

# Environments of Mid-Cretaceous Saharan dinosaurs

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## Abstract

Recent studies of the oceanic record suggest that the Earth was a global greenhouse during middle Cretaceous time. A review of topographic, sedimentary and biologic data pertaining to terrestrial mid-Cretaceous equatorial environments broadly supports the climatic inferences of marine studies. In particular, analyses of widely-occurring low latitude Saharan sediments support the Cretaceous greenhouse hypothesis. In comparison to marine ecosystems, terrestrial ecosystems respond more sensitively to atmospherically transported heat and nutrients because of the more tenuous presence of the hydrosphere on land. Indeed, the morphologies of terrestrial biota suggest that: (1) equatorial mid-Cretaceous climates were episodic rather than seasonal; (2) convective storms although infrequent were violent; and (3) a moist intertropical convergence zone was absent. Cretaceous atmospheric dynamics apparently differed importantly from those of the present. Circumstantial evidence suggests that (1) higher atmospheric carbon dioxide levels probably stimulated the emission of other greenhouse gases; and (2) higher humidity levels reduced diurnal temperature variations but impaired evaporative thermoregulatory mechanisms. That terrestrial ecosystems withstood greenhouse conditions in low latitudes as well as they did underscores the adaptability of terrestrial life. Analogies for future environmental stresses and responses, whether anthropogenic or resulting from other causes, might be found in the terrestrial record of the Cretaceous equatorial zone.

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## 1. Introduction

The marine record suggests that during middle Cretaceous time the biosphere recoiled before the effects of a global greenhouse. The purpose of this review, which was inspired by the syntheses of Georges Busson and his colleagues (Busson & Cornée, 1989; Busson et al., 1999), as well as by more recent studies, is to assess the implications of information pertaining to terrestrial environments in the Saharan region during the greenhouse interval. It has long been suspected that polar climates were warm during the Cretaceous, and that tropical and subtropical climates spread deeply into mid-latitudes. Although terrestrial Cretaceous sediments occur widely across the Sahara (Mateer et al., 1992), the

low-latitude environmental record they contain is often not easily accessible.

Accessibility is limited by a physical environment that is hostile in the extreme. The Sahara is larger than the continental United States (Fig. 1). It extends for thousands of kilometers over denuded plateaus and mountains, and across vast plains of gravel and sand. Rain typically falls in heavy torrents after years of drought. Temperatures in the shade have reached 58°C, and daily fluctuations of 30°C are common (cf. Lutgens & Tarbuck, 1998). Fossil palynomorphs are oxidized near the surface so that pollen samples must be taken from sediment cores (Schrank, 1991). Escarpments collapsed throughout the Sahara during an early Pleistocene wet interval (Busche, 2001), obscuring exposures of older strata. Veneers of wind-blown sand and coarse carbonate scree further obscure the foundered exposures. Yet the geographic extent of the Cretaceous Saharan record underscores its importance.

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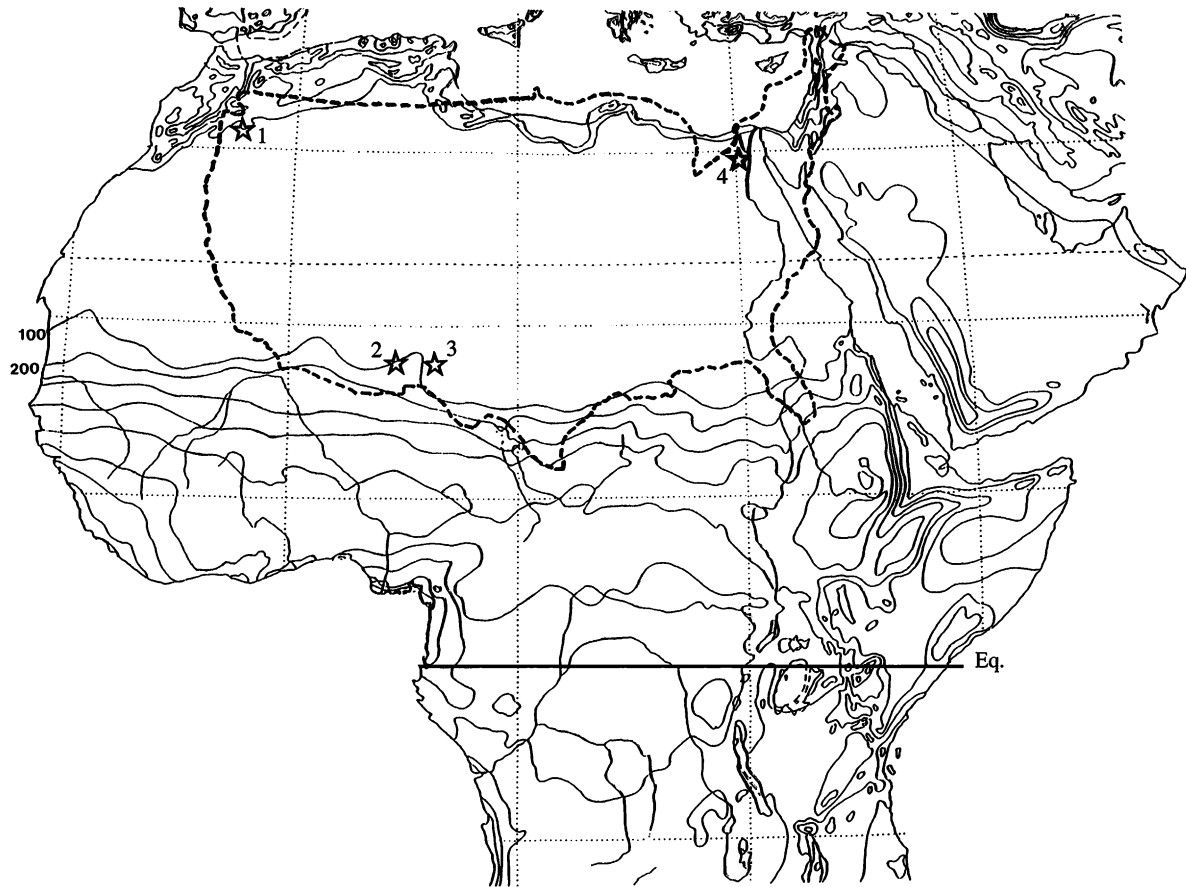


Fig. 1. North Africa and the Arabian peninsula, showing present annual rainfall (in mm). The dotted outline is that of the United States, drawn to the same scale. 'Eq' indicates the position of the equator. Stars mark the location of important dinosaur sites: 1, the Kem Kem, Morocco (cf. Russell, 1996); 2, the Falaise de Tiguidi, Niger (cf. Sereno et al., 1999); 3, Gadoufaoua, Niger (cf. Taquet, 1976), and the Bahariya Oasis, Egypt (cf. Lyon et al., 2001).

The present review begins with a discussion of the Earth's energy balance and considers how a global greenhouse can be understood in terms of this balance. It then provides evidence in support of a mid-Cretaceous greenhouse and continues with a consideration of processes presumed to have been relatively fundamental, such as those originating in the mantle. Following this, much of the review considers secondary phenomena, concluding with the more derivative responses of greenhouse dinosaurs. Some areas of knowledge are currently less well established than others. These are subjectively placed in groups, listed in reverse order of certitude in Table 1. The review concludes with comments on the relevance of conditions in equatorial lands during the mid-Cretaceous greenhouse to those anticipated for a global warming in the proximate future (Spicer et al., 1996). Advancement of knowledge of the former may also inform the latter.

## 2. Energy flow to and from the Earth's biosphere

Currently, energy flows into the Earth's biosphere from the sun, the moon, and the Earth's interior, as

depicted in Fig. 2 (Wallace & Hobbs, 1977; Berman & Evans, 1986; Chapman, 1986). All other celestial sources are too remote to provide significant contributions. The sun radiates several tens of trillions of TeraWatts (top scale), but only 173 000 TeraWatts are incident on the Earth (middle scale). Direct warming of the biosphere from geothermal sources, and lunar tidal coupling are many orders of magnitude less than solar warming (bottom scale). For comparison, the roughly ten TeraWatts of human energy consumption is indicated on the bottom scale.

Upward arrows (middle scale) denote both anisotropic (Earthlight) and isotropic (heat) radiation from the Earth to nearby space. The Earth loses heat through the latter channel because the planet is a relatively warm (300°k) body immersed in a relatively cool (3°k) cosmic sea. This loss is given by

$$P = a\sigma A(T_E - T_C)^4 \quad (1)$$

where  $P$  is the power radiated,  $a$  is the absorptivity of the Earth,  $A$  is the surface area of the Earth,  $T_E$  and  $T_C$  are the temperatures of the Earth (300°k) and the

Table 1

Environmental evidence and inferences pertaining to Aptian–Cenomanian terrestrial environments in the equatorial Saharan region. Evidence is grouped according to categories of decreasing observational support; relevant modern correlates are listed following the observational categories

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*Relatively firm evidence exists for:*

1. A general rise in sea level, accompanied by brief flooding events.
2. Intervals of widespread oceanic anoxia.
3. A trend toward increasing but variable atmospheric CO<sub>2</sub> levels.
4. A trend toward increasing but variable equatorial sea surface temperatures.
5. An enormous, low-level equatorial plain extending across the Saharan region.
6. High-energy sedimentation and poorly defined drainage, generated by convective storms.
7. Extensive droughts enduring on time scales of the life spans of terrestrial organisms.
8. High productivity in freshwater environments.
9. Angiosperm replacement of ferns and conifers, caused by irregular environmental conditions.
10. Semi-arid climates and episodic rainfall, precluding the presence of a humid, intertropical convergence zone.
11. The capacity of terrestrial ecosystems to adapt to equatorial greenhouse conditions.

