Late Cretaceous Vertebrate Fossils from the North Slope of Alaska and Implications for Dinosaur Ecology: Comment & Reply

PALAIOS, 1989, V. 4, p. 298–300

COMMENT BY:
GREGORY S. PAUL
3109 N. Calvert St., Side Apt.
Baltimore, MD 21218

Recently Parrish et al. (PALAIOS, v. 2, p. 377–389) concluded that ectothermic dinosaurs may have been able to tolerate Mesozoic polar winters. This is contrary to Paul's (1988) findings that endothermy at at least the tenrec level would have been necessary for polar dinosaurs. This note examines some of the issues raised by Parrish et al.

Parrish et al. assume that dinosaurs would have found winter conditions suitable for ectotherms at the arctic circle. However, Paul (1988) shows that even at the polar circles winter conditions were probably not adequate to sustain solar-dependent dinosaurs. Parrish et al. and I agree that dinosaurs probably did not migrate away from high-latitude polar winters.

Increasing evidence supports the view of Parrish et al. that Mesozoic polar winters, although mild by modern standards, were harsh by traditional Mesozoic criteria. Notably, Frakes and Francis (1988) have cited evidence that erratic boulders up to 3 m in diameter were carried across Jurassic-Cretaceous seas by heavy coastal or river ice at paleolatitudes higher than 65°C. They note that this confirms Mesozoic climatic models in which winter freezing occurs at high latitudes, especially inland and at high altitudes. Permanent glaciers are considered probable by Frakes and Francis, especially in the highlands. This supports the controversial assertion by Haq et al. (1987) that rapid fluctuations in Mesozoic sea levels were tied to changing glacial volumes. The combination of inland glaciation and coastal ice implies that Wolfe (1988) is overly optimistic in asserting that Mesozoic coasts escaped even temporary freezes.

Parrish et al. note that many reptiles can survive body temperatures down to −4 to −8°C, but such supercooled creatures can move little if at all below 0°C. This is virtual hibernation, something that Parrish et al. argue that large dinosaurs did not do. Nor should it be assumed that dinosaurs could survive such low body temperatures. This is because the living, winter-adapted reptile most closely related to dinosaurs, the American alligator, seems unable to survive body temperatures below −1°C in the lab or in aquatic refuges (Weigman, 1929; Gregory, 1982; Hagen et al., 1983). On the other hand, tropical caimans can survive −6°C internally. *Alligator* becomes largely inactive and no longer able to perform normal feeding and other functions at a body temperature below 16°C, and can easily be handled as its temperature drops further. Ectothermic dinosaur temperature and activity patterns would probably be simliar (as discussed in detail in Paul, 1988). It should be noted that while small or aquatic reptiles can manage some locomotory activity when their body temperatures are very low, it is questionable whether such severely cooled muscles could move the great bulk of large dinosaurs on land.

Like others, Parrish et al. did not address the most severe conditions that would have faced large dinosaurs during Mesozoic polar winters. Among these would have been extended, breezy rainstorms. Consider that if ambient air temperatures were 4°C, a 25 km/h breeze would create an effective naked skin temperature of −6°C, and a 50 km/h breeze drops it to −12°C (from National Weather Service tables). Air at −4°C and a 25 km/h wind brings skin down to −16°C, 50 km/h wind drops it to −23°C. Evaporative cooling would further plunge skin temperatures. Parrish et al. suggest that the fermentation of plant matter in the gut would help provide adequate internal heat in low metabolic rate dinosaurs. Their suggestion is perplexing, because they acknowledge that digestive activity is suppressed if body temperatures are below the upper portions of an ectotherm's preferred range. With preferred summer body temperatures of about 30°C (see Paul, 1988) even the largest ectothermic dinosaurs would become too cool to digest properly in polar winters. The relatively poor quality of winter browse would have also hindered heat production via fermentation.

