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Dyrosaurid (Crocodyliformes: Mesoeucrocodylia) Fossils from the Upper Cretaceous and Paleogene of Mali: Implications for Phylogeny and Survivorship across the K/T Boundary

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ABSTRACT

We describe new dyrosaurid fossils from three localities in Mali, representing strata of Maastrichtian, Paleocene, and Eocene ages. The fossils significantly extend the temporal and geographic ranges of several known dyrosaurid taxa. *Rhabdognathus keiniensis* and *Chenanisuchus lateroculi* are identified for the first time from Maastrichtian sediments. Additional material is referred to *Phosphatosaurus gavialoides* and, tentatively, the genus *Sokotosuchus*. These discoveries represent the first occurrence of *Chenanisuchus* and possibly of *Sokotosuchus* from Mali. Previously unknown morphological character states are incorporated into existing data matrices, reducing the amount of missing data. Phylogenetic analyses largely corroborate prior hypotheses of dyrosaurid relationships, but indicate a need for new characters to resolve the relationships of certain genera and species. The occurrence of both basal (e.g., *Chenanisuchus lateroculi*) and highly nested (e.g., *Rhabdognathus keiniensis*) members of Dyrosauridae on both sides of the K/T boundary indicates that dyrosaurid diversification was well underway by the latest Cretaceous, and that most, if not all dyrosaurid species survived the extinction event. The geology of the Mali's Tilemsi Valley is clarified; some rocks previously assigned to the Iullemmeden Basin actually represent extensions of other basins: the Taoudeni Basin and Gao Trench.

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INTRODUCTION

Dyrosaurids are extinct, longirostrine crocodyliforms known mainly from shallow marine deposits of Late Cretaceous through late Eocene age (e.g., Buffetaut, 1978a; Denton et al., 1997). Although they have been found in North America, South America, and Asia (e.g., Denton et al., 1997; Jouve et al., 2005b), the most abundant remains of dyrosaurids are known from western Africa (e.g., Buffetaut, 1978b, 1980; Brochu et al., 2002; Jouve, 2004; Jouve and Schwarz, 2004; Jouve et al., 2005a, 2005b; Jouve, 2007). Despite being relatively common components of late Mesozoic and early Cenozoic faunas in western Africa, dyrosaurids present special challenges to the interpretation of crocodyliform biostratigraphy and phylogenetics. Specifically, the naming of anatomically nonoverlapping taxa has complicated efforts to diagnose new species, to confidently refer new specimens to existing species, and to generate a stable species-level phylogeny of Dyrosauridae (Brochu et al., 2002; Jouve, 2007).

Dyrosaurids figure prominently in contemporary debates over crocodyliform systematics, and the inclusion of one or a few dyrosaurid taxa in phylogenetic analyses has significantly affected tree topology in prior analyses. Buckley and Brochu (1999) found support for a monophyletic longirostrine clade including Dyrosauridae, *Sokotosuchus*[6], *Pholidosaurus*, and Thalattosuchia (*Pelagosaurus*, Teleosauridae, and Metriorhynchidae) as the sister taxon to crown-group Crocodylia. This result, unexpected in light of more traditional hypotheses (e.g., Clark, 1994), placed several putatively basal taxa at a highly nested position within Neosuchia. When Dyrosauridae, *Sokotosuchus*, and *Pholidosaurus* are excluded from this analysis, however, Thalattosuchia occupies a more conventional position on the resulting tree, as a basal lineage of Mesoeucrocodylia. Buckley and Brochu (1999) suggested that certain conspicuous characters related to elongation of the snout artificially inflated support for a close relationship between longirostrine taxa that are actually distantly related. A subsequent analysis of a slightly modified data set (Buckley et al., 2000) did not include dyrosaurs, and accordingly recovered a basal position for Thalattosuchia.

Brochu et al. (2002) described a well-preserved dyrosaurid braincase, allowing several previously unknown cranial characters to be scored. The characters were considered representative of all dyrosaurids, and incorporated into a modified phylogeny based on the matrix of Buckley and Brochu (1999). The resulting tree placed a Dyrosauridae + *Sokotosuchus* clade at a highly nested position, as the sister taxon to Thalattosuchia + *Pholidosaurus*.

Sereno et al. (2001) and Wu et al. (2001) also considered the position of selected dyrosaurids in their phylogenetic analyses of crocodyliform relationships. Both analyses recovered a highly nested position for dyrosaurids. Wu et al. (2001) found a monophyletic Dyrosauridae (containing *Dyrosaurus* and *Hyposaurus*) as the sister taxon to the longirostrine form *Terminonaris*, with *Pholidosaurus* and Thalattosuchia as closely related but incompletely resolved taxa. Sereno et al. (2001) found support for a sister-taxon relationship between *Terminonaris* and *Sarcosuchus*, with *Dyrosaurus* and *Pholidosaurus* as successively more distant sister taxa.

Although the position of dyrosaurids among higher-level crocodyliform clades has been the subject of significant discussion, the phylogenetic relationships between individual dyrosaurid genera and species have only recently received attention. Buffetaut (1978b) presented a hypothetical tree (not based on cladistic character data) to explain the relationships among four dyrosaurid genera: *Dyrosaurus*, *Hyposaurus*, *Phosphatosaurus*, and *Rhabdognathus*. The tree placed the large-bodied, Eocene *Phosphatosaurus* at the base of the dyrosaurid radiation, with *Rhabdognathus* and *Dyrosaurus* + *Hyposaurus* as successively more highly nested taxa (fig. 1A).

To date, only two cladistic analyses have been reported that address the genus-level and, in part, species-level phylogeny of Dyrosauridae. With his redescription of the cranial anatomy of *Dyrosaurus phosphaticus*, Jouve (2005) included the first cladistic analysis of dyrosaurids. The analysis recovered a monophyletic Dyrosauridae consisting of the

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[6] Although considered a separate taxon in certain phylogenetic analyses (e.g., Clark, 1994; Buckley and Brochu, 1999; Buckley et al., 2000; Brochu et al., 2002; Pol and Norell, 2004), *Sokotosuchus* is generally considered to be a dyrosaurid (see, e.g., Buffetaut [1976] and Jouve et al. [2005b]).

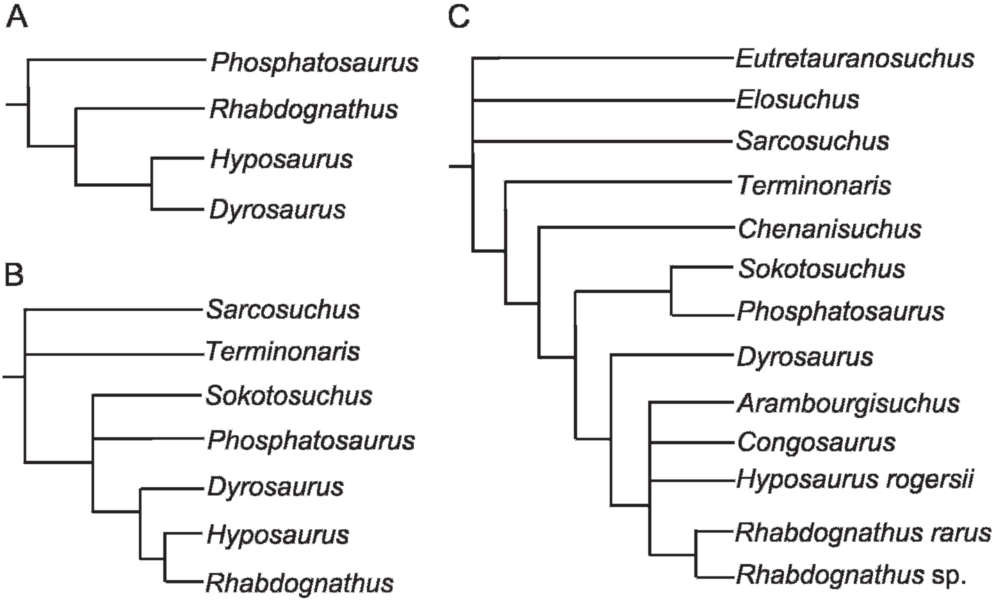

Fig. 1. Alternative hypotheses explaining the phylogenetic relationships of dyrosaurids. **A**, "manual cladogram", not based on a cladistic data matrix, hypothesized by Buffetaut (1978b). **B**, cladogram presented by Jouve (2005), based on cladistic analysis of 12 characters. **C**, cladogram presented by Jouve et al (2005b), based on cladistic analysis of 30 characters. Note basal position of *Phosphatosaurus* and highly nested position of *Hyposaurus* common to all hypotheses.

