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THE OLDEST AFRICAN CROCODYLIAN: PHYLOGENY, PALEOBIOGEOGRAPHY, AND DIFFERENTIAL SURVIVORSHIP OF MARINE REPTILES THROUGH THE CRETACEOUS-TERTIARY BOUNDARY

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ABSTRACT—A gavialoid crocodylian from the Maastrichtian of the Oulad Abdoun phosphatic Basin (Morocco) is described, representing the oldest known crocodylian from Africa. The specimen consists of a skull that exhibits several features not found in other gavialoids, and a new genus and species is erected, *Ocepesuchus eoafricanus*. A phylogenetic analysis has been conducted including 201 characters and 71 taxa, where *Ocepesuchus eoafricanus* appears as the most basal African gavialoid, and the South American gavialoids are paraphyletic. This paraphyly has strong biogeographic implications, and the previous hypothesis of South American and Asian assemblages derived from African gavialoids should be reviewed. The historical biogeography of Gavialoidea is probably more complex than previously supposed. The phosphatic deposits of Morocco provide a unique opportunity to study the vertebrate faunal turnover across the Cretaceous-Tertiary (KT) boundary. The crocodyliforms are very scarce in the Maastrichtian marine basins of Africa which are dominated by mosasaurid squamates. The latter became extinct by the KT boundary, while crocodyliforms survived and diversified in the Paleocene. Mosasaurids and crocodyliforms both lived in probably comparable marine environments during the Maastrichtian. The selectivity of the KT boundary extinctions remains to be explained; since freshwater environments are known for having been less affected by the KT crisis than marine ones, a freshwater lifestyle of the juveniles, like in extant marine crocodiles and unlike the fully marine mosasaurs, could explain this difference with regard to survivorship.

INTRODUCTION

Living crocodylians (gavials, alligators and crocodiles) are only part of a larger group, the crocodyliforms that includes an important number of extinct forms. The earliest crocodylians are known from the Late Cretaceous (80 million years (myr)) of North America and Europe, but the oldest known African crocodylian known to date was the 63 myr-old gavialoid *Argochampsa krebsi* from the Paleocene of Morocco (Hua and Jouve, 2004) (Fig. 1). Other Paleogene crocodylians are also known from the Middle Eocene (45 myr) of Egypt (Fig. 2) (Andrews, 1906). The crocodylians from the phosphatic deposits of the Oulad Abdoun Basin of Morocco are the only known African crocodylians ranging from the Maastrichtian (70 myr) to the Lower Eocene (46 myr); they have received little attention since the pioneering works of Arambourg (Arambourg, 1952). The ongoing French-Moroccan excavation program (MNHN/CNRS; FSSM; MEM; OCP; UCDJ), has led to the discovery of a large number of well preserved crocodyliform specimens from the Oulad Abdoun Basin (Hua and Jouve, 2004; Jouve, 2004; Jouve et al., 2005a, b, 2006a, b) (Fig. 1). Here we report on a new gavialoid from the Maastrichtian levels of this basin (Figs. 3, 4), which represents henceforth the oldest African crocodylian (Fig. 2). The specimen consists of a nearly complete skull that probably belongs to a small-sized adult individual.

Institutional Abbreviations—CNRS, Centre National de la Recherche Scientifique, Paris, France; FSSM, Faculté des Sciences Semlalia de Marrakech, Marrakech, Morocco; MEM, Ministère de l'Energie et des Mines, Rabat, Morocco; MNHN, Muséum Natinal d'Histoire Naturelle, Paris, France; OCP, Office Chérifien des Phosphates, Casablanca, Morocco; UCDJ, Université Chouab Doukkali, El Jadida, Morocco.

SYSTEMATIC PALEONTOLOGY
EUSUCHIA Huxley, 1875
CROCODYLIA Gmelin, 1789
GAVIALOIDEA Hay, 1930 (*sensu* Brochu, 1999)
Genus *OCEPESUCHUS*, gen. nov.

Etymology—Ocepe, dedicated to the OCP, "Office Chérifien des Phosphates", the company exploiting the phospates in Morocco and strongly participating to the excavation of the fossils, and suchus, crocodile.

Type Species—*Ocepesuchus eoafricanus* sp. nov.
Diagnosis—As for the type and only known species.

Ocepesuchus eoafricanus, n.sp.
(Fig. 3)

Etymology—eoafricanus, "dawn" and African, in reference to its ancient age relative to other African crocodylians.

Holotype—OCP DEK-GE 45, a crushed skull, lacking the ventral part and the premaxillae; housed in the geological survey of the OCP in Khouribga, Morocco (Fig. 3).

*Corresponding author.
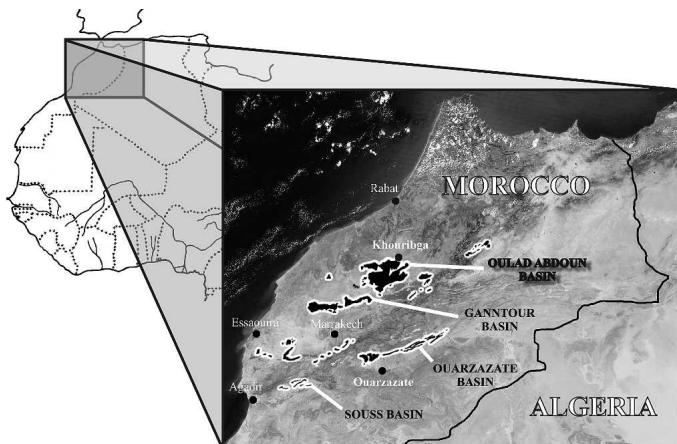
FIGURE 1. Geographic position of the marine basins of central Morocco.

Locality and Age—'Couche III', late Maastrichtian of the Oulad Abdoun Basin, Morocco.

Diagnosis—Prefrontal strongly extended anteriorly, exceeding strongly the anterior extremity of the frontal; interorbital distance very short, only slightly wider than the interfenestral bar; parietal in the interfenestral bar strongly depressed, a strong rim bordering the medial margin of the supratemporal fenestra; posterolateral process of squamosal posterolateraly oriented; posterolateral margin of the squamosal bearing a smooth dorsolateral depression, so a strong squamosal rim borders the lateral margin of the supratemporal fenestra.

DESCRIPTION

General Shape—The skull of *Ocepesuchus* is crushed and damaged, its snout extremity (premaxillae) is missing, and the bones are displaced from their original position. It is a longirostrine crocodylian, with a narrow and nearly tubular snout, that is wider than high (Figs. 3, 4). All the surface of the skull is well ornamented, with the ornamentation of the posterior part, and in particular the skull roof, showing deeper furrows and pits than the snout.

Cranial Openings—As in all crocodylians, the antorbital fenestra is absent. The orbit is rather wide, bordered medially by

the frontal, anteriorly by the prefrontal (and lacrimal ?) and laterally by the jugal. The interorbital space is narrow, the orbits being relatively closely set (Figs. 3B, 4).

The supratemporal fenestra is relatively large on the skull roof, nearly as wide as long. They are separated by a relatively narrow fronto-parietal bar. The interfenestral bar is mostly formed by the parietal, and the frontal seems to have slightly penetrated the supratemporal fenestra (Fig. 3B). The squamosal forms the posterolateral quarter of the supratemporal fenestra and its anterolateral portion (postorbital) is not preserved.

Only the posteroventral margin of the infratemporal fenestra is known. It is largely ventrally, and at least posteroventrally, bordered by the quadratojugal (Fig. 3B).

Nasal—The nasals are poorly preserved. They are narrow, and separate the maxillae. Their anterior relationships with the premaxillae are not preserved.

Maxilla—The maxilla is long, narrow, and bears closely set and circular tooth alveoli. (Fig. 3A). Its lateral margin is linear, and it is dorsally ornamented with deep ridges and furrows, whereas its lateroventral margin is ornamented with less numerous and deep furrows. Its posteroventral margin, below the jugal, bears several deep pits. The edge of the maxillary tooth alveoli is higher than the space between the toothrows (toothrow underlined). Each maxilla bears at least 15 alveoli.

Jugal—The jugal extends farther anteriorly than the anterior margin of the orbit (Fig. 4). It participates in the ventral portion of the postorbital pillar that seems to be relatively weak. The jugal exhibits an anterior elevation, which disappears just anterior to the postorbital bar (Fig. 3C). Nevertheless, the postorbital bar is directed ventrolaterally, and its base is not flushed with the lateral surface of the jugal. A small lateral jugal rim borders the base of the postorbital bar, without any dorsolateral elevation (the lower temporal bar is laterally thicker than the base of the postorbital bar). The jugal participates in the anteroventral margin of the infratemporal fenestra, but its participation in the ventral margin of this fenestra cannot be estimated. Its dorsal margin is ornamented with deep pits, whereas its ventral margin is ornamented with deep furrows that are anteroventrally oriented (Fig. 3B).

Frontal—Between the orbits, the frontal is narrow and strongly medially concave to form an anteroposterior medial depression (Fig. 3B). Its narrow anterior process extends far anteriorly, but it does not penetrate deeply between the nasals. Its contact with the nasal is short. The anterior process of the frontal, from the level of its posteriormost contact with the prefrontal
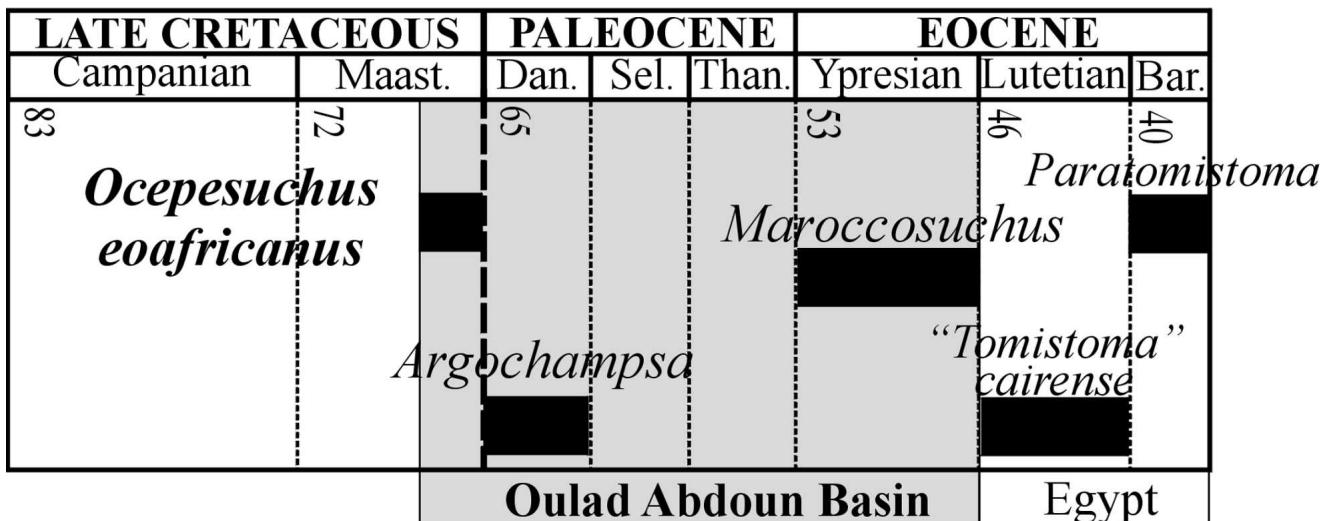

