European Goniopholididae from the Early Albian Escucha Formation in Ariño (Teruel, Aragón, Spain)

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ABSTRACT

Although goniopholidids constitute the most abundant remains of the Lower Cretaceous record of the Iberian Peninsula crocodilians, few specimens have been found complete enough to provide precise taxonomic determinations. The palaeontological site of Mina Santa María in Ariño (Teruel, Early Albian Escucha Formation) has yielded several neosuchian monotaxic concentrations. The skulls discovered at the Ariño Mine show a character combination linking them to the latter European species. The Ariño skulls share apomorphies with Anteophthalmosuchus hooleyi, Goniopholis willetti (e.g., loss of the transverse frontal crest and of the prefrontal-lachrymal crest, supratemporal fossa larger than the orbit and supratemporal fenestra subequal, among other derived characters). The new taxa, Hulkepholis plotos gen. n., sp. n. and Anteophthalmosuchus escuchae sp. n., are herein erected, and they constitute the most recent record of their

RESUMEN

A pesar de que los restos de goniofolídidos son los más abundantes del registro de cocodrilos del Cretácico Inferior de la Península Ibérica, pocos ejemplares se han descubierto lo suficientemente completos como para proporcionar determinaciones taxonómicas precisas. Las concentraciones monotáxicas de cocodrilos neosuquios descubiertas en la Mina Santa María de Ariño (Teruel, Albiense Temprano de la Formación Escucha) han proporcionado restos craneales, cuya combinación de caracteres los vincula con el clado de los Goniopholididae temporalmente más modernos. Las apomorfias compartidas (ausencia de cresta prefronto-lacrimal y de cresta frontal interorbitaria; fenestra supratemporal subigual a la órbita, siendo las fosas mucho mayores en diámetro, entre otros caracteres derivados) permiten caracterizar los dos nuevos táxones: Hulkepholis plotos gen. n., sp. n. y Anteophthalmosuchus escuchae sp.
clade in Europe. These sympatric species lived in a coastal marsh system with barrier islands and lagoon.

**Keywords**: Neosuchia, Goniopholididae, Lower Albian, Oliete sub-basin, Maestrazgo basin, Iberian Peninsula, palaeobiogeography.

1. INTRODUCTION

The goniopholidid neosuchians are one of the most common taxa of the crocodylomorph Mesozoic European record. Goniopholid-like teeth and osteoderms are dominant elements in fossil assemblages of continental lacustrine, fluviolacustrine, fluvial, freshwater lagoon to shallow offshore environments from Western Europe (Schwarz, 2002; Pouech, 2008; Salisbury & Naish, 2011). The goniopholidid Iberian record follows this same trend (see Buscalioni, 1986a, 1986b for a historical perspective) and members of the family have been identified in the Kimeridgian of the Alcobaça Formation (Portugal) (Crespo, 2002; Schwarz, 2002), and throughout the Berriasian to Upper Barremian/Aptian Formations of different Iberian basins: Cameros (Urbión, Golmayo, Castrillo de la Reina and Pinilla de los Moros Formations; Buscalioni, 1986b; Ortega et al., 1996; Fuentes-Vidarte et al., 2003), Maestrazgo (El Castellar, Camarillas, Artoles, Arcillas de Morella, and Forcall Formations; Buscalioni, 1986a; Buscalioni & Sanz, 1987; Cuenca-Bescós et al., 1999; Ruiz-Omeñaca et al., 2004; Sánchez-Hernández et al., 2007; Sastre García, 2007; Gasulla et al., 2011) and in the south Iberian sub-basin (La Huérguina Formation; Brinkmann, 1992; Buscalioni et al., 2008). However, despite its abundance, this material is fragmentary and composed by isolated, non diagnostic elements. Few Iberian specimens preserving skull elements have provided solid diagnoses as the Guimarota species *Goniopholis baryglyphaeus* (Schwarz, 2002), while others were tentatively attributed to *Goniopholis* sp. (Ortega et al., 1996), *Goniopholis cf. simus* (Buscalioni, 1986a, 1986b), and *Goniopholis cf. crassiden* (Buscalioni, 1986b; Buscalioni & Sanz, 1987) (Fig. 1).

Here we present the first evidence of complete articulated goniopholidid skulls from Early Albian Escucha Formation discovered in the locality of Mina Santa María in Ariño (Teruel, Aragón, Spain). The Ariño locality has yielded a rich vertebrate assemblage in which archosaurs are the most abundant fossils (Alcalá et al., 2012). Other isolated goniopholidid elements, of similar age (Lower Albian), have been reported at the nearby locality of Corta Barrabasa (Andorra, Teruel) (Puértolas-Pascual et al., 2012).

A taxonomic revision of the family Goniopholididae has been taking long process since the taxon was erected by Cope in 1875 based on the description of the British Purbeck crocodilian assemblages by Owen in 1842. The legate of an overflowing number of *Goniopholis* species (i.e., 22 according to Steel, 1973) was corrected by Salisbury et al. (1999), Salisbury (2002) and recently by Salisbury & Naish (2011), Andrade & Hornung (2011) and Andrade et al. (2011). Recent detailed descriptions on the European goniopholidids have revealed that this clade show a higher diversity than previously supposed (Andrade et al., 2011). Two clades have been proposed, one gathering species of the genus *Goniopholis* (*G. simus*, *G. kiplingi* and *G. baryglyphaeus*) and an unnamed clade in which the upper Barremian to Aptian goniopholidids were assembled. This last clade is defined by three terminal taxa: “Dollo-specimen”, “Hulke-specimen” and “Hooley-specimen”. In the revision of the taxonomic status of the crocodilians of the southern England Wealden Supergroup by Salisbury & Naish (2011), the authors erected the new species *Goniopholis willetti* for the “Hulke-specimen”, and the genus *Anteophthalmosuchus* for the “Hooley-specimen” (*A. hooleyi*). The “Dollo-specimen” has no formal denomination yet. The erection of the scientific name of *G. willetti*, preceding the phylogenetic revision of the family according to Andrade et al. (2011), has resulted in a paraphyletic *Goniopholis* grouping. This situation should be corrected in further analyses testing the phylogenetic definition of *Goniopholis* and its sister clade within Goniopholididae on the light of the new discoveries.

