

PHYSIOLOGICAL, MIGRATORIAL, CLIMATOLOGICAL, GEOPHYSICAL, SURVIVAL, AND EVOLUTIONARY IMPLICATIONS OF CRETACEOUS POLAR DINOSAURS

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ABSTRACT—The presence of Late Cretaceous social dinosaurs in polar regions confronted them with winter conditions of extended dark, coolness, breezes, and precipitation that could best be coped with via an endothermic homeothermic physiology of at least the tenrec level. This is true whether the dinosaurs stayed year round in the polar regime—which in North America extended from Alaska south to Montana—or if they migrated away from polar winters. More reptilian physiologies fail to meet the demands of such winters in certain key ways, a point tentatively confirmed by the apparent failure of giant Late Cretaceous phobosuchid crocodilians to dwell north of Montana. Low metabolisms were also insufficient for extended annual migrations away from and towards the poles. It is shown that even high metabolic rate dinosaurs probably remained in their polar habitats year round. The possibility that dinosaurs had avian-mammalian metabolic systems, and may have borne insulation at least seasonally, severely limits their use as polar paleoclimatic and Earth axial tilt indicators. Polar dinosaurs may have been a center of dinosaur evolution. The possible ability of polar dinosaurs to cope with conditions of cool and dark challenges theories that a gradual temperature decline, or a sudden, meteoritic or volcanic induced collapse in temperature and sunlight, destroyed the dinosaurs.

INTRODUCTION

INCREASING NUMBERS of remains show that dinosaurs lived near the North and South Poles during the Cretaceous. Clemens and Allison (1985), Davies (1987), and Brouwers et al. (1987) reported on a Maastrichtian bonebed of juvenile and adult duck-billed hadrosaurs from near the Colville River of Alaska (Figure 1). Other Arctic dinosaurs include small to large predatory theropods and large, horned ceratopsians from the Late Cretaceous (Campanian, Maastrichtian, and perhaps earlier) of northern Alaska, northwest Yukon, and western Northwest Territories (Figures 1, 2; Russell, 1973, 1984; Roehler and Stricker, 1984; Parrish et al., 1987). Pre-duckbill iguanodonts are also known from the late Early Cretaceous of Spitsbergen (Lapparent, 1962), which may have been an extension of northeastern Greenland at the time.

Just how far north these and the classic North American dinosaur sites were is not certain. The Late Cretaceous magnetic North Pole was a little north of the Bering Land Bridge (Smith et al., 1981). However, the paleomagnetic and paleospin poles were probably displaced 10° or more from one another, as they are today, and it is likely that the Late Cretaceous spin pole was closer to the modern spin pole than was the contemporary paleomagnetic pole. The exact location of the Late Cretaceous spin pole is a matter of question. Andrews (1985) used fixed hotspot data to plot it just north of Prince Patrick Island, while Courtillot and Besse (1987) used nonfixed hotspot data to put it to the north and somewhat east of Greenland (Figure 1). Although the fixity of hotspots has been questioned (Molnar and Stock, 1987), Andrews' (1985) spin polar position is not as out of line with the magnetic paleopole (~15°, about the same as today) as is the position in Courtillot and Besse (1987, ~35°). Andrews' (1985) position is also more compatible with the contemporary extent of an Arctic floral and faunal regime as far south as Montana (see below). Hence, Andrews' (1985) spin pole position is preferred here. The north Alaskan dinosaurs were a little over 10° from the Late Cretaceous spin pole relative to Andrews' (1985) position, a little less than this from the paleomagnetic pole, and 30+° from Courtillot and Besse's (1987) spin pole plot.

These may not have been the northernmost occurring dinosaurs. The close similarity between predatory theropods and other dinosaurs of Late Cretaceous Asia and western North

America suggests that dinosaurs were regularly crossing, and living upon, the Bering Land Bridge within a few degrees of the paleomagnetic pole (Clemens and Allison, 1985; Paul, 1987a). North-central Canadian and Greenlandian land often reached to within a few degrees of Andrews' (1985) and Courtillot and Besse's (1987) spin paleopole positions in the Late Cretaceous (Williams and Stelck, 1975). Whether dinosaurs lived in these areas is unconfirmed, in part because the deposits appear to be of poor suitability for preserving them (Currie, personal commun.). In the middle of the Cretaceous, Spitsbergen was about 25° from the magnetic pole, but Andrews (1985) and Courtillot and Besse (1987) agreed that it was very near to or at the true North Pole (when their data are combined with the continental plate positions as per Smith et al., 1981).

Note that if Andrews (1985) is correct, then western North American dinosaur sites were some 10° further north than usually thought. For example, the Dinosaur Provincial Park would have been at a little over latitude 60°N. This is in sharp contrast to Courtillot and Besse (1987) who place the Park further south than it is today, at ~45°N.

In the Southern Hemisphere, theropod and ornithopod dinosaurs are known at about 15–5° from the middle Cretaceous paleomagnetic pole in Australia (Douglas and Williams, 1982). Press accounts report that Late Cretaceous ankylosaur and fragmentary theropod remains have also been found on the Palmer Peninsula of Antarctica. The evidence from Late Triassic to early Early Cretaceous polar sediments is not yet adequate to determine if dinosaurs were present.

The discovery of dinosaurs in polar regions has led workers to use them to help interpret the region's paleoclimates, and determine the planet's paleoaxial tilt, but such uses may be unwarranted. Polar dinosaurs are, however, good evidence for dinosaurian endothermic homeothermy at least at the tenrec level, whether or not dinosaurs wintered over, or migrated away from polar winters. Dinosaurs can also be used to assess the validity of certain evolutionary and extinction scenarios.

USING DINOSAURS TO EXAMINE POLAR CLIMATES AND AXIAL TILT

The physiological problem.—Because dinosaurs were long thought of as naked skinned ectotherms, it was often assumed that they could only live in warm, equable climates. In 1970,

Ostrom warned against deriving climatic conclusions from the presence of dinosaurs, because they are a long extinct group whose physiology is not nearly as certain as those of extinct amphibians, archaic reptiles, lizards, turtles, crocodylians, birds, or mammals. The physiological possibilities for dinosaurs include their being endothermic homeotherms of the avian-mammalian type. The arguments for and against such a metabolism were presented in Thomas and Olson (1980); however, Russell (personal commun.) is currently more favorable towards endothermic dinosaurs. The key point is that if all dinosaurs had high metabolic rates then the group's ability to cope with cold and temperature variation may have been as good as that of birds and mammals. Thus, the value of dinosaurs as climatic indicators may be severely limited, or even nonexistent, because dinosaurs differ from late Tertiary mammals and birds whose climatic tolerances can often be estimated from very closely related living species. Despite these problems, Roehler and Stricker (1984) and Xu (1980) used the presence of Arctic dinosaurs to infer a mild climate, and Xu used them to postulate a lesser axial tilt at the time.

Insulation.—Complicating the issue is the problem of insulation, which can greatly alter an animal's ability to cope with various climates. Mosaic-pattern scale impressions are preserved with big hadrosaurs, ceratopsians, and theropods (Lull, 1933; Lull and Wright, 1942; Morell, 1987). In particular, note the naked skin recorded for large arctic hadrosaurs (Roehler and Stricker, 1984). Such examples of naked skin are often taken as evidence that these or all dinosaurs could not cope with sharply cool seasonal environments, especially the kind of severe winters that mark modern polar regions. The presence of naked skinned dinosaurs at a site continues, therefore, to often be taken as evidence for a mild climate at the time. Davies (1987) and Douglas and Williams (1982) did so in regard to the climates of polar dinosaur habitats. The latter also used naked skinned dinosaurs to argue for less axial tilt in the Cretaceous.

However, the issue of dinosaur integument is not as settled as it may appear. Although it is true that no insulation has been found associated with a small dinosaur, no scale impressions are known from small dinosaurs either. Ostrom (1978) argues that the absence of insulation with the *Compsognathus* specimen from the fine-grained Solenhofen slates is good evidence that such small theropods were naked skinned, but one could just as well argue that the lack of preserved scales shows that they were unscaled. Besides, four of the five *Archaeopteryx* specimens from the same deposits lack any trace of the soft body contour feathers—as opposed to the prominent wing plumage—one would expect to find on a flightless theropod. Because all small theropods are larger brained than living reptiles (Raath, 1977; Hopson, 1980), there is a consensus that small theropods had substantially higher metabolic rates than reptiles (various workers in Thomas and Olson, 1980). If so, insulation would be a logical requirement for maintaining a constant body temperature whether the climate be hot, cold, or even warm and equable. A few modest sized endotherms are naked skinned, including humans and some suids. However, humans use a highly developed sweat coolant system and artificial insulation, neither of which archosaurs were likely to have had. Smaller, ground-dwelling endotherms, the size of the smallest theropods, are always insulated.

