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ARTICLE

A COMPLETE SKULL OF *ALLODAPOSUCHUS PRECEDENS* NOPCSA, 1928 (EUSUCHIA) AND A REASSESSMENT OF THE MORPHOLOGY OF THE TAXON BASED ON THE ROMANIAN REMAINS

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ABSTRACT—A new eusuchian skull from the Maastrichtian locality of Oarda de Jos in the southwestern Transylvanian Basin of Romania represents the best-preserved known specimen of *Allodaposuchus precedens* Nopcsa, 1928. This new fossil allows us to clearly characterize the skull morphology of *A. precedens* and to reject the idea, as recently suggested, that the taxon could be considered a nomen dubium. Parsimony analysis confirms earlier phylogenetic hypotheses based on the fragmentary holotype from the Maastrichtian of Valioara in Haţeg Basin (Romania), as well as on putative conspecific remains from approximately coeval localities in Spain and France: *A. precedens* is a non-crocodylian eusuchian. However, some relevant morphological traits differ from what was previously reported for this taxon: the external naris is large and anterodorsally directed; the lateral profile of the skull is not festooned in dorsal view; the suborbital fenestrae reach the eighth alveolus; the postorbital bar is not massive and inset from the jugal margin; the skull table is approximately planar or medially concave and does not markedly overhang the supratemporal fenestrae; the exoccipitals are not significantly involved in the basioccipital tubera. Because the condition of most of these characters was unknown in the holotype, the morphology of the taxon was previously evaluated on non-Romanian remains only. The morphological discrepancies between Romanian and western European fossils could suggest the presence of different taxa, possibly of infra-generic rank. *Allodaposuchus* and presumably *Hylaeochampsa* are the only eusuchians showing a laterally open cranioquadrate passage.

INTRODUCTION

The history of the definition of the eusuchian taxon *Allodaposuchus precedens* Nopcsa, 1928, has been recently examined in detail by Buscalioni et al. (2001). *Allodaposuchus precedens* was originally described on the basis of isolated fragmentary cranial and postcranial bones from Vălioara, a Maastrichtian locality in the Haţeg Basin of Transylvania (Romania; Nopcsa, 1915–1916, 1928). Additional, approximately coeval remains from Spain (Armuña, Villamitjana and Laño) and France (Bellevue and Cruzy) have been referred to the same taxon in the last few years (Buscalioni et al., 2001; Martin and Buffetaut, 2005). *Allodaposuchus precedens*, formerly referred to Leidyosuchidae by Nopcsa (1928) or more generally to crocodylians (Kalin, 1955), has been considered a crocodylid by most authors (among others, Kuhn, 1936; Steel, 1973; Buffetaut, 1980; Astibia et al., 1990; Vasse, 1993; Jianu and Boekschoten, 1999), but the reassessment of its phylogenetic relationships with a cladistic approach performed by Buscalioni et al. (2001), although confirming its membership to Eusuchia, placed *Allodaposuchus* outside the crown group Crocodylia. Their analysis suggested that *Allodaposuchus* was the sister taxon of Crocodylia, "filling the gap between the Early Cretaceous (Barremian) *Hylaeochampsa* and the earliest common ancestors of Crocodylia" (Buscalioni et al., 2001:74).

Such a position has been widely accepted in general papers concerning crocodylian phylogenies and validated by other analyses based on the same character coding and matrix of *Allodaposuchus* proposed by the abovementioned authors (Brochu, 2001a, 2003, 2004; Buscalioni et al., 2003, 2004; Hua and Jouve, 2004; Delfino et al., 2005). An exception is represented by Brochu (2001b:fig. 3) that placed this taxon, without indicating any precise relationships, among the basal alligatoroids in a figure summarizing the stratigraphic distribution of this clade.

However, as already noted by Martin and Buffetaut (2005), due to the fragmentary nature of the type material and of most of the remains referred to *A. precedens*, it is not unlikely that specimens presently referred to this species actually represent different, although superficially similar taxa. The latter authors recently advanced their criticism stating that "this genus seems to have been erected on poorly diagnostic characters and the question may be asked whether *Allodaposuchus precedens* should be considered as a nomen dubium" (Martin and Buffetaut, 2005: 35). On the same dubitative line, Salisbury et al. (2006) refrained from using *Allodaposuchus* in their main phylogenetic analysis, not being convinced of its taxonomic validity as defined by Buscalioni et al. (2001), but tentatively placed it in a phylogenetic model as a non-crocodylian eusuchian, the sister taxon of *Hylaeochampsa* (Salisbury et al., 2006:fig. 5a).

The new skull described herein comes from Oarda de Jos, a Maastrichtian locality in the Transylvanian Basin of Romania, only few kilometers from the type locality of *A. precedens*, and

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thus represents a chance to widen the knowledge of its cranial osteology and to test the validity of the morphological traits associated with this taxon on the basis of the western European remains.

Institutional Abbreviations—**MAFI**, Magyar Állami Földtani Intézet, the Hungarian Geological Institute, Budapest, Hungary; **BMNH**, Natural History Museum, London, United Kingdom; **PSMUBB**, Paleontology-Stratigraphy Museum, University Babeş-Bolyai, Cluj-Napoca, Romania; **UPUAM**, Unidad de Paleontología de la Universidad Autónoma de Madrid, Spain.

GEOLOGICAL AND PALEOENVIRONMENTAL SETTINGS OF OARDA DE JOS

The skull of *Alloposuchus precedens* described here was discovered in 1999 at Oarda de Jos along the Sebeş River in the area outlined by the localities Alba Iulia, Sebeş, Vinţu de Jos (Alba District) called the "Metaliferi area" (Codrea and Dica, 2005). This area of the southwest Transylvanian Basin is just northeast of the Haţeg Basin (Fig. 1). Both areas expose continental formations belonging to post-Laramian cover that begun during the Late Cretaceous. Oarda de Jos belongs to the base of the Şard Formation, a continental pile of deposits exceeding 1000 m of thickness and extended from the Early Maastrichtian until the Late Eocene (Codrea and Dica, 2005). As a whole, this succession belongs to a braided fluvial system, with numerous internal bars, where the sediments were temporarily stocked. Sand and gravel represent the channel-fills. Peculiar red beds (red silt with pedogenic levels documented by root-marks) represent overbank accumulations. Towards its base, the fluvial system produced pond (up to small lake) deposits with gray-blackish silt clays and calcretes documenting this kind of environment. It is in one of these pond deposits that the *Allodaposuchus* skull was discovered.

Fossils are rare at Oarda de Jos but many vertebrate remains have been found in the lateral equivalent Şard Formation deposits at Vurpăr, on the other side of the Mures River, 2 km south from Oarda de Jos. At Vurpăr, the base of the Şard Formation is exposed on 70 m ("Red Continental Strata" in Therrien et al., 2002; Therrien, 2005) and has yielded remains of the euornithopods *Zalmoxes robustus* and *Z. shquiperorum*, the hadrosaurid *Telmatosaurus transsylvanicus*, the nodosaurid ankylosaur *Struthiosaurus transylvanicus*, the titanosaurid sauropod *Magyarosaurus dacus*, and the selmacryptodire turtle *Kallokibotion bajazidi*. These vertebrate taxa are all known from the Sânpetru Formation (central Haţeg Basin), and the Densuş Ciula Formation (northwest Haţeg Basin) where the holotype of *Allodaposuchus precedens* also comes from. Therefore, we consider the age of the skull of *A. precedens* from Oarda de Jos as equivalent to the *A. precedens* holotype from the Densuş Ciula Formation of Vălioara. For a long time these formations have been considered as late Maastrichtian in age but recent paleomagnetic and palynological studies suggest that they should belong to the early-late Maastrichtian boundary interval within the 31-r magnetochron (Panaiotu and Panaiotu, 2002; Van Itterbeeck et al., 2005).

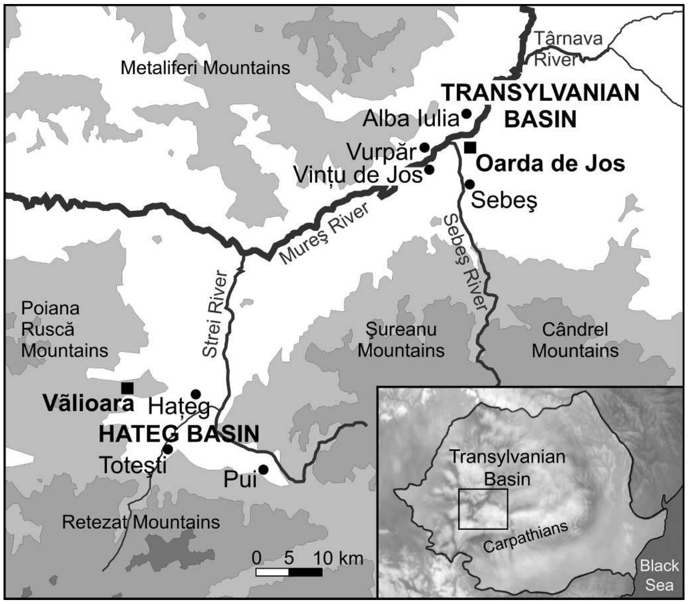


FIGURE 1. Geographic location of the principal Maastrichtian continental localities of the Transylvanian and Haţeg basins (Romania) that have yielded eusuchian remains. The new skull of *Allodaposuchus precedens* is from Oarda de Jos and the holotype material is from Vălioara.

