian plate, was first elevated above the sea about 30 million years ago. When New Guinea had built up to an extensive land area, by about 15 million years ago, it constituted the Australian plate's first tropical extension, and became for the first time a ready means of migration between Asia and Australia. New Guinea was rapidly colonized by plants and animals from Asia, some of which subsequently reached northern Australia. Land connections with Australia were first established about 7 million years ago. By this time, the mountains of New Guinea had reached sufficient height to provide habitats for some of the temperate Australian plants and animals, like the southern beech, and marsupials also came to New Guinea at about the same time. In the lee of the mountains of New Guinea, zones of low rainfall were set up, and some of the plants and animals of the drier zones of Australia also entered, to become a conspicuous element in the lowlands around Port Moresby.

Wallace's line

Wallace's line, which divides the fauna of Asia from that of Australia, was recognized first by the great naturalist Alfred Russel Wallace, who visited New Guinea and its neighbouring islands in the middle of the nineteenth century. It defines the region of mixing of the plants and animals that had evolved in the south, in Australia, with those

that had evolved in the north, in Asia, and was set up, starting about 15 million years ago, when the collision of the Australian and Asian plates finally resulted in the creation of a considerable amount of land between them.

The mountains of Malaysia, New Guinea, Australia, and New Zealand were all elevated in the past 2 to 3 million years. They now form a series of stepping stones by which some of the plants of temperate Asia have migrated into Australasia, finding ample scope for evolution there, especially in the newly-formed mountains of New Zealand. The powerful southern westerlies sweep seeds, spores, and small animals continually around the Southern Hemisphere, and many southern patterns of distribution have an origin much more recent than the events discussed in this article. Birds and ocean currents have likewise been important in setting up some southern distributions.

But these are some of the recent embellishments of the main pattern, a pattern that can be stated simply as follows. The southern lands, including India, were once joined into a huge landmass known as Gondwanaland. During the past 100 million years, this landmass has broken up progressively into the fragments we see at the present day. In Australasia, the process has involved the gradual replacement of southern plants and animals of temperate climates by those adapted to arid and tropical climates, with the survival of many ancient kinds of organisms in southeastern Australia, in Tasmania, and on islands such as New Zealand and New Caledonia that have separated from eastern Australia and become increasingly isolated by their subsequent movement.

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Australia and Gondwanaland

By JOHN R. GRIFFITHS

University of Tasmania

AUSTRALIA has not always occupied its present position on the earth's surface. In the past it lay close against Antarctica, with no intervening ocean, the Tasman Sea did not exist, and New Zealand lay much closer to eastern Australia. Over many tens of millions of years, because of the phenomenon of continental drift, the geography of the earth's surface has been constantly changing. There is no reason to suppose that drift has ceased, and it is interesting to speculate on future movements. Evidence is also available to help in reconstructing former positions of the continents, and in this article I will discuss some of the evidence which shows how Australia, Antarctica, and New Zealand can be refitted together as part of an ancient supercontinent called Gondwanaland.

The possibility of continental drift has been considered for many years, and is now generally accepted by geologists. The early ideas about drifting continents sprang largely from the realization that certain continents, such as Africa and South America, could be fitted snugly back together. Other geologists went further, suggesting that at a certain time in the past all the present continents were grouped into two "supercontinents" which they called Gondwanaland and Laurasia, and that perhaps even these were joined as one single supercontinent called Pangaea. These early theories were based on two lines of evidence—the remarkably good fits, with few gaps, possible between certain continents, and the observation that, when so fitted back together, many geological features were continuous from one continent to another, seemingly irrespective of the oceans which separate them today.

Plate tectonics

The most recent version of the continental drift theory, called plate tectonics, says essentially that the surface of the earth consists of huge rigid plates, up to 150 kilometres (about 100 miles) thick. The plates move with respect to each other, and almost all of the world's earthquakes occur

at plate edges. The upper part of a plate can consist of two different types of crust—continental and oceanic. Continental crust varies from about 20 to 50 km thick, whereas oceanic crust is only about 5 km thick. Continental crust is made up of a wide variety of rock-types, including granites, metamorphic rocks, sediments, and other igneous rocks, whereas oceanic crust is of basaltic composition with a thin covering layer of deep-sea sediments. Another distinction, very important to the geologist who is trying to fit continents back together, is that oceanic crust, as its name implies, is generally covered by about 5 km of water—the world's oceans.

Plates can move with respect to each other in three different ways. Where they are moving apart, new oceanic crust is formed between them, usually at a mid-ocean ridge. When they are in collision, one dives sharply beneath the other, and oceanic crust is consumed, usually at an oceanic trench. They can also slip sideways past each other, giving rise to large faults such as the San Andreas Fault in California. Notice that in this scheme only oceanic crust is created or consumed. Continental crust is relatively buoyant and once formed tends to ride as a "passenger" on a plate, and subsequently cannot easily be destroyed. The continents are therefore old features on the surface of the earth whereas the oceans are very much younger and are continually being created and destroyed.

Magnetic "clock"

Geophysicists have developed a technique for determining the age of formation of oceanic crust. As molten basalt solidifies to form new oceanic crust at a mid-ocean ridge it records the direction of the earth's magnetic field at that time. The earth's magnetic field "flips" periodically, so that the north and south magnetic poles are reversed. The frequency of these reversals is irregular, but their sequence during the past 80 million years has been determined and the date of each reversal established.

It is therefore possible, using this magnetic “clock”, to map the ages of the ocean floors between the continents, and, as a result, to

take successive steps backwards in time and move the continents to their former positions. Before proceeding to attempt this exercise,

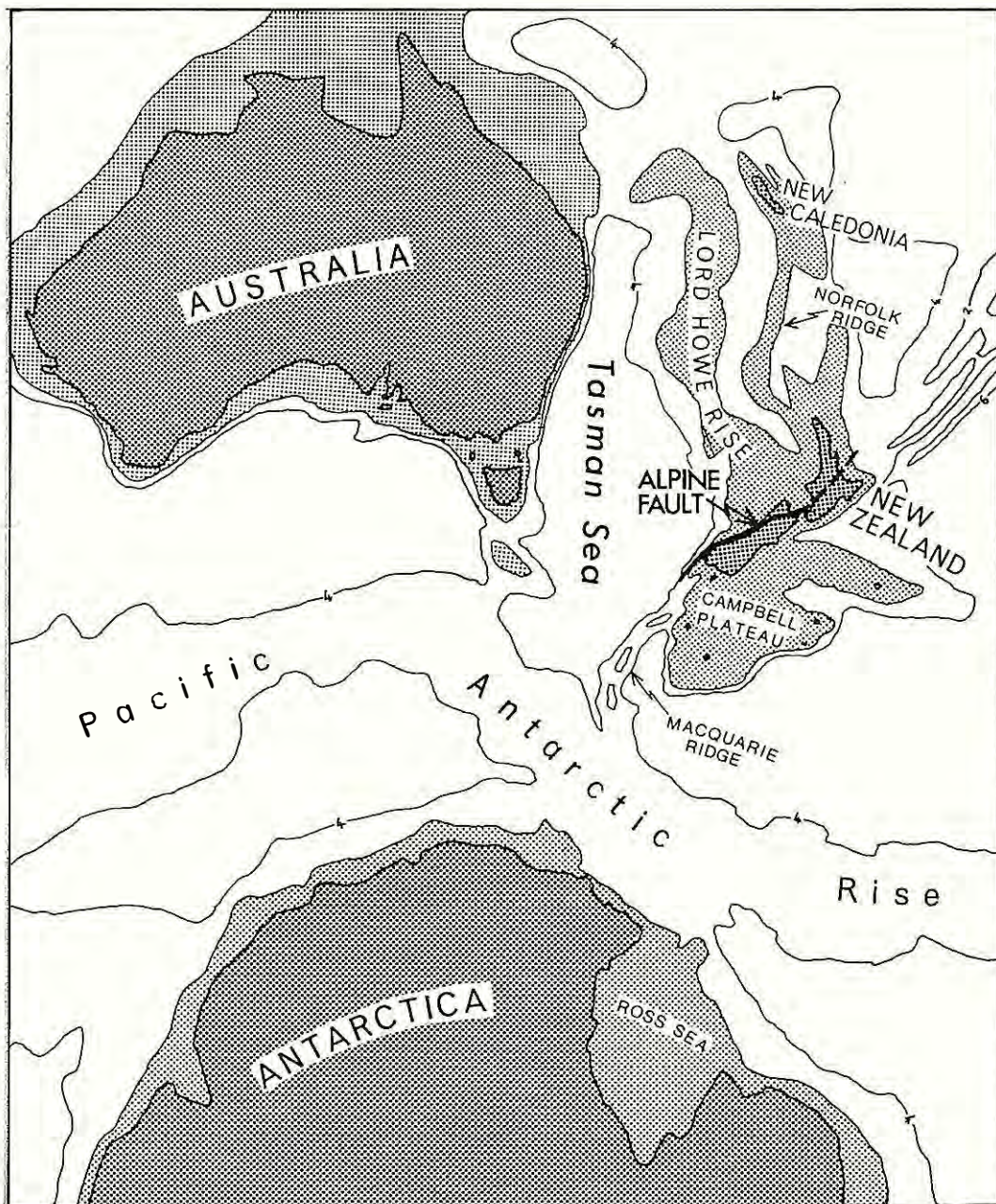
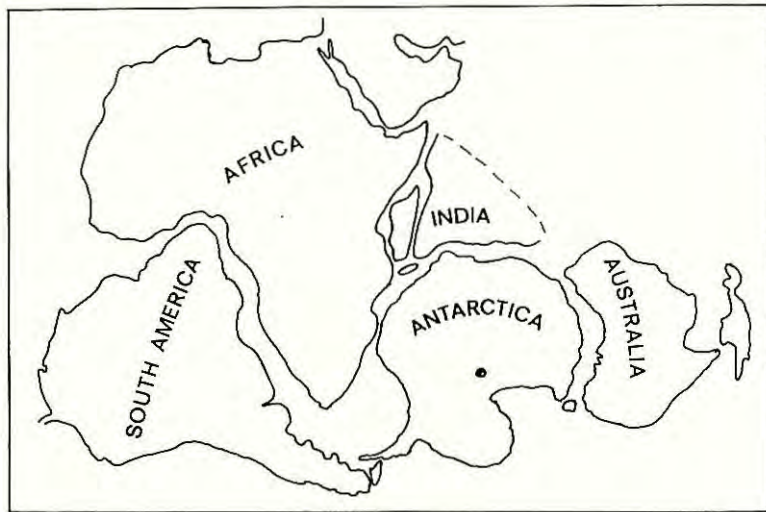


Fig. 1.—Bathymetry to the south and east of Australia, the 2, 4, and 6 kilometre submarine contours being indicated. Heavy shading indicates land areas, lighter shading areas of continental crust defined by the 2,000-metre contour.

Fig. 2.—Reassembly of the major components of Gondwanaland as they were about 100 million years ago.



one further point must be emphasized, and that is the difference between the geographer's notion of a continent and the geophysicist's definition of continental crust. The geographer recognizes continents as large areas of land bounded by water, taking the shoreline as his limits. In our geological reconstructions of "continents" we are in fact referring to areas of continental crust, which are bounded by the transition zone from continental to oceanic crust based on crustal thicknesses. Shorelines can shift rapidly in geological time, as, for example, when the sea invades large low-lying areas of land, and hence cannot be used to define the transition zone. We can, however, utilize another fact which I have mentioned, which is that oceanic crust is almost invariably covered by very deep water. We can therefore fairly accurately define the edges of the continental blocks that we are going to reassemble by selecting an intermediate bathymetric contour, thus overcoming the problem of widespread shoreline changes caused by comparatively superficial changes in sea-level. The oceans are on average about 5,000 metres deep, and in my reconstructions I have generally used the 2,000-metre submarine contour to define continental blocks. A quick glance at a map of the world's oceans will show that, although the 2,000-metre line roughly parallels the shores of the major continents, there are in places large submerged areas which are nevertheless covered by much less

than 2,000 metres of water.

These basic concepts provide the background with which to approach the question "What did Australia look like before continental drift occurred?", which I will now try to answer. Look again at a map of the seas around Australia, and it will be evident that the 2,000-metre line is far from the present coastline in places, especially in the northern regions. Off the east coast of Australia the 2,000-metre line is close to the New South Wales coast, but swings out widely around the Great Barrier Reef and encompasses much of the sea between Australia and New Guinea. Across the Tasman Sea there are other large areas covered by much less than 5,000 metres of ocean, and which break the surface in New Zealand, New Caledonia, and a few other small islands. I have indicated all the area submerged to less than 2,000 metres in figure 1, and all these areas must be considered when attempting to reassemble continental fragments in the region.

Though I have defined these as continental fragments on the basis of bathymetry alone, there is other evidence that they are really continental crust. Geophysicists have shown that the crust beneath the Lord Howe Rise, the Norfolk Ridge, and the extensive plateau southeast of New Zealand ranges up to 30 kilometres or more thick, whereas in the Tasman Sea, New Caledonia Basin and surrounding Pacific Ocean the crust is only

5 kilometres thick. The rock-types found on New Zealand, New Caledonia, and the smaller islands are typically continental, whereas oceanic basalts have been dredged from the deeper oceanic areas. So with the continental blocks—the pieces in the jig-saw puzzle—thus defined, the problem is to solve the puzzle and reassemble the pieces as they were before drift occurred.

The first stage in the reconstruction is to

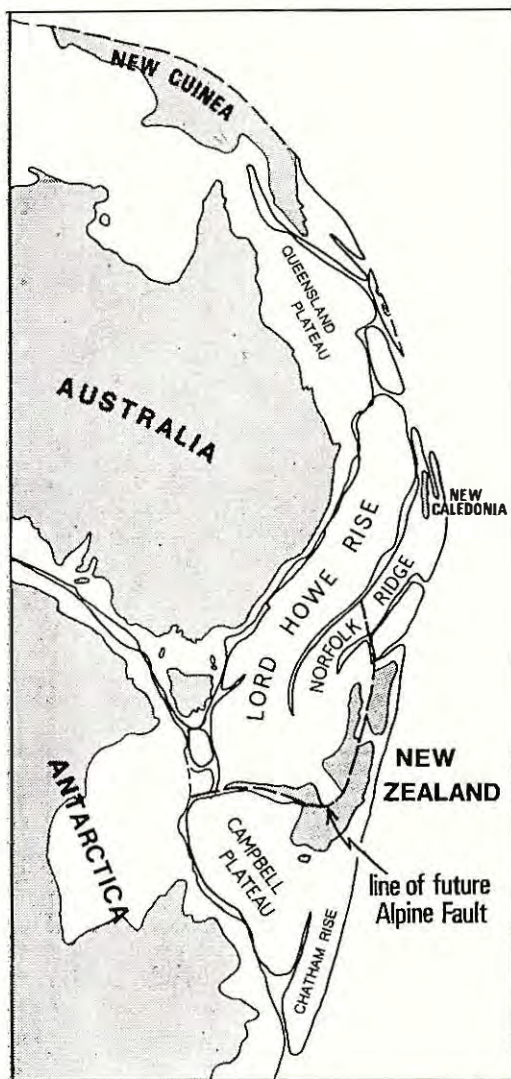


Fig. 3.—Reassembly of the Gondwanaland fragments in the southwest Pacific as they were about 100 million years ago.

reposition the major continents which formed Gondwanaland. Australia was one of these continents, and fits against Antarctica along with India, Africa, and South America (figure 2). This fit of Australia and Antarctica is confirmed by recent mapping of the magnetic pattern in the intervening ocean. This data also indicates that the split occurred about 55 million years ago, in contrast to the continental rocks on either side, which range up to 2,000 million years and more in age.