Potentially informative in regard to small dinosaurs, especially herbivorous ones, is the possible skin impression reported from one small ornithomimid (Gilmore, 1915). Unlike its large relatives, it is stated to lack scales and to have small pits instead. Unfortunately, the impressions are not currently accessible for confirmation. It is possible that the pits supported a layer of insulation, perhaps feather- or fur-like structures. Juvenile di-

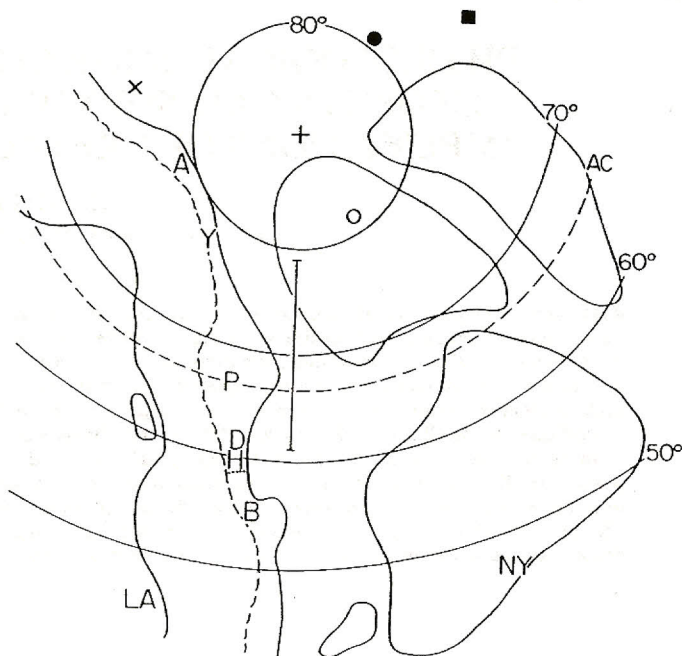


FIGURE 1—A generalized map of the North American region during the Campanian-Maastrichtian. Positions of north poles are Andrew's (1985) spin paleopole (cross) with north paleolatitudes drawn from that point, paleomagnetic pole (X), Courtillot and Besse's (1987) spin paleopole (solid square), present North Pole (solid circle), and present magnetic pole (open circle). The highland bordering the western interior seaway coastal floodplain is indicated by an irregular dashed line, note that cartographic distortion causes the floodplain to appear straight instead of properly curved. The boundary between a deciduous flora Arctic regime and a southerly phobosuchid crocodylian and evergreen fauna-flora on the coastal floodplain is indicated by a dotted line. Indicated are the dinosaur sites in Alaska (A), the Yukon and Northwest Territories (Y), Dinosaur Provincial Park (D), the wintering grounds of Arctic dinosaurs postulated by the author (B), by Hotton (1980) (H), by Axelrod (1985), and by Parrish et al. (1987) (P), and the paleo-Arctic Circle (AC). The future positions of New York and Los Angeles are plotted for comparison to the postulated migration distance, scale bar equals 2000 km. Paleopole and paleo-cartographic data from Russell (1973), Williams and Stelck (1975), Smith et al. (1981), and Andrews (1985).

nosaurus may have borne insulation that was shed as they increased in size. Because dinosaurs are a unique group of animals of unknown body covering at small sizes, an objective assessment of their possible integument should not place the burden of proof upon the seemingly radical idea of insulation, versus the traditional scaly model. Both are equally plausible at this time.

Even big dinosaurs may have grown insulative layers over their scales during cooler seasons, which they then shed before the summer. If this seasonal insulation was feathery, it could have grown at the margins of the body scales, as can occur on bird feet (Rawles, 1960), or along a limited number of tracts as on birds' bodies. Especially notable in this regard are Arctic ptarmigans, which in the spring shed the winter coat of feathers that in the fall grow directly on their feet and toes (Johnsgard, 1983). In doing so they uncover the underlying scales. Such seasonal feathers could go unrecorded if the subject died in the summer, or if the conditions were unsuitable for the preservation of feathers while being suitable for scales. Seasonal dinosaurian insulation is speculative, but not unduly so. Although the situations are not fully analogous, it is worth noting that the

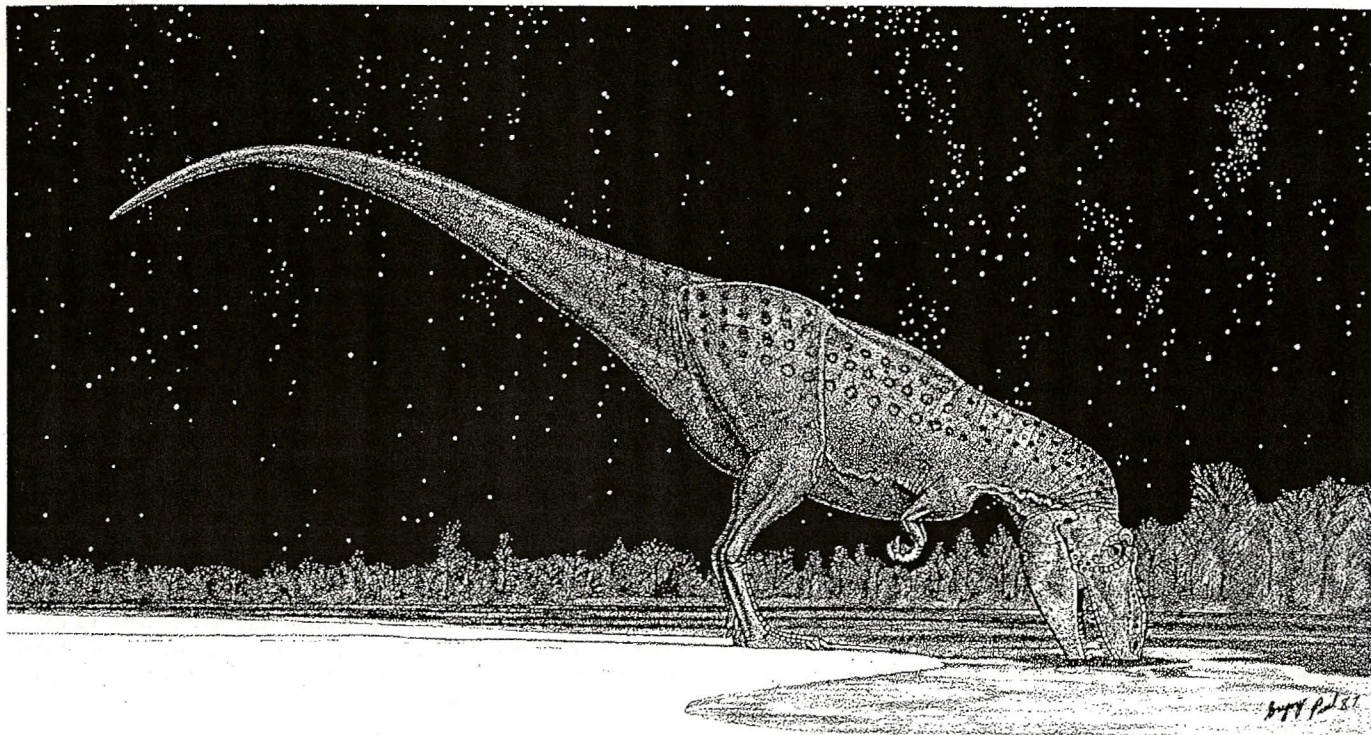


FIGURE 2—Standing in light snow a thirsty tyrannosaur, genus and species uncertain, breaks through the ice glaze edging a large river on the Late Cretaceous North Slope of Alaska. Shown under a clear moonlit winter midnight, still air temperature is projected to be -2 to -4°C , breezes would drive effective temperatures lower. Although shown naked skinned, it is possible that such big dinosaurs bore a winter pelage. Across the river stands a leafless deciduous forest.

presence of proboscideans and rhinos in Pleistocene Arctic deposits was taken as evidence of warm climates because the living tropical species are naked (Grayson, 1984), until frozen remains showed that the northern species were furry.

There are a number of ways large dinosaurs could have acquired insulation. Over the generations each species may have done so as they pushed their ranges closer to the poles. Insulation may have evolved in small, early, nonpolar archosaurs or dinosaurs, and was secondarily lost as larger nonpolar species evolved from them—much as many very large mammals have lost their insulation. In this case the genetic information for growing insulation may have already been in place, and only needed to be reactivated in polar species. Alternatively, some small insulated polar species may have evolved directly into large, seasonally insulated ones.