FIGURE 2. Stratigraphic distribution of the oldest African crocodylians [in grey, the Oulad Abdoun Basin (Morocco) stratigraphic range].
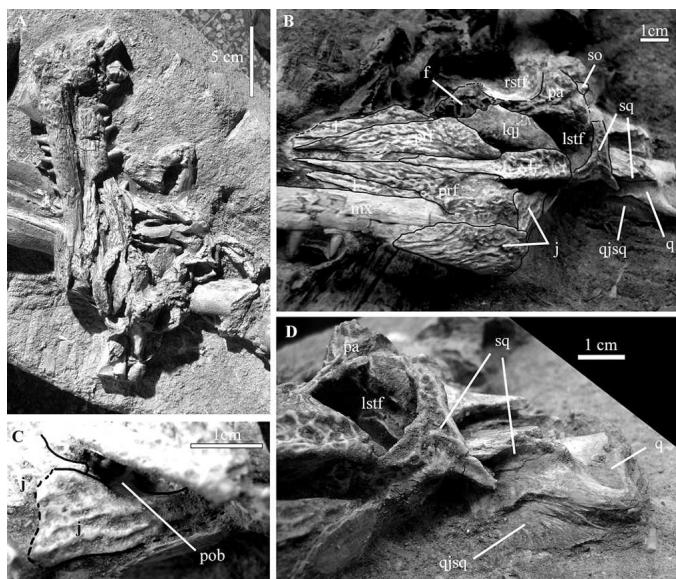
FIGURE 3. *Ocepesuchus eoafricanus* nov. gen. et sp., holotype, OCP DEK-GE 45, from the Maastrichtian of Morocco. **A**, skull in dorsal view; **B**, detail of the posterior portion of the skull; **C**, detail of the jugal; **D**, detail of the squamosal. **Abbreviations: f**, frontal; **j**, jugal; **l**, lacrimal; **lqj**, left quadratojugal; **lstf**, left supratemporal fenestra; **mx**, maxilla; **pa**, parietal; **pob**, postorbital bar; **prf**, prefrontal; **q**, quadrate; **qjsq**, quadratojugal suture on quadrate; **rstf**, right supratemporal fenestra; **so**, supraoccipital; **sq**, squamosal;.

is smooth, only its anteriormost extremity being ornamented with scarce and shallow pits (Fig. 3B). Posteriorly, its suture with the parietal could have participated slightly in the anterior margin of the supratemporal fenestra. Posteriorly to the orbits, the frontal is ornamented with deep pits.

Prefrontal—The prefrontal is narrow and extends far anteriorly. Its contact with the nasal is nearly as long as its contact with the frontal. It is strongly ornamented posteriorly with deep pits, and anteriorly with anteroposterior ridges and furrows. It forms the anteromedial margin of the orbit (Fig. 4).

Lacrimal—The lacrimal is narrow, and extends far anteriorly. It seems to reach or to slightly exceed the prefrontal anteriorly. Its ornamentation is as the one observed in the prefrontal: it is ornamented posteriorly with deep pits, and anteriorly with anteroposteriorly-oriented ridges and furrows (Fig. 4).

Parietal—The parietal is strongly damaged. Its suture with the frontal is far anteriorly positioned, and the parietal forms most of the interfenestral bar (Fig. 3B). This bar is relatively narrow, strongly ornamented with deep pits and separates the supratemporal fenestrae. The parietal in the interfenestral bar is strongly depressed, and a strong rim borders the medial margin of the supratemporal fenestra. The parietal is not preserved in the posterior margin of the supratemporal fenestra, and its suture with the squamosal cannot be discerned. The supraoccipital does not penetrate the parietal (Fig. 4).

Squamosal—The squamosal forms the posterolateral quarter of the supratemporal fenestra. Its posterolateral process is short and posterolaterally oriented (Fig. 3D), which gives a gently anteriorly concave shape to the posterior margin of the skull table (Fig. 4). The lateral margin of the squamosal is strongly ornamented with deep pits, and bears a strong dorsolateral depression. So, a strong squamosal ornamented rim borders the lateral margin of the supratemporal fenestra (Fig. 3D). The squamosal forms the posterior margin of the supratemporal fenestra, which is strongly ornamented, and as wide as the lateral margin of the
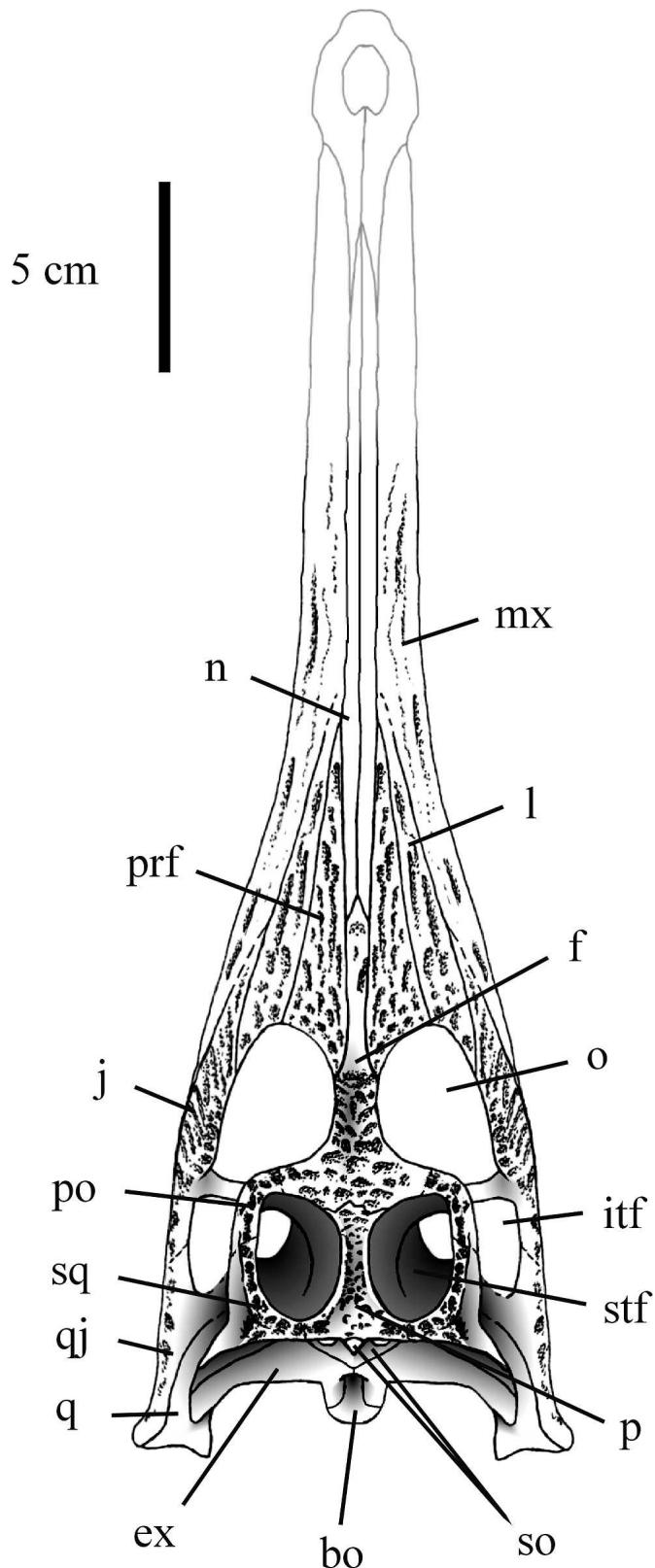
FIGURE 4. *Ocepesuchus eoafricanus* nov. gen. et sp., holotype, OCP DEK-GE 45, from the Maastrichtian of Morocco. Reconstruction of the holotype cranium in dorsal view. **Abbreviations: bo**, basioccipital; **ex**, exoccipital; **f**, frontal; **itf**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **mx**, maxilla; **n**, nasal; **o**, orbit; **p**, parietal; **po**, postorbital; **prf**, prefrontal; **q**, quadrate; **qj**, quadratojugal; **so**, supraoccipital; **sq**, squamosal; **stf**, supratemporal fenestra.

supratemporal fenestra (anterolateral portion of the squamosal). The squamosal participates in the dorsolateral part of the occipital surface, and is sutured ventrally to the exoccipital in the paroccipital process. Its dorsal surface is dorsally convex, and the skull table surface thus slopes ventrally from the sagittal axis. Posterior to the external ear, the squamosal forms a long, high blade, which sinks deeply beneath the squamosal part of the skull roof, and ventrally is sutured to the quadrate (Fig. 3).

Quadratojugal—Only the ventral portion of the left quadratojugal is preserved. It is dorsolaterally smooth and ventrolaterally strongly ornamented with deep pits (Figs. 3B, 4). No quadratojugal spine is preserved. Ventrally, the quadratojugal sends a long process and forms a large part of the ventral margin of the infratemporal fenestra. Posteriorly, it reaches the quadrate condyle, and bears at its posterior tip a small lateral protuberance (Fig. 4).

Quadrate—Anteriorly, the quadrate forms the floor of the external auditory meatus. Its participation in the margin of the infratemporal fenestra is unknown, but it is at least excluded from its posteroventral margin by the quadratojugal. The articular surface is sigmoidal, with the inner condyle being the largest. The condyle is smooth and shortly extends posteriorly (Fig. 3D). A long dorsomedial concavity can be seen for the cranioquadrate canal, and the quadrate forms its lateral margin. The suture with the exoccipital is linear at the basis of the paroccipital process. A foramen (foramen aereum ?) is present at the dorsal margin of the quadrate, at nearly its mid width.

Supraoccipital—The supraoccipital is damaged, and only its left part is preserved. It is small and excluded from the foramen magnum. The bone is sharp and forms a posterior process posterior to the skull table. It does not penetrate the parietal anteriorly, but projects posteriorly from the rear of the skull's margin (Fig. 3B). On the occipital face, it is triangular in shape and bears a posterior occipital tuberosity, which is visible in dorsal view, on each side of the posteromedial process below the posttemporal fenestra, the latter being unfortunately not preserved.

Exoccipital—The exoccipitals are the largest bones of the occipital face. They circumscribe most of the foramen magnum with the exception of the central part of the ventral border occupied by the basioccipital. The occipital surface is strongly inclined because of the orientation of the exoccipitals, which bear two posterior wings, largely visible in dorsal view (Fig. 4). The ventromedial process of the exoccipital does not reach the ventral margin of the basioccipital tubera, but remains dorsal. The exoccipital forms the dorsal, ventral and medial margins of the cranioquadrate canal.

Basioccipital—The basioccipital is poorly preserved. It forms most of the occipital condyle, and the ventral margin of the foramen magnum (Fig. 4). Its ventral part is wide, vertically oriented, and lacks a medial crest.

Teeth—Twelve maxillary teeth are preserved in situ (Fig.3A). The teeth are sharp, short, robust, close to each other, and without any striation or carina (Fig. 3A, B). Also, they are relatively straight, and weakly curved. Only their lateral sides are visible. All alveoli have nearly the same size (homodonty).

DISCUSSION

Comparison

In adult and subadult crocodylians, the dorsal surface of the skull is strongly ornamented and the interfenestral bar is wide, whereas the skull is much smoother and the interfenestral bar is narrower in juveniles than in adults (Mook, 1921; Müller, 1927:pl. 3). Moreover, in juvenile specimens the ventral margin of the orbit is laterally turned. In the specimen described here, all the dorsal surface of the skull is particularly strongly ornamented, the interfenestral bar is narrow, and the ventral margin

of the orbit is dorsomedially oriented. So, the present specimen is probably an adult, or at least a subadult.

