



## Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana

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### ABSTRACT

A high diversity of terrestrial crocodyliform species has been found in the continental Cretaceous deposits of Gondwana. They are widespread in the sedimentary basins of Brazil, Uruguay, Argentina, Bolivia, Morocco, Cameroon, Niger, Malawi, Madagascar and Pakistan, from alluvial, fluvial and lacustrine deposits. A peculiar aspect of these terrestrial crocodyliforms is that only some of them are cosmopolitan. They comprise distinct groups as the basal *Notosuchia*, baurusuchids, sphagesaurids and Sebecian peirosaurids. There is a distribution pattern of the terrestrial Crocodyliformes faunas throughout the Cretaceous. The oldest are composed of the small and probably omnivorous *Notosuchia* and *Araripesuchus*, found in Early Cretaceous deposits. In the Late Cretaceous this fauna was enriched by the medium-sized to large-size baurusuchids, sphagesaurids, peirosaurids and larger *Araripesuchus* which present specializations as active terrestrial predators. The distribution analysis of the terrestrial Crocodyliformes from Early and Late Cretaceous palaeogeographic and palaeoclimatic maps indicates that temperature was the principal influence on their Gondwanan distribution. Although expressed seasonality, aridity is a limiting factor for the distribution of extant crocodylians. The Cretaceous basal *Notosuchia*, baurusuchids, sphagesaurids, *Araripesuchus*, Sebecian peirosaurids, are found in arid climatic belts during Early and Late Cretaceous. To live in a hot and arid climate they have presumably developed ecological strategies that allowed such habits. The aridity or seasonal warm and cyclic dry and wet climate periods plays a role, that have not yet been analyzed, that may explain the domain of bizarre Crocodyliformes in Gondwana during the Cretaceous.

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### 1. Introduction

The terrestrial Cretaceous Crocodyliformes from Gondwana comprises distinct groups as the small basal *Notosuchia*, baurusuchids, sphagesaurids, *Araripesuchus* and peirosaurids. The oldest ones are probably Berriasian (Uiraúna Basin, Brazil), despite which their diversification took place during Aptian–Albian in South America and Africa. They are widespread in deposits of alluvial, fluvial and lake paleoenvironments, comprising more than 30 species (Figs. 1–4).

The taxonomic and systematic definitions are based on Sereno and Larsson (2009). Their systematic revision infers that the Notosuchian clade groups *Baurusuchus*-related taxa (*Baurusuchus*, *Stratiotosuchus*, *Penhuechesuchus*, *Pabweshi* and *Wargosuchus*), *Sphagesaurus*-related taxa (*Sphagesaurus*, *Adamantinasuchus* and *Armadillosuchus*), *Araripesuchus*, and other more basal taxa with a controversial systematic

position, such as *Notosuchus*, *Uruguaysuchus*, *Malawisuchus*, *Comahuesuchus*, *Mariliasuchus*, *Simosuchus*, *Anatosuchus*, *Yacarerani* and *Morrinhosuchus*, *Peirosaurus*, *Lomasuchus*, *Uberabasuchus*, *Montealtosuchus* and *Hamadasuchus* are defined by the same authors as part of a larger clade named Sebecia and closely related to the Paleogene *Sebecus* and the aquatic *Stolokrosuchus*, all of them nested within the most primitive Neosuchia.

A peculiar aspect of these terrestrial Crocodyliformes is that some of them are cosmopolitan, whether others seem to be endemic. Basal *Notosuchia* are found in Brazil (Uiraúna, Parnaíba, Parecis and Bauru basins), Uruguay (Litoral Basin, Guichón Formation), Bolivia (Cajones Formation), Argentina (Neuquén Basin), Africa (Malawi Dinosaur Beds, Koum, Tegama basins) and Madagascar (Mahajanga Basin). *Araripesuchus* are found in Brazil (Araripe Basin), Argentina (Neuquén Basin), Africa (Kem Kem Beds, Koum and Tegama basins) and Madagascar (Mahajanga basin). The Sebecian peirosaurids are found in Brazil (Bauru Basin), Argentina (Neuquén Basin) and Morocco (Kem Kem Beds). The Notosuchian baurusuchids are found in Brazil (Bauru Basin), Argentina (Neuquén Basin) and Pakistan (Pab Formation, Balochistan Province). The Notosuchian sphagesaurids

