

A REVISION OF THE CROCODYLIFORM *ALLODAPOSUCHUS PRECEDENS* FROM THE UPPER CRETACEOUS OF THE HATEG BASIN, ROMANIA. ITS RELEVANCE IN THE PHYLOGENY OF EUSUCHIA

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ABSTRACT—This paper describes the skull of *Allodaposuchus precedens* Nopcsa, 1928 and provides the first complete diagnosis of the species. The description of the holotype, which comes from the Upper Cretaceous deposits of Valioara in the Hateg Basin of Romania (Late Maastrichtian), is included with those of other undescribed specimens from the uppermost Cretaceous of Spain and southern France. All the specimens preserve the same anatomical region as the holotype and provide new relevant information on the genus *Allodaposuchus* and its phylogenetic position. The phylogenetic context of *A. precedens* is discussed in the context of a recent cladistic analysis of Eusuchia and its crown-group Crocodylia. *Allodaposuchus* is unambiguously the sister taxon of the crown-group Crocodylia, sharing with this clade the absence of a lingual to maxillary occlusion of the dentary teeth, and the extension of the ectopterygoid that does not reach the posterior tip of the lateral pterygoid flange, among other characters. The phylogenetic analysis also raises the problem of the ambiguous definition of Eusuchia, since the characters traditionally used in its diagnosis are multiply derived. *Allodaposuchus* is an outstanding crocodyliform providing new anatomical evidence concerning the stem-group of Crocodylia, and filling the gap between the Early Cretaceous (Barremian) *Hylaeochampsia* and the earliest common ancestor of Crocodylia.

INTRODUCTION

Nopcsa (1915–1916) described the first crocodyliform material from the Late Cretaceous of Transylvania. These specimens were collected by Ottokar Kadis in 1914 from the Densus Ciula Formation of Valioara (Late Maastrichtian in age; Weishampel et al., 1991; Grigorescu, 1992), in the Hateg Basin of what is now Romania. The collection consists of isolated remains housed in the Magyar Állami Földtani Intézet (MAFI; the Hungarian Geological Institute) in Budapest. Nopcsa originally attributed the Valioara crocodile to *Crocodylus affuvelensis*?, on the basis of comparisons with the description and figures of the Late Cretaceous crocodiles of the Fuvelian lignites of southern France provided by Matheron (1869).

In 1928, Nopcsa identified differences between the French and Valioaran specimens. He named the Valioara material *Allodaposuchus* cf. ? *affuvelensis*, emphasising that should a specific difference ever be established for the Valioara species, it should be named *A. precedens*. The material labelled as the type comprises vertebrae, teeth, appendicular elements (humeri and femora), girdle elements (ilium and coracoid), and a portion of the skull table. Although the Valioara species has become known as *Allodaposuchus precedens* (Steel, 1973), Nopcsa's formal proposal has never been honoured. In fact, the type is currently labelled *Crocodylus affuvelensis* in the MAFI collection. The similarities noted by Nopcsa between *A. precedens* and *Crocodylus affuvelensis* have not been appreciated because the specimens described by Matheron (1869) have been lost, and currently the only overlapping material is a femur (Brochu, 1997a). Up to now, the only skull material from the French Fuvelian lignite has been based on a fragment of maxilla and mandible. This specimen is housed in the Natural History Museum at Marseilles (figured in Buffetaut in 1980) and has been ascribed to the genus *Musturzabalsuchus* (Buscalioni et al., 1997).

Nopcsa (1928) related *Allodaposuchus* to *Leidyosuchus*, and included them into the subfamily Leidyosuchinae. He considered a set of characters, including the construction of the cer-

vical vertebrae and the skull table, to be of special taxonomic relevance (see also Buffetaut, 1980). Comparing *L. formidabilis* (Erickson, 1976) and *Allodaposuchus* reveals several similarities including: the anteroposterior elongation of the skull table owing to the presence of long squamosal lobules, the frontal participating in the supratemporal fossa, the projection of the articular quadrate branch quite flat and directed more caudally than ventrally, and the anteroposterior elongation of the otic recess.

In this paper we evaluate these similarities in the context of a phylogenetic analysis of Eusuchia (Fig. 1). Beforehand, we present the first comprehensive description of the skull of *Allodaposuchus precedens* and provide a diagnosis of the species based solely on the skull. The description of the Valioara specimen is presented with other undescribed specimens from Spain: Armuña (Segovia Province), Villamitjana (Lleida Province) and Laño (Treviño County); and from southern France: Bellevue (Département de l'Aude).

Institutional Abbreviations—**MAFI**, Magyar Állami Földtani Intézet, the Hungarian Geological Institute, Hungary; **MCNA**, Museo de Ciencias Naturales de Álava, Vitoria, Spain; **MDE**, Musée des Dinosaures, Espéraza, France; **UPUAM**, Unidad de Paleontología de la Universidad Autónoma de Madrid, Spain.

MATERIAL EXAMINED

The revision of the crocodyliform assemblage from the European Upper Cretaceous has provided a set of skull remains that share the same character combination as the holotype of *Allodaposuchus precedens*. Besides the holotype, the remains of three *Allodaposuchus* skulls from different French and Spanish localities have been selected for description and phylogenetic discussion. All the specimens specified below preserve the same anatomical region as the holotype, but also add important new information that allows their proper comparison. Additionally, a brief description is provided of the postcranial elements that were originally figured in Nopcsa (1915–1916) and those

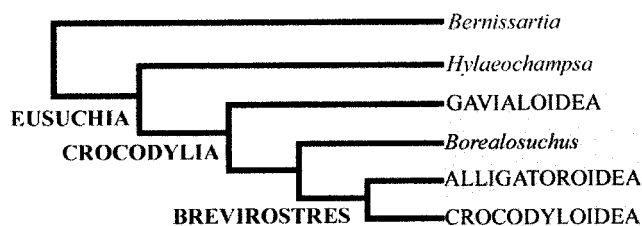


FIGURE 1. Cladogram shows the relationships within Eusuchia and its crown-group Crocodylia. Major groups of Crocodylia indicated in gray (based on Brochu, 1997a).

elements that are in the collection and belong to the Type Locality.

MAFI Ob.3131 (Figs. 2, 3) from Valioara (Hateg Basin, Maastrichtian, Hunedoara, Romania) consists of a fragment of the cranial table and frontal. The ventral side of the skull is fractured at the level of the basioccipital roof and lacks most of the neurocranium. It is the best-preserved of all the specimens examined, with the fine detail of the sutures visible. The squamosal lobules have been partially reconstructed, as well as the left quadrate, squamosal and postorbital. The left exoccipital is deformed, and the specimen lacks the anterior portion of the right quadrate. The specimen's cranial width is 175 mm (measured between the lateral surfaces of the mandibular condyles of the quadrates), and the posterior width of the cranial roof (between the squamosal lobules) is 120 mm. The distance between the mandibular condyle of the quadrate and the anterior tip of the frontal is 195 mm.

UPUAM A1 (Fig. 4) Armuña (Campanian–Maastrichtian, Segovia Province, Spain; Buscalioni and Martinez-Salanova, 1990) consists of disarticulated fragments of a skull with a few associated teeth, figured and reconstructed in Buscalioni and Sanz (1987). The skull is broken off at mid rostrum with fragments of maxilla, premaxillae, pterygoid and basioccipital. The premaxillae were restored gluing separated fragments, graphic documentation of the field work has permitted a new reassessment of the shape of the premaxillae (compare Figs. 4 and 8). The sutures and sculpture in this specimen are hidden because they are partially covered by a matrix of small- and medium-sized sand grains. The specimen has a cranial width (between the lateral surfaces of the mandibular condyles of the quadrates) of about 182 mm, and a cranial roof posterior width of 119 mm. The distance between the mandibular condyle of the quadrate and the anterior tip of the frontal is about 200 mm.

UPUAM A2 from Armuña (Campanian–Maastrichtian, Segovia Province, Spain; Buscalioni and Martinez-Salanova, 1990) contains part of the rostrum and posterior portion of skull with basicranium. The specimen is still partially included in the matrix, although it presents fine details on its ventral side.

UPUAM V1 (Fig. 5) from Vilamitjana (Tresp Basin, Maastrichtian, Lleida Province, Spain; Buscalioni et al., 1986) is an acid-prepared fragment of cranial table with the occipital and braincase regions preserved. The specimen is broken off at the frontoparietal suture, and lacks the palatal elements. Caudal ends of the squamosals are eroded. The specimen has a cranial width (between the lateral surfaces of the mandibular condyles of the quadrates) of about 162 mm, and a cranial roof posterior width of about 100 mm.