As in gavialoids (Hua and Jouve, 2004; Jouve, 2004; Jouve et al., 2006a), *Ocepesuchus* exhibits a slender-snouted morphology, an occipital surface dorsally inclined and largely visible in dorsal view, and a supraoccipital located posteriorly to the rear margin of the skull table.

O. eoafricanus differs strongly from *Argochampsa krebsi*, another gavialoid from the Paleocene of the same basin. This species has a particularly long posterior process of the squamosal, as in South American gavialoids such as *Siquisiquesuchus*, *Gryposuchus*, and *Piscogavialis*, whereas this process is very short in *Ocepesuchus* (Figs. 3D, 4). The squamosal of *O. eoafricanus* also bears further autapomorphic characters. The posterolateral process of the squamosal is posterolaterally oriented, whereas it is posteriorly directed in all other gavialoids, and it bears a lateral sulcus above the external ear, so that a strong squamosal ornamented rim borders the lateral margin of the supratemporal fenestra. If a narrow lateral lamina exists in *A. krebsi*, it is narrower, and not present in the posterior part of the squamosal. This sulcus is absent in all other gavialoids.

The interfenestral bar, formed by the parietal, is strongly depressed, and a strong rim borders the medial margin of the supratemporal fenestra. This differs from that observed in other gavialoids, where this bar is flat.

The prefrontal of *O. eoafricanus* extends far anteriorly, and is twice as long as the anterior process of the frontal. The prefrontal is much shorter in all other gavialoids. *Thoracosaurus macrorhynchus* (pers. obs.), *Eothoracosaurus mississippiensis* (Carpenter, 1983), *Gryposuchus colombianus* (Langston, 1965; Langston and Gasparini, 1995), *"Crocodylus" clavirostris* (Morton, 1845; Brochu, 2006), and *Gavialis* have a wide interorbital space, when in *Argochampsa krebsi* (Hua and Jouve, 2004; Jouve et al., 2006a), *Piscogavialis jugaliperforatus* (Kraus, 1998), *Siquisiquesuchus venezuelensis* (Brochu and Rincon, 2004), *Ikanogavialis gameroi* (Sill, 1970), and *Eosuchus* (Dollo, 1907; Swinton, 1937; Delfino et al., 2005), this distance is narrower. *Ocepesuchus eoafricanus* has a particularly narrow interorbital distance, narrower than in all above cited gavialoids.

In conclusion, the new specimen from the Maastrichtian of Morocco described herein exhibits several autapomorphies, justifying the erection of a new genus and species.

Phylogenetic Analysis

Method—*Ocepesuchus eoafricanus* was included in a matrix of 201 morphological characters (Appendix 1) and 69 ingroup taxa. *Bernissartia fagesii* and *Hyleochampsa vectiana* were used as outgroups. The matrix (Appendix 2) is mainly based on previous works (Brochu, 1997, 1999, 2004a, b, 2006; Brochu and Gingerich, 2000; Buscalioni et al., 2001; Brochu and Rincon, 2004; Hua and Jouve, 2004; Jouve, 2004; Delfino et al., 2005; Jouve et al., 2006a), whereas 7 characters were modified, 34 characters are newly included, and the coding of several taxa was changed. The maximum parsimony analysis was conducted using PAUP (version 4.0b10; Swofford, 2002), first with the "closest addition sequence" option, and second with two hundred heuristic searches with the starting order of taxa randomized for each iteration; both provide the same result. The analysis generated 1109 equally most parsimonious trees with a length of 667 steps (consistency index excluding uninformative characters: 0.37; retention index: 0.80; rescaled consistency index: 0.30).

If only 16% of the characters are coded for *Ocepesuchus eoafricanus*, 48% of the apomorphic characters for the gavialoids (Appendix 3) are coded. The high percent of missing values for *O. eoafricanus* does not seem to affect the result, as if it is deleted form the analysis, only the resolution of the basal forms (*Thoracosaurus*, *Eothoracosaurus*, *Eosuchus*) is affected. These miss-

ing data does not affect the following phylogenetic and paleo-biogeographic interpretations.

Result—The result is globally congruent with previous works, and the main differences are observed in gavialoids. In the consensus tree (Fig. 5), *Ocepesuchus eoafricanus* is more closely related to the clade formed by *Gavialis*, South American gavialoids, *Argochampsa*, and *Eogavialis*, than *Thoracosaurus*, *Eothoracosaurus*, and *Eosuchus*. *Eosuchus* is surprisingly the most basal gavialoid, whereas *Thoracosaurus* (paraphyletic herein) and *Eothoracosaurus* were considered to be more basal than *Eosuchus* in previous analyses (Brochu, 2004, 2006; Brochu and Rincon, 2004; Delfino et al., 2005). This clade (Gavialoidea, node 1, Fig. 5; Appendix 3) is supported by 13 unambiguous synapomorphies (synapomorphies observed without optimisation), whereas node 3 (Gavialoidea except *Eosuchus*; Fig. 5) is supported by three unambiguous synapomorphies: the nasals penetrate weakly between the premaxillae [95(3)], the posteroventral process of the premaxilla is long [168(1)], and the interorbital space is wide [177(1)] (strongly homoplastic: reverse condition in *Ocepesuchus*, *Argochampsa*, *Eogavialis*, *Piscogavialis*, *Ikanogavialis*, and *Siquisiquesuchus*).

The monophyly of the South American gavialoids is herein not supported, as they form a paraphyletic group, as in a previous analysis (Jouve et al., 2006a). *Gryposuchus colombianus* is more closely related to *Gavialis* than to other South American gavialoids, a node (node 11, Fig. 5) supported by 5 unambiguous synapomorphies: postorbital pillar robust and anteroposteriorly oval in cross section [70(0)], wide basisphenoid anterior to the basioccipital [113(1)], wide interorbital space [177(1)], postorbital bar vertical [184(1)], and short posterodorsal premaxillary process [192(0)] (a reversion compared to more basal gavialoids). These character states differ from those observed in other South American gavialoids, but they are shared by an undescribed gavialoid skull from Brazil figured by Sill (1970) (pers. obs.), and by *Gryposuchus neogaeus* (Gasparini, 1968; Langston and Gasparini, 1995). These two taxa could also be more closely related to *Gryposuchus* and *Gavialis* than to other South American Gavialoids. *Piscogavialis jugaliperforatus* results the sister taxa of the remainder South American gavialoids plus the Asian *Gavialis*. This latter node (node 10, Fig. 5) is supported by 2 unambiguous synapomorphies: the presence of a deep notch on the ventral margin of the orbit [139(3)] and of a quadrangular and wider than long supratemporal fenestra [199(1)]. These characters differ in *P. jugaliperforatus*, as its orbital ventral margin does not bear a prominent notch, and its supratemporal fenestra is more rounded and nearly as wide as long; these characters more resemble those found in more basal gavialoids such as *E. africanum*.

In previous works (Brochu, 2004a, 2006), the South American gavialoid clade was supported by only one unambiguous character: an elongate posterolateral squamosal process [140(2)]. This long squamosal process is also found in the African *A. krebsi* (Fig. 6), and is thus not restricted to South American gavialoids (Jouve et al., 2006a). In the present work, this character is an unambiguous synapomorphy uniting *A. krebsi*, South american gavialoids, and *Gavialis* (node 8, Fig. 5), a reversion being observed in the latter (node 12, Fig. 5).

Paleobiogeographic Implication—The phylogeny of crocodylians generally matches their stratigraphic distribution, and the earliest-known and most basal crocodylians are Late Cretaceous gavialoids and alligatoroids from North America and Europe (Brochu, 2003). Consequently, the occurrence of *Ocepesuchus eoafricanus*, the most basal (Fig. 5) and oldest known African gavialoid (Fig. 2), in Morocco is not so surprising, since this region of Africa was close to the Northern continents during the latest Cretaceous times, and the earliest African crocodylians were probably derived from North American or European forms.

The paleobiogeography of the gavialoids is particularly interesting, as in the present phylogenetic analysis, the South American gavialoids are not monophyletic. Several authors have suggested that the South American and Asian gavialoids are two monophyletic groups, each having derived from African immigrants respectively through Atlantic and Indian Oceans (Buffetaut, 1982, 1985; Brochu and Rincon, 2004). In the present work, the South American and Asian species represent only one single clade, and the South American gavialoids appear paraphyletic (Fig. 7), suggesting a more complex historical biogeography. The most parsimonious hypothesis, according with the cladogram of figure 7, suggests that the South American gavialoids derive from an African immigrant, and Asian gavialoids from a South American immigrant. This could explain the presence of a gavialoid (*"Gavialis" papuensis*) in the New Guinea area (Salomon Islands; Vis, 1905; Molnar, 1982), which Molnar (1982) regarded as closely related to the South American gavialoid *Ikanogavialis gameroi*. This hypothesis is not congruent with the stratigraphic distribution of *"G." papuensis*, from the Holocene whereas the migration to Asia occurs between the Late Paleocene and Early Oligocene. Moreover, the Atlantic is a shorter barrier than the Pacific. Two further hypotheses, less parsimonious than the previous one, can be suggested. In the first, the migration occurred from Africa to South America, followed by a return to Africa from South America, with subsequent migration to Asia. Following the phylogenetic result, this second migration should have occurred between the middle Oligocene and the Lower Miocene, but no gavialoid fossil is known from Africa during this period. The second hypothesis suggests several migrations from Africa to South America, and a later migration from Africa to Asia. Thus, the biogeographic history of gavialoids still remains poorly understood, as the present result does not allow to provide a clear and convincing hypothesis on their geographic distribution.

Differences in Marine Reptile Survivorships Through the Cretaceous-Tertiary Boundary