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# Early Cretaceous Climate

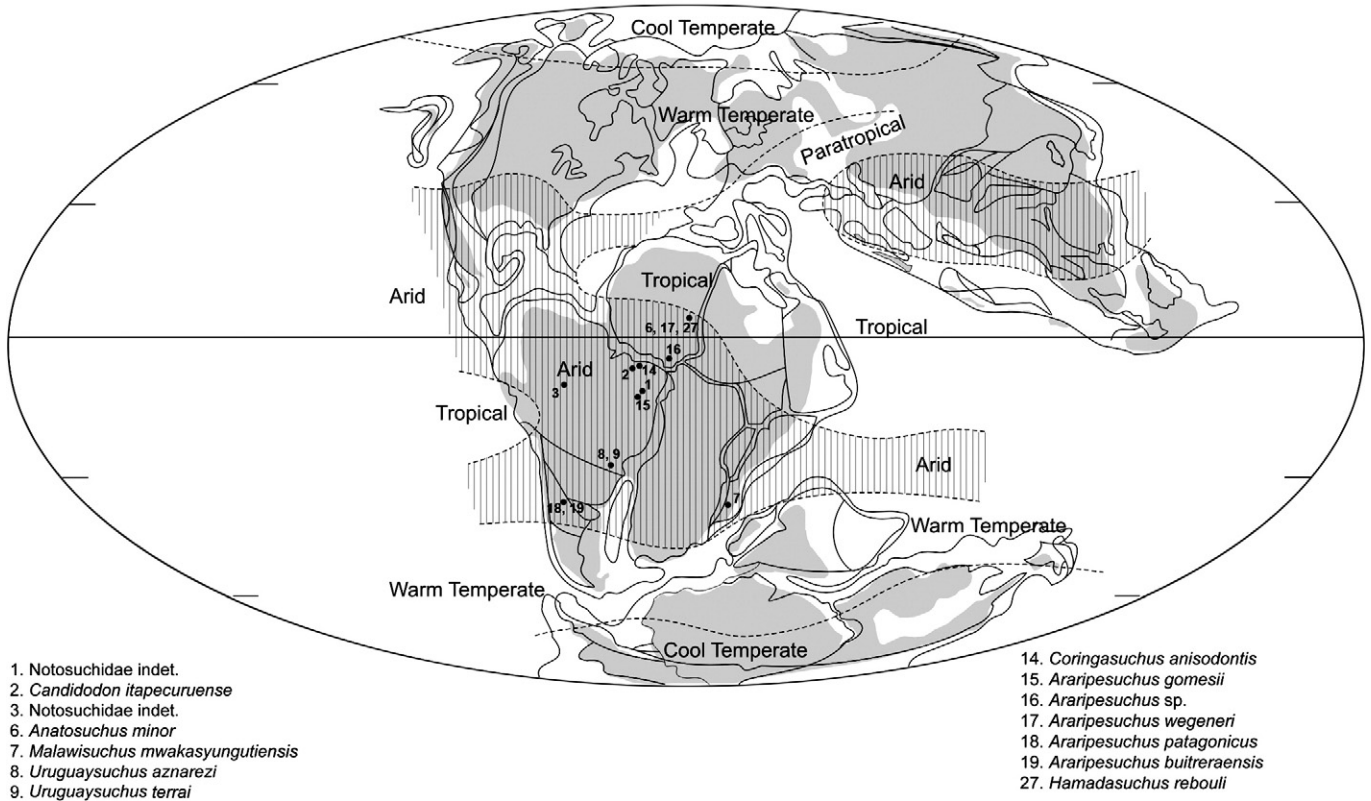


Fig. 1. Early Cretaceous climate and the distribution of the terrestrial Crocodyliformes in Gondwana. Paleoclimatic map according Scotese (2005).

are the only group still restricted to South America (Bauru Basin, Brazil) (Figs. 1 and 2).

According to Markwick (1998) the distribution of living crocodylians is climatically controlled by a mean annual temperature equal to or more than 14.2 °C, although local hydrological conditions play an important role, providing a buffer effect against temperature extremes and a fully adequate environment for the amphibious niche of the extant Eusuchia. Thus, the extant crocodylians are limited to tropical and subtropical environments. The analysis of the distribution of terrestrial Crocodyliformes carried out on the Early and Late Cretaceous palaeogeographic and palaeoclimatic maps (Scotese, 2005) shows a spatial distribution of the same pattern as that of modern crocodylians. It indicates that temperature was the principal influence on their global distribution. It is possible that these crocodyliforms developed ecological strategies that allowed them to live in a hot and arid climate. Therefore the rare Cretaceous Eusuchian crocodylians are excluded from this analysis, because they are semi-aquatic to aquatic, so they are not influenced by the terrestrial environment. Extant species are known to endure severe low humidity in the Sahara desert region, but even then are closely linked to the small aquatic habitats within the arid environment (Richardson et al., 2002).

Available data from the studied dinosaurs from Brazil, Argentina, Africa and Madagascar do not support any specific adaptation to different terrains or climates in Gondwana. In Brazil, fossils of terrestrial crocodyliforms outnumber those of dinosaurs. More specifically, the preservation of crocodyliform fossils, even from outcrops yielding dinosaurs, is outstanding. The same outcrops yield fully preserved crocodyliforms and scarce and fragmentary dinosaur fossils. These observations are relevant to the analyses undertaken here. There are no macro-fossil plants or palynomorphs associated with these crocodyliforms.

## 2. The paleobiogeographic context of the Cretaceous terrestrial Crocodyliformes of Gondwana

The paleobiogeographic synthesis of Bonaparte (1986) allowed an insight into the faunal distribution and vicariant events in Gondwana throughout the Mesozoic. However, paleobiogeographic studies concerning the distribution of terrestrial Crocodyliformes have shown conflicting results. Due the high diversity, widespread distribution and a largely terrestrial habit, the crocodyliform phylogeny is considered adequate to explore paleobiogeographical events. Turner (2004), through a cladistic paleobiogeographical method, suggested that the vicariant biogeographical pattern played a major role in determining the paleogeographical distribution of the Crocodyliformes, in spite of dispersal and regional extinction (Figs. 3 and 4).

The similarities of the vertebrate faunas across Gondwana led to the assumption of a South American–African–Madagascar–Antarctica–India–Australia (Chatterjee and Scotese, 1999) connection until the Aptian (Buffetaut and Taquet, 1979; Buffetaut, 1980, 1981, 1982). A land bridge may have existed at least up to the Albian–Cenomanian (Calvo and Salgado, 1996). Notwithstanding the opening of the South Atlantic, Buffetaut (1980, 1982) also considered the possibility of intermittent faunal interchange after the Albian, through a chain of islands between Africa and South America or even a connection through Antarctica and Australia. Ortega et al. (2000), through the analysis of *Araripesuchus*, considered that phylogenetically related taxa do not necessarily presuppose the existence of a continental nexus during the Aptian, and the archosaurian fauna could have been previously isolated in each continent. These authors postulated that the distribution of the basal Notosuchia and *Araripesuchus* does not support the hypothesis of terrestrial connections between South America and Africa after the Albian.