Unlike the large polar Ice Age mammals that retained their pelages year-round, large polar dinosaurs may have had to shed their insulation in order to avoid overheating during the relatively warmer and longer Cretaceous summers. What can be said at this time is that the possibility that dinosaurs had a winter pelage further reduces their value as climatic indicators.

Alternatively, it is possible that large dinosaurs were uninsulated. In this case their ability to cope with the cold is still not known, because this question has not been fully examined among today's big, naked skinned animals. Naked skinned, fat insulated whales, walruses, and phocid seals live in near 0°C waters, and water is a much better conductor of heat than air (Gordon et al., 1968). The fat deposits of naked skinned, domestic suids raised in the subarctic allow them to tolerate 0°C air temperatures (Gordon et al., 1968). These mammals' resistance to cold is accomplished by allowing their superficial layers to drop to near freezing so that they act like an insulative shell.

Species of mammoth lived in temperate latitudes that experienced sharp winters. Naked skinned Arctic dinosaurs may have built up heavy subcutaneous winter fat reserves for insulation which, when combined with their sometimes very large bulk, may have given them an equal or even higher tolerance to cold air temperatures. This tolerance was not likely to have been able to cope with modern Arctic winters, however.

Migration.—The final problem with using dinosaurs as indicators of polar climates is that in some areas they may have avoided winters by migrating away from the poles, a possibility further explored below.

USING POLAR CLIMATES TO EXAMINE DINOSAUR PHYSIOLOGY

Rather than using dinosaur physiology to estimate the climates of their polar habitats, it may be more useful to do the opposite. Ostrom (1980) and Bakker (1980) argued that the relatively mild conditions prevalent at the Cretaceous poles limited the significance of any physiological implications. Bakker (1986) has since become more favorable to the physiological implications of polar dinosaurs. In neither Ostrom's nor Bakker's studies was the problem examined in depth. Understanding the physiological consequences of polar dinosaurs requires that the detailed responses of various physiologies to the region's reconstructed paleoclimates be examined.

Cretaceous polar conditions.—Various non-dinosaurian lines of data are available to determine Cretaceous polar climates. The presence of relatively warmth-loving floral and faunal elements led some to speculate that the Earth's axial tilt was less in the Cretaceous and early Tertiary (Wolfe, 1980; Xu, 1980; Douglas and Williams, 1982). Geophysical, paleoclimatological, and paleontological evidence strongly contradicts this concept

(Estes and Hutchison, 1980; Axelrod, 1984; Creber and Chaloner, 1985). Specifically, the Earth is a stable gyroscope and should have retained much the same axial tilt since its formation. This is confirmed by the Cretaceous and early Tertiary polar region's deciduous floras and by their persistently small ectothermic vertebrates. Both of these became dormant during long winter nights that only high axial tilt can create.

There is little doubt that from the middle to the end of the Cretaceous, polar climates were much milder and more equable than they are today. Permanent glaciers, sea ice packs, and tundra are generally believed to have been absent (but see below). However, considerable dispute centers around just how severe winters were, and the potential coldness of the Cretaceous poles has not been widely appreciated. Axelrod (1984) estimated that the mean annual polar temperatures were about 15°C. He and Spicer and Parrish (1986) see the middle to late Cretaceous polar winters as cool, with January temperatures averaging perhaps 10°C. Axelrod (1984) noted that although 5°C may have been the normal January low in the Late Cretaceous, in his worst case scenario "regular light freezes" are considered possible and compatible with the flora. If so, occasional snowfalls may have occurred (Figure 2). Spicer and Parrish (1986) noted that the excellent preservation of fossil middle Cretaceous Arctic leaves indicates "cool or cold" conditions at the time of their preservation. Hotton (1980) believed that periodic frosts were plausible. Brouwers et al. (1987) indicated 2–4°C means in the coldest month, with frosts. Crowley et al. (1986) cited climatic models, and scattered evidence of river and coastal ice, as implying that deeper freezes regularly occurred. Using paleobotanical evidence, Parrish et al. (1987) also indicated that Late Cretaceous polar climates may have been fairly harsh, and variable in the long term. In the Cenomanian, they estimated a mean annual temperature of only 10°C, with January temperatures averaging 5°C. In the Campanian, they estimated that overall temperatures were at least 5° lower and less equable, with mean January temperatures possibly as low as -11°C. In this case, hard freezes would have occurred. Parrish and Spicer (1988) detail the evidence for changing climates, with a mean annual temperature of 7–13°C during the Albian and Cenomanian, then 10–13°C in the Coniacian, followed by a drop to only 2–8°C in the Campanian and Maastrichtian. The latter conditions especially would indicate winter freezes. Brouwers et al. (1987), however, dispute such claims of hard freezes. Cyclical climatic changes are also indicated by Hickey (1980), who argued that temperatures in Montana dropped from a high of over 20°C to 10°C at the end of the Cretaceous. If correct, then polar regions should have cooled at the same time. If Late Cretaceous polar climates did fluctuate, then it is notable that dinosaurs remained abundant regardless of the Campanian shift to colder conditions.

Brouwers et al. (1987) noted that Late Cretaceous Arctic regime of deciduous flora extended as far south as northern Montana. They suggested that this was due to low winter light levels, and following Andrew's (1985) spin polar position (Figure 1) the winter solstice sun in southern Alberta would have been above the horizon for only four hours and would have risen only 6°. At the Montana-Wyoming border a semitropical evergreen flora was dominant (Axelrod, 1984). This locale was perhaps at latitude 55°N at the time, in which case the sun would shine for nearly five hours and rise 11° above the horizon at winter solstice. In Montana and Wyoming mean annual temperatures during the Maastrichtian may have been around 20°C (Hickey, 1980). Extrapolating from Axelrod (1984), mean January temperatures may have been about 15°C, and rarely dipped below 10°C.

The zonation of the North America's western interior seaway

into cool arctic and warm gulf currents may have also contributed to the parallel development of arctic and semitropical regimes along the coastal floodplain (roughly equivalent to the humid northerly and dry southern climates of Lehman, 1987, although he puts the boundary further south).

Disagreements also cloud the Cretaceous Antarctic climate. Waldman (1971) argued that lake varves indicate seasonal hard freezes and spring snow melts, but Douglas and Williams (1982) strongly disputed this. Haq et al. (1987) suggested that periodic Antarctic glacial fields were responsible for a series of rapid sea level fluctuations in the Late Cretaceous, but this is a minority view.

It should be noted that the polar dinosaurs found so far come from coastal deposits where conditions should have been the mildest and most equable, due to the moderating effects of the oceans. It is quite possible that dinosaurs lived on high mountains near the poles, and that only the lack of suitable deposits prevents us from knowing of them. If dinosaurs lived in polar mountains then, they may have experienced more severe winter conditions.

Extensive polar winter freezing was not inherently incompatible with Late Cretaceous world geography and atmospheric chemistry. The moderating effects of the low world topography and widespread seaways were apparently insufficient to overcome a high loss of heat to the polar night (Crowley et al., 1986; Schneider, 1987). Climatic models indicate that a massive increase in the atmospheric level of CO₂ has to be invoked to prevent widespread freezes in continental interiors well south of polar regions during the Late Cretaceous. Even this may not have prevented regular polar winter freezes. Aside from the large scale fluctuations noted above, it is possible that orbital cycles forced milder, shorter term polar climatic fluctuations similar to the rainfall cycles observed in the Mesozoic (Olsen, 1986).

Regardless of how cool Cretaceous polar winters did or did not become, other weather factors may have posed serious problems for thermoregulating animals, contra Axelrod's (1984) implication that temperature was the only critical weather factor affecting polar life. Polar winter winds were probably strong, albeit not as strong as today's, because the darkened pole acted as a giant heat sink (Schneider, 1987), and also because strong winds are necessary to explain the relatively moderate Cretaceous temperature gradient. As these air masses passed over the extensive mid-latitude seas, they would have picked up considerable moisture. This moisture would then precipitate out in periodic storms as fronts and low pressure air masses cooled upon entering the polar winter nights. Some of these storms may have lasted a few days each and/or were repeated every few days over extended periods of time. The paleoecological evidence confirms that the Cretaceous polar dinosaur habitats were well watered (Axelrod, 1984; Douglas and Williams, 1982; Roehler and Stricker, 1984; Spicer and Parrish, 1986). Warmer, wetter snowfalls could be more metabolically challenging than colder ones, because the former would supply more melting water for evaporative cooling. Perhaps worst of all would be a series of storms bringing in freezing or near freezing rain and breezes. The effect of rainstorms is persistently neglected in studies of dinosaur and other animal physiology. As noted by Bakker (1980), even warm monsoonal storms could have seriously taxed the thermoregulatory capacity of large-bulk homeotherms. No mathematical models of the Spotila et al. (1973) type have been constructed to explore these problems, and they are needed.

