

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 VII

# CROCODILIAN DIVERSITY: THE INFLUENCE OF CLIMATE

*"To the rational mind nothing is inexplicable, only unexplained"*

Tom Baker (Dr Who)  
"The Robots of Death", BBC 1977

### VII.1. INTRODUCTION

The spatial distribution of fossil crocodilians has frequently been used to reconstruct paleoclimate (Berg, 1965; Donn, 1987; Habicht, 1979; Lyell, 1837; Owen, 1851), but a detailed analysis of this climate proxy has not been forthcoming until now (see Chapter IV). Even fewer workers have looked at the overall diversity pattern of crocodilians (Benton, 1985), although the history of the group has been the subject of interest since the 19th century (Woodward, 1887)

The order Crocodylia (in the traditional sense of the term as used by Romer, 1971, and Carroll, 1988) originated in the middle Triassic and together with the birds comprises the surviving members of the Archosauria (a group that also includes the extinct dinosaurs). Recent cladistic hypotheses have attempted to restrict the term Crocodylia to the crown group represented by the extant families Alligatoridae, Crocodylidae and Gavialidae (Benton and Clark, 1988; Clark, 1986). Although this restriction is not adopted here, the paleoclimatic interpretations made in this chapter and Chapter IV are based only on the

fossil members of these three families. This is because they have extant relatives and therefore analogy with recent physiology can be made with more confidence. Throughout this study, I refer to members of these three families as "crown group crocodilians."

This chapter also examines the diversity of non-crown group crocodilians, although they are not used for reconstructing paleoclimate. This includes the diversity of the "Eusuchia," a group that traditionally includes all crocodilians with full secondary palates (palatines and pterygoids fused) and procoelus vertebrae, and which thereby includes all crown group crocodilians. The "Eusuchia" probably first appeared in the Late Jurassic (Steel, 1973), although little is known of them until the middle Cretaceous and an equivocal occurrence in New South Wales (Molnar, 1980); certainly they did not begin to diversify until the Late Cretaceous. The history of "eusuchians" is largely dominated by that of crown group crocodilians.

I have also included an analysis of the "Mesosuchia," which although probably paraphyletic (Benton and Clark, 1988), represents crocodilian groups linked by two principal characters, amphicoelous vertebrae and incomplete secondary palates (palatines fused, but not pterygoids). The overall body plan of the two groups is generally quite similar. In the recent cladistic hypothesis of Benton and Clark (1988), the "Mesosuchia" and "Eusuchia," together with the "Protosuchia," comprise the Crocodylomorpha.

The principal aim of this study is to examine the effect of global climate change on the overall diversity of crocodilians, especially the crown group families.<sup>1</sup> In Chapter V

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1. The effect of climate, and especially temperature, on determining the history of life has been considered since at least Lyell:

*"...and there would also, by the formation of new mountains and other changes, be transpositions of climate, contributing, in the manner alluded to, to the local*



and Markwick (1992) I have shown that the paleodistribution of crocodilians changes in concert with known global climate changes, and that these changes imply a link between glacial ("ice-house") periods and increased aridity and continentality, and non-glacial ("hot house") periods with thermally more equable continental interiors. The effect of this transition on the Paleogene amphibian and reptile faunas of the northwestern United States has already been discussed by Hutchison (1982, 1992). Markwick (1993) has presented the preliminary results of a global study, and it is the full results of this work that are presented here. In addition, the crocodilian dataset provides an opportunity to examine diversity trends across the Cretaceous-Tertiary (K-T) boundary; if crocodilians are sensitive to climate, as shown in Chapter IV, then a climatic cause for the K-T extinction should be readily apparent in the crocodilian record. Preliminary results suggest that this is not the case (Markwick, 1994).

## VII.2. THE DATASET

The dataset used in this study is the same as that used in the distributional analyses presented in Chapter V. The database described there and in Chapter III has been designed to facilitate diversity studies--occurrence records contained within the database are used to calculate automatically the temporal range of each taxon. This assumes that the database is comprehensive. A survey of the literature, and comparison with the temporal range data given by Romer (1971) and Carroll (1988), supports this assumption for crocodilians.

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*extermination of species...For if the doctrines explained by us in regard to vicissitudes of temperature are sound, it will follow that changes of equal magnitude in the geographical features of the globe, may at different periods produce very unequal effects on climate, and, so far as the existence of certain animals and plants depends on climate, the duration of species may often be shortened or protracted, according to the rate at which the change in temperature proceeded." (p.115, 139, Lyell, 1830)*

### VII.3. DIVERSITY PATTERNS

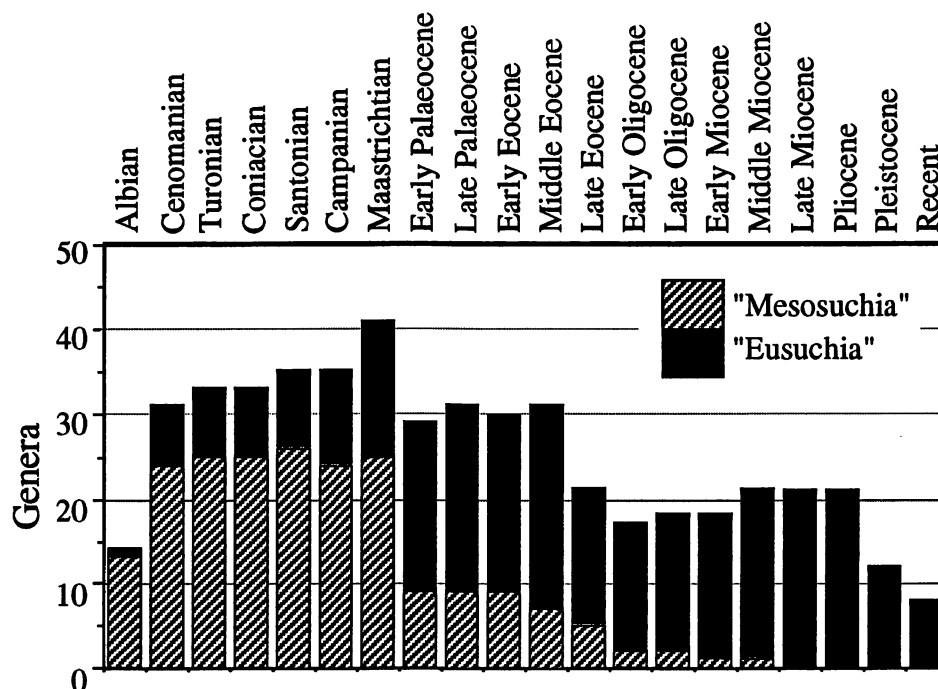
#### VII.3.1. Global Generic Diversity Patterns

Total generic diversity for all post-Aptian Crocodylia is shown in Figure VII.1. Throughout this study, I generally show diversity as bar or column charts, since this is more representative of the resolution of the data; however, point data are used for regressions from which diversification rates, etc., can be calculated. Diversities were calculated using the following equation:

$$D_t = D_{t-1} - E_{t-1} + O_t \quad (1)$$

where  $D_t$  is the diversity at time  $t$ ,  $O_t$  is the number of originations in interval  $t$ ,  $D_{t-1}$  is the diversity in the previous time interval and  $E_{t-1}$  is the number of extinctions in that interval.

Two trends are readily apparent in the diversity graph. First, overall crocodilian diversity appears to fall into two major temporal intervals: the first is from the Cenomanian to Middle Eocene, in which diversities generally range between 30 and 35 genera (with the highest diversity recorded in the Maastrichtian), and the second is from the Late Eocene to the Pliocene, during which diversities are on the order of 20 genera. The second trend, and perhaps more significant, is that the general composition of this diversity changes through time, with "eusuchian" diversity increasing as "mesosuchian" diversity decreases. The cause of this replacement is uncertain.

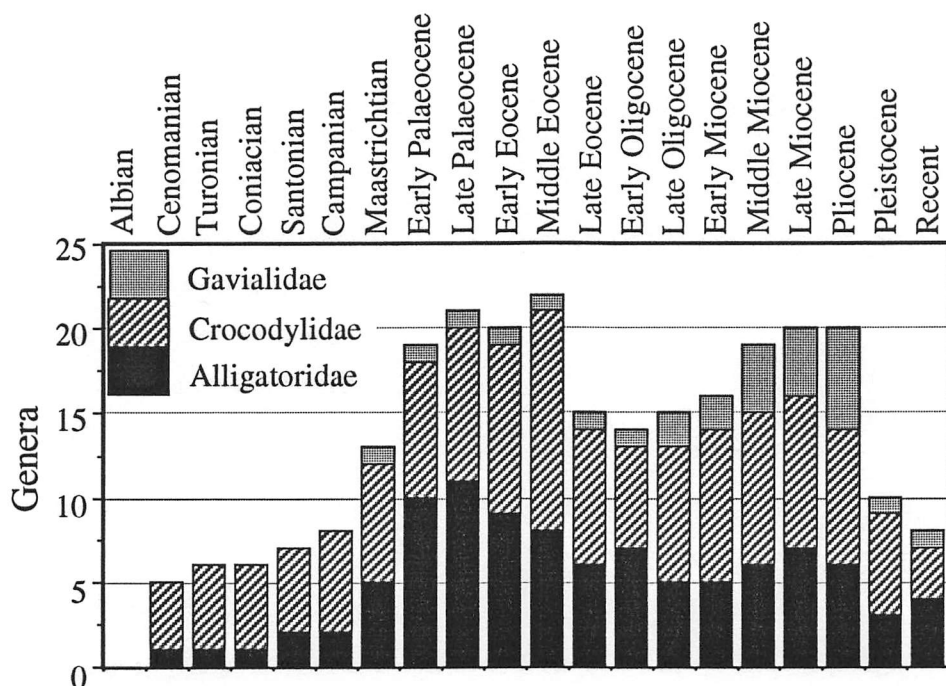


**FIGURE VII.1. The generic diversity of all crocodilians.**

Diversity is calculated using equation (1). Diversity for "eusuchian" and "mesosuchian" crocodilians is shown. The total height of each column is the total diversity ("eusuchians" plus "mesosuchians"). Stacked column charts like this are used to represent diversity in preference to point graphs because they provide a better representation of the resolution of the data (diversity is for the whole interval rather than a point in that interval).

The diversity of crown group crocodilians (the climate proxies in this study) is shown in Figure VII.2. (The similarity between "eusuchian" diversity, Figure VII.1, and crown group diversity is unsurprising since non-crown group "eusuchians" are only represented by about four genera; see Appendix B.) The trends shown in this figure suggest the following: an initial diversification through the Late Cretaceous; leveling off into the Paleogene, with an extinction "event" around the Middle-Late Eocene;<sup>2</sup> a re-

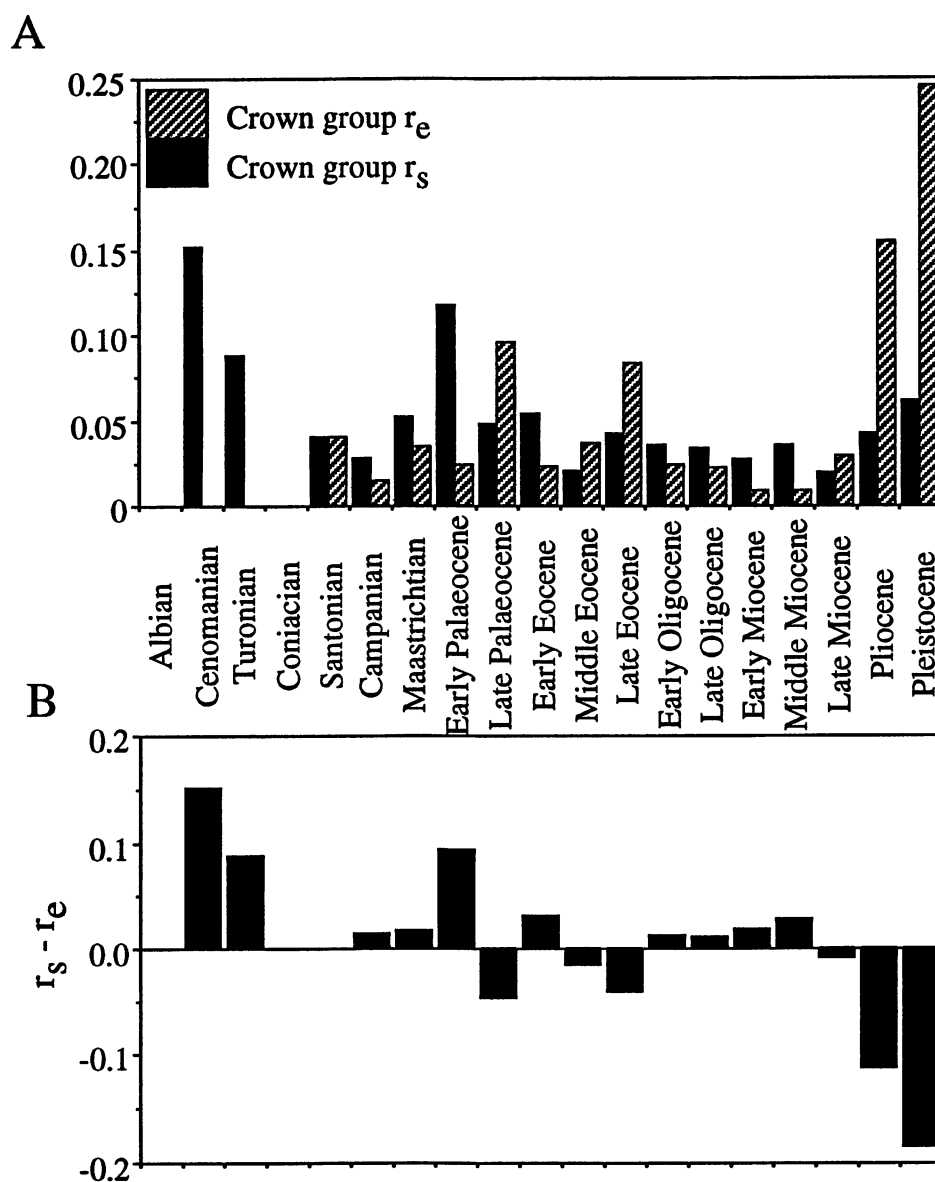
2. It must be noted that the positioning of this diversity change at the boundary, between the Middle and Late Eocene, is wholly an artifact of the temporal resolution used and need not reflect the actual position of the change.



**FIGURE VII.2. The generic diversity of crown group crocodilians (alligatorids, crocodylids and gavialids).**

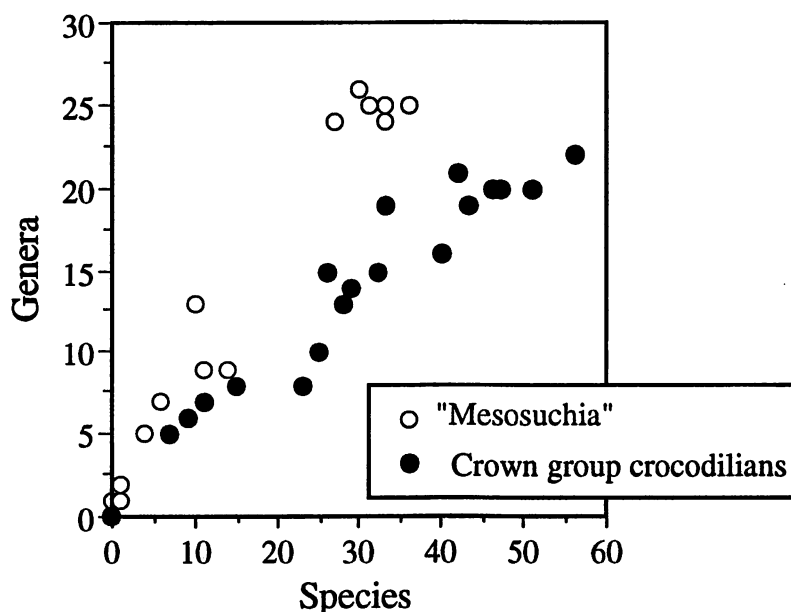
A stacked column chart of crown group crocodilian genera. Diversity calculated using equation (1). All data are included. The initial diversification of crocodylids and alligatorids during the Late Cretaceous and Early Tertiary is readily apparent. Note that the diversification of gavialids does not occur until the Neogene. Drops in diversity occur in the Late Eocene and Pleistocene.

diversification extending into the Late Miocene, followed by a second extinction in the Pliocene-Pleistocene. The coincidence of major extinctions with known global climate cooling events has already been noted in Chapter V. Per-genus rates of diversification are shown for each group in Figure VII.3, which illustrates the high extinction rates during the Pliocene-Pleistocene.



**FIGURE VII.3. A. Crown group per-genus rates of origination ( $r_s$ ) and extinction ( $r_e$ ). B. Per-genus rates of diversification through time ( $r_s - r_e$ ).**

Values are derived using the following:  $r_s = (1 / D) * (O / \Delta t)$ ,  $r_e = (1 / D) * (E / \Delta t)$ , where  $D$  = diversity in the interval,  $O$  = the number of originations in the interval,  $E$  = the number of extinctions in the interval, and  $\Delta t$  = the length of the interval in millions of years. High per-genus rates of origination (and positive values of per-genus diversification rates) in the Cretaceous produce the diversification during that period. Note that the per-genus rate of diversification is positive in the Maastrichtian despite the K-T boundary "event." High per-genus rates of extinction (and corresponding negative per-genus rates of diversification) occur in the Late Palaeocene, Late Eocene, and especially Pliocene and Pleistocene.



**FIGURE VII.4. The relation between the number of species and number of genera in each time interval.**

Solid circles, crown group crocodilian genera; open circles, "mesosuchian" genera. The systematic relationship between the generic and species diversities in each time interval implies that generic patterns may be used as a surrogate for species level patterns. The steeper slope associated with the "mesosuchian" data probably reflects an inherent taxonomic bias in this group.

The use of generic rather than species level data reflects the greater perceived robustness of generic level paleontological data. In these data, there is actually a close relationship between the number of species in an interval and the number of genera (Figure VII.4), which suggests that both should show similar patterns.<sup>3</sup> However, "mesosuchian" genera appear to be species poor relative to crown group crocodilians.

3. Sepkoski (1991) has used the observed correlation between the diversity of higher taxonomic groups and species diversity to justify the applicability of using higher taxa, which are less susceptible to the vagaries of inherent in the geological record, as surrogates for species patterns. This is supported here.

### **VII.3.1.1. Interpreting Diversity Patterns**

Fossil diversity patterns reflect the effects of two potential influences. Extrinsic (physico-biotic) factors, such as climate, which are ultimately responsible for patterns (as discussed in Chapters VI and V; extrinsic factors also include evolutionary trends such as diversification), and intrinsic factors, such as sampling, which reflect the degree of completeness of the fossil record. In order to understand the potential impact of climate on crocodilian diversity patterns it is important to differentiate between the effects of each.

#### **VII.3.1.1.1. The effect of sampling on diversity**

Paleodiversity studies are no different from any other paleoecological investigations in that they suffer from one serious drawback -- they are derived from the geological record. This record is, at best, incomplete, and what record there is, is not a random sample (see Chapter V). This places serious limitations on the confidence with which we can interpret observed patterns, and the statistical tools that can be used to examine those patterns. To this end it is important to understand the biases involved, the degree to which they influence patterns, and, where possible, to minimize their effects. This is particularly acute in the terrestrial vertebrate record, where small sample sizes and correlation problems add to this prejudicial mélange.

An indication of how these biases may affect diversity is shown in Table VII.1, in which diversity for alligatorids, crocodylids, gavialids and "mesosuchians" is recalculated for non-monotypic genera, genera that are present in more than one locality, and those occurring in more than five localities. A number of features are apparent: first, some 60-70% of crocodilian genera are monotypic. This is probably not important in itself, but calculated average longevities increase noticeably when monotypic genera are excluded.

TABLE VII.1. DATA SUMMARY

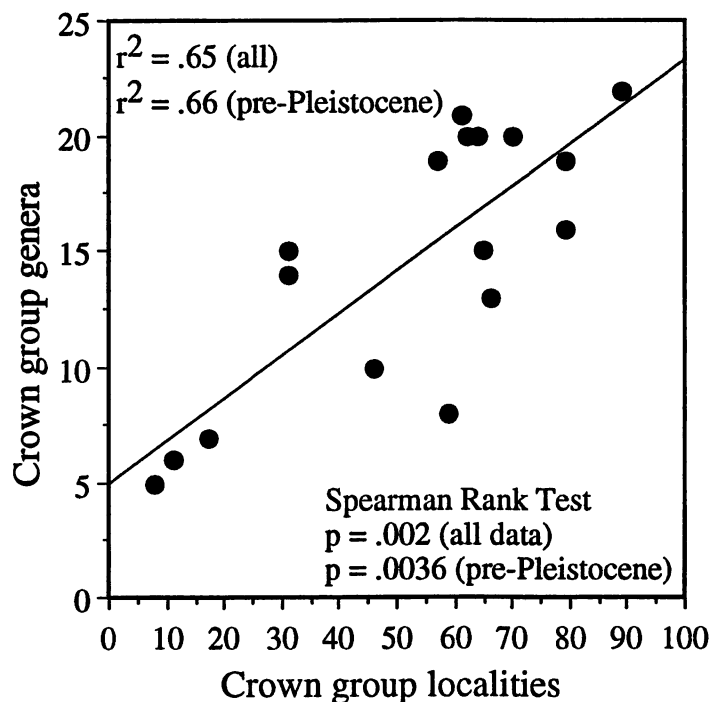
	Alligatoridae	Crocodylidae	Gavialidae	Mesosuchia
<b>USING ALL DATA</b>				
#genera	23	35	6	48
#species	71	143	19	80
#localities	217	424	75	183
#occurrences	270	455	80	197
mean generic longevity	18.9	19.4	20.8	21.2
#spp / #gen	3.09	4.09	3.17	1.67
#locs / #gen	9.43	12.11	12.50	3.81
#mono-specific genera	15	20	4	35
% mono-specific genera	65.2%	57.1%	66.7%	72.9%
<b>EXCLUDING MONOSPECIFIC GENERA</b>				
#genera	8 (34.8%)	15 (42.9%)	2 (33.2%)	13 (27.1%)
#species	56 (78.9%)	123 (86.0%)	15 (78.9%)	45 (56.3%)
#localities	173 (79.7%)	386 (91.0%)	65 (86.7%)	118 (64.5%)
#occurrences	227 (84.1%)	418 (91.9%)	70 (87.5%)	132 (67.0%)
mean generic longevity	35.1	35.1	47.83	40.4
#spp / #gen	7.00	8.20	7.50	3.46
#locs / #gen	21.63	25.73	32.50	9.08
<b>&gt;1 LOCALITY</b>				
#genera	14 (60.9%)	23 (65.7%)	4 (66.7%)	27 (56.3%)
#species	60 (84.5%)	131 (91.6%)	17 (89.5%)	58 (72.5%)
#localities	209 (96.3%)	413 (97.4%)	73 (97.3%)	162 (88.5%)
#occurrences	260 (96.3%)	443 (97.4%)	78 (97.5%)	174 (88.3%)
mean generic longevity	28.3	27.3	30.3	30.2
#spp / #gen	4.29	5.70	4.25	2.15
#locs / #gen	14.93	17.96	18.25	6.00



TABLE VII.1. continued

	Alligatoridae	Crocodylidae	Gavialidae	Mesosuchia
<b>≥5 LOCALITIES</b>				
#genera	8 (34.8%)	12 (34.3%)	3 (50.0%)	8 (16.7%)
#species	54 (76.1%)	118 (82.5%)	16 (84.2%)	33 (41.3%)
#localities	194 (89.4%)	380 (89.6%)	71 (94.7%)	107 (58.5%)
#occurrences	242 (89.6%)	413 (90.8%)	76 (95.0%)	118 (59.5%)
mean generic longevity	37.8	41.7	36.7	43.1
#spp / #gen	6.75	9.83	5.33	4.13
#locs / #gen	24.25	31.67	23.67	13.38

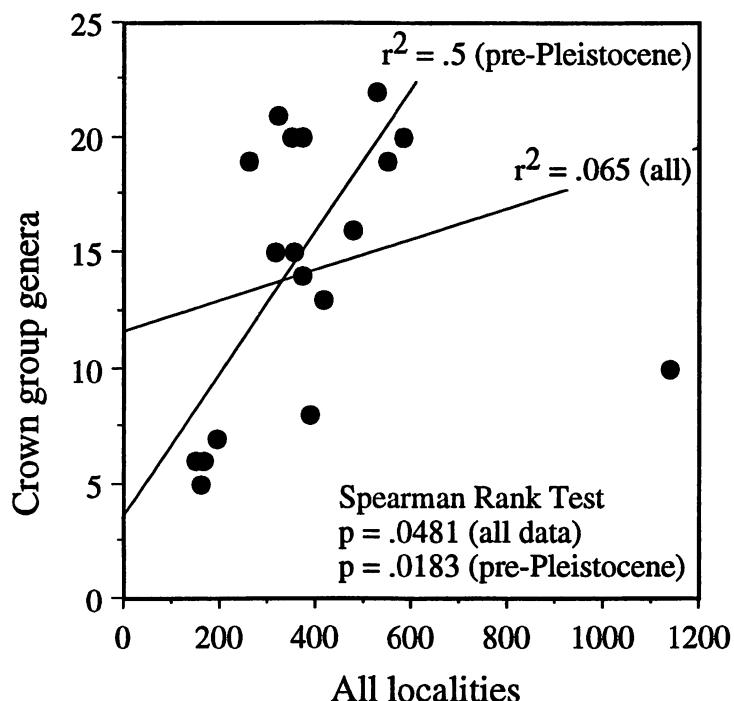
This is largely due to the fact that most monotypic genera are also restricted to one or two localities. Indeed overall, only about 60% of genera occur in more than one locality and only about 35% occur in five or more. This is a potentially more serious problem given the relatively close relationship between diversity and the number of localities present in an interval (Figures VII.5 and VII.6; note the effect of the Pleistocene). However, a sampling argument might be expected to include a relation between diversity, the number of localities, and the length of each time interval, since it might be expected that the longer the time interval the more localities there should be. But, while there is a weak relationship between the interval length and the number of localities contained (Figure VII.8), a significant relationship between diversity and the interval length is not found (Figure VII.7).