# Late Cretaceous Climate

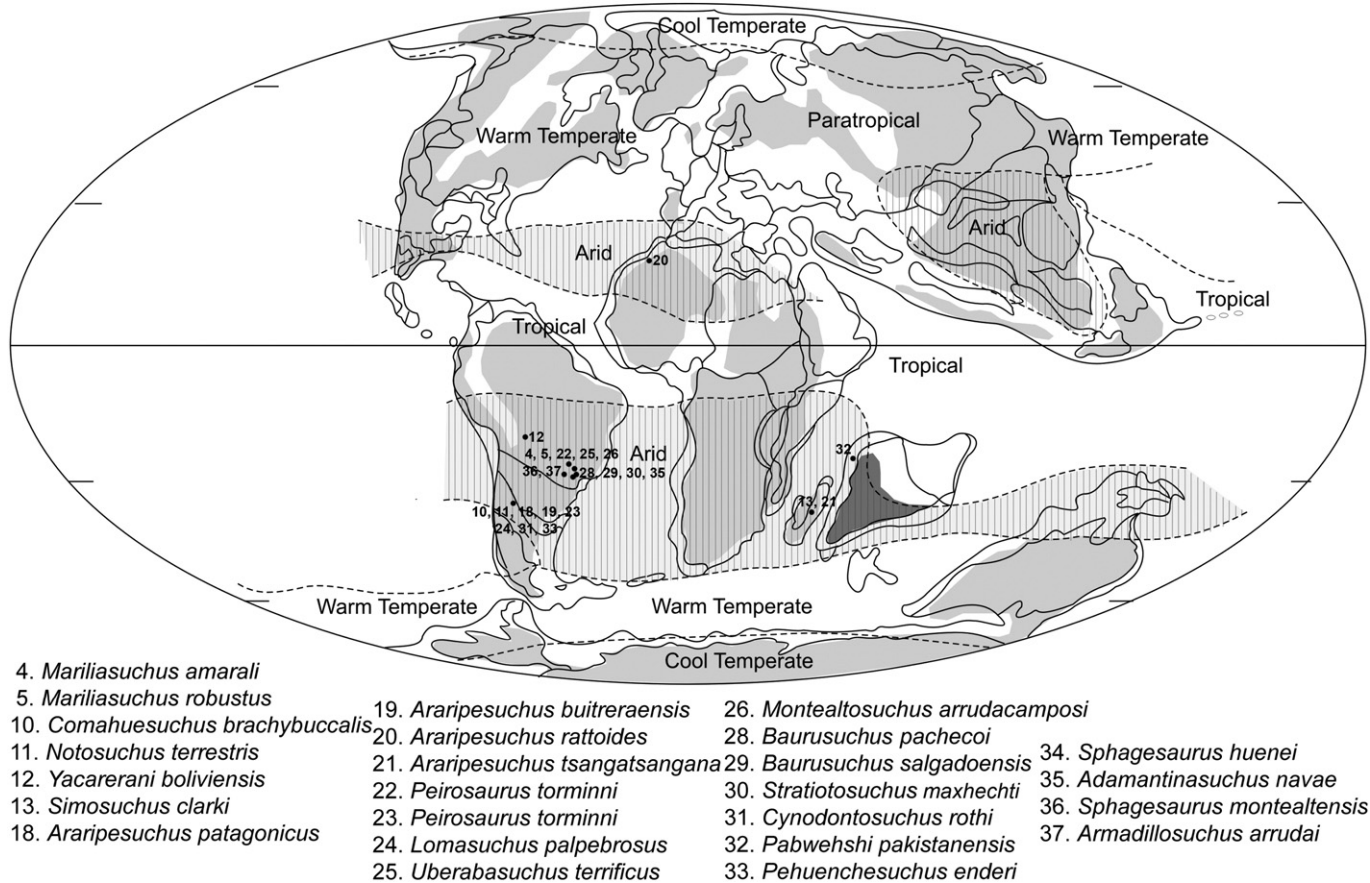


Fig. 2. Late Cretaceous climate and the distribution of the terrestrial Crocodyliformes in Gondwana. paleoclimatic map according to Scotese (2005).

Therefore, the Cretaceous paleobiogeography of Gondwana presents problems concerning the distribution of some taxa, like the *Notosuchia*, previously considered to have an exclusively Gondwanan record (Gasparini, 1971, 1996; Bonaparte, 1986; Gomani, 1997). The idea of a non-endemic tetrapod fauna during the Cretaceous in Gondwana is reinforced by the studies of Hallam (1967, 1972), Colbert (1975), Buffetaut (1987) and Molnar (1989) that noted a conflict between the idea of island continents and the distribution of vertebrate fossils. As argued by Chatterjee and Hotton (1986) and Chatterjee and Scotese (1999), India could not have been an isolated island during the Cretaceous and early Cenozoic, because there was no development of endemic faunas and floras. The lack of endemism among Indian Cretaceous terrestrial vertebrates is inconsistent with the island continent hypothesis. Based on the vertebrate terrestrial data, geological and geophysical evidence, Chatterjee and Scotese (1999, 2007), presented new paleogeographical maps to the Early and Late Cretaceous with several possible biogeographic corridors between eastern and western Gondwana.

