Reports

Evidence for Low Temperatures and Biologic Diversity in Cretaceous High Latitudes of Australia

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A diverse terrestrial biota inhabited polar latitudes during the Cretaceous, 105 to 130 Ma (million years ago), along what is now the southeast coast of Australia. This biota, from rocks in the Otway and Strzelecki groups, consisted of more than 150 taxa of vertebrates, invertebrates, and plants. Oxygen isotope ratios in diagenetic calcite suggest that mean annual temperatures were most likely less than 5°C, and rings present in the fossil araucarian-podocarp-ginko woods indicate seasonality. Southeastern Australia, thus, seems to have had a cool, seasonal, nontropical climate. Dinosaurs that have been recovered are up to five species and three genera of hypsilophodontids, all of which were endemic, and three species of theropods. The occurrence of *Allosaurus* sp. and labyrinthodont amphibians, which had become extinct elsewhere in the Jurassic, indicate that isolation may have allowed extended survival of these taxa in Australia. In that dinosaurs coped with high latitudes for at least 65 million years [Valanginian to Albian time in Australia and Campanian to Maastrictian time (80 to 65 Ma) in Alaska] suggests that cold and darkness may not have been prime factors bringing about the extinction of dinosaurs and some other groups at the Cretaceous-Tertiary boundary, unless they were prolonged.

Polar terrestrial biotas, and particularly polar dinosaur faunas, have been rarely preserved in the fossil record. Polar dinosaurs have been found in only three areas, the southeastern coast of Australia (*1, 2*), Alaska, and northern Canada (*3*). Because these sites were at latitudes greater than 70° during the Cretaceous, the inhabiting biota had to cope with 1 to 2 months of continuous darkness. Temperatures during the winter must have dropped below freezing, as recent geochemical studies have indicated (*4*). These environments were most likely places of extremes, quite cold at times, with large annual temperature ranges.

Cretaceous fossil vertebrates from southeastern Australia were described by Woodward in the early part of this century (*1*); a few additional vertebrates (*5–8*) were collected in the ensuing 80 years. Recent discoveries of dinosaur fossils, including an allosaurid theropod (*3*), have rekindled interest in the area, especially because paleogeographic reconstructions placed southern Australia well within the Antarctic Circle during the Early Cretaceous, perhaps as far south as 80°S (*9*). In this report, we describe the diverse biota from this region, including recently found dinosaur fossils, and present oxygen isotope data which indicate that southeastern Australia had a cool, nontropical climate during the Early Cretaceous.

Dinosaur fossils and their associated biota occur in Lower Cretaceous rocks in the Otway Basin (Otway Group) to the southwest and the Gippsland Basin (Strzelecki Group) to the southeast of Melbourne (Fig. 1) (*10–12*). These basins formed as a result of rifting between Australia and Antarctica early during the Cretaceous (*12*).

Up to 3 km of fluviatile and lacustrine sedimentary rocks including mudstone, coal, and volcanoclastic sandstone were deposited in these rift basins on medial to distal alluvial fans dominated by braided streams whose periodic flooding may have been related to seasonal meltwater derived from associated highlands (*13*), perhaps both the rift shoulders and intrarift volcanoes. Most tetrapod fossils have been recovered from channel lag deposits, fluviatile sandstone beds 5 to 10 m wide and 0 to 30 cm thick containing abundant intraclasts. Some have been found in large channel sandstone beds characterized by cross-bedding and lacking intraclasts. In a few cases, vertebrates have been preserved in lacustrine rocks and, in one location, in mudstones that were deposited on the floodplain, where a single footprint establishes that at least one species of dinosaur lived in situ.

The tetrapod-bearing rocks in the Otway Group range from latest Aptian to early Albian in age (*10, 13*), whereas those of the Strzelecki Group range from Valanginian to Aptian (*10*). Fission track ages for the Otway Group place it in the latter half of the Early Cretaceous (*14*). Fission track dates for the Koonwarra locality in the Gippsland Basin bracket this part of the Strzelecki Group between 115 ± 6 and 118 ± 5 Ma (million years ago) (*14, 15*). The dates for both groups are concordant with palynological determinations (*10*).