*Evidence is suggestive of:*

1. Increasingly frequent storm- (hurricane-) disturbed strata in shallow marine environments.
2. A general replacement of humid by semi-arid biota at the beginning of the interval, and a decrease in the productivity of terrestrial plants.
3. An appearance of giant pterosaurs at the beginning of the interval, in response to stronger atmospheric convection.
4. A broad alternation of relatively humid and arid environments on thousand-year time scales.
5. An absence of catastrophic equatorial thermal excursions evidenced by a general continuity of equatorial biota and moderately high diversity of large herbivores (dinosaurs).

*More evidence is particularly needed in support of:*

1. A high incidence of fires.
2. A greater water vapor content of air over the vast, semi-arid lowlands.
3. Less diurnal temperature variation than in modern semi-arid equatorial environments.
4. The frequency and amplitude of CO<sub>2</sub> and sea surface temperature excursions.
5. The relative importance of terrestrial greenhouse gas emission.
6. Terrestrial environmental correlates of oceanic anoxia.
7. The sequence and relative importance of greenhouse gases released during a deepening greenhouse.
8. Identifying the adaptations of mid-Cretaceous equatorial terrestrial ecosystems to water and heat stresses.

*Modern correlates of relevance to mid-Cretaceous climates include:*

1. High and variable marine mean annual temperatures produce a similar thermal regime in terrestrial environments at the same latitude.
  2. Anoxia in oceanic waters facilitates the accumulation of nitrous oxides and oxygen in the atmosphere.
  3. Warmer temperatures at the base of the atmosphere are correlated with a higher tropopause.
  4. A higher tropopause is associated with an increased lightning flux, and increased levels of nitrous oxide and ozone production.
  5. Highly productive equatorial wetlands release large quantities of methane.
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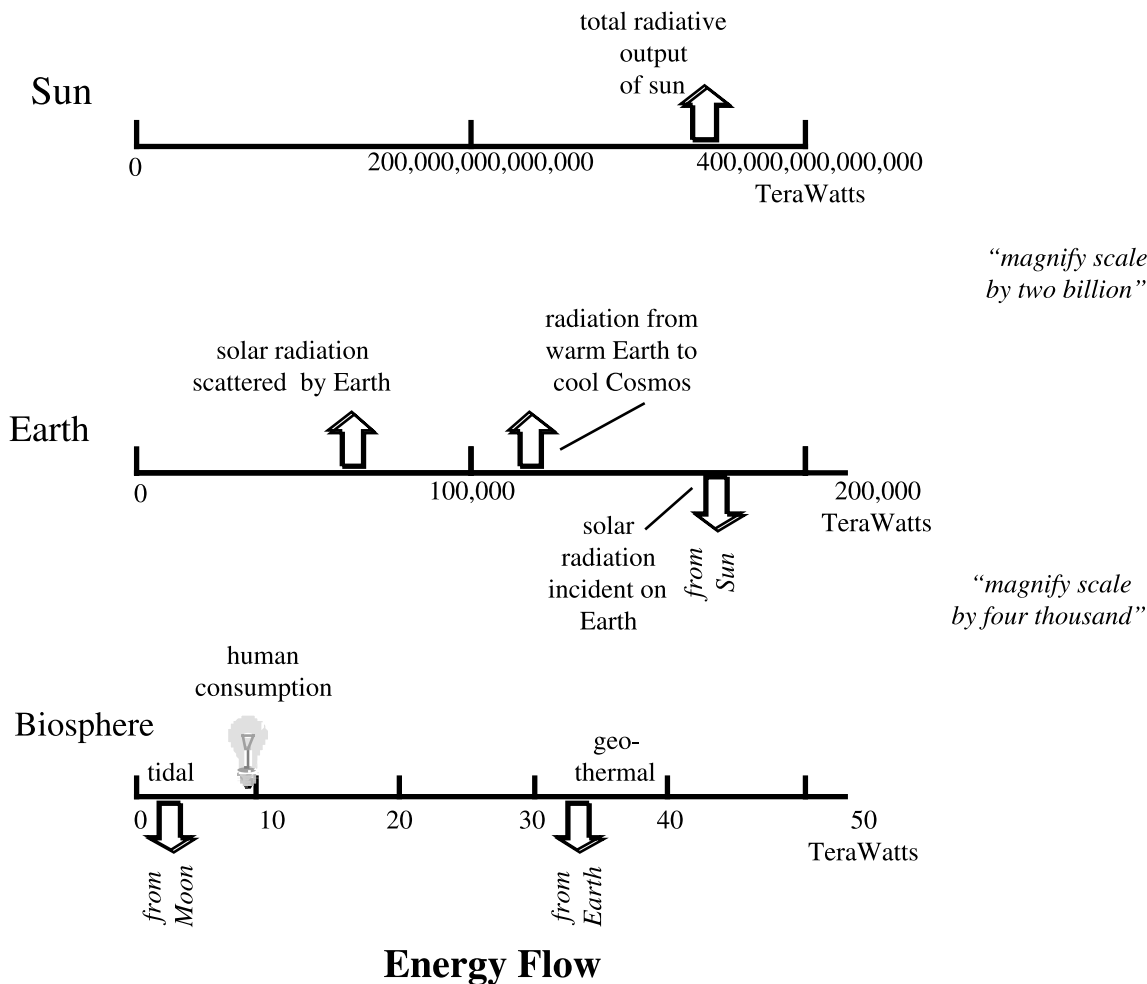


Fig. 2. Three scales of energy flow. All three axes are calibrated in TeraWatts, but each is at a vastly finer scale than the one above it. Approximately 173 000 TeraWatts of solar radiation reach the earth. A nearly equivalent power is radiated from the Earth to the relatively cool cosmos.

cosmos ( $3^{\circ}\text{k}$ ), and  $\sigma$  is the Stefan–Boltzman constant ( $5.7 \times 10^{-8} \text{ W/m}^2\text{k}^4$ ). An ideal radiator, or *black body*, has absorptivity,  $a=1$ . For the Earth,  $a$  is somewhat less than one. For the purposes of this analysis (middle scale), the Earth’s heat loss is roughly comparable to the radiative solar input, i.e. between 100,000 and 200,000 TeraWatts. Thus, the surface of the Earth is in a state of thermal equilibrium.

A survey of the literature allows one to consider how the Cretaceous equilibrium may have differed. Solar luminosity has slowly increased at rates suggesting that during mid-Cretaceous time it was about 0.9% less brilliant than at present (Sackman et al., 1993). Solar fluctuations of 0.2–0.6% may drive postglacial temperature changes on hundred- to thousand-year time scales, but the Sun appears to be unusually stable among Sun-like stars (Lockwood et al., 1997; Perry & Hsü, 2000; Bond et al., 2001). Similarly, oscillations in the pattern of the Earth’s rotation around the Sun produced no known long-lasting

climatic alterations on a scale of millions of years (cf. Zachos et al., 2001a,b; Olsen & Kent, 1999; Kuhnt et al., 2001). Since Cretaceous time, the rotation of the Earth has slowed by about a half-hour per day through gravitational interactions with the Moon (Rosenberg, 1997). The rate of rotational slowing has been modulated by tidal friction against gradually changing continental configurations (Steinberger & O’Connell, 1997; Kvale et al., 1999; Lourens et al., 2001), but the climatic effects of the slowing were probably inconsequential.

In terms of altering the Earth’s energy balance, one may conclude that any conceivable differences in the energy input to the biosphere are dwarfed by the real possibility that the atmosphere’s heat-retaining capabilities have changed through geologic time. Thus, even small differences in the Earth’s absorptivity,  $a$  in Eq (1), have the potential of significantly affecting the planet’s energy balance and thus  $T_E$ , the temperature of the Earth’s surface.

### 3. The mid-Cretaceous greenhouse

Among the more compelling paleobiologic pieces of evidence for a mid-Cretaceous global greenhouse are indications of temperate forests inside the Arctic and Antarctic circles (e.g. Herman & Spicer, 1996; Falcon-Lang et al., 2001), and isotopic signatures of unusually high sea surface temperatures preserved by planktonic foraminifera inhabiting the equatorial zone (cf. Boucot & Gray, 2001). How did such an enormous change in the distribution of planetary surface heat come about? The current consensus (e.g. Larson & Olson, 1991; Erbacher et al., 1996; Sahagian et al., 1996; Gröcke, 1997; Beerling et al., 1999; Gatzmaler et al., 1999; Gale, 2000; Kent & Olsen, 2000; Wallmann, 2001; Wilson & Norris, 2001; Wignall, 2001; Machel & Humler, 2003) holds that the greenhouse coincided with changes in mantle circulation, as manifested by: (1) a long period of unchanging geomagnetic polarity; (2) emplacement of enormous oceanic plateau basalts; (3) release of large volumes of mantle carbon dioxide; (4) rifting apart of the southern continents; (5) carbon-rich oceanic black shale deposition; and (6) elevation of sea level.

