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

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CHAPTER VIII

"THE FUTURE FORETOLD, THE PAST EXPLAINED, THE PRESENT...APOLOGIZED FOR:" GENERAL CONCLUSIONS AND FUTURE WORK

"...when you have eliminated the impossible, whatever remains, however improbable, must be the truth"

Sherlock Holmes
"The Sign of Four," Sir. Arthur Conan Doyle

There can be little doubt that the Earth's climate has changed through time, a fact recognized since the early nineteenth century. While the geological record provides the pattern of this change (the spatial and temporal distribution of paleoclimate), computer models allow us to investigate the processes responsible for patterns. But, as described in Chapter I, the success of modeling experiments can only be assessed by comparing results with the geological record (Saltzman, 1990), and our understanding of that record too often has been limited to a two dimensional view--changing climate through time. An understanding of the spatial pattern of paleoclimate is required. This has been the focus of this dissertation, in which I have used geologic data (principally fossil crocodilians--data stored in a customized relational database described in Chapter III and a detailed report given in Appendix D) to reconstruct the temporal and, more importantly, the spatial


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pattern of paleoclimate during the last 100 million years, an interval during which the Earth changed from a world without large polar ice-sheets (a "hot-house" world) to the glaciated world in which we now live (an "ice-house" world). As part of this study I have also examined the nature of the data themselves and the modern world upon which so much of our understanding of the past is based.

In this final chapter I summarize the principal conclusions of this study and also outline some of the additional questions and avenues of research that the study has spawned.

VIII.1. CONCLUSIONS: THE PRESENT

Paleoclimate interpretations from geologic data depend heavily on analogy with the Recent. For fossil crocodilians (specifically crown group crocodilians: members of the Alligatoridae, Crocodylidae and Gavialidae, which all have extant representatives), the analysis of present day climate limitations, based on the distribution of modern crocodilians and experimental observations described in Chapter IV, showed the following:

1. Temperature is the principal climatic factor responsible for limiting the distribution of crocodilians—not just the magnitude of minimum temperatures, but also their duration. This is supported by the experimental observations of Colbert et al. (1946) and Smith (1975, 1976, 1978, 1979), by the observed increase in the incidence of disease and juvenile mortality at lower temperatures (Blake and Loveridge, 1975; Coulson et al., 1973; King and Dobbs, 1975; Webb and Cooper-Preston, 1989), and by the general trends indicated by the climate station dataset
used to define the climate space presently occupied by extant crocodilians. Observed values that may be applied to fossil occurrences are as follows: MAT: ≥14.2°C (≥16.0°C is probably more applicable; there is a 95% probability that the random occurrence of a crocodilian will indicate a MAT≥18.0°C); CMM: ≥5.5°C; mean Winter T: ≥6.6°C; MART: ≤24.0°C.

2. Standing water provides an essential buffer against temperature extremes, without which a fundamental element of behavioral thermoregulation is precluded. However, this dependence on water need not reflect local precipitation--e.g., the Nile River. The absence of crocodilians can therefore reflect local hydrological conditions rather than just temperature.

3. Elevation may affect hydrology and temperature and thereby influence crocodilian distributions independent of the state of the global climate.

VIII.2. CONCLUSIONS: THE PAST

VIII.2.1. Mesozoic Glaciations?

In Chapter II the evidence for Mesozoic continental glaciations was assessed, with particular regard to the implications for eustacy. The following conclusions were reached:

1. The use of erratics in marine strata as evidence for continental glaciation is questionable, especially given the absence of other unequivocal evidence such as
striated pavements. Calculations were used to show that all of the known Mesozoic erratics can be explained using non-ice-rafting mechanisms, especially organic rafters such as trees.

2. It is postulated that the coincidence of erratic-bearing beds with marine transgressions suggests a scenario in which flooding of low-lying forested areas provides large trees with "erratics" enveloped in their roots for transport into the marine environment.

3. The use of glendonite as an indicator of glaciation is dubious. If, as has been suggested, glendonite is a pseudomorph after ikaite, then its presence suggests cold conditions only and not necessarily the existence of ice-sheets.

4. The magnitudes and frequencies of the 3rd-order eustatic curves of Haq et al. (1987) would require the presence of large (Antarctic-sized) continental glaciers for numerous intervals in the Mesozoic. In the absence of unequivocal evidence for such glaciations we conclude that the absolute magnitudes of the 3rd-order curves must be exaggerated---magnitudes of 10-20 m are acceptable. Given this, global stratigraphic correlation using such curves should be reconsidered.

