

A PRIMITIVE MARINE GAVIALOID FROM THE PALEOCENE OF MOROCCO

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ABSTRACT—The discovery of a new genus and species of gavialoid at the Danian–Thanetian boundary, in the Oulad Abdoun Basin of Morocco, is consistent with an African origin of Gavialoidea. *Argochampsia krebsi*, n.g. n.sp., exhibits a particular shape of the anterior end of its premaxillae, transversely broad and strongly bent downwards, a shape found in distantly related taxa, such as pholidosaurids and *Terminonaris*. A phylogenetic analysis, suggests that *A. krebsi* is a primitive gavialoid, placed with *Eogavialis africanum* between ‘thoracosaur’ (primitive Gavialoidea) and more derived taxa. This analysis supports the previous morphological analysis, which suggests a close relationship of Tomistominae with Crocodylinae, in contrast with the molecular analysis which give a closer relationships between *Tomistoma* and *Gavialis*. The marine nature of the layer where *Argochampsia* comes from is consistent with a marine origin for *Argochampsia*. This demonstrates the existence of marine adaptation in fossil species of primitive gavialoids, which may explain the dispersal of the fossil gavialoids to South America and Asia during and after the Oligocene.

INTRODUCTION

After the K/T crisis, marine crocodyliforms were among the largest marine predators. They were represented by three end members shared between dyrosaurids and eusuchians: a large durophagous mesorostrine form, a mid-length ichthyophagous mesorostrine to longirostrine form, and a large longirostrine crocodyliform. These specializations may have helped to avoid interspecific competition (Hua, 1997). During the Danian, all three morphotypes are occupied by dyrosaurids in Saudi Arabia (Langston, 1995) with *Hyposaurus* sp. (mid-length ichthyophagous mesorostrine form), *Phosphatosaurus* sp. (large durophagous mesorostrine form) and *Rhabdognathus* sp. (large longirostrine form). But in North Africa, though the crocodyliform fauna is dominated by dyrosaurids (Arambourg, 1952; Bergounioux, 1956), a new species of longirostrine eusuchian seems to have lived there as well.

This specimen, represented by a skull (OCP DEK-GE 1201), was found in the Oulad Abdoun basin in strata II of the ‘Grand Daoui’ area (Fig. 1), corresponding to the boundary between Danian and Thanetian (Noubhani and Cappetta, 1997). This work has taken place in collaboration between the French National Museum, the Geological Survey of Morocco and O.C.P. (Office Chérifien des phosphates).

SYSTEMATIC PALAEOLOGY

EUSUCHIA Huxley, 1875

CROCODYLIA Gmelin, 1788

GAVIALOIDEA Brochu, 1997

Genus *ARGOCHAMPSA*, gen. nov.

Etymology—Argo, from the Greek ship of Jason, champsia, Greek root for crocodile.

Type species—*Argochampsia krebsi*, sp. nov.

Diagnosis—As for the type and only known species.

Argochampsia krebsi, sp. nov.
(Figs. 2–5)

Etymology—krebsi, in honor of the late prof. B. Krebs (Berlin).

Holotype—OCP DEK-GE 1201, a nearly complete skull, with mandibular fragments, housed in the geological survey of

the OCP (‘Office Chérifien des Phosphates’) in Khouribga, Morocco (Figs. 2–5).

Type locality—‘Couche II’ of the Oulad Abdoun basin, ‘Grand Daoui’ area (Dano–Thanetian boundary).

Diagnosis—Rostrum about 70% of median length of the skull, 5 premaxillary alveoli and 26 maxillary alveoli, premaxilla transversally broad and strongly bent downwards, with first three alveoli forming a transverse row, diastema between the fourth and fifth premaxillary alveoli, nasals fused, one external foramen between maxilla and jugal, frontal modestly penetrates the supratemporal fenestra, paroccipital processes form two postero-laterally directed long narrow points.

DESCRIPTION

State of preservation—The skull is 43.3 centimetres long and has a typical longirostrine form (Busbey, 1995). It has been severely crushed at the postorbital level, and the lower bar of the infratemporal fenestrae is lacking. The rostrum has a length of 30.6 cm and a constant width of 3.2 cm, which increases drastically at the level of the lacrimal to reach approximately 13.4 centimetres.

Cranial openings—The most important morphological characters of *A. krebsi* are located on the anterior part of the snout. One of them is a pair of large premaxillary foramina, located at the level of the first premaxillary diastema (Fig. 2A, B). These circular openings (diameter approximately 1 cm) may have received the first teeth of the mandible in the living animal. The external nares are large, opened dorsally, with a pentagonal shape. They are completely included in the premaxillae, without contact with the nasal (Fig. 2A, B). The incisive foramen is elliptical and ventrally comes between the premaxillary foraminae (L: 2.3 cm; l: 0.9 cm). It is well developed, and exceeds the anterior level of the external nares (Fig. 3A, B). The more or less elliptical orbits are larger than the supratemporal fenestrae. They are separated by a relatively narrow and concave frontal (Fig. 2A, B). Posteriorly, the supratemporal fenestra is craniocaudally longer than wide, bordered caudally by the parietal and squamosal (more by the squamosal), and anteriorly by the postorbital and frontal. The postorbital constitutes half of the lateral edge, but does not contribute much to the anterior margin. The suture between the frontal and post-



FIGURE 1. Geographical position of the type locality. **A**, geographical position of the Paleocene deposits in the Oulad Abdoun basin (Morocco) of Africa (grey, Palaeocene [modified from Capetta, 1972]). **B**, simplified geological map of the Oulad Abdoun basin; Grand Daoui is the type locality (modified from Arambourg, 1952).