The onset of the greenhouse interval began near the Barremian-Aptian boundary at 121 myr (million years), and ended near the Santonian-Campanian boundary at 83.5 myr (Channell et al., 1995; Gradstein et al., 1995), thus enduring nearly 40 myr. A mantle event that altered the heat-retaining properties of the atmosphere, and thereby the Earth's absorptivity,  $a$  in Eq. (1), is accepted here as the most probable cause of the mid-Cretaceous greenhouse.

### 4. Oceanic influences

In dramatic views of Solar System objects from space the Earth is revealed as a uniquely blue planet, emphasizing the dominant presence of oceans. Appropriately, this review begins with a consideration of oceanic conditions during the interval when the record of terrestrial life in the Sahara is most complete, from Aptian to early Cenomanian time (121 to 97.5 myr, Channell et al., 1995; Prokoph et al., 2001).

The period began with an early transgressive oceanic pulse, probably due to increased magmatic underplating of the crust and a concomitant rise in sea level (cf. MacLennan & Lovell, 2002). A marine nannofossil turnover simultaneously occurred, evidently in response to increased metal and nutrient concentrations in ocean water. These events stratigraphically marked the onset of the greenhouse (Bersezio et al., 2002). The period under consideration (but not the mid-Cretaceous greenhouse) ended during the mid-Cenomanian with a great global expansion of marine waters over continental

lowlands. Simultaneous changes in the marine biotic record at the Cenomanian-Turonian boundary have been ascribed to: (1) the shifting of marine assemblages in the direction of transgressing shorelines (Gale et al., 2000; A. B. Smith et al., 2001); (2) loss of wetland habitat through sea level rise (Eaton et al., 1997); (3) overheating of equatorial surface waters (Wilson et al., 1998; Jenkyns & Wilson, 1999); (4) warming and deoxygenation of bottom waters (Kaiho, 1998); and (5) a possible bolide impact event in the North Atlantic basin (Monteiro et al., 2000). It would seem that there were no major oceanic extinction events during the early, transgressive phase of the global greenhouse.

Sea levels fluctuated at slightly less than 200 m above the present sea level during most of Jurassic–Cretaceous time. They rose above 200 m with the beginning of the Albian and peaked at 270 m near the Cenomanian-Turonian boundary (Sahagian et al., 1996). During the latter transgression, vast areas of lowland habitat in the Saharan region were submerged. Sea level fluctuations on the order of tens of meters before and after the greenhouse interval have been attributed to high latitude glaciations (Stoll & Schrag, 1996; Miller et al., 1999, but see Huber et al., 2002; MacLennan & Lovell, 2002), although there is little evidence of polar ice during middle Cretaceous time (Price, 1999; Veizer et al., 2000, but see Stoll & Schrag, 2000).

For decades it was assumed that surface temperatures of tropical oceans remained approximately constant, and that the primary effects of fluctuations in the global heat budget were expressed by thermal excursions in high latitudes. Recent reports suggest, however, that tropical sea surface temperatures were 3–4°C cooler during glacial intervals (Kerr, 2001), and that they warmed into the present interglacial. At present, deep and surface waters of tropical oceans are respectively ca. 4 and ca. 26–28°C.

Near the middle of the transgressive phase of the greenhouse interval (Albian–Cenomanian), subtropical sea surface temperatures reached ca. 30–31°C, and were higher than anywhere today, except in restricted water bodies such as the Red Sea and the Persian Gulf. They nevertheless varied as much as 6°C on time scales of ten thousand years, demonstrating that mean annual surface temperatures in low latitudes were not constant at that time (Norris & Wilson, 1998; Wilson & Norris, 2001). Isotopic data presented by Veizer et al. (2000) are also suggestive of short-term temperature fluctuations in low-latitude oceans. Deep and surface oceanic waters reached maxima of respectively ca. 20 and ca. 33–34°C during latest Cenomanian time (Clarke & Jenkyns, 1999; Huber et al., 2002; Norris et al., 2002). Coral atolls apparently died in the superheated waters of the central Pacific (Wilson et al., 1998; Jenkyns & Wilson, 1999). On land, warm forests grew at what was then 42°N latitude (Upchurch & Wolfe, 1993), suggesting that



climates as warm or warmer than the modern tropics prevailed over two-thirds of the surface of the Earth.

Over the past decade, General Circulation Models of increasing complexity and sophistication have been designed to imitate the dynamics of the mid-Cretaceous greenhouse (e.g. Barron et al., 1995; Johnson et al., 1996; Poulsen et al., 1999; Bice & Marotzke, 2001; Haupt & Seidov, 2001; Emanuel, 2002). The primary forcing factor is usually considered to have been an increase in the concentration of atmospheric carbon dioxide. The major problem to be resolved has been the exportation of sufficient heat from low latitudes to maintain polar warmth. Thus far, even very comprehensive models have yielded anomalously low winter temperatures in continental interiors inhabited by large herbivorous dinosaurs (cf. DeConto et al., 1999). The insights model studies have produced are nevertheless many and interesting (Price et al., 1998; Upchurch et al., 1999; Bice et al., 2000; Emanuel, 2002). For example, during a greenhouse interval they suggest that: (1) temperature increases were less over lands than over oceans; (2) vegetation promoted regional heating through albedo reduction; (3) mean annual temperatures in the Saharan region during the Cretaceous may have exceeded 32 °C; (4) evaporation increased (together with the greenhouse effect of water vapor); (5) hurricanes and convective storms became more frequent, but cloud cover did not increase; and (6) hurricanes mixed heat into the upper levels of the ocean, thereby promoting oceanic heat transport and the transfer of dissolved carbon dioxide to the atmosphere.

Warm, mid-Cretaceous greenhouse oceans were prone to repeated episodes of carbon-rich, black shale deposition termed ‘oceanic anoxic events’. (For a sequence and classification of carbonaceous shales, see Erbacher et al., 1996.) In one rather typical episode in late Albian time, surface and subsurface waters were mixed and the thermal gradient in the water was obscured as organic carbon accumulated on the ocean floor. This and similar episodes of black shale deposition were, therefore, not due to water stagnation, but to increased plant productivity (Wilson & Norris, 2001). Carbon derived from terrestrial plants is often abundantly represented in the black shales (Bersezio et al., 2002; Kennedy et al., 2002). The Cenomanian–Turonian marine black shale horizon contains large quantities of iron sulfide, evidently derived from marine phytoplankton productivity (Kuypers et al., 1999; Ohkouchi et al., 1999; the distribution of black shale deposition across North Africa during this interval is reviewed by Lüning et al., 2003). The removal of two oxygen sinks (reduced carbon and iron) is postulated to have greatly increased the flux of oxygen to the atmosphere (Ohkouchi et al., 1999). During Carboniferous time, the burial of enormous amounts of reduced organic carbon may have increased atmospheric oxygen concentrations to 35%

(Berner, 1999), simultaneously increasing air pressure (Gans et al., 1999) and therefore temperatures at the base of atmosphere. (For the tropospheric thermal gradient and extreme temperatures at or below sea level, see Lutgens & Tarbuck, 1998, fig. 1–14, p. 50.)

During periods of black shale deposition, deeper oceanic waters must have been suboxic to anoxic. Nitrogen is fixed in suboxic marine waters, and is currently being released to the atmosphere in climatically significant quantities as nitrous oxide, a potent greenhouse gas (Codispoti et al., 2001; for a Jurassic precedent of the denitrification of a black shale, see Jenkyns et al., 2001). Anoxia was much more prevalent in the world’s oceans during middle Cretaceous time, and its incidence varied in an episodic manner. Available data from land plant tissues, preserved in both marine (Kuypers et al., 1999) and terrestrial strata (Retallack, 2001, 2002), suggest that atmospheric carbon dioxide levels were also high and varied episodically.

In mid-Cretaceous time, the equator extended across the Saharan region from the present Liberian coast in the ‘southwest’ to the present southern tip of the Sinai Peninsula in Egypt in the ‘northeast’ (Fig. 3; cf. Wilson & Norris, 2001; Huber et al., 2002). As noted above, northern Africa was bounded on three sides by equatorial seas with surface temperatures in the general range of 30–34 °C, and exhibiting 6 °C mean annual temperature excursions on time scales of ten thousand years. That hurricanes were much more common than at present may be inferred from a correlation between their frequency and sea surface temperature (Emanuel, 2002). Shallow, epicontinental seas flooded Saharan borderlands and occasionally reached the interior. The oceans enriched the atmosphere in greenhouse gases such as carbon dioxide, water vapor (cf. Jahren & Silveira Lobo Sternberg, 2003) and nitrous oxide, the concentrations of which varied episodically, as well as facilitating an increase in the mass of atmospheric oxygen. As will be seen below, there is also evidence suggesting that the greenhouse gas composition of the atmosphere may have been affected by interactions with the terrestrial biosphere. With the exception of the North Atlantic region, mean annual isotherms at the base of the atmosphere now parallel latitude rather closely across oceans and continental lowlands (cf. Lutgens & Tarbuck, 1998, figs 3–14, 3–15). They probably did so during mid-Cretaceous time as well.

