

THE UNIVERSITY OF CHICAGO

LATE CRETACEOUS TO PLEISTOCENE CLIMATES: NATURE OF THE  
TRANSITION FROM A 'HOT-HOUSE' TO AN 'ICE-HOUSE' WORLD

VOLUME TWO

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## CHAPTER VI

# 'EQUABILITY,' CONTINENTALITY AND TERTIARY 'CLIMATE': THE CROCODILIAN PERSPECTIVE<sup>1</sup>

*"The world is full of obvious things which nobody by any chance ever observes."*

Sherlock Holmes  
'The Hound of the Baskervilles' Sir Arthur Conan-Doyle

## ABSTRACT

The distributions of fossil crocodilians are used to examine North American continental paleoclimates for four time periods in the Cenozoic. Control groups are used to 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

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1. The chapter has been modified from its published form (Markwick, 1994b) in order to make it consistent with the rest of the dissertation.

and the Pleistocene (times of major glaciation), crocodylians were restricted to more maritime localities.

## VI.1. INTRODUCTION

The traditional view of Mesozoic and early Cenozoic continental climates as being warmer and more 'equable' than present (Frakes, 1979; Lyell, 1830; Romer, 1961) 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 speculation about the validity of each approach (Archibald, 1991; Sloan and Barron, 1991; Wing, 1991). This has been compounded further 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 datasets 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 I have compiled a computerized database of some 5000 globally distributed vertebrate localities spanning the last 100 m.y. of Earth's history. The comprehensive nature of this dataset

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 (using the latest detailed maps produced by the Paleogeographic Atlas Project), this dataset 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 database, the Tertiary North American fossil crocodylian record (Figures VI.1-VI.4), as a further entry in the present discussion of the nature of Cenozoic continental climates.

## VI.2. CROCODYLIANS AS CLIMATE PROXIES

Fossil crocodylians have been used as climate proxies since at least the early nineteenth century (Lyell, 1830). 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 fossil forms occupied identical positions in climate space as their closest living relatives, need not be true (Fleming, 1829, 1830; 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; Kitts, 1963). Thus in North America we find Eocene crocodylians 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 crocodylian 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 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 an artifact of collection or taphonomic biases.

### VI.3. 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) in 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  $-4.3^{\circ}\text{C}$  by remaining torpid and submerged 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 reinforce 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 years despite a mean temperature for the coldest month that varied between  $-5.7$  and  $1.8^{\circ}\text{C}$ . However, an adult individual does not constitute a viable population, especially when it has been transposed through the intervention of humans. This 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; Webb 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. mississippiensis* (Grenard, 1991; Neill, 1971) to derive general climate characteristics that define a region rather than a point in climate space (Table VI.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.