Therrien (2005) has shown that paleoenvironmental and taphonomic conditions of the "Red Continental Strata" of Vurpăr and the Densuş Ciula Formation of Vălioara are similar, representing stable, moderately to well-drained floodplains (mature paleosols). These conditions contrast with those of the Sânpetru Formation where the paleoenvironments were unstable (immature paleosols), comprised a mosaic of wetlands, and were dominated by areas of impeded drainage (Therrien, 2005), with ferns and bryophytes, dispersed flowering plants and gymnosperm trees (Van Itterbeeck et al., 2005). The climate in the Transylvanian and Haţeg basins has been interpreted as warm subhumid with alternating wet and dry periods (Therrien, 2005). In the Maastrichtian of the "Metaliferi area," the presence of gymnosperms, but also of several angiosperms as Icacinacee, Lauracee, Mastixiacee, Euphorbiacee or Palmae seem to indicate the same warm climate (Givulescu et al., 1995; Iamandei et al., 2005).

SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Hay, 1930
EUSUCHIA Huxley, 1875
ALLODAPOSUCHUS Nopcsa, 1928
(Figs. 1–4)

Emended Diagnosis—As for the only known species.

Type Species—*Allodaposuchus precedens* Nopcsa, 1928

ALLODAPOSUCHUS PRECEDENS Nopcsa, 1928

Holotype—skull fragment MAFI Ob 3131.

Type Locality—Vălioara, Romania.

Horizon and Age—Densuş Ciula Formation, Maastrichtian, Late Cretaceous.

Referred Material From Romania—nearly complete skull PSMUBB V 438 from Oarda de Jos (Alba District).

Emended Diagnosis Based on Romanian Remains—*Allodaposuchus precedens* differs from all other non-crocodylian and crocodylian eusuchians, except probably *Hylaeochampsa vectiana*, by the presence of a cranioquadrate passage laterally open so that it is represented by a sulcus. *Allodaposuchus precedens* differs from *Hylaeochampsa vectiana* in having a broader laterally open cranioquadrate passage; less developed bosses on paroccipital processes; slender postorbital bar; upturned orbital margins; in line occlusion pattern; shallow fossa at the anteromedial corner of the supratemporal fenestra; lateral Eustachian canals opening lateral to the median Eustachian canal; considerably larger skull size.

Furthermore, *A. precedens* is characterized by the following combination of characters: fourth dentary tooth hosted in occlusion in a pit between premaxilla and maxilla; increasing size of the maxillary alveoli up to the fourth; quadrate foramen aereum far from the dorsomedial edge; quadrate-pterygoid suture linear from basisphenoid to foramen ovale; external naris large and anterodorsally oriented; premaxillary and anterior maxillary teeth rather slender, pointed and with smooth mesiodistal keels delimited, chiefly on the lingual surface, by evident grooves (ridges are developed between these two grooves); five premaxillary teeth and thirteen or fourteen maxillary teeth; brevirostrine skull (the region anterior to the orbits is only slightly longer than the posterior one) with a length that could reach at maturity at least 40 cm.

Description of Specimen PSMUBB V 438

Preservation, Form, and General Features—The skull is almost complete although the following elements or structures are variably damaged or missing: the dorsal surface of the maxillae in correspondence of the roots of the fourth maxillary teeth, the lateral edge of the same skeletal elements corresponding to the fourth right tooth and to the sixth and seventh left teeth, as well as the posterior rim of infratemporal fenestrae, the most of the pterygoids, part of the postorbital bars, of the quadrates and of the occipital condyle (Figs. 2–4). The skull cavities, like the braincase or the nasal passages, and also the empty spaces inside the maxillae, are filled with a hard matrix that keeps the bone fragments together wherever they are separated (like in the palate region). The surface is generally not abraded allowing us to confidently interpret the position of the most of the major sutures (but the lateral surface of the braincase is not fully visible). The geometric relationships among the skeletal elements constituting the skull, as well as its general shape, are mostly well preserved, allowing a clear understanding of its fine anatomy; only the interorbital area is slightly shifted to the left and the right lower temporal bar is shifted laterally due to the displacement in anterior direction of the right posterolateral sector of the skull.

A few morphological traits (such as the position of the maxillopalatine suture) can be also deduced with the aid of some blocks of rock that still preserve the imprint of the sutures or small bone fragments matching the missing parts. The rostral region is rather wide and slightly longer than the rest of the skull (the anterior corner of the orbits is located a little caudally than the mid part of the skull). The outline of the skull is not noticeably festooned in dorsal view (only a weak constriction is developed in the mid region) and recalls in general the alligatoroid condition with a large naris and wide temporal region; in lateral view, a festooned appearance is caused by a marked concavity corresponding to the premaxillo-maxillary suture (that in dorsal view does not correspond to a notch hosting a dentary tooth), and by a more modest concavity corresponding to the sixth interalveolar space (at least on the right side, because the left maxilla is not preserved in that region).

The region anterior to the orbit is slightly convex medially but structures like a median boss, preorbital ridges and canthii rostralii are not developed. A wide and shallow depression is however visible on both sides of the skull in the region anterior to the contact between maxilla, nasal and lacrimal. A weak step could possibly be developed between the orbits, linking the points where the parallel medial rim of the orbits starts to diverge anteriorly. In dorsal view, the skull table is much wider than long; it has rounded anterolateral corners and posteriorly diverging lateral margins that, although asymmetrically developed, can be considered as slightly convex. The posterior edge of the skull table is medially convex and markedly concave laterally. In occipital view, the dorsal edge of the skull table can be tentatively considered as planar because a general sloping from sagittal axis is not evident, the entire skull table being somewhat concave and only laterally slightly sloping. The entire dorsal external surface that was directly in contact with the skin is ornate with approximately the same pattern of variably sized pits, that only in the posterolateral area of the naris and on the lower temporal bar, become more elongated or somehow merge into irregular furrows. The sagittal skull length (from the tip of the premaxillae to the tip of quadrates) and maximum width (at the level of the quadratojugals) are 36 and 26 cm, respectively.

Cranial Fenestrae and Openings—The naris opens between the premaxillae and it is posteriorly reached by nasals; it is particularly large (a little wider than the width of each premaxilla), only slightly wider (55 mm) than long (50 mm), so that its shape can be considered as approximately circular; the lateral rims gradually merge with the premaxillary surface whereas the posterolateral rims are slightly raised (but not in the posterior sector where nasals reach the naris). Because the anterior rim is markedly placed ventrally to the posterior one, the naris is considered as anterodorsally oriented.