The phosphatic deposits of Morocco provide a unique opportunity to study the vertebrate faunal turnover across the Cretaceous-Tertiary (KT) boundary, as they exhibit the largest stratigraphic extension in the southern Tethys phosphogenic province, from the uppermost Cretaceous to the Lower Eocene (Lucas and Prévôt-Lucas, 1996). Mosasaurid squamate remains are particularly abundant in the Maastrichtian levels (Bardet et al., 2004, 2005a, b) but crocodyliforms remain very scarce, as suggested by the ratio crocodyliform/mosasaurid teeth (about 1/1000) observed in the Ganntour Basin (where phosphatic levels extend from the basal to the uppermost Maastrichtian; N.B., pers.obs.). Only one taxon (*Ocepesuchus*) is known in the Maastrichtian phosphates of the Oulad Abdoun Basin (Fig. 8A). On the contrary, the abundance and diversity of crocodyliforms (crocodylians and especially dyrosaurids) increase notably throughout the Paleocene and Eocene. The same diversity pattern occurs in the West African Iullemmeden Basin (Niger, Mali, and Nigeria) (Fig. 8B). In both African basins, the number of Paleocene crocodyliform species is equivalent to the number of Maastrichtian marine reptiles (1 crocodyliform species, and 5 to 7 mosasaurid and plesiosauroid species) (Fig. 8A, B). This contrasts with the condition in eastern North America (Fig. 8C), where the number of crocodyliform species is stable during the Cretaceous and Paleocene, despite comparable Maastrichtian mosasaurid and plesiosauroid diversity (Fig. 8C). This is probably due to differences between the respective environments: the Oulad Abdoun and Iullemmeden Basins were not widely open toward the ocean, contrary to the contemporaneous North American reptile-bearing deposits (Fig. 8D). Presumably, the competition between the various reptile taxa may have been more important in the relatively closed basins than in the open sea, and mosasaurid
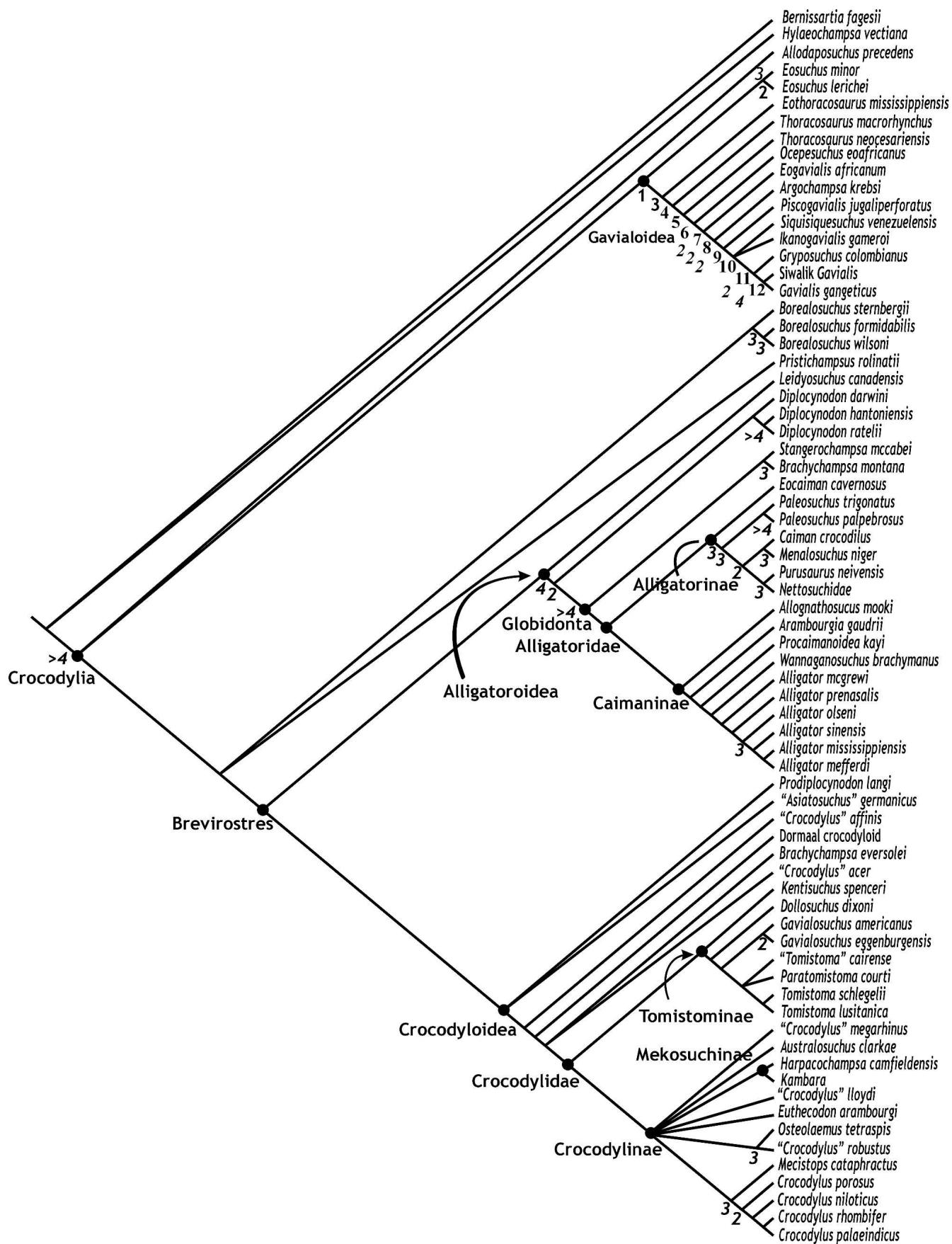
FIGURE 5.   Strict consensus tree based on 1109 equally parsimonious trees of 667 steps, based on maximum parsimony analysis of 201 characters (Appendix 1, 2). The nodes for gavialoids are labelled to provide the list of unambiguous synapomorphies (Appendix 3), and the decay index is indicated in italicized numbers (when not indicated otherwise, the decay index is 1).
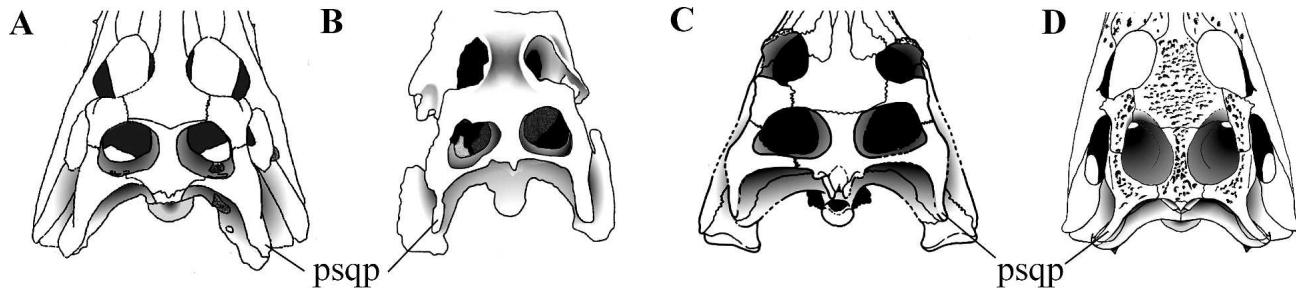
FIGURE 6. Posterior portions of several gavialoid skulls in dorsal view. **A**, *Piscogavialis jugaliperforatus* (modified from Kraus, 1998); **B**, *Siquisiquesuchus venezuelensis* (modified from Brochu and Rincon, 2004); **C**, *Gryposuchus colombianus* (modified from Langston and Gasparini, 1995); **D**, *Argochampsa krebsi* (from Jouve et al., 2006a). **Abbreviation: psqp**, posterior squamosal process.

diversity and abundance may have hampered the diversification of the African crocodyliforms during the Cretaceous.

Mosasaurids and crocodyliforms both lived in comparable marine environments during the Maastrichtian. The selectivity of the KT boundary extinctions remains to be explained, as marine crocodyliforms survived the crisis, whereas mosasaurids and plesiosaurs disappeared. Dyrosaurids are particularly abundant in the Oulad Abdoun Basin, and especially in the Lower Eocene beds, where numerous specimens of *Dyrosaurus maghribensis* have been found (Jouve et al., 2006b). In these levels, the specimens are all adults, and nearly of the same size, while juveniles are particularly scarce. Juvenile *Dyrosaurus* may have lived in freshwater environments, whereas large adults were probably marine. A comparable behaviour is observed in the extant marine *Crocodylus porosus*, and the same separation of size classes is observed in extant fresh-water *Crocodylus niloticus*, small animals being restricted to the river whereas all larger animals occupy the lake into which the river flowed (Hutton, 1989), in order to avoid intraspecific competition. By contrast, both fully grown and juvenile mosasaurids are found together in the same Maastrichtian levels, suggesting that they were probably marine during their entire life.

Marine environments are known for having been strongly affected by the KT crisis (i.e. Fara, 2000), unlike freshwater ones which have less suffered from the effects of the crisis (Bakker, 1977; Van Valen and Sloan, 1977; Sheehan and Fastovsky, 1992; Cavin, 2001). Assuming that marine crocodyliforms behaved much in the same way as living marine crocodiles, including a freshwater life cycle for the young, this may have protected them to some extent from the KT crisis, when dramatic extinction occurred in the seas, eliminating fully marine reptiles such as mosasaurids and plesiosaurs.
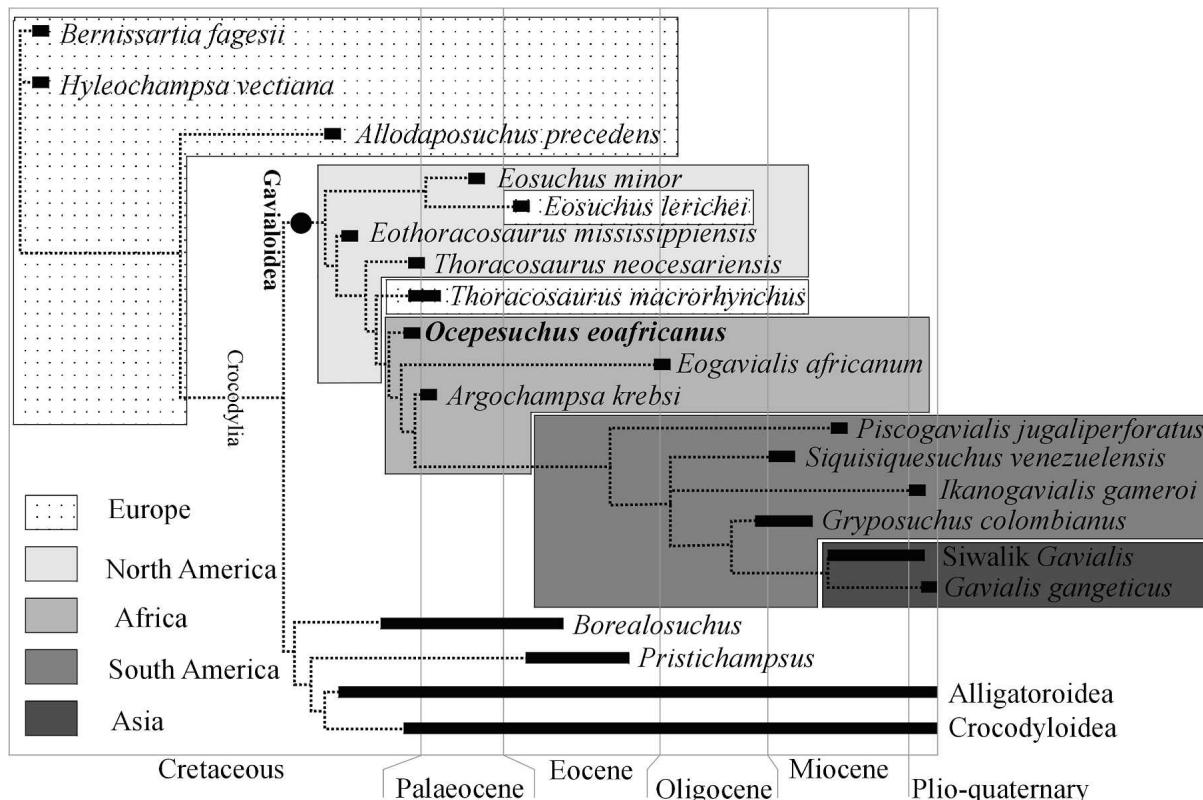
FIGURE 7. Fit of the most parsimonious cladogram (consensus) to the stratigraphic and geographic distribution. The boxes show the reconstructed paleobiogeographic history of gavialoids, according to the most parsimonious phylogeny.
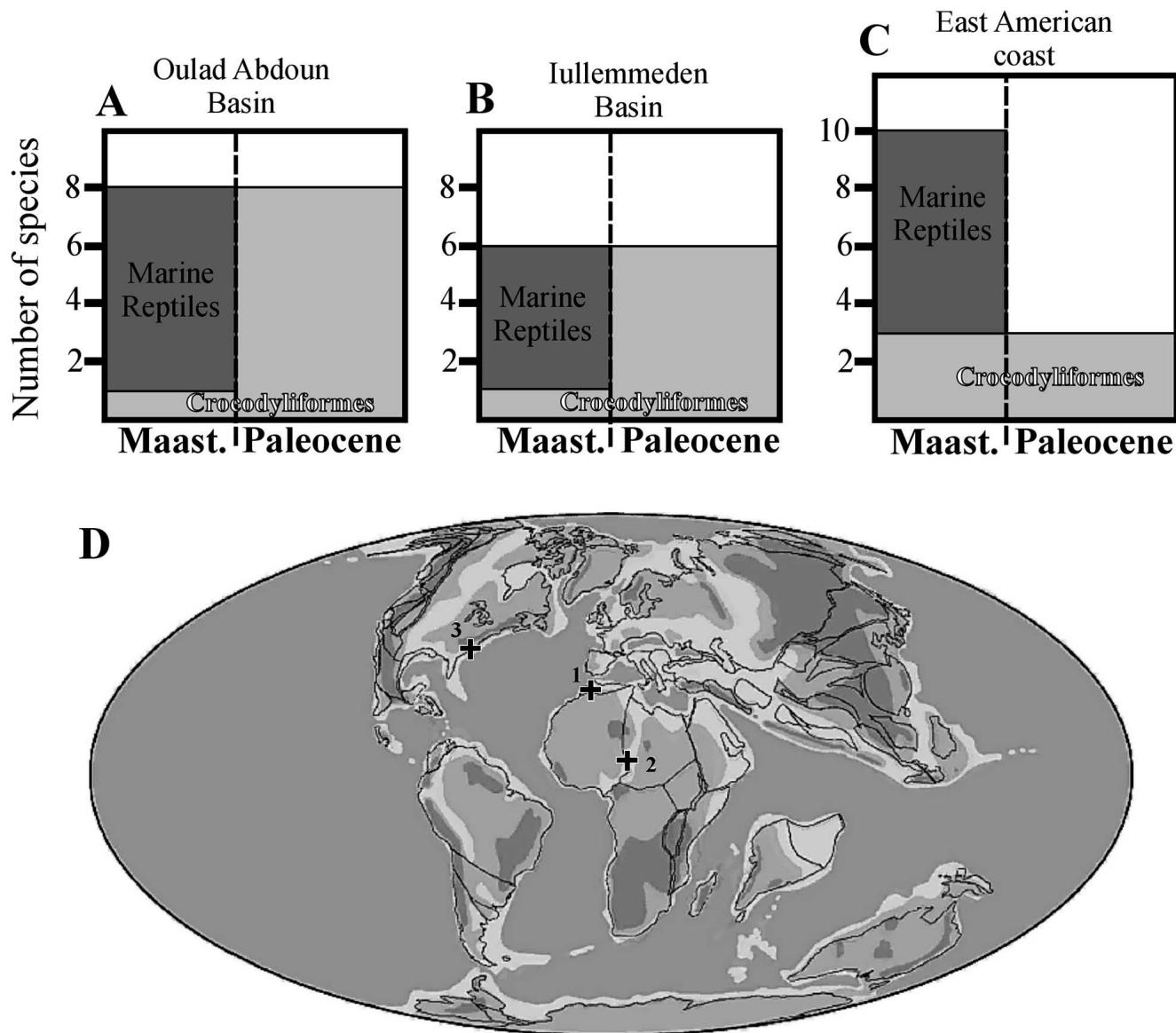
FIGURE 8. Stratigraphic distribution of Crocodyliformes compared to Late Cretaceous marine reptiles (mosasaurids and plesiosaurs), with reference to the three localities discussed in this study. **A**, Oulad Abdoun Basin (North Africa); **B**, Iullemmeden Basin (West Africa); **C**, East American Coast (U.S.A.); **D**, Maastrichtian paleogeographic map showing the Oulad Abdoun Basin (number 1) and other penecontemporaneous basins (2: Iullemmeden, West Africa; 3: New Jersey, eastern North American coast); map from Scotese (1998). See Appendix 4 for the list of taxa used.

