"Equability," continentality, and Tertiary "climate": The crocodilian perspective

Paul J. Markwick   Department of Geophysical Sciences, University of Chicago, 5734 South Ellis Avenue, Chicago, Illinois 60637

ABSTRACT

The distributions of fossil crocodilians are used to examine North American continental paleoclimates for four time periods in the Cenozoic. Control groups provide a qualitative means of examining the completeness of the record and thus the validity of crocodilian patterns. By analogy with the range of the extant American alligator, *Alligator mississippiensis*, the patterns imply that mid- to high-latitude continental interiors during the Eocene and Miocene did not undergo seasonal temperature extremes as great as those observed in such areas today. This is compatible with the paleobotanical data. During both the late Oligocene and the Pleistocene (times of major glaciation), crocodilians were restricted to more maritime localities.

INTRODUCTION

The traditional view of Mesozoic and early Cenozoic continental climates as being warmer and more "equable" than at present (Lyell, 1830; Frakes, 1979; Hutchison, 1982) has recently been challenged by the results of computer modeling experiments (Sloan and Barron, 1990, 1992). Such models produce strong thermal seasonality within large continental areas in mid to high latitudes. Caused by the low thermal capacity of land, this is a well-documented phenomenon known as continentality; the larger the continent, and consequent distance from the ameliorating effects of the oceans, the greater the disparity between winter and summer temperatures. Climatic inferences based on the interpretation of the geologic proxy data, primarily fossil faunas and floras, do not support such strong thermal seasonality during these times (Wing and Greenwood, 1993). This disparity, between climatic conclusions drawn from the geologic data and those from modeled results, has led to speculations over the validity of each approach (Sloan and Barron, 1991; Wing, 1991). The disagreement has been compounded by confusion over terminology, especially qualification of the term "equable" (Axelrod, 1992), the problem of describing "climate" for time spans on the order of millions of years, and the sparsity of large, well-constrained, global data sets of geologic proxy data (Sloan and Barron, 1990).

As more model experiments are run, and concern over future climate change increases, resolution of these issues becomes paramount. To help address this need I have compiled a computerized data base of some 5000 globally distributed vertebrate localities spanning the past 100 m.y. of Earth's history. The comprehensive nature of this data set allows for comparisons among climatically sensitive vertebrate groups, while also providing the means for analyzing the impact of nonclimate influences upon the

data used. When integrated with other data sets such as those for paleofloras and lithologies, and placed in the context of paleoenvironment and paleogeography (by using the latest detailed maps produced by the Paleogeographic Atlas Project), this data set provides an important addition to the tools necessary for understanding the geologic record of global change. In the study presented here, I submit a subset of this data base, the Tertiary North American fossil crocodilian record (Figs. 1–4), as a further entry in the present discussion of the nature of Cenozoic continental climates.

CROCODILIANS AS CLIMATE PROXIES

Fossil crocodilians have been used as climate proxies since at least the early nineteenth century (Lyell, 1830; Hutchison, 1982). Climatic inferences have been based

