

A review of *Mawsonia* from the Ilhas Group, Marfim Formation (? Late Hauterivian), Recôncavo Basin

Camila Cupello*, Léo G. C. Fragoso and Paulo M. Brito

Departamento de Zoologia, Universidade do Estado do Rio de Janeiro, R. São Francisco Xavier, 524, Maracanã – Rio de Janeiro – RJ – Cep 20550-900, Brazil.

(Received 20 May 2017; accepted 21 June 2017)

Abstract - The Mawsoniidae family includes six genera *Chinlea*, *Diplurus*, *Trachymetopon*, *Parnaibaia*, *Mawsonia* and *Axelrodichthys* with an almost worldwide occurrence ranging from the Triassic to the Late Cretaceous. The genus *Mawsonia* is widely registered from the Western Gondwana (South America and Africa) and is currently found in layers of continental origin and in association with fresh water ostracods or with a peculiar continental vertebrate fauna. Here we redescribe some nearly complete skeletons of *M. gigas*. Mawsoniids are extremely common in the Western Gondwana and, yet various specimens from different basins are referred to *M. gigas*, this type species is still one of the most poorly known species of this family. The redescription of the specimens from Recôncavo Basin confirms its classification as *M. gigas*, based mainly on the postcranial skeleton.

Keywords: Postcranium, Mawsoniidae, Actinistia, Gondwana, Lower Cretaceous

1. Introduction

The Mawsoniidae family includes six genera *Chinlea*, *Diplurus*, *Trachymetopon*, *Parnaibaia*, *Mawsonia* and *Axelrodichthys* (Schultze, 1993; Forey, 1998; Schultze, 2004; Clément, 2005; Lopez-Albarello *et al.*, 2008; Yabumoto, 2008; Dutel *et al.*, 2012; Miguel *et al.*, 2014; Dutel *et al.*, 2015), with an almost worldwide occurrence ranging from the Triassic to the Late Cretaceous (Soto *et al.*, 2012; Dutel *et al.*, 2015; Cavin *et al.*, 2016; Cupello *et al.*, 2016). The genus *Mawsonia* is widely registered from the Western Gondwana (South America and Africa) and is currently found in layers of continental origin and in association with fresh water ostracods or with a peculiar continental vertebrate fauna (Wenz, 1980; Carvalho and Maisey, 2008; Cupello *et al.*, 2012). In the Early Cretaceous of Brazil, three nominal species of *Mawsonia* were described: the type species *Mawsonia gigas* Woodward, 1907 from the ?Late Hauterivian Marfim Formation, Recôncavo Basin; *Mawsonia minor* Woodward, 1908 from the Berriasian-Hauterivian of the Morro do Barro Formation, Almada Basin; and *Mawsonia brasiliensis* Yabumoto, 2002 from the Albian Santana Formation, Araripe Basin (Yabumoto, 2002; Brito and Richter, 2015). The specific validity of many Brazilian and African *Mawsonia* is still an open debate. Based on an anatomical variety described in specimens referred to *M. gigas*, some species referred to this genus, including also the African species, had been considered as a synonym of the type species (Carvalho and Maisey, 2008).

Mawsonia is mostly known by cranial elements (Forey, 1998), and only *M. brasiliensis* has the postcranial skeleton articulated with the skull. Considering *M. minor* as a junior synonym of *M. gigas* (Carvalho, 1982), this taxon presents also a postcranial skeleton preserved, although articulated with very few posterior bones of the skull. Here we redescribe some nearly complete skeletons of *M. gigas*, focusing especially in the postcranial region and comparing them with the preserved postcranial material of other Brazilian mawsoniid species.

2. Material and methods

The specimens used in this work are: DGM 1041-P, 1045-P, 1046-P, 1047-P (part and counterpart), housed in the Departamento Nacional de Produção Mineral (DNPM, Rio de Janeiro, Brazil). This material the locality of Manguinhos, Itaparica Island, Bahia, Brazil (Late Hauterivian of the Ilhas Group, Marfim Formation, Recôncavo Basin) and were firstly studied by Carvalho (1982).