Finally, assuming that axial tilt has remained constant, the polar winter daylight was at best very short, and continuous nights could last from days to many months. Even the little, low angle sunshine available may often have been obscured by clouds, trees, and hills.

In summary, the bulk of the evidence indicates that Cretaceous polar winter conditions were broadly similar to those in today's temperate regions. Whether mild temperate or harsher models are the best is not certain, both may be appropriate if conditions fluctuated. An important proviso is that winter dark was more extended in Cretaceous polar winters than it is in modern temperate latitudes.

Implications of polar conditions for dinosaur physiology.—If dinosaurs had avian–mammalian physiologies, then the survival of small and big adults, and the latter's young, in even the harsher polar climatic scenarios, is fully explained. Seasonal insulation is not absolutely required on large dinosaurs for any of the current climatic scenarios—except for any that may have dwelled near any Antarctic ice fields—but it would have been helpful in the harsher scenarios. Insulation may have been needed on small dinosaurs, and probably would have been needed on small species. Either a tenrec–monotreme level of endothermy, or a more developed form as found in large marsupials, placentals, and birds, is plausible for polar dinosaurs, because both are good for coping with low external temperatures (Bakker, 1980). Polar dinosaur body temperatures may have been 27–30°C, as in tenrecs and monotremes, or up to 38°C, as in modern polar mammals and birds.

A second possible dinosaur physiology, in this case a “reptilian” one, is bulk endothermy. This has small dinosaurs and juveniles showing a low, reptilian grade, active metabolic rate, and the larger individuals having active metabolic rates converging with those of equal-sized endothermic homeotherms (Hotton, 1980). Since the large species had what were in effect avian–mammalian metabolic rates, it is plausible that they could have been seasonally insulated. All in all, the larger individuals should have been able to weather the severe polar winters in the open. The smaller dinosaurs could have sought refuge and hibernated, as did the similar sized reptiles living near the poles at this time and in the early Tertiary. However, it is unclear whether medium-sized individuals would have had fast enough metabolic rates to remain exposed, or been small enough to hibernate. More importantly, the juveniles and adults of big species would be unable to stay together, because the former's low metabolic rates would have forced them to hibernate. This is unsatisfactory because much evidence indicates that hadrosaurs, ceratopsians, and theropods were social and took care of their young for extended periods of time (Ostrom, 1972; Currie, 1984; Horner, 1984). Although dinosaurs probably grew rapidly (Ricqles, 1980; Bakker, 1980; Reid, 1984; Currie, 1984; Morell, 1987), it would still have taken well over a year for a two-plus-ton dinosaur to reach a large enough size to either be a fully effective bulk endotherm or leave its parents. In particular, bonebeds, including the one in the Arctic, confirm that ceratopsian and hadrosaur juveniles stayed with the adults at least until half-grown, and that it took about two years for them to reach half-adult dimensions (Currie, 1984; Morell, 1987; Horner, personal commun.). Polar dinosaurs probably bred their young before or at the beginning of summer, when food would be becoming most abundant. The juveniles would still be modest sized and accompanying their parents by their first winter, and perhaps additional winters.

A third possible, and a second “reptilian,” dinosaur physiology is bulk homeothermy. In this, active metabolic rates were low for all sizes, about seven to ten times lower than in big mammals of the same size. In general, large, low metabolic rate animals can maintain a body temperature a few degrees above average air temperatures when abundant sunlight is not available (Spotila et al., 1973; Hotton, 1980; Brisbin et al., 1982). Polar dinosaurs needed to operate most effectively during the warm, food abundant summers. So their preferred body tem-

peratures should have been fairly high, about the same as in more equatorial dinosaurs. This should have been from 30–38°C, the range seen in diurnal reptiles living in warm regions (Colbert et al., 1946; Templeton, 1970). As declining air temperatures and sunlight become unable to support the subject's preferred body temperature, activity levels progressively decline until torpor occurs. The uniquely cold-adapted tuatara remains active when body temperatures are as low as 6°C (Bogert, 1953; Templeton, 1970). However, tuataras normally operate at low body temperatures of 20°C or less. In addition, tuataras and most other cold-adapted reptiles have relatively underdeveloped metabolic and circulatory systems, including three-chambered hearts, so they may not be the best model for ectothermic dinosaurs.

The dinosaur's closest living ectothermic relatives are crocodilians. Their four-chambered hearts and sophisticated lung systems show they are more sophisticated physiologically than other living reptiles. Dinosaurs must have had four-chambered hearts in order to pump blood up to their high held heads (Ostrom, 1980). So a better model for polar ectothermic dinosaurs may be the northernmost taxon of living crocodilian, *Alligator mississippiensis* prefers body temperatures of 32–35°C (Colbert et al., 1946). It becomes largely inactive and sluggish when body temperatures drop below 16°C (Colbert et al., 1946; Axelrod, 1984). That *Alligator* has failed to develop a better active cold tolerance during the 35 million year cooling trend since the Eocene suggests that this may be the minimum temperature at which relatively sophisticated, and hence inherently hypothermally sensitive, ectothermic archosaurs can operate. Crocodilians can survive water temperatures, and presumably body temperatures, as low as about 1–2°C (Hagan et al., 1983). The alligator's basal temperatures for activity and life can be used as minimums for low metabolic rate dinosaurs.

The use of crocodilians as thermoregulatory models for ectothermic dinosaurs is complicated by the fact that even large crocodilians often retreat to relatively warm dens or waters when cold air or precipitation induced evaporation threaten to drop temperatures too far (Minton and Minton, 1973; Brisbin et al., 1982; Hagan et al., 1983). Brisbin et al. (1982) found that in extreme cases alligators survive air temperatures lower than –8°C and ice covers by hibernating in water that is 1–2°C. In this regard, large crocodilians may be somewhat superior to physiologically similar terrestrial animals in their ability to weather cold conditions.

June through August temperatures averaged as high as 20°C near the Late Cretaceous poles (Axelrod, 1984). Spotila et al. (1973) calculated that such temperatures would support an ~27°C body temperature in a large bulk homeotherm. However, polar summer solar radiation lasts much longer than in the model of Spotila et al. (up to 24 hours a day), so bulk homeothermic dinosaurs should have been able to maintain a plus 30°C constant body temperature. In spring and fall, temperatures and sunlight were less, but probably sufficient to maintain activity. From October through March, average temperatures may have been below 15°C and sunlight would have been much more limited, so activity levels would have declined drastically. If Axelrod's 10°C average for Cretaceous polar January temperatures is accepted, and with sunlight virtually absent, then bulk homeothermic dinosaurs would have experienced extremely low activity levels and torpor. As in the bulk endothermy scenario, small dinosaurs could have hibernated in dens. However, the multi-ton adults could not screen themselves from storms. Animals that size cannot lay on their sides for extended periods because the pressure on the lowermost lung results in its congestion (Taylor, 1976). The relatively tall, narrow bodies of procumbent dinosaurs could have been well ventilated by breezes. So exposed, the combination of wind chill factors with the pow-

erful coolant effect of evaporating, extended rains or wet snows could drive effective temperatures on a dinosaur's skin to well below freezing, and drop its body core temperature near to or below freezing. This would be true even when ambient air temperatures were 5–10°C and the superficial body layers were being used as an insulative shell. If one storm did not accomplish this chilling effect, a series of storms following one another too closely to allow the animal to recover might do so. This would be lethal, and if it happened frequently throughout the polar regions it could have had a devastating effect upon polar dinosaur populations. Note that storm-induced flooding would hinder the use of water as a thermal buffer. If climates were as harsh as indicated by Parrish et al. (1987), then nonstorm conditions could drop body temperatures below freezing.

Even if not directly killed by winter conditions, torporous large dinosaurs would be vulnerable to competition from, or predation by, any very large dinosaurs that developed a more active metabolism. They would also be vulnerable to predatory mammals or flightless birds that grew to large size. Since there is a consensus that small theropods had heightened metabolic rates (see above), they too may have had the potential to become large polar winter predators. The Late Triassic to latest Cretaceous may have offered 160 million years for such events to occur. Yet another nonlethal problem for large, low metabolic rate animals might be that the summer growing season near the poles was too short to sustain proper growth (Hutchison, 1982; Hagan et al., 1983).