same four taxa used by Buffetaut (1978b) along with *Sokotosuchus*. Consistent with assertions by Buffetaut (1978b, 1979a) that *Phosphatosaurus* and *Sokotosuchus* were the most primitive dyrosaurids, these two genera occupy a basal (albeit unresolved) position on Jouve's (2005) tree. In contrast to Buffetaut's (1978b) tree, however, Jouve (2005) found *Hyposaurus* and *Rhabdognathus* to be the two most highly nested dyrosaurids (fig. 1B).

A second, more comprehensive cladistic analysis was presented by Jouve et al. (2005b), and included the newly described taxa *Arambourgisuchus* and *Chenanisuchus*, two separate species of *Rhabdognathus*, and several new characters. The results again supported a basal position for *Phosphatosaurus* and *Sokotosuchus*, this time united in a monophyletic Phosphatosaurinae sensu Buffetaut (1979a). In addition, the two species of *Rhabdognathus*, *R. rarus* and *R.* sp., formed a highly nested, monophyletic genus (fig. 1C).

The dyrosaurid specimens recently described by Brochu et al. (2002), Jouve et al. (2005a, 2005b), and Jouve (2007) contribute significantly to the understanding of species diversity and evolutionary history of these marine crocodyliforms. These fossils include well-preserved cranial remains, facilitating the description of new morphological characters that describe the occipital and supratemporal regions of the skull. Jouve et al. (2005b) emphasized the dimensions of the interfenestral bar and occipital tuberosities as particularly important characters for morphological systematics of dyrosaurids. The description of new dyrosaurid specimens that preserve these regions, along with the addition of new data from known species, is expected to provide additional insights into the evolutionary history of dyrosaurids (Jouve et al., 2005b).

Because dyrosaurid occurrences span the K/T boundary, an understanding of the species-level phylogeny of the clade is important for broader studies of faunal change across this major extinction event. Some dyrosaurid lineages clearly survived the extinction, and occur on both sides of the K/T boundary, whereas others, known only from Paleogene localities, may have speciated after the event.

Importantly, certain members of purportedly basal dyrosaurid lineages (e.g., *Phosphatosaurus*, *Chenanisuchus*; Buffetaut, 1979a; Jouve et al., 2005a) are known only from Paleogene localities, implying that long ghost lineages (Norell, 1992) separate them from longer-lived taxa that occur on both sides of the K/T boundary (e.g., *Hyposaurus*). The geographic origin of dyrosaurids and their history of worldwide dispersal are also best interpreted in the context of a robustly supported phylogeny of Dyrosauridae.

Recent fieldwork in the shallow marine deposits of the Iullemmeden and Taoudeni basins of northeastern Mali has resulted in the discovery of several new fossiliferous localities (Roberts and O'Leary, 1999; Brochu et al., 2002; Tapanila et al., 2004). The rocks, which range from Maastrichtian to late Eocene in age, incorporate repeated sequences of phosphate-rich conglomerates that preserve a diverse vertebrate fauna. In addition to mammals (O'Leary et al., 2006), turtles (Gaffney et al., 2007), sharks, rays, and pycnodont fishes, an abundance of dyrosaurid crocodyliform fossils has been recovered from these localities (e.g., Brochu et al., 2002; Hill, 2006; McCartney and Hill, 2007). Here, we describe several dyrosaurid fossils from the new Malian localities. Morphological data from these specimens are incorporated into existing data matrices to test important phylogenetic hypotheses, including those relating to dyrosaurid monophyly and interrelationships of known dyrosaurid species.

ABBREVIATIONS: AMNH, American Museum of Natural History, New York; CNRST-SUNY, Centre National de Recherche Scientifique et Technologique du Mali–Stony Brook University; MM, Musée de la Compagnie des Phosphates de Gafsa, Metlaoui, Tunisie.

GEOLOGIC SETTING

Late Mesozoic rifting between South America and Africa resulted in the development of the southern Atlantic Ocean (Petters, 1979; Reyment and Dingle, 1987; Burke, 1996). Across West Africa, however, a series of other basins, including the Iullemmeden, Taoudeni, and Chad basins, were also affected by this major Gondwanan breakup event. Most notably, regional crustal attenuation, fault reactivation, and thermal subsidence resulted in the preservation of widespread Late Cretaceous–Paleogene sedimentary sequences across North and West Africa (fig. 2). This time was also characterized by globally elevated sea levels and subsequent development of a north-south trending, epicontinental seaway, known as the Trans-Saharan Sea (TSS), which inundated portions of the Taoudeni and Iullemeden basins (Greigert, 1966; Reyment, 1980).

Although deposits of the TSS are extensively preserved within the Iullemmeden Basin, which occupies most of northern Mali (east of the Adrar des Iforas Mountains), southeastern Niger, and northwestern Nigeria, there are also other excellent exposures of the TSS within two other basins in Mali. TSS deposits preserved within the Tilemsi Valley on the west side of the Adrar des Iforas are not part of the Iullemeden Basin, as suggested by Jouve (2007), but rather are part of the Taoudeni Basin (O'Leary et al., 2006: fig. 1). Late Cretaceous–Eocene TSS strata in the Tilemsi Valley overlie a deformed Pan-African suture belt that defines the eastern boundaries of the Taoudeni Basin and underlying basement rocks of the West African Craton. Moreover, the thickest sequence of TSS deposits are preserved to the south and east of the Tilemsi Valley within the Gao Trench (Détroit Soudanais), which represents a narrow, E-W trending half graben basin connecting the Taoudeni and Iullemmeden basins (fig. 2; Radier, 1959).

Sedimentary sequences across each of these basins are characterized by broad similarities in regional stratigraphy and sedimentology (e.g., see Radier, 1959; Greigert, 1966; Petters, 1979; and others), however, closer inspection reveals that significant variations exist across these basins, which have not been previously recognized or well studied (see Tapanila et al.,2008). In particular, considerable variations in thickness, lateral and vertical facies stacking patterns, and depositional environments exist between the Iullemmeden Basin, the Gao Trench, and the Taoudeni Basin (see Moody and Sutcliffe, 1993; Tapanila et al.,2008). Furthermore, the extent of the Trans-Saharan Seaway in the early Paleogene is not well understood. Its passage has been

