

A new dyrosaurid crocodyliform from the Palaeocene of Morocco and a phylogenetic analysis of Dyrosauridae

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A new genus and species belonging to Dyrosauridae, *Arambourgisuchus khouribgaensis*, from the Thanetian (Palaeocene) of Morocco, is erected. Two more or less complete skulls and three mandibular fragments enable a reconstruction of the anatomical characteristics of this species. Dyrosaurid systematics is mainly based on mandibular characters. The comparison of this new material with several dyrosaurid species previously known provides new systematic data for this group. The width of the interfenestral bar, the shape and development of the occipital tuberosities and the shape of the supraoccipital and the basioccipital are of particular importance. A phylogenetic analysis of the dyrosaurids provides an outline of the relationships between the best known species. *Chenaniusuchus lateroculi* is the most primitive dyrosaurid. *Sokotosuchus ianwilsoni* and *Phosphatosaurus gavialoides* form a clade, more closely related to other dyrosaurids than to *Chenaniusuchus lateroculi*. The relationships between *Arambourgisuchus*, *Rhabdognathus*, *Congosaurus*, and *Hyposaurus* are unclear, and the two latter taxa remain too poorly known to provide an uncontested phylogenetic result. The dyrosaurids are known from nearly all continents. The phylogenetic results suggest a North African range for basal members, and the wide distribution of *Rhabdognathus* and *Hyposaurus* confirms the possibility of transoceanic dispersal of these taxa. Unfortunately, many dyrosaurids are insufficiently known to be included in the analysis, and the present analysis considers mainly African forms. A better knowledge and the inclusion of other taxa from other geographic regions should significantly improve and modify the hypothesis.

Key words: Crocodyliformes, Dyrosauridae, *Arambourgisuchus*, Paleocene, Ouled Abdoun Basin, Morocco.

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Introduction

Due to intensive field work undertaken in Spring 2000 in the framework of an active collaboration between CNRS/MNHN, OCP, and MEM, new remains of dyrosaurid crocodiles have been recovered from the Palaeogene phosphatic deposits of the Ouled Abdoun Basin (also spelled: Oulad Abdoun) of Morocco. Among the new material, a complete skull with mandible, an almost complete skull and two mandibles, belonging to four different specimens, are referable to the same taxon. The first skull, without mandible, is missing its anterior extremity, is strongly crushed, but all its surfaces are accessible (dorsal, ventral, and occipital). A second skull with an associated mandible is more complete, but its bad preservation does not permit the examination of some details. Description of these two skulls, which complement each other, significantly improves our knowledge of this family.

The Dyrosauridae were marine crocodyliforms with a wide distribution, known from the Cenomanian to the Lutetian, and thus survived the K-T mass extinction. They were present in North America, South America, Asia, Middle East, and maybe in Europe; however, dyrosaurids were much more

numerous in Africa, where they occupied the areas of Tunisia, Algeria, Morocco, Niger, Mali, Nigeria, Congo, Egypt, Togo, Senegal, Libya, Sudan, and Ethiopia (Buffetaut 1981).

The family Dyrosauridae was erected by Stefano (1903) for the Tunisian species *Dyrosaurus phosphaticus*, a species first described as *Crocodylus phosphaticus* by Thomas (1893) based on isolated teeth and postcranial remains. In fact, the first remains of this family were described by Owen (1849) as *Hyposaurus rogersii*, who considered this species from the Maastrichtian and Palaeocene of New Jersey as a “teleosauroid”. The validity of the family has been questioned. The taxonomy was clarified by Buffetaut, who considered the Dyrosauridae as a distinct “mesosuchian” family (Buffetaut 1976, 1978, 1981).

The relationships of longirostrine forms such as the dyrosaurids strongly differ between authors, thus the dyrosaurids are of particular phylogenetic importance. Their inclusion or exclusion from phylogenetic analyses strongly influences the results (Buckley and Brochu 1999).

While numerous dyrosaurid remains are known, they are often poorly preserved, precluding a good understanding of this taxon. The systematics is especially confused, because it

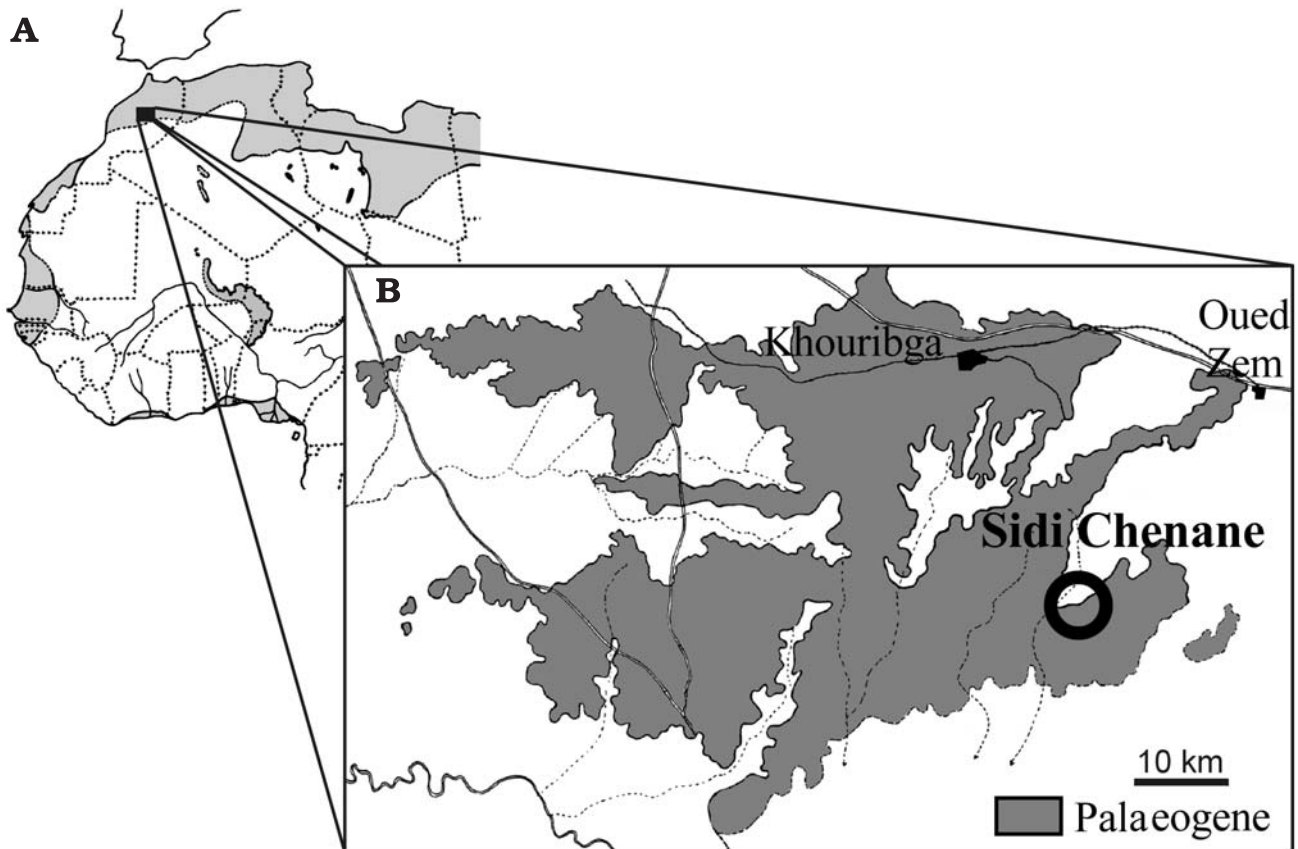


Fig. 1. Geographical position of the type locality. **A.** Geographical position of the Ouled Abdoun Basin (Morocco) in the Palaeocene deposit of Africa, (shaded area); modified from Capetta (1972). **B.** Simplified geological map of the Ouled Abdoun Basin; Sidi Chenane is the type locality (modified from Salvan 1952).

is mainly based on mandibular characters. This paper describes a new genus in detail, compares it with other dyrosaurids, and pinpoints the occurrence of important systematic characters on the skull.

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CNRS, Centre National de la Recherche Scientifique, Paris, France; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; MEM, Ministère de l'Énergie et des Mines, Rabat, Morocco; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MRAC, Musée Royal d'Afrique Centrale, Tervuren, Belgium; NHM, Natural History Museum, London, United Kingdom; NJSM, New Jersey State Museum, Trenton, New Jersey, USA; OCP DEK-GE, Office Chérifien des Phosphates, Direction exploitation de Khouribga, Service Géologie-Exploitation, Khouribga, Morocco; SUNY, State University of New York, Stony Brook, New York State, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA.

Geological setting

The Ouled Abdoun Basin, where these fossils come from, is formed by a phosphatic sequence, interbedded with differ-

ent layers of various lithologic nature in space and time. It extends from the Maastrichtian to the Lutetian, the latter represented by a calcareous “dalle à Thersitées” (Thersitean slab), which protected the less durable phosphatic sequence from erosion. The stratigraphic scale of this sequence was established in 1935 by Arambourg, who used the selachian fauna associations to distinguish the major stratigraphic levels. The selachians were used also by Arambourg (1952) and more recently by Noubhani et al. (1997) to specify the stratigraphy.

