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Latest European coelacanth shows Gondwanan affinities

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The last European fossil occurrence of a coelacanth is from the Mid-Cretaceous of the English Chalk (Turonian, 90 million years ago). Here, we report the discovery of a coelacanth from Late Cretaceous non-marine rocks in southern France. It consists of a left angular bone showing structures that imply close phylogenetic affinities with some extinct Mawsoniidae. The closest relatives are otherwise known from Cretaceous continental deposits of southern continents and suggest that the dispersal of freshwater organisms from Africa to Europe occurred in the Late Cretaceous.

Keywords: Actinistia; fossil; Cretaceous; palaeobiogeography; dispersal

1. INTRODUCTION

Since Agassiz (1839) described a tail of *Coelacanthus* from the Permian of England, coelacanth fishes have long been known as fossils. They were thought to have become extinct some 75 million years ago. The living coelacanth, *Latimeria*, from the western Indian Ocean, was described by Smith (1939), as recently was another from the Celebes Sea (Erdmann *et al.* 1998). Marine representatives of the *Latimeria* lineage are known from the Mid-Cretaceous (Albian–Turonian) chalk of England and Czech Republic with *Macropoma* (Forey 1998), and from the Late Cretaceous of North America with *Megalocoelacanthus* (Schwimmer *et al.* 1994). Alongside the *Latimeria* lineage, freshwater mawsoniid coelacanths occurred in the Late Cretaceous of Africa and Madagascar as well as in the Early Cretaceous brackish/freshwater deposits of South America. Here, we provide the first direct evidence, to our knowledge, of a continental coelacanth in the European Late Cretaceous in the form of an angular referable to a mawsoniid coelacanth. Geologically, the new find from France is about 20 million years younger than *Macropoma*. The specimen shows affinities with the *Mawsonia–Axelrodichthys* complex and indicates brackish or, more likely, freshwater dispersals between Africa and the European archipelago during the Late Cretaceous.

2. FOSSIL MATERIAL

The fossil coelacanth described here was found in 2004 during excavations at the Early Maastrichtian locality of Cruzy (southern France). The vertebrate remains were found in a lens of variegated clays cut by unfossiliferous sandy channels. The sediments of the Cruzy locality were deposited in continental environments, probably a floodplain. The fossil vertebrate assemblage comprises isolated remains of gars, lissamphibians, squamates, turtles, crocodiles, pterosaurs, ornithopod, sauropod and theropod dinosaurs, enantiornithine birds and mammals (Buffetaut *et al.* 1999).

3. RESULTS

Our identification of the specimen as a coelacanth angular is based on the rectangular outline shape, the pattern of the mandibular sensory canal and the openings from that canal (figure 1*a*, m.s.c.), the path of the groove for the external mandibular ramus of the facial nerve (figure 1*a*, gr.VII.m.ext) and the presence of a ridge on the medial side which marks the floor of the adductor fossa (figure 1*a*, r). The specimen is referred with confidence to the *Mawsonia–Axelrodichthys* complex because of an ornamentation consisting of coarse ridges radiating from a point in the posterior third of the bone, an inflated lateral surface, the few slit-like ventral openings of the sensory canal (figure 1*b*, arrows) and the well-marked medial contact surface with the prearticular (figure 1*a*, con.Part). Coelacanths other than *Mawsonia*, *Axelrodichthys*, *Lualubaea* and *Megalocoelacanthus* show an ornament upon the angular that consists of enamel-topped tubercles or ridges, or is absent altogether; a mandibular sensory canal that opens through rounded pores; an ill-defined area of contact between the angular and prearticular, and a centre of ossification on the angular that is close to the deepest part of the bone (Forey 1998). Among these coelacanths our specimen may be distinguished from *Megalocoelacanthus* because that taxon shows an angular with a posteriorly directed opening for a special subopercular branch of the sensory canal, which indicates affinities with the latimeriids (Forey 1998). We are less certain about its distinction from other coelacanths within the *Mawsonia–Axelrodichthys* complex: for this we would need more material.

4. DISCUSSION

Late Cretaceous coelacanths are represented only by the marine latimeriids and the fresh water mawsoniids. Mawsoniid coelacanths diverged from the latimeriids in the Early Mesozoic. Mawsoniid coelacanths were exclusively Mesozoic and most lived in fresh water. Typical members, such as *Mawsonia* and *Axelrodichthys*, were heavy-bodied and showed an unusual pattern of fusion between bones in the skull roof. Some grew to a large size, estimated at over 2 m, and rivalled the size of *Latimeria* today (Wenz 1981).

