New Spanish Late Cretaceous eusuchian reveals the synchronic and sympatric presence of two allodaposuchids

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ABSTRACT

The recently described clade Allodaposuchidae includes European eusuchian crocodyliforms restricted to the Late Cretaceous (Campanian and Maastrichtian). A new allodaposuchid crocodyliform is here described based on two specimens from the upper Campanian-lower Maastrichtian fossil site of Lo Hueco (Cuenca, Spain). This new taxon, *Agaresuchus fontisensis* gen. et sp. nov., is described by two complete skulls and a lower jaw associated with one of them. This new species can be distinguished unambiguously from *Lohuecosuchus megadontos*, the other allodaposuchid known from the same fossil site. The presence of two allodaposuchid crocodyliforms in Lo Hueco allows the recognition of the synchronic and sympatric existence of two representatives of this clade for the first time. The new genus *Agaresuchus*, comprises a previously described Iberian allodaposuchid species, “*Allodaposuchus*” *subjuniperus*, as *Agaresuchus subjuniperus*, new combination.

1. Introduction

Allodaposuchidae Narváez et al. 2015 is a recently described group of European eusuchian crocodyliforms of Late Cretaceous (Campanian and Maastrichtian) age. This clade forms the sister group of Crocodylia (Narváez et al., 2015) together with Hylaeochampsidae Andrews 1913, an Early and Late Cretaceous clade found predominantly, if not exclusively, in Europe (Buscalioni et al., 2011; Turner, 2015). The type species of Allodaposuchidae, *Allodaposuchus precedens* Nopcsa 1928, was initially described on fragmentary specimens from the lower Maastrichtian of Vălioara, Romania. A nearly complete skull from Oarda de Jos (Hateg Basin, Romania) was later referred to the species (Delfino et al., 2008), significantly improving the knowledge on

this taxon. Several subsequently described crocodyliforms from Campanian and Maastrichtian sites of the Iberian Peninsula and southern France were also identified as allodaposuchids (see Narváez et al., 2015). Most of them correspond to forms described in recent years. The Iberian forms include *Allodaposuchus subjuniperus* Puértolas-Pascual, Canudo, Moreno-Azanza, 2014, *Arenysuchus gascabadiolorum* Puértolas, Canudo, Cruzado-Caballero, 2011, *Musturزابalsuchus buffetauti* Buscalioni, Ortega, Vasse, 1997, *Lohuecosuchus megadontos* Narváez, Brochu, Escaso, Pérez-García, Ortega, 2015, *Allodaposuchus palustris* Blanco, Puértolas-Pascual, Vila, Marmi, Sellés, 2014 and *Allodaposuchus hulki* Blanco, Fortuny, Vicente, Luján, García-Marça, Sellés, 2015. Whether *A. subjuniperus* can be referred to *Allodaposuchus*, and whether *A. palustris* and *A. hulki* can be diagnosed, has been challenged in recent analyses (Martin et al., 2015; Narváez et al., 2015). The French forms correspond to *Massaliasuchus affuvelensis* (Matheron, 1869), *Lohuecosuchus mechinorum* Narváez, Brochu, Escaso, Pérez-García, Ortega, 2015, and specimens referred to *A. precedens* (Martin and Buffetaut, 2008; Martin et al., 2015).

Eusuchian crocodyliforms are abundant at the Spanish site of Lo Hueco in Cuenca Province (Fig. 1; Ortega et al., 2015). *Lohuecosuchus megadontos* is based on three skulls and three lower jaws from this locality (Narváez et al., 2015). Two complete skulls, and a lower jaw associated with one of these skulls, establish the presence of a second allodaposuchid at the Lo Hueco fossil site. It is closely related to “*Allodaposuchus*” *subjuniperus*, and both can be referred to a new genus. This material allows not only the description of one of the best represented allodaposuchids but, for the first time, the synchronous and sympatric coexistence of two members of Allodaposuchidae. In fact, crocodyliforms are identified in the two levels of the site with the greater abundance of fossil remains (i.e. the levels of grey marly mudstones G1

and G2, sensu Barroso-Barcenilla et al., 2009; Ortega et al., 2015). The level G1 corresponds to the proximal part of a flooded muddy plain, close to the distributary channels. The level G2 has been interpreted as the distal part of a flooded muddy plain. The same faunal composition has been recognized for both levels, separated by a short time span (Ortega et al., 2015). Skulls of *Lohuecosuchus megadontos* were identified in both levels. The holotype of the new taxon described here comes from G1, but the other skull attributed to this taxon was found in G2. Here, we describe the new species and discuss its implications for eusuchian phylogeny and biogeography.

Institutional abbreviations. HUE, Lo Hueco collection, Museo de las Ciencias de Castilla-La Mancha, Cuenca, Spain; MPZ, Museo Paleontológico de la Universidad de Zaragoza, Zaragoza, Spain.

Anatomical abbreviations. 4mt, fourth maxillary tooth; an, angular; ar, articular; bo, basioccipital; bs, basisphenoid; ch, choana; cqg, cranioquadrate groove; cr, coronoid; cv, cervical vertebra; d, dentary; ec, ectopterygoid; ex, exoccipital; f, frontal; fa, foramen aërum; fcp, foramen caroticum posterius; fe, eustachian foramen; fic, foramen intermandibularis caudalis; fm, foramen magnum; fv, foramen vagi; gf, glenoid fossa; if, incisive foramen; itf, infratemporal fenestra; j, jugal; l, lacrimal; mx, maxilla, n, nasal; na, naris; o, orbit; oc, occipital condyle; op, occlusion pits; or, otic recess; p, parietal; pa, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pob, postorbital bar; pt, pterygoid; ptf, post-temporal fenestra; q, quadrate; qj, quadratojugal; qjs, quadratojugal spine; rp, retroarticular process; sa, surangular; so, supraoccipital; sof, suborbital fenestra; sp, splenial; sq, squamosal; stf, supratemporal fenestra; sym, mandibular symphysis; xii, foramen for hypoglossal nerve (XII).

2. Materials and methods

The specimens HUE-02502 (a complete skull, the right lower jaw and a cervical vertebra) and HUE-03713 (a nearly complete skull) are from the fossil site of Lo Hueco (Cuenca, Spain), and the specimen MPZ 2012/288 (a nearly complete skull) is from the fossil site of Beranuy (Huesca, Spain). Both have been compared in detail with the type specimens of all currently known members of Allodaposuchidae: *Allodaposuchus precedens* (early Maastrichtian, Romania), *Arenysuchus gascabadiolorum* (late Maastrichtian, Spain), *Lohuecosuchus mechinorum* (late Campanian-early Maastrichtian, France), *Lohuecosuchus megadontos* (late Campanian-early Maastrichtian, Spain), *Massaliasuchus affuvelensis* (early Campanian, France), and *Musturزابalsuchus buffetauti* (late Campanian-early Maastrichtian, Spain).