Latter contributions have provided a more complex scenario on the goniopholidid diversity. The Ariño assemblage renders crucial in the understanding of the European goniopholid diversity and biostratigraphic extension during the “mid” Cretaceous. We present a
Figure 1. Goniopholididae from the Iberian Peninsula. Their chronostratigraphic record comprises the Kimmeridgian (K), Berriasian (B), Barremian (Ba), Aptian (Ap) and Early Albian (Al). Localities and taxonomic attributions are specified below each specimen. **a)** *Goniopholis baryglyphaeus* (Schwarz, 2002), in ventral view. **b)** The Berriasian *Goniopholis* sp. from Cameros (Ortega et al., 1996), in ventral view. In the Cameros specimen the lanceolate and wide choana resembles that of *G. kiplingi* and *G. simus*, differing from the long and narrow choana of the Ariño specimens. The premaxillo-maxillary suture has a W-shape different to *G. simus*; and the size of premaxillary teeth (in which the third and fourth are the largest) is similar to *G. kiplingi* and *G. baryglyphaeus* differing in this feature from the Ariño specimen. **c)** Skull material from Galve (Cabezo Santa Bárbara and Rocha-Pelejón, both Lower Barremian in age; Díaz Molina & Yébenes, 1987). On top, maxillary fragment from the Rocha-Pelejón (RPAH-203), in ventral view. The attribution to *G. cf. crassidens* (synonymous of *G. simus*, Salisbury, 2002) was based on its wide rostral proportion. On bottom, a skull table in dorsal view from the Cabezo Santa Bárbara (CBP-835) specimen. It was attributed to *cf. Goniopholis* sp. since the comparison with *G. simus* and *G. crassidens* was not definitive (Buscalioni & Sanz, 1987). **d)** The Aptian specimen from Castellón (Forcall Formation) (MSB-ref. 39484) attributed to *G. cf. simus* is based on the scarce rostral ornamentation, the presence of interorbital crest, and the configuration of the sutures between nasal, lachrymal, prefrontal and frontal. The preorbital area shows: the frontal with a truncated anterior-most tip; narrow anterior prefrontal process; and widen lachrymal and jugal. Note: see text for abbreviations.
preliminary taxonomic determination of three skulls discovered at Ariño. These skulls comprise the sole well preserved material that can be compared with the Wessex (southern England) and Bernissart (Belgium) type species of Goniopholis and Anteophthalmosuchus.

2. MATERIAL AND PRESERVATION

The palaeontological research project carried out in a partnership with the mining company SAMCA has identified a Lower Cretaceous outcrop with outstanding bone concentrations of vertebrate fossils from the Early Albian Escucha Formation. These mining operations have exposed an extensive area (15 ha) of a vertebrate bearing stratum that permitting an extensive, ongoing palaeontological salvage program of potentially great significance. The excavations at Mina Santa María, Ariño (Teruel, Spain) are performed following a single fossiliferous level (AR-1) where numerous individualized bone concentrations have been mapped. The site, dated Lower Albian (Alcalá et al., 2012; Tibert et al., in press) is placed at the Middle Interval with Coal, Lower Sedimentary Succession, Escucha Formation, according to Rodriguez-López et al. (2009). A preliminary examination of the more than five thousand identifiable vertebrate fossils recovered by the end of year 2012 has allowed us to identify numerous species of vertebrates, specifically dinosaurs (including a new genus and species of ornithopod – Proa valdearinnoensis [McDonald et al., 2012]-, thyreophorans and theropods), turtles, crocodiles and fishes (both bony and cartilaginous), as well as coprolites, plant remains (logs, plant fragments, palynomorphs, amber), bivalves, gastropods and ostracods (Alcalá et al., 2012).

Although the age and genesis of the classic locality of Bernissart (Belgium) and Ariño are not comparable, fossil preservation shares some similarities associated with pyrite oxidations. The high proportion of iron bisulphide microcrystals in Ariño’s fossils, and its instability (even in humid depressed conditions) will affect their integrity in short-term. In fact, the mechanisms directly or indirectly linked to the pyrite oxidation are often responsible for the bursting of the bone structure, having a disastrous effect on bone conservation (Leduc, 2012). The safeguarding techniques tested in Bernissart fossils have proven to be inefficient to prevent the destructive processes, but in some cases they have partially slowed them down (Leduc, 2012).

Ariño’s vertebrates follow two types of taphonomic assemblages: 1) as disperse elements all over the fossiliferous layer. Here, crocodylian osteoderms and turtle scutes result the most common elements; and 2) as monotaxic (occasionally bitaxic) concentrations of articulated or semi-articulated fossils. This taphonomic pattern is recurrent and homogeneous in the sampled horizon AR-1 (Fig. 2). The crocodyliform assemblage is the most frequent (66% of the concentrations found), with 23% of the sampled crocodyliform concentrations composed by postcranial and cranial remains. Crocodyliforms were found associated with turtles mostly (36 cases of 64 assemblages), or phytophagous dinosaurs (14 cases), or carnivorous dinosaurs (11 cases).

The studied goniopholidid assemblage is composed by cranial and postcranial elements. The concentration #62 is composed by a skull lacking premaxillae (AR-1-3422), and by two dentary fragments (AR-1-3423 and AR-1-4676) from the same individual. The concentration is also composed by postcranial isolated elements, such as paramedial not keeled osteoderms (subrectangular in shape, wider than longer, with a flat strongly ornamented dorsal surface bearing a strong anterolateral projection); amphicoelous vertebrae (centra with a neat and wide neurocentral suture, and a medially compressed body); and appendicular elements (girdle and limb fragments). AR-1-3422 is dorsoventrally compressed and laterally sheared; it bears a biting mark at the maxilla. The concentration #56 is composed by a completely articulated skull (AR-1-2045), lacking the mandible. The skull is distorted; bones are inwardly curved with important cracks at the ventral and occipital regions. The concentration #37 corresponds to a partial articulated skull (AR-1-1097) divided in two parts, maxilla and skull table. Other disarticulated skull elements are a left quadrate and a posterior fragment of the right mandible. The skull preserves sutural details but it is dorsoventrally compressed.

In the studied material there is any evidence of bone abrasion and erosion, indicating that carcasses were produced close where they were buried (autochthonous). However, skeletal disarticulations including skull detaching suggest at least a short subarial exposure previous to burial enhancing disintegration and disarticulation. In accordance with their habitat these palaeobiological entities should be considered demic (i.e., living in the ecosystem were they were produced).