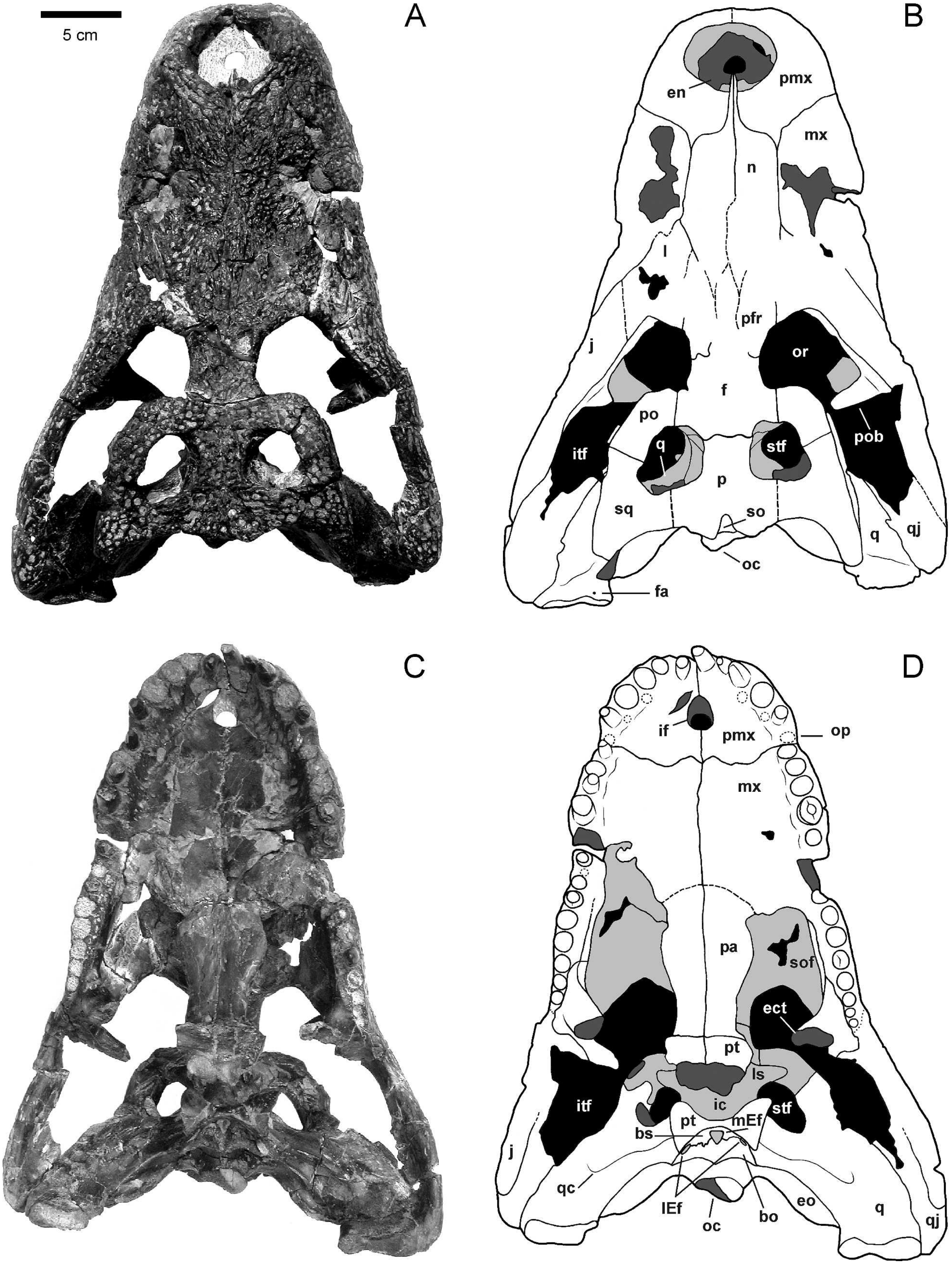
The orbits are relatively wide and short, with a well-defined and nearly straight anteromedial rim that coincides with the blade-like anterolaterally developed ventral lamina of the prefrontals (see below); the orbit rims are slightly upturned in a ridge mainly developed in the anteromedial area.

The supratemporal fenestrae are smaller than orbits, they are asymmetrically developed because the left is slightly larger than the right one; their outline is sub-trapezoidal with a wide “notch” at the posterolateral sector (more marked in the left orbit); the skull roof does not significantly overhang the fenestrae although the parietal slightly projects into the fenestra along its medial rim. There is no trace of foramina on the medial (parietal) walls. A shallow fossa (or shelf) is distinctly present at the anteromedial corner of the right fenestra whereas it is weakly developed on the left one. A shallow parasagittal groove is developed on the medial surface of the supratemporal fossa and is ventrally delimited by the suture between parietal and laterosphenoid. The geometry of the elements forming the medial and posterior wall of supratemporal fenestrae is only partly known because the bones are not completely preserved, or are hidden by hard matrix, and the development of sutures is hard to follow: the right temporal canal is hidden by matrix whereas the left one is not preserved because the surrounding skeletal elements are broken off. However, the position of the suture between the parietal and the quadrate in the left fenestra (such suture is not visible in the right one) suggests that the quadrate widely contacts the temporal canal.

Although both the infratemporal fenestrae are incomplete, they are approximately as large as the orbits; they are delimited by postorbital, jugal, and quadratojugal; because the posterior area is damaged, it is not possible to evaluate whether the quadratojugal or the jugal form its posterior angle (but, according to Buscalioni et al., 2001, it is the quadratojugal that forms such angle in *A. precedens*).

The otic recess is quite peculiar because, unlike in modern crocodylians, it does not have a sharp posterior rim but merges into the cranioquadrate sulcus. In fact, the cranioquadrate passage (or cranioquadrate canal) is laterally open being devoid of its lateral wall: the cranioquadrate passage is therefore best defined as a sulcus or canalis quadratosquamosoexoccipitalis (see Salisbury et al., 1999). Such a sulcus is developed in the exoccipital, it is ventrally delimited by the exoccipital-quadrate suture and dorsally by the exoccipital-squamosal suture. The rim of the otic recess is comprised in the quadrate (ventrally and anteriorly) and the squamosal (dorsally). Hence, the condition of characters “102” and “132” (see the phylogenetic section below) have been here considered as “non scorable,” because the otic aperture does not possess a posterior rim and there is not a squamosal-quadrate suture behind the otic recess.

The incisive foramen opens between the premaxillae, it is partly preserved on the skull and partly, just the anterior sector, on one of the blocks that embedded the skull before preparation; it is almond shaped and rather small (its maximum width is about 15 mm) and its anterior tip nearly reaches the premaxillary tooth row.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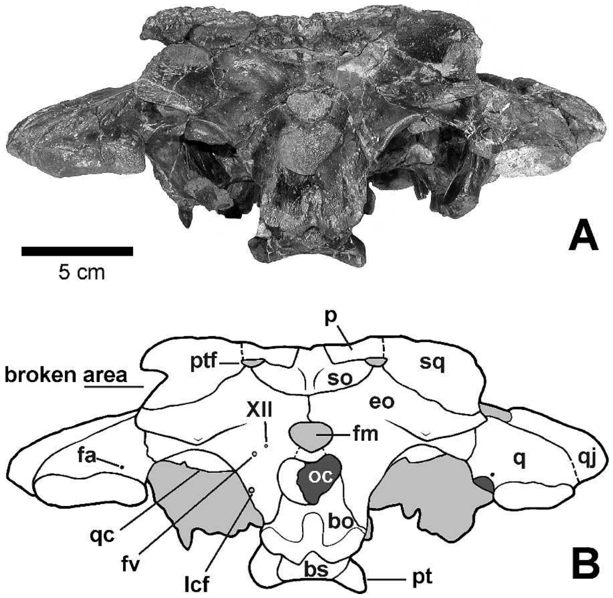

FIGURE 3. Occipital view of the *Allodaposuchus precedens* skull from Oarda de Jos, Romania, PSMUBB V 438. **A**, photograph and **B**, interpretive drawing. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **eo**, exoccipital; **fa**: foramen aereum; **fm**: foramen magnum; **fv**, foramen vagi; **lcf**, lateral carotid foramen; **oc**, occipital condyle; **p**, parietal; **pt**, pterygoid; **ptf**, posttemporal fenestrae; **q**, quadrate**; qc**, quadrate crest; **qj**, quadratojugal; **sq**, squamosal; **so**, supraoccipital; **XII**, XIIth cranial nerve.

The suborbital fenestrae are not wholly preserved but the left one is complete enough to state that its anterior rim corresponds to the anterior margin of the eight alveolus and that the posterior one probably corresponds to the end of the tooth row. The lateral rims of the suborbital fenestrae are not medially bowed but approximately straight, whilst the medial ones are markedly concave (due to the incompleteness of the pterygoids, the shape of the posterior corner is not assessable).

The opening of the internal choana preserves only the posterior and posterolateral wall but by the position of the palatine-pterygoid suture, it is clear that it was entirely surrounded by pterygoids and placed close to their posterior edge; by the inclination of the posterior wall it seems that it was slightly oriented in posteroventral direction; the posterior wall gradually merges with the ventral pterygoid surface without a marked ridge and without any deep notch, as well as without any septum.

The oval foramen is masked by matrix on both sides of the skull, but the pterygoid, quadrate and laterosphenoid converge in the area; the prootic seems to be present but its dorsal boundaries cannot by confidently described; a horizontal anteriorly directed groove originates from this area.

Although it is not completely preserved or free from matrix, the posttemporal fenestrae are quite small and delimited by parietal (dorsally), squamosal (laterally), supraoccipital and exoccipital (medio-ventrally).

The foramen magnum is partly damaged dorsally; it is mostly delimited by exoccipitals and marginally by the basioccipital (only in the median sector of the ventral surface); it is subtriangular in shape and it has a distinctly overhanging roof.

The median Eustachian canal opens between basioccipital and basisphenoid (the sutures are visible laterally to the canal on both sides); two depressions, partly filled by matrix and located laterally to the canal, are interpreted as the openings of the lateral Eustachian canals.

Premaxilla—Posterior to the naris, the premaxillae are not in contact with each other because the nasals separate them; they are slightly longer than wide (considering the processes), with weakly developed, short and narrow, dorsal processes reaching approximately the posterior limit of the third maxillary alveoli; the dorsal surface is slightly elevated along the posterolateral sector of the choana, without the development of any notch or marked depression. On the palatal surface, the premaxillo-maxillary suture is undulated but overall developed roughly perpendicularly to the sagittal axis. There are five premaxillary alveoli; the fourth is the largest (about 14 mm). The right premaxilla retains two teeth whilst the left one retains four; except the third left tooth, all the premaxillary teeth are incomplete. The first left premaxillary tooth was nearly out of its alveolus when fixed by fossilization and therefore it appears particularly long. The palatal surface hosts several evident foramina, separated by ridges and lined parallel to the tooth row.

