A marine Late Cretaceous (Maastrichtian) coelacanth from North Africa

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Abstract

An isolated, articulated, but crushed ossified lung of a mawsoniid coelacanth is reported from **uppermost** Cretaceous (upper Maastrichtian) of Oued Zem, Morocco. The specimen is the last record of a coelacanth before their pseudo-extinction at the end of the Mesozoic. The specimen is also the first record of a marine coelacanth in the Mesozoic of Morocco and the first occurrence of coelacanths in the phosphatic deposits of North Africa. The large size of the lung suggests a fish estimated at between 3.65 m and 5.52 m total body length.

1. Introduction

Coelacanths are a group of fish-like sarcopterygians, with a long and complex evolutionary history, being known as fossils from the Early Devonian (Johanson et al., 2006; Friedman, 2007; Zhu, 2012) to the Late Cretaceous (Schwimmer et al., 1994; Cavin et al., 2005; Duthel et al., 2012; Cavin et al., 2020). The fossil forms displayed diverse morphologies within an easily recognizable coelacanth body plan, and inhabited many aquatic environments (Forey, 1998), including both fresh and marine waters. Considered to have become extinct at the end Mesozoic, with no Cenozoic record, the group was rediscovered in 1938, after a gap of 70 myr, when the now iconic *Latimeria chalumnae* Smith, 1939 was discovered in the Mozambique channel off of South Africa (Smith, 1939, 1956; Thomson, 1991; Forey, 1998). Sixty years later, a second species *L. menadoensis* Pouyaud et al., 1999 was discovered in the eastern Indian Ocean, in Sulawesi, Indonesia (Erdmann et al., 1998; Erdmann, 1999; Pouyaud et al., 1999).

One of the most striking differences between the extant coelacanth species and many fossil taxa (e.g., the Paleozoic *Coelacanthus*, *Caridosuctor*, *Rhabdoderma*, *Hadronector*, *Allenkypterus*, and *Polyosteorhynchus*, and the Mesozoic *Axelrodichthys*, *Mawsonia*, *Macropoma*, *Undina*, *Coccoderma*, *Lybis*, *Laugia*, *Swenzia*, *Piveteauia*) is the presence in the fossil forms, of a calcified structure, occupying the length of the dorsal part of the abdominal cavity, and reaching back as far as the pelvic fins (Brito et al., 2010). The nature of this structure has, since the 19th century, been the subject of considerable controversy. Firstly identified as a stomach (Agassiz 1834-43) or a swim (air)-bladder (Williamson, 1849; Woodward, 1891; Lund and Lund 1985; Maissey, 1986; Forey, 1998), more recently it has been interpreted as an ossified lung (Brito et al., 2010). The presence of a lung entirely covered by true bone tissue, filling most of the abdominal cavity seems to be a synapomorphy of actinistians.

Recently, considerable progress has been made understanding the anatomy of the lung of the extant coelacanth, *L. chalumnae* (Cupello et al., 2015, 2017a,b) and its adaptation to moderately deep water (Cupello et al., 2019b) as well as in the homology between this structure and the ossified lungs of fossil coelacanths (Cupello et al., 2017a). This homology, proven in part by the presence of ossified plates in the two extant species, points to the presence of a functional lung in fossil coelacanths, especially those most closely related to *Latimeria* (e.g. *Swenzia* and *Macropoma*).

Here we describe the occurrence of an isolated coelacanth ossified lung from **uppermost** Cretaceous phosphatites from central Morocco, and discuss the implications of its discovery.

2. Locality and geological context

Specimen FSAC-CP 400 was obtained from a commercial fossil source, such that its precise locality and horizon are uncertain, but it was reported to have come from the phosphate deposits of Oued Zem on the Moroccan central Plateau des Phosphates. There are a number of aspects concerning the specimen that corroborate these details as well as some aspects that allow for considerable precision regarding its horizon and age.

The locality name of Oued Zem is frequently used for fossils from the Moroccan phosphate deposits of the central plateau, but this is just one locality among many where phosphate is extracted commercially in the Oulad Abdoun Basin. (Note that there are several other smaller basins in Morocco where phosphate is mined.). The mined area is extensive and there are many artificial exposures of the fossiliferous strata between the mining centres of Oued Zem, Khouribga and Fquih Ben Salah (Figs 1, 2). The matrix of the

described specimen is wholly consistent with derivation from this region, it being a weakly cemented pelletal phosphatite rich in vertebrate debris. The age of the specimen is clearly Cretaceous as indicated by its association with bones of a large pterodactyloid pterosaur (Fig. 3) and a tooth of the aulopiform teleost fish *Enchodus* sp. In the Oulad Abdoun Basin only the lowest two phosphatite beds, known as Couche III and IV, are of Cretaceous age, and these have been dated as Maastrichtian on account of their diverse vertebrate assemblage (Gharbi, 1998).