2.1. Abbreviations

Institutional abbreviations: AR, Ariño collection housed at Museo Aragonés de Paleontología (Fundación Conunto Paleontológico de Teruel-Dinópolis) in Teruel; BMNH, British Museum Natural History, London; IRSNB, Institut Royal des Sciences Naturelles de Belgique, RPAH, Rocha Pelejón, Herrero collection in Galve; CBP, Cabezo Santa Bárbara, Universidad Autónoma Unidad de Paleontología collection; MSB, Museo del Seminario de Barcelona.

Anatomical abbreviations: A-B, quadrate crests; an, angular; bo, basioccipital; bsp, basisphenoid; con occ, condyle occipital; cpp, craniaquadrate passage; co, choana; de, dentary; dmx, maxillary depression; ect, ectopterygoid;
3. THE ARIÑO GONIOPHOLIDIDAE ASSEMBLAGE

The revision on the phylogenetic relationships of the family Goniopholididae including a significant number of species of Mesoeucrocodylia has provided details on the character definitions and their evolutionary transformations (Andrade et al., 2011). The European Goniopholididae consists of two clades, one relates the species of the genus Goniopholis (G. simus, G. kiplingi and G. baryglyphaeus) while the other clade comprises stratigraphically the latest (Late Barremian to Aptian) goniopholidids, uniting “Dollo’s” + “Hooley’s” specimens as sister group to the “Hulke-specimen”. Each major clade is rather well...
supported by a set of unambiguous apomorphies. The three skulls from Ariño show the characteristic combination of features diagnostic of the family Goniopholididae, of which the presence of a maxillary fossa, formed by a depressed lobulated area at the level of the maxilla, jugal and lachrymal, is a clear autapomorphy. More specifically, the individuals share the apomorphies that diagnoses the triad of the latest European goniopholidids: the loss of prefrontal-lachrymal crest dorsal to the orbit, and of the transverse frontal crest; the supratemporal fenestra is subequal to the orbit, whereas the fossa is larger than the orbit; lateral process of the frontal arched laterodorsally with palpebral and postorbital curved dorsally; posterior ramus of jugal subcircular to subpolygonal in cross section; ventral margin of the jugal level with the posterior ramus; palatal ramus of maxilla takes part in the anteromedial border of suborbital fenestra; the anterior palatine process of palate is evidently longer than wider.

Recent osteological revisions on the European goniopholidid skulls focus their specific differences on the periorbital morphology (Andrade & Hornung, 2011). The periorbital morphology, as described by these authors, is compound by the arrangement and disposition of the orbit, the palpebrals, the jugal, the lachrymal and the postorbital. The configurations of the periorbital area in “Dollo’s” and “Hooley’s” specimens are similar. According to Andrade et al. (2011) both taxa constitute a node sharing features such as: the dorsal component of the orbit; prefrontals very long, reaching the postorbital anterolateral process of the orbit; jugal only forms a narrow band of bone below the orbit; palpebrals are small, robust, and rectangular or very elongated. Other shared apomorphies concern the shape of the supratemporal fossa (circular), and the very long and robust condition of the preorbital anterolateral process shielding the anterolateral section of the orbit; the nasopharyngeal duct has a deep sulcation exposed at the palatal surface. The periorbital region of the “Hulke-specimen” differs in the interorbital area having a jump-like frontal ridge; a large palpebral, triangular in shape; elongated lachrymal; the shortness of the posterior process of the prefrontal; the inclination of the postorbital bar; and the absence of an elongated anterolateral postorbital process shielding the orbit laterally (Andrade & Hornung, 2011).

The Ariño goniopholidids are herein compared to unveil major differences among specimens and with other goniopholidids. We centre the description on the rostral shape, the periorbital region and skull table, and we include other relevant parts of the skull as the pterygoidean complex and the mandible when preserved.

4. SYSTEMATIC PALAEONTOLOGY

CROCODYLIFORMES (sensu Benton & Clark, 1988)

NEOSUCHIA (sensu Benton & Clark, 1988)
Family Goniopholididae Cope, 1875
Unnamed Clade (sensu Andrade, Edmonds, Benton & Schouten, 2011)

Goniopholididae indet.  
(Figs 3, 4a; Table 1)

Description.

Skull
The skull AR-1-3422 combines a set of features shared with the clade “Dollo-specimen” + “Hooley-specimen” sensu Andrade et al. (2011). The individual age of AR-1-3422 corresponds to a subadult animal (sutures are clearly visible). This makes the comparison with the adult specimen Anteophthalmosuchus hooleyi (Salisbury & Naish, 2011) difficult. The maxillary ornamentation differs from the skull table, being composed by irregular bumps and pits, which are not so enlarged in the specimen as in Anteophthalmosuchus hooleyi, but more similar to that of the “Dollo-specimen”. The length of the postorbital region (from the anterior tip of the orbit to the quadrate articulation) is equivalent to the rostral length excluding the premaxilla. Its relative width at the level of the 5th maxillary tooth is 40 % corresponding to a moderate rostral length.

The rostral contour has a premaxillo-maxillary compression at the notch and two lateral and vertical waves (one at the level of the 6th, and a second not so pronounced at the level of the 12th tooth). The largest maxillary teeth are 4th and 5th. Each maxilla bears 19-20 teeth. The maxillary depression is placed in front of the suborbital fenestra, and it is longer than wide. The depression is formed by three lobes; the posterior lobe faces anteriorly, and the middle one is dorsally displaced. The posterior lobe level the anterolateral orbital contour.

The palatal view preserves the premaxillo-maxillary suture. The maxilla projects an anteromedial process towards the premaxilla. The pits of mandibular teeth are positioned lingual and in interalveolar spaces; medial to the 10th up to 12th alveoli, these pits are deep. Medial to the posterior alveolar series vascular foramina are wide. The posterior maxillary teeth have a medial platform. The anterior tip of the ventral projection of the ectopterygoid is short and located posterior to the alveolar series. The maxilla sends a lateral posterior projection to the suborbital fenestra that expands anteromedially. The anterior palatine process exceeds the palatal fenestra. The fenestra is very long, corresponding to 50 % of the skull length (excluding the premaxilla). The palatines are straight at the interfenestral area, and bulge slightly posteriorly. There is a median sulcus between palatines. Part of the left pterygoid is preserved; the bone forms the anteromedial border of the palatine fenestra. The palatines participate
in the anterior choanal border. The anterior choanal border is located cranial to the posterior margin of the palatal fenestra.

