THE UNIVERSITY OF CHICAGO

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

VOLUME TWO

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CHAPTER V

FOSSIL CROCODILIANS AS INDICATORS OF LATE CRETACEOUS AND CENOZOIC CLIMATES: IMPLICATIONS FOR USING PALEONTOLOGICAL DATA FOR GLOBAL CHANGE: PART 2--THE PAST

"Each fact is suggestive in itself. Together they have a cumulative force."

Sir A. Conan Doyle
Sherlock Holmes, "The adventure of the Bruce-Partington plans"

V.1. INTRODUCTION

In Chapter IV, climate, particularly temperature, was shown to be the principal limiting factor for the distribution of extant crocodilians. In this chapter, the climate space defined by those limits is applied to fossil occurrences, but not without caveats. As discussed in Chapter I, 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 distributional 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 paleoclimate 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 "paleoclimate" given the temporal disparity between geological paleoclimate (magnitudes of millions of years) and meteorological climate (being an average of 30 years of weather). These are problems that apply to all paleontological climate proxies, and thus the conclusions reached in this study may provide a template for examining other lines of evidence.

The dataset used in this study is described in Chapter III and Appendix D.

V.2. CLASSIFICATION

All living crocodilian species belong to one of three families, the Alligatoridae, Crocodylidae and Gavialidae, which are the principal representatives of what has been

traditionally called the Eusuchia. Members of this group are typified by a complete secondary palate, fused palatines and pterygoids, and procoelus vertebrae (Ross, 1989). Although this classification has been modified in recent years (Benton and Clark, 1988; Clark, 1986; Norell, 1989), I have kept to the more traditional classification given in Carroll (1988) because of its greater familiarity to non-crocodilian workers. The use of Carroll's classification scheme is discussed in section III.2.4.1. In order to mitigate potential evolutionary/physiological incongruities, only fossil members of these three extant families have been used to interpret paleoclimate. These groups represent the crown group in Clark's (1986) cladistic classification and so throughout the text are referred to collectively as "crown group crocodilians."[1] An assessment of the climatic and paleobiogeographic implications of non-crown group crocodilians is in preparation.

A complete list of the genera used in this study, with their family assignments and age ranges, is given in Appendix C.

V.3. 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 paleoclimate 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, are only influenced by issues of resolution and identification or dating errors, not by questions of representation. The

1. Clark has redefined the term "Crocodylia" to describe the node at the base of this crown group, which has led to some confusion. In this study I have retained the term's traditional breadth. The use of the collective term "crown group crocodilians" is simply a matter of convenience, given that there is no other collective term appropriate and repetition of the phrase "alligatoridae, crocodylidae and gavialidae" is cumbersome.

indicator exists at that point in time and space, and a specified climate can thereby be attributed to that point. The absence of a climate proxy is more problematic because the absence may reflect poor sampling or preservation (representation) rather than an original ecological absence. Methods based on assemblage data (floral analysis, cenograms etc.) are even 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.

V.3.1. Resolution

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

V.3.1.1. Spatial resolution

In the database "localities" (individual records in the Main Locality relation, see section III.2.3.3.) represent a variety of spatial scales: for instance, collecting sites (essentially a single point in space and time), localities (generally a composite of collecting sites within specified geographic and stratigraphic limits--this is the most common way in which the location of vertebrates is described in the primary literature), and entire outcrops of stratigraphic units, which may extend over broad geographic regions. Each locality is assigned a code which describes the spatial resolution of that locality. This is the Geographic Precision code (GP) which is described in section III.1.1. All data are entered into the database, regardless of their resolution. However, in order to mitigate the tendency for coarsely constrained data to swamp finer patterns (for instance the latitudinal range of

crocodilians), the data used in the analyses and maps in this chapter are restricted to only those "localities" that are resolved to within 100 km (GP≤3).[2]

V.3.1.2. Temporal Resolution and Time Averaging

Temporal resolution of fossil data is dictated by two factors: the resolution of the age assignment and the effects of time-averaging. For consistency, only localities whose stratigraphic ages do not exceed more than two consecutive time intervals (see Figure V.1) 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; Kidwell and Behrensmeyer, 1993) and Rogers (1993), among others, have drawn attention to the effect of time-averaging on vertebrate faunas. This takes two forms: "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; and "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. These have been discussed at length in Behrensmeyer and Chapman (1993) and Kidwell and Behrensmeyer (1993).

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2. For the present study spatial resolution does not seriously effect results, not least 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 (meters in scale) or a composite over a whole county (10's kilometers). However, there may be problems when qualitative or quantitative comparisons between localities are required. In such cases weighting localities equally regardless of their spatial resolution may be inappropriate and some consistent compositing may be required. This might be done by assigning faunas to specified sites in the same way that the modern faunas were assigned to climate stations in section IV.3.3.1. and VII.2.

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 indistinguishable from distributions based on all data (see Figure V.15).

Analytical time-averaging is a potentially more insidious problem, especially in terms of defining paleoclimate. Climate, in the modern meteorological sense, represents "average" weather, or more correctly the long-term aggregate effect of weather (Barry and Chorley, 1987), most commonly taken as a period of 30 years (Saltzman, 1990).[3] 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 paleoclimate 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

3. Saltzman (1990) suggests that climate could easily be referred to as the aggregate state over 100 or 1000 years given the small fluctuations observed over such intervals.

(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 700000^{99}; even taking "climate" as representing a 1000 year aggregate,[4] the probability is still 21000^{99}.

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 investigated with a computer program written with Ann Lottes (a former graduate student at the University of Chicago).[5] This program randomly places a specified number of localities (each representing a specified duration; viz., 30 and 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

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4. Behrensmeyer (1982) estimated that 1000 to 10,000 years was the typical period represented by vertebrate accumulations in fluvial systems, based on her observations in East Africa.

5. This program is called COEVAL and has been recently modified by David Rowley, University of Chicago.

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, paleoclimate on geological timescales should be considered as the long-term aggregate effect of climate--the "tectonic average" period of Saltzman (1990).

V.3.2. Representation

Figure V.1 shows the distribution of all crocodilian and non-crocodilian bearing vertebrate localities presently contained in the database. Only localities that are both spatially and temporally well constrained are used: GP≤3 (see section III.1.1. and Appendix D) and age assignment encompasses no more than two time intervals. From this it is clear that the spatial 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 Figures IV.1 and IV.3). This bias towards North America and Eurasia is shown in Figure V.2, which summarizes the proportion of localities by continent. The distribution of crocodilians used as climate proxies can only be understood in the context of the distribution of all vertebrate localities, since no data can lie outside of it. Fortuitously, most of the latitudinal changes that are of interest in this study occur within this northern mid-latitudinal belt, as will be shown below and as summarized by Markwick (1992).

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 megafloral record

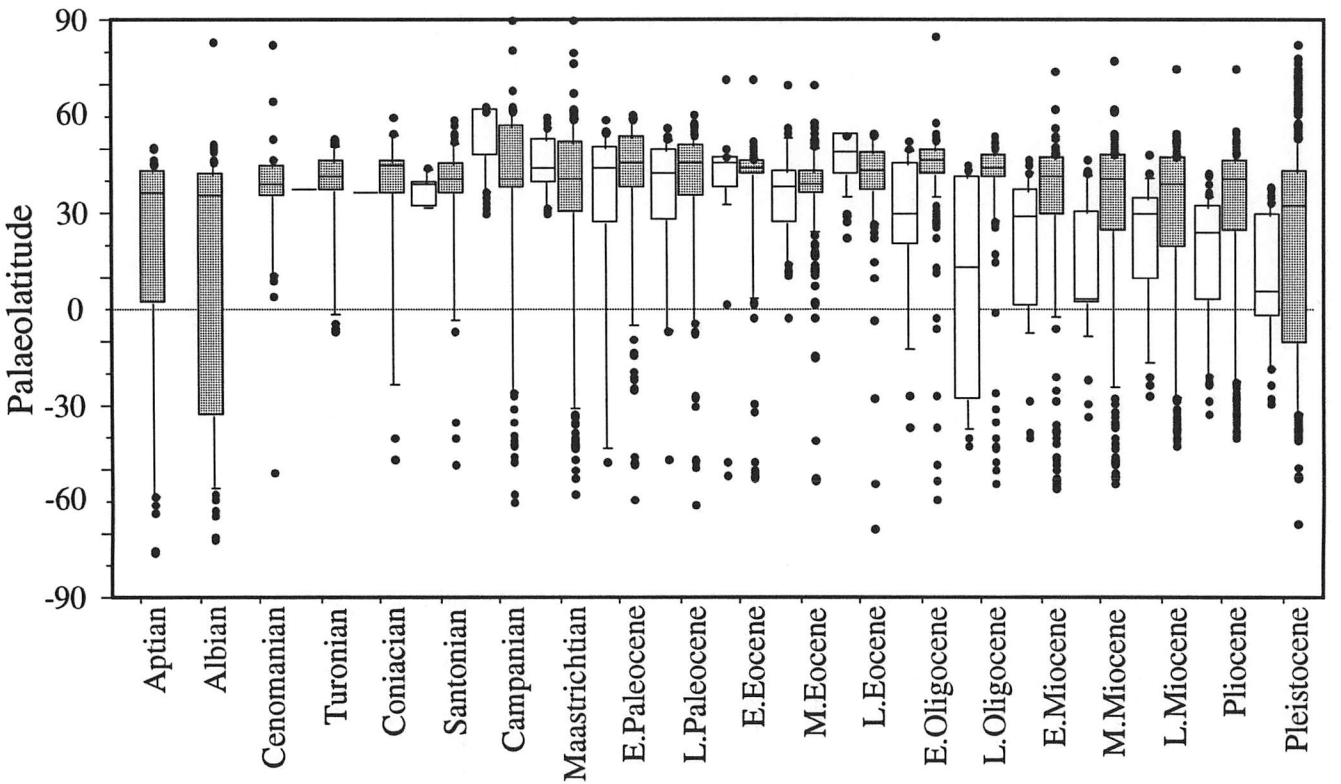

FIGURE V.1. Box plot of all vertebrate localities in the database.

Open cells = crown group crocodilian localities, shaded cells = all vertebrate localities. Only those localities which are spatially well resolved (Geographic Precision, GP ≤3) and temporally limited to no more than two consecutive time intervals are used. 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.

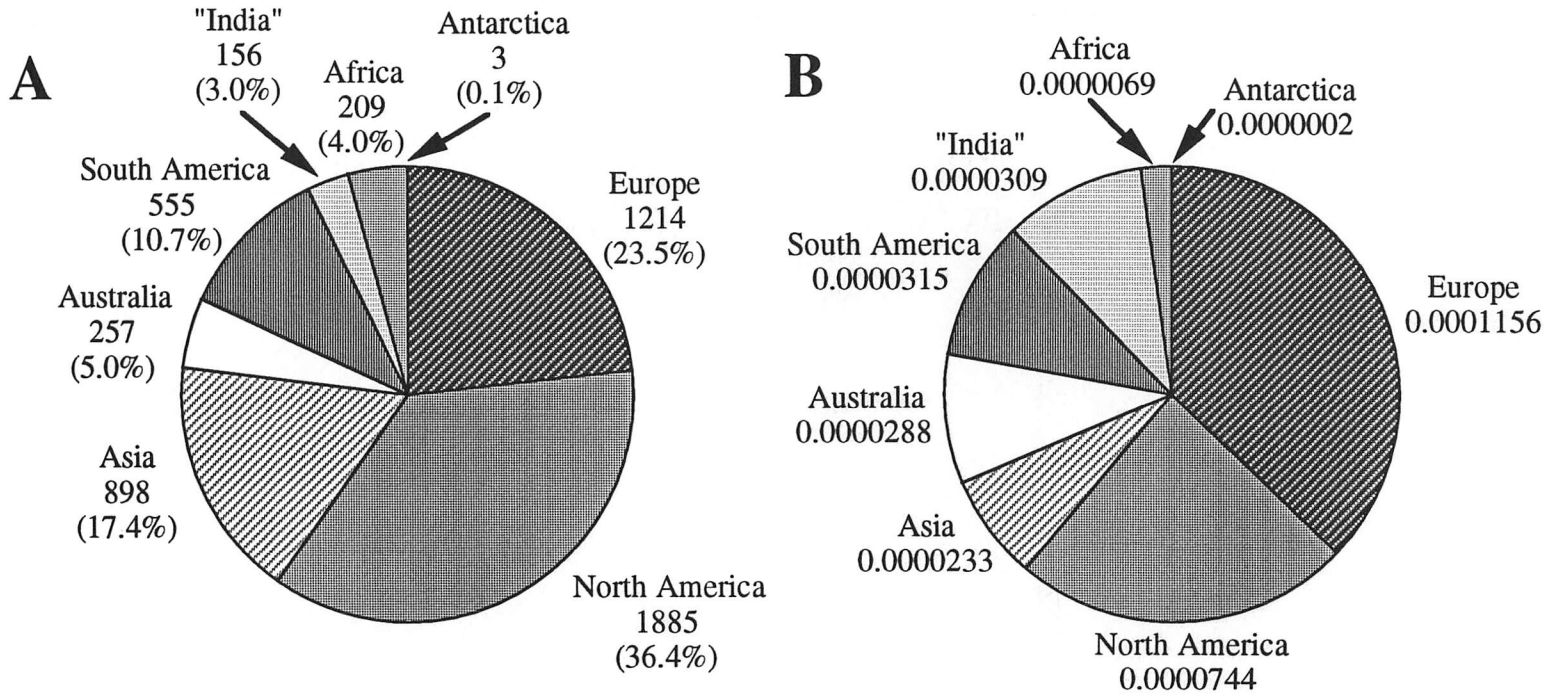

FIGURE V.2. Pie charts showing the proportion of localities in each continent (A) and normalized for area (B).

In chart A, numbers refer to the number of "localities" in the database for each continent; percentage values in parentheses represent the proportion of localities represented by that continent. B. Values given in B are the density of 'localities' per square kilometer 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.

throughout the Cretaceous and Tertiary (Boulter and Fisher, 1994; Vakhrameev, 1991) suggests that a 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 megafloral remains, but not vertebrates, are found in these latitudes.[6]

The spatial heterogeneity of fossil vertebrate localities has a temporal counterpart with the number of localities varying through time (Figure V.3). 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 Figure V.3 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 (Figure V.4), 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[7]--vertebrates act as a control on sampling. Figure V.5 shows the proportion of localities that contain crocodilians and turtles respectively. The significance of derived

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6. Research is planned to investigate this issue using empirical observations (taphonomic field experiments with Ray Rogers, Cornel College, Mount Vernon, Iowa) and a survey of the literature. This will require augmentation of the present vertebrate dataset with megafloral data.

7. This method is susceptible to spatial heterogeneites between time intervals. However, although the data are heavily biased to Eurasia and North America (Figure V.1.) this is true throughout the study interval which means that temporal trends should not be adversely affected.

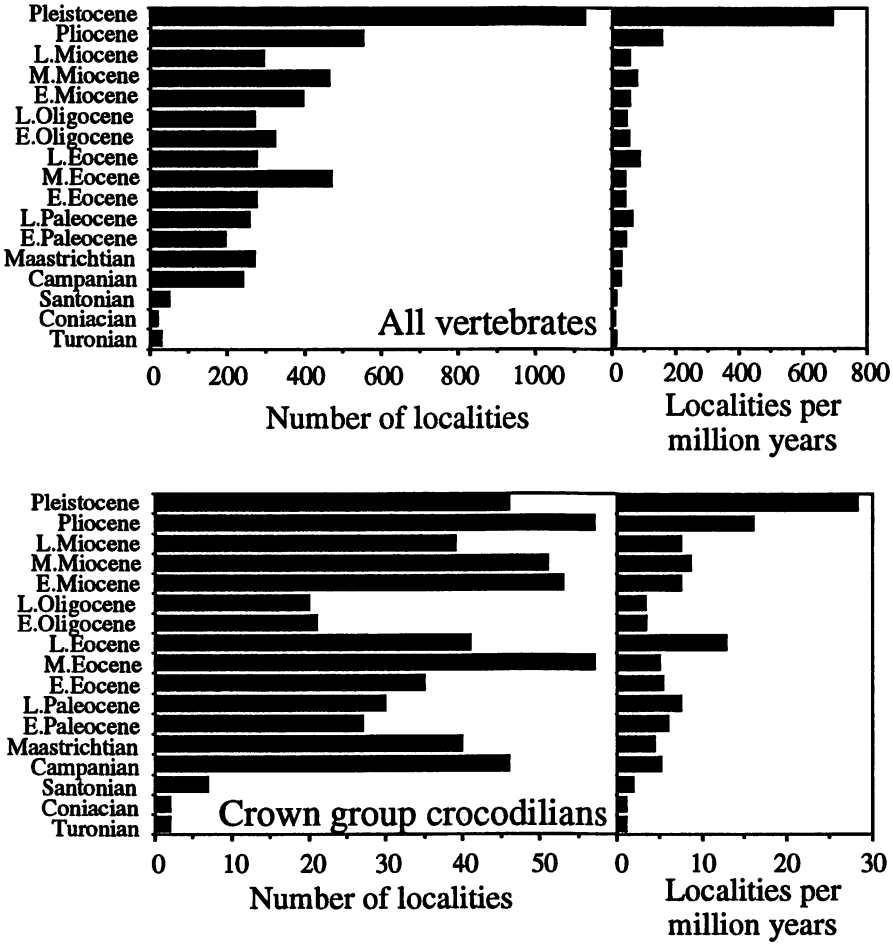


FIGURE V.3. Number and rate of localities by interval.

Bar charts showing 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≤3) and less than or equal to two consecutive time intervals (count ≤2). Note the drop in the number of crown group crocodilian localities in the Danian 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.

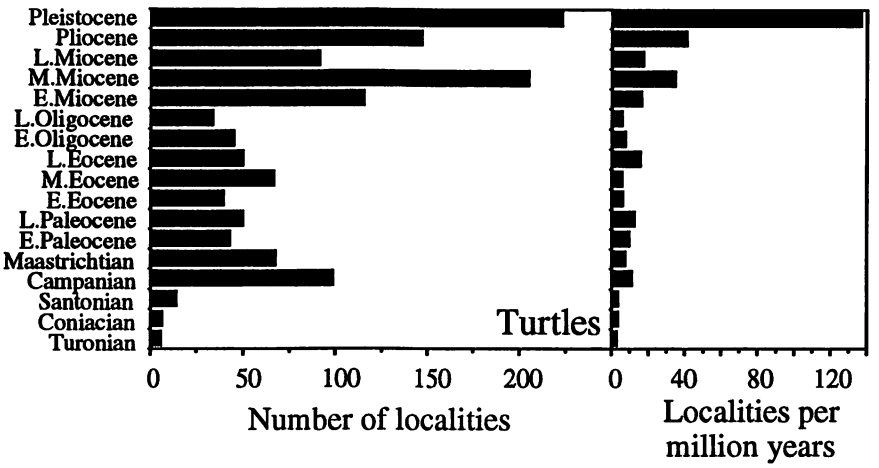


FIGURE V.3. continued.

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 affect. This is not the case for the Turonian, which occurs early in the diversification of crown group 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.

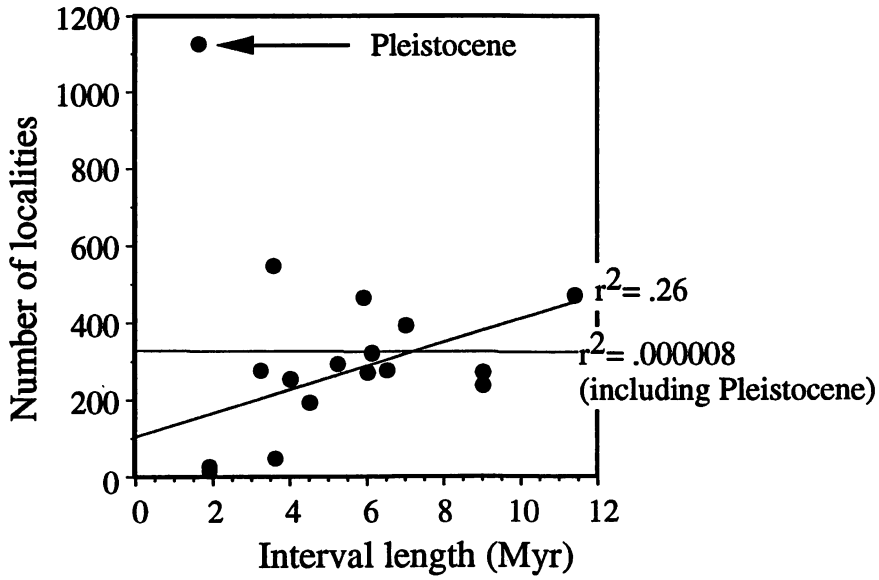


FIGURE V.4. Interval length versus number of vertebrate localities.

The number of vertebrate localities (spatial resolution, GP≤3; temporal resolution, ≤ 2 time intervals) in each time interval is plotted against the duration of that interval. Two regressions are shown: including and excluding data for the Pleistocene.

V.3.2.1. 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).[8] 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

8. Raup has referred to the effects of the "monographic bias" on diversity trends, in which the comprehensiveness of monogaphs tends to swamp derived patterns.

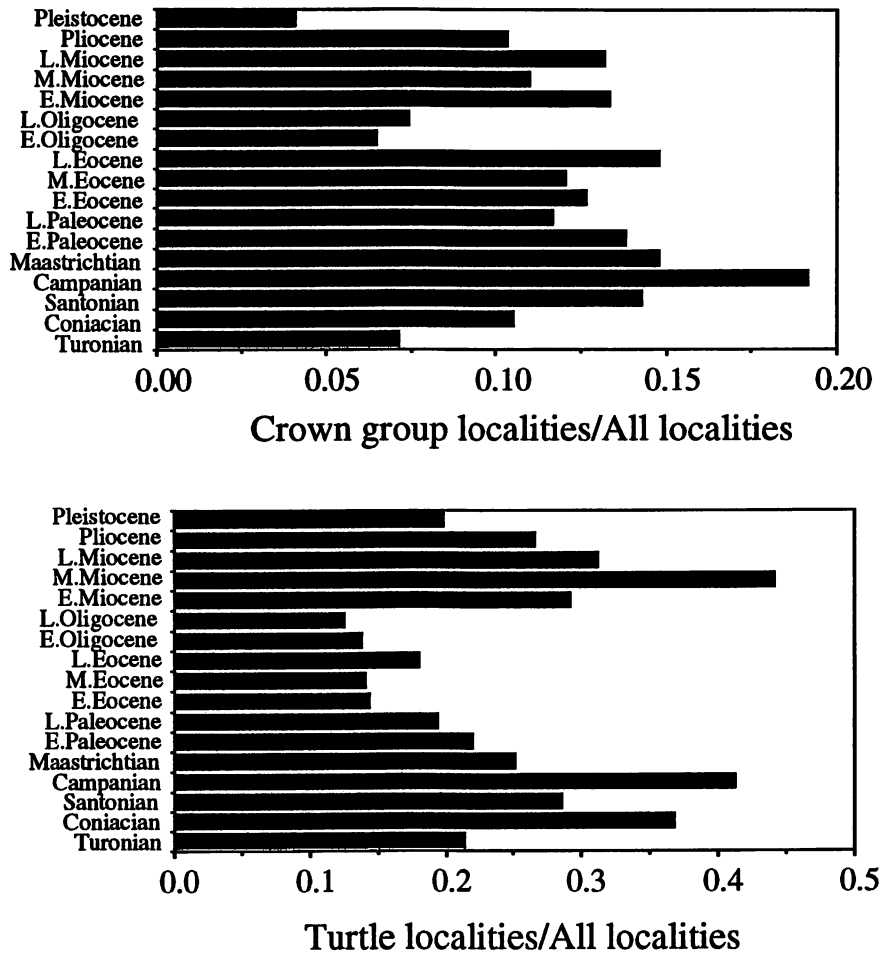


FIGURE V.5. Proportion of localities represented by crocodilians (top) and turtles (bottom).

The proportion of all localities that have associated crocodilians (spatial resolution, GP≤3; temporal resolution, ≤ two time intervals). This gives an indication of how the number of crocodilian-bearing localities varies as a function of total sampling. Consquently, it also reflects the spatial distribution of localities and thereby climate.

relegated to the "and also present were " status. Thus West (p.64, 1973) states "*The remains of lower vertebrates are present at all of these localities, as well as many other places in the New Fork-Big Sandy area. No record was kept of the occurrence of turtles because of their abundance and generally fragmentary nature.*" While this does not affect paleoclimate conclusions based solely on the presence of fossil crocodilians, conclusions based on absences may be compromised. Detailed site by site examinations of assemblage data, including studies of amphibian and reptile diversity and paleoecology, must also be viewed with caution.

V.3.2.2. Collection

Related to this publication bias is a collection bias. The interest in dinosaurs and mammals over lower vertebrates imparts not only a bias on what is written, but also what is collected. Collection may also affect distributions in a more direct way. In areas where logistics make fossil collection difficult, crocodilians may not have been recorded because nothing at all has been collected. In order to qualify this bias, plots of fossil crocodilians in this study are plotted against a backdrop of all vertebrate data, such that a visual, qualitative estimate of the area collected can be readily made--vertebrates are used as controls for collection bias.