In order to establish the phylogenetic relationships of *Ag. fontisensis*, its morphological characters were scored in the data matrix used by Narváez et al. (2015). The recently described material from Velaux-La Bastide Neuve (France), identified as *Allodaposuchus precedens* by Martin et al. (2015), cannot be coded here because it is not currently available, being under study (Valentin, com. pers.).

The recently described species *Allodaposuchus hulki* (Blanco et al., 2015) presents important problems in its phylogenetic placement due to the poor preservation and the lack of information of the skull and lower jaw. There are no evident diagnostic characters for the species and most of the autapomorphies are based on characters badly preserved and thus, difficult to assess, such as the size of the quadratojugal spine or the presence of a fossa at the anteromedial corner of the supratemporal fenestra in the

available material. Thus, *Allodaposuchus hulki* should be viewed cautiously, and a detailed review of known material should be done.

A total of 189 characters and 106 taxa were analysed. *Goniopholis simus* was selected as outgroup. The matrix was analysed with TNT (Goloboff et al., 2008) using heuristic searches based on 1000 random addition sequence replicates. Bootstrap frequencies and Bremer support values have also been calculated using TNT.

3. Systematic Paleontology

Crocodylomorpha Walker, 1970

Crocodyliformes Hay, 1930

Eusuchia Huxley, 1875

Allodaposuchidae Narváez, Brochu, Escaso, Pérez-García & Ortega, 2015

Agaresuchus gen. nov.

Type species. Agaresuchus fontisensis sp. nov.

Other included species. Agaresuchus subjuniperus, new denomination for *Allodaposuchus subjuniperus* Puértolas-Pascual, Canudo & Moreno-Azanza, 2014.

Etymology. *Agare-*, referring to Agares, a demon, one of the dukes of hell, described in demonological grimoires as an old man riding upon a crocodile (Weyer, 1583); and *-suchus*, a suffix latinized from the Greek word *souchos*, referring to an Egyptian crocodile-headed god.

Distribution. Upper Campanian-lower Maastrichtian (Upper Cretaceous) of the Iberian Peninsula.

Diagnosis. Allodaposuchid characterized by the following autapomorphies: incisive foramen located close to the premaxillo-maxillary suture; in lateral view, the anterior tip of the rostrum is flat; and dorsal projection of the nares. *Agaresuchus* shares with *Lohuecosuchus mechinorum* a massive postorbital bar. It shares with *Arenysuchus gascabadiolorum* and *Lohuecosuchus mechinorum* an anterior process of the frontal extended beyond the anterior margin of the prefrontals. *Agaresuchus* shares with *Arenysuchus gascabadiolorum* a great number of maxillary alveoli (fifteen in *Ag. fontisensis* and fourteen in *Ag. subjuniiperus*), relatively small-sized teeth, and wider interdental spaces between them compared with other allodaposuchids.

Agaresuchus fontisensis sp. nov.

Figs. 2–5

Holotype. HUE-02502, a complete skull, right lower jaw and cervical vertebra (Figs. 2–4).

Referred Material. HUE-03713, a relatively complete skull lacking the posterior region of the left quadrate, quadratojugal and jugal (Fig. 5).

Etymology. *fontis*-, from Latin word *fontis* (fonts in English), referring to Fuentes, the village in Cuenca Province, Spain where the Lo Hueco fossil locality is located; and *-ensis*, “belonging to”.

Locality and horizon. Lo Hueco fossil site, Fuentes, Cuenca Province, Castilla-La Mancha, Central Spain. Arcas-Fuentes Syncline, southwestern branch of the Iberian Ranges. Margas, Arcillas y Yesos de Villalba de la Sierra Formation; Upper Cretaceous (upper Campanian-lower Maastrichtian) (Barroso-Barcenilla et al., 2009; Ortega et al., 2015).

Diagnosis. A species of *Agaresuchus* differing from *Ag. subjuniperus* by: elongate and narrow snout; fifteen maxillary alveoli; occlusal pits between the seventh and eighth maxillary alveoli; premaxillae longer than wide; almond-shaped incisive foramen; long and thin nasals, with parallel lateral margins; lack of posterior process of the nasals between the frontal and the prefrontals (exclusive for *Ag. fontisensis*); main axis of the dorsal surface of the prefrontals parallel to the sagittal plane; narrow frontal and small interorbital space; rounded orbits relatively larger than in *Ag. subjuniperus*; choana with sagittal septum; posterolateral angle of infratemporal fenestra comprised of both the quadratojugal and jugal; anterior half of the palatines projected laterally into the suborbital fenestrae (exclusive for *Ag. fontisensis*); sharply acute anterior palatine process (exclusive for *Ag. fontisensis*).

Description. The holotype skull, HUE-02502, is complete and well-preserved, but it has some slightly damaged or displaced structures (Figs. 2-3). A cervical vertebra is embedded on the back of the left half, between the quadrate and the pterygoid, preventing the detailed observation of that region. The maximum length of this skull,

from the snout tip to the posterior margin of the quadrate condyles, is about 370 mm. Its maximum width, at the level of the lateral margins of the quadrate condyles, is approximately 220 mm. The skull of the paratype, HUE-03713, is longer than that of the holotype (maximum length approximately 430 mm). It presents lateral compression (Fig. 5). In dorsal view, the lateral outlines of both specimens are anteriorly convex, in the region where the fourth maxillary teeth are situated. However, they are slightly concave behind this area and vertical in the rear region. The orbits of *Ag. fontisensis* are rounded and slightly broadened posterolaterally. Their margins are slightly upturned with respect to the dorsal surface of the skull. The supratemporal fenestrae are circular and slightly smaller than the orbits. The infratemporal fenestrae are trapezoidal with lateral margins longer than the width of each fenestra. The suborbital fenestrae are large and elongate, anteriorly reaching the level of the eighth maxillary tooth (Figs. 2-3, 5).

The premaxillae are longer than wide. They form the anterolateral narial margin, and the nasals prevent the sagittal contact of both premaxillary branches in this area (Figs. 2A-B, 5A). In dorsal view, the premaxillae are slightly raised with respect to the rostrum. The circular external naris is large and dorsally projected, and although it does not bear ridges on its edges, the posterolateral margins appear slightly raised (Figs. 2A-B, 5A-B). Dorsally, the anterior and posterior region of the premaxilla-maxilla sutures can be clearly observed in the holotype. The premaxillae extend posteromedially, forming a short process between the nasals and the maxillae (Fig. 2A-B). In palatal view, the premaxilla-maxilla suture is convex anteriorly and extends from a deep foramen located medial to the notch for reception of the fourth mandibular tooth laterally to the midline. Medially, the premaxilla-maxilla sutures closely approach the posterior margin of the small, almond-shaped incisive foramen (Figs. 2C-D, 5C-D).

Anteriorly, the margin of the incisive foramen is very close to the first pair of premaxillary alveoli (Figs. 2C-D, 5C-D).