upon analogy with the presumed climatic tolerances of living forms as suggested by their biology and geographic distribution. This method has been criticized, however, because the basic assumption—that the position occupied in climate space by fossil forms is identical to that occupied by their closest living relatives—need not be true (Fleming, 1829; Ostrom, 1970). Unfortunately, the full physiological characteristics of any extinct organism are rarely fully realized in the preserved fossil. Consequently, reference to the Present is not only the most parsimonious guide to the geologic record (methodological uniformitarianism of Gould, 1965) but often the only guide. It is corroborating and circumstantial evidence that ultimately helps support derived climate inferences (Conybeare, 1829). Thus, in North America, Eocene crocodilians are associated with other warm-climate proxies such as salamanders and giant tortoises on Ellesmere Island (Estes and Hutchison, 1980) or palms in Wyoming (Wing and Greenwood, 1993). In addition, fossil crocodilian distributional patterns and diversity trends are entirely consistent with the Cenozoic global climate changes indicated by isotopic and sedimentological evidence (Markwick, 1992, 1993). Throughout this study the American alligator, *Alligator mississippiensis*, is used
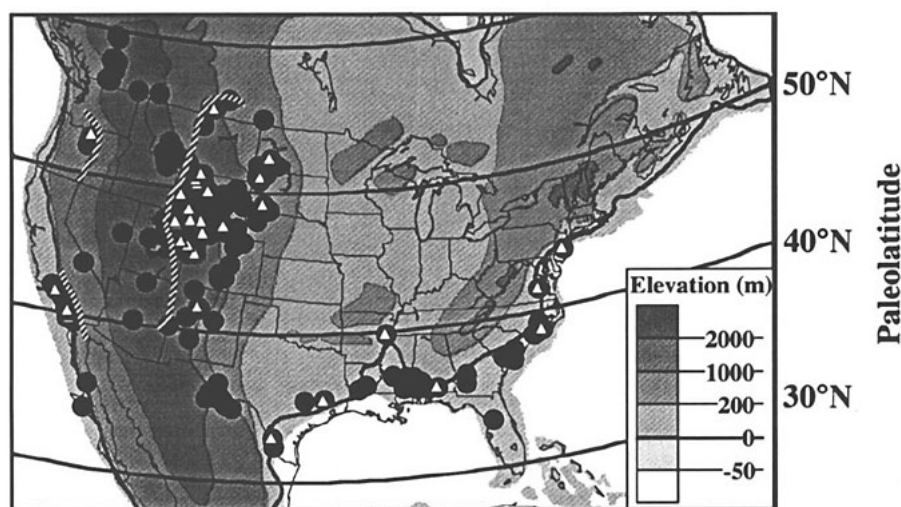

Figure 1. Distribution of Eocene vertebrates and crocodilians. Ellesmere Island localities are not shown because they do not have direct bearing on interior paleoclimates in western United States. Base map (used for all four figures) is for present day plotted on Lambert conformable conic projection. Paleogeography is for middle Eocene (Lutetian Stage). West coast and position of 2000 m contour are speculative at present. Diagonally ruled line represents conservative estimate of limit of crocodilians during Eocene. Circles—vertebrate localities; triangles—localities with fossil crocodilians.
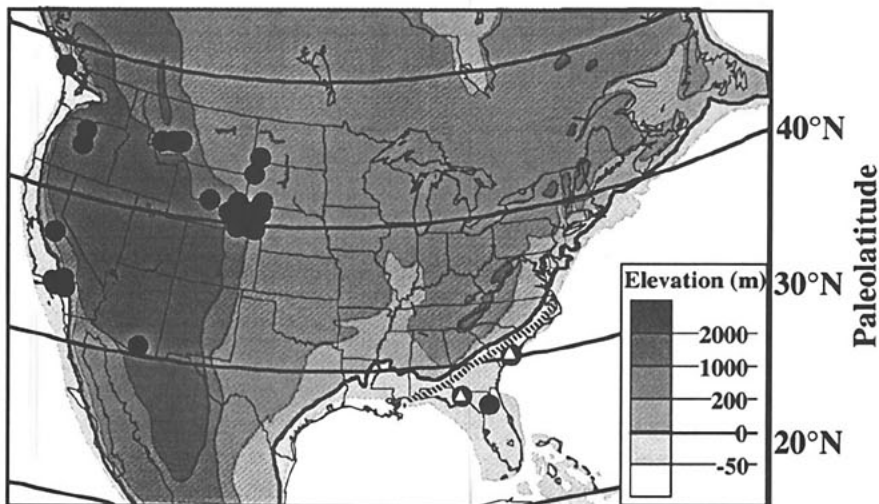
Figure 2. Distribution of vertebrates and crocodilians in late Oligocene time. Paleogeography is for Chattian Stage. Key to symbols is in Figure 1 caption.
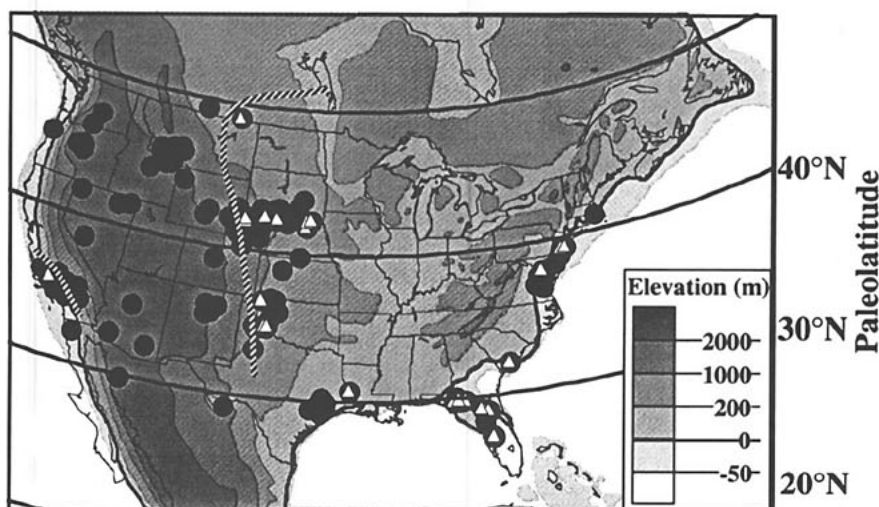