orbital is continuous with the lateral edge of the supratemporal fenestra. On the posterior wall of the supratemporal fenestra, the temporal canal is small, wider than high, surrounded dorsally by the parietal and squamosal (each for one half). Ventrally the sutures between the different bones are not visible. Only the anterior and dorsal margins of the infratemporal fenestrae are preserved, and the lower bars are completely absent. Anteriorly each is bordered by the postorbital in the postorbital pillar, and the squamosal and quadrate constitute the dorsal margin (Fig. 4A, B). The quadratojugal participates in at least the posterior margin. The posttemporal fenestrae are very reduced, with a narrow arch shape, bordered medially and ventrally by the supraoccipital and mediodorsally by the parietal (Fig. 5A, B). The squamosal seems to contribute to the dorsal edge only, and the exoccipital seems excluded from the posttemporal fenestral margin. In ventral view, only the anterior part of each suborbital fenestra is preserved. Each ends anteriorly at the level of the twentieth maxillary tooth. It is bordered medially by the palatine, anteriorly and laterally by the maxilla, and probably posterolaterally by the ectopterygoid. The pterygoid seems to participate in the suborbital fenestra only in the most posterior part (Fig. 3A, B). Only the left pterygoid is preserved, exhibiting a little more than the left anterior quarter of the choana. The choana appears rounded and not separated with a septum. The left dorsal part, preserved in place on the basisphenoid, is directed caudoventrally with a very thin separation with the basisphenoid. The posterior margin of the choana is formed by a thin pterygoidal lamina (Fig. 3A, B).

Premaxilla—The arrangement of premaxillary alveoli is striking. The premaxillae are transversally broad and strongly bent downwards with the first three alveoli of each constituting a mediolateral row (Figs. 2A, B; 3A, B; 4A, B). These first three alveoli have a uniform diameter (8 mm), are larger than the other premaxillary alveoli (about 5 mm), and are followed posteriorly by the 8 mm long first diastema. This space probably allowed reception of the second dentary tooth. The last two alveoli form an angle of 45° with the medial plane of the skull. At this level, the snout reaches its maximal width of 4.9 cm. After the fifth alveoli, at the level of the second diastema (1.4 cm long), the rostrum is narrowest (2.3 cm). The premaxillae extended dorsally as far as the level of the fifth maxillary alveoli, contact the nasals, and ventrally reach the level of the third maxillary alveoli.

Maxilla—The left maxilla has twenty six teeth, but the right has only twenty two. This difference is caused by an anomaly, since two alveoli are absent in the right tooth row between the thirteenth and fourteenth, and two others between the fourteenth and fifteenth (Fig. 3A, B). Because of the alignment of the maxillary and dentary tooth rows, these bones have festooned outlines (Fig. 2A, B). The interalveolar space and the diameter of the alveoli remain constant (respectively 4 and 6 mm, width at the first alveolus: 3.1 cm). Only one tooth is preserved (the second right tooth; Fig. 3A, B): it is curved posteriorly, circular in cross section, and no carinae are seen. On the ventral margin of the skull, the maxillary-jugal suture is posteriorly inserted in a furrow, beginning at the level of the last teeth, and ending