**FIGURE VII.5. The relation between crown group crocodilian generic diversity and the number of localities at which they are recorded.**

This relationship strongly implies a sampling bias for generic diversity (see text).

The effect of these biases on the temporal pattern of diversity is shown in Figures VII.9 and VII.10. In both cases, the Late Cretaceous diversification and Pliocene diversity drop are still clear; but, when the dataset is limited to only genera which occur in at least five localities, the Middle-Late Eocene decline in diversity disappears (Figure VII.10). This suggests that the high diversity of the Eocene is largely dictated by "rare" taxa. But, since "rare" on this criterion refers to about 65% of crown group genera (see Table VII.1),



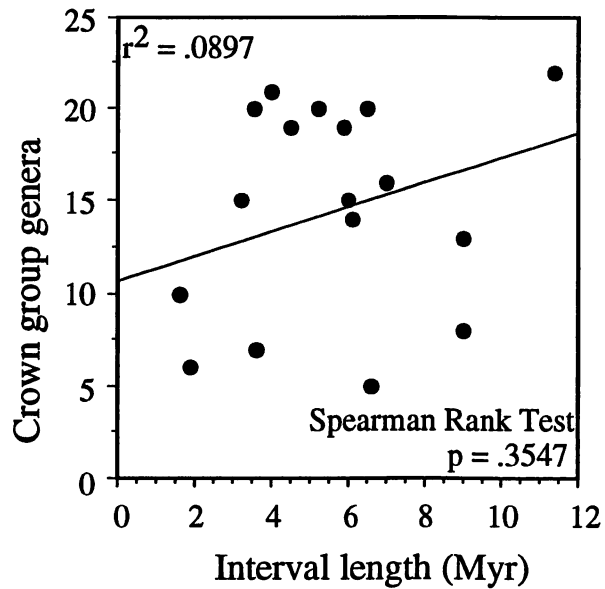
**FIGURE VII.6. The relation between crown group crocodilian diversity and the total number of vertebrate localities in each interval.**

The strong relationship between diversity and the total number of localities (although weaker than that in Figure VII.5) suggests the influence of sampling on generic diversity.

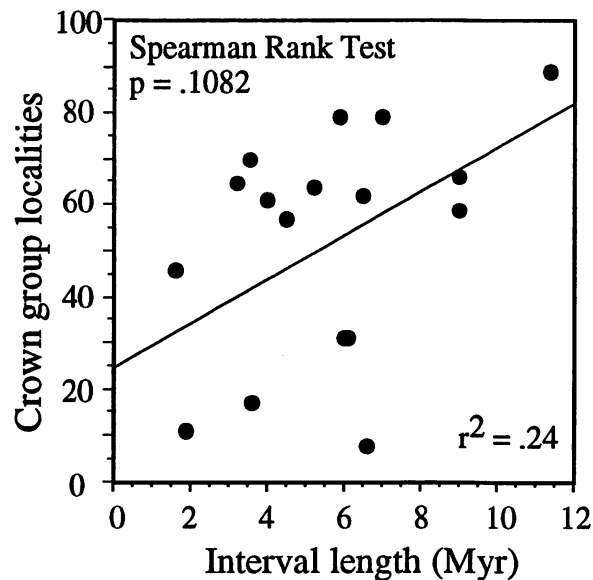
it is unclear that such an observation alone can be used to dismiss the Middle-Late Eocene diversity drop shown by the entire dataset.<sup>4</sup>

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4. This observation of temporally transitory taxa being largely responsible for high diversities during demonstrably warm periods may be analogous to the spatial variations observed in present day taxa. Stevens (1989) has noted that the latitudinal ranges of modern taxa decrease with decreasing latitude, such that in warmer climates diversity is dominated by spatially short ranged taxa. Steven's refers to this as Rapoport's Rule. Although Rapoport's Rule has been dismissed by some workers (Roy et al., 1994), my preliminary observations using the climate station faunal dataset outlined in Chapter III suggests that it is valid in terrestrial systems. An investigation of the applicability of this rule to temporal patterns (as implied above) is in progress.

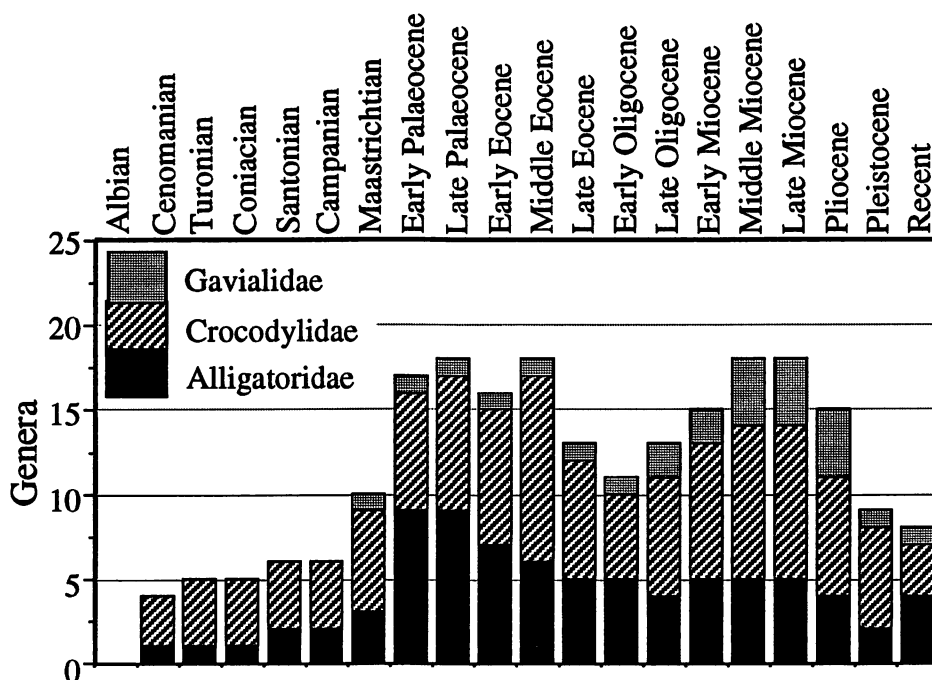


**FIGURE VII.7.** The relation between the number of localities at which crown group crocodilians are recorded and the interval length.



**FIGURE VII.8.** The relationship between crown group crocodilian diversity and the interval length (in millions of years).

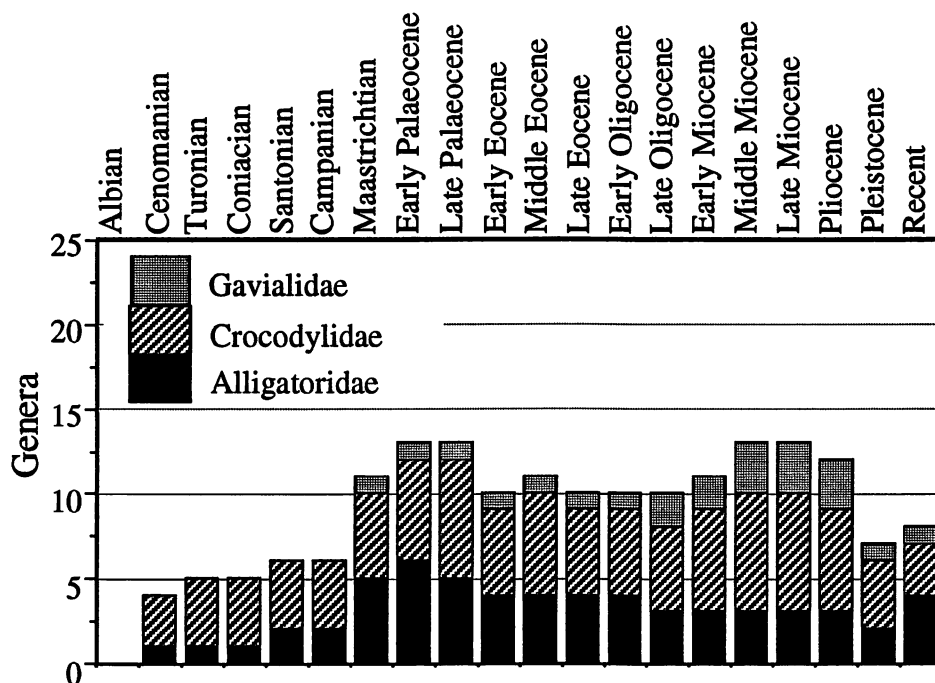
A sampling bias for dictating generic diversity (see Figures VII.5 and VII.6) would intuitively suggest a relation with the length of each interval, such that the longer intervals would contain more localities and thereby more genera. This is not observed in this graph.



**FIGURE VII.9. Crown group crocodilian generic diversity using only those genera that occur in more than one locality.**

Generic diversity is again calculated using equation (1). In this case the dataset is limited to only crown group crocodilian genera that occur in more than one locality. A similar pattern to Figure VII.2 is observed.

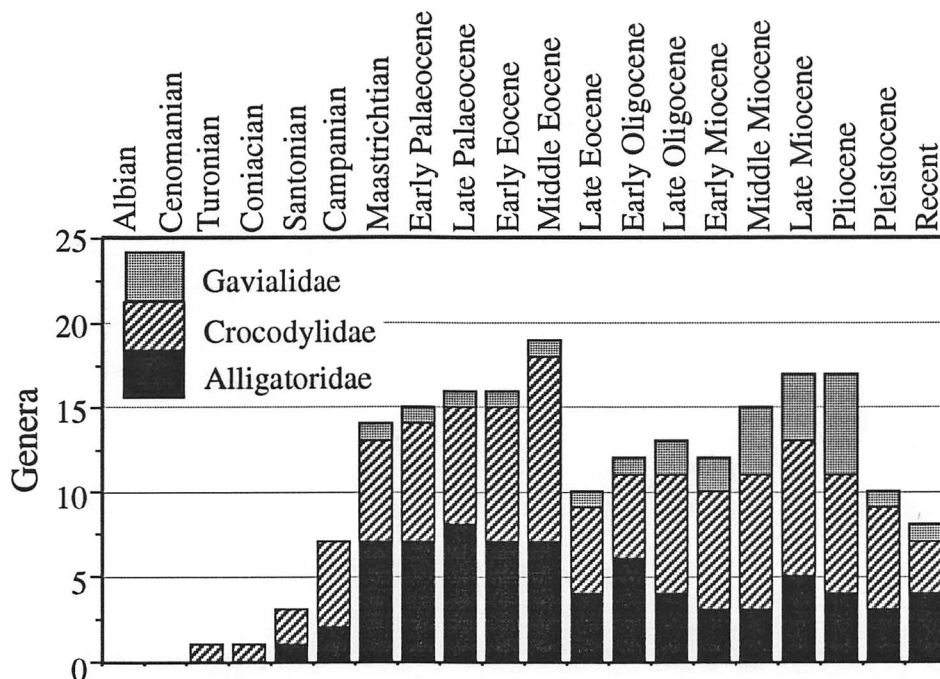
Figure VII.11 illustrates diversity based only on localities that are spatially constrained to within 100 km ( $GP \leq 3$  --see Chapters III and V) and occur in no more than two consecutive intervals. This is the same resolution used in Chapter V and so provides a direct comparison with the paleodistribution maps presented there. Again the general trends are the same, although the Late Cretaceous diversification is delayed by one stage, due, in part, to the loss of temporally poorly resolved localities (viz., localities dated as "Late Cretaceous" only). Note that in each of these figures (VII.9-VII.11), the vertical scale is the same to facilitate direct comparison.



**FIGURE VII.10. Crown group crocodilian generic diversity using only genera that occur at least five localities.**

Generic diversity using only those genera that occur in five or more localities. The Cretaceous diversification of crocodylids and alligatorids is still apparent as is the Miocene diversification of gavialids. However, the diversity trend from the Campanian to the Pliocene is much flatter than in Figure VII.2 and Figure VII.9. Nonetheless the decreased diversity in the Pleistocene is still clear.

A sampling argument to explain observed diversity trends implies that drops in diversity reflect increased incompleteness of the record. One way of assessing the degree of incompleteness is to use the difference between calculated diversities (using equation 1) and absolute recorded diversity for each interval; this is known as "gap analysis" and was invented by Paul (1985), although it has been used by others (Jablonski, 1986; Maxwell and Benton, 1990). Differences stem from the fact that a genus may not be recorded from all the intervals in which it was extant (where absences are long, such taxa have been

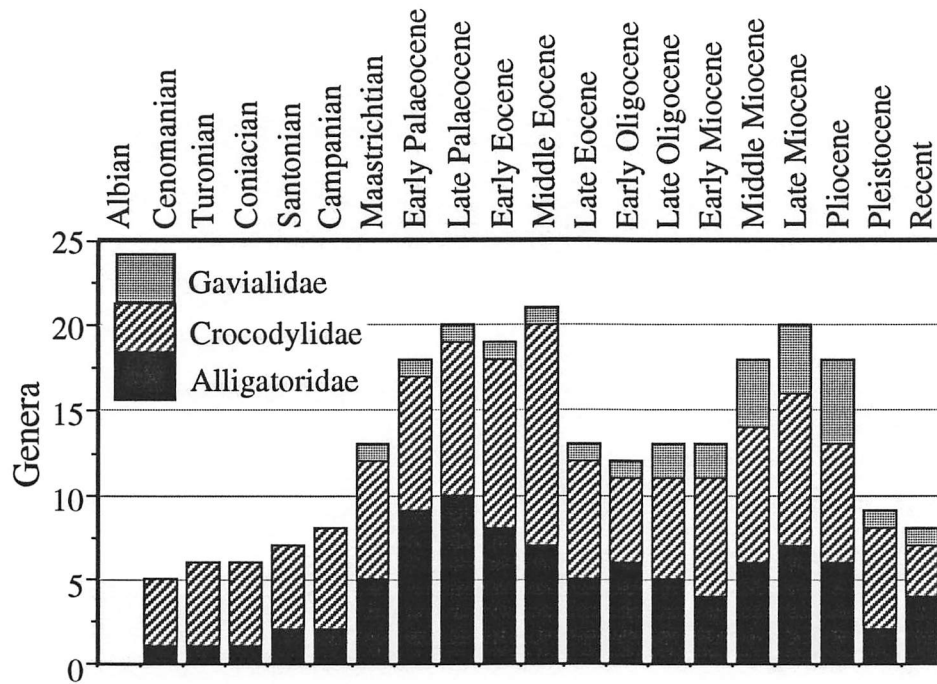


**FIGURE VII.11. Crown group crocodilian generic diversity,  $GP \leq 3$ ,  $\leq 2$  time intervals.**

Generic diversity based on occurrences from localities that have a spatial resolution of  $GP \leq 3$  (known to within 100 km) and whose age includes no more than two time intervals. The general trends are the same as those shown with the entire dataset in Figure VII.2.

referred to as "Lazarus taxa," Jablonski, 1986). Logically, the genus must be present during these intervals (this is what equation 1 dictates), and thus the absence reflects sampling problems.<sup>5</sup> Figure VII.12 shows the recorded diversity of crown group genera based only on genus counts for each interval. The difference between this figure and Figure VII.2 is therefore a measure of incompleteness, which is shown in Figure VII.13. This metric suggests that for the most part the record is relatively complete and, if interpreted

5. In looking at the spatial distribution of diversity, discussed below, qualifying incomplete sampling is more difficult to qualify because the continuous presence of a genus at any latitude or continent cannot be guaranteed, thus diversity is based on known presences only.

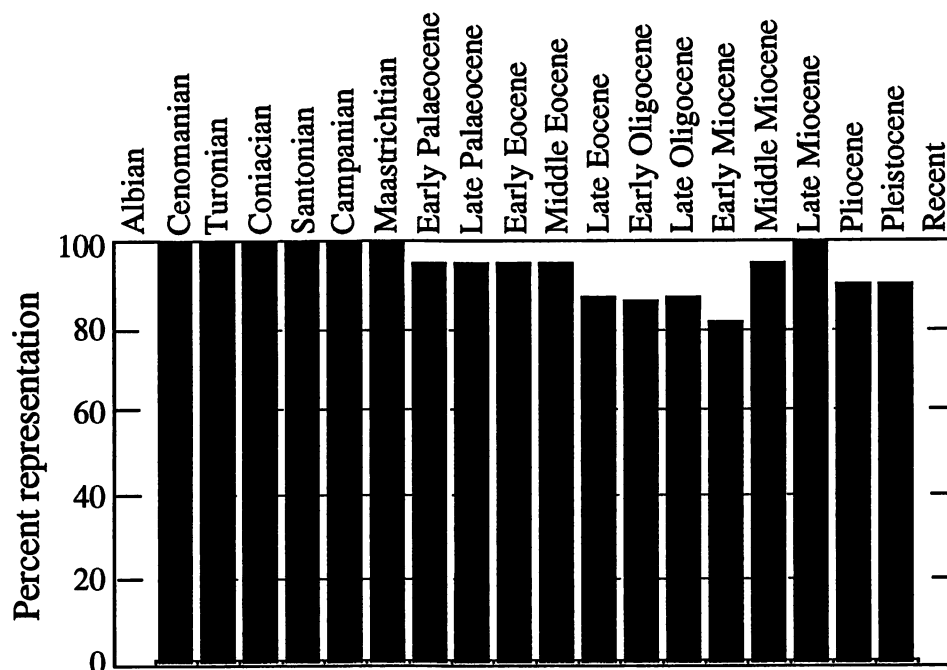


**FIGURE VII.12. Crown group crocodilian diversity based on absolute counts per interval .**

The generic diversity shown in this figure reflects absolute counts for each interval. Values are not calculated and so consequently the effects of "Lazarus genera," sensu Jablonski (1986) , are not compensated for.

literally, that both the Late Cretaceous diversification and Late Miocene-Pliocene extinction are not due to sampling. In the Paleogene, the record is shown to be up to 15% incomplete, but the question is whether this is sufficient to account for the observed diversity drops during this period (Figure VII.2). Recalculating the number of originations and extinctions in each interval, and compensating for the percentage incompleteness in each case, allows a new diversity curve to be derived. As might be expected, only slight differences are found between this "curve" and the original pattern of diversity (Figure VII.2). Therefore, based on this metric for incompleteness, the changes in observed diversity cannot be explained solely by sampling. However, this is on a global basis and may not reflect completeness on





**FIGURE VII.13.** The completeness of the record based on the ratio of observed diversity and calculated diversity; "gap analysis," sensu Paul (1985).

local or regional scales. Nor is it clear how good a measure of completeness this metric really is.

A different approach to this problem uses the relationship between generic diversity and numbers of localities (Figures VII.5 and VII.6) as a means of predicting diversity. If sampling alone drives observed diversity, then the average ratio between diversity and number of localities should be representative of the general relationship between the two. Diversities are predicted by multiplying this average value by observed numbers of localities. Results are then compared with observed diversities and the hypothesis that the two are indistinguishable (sampling drives the observed pattern of diversity, or at least that the two are closely related) assessed using the Chi-square test. For the crocodilian data, the

results suggest that this is not the case, at least not entirely. Predictions based on all localities and crown group crocodilian localities give p-values of 0.0007 and 0.0101 respectively. When the Pleistocene is ignored, p-values become 0.0030 and 0.0080 respectively, which are still very significant. The question is whether these predictions should be applied to the entire history of crown group generic diversity. In Figures VII.9 to VII.12, constraining the dataset for various sampling effects, did not change the appearance of the initial diversification of the group, a time when the completeness metric suggests the record is relatively complete (Figure VII.13). This implies that the observed Late Cretaceous - early Paleogene diversification is not simply an artifact of sampling; p-values based on the period Cenomanian-Middle Eocene are 0.001 and 0.009 using all localities and crown group localities, respectively. However, predictions for the period Late Eocene-Pliocene (again ignoring the Pleistocene, which is clearly not an artifact) give much higher p-values, 0.658 and 0.092 based on all localities and crown group localities, respectively. This suggests that the minor fluctuations during this period may indeed be due to sampling effects.

#### **VII.3.1.1.2. Extrinsic causes**

In Chapter V, the systematic distributional changes shown by crown group crocodilians through time was shown to be a response to some sort of climate signal. One would therefore anticipate that this should also be apparent in the pattern of diversity. With this in mind, an alternative explanation for the observed relationship between diversity and number of localities is postulated here. Sepkoski (1996) noted that decreases in geographic ranges (as indicated for crocodilians by the paleodistributional data presented in Chapter V; this latitudinal pattern was shown to be independent of sampling) results in reduced carrying capacities as habitat area is reduced. This can lead to a destabilization of existing competitive coexistence between species and thereby result in extinctions. Since this

decrease in geographic range also limits the area over which localities may be preserved, diversity and sampling can decrease together.

An extrinsic argument is also suggested by two further observations. First, the change in diversity with time follows a systematic trend (exponential diversification; Figure VII.1), which is difficult to explain in the context of sampling alone (note also the change in composition of crocodilian diversity through time, Figures VII.1 and VII.2); and second, while crown group diversity is related to both the diversity of crown group localities and all vertebrate localities in an interval (Figures VII.5 and VII.6), it is better correlated with the former. This is supported by an observation in Chapter V, section V.3.2, in which significant drops in the ratio of crown group localities to all localities were found in the Oligocene and Pliocene, concomitant with contraction of the latitudinal range of crocodilians and drops in diversity. (The ratio of crown group crocodilian localities to all localities was used as an indication of how closely crocodilian sampling is dictated by total sampling.) This suggested that the significant perturbations were 'real,' non-sampling effects.