The holotype comes from Sidi Chenane (Fig. 1), an area mined by O.C.P. (Office Chérifien des Phosphates), and has been found in the “C2a” stratum, which corresponds to the Thanetian (Noubhani et al. 1997).

Systematic palaeontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Mesoeucrocodylia Whetstone and Whybrow, 1983

Neosuchia Benton and Clark, 1988

Family Dyrosauridae de Stefano, 1903

Genus *Arambourgisuchus* nov.

Etymology: A patronym erected in honour of Prof. Camille Arambourg who was the first to provide an extensive study of the fossil fauna from the phosphates of Morocco, and the Greek, *suchos*, a crocodile.

Type species: *Arambourgisuchus khouribgaensis* sp. nov.

Diagnosis.—As for type and only known species.

Arambourgisuchus khouribgaensis sp. nov.

Etymology: Khouribga (place name), referring to the city near the type locality.

Holotype: OCP DEK-GE 300 (Figs. 2, 5–7), a nearly complete crushed skull, lacking the anterior part of the rostrum. Originally preserved in a phosphatic block, it has been mechanically prepared on both sides. It is very crushed and dorsoventrally flattened from the anterior level of the palatine to its posterior end. Some sutures are hardly visible, but almost all the bones can be reconstituted. All the measurements are taken for the holotype.

Type locality and horizon: The phosphate mine of Sidi Chenane, in the Ouled Abdoun Basin, Morocco; from the “couche (bed) 2a”, Thanetian (Palaeocene).

Diagnosis.—Dyrosaurid with about 20 to 21 robust but sharp teeth on the upper tooth row (on each ramus); teeth moderately elongated, with a posterior carina which ends before reaching the base of the teeth (not in the more posterior teeth), buccal and lingual surface smooth or lightly striated; interfenestral bar very narrow (sagittal crest); supraoccipital, with parietal, tapers posteriorly between the two occipital

tuberosities; occipital tuberosities well developed, and dorsoventrally flattened; suture between basioccipital and exoccipital (posteriorly to basioccipital tuberosities) deeply within a groove; mandibular symphysis long, wider than high in its median part, and ending posteriorly at the level of the sixteenth tooth; splenials end dorsally between the level of the tenth and the eleventh tooth. Differs from *Dyrosaurus* in having less numerous, and more massive teeth, a narrower interfenestral bar, a posterior wall of the supratemporal fenestra very inclined dorsally, the occipital tuberosities dorsoventrally flattened, and the supraoccipital which tapers posteriorly; from *Congosaurus* in having a longer snout, more massive and more widely separated teeth; from *Hyposaurus* in having a longer snout, and more massive teeth, more ventrally projected basioccipital tuberosities, and the supraoccipital which tapers posteriorly; from *Rhabdogna- thus* in having more ventrally projected basioccipital tuberosities, the occipital tuberosities dorsoventrally flattened, and the supraoccipital which tapers posteriorly.

Material.—In addition to the holotype there are:

OCP DEK-GE 18 (Fig. 3). An almost complete skull, with mandible. The skull is crushed, and the occipital part is strongly damaged. In the left ramus of the mandible the posterior part is missing a little behind the end of the mandibular symphysis; the right mandible is badly preserved.

OCP DEK-GE 269. A posterior part of a mandibular symphysis with five or six tooth alveoli on each side.

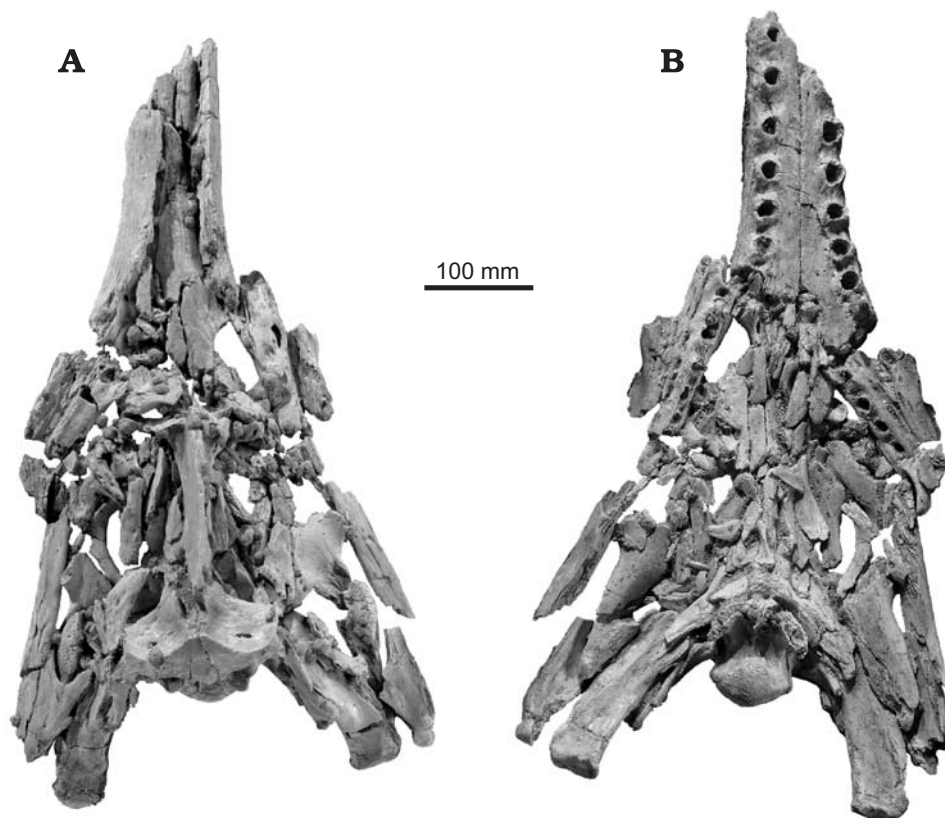


Fig. 2. *Arambourgisuchus khouribgaensis* gen. et sp. nov., OCP DEK-GE 300, Sidi Chenane, Morocco, late Palaeocene, skull in dorsal (A) and ventral (B) views.

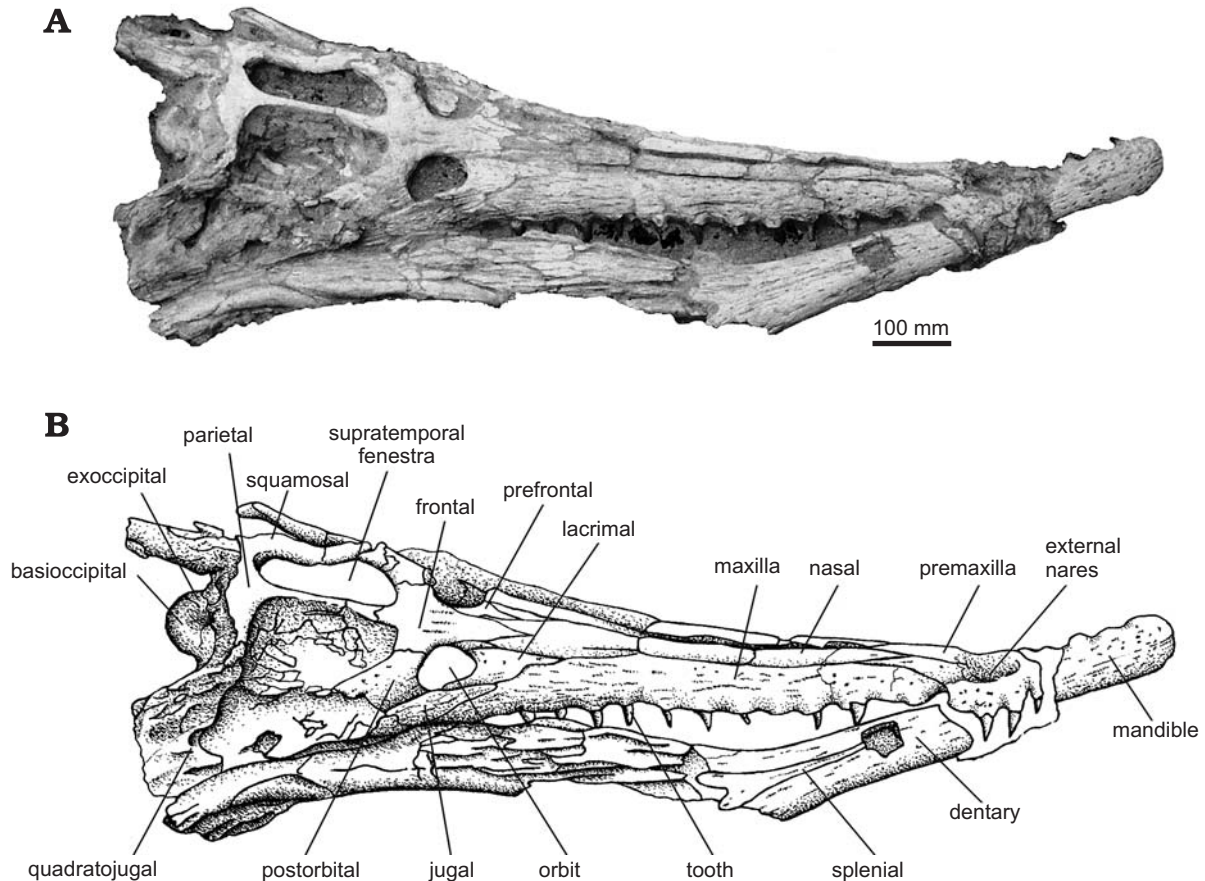


Fig. 3. *Arambourgisuchus khouribgaensis* gen. et sp. nov., OCP DEK-GE 18, Sidi Chenane, Morocco, late Palaeocene, skull and mandible in dorsal view. Photograph (A) and explanatory drawing of the same (B).

