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Pattern of biotic replacement in modern crocodiles during the Late Cretaceous

Patrones de reemplazamiento biótico en cocodrilos modernos durante el Cretácico Superior

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Abstract: The Late Cretaceous crocodylomorph record is revised in detail in order to examine the biotic replacement that characterises the appearance of the members of the Crocodylia clade. The percentages of crocodylian and non-crocodylian genera have been estimated by chronostratigraphic stage and by continent. The results show that there are a higher proportion of non-crocodylians genera (71%) in the Late Cretaceous. However, the percentage of Crocodylia increases from 6% in the Cenomanian - Santonian to 22% in the Campanian - Maastrichtian interval. Crocodylia have a pattern of expansive radiation, without involving a geographic shift of non-crocodylians crocodylomorph. The chronostratigraphic distribution of the crocodylian genera is mostly restricted to Campanian-Maastrichtian localities. Crocodylians have a non-uniform spatial distribution among continents. Two different patterns are distinguished: 1) Europe plus North America, characterised by a high proportion of Crocodylia, exceeding 50% of the total number of genera, and 2) Asia, South America and Africa, all of which have similar proportions, in which the crocodylians form less than 15% of the crocodylomorph assemblage. A large-scale expansive radiation and diversification of crocodylians is postulated for Europe and North America at the uppermost Cretaceous. The bulk of the biotic replacement occurs in the continental realm. The absence of continental members of Crocodylia in Asia, Africa and South America is significant because non-crocodylians are otherwise well-documented throughout the Upper Cretaceous. Taxonomic dissimilarity between continents is so high that no continental genera are shared between continents.

Key words: Crocodylia, biotic replacement, origin, Late Cretaceous.

Resumen: Se revisa en detalle el registro fósil de crocoylomorfos del Cretácico Superior con el fin de examinar el reemplazamiento biótico que supuso la aparición de los miembros del clado Crocodylia. Para ello se ha estimado cronoestratigráficamente y por continentes el porcentaje de crocodylianos (cocodrilos modernos miembros del "crown-group" Crocodylia) y de crocodylomorfos no-crocodylianos. En el Cretácico Superior hay una proporción elevada de géneros no-crocodylianos (71%). Sin embargo, el porcentaje de crocodylianos se incrementa de un 6% en el Cenomaniense-Santoniense a un 22% en el intervalo Campaniense-Maastrichtiense. Crocodylia se caracteriza por presentar una pauta propia de una radiación expansiva, que no implica el desplazamiento geográfico de los crocodylomorfos no-crocodylianos. La distribución cronoestratigráfica de los géneros de Crocodylia se restringe principalmente a localidades datadas como Campaniense y Maastrichtiense. Los crocodylomorfos no muestran una distribución espacial uniforme entre continentes. Se distinguen dos tipos de patrones: 1) Europa y Norte América, caracterizados por una alta proporción de géneros del clado Crocodylia, sobrepasando el 50% del número total de géneros, y 2) Asia, Sudamérica y Africa, todos con proporciones semejantes, donde Crocodylia representa menos del 15% del número total de géneros. Se propone para Crocodylia una radiación expansiva a gran escala localizada en Europa y Norte América hacia el final del Cretácico terminal. Este reemplazamiento biótico sucede en ambiente continental. La ausencia de miembros del clado Crocodylia en Asia, Africa y Sudamérica es significativa, ya que los no-crocodylianos están, por el contra, bien documentados a lo largo de todo el Cretácico Superior. Las disimilitudes taxonómicas entre continentes son tales que no se comparte ningún género.

Palabras clave: Crocodylia, reemplazamiento biótico, origen, Cretácico Superior.

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INTRODUCTION

After the first fossil-based zoogeographic model (Sill, 1968), which predated the acceptance of the concept of continental drift, other models tracing the historical divergence of living crocodilians were based on neontological studies that adopted physiological, parasitological and molecular approaches (Brooks, 1979; Taplin & Grigg, 1989; Densmore, 1983; Densmore & Owen, 1989; Densmore & White, 1991; Jackson et al., 1996). From these studies two alternative hypotheses were proposed, putting the time of divergence of modern crocodiles as being either in the Early or Late Cretaceous. This controversy has been resolved by recent phylogenetic analysis based on morphological and molecular data (Brochu, 1997a, 2001; Poe, 1996), placing the origin of the common ancestor or all modern crocodilians in the Late Cretaceous.

Modern crocodilians (the monophyletic group Crocodylia) comprise the three major lineages (Crocodyloidea, Alligatoroidea and Gavialoidea). The crocodyloids and the alligatoroids were undoubtedly present during the Late Cretaceous, but the evolutionary history of the third lineage, which gave rise to the gavials, is still debatable. Molecular data suggests that the divergence of the Gavialoidea did not occur earlier than the Late Tertiary, because of the position of *Gavialis* as a close relative of *Tomistoma.* On the other hand, morphological data, favours the basal position of the Gavialoidea, -with the genus *Thoracosaurus* being a close relative of *Gavialis*- in the Late Cretaceous (Molnar, 1994; Brochu, 1997a, 2001; Buscalioni et al., 2001), where *Gavialis*, is the sister taxon of the remaining modern crocodilians.

Markwick (1998) analysed the dynamic of the living crocodilian global diversity from their origin in the Cretaceous through the Cenozoic, with an examination of their spatial and temporal trends, based on a well documented data base of the crocodilian fossil and living species. The pattern of diversification of living crocodilians was intepreted as an initial exponential diversification through the Late Creta-ceous and Palaeocene (Markwick, 1998), originating in the northern hemisphere, Laurasia.

Late Cretaceous characterises a key period in the evolutionary history of living crocodilians. The origin of Crocodylia is a major macroevolutionary, and during this epoch a turn over event confronted the rise of diversity of Crocodylia (Alligatoroidea, Crocodyloidea and Gavialoidea) to the demise of the ancestral crocodilian species ("the mesosuchians") (Vasse & Hua, 1998; Markwick, 1998). Markwick's results are based on palaeoecological, stratigraphic and sedimentological data, demising any phylogenetic context. Cladistic phylogeny was not available to the level necessary, and instead he used a published 'traditional' classification scheme. In this paper we test recent hypotheses on the origin of modern Crocodylians using a robust phylogenetic context. This is the critical difference between the work did in Markwick (1998) and this study.

The Late Cretaceous crocodilian fossil record is here brought up to date and analysed in order to show a more complete scenario on the origin of modern crocodilians. First, we evaluate the quality of its fossil record, second, the shape of the biotic replacement. The pattern of the worldwide geographic distribution of the major clades of Crocodylomorpha during the late Cretaceous is analysed, with particular reference to the earliest genera of Crocodylia, and their spatial, ecological and chronostratigraphic distribution.