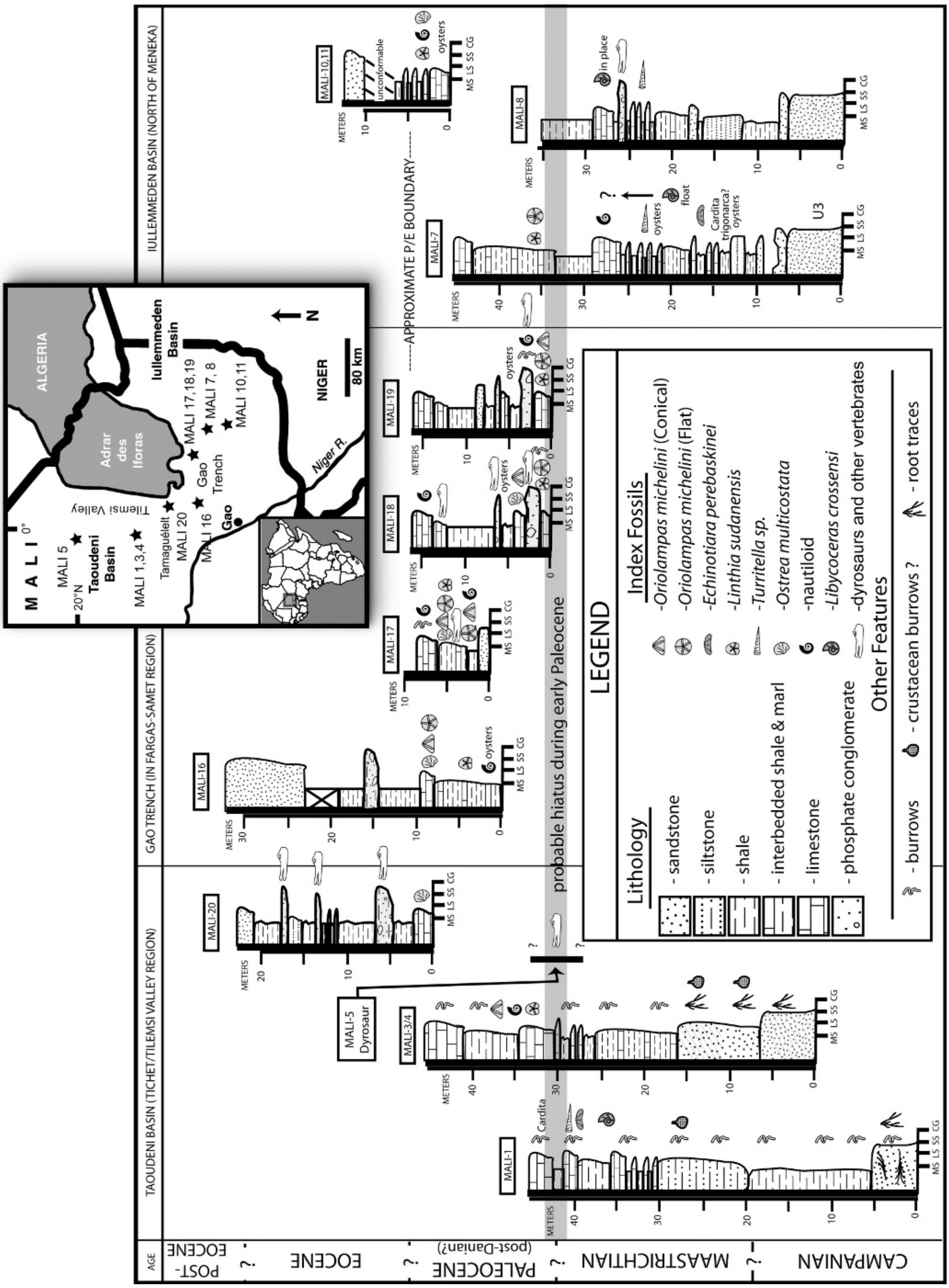

Fig. 2. Diagrammatic stratigraphic sections depicting correlations in age between strata at different Malian localities. Fossils described herein come from deposits in Mali-8 (Maastrichtian), Mali-18 (Paleocene), and Mali-20 (Eocene). Inset: map of eastern Mali showing relative locations of fossiliferous localities.

studied with standard lithostratigraphic and biostratigraphic approaches (Radier 1959; Greigert, 1966; Bellion et al., 1989, 1992), which has resulted in ambiguous age relationships and unresolved regional correlations. Patterns and frequency of early Paleogene sea level cyclicity are relatively constrained in the southern Trans-Saharan realm (i.e., Nigeria), yet unresolved in Mali, particularly between these different basins. This demonstrates the need for greater and more detailed stratigraphic work in the region, utilizing modern approaches such as sequence stratigraphy and chemostratigraphy, as well as improved biostratigraphy.

SYSTEMATIC PALEONTOLOGY

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Dyrosauridae de Stefano, 1903

Rhabdognathus Swinton, 1930

(= *Rhabdosaurus* Bergounioux, 1956)

Type Species: *Rhabdognathus rarus* Swinton, 1930; nomen dubium (Jouve, 2007).

Included Species: *R. aslerensis* Jouve, 2007; *R. keiniensis* Jouve, 2007.

Age and Distribution: Maastrichtian-Paleocene, Tilemsi Valley, Mali.

Diagnosis: As in Jouve (2007); dyrosaurid with caudal wall of supratemporal fenestra largely visible in dorsal view; interfenestral bar narrow and unornamented; occipital tuberosities long, well-developed and widely spaced; suture between parietal and supraoccipital gently sinuous ventrally (not W-shaped). See Jouve (2007) for other diagnostic characters of this genus.

Discussion: Swinton (1930) described *Rhabdognathus rarus* based on a few fragmentary, tubular segments of lower jaw from the Paleocene of Nigeria. Additional mandibular material was referred to this genus by Halstead and Middleton (1976) and Buffetaut (1980). Buffetaut (1980) also described the first cranial remains referred to *Rhabdognathus*, but did not include any characters of the skull in his emended diagnosis. Because *Rhabdognathus* could be recognized only on the basis of mandibular characters, subsequent referrals of cranial material to the genus were necessarily tentative (e.g., Langston, 1995; Brochu et al., 2002). Jouve (2007) recently revised the genus, examining all known material and recognizing two species of *Rhabdognathus*: *R. aslerensis* and *R. keiniensis*. He declared *Rhabdognathus rarus* a nomen dubium, but retained it as the type species of the genus. *Rhabdognathus compressus* (Buffetaut, 1980) was transferred to the genus *Congosaurus* on the basis of alveolar morphology.

Jouve (2007) referred to another species as "*Rhabdosaurus acutidentatus*" and attributed it to Bergounioux (1956), acknowledging that it was later transferred to *Rhabdognathus* by Buffetaut (1978b). In fact, Bergounioux (1956) named *Rhabdosaurus acutirostris* (not *acutidentatus*), which Buffetaut (1978b) transferred to *Rhabdognathus acutirostris*. The holotype and only known specimen of this species has been lost (Buffetaut, 1978b; and see Jouve, 2007), but because it consists of mandibular material, according to Jouve (2007) it can only be referred to *Rhabdognathus* sp. The two currently recognized species of *Rhabdognathus* (*R. aslerensis* and *R. keiniensis*) differ from one another primarily in characters of the occipital region (Jouve, 2007).

Rhabdognathus keiniensis Jouve, 2007

(= *Rhabdognathus rarus* Swinton, 1930 [in part])

Holotype: MNHN TGE 4031.

New Referred Specimens: CNRST SUNY 276; 277.

Locality: Mali-8; Maastrichtian phosphate conglomerate.

Diagnosis: As in Jouve (2007); *Rhabdognathus* with extremely well-developed, sharp occipital tuberosities; deeply concave caudal margin of the parietal between occipital tuberosities, the rostral extent of which reaches or almost reaches the caudal level of the supratemporal fenestra.