Each premaxilla has four rounded alveoli. Only three teeth are preserved in the left premaxilla of HUE-02502, one almost complete and two broken. Several teeth are preserved in HUE-03713: one broken tooth (the first), one replacement tooth not fully developed (the second) and one complete tooth (the third) in the left element, and one replacement tooth not fully developed (the third) and one broken tooth (the fourth) in the right premaxilla. The third premaxillary alveoli are the largest, while the first and fourth are the smallest. A pit for reception of the first mandibular tooth is present between the first and the second alveolus in each premaxillary branch. This pit is larger than both alveoli (Figs. 2C-D, 5C-D).

The maxillae are elongate, with dorsal and ventral lengths close to twice the respective widths (Figs. 2, 5). Their dorsal surfaces are abundantly ornamented. Slight depressions, near the sutures between the maxillae and the premaxillae, are identified in the maxillae of both specimens (Figs. 2A, 5A). Posteriorly, the maxillae bear distinct short processes that extend into the lacrimals. Ventrally, the maxillae participate in the posterior portions of the notch for reception of the fourth dentary teeth (Figs. 2C-D, 5C-D).

The maxillae have fifteen rounded dental alveoli aligned in a linear series. The fourth alveoli are the largest (Figs. 2C-D, 5C-D). Diameter decreases progressively from the eighth to the fifteenth alveoli, and the posteriormost alveolus is smallest. Ten complete and three broken teeth are preserved on the right maxilla of the holotype, and four complete and six broken teeth on the left. In HUE-03713, six complete and four broken teeth are preserved on the right, and, four complete teeth, one replacement tooth not

fully developed, and four broken teeth on the left. Well-developed interalveolar occlusion pits are present between the sixth through ninth alveoli (Figs. 2C-D, 5C-D).

The narrow, elongate nasals reach their maximum width where they contact the anterior processes of the lacrimals (Figs. 2A-B, 5A-B). Their medial and posterolateral margins are clearly visible on HUE-02502, however, their anterior margin cannot be observed. However, the nasals probably separate the premaxillae and anteriorly contact the posterior margin of the external naris, though without forming an internarial bar. Posteriorly, the nasals are separated by the rostral frontal process (Fig. 2A-B). In HUE-03713, the margins of the rear region of the nasals are not clearly visible (Fig. 5A-B).

The margins of the lacrimals are not clearly visible in any specimens, but can be recognized the possible outline of the bones (Figs. 2A-B, 5A-B). The lacrimals extended anteriorly further than the prefrontals, The lacrimals and prefrontals participated equally in the orbital margins, the lacrimals forming the anterior margin. Anteriorly, each lacrimal projects a short, acute process between the nasal and maxilla (Figs. 2A-B, 5A-B).

Sutures delimiting the prefrontals are clearly visible in HUE-02502, but not in HUE-03713 (Figs. 2A-B, 5A-B). The prefrontals are subrectangular in dorsal view and separated by the anterior process of the frontal (Fig. 2A-B). There is a small anterolateral process between each nasal and lacrimal. Each prefrontal forms a well-marked torus with the frontal at the level of the anteromedial corner of the orbit. The dorsal prefrontal surface is posteriorly elevated where it forms the medial wall of the orbit. The prefrontal pillars are parasagittal columnar structures extending vertically from the medial margins of the prefrontals. The medial processes of the prefrontal pillars cannot be observed. Laterally, a thin, slightly concave lamina runs the ventral surface of prefrontals.

The frontal is profusely ornamented. It has a long, narrow anterior process that reaches the nasals (Figs. 2A-B, 5A-B). The frontal participates in more than half of the medial orbital margins, forming a smooth crest, not as marked as than developed on the prefrontals and lacrimals. The frontal contacts the parietal at the level of the anterior region of the supratemporal fenestrae, by a linear suture. The frontal forms a small portion of the anteromedial corners of these fenestrae (Figs. 2A-B, 5A-B).

The dorsal surface of the parietal is flat and abundantly ornamented with large and deep depressions (Figs. 2A-B, 5A-B). The parietal forms the entire medial and posteromedial margin of the supratemporal fenestrae, and the margins are not dorsally expanded. The posterior margin of the parietal shows a slight medial depression at its contact with the supraoccipital. In occipital view, the parietal constitutes the dorsal margins of the post-temporal fenestrae (Figs. 3A-B, 5F).

The length and width of the postorbitals are subequal. The postorbitals are approximately half the length of the squamosals (Figs. 2A-B, 5A-B). They constitute the anterolateral margins of the supratemporal fenestrae. Posteromedially, they constitute half the length of the lateral margin of the fenestrae. The lateral surface of the postorbitals contacts with a thin quadratojugal process. The postorbital bars are short and robust, and extend from the anterolateral corners of the postorbitals to the ascending ramus of the jugals (Figs. 2A-B, 3C-D, 5A,F).

The dorsal surfaces of the squamosals are planar and abundantly ornamented (Figs. 2A, 5A). Caudolaterally, these elements bear long processes extending posteroventrally from the skull table surface. The posterior margin of each process is shorter than the squamosal participation in the paraoccipital process. These projections are dorsally smooth and slightly expanded posterolaterally. In occipital view, a notch separates the distal portion of these projections of the posteroventral participation of the squamosals

in the paraoccipital process. In dorsal view, the medial region of the caudal margin of each squamosal is concave and the squamosal surface behind the supratemporal fenestra is narrow. The squamosals constitute the posterolateral walls of the supratemporal fenestrae. A pair of well-developed foramina is developed here. In lateral view, each squamosal bears an elongate anterior process above the postorbital contacting the postorbital bar. The groove for insertion of the ear flap musculature is well-developed and reaches anteriorly the posterior border of postorbital. The ventral surface of each squamosal constitutes the roof of the otic recess (Figs. 3C-D, 5E). The region of contact between the squamosal and the exoccipital marks the dorsal limit of the cranioquadrate passage, which is a groove rather than an enclosed canal. The squamosals contact the quadrates anteromedially in this passage, but not posteriorly. In occipital view, the squamosal surface is depressed and its medial border constitutes the lateral margin of a marked depression next to each post-temporal fenestra (Figs. 3A-B, 5F).

The jugals form the lateral margins of the infratemporal fenestrae and the orbits (Figs. 2A-B, 5A-B). A slight dorsal crest is developed in the region defining the orbits. Anteriorly, each jugal extends to the level of the seventh maxillary alveolus as a small and acute anterior process, located near to the contact area with the lacrimal. Each ascending ramus, forming the ventral portion of the postorbital bar, has a circular cross-section. Posteriorly, the jugals end almost at the level of the caudal limit of exoccipitals. The postorbital bars are robust (Figs. 3C-D, 5F), and inset into the medial wall of the jugals. Two well-developed foramina are observed at the base of the anterior and posterior surfaces of each postorbital bar.

