

Fossil crocodilians as indicators of Late Cretaceous and Cenozoic climates: implications for using palaeontological data in reconstructing palaeoclimate

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Abstract

That the Earth's climate has cooled over the last 100 million years has been recognized since the early nineteenth century—the transition from the 'hot-house' world of the Cretaceous (a time interval without significant polar ice-sheets) to the 'ice-house' world in which we now live. Today, the dynamics (process) responsible for this change are being examined using computer models, especially General Circulation Models (GCM's). Through such work our understanding of the dynamics of the Earth system improves and our ability to predict future trends is enhanced. But, the success of modelling experiments can only be assessed by comparing results with observations (the pattern), which, for palaeoclimate, are drawn exclusively from the geological record. Palaeoclimate interpreted from geological data is invariably based on analogy with the Recent, the validity of which depends on corroboration from multiple lines of evidence. This requires the compilation and investigation of large, global datasets of well-constrained geological climate proxies.

This study uses the palaeodistribution of fossil crocodilians to examine the spatial distribution of palaeoclimate during this transition. Fossil crocodilians have a relatively good fossil record and are climatically limited in the Recent. They also provide a manageable global dataset with which to investigate other issues that impinge on the use of geologic data for reconstructing palaeoclimate: taphonomy, sampling effects, time-averaging, tectonics, and, for fossils, palaeobiogeography and evolution. As such this study provides a possible template for examining other climate proxies in order to validate and hone palaeoclimatic interpretations.

An analysis of modern crocodilians indicates that temperature is the principal influence on their global distribution, with the Coldest Month Mean temperature (CMM) of $\approx 5.5^{\circ}\text{C}$ marking the minimum thermal limit for the group, corresponding today to a minimum Mean Annual Temperature (MAT) of $\approx 14.2^{\circ}\text{C}$. The duration of warmth during the year (partly indicated by the Mean Annual Range of Temperature, MART) is also important, as this affects early juvenile development and survival. The presence of standing water provides an essential thermal buffer against temperature extremes. By analogy, the palaeodistribution of fossil crocodilians suggests the following: during the Late Cretaceous and early Palaeogene MAT's in excess of 14.2°C (CMM's $> 5.5^{\circ}\text{C}$) permeated throughout mid-latitudes and coastal regions in high latitudes; during the Oligocene the restriction of fossil crocodilians to low latitudes suggests high-latitude cooling, as indicated by numerous other lines of evidence—coeval restriction of crocodilians to coastal regions in mid-latitude North America and much of Asia, consistent with increased seasonality and aridification in

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continental interiors, may reflect local orographic changes as well as global climate change. During the Miocene fossil crocodilians return to the Great Plains of North America, but do not reoccupy the continental interior of Asia; by the Pliocene, crocodilians are again restricted to low-latitudes and coastal regions in mid-latitudes, coincident with further high-latitude cooling, and aridification and cooling of mid-latitude continental interiors. Minor distributional changes during the Holocene may reflect human effects. © 1998 Elsevier Science B.V.

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1. Introduction

That the Earth's climate has changed through time was readily apparent to early geologists. Fossil collections made in northern Europe were typified by forms more reminiscent of the present tropics than the latitudes in which they were found (Lyell, 1830, p. 92). This suggested to geologists that the Earth's surface had undergone a progressive cooling down to the present day, a view so widely accepted in the early nineteenth century that Greenough referred to it as "one of the most undoubted facts in geology" (Greenough, 1834, p. 216). Although this cooling trend was ultimately tempered by the discovery of glacial deposits from other parts of the record (Croll, 1875), the presence of 'tropical' floras in high latitudes continued to require greater warmth than at present for much of the geological past, especially the Mesozoic and early Cenozoic. This led Elie de Beaumont to postulate that polar regions, in the early Tertiary at least, were essentially ice-free (de Beaumont, 1836).

Today, palaeoclimatology is enjoying a renaissance as concerns grow over the potential effects of anthropogenically induced climate change. But, despite the development of stable isotope geochemistry, the accession of the deep-sea record and the wealth of new climatically pertinent fossil data, our fundamental understanding of palaeoclimate remains essentially two-dimensional: changes through time (for instance, a 'warm Cretaceous' followed by 'cooling to the Present Day'), as epitomized by the 'global' oxygen isotope curve (Fig. 1). Such generalities tend to obscure more 'subtle' changes, for instance the effect of continentality and development of seasonality (Markwick, 1994), which may better indicate the dynamics responsible for climate change, than simply stating

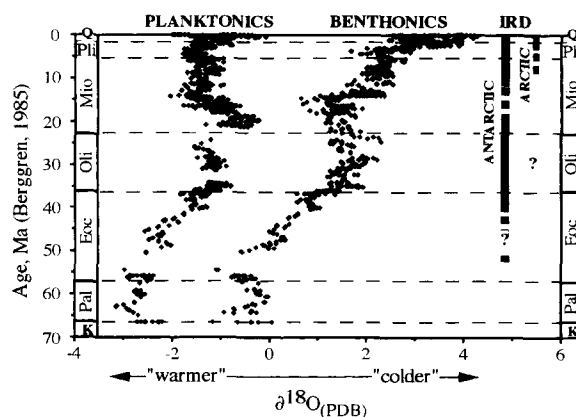


Fig. 1. The benthonic and planktonic oxygen isotope curves (modified from Markwick and Rowley, 1997; after Prentice and Matthews, 1988).

that the earth is becoming 'cooler' or 'wetter' through an interval. This has been compounded by the fact that many studies of geological-scale global climate change have been based on extrapolations from analyses of single localities or individual basins. While local changes may potentially reflect more general trends, they need not, no more than London or Chicago today represents the mean climate state of the present Earth. To understand global climate change fully we must examine palaeoclimate in all its dimensions: in short we must map palaeoclimate both spatially and temporally.

The need to understand the spatial variation of climate in the geological past has become critical with the development of computer-based equilibrium climate models, specifically General Circulation Models (GCM's). These models provide the means of examining the dynamics of palaeoclimate (the process). But modelling success can only be assessed by comparing results with observations (Lloyd, 1984; Kutzbach, 1985; Saltzman, 1990); models cannot, in themselves,

generate data. For palaeoclimate, these observations (the pattern of palaeoclimate) are derived from the Geological Record (Saltzman, 1990)—although the Geological Record cannot directly describe the dynamics (process) responsible for past climates, it may imply which processes are important through circumstantial evidence, for instance, the temporal coincidence of periods of mountain building and glaciation (Markwick and Rowley, 1997). A full understanding of palaeoclimate therefore requires both a comprehensive understanding of the spatial pattern of palaeoclimate (a ‘warm Cretaceous’ provides little comparative power) and some measure of agreement if the models are to be used to resolve dynamical questions. Unfortunately, such agreement is presently limited, and this has led to a considerable debate over the relative merits of models versus data (for instance in reconstructing Eocene continental climates: Sloan and Barron, 1990, 1991; Archibald, 1991; Wing, 1991). If we accept that each addresses a different issue (pattern or process), then such disagreements cease to be contentious and instead provide an opportunity for refining the models themselves. Thus, the goal is to seek convergence between geological data (pattern) and model results (process). Since these models are also instrumental in predicting the potential direction and nature of future climates, whether natural or anthropogenically induced, studies of the climate of the geological past have a direct application to present concerns.

Although maps showing the spatial distributions of climate proxies have been assembled for many geological intervals (viz., Vakhrameev, 1975, 1978, 1991; Frakes, 1979; Wolfe, 1985; Ziegler, 1990; Horrell, 1991; Ziegler et al., 1993), the most detailed and comprehensive compilations have been limited to the Quaternary, best represented by the work of CLIMAP (Climate/Long-Range Investigation, Mapping and Prediction) in the Pleistocene and COHMAP (Cooperative Holocene Mapping Project) in the Holocene (CLIMAP Project Members, 1976, 1984; COHMAP Project Members, 1988; one of the original aims of CLIMAP was the compilation of global data from a wide range of interdisciplinary fields, which could then be used to define boundary conditions for checking modelling results and therefore aid in

understanding the dynamics of the climate system). This partly reflects the greater availability of Quaternary data, but also, in part, its greater perceived relevance to recent climate issues—the view that climate changes over the next 50 to 100 years can only be understood by investigating historical records of climate phenomena occurring on similar time scales, which, given the temporal resolution of the geological record, effectively limits the available record to the Holocene or, at the very most, the latest Pleistocene. (It is also possible that the logistical problems associated with amassing such large datasets may have limited past efforts, especially in the absence of computerized databases). But, the pre-Pleistocene record does provide valuable information on the Earth’s climate system, especially the large-scale changes that occur on geological, or tectonic, time scales. It is upon these long-term variations that shorter-term changes are superimposed (Saltzman, 1990) and consequently they must be addressed. More importantly, if the present prediction of a doubling of atmospheric CO₂ by the year 2100 is correct (Houghton et al., 1996), then only the pre-Pleistocene record can give any indication of what the consequences of such an increase might be, either climatically or in terms of the biotic response (such CO₂ concentrations are not found in the Quaternary, but are believed to typify most of the Palaeogene, with even higher concentrations during the Cretaceous; Crowley and North, 1991; Freeman and Hayes, 1992). More fundamentally, pre-Pleistocene climates, especially those of the Cretaceous and early Palaeogene, differ substantially from that of the present, and if we cannot explain them then we may be missing a key element in understanding the Earth’s climate system. Such questions must be resolved by climate modellers, and those models must be based on an understanding of the data (pattern).

The geological record provides our only direct source of information for mapping palaeoclimate. Traditionally patterns have been based upon palaeontological information, supplemented with lithological evidence, such as coals, evaporites and soils (Ziegler et al., 1984, 1987; Retallack, 1986; Gyllenhaal, 1991; Sellwood and Price, 1994). Recent emphasis has been towards geochemical techniques, especially analyses of stable isotopes,

such as oxygen. In the debate over Eocene continental climates, isotopic interpretations have been used to corroborate model results over palaeontological inferences (Seal and Rye, 1993). But, while fossil evidence directly samples past climates (the organisms themselves are the products of evolutionary adaptations to the environments in which they lived), isotopic signals are subject to additional uncertainties associated with identifying the source reservoir and its parent isotopic composition, fractionation effects, temperature and diagenesis (Buchardt and Fritz, 1980). Although a very powerful tool (especially in the marine realm, where the signal is ‘cleaner’ and the basic shape of Cenozoic climate defined; Fig. 1), it is no palaeoclimate panacea, and resulting interpretations, as for fossils, must be corroborated by independent evidence. In terrestrial environments the sparsity of isotopic data places further emphasis on lithological and palaeontological evidence.

The interpretation of terrestrial palaeoclimate using fossil data depends heavily on analogy with the climate tolerances of Recent species (“taxonomic uniformitarianism”, Dodd and Stanton, 1981, p. 17). The validity of applying the ‘climate’ of living organisms to their extinct relatives has been questioned, given the potential for evolutionary change in physiology that are not detectable in the preserved fossil (Fleming, 1829, 1830; Ostrom, 1970). This has led to scepticism of climate interpretations derived from fossils, which has been recently compounded by the results of numerical climate model experiments that have suggested palaeoclimate scenarios that differ from those implied by fossil evidence (Sloan and Barron, 1990, 1991). But, as stated above, numerical climate models do not, in themselves, provide data, only “hypotheses to be tested continually for their simulation capabilities compared to observations” (Saltzman, 1990, p. 70). Consequently, model results cannot be used to assess the validity of fossil-derived climate interpretations. Such validation can only come from the geological record itself by intercomparisons between various geological data. I consider this to be a central tenet for reconstructing the pattern of palaeoclimate using geological information, a tenet first stated by Conybeare: “They [geologists] do not ... reason from a few detached cases, but from an induction

of the whole phenomena presented by the distribution of organic remains—from a collective view of all the analogies. Each of these analogies, taken separately, must surely, unless it can be neutralized by some countervailing argument, be allowed to constitute a probability. 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” (Conybeare, 1829, p. 143). Thus the presence of alligatorids in the Canadian Arctic of Eocene Ellesmere Island may at first be explained as either reflecting an evolutionary change in alligatorid physiology or a climate change. Consideration of the associated biota of giant tortoises and salamanders (Estes and Hutchison, 1980; McKenna, 1980) would, using Conybeare’s arguments, strengthen a climatic interpretation since the simultaneous evolution of the entire fauna seems implausible. The more corroborating evidence we can supply the more confident we can feel in our interpretations.

There are two consequences that follow from this if we are confidently to map the spatial distribution of palaeoclimate through time using geological data. First, we need a global dataset to reconstruct the pattern of global palaeoclimate; and second, we need corroborating data for this dataset (i.e., other geological data on a global scale). In short, we need a lot of data. In addition, derived climate interpretations must be gathered quickly if they are to have any impact in elucidating potential global climate changes on human time scales (say, the next fifty years). This urgency precludes the detailed re-examination of all pertinent localities around the globe, but instead directs us to the shelves of the world’s libraries. It is this source that provides the basis for the present study.

2. This study

In order confidently to make intercomparisons between multiple lines of evidence it is essential that the nature of each climate proxy be understood. This requires an understanding of not only the fossil record with its inherent biases (Part 2 of this study), but also an investigation of the climatic

limits of living relatives that are to be applied to fossil occurrences (Part 1). This study concentrates on one climate proxy, the order Crocodylia, as a means for examining these issues. As such it is intended to provide a template for future research.

The aim of this study is to map out, both spatially and temporally, the most fundamental of palaeoclimatic transitions recorded in the geological record: the change from a non-glacial to a glacial world. Although glaciations have occurred at discrete intervals throughout geologic time, the most recent case, in the Cenozoic, provides the best opportunity to examine the details of such a transition. First, the record is relatively complete. Second, extant biotic groups are well represented in the fossil record, which is vital since palaeoclimate interpretations depend heavily on analogy with the climatic constraints of living groups. Finally, plate reconstructions and palaeogeographies (especially orography), both essential GCM boundary conditions, are well constrained.

The general trend of the climate transition from the 'hot-house' world of the late Mesozoic to the 'ice-house' world of the late Cenozoic is chronicled by the oxygen isotope record (Savin et al., 1975; Matthews and Poore, 1980; Matthews, 1984; Shackleton, 1984; Miller and Fairbanks, 1985; Prentice and Matthews, 1988; see Fig. 1) with the most dramatic climate change placed within the Oligocene coincident with a significant oxygen isotopic shift and a substantial (ca. 140–180 m) and very rapid (within 0.5 Myr) 'eustatic' sea-level drop (Vail et al., 1977; Miller and Fairbanks, 1985; Haq et al., 1988; Mackensen and Ehrmann, 1992), both strongly suggestive of the formation of large continental ice-sheets. The overall nature of the change is complex and in order to understand it fully, the temporal bounds of this study encompass the full span between the middle Cretaceous and the Recent (the inclusion of the Cretaceous in this study facilitates additional questions concerning ecological differences between pre- and post-end Cretaceous mass extinction).

The fossil data used in this study comprise over 5700 globally distributed fossil vertebrate localities, taken from the literature, and include comprehensive stratigraphic, environmental and sedimentological information for each—crocodilian localities were derived from the primary literature where

possible; non-crocodilian bearing localities were initially compiled from reviews in order to more rapidly collate a dataset of the 'universe' of fossil vertebrate localities; these review-based data are now being replaced by the more detailed information from primary sources. This is augmented by data on about 17,167 extinct and living vertebrate taxa, which are represented by 26,576 fossil records (occurrences) and 51,558 recent records (linked to climate station data, see Section 5.3.1). This information is stored in a custom-designed Macintosh relational database (see Markwick, 1996). The intentional breadth of the dataset allows questions concerning evolutionary trends, palaeoecology, biogeography, taxonomy, misidentification, dating and so forth, which impinge on any interpretation of palaeoclimate to be addressed. It also provides an opportunity to investigate other vertebrate groups, such as the dinosaurs and, more importantly for palaeoclimate, other amphibians and reptiles which are climatically restricted in the Recent.

3. The study group, order Crocodylia

3.1. Classification

Living crocodiles, alligators and gavials are members of the order Crocodylia (hence the informal term 'crocodilian' or 'crocodilian'), which today comprises eight extant genera distributed throughout low latitudes Equator-ward of about 30° (Fig. 2). With the living birds, crocodilians are the surviving members of the subclass Archosauria that also includes the extinct dinosaurs. This latter relationship has motivated much of the interest in crocodilian habits and physiology as a possible guide to understanding the biology and lifestyles of that extinct group.

Although the classification of crocodilians has been modified in recent years (Clark, 1986; Benton and Clark, 1988; Norell, 1989), I have kept to the more traditional classification given in Carroll (1988) because of its greater familiarity to non-crocodilian workers (see Markwick, 1996, for further discussion). In order to mitigate potential evolutionary/physiological incongruities, only

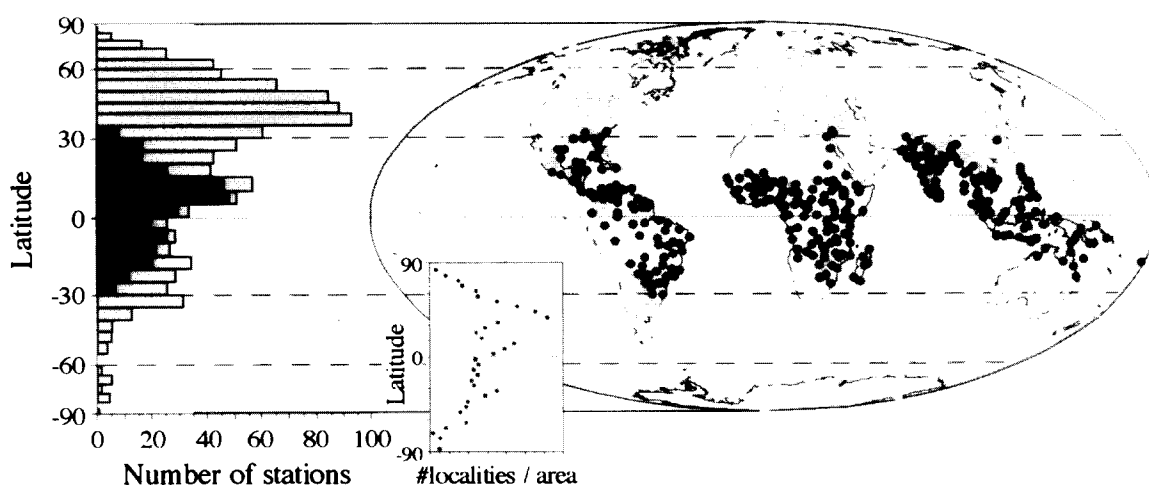


Fig. 2. The distribution of modern climate stations used in this study (for additional information see text). Stations with crocodilians are represented by black circles, all others by grey circles. The bar chart on the left of the figure shows the number of stations in each 5° latitudinal zone (the numbers of crocodilian-bearing stations in each zone are shown in black). Note the peak in northern mid-latitudes which represent stations in Europe and the United States. The inset shows the ratio of stations to area of land in each 5° latitudinal zone.

fossil members of the three extant families (Alligatoridae, Crocodylidae and Gavialidae) have been used to interpret palaeoclimate. In order to avoid repetition of the cumbersome phrase 'Alligatoridae, Crocodylidae and Gavialidae' throughout the text I refer to these groups collectively as 'crown group crocodilians', in deference to the fact that they represent the crown group in Clark's (1986) cladistic classification (Clark, 1986).

A complete list of the genera used in this study, with their family assignments and age ranges, is given in Markwick (1996).

3.2. *Crocodilians as climate proxies*

The order Crocodylia has been used as an indicator of warmth in the geological record since the early nineteenth century (Crichton, 1825; Lyell, 1830; Owen, 1850; Berg, 1965). Indeed the efficacy of this climate proxy has rarely been doubted; Matthew (1915, p. 287), in his review of the relationship between palaeoclimate and organic evolution, states that "the present limits of range [of the order Crocodylia] are conditioned chiefly by temperature and climate, and that the much wider range in the early Tertiary was due to a warmer

climate towards the poles, will hardly be questioned". Owen (1850) takes it for granted that the presence of crocodilians in the early Tertiary London Clay of England implies tropical climates. Hibbard (1960, p. 10) suggests that the value of fossil crocodilians may have been underestimated, describing them as one of "... the best indicators of temperature among the larger vertebrates". Crocodilians are not alone in providing climate information. Other vertebrates, especially mammals, have received considerable attention (Colbert, 1953, 1964a,b; Esteban and Sanchiz, 1986; Schleich, 1986; Thackeray, 1987; Janis, 1989, 1993; Repenning, 1990; Uhen, 1992; Woodcock, 1992). Moreover, since Lyell (1830), most geologists have recognized the palaeobotanical record as being the most informative for reconstructing terrestrial palaeoclimate (De Martius, 1825; Lyell, 1830; Nathorst, 1912; Seward, 1892; Wolfe, 1971). But there are a number of advantages to using crocodilians for this study: unlike the voluminous floral record, the record of crocodilians for the last 100 million years is more manageable, such that a global, comprehensive dataset can be compiled relatively quickly and intrinsic issues, such as biases in the record, can be readily examined; palaeoclimatic conclusions are derived from simple

presences rather than assemblage compositions (cf. floral physiognomic method, Wolfe, 1993) which makes them less susceptible to taphonomic influences; they are temporally long-ranged, but morphologically relatively conservative with numerous distinctive elements, especially teeth and scutes that are readily preserved in large numbers; living crocodilians are limited to warm climatic regions, more so than other ectotherms, such as snakes and turtles, that are of smaller size and therefore better able to utilize microhabitats where ambient temperatures may be warmer than observed surface temperatures (thermal climate). Consequently, fossil crocodilian occurrences might provide an indication of contemporary surface temperatures. The large size of crocodilians also increases their preservation potential in the fossil record.

In the absence of physiological evidence of climate tolerances in preserved fossils, climate interpretations using fossils, crocodilians in this case, are based on the climate tolerances of their extant relatives. In its simplest sense this is known as Nearest (or closest) Living Relative analysis (NLR). NLR requires a full understanding of the present ecological and climate requirements of living crocodilians. To this end some fundamental questions must be addressed: Are modern crocodilians climate-dependent? Is their distribution the maximum possible given their biology? What else limits crocodilian distribution? Could the present distribution be an artifact of history, man, or simple chance?

All geological climate proxies work on the fundamental assumption that geologists know the region of climate space in which these proxies can potentially exist (Fig. 3). This is analogous to petrologists defining the stability field of a mineral or mineral assemblage in a phase diagram. The problem is that this assumption is rarely met, partly because defining such boundaries is far from easy, and partly because, until recently, such details were not so crucial ('warm', 'cold', 'wet' or 'dry' sufficed). This problem is compounded by the fact that the spatial distribution of a climate proxy, especially an organism, need not necessarily be defined by only one or two parameters, but instead may be the consequence of numerous factors in

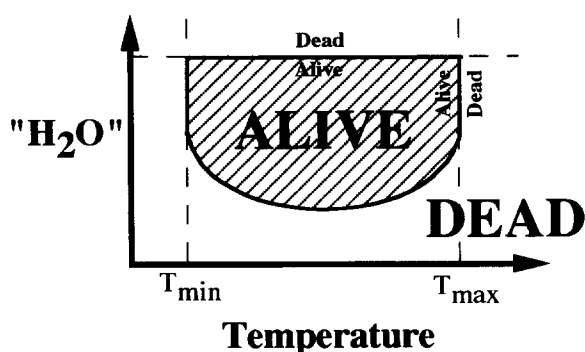


Fig. 3. The hypothetical position of extant crocodilians in two dimensional 'climate-space'.

multivariate space, including non-climatic ones, just as the stability field of a mineral phase is rarely only defined by pressure and temperature. Because of this, it is important to investigate all, or at least as many, of the factors that might influence the geographic distribution of a climate proxy, in this case crocodilians.

Our understanding of the climate tolerances of living crocodilians (and thus by analogy the climate interpretations of fossil crocodilians) comes from two principal sources: biological observations and distributional inferences. Biological observations are limited by the problems of working with such large and potentially dangerous animals (Avery, 1982), which generally restricts study to juveniles. They are also limited by ethical considerations, since the climatic limits (boundaries in climate space), especially the thermal tolerances, are fatal by definition. Consequently most palaeoclimatic interpretations have been based on distributional inferences. Thus Berg (1965) used the 10°C and 15°C winter (January, Northern Hemisphere, July in the Southern Hemisphere) isotherms for the most poleward limits of the alligators and crocodiles respectively, while Romer (1961, p. 201) pointed out that the alligator, the "most climatically venturesome of the group [Crocodylia], does not go north of regions with a mean annual temperature of about 60°F [$\approx 15.6^\circ\text{C}$] ...". This approach assumes that the present distribution of crocodilians represents occupation of the entire range of tolerable climates that crocodilians could

occupy, all other factors being equal. This need not be true.

In the following section I present a review of the limiting factors responsible for the distribution of living crocodilians, based first on empirical observations (experiment and field observations) and second on inferences based on their present geographical range, which also incorporates the consequences of biogeography, history, habitat, etc. (a more detailed review is given in Markwick, 1996). It is important to realize that the establishment of climate tolerances in the present does not automatically guarantee that fossil representatives had the same tolerances, although this is the most parsimonious assumption. Following the arguments of Conybeare (1829), validation of this assumption is based on comparisons with the interpretation of other preserved fossils. However, if we do not understand the Recent any conclusions about the past are mute.

PART 1 — THE RECENT

4. Empirical biological observations

All living crocodilians are ectothermic, and as such their body temperatures correspond closely to ambient environmental temperatures (Kirk and Hogben, 1946; Spotila et al., 1972; Smith, 1975, 1976). The environmental temperature is the temperature of the immediately adjacent environment, which may be water or mud, rather than air. Consequently changes in ambient air temperatures (weather) may be mitigated by the behaviour of the local medium.

Crocodilians, like all animals, live within a definable range of body temperatures. In the wild these are the 'critical maximum' and 'critical minimum' temperatures (Cowles and Bogert, 1944; Pough and Gans, 1982), and refer to the 'potential lethal temperature' above and below which the animal is no longer able independently to escape from imminent death. Direct measurements of critical minimum and maximum body temperatures are rare in the literature, given the deleterious effects on the subject crocodilian. For the American alligator, *Alligator mississippiensis*,

which is the best studied living crocodilian, the critical maximum is generally given as 38–39°C (Avery, 1982) and the critical minimum as about 4–5°C (Brisbin et al., 1982). This minimum value is based on a study of two large (188 and 135 kg) alligators in a pond in Barnwell County, South Carolina (32°18'N). One alligator died during this study, possibly as a result of experimentally induced stress. The other survived despite 1.5 cm thick ice and a minimum ambient water temperature of 4°C. The relation between the immediate environmental temperature (the water) and individual body temperature is clearly illustrated here (Brisbin et al., 1982). Freezing conditions and the formation of ice are not in themselves significant as long as the water temperature remains above the critical minimum body temperature and an air hole is maintained; indeed ice provides a thermal seal from external air temperature, slowing heat loss. However, freezing over of the air hole will result in drowning, and this consequently puts limits on how much ice can form and thus how cold the air can get and its duration (Brisbin et al., 1982; Child, 1987).

Other quoted minimum temperature limits are based on observed environmental temperatures. At Lake Ellis Simon, Caven County, North Carolina (35°50'40"N), Hagan et al. (1983) studied fourteen adult alligators which were fitted with transmitter collars that could measure environmental temperatures. In this experiment the coldest environmental (water) temperature was measured at 2°C, at which temperature the alligators were still able to react to the presence of the observers (mean minimum temperature for that month, February 1981, was 2.7°C). Hagan et al. (1983) also noted that many adult alligators, and some juveniles, survived in the study area during the record cold of January 1977, when the mean minimum air temperature reached –4.3°C and the lake froze over. At Elm Lake, Brazos Ben State Park, Texas, Hayes-Odum and Jones (1993) noted that the deaths of twelve adults were probably the result of one severe freeze in which air temperatures reached –13.9°C. In the Victoria Falls area, Zimbabwe, Child (1987) found that the Nile crocodile, *Crocodylus niloticus*, could survive subfreezing air temperatures in which 18% (ca. 22) of the days

between May and August were below 0°C as a consequence of elevation, although during this period only 0.9% (ca. 1 day) were below –4°C.

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 the Castle Shannon area, Allegheny County, Pennsylvania, for possibly 6 or 7 years despite the mean air temperature for the coldest month varying between –5.7 and 1.78°C (average –3.1°C) and the mean air temperature of the four coldest months varying from –0.6 to 3.3°C (average 0.5°C). However, such occurrences do not necessarily reflect where a viable crocodilian population capable of reproducing will survive (Neill, 1971; Markwick, 1994).

Crocodilian critical maximum and minimum body temperatures only provide the extreme limits within which individuals can survive. In general, crocodilians remain within their activity range (the temperature range within which crocodilians are able to maintain their body temperatures through behavioural, and to some extent physiological, means; Pough and Gans, 1982), which for *A. mississippiensis* is generally given as 25–35°C. This is also the activity range given for many other crocodilian species (Lang, 1987b; see also Johnson et al., 1976, and Fig. 4; 26–37°C, Brattstrom, 1965). The selected or ‘preferred’ temperature range (the range of temperature generally selected by the organism given the ‘choice’; Pough and Gans, 1982) for *A. mississippiensis* is taken as being 32–35°C (Brattstrom, 1965; Avery, 1982; Fig. 4). Most crocodilian environmental temperatures reflect closely the selected body temperatures and this has been recognized by zoos (Table 1).

