

A Saharan Fossil and the Dawn of Neotropical Armoured Catfishes in Gondwana

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Abstract

Siluriformes are considered as primarily freshwater and have frequently been a model for the study of historical biogeography. Among catfishes, the most diverse clade is the Loricarioidei, a Neotropical group for which the fossil record extends back to the Palaeocene of Argentina. Here we describe a fossil from the early Late Cretaceous of Morocco, exhibiting typical morphological traits of the Loricariidae. A phylogenetic analysis integrating morphological characters with a multigene database for the main loricarioid lineages and outgroups highly supports inclusion of the fossil within the Loricariidae. A time-calibrated analysis corroborates the origin of loricarioids at about 112 MYA. The presence of this loricariid in Africa provides evidence that loricarioids have diversified before the separation of Africa and South America. The Moroccan loricariid shows an ancient evolutionary history that, in Africa, ended in the Late Cretaceous but persisted in South America, later surviving the K/Pg extinction.

Keywords

Siluriformes, Loricariidae, Late Cretaceous, Africa, biogeographic range

1. Introduction

Freshwater fossil deposits from the Mesozoic of Gondwana, although rare, play a fundamental role for a better understanding historical biogeographical patterns of diversification in teleost fishes. The discovery of a new taxon from the Late Cretaceous (Cenomanian, ~100–95 million years), Jbel Oum Tkout locality (OT1), Douira Formation, Kem Kem Group of Morocco, Africa (Sereno et al., 1996; Dutheil, 1999; Ibrahim et al., 2020) caught our attention due to its taxonomic importance. In this fossil, the structure of the caudal fin, including division of hypurals into dorsal and ventral groups (de Pinna, 1996), clearly indicates that it is a teleost fish. The most notable feature of this new taxon is the presence of bony plates on the surface of the body. This feature occurs in several groups of teleost fish, including gasterosteiforms, siluriforms, syngnathiforms, and a few scorpaeniforms (Nelson et al., 2016), as well as in the aulopiform *Leptecodon rectus* Williston, 1899 from the Upper Cretaceous of Kansas (e.g. Frickhinger, 1995). The presence in the new taxon of a dorsal fin positioned anteriorly on the body, with a spine on its anterior part, excludes the possibility that the new taxon is a gasterosteiform, syngnathiform, scorpaeniforms, or an aulopiform, as none of these fishes possess these characteristics, thus leaving the possibility of it being a siluriform. Among siluriforms, bony plates on the body surface occur in families of the Loricarioidei (i.e., Callichthyidae, Loricariidae, Scoloplacidae) and the Doradidae, with both groups presently restricted to the Neotropical Region, and the Amphiliidae, a family of Siluroidei geographically restricted to Africa (Nelson et al., 2016). However, the presence of dermal plates covering the entire flank and dorsum and the presence of odontodes on the body, being more conspicuously visible on the dorsal-fin spine and on the upper and lower-most ray of the caudal fin, discard the possibility of the new taxon being an amphiliid or a doradid, supporting its inclusion among the Loricarioidei, possibly among loricariids, the only group possessing three longitudinal series of dermal plates on the flank.

Modern representatives of Siluriformes, the so-called catfishes, are among the most diverse freshwater fish groups. With a near worldwide distribution and exploiting a remarkable variety of aquatic niches, siluriforms have even few marine taxa, confined to coastal areas (Fricke et al., 2022). Their worldwide distribution and the fact that they are primarily freshwater, makes them a key group for modelling historical biogeography (Lundberg, 1993; Diogo, 2004; Briggs, 2005; Sullivan et al., 2006), capable of explaining scenarios for many other largely continental groups.

Previously, the most basal siluriforms were thought to be members of the Diplomystidae (Lundberg, 1993; Greenwood et al., 1966; Fink and Fink, 1981; 1996; Arratia, 1987), but a molecular phylogeny supports an alternative hypothesis where the Loricarioidei are the extant sister group to all other extant catfishes (Sullivan et al., 2006; Betancur et al., 2017). Loricarioidei is the most diverse clade of catfish, containing approximately 1,640 species in six families (Nematogenyidae, Trichomycteridae, Callichthyidae, Scoloplacidae, Astroblepiidae, Loricariidae) corresponding to more than 40% of catfish diversity. All known loricarioids are geographically restricted to the Neotropics.

The previous oldest known fossil loricarioid, the callichthyid *Corydoras revelatus* Cockerell, 1925, came from ~58.5 million years old (Late Palaeocene) deposits of Argentina (Reis, 1998). Other records, based mainly on isolated spines, fragments of skull and pectoral girdle elements are known from Miocene strata (Lundberg, 1997; 1998; Rubilar, 1994) with a single partial neurocranium from the ?Late Oligocene-Early Miocene of Brazil (Malabarba and Lundberg, 2007; Armbruster and Lujan, 2021). Although loricarioids have a meagre fossil record, molecular data suggests an Early Cretaceous age of around 115.8 million year for the origin for the group (Betancur et al., 2015), prior to the separation of the African and South American continents (Maisey, 2011). Within Loricarioidei, the Loricariidae (armoured catfishes) is the most speciose clade with around 1,220 species. Indeed, this makes it the most speciose family within the Siluriformes, and perhaps even within the Teleostei. Due to their

higher diversity and considerable anatomical complexity, little is known about the high-level phylogeny of Siluriformes.

Here, we describe and analyse a new genus and species from the Late Cretaceous of Morocco (Figs. 1, 2, Figs.S 1—6, supplementary material). Thus, we perform a phylogenetic analysis integrating morphological characters that can be checked in the new fossil with a multigene database for the main loricarioid lineages and outgroups, besides providing a full description of the new taxon. In addition, we test current age estimates for loricarioid lineages through a time-calibrated analysis using the new fossil (Supplementary Notes and Supplementary Methods). The discovery of a Cretaceous representative of this extant lineage is remarkable, not only for the evolutionary history of the group but also for understanding some of the evolutionary events that occurred during the early phase of the break-up of western Gondwana.

