

Origins and evolution of the Antarctic biota: an introduction

J. A. CRAME

British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

Within the last 25 years there has been a dramatic increase in our knowledge of the fossil record of Antarctica. Improved access to the remotest parts of the continent, the advent of offshore drilling and intensive study of early expedition collections have all led to the accumulation of a vast amount of data that stretches back nearly 600 Ma to the beginning of the Cambrian period. No longer can Antarctica be dismissed from our view of the history of life on earth simply because so little is known about it; it is fast becoming another crucial reference point for global palaeontological syntheses.

If, today we have an image of Antarctica as a remote, inhospitable continent that supports little life, we now know that such a view cannot be projected back indefinitely through time. Abundant plant and animal fossils from a variety of periods point to much more benign climates and immediately raise a series of interconnected questions: where did such organisms come from, how long did they persist, and precisely when (and how) did they become extinct? Can our most southerly continent throw further light on the long-term role of climate in driving evolutionary trends (e.g. Valentine 1967; Vrba 1985)?

It was with points such as these in mind that a mixed group of palaeontologists, biologists, geologists and geophysicists gathered together for an international discussion meeting on the 'Origins and evolution of the Antarctic biota' at the Geological Society, London on 24 and 25 May 1988. A further workshop day (26 May 1988) was held at the British Antarctic Survey, Cambridge and altogether over 100 scientists from some 15 different countries took part in the discussions.

Obviously, in such a short space of time, it was not possible to cover all aspects of Antarctic palaeontology, and some subjects were necessarily reviewed in greater detail than others. As Palaeozoic biotas and biogeography were to be the subject of a complementary symposium ('Palaeozoic biogeography and palaeogeography'; Oxford, 14–19 August 1988), they were not examined exhaustively here. Nevertheless it was felt to be important to spend some time considering Antarctica's first macrofossils, and

in this volume **L. R. M. Cocks** provides a brief but succinct review of Antarctica's place within Cambrian to Devonian Gondwana. It is perhaps not generally appreciated that the greater part of Antarctica's extensive Early and Middle Cambrian sedimentary record was laid down under tropical conditions. The extensive Shackleton Limestone of the Transantarctic Mountains, and its correlatives, contains abundant shelly faunas with Australian and Chinese affinities, and part of the margin of what we now know as the Gondwana supercontinent formed a reef belt that protruded 10°–20° into the Northern Hemisphere. The most abundant and characteristic early Palaeozoic fossils of Antarctica are in fact archaeocyaths and **F. Debrenne** & **P. D. Kruse** show how, in conjunction with certain skeletal cyanobacteria and algae, these primitive coral-like organisms were the primary framework-builders of the reefs. Taxonomic revisions presented by these authors confirm the particularly strong faunal links between Antarctica and South Australia in the Early Cambrian.

Amongst the inarticulate brachiopods, trilobites, primitive molluscs and other marine invertebrates that inhabited the Early Cambrian reefs and carbonate platforms, a particularly important series of monoplacophorans and gastropods has been identified by **G. F. Webers** & **E. Yochelson**. These occur in the Late Cambrian (Dresbachian) Minaret Formation of the Ellsworth Mountains and comprise some 20 taxa. The most important of these is the monoplacophoran, *Knighthoconus antarcticus*, which could well have been a direct ancestor of the cephalopods. Its 7 cm long, curving, cap-like shell bears multiple internal septa along at least one-third of its length and these are perforated by a rudimentary connecting tube (siphuncle). The stratigraphic position of this species can be demonstrated to be slightly beneath that of *Plectronoceras*, the first true cephalopod (from China).

In his review, **Cocks** points out that there is a very limited Ordovician and Silurian sedimentary and palaeontological record in Antarctica; it is likely that this was a time of extensive uplift and erosion. However, it is apparent that,

during the later part of early Palaeozoic time, profound changes were occurring in the distribution of supercontinents and the large Gondwana plate slid progressively over the contemporary south pole. By the early Middle Devonian the pole lay under either S. Africa or S. America, and Antarctica came to occupy a mid- to high-latitude position (35°–75°S depending on the reconstruction used). It has essentially maintained this ever since.