MDE C3-276 (Fig. 6) from Bellevue (Late Campanian–Early Maastrichtian, Département de l'Aude, France; Le Loeuff and Buffetaut, 1995) is a fragment of the cranial table broken off at the frontal and neurocranium, with a well-preserved occipital

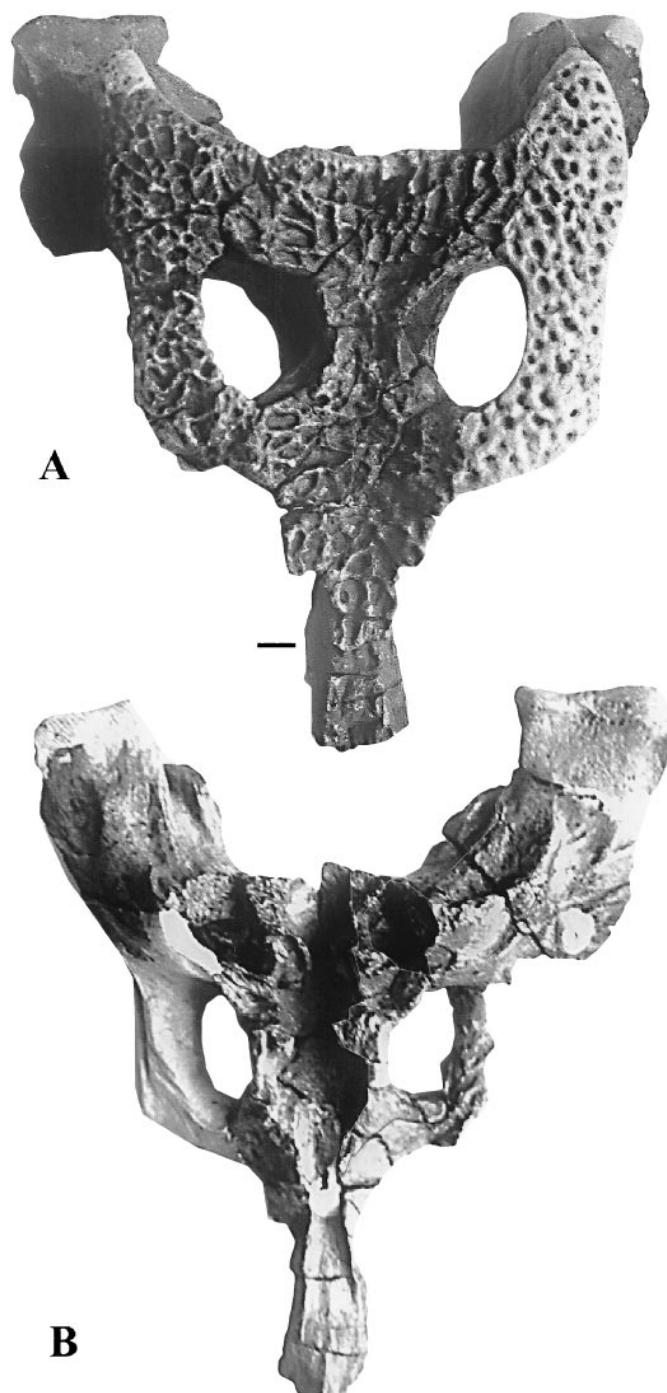


FIGURE 2. **A**, dorsal and **B**, ventral view of the skull of *Allodaposuchus precedens* (Ob3131 from Valioara, Hateg Basin, Romania, Maastrichtian). Scale bar equals 1 cm.

face. The specimen lacks most of its right side, and its left side is distorted.

MCNA LIA-41 from Laño (Campanian–Maastrichtian, Burgos Province, Treviño County, Spain; Astibia et al., 1987, 1990) is an isolated basioccipital.

The specimens considered and figured in Nopcsa are: MAFI Ob 3133: a procoelous dorsolumbar vertebra; MAFI Ob 3136, a sacral vertebra attached to the ilium and MAFI Ob 3140, two femora (left and right) from the same animal. Other isolated

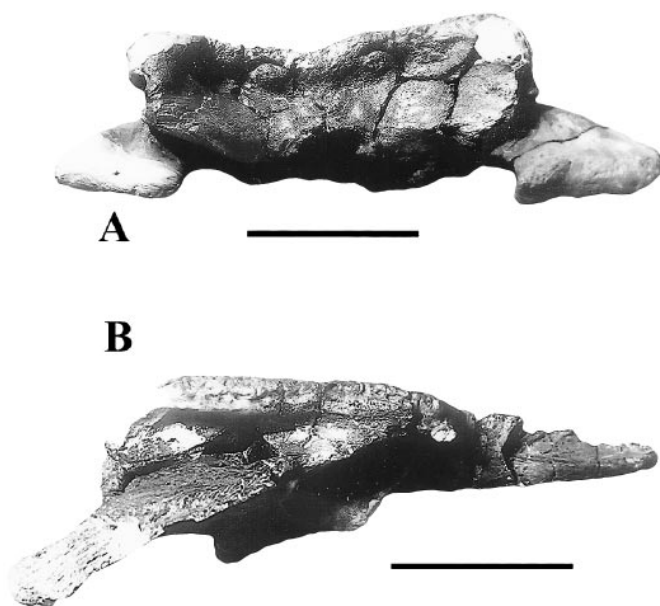


FIGURE 3. **A**, occipital and **B**, right lateral view of the holotype skull (Ob3131) of *A. precedens* in the Hungarian Geological Institute of Budapest from Valioara, Hateg Basin, Romania, Maastrichtian. Scale bar equals 5 cm.

elements in the MAFI collection are, MAFI Ob 3139, two distal femora (left and right) fragments; MAFI Ob 3138, a proximal portion of a humerus; MAFI Ob 3135, a coracoid; MAFI Ob 5727, a dorsolumbar vertebra; MAFI Ob 3134, five cervical and caudal centra; MAFI Ob 5724, a series of six small cervical (2), dorsal (2) and caudal (2) vertebrae; MAFI Ob5725, a fragment of a neurapophysis; MAFI Ob 3137, three osteoderms.

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Hay, 1930 (sensu Benton and Clark, 1988)

EUSUCHIA Huxley, 1875

ALLODAPOSUCHUS Nopcsa, 1928

Diagnosis—as for the type species (by monotypy).

Type species—*Allodaposuchus precedens* Nopcsa, 1928

ALLODAPOSUCHUS PRECEDENS Nopcsa, 1928
(Figs. 2–6)

Holotype—Together with MAFI Ob.3131 (skull fragment), Nopcsa (1915–1916, plate IV, figs. 3–5) figured in the original description a procoelous dorsolumbar vertebra (MAFI Ob 3133), a sacral vertebra attached to the ilium (MAFI Ob 3136) and two (left and right) femora (MAFI Ob 3140) from the same animal (“desselben Tieres”). However, it is not clear to us that these postcranial elements are from the same individual (MAFI Ob 3131). There are other isolated elements of the MAFI collection (MAFI Ob 3134–35; 47–38, and 5724–25, 5727) that Nopcsa did not mention. In his first discussion, naming *Allodaposuchus* in 1928, he did not explicitly list the remains referred to the type: “the remains comprise among others the top of the skull and parts of the atlas and epistropheus (axis)”. We consider solely the skull fragment (MAFI Ob 3131) as being from the holotype in this revised diagnosis of *Allodaposuchus*.

Type Locality—Valioara, Hateg Basin, Late Maastrichtian (Hunedoara County, Romania).

Related Material—Several skull fragments UPUAM V1; UPUAM A1; UPUAM A2; MDE C3–276; MCNA LIA-41.

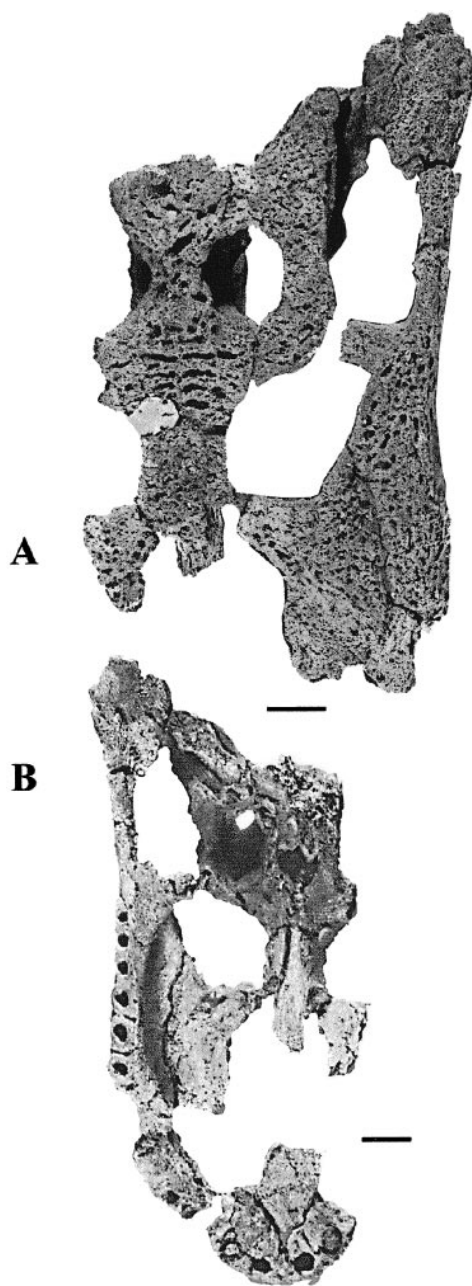


FIGURE 4. **A**, dorsal and **B**, ventral view with premaxillae and maxilla included of the skull related to *Allodaposuchus precedens* UPUAM A1 from Armuña (Segovia province, Spain, Campanian–Maastrichtian). Scale bar equals 2 cm.