2. Material and methods

2.1. Geological framework

The Jbel Oum Tkout locality (OT1) crops out within the Douira Formation of the Kem Kem Group, in southeastern Morocco, 10 Km south of Tafraoute Sidi Ali, Errachidia Province. OT1 was deposited in a low-energy seasonally dried fresh water environment (Dutheil, 1999; Garassino et al., 2006), as indicated by an absence of marine organisms and the presence of unionoid bivalve and insect larvae, restricted to freshwater. The OT1 Konservat-Lagerstätte yielded numerous fossil remains including a rich flora of gymnosperms and angiosperms, as well as unionoid bivalves, aquatic insects, isopod and decapod malacostracans, hybodont elasmobranchs and actinopterygians (Garassino et al., 2006; Filleul and Dutheil, 2001; 2004), regularly preserving finely phosphatised soft-tissues and particularly muscles (Gueriau et al., 2014; 2015). Fossils have been recovered from five centimeter-thick successive grey

illitic layers exhibiting mudcracks. The absence of marine organisms and the presence of mudcracks, unionoids and larvae of odonatopterans and ephemeropterans points to a low-energy seasonally dried freshwater habitat comparable to a small lake, pool or oxbow lake.

Excavation at the Jbel Oum Tkout locality of the Douira Formation of the Kem Kem Group in southeastern Morocco took place in spring 1999. In addition to the single specimen of *Afrocascudo*, numerous other actinopterygians were collected.

2.2. Fossil preparation

The three pieces belonging to the specimen (MHNM-KK-OT 36) were transferred on polyester resin and the clayey matrix was removed by water with peroxide, followed by mechanical preparation using pin vises and needles under a binocular microscope.

Two dermal plates were removed from the specimen during its preparation, embedded in polyester resin (GBS 1; Brot) and sectioned for the study of bone and odontode structures. Two sections were ground and polished to a thickness of about 60–80 μm and observed under transmitted natural and polarised lights with a Zeiss Axiovert 35 microscope. Pictures were taken with a digital camera Olympus Camedia C-5060. For a better observation, the matrix was eventually removed from the pictures with the software “Adobe Photoshop”.

2.3. X-ray computed tomography

Two fragments of the holotype were studied in three dimensions using synchrotron X-ray microtomography. Measurements were performed at the PSICHÉ beamline of SOLEIL Synchrotron (Saint-Aubin, France) using a pink beam (63–69 keV), a single propagation distance of 36 cm, and 3900 projections. The available field of view was extended horizontally by positioning the rotation axis off-centre, and extended vertically by using a helicoid acquisition with a continuous vertical movement of the sample during multiple rotations of the sample. The volume (5.727 μm voxel size) was reconstructed from the combined radiographs using PyHST2 software (Mirone et al., 2014), with a Paganin phase retrieval algorithm (Paganin et al.,

2002). Segmentation and three-dimensional rendering were performed at the IPANEMA laboratory, manually (every single or 5 slices) using MIMICS Innovation Suite 19.0 (Materialise) and automatically (thresholding) using 3D Slicer (<http://www.slicer.org/>) for the tail fragment and skull roof, respective.

2.4. Multispectral imaging

The specimen was further documented using multispectral imaging at the Institute of Earth Science of the University of Lausanne (Switzerland) in order to enhance the distinction between bones present as actual remains versus resin casts. Reflection and luminescence images in various spectral ranges were collected using a setup consisting of a low-noise 2.58-megapixel back-illuminated sCMOS camera with high sensitivity from 200 to 1000 nm, fitted with a UV–VIS–IR 60 mm 1:4 Apo Macro lens (CoastalOptics) in front of which is positioned a filter wheel holding eight interference band-pass filters (Semrock) to collect images in eight spectral ranges from 435 to 935 nm. Illumination was provided by 16 LED lights ranging from 365 to 700 nm wavelength (CoolLED pE-4000), coupled to a liquid light-guide fitted with a fibre-optic ring light-guide. Among the more than 90 different illumination/detection couples available, 3 of the resulting greyscale images (excitation/emission of 740/935, 365/650, and 435/435) were combined into false color RGB composite images using ImageJ to enhance contrasts or reveal details invisible in traditional photography using only visible light. Results are shown in Fig. S1B, Fig. S3D, supplementary material.

2.5. Phylogenetic analysis

The total evidence matrix used for the current analyses included 3015 base pairs and 15 morphological characters. The characters have been carefully defined to be well delimited and completely independent of each other. Terminal taxa were *Afrocascudo saharaensis*, and 12 living teleosts, including eight species representing the main lineages of the suborder

Loricarioidei, a basal representative of the order Siluriformes, and *Distichodus notospilus*, *Danio rerio* and *Chanos chanos* as out-groups. The GenBank accession number of the sequences analysed are shown in Supplementary Methods 3. Sequences were edited in MEGA 7 (Kumar et al., 2016) and aligned using *ClustalW* (Chenna et al., 2003). The molecular data were analysed in the digital platform W-IQTREE (Trifinopoulos et al., 2016) to determine the best evolutive models, which are presented in Supplementary Methods 4. Morphological characters were analysed as a single partition, sites processed as unweighted under Mk model with gamma distribution (Lewis, 2001). The phylogenetic analyses were performed in the programs IQ-TREE (Nguyen, 2015), for Maximum Likelihood (ML) and MrBayes 3.2.6 (Ronquist et al., 2012) for Bayesian inference (BI). For the ML analysis the support values were calculated by 2000 bootstrap replications. Two runs and four independent Markov Chain Monte Carlo (MCMC) were performed with 5 million generations each, sampling one of every 1,000 trees for the BI analysis. The support values of the BI analysis were calculated by posterior probability. The quality of the MCMC chains was evaluated in Tracer 1.6 (Ronquist et al., 2012), and a 25% burn-in was removed. Both analyses recovered the same topology, support values are presented in Fig. 3.