The preorbital region of AR-1-3422 lacks an interorbital crest on the wide dorsal skull surface. The sculpture at this part consists of radiating ridges from the orbital notch towards the maxilla. The orbit is subcircular in shape, and its dorsal contour is neat. The orbit has an anterior long recess where the lachrymo-jugal contacts. The lachrymal is prominent at the anterior orbital border, a similar condition occurs in the “Dollo-specimen”. The lachrymal prominence overhangs the orbital recess. A tiny foramen is inset the lachrymal notch. The anterior process of the jugal is short and extends in front of the orbital recess. The jugal forms the laterodorsal orbital margin forming an elevated crested profile. The posteromedial right orbital edge shows a sutural scar for a palpebral bone. This tiny subrectangular palpebral is in articulation at the left orbit. The prefrontal is posteriorly elongated and reaches the palpebral posterior suture. The suture between the prefrontal and lachrymal is clear, and delimited by an incision. The frontals form part of the posterior orbital margin.

The anterior frontal process is triangular in shape. The lachrymal broadly contacts the nasal in its posterior third. The jugal is a long and narrow bone, it overlays the maxilla with an extended sutural contact. The prefrontal is a narrow bone and has a curved convex suture with the

| Table 1. Skull measurements in mm. The resulting measures are affected by preservation (flattening, and distortions by curving). |
|-------------------------------------------------------------------------------------------------|
| **Skull measurements** | **AR-1-3422** | **AR-1-2045** | **AR-1-1097** |
|---------------------------------|---------------|---------------|---------------|
| Skull length (excluding premaxilla) | 198 | 320 | - |
| Length from the 1<sup>st</sup> maxillary tooth to the anterior border of the suborbital fenestra | 100 | 155.5 | - |
| Width of the interorbital space | 80 | 50 | - |
| Skull width at 5<sup>th</sup> alveoli | 90 | 65 | 100 |
| Width of the quadrate condyle including the quadratojugal extension | 38 | 60 | 62 |
| Skull table length: postorbital to parietal posterior margin | 75 | 11 | - |
| Mid width of the skull table | c. 14 | 11.4 | 18 |
Frontal. Rostrally, the prefrontal ends in an acute process. Ventrally the prefrontals extend transversally at the level of the prefrontal pillars reaching the lachrymals, and leaving a narrow through between the suborbital fenestra and the maxillary sinus.

The skull table is characterized by a relatively narrow anterior and lateral bars (subequal to less than the intertemporal bar). The supratemporal fossae are wide, and the supratemporal fenestra is of subequal size to the orbit. The fossa is subcircular in shape, with a curved lateromedial margin. Parietals are unfused at the skull table. The frontals form part of the anteromedial border of the supratemporal fossa. At that area the frontals are laterodorsally expanded. The laterosphenoid has a transverse anterior edge, and forms the floor of the supratemporal fossa generating a sharp flatten rim. The parieto-frontal suture is placed at midlength of the fenestra, and it has a straight suture with a mid posterior peak. The posterior projection of the squamosal surpasses the paraoccipital process and is laterally directed. The squamosal-postorbital suture divides dorsally the cranial table in two unequal portions with the squamosal twice as long. The squamosal suture is anterolaterally directed. Laterally the squamosal projects an anterior process that reaches the posterior dorsal edge of the postorbital bar. The anterior border of the postorbital is transverse, and anterolaterally projects a protuberance (broken at the tip).

The infratemporal fossa faces laterodorsally. At the infratemporal fenestra the section of the jugal is rounded to subpolygonal. The jugal bar is inset, and placed at a depressed platform formed by a long medial extension of the jugal and the ectopterygoid. The bar is not fully preserved, but dorsally it is set below the postorbital anterior expansion. The jugal sutures the quadrate to the quadrate articulate anterior to the caudolateral border of the infratemporal fenestra, and extends posteriorly in oblique contact. The suture between the jugal and quadrate is ventrally exposed, showing the long posterior jugal process that bends rostrally to enter into the infratemporal fenestra. The quadrate projects into a short and stout spine. The quadrate and quadrate area is dorsally broad and long. The area has a peculiar unsculptured depressed surface at the otic area with a dorsoventrally low recess at the quadrate. As in other European goniopholidids the cranio-quadrate passage is opened forming a lateral sulcus running ventral to the paraoccipital process and dorsal to the quadrate surface, in which the squamosal lateroventral lamina does not suture with the dorsal surface of the quadrate.

The occipital area (Fig. 4a) is characterized by the relative low quadrate articulation. The dorsal quadrate surface has a mid dorsal crest, delimiting its medial convex contour. The quadrate articulation has a ventrally twisted medial condyle. The ventral surface of the quadrate has a developed crest B for the attachment of the mandibular adductor. The basioccipital is dorsoventrally short but laterally expanded. The ratio between quadrate articulation width and the mid occipital width (mid Eustachian canal to lateral quadrate condyle) is 3.7.

**Mandible**

Two disarticulated fragments of dentaries with eighteen alveoli and teeth in situ were preserved. The dentary when reconstructed has a spatulate anterior outline, with the third tooth almost in line with the first and second, and the fourth posterior to the third. The symphysial area is massive in
relation to the dentary ramus, and the lateral profile of the
dentary symphysis is elevated at the third and fourth teeth.
The set of vascular foramina placed medial to the alveoli
are wide. Third and fourth alveoli are confluent and have
twice the diameter of the 6th to 9th alveoli, the alveolar
diameter increase from the 10th on, forming a peak at the
11th and 12th. The alveoli have thin interalveolar spaces. In
dorsal aspect the symphyseal area extends to the
fifth to sixth alveoli. At midlength, the dentary is deep and has a
quadrangular cross-section. The Meckelian canal is centred
sixth alveoli. At mid length, the dentary is deep and has a
quadrangular cross-section. The Meckelian canal is centred
on the postorbital bar.

Type locality. Cuckfield, West Sussex (unknown exact
location), Grinstead Clay Formation, United Kingdom.