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

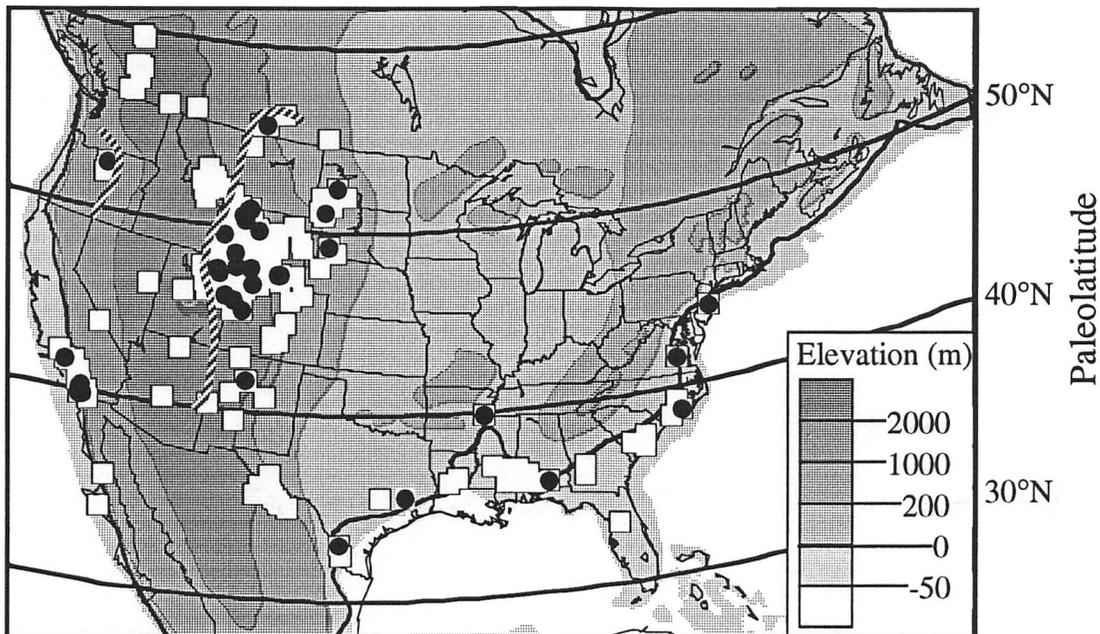
	Latitude	Elevation (m)	CMM (CMM) (°C)	Mean length of freeze-free period (days)	MART (°C)	MAT (°C)
Present crocodilian range in North America*	-	<250	>7.0 (>1.5)	>220	<21.1	>16
Biological limits for <i>A. mississippiensis</i> †	-	-	critical min.=4-5 activity min.=25	-	-	-
St. Louis, Missouri§	38°38'N	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; CMM-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



**FIGURE VI.1. Distribution of vertebrate and crocodilian localities during Eocene.**

Ellesmere Island localities are not shown since they do not have direct bearing on interior paleoclimates in the 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 at this time. White filled squares - vertebrate localities, black filled circles - localities with fossil crocodilians (note that in this chapter black filled circles represents all crocodilians rather than only crown group crocodilians--see Chapter V).