Tests of whether bulk homeothermic archosaurs can cope with polar conditions.—Tests of the ability of very large (over 500 kg) known ectotherms to tolerate Late Cretaceous type polar winters are available. The first is provided by the middle to late Permian pareiasaurs of Africa and Europe, which reached up to 1,000 kg. They are sometimes common in South African deposits that were then very close to the South Pole (Bakker, 1975). A great glaciation had ended by the middle Permian, so polar winters were relatively mild, with regular freezes and snowfalls possible (Parrish et al., 1986). However, pareiasaurs were so different from dinosaurs that their ability to withstand such winters may not be comparable. Pareiasaurs were archaic reptiles that must have had three-chambered hearts, hence the polar examples may have been as cold adapted as tautaras. Their short necks, tails, and appendages and semispherical bodies may have rendered them less vulnerable to heat loss than the more slenderly built dinosaurs. Being low-slung, broad-bodied, swamp dwellers (Houghton and Boonstra, 1929–1934), they may have been able to enhance their resistance to freezing conditions by seeking partial shelter in swamp waters and muds. This also would have helped isolate them from the therapsid predators of the region, which may have had tenrec-type physiologies (Bakker, 1980). Further protecting the pareiasaurs from predation may have been their much larger size relative to the more common species of predatory therapsids (Bakker, 1975) and their substantial armor.

Turtles are another group of known ectotherms found in Late Cretaceous–Eocene near-polar or polar regions. Turtles with shells up to 1 m across are known from the Late Cretaceous of Alberta, but they were flat-shelled, semiaquatic, and able to seek shelter and hibernate in bottom muds, like the big snapping turtles of Massachusetts (Mlynarski, 1976; Fox, Brinkman, and Currie, personal commun.). Terrestrial, arched-shelled turtles that lived at the locations under consideration, such as the Cretaceous *Boremys* of Alberta, and small Eocene Arctic tortoises, were much smaller and could easily shelter themselves.

During Pleistocene interglacials, giant tortoises of about 100 kg lived as far north as central Illinois (Mlynarski, 1976; Hibbard, 1960; King and Saunders, 1986). Living nonburrowing

and nonaquatic species of large and giant tortoises cannot tolerate the freezes of colder Florida winters (Hibbard, 1960), and Hutchison (1982) suggested that giant tortoises cannot tolerate average winter temperatures below about 10°C. The ultimate cold resistance of giant northern tortoises is not certain because the living species come from a few tropical islands. Human predation may be responsible for the elimination of giant tortoises from cooler continental climes (Martin, 1984). Giant tortoises may have been able to tolerate sharper temporary temperature drops than ectothermic dinosaurs because of a less derived physiology and because their thick surface armor may have acted as a partial thermal shell against evaporative and wind-chill cooling. The extensive armor also made them invulnerable to attacks by big mammalian carnivores. Still, long-term freezing would likely be lethal, and there are arguments based partly on the giant tortoise's presence, as well as floral data, that past interglacials were much milder and more equable than today (Hibbard, 1960; King and Saunders, 1986). In that case, the northern giant tortoises did not experience extended freezing conditions. Giant tortoises offer evidence that big ectotherms do not readily tolerate polar conditions.

Perhaps the most useful test of the problem centers around crocodylians. To date, the only known polar crocodylians are small early Tertiary forms (Estes and Hutchison, 1980). Examples of the size of *Alligator mississippiensis* or *Crocodylus niloticus* have not been found. No crocodylians have been reported from the Cretaceous Arctic (Brouwers et al., 1987; the report of a large "crocodile-like" reptile in Dusheck, 1985, is erroneous?, Clemens, personal commun.) or Antarctic regions (Douglas and Williams, 1982). Small crocodylians were generally the case in the Campanian and Maastrichtian communities of Alberta (Steel, 1973; Currie and Brinkman, personal commun.). These small crocodylians were reminiscent of modern *Alligator sinensis*, which refuges in dens and hibernates through the cool eastern Chinese winter (Minton and Minton, 1973). The only exceptions are some fragmentary remains of a large crocodylian of unknown type from the early Campanian Milk River Formation, just above the Alberta–Montana border (Fox, personal commun.).

Giant, multi-ton phobosuchid crocodylians were present in the Campanian and Maastrichtian of much of the western United States as far north as Montana, including the U.S. portion of the Judith River Formation (Steel, 1973; Baird and Horner, 1979). Extensive prospecting has failed to find them in Alberta, including its Judith River beds (Brinkman, personal commun.), and they are so far lacking from any sites further north. This is significant because the Campanian–Maastrichtian formations of the Arctic and Alberta supported rich dinosaur faunas similar to Montana's. Also, the Arctic, Alberta, and Montana sediments were deposited under broadly similar, well-watered coastal floodplain and deltaic conditions, with many large rivers available for giant crocodylians (see above references). The absence and presence of phobosuchids in the Alberta and Montana portions, respectively, of the Judith River—whose dinosaur faunas and sediments are very alike—is especially significant. As a test of the ability of ectothermic archosaurs to cope with polar conditions, giant crocodylians indicate that even southern Alberta winters were too cool and sunless to support such creatures. One possibility is that the Alaskan–Canadian winter weather was directly lethal to crocodylians too gigantic to den-in during the winter. This is most plausible in the more northern locales, especially if the harsher climatic scenarios are correct. It is less so in Alberta where relatively warm waters should have been available as a buffer against cold and precipitation. In that case, more metabolically active tyrannosaurs may have waded in the shallows in the winter, hoping to stumble upon hibernating

phobosuchids. Low body temperature alligators are so lethargic that 100+ kg specimens can be readily captured and handled by humans (Colbert et al., 1946; Brisbin et al., 1982). Multiton endothermic tyrannosaurs would have had little trouble dragging torporous phobosuchids ashore and dispatching them. Such depredations may have been at least partly responsible for the giant crocodylian's fauna to inhabit northern regions, especially Alberta.

Phobosuchids were relatively common only in such southern locales as Texas. In Montana and Wyoming they were rare, and this indicates that winter conditions there were marginally able to support very large bulk homeothermic archosaurs that could retreat to water when necessary. It is possible that giant crocodylian habitation this far north was cyclical, tied to periodic warming trends. Also note that the semiaquatic, short-limbed crocodylians may have been unable to migrate substantial distances, unless they used the coastal waters as a swimming route. The modern semimarine, estuarine crocodile shows such a tolerance for salt water.

Like phobosuchids, giant sauropod dinosaurs are also absent from the Late Cretaceous communities of the Arctic, Alberta, and perhaps even Montana and Wyoming (Russell, 1984). Unlike crocodylians, however, sauropods are animals of less certain physiology that appear to have preferred habitats with a sharp dry season and open forest canopies. Late Cretaceous sauropods were present in such interiorly placed formations as Mongolia's Nemegt and Utah's North Horn, which were substantially drier than the coastal habitats (Osmolska, 1980; Bakker, 1986; Lehman, 1987). Perhaps the more dense forest canopies of the well-watered Alaska-Wyoming coastal floodplain were too great a hindrance to the movement of these long-necked creatures. Giraffes likewise prefer open, seasonally dry woodlands. Seasonally dry polar dinosaur habitats have not been found, so the true reason for the sauropod's absence, whether physiological or choice of habitat, is not yet tested.

USING PHOBOSUCHID CROCODYLIANS TO EXAMINE ARCTIC CLIMATES

More evidence is needed, but since phobosuchids were very large archosaurs that were definitely ectothermic, uninsulated, and lacked heavy, turtle-grade armor, they may be good paleoclimatic indicators. This possibility is confirmed by the way in which the phobosuchid's decrease in abundance was paralleled by the decreasing abundance of evergreens, winter light, and winter temperatures approaching the North Pole. Phobosuchids therefore strengthen the observation that such classic southern Alberta sites as Dinosaur Provincial Park were laid down under conditions that were essentially subarctic, albeit in the Cretaceous style.

THE PROBLEM OF MIGRATING POLAR DINOSAURS

Migration distances.—The polar dinosaurs' alternative to wintering over was to migrate towards the equator and back again (Figure 3; Russell, 1973; however, Russell, personal comm., no longer fully supports this scenario; Hotton, 1980; Axelrod, 1984; Parrish et al., 1987). Note that Hotton, who has postulated polar dinosaur migration in the greatest detail, envisioned bulk endothermic dinosaurs as making the migration. Hotton (1980) also asserted that the heavily armored ankylosaur and nodosaur dinosaurs were unable to migrate long distances. However, armored dinosaurs had moderately long, fully erect limbs, similar in most regards to other large dinosaurs, and were fully competent walkers and runners (Carpenter, 1982; Paul, 1987b).

