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

VOLUME ONE

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CHAPTER IV

FOSSIL CROCODYLIANS AS INDICATORS OF LATE CRETACEOUS AND CENOZOIC CLIMATES: IMPLICATIONS FOR USING PALEONTOLOGICAL DATA FOR GLOBAL CHANGE: PART 1--THE PRESENT

"There is nothing more deceptive than an obvious fact"

Sherlock Holmes
"The Boscombe Valley Mystery", Sir Arthur Conan Doyle

IV.1. INTRODUCTION

In order confidently to make intercomparisons between multiple lines of evidence it is essential that the nature of each climate proxy be understood. This requires an understanding of not only the fossil record with its inherent biases (addressed in Chapter V), but also an investigation of the climatic limits of living relatives that are to be applied to fossil occurrences. This study concentrates on one climate proxy, the order Crocodylia, as a means for examining these issues. As such it is intended to provide a template for future research.

In the absence of physiological evidence of climate tolerances in preserved fossils, climate interpretations using fossil crocodilians are based on the climate tolerances of their extant relatives. In its simplest sense this is known as Nearest (or closest) Living Relative analysis (NLR). NLR requires a full understanding of the present ecological and climate requirements of living crocodilians. To this end some fundamental questions must be addressed: are modern crocodilians climate dependent? is their distribution the maximum possible given their biology? what else limits crocodilian distribution? could the present distribution be an artifact of history, man, or simple chance? It is important to realize that the establishment of climate tolerances in the present does not automatically guarantee that fossil representatives had the same tolerances, although this is the most parsimonious assumption. Following Conybeare's (1829), arguments validation of this assumption is based on comparisons with the interpretation of other preserved fossils. However, if we do not understand the Present any conclusions about the past are mute.

IV.1.1. The Study Group, Order Crocodylia

The order Crocodylia has been used as an indicator of warmth in the geological record since the early nineteenth century (Berg, 1965; Crichton, 1825; Lyell, 1830; Owen, 1850).¹ Indeed the efficacy of this climate proxy has rarely been doubted; Matthew (p.287,

1. The significance of the presence of fossil crocodilians in higher latitudes is emphasised by a report quoted in Crichton (p. 215, 1825) about a crocodile that was brought to Versailles in the eighteenth century:

"Disons d'abord, que le spectacle de cet animal vivant, déjà si propre par lui-même à exciter la curiosité, parut surtout extraordinaire par la circonstance de la saison où étoit alors, et par celle du climat. Car le froid est tellement contraire au crocodile qu'en Amérique et en Egypte même, au rapport des auteurs, cet animal ne peut passer les nuits d'été que dans l'eau, qui alors est beaucoup plus chaude que l'air. Ceux qui avoient approtté par terre depuis le Rochelle, le crocodile dont il s'agit, dirent qu'ils l'avoient cru mort plusieurs fois, et n'avoient pu le faire revenir qu'en le mettant auprès du feu." This crocodile lived only a little more than a month.

1915), in his review of the relationship between paleoclimate and organic evolution, states that "*the present limits of range [of the order Crocodylia] are conditioned chiefly by temperature and climate, and that the much wider range in the early Tertiary was due to a warmer climate towards the poles, will hardly be questioned.*" Owen (1850) takes it for granted that the presence of crocodilians in the early Tertiary London Clay of England implies tropical climates. Hibbard (p.10, 1960) suggests that the value of fossil crocodilians may have been underestimated, describing them as one of "*...the best indicators of temperature among the larger vertebrates.*" Crocodilians are not alone in providing climate information. Other vertebrates, especially mammals, have received considerable attention (Colbert, 1953, 1964a, 1964b; Esteban and Sanchiz, 1986; Graham, 1986; Janis, 1989, 1993; Repenning, 1990; Schleich, 1986; Thackeray, 1987; Uhen, 1992; Woodcock, 1992). Moreover, since Lyell (1830), most geologists have recognized the paleobotanical record as being the most informative for reconstructing terrestrial paleoclimate (Wolfe, 1971). But there are a number of advantages to using crocodilians for this study: unlike the voluminous floral record, the record of crocodilians for the last 100 million years is more manageable, such that a global, comprehensive dataset can be compiled relatively quickly and intrinsic issues, such as biases in the record, can be readily examined;² paleoclimatic conclusions are derived from simple presences rather than assemblage compositions (cf., floral physiognomic method, Wolfe, 1993) which makes them less susceptible to taphonomic influences; they are temporally long-ranged, but morphological relatively conservative with numerous distinctive elements, especially teeth and scutes that are readily preserved in large numbers; living crocodilians are limited to warm climatic regions--more so than other ectotherms, such as snakes and turtles, that are

2. This being said, the present dataset is part of a larger project aimed at ultimately collecting not only vertebrate information but also floral data. Lithological data have already been compiled for the study period through the efforts of the Paleogeographic Atlas Project.

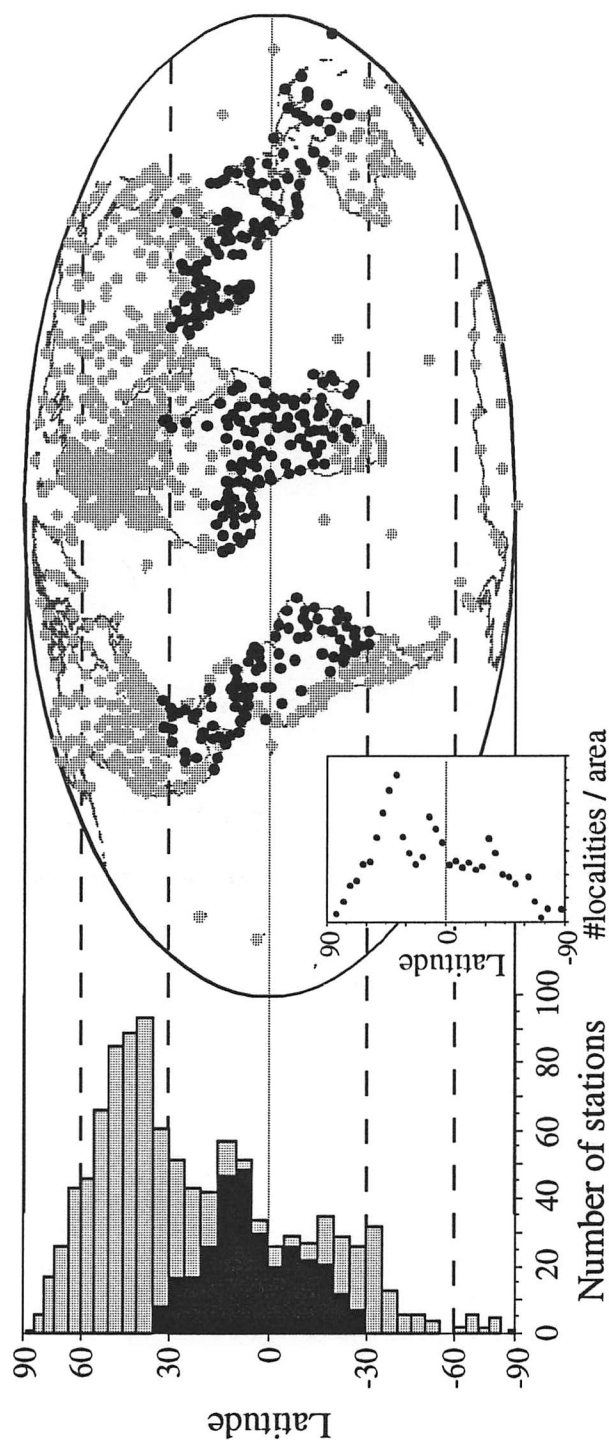


FIGURE IV.1. The distribution of modern climate stations used in this study.

Data from Müller (1982). For additional information see text and Chapter VII. Stations with crocodilians are represented by black circles. The bar chart on the left of the figure shows the number of stations in each 5° latitudinal zone (the number of crocodilian-bearing stations in each zone are shown in black). Note the peak in northern mid-latitudes which represent stations in Europe and the United States. The insert shows the ratio of stations to area of land in each 5° latitudinal zone.

of smaller size and therefore better able to utilize microhabitats where ambient temperatures may be warmer than observed surface temperatures (thermal climate).³

Living crocodiles, alligators and gavials are members of the order Crocodylia (hence the informal term crocodylian or crocodilian), which today comprises seven extant genera distributed throughout low latitudes equatorward of about 30° (Figure IV.1). With the living birds, crocodilians are the surviving members of the subclass Archosauria that also includes the extinct dinosaurs. This relationship has motivated much of the interest in crocodilian habits and physiology as a possible guide to understanding the biology and lifestyles of that extinct, but popular, group.

Our understanding of the climate tolerances of living crocodilians (and thus by analogy the climate interpretations of fossil crocodilians) comes from two principal sources: biological observations and distributional inferences. Biological observations are limited by the problems of working with such large and potentially dangerous animals (Avery, 1982), which generally restricts study to juveniles. But, they are also limited by ethical considerations, since the climatic limits, especially the thermal tolerances, are fatal by definition. Not surprisingly, the degree to which experiments can represent reality has been questioned, being likened by Bogert (1959) to the inability of a man "*with a heavy iron ball chained to one leg [to] demonstrate how fast he can run.*" Consequently most paleoclimatic interpretations have been based on distributional inferences. Thus Berg (1965) used the 10 °C and 15 °C Winter (January, northern hemisphere, July in the southern hemisphere) isotherms for the most poleward limits of the alligators and crocodiles respectively, while

3. Hibbard (1960) suggested that the large size of the giant tortoise *Geochelone* prevents individuals from burrowing and thereby escaping extreme ambient surface temperatures. Consequently, fossil occurrences might provide an indication of contemporary surface temperatures. The large size of crocodilians and giant tortoises also increases their preservation potential in the fossil record.

Romer (p.201, 1961) pointed out that the alligator, the “*most climatically venturesome of the group [Crocodylia], does not go north of regions with a mean annual temperature of about 60°F...*” (60°F being equivalent to $\approx 15.6^{\circ}\text{C}$). This approach, however, assumes that the present distribution of crocodilians represents occupation of the entire range of tolerable climates, which crocodilians could occupy, all other factors been equal. This need not be true. More recent studies using crocodilians as paleoclimatic proxies have also included empirical observations in order to constrain fossil interpretations (Habicht, 1979; Markwick, 1994).

In the following sections I present a review of the limiting factors for the distribution of living Crocodylia based first on empirical observations (experiment and field observations) and second on inferences based on their present geographical range, which also incorporates the consequences of biogeography, history, habitat, etc.

IV.2. EMPIRICAL BIOLOGICAL OBSERVATIONS

IV.2.1. Basic Physiology

All living crocodilians are **ectothermic**, which means that their body temperatures depend primarily upon absorption of energy from the environment. They are also generally considered **poikilothermic** (the modern equivalent of the archaic ‘cold-blooded’), a term which describes the pattern of temperature regulation rather than the source of energy and denotes large variations in body temperature that are the results of changing environmental conditions. However, like most reptiles, crocodilians are able to maintain relatively constant body temperatures through behavior. This is a characteristic of

homeothermy (= homoiothermy = warm-blooded), and crocodilians might be better described as **ectothermic homeotherms**.⁴

Ectotherms consume relatively small amounts of energy--energy that is then efficiently converted to biomass; indeed, in reptiles as a whole the resting and active metabolism is only about 10% that of a bird or mammal of equivalent size (Lang, 1987b). But, unlike endotherms, ectotherms are incapable of sustained activity--they fatigue easily and recover slowly (Bennett and Ruben, 1979)--nor are they able to decouple their body temperatures from the ambient temperature.

IV.2.2. Terminology

All animals (ectotherms and endotherms) live within a definable range of body temperatures. The upper and lower limits are termed the **Lethal Maximum** and **Lethal Minimum** respectively, above and below which the animal suffers physiological damage after only short exposure (Pough and Gans, 1982) and then dies (Cowles and Bogert, 1944). However, in the literature most biologists refer to the upper and lower limits as the **Critical Maximum** and **Critical Minimum** (Cowles and Bogert, 1944; Pough and Gans, 1982). These refer to the "potential lethal temperature" above and below which the animal is no longer able independently to escape from imminent death and which under laboratory conditions is basically the time at which to stop the experiment. In the ecological sense this is the lethal maximum and minimum. Within these "critical" temperatures are the **voluntary minimum** and the **voluntary maximum**, the temperatures at which the animal ceases activity and moves into shelter (whether this be the shade or water). The

4. A full summary of terminology is given in Pough and Gans (1982).

temperature range between these two voluntary temperatures is the **activity temperature range** within which crocodilians are able to maintain their body temperatures through behavioral, and to some extent physiological, means. A further distinction is given by the recognition of a **preferred temperature range** or **selected temperature range**, which is the range of temperature generally selected by the organism given the 'choice'.

IV.2.3. Environment Verses Body Temperatures

As ectotherms, crocodilian body temperatures should correspond closely to ambient environmental temperatures. This has been demonstrated experimentally. Kirk and Hogben (1946) found that within 6 hours of suddenly dropping the air temperature from 32 °C to 10 °C, alligator body temperatures were within 1 °C of the air temperature. Similar results were found by Smith (1975, 1976), who noted that differences in the rate of heating and cooling were also dependent on whether the individual was in water or air. Spotila et al. (1972) state that when "*an alligator enters water its body temperature quickly converges toward water temperature and then remains approximately equal to it.*" The importance of water in regulating temperature will be discussed later, but an important note to add here is that for individual crocodilians the environmental temperature is the temperature of the immediately adjacent environment, which may be water or mud, rather than air. Consequently changes in ambient air temperatures (weather) may be mitigated by the behavior of the local medium. This will become important later in discussing the survival of alligator individuals at the periphery of their climate range.

IV.2.4. Crocodilian Thermal Limits

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

Other quoted minimum temperature limits are based on observed environmental temperatures. At Lake Ellis Simon, Caven County, North Carolina (35°50'40"N), Hagan et al. (1983) studied 14 adult alligators which were fitted with transmitter collars that could measure environmental temperatures. In this experiment the coldest environmental (water) temperature was measured at 2°C, at which temperature the alligators were still able to react to the presence of the observers (mean minimum temperature for that month, February

1981, was 2.7°C). Hagan et al. (1983) also noted that many adult alligators, and some juveniles, survived in the study area during the record cold of January 1977, when the mean minimum air temperature reached -4.3 °C and the lake froze over.⁵ At Elm Lake, Brazos Ben State Park, Texas, Hayes-Odum and Jones (1993) noted that the deaths of 12 adults were probably the result of one severe freeze in which air temperatures reached -13.9 °C.⁶ In the Victoria Falls area, Zimbabwe, Child (1987) found that the Nile crocodile, *Crocodylus niloticus*, could survive subfreezing air temperatures in which 18% (≈ 22) of the days between May and August were below 0 °C as an artifact of elevation, although during this period only 0.9% (≈ 1 day) were below -4 °C.

Data from escaped alligators across the United States reinforce the idea that individual adults can tolerate quite low temperatures. Barton (1955) described an alligator that seems to have survived in the Castle Shannon area, Allegheny County, Pennsylvania, for possibly 6 or 7 years despite the mean air temperature for the coldest month varying between -5.7 and 1.78 °C (average -3.1 °C) and the mean air temperature of the four coldest months varying from -0.6 to 3.3 °C (average 0.5 °C). However, such occurrences do not necessarily reflect where a viable crocodilian population capable of reproducing will survive (Markwick, 1994; Neill, 1971).

5. It should be noted here that the ambient air temperature need not be exactly the same as the 'environmental' temperatures experienced by the alligator individuals, which would be the temperature of the water, which was not reported in this study.

6. In general it seems that sustained cold temperatures will limit crocodilian distributions as noted in Anthony Haswell's 1802 account of the explorations of Captain Matthew Phelps (cited in Neill, p.193, 1971):

"There are likewise Alligator or Crocodiles in these rivers.... One perculiarity of these creatures, which fell within my observation, was their incapability to bear excessive cold. I have seen in passing up the Big Black, at times, thirty or forty of these creatures, sleeping on the shore, or sunning on old logs, and generally killed a number, on the tails of which the inhabitants make an agreeable repast; but in going up the river after the hard winter of 1779 and 1780, I saw but one live one, while the shores were lined in a manner with dead ones, and the air perfectly tainted."

Crocodylian critical maximum and minimum body temperatures only provide the extreme limits within which individuals can survive. In general, crocodilians remain within their activity range, which for the *A. mississippiensis* is generally given as 25-35 °C. This is also the activity range given for many other crocodilian species (Lang, 1987b; see also Johnson et al., 1976, and Figure IV.2; 26-37 °C in the earlier literature, Brattstrom, 1965). The preferred or selected temperature range for *A. mississippiensis* is taken as being 32-35 °C (Avery, 1982; Brattstrom, 1965; Figure IV.2). Most crocodilian environmental temperatures reflect closely the selected body temperatures and this has been recognized by zoos; for instance, an exhibit at Lincoln Park Zoo, Chicago, maintained the water temperature at 24-27 °C for *Tomistoma schlegeli* and around 24 °C for *Crocodylus intermedius* (Almandarz, 1975) (Table IV.1). The most significant feature of these temperatures is the difference between critical maximum and voluntary maximum which is only about 3 °C and that between critical minimum and voluntary minimum which is about 22 °C. This suggests that alligators can cope with decreases in temperatures below their 'optimum temperature range' better than increases, and that despite the overall temperature tolerances of alligators, given the choice, they 'prefer' the warmer end of the range. This is consistent with the results of Colbert's experiments in the 1940's (Colbert et al., 1946). This is intuitive when we consider that like all animals crocodilians need to get the maximum amount of energy with the minimum of expenditure and as ectotherms this is far easier at higher temperatures. A similar result was found by Spotila and workers using a slightly different approach in which they calculated energy budget models for *A. mississippiensis* (Spotila et al., 1973; Spotila et al., 1972; Spotila and Standora, 1985). They concluded that when an alligator is at its selected body temperature, it is restricted to a small portion of its climate space (the multidimensional space defined by climate

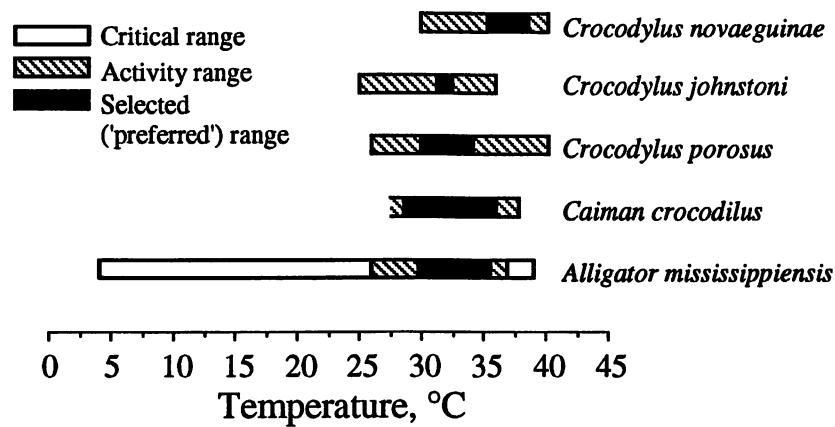


FIGURE IV.2. The critical, activity and selected temperature ranges for five crocodilians.

Data from the following sources: *Alligator mississippiensis*, Avery (1982), Brattstrom (1965), Brisbin et al. (1982), Colbert et al. (1946), Lang (1987), and Smith (1975, 1976); *Caiman crocodilus*, Diefenbach (1975); *Crocodylus porosus*, *Crocodylus johnstoni* and *Crocodylus novaeguinae*, Johnson (1974 and Johnson et al. (1976). Note that critical temperatures are presently only known for *Alligator mississippiensis*, based almost exclusively on observations in the wild.

parameters) and that while large alligators can operate outside their climate space, because they can store large amounts of heat, small individuals are more restricted (Spotila et al., 1972).

