

# 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 1a, m.s.c.), the path of the groove for the external mandibular ramus of the facial nerve (figure 1a, gr.VII.m.ext) and the presence of a ridge on the medial side which marks the floor of the adductor fossa (figure 1a, 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 1b, arrows) and the well-marked medial contact surface with the prearticular (figure 1a, 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

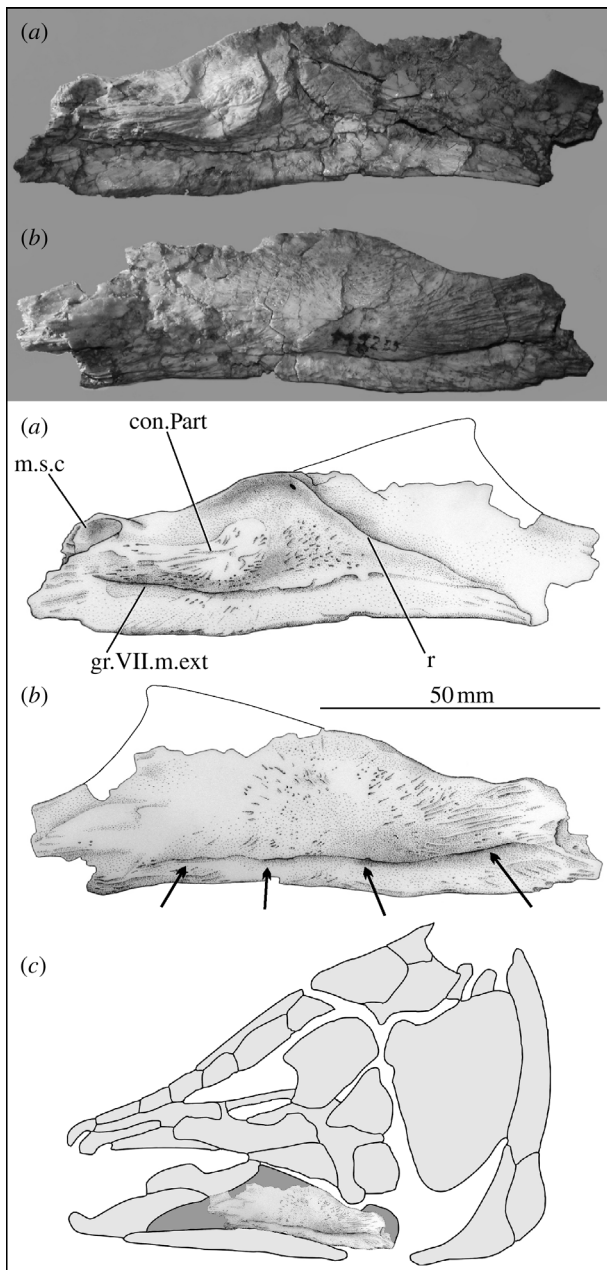


Figure 1. Left angular of a mawsoniid coelacanth from the Early Maastrichtian locality of Cruzy, southern France (M2205, collection Association culturelle, archéologique et paléontologique de l'Ouest biterrois). (a) Internal views, (b) lateral views and (c) location of the bone within the outline of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

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 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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- Agassiz, L. 1839 *Recherches sur les poissons fossiles*, vol. 2. Neuchâtel: Published by the author, Petitpierre.
- Buffetaut, E. 1989 Archosaurian reptiles with Gondwanan affinities in the Upper Cretaceous of Europe. *Terra Nova* 1, 69–74.
- Buffetaut, E., Le Loeuff, J., Tong, H., Duffaud, S., Cavin, L., Garcia, G., Ward, D. & L'association Culturelle, Archéologique Et Paléontologique De Cruzy 1999 Un nouveau gisement de vertébrés du Crétacé supérieur à Cruzy (Hérault, Sud de la France). *C. R. Acad. Sci. Paris, Sciences de la terre et des planètes* 328, 203–208.
- Cavin, L. & Forey, P. L. 2004 New mawsoniid coelacanth (Sarcopterygii: Actinistia) remains from the Cretaceous of the Kem Kem beds, SE Morocco. In *Mesozoic fishes III* (ed. A. Tintori & G. Arratia), pp. 493–506. Munich: Dr Pfeil Verlag.
- Cavin, L., Martin, M. & Valentin, X. 1996 Découverte d'*Atractosteus africanus* (Actinopterygii: Lepisosteidae) dans le Campanien inférieur de Ventabren (Bouches-du-Rhône, France). Implications paléobiogéographiques. *Revue de Paléobiologie* 15, 1–7.
- Erdmann, M. V., Caldwell, R. L. & Kasim Moosa, M. K. 1998 Indonesian 'king of the sea' discovered. *Nature* 395, 335.
- Forey, P. L. 1998 *History of the coelacanth fishes*. London: Chapman & Hall.
- Gottfried, M. D., Rogers, R. R. & Curry Rogers, K. 2004 First record of Late Cretaceous coelacanths from Madagascar. In *Recent advances in the origin and early radiation of vertebrates* (ed. G. Arratia, M. V. H. Wilson & R. Cloutier), pp. 687–691. Munich: Dr Pfeil Verlag.
- Hay, W. W. *et al.* 1999 An alternative global Cretaceous paleogeography. In *Cretaceous ocean/climate systems* (ed. E. Barrera & C. C. Johnson), pp. 1–48. *Geological Society of America, Special Paper* 332. Boulder, Co: Geological Society of America.
- Le Loeuff, J. 1991 The Campano–Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world; palaeobiogeographical implications. *Cretaceous Res.* 12, 93–114.
- Maisey, J. G. 2000 Continental break up and the distribution of fishes of Western Gondwana during the Early Cretaceous. *Cretaceous Res.* 2000, 281–314.
- Rage, J. C. 1997. Terrestrial trans-Tethyan dispersals: an overview. Geological Society of Denmark, On Line Series, 1: [http://www.2dgf.dk/publikationer/DGF\\_On\\_Line/Vol\\_1/tethys.htm](http://www.2dgf.dk/publikationer/DGF_On_Line/Vol_1/tethys.htm).

- Scotese, C. R. 2003 Paleomap project. See [www.scotese.com](http://www.scotese.com).
- Schwimmer, D. R., Stewart, J. D. & Williams, G. D. 1994 Giant fossil coelacanth of the Late Cretaceous in the eastern United States. *Geology* **22**, 503–506.
- Smith, J. L. B. 1939 A living fish of Mesozoic type. *Nature* **143**, 455–456.
- Wenz, S. 1981 Un coelacanth géant, *Mawsonia lavocati* Tabaste, de l'Albien-base du Cénomanién du sud marocain. *Annales de Paléontologie (Vertébrés)* **67**, 1–20.