

Technical Note

On the Occurrence of the Gar *Obaichthys africanus* Grande in the Cretaceous of Portugal: Palaeoecological and Palaeobiogeographical Implications

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Abstract: Several disarticulated fish scales and a vertebral centrum were collected from the uppermost middle to lowermost upper Cenomanian beds of the vertebrate fossil site of Casais dos Carecos (Baixo Mondego region, Coimbra, West Portugal), corresponding to shallow carbonate and mixed facies (“Unit B”) of the Tentúgal Formation. The taphonomic preservation of these remains is adequate for their detailed taxonomical study. The scales are diagnosable for the species *Obaichthys africanus* Grande, as each one has a strong spine protruding from the middle of the posterior border in a rostro-caudal direction, a dorsoventral peg and socket, and a small anterodorsal process for articulation of adjacent scales. The sculpture with ganoid ridges and grooves distinguishes the studied remains from those of *O. decoratus* Wenz and Brito, which display rounded tubercles. The isolated Lepisosteioidea centrum is tentatively attributed to *O. africanus* as well, as it was found together with the scales, and no other compatible remains were found in the site. The fish material reported here constitutes the first record of *O. africanus* in the Baixo Mondego region and northern ranges of the Albian–Turonian West Portuguese Carbonate Platform, as well as in the uppermost middle to basal upper Cenomanian of Portugal.

Keywords: Cenomanian; Lepisosteioidea; Obaichthyidae; scales; Casais dos Carecos (Coimbra)



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1. Introduction

Lepisosteioidea scales have been scarcely recorded in the Cenomanian of Portugal since the late 19th century, and they were tentatively classified at that time as “ganoid fish” [1] and “Paleoniscidae indet” [2]. All these early findings were collected from the section of Pendão (Belas, Sintra, northwest of Lisbon) and housed at the Geological Commission of the Kingdom (later renamed the Geological Museum of the National Laboratory of Energy and Geology), in Lisbon. These scale remains were found during extensive fieldwork carried out by Paul Léon Choffat (1849–1919), which resulted in the first full definition of the Cretaceous stratigraphic setting of Portuguese South Estremadura and its main faunas e.g., [3–6]. They were collected from shallow carbonate platform beds assigned to the “*Exogyra pseudofrancica* level” of the local “Bellasian” stage [1,7]. Based on micropalaeontological data [5,8,9], this oyster-rich level, with North African affinities, was positioned in the lower Cenomanian [10,11]. These Lepisosteioidea scales from Portugal were subsequently mentioned by Ernst Stromer (1871–1952), who related them with remains collected in the Cenomanian of Egypt [12] (p. 42), as well as in the description of *Stromerichthys aethiopicus* Weiler [13] (p. 30), thus reinforcing the Tethyan affinities of the Portuguese materials.

Additional scales, identified as aff. *Stromerichthys* sp. [13], *S. aethiopicus* Weiler [13], *Paralepidosteus cacemensis* Jonet [14], and “*Lepidotus*” *minimus* Jonet [14], were recorded by the Portuguese Geological Survey during cartographic works carried out in the areas of Lisbon, Sintra, and Cascais. After their study [14–17], these remains considerably increased the number of lepisosteiform findings in the lower Cenomanian of Portugal.

In recent years, the scales mentioned above and previously classified as “*Paleoniscidae* indet” and *S. aethiopicus* were reidentified [18] as *Obaichthys africanus* Grande [19]. The same authors [18] also cautiously re-assessed the scales previously classified as *P. cacemensis* and *L. minimus* [14] as probably corresponding to *Dentilepisosteus kemkemensis* Grande [19].

Despite these common early Cenomanian records, until this work, *Lepisosteioidea* scales remained unknown from higher levels of the carbonate platform, namely at the uppermost middle to lowermost upper parts of the Cenomanian, both with a significant stratigraphic record available in the onshore ranges of the West Portuguese Margin (WPM) [20–22].

In the present work, new well-preserved *Obaichthyidae* remains are reported from Cenomanian carbonate platform beds exposed near Casais dos Carecos (Coimbra), in the Baixo Mondego region of West Portugal, about 200 km northward of Lisbon. These are not only the first scales to be collected in the middle Cenomanian beds of the country, but also the first ones to be identified in the northern ranges of the WPM. The purpose of this study is to present a detailed morphological description and taxonomic identification of these new remains. The here-provided data expand the known stratigraphic and palaeobiogeographical ranges of *Lepisosteioidea* fishes and improve our knowledge regarding the rich vertebrate faunas and palaeoenvironmental evolution of the Tethyan WPM during the Cenomanian, e.g., [20–25].