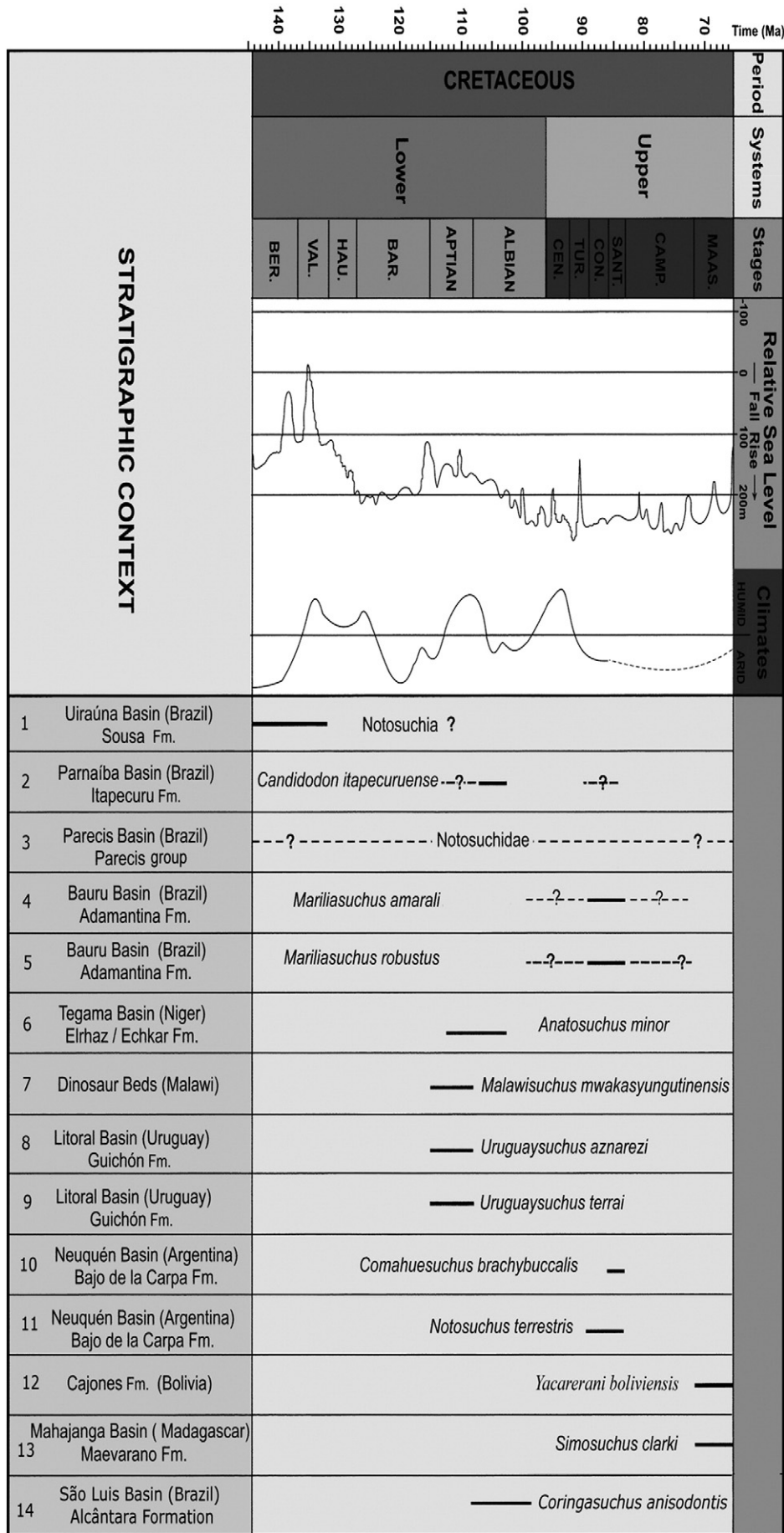
Then, the main concern is to explain the paleogeographic models where continental connections throughout the Cretaceous did not exist. The plate tectonic and paleogeographic reconstructions of Barron (1987), Barron et al. (1981), Hay et al. (1990), Scotese (1991) and Scotese et al. (1988) assumed that Eurasia, Greenland, North America, South America, Africa, Madagascar, India, Australia, and

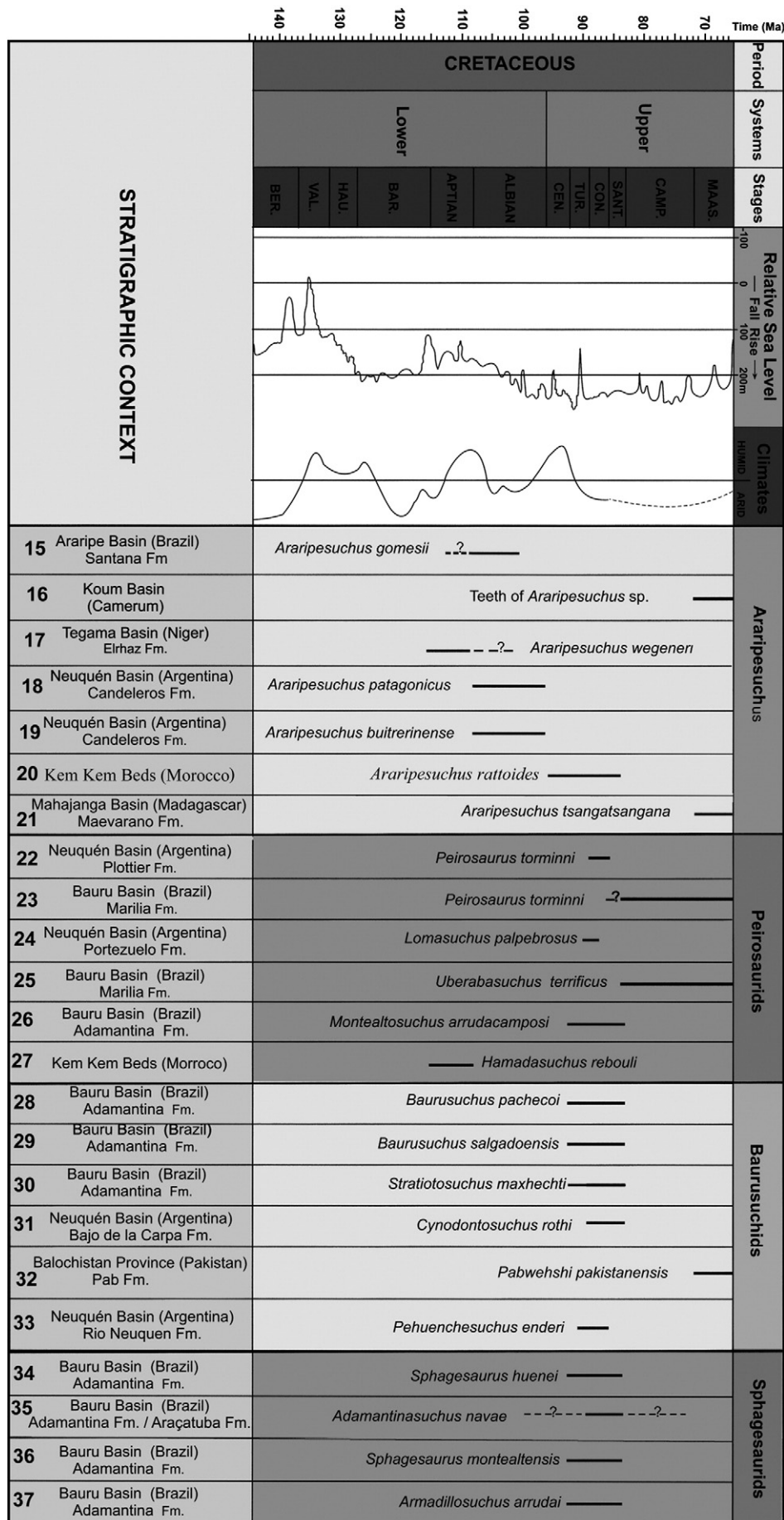
Antarctica were separated by the end of the Early Cretaceous, without any later connections, by deep ocean passages between these major continental blocks.