This analysis and the compiled characters matrix represent a hypothesis that is likely to evolve as new observations and discoveries are made.

2.6. Divergence-time estimation

The divergence time analysis was performed in MrBayes 3.2.6, using the concatenated dataset with the same partitions as described above. A normal uncorrelated relaxed clock model which emphasizes the minimum age was applied. The time calibrated analysis was performed with 100 million generations, two runs and four independent MCMC a sampling frequency of 1000. The software Tracer v. 1.6 (Rambaut et al., 2014) was used to evaluate

the value of parameters of the analysis, convergence of the MCMC chains, sample size and the stationary phase of the chains. A Birth-Death speciation process was applied for the tree prior (Gernhard, 2008). Three calibration points were included in the analysis, (1) *Afrocas- cudo saharaensis*, based on the age of the fossil (minimum and maximum ages of 95 Ma and 100 Ma, standard deviation 1.0); (2) on the diversification between *Corydoras aenus* and *Cal- lichthys callichthys* based on the Late Palaeocene species *Corydoras revelatus* (minimum and maximum ages of 58.2 Ma and 58.5 Ma, standard deviation 1.0) (Lundberg et al., 2007); and (3) at the root of three based on the origin of Ostariophysi (minimum and maximum ages of 126.3 Ma and 158.3 Ma, standard deviation 1.0) (Benton et al., 2015). The analysis was performed on the CIPRES Science Gateway (Miller et al., 2010). The calibrated tree present- ing divergence time estimations means and 95% highest posterior densities are presented in Supplementary Methods 5.

3. Results

3.1. Systematic palaeontology

Siluriformes Cuvier, 1817

Loricarioidei (*sensu* Howes, 1983)

Loricariidae Rafinesque, 1815

Genus *Afrocas- cudo* gen. nov. (monotypic genus)

Etymology: *Afrocas- cudo* after *Afro*, Africa (in Latin) and *cas- cudo* (in Portuguese), the com- mon name by which armoured catfishes (generally Loricariidae) are known in Brazil, the country where there is the greatest diversity of this family.

Diagnosis for monotypic genus and species: *Afrocasudo* differs from all other teleost fishes, except loricarioid catfishes, by the presence of dermal plates ornated with odontodes on the flank (vs. absence). *Afrocasudo* is distinguished from all loricarioid catfishes, except members of the clade comprising Astroblepidae, Callichthyidae, Loricariidae, and Scoloplacidae, by having reduced mesethmoid cornua (vs. well-developed in Nematogenyidae and Trichomycteridae), three or four branchiostegal rays (vs. eight or more), the presence of a lateral connecting bone (vs. absence), and the dorsal hypural elements fused to the compound caudal centrum (vs. unfused); from all loricarioid catfishes, except members of the clade comprising Astroblepidae, Loricariidae, and Scoloplacidae, by the lateral connecting element being ossified (vs. unossified when present); from all loricarioid catfishes, except members of the clade comprising Astroblepidae and Loricariidae, by the absence of parapophyses (vs. presence) and the parhypural fused to the ventral hypural plate (vs. unfused); from all loricarioid catfishes, except members of the Loricariidae, by the presence of three longitudinal rows of dermal plates on the flank (vs. two rows or rows absent) and presence of dermal plates on the cheek region (vs. absence); *Afrocasudo* is distinguished from all Loricariidae, except the *Acanthicus* group, by the presence of prominent odontodes, arranged in a longitudinal row, along each row of flank dermal plates (vs. odontodes minute, not arranged in longitudinal rows); *Afrocasudo* has the dorsal fin defensive spine covered with numerous odontodes.

Type and only species: *Afrocasudo saharaensis* sp. nov.

Holotype: MHNM-KK-OT 36 a—c (Figs.1, 2, Figs.S 1—6, supplementary material), belongs to the Musée d'Histoire naturelle de Marrakech, Morocco (MHNM). The specimen is formed by three distinct pieces, collected still articulated, in the field.

Type locality: The Jbel Oum Tkout locality (OT1) crops out within the Douira Formation of the Kem Kem Group, in southeastern Morocco, 10 Km south of Tafaout. This locality is early Cenomanian (Late Cretaceous) in age (Sereno et al., 1996; Dutheil, 1999; Ibrahim et al., 2020). The fossiliferous bed is a 50 to 150 cm centimeter-thick successive grey illitic layers exhibiting mudcracks. Additional details regarding the locality, sedimentary environment, and palaeobiota are provided in the Geological framework.

3.2. Description

The holotype represents a nearly complete, small sized fish, lacking large parts of the head, pectoral and pelvic fins. Dorsal and lateral surfaces of the head and the body are entirely covered by bony plates coated by numerous odontodes directed obliquely backwards. This specialised armoured morphology is unique among catfish and represents a synapomorphy of the family Loricariidae, the suckermouth armoured catfish (Alexander, 1996; Rivera-Rivera and Montoya-Burgos, 2017; Mori and Nakamura, 2022). The specimen has an elongated body, progressively tapering from the cleithrum to the end of caudal peduncle, with total length of approximately 74 mm and a preserved maximum depth (although the anterior part of the body is distorted) of 9 mm. The head occupies about 35% of the total body length.

The roof of the skull is triangular in shape, narrow anteriorly, forming a long and pointed snout. The skull roof expands posteriorly into the orbit region, becoming wider mainly in the occipital region. (Fig. 1A, Fig. S1, supplementary material). The arrangement of the cranial bones shows a similar pattern to those of extant loricariids including paired nasals, frontals, sphenotics, compound pterotics, and a parieto-supraoccipital. No cranial fontanelle is present. The nasals are very elongated bones (Fig. 1B), probably surpassing the anterior margin of lateral ethmoid; posteriorly they are connected to the frontals. The frontals are as long as nasals. They form almost the entire dorsal margin of the orbits, contacting posterolaterally the somewhat square-shaped sphenotics and meeting medially the parieto-supraoccipital. The

parieto-supraoccipital is about as wide as long. It contacts anteriorly the sphenotics and the frontals and laterally the compound pterotics (Fig.1A, Fig. S1, and supplementary material). As in other loricariids, scoloplacids, and astroblepids, the compound pterotics (pterotics + supraclithra) are greatly expanded laterally, forming most of the posterolateral part of the skull (Schaeffer, 1987) (Fig.1C, Figs. S1–3 supplementary material). These bones are covered with numerous odontodes of different sizes (Fig.1C). The skull roof is posteriorly limited by four roughly square-shaped plates.