OCP DEK-GE 1200. The anteriormost portion of a mandibular symphysis exposed in ventral view.

Description

Cranial openings.—The external nares are poorly preserved. They seem large, dorsally directed, and surrounded by the premaxillae only.

The orbits are rounded, dorsolaterally oriented, bordered posterolaterally by a prominent anterolateral postorbital process typical of dyrosaurids.

The supratemporal fenestrae are longer (about 17 cm) than wide (about 6 cm), separated medially by a very narrow interfenestral bar constituted by the frontal (for about one fifth) and in a major part by the parietal (Figs. 2A, 4A). The fenestra appears to be bordered laterally more by the postorbital than by the squamosal. The posterior margin is constituted for about the same proportion by squamosal and parietal.

The infratemporal fenestra is not preserved, but can be reconstructed after the holotype (OCP DEK-GE 300; Figs. 2A, 4A). It is anteriorly limited by the postorbital bar, constituted half by the postorbital and jugal, this latter constituting the major part of the ventral margin. The quadratojugal borders the posterior margin, constitutes the posterior part of the dorsal edge, excluding the quadrate from the dorsal margin. It participates for a small length to the ventral edge.

The temporal canal, wider than high, is largely surrounded by the parietal (two third), with the squamosal contributing to its lateral margin.

The suborbital fenestra is formed medially by the palatine and the pterygoid, posterolaterally by the ectopterygoid, and anterolaterally by the maxilla (Figs. 2B, 4B). The medial and lateral edges are curved, and the most posterior part is acute and bears the ectopterygoid-ptyergoid suture.

The choanae are deep, ventrally oriented (slightly caudally), and separated by a pterygoidian septum (Figs. 2B, 4B). They are largely surrounded by the pterygoid, only the most anterior border being formed by the palatine. The choanae are not very abruptly pierced within the pterygoids: the choanae lie within a depression on the ventral pterygoid surface. The depression extends posterolaterally on to the lateral branch of the pterygoid, tapering before the pterygoid contacts the ectopterygoid. Thus, the choanal margin is not abrupt.

On the occipital face, the parietal forms the dorsomedial quarter of the posttemporal fenestra (Fig. 5). The squamosal contributes to it dorsolaterally (less than the lateral half), and very slightly to the ventrolateral margin. The supraoccipital constitutes a small part of the ventral margin of the posttemporal fenestra (the rest formed by exoccipital), but constitutes the major part of this same margin to contact the

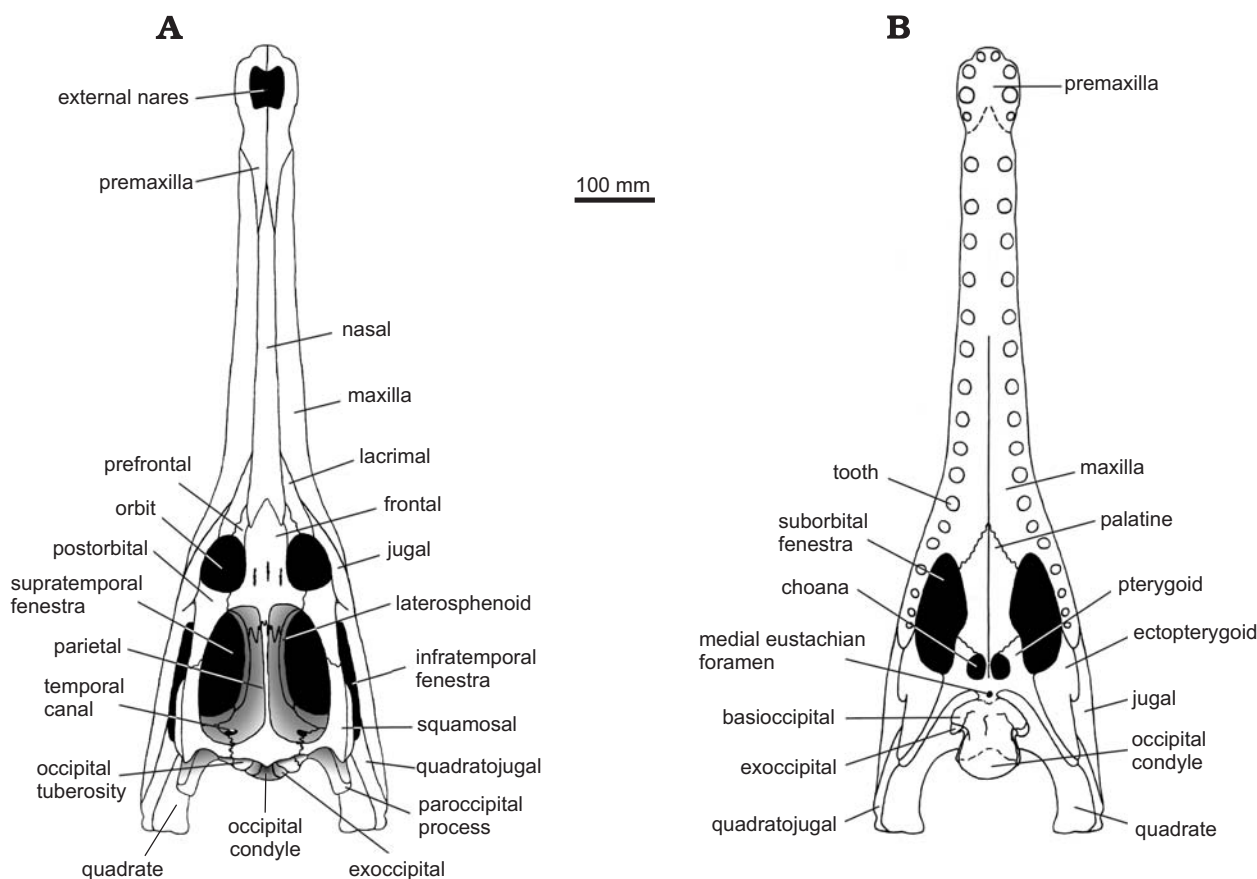


Fig. 4. *Arambourgisuchus khouribgaensis* gen. et sp. nov., reconstruction of skull in dorsal (A) and ventral (B) views.

squamosal more deeply within the posttemporal fenestra (excluding the exoccipital) (Fig. 5).

Premaxilla.—The premaxilla is only preserved on OCP DEK-GE 18 (Fig. 3). It is crushed, but its general shape can be reconstructed. Only the three first right teeth are preserved, but four teeth seem to have existed on each premaxilla. The first tooth is smaller than the two other, and a deep concavity is present between the first and the second. The second tooth is larger, but less than the third tooth which seems to be the largest (apparently confirmed by the large space between the second and third mandibular tooth). The fourth premaxillary tooth is not preserved on the skull of OCP DEK-GE 18, but the space between its third and fourth mandibular teeth is short (as in OCP DEK-GE 1200), implying the fourth tooth would have been the smallest. The space between the fourth and the first maxillary tooth is large, due to the large size of the fourth dentary tooth, and the premaxilla-maxilla suture is at this level on the lateral surface of the snout.

The dorsal posterior process of the premaxilla is long and ends posteriorly at the level of the third maxillary tooth (Fig. 3).

Maxilla.—The number of teeth on each maxilla can be estimated to about 17 (Fig. 3). The snout is relatively narrow, slender, and exhibits a longirostrine type morphology (Figs. 2–4). The maxilla is relatively sculptured laterally compared to other skull area, with longitudinal deep ridges and furrows.

The alveoli are well developed, circular, with their base in relief and very marked ventrally (Fig. 2B). They are largely spaced (interalveolar space larger than the alveoli diameter for the teeth anterior to the thirteenth one), diameter and space decreasing posteriorly from the thirteenth tooth.

The maxilla is laterally straight, and the tooth row does not display a festooned outline in dorsal view. Occlusal pits are present from the space between the twelfth and thirteenth right maxillary alveoli, and between the thirteenth and fourteenth left alveoli. These pits, lined with the alveoli tooth row, increase in depth posteriorly. Anteriorly, the space between the right and left alveoli is large (twice the diameter of the alveoli) and increases posteriorly.