Although palynomorphs of probable Early Devonian age are known from the Beacon Supergroup of southern Victoria Land (Kyle 1977), the most characteristic fossils of this age comprise a series of marine invertebrates from the Horlick Mountains, Ohio Range, Transantarctic Mountains. These clearly have Malvinokaffric Province (i.e. cool-water) affinities (Doumani *et al.* 1965) and testify to the comparatively high-latitude position of Antarctica in the Early Devonian. Some Lower Devonian fish fossils have been recorded from both the Horlick and Ellsworth mountain ranges and Middle–Late Devonian plant remains are known from the Ruppert Coast of Marie Byrd Land (Grindley *et al.* 1980); however, these are overshadowed in both stratigraphical and biogeographical importance by the Givetian (late Middle Devonian) Aztec Siltstone fish fauna from southern Victoria Land.

In a comprehensive review, **G. C. Young** shows that the Aztec fauna comprises not only the oldest but also one of the most diverse fossil vertebrate assemblages yet found in Antarctica. Over 30 taxa have so far been identified and these belong to four major groups of jawed fishes — the placoderms (armoured fishes), acanthodians (spiney-finned fishes), chondrichthyans (sharks and their relatives) and osteichthyans (boney fish) — and one group of agnathans (primitive jawless vertebrates; the thelodontids). The fauna has its strongest biogeographic links with eastern Australia and indicates that a distinctive East Gondwana vertebrate faunal province persisted until at least the end of the Middle Devonian (Young 1981). By the latest Devonian the vertebrate faunas of Euramerica and East Gondwana are much more similar, particularly in the composition of their respective freshwater assemblages. **Young** links this change to major palaeogeographic reconstructions and suggests that this may have been the time when the ocean separating these two supercontinents disappeared. The presence of a significant number of primitive taxa (or paraphyletic stem groups) in Antarctica and Australia suggests that this extensive continental region was the site of origin of major groups of

phyllolepid placoderms, xenacanth sharks and bothriolepid antiarchs.

Collision of the Gondwana and Baltica/Laurentia blocks in the latest Devonian to form the single supercontinent of Pangea radically alters our view of the subsequent evolution of life in the southern high latitudes. It has traditionally been felt that the classic ‘Gondwana’ sequences in these regions, comprising Permian–Carboniferous non-marine glacial facies overlain by coal measure facies containing a *Glossopteris* flora and Triassic non-marine facies with a *Lystrorhynchus* fauna and *Dicroidium* flora, were the product of supercontinent isolation. However, viewed in terms of the single supercontinent model, it would now appear that these classic sedimentary facies and biotas can be re-interpreted as austral components of a Pangean super-sequence (Veevers 1988). The basal glacial successions reflect the mid- to high southern latitudes and succeeding beds contain a provincial biota separated from boreal Pangea on the east by the Tethyan gulf and on the west by a tropical land zone (Veevers 1988, fig. 2c). Although Veevers dates the coalescence of Gondwana and Euramerica slightly later (mid-Carboniferous, c. 320 Ma), it is clear from his reconstruction that the classic *Glossopteris* flora now has a distinctly austral aspect.

Dicynodonts, a widespread, morphologically diverse group of mammal-like reptiles prevalent during the Permian and Triassic, are the subject of a comprehensive review by **S. L. De Fauw**. Essentially composed of herbivores, this group appears to have undergone two significant adaptive radiations: one in the Late Permian (Tatarian) and the other in the early Middle Triassic (Anisian). Both radiations were undoubtedly aided by the development of homogeneous Gondwana floras (the *Glossopteris* and *Dicroidium* floras, respectively), but it is important to emphasize that many genera achieved very widespread distributions in Pangea. The equatorial barrier does not appear to have been impenetrable to terrestrial vertebrates (see also Chatterjee 1987), and of the 35 known dicynodont genera approximately 11 are known from two or more cratonic regions. *Lystrorhynchus*, the famous dicynodont from the Fremouw Formation of Antarctica, is now known to have been particularly widely dispersed. Semi-aquatic and probably able to forage for a variety of food types, it may have been the most successful mammal-like reptile of all time.