The quadratojugals are long and narrow. They are ornamented only on their posterior regions (Figs. 2A-B, 5A-B). The quadratojugals constitute the rear margins of the infratemporal fenestrae with sutures between the jugals and the quadratojugals in the

posterior corner of these fenestrae. The left quadratojugal of HUE-02502 preserves a thin spine extending anteromedially more than half of the length of the infratemporal fenestra (Fig. 2A-B). The anteromedial development of the quadratojugals excludes the quadrates from the infratemporal fenestral margins. The quadratojugals extend almost to the posterolateral end of the quadrates with no condylar contribution (Figs. 2, 3, 5).

The quadrate rami are long with respect to those of the squamosals. They are laterally expanded. The quadrate surfaces are smooth. Each foramen aëreum opens dorsally at the end of a marked crest (Figs. 2A-B, 5A-B). The quadrates and squamosals do not contact in the posterior region of the otic aperture. Therefore, the cranioquadrate passage is opened (Figs. 3C-D, 5E). The quadrates constitute the posterior walls of the supratemporal fossae, preventing parietal-squamosal contact in this region. In ventral view, well-developed longitudinal ridges can be recognized in a similar position to crests B (*sensu* Iordansky, 1973) parallel to the medial margins of the quadrates from their posterolateral angles. Likewise, modest crests ventromedially constrain the supratemporal fenestrae (Fig. 2C-D). Both crests delimit a groove extending to the trigeminal foramen. There is a small depression between the hemicondyles of each quadrate. As can be observed in HUE-02502, both hemicondyles of the quadrates form a well-marked flange in which the smaller and more dorsally extensive medial hemicondyle is directed ventrally (Figs. 2, 3A-B).

The palatines are mediolaterally narrow (Figs. 2C-D and 5C-D). Their lateral margins are subparallel, with a marked change of curvature at their approximate midpoint, which makes the anterior half almost twice wider than the posterior region. The sutures of the palatines with the pterygoids do not reach the posterior margin of the suborbital fenestrae. The rostral process formed by the palatines is acute and extends beyond the anterior margin of the suborbital fenestra (Figs. 2C-D, 5C-D). In the anterior

half of the palatines, marked expansions of the anteromedial margins of suborbital fenestrae are observed (Figs. 2C-D, 5C-D).

The ectopterygoids are robust. Posteriorly, they do not reach the caudal borders of the pterygoid wings (Figs. 2C-D, 5C-D). The ectopterygoid-ptyergoid sutures are slightly curved. The maxillary ectopterygoid rami are anteriorly acute and form the medial borders of the last four maxillary alveoli (Figs. 2C-D, 5C-D). Their participation in the postorbital bar is unclear.

The pterygoids in the holotype are incomplete. The right pterygoid lacks its posteromedial process, while the left one lacks its posterolateral corner (Fig. 2C-D). In HUE-03713, the left pterygoid is broken posteriorly (Fig. 5C-D). In both specimens, the pterygoids are much expanded caudally, and their dorsal surface is nearly flat with modest central concavities. The pterygoids have large lateral wings that almost reach the posterior border of the quadrate condyles. The caudal ends of the pterygoid wings exceed the posterior limit of the posteromedial processes of the pterygoids. The pterygoids are posteriorly expanded (Figs. 2C-D, 5B). The choana is completely surrounded by the pterygoids and is located near the distal margin of these plates. It is circular and projects posteroventrally. The choana is sagittally septate (Figs. 2C-D, 5C-D).

The laterosphenoids of HUE-03713 are covered with sediment, but the right laterosphenoid of HUE-02502 is almost complete. It has a triangular dorsal process and an anteroposteriorly oriented capitate process. Anteriorly, it contacts the postorbital in a region where a marked notch is developed. Longitudinally, each laterosphenoid has a ridge running from the anterior margin of the trigeminal foramen to the middle of the anterior border of the element. The prootics are not visible.

In occipital view, the supraoccipital is wider than tall and has a subtriangular shape (Figs. 3A-B, 5F). A marked sagittal nuchal crest is present posteriorly. The supraoccipital completely surrounds the post-temporal fenestrae, which are transversely elongated. The ventral margins of the post-temporal fenestrae are thickened and posteriorly projected. In dorsal view, the supraoccipital constitutes the posteriormost surface of the medial region of the skull table and contacts the parietal (Figs. 2A-B, 5A-B).

The exoccipitals constitute most of the occipital surface (Figs. 3A-B, 5F). In occipital view, the dorsal halves of the exoccipitals are depressed at their contact areas with the squamosals. The exoccipitals meet above the foramen magnum, forming a prominent posteriorly-projecting shelf along its dorsal margin. The ends of the paroccipital processes are ventrolaterally projected on the dorsal surfaces of the quadrates. They exceed the level of the medial margin of the quadrate condyles. In the medial margin of each exoccipital, near its contact with the basioccipital, several foramina are located: the large foramen vagi, two hypoglossal foramina (XII) located laterally near the foramen vagi; and the more ventrally positioned foramen caroticum posterius (Figs. 3A-B, 5F). In lateral view, the exoccipitals prevent contact between the quadrates and the squamosals on the interior walls of each otic region (Figs. 3C-D, 5E).

The posteroventral region of the basisphenoid can be observed in occipital view, where it contacts the pterygoids along ventromedially directed sutures (Figs. 3A-B, 5F). The basisphenoid comprises the ventral margin of the median Eustachian foramen. Its lateral expansions are hidden below the basioccipital, at the level of the lateral Eustachian foramina. Therefore, the basioccipital contact the pterygoids on both sides of the median eustachian foramina. It is possible to see the basisphenoid rostrum on the right lateral side in HUE-02502. A well-marked foramen, possibly corresponding to

cranial nerves II, III or IV, is preserved on the posterodorsal part of the basisphenoid rostrum in HUE-02502 (Fig. 3A-B).

The basioccipital is a sub-rhomboidal element. It constitutes most of the occipital condyle, which does not have a developed neck (Figs. 3A-B, 5F). The dorsal wall of the condyle forms the ventral margin of the foramen magnum. Several well-marked foramina are recognized in the ventral wall of the occipital condyle of HUE-02502. The basioccipital plate is vertical. It presents two longitudinal ridges ventromedially directed to both sides of the sagittal axis. These ridges reach the ventral margin of the basioccipital plate, where a well-developed sagittal notch is formed, bounding the dorsal margin of the median Eustachian foramen (Figs. 3A-B, 5F). The basioccipital tubera show a marked transverse flange on both sides of this notch.

Lower jaw: The maximum length of the right lower jaw of HUE-02502, from the tip of the retroarticular process to the anterior tip of the dentary, is about 415 mm. Its maximum height, from the ventral margin of the dentary to the posterodorsal rim of the glenoid fossa, is approximately 88 mm (Fig. 4A-F).