If big polar dinosaurs were bulk homeotherms, how far north

could they be in the winter and still keep warm? Phobosuchids are the best model available. But it is unlikely that on the one hand dinosaurs used water as a thermal buffer, while on the other hand tyrannosaurs may have been suppressing Alberta's phobosuchid populations. The combined scarcity of phobosuchids and evergreens can be taken to indicate that at the Alberta-Montana border winters were unable to support large ectothermic dinosaurs. It is here inferred that the dinosaur's inability to employ water as a thermal refuge would have forced them to winter even further south than the northernmost giant crocodylians, at perhaps the Montana-Wyoming border. If so, then some of the dinosaurs known from Montana may have been winter residents that summered in Alaska (Figure 3). Since Montana was then at 55°N by Andrew's (1985) measure, this latitude is considered the highest for wintering ectothermic dinosaurs.

To the south of the north Alaskan Cretaceous dinosaurs were mountains and ocean (Figure 1). Note that Alaskan dinosaurs had the option of migrating either further into North America or into Asia. North America's coastal floodplain seems to have offered the easier route southward, so it is assumed that the dinosaurs migrated southeastward along the floodplain to reach the Montana-Wyoming border. The shortest path around the curve of western highlands was some 3,700 km long. Detours around high topography, uncrossable watercourses, and the sometimes dense vegetation could increase this value by perhaps a quarter, so total roundtrip distance would have been about 9,200 km. In order to avoid crowding together at the Montana-Wyoming border, summer dinosaur populations south of Alaska would probably have migrated in a parallel displacement pattern (Hotton, 1980). Although migration distances would dwindle progressively southwards, some populations could have traveled as far south as New Mexico. Note that if Bering dinosaurs also migrated down the American coastal floodplain, then they may have had to migrate even further than the Alaskan populations. Even if the spin paleopole was closer to the paleomagnetic pole than Andrews (1985) calculated, and the summering locale was at 55°N, then the Bering dinosaur populations would still have to migrate about 9,200 km. This distance is also only a little more than the north-south distance, with detours, that dinosaurs in Greenland or north-central Canada would have had to take, or the southern dinosaurs from the South Pole to 55°S. Hotton (1980) postulated dinosaur migrations of similar magnitude (6,400 km roundtrip distance not including detours). Axelrod (1984) and Parrish et al. (1987) suggested that dinosaurs could have wintered at the polar circles. This, of course, presumes that they could tolerate a near absence of sunlight for extended periods.

The distance calculated here equals a trip from New York to Los Angeles and back. Marine swimmers and flying creatures can migrate even greater distances because of their relatively low cost of travel per unit distance, but, except for technology exploiting humans, no living land animal travels so far in a single year (even cross-continent hikers have always used at least some roads and prepackaged food). Notably, migrations are longest for Arctic species, with annual roundtrip migration distances being 2,000–2,500+ km for caribou and polar bears, 500 km for Serengeti wildebeest, and 150 to perhaps 1,250 km for African elephants (Banfield, 1974; Stirling and Kiliaan, 1980; Maddock, 1979; Laws et al., 1975; Eltringham, 1982).

Migrating baby dinosaurs.—Brouwers et al. (1987) suggested that presence of young Arctic hadrosaurs hindered long migrations of their species. However, this is not the case with the young of caribou, polar bears, and wildebeest, which accompany their parents on long migrations. As noted above, hadrosaurs

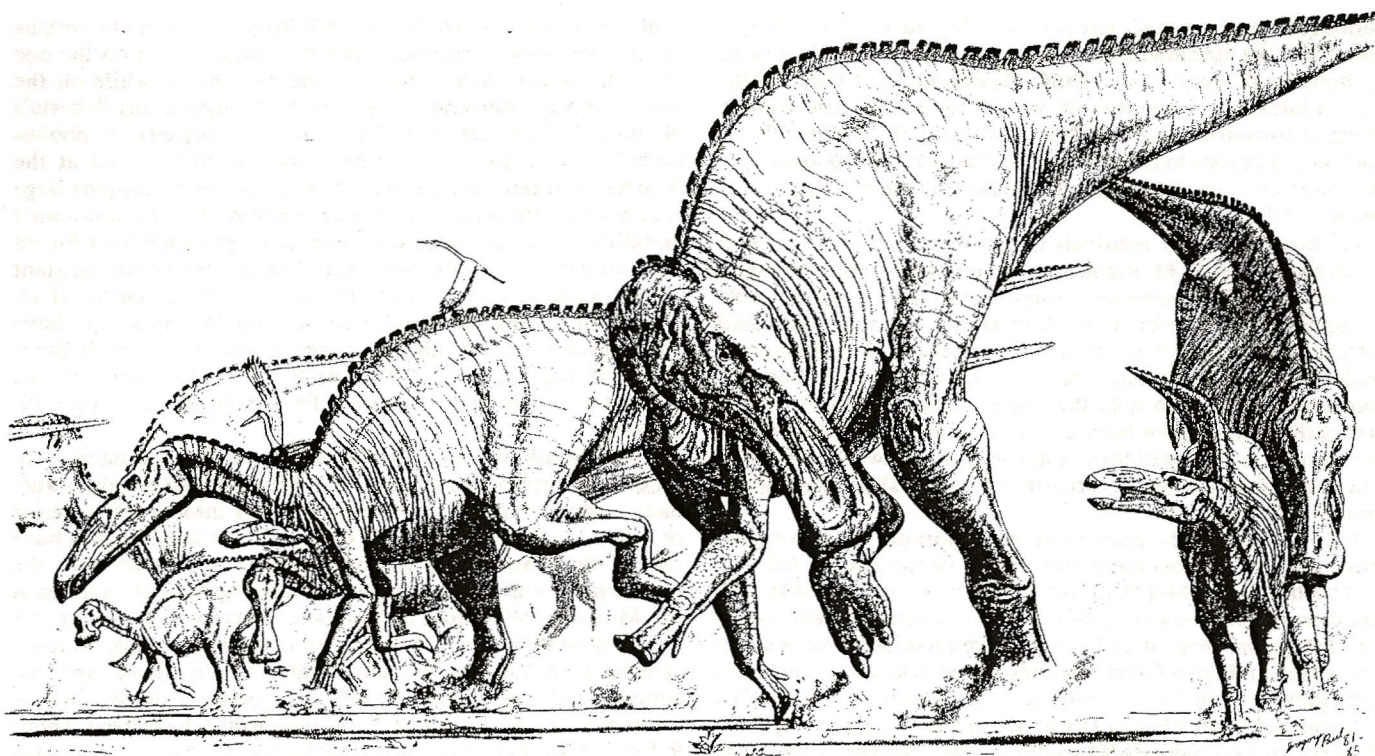


FIGURE 3—If polar dinosaurs migrated, then the Maastrichtian duckbill *Edmontosaurus copei* could have been a winter resident of Montana, where it is found, and summered in northern Alaska. The well-developed limbs of both adult and young were good for long distance travel, but prohibitive energy costs made such continent-length migrations impractical (see Figure 1).

grew rapidly. Assuming Arctic species hatched in the spring in northern rookeries, by the time of their fall migration they may have been as large as or larger than the migrating juveniles of caribou, wildebeest, etc. The limbs of hadrosaur youngsters would have been well developed by that stage (Figure 3), and energy consumption per unit of distance traveled is about the same relative to metabolic rate regardless of size (both scale close to $M^{0.75}$; Fedak and Seeherman, 1979; MacMahon, 1984). So hadrosaur young should have been able to keep up with the adults (Figure 3).

Migratory energetics.—Energetic concerns may have limited the migrations of adults and juveniles alike. For a 2.5 ton dinosaur, the annual cost of migrating 9,200 km would be about 10,800,000 kcal/year (from Fedak and Seeherman, 1979, with locomotory cost scaled elastically to $W^{0.75}$ as per MacMahon, 1984). The ultimate migratory abilities of large land ectotherms are not known—all the living species (tortoises, komodo monitors) live on small islands—but it is probably limited. A 2.5 ton bulk homeothermic dinosaur would have an active yearly energy budget of about 1,850,000 kcal (Bennett and Dawson, 1976), only a sixth of the calculated yearly migration expenditure. It is questionable whether a low metabolic rate ectotherm could boost its total metabolic rate to what was, in effect, an endothermic level; no known living ectotherm does so. Even if the distance traveled was only half that estimated here, an ectotherm would be hard pressed to meet the journey's metabolic needs. If migratory energy costs were limited in order to only double total yearly metabolic expenditures, then total roundtrip distances for an ectotherm would be about 1,500 km, insufficient to escape polar winter regimes.