In ventral view some bones of the neurocranium can be observed. They are paired orbitosphenoids, prootics, exoccipitals and compound pterotics, and median mesethmoid, parasphenoid, and basioccipital (Fig. 2A,B, Fig. S2A, supplementary material). Note that some of these bones have been destroyed during preparation and are only preserved as casts in the polyester resin; they can therefore not be observed in the microtomography data. Bones preserved as resin casts appear translucent greyish, while actual bone remains exhibit much more texture and a very different color (see e.g., the pterotic in Fig. 2A, fin rays in Fig. 2D, Fig. S5B, C, supplementary material, and posterior plates between odontodes in Fig. S5E, supplementary material). We further enhanced the distinction between bone remains and casts by exploiting the different luminescence properties of apatite (the main mineral component of bone) and the resin using multispectral imaging (Fig. S1B, S3D, supplementary material).

The neurocranium is narrow anteriorly, widening posteriorly reaching its maximum width in the occipital region. Although displaced and broken caudally, the mesethmoid is quite straight and slender, widening slightly posteriorly (Fig. 2A–C). Anteriorly, it shows a reduced and rounded anterolateral cornua, followed by a small mesethmoidal disc (Fig. 2C).

Although incomplete, the orbitosphenoid is a somewhat rectangular bone. It sutures the prootic posteriorly. The prootic is larger than the orbitosphenoid and forms the ventrolateral floor of the neurocranium. It sutures posteriorly to the basioccipital, the exoccipital, and the

compound pterotic.

The basioccipital contacts anteriorly with the parasphenoid, posteriorly the Weberian complex, and laterally sutures to the prootic and exoccipital (Fig. 2A, B, Fig. S2, supplementary material). The basioccipital lateral process contacts the mesial end of the ossified Baudelot's ligament of the compound pterotic forming a distinct wall as in many loricariids (Fig. 2B, Fig. S2, supplementary material). The exoccipital is a small bone posteriorly limited by the basioccipital lateral process as in other loricariids.

Only the posterior third of the parasphenoid is preserved; it is wide, sharing a large interdigitated suture with the basioccipital. The hyoid arch presents four branchiostegal rays.

The Weberian complex centrum is short and almost square shaped, having about the same length as the sixth centrum (Fig. 2A, B, Fig. S2, supplementary material). This centrum contacts the basioccipital anteriorly and the sixth centrum posteriorly. Laterally, the transverse process has its distal margin rounded. It is easily distinguished from the compound pterotic, with approximately the same length of this bone. The sixth centrum is partially preserved and articulates with the first pair of ribs. Although not all vertebrae, especially those of the posterior region of the body, are preserved we estimate the number of vertebrae at approximately 30, including the five forming the Weberian apparatus. The vertebrae are strongly ossified, with distally expanded neural and haemal spines that meet the dorsal and ventral plates of the skin surface (Fig. 1C, Fig. S3, supplementary material). Vertebral parapophyses are absent.

Although slightly displaced, the caudal-fin skeleton consists of the compound centrum (PU1 + U1) fused to the dorsal hypural elements. The dorsal hypural element is superimposed by large and continuous expansion of the neural spine of the second pleural centrum, that almost reaches the posterior border of the hypural plates. The ventral plate has the same size as the dorsal one and is the result of the fusion between parhypural with the hypural element as in other loricariids and astroblepids (Lundberg and Baskin, 1969; Schaeffer, 1997)

(Fig. 2E, Fig. S4 , supplementary material).

Although the terminal part of the caudal fin is not preserved, the fin seems to have a symmetrically rounded distal margin (Fig. 1E, 2D, E). It displays several dorsal procurrent rays (the ventral ones are not preserved), two unbranched and 12 branched rays. The caudal peduncle is covered by three rows of plates.

The dorsal fin consists of a small, elliptical, anterior spinelet, a large defensive spine, and eight or nine branched rays (Note that because some rays may be misaligned due to a detachment of the lepidotrichia the precise number of fin rays is really difficult to assess with confidence). The defensive spine is covered with numerous odontodes (Fig. 1E, Fig. S5 A–C, supplementary material). The dorsal-fin inserts slightly more posterior to the pelvic-fin origin. The dorsal fin pterygiophores have their distal half slightly curved posteriorly. Well-ossified ribbonlike lateral connecting elements are present. The connecting bone is dislocated and covered by numerous fragments of plates, broken during the taphonomic process (Fig. 1E).

No distal radials precede the spines, although they are associated with the branched rays. The pelvic fin is well-developed, presenting an unbranched ray, covered with numerous odontodes, and five branched rays, all arranged parallel to each other (Fig. 1E, Fig. S5A, supplementary material). Although the anal fin is not preserved, we can see the impression of four rays in the resin.