3. Materials and methods

The specimen is accessioned in the collection of the Department of Geology, Hassan II University of Casablanca, Morocco, number FSAC-CP 400. It comprises a partially crushed, incomplete ossified lung of an actinistian partly embedded in a block of phosphate matrix with a backing of reinforced plaster of Paris on the back and on three sides. The plaster has been reinforced with two steel rods. The specimen was originally collected on a larger slab that incorporated several bones of a large pterodactyloid pterosaur of indeterminate generic identity (Fig. 3). Initial crude preparation had exposed some bones, but left many covered by matrix. Furthermore, a coating with a lacquer of unknown composition, but soluble in acetone had been applied to the surface, imparting a brownish colour to the bones. Preparation by one of the authors (RES) removed the brown coating and further exposed the bones using a Dremel™ tool with rotary cutting disc, dental tools and fine brushes. Acetone was used to remove resin that had impregnated the sediment.

A coat of paraloid was applied to consolidate the surface. A thin section was prepared from part of one bony plate following standard protocols for geological thin section

preparation. It was subsequently examined under a petrological polarising using PPL and XPL. The specimen was photographed using standard digital photographic techniques.

4. Results

4.1 Systematic palaeontology

Sarcopterygii Romer, 1955

Actinistia Cope, 1871

Latimerioidei Schultze, 1993

Mawsoniidae Schultze, 1993

4.1.1 Remark

Presently it is not possible to distinguish different coelacanth genera based on the overall morphology or the histology of the ossified lung plates. Species of mawsoniid such as *Axelrodichthys araripensis* Maisey, 1986, *Mawsonia brasiliensis* Yabumoto, 2002, and *Parnaibaia maranhaoensis* Yabumoto, 2008 or the latimeriid *Macropoma mantelli* (Agassiz, 1835) and *Swenzia latimerae* (Clément, 2005) present proportionally and similar large bony plates. However, we regard specimen FSAC-CP 400 as belonging to a mawsoniid as its lung is subdivided into two or three chambers (Fig. 4), a character found in Mawsoniidae and in the Whiteiidae, such as *Piveteauia*, although in this genus the bony plates covering the lung are very small (cf., Lehman, 1952, Clément, 1999). In Latimeriidae the lung is a single chambered structure (Cupello, 2019a).

4.2 Description

Specimen FSAC-CP 400 is a partial calcified coelacanth lung, here interpreted as representing the anterior chamber of a mawsoniid coelacanth lung (Fig. 5). This piece measures 300 mm in length and 220 mm in height or width (this dimension cannot satisfactorily be determined) presenting a slight constriction at the anterior and posterior ends. The specimen lies on a slab of phosphatite matrix measuring approximately 370 mm by 345 mm and, including its plaster of Paris backing, a thickness of approximately 80 mm.

The lung is a very well-ossified structure, formed by numerous large, superimposed and multilayered bony plates, separated (in the living individual) by unossified connective tissue. All the plates are gently concave and have a very smooth, almost polished surface texture (Figs. 5A,D).

A histological detail of a bony plate shows that it is composed by primary pseudo-lamellar cellular bone (Fig. 6A-G) in which many star-shaped osteocytes are seen (Fig. 6H). These osteocytes present numerous ramified cytoplasmic extensions (Fig. 6I).

4.3 Morphometric analysis

Specimen FSAC-CP 400 undoubtedly represents a large coelacanth as evident by the abnormal size of the ossified organ (Fig. 4,5). We attempted to quantify the standard length of the coelacanth when alive using scaling ratios from several coelacanth taxa which are known as complete individuals with an ossified organ (see Table 1).