For comparison, we used the holotype of *M. minor* NHMUK PV 10567 and NHMUK PV 10568, deposited at the Natural History Museum of the United Kingdom (London, England); the holotype of *M. brasiliensis* KMNH VP 100,247, housed on the Kitakyushu Museum of Natural History and Human History (Kitakyushu, Japan); and two specimens of *Axelrodichthys araripensis*, KMNH VP 100,329 housed also at the KMNH (Kitakyushu, Japan) and UERJ-PMB 468b housed at the Universidade do Estado do Rio de Janeiro. Measurements of all the speci-

*Author for correspondence: camila.dc@gmail.com

mens were taken with a caliper and using the software ImageJ (Rasband, 2016) (Fig. 1).

Abbreviations: CL, caudal lobe; D1, first dorsal fin; sCP, superior caudal peduncle; SL, standard length.

Institutional abbreviations: DGM, Divisão de Geologia e Mineralogia, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brasil; KMNH, Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan; NHMUK, Natural History Museum United Kingdom, London, United Kingdom; UERJ, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, Brazil.

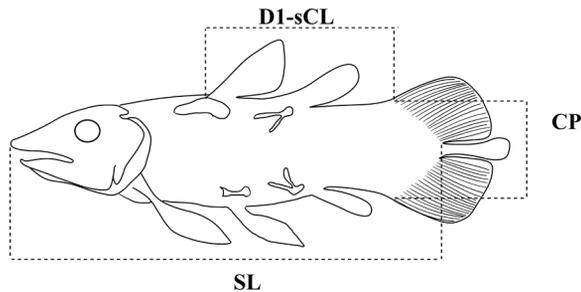


Figure 1. Measurements used in comparisons with the postcranial skeleton of other Brazilian mawsoniid species. CP, caudal peduncle; D1, first dorsal fin; sCL, superior caudal lobe; SL, standard length. Modified from Forey (1998).

3. Systematic Palaeontology

Actinistia Cope, 1871

Latimerioidei Schultz, 1993

Mawsoniidae Schultz, 1993

Mawsonia Woodward, 1907

Mawsonia gigas Woodward, 1907

Type species: Holotype NHMUK PV P 10355; Paratypes NHMUK PV P 10356, 10357

Type locality: Ilhas Group, Marfim Formation (? Late Hauterivian), Recôncavo Basin, Almeida Brandão, municipality of Salvador, state of Bahia.

Distribution: other references to this species were cited from Almada Basin, Tucano Basin, Iguatu Basin, Araripe Basin, and Sanfranciscana Basin.

3.1 Descriptions (Figs. 2 and 3)

Opercular series

The impression of the right opercle is preserved (DGM 1047-P) (Fig. 2 B). It has an overall triangular shape although the posterior edge is not evident. From a close range, it is possible to observe weak radiating ridges departing from the point of suspension of the operculum (Fig. 2 B).

Postcranial skeleton and fins

In DGM 1047-P the right cleithrum is partially preserved, presenting a medial expansion (Fig. 2 A). On another specimen, DGM 1041-P, the right disarticulated pectoral fin is preserved in and displays about 20 fin rays (Fig. 3 B). The basal plate of the pelvic fin is displaced in DGM 1047-P and display a flat “V” shape with two diverging

projections. In the same specimen (DGM 1047-P), the lobed pelvic fin is located at the level of the first dorsal fin and display about 16 rays (some also showing their hollow aspect). The basal plate of the first dorsal fin is disarticulated and displaced and the first dorsal fin presents about 8 rays, some of which are broken longitudinally and display a hollow interior (DGM 1047-P). Although it was not easily identified, we have counted about 20 rays in the superior and inferior caudal lobes (DGM 1046-P, DGM 1047-P) (Fig. 2 A and 3 A). In comparison, the rays seem to be as stout as in the holotype of *M. minor* (part and counterpart NHMUK PV P 10567, NHMUK PV P 10568). No trace of denticles has been observed on the rays of the first dorsal or caudal fin rays. None of the specimens present the epicaudal lobe preserved. About 19 pleural ribs were observed on the abdominal cavity of DGM 1047-P (Fig. 2 A). Some lung plates are preserved on the counterpart of this specimen (DGM 1047-P) and no constrictions has been observed (Fig. 2 B).