The contact with the palatines is expected between the level of the eleventh and twelfth maxillary alveoli (OCP DEK-GE 300; Fig. 4B). The maxilla contacts the ectopterygoid medially, and ends ventrally on the jugal. Dorsally, the maxillae are separated by the nasal.

Nasal.—The nasal is a single bone (the two nasals are fused), ornamented with only discrete and sparse furrows. It is narrow between the maxillae, and its anterior process penetrates deeply between the posterior premaxillae processes, but terminates 7 cm (in OCP DEK-GE 18) posterior to the external nares, which it does not reach (Fig. 3). The nasal is narrow anteriorly between the maxillae, with a constant width from the posterior contact with the premaxillae to the anterior contact with

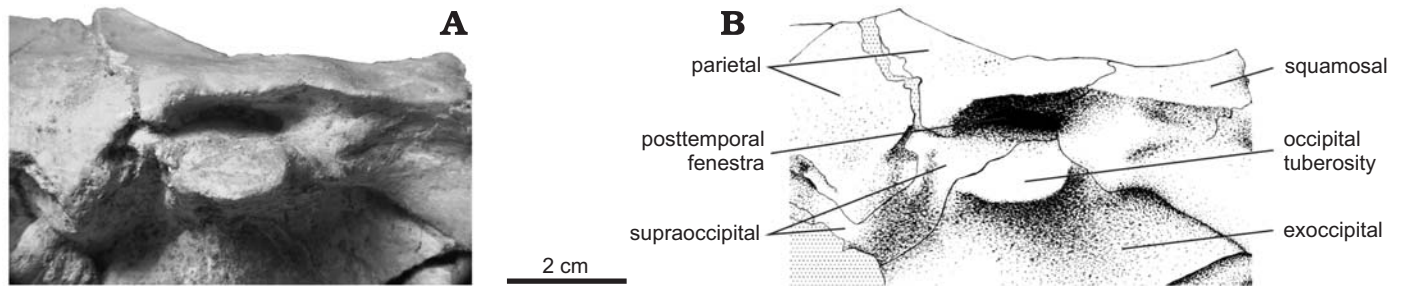


Fig. 5. *Arambourgisuchus khouribgaensis* gen. et sp. nov., OCP DEK-GE 300, Sidi Chenane, Morocco, late Palaeocene, detail of the right posttemporal fenestra in posterior view. Photograph (A) and explanatory drawing of the same (B).

the lacrimals. Then, it widens posteriorly and finally sends a long posterior process between frontal and prefrontal (Fig. 4).

Prefrontal.—Only the right prefrontal is preserved (on OCP DEK-GE 300; Fig. 2A), almost complete (the most anterior part is absent). It is short, narrow and longer than wide (Figs. 2A, 4A). Dorsally, the contact with the frontal is as long as its contact with the nasal.

Lacrimonal.—The right lacrimonal of specimen OCP DEK-GE 18 is well preserved (Fig. 3), and is well anteriorly expanded, reaching the level of the tenth maxillary tooth. Its ornamentation is very light, with some shallow pits. It is large, and forms the anterior margin of the orbit.

Frontal.—It extends anteriorly within the nasal as far as the prefrontal, and its width, at the orbital level appears moderate (Figs. 2A, 4A). Its lateral extension is short, and contacts the postorbital to constitute the postorbital bar. Posteromedially, at the angle between the postorbital bar and the interfenestral bar, the frontal forms a very light dorsal overhang within the supratemporal fenestra. Ventrally, and below this overhang, the frontal contacts an extremely laterally elongated laterosphenoid in a flat lateroventral extension. Posteromedially, the frontal takes part in the narrow interfenestral bar (1 cm width), since its total proportion is about one-fifth of the total length (Figs. 2A, 4A).

The frontal is smooth, without ornamentation, with only three medial grooves between the orbits.

Parietal.—The interfenestral bar, formed by the frontal and the parietal, decreases in width just posteriorly to the contact between these two bones: the width, which reached 1 cm anteriorly, is only 0.5 cm in width posterior to the suture (OCP DEK-GE 300; Figs. 2A, 4A). Anteroventrally, its contact with the laterosphenoid is visible, with a long anterior process between the frontal and the laterosphenoid, reducing the contact between these two bones.

Ventrally, the parietal-laterosphenoid suture appears parallel to the skull roof. Posteriorly, the interfenestral bar is broken and separated from the occipital part of the skull. In the angle between the interfenestral bar and the posttemporal bar (formed by the parietal and squamosal), the parietal sends an anterodorsal overhang into the supratemporal fenestra. This overhang is more developed than the anterior one, beginning laterally about 1 cm medial to the squamosal-parietal

suture, and appears to end rapidly in the interfenestral bar. The posterior wall of the supratemporal fenestra is very inclined posteriorly, and is largely visible in dorsal view (Figs. 2A, 4A). The parietal-quadratojugal suture, visible in dorsal view on the posterior wall of the supratemporal fenestra, continues in the same direction as the parietal-laterosphenoid suture. It extends dorsally to join the squamosal-quadratojugal suture at the same level (in the right supratemporal fenestra) or slightly below the temporal canal (in the left supratemporal fenestra), about 1 cm laterally to the temporal canal. The ventral squamosal-parietal suture joins the temporal canal in its most lateral part, continues dorsally to this one (crosses the temporal canal medially, in its one-third dorsomedial part), and continues in a vertical direction (with zigzag).

The parietal is not ornamented on either the interfenestral bar or on the posterior skull roof. It contributes to half of the posterior wall of the supratemporal fenestra, and tapers posteromedially with a strong and acute process in the occipital face between the occipital tuberosities. The dorsal surface of this process is posteroventrally inclined, and the supraoccipital forms its ventrooccipital part (Fig. 6).

Postorbital.—It is badly preserved on OCP DEK-GE 18 (Fig. 3), and extremely fractured in OCP DEK-GE 300 (Fig. 2A). The postorbital bar, comprised of the postorbital and the jugal, seems to be gently concave medially. It was probably inclined ventrolaterally, not ornamented, mediolaterally flat and longer than wide.

The postorbital is the most important part of the lateral arcade of the supratemporal fenestra (Figs. 2A, 4A, 7). It appears dorsally and laterally ornamented with spaced pits, contacts the squamosal posteriorly, and the quadratojugal posteroventrally. It seems to participate largely to the dorsal margin of the infratemporal fenestra (Fig. 7). Anteriorly, it bears a robust lateral process, directed anteroventrally, and ornamented with deep furrows, which seems to contact the ventral margin of the orbit (jugal) (Figs. 3, 4A).

Squamosal.—The squamosal forms the posterolateral part of the supratemporal fenestra. It is relatively narrow at the level of the posttemporal bar (1.5 cm in its minimum antero-posterior length) (Fig. 2A). Weakly high in the posterior wall of the supratemporal fenestra, it constitutes the major part of the dorsal border of the temporal canal. It contacts the postorbital anterolaterally, but is separated from the quadrato-

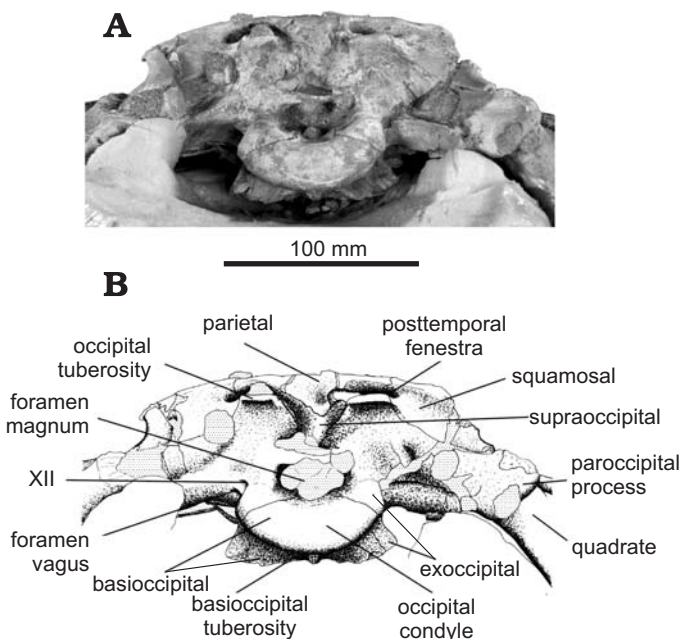


Fig. 6. *Arambourgisuchus khouribgaensis* gen. et sp. nov., OCP DEK-GE 300, Sidi Chenane, Morocco, late Palaeocene, skull in occipital view. Photograph (A) and explanatory drawing of the same (B).

jugal by the quadrate. It takes part in the dorsal part of the external ear, and sends an important squamosal wing roofing the external otic aperture (Fig. 7). Posterior to the ear, the squamosal constitutes a long and high blade sinking deeply beneath the skull roof and forms the anterior wall of the paroccipital process. The paroccipital process extends more ventrally than the level of the skull roof.