Stratigraphical distribution. Valanginian to Lower
Albian.

Hulkepholis willetti Salisbury & Naish (2011)

Holotype. BMNH 001876, a nearly complete skull,
Salisbury & Naish (2011; figs 24.2-24.4).

Diagnosis. Choana midway between palatines and
pterygoid, absence of postorbital palpebral.

Type locality. Cuckfield, West Sussex (unknown exact
location), Grinstead Clay Formation, United Kingdom.

Hulkepholis plotos Salisbury & Naish (2011)

Holotype. AR-1-3423, the Guimarota Goniopholis
sp. n., Lower Albian, Teruel, Spain.

Type species. Hulkepholis (=Goniopholis) willetti
(see Salisbury & Naish, 2011; figs 24.2-24.4). Related
species: Hulkepholis plotos sp. n., Lower Albian, Ariño,
Teruel, Spain.

Derivatio nominis. From the Greek πλοτός, the drifter.

Holotype. AR-1/56, a partial skeleton deposited at
Museo Aragonés de Paleontología/Fundación Conjunto
Paleontológico de Teruel-Dinópolis (Teruel, Spain),
composed by skull (AR-1-2045), 3 vertebræ (AR-1-2048,
AR-1-4859, AR-1-4860), a rib (AR-1-2046), a metapodial
(AR-1-2048), and 3 osteoderms (AR-1-2049, AR-1-4861,
AR-1-4862).

Diagnosis. Choana with the anterior edge posterior to
the palatal fenestra edge, enclosing most of the choanal
aperture within the pterygoid, the basioccipital lateral
tubera pendulous extending ventral to the Eustachian
medial foramen, the postorbital palpebral projecting
with an anterolateral wide lamina towards the mid orbit,
expanded articular quadrate that is wider than the mid
rostral width at the suborbital fenestra.

Type locality. Site AR-1, Mina Santa María, Ariño,
Teruel Province, Spain.

Stratigraphical distribution. Middle Interval with
Coal, Lower Sedimentary Succession, Escucha Formation
(Rodríguez-López et al., 2009), Lower Albian (Alcalá et
al., 2012, Tibert et al., in press).
**Description.** The skull AR-1-2045 has the combination of features of the “Hulke-specimen” (Andrade & Hornung, 2011) recently described as *Goniopholis willetti* (Salisbury & Naish, 2011). The rostral ornamentation is profuse and dense, configured by ridges and occasional subcircular pits. The hump-like interorbital ridge might be present although it is not so evident since this area is deformed and fractured in the specimen. The rostrum is elongate and rather narrow, and comprises 59% of the skull length (excluding the premaxilla), while the relative width to the rostral length at the level of the fifth maxillary tooth is 22%. The maxillary contour presents an anterior lateral to vertical wave up to the 6th-7th teeth, and a second one better exposed laterally at the 11th tooth. In lateral view, the maxillary alveolar border is unornamented posterior to the 6th alveolus. The maxillary depression is longer than it is wide, and its posterior contour placed at the level of the suborbital fenestra. The maxillary depression has 3 or more widen lobes separated by uncompleted ridges. The anterior premaxillary border is straight and somehow depressed. The premaxilla shows the goniopholidid T-shape although their lateral borders do not surpass the maxillary ones. The anterior border of the premaxilla is deeply verticalized, and the external nare is unique and faces dorsally. The nares are subcircular in shape. The perinarial fossa has verticalized marginal walls. The fossa spread ventrally forming a narial floor. The nares have a perinarial dorsolateral crest ending posteriorly in a knob. Nasals in *Hulkepholis* (=*Goniopholis*) *willetti* do not enter the nares. In AR-1-2045 the area is deformed and downturned forcing the anterior projection of nares. Nonetheless, the premaxillary mid suture posterior to the nare is partially exposed. The premaxillo-maxillary suture is posteriorly projected reaching the level of the second-maxillary tooth. Nasals have parallel sides, although they widen posteriorly forming a curved lateral contour.

The palatal view preserves the premaxilo-maxillary suture placed at the level of the first maxillary tooth, projects its anteriormost tip towards the premaxilla. Ventrally the premaxilla bends at the level of the 4th alveolus leaving a wide notch laterally. The premaxilla bears 5 alveoli although the fifth, which is posterolateral placed, is almost completely reduced. The size of the premaxillary teeth is 5c<4c<3c<2c. The foramen incisivum is a slit like almost closed fenestra. A deep pit for the mandibular tooth is placed lingual in between the first and second, and a second pit is placed lingual to the third in the premaxilla. Each maxilla bears 23-24 alveoli. The interalveolar space is wide (as wide as the alveolar diameter) and subequal, except for the rear maxillary teeth. There are two relevant pits in the maxilla, one placed posterior to the 7th and the other placed between the 8th and 9th alveoli. The foramina for reception of mandibular teeth are interforaged along the maxilla (between alveoli). The opening of the trigeminal foramen is medial to the 13th alveolus. The posterior maxillary series has a medial shelf. The ectopterygoid anterior projection is short and rounded, and it is placed medial to the last maxillary alveolus. Palatines are straight and they are prolonged beyond the palatal fenestra forming a lobate (round) suture. The palatine bar widens posteriorly. The pterygoids extend along the skull table length. They are formed by a flat lamina with a thick lateral wing. The ectopterygoid contacts the pterygoid rostrally and does not reach the posterior pterygoid margin. The choana is posteriorly placed; its anterior border at the level of the posterior margin of the suborbital fenestra. It is formed by two narrow and long openings divided by a thick septum. The palatines are involved in the formation of the anterior part of the choana, and they have two medial short ventral projections to the mid septum. Laterally the pterygoids have a concave posterior surface. The posterior pterygoid lamina folds medially, exposing a vertical strand of bone. This fold lies anterior to the basioccipital tubera, leaving a wide space where the Eustachian canal opens. The contact leaves a neat suture between the basioccipital and the pterygoids with no apparent ventral exposition of the basisphenoid.