The next stage is to fit the Campbell Plateau against Antarctica. The magnetic record has not yet been fully mapped in this region, and little data is available from south of the Pacific-Antarctic Rise. However, using the general principle that the magnetic record is symmetrical about the mid-ocean ridges, we can extrapolate the available data to south of the ridge. Successive steps backward in time then swing the Campbell Plateau back to fit against Antarctica, with a reasonably good fit of the 2,000-metre contours (figure 3). This separation began about 80 million years ago.

East of Australia, recent results indicate that the Tasman Sea is also less than 80 million years old, and that the Lord Howe Rise originally lay against eastern Australia. To complete the reconstruction it is then necessary to shift the southern end of the Lord Howe Rise about 1,000 kilometres west with respect to the Campbell Plateau. Study of the geology of New Zealand shows that just such a displacement has taken place, deforming the rocks in New Zealand and giving rise to the great Alpine Fault which cuts New Zealand in two (figures 1, 3). When this 1,000 kilometre displacement is reversed, the remaining continental fragments fall into place as shown in figure 3, thus completing the reconstruction.

Geologically we can now look at the reconstruction and see if in fact we can match up the rock sequences across the much younger oceans. This is made a little difficult in this region because of the extensive ice-cover of Antarctica, and the submergence of much of the continental crust to the east, but nevertheless correlations do exist. On the broadest scale we can recognize several belts, each characterized by a sedimentary sequence of a particular age which has been

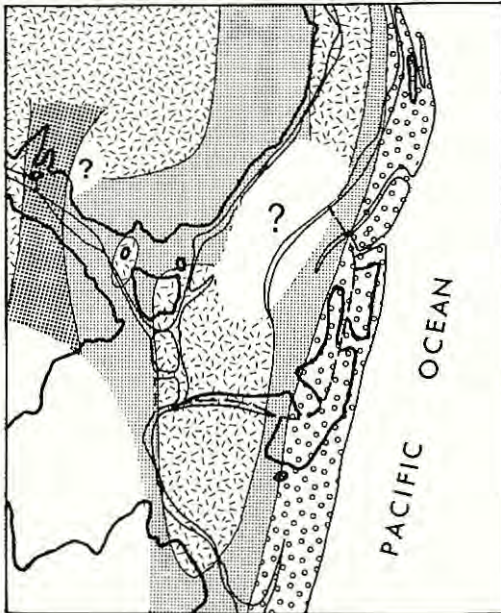


Fig. 4.—The position of major geological divisions as they appear on the reconstruction shown in fig. 3 (see text). Dashes indicate Precambrian shield and "islands"; heavy dots, Adelaide-Ross geosyncline; light dots, Tasman Orogenic Zone; open circles, New Zealand geosyncline.

subsequently deformed during orogenic (mountain-building) activity. These major geological divisions are indicated in figure 4. Generally the rocks become younger eastwards, suggesting gradual accretion onto the old Australian shield, but recent studies indicate further complications in that large "islands" of older rocks occur within younger belts. These islands were once probably separated from the rest of Australia by small oceans, which have been subsequently swallowed during a much earlier episode of continental drift.

Thus from the Precambrian shield (see figure 4) we pass eastwards into the Ross-Adelaide geosyncline (Precambrian-Lower Paleozoic), and then into the very complex Tasman Orogenic Zone (Lower-Upper Paleozoic). Two possible Precambrian "islands" which we have identified are shown within this belt. During the orogenic activity affecting this zone, these islands have probably been swept westwards on a plate until they collided with the rest of Australia. After this the New Zealand geosyncline

began to develop along the Gondwanaland margin. This was originally a linear feature, but has been very severely distorted during the latest episode of continental drift, which has shifted the Gondwanaland fragments to their present positions.

Continental drift is almost universally accepted today. In recognizing the existence of supercontinents such as Gondwanaland, and trying to fit their fragments back together, many other geological problems are simplified. The theory has much wider implications, however, as it has a direct bearing not only on earth sciences but also on biological sciences through its implications in the study of plant and animal distribution and evolution, and it should continue to prove valuable in helping to solve many outstanding biological and geological problems.

[The illustrations in this article are by the author.]

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A.C.T. WILDFLOWERS

WILDFLOWERS OF THE AUSTRALIAN CAPITAL TERRITORY, by Thelma and George Chippendale; *Jacaranda Wildflower Guides*, Vol. 6, Jacaranda Press, Brisbane, 1972; \$1.95.

Like its companion volumes (*Wildflowers of N.S.W.*, *Wildflowers of Victoria*, etc.) this pocket-size booklet illustrates and describes exactly fifty common species. The illustrations are photographic and very variable in quality, some excellent, some poor, some sideways, at least one (page 7) upside-down. The text is by a professional botanist and his wife and is therefore authentic.

Apparently the vogue for wildflower picture books these days is such that publishers find it profitable to churn them out. For practical purposes one is bound to wonder at the utility of a book which deals with a mere fifty species. In some of the larger "coffee-table" editions the photography in itself is outstanding or the scope and scholarship of the work compel respect, but the pocket-size work under discussion does not possess these qualities. Perhaps a newcomer to the A.C.T. might find it useful to the beginner, but even he would be left puzzling over many species not mentioned in it.—*J. S. Beard, Director and Chief Botanist, Royal Botanic Gardens, Sydney.*

THE FACE OF THE EARTH

By S. WARREN CAREY

Professor of Geology, University of Tasmania

DAS *Anlitz der Erde*, or "The Face of the Earth", was the title of the first great *magnum opus* on the gross surface features of the earth by Eduard Suess late last century. A recent British television documentary with the same purpose bore the same title. Suess' masterpiece was the product of one great mind. The TV show was produced by a very large team. Suess wrote for a scientific oligarchy. The TV documentary was directed at the man in the street. In Suess' day the only bird's-eye view was from a mountain-top. In this decade all have seen the face of the whole earth as viewed from the moon. From nineteenth-century elitism to twentieth-century mass communication, what has really happened to the science of the earth?

All early science was egocentric, in that it assumed that things have always been much as we now see them, at least since the earliest beginning too hazed in ignorance to discuss. A century ago geologists believed that the mass, volume, and diameter of the earth were fixed inheritances, that the axial tilt to the ecliptic was immutable, that the earth was a dying body dissipating primal heat from a still molten core, that magnetic north was north and south was south and always had been so, that physical constants had been and would remain constants, and that continents were fixed permanent features which heaved and sagged from time to time against an ebbing and flooding sea. The geologist's task was to describe and understand the details of a planet on which the really big things had happened eons ago as a prologue before their saga opened.

During the nineties Suess knew this had to be changed, for he recognized that 200 to 300 million years ago Africa, South America, India, and Australia had been a super-continent sharing the *Glossopteris* flora and a common ice age. [*The Face of the Earth*, trans. Sollas 1906, Oxford, vol. III, p. 254.] But Suess assumed, not that Africa and the rest had moved, but that the parts between had foundered to form new oceans. Wegener upset the calm by concluding that at the time in question all the main land

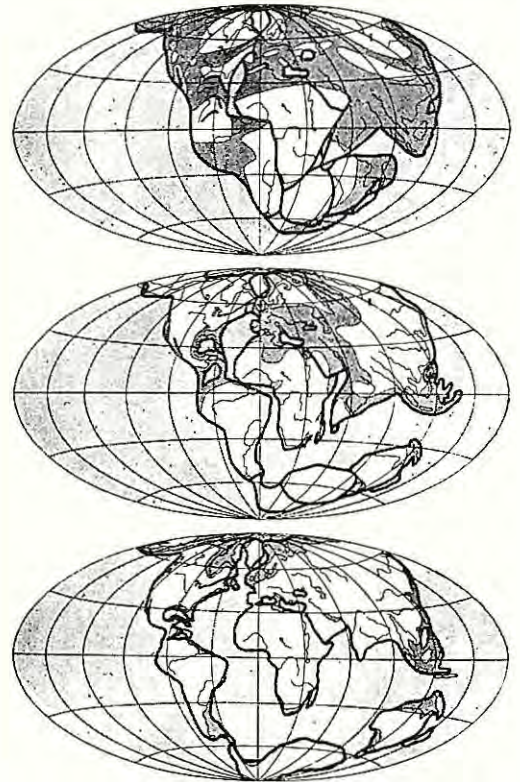


Fig. 1.—Dispersal of Pangaea according to Wegener. Late Palaeozoic (top) to the present (bottom) on a Mollweide projection. Shallow seas are shaded.

masses of the world had been a single great continent, Pangaea, which had disrupted into separate blocks that drifted apart like great tabular icebergs, opening the Arctic, Atlantic, and Indian Oceans and reducing the area of the Pacific by a like amount (fig. 1). During the thirties and forties and early fifties Wegener's ideas were generally rejected as a fantasy—fascinating but false. During the fifties a few of us, who had recognized the truth of Wegener's separations, realized that the earth had to be expanding and that oceans generally represent new crustal growth separating dismembered earlier crust. This too was, and is, largely scorned. During the late fifties also, new palaeomagnetic data

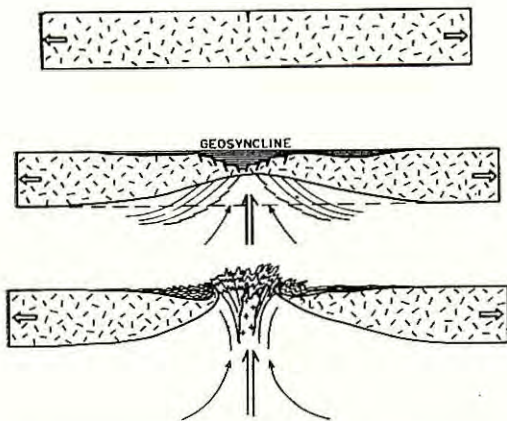


Fig. 2.—The development of sedimentary troughs (geosynclines) and the process of mountain building (orogenesis) on an expanding earth. [Diagram by the author.]

strongly supported intercontinental separations along Wegener lines. This, together with vastly improved information about the ocean floors, led to a new generation of "continental drifters" who accepted the separation of continents but assumed that whereas new oceanic crust was added in the separating regions, this was balanced by swallowing ("subduction") of old ocean crust in the ocean trenches. Under the slogans "new global tectonics" and "plate tectonics" these views, with British and American sponsorship, have reached a hit-popularity worthy of Presley and the Beatles.

Today there are three competing theories: (1) this plate-tectonics conveyor-belt model, currently commanding overwhelming popular appeal; (2) a small group led by Meyerhoff, Stehli, and Teichert in America and quite a number in Russia, who believe that the continents and ocean basins remain now more or less where they have always been; and (3) a small third group—for which I will accept blame that any others may not wish to accept—who are convinced that the earth is expanding and that the separation of the continents by growth of new oceans is not extensively compensated by the swallowing of old crust elsewhere.

The "new" global tectonics has "discovered" that Wegener, long spurned and sneered at, was essentially right in his separation of the continents, which a few of us knew all along. The vast new data about the ocean floors have left no remaining doubt

that all the ocean floors are young and represent new growth separating blocks and slices of old crust. But unfortunately this has been tied to the old false axiom that orogenic belts and ocean trenches represent zones of intense crustal shortening, contraction and swallowing of crust, a view held firmly by Suess and others a century ago. In the long run this will be recognized as the greatest false trail in the history of geology. This compressional orogenesis misconception is primarily held by the English-speaking schools. The Russians and many European geologists (e.g., van Bemmelen) have always recognized that gravity is the prime mover, that orogenesis is essentially an upward diapiric (piercing through) process originating at great depth, and that the horizontal overthrusting and overfolding in all fold belts is a secondary spreading under gravity (fig. 2). Enormous amounts of work have been done by geologists and geophysicists who have jumped on the plate-tectonics bandwagon to rationalize the data of earthquakes, of volcanism and plutonism, and of metamorphism and heat flux, to fit the concept of wholesale swallowing of crust there, hundreds of millions of cubic kilometres of it, as fast as new ocean crust is developed elsewhere. But all these data fit as well (usually better) into the proper concept of upward diapirism and crustal extension in these zones.

The plate-tectonics bandwagon now is very close to the views I taught 20 years ago, when most scorned them. I pursued these ideas for more years than any of the new generation of plate tectonicists. I have no doubt that when they have studied them for as many years as I did, they will come round to the same conclusion that I did—that they will not work for the whole earth, and that gross expansion is inescapable (*Search*, vol. I, no. 5, pp. 178-189). Meservey has also pointed out (*Science*, 31st October, 1969, pp. 609-611) that the plate-tectonic model is geometrically impossible without major crustal expansion, using one of the arguments which I have presented to my students for a decade.

The cause of earth expansion remains an enigma. But this is a common state in the history of science. Frequently a great empiricism has been in conflict with the

current theoretical model of nature—as, for example, when Kelvin told the geologists that their claims about the great age of the earth just had to be wrong by two orders of magnitude. The discovery of radioactivity was the missing link which eventually set this right. But even for the expanding earth the answer may be in sight. Hoyle and Narlikar (*Nature*, vol. 233, pp. 41–44) have suspected from their studies in cosmology that the gravitational constant may well be diminishing with time. Now the gravity potential energy of the earth accounts for 61 per cent of its total energy (elastic compression 22 per cent, heat 8 per cent, radioactivity 2 per cent, etc.). The gravitational potential energy involves the gravitational constant, G , and the radius. Hence, if G changes the earth radius must increase inversely. The estimated average rate given by Hoyle and Narlikar (10^{-10} /year) would correspond to a circumference increase of about 2 mm per year or 400 km since the Triassic. Observed rates are greater than this but empiricism indicates that the expansion rate has been increasing with time, so that rates during the last 200 million years were much faster than this average. Also, the expansion is increased by other feedbacks. Throughout the earth there are phase transitions where minerals condense to denser forms. At a given temperature these depend on pressure. If G diminishes so does the pressure at all depths, and minerals change phase to their less dense forms, resulting in further expansion. Gravity differentiation within the earth also results in expansion, because if a uniform sphere progresses to a radially differentiated one, the total potential energy is greatly reduced. At constant temperature this would result in expansion to conserve energy, or if all this lost energy were dissipated as heat the rising temperature would further shift the phase transition boundaries, with denser phases becoming less dense, and hence there would be further expansion.

When the 1928 symposium in Tulsa rejected Wegener, continental drift became dirty words for a quarter of a century, until a new generation rediscovered it. Observing the current triumphal march of the half-right “new” plate tectonics with its subductive anti-truth, we might expect to wait another quarter of a century and the emergence of

another generation before the reality of the earth expansion is recognized.

Fortunately, however, three brilliant experiments are contemplated which should settle the matter within a decade:

(1) Apollo 15 placed a corner-cube reflector on the moon which will return any light directed onto it back along the path it came. Modern technology has also yielded laser light which has three special properties: the beam can be made much narrower than the best searchlight, it contains only a single wave-length (colour), and (most important) it is coherent. (If we had fifty propellers all turning at different speeds, this would correspond to white light, which is a mixture of all colours; if all the propellers turned at the same speed, this would correspond to light of a single colour; if, in addition, the propeller blades remained parallel to each other as they turned so that they all pointed upwards at the same instant, this would correspond to coherent light). The important point is that coherent light reflected back from a corner-cube to its source interferes with the outgoing beam in such a way that the distance to the corner cube can be measured very accurately. To do this to the moon requires a very good telescope because the returning beam is extremely weak, but it can be done. The proposal is to do just this from observatories at Honolulu, Tokyo, and Canberra, and if this is repeated for different positions of the moon, not only can the distances from these observatories to the moon be measured, but also their distances from each other, with an accuracy of a few centimetres. Now according to the newly-fashionable theory each of these observatories must be getting closer to each other by a decimetre or so per year, but according to the expanding-earth theory they should be getting further apart. A few years' observations should prove who is right.