If ectothermic polar dinosaurs could produce nearly as much

energy as endotherms, it can be asked why they did not develop the body temperature control systems needed to remain near the poles? Then they could have withstood cool winters instead of having to burn the same energy migrating away from them.

In contrast to bulk homeothermy, either Hotton's type of bulk endothermic dinosaur or an endothermic homeothermic dinosaur of 2.5 tons would have a yearly energy budget up to 10 times greater (Gessamen, 1979), and might have been able to handle the extra energy expenditure of hyperlong migrations. Tenrec-level endothermy could provide sufficient energy. However, bulk endothermic adult dinosaurs would still face the problem of their low metabolic rate juveniles, which would be unable to keep up with the former. Again, it is endothermic homeothermy that offers a full basis for extended migrations of polar dinosaur adults and their juveniles.

It is, however, improbable that even fully endothermic dinosaurs would have practiced such journeys. After all, caribou, musk oxen, and wolves withstand much harsher modern Arctic winters, in which the flora is far more severely limited than it was in the Mesozoic. Rather than expend great amounts of energy migrating continental distances, it is much more likely that polar dinosaurs built up fat reserves for the winter. The fat could have doubled as insulation. Polar dinosaurs could have supplemented their energy needs with the twigs and bark of dormant deciduous vegetation, the needles and leaves of evergreens, and subaquatic rhizome-mat vegetation (Brouwers et al., 1987). The moas of New Zealand lived year round on a diet of nondormant twigs (Trotter and McCulloch, 1984). Evergreen conifers and dicotyledons (in austral regions) were present near the poles, especially in Late Cretaceous southeastern Australia (Douglas and Williams, 1982; Axelrod, 1984). As noted in Axel-

rod (1984), evergreen conifer needles probably maintained a high nutritional quality in winter. Some modern animals browse on conifers regularly or during the winter (Ullery et al., 1964; Fenna and Boag, 1974), confirming that polar dinosaurs may have been able to also. Russell (1973) suggested that the big-eyed dinosaurs preferred well-lit conditions, and that they migrated away from winter darkness. But large eyes can enhance dim-light-condition light gathering abilities too, so dinosaur eye size does not tell us whether their owners migrated or not.

Other migratory factors.—Feeding time versus migrating time may also pose a problem for large endothermic herbivores. If a polar dinosaur spent eight months a year migrating 9,200 km per hour, at a typical walking speed of 5 km/hour, it would have averaged nearly eight hours a day migrating. Large endotherms spend up to 14 hours each day searching for and browsing upon suitable plants (Guy, 1975), and much of the rest of the day is devoted to obtaining water, resting, and other activities. Even if some feeding occurred while migrating, it is questionable whether the extra time load of migration could have been accommodated.

Regarding low metabolic rate dinosaurs, Cowles and Bogert (1944) showed that predators and herbivores of such physiology can digest food only when their body temperatures are in the upper portion of their tolerance range. Since these temperatures must have been high in ectothermic dinosaurs in order to accommodate summer feeding (see above), then the relatively low body temperatures that would have resulted from wintering over would have prevented them from feeding during that season. This would not have been a serious problem, for the relatively low food requirements of ectotherms gives them a high tolerance for extended food deprivation. This tolerance is reinforced if extensive fat deposits are available to draw upon and if low body temperatures further reduce metabolic rates.

In any case, not all Arctic dinosaurs may have been able to migrate away from polar winters. In middle Campanian–early Maastrichtian times the north-central Canadian landmass, Keewatin, was isolated from western North America by the broad interior seaway, and seems to have been cut off from eastern North America by a narrower seaway crossing the Hudson Bay area (Figure 1; Williams and Stelck, 1975). If dinosaurs were present in Keewatin at that time, then they may have been barred from migrating further south than the Arctic Circle. The mid-Cretaceous dinosaurs on Spitsberg may have migrated south via Greenland. Both they and any Late Cretaceous dinosaurs that were on Greenland could have reached 55°N, but the summer dinosaur populations would have been crowded together at the island's southern tip.

The problem of whether polar dinosaurs were or were not migratory can be examined by comparing the degree of taxonomic differences between polar and neighboring populations. Migration might cause a high degree of mixing between adjoining populations. This may not be a simple problem, however. Habitat differences can cause even nearby locales to have very different faunas, while distant faunas can be very alike if the habitat's rainfall and floral patterns are similar, even if migrational intermixing does not occur. It is possible that the Alaskan dinosaurs were cold-adapted subspecies of some of the same species present in Alberta.

Short migrations.—Of course, some polar dinosaur populations may have made shorter, caribou- or polar bear-length migrations in order to take advantage of seasonal changes in regional conditions. In particular, higher, cooler elevations attractive in the summer may have been abandoned for more comfortable lower altitudes in the winter.

POLAR DINOSAUR EVOLUTION

For typical reptiles, the polar regions have always represented the "edge" of their world, or have been beyond its borders. At any given time, including the Mesozoic, only a few species have been able to move away from the abundant diversity of reptiles paralleling the equator into the winter darkness and cold. This is quite different from mammals, which even at the height of the Pleistocene produced an array of cold-tolerant species. The apparent diversity of what may have been a permanent polar dinosaur fauna suggests that their polar populations were a flourishing and integral part of their world population, one that may have produced an array of aboriginal polar species, some of which may have invaded more equatorial climes. Notably, Arctic plants may have formed such a center of evolution and radiation (Hickey et al., 1983; Hickey, personal commun.), although this thesis is disputed by Spicer et al. (1987). If polar dinosaurs were evolutionarily so active, then they were, once again, more like mammals than reptiles.

POLAR DINOSAUR EXTINCTION

Introduction.—Over the years a worldwide decline in temperatures at the end of the Cretaceous has been cited as the reason for the dinosaur's extinction. A more recent variation argues that a short-term false "winter" or "fall," created by a global dust cloud thrown up by the impact of a giant meteorite or intense vulcanism, destroyed the dinosaurs via cold and darkness. It is beyond the scope of this paper to examine these theories in full detail, the following are some observations on how polar dinosaurs fit into the problem.

Gradual changes.—Some have suggested that a relatively gradual temperature decline at the end of the Cretaceous, and/or increased seasonability, directly afflicted the dinosaurs. This view has been applied to both endothermic (Russell, 1965; Bakker, 1972) and essentially ectothermic (Axelrod and Bailey, 1968; Benton, 1979) dinosaurs. That dinosaurs inhabited relatively cool polar regions strongly indicates that they should have been thermoregulatorily able to cope with the modest and gradual temperature declines often thought to have occurred at the end of the Cretaceous. This is especially so in view of the fact that most dinosaur populations were free to shift equatorwards in step with their preferred temperature regime. This was dramatically demonstrated in the Pleistocene when relatively tropical interglacial hippopotamus communities repeatedly withdrew from England and Europe as cold conditions arrived (Grayson, 1984), were replaced by woolly mammoth communities moving in from the north, and then moved back again as warmer conditions returned. The north-south trend of easily traveled flatlands in many regions, such as western North America, would have facilitated such population shifts in the Cretaceous.

Others argue that declining and/or more seasonal terminal Cretaceous temperatures altered the flora to the dinosaur's detriment (Van Valen and Sloan, 1977; Stanley, 1987). Interestingly, the changes observed in western North American floras seem to lessen proceeding north from New Mexico to Alberta (Wolfe and Upchurch, 1986). The changes in polar floras are not well documented, but it appears that already cool-adapted deciduous plants were better able to weather the supposed temperature declines. If so, then it can be argued that polar floras should have acted as a botanical reserve able to support dinosaurs during the crisis, and then recolonize more southerly climes in tandem with the dinosaurs.

Catastrophic changes.—The shock effect of an extremely sud-

den decline, albeit a brief one of few months duration, in temperature, equability, and sunlight due to a dust and soot cloud induced winter may be more detrimental to life than a slow, long-term cooling of equal or lesser magnitude (Silver and Schultz, 1982; Alvarez, 1986; Alvarez, 1987; Officer et al., 1987; Courtillot and Besse, 1987; Crutzen, 1987). An important problem is that animal populations cannot move rapidly enough to avoid such changes. For polar animals the onset of winter conditions in spring, summer, or fall could leave them and the plants they depended upon unprepared to cope with the kind of conditions they would be ready for by true winter. If the impact or eruption occurred in winter, then the increased degradation of conditions could overtax the plant's and animal's wintering abilities.