LITERATURE CITED

Andrews, C. W. 1906 A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt. British Museum of Natural History, London, 324 pp.

Arambourg, C. 1952. Les vertébrés fossiles des gisements de phosphates (Maroc, Algérie, Tunisie). Notes et Mémoires du Service Géologique du Maroc 92:372 p.

Bakker, R. T. 1977. Tetrapod Mass Extinctions—A model of the regu-

lation of speciation rates and immigration by cycles of topographic diversity; pp. 439–468 in A. Hallam (ed.), Patterns of evolution as illustrated by the fossil records. Elsevier, Amsterdam.

Bardet, N., X. Pereda Suberbiola, F. Bouyahyaoui, M. Iarochène, B. Bouya, and M. Amaghzaz. 2004. *Mosasaurus beaugei* Arambourg, 1952 (Squamata, Mosasauridae) from the Late Cretaceous Phosphates of Morocco. Geobios 37:315–324.

Bardet, N., X. Pereda Suberbiola, M. Iarochène, B. Bouya, and M. Amaghzaz. 2005a. A new species of *Halisaurus* from the Late Cretaceous phosphates of Morocco, and the phylogenetical relationships of the Halisaurinae (Squamata: Mosasauridae). Zoological Journal of the Linnean Society 143:447–472.

Bardet, N., X., Pereda Suberbiola, M., Iarochène, M., Amalik, and B. Bouya. 2005b. Durophagous Mosasauridae (Squamata) from the Upper Cretaceous phosphates of Morocco, with the description of a new species of *Globidens*. Netherlands Journal of Geosciences 84: 447–472.

Brochu, C. A. 1997. Morphology, fossils, divergence timing, and the phylogenetic relationships of *Gavialis*. Systematic Biology 46: 479–522.

Brochu, C. A. 1999. Phylogenetics, taxonomy, and historical biogeography of Alligatoroidea. Journal of Vertebrate Paleontology, Supplement to number 2 (Memoir 6):9–100.

Brochu, C. A. 2003. Phylogenetic approaches toward crocodylian history. Annual Revues of Earth Planet Sciences 2003:357–397.

Brochu, C. A. 2004a. A new Late Cretaceous gavialoid crocodylian from Eastern North America and phylogenetic relationships of thoracosaurs. Journal of Vertebrate Paleontology 24:610–633.

Brochu, C. A. 2004b. Alligatorine phylogeny and the status of *Allognathosuchus* Mook, 1921. Journal of Vertebrate Paleontology 24: 857–873.

Brochu, C. A. 2006. Osteology and phylogenetic significance of *Eosuchus minor* (Marsh, 1870) new combination, a longirostrine crocodylian from the late Paleocene of North America. Journal of Paleontology 80:162–186.

Brochu, C. A., and P. D. Gingerich. 2000. New Tomistomine crocodylian from the Middle Eocene (Bartonien of Wadi Hitan, Fayum Province, Egypt). Contribution from the Museum of Paleontology, the University of Michigan 30:251–268.

Brochu, C. A., and A. Rincon. 2004. A gavialoid crocodylian from the Lower Miocene of Venezuela. Special Papers in Palaeontology 71: 61–79.

Buffetaut, E. 1982. Systématique, origine et évolution des Gavialidae sud-américains. Geobios, Mémoire spécial 6:127–140.

Buffetaut, E. 1985. The place of *Gavialis* and *Tomistoma* in Eusuchian evolution: a reconciliation of palaeontological and biochemical data. Neues Jahrbuch für Geologie und Paläontologie, Monatshefte 12: 707–716.

Buscalioni, A. D., F. Ortega, D. B. Weishampel, and C. M. Jianu. 2001. A revision of the Crocodyliform *Allodaposuchus precedens* from the upper Cretaceous of the Hateg basin, Romania. Its relevance in the phylogeny of Eusuchia. Journal of Vertebrate Paleontology 21: 74–86.

Buscalioni, A. D., and J. L. Sanz. 1990. *Montsecosuchus depereti* (Crocodylomorpha, Atoposauridae), new denomination for *Alligatorellus depereti* Vidal, 1915 (Early Cretaceous, Spain): redescription and phylogenetic relationships. Journal of Vertebrate Paleontology 10: 244–254.

Carpenter, K. 1983. *Thoracosaurus neocesariensis* (de Kay, 1842) (Crocodylia : Crocodylidae) from the Late Cretaceous Ripley Formation of Mississippi. Mississippi Geology 4:1–10.

Cavin, L. 2001. Effect of the Cretaceous-Tertiary event on bony fishes; pp. 141–158 in E. Buffetaut and C. Koeberl (eds.), Geological and Biological Effects of Impact Events. Springer Verlag.

Delfino, M., P. Piras, and T. Smith. 2005. Anatomy and phylogeny of the gavialoid crocodylian *Eosuchus lerichei* from the Paleocene of Europe. Acta Palaeontologica Polonica 50:565–580.

Dollo, L. 1907. Nouvelle note sur les Reptiles de l'Eocène inférieur de la Belgique et des régions voisines (*Eosuchus lerichei, Eospharsis gigas*). Bulletin de la Société Belge de Géologie 21:81–85.

Fara, E. 2000. Diversity of Callovian-Ypresian (Middle Jurassic-Eocene) tetrapod families and selectivity of extinctions at the K/T boundary. Geobios 33:387–396.

Gasparini, Z. B. 1968. Nuevos restos de *Rhamphostomopsis neogaeus*

(Burm.) Rusconi 1933, (Reptilia, Crocodilia) del "Mesopotamiense" (Plioceno medio-superior) de Argentina. Ameghiniana 5:199–311.

Gmelin, J. F. 1789. Regnum animal ; pp. 1033–1516 in G. E. Beer (ed.), Caroli a linne systema naturae per regna tri naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Leipzig.

Hay, O. P. 1930. Second bibliography and catalogue of the fossil vertebra of North America. Carnegie Institute of Washington, Washington, 415 pp.

Hua, S., and S. Jouve. 2004. A primitive marine gavialoid from the Paleocene of Morocco. Journal of Vertebrate Paleontology 24: 344–353.

Huxley, T. H. 1875. On *Stagonolepis robertsoni*, and on the evolution of the Crocodilia. Quarterly Journal of the Geological Society of London 31:423–438.

Hutton, J. 1989. Movement, home range, dispersal and the separation of size classes in Nile Crocodiles. American Zoologist 29:1033–1049.

Jouve, S. 2004. Etude des Crocodyliformes fini Crétacé-Paléogène du Bassin des Oulad Abdoun (Maroc) et comparaison avec les faunes africaines contemporaines: systématique, phylogénie et paléobiogéographie. Ph.D. dissertation, Muséum National d'Histoire Naturelle, Paris, 651 pp.

Jouve, S., B. Bouya, and M. Amaghzaz. 2005a. A short-snouted dyrosaurid (Crocodyliformes, Mesoeucrocodylia), from the Palaeocene of Morocco. Palaeontology 48:359–369.

Jouve, S., M. Iarochène, B. Bouya, and M. Amaghzaz. 2005b. A new crocodyliform dyrosaurid from the Palaeocene of Morocco and a phylogenetic analysis of Dyrosauridae. Acta Palaeontologica Polonica 50:581–594.

Jouve, S., M. Iarochene, B. Bouya, and M. Amaghzaz. 2006a. New material of *Argochampsa krebsi* (Eusuchia: Gavialoidea) and phylogenetic implications. Geobios 39:817–832.

Jouve, S., M. Iarochène, B. Bouya, and M. Amaghzaz. 2006b. A new species of *Dyrosaurus* (Crocodylomorpha, Dyrosauridae) from the Early Eocene of Morocco: phylogenetic implications. Zoological Journal of the Linnean Society 148:603–656.