(2) Particle physicists with access to the high-energy Brookhaven accelerator propose to send a pulsed beam of neutrinos right through the earth from Chicago to Cocos Island in the Indian Ocean and to measure the length of this chord with an accuracy of a few centimetres. This again would, after a few years of repetition, prove whether the

earth is expanding or not. Neutrinos are the most elusive of all subatomic particles. They have no rest-mass, no charge, and so do not respond to magnetic fields. They can go right through an atom and even a nucleus with rarely any interaction, and so the bulk of them will pass right through the earth. To contemplate focussing them into a pulsed beam is to ask for the near-impossible, but a statistical approach to this seems practicable.

(3) A Japanese geophysicist working in Paris claims to have developed a technique to measure absolute gravity to an accuracy of a few microgals (better than one hundred-millionth part of the gravity acceleration). This is precise enough to show up the expansion of the earth in a few years, although here again fastidious care would be necessary to correct for several other known perturbations of gravity.

And so we wait.

NEW BOOKS REVIEWED

MOSQUITOES, by J. D. Gillett; *The World Naturalist series*; Weidenfeld and Nicolson, London, 1971; \$18.50.

This book is an interesting and informative addition to the World Naturalist Series.

Professor Gillett devotes the early chapters to the various stages of the life-history of mosquitoes, and follows on with a series of chapters on the more modern research problems associated with mosquitoes, such as the feeding cycle, the ovarian cycle, circadian rhythm and strains and species.

There is, naturally enough, a considerable bias to the important research work carried out in Africa in the past 20 years, in which the author and his colleagues played important roles in unfolding the ecology of sylvan yellow fever. In the accounts of this and other research, details of the problems which had to be overcome in carrying into effect definitive experiments are sometimes included. These give the reader an insight into physical and operational difficulties which can only be fully appreciated by the field or laboratory worker who has attempted comparable studies.

The Australian reader will not appreciate the inclusion of Australia in the distribution of filariasis, and will be surprised at the failure to mention *Aedes polynesiensis* as the most important Pacific vector of this disease. Australian workers will be unable to find any justification for the segregation of New Guinea from the rest of the Australian region in the regional lists of species, nor for the inclusion of Micronesian species in the Australia list. Indeed the regional lists have no relevance to the rest of the book. Plate 17, depicting mosquitoes feeding on a caterpillar, is a questionable inclusion, as the insects appear to be biting-midges and not mosquitoes.

In the body of the text the information presented is at a fairly advanced level, but the easy style ensures relaxed and informative reading to anyone interested in biological knowledge for its own sake. For this reason it would be fair to emphasize that readers at all levels of biological training would find the book profitable and enjoyable. The final chapter on mosquitoes and history is an interesting and salutary reconstruction of the dramatic episodes of mosquito-borne disease of the past and even recent years.—*David Lee, School of Public Health and Tropical Medicine, University of Sydney.*

SYNOPSIS OF ANIMAL CLASSIFICATION, by R. B. Clark and A. L. Panchen; Chapman and Hall, Ltd, London, 1971; \$5.30.

The time devoted to systematic zoology (animal classification) in university zoology courses has been greatly reduced over the last decade. Instead, far more emphasis is being placed upon ecology, physiology, biochemistry, etc. While this may be extremely valuable, the student is still expected to be able to put a name to an animal and place it within the relevant group, for it is important for a physiologist or ecologist to know which animals he is in fact dealing with.

Clark and Panchen have attempted to solve this dilemma by *Synopsis of Animal Classification*, which was written to be used in conjunction with zoology practicals at the University of Newcastle, England, and from my own experience it was successful. In a short but good introduction the reasons and principles used in classifying animals are given. Each phylum or group of animals is then discussed. The basic morphological characteristics of the phylum and the major subdivisions within that phylum are given, together with simple diagrams. Obviously, a book of this size cannot deal with the characteristics of the genera and species within the subdivisions. But this is not the aim of the book; instead, it is to provide a student with the basic morphological characteristics of the phylum, etc., which should enable him to place an unknown animal in the correct phylum, class, and order. For once the underlying principles of animal classification have been grasped, some rhyme and reason is introduced into systematic zoology.

This book will, I think, be useful to high school and university students and to their teachers, who are faced with having to teach systematic zoology in a very limited period of time. It will also have some value for the keen amateur, especially those who are interested in identifying the minor invertebrate phyla, e.g. nemerteans, sipunculids, echiuroids, which are to a large extent ignored by popular books. It is a pity, however, that such a useful little book should retail here in Australia for \$5.30, which may put it beyond the range of some students, whereas in England the recommended price is £1.60—*Pat Hutchings, Assistant Curator of Marine Invertebrates, Australian Museum.*

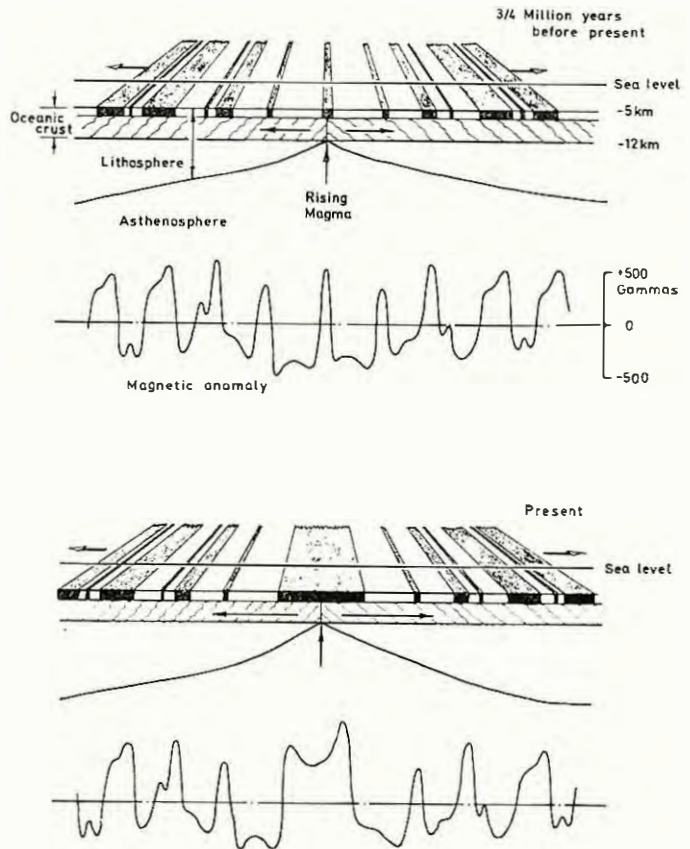
Plate Tectonics: A Dynamic Approach to Modern Geological Theory

By DAVID A. FALVEY
Royal Australian Navy Research Laboratory

UNTIL just this decade geology was always relegated to the position of the arch-descriptive science—even an “art form”. In the important areas of study, such as mountain building (orogenesis), it totally lacked the predictive, or even physically feasible, working model that, for example, atomic theory had provided for chemistry in the nineteenth century. The “new” geology had its conception during the 1960’s, when the newest branch of the science, oceanography, uncovered remarkable evidence in support of a modified form of the old, and

largely discredited, theory of continental drift, put forward early this century by Alfred Wegener. This modified theory became known as “sea-floor spreading” and was due primarily to the work of H. H. Hess, and also R. S. Dietz. Whereas the continental drift hypothesis held that continents floated upon, and moved over, more or less fixed oceanic crust, sea-floor spreading implies the welding of continental to oceanic crust, and their joint movement as if forming the skin of a conveyor belt. Two such “belts” rise and move in opposite

The Vine-Matthews hypothesis. — A natural remanent magnetism is frozen into new oceanic crust formed at a mid-ocean ridge as described by the sea-floor spreading theory of Hess and Dietz. A pattern of main magnetic field reversals may be sensed by measuring marine magnetic anomalies in the present earth’s field. Black stripes represent the present-day, or normal field direction, and white stripes the reversed field direction. The upper cross-section represents a mid-ocean ridge three-quarters of a million years before the lower one. Note that the oceanic crust and its characteristic magnetic anomalies are shifted symmetrically left and right of the ridge. [Diagram by the author, after Vine.]

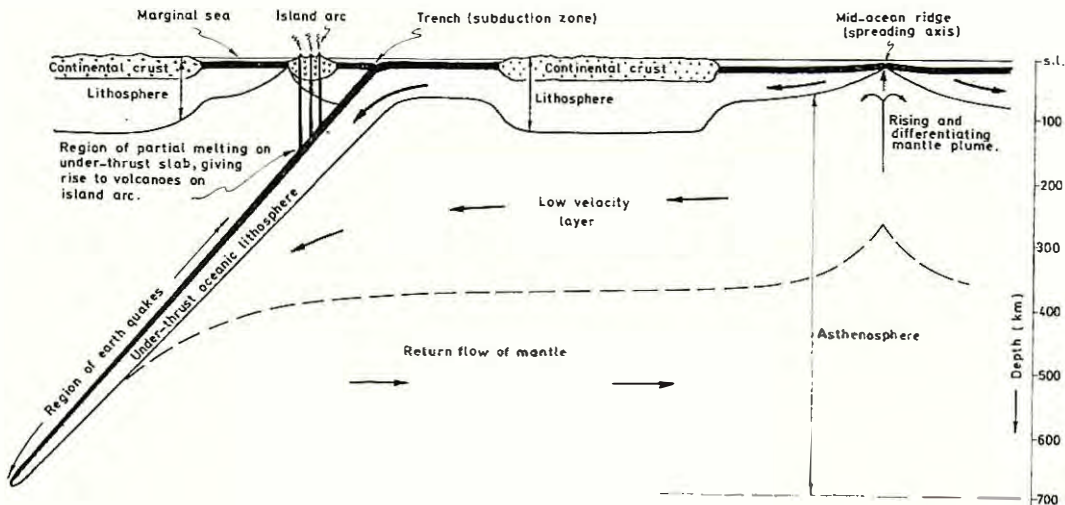


directions, at the mid-oceanic ridges, where the oceanic crust portion of the belt (only) is created from the solidification of liquid volcanic material which rises up from the earth's mantle.

A means of measuring relative rates of sea-floor spreading (i.e., the speed of one "belt" relative to the other on the opposite side of a mid-oceanic ridge) was devised by F. J. Vine and D. H. Matthews in 1963. Volcanic material, which composes oceanic crust (basalt or oceanic tholeiite), contains a mineral, magnetite, which, upon cooling from high temperature in the presence of the earth's main magnetic field, acquires its own magnetism. Thus, oceanic crust has a natural remanent (remnant) magnetism (N.R.M.) which is acquired by the crust at the time of its formation at the mid-oceanic ridge. The direction of the N.R.M. is such as to align north-to-south in the earth's main magnetic field just like a compass needle. However the earth's main field periodically reverses its direction—the north magnetic pole has occasionally been south, while the geographic pole is fixed. Thus the oceanic crust preserves a memory of these periodic field reversals by the changing sense of the N.R.M. frozen into the basalt of the oceanic crust. This may be measured by a ship at sea as a small variation, or anomaly,

imprinted on the earth's main magnetic field. These oceanic magnetic anomalies are just like morse code on a tape recorder. Since, from other data on continental volcanics we know this code—i.e., the pattern of main field reversals through recent geological time—we may determine the speed of the tape, i.e., the oceanic crust. This gives the rate of sea-floor generation at a mid-oceanic ridge (and also its direction of motion).

Many scientists (including the author!) remained sceptical of the absolute ability of marine magnetic anomaly patterns to describe a history of oceanic crustal growth. However, in 1968 results from the Deep Sea Drilling Project of the U.S.A. dispelled all doubt. Rocks drilled from oceanic crust near the South Atlantic Ridge were found to be younger in age than those more distant from the ridge—a relationship described almost exactly by the magnetic anomaly pattern suggested by the sea-floor spreading hypothesis. Thus far, a qualitative theory existed which described the growth of new sea floor by accretion at a mid-oceanic ridge, and its lateral spreading, away from that ridge through time, producing growing ocean basins. The new theory satisfied the old continental drift concept because continents would be moved apart by oceanic



Cross-section of lithosphere plate.—Oceanic lithosphere is generated at a mid-oceanic ridge (right), moves to the left, and is underthrust and returned to the asthenosphere. Partial melting of the under-thrust slab gives rise to a volcanic arc behind the subduction zone. Sometimes marginal basins grow behind volcanic chains, and consequently give rise to an island arc. Continental material is carried about by the growth and destruction of oceanic lithosphere. [Diagram by the author.]

crust accreting at a ridge, hence the name "mid-ocean" ridge. Iceland, in the North Atlantic, is a portion of the mid-ocean ridge exposed above sea-level. Growth along this ridge separates North America and Europe further apart and causes Iceland to grow wider by 2 cm a year, or by 20 metres since the island was first settled about the year 1000.

Patterns of earthquakes as "plate" boundaries

Nearly all the world's major earthquakes (there are none within Australia) occur in very narrow zones or belts which are all interlocked like a network. Very simply, there are two types of geographic features associated with earthquake (or seismic) belts:

- The mid-oceanic ridges: the sites of generation of oceanic crust by sea-floor spreading are also sites of shallow seismic activity;

- The deep-sea trenches and island or volcanic arcs: most of the world's earthquakes occur at or behind these regions, which mainly encircle the Pacific Ocean. The zone of earthquakes begins at the trench and dips down at about 50° beneath the island arc or volcanic arc, sometimes to as deep as 700 kilometres (about 470 miles). This is interpreted to demonstrate the underthrusting (subduction) of oceanic crust beneath the island or volcanic arc, just like the down-turning edge of a conveyor belt beneath a fixed belt. The earthquake zone marks the plane of contact between the stable and underthrust blocks. Partial melting of this underthrust slab is thought to produce the volcanic extrusives of the arc, which occurs behind all trenches.