The dentary is elongate and forms almost three-quarters of the length of the mandible (Fig. 4A-B). The most anterior part of the dentary forms a short symphysis that reaches posteriorly the level of the fourth alveolus (Fig. 4C-D). It bears seventeen alveoli. Six complete and eleven incomplete teeth are preserved (Fig. 4A-F). The alveoli are well spaced, especially the anteriormost three. The dentary forms two concave waves in lateral view, one from the first to the third alveoli, and the other from the fourth to the eighth (Fig. 4A-B). The largest tooth in the series is the fourth. Behind this, three small alveoli, and a substantial diastema between the seventh and eighth alveoli for reception of the fourth maxillary tooth, are identified. Posterior to the diastema, the dentary forms a convex dorsal wave reaching the tenth alveolus. The tooth row is linear

behind the diastema. In the posterior half of the tooth row, the tenth and eleven alveoli are largest. There are shallow dorsolateral depressions for reception of maxillary teeth from the twelfth through seventeenth alveoli. There are parallel foramina lingually along the whole tooth row (Fig. 4A-D). The entire dentary is heavily vascularized in labial and ventral views (Fig. 4A-D). A longitudinal groove appears parallel to the tooth row in the posterodorsal part of the labial surface (Fig. 4A-B). There is no external mandibular fenestra.

The splenial is smooth. No foramen is observed on its surface (Fig. 4C-D). Its anterior margin is thin and reaches the level of the fourth dentary tooth, without contacting the mandibular symphysis. Due to the presence of the Meckelian groove, the splenial has a bifurcated end. The ventral process of its anterior border is slightly longer than the dorsal process. A shallow elongate depression is present in its medioventral region. Behind this, another smaller and oval-shaped depression is also developed. The dorsal margin of the splenial contributes to the last seven dentary alveoli (Fig. 4C-F). Posteriorly the splenial forms the anterior half of the foramen intermandibularis caudalis (Fig. 4C-D).

The coronoid is crescent-shaped (Fig. 4C-D). Its anterior portion is slightly depressed and surrounds the foramen intermandibularis medius. Its posterior margin has a dorsal notch. This margin constitutes the anterodorsal edge of the mandibular fossa. The almost horizontal posterodorsal margin of the coronoid medially overlaps the splenial (Fig. 4C-D).

The angular extends longitudinally from the posterior tip of the retroarticular process to an acute ventral process at the level of the sixteenth dentary alveolus. This element constitutes almost half the length of the mandibular ventral surface (Fig. 4A-D). Its labial and ventral surfaces are extensively ornamented except in the posterior region,

where this bone is as smooth as its entire lingual surface. The angular forms the posterior half of the foramen intermandibularis caudalis. Its anterior process does not extend dorsally beyond the anterior margin of this foramen (Fig. 4C-D). A shallow, elongate depression is situated below the foramen intermandibularis caudalis, in the ventrolingual region of the angular. A well-developed ridge, which reaches its dorsal margin, is observed in the upper half of its posterior surface.

The long, narrow surangular forms a flat and elongated dorsal shelf extending from the end of the tooth row to the posterior end of the retroarticular process (Fig. 4A-F). Labially, it has two anterior processes surrounding a foramen at the posterior region of the longitudinal posterodorsal groove of the dentary (Fig. 4A-B). The dorsal process is longer than the ventral, and it reaches the posterior margin of the last alveolus, preventing contact between the splenial and dentary. The labial surface of the surangular is profusely ornamented except on the anterior and posterior processes (Fig. 4A-B).

The retroarticular process is high and projects posterodorsally. It is comprised mostly by the articular and its dorsal surface is concave. The foramen aëreum is in the middle area of the anterior margin of the process, but it is not clearly visible. The glenoid fossa is divided by a well-developed longitudinal ridge. The medial face of the articular is concave and has a well-defined posterodorsal foramen on its surface.

Dentition: There are four premaxillary teeth, fifteen maxillary teeth, and seventeen dentary teeth. The fourth tooth is largest both in the maxilla and the dentary. A pit is present on the maxilla, between the seventh and eighth alveoli, where the eleventh dentary tooth occludes. Other dentary teeth occlude lingual to the maxillary tooth row. All preserved teeth are conical, sharp, and with short crowns. They have two

longitudinal mesiodistal carinae dividing the crown into a flat lingual facet and a larger and slightly concave labial facet. The enamel is unornamented.

Cervical vertebra: A strongly procoelous vertebra is identified on the back of the left half of the skull of the holotype between the quadrate and the pterygoid (Fig. 3A-B). Few informative characters can be recognized. It is approximately 40 mm in length and 80 mm in height. Its centrum is slightly taller than wide, and it is twice as long as tall. The body is laterally compressed. In the rear region of the centrum, the condyle bears a prominent cotyle. The neural arch cannot be observed. The neural spine is high, but the top is hidden by the left ectopterygoid. The parapophyseal facets are ventrally displaced with respect to the transverse processes. The ventral surface of the centrum is rostrocaudally keeled and bears a well-developed hypapophysis.

Agaresuchus subjuniperus comb. nov.

Holotype. MPZ 2012/288, a nearly complete skull.

Locality and horizon. Municipality of Beranuy, near the village of Serraduy del Pon, Huesca Province, Aragón, northeastern Spain. Conqués Formation, Tremp Group, Upper Cretaceous (upper Maastrichtian; Puértolas-Pascual et al., 2014).

Emended diagnosis. A species of *Agaresuchus* differing from *Ag. fontisensis* by: relatively short and rounded snout; fourteen maxillary alveoli; absence of occlusion pits between seventh and eighth maxillary teeth; premaxillae wider than long; drop-shaped incisive foramen (exclusive for *Ag. subjuniperus*); expanded lateral margins of the nasals in their middle area (exclusive for *Ag. subjuniperus*); presence of a posterior

process of the nasals between the frontal and the prefrontals; main axis of the dorsal surface of the prefrontals converge anteriorly; wide frontal and broad interorbital space (exclusive for *Ag. subjuniperus*); small, crescent-shaped, obliquely oriented orbits; unseptate choana; quadratojugal alone comprises the posterolateral corner of the infratemporal fenestra; absence of lateral projections of the anterior half of the palatines into the suborbital fenestrae; rounded anterior palatine process.

Description. See Puértolas-Pascual et al. (2014).

4. Discussion

4.1. Identification of Agaresuchus as an allodaposuchid and comparison with the other members of this clade

Agaresuchus is a member of Allodaposuchidae (see Narváez et al., 2015) based on the presence of shallow fossae at the anteromedial corners of the supratemporal fenestrae; the tenth alveolus is the largest behind the fourth in the dentary tooth row (not known in *Ag. subjuniperus*); broad cranioquadrate passages, represented by laterally-open sulci, without defined posterior margins of the otic apertures, and without quadrate-squamosal contact posterior to the external otic aperture; presence of tubercles on the ventrolateral margin of the paraoccipital processes (not known in *Ag. subjuniperus*); absence of external mandibular fenestrae (not known in *Ag. subjuniperus* and shared by other basal member of Eusuchia as hylaeochampsids and paralligatorids, and derived neosuchians); notches for reception of the fourth dentary teeth between the premaxillae and the maxillae; maxillae excluded from the lower temporal bars; anterior

tip of the frontals constituting a simple acute point; lacrimals larger than prefrontals; nearly horizontal skull table, with significant posterolateral squamosal rami along the paroccipital processes; wide suborbital fenestrae; lack of protuberances in the ventral surface of the quadrate rami; presence of prominent quadratojugal spines; quadrate rami extending beyond the level of the occipital condyles; upturned dorsal edges of the orbits; dermal bones of the skull roof overhanging the rim of the supratemporal fenestrae; quadrate foramen aëreum on the dorsal surface of the quadrates; and festooned dorsolateral surface of the dentary, describing two concave waves (not known in *Ag. subjuniperus*).