V.3.2.3. 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. Basin formation therefore determines this

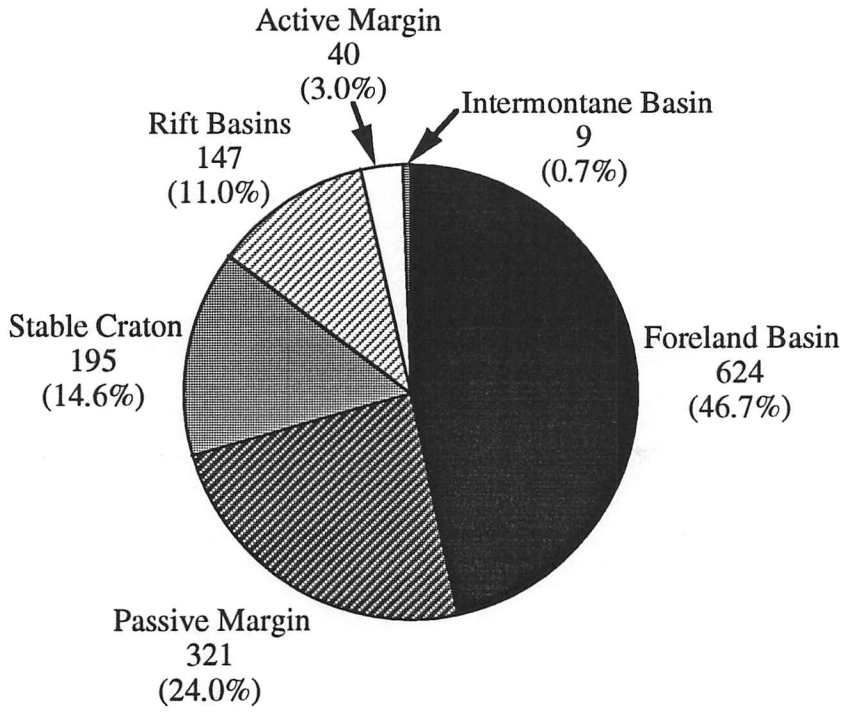


FIGURE V.6. Pie chart showing proportion vertebrate localities represented by each basin type.

distribution (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 as a function of basin type is shown in Figure V.6. 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) is suggestive of a bias towards certain tectonic settings. As with collection biases, the effects of tectonics can again be constrained using control groups. In this respect vertebrates or rock outcrop form a suitable control on the potential distribution of climate proxies.

V.3.2.4. 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; Behrensmeyer and Chapman, 1993; Behrensmeyer et al., 1992; Behrensmeyer et al., 1979). As with other representation biases, taphonomic biases do not influence the paleoclimate 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: in the case of this study, does the absence of a fossil crocodilian provide climate information? As already stated, this is especially important in defining trends in the data.

The terrestrial geological record is heavily biased towards aquatic environments (Figure V.7), especially in older deposits. This reflects the fact that regions with active accumulation are generally also loci for water accumulation. Crocodilians, as semi-aquatic animals, should consequently have a relatively good fossil record.[9] Accordingly, the general distribution of fossil crocodilians should not be delimited by the lack of representation of aquatic settings, but other factors such as the nature of the aquatic

9. Throughout the Cretaceous and Cenozoic, non-marine crocodilians are postcranially relatively conservative (Langston, 1973) suggesting little change in their association with aquatic habitats. Indeed, 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 (Buffetaut, 1988; Langston, 1975), 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.

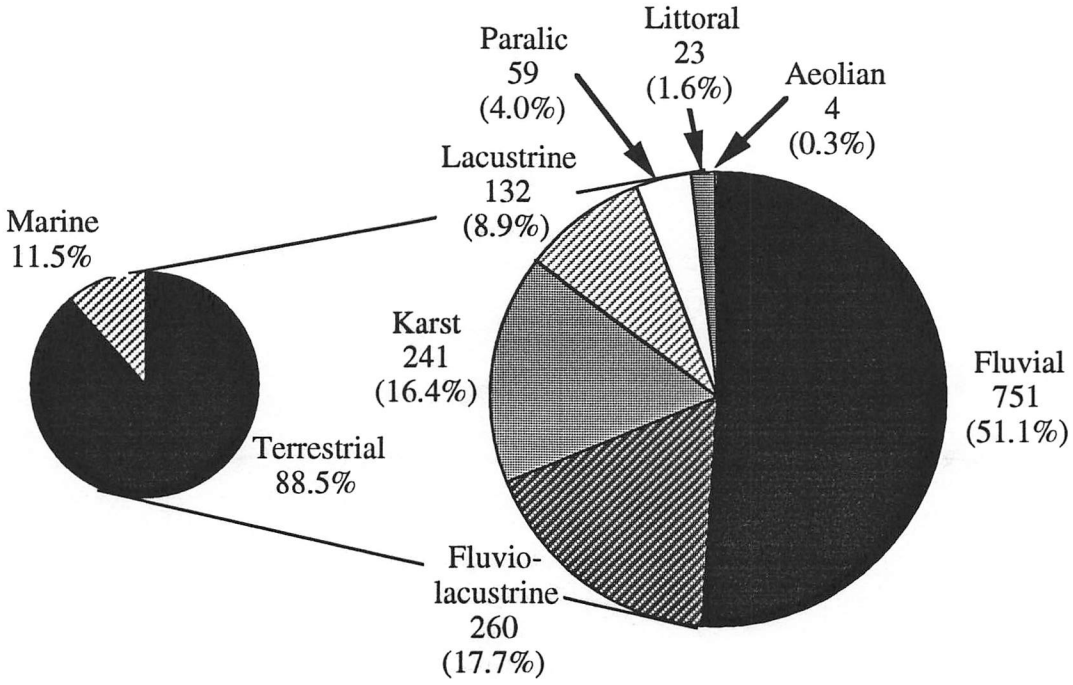


FIGURE V.7. Pie charts showing the distribution of environments in the fossil dataset.

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.

environment--ephemeral or permanent--and climate.[10] The nature of the aquatic environment can be constrained using sedimentological data such as paleosols--caliches.

Nonetheless, even given a suitable environment, fossils need not be preserved. For vertebrates, empirical studies in Africa have shown that size is an important taphonomic

10. The effect of different hydrologies in determining the relative abundances of fossils has been discussed by Wood (1973) in reference to the pelomedusid turtles *Pelusios* and *Pelomedusa*. Today *Pelusios* lives in permanent rivers and lakes, and *Pelomedusa* in intermittent seasonal water bodies and high elevations. Wood suggests that this difference in habitat may explain the prevalence of *Pelusios* in the fossil record compared with the sparsity of *Pelomedusa*.

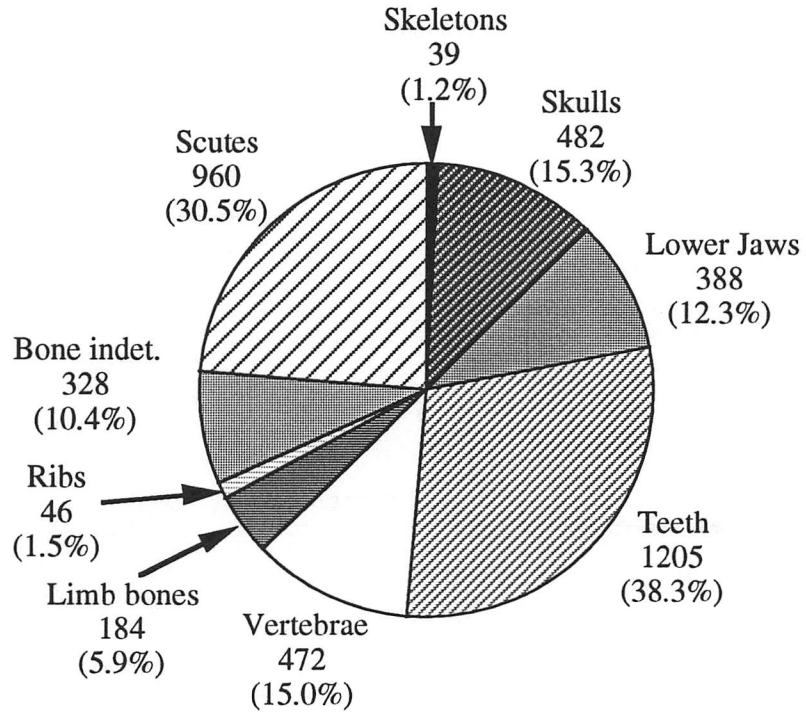


FIGURE V.8. Pie chart showing distribution of crown group crocodilian specimens recorded in the database.

Not all reports of fossil crocodilians in the literature give specimen information. Where information is available it is subject to two biases: 1. what specimens are identifiable as crocodilian (e.g., ribs are difficult to discern as crocodilian except when associated with known crocodilian material); 2. under-reporting of very common elements--actual numbers of teeth and scutes are rarely reported, usually they are summarized as simply "teeth [or scutes] present," which in the database is recorded as a minimum number of specimens (MNS), such that "teeth" will be recorded as "2" specimens. Skulls include skull fragments as well as complete skulls. Individual elements of complete skeletons are not reported separately in the database.

bias in fluvial systems, with larger animals, especially those greater than about 15 kilograms, being more likely to have elements preserved (Behrensmeyer et al., 1979). This essentially reflects the greater resistance of large elements to physical breakdown. 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 (Figure V.8) and, although not generally diagnostic for finer taxonomic levels, they are recognizably crocodilian. The relative abundance of teeth reflects the fact that crocodilians shed their teeth continuously and over two years will have replaced all of them. For the American crocodile, *Crocodylus acutus*, this means 70 teeth (Neill, 1971) and given an average longevity of crocodilians of 30 years, an individual may generate over 1000 teeth.

V.3.2.4.1. Taphonomic control groups

Given the potential taphonomic biases described above, crocodilians are eminently preservable: they live in aquatic environments, are large, and have common identifiable elements. Therefore, if a vertebrate record exists for a place and time where crocodilians once lived, there should be evidence of their presence. Consequently, absences in a faunal list should reflect original ecological absence. Nonetheless, a more rigorous qualification of significant absence is desirable. This qualification is based on the use of control groups, which have already been described in the context of controlling for potential sampling biases (section V.3.2.).

The concept of taphonomic control groups was first described by Bottjer and Jablonski (1988) in their study of marine invertebrate onshore-offshore patterns. 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 behavior and only differs from the study group in the factor being investigated. For crocodilians, the taphonomic control group is the turtles, which have a good fossil record (turtle shell being one of the more ubiquitous elements at many vertebrate sites) and ecologically are mainly dependent on aquatic environments. The basic difference between the two groups is that turtles can occupy regions that are climatically

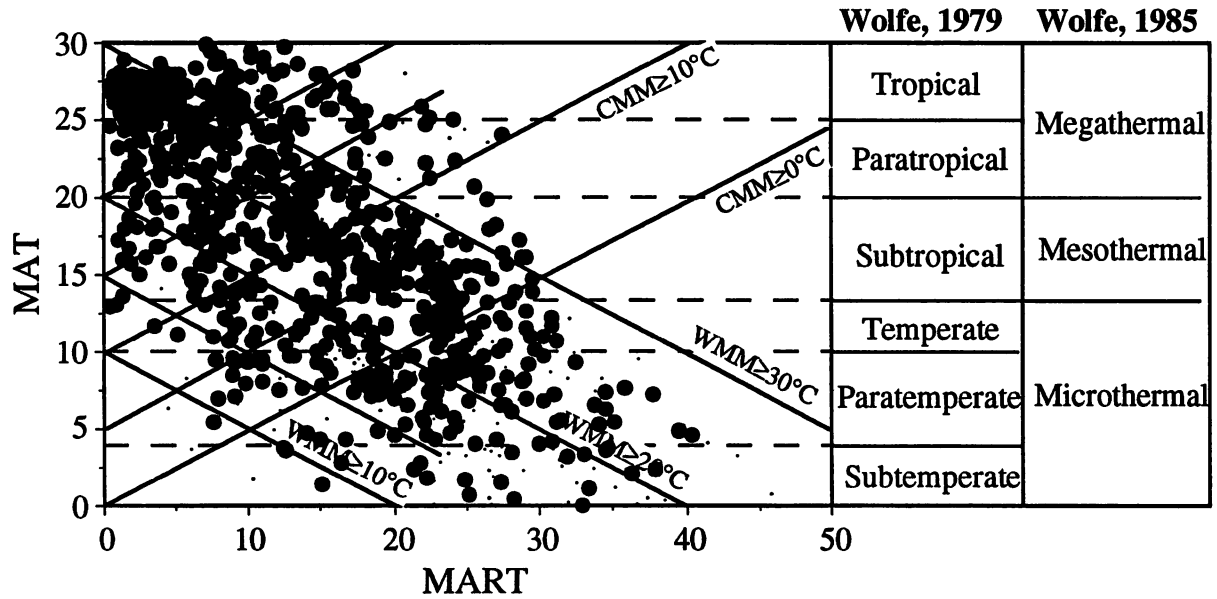


FIGURE V.9. The distribution of climate stations with turtles in MAT-MART climate space.

Turtles, per se, are not as climatically restricted as crocodilians (Figure IV.8). Consequently, they provide an excellent taphonomic control for examining significant absences of crocodilians due to climate.

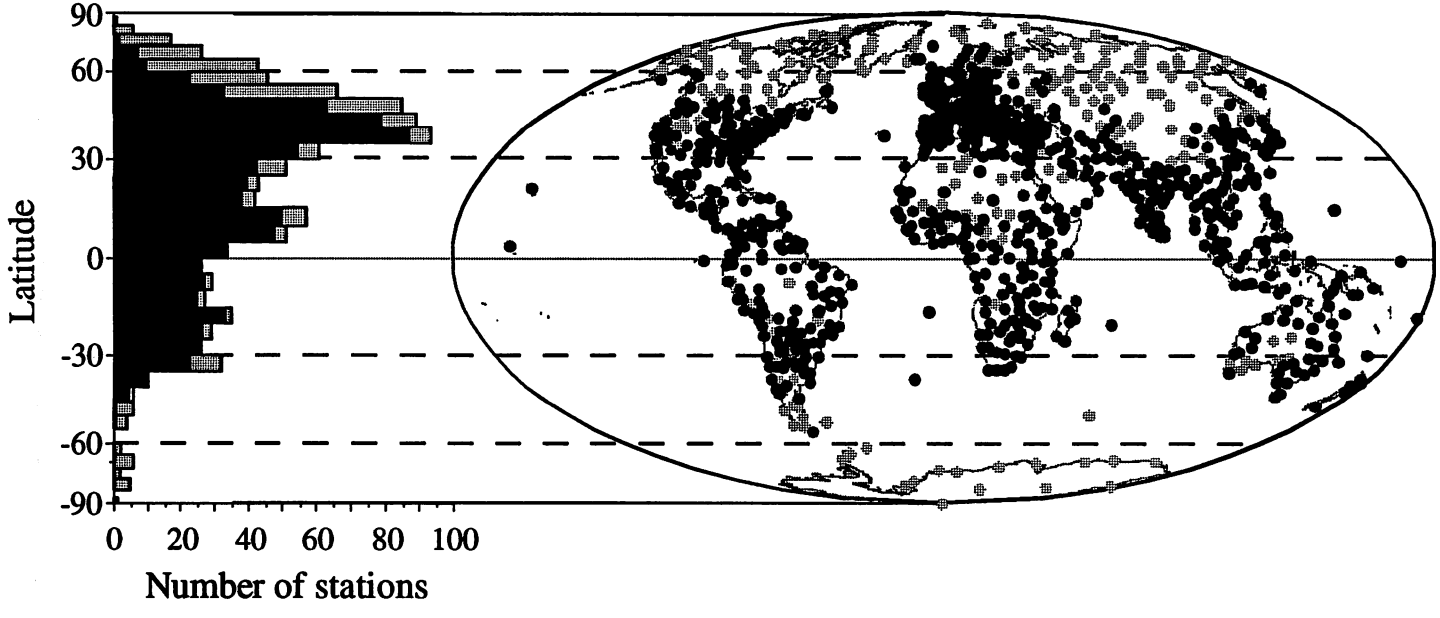


FIGURE V.10. Turtle bearing stations as a function of latitude.

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.

(especially thermally) too extreme for crocodilians (Figure V.9; compare with Figure IV.8), although subgroups of the turtles, such as the land tortoises, are more restricted (see Figure IX.3). This is reflected in turtles occupying a greater latitudinal range than crocodilians (Figure V.10; cf., Figure IV.1). The validity of using turtles as the taphonomic control is shown using the present day climate station dataset (section IV.3.3.1.). Of the 304 crocodilian bearing stations in this dataset 95.1% also have turtles.[11] 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.

The relationship between crocodilians and turtles exhibited by the climate station dataset can also be used to assess the completeness of the fossil dataset. Assuming that the relationships observed for the Recent also apply to the geologic past, then there is a 95% probability that given a fossil crocodilian there should also be a fossil turtle. However, in the dataset only 77.5% of fossil crocodilian localities, which contain other data, also contain turtles. This suggests that the turtle dataset may be incomplete, and therefore the absence of a turtle from a faunal list may be an artifact of the data collection process--the initial emphasis on fossil crocodilians. This is an area for future data compilation.

The proportion of turtle-bearing stations in each latitudinal zone is not randomly arrayed, but decreases monotonically at high latitudes, a pattern also observed for crocodilians (Figure V.11., cf. Figure IV.9--crocodilians). However, throughout the latitudinal range of crocodilians, between about 30° north and south, almost all stations bear turtles. Thus for the distribution of crocodilians, turtle-bearing stations can be used as a

11. This 4.9% discrepancy may be an artifact of the method--crocodilian distributions are based on area data which may overestimate ranges, turtles on published point data which tends to underestimate ranges.

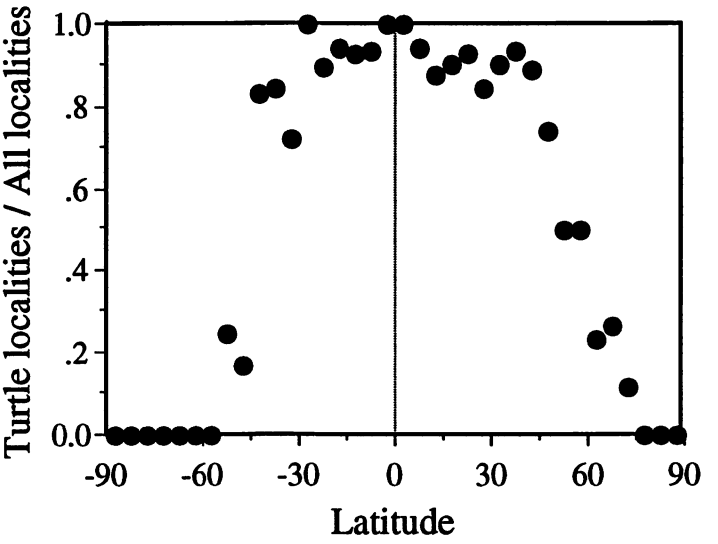


FIGURE V.11. Turtle bearing stations as the proportion of all localities in each 5° latitudinal zone.

surrogate for all stations (Figure V.12). Consequently, the relationships observed between the proportion of crocodilian-bearing stations and MAT, or other climate proxies (see section IV.3.3.2.), are also true for the proportion of crocodilian-bearing stations as a function of those with turtles. Application of these climate relationships to the geologic record may be made with more confidence using the ratio of crocodilian to turtle bearing localities, since fossil turtles provide qualification of significant fossil crocodilian absences (see above). Given this, changes in this ratio through time provide a potential indication of "global" temperature changes. This is shown in Figure V.13. The potential application of this is developed in section V.5.

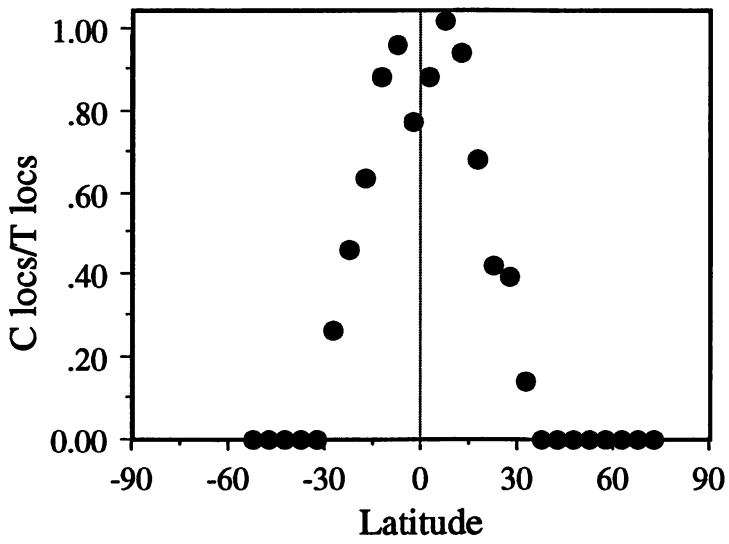


FIGURE V.12. The proportion of turtle stations with crocodilians for each 5° latitudinal band.

The trend shown here is essentially indistinguishable from that for the ratio of crocodilian-bearing stations to all stations shown in Figure IV.7. This is important when looking at the fossil record where the completeness of all localities is uncertain, but where we can constrain crocodilian occurrences using turtles.

V.3.2.5. History: Paleobiogeography

One influence on the distribution of living organisms is history. Organisms do not instantaneously appear throughout the world but originate from the evolution of a single individual to develop new populations 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 organisms' viable climate space. The distribution of modern and fossil occurrences of each crown group crocodilian family is shown in Figure V.14. These reveal that neither alligatorids nor gavialids are

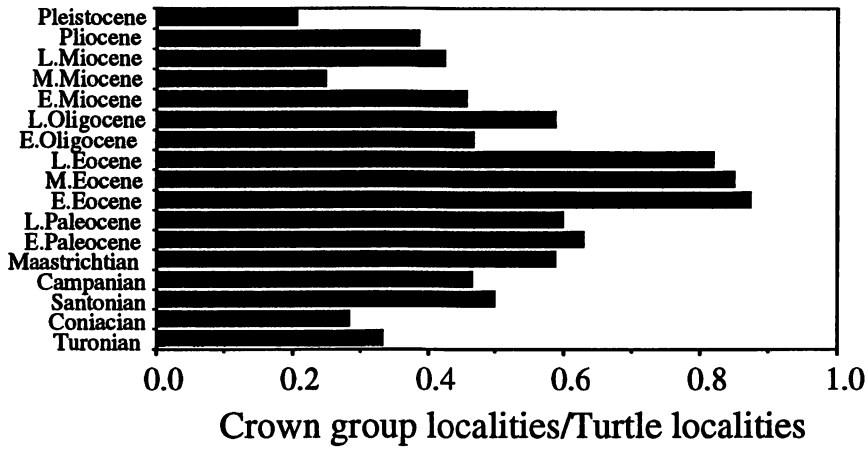


FIGURE V.13. The ratio of crown group crocodilian localities to turtle localities for each interval.

The ratio of localities with crown group crocodilians to those with turtles is shown as a function of time. The use of this ratio as a potential indicator of temperature is discussed in section V.3.2.4.1. If applicable to the geologic past then the ratio of crown group crocodilian localities to turtle localities through time should reflect a generalized paleotemperature signal. This suggests cooling from the Oligocene to the Recent. Note that crown group crocodilians are diversifying through the late Cretaceous and Paleocene and so the ratio during these time intervals is probably dominated by this evolutionary signal (see Chapter VII).

historically found in Africa or Australia, although their relatives, the Crocodylidae, occur on both continents. Modern alligators, caimans and gavials all lack the salt glands that enable many crocodiles to invade saline habitats. 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.[12] Given this, the historical expansion of these two families into South America, North America, Europe and Asia must have been made via

12. By the Miocene, when Africa and Eurasia collide, 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.

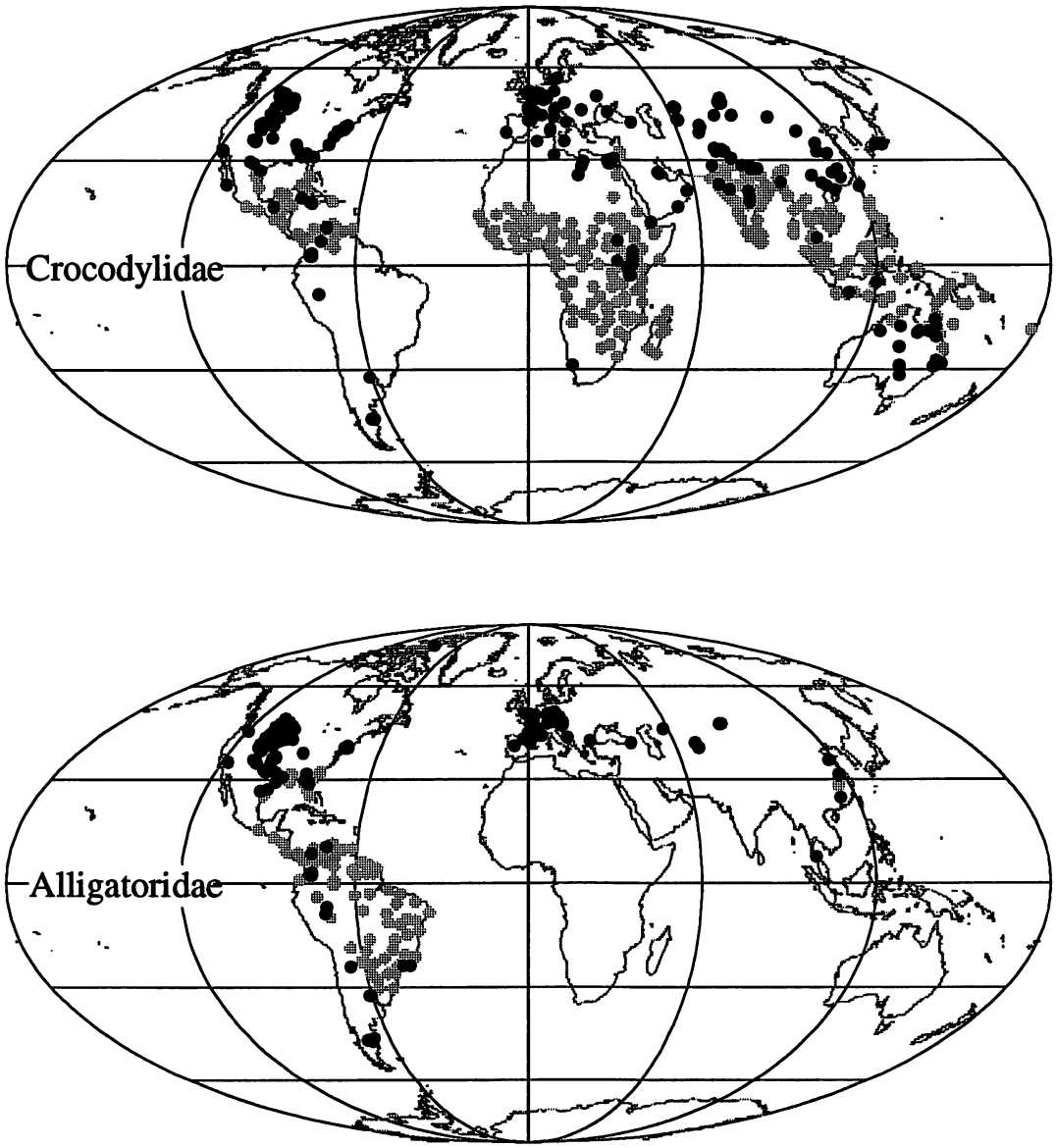


FIGURE V.14. Maps showing distribution of alligatorids, crocodylids and gavialids.