3.2 Comparative measurements

The skull is not completely preserved on DGM 1047-P but a comparison with *M. brasiliensis* can provide an idea of the standard length of the specimen. The standard length (SL, Fig. 1) of *M. brasiliensis* is of 120 cm and the distance between the base of the first dorsal fin and the base of the superior caudal lobe (as we will refer here as D1-sCL) is of 68.4 cm. On DGM 1047-P D1-sCL is 18.5 cm, giving a proportioned SL of 32.4 cm.

Another useful measurement in this case is the height of the caudal peduncle (CP, Fig. 1) taken between the bases of the superior and inferior caudal lobes (after Forey, 1998; see page 298, Fig 11.1). We compared the measurements of the specimens here described with other mawsoniid species with the postcranial skeleton preserved: *A. araripensis*, (the adult specimen KMNH VP 100,329 and a probable a juvenile UERJ-PMB 468b), and an adult specimen of *M. brasiliensis* (KMNH PV 100,247) (Table 1).

The estimated length of the specimen DGM 1047-P is of about 32.4 cm TL. We estimate also that its proportions are closer in value to the juvenile specimen of *A. araripensis* (UERJ-PMB 468b) than to the adult specimens of *M. brasiliensis* (KMNH VP 100,247) and *A. araripensis* (KMNH VP 100,329) (Table 1). Therefore, we support that DGM 1047-P is a juvenile, already proposed by Carvalho (1982), based on its estimated length and proportions.

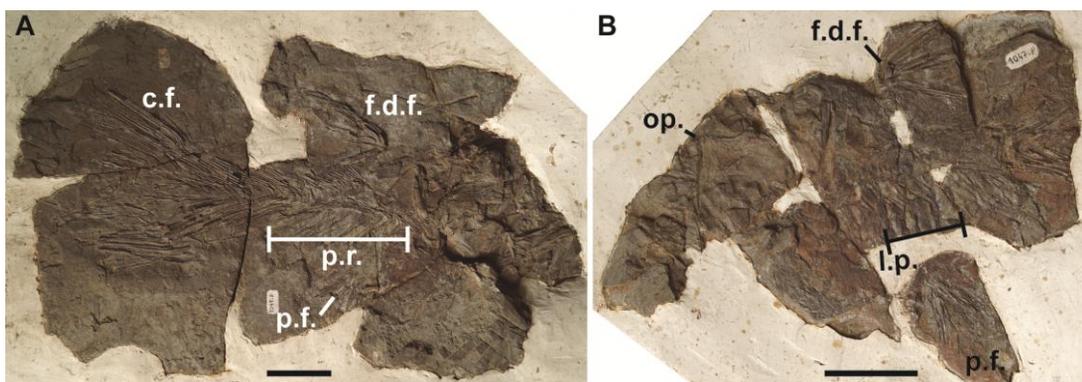


Figure 2. *Mawsonia gigas* DGM 1047-P. A, part of the specimen. B, counterpart of the specimen. Abbreviations, c.f., caudal fin; f.d.f., first dorsal fin; l.p. lung plates; op., opercle, p.f., pelvic fin; p.r., pleural ribs. Scales, 5 cm.

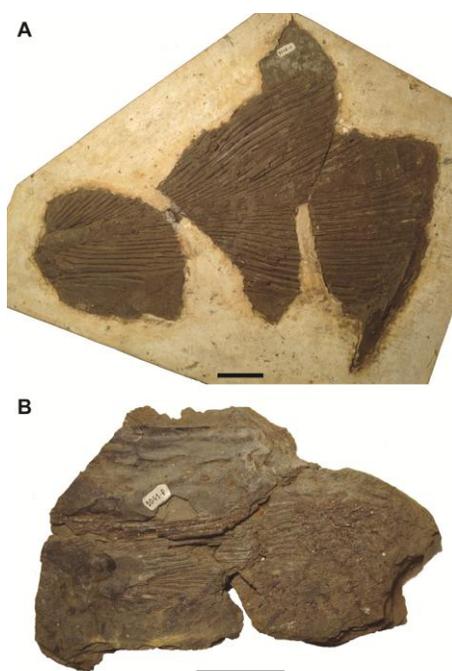


Figure 3. Caudal and pectoral fins of *Mawsonia gigas*. A, caudal fin of DGM 1046-P. B, Right pectoral fin of DGM 1041-P. Scales, 5 cm.