The new allodaposuchid, *Agaresuchus*, is not only characterized by several autapomorphies, but also by an exclusive combination of characters. *Agaresuchus* bears four premaxillary teeth. Among allodaposuchids, only the left premaxilla of *Allodaposuchus hulki* and the holotype of *Lohuecosuchus megadontos* share this feature. However, the other two known skulls of *Lohuecosuchus megadontos* (i.e. some of the paratypes) bear five alveoli in each ramus. Therefore, this character is variable in *Lohuecosuchus*. Other allodaposuchids bear five premaxillary teeth.

However, this character can also vary ontogenetically in most living crocodylians. The small second premaxillary alveolus is often allometrically crowded out by the much larger first or third alveoli; only *Paleosuchus* among living crocodylians has four premaxillary alveoli throughout ontogeny (Mook, 1921; Kälin, 1933). Discovery of very small specimens of *Agaresuchus* will allow us to test use of a four-toothed premaxilla as diagnostic for the lineage.

While the incisive foramen of *Agaresuchus* is near the premaxillo-maxillary suture, a substantial space between the posterior margin of the incisive foramen and the

maxilla is present in all other allodaposuchids. This argues against the suggestion that this morphology is pathological in *Agaresuchus subjuniperus* (Martin et al., 2015).

As mentioned, the naris of *Agaresuchus* is dorsally oriented. The nares of other allodaposuchids (and of most other non-crocodylian eusuchians) are oriented anterodorsally. Dorsal narial projection also arose multiple times in Crocodylia.

The anterior process of the frontals in *Agaresuchus* extends beyond the anterior margin of the prefrontals. This feature is also present in *Arenysuchus gascabadiolorum* and *Lohuecosuchus mechinorum*.

The nasals of *Agaresuchus fontisensis* do not project between the frontal and the prefrontals. The nature of this feature is unknown in *Ag. subjuniperus*. This character is not shared with the other members of Allodaposuchidae.

The postorbital bar of *Agaresuchus* is massive, a character only shared with *Lohuecosuchus mechinorum* within Allodaposuchidae, and with hylaeochampsids, gavialoids and some few crocodyloids within Eusuchia. Robust postorbital bars are probably plesiomorphic for Eusuchia with reductions to a more slender element arising independently (and possibly with reversals to a more robust bar in slender-snouted crocodylians, depending on how the gharials are related to each other).

Agaresuchus shares with *Arenysuchus gascabadiolorum* a larger number of maxillary alveoli compared to other allodaposuchids, relatively small teeth, and wider interalveolar spaces between them. On the other hand, *Ag. fontisensis* has the largest number of dentary alveoli –seventeen– among allodaposuchids. The dentary is unknown for *Ag. subjuniperus*. Some *Lohuecosuchus megadontos* dentaries have fourteen alveoli, and others have fifteen. *Massaliasuchus affuvelensis* has fifteen, and *Musturzabalsuchus buffetauti* and the allodaposuchid from Velaux-La Bastide Neuve have sixteen.

The choana of the only species of *Agaresuchus* where this element is known, *Ag. fontisensis*, is sagittally septate. This feature is similar to that of the allodaposuchid from Velaux-La Bastide Neuve, while other known allodaposuchids lack a choanal septum. Choanal septa appear in some neosuchians as *Theriosuchus pusillus*, *Goniopholis simus*, *Bernissartia fagesii* and *Isisfordia duncani*, as well as some crocodylians such as *Boverisuchus vorax*, *Borealosuchus*, and many alligatoroids and crocodyloids.

Dorsal supraoccipital exposure in *Agaresuchus* (only known in the dorsal view of the skull table of *Ag. fontisensis*) is similar to that of *L. mechinorum* and *Al. precedens* (based on the specimen from Oarda de Jos), but with a less development than in the holotype of *Al. precedens*.

The dorsal surface of the dentary in *Agaresuchus fontisensis* describes two well-developed concave waves. However these waves are not as marked as in the paratypes of *Musturzabalsuchus*, the now-lost jaw of *Massaliasuchus* (see Matheron, 1869), or the dentary of the allodaposuchid from Velaux-La Bastide Neuve (based on Martin et al., 2015). Curvature of the dorsal surface of the dentary in *Agaresuchus* is less pronounced than in *Musturzabalsuchus* and *Massaliasuchus*. The dorsal surface of the ninth mandibular alveolus of *Agaresuchus* is posteriorly roughly flat compared with *Musturzabalsuchus* and *Massaliasuchus*.

All defined Iberoarmoric an allodaposuchids differ from Romanian *Allodaposuchus precedens* (the only known representative of *Allodaposuchus*). The Iberoarmoric an forms are characterized by the presence of a notch between the premaxilla and the maxilla for reception of the fourth mandibular tooth; the presence of a small medial jugal foramen (except in the allodaposuchid from Velaux-La Bastide Neuve); and the non-linear dental occlusion pattern. These differences confirm the restriction of *Allodaposuchus* to specimens from eastern Europe (Narváez et al., 2015).

4.2. Comparison between the species of *Agaresuchus*

Puértolas-Pascual et al. (2014) diagnosed *Agaresuchus subjuniperus* (as *Allodaposuchus subjuniperus*) with the following autapomorphies: wide and short premaxillae; small teardrop-shaped incisive foramen, almost reaching the premaxillo-maxillary suture; wide, rounded, leaf-shaped nasals, with gradual lateral expansion; small, crescent-shaped, obliquely oriented orbits; and extremely wide frontal. Both the position of the incisive foramen in relation to the premaxillo-maxillary suture and the projection of the nares are shared between *Ag. subjuniperus* and the new species *Ag. fontisensis* and can be viewed as diagnostic of *Agaresuchus*. The size of the premaxillae clearly differs between the two species of *Agaresuchus*; as indicated by Puértolas-Pascual et al. (2014), the premaxillae of *Ag. subjuniperus* are short and wide, forming a rounded snout. *Agaresuchus fontisensis* premaxillae are longer than wide, leading to an elongate snout, similar to that recognized in *Arenysuchus gascabadiolorum*.