IV.2.5. Importance of Size

The importance of size was clearly demonstrated in Colbert et al's (1946) original experiments in the 1940's, with the smaller alligators always being the first to react to heating or cooling. Subsequent workers have found the same pattern. Diefenbach (1975) studying *Caiman crocodilus* found that while small (<45 cm total length) animals had

selected temperatures in the range 28.5-31.5 °C (with maximum voluntary temperatures of 36 °C), large animals (>75 cm) had selected temperatures in the range 32.0-36.2 °C (maximum voluntary temperature of 37.6 °C). The heating rates were almost three times faster in the smaller animals. Avery (1982) noted that the selected body temperatures are 2.2 °C higher in large alligators than they are in juveniles, although Johnson (1974) found that in *Crocodylus porosus*, and to a degree in *Crocodylus novaeguinae*, there was an inverse relationship between size and mean selected temperature. Coulson et al. (1989) found that the metabolic rate is a function of size and temperature with the lower metabolic rates corresponding to larger animals and colder temperatures.

This size-based differential response to thermal changes is a direct consequence of ectothermy and the lack of an internal source of energy. Ectotherms gain and lose heat as a function of their heat capacity and the surface area across which heat is gained or lost to the environment. Heat capacity refers to the heat necessary to raise the temperature of a unit volume of a substance 1 °C (given in units of $\text{J m}^{-3} \text{ }^{\circ}\text{C}^{-1}$, where J is joules). From this it is clear that the larger an individual is the more heat or energy is required to raise its body temperature, and the longer it takes to lose heat. This is further exaggerated by the decrease in the surface area to volume ratio with increasing size, which decreases the area over which heat may be gained or lost relative to the volume of the body that must be heated or cooled respectively. This means that very large ectotherms of dinosaur proportions would have been able to maintain sufficient body temperatures during cold periods by virtue of thermal inertia. This is known as inertial homeothermy or gigantothermy (Hotton, 1980).

This difference in the extent to which large and small individuals can cope with temperature has important ecological implications because it places limits on the survival of

TABLE IV.1. ZOO ENVIRONMENTAL TEMPERATURES

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

a viable population, such that the occurrence of individual adults is constrained in large part by the ability of juveniles to survive. This must also apply to the geological record where the occurrence of a fossil must, using parsimony, imply the contemporary presence of a population rather than the consequences of an errant wandering individual (Markwick, 1994).

IV.2.6. The Consequences of Extreme Temperatures

As body temperatures fall below the minimum voluntary temperature (below the activity range), crocodilians become torpid, falling into what King and Dobbs (1975) described as a "semi-hibernation." Neill (1971) noted that this torpidity led to death for

American crocodiles, *Crocodylus acutus*, kept in water at about 18.3 °C. However, this cold induced torpidity has proven useful for transporting zoo specimens. Almandarz (1975) at Lincoln Park zoo, Chicago, found that *Tomistoma schlegeli* became torpid when the water temperature was chilled to 11 °C (in 5 hours) and *Crocodylus intermedius* was quiet by 8.9 °C and torpid by 7.2 °C (after almost 5 hours), at which point they could be transported. The difference may be due to the larger size of the *Crocodylus intermedius*. King and Dobbs (1975) note that American alligators in zoos can tolerate temperatures as low as 5-10 °C for short spells without affecting breeding success, although they do note that animals subjected to low temperatures are more prone to hypoglycemic shock and gout than ones that are kept warm. Coulson et al. (1973) found that although *A. mississippiensis* inhabits regions which are largely sub-tropical, they need very high temperatures for satisfactory growth and physiological function; that with exposure to 18 °C some impairment of renal function may result; and that at temperatures below 18 °C the ability to synthesize NH_4HCO_3 is reduced and as a consequence NaCl is lost to the urine. Coulson concluded that even in winter, temperatures between 29 and 31 °C seem best for alligators.

IV.2.6.1. Effect on Feeding

Lang (1979) found that while digestion was promoted by an increase in body temperature, appetite itself seemed to depend on heat availability rather than proximate temperatures. This would seem to agree with the experiments of Coulson and Hernandez (1964) who found that appetite was suppressed with the onset of fall and winter irrespective of temperature or photoperiod. However, Coulson et al. (1973) noted that for *A. mississippiensis* the desire for food was diminished or absent below 22 °C regardless of

season. Joanen et al. (1987) observed that in Louisiana, *A. mississippiensis* only feeds between March and October, although during the fasting period the average temperature of the coldest month is 8.5 °C, well above freezing, compared with the mean temperature during the active period of 26.5 °C. Lang (1979) also referred to this fasting, noting that in captivity low temperatures lead to loss of appetite in alligators, caimans and Nile crocodiles. Lang (1979) further observed that the lowest body temperatures during fasting were 13 °C in *Alligator mississippiensis* compared with 18.2 °C for *Crocodylus acutus*, a difference that might reflect their geographic distribution. In Zimbabwe, Blake and Loveridge (1975) suggested that cold might be the most important cause of crocodile mortality because of its suppression of appetite and the consequent increased susceptibility to disease.

IV.2.6.2. Effect on Juvenile Survival

Although the extremes of temperature are clearly important, Hagan et al. (1983) concluded that the northern range of *Alligator mississippiensis* may not be affected as much by the severity as by the duration of the winter. This is most significant for the earlier developmental stages prior to sexual maturity. Joanen and McNease (1979) found that the nesting of *Alligator mississippiensis* in captivity occurs within a two week period which is directly related to air temperature, with higher temperatures leading to earlier nesting. Further observations in western Louisiana support this fact, with nesting in the wild occurring earliest (in late May - early June) when the March-April-May ambient temperatures are highest (average of 21.4 °C); the bulk of nesting again taking place in a two week period each year. Egg laying was delayed until late June - early July in the coldest years when the temperatures for March-April-May averaged only 18.3 °C (Joanen and McNease, 1989).

Postponement of nesting and egg laying limits the season available for incubation and successful hatching and may impair subsequent growth rates. Growth rates are also directly related to the incubation temperature, which is inversely related to the total incubation time (Joanen and McNease, 1989). Joanen et al. (1987) found that the poorest growth rates were found in crocodiles incubated at extreme temperatures (32.8 °C and 29.4 °C). This was also found by Hutton (1989) for *Crocodylus niloticus*; hatchlings incubated at 34 °C outgrew those incubated at 28 °C and 31 °C within 3 months even though they were shorter at hatching. Blake and Loveridge (1975) noted that growth rates of *Crocodylus niloticus* at rearing stations in Zimbabwe (Kariba, Binga and Victoria Falls) were twice that of hatchlings in the wild. Where hatching was continued into January, success rate was poor (Victoria Falls 1971-73 and Binga 1968), which could be indicative of incubation temperatures having been too low. These authors also noticed that there was a substantial slowing of growth in the colder months. An additional limit was noted by King and Dobbs (1975) who found that at temperatures less than 21 °C the umbilicus did not properly heal and the hatchlings eventually died. Coulson et al. (1973) noted that high temperatures facilitate absorption of yolk sac which seems to reduce mortality rate. Webb and Cooper-Preston (1989), studying *Crocodylus porosus* in Northern Australia, noted that higher mortality rates occur for eggs incubated in nests at temperatures of 33.1-35.0 °C and 28.1-29.0 °C compared with those incubated between 29.1 and 33.0 °C. This trend continued for at least the first two years of life with higher mortality rates for individuals incubated at lower temperatures. As with *Alligator mississippiensis*, the mean size of Australian *Crocodylus porosus* is highly dependent upon incubation temperatures with smaller individuals for lower incubation temperatures. The maximum survival percentage was for those individuals incubated at 32 °C (87%) and the lowest for those incubated at

29.0 °C (44%). In Uttar Pradesh, northern India, Whitaker (1987) noted that when water temperatures fell to 5-10 °C, rearing pens containing hatchlings of *Gavialis gangeticus* had to be covered with plastic sheeting and heating bulbs installed for the hatchlings to bask under.

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

IV.2.7. Thermoregulation

The process of regulating temperature within the limits described above is known as thermoregulation. The field of reptilian thermoregulation was initially defined by Cowles and Bogert in the 1940's (Cowles and Bogert, 1944) through their field analyses of desert lizard behavior in California (see Pough and Gans, 1982, for a more recent glossary, which is the source for the definitions used in this study). The crocodilians that have been studied can regulate their body temperatures so as to remain within their activity ranges despite often quite large discrepancies with the environmental temperatures. This is generally through behavioral means (Johnson, 1973; Lang, 1987a, 1987b; Smith, 1975) in which water plays an extremely important part (Johnson et al., 1976; Spotila et al., 1972), but can also be through physiological controls such as subcutaneous peripheral blood flow

(Smith, 1976). Other ectotherms can survive extremely low temperatures through other mechanisms such as depressing the supercooling and freezing points of body fluids or, more surprisingly, by tolerating ice formation in extracellular fluid spaces. An extensive study of the last of these, known as freeze tolerance, has been done recently (Storey, 1990; Storey and Storey, 1988), but this only seems applicable to small ectothermic tetrapods.

IV.2.7.1. Behavioral Thermoregulation

Crocodylians will behave so as to remain in their selected temperature range, using as little energy as possible. Diefenbach found that *Caiman crocodilus* behaved in a similar way to “*heliothermic lizards, which attain and maintain a range of selected temperatures by sequential movements and body orientation relative to the sun or other heat radiating objects in their surroundings*” (p.536, Diefenbach, 1975). For instance, if the water becomes too cold, crocodylians will bask in the sun until they reach the upper limit of their selected (“preferred”) temperature range at which point they return to the water or seek the shade. Cott (1961) found that the time in the morning at which the *Crocodylus niloticus* moved onshore depended on the air temperature, such that on cooler (cloudier) mornings it occurred later. The use of warm substrates (**thigmothermy**) has also been found to be important (Smith, 1975). Cott also noted the importance of gaping at least in *Crocodylus niloticus* (if the crocodile has its mouth tied shut its temperature rises beyond its normal activity range). Johnson (1974) also found that gaping reduced head temperatures in *Crocodylus porosus*. However, other workers have found no such significance to gaping (in *Caiman crocodilus*, Diefenbach, 1975; and *Crocodylus acutus*, Johnson et al., 1978).

The most important behavioral response to temperature extremes (hot and cold) is to seek water. Smith (1975) noted that during hot afternoons an alligator at Waco, Texas, would often retreat to the bottom of the zoo pond. Similarly, Diefenbach (1975) found that overheating in *Caiman crocodilus* was mitigated by immersion in water. Brisbin et al. (1982) described how *Alligator mississippiensis* would escape cold weather by submerging in deep pools using their snouts to maintain an air hole through the accumulating ice. This was termed the "icing response" by Hagan et al. (1983) who observed this behavior in alligators in North Carolina. The "icing response" was only found to occur when there was ice present at the den, and when the water temperature was $\leq 5^{\circ}\text{C}$.

Spotila et al. (p.1094, 1972) noted that "*Water is the most important part of an alligator's habitat because it acts as a substitute for blackbody conditions and insures maximum utilization of an alligators potential climate space*" and that "*If alligators are deprived of water their activity is greatly restricted and their chance of survival is greatly reduced.*" They also noted the importance of vegetation to provide shade for alligators. (It should be noted here that the presence of standing water need not reflect local precipitation, as the Nile valley in Egypt attests; therefore precipitation need not be an accurate indicator of suitable environments for crocodilians; the significance of this is discussed later). A further response to temperature has been reported by Groombridge (1987), who noted that *Alligator sinensis* is active diurnally in May (Nanjing mean daily temperature 20.5°C) after resurfacing after the winter (Nanjing mean winter temperature 3.7°C) but will become nocturnal in June (Nanjing mean daily temperature 24.7°C) and the summer (Nanjing mean summer temperature of 26.9°C). This has also been observed in *Alligator mississippiensis*, which are diurnal in colder weather and nocturnal in warmer weather (Smith, 1975).

A possible behavioral response to environmental inclemency is the "gator-hole," a large, deep, often circular, basin dug by *Alligator mississippiensis* usually in soft substrate (they often utilize sinkholes in Florida). These often provide the only source of water during dry periods. Indeed Neill has suggested that "*probably the impulse to dig a basin was originally evolved not as a method of coping with low temperatures of winter, but with lowering of water table in a dry season*" (p.273, Neill, 1971). This seems more likely given that irrespective of the buffering effect of water to climate change, sustained or extreme cold will freeze a "gator hole" with the "gator" in it regardless ("gator holes" have been shown to be taphonomically significant and may be important in the geological record, Leite and Breithaupt, 1990).

IV.2.7.2. Physiological Thermoregulation

For large individuals of *Alligator mississippiensis*, warming rates were found to be twice cooling rates, a difference that is greater than that in any other reptile (Johnson et al., 1978; Smith, 1975). Johnson et al. (1978) suggested that this might explain their success in temperate North America. Mechanisms for warming rates are not fully understood, although Smith (1975, 1976) noted that the heart rate of a warming animal exceeded that of a cooling animal at the same temperature, and that endogeneous heat production was large enough to maintain the body temperature several degrees above the temperature of the water regardless of outside sources of energy. Since dead animals heat and cool at the same rate and at a rate considerably slower than live animals (Smith, 1976), Grigg and Alchin (1976) suggested that the heating and cooling discrepancy is physiological. Again, size is important with the difference between heating and cooling rates increasing with increasing body mass. Smith (1976) suggested this might be due to the concomitant increase in

integument thickness in larger animals. Smith also noted that during warming the subcutaneous temperature was greater than stomach temperature, while during cooling it was less than the temperature of the stomach suggesting that the alligator is using its periphery as an insulating shell. During warming, increased peripheral blood flow reduces the subcutaneous to stomach temperature differences (Smith, 1976). It is of interest to note that the osteoderms of *Alligator mississippiensis* are highly vascularized and may have a thermal function in the sense of peripheral blood flow (Lang, 1987b). Smith found that alligators cooled and warmed more quickly in water than in air in his experiments, although further work showed that larger alligator individuals cooled more slowly in water than they heated in air (Smith, 1976).

The above results were found using *Alligator mississippiensis* but research by Grigg and Alchin (1976) found similar evidence for physiological thermoregulation in the Australian freshwater crocodile *Crocodylus johnstoni*. In this case, the cooling rate was found to be about 80% of the heating rate in both air and water, although heating in air was not always faster than cooling in air, and in one case a crocodile cooled twice as fast as it heated. Again, heat transfer was seen to be much quicker in live animals as opposed to dead animals, with large temperature gradients developing between surface and core in dead crocodiles. This was further emphasized by the ability of *Crocodylus johnstoni* to heat its whole body when only either the head or body were warmed, a warming that was much slower in dead crocodiles. Experiments have also indicated that most crocodilians show a temperature gradient between head and body of generally about 1 to 2 °C, although 4.2 °C has been observed in *Alligator mississippiensis* (Johnson et al., 1978); *Crocodylus novaeguinae* show similar selected temperature gradients of 1-2 °C (Johnson, 1974). As in the case of *Alligator mississippiensis*, the heart rate was more rapid during heating than

during cooling. In the view of Grigg and Alchin (1976), “*The dilation or constriction of cutaneous blood vessels and the acceleration or deceleration of heart rate are seen as separate responses to surface heating and cooling. Together they promote heat gain or retard heat loss and provide physiological mechanisms contributing to thermoregulation in C. johnstoni.*”

A slightly different physiological response is shown by the common caiman (*Caiman crocodilus*), which is usually marked with black bands on a background of olive or yellowish brown, but which will darken when it is chilled, becoming so dark that the crossbands are no longer visible. On warming the original coloration returns. The darker color absorbs more heat and is the result of the expansion of melanophores (concentrations of dark pigments in skin cells) which react to cold. The question in this case is why a tropical species would need to do this (Neill, 1971). Diefenbach (1975) noted that adult individuals of *C. crocodilus* can maintain body temperatures 4 °C higher than their surrounding environments as long as their dorsums are exposed to a heat source, and he suggests that such individuals in nature may seek warm areas.

IV.2.8. Hibernation and Aestivation

Crocodylian hibernation is problematic. Mazzotti (in Ross p.270, 1989) is categorical: “*Contrary to many published reports, crocodilians do not survive cold winter temperatures by hibernating,*” while Bellairs (p.230, 1970) states “*All temperate zone reptiles hibernate for several months in the year.*” Not surprisingly there is a considerable literature on the subject which Neill (p.269, 1971) has described as “*...confused and contradictory.*” The problem is one of how hibernation is defined. For simplicity I have followed Neill (1948),

who used it to “*include any sort of retreat from winter conditions, whether or not actual dormancy is involved.*” The reason for this is that however hibernation is defined ectotherms are still subject to immediate environmental temperatures. Thus, while hibernating mammals store large amounts of fat as a winter energy source and also as insulation, for reptiles that insulation is external whether it be mud or water. Because of their large size, crocodilians would have problems isolating themselves from the environment without the buffering effect of water, and since water itself can not sustain its temperature indefinitely, in areas where sub-zero temperatures persist for any length of time crocodilians will be precluded. Similarly, dens and burrows in river banks are also limited in the degree to which they can buffer an individual from external temperature extremes, although many species are known to dig such burrows (Groombridge, 1987; Neill, 1971). Indeed, alligators have a bony septum extending longitudinally through the nasal cavity (absent in caimans) which strengthens the snout, presumably for burrowing (Neill, 1971).

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

Despite these questions about reptilian and hence crocodilian hibernation we still note that it is often accepted; for instance, Tulsa zoological park provides an “hibernation den” for their American alligators, which is maintained at 8 °C (Wright, 1981).

IV.2.9. Non-thermal Climatic Constraints

Although temperature is the dominant limiting factor for crocodilians, the presence of standing water is clearly important. Neill (1971) notes that the western limit of crocodilians in the United States is more limited by lack of water than temperature and that this has important implications for the fossil record, as will be illustrated later. As noted in the thermoregulation section, water provides an extremely important thermal buffer. This does not require a relationship with precipitation, as stated earlier. Gorzula (1987) noted how during the dry season in the western Llanis area of Venezuela (March and April) almost all individuals of *Caiman crocodilus* concentrated in refuge lagoons. Groombridge (1987) observed that *Crocodylus palustris* may wander great distances during dry and monsoonal seasons.

Hydrology also affects nesting and consequent survival of juveniles. Joanen and McNease (1989) found that prolonged drought will cause egg desiccation, which is a serious mortality factor. They also point out the effect of floods on mortality, and note that tropical storms in coastal Louisiana can destroy 80-90% of nests. The importance of flooding was also noted by Blake and Loveridge (1975). For *Alligator mississippiensis* in Louisiana, Joanen and McNease (1989) found no significant relationship between rainfall and time of nesting activity, although water levels did effect the density of nesting. This is not always the case; some crocodilian species nest specifically in the wet season, others during the dry season. For instance *Crocodylus niloticus* in Zambia lays its eggs in late August - September coincident with the seasonal fall of the water table which exposes suitable nesting sites; in the Lake Victoria area there are two dry seasons and as a

consequence some crocodiles lay there their eggs in August - September while others take the second opportunity in December - January (Neill, 1971). Webb et al. (1987b) note that in both *Crocodylus johnstoni* and *Crocodylus porosus* of Northern Australia a delay in the wet season by only two weeks can greatly reduce nesting activity (by 30-50% in the case of the 1982/83 wet season), although in this case a note should be made that the 1983 dry season was also particularly cool.

In northern Papua New Guinea, Hollands (1987) reported that 15% of *Crocodylus novaeguinae* eggs and 20% of *Crocodylus porosus* egg clutches studied were lost to flooding (in both cases a higher percentage, 22% and 33% respectively, were lost to predation). In northern Australia, Webb et al. (1987b) noted that for *Crocodylus porosus* rising water levels in the rainy season can account for the loss of 100% of eggs in some areas (overall the mean egg survivorship is estimated to be 25% for this species in northern Australia). Other weather phenomena can also effect mortality rates; for instance a severe hail storm in the Lake Kariba area of Zimbabwe almost decimated all of the crocodile eggs (Child, 1987).