Unfortunately specimen FSAC-CP 400 is incomplete longitudinally and therefore its original length is difficult to estimate due to the diversity of coelacanth organ morphologies. However, a gentle curvature of the bony plates both anteriorly and

posteriorly suggest that it is a near complete chamber of moderately short low ratio, unlike the elongate, tubular ossified structure found in latimeriids such as *Macropoma*. Consequently, we calculated standard length from the organ width (220 mm max. in FSAC-CP 400). A scaling ratio for each compared taxon was calculated by dividing the total standard length of the coelacanth skeleton (measured from tip of snout to base of epicaudal fin lobe), divided by the maximum width (height) of its ossified organ. This scaling ratio was then multiplied by the width of FSAC-CP 400 to calculate the standard length of the original coelacanth. This method was performed using the following taxa: *Axelrodichthys araripensis*, *Mawsonia brasiliensis*, *Macropoma mantelli* and *Macropoma speciosum*. These Mesozoic taxa were selected as there are examples known consisting of complete individuals with a well-preserved organ.

4.3.1 Results

Based on the measured taxa, we recognise two broad morphologies for coelacanth ossified organs. These morphotypes are 1, multilobated (e.g. multilobed (*Axelrodichthys*, *Mawsonia*) and 2, unilobed elongate (e.g. the latimeriid *Macropoma*).

When FSAC-CP 400 is compared with multilobated Morphotype 1 organ-bearing *Axelrodichthys araripensis* (220 mm x 16.6), FSAC-CP 400 has an estimated original standard length of 3.65 m. By contrast, when compared with another mawsoniid with morphotype 1 ossified organ, *Mawsonia brasiliensis* (220 mm x 25.1), FSAC-CP 400 has an estimated original standard length of 5.52 m.

Contrastingly, scaling FSAC-CP 400 to a unilobed organ coelacanth (morphotype 2) an estimated standard length of 3.26 m is found based on *Macropoma mantelli* (220 mm x 14.8) or 3.04 m after *M. speciosum* (220 mm x 13.8).

Although due to the incompleteness of the specimen, it is difficult to determine which of the two organ morphotypes correspond with. However, its relatively low length/width aspect ratio and a gentle tapering towards both ends, strongly suggest a morphotype 1, affinity. Correspondingly, we regard FSAC-CP 400 as a mawsoniid coelacanth, rather than a latimeriid, likely with a standard length of between 3.65 m and 5.52 m.

5. Discussion.

The new specimen described here most likely represents the anterior chamber of a mawsoniid coelacanth lung, very similar to the one described for *Mawsonia brasiliensis* Yabumoto, 2002 from the Santana Formation, Araripe Basin, Brazil. The presence of a lung with chambers, excludes the possibility that the specimen is a Latimeriidae.

During the Mesozoic (especially in the Late Jurassic and Cretaceous) coelacanths were represented by two families: Latimeriidae, with typical marine genera, including the extant *Latimeria* Smith, 1939 and the Mawsoniidae. Mawsoniids have a temporal range from the Late Triassic to Late Cretaceous (Cupello et al., 2016; Cavin et al., 2019) and occur in freshwater, brackish, and marine palaeoenvironments.

Mawsoniidae comprises numerous genera distributed in North and South America, Africa, Madagascar, and Europe (Mawson and Woodward, 1908; Schultze, 1993; 2004; Forey, 1998; Gottfried et al., 2004; Clément, 2005; Yabumoto, 2008; Soto *et al.* 2012; Dutel *et al.*, 2014; 2015; Cavin *et al.*, 2013, 2016; 2019; Deesri et al., 2018) although the family is especially well documented in several Upper Jurassic and Lower Cretaceous Western Gondwanan basins as well as in Upper Cretaceous localities from North Africa

(for details see Cavin 2017). All these taxa are considered as freshwater and/or brackish taxa. Except for an indeterminate taxon from the Triassic and the genus *Trachymetopon*, from the Jurassic of Europe (Deesri et al., 2018; Dutel *et al.*, 2014; 2015). The latest occurrence of mawsoniids are examples from the Late Cretaceous (Early Campanian to Early **Maastrichtian**) of Europe (Cavin and Forey, 2004; Cavin et al., 2017, 2020).

In Africa, mawsoniids are known by the species *Lualabaea lerichei* Saint-Seine and Casier, 1955, from the Late Jurassic of Democratic Republic of the Congo, and by three species of the genus *Mawsonia*: *M. tegamensis* Wenz, 1975 from the Lower Cretaceous of Niger; *M. lavocati* Tabaste, 1963 from the ?Albian-Cenomanian Kem Kem Group, Southeastern Morocco; and *M. soba* Brito et al., 2018 from the pre-Aptian Babouri Figuil Basin of Northern Cameroon. Two other nominal species, *M. libyca* Weiler, 1935 and *M. ubangiana* Casier, 1961 are considered as junior synonyms of *M. gigas* Woodward, 1907 from the Ilhas Group, Marfim Formation (?Late Hauterivian) of the Recôncavo Basin, Brazil (Forey, 1998; Brito and Richter, 2015).