An alternative global Cretaceous paleogeography, to these traditional models, was proposed by Hay et al. (1999) and in a paleobiogeographic perspective by Sampson et al. (1998), Krause et al. (2006) and Chatterjee and Scotese (2007). Their global plate tectonic reconstructions present three continental blocks during Early Cretaceous (North America–Eurasia, South America–Antarctica–India–Madagascar–Australia, and Africa), a large open Pacific Basin, a wide eastern Tethys and a circum-African seaway extending from the western Tethys region through the North and South Atlantic into the juvenile Indian Ocean between Madagascar–India and Africa. There were no deep-water passages to the Arctic. The proposal of Hay et al. (1999), of an Early Cretaceous Earth with a long, narrow, sinuous ocean basin extending off the Tethys, contrasts strongly with the traditional view of separated island continents.

### 3. The climatic control of the distribution of modern crocodiles

Climatic interpretations using fossil crocodiles are based on the climate and temperature tolerances of their extant relatives. All living species are ectothermic, and as such their body temperatures correspond closely to environmental temperatures, that in turn





correspond to the temperature of the immediately adjacent environment, which may be water or mud, rather than air (Markwick, 1998). Biological observations of living species allowed Markwick (1998) to consider that temperature is the limiting factor to the distribution of crocodylians and that climate can be inferred through the paleobiogeography of this group. Basal *Notosuchia*, sphagesaurids, baurusuchids, *Araripesuchus*, and the Sebecian peirosaurids were clearly terrestrial animals, living in an environment marked by rainy and dry seasons in an arid climate. Therefore, this uniformitarian approach may be not adequate in the case of the fossil groups of Gondwana.

The observations on the distribution of modern crocodiles by Markwick (1998) indicate that temperature is the principal influence on their global distribution, with the coldest monthly mean temperature of 5.5 °C marking the minimum thermal limit for the group, corresponding today to a minimum mean annual temperature of 14.2 °C. For the living species *Alligator mississippiensis* the optimal temperature is taken as being 32–35 °C. The duration of warmth during the year is also important, as this affects sex determination, early juvenile development and survival. The presence of standing water or burrows provides an essential thermal buffer against temperature extremes (Campbell and Mazzotti, 2004).

Coulson et al. (1989) and Markwick (1998) 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 (Markwick, 1998). This could be used to infer physiological aspects of the large *Notosuchia* such as baurusuchids and sphagesaurids, and Sebecia such as the peirosaurids from the Late Cretaceous. As an individual grows larger, the greater its body surface area becomes, hence, the more heat or energy is required to raise its body temperature, and the longer it takes to lose heat. This inertial homeothermy has been used to suggest that very large ectotherms would have been able to maintain sufficient body temperatures during cold periods by virtue of thermal inertia. Seymour et al. (2004) even suggest that extant and fossil crocodylians could be homeothermic animals, a primitive ancestral trait among archosaurs. Then, baurusuchids, peirosaurids and sphagesaurids would have been able to wander large distances, withstanding the heat and low humidity, as active predators in a harsh environment (Vasconcellos, 2006).

Other characteristics are unique to these taxa. The morphofunctional and ecological inferences used to determine their terrestrial habits were based on skull characters (position and orientation of orbits and external nares and rostral shape) and some postcranial features (appendicular bone shape and stoutness, osteoderms, pelvic girdle morphology and, shape of manus and pes) discussed by Pol (2005), Marinho et al. (2006) and Vasconcellos (2009). All them show a profound adaptation to fully terrestrial niches and even cursoriality.

#### 4. The climatic role in the paleobiogeographic distribution of Cretaceous Crocodyliformes

The Cretaceous is generally considered as an ice-free period, although there are several reports of deposits formed by ice transport at high-latitude sites (Gregory et al., 1989). During this period, what is possibly one of the warmest intervals in Earth history, the climate

was in an extreme 'greenhouse' mode (Barron and Pettersson, 1989; Spicer and Corfield, 1992; Barron et al., 1993; Tajika, 1999).

From the marine record, a cool interval in the Early Cretaceous is followed by warming lasting until the late Albian. The stable isotope evidence and paleobotanical data indicates in mid-Cretaceous a warm, equable condition of the ocean waters (Crowley and North, 1996; Herman and Spicer, 1996; Fassell and Bralower, 1999). Then, hurricane formation should have been more frequent in the mid-Cretaceous than in the Early Cretaceous when ocean temperatures were likely to have been cooler. The analysis presented by Lloyd (1982) based on paleogeography, ocean circulation and temperature indicated that there was greater seasonality of wind patterns during the mid-Cretaceous, leading to more extreme climates over the continents, with slightly equator-ward positions of the subtropical anticyclones and monsoonal regimes over the continental margins bordering Tethys and the central Atlantic. The latitudinal distribution of relative humidity presented by Ufnar et al. (2002) for the mid-Cretaceous, indicates dry belts in the paleolatitudes of 20–40° and 60–80°. These can also be observed in the paleoclimatic maps of Scotese (2005).