The most significant feature of these temperatures is the difference between critical maximum and voluntary maximum which is only about 3°C, and that between critical minimum and voluntary minimum which is about 22°C. This suggests that alligators can cope with decreases in temperatures below their ‘optimum temperature range’ better than increases, and that despite the overall temperature tolerances of alligators, given the choice, they ‘prefer’ the warmer end of the range. This is

consistent with the results of Colbert’s experiments in the 1940’s (Colbert et al., 1946). This is intuitive when we consider that like all animals, crocodilians need to get the maximum amount of energy with the minimum of expenditure and as ectotherms this is far easier at higher temperatures. A similar result was found by Spotila and workers using a slightly different approach in which they calculated energy budget models for *A. mississippiensis* (Spotila et al., 1972, 1973; Spotila and Standora, 1985). They concluded that when an alligator is at its selected body temperature, it is restricted to a small portion of its climate space (the multidimensional space defined by climate parameters) and that while large alligators can operate outside their climate space, because they can store large amounts of heat, small individuals are more restricted (Spotila et al., 1972).

4.1. Importance of size

The importance of size was clearly demonstrated in the experiments of Colbert et al. (1946) in the 1940’s, with smaller alligators always being the first to react to heating or cooling. Subsequent workers have found the same pattern, for instance Diefenbach (1975), who found that heating rates in *Caiman crocodilus* were almost three times faster in the smaller individuals than the largest. Coulson et al. (1989) found that the metabolic rate is a function of size and temperature with the lower metabolic rates corresponding to larger animals and colder temperatures.

This size-based differential response to thermal changes is a direct consequence of ectothermy and the lack of an internal source of energy. Ectotherms gain and lose heat as a function of their heat capacity and the surface area across which heat is gained or lost to the environment: the larger an individual, the more heat or energy is required to raise its body temperature, and the longer it takes to lose heat. This is further exacerbated by the decrease in the surface area to volume ratio with increasing size, which decreases the area over which heat may be gained or lost relative to the volume of the body that must be heated or cooled respectively. This is the basis of ‘inertial homeothermy’ or ‘gigantothermy’

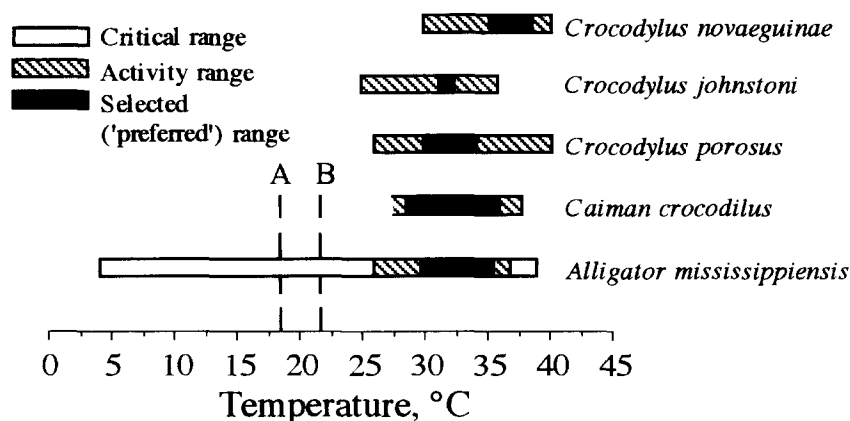


Fig. 4. The critical, activity and selected temperature ranges for five crocodilians. Data from the following sources: *A. mississippiensis*, Colbert et al. (1946), Brattstrom (1965), Smith (1975, 1976), Avery (1982), Brisbin et al. (1982), Lang (1987b); *C. crocodilus*, Diefenbach (1975); *C. porosus*, *Crocodylus johnstoni* and *C. novaeguinae*, Johnson (1974), Johnson et al. (1976). Note that critical temperatures are presently only known for *A. mississippiensis*, based almost exclusively on observations in the wild. The dashed lines represent for *A. mississippiensis*: (A) the temperature (18°C) below which renal function may be impaired (Coulson et al., 1973); (B) the temperature (22°C) below which appetite is suppressed (Coulson et al., 1973; Joanen et al., 1987).

Table 1

Environmental temperatures used in various zoos as an indication to possible selected ('preferred') temperatures

Species	Zoo	Water temperature (°C)
<i>Tomistoma schlegelii</i>	Lincoln Park, Chicago	24–27 (Almandarz, 1975)
<i>Crocodylus intermedius</i>	Lincoln Park, Chicago	24 (Almandarz, 1975)
<i>Osteolaemus tetraspis tetraspis</i>	Ueno Zoo, Tokyo	21–30 (generally 26) (Hara and Kikuchi, 1978)
<i>Osteolaemus tetraspis tetraspis</i>	Metro Toronto Zoo	24–27 (Teichner, 1978)
<i>Osteolaemus tetraspis tetraspis</i>	Memphis Zoo	24–29 (Beck, 1978)
<i>Crocodylus porosus</i>	Melbourne Zoo	27–30 (Dunn, 1981)

(Hotton, 1980), which has been used to suggest that very large ectotherms of dinosaur proportions would have been able to maintain sufficient body temperatures during cold periods by virtue of thermal inertia, without having to be endothermic.

This difference in the extent to which large and small individuals can cope with temperature has important ecological implications because it places limits on the survival of a viable population, such that the occurrence of individual adults is constrained in large part by the ability of juveniles to survive. This must also apply to the geological

record where the occurrence of a fossil must, using parsimony, imply the contemporary presence of a population rather than the consequences of an errant wandering individual (Markwick, 1994).

4.2. The consequences of extreme temperatures and other climatic factors

As body temperatures fall below the activity range, crocodilians become torpid. Although this cold-induced torpidity has proven useful for transporting zoo specimens (Almandarz, 1975), sus-

tained exposure to cold (even above the critical minimum) can be detrimental. Neill (1971) noted that torpidity led to death for American crocodiles, *Crocodylus acutus*, kept in water at about 18°C; Coulson et al. (1973) found that below 18°C renal function was impaired in individuals of *A. mississippiensis* (Coulson concluded that even in winter, temperatures between 29 and 31°C seem best for alligators). King and Dobbs (1975) noted that American alligators in zoos can tolerate temperatures as low as 5–10°C for short spells without affecting breeding success, but that animals subjected to low temperatures are more prone to hypoglycemic shock and gout than ones that are kept warm.

Blake and Loveridge (1975) suggested that cold might be the most important cause of Nile crocodile mortality in Zimbabwe, because of its suppression of appetite and the consequent increased susceptibility to disease. The relation between low temperatures and suppression of appetite has also been noted for alligators and caimans (Coulson and Hernandez, 1964; Lang, 1979). Coulson et al. (1973) found that for *A. mississippiensis* the desire for food was diminished or absent below 22°C, and this is supported by observations of Joanen et al. (1987) in Louisiana that *A. mississippiensis* only feeds between March and October when the mean temperature is 26.5°C. During the rest of the year alligators fast, even though the average temperature of the coldest month in this period is well above freezing (8.5°C).

There have been far fewer studies of the effects of high temperatures, although experiments of Colbert et al. (1946) in Florida, demonstrate that without access to water, alligators rapidly suffer heat exhaustion and die.

Although the extremes of temperature are clearly important, Hagan et al. (1983) concluded that the northern range of *A. mississippiensis* may not be affected as much by the severity as by the duration of the winter. This is most significant for the earlier developmental stages prior to sexual maturity. Joanen and McNease (1979) found that the nesting of *A. mississippiensis* in captivity occurs within a two-week period which is directly related to air temperature, with higher temperatures leading to earlier nesting. Further observations in western

Louisiana support this fact, with nesting in the wild occurring earliest (in late May–early June) when the March–April–May ambient temperatures are highest (average of 21.4°C), the bulk of nesting again taking place in a two-week period each year. Egg laying was delayed until late June–early July in the coldest years when the temperatures for March–April–May averaged only 18.3°C (Joanen and McNease, 1989). Postponement of nesting and egg laying limits the season available for incubation and successful hatching and may impair subsequent growth rates.

Growth rates are also directly related to the incubation temperature, which is inversely related to the total incubation time (Joanen and McNease, 1989). Joanen et al. (1987) found that the poorest growth rates were found in alligators incubated at extreme temperatures; this has been found also for *C. niloticus* (Blake and Loveridge, 1975; Hutton, 1989), and *Crocodylus porosus* in northern Australia (Webb and Cooper-Preston, 1989). Fuller (1981, cited by Hagan et al., 1983) reported that growth rates of *A. mississippiensis* in North Carolina are about one half those reported in Louisiana. Slower growth rates and small size make individual juveniles more vulnerable to predation, and there are a number of animals more than happy to feast on crocodilian eggs and juveniles (for instance the Nile monitor in Zimbabwe, Child, 1987).

An additional limit was noted by King and Dobbs (1975) who found that at temperatures less than 21°C the umbilicus did not properly heal and the hatchlings eventually died. Coulson et al. (1973) noted that high temperatures facilitate absorption of yolk sac which seems to reduce mortality rate.

An additional consequence of incubation temperature is sex determination. This has been discussed at length by numerous authors (Bull, 1987; Deeming and Ferguson, 1989). Experiments show that at lower temperatures females predominate (100% female at incubation temperatures of 30°C, while 34°C produces 100% males, Deeming and Ferguson, 1989). To date, five species of the genus *Crocodylus* and three species of alligatorids have been recorded as exhibiting temperature-dependent

sex determination, although the pattern in each varies (Lang et al., 1989).

Although temperature is the dominant limiting factor for crocodilians, the local hydrology is also very important. Water provides a thermal buffer against temperature extremes, but it can also affect nesting and consequent survival of juveniles. Joanen and McNease (1989) found that prolonged drought will cause egg desiccation, which is a serious mortality factor. They also point out the effect of floods on mortality, and note that tropical storms in coastal Louisiana can destroy 80–90% of nests. The importance of flooding was also noted by Blake and Loveridge (1975). In northern Papua New Guinea, Hollands (1987) reported that 15% of *Crocodylus novaeguinae* eggs and 20% of *C. porosus* egg clutches studied were lost to flooding (in both cases a higher percentage, 22% and 33% respectively, were lost to predation). In northern Australia, Webb et al. (1987) noted that for *C. porosus* rising water levels in the rainy season can account for the loss of 100% of eggs in some areas (overall the mean egg survivorship is estimated to be 25% for this species in northern Australia). Other weather phenomena can also effect mortality rates; for instance a severe hail storm in the Lake Kariba area of Zimbabwe almost decimated all of the crocodile eggs (Child, 1987).

4.3. Thermoregulation

The process of regulating temperature within the limits described above is known as thermoregulation (Cowles and Bogert, 1944; Pough and Gans, 1982). Crocodilians can regulate their body temperatures so as to remain within their activity ranges despite often quite large discrepancies with the environmental temperatures. This is generally through behavioural means (Johnson, 1973; Smith, 1975; Lang, 1987a,b). For instance, if the water becomes too cold, crocodilians will bask in the sun until they reach the upper limit of their selected ('preferred') temperature range at which point they return to the water or seek the shade. Groombridge (1987) noted that *Alligator sinensis* is active diurnally in May (mean daily temperature $\approx 20.5^\circ\text{C}$), but becomes nocturnal in the summer as temper-

atures rise (mean summer temperature, $\approx 26.9^\circ\text{C}$). This has also been observed in *A. mississippiensis* (Smith, 1975). Other behavioural responses include the use of warm substrates (thigmothermy; Smith, 1975) and gaping (Cott, 1961; Johnson, 1974), although this has been disputed (Diefenbach, 1975; Johnson et al., 1978).

The most important behavioural response to temperature extremes (hot and cold) is to seek water (Spotila et al., 1972, p. 1094: "Water is the most important part of an alligator's habitat because it acts as a substitute for blackbody conditions and insures maximum utilization of an alligators potential climate space ... If alligators are deprived of water their activity is greatly restricted and their chance of survival is greatly reduced"; Neill, 1971, notes that the western limit of crocodilians in the United States is more limited by lack of water than temperature and that this has important implications for the fossil record, as will be illustrated later). Smith (1975) noted that during hot afternoons an alligator at Waco, Texas, would often retreat to the bottom of the zoo pond. Similarly, Diefenbach (1975) found that overheating in *C. crocodilus* was mitigated by immersion in water. Brisbin et al. (1982) described how *A. mississippiensis* would escape cold weather by submerging in deep pools using their snouts to maintain an air hole through the accumulating ice. This was termed the 'icing response' by Hagan et al. (1983) who observed this behaviour in alligators in North Carolina. The 'icing response' was only found to occur when there was ice present at the den, and when the water temperature was $\leq 5^\circ\text{C}$.

In order to maintain a ready source of water, *A. mississippiensis* digs large, deep, often circular, basins in soft substrate called 'gator-holes' (they often utilize sinkholes in Florida). These often provide the only source of water during dry periods. Neill has suggested that "probably the impulse to dig a basin was originally evolved not as a method of coping with low temperatures of winter, but with lowering of water table in a dry season" (Neill, 1971, p. 273). This seems more likely given that irrespective of the buffering effect of water to climate change, sustained or extreme cold will freeze a 'gator hole' with the 'gator' in it ('gator holes' have been shown to be taphonomi-

cally significant and may be important in the geological record, Leite and Breithaupt, 1990).

It should be noted here that the presence of standing water need not reflect local precipitation, as the Nile River in Egypt attests; therefore precipitation need not be an accurate indicator of suitable environments for crocodilians.

To a lesser extent crocodilians can also regulate their body temperatures through physiological controls such as subcutaneous peripheral blood flow (Smith, 1975, 1976; Grigg and Alchin, 1976; Johnson et al., 1978). During warming, increased peripheral blood flow reduces the subcutaneous to stomach temperature differences (Smith, 1976). Size is important with the difference between heating and cooling rates increasing with increasing body mass. Smith (1976) suggested this might be due to the concomitant increase in integument thickness in larger animals. It is of interest to note that the osteoderms of *A. mississippiensis* are highly vascularized (Lang, 1987b).

A slightly different physiological response is shown by the common caiman (*C. crocodilus*). This species is usually marked with black bands on a background of olive or yellowish brown, but these will darken when the individual is chilled, becoming so dark that the crossbands are no longer visible. On warming the original colouration returns. The darker colour absorbs more heat and is the result of the expansion of melanophores (concentrations of dark pigments in skin cells) which react to cold. Juvenile alligators have similar strips, which may serve the same function.

Other ectotherms can survive extremely low temperatures by depressing the supercooling and freezing points of body fluids or, more surprisingly, by tolerating ice formation in extracellular fluid spaces. An extensive study of the last of these, known as freeze tolerance, has been done recently (Storey and Storey, 1988; Storey, 1990), but this only seems applicable to small ectothermic tetrapods.

4.4. Hibernation and aestivation

Crocodilian hibernation is problematic. Mazzotti (in Ross, 1989, p. 270) is categorical: “Contrary to many published reports, crocodilians

do not survive cold winter temperatures by hibernating”, while Bellairs (1969, p. 230) states “All temperate zone reptiles hibernate for several months in the year”. Not surprisingly there is a considerable literature on the subject which Neill (1971, p. 269) has described as “... confused and contradictory”. The problem is one of how hibernation is defined. For simplicity I have followed Neill (1948), who used it to “include any sort of retreat from winter conditions, whether or not actual dormancy is involved”. The reason for this is that however hibernation is defined, ectotherms are still subject to immediate environmental temperatures. Thus, while hibernating mammals store large amounts of fat as a winter energy source and also as insulation, for reptiles that insulation is external whether it be mud or water. Because of their large size, crocodilians would have problems isolating themselves from the environment without the buffering effect of water, and since water itself cannot sustain its temperature indefinitely, in areas where sub-zero temperatures persist for any length of time crocodilians will be precluded. Similarly, dens and burrows in river banks are also limited in the degree to which they can buffer an individual from external temperature extremes, although many species are known to dig such burrows (Neill, 1971; Groombridge, 1987).

A further distinction between endotherms and reptiles was noted by Case (1976), who observed that in endotherms it is the lack of available food resources that is the stimulus for hibernation, while in reptiles the metabolic rate is more a result of temperature and so the ultimate environmental factor responsible for hibernation in reptiles should be thermal suitability of environment. “This difference between reptiles and endotherms is reflected in the observation that heliothermic lizards often learn a feat more rapidly when given a heat reward rather than food” (Case, 1976, p. 86).

5. Climate inferred from biogeography

The empirical biological observations, described above, show the importance of temperature for limiting the distribution of extant crocodilians; not only the extremes of temperature, but also the

duration. Water was shown to provide an essential buffer to temperature extremes. Such observations help bound the region in climate space within which crocodilians can potentially survive. The nature of this region has also been investigated using steady-state energy balance models in which intrinsic properties such as metabolic rate and integument emissivity (insulation and water loss) are taken into account (Porter and Gates, 1969; Spotila et al., 1972). Results for *A. mississippiensis* support empirical observations, especially the fundamental importance of water (Spotila et al., 1972). However, it is important to understand how the geographic distribution of crocodilians reflects these physiological limitations and to what extent it is dictated by other factors.

5.1. Historical artifact—the effect of humans

Historical distributions of crocodilians are known to have differed slightly from those of the late twentieth century. Ross (1989, p. 72) refers to the discovery of two skulls of *Tomistoma schlegelii* from Guangdong, China, which indicate that their range was much larger in the past, possibly as recently as the Ming Dynasty (1368–1644). Morgan et al. (1993) report on the historical disappearance of *Crocodylus rhombifer*, amongst other vertebrates, from Grand Cayman in the Caribbean, which the authors suggest to be the result of a combination of human habitat destruction and predation. Neill (1971) notes that historical remains of *C. niloticus* are known from regions of Africa that are now too dry for the species, while historical records of eggs in Israel and south-west Syria suggest that the range extended into this region also—Werner (1988) notes that *C. niloticus* survived in the Kabara swamps and Nahal Taninim (River of Crocodiles) of coastal Israel until about 1900, when they were finally eradicated by hunting, compounded by swamp-draining. Neill also reports on the known contraction of the range of *C. niloticus*, which vanished from the Seychelles by about 1800, the Nile delta by the latter 1700's, and by 1870 effectively from all of the Nile below Aswan. Anderson (1898) provides an excellent account of the historical distribution of *C. niloticus*, noting that there are accounts of crocodiles

being seen in Syria and even Sicily during mediaeval times. In North America, *A. mississippiensis* was historically reported as far north as the Dismal Swamp, on the border between North Carolina and Virginia (Neill, 1971). Hunting has also had a devastating effect on populations of all species (Turner, 1977). Although human activity is probably primarily responsible for these changes (especially through drainage), it should be noted that through historical times there have also been minor climate changes (Lamb, 1982, 1985), which might account for some distributional changes.

5.2. Ecological limitations

Some distributional anomalies may also be explained by ecological requirements. For instance, Neill (1971) suggests that the absence of *C. acutus* from the Bahamas is due to the fact that the hatchlings cannot survive strongly saline water; although adults could swim across sea to an island, they could not establish a population on it unless it offered freshwater streams or heavy runoff. This may also explain the historical absence of alligatorids in Africa. Modern alligatorids lack salt glands and are restricted to mostly freshwater habitats (Taplin and Grigg, 1989). For most of the last 100 million years Africa was isolated by seaways from Eurasia and any potential source of alligatorids (this is discussed further in Section 7.2.5).

5.3. The climate of living crocodilians

5.3.1. The dataset

In order to examine the influence of climate on the distribution of crocodilians, I have computerized a dataset of 1060 climate stations compiled by Müller (1982) (Fig. 2). Each station contains monthly data for fourteen climate parameters including mean daily temperature, mean precipitation, radiation and potential evapotranspiration. Additional parameters and summary metrics have been calculated using these data, together with information from other sources, including satellite-derived measures of 'productivity' (see Markwick, 1996). Non-avian tetrapod faunal lists have been assigned to each station by overlaying climate station distributions onto published species distri-

bution maps (Hall and Kelson, 1959; Van der Brink, 1967; Arnold and Burton, 1978; Cook, 1984; Stebbins, 1985; Branch, 1988; Bouchardy and Moutou, 1989; Eisenberg, 1989; Kingdon, 1990; Conant and Collins, 1991; Grenard, 1991; Cogger, 1992; Redford and Eisenberg, 1992; Strahan, 1992). A 50 km radius circle was drawn around each site, in order to allow for the potential distribution of sub-environments as represented by the faunal list for each station, and an occurrence registered where the taxon's distribution intersected this circle. In areas with rapid relief changes, such as the Alps, this methodology mixes high and low elevation faunas, but these points do not significantly effect derived regressions. The propensity for stations to occur in lowland sites reflects Müller's original requirements: acceptable stations must contain data for a large array of climate parameters representing time series on the order of 30 years (typical of 'climate'). Consequently, most stations are located in large towns or cities that historically occupy lowland sites. This bias closely mimics the biases in the geological record that tend to over-represent low elevation environments. Similarly, the distribution of stations is numerically biased towards the Northern Hemisphere, especially North America and Europe (Fig. 2), which is also the case with the fossil data (Fig. 5). A consequence of using town- or city-based climate stations is the effect that urbanization has on observations. This depends on the size of the urban area. For Chicago this urban effect results in the city's MAT being $\approx 0.6^\circ\text{C}$ higher than adjacent rural areas; New York City has a MAT $\approx 1.1^\circ\text{C}$ higher than adjacent areas (Peterson, 1973). For most of the cities and towns used by Müller (1982), which are smaller than either Chicago or New York, this effect is insignificant compared to the magnitudes of the climate patterns being investigated.

Two caveats concerning this method must be made. First, the crocodilian distribution maps used for the study are unfortunately relatively coarse (except for North America, Australia and southern Africa). The result is that the maps tend to overestimate the extent of the present crocodilian range. Second, distributions reflect essentially those of the twentieth century, or some part of it. Thus

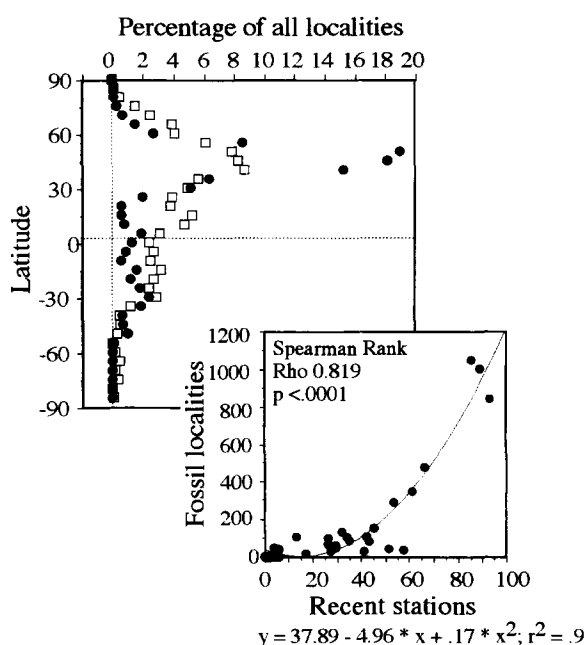


Fig. 5. The relationship of fossil localities and modern climate stations with latitude. For each 5° latitudinal (palaeolatitude for fossil localities) zone, the number of fossil localities (black circles) and modern climate stations (open squares) is shown as a percentage of all localities or stations in the entire dataset. The biases in both datasets have the same sign, suggesting that conclusions based on the present dataset can be confidentially applied to the fossil data. The number of localities and stations is closely related to the area of land at each latitude. INSET (bottom right): this shows the number of fossil localities versus the number of climate stations for each 5° latitudinal zone. In this case the absolute number of localities for each 5° zone is used.

today there are no crocodilians in Israel or the lower Nile, but these are included in the climate station set because of their earlier presence (the inclusion of the Jerusalem climate station in the dataset is based on the distribution map given in Neill, 1971, and the known historical occurrences in Israel; Jerusalem lies on the limit of crocodilian climate space as defined by the station dataset). In general, where historical absences can be clearly demonstrated to have been induced by human activity, the presence is included here.

5.3.2. Results

The basic results are presented as a series of frequency and percentile plots (Fig. 6). Eighteen

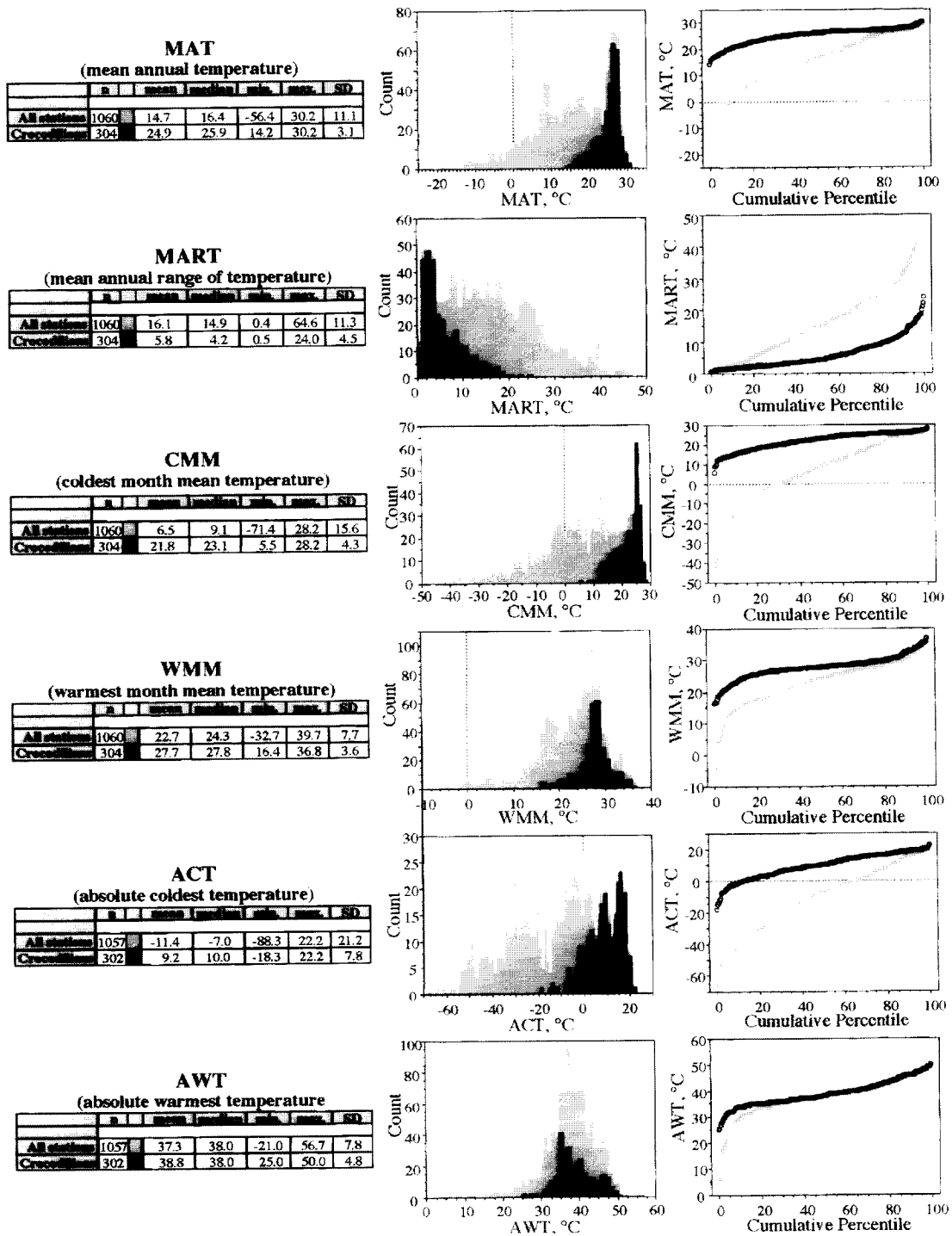


Fig. 6. Graphs showing the frequency distribution of stations for 18 commonly quoted climate parameters. In each case the distribution occupied by crocodilians (black) is superimposed on the distribution of all stations in the dataset (grey). These distributions define the climate space occupied by extant crocodilians, but not necessarily the full space that could potentially be occupied, all other factors being equal.

mean Winter T
(mean daily temperature for winter months)

	n	mean	median	min.	max.	SD
All stations	1060	7.5	9.8	-69.5	29.3	15.3
Crocodiles	304	22.6	23.9	6.6	29.3	4.3

mean Spring T
(mean daily temperature for spring months)

	n	mean	median	min.	max.	SD
All stations	1060	14.5	15.4	-56.3	33.7	12.0
Crocodiles	304	25.9	26.7	15.6	33.7	3.6

mean Summer T
(mean daily temperature for summer months)

	n	mean	median	min.	max.	SD
All stations	1060	21.4	23.0	-36.9	36.7	7.7
Crocodiles	304	26.2	26.8	14.7	36.3	3.2

mean Autumn T
(mean daily temperature for autumn months)

	n	mean	median	min.	max.	SD
All stations	1060	15.4	17.0	-63.1	31.1	11.0
Crocodiles	304	25.0	26.0	13.8	31.1	3.1

