Available online at www.sciencedirect.com

SCIENCE DIRECT®

Palaeogeography, Palaeoclimatology, Palaeoecology 214 (2004) 225–231

PALAEO

www.elsevier.com/locate/palaeo

Polar dinosaurs and the question of dinosaur extinction: a brief review

Eric Buffetaut*

Centre National de la Recherche Scientifique, 16 cour du Liégat, Paris 75013, France

Received 4 September 2003; received in revised form 6 February 2004; accepted 15 February 2004

Abstract

Although the physiology of dinosaurs is still a matter of controversy, there is no doubt that some of them were able to live in environments that were too cold for ectothermic reptiles, as shown by discoveries of Jurassic and Cretaceous polar vertebrate assemblages which contain dinosaurs but lack turtles and crocodiles. This adaptation of dinosaurs to cool climates invalidates hypotheses according to which dinosaur extinction at the end of the Cretaceous was a result of long-term climatic cooling. The pattern seen at the K/T boundary, with the disappearance of dinosaurs and the survival of ectothermic reptiles, is completely different from that seen in Arctic regions during the Late Cretaceous, where ectotherms disappeared, while dinosaurs subsisted, during cooler periods. The idea of an intense and enduring cold spell at the K/T boundary, caused by the Chicxulub impact, is extremely unlikely in view of the pattern of vertebrate extinction (survival of endotherms, extinction of dinosaurs). Models of environmental events following the impact must take this palaeontological constraint into consideration.

Keywords: Dinosaurs; Polar regions; Ecology; Climate; Extinction

1. Introduction

Dinosaurs are still frequently seen as "tropical" animals, which flourished under the warm equable climates of the Mesozoic. This picture of warmth-loving dinosaurs probably applies to many dinosaur assemblages, but recent discoveries of "polar" dinosaurs, which lived close to the Mesozoic poles, have shown that some of these animals lived under climatic conditions which cannot be considered as tropical.

Beyond the interesting problems posed by the adaptation of dinosaurs to life at high latitudes (and notably to extensive periods of darkness), these finds of polar dinosaurs have a bearing on the question of dinosaur extinction. Gradual climate change—usually seen as change towards colder and/or more contrasted climates, although a trend towards warmer temperatures has also been suggested (Cowles, 1939, Cloudsley-Thompson, 1978)—has frequently been put forward as one of the main causes of dinosaur

* Tel.: +33 145 84814; fax: +33 145 848145.
E-mail address: Eric.Buffetaut@wanadoo.fr.

0031-0182/$ - see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2004.02.050

extinction, a hypothesis clearly advocated by Audova as early as 1929 (Audova, 1929). As noted by Cloudsley-Thompson (1978, p. 68), "until 1939, it had been tacitly assumed that the extinction of the dinosaurs might have been caused by gradually falling temperatures...", and this assumption is still an important component of many theories about the K/T mass extinction. Climatic cooling is often mentioned as one of the main factors in an extinction event brought about by a combination of causes (Swinton, 1970; Sloan et al., 1986; Taquet, 1994), it plays a key role in some hypotheses linking dinosaur extinction with a major regression at the end of the Cretaceous (Ginsburg, 1964, 1984, 1986; Jaeger, 1986), and it resurfaces again and again as one of the important components in more elaborate hypotheses involving complex causes, such as the "volcanism plus regression" hypothesis of Officer et al. (1987) or the "Pele hypothesis" of changes in atmospheric composition (Landis et al., 1996). Sloan (1976, p. 134) summarised his view about the extinction of North American dinosaurs in straightforward terms: "In view of the progressive reduction in numbers of dinosaurs and the simultaneous changes in plants over this stratigraphic interval, a change to a cooler, more continental climate provides both a sufficient and an observed cause for the extinction of this community of dinosaurs". In an extreme form, a glaciation (for which there is no factual evidence, although mountain glaciers may have existed: see Spicer and Corfield, 1992) was postulated to account for both marine regression and climatic cooling in the Late Cretaceous (Ginsburg, 1986). One of the reasons why climate change has been considered as so important in dinosaur extinction is that these animals have often been portrayed as sensitive to climatic fluctuations (Ginsburg, 1986), largely on the basis of extrapolations from living reptiles which are in all likelihood unwarranted. The purpose of the present short review is to discuss what polar dinosaurs can tell us about the climatic adaptability of dinosaurs, and the role that climate change may have played in their extinction.