One of the most significant palaeontological discoveries yet made in Antarctica is that of a series of fossil forests. Characterized by both petrified logs and in situ stumps bearing clearly-

defined annual growth rings, they are now known from the Permian and Lower Triassic of the Transantarctic Mountains, the Lower Cretaceous of Alexander Island and the Upper Cretaceous–lower Tertiary of the northern Antarctic Peninsula region (e.g. Creber & Chaloner 1984). So striking is their abundance and diversity, and so mild the climatic deductions made from them, that it was thought at one time that they may indicate periods of fundamental change in the growing conditions in polar regions (perhaps related to shifts in the tilt of the earth's axis; e.g. Jefferson 1983). However, **W. G. Chaloner** & **G. T. Creber** have been interested in this problem for some time, and in their review of the phenomenon of forest growth in Antarctica they suggest that the only factor which inhibits tree growth in the highest latitudes at the present day is temperature. It is now apparent that the annual input of solar energy to the polar regions is sufficient to produce large annual growth rings and it has been demonstrated that many evergreen trees can tolerate long, dark winters. Studies on the composition of both living and fossil forests have shown that the low angle of sunlight does not cause excessive mutual shading of trees.

It has long been suspected that many of the key elements of today's Southern Hemisphere humid and perhumid forests could be traced well back into the Mesozoic period. This is particularly so for certain lycopods, ferns, araucarians and podocarps which may belong to lineages originating as early as the early Jurassic, or even the late Triassic (Fleming 1963, 1975). Certainly, elements of the extensive Late Jurassic evergreen coniferous rainforests that covered much of the southern Gondwana margins have persisted to the present day (Jefferson 1983; Dettman 1986).

If much of the early evidence for the antiquity of austral forest floras came from macro-palaeobotany, much of the latest information stems from a proliferation of palynological investigations. Utilizing both on- and offshore successions, and a wide variety of palynoflora taxa, it is now possible to establish at least the Cretaceous ancestry of a number of living groups. **M. E. Dettmann**, for example, shows how the fern *Lophosoria*, which is restricted to South and central America, had a much wider distribution in the Cretaceous and Tertiary. Traced by its unique spore, *Cyatheacidites annulatus* (Dettman 1986), this genus can be shown to have its earliest stratigraphic occurrence (in basal Cretaceous strata) in the Antarctic Peninsula–South America region; it then migrated eastwards to Australia (where it

occurs in later Cretaceous beds) and northwards through South America. Similarly, the gymnosperm *Dacrydium balansae*/*D. bidwillii* alliance is now distributed from South America, through New Zealand, to certain Pacific islands and Malaysia. Its history can be traced by the pollen genus *Lygistepollenites* and the oldest occurrences (Coniacian–Santonian) shown to be on the Antarctic Peninsula and in southeast Australia.

Particularly important in confirming the high-latitude origins of a number of angiosperm lineages has been the elucidation of the Cretaceous–Tertiary boundary section on Seymour Island by **R. A. Askin**. Data from here are important in confirming that species from a range of families, which includes the Fagaceae, Myrtaceae, Proteaceae, Winteraceae, Casuarinaceae, Gunneraceae, Bombacaceae and Loranthaceae, have late Cretaceous–early Tertiary first appearances somewhere along the southern Gondwana margins. It should be emphasized, however, that not all these families necessarily originated in this region. Myrtaceous pollen, for example, is known from early Campanian and Maastrichtian sediments on the Antarctic Peninsula; this occurrence clearly predates Paleocene records in Australia and New Zealand, but postdates those from undifferentiated 'lower Senonian' in Borneo and Santonian in Gabon. In her paper, **Dettmann** speculates that a number of austral angiosperm taxa may actually have had northern Gondwanan or even Laurasian origins and then migrated via a South America–Antarctica–Australia route.