## 5. Terrestrial topography

When Africa and South America separated early in Cretaceous time, a major fault system propagated across Africa to the east, parallel to but about 2000 km south of the mid-Cretaceous equator. Extensional faulting occurred along the borders of the system, and in central

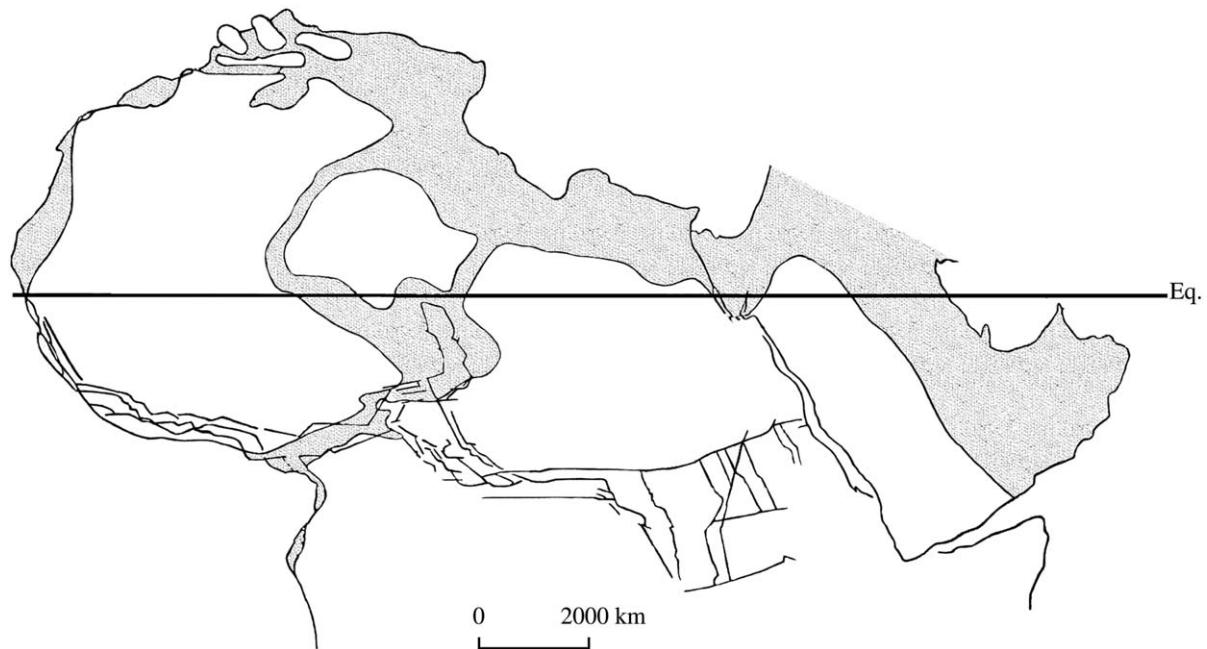


Fig. 3. Mid-Cretaceous (late Cenomanian) topography of North Africa-Arabia. The heavy line indicates the position of the paleo-equator (cf. Wilson & Norris, 2001; Huber et al., 2002). The late Cenomanian shoreline is after Andreu (1993, fig. 10; inundated regions are shown in grey). The linear features south of the paleo-equator follow rift escarpments active earlier in Cretaceous time (after Maurin & Guiraud 1993, fig. 2).

Africa, Morocco and Libya (Genik, 1992; Guiraud & Maurin, 1992; Maurin & Guiraud, 1993; Wennekers et al., 1996; Feist et al., 1999; Guiraud & Bosworth, 1999). As in East Africa today, these intracontinental rifts were bordered by highlands and often contained lakes (cf. Bussert, 1993b). Most of the rift topography in the Saharan region was then buried beneath a thick sheet of clastics (200–1000 m) derived from highlands along the major transcontinental fault system to the south. The detrital series was followed by an Aptian transgression into the central Sahara, approximately contemporaneous with an oceanic black shale depositional event. Another, thinner detrital series of Albian–Cenomanian age followed (Busson & Cornée, 1989; Beauchamp et al., 1990; Lefrance & Guiraud, 1990; Bussert, 1993b). There were as yet no mountains in the central Sahara, nor had the Red Sea rift formed (Sahagian, 1988; McClay, 2000). The Saharan region was a flat, low-lying equatorial plain extending 16,000 km from east to west, and bordered to the north by an equally uniform, shallow sea (Andreu, 1993). Between the land and the sea in the west were enormous evaporitic lagoons (Busson & Cornée, 1989) and in the east clastics accumulated from continental sources (J. B. Smith et al., 2001), both of middle Cenomanian age.

Busson & Cornée (1989) discuss patterns of mid-Cretaceous sedimentation in the continental interior of the Sahara by appealing to descriptions of modern detrital sedimentation in the Darfour Plateau of western Sudan. Torrential rains and local tornadoes characterize

the short wet season in the Darfour. The storms heavily erode even minor relief and transport sedimentary particles for distances of a few tens of meters to several kilometers in indistinct channels across flat terrain. Currents abruptly fail after the passing of storms, leaving behind a deposit that is highly variable in thickness and distribution, and includes normal fluvial sediments, aeolian sand, deltaic structures, mud-drapes, poorly sorted gravels and clay balls. The example of the Darfour illustrates a sedimentary mechanism by which even coarse materials can be moved over immense distances and almost imperceptible slopes. Within mid-Cretaceous sequences are indications of aridity, including dunes and ventifacts, and aeolian dust in offshore marine strata. The distribution of remains of aquatic organisms provides evidence of great expanses of wetlands. Alternating dry and wet intervals on multi-year, or thousand-year time scales over sub-continental areas distributed alternating arid and wet facies over areas many times larger than the largest modern deltas. The sediments were transported across a gigantic, low-lying tropical plain the dimensions of which are approached nowhere on Earth today.

With the onset of oceanic black shale deposition and a global rise in sea level in late Cenomanian time (Prokoph et al., 2001; Gale et al., 2002), a film sea (*mer pelliculaire*) spread south over the evaporitic lagoons and more coastal margins of the plain. It passed deep into the Saharan region to merge with the South Atlantic near the present Niger delta. Marine carbonates

rest directly upon Paleozoic strata without intervening deltaic deposits in Morocco and Algeria, suggesting local aridity (Ferrandini et al., 1985; Busson & Cornée, 1989; Busson et al., 1999). Deeper into the continent, in the Iullemeden Basin of Niger, clays washed into the seaway from surrounding lands indicate a more humid climate (Meister et al., 1992; Pascal et al., 1993). Based on sedimentary lamina reflecting periodicities in the Earth's orbit, the flooding event lasted ca. 320 thousand years (Prokoph et al., 2001; intervals of black shale deposition varied according to local conditions; Lüning et al., 2003). The rapidity with which the shallow (50–100 m deep) sea crossed the Sahara is evidence of the flatness of the terrain it inundated.

## 6. Terrestrial climates

In shallow marine environments, the wavelength of large-scale cross stratification reflects the intensity of passing storms. Average wavelength rapidly increased to a maximum during the transgressive phase of the mid-Cretaceous greenhouse (Ito et al., 2001), suggesting a simultaneous global increase in the frequency of land-falling hurricanes. The storms would likely have landed along the eastern coast of the African-Arabian continent (cf. Lutgens & Tarbuck, 1998, fig. 11-3). The probability of great floods also increases with greenhouse gas concentrations in the atmosphere (Milly et al., 2002).

Mean annual temperatures similar to surface temperatures of adjacent oceans could be expected to prevail over continental regions, although terrestrial diurnal fluctuations would be greater than those over oceans. The fluctuations might have been dampened somewhat by a more rapid rate of planetary rotation and a greater water vapor content of the atmosphere during the mid-Cretaceous greenhouse (cf. Jahren & Silveira Lobo Sternberg, 2003). In semi-arid to arid terrestrial environments, frontal systems produce a relatively continuous, gentle rain, and the resulting sedimentary flux is predominantly fine-grained and well stratified. In the case of more violent convective storms, sediments are sandy and coarse-grained (Maley, 2000). The volume of coarse-grained sediment transported by ephemeral rivers is several hundred times greater than in perennial rivers of humid regions (Larrone & Reid, 1993), and the frequency of severe floods is also greater in arid lands (Molnar, 2001). Semi-arid climates would have increased the erosional efficaciousness of mid-Cretaceous convective storms.

In the mid-Cretaceous Sahara, the equator extended across a low, flat plain where sedimentary processes reflected heavy but sporadic rainfall, and alternating arid to semi-arid and pluvial intervals. Thus, the sedi-

mentary record indicates the absence of high, annually sustained rainfall that is typical of the modern inter-tropical convergence zone. The equatorial humid belt was apparently half of its present width during Late Triassic time (Kent & Olsen, 2000) and one-third of its present width during the latest Cretaceous (cf. Upchurch et al., 1999, fig. 1). These circumstances, further abetted by weak polar fronts (Ziegler et al., 1987; Farrell, 1990; Spicer et al., 1996), suggest that the equatorial humid belt was replaced by a broad zone of convective circulation during the mid-Cretaceous greenhouse. It is perhaps noteworthy that giant pterosaurs (with wingspans of 5–12 m) appear in the geologic record near the Barremian-Aptian boundary (cf. Martill et al., 1996), with the presumed onset of strong, greenhouse atmospheric convection.