Plate motions

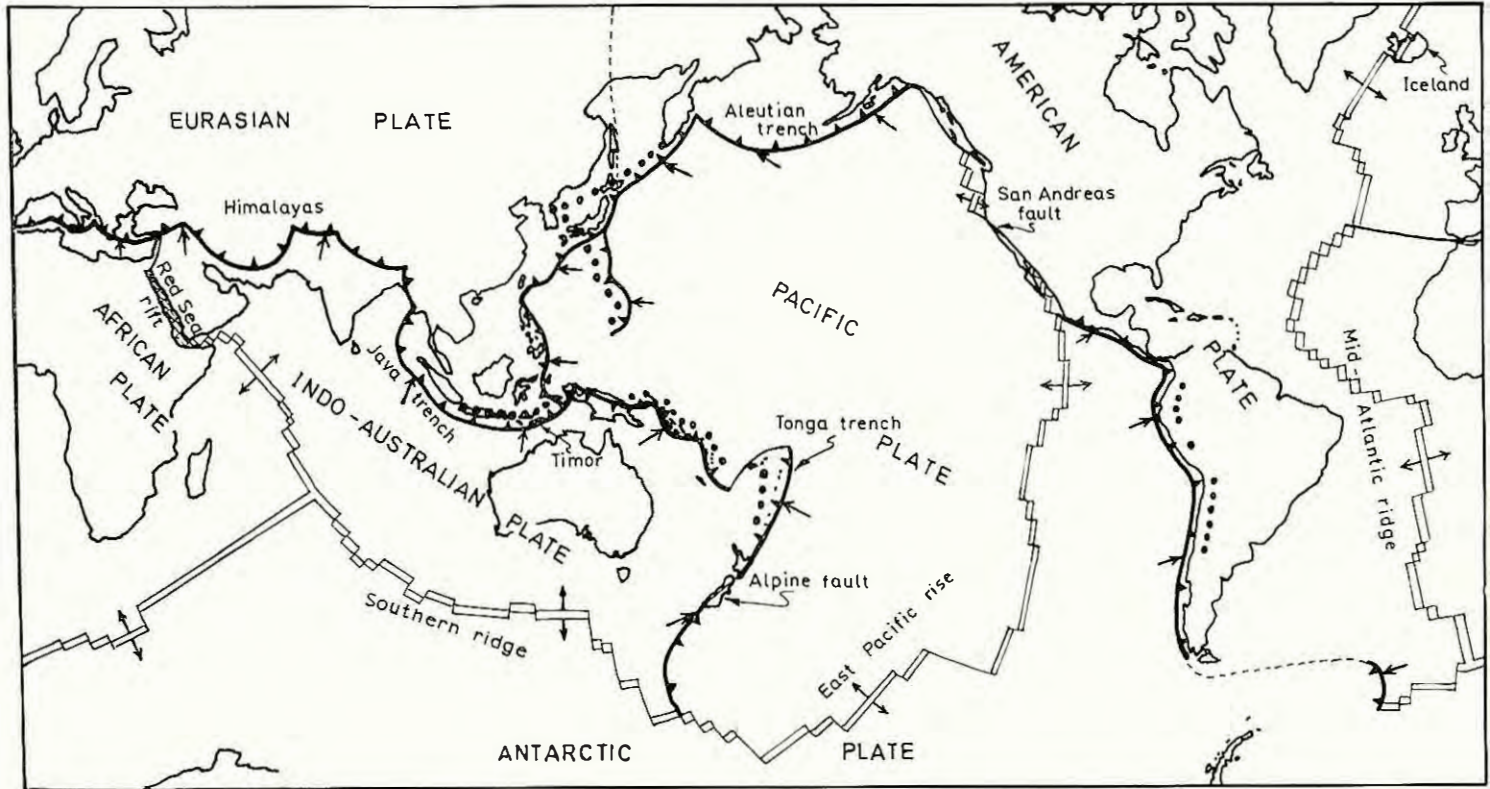
The rigid, moving plates just described consist of more than just the superficial (oceanic or continental) crust. It is possible to measure the travel time of sound or shock waves from earthquakes to various detectors (called seismometers). From these observations one may compute changes in the velocity of such shock waves with depth through the earth (P-waves or pressure waves travel through both solids and liquids; S-waves or shear waves travel only through solids). At depths of about 70 kilometres beneath oceanic crust and about 100-150 kilometres beneath continental crust, the velocity of S-waves, in particular, suddenly

drops by about 10 per cent. Here, the earth's mantle becomes suddenly weaker and more plastic. The relatively stronger material above these depths is called the lithosphere, and indicates the depth extent of the rigid plate (much deeper than the crust-mantle boundary, which is a chemical, not mechanical, boundary). The mantle below the lithosphere is called the asthenosphere. The low velocity layer extends to 200-300 kilometres, and is the near-fluid material which carries the moving plates. A good analogy is pack ice floating on sea-water.

The motion of a plate over the asthenosphere is difficult to describe relative to a fixed point, such as the geographic north pole, except by reference to palaeomagnetic data. However, it is easy to describe the motion of two or more plates relative to each other, and without reference to the present latitude-longitude grid. Hence, both theory and observation are important:

- Long before this century it was realized that any simple movement from one spot to another on a sphere, like the earth, could be described by a rotation about some axis, which passes through the centre of the sphere. The intersection of the axis with the surface of the sphere is called the pole of rotation. Any path segment on the earth, be it a small circle or great circle, has a unique axis and pole of rotation. A specific example is the way in which east-west latitude lines have a pole of rotation at the north (or south) pole, i.e., any east-west motion may be described by a rotation about the north (or south) pole. For our purpose, imagine the north and south pole and its latitude-longitude grid to be free to move anywhere over the earth to describe the motion of one plate relative to another.

- The pole of rotation, which describes the drift of South America from Africa, lies between the southern tip of Greenland and Ireland (60° N and 30° W). With a piece of string (or perspex cap) hold the pole fixed there on a globe, and trace the drift path—Ghana to the mouth of the Amazon River, the mouth of the Orange River (in South West Africa) to near Montevideo (in Uruguay), etc. Note that, as you trace drift paths further south, the path length increases, until a maximum is reached for the path through Walvis Bay, South West Africa, to the southernmost part of Brazil. This



Spreading ridge & transform fault offset.



Trench or fold mountain belt.



Deep earthquake locations.

World-wide mosaic of plates.—The six major lithosphere plates are outlined by narrow zones of earthquakes. All tectonic activity—i.e., spreading apart at ridge axes, lateral slipping at transform faults, and convergence at subduction zones or mountain belts—is confined to the plate boundaries. [Diagram by the author, after Le Pichon.

implies an increase in spreading rate, from the pole, down to the equator of rotation. Indeed, such an increase has been measured here (and elsewhere) using sea-floor spreading rates determined from oceanic magnetic anomaly patterns previously described.

It is also important to note that the South Atlantic ridge is made up, in detail, of two types of segments, each at right angles to the other: the actual ridge segments which are longitudinal to the pole of rotation along which the new oceanic crust is formed, and offsets in the ridge (called transform faults) which are latitude circles to the pole of rotation. Transform faults are a special kind of plate boundary where neither compression nor tension occurs—the plates merely slip past each other without deforming or tearing.

There are six major plates over the earth at this time—Pacific, Africa, Australia, Eurasia, and America—and all of these plates interact with each other. The place where three plate boundaries meet is called a triple junction. A ridge-ridge-ridge triple junction

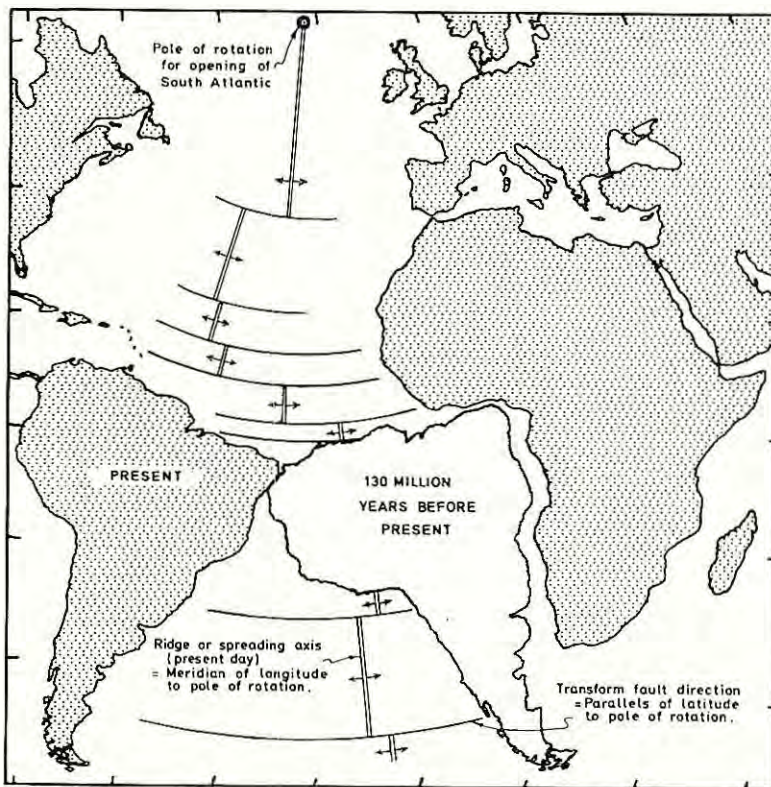
occurs in the centre of the Indian Ocean, and a ridge-ridge-transform triple junction occurs south of New Zealand. Plate motions may also be described mathematically. Since the spreading rate between Australia–Antarctica and Pacific–Antarctica can be calculated by magnetic anomalies, then the subduction rate between the Australian and Pacific plates (say, at the Tonga Trench) may be calculated (about 10 centimetres. or about 4 inches. a year).

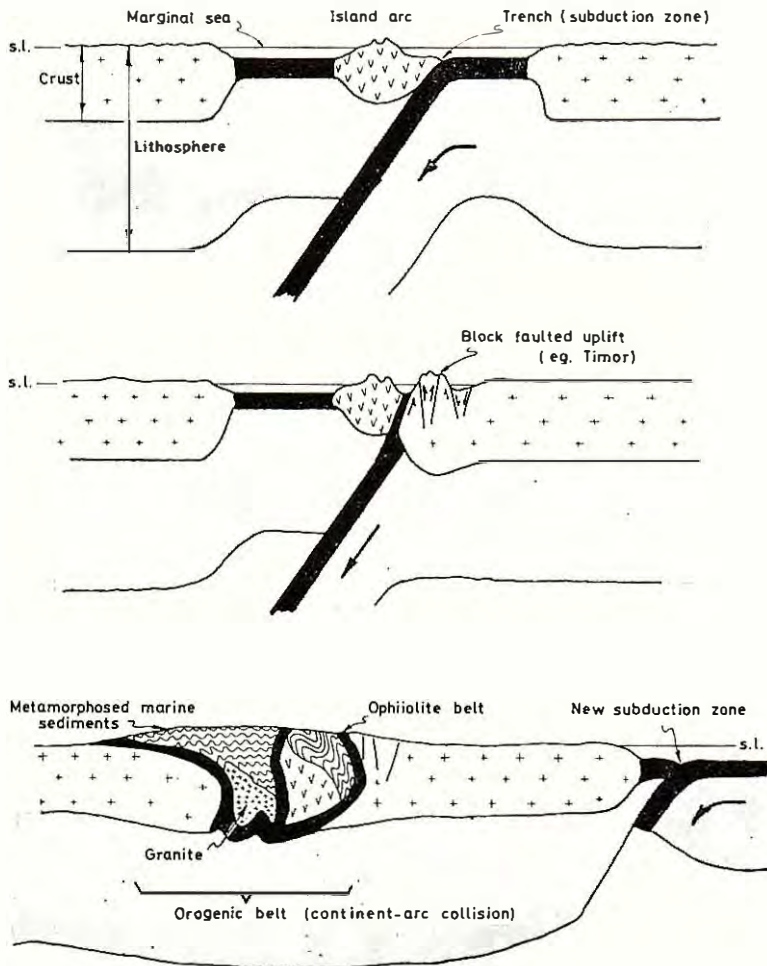
Thus it must be emphasized that plate tectonics does not permit the random, *ad hoc* motions, such as those commonly proposed in the old days of “continental drift”. The motions of plates are all interdependent and subject to fairly rigid conditions concerning plate boundary orientation and spreading or subduction rates.

Mountain building

The origin of folded mountain belts (narrow, elongate belts of deformed and metamorphosed rocks, generally derived

Spreading as a rotation on a sphere.—The break-up of South America and Africa demonstrates the mathematical description of sea-floor spreading. The motion of the continents from 130 million years ago to the present can be described as a rotation about an axis through the earth. The spreading ridge lies on radial lines from the pole of rotation, while transform faults lie on arcs of circles. [Diagram by the author.]





Mountain building by continent-island arc collision.— This appears to be an inevitable consequence of continental break-up by sea-floor spreading and subduction of oceanic crust at trenches. About 20 million years may separate each cross-section, beginning at the top. Collapse of the marginal basin between the middle and later stages may be facilitated by the formation of an intermediate subduction zone within the marginal sea. Upon completion of the orogeny a new subduction may form to maintain the global balance of spreading and subduction. [Diagram by the author, after Dewey.]

from uplifted marine sediments) may be discovered from the following observations, and also from corollaries of the above theory of plate motion:

- As stated above, mid-oceanic ridges generate only oceanic crust. As well, trenches, as they operate today, consume only oceanic crust.

- Mountain belts contain a number of distinctive rock types, including marine sediments, and a characteristic assemblage of basaltic-like rocks called an "ophiolite suite". The latter are considered slices of oceanic crust and upper mantle.

- A trench could, without conceivable difficulty, swallow an entire ocean basin. Thus, it is geometrically possible, and

statistically likely, that a continent may encounter an active trench.

- The continental crust is composed of lower-density material than oceanic crust. It also stands at least 5 kilometres above the ocean floor, and the continental lithosphere is also 30–40 kilometres thicker than oceanic lithosphere.

It has been proposed that subduction of a continental portion of a plate is not possible. Thus the collision of a continent with a trench-volcanic arc is considered to result in a fold mountain belt. The Himalayan mountains have presumably resulted from the collision of the Indian part of the Australian plate with the Eurasian plate. The shallow earthquakes indicate a still

active, compressive plate boundary, but no subduction (subduction at trenches involves very deep earthquakes as well). When deformation is complete, India will be welded to the Eurasian plate and a new trench-type plate boundary must come into being, to preserve the world-wide balance of crust generated at ridges and destroyed at trenches.

Driving mechanism for sea-floor spreading

One problem exists at the present time, in this apparently elegant theory—no clear mechanism! The basic conditions seem to involve convective overturn in the asthenosphere, rising beneath ridges and sinking beneath trenches. A number of energy sources are proposed; most involve utilization of the energy dissipated in the earth-moon tidal system. A. E. Ringwood, of the Australian National University, has recently suggested that phase changes, from low to high density rock, in the underthrust slab beneath a trench, actually pull the oceanic part of a plate into the trench. Thus, the whole mantle would behave like a huge chemical engine, in principle little different from a steam engine, and driven by the progressive differentiation of the mantle.

The author wishes to thank Dr G. H. Packham, Margaret Falvey, Diana Packham, and Eric Kaye for their assistance in the preparation of this article. Garnet Cook (Royal Australian Navy Research Laboratory) assisted in drafting the figures.

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NEW BOOK ON BARRIER REEF

THE GREAT BARRIER REEF, by Isobel Bennett; Lansdowne Press Pty Ltd, Melbourne, 1971; 183 pages; price, \$12.95.

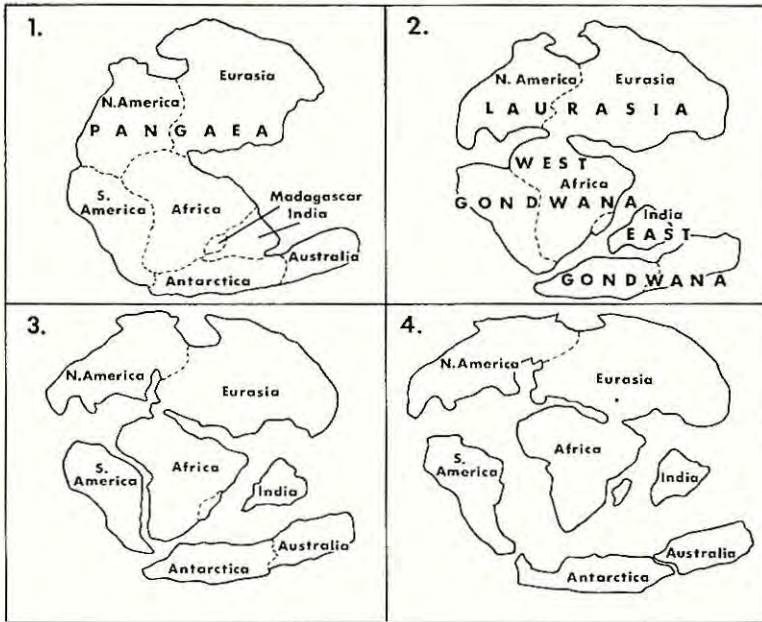
Miss Isobel Bennett's new book on the Great Barrier Reef is a most worthwhile addition to the growing literature on this fascinating marine area. The photographs in this book, the majority of which are by the author, are lavish in their numbers and of a very high standard. There is no doubt that this is the fullest visual statement on the reef in any book, and there is a good balance between photographs that provide rich, aesthetic pleasure and those giving much factual material.