2. Geological and Stratigraphic Settings

The *Lepisosteioidea* material studied here was sampled in the vertebrate fossil site of Beiraterria quarry (40°15′10.9″ N, 8°34′13.3″ W), near the village of Casais dos Carecos, in the Coimbra municipality of the Baixo Mondego region (Figure 1A,B). It was found in local basal levels of the Cenomanian–Turonian West Portuguese Carbonate Platform (WPCP, a part of the post-rift series of the West Portuguese Margin), where transgressive beds of the Tentúgal Formation (Fm) overlay the lower to middle Cenomanian alluvial to tidal flat coarse sandstones of the Figueira da Foz Fm [26,27] (Figure 1C).

The lower part of the Tentúgal Fm consists of a basal member (“Unit B”) sensu [7,20,28–31] of uppermost middle to basal upper Cenomanian fine-grained sandstones, interbedded with sandy limestones, mudstones, and marls with low-diversity bivalve assemblages dominated by the oyster *Gyrostroma ouremensis*, together with *Septifer lineatus* and *Anisocardia orientalis* (Figure 1C). Besides *Obaichthys africanus*, the local vertebrate assemblage yields diverse remains of lamniform sharks, enchodontids, obaichthyids, rare turtle plates, and the recently described *Pythonomorpha* lizard *Carentonosaurus soaresi* and *Crocodylomorpha* *Portugalosuchus azenhae*.

The shallow-water sequence of “Unit B” is overlaid by a transgressive surface with a set of nodular marly carbonates, with a rich and diverse carbonate shelf fauna (“Unit C”) (Figure 1C). These beds yield an early late Cenomanian ammonite assemblage with *Neolobites vibrayeanus* and *Calycceras naviculare* [7,20,21,28,32,33]. The succession continues upwards with a bed of whitish massive limestones, packstone to grainstone (“Unit D”), with abundant fragments of scleractinian corals, mollusks, and the echinoid *Anorthopygus michelini* (Figure 1C). Outside the quarry area (Figure 2), the Tentúgal Fm finishes with a few meters of greyish marls with nodular limestone layers (“Units E and F”), where a middle upper Cenomanian assemblage of Tethyan ammonites with *Vascoceras gamai* can be recognized [20,21,33].