5. Despite the doubts expressed concerning the purported evidence for large-scale continental glaciation during the Mesozoic, this work has highlighted the need to recognize the spatial variation in climate during "hot-house" intervals. Consequently the perception of 'global' warmth must be tempered.
VIII.2.2. Crocodilian Distributions

The main emphasis of this dissertation is the reconstruction of the pattern of paleoclimate using the paleodistribution of fossil crocodilians. Although fossil crocodilians provide only one line of evidence and should not be seen as the definitive climate proxy or be considered in isolation, they are an ideal vehicle for examining patterns for the following reasons: they are climatically restricted in the Recent; they have a relatively good fossil record; and the dataset is of manageable size. These factors also allow other issues to be addressed: taphonomic effects, sampling biases, paleoclimate resolution, qualification of data absences, and the logistics of collecting such a large dataset. These issues were examined in Chapters V and VI with the following principal conclusions:

1. Qualifying absences. Control groups (turtles as the taphonomic control, all vertebrates as the collection control) provide a means of qualifying significant absences of the climate proxy (crown group crocodilians).

2. Paleolatitude. The paleolatitudinal range of crocodilians is found to reflect known climatic changes: during "hot-house" intervals crocodilians extend into high latitudes, but are restricted to low latitudes during "ice-house" intervals especially in the Late Oligocene and Pliocene-Recent. For the northern hemisphere, which dominates the preserved record, the Late Oligocene latitudinal fall was not as great as that in the Plio-Pleistocene, and seems to have been restricted to North America (see below).
3. Continentality. During the Late Oligocene and Pliocene-Recent, crocodilians in mid-latitudes become limited to maritime localities, concomitant with the observed contraction in their paleolatitudinal range. This is interpreted to reflect increases in thermal seasonality and aridity in mid-latitude continental regions (Chapter VI). These changes may have been exacerbated by increased topography, especially in North America (from the Late Eocene on, crocodilians are precluded from the Rocky Mountain region; see below).

4. Elevation. In Asia and North America uplift of the Tibetan Plateau and Rocky Mountain-Great Plains regions, respectively, may be partly responsible for the observed changes in crocodilian distributions during the Tertiary. As these areas rose, local temperatures decreased below the threshold for crocodilian survival—changes in local hydrology may also have been affected.

5. Biogeography. The distributional data also points to biogeographic effects influencing distributions, apparently independent of climate. Crown group crocodilians are precluded from the southern hemisphere until after the K-T boundary, when their southward expansion may occur in response to the preferential extinction of "mesosuchians" during this mass-extinction event. The exclusions of alligatorids and gavialids from Australia and Africa may reflect the lack of contemporary freshwater links to these regions—today both families are restricted to freshwater environments.
VIII.2.3. Crocodilian Diversity

In Chapter VII the diversity of crocodilians was investigated with the following conclusions:

1. Crown group crocodilians diversify exponentially through the Late Cretaceous and into the early Paleogene. There is no observed change in this trend across the K-T boundary.

2. Generic and species diversity falls in the Middle-Late Eocene, rediversifies exponentially in the Miocene, and then falls again in the Plio-Pleistocene. The coincidence of intervals with low diversity and paleolatitudinal range contraction is postulated to reflect lowered carrying capacities due to habitat restriction. Although the Middle-Late Eocene drop in diversity precedes the Late Oligocene paleolatitudinal range contraction, it does coincide with the preclusion of crocodilians from the Rocky Mountain region and central Asia. This may represent local responses to uplift rather than to global climate change.

3. The K-T boundary. While crocodilian diversity clearly responds to these long-term climate changes (Late Eocene-Oligocene, and Pliocene) there is little response to the K-T "event"; 30% of crown group crocodilian genera do become extinct at this boundary, but the exponential diversification of the group continues largely uninterrupted due to high origination rates in the Early Paleocene. This is consistent with a rapid "recovery" during this period, suggesting that whatever occurred at the K-T boundary was quickly resolved (within the 4.6 Myr of the
Early Paleocene). In addition, drops in observed diversity are apparent throughout the entire latitudinal range of the group at this time, but with no recognizable change in the poleward limits of the latitudinal range itself. The response of crown group crocodilians to the K-T boundary is in stark contrast to that of the "Mesosuchia," which do seem to undergo a major extinction at this time. Expansion of crown group crocodilians into the southern hemisphere does not occur until after this event, and circumstantially appears to be in response to the demise of "mesosuchians." However, the reason for this differential response to whatever occurred at the K-T boundary is presently unclear.

4. Paleolatitudinal Diversity. There is evidence for a bimodal paleolatitudinal distribution in the diversity of crocodilians during the Late Cretaceous and Paleogene, with peaks in mid-latitudes. A third peak in equatorial regions increases throughout the Paleogene and into the Neogene, towards the end of which they converge into a single equatorial peak.