Table 1. Comparative measurements and proportions among juvenile and adult specimens of mawsoniid species with the postcranial skeleton preserved. Abbreviations: CP, caudal peduncle and SL, standard length.

	CP	SL	CP/SL
<i>M. gigas</i> DGM 1047-P	8.66 cm	32.4 cm	0.267284
<i>M. brasiliensis</i> KMNH VP 100,247	16.91 cm	120 cm	0.140917
<i>A. araripensis</i> UERJ PMB 468b	5.2 cm	20.84 cm	0.24952
<i>A. araripensis</i> KMNH VP 100,329	13.2 cm	89.38 cm	0.147684

4. Discussion and conclusion

Mawsoniids are extremely common in the Western Gondwana and, yet various specimens from different basins are referred to *M. gigas*, this type species is still one of the most poorly known species of this family. The redescription of the specimens from Recôncavo Basin confirms its

classification as *M. gigas*, based mainly on the postcranial skeleton. The material here reviewed is signed to the genus *Mawsonia* based on the opercle ornamentation composed by radiating ridges from the suspension point and based on the absence of denticles on the first dorsal and caudal fin rays (Woodward, 1907; 1908). Comparing the

specimens here described with the other Brazilian mawsoniid genera, it differs from *Axelrodichthys* by the triangular shape of the opercle (*Axelrodichthys* have a sub-semicircular opercle) and from *Axelrodichthys* and *Parnaibaia* by the absence of denticles on the rays of the caudal and dorsal fins (fin rays of *Axelrodichthys* and *Parnaibaia* hold few denticles; Maisey, 1986; Yabumoto, 2008). We identified the material as *M. gigas* based also on the number of rays in the first dorsal fin; on the approximate number of rays of the upper and lower lobes of the caudal fin; and on the position of the pelvic fin in relation to the first dorsal fin (Forey, 1998; Brito and Richter, 2015). Comparing the specimens here described with the other Brazilian species of *Mawsonia* that present the postcranial skeleton, the material collected at the Recôncavo Basin differs from *M. brasiliensis* from the number of rays of the first dorsal fin (8 in *M. gigas* and 10 in *M. brasiliensis*) and from the number of rays of the caudal fin (although the caudal fin described for *M. brasiliensis* was not complete) (Yabumoto, 2002). Also, the number of rays of the pelvic fin differs between our specimen and *M. brasiliensis* (about 16 for DGM 1047-P and 22 for *M. brasiliensis*) (Yabumoto, 2002). Among extant coelacanths, meristic data have been used as an additional argument to differentiate the two species *Latimeria chalumnae* Smith, 1939 and *Latimeria menadoensis* Pouyaud *et al.*, 1999 (Pouyaud *et al.*, 1999).

Wenz (1980) gives an estimative of about 3.5 m total length (TL) for some specimens of *M. gigas*. We recurred to *M. brasiliensis* to obtain a more precise estimated standard length, since the holotype of this specimen is the most complete *Mawsonia* found thus far, with the skull still attached to the postcranial skeleton (see Yabumoto, 2002). Here we estimate the length of DGM 1047-P of about 32.4 cm TL and support that this specimen is a juvenile, as already proposed by Carvalho (1982). Just for comparison, the smallest specimen of the extant coelacanth *L. chalumnae* caught in free swimming (outside female body) (CCC 94) has 42.5 cm TL (Nulens *et al.*, 2011). We suggest also that small juveniles of *M. gigas* and *A. araripensis* would present an allometric growth, becoming slenderer as the holotype of *M. brasiliensis* (KMNH VP 100,247) and the large adult specimen of *A. araripensis* (KMNH VP 100,329; Table 1).