In mentioning the photographs first, I do so not to denigrate the text but because one's first impressions of the book are visual. Miss Bennett gives a very full statement of the physical structure of the reef, based largely on Professor W. G. H. Maxwell's *Atlas of the Great Barrier Reef* (1968, Elsevier, London) and her own experiences. Chapters on coral cays and their plants and animals, continental islands and near shore fringing reefs, reef-building corals, and coral reef animals are all clearly written and make good attempts to capture the variety and beauty of the reefs and their flora and fauna.

As this is the richest marine ecosystem that exists, no single book can hope to portray all its variety, but Isobel Bennett's book comes nearest to doing so.

I recently visited the reef with Miss Bennett's book in hand and found it a mine of information and an excellent complement to Gillett and McNeill's *The Great Barrier Reef and Adjacent Isles* (A. K. Murray, Sydney). For example, the latter book figures over three times as many molluscs, but Miss Bennett's figures about twice as many echinoderms and corals. There are a few errors, mostly of little consequence. However, surely the colour photograph labelled "Russell Island" is Little Fitzroy? It was also a little surprising to see in the list of books written by Miss Bennett the classic *Australian Seashores*, recorded as being by Miss Bennett and W. J. Dakin, without the addition of the third, not inconsiderable, author.

This book is invaluable on the reef itself and a delight in an armchair. At \$12.95, it is not a cheap book but the reef-lover is well advised to start saving.—F. H. Talbot, Director, Australian Museum.



Successive stages in the break-up of Pangaea. [From Fooden, 1972.]

ZOOGEOGRAPHY OF FOSSIL AND LIVING TURTLES

By RUSSELL A. MITTERMEIER
 Graduate Student at Harvard University, U.S.A.

SEVERAL groups of animals exhibit what zoogeographers call disjunct distribution patterns; in other words, their representatives are found in widely separated corners of the globe, but nowhere in between. Such unusual distribution patterns have long been cited as proof of continental drift, the rationale being that the present situation could have come about only if the geographical areas in question had once been connected. Many of the striking examples of disjunct distribution, such as the lungfishes, the marsupials, the ratite birds (of which the emu is one), the iguanid lizards, the meiolaniid turtles, the *Podocnemis* turtles, and the chelid turtles, are found in the Southern Hemisphere and, at first glance, appear to provide solid evidence for the theory of continental drift. In this article, we will briefly investigate three of these groups, the meiolaniid, *Podocnemis* and

chelid turtles, and try to determine if their zoogeography can really be used to support continental drift.

First, let us take a brief look at the turtles we will be dealing with. The meiolaniid turtles are an extinct group known only from fossils found in South America and the Australian region. One of the most interesting things about these turtles is that they have two horns on their heads. Two genera, *Crossochelys* and *Niolamia*, are known only from Patagonia in Argentina and have one species each. The third genus, *Meiolania*, is composed of three species, *M. platyceps* from Lord Howe Island, *M. mackayi* from Walpole Island, and *M. oweni* from Queensland (see the diagram on the next page and the world map on page 267). The three *Meiolania* are all Pleistocene in age, whereas *Crossochelys* is Eocene and *Niolamia* Cretaceous or Eocene.

Both the chelid turtles and *Podocnemis* are members of the suborder Pleurodira, the side-necked turtles. They differ from other living turtles (suborder Cryptodira—for example, modern sea turtles) in that their necks are pulled into the shell sideways, rather than straight back. The genus *Podocnemis* is represented by seven living species in South America and one on the island of Madagascar (see world map). Several fossil forms are known from Africa and South America. All the living species inhabit fresh water. The chelid turtles are found in Australia, New Guinea, and South America. In Australia and New Guinea, they constitute most of the freshwater turtle fauna. They are represented by the genera *Chelodina*, *Emydura*, *Elseya*, and *Pseudemydura*, known in Australia as long-necked tortoises, short-necked tortoises, snapping tortoises, and the western swamp tortoise, respectively. The South American genera include *Phrynops* (toad-headed turtles), *Hydromedusa* (Argentinian snake-necked turtles), *Platemys* (twist-neck turtles) and *Chelys* (the matamata). The fossil record of the chelids is fragmentary and of little use in the present discussion.

What bearing, if any, does the distribution of these turtles have on continental drift?

To fully understand the problem, it is necessary to look at all the possible explanations for their distribution:

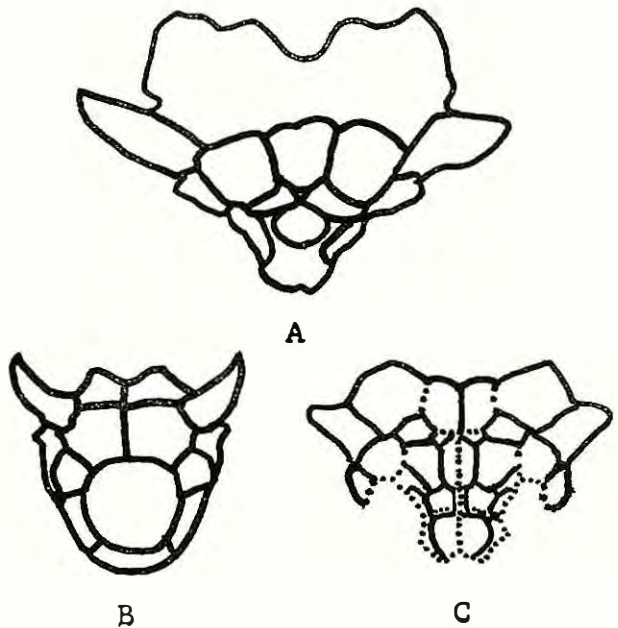
(1) The distribution of the meiolaniid, *Podocnemis*, and chelid turtles is the result of continental drift. In other words, the now widely-separated members of each group once occurred on the same landmass and became separated from each other by the drifting apart of the continents.

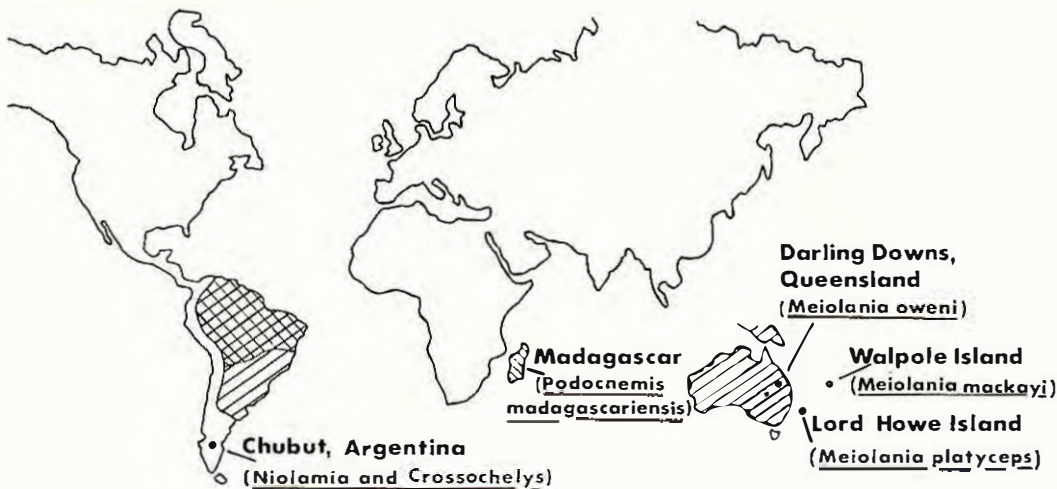
(2) The distribution of these turtles can be accounted for by the existence of now-submerged land bridges between South America and Africa and South America and Australia. At some time in the past, when these bridges were not submerged, the turtles were able to cross over them from one continent to another.

(3) The turtles in question were once cosmopolitan in distribution—that is, they were once found in the Northern Hemisphere continents as well. Their ancestors could have originated in the Northern Hemisphere, migrated to South America via North America and to Australia via certain South East Asian islands, and then later could have become extinct in the Northern Hemisphere.

(4) The resemblances between the meiolaniids and chelids in South America

Dorsal surfaces of the skulls of the three genera of Meiolaniidae. *Niotamia* (A) and *Meiolania* (B) are shown one-eighth their natural size; *Crossochelys* (C) is shown a quarter its natural size. [From G. G. Simpson, 1938.]





The distribution of Meiolaniidae, living Podocnemis, and living Chelidae. [Map by the author and Gail Anderson.]

and Australia and the *Podocnemis* in South America and Africa are the result of parallel or convergent evolution, and the animals are not really as closely related as they appear to be.

(5) The distribution of these turtles can be explained in other ways, without reference to continental drift, land bridges, north to south migrations or parallelism-convergence. Some of the possibilities are:

(a) the animals were rafted from one continent to another on floating vegetation or debris of some kind;

(b) the animals could float by themselves and were carried by ocean currents;

(c) the animals were at one time marine and were able to cross the ocean barrier under their own power.

How does available information on these three turtle groups line up with each of the five alternatives?

(1) The most recent continental drift reconstructions, based on geophysical studies, suggest that, at the end of the Paleozoic, all of the earth's crust was united in a single supercontinent called Pangaea. Near the close of the Triassic, this supercontinent started to split into two parts: Laurasia—West Gondwana (including what is now North America, South America, Eurasia, excluding India, and Africa) and East Gondwana (including what is now Australia, New

Zealand, New Guinea, Antarctica, and India). While this split was taking place, India was also separating from East Gondwana and moving northward, while North America was drifting away from Africa and South America. In the Upper Jurassic or Lower Cretaceous, South America started to split from Africa. In the Cretaceous, Madagascar moved away from Africa, and Australia—New Guinea left Antarctica and headed north (Dietz and Holden, 1970; Fooden, 1972).

The possibility that South America might once have been connected directly with Africa, and South America and Australia indirectly connected via Antarctica, seems at first to fit nicely with the turtle distribution data. We (and many other students before us) are attracted to the explanation that *Podocnemis* was found in South America and Africa prior to the separation of those two continents and that the chelids and meiolaniids found their way from South America to Australia (or *vice versa*) via Antarctica or originated in Antarctica and spread to Australia and South America. However, if we keep in mind the time periods involved, our initially attractive explanation loses a great deal of its glamour.

The oldest *Podocnemis* fossils are from the Cretaceous (*P. elegans* from Brazil), some time after the separation of South America and Africa. In addition, *Niolamia*, the

Two living Podocnemis. — *P. expansa* (right) and *P. madagascariensis* (below). *P. expansa* occurs in northern South America; *P. madagascariensis* is from the island of Madagascar. [Photos by the author at the Goeldi Museum, Belém, Brazil, and Tapir Research Institute, Claremont, California, U.S.A.]



oldest known meiolaniid, is Cretaceous or Eocene in age and therefore from a period many millions of years after the separation of South America from Australia and Antarctica. Whether or not much older meiolaniids actually existed prior to the separation of these continents is impossible to determine at present. If common ancestors were not present in the continents in question before they split (and fossil evidence available at this time suggests that they were not) then it becomes most difficult to explain the distribution patterns of these turtles solely by continental drift.

How then can these patterns be explained? Alternative 2, that now-submerged land bridges once existed between the southern continents, is unlikely on the basis of geological evidence now available. Alternative 3, that the turtles were once cosmopolitan in distribution but became extinct in the Northern Hemisphere, is not

supported by the present fossil record. However, it cannot be totally discounted, especially in the case of the meiolaniids, since future fossil finds might demonstrate its validity. Alternative 4, that the turtles under consideration are not as closely related as they appear to be, can probably be ruled out for the chelids and *Podocnemis*. The similarities between members of each of these groups are so great that they almost certainly are the result of common ancestry and not parallelism or convergence. In the case of the meiolaniids, convergence might have occurred. G. G. Simpson, in the most recent authoritative work on these animals, stated: "There is a possibility that *Meiolania* is convergent toward the South American genera, a member of the same broad group but developing horns independently, but this possibility is slight and the great probability is that the relationship is closer, special to these three genera, and that a family, Meiolaniidae, of horned turtles is a natural unit".

Finally, we come to alternative 5, the chance that the distribution patterns of these turtles can be accounted for by means other than continental drift, land bridges, cosmopolitan distribution, or parallelism-convergence. This would certainly appear to be the case for the meiolaniids. Charles Anderson, a former Director of the Australian Museum, conducted an extensive study of *Meiolania* fossils, the results of which were published in 1925 and 1930. He concluded that *M. platyceps* and *M. mackayi* were

primarily terrestrial, but also may have occupied estuarine or shore habitats and were probably capable of undertaking sea voyages. In particular, Anderson cited the presence of *M. mackayi* on Walpole Island, a coral outcropping apparently never connected to any larger landmass, as evidence that *Meiolania* species were able to traverse considerable stretches of ocean. Other students went so far as to state that *M. platyceps*, the Lord Howe Island form, was marine and, like today's green sea turtle (*Chelonia mydas*), only came ashore to lay eggs. G. G. Simpson agreed with Anderson: "It is almost certain that some or all members of the family could swim well; given some fifty or sixty million years they might have reached almost any place, under no necessity of getting there without wetting their feet".

Pretty much the same is true of *Podocnemis*. All living members of the genus are freshwater turtles. However, Roger Wood, of Harvard, recently conducted a study of fossil *Podocnemis* and decided that many of the now extinct types were marine or estuarine and that the ancestors of modern forms were more than likely capable of long ocean journeys.

It therefore appears that the disjunct distributions of the Meiolaniidae and *Podocnemis* can easily be explained without recourse to continental drift. Chelid history is, however, somewhat more hazy. The fossil record tells us almost nothing; so we can only guess at the means by which the ancestors of modern chelids reached their widely separated homelands. Although it is possible that they moved from Australia to South America (or vice versa) via Antarctica or that they even originated in Antarctica, we presently have no evidence supporting either of these contentions. On the other hand, we don't have any evidence suggesting that chelid ancestors were marine, either.

Rafting, or some other form of accidental marine transport, are also possibilities that cannot be ignored. Even today, in large rivers like the Amazon in South America, large masses of vegetation become dislodged from river banks and float out to sea. Chelid turtles and many other small animals sometimes inhabit such river-bank vegetation and could occasionally wind up in sections that happen to break loose and get carried

out to sea. Since turtles can survive long periods without eating, it is not impossible that such stowaways could eventually be cast ashore on some other continent. And, as G. G. Simpson has said, given millions of years for something like this to occur, such an "improbable" event becomes highly probable.

On the basis of this brief discussion, we must conclude that the zoogeographic distribution of turtles does not provide very solid support for continental drift. Freshwater turtles are hardy animals that can go for long periods without food and can usually tolerate salt water. Even terrestrial turtles can float and could be carried by ocean currents if they somehow got washed out to sea (as must have occurred with the ancestors of the giant land tortoises, genus *Geochelone*, now found on the Galapagos and Aldabra islands). Furthermore, many turtles that are now restricted to fresh water apparently once had marine or estuarine ancestors capable of widespread oceanic dispersal.

This is not to imply that continental drift is not a real phenomenon. I personally feel that the body of knowledge provided by geophysics, oceanography, and other branches of zoogeography makes an excellent case for continental drift. This article has merely tried to show that we must be careful about jumping to conclusions on the basis of inadequately studied information, however nicely that information happens to fit our theories. Our data become a solid foundation for theory only after we have examined many alternative explanations of it and thoroughly understand its finer details.

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PERMIAN MOLLUSCS AND CONTINENTAL DRIFT

By J. M. DICKINS

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THE distinctive climatic features of the Permian period have long excited interest. The period extended from about 280 to 230 million years ago—the last period of the Palaeozoic era which preceded the Mesozoic era, or the age of reptiles. In Europe Permian rocks were worked for copper and salt formed in a sea associated with a warm, arid climate. In North America reefs grew in seas which had invaded the continent, and large salt deposits were formed under conditions similar to those in Europe.