VIII.3. THE FUTURE

This project has depended heavily on the compilation of large amounts of data—not just information on fossil crocodilians, but also on the control groups and corroborating proxies, lithologic and environmental data, and more recently a survey of the climate distribution of modern organisms (Chapter IV). The result has been a dataset that has provided me with the opportunity to address issues that go way beyond the limits of the present dissertation: questions of paleobiogeography, biodiversity (fossil and recent), paleoecology, mass-extinction, mega-biases, and taxonomic heterogeneity's. Part of the
FIGURE VIII.1. Recent North American reptilian generic diversity as a percentage of the non-avian tetrapod fauna.

This dataset breaks down diversity into 5 x 5 grid squares. The new dataset assigns faunal and floral lists to climate stations and therefore provides more precise information. The same trends are found using each method. Note the decline in relative diversity with increasing latitude, and thereby temperature.

power of the dataset is its integration of modern and fossil data. The Recent provides the template for examining the past, but the Recent is also the sum of its history. A full understanding of the Earth System requires examination of issues from both perspectives, and the dataset used in this study has been designed to facilitate exactly this dual approach.

Figure VIII.1 shows the proportion of the non-avian tetrapod generic fauna of North America that comprises reptiles. It is based on a pilot survey of modern vertebrate diversity using genus counts for each 5° x 5° grid square. While this dataset provided a
general view of diversity trends, and hinted at a circumstantial relation with climate, it did not provide the means for further analysis. This shortcoming was the motivation for creating the climate station-based faunal dataset described in Chapters III and IV. Not only can this dataset be used to define the climate space occupied by any organism or taxonomic group—the distribution of palms and the giant tortoise *Geochelone* in the MAT-MART climate space is shown in Figure VIII.2—but also to examine larger scale patterns: for instance, latitudinal diversity gradients (Figure VIII.3) and the relationship between net primary productivity (NPP; using NDVI as a surrogate) and biodiversity (Figure VIII.4). This modern dataset also lends itself to analysis through multivariate statistical techniques, such as Correspondence Analysis (CA), which can be used to examine the relationship of whole assemblages to one another, or even to environmental metrics (Canonical Correspondence Analysis, CCA, Ter Braak, 1987-1992). For example, Figure VIII.5 shows the results of a correspondence analysis of North American non-avian tetrapod genera. Axis 1 appears to correlate with generic diversity (shading on figure), but also with latitude and MAT (insert, Figure VIII.5), while axis 2 correlates with precipitation (insert, Figure VIII.5). These relationships suggest a link between faunal composition, diversity, and climate. This can be examined more closely by analyzing particular groups, such as amphibians, which would be expected to show a greater relationship with water than temperature. Figure VIII.6 shows a correspondence analysis of Australian amphibian species. In this case axis 1 shows the strongest relationship with precipitation and axis 2 with temperature (MAT; inserts Figure VIII.6), consistent with amphibian physiology. There is also a biogeographic effect here as recorded by the "U" shaped relationship between diversity and MAT.

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2. Lieth notes that "The optimum temperature for productivity, in the range of 15°-25°C, agrees with the optimum temperature range for photosynthesis." (p.242, Lieth and Whittaker, 1975). This range is very similar to the thermal limits of crocodilians; a comparison of the spatial distribution of regions of high primary productivity (see Figure 2-1, p.14, Lieth and Whittaker, 1975) and that of crocodilians, shows that the two are very similar. Lieth's productivity is based on ground observations (g C / m² / yr) but the satellite based NDVI data shows the same spatial distribution.
FIGURE VIII.2. The position of the giant tortoise Geochelone (top), and palms (bottom), in MAT-MART climate space.

Small dots represent all climate stations in the dataset that fall within the limits shown. CMM refers to Coldest Month Mean temperature and WMM refers to Warmest Month Mean temperature. Use of these diagrams facilitates direct comparisons with Wolfe's work on modern and fossil floras and can be created for most terrestrial organic groups at any prescribed taxonomic level.
FIGURE VIII.3. Recent species diversity as a function of absolute latitude.

Data are from the compilation of Recent faunal information stored in the Vertebrate Database.
FIGURE VIII.4. The relationship between non-avian tetrapod generic diversity and "productivity" (represented by NDVI).

Note that the "humped-shaped pattern" predicted by Rosenzweig (Rosenzweig and Abramsky, 1993) is not seen (this predicts that peak diversity does not coincide with peak productivity, but at some intermediate value). However, some subsets of the data do show the hump, for instance North American rodents, although European rodents do not. The implication is that the hump is a biogeographic artifact. See Chapters III and IV for discussion of NDVI as a proxy for Net Primary Productivity (NPP).
FIGURE VIII.5. A Correspondence Analysis of North American vertebrate faunas (genera).