2. Temperature requirements of dinosaurs

Dinosaurs were once generally considered as indicative of warm climates, under the assumption that they were basically giant versions of modern reptiles, at least from a physiological point of view. Colbert (1962, p. 230), for instance, considered that "by virtue of their limited temperature tolerances the dinosaurs, like modern crocodilians, could have lived only in tropical and subtropical climates". The tropical distribution of present-day large reptiles, such as crocodiles and the largest terrestrial turtles, lizards and snakes, was widely considered as indicating that the even larger dinosaurs must have lived in warm environments—hence the well-known reconstructions by Charles Knight, Zdenek Burian and other artists of dinosaurs wallowing in tropical swamps.

Our general conception of dinosaurs has changed drastically since the late 1960s, and it has become clear that they were not simply scaled-up lizards or crocodilians. In particular, the question of the thermal physiology of dinosaurs has been the subject of much controversy. The debate on the "warm-blooded dinosaurs", which started in the 1970s, cannot really be considered as having reached its conclusion, insofar as there is no complete consensus on whether dinosaurs were endothermic or not. Besides the point that there were certainly physiological differences among dinosaurs, they may have had physiologies that have no exact equivalents in the present world (Padian, 1997; Reid, 1997), which would make them difficult to reconstruct. Be that as it may, the concept of dinosaurs as strictly bound to warm climates, like modern giant reptiles, has also been challenged by discoveries of dinosaur remains in polar regions, which in the Mesozoic already were at high latitudes [in the Maastrichtian, the North Slope of Alaska, for instance, may have been at about 85°N (Spicer and Parrish, 1990), i.e., farther north than today]. There is considerable evidence that such polar dinosaurs, whatever their metabolism was, lived under climates which were definitely not "tropical". This has interesting implications for temperature tolerance in dinosaurs, irrespective of their physiology.

3. Polar dinosaurs

The first record of polar dinosaurs is probably that of *Iguanodon* footprints from Svalbard, discovered during an excursion of the International Geological Congress (Lapparent, 1960). Since then, dinosaur discoveries from localities which were beyond the northern or southern polar circle in the Mesozoic, or close to it, have multiplied (see Rich et al., 1997, for a review, and Case et al., 2000, Fiorillo and Gangloff, 2000 and Rich et al., 2002, for complements about more recent finds). Jurassic polar dinosaurs are known from Antarctica, Australia, Siberia and Alaska. Cretaceous polar dinosaurs are known from Antarctica, New Zealand, Australia, Siberia, Svalbard, Canada and Alaska. They belong to various taxa, including large and small theropods, prosauropods, hypsilophodontids, iguanodontids, hadrosaurs, ankylosaurs and ceratopsians. Admittedly, relatively few detailed studies have yet been published about those polar assemblages (the most thoroughly studied fauna probably being that from the Lower Cretaceous of Australia: see Rich and Vickers-Rich, 2000 and Rich et al., 2002, and references therein), and no very clear pattern emerges in terms of systematic distribution of polar dinosaurs, except that fairly diverse taxa apparently were able to live under polar conditions. However, some groups of dinosaurs have not yet been found in such environments, notably sauropods [interestingly, in the Late Cretaceous of North America, sauropods appear to be restricted to the southern part of the continent (Lehman, 1987), which may indicate a preference for warmer climates].

