

niches, but in any case conditions for it are probably restricted. Plausible examples may require consideration of ecological and evolutionary processes on different temporal or spatial scales, so that a trait conferring a fitness disadvantage under some ecological conditions can persist.

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Polar Dinosaurs and Ancient Climates

Michael J. Benton

Dinosaur skeletons have recently been found well within the contemporary Arctic and Antarctic Circles. These discoveries have surprised palaeontologists who regarded the dinosaurs as warm-adapted animals. New geological evidence suggests that these polar areas were also rather colder than had been thought, and this raises further problems in interpreting dinosaurian palaeobiology: were the dinosaurs fully endothermic and able to survive the darkness and cold of the polar regions, or could they undertake vast annual migrations of 3000–4000 km?

Dinosaurs are usually pictured against a background of damp tropical jungle-like foliage or sandy deserts. Most fossil skeletons of dinosaurs have been found associated with tropical or subtropical floras, and often with various sedimentological indicators of humid or arid conditions. Further, their postulated thermal physiology and naked skin was taken to indicate a preference for the environments favoured by living reptiles. New findings, however, show that dinosaurs lived within the ancient Arctic and Antarctic Circles^{1–8} (Fig. 1), and that these zones may have been covered extensively with ice⁹, although this idea is controversial^{10–12}. Should we now

imagine dinosaurs as thermally insulated warm-blooded animals that ploughed through snowdrifts and scraped the ice off the ground to find food?

The first polar dinosaur remains to be reported were some ornithopod footprints from Spitsbergen¹³, which lay at about 60°N in the Early Cretaceous. Further footprints, skin impressions and bones have been reported over the past 30 years from the mid and Late Cretaceous (114–66 million years ago) of the North Slope of Alaska, as well as from the Northwest Territories and Yukon Territories of Canada. Much of this material was collected by prospecting parties from coal and oil companies, and the specimens have only recently been described^{1–3}.

The North Slope of Alaska today lies at latitude 69°N, but geologists estimate that this area was further north in the Late Cretaceous, at 75–85°N. The climate appears to have been cool temperate in the Late Cretaceous, based on studies of the fossil plants. The flora consisted of deciduous plants which shed their leaves and died back or lay dormant in winter. Cross-sections of the fossil wood also show that growth ceased in winter^{2,12,14}. The Alaskan fossils include a freshwater dermatemyd turtle, a freshwater clam bearing tooth marks of a crocodilian or dinosaur, an ornithopod dinosaur footprint, isolated bones of ceratopsian dinosaurs (an occipital condyle, a horn core, and a partial femur) and hadrosaurs, and

teeth of a tyrannosaur and a troodont^{1–3}. (See Box 1 for a glossary of taxa.)

The southern polar dinosaurs were first recorded in 1906, when Woodward¹⁵ reported a lungfish specimen and a dinosaurian claw from the Early Cretaceous (130–105 million years ago) of Victoria, southeastern Australia. Further isolated fossils were found sporadically after 1906, but recent systematic collecting has yielded an extensive fauna^{4,5}. The area lay as far south as 70–85°S in the Early Cretaceous, and it must have experienced up to three months of effective darkness in the austral winter. The fossil plants and invertebrates, and the geochemistry, indicate a cool humid climate.

So far, the Victorian flora and fauna consists of more than 150 species: deciduous and evergreen trees, bushes and low ground cover, aquatic and terrestrial invertebrates (ostracods, cladocerans, other crustaceans, spiders, insects, earthworms, bryozoans, bivalves), fishes (bony fishes, lungfishes), turtles, lizards, pterosaurs, freshwater(?) plesiosaurs, birds and dinosaurs. A jaw bone of a temnospondyl amphibian has also been found: the last survivor of a group that had died out elsewhere long before the Early Cretaceous. The dominant dinosaurs are three or four genera of small- to medium-sized hypsilophodont ornithopods, and other less-complete remains indicate the presence of two or three theropods.

A single vertebra of a theropod(?) dinosaur has also been recorded from the latest Cretaceous of North Island, New Zealand⁶, in an area that

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lay further south than the Australian faunas, and well within the Antarctic Circle. No other vertebrate fossils were found associated with this bone, but several must have existed, presumably ancestors of the modern flightless birds, a sphenodontid reptile and a leiopelmatid frog, since New Zealand may already have been separate from Antarctica and Australia by latest Cretaceous times.

Dinosaurs have also been reported recently from the Antarctic continent, presently lying within polar latitudes, but probably just north of 60°S in the Cretaceous. These include an ankylosaur from James Ross Island⁷ and a hypsilophodontid from Vega Island, which lies nearby⁸. These southern forms – from Antarctica, Australasia, and also from southern South America – indicate a specialized southern-continent fauna that shared many characteristics. The late Cretaceous mammals of Argentina and Bolivia^{16–19}, in particular, show how South America, Antarctica and Australia formed a rather isolated evolutionary zone focused close to the South Pole; this continued into the Palaeocene and Early Eocene (65–45 million years ago), when South American-style mammals (marsupials, megatherioids) and birds (phororhacoids) lived in Antarctica²⁰.