Maxilla—There is only minimal medial expansion of the dorsal surface of maxillae because of the width of nasals; on both sides, it is fractured and incomplete in the area corresponding to the roots of the enlarged fourth teeth. The maxillae are rather flattened anteriorly but their posterolateral surface is nearly vertical. The right maxilla hosts 13 alveoli, the left 14; the last alveolus on the left element is quite small and developed in posteroventral direction and it could be supernumerary. The central part of the tooth row is missing, but the number of tooth positions is testified by one of the blocks that embedded the skull. The fourth alveolus is the largest (about 16 mm). Three teeth are preserved on the right side and one (the only one that is nearly complete) on the left side (plus two extremely fragmentary teeth on both sides). The tooth row is approximately linear posteriorly, and is barely convex only in the region of the fourth tooth. Although the middle part of the maxilla-lacrimal suture is not well preserved, it is possible to tentatively interpret a faint line on the left maxilla as the evidence for the presence of a modest maxillary process entering the lacrimal.

The palatal surface of the maxillae is severely damaged and incomplete but the line of foramina described for the premaxillae is also present on maxillae; there is no trace of a large foramen for the palatine ramus of the trigeminal nerve (cranial nerve V).

Nasal—The limits of the nasal are visible anteriorly but not very well posteriorly and medially. The nasals are markedly wide in the median region and they are so anteriorly elongated that, after an abrupt reduction toward the end, they reach the premaxillae and the naris (also on the dorsal surface), slightly entering it. They, along with the anterior process of frontal, are not elevated into a boss and seem not to have had a proximal trans-

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FIGURE 2. Dorsal (**A**, **B**) and ventral (**C**, **D**) views of the *Allodaposuchus precedens* skull from Oarda de Jos, Romania, PSMUBB V 438. **A**–**C**, photograph and **B**–**D**, interpretive drawing. The sutures of the skeletal elements placed just anteriorly to the orbits are here tentatively reconstructed; the dashed lines do not necessarily represent the true morphology of the frontal process nor the position of the suture between the nasals. **Abbreviations**: **bo**, basioccipital; **bs**, basisphenoid; **ect**, ectopterygoid; **en**, external naris; **eo**, exoccipital; **f**, frontal; **fa**: foramen aereum; **ic**, internal choana; **if**, incisive foramen; **itf**, infratemporal fenestra; **j**, jugal; **l**, lacrimal; **lEf**, lateral Eustachian foramen; **ls**, laterosphenoid; **mEf**, median Eustachian foramen; **mx**, maxilla; **n**, nasal; **oc**, occipital condyle; **op**, occlusal pit; **or**, orbit; **pa**, palatine; **pfr**, prefrontal; **po**, postorbital; **pob**, postorbital bar; **p**, parietal; **pt**, pterygoid; **pmx**, premaxilla; **q**, quadrate; **qc**, quadrate crest; **qj**, quadratojugal; **sof**, suborbital fenestra; **sq**, squamosal; **stf**, supratemporal fenestra; **so**, supraoccipital.

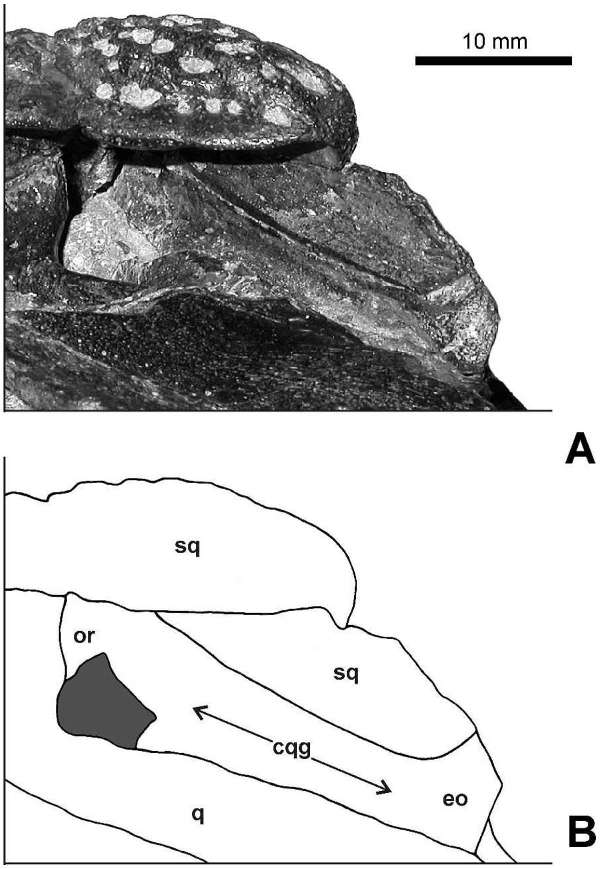

FIGURE 4. Left lateral view of the otic region of *Allodaposuchus precedens* from Oarda de Jos, Romania, PSMUBB V 438. **A**, photograph and **B**, interpretive drawing. Note that squamosal and quadrate are not in contact in the area posterior to the otic notch and that they are separated by the exoccipital. **Abbreviations**: **cqg**, laterally open cranioquadrate groove, named in the text "canalis quadratosquamosoexoccipitalis" to better define its morphology; **eo**, exoccipital; **q**, quadrate**; or**, otic recess; **sq**, squamosal.

versal end at the level of the frontal process but to taper gradually.

Lacrimal—Even if most of the sutures are not confidently visible, tentatively interpreting some "lines" on the left side of the skull as the lateral sutures, the lacrimals are apparently longer than the prefrontals and seem to host a posteriorly directed maxilla process. Along the orbital rim, the lacrimals are rather thickened, forming a dorsal ridge; at the anterior corner of the orbits, on the vertical wall, there is a lacrimal duct whose ventral rim has not been preserved on both sides of the skull.

Prefrontal—The limits of the prefrontals are not visible, except in the orbital region (and mainly on the right one). The prefrontals are not in contact with each other because they are separated by the frontal. The prefrontal pillars are broken off nearly at their base, but the remaining portion (the contiguity of these structures with the prefrontal cannot be directly established due to the preservation) has a peculiar lateral expansion that forms a lamina (best seen on the right side), vertically expanded and with a ventral sharp edge, also developed under the anteromedial margin of the orbit (lacrimal) up to the anterior corner where the lacrimal duct opens. The status of the characters concerning the prefrontal pillar has not been scored for the phylogenetic analysis due to such peculiar morphology (as character 137) or incomplete preservation (as characters 99, 136, 138).

Frontal—The sutures delimiting the anterior process of the frontal are not clearly visible, therefore its length and relationships with the prefrontals and nasals can only be tentatively assessed: the frontal process seems to taper anteriorly to a point (but the anterior left lateral sutures are even less visible than the right), and appears to be slightly shorter than the prefrontal. The frontal forms a little less than half of the medial rim of the orbit and constitutes the anteromedial corners of supratemporal fenestrae because the frontoparietal suture extensively enters the supratemporal fenestrae; such suture has been considered here as linear since it does not describe any wide concavity or convexity but it is slightly undulated. The frontal, along with the parietal, forms a well-developed shelf in the right fossa (where the shelf represents the top of the lateral expansion of the laterosphenoid) but it is only slightly outlined in the left one (where it is not so flat and with vaguely defined posterior edge; the posterolateral edge of the shelves is marked in Fig. 2B). The dorsal surface of the frontal is slightly concave.

Parietal—The parietal slightly overhangs the medial and half of the posterior rim of supratemporal fenestrae. Its dorsal surface is markedly convex at the level of the posterior margin of the supratemporal fenestrae. Given that the frontal forms the anteromedial edge of the supratemporal fenestrae, the parietal does not meet the postorbital on the skull table. The posterior edge of this element is convex and, along with the supraoccipital, confers to the skull table a medially convex posterior outline.

Supraoccipital—The supraoccipital is wider than tall on the occipital region of the skull but only modestly exposed dorsally on the skull table; because its dorsocaudal region is partly absent, it is not possible to evaluate the shape of the median posterior tip (acute or not) of the skull table. A marked sagittal ridge is visible in occipital view.

Postorbital—The postorbitals constitute the anterolateral sector of the supratemporal fenestrae and, although slightly asymmetrical, confer rounded anterior corners to the skull table. The postorbital participates in the postorbital bar with a ventral projection, forming the posterodorsal section of the bar. The left postorbital bar is completely broken off, whereas the right one is partly preserved (only the dorsal part is missing); the preserved section allows an assessment of the bar development: it is here considered as "slender" because, although it is not as slender as in *Crocodylus cataphractus*, its thickness is far from the massive condition shown at maturity by *Gavialis gangeticus* (the only living taxon with a massive postorbital bar; therefore character 70 has been scored as 1).