The tropopause is more elevated in the tropics than at higher latitudes. Convective clouds in the tropics can accordingly attain greater elevations before their ascent is restrained by stable air at the base of the tropopause. Heating at ground level largely controls the elevation of the tropopause (Farrell, 1990; Thurnburn & Craig, 1997), so that during the mid-Cretaceous greenhouse convective clouds must have soared to higher elevations than at present. Lightning is also concentrated over the continents in the equatorial zone, and its frequency is very sensitive to cloud height (Price & Penner, 1997). Lightning produces nitrous oxide and ozone (Pickering et al., 1998; Hauglustaine et al., 2001; Tie et al., 2001), both of which are efficient greenhouse gases. Large mid-Cretaceous fluxes of lightning would thus have increased the greenhouse effect, and in the case of nitrous oxides also been a source of fixed nitrogen. Plants assimilate nitrous oxides directly from the atmosphere through the leaves (Siegwolf et al., 2001). Local tradition in rural areas of the southeastern United States asserts that summer storms with numerous lightning discharges improve garden growth.

Evidence derived from the current behavior of the atmosphere suggests that convective storms were more violent during mid-Cretaceous time. A modern convective storm in the Sahara, at a flat interface between land and sky, has been described by Cloudsley-Thompson (1984, p. 3): “. . . we were struck by a devastating thunder-storm one evening in northern Chad . . . We barely had time to secure our possessions in the sudden gale before there was a torrential down-pour. Within a few minutes, the entire landscape, brilliantly illuminated by the continual lightning, was inundated. Looking out from our vehicle, we seemed to be floating in a vast sea, the ripples from the wind giving the appearance of rapid currents. When the rain stopped abruptly after six hours, we literally had to shout to be heard above the fantastic chorus of croaking toads and stridulating insects. By sunrise all was quiet, and less than 20 km further on the ground was bone dry.”



## 7. Vegetation

Atmospheric carbon dioxide concentrations greatly affect global plant productivity and global temperatures. It is suspected that CO<sub>2</sub> concentrations during Mesozoic times: (1) were higher than at present; (2) were controlled by processes very sensitive to changes in fluxes from dynamic and massive carbon reservoirs; and (3) fluctuated on geologically short time scales. Considerable research on the history of atmospheric carbon dioxide concentrations is currently underway (e.g. Royer et al., 2001; Beerling & Royer, 2002; Retallack, 2002).

Atmospheric effects on global vegetation models provide interesting insights. Assuming three times present levels of atmospheric carbon dioxide and an atmospheric oxygen content of 26%, the primary productivity of green plants approximately doubles (Beerling et al., 1999). Since much of the world's petroleum derives from low-latitude source strata of Cretaceous age, the productivity of low-latitude marine Cretaceous plants may have been high (Beydoun, 1998; Lüning et al., 2003). However, contemporaneous terrestrial productivity in equatorial regions may have been exceeded by that in mid-latitudes (Ziegler et al., 1987). Elevated carbon dioxide levels promote gigantism in coniferous trees, with height increasing more rapidly in mid-latitudes and girth in low latitudes. If conifers can escape fire and hurricanes, they can also escape competition from angiosperms (Osborne & Beerling, 2002). Fossil charcoal occurrences increased from Late Jurassic through Early Cretaceous time (Scott, 2000), as did the incidence of low-latitude hurricanes (Ito et al., 2001) and probably also convective storms on land (Busson & Cornée, 1989). Angiosperms originated and initially proliferated in low latitudes during the Aptian–Cenomanian interval in a region that was dominated to an extreme degree by unstable, quasi-fluvial environments (Busson & Cornée, 1989), and were presumably propelled to higher latitudes along seasonally-disturbed river margins (Wing & Boucher, 1998) by the waxing phase of a global greenhouse.

Plant fossils show evidence of a climatic change that occurred throughout the Saharan region near the beginning of the mid-Cretaceous greenhouse. An abundance of ferns and significant presence of cycad-like plants and primitive conifers, suggesting mesic climates, characterize Neocomian palynofloras in Saharan Algeria and Tunisia. An abrupt floral change coincided with a Barremian influx of xeric conifers and ephedrales, which continued as dominants through Cenomanian time (Reyre, 1973; Tekbali, 1994). Leaf assemblages from southern Tunisia indicate a change within Aptian time from a fern-dominated flora to one containing different ferns and gymnosperms, and angiosperms (Barale et al., 1997; Barale & Ouaja, 2001). In palynofloras from

central Egypt, as well as in many areas of Africa, ferns and mesic conifers were replaced as dominants in Barremian–Aptian time by xeric conifers, ephedroids and angiosperms. The floral change suggests an expansion of warmer and semiarid climates, and steppe-like landscapes (Hendriks & Schrank, 1990; Schrank, 1991; Schrank & Nesterova, 1993; Schrank & Mahmoud, 2002). Angiosperm leaves from the Cenomanian of Lebanon, southern Egypt and Sudan indicate a warm and semi-arid climate (Wolfe & Upchurch, 1987; Dilcher & Basson, 1990; Krassilov & Bacchia, 2000; Lyon et al., 2001). Exceptions to a general change from mesic to semi-arid floras during Barremian–Aptian time were due to more local, tectonic factors. For example, hyperarid Aptian climates within the Atlantic rift became more mesic with the entry and expansion of marine waters during Albian–Cenomanian time (Salard-Cheboldaëff & Dejax, 1991; Rossetti et al., 2001). And mesic, montane vegetation on Albian rift shoulders in Sudan was gradually replaced by plants of semi-arid facies with the erosion and lowering of the highlands into late Cenomanian time (Awad & Schrank, 1993; Bussert, 1993a,b).

Wolfe & Upchurch (1987) and Ziegler et al. (1987) emphasized that unstable terrain, aseasonal rainfall and significant water stress precluded the existence of closed-canopy, equatorial forests. Schrank & Nesterova (1993) further noted that extreme aridity would not support any significant vegetation, and preferred to use terms such as steppe and semi-desert to describe mid-Cretaceous low-latitude plantscapes. Paleobotanic evidence is consistent neither with rainforests such as those of the modern intertropical convergence zone nor with the extreme desert that now exists in much of the Saharan region. It points instead to the widespread development of a low-latitude, aseasonal, semi-arid climatic regime that has since vanished. Because the mid-Cretaceous greenhouse was marked by the expansion of angiosperms in the Saharan region (Schrank & Nesterova, 1993), perhaps angiosperm ecology in semi-arid regions today offers some insights into plantscapes in mid-Cretaceous equatorial regions. In terms of time available for adaptation, it should be recalled that arid conditions in the Sahara have persisted intermittently for at most 6 myr (Busche, 2001), whereas the mid-Cretaceous greenhouse endured for approximately 40 myr.

The wood of mid-Cretaceous angiosperms is often pithy and suited for water- and nutrient storage rather than supporting great heights (Wolfe & Upchurch, 1987). A modern, if somewhat extreme, analogue might be the stout and flat-crowned baobab, belonging to a plant family recorded in Late Cretaceous strata (Wheeler & Lehman, 2000; Elisabeth Wheeler, pers. comm. 2001). This tree is long-lived, resistant to drought and fire, and common in tropical savannahs. It attains a

maximum girth of 20 m and swells after heavy rains. The edible foliage is shed during times of water scarcity, and the seeds germinate after passing through the guts of large herbivores (Von Maydell, 1990). In general, leaves in warm, arid environments are grey, grey-green or even white in order to reflect heat. A leaf up to 1 cm in breadth can remain below the lethal temperature of 46°C on a calm day with its stomata closed; a larger leaf must invest water in evapotranspiration through open stomata for cooling. The annual habit is very successful in warm, arid climates, and the abundance of annuals increases with dryness until aridity becomes extreme. Longevity promotes competitiveness in polar and wet-tropical environments, but perennials must be widely spaced to survive in arid conditions (Dimmit, 2000a,b). Pollinating bees are most abundant and diverse in deserts and savannahs, and the region of Tucson, Arizona, may support more varieties of bees than anywhere else on the globe (Buchman, 2000). Rainfall in the Sonoran region is often episodic on multi-year time scales (Dimmit, 2000b): “. . . most of the time it’s just brown gravel and brown bushes. Then one spring travelers were astonished to discover the ground between the bushes literally carpeted with flowers. It happened in March 1998 when for three weeks the freeway bisected a nearly unbroken blanket of desert sunflowers forty miles long and ten miles wide . . . In the decades between 1940 and 1998 there have been only four documented drop-everything-and-go-see-it displays [of annuals] in Arizona.”