CROCODYLOMORPHA PHYLOGENY

The Crocodylomorpha are a monophyletic group that comprises the set of basal crocodylomorphs and the Mesoeucrocodylia. In figure 1 we depict a compound dendrogram gathering the taxonomically congruent phylogenies of Crocodylomorpha, and trying to render the greatest possible amount of terminal taxa (for the phylogenies used, see figure caption). The node Mesoeucrocodylia is defined by two major clades: Ziphosuchia plus (*Araripesuchus* + Neosuchia) (Ortega *et al*., 2000). The inclusion of the clades Ziphosuchia and Neosuchia is important, because it marks a drastic change in the explanation of their evolutionary history and the definition of "mesosuchians". One of our objectives is to check the extent that this dichotomy, implying the differentiation of two *a priori* independent evolutionary histories in Crocodylomorpha, would affect the final shape of the Late Cretaceous biotic replacement.

The clade Ziphosuchia consists of a set of sister groups whose terminal taxa are Cretaceous and Cenozoic species with mostly a gondwanan fossil record (Fig. 1, see also figure caption for the diagnosis of the clade). The clade Neosuchia, on the other hand, includes a set of successive sister groups, in which are pla-

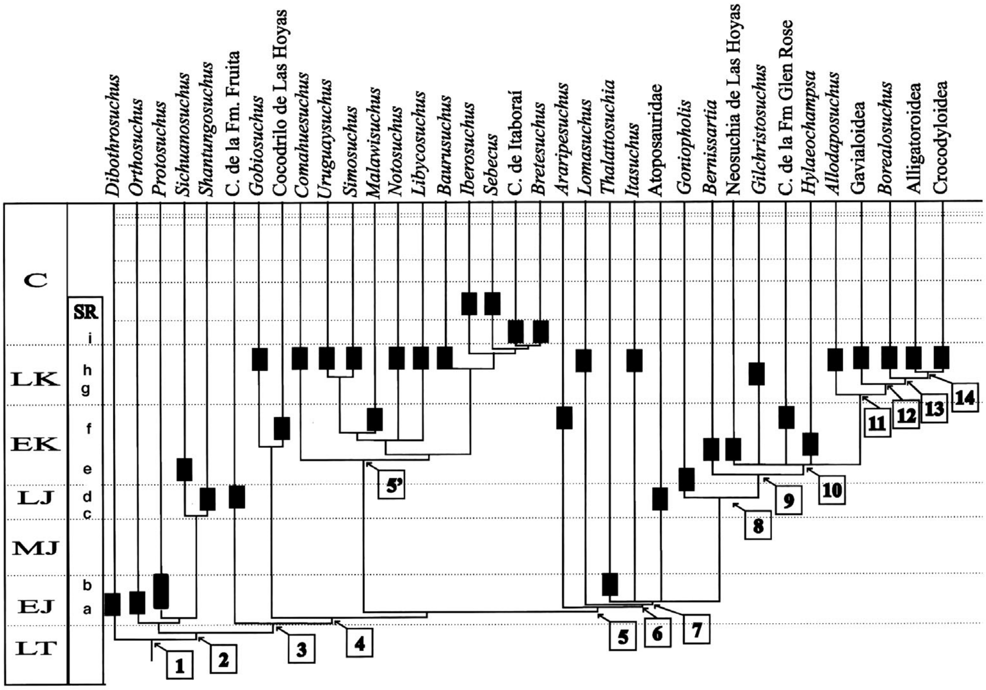

Figure 1.- Time-calibrated dendrogram between major Crocodylomorpha clades. The dendrogram is based on different phylogenetic hypotheses (Ortega et al., 2000; Buscalioni et al., 2001; Buckley et al., 2000). Black squares denote the first evidence for each terminal taxa. The branching order has been specified to fix the clade rank (represented in boxes: 1 to 14, see figure 3). Relevant nodes are: 1) Crocodylomorpha; 2) Crocodyliformes; 3) Mesoeucrocodylia; 5) Neosuchia; 5') Ziphosuchia; 11) Eusuchia; and 12) Crocodylia. On the left SR column specified the stratigraphic rank for each node (see figure 3): a) Sinemurian; b) Toartian; c) Oxfordian; d) Kimmeridgian; e) Berriasian-Barremian; f) Aptian; g) Coniacian, h) Santonian; and i) Campanian.

Figura 1.- Dendrograma calibrado temporalmente para los principales clados de Crocodylomorpha. El dendrograma se fundamenta en diversas hipótesis filogenéticas (Ortega et al., 2000; Buscalioni et al., 2001; Buckley et al., 2000). Los cuadrados negros señalan el primer registro de cada taxon terminal. El orden de divergencia (representado en cajetines del 1 al 14) se considera con el fin de fijar el grado dentro de los clados propuestos (véase figura 3). Los nodos mayores son: 1) Crocodylomorpha; 2) Crocodyliformes; 3) Mesoeucrocodylia; 5) Neosuchia; 5') Ziphosuchia; 11) Eusuchia, and 12) Crocodylia. En la columna de la izquierda (SR) se especifica el nivel estratigráfico para cada nodo: a) Sinemuriense; b) Toartiense; c) Oxfordiense; d) Kimmeridgiense; e) Berriasiense-Barremiense; f) Aptiense; g) Coniaciense, h) Santoniense; and i) Campaniense.

ced the stem-group of the living crocodilians, this latter defining the node Eusuchia (Fig. 1). The neosuchian fossil record extends from the Jurassic on, and its species had a cosmopolitan and Neopangeic distribution. Within Eusuchia, the term Crocodylia (according to Benton & Clark, 1988 and Brochu, 1997 a, b) designate just the crown-group composed by three major lineages of extant crocodylomorphs (Crocodyloidea, Alligatoroidea and Gavialoidea).

The phylogenetic pattern allows us to draft a scenario of the evolutionary history of the Crocodylomorpha. It can be pointed out that during the Late Cretaceous a broad spectrum of clades still persisted. The taxonomic differences are made up by a mixture of historical entities or members that belong to a wide range of clades: 1) the crocodyliform *Gobiosuchus*, 2) Ziphosuchia (*sensu* Ortega et al., 2000, node 5' in Fig. 1), 3) Neosuchia (node 5 in Fg. 1), and 4) its crown-group Crocodylia (node 12 in Fig 1). However, when the faunistic content is plotted against a Late Cretaceous palaeogeography, a spatial pattern emerges, each continent preserved part of the history of the crocodyliforms during the Late Cretaceous (see Fig. 2).