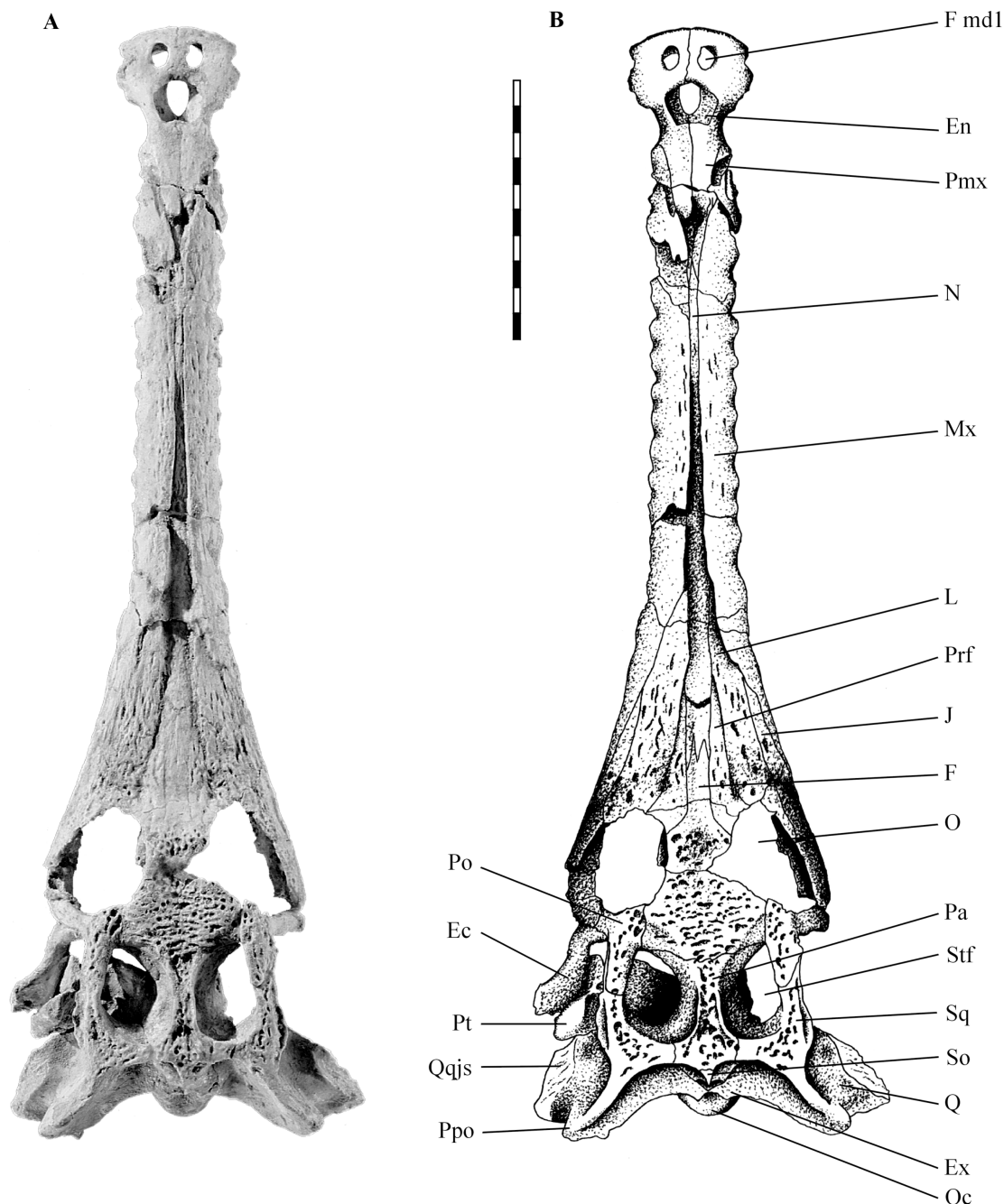


FIGURE 2. *Argochampsia krebsi*, nov. gen. et sp., holotype, SMG-C1, from the Paleocene of Morocco. Skull in dorsal view. Scale bar equals 10 cm. **Abbreviations:** Oc, occipital condyle; Ec, ectopterygoid; En, extenal nares; Ex, exoccipital; F, frontal; Fmd1, foramen for first dentary tooth; J, jugal; L, lacrimal; Mx, maxilla; N, nasal; O, orbit; Pa, parietal; Pmx, premaxilla; Po, postorbital; Ppo, paraoccipital process; Prf, prefrontal; Pt, pterygoid; Q, quadrate; Qqjs, quadrate-quadratojugal suture; So, supraoccipital; Sq, squamosal; Stf, supratemporal fenestra.

posteriorly with a foramen (Fig. 3A, B). Therefore, the jugal forms a small lateral ridge, bordering the last alveoli and the foramen situated between the maxilla and jugal.

Nasal—The nasal bones are fused, are 15.5 cm long, have a maximum width of 1.1 cm, and a narrow anterior width (0.3 cm). They separate the maxillae to contact the premaxillae (Fig. 2A, B). This contact is shallow, penetrating very little between premaxillae. Their ornamentation is very modest.

Lacrimal—The lacrimals are densely ornamented and form the anterior walls of the orbits (Fig. 2A, B). They extend from the level of the fourteenth to the twenty fifth maxillary alveoli,

extend further anteriorly than the prefrontals (total length: 9.7 cm), and contact the nasals for at least 3 cm.

Prefrontal—The prefrontals extend 1.5 cm anterior to the anterior process of the frontal (maximal length: 5.8 cm). Sutures with the lacrimals can be seen on the ventral surface (Fig. 3A, B), through the suborbital fenestrae. The prefrontal pillar is antero-posteriorly long, laterally narrow, and the suture between the prefrontal and palatine is horizontal at mid height.

Frontal—The frontal extends 3 cm anterior to the orbits, and posteriorly participates in the anterior border of the supratemporal fenestra (Fig. 2A, B). Its ornamentation is dense, and it

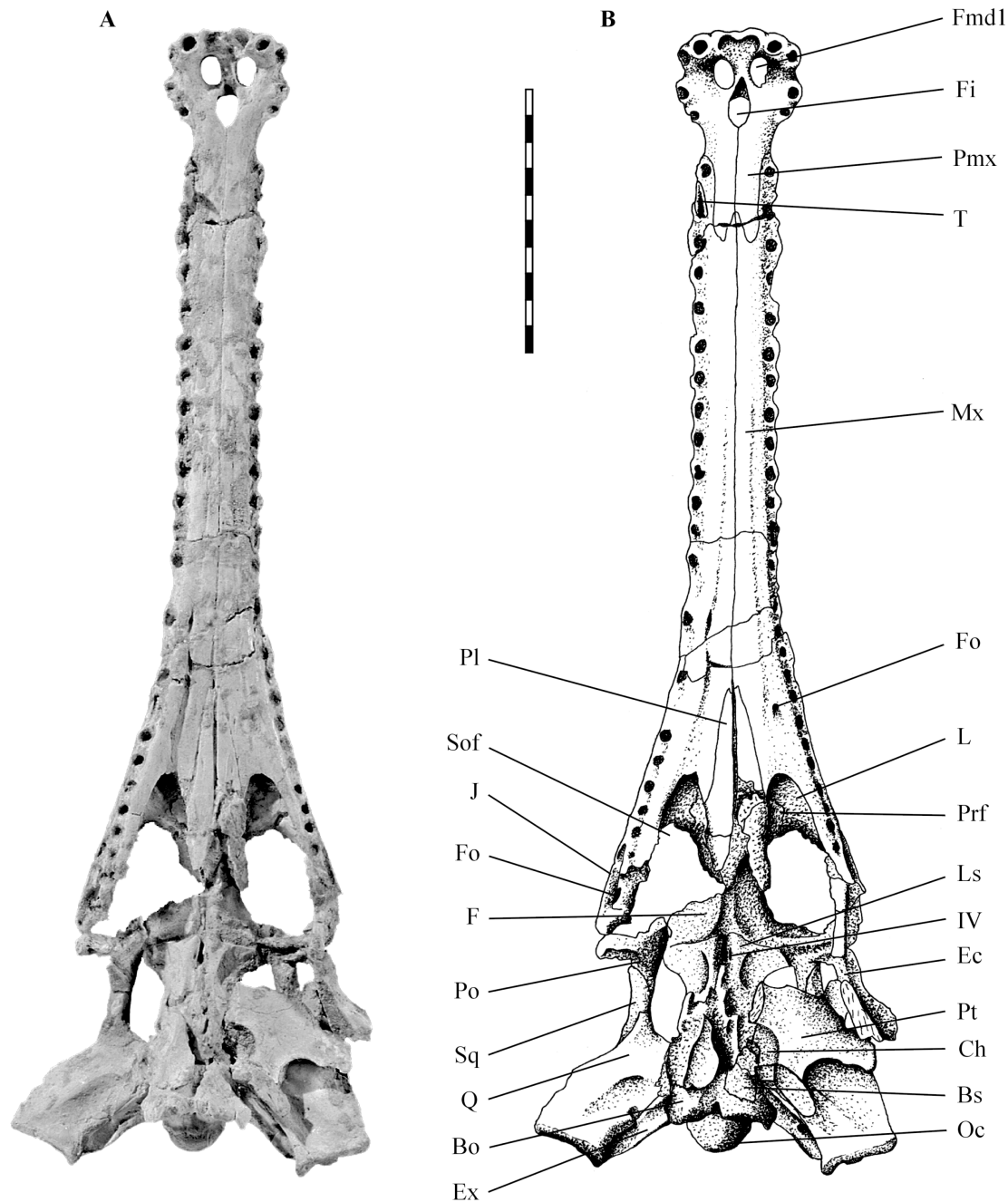


FIGURE 3. *Argochampsia krebsi*, nov. gen. et sp., holotype, SMG-C1, from the Paleocene of Morocco. Skull in ventral view. Scale bar equals 10 cm. **Abbreviations:** Bo, basioccipital; Bs, basisphenoid; Ch, choana; Oc, occipital condyle; Ec, ectopterygoid; Ex, exoccipital; F, frontal; Fi, foramen incisivum; Fmd1, foramen for first dentary tooth; Fo, foramen; J, jugal; L, lacrimal; Ls, laterosphenoid; Mx, maxilla; Pi, palatine; Pmx, premaxilla; Po, postorbital; Prf, prefrontal; Pt, pterygoid; Q, quadrate; Sof, suborbital fenestra; Sq, squamosal; T, tooth; IV, foramen for cranial nerve IV.