#### **VII.3.1.1.3. Intrinsic or extrinsic?**

The relationship between diversity and sampling can be explained in at least two ways: 1. Collection bias -- workers may tend to name new taxa with each new find, and thus the number of taxa named will be directly related to the number of 'finds' (localities); 2. Publication bias -- having found a new taxon the urge to publish is higher than for an existing taxon (an analysis of specimen counts in the database shows a preponderance of skulls and lower jaws, not because of their greater preservational potential but because of the larger numbers of type specimens recorded in the literature relative to 'average' finds). These biases have already been explored in Chapter V. Sampling bias can also be induced

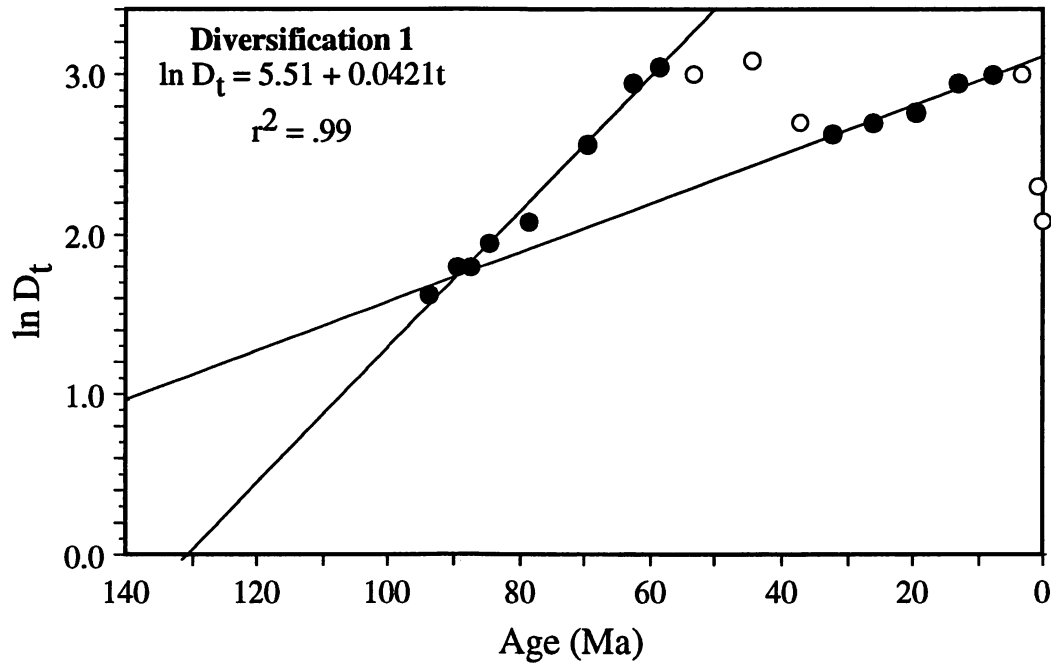
by extrinsic factors, such as climate. In the Oligocene, for instance, the formation of large continental ice-sheets resulted in a eustatic sea-level fall. The concomitant lowering of base-level would be predicted to reduce deposition in terrestrial environments and thereby limit available preserved rocks to sample (see also Hutchison, 1982). The use of distributional control groups in Chapter V shows that this cannot be used to explain observed patterns, and therefore cannot be used to explain diversity trends.

Even if sampling and diversity are strongly correlated, this does not automatically imply cause and effect. As suggested in section VII.3.1.1.2 the two could both be responding to the same extrinsic cause. Differentiating between these opposing hypotheses is difficult, because the signals are essentially the same. Nonetheless the evidence so far presented tends towards an extrinsic cause for at least the initial diversification of crown group crocodylians and the Plio-Pleistocene extinction, and probably for the rest of the record as well.

If these arguments in favor of an extrinsic cause are robust, then it should be possible to identify the governing mechanisms directing the pattern of diversity. It should also be possible to identify biogeographical and historical changes in diversity. This is because coherent patterns in both cases would not be expected using a purely sampling-based hypothesis.

#### **VII.3.1.1.4. Diversification models**

In order to understand diversity patterns, paleontologists have applied population dynamical methods of demographers and biologists to model paleodiversification patterns (Sepkoski, 1991). Such models take two basic forms, exponential growth, given by the equations,



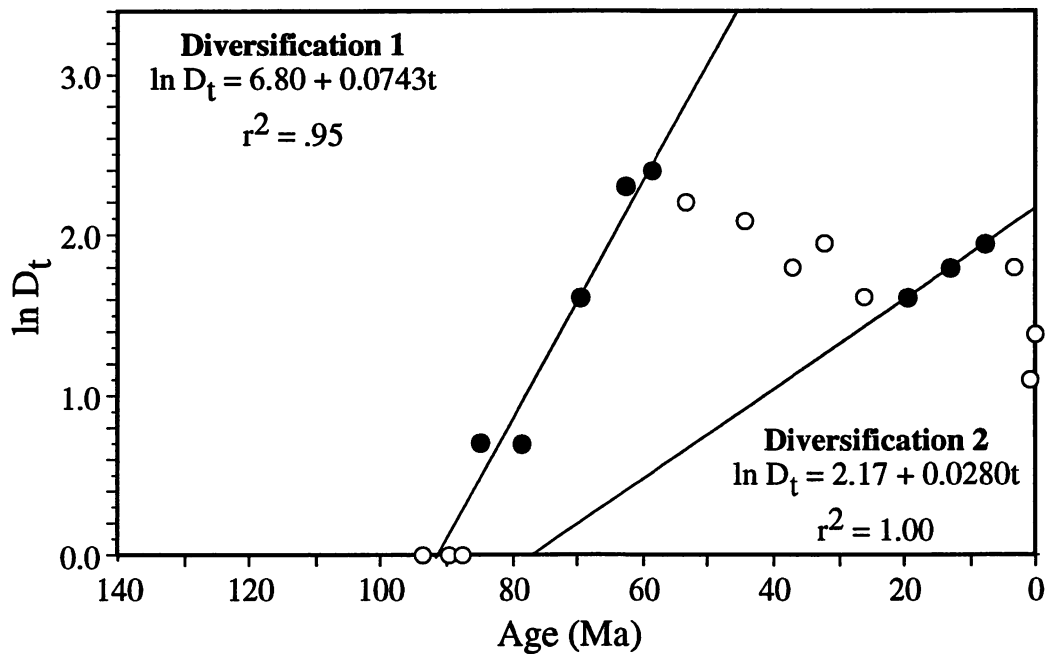
**FIGURE VII.14. Log crown group crocodilian generic diversity.**

Two separate periods of exponential diversification are shown (filled circles). Linear regressions through these diversifications shown extremely good fits with an  $r^2$  of .99 for the Late Cretaceous through Paleocene diversification, and .97 for the second diversification in the middle through late Tertiary. These are separated by extinctions, the most extreme being that in the Pleistocene. Extrapolation of the initial diversification to the x-axis implies that the origin of the group occurred in the Early Cretaceous.

$$D_t = D_0 e^{rt} \quad (2)$$

$$\ln D_t = \ln D_0 + r t \quad (3)$$

(where  $D_t$  = diversity at time  $t$ ,  $D_0$  = initial diversity,  $r$  = rate of diversification), and logistic growth in which exponential diversification is limited by some threshold diversity,  $D_e$ ,



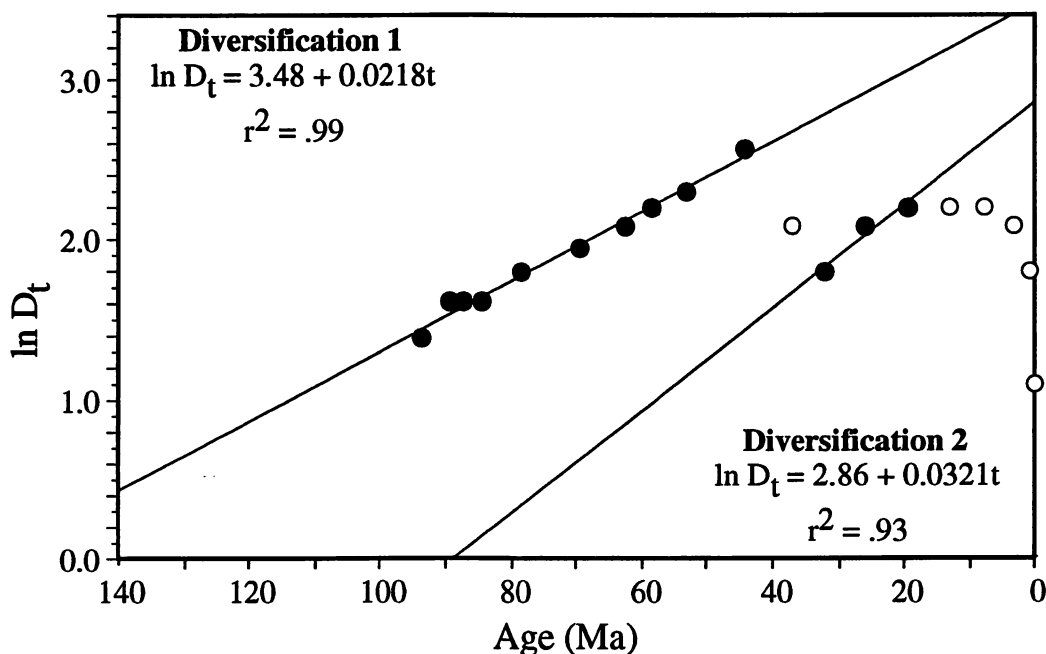
**FIGURE VII.15. Log alligatorid generic diversity.**

Two separate periods of diversification ( $r^2 = .95$  and  $1.00$ , for the Late Cretaceous-Paleogene and Neogene diversifications respectively) are shown. The Pleistocene extinction is sharp, but the decline in diversity during the Paleogene appears gradual.

$$D_t = D_e / [1 + (D_e / D_0 - 1) * \exp(-rt)] \quad (4)$$

Equations after Sepkoski (1991).

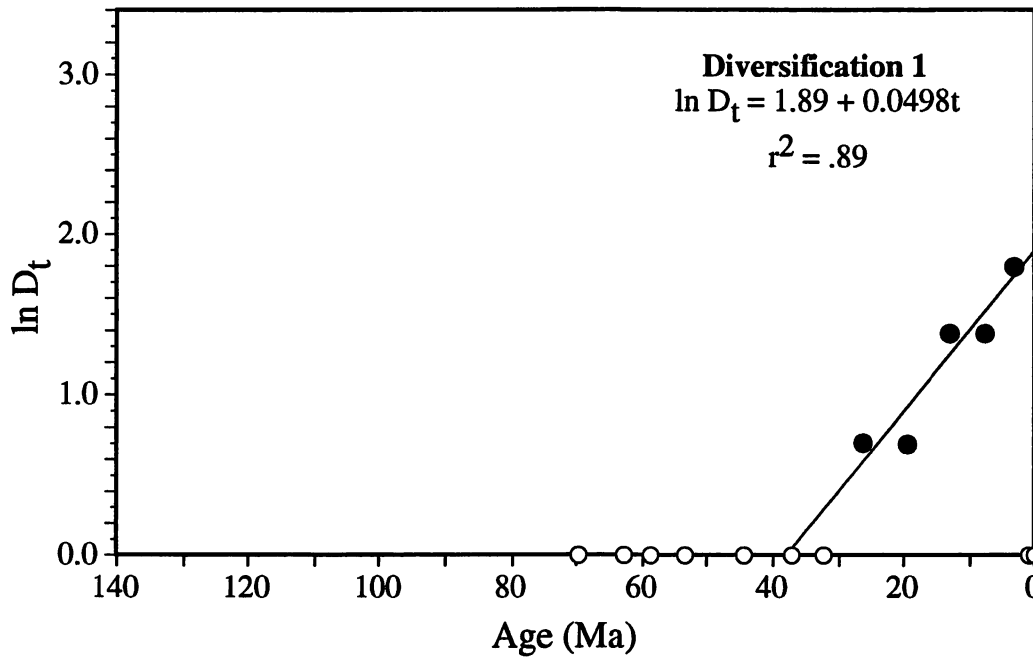
The diversity patterns shown in Figure VII.2 suggest two phases of diversification, followed in each case by a leveling off in diversity, terminated by extinction. In gross appearance these suggest a logistic rather than exponential model of diversification. I begin by examining the trends in more detail using plots of natural log of diversity against time (Figures VII.14-VII.17). In each case the phases of diversification show significant



**FIGURE VII.16. Log crocodylid generic diversity.**

Two separate periods of diversification are shown. The diversification rate implied by the regression through the first diversification is much lower than that for alligatorids, although the rate for the second diversification is similar in both cases. Extinctions in both the Paleogene and Pleistocene are indicated.

linearity (note that gavialids only show one round of diversification, Figure VII.17). More significantly, the slowing in diversification, which would be expected in a logistic model of growth, is not well defined; instead exponential diversification can be interpreted to continue until the "equilibrium" level is reached. Attempts to fit logistic and exponential models to the data are shown in Figure VII.18.



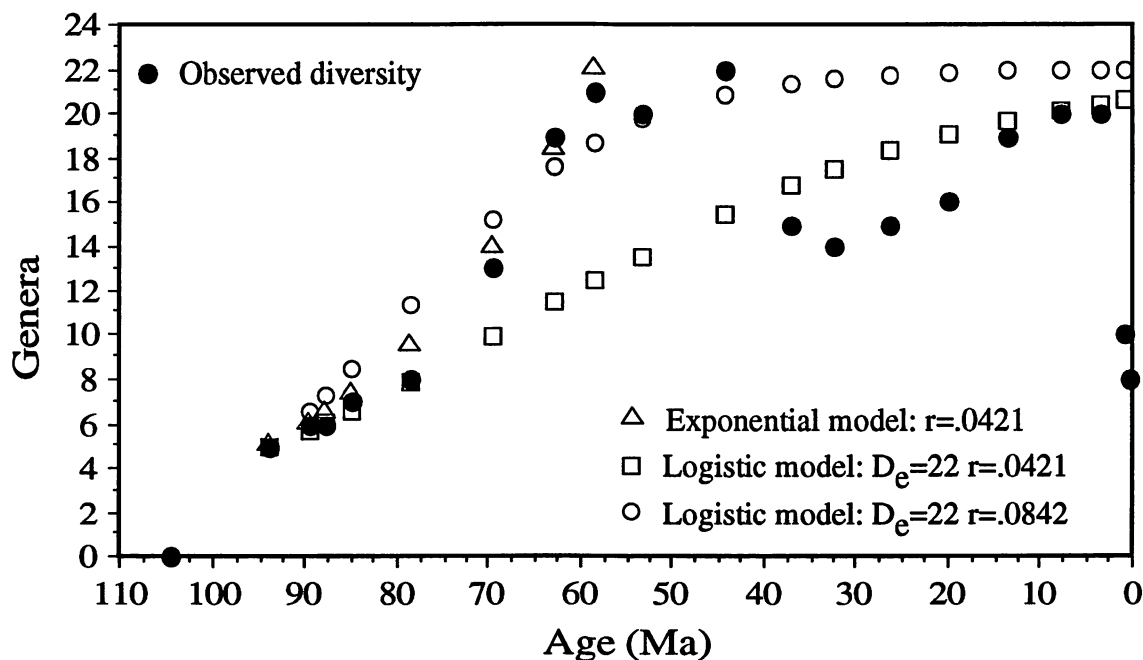
**FIGURE VII.17. Log gavialid generic diversity.**

Only one phase of diversification is seen in the history of gavialids. This is followed by an extinction in the Pleistocene.

Although in this study I have concentrated on generic diversity, specific diversity trends are very similar. This is shown in Figure VII.19 and Figure VII.20. The Late Eocene extinction event is more pronounced than for generic diversity, but the better fit of exponential rather than logistic diversification is the same.

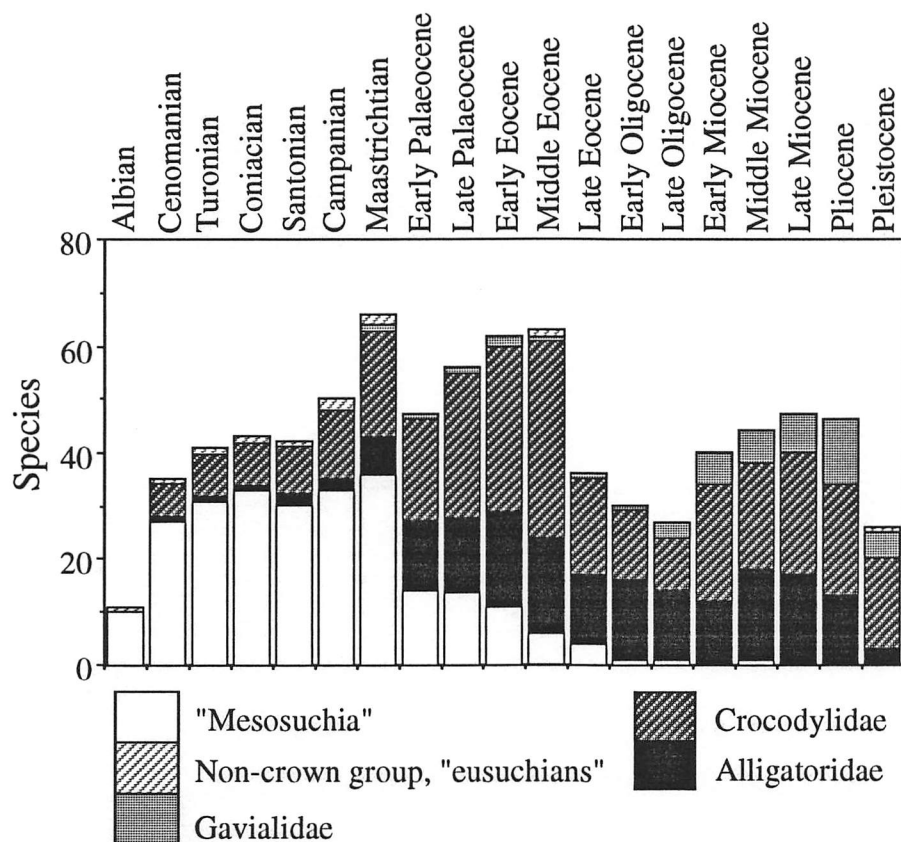
In Figure VII.21 "mesosuchian" diversity is shown. In this case an early diversification is suggested only by one datapoint, with the earlier history beyond the range of the present study period. However, through the Late Cretaceous diversity remains relatively constant, suggesting, perhaps, some equilibrium level. Diversity then decreases through the Cenozoic in a nearly exponential decline.





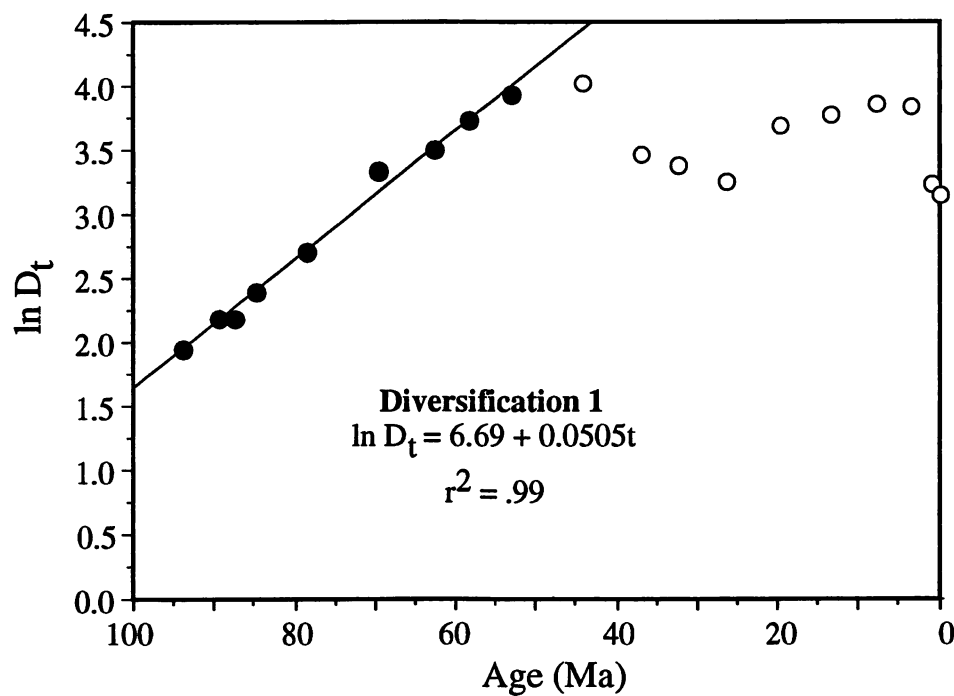
**FIGURE VII.18. Modeled diversification trends for crown group crocodilians using exponential and logistic models.**

Diversity curves are derived for logistic and exponential models of diversification using specified values for diversification rate,  $r$ , and equilibrium diversity,  $D_e$ . A leveling off is suggested by the pattern of crown group diversity, reminiscent of, but not consistent with a purely logistic growth (given the diversification pattern). An alternative model for diversification is thereby required.



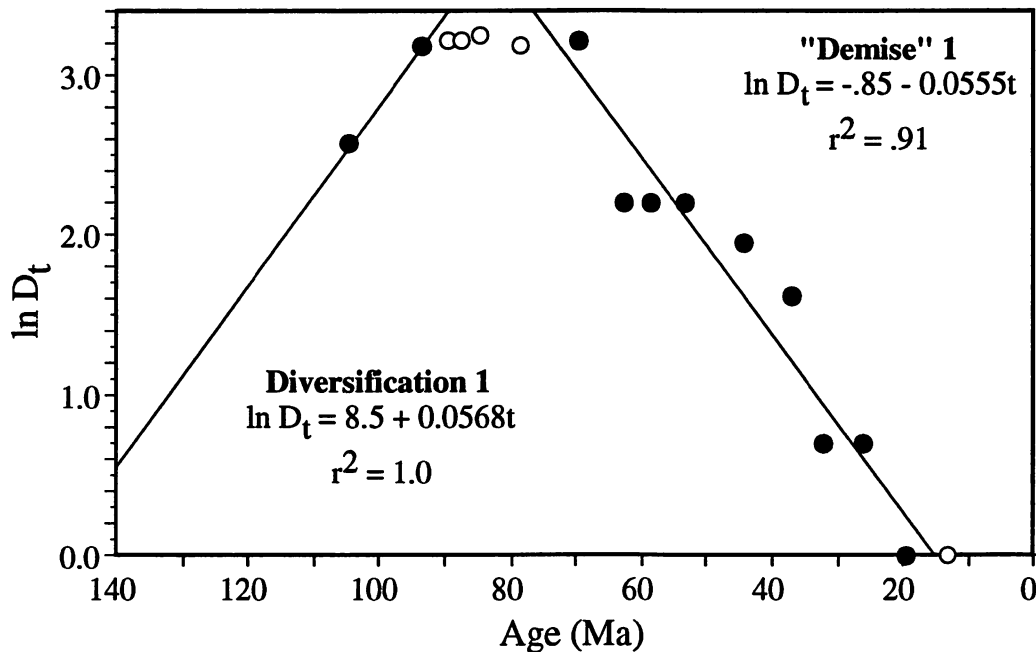
**FIGURE VII.19. Crocodilian species diversity.**

Diversity is calculated using equation (1). The overall pattern is the same as that for generic level data (Figures VII.1 and VII.2) as would be expected given the close relationship between species and generic diversity (Figure VII.4). The principal difference is that species diversity patterns intensify the Late Eocene extinction.