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.

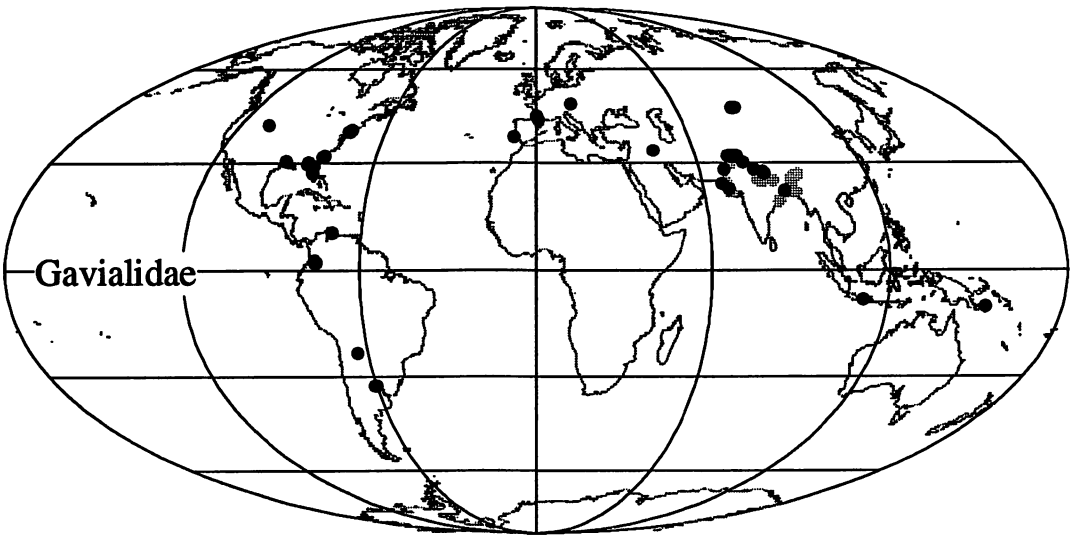


FIGURE V.14. continued.

land bridges. Those between the last three must have been via high-latitude land bridges, which has direct implications for paleoclimate.

V.3.3. Errors

V.3.3.1. Misidentification

Misidentification is a potential source of error that may influence distributions. 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 Paleogene of Antarctica, also on the basis of jaw fragments, which has subsequently been re-identified as a fish (Case, personal communication). A survey of the literature suggests that such

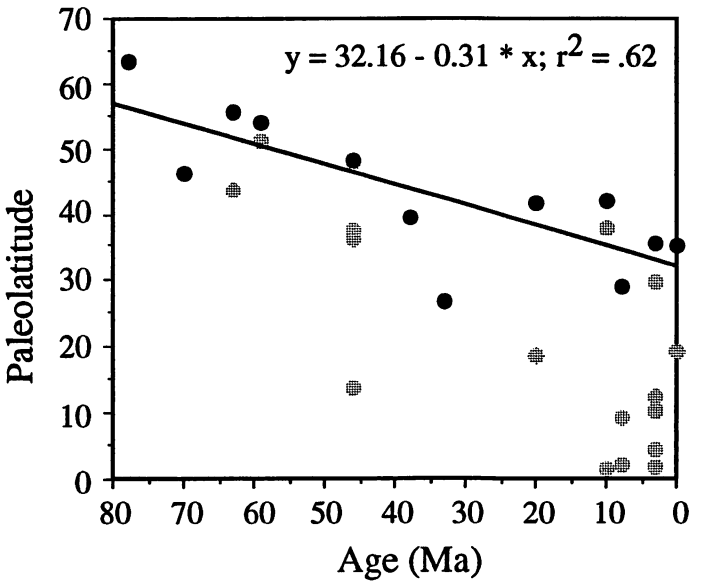


FIGURE V.15. Distribution of crown group crocodilian localities which have complete skulls preserved.

Each black or gray dot represents a locality. The regression is drawn through the maximum northern paleolatitude for each time interval (represented by the black dots; see Figure V.1 for intervals) and shows the general equatorward trend through the Cenozoic. In order to assess the significance of the changes in latitude, a Chi-square test is calculated using the average maximum paleolatitude as the predicted result (assuming that the distribution is random: average paleolatitude is 43.3°, median is 42.1°). The null hypothesis is that the two distributions are indistinguishable. A p value of 0.0013 indicates that the null hypothesis is false and the distribution is significant.

misidentifications are the exceptions. Nonetheless, 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 level (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). The paleolatitudinal trends given by these data are shown in Figure V.15 and are essentially indistinguishable from that using all data (Figure V.16).

V.3.3.2. Dating

The effect of temporal resolution on geologic patterns and trends has already been discussed in section V.3.1.2., but results can also be influenced by the accuracy of age assignments. In general, these ages are based on biostratigraphy. Errors may occur due to incorrect placement of a fauna within a biostratigraphic scheme (resulting from insufficient faunal information or misidentification), poor correlation between geographically disparate stratigraphies (especially when comparing global faunas), incorrect correlation of local terrestrial units with the global marine standard, and/or imprecision in constraining biostratigraphically derived relative ages in absolute time. As more precise absolute ages and biostratigraphic studies become available, these problems are becoming less significant. Consequently, in order to minimize such errors, age assignments used in this study are based on the most recent published accounts (see Chapter III). Unfortunately this is not a guarantee of truth.

An inspection of age assignments for localities, made during the compilation of the dataset, has shown that where changes have been made over the last 100 years they have generally not exceeded more than one sub-epoch (e.g. Early Pliocene to Late Miocene).[13] Problematic assignments are concentrated at key chronostratigraphic boundaries, for

13. In some cases age assignments have changed by more than one sub-epoch. An example is the Hornerstown Formation, New Jersey, which has varied in age from the Cretaceous to the Eocene and Palaeocene (Miller, 1956; Olsson, 1963; Richards and Gallagher, 1974)--in this study the Hornerstown Formation is placed across the K-T boundary (late Maastrichtian to early Thanetian) based on the COSUNA (Correlation of Stratigraphic Units of North America Project) stratigraphic scheme (Jordan and Smith, 1983). The Hornerstown Formation contains vertebrates that are distinctly Cretaceous (mosasaurs, plesiosaurs and goniopholid crocodilians). Consequently the extension of the Hornerstown into the early Palaeocene raises some problems, although Richards and Gallagher (1974) suggest the possibility of reworking. Another issue here is the definition of stratigraphic unit boundaries, which can change position relative to one another.

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 USSR Korobkov (1963) suggested that all dates formerly assigned to the Lower Oligocene (Rupelian) should be reassigned to the Upper 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 V.3.1.2.).

Dating errors are a problem, especially for global studies. Resolution of these issues requires globally based terrestrial correlations, and the present database provides a potential tool for this. With complete faunal lists it should be possible to constrain relative time better using a method such as Alroy's conjunction-disjunction (Alroy, 1992, 1994). This is a direction for future study.

V.4. TRENDS

Figure V.16 shows the paleolatitudinal distribution of crown group crocodilians in the context of all fossil vertebrates (spatial and temporal resolution, GP≤3, ≤2 time intervals, respectively; see section V.3.1). A detailed view of the region between 30° and 80° north paleolatitude, which represents the best sampled area of the globe (see section V.3.2), is given in Figure V.17. 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: Estes and Hutchison, 1980; McKenna, 1980; West et al., 1977). However, the group does not expand into the southern hemisphere until the Paleocene (a possible explanation of this pattern is discussed in Chapter VII). The Middle and Late Eocene record is poorly represented in southern latitudes, but from the Oligocene to the Recent there is a general equatorward retreat of crocodilians. In the northern hemisphere, an equatorward shift is seen during the Oligocene and again in the 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 equatorward shifts at times of polar cooling. The general similarity of this trend with that implied by the marine isotopic signal supports this supposition (Figure II.1). This trend is also indicated by the floral record (p.203, Frakes, 1979) and the Cenozoic history of glaciation outlined in Chapter II.

The trends shown in Figure V.16 and V.17 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

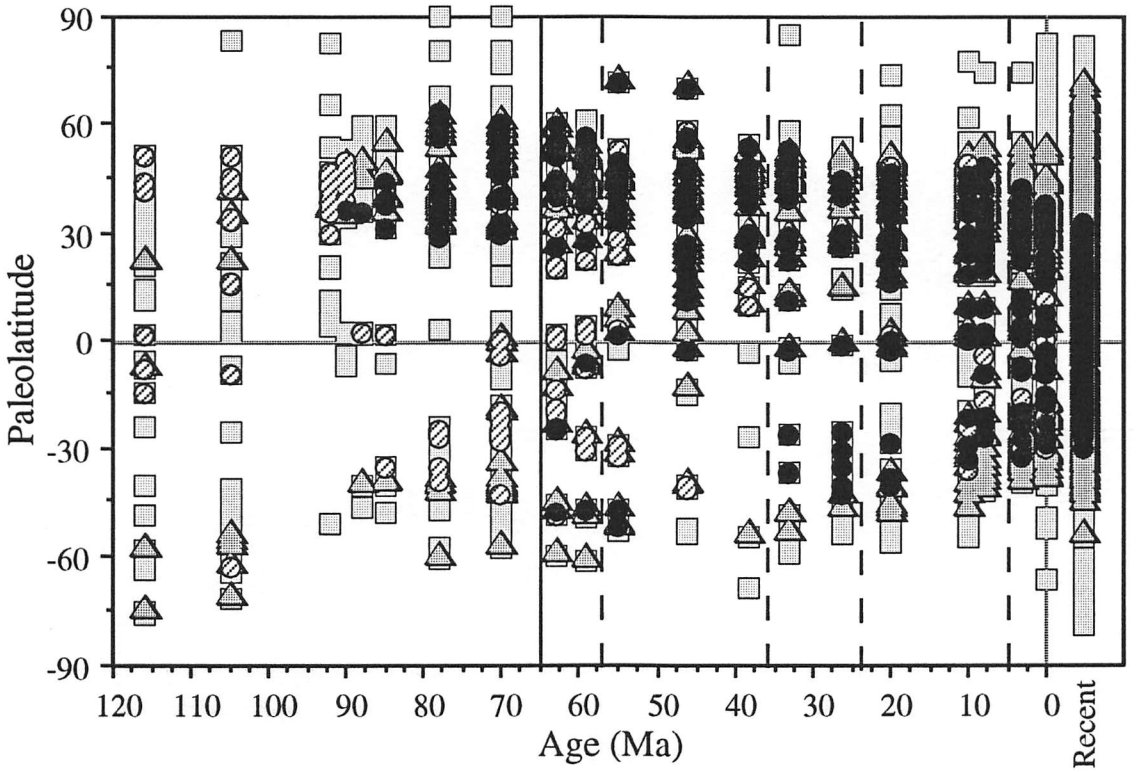


FIGURE V.16. The paleolatitudinal distribution of crocodilian and non-crocodilian vertebrate localities.

Crown group crocodilians (black circles) are shown against a backdrop of all crocodilians (diagonally shaded circles), turtles (medium gray triangles) and vertebrates in general (light gray squares--white squares on later maps). 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 figure 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.

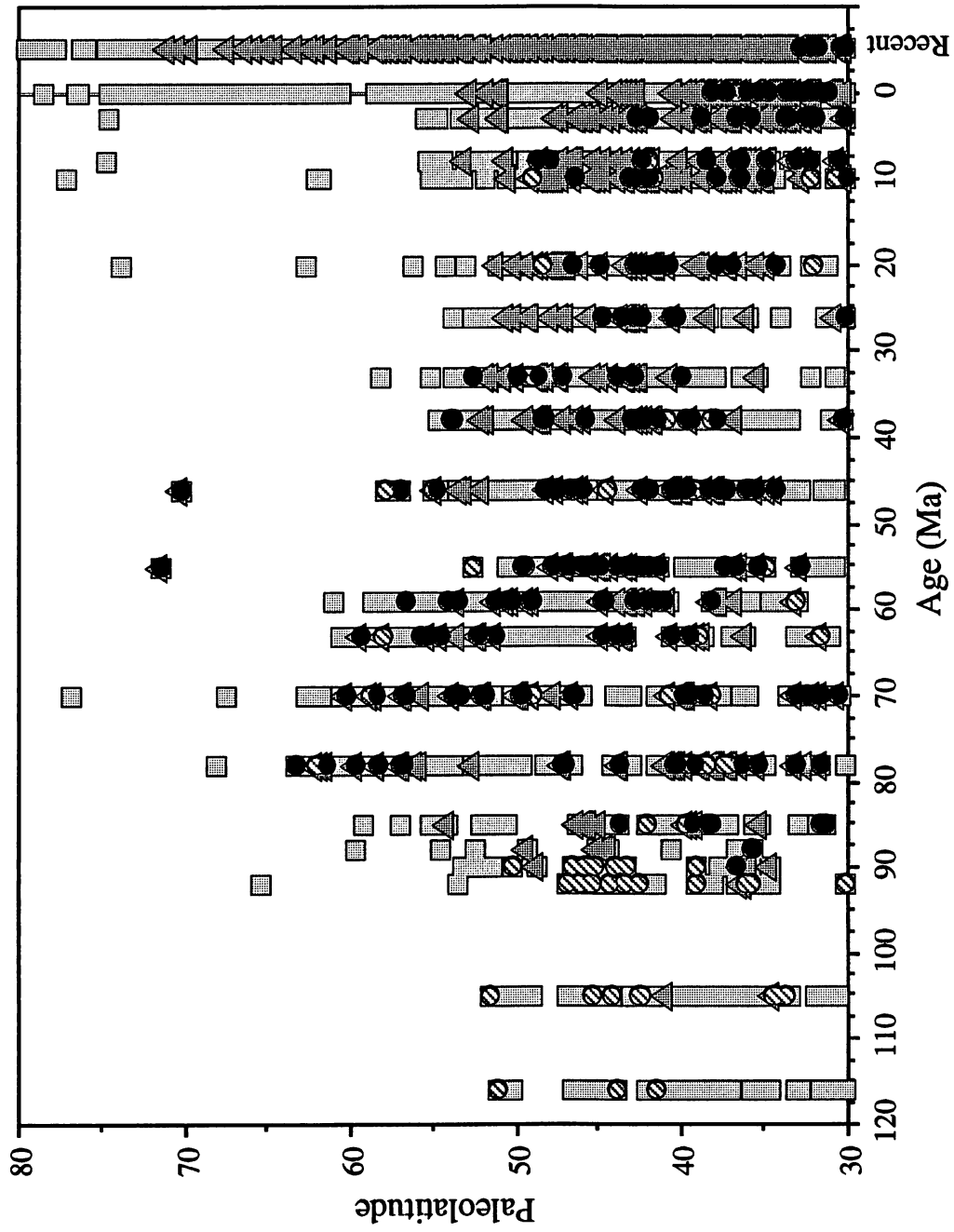


FIGURE V.17. Paleolatitudinal distribution of crown group crocodilians in the Northern Hemisphere.

This is a detailed view of the region between 30 and 80° N paleolatitude from Figure V.16. See Figure V.16 caption for further information.

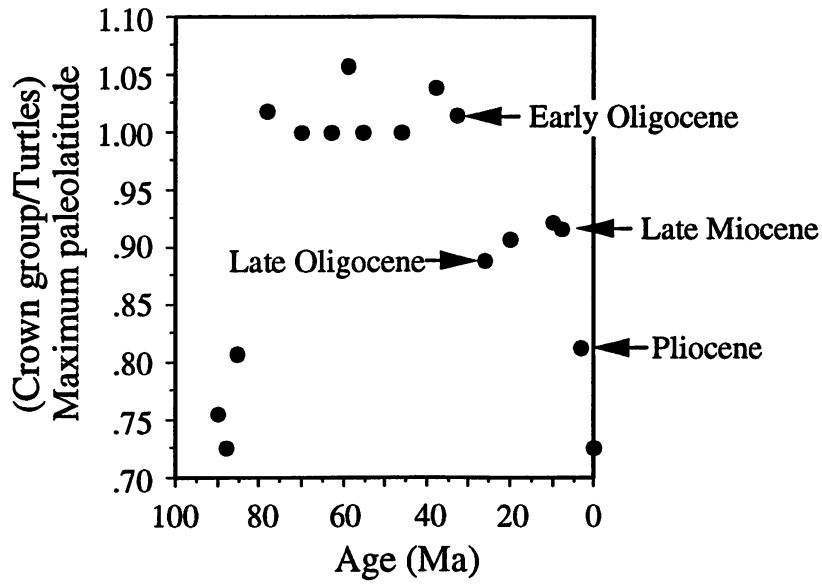


FIGURE V.18. The ratio of the maximum paleolatitudes represented by crown group crocodilians and turtles through time.

The significance of the equatorward 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 equatorward shifts of crocodilians in the Oligocene and Pliocene are clearly shown in this diagram.

appear well constrained, but Late Cretaceous and early Paleogene trends are limited by available data. This is shown more clearly in Figure V.18, which shows the proportion of the latitudinal range represented by turtles (localities in which crocodilians could be preserved if they had originally been present; see section V.3.2.4.1) that have crown group crocodilians.

While control groups provide a qualitative assessment of the significance of trends, this assessment can also be made quantitatively. However, quantitative methods are

susceptible to the effects of inhomogeneities within datasets, especially differences in sampling density between intervals--the Late Oligocene, during which the latitudinal distribution of crocodilians is restricted to low paleolatitudes (Figure V.17), has the fewest number of crown group crocodilian localities of any time interval in the post-Santonian (Figure V.3). It will be argued later that these differences in the numbers of localities represent real differences in the frequency of crocodilians through time (related to restriction of latitudinal ranges). However, here, a resampling technique (rarefaction: sampling without replacement) is used to look at the significance of the Oligocene low to see if it can be explained by sampling alone: for each interval, from the Campanian to the Pleistocene (the pre-Campanian intervals are ignored because of their overall low representation during the initial diversification of the group; see Chapter VII), 10 localities (the number of localities in the Late Oligocene distribution) 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 10 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 are given in Figure V.19 and show that even when sampling is taken into account there is a 95% probability that the Late Oligocene paleolatitude low is significant relative to the entire dataset with p=0.0376 (pre-Late Oligocene p=0.1164).[14]

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 paleolatitude of less than or equal to the Late Oligocene value of 44.9°, given the Late Oligocene sample size of 10 localities between 0 and 90°N. This

14. One potential problem in using resampling is that it assumes that each locality in the dataset is of equal "weight" and this is not necessarily the case. Heterogeneities in the definition of a "locality" have already been discussed in section V.3.1.1.

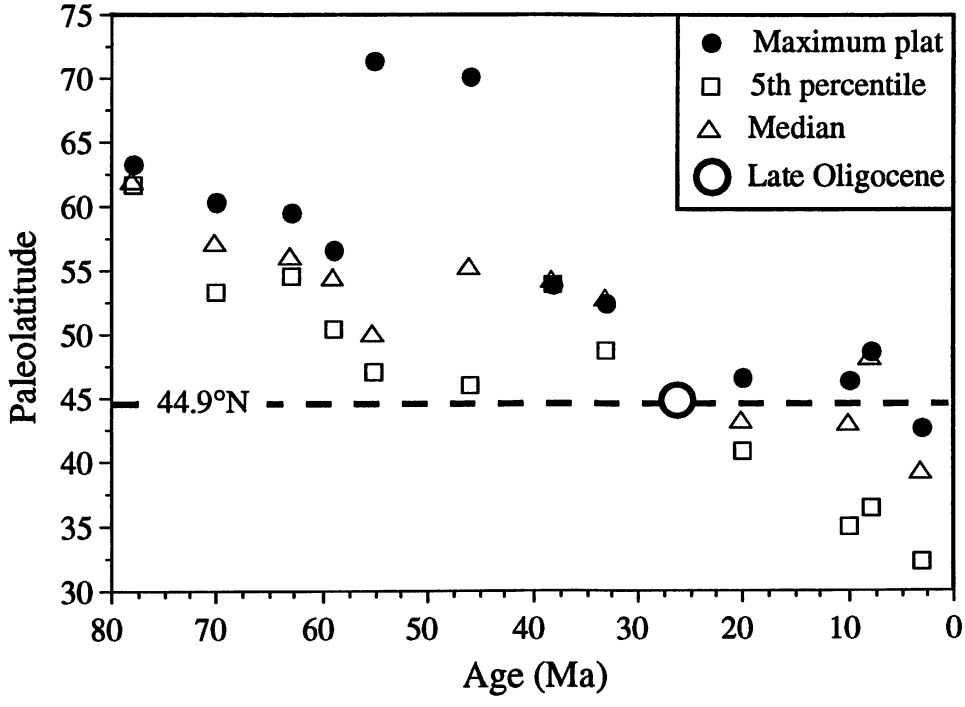


FIGURE V.19. Resampled crown group crocodilian paleolatitudinal distributions.

The observed northern paleolatitudinal limit of crown group crocodilians (GP≤3, ≤2 intervals) is represented by black circles. 44.9°N represents the maximum poleward extent of crown group crocodilians during the Late Oligocene (large circle). The influence of sampling on this distribution, particularly its effect on the Oligocene low, is assessed using resampling without replacement (pre-Campanian intervals are ignored because of their overall low representation during the initial diversification of the group; see Chapter VII). In each case 10 localities (the number of crown group crocodilian localities in the Late Oligocene) are randomly taken from all of the localities in that interval (northern hemisphere only). The maximum latitude amongst these 10 is then recorded. This is repeated 1000 times and the distribution examined. The median of this distribution is represented by open triangles, the 5th percentile values by open squares (95% of results lie poleward of this value). A Chi-square Test is used to assess how significantly different these distributions are from the Late Oligocene value (44.9°). The results show that even when sampling is taken into account we can be ≈90% certain (p=0.1164, lower 5th percentile; p=.0105, median) that the Late Oligocene paleolatitudinal low is lower than the poleward limit of preceding intervals.

analysis is also made for a subset of the dataset, all localities that occur below 55.9°N paleolatitude, the most poleward vertebrate locality in the Late Oligocene. The results are shown in Table V.1. and illustrate again that the variations in observed paleolatitudinal trends are not simply an artifact of sampling.

TABLE V.1. RESAMPLING RESULTS
P values for the probability that resampling crown group crocodilians in each interval for the sampling level in the Late Oligocene (10 localities) that the maximum paleolatitude will be below the Late Oligocene.

Interval	Number of localities	Maximum Paleolatitude	P for max. plat≤44.9° 10 locs only	Number of localities plat≤53.9°	P 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

If sampling is not entirely responsible for observed patterns, then there are some other relationships that require explanation, in particular the strong correlation between the maximum paleolatitude occupied by crocodilians in an interval and the duration (in millions of years) of that interval (Figure V.20). It is posible that this may reflect an intrinsic property of warm periods ("hot-house" worlds), that they are generally more "stable" than

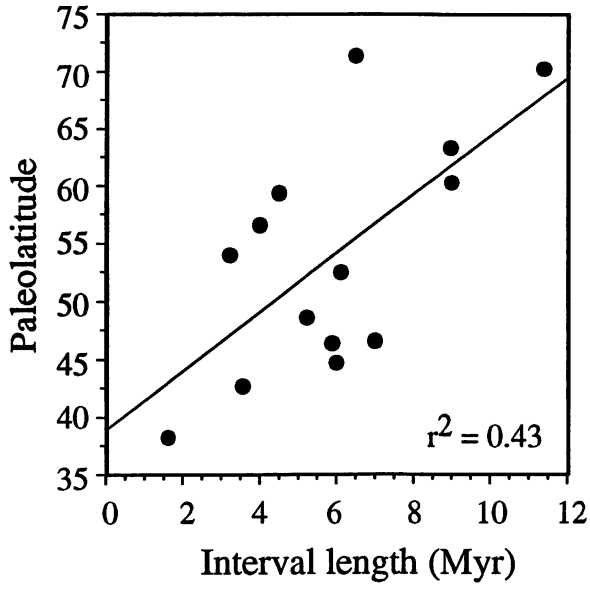


FIGURE V.20. Interval length versus maximum crown group paleolatitude.

This graph shows the relationship between the length of each time interval and the maximum paleolatitude reached by crown group crocodilians in that interval. The positive correlation between the two is suggestive of some underlying cause. As discussed in the text this does not appear to be due to sampling alone.

glacial worlds (less susceptible to short-term climate fluctuations). After all, stratigraphic intervals are defined on observed changes in the geological record; if short term climate changes during "ice-house" have larger effects than those of "hot-house" intervals then they are more likely to be recorded in the geologic record and thereby provide the opportunity for finer stratigraphic divisions.