separates the orbits with a minimal width of 2.5 cm. The suture with the parietal occurs at the anterior end of the interfenestral bar (total length: 8.6 cm), and the suture with the laterosphenoid is on the margin of the supratemporal fenestra.

Jugal—The jugals extend anteriorly to the level of the eighteenth maxillary alveoli. As seen above, a foramen (L: 1.1 cm), visible from both sides, ventrally separates the maxilla from the jugal and terminates 6 mm from postorbital bar. In dorsal view, each foramen borders the external face of the orbit. The jugal exhibits an anterior elevation, which disappears just before the

postorbital bar (Figs. 2A, B; 4A, B). Nevertheless, the postorbital bar is directed laterally, and its base is not flush with the lateral surface of the jugal. A little lateral jugal rim borders the base of the postorbital pillar, without presence of a dorsolateral elevation (the lower temporal bar is laterally thicker than the base of the postorbital bar).

Quadratojugal—These are extremely badly preserved, and only the posterior process, forming the posterior margin of the infratemporal fenestra, can be reconstructed.

Postorbital—The postorbitals form the antero-lateral quarter

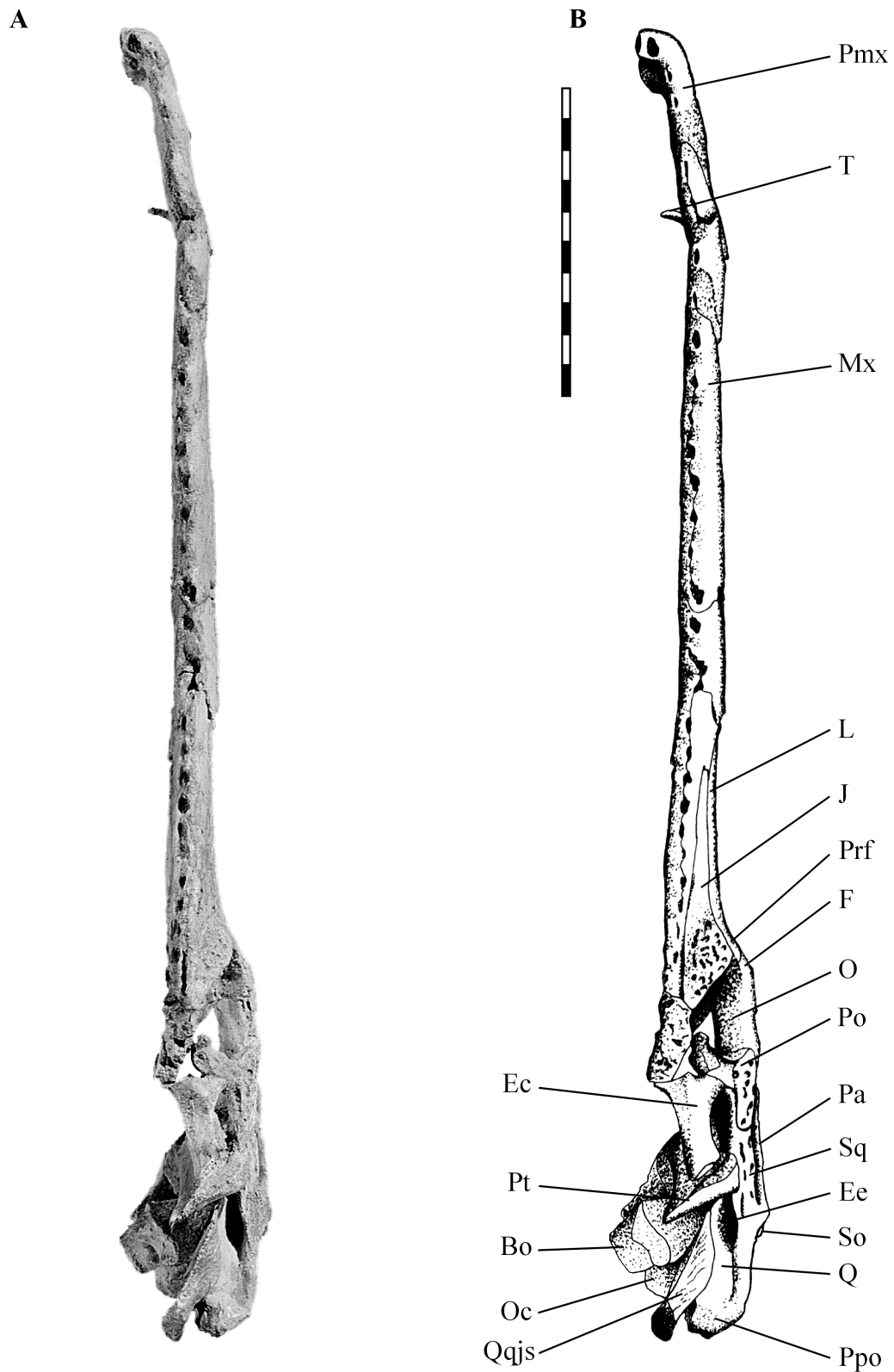


FIGURE 4. *Argochampsia krebsi*, nov. gen. et sp., holotype, SMG-C1, from the Paleocene of Morocco. Skull in lateral view. Scale bar equals 10 cm. **Abbreviations:** Bo, basioccipital; Oc, occipital condyle; Ec, ectopterygoid; Ee, external ear; F, frontal; J, jugal; L, lacrimal; Mx, maxilla; O, orbit; Pa, parietal; Pmx, premaxilla; Po, postorbital; Ppo, paraoccipital process; Prf, prefrontal; Pt, pterygoid; Q, quadrate; Qqjs, quadrate-quadratojugal suture; So, supraoccipital; Sq, squamosal; T, tooth.