Revised Diagnosis—Autapomorphic traits: posterior bottom of supratemporal fossa built by a wide quadrate shelf without contribution of squamosal or parietal. Frontal forming just the caudomedial edge of orbit and vertical suture with prefrontal on the medial orbital contour. The following characters correspond to those provided by the related material but unknown in the holotype: retroverted basioccipital plate (similar to the condition seen in *Eogavialis africanum*). Premaxillae twice as wide as long (distance from the anterior tip to the premaxillo-maxillary lateral suture). In ventral view, lachrymal contacting frontal, almost hiding prefrontal ventral face. Suborbital fenestra more than half the anteroposterior length of maxilla, reaching the fourth maxillary tooth. Derived traits for basal neosuch-

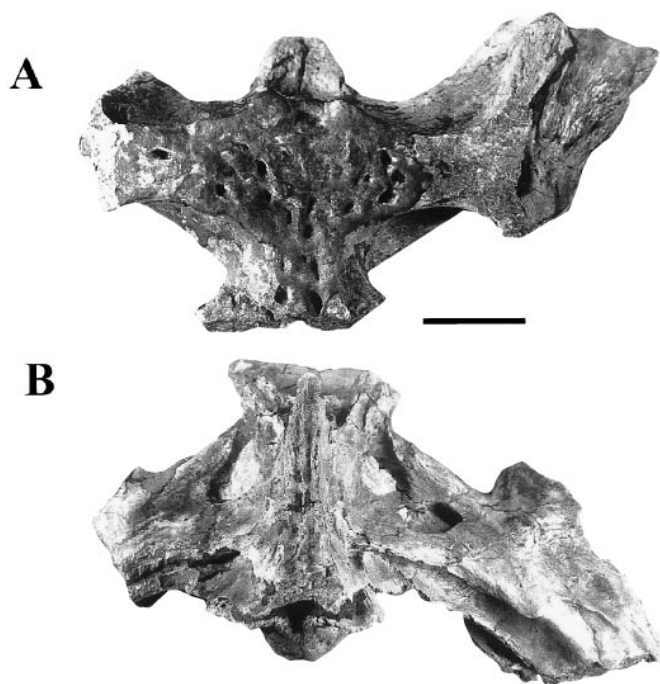


FIGURE 5. **A**, dorsal and **B**, ventral view of the fragment of skull related to *A. precedens* UPUAM V1 from Vilamitjana (Trepn Basin, Lleida province, Spain, Maastrichtian). Scale bar equals 2 cm.

chians and shared with *Goniopholis simus* and probably *Hylaeochampsia vectiana*: laterally opened cranioquadrate groove. Derived traits shared with *Hylaeochampsia*: prominent protuberance along paraoccipital process set ventrally on its occipital surface and medial to cranioquadrate passage; extensive flat occipital surface of quadrate, verticalized posterior wall of the supratemporal fossa becoming deep so that contour of fenestra and fossa match each other. A prominent tubercle on the ventral surface of the quadrate, derived and shared with *Hylaeochampsia*, *Shamosuchus* and *Brachychampsia*.

DESCRIPTION

Skull

General Description—The general description of the skull is based on all the specimens referred to above (Figs. 7, 8). The skull of *Allodaposuchus precedens* is moderately long, the rostrum being slightly longer than the postrostral length (measured from the anterior tip of the orbits to the posterior margin of the supraoccipital). The estimated cranial length of the biggest individual (UPUAM A1) is 320 mm. The surface of the bones is profusely ornamented. In lateral view the profile of the rostrum is straight to slightly convex. The maxillae are festooned in dorsal view at their anterior end and constricted in the middle. The maxillae have verticalized posterior lateral walls, and 12 teeth each. A deep vertical notch delimits the contour between the premaxillae and maxillae in lateral view. The premaxillae are wide and short. The external naris is undivided and almond-shaped. The orbit, which is one quarter the length of the rostrum, is wider than the supratemporal fenestra and faces dorsally.

The cranial table is subrectangular and its anteroposterior length is greater than the width owing to the posterior projections of the squamosals. The bones of the cranial table are ornamented with wide pits. The skull table is constricted at mid-length owing to the development of squamosal grooves for the

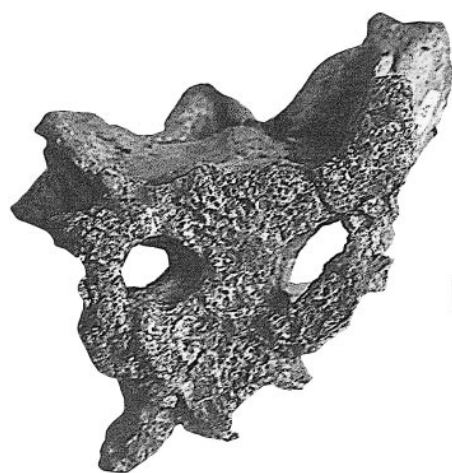


FIGURE 6. Dorsal view of the skull fragment related to *A. precedens* (MDE C3-276) from Bellevieu (Département de L'Aude, France, Late Campanian–Early Maastrichtian). Scale bar equals 1 cm.

external ear valve musculature. Each supratemporal fossa is located in the centre of its half of the table, being almost equidistant from the anterior, posterior and lateral borders of the table. The lateral edge of the postorbital is rounded. The frontal is moderately depressed transversely between the orbits and forms part of the supratemporal fossa. The dorsal surface of the parietal is narrow in the intratemporal area and is sagittally depressed posteriorly. The depth of this depression varies among the specimens; UPUAM A1 even has a sagittal groove in this area. The parietal does not contact the postorbital in the skull table, being separated there by the frontal. The supraoccipital has a short contribution on the dorsal surface of the skull table. The skull table occipital contour is strongly concave because of the squamosal posterior lobules. This curvature is overemphasised in the holotype owing to the reconstruction of this part.

In occipital view the paraoccipital process is medially placed with respect to the articular condyles of the quadrate. In dorsal view the articular branch of the quadrate is short to the rear of the paraoccipital process in the Valioara specimen. However, this length varies in UPUAM A1 and UPUAM V1, being around 15–20% longer than in the holotype. Ventrally the quadrates have strong ridges that deform its ventral surface. Laterally the cranioquadrate groove is opened in the otic area, thus avoiding outermost contact between the quadrate and squamosal behind the otic notch. The otic vestibule is elongated anteroposteriorly. The basioccipital, which has expanded tubera, projects caudally rather than ventrally, as in *Crocodylia*, or anteriorly, as in basal neosuchians.

Premaxilla—The premaxilla is deep in lateral view and seems to be extremely short and transversely wide (twice as wide as it is long from the premaxillomaxillary notch to the anterior premaxillary tip). Three alveoli are preserved. A fourth or even a fifth alveolus may have been present, but this part of the premaxilla has been restored (Figs. 7, 8). A notch is present behind the last premaxillary tooth. The anterior wall of the premaxillae beyond the external nares is vertical. In dorsal aspect the anterior outline is rounded. The external naris is dorsally placed and behind the anterior contour of the rostrum. A depressed perinarial area is not manifest. No incisive foramen is apparent on the specimen as preserved. Occlusal pits for the mandibular teeth are present between the interalveolar walls. A pit for the reception of a third and/or fourth mandibular tooth

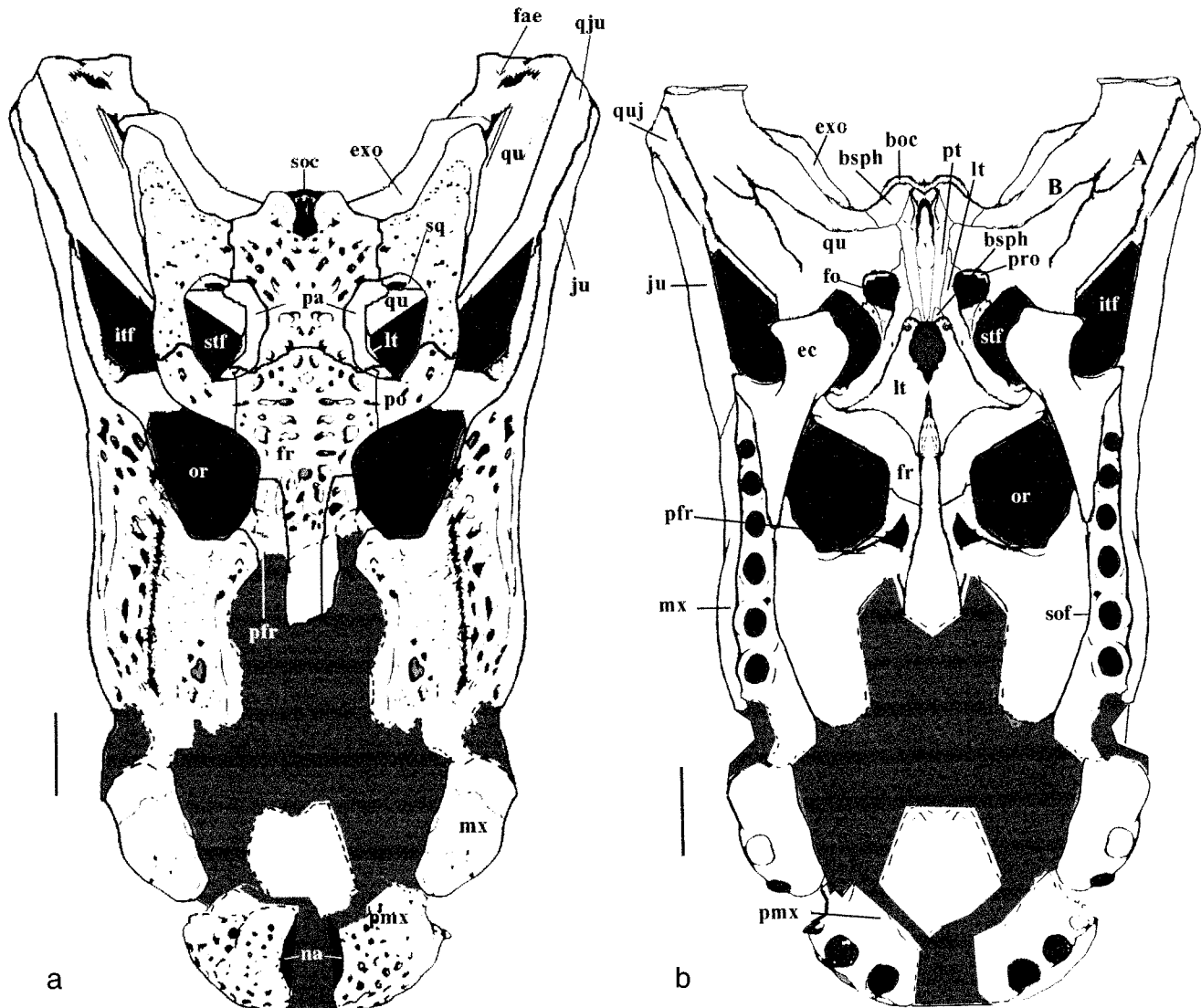


FIGURE 7. **Left (a)**, Schematic reconstruction of the skull of *Allodaposuchus precedens* in dorsal view, based on the anatomical details of the holotype (Ob3131) and other specimens referred to this species, especially UPUAM A1. **Abbreviations:** **exo**, exoccipital; **fae**, foramen aerum; **fr**, frontal; **itf**, infratemporal fenestra; **ju**, jugal; **lt**, laterosphenoid; **mx**, maxillae; **na**, external naris; **or**, orbit; **pa**, parietal; **pfr**, prefrontal; **po**, postorbital; **qu**, quadrate; **qju**, quadratojugal; **soc**, supraoccipital; **sq**, squamosal; **stf**, supratemporal fenestra. In the schema some areas (i.e., supratemporal fossa) have been forced in order to show the relationships among the bones. Damaged or missing parts shown in gray. The sculpture does correspond to UPUAM A1. Scale bar equals 3 cm.