The Australian Early Cretaceous vertebrate fauna (Fig. 2) is a varied terrestrial

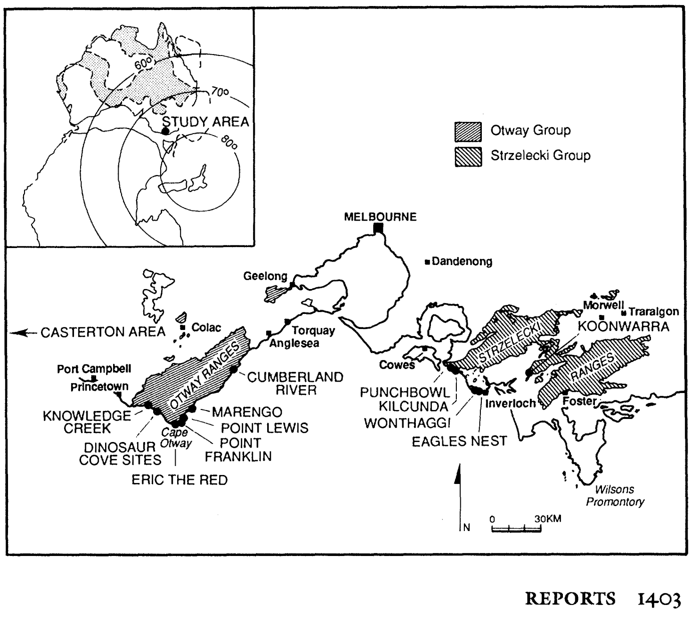

Fig. 1. Map of Australia with study area and location of sites with Early Cretaceous fossils (Fig. 2). Land and seaways (shaded areas) are mapped on the Australian continent only (inset). Modified from Frakes *et al.* (*31*).

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assemblage that is characterized by endemic and relict species. The dinosaur faunas are dominated by large-eyed, large-brained hypsilophodontids as well as theropods. Such variety and taxonomic composition may reflect both the polar climate and the isolation of this area during Early Cretaceous times.

We have found three, to perhaps five, species of hypsilophodontid dinosaurs (*16*), and at least two, possibly three of these, are new. Only one partial skeleton (that of the smallest genus) has been found; all other material is disarticulated. Femora dominate, but some dental and cranial material, as well as other postcranial elements, have been identified, clearly indicating taphonomic biasing.

Theropods, at least three species, are the only other dinosaurs represented. *Allosaurus* sp. (*2*) is the largest of the three, but the Australian specimen is from a small individual that would have been no more than 2 m high.

A varied biota of plants, invertebrates, and vertebrates comprising more than 150 taxa is associated with these dinosaurs. Forests of both deciduous and evergreen trees were dominated by ginkgoes, podocarps, and araucarian conifers. The undergrowth contained *Taeniopteris daintreei*, pentoxylaleans, ferns, sphenopsids, and both ground and epiphytic bryophytes (*10, 11*). Sclerophyllous ferns characterized forest fringes, and *Lycopodium* and sphagnalean mosses were in more open moorlands (*10*). *Isoetales*, hepatics, and algae dominated aquatic environments (*10*).

More than 80 species of invertebrates are known, most of which are insects primarily from the Koonwarra locality in the Gippsland Basin (Fig. 1) (*17*). Ostracods, syncarids, anostracans, cladocerans (all crustaceans), spiders, possibly earthworms, freshwater bryozoans, and unionoid bivalves are present (*17*). The fossil evidence indicates that among the 12 orders of insects, the hemipterans, coleopterans, and dipterans were the most diverse. Immature individuals of the aquatic Ephemeroptera and Diptera are the most abundant fossils.

Vertebrate faunas include a variety of fish (dipnoans, actinopterygians) (*8*), turtles (*5*), lepidosaurs (*6*), pterosaurs, plesiosaurs (presumably freshwater forms) (*2, 16*), birds (*7*), and a labyrinthodont amphibian (Fig. 3) (*16a*). Apart from dinosaurs, turtles are the most common terrestrial fauna, and are represented by limb bones, vertebrae, a lower jaw, and two partial carapaces (*2, 16*). The lack of any derived character in these turtles prevents assigning them to either cryptodires or pleurodires (*18*).

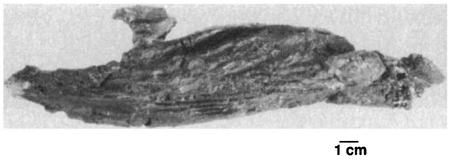

Fig. 3. Possible labyrinthodont lower jaw from the Strzelecki Group, Early Cretaceous, southeastern Australia.

Fish are well represented, especially from the Koonwarra locality (Fig. 1). Ceratodontid lungfish, coccolepidid palaeonisciforms, archaeomaenid pholidophoriforms, and two clupeiform groups, the Australian koonwarrids, as well as an endemic species of leptolepid, have been identified (*8*).

Five feathers from the Koonwarra locality are the only indication that birds were present in the region during the Early Cretaceous. Unfortunately, because of poor preservation, their familial level identity cannot be discerned (*7, 19*).