The same phenomenon is repeated in the modern Sahara (Gautier, 1935, p. 21): “Should a heavy rain fall, the (dormant) seed . . . utilizes it with an admirable speed and energy. In an astonishingly short number of days it germinates, pushes up its stem, spreads out its flowers, and forms new seeds . . . Then, after a brief existence, the ashab dies; but the new seed, carried by the wind . . . will wait, ten years if need be, for the next storm. During their short span of life however, these plants, whose every effort is expended for the purposes of reproduction, have been veritable bouquets of flowers; and these clumps of flowers are the pasturage. The camels are very partial to them, and it is a ludicrous sight to see the delicate blossoms swallowed up by their filthy jaws.”

## 8. Fauna

As can readily be imagined, the reworking of surficial sediments by torrential storms is highly destructive to animal skeletons. In other areas of the world, beautifully preserved fossils are recovered from laminated lake deposits and fluvial sands left behind within rapidly and continuously aggrading fluvial plains; in the mid-Cretaceous of the Sahara usually only the more robust

fragments were scattered, and preserved in isolation. Insect body fossils from Cretaceous strata in other regions suggest that a diversification of social insects, such as termites, ants and bees, as well as pollinating flies and lepidopterans, accompanied the radiation of the angiosperms. Most of these groups have modern distributions that are concentrated in areas of arid or Mediterranean climates that resemble ‘refugia’ or fragments of the semi-arid Cretaceous equatorial zone (Grimaldi, 1999, 2000).

Insect galleries identified as pertaining to termites occur in the Upper Jurassic of North America (Hasiotis, 1996), and impressions of flying termites are preserved in lagoonal strata of Aptian–Albian age in Brazil (Martill, 1993). In Africa today, termites create mounds up to 9 m in height, and dominate tropical and subtropical soils to an extent comparable to the domination of temperate soils by earthworms (White, 1983). In subtropical deserts in North America the biomass of termites can approximate 30 kg per hectare, exceeding that of cattle by an order of magnitude; they are important sources of methane and fixed nitrogen (Jones & Nutting, 1989; MacKay et al., 1989). According to Wuebbles & Hayhoe (2002), methane is released by termites and vertebrate herbivores consuming poor quality browse (cf. dinosaurs), and particularly from warm, low-latitude wetlands. Methane is oxidized by the hydroxyl radical (cf. high nitrous oxide and ozone concentrations in the troposphere during the mid-Cretaceous). These authors note that the combined effects of other greenhouse gases, including methane, equals that of carbon dioxide, amplifying the total greenhouse effect. The consequences of the expansion of subtropical climates over much of the Earth during the mid-Cretaceous for the production of greenhouse gases other than carbon dioxide remain to be evaluated.

Within the Saharan region, freshwater pelecypods and gastropods inhabited temporary lakes and streams under semi-arid conditions, and were adapted to resist droughts (Busson & Cornée, 1989). Lungfish teeth are particularly abundant (Tabaste, 1963) and freshwater vertebrate occurrences are widespread (e.g. Tabaste, 1963; Taquet, 1976; Buffetaut & Rage, 1993; Russell, 1996; Sereno et al., 1996; Lapparent de Broin, 2000a; Cavin et al., 2001), providing evidence of extensive, temporary wetlands (Busson & Cornée, 1989). Rapidly evolving, semi-aquatic to aquatic turtles and crocodiles were closely related to forms from South America. Differences appear to be due to the isolating effects of Atlantic Rift topography and the subsequent marine flooding of the zone rather than environment (Lapparent de Broin, 2000a,b). The dimensions of some of the fish (up to 3.5 m in length, cf. Wenz, 1980) and crocodiles (up to 11.5 m in length, *Sarcosuchus*, Taquet, 1976; Sereno et al., 2001; *Stomatosuchus*, J. B. Smith et al., 2001; *Elosuchus*, Lapparent de Broin,

2002) suggest highly productive aquatic environments. Piscivorous dinosaurs were also abundant (Taquet, 1984; Sereno et al., 1998; Taquet & Russell, 1998).

Small terrestrial vertebrates were certainly present, as indicated by remains of frogs, lizards and an unusual variety of snakes (cf. Sereno et al., 1996; Rage & Werner, 1999; Rauhut, 1999), and small terrestrial crocodiles (cf. Buffetaut, 1976; Buffetaut & Taquet, 1979; Buffetaut, 1994; Gomani, 1997). Isolated teeth and skeletal parts of juvenile or small adult theropod dinosaurs are present but not common (Taquet, 1976; Russell, 1996; Sereno et al., 1996; Rauhut, 1999). Rare but diverse teeth of tiny mammals have been recovered from a Neocomian locality in Morocco (Sigogneau-Russell, 1995), and a recent molecular phylogeny (Murphy et al., 2001) links the time of origin of afrotheres to that of the mid-Cretaceous separation of Africa from South America. Mammals must have inhabited the Saharan region during mid- and late Cretaceous time, although their diversification is not yet documented by fossils. Small terrestrial vertebrates were thus present, but their environmental significance is unknown.

Across the Sahara, Cretaceous dinosaurs preferentially occur in three horizons (Taquet, 1980). Remains of pre-Aptian (pre-greenhouse) dinosaurs occur in Niger, where the most abundantly preserved terrestrial vertebrate is the large (length ca. 21 m) sauropod *Jobaria*, and the most completely known theropod is *Afrovenator* (length ca. 8 m). At least two additional theropods of smaller dimensions and uncertain affinities were also present. The two larger dinosaurs are morphologically primitive (Sereno et al., 1994, 1999). Thus, in the Saharan region, both Neocomian plants and dinosaurs seem to have been of a 'Jurassic' aspect.

Most greenhouse dinosaur occurrences are in Aptian or Cenomanian strata (Taquet, 1980; Sereno et al., 1996, 1999), separated from each other by ca. 20 myr in age. Faunal similarities between the two horizons include the common occurrence of spinosaurs, rebbachisaurids, and titanosaurs. The Cenomanian localities have produced few indications of the presence of ornithomimids, but have yielded remains of carcharodontosaurs, dicraeosaurs and giant titanosaurs, which have not been identified in the older horizon. To what extent these differences are the result of faunal or environmental evolution, local environmental conditions or incomplete sampling is unknown. The dinosaurs from both horizons are here considered as a group.

The remains of greenhouse dinosaurs are remarkably incomplete. In only four mid-Cretaceous forms (all from the Aptian of Niger) is the skeleton sufficiently well known to reveal the body form: *Cristatusaurus* (Sereno et al., 1998; Taquet & Russell, 1998), *Lurdusaurus* (Taquet & Russell, 1999), *Ouranosaurus* (Taquet, 1976) and *Nigersaurus* (Sereno et al., 1999). The shapes of Saharan abelisaurids, dicraeosaurs and rebbachisaurids

may have approximated those of their closely related Argentinian counterparts (cf. Bonaparte et al., 1990; Salgado & Bonaparte, 1991; Calvo & Salgado, 1995), for intermittent contacts between the two continents probably did not end until late Albian time (Pletsch et al., 2001). However, Argentinian dinosaurs inhabited more southerly latitudes and may have possessed body forms less well adapted to equatorial stresses.

Evidence of dinosaurian diversity is manifest in isolated bones and skeletal parts (cf. Russell, 1996). The diversity of smaller forms has not been well sampled, although animals on the order of 1–2 m in length are uncommon in modern heat- and water-stressed environments (Willmer et al., 2000). Nevertheless, dinosaurian diversity levels seem comparable to those in most Late Cretaceous temperate assemblages in North America, with the notable exception of that of the Dinosaur Park Formation in Alberta (Russell & Manabe, 2002). With the exception of one published record (*Paralititan*, length ca. 40 m; J. B. Smith et al. 2001, fig. 2d), Saharan herbivorous dinosaurs were not large. They attained lengths in the range of 6–15 m. Late Jurassic sauropods frequently attained lengths of 22–26 m (Russell & Zheng, 1993). Sauropods appear to have been very common and may even have been the dominant herbivores (cf. Russell, 1996; Sereno et al., 1999). The mandible of the titanosaur *Malawisaurus* (Jacobs et al., 1993) and the skull of the pre-angiosperm *Jobaria* (cf. Sereno et al., 1999, fig. 2b) suggest browsing habits. The short stature and slender but transversely truncated beaks of the ornithomimids *Ouranosaurus* (Taquet 1976, fig. 10b) and *Lurdusaurus* (Taquet & Russell, 1999, fig. 1) are congruent with selective, low-level feeding. The expanded, blunt muzzle of the rebbachisaurid *Nigersaurus* (Sereno et al., 1999) strongly implies feeding on herbaceous vegetation. It would appear that herbaceous or low-stature vegetation composed largely of primitive angiosperms provided a major source of food for a dinosaurian assemblage in which sauropods comprised a very important component (cf. Russell et al., 2001). Body size often reflects the abundance of fodder. Thus the large size of freshwater fishes and the small size of the dominant terrestrial herbivores could be taken as evidence of the generally higher productivity of freshwater bodies and lower productivity of terrestrial environments in the mid-Cretaceous Sahara relative to those in well-studied Late Jurassic environments (cf. Burness et al., 2001; Chure et al., 1998; James Kirkland, pers. comm. 2002).