What exactly polar environments were in the Mesozoic is an important but incompletely understood point. As shown by palaeobotanical evidence, there can be no doubt that polar regions were warmer in the Mesozoic than they are today, with no development of extensive ice caps. However, it would be misleading to think of a single "Mesozoic" polar climate, as climatic conditions clearly changed over time (Spicer and Parrish, 1990), some periods being warmer than others. The Turonian–Coniacian time interval thus seems to have been remarkably warm, notably on the basis of vertebrates from Axel-Heiberg Island in Arctic Canada: an estimated mean annual temperature above 14 °C has been suggested (Tarduno et al., 1998). Temperature estimates for other places and periods are much lower, however (Spicer and Parrish, 1990). A mean annual temperature of about 5 °C has been suggested (Spicer and Parrish, 1990; Spicer and Corfield, 1992) for the early Maastrichtian of northern Alaska, on the basis of plant remains. Rich et al. (1988) indicate mean annual temperatures below 5 °C for the Early Cretaceous of southeastern Australia, based on oxygen isotopes in diagenetic calcite, which may be supported by cryoturbation structures (Vickers-Rich et al., 1999). In both instances, cold spells below freezing point probably occurred.

An aspect of polar conditions which cannot have been much different from the present situation, however, is polar night. How polar dinosaurs (and other vertebrates) responded to long periods of darkness is uncertain—both overwintering by feeding on low-quality forage and migration to lower latitudes have been suggested (Parrish et al., 1987). Fiorillo and Gangloff (2000) have interpreted the dominance of the small large-eyed theropod *Troodon* in Maastrichtian tooth assemblages from Alaska as a result of adaptation to low light conditions while overwintering at a high latitude. Similarly, the Early Cretaceous hypsilophodontids from southeastern Australia are interpreted by Vickers-Rich et al. (1999) as having been adapted to year-round activity at high latitudes, whereas the supposed ornithomimosaur *Timimus* may have hibernated.

An especially interesting point, from the point of view of temperature tolerance in dinosaurs, is the occurrence of polar vertebrate assemblages containing dinosaurs in which ectothermic reptiles (known to have been so because they have living representatives) are absent or very scarce. While isolated finds of dinosaur remains in polar regions are not significant in this regard, several sites are known at which fossil remains occur in sufficient abundance to provide a reliable picture of vertebrate diversity. Both the Early Cretaceous assemblage from the Otway Group of Australia (Rich and Vickers-Rich, 2000, Rich et al., 2002, and references therein) and the Maastrichtian assemblage from the Kogosukruk Tongue (Prince Creek Formation) of northern Alaska (Parrish et al., 1987; Clemens and Nelms, 1993) are especially important in this respect. Both are characterised by the presence of various dinosaurs. In the Otway Group, some apparently scarce ectothermic tetrapods occur, as shown by the presence of crocodilians (Rich and Vickers-Rich, 2000), turtles (Gaffney et al., 1998) and temnospondyl amphibians (Warren et al., 1997). The temperature requirements of temnospondyls are unknown, but the occurrence of crocodilians and turtles is not consistent with prolonged cold spells. No ectothermic reptiles such as crocodiles and turtles (which occur in abundance in contemporaneous vertebrate assemblages from lower latitudes) are known from the Prince Creek Formation of Alaska. An inescapable conclusion seems to be that dinosaurs were able to withstand climatic conditions which were too harsh for ectothermic reptiles. Thus, despite the uncertainties which remain concerning dinosaur metabolic rates, palaeoecological evidence strongly suggests that they were more resistant to cool temperatures than, for instance, crocodiles and turtles.

4. Consequences for dinosaur extinction

The now well-attested occurrence of polar dinosaurs which were able to withstand cool climates unsuitable for ectothermic reptiles has a bearing on the question of the causes of the mass extinction at the Cretaceous–Tertiary boundary. To put it simply, the fact that ectothermic reptiles generally survived the boundary, whereas dinosaurs did not, shows that climate deterioration was not a significant extinction factor. Our understanding of climate change during the Late Cretaceous is still fraught with uncertainties, although a cooling trend from the extremely high temperatures of the Turonian seems perceptible, with, probably, a warming up at the end of the Maastrichtian. What can be said, however, is that cooler climates at the end of the Cretaceous are extremely unlikely to have led to dinosaur extinction. It has already been pointed out (Tatarinov, 1986; Buffetaut, 1987) that tropical dinosaurs also became extinct at the K/T boundary, in environments which certainly did not become significantly cooler. More importantly in view of the abovementioned discoveries in the polar regions, the predictable results of a cooling trend are that ectothermic reptiles would have been more affected than dinosaurs. The fossil record shows exactly the reverse.