Figure 3. Distribution of vertebrates and crocodilians in Miocene time. Paleogeography is for middle Miocene. Key to symbols is in Figure 1 caption.
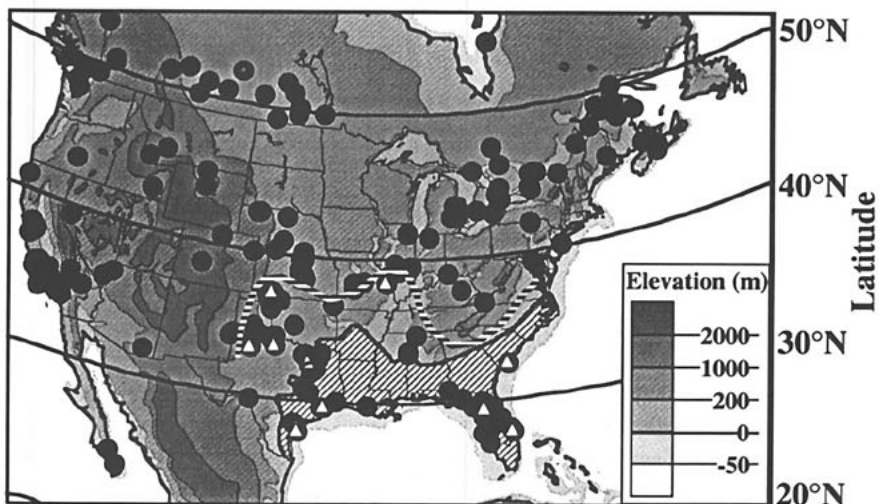

Figure 4. Distribution of vertebrates and crocodilians in Pleistocene and early Holocene time. Topography is for present day. Shaded area in southeastern United States represents present distribution of crocodilians in North America (Neill, 1971). Key to symbols is in Figure 1 caption.

to represent the minimum climatic tolerances of all crocodilians; it is the best studied of living crocodilians and is found in the highest latitudes; thus, it should provide the minimum temperature requirements of the group.

Crocodilians are relatively well represented in the fossil record, but to determine their distributions more precisely I have used control groups. The method is similar to that employed by Bottjer and Jablonski (1988) for their "taphonomic controls" in which the presence of a taxon with preservational characteristics similar to those of the taxon of interest is used to qualify significant absences. In this study, noncrocodilian vertebrates provide a broad-based control group; thus, the absence of crocodilians at a vertebrate locality is considered to reflect environmental factors (including climate) and not just to be an artifact of collection or taphonomic biases.