The southern continents in the early part of the Permian, at least, presented a very different picture. Vast ice fields were formed in South Africa, India, and Australia, and recently evidence for widespread glaciation has been discovered in Antarctica. Associated with the glaciation were a distinctive marine fauna—the *Eurydesma-Deltopecten* fauna (*Eurydesma* and *Deltopecten* are both bivalves or pelecypods)—and the *Gangamopteris-Glossopteris* flora on land.

It was these geological features which first led to a hypothesis of a large southern continent which was called Gondwanaland after an ancient Indian people. These features also strongly influenced Wegener

and Du Toit in putting forward the continental drift hypothesis for the southern continents.

Nature of the Permian marine molluscan fauna

In Australia, the Permian was a time of great changes—formation of large sea basins on the present land area, mountain-building, and volcanic and earthquake activity. The seas were populated by a rich fauna, although at times the variety was limited by the cold.

Bivalves (pelecypods, i.e., forms related to the cockles and mussels) and gastropods (including sea snails) were well represented, but the other major molluscan group, the ammonoids (extinct forms related to the pearly *Nautilus*) were rarer. The poor representation of the ammonoids is taken to reflect the general cold to coolish waters which persisted for most of the Permian, along with absence of colonial corals, fusulinids (an extinct group of foraminifera, single-celled animals with shells), and brachiopods (lamp shells) which typified warm-water faunas of this time.

In the earliest part of the Permian (the Sakmarian) the *Eurydesma-Deltopecten* fauna is found in eastern and western Australia



From the left: *Eurydesma*, a marine pelecypod associated with cool water in Australia, India, South Africa, and South America; *Deltopecten*, a marine pelecypod found with *Eurydesma* in Australia, India, and South America; *Atomodesma exarata*, a mid-Permian marine pelecypod found in Australia, Indonesia, and Siberia. [Photos: G. T. Reid and H. M. Doyle.]

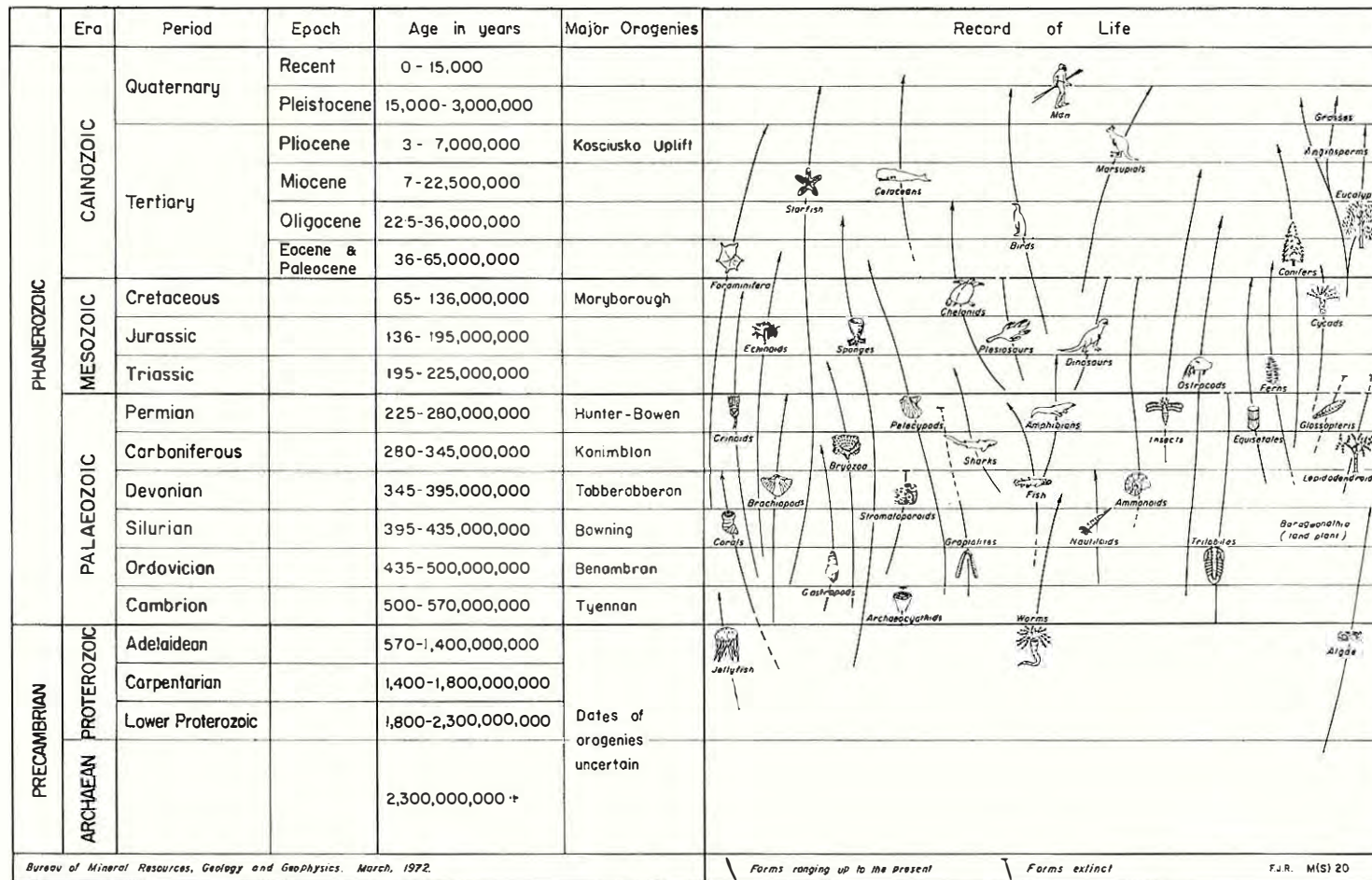
(Western Australian and western Northern Territory), India, Southwest Africa, and Argentina. The faunas are all of similar age and appear to date the main glaciation everywhere as earliest Permian, except possibly Antarctica, where no marine fossils have been found. The Australian faunas, however, most resemble those of India. During the Palaeozoic and into the Tertiary (age of mammals) a seaway (the Tethyan Sea) persisted from Europe through the Mediterranean, Asia Minor, and Southern

Asia. Tethyan links are shown by the early Permian ammonoid faunas from Western Australia. [The Permian is commonly divided into two subdivisions, the Lower and Upper Permian Series, the Lower Permian Series comprising the Sakmarian, Artinskian and Kungurian Stages, and the Upper Permian the Kazanian and Tatarian Stages.]

Although not as close as that from India, the fauna from Argentina shows a close relationship to that of eastern and western Australia, as well as to that of southern



Areas of marine Permian sedimentation in Australia. [Map by the author.]



Bureau of Mineral Resources, Geology and Geophysics. March, 1972.

Forms ranging up to the present

Forms extinct

F.J.R. M(S) 20

Geological time-scale and Australian record of life. [Diagram by Palaeontology Group, Bureau of Mineral Resources.]

Africa and Europe, and migration must have been possible between these areas at this time. This southern fauna is absent or poorly represented in the Northern Hemisphere.

In later Permian time (Artinskian to Kungurian) slightly warmer conditions are found, especially in western Australia. Many species and genera of bivalves and gastropods, as well, indeed, as brachiopods and polyzoans (sea mats) appear in the marine faunas related to species found elsewhere only in the Tethyeen region, especially India and Indonesia (Timor). Although some migration was possible between eastern and western Australia, the persistence of many of the earlier forms in eastern Australia indicates that here the water remained cooler.

An interesting feature of this time is that, although judging from their faunas waters in Indonesia and southeast Asia were warm-tropical, some of the forms found in the temperate region represented by western Australia are again found in Siberia, apparently reflecting a corresponding northern temperate zone.

Mid-Permian sea snails have only recently been described from Malaya by Dr R. L. Batten, of the American Museum of Natural History, New York. The fauna contains many species related to sea snails found in western Australia despite the apparently somewhat warmer waters of Malaya.

In Australia the youngest marine faunas are found only in western Australia, and it is these faunas that show the closest relationships to any outside Australia. Many of the species lived also in Timor and India, across which stretched the Tethyeen seaway, and some of the species of bivalve are found as far away as Europe, emphasizing the freedom available for migration along this route. No other Australian Permian bivalve fauna had such a close identity with shells from outside.

Interpretations and conclusions

If we look at all of the Permian, the faunal links with Timor, Malaya, and India are so strong that it is difficult to hold any view other than that at this time Australia was close to Indonesia and southeast Asia. Even in earliest Permian times, when links with South America can be seen, the Tethyeen influence is shown by the ammonoids.

This appears contrary to the current views

on continental drift, according to which Australia should be close to southern Africa, South America, and possibly India, but not to southeast Asia and least of all to that part of the Tethyeen region passing through Asia Minor to Europe.

In mid-Permian time this discrepancy is emphasized by the warm-water faunas close to the present equator, with the matching temperate belts on either side in Australia and Siberia.

The distribution of the early Permian cool-water fauna in the Southern Hemisphere could be explained by a somewhat more marked asymmetry of ocean currents than at present. Even at the present time the tropical climatic belt is displaced to the north because of the asymmetry of land and sea. This explanation could also apply to the southern glaciation if associated with an overall cooling of the earth. The main barrier to migration of marine organisms seems to be not distance but finding satisfactory conditions for life and growth on arrival.

Bringing all the glaciated areas together as in continental reconstructions for the Permian, on the other hand, raises a very difficult problem. The glaciated continent formed would be so large that it would be difficult for the inland glaciers to receive sufficient precipitation to maintain themselves. These problems are to be discussed at the Third Gondwana Symposium, to be held in Canberra, A.C.T., Australia, in August, 1973. At the Second Gondwana Symposium, held in South Africa in 1970, some workers suggested that the large continent (Gondwanaland) may have moved across the pole between Lower Carboniferous and Permian, but others pointed out that the fossil evidence (floral as well as faunal), which indicated widespread early Permian glaciation, precluded this.

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INSECTS AND CONTINENTAL DRIFT

By DAVID K. McALPINE

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THE insects of the world's southern continents (excluding Antarctica, which now has almost no insect fauna) and of New Zealand include many groups unfamiliar to students from the Northern Hemisphere. If each of these groups is taken separately and its present world distribution examined, a bewildering variety of patterns is seen. It is certain that a great number of different factors have operated to produce these patterns. There has been much invasion of new territory by insect groups when opportunities arose, much extinction of insect groups in places where they were once plentiful, and also there have evolved new species with different potential for dispersal from their ancestors. The fossil record of insects of past ages gives only occasional glimpses of small sections of what has existed, and is therefore only a very slight help in telling us of past faunas. In the Tertiary Period (from 70 million to 1 million years ago) the most extensive known fossil fauna is that preserved in Baltic amber, but it is not certain if this belongs to the lower

Oligocene or upper Eocene (from 45 million to 35 million years ago), and there is nothing comparable to this for the Southern Hemisphere.

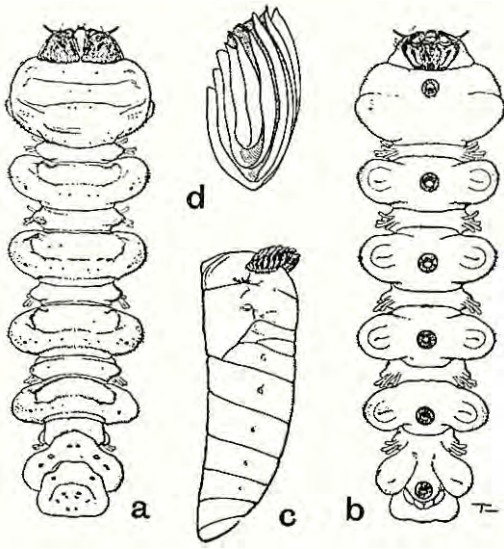
It is evident that much detail of the origins of southern insect faunas is obscured by gaps in our knowledge. Yet it is to the credit of certain perceptive entomologists that they were able to find convincing support in the data of insect geography for the theory of continental drift at a time when the geological evidence, now so impressive, was largely unavailable.

Distribution patterns

Among the many kinds of distribution pattern for southern insect groups, we repeatedly find one that includes Australasia and South America only, and more particularly the temperate zone within these regions. Hennig has used the term AS-group for the groups having this kind of distribution. Some other insect groups, smaller in number than the above, are restricted to Australasia, South America,



The wingless cylindrical cricket (family Cylindrachetidae) is a representative of an isolated insect group now restricted to Australia, New Guinea, and southern South America. Length, about 44 millimetres (1 $\frac{3}{4}$ inches). [Photo: Author.]



Larva (a, b) and pupa (c) of the primitive net-veined midge *Edwardsina*; shows the complex respiratory organ of the pupa. Length of larva, 10 millimetres (two-fifths of an inch). [After Edwards. By courtesy of the Trustees of the British Museum (Natural History).]

and southern Africa. This is, of course, the kind of distribution we could expect if these surviving members of the group are the descendants of forms originating in Gondwanaland before it became completely broken up (as explained elsewhere in this issue). The pattern would only remain recognizable today if the insects were sufficiently sedentary to remain on the same land surfaces without effective dispersal over the sea, and also provided they were able to survive the changing physical and biological environment through the ages. The insects of Australasia would have been adapted to cool conditions, but probably not to a frigid climate, after the beginning of the Mesozoic. Perhaps most surviving forms in Australasia would have been subjected to an environment resembling that of the present South Island of New Zealand, though it is to be expected that the much larger and more varied land surfaces of Australia and South America provided greater opportunities for survival for many insects. Now, the New Zealand insect fauna contains a very high proportion of species of two-winged flies (Diptera) exceeding in number either the Hymenoptera (wasps, ants, bees) or Lepidoptera (moths, butterflies). This is in sharp contrast to the

situation in Australia and other warmer countries, where the Diptera have a smaller representation than the Lepidoptera and Hymenoptera. The two-winged flies of New Zealand are particularly well represented by fragile, cool-forest types belonging to the older families of the order. It is precisely such groups of flies as these which predominate among the recognized AS-groups of insects.

AS-group examples

At this stage it will be useful to look at some of the well-known examples of AS-groups. The moss bugs of the family Peloridiidae (order Hemiptera) are small flat insects under a quarter of an inch (6 mm) long which live only on wet moss or liverworts in cool localities. They are known only from Australia, New Zealand, and South America. They are predominantly flightless forms, and many of the species are restricted to certain mountain-tops. They are a primitive group of bugs (Hemiptera) only remotely related to other living forms.

The elongate weevils of the family Belidae are best represented in Australia but also occur in New Guinea, New Zealand, and Chile. In Australia they are not restricted to the temperate zone, but a relatively late radiation of the group probably accounts for their entering the tropics, including New Guinea. The cylindrical crickets, family *Cylindrachetidae*, also constitute an AS-group which extends to New Guinea, but in this case there is no representation in New Zealand. They are wingless burrowers living mainly in dry, sandy places. Stoneflies (order Plecoptera) are rather sluggish insects of limited flying ability found generally near clear, running water, especially mountain streams in which the larvae live. The Australian species all belong in four families of the order, three of which are AS-groups. The fourth family is not itself an AS-group, but one subfamily of it is restricted to Australia, New Zealand, South America, and southern Africa.

The pigmy scorpion-flies of the family Nannochoristidae (order Mecoptera) are another typical AS-group (southern Australia, New Zealand, southern South America). They are restricted to cool localities where their larvae (the only known aquatic mecopterous larvae) live in shallow

fresh waters. The adults do not seem to wander far from the larval habitat. Scorpion-flies are an ancient order of insects, much more numerous at the end of the Palaeozoic than they are at present. A fossil from the Upper Permian of Belmont, New South Wales, named *Robinjohnia tillyardi*, has been referred to the family Nannochoristidae. This would seem to demonstrate that this family has indeed existed on the Australian continent since the breaking up of Gondwanaland.