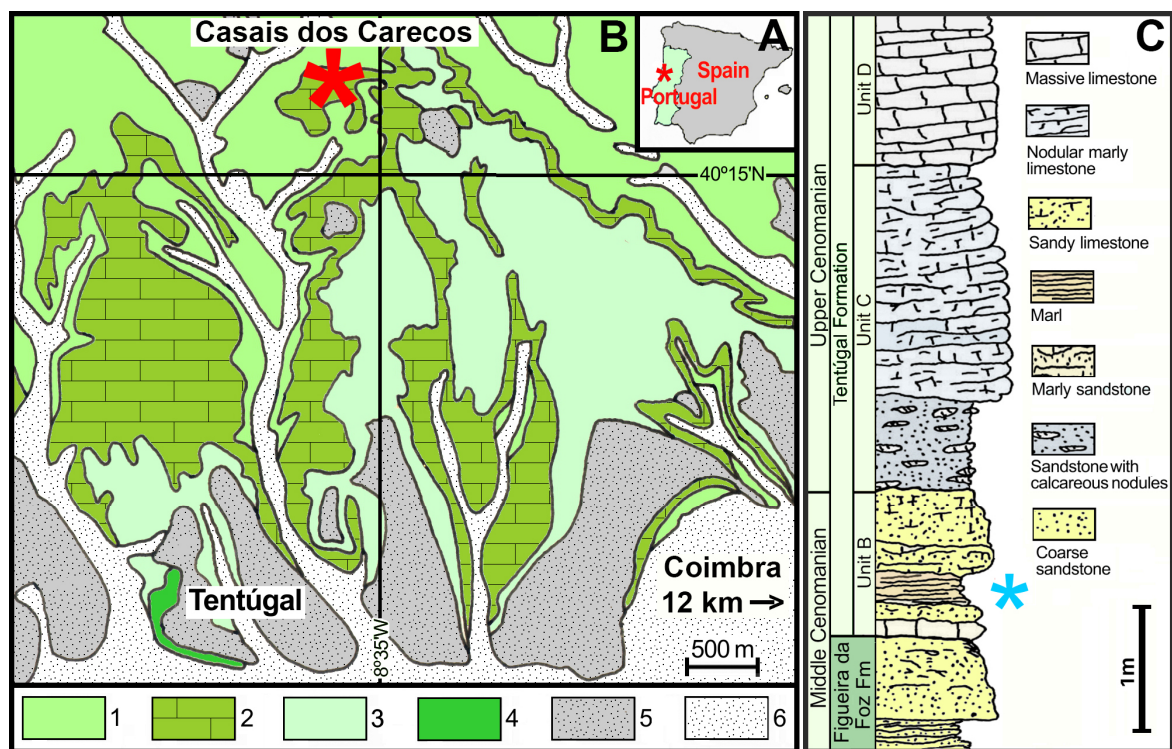


Figure 1. Geographical and geological context of the Beiraterria quarry vertebrate fossil site, Casais dos Carecos, Coimbra (Baixo Mondego region of West Portugal). (A) General location of the site in the Iberian context. (B) Simplified geological map with the Cretaceous and Quaternary units of the Baixo Mondego region and the location of the Beiraterria quarry. Cretaceous—1: Figueira da Foz Formation (upper Aptian to middle Cenomanian alluvial to marginal marine coarse sandstones); 2: Tentúgal Formation (uppermost middle Cenomanian to lower Turonian platform carbonates); 3: Furadouro Formation (lower to upper Turonian marginal marine to alluvial micaceous sandstones); 4: Oiã Formation (Coniacian and Santonian alluvial coarse sandstones); Pleistocene—5: Fluvial terraces; Holocene—6: Alluvial surface deposits. (C) Stratigraphic section of the uppermost middle to upper Cenomanian transgressive carbonate platform succession at the site. Red asterisks indicate the location of the site, and blue asterisk indicates the levels with *Obaichthys africanus* Grande [19].



Figure 2. Cont.