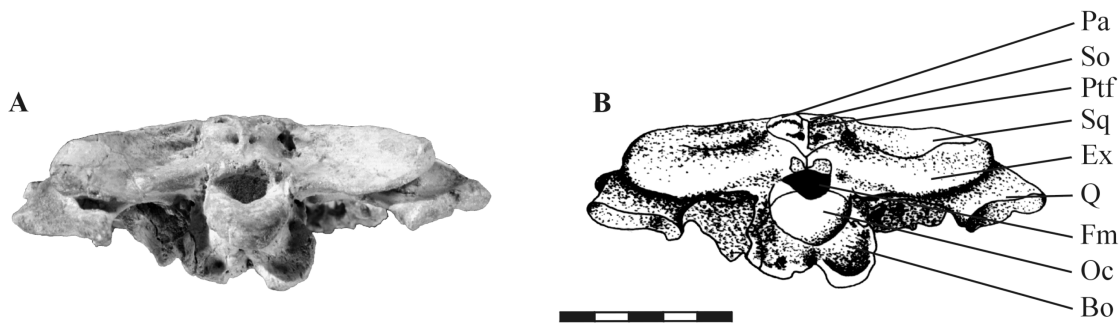


FIGURE 5. *Argochampsia krebsi*, nov. gen. et sp., SMG-C1, holotype, from the Paleocene of Morocco. Skull in occipital view. Scale bar equals 5 cm. **Abbreviations:** Bo, basioccipital; Oc, occipital condyle; Ex, exoccipital; Fm, foramen magnum; Pa, parietal; Ptf, posttemporale fenestra; Q, quadrate; So, supraoccipital; Sq, squamosal.

of the supratemporal fenestrae. They are densely ornamented dorsally, and contribute to the half dorsal part of the postorbital pillar. Their contact with parietal cannot be seen in dorsal view in the supratemporal fenestrae, and this contact may not exist, precluded by the laterosphenoid.

Parietal—The parietal comprises the major part of the interfenestral bar (Fig. 2A, B). It is densely ornamented with deep pits and contributes to the posterior wall of the supratemporal fenestra. It constitutes the dorsal part of the temporal canal and the medio-dorsal margin of the posttemporal fenestra.

Squamosal—Nearly a quarter of the supratemporal fenestra is constituted by a densely ornamented squamosal (Fig. 2A, B). It forms a bony wing laterally, roofing the recessus oticus externus (Iordansky, 1973). Anteroventrally, the squamosal forms the dorsal border of the infratemporal fenestra, and contacts the postorbital bar (Fig. 4A, B). Caudo-externally, each terminates at a point on the paroccipital process.

Supraoccipital—The supraoccipital is small and excluded from the foramen magnum. It is exposed on the skull roof, not embedded within the parietal, but projected posteriorly from the rear of the skull's margin (Fig. 2A, B). On the occipital face, it bears two posterior occipital tuberosities, largely visible in dorsal view, on each side of the postero-medial point, under the posttemporal fenestra.

Exoccipital—The occipital face (height: 4.5 cm) of *Argochampsia* is inclined because of the orientation of the exoccipitals, which bear two posterior wings, largely seen in dorsal view (Fig. 2A, B). The exoccipitals are the largest bones of occipital face (Fig. 5A, B). They circumscribe most of the foramen magnum with the exception of the central part of the ventral border occupied by the basioccipital. The foramen magnum has an elliptical shape (w: 1.7 cm; h: 1.2 cm), and the exoccipitals are sutured in a ridge overhanging it. Ventrally, each bone is indented before joining the quadrate. They contribute in the lateral face of the basioccipital tuberosities. The fracture of the skull does not allow precise description of the cranial nerve foramina and carotid foramen. Only a deep damaged foramen is visible laterally to the occipital condyle, roofed by the exoccipital. The cranio-quadrate canal opens largely laterally, and is surrounded for three-quarters by the exoccipital. A ventral projection of the exoccipital hides the posterior opening of cranio-quadrate canal from occipital view. Only its ventral limit is bordered by quadrate.

Basioccipital—The basioccipital forms the occipital condyle (width: 2.5 cm; medial height: 1.3 cm) and nearly all of the basioccipital apophyses (Fig. 5A, B). These latter are large, constituted in two parts extended laterally, separated by a deep pit, with caudally oriented edges. Each of these apophyses has nearly the width of the condyle. The basis of the apophyses is

uneven, probably for the insertion of the *musculus longissimus capitis profundus* and *rectus capitis anterior* (Broin, 1965).

Quadrate—Anteriorly, the quadrate constitutes the floor of the external auditory meatus, and laterally, the suture with the missing quadratojugal is trapezoidal (Fig. 4A, B). It participates in the postero-dorsal corner of the infratemporal fenestra. The articular surface (total length: 3 cm) is sigmoidal with the inner condyle the largest. It is directed posteromedially and ventrally. Ventrally a smooth ridge, parallel to the suture with the quadratojugal, starts from the prootic and joins the external condyle (distance between both condyles: 13.3 cm). The suture with the exoccipital is linear at the basis of the paroccipital process.

Palatine—In ventral view, the palatine bones are inserted at the level of the seventeenth maxillary alveoli (distance between the anterior margin of the palatine and the premaxillae: 17 cm), far in front of the suborbital fenestra (distance: nearly 3 cm). Caudally, they have been crushed and their posterior part is missing (width between suborbital fenestra: 2.4 cm). Nevertheless, a portion still in contact with the pterygoid shows that the suture between these two bones was perpendicular to the medial plane.