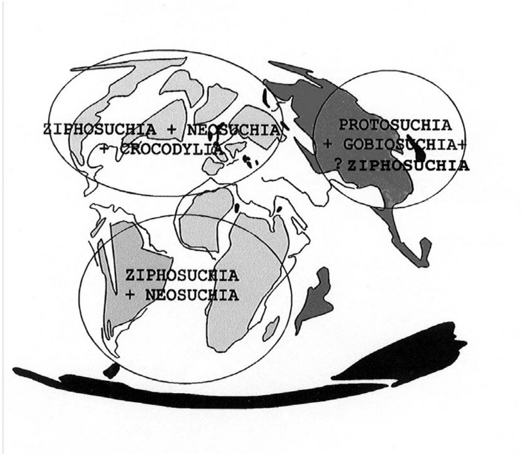

Figure 2.- Late Cretaceous palaeogeography (SMITH et al., 1994), and the distribution of Crocodylomorpha). Only has been considered genera from the continental realm. Note the absence of continental members of the clade Crocodylia in Africa, South America, Madagascar, and Asia. The crocodilian fossil record of India is ambiguous, and only represented by isolated teeth.

Figura 2.- Mapa paleobiogeográfico del Cretácico Superior (SMITH et al., 1994) donde se muestra la distribución de Crocodylomorpha. Se han considerado exclusivamente géneros de ambientes continentales. Nótese la ausencia de miembros del clado Crocodylia en Africa, Sudamérica, Madagascar y Asia. El registro fósil de cocodrilos en India es ambiguo y sólo está representado por dientes aislados.

It may be seen that *Gobiosuchus* is a relict of the Pangeic distribution of basal Crocodyliformes in Asia. Ziphosuchians are placed, according to "well-sampled" genera in Africa, Madagascar and South America. Isolated teeth with serrated margins (ziphodont teeth) have been described in the Maastrichtian inter-trappean beds of Naskal (India) (PRASAD & LAPPARENT DE BROIN, 2002). An endemic fauna has been postulated for these continents on several occasions (BONAPARTE, 1991, 1996). However, several authors recognise "notosuchian" relatives in Asia during the latest Cretaceous (EFIMOV, 1988), suggesting that Ziphosuchia were more globally distributed by then.

Neosuchians (excluding the members of Crocodylia) have a broad spatial distribution throughout the four continents analysed due to their early diversification in Pangea. One of the remarkable features dealing with the distribution of the continental genera in the Upper Cretaceous is that North America and Europe accommodate either the stem-group of Crocodylia and members of Crocodylia itself. Both *Hylaoechampsa* and *Allodaposuchus* are laurasiatic endemicities. Thus, regarding the phylogenetic hypothesis, probably an *in situ* radiation of Crocodylia occurred in Laurasia at the end of the Cretaceous.

CROCODYLOMORPHA AND THE QUALITY OF ITS FOSSIL RECORD

The compound dendrogram of Crocodylomorpha (gather other taxonomically congruent phylogenies, see figure 1 caption) is used to explore the quality of its fossil record. This will be achieved by means of a quantitative approach testing the congruence between the phylogenetic pattern and the crocodylomorph fossil record. We have followed the Spearman Rank Correlation method (NORELL & NOVACEK, 1992) to compare the fossil record completeness of crocodylomorphs, and that of its crown-group Crocodylia. Both explorative approaches give a significant correlation between the earliest record for each node, and the rank of derivation of the cladogram (Fig. 3).

Crocodylomorpha shows a good assessment on the quality of its fossil record ($S = 0.80$, $P<0.01$). From a comparative point of view the quality of the fossil record of Crocodylia is similar to that for other groups (e.g. Squamata in NORELL & NOVACEK, 1992). Node branching and fossil order fail throughout some Neosuchia clades (clade ranks 5 to 10). These stratigraphic mismatches may be detected on a calibrated phylogeny, revealing that the phylogenetic position of the marine crocodiles (Thalattosuchia) in

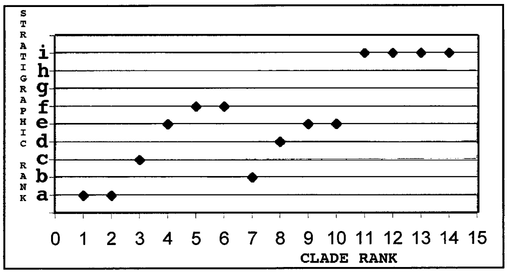

Figure3.- Resulting plot from the Spearman correlation between the clade rank (1 to 14 in x-axis) and stratigraphic rank (a to i in y-axis). Compare the result with data in figure 1.

Figura 3.- Diagrama resultante de la correlación no paramétrica de Spearman entre el grado dentro de los clados (1-14 en el eje x) y el nivel estratigráfico (a-i en el eje y). Compárese el resultado con la figura 1.

the dendrogram, and their low stratigraphic record (Lower Jurassic, Toarcian) is determinant in the output of the stratigraphic gaps. The calibrated phylogeny hypothesises a common mesoeucrocodylian (Ziphosuchia + (*Araripesuchus* +Neosuchia)) ancestor at least by the Early Jurassic. Thus, it may be concluded that the worst fossil record of Mesoeucrocodylia corresponds to the mid- Jurassic and very early Cretaceous periods, although they are fairly well represented throughout the mid (Barremian-Albian) and uppermost Cretaceous (Campanian-Maastrichtian). Its bias follows the same trend as seen in the entire continental tetrapod record, whose early Late Cretaceous records have relatively low values of metric completeness (Turonian: 21.6; Coniacian: 28.6; Santonian: 37.2) with respect to the two latest stages (Campanian: 84.7; Maastrichtian: 95.1; BENTON, 1987).

The fossil record of the basal eusuchians and Crocodylia, spanning from the Barremian to the Palaeocene, is congruent with its nodal pattern. The stratigraphic hiatus find on the calibrated phylogeny of Crocodylia reveals that there is a gap of about 30 million- years spanning from the Albian to the Campanian (Fig. 1). According to the phylogenetic pattern, this gap should affect the estimation of diversity of basal eusuchians (i.e. *Hylaeochampsa*, Las Hoyas crocodile, *Gilchristosuchus*, Glen Rose crocodile) since the timing of divergence of the closest relative of Crocodylia (*Allodaposuchus precedens*) is placed at the Campanian-Maastrichtian (BUSCALIONI et al., 2001), and members of the Crocodylia diversified throughout the Uppermost Cretaceous.

PATTERN OF THE BIOTIC REPLACEMENT OF CROCODYLIA

Research into Late Cretaceous vertebrates during the last ten years has yielded a better understanding of the terminal Cretaceous in the northern and southern continents (see RUSSELL, 1993, 1995, for sources of recent literature and taxa involved). Furthermore, the revision of old taxa is yielding a more comprehensive perspective of the world-wide diversity of Upper Cretaceous crocodilians (VASSE, 1993; NORELL et al., 1994; WILLIAMSON, 1996; SALISBURY & WILLIS, 1996; WU et al., 1996; BUSCALIONI et al., 1997; 1999; BROCHU, 1997b, 1999, 2001; VASSE & HUA, 1998).

THE DATA COLLECTED

New data based on revisions of the Upper Cretaceous fauna of South America, North America, Asia, Africa, Madagascar and Europe, spanning the Turonian to Maastrichtian, are presented in Tables 1 and 2. Unreliable or contentious evidence, such as that where classification was based on isolated teeth, has been omitted. Data have been collected at the specific level (Tables 1 and 2), although we consider them at the generic level to evaluate the biotic replacement.