Due to the distortion of the anterior part of the body, the pectoral girdle and the fins are much damaged, raising difficulties in locating some anatomical structures such as the coracoids. The bones of the pectoral girdle support numerous odontodes of varying sizes. The largest ones at the anterior and lateral edges of the cleithra. Although lost during preparation, the cleithrum was a remarkably massive bone, disposed in horizontal and vertical planes (Fig. S3A, supplementary material). The right pectoral-fin spine, although broken in two parts and much worn, is present. The spine is well ossified and gently curved. In ventral view, the base shows a well-developed, somewhat rounded ventral articular process (Fig. 1D). Both,

the base and part of the spine shaft are covered with relatively prominent odontodes. Three or four rays belonging to the pelvic fin are present immediately behind the pectoral girdle. The pelvic girdle was not preserved. The cranial plates are ornamented with numerous odontodes or pits where the odontodes were inserted (Fig. 1A, B, Fig. 2A, Fig. S1, supplementary material). In the anterior region of the body, dermal denticles form four distinct longitudinal rows of bigger odontodes going from the most anterior region of the skull to at least the first postcranial plates. On the postcranial plates, the odontodes are positioned in a series of three or four odontodes aligned in their medial part (Fig. 1E–G, Fig. S5D, E, supplementary material). All odontodes are conical true teeth constituted by enamel surrounding a central pulpar cavity which communicate with the vascular network of the bony plate (Sire and Meunier, 1993) (Fig. S4E, F, Fig S6, supplementary material).

There is only one other occurrence of odontodes from the Cretaceous of northern Africa: 6 hemisegments of lepidotrichia bearing one or two hook-like odontodes from older deposits (pre-Aptian) of southern Tunisia. However, the rays that bear odontodes in Loricariidae and our new fossil are not subdivided into hemisegments, and the Tunisian fossils were instead considered to belong to an actinistian (Cuny et al., 2010).

4. Discussion

4.1. Phylogenetic relationships

To test relationships of *Afrocasudo* with other loricarioids, we used an integrated morphological and multigene database (Supplementary material 1–5). Within this phylogenetic context, the loricarioid monophyly is corroborated, but the resulting topology differs from the hypothesis of previous authors (Diogo, 2004; de Pinna, 1998) by the Nematogenyidae being retrieved as sister to all other Loricarioidei, instead of sister to only the Trichomycteridae. In the analysis, *Afrocasudo* emerges with high support as a member of the Loricariidae (Fig. 3).

Afrocascudo is clearly a siluriform on account of many derived characters such as the fusion of the parietals with the supraoccipital, the possession of spiny rays anterior of the dorsal and pectoral fins, and a complete lack of scales (Fink and Fink, 1981). It is a member of Loricarioidei as it possesses an encapsulated Weberian apparatus and has numerous odontodes. Within loricarioids, *Afrocascudo* appears to belong in a clade with callichthyids, scoloplacids, astroblepids and loricariids as it has a shortened mesethmoid cornua. Furthermore, *Afrocascudo* has laterally expanded compound pterotics that form the largest part of the lateral skull as in scoloplacids (astroblepids + loricariids) (de Pinna, 1998). Similarly, the presence of two hypural plates, also found in astroblepids and loricariids, confirms its position in this clade (Rivera-Rivera and Montoya Burgos, 2017). Within Loricarioidei, *Afrocascudo* possesses several characters that place it in Loricariidae: ossified dermal plates on head, absent in callichthyids, scoloplacids, and astroblepids (de Pinna, 1998) and body, trunk with a series of three dermal plates (Alexander, 1966; Schaeffer, 1987; 2003; Baskin, 2016; Mori and Nakamura, 2022), and well ossified vertebrae in which the neural and haemal spines are expanded and compressed meeting the dorsal and ventral plates of the skin surface (Lundberg, 1993). Importantly, the arrangement of the odontodes of the post-cranial dermal plates is unlike that of most of the extant Loricariidae, where the odontodes are arranged in several longitudinal rows. In *Afrocascudo* they form a single row of three or four, resembling the pattern found in *Acanthicus* and in scoloplacids, although in the latter there are only two dermal plates on the flank of the body and the odontodes are all of the same size. Thus, *Afrocascudo* shows that the loricariid body plan was already present by mid-Cretaceous times.

4.2. Timing of Loricarioidei origin

Our time-calibrated analysis provides support for a Lower Cretaceous (Aptian ~112,32 MYR) split between the Diplomystidae and the Loricarioidei, prior to the separation of western Gondwana. The crown group loricarioids first appeared in the Albian (~110,71 MYR) while

the separation between *Afrocasudo* and the Neotropical Loricariidae would have mostly likely occurred between ~95 and 100 MYR, indicating diversification of this group in the Early Cretaceous prior to the Cenomanian and coinciding with the definitive separation of Africa and South America.

4.3. A Gondwanan biogeographical history

Afrocasudo also sheds light on some evolutionary events that occurred during the early phase of the break-up of western Gondwana. The presence of this well-defined lineage of loricarioid catfish, currently typical of the Neotropical region, supports the existence of a common and endemic western Gondwana fresh-water ichthyofauna before the complete separation of Africa and South America. Until the Albian a persistent land connection permitted substantial biotic exchanges that maintained relatively uniform continental faunas (Medeiros et al., 2014; Veiga et al., 2019). After the final separation of western Gondwana, when dispersal routes between these land masses were finally severed and deeper oceanic barriers developed, the once cosmopolitan freshwater fish assemblages experienced distinct fates: in Africa they survived for some time until becoming extinct probably by the transitional marine episodes of the late Cenomanian-Turonian, which flooded the northern part of this continent (Reyment, 1980) whereas in South America, the Loricarioidei not only survived but became a diverse and widespread group.

Except for the genus *Lacantunia* and freshwater ariids, no extant African siluriform (Lundberg et al., 2007) taxon is a sister group to any South American lineage (Greenwood, et al. 1966; Lavoué, 2020). It seems that the extant African catfish families reached the continent after dispersal events from Asia (Lavoué, 2016), with a fossil record extending back only to the Coniacian Santonian of Niger and Palaeocene of Nigeria (White, 1934; Patterson, 1993; Murray and Holmes, 2022). Thus, the Jbel Oum Tkout loricariid, was part of an old evolutionary story that, in Africa, ended at the beginning of the Late Cretaceous, most likely

corresponding to the early Cenomanian-Turonian transgression.