It seems to be possible to conclude that Antarctica was both an important source area and dispersal corridor (during the early Cretaceous–early Tertiary period) for austral plants now living at mid- to low latitudes. Quite why a number of major groups should either originate in, or disperse through, the highest southern latitudes is not readily apparent, but, as **Askin** points out, the climate during this period was for the most part mild and equable. Indeed, it could well be that an unusual combination of climatic conditions (comprising a polar winter/summer light cycle, low light angles and relatively mild and wet weather at the poles) provided an unique stress impetus for diversification of a wide variety of taxa. We will return to polar origination events and the time-discrepancy of high- and lower-latitude occurrences of taxa (often referred to as heterochroneity) below.

We know that for much of the Cretaceous Antarctica was covered by thick forests,

but which animals may have inhabited them? Although the Cretaceous terrestrial and freshwater faunal record from the continent is still poor, **T. H. Rich, P. V. Rich, B. Wagstaff, J. McEwen-Mason, C. B. Douthitt & R. T. Gregory** maintain that it is possible to speculate on the composition of at least the Early Cretaceous biotas by close comparison with southeastern Australia. At this time the two continents were of course still joined and it is estimated that the terrestrial vertebrates preserved within the Otway and Gippsland basins could have lived at as high a palaeolatitude as 85°S! Hypsilophodont dinosaurs are particularly common in these Victoria coast assemblages, and there is at least one theropod, *Allosaurus* sp.. Turtles are common too, although they seem to belong to primitive types, and there is a variety of fish (including ceratodont lungfish and the unique Australian koonwarrids), lepidosaurs, pterosaurs, plesiosaurs (presumably freshwater) and birds, together with a possible labyrinthodont amphibian. That dinosaurs could have lived in southeastern Australia (and thus Antarctica too) is not altogether surprising for they have been known for some time from Late Cretaceous deposits on the North Slope of Alaska. **Rich et al.** believe it unlikely that the herbivorous hypsilophodontids would have migrated vast distances to areas of winter daylight and suggest instead that a large brain and eyes may have pre-adapted them to the low light conditions of polar habitats.

By comparing assemblages from both Australia and southern South America, **R. E. Molnar** has suggested that the one dinosaur known from the Late Cretaceous of Antarctica (an ankylosaur from James Ross Island; Olivero et al. in press) was part of a terrestrial fauna that included hypsilophodontids, pterosaurs, ratites, sphenodontians, leiopelmatid frogs and ceratodontid lungfish. In reviewing austral Mesozoic terrestrial vertebrate faunas, he was struck by the fact that three of the fifteen known genera from the Jurassic–Cretaceous of Australia (*Allosaurus*, *Austrosaurus* and *Siderops*) seem to have been relicts. Coupled with the occurrence of the apparent labyrinthodontid amphibian, this could be taken to indicate one of two things: either there was some form of geographical barrier protecting the Australian region (and Antarctica too?), or certain taxa may have preferentially survived in polar regions (cf. Vermeij 1987).

Returning to the marine realm, **G. R. Stevens** indicates that a distinctive cool-temperate Maorian province can be detected within the Triassic invertebrate assemblages known from

New Caledonia, Papua New Guinea and South America. However in the Jurassic, eastern Gondwana rotated in a direction away from the South Pole and this led directly to a substantial improvement in global climates. Simultaneously, new shallow-water migration routes were established around the southern Gondwana margins and by the Middle Jurassic warm-temperate Tethyan faunas were able to spread to Australia, New Caledonia, New Zealand and West Antarctica. Such a scenario is certainly borne out by the belemnite assemblages described by **P. Doyle & P. J. Howlett**, for in the Middle–Late Jurassic a distinctive *Belemnopsis–Hibolithes–Duvallia* fauna can be traced southwards from European Tethys to the Gondwana margins. Local endemic centres can be identified at this time, such as in the embryonic trans-Gondwana seaway, but they are only discernible at the species level.

By the Early Cretaceous, extensive rifting had occurred across Gondwana and the proto-Indian and South Atlantic oceans were beginning to form. This in turn led to a reversal of the rotation of the eastern Gondwana block and the re-introduction of its southern margins into the highest latitudes. Here, a cool-temperate molluscan fauna developed, with one of its most important components being the endemic belemnite family, the Dimitobelidae. Further opening of the Atlantic and Indian oceans occurred throughout the Late Cretaceous and it was at this time that New Zealand's land links with the rest of Gondwana were severed by the formation of the Tasman Sea. However, as **Stevens** points out, there were still good Late Cretaceous shallow-marine connections between New Zealand, West Antarctica and South America. A cool-temperate Weddellian Province can be established between these localities until well into the Paleogene (Zinsmeister 1982).