PRESENT-DAY CROCODILIANS

All animals live within definable body-temperature limits (critical temperatures) above and below which they die. For ectotherms, whose body temperatures depend primarily upon absorption of energy from the environment (Pough and Gans, 1982), these critical temperatures are directly related to environmental temperatures. For *A. mississippiensis*, the maximum and minimum critical temperatures are generally given as 38–39 °C (Avery, 1982) and 4–5 °C (Brisbin et al., 1982), respectively. Generally, however, ectotherms keep within a smaller "activity" temperature range, which for *A. mississippiensis* is about 25–35 °C, a range also applicable to many other crocodilian species (Lang, 1987). As temperatures drop below this activity range, crocodilians lose their appetites, their metabolic rates diminish, and they become increasingly torpid, which makes them more susceptible to disease. Only an external stimulus, an increase in temperature, can prevent them from ultimately "shutting down" completely and dying (Neill, 1971). This preference for warmth was noted by Colbert et al. (1946) from experiments, which have been born out by observational data, that showed that alligators and other crocodilians will act to remain within this activity range through a process known as thermoregulation. Although partly physiological (Johnson et al., 1978), most thermoregulation is behavioral and includes basking, gaping, and immersion in water. For crocodilians, water is extremely important as it provides a buffer against climatic extremes, both hot and cold (Smith, 1975). *A. mississippiensis* has been documented to survive air temperatures as low as −4.3 °C by remaining torpid and sub-

TABLE 1. CLIMATE DATA FOR AREAS AND LOCATIONS REFERRED TO IN THE TEXT

	Latitude	Elevation (m)	CMM (°C)	CMMM (°C)	Mean length of freeze-free period (days)	MART (°C)	MAT (°C)
Present crocodilian range in North America*	-	<250	>7.0	>1.5	>220	<21.1	>16
Biological limits for A.mississippiensis [†]	-	-	critical min.=4-5 activity min.=25		-	-	-
St. Louis, Missouri[§]	38°38'N	142	-0.1	-4.4	180	26.5	13.3
Omaha, Nebraska[§]	41°18'N	337	-5.4	-10.6	160	31.2	10.8
Cheyenne, Wyoming[§]	41°09'N	1871	-3.6	-9.4	120	22.8	7.0

Note: CMM-coldest month mean temperature; CMMM-coldest month mean daily minimum temperature; MART-mean annual range of temperature; MAT-mean annual temperature.

*Data from Baldwin (1973) ostensibly for the period 1931-1960, based on comparison with the crocodilian distribution map given in Neill (1971).

[†]Critical and activity temperatures for *Alligator mississippiensis* for comparison with temperatures indicated by their present geographic distribution.

[§]Data from Müller (1982), for the period 1931-1960.

merged in water (Hagan et al., 1983), even with surface ice 1.5 cm thick, as long as an air hole remained to prevent drowning (Brisbin et al. 1982). Data from escaped alligators across the United States reinforces the idea that individual adults can tolerate quite low temperatures; Barton (1955) described an alligator that seems to have survived in Allegheny County, Pennsylvania, for possibly 6 or 7 yr despite a mean temperature for the coldest month that varied between −5.7 and 1.8 °C. However, an adult individual does not constitute a viable population, especially when it has been transposed through human intervention. This concept is important because in the geologic record the presence of a fossil crocodilian must, in terms of simple probability, be seen as evidence of a population rather than as the wanderings of an errant individual. The viability of populations is a function of not only minimum temperatures but more especially of the length of the active season. An extended cold season can result in the postponement of nesting and egg laying such that the season available for incubation and successful hatching may be limited (Joanen et al., 1987) and subsequent growth rates low. Fuller (cited in Hagan et al., 1983) noted that the growth rates of *A. mississippiensis* in North Carolina are about one half those reported in Louisiana, which makes the North Carolina crocodilians more liable to predation. Suggestions that crocodilians hibernate to escape temperature extremes are problematic and depend on the definition of "hibernation" used.

Climatic tolerances based upon isolated observational or experimental data may be founded upon a particular aspect of climate such as the absolute minimum air temperature survivable. However, crocodilian distributions, as for most organisms, are not defined by a single climate parameter but by a combination of factors (Sloan and Barron, 1992). A more meaningful approach is to use the climatic data applicable to the present-day geographic distribution of *A. mississip-*

piensis (Neill, 1971) to derive general climate characteristics that define a region rather than a point in climate space (Table 1). This is appropriate if present-day alligators are occupying the fullest geographic range allowed by climate rather than a range limited by the effects of Pleistocene glacial climates (Joysey, cited in, but dismissed by, Colbert, 1964). With this approach, temperature (magnitude and duration) appears to be the most important limiting factor for *A. mississippiensis*; there appears to be no relation to precipitation patterns. The presence of water, although important, need not necessarily reflect local precipitation, as the presence of *Crocodylus niloticus* in the Nile River illustrates. It should be noted that the ambient air temperature implied by the climate data may not exactly reflect the immediate environmental temperature for the alligator, which, when in water, would be that of the water body.