During the Early Cretaceous, the western Gondwanan palaeoichthyofauna was dominated by polypteriforms, halecomorphs, ginglymoids and basal teleosts such as goniorhynchiforms, elopomorphs, and clupeomorphs, as well as lobed finned fishes such as lungfishes and mawsoniid coelacanths (Veiga et al., 2019; Cavin, 2010). Much of this ichthyofauna appears to have become extinct or was greatly reduced by the end of the Cretaceous. Therefore, the discovery of *Afroscudo* further offers an exceptional example of how some of the most important freshwater lineages among vertebrates, such as loricariids, today restricted to the Neotropical region, originated in Gondwanan ecosystems and later survived the K/Pg extinction; this has been confirmed in the case of neobatrachians (Agnolin et al., 2019) and must be the case for other groups of freshwater fishes. However, our understanding of their diversification remains vague due to the scarcity of relevant fossils, probably linked to special palaeoecological conditions and selective preservation biases. Evidence from more Cretaceous freshwater strata of eastern Gondwana will hopefully provide new data for testing phylogenies and evolutionary scenarios and will further document the origin of other neotropical clades.

5. Conclusions

Afroscudo saharaensis represents the oldest known catfish and the oldest known fossil loricarioid, currently endemic of the Neotropical region. This discovery supports the existence of a common and endemic western Gondwana fresh water ichthyofauna before the complete separation, in the Albian, of Africa and South America. A phylogenetic analysis integrating morphological characters with a multigene database for the main loricarioid lineages and outgroups highly supports inclusion of the fossil within the Loricariidae. A time-calibrated analysis corroborates the origin of loricarioids at about 112 MYA.

The presence of this loricariid in Africa provides evidence that loricarioids have diversified before the separation of Africa and South America. The Moroccan loricariid shows an ancient evolutionary history that, in Africa, ended in the Late Cretaceous but persisted in South America, later surviving the K/Pg extinction.

Data accessibility. The holotype of *Afrocascudo saharaensis* belongs to the Musée d'Histoire naturelle de Marrakech, Morocco (registration number MHNM-KK-OT 36 a—c). The material is currently housed at the Muséum national d'Histoire naturelle (Paris, France) for study, within an agreement between both museums. Correspondence and requests for materials should be addressed to P.M.B. or D.B.D. The synchrotron X-ray microtomography datasets (tomographic slices) used in this study are available on Figshare (<https://doi.org/10.6084/m9.figshare.23669274.v1>). High-resolution versions of the figures are available on Zenodo (<https://doi.org/10.5281/zenodo.10019045>; the access is restricted during peer-review, please use this temporary link for access in the meantime: [### **Declaration of Competing Interest**](https://zenodo.org/records/10019045?token=eyJhbGciOiJIUzUxMiIsImIhdCI6MTY5NzY3MDE2NCwiZXhwIjoxNzAyNzcxMTk5fQ.eyJpZCI6ImY3ZDFmODkwLWNmMzltNDkzMS05NzcxLTc2MDRIODg1ZDcwYyIsImRhdGEiOnt9LCJyYW5kb20iOiIwY2ZjNjdhYzJiZGVkYzI3ZDY0MTE5MzhhODRiZGZGNiZSJ9.cKkKZeLX1xs1X7cM7oKsM7NBXu5_sSCO428pYwXoG6Hd8hpkTcC4gz7KwZGsayG_6KqWzMPKRPbljvKHOSaTwQ).”</p></div><div data-bbox=)

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary Material

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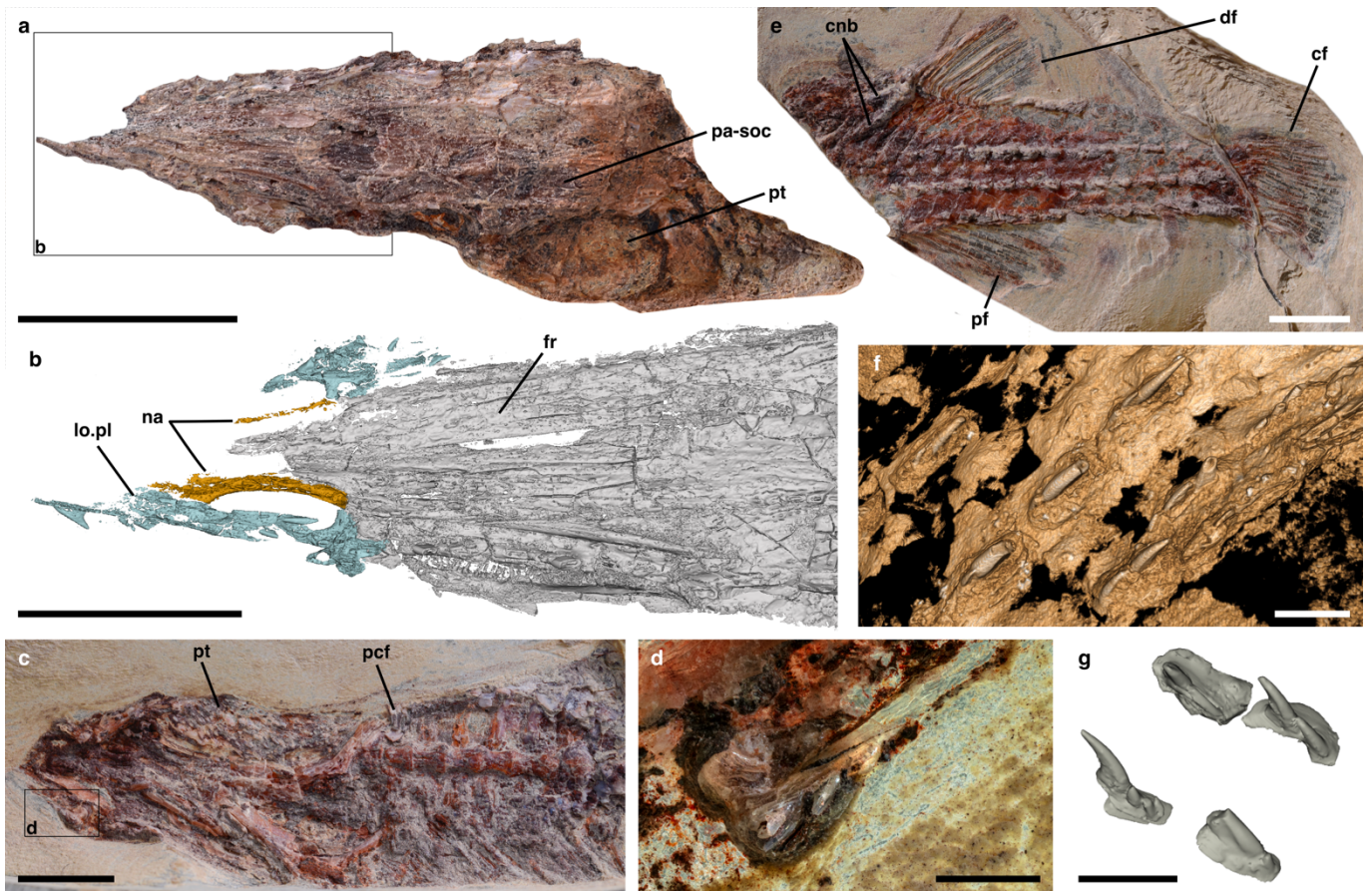