The incisive foramen is drop-shaped in *Ag. subjuniperus* (exclusive within Allodaposuchidae) and almond-shaped in *Ag. fontisensis*. The nasals of both *Agaresuchus* species differ; *Ag. subjuniperus* has a leaf-shaped nasals, and they are centrally laterally widened much more than in any other allodaposuchid. On the other hand, *Ag. fontisensis* shares with other allodaposuchids the presence of parallel lateral nasal margins. The nasals of both species of *Agaresuchus* are more elongate and thinner than those of other members of this clade.

The relative size of the orbits of *Ag. subjuniperus* is smaller than that of *Ag. fontisensis* and other allodaposuchids. In addition, *Ag. subjuniperus* possesses a larger interorbital space than any other allodaposuchid.

Furthermore, Puértolas-Pascual et al. (2014) included in the diagnosis of *Ag. subjuniperus* the following unambiguous autapomorphies: massive postorbital bar; almond-shaped naris, longer than wide and dorsally oriented; premaxillae with four teeth; and large maxillary foramen for palatine ramus of cranial nerve V. The massive postorbital bar (shared with *Lohuecosuchus mechinorum*), the dorsal projection of the nares and the presence of four premaxillary teeth (shared with *Allodaposuchus hulki*) are present in both species of *Agaresuchus*. The presence of rounded, non-separate nares contacting the nasals is shared with all allodaposuchids.

Finally, Puértolas-Pascual et al. (2014) characterized the maxillary foramen for the palatine ramus of cranial nerve V of *Ag. subjuniperus* as large. Although *Ag. subjuniperus* shows a well-marked foramen in the palatal surface, at the level of the eighth alveolus, this element does not reach the dimensions of the foramina in some crocodyloid taxa as *Asiatosuchus germanicus*, *Prodiplocynodon langi*, *Crocodylus affinis* or *Crocodylus depressifrons*. In fact, it is a relatively small foramen, as that present in all the allodaposuchids.

Furthermore, *Ag. fontisensis* does not show a large lacrimal-nasal contact as in *L. megadontos*, *L. mechinorum* or *Ag. subjuniperus*. It is short as in *Allodaposuchus precedens* from Oarda de Jos.

The position of the quadratojugal-jugal sutures differs in both species of *Agaresuchus*. In *Ag. fontisensis*, these sutures form the posterolateral corners of the infratemporal fenestrae, as in *L. megadontos*. This character is only shared by a few eusuchians such as *Deinosuchus riograndensis* and some crocodyloids. The quadratojugals of *Ag. subjuniperus* and other allodaposuchids form the posterior corners of the infratemporal fenestrae. This feature is common in most lineages of Eusuchia.

Agaresuchus fontisensis has a lingual occlusion between the maxillae and the jaws, with the presence of several occlusion pits between the sixth and the seventh, seventh and eighth, and eighth and ninth maxillary alveoli. Within Allodaposuchidae, this kind of occlusion only appears in the specimens of Velaux-La Bastide Neuve, being less pronounced. Moreover, this character is very uncommon within Eusuchia, and only appears in some representatives of several groups that conforms the lineage, as *Borealosuchus*, *Planocrania hengdongensis* in planocraniids, *Diplocynodon hantoniensis* and some caimanines in Alligatoroidea, and some species of *Crocodylus* in Crocodyloidea. The occlusion pattern in *Ag. subjuniperus* is lingual, as in *Lohuecosuchus megadontos*, with absence of occlusion pits.

Agaresuchus fontisensis bears fifteen alveoli in its maxillary tooth row, a similar number as that tentatively interpreted for *Arenysuchus gascabadiolorum*, and one more than that in *Ag. subjuniperus* and *Allodaposuchus precedens* (based in the specimen from Oarda de Jos).

Agaresuchus fontisensis shares with *Allodaposuchus precedens* and *Arenysuchus gascabadiolorum* an anterior process of each lacrimal, located between the maxilla and the nasal. This is absent in *Ag. subjuniperus* and *Lohuecosuchus*.

The anterior half of the palatines of *Ag. fontisensis* projects laterally into the suborbital fenestrae. This character is not present in any other allodaposuchid, and it is irregularly distributed within Eusuchia. It is present in *Borealosuchus*, in some alligatoroids such as *Leidyosuchus*, *Diplocynodon muelleri*, *Alligator olseni*, *Paleosuchus*, and in some crocodyloids such as *Osteolaemus tetraspis* and *Voay robustus*.

The anterior processes of the palatines in *Ag. fontisensis* are wide, as is common in allodaposuchids, but are rostrally pointed, with a unique morphology within the

clade. Anteriorly, the tip of each process reaches the level of anterior margin of the suborbital fenestrae, without extending significantly beyond the margins. The anterior palatine processes in *Ag. subjuniperus* are wide and rounded, extending significantly beyond the anterior margins of the suborbital fenestrae.

4.3. Results of the phylogenetic analysis

The analysis performed here recovered 2161 most parsimonious trees of 780 evolutionary steps, with a consistency index (CI) of 0.314 and a retention index (RI) of 0.790. The topology of the strict consensus tree (Fig. 6) is very similar to that obtained by Narváez et al. (2015), although there are some differences relative to the base of Eusuchia. The obtained strict consensus shows a more derived position for Allodaposuchidae as the sister group of Crocodylia. The monophyletic clade composed by *Pachycheilosuchus*, *Shamosuchus*, *Pietraroiasuchus*, *Acynodon*, *Iharkutosuchus* and *Hylaeochampsia* (Hylaeochampsidae sensu Buscalioni et al., 2011) constitutes the sister taxa of Allodaposuchidae + Crocodylia. Thus, *Pietraroiasuchus*, *Pachycheilosuchus* and *Shamosuchus* are placed as eusuchians, a position suggested in several previous phylogenetic analysis (Buscalioni et al., 2011; Turner, 2015).

In this analysis, Eusuchia is supported by the presence of procoelous presacral vertebral centra (character 21, state 1), a wide and rounded olecranon process of the ulna (character 29, state 1), non-septate choanae (character 125, state 0), and thin and rod-like posterior cervical neural spines (character 189, state 1).

The clade formed by allodaposuchids and crocodylians is supported by the presence of a posterodorsally projected retroarticular process (character 71, state 1); presence of a sulcus between the articular and the surangular (character 74, state 0); a palatine-

pterygoid suture far from the posterior angle of the suborbital fenestra (character 118, state 1); choana entirely surrounded by the pterygoids (character 121, state 1); anterior tip of the frontal forming a simple acute point (character 131, state 0); mature skull with nearly horizontal sides and significant posterolateral squamosal rami along the paroccipital process (character 158, state 1); and posteriorly oriented external surface of the basioccipital ventral to the occipital condyle at maturity (character 170, state 1).

Allodaposuchidae is supported by the presence of nasals contacting external naris, but not bisecting it (character 82, state 1); the fourth maxillary alveolus being the largest in the tooth row (character 93, state 2); upturned dorsal edges of the orbits (character 137, state 1); caudal margin of the otic aperture not defined and gradually merging into the exoccipital (character 149, state 0); linear frontoparietal suture between the supratemporal fenestrae (character 151, state 1); and dermal bones of the skull roof overhanging the rim of the supratemporal fenestra (character 152, state 1).