FOSSIL CROCODILIAN DISTRIBUTIONS AND INFERRED PALEOCLIMATE

The distribution of fossil crocodilians in North America, south of Hudson Bay, for four Cenozoic time intervals (Figs. 1–4) are plotted on present-day base maps with superimposed paleogeography and lines of paleolatitude. North American motion during this period was minor and does not account for the changes in crocodilian distributions.

Eocene

Crocodilian and noncrocodilian vertebrate localities are widely distributed in the Eocene strata of North America up to lat ~50°N (Fig. 1). The paucity of vertebrate data north of this latitude, with the significant exception of Ellesmere Island (Estes and Hutchison, 1980), remains a problem. By analogy with the modern distribution of *A. mississippiensis*, I infer that the climate of areas that had fossil crocodilians during the Eocene was not any more extreme than that of the present-day maritime southeastern

and southern United States (see Table 1). MacGinitie (1969) reached a similar conclusion for Eocene Wyoming on the basis of flora of the Green River Formation, and Wing and Greenwood (1993), also using floras, inferred coldest-month mean temperatures of 8–10 °C and mean annual temperatures of no less than 12–18 °C for the region between 40°N and 50°N. The crocodilians do not preclude thermal seasonality, as is often implied by the term "equable," but imply that the seasonality was not as great as that observed in similar continental settings today (compare with the data for present-day Cheyenne in Table 1). Although the ameliorating effects of the Cretaceous Western Interior Seaway had been removed by the Eocene, it is possible that remnants of the Cannonball Seaway remained into this time at least in the form of an expanded Hudson Bay (Fig. 1). If true, this additional inland water may explain the apparent warmth of the Rockies region.

Late Oligocene

During the late Oligocene, North American crocodilians were found only in maritime localities (Fig. 2). Other vertebrates are known from the continental interior, but the number of localities represented, even allowing for the shorter length of the late Oligocene compared to the Eocene or Miocene, is greatly reduced. The overall lack of crocodilian localities may partly reflect this paucity. However, the number of crocodilian localities diminishes proportionally more than vertebrate localities in general (from 17% to 6.5% of all vertebrate localities). In combination with the contemporary distribution of control points in interior sites, this fact would seem to indicate that the absence of crocodilians there is significant. Perhaps more significantly, the nature of the crocodilian fauna changed at this time, with the loss of all members of the family Crocodylidae. From the late Oligocene until the present, the family Alligatoridae remains the dominant group in North America in terms of both generic diversity and numbers of localities where it is found. It is this family that today includes the most poleward members of the Crocodylia, *A. mississippiensis* and *A. sinensis*.

Miocene

Fossil crocodilians are found in Miocene fluvial deposits of the Great Plains, which may have been at elevations similar to the present (the linearity of crocodilian localities in Nebraska, South Dakota, and eastern Wyoming may mark the traces of the paleo-Niobrara or Platte river systems, which had their sources to the west). The contrast between the climate of this region in the Mio-

cene and that of today can be best illustrated by comparing the climate implied by the present distribution of *A. mississippiensis* with the climate of Omaha, Nebraska, situated close to the Miocene crocodilian locations (Table 1). This return of crocodilians to the continental interior is consistent with the renewed global warmth implied by other evidence such as the marine isotopic record (Miller and Fairbanks, 1985).

Pleistocene-Holocene

With the establishment of ice sheets at both poles and consequent changes in the global climate system, the crocodilians were once more restricted to the major river systems of Texas and the coastal plain of the southern and southeastern United States. Migrations up the Mississippi, Red, and Brazos rivers, for example, during warmer interglacial climates may explain the presence of crocodilians beyond their historical distribution (see Fig. 4). The distribution of noncrocodilian vertebrate localities shows that the crocodilian distribution shown for this time is well constrained.