In occipital view, the squamosal contributes dorsolaterally to the posttemporal fenestra (less than the lateral half), and to a small lateral part of the occipital tuberosity. It contributes to a small part to the occipital face, and more posteriorly, it participates in the dorsal edge of the paroccipital process, ending before the extremity one of the process (Fig. 6).

Jugal.—Very fragmentary (Fig. 2A), the jugal forms the lateroventral edge of the orbit, and the ventral part of the postorbital pillar (Fig. 4A). There is no lateral jugal edge raised bordering this pillar, and the postorbital pillar is not laterally in continuity with the lateral edge of the jugal. The postorbital bar is displaced medially and is not laterally in alignment with the lateral jugal edge. The base of the postorbital pillar is completely pierced by a foramen, antero-posteriorly directed. Apparently, the posterior aperture of this foramen is situated on the external face of the postorbital pillar. Posteriorly, the internal part of the jugal is exposed and exhibits a deep and long groove, including two distinct foramina (Fig. 2A).

The jugal is laterally ornamented with spaced deep pits. Posteriorly, it is high, slightly convex dorsally, lateromedially narrow and ends just before the quadratojugal lateral notch (see below). Anteriorly, it reaches the level of the anterior process of the prefrontal (Figs. 3, 4A).

Quadratojugal.—It is well developed, and contributes to the jaw joint for one quarter (Fig. 2). It is laterally straight, and extends slightly ventrally in its posterior portion. A deep lateral notch just before the articulation marks off the jaw joint segment (preserved on the right quadratojugal). Medially, the contact with the jugal is long, and the space between the quadratojugal and the ectopterygoid is small on the jugal (2 cm).

The quadratojugal constitutes the posterior edge of the infratemporal fenestra, and forms a part of its dorsal margin (Fig. 7). Dorsolaterally, it is separated from the squamosal by the quadrate (there is no contact with the squamosal).

Supraoccipital.—It is a small bone, “V” shaped in posterior view, which contributes to the posteromedial occipital process with the parietal (Figs. 2A, 4A, 6). It forms the medioventral mid part of the posttemporal fenestra, posteriorly on the occipital tuberosity, but contacts the squamosal one centimeter anteriorly, within the posttemporal fenestra (Fig. 5). It does not seem to contribute to the occipital tuberosities.

Exoccipital.—They form the main part of the occipital face, contributing laterally to the occipital condyle (each exoccipital constitutes to one third of the half width), and almost completely surround the foramen magnum (three-quarter) (Fig. 6). Dorsally, they form the occipital tuberosities, which are well developed, dorsoventrally flattened, and posteriorly directed under the posttemporal fenestra. Laterally, they constitute the main part of the robust paroccipital process, and surround dorsally, medially and ventrally to the cranio-quadrate canal. The paroccipital process is flat, composed of the exoccipital and squamosal, and its posterior extremity is quadrangular.

Ventrally, the exoccipitals contribute posterolaterally, one-third to each basioccipital tuberosity in a very broad ventral process (Figs. 2B, 4B, 6B). The suture between the basioccipital and the exoccipital, posteriorly to the basioccipital tuberosities, lay deeply in a cavity.

The foramen for nerve XII is small and laterally directed on the exoccipital. The vagus foramen and posterior carotid foramen are situated anterior to the foramen for nerve XII, and directed ventroposteriorly (Fig. 6).

Basioccipital.—It constitutes the main part of the occipital condyle, which is very wide. Its anterior part (basioccipital tuberosities) is not strongly projected ventrally and therefore does not proceed ventrally to the occipital condyle in occipital view (Fig. 6). The area between the basioccipital tuberosities and the occipital condyle is gently curved dorsally, almost horizontally oriented. In ventral view, the posterior margin of the basioccipital tuberosities is concave anteriorly, relatively thin in its medial part (just behind the medial eustachian foramen), with a small medial ridge posteriorly to the medial eustachian foramen (Figs. 2B, 4B). The anteroposterior thinness of the medial part of the basioccipital, posterior to the medial eustachian foramen, separates the two basioccipital tuberosities, each one having a “drop” shape in ventral view (Figs. 2B, 4B).

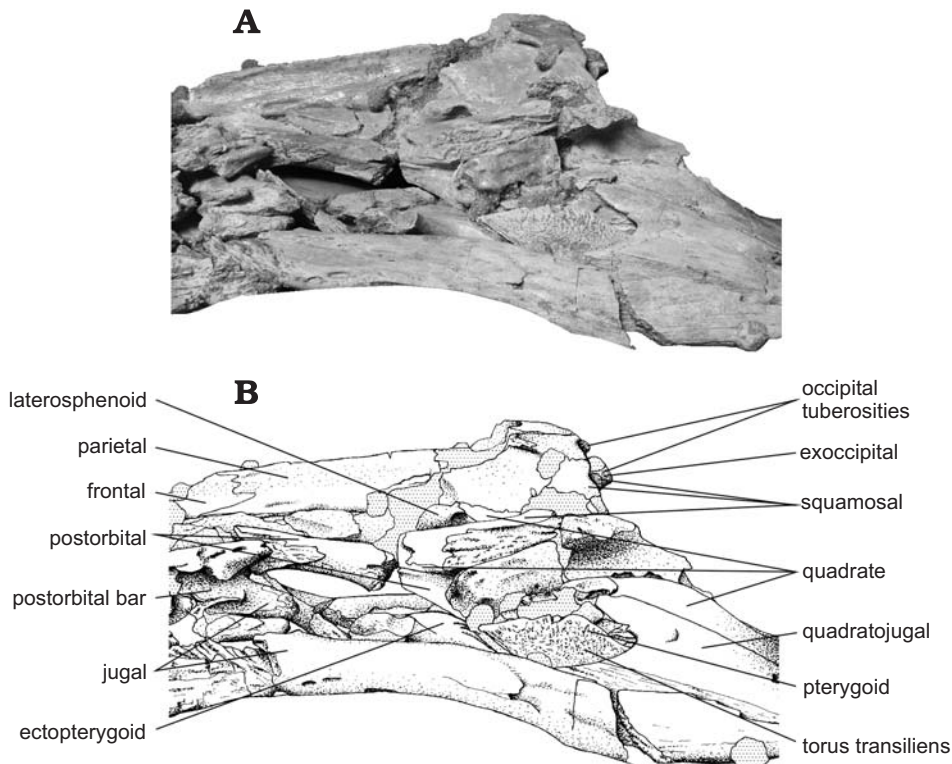


Fig. 7. *Arambourgisuchus khouribgaensis* gen. et sp. nov., OCP DEK-GE 300, Sidi Chenane, Morocco, late Palaeocene, detail of the left posterior part of the skull in left lateral view. Photograph (A) and explanatory drawing of the same (B).

Basisphenoid.—It seems to enclose completely the medial eustachian foramen, but the limit between basioccipital and basisphenoid cannot be seen. The bone is narrow laterally to the medial eustachian foramen, with a lateral “pinching” (Figs. 2B, 4B).

Quadrate.—It is long, posteroventrally directed, and forms the jaw joint with the quadratojugal (Figs. 2A, 4). In the supratemporal fenestra, it contacts the squamosal lateral to the temporal canal. Anterolaterally, it slips in between the squamosal and the quadratojugal by a thin anterior process that contacts the postorbital. Anteriorly, on its ventral face, the quadrate bears a small crest at its mid width, which probably corresponds to the “crest B” of Iordansky (1964, 1967, 1973).

Palatine.—The palatines are very crushed (Fig. 2B). They seem enlarged and curved laterally before contacting the maxillae anteriorly. This contact, due to the bad preservation, is not available. Its posterior border seems flattened, enlarged posteriorly and deviates laterally before joining the pterygoid (lateral border of the palatine not parallel, but laterally curved anteriorly and posteriorly, medial border of suborbital fenestra medially curved). The contact with the pterygoid is not clearly visible, but it seems to form only the anterior part of the choanae (Fig. 4B).

Ectopterygoid.—The left ectopterygoid is well preserved (Fig. 2B). It is wide and twisted between its contacts with the jugal and the pterygoid. It curves gently anteriorly to form the posterolateral part of the suborbital fenestra (Fig. 4B). The posterior process is wide, decreasing posteriorly, and covers the pterygoid almost as far as its posterior extremity

(Fig. 2B). Its contact with the maxilla seems short, whereas that with the jugal is long.

Pterygoid.—The pterygoids are damaged (Fig. 2B), but their shape can be traced out. Anteriorly, they almost completely surround the choanae. A septum, formed by the pterygoids separates the choanae in two openings (Fig. 4B).

The pterygoids diverge posterolaterally to form two lateral wings in contact with the ectopterygoid. In front and anterolaterally to the choanae, they seem flattened and enlarged laterally; they are anteroposteriorly narrow between the choanae and their contact with the ectopterygoids (Fig. 4B). Contact with the ectopterygoid is small, and increases rapidly lateroposteriorly with the increase of the anteroposterior length of the pterygoid wing. The lateral part of this wing is extremely thickened dorsoventrally to form a strong *torus transiliens*, with a very important anterior thickening, decreasing progressively posteriorly (Fig. 7).