One can thus compare the effects of Late Cretaceous cooling on polar vertebrate assemblages with those of K/T boundary events on vertebrate assemblages worldwide (Fig. 1). In mid-Cretaceous times, both dinosaurs and turtles occurred in Alaska (Parrish et al., 1987), and there is convincing evidence from Arctic Canada that relatively high temperatures still prevailed there in the Turonian–Coniacian, at a time when turtles were still present on Axel-Heiberg Island (Tarduno et al., 1998). By Maastrichtian times, however, temperatures in

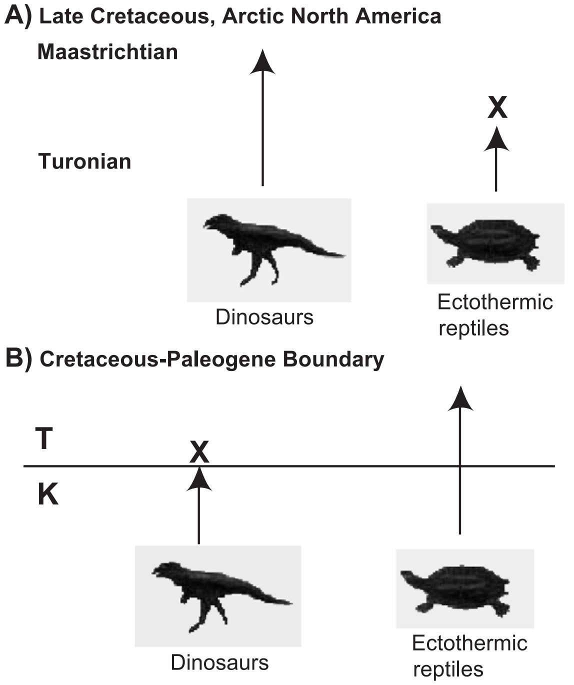

Fig. 1. A diagrammatic comparison of extinction patterns during the Late Cretaceous in Arctic North America (A) and at the Cretaceous–Tertiary boundary (B) worldwide. Whereas both dinosaurs and ectothermic reptiles (such as turtles) are present in Arctic North America at the beginning of the Late Cretaceous, by Maastrichtian times, ectothermic forms have disappeared while dinosaurs are still present, suggesting that climatic deterioration led to the local extinction of ectotherms but was not fatal to polar dinosaurs. A completely different pattern is seen at the Cretaceous–Tertiary boundary, with dinosaurs becoming extinct world-wide while ectotherms were little affected. Whatever happened at the Cretaceous–Tertiary boundary, it is therefore unlikely that temperature decline was an important factor in the mass extinction.

Arctic North America had cooled so much that turtles no longer occurred there (Brinkman, 2003), but dinosaurs were still present. At the K/T boundary, a completely different pattern emerges: Assemblages in which both dinosaurs and turtles (and other ectothermic reptiles) occur are replaced everywhere by impoverished faunas which still contain turtles (and other ectothermic reptiles), but from which dinosaurs are absent. The effects of a long-term cooling trend on Cretaceous vertebrate assemblages at high latitudes are thus clear (survival of dinosaurs, local disappearance of ectotherms), and they are completely unlike those of K/T boundary events (global extinction of dinosaurs, survival of ectotherms).