Plant (*10, 11*) and invertebrate assemblages (*17*) are consistent with a cool, humid climate, and the presence of distinct tree rings reflects some seasonality. The vertebrates of the Otway and Strzelecki groups (*16*) provide little paleoclimatic information, although earlier workers have suggested that the fauna indicated a relatively equable climate with no widespread winter freezing (*20*).

The Early Cretaceous vertebrate faunas of Victoria are unusual in that they were dominated by several different hypsilophodontid dinosaurs. The Australian hypsilophodontids are endemic at the generic level, but clearly belong in the family Hypsilophodontidae. Some form of isolating barrier, climatic or geographic, must have allowed development of the endemic biota. The numerical dominance of the hypsilophodontids among the dinosaurs could be a result of selective preservation related to their small size and the limited nature of the total sample (a few hundred reasonably complete isolated bones, teeth, and one skeleton). The only other dinosaur remains are fragments of smaller theropods (*16*).

Another explanation may be that these two groups of dinosaurs were among those particularly well adapted to high-latitude climates. On the North Slope of Alaska, hadrosaurs are dominant and theropods and ceratopsians scarce in Late Cretaceous faunas from comparable latitudes to those in Australia (*3*). The Alaskan hadrosaurs are about ten times as large in linear dimensions as the Victorian hypsilophodontids, but

	W **Otway Basin**										**Gippsland Basin** E					
Locality **Taxa**	Casterton	Dinosaur Cove West	Dinosaur Cove East	Slippery Rock	Knowledge Creek	Eric the Red	Point Franklin	Point Lewis	Marengo	Cumberland River	Punch Bowl	Kilcunda	Eagles Nest	Cape Paterson	Koonwarra	Wonthaggi
Dinosaur indet.		●	●	●		●	●	●	●		●		●			
Fulgurotherium australe			●									●	●			
Victorian hypsilophodont A		●	●	●												
Victorian hypsilophodont B		●	●	●				●								
Victorian hypsilophodont C			●	●												
Victorian hypsilophodont D														●		
Theropoda								?	●							
Allosaurus sp.													●			
Dinosaur footprint					●											
Testudines		●	●	●									●			●
Chelycarapookus arcuatus	●															
Plesiosaur		●		●						●			?			
?Lepidosaur													●			
Pterosaur			●	?												
Aves															●	
Labyrinthodont											●					
Pisces				●												
Ceratodontidae				●												
Ceratodus avus													●			●
Ceratodus nargun								●								
Ceratodus sp.															●	
Coccolepis woodwardi															●	
Wadeicthys oxyops															●	
Koonwarria manifrons															●	
Leptolepis koonwarri															●	
Palynological age	–	L. Ap. - E. Al			–	L. Ap. - E. Al.				–	B.- Ap.		V.- B.	–	B.- Ap.	–

Fig. 2. Known occurrences of Early Cretaceous fossil vertebrates in the Otway and Strzelecki groups, southeastern Australia. L. Ap., late Aptian; E. Al., early Albian; B.-Ap., Barremian to Aptian; V.-B., Valanginian to Barremian.

both families of dinosaurs were bipedal herbivores and are grouped together as ornithopods.

One Victorian hypsilophodontid is represented by an associated partial skeleton and skull. The material is from a juvenile of no more than one-third its adult weight, on the basis of a comparison of femoral sizes within the species. An endocast of the brain is preserved. The estimated archosaur encephalization quotient [*EQ* of Jerison (*21*), as modified by Hopson (*22*)] ranges between 1.1 and 1.8, depending on the adult size of the animal. Hopson (*22*) reported a maximum archosaur *EQ* of 1.5 for ornithopods. The form of the brain in dorsal view is similar to that of the small theropod *Stenonychosaurus inequalis* (*16, 22, 23*). The two differ in that *S. inequalis* has a much higher archosaur *EQ* (5.8), and the new Victorian hypsilophodontid has a distinct pineal body, whereas *S. inequalis* does not (unlike some other small theropods). In contrast to other hypsilophodontids for which the dorsal aspect of the brain endocast is known (*Hypsilophodon foxii*, *Dryosaurus lettowvorbecki*, and an as yet unnamed specimen from the Proctor Lake Site, Texas), that of the Victorian specimen has prominent optic lobes. This, together with its large brain and large eyes, suggests that the Victorian form may have been best adapted among hypsilophodontids for coping with the long periods of darkness or dusk associated with polar habitats.