P (year)
(mean annual precipitation)

	n	mean	median	min.	max.	SD
All stations	1045	984.3	735	1	10798	906.7
Crocodiles	304	1640.8	1393	8	10798	1141.6

mean P range
(mean range of precipitation between highest and lowest mean monthly values)

	n	mean	median	min.	max.	SD
All stations	1045	145.3	84	0	2682	179.8
Crocodiles	304	289.7	238	1	2682	246.4

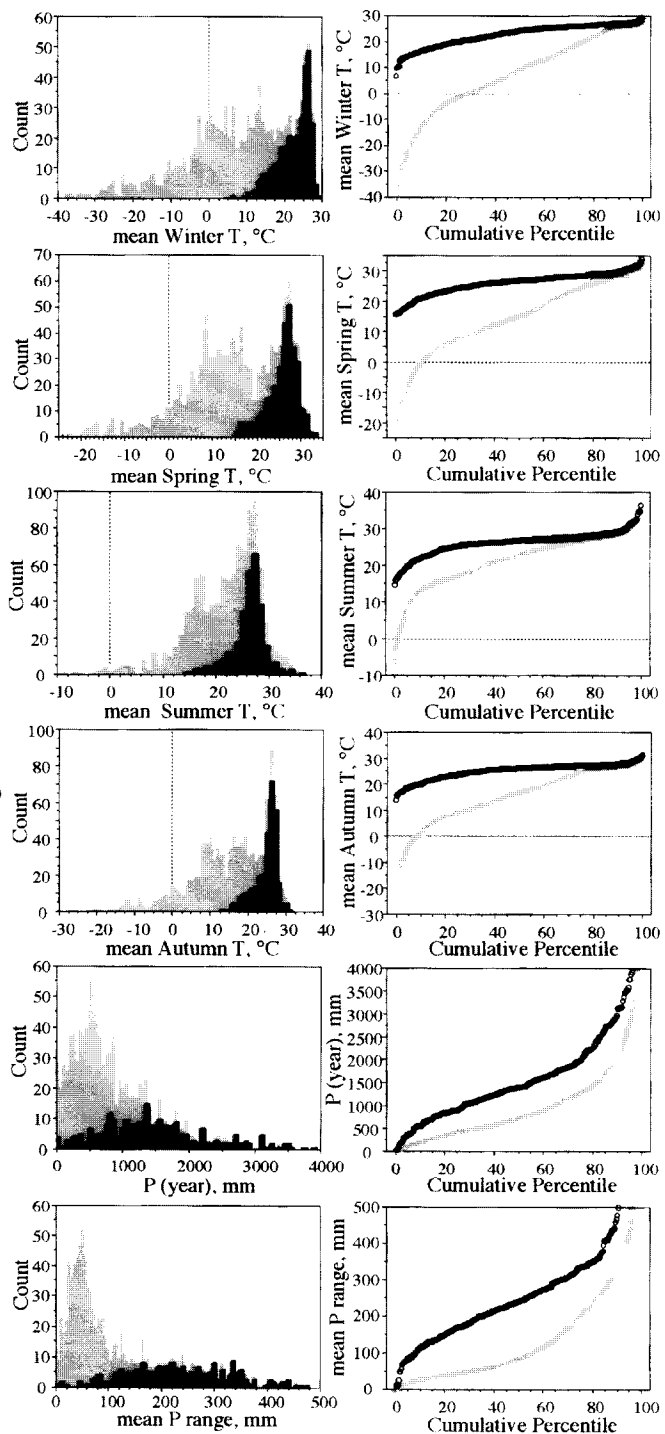


Fig. 6. (continued)

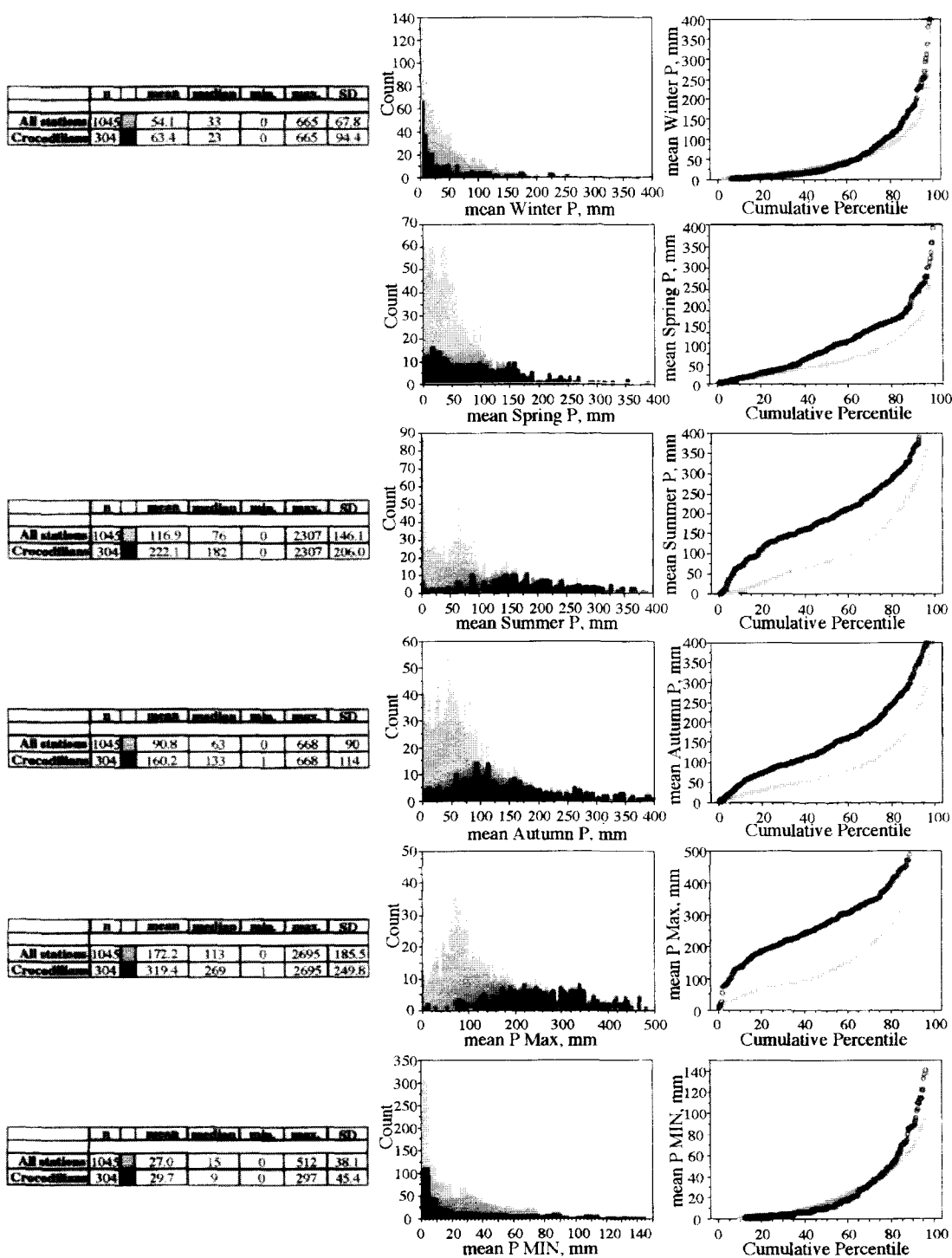


Fig. 6. (continued)

climate parameters are illustrated. These represent the most pertinent parameters for this study and include those most commonly quoted by palaeoclimatologists. A more comprehensive selection is given in Markwick (1996). An important attribute of the climate space defined in these diagrams is that it represents the space in which crocodilians do exist today. In each case the distribution of crocodilian-bearing stations is superimposed on the distribution of all stations. The disparity between the two gives a measure of how significantly the geographic distribution of crocodilians is defined by that parameter. This is assessed quantitatively using the Mann–Whitney non-parametric test, which tests the hypothesis that the two distributions represent two ‘sub-populations’ drawn from the same ‘population’ (population in the statistical sense); the results are expressed as a probability (following convention, at p -values lower than 0.05 the hypothesis is rejected). For example, a statistically significant ($p < 0.0001$) disparity is shown for MAT, with crocodilians only occupying those stations at the warmest extreme of the distribution.

The results of the Mann–Whitney test suggest that the distribution of crocodilian-bearing stations is significantly distinct ($p < 0.05$) from that of non-crocodilian bearing stations for all the climate parameters shown in Fig. 6: p -values of < 0.0001 for all parameters except mean Winter P ($p = 0.0122$), minimum annual precipitation ($p = 0.0447$) and AWT ($p = 0.0159$). This is not true for the absolute range of values. Minimum values for thermal parameters are generally higher for crocodilian-bearing stations, but maximum and minimum values for precipitation parameters are indistinguishable from those of non-crocodilian stations. Consequently, the presence of crocodilians cannot be used to retrodict the absolute limits of precipitation. Nonetheless, it is tempting to use these percentile plots to derive the probability that any climate parameter, including precipitation, will be greater or less than a specified value, given the presence of a crocodilian. This assumes that each parameter in some way controls crocodilian biogeography and this need not be true—derived probabilities may only apply to the present. If this information is to be of any use for retrodicting

palaeoclimate based on fossil crocodilians, it is essential to determine the relative contribution of each parameter in limiting the spatial distribution of modern crocodilians. Unfortunately, this is hindered by the following: the large number of climate parameters, the close correlations between them, and the possibility that the influence of any parameter may not be important over the entire geographic range of crocodilians. In short, correlation does not automatically mean causation.

The first of these problems can be readily solved by using Principal Component Analysis (PCA) to reduce the number of parameters to a manageable few. An analysis of sixteen of the precipitation and temperature metrics from Fig. 6 (MART and mean P range are excluded because they are calculated from other parameters in the analysis) reduces the number of parameters to three interpretable factors (Table 2; five other factors were recognized in the analysis, but they do not account for a significant proportion of the scatter in the data), with the first component (PC 1) representing ‘climate’ and dominated by temperature (accounting for 52.7% of the scatter; there is a strong linear relationship

Table 2

Results of a principle components analysis of sixteen precipitation and temperature parameters (see Fig. 6 for explanation of abbreviations)

Climate parameter	PC 1 variance: 52.7%	PC 2 variance: 25.7%	PC 3 variance: 8.3%
MAT	.963	–.247	.044
CMM	.944	–.115	.050
ACT	.915	–.051	.038
AWT	.448	–.631	.122
WMM	.802	–.465	.045
mean Winter T	.947	–.123	.041
mean Spring T	.954	–.260	.008
mean Summer T	.817	–.446	.089
mean Autumn T	.958	–.252	.055
Annual P	.590	.772	–.146
mean Winter P	.262	.660	.608
mean Spring P	.476	.744	.109
mean Summer P	.521	.507	–.599
mean Autumn P	.572	.699	–.062
mean maximum annual P	.521	.457	–.504
mean minimum annual P	.183	.729	.528

between MAT and PC 1 scores), the second (PC 2) distinguishing between temperature and precipitation (25.7% of the distribution; PC 2 scores correlate best with precipitation) and the third (PC 3) by a subset of precipitation metrics, perhaps representing seasonality (8.3% of the distribution).

The distribution of crocodilians in this PCA space is shown in Fig. 7, and its significance assessed using the Mann–Whitney test. This shows that crocodilians are statistically significantly distributed with respect to ‘temperature’ (PC 1; $p < 0.0001$) and not ‘precipitation’ (PC 2; $p = 0.2620$), supporting previous observations, but it still does not give any indication as to which temperature parameter (or combination of parameters) is the most important (loadings for thermal parameters on PC 1 are all very similar, except for AWT). Nor does it provide quantitative limits to crocodilian climate space, which is essential if fossil

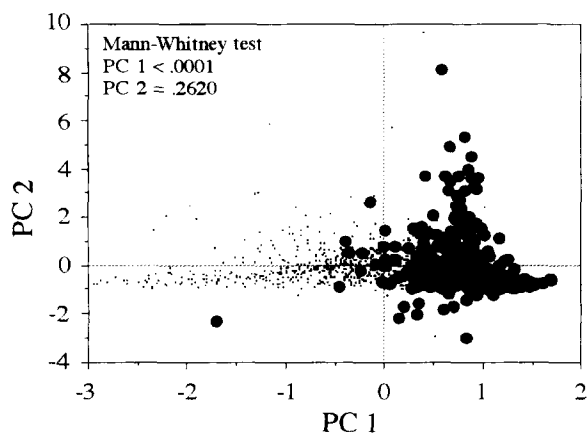


Fig. 7. A graph of component 1 and component 2 scores from a Principal Component Analysis (PCA) of sixteen climate parameters. Scores used here are unrotated scores from a PCA using the Statview statistics software (Haycock et al., 1992–1993). The sixteen climate parameters used are given in Table 2, which also gives the unrotated loadings for each factor (PC 1, accounting for 52.7% of the scatter, is dominated by temperature, and PC 2, accounting for 25.7% of the distribution, by precipitation). The position of stations with crocodilians on this graph are represented by the larger filled circles. The Mann–Whitney non-parametric test is used to examine whether these stations are significantly distributed along either axis. Derived p -values show that crocodilians are significantly distributed along PC 1 (‘temperature’), but not along PC 2 (‘precipitation’).

crocodilians are to be of any use in retrodicting climate.

The importance of temperature is again suggested by the present latitudinal restriction of crocodilians (Fig. 2), since latitude and temperature are closely related (Fig. 8, top). Although restricted to low latitudes, latitude per se is not the constraining factor, as is evident from the greater latitudinal range occupied by the group in the geological past—fossil crocodilians are known to have occurred up to 80°N palaeolatitude (Ellesmere Island) in the Early Eocene. A Spearman Rank test shows that precipitation is also significantly correlated with latitude

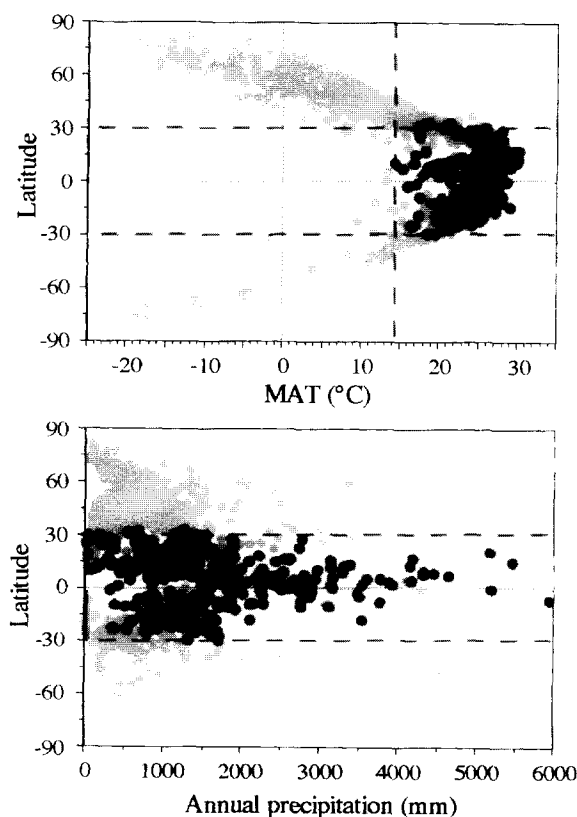


Fig. 8. The relationship between mean annual temperature (MAT) and precipitation with latitude. In both figures black circles are stations with crocodilians present. Only MAT's $> -25^{\circ}\text{C}$ are included in the top figure, and stations with annual $P \leq 6000$ mm in the lower figure. The spread of data in equatorial regions towards lower temperatures is due to the higher elevation of many of these stations.

Table 3
Correlation matrix for seventeen climate parameters including the sixteen parameters used in the factor analysis shown in Fig. 8 and Table 2 (see Fig. 6 for explanation of abbreviations)

	MAT	MART	CMM	ACT	AWT	WMM	Winter			Spring			Summer			Autumn			P (year)	Winter			Spring			Summer			Autumn			mean P	min
							mean T	mean T	mean T	mean T	mean T	mean T	mean T	mean T	mean T	mean T	mean T	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	mean	
MAT	1.000																																
MART	-.774	1.000																															
CMM	.966	-.909	1.000																														
ACT	.920	-.899	.964	1.000																													
AWT	.538	-.006	.358	.261	1.000																												
WMM	.860	-.347	.707	.644	.794	1.000																											
mean T Winter	.970	-.902	.999	.965	.366	.717	1.000																										
mean T Spring	.993	-.753	.952	.899	.553	.863	.957	1.000																									
mean T Summer	.875	-.382	.728	.665	.780	.988	.736	.872	1.000																								
mean T Autumn	.996	-.764	.959	.919	.538	.861	.963	.982	.877	1.000																							
P (year)	.358	-.478	.425	.452	-.169	.146	.423	.353	.161	.351	1.000																						
mean P Winter	.106	-.271	.181	.217	-.184	-.052	.171	.071	-.010	.112	.584	1.000																					
mean P Spring	.267	-.383	.328	.346	-.163	.088	.326	.251	.110	.265	.865	.637	1.000																				
mean P Summer	.338	-.366	.364	.373	-.072	.199	.367	.356	.189	.328	.832	.097	.579	1.000																			
mean P Autumn	.370	-.512	.448	.484	-.185	.140	.445	.361	.159	.359	.901	.557	.710	.653	1.000																		
mean P max	.351	-.363	.374	.387	-.028	.225	.376	.359	.214	.344	.691	.219	.497	.725	.596	1.000																	
mean P min	.014	-.188	.085	.097	-.245	-.127	.075	-.007	-.090	.014	.588	.779	.665	.198	.550	.198	1.000																

1042 observations were used in this computation.

($p < 0.0001$: testing the null hypothesis that the two variables are not correlated). However, the distribution of crocodilian-bearing stations shown in Fig. 8 (bottom) does not reveal a systematic preference for sites with high precipitation—crocodilians in low latitudes occur at stations with annual precipitation values that encompass the whole range of potential values. The relation between crocodilian-bearing stations and stations with high precipitation is therefore considered here to be a coincidence—crocodilians are restricted to low latitudes and low latitudes include areas with very high precipitation. Again, the implication is that temperature and not precipitation is the dominant climatic factor limiting crocodilians. Nonetheless, water is important for crocodilians, as discussed in Section 4.3, and although crocodilians are latitudinally restricted there is also a distinct asymmetry in the distribution that coincides with the distribution of aridity on the globe. This is discussed later.

The close correlation among climate parameters is a more insidious problem to solve. Table 3 gives the correlation matrix for the sixteen parameters used in the principal components analysis above (MART is also included; correlation and partial correlation matrices are used in preference to a covariance matrix because of the large disparity in the magnitude of values for temperature and precipitation parameters). Of the thermal parameters, all except AWT are very closely related, which is what its lower loading score on the thermal axis (PC 1) in the PC analysis shows (Table 2). A partial correlation matrix of these parameters (excluding MART, which is not included in this matrix because it is derived from CMM and WMM) is shown in Table 4 (for each pair of variables the effects of all the others are removed); but while this shows a strong correlation between seasonal and annual values of temperature and precipitation respectively, again it does not help in defining which parameters are important for limiting the spatial distribution of crocodilians. It does, however, indicate which parameters might have influences that will be difficult to discriminate.

All of the evidence so far presented has indicated the greater significance of thermal parameters, especially the cold temperature parameters, in lim-

iting the spatial distribution of crocodilians. The empirical biological data, discussed earlier, support this, but also suggest that the limits of crocodilian distribution may be defined not only by absolute cold, but also by the duration of the cold season. This 'duration' can be represented in two ways: as a count of consecutive months above a certain temperature, or as the mean annual range of temperature (MART). MART has additionally been used as an indication of 'continentality', which has become an important issue in the palaeoclimate literature (Sloan and Barron, 1990, 1992; Markwick, 1994; measures of continentality invariably use MART as an input variable, for instance Conrad's continentality formula and Gorczynski's continentality index; Barry and Chorley, 1987). The effect of this on climate can be seen by comparing the monthly temperature profiles of London and Chicago. Although these two cities have similar MAT's (10.5°C and 10.7°C, respectively) the MART in each case is quite different (13.4°C and 27.6°C, respectively)—London is maritime (also influenced by the Gulf Stream), Chicago continental. Plots of MAT versus MART have been used extensively by Wolfe for floral assemblages in order to accommodate these effects (Wolfe, 1971, 1979, 1993; Wolfe and Poore, 1982). Fig. 9 shows the distribution of crocodilians in this thermal climate space, which facilitates comparisons with Wolfe's work (the distributions of turtles and palms in this climate space are given in Markwick, 1996). Some interesting features are apparent from this figure. First, the distribution appears limited by CMM rather than MAT or WMM, based on the geometry of the lower bounding line. Second, the stations at the periphery of the distribution are those from the northern limit of the geographic range, Nanchang, Vicksburg, Charleston and Jerusalem. Finally, as one nears the limits of the MAT–MART climate space occupied by crocodilians, the proportion of crocodilian-bearing stations diminishes (towards the bottom right of the distribution and lower MAT's and higher MART's).

The gradient in the proportion of crocodilian-bearing stations exhibited in Fig. 9 is also evident in the latitudinal distribution of crocodilians (Fig. 10). Towards the poleward limits of their

Table 4
Partial correlation matrix for sixteen climate parameters including the sixteen parameters used in the factor analysis shown in Fig. 7 and Table 2 (see Fig. 6 for explanation of abbreviations)

	MAT	CMM	ACT	AWT	WMM	mean T Winter	mean T Spring	mean T Summer	mean T Autumn	P (year)	mean P Winter	mean P Spring	mean P Summer	mean P Autumn	mean P max	mean P min
MAT	1.000															
CMM	.0007	1.000														
ACT	.0010	-.023	1.000													
AWT	.025	.086	-.244	1.000												
WMM	-.027	-.282	.0093	.188	1.000											
mean T Winter	.964	.251	.032	-.047	.078	1.000										
mean T Spring	.996	-.015	-.0098	-.012	.044	-.951	1.000									
mean T Summer	.987	.047	-.0097	-.019	.151	-.967	-.981	1.000								
mean T Autumn	.990	-.015	.029	-.025	.037	-.942	-.988	-.967	1.000							
P (year)	.015	-.073	.035	-.016	-.064	.0048	-.017	-.0006	-.023	1.000						
mean P Winter	-.015	.075	-.033	.017	.064	-.0058	.016	.0002	.022	1.000	1.000					
mean P Spring	-.016	.070	-.036	.015	.064	-.0033	.017	.0002	.023	1.000	1.000	1.000				
mean P Summer	-.015	.074	-.035	.016	.065	-.0053	.017	.0004	.023	1.000	1.000	1.000	1.000			
mean P Autumn	-.015	.072	-.034	.014	.065	-.0046	.016	.0007	.022	1.000	1.000	1.000	1.000	1.000		
mean P max	.046	.0002	-.014	-.031	.100	-.048	-.042	-.063	-.039	.023	-.021	-.023	-.020	-.022	1.000	
mean P min	.0097	.121	-.144	-.057	-.044	-.040	-.026	-.0077	-.0062	.0029	.0049	.0018	-.0031	-.0009	-.123	1.000

1042 observations were used in this computation.

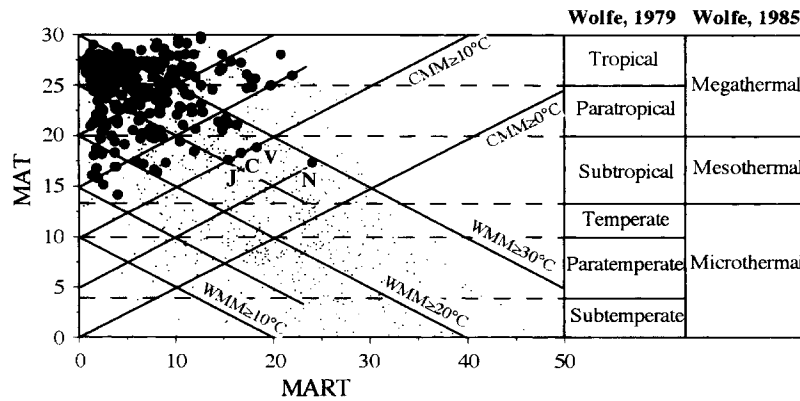


Fig. 9. The distribution of crocodilians in MAT–MART climate space. Each dot represents a climate station from the dataset (stations outside of the plot bounds are excluded); stations with crocodilians are represented by the large black circles. This type of diagram has been used extensively by palaeobotanists, following the work of Wolfe, for examining the position of modern and fossil floras in climate space. The advantage of this plot is that all pertinent thermal parameters can be represented by it, which is preferable to plotting the position of each group in bivariate plots representing every possible combination of thermal parameters (compare with Fig. 6). Terminology is that of Wolfe (1979, 1985).

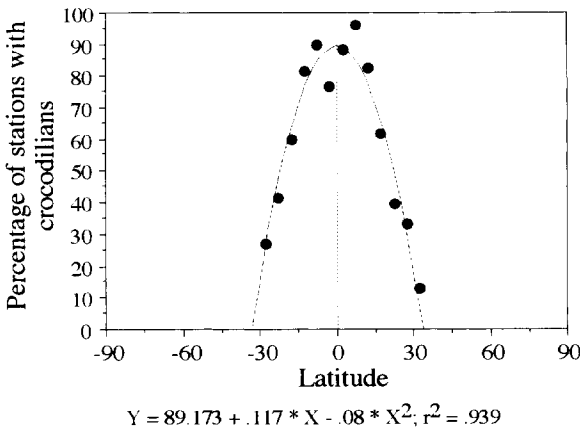


Fig. 10. The percentage of all stations in each 5° latitudinal band that have crocodilians assigned to them. A second-order polynomial is fitted through the data. A similar relationship is also found when using 1° latitudinal zones rather than 5° zones. In the case of 1° zones the fit through the data is not quite as good as that shown in this figure ($r^2=0.68$), although the intercept with the x -axis is the same in both cases, $\pm 34.1^\circ$ latitude.

latitudinal range, crocodilians are increasingly spatially restricted (Fig. 2). As already noted, latitude cannot directly affect distributions, but temperature can. Fig. 11 shows the relationship between MAT and the proportion of crocodilian-bearing stations for each degree increment. From this it is

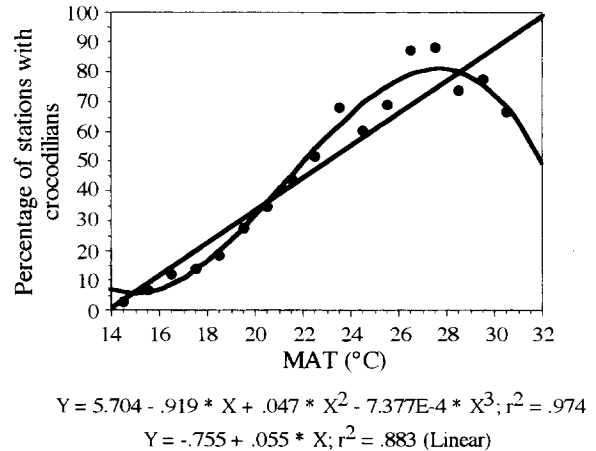


Fig. 11. The percentage of all stations that contain crocodilians, as a function of MAT. Black circles represent all crocodilian-bearing localities. Percentages represent the proportion of all stations that contain crocodilians for each value of MAT (1°C increments). Although a third-order polynomial gives the best fit through the data ($r^2=0.974$), a linear regression also gives a very good fit ($r^2=0.883$), and for reasons of parsimony is to be preferred.

clear that the minimum MAT of 14.2°C defined by the present spatial distribution of crocodilians (Fig. 6) is not the only limit on crocodilian distribution, since there are stations with higher temperatures but no crocodilians (see also the frequency

plots in Fig. 6). However, a linear regression through this trend predicts a minimum limit of $14.9 \pm 1.7^\circ\text{C}$ (assigned errors represent a single standard deviation derived from the residuals of the linear regression). This is indistinguishable from the observed minimum. Similar trends are found for other climate parameters. In each case minimum limits derived from calculated linear regressions give values that are close to observed minimums: calculated minimums derived from linear regressions are given for the following thermal parameters (values in parentheses are observed minimum values from Fig. 6): ACT, $-11.7 \pm 5.1^\circ\text{C}$ (-18.3°C); MMDC, $2.8 \pm 3.6^\circ\text{C}$ (4.0°C); CMM, $8.3 \pm 2.1^\circ\text{C}$ (5.5°C); mean Winter T, $9.01 \pm 1.8^\circ\text{C}$ (6.6°); maximum MART, $18.8 \pm 3.0^\circ\text{C}$ (24.0°C). A relationship is also found between annual precipitation and the proportion of crocodilian-bearing stations in each 50 mm increment. However, as discussed above, this latter relationship may reflect covariance between temperature, or latitude, and precipitation, rather than the dependence of crocodilians on precipitation.