Laterosphenoid.—Anteriorly, it is laterally expanded ventrally to the frontal, and its anterior margin is lateromedially directed (Figs. 2A, 4A). The posterior part is dorsoventrally crushed, and its shape is hardly distinguished (Fig. 2). Suture with the frontal and parietal (in continuity) seems horizontal, parallel to the skull roof (dorsal limit of the interfenestral bar).

Mandible.—Two isolated mandibular fragments have been found, one anterior, preserved from the first to the twelfth tooth (OCP DEK-GE 1200; Fig. 8A), and a more posterior part, including the eleventh to the sixteenth teeth (OCP DEK-GE 269; Fig. 8B, C). Unfortunately, only a small part of its posterior branch is preserved on the specimen OCP DEK-GE 300, but too poorly preserved to be interpreted. The

first tooth is relatively robust (Fig. 8A), the second alveolus smaller, and the space between it and the third one is greater than between the other. The third tooth is about the same size as the second, and it is near the very enlarged fourth. This one has its alveolar edge higher dorsally. The next alveoli seem relatively regular in their spacing and diameter.

The mandible is wider than high (Figs. 3, 8B, C), lacks festooned outlines, and there are occlusal pits posterior to the fifteenth teeth (OCP DEK-GE 269; Fig. 8B).

The symphysis ends posteriorly at the level of the sixteenth tooth, and the splenial ends anteriorly between the tenth and the eleventh (Fig. 3).

Teeth.—They are robust, not very slender, but relatively sharp, with posterior carinae which ends before the base of the teeth, when the anterior one reaches the base. The superficial striae are variably present on some of the teeth, and are absent or weak.

Discussion

Comparison.—The dyrosaur cranial skeleton is relatively well known in its general morphology due to the descriptions of *Dyrosaurus phosphaticus* (Thévenin 1911; Piveteau 1935; Bergounioux 1956; Moody and Buffetaut 1981; Hua 1995; Jouve 2005), *Hyposaurus rogersii* (Troxell 1925; Parris 1986; Denton et al. 1997), *Phosphatosaurus gavialoides* (Bergounioux 1956; Buffetaut 1978; Moody and Buffetaut 1981), *Sokotosuchus ianwilsoni* (Halstead 1973; Buffetaut 1979), *Rhabdognathus* (Buffetaut 1980; Langston 1995; Brochu et al. 2002), *Congosaurus bequaerti* (Dollo 1914; Swinton 1950; Buffetaut 1976; Jouve and Schwarz 2004) and *Chenanisuchus lateroculi* (Jouve et al. 2005).

In spite of the abundance of cranial material, the diagnoses of dyrosaurid species are mainly based on mandibular characters. Comparison of these specimens with other species will demonstrate the great importance of skull characters in dyrosaurid systematics.

The presence of large occipital tuberosities, and the supra-temporal fenestra largely longer than wide support the assignment of *Arambourgisuchus khouribgaensis* to Dyrosauridae. It is a large species, with a skull length estimated to about 100 cm (OCP DEK-GE 18), with a high antorbital length / total length ratio (71%, Table 1). This ratio illustrates the extreme elongation of the snout, which is proportionally one of the longest of the dyrosaurids. In *Dyrosaurus phosphaticus*, the snout is very elongated, without lateral “festooned” outlines, but *A. khouribgaensis* differs in being more robust, with larger, less numerous and more massive teeth (Figs. 3, 8B, C). The teeth are more slender than those of *Phosphatosaurus gavialoides*, which has blunt teeth (Bergounioux 1956); the teeth of *A. khouribgaensis* are sharp (Fig. 8C).

The interfenestral bar varies among dyrosaurids. In *A. khouribgaensis*, it is very narrow (Figs. 2A, 3, 4A), as in *P. gavialoides* and *Rhabdognathus* (some millimeters), when it

Table 1. Measurements of the skull of different dyrosaurids. Abbreviations: DL, dorsal length of the skull; PreoL, preorbital length; R, ration, preorbital length/dorsal length.

	DL (cm)	PreoL (cm)	R (PreSL/DL)
<i>R. rarus</i>	73.1	53.4	73.05
<i>D. phosphaticus</i>	104	75	72.12
<i>A. khouribgaensis</i>	100	71.5	71.50
<i>P. gavialoides</i>	107	72	67.29
<i>S. ianwilsoni</i>	60.1	39.7	66.06
<i>H. rogersii</i>	42.9	28.2	65.73

is relatively wider in *D. phosphaticus* (about 1 cm) (personal observations) and *C. lateroculi*. This character is apparently not related with the snout length, since a narrow interfenestral bar can be found indifferently in long-snouted (*R. rarus*) or short-snouted species (*P. gavialoides*).

In *A. khouribgaensis*, the posterior wall of the supra-temporal fenestra (formed by the squamosal, parietal and quadrate) is very inclined dorsally, making it largely visible in dorsal view (Figs. 2A, 4A); a similar condition is observed in the *Rhabdognathus* sp., a skull from Mali described by Brochu et al. (2002) (personal observations). In *Dyrosaurus* and *C. lateroculi*, it is almost vertical, and faintly visible in dorsal view (Jouve et al. 2005; Jouve 2005).

The shape of the occipital tuberosities has been neglected until now. Buffetaut (1976), considering this character at the familial level, never made distinction between the different species (Buffetaut 1978, 1980, 1981), and only mentioned “a greater development in early Tertiary forms” (Buffetaut 1979: 35). In fact, more differences than previously supposed are observed. In *A. khouribgaensis* they are well developed, dorsoventrally flattened, and the supraoccipital tapers posteriorly between these two structures (Figs. 2A, 3, 4A). In *Dyrosaurus phosphaticus*, contrary to Buffetaut (1978) and Denton et al. (1997), they are not the largest of the dyrosaurids; they are fairly developed, with a “quadrangular” shape, and a posteriorly straight supraoccipital with a very tight dorsoventrally oriented medial ridge between them (Jouve 2005). The occipital tuberosities are rounded, sharp, particularly well developed and projected posteriorly in *Rhabdognathus rarus*, a skull from Mali described by Buffetaut (1980). In this species, the supraoccipital is strongly concave anteriorly, and the posterior limit of the skull roof, at the level of the supraoccipital, is more anteriorly situated than the posterior limit of the supratemporal fenestra (Buffetaut 1980: fig. 1, pl. 2; and personal observations). In *Rhabdognathus* sp., the tuberosities are weaker than in *R. rarus*, and the posterior margin of the parietal is much less anteriorly concave (Brochu et al. 2002; personal observations). *Hyposaurus rogersii*, exhibits strong tuberosities, dorsoventrally flattened, as *A. khouribgaensis*, but the whole of the posterior margin of the skull roof is anteriorly concave (Denton et al. 1997; personal observations). In *Sokotosuchus ianwilsoni* (Halstead 1973; Buffetaut 1979), as in *Chenanisuchus lateroculi* (Jouve et al. 2005), the occipital tuberosities are

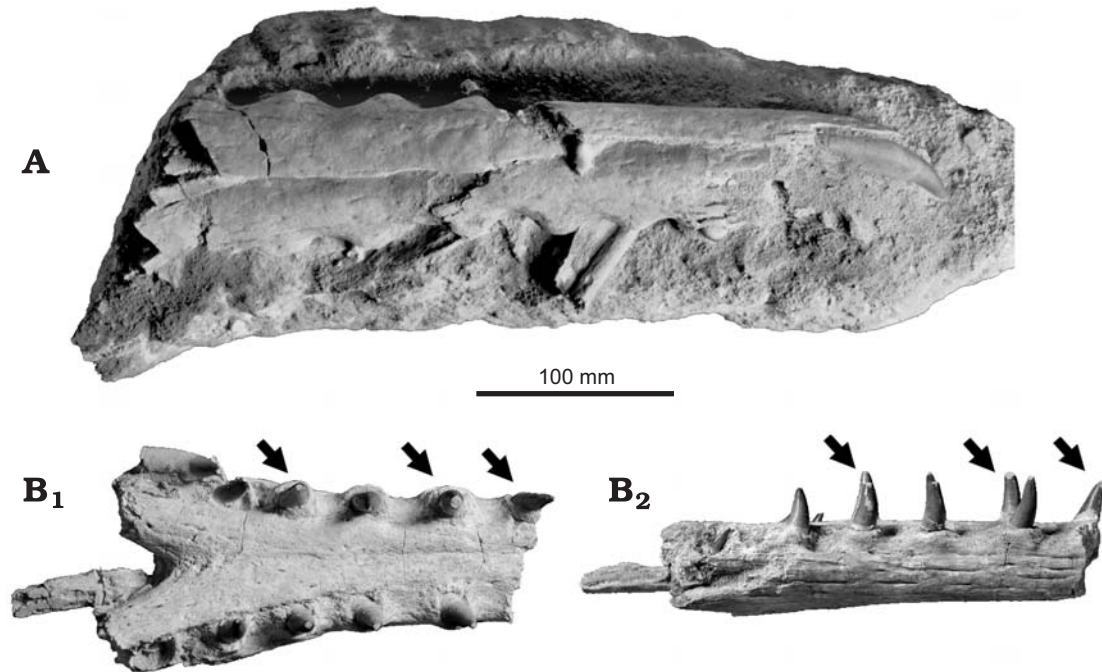


Fig. 8. *Arambourgisuchus khouribgaensis* gen. et sp. nov., Sidi Chenane, Morocco, late Palaeocene. Elements of mandibles. **A.** OCP DEK-GE 1200 in ventral view. **B.** OCP DEK-GE 269 in dorsal (**B₁**) and lateral (**B₂**) views. The arrows indicate the teeth that have been added recently, and which do not belong to the same specimen.

extremely reduced, with the posterior margin of the skull roof straight.