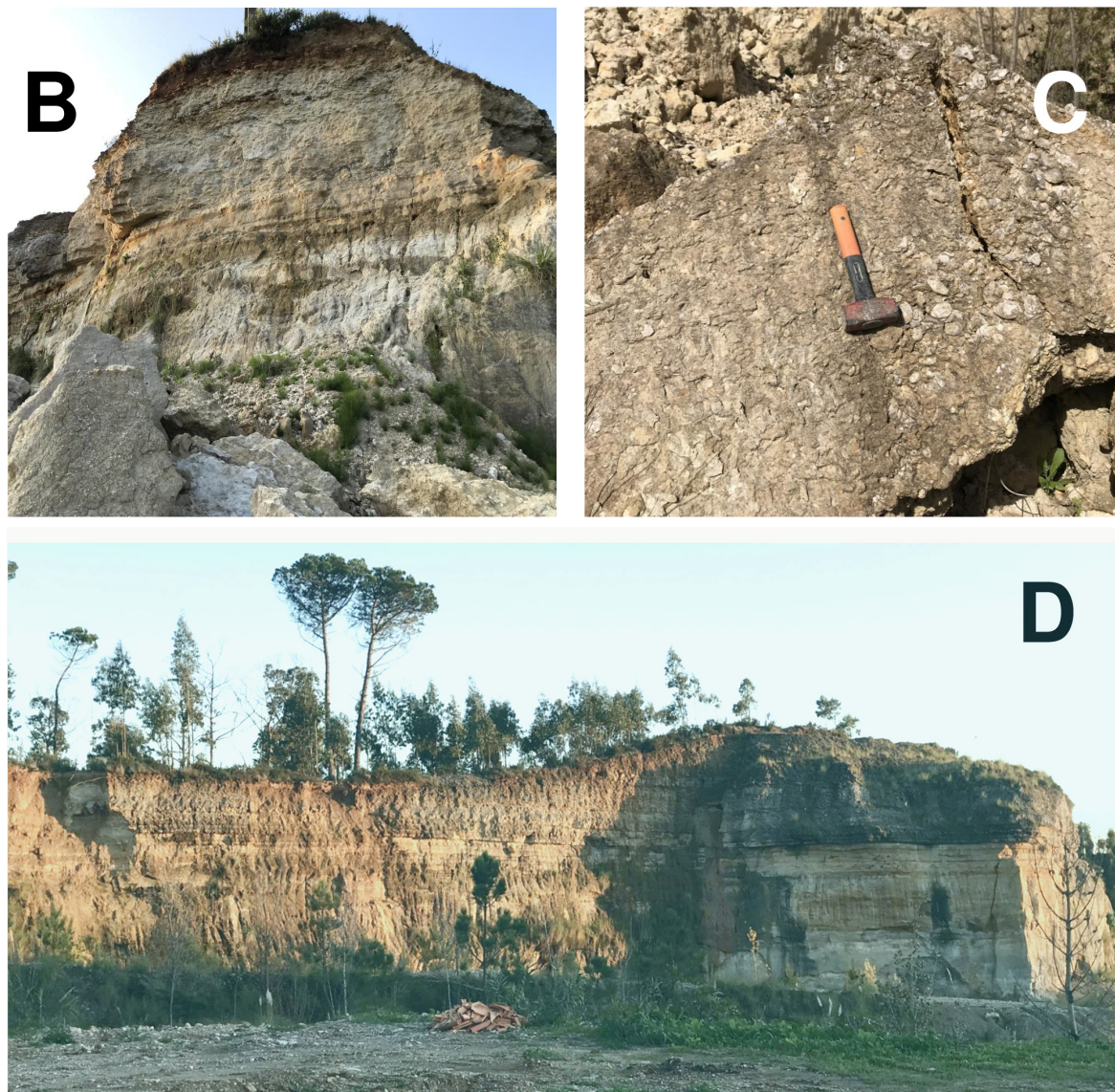


Figure 2. Panoramic views of Beiraterria quarry vertebrate fossil site, Casais dos Carecos, Coimbra (Baixo Mondego region of West Portugal), showing the middle and upper Cenomanian succession. (A) Panoramic view of the west front of the quarry. (B) Detailed view of the north front of the quarry. (C) Block from “Unit B” of Tentúgal Formation with a pavement of *Gyrostrea ouremensis*. (D) Panoramic view of the east front of the quarry.

3. Materials and Methods

The studied scales and vertebral centrum were found disarticulated and collected in situ, between 2019 and 2023, from a few collapsed quarry face blocks that correspond to the top of “Unit B” (specimens DCT-CC-15, DCT-CC-16, DCT-CC-17, DCT-CC-18, DCT-CC-19, DCT-CC-32) or obtained from the screen washing of a 100 kg bulk sample of sediments collected between January and February of 2023 (specimen DCT-CC-34). The scales were cleaned using mechanical tools, examined using a Leica® MZ 16A binocular stereomicroscope, and photographed with a Canon® EOS 550D camera with a Sigma® 50 mm F2.8 DG macro lens and an Olympus® E-M5II camera.

Suprageneric classification followed López-Arbarelo [34]. All specimens are housed (with additional unnumbered fish remains from the same locality) in the palaeontological collections of the Department of Earth Sciences, University of Coimbra (DCT-CC), Portugal.

4. Material Description

The six complete, or almost complete, isolated scales (DCT-CC-15, DCT-CC-16, DCT-CC-17, DCT-CC-18, DCT-CC-32, and DCT-CC-34, Figure 3), and the opisthocoelous vertebral centrum (DCT-CC-19, Figure 4) show an adequate taphonomic preservation state for morphological description and taxonomic study, with no signs of distortion or intensive abrasion, and many diagnostic characteristics are still present. The six examined scales are well preserved, with a shiny ganoine layer on their exterior surface and a bony basal plate on their interior face.