More than half of the hypsilophodontid specimens from Victoria are of juveniles. No fossil eggshells have been found, but southeastern Australia seems to have been an Early Cretaceous dinosaur nursery. Whether dinosaurs occupied the area seasonally (like caribou and so forth) and then migrated away from the pole during the winter or remained is uncertain (*16, 20*). Estimates of the paleolatitudinal position of southern Victoria vary between 70° and 80°S (*9*); therefore, the distance that they would need to have traveled to reach areas with partial winter daylight is uncertain. If the latitude was near 80°S, however, small hypsilophodontids most likely could not have migrated annually to areas of winter daylight. Had they remained in the area all year, food would have been available. Many of the forest trees, such as the araucarians, would have retained green forage even during several months of darkness.

Plants, invertebrates, and many vertebrates (ceratodont lungfish, actinopterygians, turtles, and so forth) must have overwintered. With the possible exception of the *Allosaurus* sp., all of the animals were small enough to have found shelter readily by burrowing.

To estimate paleotemperature we determined oxygen isotope ratios on calcite concretions in sandstones of the Otway and Strzelecki groups (*4*). These concretions have been thought to have formed predominately during early diagenesis (*4, 24*), and they probably reflect the $^{18}O/^{16}O$ of the local meteoric water at the time of their formation. The concretions yielded some of the lightest $\delta^{18}O$ values that have been measured in sedimentary rocks [as light as 3.6 per mil (*4*)]. Most of the $\delta^{18}O_{SMOW}$ (standard mean ocean water) values cluster around 10.5 per mil (*4*), indicating that local meteoric waters were ^{18}O-depleted, with mean $\delta^{18}O$ values approaching −20 per mil. Comparison with modern data on soil carbonates (*25*) and meteoric waters (*26, 27*) suggests that the Cretaceous polar environment of southeastern Australia may have been far from equable, with mean annual temperatures less than 5°C and perhaps as low as −6°C (Fig. 4). Sedimentological evidence from central Australia likewise suggests that conditions could produce winter ice during the Early Cretaceous (*28*).

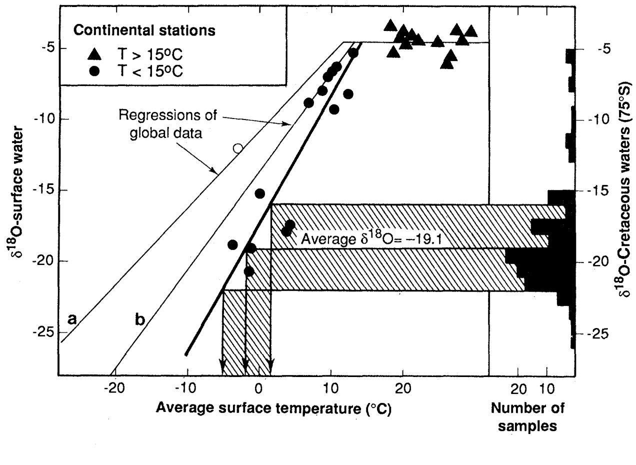

Fig. 4. Calculated surface water $\delta^{18}O$ values for the Otway and Gippsland basins. We assumed that $\delta^{18}O_{calcite} \approx \delta^{18}O_{water} + 29.4$ (*4*). Use of such a relation implies that the subsurface change in $\delta^{18}O$ (the ^{18}O-shift) of diagenetic fluids roughly parallels fractionation curves such as calcite-water. If calcite concretions could grow from "unshifted" meteoric waters at 50°C, the mean value of the histogram would shift upward to ≈ −14 per mil. The average $\delta^{18}O$ of the water distribution, truncated at $\delta^{18}O = -10$, is −19.1, and the diagonally ruled area brackets one standard deviation from the mean. The arrows bounding the field point to the estimates of average surface temperature. The regression of continental precipitation data (bold line) for stations with average surface T < 15°C (*4*) gives the warmest temperatures and the steepest descent on a $\delta^{18}O$ versus temperature plot. We have chosen the continental regression line (bold line) because it possibly mimics the shift to the right of the global precipitation line predicted by Rayleigh models if Cretaceous oceans were warmer. For comparison, the regression of the International Atomic Energy Agency (IAEA) global network (a) for the years 1953 to 1975 (*27*) and the regression line of Dansguard (b) (*30*) are shown. Modified from Gregory *et al.* (*4*).