Late Cretaceous orography strongly influenced the distribution of precipitation and the paleogeographic distribution of deserts. Large intercontinental deserts dominated the low-lying continental interiors of South America, Africa, and southwest Asia (De Conto et al., 1999). Increased greenhouse gases in the atmosphere could explain the generally warm state of Late Cretaceous climates (Frakes, 1999); although some authors (Barrera, 1994; D'Hondt and Arthur, 1996) considered the temperature of the Maastrichtian sea surface waters to have been lower than those of today. The Santonian–Campanian was generally a cool time, except for a strong warming in the marine environment in the late Campanian. For the continental landmasses, there was continuous warming from the Albian to a peak in the Turonian, and there is no evidence of a reversal to cooling in the Cenomanian, as seen in the marine record. A Coniacian–Santonian warming is poorly defined, being seen only in the high-latitude data. Comparisons of selected Cretaceous temperature gradients with those of the present reveal that continental gradients may have been warmer than at present. During latest Cenomanian–earliest Turonian there was an ultra-thermal greenhouse event (Frakes, 1990), and the reptile assemblage of Turonian–Coniacian from the Arctic indicates a mean annual temperature exceeding 14 °C. These high polar temperatures implied raised equatorial temperatures (Tarduno et al., 1998). Parrish and Spicer (1988), based on terrestrial vegetation, inferred Arctic temperatures no higher than 13 °C during Albian–Coniacian. There, the Campanian and Maastrichtian mean annual Arctic temperature would have been about 2–8 °C. The Amiot et al. (2004) analysis reveals a similar signature from the point of view of continental vertebrates. Therefore the Campanian climate in lower latitudes was warm and wet, with a global mean annual temperature of 24.1 °C (about 10 °C higher than today) (Barron and Pettersson, 1989; Barron et al., 1993). The high-latitude continental landmasses close to the polar oceans, were not cold enough to induce ice sheet formation. Model simulations of Upchurch et al. (1999) demonstrated an important climatic linkage between the oceans and the land surface in the Maastrichtian. Sea ice development is inhibited by warmer oceans, which delay the formation of sea ice in winter and reduce both its thickness and fractional cover. The warm high-latitude temperatures during the Late Cretaceous could have resulted from the interaction of increased pCO<sub>2</sub>, paleogeography, and a reduced surface albedo due to forest vegetation (Donnadieu et al., 2006). The climatic fluctuations inferred for the Sergipe Basin during Late Cretaceous by

Carmo and Pratt (1999) suggests a high degree of biotic sensitivity to continental climatic variability at low latitudes under global greenhouse conditions. Then, the equatorial climatic dynamics probably affected large portions of the evolving South Atlantic Ocean due to the narrow, elongate shape of the oceanic passage and the close proximity of Africa and South America.

During the Cretaceous, tectonics and climate were both directly and indirectly related, through uplift, atmospheric circulation, the hydrologic cycle, and volcanism (Hay, 1996; Poulsen et al., 1999). The Cretaceous was a highly active period tectonically, with many different landmass configurations. During this time, the rifting of continental blocks involved broad upwarping followed by subsidence of a central valley and uplift of marginal shoulders. Hay (1996) demonstrated that in this context the result is an evolving regional climate consisting first of a vapor-trapping arch, followed by a rift valley with freshwater lakes and playa lake deposits, culminating in an arid rift bordered by mountains intercepting incoming precipitation.

Gondwana, as a large continent, caused disruption of zonal atmospheric circulation and the establishment of monsoonal circulation. The great land area of Gondwana would have changed the paths of the wind systems (controlled by the tropical Hadley cells, mid-latitude Ferrel cells, and polar cells), creating an oceanic subtropical high-pressure and high mid-latitude low pressure cells and increasing poleward heat and moisture transport in the Southern Hemisphere. In general, rainfall was controlled by the zonal pattern and was heaviest on the windward sides of mountains and where airflow crossed the coastline into the continent. Besides this, there was the strongly seasonal monsoon. The seasonality would have been strong because of the isolation of the continental interior from the ameliorating influence of the surrounding ocean. Seasonality would have been particularly strong when the continent was centered in mid-latitudes, covering regions of maximum cooling and heating. Both temperature and precipitation would have fluctuated strongly with the seasons (Riccardi, 1988; Parrish, 1990; Scherer and Goldberg, in press).

Aridity is another aspect of the greenhouse effect in the landmasses of Gondwana. There is a strong dependence of water vapor content on temperature at the surface. The increase in the evaporative capacity of warmer air over land may not be satisfied by the moisture available, and as a result, global warming increases the aridity of land areas on a global scale (Wolfe and Upchurch, 1987; Hay, 1996; Price et al., 1998). Volcanic activity can also influence the climate, due to effects on sea level changes, paleobathymetry, oceanic circulation, and chemistry of the atmosphere and hydrosphere (Budyko and Ronov, 1979; Schlanger and Arthur, 1990). Khadkikar et al. (1999) interpreted the Maastrichtian semi-arid climate of the Indian Peninsula as the result of Deccan volcanism. Basaltic volcanism was a significant mechanism of introducing aerosols into the atmosphere, allowing short-term global surface cooling. On the local scale, this volcanism may lead to aridity, as it produced fresh barren xeric landscapes. Between 65.5 and 65.3 Ma high climatic and oceanic variability occurred, that warmed globally by 3–4 °C. Barrera and Savin (1999) interpreted this global warming as related to the Deccan Trap volcanism at the end of the Cretaceous.

The global Cretaceous paleogeography of Hay et al. (1999), showing an Early Cretaceous Earth with a long, narrow, sinuous ocean basin extending off the Tethys, provides a markedly different set of boundary conditions for a climate model and also to the possibilities of dispersal of the terrestrial crocodyliforms. During the first stages of the South Atlantic opening, the Falkland Plateau carried Madagascar–India–Antarctica–Australia with it in an arc. Subsequently, South America and Africa separated along a transform fault between the northeastern margin of Brazil and Guinea coast of Africa. Although Antarctica moved south, the Antarctic Peninsula remained in contact with the southern Andes, forming a continuous mountain chain that was not interrupted until the Oligocene. In the Indian Ocean, India first moved south with Antarctica and Madagascar. In the

Early Cretaceous, India began to rotate away from Antarctica, moving along a transform fault and sliding past Madagascar. However, it remained connected to Antarctica by a land bridge until final separation in the Late Cretaceous, when it also separated from Madagascar (Sampson et al., 1998; Krause et al., 1998; Hay et al., 1999; Krause, 2003; Krause et al., 2006, 2007; Sereno et al., 2004; Sereno and Brusatte, 2008). Chatterjee and Scotese (1999) pointed out that the evolution of the Indian plate is the most complex and least understood of all Gondwanan landmasses. As India did not rift apart from Pangea in one simple motion, but during several distinct episodes, even during the Cretaceous there was contact of India with adjacent landmasses that allowed transcontinental migration routes. Deep-water passages between the Tethys, the Atlantic, the Pacific, and the developing Indian Ocean formed during the Late Cretaceous. There were many isolated land areas in the Late Cretaceous, but mostly they were separated by epicontinental seas (Hay et al., 1999).