The gradient shown by the grayscaling represents the generic diversity at each station (black, lowest diversity, light gray, highest). The inserts show the relationship between axis 1 and MAT, and axis 2 and annual precipitation. The minor arch effect seen here is an artifact of the method. The spread of data at low diversities represents the higher potential for differences possible when low numbers are considered. In paleoecological studies, sites with low diversities are often ignored. The problem is that in the case shown in this figure these stations do have low diversities and the faunas are different. Further analysis is therefore required, which the breadth of dataset facilitates.
FIGURE VIII.6. A Correspondence Analysis of Australian amphibian faunas (species).

The gradient shown by the grayscaling represents the species diversity at each station (black, lowest diversity, light gray, highest). The inserts show the relationship between axis 1 and annual precipitation, and axis 2 and MAT. In this case diversity is positively correlated with precipitation rather than temperature (MAT) as shown in Figure VIII.5, reflecting the physiological constraints of amphibians.
between annual precipitation and axis 1. This is probably due to the isolation of southwestern Australia from the other areas of moderate to high precipitation.

These are just a few of the questions that can be addressed using this dataset. But as well as investigating modern patterns, the climate station faunal dataset can also be used to model the fossil record, for instance by degrading the modern record to emulate the effects of mega-biases such as taphonomy. The results can then be directly compared with the fossil data contained within the same database. Again, the dataset has been designed with such tasks in mind.

Patterns and relationships established in the Recent provide predictions for the past. Although in this study I have concentrated on crocodilians (as a template for the examination of other types of data), the fossil dataset also includes information on other vertebrates (for instance tortoises may be defined in climate space using the modern data, Figure VIII.2, and then their distribution examined through time, Figure VIII.7). It also includes data on lithologies (Figure VIII.8) and floras (the integration of floral data is in progress). Again, the Recent provides the template for the past, but is itself the consequence of its history. With this dataset, issues can be addressed from both perspectives.

VIII.4. FINAL THOUGHTS

An understanding of Global Change requires an examination of global patterns; the record of a single locality or region cannot be used as a proxy for the whole planet, just as a single adjective cannot be used to describe an entire geologic interval. Like an impressionist painting, if we stand too close we may identify individual "colors" but little else; only when
FIGURE VIII.7. The paleolatitudinal distribution of the genus *Geochelone* (black circles), superimposed on that of the family Testudinidae (light gray circles).

The distribution of giant tortoises, *Geochelone*, is shown to become increasingly restricted to low latitudes towards the Recent. This is not seen in the family Testudinidae as a whole. The difference is almost certainly a function of size and the greater difficulty that *Geochelone* has in isolating itself from environmental extremes. The use of this group as a climate proxy has been advocated by several authors (Brattstrom, 1961; Graham, 1986).
FIGURE VIII.8. The distribution of Recent peats (black circles) and evaporites (gray diamonds).

Data are from the Lithological Database of the Paleogeographic Atlas Project. The bar charts show the absolute number of peat (black) and evaporite (gray) occurrences, and the percentage of all occurrences (peats + evaporites) represented by each lithology. Each bar represents counts for 5° latitudinal zones. The arid zones, referred to in Chapter IV as a major limiting factor in determining crocodilian distributions, are readily apparent in this figure.
we step back and look at the larger scale patterns does the overall picture become clear. This necessitates a breadth reminiscent of a nineteenth century inquiry. As a consequence, the study presented in this dissertation is not an end in itself; it is not a test of a single hypothesis, nor is it the product of a dissertation recipe. Nonetheless, it provides a template for examining the Earth System, past and present, and has clearly demonstrated that coherent patterns exist. For the paleoclimate of the last 100 million years, the dissertation shows that whether we examine the paleodistribution of fossil crocodilians (Chapter V) or their diversity (Chapter VII), whether we consider floras (Wing and Greenwood, 1993), tortoises (Graham, 1986), or even the general trends of the marine isotopic record (Chapter II), the patterns all indicate the same interpretation of global change. Given this, we must accept the validity of the interpretation:

"The united force arising from the constant repetition of these analogies, without the occurrence of one solitary analogy of a contrary tendency, must, to ordinary understandings, multiply that probability till it assumes the highest rank of which probable reasoning admits" (p. 143, Conybeare, 1829).

If we do not, then all of the coincidences suggested by the geological record and analysis of the Recent are no more than that--just coincidences. If that is true, then we can never hope to understand the past or the present and will be forced to conclude that everything is ruled by nothing other than chance, and that, in the words of Conan Doyle's Sherlock Holmes "is unthinkable."