FIGURE 8. **Right (b)**, Schematic reconstruction of the skull of *Allodaposuchus precedens* in ventral view, based on the anatomical details of the holotype (Ob3131) and other specimens referred to this species, especially UPUAM A1 for the rostral portion, and UPUAM V1 for the basicranium. **Abbreviations:** **boc**, basioccipital; **bsph**, basisphenoid; **ec**, ectopterygoid; **exo**, exoccipital; **fr**, frontal; **fo**, foramen ovale; **itf**, infratemporal fenestra; **ju**, jugal; **lt**, laterosphenoid; **mx**, maxilla; **or**, orbit; **pa**, parietal; **pfr**, prefrontal pillar; **pm**, premaxilla; **po**, postorbital; **pro**, prootic; **pt**, pterygoid; **qu**, quadrate; **qju**, quadratojugal; **sq**, squamosal; **sof**, suborbital fenestra; **stf**, supratemporal fenestra; **A** and **B**, muscle scars on the quadrate. Damaged or missing areas shown in gray. Scale bar equals 3 cm.

is located at the uppermost part of the premaxillo-maxillary notch.

Maxilla—The maxillae are longer than wide, and on the dorsal surface are ornamented with deep pits of 5 mm diameter. Dorsal to the toothrow, the surface of the bone is smooth, except for a line of foramina that runs anteroposteriorly. Posteriorly, the lateral walls of the maxillae are vertical. The maxilla slopes progressively in height (from 40 to 18 mm) to its anterior end, becoming flattened. Anteriorly, the maxilla contains alveoli for a small first tooth and a large second one, followed by collapsed third and fourth alveoli. The alveolar closure might

be attributable to pathology, although it cannot be ruled out that these two teeth should have been resorbed during ontogeny. However, only the left maxilla is preserved, and additional material would be needed to confirm the latter suggestion. Behind these collapsed alveoli, a part of the tooth row equivalent to two alveoli has been destroyed, and behind these in turn there are six additional alveoli. From the seventh to the final alveolus the anteroposterior diameter decreases gradually from 11 to 5 mm, and the labiolingual diameter from 7 to 5 mm. These alveoli are located at the lateral border of the maxilla, and thick interalveolar walls separate them. They have an ovate mesio-

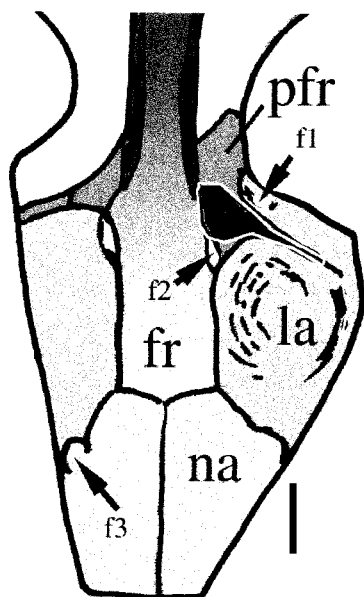


FIGURE 9. Schema of the ventral view of the skull fragment UPUAM A2 from Armuña (Segovia province, Spain, Campanian-Maastrichtian) showing the relationships among bones of the rostrum and orbital area. **Abbreviations:** fr, frontal; la, lacrymal; na, nasal; pfr, prefrontal. Note that lacrimal contacts frontal preventing the prefrontal anterior projection. In black, section of the prefrontal pillar. **F1**, lacrimal foramen at the orbital margin; **f2**, foramen located at the top of the prefrontal pillar; **f3**, anterior notch for the emergence of the lacrimal duct. Olfactory bulbs lodged on the lacrimals. Scale bar equals 2 cm.

distal contour. There are four occlusal interalveolar pits, indicating that the mandibular teeth interlocked, although the pits are not as well-aligned with the maxillary dentition as in *Crocodylus niloticus*. The suborbital fenestra is as long as in *Borealosuchus*. The suborbital fenestra is more than half the anteroposterior length of the maxilla ending at the fourth maxillary tooth.

Nasal—Only the posterior portion of the nasals have been preserved in ventral view in specimen UPUAM A2. The frontonasal suture is transverse, without any posterior parasagittal wedges of the nasals.

Lacrimal—The sutures outlining the lacrimal are obscured in UPUAM A1, and a ventral view is available in UPUAM A2. In the latter specimen, the lacrimal contacts along its entire medial edge with the frontal (Fig. 9). The lacrimal has a short suture with the nasal.

Prefrontal—The prefrontal is not complete in UPUAM A1, but broken medially. The prefrontal forms much of the orbital margin on the interorbital area, but it is short beyond the orbits. In UPUAM A2, it is complete, although only in ventral view. In ventral aspect, the prefrontal lacks a sharp anterior projection between lacrimal and frontal. The prefrontal pillar is medially columnar. The pillar is not anteriorly expanded, but forms a thin lamina laterally at the orbital margin underlying the lacrimal. This lamina forms the posterior wall of a deep concavity, in which the olfactory bulbs are lodged (Fig. 9). The transverse development of this lamina is similar to that of *Hylaeochampsia*.

Frontal—The fused frontal bears a long and narrow anterior process, as is found in *Borealosuchus formidabilis* and *B. wilsoni*, but unlike *Hylaeochampsia vectiana*. A shallow transverse preorbital ridge is located on the anterior third of the dorsal surface of the frontal. The frontal has only limited exposure on the orbital rim owing to the length of the prefrontal. The frontal

meets the parietal at the anterior border of the supratemporal fenestra, and this suture tapers caudally to the midline. The frontal cristae cranii are sharply ridged.

Postorbital—The large postorbital is about half the length of the squamosal. It forms the anterolateral corner of the skull table, and extends posteriorly to midway along the length of the supratemporal fenestra. The lateral face of the postorbital is long, contacting a slender projection of the quadratojugal ventromedially, so that the postorbital forms the dorsal margin of the infratemporal fenestra. The postorbital bar is massive, subovate in cross-section, and inset from the overhanging dorsal corner of the table. The postorbital bar is prolonged into two laminae: one facing anteriorly and the other lateroposteriorly. A spine is highly visible on the anterior edge of the dorsal part of the bar. A foramen within a depression is present on the lateral surface of the postorbital at the top of the postorbital bar. The postorbital meets the frontal medially and contacts a reduced part of the parietal and frontal at the anterior border on the supratemporal fossa.

Parietal—The posterolateral edge of the parietal is indented, and the dorsal surface is flat, except posteriorly, where the parietal is depressed at the midline. This depression continues toward the occipital plane, ending above the supraoccipital ridge. The suture between the parietal and supraoccipital is unclear on the dorsal surface of the cranial table, and the relationship between these two bones is better observed in occipital view. The parietal and squamosal together form a rim overhanging the supratemporal fenestra. The parietal expands laterally at the anterior part of the supratemporal fossa, whereas a sulcus is present on the anteromedial corner of the fossa. The foramen for the orbitotemporal artery is destroyed in the holotype and in UPUAM A1. In UPUAM V1, this foramen is slit-like (lateromedially long), and the parietal forms its postero-medial edge. Above the temporo-orbital foramen, the parietal and squamosal contact each other on the posterior wall, but the quadrate forms part of the anterior border of the foramen.

Supraoccipital—As occurs in *Hylaeochampsia* and other neosuchians such as *Goniopholis*, it is much wider than it is tall in occipital view, and it has a subtrapezoidal contour (Fig. 10). The post-temporal processes for the attachment of *M. spinialis capitis* are roughened. The holotype has a smooth median nuchal crest. This midcrest is thicker in the UPUAM A1 and UPUAM V1 specimens.

Squamosal—The squamosal has a flat dorsal surface, except posterolaterally, where it slopes ventrally. The end of this long portion of the squamosal forms a smooth posterior projection (the squamosals have been reconstructed on the holotype). The tip of the squamosal lobule is aligned with the paraoccipital process. In lateral view, the squamosal does not form a wide platform, as seen in *Crocodylus*, but forms a thin rim that expands slightly posteriorly to allow attachment of the ear flaps (Fig. 11). An anterior process of the squamosal passes under the postorbital ending above the postorbital bar. In lateral view, a ventrally projected spike of the squamosal divides the dorsal contact between the quadratojugal and quadrate (Fig. 11). The squamosal forms the roof of the otic recess, and its relationship with the exoccipital and quadrate is visible in lateral view. The contact between the squamosal and the quadrate occurs in the anterior part of the squamosal, since posteriorly (dorsal to the laterally opened cranioquadrate groove) the squamosal contacts the exoccipital. The suture between the squamosal and exoccipital, on the occipital face, runs almost anteroposteriorly owing to the long posterior projection of the squamosal lobules. The participation of the squamosal on the occiput is restricted by the marked expansion of the exoccipitals.

