

## RAPID COMMUNICATION

# A mawsoniid coelacanth (Sarcopterygii: Actinistia) from the Rhaetian (Upper Triassic) of the Peygros quarry, Le Thoronet (Var, southeastern France)

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### Abstract

Remains of a coelacanth specimen are described from Rhaetian deposits of the Var Department, southeastern France. They comprise the lower part of a branchial apparatus associated with a left lower jaw and a basisphenoid. Osteological features of the angular and basisphenoid and the teeth ornamentation allow the inclusion of the specimen in the mawsoniid family, genus and species indeterminate. Mawsoniids are known in freshwater environments from the Triassic of North America and from the Cretaceous of Western Gondwana and Europe, as well as from Late Jurassic marine environments from Europe. The new discovery here reported represents the first coelacanth from the marine Triassic of France and improves the understanding of the palaeobiogeography of the Mawsoniidae.

Keywords: Mesozoic, Sarcopterygii, Europe, systematic, palaeobiogeography

### 1. Introduction

The coelacanths, or actinistians, form a clade that split from other sarcopterygians in Early Devonian time, i.e. more than 400 Ma ago. However, the group has never been diversified and comprises today a single genus with two species. The highest, although moderate, peak of diversity was reached in Early Triassic time (Forey, 1998; Schultze, 2004; Cavin, Furrer & Obrist, 2013; Romano *et al.* 2016), and it has been hypothesized that these fishes benefited from the decrease in diversity of the ray-finned fishes after the Permian–Triassic

mass extinction to thrive a little (Wen *et al.* 2013). During most of the history of the group, coelacanths had representatives in both marine and freshwater environments. Most of the Early Triassic record is from marine environments, but the proportion changes towards freshwater environments in Late Triassic time (Forey, 1998). From the Late Triassic period onwards, only two families are present in the fossil record, the mawsoniids and the latimeriids (plus the stem latimeroid *Coccoderma* in Late Jurassic time) until Late Cretaceous time (Forey, 1998). Here, we describe fragmentary remains of coelacanths from marine deposits of Late Triassic age in southeastern France that can be referred with some confidence to the mawsoniids. The Rhaetian deposits of the Provence region have already yielded isolated fish remains, mostly teeth and ganoid scales referable to hybodont sharks, various 'ganoid' ray-finned fishes (Corroy, 1934) and marine reptiles (Bardet & Cuny, 1993; Bardet *et al.* 2013; Fischer *et al.* 2014). But, as far as we are aware, the present contribution describes actinistian remains for the first time.

### 2. Geographical and geological setting

The Peygros quarry is located in the Var Department in Le Thoronet municipality (Fig. 1). The quarry, located in a hill called Darboussière, was exploited over several years for its bauxite deposits by the Peychiney and SABAP companies (now affiliated with the Rio Tinto quarry consortium).

The Cabasse – Le Thoronet syncline is composed of Jurassic and Triassic limestone, marl and claystone beds. The unit corresponds to a thrust sheet with sediments ranging from the Keuper to the Hettangian above an autochthonous Triassic to Bathonian unit with Cretaceous bauxite locally. Several faults cause reverse contacts between Triassic and