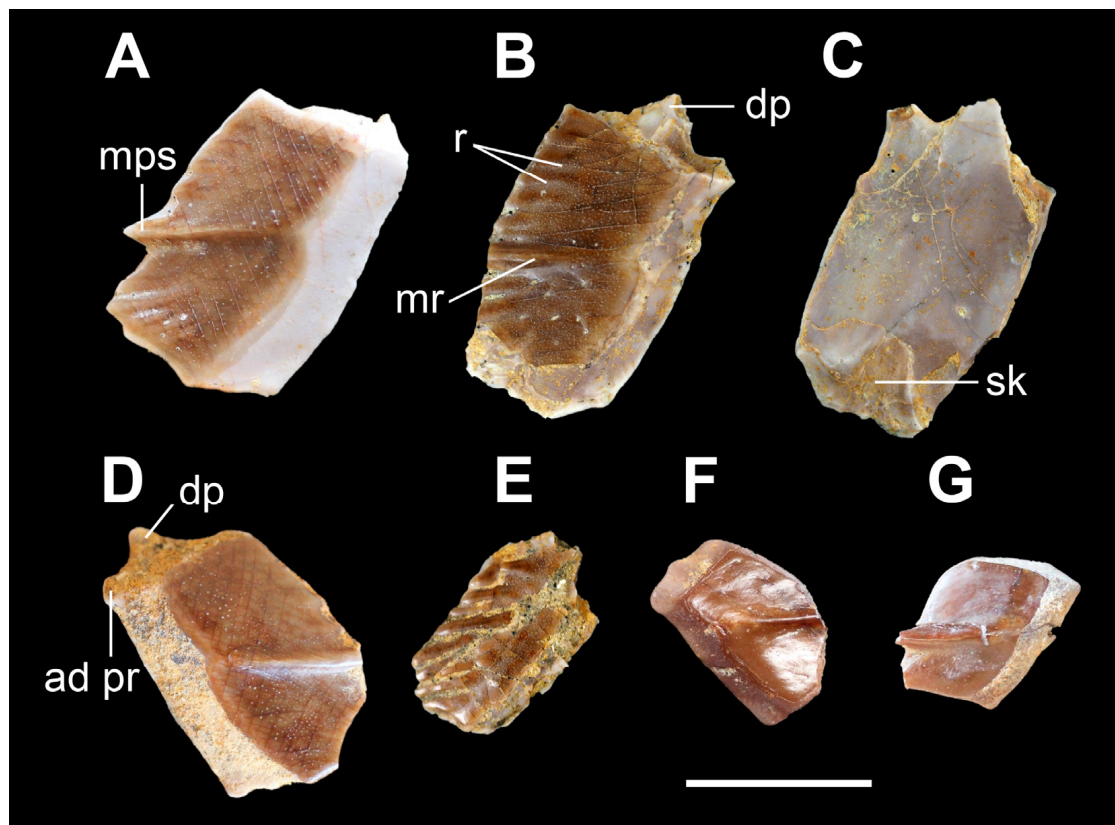


Figure 3. *Obaichthys africanus* Grande [19]; scales from Beiraterria quarry vertebrate fossil site, Casais dos Carecos, Coimbra (Baixo Mondego region of West Portugal). (A) DCT-CC-15, external view. (B,C) DCT-CC-17, external (B) and inner (C) views. (D) DCT-CC-16, external view. (E) DCT-CC-18, external view. (F) DCT-CC-32, external view. (G) DCT-CC-34, external view. Abbreviations: ad pr, anterior dorsal process; dp, dorsal peg; mps, strong middle posterior spine; mr, median ridge; r, ridges; sk, socket. Scale bar = 1 cm.

The scales DCT-CC-15 (Figure 3A), DCT-CC-17 (Figure 3B,C), and DCT-CC-16 (Figure 3D) are rectangular, deeper than wide. These specimens display anteroposterior ridges on the ganoine layer. The median ridge is more pronounced and forms a spine projecting caudally. The median ridge (that forms a spine) and the other secondary ridges are subparallel (Figure 3A,B). DCT-CC-16 and DCT-CC-17 have a peg-and-socket dorsoventral articulation, comprising a dorsal spine-like peg (Figure 3B,D) which fits to a narrowed socket on the medial surface of the scale (Figure 3C). The anterior area does not present any processes and was just overlapped by an adjacent scale, or it has a small longitudinal anterodorsal process, for articulation (Figure 3D). The specimen DCT-CC-18 is incomplete, but it exhibits well-defined anteroposterior, almost equally subparallel, ridges (Figure 3E). The scales DCT-CC-32 (Figure 3F) and DCT-CC-34 (Figure 3G) have sub-rhombic outlines and only present the median ridge, while the secondary ridges are not clearly observed.