With skin temperatures so extremely low, ectothermic polar dinosaurs could have been frostbitten. Worse, they probably could not maintain their body core temperatures above lethal levels, even if they were well below 0°C. Even if they did avoid lethal lows, they would be virtually immobile and subject to predation by any endothermic predators that evolved to take advantage of the situation, even small, big-brained, feathered theropods would have been a threat.

The suggestion by Parrish et al. that dinosaurs escaped sharp chills by retreating to watercourses also fails to consider extended rainstorms. These would have turned the rivers into swift, deep, turbulent water hazards. Polar dinosaurs, the ceratopsids most of all, were less adapted for swimming than crocodilians, so they would have been more suceptible to drowning. Total, rather than partial, immersion is crucial to using water as a thermal buffer, otherwise any exposed skin would be subject to frostbite, especially if wet. Crocodilians can remain totally immersed while escaping floods by swimming into very shallow water. This option was not available to the deep-bodied, erect-limbed dinosaurs.

Lakes might appear to be safer than rivers in a flood, but big dinosaurs would have to retreat to water over 2 m deep, well away from a shoreline that they could not see on a dark and stormy polar night. Drifting and slippage on bottom muds into deeper water would be constant problems, as would entrapment in soft bottom muds. Adding to the dinosaur's travails would be large storm-blown waves.

Even when not flooding, Mesozoic coastal rivers at the poles may have been very cool because of their origin from interior highlands, perhaps from snow packs or glaciers. To that must be added a "water chill" factor—and flowing water is a much better conductor of heat than moving air. So chilled, the dinosaurs' sluggishness would have increased the danger of drowning, or of miring in muds. Indeed, if body temperatures declined too much they may have been immobilized and unable to avoid drowning. Detailed heat flow studies are needed to better understand these problems. Also questionable is whether polar ceratopsids, with their heavy, low-set heads, could have breathed properly while remaining almost totally immersed for long periods of time.

The break-up and drifting of even relatively thin sheets of ice would be an added danger to dinosaurs in flooding polar rivers, even more so if the sheets piled up into thicker slabs. The same would be true of wind-blown ice sheets in large lakes. Of course, freshwater ice sheets thick enough to carry boulders (noted above) would have directly barred dinosaurs from using water as a thermal buffer.

The dreadful conditions that seem to have plagued polar rivers and lakes in Mesozoic winters offer an explanation for the apparent absence of giant phobosuchid crocodilians from Alberta on north (Paul, 1988, Alberta may then have not been far below the Arctic paleocircle). If such semi-aquatic archosaurs could not dwell in polar watercourses, it is unlikely that terrestrial dinosaurs could have either. In all, the idea of ectothermic dinosaurs using water as a buffer against polar winters, although not strictly impossible, is awkward and contrived. It is more plausible to envision polar dinosaurs as endotherms. With their warm breaths condensing in the chill wind of a winter rain, their thermoregulatory abilities would have allowed them to stay away from storm-churned, ice-filled waters.

REPLY BY:
J.T. PARRISH
Department of Geosciences
University of Arizona
Tucson, AZ 85721

J.M. PARRISH
Department of Biology
Northern Illinois University
DeKalb, IL 60115

J.H. HUTCHISON
Museum of Paleontology
University of California
Berkeley, CA 94720

R.A. SPICER
Department of Earth Sciences
Oxford University
Oxford, OX1 3PR, U.K.

In his enthusiastic portrayal of freezing dinosaurs, Paul takes us (Parrish et al., 1987) to task partly on evidence presented in publications by Paul (1988), Frakes and Francis (1988), and Wolfe (1988), none of which, of course, had appeared until after our paper was published (indeed, the paper by Paul was still in press when we first received his comment). We welcome the opportunity to discuss our paper in light of the new information presented in the papers mentioned by Paul. In addition, we would like to clear up some evident misconceptions and point out an erratum in our paper.