While the previous trends have concentrated on all crown group crocodilians, Figure V.21 shows the paleolatitudinal distribution of alligatorids, crocodylids and gavialids separately. All three families show similar trends, although in the post-Oligocene

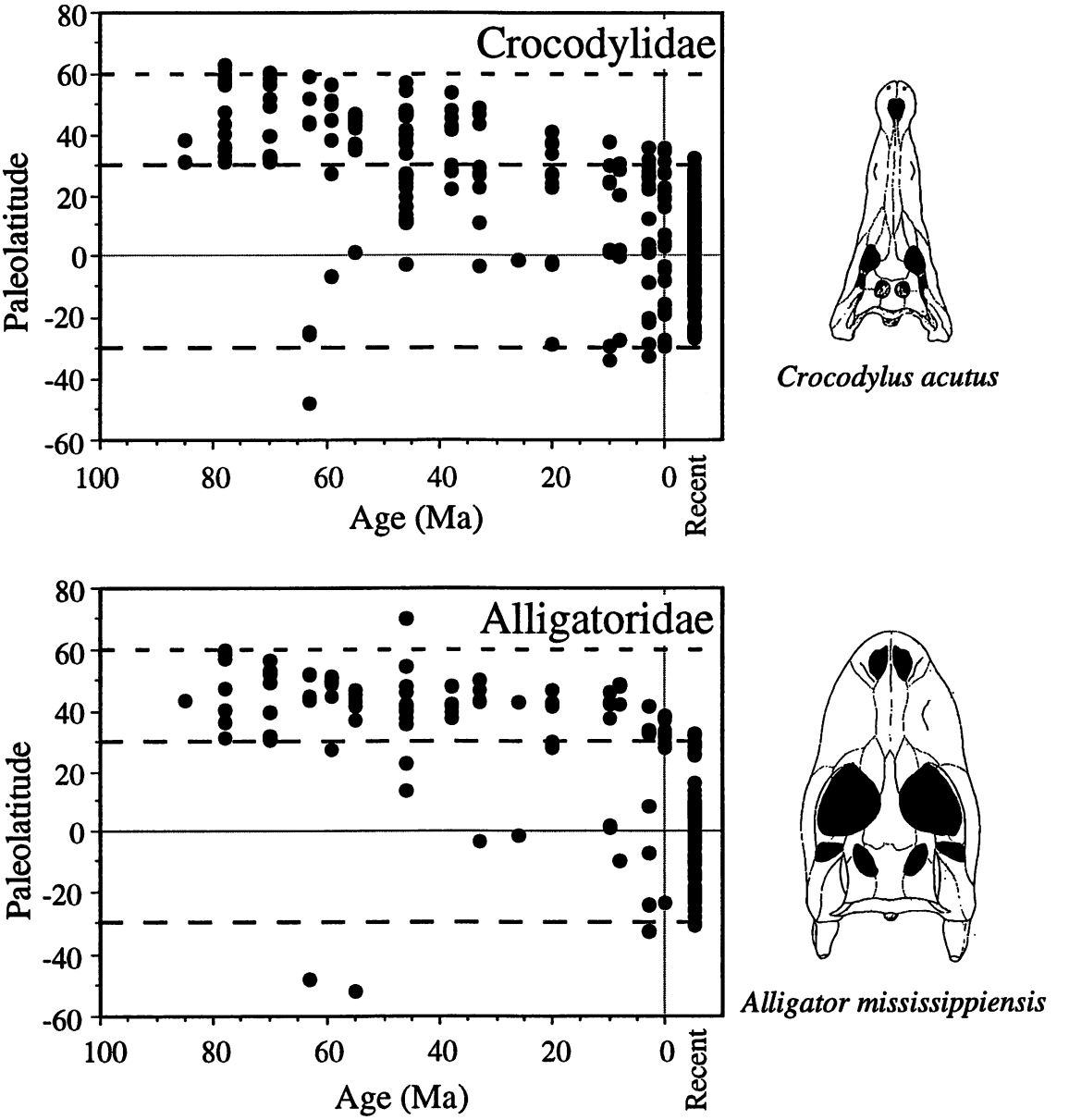


FIGURE V.21. Paleolatitudinal distribution of each crown group family through time.

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 Chapter VII). Note also that after the Oligocene the highest northern latitude occurrences are restricted to alligatorids.

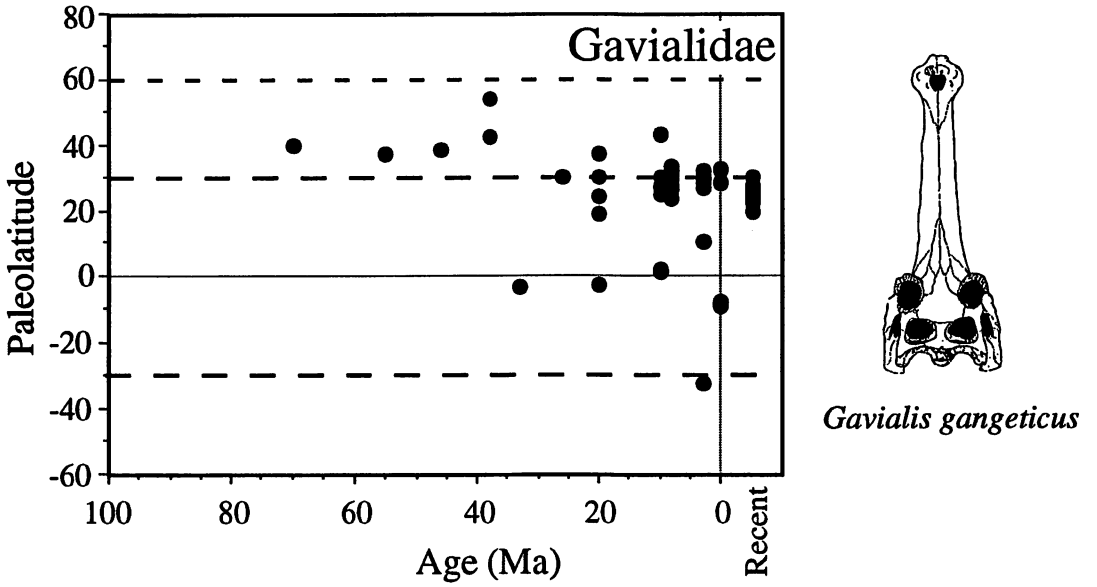


FIGURE V.21. continued.

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.

V.5. LATITUDINAL GRADIENTS

In section V.3.2.4.1, the ratio of crocodilian to turtle bearing climate stations was shown to vary systematically with latitude and thereby with temperature. 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. Figure V.22 shows the relationship between the ratio of crocodilian to turtle bearing stations in each 5° latitudinal zone and the mean MAT for that zone. The derived regression

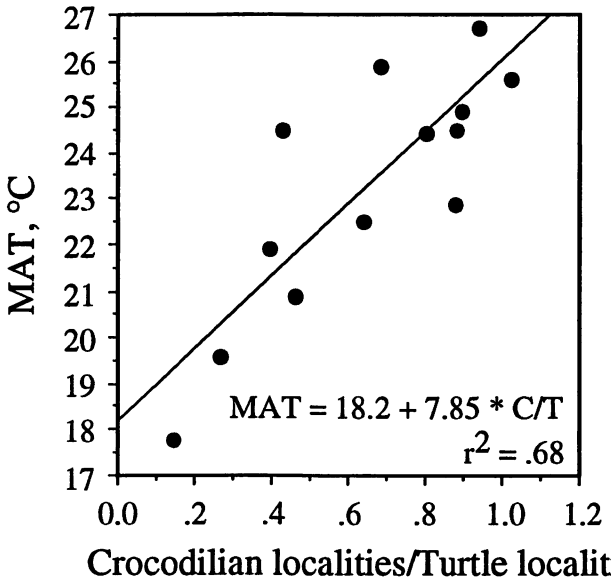


FIGURE V.22. The relationship between the ratio of crocodilian to turtle localities and MAT (°C) for each 5° latitudinal zone.

This is derived from the present day climate station dataset. Compare with Figure V.12.

is used to retrodict the average MAT for each 5° paleolatitudinal zones in each time interval used in the study. The results are shown in Figure V.23.

The retrodicted thermal gradients in Figure V.23 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; the extremely high temperatures retrodicted for a number of time intervals, for instance the 96.7°C score in the Late Eocene, are a consequence of undersampling of turtles in the database. Steepened gradients are also retrodicted for the glacial world of the late Oligocene, but those of the Miocene and Pliocene are similar to that

of the Recent. In the Paleogene 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.

While the general difference between Paleogene and Neogene gradients are consistent with paleoclimate interpretations based on other evidence, the absolute values calculated for mid and high latitudes are much higher than retrodicted using 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 IV.3.3.2. and Figure IV.15). 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 Figure V.23 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

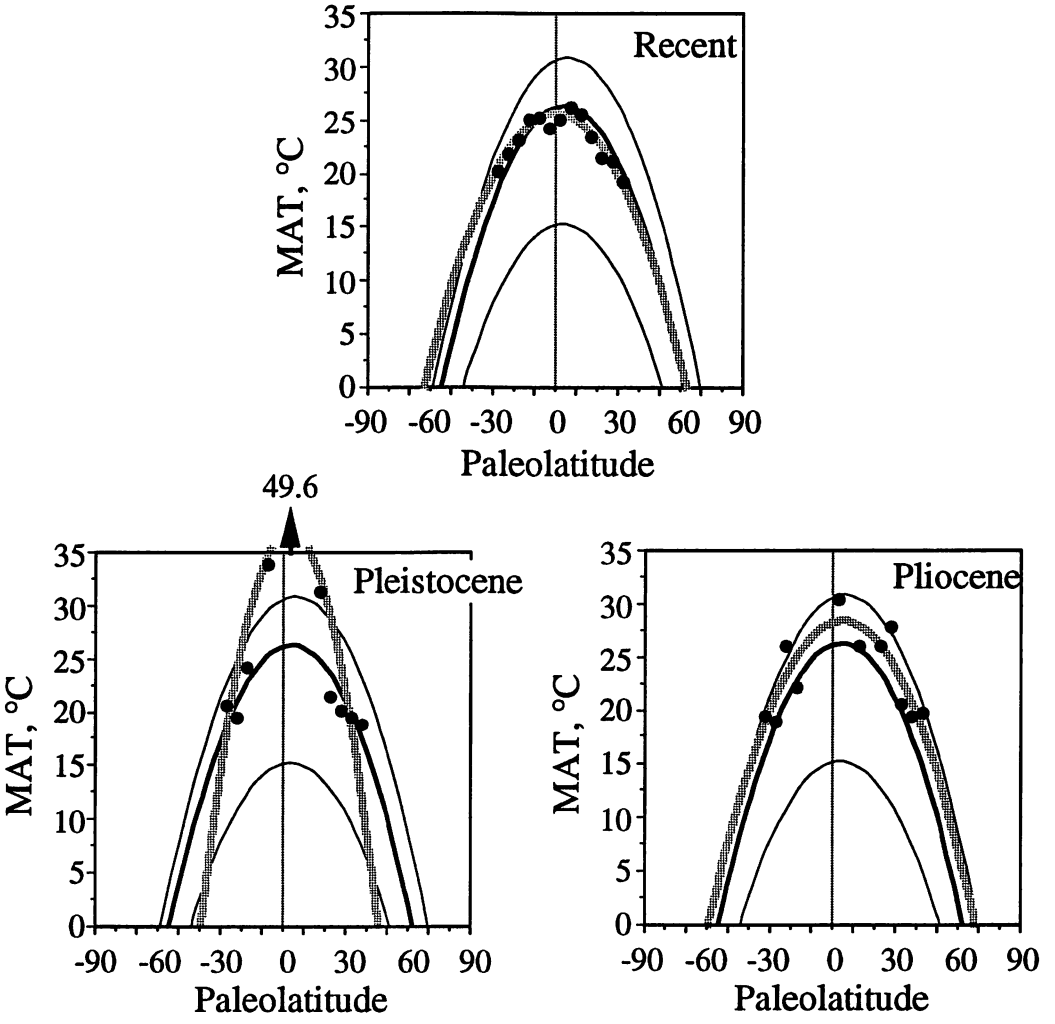


FIGURE V.23. Thermal gradients determined using the ratio of crocodilian to turtle localities.

Paleotemperature values for each 5° paleolatitudinal zone are calculated using the regression given in Figure V.22. A second-order polynomial is drawn through these results (thick gray 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 minimum MAT in each zone, the upper line the maximum MAT.

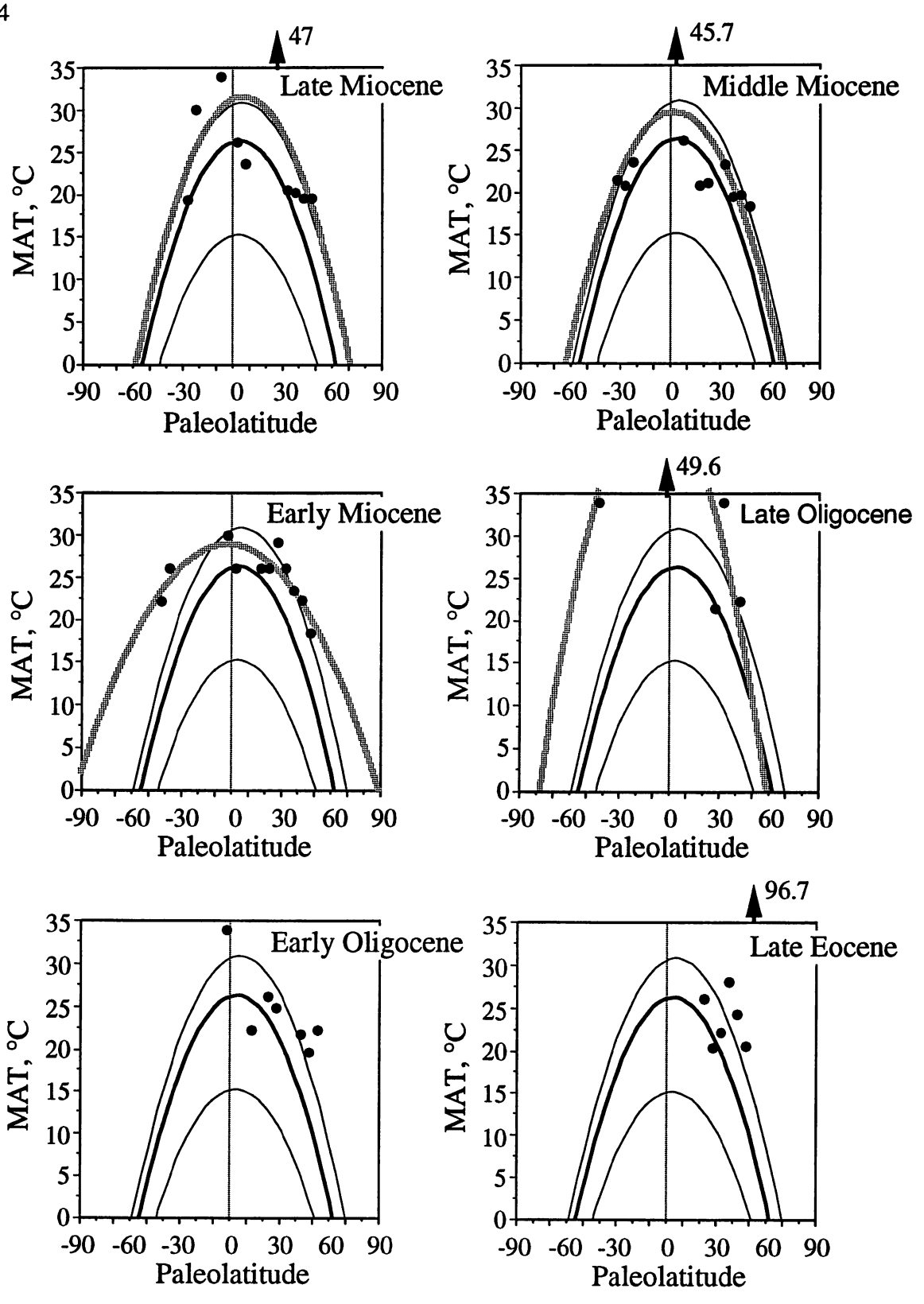


FIGURE V.23. continued.

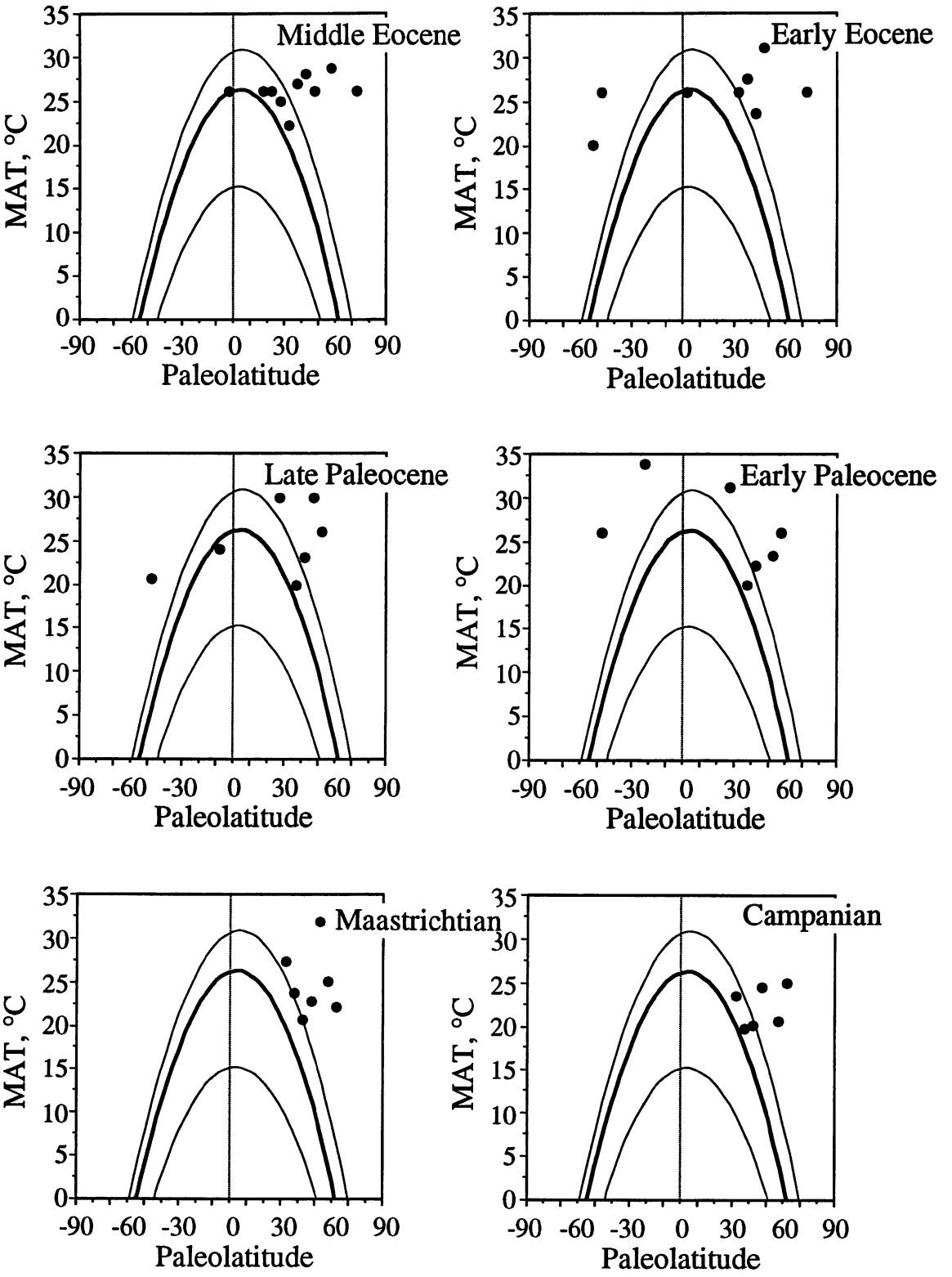


FIGURE V.23. continued.

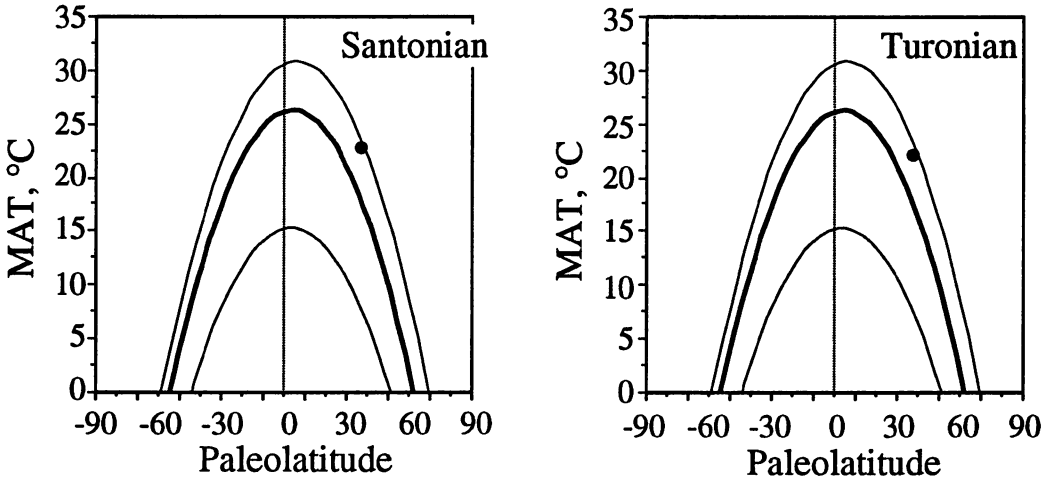


FIGURE V.23. continued.

Cenozoic. The relationship between mid-latitude aridity and periods of glaciation is an important one and is developed further in the following section.

V.6. MAPS

While changes in the latitudinal range of crocodilians indicate the general trend of global paleoclimate, comparable with that indicated by the marine isotopic record (Figure II.8), an understanding of the dynamics responsible for paleoclimate can only be understood through the examination of the spatial pattern of climate proxies (see Chapter I). In this section the spatial pattern of crocodilians is shown on a series of plate reconstruction maps. Control groups for taphonomy (turtles) and collection/tectonics (vertebrates in general) are also plotted (note that these may be obscured by the crocodilian data which are superimposed on this information). Non-crown group crocodilians are also plotted; this not only includes "mesosuchian" occurrences, but also indeterminate data, in which poor specimen fidelity precludes finer level identification. Temporal resolution is determined by only using data that occur in no more than two intervals (see section V.3.1.2). However, in

order to include the maximum amount of information, maps are presented for two temporal resolutions - "Epoch" level (Upper Cretaceous, Paleocene, Eocene, Oligocene, Miocene, Pliocene, and Pleistocene) and stage / sub-epoch level (Cenomanian, Turonian, Early Eocene, etc.). Consequently, poorly resolved localities, such as those in the dataset dated as "Late Cretaceous," appear on the Epoch level maps, but do not appear on the more finely resolved maps.

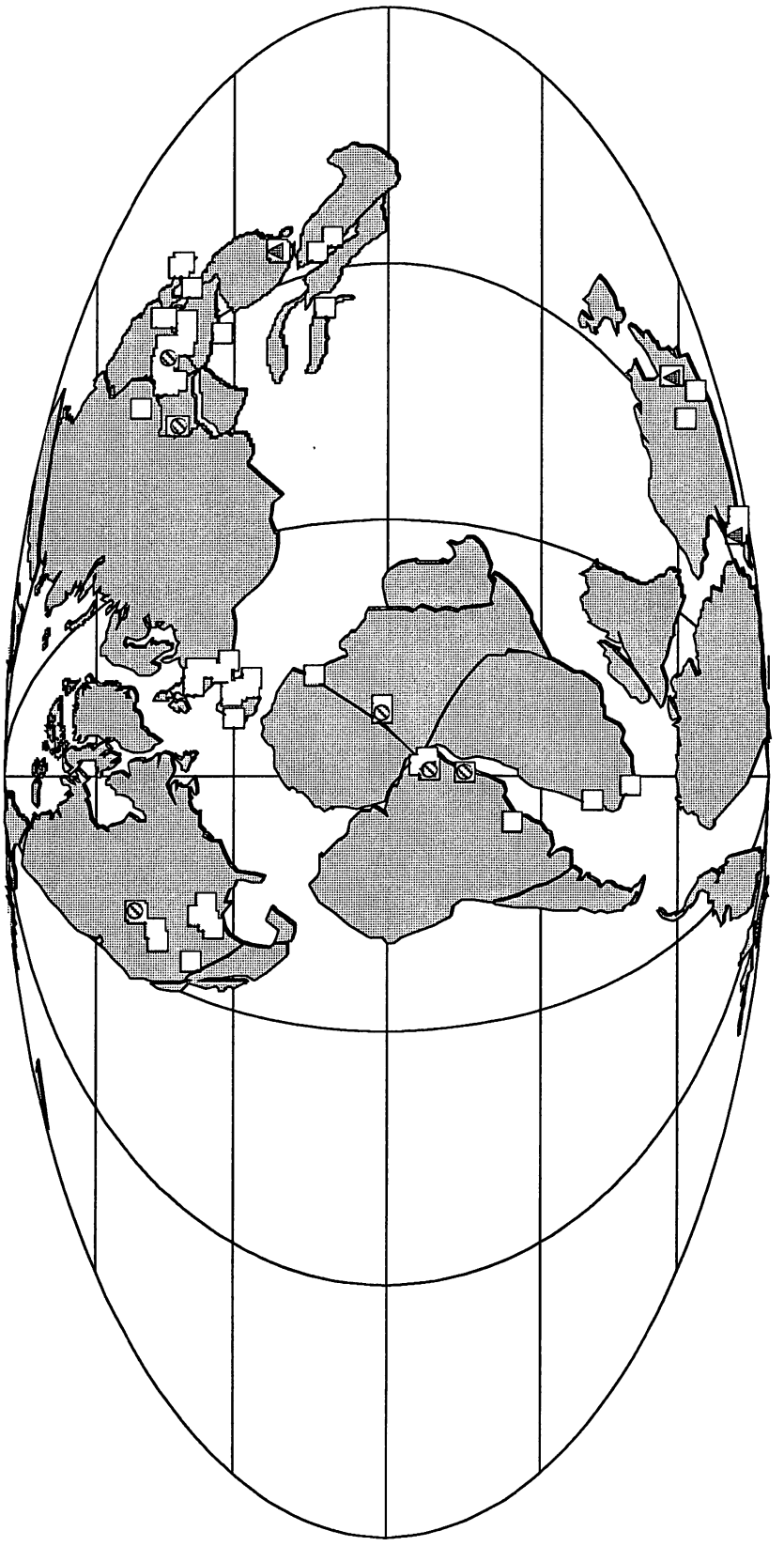
A detailed synopsis of the paleoclimate of each interval is beyond the purview of this study; to this end, text associated with each map is kept to a minimum. For excellent reviews of the terrestrial climate record through this period, readers are referred to Frakes (1979), Crowley and North (1991), and especially Behrensmeyer et al. (1992).