These relationships are consistent with, or at least suggestive of, an hypothesis that postulates that as temperature decreases, conditions become increasingly deleterious for crocodilians, and their survival becomes progressively dependent on additional factors. In order to investigate this, the geographic distribution of each climate parameter is compared with that of crocodilians (Fig. 2). For example, Fig. 12 shows the distribution of all climate stations that have MAT's of at least 14.2°C , the minimum MAT for crocodilians given in Fig. 6. Spatial discrepancies between this distribution and that of crocodilians show the regions where MAT alone does not account for the absence of crocodilians (the principal discrepancies are the southwestern United States, western Mexico, western South America, the Mediterranean region, saharan North Africa, Arabia, southern China and most of Australia). In this case, only 50.2% of climate stations that satisfy the minimum MAT requirements actually bear crocodilians (this should be equal to the region below the regression in Fig. 11). Each climate (and non-climate) parameter is examined in turn. CMM, mean Winter T, mean Autumn T and ACT all show a similar pattern of discrepan-

cies to MAT with crocodilian-bearing stations accounting for 50.3%, 51.1%, 47.5% and 44.9%, of all potential stations, respectively. Using the maximum limit of MART (24.0°C ; Fig. 6) as the limiting factor is less successful, only 36.9% of these stations have crocodilians, which is consistent with the results plotted in Fig. 9 that suggest that regardless of MART, crocodilians can only exist in regions with minimum temperatures above some threshold value. Neither precipitation minimum nor maximum values are at all useful in defining crocodilian biogeography.

Although discrepancies can be partially minimized by taking less conservative limits (for instance using 14.0°C as the minimum limit for CMM, the 5th percentile in Fig. 6, 73.6% crocodilian-bearing), or using multiple limits (Fig. 13, which shows the distribution of climate stations which have at least minimum values for the following thermal parameters, MAT, MART, CMM, ACT, MMDC, mean Winter T, and the number of months with temperatures greater than 10°C), the regions of discrepancy remain problematic: Australia, southwestern Africa, North Africa, Arabia, southwestern United States and western Mexico, western South America, the Mediterranean, and southern China. However, most of these areas do share a common climate signature: they are arid. This suggests strongly that the exclusion of crocodilians from these regions, and thereby the only partial occupation of their potential thermal climate space, is a function of hydrology. (The absence of crocodilians from the perennial Orange River in the Kalahari Desert is problematic, since despite being in an arid region one would assume that it provides similar aquatic habitats to the River Nile, where crocodiles do occur. A number of explanations come to mind. It is possible that the limited riparian vegetation of the Orange River (Corvinus and Hendey, 1978) does not provide a suitable habitat. Alternatively, the absence of crocodilians may reflect a historical artifact: once eliminated from the entire Orange River drainage system they were physically impeded by geographic barriers from returning when the climate ameliorated. However, a climate explanation is not ruled out as this region is very

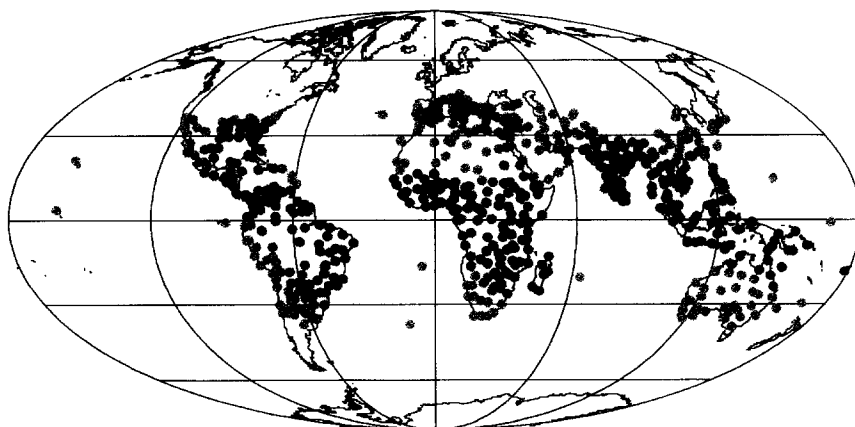


Fig. 12. The global distribution of all climate stations with $\text{MAT} \geq 14.2^\circ\text{C}$ (light grey circles) and crocodilian-bearing stations (black circles). 14.2°C represents the minimum MAT represented by the present crocodilian distribution (see Fig. 6). Only 50.2% of stations with $\text{MAT} \leq 14.2^\circ\text{C}$ are crocodilian-bearing. This suggests that some other limiting factor(s) is also at work.

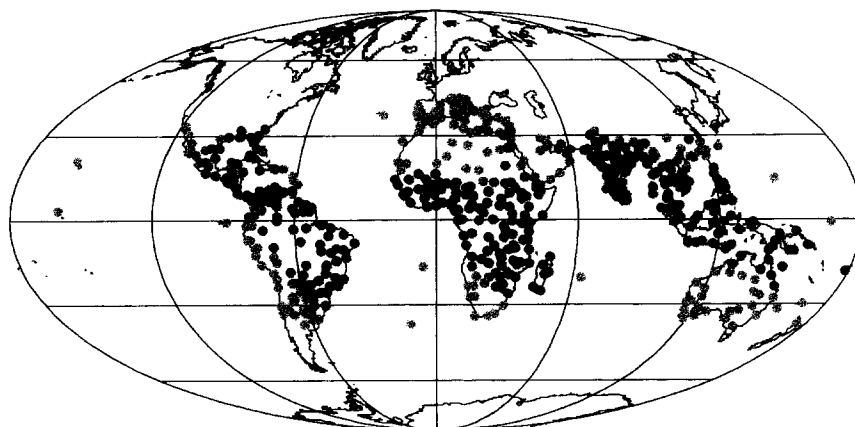


Fig. 13. The global distribution of all stations with specified minimum thermal limits compared with the observed distribution of extant crocodilians. Black circles represent crocodilian-bearing stations, grey circles represent stations which have minimum temperatures for the following parameters, $\text{MAT} (\geq 14.2^\circ\text{C})$, $\text{MART} (\leq 24.0^\circ\text{C})$, $\text{CMM} (\geq 5.5^\circ\text{C})$, $\text{ACT} (\geq -18.3^\circ\text{C})$, $\text{MMDC} (\geq 4.0^\circ\text{C})$, mean Winter T $(\geq 6.6^\circ\text{C})$ and $\text{moT} \geq 10^\circ\text{C}$ (≥ 9 months), as defined by the observed distribution of crocodilians (Fig. 6). 60% of the climate space defined using these values is occupied by crocodilians.

close to the minimum limit of CMM for crocodilians.)

Topography also plays an important rôle in limiting the distribution of crocodilians: it affects drainage and the distribution of standing water; it provides physical barriers to migration; it influences regional climate, especially through orographically enhanced precipitation and aridity (rain shadow). Most significantly, it affects local temperatures, which decrease with increasing ele-

vation. This is the 'lapse rate', and is generally taken as $\approx 6^\circ\text{C}/\text{Km}$ (the 'environmental lapse rate'; this is a simplification because observed lapse rates vary with location and time; Barry, 1992). In order to understand the effect of elevation, this lapse rate is used to recalculate the observed MAT for each station to its sea-level equivalent. Fig. 14 shows the distribution of all stations with sea-level MAT's ≥ 14.2 (the thermal limits for crocodilians defined by the modern crocodilian dataset). The

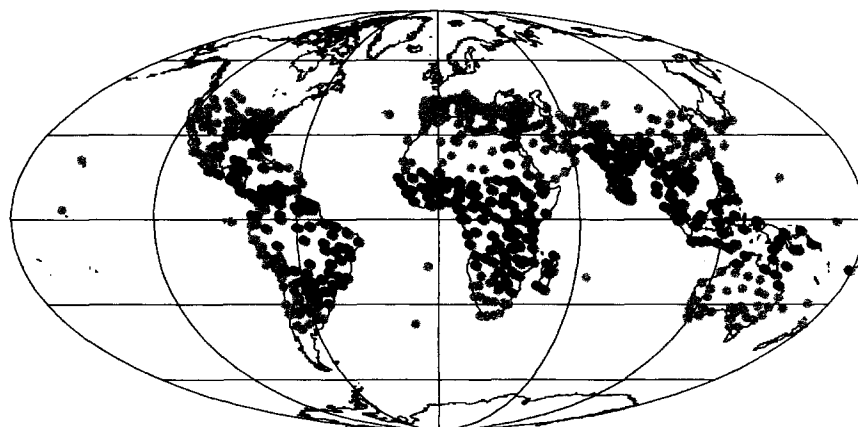


Fig. 14. The global distribution of stations with calculated sea-level values of MAT $\geq 14.2^{\circ}\text{C}$ (grey circles), crocodilian-bearing stations (black circles). Values are calculated by taking the observed elevation and MAT for the station, and deriving what the MAT would be if the site were at sea level, assuming a lapse rate of $6^{\circ}\text{C}/\text{km}$. The distributions shown in this figure are similar to those given in Fig. 12; reflecting the preponderance of low elevation sites in the original dataset. Discrepancies occur in North America (the central Rockies region) and the area in and around Afghanistan.

discrepancies between the distributions shown in this figure and those in Fig. 13 give an indication of areas where elevation may, through temperature, influence the distribution of crocodilians. The principal discrepancies are in North America and central Asia. Because topography changes through time, these differences have implications for past climatic reconstructions.

6. The Recent: discussion and conclusions

Climate interpretations based on fossil crocodilians are dependent upon analogy with the constraints dictated by present-day physiologies. An understanding of these constraints is therefore essential. Experimentally defined limits, akin to phase boundaries defined by petrologists, have been found in some cases (Colbert et al., 1946), but in general are precluded on ethical grounds since for crocodilians the pertinent 'phase boundary' is 'dead' or 'alive'. Regardless, derived results may only be applicable to individuals rather than populations and do not take account of additional factors, such as the importance of water (an initial experimental problem observed by Colbert et al., 1946). As described above, individual adults may survive in regions outside their present geographic

and climatic range (e.g. Pennsylvania, Barton, 1955), but populations are more restricted due largely to the greater vulnerability of juveniles.

As a consequence of these experimental limitations, the climate space occupied by extant crocodilians is defined ostensibly on circumstantial evidence derived from the group's present spatial distribution. The validity of derived boundaries is therefore dependent upon the degree to which the geographic range replicates the full potential range dictated by the physiological dependence on climate. This is addressed here using a dataset of globally distributed climate stations with associated faunal lists.

Temperature is shown to be the single most important factor in limiting the present distribution of crocodilians. This is indicated by the experimental work of Colbert et al. (1946) and subsequent field observations. It is also suggested by the restriction of the group to low latitudes and by the results of a principal components analysis of sixteen climate parameters, which shows crocodilians significantly ($p < 0.0001$, Mann-Whitney test) distributed along the temperature-dominated first axis (Fig. 7). Although most thermal parameters are closely correlated with one another (Tables 3 and 4), the geometry of the climate space occupied by crocodilians in MAT-MART space

(Fig. 9) suggests that CMM is the main limiting thermal metric. A minimum value of about 5.5°C is found (Fig. 6). The similarity of this figure with the observed critical minimum body temperature for *A. mississippiensis* of 4–5°C (Brisbin et al., 1982) is suggestive, although a less conservative minimum value of about 14.0°C replicates the observed distribution of crocodilians far better. This latter value represents the 5th percentile from the CMM percentile plot in Fig. 6 (95% of crocodilian-bearing stations have CMM's above this value). Warm-temperature metrics, especially AWT, are shown not to be important.

While the empirical data suggest that the duration of the cold season may greatly influence the survival of juveniles and thereby the viability of a population, this is not obvious from the climate station dataset. It is postulated here that this may be a consequence of the present relationship between absolute temperature (such as MAT, CMM, etc.) and the range of temperature (MART)—all areas which exceed the minimum thermal limits by default have MART's within acceptable values. Nonetheless, seasonality must be considered as a potential limiting factor in geologic periods when the relationship may have been different.

Although minimum-temperature limits can be assigned to the distribution of crocodilians, not all stations within these limits have crocodilians. The proportion that do, is found to increase linearly with increasing temperature (Fig. 11), which suggests a systematic cause. This can be examined by comparing maps of the distribution of stations which satisfy minimum thermal requirements and the present geographic distribution of crocodilians. Spatial discrepancies between the two are found generally to be regions of aridity. These results suggest that as the thermal limit of crocodilian climate space is approached the presence of standing water becomes increasingly important in order to mitigate the effects of temperature extremes. (The distribution of temperature and hydrology may both be influenced by topography.)

The relationship between the proportion of stations with crocodilians and temperature has important implications for retrodicting palaeoclimate. It shows that while the presence of a fossil crocodilian

signifies a specified minimum temperature, the absence of fossil crocodilians does not automatically mean temperatures less than this value. Nonetheless the frequency distributions in Fig. 6 can be used to assign probabilities to the presence or absence of a fossil crocodilian signifying a specific temperature or range of temperatures. However, this assumes that the frequency distribution observed in the Recent may be applied verbatim to the fossil record, which may not be realistic. With decreasing temperature, the shape of this frequency distribution is increasingly determined by the spatial distribution of aridity, a distribution that may have been radically different in the geologic past.

The empirical and circumstantial evidence presented here thus suggest the following: (1) crocodilians are primarily limited by ambient minimum temperatures, $\text{CMM} \geq 5.5^\circ\text{C}$; (2) the duration of the cold season (consecutive months above a specified temperature and MART) is an important determinant of the viability of a population through effects on the survival of juveniles; (3) the presence of standing water provides an essential buffer against temperature extremes, such that aridity is an important limiting factor especially at the poleward limits of the crocodilian geographic range. The presence of fossil crocodilians therefore indicates not only palaeotemperature, but also local palaeohydrology.

PART 2 — THE PAST

Having established the climate-space represented by crocodilians in the Recent (Part 1), this can then be applied to fossil occurrences, but not without caveats. As discussed in the introduction, the validity of directly applying recent physiological constraints to fossil relatives has been questioned. Thus, the presence of a fossil individual in an area in which its extant relatives no longer live may be interpreted to reflect not environmental transience, but rather physiological changes, or even a combination of the two. In the case of crocodilians, however, it is difficult to support a purely physiological explanation, because multiple, rapid transitions from warm- to cold-bloodedness and back, are required to explain observed distri-

butional patterns; transitions that require substantial internal biological changes (Ruben, 1995).

While climate change is the more parsimonious solution, the degree to which present-day limits can be applied verbatim to the past can only be assessed by comparison with the results of other lines of evidence (Conybeare, 1829). Given the sparsity of well-constrained global datasets, such comparisons are difficult. Consequently, in this study, support for interpreted climate patterns based on crocodilians comes largely from more general circumstantial evidence, such as the marine isotopic record and lithological evidence from Antarctica and its environs, or from local studies.

Regardless of how inviolate such a literal uniformitarian approach may be considered, there are other intrinsic problems that must be accounted for when reconstructing palaeoclimate from geological climate proxies. These are the biases that act on the geological record itself: taxonomy, dating, misidentification, preservational biases (taphonomy), and collection biases. In addition, there is the question of what is meant by ‘palaeoclimate’ given the temporal disparity between geological palaeoclimate (magnitudes of millions of years) and meteorological climate (being an average of 30 years of weather). These are problems that apply to all palaeontological climate proxies, and thus the conclusions reached in this study may provide a template for examining other lines of evidence.

7. Biases

Biases in the geological record fall into three main categories: resolution (spatial and temporal), representation (collection and preservation), and errors (misidentification, incorrect dating). The influence of each on the interpretation of palaeoclimate depends on the questions being asked and methods employed. Climate interpretations based solely on the recognized presence of a climate proxy, such as a crocodilian (this study), are only influenced by issues of resolution and error, not by representation: the indicator exists at that point in time and space, and a specified climate can thereby be attributed to that point. Interpretations

based on the absence of a climate proxy are more problematic because the absence may reflect poor sampling or preservation (representation) rather than an original ecological absence. Methods based on assemblage data are more susceptible to this kind of representation bias. An understanding of the trends in climate over time or changes in patterns based on proxy data requires that some qualification of absences be made. In this section I describe some of the major biases, how they may affect palaeoclimate interpretations, and how they can be qualified (see Markwick, 1996, for a fuller account).

7.1. Resolution

The resolution of palaeoclimate patterns interpreted from geological climate proxy data is dependent upon the spatial and temporal resolution of the data itself.

7.1.1. Spatial resolution

A ‘locality’ (an individual spatial–temporal record in the database, see Markwick, 1996) may represent a variety of spatial scales: a hand-specimen characterizes a single definable point in space; a composite of sampling sites or a review of a stratigraphic unit, may encompass a broad geographical area that must be defined. For this study spatial resolution does not seriously affect results, because the published size of the distribution maps cannot differentiate the finest spatial resolution; a printed datapoint may itself cover a 500 km area of space regardless of whether it represents an individual collecting site (metres in scale) or a composite over a whole county (10’s of kilometres).

A related issue is the inexactness in defining the position of a locality: how precisely its position is known. This is dealt with in the database by an arbitrary code that allows the database to be sorted as appropriate: this is the Geographic Precision code (GP: 1, known within 1 km; 2, within 10 km; 3, within 100 km; 4, within 500 km; 5, not known to within 500 km; Markwick, 1996). In this study I have restricted the dataset to only those ‘localities’ that are resolved to within 100 km ($GP \leq 3$).

7.1.2. Temporal resolution and time-averaging

Temporal resolution of fossil data is dictated by two factors: (1) the resolution of the age assignment; (2) the effects of time-averaging. For consistency, only localities whose stratigraphic ages do not exceed more than two consecutive time intervals (see Fig. 15) are considered. This then is the temporal resolution of the study. This not only limits the number of datapoints available, but also limits the geographic spread of the data because many parts of the world remain stratigraphically poorly resolved.

Behrensmeyer (1982), Behrensmeyer and Hook (1992) and Rogers (1993) have drawn attention to the effect of time-averaging on vertebrate faunas. This takes two forms: (1) 'taphonomic time-averaging' (Behrensmeyer and Chapman, 1993), due to physical mixing, in which reworking of older sediments leads to incorporation of earlier faunal elements within the contemporary fauna; (2) 'analytical time-averaging' due to the disparity

between the time represented by a single fauna and the length of geological intervals that can be confidently correlated over large regions.

The effects of taphonomic time-averaging (reworking) can be assessed by looking at the degree of abrasion or disarticulation of specimens at a site, as well as by noting the potential sources for reworked specimens and the distance of transport possible. For the present study taphonomic time-averaging is not a major contributor to the overall patterns observed: distributions derived from occurrences of fragile fossil crocodilian material, such as complete, articulated skulls that are unlikely to survive reworking, are statistically indistinguishable from distributions based on all data.

Analytical time-averaging is a potentially more insidious problem, especially in terms of defining palaeoclimate. Climate, in the modern meteorological sense, represents 'average' weather, or more correctly the long-term aggregate effect of weather

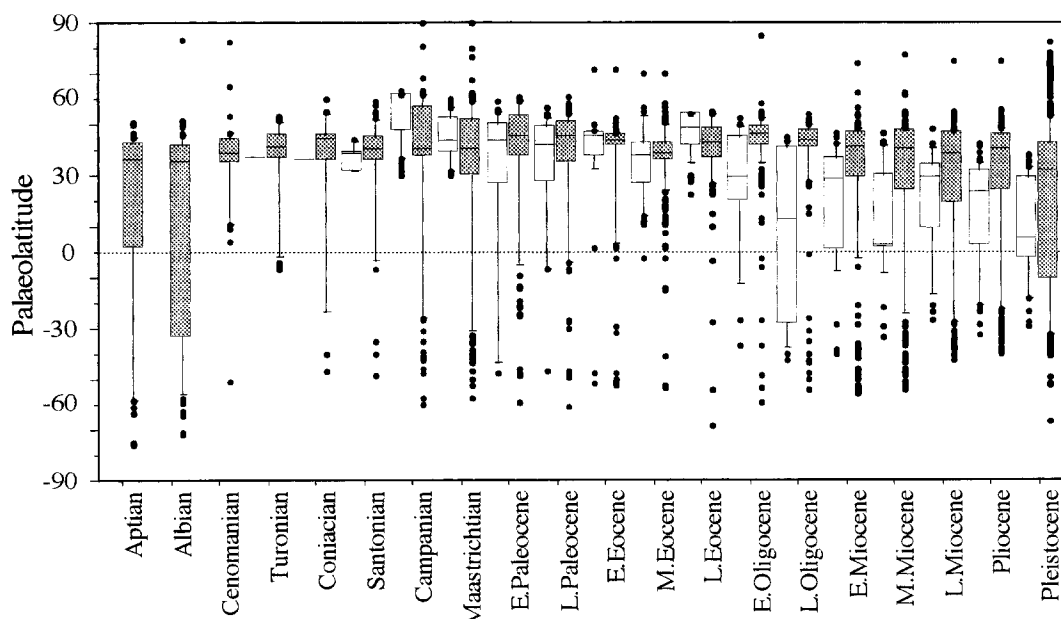


Fig. 15. Box plot of all vertebrate localities in the database. Open boxes: crown group crocodilian localities. Shaded boxes: all vertebrate localities. Only those localities which are spatially well resolved ($GP \leq 3$) and temporally limited to no more than two consecutive time intervals. In each case, boxes are bounded by the 25th and 75th percentiles and bisected by the 50th percentile; the lines are drawn out to the 10th and 90th percentiles; points outside of these limits represent all points in the tails of the distribution. The bias of the Northern Hemisphere is readily apparent. In addition, only after the Eocene do the majority of crocodilian localities occur in lower palaeolatitudes than the majority of all vertebrate localities.

(Barry and Chorley, 1987), most commonly taken as a period of 30 years (Saltzman, 1990). An individual crocodilian has a life expectancy in captivity of about 30–40 years (Bowler, 1977), so assuming that fossil crocodilians had similar longevities, the climate interpreted from an individual fossil crocodilian specimen is comparable with what we think of as ‘climate’. Although an individual fossil crocodilian may represent the meteorological climate at the place and time where it lived, that climate may not be representative of the entire geologic interval. Analytical time-averaging exacerbates this problem because the reconstruction of global palaeoclimate requires more than one individual and these additional datapoints may represent life-times, and thereby meteorological climates, from anywhere within the geologic interval in question. The magnitude of this problem can be demonstrated quantitatively by calculating the probability that all localities in an interval represent the same ‘climate’ period. For example, the Eocene is 21.1 million years long (Harland et al., 1990). Dividing this into a series of ‘climate’-sized segments of 30 years and given 100 Eocene localities, the probability that all 100 localities represent exactly the same 30-year segment is 1 in 700000⁹⁹; even taking ‘climate’ as representing a 1000-year aggregate (Saltzman, 1990; also based on the estimate of Behrensmeyer (1982) that 1000 to 10,000 years is the typical period represented by vertebrate accumulations in fluvial systems, based on her observations in East Africa and North America), the probability is still 21000⁹⁹.

Another approach to this problem is to ask how many overlaps between localities should be expected if localities are randomly distributed through a geologic interval. This is examined using a program called COEVAL written by Ann Lottes and David Rowley at the University of Chicago. This program randomly places a specified number of localities (each representing a specified duration; viz., 30 or 1000 years) within the interval of interest and then counts the number of overlaps (overlaps can be between any two localities and do not have to all temporally co-occur). Simulations of 1000 runs have been made for the Eocene (21.1 million years long) and Early Eocene (6.5 million years

long). Results suggest that amongst the 215 Eocene crocodilian localities contained in the dataset, there is a 95% probability that there will be no more than three overlaps in the entire interval, and indeed only a 50% probability that there will be any overlaps at all (taking localities to represent 30 years each; if localities represent 1000-year durations there is a 95% probability that there will be no more than 5 overlaps). This problem is not resolved by using finer intervals of geologic time because of the concomitant decrease in the number of localities. For the Early Eocene the problem is indeed exacerbated; taking localities to represent 30-year durations there is only a 9% probability that any of the 84 crocodilian localities will overlap in time, and a 99% probability that there will be no more than 1 overlap. Given this, is the ‘climate’ of the Eocene, Early Eocene, or any other geological interval comparable with meteorological climate? For one locality the two are comparable, but as soon as more localities are considered, especially for global studies, this comparability becomes more tenuous due to the effects of analytical time-averaging. Consequently, palaeoclimate on geological timescales may better be considered as the long-term aggregate effect of climate—the ‘tectonic average’ period of Saltzman (1990).

7.2. Representation

Fig. 15 shows the spatial and temporal distribution of all crocodilian- and non-crocodilian-bearing vertebrate localities presently contained in the database. The distribution of data is neither homogeneous nor random. The most distinct pattern is the numerical bias for localities to occur in Northern Hemisphere mid-latitudes (see also Figs. 2 and 5): North America and Europe between them account for about 60% of all fossil localities in the database (Fig. 16).

The paucity of fossil vertebrates in high latitudes above 45–50° has been documented by numerous workers (Dorr, 1964, in Alaska, and Belyaeva, 1962, in Siberia). However, the reason for this paucity remains unclear. From the Late Miocene to the Recent, high-latitude fossil vertebrates are reported, which suggests that whatever the cause it has a temporal component. The existence of a high-latitude megafossil record throughout the

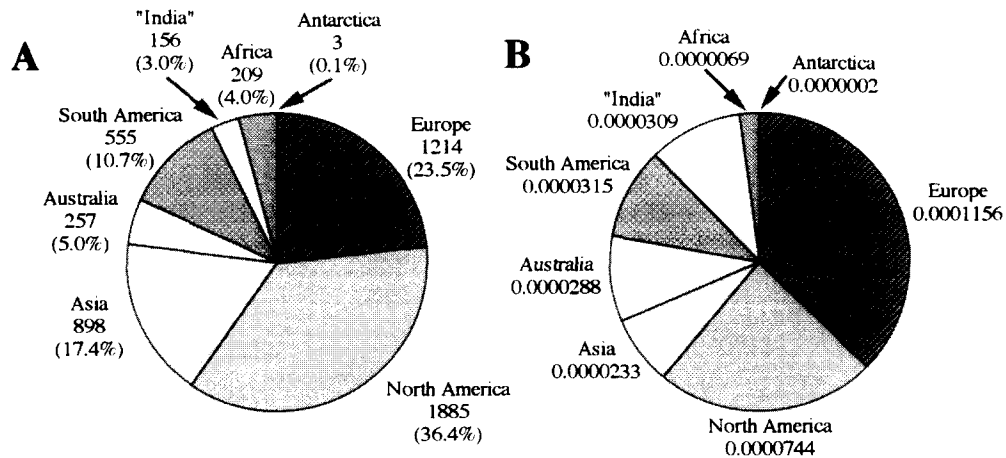


Fig. 16. Pie charts showing the proportion of localities in each continent (A) and normalized for area (B). In (A), numbers refer to the numbers of 'localities' in the database for each continent; percentage values in parentheses represent the proportion of localities represented by each continent. (B) Values are the density of 'localities' per square kilometre for each continent. Asia does not include the Indian subcontinent (India, Pakistan, Bangladesh and Ceylon) which is considered under 'India'. The bias of Europe and North America is again clearly shown by the number of localities by continent (A). Normalizing for area does not eliminate this bias.

Cretaceous and Tertiary (Vakhrameev, 1991; Boulter and Fisher, 1994) suggests that a fossil record is present in these areas. It is postulated here that the absence of fossil vertebrates may reflect taphonomic factors, especially enhanced bone dissolution due to more acidic hydrologic conditions. This would at least explain why megafloal remains, but not vertebrates, are found in these latitudes.

The spatial heterogeneity of fossil vertebrate localities has a temporal counterpart with the number of localities varying through time (Fig. 17). Potential sampling inhomogeneities associated with differences in the lengths of sampled intervals are compensated for by normalizing counts for interval length to obtain a rate. In Fig. 17 these calculated rates show a general increase towards the Recent. This increase is analogous to the 'Pull of the Recent' discussed by Raup (1972, 1976), except that it is not due to the range extension bias inherent in including extant taxa but simply the better preservation of younger rocks (Gilluly, 1949, 1969; Gregory, 1955). However, in this dataset no strong relationship is found between the interval length and the number of localities, so that normalizing for interval length may not be necessary.