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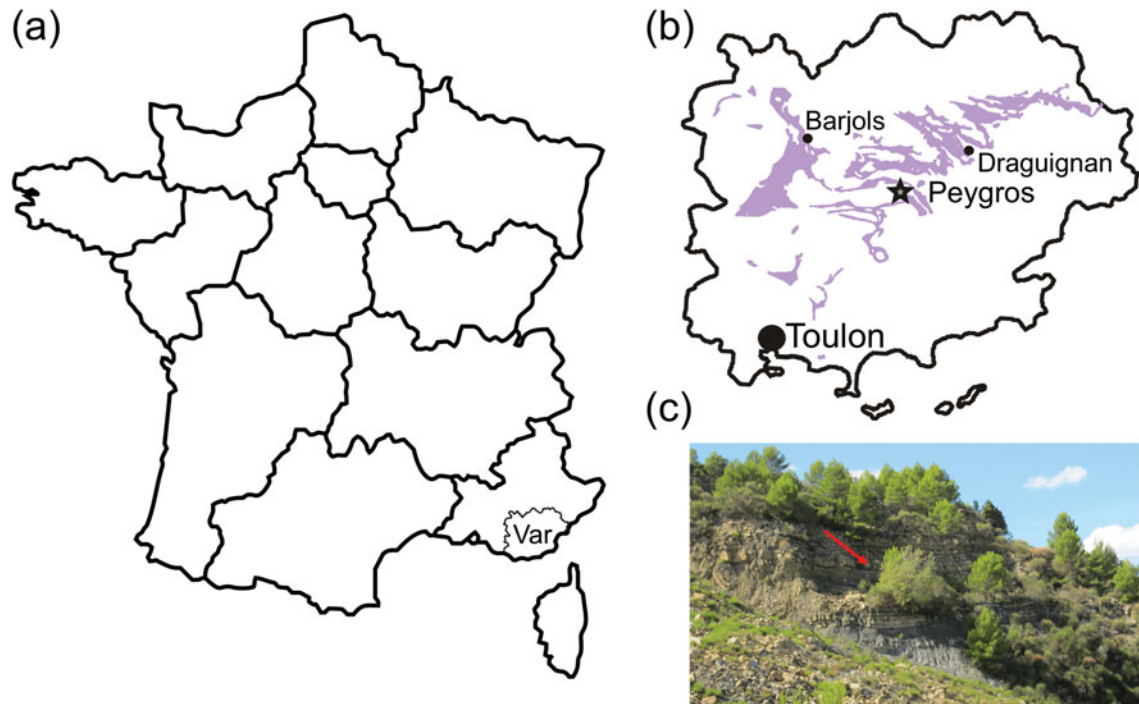


Figure 1. (Colour online) (a) Map of France with its Regions and the Var Department with (b) localization of the site (star) in the Var Department, with the distribution of the Upper Triassic in purple; (c) view of the outcrop with arrow showing the fossiliferous bed that yielded PEY-2015.5.1.

Jurassic outcrops, and Cretaceous bauxite deposits. The outcrops present an alternation of dark grey calcareous marl and grey argillaceous beds. The cliff is unstable and several blocks collapse because of gravitational crumbling exacerbated by atmospheric perturbations and cryoclasty during cold winters. The fossils were found in the talus cone under the cliff.

The presently described specimen was discovered during the course of a field survey of the Peygros quarry in September 2015.

### 2.a. Material

The fossil described here is housed in the Departmental Natural History Museum of Var, SE France under the collection number PEY-2015.5.1 (PEY-2015.5.1.1 for the skull and PEY-2015.5.1.2 for the basisphenoid). The specimen was embedded in a block of coarse-grained argillaceous limestone. The only preserved bones are a series of ceratobranchials, which articulated with basibranchial supporting tooth plates, as well as the left lower jaw with both gular plates. A basisphenoid was found close to the rest of the bones and can be referred with confidence to the same specimen. The main specimen was prepared mechanically with a steel needle and final preparation was performed with diluted (*c.* 10%) acetic acid.

### 3. Systematic palaeontology

ACTINISTIA Cope, 1871  
 LATIMERIOIDEI Schultze, 1993  
 MAWSONIIDAE Schultze, 1993  
 gen. et sp. indeterminate

#### 3.a. Lower jaw and gular plates

The preserved part of the left lower jaw comprises the angular, prearticular and principal coronoid (Fig. 2a, d). Pieces

of the dentary or the splenial are present but poorly preserved. The general shape of the lower jaw is proportionally elongate and shallow. The prearticular, located on the lingual side of the mandible is elongate and shallow (Fig. 2a). It occupies nearly the entire length of the lower jaw. Its lingual face is fully covered with tiny teeth that are regular in shape and size. Each tooth is rounded and slightly flattened and marked with fine striations radiating from the apex. The posterior part of the bone is poorly preserved, but a narrowing is present. The principal coronoid is large, elongated and poorly preserved (Fig. 2a, d). It wedges between the angular laterally and the prearticular medially at the level of the maximum depth of the angular. The angular (Fig. 2d) was likely long and shallow, but its anterior part is damaged. The dorsal margin forms a concavity at the level of the principal coronoid while the ventral margin is approximately straight. Its lateral surface is ornamented with faint grooves in its dorsal part, strong pits and deep grooves above the course of the sensory canal, and is almost smooth in the ventral part. The mandibular sensory canal is marked with at least four large oval openings located under a ridge situated beneath the ornamented part. The posterior opening of the mandibular canal, which connected to the preopercular sensory canal, is visible at the posterodorsal corner of the bone. Two gular plates are preserved, but their shape cannot be reconstructed. The outer surface of each gular is smooth.