Description: CNRST SUNY 276 and CNRST SUNY 277 exhibit a similar general morphology. Both specimens preserve the caudal region of the skull roof, including parts of the parietal, squamosal, supraoccipital, and

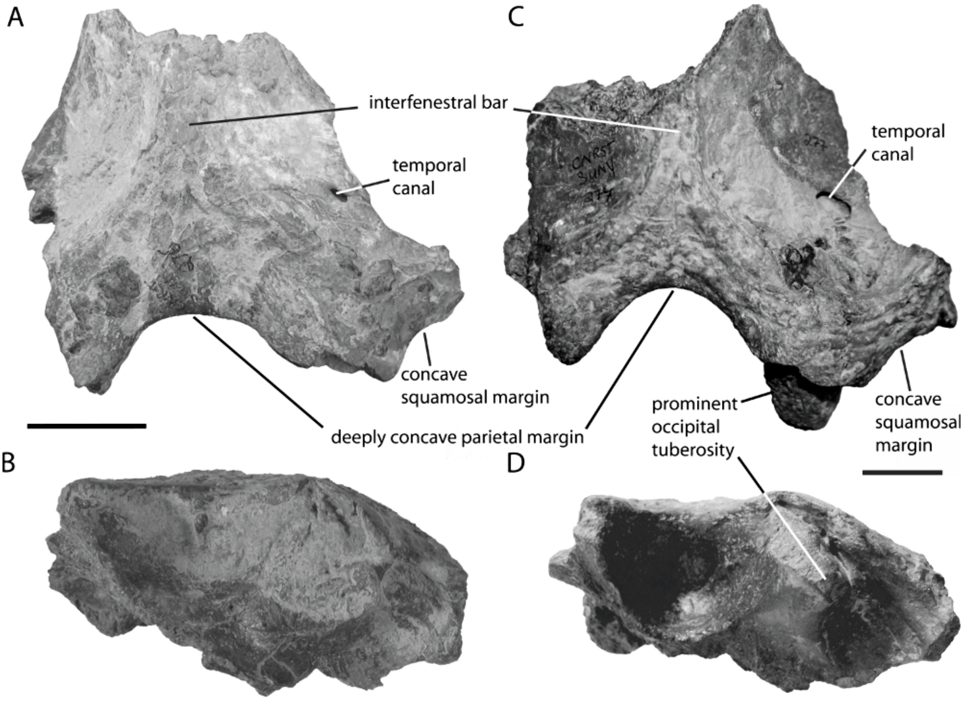

Fig. 3. *Rhabdognathus keiniensis*. Partial skull roof and occiput of two individuals. CNRST SUNY 276 in **A**, dorsal and **B**, occipital views. CNRST SUNY 277 in **C**, dorsal and **D**, occipital views. Scale bars equal 2 cm.

exoccipital elements. They can be identified as dyrosaurids on the basis of closely spaced otic capsules, relatively large supratemporal fenestrae, and prominent occipital tuberosities.

In dorsal view, CNRST SUNY 277 exhibits a deeply excavated caudal border of the parietal, forming a deep, U-shaped concavity (fig. 3). The parietal forms the caudomedial border of the supratemporal fenestrae. On the right side, the parietal articulates laterally with the squamosal, which forms the caudolateral border of the supratemporal fenestra. The caudal wall of each supratemporal fenestra slopes gently rostrally, and is largely visible in dorsal view. The occipital tuberosities are well developed and prominent, and visible in dorsal view, extending beyond the caudal margin of the skull roof.

In occipital view, the space between the occipital tuberosities forms a deep, hemispherical concavity whose rostralmost extent is formed by the supraoccipital. The parietal is visible as a narrow strip in occipital view, contributing to the dorsal margin of the supraoccipital region. The right posttemporal fenestra is preserved, roofed primarily by the parietal with only a small contribution from the squamosal. The occipital tuberosities are composed entirely of the exoccipitals, which also articulate with the squamosals along an oblique suture.

The morphology of CNRST SUNY 276 compares closely with that of CNRST SUNY 277, being slightly smaller in all dimensions. The distal ends of the occipital tuberosities are broken, and their caudal extent cannot be determined. Additionally, the concavity between the occipital tuberosities is somewhat less pronounced, and the supraoccipital bears a weak median ridge.

PHOSPHATOSAURUS Bergounioux, 1955

PHOSPHATOSAURUS GAVIALOIDES Bergounioux, 1955

HOLOTYPE: MM D15.

New Referred Specimens: CNRST SUNY 275, articulated dentaries and splenials with one replacement tooth.

Locality: Mali-20; Eocene phosphate conglomerate.

Description: CNRST SUNY 275 (fig. 4) is recognized as a dyrosaurid on the basis of a relatively small alveolus for the seventh dentary tooth. It is referred to *Phosphatosaurus gavialoides* on the basis of several characters, including large size, nonhomodont dentition, robust teeth with straight carinae and longitudinally striated enamel, and a spoon-shaped lateral expansion of the rostral portion of the mandible. In addition, CNRST SUNY 275 possesses a splenial symphysis that reaches the level of the ninth alveolus, and a mandibular symphysis that is inclined caudodorsally when viewed from the lateral side. Both of these features have been described in a specimen referred to *Phosphatosaurus* sp. (Buffetaut, 1979b).

Examination of the specimen allows the interpretation of certain character states that could not be identified in previously known specimens of *Phosphatosaurus*. Jouve et al. (2005b) coded the character describing the seventh mandibular tooth as unknown for *Phosphatosaurus* in their analysis. Buffetaut (1979b), however, described a fragment of the mandibular symphysis of *Phosphatosaurus* sp. from the Paleocene of Niger that preserves the seventh through tenth alveoli. The specimen shows the presence of a small seventh dentary alveolus in *Phosphatosaurus*. CNRST SUNY 275 further corroborates this interpretation, as its seventh alveolus is comparatively small on both sides. The specimen shows an unusual variation of this character, however. In CNRST SUNY 275, both the sixth and seventh dentary teeth are small in size, and are closer to one another than to the fifth or eighth tooth. Although this character has not been reported in dyrosaurids before, such "alveolar couplets" occur in certain

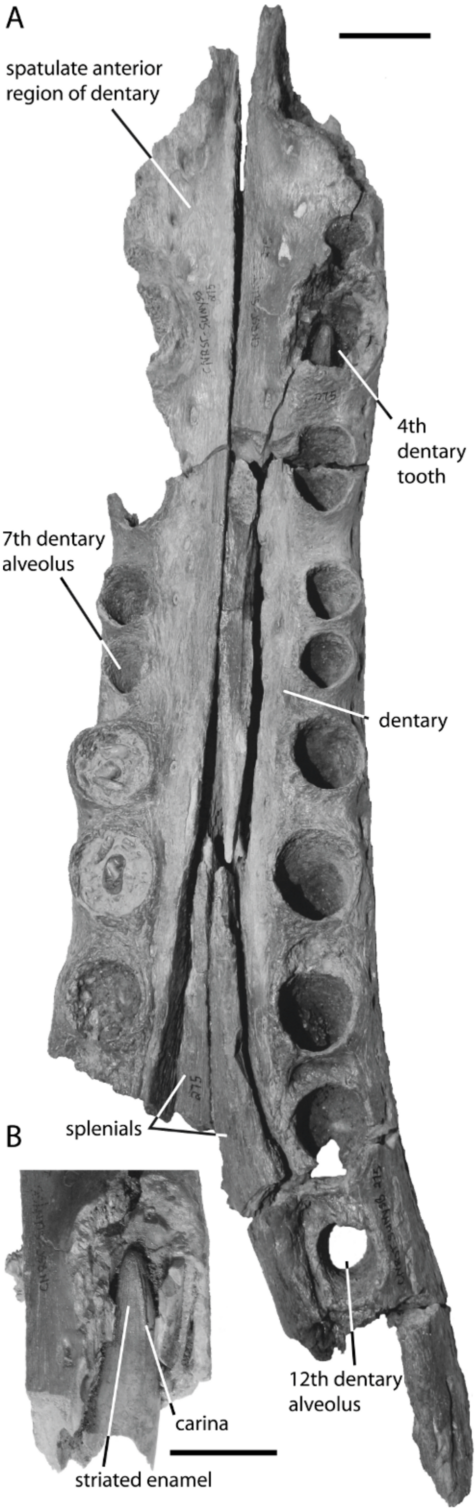

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Fig. 4. *Phosphatosaurus gavialoides*. CNRST SUNY 275, partial lower jaw with one replacement tooth. Inset: detail of tooth showing features of enamel. Scale bars equal 2 cm.

other longirostrine crocodyliforms, notably *Eosuchus minor* (Brochu, 2006). The diastemata on either side of the alveolar couplets presumably served to receive comparatively larger maxillary teeth.