The abundant early Campanian–late Eocene marine invertebrate faunas of the James Ross Island region have been investigated by **R. M. Feldmann & D. M. Tschudy**. They are particularly interested in an unusually rich decapod crustacean fauna which occurs in association with ammonites, bivalves, gastropods, echinoderms and brachiopods. Concentrating on the macrurous decapods (lobsters), they have been able to identify four species in the shallow-water Campanian–Paleocene Lopez de Bertodano Formation. *Hoploparia stokesi* is extremely abundant, but shows no clear-cut evolutionary trends in shape over a 20 Ma period. *Metanephrops jenkinsi*, a probable derivative of *H.*

stokesi, is particularly noteworthy as it extends the range of the genus back from the Pliocene to the Campanian. *Metanephrops* today is in fact only known from outer shelf/slope habitats at lower latitudes, and **Feldmann & Tschudy** believe that this may be another example of a marine invertebrate taxon that originated in the Late Cretaceous–early Tertiary of the James Ross Island region and then dispersed slowly to lower latitudes through the Cenozoic. So far, at least five bivalve, one gastropod, three echinoderm, seven decapod and two brachiopod genera known previously from either the late Cenozoic or Recent of mid- to low-latitude regions can be shown to have their earliest stratigraphic occurrences at this Antarctic locality (Zinsmeister & Feldmann 1984; Crame 1986; Wiedman *et al.* 1988). This is another striking example of high-latitude heterochrony.

Marine vertebrates from the Lopez de Bertodano Formation include teleost fish, sharks, mosasaurs and plesiosaurs. The last two groups have been studied by **S. Chatterjee & B. J. Small** as they almost certainly occupied the top-predator niches filled at the present day by seals and whales. Material belonging to two separate plesiosaur families, the Plesiosauridae and Cryptoclididae, has now been identified, and a new species within the latter taxon is described (*Turneria seymourensis* sp. nov.). Interestingly enough, it would appear that cryptoclidids fed by sieving food particles through a mesh formed by their slim, delicate, interlocking teeth. **Chatterjee & Small** speculate that they may even have fed on *Hoploparia*, in a manner analogous to that of crabeater seals feeding on krill.

In a stimulating new hypothesis to account for the origin of the Australian marsupials, **J. A. Case** suggests that Zinsmeister's (1982) Weddellian Province can also be identified in the terrestrial realm. Here it is characterised, in the Paleocene and Eocene of South America, south-east Australia and Antarctica (Seymour Island), by two key elements: *Nothofagus* and marsupials. **Case** points out that, just as the concept of high-latitude heterochrony can be used to account for the origin of certain plant and marine invertebrate taxa within the province, so it may also be applicable to terrestrial vertebrates too. In its original formulation (Zinsmeister & Feldmann 1984), the concept was split into two distinct components: first, the high latitudes may serve as centres of origin for taxa which can 'escape' under existing climatic conditions, and second, they may serve as 'holding tanks' for new taxa which remain isolated

until suitable conditions develop for their dispersal.

It is this second aspect of heterochrony which may have been crucial here, with Australian marsupial radiation being closely linked to habitat diversification. New stem taxa are held to have evolved in the latest Cretaceous–early Tertiary Weddellian Province but these could not proliferate in the uniform cool-temperate closed rainforests. However, by the mid- to late Eocene, Australia had separated sufficiently from Antarctica to generate much more diverse open-forest habitats and this provided the trigger for extensive family-level cladogenesis to occur.