#### 3.b. Basisphenoid

The basisphenoid is incomplete (Fig. 2c). The *processus connectens* are elongated but they apparently do not reach the parasphenoid ventrally. The sphenoid condyles are large, close to each other and protrude dorsally. The antotic processes are not preserved and the *dorsum sella* appears to be short and narrow. Fragments of the posterior extremity of the parasphenoid are still attached to the ventral margin of the basisphenoid.

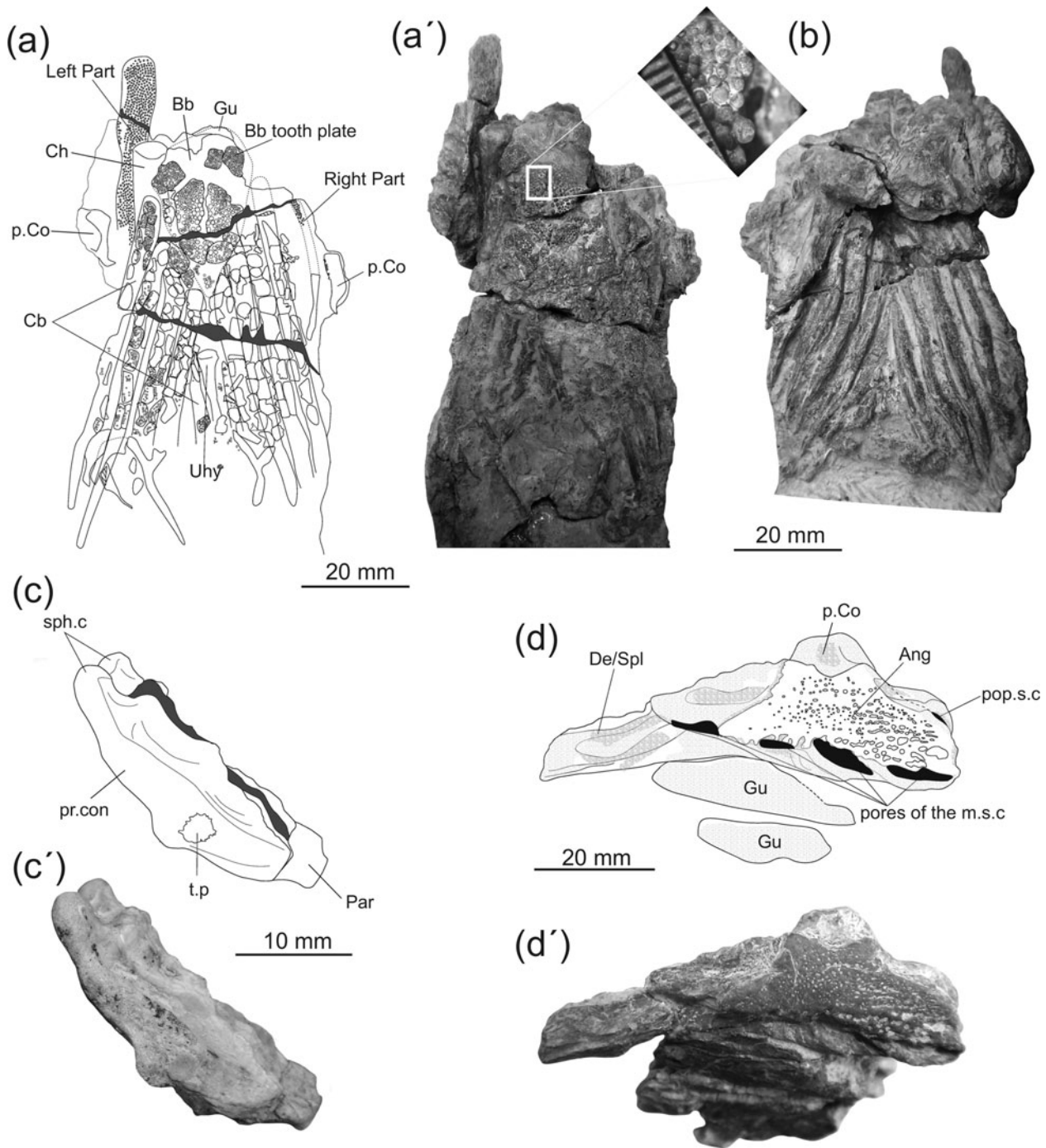


Figure 2. The Mawsoniidae gen. et sp. indet. (PEY-2015.5.1) from the Rhaetian of Peygros. (a) Interpretative drawing and (a') photograph of the complete specimen (except the basisphenoid) in dorsal view, with a close-up of teeth from a basibranchial tooth plate; (b) photograph of the complete specimen in ventral view; (c) interpretative drawing and (c') photograph of the basisphenoid in right lateral view; (d) interpretative drawing and (d') photograph of the left lower jaw in lateral view. Abbreviations: Ang – angular; Bb – basibranchial; Cb – ceratobranchial; Ch – ceratohyal; De – dentary; Gu – gular plate; m.s.c – mandibular sensory canal; p.Co – principal coronoid; Par – parasphenoid; Part – prearticular; pop.s.c – preopercular sensory canal; pr.con – processus connectens; sph.c – sphenoid condyles; Spl – splenial; t.p – tooth plates; Uhy – urohyal.

**3.c. Branchial apparatus and tooth plates**

The anteroventral portion of the branchial arches is preserved (Fig. 2a, b). The anterior extremity of the left ceratohyal is visible dorsally, wedged between the basibranchials and the left lower jaw, and its posterior part is visible in lateral view. There are five arches represented by ceratobranchials, which are large, stout and curved elements. Each ceratobranchial is excavated by a deep groove ventrally for

the afferent branchial artery (Fig. 2b) and is covered dorsally by tooth plates arranged along two parallel series (Fig. 2a). Each tooth plate is quadrangular and slightly curved, thus forming a zig-zag pattern along a series. Each bears tiny villiform teeth which show ridges radiating from the centre of the crown, as present on the prearticular (Fig. 2a', close-up). The basibranchial is large and roughly trapezoidal in shape and supports the first four pairs of branchial arches. The fifth pair of ceratobranchials is located more