Pterygoid—Only the left pterygoid is preserved, and its caudal process joins the medial plane presumably surrounding the choanae (L: 1.7 cm; $\frac{1}{2}$ W: 1 cm). This bone is well developed with a lateral extension forming a wing, bends ventrally to 45°, and its width (4.6 cm) is greater than its length (4.3 cm). The lateral border of the wing is underlined by an osseous rim (torus transiliens). The insertion of the ectopterygoid is difficult to locate but seems to be at the externo-lateral border of the pterygoid (Fig. 3A, B).

Ectopterygoid—Only the left ectopterygoid is present (total length nearly 4 cm). It has the shape of an 'H' twisted at 90° (Figs. 3A, B; 4A, B). The anterior face has two kidney-like insertion surfaces but it is impossible to know which bone (postorbital, jugal, or maxilla) was located here. The suture with the pterygoid is invisible, but it is preserved medio-dorsally on the postorbital pillar, where it seems to contact the squamosal (the dorso-ventral crushing makes this interpretation uncertain).

Laterosphenoid and prootic—Without the posterior part of the palatine, the laterosphenoids and prootics are visible (Fig. 3A, B). Anteriorly the laterosphenoids are dorso-ventrally flattened, attached to the ventral surface of the frontal, and their anterior margins are perpendicular to the medial plane. They become thin posteriorly, and contact with the parietal cannot be seen. Medially, a foramen probably corresponding to nerve IV can be seen. A foramen, probably for nerve V, lies between the laterosphenoid and prootic. The exact limits of the prootic with the basisphenoid are unclear.

Basisphenoid—The basisphenoid rostrum is broken anteri-

only. Caudally, the basisphenoid extends the ventral face of the basioccipital apophyses by a triangular process. The median eustachian foramen lies between these apophyses (Fig. 3A, B).

COMPARISON AND DISCUSSION

The most striking character of this specimen is the shape of its premaxilla, with its anterior end transversally broad and strongly bent downward, an anatomical layout only seen among pholidosaurids and *Terminonaris*. This character could be interpreted as a mechanical process allowing precise occlusion between the skull and the mandible among some long snouted forms. According to different phylogenetic analyses, this character may have been acquired independently within these different taxa (Wu et al., 2001) or not (Sereno et al., 2001). Nevertheless, *A. krebsi* is distantly related to both, and this morphology is unique among eusuchians.

Snout shape is very labile within Crocodylia (Kälin, 1955; Langston, 1973; Busbey, 1995; Russell and Wu, 1997; Brochu, 2001), and a similar slender snout morphology may have arisen at least six times (Brochu, 2001) during crocodylian evolution. Some species have a very unstable nomenclature according to the different authors, and assignment of some species to Tomistominae or to gavialoids is still debated. *Argochampsia krebsi*, with its homodont maxillary teeth, the frontal within the supratemporal fenestra, and its basioccipital tuberosities is related to the slender snouted Gavialoidea. Maxillary homodonty is present within Crocodylia only in Gavialoidea; in Tomistominae, as in other derived crocodyloids, the 5th maxillary alveolus is the largest (Brochu, 1997b).

In *Argochampsia*, the frontal penetrates the supratemporal fenestra less posteriorly than in the more derived taxa; in 'thoracosaurus', the basalmost gavialoids (Brochu, 1997a, b, 1999, 2002; Brochu and Gingerich, 2000), the frontal is deep in supratemporal fenestra, comprising the anterior quarter of interfenestral bar, but in the most derived, *Gavialis gangeticus*, there is a modest or no penetration of frontal that varies ontogenetically as the fenestra grows beyond the frontoparietal suture.

Much of the confused taxonomy of the longirostrine taxa is due to the position of the nasal in relation to the premaxilla, which touch each other in all tomistomines and primitive gavialoids, but are separated in more derived gavialoids (Langston, 1965). In *A. krebsi*, the very narrow nasal, contacts the premaxillae, but barely penetrates them. This seems to be the condition in primitive Gavialoidea (*Eogavialis africanum*, *A. krebsi* and *Gryposuchus colombianus*), and a difference with Tomistominae, whose nasals penetrates deeply between premaxillae. The condition of this character is unclear among 'thoracosaurus', the basalmost group of gavialoids (Buffetaut, 1985; Brochu, 1997a, b, 1999, 2000a, 2000b, 2001); some species show this contact (*Thoracosaurus macrorhynchus*, (Blainville, 1955)), but others may have lost it as in *Thoracosaurus scanicus* (Troedsson, 1924) and *Thoracosaurus neocesariensis* (Carpenter, 1983). The condition in these two taxa is probably due to misinterpretation (Brochu, pers. comm.), but contact certainly does not exist in the most derived gavialoids (*G. lewisi* and *G. gangeticus*).

The presence of the basioccipital tuberosity is an important character, since it is particular to the most derived gavialoids (Hecht and Malone, 1972; Langston, 1965). This character is observable in our specimen, where the basioccipital is ventrally short and its medial groove, back to the medial eustachian foramina, is deep. In 'thoracosaurus', as in other crocodylians, this groove does not exist, and the basioccipital is ventrally long and rounded.

In *A. krebsi*, the supraoccipital participates in the skull roof. This can be observed in several eusuchians (Brochu, 1999), and is visible in Gavialoidea (*T. macrorhynchus*, *A. krebsi*, *Gry-*

posuchus colombianus, *G. gangeticus*, and in *Thecachampsoides minor* [Leidy, 1865], a primitive gavialoid [Brochu, 2002], but with a different aspect. In other crocodylians, when the supraoccipital contributes to the skull roof, it is embedded within the parietal. In *A. krebsi*, as in other gavialoids (except apparently in *Eogavialis africanum* [Andrews, 1906; Müller, 1927] and in the specimen described as *T. neocesariensis* by Carpenter [1983] [Brochu, pers. comm.]), the supraoccipital is embedded not within the parietal, but posterior to the parietal's caudal margin. In *A. krebsi*, as in *G. gangeticus*, *Piscogavialis jugaliperforatus* and *Gryposuchus colombianus*, in addition, the dorsal extent of the supraoccipital is slender and points posteriorly.

The absence of the posterior part of the palatine in *A. krebsi* enables access to the laterosphenoid. The shape of its capitata process, laterally oriented (anterior margin perpendicular to the medial plan), is a condition observed in all gavialoids, and different from the posterolaterally-oriented margin seen in other crocodylians.