Within Allodaposuchidae, *Allodaposuchus precedens* is diagnosed here by the presence of a very large medial jugal foramen (character 102, state 1); and anteroposteriorly wide basisphenoid ventral to the basioccipital (character 172, state 1). The other members of Allodaposuchidae are grouped in a clade supported by the presence of a basisphenoid exposed as a broad sheet ventral to the basioccipital, the pterygoid being tall ventral to the median Eustachian opening (character 173, state 0). *Arenysuchus gascabadiolorum* is supported by the presence of a skull table with broad curvature and short posterolateral squamosal rami along paroccipital process (character 158, state 0).

Lohuecosuchus and *Agaresuchus* are placed in a clade diagnosed by the presence of a lateral carotid foramen which opens dorsal to the basisphenoid (character 169, state 1). *Lohuecosuchus* is supported by a naris wider than long (character 83, state 1),

prominent preorbital ridges (character 97, state 1), and a straight pterygoid ramus of the ectopterygoid, resulting in a linear posterolateral margin of the suborbital fenestra (character 119, state 0). *Lohuecosuchus mechinorum* is diagnosed by the presence of a basisphenoid not broadly exposed ventral to the basioccipital, the pterygoid being short ventral to the median Eustachian opening (character 173, state 1); and a maxillo-palatine suture that intersects suborbital fenestra nearly at its anteriormost limit (character 187, state 1). *Lohuecosuchus megadontos* is supported by the presence of deep notch lateral to the naris (character 86, state 1), prominent canthi rostralii (character 96, state 1), and quadratojugal-jugal suture forming the posterior angle of infratemporal fenestra (character 142, state 2).

Agaresuchus is supported by the dorsal projection of the nares (character 81, state 1) and the presence of only four premaxillary teeth (character 87, state 1). *Agaresuchus. subjuniperus* is distinguished by a maxillo-palatine suture that intersects suborbital fenestra nearly at its anteriormost limit (character 187, state 1). *Agaresuchus fontisensis* is diagnosed by a lingual occlusion pattern with the presence of pits between seventh and eighth maxillary teeth (character 92, state 1); lateral projections of the edges of palatines into suborbital fenestrae (character 117, state 1); and the quadratojugal-jugal suture forming the posterior angle of infratemporal fenestra (character 142, state 2).

5. Conclusions

Study of the eusuchian crocodyliforms from the Upper Cretaceous fossil site of Lo Hueco (Cuenca, Spain) confirms the existence of two different species: *Lohuecosuchus megadontos* Narváez et al., 2015 and *Agaresuchus fontisensis* described here. These two

eusuchians allow a review of the phylogenetic position of several European Campanian-Maastrichtian specimens. As suggested by Narváez et al. (2015), the genus *Allodaposuchus* should be restricted to specimens from central and eastern Europe (Nopcsa, 1928; Delfino et al., 2008), while both in the Iberian Peninsula and in southern France, allodaposuchid specimens are identified as members of a clade. Thus, a vicariant distribution pattern, like that recognized for other European Late Cretaceous vertebrate clades (Le Loeuff, 1991; Pereda-Suberbiola, 2009; Weishampel et al., 2010; Csiki-Sava et al., 2015), is identified for this lineage of crocodiles.

In addition, the phylogenetic analysis reveals a more derived position for Allodaposuchidae than that proposed by Narváez et al. (2015). This clade is here supported as the sister group of Crocodylia. The lineage including Hylaeochampsidae is obtained as the most basal clade within Eusuchia, but an in-depth review of this group is necessary in order to clarify the phylogenetic position of *Pietraroiasuchus*, *Pachycheilosuchus* and *Shamosuchus*.

The study of *Ag. fontisensis* has allowed attribution of another species to *Agaresuchus*: *Allodaposuchus subjuniperus* (Puértolas-Pascual et al, 2014).

On the other hand, the description of a new eusuchian member belonging to Allodaposuchidae in Lo Hueco allows recognition for the first time of the synchronic and sympatric existence of two representatives of this clade. Therefore, the allocation of fragmentary material found in a single locality or area to the same taxon must be considered with caution.

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Figure captions

Fig 1. Geographic location of the sites where the European crocodyliform *Agaresuchus* gen. nov. has been identified. Lo Hueco (Cuenca, Spain), type locality of *Agaresuchus*

fontisensis sp. nov.; and Beranuy (Huesca, Spain), type locality of *Agaresuchus subjuniperus* comb. nov.

Fig 2. Skull HUE-02502, holotype of *Agaresuchus fontisensis* gen. et sp. nov., from the upper Campanian-lower Maastrichtian site of Lo Hueco (Cuenca, Spain). (A, B) Dorsal views. (C, D) Ventral views. A and C, photographs of the specimen. B and D, interpretative drawings. Sutures are figured with plain lines. The dashed lines represent tentatively reconstructed sutures. The lined areas represent broken bones.

Fig 3. Skull HUE-02502, holotype of *Agaresuchus fontisensis* gen. et sp. nov., from the upper Campanian-lower Maastrichtian site of Lo Hueco (Cuenca, Spain). (A, B) Posterior views. (C, D) Lateral views. A and C, photographs of the specimen. B and D, interpretative drawings. Sutures are figured with plain lines. The dashed lines represent tentatively reconstructed sutures. The lined areas represent broken bones.

Fig 4. Right jaw HUE-02502, holotype of *Agaresuchus fontisensis* gen. et sp. nov., from the upper Campanian-lower Maastrichtian site of Lo Hueco (Cuenca, Spain). (A, B) Lateral views. (C, D) Medial views. (E, F) Dorsal views. A, C and E, photographs of the specimen. B, D and F, interpretative drawings. Sutures are figured with plain lines. The dashed lines represent tentatively reconstructed sutures. The lined areas represent broken bones.

Fig 5. Skull HUE-03713, paratype of *Agaresuchus fontisensis* gen. et sp. nov., from the upper Campanian-lower Maastrichtian site of Lo Hueco (Cuenca, Spain). (A, B) Dorsal views. (C, D) Ventral views. (E) Lateral view. (F) Posterior view. A, C, E and F,

photographs of the specimen. B and D, interpretative drawings. Sutures are figured with plain lines. The dashed lines represent tentatively reconstructed sutures. The lined areas represent broken bones.

Fig 6. Calibrated cladogram corresponding to the strict consensus tree obtained in the phylogenetic analysis. The black rectangles represent the stratigraphic distribution of each taxon. Numbers at nodes indicate bootstrap frequencies over 50%, and Bremer support, over 2 (in parentheses).

Appendices

A. Data Matrix (TNT).

B. List of several measurements of the skull of the holotypes of the two known species of *Agaresuchus*, HUE-02502 (*A. fontisensis*) and MPZ 2012/288 (*A. subjuniperus*) (modified from Puértolas-Pascual et al., 2014).

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

Figure 6