CNRST SUNY 275 also allows interpretation of Jouve et al.'s (2005b) character describing the relative width of the mandibular symphysis. It is clearly wider mediolaterally than it is high dorsoventrally, giving the symphysis a wide, oval cross section along its entire length. Nothing is preserved of the external mandibular fenestra, if one existed in this taxon.

Dyrosauridae de Stefano, 1903

cf. Phosphatosaurinae Buffetaut, 1979a

New Referred Specimens: CNRST SUNY 279, caudal region of skull roof and occiput.

Locality: Mali-18; Paleocene phosphate conglomerate.

Description: CNRST SUNY 279 preserves the caudal region of the skull roof of a large dyrosaurid (fig. 5). The specimen is recognized as a dyrosaurid on the basis of a dorsoventrally high occipital region, pronounced medial expansion and midline contact of the otic capsules, and large supratemporal fenestrae separated by a relatively narrow interfenestral bar. Although occipital tuberosities were present, their extent cannot be determined due to breakage at the bases of both processes. The specimen preserves most of the parietal and paired squamosals, along with the supraoccipital and portions of the exoccipital elements. The dorsal surface of the skull roof is robustly ornamented with deep pits. The dorsal surface of the interfenestral bar is broken, however, and the extent of ornamentation on this structure cannot be assessed. The caudal margin of the skull roof is not straight, but moderately invaginated, forming a wide V-shape. This differs from the deep, U-shaped concavity seen in *Rhabdognathus keiniensis*, which may extend rostrally beyond the caudal border of the supratemporal fenestra. Based on its large size, this specimen probably represents a member of Phosphatosaurinae, the taxon that includes *Phosphatosaurus* and *Sokotosuchus* (Buffetaut, 1979a; but see Jouve et al., 2005b).

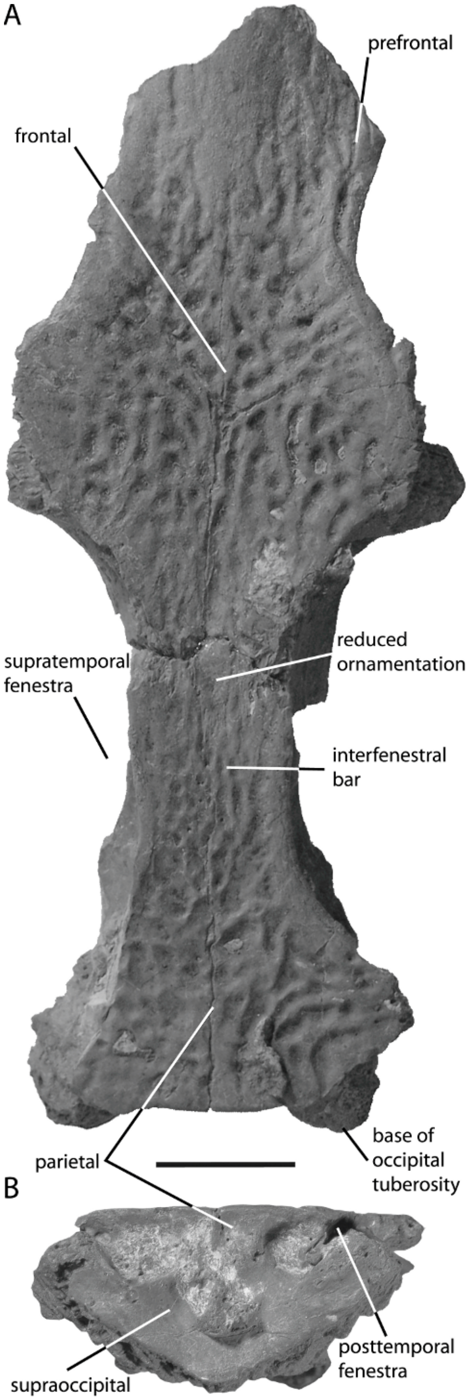

Fig. 5. *Chenanisuchus lateroculi.* CNRST SUNY 280, partial skull roof and occiput in **A**, dorsal and **B**, occipital views. Scale bar equals 2 cm.

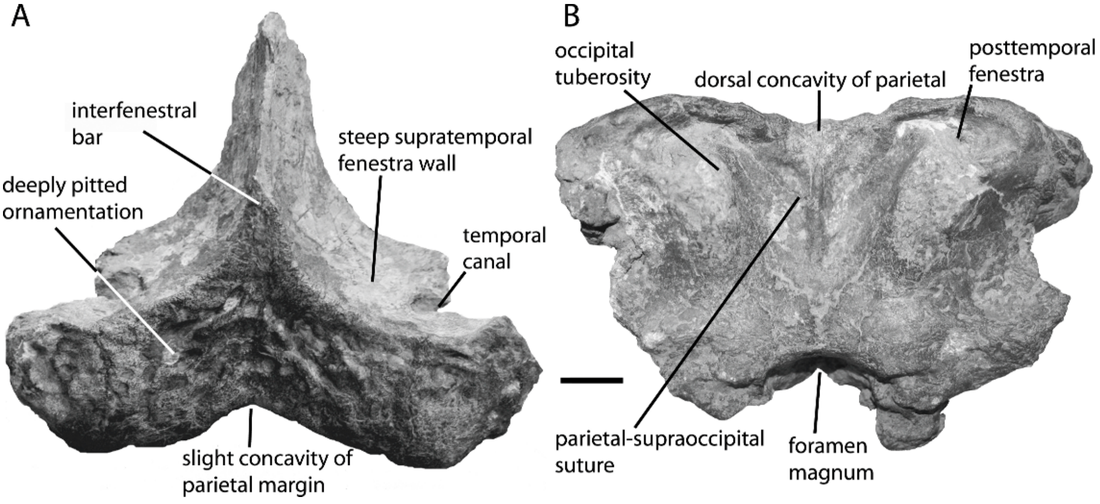

Fig. 6. cf. *Sokotosuchus*. CNRST SUNY 279, partial skull roof and occiput in **A**, dorsal and **B**, occipital views. Scale bar equals 2 cm.

The gently invaginated caudal parietal margin compares more closely with that of *Sokotosuchus* than with the straight parietal margin of *Phosphatosaurus* (e.g., Halstead, 1975; Buffetaut, 1979a; Jouve et al., 2005a).

Chenanisuchus Jouve et al., 2005a

Chenanisuchus lateroculi Jouve et al., 2005a

Holotype: OCP DEK-GE 262 (Jouve et al., 2005a).

New Referred Specimen: CNRST SUNY 280.

Locality: Mali-8; Maastrichtian phosphate conglomerate.

Description: CNRST SUNY 280 consists of the frontoparietal portion of the skull roof with portions of the articulated prefrontals and supraoccipital elements (fig. 6A). The specimen is identified as a dyrosaurid based on the presence of otic capsules that closely approach one another medially, and an occipital exposure of the parietal. Although the lateral margins of the supratemporal fenestrae are not preserved, they can be confidently reconstructed as rostrocaudally elongate, based on the size of the preserved supraoccipital (fig. 6B). In addition, the supraoccipital contributes to the bases of occipital tuberosities, although their full extent is not known.

The specimen compares most closely with the description of *Chenanisuchus lateroculi* (Jouve, 2005a). The skull roof is flat and ornamented with moderately deep pits separated by rounded ridges. The ornamentation is most pronounced at the centers of the frontal and parietal, but diminishes in the vicinity of the frontoparietal and frontonasal sutures. The ornamentation extends fully to the straight caudal margin of the parietal, differing slightly from the condition in the holotype of *C. lateroculi*, in which ornamentation is lacking in this region.