To evaluate the biotic replacement we have compared two groups of crocodylomorphs; the Crocodylia, and the non-crocodylians, which have been divided into the clades comprising: gobiosuchians, ziphosuchians and the basal members of the neosuchia clade. Within all the Late Cretaceous Crocodylia there are three problematic genera: *Dolichochampsa*, *Aigialosuchus*, and the Stromatosuchidae. In order not to exclude any taxa, we have also considered them in the present evaluation, even though they do not influence the overall pattern of replacement.

Finally, genera are grouped into two categories to consider the environmental context of the replacement. We separate the coastal to marine inhabitants (including the long- and narrow-snouted thalattosuchians, pholidosaurids, dyrosaurids, tomistomids, gavials and thoracosaurians) from the remainder of the crocodylomorphs, which are characterised here as continental inhabitants. These categories are based on morpho-functional aspects of crocodilian anatomy, and the combination of the following features: large basioccipital tubera, large supratemporal fenestrae, a long tubular rostrum, and an extensive involvement of the splenial in the mandibular symphysis, has been taken as indicative for coastal to marine inhabitants (CLARK, 1986, BROCHU, 2001).

THE BIOTIC REPLACEMENT

A consideration of all genera suggests that a prolonged radiation of Crocodylia occurred during the Late Cretaceous. The proportion of total non-crocodylians (70.8%) is much greater than that of the Crocodylia (29.1%), and the absolute number of non-crocodylians increased in the uppermost Cretaceous (Table 3).

In figure 4 we plotted the number of genera against chronostratigraphic intervals. In terms of the biotic replacement, Crocodylia diversified in an expansive

EUROPE. Number of genera: 4. Cen-Sa=0; Ca-Maa=4

TAXON	AGE (LOCALITY)	COUNTRY
Acynodon lopezi, A. iberoccitanus (AL)	Ca-Maa (Quintanilla del Coco, Laño, Fox Amphoux)	Spain, France and Romania
Aigialosuchus villandensis (UND)	Maa	Scantia
Thoracosaurus Maacrorhynchus, Th. Neocesarensis (GA)	Maa. (Saint Pierre, Maaastrich)	Netherlands, Belgium and France
Musturzabalsuchus buffetauti (=*C. affuvelensis) (AL)*	Ca-Maa (Laño, Fuveau)	Spain and France

NORTH AMERICA Number of genera: 8 Cen-Sa=0; Ca-Maa=8

TAXON	AGE (LOCALITY)	COUNTRY
? *Brachychampsa sealeyi (AL)*	Ca.	USA-New Mexico
Brachychampsa montana (AL)	Maa (Hell Creek beds)	USA-Dakota and Montana
Albertochampsa langstoni (AL)	Ca (Judith. River Fm.)	Canada
Stangerochampsa mccabei (AL)	Maa (Morshoe Fm.)	Canada
Deinosuchus rugosus, D. riograndensis, D. (=*Phobosuchus) hatcheri (AL)*	Ca (Gulf of Mexico, Aguja Fm, and Judith River Beds)	Mexico, USA-Texas and Montana
Bottosaurus (=?*Brachychampsa) perrugosus B.* (=?*Brachychampsa) harlani (AL)*	Ca-Maa (OldMaan Fm, Greensands.)	Canada-Alberta and USA-New Jersey
Thoracosaurus neoCensarensis (GA)	Maa (Greensands)	USA-New Jersey
Thoracosaurus (=*Holops) brevispinus (GA)*	Maa (Greensands)	USA-New Jersey
Prodiplocynodon langi (CO)	Maa (LanCen Fm.)	USA-Wyoming
Leidyosuchus canadensis (= *L. gilmorei) (AL)*	Ca (Judith River Fm, OldMaan Fm.)	Canada-Alberta
Leidyosuchus sp. (AL)	Maa (Fox Hill Fm.)	USA-North Dakota
Borealosuchus (=*Leidyosuchus) sternbergii (BC)*	Maa (LanCen Fm.)	USA-Wyoming

ASIA. Number of genera: 1. Cen-Sa=0; Ca-Maa=1

TAXON	AGE (LOCALITY)	COUNTRY
EotomistoMaa multidentata (=*Thoracosaurus petrolica)* (GA)	Ca-Maa (Inner Mongolia)	China

SOUTH AMERICA. Number of genera: 1. Cen-Sa=0; Ca-Maa=1

TAXON	AGE (LOCALITY)	COUNTRY
Dolichochampsa miniMaa (UND)	Maa (Salta-Jujuy)	Argentina and Bolivia

AFRICA.Number of genera: Cen-Sa=1; Ca-Maa=0

TAXON	AGE (LOCALITY)	COUNTRY
?Thoracosaurus cherifiensis (GA)	Co-Tu	Morocco

Table 1.- Late Cretaceous Crocodylia .
Tabla 1.- Crocodylia del Cretácico Superior.

Tabla 2.- Late Cretaceous non-crocodylian crocodiles.
Tabla 2.- Cocodrilos no-cocodrilianos del Cretácico Superior.

Abbreviations: Cen, Cenomanian; Tu, Turonian; Co, Coniacian; Sa, Santonian; Ca, Campanian; Maa, Maastrichtian. In brackets is added the phylogenetic group of each taxa: AL, Alligatoroidea, CO, Crocodyloidea; GA, Gavialoidea; BC, basal Crocodylia; UND, undetermined; N, Neosuchia; Z, Ziphosuchia; P, Protosuchidae.

Source of data: **Europe** Astibia et al., 1987, 1990, 1999; Buffetaut, 1978, 1979a, 1980, 1989; Buffetaut & Pouit, 1994; Buffetaut et al., 1981; Buscalioni et al., 1997, 1999; Koken, 1888; Le Loeuff, 1991; Laurent et al., 2000; Mulder, 1997; Mulder et al., 1998; Nopcsa, 1915, 1923; Persson, 1959;. Pol et al., 1992; Sigé et al., 1997; Troxell, 1925; Vasse, 1993, 1995.

North America: Archibald & Bryant, 1990; Brochu, 1997 a, b, 1999, 2001; Carpenter, 1983; Colbert, 1954; Denton et al., 1994; Erickson & Brochu, 1999; Gilmore, 1910; Lucas & Sullivan, 1986; Norell et al., 1994; Mook, 1925, 1941; Rodriguez de la Rosa, 1996; Sahni, 1972; Schwimmer & Williamns, 1996; Sankey, 1996; Williamson, 1996; Wu et al,. 1996, 2001; Young-Nam, 1997.