**FIGURE VII.20. Log crown group crocodilian species diversity.**

The initial diversification of crown group crocodilians is again clearly shown, continuing uninterrupted through the Late Cretaceous and early Paleogene. The rate of diversification (0.0505) is similar to that for genera (0.0421). Drops in diversity during the Late Eocene and Pleistocene are also seen.



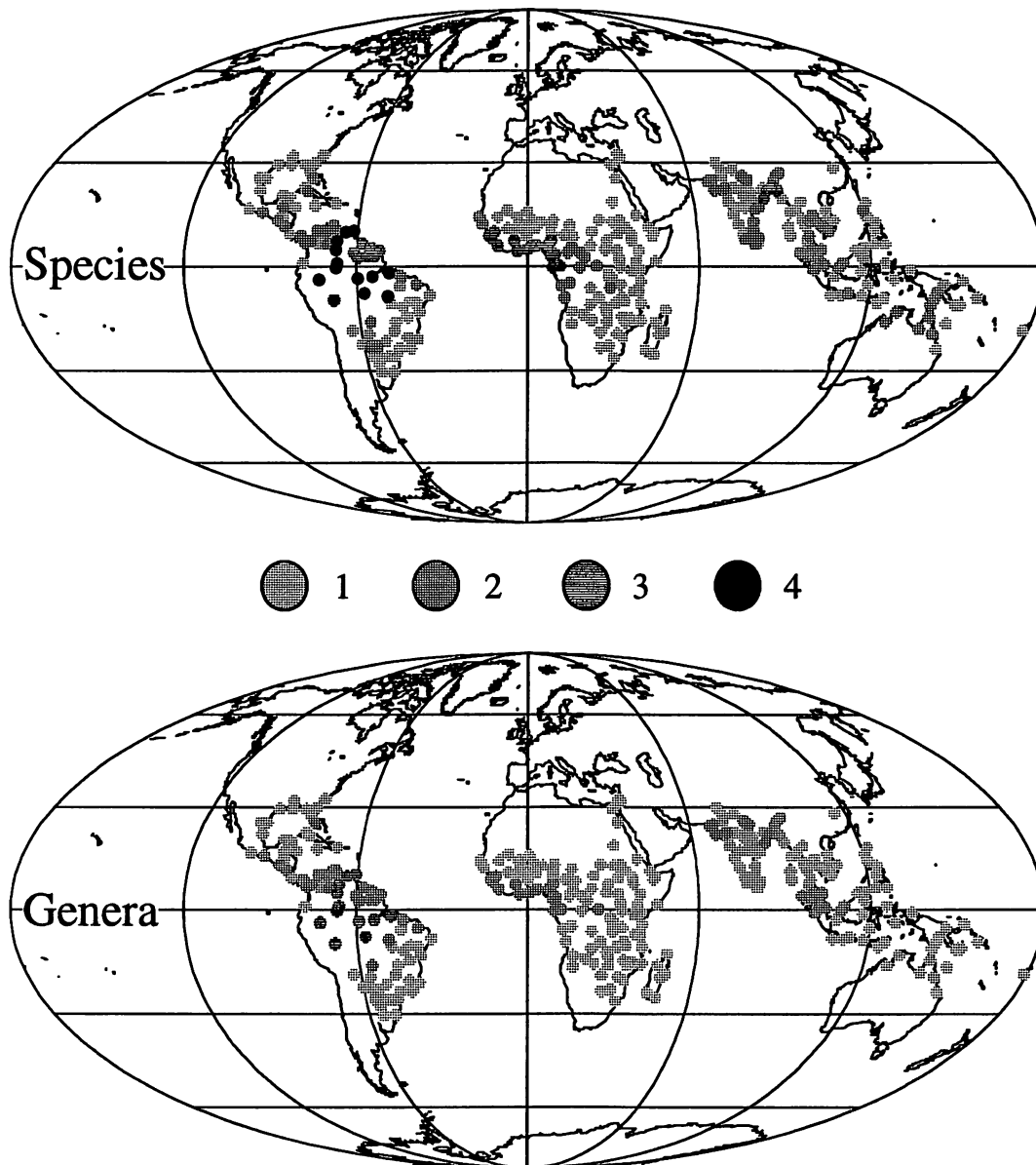
**FIGURE VII.21. Log "mesosuchian" generic diversity.**

"Mesosuchian" diversity patterns through this interval are generally opposite in sign to those of crown group crocodilians. The initial diversification shown is difficult to qualify since the present dataset does not extend to the origins of the "group." However, during the Late Cretaceous "mesosuchian" diversity appears relatively constant, suggestive of some "equilibrium level." This ends at the K-T boundary, where "mesosuchians," in contrast to crown group crocodilians, experience a major extinction. The straight line fit for the demise in diversity after the Cretaceous is consistent with exponential decay, although why this should be so is unclear. However, the pattern is also consistent with a leveling off after the K-T (perhaps due to a new equilibrium level) into the Middle Eocene, and then decreases to the Pleistocene and final extinction of the group. In the post-Paleocene, the "Mesosuchia" are represented almost solely by the Sebecidae, which may reflect a further clade, the taxonomic position of which is unclear. Investigation of the interaction between "mesosuchian" and crown group (or "eusuchian") diversification using a coupled logistic model (Sepkoski, 1991) is untenable given that the diversification of crown crocodilians is itself clearly not following a simple logistic path (See Figure VII.18).

### VII.3.2. Spatial Variations in Diversity

In order to understand fully the trends in global crocodilian diversity described above, it is important to see how diversity changes spatially (in the same way that distributional trends are better understood by looking at spatial changes -- Chapter V). At the present day, crocodilian diversity, like for so many other groups, increases with decreasing latitude (Figure VII.22). But, environmental factors, such as climate, are not the only influences on this pattern. As described in Chapter V, the paleobiogeography of crocodilians must also be seen in the context of history and this is also apparent in the spatial distribution of diversity; evolution works at the individual level and consequently a group cannot instantaneously appear everywhere. How this is ultimately represented in the fossil record is dependent on the temporal resolution of the analysis, which here is the sub-epoch level (stages in the Cretaceous; given the length of these intervals, individual genera may appear to originate in more than one place).

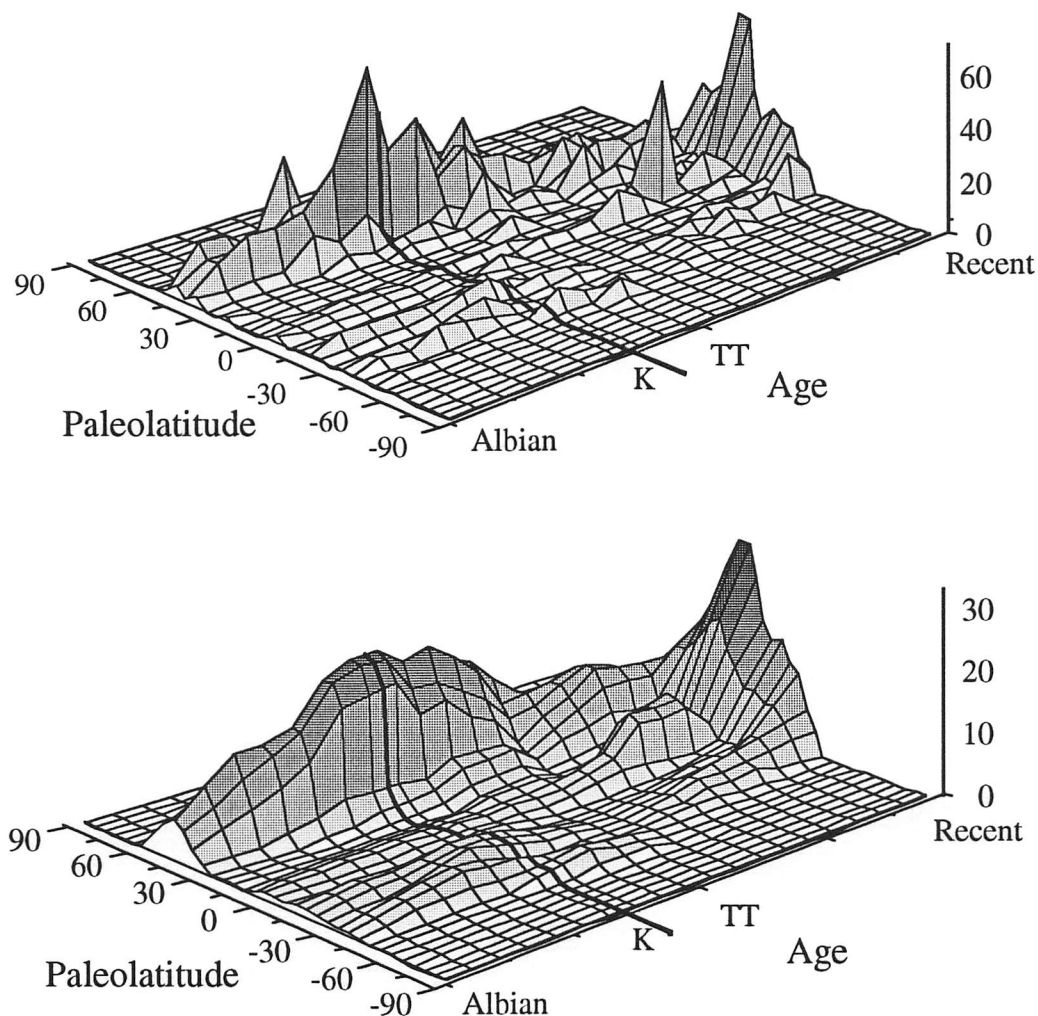
The spatial distribution of diversity is displayed in two ways in this study. As a function of paleolatitude, in which standing diversity for each interval is summed for 5° latitudinal bands, and by continent. In both cases, diversity represents the observed standing diversity, since the continuous presence of a genus at any one place cannot be assumed regardless of its temporal existence before and after the interval in question (compare with the global trends discussed above which use equation 1). This follows from the fact that an absence may not be an artifact of preservational bias, but a real effect due to range changes. A consequence of this method is that changes in diversity between intervals are exacerbated. This must be borne in mind when looking at the patterns.



**FIGURE VII.22.** The modern day distribution of crocodilian specific and generic diversity.

### VII.3.2.1. Diversity by Paleolatitude

The use of 5° latitudinal bands, rather than a more finely resolved division, reflects the sparsity of fossil data. Experimentation with the dataset has shown that a finer division, such as 1° latitudinal zones, is more susceptible to the vagaries of sampling, producing an increased disparity between poorly sampled and well sampled areas. Analysis of modern day latitudinal trends (see Chapter IV) has shown that a 5° division not only replicates trends based on more finely resolved data, but also removes the noise inherent in a finer resolution. However, which 5° zones are chosen (whether boundaries are placed on the fives or in between) is arbitrary. Potential consequences of these decisions may be mitigated by averaging adjacent values, although such averaging decreases further the resolution of the dataset. Nonetheless, such averaging is applied to the data to produce three dimensional surface diagrams. This is done using the smoothing function in Spyglass Transform (Spyglass, 1990-1993), which averages each point with its eight neighbors. Since in each data array the columns represent time intervals, the averaging also affects the temporal resolution. Consequently, sudden changes, especially those connected with short-term extinction events, are smoothed out, while more general trends are well replicated. With this in mind the 3D surface diagrams are provided as a visualization aid only; hence I have generally not provided a corresponding labeled vertical axis in order to avoid misunderstanding and temptation. In each case an array showing the actual observed values is presented, and it is to these that readers should refer (zero values shown on the figures provide a control on the data, showing where other crocodilian data are present; see Chapter V for discussion of control groups). To show how this works, Figure VII.23 illustrates what happens when the distribution of all crocodilian localities through time is smoothed using



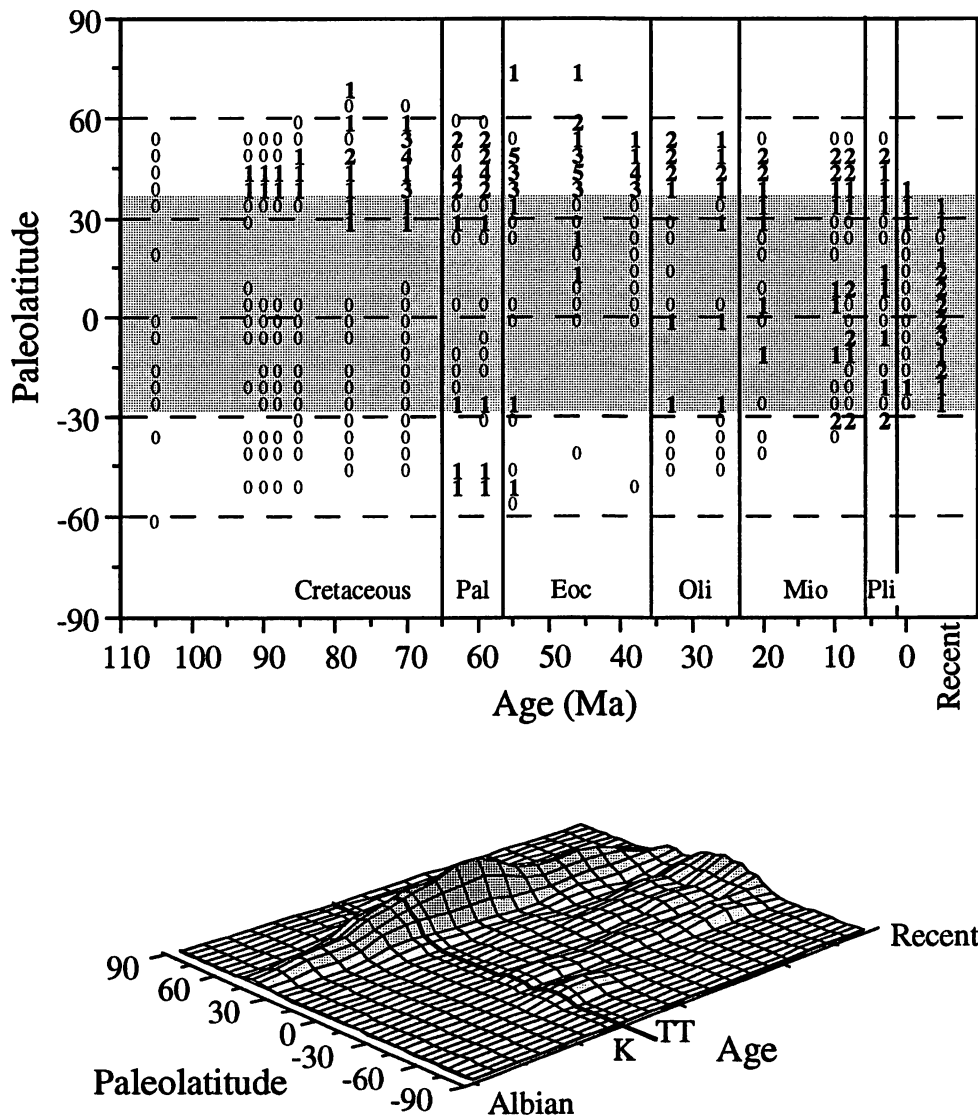
**FIGURE VII.23.** The paleolatitudinal distribution of all crocodilian localities as a function of time. Unsmoothed (top), smoothed (bottom).

Surface plots of the number of crocodilian localities in  $5^\circ$  latitudinal zones for each time interval. Counts represent absolute numbers of localities in each case. These data are stored as Spyglass Transform data arrays (Spyglass, 1990-1993). The bottom figure shows how the same data look after being smoothed once by averaging each point with its eight neighbors. This smoothing changes the absolute values (as the z-axis scales show in this figure, and consequently such plots should not be used to obtain data values) but, overall, general trends are well replicated and easier to visualize (see text). Note that the sampling "diversity" clearly shows the bias towards northern mid-latitudes throughout the Late Cretaceous and Paleogene, but that this bias shifts to low latitudes during the Neogene.



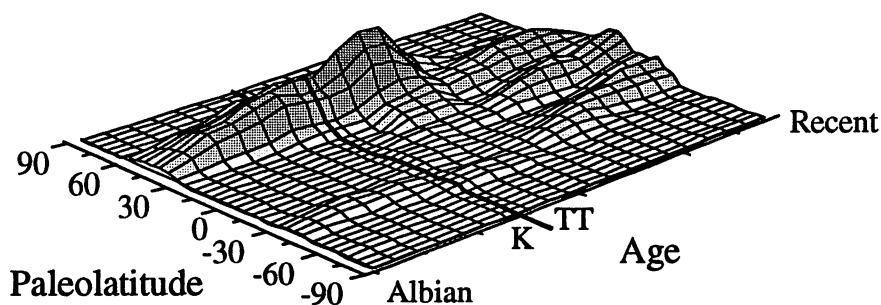
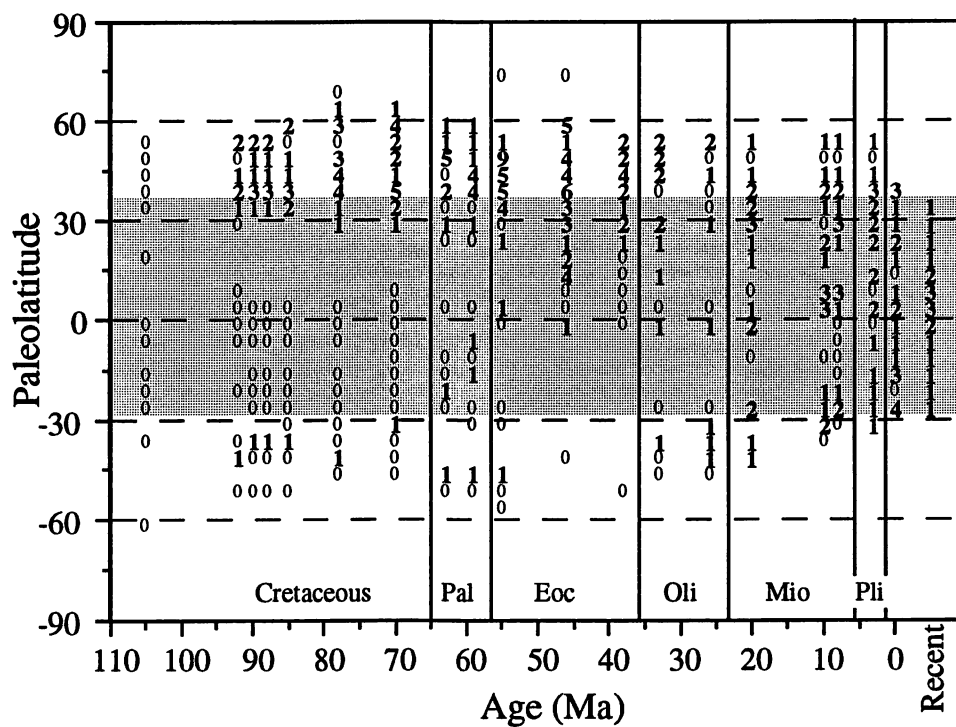
the algorithm stated above. The general trends remain unchanged but sudden shifts are subdued.

One persistent problem in examining paleolatitudinal diversity patterns is the question of temporal resolution. For the distributional maps given in Chapter V this was qualified by limiting the dataset to only those localities that are known spatially to within 100 km ( $GP \leq 3$ ) and no more than two time intervals, with data shown at both the epoch and sub-epoch/stage level. For distributional patterns, poorly resolved data do not influence general paleoclimatic conclusions. But for diversity trends, based on a more detailed exploration of the dataset (genus occurrences, rather than "crown group crocodilian" occurrences--Chapter V), poorly resolved data are important, and often provide the only evidence for the presence of a taxon, especially during the Cretaceous. Consequently, diversity plots shown in this chapter are based on all data. Nonetheless, an analysis of diversity trends based on a temporally constrained subset of the dataset (localities that occupy no more than two time intervals) shows only minor differences with trends based on the entire dataset, with two systematic exceptions: Cretaceous diversifications are delayed using the temporally constrained dataset, such that diversification rates are much higher than the trends shown here; and overall magnitudes are lower, although qualitative patterns remain unchanged. Specific differences occur due to the effects of individual aberrant localities; for instance the presence of crown group crocodilians in the pre-Paleocene southern hemisphere is based solely on one locality, Nagpur, India, which is dated as Late Cretaceous to Paleocene (Sahni et al., 1984; see discussion in Chapter V). Such aberrations are generally easy to spot and are referred to in the text and figure captions where appropriate. Figures VII.24 to VII.31 show the latitudinal distribution of generic diversity for each of the major crocodilian taxonomic groups discussed in the text.



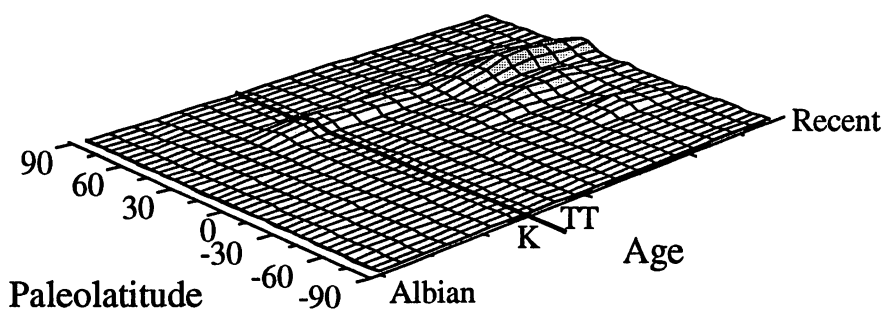
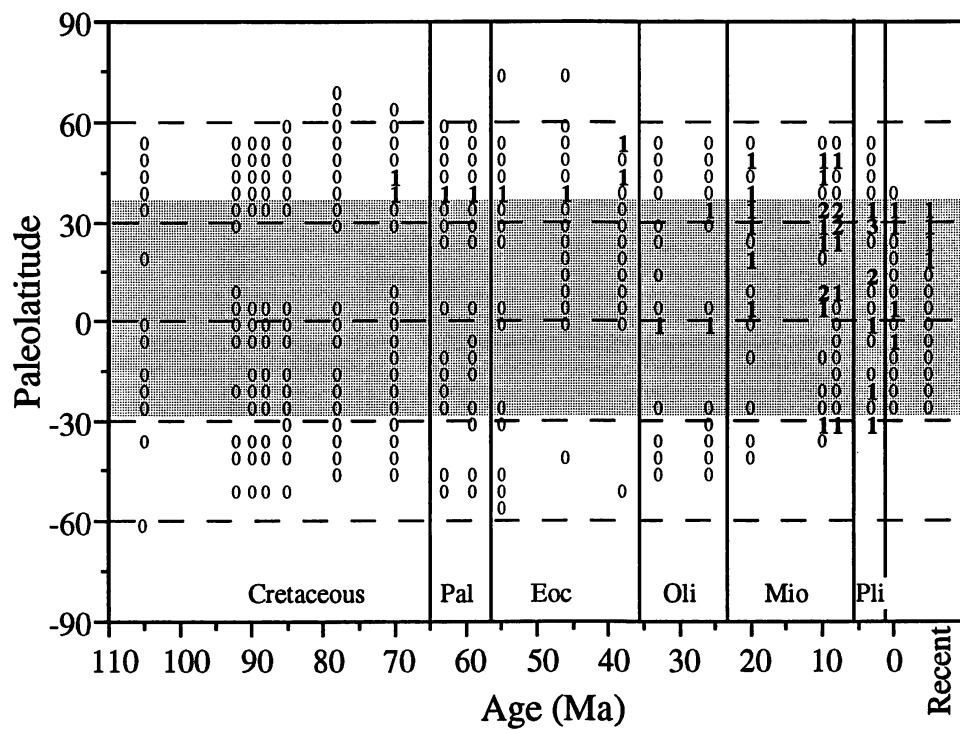
**FIGURE VII.24. The paleolatitudinal distribution of all alligatorid genera through time.**

Values represent absolute diversity counts in each 5° latitudinal zone and for each time interval using the entire crocodilian dataset. Zero values represent points where crocodilian data exist, but where alligatorids are not represented. The gray shaded region represents the approximate latitudinal range occupied by modern crocodilians. The smoothed surface plot (see Figure VII.23 caption) shows the data given in the data array. The early diversification of alligatorids in the northern hemisphere is clear. Expansion into the southern hemisphere occurs only after the K-T boundary. (The recent data is offset from 0 Ma in order that it not obscure the Pleistocene data.)