An alternative means of compensating for sampling effects is to examine the temporal changes of each vertebrate fossil group in the context of all available vertebrate fossil localities—vertebrates act as a control on sampling. This method is susceptible to spatial heterogeneities between time intervals; however, although the data are heavily biased to Eurasia and North America (Fig. 15) this is true throughout the study interval which means that temporal trends should not be adversely affected. Fig. 18 shows the proportion of localities that contain crocodilians and turtles, respectively. The significance of derived crown group crocodilian trends is examined by using the average ratio between crocodilian-bearing and all localities to predict the number of crown group crocodilian localities in each interval. The chi-square test is used to examine the significance between actual and predicted values: p -values for all intervals and for the subset excluding the Turonian, Pleistocene and Oligocene are 7.26×10^{-12} and 0.307, respectively. This suggests that, in general, the number of crocodilian localities in an interval is a function of the total number of all localities, which implies a potential sampling effect. This is not the case for the Turonian, which occurs early in the diversification of crown group

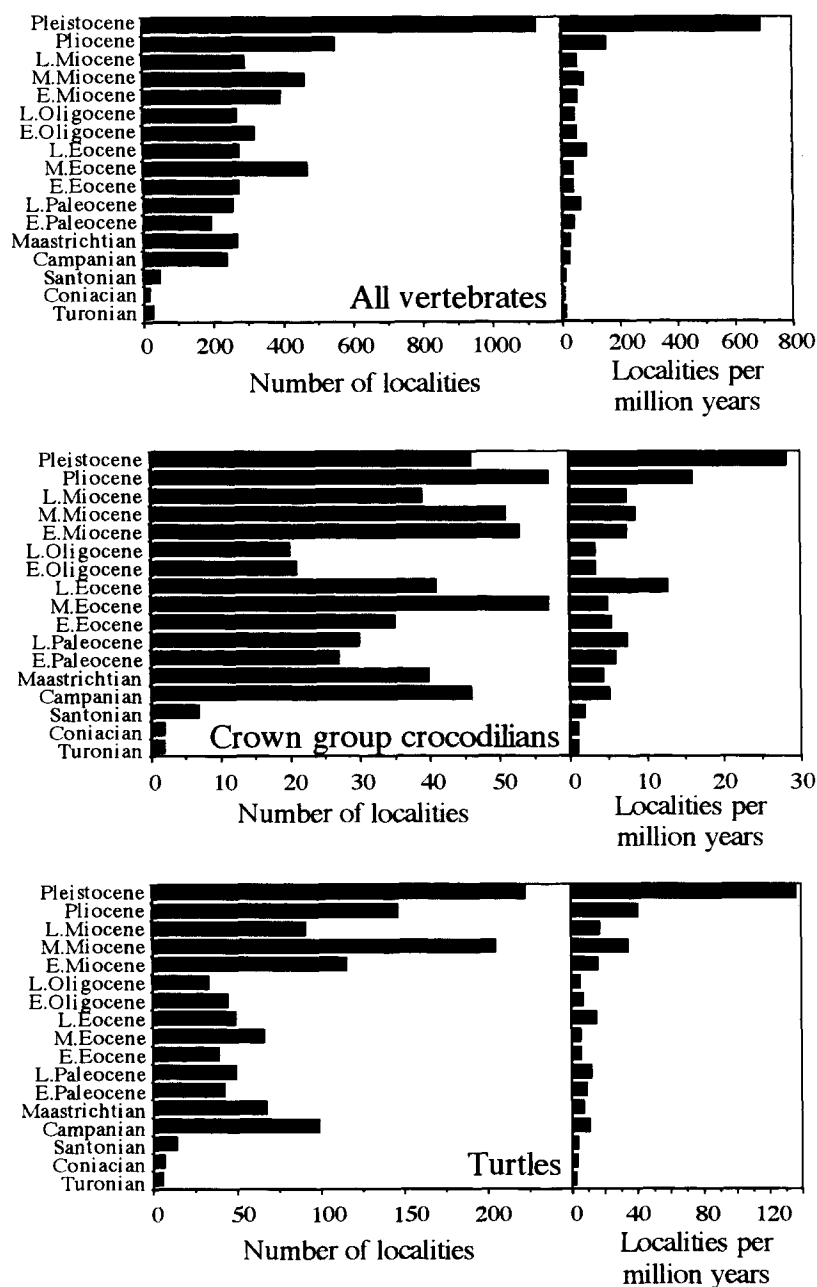


Fig. 17. Number and rate of localities by interval. Bar charts show the number of all vertebrate localities, crown group crocodilian localities and turtle localities in each time interval. The dataset is limited to localities that are spatially and temporally resolved to within 100 km ($GP \leq 3$) and less than or equal to two consecutive time intervals ($count \leq 2$). Note the drop in the number of crown group crocodilian localities in the Early Paleocene and Oligocene. The number of localities per million years (rate) is shown for each subset of the data. In all three cases the rate increases towards the Pleistocene perhaps reflecting the effects of the 'Pull of the Recent'. For crown group crocodilians the Oligocene values are still low compared with other intervals.

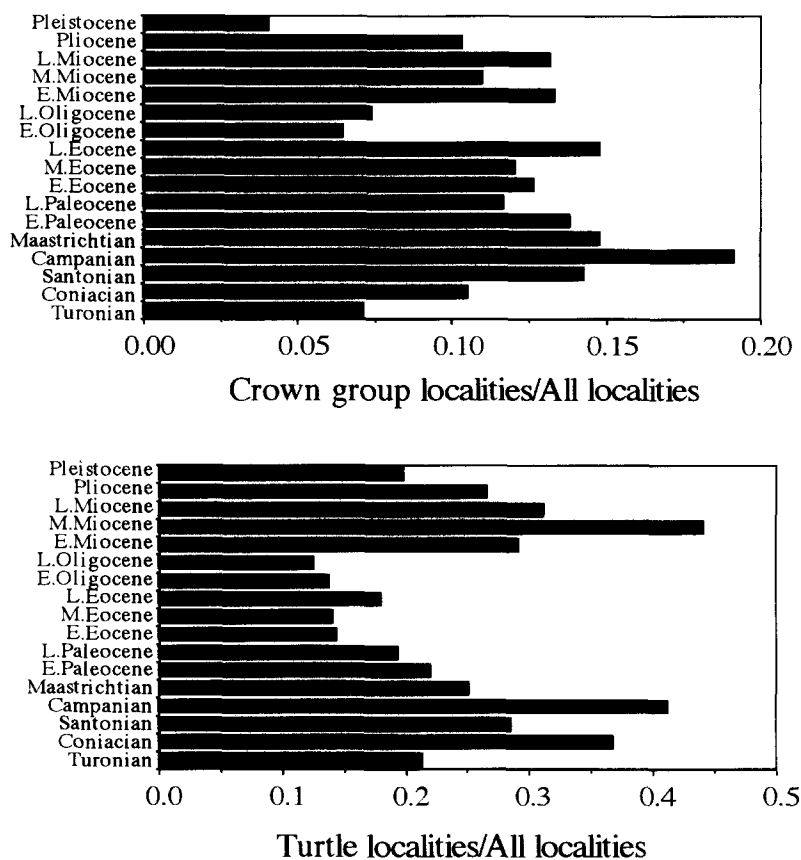


Fig. 18. Proportion of localities represented by crocodilians (top) and turtles (bottom). The proportion of all localities which have associated crocodilians (spatial resolution, $GP \leq 3$; temporal resolution, ≤ 2 time intervals). This gives an indication of how the number of crocodilian-bearing localities varies as a function of total sampling. Consequently, it also reflects the spatial distribution of localities and thereby climate (see text).

crocodilians—an artifact of evolutionary history—and the Pleistocene and Oligocene, which are times of global cooling—a climatic cause. The use of control groups is developed further in the following sections.

7.2.1. Reporting

The published literature is not an exact account of the fossil record, but a biased consequence of what is reported—largely dictated by the interests of authors and their peer reviewers. The potential consequences of this bias have been discussed by Koch (1978) and Raup (1972, 1976); Raup has referred to the effects of the ‘monographic bias’ on diversity trends, in which the comprehensive-

ness of monographs tends to swamp interpretations). Lower vertebrates, including crocodilians, are especially susceptible to this problem. With the overwhelming interest in dinosaurs in the Mesozoic and mammals in the Tertiary, lower vertebrates (amphibians and reptiles) are typically relegated to the ‘and also present were’ status. While this does not affect palaeoclimate conclusions based solely on the presence of fossil crocodilians, conclusions based on absences may be compromised.

7.2.2. Collection

Collection may bias the record through interest (viz., dinosaurs and mammals over lower verte-

brates) and logistics (difficult accessibility may preclude collection of any fossils). In order to qualitatively represent the area of potential fossil crocodilian collection, fossil crocodilian occurrences are plotted on backdrop of all vertebrate data—vertebrates are used as ‘controls’ for collection bias.

7.2.3. Tectonics

While collection is dependent upon interest and logistics, the fundamental limit on the occurrence of fossil vertebrates is the preservation of the rocks that may contain them. Sediments are not randomly distributed on the Earth, but accumulate where local base-levels are high enough to allow accumulation (the Pleistocene peak in localities reflects the fact that there has not been adequate time for erosion to erase localities outside of basin boundaries). The distribution of localities in the database as a function of basin type is shown in Fig. 19. The high proportion of foreland basin localities may partly reflect a collection bias—most foreland basin localities are from North America. Nonetheless, the dominance of foreland basin and passive margin localities (about 70% of all vertebrate localities in the database) is suggestive of a bias towards certain tectonic settings. As with collection biases, the effects of tectonics can

again be constrained using control groups—all fossil vertebrates or rock outcrop.

7.2.4. Taphonomy

Even given suitable basins in which to preserve rocks, there are other physical biases that may preclude or dictate what fossils can be preserved. For vertebrates, these taphonomic (preservational) biases have been extensively discussed by Behrensmeyer (1982, 1991) and co-workers (Behrensmeyer et al., 1979, 1992; Behrensmeyer and Chapman, 1993). As with other representation biases, taphonomic biases do not influence the palaeoclimate interpretations based on the presence of a climate proxy—the indicator exists at that point and no further qualification is required. Nonetheless, taphonomy is important in understanding the climatic significance of the absence of such information, which, as already stated, is especially important in defining trends in the data.

The terrestrial geological record is heavily biased towards aquatic environments (Fig. 20), especially in older deposits, because regions with active sediment accumulation are generally also loci for water accumulation. Throughout the Cretaceous and Cenozoic, non-marine crocodilians are postcranially relatively conservative (Langston, 1973), suggesting little change in their association with aquatic habitats. Only two groups appear to have shown any penchant to go beyond the aquatic environment during the last 100 million years: the sebecosuchids, whose taxonomic position remains problematic, but whose dinosaur-like serrated teeth suggest a fully carnivorous habit (Langston, 1975; Buffetaut, 1988), and pristichampsids, some of which appear to have been hoofed, suggesting full terrestriality (Hecht and Archer, 1977; Ross, 1989); however, neither group influences palaeoclimate interpretations based on spatial distributions, because they are invariably associated with other crocodilians. Consequently, crocodilians, as semi-aquatic animals, should have a relatively good fossil record. Accordingly, the general distribution of fossil crocodilians should not be delimited by the lack of representation of aquatic settings, assuming these were generally present to accumulate and preserve vertebrates, but other factors such as the nature of the aquatic environment

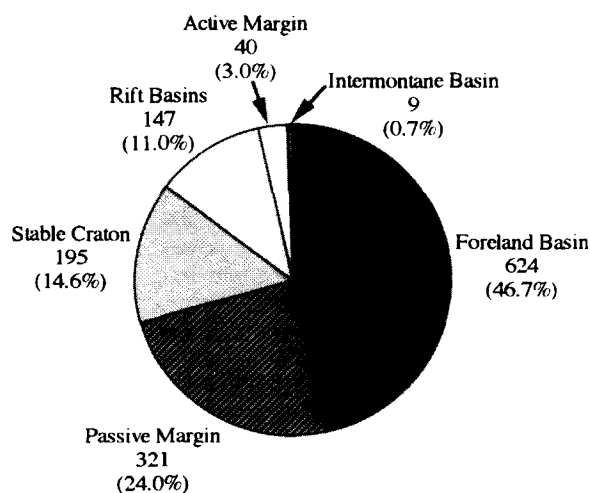


Fig. 19. Pie chart showing proportion of vertebrate localities in the database represented by each basin type.

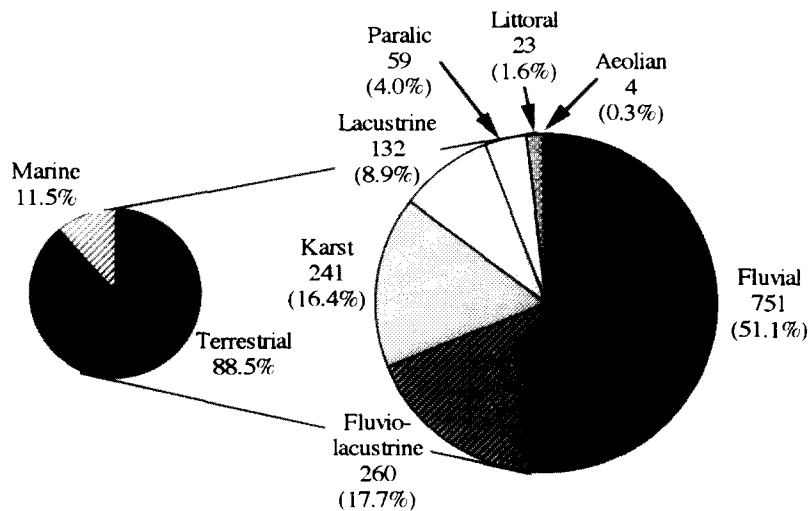


Fig. 20. Pie charts showing the distribution of environments in the fossil dataset. Numbers represent the number of localities for each environment (note that not all localities presently in the database have assigned environments); percentages refer to the proportion of all localities represented by localities from that environmental setting. 'Karst' environments include fluvial and lacustrine settings where these occur in sinkholes and caves.

(ephemeral or permanent) and climate. The nature of the aquatic environment can be constrained using sedimentological data such as palaeosols.

Behrensmeyer et al. (1979) have shown, through empirical studies in Africa, that size is an important taphonomic bias in fluvial systems, with larger animals, especially those more than about 15 kg, being more likely to have elements preserved. This essentially reflects the greater resistance of large elements to physical breakdown. Although there are few published weight measurements for extant crocodilians, most adults are certainly heavier than 15 kg: a relatively small American alligator, 1.98 m long, weighed 24.5 kg (Bellairs, 1969), while the two alligators in the study of Brisbin et al. (1982) (see Section 4) weighed 188 and 135 kg.

The number of taxonomically identifiable elements is also important: the more elements, the more chance of being recognized and reported. In the fossil record, scutes and teeth are the most common crocodilian material found (Markwick, 1996) and, although not generally diagnostic for finer taxonomic levels, they are recognizably crocodilian (an individual crocodilian may generate over 1000 teeth during its lifetime; Markwick, 1996).

7.2.4.1. Taphonomic control groups. The concept of taphonomic control groups was first described by Bottjer and Jablonski (1988). It is based on the postulate that a significant absence in one fossil group, due to some factor such as environment or climate, can be constrained by the presence of another fossil group that has a similar taphonomic behaviour and only differs from the study group in the factor being investigated. For crocodilians, I have used turtles as the taphonomic control group; they have a good fossil record (turtle shell being one of the more ubiquitous elements at many vertebrate sites), are ecologically mainly dependent on aquatic environments, but as a group occupy regions that are climatically (especially thermally) too extreme for crocodilians (Fig. 21; compare with Fig. 10; subgroups of the turtles, such as the land tortoises, are more restricted, Markwick, 1996). This is reflected in turtles occupying a greater latitudinal range than crocodilians (Fig. 22; cf., Fig. 2). The validity of using turtles as the taphonomic control is shown using the present-day climate station dataset (Section 5.3.1); of the 304 crocodilian-bearing stations in this dataset 95.1% also have turtles. (This 4.9% discrepancy may be an artifact of the method: crocodilian

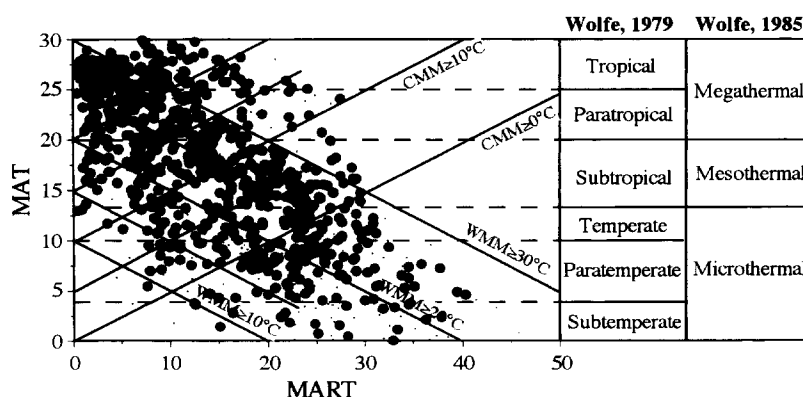


Fig. 21. The distribution of climate stations with turtles in MAT–MART climate space. Turtles, per se, are not as climatically restricted as crocodilians (Fig. 9). Consequently, they provide an excellent taphonomic control for examining significant absences of crocodilians due to climate.

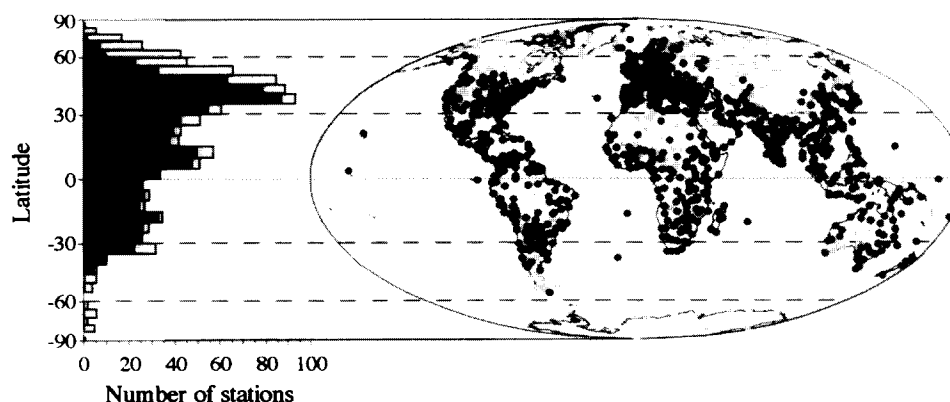


Fig. 22. Turtle-bearing stations as a function of latitude. The extension of turtles into high latitudes is due, in part, to the distribution of marine turtles, as they follow the poleward extension of warm low-latitude ocean currents. In low latitudes turtles occupy almost all stations.

distributions are based on area data which may overestimate ranges, turtles on published point data which tends to underestimate ranges.) In contrast only 35.4% of the 816 localities with turtles have crocodilians. Given these arguments, a fossil fauna that contains a fossil turtle but no crocodilian should be seen as reflecting the original absence of the latter and not the effects of taphonomy.

7.2.5. History: palaeobiogeography

Organisms do not instantaneously appear throughout the world, but originate from the evolution of a single individual to develop new popula-

tions at one point in space. Although subsequent expansion may occur, there may be non-climatic reasons why this does not lead to the immediate and full occupation of all geographic areas within the organism's viable climate space.

The distribution of modern and fossil occurrences of each crown group crocodilian family is shown in Fig. 23. These reveal that neither alligatorids nor gavialids are historically found in Africa or Australia, although their relatives, the Crocodylidae, occur on both continents. Modern alligators, caimans and gavials lack the salt glands that enable many crocodiles to invade saline habitats, and although some alligatorids are found in

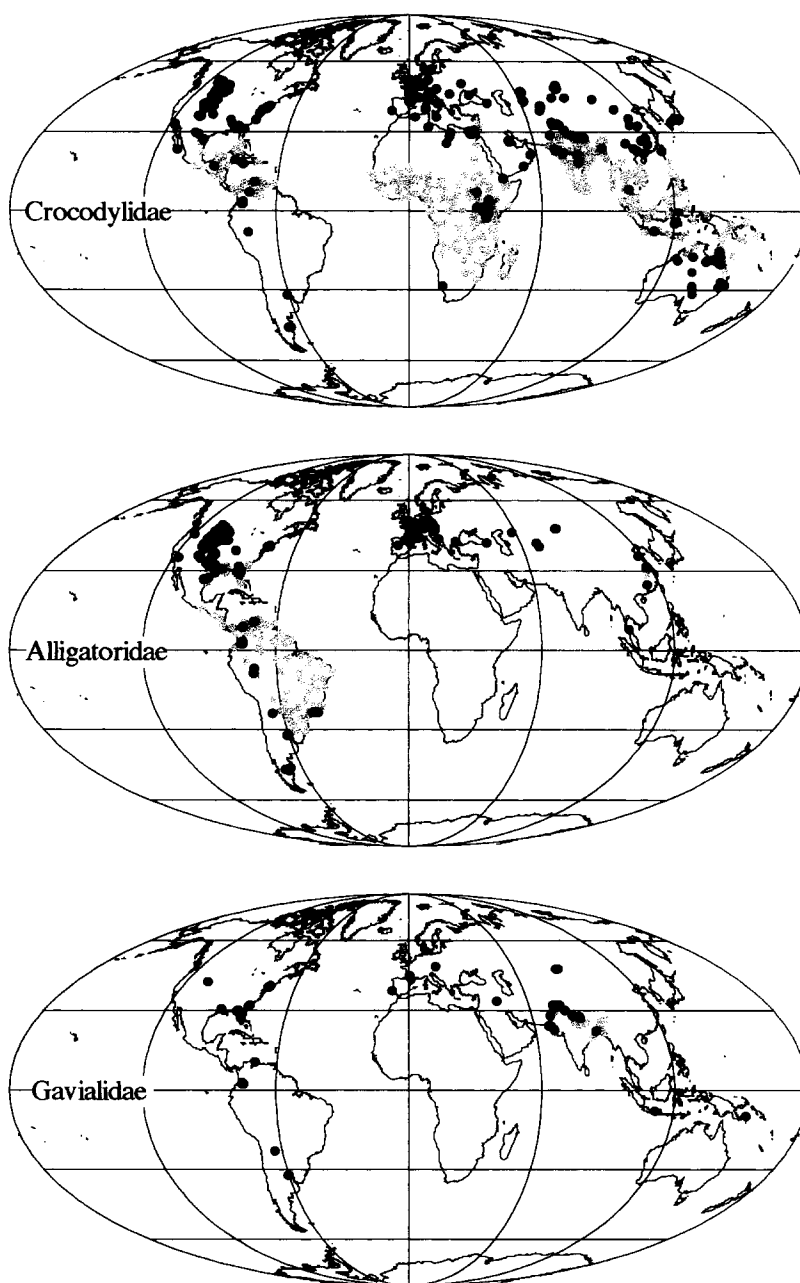


Fig. 23. Maps showing distribution of alligatorids, crocodylids and gavialids. Light shading represents the present distribution (climate station dataset). Black dots represent their fossil distribution. Note the absence of gavialids and alligatorids from Australia and Africa.

estuarine habitats, crocodylids are much better adapted to such environments (Jackson et al., 1996). This has generated considerable interest in the role osmoregulatory physiology may have

played in the palaeobiogeographical history of crocodilians (Densmore, 1983; Brooks and O'Grady, 1989; Taplin and Grigg, 1989; Jackson et al., 1996), because if this biological difference is

also true for their fossil relatives, then the presence of marine seaways isolating Africa and Australia from the rest of the terrestrial world may explain the failure of alligatorids and gavialids to expand into these two continents. (By the Miocene, when Africa and Eurasia collided, alligatorids have already become restricted to central and eastern Asia and western Europe. Their absence from the region in between, which is the site of a Miocene land connection, may explain why they do not enter Africa at this time). Given this, the historical expansion of these two families into South America, North America, Europe and Asia must have been made via land bridges; those between the last three must have been via high-latitude land bridges, which has direct implications for the contemporary palaeoclimate in those latitudes.

7.3. Errors

7.3.1. Misidentification

Misidentification is a potential source of error that may influence distributions. Although rare, misidentifications of crocodilians have occurred; for example, in 1944, Kellogg described a new genus of long-snouted dolphin, *Megalodelphis magnidens*, based on part of a lower jaw, a lower jaw that Morgan (1986) later reinterpreted as part of a crocodile. Conversely, Case et al. (1987) described the presence of a crocodilian in the Palaeogene of Antarctica, also on the basis of jaw fragments, which has subsequently been re-identified as a fish (Case, pers. commun.). The potential effects of misidentification can be mitigated by only accepting identifications based on complete, or essentially complete, skulls, which are more difficult to misidentify at the level of family, suborder or order (specimen information is stored within the database in order to facilitate such checks, although it is implicit in taxonomic assignments that the material be identifiable). For the present study such problems are negligible; trends based on such data are indistinguishable from those using all data.

7.3.2. Dating

In order to minimize the effects of inaccurate dating, age assignments used in this study are

based on the most recent published accounts. Unfortunately this is not a guarantee of truth. However, an inspection of localities in the database where age assignments have been amended over the last 100 years, suggests that in general such changes have not exceeded more than one subepoch (e.g. Early Pliocene to Late Miocene). Problematic assignments are concentrated at key chronostratigraphic boundaries, for instance the Eocene–Oligocene boundary (Prothero and Berggren, 1992), where the Chadronian Land Mammal Age in North America has recently been reassigned to the Late Eocene from the Early Oligocene; in the former U.S.S.R., Korobkov (1963) suggested that all dates formerly assigned to the Early Oligocene (Rupelian) should be reassigned to the Late Eocene. Whether this change should be applied globally remains uncertain. This then defines the temporal resolution of the dataset—plus or minus one subepoch (see also Section 7.1.2).

8. Trends

Fig. 24 shows the palaeolatitudinal distribution of crown group crocodilians in the context of all fossil vertebrates (spatial and temporal resolution, GP3, two time intervals, respectively; see Section 7.1). A detailed view of the region between the 30° and 80°N palaeolatitudes, which represents the best sampled area of the globe (see Section 7.2), is given in Fig. 25. The overall trends revealed in these figures show the expansion of crown group crocodilians into northern high latitudes during the Late Cretaceous, with the greatest poleward range found in the Early Eocene (the Ellesmere Island fauna, Canada: West et al., 1977; Estes and Hutchison, 1980; McKenna, 1980). However, the group does not expand into the Southern Hemisphere until the Paleocene (a possible explanation of this pattern is discussed in Markwick, 1996)—the Middle and Late Eocene record is poorly represented in southern latitudes, but from the Oligocene to the Recent there is a general Equator-ward retreat of crocodilians. In the Northern Hemisphere, an Equator-ward shift is seen during the Oligocene and again in the

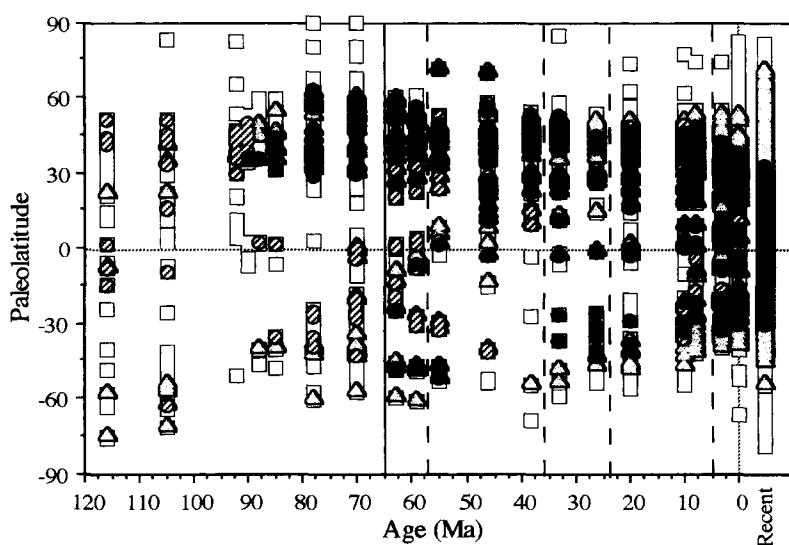


Fig. 24. The palaeolatitudinal distribution of crocodilian and non-crocodilian vertebrate localities. Crown group crocodilians (black circles) are shown against a backdrop of all crocodilians (open circles), turtles (medium grey circles) and vertebrates in general (white squares). The dataset used here has the following spatial and temporal resolution: GP ≤ 3 , ≤ 2 time intervals. The solid vertical line at 65 Ma is the K–T boundary, and dashed vertical lines are the boundaries between the epochs of the Tertiary. This provides a visual impression of times when the poleward limit of crocodilians is well constrained (significant absences are indicated by the presence of turtles—taphonomic controls—and all other vertebrates—collection controls). These intervals include the Late Cretaceous and the Neogene to Recent, in which the poleward limit can be assumed to be the actual limit rather than a reflection of preservation.

Pliocene, separated by a slight latitudinal expansion through the Miocene. The Pliocene to Recent history is one of increasingly limited range. These latitudinal changes are interpreted as reflecting general thermal conditions, with Equator-ward shifts at times of polar cooling. The general similarity of this trend with that of the marine oxygen isotope curve (Fig. 1) supports this supposition. This trend is also indicated by the floral record (Frakes, 1979) and the Cenozoic history of glaciation (Markwick and Rowley, 1997).

The trends shown in Figs. 24 and 25 are qualified using control groups: vertebrates as a whole controlling for collection and tectonic biases, turtles controlling for taphonomic bias. Given these controls, observed trends during the Oligocene to Recent appear well constrained, but Late Cretaceous and early Palaeogene trends are limited by available data. This is shown more clearly in Fig. 26, which shows the proportion of the latitudinal range represented by turtles (localities in which crocodilians could be preserved if they had origi-

nally been present; see Section 7.2.4.1) that have crown group crocodilians.