The periorbital region is characterized by the orbit, which is surrounded by a prominent thick dorsally turned border. This border has a sutural scar for a palpebral extended from the posteromedial border to the medial lacrimal edge. This palpebral is not preserved (Fig. 5c). The postorbital itself shows a sutural anterior border where a palpebral sets avoiding a direct contact of the frontal at the posterior orbital border, thus, being the prefrontal in contact with the postorbital ventral to the orbit. The postorbital is anteriorly cupped and a dorsally protuberant palpebral covers this space. The suture between the postorbital and its palpebral is exposed even laterally. This palpebral curve laterally forming the anterolateral extension of the postorbital process that prolongs towards the lateral contour of the orbit. In *H. willetti* this process is described as rostral tuberosity. This rostral tuberosity is also present in AR-1-2045 specimen at the postorbital bar. However, the development of the process exceeded this condition, and differs from that of AR-1-1097 and *H. willetti* in its robustness because its ventral margin extends ventral to the squamosal lateral shelf. The stout postorbital tip bends ventrally and reaches the mid-lateral orbital contour as in Ariño. The lacrimal presents an anterior deep and narrow recess at the orbital edge. The jugal forms a thick and deep lateral orbital contour but without an elevated border. Lacrimal and prefrontal sutures and their contacts with nasals are obscured.

The cranial table contains long subquadrangular supratemporal fossae. The supratemporal fossa is twice longer than the orbital diameter, although the fenestra is subequal or smaller than the orbit. The anterior and lateral bars of the skull table are wider than the intertemporal bar. The squamosal-postorbital suture divides the cranial table into two subequal portions. The postorbital has an...
Figure 5. Specimen AR-1-2045 from Mina Santa María, Ariño (Lower Albian, Escucha Formation, Teruel Province) corresponding to the holotype of *Hulkepholis plotos* sp. n. a) Dorsal view. b) Ventral view. c) Detail of the left periorbital region and skull table in lateral view. Notice that the profile of the prefrontal palpebral (pab, in grey) has been reconstructed, connecting the lachrymal knob and the postorbital palpebral (po pab). The black arrow points the anterior process of the postorbital palpebral underlying the postorbital tuberosity. The white arrow points the sulcus of the jugal. Note: see text for abbreviations.
Genus *Anteophthalmosuchus* Salisbury & Naish, 2011

*Anteophthalmosuchus escuchae* sp. n.  
(Figs 4c, 6-9; Table 1)

**Derivatio nominis.** Dedicated to Escucha Formation.

**Holotype.** AR-1/37, a partial skeleton deposited at Museo Aragonés de Paleontología/Fundación Conjunto Paleontológico de Teruel-Dinópolis (Teruel, Spain), composed by a disarticulated but associated skull (AR-1-1097, including the mandible), 11 isolated teeth (AR-1-1051, AR-1-1096, AR-1-1106 to AR-1-1109, AR-1-1140, AR-1-1167 to AR-1-1169), 17 vertebrae (AR-1-1187, AR-1-1192, AR-1-1196, AR-1-1346, AR-1-1348 to AR-1-1350, AR-1-1355), 6 ribs (AR-1-1193, AR-1-1194, AR-1-1335, AR-1-1337, AR-1-1339, AR-1-1341), a limb bone (AR-1-1095), and 16 dermal armor plates (AR-1-1043, AR-1-1047 to AR-1-1049, AR-1-1098, AR-1-1160, AR-1-1165, AR-1-1195, AR-1-1196, AR-1-1346, AR-1-1348 to AR-1-1350, AR-1-1352 to AR-1-1354).

**Diagnosis.** *Anteophthalmosuchus escuchae* differs from *Anteophthalmosuchus hooleyi* in the palatine-maxillary suture anteriorly convex and longer than wider; the caudal inclination of the mandible, and angular forming the posterior mandibular contour, laterally occupying one third of the mandible height.

**Type locality.** Site AR-1, Mina Santa María, Ariño, Teruel Province, Spain.

**Stratigraphical distribution.** Middle Interval with Coal, Lower Sedimentary Succession, Escucha Formation (Rodríguez-López et al., 2009), Lower Albian (Alcalá et al., 2012, Tibert et al., in press).

**Description.**

**Skull**

The skull AR-1-1097 is related to the “Hooley-specimen” (Andrade & Hornung, 2011) that has been recently described as *Anteophthalmosuchus hooleyi* by Salisbury & Naish (2011). The rostral ornamentation is dense and organized with a uniform pattern of regular subcircular pits (Fig. 6). The maxilla is ornamented with radiating ridges at its jugal and lachrymal contact. The maxilla has more than 14 teeth (4th and 5th teeth being the largest), with two lateral waves at the level of the 6th, and at the 11th tooth. The lateral margin of the maxilla has a simple band over the alveolar border (Fig. 7). The specimen preserves the anteromedial contour of the orbit, which is deprived of crests. The anterior jugal suture is narrow and ends in an acute, narrow triangular process. The maxillary depression is not preserved, although at that level the maxilla lacks ornamentation; nasals are partially preserved. They broaden with a convex lateral contour posteriorly.

In ventral view the maxilla preserves pits of reception for mandibular teeth, which are placed at the interalveolar spaces from 9th to 12th alveoli. The interalveolar spaces are wide, being maximal at the 10th and 11th. The maxilla holds a posterolateral process that enters the suborbital (palatal) fenestra although its medial contour is obscured. The palatine anterior process surpasses anteriorly the palatal fenestra, and has a rounded convex edge. This suture is different in *Anteophthalmosuchus hooleyi* with a subrectangular palatine suture. The ventral surface of the portion comprising the posterior part of the skull preserves a medial depression at the postorbital in where
the laterosphenoid head contacts, and the area where the bar sets (Fig. 8). In ventral aspect, the relative short length of the jugal, its polygonal cross section, and the suture with the ectopterygoid becomes visible. The ectopterygoid has an acute posterior extension. The quadratojugal projects with strong process that reaches the tip of the dorsal postorbital bar medially and laterally, and contacts with the postorbital anterior projection. A large medial Eustachian opening is visible. The suture between the basisphenoid and basioccipital divides this opening. The quadrate ventral surface exhibits its suture with the pterygoid (Fig. 8), and a developed crest B that posteriorly ends into a reticulate area as occurs in *G. baryglyphaeus*. Between crests B and A there the surface is deeply concave.