Carvalho and Maisey (2008) described some morphologically variability between specimens referred to a single population of *M. gigas* and pointed to an intraspecific wide variability. Concerning *M. minor*, Carvalho (1982) argued that the difference in the strength of the ornamentation and the size of the specimen, proposed as a diagnostic character for this species from the Berriasian-Hauterivian of Morro do Barro Formation, Almada Basin (southern Bahia) (Woodward, 1908), are not sufficient to separate this taxon from the type species. The morphological structures described here points to this synonym, although a more detailed revision of specimens from the Almada Basin is needed. Nothing is more relative than the concept of fossil species. Specimens referred to *M. gigas* are registered in different geological formations with pos-

sible different ages, suggesting different paleoenvironments. These basins constitute a sequence of fresh and probably brackish water lakes from the rift phase of breakup of western Gondwana. The Marfim Formation most probably constitutes, by its vertebrate fauna and geology, one of those palaeolakes.

The “Afro-Brazilian lakes” are analogous to the nowadays Rift Lakes of East Africa (Maisey, 1991). Although it is estimated that the genus *Mawsonia* might have had a slow morphological evolution (Cavin and Guinot, 2014; Cavin *et al.*, 2016), more than one species may have inhabited these lakes. This possible specific richness was due to the isolation between these lakes and the subsequent reproductive isolation during the pre-rift/rift. However, the weak number of specimens of *Mawsonia*, mainly of complete specimens with the skull articulated to the postcranial skeleton, as well as the restrictions on information from the fossil record, do not allow to support diagnostic differences to distinguish various different taxa on the “Afro-Brazilian lakes”, notably to *M. gigas*.

Acknowledgements

We are grateful to E. Bernard and M. Richter (Natural History Museum, UK), Y. Yabumoto (Kitakyushu Museum of Natural History and Human History, Japan), and R. Machado (Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil) for providing access to the fossil fish collections. C. Cupello was supported by Capes fellowships (proc n°. BEX 0346/13-6 and Programa Nacional de Pós Doutorado PNPd/Capes) and CNPq (proc n°. 142252/2011-5). L.G. Fragoço was supported by a FAPERJ fellowship (E-26/100-937/2010). P.M. Brito’s research has been partially supported by CNPq (proc n°. 304082/2013-9).

References

- Bruto, P. M. and Richter, M. 2015. The contribution of Sir Arthur Smith Woodward to the palaeoichthyology of Brazil—Smith Woodward’s types from Brazil. Geological Society, London, Special Publications 430, 201-217.
- Carvalho, M. S. S. 1982. O gênero *Mawsonia* na ictiofauna do Cretáceo do estado da Bahia. Anais da Academia Brasileira de Ciências 54, 519-539.
- Carvalho, M. S. S. and Maisey, J. G. 2008. New occurrence of *Mawsonia* (Sarcopterygii: Actinistia) from the Early Cretaceous of the Sanfranciscana Basin, Minas Gerais, southeastern Brazil. Geological Society, London, Special Publications 295, 109-144.
- Cavin, L. and Guinot, G. 2014. Coelacanths as “almost living fossils”. *Frontiers in Ecology and Evolution* 2, 49.
- Cavin, L., Valentin, X. and Garcia, G. 2016. A new mawsoniid coelacanth (Actinistia) from the Upper Cretaceous of southern France. *Cretaceous Research* 62, 65-73.
- Clément, G. 2005. A new coelacanth (Actinistia, Sarcopterygii) from the Jurassic of France, and the question