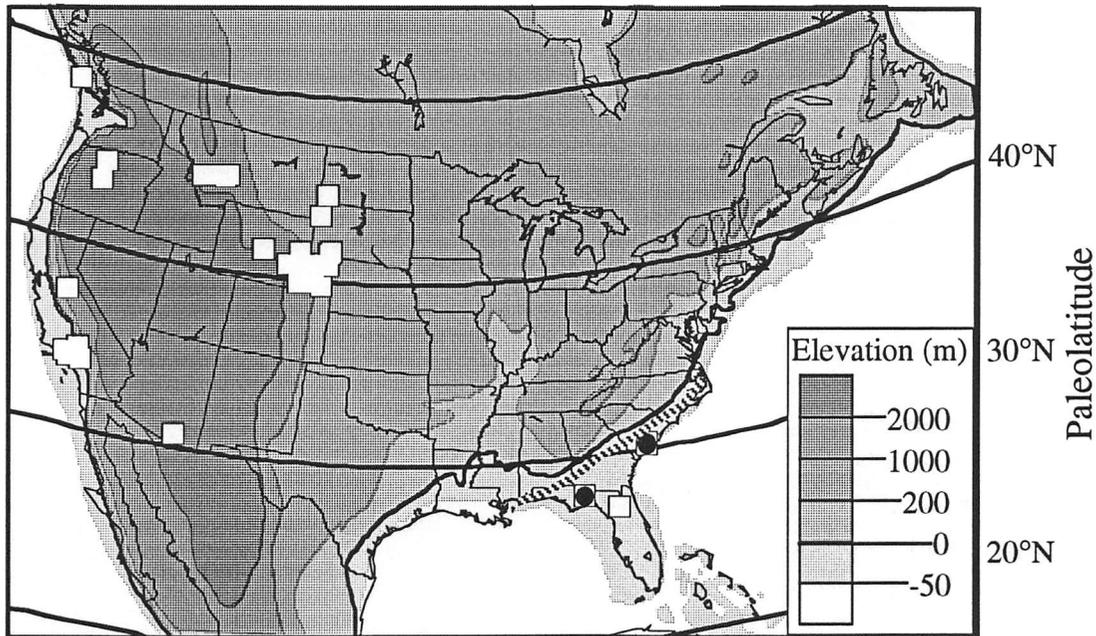
#### **VI.4. FOSSIL CROCODYLIAN DISTRIBUTIONS AND INFERRED PALEOCLIMATE**

The distributions of fossil crocodilians in North America, south of Hudson Bay, for four Cenozoic time intervals (Figures VI.1-VI.4) are plotted on present-day base maps with superimposed paleogeography and lines of paleolatitude. North American motion

during this period is minor and does not account for the changes in crocodilian distributions.

#### VI.4.1. Eocene

Crocodylian and noncrocodylian vertebrate localities are widely distributed in the Eocene strata of North America up to  $\approx 50^{\circ}\text{N}$  paleolatitude (Figure VI.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 VI.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 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 VI.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 (Figure VI.1). If true, this may explain the apparent warmth of the Rocky Mountain region.

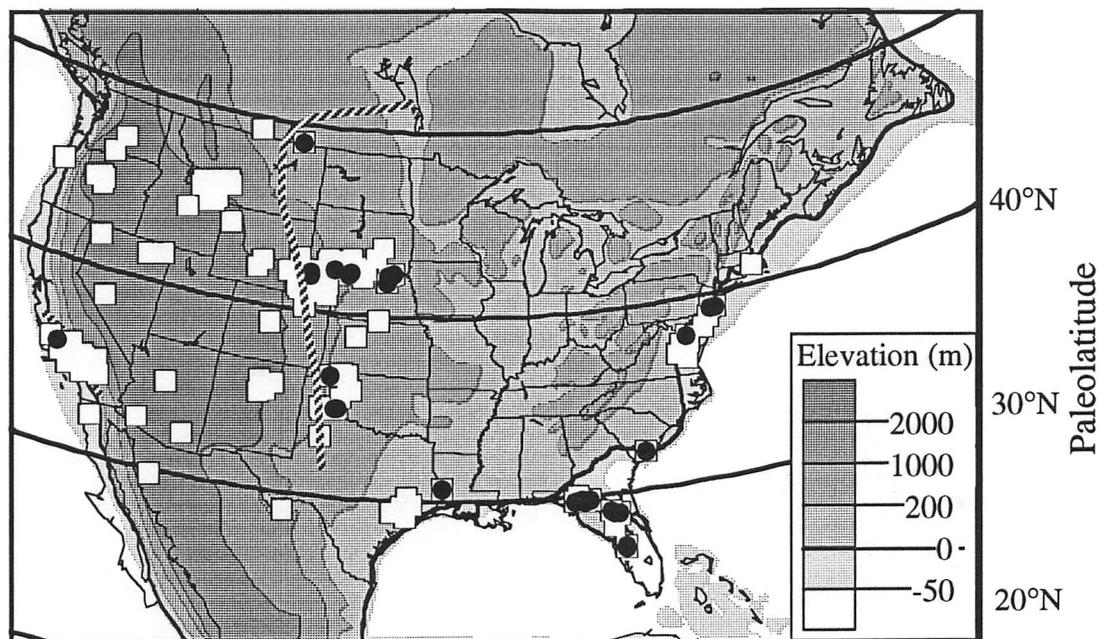


**FIGURE VI.2. Distribution of vertebrates and crocodilians in Late Oligocene.**

Paleogeography is for Chattian Stage. For key to symbols see Figure VI.1.