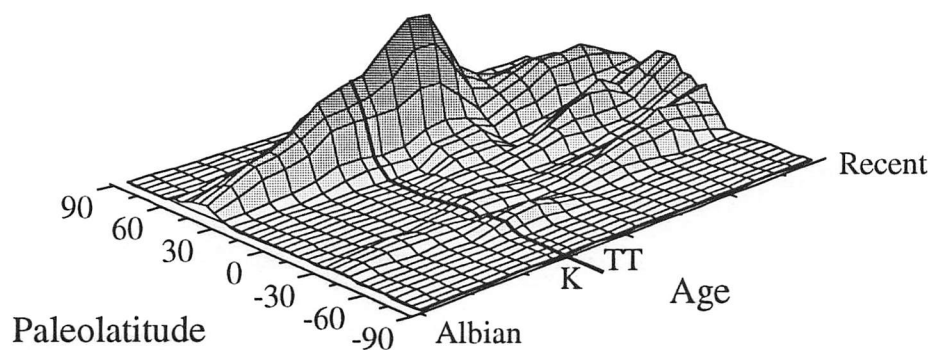
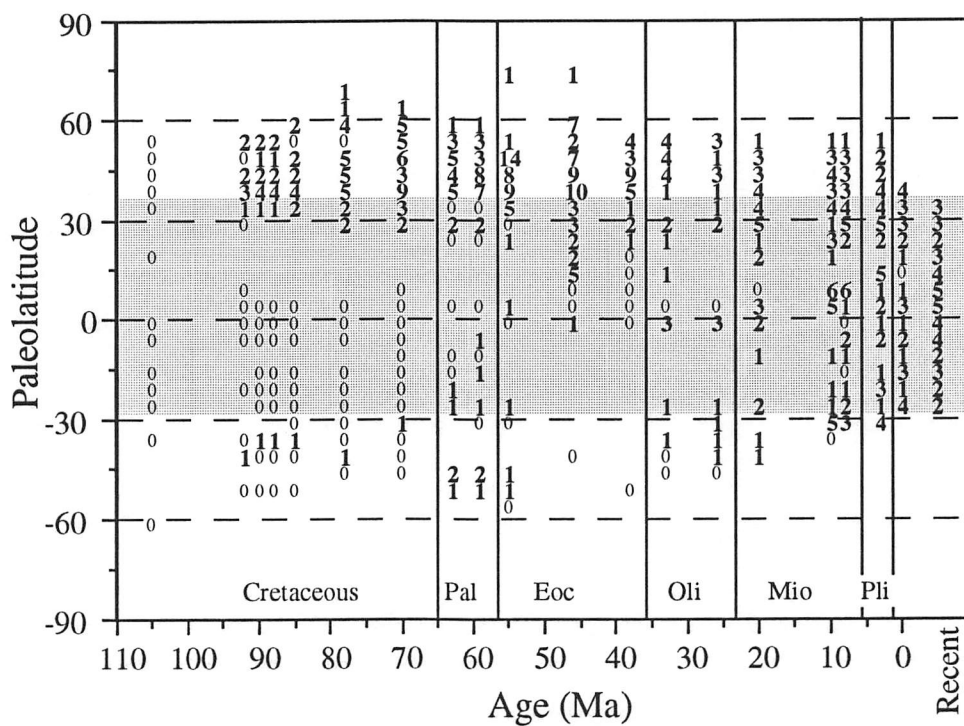
**FIGURE VII.25. The paleolatitudinal distribution of all crocodylid genera through time.**

See caption, Figure VII.24, for details. The occurrence of crocodylids in the southern hemisphere prior to the Tertiary is based on one poorly constrained occurrence in India, which may be ignored (e.g. Nagpur, see text; the paleolatitudinal variation of this one locality represents the motion of India during the Late Cretaceous).



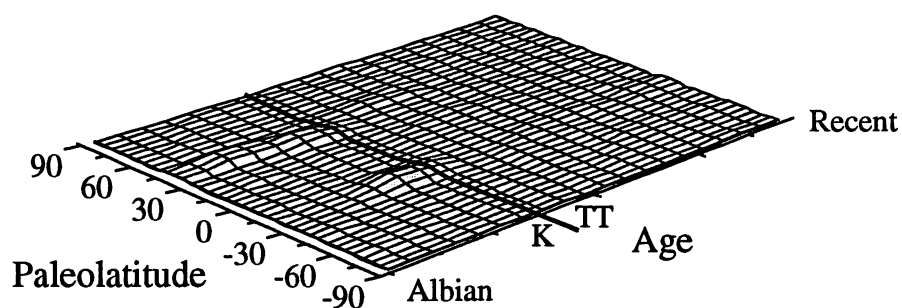
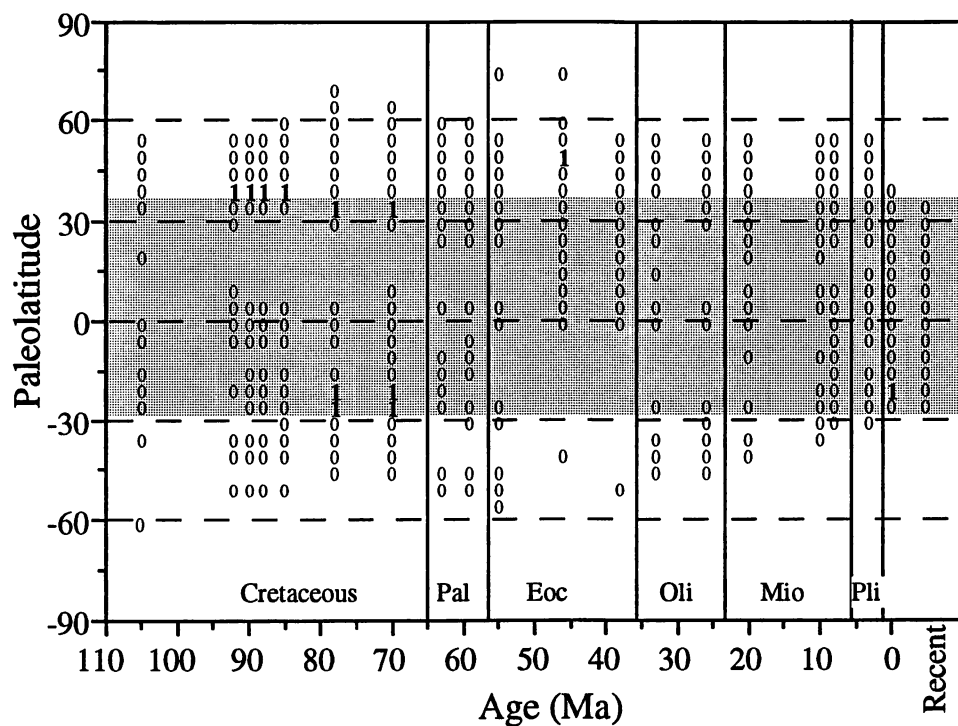
**FIGURE VII.26.** The paleolatitudinal distribution of all gavialid genera through time.

See caption, Figure VII.24, for details. Gavialids are shown to originate in the northern mid-latitudes during the Late Cretaceous and to have never have been particularly diverse in any place.



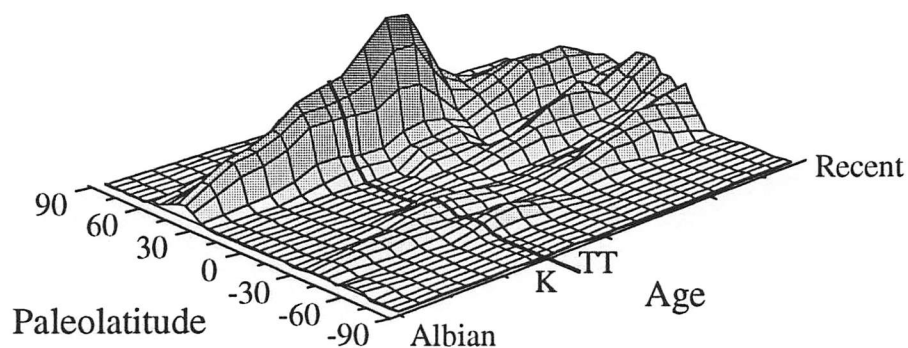
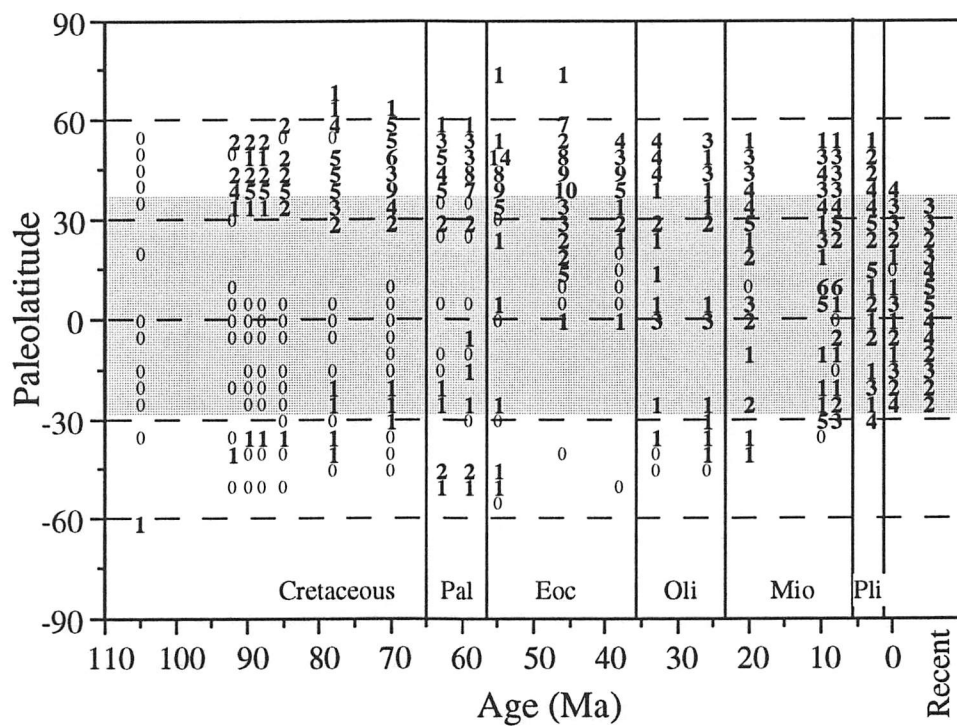
**FIGURE VII.27.** The paleolatitudinal distribution of all crown group genera through time.

See caption Figure VII.24, for details. This distribution represents the sum diversity of crocodylids, alligatorids and gavialids.



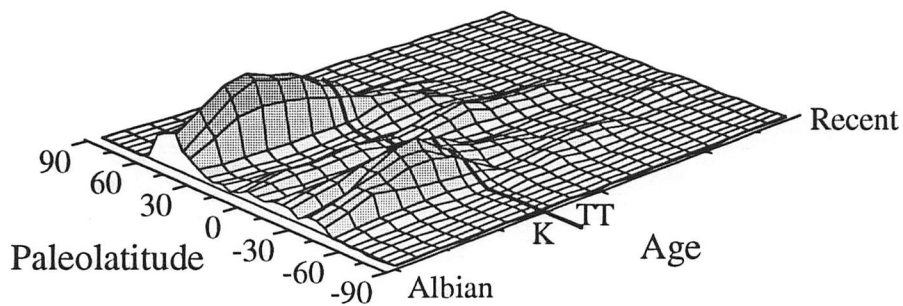
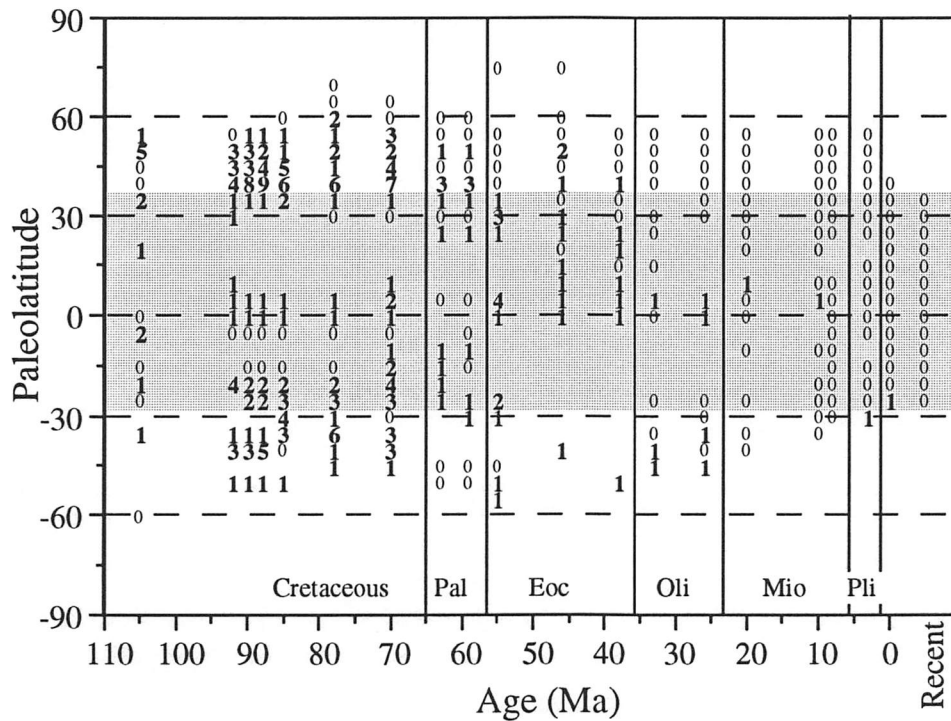
**FIGURE VII.28.** The paleolatitudinal distribution of all non-crown group "eusuchian" genera through time.

See caption, Figure VII.24, for details. No trends are apparent given the few genera represented.



**FIGURE VII.29.** The paleolatitudinal distribution of all "eusuchian" genera through time.

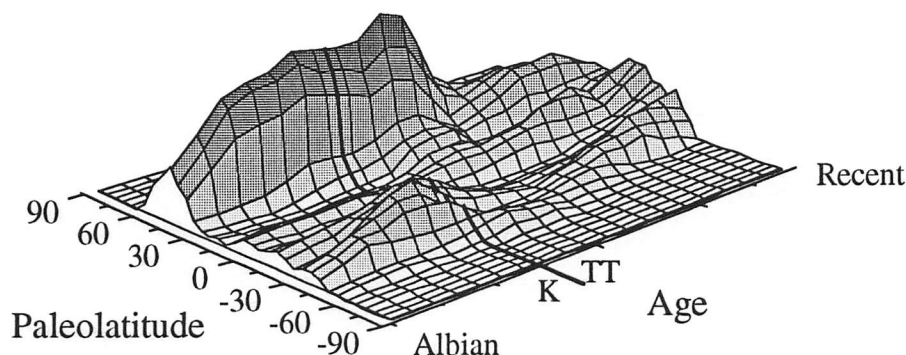
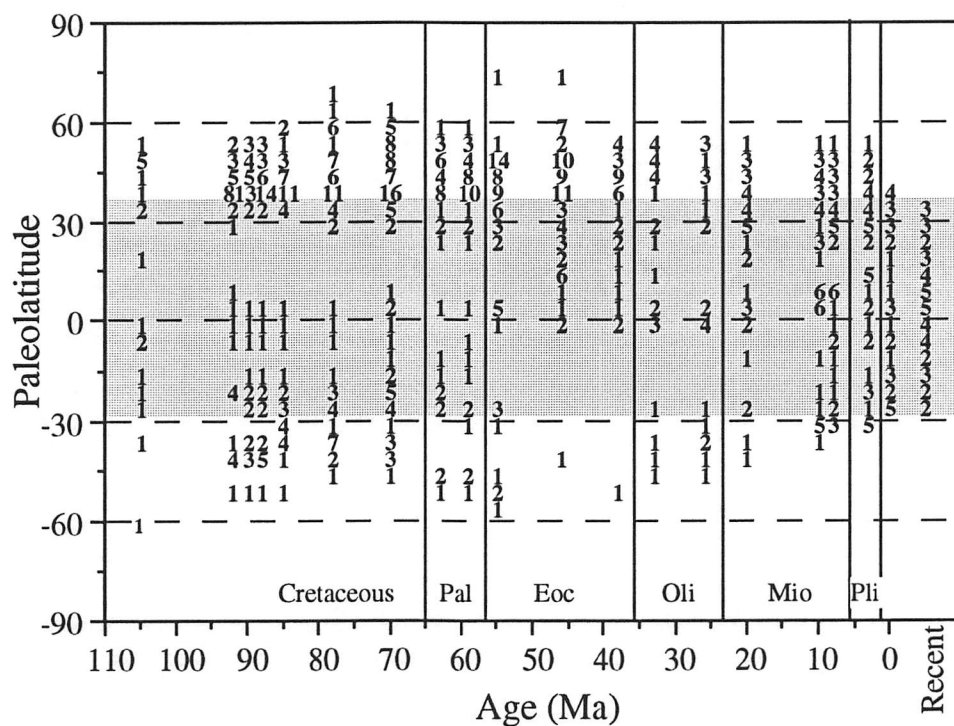
See caption, Figure VII.24, for details.



**FIGURE VII.30. The paleolatitudinal distribution of "mesosuchian" genera through time.**

See caption, Figure VII.24, for details. The overall trends in this figure illustrate relatively high "mesosuchian" diversities in northern and southern mid-latitudes, with lower diversities in equatorial regions. Diversities in all paleolatitudes decrease after the Cretaceous, but only after the Eocene does the group become paleolatitudinally more restricted.





**FIGURE VII.31. The paleolatitudinal distribution of all crocodilian genera through time.**

See caption, Figure VII.24, for details. The northern hemisphere highs are readily apparent in this figure, dropping in the Late Eocene. A more interesting trend is shown by the bimodal peak in diversity during the Late Cretaceous. In the Paleogene, equatorial diversities begin to increase creating a trimodal pattern, which coalesces to form one equatorial peak at the present. Given the small numbers represented, it is presently difficult to assess how ubiquitous such trends are, although such a bimodal distribution of diversity and productivity has been suggested by other workers. Normalizing for the effects of sampling (by dividing the diversity in each grid square by the number of localities: not shown) makes these trends all the more prominent, while also balancing peaks in northern and southern hemispheres.

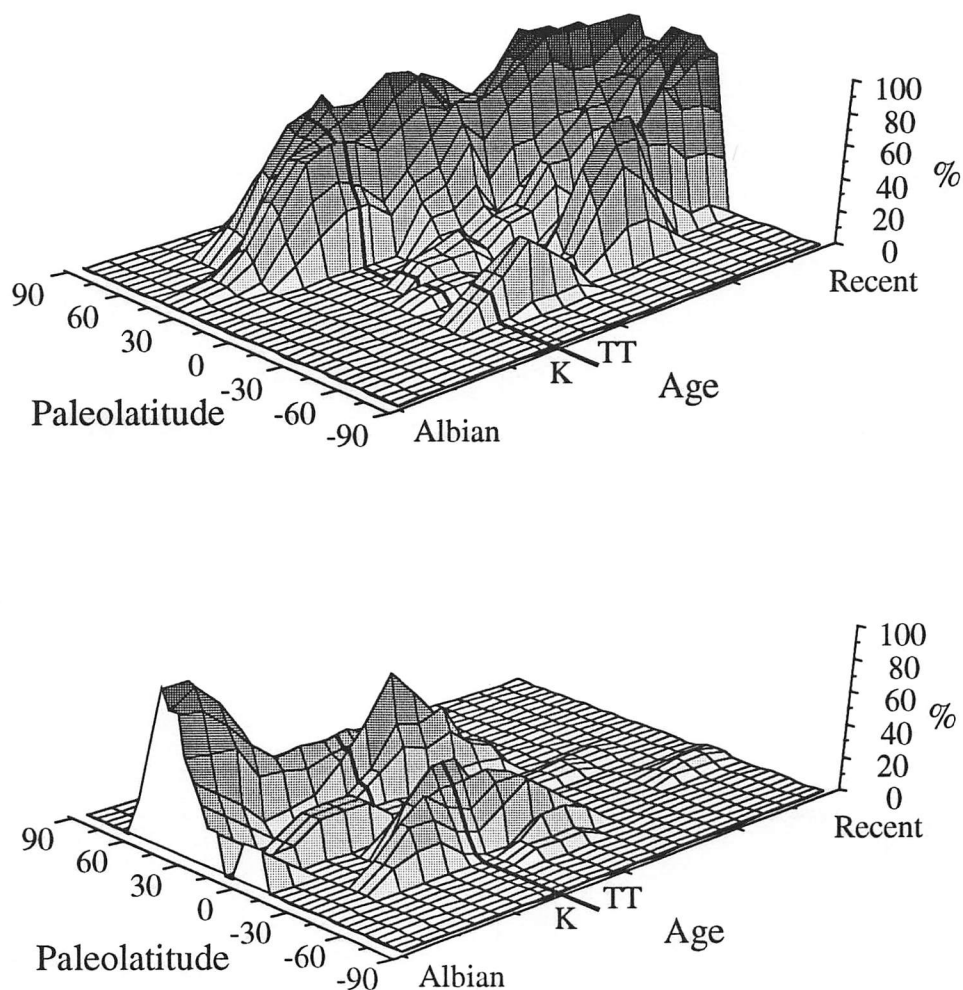
A number of trends are apparent in this dataset. Crown group crocodilians are shown to be of northern hemisphere origin, which corroborates not including the Lightning Ridge "eusuchian" (Molnar, 1980) in the crown group. Not until the Paleocene does this group expand into southern latitudes (ignoring the Nagpur locality; Figure VII.25). This expansion appears to be at the expense of "mesosuchians" which unlike "eusuchians" do suffer a major extinction at the K-T boundary. The changes in diversity between these two groups is illustrated in Figure VII.32, which illustrates the percentage of the total crocodilian generic diversity represented by crown group crocodilians and "mesosuchians".

