New data on dwarf crocodylomorphs (Atoposauridae) from the Upper Jurassic of Portugal

Puértolas-Pascual, E.[1,2,3], Beccari, V.[4,5], Quaranta, M.[6,7]

1: Grupo Aragosaurus-IUCA, Paleontologia, Facultad de Ciencias, Universidad de Zaragoza, C/Pedro Cerbuna, 12, 50009 Zaragoza, (Zaragoza, Spain). eduardo.puertolas@gmail.com
2: GeoBioTec, Departamento de Ciências da Terra FCT, Universidade Nova de Lisboa, 2829-516 Campus Monte de Caparica, (Caparica, Portugal).
3: Museu da Lourinhã, Rua João Luis de Moura, 95, 2530-158 Lourinhã, (Lisboa, Portugal).
4: Bayerische Staatssammlung für Paläontologie und Geologie, Richard-Wagner-Straße 10, 80333 (Munich, Germany).
5: Department of Earth and Environmental Sciences, Ludwig-Maximilians-Universität, Theresienstraße 41, 80333 (Munich, Germany).
6: Departamento de Estatística e Investigação Operacional, Faculdade de Ciências da Universidade de Lisboa, Campo Grande, 1749-016, Lisboa (Lisboa, Portugal).
7: CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Instituto Superior de Agronomia, Universidade de Lisboa (Lisboa, Portugal).

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Introduction

The Lourinhã Formation (Late Jurassic, Kimmeridgian–Tithonian) in western Portugal is one of the richest fossil-bearing units of this age in Europe, particularly known for its exceptional vertebrate record. This formation has yielded abundant remains of dinosaurs, mammals, turtles, and pterosaurs, but also preserves a notably diverse assemblage of crocodylomorphs. Within the Lusitanian Basin, crocodylomorph fossils have been recovered from both macrofossil sites and microvertebrate assemblages, spanning a wide range of body sizes, morphologies, and ecological adaptations. Notably, the Guimarota lignite mine (further north, in the Alcobaça Formation, near the city of Leiria) produced *Knoetschkesuchus guimarotae*, originally described as *Theriosuchus guimarotae* (Schwarz et al., 2017), one of the best-known atoposaurids from the Iberian Peninsula, as well as the medium-sized goniopholidid *Goniopholis baryglyphaeus* (Schwarz, 2002). Additional taxa such as *Lisboasaurus estesi* and *Lusitanisuchus mitracostatus*, small mesoeucrocodylians of uncertain affinities, were originally identified as anguimorph lizards or even maniraptoran theropods, but were later reassigned to Crocodylomorpha (Buscalioni et al., 1996; Schwarz & Fechner, 2004). These taxa, known from Guimarota and possibly Lourinhã, further highlight the taxonomic and ecological diversity of crocodylomorphs in the Portuguese Upper Jurassic.

In the Lourinhã area specifically, some neosuchian taxa have been described based on more complete material. These include *Ophiussasuchus paimogonectes* (López-Rojas et al., 2024), a newly described goniopholidid skull from Paimogo beach. In addition, postcranial material and isolated teeth from Valmitão and other localities have been attributed to several taxa, including *Lusitanisuchus*, Atoposauridae, Goniopholididae, Bernissartiidae, and undetermined mesoeucrocodylians, suggesting a higher diversity than previously recognized based on skeletal remains alone (Guillaume et al., 2020). Despite this diversity, the record of atoposaurids in the Lourinhã Formation remains sparse and fragmentary, mostly limited to isolated teeth and cranial fragments recovered from microvertebrate-rich layers. These small-sized remains from dwarf crocodylomorphs are crucial for understanding the evolutionary history of Atoposauridae and their phylogenetic and biogeographic patterns in western Europe. The present study

contributes new data to this group, based on previously undescribed material from three fossiliferous sites, Zimbral, Porto das Barcas, and Peralta Sul, located along the coastal cliffs of Lourinhã. The specimens under study comprise ML2631, a skull table that was preserved in a nodule from Zimbral; ML2322, a partial skeleton including cranial elements from Porto das Barcas; and ML2688, an articulated partial skeleton preserving most of the posterior body region, from Peralta Sul. All three specimens were prepared at the Museu da Lourinhã laboratory. Since portions of the surrounding rock matrix could not be removed mechanically, they were micro-CT scanned at the Micronsense facilities (Leiria, Portugal) to reveal hidden anatomical features and allow the digital reconstruction of internal bony cavities.