Although it is generally assumed that the best record of the deterioration of Cenozoic climates and onset of glaciation in Antarctica is contained in marine cores (e.g. Leg 113 scientific party 1987; Leg 119 scientific party 1988), there are also some important terrestrial sequences to be considered. **K. Birkenmajer & E. Zastawniak** indicate that a long sequence of late Mesozoic–Tertiary floras is contained within the volcanoclastic sediments interbedded with a thick volcanic pile on King George Island, South Shetland Islands. Radiometric dating of the volcanics has enabled the plants to be grouped into a series of discrete assemblages, which can then be analysed palaeoecologically. The results of this study, in conjunction with sedimentological investigations of intercalated glacial deposits, have been used to construct a 'climatostratigraphy' for the South Shetland Islands. Warm phases are identified in the Late Cretaceous–Paleocene, middle Eocene–early Oligocene, late Oligocene (in part) and at the Oligocene–Miocene boundary; intervening cold ones are identified in the early Eocene (the Krakow Glaciation) and late Oligocene (Polonez and Legru glaciations, separated by the Wesele Interglacial).

In a review of the evolution of the Antarctic fish fauna, **J. T. Eastman & L. Grande** demonstrate that the dominant living group, the notothenioids, have no fossil record. Their rise to prominence seems to have been a consequence of the thermal isolation of Antarctica, which was partially achieved after the final (deep water) separation of Australia in the late Eocene–early Oligocene (38 Ma) and completed on the formation of the Drake Passage at the Oligocene–Miocene boundary (23 Ma) (e.g. Kennett 1977). With the formation of the Antarctic Convergence, it is likely that the southward migration/colonization by most pelagic fishes would have been prohibited; the ancestral notothenioid stocks could then de-

velop unchallenged in the vast Southern Ocean.

Eastman & Grande point out that the most logical explanation for the replacement of the Seymour Island Tertiary fish fauna by a relatively depauperate Recent one is the 15°C decline in temperature over a 50 Ma period. Nevertheless this should not have been an insurmountable evolutionary problem, for this averages out to a decrease of only 0.03°C per 100 000 years. Adaptation to low temperature as such presents few major biological obstacles and literally thousands of species have accomplished it (Dunbar 1968; Clarke 1988). Other ecological restraints, such as limited habitat space and trophic resources, are far more likely to have inhibited the development of the Antarctic fish fauna.

A more general survey of the Southern Ocean marine fauna by **A. Clarke & J. A. Crame** reveals that a substantial part of it may have evolved in situ over a long period of time. A number of living invertebrate groups, such as the pycnogonids, certain gastropods (trochids, littorinids, trichotropids and buccinaceans), echinoderms (ophiuroids, ctenocidarid cidaroids and schizasterid spatangoids) and ascidians, appear to be the products of adaptive radiations that began in the Cenozoic, or even, in some instances, the late Mesozoic. Far greater areas of shallow-water habitats were available for colonisation in the geological past; even after the onset of the main ice caps, substantial de-glaciations occurred in interglacial periods.

Turning to more physiological matters, **Clarke & Crame** consider the slow growth rates, extended development times and low metabolic rates of cold-water ectotherms (cold-blooded organisms). Low temperature is of course the traditional explanation for all these phenomena, but it seems somewhat paradoxical to suggest that it should hinder some processes such as growth, but not others such as locomotion. There is in fact a great energetic benefit to be derived from living in cold water, because basic maintenance costs are so low (Clarke 1988). The real problem for organisms in polar waters seems to be adapting to a severely pulsed food supply.

Using evidence gleaned from both the austral fossil record and the adaptations and distribution of living organisms, **R. E. Fordyce** suggests that the formation of the Southern Ocean may have had a seminal influence on the development of certain groups of marine mammals. The formation of the circum-Antarctic current, psychrosphere and Atlantic Convergence almost certainly provided the stimulus to develop new feeding strategies.

Fossil evidence from both Antarctica (Seymour Island) and New Zealand supports the conclusion that, within the Cetacea (whales and dolphins), the filter-feeding Mysticeti and echolocating Odontoceti arose from the primitive Archeoceti in the latest Eocene—earliest Oligocene interval. Both groups certainly appear to have then proliferated in the mid- to high southern latitudes through the Oligocene. Lobodontine phocids (true seals) radiated in the Southern Ocean region in approximately the late Miocene, and perhaps excluded certain otariids (fur seals and sea lions), such as *Arctocephalus*, from high-latitude pagophilic lifestyles.