The interfenestral bar is relatively wide, and does not form a peaked sagittal crest as in *Rhabdognathus* and *Hyposaurus*. Instead, the dorsal surface slightly overhangs the base of the bar, forming a broad, T-shaped cross section as in *Chenanisuchus lateroculi*. The suture between the frontal and prefrontal elements is not L-shaped, as in other specimens of *Chenanisuchus*, but instead is straight and diagonal, as in all other dyrosaurids in which it is known, forming an angle of about 50 degrees with the long axis of the skull. We do not consider this character to represent an interspecific variation, and accordingly refer this specimen to *C. lateroculi*.

PHYLOGENETIC ANALYSIS

To test hypotheses of dyrosaurid relationships (e.g., Buffetaut, 1978b; Jouve, 2005; Jouve et al., 2005b) we performed a phylogenetic analysis using previously recognized and new characters of cranial morphology.

METHODS: We evaluated the phylogenetic relationships of ten dyrosaurids with respect to four non-dyrosaurid outgroup taxa. Using the data matrix of Jouve et al. (2005b) as a basis, we re-coded certain characters, provided previously unknown character states based on our new observations, and added seven new characters (appendix 1). The resulting data matrix included 14 taxa and 39 characters (appendix 2). The data matrix and supporting information, including additional photographs of the specimens, is available to the reader at http://www.morphobank.org. The character data were analyzed using a branch-and-bound parsimony search in PAUP*4.0b10 (Swofford, 2003; hereafter PAUP). All characters were unweighted and unordered, and *Eutretauranosuchus*, *Elosuchus*, *Sarcosuchus*, and *Terminonaris* were fixed as outgroups (after Jouve et al., 2005b). A strict consensus tree was calculated, and resulting polytomies were further resolved using the agreement subtrees function. This function identifies certain taxa that contribute to decreased resolution in the consensus tree (“wildcard taxa”; Nixon and Wheeler, 1992). Removing such taxa a posteriori preserves phylogenetic signals that are common to all most parsimonious trees.

RESULTS: The analysis produced 10 most parsimonious trees. The strict consensus of these trees (fig. 7, inset A) supports dyrosaurid monophyly based on 14 synapomorphies. *Phosphatosaurus* and *Sokotosuchus* are sister taxa to one another, corroborating assertions by Buffetaut (1979a) of a monophyletic Phosphatosaurinae. This clade forms a trichotomy with *Chenanisuchus* and a clade containing all other dyrosaurids. The remaining dyrosaurids are contained in a largely unresolved polytomy, with the exception that the two species of *Rhabdognathus* are recovered as sister taxa. A close relationship between *Dyrosaurus phosphaticus* and *D. maghribensis* was not recovered.

A single optimal agreement subtree was found (fig. 7). As in the strict consensus, the agreement subtree indicates that *Phosphatosaurus* and *Sokotosuchus* are united in a monophyletic Phosphatosaurinae at the base of the dyrosaurid radiation. *Rhabdognathus* is monophyletic, and *Hyposaurus*, *Arambourgisuchus*, *Dyrosaurus maghribensis* and *D. phosphaticus* represent successively more distant sister taxa. In this analysis, therefore, members of the genus *Dyrosaurus* represent a paraphyletic assemblage. *Chenanisuchus*, *Congosaurus*, and *Elosuchus* do not appear on the agreement subtree, indicating their “wildcard” status.

In eight of the 10 most parsimonious trees, *Chenanisuchus* is resolved as the most basal member of the ingroup and therefore represents the sister taxon to all other dyrosaurids. In the other two most parsimonious trees, Phosphatosaurinae (*Phosphatosaurus* + *Sokotosuchus*) is the most basal dyrosaurid lineage, lying immediately basal to the position of *Chenanisuchus*. In either scenario, *Chenanisuchus* is resolved as one of the most basal dyrosaurids, but its slightly variable position excludes it from the agreement subtree. The position of *Congosaurus* is more highly variable; in the 10 most parsimonious trees, this taxon is allied alternatively with *Hyposaurus*, *Rhabdognathus*, *Dyrosaurus phosphaticus*, or as the sister taxon to the four most highly nested ingroup taxa (fig. 7).

All possible scenarios illustrated by this analysis indicate a highly nested position for the genus *Rhabdognathus* and a basal position for *Chenanisuchus*, supporting the hypothesis of Jouve et al. (2005b). The discovery of members of both of these genera in Cretaceous rocks (this paper) significantly shortens ghost lineages for these taxa and dates the main diversification of dyrosaurids to the late Cretaceous. Sizeable ghost lineages are still implied for *Dyrosaurus maghribensis*, *Congosaurus*, and *Arambourgisuchus*. An implied ghost lineage also separates Dyrosauridae from its putative closest relative, *Terminonaris*.

DISCUSSION

The phylogenetic analysis presented here supports certain major divisions of Dyrosauridae, and largely corroborates prior hypotheses of dyrosaurid relationships advanced