An isolated left quadrate exposed the cranioquadrate sulcus (Fig. 8). The quadrate forms the ventral floor of the otic recess. Lateral to the otic recess a preotic foramen is exposed. Caudally the quadrate has two sulci, one laterally exposed directed to the preotic foramen, and a second medial one directed to the external otic recess. This medial sulcus ends in a dorsal posterior foramen. Both sulci are separated by a dorsal elevation of the quadrate. The ventral lamina of the squamosal and the paraoccipital process sutures are medially to both sulci.

The skull table is characterized by a wide supratemporal fossa, with a curved lateromedial margin. The skull table has lateral and anterior bars lesser to subequal to the intertemporal bar. The squamoso-postorbital suture divides the cranial table in two unequally portions being the postorbital longer than the squamosal. The squamosal posterior corner is prominent and is projected caudally more than laterally. The frontal forms an oblique, anterolaterally directed suture with the postorbital. The postorbital forms a concave cup forming the posterior orbital wall. A long and sharp postorbital anterolateral spine shields laterally the orbit. This spine is dorsally ornamented. The dorsal base of the postorbital bar extends anteroposteriorly, and has a lateral tubercle.

The infratemporal area occupies half the skull table length (Fig. 7). The jugal is subequally wide at its anterior and posterior edges. Laterally the jugal is profusely ornamented, at the infratemporal area. As in the other specimens it has a smooth dorsal edge posterior to the jugal dorsal process. Posteriorly, the jugal contacts the quadratojugal anterior to the posterior infratemporal corner in a dorsally flexed but caudally long suture. In lateral view, the squamosal anterolateral process ends quite posterior to the postorbital bar. The lateral edge of the skull

Figure 6. Specimen AR-1-1097 from Mina Santa María, Ariño (Lower Albian, Escucha Formation, Teruel Province) corresponding to the holotype of *Anteophthalmosuchus escuchae* sp. n. a) Rostral fragment in ventral view. b) Rostral fragment in dorsal view. Note: see text for abbreviations.
The skull table is smooth and separated by a deep sulcus from its dorsal ornamented part. The sulcus extends from the otic region to the postorbital region, including the prominent anterior extension of the postorbital corner.

The occipital area is characterized by a laterally enlarged basioccipital (Fig. 4c), and occipital condyle. The occipital condyle protrudes caudally surpassing the basioccipital tubera posterior contour. The occipital condyle diameter is diminished, and as described for Anteophthalmosuchus hooleyi, the foramen magnum opening is otherwise laterally widened. The quadrate articulation has a twisted medial condyle and its medial surface gently slopes from the dorsal plane. The dorsal quadrate surface has two foramina aereum (Fig. 4c). The ratio between quadrate articulation width and the mid occipital width is 2.8.

Figure 7. Specimen AR-1-1097 from Mina Santa María, Ariño (Lower Albian, Escucha Formation, Teruel Province) corresponding to the holotype of Anteophthalmosuchus escuchae sp. n. Skull table in lateral view, right side, and rostral fragment in lateral view. The rostral fragment has been rotated in order to show the general lateral aspect of the skull, although it corresponds with the left lateral aspect. Note: see text for abbreviations.

Figure 8. Schematic interpretation of the specimen AR-1-1097 from Mina Santa María, Ariño (Lower Albian, Escucha Formation, Teruel Province) corresponding to the holotype of Anteophthalmosuchus escuchae sp. n. a) Isolated left quadrate in dorsal view showing the interpretation of the otic area and the sulcus of the cranio-quadrate passage (s cqp). b) Ventral view of the posterior skull fragment. Note: see text for abbreviations.
Mandible

The posterior part of the mandible differs from *G. baryglyphaeus* and *G. simus* in several features. The posterior part is profusely ornamented with pits 3 mm wide (Fig. 9). The posterior border of the mandible is inclined, and the angular reaches the retroarticular process ventrally, while the surangular is laterally placed at this area. It has no external fenestra but a longitudinal long suture between the angular and surangular.

The retroarticular process has a horizontal profile slightly elevated from the dorsal mandibular margin. The retroarticular process is very long (about mid length of the surangular). It is medially curved (although preservation may enhance this feature). It has a sharp medial lamina that extends from the glenoid medial surface with a straight edge but curves posteriorly toward the tip. The retroarticular dorsal surface is deeply concave. Laterally it contacts with the surangular that at that level is thick. The tip of the retroarticular process does not deflect either dorsally not caudally as in *G. simus*. The glenoid area is placed ventrally to the retroarticular process, and faces cranially instead of dorsally. The glenoid bears two cotylar surfaces divided by an oblique ridge that projects medially. The ridge ends in a tubercle that forms the anteromedial border of a convex medial edge. The medial cotyle is shorter than the lateral one but deeper. The posterodorsal rim of the glenoid articulation has a mid rim. The ventral process of the articular shows a continuous sutural area with the surangular and inset in the ventral angular recess.

The surangular is longitudinally short. It projects with a dorsal spine reaching the tooth row, while the dentary project a posterior acute forked process. The process is visible in lateral view. At that level the dentary (30 mm) is low in contrast with the posterior mandibular height (70 mm). At the inner side the surangular shows a wide sutural contact with the splenial. The dorsal border of the surangular is straight and medially thick.

Figure 9. Specimen AR-1-1097 from Mina Santa María, Ariño (Lower Albian, Escucha Formation, Teruel Province) corresponding to the holotype of *Anteophthalmosuchus escuchae* sp. n. Right mandible in lateral view. Note: see text for abbreviations.

5. DISCUSSION

The European goniopholidids are composed by the three species *G. baryglyphaeus*, *G. simus* and *G. kiplingi* subsumed in the genus *Goniopholis*, plus a sister clade that includes *Hulkepholis* (=*Goniopholis*) *willetti* (for the “Hulke-specimen”), *Anteophthalmosuchus* (for the “Hooley-specimen”, *A. hooleyi*), and the “Dollo-specimen” (Andrade et al., 2011; Salisbury & Naish, 2011). The biochronological interval of the *Goniopholis* clade spans from the Kimmeridgian to the Berriasian, while its sister group was known from the Valanginian to the Aptian. The Ariño Lower Albian assemblage is therefore the latest identifiable record of the Goniopholididae (Fig. 10). The Iberian fossil record supports the basal dichotomy in the evolution of Goniopholididae because the Ariño goniopholidids share the apomorphies related to the latest members of this family (see Section 3). Furthermore, the Ariño specimens contribute to a better understanding of the clade with preserved postcranial elements in association,
and skull features not clear or not exposed previously on the southern England holotypes of *Anteophthalmosuchus hooleyi* (i.e., the quadrate configuration, and the mandibular retroarticular region) and “*Goniopholis*” *willetti* (i.e., periorbital region), that could be currently attributed to the new genus *Hulkepholis*.