Asia: Efimov, 1988; Konzhukova, 1954; Kordikova et al., 1996; Malone, 1979; Mook, 1924; ; Osmolska, 1972;Rana, 1990; Shuonan et al., 1985; Young, 1964; Steel, 1973; Storrs & Efimov, 2001; Taplin & Grigg, 1989. **South America**: Bertini, 1994; Gasparini et al., 1991, 1993, Gasparini, 1996; Gasparini & Buffetaut, 1980; Price, 1950 a,b;. Almeida Campos et al., 2001; Riff & Kellner, 2001.**Africa and Madagascar**: Buffetaut, 1974, 1979b, 1994, 1985; Buffetaut et al., 1990; Buckley & Brochu, 1996; Krause et al., 1999; Nopcsa, 1926; Stromer, 1914; Sereno et al., 1996; Sues, 1980.

EUROPE. Number of genera: 5. Cen-Sa=.2; Ca-Maa=4

TAXON	AGE (LOCALITY)	COUNTRY
?Dyrosaurid (N)	Cen-Ca-Maa (Nazare, Aveiro)	Portugal
Allodaposuchus precedens (N)	Ca-Maa (Valioara, Armuña, Tremp, Bellevue)	Romania, Francen and Spain
Doratodon cacharidens (Z)	Ca (Gosau Fm., Valiora)	Austria and Romania
Terminonaris (=Teleorhynus browni) (N)	Cen	Germany
Ischyrochampsa meridionalis(N)	Ca-Maa (St. Estève-Janson)	Francen

NORTH AMERICA. Number of genera: 5. Cen-Sa=3; Ca-Maa=3

TAXON	AGE (LOCALITY)	COUNTRY
Hyposaurus rogersii(N)	Ca-Maa (Greensand Fm.)	USA-New Jersey and Alabama
Terminonaris robusta (=Teleorhynus mesabiesis) (N)	Tu (Benton Shale, Coleraine Fm, Favel Fm..)	USA-Montana, Minnesota, Saskatchewan
Gilchristosuchus palatinus(N)	Sa-Ca (Milk River Fm.)	Alberta-Canada
Goniopholididae(N)	Ca (Cenrro del Pueblo Fm.)	Mexico
Goniopholis kirtlandicus(N)	Maa (Kirtland Fm.)	USA-New Mexico
Woodbinesuchus byersMaauriCeni(N)	Cen (Woodbine Fm.)	USA-Texas

ASIA. Number of genera: 5. Cen-Sa=3; Ca-Maa=3

TAXON	AGE (LOCALITY)	COUNTRY
Kanjasuchus extensus; K. borealis(N)	Tu-Sa (Dzhara-Khudduk, and Fergana Basin)	Uzbekistan, Tadzhikistan
Turanosuchus aralensis(N)	Tu-Sa	Mongolia and Kazakhstan
Gobiosuchus kielanae; G. parvus(G)	Ca (Djadokhta Fm.)	Mongolia
Artzosuchus brachyCenphalus (P or Z)	Ca (Djadokhta)	Mongolia
Shamosuchus djadochtaensis ;S. Maajor; S. gradilifrons; S. Ulgicus; S. anCenstralis; S. ulanicus; S. tersus S. borealis, S. karakalpakensis; S. Occidentalis(N)	Tu-Maa	Uzbekistan, Sheichdzheili, Dzharakhuduk, Mongolia

SOUTH AMERICA. Number of genera: 13. Cen-Sa=4; Ca-Maa=11

TAXON	AGE (LOCALITY)	COUNTRY
Notosuchus terrestris(Z)	Co-Sa (Neuquén)	Argentina
Comahuesuchus brachibuccalis(Z)	Co-Sa (Neuquén)	Argentina
Uruguaysuchus aznarezi(Z)	Sa-Ca (Guichón)	Uruguay
Uruguaysuchid gen et sp nov. *(Z)*	Ca-Maa (AdaMaantina Fm.)	Brazil
Peirosaurus torminni(N)	Co-Maa (Minas Gerais, Neuquén)	Brazil and Argentina
Lomasuchus palpebrosus(N)	Co-Maa (Neuqén)	Argentina
Stratiotosuchus Maaxhechti (Z)	Ca-Maa (AdaMaantina Fm.)	Brazil
Hyposaurus derbianus(N)	Maa (Pernambuco)	Brazil
Cynodonthosuchus rothi(Z)	Ca-Maa (Neuquén)	Argentina
Brasileosaurus pachecoi(Z)	Ca-Maa (AdaMaantina Fm.)	Brazil
Sphagesaurus huenei(Z)	Ca-Maa (AdaMaantina Fm.)	Brazil
Itasuchus jesuinoi(N)	Ca-Maa (Peiropolis)	Brazil
Baurusuchus pachecoi(Z)	Ca-Maa (AdaMaantina Fm.)	Brazil
Baurusuchus n. sp. *(Z)*	Ca-Maa (Maarilia Fm.)	Brazil
?Goniopholis paulistanus(N)	Ca-Maa (AdaMaantina Fm.)	Brazil

AFRICA. Number of genera: 6 Cen-Sa=5; Ca-Maa=1

TAXON	AGE (LOCALITY)	COUNTRY
Dyrosaurus sp (N)	Cen	North Sudan and Egypt
Sokotosuchus ianwilsoini (N)	Maa (Sokoto)	Nigeria, Egypt and Morocco
Libycosuchus brevisrostris(Z)	Cen (Baharija)	Egypt
Aegyptosuchus peyeri(N)	Cen (Baharija)	Egypt
Trematochampsa taqueti(N)	Sa	Niger
HaMaadasuchus rebouli(Z)	Cen (HaMaada)	Morocco
Stomatosuchus inermis(N)	Cen (Baharija)	Egypt

MAADAGASCAR. Number of Genera: 4. Cen-Sa=0; Ca-Maa=4

Trematochampsa oblita(N)	Ca (Maevarano Fm.)	Madagascar
Mahajangasuchus(N)	Ca	Madagascar
Simosuchus clarki (Z)	Ca	Madagascar
Araripesuchus sp. *(N)*	Ca (Maevarano Fm.)	Madagascar

	Absolute number of genera	Cenomanian to Santonian	Campanian to Maastrichtian
Non-crocodylians	34	16	21
Crocodylians	14	1	14

Table 3.- Total number of Late Cretaceos crocodylomorphs.
Tabla 3.- Número total de crocodilomorfos del Cretácico Surperior.

radiation during the Campanian-Maastrichtian transition, nonetheless, there was not a concomitant extinction of the non-crocodylians. It is shown that the K/T affected both groups, non-crocodylians decreased in the number of genera, whereby most Crocodylia genera were replaced by new ones during the Paleocene (see the figure 4 caption for the taxa involved in the graphic, also MARKWICK 1998).

CHRONOSTRATIGRAPHIC DISTRIBUTION

Our knowledge of the early history of the Crocodylia is biased. When evaluated by stage, the crocodylians represent 6.25% of the total genera in the Cenomanian-Santonian interval (only 1/16), and 21.53% in the Campanian-Maastrichtian interval, in which the relative number of non-crocodylians decreases. The entire Late Cretaceous crocodilian fossil record is mainly if not totally from Campano-Maastrichtian localities (Table 3).