Kraus, R. 1998. The cranium of *Piscogavialis jugaliperforatus* n.gen., n.sp. (Gavialidae, Crocodylia) from the Miocène of Peru. Paläontologische Zeitschrift 72:389–406.

Langston, W. 1965. Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia. University of California Publications in Geological Sciences 52:1–157.

Langston, W., and Z. B. Gasparini. 1995. Crocodilians, *Gryposuchus*, and the South American Gavials; p. 113–154 in R. F. Kay, R. H. Madden, R. L. Cifelli, and J. J. Flynn (eds.), Vertebrate paleontology in the Neotropics : the Miocene fauna of La Venta, Colombia. Smithonian Institution Press, Washington D.C.

Lucas, J., and L. Prévot-Lucas. 1996. Tethyan phosphates and bioproductites; pp. 367–391 in A. E. M. Nairn, L.-E. Ricou, B. Vrielynck, and J. Dercourt (eds), The Ocean Basins and Margins. Plenum Press, New York.

Molnar, R. E. 1982. A longirostrine crocodilian from Murua (Woodlark), Solomon sea. Memoirs of the Queensland Museum 20:675–685.

Mook, C. C. 1921. Individual and age variation in the skull of recent crocodilia. Bulletin of the American Museum of Natural History 44:51–66.

Morton, M. D. 1845. Description of the head of a fossil crocodile from the Cretaceous strata of New Jersey. American Journal of Sciences 48:265–267.

Müller, L. 1927. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägypteus. Abhandlungen Bayerisch Akademie der Wissenschaften. Mathematisch-Naturwissenschaftelischt abtelund 31:1–97.

Ortega, F., Z. B. Gasparini, A. D. Buscalioni, and J. O. Calvo. 2000. A new species of *Araripesuchus* (Crocodylomorpha, Mesoeucrocodylia) from the Lower Cretaceous of Patagonia (Argentina). Journal of Vertebrate Paleontology 20:57–76.

Scotese, C. R. 1998. Quicktime Computer Animation, PALEOMAP Project. Department of Geology, University of Texas, Arlington, TX.

Sheehan, P. M., and D. E. Fastovsky. 1992. Major extinctions of landdwelling vertebrates at the Cretaceous-Tertiary boundary. Geology 20: 556–560.

Sill, W. D. 1970. Nota preliminar sobre un nuevo Gavial del Plioceno de

Venezuela y una discusión de los Gaviales sudamericanos. Ameghiniana 7:151–159.

Swinton, W. E. 1937. The crocodile of Maransart (*Dollosuchus dixoni* (Owen)). Mémoire du Musée Royale d'Histoire Naturelle de Belgique 80:1–46.

Swofford, D. L. 2002. PAUP 4.0b10. Illinois Natural History Survey, Champaign, IL.

Van Valen, L. M., and R. E. Sloan. 1977. Ecology and the extinction of the dinosaurs. Evolutionary Theory 2:37.

Vis, C. W. D. 1905. Fossil vertebrates from New Guinea. Annals of the Queensland Museum 6:26–31.

Wu, X.-C., D. B. Brinkman, and R. C. Fox. 2001. A new crocodylian (Archosauria) from the basal Paleocene of the Red Deer River Valley, southern Alberta. Canadian Journal of Earth Sciences 38: 1689–1704.

APPENDIX 1. The characters used in the present analysis are mainly from Brochu (1997, 1999, 2004a, b, 2006), Brochu and Gingerich (2000), Buscalioni et al. (2001), Brochu and Rincon (2004), Hua and Jouve (2004), Jouve (2004), Delfino et al. (2005), and Jouve et al. (2006a). Characters 198, 199, and 201 are new. Origin of characters is provided after the definition.

Only the new or modified characters, relative to Brochu (1999), are listed below, see the above cited references for a complete list of characters.

70. Postorbital bar massive and anteroposteriorly oval in cross section (0) or slender and rounded in cross section (1). [Modified from Brochu, 1997 (70)].

82. Supraoccipital exposure on dorsal skull table small (0), points posteriorly to the caudal margin of the parietal (1), absent (2), large (3), or large such that parietal is excluded from posterior edge of table (4). (Hua and Jouve, 2004, modified from Brochu 1999).

93. Lacrymal makes broad contact with nasal and there is no posterior process of maxilla (0), maxilla sends posterior process within lacrymal or between lacrymal and nasal (1), or maxilla sends posterior process between lacrymal and prefrontal (2). [Modified from Brochu, 1997 (character 93)].

95. External naris bisected by nasals (0), nasals contact external naris but do not bisect it (1), nasals excluded, at least externally, from naris and nasals and premaxillae still in large contact (2), nasals excluded from naris and nasals and premaxillae in weak contact (3), or nasals and premaxillae not in contact (4). [Modified from Brochu, 1997 (character 95)].

124. Incisive foramen small and less than half the greatest width of premaxillae (0), extremely reduced and thin (1), large and more than half the greatest width of premaxillae (2), or large and intersects premaxillary-maxillary suture (3). [Modified from Brochu, 1997 (character 124)].

139. Lateral edge of the jugal raises laterally to the postorbital bar and a gutter separates this edge from the postorbital bar (0), or lateral edge of the jugal raises laterally to the postorbital bar, and projects a shelf laterally to the postorbital bar, and the dorsal margin of the jugal is not gently convex dorsally, but shows a gentle step in lateral view (1), or lateral edge of the jugal raises laterally to the postorbital bar, but there is no or shallow gutter between the latter and postorbital bar, and the dorsal margin of the jugal is not gently convex dorsally but exhibits a step in lateral view (2) or no jugal lateral edge laterally to the postorbital bar, jugal not widens laterally and presence of a prominent notch on the ventral margin of the orbit (3). [Brochu, 1997 (139 and 146)].

140. Mature skull table with broad curvature; short squamosal prongs (0), with nearly horizontal sides; significant squamosal prongs (1), or long squamosal process (2). (Brochu, 2004, modified from Brochu, 1999).

146. Anterolateral border of the suborbital fenestra narrow (0) or very broad (1) (adapted from Wu et al., 2001).

165. Edge of the maxillary tooth alveoli lower or at the same level than the space between toothrow (0), or edge of the maxillary tooth alveoli higher than the space between toothrow (toothrow underlined) (1). (Hua and Jouve, 2004).

166. Ventral border of the exoccipital: convex and ventrally projected, hiding the posterior opening of the cranioquadrate passage from the occipital view (0); straight, sharpen or smoothly convex and does not hide the posterior opening of the cranioquadrate passage from occipital view (1). (Buscalioni et al., 2001, modified from Buscalioni and Sanz, 1990; Ortega et al., 2000, character 160).

167. Occipital surface sloped, visible in dorsal view (0) or vertical and not visible in dorsal view (1) at maturity. [Modified from Hua and Jouve, 2004 (167)].

168. Ventral premaxilla-maxilla suture short and ends posteriorly before the 3rd maxillary teeth (0), or elongated and extends or exceeds the 3rd maxillary alveoli (1) [Modified from Jouve, 2004 (168)].

169. Less than 18 teeth (0), 18 to 22 teeth (1), or more than 22 teeth (2) on maxilla. [Modified from Jouve, 2004 (169)].

170. Lateral edge of the skull table at the level of the postorbital-squamosal suture situated laterally at the same level as (0), or medially to (1) the quadrate condyle in dorsal view at maturity. [Modified from Jouve, 2004 (170)].

171. Frontal ends at the same level or posterior (0) or extends well anterior (1) to the anterior extension of the prefrontal. [Modified from Jouve, 2004 (172)].

172. Maxillary posterior process without tooth, short or absent (0) or long, longer than the distance between the three last teeth (1) in ventral view. [Jouve, 2004 (173)].

173. The ectopterygoid does not extend (0) or extends anteriorly beyond (1) the anterior quarter of the suborbital fenestra. [Modified from Jouve, 2004 (174)].

174. Anterior process of jugal extends anterior or at the same level as (0), or well posterior to (1) the anterior process of frontal. [Modified from Jouve, 2004 (177)].

175. Anterior process of frontal extending far anterior (0) or at the same level or posteriorly (1) to the anterior margin of the orbit. [Modified from Jouve, 2004 (178)].

176. Symphysis less extended posteriorly than the level of the thirteenth dentary tooth (0), extended between the level of the fourteenth and twentieth tooth (1) or extended beyond the twenty first tooth (2). [Jouve, 2004 (180)].

177. Interorbital space narrower (0), or broader (1) than the minimal width of the rotrum. [Jouve, 2004 (181)].

178. Ventral margin of jugal strongly convex dorsally (0) or straight (1). [Jouve, 2004 (182)].

179. Posterior edge of the supratemporal fenestra thick (0) or thin (1). [Jouve, 2004 (184)].

180. Presence (0) or absence (1) of a medial crest on the basioccipital. [Jouve, 2004 (185)].

181. Posterior process of jugal ends posteriorly to (0) or at the level as (1) the posterior margin of the basioccipital tubera. [Modified from Jouve, 2004 (186)].

182. Absence (0) or presence (1) of a posterior dentary process between splenial and angular on the ventral side. [Jouve, 2004 (187)].

183. Infratemporal fenestra not or slightly (0), or largely (1) visible in ventral view, laterally to the pterygoid flange. [Jouve, 2004 (189)].

184. Postorbital bar strongly inclined laterally (0), or vertical and not visible in dorsal view (1). [Modified from Jouve, 2004 (192)].

185. Dorsal margin of the articular on retroarticular process largely visible in lateral view (0), or slightly or not visible in lateral view (1). [Jouve, 2004 (194)].

186. Posterior margin of the orbit anterior to the posterior margin of the suborbital fenestra (0), or posterior or at the same level than the posterior margin of the suborbital fenestra (1). [Modified from Jouve, 2004 (195)].

187. Posterior surface of basioccipital ventral to the occipital condyle long, flat and nearly vertical (0), or short and gently curved (1). [Jouve, 2004 (197)].

188. Absence (0) or presence (1) of a smooth medial depression ventral to the basioccipital and posterior to the medial eustachian foramen. [Modified from Jouve, 2004 (198)].

189. Ventral processes of the exoccipital oriented ventrally or medioventrally (0), or oriented lateroventrally (1) in occipital view. [Jouve, 2004 (176)].

190. Retroarticular process does not extend posterodorsally beyond the posterior edge of the articular fossa (0) or extending posterodorsally beyond the posterior edge (1) [Modified from Jouve, 2004 (201); adapted from Wu et al., 2001].

191. Splenial extensively (0), or not extensively (1) involved in the formation of the dorsomedial wall of the posteriormost four alveoli [Modified from Jouve, 2004 (202); adapted from Wu et al., 2001].

192. Distance between the tip of the snout and the anteriormost position

of the premraxilla-maxilla suture in dorsal view is larger (0), or smaller (1) than the distance between the anteriormost position of the premaxilla-maxilla suture in dorsal view and the posterodorsal extremity of the premaxilla. [Jouve, 2004 (205)].

193. Length of the posterior process of the premaxilla: distance between the posterior margin of the external nares to the posterodorsal extremity of the premaxilla is less than twice longer (0), or at least twice longer (1) than the length between the tip of the snout and the posterior margin of the external nares. [Modified from Jouve, 2004 (207)].