The large, conspicuously coloured flies of the genus *Pelecorhynchus*, perhaps to be placed in a family to themselves, are allied to the biting March-flies or horse-flies of the dipterous family Tabanidae. They are confined to southeastern Australia and southern South America. Many of them live in mountain habitats.

Trichophthalma is a genus of tangle-vein flies (family Nemestrinidae) restricted to Australia, where it lives at all latitudes, and to the southern part of South America. Its occurrence in hot, open country on Cape York Peninsula and islands of Torres Strait is not typical of AS-groups. Yet *Trichophthalma* has not been found further northwards beyond Australia, perhaps because it is not an inhabitant of tropical rainforests.

Among the smaller, more delicate flies of the order Diptera are the dance-flies (family Empididae). Despite their often fragile appearance many of these are predaceous on other small insects. They are particularly abundant in cool, moist climates such as that of New Zealand. One subfamily of dance-flies, the Ceratomerinae, is restricted to southern Australia, New Zealand, and southern South America. In Australia the ceratomerines are found in damp shady situations, particularly on damp rocks at the margins of streams. Apart from this group, there are several other AS-groups among the genera of Empididae.

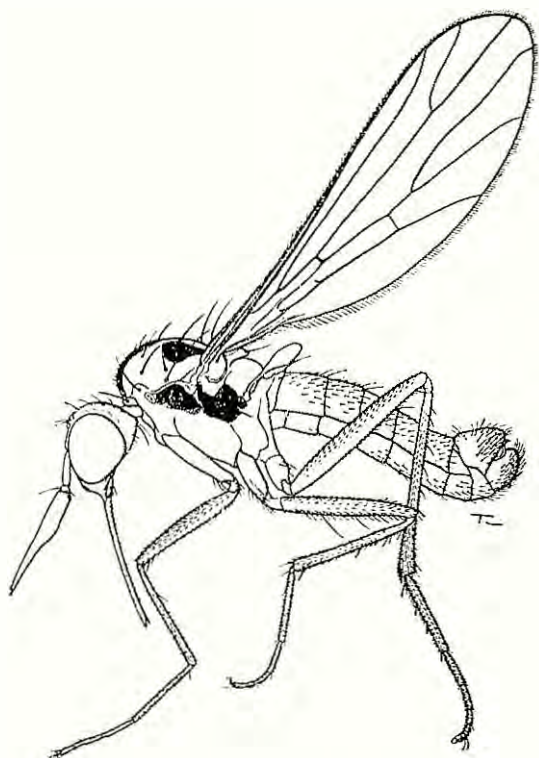
The net-veined midges of the family Blephariceridae inhabit the vicinity of waterfalls and torrents. The peculiar larvae attach themselves to rock surfaces by suckers on their lower surface in places of greatest water movement. The most primitive net-veined midges, as determined by structure of wings and other parts, belong in the genus *Edwardsina*, distributed in southern

Australia, New Zealand, and southern South America.

The list of AS-groups found in the Insecta could be greatly prolonged, but these examples suffice to show that AS-groups occur with rather high frequency in south-temperate insect faunas. It remains to be decided if these modern distribution patterns are the direct result of the fragmentation of the distribution of ancestral Gondwanaland inhabitants by the process of continental drift.

Insects' ability to cross oceans

It has been suggested by those who oppose the theory which explains AS-distributions as the result of continental drift that there may be a tendency to underestimate the ability of insects to disperse themselves across oceans. It is known that the insects of many oceanic islands have arrived across considerable expanses of ocean. A variety of smaller insect types has been netted by screening large volumes of air over the Pacific and Southern Oceans. These "correlate extremely well with the prevailing representation of insects on the more isolated islands" (Gressitt, 1961). The fact that many, perhaps almost all, insects carried by air currents would be dead on arrival becomes less significant over very long periods of time. If the chances of a species spreading to colonize a particular island from its continental home are 1 to 10 million in 1 year, then the statistical probability for 10 million years is one successful colonization. If there are many such continental species with a similar potential for colonizing an island, then the probability that one or more will be successful is accordingly increased. Returning to the problem of dispersal of insects of AS-groups, it could perhaps be argued that, as these are largely "old" groups of insects (pre-Tertiary), the probability of their spread across oceans is not to be excluded. While admitting that the age of these groups renders the history of their dispersal all the more obscure, this line of argument does not seem applicable to most of our examples. The AS-groups consisting of small, light, flying insects are those least capable of surviving away from their special habitat. The larger and heavier insects, such as the flightless cricket-like cylindrachetids and the nemestrinid flies,



A dance fly, *Ceratomerus virgatus*, from New Zealand. It is a representative of a group restricted to the cooler parts of Australia, New Zealand, and South America. Length, 4 millimetres (one-sixth of an inch). [After Collin. By courtesy of the Trustees of the British Museum (Natural History).]

for all their skill in flight, are not the kinds of insects to be carried far in air currents. Although the chances of an event of low probability taking place are increased with increasing time-opportunity, the chances for an impossible event are not. The sum of 10 million zeros is zero still. The latter statistic seems most applicable to our AS-groups.

Diagrams based on the geological evidence for continental drift show the separation of South America from the persisting Antarctic-Australian land mass to be at least as early as the separation of Africa. It is a little puzzling then to find that there are so many more southern groups held in common between Australasia and South America than between Australia and Africa or even southern Africa and southern South America. It is possible that Africa, moving

more rapidly northwards, received a warmer climate at a comparatively early date. Australasia started its northern journey much later, and South America both maintained a high-latitude zone and also early acquired a mountain chain sheltering cool-climate organisms. In addition, South America may not have moved so far from Antarctica for some time after its separation, thus enabling some faunal interchange with Australasia via Antarctica before the latter became too cold. These considerations would seem to account for the fact that Africa figures relatively infrequently in the distribution pattern of insects with extensive southern distributions.

A further difficulty in the derivation of the old southern insect groups from purely southern ancestors lies in the fact that we have only a little knowledge of what extinction of insect groups took place on the northern continents between the Mesozoic Epoch and the present. Could these southern groups have once been world-wide? During the Tertiary Period there was a great evolutionary radiation of many animal groups and these must have hard-pressed many pre-existing types through competition and predation. The more complete fossil record of land vertebrates shows a repeating picture of the overthrow of one ruling type and its replacement by the changing descendants of some lesser light. Something similar has undoubtedly happened among the insects. The most primitive living termite, *Mastotermes darwiniensis*, is the only representative of a purely Australian family, but fossil representatives of this family have been found in Northern Hemisphere Tertiary deposits, providing a clear case of northern extinction of a now purely southern group. This is not, however, one of the AS-groups and its present distribution is tropical only. Also, as only one species of the group has survived anywhere, this is not a good statistic for basing a generalization. A different picture is provided by the primitive flies of the family Sciadoceridae, which, because of their unique position in the phylogeny of Diptera, have been called "the most wonderful flies in the world". Of the two living species, one lives in the south of South America, the other in Australia and New Zealand. The latter species extends

just within the tropics in Queensland but, exists there only in mountain forest at an altitude of at least 600 metres (about 2,000 feet). Here is a typical AS-group as judged from present-day distributions. But here the fossil evidence steps in and destroys any notions of an ancient southern dispersal. The living South American sciadocerid is almost identical with a European Baltic amber fossil—they cannot even be put in separate genera—and there are more ancient Cretaceous sciadocerids from Canadian amber. With our still limited knowledge of the early Diptera, might there yet be many more southern groups that once lived in the Northern Hemisphere?

Support for Wegener theory

I would like to close with the idea that the very numerous southern insect groups living in more than one of the southern landmasses have provided good statistical support for the Wegener theory of the origin of the southern continents from a single landmass. The validity of this kind of reasoning has been borne out by the fact that much evidence from other sources has led to the same conclusions. It is best to remember that the entomological evidence is cumulative. Perhaps for no single insect group of restricted southern distribution can we be certain that it has never existed on northern continents, but it is improbable that more than a few of them did so without leaving any evidence of their presence.

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BUTTERFLY BOOK REVIEWED

BUTTERFLIES OF THE AUSTRALIAN REGION, by Bernard D'Abbrera; Lansdowne Press, Melbourne, 1971; 415 pages; price, \$29.50.

This is the first book to deal exclusively with the butterflies of the region from the Moluccas and Timor in the west to New Zealand and Fiji in the east. The Hesperioidea or Skippers are not included, as the author plans that they should appear in a later publication.

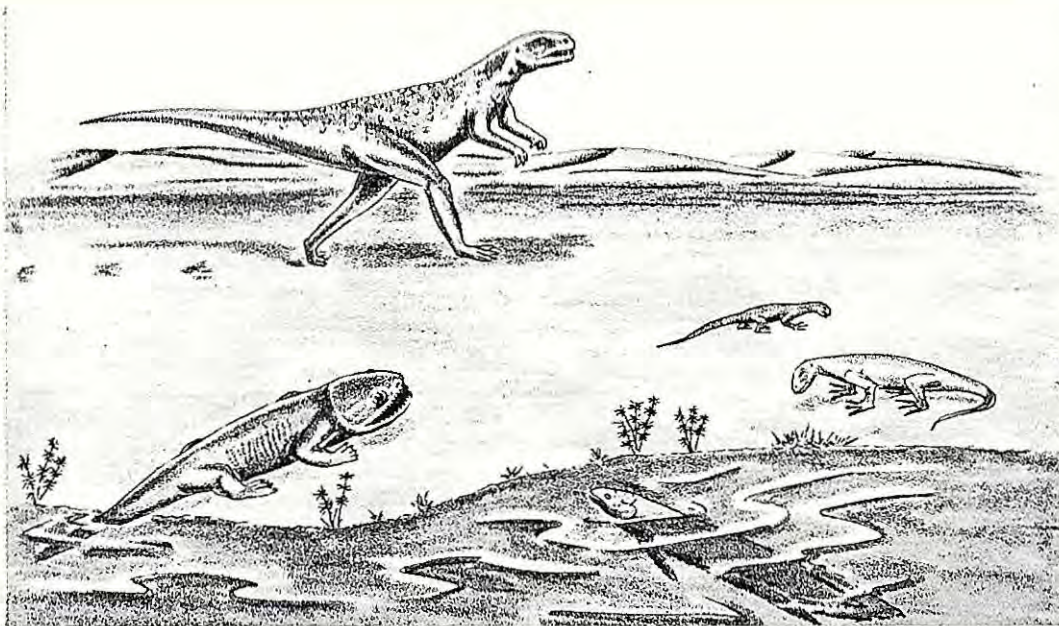
Following introductory sections on the butterfly-mimicry, variation, nomenclature, classification, a short history of the collection and study of butterflies, and a glossary, the bulk of the book lists and illustrates most of the species and subspecies recorded from the Australian region. Most of the illustrations are of set specimens, but the author has included a number of photographs showing live specimens of larvae, pupae, and imagines. At the end of the book there are a select bibliography and an index.

Few will doubt that the illustrations alone make this a magnificent book of inestimable value to students of Lepidoptera. However, a glance at the bibliography and the text reveals that the author has paid little attention to recent literature on the butterflies of the region, particularly that of Australian workers. Numerous errors in nomenclature and distribution are the result, and it is impractical to try to list all of these. One statement that requires correcting appears on page 112. Here the author suggests that only one specimen of *Graphium meeki* exists in a museum—a female in the British Museum, from Santa Isabel. However, there is also a female of this species in the Australian Museum collection, from Bougainville, in the Solomons.

It appears that most of the author's research was carried out in the British Museum, and I feel that a much clearer picture would have emerged from time spent studying the major private and institutional collections throughout the region itself.

A book of this kind is hardly the place for descriptions of new species and subspecies, yet some fourteen of these appear. These descriptions are inadequate, and would have been better placed in an entomological journal.

Despite the many errors in the text and the transposition of names on the plates, the excellent photography allows for the identification of most of the butterfly species of the region. As a result, the book should increase the interest now being shown, thus adding to our extremely incomplete knowledge of the life-histories, distribution, and nomenclature of the butterflies of the Australian region.—John V. Peters.



This may have been a typical scene in eastern central Queensland early in the Triassic period, over 200 million years ago. A lungfish (lower right) is in a channel, and a labyrinthodont amphibian (lower left) is emerging from it. Small reptiles, superficially resembling lizards, forage on the banks, and a bipedal thecodont, about 5 feet high, is running in the background. [Drawing by Alex Ritchie.]

Triassic Amphibians and Reptiles of Australia in Relation to Gondwanaland

By ANNE WARREN

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FOR some time it has been fashionable to publish lists of the various reptiles present in Permian and Triassic deposits of the southern continents and to show how alike these lists are, the resulting "evidence" being used in support or otherwise of the concept of an ancient continent, Gondwanaland. Initially these lists dealt with southern Africa and southern South America but, as our knowledge of vertebrate-bearing deposits increased, faunal lists became available for India and Madagascar and, most recently, for Australia and Antarctica. The emphasis

has been on reptilian faunas because in all of the southern continents except Australia reptiles were the most commonly found fossils. In Australia, however, fossil amphibians by far outnumber reptiles in all known Permo-Triassic deposits. In fact, only in the Northern Hemisphere, in the Lower Trias of North America, Germany, East Greenland, Spitsbergen, and Russia do amphibian remains similarly outnumber those of reptiles. Perhaps an even more puzzling aspect of the Australian faunas is the fact that the reptiles that have been

found are those which are the least common in all other southern continents. Thus, of the four subclasses of early terrestrial reptiles Australia has a few representatives of the Anapsida (family Procolophonidae), the Lepidosauria (order Eosuchia), and the Archosauria (order Thecodontia), but none of the Synapsida, which are the most commonly found component of Permo-Triassic faunas in the other Gondwanaland members.

Incomplete fossil records

In theory, comparison of the faunas of the five supposed Gondwanaland members in pre-drift times should give a measure of the degree of association of the continents, and the faunas should diverge from each other as the continents moved apart. In practice the situation is not so clear-cut, as the fossil record is far from complete in any continent and the known fossiliferous strata in the various continents rarely coincide in age. For instance, until recent discoveries were made in South America and India the only fossiliferous deposits known from the Middle Trias were the Manda Beds, East Africa. In addition one must be careful of circular arguments, as past estimates of the times at which continental drift has taken place have been based on the distribution of fossils as well as times of sea-floor spreading, vulcanism, and palaeomagnetism.

Although the component parts of Gondwanaland undoubtedly separated at different times, it is currently thought that the break-up of the continents began in the Trias with most dispersal taking place in the Cretaceous and Cenozoic, the link between Antarctica and Australia being the longest-lasting intercontinental connection. Thus, the Permian and Triassic faunas of the member continents of Gondwanaland should be essentially similar or at least more alike than are the faunas of those continents today.

Faunal list

A conservative faunal list of the amphibians and reptiles now known from the Permian and Trias of Australia is given below, together with the approximate size of each animal.

In New South Wales the Permian Newcastle Coal Measures of the Sydney Basin have yielded amphibians of the family Brachyopidae, short-skulled labyrinthodont amphibians which would have looked rather like large salamanders and which lived in fresh water and actively hunted fish for food. The two known forms are *Bothriceps australis* (14 inches) and *B. major* (24 inches).

Reptilian footprints are known from the Upper Permian Coalcliff Sandstone in the Sydney Basin but bones have not, as yet, been discovered.

In Triassic deposits amphibian-reptilian faunas have been discovered in Western Australia, Tasmania, Queensland, and New South Wales.