While control groups provide a qualitative assessment of the significance of trends, this assessment can also be made quantitatively. Rarefaction (resampling without replacement) is used here to test whether the restriction of fossil crocodilians to lower latitudes during the Late Oligocene (Fig. 25) is a function of sampling alone (the Late Oligocene has the lowest number of crown group crocodilian localities of any time interval in the post-Santonian, Fig. 17). For each interval, from the Campanian to the Pleistocene, ten localities (the number of localities in the Late Oligocene Northern Hemisphere) are randomly taken from all of the localities in that interval (Northern Hemisphere only) using the Resampling Stats software (Bruce, 1995). The maximum latitude among these ten is then recorded. This is repeated 1000 times and the distribution compared with the observed distribution of localities using the chi-square test. The results show that the Late

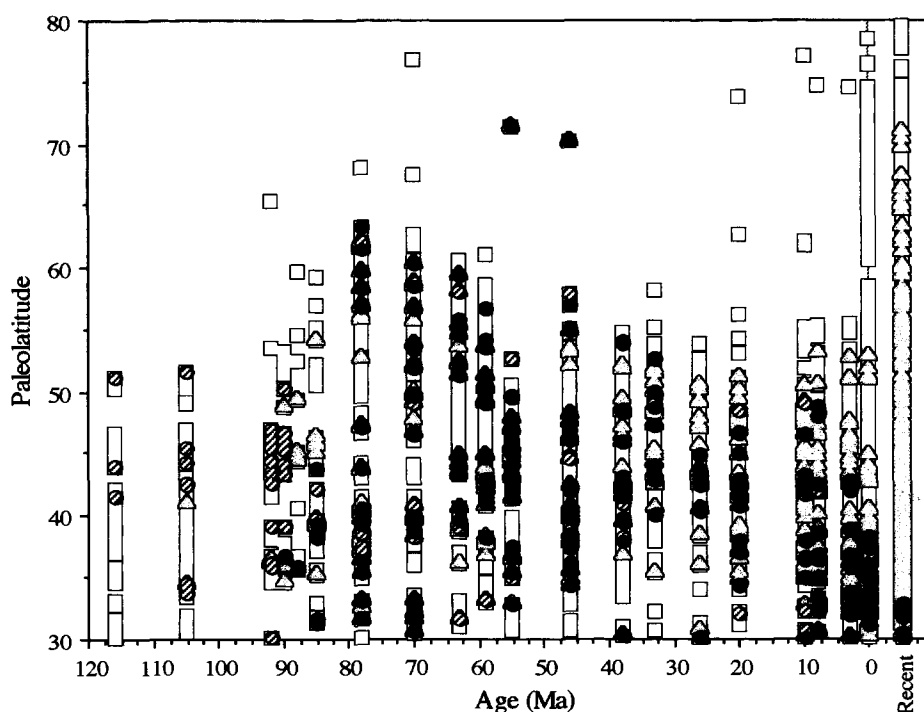


Fig. 25. Palaeolatitudinal distribution of crown group crocodilians in the Northern Hemisphere. This is a detailed view of the region between 30 and 80°N palaeolatitudes from Fig. 24. See Fig. 24 caption for further information.

Oligocene palaeolatitudinal restriction is not necessarily a function of low sampling ($p=0.0376$; testing the hypothesis that the two distributions are indistinguishable).

Another way of examining the significance of sampling on the distribution is to ask what the probability is that a random resampling of crown group localities in each interval would produce a maximum palaeolatitude of less than or equal to the Late Oligocene value of 44.9°, given the Late Oligocene sample size of ten localities between 0 and 90°N. This analysis is also made for a subset of the dataset, all localities that occur below 55.9°N palaeolatitude, the most poleward vertebrate locality in the Late Oligocene. The results are shown in Table 5 and illustrate again that the variations in observed palaeolatitudinal trends are not simply an artifact of sampling.

While the previous trends have concentrated on all crown group crocodilians, Fig. 27 shows the palaeolatitudinal distribution of alligatorids, crocodylids and gavialids separately. All three families

show similar trends, although in the post-Oligocene Northern Hemisphere alligatorids dominate the higher latitudes, crocodylids never reoccupying these latitudes. Whether this reflects greater tolerance of cold conditions by alligatorids is unclear, but is not suggested by the limited available experimental data.

9. Latitudinal gradients

Fig. 10 showed how the proportion of climate stations with crocodilians varied systematically with latitude and thereby with temperature (Fig. 11). If this relationship holds for the fossil record then it provides the opportunity to retrodict temperatures and thereby latitudinal thermal gradients, which are an important GCM boundary condition. Fig. 28 shows the relationship between the ratio of crocodilian- to turtle-bearing stations in each 5° latitudinal zone and the mean MAT for that zone (turtle-bearing stations are used as a

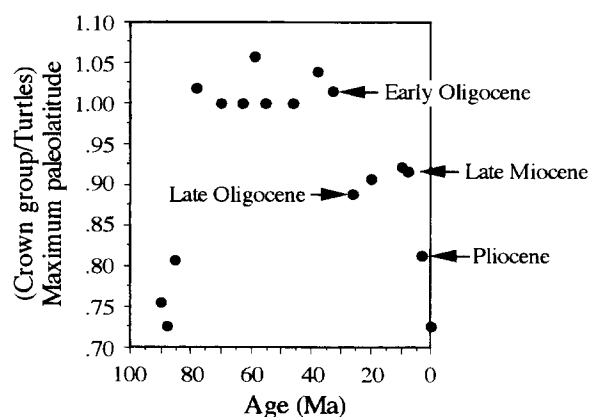


Fig. 26. The ratio of the maximum palaeolatitudes represented by crown group crocodilians and turtles through time. The significance of the Equator-ward trend in crocodilians can be qualified using the taphonomic control group, turtles. The ratio between the two gives an indication of how much of the latitudinal range occupied by the control group is also occupied by crocodilians. From the very Late Cretaceous to the Early Oligocene crocodilians and turtles both occur in the most poleward localities (values greater than 1 reflect undersampling of turtles). The subsequent Equator-ward shifts of crocodilians in the Oligocene and Pliocene are clearly shown in this diagram.

surrogate for climate stations in general: this does not affect the modern relationship, but allows for some control of taphonomic effects when applied

to the geological past). The derived regression is used to retrodict the average MAT for each 5° palaeolatitudinal zone in each time interval used in the study, of which four are shown in Fig. 29 (see Markwick, 1996, for the complete results).

The retrodicted thermal gradients in Fig. 29 show a number of interesting results. The method replicates the Recent well, although there is a slight hemispheric offset. In the Pleistocene, gradients are steep. In part this reflects the effects of the 49.6°C value in low latitudes, which seems wholly unreasonable even though adjacent latitudinal zones also have high values. Steepened gradients are also retrodicted for the glacial world of the Late Oligocene, but those of the Miocene and Pliocene (e.g., Middle Miocene, Fig. 29) are similar to that of the Recent. In the Palaeogene and Late Cretaceous, the record is mostly restricted to the Northern Hemisphere. Derived gradients during these times are very shallow with warm temperatures extending into high latitudes (e.g. Early Eocene, Fig. 29).

While the general difference between Palaeogene and Neogene gradients are consistent with palaeoclimate interpretations based on other evidence, the absolute values calculated for mid and high latitudes are much higher than retrodicted using

Table 5
Resampling results

Interval	Number of localities	Maximum palaeolatitude (degr.)	<i>p</i> for max. plat. ≤44.9°, 10 locs only	Number of localities plat. ≤53.9°	<i>p</i> for max. plat. ≤53.9°, 10 locs only
Campanian	46	63.4	<0.001	15	0.005
Maastrichtian	40	60.4	<0.001	32	<0.001
Early Paleocene	22	59.5	0.003	17	0.164
Late Paleocene	26	56.7	<0.001	24	0.004
Early Eocene	34	71.4	<0.001	33	<0.001
Middle Eocene	57	70.3	0.064	51	0.169
Late Eocene	41	54.0	<0.001	38	<0.001
Early Oligocene	17	52.6	0.004	17	0.004
Late Oligocene	10	44.9	1	10	1
Early Miocene	42	46.7	0.6	42	0.6
Middle Miocene	46	46.5	0.774	46	0.774
Late Miocene	33	48.7	0.42	33	0.42
Pliocene	47	42.8	1	47	1
Pleistocene	31	38.3	1	31	1

Values of *p* for the probability that resampling crown group crocodilians in each interval for the sampling level in the Late Oligocene (10 localities) and that the maximum palaeolatitude will be below the Late Oligocene.

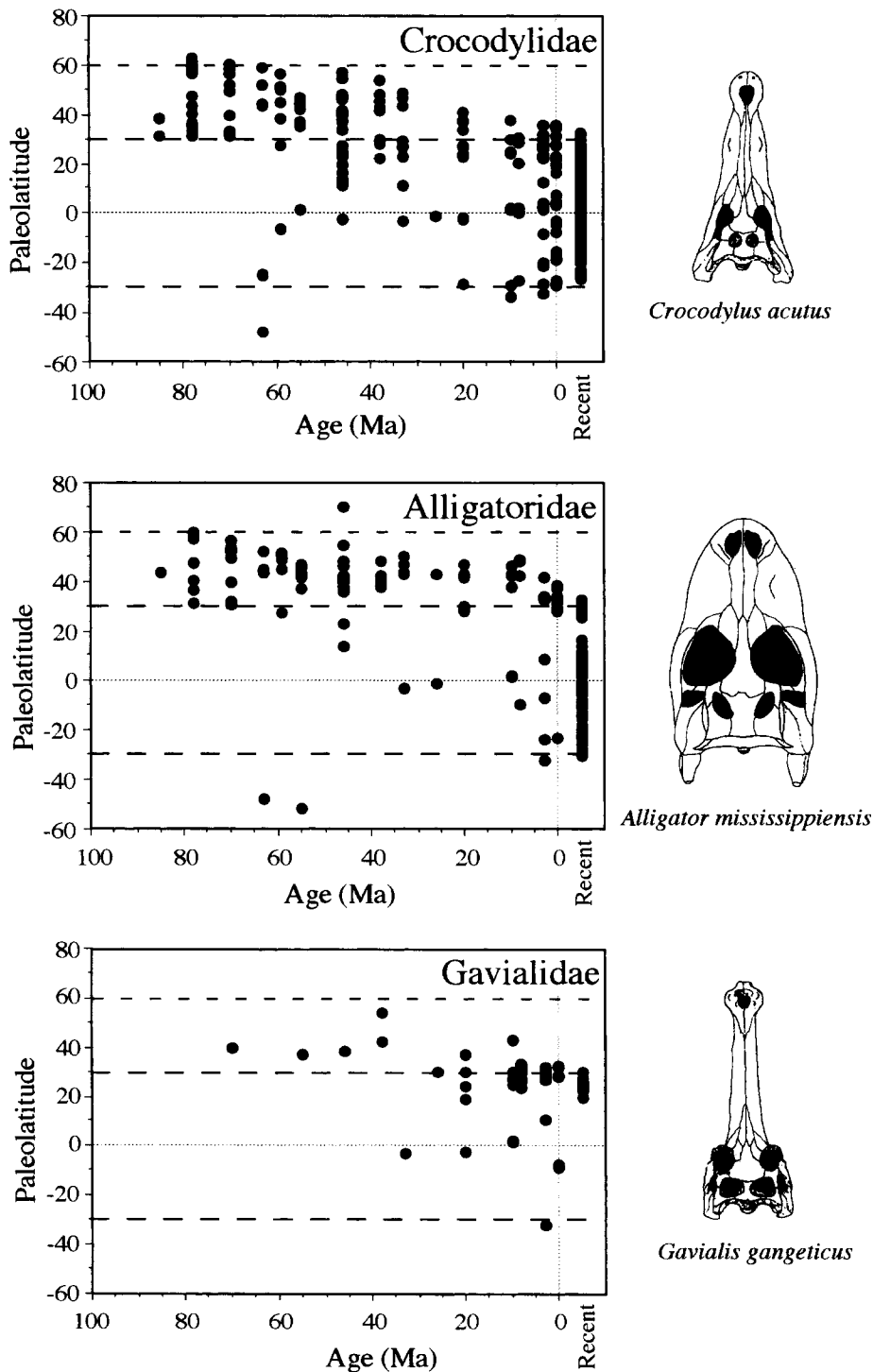


Fig. 27. Palaeolatitudinal distribution of each crown group family through time. Each point represents a locality that contains a representative of the specified family. Spatial and temporal resolution: GP ≤ 3 , ≤ 2 intervals. Skull figures are modified from Iordansky (1973). The bias of the Northern Hemisphere is again clear. Note that based on the limited evidence crown group crocodilians only expand into the Southern Hemisphere after the K–T boundary (see Markwick, 1996). Note that after the Oligocene the highest northern latitudes are restricted to alligatorids.

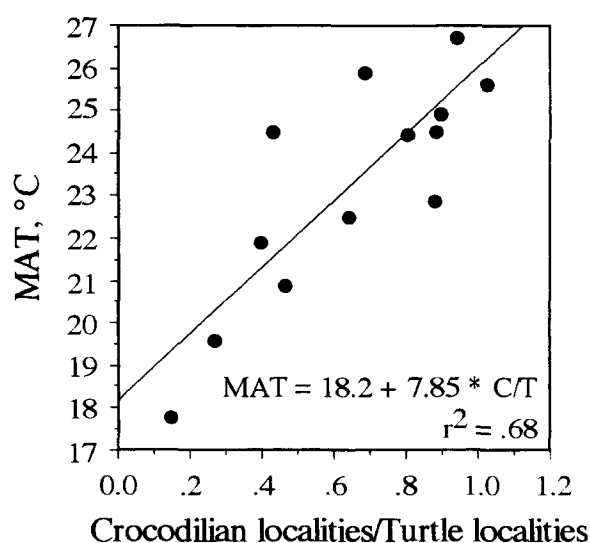


Fig. 28. The relationship between the ratio of crocodilian to turtle localities and MAT (°C) for each 5° latitudinal zone. This is derived from the present-day climate station dataset.

other methods, for instance floral physiognomy (Greenwood and Wing, 1995) and marine oxygen isotopes (Zachos et al., 1994). This almost certainly reflects an intrinsic effect of the method. The ratio of modern crocodilian- to turtle-bearing climate stations is not only a function of temperature but also a consequence of the longitudinal distribution of aridity (see Section 5.3.2). If the distribution of aridity changes with time then the relationship between this ratio and temperature should also change, such that cooler regions will have higher ratios; unfortunately the method is calibrated using only the present relationships. This does not contradict the overriding importance of temperature as the limiting factor restricting the spatial distribution of crocodilians. As the region of aridity decreases, the area in which crocodilians can survive increases, reflecting more standing water and vegetation for buffering the effects of extremes of temperature at the peripheries of crocodilian thermal climate space. Given this, the gradients shown in Fig. 29 also provide information about the degree of aridity in each time interval. The Neogene and Pliocene are similar to the Recent, but the disparity between the results shown for the Eocene and those derived by the

floral data of Greenwood and Wing (1995) may be interpreted as reflecting less extensive regions of aridity at that time, especially in mid-latitudes where most of the data are concentrated. It may also reflect distributional sampling bias, but this is not borne out by the maps shown below, which suggest that the longitudinal coverage in northern mid-latitudes is quite comprehensive for at least the Cenozoic. The relationship between mid-latitude aridity and periods of glaciation is an important one and is developed further in the following section.

10. Maps

In this section the palaeodistribution of fossil crown group crocodilians is shown on a series of plate reconstruction maps (Figs. 30–54: see caption of Fig. 30 for details). Each occurrence of this climate proxy represents for that locality the climate defined in Part 1 of this study: CMM $\geq 5.5^{\circ}\text{C}$ (by inference MAT $\geq 14.2^{\circ}\text{C}$, mean Winter T $\geq 6.6^{\circ}\text{C}$) and the presence of standing water. A detailed synopsis of the palaeoclimate of each interval is beyond the purview of this study; to this end, text associated with each map is kept to a minimum. For excellent reviews of the terrestrial climate record through this period, readers are referred to Frakes (1979), Crowley and North (1991), and Behrensmeyer et al. (1992).

10.1. Cretaceous

The middle Cretaceous terrestrial record is poorly represented, due in part to the concomitant high sea-level which greatly reduces the available land area on which to preserve a terrestrial record. Maps for the Aptian through Turonian are shown in Figs. 30–33. Although crocodilians in general are relatively well distributed throughout the world at this time, crown group crocodilians have only a limited representation and are restricted entirely to the Northern Hemisphere. One of the earliest occurrences of a 'eusuchian' grade crocodilian (the 'Eusuchia' include all crown group crocodilians) is in the Albian aged Griman Creek Formation of Australia. Referred to as *Crocodylus selaslophensis*,

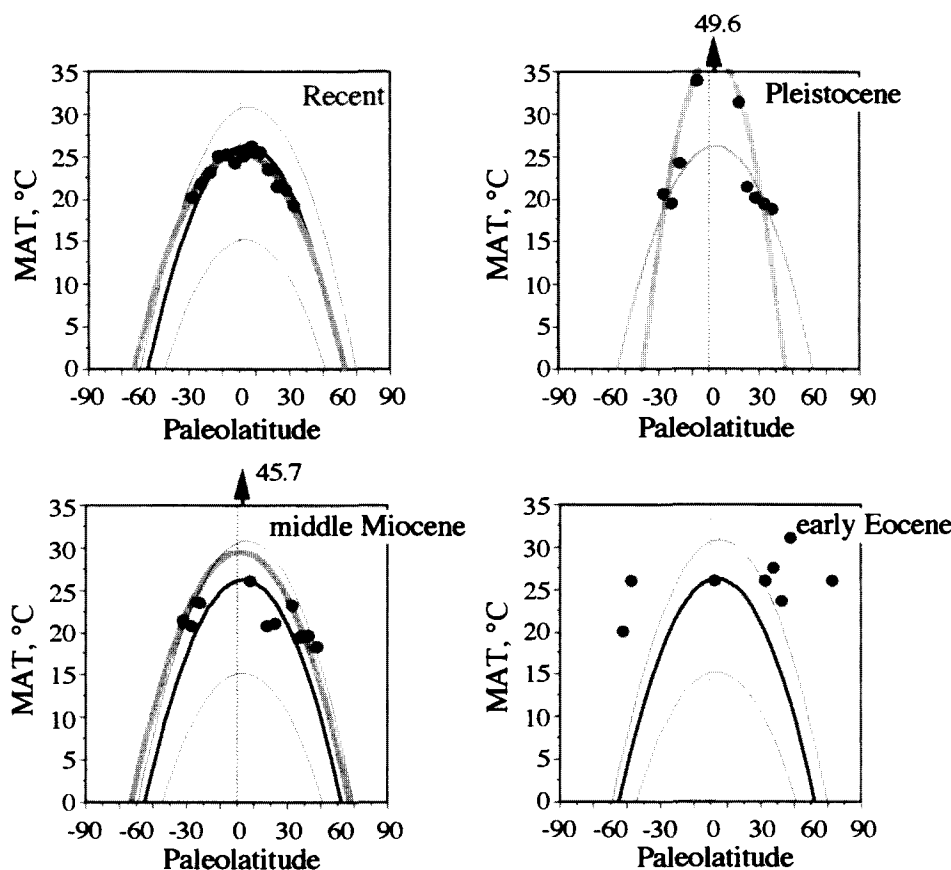


Fig. 29. Thermal gradients determined using the ratio of crocodilian to turtle localities. Palaeotemperature values for each 5° palaeolatitudinal zone are calculated using the regression given in Fig. 28. A second-order polynomial is drawn through these results (thick grey line) for post-Early Oligocene times; this represents the best fit thermal gradient. These time intervals have similar gradients to the Recent, but differ from those retrodicted for earlier intervals, which are flatter. See text for discussion. Arrows and adjacent values represent results above the limit of the y-axis for the palaeolatitudinal position shown. The bold black line represents the Recent gradient—mean MAT for each 5° zone of latitude. The lower thin black line represents the Recent minimum MAT in each zone, the upper line the maximum MAT.

the true relationships of this taxon remain unclear (Molnar, 1980), and consequently it is not shown on the maps as a crown group crocodilian.

As crown group crocodilians diversify through the Late Cretaceous (Markwick, 1993, 1996), their spatial distribution also expands (Figs. 34–38), such that by the Santonian (Fig. 36) they are well distributed throughout the Northern Hemisphere, except the Far East. However, crocodilians in the Southern Hemisphere remain exclusively represented by ‘mesosuchians’, or ‘indeterminate’ crocodilians, until the Paleocene, with one exception (Fig. 34): a temporally poorly resolved locality

near Nagpur, India, which is dated as Upper Cretaceous–Paleocene (Sahni et al., 1984).

In the Campanian the distribution of crown group crocodilians depends largely on the position of seaways; the northernmost Campanian localities lie along the edge of the Western Interior Seaway of North America (Figs. 32 and 33). This reflects a preservational bias and the importance of seaways as conduits of heat to high latitudes (Valdes et al., 1996). This is consistent with the floral interpretations of Wolfe and Upchurch (1987; Upchurch and Wolfe, 1993), who interpreted megathermal climates (MAT $\geq 20^{\circ}\text{C}$) extending to

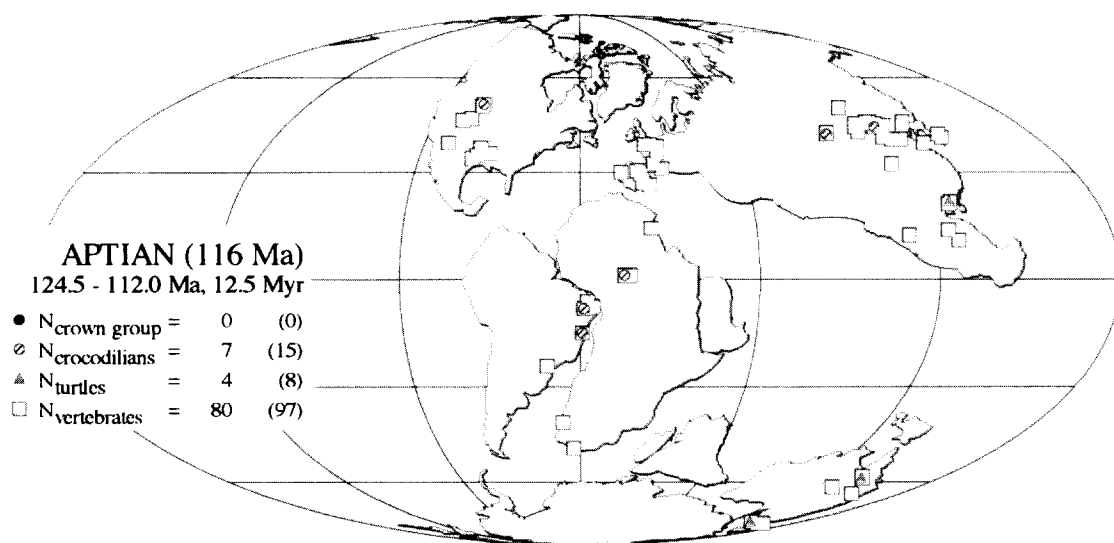


Fig. 30. Aptian map (116 Ma). In each of the following maps (Figs. 42–66) the distribution of vertebrates (white squares), turtles (grey triangles), crocodilians (cross-hatched circles) and crown group crocodilians (black circles) is shown. Data are restricted to those localities with $GP \leq 3$ and which occur in no more than two time intervals (note that for Figs. 34, 39, 42, 46 and 49 the maps show data for the entire epoch in each case, including the Late Cretaceous; consequently in these cases intervals are much coarser, e.g. two intervals could mean 'Eocene–Oligocene'). The numerical date given in parentheses on each map is the reconstruction age used for the basemap. Below this is given the numerical age range of the interval and its duration in millions of years (Myr). These numerical ages are those of Harland et al. (1990). Each map also includes the number of localities represented by each data type (e.g. ' $N_{\text{crown-group}}$ ' is the number of crown group crocodilian localities shown on the map); the values in parentheses represent the total number of localities (including those whose age assignments span more than two time intervals) in the dataset that range through the time interval of the map. In order to aid clarity vertebrate localities are plotted first and then filled with white such that overlapping localities form one large white area. The symbol for turtles (grey triangles; includes all turtles, including tortoises and marine forms) is then superimposed onto these data. Crocodilian data are then placed on top of the vertebrate and turtle symbols, such that in most instances turtle biogeography is obscured. For the present study this is not important because turtles are only being used to qualify the absence of crocodilians. Basemaps courtesy of Dr. David Rowley, University of Chicago (unpublished work).

about 40°–50°N palaeolatitude and mesothermal conditions (MAT 13–20°C) as far as about 60°. (From Fig. 9 modern crocodilians only occur in meso- and mega-thermal climate regions.) Only the Mongolian and northern Chinese localities appear landlocked, where the development of caliches during the middle Campanian (Djadokhta Formation) suggests increasing aridity during this time (Jerzykiewicz and Russell, 1991). These localities are dominated by non-crown group crocodilians. This pattern continues into the Maastrichtian.

10.2. Tertiary

With the Paleocene, crown group crocodilians expand their range into South America, India, eastern Asia and Australia, but apparently not

into either Antarctica or Africa (neither of which have a good fossil record at this time). These distributional changes may be in response to the large number of 'mesosuchian' extinctions at the K–T boundary (Markwick, 1996). Regardless, they provide the opportunity to interpret the palaeoclimate of a much broader region: during the Paleocene the Americas from Patagonia in the south ($\approx 50^\circ$) to Alberta and Saskatchewan in the north ($\approx 60^\circ\text{N}$) experienced CMM's $\geq 5.5^\circ\text{C}$ and MAT's $\geq 14.2^\circ\text{C}$ (note the absence of data in low latitudes). This is consistent with the flatter thermal gradients shown for this interval in Fig. 29. In almost all of these cases, as for the Late Cretaceous, faunas are associated with the distribution of marine seaways and embayments. Again, exceptions to this lie in northern China and

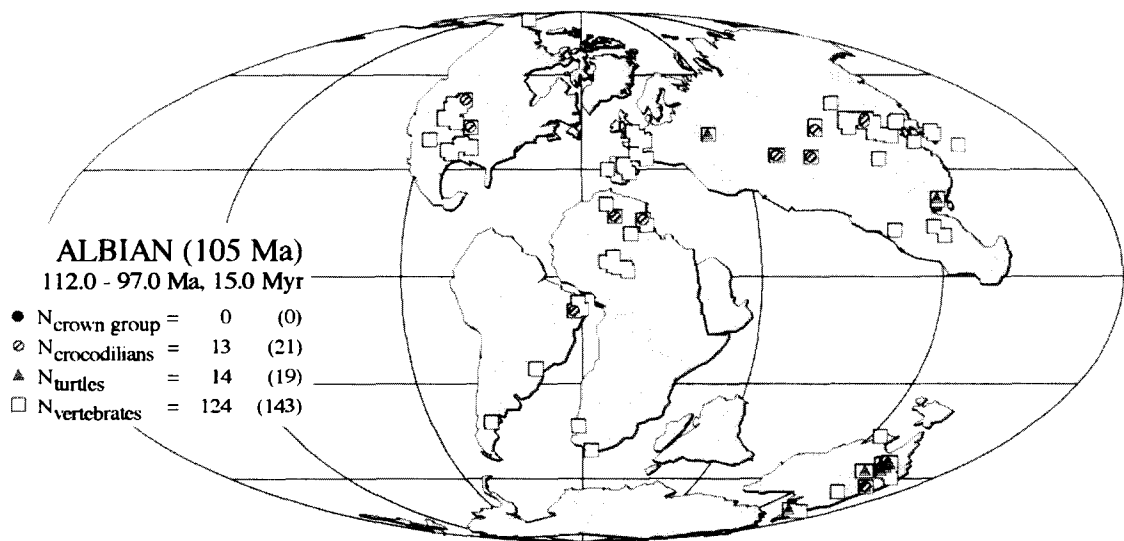


Fig. 31. Albian map (105 Ma). See Fig. 30 for key and further details.

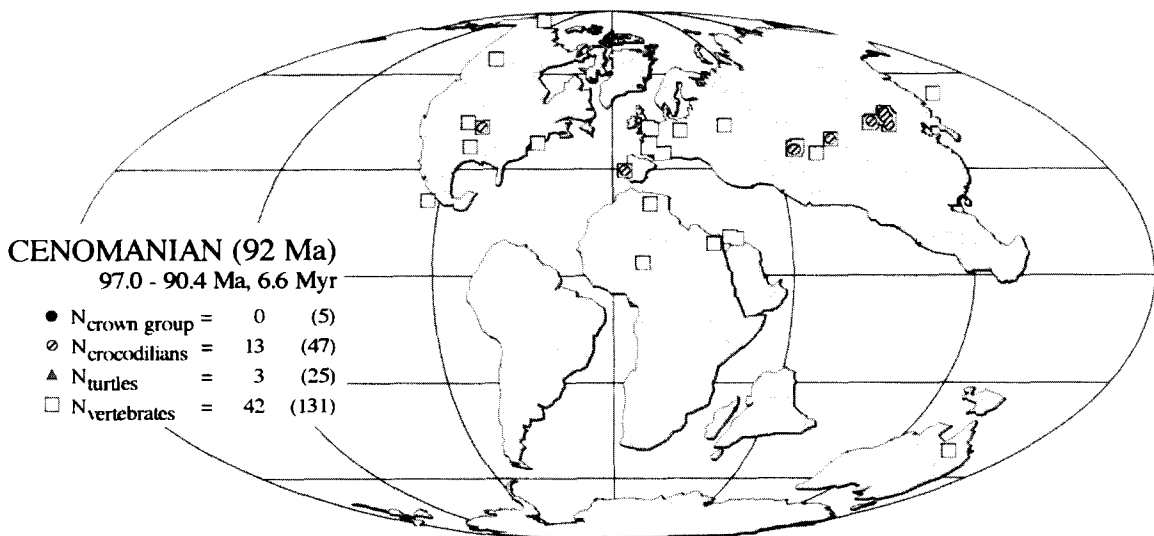


Fig. 32. Cenomanian (92 Ma). See Fig. 30 for key and further details.