V.6.1. Cretaceous

One of the earliest occurrences of an "eusuchian" grade crocodilian is in the Albian aged Griman Creek Formation of Australia. Referred to as *Crocodylus selaslophensis*, the true relationships of this taxon remain unclear (Molnar, 1980), and consequently it is not shown on the maps as a crown group crocodilian. In general, 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 figures V.24-V.27. 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.

FIGURE V.24. Aptian map (116 Ma).

In each of the following maps the distribution of vertebrates (open squares), turtles (grey triangles), crocodilians (cross-hatched circles) and crown-group crocodilians (black circles) is shown. Data are restricted to those localities with GP less than 3 and which occur in no more than two time intervals (note that for Figures V.28, V.33, V.36, V.40, and V.43 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 absolute dates given in the caption title are the reconstruction ages used for the map. In order to aid clarity vertebrate localities are plotted first and then the filled with white such that overlapping localities form one large white area. The symbol for turtles (gray triangles) is then superimposed onto these data--remember that this includes all turtles, including tortoises and marine forms. 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.



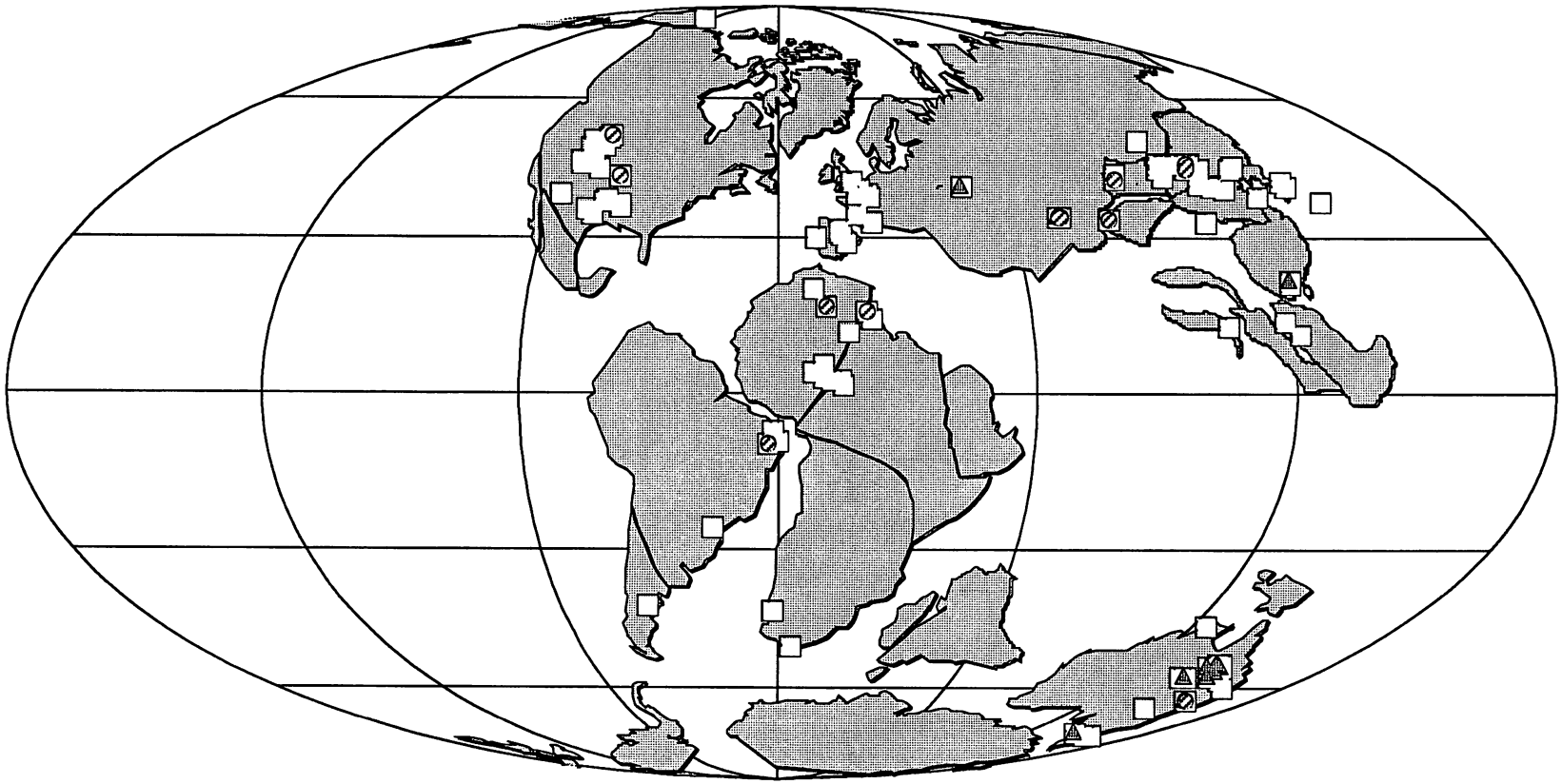


FIGURE V.25. Albian map (105 Ma).

See Figure V.24 caption for key and further details.

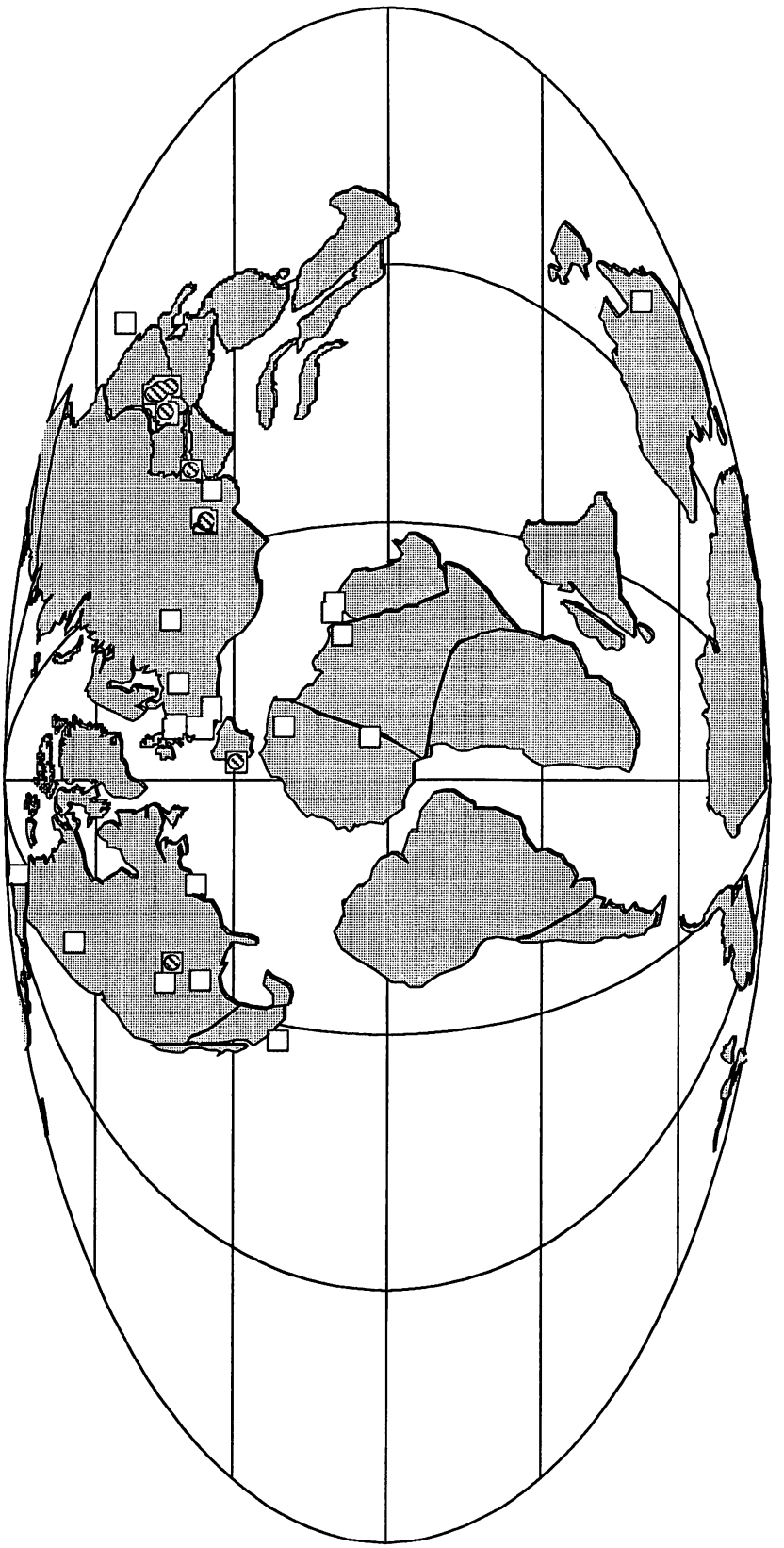


FIGURE V.26. Cenomanian (92 Ma).

See Figure V.24 caption for key and further details.

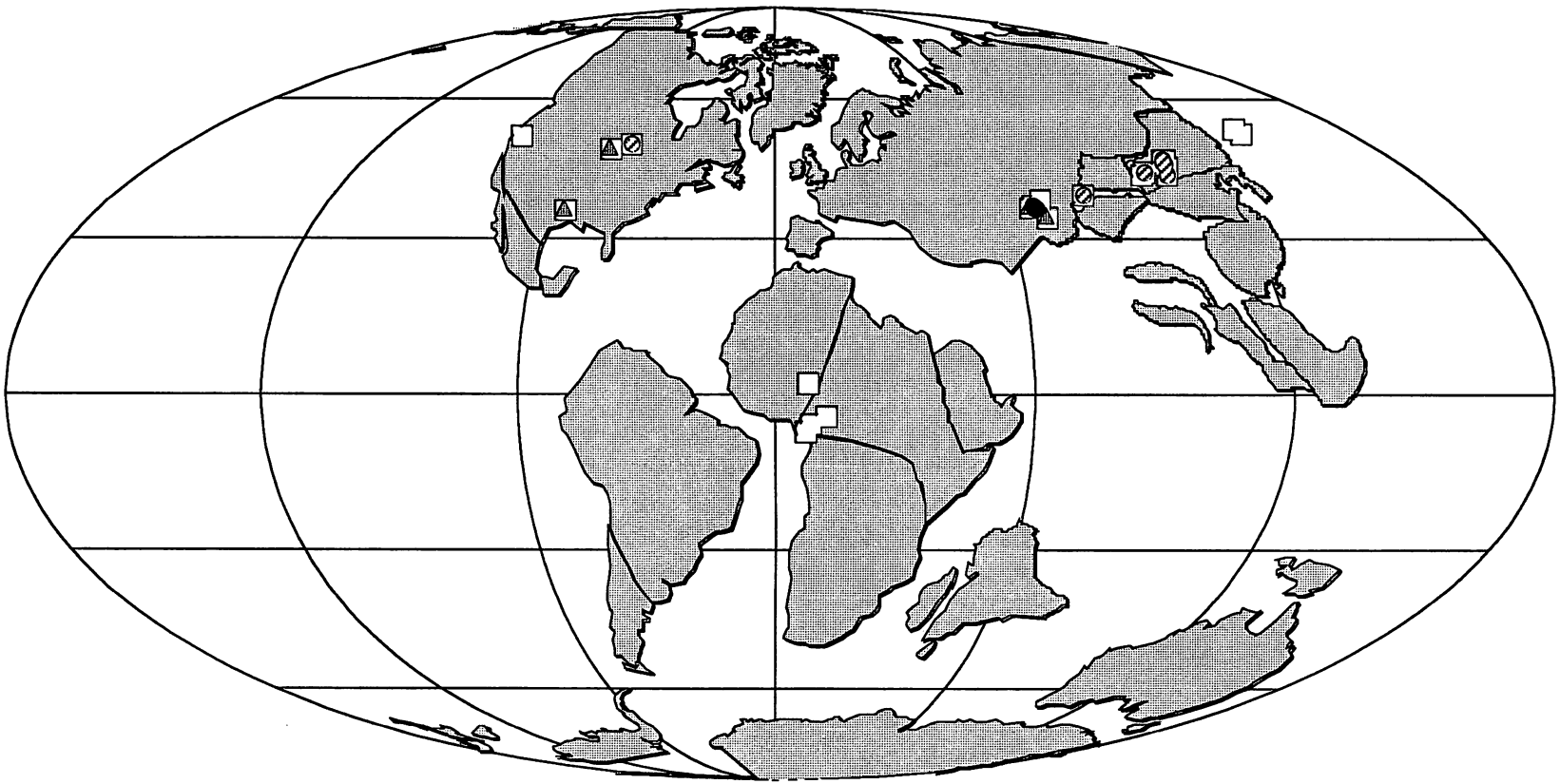


FIGURE V.27. Turonian (90 Ma).

See Figure V.24 caption for key and further details.

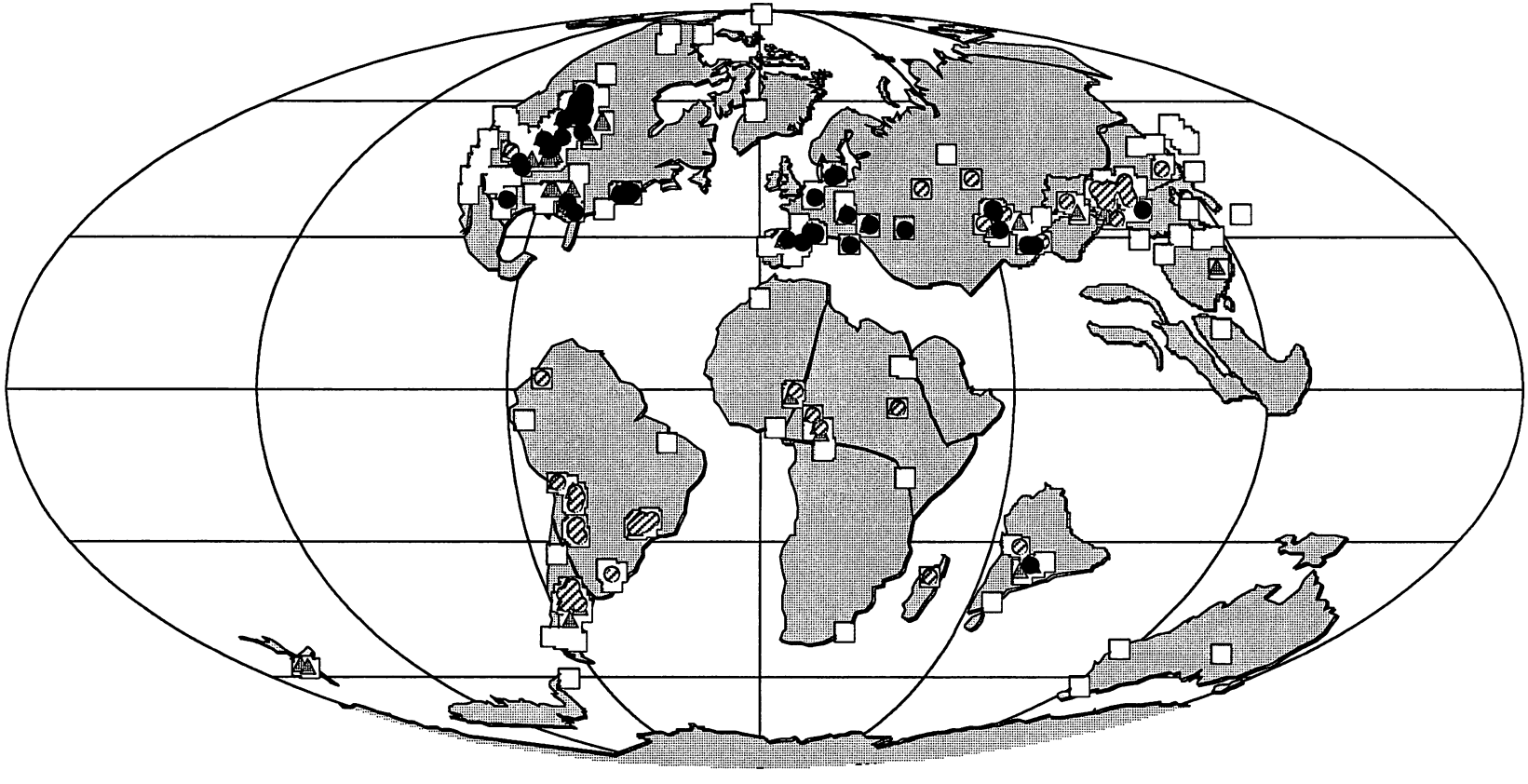


FIGURE V.28. Senonian (70 Ma).

See Figure V.24 caption for key and further details. This figure includes all occurrences dated as Senonian (Coniacian-Maastrichtian). Note that the crown group crocodilian occurrence in India represents a temporally poorly resolved locality: Nagpur, which is dated as Upper Cretaceous to Palaeocene and includes both dinosaurs and a Paleocene fauna (Sahni et al., 1984) . By the Paleocene crown group crocodilians are well represented in India.

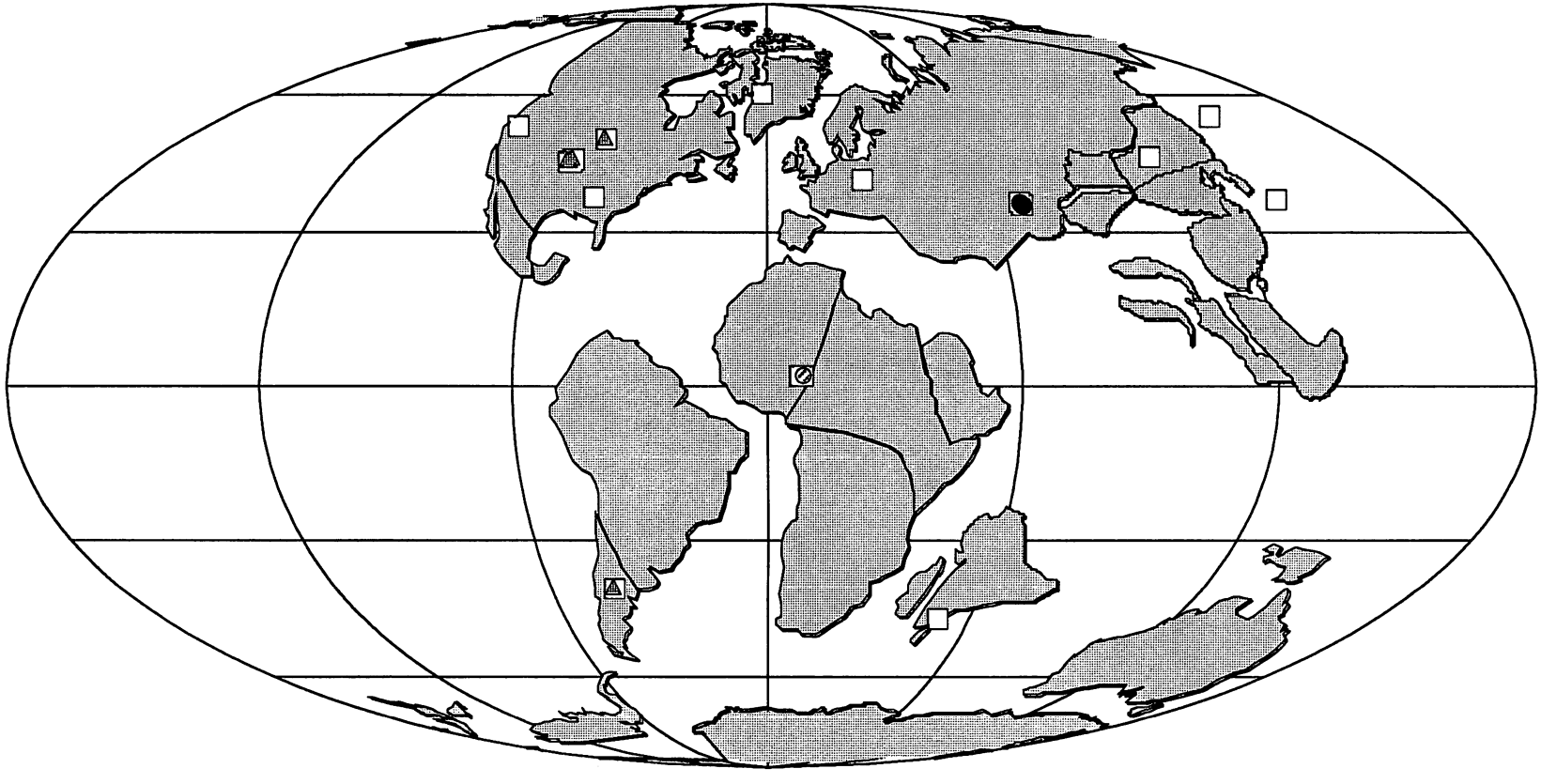


FIGURE V.29. Coniacian map (88 Ma).

See Figure V.24 caption for key and further details.

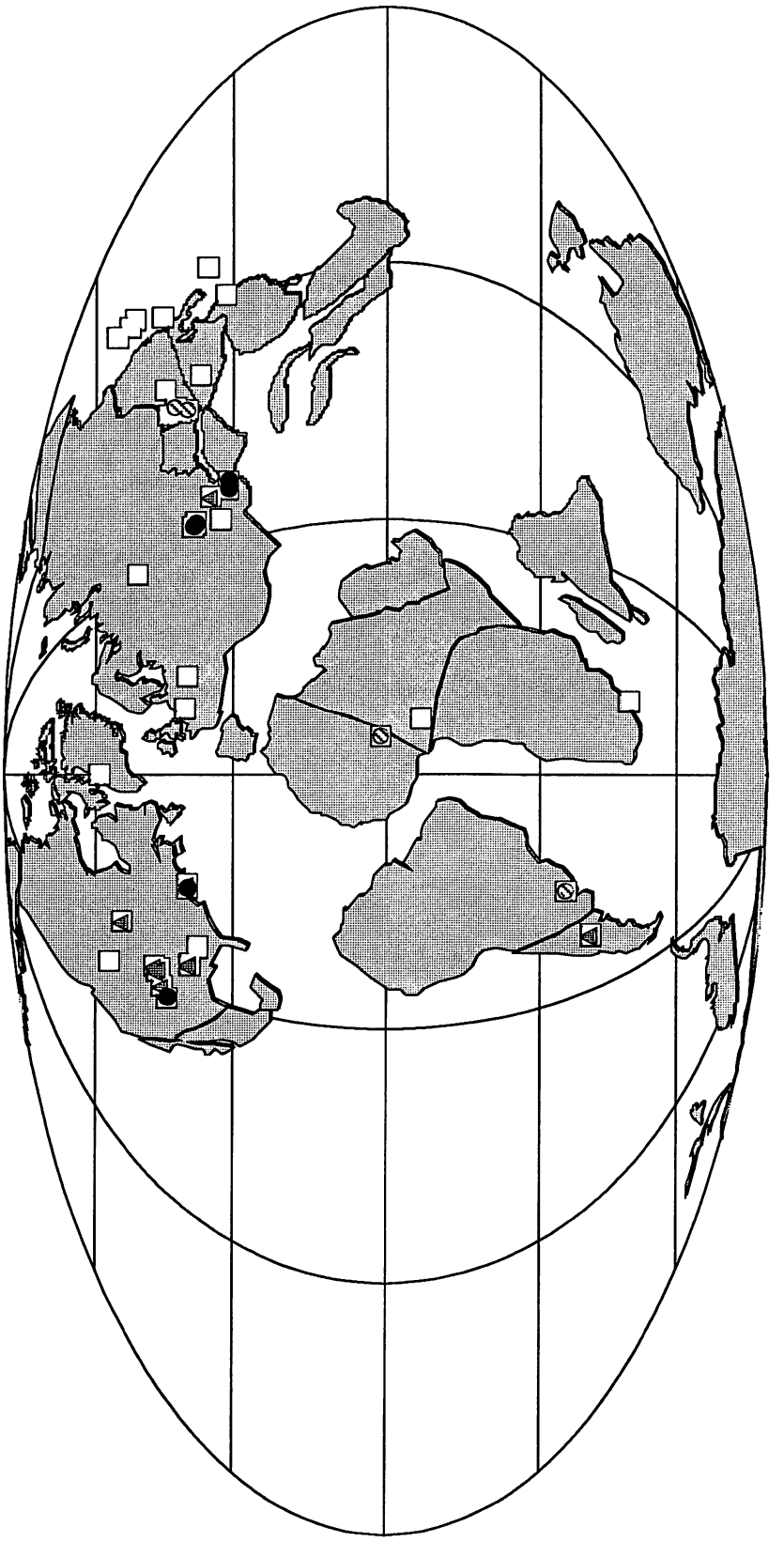


FIGURE V.30. Santonian map (85 Ma).

See Figure V.24 caption for key and further details.

As the crown group crocodilians diversify through the Late Cretaceous (Markwick, 1993; see also Chapter VII), their spatial distribution also expands, such that by the Santonian (Figure V.30) they are well distributed throughout the northern hemisphere. However, occurrences in the southern hemisphere are dominantly represented by "mesosuchians" or indeterminate crocodilians. The only exceptions to this are in central India where poorly resolved occurrences result in the representation of crocodylids near Nagpur (Sahni et al., 1984). These are shown on Figure V.28. Ignoring these occurrences, crown group crocodilians do not extend into the southern hemisphere until the Paleocene.

The limited distribution of crown-group crocodilians prior to the Campanian means that paleoclimate inferences at these times must rely on other proxies, which thankfully are readily available (Frakes, 1979; Spicer and Corfield, 1992; Vakhrameev, 1991). The significance of this for paleoclimate inferences has already been discussed above. By the Campanian, however, it seems that crown group crocodilians are well ensconced and, allowing for collection and taphonomic biases, the distribution shown is the full distribution possible given the climate. This distribution depends largely on the position of seaways through this interval; indeed the northernmost localities through this time are closely tied to the western Interior Seaway of North America (Figure V.31-V.32). Only the Mongolian and northern Chinese localities appear landlocked, where the development of caliches during the middle Campanian (Djadokhta Formation, e.g., at sites such as Bayn Dzak) suggests increasing aridity during this time (Jerzykiewicz and Russell, 1991). However, these localities are dominated by non-crown group crocodilians. This pattern continues into the Maastrichtian.