A further trend apparent in the data is that peak diversity occurs in the northern mid-latitudes during the Cretaceous and early Tertiary, but then moves to lower latitudes during the middle Cenozoic. Whether this reflects an actual difference in the distribution of biodiversity between "hot-house" and "ice-house" worlds or is an artifact of sampling, is unclear.<sup>6</sup>

In terms of the composition of this diversity, it is clear from these figures that all crown group families originate in North America, although subsequent histories differ. A more detailed multivariate analysis is in progress, but for the moment these figures provide the basic trends which are readily apparent. This history can also be examined by looking at the distribution of first (FA) and last (LA) appearances. Values are calculated by taking the complete range of each genus and then looking at the paleolatitudinal zones occupied by the genus at the beginning and end of this range. Given the temporal resolution of the data, both FA and LA for a genus may occupy more than one paleolatitudinal zone. Each case

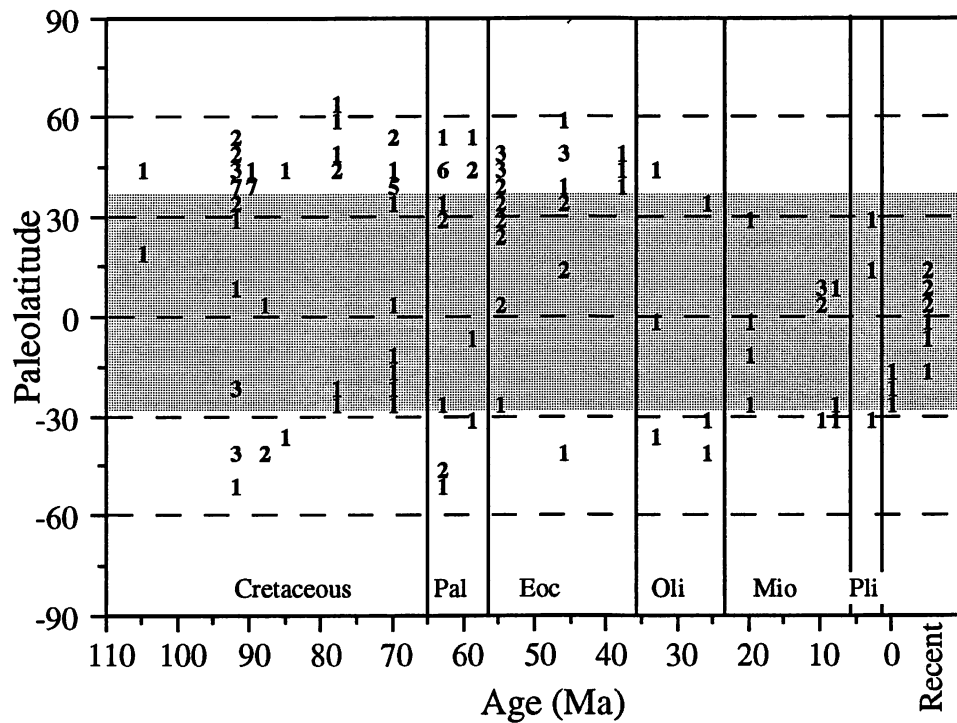
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6. The peak diversity of Jurassic floras appears to also occur in midlatitudes rather than equatorial regions (pers. comm. A. Rees and A. M. Ziegler). Further work on this issue is in progress.



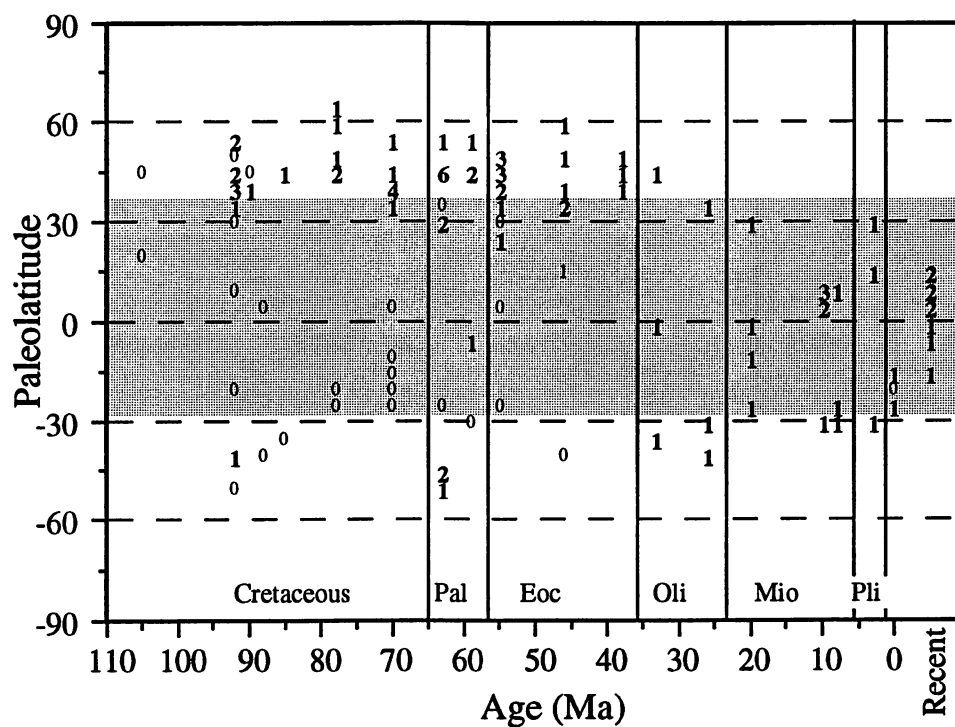
**FIGURE VII.32. The percentage of diversity represented by crown group crocodilians (top) and "mesosuchians" (bottom) as a function of paleolatitude and time.**

The percentage composition of crocodilian diversity is calculated for each 5° paleolatitudinal band in each time interval. In each case the percentages are represented by surface diagrams in which the data have been smoothed once using the algorithm described in the caption for Figure VII.24.



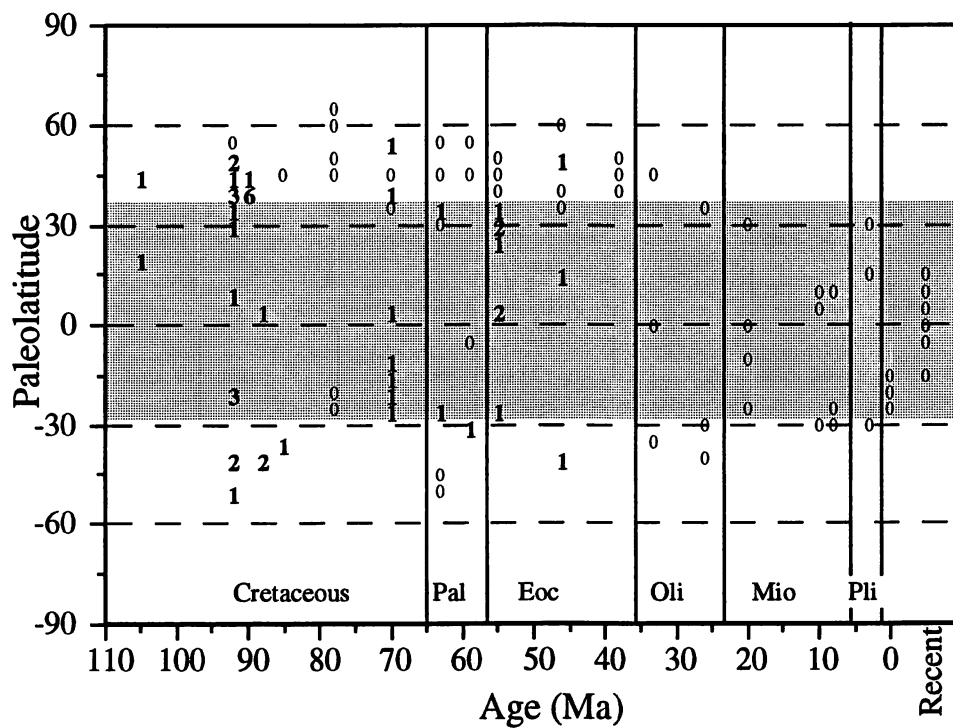
**FIGURE VII.33. The paleolatitudinal distribution of generic first appearances (FA's) for all crocodilians as a function of time.**

In each of the following figures the paleolatitudinal zone in which each genus first appears counts as a score and these are summed in each case to produce the distribution of first appearances through time.



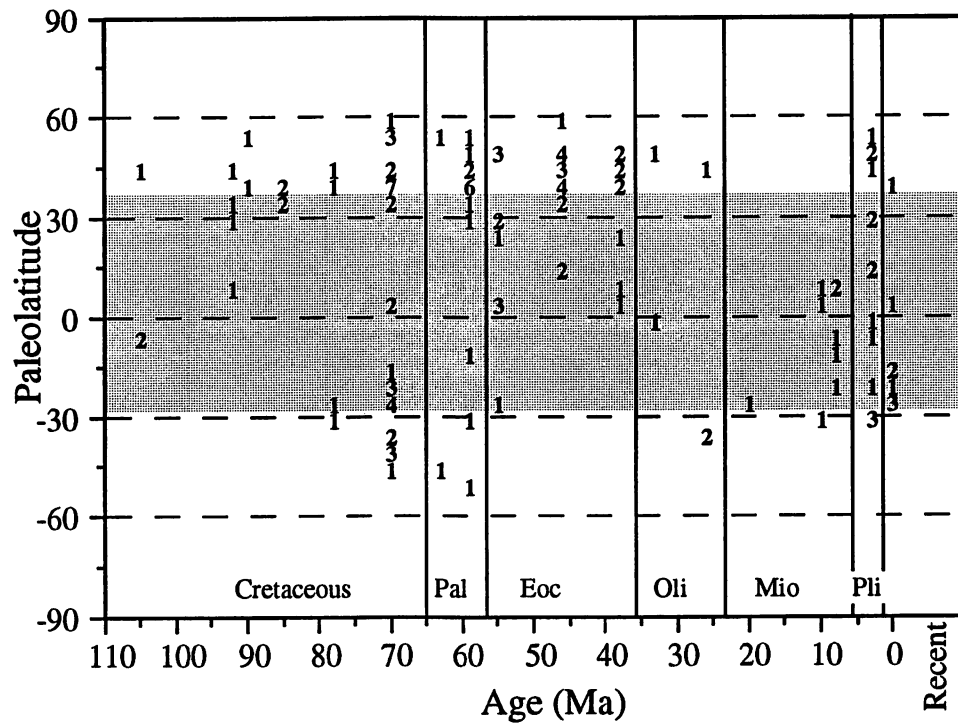
**FIGURE VII.34. The paleolatitudinal distribution of generic first appearances (FA's) for all crown group crocodilians as a function of time.**

See caption, Figure VII.33, for details. The Cretaceous southern hemisphere FA is due entirely to the poorly resolved Indian locality of Nagpur and may be ignored (see text).



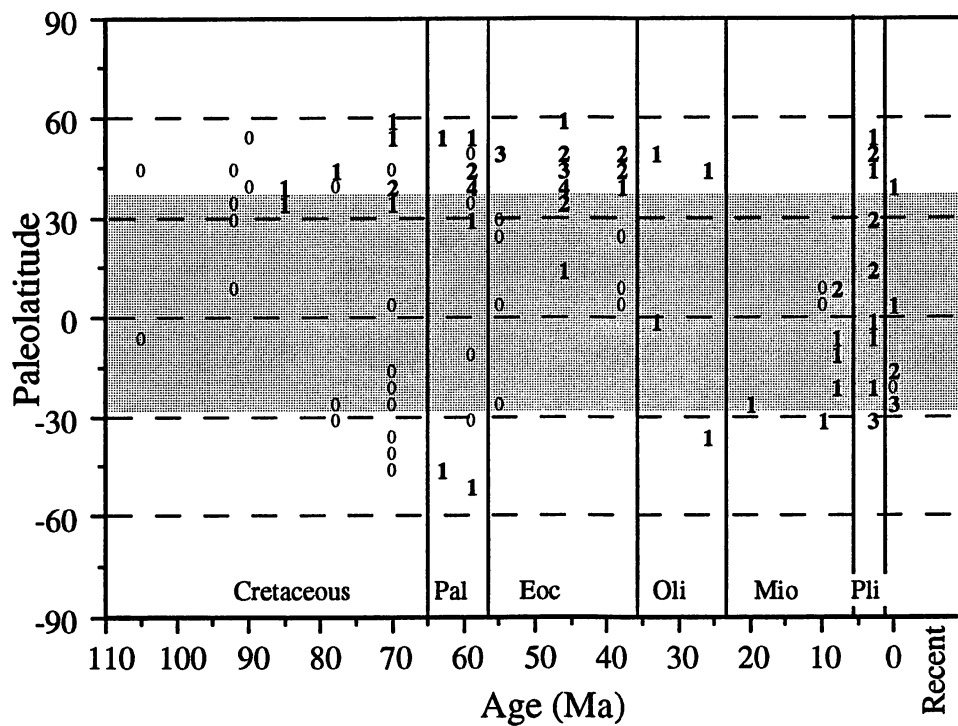
**FIGURE VII.35.** The paleolatitudinal distribution of generic first appearances (FA's) for all "mesosuchians" as a function of time.

See caption, Figure VII.33, for details.



**FIGURE VII.36. The paleolatitudinal distribution of generic last appearances (LA's) for all crocodilians as a function of time.**

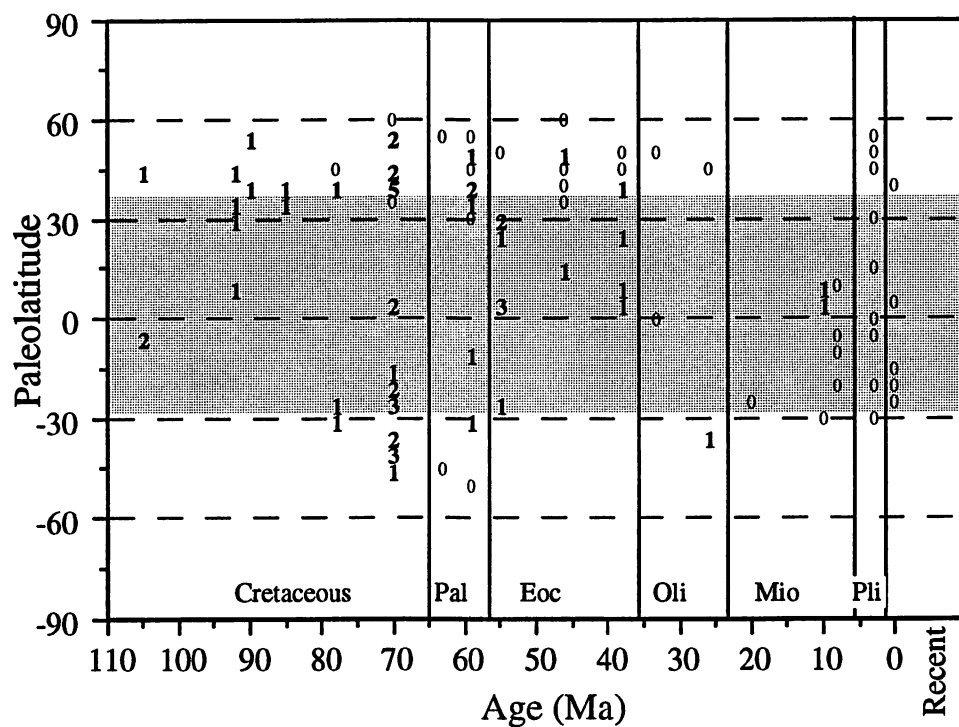
In each of the following figures the paleolatitudinal zone in which each genus last appears counts as a score and these are summed in each case to produce the distribution of last appearances through time.



**FIGURE VII.37. The paleolatitudinal distribution of generic first appearances (LA's) for all crown group crocodilians as a function of time.**

See caption, Figure VII.36, for details.



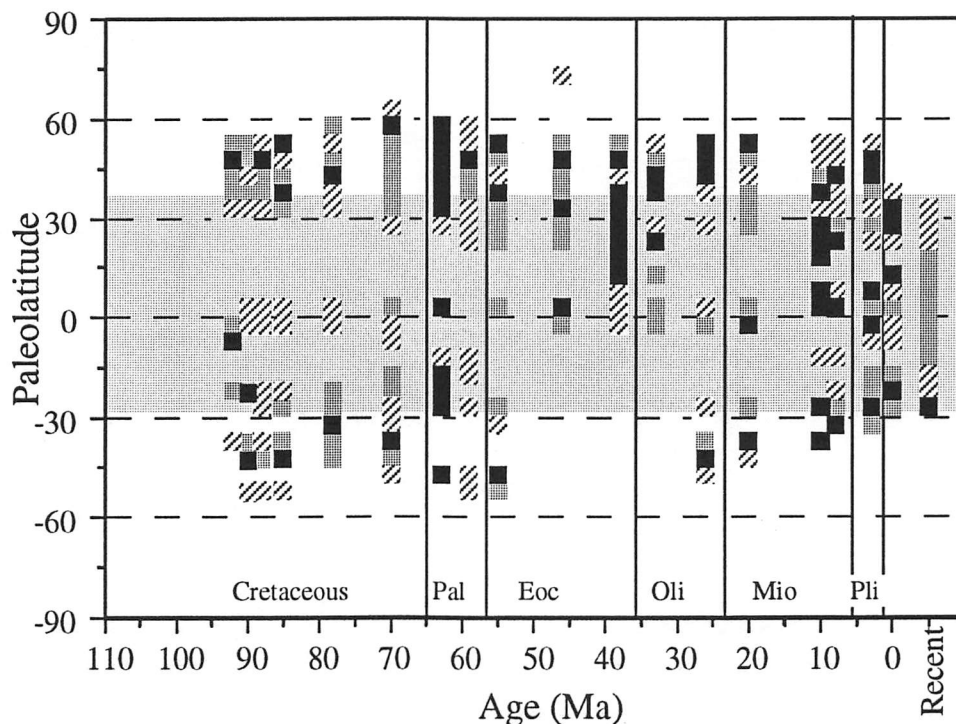


**FIGURE VII.38.** The paleolatitudinal distribution of generic first appearances (LA's) for all "mesosuchians" as a function of time.

See caption, Figure VII.36, for details.

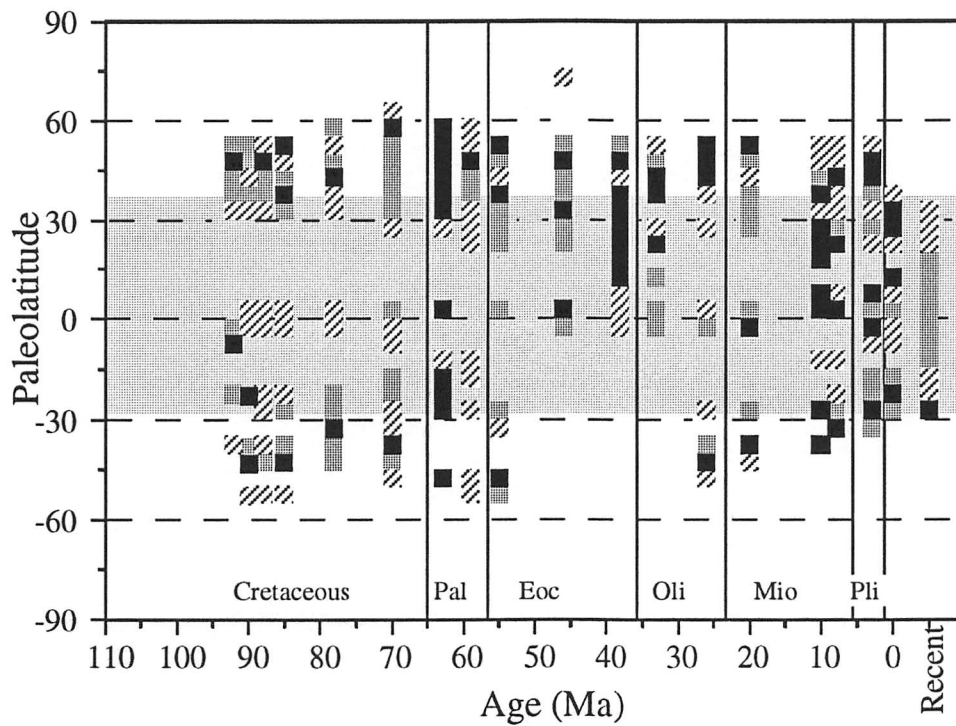
counts as a score. The results are shown in Figures VII.33-VII.38. Again the northern hemisphere bias is apparent.

The trends given in the above figures can be summarized by showing the direction (increase or decrease in diversity) in consecutive intervals. Thus decreases in diversity between two intervals at each paleolatitudinal band are recorded in the second interval. These results are shown in Figures VII.39-VII.41. This portrayal does not show the magnitude of the changes and this must be borne in mind. The Middle to Late Eocene transition shows a general decrease in diversity throughout the recorded range, consistent with the global diversity trends discussed above. However, there is a general decrease in diversity over the K-T transition, which represents the 30% turnover observed in the global dataset. Another interesting observation is that in the Miocene the main change using this method appears to be the Early-Middle transition rather than the Late Miocene. Again it must be borne in mind that these plots are dependent on sampling. The transition to the Recent shows extinctions at the poleward peripheries of the latitudinal range, with increases in low latitudes.



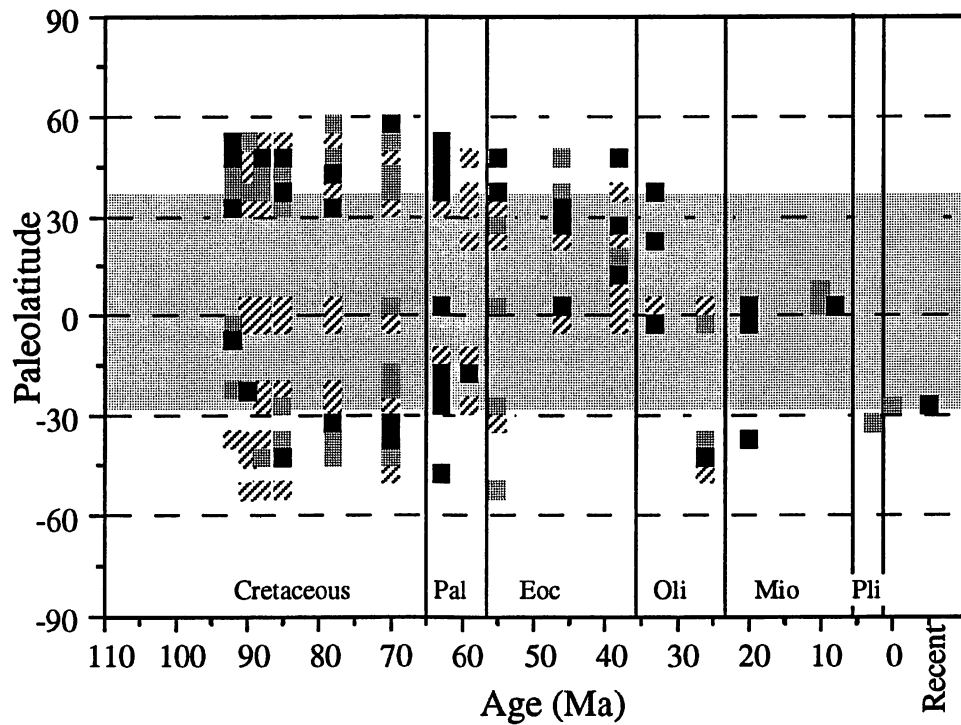
**FIGURE VII.39. The direction of crocodilian diversity between consecutive intervals.**

This figure, and the next two, summarize the diversity data and express them as simply the direction of diversity between consecutive intervals. Black squares represent decreases in diversity from the preceding interval, gray, increases, and cross hatched represents no change. However, this does not provide any indication of the magnitude of the change. All data are used in each case. Where there is no preceding data, no trend is shown. Similarly the absence of data is not assumed to mean a diversity of zero, and consequently high latitude extinctions in the Pleistocene do not show up in this type of figure. This figure shows the trends for all crocodilians. Notice the general decrease in diversity between the Maastrichtian and Early Paleocene, irrespective of paleolatitude. The extinction between the Middle and Late Eocene is also apparent, although whether this change continues into the southern hemisphere is precluded by lack of data. A further major drop in diversity is seen between the Early and Middle Miocene, a change not seen in the global diversity patterns in Figure VII.1. Assuming that high latitude absences in the Pleistocene are real (which is strongly suggested by the good preservational control on Pleistocene distributions--see Chapter V), then the Pleistocene extinctions seem mostly restricted to high northern latitudes based on the available data. Notice that in the transition from the Pleistocene to the Recent the low latitudes show an increase in diversity, higher latitudes no change and the highest latitudes decreases.