Mongolia, suggesting that the continental interiors too were thermally relatively moderate. However, whether such temperatures expanded as far poleward in these continental regions as they did in the contemporary Americas, is obscured by the lack of data.

The Eocene record is much larger than that of the Paleocene, but the distribution of crown group

crocodilians is quite similar (Fig. 42). Crown group crocodilians are well represented throughout the northern continents south of 60°. As for the Late Cretaceous and Paleocene, the northern limit of crocodilians is dictated by the limits of the record so that their true poleward extent is unresolvable. However, in the Early Eocene (Fig. 43), the presence of crocodilians and giant tortoises on

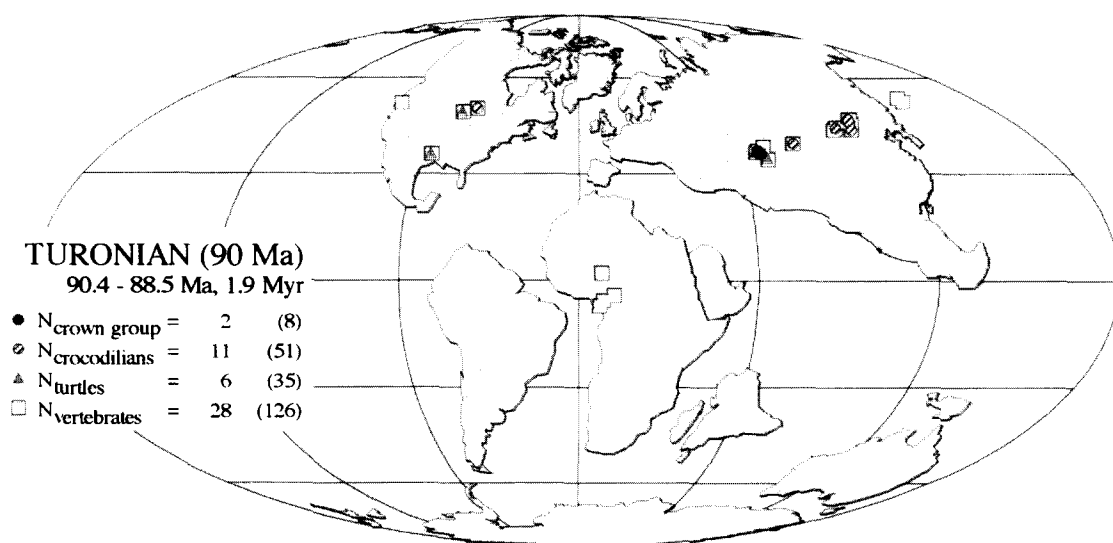
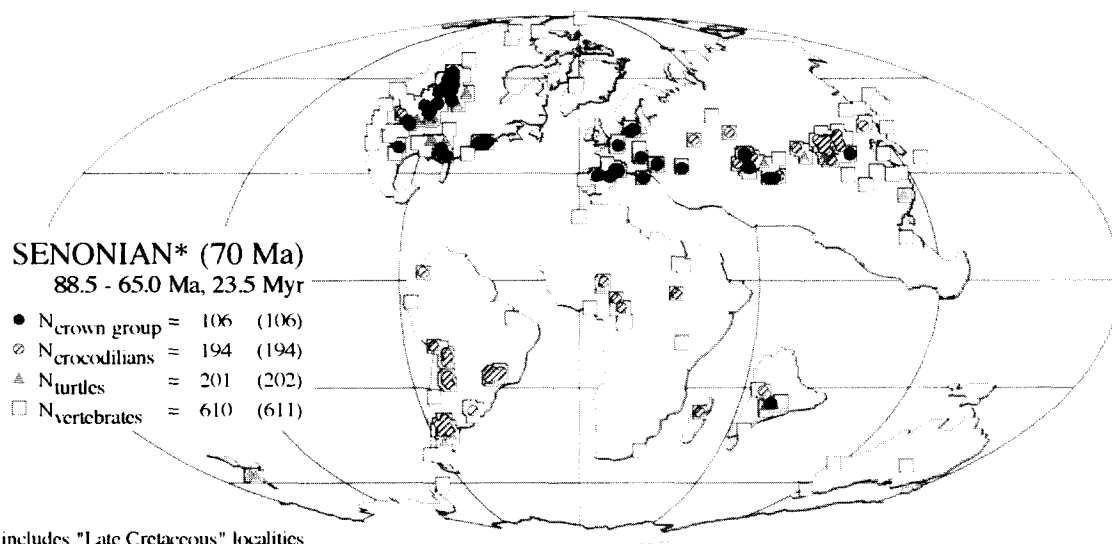


Fig. 33. Turonian (90 Ma). See Fig. 30 for key and further details.



* includes "Late Cretaceous" localities

Fig. 34. Senonian (70 Ma). See Fig. 30 for key and further details. This figure includes all occurrences dated as 'Late Cretaceous' (Coniacian–Maastrichtian). Note that the crown group crocodilian occurrence in India represents a temporally poorly resolved locality: Nagpur, which is dated as Late Cretaceous to Paleocene and includes both dinosaurs and a Paleocene fauna (Sahni et al., 1984). By the Paleocene crown group crocodilians are well represented in India.

Ellesmere Island at a palaeolatitude of $\approx 71.4^\circ$ (Estes and Hutchison, 1980) suggests that warm temperate to 'tropical' climates ('Mesothermal' of Wolfe and Upchurch, 1987; MAT ≥ 14.2 , CMM $\geq 5.5^\circ\text{C}$, based on crocodilians, this study) occurred within the Arctic Circle. (The MAT and

CMM of this region today is about -14.4°C and -31.5°C —data for Sachs Harbour, Banks Island, at 71.9°N .) There are no data to examine whether these climates also extended into the continental interior of Canada (Canadian Shield). In Eurasia crocodilians extend northward into southern

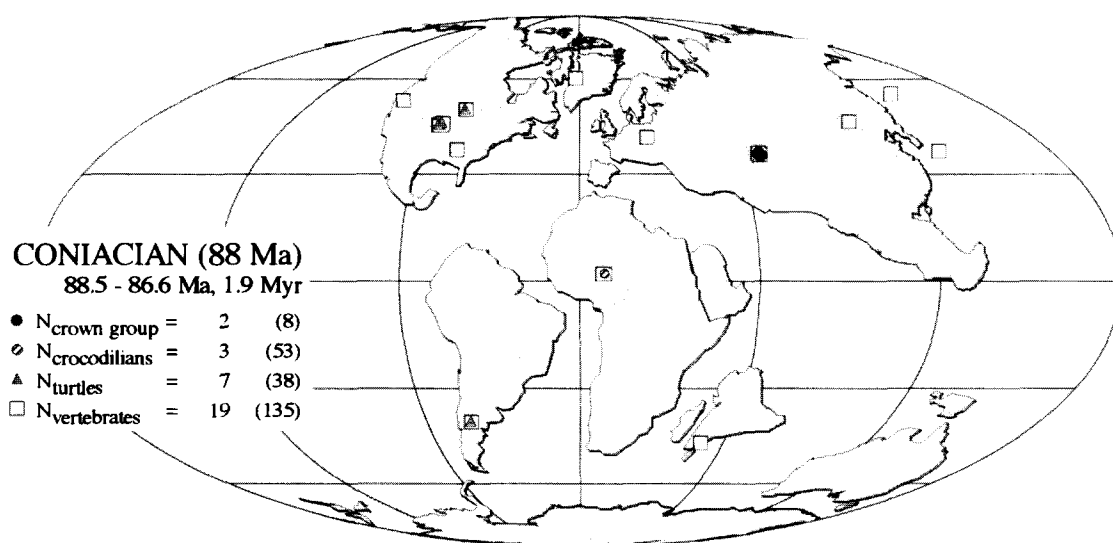


Fig. 35. Coniacian map (88 Ma). See Fig. 30 for key and further details.

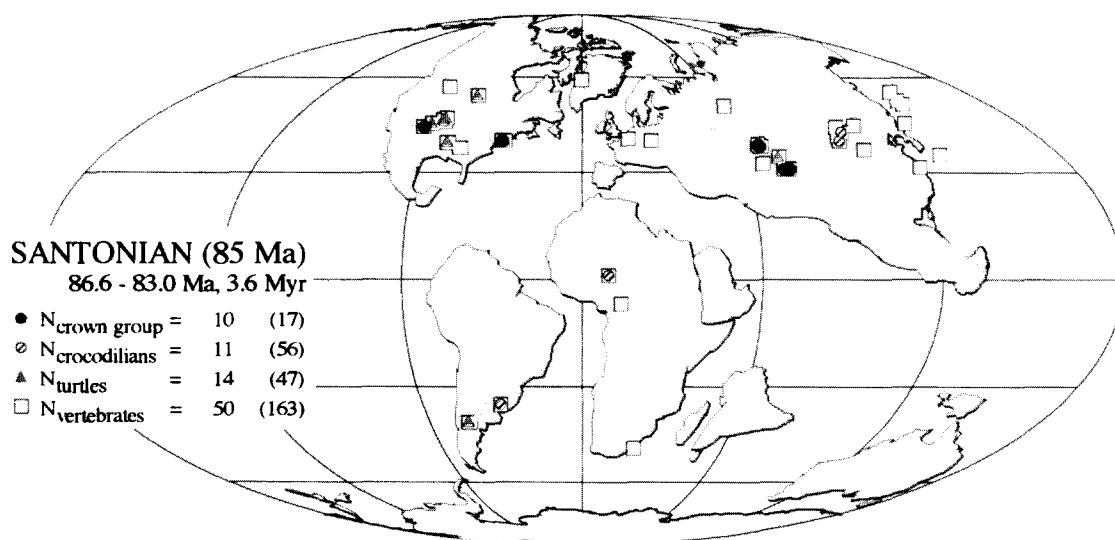


Fig. 36. Santonian map (85 Ma). See Fig. 30 for key and further details.

Britain and the Lake Zaysan area of eastern Kazakhstan. This interval represents a climate 'optimum' for most workers (Wing and Sues, 1992; Wing and Greenwood, 1993).

An important difference between the Paleocene and the Eocene is that by the latter the interior seaway of North America has largely disappeared and therefore does not play a major role in deter-

mining the distribution of warm climates (Sloan and Barron, 1990, 1992; Wing and Greenwood, 1993; Markwick, 1994; Wolfe, 1994) and crown group crocodilians. Increased continentality is also interpreted for central and eastern Asia (Kazakhstan through to China). The much warmer winters interpreted for these regions by the presence of crocodilians ($\text{CMM} \geq 5.5^\circ\text{C}$)

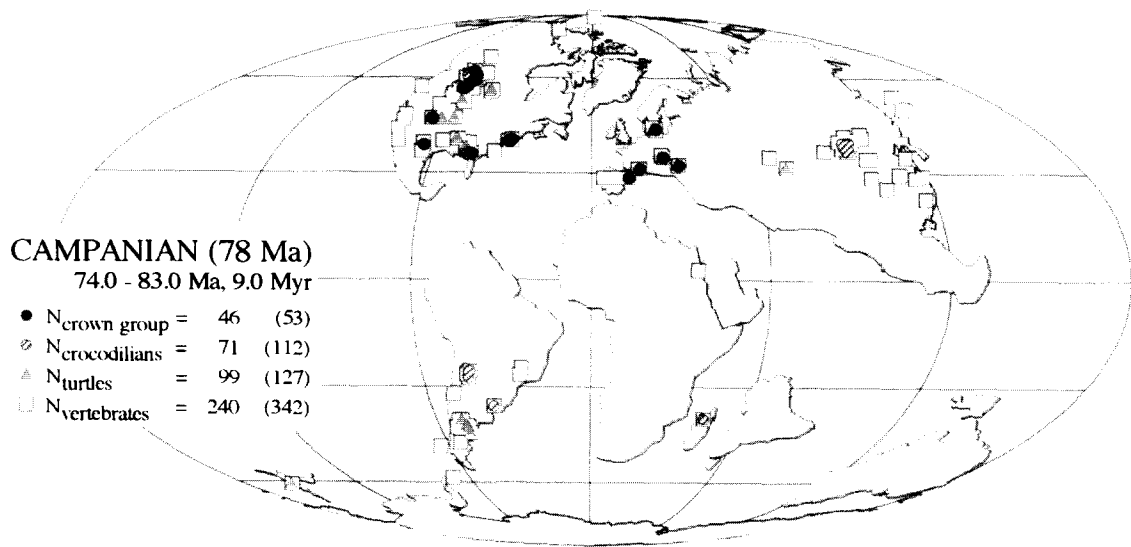


Fig. 37. Campanian map (78 Ma). See Fig. 30 for key and further details.

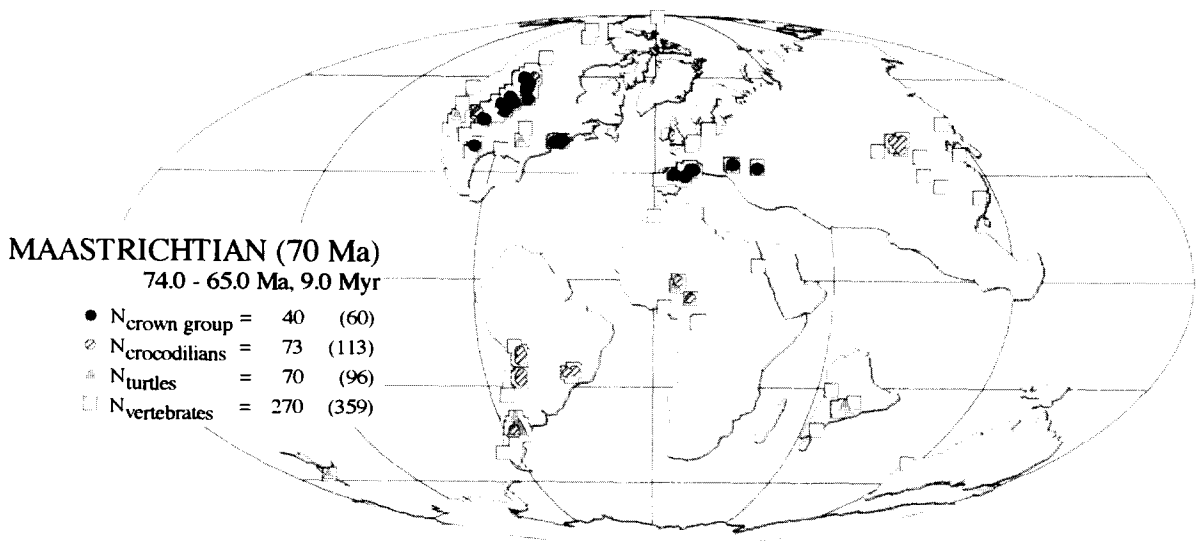


Fig. 38. Maastrichtian map (70 Ma). See Fig. 30 for key and further details.

implies thermally more 'equable' conditions than experienced by similar areas today.

By the Late Eocene (Fig. 45) the distribution of crown group crocodilians has become more sparse. They are absent from Argentina, reflecting the impoverishment of the Southern Hemisphere vertebrate record for the Middle and Late Eocene rather than a climatic signal. In North America,

crocodilians are restricted to the easternmost Eocene outcrops of the west, being excluded from the Rocky Mountain region, to which they do not return, and the west coast. Evidence suggests that this is not simply due to cooling, but also to increasing aridity in these areas (Leckie and Cheel, 1989, in the Cypress Hills area; Peterson and Abbott, 1979, in California; Roehler, 1992, in the

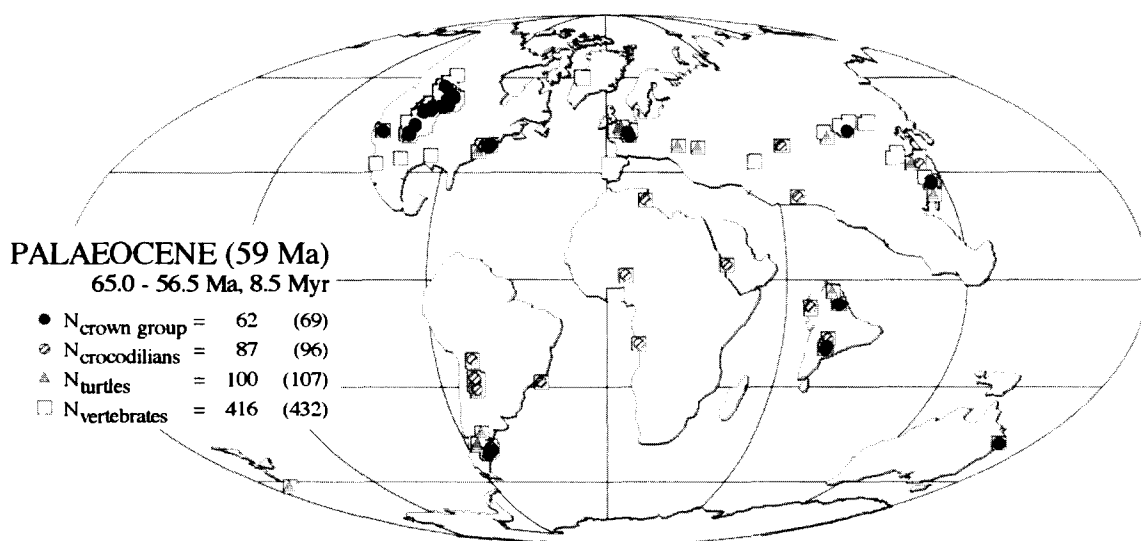


Fig. 39. Paleocene map (59 Ma). See Fig. 30 for key and further details.

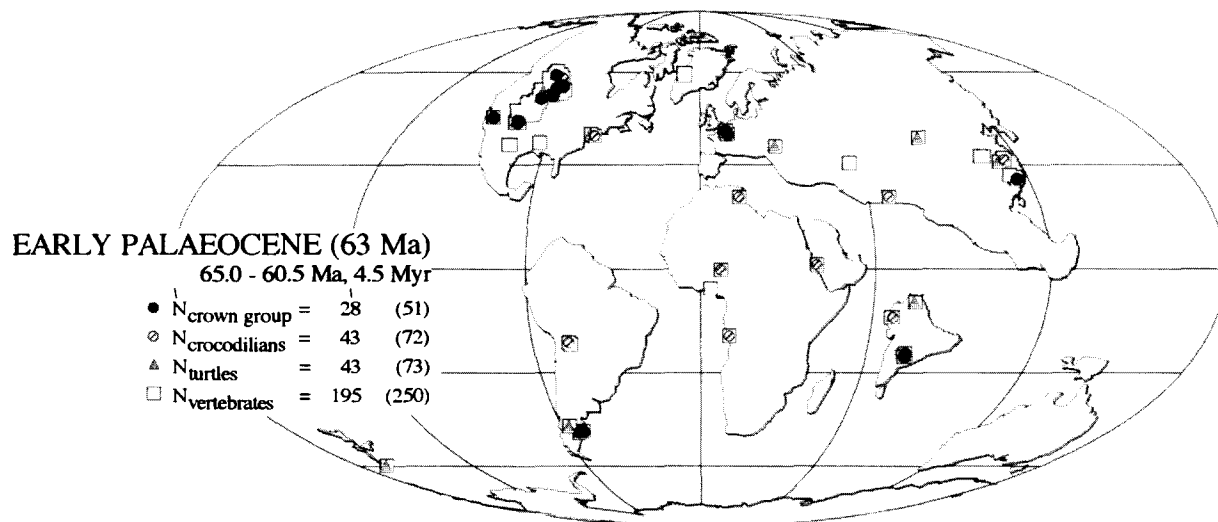


Fig. 40. Early Paleocene (Danian) map (63 Ma). See Fig. 30 for key and further details.

central Rocky Mountain region). A similar increase in aridity has also been noted by Tang and Zhou (1965) in the Late Eocene of South China with the development of evaporites, although crocodilians remain along the south coast of China until the Early Miocene.

In North America, these thermal and hydrological changes may be in response to the continuing uplift of the Rocky Mountain region; the restric-

tion of crocodilians to the Great Plains, Gulf and East coast during the Late Eocene, may partly reflect a regional rather than global climate change, with the elevation of the area reaching the threshold for crocodilian survival ($\text{MAT} \geq 14.2^\circ\text{C}$) as temperatures (average and seasonal) change with altitude.

Globally, this is the time at which there is the first clear evidence of glaciation on Antarctica

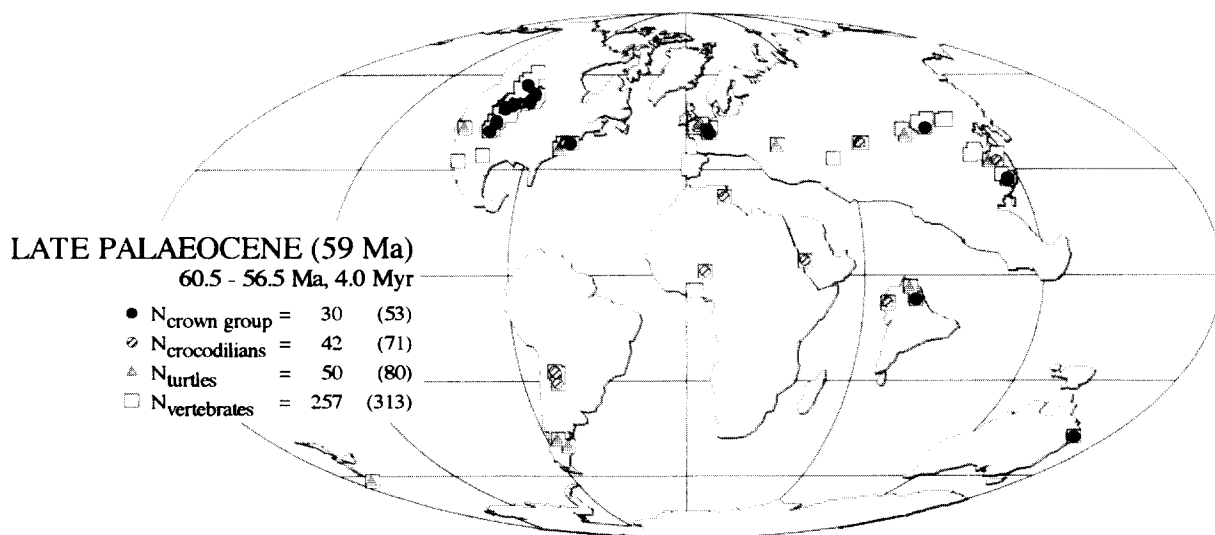


Fig. 41. Late Paleocene (Thanetian) map (59 Ma). See Fig. 30 for key and further details.

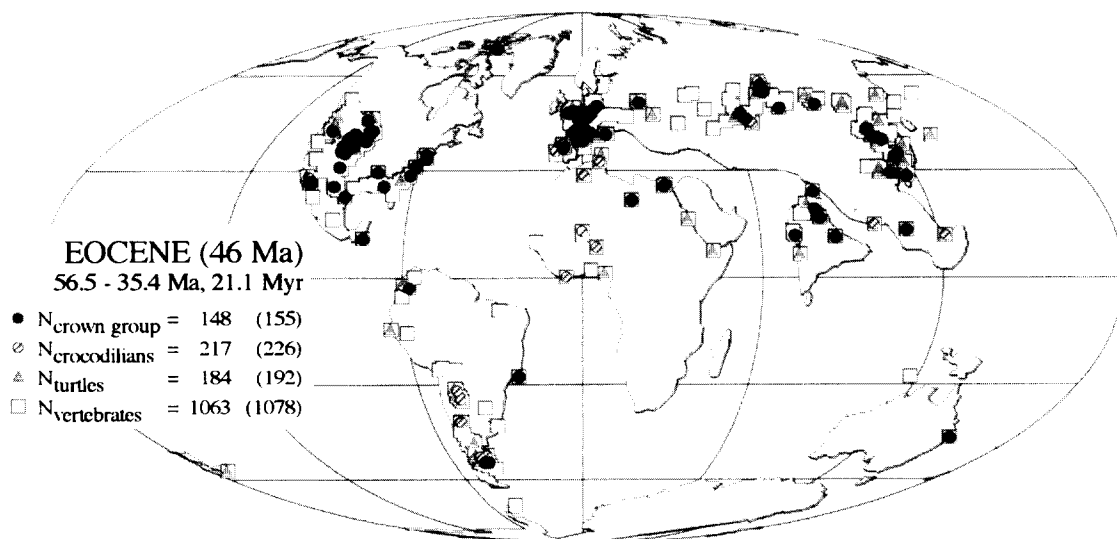


Fig. 42. Eocene map (46 Ma). See Fig. 30 for key and further details.

(Barrett, 1986; Birkenmajer et al., 1989; Hambrey et al., 1989, 1991; Barron et al., 1991; Ehrmann, 1991; Mackensen and Ehrmann, 1992), although evidence for earlier ice has been described (Geitzenauer et al., 1968; Birkenmajer, 1987). It is probable that this is the cause of, or at the least related to, the changes observed in the ocean record as revealed by the sedimentary record of

hiatuses (Keller et al., 1987; Miller et al., 1993), and especially the oxygen isotopic record (Miller and Fairbanks, 1985; Miller et al., 1987; Prentice and Matthews, 1988; Barrera and Huber, 1991; Mackensen and Ehrmann, 1992; Miller, 1992). It seems probable that these oceanographic changes influenced upwelling systems and thereby coastal climates in western U.S.A., and South America,

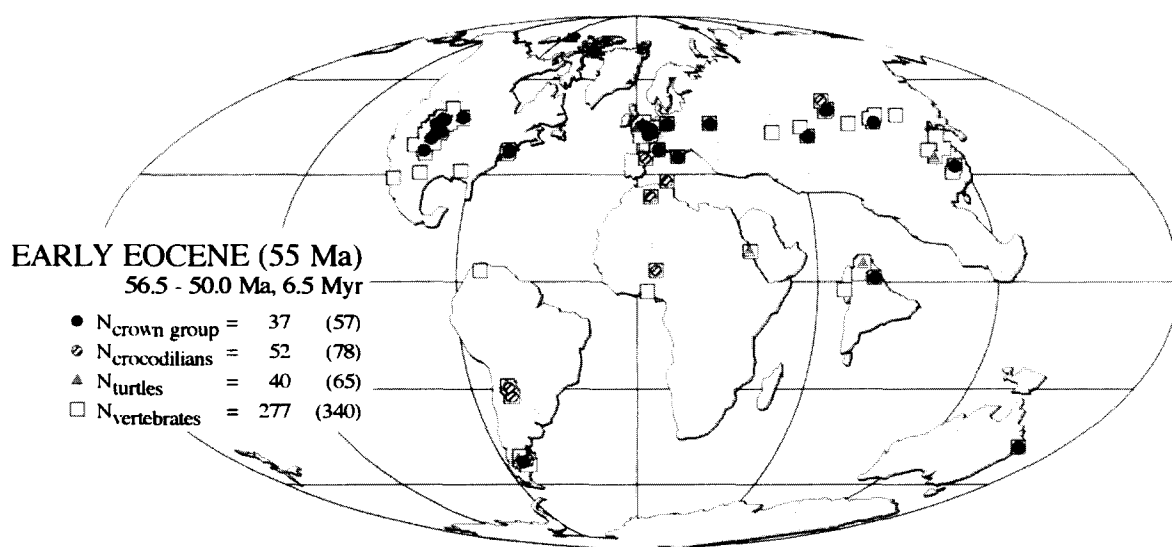


Fig. 43. Early Eocene map (55 Ma). See Fig. 30 for key and further details.

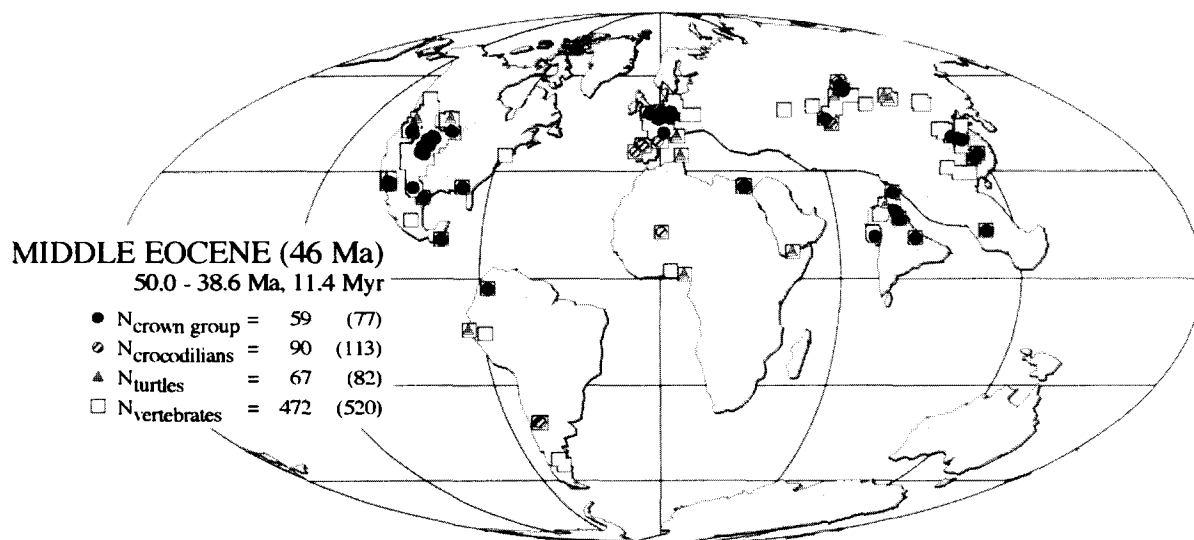


Fig. 44. Middle Eocene map (46 Ma). See Fig. 30 for key and further details.

but the process by which this may have influenced continental interior climates is less clear.