According to Clemens and Nelms (1993), the occurrence of dinosaurs in the Maastrichtian of northern Alaska, where no ectothermic reptiles were present, shows that (1) dinosaurs (or at least the polar forms) were endothermic, and 2) the pattern of extinction seen at the K/T boundary contradicts the hypothesis of an impact-induced period of cold and darkness as the cause of dinosaur extinction. Their first conclusion is in all likelihood correct, as it convincingly explains the unusual composition of the Alaskan assemblage (and of other Mesozoic polar faunas). Their second conclusion is based on the idea that endothermic polar dinosaurs, being adapted to cold and darkness, should not have perished during the "impact darkness" following the Chixculub impact, at a time when ectothermic reptiles survived. As noted by Buffetaut (1994), the evidence from the Maastrichtian of Alaska does contradict simplistic models of impact-induced extinction, in which dinosaurs simply "froze to death" during a sudden and severe cold spell—which in all likelihood never happened, as shown by the survival of ectothermic reptiles. According to more sophisticated models (Buffetaut, 1984, 1990; Sheehan and Fastovsky, 1992), selective extinctions at the K/T boundary are mainly the result of food-chain collapse caused by the cessation or reduction of photosynthesis, itself a result of reduced light intensity caused by the introduction of huge amounts of "dust" in the atmosphere at the time of the impact. Clemens and Nelms (1994, p. 192) have countered that polar dinosaurs stayed at high latitudes throughout the year and "were adapted to survive through periods of darkness of several month's duration when there was cessation of primary productivity of the plants". This is based on their claim that the Maastrichtian dinosaurs of Alaska did not migrate southward during the winter because of the occurrence of remains of very young individuals, possibly hatchlings, which supposedly would not have been able to engage in long migrations. This, however, does not explain how those dinosaurs subsisted during the polar night. Based on comparison with musk-oxen, Parrish et al. (1987) have suggested that Alaskan herbivorous dinosaurs may have survived on poor-quality food consisting of dead foliage and twigs. However, such a possible adaptation to the polar night implies that this kind of winter food supply was renewed every year during the polar summer. Things would have been different in the case of impact-induced darkness, which was not of a seasonal character. Plant devastation at the K/T boundary occurred both in the northern and southern hemispheres (Vajda et al., 2001), and probably corresponds to a period of reduced light having lasted longer than the duration of polar night (although estimates of that duration are variable). Even if polar dinosaurs were able to subsist on poor-quality food for some time, a photosynthetic crisis of some duration would have been fatal to them because even this food resource would have become exhausted.

5. Conclusions

The idea that dinosaurs were simply scaled-up versions of present-day reptiles has long been discredited. However, the implications of this new interpretation in terms of temperature tolerance are not always perceived, especially concerning the possible causes of dinosaur extinction. The metabolism of dinosaurs is not yet completely understood, however. The Mesozoic vertebrate assemblages from polar regions which contain dinosaurs, but sometimes lack other reptiles, show that dinosaurs were able to live under relatively cool climates. The diversity of taxa found at high latitudes shows that this resistance to cold was widespread among dinosaurs.

One obvious conclusion to be drawn from the existence of polar dinosaurs is that global cooling cannot be considered as a significant factor in dinosaur extinction, all the more so that it should have resulted in extinctions among other reptiles which are not shown by the fossil record at the K/T boundary. More generally, it should be remembered that in the geologically recent past, global cooling has not resulted in mass extinction, as shown by the example of Pleistocene glaciations, which casts serious doubt on gradual temperature decline as a potential cause for the extinctions of the K/T boundary. On the other hand, the survival of those reptiles also clearly shows that there cannot have been an intense protracted cold spell as a consequence of the Chicxulub impact. Models of the consequences of the impact must take this piece of palaeontological evidence into account if a realistic picture of what happened at the K/T boundary is to be achieved.

The question of what polar dinosaurs did during the polar night remains largely unanswered. However, even if they were able to subsist on low-quality food during the annual periods of darkness, it is unlikely that they could have survived a year or two "without a summer", following the Chicxulub impact, since food resources would not have been renewed because of enduring reduction of photosynthetic activity.