As Mayhew et al. (2008) demonstrated, global climate explains substantial variation in the fossil record due to accelerated rates of extinction and origin of species, genera and even families. The stratigraphic context of the Cretaceous terrestrial Crocodyliformes also reinforces this idea of a climate-controlled distribution of faunas. In the Early Cretaceous north and northeastern Brazilian basins of Parnaíba and Araripe, *Candidodon itapecuruense* (Aptian) is found in fluvial-lacustrine sediments and *Araripesuchus gomesii* occurs in carbonate nodules of the Santana Formation (Aptian–Albian), both in a context of an arid climate. The palaeoenvironmental setting of the fine sandstones where the Late Cretaceous species of the Bauru Basin (Brazil), where *Mariliasuchus amarali*, *Mariliasuchus robustus*, *Baurusuchus pachecoi*, *Baurusuchus salgadoensis*, *Stratiotosuchus maxhechti*, *Sphagesaurus huenei*, *Sphagesaurus montealtensis*, *Adamantinasuchus navae*, *Armadillosuchus arrudai*, *Peirosaurus torminni*, *Uberabasuchus terrificus*, *Montealtosuchus arrudacamposi* and *Morrinhosuchus luziae* are found, have been interpreted as deposited during sudden floods on alluvial plains during a dry and hot season (Mezzalana, 1980; Soares et al., 1980; Lima et al., 1986; Campanha et al., 1992; Bertini, 1994; Fulfaro et al., 1994, 1999; Silva et al., 1994; Fernandes and Coimbra, 1996; Alves and Ribeiro, 1999; Andreis et al., 1999; Batezelli et al., 1999; Etchebehere et al., 1999; Carvalho and Bertini, 2000; Campos et al., 2001; Dias-Brito et al., 2001; Fernandes et al., 2003; Pol, 2003; Carvalho and Bertini, 1999; Carvalho et al., 2004, 2005, 2007; Nobre and Carvalho, 2006; Vasconcellos, 2009; Iori and Carvalho, 2009; Vasconcellos and Carvalho, 2010). The occurrence of almost complete articulated skeletons, as for *Mariliasuchus amarali*, *Baurusuchus salgadoensis*, *Uberabasuchus terrificus*, *Adamantinasuchus navae* and *Montealtosuchus arrudacamposi*, suggests these crocodyliforms could dig large, deep excavations in the soft substrates that, like the “alligator holes” of extant alligators assisted thermoregulation (Cott, 1961; Richardson et al., 2002; Campbell and Mazzotti, 2004; Palmer and Mazzotti, 2004; Vasconcellos and Carvalho, 2006). These excavations also retain water during dry periods. This ethological aspect probably allowed them to live in more terrestrial and arid environments (Campos et al., 2005; Vasconcellos and Carvalho, 2006) than other crocodyliforms. Alternatively, these animals could have used the burrows only during hot days, being active at dawn and dusk. It seems also plausible to imagine use of a shelter in the shade during the hottest periods, and nocturnal activity (Stéphane Jouve, 2010, pers. comm.). Freshwater ponds and rivers were scarce, generally drying out during long droughts. This was a very restrictive factor and the fauna and flora of this region should be well adapted to endure these severe environmental conditions. Flash floods during rainy seasons represented catastrophic events that allowed the fossilization of articulated skeletons. Goldberg and Garcia (2000) have interpreted an increase in aridity through time, from the Early to the Late Cretaceous. In the northern region of the Bauru Basin (Uberaba County), Garcia et al. (1999) argued that the paleoclimatic conditions changed to become more arid during the Maastrichtian. This aridity

was considered by Goldberg and Garcia (2000) to reflect the global climatic conditions and the existence of topographic heights that allowed the development of a dry microclimate in the region. The more humid climate was restricted to the surrounding mountains that acted as geographic barriers to the entry of humid winds. The climatic seasonality was marked by longer dry intervals interrupted by periods of heavy rains, when small lakes and temporary ponds, which were relatively deep during the flood periods (Senra and Silva e Silva, 1999), supported an abundant and diversified flora and fauna.

In the Neuquén Basin (Argentina), the species *Notosuchus terrestris*, *Araripesuchus patagonicus*, *Araripesuchus buitieraensis*, *Comahuesuchus brachybuccalis*, *Peirosaurus torminni*, *Lomasuchus palpeprobus*, *Cynodontosuchus rothi*, *Pehuenchesuchus enderi*, *Wargosuchus australis* and from Litoral Basin (Uruguay), *Uruguaysuchus asnarezi* and *Uruguaysuchus terrai* are found in red beds (Woodward, 1896; Rusconi, 1933). The Argentinean specimens occur in successions of massive coarse and medium-grained sandstones and conglomerates, fine sandstones, siltstones and mudstones deposited in fluvial environments under braided and meandering regimes (Leanza et al., 2004; Pol and Gasparini, 2007). *Araripesuchus patagonicus* from the Candeleros Formation occur in medium- to fine-grained sandstones with pelitic intraclasts in tabular bodies. Rapid sedimentation was interpreted from the presence of articulated specimens. The depositional environment was fluvial, subjected to a regime of sporadic seasonal flooding, in a climate with alternate rainy and dry periods (Ortega et al., 2000). In Uruguay (Litoral Basin, Guichón Formation), *Uruguaysuchus asnarezi* and *Uruguaysuchus terrai* are found in a succession of argillaceous fine sandstones, reddish, with climbing ripples, laminar and cross stratification, pedogenetic structures (root bioturbation) and carbonate nodules. There are also reddish and brown mudstones where *Uruguaysuchus* occur. Aguilar and Perea (2003) interpreted these deposits as fluvial bars and abandoned channels, in environmental conditions of low humidity.