There is no doubt now that dinosaurs inhabited polar regions, both north and south, in the Mesozoic. How do these findings relate to palaeoclimatic models, and to ideas about the thermoregulation and behaviour of the dinosaurs? The latter topic became a *cause célèbre* when Bakker²¹ suggested that the presence of polar dinosaurs indicated that they were fully endothermic animals, a proposition hotly denied at the time by his critics.

Mesozoic climates

Mesozoic climates are widely interpreted as having been warmer globally than they are today, with a lower temperature gradient from the poles to the equator, and with less-marked seasonality generally^{10–12,22}. The evidence comes from studies of fossil plants and marine organisms, palaeogeography and climatic modelling, oxygen isotope measurements and, in particular, the supposed absence of ice at the poles. Frakes and Francis⁹ reported 'dropstones' (large boulders dropped on to the sea floor from the bottoms of icebergs) from a range of Jurassic and Cretaceous sediments from both southern and northern polar regions, and they proposed that ice developed at least during certain seasons of the year.

Other authors^{10–12} doubt the pres-

ence of polar ice in the Cretaceous, although the geological evidence from Alaska might allow montane glaciers and winter snow. The shape of the earth, its orbit pattern and its obliquity mean that the polar dinosaurs experienced dark and cold seasons of one to three months duration, increasing poleward, just as today. There is much debate at present about just how cold the cold season was. Simple climatic modelling based on the distribution of Cretaceous continents and oceans, and on continental topography, suggests global temperatures 3.7°C above present values²³, but more sophisticated models might be required. The mean annual temperature for the North Slope of Alaska was estimated in this way to be 0–2°C¹⁷, whereas estimates based on fossil plants indicate values of 5–13°C for different times during the Late Cretaceous¹², with lowest mean winter temperatures of –11°C. The Australian polar localities also seem to have had cool temperate climates, with mean annual temperatures estimated by oxygen isotope analyses as 0–5°C^{4,5}.

Dinosaurs in cold conditions: endothermy or ectothermy?

How did dinosaurs survive in these polar regions? Although they were not as cold as the poles today, these regions experienced freezing temperatures and weeks or months of darkness each winter at least. Did the cold-blooded (ectothermic) dinosaurs stay put and hibernate, stay put and suffer, migrate vast distances to escape the cold, or were they warm-blooded (endothermic) and able to remain active all winter?

Parrish and colleagues² argue that the Alaskan dinosaurs did not hibernate, since they were too large to shelter in deep caves or holes in the ground. They accept that endothermic dinosaurs could have survived the northern winter relatively readily, while even ectothermic forms could have toughed it out if the cold snaps were brief. Otherwise, they speculate, it would have been necessary to migrate, down to the Cretaceous Arctic Circle at the furthest – a distance of 2100 km, at a steady rate of 24 km per day. The distance could have been less if the dinosaurs were more sensitive to temperature than light. If migration were the order of the day for the dinosaurs, how did the (unquestionably ectothermic) freshwater turtle keep up? Doubtless, it could have hibernated, as its temperate-zone fellows do today.

Paladino and colleagues²⁴, however, believe that the dinosaurs were ectothermic, as is indeed suggested

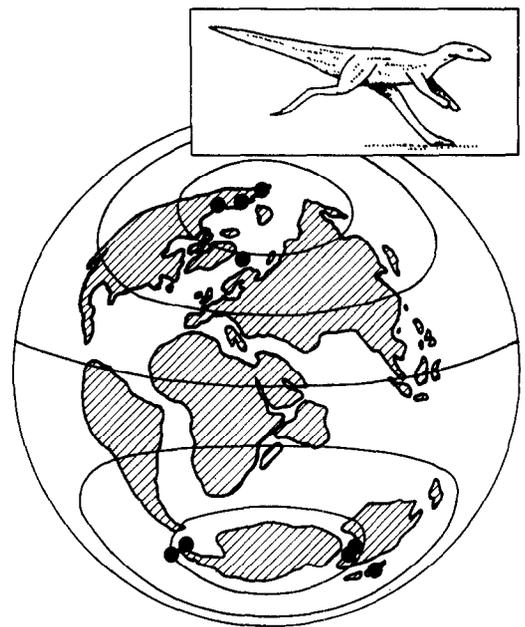


Fig. 1. A map of the Late Cretaceous world, showing the distribution of modern continents at the time, and localities of recent polar dinosaur finds (black circles). A hypsilophodontid, typical of the new Australian discoveries, is shown at the top. (Based on several sources.)

by most evidence, and that they could have stayed in the far north, displaying reasonable levels of activity. The key is physiological: like modern giant marine turtles, they were probably gigantothermic, that is, able to maintain their core body temperatures at high constant levels, despite possible low ambient temperatures, because of their large body sizes, low metabolic rates, circulatory control and insulation by superficial tissues. This could not apply, of course, to some of the smaller dinosaurs from the Australian polar localities; these, if ectothermic, may well have had to migrate or hibernate.