We did not assume, as Paul claims, that dinosaurs were ectothermic nor that, if ectothermic, they could have survived the Arctic winters. Nor do we assume that dinosaurs were solar-dependent, as Paul apparently does. Other physiological adaptations, such as countercurrent mechanisms and subcutaneous fat distribution, could conserve the heat of fermentation and muscular activity in the absence of sunlight. We merely discussed a few points in light of new information, presented by us and others, relevant to overwintering at the pole for both the ectothermic and endothermic cases. We also suggested migration as a possibility for overwintering strategy, and we went so far as to point out that the required pace for migration would have been leisurely (24 km/day, *not* 12 km/day, as mistakenly appeared in print). Our paper was intentionally inconclusive because we did not feel that enough evidence existed to draw a firm conclusion for either strategy. It should be noted that modern ectotherms as a whole have developed a variety of physiological as well as behavioral mechanisms for optimizing activity in different thermal regimes (e.g., Schmidt-Neilsen, 1983) and it is a reasonable assumption that ectothermic dinosaurs could have done so as well.

Frakes and Francis' (1988) paper suggesting the possibility of sea ice at high northern latitudes in the Cretaceous was preceded by a similar suggestion by Kemper (1987, cited by us); their conclusions on freezing conditions at altitude also follow from our work (Spicer and Parrish, 1986; Parrish and Spicer, 1988). Kemper's (1987) conclusions were based on the existence of glendonites in Early Cretaceous sediments on the North Slope of Alaska. This represents more conclusive evidence of freezing conditions, in our opinion, than the existence of clasts in the Pebble Shale, the unit to which Frakes and Francis (1988) referred, although not by name. Although evidence seems better that glacial erratics exist in *southern* latitudes (the 3 m boulders to which Paul refers), we are not satisfied that the erratics in the Pebble Shale, which have been examined by one of us (JTP), were not deposited from root balls. Given the amount of forest vegetation in Siberia and on the North Slope in the Cretaceous, it seems extremely likely to us that rootballs would be the primary source for these clasts. The troubling thing about all Mesozoic "glacigenic" deposits is that they consist entirely of dropstones in fine-grained (and sometimes not so fine) sediments. No other glacial epoch is represented solely by scattered dropstones in marine sediments. Apart from the dropstones, which have an alternate explanation, none of the criteria by which glacial deposits are distinguished from the myriad other similar deposits have been found in Mesozoic rocks (i.e., striated clasts, polished pavements, roches moutonnées, etc.; Hambrey and Harland, 1981). These would be expected even if the glaciers were solely montane. In any case, we explicitly stated that neither the plants nor the organisms exclude freezing temperatures. Indeed, we agree with Paul that Wolfe probably was optimistic in his suggestion that the winter temperatures could have remained above freezing (see Brouwers et al., 1988, reply to Wolfe, 1988).

Our point about the browse was that it was *not* poor quality, if the survival capabilities of modern herbivores are any guide (that modern herbivores are not a good analogue is arguable, but Paul, having concluded that dinosaurs were endothermic, clearly wouldn't take issue with this). It is true, as Paul states, that the browse would have been lower quality in the winter, although we are not aware that fermentation would be less under those circumstances.

The bulk of Paul's dramatic discussion is directed toward a remark in our paper that was so minor that we hesitate to dignify it with a long discussion. This suggestion was that in really bad conditions, dinosaurs might have retreated temporarily to watercourses. We did not pretend in our paper to provide a comprehensive discussion of physiology, and we did not discuss chilling by wind and water, although we did explicitly raise the possibility of frostbite and mentioned that dinosaur skin does not seem likely to have been an effective barrier to heat loss. We should mention, however, that the minor lacustrine deposits on the North Slope are not particularly fine-grained nor clayey except very locally (scale of a few meters), and the lakes were rather shallow, so the picture of dinosaurs becoming bogged down in the mud far from the shoreline, swamped by storm waves and ice floes, is not supportable. The possibility that the water was ice-cold is entirely consistent with the conditions we described. Until models of heat flow between dinosaurs and water are published, which would provide useful information to the debate about dinosaur physiology, we decline to speculate on the effects of chilling beyond the cautious statements in our paper.