Squamosal—Despite the incompleteness of the left element and the erosion of the posterior edges of both, the squamosals are clearly characterized by long posterior "lobules" but weakly developed lateral prongs that do not significantly extend laterally to the dorsal surface of the squamosals (this is part of the definition of character "140" with status "0").

On the lateral surface, a ventral process of the squamosal separates the quadrate and the quadratojugal. The rims of the groove for the attachment of musculature for the ear valve are approximately parallel. The squamosal-exoccipital suture corresponds to the dorsal limit of the canalis quadratosquamosoexoccipitalis. As for the relationships with the exoccipitals on the occipital surface, the suture between these two elements slopes ventrolaterally, but each squamosal does not laterally surpass the paroccipital process of exoccipital.

Jugal—The jugal extends posteriorly nearly to the level of the paroccipital processes of exoccipitals (best seen on the left side of the skull). Along the orbit, the jugal dorsal margin is elevated into a ridge, slightly convex and not notched in the area of the postorbital bar. The jugal participates in the postorbital bar with a dorsal projection, forming the anteroventral section of the bar. The type of insertion of the postorbital bar on the jugal surface can be defined as 'inset.' Along the lower temporal bar, the jugals are rather slender and nearly cylindrical in their median region. A large medial jugal foramen is placed on the inner jugal surface anteriorly to the root of the postorbital bar; on the right jugal, the posteroventral rim of the foramen is broken off, but the inner cast of the foramen indicates its size.

Quadratojugal—The development of the quadratojugal spine and the degree of participation of the quadratojugal to the lower temporal bar cannot be evaluated due to its incompleteness. The anterior development of the quadratojugal along the dorsal rim of the lower temporal fenestra prevents the quadrate to contact the fenestra. The medial area, approximately posterior to the lower temporal fenestra, is devoid of any ornamentation.

Quadrate—The quadrates are particularly short posterior to the squamosals. Their dorsal surface is smooth. The quadrate is not in contact with the postorbital at the dorsal angle of infratemporal fenestra. The quadratoexoccipital suture corresponds to the ventral limit of the canalis quadratosquamosoexoccipitalis. From the posteroventral corner of the otic recess (formed entirely by the quadrate), an evident small groove develops in posterolateral direction; the lateral margin of such groove becomes a rather sharp ridge, linking the area close to the posterior tip of the squamosals to nearly the posterolateral tip of the quadrato-quadratojugal suture; posteriorly to this ridge, the quadrates have an orientation of about 45° in lateral view.

The location of the foramen aereum is indicated more than by the foramen itself, which is rather small and surrounded by other foramina, by the presence of a dorsal ridge developed anteriorly to the foramen; this foramen is about one centimetre from the medial edge of quadrate.

The condyles are fairly damaged (particularly the right one) but the area between the hemicondyles is nearly rectilinear dorsally and slightly concave ventrally; the left condylar area has a small ventrally reflected hemicondyle. The quadrate-pterygoid suture along the lateral braincase wall is approximately linear (although markedly following a zigzag line). The ventral surface of quadrates is characterized by a strong, nearly blade-like, quadrate crest that abruptly ends forming (best preserved on the right) a small tubercle; such crest is so developed in ventral direction that can be seen in caudal view (Fig. 3B).

Vomer—There is no trace of the vomer on the palate.

Palatine—The palatines are severely damaged in the anterior region, so that their gross morphology and the sutures with the maxillae are not directly recognizable; however, a fragment of the rock that embedded the skull prior to the preparation, preserves the cast of the surface and shows part of the sutures between the palatines, the maxillae, the palatine and the maxillae as well as a convexity corresponding to the anterior end of left suborbital fenestra; it is therefore possible to state that the anterior edge of palatines was rounded and broad and that they extended beyond the anterior end of suborbital fenestrae. The lateral edges of palatines diverge considerably in an anterior direction for more than the anterior half; they are nearly parallel in the median sector and gently flare near the palatine-pterygoid suture. Although the posterior region of the suborbital fenestrae is broken off, the palatine-pterygoid suture apparently did not reach the posterior angle of the fenestrae, given that the left suture ends about 10 mm far from the posterior tip of the preserved portion of the pterygoid that could constitute the posterolateral rim of the fossa. The preserved section of the palatine-pterygoid suture is anteriorly convex.

Pterygoid—Pterygoids are scantily represented by only two fragments: a median fragment close to the palatines and another median fragment in the area posterior to the choana (these elements only preserve the posterior wall and rim of the choana). The lateral processes of the pterygoids are largely damaged but rather strongly developed ventrally to the median Eustachian opening.

Ectopterygoid—The posterior part of the ectopterygoids is not preserved. The anterior process of the ectopterygoid tapers to a point and abuts the posterior maxillary alveoli on both sides of the skull: the ectopterygoid constitutes the medial wall (at least at the surface) of the last two alveoli and a half, but the anterior tip of the left element extends anteriorly up to the level of the fourth alveolus from the end. The ectopterygoid significantly participates in the postorbital bar.

Prootic—Even though the sutures are not easily recognizable on the right side of the braincase, it seems that the prootic is exposed ventrally to the foramen ovale, between the quadrate, pterygoid and laterosphenoid.

Laterosphenoid—The laterosphenoids are not complete mainly because their anteriormost region is missing. The remnants of the capitate processes are markedly expanded laterally under the anterior margin of the supratemporal fenestrae, where they reach the postorbital. Therefore the laterosphenoid-frontal suture is linear and transversally oriented in a lateral direction but from the available scars on the frontal, it tends to be rather anteroposteriorly oriented in its cranial sector.

Exoccipital—The exoccipitals form the majority of the occipital surface of the braincase and the ventral region of the occipital condyle. Their ventral region is characterized by a marked ventral convexity, whose tip is medial to the "opening" of the canalis quadratosquamosoexoccipitalis. A small and flat tubercle is developed slightly medially to the ventral tip of such convexity. The paroccipital processes are only weakly developed laterally to the "opening" of the canalis quadratosquamosoexoccipitalis. The lateral tips of paroccipital processes correspond approximately to the quadrate medial hemicondyles and are slightly internal to the quadrate foramina aerea. In posterior view, the ventral extent of the exoccipitals nearly reaches the dorsal edge of the basioccipital tubercles, without actually contributing to such structures. The foramina lateral to the occipital condyle are partly damaged but, mainly on the left side, it is possible to identify, in a medial position, the small opening for the XIIth cranial nerve and lateroventrally to this, the large opening of the foramen vagi. The lateral carotid foramina have been damaged and, mostly the right one, now open above their original position.

Basioccipital—The basioccipital forms the largest part of the occipital condyle and of the tubercles that are well developed in ventral direction with a 'w'-shaped tuberosity at the ventral edge (the median 'vertical' segment is particularly large and marked). In ventral view, the basioccipital is rather anteroposteriorly thick caudally to the basisphenoid.

Basisphenoid—The basisphenoid is visible in the anterolateral surface of the braincase. It is delimited by the quadrate dorsally and anteriorly, and by the pterygoid anteriorly. Moreover, it is exposed in occipital view, below the ventral margin of the basioccipital, as an anteroposteriorly thin lamina, and relatively well exposed, having the shape of a rectangle wider than high (but at least 7 mm high). The basisphenoid rostrum is broken off. Below the foramen ovale it is not possible to evaluate the basisphenoid exposure and the presence or absence of a sulcus laterally to the rostrum because of the absence of clearly visible sutures and generally poor preservation of the bones. The dorsal edge of the basisphenoid is nearly at the level of the lateral carotid foramen.

Dentition and Occlusion Pattern—The alveoli of the premaxillae and the anterior part of the maxillae (the ones not corresponding to the suborbital fenestrae) are not located at the same level as the palatal shelf but about 15–18 mm below it, at the top of an elevated alveolar shelf.

There are 5 alveoli on the premaxillae and 13 (right side) or 14 (left one) on the maxillae. Although the rims of the alveoli are poorly preserved, so that it is not possible to take precise measurements of alveolar diameters, they are all approximately circular and the size of the largest (the fourth in both cases) is about 14 mm on the premaxilla and 16 mm on the maxilla; maxillary alveoli nine and ten are slightly larger than the others. No evident diastema are present.

Depressions interpreted as occlusal pits are present on both premaxillae, medially to the tooth row at the level of the third and fourth interalveolar spaces. Well-marked interalveolar pits are located between the last premaxillary alveolus and the first maxillary one. They are mainly developed on the premaxilla, but the posterior wall of these pits interests also the maxilla, and corresponds to an evident vertical notch in lateral view but not in dorsal view (it seems that the pit lost its lateral wall because of the erosive activity of the corresponding dentary tooth). The skull is therefore festooned in lateral but not in dorsal view. The left pit is free of matrix and appears to be rather deep and separated by a ridge from another smaller pit.