In *A. krebsi*, the maxillary tooth row is underlined, with the space between tooth row lower than the alveolar border. This character, observed in more derived gavialoids, is less clear in 'thoracosaurus', where this character is clearly present in the posterior tooth row, but the alveoli and space between tooth row seems to be at the same level in the anterior of the rostrum (pers. obs. on *Thoracosaurus macrorhynchus*). Nevertheless, in crocodylians, each alveolus is bordered with a little rim, which is absent in other gavialoids, even in 'thoracosaurus.'

In *A. krebsi*, the exoccipitals form a posterior plate, making the occipital face strongly incline anterodorsally, and visible in dorsal view. This inclination can be observed in other gavialoids, contrary to the condition seen in almost all other crocodylians, where the orientation of the occipital face is vertical. This inclination can also be observed in some taxa more primitive than Gavialoidea, such as in *Allodaposuchus precedens* Nopcsa, 1925 (Buscalioni et al., 2001) and *Bernissartia fagesii* Dollo, 1883 (Buscalioni et Sanz, 1990).

Phylogenetic implications—The phylogenetic position of Gavialoidea and its exact relationships with Tomistominae are still debated (Buffetaut, 1985; Tarsitano et al., 1989; Poe, 1996), especially between morphological (Benton and Clark, 1988; Norell, 1989; Brochu, 1997a, b, 1999, 2002; Brochu and Gingerich, 2000) and molecular analysis (Densmore, 1983; Densmore and Owen, 1989; Densmore and White, 1991; Hass et al., 1992; Gatesy, 1992). A maximum parsimony analysis, using 66 taxa and 167 discrete morphological characters (Appendix 1 and 2), was performed with PAUP 3.1.1 (Swofford, 1993), trying to bring new data to this discussed phylogeny. Characters are mainly based on Brochu (1997b, 1999), on Brochu and Gingerich (2000) for *Thoracosaurus neocesariensis* and *Paratomistoma courti*, on Buscalioni et al. (2001) for the Las Hoyas Neosuchia, *Allodaposuchus precedens*, modifications in *Bernissartia fagesii* and *Hyleochampsia vectiana*, and for character 166. Character 82 is modified, with introduction of a new character state (82(1)), and characters 165 and 167 are new.

The result shows the position of *Argochampsia krebsi* within Gavialoidea and the basal position of 'thoracosaurus' in this group (Fig. 6). At the present time, 'thoracosaurus' include three taxa: *Thoracosaurus neocesariensis* (Kay, 1842) from the Maastrichtian and Palaeocene of New Jersey (Carpenter, 1983); *T. macrorhynchus* (Blainville, 1855) from Danian of France (Gervais, 1958; Piveteau, 1927), and *T. scanicus* Troedsson, 1924 from the Danian of Sweden (Troedsson, 1924), but some disagreements in the reliability of some characters, in particular absence or presence of an antorbital fenestra in *T. neocesariensis* (Carpenter, 1983; Laurent et al., 2000), make the systematics of this group uncertain. Indeed, if the absence of an antorbital fenestra is confirmed for *T. neocesariensis* (Carpenter, 1983;

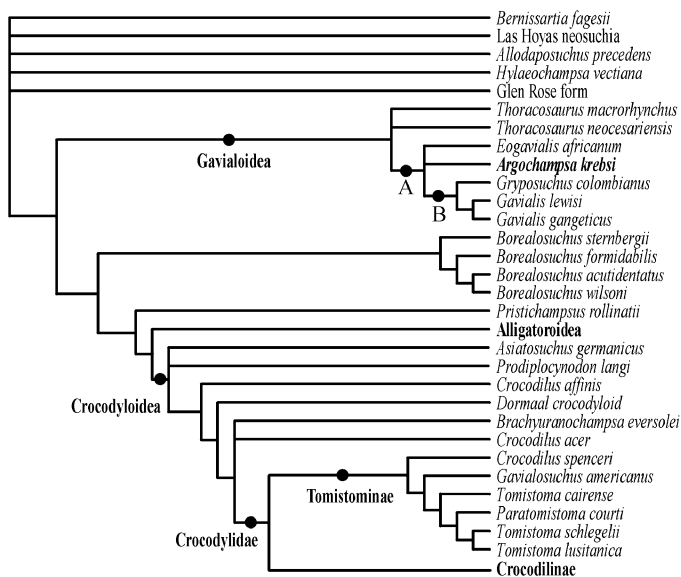


FIGURE 6. Cladogram showing phylogenetic position of *Argochampsa krebsi*, nov. gen. et sp. based on strict consensus of most parsimonious trees (length, 512; consistency index (excluding autapomorphies): 0.407; retention index, 0.818) generated using PAUP (version 3.1.1.) (Swofford, 1993). The composition of Alligatoroidea and Crocodylinae are not detailed. For character list and taxa/character matrix see Appendix 1 and 2.

Brochu, pers. comm.), the specimen described by Laurent et al. (2000) is a new species diagnosed by the presence of an antorbital fenestra, unless this fenestra is an artifact as well.

As in all members of Gavialoidea, ‘thoracosaurus’ possess a deep and wide splenial symphysis longer than five alveoli. Within this clade, one unambiguous synapomorphy unites the African gavialoids (*Argochampsa* and *Eogavialis*) to South American (*Gryposuchus*) and Indian (*Gavialis*) gavialoids (Fig. 6, node A): a basisphenoid antero-posteriorly wide ventral to basioccipital. A small, posteriorly-projected posterior pterygoid process is an unambiguous apomorphy of the clade containing *Gryposuchus* and *Gavialis* (Fig. 6, node B).

All molecular analyses relate *Tomistoma* to *Gavialis* (Densmore, 1983; Densmore and Owen, 1989; Densmore and White, 1991; Hass et al., 1992; Gatesy, 1992). The position of Tomistominae closer to Gavialoidea than to Crocodyloidea defended by molecular analysis is not confirmed by this work, mainly based on preceding morphological analysis with the same results as those obtained herein. As with previous morphological analyses, addition of a new gavialoid species is consistent with a basal position of Gavialoidea within Crocodylia, and the membership of Tomistominae within Crocodyloidea.