Geological and geographical settings

The crocodylomorph fossil material comes from coastal outcrops in western Portugal, near the town of Lourinhã (Lisboa district, Oeste region), where Upper Jurassic strata of the Lusitanian Basin are well exposed. The Lusitanian Basin is a Mesozoic rift basin developed along the western margin of the Iberian Plate during the opening of the North Atlantic, and it preserves a thick sedimentary succession spanning from the Late Triassic to the Late Cretaceous. During the Late Jurassic, the basin experienced an active rifting phase associated with syn-sedimentary faulting and the development of nested sub-basins, such as Consolação, where the studied outcrops are located. This phase led to marked lateral facies changes and the accumulation of thick continental successions dominated by fluvial and deltaic systems (e.g., Taylor et al., 2014; and references therein).

All the specimens described in this study were recovered from microvertebrate-bearing levels in the lower part of the Praia Azul Member (Lourinhã Formation), within the Consolação Sub-basin. The Lourinhã Fm, dated to the upper Kimmeridgian–lower Tithonian, represents fluvio-deltaic environments interbedded with shallow marine incursions. Within this formation, the Praia Azul Member records alternating marine-influenced and continental deposits, reflecting three major transgressive episodes (e.g., Taylor et al., 2014; and references therein). The crocodylomorph fossils were recovered from sediments deposited between the first and second transgressive episodes. The fossil-bearing horizons consist predominantly of grey marls and silts, interpreted as low-energy floodplain or shallow lagoonal settings. Despite coming from different localities (Zimbral, Porto das Barcas, Peralta Sul), all specimens share a comparable stratigraphic context within the lower Praia Azul Member, dating to the late Kimmeridgian–early Tithonian transition (Late Jurassic).

Anatomical description

The specimen ML2631 consists of a skull table (3.6 cm in length) with an associated braincase, recovered from a nodule at the microvertebrate site of Zimbral (Lourinhã). Although the specimen was micro-CT scanned, the presence of dense mineral veins (likely indicating the nodule is a septarian concretion) caused significant imaging artefacts, which obscured some regions of the skull and complicated segmentation. Despite these limitations, we were able to digitally reconstruct most of the skull as well as several internal structures, including the brain cavity, inner ear, and cranial nerve pathways. The specimen exhibits several morphological features that support its referral to Atoposauridae indet. (Pochat-Cottilloux et al., 2024). Notably, the quadrate, squamosal, and otoccipital do not meet to enclose the cranioquadrate passage. A shallow sulcus or fossa is present at the suture between the parietal and squamosal. Although this feature is strongly developed in some notosuchians (*Notosuchus*) and paralligatorids (*Wannchampsus*), in ML2631 it is more subtle and restricted to the anterior part of the

suture, resembling the condition observed in some atoposaurids such as *Theriosuchus pusillus* and *Varanosuchus*. A low sagittal crest is also present along the dorsal surface of the parietal and frontal. The lateral margin of the squamosal shows a discontinuous groove for the ear valve musculature, a pattern also seen in atoposaurids such as *Aprosuchus* and *Varanosuchus*, as well as in paralligatorids like *Paralligator* and *Shamosuchus*. Although typical atoposaurids possess a squamosal prong with a depression along its posterolateral margin, this feature could not be confidently assessed in ML2631, as the corresponding region was partially affected by erosion.