Acknowledgments

This paper has benefited from discussions with Vivi Vajda (Lund) and Don Brinkman (Drumheller), and from helpful comments by referees (Thomas Rich and Martin Sander). Funding for research on dinosaur extinction was provided by the ECLIPSE programme of the Centre National de la Recherche Scientifique.

References

Audova, A., 1929. Aussterben der mesozoischen Reptilien. Palaeobiologica 2 (222–245), 365–401.

Brinkman, D.B., 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. Can. J. Earth Sci. 40, 557–571.

Buffetaut, E., 1984. Selective extinctions and terminal Cretaceous events. Nature 310, 276.

Buffetaut, E., 1987. Why the Maastrichtian regression did not cause terminal Cretaceous mass extinctions. Mém. Soc. Géol. Fr. 150, 75–80.

Buffetaut, E., 1990. Vertebrate extinctions and survival across the Cretaceous–Tertiary boundary. Tectonophysics 171, 337–345.

Buffetaut, E., 1994. Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. Comment. Geology 22, 191.

Case, J.A., Martin, J.E., Chaney, D.S., Reguero, M., Marenssi, S.A., Santillana, S.M., Woodburne, M.O., 2000. The first duck-billed dinosaur (Family Hadrosauridae) from Antarctica. J. Vertebr. Paleontol. 20, 612–614.

Clemens, W.A., Nelms, L.G., 1993. Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. Geology 21, 503–506.

Clemens, W.A., Nelms, L.G., 1994. Paleoecological implications of Alaskan terrestrial vertebrate fauna in latest Cretaceous time at high paleolatitudes. Reply. Geology 22, 191–192.

Cloudsley-Thompson, J.L., 1978. Why The Dinosaurs Became Extinct. Meadowfield Press, Shildon. 85 pp.

Colbert, E.H., 1962. Dinosaurs. Their Discovery and Their World. Hutchinson, London. 288 pp.

Cowles, R.B., 1939. Possible implications of reptilian thermal tolerance. Science 90, 465–466.

Fiorillo, A.P., Gangloff, R.A., 2000. Theropod teeth from the Prince Creek Formation (Cretaceous) of northern Alaska, with speculations on Arctic dinosaur paleoecology. J. Vertebr. Paleontol. 20, 675–682.

Gaffney, E.S., Kool, L., Brinkman, D.B., Rich, T.H., Vickers-Rich, P., 1998. *Otwayemys*, a new cryptodyran turtle from the Early Cretaceous of Australia. Am. Mus. Novit. 3233, 1–28.

Ginsburg, L., 1964. Les régressions marines et le problème du renouvellement des faunes au cours des temps géologiques. Bull. Soc. Géol. Fr. 6, 13–22.

Ginsburg, L., 1984. Théories scientifiques et extinction des dinosaures. C. R. Acad. Sci. Paris 298 (II), 317–320.

Ginsburg, L., 1986. Régressions marines ou catastrophes cosmiques: comment juger les théories sur l'extinction des dinosaures. Bull. Cent. Rech. Explor. Prod. Elf-Aquitaine 10, 433–436.

Jaeger, H., 1986. Die Faunenwende Mesozoikum/Känozoikum-nüchtern betrachtet. Z. Geol. Wiss. 14, 629–656.

Landis, G.P., Rigby, J.K., Sloan, R.E., Hengst, R., Snee, L.W., 1996. Pele hypothesis: ancient atmospheres and geologic-geochemical controls on evolution, survival, and extinction. In: Macleod, N., Keller, G. (Eds.), Cretaceous–Tertiary Mass Extinctions. Biotic and Environmental Changes. Norton, New York, pp. 519–556.

Lapparent, A.F.de., 1960. Découverte de traces de pas de dinosauriens dans le Crétacé du Spitzberg. C. R. Acad. Sci. Paris 251, 1399–1400.

Lehman, T.M., 1987. Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America. Palaeogeogr. Palaeoclimatol. Palaeoclimatol. 60, 189–217.

Officer, C.B., Hallam, A., Drake, C.L., Devine, J.D., 1987. Late Cretaceous and paroxysmal Cretaceous/Tertiary extinctions. Nature 326, 143–149.