Crocodilians, then, have a precarious early life, and even having survived the egg stage, Child (1987) estimates for the Nile crocodile that hatchling mortality in the wild is probably greater than 95%. As growth proceeds the vulnerability of crocodilians decreases, although Child suggests that where growth rates are slow a high probability of mortality may exist for six or more years. For *Crocodylus johnstoni* in northern Australia Webb et al. (1987a) estimate survivorships as 30% for the egg stage, 12% between hatchling and 1 year, and 85% for 1 to 10 years.

Mortality rates are not only a function of incubation temperature, aridity and flooding. The effects of predation on both eggs and juveniles are important and linked to temperature through growth rates as Fuller, 1981 (cited by Hagan et al., 1983) reported for North Carolina where the growth rates of *Alligator mississippiensis* are about one half those reported in Louisiana. This makes them more liable to predation, and there are a number of animals more than happy to feast on crocodilian eggs and juveniles (for instance the Nile monitor in Zimbabwe, Child, 1987). In Zimbabwe, Blake and Loveridge (1975) reported nest predation to be as high as 49.4% three weeks after laying.

IV.3. CLIMATE INFERRED FROM BIOGEOGRAPHY

The empirical biological observations, described above, show the importance of temperature for limiting the distribution of extant crocodilians; not only the extremes of temperature, but also the duration. Water was shown to provide an essential buffer to temperature extremes. Such observations help bound the region in climate space within which crocodilians can potentially survive.⁷ However, it is important to understand how the geographic distribution of crocodilians reflects these physiological limitations and to what extent it is dictated by other factors.

IV.3.1. Historical Artifact - the Effect of Humans

Historical distributions of crocodilians are known to have differed slightly from those of the late twentieth century. Ross (p.72, 1989) refers to the discovery of two skulls

7. The nature of this region has also been investigated using steady state energy balance models in which intrinsic properties such as metabolic rate and integument emissivity (insulation and water loss) are taken into account (Porter and Gates, 1969; Spotila et al., 1972). Results for *Alligator mississippiensis* support empirical observations, especially the fundamental importance of water (Spotila et al., 1972).

of *Tomistoma schlegelii* from Guangdong, China, which indicate that their range was much larger in the past, possibly as recently as the Ming Dynasty (1368-1644). Morgan et al. (1993) report on the historical disappearance of *Crocodylus rhombifer*, amongst other vertebrates, from Grand Cayman in the Caribbean, which the authors suggest to be the result of a combination of human habitat destruction and predation. Neill (1971) notes that historical remains of *Crocodylus niloticus* are known from regions of Africa that are now too dry for the species, while historical records of eggs in Israel and south west Syria suggest that the range extended into this region also. Werner (1988) notes that *Crocodylus niloticus* survived in the Kabara swamps and Nahal Taninim (River of Crocodiles) of coastal Israel until about 1900, when they were finally eradicated by hunting, compounded by swamp-draining. Neill also reports on the known contraction of the range of *Crocodylus niloticus* which vanished from the Seychelles by about 1800, the Nile delta by the latter 1700's, and by 1870 effectively from all of the Nile below Aswan. Anderson (1898) provides an excellent account of the historical distribution of *Crocodylus niloticus* noting that there are accounts of crocodiles being seen in Syria and even Sicily during Mediaeval times. In North America *Alligator mississippiensis* was historically reported as far north as the Dismal Swamp, on the border between North Carolina and Virginia (Neill, 1971), and indeed escaped alligator "pets" have been sited on numerous occasions throughout southeastern Virginia (Clarke, 1953). Although human activity is probably primarily responsible for these changes (especially through drainage), it should be noted that through historical times there have also been minor climate changes (Lamb, 1982, 1985), which might account for distributional changes. Hunting has had a devastating effect on populations of all species (Turner, 1977)

IV.3.2. Ecological Limitations

Some distributional anomalies may also be explained by ecological requirements. For instance, Neill (1971) suggests that the absence of *Crocodylus acutus* from the Bahamas is due to the fact that the hatchlings cannot survive strongly saline water; although adults could swim across sea to an island, they could not establish a population on it unless it offered freshwater streams or heavy runoff. This may also explain the historical absence of alligatorids in Africa. Modern alligatorids lack salt glands and are restricted to mostly freshwater habitats (Taplin and Grigg, 1989). For most of the last 100 million years Africa was isolated by seaways from Eurasia and any potential source of alligatorids (this is discussed further in section V.3.2.5).

IV.3.3. The Climate of Living Crocodilians

IV.3.3.1. The Dataset

In order to examine the influence of climate on the distribution of crocodilians, I have computerized a dataset of 1060 climate stations compiled by Müller (1982) (Figure IV.1). Each station contains monthly data for 14 climate parameters including mean daily temperature, mean precipitation, radiation and potential evapotranspiration. Additional parameters and summary metrics have been calculated using these data. Non-avian tetrapod faunal lists have been assigned to each station by overlaying climate station distributions onto published species distribution maps (Arnold and Burton, 1978; Bouchardy and Moutou, 1989; Branch, 1988; Cogger, 1992; Conant and Collins, 1991; Cook, 1984; Eisenberg, 1989; Grenard, 1991; Hall and Kelson, 1959; Kingdon, 1990; Redford and

Eisenberg, 1992; Stebbins, 1985; Strahan, 1992; Van der Brink, 1967). A 50 km radius circle was drawn around each site, in order to allow for the potential distribution of sub-environments as represented by the faunal list for each station, and an occurrence registered where the taxon's distribution intersected this circle. In areas with rapid relief changes, such as the Alps, this methodology mixes high and low elevation faunas, but these points do not significantly effect derived regressions. The propensity for stations to occur in lowland sites reflects Müller's original requirements: acceptable stations must contain data for a large array of climate parameters representing time series on the order of 30 years (typical of "climate"). Consequently, most stations are located in large towns or cities that historically occupy lowland sites.⁸ This bias closely mimics the biases in the geological record that tend to over-represent low elevation environments. Similarly, the distribution of stations is also numerically biased towards the northern hemisphere, especially North America and Europe (Figure IV.1), which is also the case with the fossil data (Figure IV.3). Although complete non-avian tetrapod lists are being compiled for all stations, at present the dataset includes the following: complete lists for North America, Europe and Australia; reptile lists for southern Africa; and mammal data for Arabia and northern and southern South America. However, crocodilian and turtle data are available for all stations. These data have been entered into a customized, fully relational computer database using the Helix Express software (NorthCon Technologies, 1992) for Macintosh computers. This database is the same database that contains the 5700 fossil vertebrate localities used for paleoclimatic studies (Markwick, 1994) and discussed in Chapter III and Appendix D. The advantage of including present and fossil data in the same database is that the two kinds can

8. The influence of urbanization on local climates depends on the size of the urban area. For Chicago this urban effect results in the city's MAT being $\approx 0.6^{\circ}\text{C}$ higher than adjacent rural areas; New York City has a MAT $\approx 1.1^{\circ}\text{C}$ higher than adjacent areas (Peterson, 1973). For most of the cities and towns used by Müller (1982), which are smaller than either Chicago or New York, this effect is insignificant compared to the magnitudes of the climate patterns being investigated.

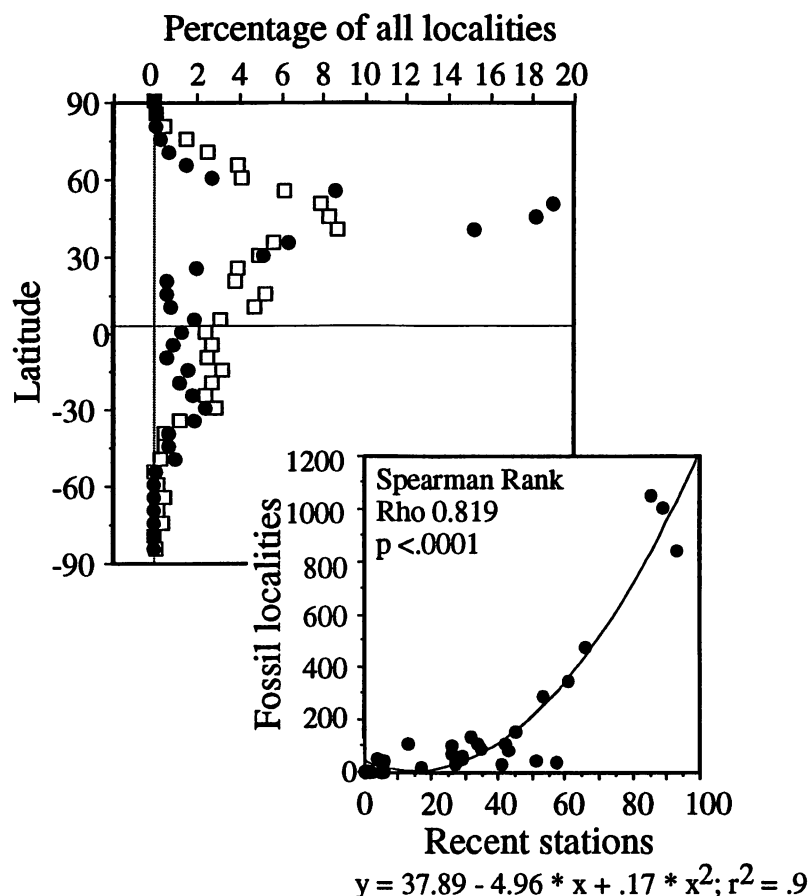


FIGURE IV.3. The relationship of fossil localities and modern climate stations with latitude.

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

then be directly linked in order to automatically derive climates for fossil vertebrate faunas based on their composition. This customized database is designed to facilitate analysis at any specified taxonomic level, which greatly expands the power of this dataset.

A number of caveats concerning this method must be made. First, the crocodilian distribution maps used for the study are unfortunately relatively coarse (except for North America, Australia and southern Africa). The result is that the maps tend to overestimate the extent of the present crocodilian range; for instance in southern India the method described above places the mugger crocodile (*Crocodylus palustris*) at elevations of about 2343 m (Kodaikanal), although Daniel (1983) states that *C. palustris* occurs in hills up to 600 m. But Daniel's work is also quite coarse. Given this uncertainty, this station is included in the analyses shown here.⁹ A second caveat is that distributions reflect essentially those of the twentieth century, or some part of it. Thus today there are no crocodilians in Israel or the lower Nile, but these are included in the climate station set because of their earlier presence (the inclusion of the Jerusalem climate station in the dataset is based on the distribution map given in Neill, 1971, and the known historical occurrences in Israel; however, the accuracy of Neill's maps is uncertain and readers should note that this occurrence lies on the limit of crocodilian climate space as defined by the station dataset). In general, where historical absences can be clearly demonstrated to have been induced by human activity, the presence is included here.

9. Inclusion of this site results in the minimum Mean Annual Temperature (MAT) for the crocodilian distribution being 14.2°C. However, if the dataset is limited to only stations below 1500 m then the minimum MAT becomes 16.4°C, a value similar to that estimated by Markwick (1994) based on the present distribution of *Alligator mississippiensis*. The use of the entire dataset thus provides a conservative estimate of the minimum temperatures that crocodilians can endure. Analysis has shown that inclusion of high elevation sites mostly affects minimum values of MAT and warm thermal metrics, such as WMM and Summer T.

IV.3.3.2. Results

The basic results are presented as a series of frequency and percentile plots, one each for each climate parameter (Figure IV.4). In each case the distribution of crocodilian-bearing stations is superimposed on the distribution of all stations. The disparity between the two gives a measure of how significantly the geographic distribution of crocodilians is defined by that parameter. This can be assessed quantitatively using the Mann-Whitney non-parametric test, which tests the hypothesis that the two distributions are the same. For example, a large disparity is shown for MAT, with crocodilians only occupying those stations at the warmest extreme of the distribution ($p = .0001$, using the Mann-Whitney Test). Conversely, the frequency distributions for mean winter precipitation (mean Winter P) are very similar, suggesting that this metric is not important for limiting crocodilians ($p = .0122$ using the Mann-Whitney Test). An important attribute of the climate space defined in these diagrams is that it represents the space in which crocodilians *do* exist today.

The results of the Mann-Whitney Test suggest that the distribution of crocodilian-bearing stations is significantly distinct from that of non-crocodilian bearing stations for all but a few of the climate parameters shown in Figure IV.4.¹⁰ However, this is not consistently true for the absolute range of values. Minimum values for thermal parameters are generally higher for crocodilian-bearing stations, but maximum and minimum values for precipitation parameters are basically indistinguishable from those of non-crocodilian stations. Consequently, the presence of crocodilians cannot be used to retrodict the absolute limits of precipitation. Nonetheless, the percentile plots can be used to derive the

10. The exceptions are the following parameters from Figure IV.4: mean Winter P ($p = .0122$); minimum P ($p = .0447$); mo $P \geq 0\text{mm}$ ($p > .9999$); mo $P \geq 20\text{mm}$ ($p = .8043$) and AWT ($p = .0159$). All other parameters return p values of $< .0001$. Note that crocodilians are even significantly distributed with respect to wind speed.

probability that any climate parameter, including precipitation, will be greater or less than a specified value, given the presence of a crocodilian. But, this assumes that each parameter in some way controls crocodilian biogeography and this need not be true--derived probabilities may only apply to the present. If this information is to be of any use for retrodicting paleoclimate based on fossil crocodilians, it is essential to determine the relative contribution of each parameter in limiting the spatial distribution of modern crocodilians. Unfortunately, this is hindered by the following: the large number of climate parameters, the close correlations between them, and the possibility that the influence of any parameter may not be important over the entire geographic range of crocodilians. In short, correlation does not automatically mean causation.

The first of these problems can be readily solved by using Principal Component Analysis (PCA) to reduce the number of parameters to a manageable few. An analysis of 16 precipitation and temperature metrics reduces the number of parameters to three interpretable factors (Table IV.2; five other factors were recognized in the analysis, but they do not account for a significant proportion of the scatter in the data), with the first component (PC 1) representing "climate" and dominated by temperature (accounting for 52.7% of the scatter; there is a strong linear relationship between MAT and PC 1 scores), the second (PC 2) distinguishing between temperature and precipitation (25.7% of the distribution; PC 2 scores correlate best with precipitation) and the third (PC 3) by a subset of precipitation metrics, perhaps representing seasonality (8.3% of the distribution).

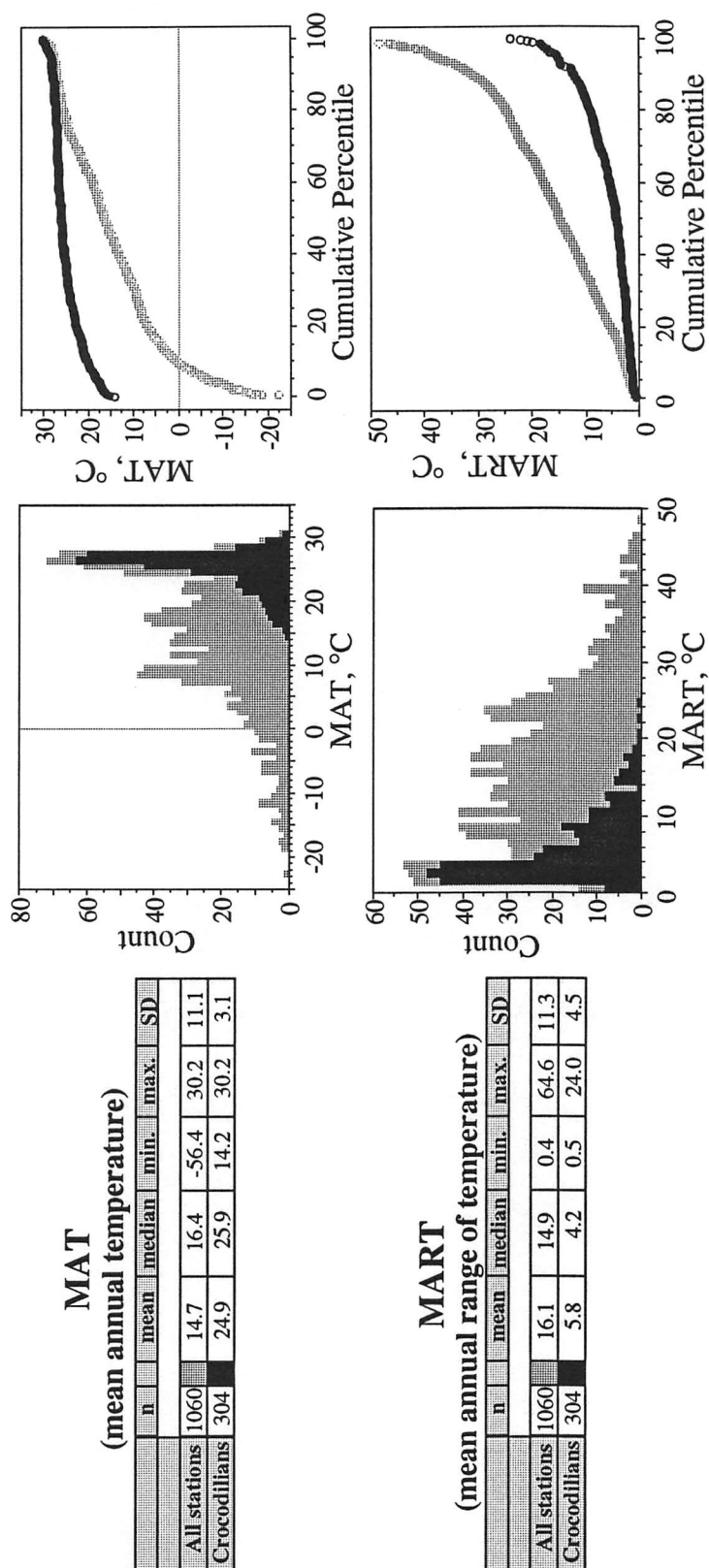


FIGURE IV.4. Graphs showing the frequency distribution of stations for specified climate parameters.

Frequency and percentile plots are given for a selection of the climate parameters stored in the Vertebrate Database (Chapter III; see Appendix D for further details and a summary of all metrics presently available in the database together with those that may be calculated). In each case the distribution occupied by crocodylians (black) is superimposed on the distribution of all stations in the dataset (gray). These distributions define the climate space occupied by extant crocodylians, but not necessarily the full space that could potentially be occupied, all other factors being equal. See text for further details.