Ariño skulls AR-1-3422 and AR-1-1097, apart of the medium sized rostral length, have strong phenotypic similarities. They share the features of the clade *Anteophthalmosuchus hooleyi* + “Dollo-specimen” (Andrade et al., 2011): dorsal component of the orbit; shape of the supratemporal fossa, nasopharyngeal duct sulcate. Not all the synapomorphies diagnosing this group (see Section 3) can be fully tested in the two Ariño individuals (even some as relevant as the long and robust condition of the preorbital anterolateral process shielding

Figure 10. Calibrated cladogram showing the basal dichotomy of the two European clades, according to Andrade et al. (2011). Box in grey remarks the time interval delimiting a potential ghost lineage. 1. *Anteophthalmosuchus hooleyi*, 2. *Anteophthalmosuchus escuchae*, 3. *Hulkepholis willetti*, and 4. *Hulkepholis plotos*. The presence of *Goniopholis simus* is expected to be expanded in the Cretaceous.
the orbit) mainly due to preservation. Despite that, AR-1-1097, the worst preserved, has the same combination of traits as Anteophthalmosuchus hooleyi (Salisbury & Naish, 2011), while AR-1-3422 bears the remaining traits diagnosing the clade: prefrontal very long reaching the posteromedial borders of the orbit; jugal only forms a narrow band of bone below the orbit; palpebrals small and rectangular.

According to the diagnosis provided by Salisbury & Naish (2011) for Anteophthalmosuchus hooleyi, the Ariño and Wessex specimens share: i) the sculpture of the cranial table, infratemporal and rostral areas with regular and wide pits, ii) the lateral bowed process of the postorbital encircling the orbit, iii) the occipital condyle width lesser than the foramen magnum, iv) the absence of a mandibular fenestra, v) the greater length of the postorbital at the dorsal cranial table, vi) the short lateral squamosal projection that does not reach the postorbital bar. Differences confirming the newly described species Anteophthalmosuchus escuchae are based on: the shape of the palatine-maxillary suture, anteriorly convex and longer than wider in A. escuchae but subquadrangular in A. hooleyi; the caudal inclination of the mandible in A. escuchae instead of orthogonal, and the disposition of the angular forming the posterior mandibular contour, and laterally occupying one third of the mandible height in A. escuchae.

There are some differences between the specimens AR-1-3422 and AR-1-1097, based on the squamosal-postorbital lateral suture, the shape of the jugal-quadratojugal suture, and the diameter and disposition of the occipital condyle. In the light of these differences we tentatively suggest that Ariño AR-1-3422 could be considered a distinct species from A. escuchae. However, AR-1-3422 should be first compared with the “Dollo-specimen” for its definitive determination.

The specimen AR-1-2045 clearly differs from AR-1-3422 and AR-1-1097 in its longirostral configuration, and periorbital region (with a triangular and wide palpebral). The specimen AR-1-2045 is herein related to Hulkepholis willetti (= Goniopholis willetti), based on the diagnosis provided for this species (Salisbury & Naish, 2011). They share: i) a long and narrow rostrum, ii) a similar premaxillary tooth arrangement being the 5<4<3<2, iii) an interorbital hump, iv) the squamosal tip with a rounded and short boss, v) a large and triangular palpebral, vi) the frontal exclusion at the orbital contour, vii) almost fused parietals, ix) postorbital as long as the squamosal. We herein described the new species Hulkepholis plotos, which differs from H. willetti in the posterior position of the choana, the pendulous basioccipital, and development of the anterolateral projection of the postorbital affected by the extension of the palpebral underlying the postorbital anterior tuberosity, and by the lateromedially expanded quadrato articulation of the Ariño species. The absence of a postorbital palpebral might be due to preservation in the Wessex specimen, a condition that should be confirmed.

We have proposed the new genus Hulkepholis based on the phylogenetic dichotomy of the two European clades (Fig. 10). Both clades are robustly supported according to Andrade et al. (2011), and all of the Ariño specimens support this evolutionary divergence. Nonetheless, two of the synapomorphies that diagnose the Goniopholis sensu stricto species are shared by Anteophthalmosuchus hooleyi (i.e., anterior face of the palatal process truncate with a transverse suture, see Salisbury & Naish, 2011, fig. 24.7, p. 320), and A. escuchae (i.e., absence of external mandibular fenestra, note that G. simus has an external mandibular fenestra according to Salisbury et al., 1999). The expectation of validating the monophyletic status of the genus Goniopholis will require the inclusion of the Ariño species in a further phylogenetic analysis.

The Latest Hauterivian to Early Albian rifting phase of the Iberian basin was associated with a major transgression episode that was interrupted by a short-lived early Aptian regression and terminated by the mid Albian regression. These regressions resulted in the progradation of deltaic complexes that linked to some tectonic processes, generating during mid Albian the accumulation of thick deltaic and lacustrine successions such as the coal bearing Escucha Formation (Martín-Chivelet, 2002). The stratigraphical and sedimentological analyses of Ariño, where the bonebeds have been found, indicate a sedimentary coastal system with barrier islands and marshes (Rodríguez-López et al., 2009). The coal layers were produced in back-barrier marshes associated with a barrier-lagoon system; at that environmental system two ecomorphotypes of crocodyliforms concurred: Hulkepholis plotos as a long-snouted species, and a second species with a moderate wide and medium sized rostrum. Populations of sympatric recent species occupy either different niches (habitat partitioning) or exploit recourses according to time partitioning (see Salisbury & Naish, 2011 for profuse examples). The longirostral H. plotos might be considered as an active aquatic predator, based on its rostral shape and homodonty. The occurrence of species related to Anteophthalmosuchus hooleyi and Hulkepholis willetti reflects similarities between the neosuchian assemblage of Ariño and the Wessex-Weald basin of southern England never reported before. In addition, if AR-1-3422 were related to the goniopholidid species from Bernissart (Belgium) a further indication of geographical connection between these areas should be undertaken.
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