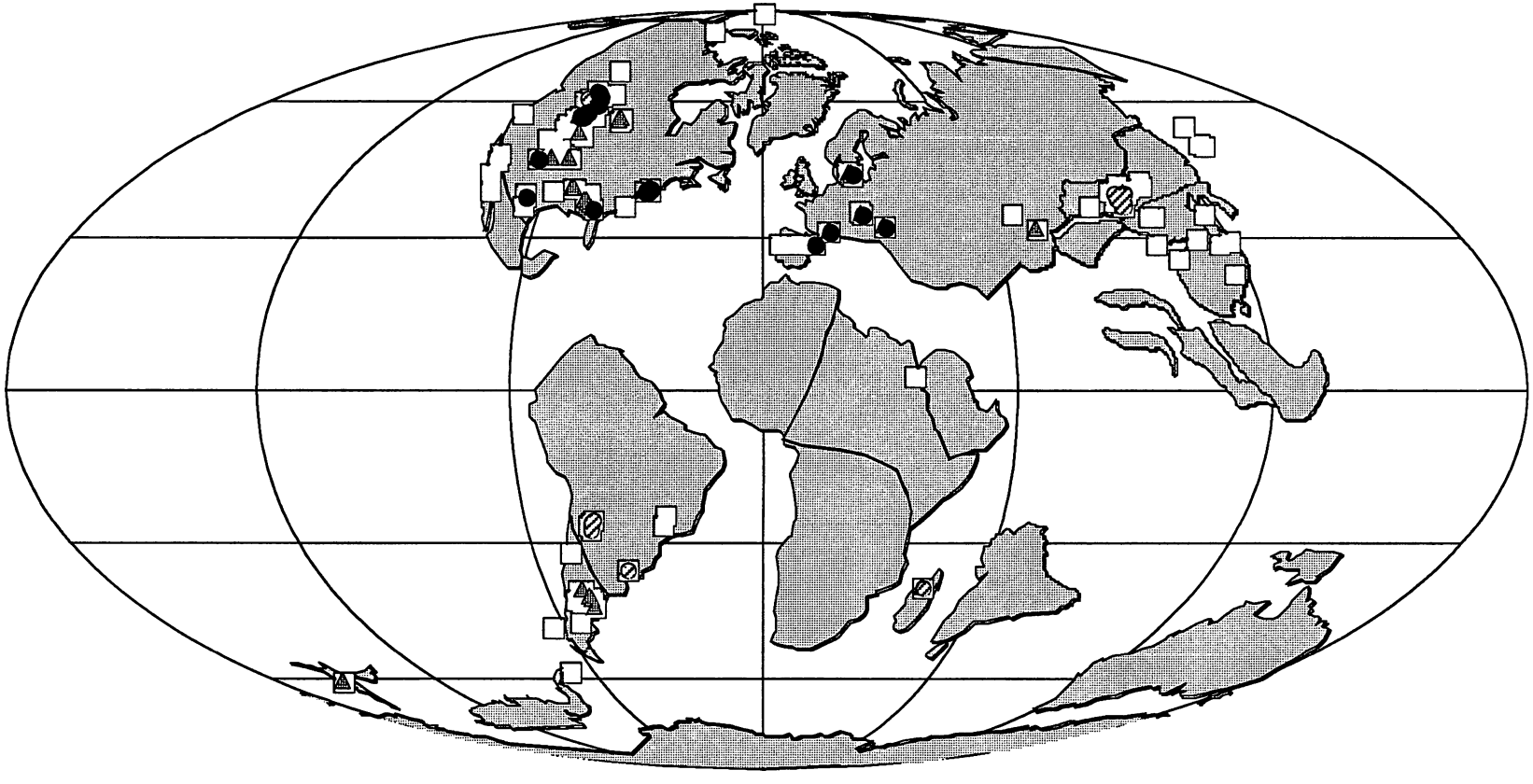


FIGURE V.31. Campanian map (78 Ma).

See Figure V.24 caption for key and further details.

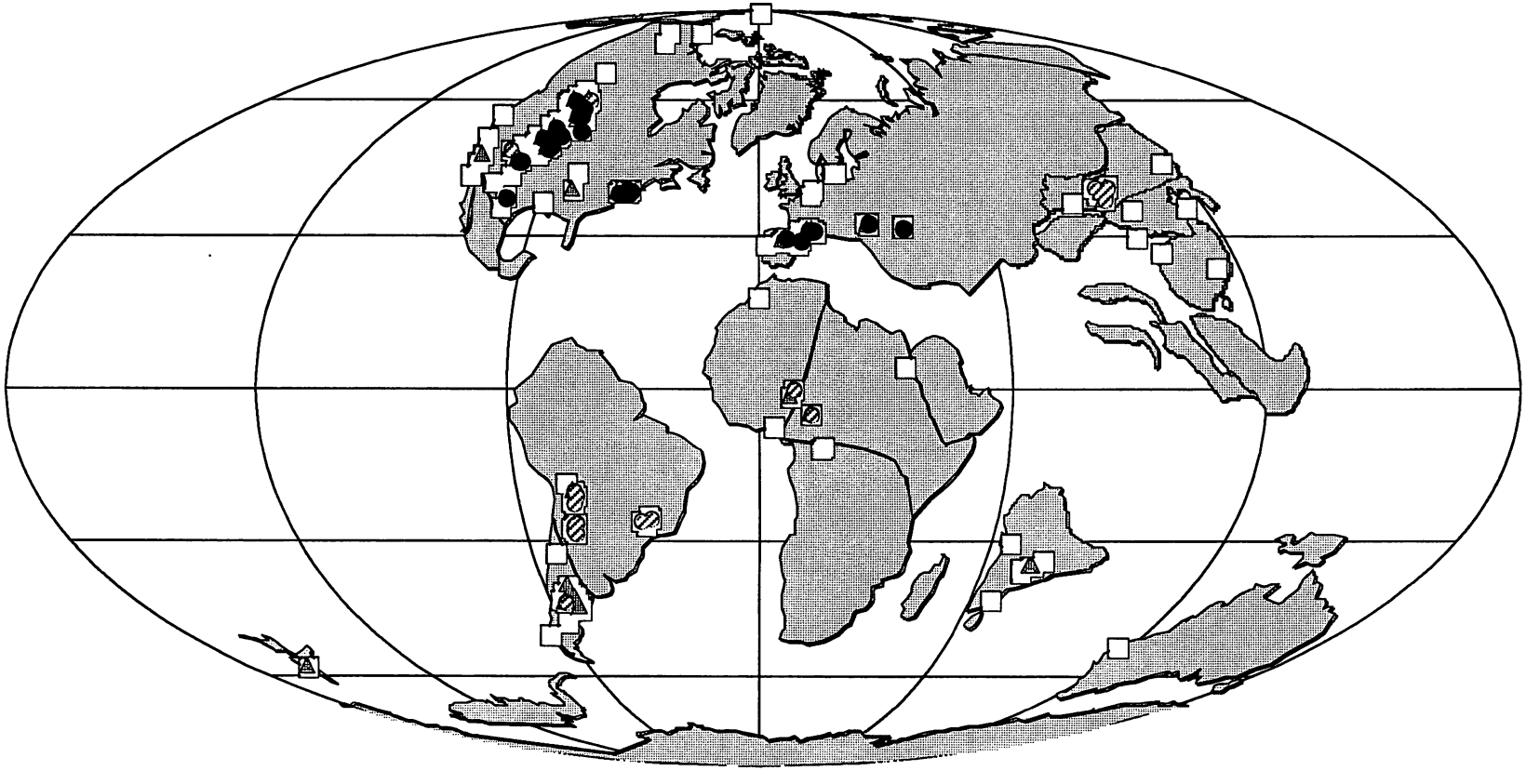


FIGURE V.32. Maastrichtian map (70 Ma).

See Figure V.24 caption for key and further details.

In North America, the paleoclimate implied by the distribution of crocodilians is consistent with the floral interpretations of Wolfe and Upchurch (1987; Upchurch and Wolfe, 1993) using foliar physiognomy, with megathermal climates extending to about 40°-50°N paleolatitude and mesothermal conditions as far as about 60° . From Figure IV.8 modern crocodilians only occur in meso- and mega-thermal climate regions (compare with figures V.27-V.32).

V.6.2. Tertiary

With the Paleocene, crown-group crocodilians become more widespread, with occurrences in South America, India and Australia, but apparently not in either Antarctica or Africa (neither of which have a good fossil record at this time). They also extend into eastern Asia. It is tempting to see this as reflecting some response to extinctions at the K-T boundary, which include the extinction of many "mesosuchian" groups (see Chapter VII). Nonetheless if all crown group occurrences represent the climate space defined by extant representatives, it is clear that the climate of both hemispheres was typified by much warmer temperatures during this time. Indeed, the present relationships suggest that during the Paleocene MAT's from Patagonia in the south (≈50°) to Alberta and Saskatchewan in the north (≈60°N) lay above at least 14.2 °C, with a 95% probability that they lay above 18 °C. This is consistent with the flatter thermal gradients shown for this interval in Figure V.23. In almost all of these cases, faunas are associated with the distribution of marine seaways and embayments. Again, exceptions to this lie in northern China and Mongolia, suggesting that the continental interiors too were relatively moderate.

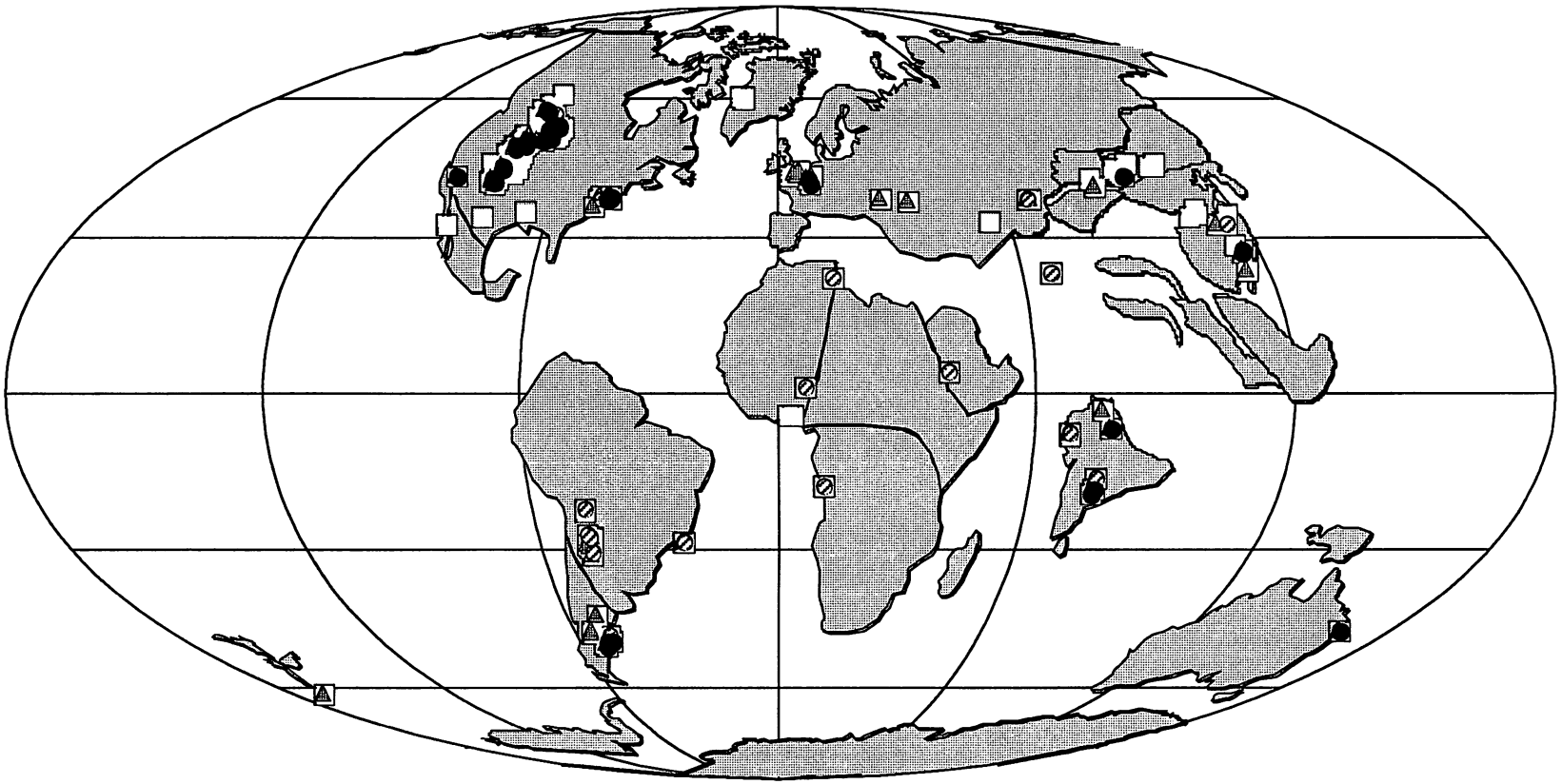


FIGURE V.33. Paleocene map (59 Ma).

See Figure V.24 caption for key and further details.

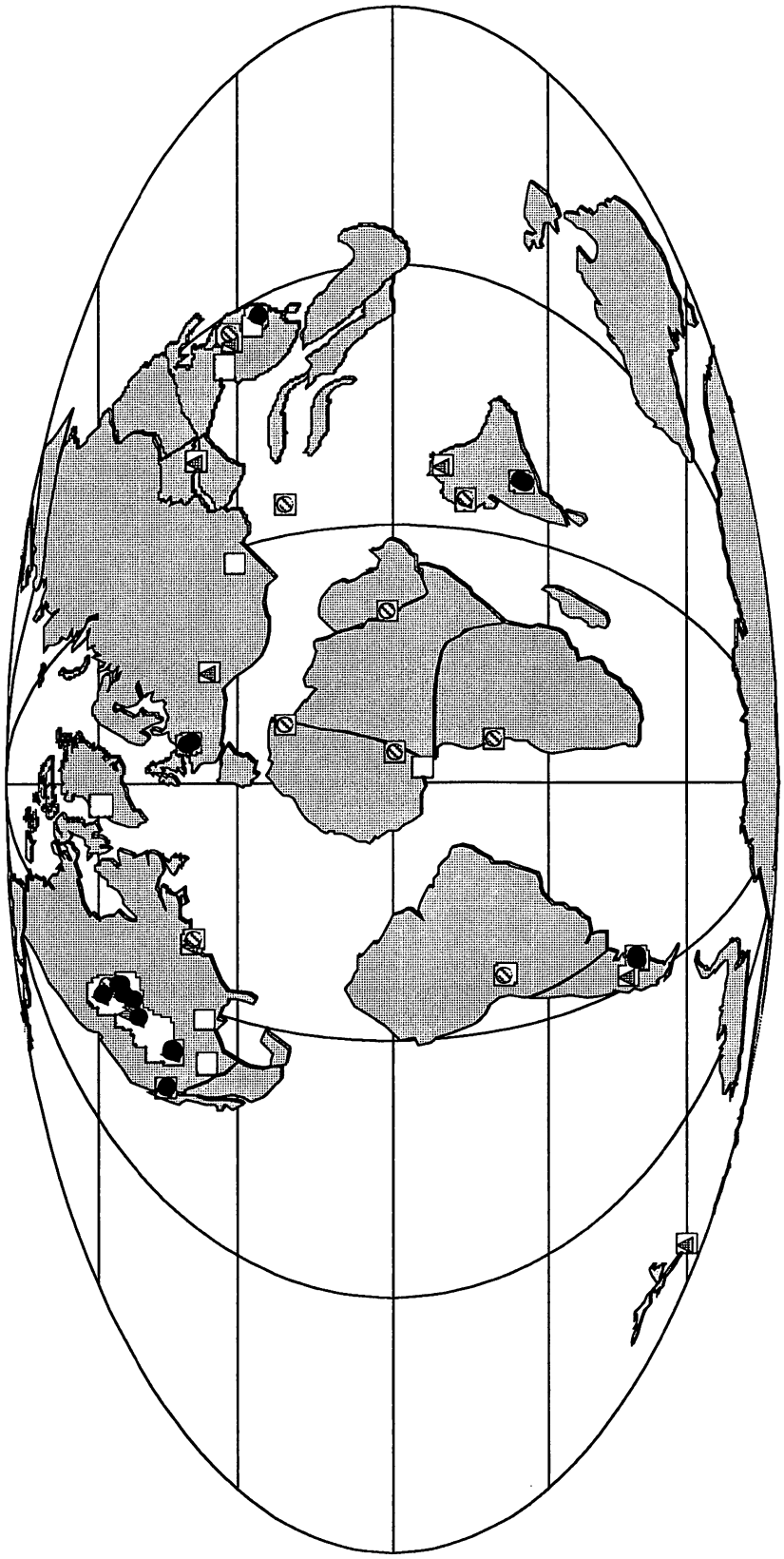


FIGURE V.34. Early Paleocene (Danian) map (63 Ma).

See Figure V.24 caption for key and further details.

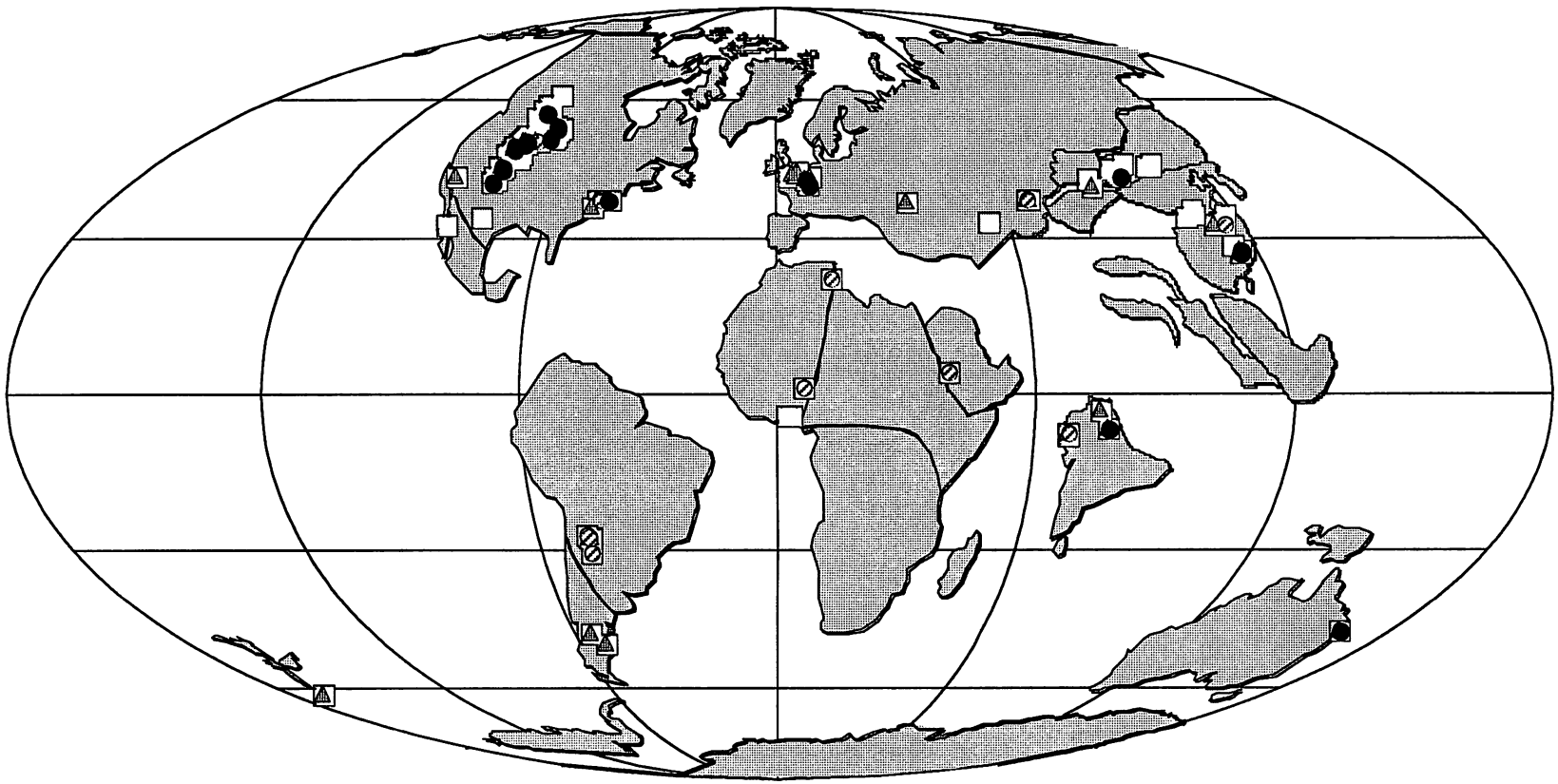


FIGURE V.35. Late Paleocene (Thanetian) map (59 Ma).

See Figure V.24 caption for key and further details.

The Eocene record differs little from that of the Paleocene except that it appears far more complete (Figure V.36). Crown-group crocodilians are well represented throughout the northern continents south of 60°, although as found for the Late Cretaceous and Paleocene, the northern limit of crocodilians is dictated by the limits of the record so that the true poleward extent is unresolvable. However, in the Early Eocene the Ellesmere Island fauna, which includes crocodilians and giant tortoises (Estes and Hutchison, 1980), suggests that warm temperate to tropical climates ("Mesothermal" of Wolfe and Upchurch, 1987) occurred in the Arctic, although such climates may not have extended into the central parts of continental interiors in Canada (Canadian Shield). Unfortunately, conclusions on this area are precluded by the lack of data. In Eurasia crocodilians extend northward into southern Britain and the Lake Zaysan area of eastern Kazakhstan. This interval represents a climate optimum for most workers (Wing and Greenwood, 1993; Wing and Sues, 1992).

An important difference between the Paleocene and the Eocene is that by the latter the interior seaways of the northern Hemisphere have largely disappeared (totally in North America), and therefore do not play a major role in determining the distribution of warm climates and crown group crocodilians. This is not only true in North America, where it has been discussed at length (Markwick, 1994b; Sloan and Barron, 1990, 1992; Wing and Greenwood, 1993; Wolfe, 1994), but also in central and eastern Asia (Kazakhstan through to China). This climatic regime during the early Paleogene is fundamentally different from that of the present day in which continental interiors undergo extreme thermal seasonality with very cold winters and hot summers. As documented by Markwick (1994b), it is the climatic evolution of these continental interior climates through the Tertiary that may provides us with the best guide to the nature of dynamical changes through this period.

Although by the Late Eocene the distribution of crocodilians has become more sparse, the overall latitudinal range appears little changed from the Early Eocene. Crown group crocodilians are not represented in Argentina by this time, reflecting the impoverishment of the southern hemisphere vertebrate record for the Middle and Late Eocene. However, in North America, crocodilians are restricted to the eastern most Eocene outcrops of the west, being excluded from the Rocky Mountain region to which they do not return. In addition, crocodilians have disappeared from the west coast. In both cases it seems that this is not only a reflection of cooling, but also of increased aridity. This has been documented by numerous workers including Leckie and Cheel (1989) in the Cypress Hills area, Peterson and Abbott (1979) in California (based on paleosol evidence) and Roehler (1992) in the 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.

During the Paleogene, the Rocky Mountain region continues to subject to uplift. Thermal and hydrological changes may be in response to this change in topography. Consequently, the restriction of crocodilians to the Great Plains, Gulf and East coast during the Late Eocene, may partly reflect a local rather than global climate change, with the elevaton of the area reaching the threshold for crocodilian survival (MAT $\geq$14.2°C) as temperatures change with altitude.

Globally, this is the time at which there is the first clear evidence of glaciation on Antarctica (Barrett, 1986; Barron et al., 1991; Birkenmajer et al., 1989; Ehrmann, 1991; Hambrey et al., 1991; Hambrey et al., 1989; Mackensen and Ehrmann, 1992), although evidence for earlier ice has been described (Birkenmajer, 1987; Geitzenauer et al., 1968). It is probable that this is the cause of, or at the least related to, the changes observed in the

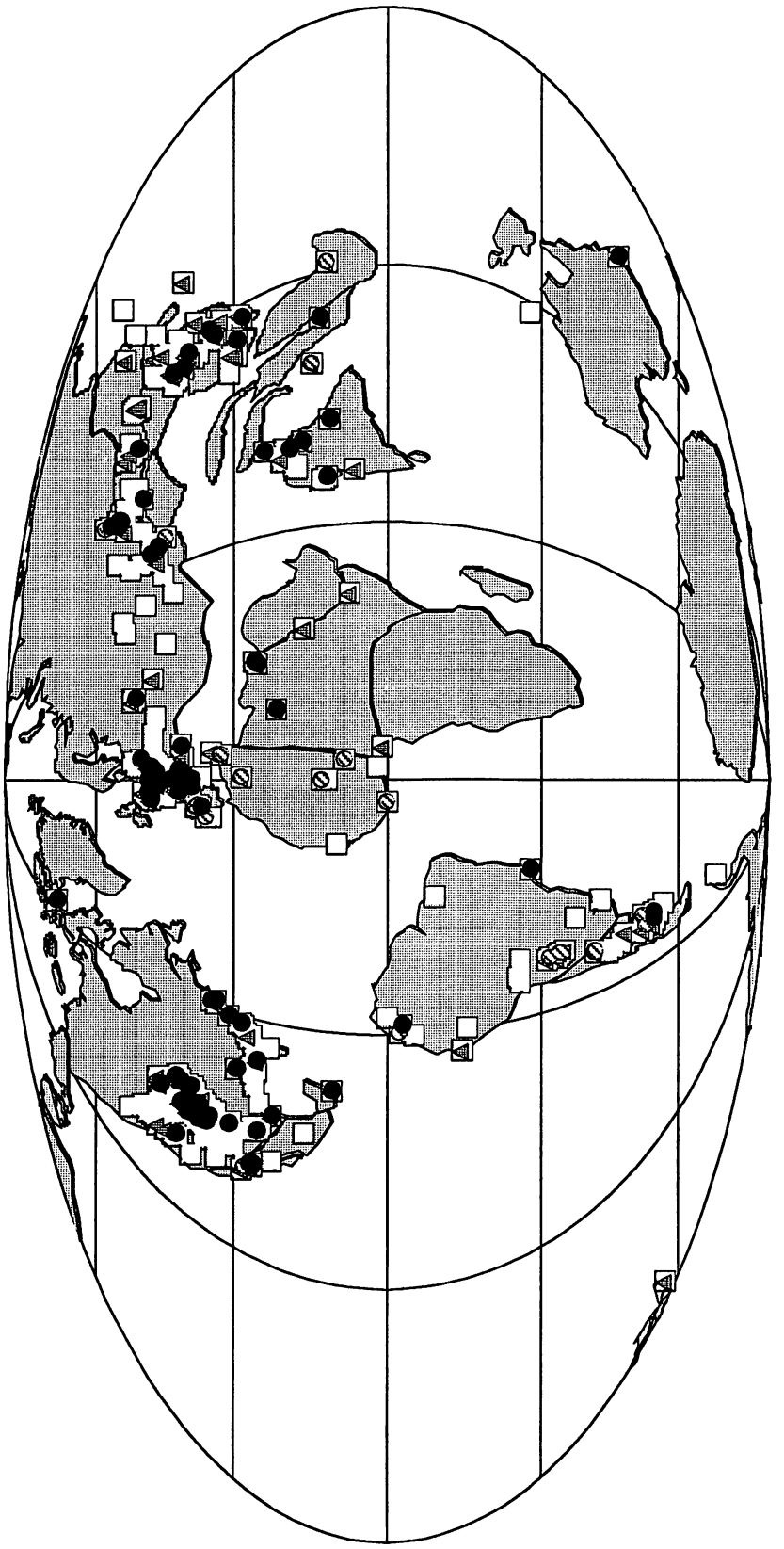


FIGURE V.36. Eocene map (46 Ma).