The bias is especially noticeable in North America and Europe, where the record of Crocodylia is absent throughout the Cenomanian and Santonian, and the non-crocodylians are represented by just two species (*Gilchristosuchus palatinus* and *Woodbinesuchus byermauricei*) . The Cenomanian and Santonian fossil record is better represented in Asia, Africa and South America. However, the absence of crocodylians is of particular significance in these continents since non-crocodylians are otherwise well-documented (Table 4). This presents us with another peculiarity of the crocodilian Upper Cretaceous record: its biogeographic heterogenity.

SPATIAL PATTERN OF DIVERSIFICATION

A closer evaluation of the percentages of crocodylians and non-crocodylians by continent reveals that the Late Cretaceous crocodilian faunal assemblage is not uniformly distributed. Two different patterns of proportions emerge from a classification of the data

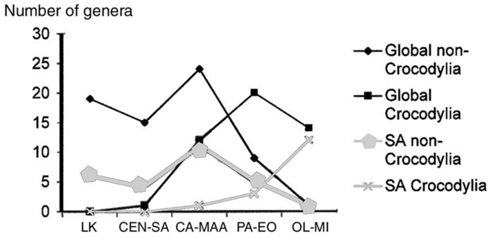

Figure 4.- Diversity throughout the Cretaceous and Miocene according with world-wide and South American Crocodylomorpha genera. Genera that have been regarded for the elaboration of the graphic: **LK non-crocodylians**: *Edentosuchus*; *Uñasuchus*; Glen Rose crocodile; *Montsechosuchus*; *Bernissartia*; *Araripesuchus*; *Meridiosaurus*; *Itasuchus*; *Amargasuchus*; *Dzungarisuchus*; *Sarcosuchus*; *Teleorhinus*; *Oweniasuchus*; *Vectisuchus*; *Theriosuchus*; *Goniopholis*; *Pholidosaurus*; *Dakosaurus*; *Hylaeochampsa*. The Cenozoic selected genera are just to indicate the chief lines of the structure of the biotic replacement, and do not represent a detailed list of the real diversity. **PA-EO non-crocodylians**: *Phosphatosaurus*; *Sebecus*; *Ilchunaia*; *Dyrosaurus*; *Bretesuchus*; *Iberosuchus*; *Bergisuchus; Wannosuchus*; *Rhabdognathus*. **PA-EO crocodylians**: *Necrosuchus*; *Eocaiman*; *Allognathosuchus*; *Maroccosuchus*; *Wannaganosuchus*; *Planocrania*; *Akantosuchus*; *Leidyosuchus*; *Atlantosuchus*; *Ceratosuchus*; *Brachyuranochampsa*; *Diplocynodon*; *Asiatosuchus*; *Arambourgia*; *Pristichampsus*; *Eogavialis*; *Dollosuchus*; *Crocodylus*; *Tomistoma*; *Procaimanoidea*. **OL-MI non-crocodylians**: *Sebecus* **OL-MI crocodylians**: *Hispanochampsa*; *Alligator*; *Caimanoidea*; *Gavialis*; *Caiman*; *Diplocynodon*; *Allognathosuchus*; *Crocodylus*; *Tomistoma*; *Rhamphostomopsis*; *Hesperogavialis*; *Gavialoidea*; *Euthecodon*; *Mourasuchus*.
Abbreviations: LK, Late Cretaceous; PA, Paleocene; EO, Eocene; OL, Oligocene; MI, Miocene.
Figura 4.- Diversidad estimada a lo largo del Cretácico y Mioceno del registro mundial y Sudamericano de Crocodylomorpha. Los géneros reseñados son los considerados para la elaboración de la gráfica. Los géneros seleccionados del Cenozoico no incluyen toda la diversidad conocida y sólo muestran las directrices del reemplazamiento biótico.
Abreviaturas: LK, Cretácico superior; PA, Paleoceno; EO, Eoceno; OL, Oligoceno; MI, Mioceno.

CONTINENTS	Turonian-Santonian	Campanan-Maastrichtian
EUROPE	**2**	**8**
NORTH AMERICA	**3**	**11**
ASIA	**3**	**4**
SOUTH AMERICA	**4**	**12**
MADAGASCAR	**0**	**4**
AFRICA	**5**	**2**

CONTINENTS	Turonian-Santonian		Campanan-Maastrichtian	
	NON-CRO	**CROCODYLIA**	**NON-CRO**	**CROCODYLIA**
EUROPE	**2**	**0**	**4**	**4**
NORTH AMERICA	**3**	**0**	**3**	**8**
ASIA	**3**	**0**	**3**	**1**
SOUTH AMERICA	**4**	**0**	**11**	**1**
MADAGASCAR	**0**	**0**	**4**	**0**
AFRICA	**5**	**1**	**1**	**1**

TABLE 4.- a. Total number of Late Cretaceous crocodylomorphs genera per continents and stages. b. Total number of Late Cretaceous genera phylogenetically arranged (non-crocodylia and crocodylia) per continents and stages.
Tabla 4.- a. Número total de géneros de crocodilomorfos por continente y piso. b. Número total de géneros ordenados filogenéticamente (no-crocodylia y crocodylia) por continente y piso.

by continent: Europe and North America, and Asia, South America and Africa. Europe and North America are characterised by a high proportion of Crocodylia, comprising more than 50% of the total crocodilian fauna. On the other continents (Asia, South America and Africa), the number of Crocodylia did not exceed that of non-crocodylians: the latter constituted more than 80% of the total crocodilian assemblage.

The expansive radiation has a geographical component. The European and North American pattern of Crocodylia expansion occurred in a large-scale event broadly differing form Asia, South America and Africa. This conclusion confirms the results based on a recent analysis of crocodilian diversity carried out by MARKWICK (1998). Therefore, Europe and North America reflect the expansion and diversification of Crocodylia earlier than do Asia, Africa and South America. Of these latter three, South America is the only continent that maintains a high proportion of non-crocodylians (more than 60%) in its faunal assemblage up to the end of the Eocene (see data in GASPARINI, 1996, and Fig. 4). The final replacement of the primitive fauna by Crocodylia did not occur until the Oligocene-mid Miocene.

THE MAGNITUDE OF THE REPLACEMENT: ITS REALM AND TAXONOMIC DISSIMILARITY

The magnitude of the large-scale biotic replacement is significant in the continental realm mainly restricted to freshwater and transitional depositional environments. Members of the clade Crocodylia became the predominant elements in the northern hemisphere assemblage (e.g., *Borealosuchus* (=*Leidyosuchus canadensis*) and the alligatoroids), specifically in North America and Europe. The expansion of Crocodylia appears to have been a small-scale event in Asia, South America and Africa based exclusively on the presence of coastal dweller members (*Hyposaurus*, *Thoracosaurus* and *Dolichochampsa*) and the lack of continental members of Crocodylia (Table 5).