- of the closest relative fossil to *Latimeria*. *Journal of Vertebrate Paleontology* 25, 481-491.
- Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. *Transactions of the American Philosophical Society*, 445-483.
- Cupello, C. D., Bermúdez-Rochas, D. D., Martill, D. M. and Brito, P. M. 2012. The hybodontiformes (Chondrichthyes: Elasmobranchii) from the Missão Velha Formation (? Lower Cretaceous) of the Araripe Basin, North-East Brazil. *Comptes Rendus Palevol* 11, 41-47.
- Cupello, C., Batista, T. A., Fragoso, L. G., and Brito, P. M. 2016. Mawsoniid remains (Sarcopterygii: Actinistia) from the lacustrine Missão Velha Formation (Lower Cretaceous) of the Araripe Basin, North-East Brazil. *Cretaceous Research* 65, 10-16.
- Dutel, H., Maisey, J. G., Schwimmer, D. R., Janvier, P., Herbin, M. and Clément, G. 2012. The giant Cretaceous coelacanth (Actinistia, Sarcopterygii) *Megalocoelacanthus dobiei* Schwimmer, Stewart and Williams, 1994, and its bearing on Latimerioidei interrelationships, Chicago. *PLoS One* 7, e49911.
- Dutel, H., Herbin, M. and Clément, G. 2015. First occurrence of a mawsoniid coelacanth in the Early Jurassic of Europe. *Journal of Vertebrate Paleontology* 35, e929581.
- Forey, P. L. 1998. *History of the Coelacanth Fishes*. Springer Science & Business Media, 419p.
- Lopez-Arbarello, A., Rauhut, O. W. and Moser, K. 2008. Jurassic fishes of Gondwana. *Revista de la Asociación Geologica Argentina* 63, 586-612.
- Maisey, J. G. 1986. Coelacanths from the Lower Cretaceous of Brazil. *American Museum novitates*; no. 2866.
- Maisey, J. 1991. *Santana Fossils: An Illustrated Atlas*. T. F. H. Publications, Neptune City, NJ.
- Miguel, R., Gallo, V. And Morrone, J. J. 2014. Distributional patterns of †Mawsoniidae (Sarcopterygii: Actinistia). *Anais da Academia Brasileira de Ciências* 86, 159-170.
- Nulens, R., Scott, L. and Herbin, M. 2011. An Updated Inventory of all Known Specimens of the Coelacanth *Latimeria* spp South African Institute for Aquatic Biodiversity 3, 1-52.
- Pouyaud, L., Wirjoatmodjo, S., Rachmatika, I., Tjakrawidjaja, A., Hadiaty, R. and Hadie, W. 1999. Une nouvelle espèce de coelacanth: preuves génétiques et morphologiques. *Comptes Rendus de l'Académie des Sciences-Series III-Sciences de la Vie* 322, 261-267.
- Rasband, W. S. and Imagej, U. S. 1997-2016. National Institutes of Health, Bethesda, Maryland, USA, <https://imagej.nih.gov/ij/>.
- Schultze, H. P. 1993. Osteichthyes: Sarcopterygii. In: Benton, M. J. (Ed.), *The Fossil Record* 2. Chapman & Hall, London, 657-663.
- Schultze, H. P. 2004. Mesozoic sarcopterygians. *Mesozoic Fishes* 3, 463-492.
- Smith, J. L. B. 1939. A living fish of Mesozoic type. *Nature* 143, 455-456.
- Soto, M., De Carvalho, M. S., Maisey, J. G., Perea, D. and Silva, J. D. 2012. Coelacanth remains from the Late Jurassic? earliest Cretaceous of Uruguay: the southernmost occurrence of the Mawsoniidae. *Journal of Vertebrate Paleontology* 32, 530-537
- Wenz, S. 1980. A propos du genre *Mawsonia*, Coelacanth géant du Crétacé inférieur d'Afrique et du Brésil. *Mémoires de la Société géologique de France* 39, 187-190.
- Woodward, A. S. 1907. Notes on some Upper Cretaceous Fish remains from the Province of Sergipe and Pernambuco, Brazil. *Geological Magazine* 4, 193-197.
- Woodward, A. S. 1908. On some fossil fishes discovered by Prof. Ennes de Souza in the Cretaceous formation at Ilheos (State of Bahia), Brazil. *Quarterly Journal of the Geological Society* 64, 358-362.
- Yabumoto, Y. 2002. A new coelacanth from the Early Cretaceous of Brazil (Sarcopterygii, Actinistia). *Paleontological Research* 6, 343-350.
- Yabumoto, Y. 2008. A new Mesozoic coelacanth from Brazil (Sarcopterygii, Actinistia). *Paleontological Research* 12, 329-343.