194. Anterolateral margin of the suborbital fenestra longer (0) or as long as, or shorter (1) than the posterolateral margin. [Modified from Jouve, 2004 (149); adapted from Wu et al., 2001].

195. Posterior maxillary alveoli round (0) or mediolaterally compressed (1). [Brochu, 2004b (165)].

196. Dentary symphysis extends to sixth through eighth dentary alveolus (0), fourth or fifth alveolus (1), or exceeds the eighth alveolus (2). [Modified from Brochu, 2004b (166)].

197. Largest dentary alveolus immediately caudal to fourth is (0) 13 or 14, (1) 13 or 14 and a series behind it, (2) 10, 11, or 12, or (3) homodonty. [Modified from Brochu, 2004b (167)].

198. Anterolateral limit of the maxilla-premaxilla suture in dorsal view: at the level as or posterior (0), or far anterior (1) to the posterior margin of the external nares. (New).

199. Supratemporal fenestra small and rounded (0), or large, quadrangular, and much wider than long (1) at maturity. (New).

200. Foramen aereum small or absent (0) or comparatively large (1). [Brochu, 2006 (165)].

201. Anterior margin of suborbital fenestra: exceeds strongly (0) or does not exceed (1) the level of the anterior margin of orbit. (New).

APPENDIX 2. There are 201 characters for 71 taxa, analysed with Paup 4.0b10. (Swofford, 2002). ? = missing data or not applicable. All characters are treated as unordered. The matrix is based on Brochu (1999, 2004), and Brochu and Gingerich (2000), and taxa and characters modified as newly included characters are listed below.

	10	20	30	40	50	60
Bernissartia fagesii	??11? 1210? 010??	??00? ?0?0? 0000?	?0001 00010 0000?	????0 100?? ????1	10???		
Hylaeochampsa vectiana	????? ????? ?????	????? ????? ?????	????? ????? ?????	????? ????? ?????	?????		
Gryposuchus colombianus	??1?0 ????? 00???	??1?? ??000 ?????	????? ????0 ?0300	00001 11110 0???0	01000		
Osteolaemus tetraspis	??100 11001 00100	?1101 01001 11112	01011 11111 10111	00001 01110 01001	11000		
"Crocodylus" robustus	????? ????? ??1??	??10? ????? ?111?	?101? ????1 10111	00011 01110 0??01	11000		
"Crocodylus" lloydi	????? ????? ?????	????? ????? ?????	????? ????? ??1??	????? ????? ?????	?????		
Tomistoma schlegelii	02100 10011 00100	01101 00001 11111	00011 01301 10400	01001 01100 00000	01000		
Gavialosuchus americanus	02100 1?000 00100	0010? ?0101 1?11?	?01? 0??1 ??412	????1 01110 00???	?1000		
"Tomistoma" cairense	????? ????? ?????	????? ????? ?????	????? ????? ??402	????1 01??? ????0	?1?00		
Kentisuchus spenceri	????? ????? ?????	??1?? ????? ?????	????? ????? ??411	?0?01 ?1?? ????1	?1?00		
G. eggenburgensis	????? ????? ?????	??1?? ????? ?????	????? ????? ?????	????? ????? ?????	?????		
Kambara	????? ????? ?????	??1?? ????? 1?11?	?0011 0???1 10111	?0001 011?? ????1	11?00		
Allodaposuchus precedens	????? ????? ?????	????? ????? ?????	????? ????? ?????	????? ????? ?????	?????		
Argochampsa krebsi	??11? ????? 0??00	??1?0 ????? 0????	????? 0???? ?23??	?3??? ?11?? ?????	?????		
Piscogavialis jugaliperforatus	????? ????? ?????	????? ????? ?????	????? ?0??? ??3??	??0?? ?11?? ?????	01???		
Ikanogavialis gameroi	????? ????? ?????	????? ????? ?????	????? ????? ??30?	??00? ?11?? ????0	?1?00		
Dollosuchus dixoni	0010? 1???1 ?????	??1?? ????0 11???	?0010 ????? ??4??	?00?1 111?? ????1	01??0		
Harpacochampsa	????? ????? ?????	????? ????? ?????	????? ????? ?????	????? ????? ?????	?????		
Eothoracosaurus	????? ????? ?????	??1?? ??00 ?????	??0?0 0???0 ??30?	?1001 1?1?? ????0	?????		
Ocepesuchus	????? ????? ?????	????? ????? ?????	????? ????? ?????	????? ????? ?????	?????		
Eosuchus minor	???1? 1???? 0????	??11? ?00?0 ?100?	?0000 00??0 ?0300	00001 1110? 0??00	?1?00		
Eosuchus lerichei	???0? 1???? ?????	??1?? ????? ?1???	????0 ????? ??3??	????? ?11?? ?????	?????		
Siquisiquesuchus	????? ????? ?????	??1?? ????? ?????	??0?? ????? ??30?	0??01 ?110? 0????	?????		

	70	80	90	100	110	120	130
Bernissartia fagesii	00000 000?2 ?0000	00101 10030 1?101	?00?0 00101 00000	?000? 000?0 ???0?	?????
Hylaeochampsa vectiana	????0 100?? 1?0?0	00?01 100?0 0110?	?0?0 00100 00000	?00?? 0101? ???0?	000?1
Gryposuchus colombianus	00200 10010 10210	11011 10040 01103	?0200 00200 00000	?0100 00010 00010	00000
Osteolaemus tetraspis	00011 10111 00210	20101 11110 01010	11100 01101 00001	03000 00011 01100	01111
"Crocodylus" robustus	00011 10111 00211	22101 01110 01011	?0100 01100 10001	03000 00001 0?100	01111
"Crocodylus" lloydi	??01 10?11 00211	2010? 00?1? 011?1	?0100 01100 0?000	0300? ?00?1 01100	0?111
Tomistoma schlegelii	00201 10000 10210	22101 10010 01102	01100 01100 00001	03000 00101 01100	11111
Gavialosuchus americanus	002?1 10000 1021?	22011 00010 0?102	?0100 01100 00000	030?0 00101 ?1100	0?1?0
"Tomistoma" cairense	002?1 100?0 1?2??	20?11 00040 ?100?	????0 0?100 000?0	?30?0 0010? 011??	0?1??
Kentisuchus spenceri	000?1 100?? ?0210	20?01 00010 01101	?0?0 0?100 ??000	?30?? 00??? ??100	0?1?1
G. eggenburgensis	????1 10??0 ?021?	2?011 ?0010 01102	??00 0?100 ??0?0	?0??? 001?? ??10?	0???1
Kambara	00001 10112 00211	20101 00010 0010?	?0100 11000 00001	00000 00101 10001	11100
Allodaposuchus precedens	????1 10?00 10210	0000? 01??? 00???	?0?0 0?100 ?0?0?	000?0 0??11 100??	?0011
Argochampsa krebsi	??2?1 100?0 00210	110?? 10?4? ?1003	?0?0 00100 ?00?0	00??? ?01?? ?0000	0??0
Piscogavialis jugaliperforatus	??2?1 100?0 00211	21011 00040 01?03	?12?0 0?100 ?0000	?00?? 001?0 00010	00??0
Ikanogavialis gameroi	?02?1 10??? ?020?	210?? 10?40 0?1?3	?02?0 0?20? ??0?0	?00?? ?010? 0?01?	??0??
Dollosuchus dixoni	??2?1 100?0 ?021?	22011 00010 01002	?11?0 0?000 000?0	?3??? 0001? 0?100	0????
Harpacochampsa	??01 ?0?12 ?0211	211?? ?0?1? 011?1	?1??? ????? ?????	?000? 0?00 0?100	?1???
Eothoracosaurus	??2?1 100?0 1021?	00?11 00040 01?03	?00?0 00000 00000	000?? ?0100 0?0?0	?????
Ocepesuchus	????1 ????0 ?????	?1??? 10?4? ?00??	????0 0?10? ?????	????? ?2??? 1?0??	?????
Eosuchus minor	?02?1 100?0 10210	20011 00040 01002	?0000 0?100 00000	030?? ?0100 00000	0?0?1
Eosuchus lerichei	??201 100?0 ?021?	2?011 00040 01002	?00?0 0?100 ?0000	0300? 00100 0?000	0????
Siquisiquesuchus	??2?? 1???0 ?021?	?1?1? ?0?40 01?0?	?02?? 00100 ??000	?0??? ??10? 0?0??	??0??

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                                1     1     1     1     1     1     2
                                4     5     6     7     8     9     0
                                0     0     0     0     0     0     0

Bernissartia fagesii            0??00 ???00 00000 00?00 001?? ????? 00??0 00?0?  00010 00?0? 0?0?0 0??00 00000 ??000 1
Hylaeochampsa vectiana          00000 0?000 0?00? 100?0 00??? ????? ??0?0 01??0  00?01 ?0?00 ????? 0000? ????0 ??00 1
Gryposuchus colombianus         00000 ???32 10001 00?10 100?? ????? 000?1 00?10(01)010011111 1?110 01111 10100 23010 1
Osteolaemus tetraspis           00010 11121 10010 00011 00110 10101 01110 11001  00000 00000 00001 10001 10000 12000 0
“Crocodylus” robustus           00010 11101 10010 00011 001?? ????? 01110 11001  00000 00000 00001 10001 10000 02000 0
“Crocodylus” lloydi             00?10 11101 10010 00??1 0?1?? ????? 0?0?? 1?001  ?0??? ?000? ????? ?00?? ?00?0 02000 0
Tomistoma schlegelii            00010 11101 10001 00010 00110 10101 01010 11001  00000 10000 00001 10001 11100 20000 0
Gavialosuchus americanus        00010 ???11 10001 00?10 0011? ????? 00010 1?001  00000 00000 1?00? ?000? 10100 02000 0
“Tomistoma” cairense            00?10 ???01 1?00? 0???0 001?? ????? ?10?? ?1??1  0??01 ?0000 ??001 1000? ??00 ??000 0
Kentisuchus spenceri            ??10 ???01 10001 00?10 001?? ????? 010?0 ?1001  00000 00000 0?001 1000? ?0100 0?000 0
G. eggenburgensis               ????0 ?0111 10001 0???0 ????? ????? 0??0 11001  0?000 ?0000 0??0? ?000? ??100 ??000 0
Kambara                         010?0 10101 ?0110 01010 010?? ???01 0?000 11001  00000 00000 ??001 1000? ?0000 0?000 0
Allodaposuchus precedens        00000 ???01 0000? 00??0 00??? ????? ??0?0 00?00  ?00?0 ?0000 0??0? ?000? ??00 ?000 0
Argochampsa krebsi              ?0010 ?1?12 10001 0???0 1?0?? ????? 0?0?1 00120  0?000 ?0?01 1?10? 0111? ?1000 23000 0
Piscogavialis jugaliperforatus  00000 ???12 10001 0??10 100?? ????? 0?0?1 00120  1111? 2011? 1?10? 01?1? 11100 23000 0
Ikanogavialis gameroi           0??00 ???32 10001 00?0 1???? ????? 00??? ?0?20  ?1010 20?1? ????? 0?11? ?1100 23010 0
Dollosuchus dixoni              ??10 ???01 10001 00?0 0?0?? ????? 000?0 11001  00000 00010 0??01 10001 10100 02000 0
Harpacochampsa                  ?101? ????? 10??0 ?0??0 0?0?? ????? 0?0?? 1?0?1  ?0??? ??000 0?10? ?000? ?00?? ??0?0 ?
Eothoracosaurus                 ?0?00 ???11 10001 00?1? 00??? ????? 00??1 00110  1?010 11000 0??01 ?0001 000?0 ?3000 0
Ocepesuchus                     ????0 ???11 ??00? ?????0 0???? ????? ????1 ?0???  0??0 ?0?0? ????? ?000? ????? ??00 ?
Eosuchus minor                  00001 0?011 10001 00?1? 100?? ????? 000?1 0100?  00000 ?0?00 0??1 00001 ?0100 ?3001 0
Eosuchus lerichei               000?1 ?0?11 10001 0??10 10??? ????0 ?0?11 0100?  00000 10?00 0???? 0000? 00100 23001 0
Siquisiquesuchus                ??00 ???32 10001 00??? 1???? ????? 00??1 ?0?20  ?1?? 20?1? ????0 000?? ?11?0 2301? 1
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                             1 1 1 1 1 1 1   1       1       1       2
                     7 8 9 9 2 3 3 4 4 4 6   7       8       9       0
                     0 2 3 5 4 5 9 0 6 9 5   0       0       0       0