E. Thomas considers the fact that polar cooling had major effects on the formation of bottom water, and this in turn is reflected in the composition of benthic foraminiferal assemblages. She describes a new sequence of Late Cretaceous (Maastrichtian) to late Miocene taxa that were obtained during ODP Leg 113 drilling on Maud Rise. They are all lower bathyal to upper abyssal types and analysis of them reveals distinct compositional shifts at seven levels (early/late Paleocene boundary, latest Paleocene, early Eocene, early middle Eocene, middle middle Eocene, earliest Oligocene, middle Miocene). At two of these, the early Eocene and early middle Eocene, the changes are particularly striking and suggest that the formation of bottom water may have been very different from preceding and succeeding periods. The marked lack of spiral forms and dominance of buliminids can be linked to lower oxygen levels and higher nutrient supply. These may have been times when deep waters were formed by evaporation at low latitudes (to form warm saline bottom water) rather than in polar regions.

Finally, **L. E. Watling & M. H. Thurston** consider a method of investigating the origins and evolution of an Antarctic amphipod family, the Iphimediidae, without recourse to the fossil record. Using a combination of phylogenetic (cladistic) and biogeographic data, they show that the most primitive members of the family are distributed primarily outside Antarctica; these are inferred to be the relicts of a former global distribution. The evolution of the family is then marked by a basic reorganization of the mouth field appendages which led directly to a major radiation of taxa. It is suggested that this occurred in the Antarctic region at approximately the Eocene—Oligocene boundary, with the cool waters of the embryonic Southern Ocean acting as an incubator for the evolutionary advance. With the possession of a new scissors-like mandible, the family spread swiftly

outwards from the Antarctic (principally through the genus *Iphimedia*; approximately 35 species worldwide) and successfully colonised the thermally changing global ocean.

Summary

The new, but still fragmentary, fossil record that we have from Antarctica indicates that a surprisingly wide variety of organisms has lived on or around our southernmost continent. Since the early Middle Devonian (385 Ma ago), when Antarctica (within Gondwana) reached approximately its present position, it has been colonized by a succession of plants and animals that shows signs of being as complex as those on any other continent.

Vast habitat areas available for occupation by both terrestrial and marine organisms, coupled with equable climates for very long periods of time, certainly contributed towards this proliferation of life. The southern margins of

Antarctica (and Gondwana) seem to have been particularly important dispersal routes and undoubtedly served as a major corridor for floral and faunal interchange between the high and low southern latitudes.

What is perhaps more surprising is to find that a number of plant and animal groups seem to have both originated in, and then radiated from, the high southern latitudes. Even after the marked deterioration of climates and loss of habitats through the Cenozoic, there still appear to have been adaptive radiations (especially in the marine realm).

Could it be that temperate, cool-temperate and even cold-temperate regions of the world have been more effective in the process of species diversification than hitherto recognized? The improved fossil record from Antarctica may be crucial in determining the contribution of high-latitude regions to the global species pool.