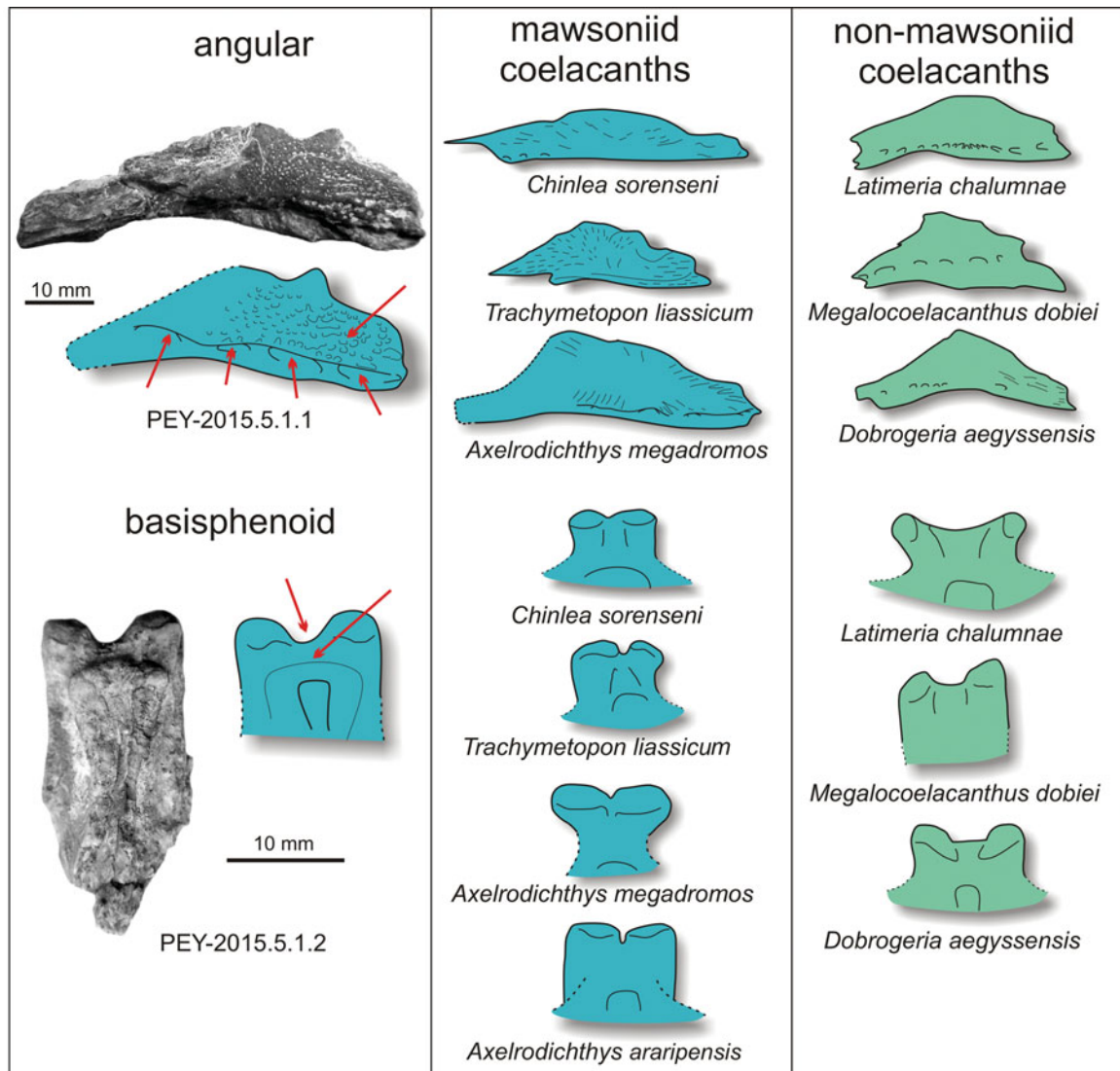


Figure 3. (Colour online) Comparison of the angular and basisphenoid of PEY-2015.5.1 (left column) with similar bones of mawsoniids (central column) and non-mawsoniid genera (right column). Mawsoniid characters are shown with red arrows (see text for details). Redrawn from Schaeffer (1967): *Chinlea sorenseni*; Dutel, Herbin & Clément (2015): *Trachymetopon liassicum*; Cavin, Valentin & Garcia (2016): *Axelrodichthys megadromos*; Maisey (1986): *Axelrodichthys araripensis*; Forey (1998): *Latimeria chalumnae* (angular); Schaeffer (1952): *Latimeria chalumnae* (basioccipital); Dutel *et al.* (2012): *Megalocoelacanthus dobiei*; Cavin & Grädinaru (2014): *Dobrogeria aegyssensis*.

posteriorly. The basibranchial is covered with tooth plates, which are much larger than those on the ceratobranchials. The basibranchial teeth vary in size, with the largest ones located along the medial margins of the large posterior tooth plates. Although they are not perfectly preserved, we recognized a pair of large and elongated tooth plates located posteriorly preceded by an indeterminate number of smaller tooth plates anteriorly, laterally and possibly posteriorly. The anterior extremity of the urohyal with its visible articulated head, which originally articulated with the posterior tip of the basibranchial, is preserved in between the anterior extremities of the fifth pair of ceratobranchials.