See Figure V.24 caption for key and further details.

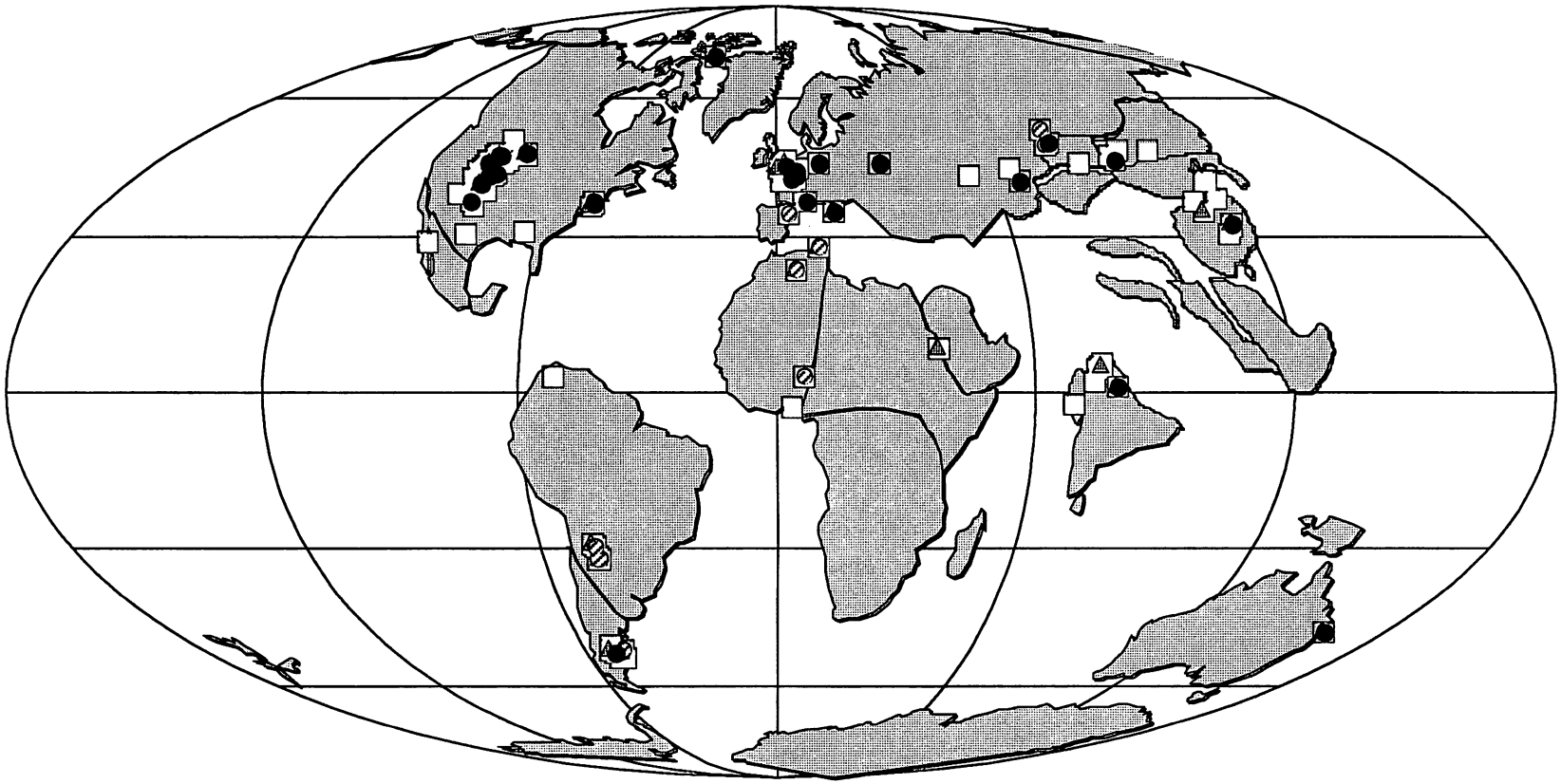


FIGURE V.37. Early Eocene map (55 Ma).

See Figure V.24 caption for key and further details.

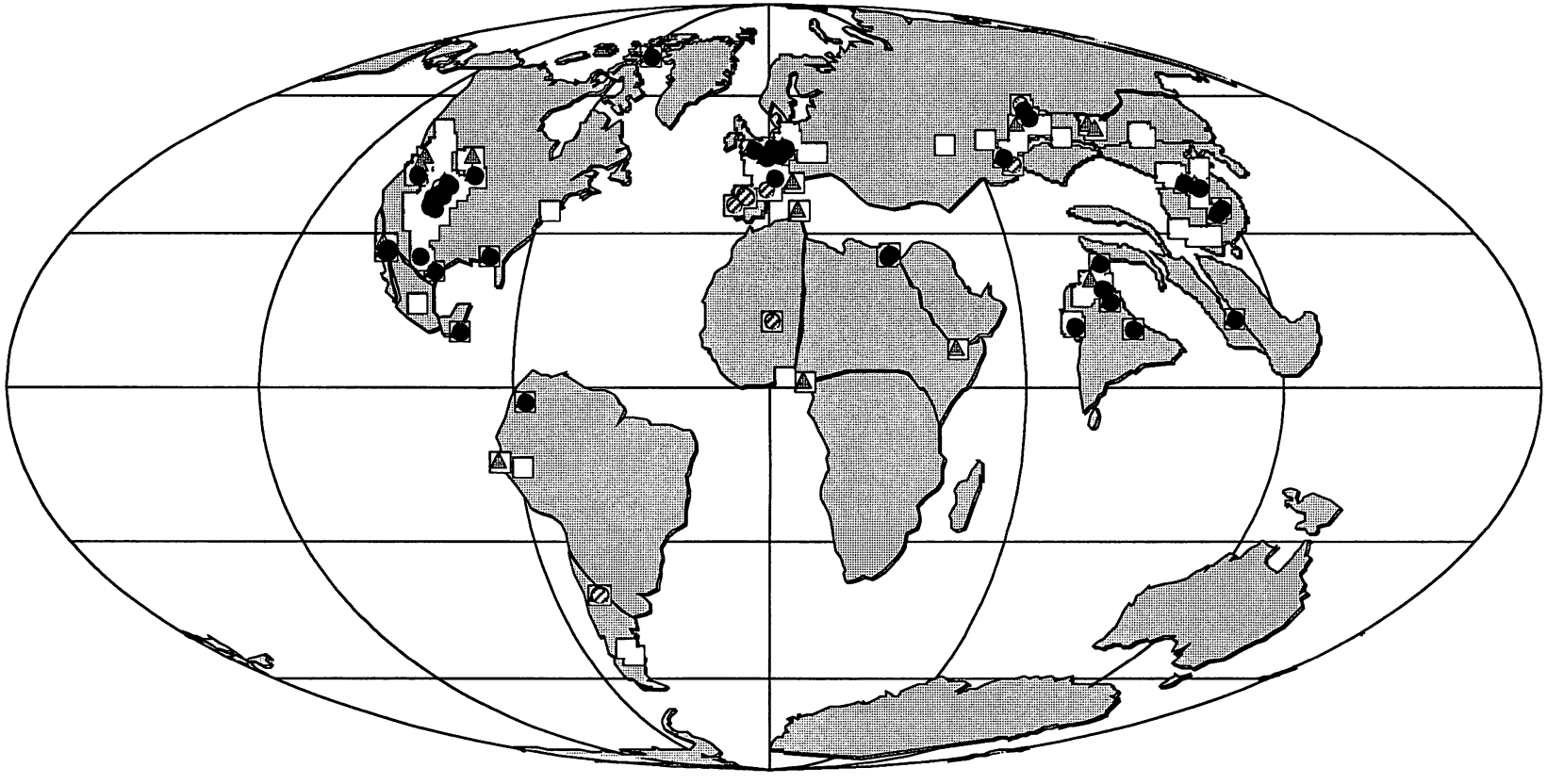


FIGURE V.38. Middle Eocene map (46 Ma).

See Figure V.24 caption for key and further details.

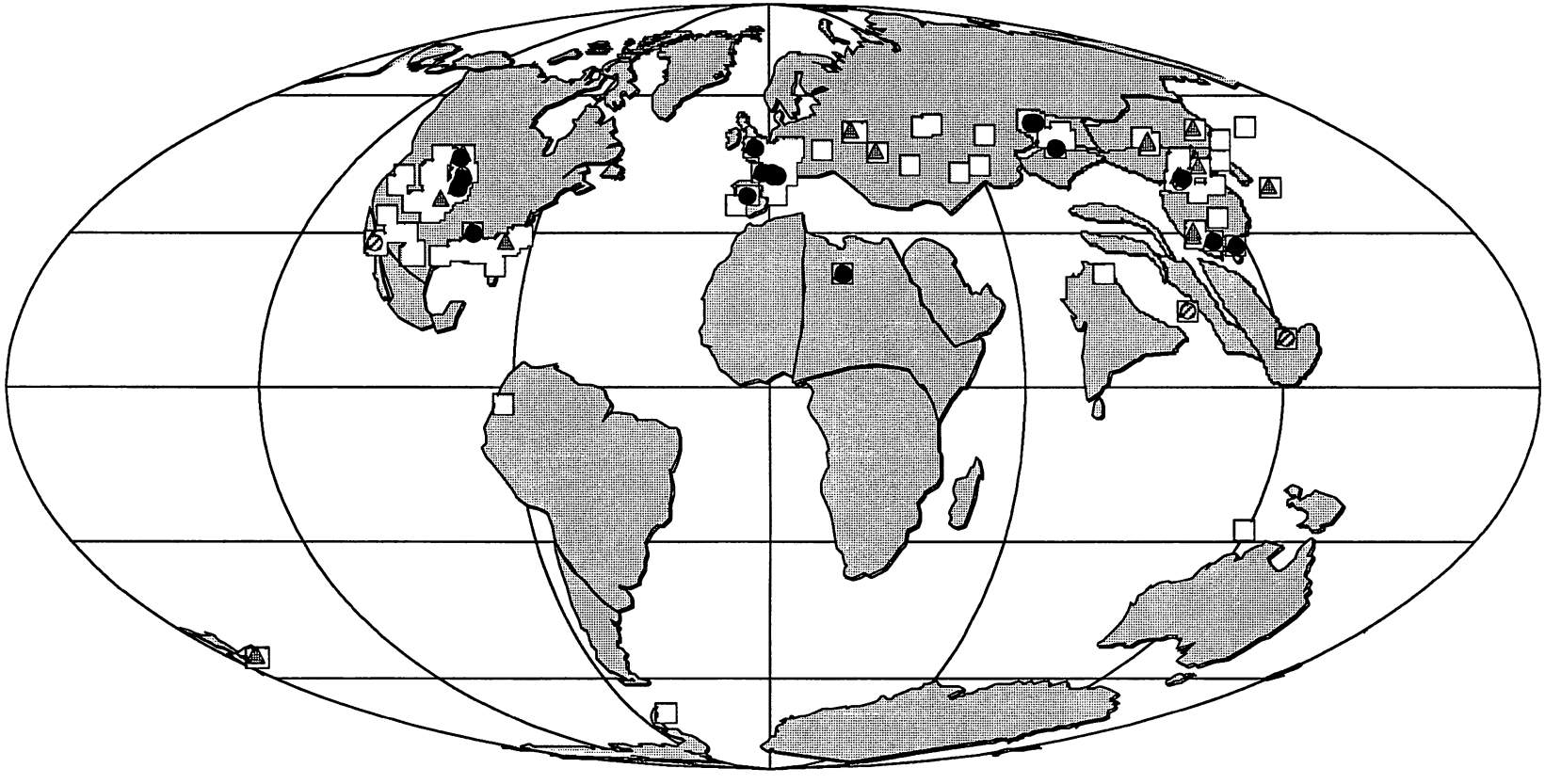


FIGURE V.39. Late Eocene map (38 Ma).

See Figure V.24 caption for key and further details.

ocean record as revealed by the sedimentary record of hiatuses (Keller et al., 1987; Miller et al., 1993), and especially the oxygen isotopic record (Barrera and Huber, 1991; Mackensen and Ehrmann, 1992; Miller, 1992; Miller and Fairbanks, 1985; Miller et al., 1987; Prentice and Matthews, 1988; see also Figure II.8). It seems probable that these oceanographic changes influenced upwelling systems and thereby coastal climates in western USA and South America, 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 record in the Early Oligocene and only coastal occurrences in the Late Oligocene, Markwick, 1994b), 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 Miocene (Figure V.45; Kintykche, central Priaral'e, Kazakhstan, Efimov, 1988). As indicated by the distribution of other vertebrates and turtles through this period, it is clear that this absence is not simply an artifact of collection or taphonomic bias. In contrast, an Australian record develops at this time.

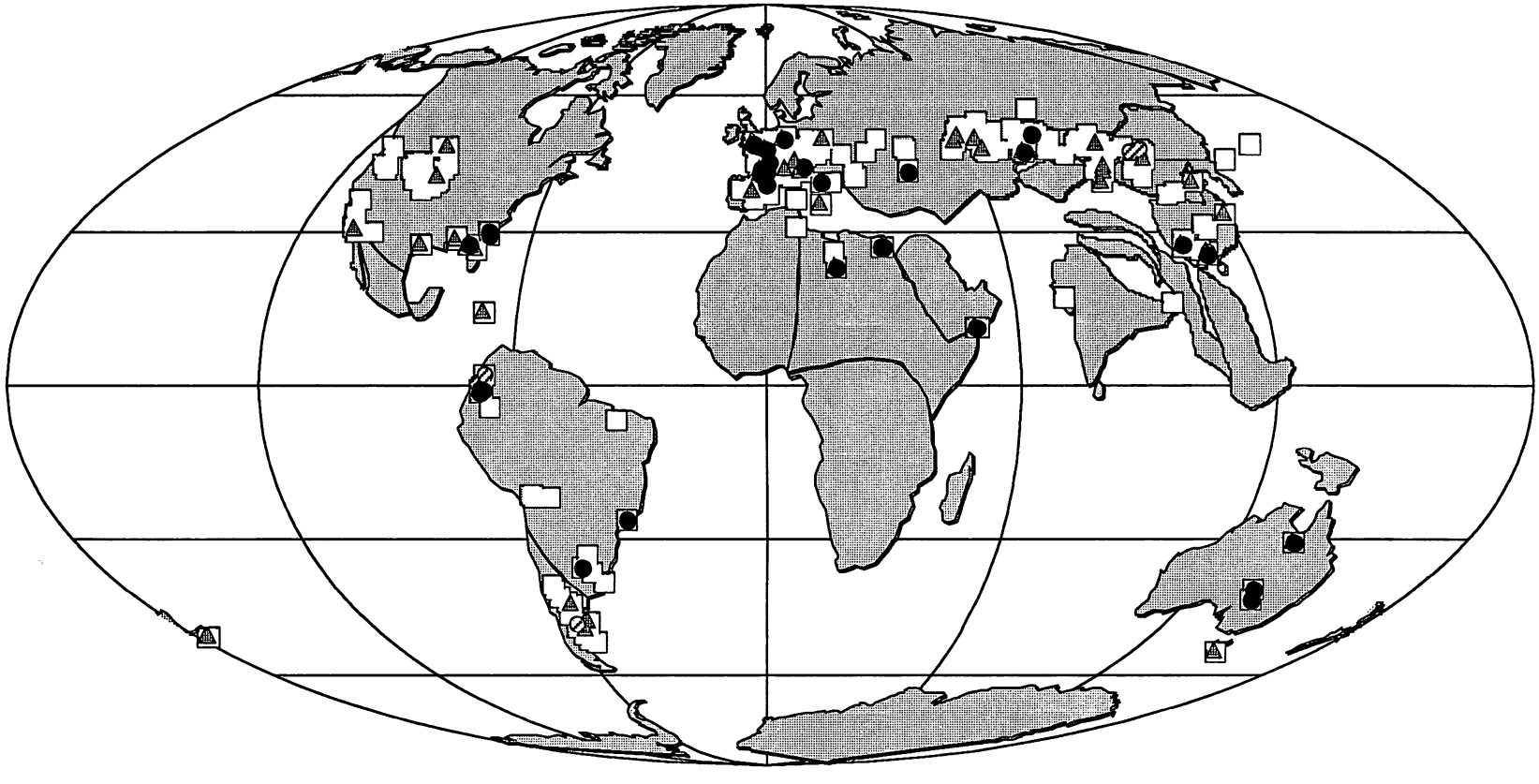


FIGURE V.40. Oligocene map (26 Ma).

See Figure V.24 caption for key and further details.

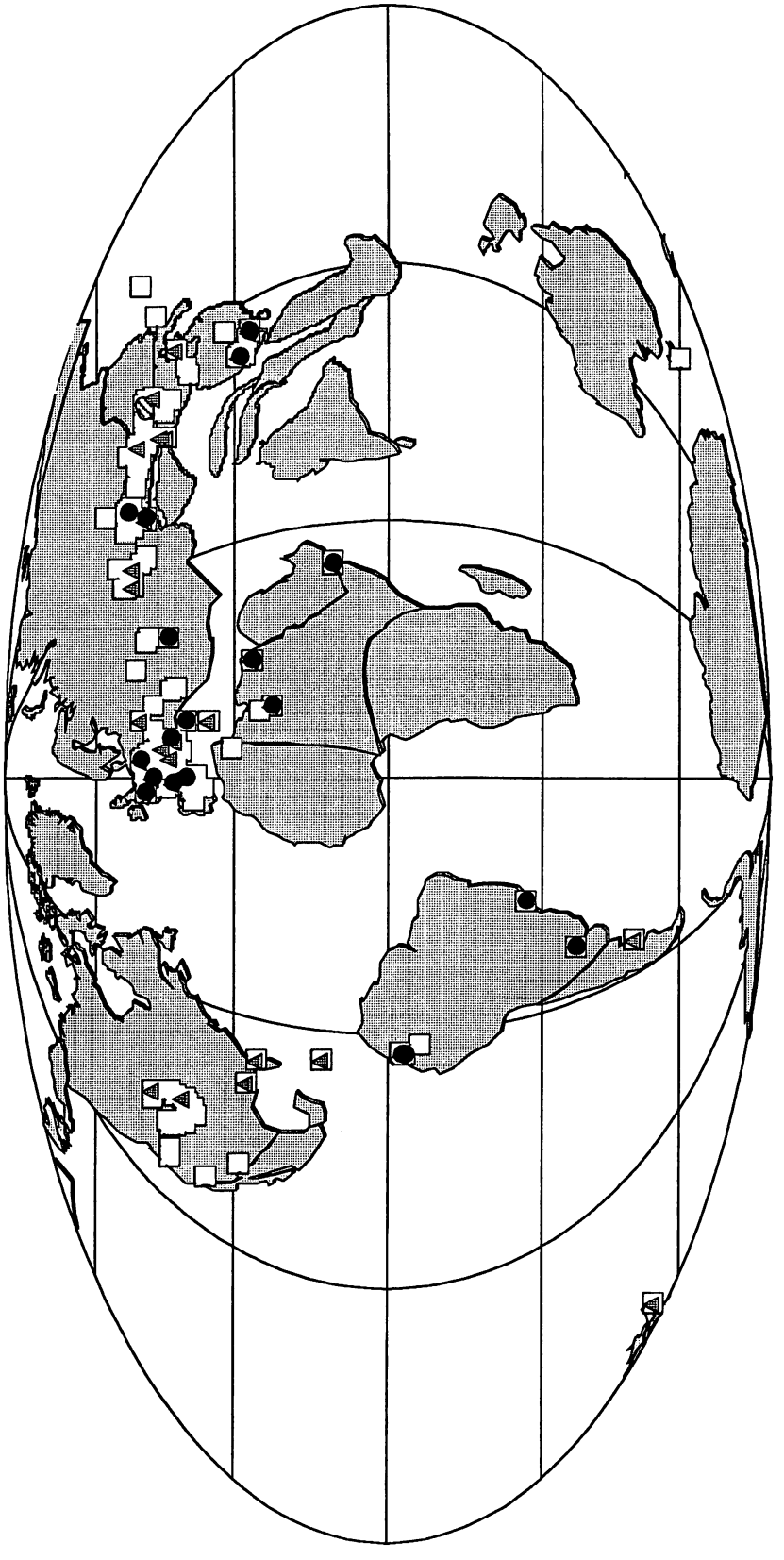


FIGURE V.41. Early Oligocene map (33 Ma).

See Figure V.24 caption for key and further details.

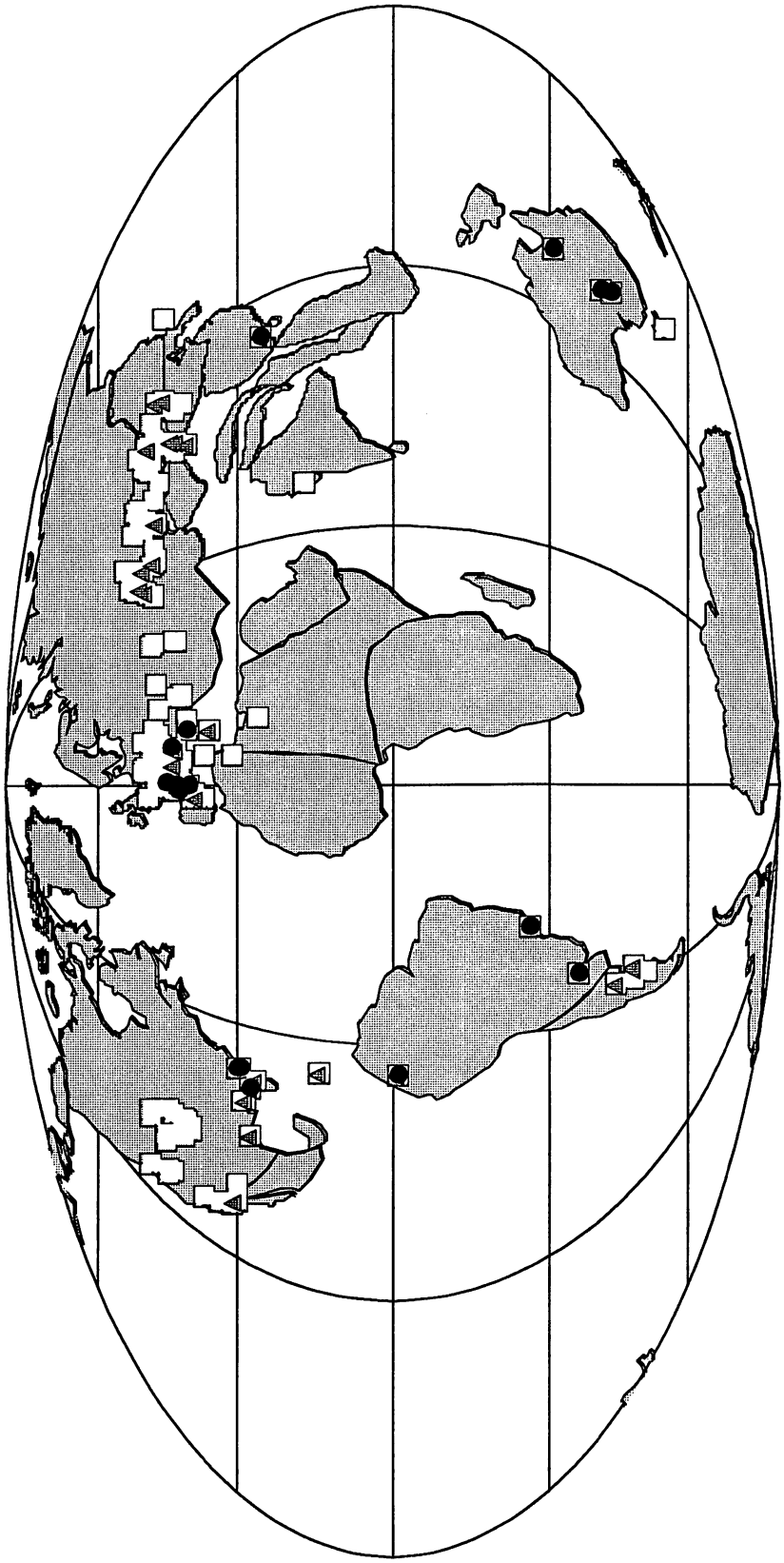


FIGURE V.42. Late Oligocene map (26 Ma).

See Figure V.24 caption for key and further details.

With the Miocene, crocodilians return to the Great Plains of North America and extend south into southern Africa.

During the Late Miocene and Pliocene the climate changes again with a trend towards increased aridity 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, 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.