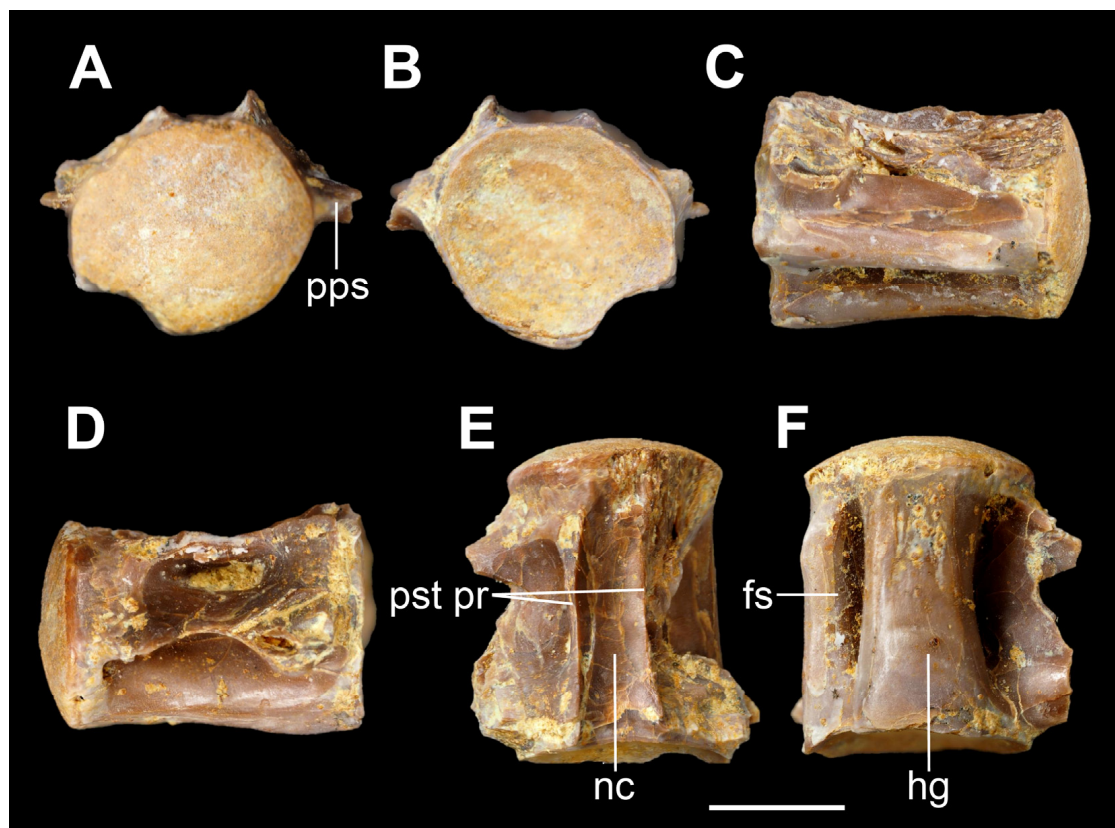


Figure 4. *Obaichthys africanus* Grande [19]; vertebral centrum DCT-CC-19 from Beiraterria quarry vertebrate fossil site, Casais dos Carecos, Coimbra (Baixo Mondego region of West Portugal). (A–F) Anterior (A), posterior (B), right lateral (C), left lateral (D), dorsal (E), and ventral (F) views. Abbreviations: fs, lateral fossa; hg, hemal groove; nc, neural canal; pps, parapophyses; pst pr, longitudinal parasagittal ridges. Scale bar = 0.5 cm.

The opisthocelous vertebral centrum DCT-CC-19 (Figure 4) was collected together with the three larger scales (DCT-CC-15, DCT-CC-16 and DCT-CC-17). Only the base of the laterally oriented parapophyses is conserved (Figure 4A,B). The neural canal and the hemal shallow groove are well preserved (Figure 4E,F). In the dorsal view, it presents a pair of longitudinal parasagittal ridges that delimit the neural canal (Figure 4E). In the ventral view, the hemal groove is wider than the neural canal (Figure 4F). Both the dorsal and ventral sides have two lateral fossae, of which the ventral ones are larger (Figure 4F).

5. Discussion

5.1. Taxonomic Remarks

Unlike in Lepisosteidae [35], the Obaichthyidae [19] scales are characteristically of a palaeoniscoid type [36] (pp. 757–758), with three layers: ganoine, dentine, and a bony basal plate [19,37,38]. Moreover, among Lepisosteioidea [39], the Obaichthyidae flank scales have a single or several larger prominent spines at their posterior margin [19].

The features of the studied scales fully correspond to those of the genus *Obaichthys* [40], as most of them are much deeper than wide [19], and they have a strong spine protruding from the middle of the posterior border in a rostrocaudal direction [19,34], a dorsoventral peg and socket, and a small anterodorsal process for the articulation of adjacent scales [41].

In further detail, they show the typical sculpture of the scales of *Obaichthys africanus* Grande [19], with ganoid ridges and grooves, which clearly distinguishes them from those of the West Gondwanan species *Obaichthys decoratus* Wenz and Brito [40], which presents rounded tubercles arranged around a central longitudinal thickening [19,37]. Besides

the morphological differences, the known records of this last species are Albian in age, e.g., [40,41].

Studies carried out on the microstructure of the scales revealed that the ridges of the *O. africanus* scales are formed by an accretion of pluristratified ganoine over individualized concentrated dentine units that sustain the ridges [38]. In the grooves, the dentine units are very thin or even absent. The scales of *O. africanus* display dentine units comparatively more developed than those of *O. decoratus* [37]. However, no studies have been carried out on the microstructure of *O. africanus* scales from Casais dos Carecos.

Comparing the scales from Casais dos Carecos to those assigned to other genera, the remains presently described differ from those of *Dentilepisosteus* [19] because the latter have a rhomboid outline. Scales attributed to *Dentilepisosteus kemkemensis* Grande [19], are rather different, as they show elongated patches of ganoine separated by a groove which goes down to the bony tissue, e.g., [18]. *Dentilepisosteus laevis* Wenz and Brito [40] has scales displaying posterior marginal spines where the further posteroventral spine is more protuberant, e.g., [19,34,42]. *Stromerichthys* [13] seems to be a genus erected on a mixture of remains belonging to different taxa [18]. Among the diverse original material, the morphology of the scales of the genotype *Stromerichthys aethiopicus* Weiler [13] fully corresponds to that of *O. africanus*.