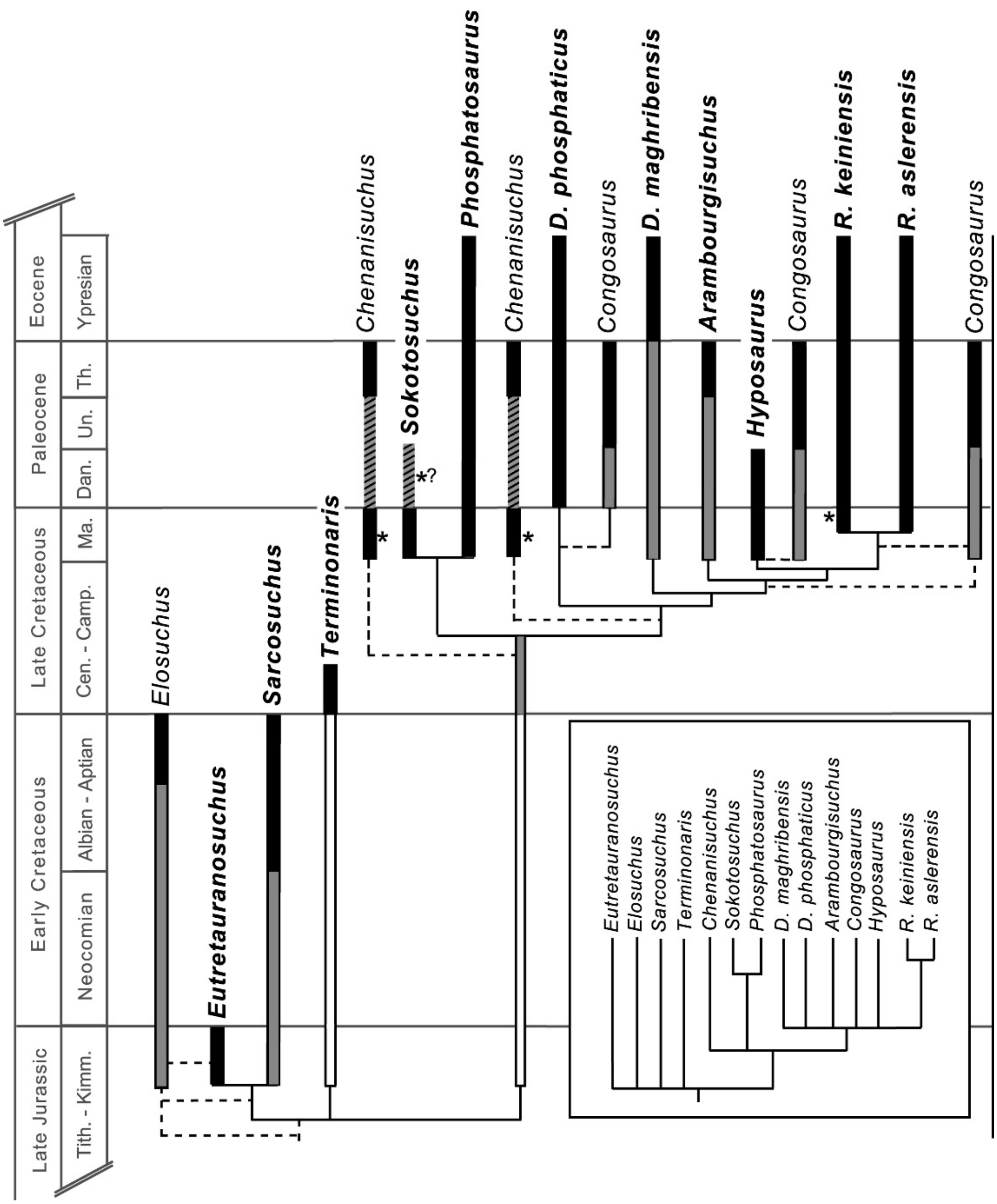

Fig. 7. Phylogenetic relationships and stratigraphic distribution of 10 dyrosaurid taxa and four outgroups, derived from ten equally most parsimonious trees. Tree length = 66 steps; CI = 0.6522; RI = 0.7576; RCI = 0.4941. Inset shows strict consensus of 10 most parsimonious trees; larger cladogram based on the single agreement subtree, which excluded *Chenanisuchus*, *Congsaurus*, and *Elosuchus*. Fine black lines depict the hypothesized phylogenetic relationships based on the current analysis. Bold black bars indicate the known stratigraphic ranges of taxa; solid gray bars represent inferred occurrences of taxa (i.e., ghost lineages). Alternative positions of *Chenanisuchus* (two alternatives) *Congosaurus* (four alternatives), and

by Buffetaut (1978b), Jouve (2005), and Jouve et al. (2005b). There is evidence in support of a monophyletic Phosphatosaurinae, a clade of large-bodied dyrosaurids including *Phosphatosaurus* and *Sokotosuchus*. The relationships among more highly nested dyrosaurids, however, remain partially ambiguous. In particular, inclusion of *Congosaurus* and *Chenanisuchus* contributes to instability of highly nested dyrosaurid clades in the strict consensus, because these genera are alternatively allied with several other taxa.

Jouve et al. (2005b) indicated that the large amount of missing data for *Congosaurus* may contribute to its unresolved phylogenetic position. This problem persists in the current analysis, where 50% of character data are missing for this genus. In contrast, *Chenanisuchus* has only 21% missing data, but is still identified as a "wildcard taxon" (Nixon and Wheeler, 1992). The previously unknown character states scored here for *Phosphatosaurus* slightly reduce the amount of missing data for this taxon, and may contribute to its stable phylogenetic position relative to prior analyses.

Also of interest in the current analysis are the relationships of the species of *Dyrosaurus*. Although several species have been attributed to this genus, Buffetaut (1978b) retained only *D. phosphaticus* (see also Jouve, 2005, for a discussion of synonymy of named *Dyrosaurus* species). Recently, Jouve et al. (2006) assigned a nearly complete dyrosaurid skeleton to *Dyrosaurus maghribensis*, diagnosing the genus with several cranial characters. Most of these characters were incorporated into the current analysis, but we did not recover the two species as sister taxa. Instead, the agreement subtree indicates that they comprise a paraphyletic grouping that lies basal to other derived (i.e., hyposaurine) dyrosaurids.

The fossils described here provide new information about the anatomy, temporal distribution, and evolutionary history of dyrosaurid crocodyliforms. Importantly, these new specimens demonstrate at least two temporal range extensions, providing evidence for two (and possibly three) new cases of genus-level survivorship across the K/T boundary (fig. 7). Several taxa previously known exclusively from either the Mesozoic or Cenozoic are now demonstrated to occur on both sides of the K/T boundary.

In his revision of the genus *Rhabdognathus*, Jouve (2007) recorded occurrences of the two constituent species of mainly from the Paleocene. Brochu et al. (2002) had broadly dated *Rhabdognathus aslerensis* (originally described as cf. *Rhabdognathus* sp.) as Maastrichtian-Paleocene, but suggested that the rocks containing the specimen were most likely Paleocene in age. *Rhabdognathus keiniensis* (= *R. rarus*, in part) was known only from Paleocene deposits (Jouve, 2007). The two specimens of *R. keiniensis* described here, CNRST SUNY 276 and 277, were found in rocks that are unequivocally dated to the Maastrichtian. These fossils therefore represent the first definitive evidence of the genus *Rhabdognathus*, and the first occurrence of *R. keiniensis*, in the Mesozoic.

The single specimen of *Chenanisuchus lateroculi* described here is similarly important. Previously, *C. lateroculi* was known from two specimens of Late Paleocene (Thanetian) age from Morocco (Jouve et al., 2005a). CNRST SUNY 280 comes from the Maastrictian locality Mali-8, indicating both a temporal and geographic range extension for this basal dyrosaurid. The large dyrosaurid represented by CNRST SUNY 279 might be referable to the genus *Sokotosuchus*, based on a combination of two characters: large size and a gently concave caudal parietal margin. In the absence

←

Elosuchus (three alternatives), are indicated by dashed lines. Hatched gray bars indicate strata where the occurrence of a taxon is uncertain. White bars represent the possible ghost lineages based on one alternative placement of *Elosuchus*. Several new occurrences of taxa are reported here that indicate survivorship across the K/T boundary (asterisks). The primary radiation of dyrosaurids took place before the K/T boundary, and most dyrosaurid lineages survived this major extinction event. Age abbreviations: Camp. = Campanian; Cen. = Cenomanian; Dan. = Danian; Kimm. = Kimmeridgian; Ma. = Maastrichtian; Tith. = Tithonian; Un. = Unnamed Paleocene unit.

of additional diagnostic characters, however, this assignment is tentative. If this specimen does represent *Sokotosuchus*, it is the first occurrence of this genus from the Cenozoic of Mali, having previously been reported only from the Cretaceous of Nigeria (Halstead, 1975; Buffetaut, 1979a).

Jouve et al. (2005b) noted that the phylogenetic relationships of dyrosaurids, based on cranial morphology, did not correspond with the stratigraphic distribution of taxa. Specifically, the basal position of *Chenanisuchus* was inconsistent with its Late Paleocene occurrence. CNRST SUNY 280 significantly shortens the ghost lineage for this genus, and indicates that remains of *Chenanisuchus* may also occur in temporally intervening lower Paleocene deposits. The highly nested genus *Rhabdognathus*, also known from Paleogene localities, is now unequivocally reported from Maastrichtian sediments. Despite being among the most highly derived dyrosaurids, the two species of *Rhabdognathus* clearly diverged from one another and from *Hyposaurus* before the latest Cretaceous.

Jouve et al. (2005b) noted that the divergence of *Dyrosaurus* from more derived taxa must have occurred by the late Cretaceous, based on the occurrence of *Hyposaurus* in Maastrichtian strata. Our analysis further supports this hypothesis, with the addition of the Maastrichtian occurrence of *Rhabdognathus keiniensis*. Moreover, the Maastrichtian occurrence of *Chenanisuchus lateroculi*, one of the most basal dyrosaurids, suggests that a major radiation of dyrosaurids took place before the beginning of the Cenozoic, and that most dyrosaurid lineages survived the K/T event. This corroborates provisional reports of dyrosaurids from even earlier (Cenomanian) sediments (Buffetaut and Lauverjat, 1978; Churcher and Russell, 1992; Lamanna et al., 2004).

Several vertebrate clades are known to have survived the K/T extinction event. In addition to avian dinosaurs and mammals, members of both crown-group Crocodylia (the clade including the common ancestor of all living crocodylians and all of its descendants, both living and extinct), and stem crocodylians (the wholly extinct species that lie outside crown crocodylians as their closest relatives) survived the event. The relative number of species occurring on both sides of the K/T boundary provides important information about survivorship and is relevant to questions about how diversity has changed through time.