To estimate the paleotemperature, we assumed that (i) the concretions record the $\delta^{18}O$ of the local ground water, which averages the local precipitation, and not some exotic water derived from another climate regime; (ii) the concretions have not been recrystallized at higher temperatures; and (iii) surface temperature and the $\delta^{18}O$ of precipitation were related in the Cretaceous. The first assumption is justified because the carbonates formed during diagenesis and because the climate is inferred to be wet. Arid regions are the only modern environments where ground water commonly reflects the $\delta^{18}O$ of an exotic source region (*29, 30*). The concretions may have recrystallized; however, the $\delta^{18}O$ values for much of the calcite are lower than the normal values expected for host sediments such as those enclosing the concretions in the Otway and Strzelecki groups. Therefore, subsurface recrystallization at elevated temperatures under conditions of a low water to rock ratio would require fluids with $\delta^{18}O$ values less than −20 per mil. In order to maximize the estimated mean annual temperature we used the regression line for modern continental stations (Fig. 4). This line gives a maximum estimate because it has a steeper slope on a graph of $\delta^{18}O$ versus temperature than regressions of earlier data and thus may more accurately mimic the effect of warm Cretaceous oceans on the temperature-$\delta^{18}O$ relation (*30*).

The Early Cretaceous climate of southern Victoria was most likely temperate, humid, and subject to seasonal extremes. The biota was diverse and contained temporal relicts such as the allosaurids and labyrinthodonts (*2, 16a*), which indicates isolation of this part of Gondwana during the Early Cretaceous. Together with the Late Cretaceous Alaskan occurrence, the presence of dinosaurs in Australia during the Early Cretaceous indicates that some ornithopod and theropod dinosaurs managed well under such conditions for at least 55 million years. Their presence near the poles was an enduring association, not a single random event. Any theory regarding dinosaur extinction must account for this type of adaptability in some dinosaurs. A prolonged period of darkness alone could have brought about the Cretaceous-Tertiary boundary extinction event only if its duration was greater than 3 to 5 months or if the dinosaurs were occupying high latitudes only during part of the year, which may be unlikely for some of the small, large-eyed, large-brained Victorian hypsilophodontids.

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X-ray Scattering Studies of Aligned, Stacked Surfactant Membranes

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X-ray scattering studies were performed to understand the structure and correlations in the lamellar phases of thick, freely suspended films of (i) the hydrated phospholipid dimyristoylphosphotidylcholine (DMPC) and (ii) the ternary system consisting of the surfactant sodium dodecyl sulfate (SDS), cosurfactant (pentanol), and water. The films were drawn in a temperature- and humidity-controlled environment, where the layers were oriented to within 0.1°. In the DMPC system, this made it possible to directly observe the orientation of the $P_{\beta'}$ modulation and to identify phase $L_{\beta'}$ as three distinct phases distinguished by the direction of chain tilt with respect to the lattice. In the L_α phase of the ternary system, power law behavior of the (0,0,L) structure factor arising from the algebraic decay of layer correlations was observed in single crystals.

SINCE THE LIPID MOSAIC MODEL OF cell membranes was proposed (*1*), much work has been done to understand the details of their function and structure. Although actual cell membranes consist of many components including lipids, cholesterol, and proteins, a great deal can be learned from the study of simple model systems that contain either a subset of those components or components similar to those found in real membranes. These are lyotropic, liquid crystalline phases (*2–5*), which are also of scientific interest because they are prototype models for elucidating the nature of phases and their transitions in two-dimensional (2D) systems. Furthermore, because of their ability to buckle out of their 2D plane, these phases provide real models for studies of the statistical physics of crumpled surfaces imbedded in three-dimensional (3D) space (*6*).

The high-water-content portion of the phase diagram of phospholipids was known to consist of three lamellar regions. The L_α phase, characterized by disordered chains and a lack of positional order within the layer, has been the subject of a great deal of study (*2–5*) because surfactants in most living membranes are in this state. The $P_{\beta'}$ phase is of particular interest as a result of the presence of a long wavelength ($80\ \text{Å} < \lambda < 120\ \text{Å}$) modulation of the layers. The $L_{\beta'}$ phase was believed to have tilted molecules and, although occupying a large portion of the phase diagram, it was largely ignored. We have expanded on a technique (*7*) by which we can produce extremely well-aligned, freely suspended films of the samples in continuously variable humidity con-

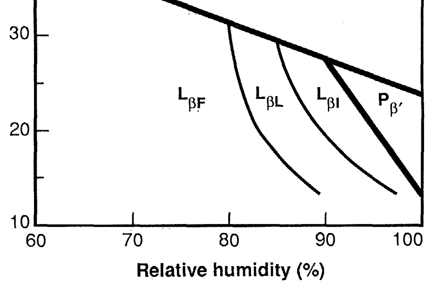

Fig. 1. The temperature-humidity phase diagram of DMPC. Because both axes are related to thermodynamic potentials, there are no two-phase regions. Note that the phase previously known as $L_{\beta'}$ is, in fact, three distinct phases, $L_{\beta F}$, $L_{\beta L}$, and $L_{\beta I}$.

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