Borealosuchus formidabilis      1 0 0 2 0 1 0 1 0 1 0  10011 0?000 00000 00001 10001 10100 02000 0
Borealosuchus wilsoni           1 0 0 2 ? 1 0 1 0 1 0  ??01? ?0??? ?0?00 ????? ????? ?0000 ??000 0
Borealosuchus sternbergii       1 0 0 2 0 1 0 1 0 1 0  10011 000?0 00000 00001 10001 10000 00000 0
Leidyosuchus canadensis         1 0 0 1 0 0 2 1 1 1 0  ?0011 00000 00000 0?000 10000 00010 00000 0
Thoracosaurus macrorhynchus     1 1 0 3 0 0 1 1 0 1 1  00110 0??00 11000 0?10? 0000? 01100 23000 0
Eogavialis africanum            0 1 0 2 1 0 1 1 0 1 1  00100 00000 10100 1?110 00011 11100 23000 0
Siwalik Gavialis                0 1 ? 4 1 0 3 1 0 1 1  001?0 11110 ?1111 1?110 0111? ?0010 23010 1
Gavialis gangeticus             0 1 1 4 1 0 3 1 0 1 1  00120 11110 21111 11110 01111 10010 23010 1
Pristichampsus rollinatii       1 0 0 1 0 0 0 1 0 1 ?  1?001 00010 00000 0??0? ?000? ?0001 ?2000 0
Diplocynodon hantonensis        1 0 0 2 0 0 2 1 ? 1 0  11001 ?000? 00000 00001 10000 00000 00000 0
Diplocynodon ratelii            1 0 0 2 0 0 2 1 ? 1 0  11001 10000 00?00 00001 1000? 00000 ?0000 0
Diplocynodon darwini            1 0 0 2 0 0 2 1 1 1 0  11001 ????? 00000 00?01 10??0 00000 00000 0
Stangerochampsa mccabei         1 0 2 1 3 0 2 1 1 1 0  11001 00101 00000 0??01 1000? 01010 01100 1
Brachychampsa montana           1 3 2 1 3 0 2 1 1 1 0  11001 00101 ?0000 00?01 10000 ?1010 01100 1
Alligator sinensis              1 2 1 0 0 0 2 1 1 1 0  11?01 00001 00000 0?001 10000 00010 10100 1
Alligator mississippiensis      1 2 1 0 0 0 2 1 1 1 0  11001 00000 00000 00001 10000 00010 10100 1
Alligator mefferdi              1 2 1 0 0 0 2 1 1 1 0  11?01 ?00?1 00000 00001 10000 000?0 10100 1
Alligator olseni                1 2 1 0 0 0 2 1 1 1 0  ?1001 00101 ?0000 00001 100?0 00010 10100 1
Alligator mcgrewi               1 2 1 0 0 0 2 1 1 1 0  11001 0?001 00000 00001 10000 00010 00100 1
Alligator prenasalis            1 0 1 0 0 0 2 1 1 1 0  11001 00?01 0000? 00?01 ?0000 000?0 01100 1
Allognathosuchus mooki          1 0 1 1 2 0 2 1 1 1 0  1100? 00101 0?0?0 00?0? 1000? 000?0 01000 1
Wannaganosuchus brachymanus     1 2 1 1 0 0 2 1 1 1 0  11001 00001 00000 0?00? 100?? ?0010 01100 1
Procaimanoidea kayi             1 2 1 ? ? 0 2 1 1 1 0  ?1??1 00001 00000 00001 100?0 0??11 10?00 1
Arambourgia gaudryi             1 0 1 1 ? 0 ? 1 ? 1 0  11??0 0???1 00000 0??01 1000? ?00?1 10000 1
Eocaiman cavernosus             1 4 ? ? ? ? 2 1 1 ? ?  ????? 0000? 000?? ???0? ????? 0??10 ????0 1
Purussaurus neivensis           1 4 1 1 2 0 2 1 1 1 ?  ?1001 01001 ?0000 0?00? 10000 ?0000 ??100 0
Nettosuchidae                   1 4 0 2 0 0 2 1 1 1 0  ?1021 0?001 00000 0?10? 100?0 ?1000 1?100 0
Caiman crocodilus               1 4 1 1 0 0 2 1 1 1 0  11001 00001 00000 00001 10000000(01)012000(01)
Melanosuchus niger              1 4 1 1 0 0 2 1 1 1 0  11001 00001 00000 00001 10000 00000 12000 0
Paleosuchus trigonatus          1 3 0 1 0 0 2 1 0 1 0  11001 00000 000?0 00001 10000 00000 12000 0
Paleosuchus palpebrosus         1 3 0 1 0 0 2 1 0 1 0  11001 00000 000?? 0?001 1??0 00000 12000 0
Crocodylus cataphractus         1 0 0 2 0 0 0 1 0 1 0  11001 01100 00000 00001 10001 10000 0?000 0
Crocodylus niloticus            1 0 0 1 0 0 0 1 0 1 0  11001 00100 00000 00001 10001 10000 12000 0
Crocodylus porosus              1 0 0 1 0 0 0 1 0 1 0  11001 00100 00000 00001 10001 10000 12000 0
Crocodylus rhombifer            1 0 0 1 0 0 0 1 0 1 0  11001 00000 00000 0?001 10001 10000 12000 0
“Crocodylus” palaeindicus       1 2 0 1 0 0 0 1 0 1 0  ?1001 ??0?? ?000? ??00? 1000? ?0000 1?000 ?
“Crocodylus” megarhinus         1 ? 2 1 0 0 0 1 ? 1 0  11001 ?0??? ?0000 0??01 ?000? ?00?0 ??000 ?
Euthecodon arambourgi           1 0 ? 3 1 0 0 1 0 ? 0  ?110? 0?00? ?0000 0??0? ????? ?01?0 23000 0
Tomistoma lusitanica            1 2 0 2 0 0 0 1 0 1 0  11001 0??00 0000? 00001 ?00?1 10100(02)20000
Brachyuranochampsa eversolei    1 0 0 1 ? 0 0 1 0 1 0  11001 0?0?0 ?0000 0?00? 1000? ?0010 02000 0
Dormaal crocodyloid             1 3 ? 1 0 0 0 1 0 1 0  11001 ?0000 00000 0?001 10001 10000 ???0 ?
“Crocodylus” acer               1 0 0 1 0 0 0 1 0 1 0  11001 00000 ?0000 0?00? 1000? ?0000 ??00 0
“Crocodylus” affinis            1 0 0 1 0 0 0 1 0 1 0  11001 00000 00000 00001 10001 10000 02000 0
Asiatosuchus germanicus         1 0 0 1 0 0 0 1 ? 1 0  110?1 0???1 0000? 00?01 1??0 000?0 00000 ?
Prodiplocynodon langi           1 0 ? 1 0 0 0 1 0 1 0  11001 ?00?? ?0000 0?00? 1000? ?00?0 ??000 ?
Australosuchus clarkae          1 2 0 1 0 0 0 1 0 1 ?  ??001 01?00 ?000? 00?0? 1???? ?00?0 ??000 ?
Thoracosaurus neocesariensis    1 1 0 3 0 0 1 1 0 1 1  00??? 0?000 ?1?00 ???1? 000?? ????0 23000 0
Paratomistoma courti            1 0 0 ? ? ? ? ? 1 0 ? 1  ?1??? 1?00 ??00 ???1 ?0001 ????0 ??00 ?
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APPENDIX 3.   Apomorphy list for Gavialoidea

Only the unambiguous synapomorphies are listed. (See Fig. 5 for node number).

Node 1: Gavialoidea: 19(1), 35(0), 43(3), 68(2), 84(1), 89(4), 118(1), 119(0), 139(1), 145(1), 153(0), 165(1), 176(1).

Node 2: *Eosuchus*: 81(2), 112(3), 135(1), 151(1), 167(1), 200(1).

Node 3: 95(3), 168(1), 177(1).

Node 4: 82(1).

Node 5: 86(1).

Node 6: 177(0).

Node 7: 151(1), 189(1).

Node 8: 140(2), 180(1), 187(1), 188(1).

Node 9: 171(1), 173(1), 174(1), 179(1).

Node 10: 139(3), 199(1).

Node 11: 70(0), 113(1), 177(1), 184(1), 192(0).

Node 12: *Gavialis*: 95(4), 140(1), 193(0), 194(1).

APPENDIX 4.   List of taxa used in Fig. 8 (D, Dyrosauridae; G, Gavialoidea; M, Mosasauridae; P, Plesiosauroidea).

MAASTRICHTIAN

Marine reptiles

Oulad Abdoun Basin—*Mosasaurus beaugei* (M); *Platecarpus ptychodon* (M); *Halisaurus arambourgi* (M); *Globidens phosphaticus* (M); *Prognathodon* sp. (M); *Carinodens belgicus* (M); "*Plesiosaurus*" *mauritanicus* (P).

Iullemmeden Basin—*Goronyosaurus nigeriensis* (M); *Igdamanosaurus aegyptiacus* (M); *Pluridens walkeri* (M); *Mosasaurus* sp. (M); Plioplatecarpinae indet. (M).

Eastern American coast—*Mosasaurus hoffmani* (M); *Mosasaurus conodon* (M); *Plioplatecarpus marshi* (M); *Halisaurus platyspondylus* (M); *Prognathodon rapax* (M); *Leiodon sectorius* (M); Elasmosauridae indet. (P).

Crocodyliformes

Oulad Abdoun Basin—*Ocepesuchus eoafricanus* (G).

Iullemmeden Basin—*Sokotosuchus ianwilsoni* (D).

Eastern American coast—*Hyposaurus rogersii* (D); *Thoracosaurus neocesariensis* (G); *Eothoracosaurus missippiensis* (G).

PALEOCENE

Crocodyliformes

Oulad Abdoun Basin—*Phosphatosaurus* sp. (D); *Hyposaurus paucidens* (D); *Hyposaurus* sp. (D), *Chenanisuchus lateroculi* (D); *Arambourgisuchus khouribgaensis* (D); *Atlantosuchus coupatezi* (D); *Argochampsa krebsi* (G); Crocodyliformes indet.

Iullemmeden Basin—*Rhabdognathus keiniensis* (D); *Rhabdognathus aslerensis* (D); *Congosaurus compressus* (D); *Congosaurus bequaerti* (D); *Hyposaurus* sp (D); *Hyposaurus* sp. (D).

Eastern American coast—*Hyposaurus rogersii* (D); *Thoracosaurus neocesariensis* (G); *Eosuchus minor* (G).