Therefore, the new specimen described here represents the youngest Mawsoniidae known in Africa, as well as the only representative of this family in a marine environment on this continent. **If this specimen was not transported from a river system, the presence** of a representative of this family in an unequivocally marine environment facilitates the understanding of possible routes of dispersion between Africa and the European archipelago.

6. Conclusions

The new specimen described here represents the youngest coelacanth from the Mesozoic of Africa. Its ossified lung subdivided into chambers, the shape and size of the plates, and the overall size of the specimen allow us to diagnose it as a mawsoniid. In Gondwana the

Mawsoniidae, until now were represented only by freshwater or brackish forms. The specimen from Morocco together with the mawsoniid from southern France, represent the last known coelacanths before the Cretaceous / Paleogene extinction.

If we accept this coelacanth as marine, the Oued Zem coelacanth indicates a return to the marine environment by the Mawsoniidae by the end of the Cretaceous. The conquest of this marine environment facilitates the understanding of possible routes of dispersion between Africa and Europe of coelacanths during the late Mesozoic. The new specimen also confirms that mawsoniids remained very large fishes with standard lengths in the range between 3.65 m and 5.52 m.

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Figure Captions

Fig. 1. Outline map of the distribution of phosphate deposits in the Oulad Abdoun Basin. Basic outline and roads based on Google Earth. Geology from Bardet et al., (2010).

Fig. 2. Simplified stratigraphic scheme for the Oulad Abdoun Basin. Based on Yans et al., (2014).

Fig. 3. The original slab, as purchased, with the coelacanth ossified lung in close proximity to a series of associated, but disarticulated wing elements of a large, but indeterminate petrosaur; *prima facie* evidence that the specimen is from the Cretaceous part of the Phosphate Series sequence.

Fig. 4. The specimen of coelacanth lung FSAC-CP 400 showing its likely position as the anterior chamber in a mawsoniid coelacanth. The dotted outline of the organ is based on *Mawsonia brasiliensis* from the Cretaceous of Brazil. Scale bar equals 30 mm. Modified and redrawn from Cavin et al., 2020.

Fig. 5. The specimen of coelacanth lung FSAC-CP 400 in A, ?lateral view; B, slightly oblique lateral view in posterior aspect; C, in posterior view and D, detail of overlapping bony plates. Scale bars = 50 mm.

Fig. 6. Histological section through a single bony ossified lung lamina of specimen FSAC-CP 400. Single lamina cut perpendicular to its flat surface showing multilayered histology in A, Plane polarised light (PPL); B, in crossed polarised light (XPL) and C, in XPL with sensitive tint plate. Single lamina at slightly higher magnification to better show internal finer-scale laminar bone tissue, D, plane polarised light (PPL); E, in crossed polarised light (XPL) and F, in XPL with sensitive tint plate. G, detail of fine laminae in XPL with stage rotated slightly to enhance contrast. H, I, osteocyte lacunae within laminar bone at high magnification to show stellate pattern.

Table 1. Selected measurements of coelacanth ossified lungs and total length used to estimate standard length of specimen FSAC-CP 400. * = standard length measured from tip of snout to base of epicaudal fin lobe.

Figure 1

Figure 2

Figure 3

Figure 4 revised

Figure 5

Figure 6

Table 1.

Taxon	Horizon	Age	Lung length	Lung width	Standard length*	Lung length scale factor	Lung width scale factor	Reference
<i>Axelrodichthys araripensis</i>	Santana Fm.	Aptian-Albian	30 cm	7.5 cm	125 cm	X 4.2	X 16.6	Brito et al., 2010
<i>Mawsonia brasiliensis</i> (Holotype)	Santana Fm.	Aptian-Albian	40 cm	5.7 cm	143 cm	X 3.8	X 25.1	Yabumoto, 2002
<i>Macropoma mantelli</i> (Holotype)	Chalk Grp.	Turonian	16 cm	3.1 cm	46 cm	X 2.9	X 14.8	Woodward, 1891
<i>Macropoma speciosum</i> (Holotype)	Bohemian Plans	Turonian	6.2 cm	1.2 cm	16.5 cm	X 2.7	X 13.8	Reuss, 1857

* = standard length measured from tip of snout to base of epicaudal fin lobe.