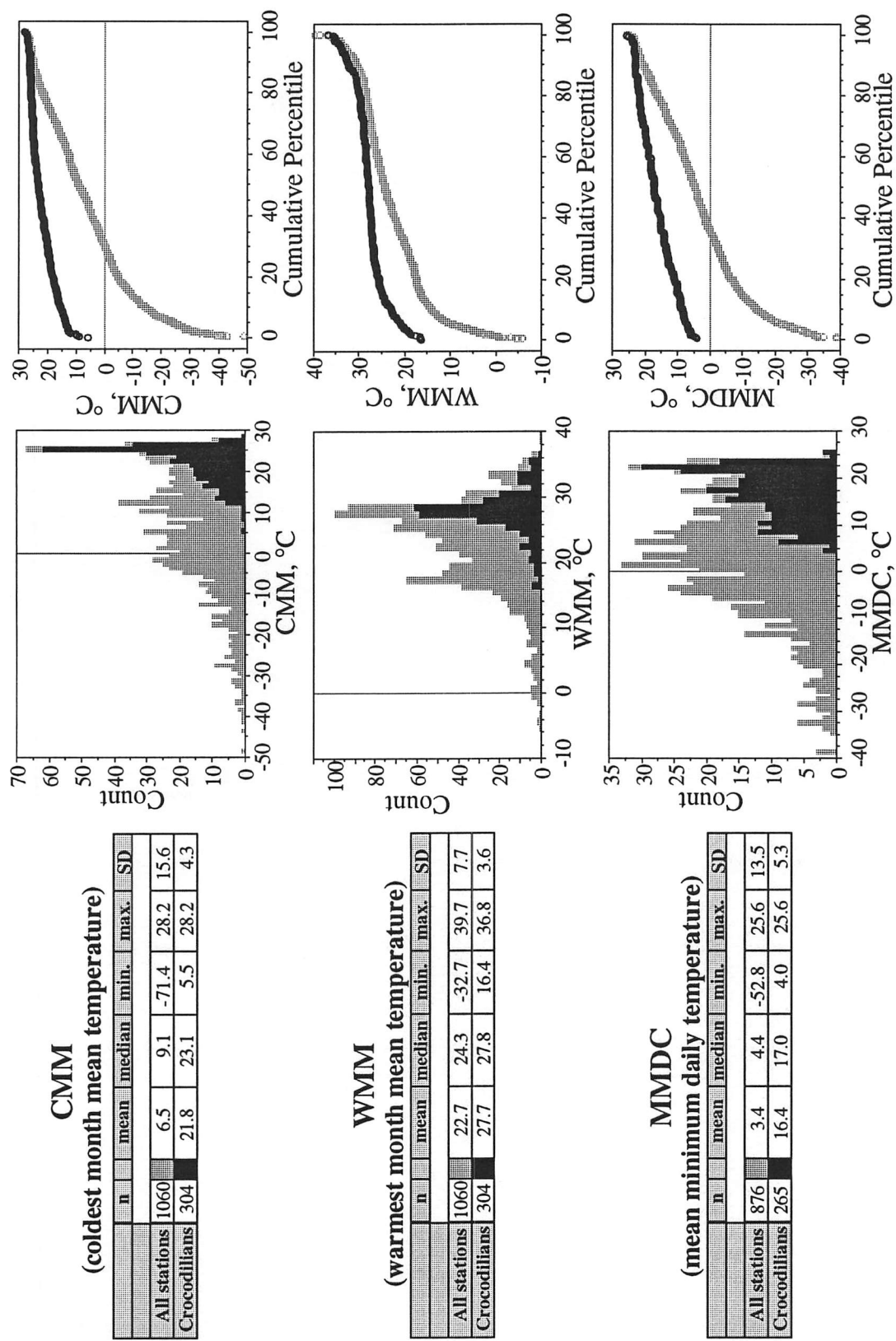


FIGURE IV.4. continued.

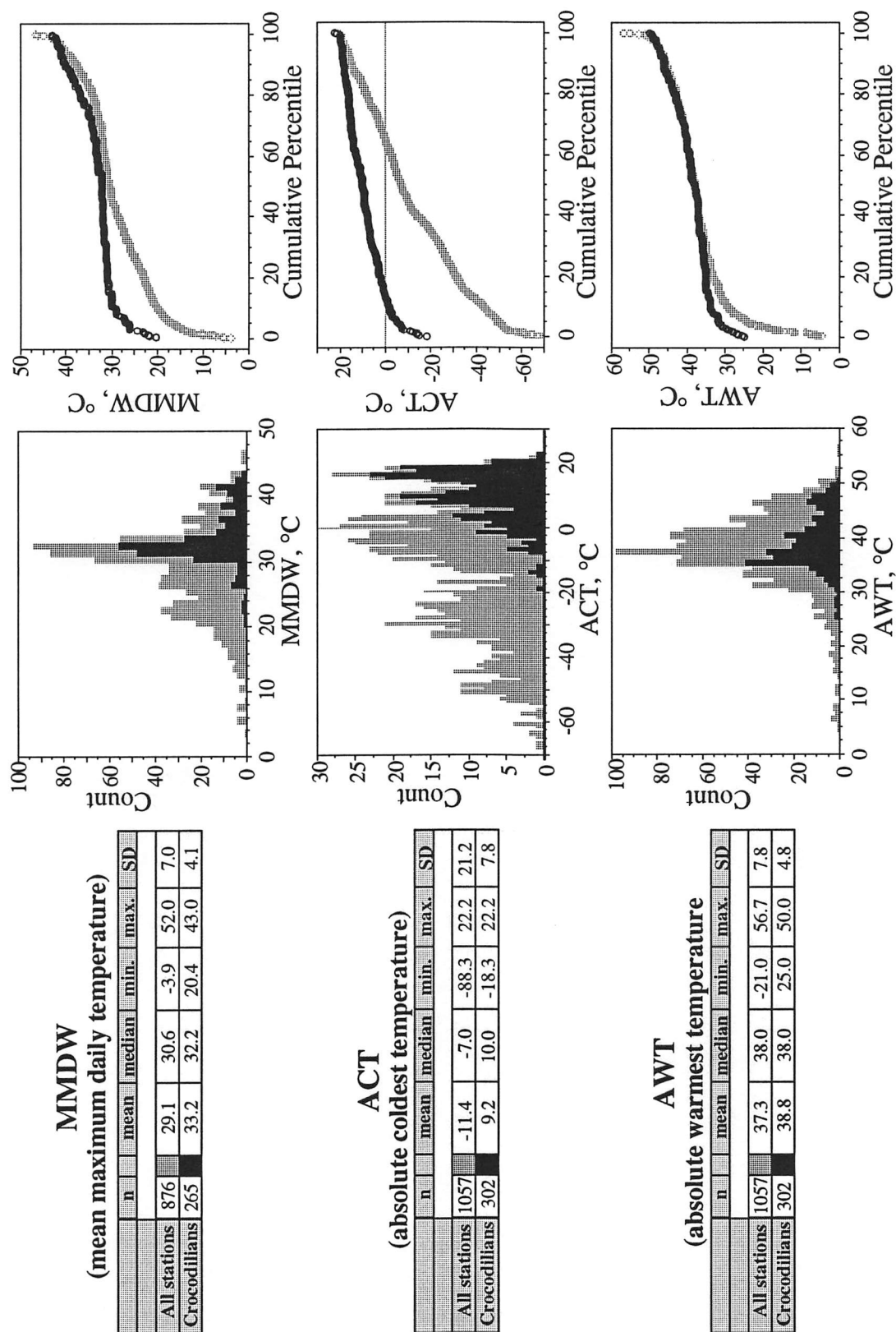


FIGURE IV.4. continued.

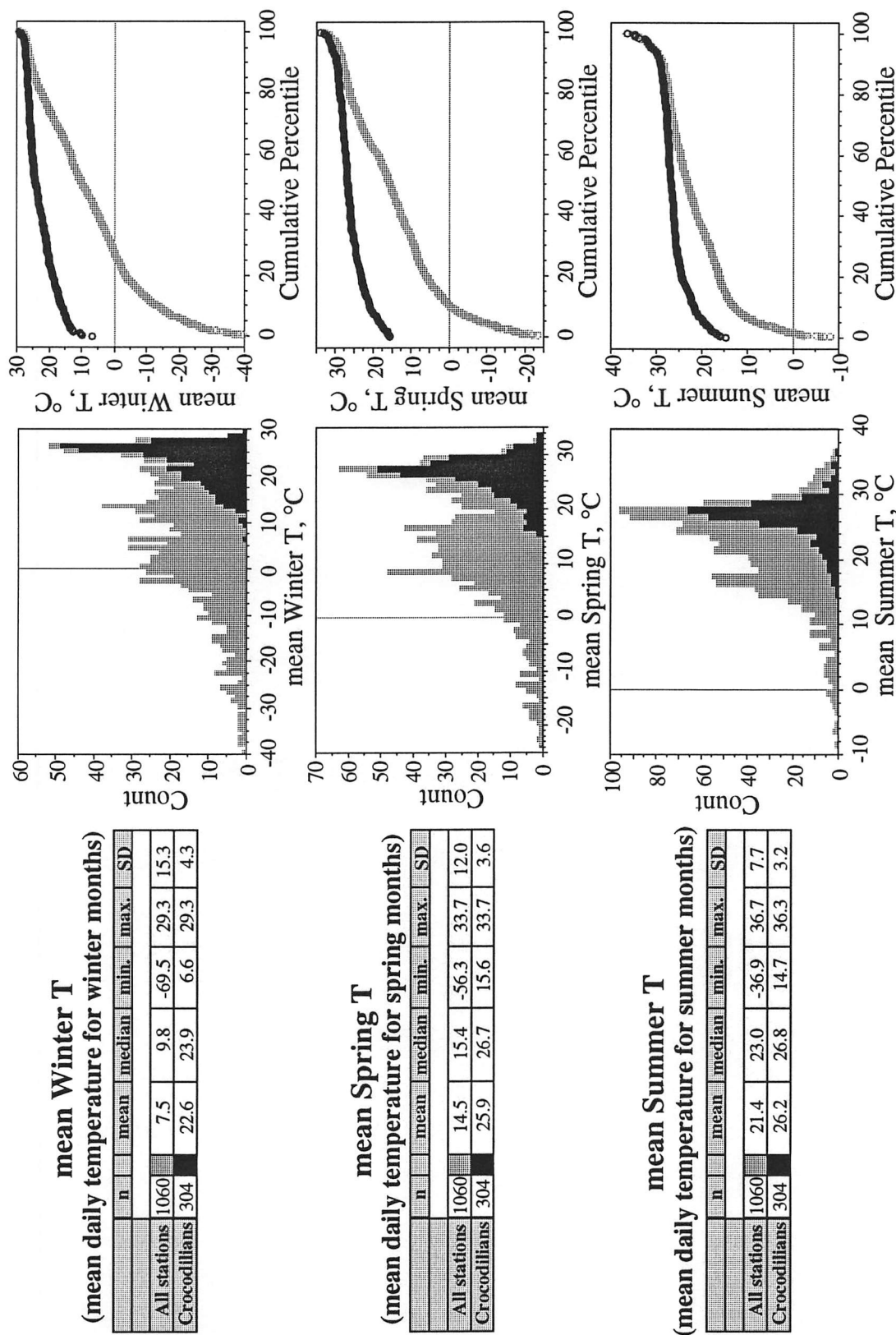


FIGURE IV.4. continued.

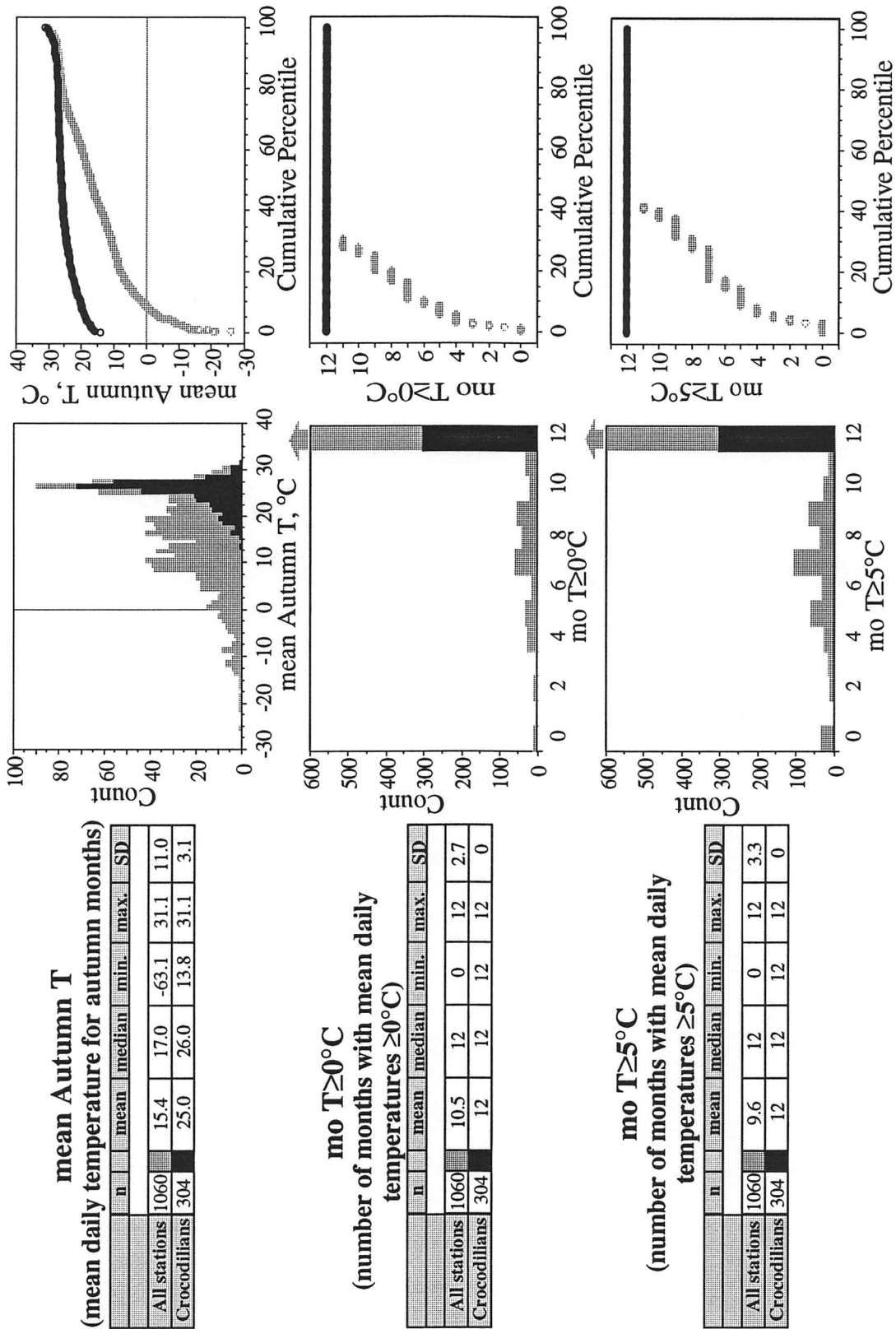


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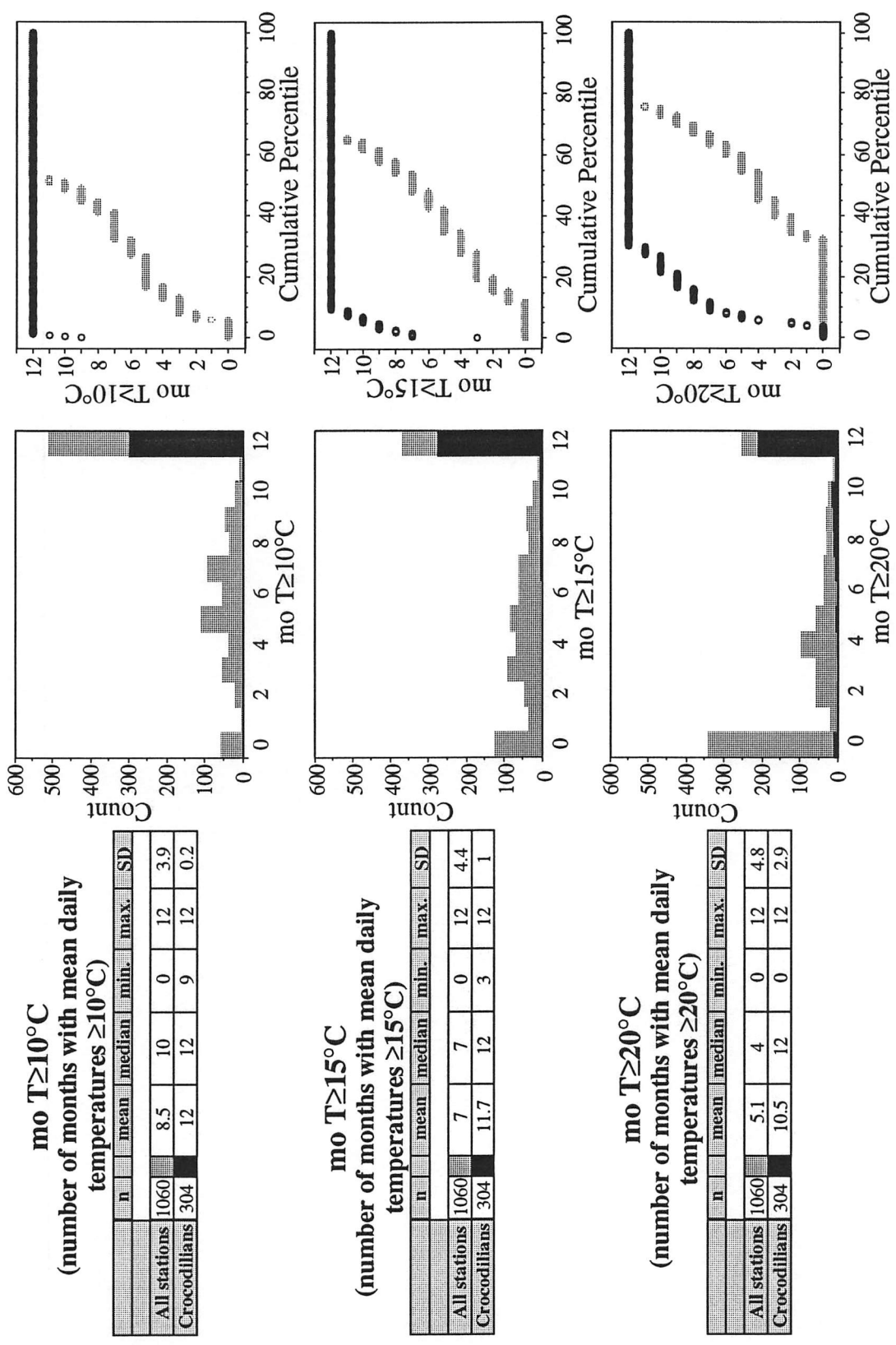
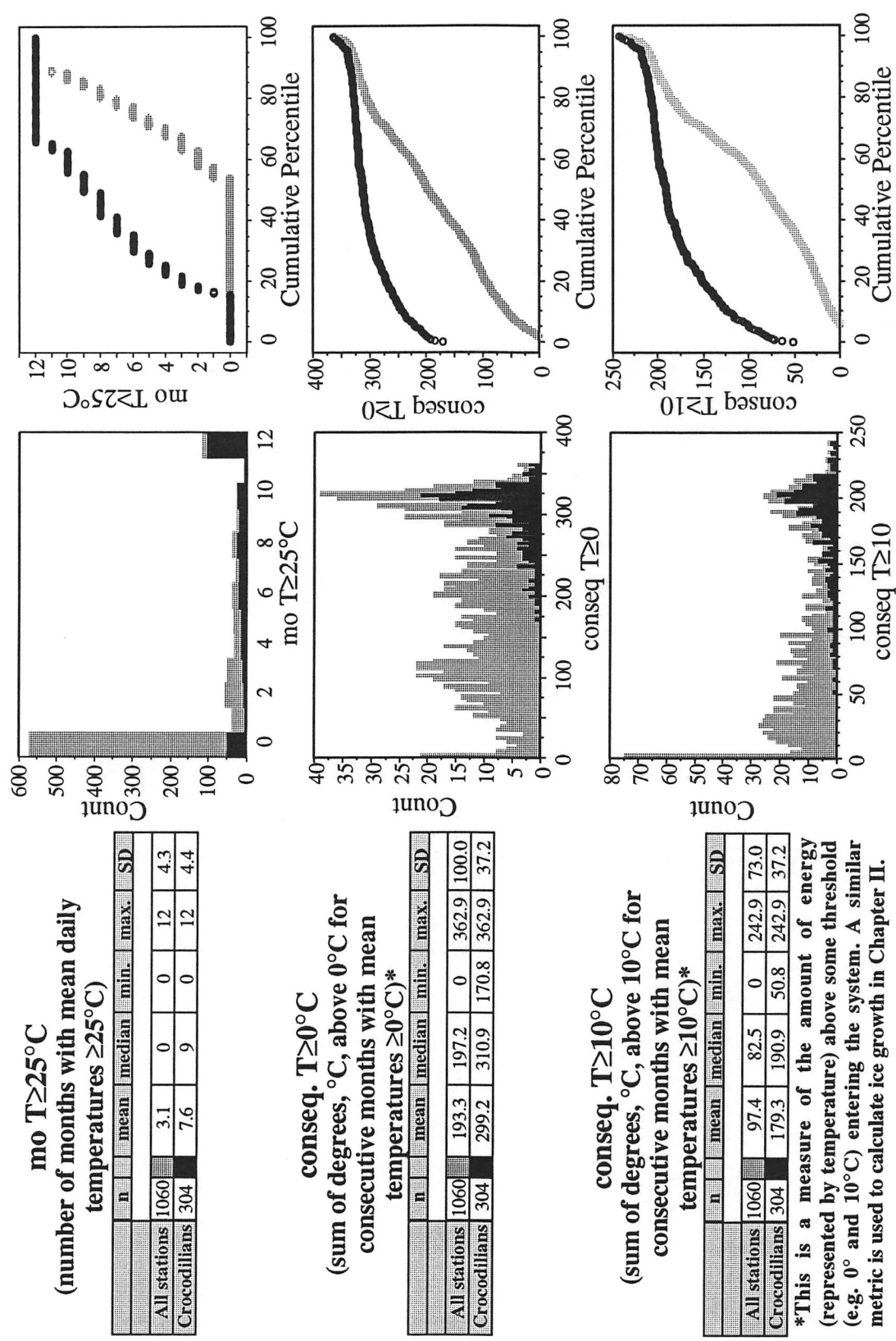


FIGURE IV.4. continued.