Figure 1. *Afrocasudo saharaensis* gen. et sp. nov., holotype MHNM-KK-OT 36 a—c. a, MHNM--KK-OT 36 a, skull in dorsal view. b, 3D rendering of the anterior part of the skull in dorsal view. c, MHNM-KK-OT 36 b (mirrored), ventral view of skull and first free vertebrae. d, Close-up view of the pectoral fin spine base. e, MHNM-KK-OT 36 c, postcranial region in lateral view, showing dorsal, pelvic and caudal fins. f, g, 3D rendering of the odontodes of the caudal region, top view (f) and lateral view (g). Abbreviations: cnb, connecting bone; df, dorsal fin; lo.pl, infraorbital plate; pa-soc, parieto-supraoccipital; fr, frontal; na, nasal; pcf, pectoral fin; pf, pelvic fin; pt, pterotic-supracleithrum. Scale bars, 10 mm (a), 5 mm (b, c, e), 1mm (d, f, g).

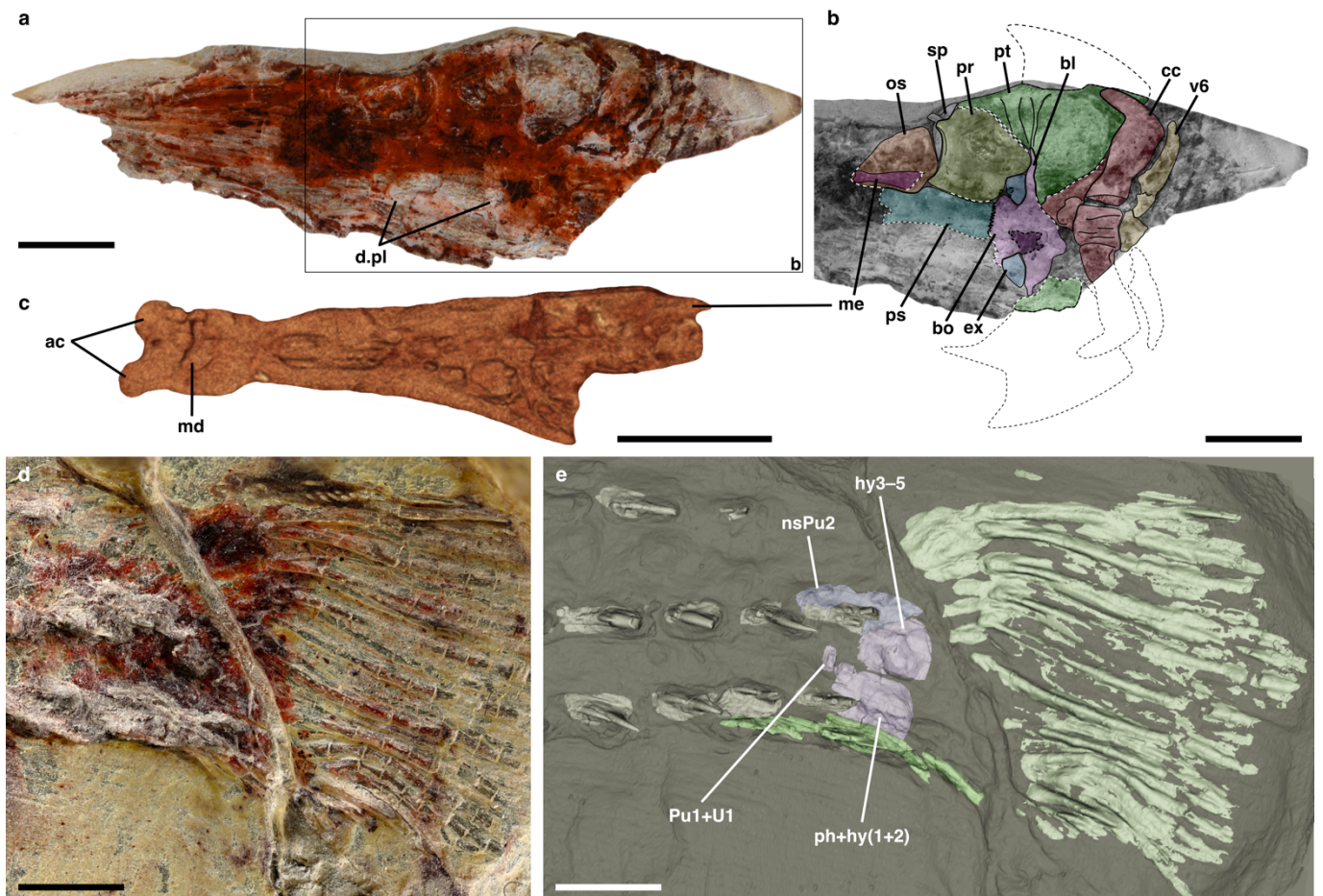


Figure 2. *Afrocasudo saharaensis* gen. et sp. nov., holotype MHNM-KK-OT 36 a—c. a, MHNM-KK-OT 36 a, skull in ventral view. b, Interpretative drawing of the brain case (some bones are preserved as casts in the polyester resin). c, 3D rendering of the mesethmoid in ventral view. d, MHNM-KK-OT 36 c, close-up of caudal region. e, 3D rendering of part of caudal endoskeleton shown in lateral view. Abbreviations: ac, mesethmoid anterior cornua; bl, basioccipital lateral