The physiological reactions of humans may serve to illustrate those of larger-bodied terrestrial vertebrates exposed to relatively mild maximum temperatures (ca. 34°C) of an equatorial mid-Cretaceous day. At this temperature and a relative humidity of 10% a comfortable body temperature can be maintained through sweating; at a relative humidity of 50% it becomes

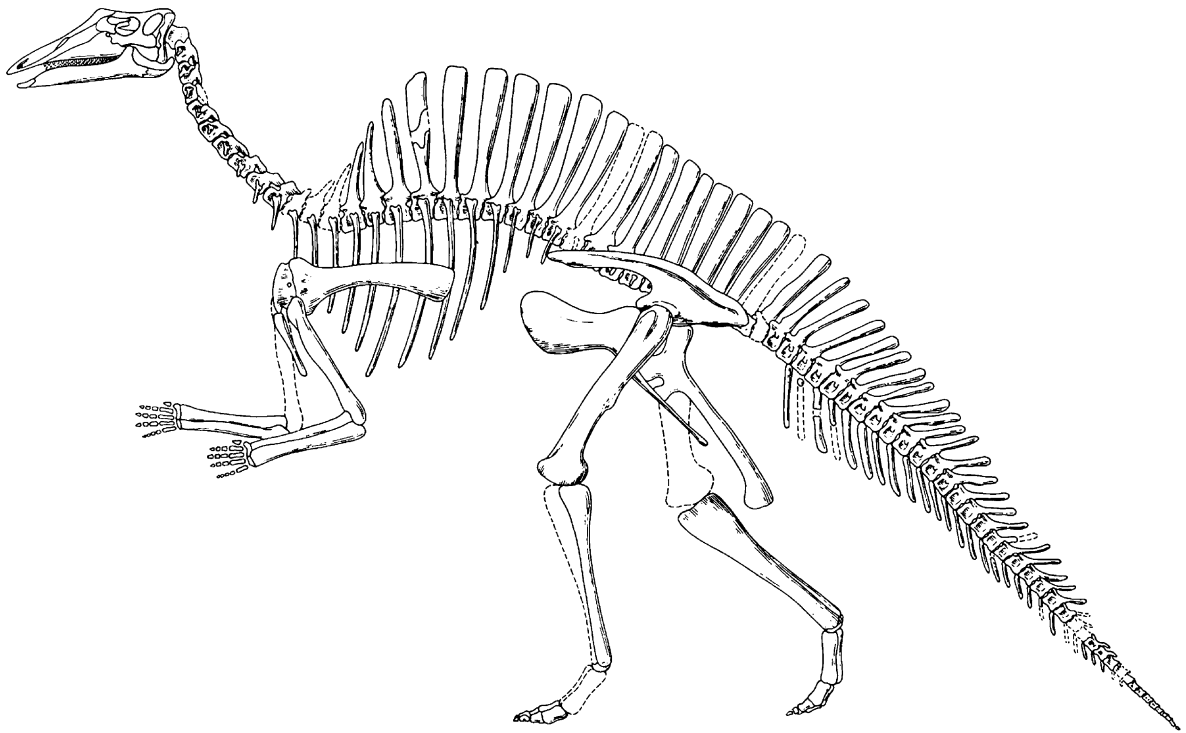


Fig. 4. *Ouranosaurus nigeriensis*, after Taquet (1976, fig. 73).

unbearably hot (Lutgens & Tarbuck, 1998, p. 85). Sweat production sharply increases above 30°C, and if night temperatures do not fall substantially below 37°C (normal body temperature) a physiological crisis seems to be approached (Lee, 1964). At 50°C in a low-humidity environment a person can walk for only a few hours during the day without drinking, and can survive for 24 hours only by walking at night. In the humid tropics, heat stress is less because of lower daytime highs and intermittent cloud cover (Adolph, 1969). When daily maximum temperatures reached 50°C during a recent (2002) heat wave in India both humans and animals began to die (U. C. Mohanti, pers. comm. 2002); Spicer et al. (1996) postulated this temperature as typical for the mid-day in Cenomanian low-latitude terrestrial environments. As ambient temperatures rise above levels tolerated by vulnerable tissues (e.g. in the range of 40–55°C), survival increasingly becomes a function of water availability and evaporative cooling. If the temperature and heat capacity of the Saharan atmosphere were greater than at present, mechanisms to balance a particularly critical water budget would have been highly developed in mid-Cretaceous Saharan dinosaurs (Claude Piantadosi, pers. comm. 2002).

Skeletal configurations in terrestrial vertebrates may reflect posture, weight, feeding habits, defense and locomotion, but they do not reflect climate well. The results of parallel selection among modern vertebrates inhabit-

ing episodically heat- and water-stressed environments have been well reviewed (cf. Schreider, 1963; Dawson & Schmidt-Nielson, 1964; Macfarlane, 1964; Schmidt-Nielson, 1964; Schmidt-Nielson & Dawson, 1964; Willmer et al., 2000). On this basis, the appearance of an equatorial mid-Cretaceous dinosaur might be expected to resemble those of ostriches and camels. Accordingly it might be pale brown with darker flanks, and possess a relatively long neck and tail. Its legs would be long and tough-skinned, terminating in feet with dark corneous pads. It would thermoregulate by remaining inactive during the heat of the day, panting, orienting itself head-on to the sun to minimize exposure, shedding heat convectively through dewlaps and skin folds, re-radiating at night heat absorbed by day, and shunting blood from the nasal area to cool the brain. It would forage at night and obtain much of its water from food. Its metabolic rate would be low, and a considerable portion of its body weight would be in fat. An opportunity to wallow in water or mud in temporary ponds would not be missed. The paucity and transitory nature of water sources would result in roaming herds; thus animals would tend to gregarious and nomadic. Strongly dependent offspring would not survive, so animals would bear precocial young.

The skeleton of an equatorial iguanodont *Ouranosaurus* (Fig. 4; Taquet, 1976, fig. 73) can be compared with that of the mid-latitude *Iguanodon bernissartensis* (Fig.



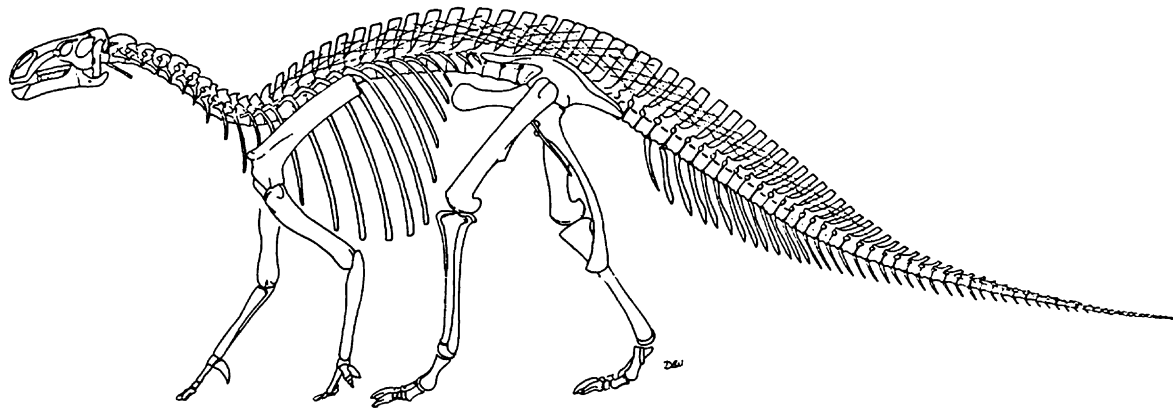


Fig. 5. *Iguanodon bernissartensis*, after Norman (1980, fig. 84).

5; Norman 1980, fig. 84) to reveal indications of adaptation to equatorial environments. In *Ouranosaurus*, the ribs, forelimbs and tail are shorter and more lightly constructed, and the dorsal spines are vertical and relatively much longer than in *Iguanodon*. Scaling lengths from skeletal reconstructions and calculating body weights from femoral circumferences, both derived from illustrations or published sources, *Ouranosaurus* was about 6 m long and weighed about 1000 kg (Taquet, 1976, figs. 62, 73), and *Iguanodon* was about 8.4 m in length and weighed about 3000 kg (Norman, 1980, figs. 68, 75). *Lurdusaurus* (Taquet & Russell, 1999) was a stocky, equatorial iguanodont about 8.6 m long, and weighed about 5500 kg. Its broad belly was carried 70 cm above the ground, whereas that of *Ouranosaurus* was easily 1 m off the ground (Taquet, 1976, fig. 73). *Sarcosuchus* was a giant aquatic crocodile estimated to have had a length of 11.5 m and a weight of about 8000 kg (Taquet, 1976; Sereno et al., 2001).

Appropriate weight/length ratios for the four animals are: *Ouranosaurus*, 170 kg/m; *Iguanodon*, 360 kg/m; *Lurdusaurus*, 630 kg/m; *Sarcosuchus*, 700 kg/m. *Ouranosaurus* was thus much more slender than its mid-latitude contemporary *Iguanodon*. *Lurdusaurus* was a ponderous animal the proportions of which approached those of the giant crocodile.