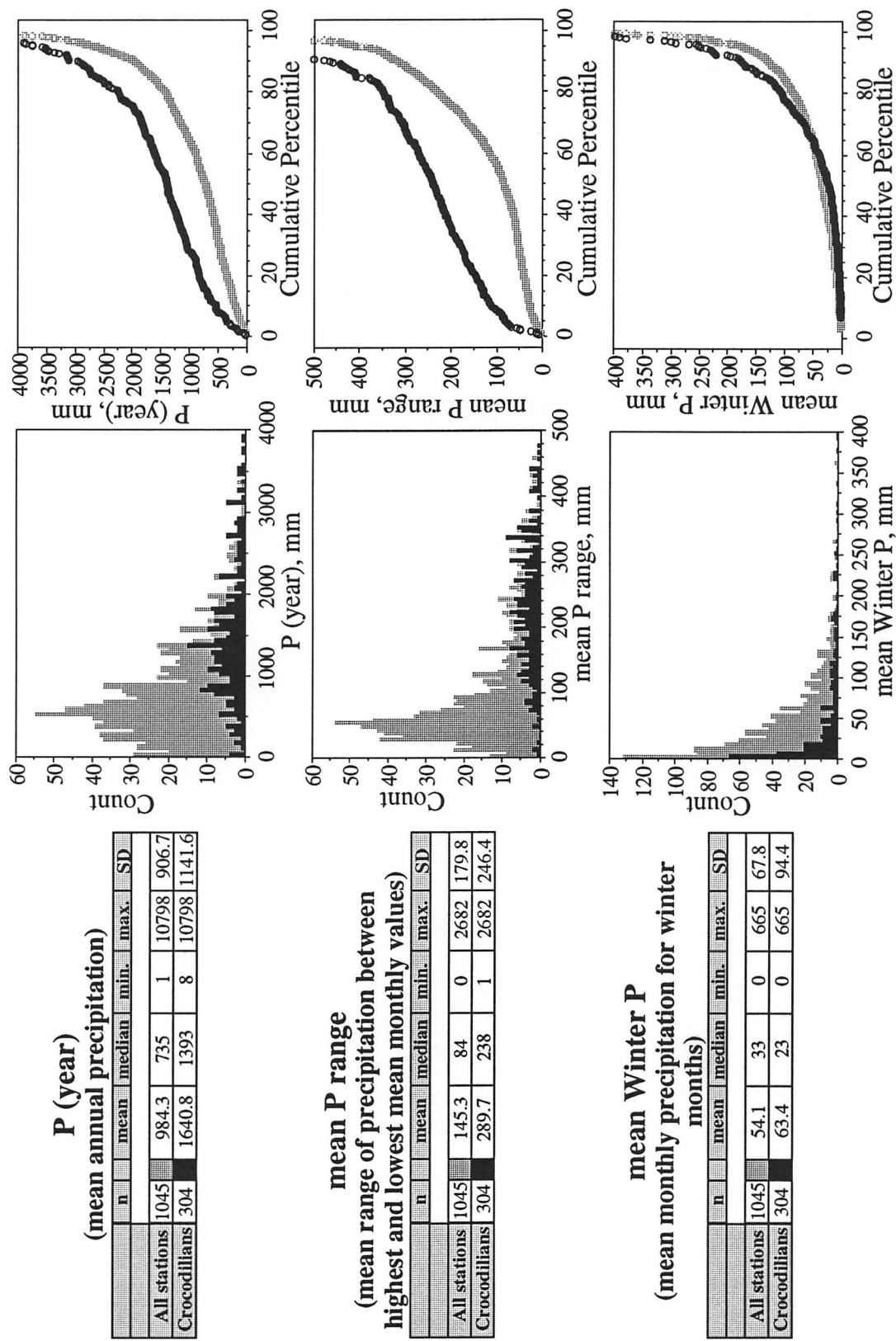


FIGURE IV.4. continued.

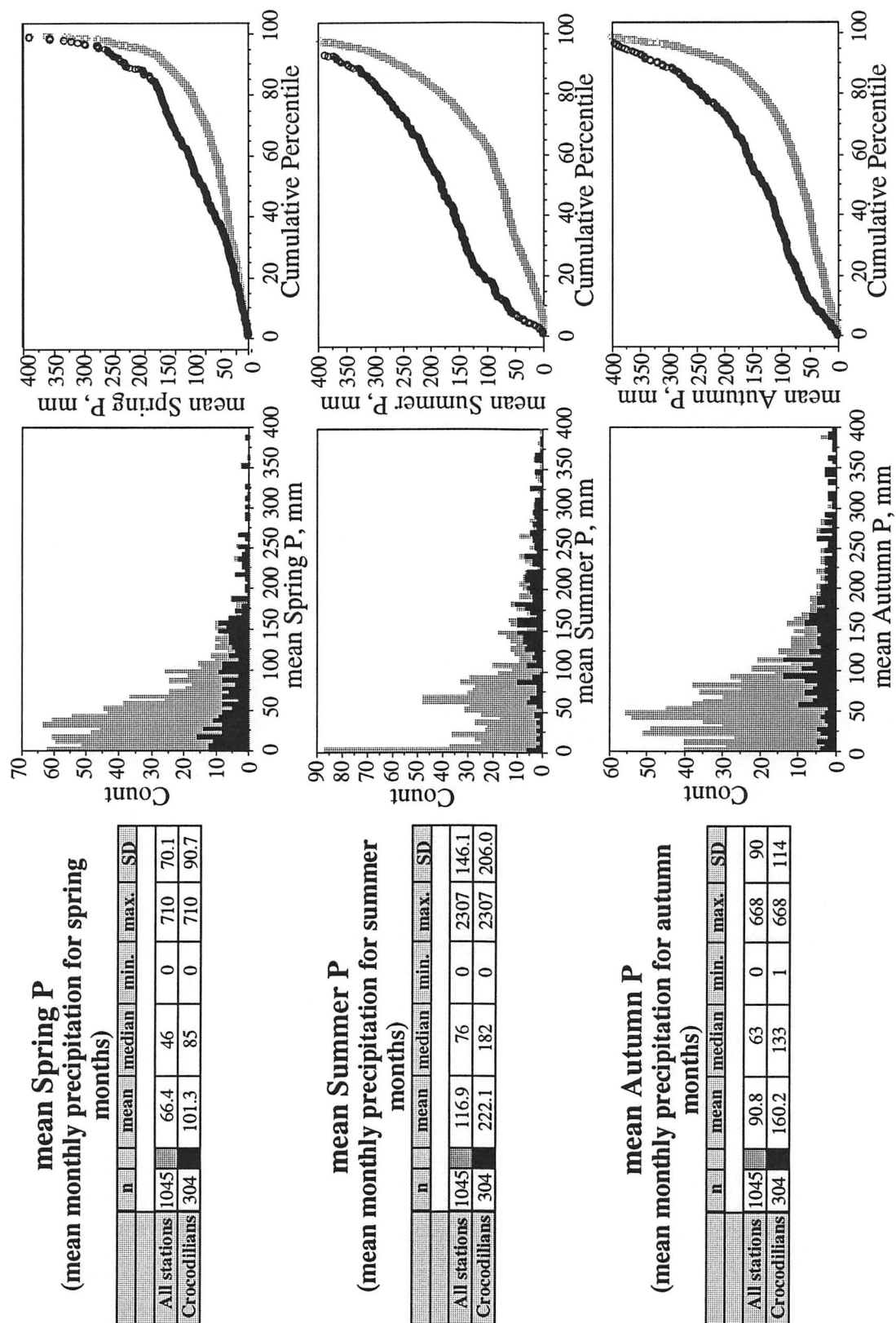
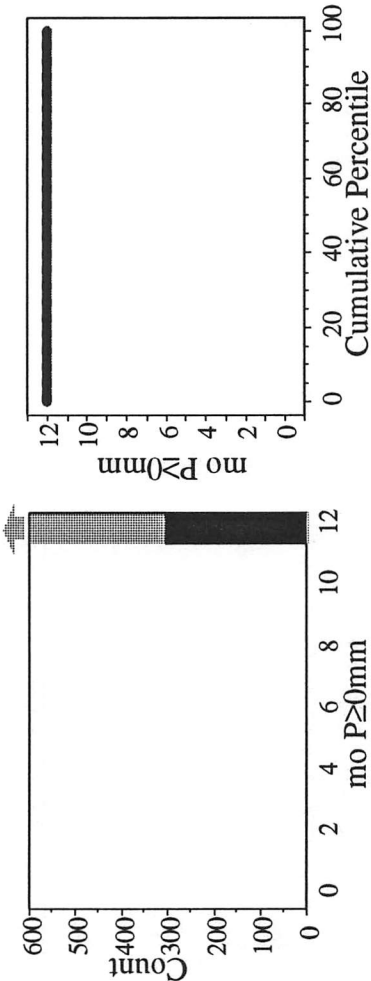


FIGURE IV.4. continued.

mo $P \geq 0\text{mm}$

(number of months with mean precipitation $\geq 0\text{mm}$)

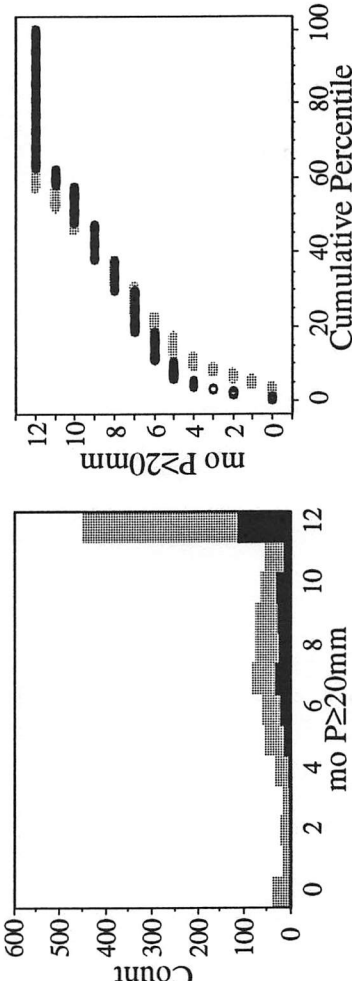
	n	mean	median	min.	max.	SD
All stations	1045	12	12	12	12	0
Crocodillians	304	12	12	12	12	0



mo $P \geq 20\text{mm}$

(number of months with mean precipitation $\geq 20\text{mm}$)

	n	mean	median	min.	max.	SD
All stations	1045	9	10	0	12	3.5
Crocodillians	304	9.2	10	0	12	2.9



mo $P \geq 40\text{mm}$

(number of months with mean precipitation $\geq 40\text{mm}$)

	n	mean	median	min.	max.	SD
All stations	1045	7	7	0	12	4
Crocodillians	304	8.3	8	0	12	3.1

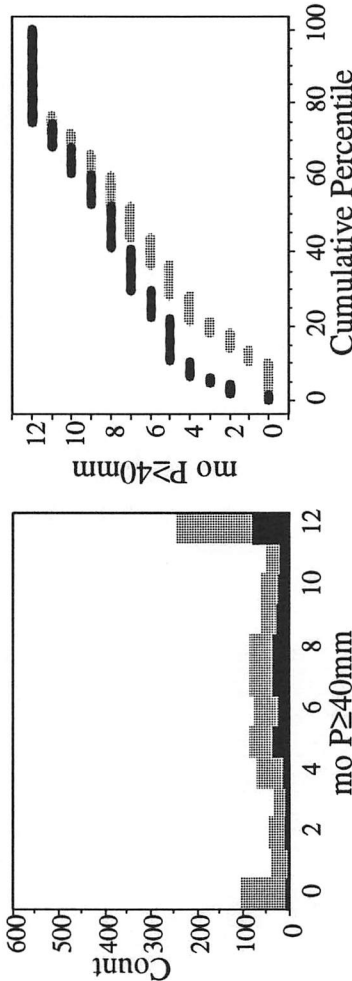


FIGURE IV.4. continued.

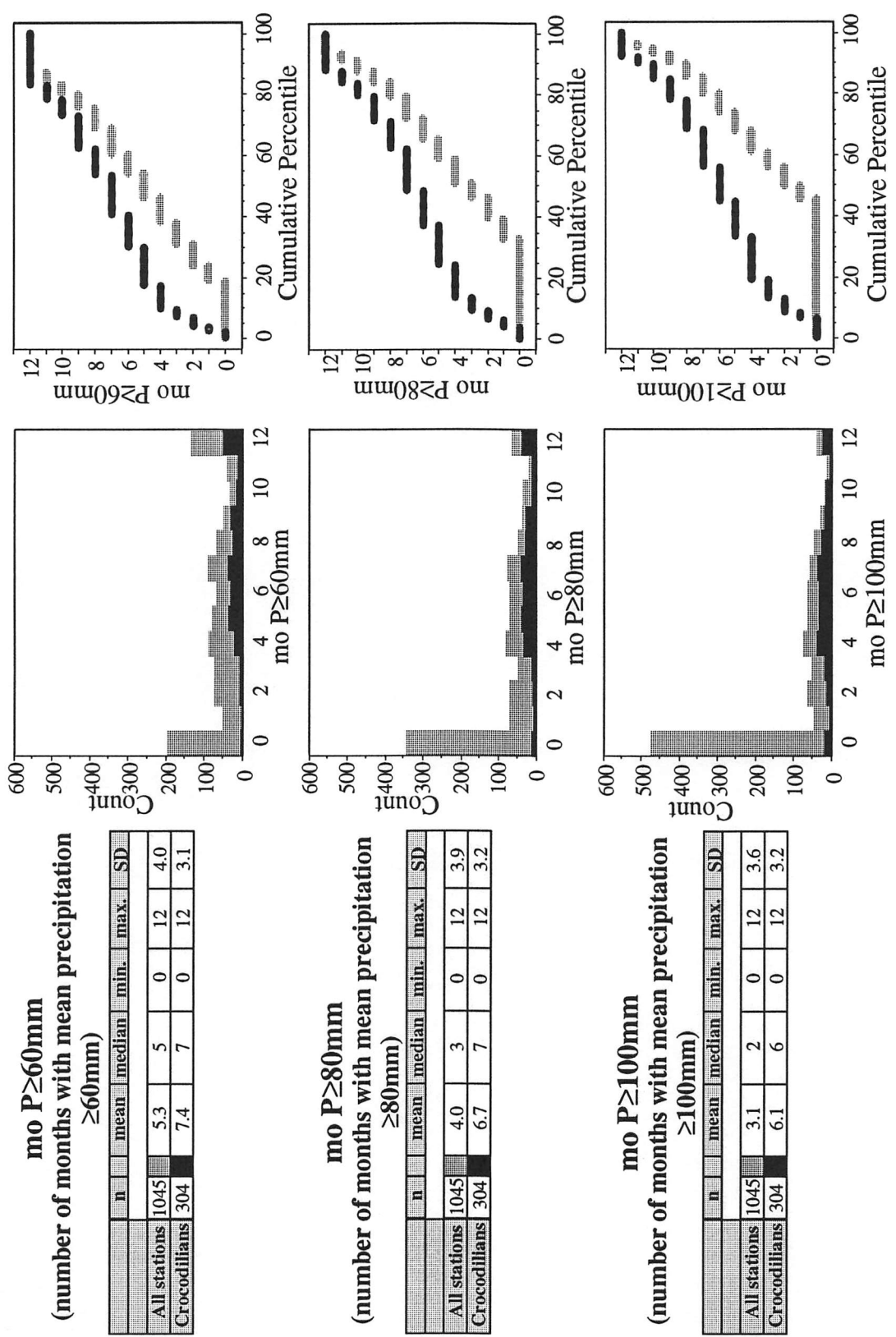


FIGURE IV.4. continued.

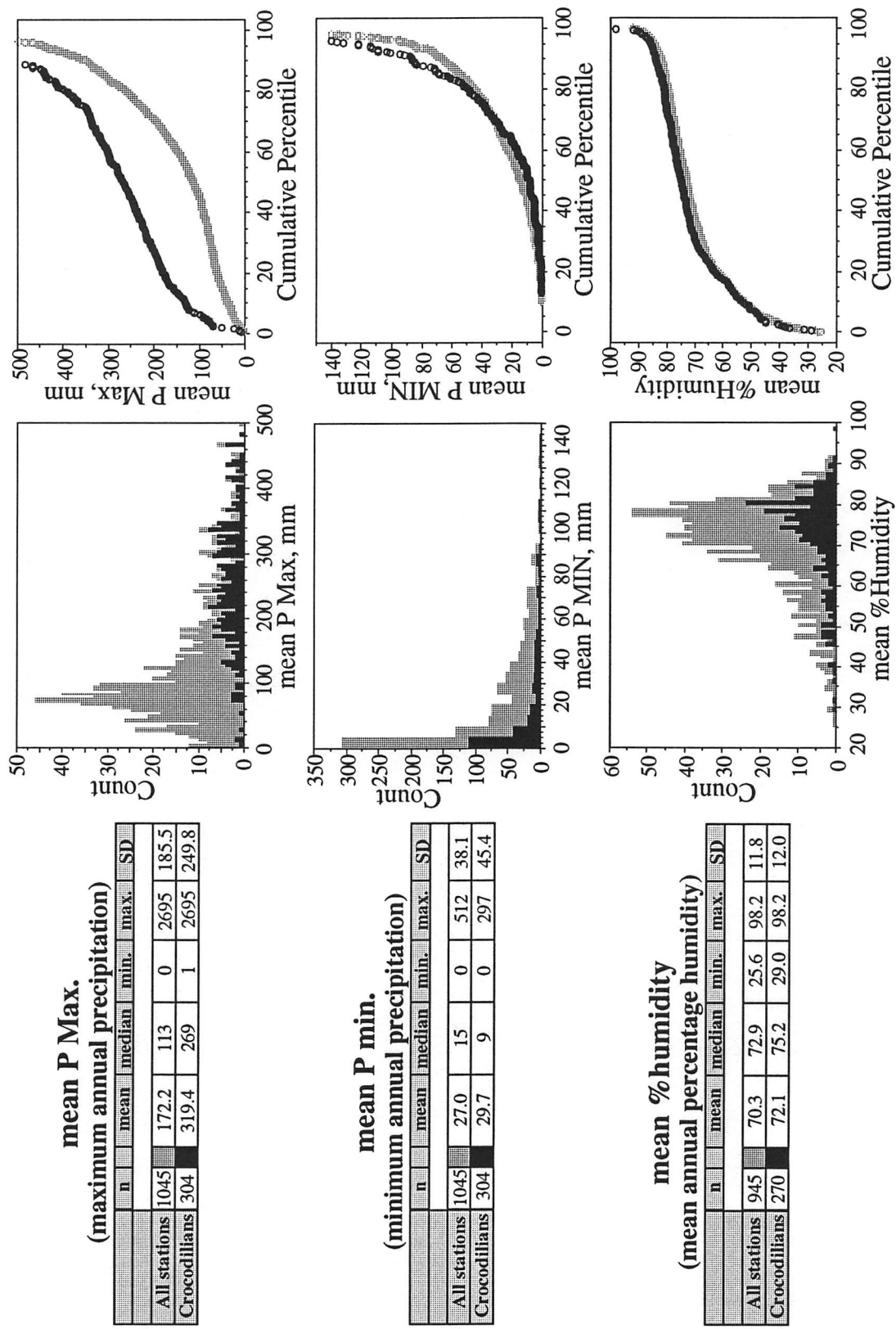


FIGURE IV.4. continued.