Quadrate—The posterior branch of the quadrate is short. The longitudinal axis of this branch is almost horizontally oriented. The medial articular condyle is dorsoventrally expanded,

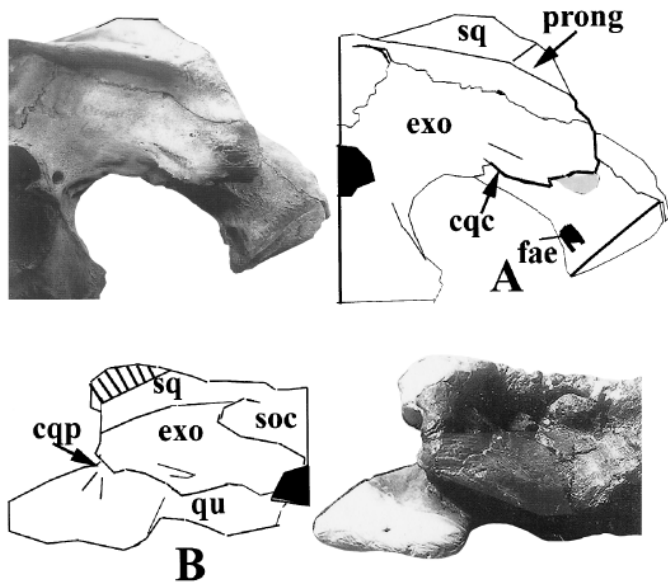


FIGURE 10. Occipital view of **A**, *Gavialis gangeticus*, and **B**, *Allodaposuchus precedens* (MAFI Ob3131). **Abbreviations:** **cqc**, cranioquadrate canal; **cqp**, cranioquadrate passage; **exo**, exoccipital; **fae**, foramen aerum; **qu**, quadrate; **sq**, squamosal; **soc**, supraoccipital. Note how the sharp ventral edge of the exoccipital medial to the paraoccipital process overhangs the quadrate in *Allodaposuchus*. Compare the thickness of the prong in *Gavialis* and *Allodaposuchus*.

being higher than the lateral one. The foramen aerum is located midway between the paraoccipital process and the mandibular articulation, but it does not form a notch. The quadrate lacks a dorsal projection contacting the base of the squamosal at the otic notch. As a result, there is a laterally open groove, as seen in some species of *Goniopholis* (Salisbury et al., 1999) and probably in *Hylaeochampsia vectiana*.

The dorsal surface of the quadrate at the otic recess displays a rim and associated sulcus that together extend cranio-caudally and parallel to the cranioquadrate groove. The outer half of the anterodorsal surface of the quadrate is wide and is deflected laterally. There is a small opening on the anterodorsal surface of the quadrate, anterior to the otic notch, that corresponds to the siphonial opening. In ventral view, the suture with the quadratojugal runs almost parallel to the sagittal plane, although it curves abruptly toward the postorbital bar at the infratemporal fenestra. The ventral surface of the quadrate is convex medially, and possesses marked crests associated with depressed areas (Fig. 8). One of these, corresponding to muscle scar "B" of Iordansky (1973), extends parallel to the suture with the exoccipital. A second crest, corresponding topographically to Iordansky's "A" crest, extends laterally. Both crests merge posteriorly to form a tubercle. The region between these crests is elevated with respect to the rest of the ventral surface of the quadrate. In all details, the ventral surface of the quadrate of *Allodaposuchus* is similar to that of *Hylaeochampsia* and *Shamosuchus*. The surface of the quadrate is broad and flat, facing occipitally.

Quadratojugal—The quadratojugal forms the posterior margin of the infratemporal fenestra where it becomes a thin lamina. There is no indication of a quadratojugal spine owing to preservation. Anterodorsally, the quadratojugal is narrow, and posteriorly curves laterally and expands ventrally. In ventral view, the quadrate overlaps the quadratojugal laterally. In ventral view, the jugo-quadratojugal suture is partially hidden, be-

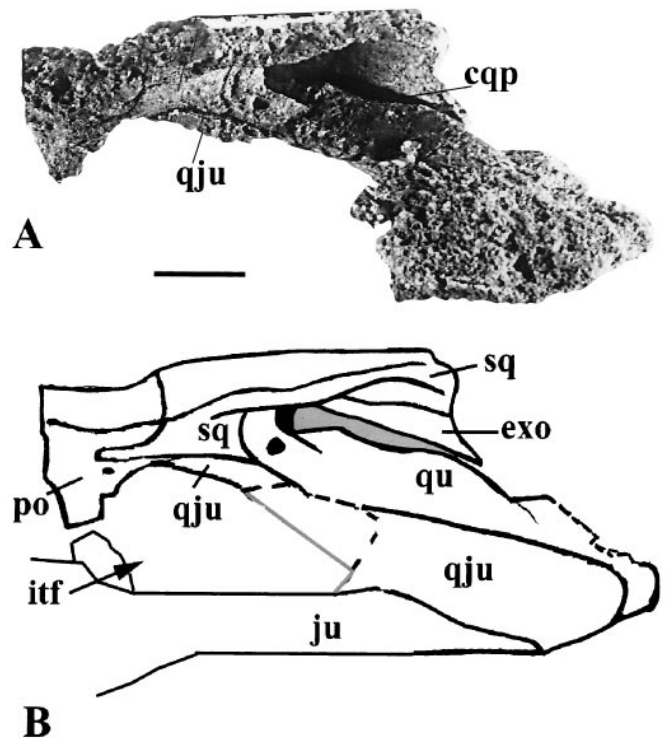


FIGURE 11. **A**, lateral view of UPUAM A1 from the Upper Cretaceous of Armuña (Spain) and **B**, schema showing the relationships among the bones around the infratemporal fenestra and otic region. Note the oblique displacement of the postorbital bar on the jugal. **Abbreviations the same as in Figure 7;** **cqp**, cranioquadrate passage. The squamosal (**sq**) divides the quadratojugal and quadrate at their dorsal connection. Scale bar equals 2 cm.

cause it is placed on the inner side of the verticalized ventral quadratojugal expansion.

Jugal—The anterior part of the jugal is dorsoventrally wider than the posterior one. The jugal forms most of the massive postorbital bar that originates from its dorsal edge posteriorly and becomes inset in its anterior part, as also occurs in *Hylaeochampsia* and *Gavialis gangeticus*. The jugal forms a thickened elevated rim at the orbital margin. A large foramen opens anteromedially on the jugal. The posterior portion of the jugal is a subcylindrical bar that provides the base of a long and wide infratemporal fenestra, ending in a narrow spine that contacts the quadratojugal lateroventrally. In UPUAM A1, the jugal surpasses posteriorly the paraoccipital process.

Exoccipital—The exoccipitals constitute most of the occiput. They meet above the foramen magnum to form a prominent rim. In MAFI Ob.3131, the ventral region of the exoccipitals is missing at the level of the mid-foramen magnum. Medial to the cranioquadrate sulcus the exoccipital forms an expanded ventral lamina that overhangs the medial face of the quadrate (Fig. 10). The prominent profile of the ventral edge of the exoccipital is similar to that of *Hylaeochampsia*, *Goniopholis*, and *Bernissartia*. On the ventral edge of the paraoccipital process there is a thick tubercle. In the best-preserved occiput (UPUAM V1), the participation of the exoccipital in the occipital condyle is very short.

Basioccipital—The ventro-occipital area of the braincase is preserved in UPUAM V1 and MDE (C3-276). The basioccipital forms most of the occipital condyle. Its ventral margin is directed caudoventrally, rather than ventrally (Fig. 12). The basioccipital plate is retroverted and turned upward, a condition

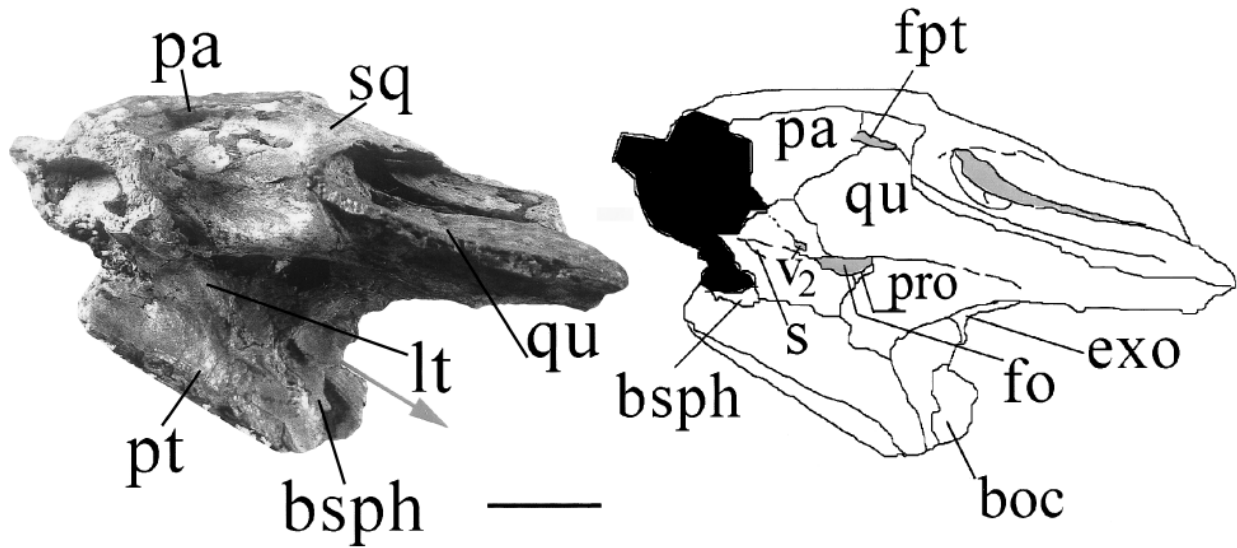


FIGURE 12. (Left) Lateroanterior view and (Right) Schema of the specimen UPUAM V1 from Villamitjana (Trempe Basin, Spain). **Abbreviations:** boc, basioccipital; bsph, basisphenoid; exo, exoccipital; fo, foramen ovale; fpt, posttemporal fenestra; lt, laterosphenoid; pa, parietal; pro, prootic; pt, pterygoid; qu, quadrate; s, sulcus for the emergence of the ophthalmic ramus of the trigeminal nerve; sq, squamosal; V1, maxillary branch of the trigeminal nerve. The grey arrow shows the caudoventral direction of the basioccipital plate. Scale bar equals 1 cm.