In dyrosaurids, different basioccipital shapes can be observed, more or less projected below the level of the occipital condyle or ventrally short. In *A. khouribgaensis*, the basioccipital is moderately ventrally projected, and the area between the occipital condyle and the basioccipital tuberosities is gently convex dorsally, with a long distance between the occipital condyle and the medial eustachian foramen in ventral view (Figs. 2B, 4B). In *Dyrosaurus phosphaticus*, the basioccipital tuberosities are more ventrally projected and more clearly convex dorsally, reducing the distance between the occipital condyle and the medial eustachian foramen (Jouve 2005); the basioccipital tuberosities are more largely exposed in occipital view. In *Rhabdognathus* (Buffetaut 1980; Brochu et al. 2002; personal observations) and *H. rogersii* (personal observations), the basioccipital tuberosities are less ventrally projected and almost invisible in occipital view; the basioccipital tuberosities are almost vertical and long ventrally in some remains from Mali (personal observations), with a smaller distance between the occipital condyle and the medial eustachian foramen in ventral view. The same condition is observed on a misidentified dyrosaurid occipital that Thévenin (1911) attributes to *D. phosphaticus* (Thévenin 1911: 104 and fig. 7), and which clearly belong to a different species (deep cavity between occipital tuberosities which are more greatly developed).

Thus, *A. khouribgaensis* differs from other dyrosaurids by its following combination of character states: the narrow interfenestral bar, the important incline of the posterior wall of its supratemporal fenestra, its occipital tuberosity dorsoventrally flattened, a parietal-supraoccipital which tapers

posteriorly, and the moderate ventral projection of its basioccipital tuberosities.

Phylogenetic analysis.—Only a very simple phylogenetic analysis (a “hand-made cladogram”) including four taxa (*Phosphatosaurus gavialoides*, *Rhabdognathus*, *Hyposaurus*, and *Dyrosaurus phosphaticus*) has been proposed for the dyrosaurids (Buffetaut 1978), a group which is generally poorly known, and often inadequately described. Several recent descriptions of new species (Jouve et al. 2005) or reviews of old ones (Jouve and Schwarz 2004), resulted in a better knowledge of the clade. All species known by cranial material have been used in the present paper. Species or specimens only known by mandibular elements, such as *Hyposaurus derbianus* from Brazil (Cope 1885), and *Hyposaurus* from Mali (Swinton 1930; Buffetaut 1980), have not been included herein.

The relationships of the dyrosaurids with other Crocodyli-formes have often been discussed (Clark 1994; Wu et al. 1997, 2001; Larsson and Gado 2000; Brochu et al. 2002; Pol 2003). These analyses found dyrosaurids to be closely related to *Terminonaris* and *Sarcosuchus* (Wu et al. 2001; Sereno et al. 2001, 2003); consequently these taxa have been used herein as outgroups. *Elosuchus*, even if it is considered as a Peirosauridae following Lapparent de Broin (2002), is probably closely related to the dyrosaurids (Jouve 2004). Indeed, it has an anterolateral postorbital process and its lateral eustachian foraminae are located dorsally to the medial one, as in all dyrosaurids (Brochu et al. 2002). It has thus also been added to the analysis as an outgroup. All taxa used here as outgroups are longirostrine forms, as the ingroup taxa. To avoid the problem of optimisation of the features related to longirostry,

a closely related, non longirostrine form, the goniopholidid *Eutreauranosuchus delfsi* (Mook, 1967) (Clark 1994; Sereno et al. 2001, 2003; Brochu et al. 2002), was included as an outgroup. The characters used in the present analysis (Appendix 1) are new, or inspired by previous phylogenetic analyses on crocodyliforms (Benton and Clark 1988; Wu et al. 2001). They are mainly the result of the comparison of all species and specimens studied by the authors (Jouve 2004).

Branch and Bound searches were performed using PAUP* (version 4.0b10; Swofford 2002) and multistate characters are unordered (Appendix 2). The analysis has generated five most parsimonious trees with a length of 44 steps (C.I. excluding uninformative characters: 0.66; R.I.: 0.85; R.C.: 0.62) (Fig. 9).

The outgroup is not a monophyletic assemblage, as *Sarcosuchus* and *Terminonaris* share a more recent common ancestry with the Dyrosauridae than they do with the Goniopholididae (Clark 1994; Wu et al. 1997, 2001; Larsson and Gado 2000; Brochu et al. 2002; Pol 2003, Wu et al. 2001; Sereno et al. 2001, 2003). Thus, the monophyly of the Dyrosauridae can be tested. If each outgroup is considered successively as the first outgroup, the results do not differ within the ingroup, being monophyletic each time. Monophyly of Dyrosauridae is supported by seven synapomorphies [characters: 2(1), 3(1), 5(1), 15(1), 17(1), 19(1), 26(1)], many of which were traditionally considered as diagnostic of the dyrosaurids (Buffetaut 1976, 1978, 1980, 1981). The relationships of this clade with *Terminonaris* seems to be confirmed, or at least does not contradict the results of Wu et al. (2001), and *Terminonaris* is more closely related to the Dyrosauridae than the other considered outgroups, *Sarcosuchus*, *Eutreauranosuchus*, and *Elosuchus*. Nevertheless this result must be relativised, and this relationship should be tested in the framework of all Crocodyliformes.

For the ingroup relationships, if the present result differs significantly from previous Buffetaut's hypothesis (Buffetaut 1978), the primitive condition of *Phosphatosaurus*, compared to those of *Dyrosaurus*, *Hyposaurus*, and *Rhabdognathus* seems to be confirmed. In the present work, the short-snouted *Chenanisuchus lateroculi* is the most primitive dyrosaurids, and *Phosphatosaurus* and *Sokotosuchus* forms a clade. The possible existence of this clade has been suggested by Buffetaut (1979), who named it Phosphatosaurinae, but it seems premature, due to the poor knowledge of the anatomy of these two species, to consider this phylogenetic relationships as definitive and this name as valid.

In the tree provided by Buffetaut (1978) and corrected at the end of his paper, *Rhabdognathus* shares a more recent common ancestor with *Dyrosaurus* than *Hyposaurus*, based on the snout length and shape of the mandibular cross section (Buffetaut 1978, 1981). In our analysis, *Rhabdognathus* shares a more recent common ancestor with *Hyposaurus* than *Dyrosaurus* (node 7, Fig. 9), a clade supported by three synapomorphies [characters: 10(1), 11(1), 13(1)]. If, as suggested by Buffetaut (1978), *Dyrosaurus* is forced to be more closely related to *Rhabdognathus* than to *Hyposaurus*, the consensus tree is five steps longer (49 steps; CI: 0.65; RI:

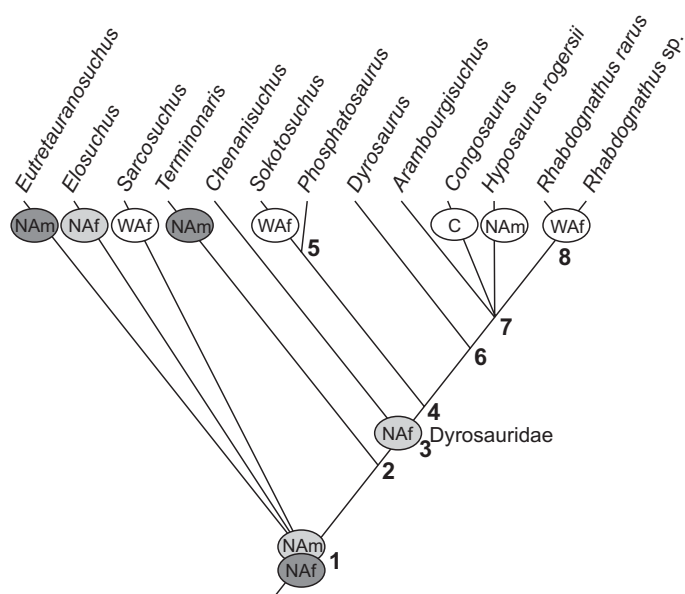


Fig. 9. The strict consensus of the five most parsimonious trees of Dyrosauridae found based on a cladistic analysis of 13 taxa and 30 characters (Appendices 1 and 2), and historical biogeography. Tree length: 44 steps long (C.I. excluding uninformative characters: 0.66; R.I.: 0.85; R.C.: 0.62). Land area abbreviations in the circles indicate optimised transformations on the tree, with two alternative results in light grey, and dark grey. Abbreviations: C, Congo; NAF, North Africa; NAm, North America; WAF, West Africa.