The Late Cretaceous crocodilian assemblage is characterised by very great taxonomic dissimilarity at the generic level (Table 5). The only genera common to continents are the coastal ones (e.g., the dyrosaurids occur in Europe and Africa, *Hyposaurus* occurs in North America and South America, and the crocodylian gavialoid *Thoracosaurus* occurs in North America, Europe, Asia and Africa). There is a worldwide distribution of coastal organisms, however, dyrosaurids tend to be placed in the Tethys realm in both hemispheres, while thoracosaurids occur at a higher latitude in the northern hemisphere, with the exception of *Thoracosaurus cherifiensis* (from the Kem Kem Formation in southern Morocco, LAVOCAT, 1955; SERENO et al., 1996), which is a long-known but unrevised species, and probably it is not a member of the Crocodylia at all (Broin de Lapparent, pers.com.). In Europe the distribution of *Thoracosaurus* is grounded on the localities of the northern landmasses (Belgium, Holland, France and Denmark, see Table 1).

Continental genera do not occur on more than one continent, implying that there were no invasive radiations between them. Regional endemism composed of non-crocodylians has been postulated for the southern continents after the mid-Mesozoic (MOLNAR, 1994, GASPARINI, 1996). None of the South American genera is present in Africa. Nonetheless, the data show that endemicity can also account for the continental members of Crocodylia and for the non-crocodylians in North America, Europe and Asia.

The continental assemblages of North America and Europe were highly diversified into distinct genera during the Upper Cretaceous. This trend of endemicity, despite the turn-over event at the K/T boundary, continues throughout the Paleocene and Eocene, with little resemblance between European and North American continental crocodilian faunas during the Tertiary (NOVACEK et al., 1991).

CROCODYLOMORPHA ASSEMBLAGE DURING THE LATE CRETACEOUS: BIOGEOGRAPHIC IMPLICATIONS

North America and Europe encompass all the basal members of Crocodylia (*Borealosuchus*, BROCHU 1997 b) and the early crocodyloid *Prodiplocyno-*

CONTINENTS	Non-crocodylian		Crocodylian	
EUROPE	**5**	**3**	**4**	**2**
NORTH AMERICA	**5**	**3**	**8**	**7**
ASIA	**5**	**4**	**1**	**0**
SOUTH AMERICA	**13**	**11**	**1**	**0**
MADAGASCAR	**4**	**4**	**0**	**0**
AFRICA	**6**	**5**	**1**	**0**
	Total	Continental	Total	Continental

	AFRICA	EUROPE	ASIA	NORTH AMERICA	SOUTH AMERICA
AFRICA	**-**				
EUROPE	**2**	**-**			
ASIA	**1**	**1**	**-**		
NORTH AMERICA	**1**	**2**	**1**	**-**	
SOUTH AMERICA	**0**	**0**	**0**	**2**	**-**
MADAGASCAR	**1**	**0**	**0**	**0**	**0**

able 5: a. Total number of Late Cretaceous crocodylomorphs genera compared with continetal ones per continent. b. Shared Late retaceous crocodilian genera among continents.

Table 5: a. Total number of Late Cretaceous crocodylomorphs genera compared with continetal ones per continent. b. Shared Late Cretaceous crocodilian genera among continents.

Tabla 5.- a. Número total y continental de géneros de crocodilomorfos por continente. b. Numero de géneros de crocodilianos del Cretácico Superior compartidos entre continentes.

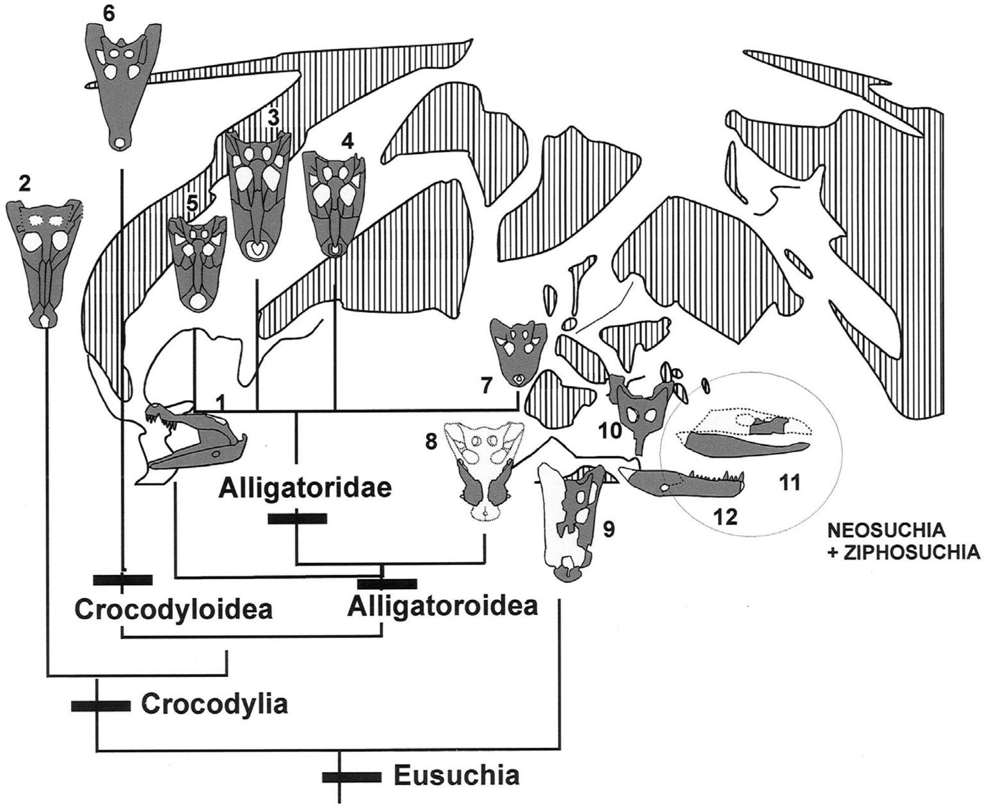

Figure 5.-North America and Europe palaeogeography. Only continental genera have been represented in the figure: 1, *Deinosuchus*; 2, *Borealosuchus*; 3, *Albertochampsa*; 4, *Stangerochampsa*; 5, *Brachychampsa*; 6, *Prodiplocynodon*; 7, *Acynodon*; 8, *Musturzabalsuchus*; 9 and 10, *Allodaposuchus*; 11, *Doratodon*; 12, *Ischyrochampsa*.
Members of Eusuchia and Crocodylia have been ordered according their phylogenetic relationships. Note that more than the 50% of the taxa belong to the clade Alligatoroidea. Only two of the continental genera belong either to non-eusuchian Neosuchia (12) or Ziphosuchia (11).
Figure 5.- Paleogeografía de Norte América y Europa. Sólo los géneros procedentes de ambientes continentales se han representado en la figura. Los miembros de Eusuchia y Crocodylia se han ordenado según sus relaciones filogenéticas. Nótese que más del 50% de los taxa pertenecen al clado Alligatoroidea. Sólo dos de los géneros procedentes de ambientes continentales pertenecen a Neosuchia (no eusuquianos) (12) o a Ziphosuchia (11).

don (BROCHU, 1997 b), and the alligatoroids (*Brachychampsa*, *Stangerochampsa*, *Leidyosuchus canadensis*, *Deinosuchus*, *Acynodon*, *Musturzabalsuchus* and *Albertochampsa*). Alligatoroids were highly diversified into distinct genera by the uppermost Cretaceous, forming more than the 50% of the crocodylian genera. In the continental realm, an *in situ* radiation of the alligatoroid Crocodylia occurred in Laurasia at the end of the Cretaceous. The relationship of the North American and European alligatorids suggests the existence of a common ancestor placed in a single area (Fig. 5).