#### 4. Discussion and conclusion

Among Osteichthyes, the coelacanths show autapomorphic features in the basisphenoid and in the lower jaw, such as the presence of *processus connectens* in the former and of an angular with a typical shape in the latter (Forey, 1998). These features occur in PEY-2015.5.1, which leaves no doubt about

the attribution of the Peygros remains to this clade. On the other hand, these osteological elements as well as the rest of the anatomy of the coelacanths are fairly uniform among most species of the clade, making a precise identification difficult. A few features, however, allow some systematic precisions. The presence of teeth with radiating ridges is a character present in derived mawsoniids (*Mawsonia* and *Axelrodichthys*), but also in the latimeriid *Libys*, and in some more basal coelacanths (*Axelia*, *Spermatodus*; Forey, 1998.) The ornamentation of the angular (Fig. 3, top), consisting of grooves and ridges rather than tubercles, and the lateral surface with a few slit-like ventral openings of the sensory canal under a ridge, is reminiscent of the situation in most mawsoniids (Forey, 1998; Cavin, Valentin & Garcia, 2016). In the North American Triassic mawsoniid *Diplurus*, the angular is smooth (Schaeffer, 1952), but it appears to be ornamented with a similar pattern in another Triassic mawsoniid from North America, *Chinlea sorenseni* (Schaeffer, 1967, plate 28, fig. 2). In latimeriids and in most other non-mawsoniid species without a granular ornamentation,