In *Ouranosaurus* (Fig. 4) the surface area of the body was further increased by the presence of a large, thin, fan-like structure resulting from the elongation of the thoracic vertebral spines (Taquet, 1976). Similar fan-like structures occur in representatives of three other groups of equatorial mid-Cretaceous dinosaurs: spinosaurs (*Spinosaurus*, Strömer, 1915), rebbachisaurids (*Rebbachisaurus*, McIntosh, 1990, p. 393) and dicraeosaurs (cf. the base of a cervical spine incorrectly referred to *Rebbachisaurus* by Russell, 1996, fig. 29). Such structures are certainly absent in the hippo-like *Lurdusaurus* and the piscivorous spinosaur *Cristatusaurus* (Taquet, 1984; Sereno et al., 1998; Taquet & Russell, 1998). Vertebral

fans are otherwise known in the geologic record only in Early Permian pelycosaurs (Romer & Price, 1940) and an aberrant middle Triassic archosaur (Zhang, 1975). Their occurrence by chance in four groups of mid-Cretaceous Saharan dinosaurs is hardly likely.

The effect of the presence of back fans is to increase surface area in a manner analogous to the slenderness of the extremities of *Ouranosaurus* and modern heat- and water-stressed animals. They are here considered as heat-radiating devices and evidence of terrestrial habits. In the case of *Lurdusaurus*, *Cristatusaurus* and the large crocodile *Sarcosuchus*, it is suspected that the animals exploited the greater productivity of aquatic environments and the thermal inertia of water to avoid the stresses of terrestrial habitats.

Several strategies employed by dinosaurs to circumvent stresses of heat and aridity within the mid-Cretaceous equatorial zone may thus include: (1) thermal inertia inherent in large dinosaurs taking advantage of diurnal temperature fluctuations; (2) shielding their small brains from extreme heat by circulating cool blood from narial passages to the brain area (e.g. rare giants such as *Paralititan*); (3) a relatively large area for convective heat loss (e.g. 'finbacks' such as *Ouranosaurus*); (4) utilizing the thermal inertia and/or evaporative cooling of water (e.g. 'hippos' such as *Lurdusaurus*).

Among the hazards for animals inhabiting terrestrial habitats would have been the high incidence of torrential rainfalls and flooding across flat terrain with variable substrates. Many mass deaths surely must have occurred through the drowning or miring of young and weakened animals (cf. Mellink & Martin, 2001). Although aquatic animals may have preferentially survived such floods, the vastness of the African-Arabian plain must have impaired the use of migration as an effective means for them to avoid regional drought. By escaping in the dimension of time, through aestivation, lungfish may have adopted the most secure route.

## 9. Conclusions

A mantle event that altered the Earth's energy balance by affecting the heat-retaining properties of the atmosphere is considered as the most probable cause of a mid-Cretaceous greenhouse that lasted nearly 40 myr. At greenhouse extremes, tropical or subtropical climates prevailed over two-thirds of the Earth's surface. The present review, which is focused on the terrestrial record in low latitudes during the early part of this interval, complements and extends information on global climates gained from more extensive studies of low-latitude marine environments and high latitude terrestrial environments.

The equator then crossed a very broad (ca. 16 000 km), low and homogeneous plain extending across northern Africa and Arabia. Relief was minimal, as evidenced by the great horizontal effects of changes in sea level. The plain constituted a vast and topographically simple interface between the base of the atmosphere and the surface of the Earth. It was bordered by rift highlands 2000 km to the south of the equator that provided a declining flux of sediments to the north. Because of rapid and fine-scale changes of facies in relatively high-energy environments of deposition, the terrestrial record preserved in these sediments is fragmentary and difficult to correlate precisely in time. The record does, however, reveal the paramount role of the atmosphere's response to greenhouse forcing in shaping terrestrial equatorial environments.

The dynamics of the ocean-atmosphere system at the time produced mean annual temperatures in the range of 30–34°C across equatorial lands where it is presently ca. 27°C. Diurnal excursions were probably reduced by greater atmospheric humidity, thereby avoiding lethal mid-day temperatures. Equatorial oceanic temperatures normally fluctuated 6°C on ten thousand year time scales, and these fluctuations were probably felt over equatorial continents. During periods of oceanic black shale deposition, atmospheric partial pressures of oxygen and nitrous oxides probably rose, and sea levels rose to a maximum of ca. 270 m (the rise in sea level if all present polar ice melted today would be ca. 80 m; cf. Clark & Mix, 2000). The result would have been warmer temperatures and loss of lowland habitat. Other short thermal excursions may have been driven by the release of methane hydrates (Jahren et al., 2001), and changes in the tempo of lava flooding and storm mixing of ocean surface waters. The incidence of hurricanes was higher during the mid-Cretaceous greenhouse. Heating at the base of the atmosphere would have elevated the tropopause (from 10–15 to 20–30 km, Farrell, 1990; see also Thuburn & Craig, 1997). Thermal excursions in marine environments may have produced mass deaths from heating and flooding in terrestrial environments.

The mid-Cretaceous atmosphere was relatively rich in greenhouse gases. In terrestrial environments the release of nitrous oxide and ozone by lightning in violent convective storms transformed methane generated in wetlands into carbon dioxide. Insect and vertebrate herbivores also generated considerable carbon dioxide through methane oxidation. Evidence of aseasonal, torrential rainfall and sheet flooding is preserved in high-energy sediments of diverse grain sizes that reflect unstable drainage patterns. The extent of wet- and dry-facies sediments across the immense equatorial plain suggests multimillennial periods of pluviosity and aridity. A variety of freshwater and terrestrial organisms show evidence of adaptation to semi-arid climates and episodic drought. There was no wet intertropical convergence zone.

Floral and faunal changes approximately coincided with the onset of the mid-Cretaceous greenhouse. The expansion of steppe-like landscapes suggests decreased water availability. Violent storms (with attendant windfalls, lightning generated fires, and erratic and unstable drainage patterns) may have been responsible for a decline in the abundance of large conifers. Flowering herbs and lower stature vegetation proliferated, as did insects that could efficiently pollinate disjunct associations of flowering plants generated by irregular rainfall. Flowering plants entered higher latitudes via disturbed areas bordering stream courses.

Giant pterosaurs made their appearance near the onset of the greenhouse, possibly as a result of increased lift associated with stronger atmospheric convection. With their huge surface/volume ratios it might be expected that they were very vulnerable to overheating. In addition to holding their folded wings to minimize intercepted light, they had the option of soaring to higher, cooler levels several kilometers higher in the atmosphere, as do modern vultures (Cook, 1997; Ferguson-Lees & Christie, 2001). Herbivorous dinosaurs were generally smaller than those typical of pre-greenhouse environments, suggesting a decline in the productivity of terrestrial vegetation. Among herbivorous dinosaurs, the broad muzzles of abundant, small sauropods were best suited for cropping herbaceous angiosperms. Dinosaurs apparently avoided heat stress through structures that increased bodily surface area, amphibious habits, and (less frequently) the thermal inertia of large bodies. The huge dimensions of freshwater fishes and crocodylians suggest that intermittent bodies of water were highly productive.

Although dinosaurian diversity does not seem to have been unusually low, terrestrial ecosystems appear to have been subjected to greater stresses than those typical of pre-greenhouse environments. Episodic extremes may have taken mid-Cretaceous Saharan ecosystems near tolerance limits. As noted above, terrestrial sediments show indications of alternating pluvial and arid climates

on multimillennial time scales. Evidence of alternations of terrestrial climates in Africa, as indicated by wind-blown dust in a mid-Atlantic core of early Albian age, occurs on similar time scales and is thought to be due to changing orbital (Milankovitch) parameters (Hoffman et al., 2001). Intervals when tolerance limits were closely approached in continental environments may more easily be detected in the marine record than in the terrestrial paleontological record.

There is little question that humans and modern, temperate agriculture would be physiologically challenged by the heightened need to rely on evaporative cooling under mid-Cretaceous equatorial conditions. It is interesting to note that terrestrial ecosystems showed as much continuity as they did through 20 myr of variable but generally deepening mid-Cretaceous greenhouse climates. They apparently accommodated stresses similar to those anticipated to occur in a future greenhouse, whether anthropogenic or not (Robinson & Robinson, 1997). With this in mind, useful climatic information might be obtained from Saharan mid-Cretaceous environments by applying isotopic applications analogous to those used with such success in the marine fossil record. Strata rapidly deposited under hypoxic conditions beneath marginal seas and deep lakes in the trans-African rift zone could yield high-resolution data on continental climatic excursions. Studies of organismal responses to gas partial pressures, such as the relationship between carbon dioxide levels and stomata in plants, could be compared with the mid-Cretaceous record, and atmospheric circulation models should continue to be expanded to include continental climates. The dependency of the terrestrial biosphere on the atmosphere is so profound that it could be regarded simply as a gigantic ‘air-plant’.

The exploration of the mid-Cretaceous greenhouse will be as fascinating in itself as it may be relevant to modern environmental concerns. The prospect stimulates the imagination, which in turn generates hypotheses: the brief, quasi-temperate dawn, the delicate scent of a primitive flower, the cacophony of reptilian squawks and bellows following heavy rains, savannahs dotted by bottle trees and finbacked ‘camels’, thin, yellow lines of diminutive sauropods grazing across green and golden prairies of flowers, lofty dots representing giant pterosaurs circling high in cooler levels of the torrid afternoon sky, and distant lightning storms towering higher than Mount Everest in the sunset.

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