However, this is by no means certain. It is difficult to assess the full effects of a terminal Cretaceous meteoritic or volcanic dust cloud, because the false winter models have so far been based on a modern nuclear war. More refined models indicate that a nuclear winter would be less intense than originally thought, and might be better called a false "fall" (Berger, 1986; Schneider, 1987). On the other hand, the amount of fine-grained material that would be injected into and suspended in the atmosphere by a giant impact or by intense vulcanism, and from subsequent wildfires, would be much greater than in a nuclear war (Silver and Schultz, 1982; Berger, 1986; Crutzen, 1987). How much difference this would make is not clear, because the solar screening performance and longevity of a nuclear smoke cloud is thought to be roughly similar to that of a meteoritic or volcanic dust cloud (Silver and Schultz, 1982; Berger, 1986). Also unclear is whether or not the Cretaceous-Tertiary distribution of continents, topography, and climatic systems would modify the extent and severity of a false winter. In this discussion, nuclear "winter/falls" (Berger, 1986; Schneider, 1987) are used as the baseline for much of the following—with the exception that a nuclear soot cloud would be largely restricted to the Northern Hemisphere, while the terminal Cretaceous dust and soot cloud was worldwide in extent.

Assuming axial tilt was unchanged at the end of the Cretaceous, winter polar sunlight could not be decreased much or any more than it already was in daily intensity. So a dust cloud induced collapse of the photosynthetic based food chain would not occur. Temperature declines should have been relatively modest near the poles, especially along coastlines (Berger, 1986; Schneider, 1987). Wintering coastal Cretaceous polar faunas and floras might therefore have been highly resistant to a false winter or fall. In this case, they could have constituted a reserve population able to recolonize the rest of the world. Especially small, insulated theropods could have fed on the carcasses of large dinosaurs killed by a catastrophe and on the surviving small reptiles and mammals. This would be most plausible if the true winter were a mild one and the dust cloud arose in early winter. In this case, a false winter might only degrade the situation to the status of a severe winter that the resident dinosaurs and plants could cope with.

Even if dark and cooling occurred during a polar summer, the deciduous flora and dinosaurs should have been much more able to survive the unexpected winter conditions than more equatorial species. The combination of a normal winter, followed by a false winter in the summer, followed by a normal winter would most seriously stress a polar fauna and flora.

However, such an extended winter would not happen at both poles, because the effects of an impact or eruption would have been asymmetrical in the two hemispheres. While one pole might lose a whole summer between two winters, the other

would only experience a winter harsher than it would otherwise have been. The degree of asymmetry would be highest if the impact or eruption occurred in the winter or summer season, less so in the spring or fall season. Whalley (1987) commented on the asymmetric effects of an impact in regard to Cretaceous insects, and Wolfe (1987) suggested that Southern Hemisphere Cretaceous-Tertiary plants were far less affected by a meteoritic catastrophe than was the northern flora.

A greenhouse effect may have followed the initial temperature drop, increasing world temperatures perhaps 10°C for hundreds or thousands of years (Crutzen, 1987). In the winter this would only serve to lift a polar region's temperatures towards more comfortable levels. Summer polar temperatures would have been boosted to a mean of perhaps 30°C, with occasional highs reaching 35–40°C. This may have been uncomfortable or even somewhat stressful for dinosaurs used to cooler conditions. But since the temperatures of their bodies were likely to have been as high as 38°C, and their uninsulated bodies could readily shed excess heat, such temperatures would hardly have been lethal. Shade and water also would have provided relief. The increased summer temperatures would have promoted plant growth.

Droughts that might accompany a false winter could be limited to the equatorial monsoons (Berger, 1986), or they might occur in the polar winter when plants were already dormant. On the other extreme, excessive snowfalls may have blanketed continental interiors (Silver and Schultz, 1982), but not the warmer coastlines where many polar dinosaurs lived.

Other possible aftereffects of an impact or eruption could last from years to millennia (Officer et al., 1987; Crutzen, 1987). These include extremely poisonous air pollution, acid rain, ozone layer depletion, and wildfires, among others. These factors would affect polar dinosaurs in much the same manner as more equatorial species. For example, although excessive summer ultraviolet radiation levels would be lessened by the lower angles of summer sunlight above the polar circles, this would be countered by the relatively longer daylight hours.

Yet, the above problems may not be as daunting as they appear. Until now, examination of the impact scenario of dinosaur extinction has been largely limited to the end of the Cretaceous, but important tests are provided by other giant impacts during the dinosaur's reign (Olsen and Sues, 1986; Boslough, 1987; Hsu, 1987; Paul, 1988). The eastern Quebec Manicouagan impact took place in the Late Triassic or Early Jurassic, perhaps at the boundary. Although as large as or larger than the supposed Cretaceous impact, no extraordinary extinction of dinosaurs is discernible at that time; indeed, at least some genera survived. Dinosaurs also survived another possible impact in the Late Triassic, another in the Early Jurassic, and the digging of the giant Duolun crater in the Late Jurassic in China, and more such events are likely to be found. Polar dinosaurs may have been survivors of these great meteorite falls, perhaps the sole ones. The scale and effects of vulcanism during the dinosaur era have not been closely examined. The possibility that the terminal Cretaceous event was larger than thought, that there were multiple impacts or eruptions, or that an impact led to multiple eruptions (Alvarez, 1986; Officer et al., 1987) further confuses the issue.

The apparent ability of dinosaurs to weather over polar winter coolness and dark, and their probable endothermy, does not prove that they could have survived a meteoritic or volcanic winter, but it does challenge the concept (Clemens and Allison, 1985; Brouwers et al., 1987). That a greenhouse effect would be buffered in polar regions implies the same. Officer et al. (1987) noted that those animals that did survive the effects of a volcanic

cooling would most likely be those from more polar latitudes. Clearly the problem is very complicated, and the possibility that polar regions acted as a dinosaurian refuge has received insufficient attention. There is a great need for paleoclimatic models to directly address this complex of problems.

CONCLUSIONS

The deciduous flora and lack of giant phobosuchid crocodilians from Late Cretaceous Alaska to northern Alberta suggest that the winter climate included extended dark, light frosts, and occasional snowfalls, if not harsher conditions. The same two factors also support the placement of southern Alberta just south of the Paleo-Arctic Circle, because only high latitudes could create such conditions on a coastal floodplain when the general world climate was so warm. That the region was as far south as 45°N is unlikely.

In the absence of any direct evidence of a winter pelage, the naked skin known for some large Arctic dinosaurs can be taken as very tentative evidence that Mesozoic polar climates were more moderate than at present. However, since we do not know a priori the physiology of dinosaurs, the absolute nature of polar dinosaur winter insulation, or whether polar dinosaurs wintered over or migrated, they cannot be used as proofs of past polar environments or axial tilts at this time. If they are shown to be endothermic and at least seasonally insulated, then they never can be.

The cold and low light-coping abilities of polar dinosaurs challenges the concept that a gradual temperature decline caused the destruction of dinosaurs. It also questions whether a sudden drop in temperatures and sunlight due to an extraterrestrial impact or volcanism was the extinction agent. Likewise, a rise in temperatures would do little, if any, harm to polar dinosaurs.

Cretaceous polar climates can be used to explore dinosaur physiology. Even the milder winters postulated by some would have spawned cooling storms probably intolerable to large bulk homeothermic dinosaurs, or to social bulk endothermic dinosaurs accompanied by their young. If winters were harsher, as was possible, then this is even more true. Nor could such dinosaurs successfully migrate away from polar winters. The absence of giant crocodilians near the Cretaceous poles tentatively confirms that polar winters were too harsh for ectotherms of such size. That dinosaurs of similar bulk were able to inhabit the same polar locales in abundance indicates that they were more endothermic than typical reptiles. This is true whether polar dinosaurs used higher metabolic rates to tolerate the winters or migrated away from them. Unlike alternative physiologies, only avian-mammalian endothermic homeothermy of at least the tenrec level offers a full explanation of how both large dinosaurs and their juveniles could either cope with the winters, whether they were relatively mild or harsh, or mount hyperlong migrations away from them. Endothermy also gave small adult dinosaurs the option of either staying highly active or of hibernating through the polar winter. The possibility that ecological factors aside from winter cold may have barred sauropods from sampled polar sites complicates investigation of that group's physiology.

If polar dinosaurs were permanent residents, then they may have been a center of dinosaur evolution, one that may have contributed to more equatorial faunas.

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