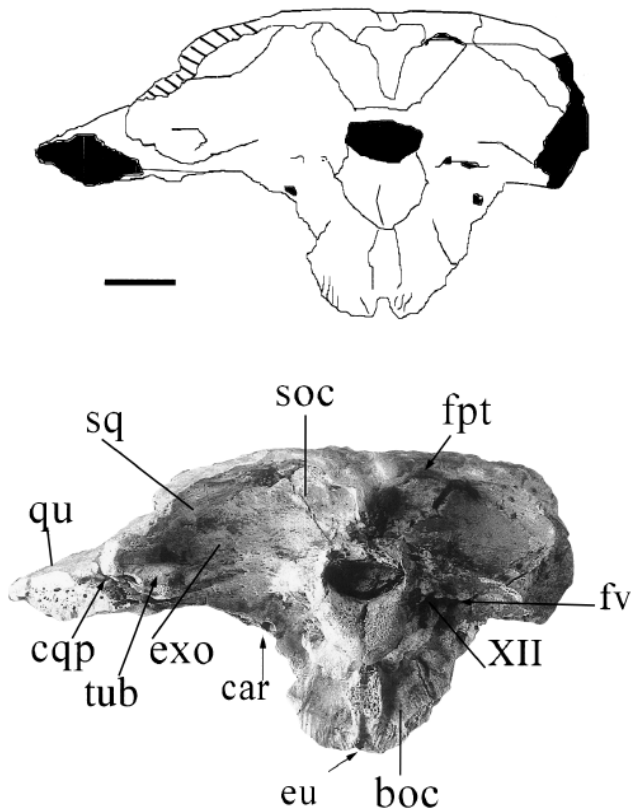


FIGURE 13. A, occipital view and B, schema of the specimen UPUAM V1 from Villamitjana (Trempe Basin, Spain). **Abbreviations:** boc, basioccipital; tub, tuberosity placed at the ventral margin of the paroccipital process; car, carotid foramen; cqp, cranioquadrate passage; eu, median eustachian opening; exo, exoccipital; fpt, posttemporal fenestra; fv, foramen vagii; sq, squamosal; soc, supraoccipital; XII, nerve XII. Dashed lines depicting eroded zones. Scale bar equals 1 cm.

comparable to that of long-snouted members of Crocodylia such as *Gavialis gangeticus*, and particularly in *Eogavialis africanum* (BMNH R.3325) (Hecht and Malone, 1972; Buffetaut, 1982). The basioccipital has a median crest and divergent basitubera. It is covered anteriorly and laterally by the basisphenoid. The carotid foramen is located midway between the exoccipital and basisphenoid, and this foramen is lateral to the openings for the IX, X and XI cranial nerves (Fig. 13).

Basisphenoid, Laterosphenoid and Prootic—The basisphenoid rostrum, the dorsum sellae, and the hypophyseal fossa are visible on the broken section at the front of the braincase in UPUAM V1 and UPUAM A2. The quadrate has a large ventral process that articulates with the lateral wall of the braincase. Thus, the quadrate-ptyergoid joint is not aligned with the basisphenoid-laterosphenoid suture. In MAFI Ob.3131 and in UPUAM A1 the laterosphenoid expands laterally. The capitate process of the laterosphenoid is long, comprising almost one third of the total laterosphenoid length. The anterodorsal margin of the laterosphenoid is strongly concave and the cotylar crest divides the laterosphenoidal surface into two parts. In Crocodylia, these parts correspond to anterior and posterodorsal faces (Iordansky, 1973). In *Allodaposuchus*, this crest is sharp and its ventral part is thickened. The disposition of the laterosphenoid in *Allodaposuchus* differs from the extant crocodyles in the orientation of the two areas divided by the cotylar crest: the anterior surface faces almost ventrally, whereas the posterior one faces nearly laterodorsally. The disposition of the laterosphenoid in *Allodaposuchus* and *Hylaeochampsia* determines their degree of inclination or verticalization of the neurocranium. The angle formed by the line running from the dorsal border of the postorbital bar to the base of the quadrate lateral condyle, all with respect to the skull roof is 20° in *Allodaposuchus*, against 30° in *Osteolamus*, *Crocodylus rhombifer*, and *Paleosuchus trigonatus*. The notches and foramina associated with the cranial nerves are well-preserved in UPUAM V1 (Fig. 12) the foramen for the olfactory nerve (c.n. I), the exit for the trochlear nerve (c.n. IV) situated on a depressed area, and the exits of the trigeminal nerve. The laterosphenoid also forms the anterior edge of the foramen ovale, but no trigeminal bridge for the ramus ophthalmicus (c.n. VI) is apparent. However, there is a pro-

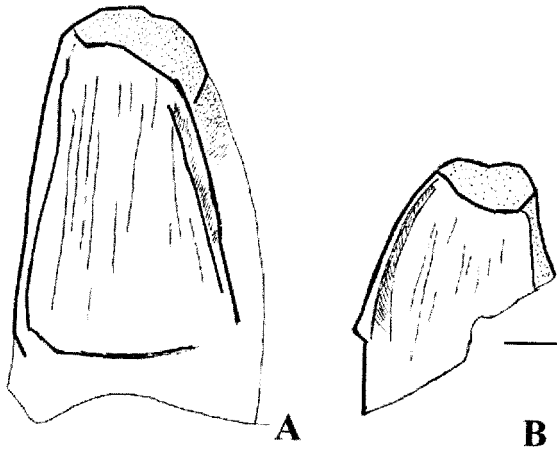


FIGURE 14. Tooth crowns located in situ in the skull UPUAM A1 from Armuña. **A**, third premaxillary tooth and **B**, the first maxillary tooth. Scale bar equals 2 cm.

nounced sulcus that runs cranially from the foramen ovale. The laterosphenoid also forms the lateral edge of the groove for the maxillary ramus (c.n. V_2) of the trigeminal nerve. At this level, the laterosphenoid expands to form a salient bridge. The posteroventral part of the laterosphenoid is long. In MAFI Ob.3131, the prootic exhibits its contact with the quadrate along a transverse suture. The tympanic capsule and the dorsal surface of the basioccipital are also exposed, but no sutures can be recognized. The prootic is slightly exposed on the lateral surface of the braincase.

Ectopterygoid and Pterygoid—UPUAM A1 preserves portions of ectopterygoids and pterygoids (the palatines are unknown). The ectopterygoid contacts the maxilla along the medial alveolar series and jugal posteriorly. A long anterior process of the ectopterygoid contacts the border of the two final alveoli and extends up to the fourth alveolus. The ventral process of the ectopterygoid does not extend to the posterior tip of the pterygoid flange. Dorsally, the ectopterygoid ascends on the inner posterior side of the postorbital bar. The ectopterygoid does not project a spine on the medial side of the jugal behind the postorbital bar. In what is preserved in UPUAM A1, the dorsal surface of the pterygoid is concave and the pterygoid flange is long and thick. Part of the nasopharyngeal canal corresponding to the choanal region is also preserved in UPUAM A1. In this region, the posterior part of the pterygoid is tall and bears two prominent projections behind the choana. The choana is not completely preserved in any specimen, but information provided by the material from Armuña and Bellevue indicates that this opening is very posteriorly placed, projects ventrally and is surrounded by the pterygoids. In addition, it is likely that the choana is longer than it is wide.

Dentition—Two premaxillary teeth and a single maxillary tooth are preserved in situ on UPUAM A1 (Fig. 14). These teeth have a similar conical crown morphology. The carinae are strong and the surface of the enamel is delicately wrinkled.

Postcranium

All the postcranial elements from the MAFI collection labelled as *Crocodylus affuvelensis* have the peculiar traits of crocodylians. The vertebrae MAFI Ob 5724 (length about 26 mm) are strongly procoelous. The cervical centra have fused neurocentral sutures, indicating maturity. On the other hand, the MAFI Ob 3134 series, also procoelous, are larger than MAFI Ob 5724 (length about 36 mm). The difference in size of the

two vertebral series denotes the presence of two distinct individuals. Additionally, there are two thoracicolumbar vertebrae (MAFI Ob 3133 and MAFI Ob 5727). In MAFI Ob 3133 the transverse processes arise from the ventral region of the prezygapophyses, and dorsally both structures are linked by a continuous concave surface. This feature was discussed for other isolated vertebrae from the Upper Cretaceous of Spain (Buscalioni et al., 1986).

There are four femora in the collection (MAFI Ob 3139 and MAFI Ob3140). MAFIOb 3140 includes a complete left femur (of which the proximal area has been reconstructed), and a proximal fragment of a right femur. The shaft of the complete femur is long (185 mm) but narrow (18 mm). The lateral distal condyle is developed, as in *Borealosuchus* (Erickson, 1976). The femora have three sharp ridges, the largest corresponding to *M. adductor femoralis*. MAFI Ob 3139 includes two distal fragments, both of which have thicker shafts than the other specimens. MAFI Ob 3136 is an iliac blade (94 mm long). It has a short anterior tubercle, situated towards the rear of the acetabular margin. The posterior iliac process ends in a stout tubercle. The dorsal margin of the iliac blade is straight in lateral aspect.

THE PHYLOGENETIC POSITION OF *ALLODAPOSUCHUS*

Discussion

Our discussion of the phylogenetic position of *Allodaposuchus* is mainly based on Brochu's (1997a, b, 1999) analyses of Eusuchia and its crown group Crocodylia. Following Brochu's approach, 164 characters were scored for *Allodaposuchus precedens*, adding this species to his data matrix composed of 61 taxa (Brochu, 1997a). Additionally, we have incorporated an extra taxon into the data matrix (the Las Hoyas Neosuchia from the Barremian of Las Hoyas, Cuenca, Spain). We have also included two new characters in the data matrix, and finally, we have improved the information on *Bernissartia* by including data from the Spanish specimen from the Lower Cretaceous of Galve (Teruel, Spain; Buscalioni and Sanz, 1990; see Appendix 1 for character definition and Appendix 2 for data matrix). The phylogenetic analysis was carried out using PAUP version 3.1 (Swofford, 1992), and was based on 166 characters (all considered as non-additive). *Bernissartia* was designated as the outgroup. The analysis retained 2,160 trees of 499 steps (with a consistency index of 0.41, and a retention index of 0.81) with an heuristic approach by simple stepwise addition, and branch-swapping tree bisection and reconnection routine.