The specimen ML2322 is a partial skeleton recovered from the site Peralta Sul. The preserved material includes a fairly complete skull (estimated total skull length: 6.3 cm; skull table: 2 cm), lower jaws, osteoderms, cervical, dorsal and caudal vertebrae, a coracoid, part of the ilium, and most of the forelimb and hindlimb bones. Thanks to the micro-CT scan, some endocranial cavities could also be segmented. Most of the features observed in ML2631 are also present in ML2322. In addition, ML2322 displays several traits typically found in atoposaurids. These include a broad oreinirostral rostrum and teeth with the characteristic atoposaurid morphology: the crowns are slightly compressed labiolingually, and the lingual surface is ornamented with centrally oriented apical ridges and fan-shaped lateral ridges extending toward the carinae. Unlike ML2631, the right squamosal in ML2322 is well preserved and clearly exhibits a squamosal prong with a depression along its posterolateral margin, forming a distinct step. As in atoposaurids, the dorsal osteoderms are arranged in two parallel rows and bear an anterior process or peg located anterolaterally. Compared to the condition in goniopholidids, this peg is less developed, and the lateral margin of the osteoderm is less ventrally inclined.

Specimen ML2688 was recovered in Porto das Barcas locality, notably found in association with a nearly complete skeleton of a juvenile ornithopod dinosaur. It consists of a partial postcranial skeleton preserved in articulation, including sixteen vertebrae (pre-sacral, sacral, and caudal), the right ilium, an almost complete right hindlimb, and over 100 osteoderms. The osteoderms show the distinctive arrangement pattern observed in atoposaurids: two paramedian rows of rectangular, lateromedially oriented osteoderms in the sacral region, and four rows of anteroposteriorly aligned square osteoderms in the caudal region. These features, together with the small overall body size (estimated at ~1.5 m based on femur dimensions) and general neosuchian morphology, suggest affinities with Atoposauridae. However, due to the absence of cranial material and the relatively large size of the individual (considerably exceeding the typical body length of atoposaurids, which usually do not surpass 0.5 m) its precise taxonomic assignment and comparison with the other two specimens remain tentative.

Ontogenetic considerations

Specimens ML2631 and ML2322 likely belong to the same taxon, as they present similar morphology and originate from laterally equivalent levels within the same facies. However, a comparison of their skull table lengths (3.6 cm in ML2631 and 2.0 cm in ML2322) shows that ML2631 is 1.8 times longer. Consequently, the morphological differences observed between the two specimens may be explained by ontogenetic variation. These differences include, for example, a more pronounced sagittal ridge on the dorsal surface of the skull table and more developed tuberosities on the basioccipital, supraoccipital, and quadrate in ML2631. In contrast, ML2322 shows a lower degree of cranial suture fusion, the absence of a sulcus at the squamosal–parietal suture, the presence of a squamosal lobe with a depressed posterolateral margin, and a more juvenile brain morphology. Regarding the postcranial skeletons of ML2322 and ML2688, the

latter is considerably larger, with a femur length of 10.5 cm compared to 4.2 cm in ML2322 (that is, 2.5 times longer). Despite the shared osteoderm morphology between the two, the greater robustness of the long bones in ML2688 could also reflect ontogenetic differences rather than taxonomic disparity. Finding additional overlapping material and new specimens could help resolve these uncertainties.

Conclussions

The newly described atoposaurid specimens from the Upper Jurassic of the Lourinhã Formation significantly expand our knowledge of the diversity, morphology, and ontogenetic variation within this clade in the Iberian Peninsula. The comparative analysis of three well-preserved individuals from stratigraphically equivalent levels suggests the presence of at least one dwarf atoposaurid taxon, possibly represented by different growth stages. Although one of the specimens (ML2688) is unusually large for the group (an estimate of 1.5 m in total length), its anatomical features and osteoderm arrangement are consistent with atoposaurid morphology, highlighting the need for further investigation.

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