Box 1. Guide to polar animal groups

- Ankylosaur, armoured tank-like dinosaur
- Ceratopsian, horned dinosaur
- Dermatemyid, freshwater turtle found today only in Central America
- Hedrosaur, plant-eating duck-billed dinosaur
- Hypsilophodontid, small bipedal herbivorous dinosaur
- Leiopelmatid, small frog restricted to New Zealand
- Megatherioid, extinct giant ground sloth
- Ornithomimid, unarmoured bipedal herbivorous dinosaur
- Plesiosaur, long-necked marine fish-eating reptile
- Phororhacoid, fossil flightless hunting bird of South America
- Pterosaur, flying reptile of the Mesozoic
- Sphenodontid, long-lived lineage of lizard-like animals, formerly global in distribution, now found only in New Zealand
- Temnospondyl, broad-skulled primitive fossil amphibian
- Theropod, bipedal carnivorous dinosaur
- Troodont, small advanced theropod dinosaur
- Tyrannosaur, large theropod dinosaur

Paul²⁵ takes an opposing view, arguing that all dinosaurs were simple endotherms (as birds and mammals are) and that polar forms were thus able to shrug off the cold, or to migrate away much more effectively. He does not favour migration since he estimates that the one-way distance from the North Slope of Alaska to warm conditions was 3700–4600 km, not 2100 km (Ref. 2), and he pictures large dinosaurs, possibly bearing a seasonal covering of feathery 'hair', standing about gloomily in the dark icy polar winds. This is unlikely, however, in view of the fact that all kinds of skin impressions show that dinosaurs were covered with scales and not hair. Indeed, a hadrosaur skin impression from the Alaskan North Slope^{1–3} confirms their naked skin.

After 20 years of argument over the thermal physiology of dinosaurs, Paul's acceptance²⁵ of simple endothermy seems hard to credit, in the absence of any evidence for it. Equally, a great deal more work is

required to establish just what those Cretaceous polar winters were like some 100 million years ago.

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Letters to the Editor

Demographic Growth Analysis

The strength of a dynamic modular approach to an understanding of process-function physiology derives from an analysis of modular life history. A leaf module has a discrete lifespan¹, with a physiology (and physiological efficiency) that may change over time. Similarly, a flower module may develop fruit and become a major sink for resources as it matures².

Ten years ago, Hunt and Bazzaz³ were in fact the first to apply modular demographic analysis and plant growth analysis in parallel, at the suborganismal level. In addition, in their recent *TREE* article, McGraw and Garbutt⁴ seem unaware of a *third* approach to the analysis of plant growth, derived from agricultural and horticultural science: yield-component analysis, where plant development is subdivided into a number of ontogenic stages. Individual components of yield represent these stages and plant yield or productivity can be calculated as the mathematical product of the individual yield components^{2,5,6}.

Both yield-component analysis and classical growth analysis subdivide yield into separate elements. Growth

analysis explores indices of the efficiency and extent of the assimilatory system, the duration of production and quality of yield. Yield-component analysis views yield as a consequence of a temporal sequence of distinct stages; growth analysis examines the collective and continuous operation of contributing processes. The two techniques therefore illuminate different aspects of the origin of plant yield.

To integrate these perspectives and provide both conceptual and practical links between yield-component analysis and plant growth analysis, we merged the two techniques into a composite procedure, sequential plant-growth analysis⁷. This composite approach treats some of the traditional indices of plant growth – including leaf-area ratio, leaf-area index, unit leaf rate, relative growth rate, crop growth rate and harvest index – as yield components. Regression analysis is used to quantify the contributions of individual yield components to variations in growth and yield. Both fitted curves and trends in coefficients of determination can illustrate the time course of relationships during development.

Later, Jolliffe and Courtney⁸ extended this concept by exploring the contributions made by individual components to the performance of the whole plant, such as, for example, the additive contributions made by different plant parts to overall unit leaf rate. For multiplicative components, the relative growth rate of yield was determined as the sum of the relative growth rates of yield components. Furthermore, allometric relationships among components and the whole were defined, further linking the three different approaches for analysing plant growth.

Each of the analytic approaches mentioned above (modular demography, sequential yield-component analysis and traditional growth analysis) addresses slightly different issues; no approach is intrinsically superior. Unification of these approaches to the analysis of plant growth should continue, incorporating perspectives from related disciplines.

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