The topology of all the trees maintains the major crocodylian groups (Fig. 15), reinforcing the previously proposed stem-based groups for Crocodylia: Gavialoidea, Crocodyloidea and Alligatoroidea (Norell et al., 1994; Brochu, 1999). In this analysis Gavialoidea is the sister taxon of all remaining Crocodylia. *Thoracosaurus* is placed within Gavialoidea, whereas the genus *Tomistoma* is placed within Crocodyloidea. The consensus tree in Figure 15 reflects the lability of the relationships between the members of Alligatoridae, basal Crocodyloidea, and within minor clades of Crocodylidae.

Crocodylia (Node 3) is unambiguously diagnosed by the construction of the skull table with nearly horizontal sides and significant squamosal prongs (character 140). Squamosal "prongs" in *Allodaposuchus* are as short and narrow (almost constituting a lamina) as in *Hylaeochampsia*, making up less than half of the lateral margin of the occipital edge of the skull, whereas the crocodylian prongs are broad and make up most of the lateral margin of the occiput (Fig. 10). The occiput of all the members of Crocodylia have exoccipitals with a small or no boss on the paraoccipital process, and long processes lateral to the cranioquadrate opening (character 141). The absence of a fossa at the anteromedial corner of the supratermporal

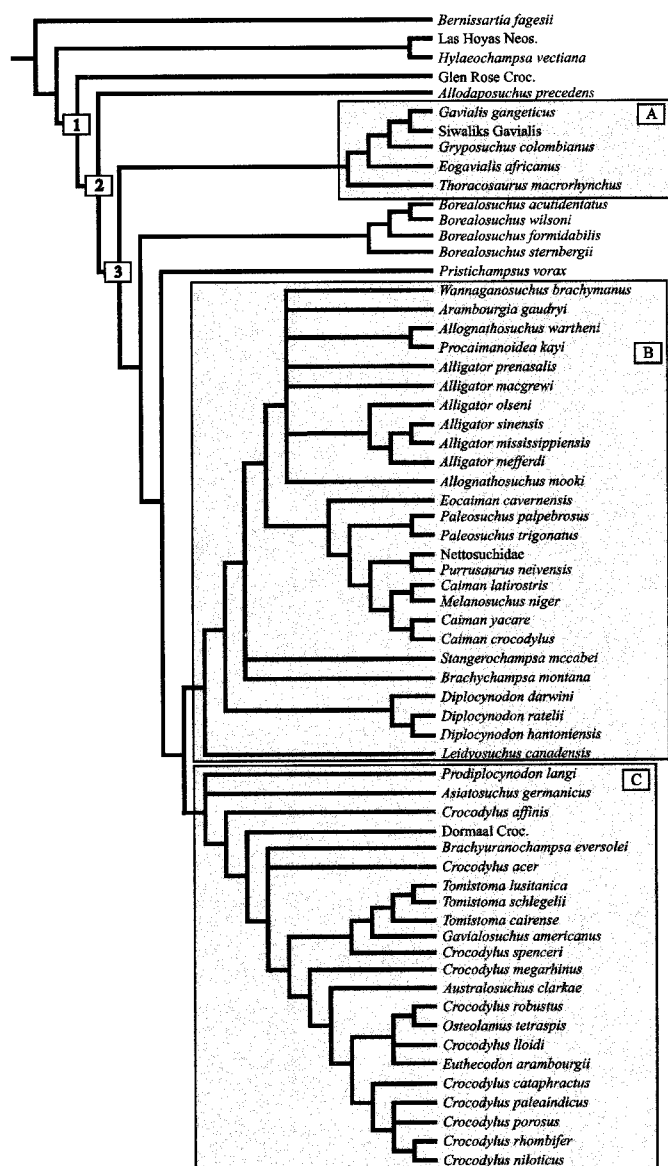


FIGURE 15. Phylogenetic position of *Allodaposuchus precedens*. The cladogram shows the strict consensus tree of 2160 trees (499 steps with a consistency index of 0.41, and a retention index of 0.81) in which the unsolved nodes are mainly within Alligatoridae (B). **Abbreviations:** A, Gavialoidea; B, Alligatoroidea, and C, Crocodyloidea. Nodes 1, 2 and 3 (Crocodylia) are diagnosed as follows; ACCTRANS or DELTRANS optimized characters with asterisk:

- Node 1:** 18 (1); 35 (1); 52 (1)
- #18: Presacral centra amphicoelous (0); procoelous (1). #35: Dorsal osteoderms not kelled (0); kelled (1). #52: Alveoli for dentary teeth 3 and 4 nearly the same size and confluent (0); fourth alveolous larger than third and alveoli separated (1)
- Node 2:** 71* ACCTRAN (1); 78 (2); 149 (1); 79* DELTRAN (1); 151* DELTRAN (1)
- #71: Anterior border of the internal choana is comprised of the palatines (0) or choana entirely surrounded by pterygoids (1). Character shared with *Hylaeochampsia* and Las Hoyas crocodile. #78: All dentary teeth occlude lingual to maxillary teeth (0); occlusion pit between 7th and 8th maxillary teeth and all other dentary teeth occlude lingually (1); dentary teeth occlude in line with maxillary tooththrow (2). #79: Naris projected anterodorsally (0); dorsally (1); #149: Ectopterygoid extends (0) does not extend (1) to posterior tip of lateral pterygoid flange at maturity. #151: Otoccipitals terminate dorsal to basioccipital tubera (0); send robust process ventrally and participate in basioccipital tubera (1); or send slender process ventrally to basioccipital tubera (2).
- Node 3:** 50* (1); 53* (1); 62* (1); 92 (1); 140 (1); 141 (1); 165 (1);

fenestra is another diagnostic trait of Crocodylia (character 92). A set of characters based on the mandible (the posterodorsal projection of the retroarticular, anterodorsal projection of the anterior dentary teeth, and the presence of an external mandibular fenestra; characters 50, 53 and 62, respectively) also diagnoses Crocodylia, but these are unknown in *Hylaeochampsia* and *Allodaposuchus*. All the above characters have been previously listed as synapomorphies for Crocodylia in Brochu's (1999) results.

The characters added to Brochu's matrix (number 165 and 166) are also involved in the diagnosis of Crocodylia. One of these characters (number 166) concerns the shape of exoccipitals. Crocodylia has a straight or sharpened exoccipital ventral edge (the latter being the case in *Gavialis gangeticus*) (Fig. 10). The large ventrolateral expansion of the exoccipitals overhanging the quadrate in *Hylaeochampsia*, *Allodaposuchus*, and *Bernissartia* is considered to be reminiscent of Neosuchia (Buscalioni and Sanz, 1990; Clark and Norell, 1992). The second character incorporated (number 165) deals with the morphology of the prefrontal pillar. Members of Crocodylia modify the shape of the prefrontal pillars from a transversely expanded lamina at their dorsal half (primitive condition) to a fully columnar pillar. In the description of *Hylaeochampsia vectiana* one of the features mentioned was the presence of the unusually extensive prefrontal pillars, which Clark and Norell (1992) related to the presence of posterior tribodont (bulky and voluminous) teeth. The presence of a transverse wall in front of the orbits is common in ziphosuchian crocodyliforms such as *Notosuchus* and *Baurusuchus*. *Araripesuchus* (Ortega et al., 2000) and other neosuchians such as *Bernissartia*, the Las Hoyas Neosuchia, *Hylaeochampsia* and *Allodaposuchus*, share a transversely expanded pillar at its dorsal half but are ventrally columnar. It can be concluded that the transverse expansions of the pillars are not associated with tribodont teeth, since these taxa have a wide variety of tooth shapes.

In all the resulting trees *Allodaposuchus* is placed as the closest relative of the crown-group Crocodylia (Node 2). *Allodaposuchus precedens*, which has an interdigitating dentary occlusion, shares the absence of a lingual to maxillary occlusion of dentary teeth (character number 78) with the remainder of Crocodylia. As in Crocodylia, the ectopterygoid does not reach the posterior tip of lateral pterygoid flange (character number 149). However, the trait is unknown in *Hylaeochampsia*. The maxillary-dentary tooth occlusion and the ectopterygoid extension were formerly assessed as synapomorphic traits of Crocodylia (Brochu, 1999). Together with Gavialoidea members, *Allodaposuchus* has long otoccipitals from which extend ventrally a robust process that participates in the basioccipital tubera (number 151), and the extension of the premaxillary dorsal surface rostral to the external nares (number 79). The reversal of both traits diagnoses the clade Borealosuchus + Pristichampsus + Brevirostres (Fig. 1) (otoccipitals terminating dorsal to basioccipital tubera, and external nares anterodorsally projected).

One of the consequences resulting from the analysis with the inclusion of the Las Hoyas crocodile, *Bernissartia* and the Glen Rose Form is that it introduces multiple derivations into the characters traditionally diagnosing Eusuchia, making its definition ambiguous. The name Eusuchia included those crocodyliforms whose choana lies within the pterygoids and procoelous vertebrae (Clark and Norell, 1992). Due to the presence of the first character in *Hylaeochampsia* (and a combination of traits confined to advanced neosuchians), Eusuchia was defined

←
166 (1).
Characters 50, 53, and 62 ACCTRAN optimization, and unknown in *Allodaposuchus*.

as the last common ancestor of *Hylaeochamps* and *Crocodylia* and all of its descendents (Clark and Norell, 1992; Brochu, 1999). However, in our analysis the Glen Rose Form is placed within the ingroup as the sister taxon of *Allodaposuchus* plus *Crocodylia*, whereas *Hylaeochamps* (forming a clade with the Las Hoyas Neosuchia) is removed as its closest sister group. The clade formed by *Hylaeochamps* and Las Hoyas Neosuchia is based on the pterygoidean position of the choana (character 71), and on the telescoped shape of the orbital margin (character number 103) convergent with some Gavialoidea.