Paleobiogeographic implications—Living *Gavialis* is a fresh water crocodile, but a description of the anatomy of its buccal cavity has shown existence of salt glands on their tongue, even if it is unclear that they are functional (Taplin, 1985; Taplin et al., 1989). This new species, from a marine environment, probably had functional salt glands, suggesting that no obstacle precluded a marine dispersal of gavialoids. The buccal condition of living *Gavialis* may represent secondary reduction from a marine adapted condition in its ancestry (Taplin et al., 1989).

This new species seems to confirm the presence of basal gavialoids in Africa. Presence of this group later in South America from the Miocene (with *Piscogavialis jugaliperforatus* Kraus, 1998 and *Gryposuchus colombianus* [Langston, 1965; Langston and Gasparini, 1995]) and from the Lower Miocene

of Asia (*Gavialis curvirostris* Lydeker, 1886 and *Gavialis breviceps*, Pilgrim, 1912 [Pilgrim, 1912]), suggests that gavialoid dispersal might have been made from Africa, probably during Oligocene, across Atlantic and Indian Ocean (Buffetaut, 1978, 1982), with marine adapted condition forms such as *A. krebsi*.

In conclusion, the study of fossils from the Moroccan phosphates has just begun. Their story is incomplete but the existence of *Argochampsa*, a primitive gavialoid, underlines their importance.

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APPENDIX 1

The characters listed below are used to discern relationships within Eusuchia together with *Bernissartia fagesii*, and the new genus described in this paper.

Character 82 is modified from Brochu (1999), with introduction of a new character state (82(1)), and characters 165 and 167 are new.

82. Supraoccipital exposure on dorsal skull table small (0), points posteriorly to the caudal margin of the parietal (1), absent (2), large (3), or large such that parietal is excluded from posterior edge of table (4). (Modified from Norell, 1988, character 11)
165. Edge of the maxillary tooth alveoli lower or at the same level than the space between tooththrow (0), or edge of the maxillary tooth alveoli higher than the space between tooththrow (tooththrow underlined) (1).
167. Occipital surface inclined (0) or “verticalized” (1).

APPENDIX 2

There are 167 characters for 66 taxa, analysed with Paup 3.1.1. (Swofford, 1993). ? = missing data or not applicable. Characters are mainly based on Brochu (1997, 1999), on Brochu and Gingerich (2000) for *Thoracosaurus neocesariensis* and *Paratomistoma courti*, on Buscalioni et al. (2001) for the Las Hoyas Neosuchia, *Allodaposuchus precedens*, modifications in *Bernissartia fagesii* and *Hyleochampsia vectiana*, and for character 166.

	11
	866
	257
<i>Bernissartia fagesii</i>	000
Glen Rose form	???
<i>Hyleochampsia vectiana</i>	001
<i>Borealosuchus formidabilis</i>	000
<i>Borealosuchus sternbergii</i>	000
<i>Borealosuchus acutidentatus</i>	000
<i>Borealosuchus wilsoni</i>	000
<i>Leidyosuchus canadensis</i>	000
<i>Thoracosaurus macrorhynchus</i>	110
<i>Eogavialis africanum</i>	210
<i>Gryposuchus colombianus</i>	110
<i>Gavialis lewisi</i>	011
<i>Gavialis gangeticus</i>	110
<i>Pristichampsus rollinatti</i>	0??

<i>Diplocynodon darwini</i>	001	<i>Crocodylus niloticus</i>	001
<i>Diplocynodon ratelii</i>	001	<i>Crocodylus palaeindicus</i>	201
<i>Diplocynodon hantoniensis</i>	001	<i>Osteolaemus tetraspis</i>	001
<i>Alligator mississippiensis</i>	201	<i>Crocodylus robustus</i>	201
<i>Alligator sinensis</i>	201	<i>Crocodylus lloidi</i>	0??
<i>Alligator mefferdi</i>	201	<i>Crocodylus megarhinus</i>	?01
<i>Alligator olseni</i>	201	<i>Australosuchus clarkae</i>	0??
<i>Alligator mcgrewi</i>	201	<i>Euthecodon arambourgii</i>	001
<i>Alligator prenasalis</i>	001	<i>Tomistoma schlegelii</i>	001
<i>Allognathosuchus mooki</i>	001	<i>Tomistoma lusitanica</i>	001
<i>Allognathosuchus wartheni</i>	001	<i>Tomistoma cairense</i>	0?1
<i>Wannaganosuchus brachymanus</i>	001	<i>Crocodylus spenceri</i>	001
<i>Procaimannoidea kayi</i>	201	<i>Gavialosuchus americanus</i>	20?
<i>Arambourgia gaudryi</i>	001	<i>Brachyuranochampsia eversolei</i>	000
<i>Stangerochampsia mccabei</i>	001	<i>Dormaal crocodyloid</i>	0??
<i>Brachichampsia montana</i>	301	<i>Crocodylus acer</i>	001
<i>Eocaiman cavernensis</i>	4??	<i>Crocodylus affinis</i>	001
<i>Purussaurus neivensis</i>	??1	<i>Asiatosuchus germanicus</i>	001
<i>Mourasuchus</i>	401	<i>Prodiplocynodon langi</i>	001
<i>Caiman yacare</i>	401	<i>Thoracosaurus neocesariensis</i>	110
<i>Caiman crocodilus</i>	401	<i>Paratomistoma courti</i>	010
<i>Caiman latirostris</i>	401	<i>Allodaposuchus precedens</i>	000
<i>Melanosuchus niger</i>	401	<i>Las Hoyas Neosuchia</i>	0??
<i>Paleosuchus trigonatus</i>	301	Character states for new genus and species	
<i>Paleosuchus palpebrosus</i>	301	<i>Argochampsia krebsi</i>	
<i>Crocodylus cataphractus</i>	001	????????????????????????????	
<i>Crocodylus rhombifer</i>	001	????????????????????????????	
<i>Crocodylus porosus</i>	001	?????1100?00021?11??10?4??	
		1002?0?000?0?00?003??01??	
		??0000??0?0010?1?11100010??	
		101?0?????0?0?100	