The largest changes in the global climate system appear to occur in the Oligocene with the greatest expansion of the Antarctic ice-sheet (Zachos et al., 1992). While this coincides with large changes in the distributional range of crocodilians in North America (with apparently no crocodilian record in

the Early Oligocene and only coastal occurrences in the Late Oligocene, Markwick, 1994), and may explain the rarity of crocodilians in Patagonia (Chiappe, 1988), little effect is seen in Europe. This has been recognized by other workers (Prothero, 1994). In central Asia, crocodilians disappear completely by the Late Oligocene and do not return, with one exception in the Middle

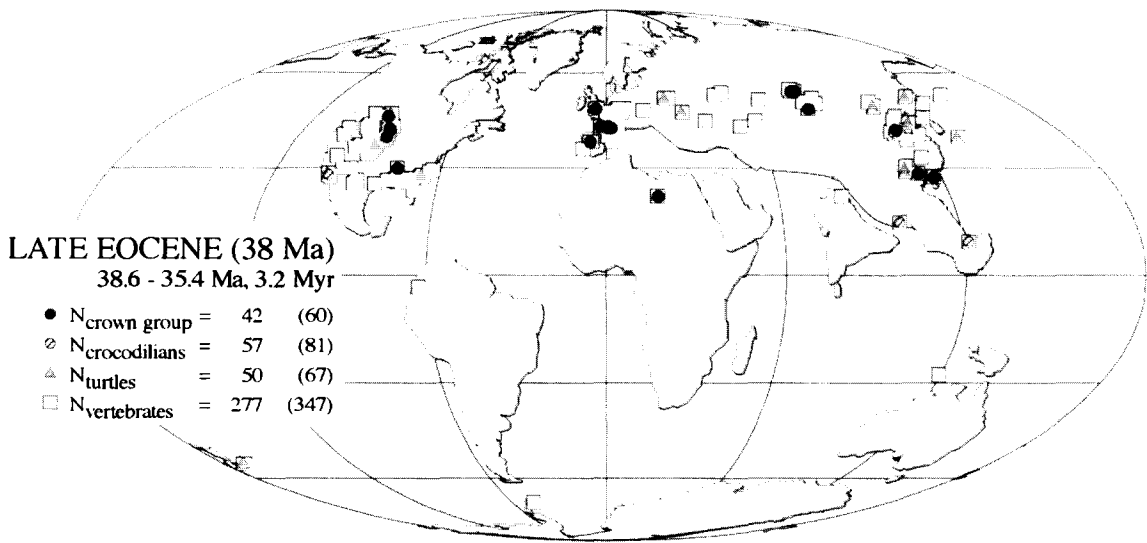


Fig. 45. Late Eocene map (38 Ma). See Fig. 30 for key and further details.

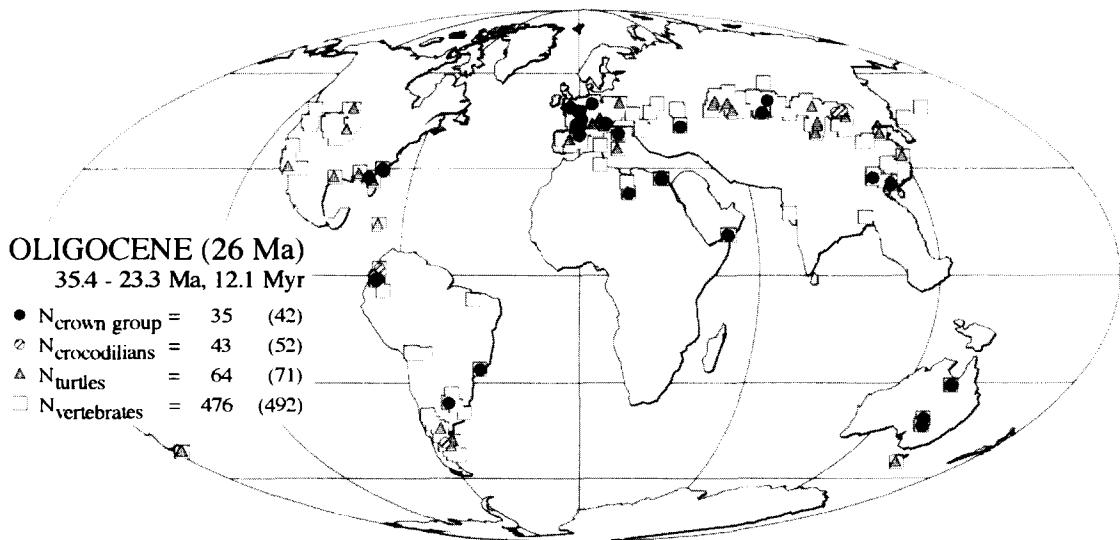


Fig. 46. Oligocene map (26 Ma). See Fig. 30 for key and further details.

Miocene (Fig. 51; Kintykche, central Priaral'e, Kazakhstan, Efimov, 1988). As indicated by the distribution of control groups (vertebrates and turtles) through this period, it is clear that this absence is not simply an artifact of collection or taphonomic bias. As for North America, this increasing climatic 'continentality' (thermal seasonality and aridity) in central Asia through this

time, may represent a climatic response to regional uplift.

The return of crocodilians to the Great Plains of North America in the Early Miocene may indicate at least a regional amelioration of temperatures; but during the Late Miocene and Pliocene the climate changes again with a trend once more towards increased aridity and thermally, highly

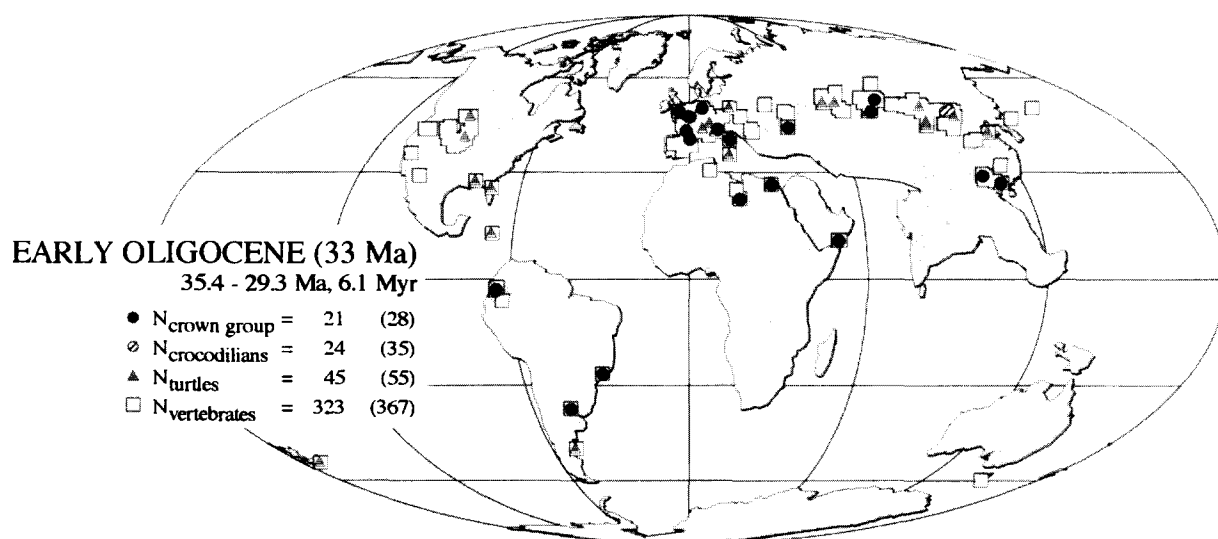


Fig. 47. Early Oligocene map (33 Ma). See Fig. 30 for key and further details.

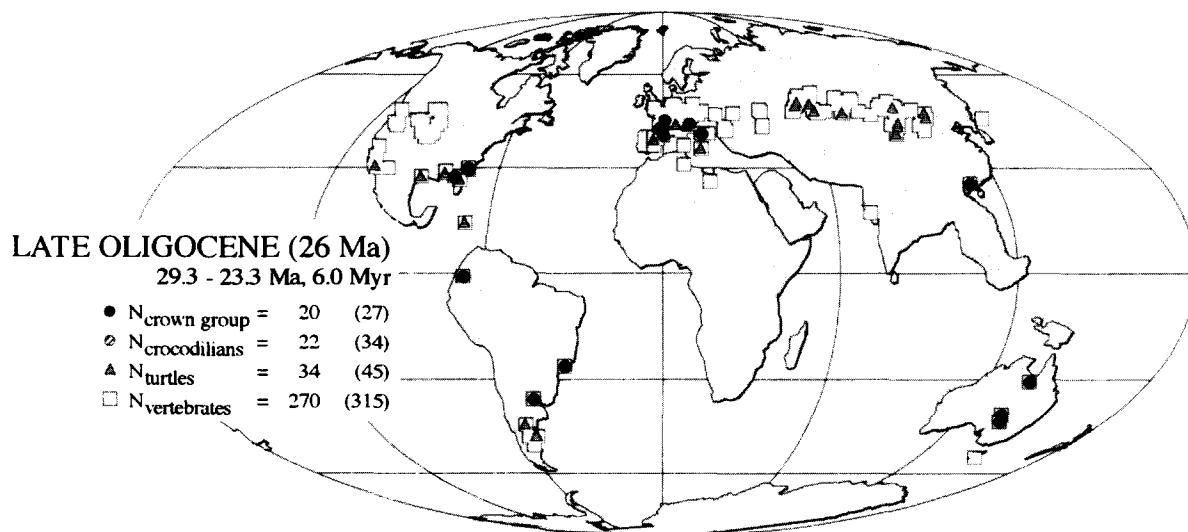


Fig. 48. Late Oligocene map (26 Ma). See Fig. 30 for key and further details.

seasonal climates in continental interiors. This is apparent in northwest Texas where faunas become typified by less aquatic forms and mammals typical of open grasslands; for example, at Crawfish Draw, Crosby County, crown group crocodilians (*Alligator* sp.) are represented by a single tooth and turtles by tortoises. Sediments in this region are typified by the development of caliches (Gustavson, 1990; Schultz, 1990). The appearance

of open-habitat mammals, especially grazing ungulates, during the Miocene, provides further evidence of a change to drier grassland environments, especially in North America and East Africa (Janis, 1993).

With the Pliocene (Fig. 53), crocodilians in Eurasia are restricted to southern Europe, while in both Australia and North America occurrences are limited to more coastal locals and lowland rivers.

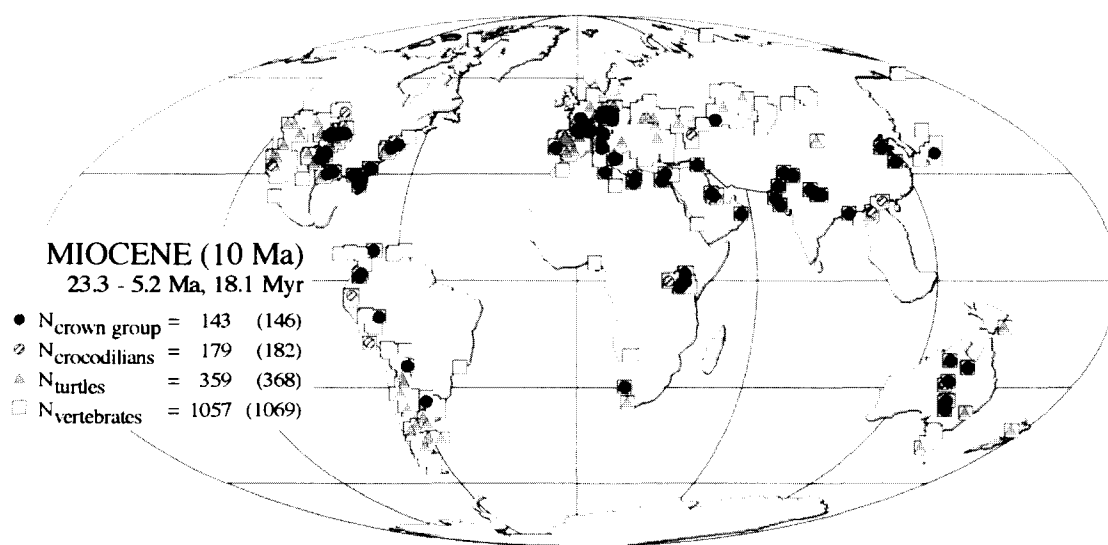


Fig. 49. Miocene map (10 Ma). See Fig. 30 for key and further details.

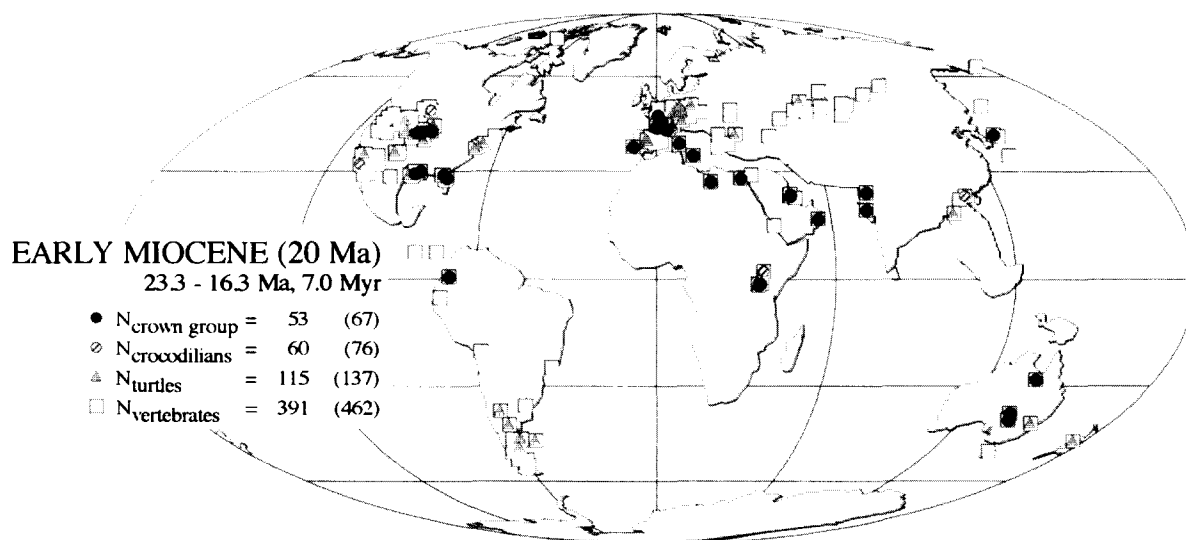


Fig. 50. Early Miocene map (20 Ma). See Fig. 30 for key and further details.

10.3. Quaternary

The Pleistocene record is, not surprisingly, the most complete of those surveyed in this study. Consequently, the limits on crocodilian ranges are better constrained (Fig. 54). As observed in the Pliocene, crocodilians are restricted to low lati-

tudes and coastal regions in mid-latitudes. There is no evidence of crocodilians in Europe at this time. In North America, Preston (1979) notes that by the latest Blancan tortoises are the principal turtle element of mid-continent faunas, which further indicates the presence of aridity throughout this region. Decreasing 'equability' and increasing

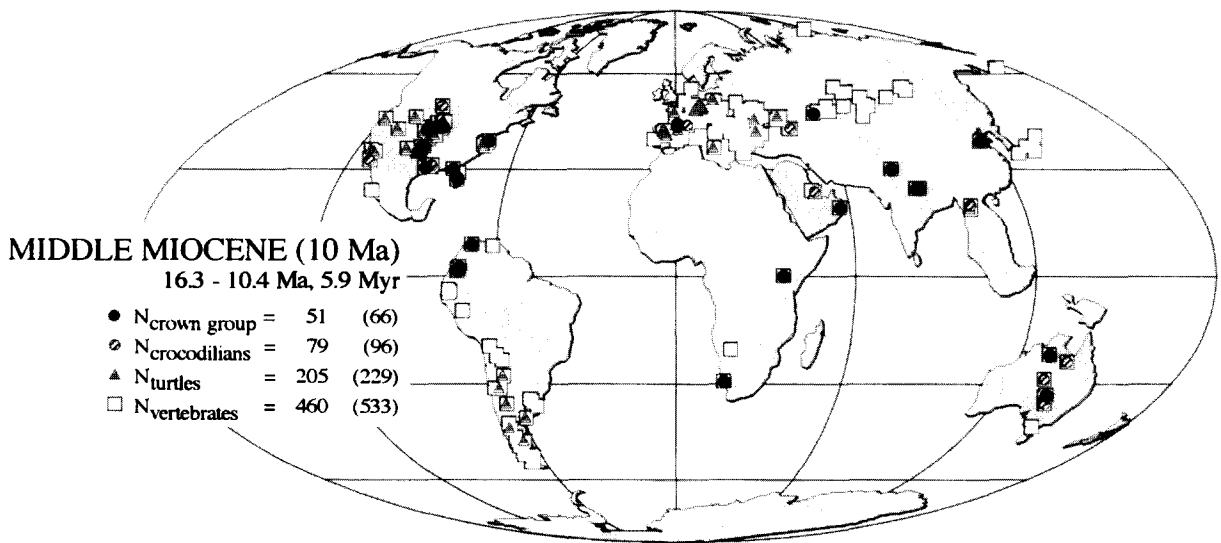


Fig. 51. Middle Miocene map (10 Ma). See Fig. 30 for key and further details.

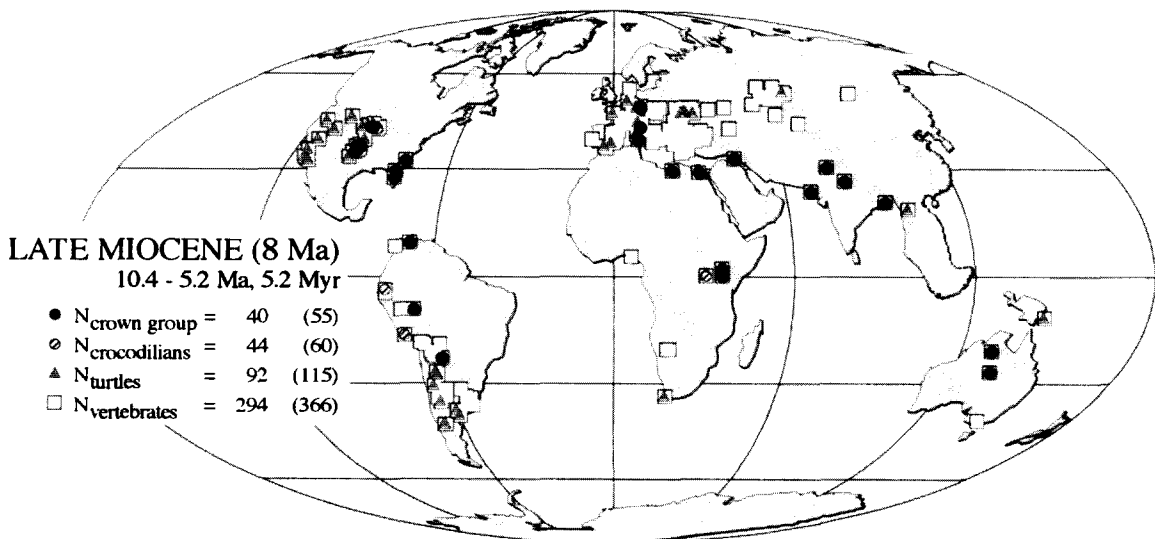


Fig. 52. Late Miocene map (8 Ma). See Fig. 30 for key and further details.

aridity has also been suggested as the cause of extinctions in Australia towards the Late Pleistocene (Lundelius, 1983).

11. Conclusions

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 palaeoclimate), numerical climate models allow us to investigate the processes responsible for observed patterns. But, such models do not, in themselves, provide data, only "hypotheses to be tested continually for their simulation capabilities compared to observations" (Saltzman, 1990, p. 70). For palaeo-

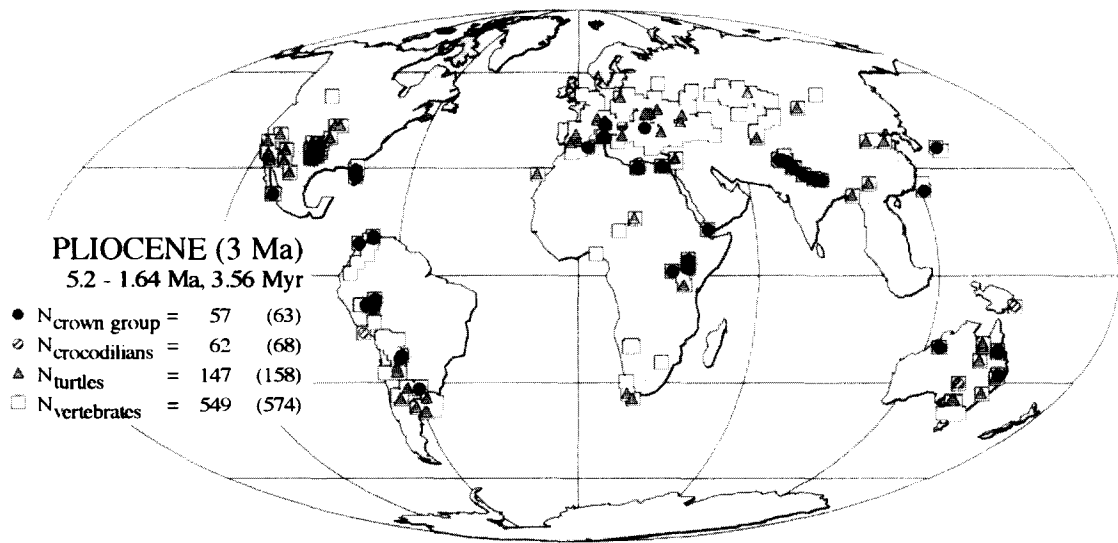


Fig. 53. Pliocene map (3 Ma). See Fig. 30 for key and further details.

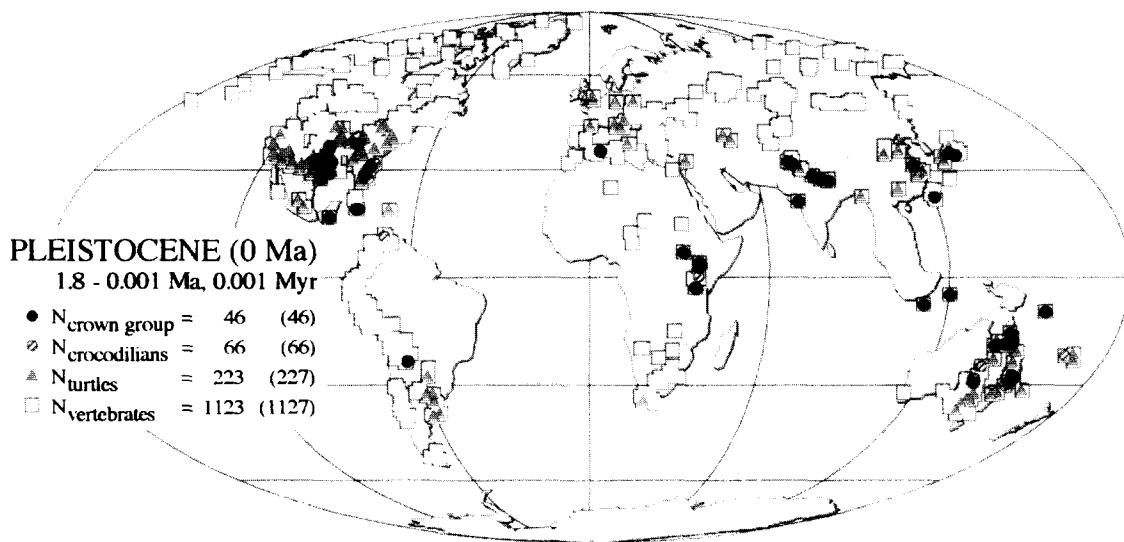


Fig. 54. Pleistocene map (0 Ma). See Fig. 30 for key and further details.

climate these observations are derived from the geological record. This study has used a detailed examination of one geological climate proxy—crown group crocodilians (members of the Alligatoridae, Crocodylidae and Gavialidae, which all have extant representatives)—to address what must be understood of any proxy if it is to be used

to constrain palaeoclimate. The principal results are summarized as follows.

11.1. Constraining the recent—the climate represented by crocodilians

(1) Temperature is the principal climatic factor

responsible for limiting the distribution of Recent crocodilians—not just the magnitude of minimum temperatures ($\text{CMM} \geq 5.5^\circ\text{C}$, today this corresponds to a $\text{MAT} \geq 14.2^\circ\text{C}$ and mean Winter $T \geq 6.6^\circ\text{C}$), but also their duration.

- (2) Standing water provides an essential buffer against temperature extremes, without which a fundamental element of behavioural thermoregulation is precluded. The absence of crocodilians can therefore reflect local hydrological conditions rather than just temperature. This dependence on water need not reflect local precipitation (e.g., the Nile River).
- (3) Elevation may affect hydrology and temperature and thereby influence crocodilian distributions independent of, or in addition to, the state of the global climate.

11.2. Constraining the past

The palaeodistribution of fossil crown group crocodilians maps out the distribution of the climate represented by Recent crocodilians. But, the geological record is not an unbiased witness of the past. Consequently, the nature of the geological data must be considered before palaeoclimatic conclusions are drawn.

- (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). However, while the presence of a fossil crown group crocodilian carries with it a specific climatic interpretation, an absence need not: a fossil crocodilian may imply a $\text{MAT} \geq 14.2^\circ\text{C}$, but a controlled absence need not mean a $\text{MAT} < 14.2^\circ\text{C}$.
- (2) Biogeography. The distributional data also point 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 exclusion of alligators

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.

11.3. The pattern of palaeoclimate over the last 100 million years

The history of the Earth’s climate over the last 100 million years is dominated by the transition from the largely ice-free (‘hot-house’) world of the Mesozoic and early Cenozoic, to the glacial (‘ice-house’) world of the Recent. In this study, the palaeoclimate interpreted from the palaeodistribution of fossil crocodilians, corroborates this overall trend, but also provides a spatial dimension to this transition that has been previously lacking.

- (1) Palaeolatitude. During ‘hot-house’ intervals (Cretaceous–late Palaeogene) crocodilians extend into high latitudes, but are restricted to low latitudes during ‘ice-house’ intervals, especially in the Late Oligocene and Pliocene–Recent. This implies large thermal changes in high latitudes. For most of the Campanian–Middle Eocene, fossil crocodilians occur up to at least 60°N palaeolatitude (Fig. 35), thereby implying for those regions $\text{MAT}'s \geq 14.2$ and $\text{CMM} \geq 5.5^\circ\text{C}$; today the MAT at $60^\circ \approx 1.2 \pm 5.2^\circ\text{C}$, and the $\text{CMM} \approx -12.5 \pm 7.1^\circ\text{C}$ (errors are 1 SD). This suggests a change in MAT and CMM over the last 40 million years of $\approx 13^\circ\text{C}$ and $\approx 18^\circ\text{C}$, respectively, at these latitudes, with the concomitant change in latitudinal thermal gradients.
- (2) The preserved record of fossil crocodilians during the Late Cretaceous and early Palaeogene is biased towards continental seaways that may have formed conduits for moving heat poleward; the thermal climate of high-latitude continental interiors is unknown and may not have been so pleasant.
- (3) Continentality. During the Late Oligocene and Pliocene–Recent, crocodilians in mid-latitudes become restricted to maritime localities, concomitant with the observed contraction in their palaeolatitudinal range. This is interpreted to reflect increases in thermal seasonality

and aridity in mid-latitude continental regions. This strongly implies a link between increased 'continentality' (as expressed by seasonality and increased aridity) and 'ice-house' climate regimes (cooler temperatures).

- (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. Such elevation effects are superimposed upon the signal of global climate change.

11.4. *Implications for reconstructing palaeoclimate*

- (1) Palaeoclimate must be seen in the context of temporal and spatial changes. Only by using a global dataset can spatial heterogeneities in the success of modelling be recognized. 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.
- (2) By establishing numerical limits to crocodilian climate space (i.e. $\text{CMM} \geq 5.5^\circ\text{C}$) discrepancies between data and models can be not only recognized but quantified. Such quantification is important, but must be constrained—numbers in themselves are meaningless.
- (3) The Recent provides the template for the past, but is itself the consequence of its history; by examining both we may come to a fuller understanding of each. Any examination of the past must begin with an understanding of the Present Day, for which we have the most complete and accessible global record.
- (4) Corroboration of palaeoclimate interpretations derived from a single climate proxy comes from an examination of other proxies. A consideration of all of the evidence is essential.
- (5) Global palaeoclimate on geological timescales may better be considered as the long-term aggregate effect of climate.

An understanding of palaeoclimate requires a multidisciplinary approach and the compilation and investigation of large, global datasets of well-constrained geological and Recent data. Such an approach requires a methodological shift, back to a holistic, 'inquiry' approach to science.

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