**FIGURE VII.40. The direction of crown group crocodilian diversity between consecutive intervals.**

See Figure VII.39 caption for key to symbols. Trends shown by the crown group crocodilians follow those of all crocodilians (see caption for Figure VII.39).



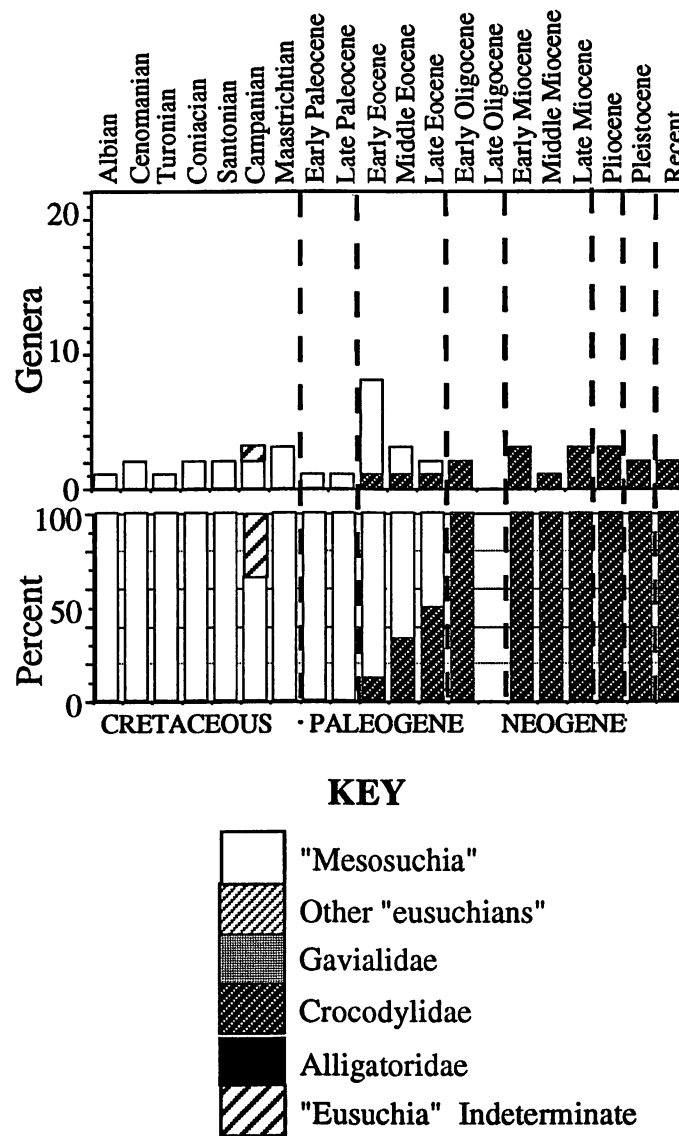
**FIGURE VII.41. The direction of "mesosuchian" diversity between consecutive intervals.**

See Figure VII.39 caption for key to symbols. Again, the transition from Maastrichtian to Early Paleocene is marked by a general decrease in diversity. A further major change is seen across the Late Eocene - Early Oligocene transition, with "mesosuchians" finally precluded from northern latitudes.

### VII.3.2.2. Diversity by Continent

Another way of looking at the historical component of diversity is to examine the changes in diversity by region. Here this is done by continent. While this oversimplifies biogeographic regions, it does represent the basic tectonic divisions through this interval. The results are presented in Figures VII.42-VII.48. Again the bias of the northern hemisphere is readily apparent. The highest diversity in North America is reached in the Late Cretaceous and early Tertiary, the record from the Late Eocene to the Recent being low and essentially flat. In Europe peak diversity occurs in the Eocene, as it does in Asia (the diversity high in the Late Cretaceous of Asia is largely driven by "mesosuchians"). Elsewhere the record is limited and diversities remain low. In India the first appearance of gavials does not occur until after collision of India with Eurasia, suggesting that the present restriction of gavials to non-marine environments may be historically true as well.

Another way of aiding understanding of these trends is shown in Figure VII.49, which presents the proportion of the total diversity represented by the diversity of each continent. What should be borne in mind with these figures is that the occurrence of one genus in more than one continent scores in each instant and so the sum of continental diversity is greater than the global diversity for each group. Nonetheless the overall trends are informative. We can see the origin of both alligatorids and gavialids in North America, crocodylids occurring first in at least three continents (North America, Asia and Europe, which together formed Laurasia). The occurrence in India has already been discussed and probably should be ignored until the Paleocene. For the "mesosuchians" the change in overall distribution seems to occur in the Early Eocene and especially at the end of that Epoch, despite the major extinction of the group at the K-T. Having said this, Figure



**FIGURE VII.42. African crocodilian generic diversity and percentage composition.**

The key shown here also applies to figures VII.43-VII.48. The full dataset is used in these diagrams.

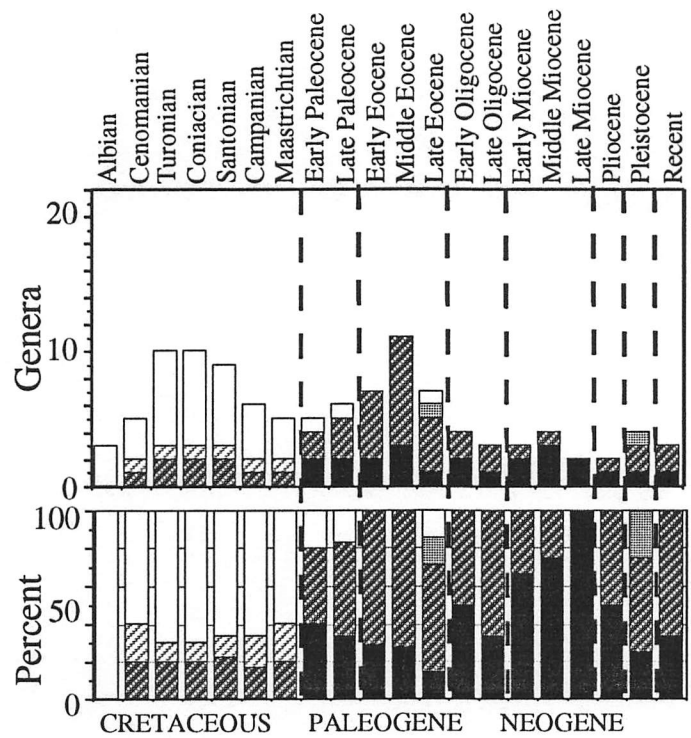


FIGURE VII.43. Asian crocodilian generic diversity and percentage composition.

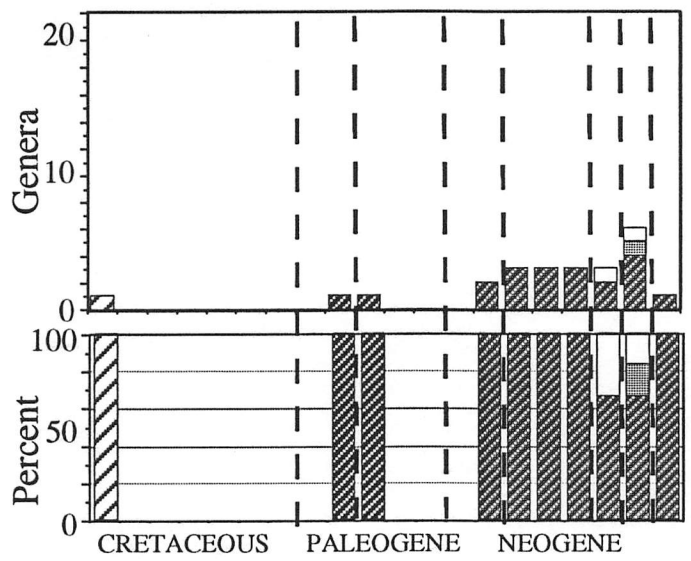
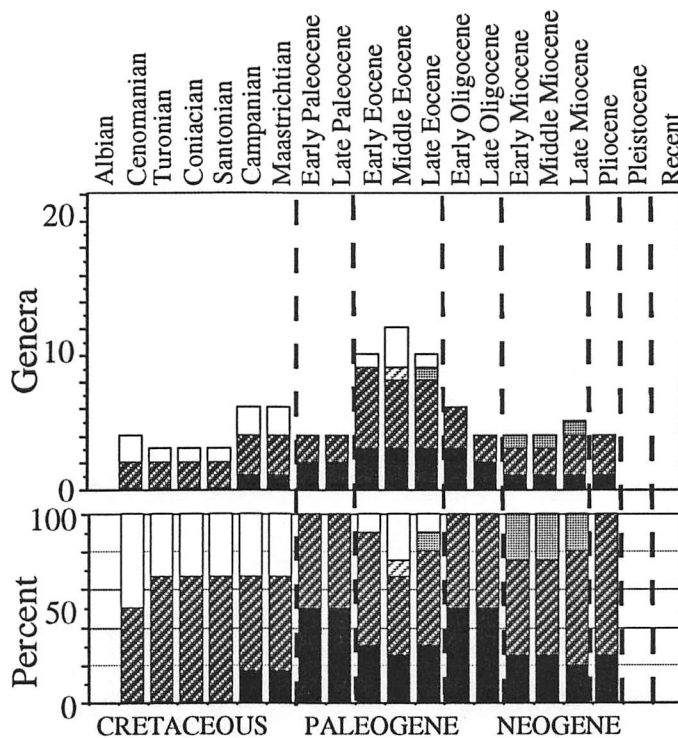


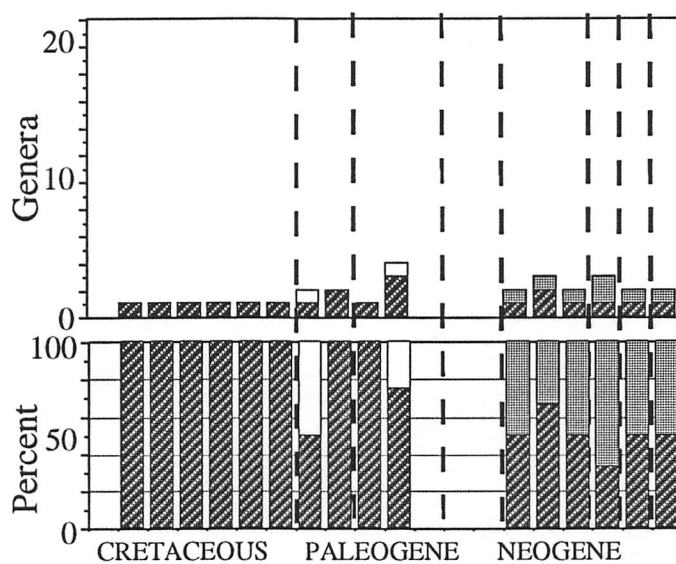
FIGURE VII.44. Australian crocodilian generic diversity and percentage composition.

See Figure VII.43 for stage names.



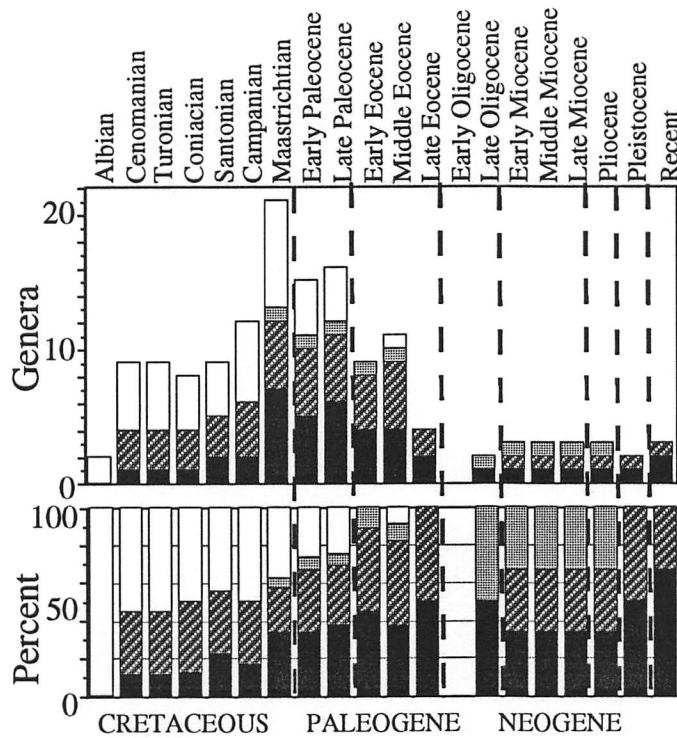


**FIGURE VII.45. European crocodilian generic diversity and percentage composition.**



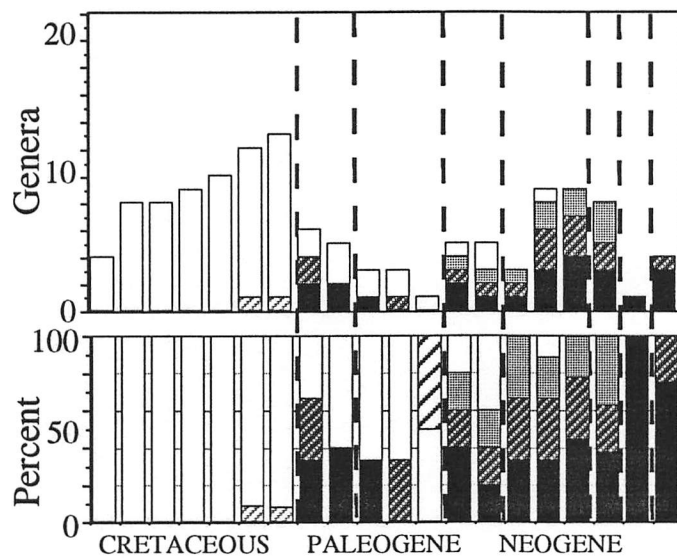
**FIGURE VII.46. "Indian" (includes Pakistan and Bangladesh) crocodilian generic diversity and percentage composition.**

The crocodilian genus in the Cretaceous is an artifact of the temporally poorly resolved locality at Nagpur (see text).



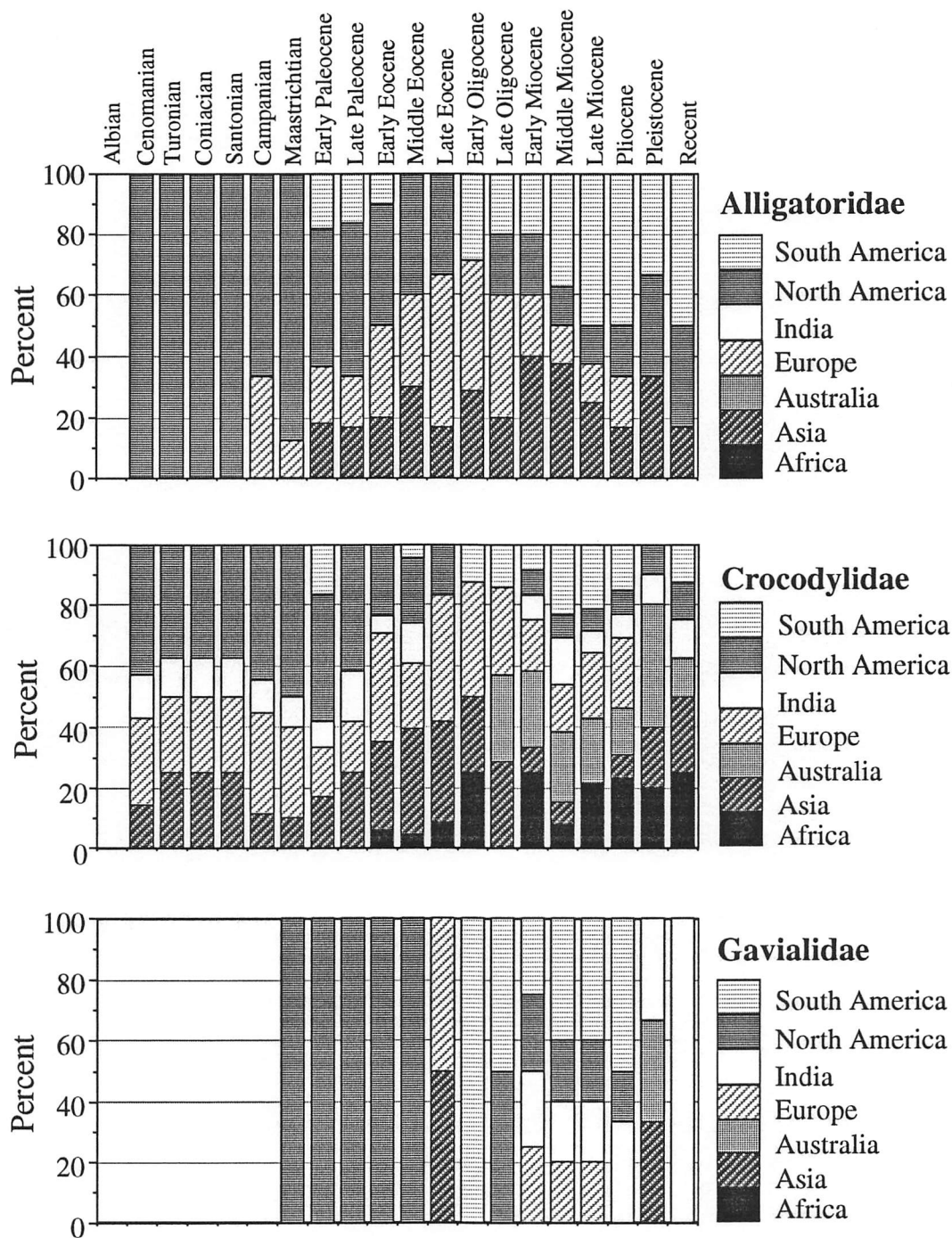
**FIGURE VII.47. North American crocodilian generic diversity and percentage composition.**

See Figure VII.42 for key.



**FIGURE VII.48. South American crocodilian generic diversity and percentage composition.**

See Figure VII.42 for key.



**FIGURE VII.49. Proportion of crocodilian diversity represented in each continent.**

The proportion of global generic diversity for each crocodilian group which is represented in each continent. The stage names given on the top plots apply to all graphs in this figure.

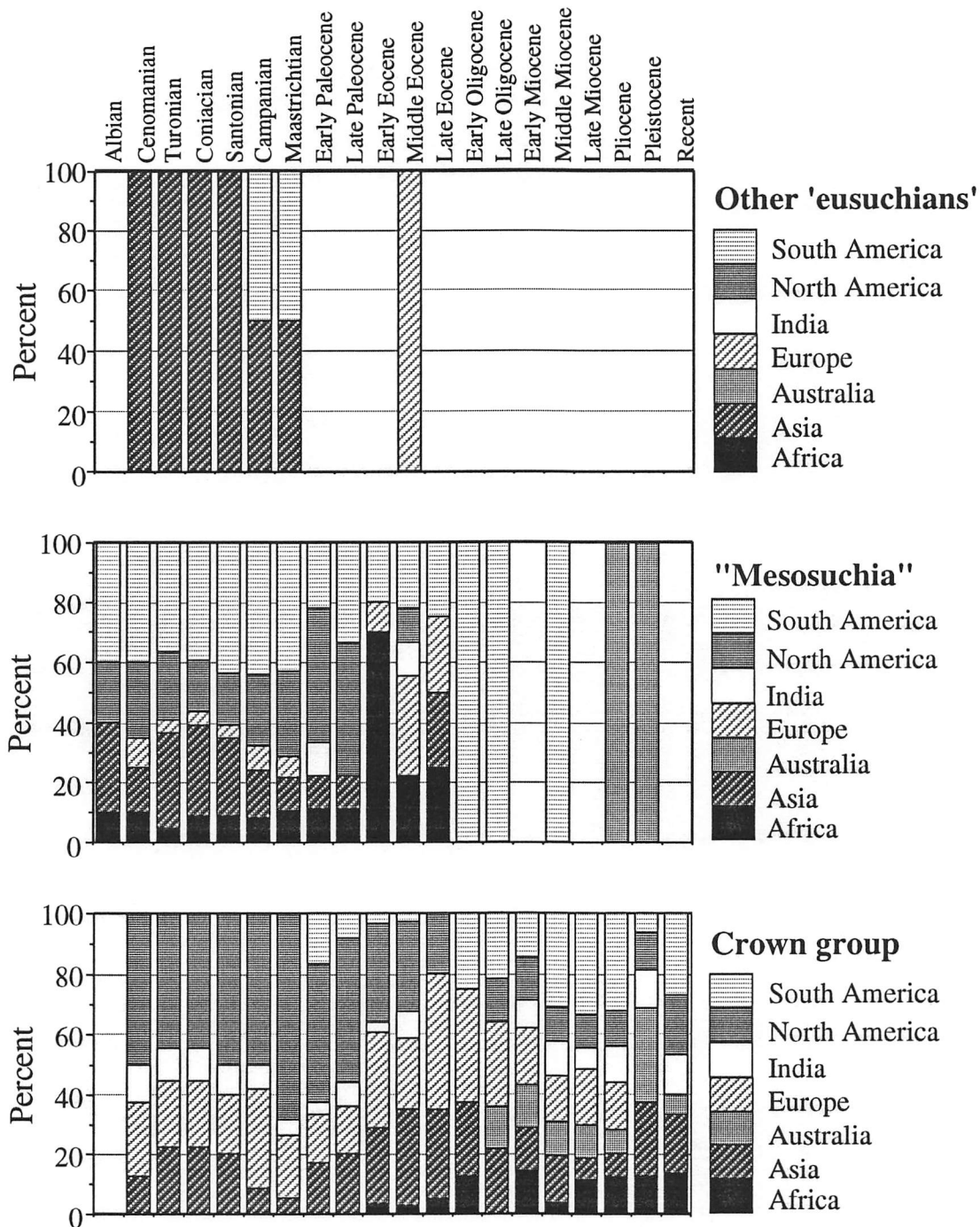


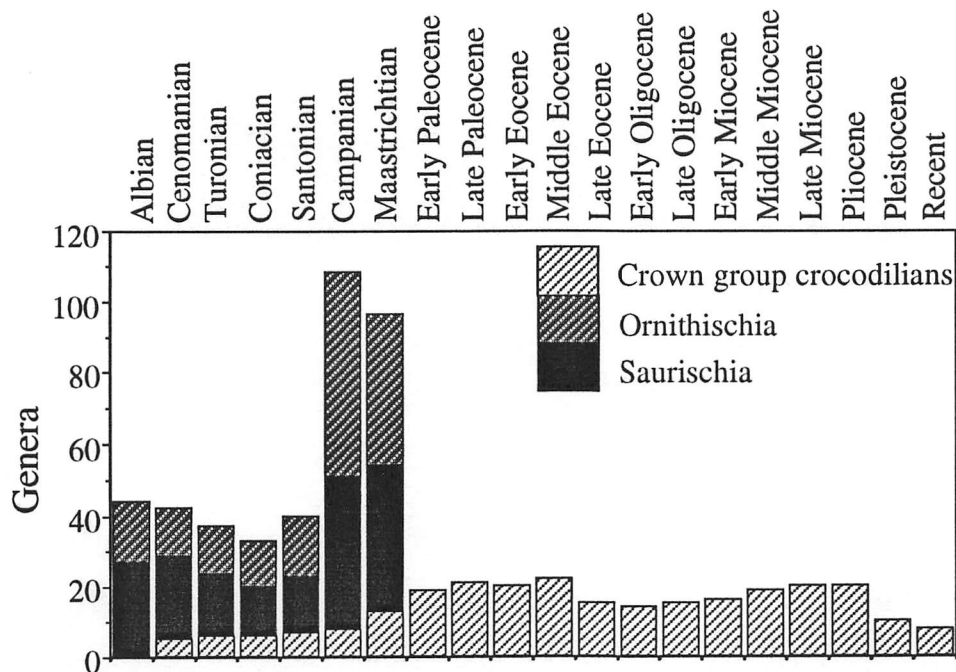
FIGURE VII.49. continued.