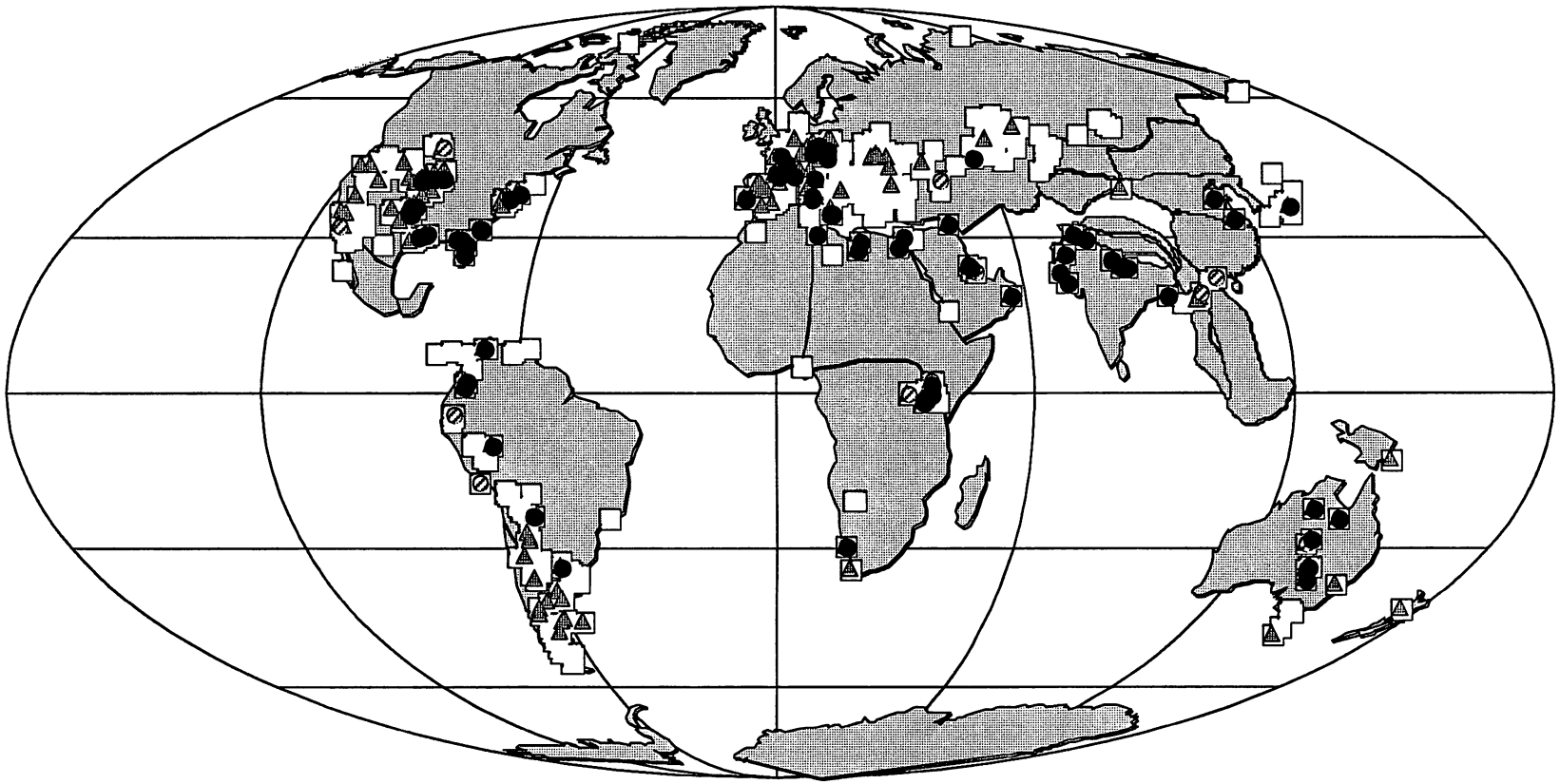


FIGURE V.43. Miocene map (10 Ma).

See Figure V.24 caption for key and further details.

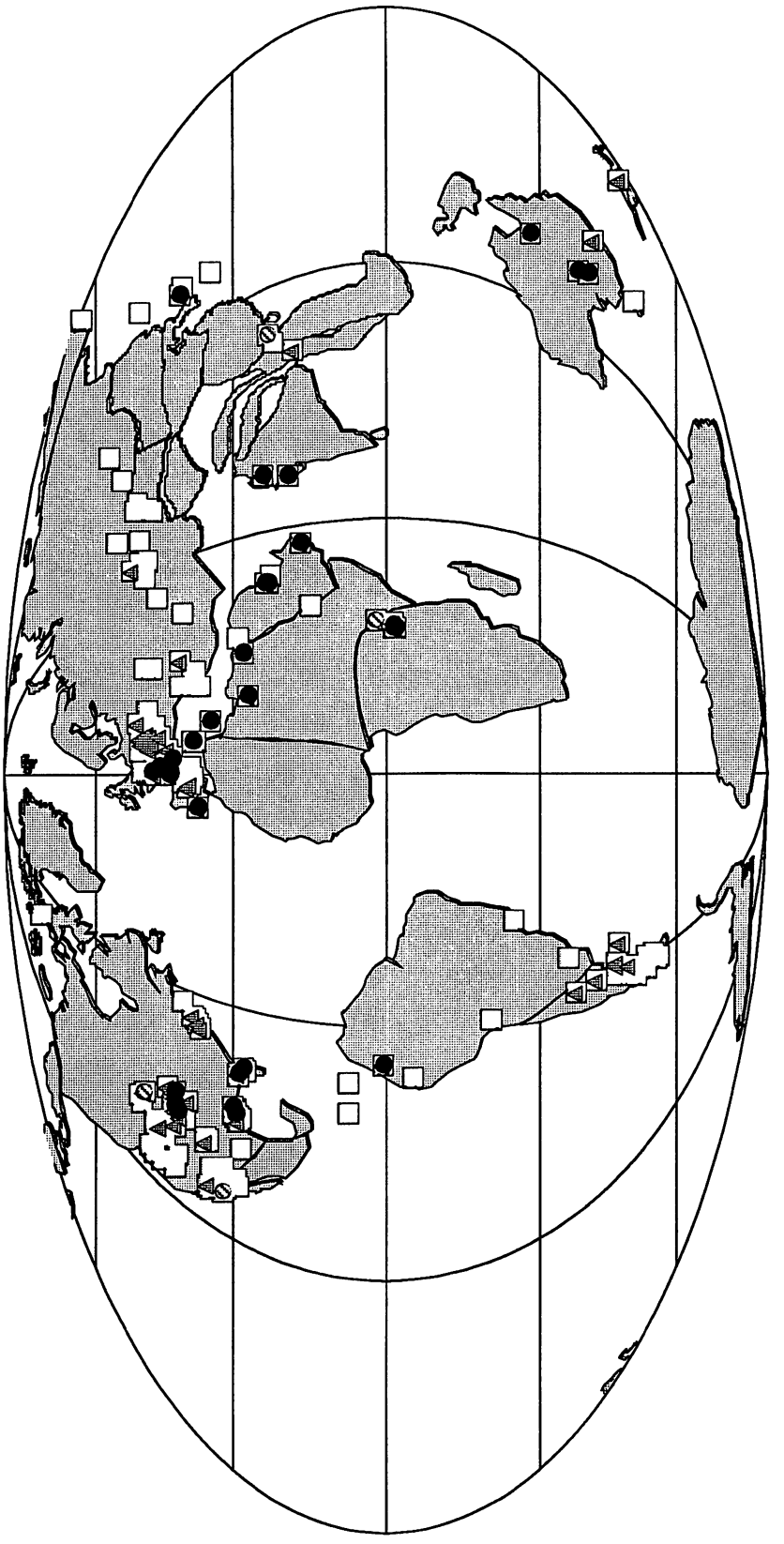


FIGURE V.44. Early Miocene map (20 Ma).

See Figure V.24 caption for key and further details.

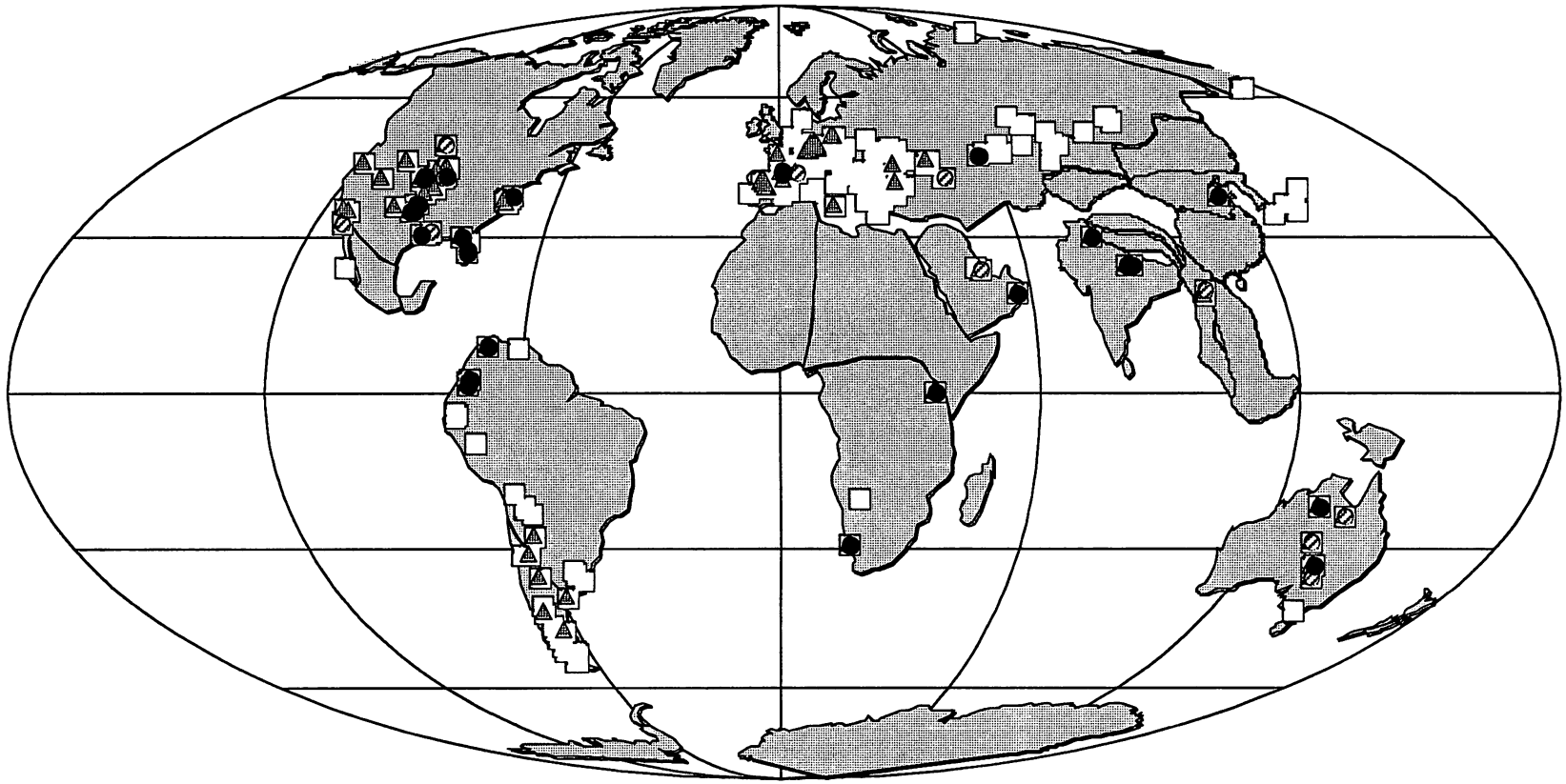


FIGURE V.45. Middle Miocene map (10 Ma).

See Figure V.24 caption for key and further details.

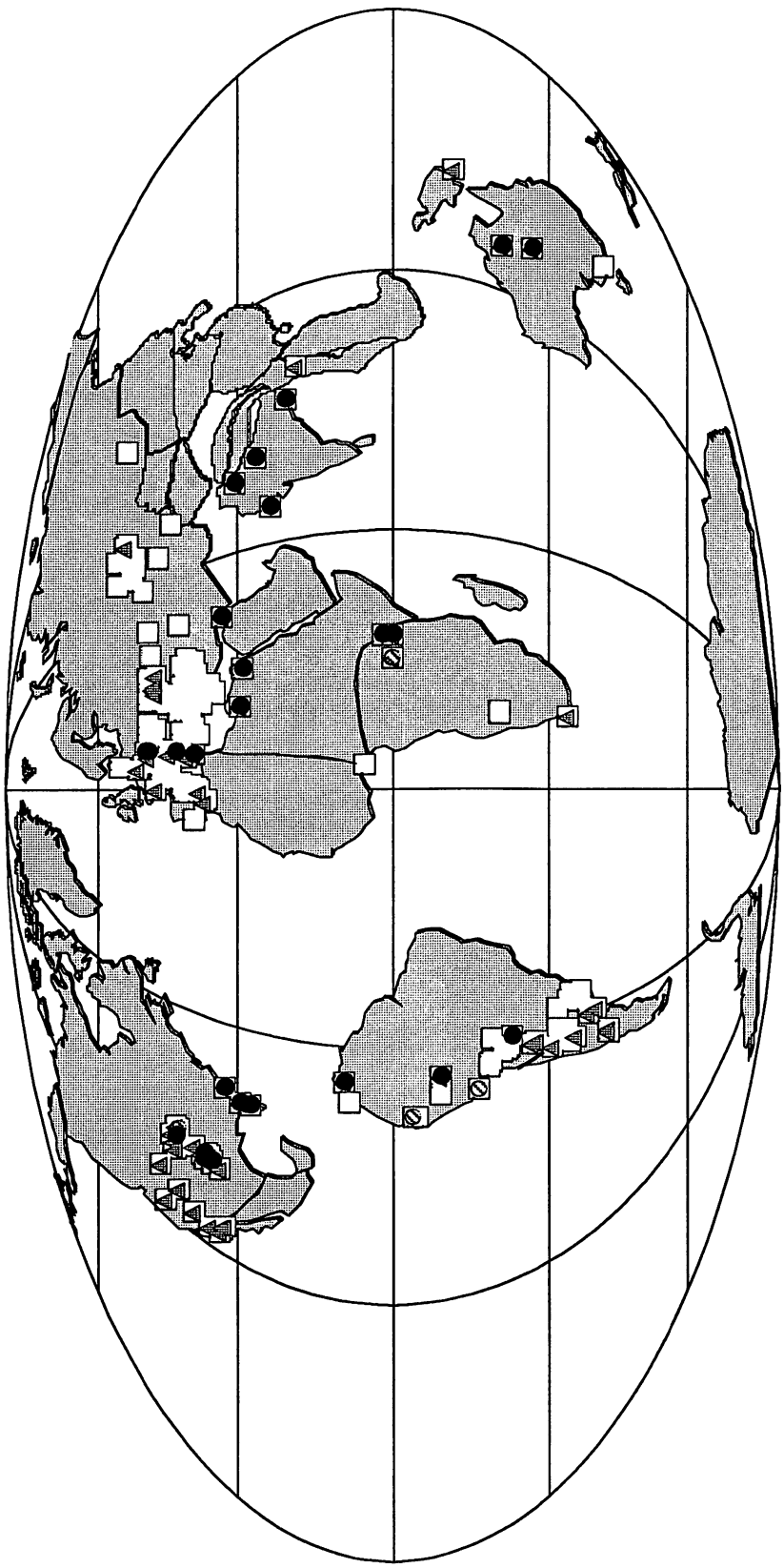


FIGURE V.46. Late Miocene map (8 Ma).

See Figure V.24 caption for key and further details.

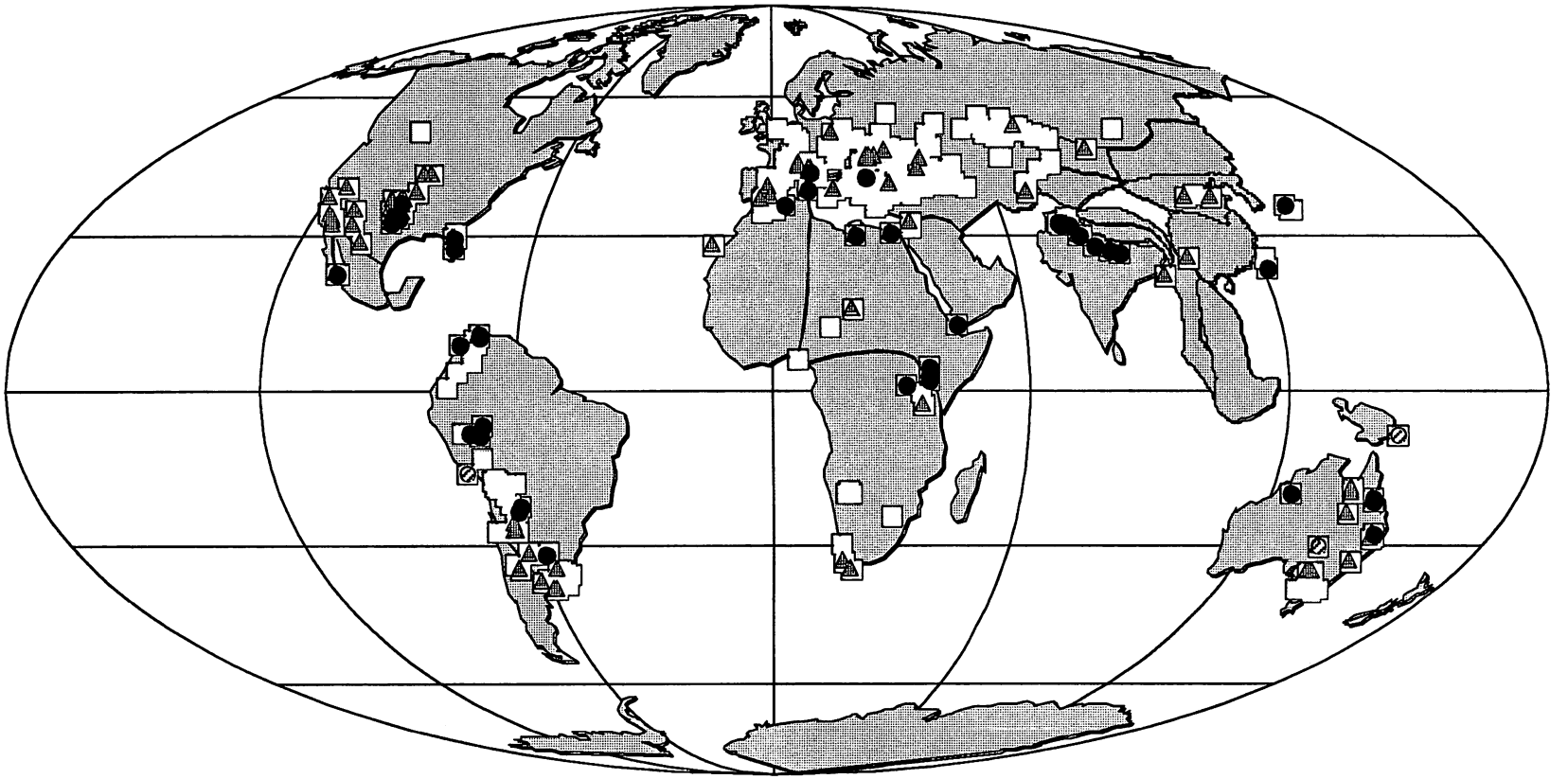


FIGURE V.47. Pliocene map (3 ma).

See Figure V.24 caption for key and further details.

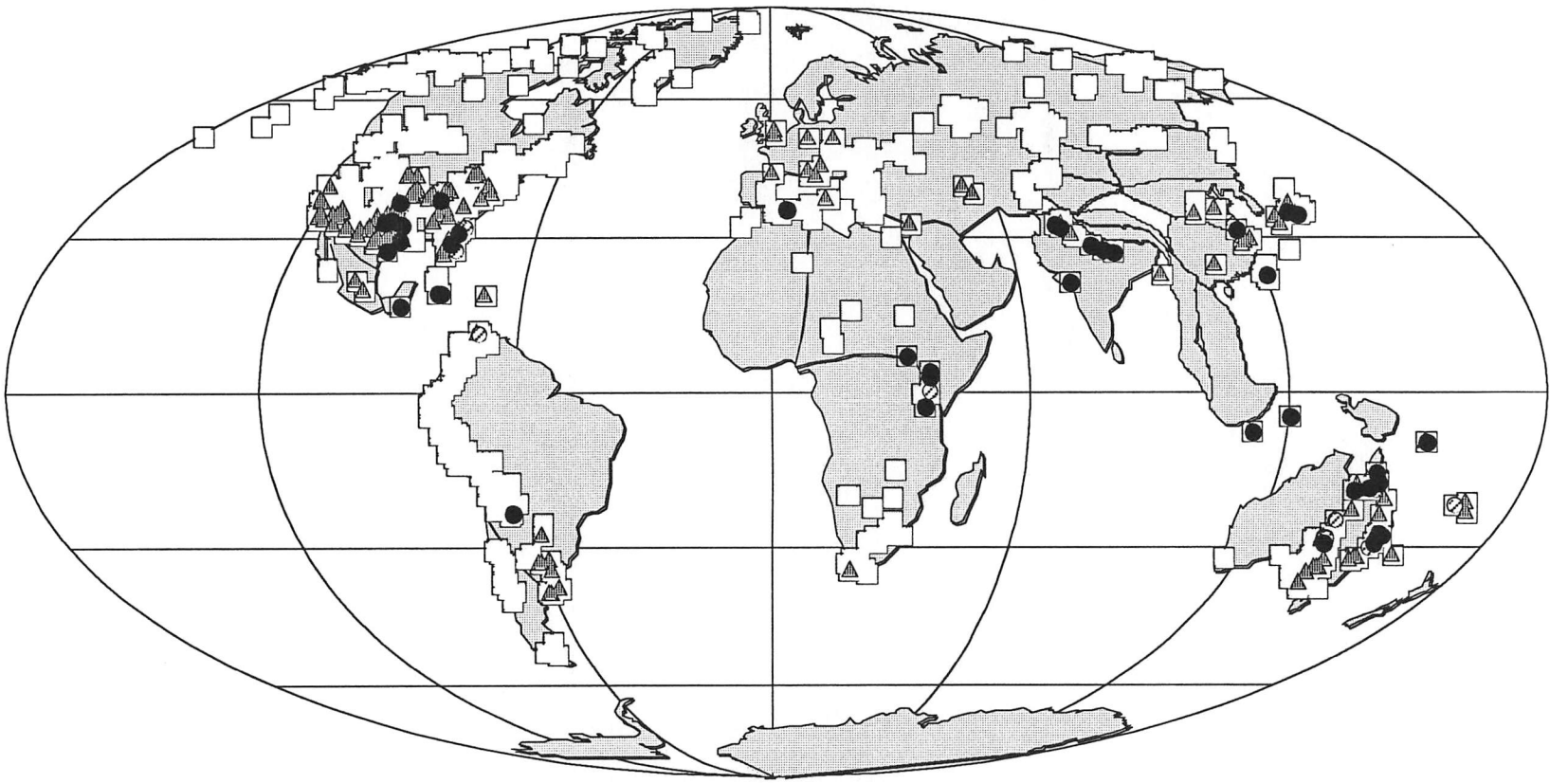


FIGURE V.48. Pleistocene map (0 Ma).

See Figure V.24 caption for key and further details.

V.6.3. 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 (Figure V.48). As observed in the Pliocene, crocodilians are restricted to low latitudes 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 aridity has also been suggested as the cause of extinctions in Australia towards the late Pleistocene (Lundelius, 1983). This seems borne out by the distribution of Australian crocodilians which disappear from the continental interior about this time, retreating northward along rivers that no longer reach South Australia (compare Figure V.48 with Figure IV.1).

V.7. CONCLUSIONS

The distribution of fossil crocodilians provides one means of reconstructing the pattern of paleoclimate, based on analogy with the climate space occupied by their extant relatives (Chapter IV). But, the geological record is not an impartial witness of the past. Consequently, the nature of the geological data must be considered before paleoclimatic conclusions are drawn. While presences are unequivocal, absences are not. In this chapter, control groups are used to control for the effects of collection and taphonomic biases and thereby qualify significant absences of fossil crocodilians; absences do not specify an absolute temperature limit; however, they may imply the proximity of crocodilian thermal bounds. This can be tested using the interpretation of paleohydrological conditions at a

locality where fossil crocodilians are absent. The presence of caliches, for instance, might suggest arid conditions (Gyllenhaal, 1991) that might preclude permanent bodies of standing water and thereby crocodilians, without indicating MAT's of less than 14.2°C. While such relationships are suggestive, they are not conclusive. Corroboration of derived paleoclimate interpretations comes from comparisons with the inferences of other climate proxies.

In terms of paleoclimate history, the crocodilian dataset indicates two important trends: first, latitudinal ranges of crocodilians respond to climate such that during glacial ("ice-house") intervals ranges are compressed; second, during these intervals crocodilians are restricted to more maritime localities. This strongly implies a link between increased "continentality" (as expressed by seasonality and increased aridity) and "ice-house" climate regimes (cooler temperatures). During "hot-house" intervals, aridity and thermal seasonality in the mid-latitudes is reduced, as indicated by the expansion of crocodilians throughout these latitudes. This is consistent with previous observations that during "hot-house" periods, mid-latitudes become the locus of high productivity. In North America especially, some of these observed changes in the distribution of crocodilians may reflect local changes in temperature and hydrology due to uplift. Such elevation effects are superimposed upon the signal of global climate change.

Embedded within these patterns of the climate proxy are paleobiogeographic histories: the preclusion of the predominantly freshwater alligatorids and gavialids from Australia and Africa, and the Mesozoic restriction of crown group crocodilians to the northern hemisphere, expanding south only after the K-T boundary. The utility of the dataset employed in this study is that such issues can be readily addressed, issues that at first glance may not appear to impinge on paleoclimate, but can, in fact, clearly affect the

significance of absences of the climate proxy--the reconstruction of paleoclimate is not simply a question of plotting the distribution of the climate proxy.