0.78; RC: 0.51) than if *Rhabdognathus* and *Hyposaurus* share a more recent common ancestor. If *Dyrosaurus* is forced to be more closely related to *Hyposaurus* than to *Rhabdognathus*, as first suggested by Buffetaut (1978), the consensus tree is four steps longer than if *Rhabdognathus* and *Hyposaurus* share a more recent common ancestor. Thus, the results we present here are more parsimonious than the trees proposed by Buffetaut (1978).

A nearly complete skull was described as *Rhabdognathus rarus* by Buffetaut (1980), and a second skull was tentatively referred to cf. *Rhabdognathus* sp. by Brochu et al. (2002). These two specimens, included in our phylogenetic analysis, form a clade, confirming that they could be congeneric. The node is weakly supported (node 8, Fig. 9) by only two synapomorphies: the lateral margin of the supratemporal fenestra is thin and smooth [16(1)], the dorsal margin of the parietal is slightly ornamented [27(2), convergent with *Hyposaurus*]. Accordingly, the possible congeneric identification of these taxa should be considered with caution, until further specimens are discovered.

Some problems occur with *Arambourgisuchus*, *Hyposaurus*, and *Congosaurus* relationships. Recent taxonomic revision had tentatively stated that, contrary to Buffetaut (1980), *Congosaurus* was distinct from *Hyposaurus* (Jouve and Schwarz 2004). In the present analysis, the relationships of *Congosaurus bequaerti*, *Hyposaurus rogersii* (the single species of this genus considered in the analysis), and *Arambourgisuchus khouribgaensis* are unresolved. This could be due to missing information from the postorbital part of the

skull of *C. bequaerti*, precluding its complete coding (54.3% of missing data). In addition, several other species of *Hyposaurus* and *Congosaurus* have been mentioned in Brazil (Jouve 2004), western Africa (Buffetaut 1980; Jouve 2004) or Morocco (Jouve 2004). Therefore, the addition of better preserved material in phylogenetic analysis could considerably change the current proposed relationships.

The dyrosaurids were long considered an African group (Buffetaut 1981), but they are now known from nearly all continents. The dyrosaurids presented here are primarily African forms, except for *Hyposaurus*, which is also present in North America (Troxell 1925; Parris 1986; Denton et al. 1997), Saudi Arabia (Langston 1995), and South America (Cope 1885, 1886), and *Rhabdognathus*, which is also present in Saudi Arabia (Langston 1995). *Phosphatosaurus*, *Dyrosaurus*, *Chenanisuchus*, *Hyposaurus*, *Rhabdognathus*, and *Arambourgisuchus* are from North Africa. *Sokotosuchus*, *Hyposaurus*, and *Rhabdognathus* are found in the Iullemeden Basin, West Africa. The phylogenetic results suggest a North African range for basal members (Fig. 9), with a dispersal to other areas from this region. The wide distribution of the genera *Hyposaurus* and *Rhabdognathus* accentuates the possibility of transoceanic dispersal of the dyrosaurids, confirming the previous hypothesis of a dispersal from North Africa. Unfortunately, many dyrosaurids are insufficiently known to be included in the present work, and their taxonomic status remains unclear. The species used here, which are the best known, are mainly African forms; inclusion of other taxa from various geographic areas could be palaeobiogeographically important, and could significantly improve and modify the present hypothesis.

The phylogenetic relationships do not match particularly well with the stratigraphic distribution of the taxa, because the most basal taxon is known from the Palaeocene (*Chenanisuchus*), while the Late Cretaceous *Sokotosuchus* is closely related to the early Eocene *Phosphatosaurus*. *Hyposaurus* is also reported from the Maastrichtian, which calibrates the split between *Dyrosaurus* (early Eocene) and more derived taxa to at least the Late Cretaceous. Splits between most of the taxa seem to occur in the Maastrichtian or early Palaeocene. The branches are long for the Eocene *Phosphatosaurus* and *Dyrosaurus*. Nevertheless, the stratigraphic distribution is not particularly extensive, and there are no unusually long ghost lineages.

The result presented herein is not strongly supported, since the decay index (Bremer 1994) is very low and is 1 for all nodes, except for node 3 (DI: 2) and node 5 (DI: 2) (Fig. 9). This is probably due to the low resolution of some taxa including *C. bequaerti* (54% of missing data), *S. ianwilsoni* (42.9% of missing data) and *P. gavialoides* (48.6% of missing data). Moreover, the comparison is often limited by the preservation of the specimens, which precludes the definition of new characters. As a result, new material of previously described species is needed, and could provide new information and enable the definition of new characters, modifying or improving the phylogenetic relationship hypothesis presented here.

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Appendix 1

List of characters used in this study.

1. Retroarticular process short (0) or extremely long and postero-dorsally curved (1).
2. Posteromedial wing of the retroarticular process dorsally situated or at mid height (0) or ventral (1) on the retroarticular process.
3. Occipital tuberosities absent (0), small (1) or strongly developed (2).
4. Palatine participates to the anterior margin or not (0) or only to the anteromedial margin (1) of the choanae.
5. Exoccipital participates slightly (0) or largely (1) to the occipital condyle.
6. Coronoid present (0) or absent (1).
7. Basisphenoid rostrum short (0) or extremely long anteriorly (1).
8. Seventh mandibular tooth about as large as the others dentary teeth (0) or smaller and close to the height (1).
9. Anterolateral postorbital process absent or small (0) or contact the dorsal margin of jugal (1).
10. Posterior wall of supratemporal fenestra almost vertical, and almost not visible in dorsal view (0) or dorsally inclined, largely exposed in dorsal view (1).
11. Posterior margin of skull roof straight (0), or strong anterior concavity of the posterior margin of parietal (1).
12. Lacrimal-nasal contact twice longer (0) or about equal (1) to the prefrontal-nasal contact.
13. Ventral part of basioccipital vertical, largely visible in occipital view (0) or strongly inclined, weakly visible in occipital view (1).
14. Antermost point of the posterior margin of the pterygoidian wing about at the level (0) or far anterior (1) to the medial eustachian foramen.
15. Supratemporal fenestra anteroposteriorly short (0) or strongly elongated (1).
16. Lateral margin of the supratemporal fenestra relatively wide and ornamented (0) or thin and not ornamented (1).
17. Symphysis wider than high (0) or about as wide as high (1).
18. Interfenestral bar wide (0) or narrow (1).
19. Quadratojugal does not participate (0) or participates largely (1) to the cranial condyle for articulation with the jaw.
20. External mandibular fenestra wide (0), absent or reduced to a thin slot (1).
21. Robust teeth with very wide alveoli (0) or thin and long teeth (1).
22. Interorbital space wide (0) or narrow (1).
23. Anterior carina of tooth dorsoventrally straight (0) or strongly medially "twisted" (1).
24. Premaxillae strongly differentiated from lateral margin of maxilla (0) or slightly or not differentiated (1).
25. Variation in maxillary tooth size (0) or homodonty in size (1).
26. 5 (0) or 4 (1) premaxillary teeth.
27. Parietal strongly dorsally ornamented with deep pits (0), or smooth (1), or slightly ornamented (2).
28. Occipital tuberosity rounded (0) or dorsoventrally flat (1).
29. Posterior margin of squamosal lateral to occipital tuberosity straight (0) or anteriorly concave (1).
30. Interfenestral bar ornamented (0) or not ornamented (1).

Appendix 2

Data matrix used for phylogenetic analysis of Dyrosauridae. Missing or unknown data are represented by "?".

<i>Eutretauranosuchus</i>	00000	0?000	01000	00000	010?0	?0N00
<i>Elosuchus</i>	0?010	?0000	0?010	00000	00000	00N00
<i>Sarcosuchus</i>	00000	00000	00000	00001	00000	00N00
<i>Terminonaris</i>	?0000	??000	01010	00001	10011	00N00
<i>Arambourgisuchus</i>	??211	??111	01011	0011?	11011	11111
<i>Hyposaurus</i>	11211	1?111	1?101	00110	11111	12101
<i>Rhabdognathus</i> sp.	??211	?1?11	10111	1111?	110??	?2011
<i>R. rarus</i>	??2?1	???11	1?1?1	1111?	11??1	?2011
<i>Dyrosaurus</i>	1?211	?1110	00001	01111	11011	10000
<i>Chenaniusuchus</i>	111?1	???00	000?1	0101?	10011	10000
<i>Sokotosuchus</i>	??1??	???00	0?0?1	0?1??	01?00	10001
<i>Phosphatosaurus</i>	???1?	?????	0?0?1	??1??	01000	10?01
<i>Congosaurus</i>	11???	1?1??	?1???	?1??1	11011	1????