The distribution of these faunas in South America, besides being controlled by the well-marked seasons, was also controlled by the regional tectonics. The drainage history of South America, as shown by Potter (1997), was subject to tectonic control first by regional uplifts and associated aulacogens and later (100 Ma) by colliding plates, which reversed paleoslopes on much of the South American platform. During the Early Cretaceous, the drainage in Patagonia (including Magallanes and Neuquén basins) was towards the paleo-Pacific and sediment source areas were to the East and North. A compressional tectonic event, related to the South America–Africa rifting, reversed the slope to the southeast, allowing a distinct connection of the fluvial network. Musacchio (2000), based on charophyte distribution, proposed that there was a break-down of the biogeographic isolation between the southern and northern regions of South America during the Aptian. The connections of the drainage system of southern Argentina and central South America (e.g. Bauru Basin) from the Aptian to the Late Cretaceous probably allowed the interchange of the crocodyliforms and the occurrence of common taxa of Peirosauridae (*Peirosaurus torminni*) and Baurusuchidae (*Cynodontosuchus rothi*) both in Argentina and Brazil (Gasparini et al., 1991, 2007). Also concerning the terrestrial groups, *Comahuesuchus brachybuccalis* (Argentina), according to Martinelli (2003) is closely related to *Malawisuchus mwakasyungutiensis* (Malawi) and to *Sphagesaurus huenei* (Brazil). Other terrestrial crocodyliforms such as the baurusuchids also indicate these relationships. Wilson et al. (2001) considered an Early Cretaceous, or even a Late Cretaceous Gondwanic 'terrestrial route' between South America and Indo-Pakistan via Antarctica, to explain the presence of this group in the Indian subcontinent (today, Asia). Later, during the Paleogene, their dispersal through Eurasia allowed them to reach North Africa and Iberia, an alternative and plausible 'land corridor' to the classic South America–Madagascar–Africa connection.

*Araripesuchus* sp. also exhibit a broad distribution, as they occur in Brazil, Argentina (South America), Cameroon, Morocco, Republic of Niger (Africa) and Madagascar. In the Mahajanga Basin (Madagascar), the Maastrichtian strata (Maevarano Formation, Anembalemba Member) that yield *Araripesuchus tsangatsangana*, *Simosuchus clarki* and *Mahajangasuchus insignis*, consist of complexly interbedded sandstones facies, that accumulated in a broad channel-belt system characterized by shallow flow and an ephemeral discharge regime prone to floods (Buckley et al., 2000; Turner, 2006; Turner and Buckley, 2008). The sandstone facies (massive sandstones poorly sorted), in which numerous bonebeds are generally found, is interpreted by Rogers et al. (2000) to represent events of rapid sediment dumping presumably during floods in aggrading channel belts. This signal of discharge variability, presumably reflects seasonality in the Late Cretaceous of northwestern Madagascar, in a climate marked by distinct rainy and dry seasons. The Malawi crocodyliform *Malawisuchus mwakasyungutiensis* comes from Aptian red beds of the Mwakasyunguti area, Karonga District (Gomani, 1997). In Cameroon (Koum Basin) the isolated teeth considered by Jacobs et al. (1990) to pertain to aff. *Araripesuchus* sp. are found in clastic sediments. All these fossils occurred in fluvial deposits, in an arid climatic belt during Lower Cretaceous as presented by Scotese (2005) (Krause et al., 1998; Krause et al., 2006).

*Pabweshi pakistanensis* from Pab Formation (Pakistan, Maastrichtian) is known from deposits of upwardly-fining sandstones, with poor sorting, where there is an upwardly-decreasing bed thickness, with trough cross-bedding. There are silty to muddy matrices in the upper part of the sandstones. This succession was interpreted by Wilson et al. (2001) as fluvial (overbank) deposits.

The wide extent of the Gondwanan landmass, even when it began to break up, implies that the interior of the continent was arid. Even in the absence of mountains, warm winds flowing landward lose their moisture over land because heating drives the air masses upward. Thus, in low latitudes, rainfall not only would have been seasonal, but also confined to coastal regions. Although the interior of a large continent would receive little precipitation at any latitude, climate would not be uniformly arid over the entire continent. At high latitudes, where temperatures are cooler and evaporation rates correspondingly lower, the climate may appear to have been humid, even though precipitation was relatively low. Conversely, at low latitudes, aridity will be more severe with low rainfall due to temperature and lower evaporation rates (Parrish, 1990).

Wherever the pattern of vicariance, dispersal and distribution of these terrestrial crocodyliforms, the paleoenvironmental conditions were similar. The main environmental control was certainly the arid climate. This could be reflected in the morphology and paleoecology of these crocodyliforms, which have lateral orbits, external nares placed anteriorly, differentiated teeth along the tooth row and erect limb posture. This anatomical pattern implies ambulatory, or even cursorial habits, in continental terrestrial environments (Vasconcellos et al., 2005; Vasconcellos and Carvalho, 2007).

## 5. Conclusions

Climate's role in the control of the fossil crocodyliform distribution has been generally neglected. The clues to understand the high diversification of the terrestrial crocodyliforms, with some 'bizarre' morphotypes, are related to the climatic pattern and to the paleogeographic models of Gondwanan evolution throughout the Cretaceous.

The marked seasonality, with distinct rainy and dry seasons, as interpreted for the deposits of distinct ages where the terrestrial Cretaceous crocodyliforms have been found, are indicative of stressed and fragile ecosystems.

Climatic interpretations using fossil crocodylians are based on the climatic tolerance of their extant relatives. Therefore, this uniformitarian approach may not be appropriate in the case of the fossil groups



of Gondwana. Basal *Notosuchia*, *Araripesuchus* and some *Sebecia* were clearly terrestrial animals, living in semi-arid environments markedly distinct from the swampy areas that are the preferred habitats of the amphibious extant crocodiles, gharials and alligators.

There is a distinct distribution pattern of the terrestrial crocodyli-form faunas throughout Cretaceous. The oldest ones are the small and omnivorous *Notosuchia* and *Araripesuchus*, found preferentially in Early Cretaceous deposits. They are followed by larger *Notosuchia* (baurusuchids, sphagesaurids) and *Araripesuchus*, and Sebecian peirosaurids, with specializations indicating active terrestrial predatory habits. Probably, they temporally succeed the Basal *Notosuchia* and *Araripesuchus* faunas. Those larger Crocodyliformes were in some way, a response to a significant environmental change, probably a hotter and drier climate in the Late Cretaceous Gondwanan landmasses.

The aridity, or maybe a seasonal warm and dry climate, that alternated with wetter periods, played a role, that has not yet been analyzed, that may explain the domain of these bizarre crocodylians in Gondwana during the Cretaceous.

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