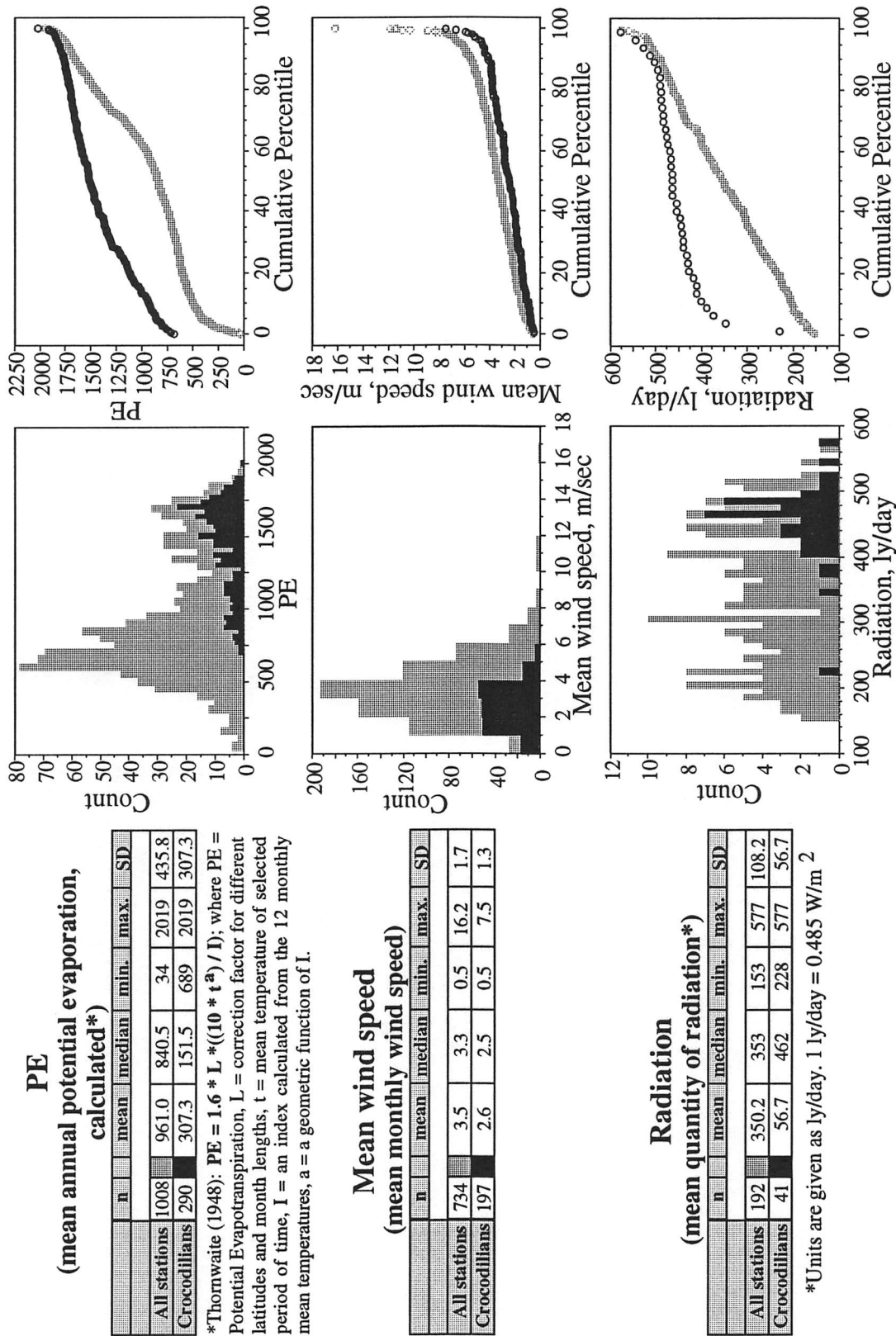


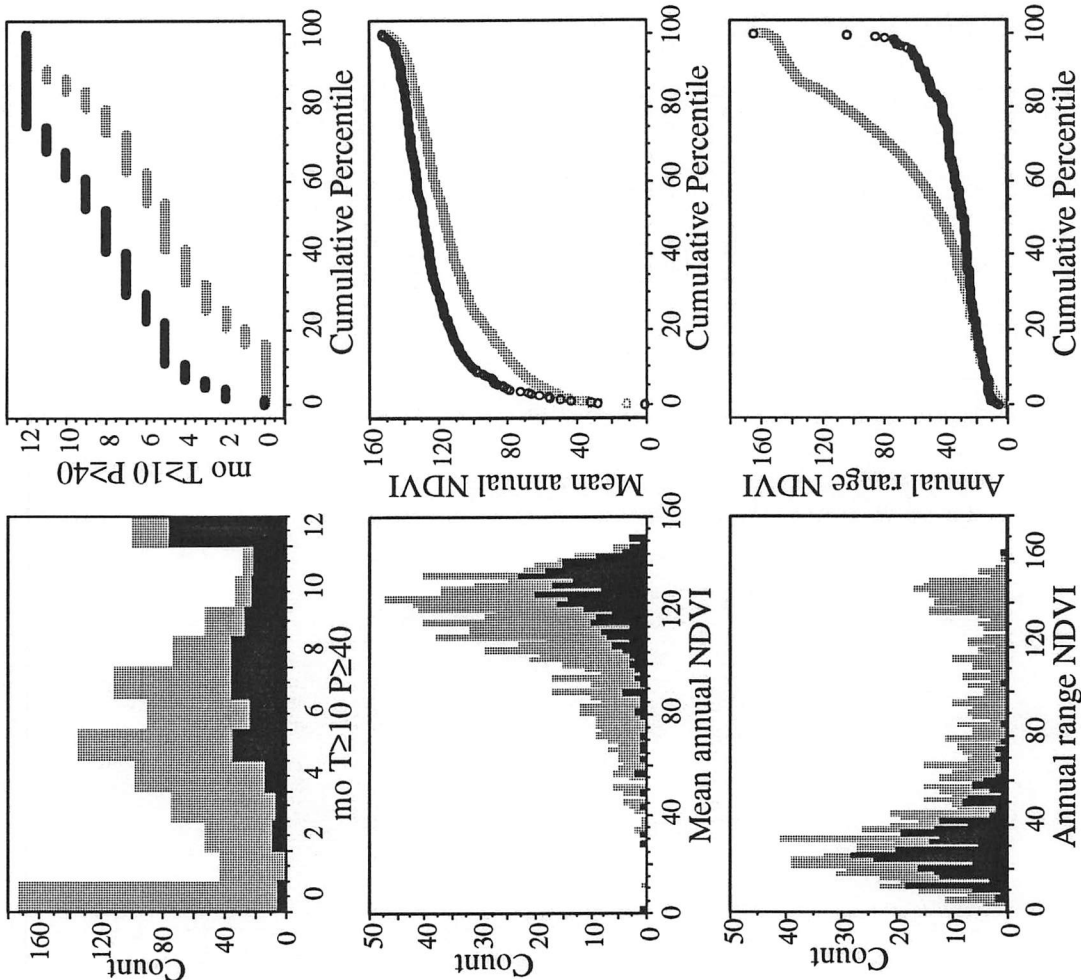
FIGURE IV.4. continued.

mo T \geq 10°C P \geq 40mm

(number of months with mean temperature \geq 10°C and mean precipitation \geq 40mm*)

	n	mean	median	min.	max.	SD
All stations	1060	5.3	5	0	12	3.7
Crocodillians	304	8.2	8	0	12	3.1

*This is the combination of T and P used by Lottes and Ziegler (1994) as a proxy for the distribution of primary productivity, as represented by the NDVI data (see text).



mean NDVI
(mean annual NDVI*)

	n	mean	median	min.	max.	SD
All stations	941	111.3	116.9	0.8	152.3	24.3
Crocodillians	281	123.4	128.5	0.8	152.3	21.2

*NDVI = Normalized Difference Vegetation Index. This is used as a proxy for Net Primary Productivity (NPP). See text for details.

	n	mean	median	min.	max.	SD
All stations	941	59.9	43	3	161	44.5
Crocodillians	281	29.0	26	5	146	15.3

FIGURE IV.4. continued.

TABLE IV.2. PRINCIPAL COMPONENTS ANALYSIS, UNROTATED LOADINGS

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

The distribution of crocodilians in this PCA space is shown in Figure IV.5, and its significance assessed using the Mann-Whitney Test. But, while this shows that crocodilians are significantly distributed with respect to temperature (PC 1; $p < .0001$) and much less so with precipitation (PC 2; $p = .2620$)--supporting previous observations--it still does not give any indication as to which temperature parameter (or combination of climate parameters) is the most important (loadings for thermal parameters on PC 1 are all very similar, except for AWT). Nor does it provide quantitative limits to crocodilian climate space, which is essential if fossil crocodilians are to be of any use in retrodicting climate.

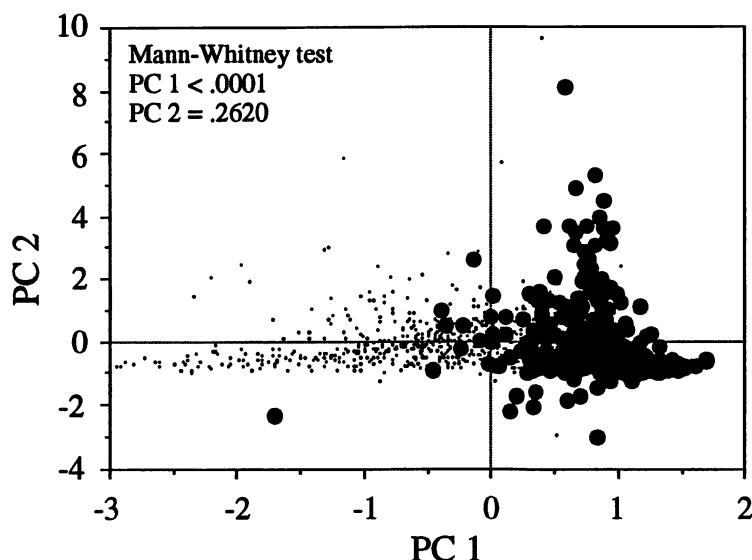


FIGURE IV.5. A graph of component 1 and component 2 scores from a Principal Component Analysis (PCA) of 16 climate parameters.

Scores used here are unrotated scores from a PC Analysis using the Statview statistics software (Haycock et al., 1992-1993). The 16 climate parameters used are given in Table IV.2, which also gives the unrotated loadings for each factor (PC 1, accounting for 52.7% of the scatter, is dominated by temperature, and PC 2, accounting for 25.7% of the distribution, by precipitation). The position of stations with crocodilians on this graph are represented by the larger filled circles. The Mann-Whitney non-parametric test is used to examine whether these stations are significantly distributed along either axis. Derived p values show that crocodilians are significantly distributed along PC 1 ("temperature"), but not along PC 2 ("precipitation").

The importance of temperature is again suggested by the present latitudinal restriction of crocodilians (Figure IV.1),¹¹ since latitude and temperature are closely related (Figure IV.6, top). But, a Spearman Rank Test shows that precipitation is also significantly correlated with latitude ($p < .0001$). However, the distribution of crocodilian bearing

11. Although the present distribution of crocodilians is restricted to low latitudes (Figure IV.1), latitude *per se* is not the constraining factor, as is evident from the greater latitudinal range occupied by the group in the geological past (Chapter V). Fossil crocodilians are known to have occurred up to 80°N palaeolatitude in the Early Eocene--Ellesemere Island.

stations shown in Figure IV.6 (bottom) does not reveal a systematic preference for sites with high precipitation--crocodilians in low latitudes occur at stations with annual precipitation values that encompass the whole range of potential values. The relation between crocodilian bearing stations and stations with high precipitation is therefore considered here to be a coincidence--crocodilians are restricted to low latitudes and low latitudes include areas with very high precipitation. Again, the implication is that temperature not precipitation is the dominant climatic factor limiting crocodilians. Nonetheless, water is important for crocodilians, as discussed in sections IV.2.7.1 and IV.2.9, and although crocodilians are latitudinally restricted there is also a distinct asymmetry in the distribution that coincides with the distribution of aridity on the globe. This is discussed later.

The close correlation among climate parameters is a more insidious problem to solve. Table IV.3 gives the correlation matrix¹² for the 16 parameters used in the Principal Components Analysis above (MART is also included). Of the thermal parameters, all except AWT are very closely related, which is what its lower loading score on the thermal axis (PC 1) in the PC analysis shows (Table IV.2). A partial correlation matrix of these parameters (excluding MART, which is not included in this matrix because it is derived from CMM and WMM) is shown in Table IV.4 (for each pair of variables the effects of all the others are removed); but while this shows a strong correlation between seasonal and annual values of temperature and precipitation respectively, it does not help in defining which parameters are important for limiting the

12. Correlation and partial correlation matrices are used in preference to a covariance matrix because of the large disparity in the magnitude of values for temperature and precipitation parameters.

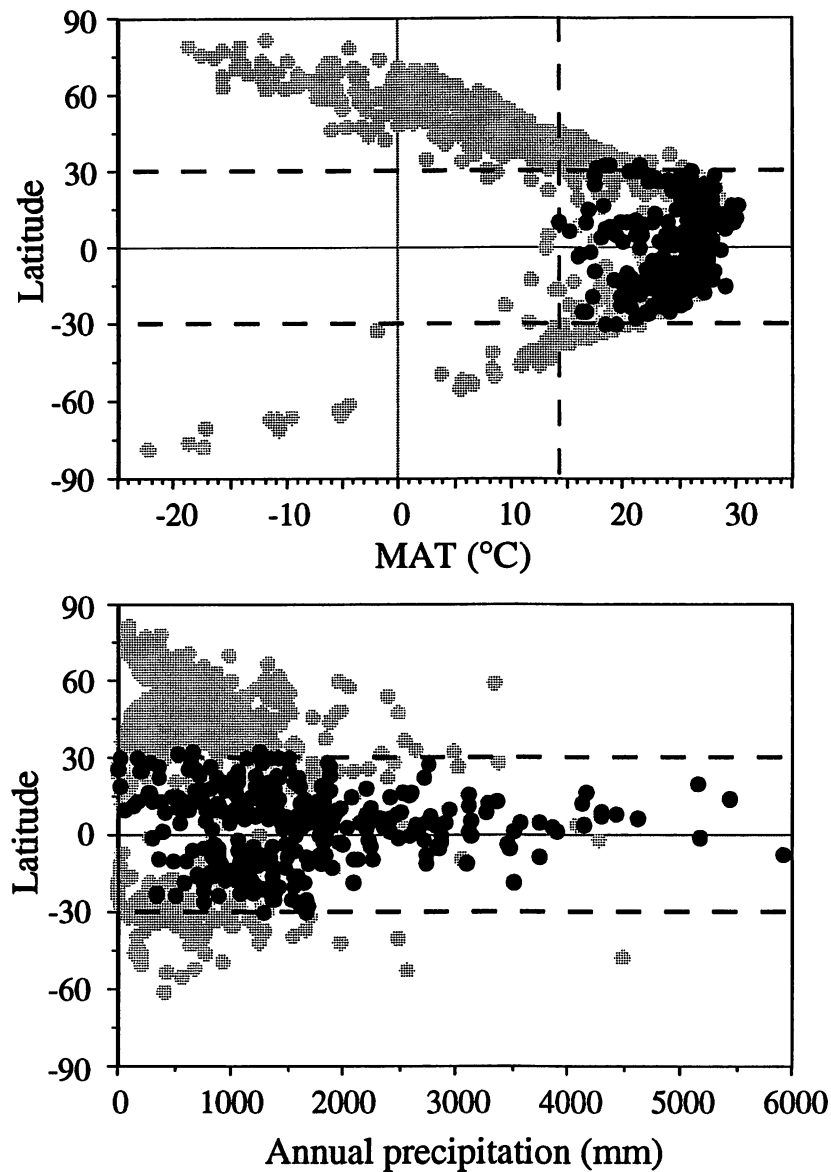


FIGURE IV.6. The relationship between mean annual temperature (MAT) and precipitation with latitude.

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

spatial distribution of crocodilians. It does, however, indicate which parameters might have influences that will be difficult to discriminate

All of the evidence so far presented has indicated the greater significance of thermal parameters, especially the cold temperature parameters, in limiting the spatial distribution of crocodilians. The empirical biological data, discussed earlier, supports this, but also suggests that the limits of crocodilian distribution may be defined not only by absolute

TABLE IV.3. CORRELATION MATRIX FOR A SELECTION OF THERMAL AND PRECIPITATION PARAMETERS

1042 observations were used in this computation.

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

TABLE IV.3. continued

	mean T Autumn	P (year)	mean P Winter	mean P Spring	mean P Summer	mean P Autumn	mean Pmax	mean Pmin
MAT								
MART								
CMM								
ACT								
AWT								
WMM								
mean T Winter								
mean T Spring								
mean T Summer								
mean T Autumn	1.000							
P (year)	.351	1.000						
mean P Winter	.112	.584	1.000					
mean P Spring	.265	.865	.637	1.000				
mean P Summer	.328	.832	.097	.579	1.000			
mean P Autumn	.359	.901	.557	.710	.653	1.000		
mean P max	.344	.691	.219	.497	.725	.596	1.000	
mean P min	.014	.588	.779	.665	.198	.550	.198	1.000

cold, but also by the duration of the cold season. This "duration" can be represented in two ways: as a count of consecutive months above a certain temperature ($mo \geq 5^{\circ}\text{C}$, $mo \geq 10^{\circ}\text{C}$, etc., in Figure IV.4), or as the mean annual range of temperature (MART). MART has additionally been used as an indication of "continentality,"¹³ which has become an important issue in the paleoclimate literature (Markwick, 1994; Sloan and Barron, 1990, 1992). The effect of this on climate can be seen by comparing the monthly temperature

13. Measures of continentality invariably use MART as an input variable; thus Conrad's formula (k) is defined as

$$k = ((1.7A) / \sin(\phi + 10)) - 14$$

where A is the MART and ϕ is latitude. Gorczynski's continentality index (K) is similar :

$$K = 1.7 (A / \sin\phi) - 20.4$$

Information from Barry and Chorley (1987).