process; bo, basioccipital; cc, Weberian complex centrum; d.pl, dermal plates; ex, exoccipital; hy3-5, fusion of hypural plates 3, 4 and 5 (plus uroneural and epural); md, mesethmoid disc; me, mesethmoid; nsPu2, neural spine of second pretrial centrum; os, orbitosphenoid; ph+hy (1+2), fusion of parhypural and hypural plates 1 and 2; pr, prootic; ps, parasphenoid; pt, pterotic-supracleithrum; Pu1+U1, fusion of first pleural centrum and first ural centrum; sp, sphenotic; v6, sixth vertebrae. Scale bars 5 mm (a, b), 2 mm (d, e), 1 mm (c).

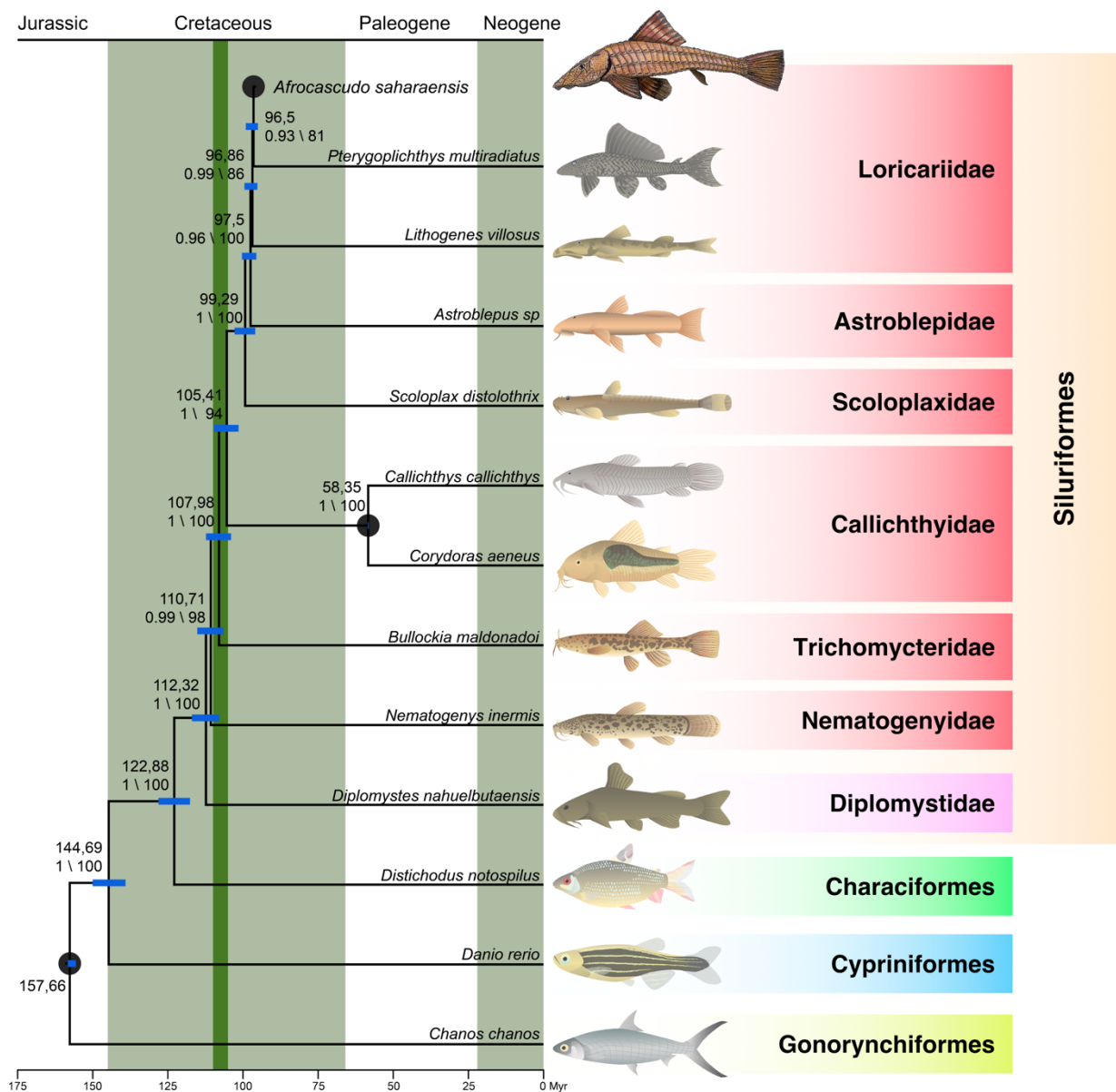


Figure 3. Time-calibrated phylogenetic placement of *Afrocascudo saharaensis* gen. et sp. nov. Time calibrated analysis recovered the same topology as IB and ML analyses. Black circles indicate the calibration points. Values near the nodes indicate divergence-time estimation mean (above) and Posterior probability IB analysis followed by Bootstrap of ML analysis (below). Blue bars indicate 95% highest posterior credibility intervals of divergence times, dark green column indicates the disjunction between South America and Africa. Illustration represent the sampled terminal species. The reconstruction of the new taxon, *Afrocascudo saharaensis*, is highlighted in the drawing.