Another interalveolar pit is located on the right maxilla (the corresponding sector on the left maxilla is not preserved) in the interalveolar space between the sixth and the seventh alveolus, but it is placed slightly more lingually than the pit between the premaxilla and the maxilla. The depressions visible on the same maxilla, lingually to the interalveolar spaces seven and eight, are here interpreted as artefacts due the irregularity of their surface. With the exception of the sixth, the interalveolar spaces on the maxillae are extremely narrow and therefore unsuitable to record an occlusal pit.

On the basis of clear interalveolar pits between premaxilla and maxilla and in the sixth right interalveolar space of the maxilla, the pattern of dentary-maxillary occlusion has been tentatively considered as in-line.

None of the teeth is perfectly preserved but the third left premaxillary tooth and the tenth right maxillary tooth are informative enough to permit a complete description of the tooth morphology. The premaxillary tooth has a rather slender and pointed crown (21 mm tall and 11 mm wide at the base); it bears two very well-developed mesiodistal keels, delimiting a wide lateral surface and a narrow medial surface; the keels are smooth (not crenulated or serrated) and are particularly well marked: indeed, a proportionally wide groove is developed medially to them on the medial surface (a less marked groove is developed in another tooth also on the lateral surface); both tooth sides bear ridges whose number varies from six to eight. Because of the presence of lateral (slightly concave) grooves, the ridges are limited to the slightly convex central area of the tooth; the ridges on the lateral surfaces seem to be more spaced out, but missing in the area close to the keel. Other premaxillary teeth and the first and third maxillary teeth have a similar morphology.

The tenth right maxillary tooth is nearly complete but apically damaged; it is rather small (about 10 mm tall and 9 mm wide at the base), not as elongated and slender as the anterior ones, but not blunt; the two keels are present but the shallow grooves delimiting the ridges (mostly) on the medial surface are not present; ridges are developed on the medial surface only.

COMPARISONS

Referral of the New Romanian Material to *Allodaposuchus precedens* as Defined by Nopcsa

The morphological comparison of the skull PSMUBB V 438 from Oarda de Jos with the *Allodaposuchus precedens* type MAFI Ob 3131 from Vălioara clearly indicates that these two fossils belong to the same taxon despite the presence of some minor differences that could be due to ontogenetic or intraspecific variation.

Relevant affinities between the two fossils concern the morphology of and the relationships between the cranioquadrate passage (actually transformed into the canalis quadratosquamosoexoccipitalis) and the otic recess, the presence of a protuberance on the paroccipital process, the position of the foramen aereum on the quadrate, the presence of a shelf at the anteromedial corner of the supratemporal fenestrae, the size of the medial jugal foramen and the tooth morphology.

In MAFI Ob 3131, the otic region is similar to that described for PSMUBB V438, but less well preserved. In both cases, there is no posterior rim on the otic recess, because the cranioquadrate passage is laterally open and the resulting sulcus is developed in the exoccipital, between the squamosal and the quadrate (therefore, the latter do not contact each other laterally). Also in the holotype, a smaller groove is present laterally and parallel to the canalis quadratosquamosoexoccipitalis. A rather prominent tubercle on each paroccipital process is clearly visible in MAFI Ob 3131: they form a well-developed, nearly horizontal (or a little sloping laterally) ridge that abruptly ends toward its medial edge, where it reaches its maximum height (medially to the ventralmost tip of the exoccipital). Therefore, they form a posteroventrally directed protuberance similar to the much better expressed paroccipital bosses of *H. vectiana* (BMNH R177). In PSMUBB V 438, bosses on the paroccipital process are not so prominent and they are slightly flattened; and, because character "141" links together the prominence of the bosses along with the development of exoccipital processes laterally to cranioquadrate opening (structures that, without any doubt, are only weakly developed, both in the holotype and in PSMUBB V 438), character "141" was scored in the same way in both cases. The foramen aereum is visible only on the right quadrate in MAFI Ob 3131, where it is laterally placed as in PSMUBB V 438, although not corresponding to an elevated ridge as in the latter. On the holotype, a strong shelf is developed at the anteromedial corner of the supratemporal fenestrae. The shelf is formed by the frontal and the parietal and is laterally delimited by a horizontal ridge (as in PSMUBB V 438, the shelf and the ridge is much more defined on the right side). A shallow groove below this ridge partially hosts the suture between the parietal and laterosphenoid (therefore the suture does not correspond to the ridge). The medial jugal foramen is rather large both in PSMUBB V 438 and in the jugal fragment associated to MAFI Ob 3131.

Several isolated teeth are associated with the holotype MAFI Ob 3131: collection number MAFI U 12685 corresponds to approximately 170 teeth, whose morphology usually falls in the range shown by PSMUBB V 438. The most elongated are morphologically congruent with the anterior teeth of the Oarda specimen, because they are characterized by two distinct mesiodistal keels separating a lingual surface that is smaller than the labial one, both characterized by longitudinal ridges that are not developed in the groove along the keels. Some smaller and less slender teeth, without evident ridges, could belong to the posterior region of the dentary or maxillary tooth rows.

A further similarity could be the presence of a marked transverse ridge developed on the frontal process of MAFI Ob 3131, approximately at the anterior corner of the orbits, and the weakly developed step visible on PSMUBB V 438. It is worth noting, however, that this feature is rather widespread among extant and fossil crocodyliforms (among others, some species of *Goniopholis*, *Diplocynodon*, and *Alligator*; Brochu, 1999; Salisbury et al., 1999).

The main difference between MAFI Ob 3131 and PSMUBB V 438 is related to the development of the frontal process, which is moderately long, anteriorly truncated and slightly flaring in the Vălioara specimen. The shape and development of this process is different in the proposed reconstruction of the Oarda skull (Fig. 2B), where the absence of clearly visible sutures along with as the apparent asymmetry of the nasal suture (marked with a dashed line), render such morphology too speculative to develop any further consideration. A minor difference concerns the condylar ramus of the quadrates that is more anteroposteriorly developed in MAFI Ob 3131 than in PSMUBB V 438; in the latter the condylar ramus is much more developed in ventral direction. It is also worth noting that in MAFI Ob 3131 the quadrate medial hemicondyle is small, not dorsally developed and without any dorsal notch corresponding to the foramen aereum. The quadrate crest is rather high and strong both in MAFI Ob 3131 and PSMUBB V 438; however, in the former it does not actually end with a tubercle as in the latter.

Differences Between the Romanian Material and Western European Material

Several differences between the Oarda skull and the west European specimens described by Buscalioni et al. (2001) can be pointed out. The most striking differences concern the following characters: general shape of the head and lateral festooning of the snout, orientation and shape of the external naris, shape of the frontoparietal suture, anterior extension of the suborbital fenestrae, appearance and insertion of the postorbital bar, relationships between the squamosal and the quadrate, shape of the skull table in occipital view, degree of overhanging of the skull table on the supratemporal fossae and the participation of the exoccipitals in the basioccipital tuber.

The outline of the skull in dorsal view of PSMUBB V 438 is characterized by a wide posterior sector nearly uniformly tapering in an anterior direction up to the level of the anterior rim of the naris; a weak change in the lateral profile corresponds to the jugal-maxillary contact (a concavity) and to the enlarged fourth maxillary tooth (a weak convexity); the reconstruction of the head of *A. precedens* provided by Buscalioni et al. (2001) is considerably narrower posteriorly and shows some sort of lateral festooning (explicitly mentioned in the description of the maxillae; Buscalioni et al., 2001:77 and fig. 7). The presence or absence of a laterally open notch at the limit between the premaxillae and maxillae, and the consequent pattern of occlusion of the fourth dentary tooth, has been discussed at length by Brochu (1999, 2003) and may reflect ontogenetic variability. The absence of juvenile specimens in the material described by Buscalioni et al. (2001) from Spain and France and in the material from Vălioara and Oarda de Jos, hinders a precise assessment. However, the condition shown by the Oarda skull is clear: there is no evidence of lateral festooning and the morphology in earlier ontogenetic stages should have been the same. It is worth noting that according to Buscalioni et al. (2001:77–78), “a notch is present behind the last premaxillary tooth” and “a pit for the reception of a third and/or fourth mandibular tooth is located at the uppermost part of the premaxillo-maxillary notch” but character “77” has been scored non accordingly as “0” (that is to say: dentary tooth 4 occludes in a notch between premaxilla and maxilla early in ontogeny).

The frontoparietal suture is described as anteriorly convex by Buscalioni et al. (2001), but is it is hardly visible in the holotype (it could be represented by some faint lines marked in orange) and is it is slightly undulating in the Oarda specimen.