TABLE IV.4. PARTIAL CORRELATION MATRIX FOR A SELECTION OF THERMAL AND PRECIPITATION PARAMETERS

1042 observations were used in this computation

	MAT	CMM	ACT	AWT	WMM	mean T Winter	mean T Spring	mean T Summer
MAT	1.000							
CMM	.0007	1.000						
ACT	.0010	-.023	1.000					
AWT	.025	.086	-.244	1.000				
WMM	-.027	-.282	.0093	.188	1.000			
mean T Winter	.964	.251	.032	-.047	.078	1.000		
mean T Spring	.996	-.015	-.0098	-.012	.044	-.951	1.000	
mean T Summer	.987	.047	-.0097	-.019	.151	-.967	-.981	1.000
mean T Autumn	.990	-.015	.029	-.025	.037	-.942	-.988	-.967
P (year)	.015	-.073	.035	-.016	-.064	.0048	-.017	-.0006
mean P Winter	-.015	.075	-.033	.017	.064	-.0058	.016	.0002
mean P Spring	-.016	.070	-.036	.015	.064	-.0033	.017	.0002
mean P Summer	-.015	.074	-.035	.016	.065	-.0053	.017	.0004
mean P Autumn	-.015	.072	-.034	.014	.065	-.0046	.016	.0007
mean P max	.046	.0002	-.014	-.031	.100	-.048	-.042	-.063
mean P min	.0097	.121	-.144	-.057	-.044	-.040	-.0026	-.0077

TABLE IV.4. continued.

	mean T Autumn	P (year)	mean P Winter	mean P Spring	mean P Summer	mean P Autumn	mean Pmax	mean Pmin
MAT								
CMM								
ACT								
AWT								
WMM								
mean T Winter								
mean T Spring								
mean T Summer								
mean T Autumn	1.000							
P (year)	-.023	1.000						
mean P Winter	.022	1.000	1.000					
mean P Spring	.023	1.000	-1.000	1.000				
mean P Summer	.023	1.000	-1.000	-1.000	1.000			
mean P Autumn	.022	1.000	-1.000	-1.000	-1.000	1.000		
mean P max	-.039	.023	-.021	-.023	-.020	-.022	1.000	
mean P min	-.0062	.0029	.0049	.0018	-.0031	-.0009	-.123	1.000

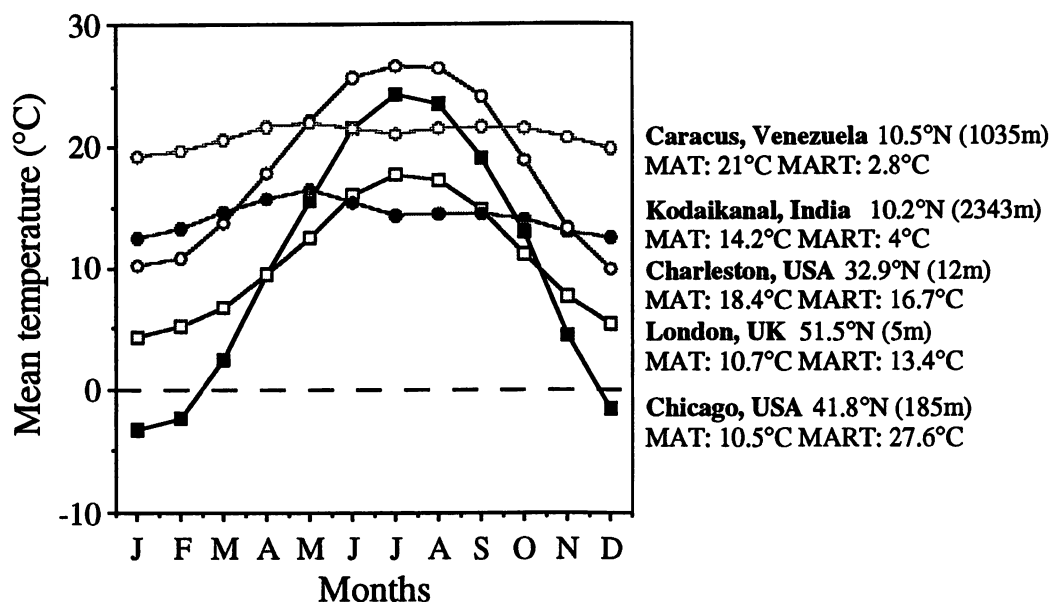


FIGURE IV.7. Monthly mean temperature distributions for selected climate stations.

The mean monthly temperature distribution is shown for five climate stations. Two of them, Chicago and London, have very similar MAT's (10.5 and 10.7 °C respectively), but different MART's (27.6 and 13.4°C respectively) reflecting the effect of continentality--although there is some ameliorating effects in Chicago due to adjacent Lake Michigan. Crocodilians cannot survive in either place today. In contrast, crocodilians are known from near Charleston, NC, which represents the approximate northern limit of crocodilians in North America, and Caracas (Venezuela) and Kodaikanal (India) which represent the crocodilian distribution at low latitudes. See text concerning Kodaikanal, which although within the range of crocodilians shown on most maps, is at high elevations (2343m) and almost certainly does not have local crocodilians. The distribution of crocodilians is therefore represented by thermal distributions that are not only warmer in absolute terms, but which also have flatter distributions (low MART). This is clearly shown in Figure IV.8.

profiles of London and Chicago (Figure IV.7). Although these two cities have similar MAT's (10.5°C and 10.7°C, respectively) the MART in each case is quite different (13.4°C and 27.6°C, respectively)--London is maritime (also influenced by the Gulf Stream), Chicago continental. Plots of MAT verses MART have been used extensively by Wolfe for

floral assemblages in order to accommodate these effects (Wolfe, 1971, 1979, 1993; Wolfe and Poore, 1982). Figure IV.8 shows the distribution of crocodilians in this thermal climate space, which facilitates comparisons with Wolfe's work (the distributions of turtles and palms in this climate space are shown in Figure IX.2). Some interesting features are apparent from this figure. First, the distribution appears limited by CMM rather than MAT or WMM, based on the geometry of the lower bounding line. Second, the stations at the periphery of the distribution are those from the northern limit of the geographic range, Nanchang, Vicksburg, Charleston and Jerusalem. Finally, as one nears the limits of the MAT-MART climate space occupied by crocodilians, the proportion of crocodilian-bearing stations diminishes (towards the bottom right of the distribution and lower MAT's and higher MART's).

The gradient in the proportion of crocodilian-bearing stations exhibited in Figure IV.8 is also evident in the latitudinal distribution of crocodilians (Figure IV.9). Towards the poleward limits of their latitudinal range, crocodilians are increasingly spatially restricted (Figure IV.1). As already noted, latitude cannot directly effect distributions, but temperature can. Figure IV.10 shows the relationship between MAT and the proportion of crocodilian-bearing stations for each degree increment. From this it is clear that the minimum MAT of 14.2°C defined by the present spatial distribution of crocodilians (Figure IV.4) is not the only limit on crocodilian distribution, since there are stations with higher temperatures but no crocodilians (see also the frequency plots in Figure IV.4). However, a linear regression through this trend predicts a minimum limit of $14.9 \pm 1.7^\circ\text{C}$.¹⁴ This is indistinguishable from the observed minimum. Similar trends are found for other climate

14. Assigned errors represent a single standard deviation derived from the residuals of the linear regression.

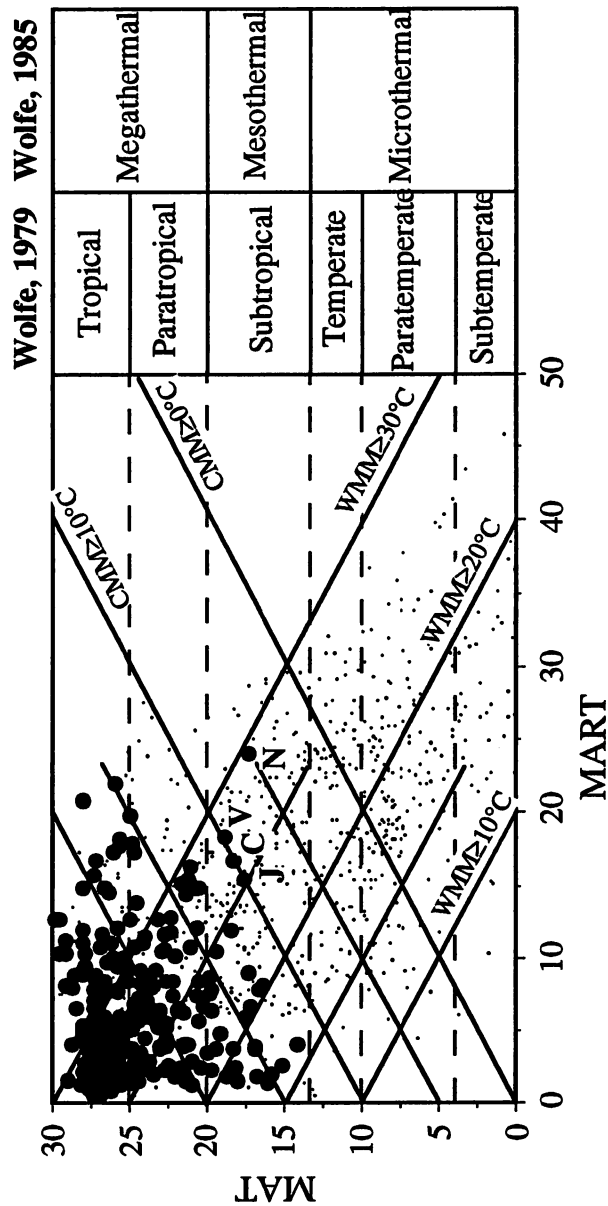


FIGURE IV.8. The distribution of crocodilians in MAT-MART climate space.

Each dot on this figure represents a climate station from the dataset (stations outside of the plot bounds are excluded); stations with crocodilians are represented by the large black circles. This type of diagram has been used extensively by paleobotanists, following the work of Wolfe, for examining the position of modern and fossil floras in climate space. The advantage of this plot is that all pertinent thermal parameters can be represented by it, which is preferable to plotting the position of each group in bivariate plots representing every possible combination of thermal parameter (compare with Figure IV.4). Terminology is that of Wolfe (1979, 1985).

parameters. In each case minimum limits derived from calculated linear regressions give values that are close to observed minimums.¹⁵ A relationship is also found between annual precipitation and the proportion of crocodilian-bearing stations in each 50mm increment. However, as discussed above, this may reflect covariance between temperature, or latitude, and precipitation, rather than the dependence of crocodilians on precipitation.

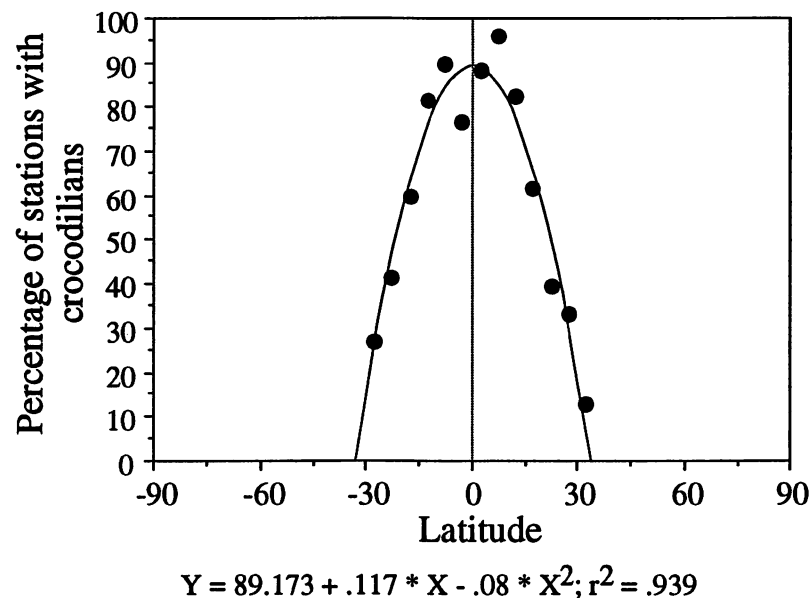
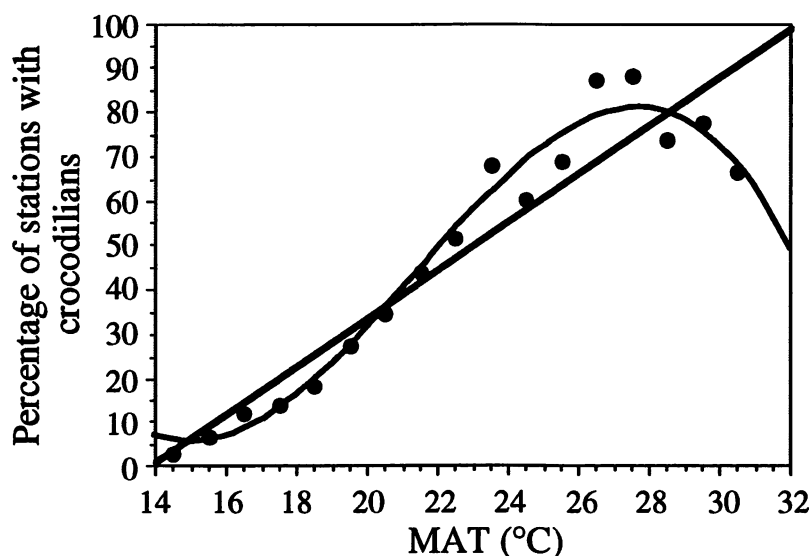


FIGURE IV.9. The percentage of all stations in each 5° latitudinal band that have crocodilians assigned to them.

A second order polynomial is fitted through the data. A similar relationship is also found when using 1° latitudinal zones rather than 5°. In the case of 1° zones the fit through the data is not quite as good as that shown in this figure ($r^2 = .68$), although the intercept with the x-axis is the same in both cases, $\pm 34.1^\circ$ latitude.

15. Calculated minimums derived from linear regressions are given for the following thermal parameters (values in parentheses are observed minimum values from Figure IV.4): ACT, $-11.7 \pm 5.1^\circ \text{C}$ (-18.3°C); MMDC, $2.8 \pm 3.6^\circ \text{C}$ (4.0°C); CMM, $8.3 \pm 2.1^\circ \text{C}$ (5.5°C); mean Winter T, $9.01 \pm 1.8^\circ \text{C}$ (6.6°). Maximum MART, $18.8 \pm 3.0^\circ \text{C}$ (14.2°C).



$$Y = 5.704 - .919 * X + .047 * X^2 - 7.377E-4 * X^3; r^2 = .974$$

$$Y = -.755 + .055 * X; r^2 = .883 \text{ (Linear)}$$

FIGURE IV.10. The percentage of all stations that contain crocodilians, as a function of MAT.

Black circles represent all crocodilian-bearing localities. Percentages represent the proportion of all stations that contain crocodilians for each value of MAT (1°C increments). Although a 3rd-order polynomial gives the best fit through the data ($r^2 = .974$), a linear regression also gives a very good fit ($r^2 = .883$), and for reasons of parsimony is to be preferred.

These relationships are consistent with, or at least suggestive of, an hypothesis that postulates that as temperature decreases, conditions become increasingly deleterious for crocodilians, and their survival becomes progressively dependent on additional factors. In order to investigate this, the geographic distribution of each climate parameter is compared with that of crocodilians (Figure IV.1). For example, Figure IV.11 shows the distribution of all climate stations that have MAT's of at least 14.2°C--the minimum MAT for crocodilians given in Figure IV.4. Spatial discrepancies between this distribution and that

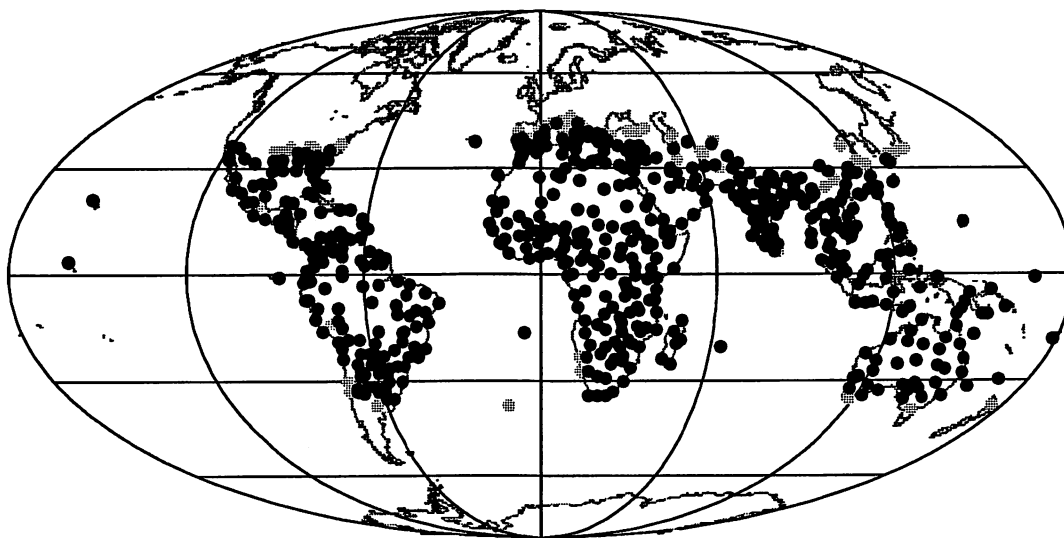


FIGURE IV.11. The global distribution of stations with MAT $\geq 14.2^{\circ}\text{C}$.

The global distribution of all climate stations with MAT $\geq 14.2^{\circ}\text{C}$ (light gray circles) and $\geq 16.0^{\circ}\text{C}$ (black circles). 14.2°C represents the minimum MAT represented by the present crocodilian distribution (see Figure IV.4); 16.0°C represents the minimum MAT for crocodilians given by Markwick based on the present distribution of *Alligator mississippiensis* in North America (Markwick, 1994) --it is also the minimum MAT based on the climate station data when only stations situated below 1500 m are considered. Only 50.2% of stations with MAT $\geq 14.2^{\circ}\text{C}$ are crocodilian-bearing. This suggests that some other limiting factor(s) is also at work.

of crocodilians (Figure IV.1) show the regions where MAT alone does not account for the absence of crocodilians. In this case, only 50.2% of climate stations that satisfy the minimum MAT requirements actually bear crocodilians (this should be equal to the region below the regression in Figure IV.10.). Iterative examination of each climate (and non-climate) parameter in this way, provides the means of understanding the causes of these discrepancies and thereby the actual limitations on the distribution of crocodilians.

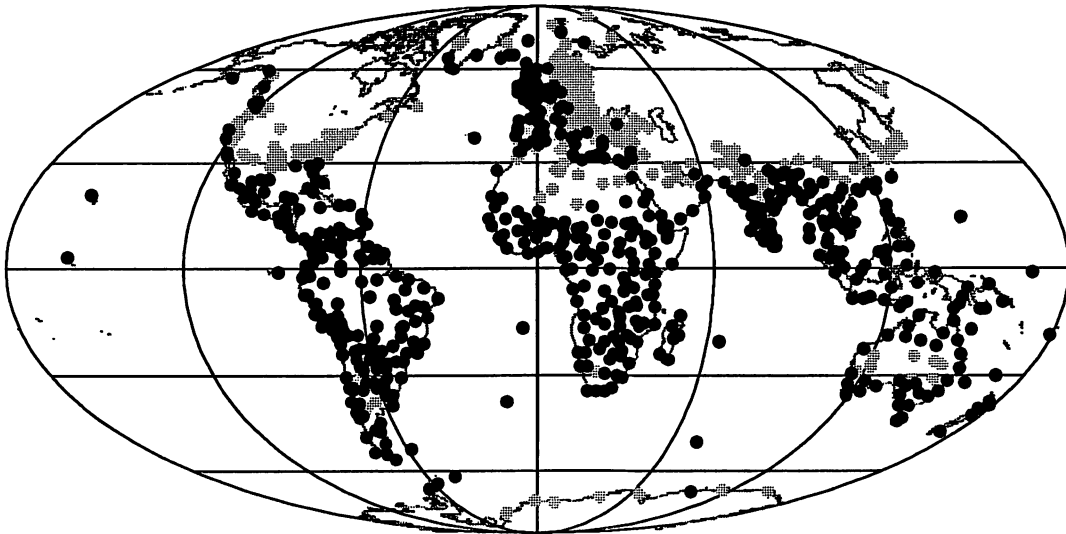


FIGURE IV.12. The global distribution of stations with $MART \leq 24.0^{\circ}\text{C}$.

The global distribution of all climate stations with $MART \leq 24.0^{\circ}\text{C}$ (light gray circles) and $\leq 15.5^{\circ}\text{C}$ (black circles). 24.0°C represents the maximum MART represented by the present crocodilian distribution (see Figure IV.4); 15.5°C represents the 5th percentile from the MART percentile plot in Figure IV.4.--95% of crocodilian-bearing stations have MART's below this value. Only 36.9% of stations with $MART \leq 24.0^{\circ}\text{C}$ have crocodilians.