the angular is smooth (Forey, 1998). The basisphenoid PEY-2015.5.1.2 possesses several features pointed out by Dutel, Herbin & Clément (2015) as diagnostic of mawsoniids, such as a narrow *dorsum sella* and close sphenoid condyles separated by a marked notch, a pattern which differs in the latimeriids and other non-mawsoniid species (Fig. 3, bottom). In particular, the short *dorsum sella* and the well-defined sphenoid condyles separated by a small depression are characters present in the basal mawsoniids *Chinlea* and *Diplurus* (Schaeffer, 1967), and in the derived mawsoniids *Mawsonia* and *Axelrodichthys* (Maisey, 1986; Carvalho & Maisey, 2008). In non-mawsoniid coelacanth, for instance *Latimeria*, *Megalocoelacanthus* or *Dobrogeria*, when visible the sphenoid condyles are less marked and separated by a wider gap (Forey, 1998; Dutel *et al.* 2012; Cavin & Grădinaru, 2014). Recently, the Early Jurassic *Trachymetopon liassicum* was included in the mawsoniids by Dutel, Herbin & Clément (2015). This genus, originally described from the Lower Toarcian marine locality of Holzmaden (Hennig, 1951) was subsequently recorded in the Upper Callovian of the Vaches Noires in Normandy (Dutel, Penneret & Penneret, 2014). As far as it can be assessed from the published data, the angular and the basisphenoid of *Trachymetopon* are reminiscent of the specimen from Peygros. However, given the fragmentary state of our specimen and pending a more precise comparison, we prefer not to include PEY-2015.5.1 in the genus *Trachymetopon*, but to regard it as an indeterminate mawsoniid.

Mawsoniids from Upper Triassic and Lower Jurassic strata are known exclusively from freshwater environments in North America (*Chinlea* and *Diplurus*; Schaeffer, 1967). During Cretaceous time, representatives of the family occurred mostly in continental deposits of Western Gondwana with *Mawsonia* and *Axelrodichthys* (South America and Africa; Maisey, 2000). The last mawsoniid genus is *Parnaibaia*, from the Upper Jurassic or Lower Cretaceous continental deposits of the Parnaiba Basin in Brazil (Yabumoto, 2008). In 2004, Gottfried, Rogers & Curry Rogers recorded an occurrence of a mawsoniid in the Coniacian/Santonian of Madagascar and in 2005, Cavin *et al.* reported an occurrence of a mawsoniid belonging to the *Mawsonia/Axelrodichthys* complex in the Campanian / Lower Maastrichtian of Cruzy, France, both localities corresponding to freshwater environments. Cavin *et al.* (2005) suggested that the presence of a mawsoniid in the Upper Cretaceous of Europe was the result of dispersal from Gondwana, which has yielded older and more diverse species of *Mawsonia* and *Axelrodichthys*. Following the attribution of the Jurassic *Trachymetopon* to the mawsoniids, Dutel, Herbin & Clément (2015) suggested that Late Cretaceous European mawsoniids might represent the upshot of the evolution of a European lineage rather than the result of a northward dispersal from Gondwana. However, the recent inclusion of the Late Cretaceous mawsoniids from France in the genus *Axelrodichthys* (Cavin, Valentin & Garcia, 2016) makes this hypothesis less likely because *Trachymetopon* is resolved as the sister genus of the pair *Mawsonia–Axelrodichthys* (Dutel, Herbin & Clément, 2015). However, it should be pointed out that the diagnoses of most of the mawsoniid species are in need of revision and their phylogenetic relationships are still poorly supported, making any palaeobiogeographical scenario very weak. The discovery of PEY-2015.5.1 in Peygros is a confirmation that marine mawsoniids were roaming the European seas until latest Triassic time. New discoveries would help to better define mawsoniid taxa, and would help to understand their obviously complex evolutionary history.

Although Rhaetian bone beds containing remains of fishes and marine reptiles were reported from Provence as early

as the 1860s (Coquand, 1868; Dieulafait, 1869), little has been published on these ichthyofaunas, with the exception of Corroy's brief note on the topic (Corroy, 1934). The find of a coelacanth, a taxon hitherto unreported from the Triassic of Provence, in the Rhaetian beds of the Peygros quarry, together with other vertebrate remains (Amiot *et al.* 2016), suggests that further fieldwork at Peygros and similar outcrops may lead to additional significant discoveries in these deposits.

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