Asia represents a special case. It is a northern continent, and interchanges of faunas between North America and Asia have been repeatedly recorded (e.g., hadrosaurs, ceraptosians, ankylosaurs, tyrannosaurs, and dromeosaurs, see HALLAM, 1994). However, there is no record of continental members of Crocodylia in Asia. Alligatorids do not reach Asia until the Paleocene (*Eoalligator chunyii* YOUNG, 1964). Until now, evidence of Late Cretaceous alligatorids based on isolated teeth from China is unreliable

"Alligatorids" isolated teeth from the Indian Deccan (RANA, 1990) have been also used as the combined

PERCENTAGES	NUMBER OF GENERA	GROUPS
8.3	**1**	BASAL CROCODYLIA[1]
58.4	**7**	ALLIGATOROIDEA[2]
8.3	**1**	CROCODYLOIDEA[3]
8.3	**1**	GAVIALOIDEA[4]
16.7	**2**	UNDETERMINED [5]

1: *Borealosuchus*; 2: *Leidyosuchus canadensis, Deinosuchus; Albertochampsa; Brachychampsa; Stangerochampsa; Acynodon; Musturzabalsuchus*. 3: *Prodiplocynodon*. 4: *Thoracosaurus*. 5: *Dolichochampsa; Aigialosuchus*.

Table 6.- Crocodylian Late Cretaceous genera by groups
Tabla 6.- Géneros de cocodrilianos del Cretácico Superior ordenados por grupos.

evidence with pelobatid frogs from the Talli Formation, and paleoryctid mammals in the intertrappean beds of Asifabad, to imply the existence of a dispersal corridor for faunal interchange between Asia and India near the Cretaceous-Tertiary boundary (Sahni et al., 1982; Jaeger et al., 1989; Prasad & Sahni, 1988; Rana, 1990; Prasad et al., 1995). The presence of Upper Cretaceous alligatorids in India is spurious evidence since it is based on these isolated elements (the same opinion is shared in a recent contribution of Prasad & Lapparent de Broin (2002) based on a detailed study of isolated teeth from the Maastrichtian of Naskal in India). "Alligatorid" voluminous crushing teeth, might belong to advanced neosuchians (e.g., *Shamosuchus* already recorded in Asia). The Indian Late Cretaceous crocodilian fauna is not determinant because of its fragmentary nature, concerning crocodylomorphs, it may share Asiatic or Madagascar elements.

Some authors have suggested that Africa boasted a faunistic profile similar to that of South America by the end of the Cretaceous (Buffetaut & Rage, 1993). This is based on putative phylogenetic relationships between some African (*Libycosuchus* and trematochampsids) and South American (related to the notosuchids and the peirosaurids, respectively) taxa (see also Gasparini, 1996). The strongest paleobiogeographic relationships between Africa and South America is based on the notosuchids. In recent phylogenetic analyses (Ortega et al., 1995; Ortega et al., 2000) (Fig. 1), *Notosuchus, Sphagesaurus* and *Libycosuchus* have been postulated as being members of the clade Ziphosuchia, suggesting a common Gondwanan ? Jurassic ancestor . On the other hand, *Trematochampsa*, and peirosaurids (*Peirosaurus*, *Lomasuchus*) do not constitute a monophyletic group, but are members of the Neosuchia clade (see also Buckley at al., 1999). Recent discoveries in Madagascar (Krause et al., 1999) sketch a Late Cretaceous crocodilian fauna similar to that of Africa and South America.

This Late Cretaceous scenario implies the appearance of Crocodylia in South America and Asia Tertiary as invasive radiations. This is consistent with the first Paleocene records of alligatorids. The invasive radiations of Alligatoridae gave rise to the modern lineage of caimans and to the bizarre extinct nettosuchians (the first occurrence is *Eocaiman*, Simpson, 1933; Estes & Baez, 1985) in South America during the Cretaceous-Paleocene transition (Pascual et al., 1996) when South America may have been in intermittent contact with North America.

CONCLUSIONS

The analysis of the biotic replacement of Crocodylia shows that explanation of the actual geographic distribution of modern crocodiles (Alligatoridae, Crocodylidae and Gavialidae) is not straight forward. Although recent crocodiles extend nowadays along a circumtropical ring, the earliest members of the clade Crocodylia originate in the northern continents of North America and Europe. The burst of their radiation appears associated to the continental realm. The continental assemblages of North America and Europe were highly diversified into distinct genera as a result of vicariant events (Buscalioni et al., 1997) during the uppermost Cretaceous. This trend of endemicity continued throughout the Paleocene and Eocene, with little resemblance between European and North American continental crocodilian faunas during the Tertiary.

This Late Cretaceous scenario here drawn allows us to establish the following implications and predictions:

1) Phylogenetically, the basal members of Crocodyloidea, Alligatoroidea and Alligatoridae should be Laurasiatic in origin.

2) The absence of crocodylians in Asia, South America, Madagascar and Africa is significant and it is not due to biases.

3) The first appearances of crocodylians in South America and Asia should be invasive radiations.

Crocodylia had a prolonged radiation that began during the uppermost Cretaceous and spanned up to the Paleocene-Eocene. There was not neither a concomitant extinction nor a geographic shifting of non-crocodylians throughout this radiation, even in those areas inhabited by crocodylians and non-crocodylians. Late Cretaceous localities in Europe have recorded associations (not based on isolated teeth) between earliest members of Crocodylia and ziphosuchians (i.e. Chera in Spain (Company et al., 1999) and in Gosau Formation in Austria (Company et al, in prep.). Also, has been discovered the presence of non-crocodylian neosuchia coexisting with earliest members of Crocodylia (e.g. Milk River Formation in Canada, Wu & Brinkman, 1993). These associations suggest that there was not a competitive exclusion between crocodylomorphs along the biotic replacement. Instead, the coexistence reveals distinct ecological, physiological and/or morphological capacities in resource partitioning.

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