In addition to the scales studied here, other remains assignable to *O. africanus* have been reported as Poisson ganoïdes [1] (p. 55); as Paleoniscidae indet. [2] (pp. 12–13, pl.1, figures 1–5); as *Stromerichthys aethiopicus* Weiler [13] (pp. 26–31, pl.2, figures 16, 29–34, pl.3, figures 7, 17, 20, 23), [14] (pp. 205, 219, pl.2, figures 1–4), [16] (pp. 33–37, pl. 1, figures 1–16), [43] (pl.11, figures 6–7, 9), and [44] (pp. 397–398, figure 5B,C); as *Stromerichthys* sp. [14] (pp. 205, 219–220, pl.2, figures 5–9), [16] (pp. 33–37, pl.1, figures 17–18), [45] (pp. 80–81, pl.4, figure 10), [46] (p. 931, figure 2C), and [47] (p. 233, figure 3C,D); and as *O. africanus* [18] (pp. 10–13, figure 6), [19] (pp. 687–689, figure 480A–H), [38] (pp. 123, 127, figures 1C–E, 4A–H), [48] (pp. 49, figure 5L), [49] (pp. 9–10, figure 8M), [50] (table 8, figure 61I–J), [51] (pp. 3, 5, figure 2A–D), and [52] (p. 43, figure 18A–C), among others.

The opisthocelous vertebral centrum is distinctive of Lepisosteioidea [53], showing its characteristic features, e.g., [34], and it could correspond to various taxa, e.g., [19]. The left parapophysis is partially preserved, and its morphology does not seem to be a peg-like as in other gars, but is instead expanded with laminar bone as described in the diagnosis of the genus *Obaichthys* [19] (p. 661, figure 478B). Additionally, the centrum is tentatively assigned to *O. africanus* as it has been found together with the more diagnostic scales and no remains referable to a different Lepisosteioidea species have been collected in this fossil site.

5.2. Scales and Vertebral Centrum Position

Considering the morphology of palaeoniscoid-type scales [54] and the position of the articular processes, the *O. africanus* remains DCT-CC-15, DCT-CC-17 and DCT-CC-34 have been located on the right flank, and DCT-CC-16 and DCT-CC-32 on the left flank. In further detail, scales with a well-developed and high peg, such as DCT-CC-16 and DCT-CC-17 (Figure 3B–D), were probably located in a central position regarding the lateral line scales. DCT-CC-32 and DCT-CC-34 (Figure 3F,G) have an undeveloped dorsal process and a dimension ratio not much higher than wide, which, compared with scales reported from other Obaichthyidae, could correspond to a more peripheral position (ventral for DCT-CC-34) regarding lateral line scales, e.g., [19,42].

Studies on vertebrae from *O. decoratus* and *D. laevis* [19] (pp. 683, 713) verified that the parapophyses on the anterior centra are projected laterally, but the parapophyses on the posterior abdominal centra are more ventrally projected. Additionally, the research of the same author on extant Lepisosteidae reveals that the centra become laterally compressed in the posterior elements of the vertebral series. Hypothetically, *O. africanus* vertebrae could present the same characteristics. Regarding the centrum found with these scales, only the bases of the parapophyses are conserved, but their positions point to a lateral projection (e.g., Figure 4A). It is not laterally compressed (Figure 4A,B) as in posteriormost abdominal,

caudal, preural and ural vertebrae from extant Lepisosteidae [19] (figures 79–81). The general morphology and described features of this centrum are compatible with a more anterior than posterior abdominal position along the spine.

5.3. Palaeoecology and Palaeogeography

The *O. africanus* scales from Casais dos Carecos display a good preservation state, suggesting that they are sub-autochthonous. Thus, it is also likely that this obaichthyid was an euryhaline or salt-tolerant fish that could occasionally swim through coastal marine waters, despite being previously described from freshwater to brackish facies, e.g., [18]. This behaviour would not be unprecedented since extant species of Lepisosteidae, such as *Lepisosteus osseus* (Linnaeus) [55], *Atractosteus spatula* (Lacépède) [56], and *A. tristoechus* (Bloch and Schneider) [57], are mainly found in freshwater environments, but they have the ability to swim in nearby marine ones, e.g., [19,58]. The same behavior has been already suggested for *O. decoratus* [19].

The occurrence of *O. africanus* in carbonate and mixed facies with a rather diverse assemblage of shallow marine taxa, mostly invertebrate species, also suggests a palaeogeographic setting where inner shelf to tidal flat coastal environments established the transition between the WPCP and extensive alluvial systems located eastwards, e.g., [20,21,24].

It is likely that *O. africanus* had a quite wide range in marginal marine areas located around the Iberian basins and carbonate platforms (Figure 5). Fossil remains today assigned to this species [18] have been recorded in the Cenomanian of Portugal [1,2,14–17,59]. In Spain, *O. africanus* scales have been identified in Cenomanian coastal deposits of the Cantabrian Ranges, in La Cabaña [60], and the Iberian Ranges, in Algora [47,51,52]. Outside Iberia, *O. africanus* has been recorded in the Cenomanian of France [45,46]; Morocco, e.g., [18,43,50,61]; Algeria [48,49]; and Egypt [13] (Figure 5).