CONCLUSIONS

By analogy with the climate limitations of living alligators, the distribution of fossil crocodilians implies that both Eocene and Miocene interior climates in North America were warmer and underwent less thermal seasonality than at present with coldest-month mean temperatures of >7 °C, mean annual temperatures of >16 °C, and mean annual temperature ranges of <21.1 °C. For the Eocene, which has been the subject of recent work, these results agree with the climate implied by the floral data (Wing and Greenwood, 1993). The distributional changes portrayed here are also consistent with an overall latitudinal pattern showing equatorward shifts in crocodilian ranges during times of purported glaciation at high latitudes (Markwick, 1992). Along with the interpretation of such glacial periods is the interpretation of increased aridity in continental interiors, which has also been used to explain vertebrate distributions through this period (Hutchison, 1982, 1992). It is unclear what ultimate causes were responsible for the Cenozoic climatic changes suggested by the proxy data, but it is not perhaps insignificant that recent modeling experiments have highlighted the importance of uplift in the Rockies for cooling climates and creating increased aridity in the Great Plains (Kutzbach et al., 1989). The climatic implications of an ice-free Arctic have yet to be explored and may also be important.

As interest in global change increases, the need for large global data sets of geologic climate proxy data becomes more pressing, as does the need for a fuller understanding of the limitations and biases such data sets inherently include.

REFERENCES CITED
Avery R. A., 1982, Field studies of body temperatures and thermoregulation, *in* Gans, C., ed., Biology of the Reptilia, Volume 12, Physiology C, Physiological ecology: London, Academic Press, p. 94–166.

Axelrod, D. I., 1992, What is an equable climate?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 91, p. 1–12.

Baldwin, J. L., 1973, Climates of the United States: Washington, D.C., National Oceanic and Atmospheric Administration, 113 p.

Barton, A. J., 1955, Prolonged survival of a released alligator in Pennsylvania: Herpetologica, v. 11, no. 3, p. 210.

Bottjer, D. J., and Jablonski, D., 1988, Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates: Palaios, v. 3, p. 540–560.

Brisbin, I. L., Jr., Standora, E. A., and Vargo, M. J., 1982, Body temperatures and behavior of American alligators during cold winter weather: American Midland Naturalist, v. 107, no. 2, p. 209–218.

Colbert, E. H., 1964, Climatic zonation and terrestrial faunas, *in* Nairn, A. E. M., ed., Problems in palaeoclimatology: London, Interscience, p. 617–638.

Colbert, E. H., Cowles, R. B., and Bogert, C. M., 1946, Temperature tolerances in the American alligator and their bearing on the habits, evolution, and extinction of the dinosaurs: American Museum of Natural History Bulletin, v. 86, no. 7, p. 327–374.

Conybeare, W. D., 1829, Answer to Dr Fleming's view of the evidence from the animal kingdom, as to the former temperature of the northern regions: Edinburgh New Philosophical Journal, v. 7, p. 142–152.

Estes, R., and Hutchison, J. H., 1980, Eocene lower vertebrates from Ellesmere Island, Canadian Arctic Archipelago: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 30, p. 325–347.

Fleming, R. J., 1829, On the value of the evidence from the animal kingdom, tending to prove that the Arctic regions formerly enjoyed a milder climate than at present: Edinburgh New Philosophical Journal, v. 6, p. 277–286.

Frakes, L. A., 1979, Climates through geologic time: Amsterdam, Elsevier, 310 p.

Gould, S. J., 1965, Is Uniformitarianism necessary?: American Journal of Science, v. 263, p. 223–228.

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, no. 4, p. 402–404.

Hutchison, J. H., 1982, Turtle, crocodilian, and champsosaur diversity changes in the Cenozoic of the north-central region of western United States: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 37, p. 149–164.