The principal discrepancies between MAT (Figure IV.11) and the distribution of crocodilians are in the following regions: the southwestern United States, western Mexico, western South America, the Mediterranean region, saharan North Africa, Arabia, southern China and most of Australia. The question is, what accounts for these differences? Figure IV.12 shows the distribution of all stations with MART less than or equal to 24°C (the maximum value for MART from Figure IV.4). Only 36.9% of these stations have crocodilians, which strongly suggests that MART ("equability"), like MAT, is not the sole limiting factor for crocodilians. This is consistent with the results plotted in Figure IV.7

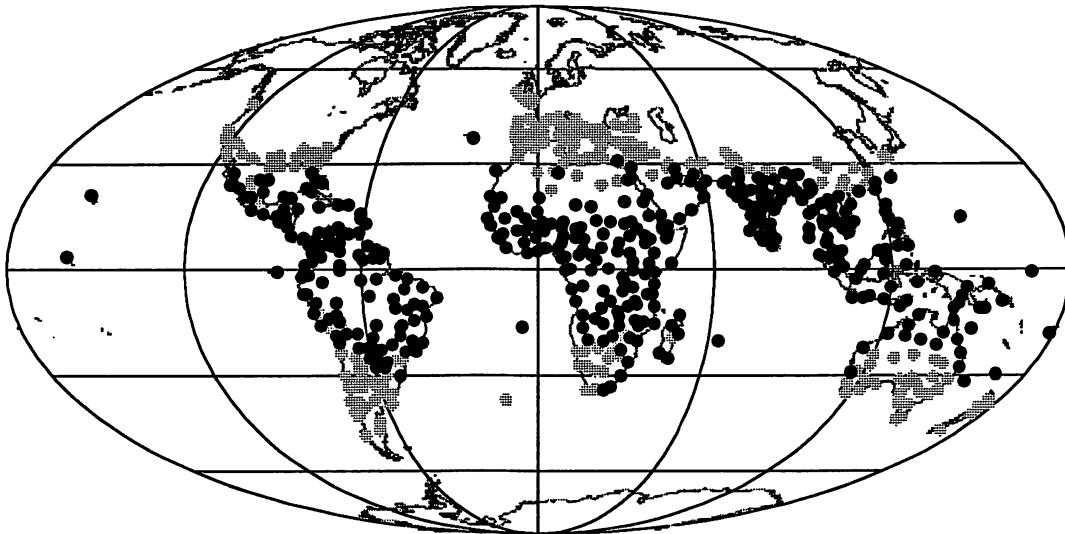


FIGURE IV.13. The global distribution of stations with $\text{CMM} \geq 5.5^\circ\text{C}$.

The global distribution of all climate stations with $\text{CMM} \geq 5.5^\circ\text{C}$ (light gray circles) and $\geq 14.0^\circ\text{C}$ (black circles). 5.5°C represents the minimum CMM represented by the present crocodilian distribution (see Figure IV.4); 14.0°C represents the 5th percentile from the CMM percentile plot in Figure IV.4.--95% of crocodilian-bearing stations have CMM's above this value. 50.3% of stations with $\text{CMM} \geq 5.5^\circ\text{C}$ have crocodilians; 73.6% of stations with CMM's $\geq 14.0^\circ\text{C}$ have crocodilians.

and Figure IV.8, which suggest that regardless of MART, crocodilians can only exist in regions with minimum temperatures above some threshold value. Whatever the case, MART limits cannot explain the discrepancies shown for MAT in Figure IV.11.

The importance of CMM for limiting crocodilians has already been suggested by their distribution in MAT-MART space (Figure IV.8). Figure IV.13 shows the distribution of all stations with minimum CMM's of at least 5.5°C . The major areas of discrepancy are similar to those found for MAT. However, a better fit is found when only those stations

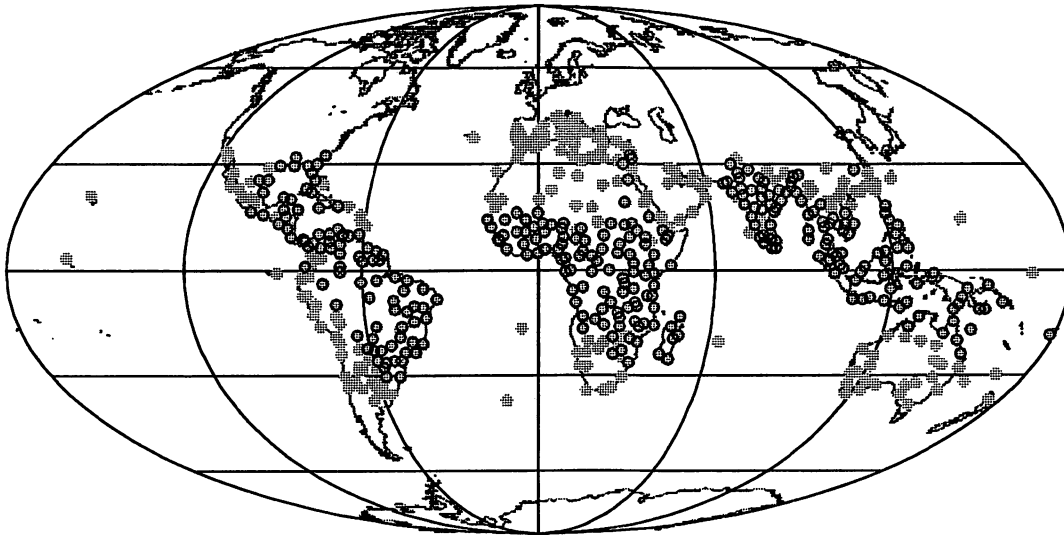


FIGURE IV.14. The global distribution of all stations with specified minimum thermal limits compared with the observed distribution of extant crocodilians.

Open circles represent crocodilian-bearing stations, grey circles represent stations which have minimum temperatures for the following parameters, MAT ($\geq 14.2^{\circ}\text{C}$), MART ($\leq 24.0^{\circ}\text{C}$), CMM ($\geq 5.5^{\circ}\text{C}$), ACT ($\geq -18.3^{\circ}\text{C}$), MMDC ($\geq 4.0^{\circ}\text{C}$), mean Winter T ($\geq 6.6^{\circ}\text{C}$) and moT $\geq 10^{\circ}\text{C}$ (≥ 9 months), as defined by the observed distribution of crocodilians (Figure IV.4). 60% of the climate space defined using these values is occupied by crocodilians.

with CMM's of greater than or equal to 14.0°C (the 5th percentile from the CMM percentile plot, Figure IV.4) are considered--stations in the Mediterranean region, central Australia, southwestern South America and southwestern Africa are excluded, having values less than 14.0°C . The choice of the 5th percentile is arbitrary, but is suggestive of the pattern of CMM values--the absolute minimum value derived from the climate stations dataset is a function of the dataset and may represent too conservative an estimate.

No single parameter exactly replicates the distribution of present crocodilians. Figure IV.14 shows the distribution of climate stations which have at least minimum values for the following thermal parameters, MAT, MART, CMM, ACT, MMDc, mean Winter T, and $moT \geq 10$. This combination of factors successfully replicates the observed distribution of crocodilians in the southeastern United States, suggesting that temperature does limit the northern extent of crocodilians in North America. But, the other regions of discrepancy seen for individual thermal metrics (excluding MART) remain problematic: Australia, southwestern Africa, North Africa, Arabia, southwestern United States and western Mexico, western South America, the Mediterranean, and southern China. The use of less conservative limits for parameters, especially CMM (Figure IV.13), can account for some of these discrepancies, but not all. However, most of these areas do share a common climate signature, they are arid--the Sahara, Arabia and the preponderance of west coast discrepancies associated with coastal upwelling systems.¹⁶

The importance of water for crocodilian thermoregulation has already been discussed in section IV.2. Water provides a thermal buffer against extremes of temperature, both hot and cold. Consequently, at the limits of the thermal climate space the importance of water should be the greatest. Figure IV.15 shows the distribution of climate stations with precipitation of at least 8mm (the minimum defined by the distribution of crocodilian-bearing climate stations, Figure IV.4). As noted earlier, this minimum limit is not very informative--crocodilians are not dependent on precipitation *per se*, but on the presence of

16. The absence of crocodilians from the perennial Orange River in the Kalahara Desert is problematic, since despite being in an arid region one would assume that it provides similar aquatic habitats to the River Nile, where crocodiles do occur. A number of explanations come to mind. It is possible that the limited riparian vegetation of the Orange River (Corvinus and Hendey, 1978) does not provide a suitable habitat. Alternatively, the absence of crocodilians may reflect an historical artifact--once eliminated from the entire Orange River drainage system they were physically impeded by geographic barriers from returning when the climate ameliorated. However, a climate explanation is not ruled out and as shown in Figure IV.13 this region is very close to the minimum limit of CMM for crocodilians.

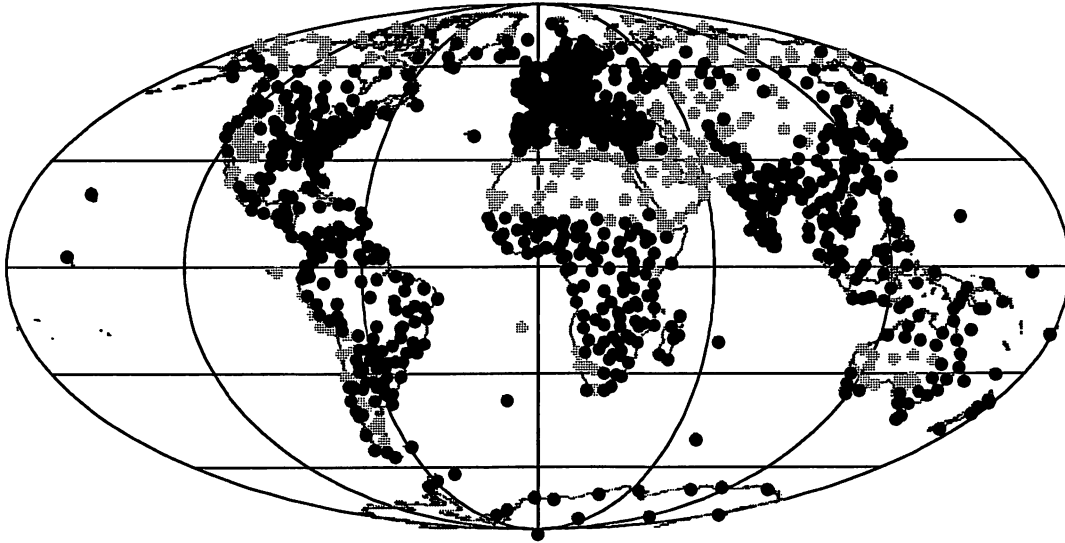


FIGURE IV.15. The global distribution of stations with annual $P \geq 8\text{mm}$.

The global distribution of all climate stations with annual $P \geq 8\text{mm}$ (light gray circles) and $\geq 340\text{mm}$ (black circles). 8mm represents the minimum CMM represented by the present crocodilian distribution (see Figure IV.4); 340mm represents the 5th percentile from the annual P percentile plot in Figure IV.4.--95% of crocodilian-bearing stations have annual P above this value. 29.2% of stations with annual $P \geq 8\text{mm}$ have crocodilians. The distribution of stations with $\geq 340\text{mm}$ shows the distribution of the Earth's major desert regions.

standing water. This is clearly indicated by the presence, at least historically, of crocodilians along the River Nile where precipitation is low. Nonetheless, less conservative minimum values for precipitation (for instance $\geq 340\text{mm}$) do replicate the regions of aridity quite well and are at least suggestive of the general availability of water.

Topography also plays an important rôle in limiting the distribution of crocodilians: it affects drainage and the distribution of standing water; provides physical barriers to migration; influences regional climate, especially through orographically enhanced

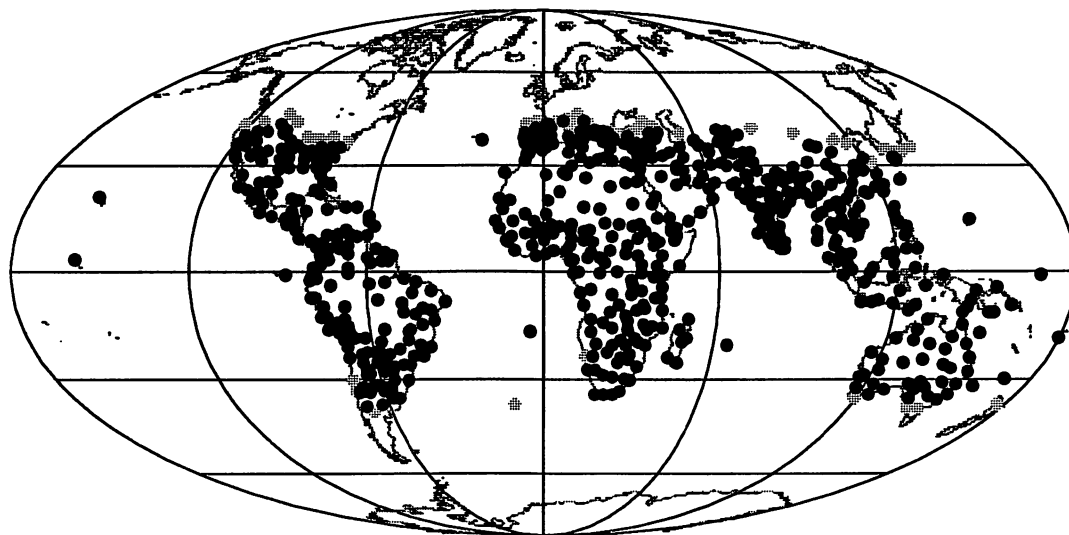


FIGURE IV.16. The global distribution of stations with calculated sea-level values of MAT $\geq 14.2^{\circ}\text{C}$ and $\geq 16.0^{\circ}\text{C}$.

Gray circles represent stations with MAT $\geq 14.2^{\circ}\text{C}$. Black circles, stations with MAT $\geq 16.0^{\circ}\text{C}$. Values are calculated by taking the observed elevation and MAT for the station, and deriving what the MAT would be if the site were at sea-level, assuming a lapse rate of $6^{\circ}\text{C}/\text{Km}$. The distributions shown in this figure are similar to those given in Figure IV.11; reflecting the preponderance of low elevation sites in the original dataset. Discrepancies occur in North America (the central Rockies region) and the area in and around Afghanistan.

precipitation and aridity (rain shadow). Most significantly, it affects local temperatures, which decrease with increasing elevation--this is the "lapse rate," and is generally taken as $\approx 6^{\circ}\text{C}/\text{Km}$ (the "environmental lapse rate"--this is a simplification because observed lapse rates vary with location and time, Barry, 1992). In order to understand the effect of elevation, this lapse rate is used to recalculate the observed MAT for each station to its sea-level equivalent. Figure IV.16 shows the distribution of all stations with sea-level MAT's ≥ 14.2 and $\geq 16.0^{\circ}\text{C}$ (the thermal limits for crocodilians defined by the modern crocodilian dataset; cf., Figure IV.14). The discrepancies between the distributions shown in this

figure and those in Figure IV.14 give an indication of areas where elevation may, through temperature, influence the distribution of crocodilians. The principal discrepancies are in North America and central Asia. Because topography changes through time, these differences have implications for past climatic reconstructions. This is discussed further in Chapter V.

IV.4. DISCUSSION AND CONCLUSIONS

Climate interpretations based on fossil crocodilians are dependent upon analogy with the constraints dictated by present day physiologies. An understanding of these constraints is therefore essential. Experimentally defined limits, akin to phase boundaries defined by petrologists, have been found in some cases (Colbert et al., 1946), but in general are precluded on ethical grounds since for crocodilians the pertinent "phase boundary" is "dead" or "alive." Regardless, derived results may only be applicable to individuals rather than populations and do not take account of additional factors, such as the importance of water (an initial experimental problem observed by Colbert et al., 1946). As described above, individual adults may survive in regions outside their present geographic and climatic range (e.g. Pennsylvania, Barton, 1955), but populations are more restricted due largely to the greater vulnerability of juveniles.

As a consequence of these experimental limitations, the climate space occupied by extant crocodilians is defined ostensibly on circumstantial evidence derived from the group's present spatial distribution. The validity of derived boundaries is therefore dependent upon the degree to which the geographic range replicates the full potential range

dictated by the physiological dependence on climate. This is addressed in this chapter using a dataset of globally distributed climate stations with associated faunal lists.

Temperature is shown to be the single most important factor in limiting the present distribution of crocodilians. This is indicated by the experimental work of Colbert et al. (1946) and subsequent field observations. It is also suggested by the restriction of the group to low latitudes and by the results of a Principal Components Analysis of 16 climate parameters, which shows crocodilians significantly ($p < .0001$, Mann Whitney Test) distributed along the temperature dominated first axis (Figure IV.5). Although most thermal parameters are closely correlated with one another (Table IV.3 and IV.4), the geometry of the climate space occupied by crocodilians in MAT-MART space (Figure IV.8) suggests that CMM is the main limiting thermal metric. A minimum value of about 5.5°C is found (Figure IV.4). The similarity of this figure with the observed critical minimum body temperature for *Alligator mississippiensis* of 4-5°C (Brisbin et al., 1982) is suggestive, although a less conservative minimum value of about 14.0°C replicates the observed distribution of crocodilians far better. This latter value represents the 5th percentile from the CMM percentile plot in Figure IV.4 (95% of crocodilian-bearing stations have CMM's above this value). Warm temperature metrics, especially AWT, are shown not to be important.

While the empirical data suggest that the duration of the cold season may greatly influence the survival of juveniles and thereby the viability of a population, this is not obvious from the climate station dataset. It is postulated here that this may be a consequence of the present relationship between absolute temperature (such as MAT, CMM, etc.) and the range of temperature (MART)--all areas which exceed the minimum

thermal limits by default have MART's within acceptable values. Nonetheless, seasonality must be considered as a potential limiting factor in geologic periods when the relationship may have been different.

Although minimum temperature limits can be assigned to the distribution of crocodilians, not all stations within these limits have crocodilians. The proportion that do is found to increase linearly with increasing temperature (Figure IV.10), which suggests a systematic cause. This can be examined by comparing maps of the distribution of stations which satisfy minimum thermal requires and the present geographic distribution of crocodilians. Spatial discrepancies between the two are found to be generally regions of aridity. These results suggest that as the thermal limit of crocodilian climate space is approached the presence of standing water becomes increasingly important in order to mitigate the effects of temperature extremes. (The distribution of temperature and hydrology may both be influenced by topography).

The relationship between the proportion of stations with crocodilians and temperature has important implications for retrodicting paleoclimate. It shows that while the presence of a fossil crocodilian signifies a specified minimum temperature, the absence of fossil crocodilians does not automatically mean temperatures less than this value. Nonetheless the frequency distributions in Figure IV.4 can be used to assign probabilities to the presence or absence of a fossil crocodilian signifying a specific temperature or range of temperatures. However, this assumes that the frequency distribution observed in the Recent may be applied verbatim to the fossil record. This may not be realistic. With decreasing temperature, the shape of this frequency distribution is increasingly determined

by the spatial distribution of aridity, a distribution that may have been radically different in the geologic past (see Chapter V).

To sum up, the empirical and circumstantial evidence presented in this chapter suggest the following: 1. crocodilians are primarily limited by ambient minimum temperatures (CMM); 2. the duration of the cold season (consecutive months above a specified temperature and MART) is an important determinant of the viability of a population by affecting the survival of juveniles; 3. the presence of standing water provides an essential buffer against temperature extremes, such that aridity is an important limiting factor especially at the poleward limits of the crocodilian geographic range. The presence of fossil crocodilians therefore indicates not only paleotemperature, but also local paleohydrology.