References

- CHATTERJEE, S. 1987. A new theropod dinosaur from India with remarks on the Gondwana — Laurasia connection in the Late Triassic. *In*: MCKENZIE, G. D. (ed.) *Gondwana six : stratigraphy, sedimentology and paleontology*. American Geophysical Union Monograph, **41**, 183–189.
- CLARKE, A. 1988. Seasonality in the Antarctic marine environment. *Comparative Biochemistry & Physiology*, **90B**, 461–473.
- CRAME, J. A. 1986. Polar origins of marine invertebrate faunas. *Palaeos*, **1**, 616–617.
- CREBER, G. T. & CHALONER, W. G. 1984. Climatic indications from growth in fossil woods. *In*: BRENCHLEY, P. J. (ed.) *Fossils and climate*. Wiley, Chichester, 49–74.
- DETMANN, M. E. 1986. Significance of the Cretaceous — Tertiary spore genus *Cyathacidites* in tracing the origin and migration of *Lophosoria* (Filicopsida). *Special Papers in Palaeontology*, **35**, 63–94.
- DOUMANI, C. A., BOARDMAN, R. S., ROWELL, A. J., BOUCOT, A. J., JOHNSON, J. G., MCALESTER, A. L., SAUL, J., FISHER, D. W. & MILES, R. S. 1965. Lower Devonian fauna of the Horlick Formation, Ohio Range, Antarctica. *Antarctic Research Series*, **6**, 241–281.
- DUNBAR, M. J. 1968. *Ecological development in polar regions. A study in evolution*. Prentice-Hall, Englewood Cliffs, N. J.
- FLEMING, C. A. 1963. Paleontology and southern biogeography. *In*: GRESSITT, J. L. (ed.) *Pacific basin biogeography*. Bishop Museum Press, Honolulu, 369–385.
- 1975. The geological history of New Zealand and its biota. *In*: KUSCHEL, G. (ed.) *Biogeography and ecology in New Zealand*. Monographiae Biologicae, **27**, W. Junk, The Hague, 1–86.
- GRINDLEY, G. W., MILDENHALL, D. C. & SCHOPF, J. M. 1980. A mid-late Devonian flora from the Ruppert Coast, Marie Byrd Land, West Antarctica. *Royal Society of New Zealand Journal*, **10**, 271–285.
- JEFFERSON, T. J. 1983. Palaeoclimatic significance of some Mesozoic Antarctic fossil floras. *In*: OLIVER, R. L., JAMES, P. R. & JAGO, J. B. (eds) *Antarctic earth science*. Australian Academy of Science, Canberra, 593–598.
- KENNETT, J. P. 1977. Cenozoic evolution of Antarctic glaciation, the circum-Antarctic Ocean, and their impact on global paleoceanography. *Journal of Geophysical Research*, **82**, 3843–3860.
- KYLE, R. A. 1977. Devonian palynomorphs from the basal Beacon Supergroup of south Victoria Land, Antarctica. *New Zealand Journal of Geology and Geophysics*, **20**, 1147–1150.
- LEG, 113 SHIPBOARD SCIENTIFIC PARTY 1987. Glacial history of Antarctica. *Nature*, **328**, 115–116.
- LEG, 119 SHIPBOARD SCIENTIFIC PARTY 1988. Early glaciation of Antarctica. *Nature*, **333**, 303–304.
- OLIVERO, E. B., GASPARINI, Z., RINALDI, C. A. & SCASSO, R. In press. First record of dinosaurs in Antarctica (Upper Cretaceous, James Ross Island) : palaeogeographical implications. *In*: THOMSON, M. R. A., CRAME, J. A. & THOMSON, J. W. (eds). *Geological evolution of Antarctica*. Cambridge University Press, Cambridge.
- VALENTINE, J. W. 1967. The influence of climatic fluctuations on species diversity within the Tethyan provincial system. *In*: ADAMS, C. G. & AGER, D. V. (eds). *Aspects of Tethyan biogeography*. Systematics Association Publication, **7**, 153–166.

- VEEVERS, J. J. 1988. Gondwana facies started when Gondwanaland merged in Pangea. *Geology*, **16**, 732–734.
- VERMEIJ, G. J. 1987. *Evolution and escalation*. Princeton University Press, Princeton.
- VRBA, E. S. 1985. Environment and evolution : alternative causes of the temporal distribution of evolutionary events. *South African Journal of Science*, **81**, 229–236.
- WIEDMAN, L. A., FELDMANN, R. M., LEE, D. E. & ZINSMEISTER, W. J. 1988. Brachiopoda from the La Meseta Formation (Eocene), Seymour Island, Antarctica. In: WOODBURN, M. O. & FELDMANN, R. M. (eds), *Geology and paleontology of Seymour Island*. Geological Society of America Memoir, **169**, 449–457.
- YOUNG, G. C. 1981. Biogeography of Devonian vertebrates. *Alcheringa*, **5**, 225–243.
- ZINSMEISTER, W. J. 1982. Late Cretaceous — early Tertiary molluscan biogeography of the southern circum-Pacific. *Journal of Paleontology*, **56**, 84–102.
- & FELDMANN, R. M. 1984. Cenozoic high latitude heterochrony of southern hemisphere marine faunas. *Science*, **224**, 281–283.