The orientation of the naris (anterodorsal) and the approximately oval outline (slightly wider than long) clearly shown by the Oarda specimen does not match the descriptions available for *A. precedens* based on the French and Spanish remains. As indicated by Buscalioni et al. (2001:77 and fig. 7), the morphology of the naris (“almond shaped” and “dorsally placed”; but character 161 has not been scored) and that of the anterior region of the snout are markedly different from the ones here depicted in Figure 2B. It is questionable if such differences are only due to incompleteness of the western European remains (the naris characters have been probably evaluated on the basis of isolated fragments whose precise topographic relationships cannot be established), to intraspecific variability, or even to interspecific characters.

The development of the suborbital fenestra as described by Buscalioni et al. (2001:79), “more than half the anteroposterior length of the maxilla ending at the fourth maxillary tooth,” strongly differs from what is seen in the Oarda specimen, whose left suborbital fenestra (although not complete) has an anterior margin visible with confidence and reaching the anterior rim of the eight tooth.

The postorbital bar of the western European specimens was described as massive and flush with the lateral jugal surface by Buscalioni et al. (2001), but the Oarda specimen (as well as the jugal fragment associated to type specimen MAFI Ob 3131) shows postorbital bars rather slender and clearly set in from the lateral jugal surfaces. It is not unlikely that such differences are related to different interpretation of a similar morphology.

The peculiar morphology of the laterally open cranioquadrate passage significantly alters the geometric relationships of the lateral wall of the skull table and the posterior margin of the external auditory meatus so that character 132 cannot be scored being the squamosal and quadrate not in contact. Buscalioni et al. (2001:77) scored this character despite explicitly stating “laterally the cranioquadrate groove is opened in the otic area, thus avoiding outermost contact between the quadrate and squamosal behind the otic notch.”

The dorsal profile of the skull table is considered by Buscalioni et al. (2001) as “laterally sloping from sagittal axis.” The shape of the skull table of PSMUBB V 438 is rather irregular, but there is a median concavity and only a modest sloping in the lateral region, the condition of this character has been here considered as “planar.” The same can be observed in MAFI Ob 3131 where the skull table is clearly medially concave and only the right squamosal lobule seems to be laterally sloping (the entire left squamosal is reconstructed as well the lobule of the right one, but from the preserved part it is clear that the lobule sloped slightly). The degree of overhanging of the margins of the supratemporal fossae seems to be a rather variable character: indeed, modern taxa that are considered as having non overhanging supratemporal fenestrae (such as *Crocodylus*), show in some cases a modest development of the skull table toward the centre of the fenestrae (Delfino, pers. obs.). In agreement with such taxa, the weak development of the parietal in the medial area of the supratemporal fenestrae shown by the Oarda specimen and by MAFI Ob 3131 (where the supratemporal fenestrae have overhanging margins only along the medial and anterolateral rims) has been considered as insufficient to consider the skull roof as overhanging the rim of the supratemporal fossae. In PSMUBB V438, the exoccipitals do not send robust ventral processes participating in the basioccipital tubera as scored by Buscalioni et al. (2001) for the western European specimens. A further difference between the Romanian skulls and the French material concerns the fact that the Cruzy specimen recently reported by Martin and Buffetaut (2005) does not show a supraoccipital participating to the dorsal surface of the skull table.

Taxonomic Conclusions

In light of the above observations, we feel that the new material described herein from Romania can confidently be referred to *Allodaposuchus precedens* Nopsca, 1928. Material from western Europe (France and Spain) tentatively referred to *Allodaposuchus* by Buscalioni et al. (2001) is here considered representative of a different taxon (or taxa); it should be excluded from *Allodaposuchus precedens* and reassigned pending further investigation.

PHYLOGENETIC ANALYSIS

The completeness of the Oarda skull described here allows to perform a new phylogenetic analysis of *Allodaposuchus pre-*

cedens based on the Romanian remains. In order to assess the relationships of *A. precedens* within the non-crocodylian eusuchians, the analysis has been performed with the dataset used by Salisbury et al. (2006), that is represented by 42 ingroup taxa and four non-eusuchian outgroups scored for 176 discrete morphological characters (see Salisbury et al. (2006) for taxa and character list, data matrix and analysis protocol). Minor differences are the following: state of character 69 of *Isisfordia* has been changed from 1 to 0 after a personal communication by S. Salisbury, and character 132 has scored as unapplicable for *Hylaeochampsa vectiana* because of the peculiar morphology of the otic area and its relationships with the cranioquadrate passage. The latter is completely encircled by bone in all Crocodylia and the same condition is shown by *Bernissartia fagesii* (Norell and Clark, 1990) and nearly all the outgroups of Crocodylia; but it is laterally open, and therefore represents a sulcus, in basal crocodyliforms such as *Hemiprotosuchus*, *Ortosuchus* and *Protosuchus* (see supplementary information in Buckley et al., 2000), as well as for *Goniopholis* (Salisbury et al., 1999).

The condition of *Hylaeochampsa vectiana* was controversial: Clark and Norell (1992:8) state that "medially, the quadrate contacts the exoccipital and with it and the squamosal encloses the cranioquadrate passage" (nothing is said about the lateral development of such bones). Salisbury et al. (1999) report that in *H. vectiana* the canalis (= sulcus) quadratosquamosoexoccipitalis is not exposed laterally because it is enclosed by the lamina ventrolateralis of the squamosal. A different opinion is expressed by Buscalioni et al. (2001:77) who wrote that this taxon "probably [has a] laterally open cranioquadrate groove". The reexamination of the type specimen of *Hylaeochampsa vectiana* Owen, 1874, BMNH R177, revealed that very probably the cranioquadrate passage is laterally open but that squamosal and quadrate are not as widely spaced as in *Allodaposuchus*, and probably quite close (nearly in contact?) in the posterior area. The left side of BMNH R177 is more informative than the right one because the latter is partly masked by a whitish matrix. The left otic notch is devoid of any posterior rim and its inner wall gradually merges with the cranioquadrate "passage" without any visible breakage witnessing a suture between the squamosal and the quadrate. Despite the fact that the posterolateral tip of squamosal is broken off, the absence of a clear sutural area on the preserved quadrate is here considered as an indication of lateral opening of the passage. The fact that this peculiar morphology is also present in some neosuchians indicates that it could be considered a symplesiomorphy within Crocodylomorpha.

The character coding presented here for the Oarda specimen (the skull PSMUBB V 438; reported in Appendix 1) is fully redundant ("states are identical for those characters coded in common, but [. . .] some characters are coded for one but not the other"; Brochu, 2004:870) with the one that can be obtained from the holotype of *A. precedens* MAFI Ob 3131, but much more informative because many characters can not be scored in the latter. The matrix was processed with PAUP 4.0b10* (Swofford, 2001). Outgroups were forced to be paraphyletic. The results of the phylogenetic analyses are presented in Figure 5 along with a summary (Fig. 5A) of the phylogenetic arrangement proposed by Buscalioni et al. (2001:fig. 15). For the sake of simplicity, the three clades with extant members as well as the four *Borealosuchus* species included in the analyses are represented in the figures by one terminal taxon only.

This analysis confirms the relationships suggested by Buscalioni et al. (2001) based on a character matrix that includes the holotype of *A. precedens* from Romania and the putative *A. precedens* remains from western Europe: *Allodaposuchus* is a non-crocodylian eusuchian. The strict consensus tree (Fig. 5B) offers poorly resolved relationships among the outgroups and non-crocodylian eusuchians. A better resolution is offered by a 76% majority-rule consensus (Fig. 5C). In both the analyses, the relationships of the clade *Borealosuchus* are those already obtained by Salisbury et al. (2006).

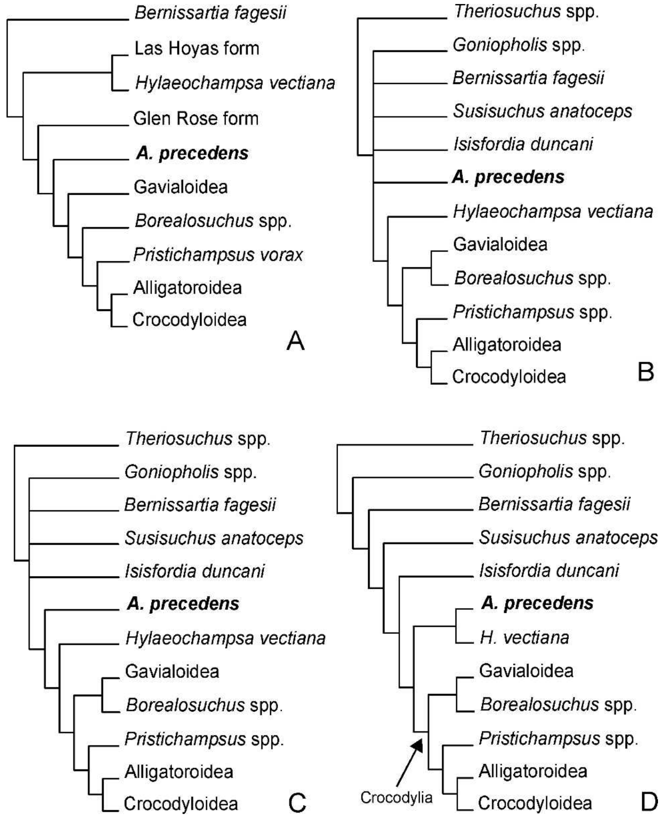

FIGURE 5. Schematic summary of the phylogenetic relationships of *Allodaposuchus precedens* (see text for details and statistics). Because the arrangement of taxa in each single clade is not a goal of these analyses, for the sake of clarity only the name of the clade (or the genus name in the case of *Borealosuchus*) is shown in the cladograms. **A**, topology from Buscalioni et al. (2001:fig. 15) here shown for comparison.; **B**, strict consensus tree resulting by the application of the dataset of Salisbury et al. (2006) to the new character coding of the *A. precedens* skull PSMUBB V 438; **C**, as in B but 76% majority-rule consensus of 63 trees; **D**, as in A but with the addition of one state to characters 102 and 132. Only the topology of the last tree is congruent with that obtained by Salisbury et al. (2006:fig. 5a).