Some scales attributed to *Stromerichthys* have been reported from the Albian of the Congo Basin [62] (pl.4, figures 15–16), but they could belong to different Obaichthyidae which present affinities with correlative Brazilian forms [18].

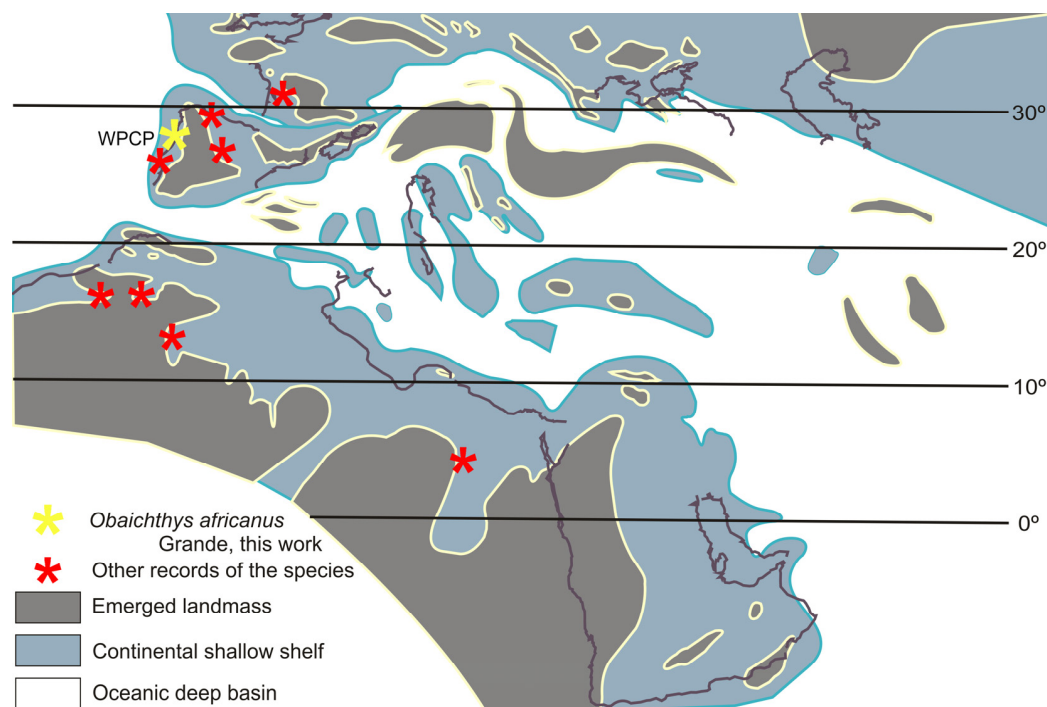


Figure 5. Palaeobiogeographical distribution of *Obaichthys africanus* Grande [19] in the Cenomanian of the Mediterranean Tethys. Yellow asterisk indicates the location of the remains from the Baixo Mondego region (West Portuguese Carbonate Platform (WPCP)) presented in this work, and red asterisks indicate other records of the species. Palaeogeographical map modified from [63–65].

Other members of Obaichthyidae seem to be represented essentially in the Lower Cretaceous of northeastern Brazil, and the Lower Cretaceous to Cenomanian of northern Africa, e.g., [42]. As a whole, the presence of the genera *Obaichthys* and *Dentilepisosteus* in the Cenomanian of Iberia, e.g., [14,52], this work, discloses Gondwanan influences on the existing Lepisosteioidea fauna at the time.

6. Conclusions

The rectangular to subrhombical shape of the Casais dos Carecos fish scales and their ornamentation, accompanied by a middle ridge forming a caudally directed spine, with other subparallel secondary ridges, are typical features of *Obaichthys africanus* Grande. The vertebral centrum is cautiously attributed to *O. africanus*, as its parapophyses seem of the *Obaichthys* type, with laminar bone, and as it was found associated with the scales and no other Lepisosteioidea species remains were found in Casais dos Carecos.

Based on these new remains, *O. africanus* is recognized for the first time in Cenomanian beds from the northern ranges of the West Portuguese Carbonate Platform, where it stands out as an interesting addition to the local vertebrate diversity of the Upper Cretaceous units from the Baixo Mondego region. Moreover, these are the first *Obaichthys* remains collected in the middle to basal upper Cenomanian beds of Portugal.

The presently known palaeobiogeographic distribution of this species encompasses an area in the Mediterranean Tethys, between the central western Iberian Archipelago and the carbonate platforms of southwestern France and northern Africa.

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