Padian, K., 1997. Physiology. In: Currie, P.J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 552–557.

Parrish, J.M., Parrish, J.T., Hutchison, J.H., Spicer, R.A., 1987. Late Cretaceous vertebrate fossils from the North Slope of Alaska and implications for dinosaur ecology. Palaios 2, 377–389.

Reid, R.E.H., 1997. Dinosaurian physiology: the case for "intermediate" dinosaurs. In: Farlow, J.O., Brett-Surman, M.K. (Eds.), The Complete Dinosaur. Indiana University Press, Bloomington, pp. 449–473.

Rich, T.H., Vickers-Rich, P., 2000. Dinosaurs of Darkness. Indiana University Press, Bloomington. 222 pp.

Rich, P.V., Rich, T.H., Wagstaff, B.E., McEwen Mason, J., Douthitt, C.B., Gregory, R.T., Felton, E.A., 1988. Evidence for low temperatures and biologic diversity in Cretaceous high latitudes of Australia. Science 242, 1403–1406.

Rich, T.H., Gangloff, R.A., Hammer, W.R., 1997. Polar dinosaurs. In: Currie, P.J., Padian, K. (Eds.), Encyclopedia of Dinosaurs. Academic Press, San Diego, pp. 562–573.

Rich, T.H., Vickers-Rich, P., Gangloff, R.A., 2002. Polar dinosaurs. Science 295, 979–980.

Sheehan, P.M., Fastovsky, D.E., 1992. Major extinctions of land-dwelling vertebrates at the Cretaceous–Tertiary boundary, eastern Montana. Geology 20, 556–560.

Sloan, R.E., 1976. The ecology of dinosaur extinction. In: Churcher, C.S. (Ed.), Athlon. Essays in Palaeontology in Honour of Loris Shano Russell. Royal Ontario Museum, Toronto, pp. 134–154.

Sloan, R.E., Rigby, J.K., Van Valen, L.M., Gabriel, D., 1986. Gradual dinosaur extinction and simultaneous ungulate radiation in the Hell Creek Formation. Science 232, 629–633.

Spicer, R.A., Corfield, R.M., 1992. A review of terrestrial and marine climates in the Cretaceous with implications for modelling the "Greenhouse Earth". Geol. Mag. 129, 169–180.

Spicer, R.A., Parrish, J.T., 1990. Late Cretaceous–early Tertiary palaeoclimates of northern high latitudes: a quantitative view. J. Geol. Soc. (Lond.) 147, 329–341.

Swinton, W.E., 1970. The Dinosaurs. George Allen and Unwin, London. 331 pp.

Taquet, P., 1994. L'empreinte des dinosaurs. Odile Jacob, Paris. 363 pp.

Tarduno, J.A., Brinkman, D.B., Renne, P.R., Cottrell, R.D., Scher, H., Castillo, P., 1998. Evidence for extreme climatic warmth from Late Cretaceous Arctic vertebrates. Science 282, 2241–2244.

Tatarinov, L.P., 1986. The process of extinction among continental vertebrates during the transition from the Cretaceous to the Palaeogene. In: Roček, Z. (Ed.), Studies in Herpetology, Prague, pp. 97–100.

Vajda, V., Raine, J.I., Hollis, C.J., 2001. Indication of global deforestation at the Cretaceous–Tertiary boundary by New Zealand fern spike. Science 294, 1700–1702.

Vickers-Rich, P., Rich, T.H., Constantine, A., 1999. Environmental setting of the polar faunas of southeastern Australia and adaptive strategies of the dinosaurs. In: Tomida, Y., Rich, T.H., Vickers-Rich, P. (Eds.), Proceedings of the Second Gondwanan Dinosaur Symposium, National Science Museum Monographs, Tokyo, vol. 15, pp. 181–195.

Warren, A., Rich, T.H., Vickers-Rich, P., 1997. The last last labyrinthodont? Palaeontogr. Abt. A 247, 1–24.