Late Cretaceous occurrences of Africa and Madagascar (Gottfried *et al.* 2004) are exclusively from fresh water. Both *Mawsonia* and *Axelrodichthys* are known in the Early and Middle Cretaceous of both sides of the proto South Atlantic (Cavin & Forey 2004) showing a vicariant biogeographic pattern (Maisey 2000). The exclusive occurrences of

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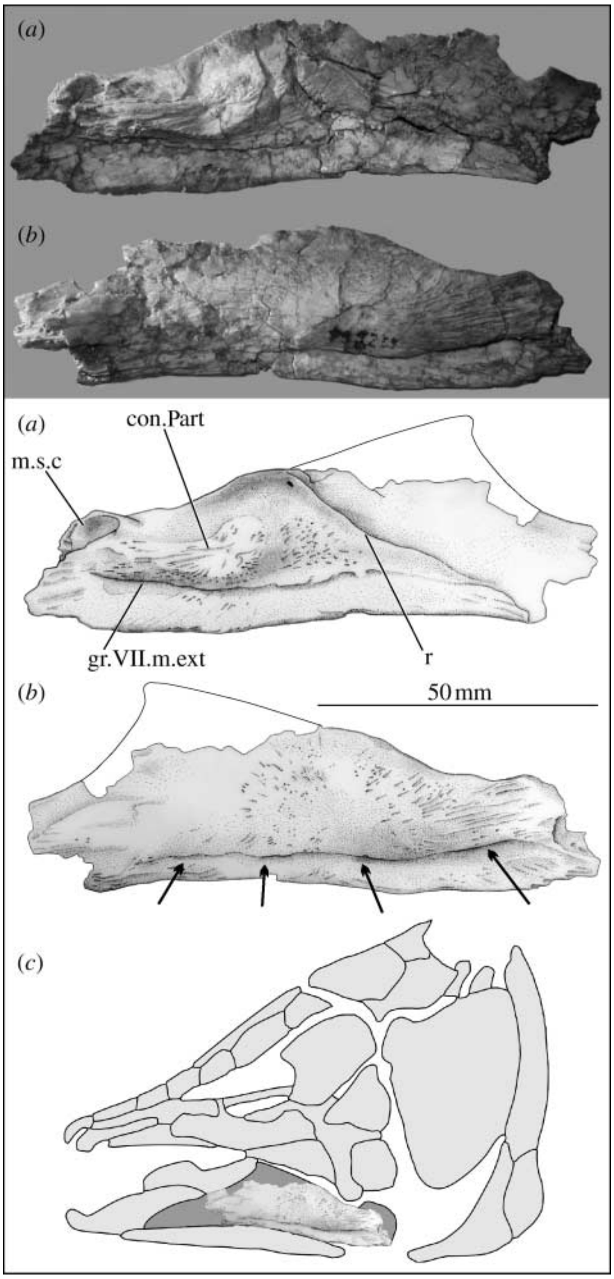

Figure 1. Left angular of a mawsoniid coelacanth from the Early Maastrichtian locality of Cruzy, southern France (M2205, collection Association culturelle, archéologique et paléontologique de l'Ouest biterrois). (*a*) Internal views, (*b*) lateral views and (*c*) location of the bone within the outline of a mawsoniid skull.

mawsoniids in fresh waters of Africa (Cavin & Forey 2004) and Madagascar (Gottfried *et al.* 2004) during the Late Cretaceous strongly suggest that mawsoniids reached the European archipelago by dispersal from Africa. We cannot exclude the possibility that dispersal polarity was from Europe to Africa. However, in the absence of contradictory information, we accept that the earlier and more widespread occurrence on and around the southern continents suggests that this is the more likely starting point. Although reconstructed maps show a wide marine barrier between Africa and the European archipelago in the Late Cretaceous (Hay *et al.* 1999; Scotese 2003), dispersal events have already been detected for tetrapods (Buffetaut 1989; Le Loeuff 1991) and freshwater fishes (Cavin *et al.* 1996), probably via a discontinuous route (Rage 1997).

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