In the Fitzroy Trough, to the southwest of the Kimberleys, W.A., the Lower Triassic Blina Shale has produced a variety of amphibians (Cosgriff, J. W., 1965). The family Brachyopidae again occurs, with *Blinasaurus henwoodi* (20 inches), and another amphibian family, the Rhytidosteidae, is represented by *Deltasaurus kimberleyensis* (36 inches), which had a short, triangular skull and probably looked rather like the brachyopids.

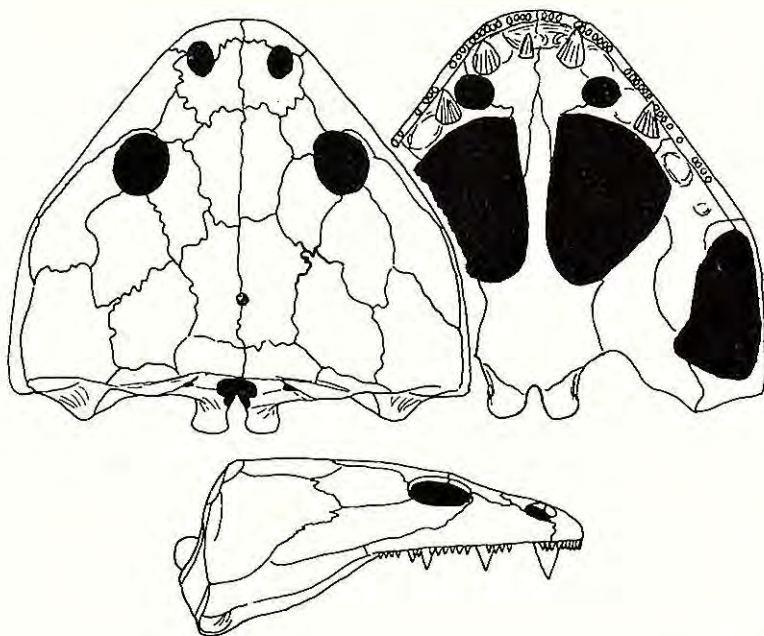
The amphibian family Trematosauridae is represented in the Blina shale by fragments of narrow-snouted forms which were active fish eaters. Similar forms have been found in marine sediments in the Northern Hemisphere. The Capitosauridae, large, dorso-ventrally flattened labyrinthodonts, looking superficially like crocodiles, were also present, e.g., *Parotosaurus* sp. (36 inches), which probably led a rather sedentary life and fed on small fish and detritus.

Fragments of probable thecodont reptiles have also been recovered from the Blina Shale. These were a diverse bipedal or quadrupedal group which gave rise to dinosaurs during Triassic times.

Father south, in the Perth Basin, W.A., the rhytidosteid amphibian *Deltasaurus pustulatus* (15 inches) has been recorded from the Kockatea Shale.

In Tasmania the Lower Triassic Knocklofty Formation has yielded the same amphibians as the Kimberley deposits (*Blinasaurus* sp.,

An attempted reconstruction of the skull of the brachyopid amphibian *Brachyops allos* Howie, from the Lower Triassic Rewan Formation of Queensland. Dorsal (left), ventral, and lateral views. The length of the skull is approximately 13 centimetres (about 5 inches). [Redrawn from Howie, 1972.]



Deltasaurus kimberleyensis, *Parotosaurus* sp.) together with undescribed remains of a small amphibian group known as the lydekkerinids. The thecodont reptile *Chasmatosaurus* sp.—also known from Lower Triassic deposits in South Africa and eastern and southern Asia—is reported from the Knocklofty Formation in Tasmania.

Rewan Formation finds

In the last few years in the Bowen Basin of Queensland the Rewan Formation (Lower Trias) has been found to contain both amphibian and reptile remains (Bartholomai and Howie, 1970), and the following forms have been recorded. The amphibians include the brachyopid *Brachyops allos* (20 inches), the rhytidosteid (?) *Deltasaurus*, unidentified fragments of a trematosaurid, the capitosaur *Parotosaurus* sp., and a representative of a hitherto unknown family, *Rewana quadricuneata* (30 inches).

Reptiles are represented in the Rewan Formation by fragments of unidentified thecodonts (which may have been about 5 feet in length) and by the skulls of procolophonids, small lizard-shaped cotylosaurid reptiles, one group of which is thought to have given rise to modern turtles and tortoises (the Chelonia). Other

skulls from the same deposits belong to eosuchian reptiles, small lizard-like animals (8 inches), which later gave rise to modern lizards and snakes.

Farther south in Queensland the jaw of a capitosaurid labyrinthodont, *Austropelor wadleyi*, was found in sediments of Lower Jurassic age near Brisbane, but it may have been reworked from earlier Triassic beds.

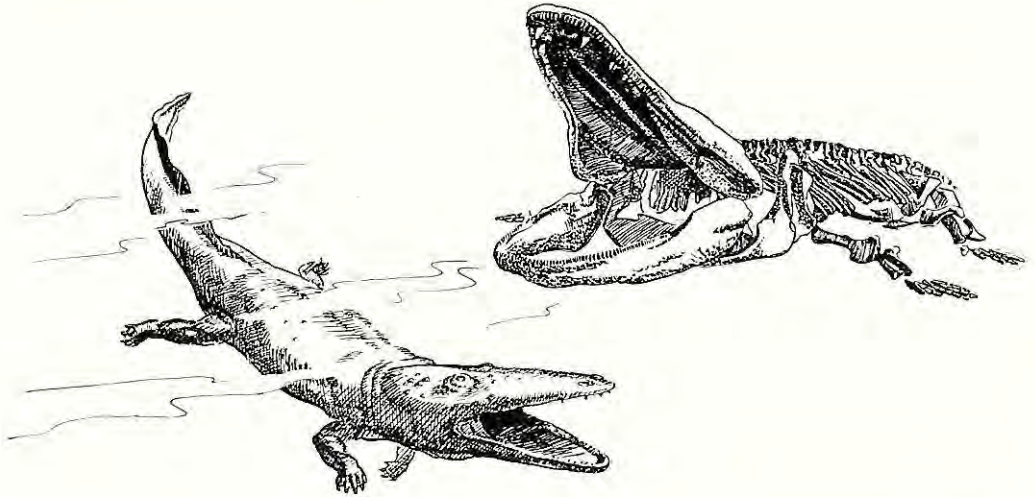
Footprints of both amphibians and reptiles are known in the Queensland Trias.

Fossil amphibians from Sydney Basin

Fossil amphibians have been discovered at several sites in the Trias of New South Wales, all in the Sydney Basin.

The Lower Triassic Narrabeen Group (Newcastle Formation, Gosford Subgroup) has yielded the brachyopid *Blinasaurus (Platyceps) wilkinsoni* (4 inches), the capitosaurid *Parotosaurus* sp. nov. of Cosgriff, and the femur of a very large capitosaurid. Both reptilian and amphibian footprints have been discovered in this formation.

The Hawkesbury Sandstone (Middle Trias) contains the capitosaurid *Parotosaurus brookvalensis*, a (?) *Mastodonsaurus* (6 feet)



A skeleton (right) and reconstruction of *Paracyclotosaurus davidi* Watson, from the Triassic of St Peters, Sydney. The animal was over 9 feet long. [Drawing by Janet Boddy.]

and labyrinthodont footprints. The overlying Wianamatta Group in the Sydney Basin has produced a similar fauna, including a new genus of brachyopid amphibian, a spectacular skeleton of the capitosaurid *Paracyclotosaurus davidi* (over 9 feet) from St Peters, Sydney, and (?) *Mastodonsaurus* and labyrinthodont footprints.

Using data of Cosgriff and Anderson and Anderson, the table opposite has been drawn up to relate age and composition of the various Australian fossil deposits to those of the rest of the southern continents. The stratigraphic correlations are based on the scant existing paleobotanical and paleozoological evidence, and are tentative. Cosgriff's placing of the Tasmanian fossils above the level of the *Lystrosaurus* Zone, despite the presence there of a chasmatosaurid reptile, is supported by the fact that the tubular horns of parotosaurs from the Rewan Formation in Queensland are very similar to isolated tubular horns from the Knocklofty Formation of Tasmania. *Parotosaurus* is only found above the *Lystrosaurus* Zone.

From the table it can be seen that no groups of amphibians or reptiles are exclusive to Australia: all have been found in other southern continents, as they have also in parts of the Northern Hemisphere.

While I believe that continental drift did occur, I cannot maintain that the facts set out above are proof that it did. For instance, the absence from Australia of *Lystrosaurus* or any other member of the subclass Synapsida could be used as evidence against the theory. However, the more fossil deposits that are found the more alike the Permo-Triassic faunas of all continents become and the harder it is to accept any zoogeographical theories that are not based on the concept of a Gondwanaland or a Pangaea. Let us hope that a bone bed of synapsid reptiles will soon be found in Australia.

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Table showing amphibians and reptiles found in the Upper Permian and Lower to Middle Trias of Australia with those recorded from other parts of Gondwanaland for comparison. Various groups are represented by the code letters BR TCLThPES where present and by a hyphen where a particular group (or groups) has not been found. For example, in BR -CLTh - - - T, P, E, and S have not been found. The upper and lower limits of each formation are not shown. Amphibians: B, family Brachyopidae; R, family Rhytidosteidae; T, family Trematosauridae; C, family Capitosauridae; L, family Lydekkerinidae. Reptiles: Th, order Thecodontia; P, family Procolophonidae; E, order Eosuchia; S, subclass Synapsida.

	WESTERN AUSTRALIA	WESTERN AUSTRALIA	TASMANIA	QUEENSLAND	NEW SOUTH WALES
205 million years ago					
MIDDLE TRIASSIC					Wianamatta Group B--C----- Hawkesbury Sandstone ---C-----
215 million years ago					
LOWER TRIASSIC				Rewan Formation BRTC-ThPE-	Gosford Sub Group B--C-?Th---
225 million years ago	Blina Shale BRTC-Th---	Kockatea Shale -R-----	Knocklofty Formation BR-CLTh---		
UPPER PERMIAN					Newcastle Coal Measures B-----
	SOUTHERN AFRICA	MADAGASCAR	ANTARCTICA	INDIA	SOUTH AMERICA
205 million years ago					
MIDDLE TRIASSIC	Manda Formation ---C-Th--S Luangwa Valley ---C-Th--S			Yerrapalli Formation B--C-Th--S	----Th--S
215 million years ago					
LOWER TRIASSIC	Cynognathus Zone BRTC-ThP-S				-----S
225 million years ago		BRTC--PE-			
UPPER PERMIAN	Lystrosaurus Zone ----LThPES Daptocephalus Zone		Fremouw Formation ----LThPES	Panchet Formation B---ThP-S	

MEET OUR CONTRIBUTORS . . .

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J. M. DICKINS has worked as a palaeontologist and stratigrapher since joining the Commonwealth Bureau of Mineral Resources, Geology and Geophysics, in 1948. He has participated in regional geological and palaeontological studies of Permian rocks in Queensland, New South Wales, Tasmania, Western Australia, and Northern Territory. He has described marine pelecypods (bivalves) and gastropods from Queensland, Western Australia, Northern Territory, and southern Africa, and has studied the faunas of India, South America, and Malaysia. Dr Dickins is chairman of the organizing committee of the Third Gondwana Symposium, to be held in Canberra from 20th to 25th August, 1973, under the sponsorship of the Australian Academy of Science and the International Union of Geological Sciences.

DAVID A. FALVEY is 27, and was born in Sydney. He graduated from the University of Sydney in 1967 with a B.Sc. in geophysics and applied mathematics, and this year completed a Ph.D. at the University of New South Wales in the field of marine geology and geophysics. His research interests have been concerned with the origin, structure, and patterns of sedimentation of continental margins. He is also interested in the theoretical aspects of orogenesis and mountain building. He has worked at the Royal Australian Navy Research Laboratory on problems related to these matters.

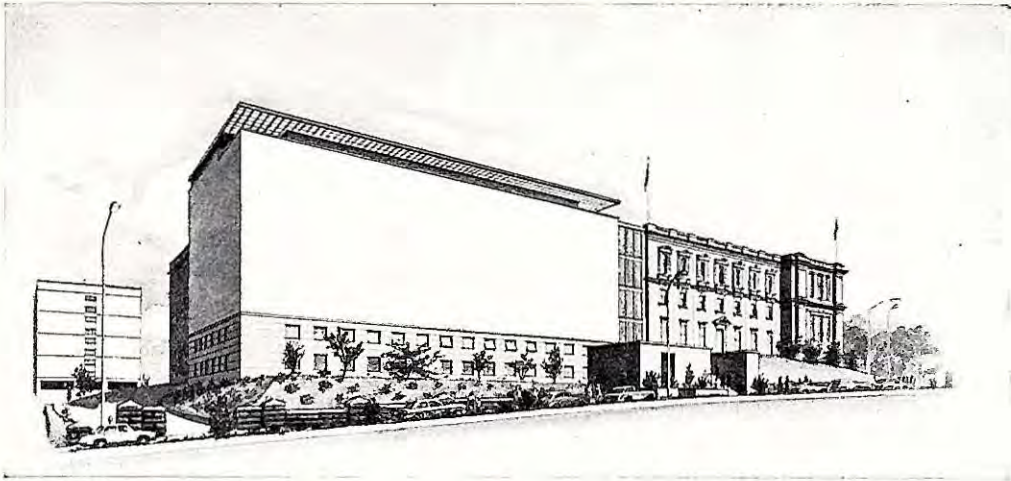
JOHN GRIFFITHS majored in Geology at the University of Cambridge, England, and gained his degree in 1969. Since then he has been working at the University of Tasmania, supported by an Esso postgraduate scholarship. He is currently completing a Ph.D. thesis on the relations of Australia, Antarctica, and New Zealand with respect to continental drift. He is particularly interested in the applications of the new ideas of plate tectonics to the solution of geological problems.

DAVID K. McALPINE is a Curator and Research Scientist in the Entomology Department of the Australian Museum. He was born in Australia and educated at Sydney Grammar School and the University of Sydney, receiving the degree of M.Sc. After joining the Australian Museum staff he studied at the Imperial College, University of London, where he received the degree of Ph.D., and at the British Museum (Natural History). He has a wide interest in natural history, but his special research interest is the systematics, biology, and evolution of the Acalyptrate Diptera (fruit-flies and related families), particularly those of Australasia.

RUSSELL A. MITTERMEIER received his B.A. from Dartmouth College, New Hampshire, U.S.A., in 1971, and is now a graduate student in biological anthropology at Harvard University. His main interests are primatology (especially behaviour and ecology of New World monkeys), herpetology (especially turtles), and wildlife conservation. In connection with these interests, he has travelled to some forty countries, has conducted fieldwork on monkeys in Panama, the Amazon region of South America, and East Africa, and has studied turtles in the United States, Mexico, and Central America. He is currently working on locomotion of New World monkeys and the taxonomy of the turtle genus *Podocnemis*. At Harvard, he is studying under Irven DeVore in anthropology and Ernest Williams in herpetology.

PETER H. RAVEN is Director of the Missouri Botanical Garden, St Louis, Missouri, U.S.A., and Professor of Biology, Washington University, St Louis. He came to St Louis in 1971 after 9 years as an Associate Professor at Stanford University. He and his wife spent 1969-70 in New Zealand, where he was a Senior Research Fellow, N.Z. National Research Advisory Council. His chief interests are plant taxonomy and geography, especially of the evening primrose family (Onagraceae).

ANNE WARREN was an undergraduate at the University of Sydney and went on to Cambridge, England, to work for her Ph.D. in vertebrate palaeontology. This involved a study of capitosaurid labyrinthodonts (Amphibia) from Tanzania, and prompted her on her return to Australia in 1967 to look for labyrinthodonts in the Australian Permo-Trias. In 1969 a Lower Triassic fauna was located in south-central Queensland, and since then she has been working on the fauna's several labyrinthodont species.



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