The discovery of new instances of dyrosaurid taxa crossing the K/T boundary, presented here, corroborates the hypothesis that crocodyliforms were largely unaffected by this mass extinction event (e.g., Markwick, 1998; Fara, 2000). This hypothesis contradicts a recent molecule-based study by Roos et al. (2007) who, on the basis of molecular clock studies using mitogenomic data, inferred that only three lineages leading to the modern crocodylian clades Alligatorinae, Caimaninae, and Crocodylidae survived the event. In fact, many members of crown-group Crocodylia are known from the fossil record to occur on both sides of the K/T boundary (e.g., Markwick, 1998). These include both basal and highly nested members of each of the three clades mentioned by Roos et al. (2007). In addition, numerous stem taxa are known to have survived the extinction event, notably dyrosaurids, goniopholids, and trematochampsids (Markwick, 1998). This pattern of survivorship, illuminated by paleontological studies, indicates that exclusive reliance on molecular data can generate incomplete or erroneous inferences about evolutionary history.

Survivorship across mass extinction events is generally considered to be nonrandom (e.g., McKinney, 1997; Jablonski, 2001; Lockwood, 2003). Differential extinction or survival may be linked to the ecological, reproductive, or life history strategies of an organism or clade. Recently Georgi (2006) investigated the inner ear morphology of Malian dyrosaurids, and concluded that dyrosaurids were adapted for walking along the sea floor, rather than swimming. This hypothesis is supported by the absence of swimming adaptations, including paddlelike limbs, found in other marine-crocodyliforms. This unique behavioral feature of dyrosaurids may have contributed to their survival across the K/T event, which saw the demise of potentially closely related, longirostrine, marine crocodyliform clades such as metriorhynchids and teleosaurids.

The diversification of dyrosaurids before the Cenozoic and widespread survivorship across the K/T extinction is intriguing in the context of other large clades that occur exclusively on one side of this event. Refinement of phylogenetic hypotheses will help to further reconstruct the evolutionary history of this group, and address its implications for clade survival and diversification before, during, and after mass extinction events. Such future studies will depend largely, as noted by Jouve (2007), on the discovery of new species and anatomically complete specimens of known species.

NOTE ADDED IN PROOF: While this paper was in press, an article was published (Jouve et al., 2008) describing new material of the Paleocene dyrosaurid *Atlantosuchus coupatezi*. A more comprehensive phylogenetic analysis was presented therein, including new characters, some of which describe the same morphology as our own. A preliminary inclusion of our nonoverlapping characters into the new data matrix of Jouve et al. (2008) upholds most of the phylogenetic groupings supported by both analyses, but still differs by failing to recover a monophyletic *Dyrosaurus* and providing equivocal results on the positions of *Congosaurus* and *Chenanisuchus* (Fig. 7).

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APPENDIX 1

CHARACTER LIST

Characters 1–30 originate from the study of Jouve et al. (2005b). Character definitions are the same as in that publication unless otherwise noted. Additional characters (31–39) are defined below, along with their sources, where applicable. Characters 31 and 32 were excluded from the analysis because Jouve (2004, 2007) considered characters of symphysis length to vary during ontogeny, rendering them unsuitable for generic or specific diagnosis. The exclusion of these two characters reduces the resultant tree length but does not otherwise influence the outcome of the analysis.

1. Retroarticular process: short (0); extremely long and posterodorsally curved (1).
2. Position of posteromedial wing of retroarticular process: dorsally situated or at mid-height of retroarticular process (0); ventrally situated (1).
3. Occipital tuberosities: absent (0); small (1); strongly developed.
4. Palatine participation in choanae: palatine contributes to the rostral margin or not at all (0); palatine contributes to the rostromedial margin.
5. Exoccipital contribution to occipital condyle: slight (0); large (1).
6. Coronoid: present (0); absent (1).
7. Basisphenoid rostrum length: short (0); extremely long rostrally (1).
8. Seventh dentary tooth size: similar in size to other dentary teeth (0); small and close to eighth dentary tooth.
9. Anterolateral process of postorbital: absent or small (0); contacts dorsal margin of jugal.
10. Posterior wall of supratemporal fenestra: almost vertical and almost not visible in dorsal view (0); dorsally inclined, largely visible in dorsal view.
11. Caudal margin of parietal: straight (0); slight concavity extending rostrally (1); deep, U-shaped concavity (2); convex (3). Modified from Jouve et al. (2005b).
12. Lacrimal-nasal contact, relative to prefrontal-nasal contact: twice as long (0); equal in length (1); shorter (2).
13. Ventral part of basioccipital: vertical, largely visible in occipital view (0); strongly inclined, weakly visible in occipital view (1).
14. Rostralmost point of caudal margin of pterygoid wing: at the level of the medial Eustachian foramen (0); far rostral to the medial Eustachian foramen (1).
15. Supratemporal fenestra: rostrocaudally short (0); strongly elongated (1).
16. Lateral margin of the supratemporal fenestra: relatively wide and ornamented (0); narrow and unornamented (1).
17. Mandibular symphysis: wider than high (0); about as wide as high (1).
18. Interfenestral bar: wide (0); narrow (1).
19. Quadratojugal contribution to articular surface of craniomandibular joint: absent (0); present (1).
20. External mandibular fenestra: wide (0); absent or reduced to a thin slot (1).
21. Teeth: robust with wide alveoli (0); thin and long (1).
22. Interorbital space: wide (0); narrow (1).
23. Anterior carina of tooth: dorsoventrally straight (0); strongly medially “twisted”.
24. Premaxillae: strongly differentiated from lateral margin of maxillae by a notch (0); slightly or not at all differentiated (1).
25. Maxillary tooth size: variable (0); homodont (1).
26. Premaxillary tooth count: five (0); four (1).
27. Parietal ornamentation: strong with deep pits (0); smooth (1); slightly ornamented (2).
28. Occipital tuberosity shape: rounded (0); dorsoventrally flattened (1).
29. Caudal margin of squamosal lateral to occipital tuberosity: straight (0); concave rostrally.
30. Interfenestral bar: ornamented (0); unornamented (1).
31. Caudalmost extent of mandibular symphysis: no further than 12th dentary alveolus (0); caudal to 12th dentary alveolus (1).
32. Rostral extent of splenial: reaches 5th dentary tooth (0); does not reach fifth dentary tooth (1).
33. Length of snout: less than 68% of skull length (0); greater than 68% of skull length (1). From Jouve (2005).
34. Caudal portion of nasal bones: completely fused (0); unfused (1). From Jouve (2005).
35. Dorsal surface of parietal: flat (0); depressed (1).
36. Rostral margin of supratemporal fenestra: straight (0); strongly curved (1).
37. Frontal ornamentation: strong with deep pits (0); smooth (1); slightly ornamented (2).
38. Parietal-supraoccipital suture morphology: W-shaped (0); gently sinuous (1)
39. Spacing between maxillary teeth: increasing between 7th and 11th teeth (0); relatively constant (1).

APPENDIX 2

DATA MATRIX

Eutretauranosuchus
000000?00001000000000010?0?0-00????0?---

Elosuchus
0?010?00000?0100000000000000-00????0000-

Sarcosuchus
0000000000000000000010000000-00?111?0---

Terminonaris
?0000??00001010000011001100-001111010--

Arambourgisuchus
??211??111310110011?1101111111111110021-1

Hyposaurus
112111?1111?111001101111112101000012201

Rhabdognathus aslerensis
??211?1?11101111?11?110???2111???11221-

Rhabdognathus keiniensis
??2?1???112?1?11111?11??1?20111?1111210

Dyrosaurus phosphaticus
1?211?1110010110111111011100001?1002201

Dyrosaurus maghribensis
1121111110010010-11111-111100011100220-

Chenanisuchus
111?1???00000?10101?1001110000??010200-

Sokotosuchus
??1????000?0?10?1??01?0010001??011100-

Phosphatosaurus
???1???1??0?0?1?01??0100010?010100120-1

Congosaurus
11???1?1???1????1??1110111????1100??2?1

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