In the topology presented in Figure 5B, the node of *A. precedens* is supported by the following character states:

> 70(1), slender postorbital bar; 77(1), fourth dentary tooth occludes in a notch; 78(2), dentary teeth occlude in line with the maxillary tooth row; 89(2), fourth maxillary tooth is the largest; 92(0), presence of a shallow fossa at the rostromedial corner of supratemporal fenestra; 103(1), upturned dorsal edges of orbits; 120(1), medial jugal foramen very large; 121(1), foramen aerum on dorsal surface of quadrate; 127(1), quadratopteygoidal suture linear from basiphenoid exposure to foramen ovale; 147(1), lateral Eustachian canals open lateral to medial Eustachian canal; 172(1), secondary choanae situated towards the caudal margin of the pterygoid; 174(1), occipital surface ventral to basioccipital condyle roughly parallel to the transverse plane.

Parameters for the topology summarized in Figure 5B are the following: number of trees retained = 63; tree length = 514; consistency index (CI) = 0.4397; homoplasy index (HI) = 0.5603; CI excluding uninformative characters = 0.4228; HI excluding uninformative characters = 0.5772; retention index (RI) = 0.7422; rescaled consistency index (RC) = 0.3263. In order to include in the analysis the peculiar morphology of the region posterior to the otic notch, a third analysis has been performed adding a state to characters 102 and 132.

The new definitions of these characters are the following:

102. Caudal margin of otic aperture not defined and gradually merging into the exoccipital (0) or smooth and continuous with the paraoccipital process (1) or caudal margin of otic aperture inset (2). (Modified from Salisbury et al., 2006, character 102).
132. Quadrate and squamosal not in contact on the external surface of the skull, posteriorly to the external auditory meatus (0) or quadratosquamosal suture extends dorsally along caudal margin of the external auditory meatus (1) or extends only to the caudoventral corner of the external auditory meatus (2). (Modified from Brochu, 1999, and Salisbury et al., 2006, character 132).

For both characters, state 0 has been assigned to *Goniopholis*, *Hylaeochampsa* and *Allodaposuchus*. The rest of the taxa have been re-scored for both characters simply changing state 0 in 1 and state 1 in 2. (For the complete data matrix see the nexus file provided as Supplementary Data 1, www.vertpaleo.org/jvp/JVPcontents.html.)

The strict consensus tree obtained with this matrix (Fig. 5D) shows a topology fully congruent with that published by Salisbury et al. (2006:fig. 5a). *Allodaposuchus* is a non-crocodylian Eusuchian, the sister taxon of *Hylaeochampsa*.

In the topology presented in Figure 5D, the clade represented by *Hylaeochampsa vectiana* and *Allodaposuchus precedens* is supported by the following character states:

> 89(2), the fourth maxillary tooth is the largest; 102(0), caudal margin of otic aperture not defined and gradually merging into the exoccipital; 103(1), dorsal edges of orbits upturned; 120(1), medial jugal foramen very large; 121(1), foramen aereum on dorsal surface of the quadrate; 132(0), quadrate and squamosal not in contact on the external surface of the skull, posteriorly to the external auditory meatus; 141(0), exoccipital with prominent boss medial to the paroccipital process and process lateral to the caudal aperture of the cranioquadrate canal short.

The node of *A. precedens* is supported by the following character states:

> 78(2), dentary teeth occlude in line with the maxillary tooth row; 92(0), shallow fossa at rostromedial corner of supratemporal foramen; 119(0), basisphenoid not broadly exposed ventral to the basioccipital at maturity in occipital aspect and pterygoid dorsoventrally short ventral to median Eustachian opening; 127(1), quadratopterygoidal suture linear from basisphenoid exposure to the foramen ovale; 130(0), capitate process of laterosphenoid oriented laterally; 147(1), Lateral Eustachian canals open lateral to medial Eustachian canal.

Parameters for the topology summarized in Figure 5D are the following: number of trees retained = 6; tree length = 499; consistency index (CI) = 0.4569; homoplasy index (HI) = 0.5431; CI excluding uninformative characters = 0.4401; HI excluding uninformative characters = 0.5599; retention index (RI) = 0.7576; rescaled consistency index (RC) = 0.3462.

DISCUSSION

The skull from the Maastrichtian of Oarda de Jos, PSMUBB V438, is one of the most informative Late Cretaceous eusuchian fossils from Europe, and adds considerable information to faunal assemblages that few years ago had been appropriately defined as “a huge puzzle composed mostly of isolated bones, teeth and osteoderms” (Buscalioni et al., 1999:214). Very strong morphological similarities with the type of *Allodaposuchus precedens* Nopcsa, 1928, not to mention their geographic provenience and chronological allocation, indicate that they belong to the same taxon, a taxon that can be considered valid and whose skull anatomy can be now described in detail.

Despite a superficial alligatoroid appearance of the skull, *A. precedens* is a non-crocodylian eusuchian. It is characterized by an internal choana placed close to the posterior edge of the pterygoids and, most likely, by procoelous vertebrae. No vertebrae or postcranial remains have been found along with the skull from Oarda de Jos. However, the vertebrae associated with the holotype from Vãlioara, representing all the vertebral districts, are clearly procoelous (MAFI Ob 3133, 3134, 5724, 5726, 5727). At the same time, *A. precedens* shows, probably along with *Hylaeochampsa vectiana* from the Barremian of the Isle of Wight, a character that is unique among Eusuchia: a laterally open cranioquadrate passage transformed in a sulcus.

The Oarda de Jos skull suggests that *A. precedens* was a carnivorous animal reaching a total length of at least three meters. The long, robust but pointed teeth, as well as the absence of bulbous crushing posterior crowns (as in the Upper Cretaceous *Brachychampsa*; see Williamson, 1996), suggest that this animal was a generalized predator, not particularly well-adapted to eat fish or hard-shelled prey. The cranial osteology of *A. precedens* is however not completely known. No lower jaws are preserved among the material from Vãlioara or Oarda de Jos or from the localities in southern France and northern Spain; however, a very well preserved lower jaw from Laño (latest Cretaceous, Spain) that could possibly belong to this or a closely related taxon (Astibia et al., 1990) has not been studied yet.

The apparent morphological differences between the *A. precedens* specimens from Romania and those referred to the same taxon by Buscalioni (2001) from western Europe could reflect a different interpretation of the same structures, intraspecific variability or even the presence of different taxa. The latter option seems likely and has been already suggested by Martin and Buffetaut (2005). From a general point of view, not even considering the debated nature of island or outpost of the Haţeg basin during the Upper Cretaceous (Jianu and Boekschoten, 1999, and references therein), it is worth mentioning that Rage (2002) recently underlined that despite previous hypotheses of homogeneous European latest Cretaceous vertebrate assemblages, new evidence suggests that faunas from different regions are not identical, and could have a rather complex taxonomic composition and geographic origin.

The knowledge about the phylogenetic relationships among the Cretaceous taxa directly related to the crown group Crocodylia is rather unstable at the moment (compare phylogenies in, among others, Buscalioni et al., 2001 and 2003) and is primarily affected by a poor fossil record. As shown by the recently described *Isisfordia duncani* (Salisbury et al., 2006) from the latest Albian-earliest Cenomanian, the chance to contribute to fix such instability lies in the collection of fossil material sampling the long gap (about 40 My long) between the Barremian and the Campanian.

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APPENDIX 1. Character coding (176 characters) of *Allodaposuchus precedens* based on the isolated skull from Oarda de Jos, Romania (PSMUBB V 438), following the character list and definitions by Salisbury et al. (2006). Note that the coding presented here slightly differs from that published by Salisbury and co-workers. The topology resulting from the analysis of this coding is shown in Figure 5B and C.

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?????????? ?????????1 10???11200 00?0100?2? 00??1?0??0
00100?0000 0?1???0001 1?100010?0 ?N0?0???00 0000011??0
001??????? 0?0?0??0?? ?1?111