This solution, in which the Glen Rose Form is placed as the sister taxon of *Allodaposuchus* plus *Crocodylia* (see Fig. 15, Node 1), is supported by apomorphies shared by *Crocodylia*, which are symplesiomorphies in *Bernissartia* and the Las Hoyas Neosuchia, but scored as missing in *Hylaeochamps* and *Allodaposuchus*. The Glen Rose Form has procelous vertebrae (character number 18). The mandibular fourth alveolous is larger than the third and both alveoli are separated (trait number 52): shared by the Glen Rose Form, Gavialoidea and other major members of *Crocodylia* (*Crocodyloidea*, *Pristichampsus*). Unlike the plesiomorphic condition characterized by the confluence of the third and fourth alveoli, the Glen Rose Form lacks keels on the osteoderms (trait number 35). The presence of double-keeled rows of osteoderms is a symplesiomorphy of *Bernissartia* and the Las Hoyas Form (Ortega and Buscalioni, 1995). Since many of these traits concern postcranial evidence, the position of the Glen Rose Form could result from nonpreservation of these features in *Hylaeochamps*.

Therefore, the relationships among the above characters are more congruent for the node defined by (Glen Rose Form + *Allodaposuchus* + *Crocodylia*) than for any other subgroup based on the pterygoidean position of the choana. The position of the choana is a conflicting character among the more advanced neosuchians, and although in *Allodaposuchus precedens*, *Hylaeochamps vectiana* and the Las Hoyas Neosuchia the choana is surrounded by the pterygoids (character number 71), the trait may be independently derived. Other neosuchians as *Brillianceausuchus* (Michard et al., 1990; Brochu, 1999) strengthen the homoplastic nature of this trait, indicating that the evolution of the position of the choana is not as simple as has been supposed. The placement of the Eusuchia node is unstable because it depends on the distribution of conflicting or missing characters throughout the taxa that conform the stem-group of *Crocodylia* (i.e., the pterygoidean position of the choana, the procelous vertebral morphology, the confluence of third and fourth dentary alveoli, and the dorsal armor).

The Outstanding Nature of *Allodaposuchus* in the Phylogeny of Eusuchia

Restricting the name *Crocodylia* to the crown-group including the last common ancestor of Gavialoidea and *Brevirostres* (see Fig. 1) and all of its descendents, *Allodaposuchus* should be designated as the closest sister group of *Crocodylia*. The phylogenetic position of *A. precedens* is chronostratigraphically congruent, since it fills the gap between a set of the Early Cretaceous advanced neosuchians (i.e., the Barremian *Hylaeochamps* and the Las Hoyas Form, and the Albian–Aptian Glen Rose Form), and the Late Cretaceous *Crocodylia Thoracosaurus cherifiensis* from Morocco (Steel, 1973). This conclusion has implications for the hypotheses concerning the Laurasian origin of *Crocodylia* (Jackson et al., 1996). The confidence placed in this hypothesis of the endemic Laurasian distribution of the stem members of *Crocodylia* still depends on the phylogenetic position of the longirostrine Eusuchia *Dolichochoamps* from Argentina (Gasparini and Buffetaut, 1980), and the controversial African taxon *Stomatosuchus inermis*, which is known only from Stromer's (1925) description.

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APPENDIX 1

Character list used in the phylogenetic analysis corresponds to the 164 characters published by Brochu (1997a), and two (165 and 166) additional ones whose definition is below provided.

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165. Prefrontal pillars transversely expanded at their dorsal half and columnar ventrally (0); narrow or longitudinally expanded at their dorsal part and columnar ventrally (1). (Modified from Ortega et al., 2000, character 30). This trait considers the primitive state as an independent prefrontal pillar morphology from that of narrow and cylindrical, or anteroposteriorly expanded. The trait #137 (dorsal half of the prefrontal pillar narrow, 0; or expanded anteroposteriorly, 1) from Brochu (1997a) distinguishes between the two derived states of the prefrontal pillar morphology. As shown the data matrix below, we have not scored the trait #137 when the prefrontal pillar is transverse.
166. Ventral border of the exoccipital: convex and ventrally projected hiding the posterior opening of the cranioquadrate passage from the occipital view (0); straight, sharpen or smoothly convex and does not hide the posterior opening of the cranioquadrate passage from occipital view (1). (Modified from Buscalioni and Sanz, 1990; Ortega et al., 2000, character 160).
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APPENDIX 2

Data matrix used in the analysis relies in the 164 characters scored by Brochu (1997a) for 58 fossil and extant Crocodylia together with *Hylaeochampsa* and two derived neosuchians (*Bernissartia*, Glen Rose Form). Below is annotated the character scores for new taxa and the modifications done over the data matrix provided by Brochu (1997a). Character score for *Bernissartia* has been improved introducing information from the specimen CR82 (Lower Cretaceous–Barremian–of Galve, province of Teruel) housed at the Museo Municipal de Galve (province of Teruel, Spain). Las Hoyas Neosuchia (LH13370) is from the Lower Cretaceous (Barremian) of Las Hoyas (province of Cuenca, Spain) provisionally housed at the Unidad de Paleontología, Universidad Autónoma de Madrid (Spain). Characters 102 and 135 for *Hylaeochampsa vectiana* are modified from Brochu's data matrix. The character coding of *Allodaposuchus precedens* is based on the holotype (MAFI Ob 3131 from the Maastrichtian of Valiora, Romania) and on related material from the Campanian–Maastrichtian of Spain and France. A list of the crown-group taxa with the scores for characters 165 and 166 is also provided. ? = missing data; N = not applicable.

<i>Bernissartia</i>	??11?1210?	010????00?	?0?0?0000?	?000100010	0000??N?00
	100??00?1	10?NN0?000	0??010000	00?0110030	1??01?00?0
	0000100?00	?000?000?0	0??0?0???	0??00?N?00	0000000?00
	001???????	00?000			
Las Hoyas	?0?11??00	0??01100?1	0?0??1????	?0?0101011	000??N?00
	?0?NN?0?0	1?0?0?000?	0000110030	?0??1?00?0	0?21000???
	100??0?0?1	??02??????	??0??N?10	0000000?00	?02???????
<i>Hylaeochampsa</i>	??????????	??????????	??????????	??????????	??????????
	??????????	100??1?0?0	00?01100?0	0110??0?0	0?20010000
	??0??000?1	000000N000	0?000000?0	00????????	??0?00
<i>Allodaposuchus</i>	??????????	??????????	??????????	??????????	??????????
	??????????	10?0010210	0000?01???	00?????0?0	0N000?0?0?
	100??00011	00000?N?00	0000?00?10	10????????	?0?0?0
<i>Borealosuchus formidabilis</i>	11		<i>Borealosuchus sternbergii</i>		?1
<i>Borealosuchus acutidentatus</i>	??		<i>Borealosuchus wilsoni</i>		??
<i>Leidyosuchus canadensis</i>	??		<i>Thoracosaurus macrorhynchus</i>		??
<i>Eogavialis africanum</i>	?1		<i>Gryposuchus colombianus</i>		??
Siwaliks gavial	?1		<i>Gavialis gangeticus</i>		11
<i>Pristichampsus vorax</i>	?1		<i>Diplocynodon darwini</i>		11
<i>Diplocynodon ratelii</i>	11		<i>Diplocynodon hantoniensis</i>		11
<i>Alligator mississippiensis</i>	11		<i>Alligator sinensis</i>		11
<i>Alligator mefferdi</i>	11		<i>Alligator olseni</i>		??
<i>Alligator mcgrewi</i>	?1		<i>Alligator prenasalis</i>		11
<i>Allognathosuchus mooki</i>	?1		<i>Allognathosuchus wartheni</i>		?1
<i>Wannaganosuchus brachymanus</i>	?1		<i>Procaimanoidea kayi</i>		??
<i>Arambourgia gaudryi</i>	?1		<i>Stangerochampsa mccabei</i>		?1
<i>Brachychampsa montana</i>	?1		<i>Eocaiman cavernensis</i>		??
<i>Purrosaurus neivensis</i>	??		Nettosuchidae		??
<i>Caiman yacare</i>	11		<i>Caiman crocodilus</i>		11
<i>Caiman latirostris</i>	11		<i>Melanosuchus niger</i>		11
<i>Paleosuchus trigonatus</i>	11		<i>Paleosuchus palpebrosus</i>		11
<i>Crocodylus cataphractus</i>	11		<i>Crocodylus rhombifer</i>		11
<i>Crocodylus porosus</i>	11		<i>Crocodylus niloticus</i>		11
<i>Crocodylus palaeindicus</i>	??		<i>Crocodylus robustus</i>		11
<i>Crocodylus lloidi</i>	?1		<i>Crocodylus megarhinus</i>		??
<i>Crocodylus spenceri</i>	??		<i>Crocodylus acer</i>		?1
<i>Crocodylus affinis</i>	?1		<i>Osteolaemus tetraspis</i>		11
<i>Australosuchus clarkae</i>	??		<i>Euthecodon arambourgii</i>		??
<i>Tomistoma schlegelii</i>	11		<i>Tomistoma lusitanica</i>		?1
<i>Tomistoma cairensis</i>	??		<i>Gavialosuchus americanus</i>		11
<i>Brachyuranochampsa eversolei</i>	?1		Dormaal crocodile		??
<i>Asiatosuchus germanicus</i>	11		<i>Prodiplacynodon langi</i>		11