#### VI.4.2. Late Oligocene

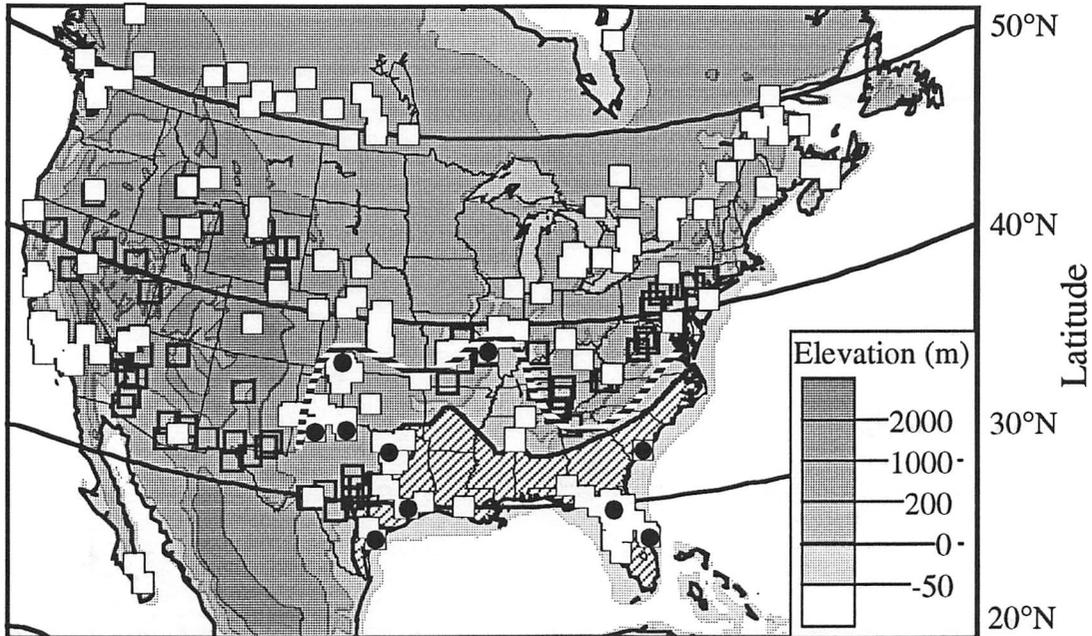
During the Late Oligocene, North American crocodilians are found only in maritime localities (Figure VI.2). Other vertebrates are known from the continental interior, but the number of localities represented, even allowing for the shorter length of the Late Oligocene compared to the Eocene or Miocene, is greatly reduced. The overall lack of crocodilian localities may partly reflect this. However, the number of crocodilian localities proportionally diminishes 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 would seem to indicate that the absence of crocodilians there is



**FIGURE VI.3. Distribution of vertebrates and crocodylians in Miocene.**

Paleogeography is for Middle Miocene. For key to symbols see Figure VI.1.

significant. Perhaps more significantly, the nature of the crocodylian 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*.



**FIGURE VI.4. Distribution of vertebrates and crocodilians in Pleistocene and early Holocene.**

Topography is for present day. Shaded area in southeastern United States represents present distribution of crocodilians in North America (Neill, 1971). Open squares--vertebrates recorded from cave deposits. For key to other symbols see Figure VI.1.

### VI.4.3. Miocene

In the Miocene fossil crocodilians are found in the 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 Miocene and that experienced 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 VI.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).

#### **VI.4.4. Pleistocene-Holocene**

With the establishment of ice sheets at both poles and consequent changes in the global climate system, 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 rivers such as the Mississippi, Red and Brazos Rivers during warmer interglacial climates may explain the presence of crocodilians beyond their historical distribution (see Figure VI.4). The distribution of non-crocodilian vertebrate localities shows that the crocodilian distribution shown for this time is well constrained.

### **VI.5. 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  $>7$  °C, mean annual temperatures  $>16$  °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). Concomitant with these glacial periods is the interpretation of increased aridity in continental interiors, which has also been used to

explain vertebrate distributions through this period (Hutchison, 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 Rocky Mountains for cooling climates and creating increased aridity in the Great Plains (Kutzbach et al., 1989; Ruddiman and Kutzbach, 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 datasets of geologic climate proxy data becomes more pressing, as does a fuller understanding of the limitations and biases such data sets inherently include.