Hutchison, J. H., 1992, Western North American reptile and amphibian record across the Eocene/Oligocene boundary and its climatic implications, *in* Prothero, D. R., and Berggren, W. A., eds., Eocene-Oligocene climatic and biotic evolution: Princeton, New Jersey, Princeton University Press, p. 451–463.

Joanen, T., McNease, L., and Ferguson, M. W. J., 1987, The effects of egg incubation temperature on post-hatching growth of American alligator, *in* Webb, G. J. W., et al., eds., Wildlife management: Crocodiles and alligators: Chipping Norton, New South Wales, Surrey Beatty and Sons Pty. Limited and Conservation Commission of the Northern Territory, p. 533–537.

Johnson, C. R., Voigt, W. G., and Smith, E. N., 1978, Thermoregulation in crocodilians—III. Thermal preferenda, voluntary maxima, and heating and cooling rates in the American alligator, *Alligator mississippiensis*: Zoological Journal of the Linnean Society, v. 62, p. 179–188.

Kutzbach, J. E., Guetter, P. J., Ruddiman, W. F., and Prell, W. L., 1989, Sensitivity of climate to late Cenozoic uplift in southern Asia and the American West: Numerical experiments: Journal of Geophysical Research, v. 94, p. 18,393–18,407.

Lang, J. W., 1987, Crocodilian thermal selection, *in* Webb, G. J. W., et al., eds., Wildlife management: Crocodiles and alligators: Chipping Norton, New South Wales, Surrey Beatty and Sons Pty. Limited and Conservation Commission of the Northern Territory, p. 301–317.

Lyell, C., 1830, Principles of geology, being an attempt to explain the former changes of the Earth's surface, by reference to causes now in operation (first edition): London, John Murray, 511 p.

MacGinitie, H. D., 1969, The Eocene Green River flora of northwestern Colorado and northeastern Utah: University of California Publications in Geological Sciences, v. 83, 202 p.

Markwick, P. J., 1992, Fossil Crocodilian distributions, Upper Cretaceous to Present: Implications for paleoclimate, *in* Lidgard, S., and Crane, P. R., eds., North American Paleontological Convention, 5th, Abstracts and Program: Chicago, Paleontological Society, p. 198.

Markwick, P. J., 1993, Crocodilian diversity and distributional responses to climate changes over the last 100 Ma: Geological Society of America Abstracts with Programs, v. 25, no. 3, p. 65.

Miller, K. G., and Fairbanks, R. G., 1985, Cenozoic δ^{18}O record of climate and sea level: South African Journal of Science, v. 81, p. 248.

Müller, M. J., 1982, Selected climatic data for a global set of standard stations for vegetation science: The Hague, Netherlands, Dr. W. Junk, 306 p.

Neill, W. T., 1971, The last of the ruling reptiles. Alligators, crocodiles, and their kin: New York, Columbia University Press, 485 p.

Ostrom, J. H., 1970, Terrestrial vertebrates as indicators of Mesozoic climates, *in* Proceedings, North American Paleontological Convention: Chicago, Allen Press, p. 347–376.

Pough, F. H., and Gans, C., 1982, The vocabulary of reptilian thermoregulation, *in* Gans, C., ed., Biology of the Reptilia, Volume 12, Physiology C, Physiological ecology: London, Academic Press, p. 17–23.

Sloan, L. C., and Barron, E. J., 1990, "Equable" climates during Earth history?: Geology, v. 18, p. 489–492.

Sloan, L. C., and Barron, E. J., 1991, " 'Equable' climates during Earth history?": Reply: Geology, v. 19, p. 540–542.

Sloan, L. C., and Barron, E. J., 1992, A comparison of Eocene climate model results to quantified paleoclimatic interpretations: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 93, p. 183–202.

Smith, E. N., 1975, Thermoregulation of the American alligator, *Alligator mississippiensis*: Physiological Zoölogy, v. 48, p. 177–194.

Wing, S. L., 1991, " 'Equable' climates during Earth history?": Comment: Geology, v. 19, p. 539–540.

Wing, S. L., and Greenwood, D. R., 1993, Fossils and fossil climate: The case for equable continental interiors in the Eocene: Royal Society of London Philosophical Transactions, ser. B, v. 341, p. 243–252.