VII.64 shows that the composition of the crocodilian faunas in South America change at this boundary with the introduction of crown group crocodilians, a change already described earlier. It should be noted at this point that the term "mesosuchia" incorporates potentially disparate phylogenetic groupings. Indeed the lingering members of this "group" during the middle and late Tertiary are in fact dominated by a single family, the Sebecidae, which has been raised to a higher taxonomic level by other workers (Steel, 1973).

### VII.3.3. Extinction and the K-T Boundary

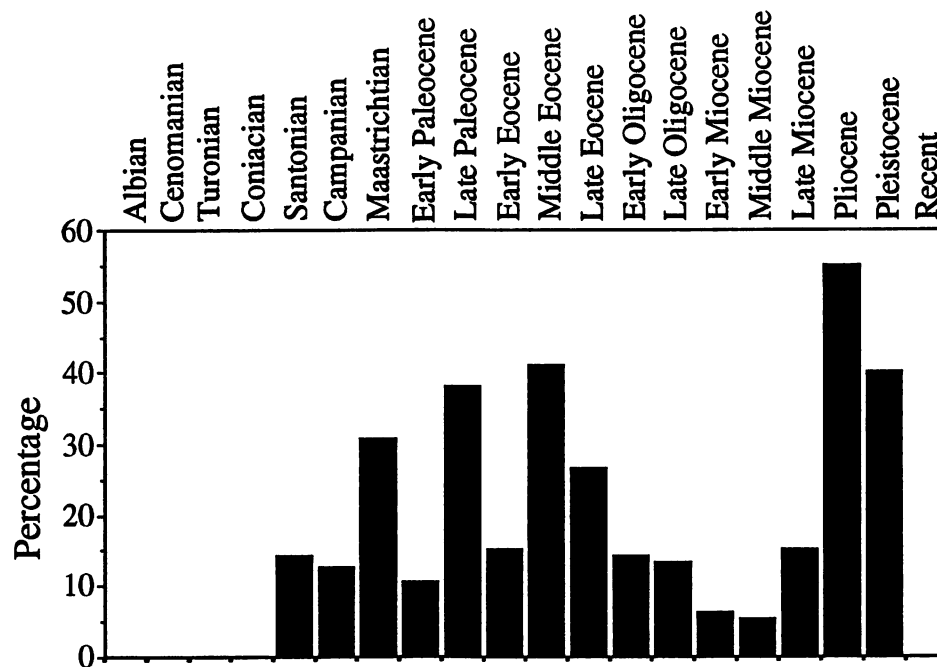
One perhaps surprising observation of the pattern of crown group crocodilian diversity is that while there are two clearly apparent extinction events (Figure VII.2), neither occurs at the K-T boundary. Indeed, for crown group crocodilians, approximately exponential diversification continues over this boundary (Figures VII.14-VII.16). That crown-group crocodilians seem little affected at the K-T has already been observed on a local scale by Hutchison (1982). The two observed crocodilian extinctions (Middle/Late Eocene and Late Miocene/Pliocene) are coeval with known climatic changes (see the marine isotopic curve, Figure II.13) and are also reflected in the crocodilian distributional changes presented in Chapter V. This has been used by Markwick (1994) to suggest that whatever caused the observed mass extinctions in other groups at the K-T (Figure VII.50), it was not a long-term climate change.

Percentage turnover at the K-T boundary (Figure VII.51) shows a change of about 30%, but it is unclear how significant a turnover this is. Higher turnovers are shown at the end of the Late Paleocene, Middle Eocene, Pliocene and Pleistocene. Indeed, per-genus rates of extinction during the K-T transition remain low (Figure VII.3). What differentiates the change at the K-T from the other intervals of high turnover is that it is followed by a



**FIGURE VII.50. Dinosaur and crown group crocodilian generic diversity.**

Diversities calculated using equation (1). Besides containing data on crocodilians and turtles the dataset used in this study also contains information on all other vertebrates, including dinosaurs. Here the generic diversity of saurischian and ornithischian are shown using a stacked column plot. Upon this is superimposed the diversity of crown group crocodilians (i.e. the total height of Cretaceous columns is the sum of dinosaur diversity only). The major extinction suffered by dinosaurs at the K-T boundary is not represented in the crocodilian data.

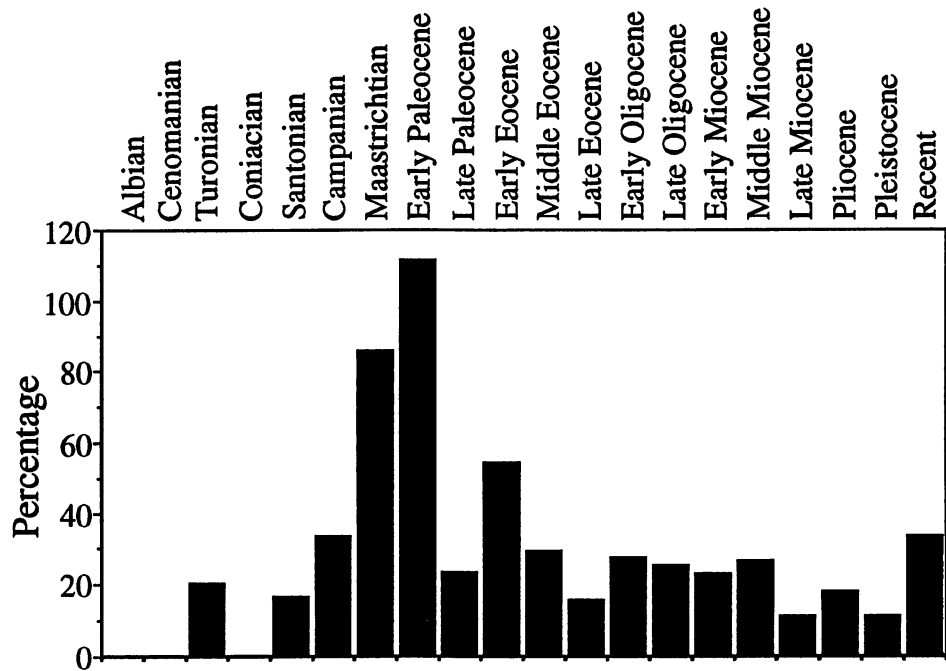


**FIGURE VII.51. Percentage turnover of crown group crocodilian genera.**

The number of crown group genera that become extinct in an interval as a percentage of the standing generic diversity. As calculated from:  $(E / D) * 100$ , where E is the number of extinctions in the interval and D is the standing diversity calculated from equation (1). Note that the highest peaks are in the Pliocene ( 55%) and Pleistocene ( 40%), when we see the greatest drop in crown group crocodilian generic diversity; the Middle Eocene ( 40%) when we see the other major drop; the Late Paleocene ( 40%) and Maastrichtian ( 30%). The relatively high turnovers in the Late Paleocene and Maastrichtian are both compensated by extremely high numbers of originations in the subsequent time interval (Figure VII.52).

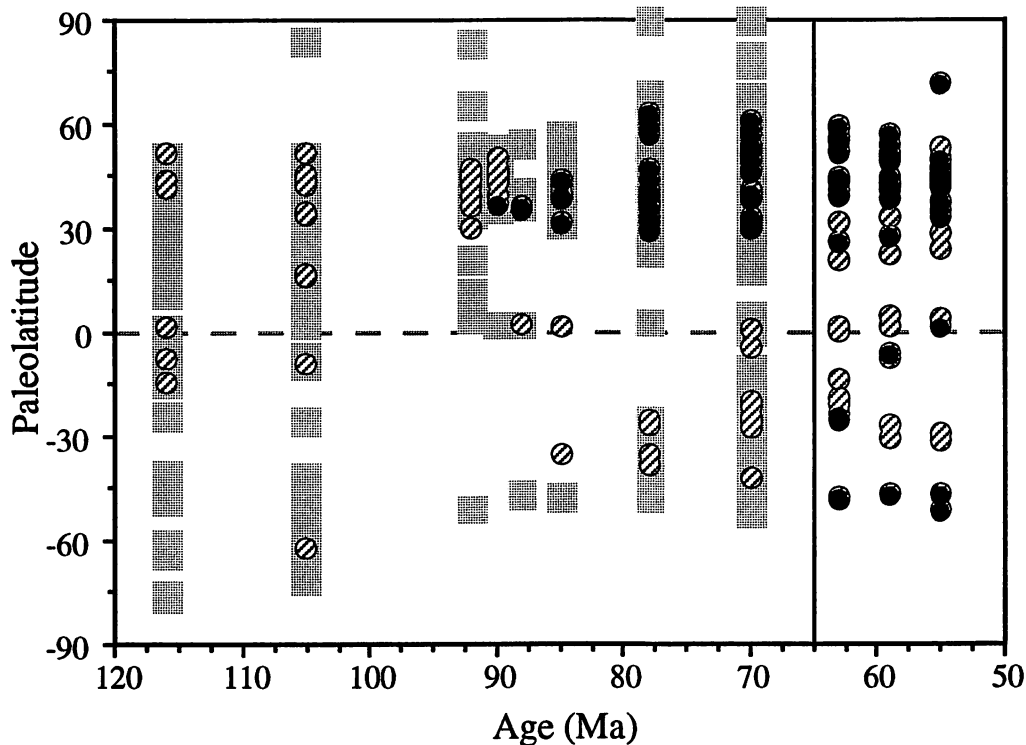
interval with very high per-genus rates of origination (Figure VII.3; the relatively low origination rates after the other "extinction events" may suggest some longer-term environmental constraint and thereby a lower generic "carrying capacity"). This is even more apparent when originations are plotted as a percentage of all survivors from the preceding interval (Figure VII.52; in this case the highest value is for the Early Paleocene). These observations are consistent with an hypothesis of a short-term extinction event (the 30% turnover), with immediate recovery. It is also consistent with a more insidious explanation, that the changes over the K-T are taxonomic. This is more difficult to qualify (needs cladistic analysis), but in any case would mean that actual turnover is lower than shown. Regardless, the K-T "event" appears to have had little long-term 'impact' on crown group crocodilian diversity, an effect that would be anticipated if climate were solely responsible for extinctions at this juncture, even if the climate change were short term--given its deleterious effect on dinosaurs. A climate change might also be expected to affect high-latitude taxa more than low latitude forms--especially a cooling--but the paleolatitude distribution of crown group crocodilian extinctions shows no such systematic differences (Figure VII.40; note that such a differential response is seen in the transition from the Pleistocene to the Recent). This distribution represents the sum diversity of crocodylids, alligatorids and gavialids. Throughout the Late Cretaceous the latitudinal range of dinosaurs extends far beyond the poleward limit of crocodilians (Figure VII.53). This suggests that dinosaurs may have been able to withstand cooler conditions than crocodilians (note the absence of crocodilians from the high latitude dinosaur localities of the Colville River, Alaska, Parrish et al., 1987; Otway Basin, southern Australia, Colbert, 1991; and especially Antarctica, Rich et al., 1988). Given this it is difficult to see how a purely climatic explanation for the K-T extinctions can possibly account for the preferential destruction of a more cold-resistant group and the survival of a demonstrably cold-sensitive group.





**FIGURE VII.52. The number of crown group crocodilian origins as a percentage of the surviving genera from the preceding interval.**

This shows the number of origins in each interval as a function of the number of survivors from the preceding interval: essentially the number of genera from which new genera can appear. Values are calculated using:  $(O_t / S_{t-1}) * 100$ , where  $O_t$  is the number of origins in the interval and  $S_{t-1}$  is the number of surviving genera from the previous interval,  $t-1$  (such that  $S_{t-1} = D_{t-1} - E_{t-1}$ ). The very high values for the Maastrichtian, Early Paleocene and, to a lesser extent, that of the Early Eocene, show why these intervals do not show up as times of drops in diversity. Interestingly, the increase from the Santonian through Early Paleocene is exponential (a linear regression through the natural log of this data for these four intervals gives an  $r^2$  of 0.97; an  $r^2$  of 1.00 is obtained when the Early Paleocene value is ignored). However, it is unclear why this should be true, since it suggests that the exponential increase in origins is independent of the number of genera from which to originate.



**FIGURE VII.53. The paleolatitudinal distribution of dinosaurs and crocodilians.**

Gray squares, dinosaur localities; diagonally filled circles, crocodilian localities; black circles, crown group crocodilians. The latitudinal range of dinosaurs is shown to consistently extend beyond the most poleward limit of crocodilians throughout the Late Cretaceous. This suggests that dinosaurs may have been able to withstand cooler climates than crocodilians, which would preclude any extinction theory based on climate change alone. There is no systematic equatorial shift in the poleward limit of crocodilians across the K-T boundary, as is observed at documented cooling 'events' in the Late Eocene-Oligocene and Pliocene (see Figures V.16 and V.17).

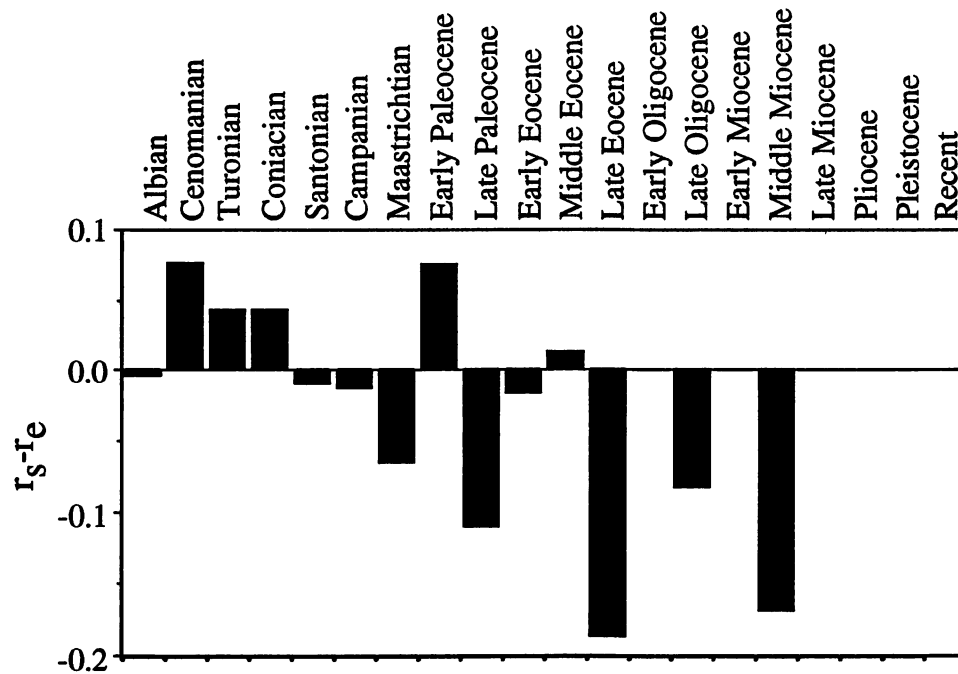
In contrast to crown group crocodilians, "mesosuchian" crocodilians do show a major extinction at the K-T boundary (Figure VII.1). Per-genus extinction rates are high (Figure VII.54) with about 80% of genera from the Maastrichtian being absent from the Early Paleocene (Figure VII.55). Perhaps in response to this extinction, crown group crocodilians subsequently expand their range (although this does not alter their pattern of diversification), especially in South America and Asia (the response in Australia and India is unknown due to the poor record during these times). Although, as found for crown group crocodilians, "mesosuchian" per-genus rates of origination are relatively high in the Early Paleocene. What is less clear is why "mesosuchian" crocodilians should be so adversely affected by the K-T event, and not "eusuchians." In overall body plan they are very similar, and there is little to suggest any major ecological difference between them, excluding the exclusively marine forms such as the thalattosuchids (Figure VII.56).<sup>7</sup> Whether the possession of a full secondary palate in "eusuchians" influenced this differential survival is also difficult to imagine, but clearly there was some difference.

## VII.4. CONCLUSIONS

The diversity data presented in this study suggest that extrinsic factors, evolution and climate, are a greater influence on observed patterns than intrinsic factors such as sampling and taphonomic biases. This is particularly true for the initial diversification of crown group crocodilians during the Late Cretaceous and early Paleogene. Although a leveling of diversity is implied in this pattern of diversification, an exponential model of diversification fits the data better than a logistic model--"recovery" in the Miocene is shown

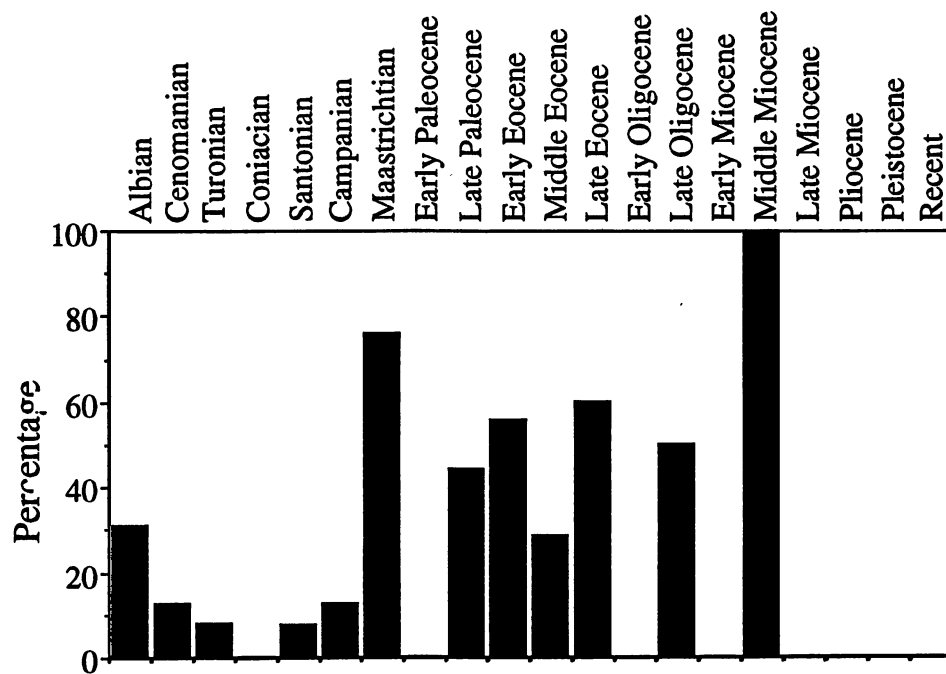
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7. The preliminary results of this study presented by Markwick (1993) suggested a differential response to the K-T by marine and non-marine crocodilians. This is not seen when the entire dataset is considered.



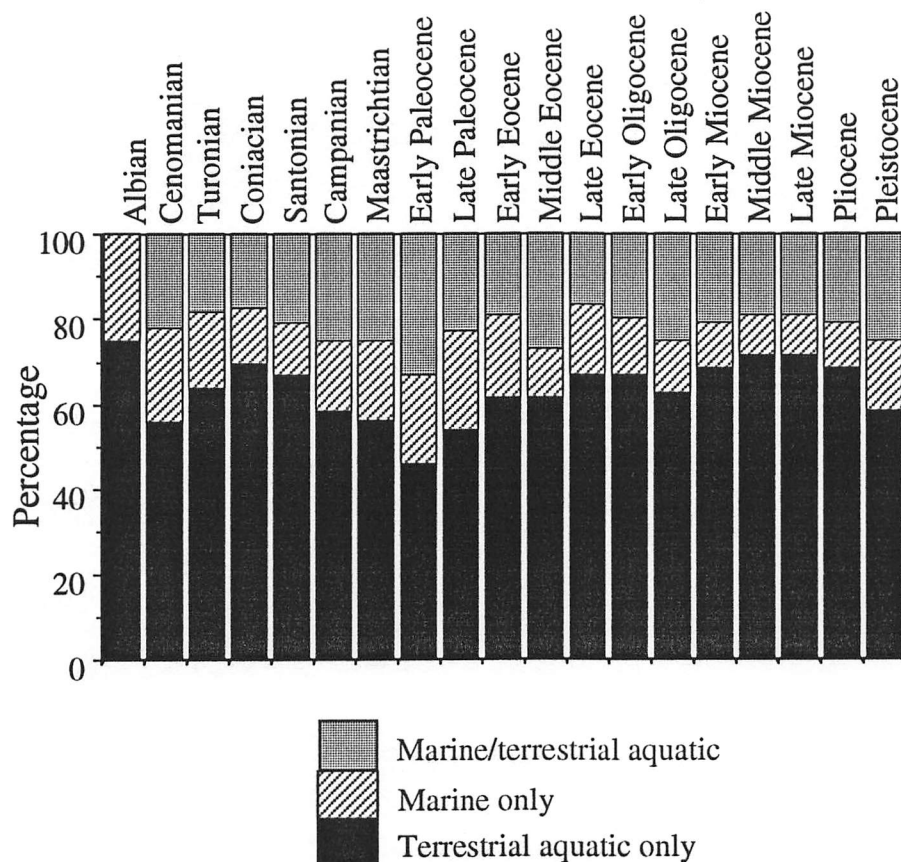
**FIGURE VII.54.** The per-genus rate of diversification for the "Mesosuchia."

The values of  $r_s$  and  $r_e$  are calculated using the equations given in the caption for Figure VII.3. The dominant trend here is the increasingly negative per genus diversification rates through the Cenozoic. Unlike crown group crocodilians, the per-genus diversification rate is negative in the Maastrichtian, but like the crown group, the rate is highly positive in the Early Paleocene, again suggestive of an immediate rebound to what ever perturbed the system at the K-T. However the trends are also consistent with a taxonomic artifact argument (different workers in the Cretaceous and Tertiary); however a preliminary qualitative assessment of the data does not show any clear evidence for this at present.



**FIGURE VII.55. Percentage "mesosuchian" turnover.**

The number of "mesosuchian" genera that become extinct in an interval as a percentage of the standing generic diversity. See caption for Figure VII.51 for equation. Note the very high values for percentage turnover through the Cenozoic.



**FIGURE VII.56. Crocodilian diversity as a function of gross ecology.**

In this figure crocodilian diversity ("mesosuchians" and "eusuchians") is shown as a function of the paleoenvironments in which they are found. Genera for which the environments are unknown are not included.

to also follow an exponential function. Diversity drops in the Late Eocene and Pleistocene are coincident with known global climate changes, suggesting a causal relationship.

There is little evidence in the crown group crocodilian data to suggest a major "crisis" at the K-T boundary. But, this is not to say there was no response. A turnover of about 30% has been noted above, although the diversification rate through this interval shows no major perturbation. In part this is a function of very high origination rates in the Early Paleocene, rates that are consistent with a rapid recovery during this period, suggesting that whatever occurred at the K-T was rapidly resolved and "normality" resumed. Drops in observed diversity are apparent throughout the entire latitudinal range at this time. The response of crown group crocodilians to the K-T is in stark contrast to that of the "Mesosuchia," which do seem to undergo a major extinction at this time. It is postulated that this extinction allowed crown group crocodilians to expand their spatial ranges, especially into the southern hemisphere, which in the Cretaceous was dominated, almost exclusively, by "mesosuchians."

The strong relationship between taxonomic diversity and sampling (the number of localities) is interpreted here to reflect the response of both to the effects of climatically induced range restriction, with a concomitant reduction in the carrying capacity of the geographic range (or simply a loss of spatially restricted genera) resulting in lowered global diversity, and a decrease in the potential area of preservation resulting in a reduction in the number of localities .

Finally, this study again indicates the benefits of computer-based, global datasets for addressing geological, and especially paleoecological, questions--questions, that require

an examination of both spatial and temporal patterns, as well as the inherent biases that can influence them.