Paul considers the absence of deinosuchian crocodilians from Alberta northward to be possibly related to the inhospitable conditions he envisions for the Cretaceous Alaskan waterways. The crocodilian genus *Deinosuchus* does have a geographic distribution apparently restricted to the U.S. The absence of *Deinosuchus* from southern Canada is of biogeographic significance, but no more so than its absence from Eurasia. No paleoclimatological conclusions should be drawn from this distribution; it could be a result of restricted habitat preference (e.g., large bodies of water rather than rivers) or simply taphonomic bias.

Our knowledge of the vertebrate fauna of Alaska is relatively limited, consisting of the taphonomically skewed hadrosaur localities from Ocean Point (Brouwers et al., 1987) and the isolated occurrences reported by Parrish et al. (1987). However, intensive search of the abundant assemblages at Ocean Point makes it likely that were crocodilians present, we probably would have detected them by this time (Hutchison, pers. obs.).

REFERENCES

BROUWERS, E.M., CLEMENS, W.A., SPICER, R.A., AGER, T.A., CARTER, L.D., and SLITER, W.V., 1987, Dinosaurs on the North Slope, Alaska: High-latitude latest Cretaceous environments: Science, v. 237, p. 1608–1610.

BROUWERS, E.M., SPICER, R.A., and CLEMENS, W.A. 1988, Arctic dinosaurs and terminal Cretaceous extinctions: Response: Science, v. 239, p. 11.

FRAKES, L.A., and FRANCIS, J.E., 1988, A guide to Phanerozoic cold polar climates from high-latitude ice-rafting in the Cretaceous: Nature, v. 333, p. 547–549.

GREGORY, P.T., 1982, Reptilian hibernation, *in* GANS, C. and POUGH, F.H., eds. Biology of the Reptilia, Vol. 13: Academic Press, London, p. 53–154.

HAGAN, J.M., SMITHSON, P.C., and DOERR, P.D., 1983, Behavioral response of the American alligator to freezing weather: Journal of Herpetology, v. 17, p. 404–406.

HAMBREY, M.J., and HARLAND, W.B., 1981, Criteria for the identification of glacigenic deposits, *in* HAMBREY, M.J., and HARLAND, W.B., eds., Earth's Pre-Pleistocene Glacial Record: Cambridge University Press, Cambridge, p. 14–17.

HAQ, B.U., HARDENBOL, J., and VAIL, P.R., 1987, Chronology of fluctuating sea levels since the Triassic: Science, v. 235, p. 1156–1167.

KEMPER, E., 1987, Das Klima der Kreide-Zeit: Geologisches Jahrbuch, Reihe A, v. 96, p. 5–185.

PARRISH, J.M., PARRISH, J.T., HUTCHISON, J.H., and SPICER, R.A., 1987, Late Cretaceous vertebrate fossils from the North Slope of Alaska and implications for dinosaur ecology: PALAIOS, v. 2, p. 377–389.

PARRISH, J.T., and SPICER, R.A., 1988, Late Cretaceous vegetation of the North Slope of Alaska: A near-polar temperature curve: Geology, v., 16, p. 22–25.

PAUL, G.S., 1988, Physiological, migratorial, climatological, geophysical, survival, and evolutionary implications of Cretaceous polar dinosaurs: Journal of Paleontology, v. 62, p. 640–652.

SCHMIDT-NEILSON, K., 1983, Animal Physiology: Adaptation and Environment: Cambridge University Press, New York, 600 p.

SPICER, R.A., and PARRISH, J.T., 1986, Paleobotanical evidence for cool North Polar climate in middle Cretaceous (Albian-Cenomanian) time: Geology, v. 14, p. 703–706.

WEIGMANN, R., 1929, Die Wirkung starker Abkuhlung auf Amphibien und Reptilien: Zeitschrift für wissenshaftliche Zoologie 134, p. 641–692.

WOLFE, J.A., 1988, Arctic dinosaurs and terminal Cretaceous extinctions: Discussion: Science, v. 239, p. 10–11.