

The second record of a mawsoniid coelacanth from the Lower Cretaceous Crato Formation, Araripe Basin, northeastern Brazil, with comments on the development of coelacanths

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Abstract

A well-preserved fossil coelacanth from the Lower Cretaceous Crato Formation in Araripe basin, northeast Brazil, is the second record of a coelacanth from this formation. The new specimen is slightly larger than the first one, with an estimated total length of about 100 mm. It is identified as *Axelrodichthys araripensis* MAISEY, 1986, based on the following features: the dorsal outline of the head is concave, the deepest portion of the lower jaw is located anteriorly, and the median extrascapular bone is present. The longer fin rays and the larger head as compared to those of adults are characteristics of juveniles of this species. The lung is already covered with thin, calcified plates at this stage. The toothed dermopalatine and ectopterygoid are described in this species for the first time. The scales have minute tubercles on the exposed area. The fact that the specimens of *Axelrodichthys* from the Crato Formation are juveniles as also are specimens of other species found in the Santana and the Crato formations led us to suggest paleoecological implications related to their reproductive biology.

Introduction

The Araripe basin in northeast Brazil is well known as a Lagerstätte for Early Cretaceous animals and plants, especially fossil fishes. Fossils are especially well preserved in two geological formations of this basin: The Albian Santana Formation with 26 nominal species of fossil fishes and the slightly older (Aptian) Crato Formation with 10 species (BRITO & YABUMOTO 2011). The species of the Crato Formation are: *Lepidotes* sp., *Araripelepidotes* cf. *temmurus* (AGASSIZ 1841), *Obaichthidae* gen. et sp. indet., *Cratoamia gondwanica* BRITO, YABUMOTO & GRANDE, 2008, *Placidichthys bidorsalis* BRITO, 2000, *Vinctifer longirostris* SANTOS, 1990, *Cladocyclus gardneri* AGASSIZ, 1841, *Dastilbe crandalli* JORDAN, 1910 (the most abundant fossil fish), *Santanaichthys* cf. *diasii* (SANTOS 1958) and *Axelrodichthys* sp. (see BRITO 2007). The last species, represented by a juvenile, was the first coelacanth reported from the Crato Formation (BRITO & MARTILL 1999). Among these taxa, *Cratoamia gondwanica* and *Dastilbe crandalli* have not been recorded from the Santana Formation.

In the present study, we describe a second specimen of the coelacanth *Axelrodichthys*, also considered to be a juvenile, and compare it with the specimens from the Santana Formation. Both specimens of coelacanth from the Crato Formation were collected in the commercial quarries for laminated limestones found near the town of Nova Olinda, State of Ceará. The age of the Crato Formation is considered as Aptian (see MARTILL & HEIMHOFER 2007).

Four nominal species of coelacanths have been described from the Mesozoic deposits of Brazil: *Mawsonia gigas* WOODWARD, 1907, from the Ilhas Group of Bahia, *M. brasiliensis* YABUMOTO, 2000, and *Axelrodichthys araripensis* MAISEY, 1986, from the Santana Formation of the Araripe basin, and *Parnaíbaia maranhaoensis* YABUMOTO, 2008, from the Pastos Bons Formation of the Parnaíba Basin.

Material and methods

The new specimen here described is deposited in the Kitakyushu Museum of Natural History and Human History, Kitakyushu, Japan under the number KMNH VP 100,262. It is an almost complete specimen, lacking only the caudal peduncle. The new specimen is slightly larger than the first one described from the same Formation and determined as *Axelrodichthys* sp. (see BRITO & MARTILL 1999); the latter specimen is catalogued under the number MPSC-287 (Museum of Santana do Cariri, Ceará, Brazil).

Meristic characters and measurements were taken according to FOREY (1998: 298). Terminology of coelacanth bones follows FOREY (1998) and ARRATIA et al. (2000). To avoid possible confusion of names, the terminology for the caudal region proposed by UYENO (1991) will be presented in parentheses in the text.

Systematic paleontology

- Order Coelacanthiformes HUXLEY, 1861
- Suborder Latimerioidei SCHULTZE, 1993
- Family Mawsoniidae SCHULTZE, 1993
- Genus *Axelrodichthys* MAISEY, 1986

Axelrodichthys araripensis MAISEY, 1986

Figs. 1–4

1999 *Axelrodichthys* sp.: BRITO & MARTILL, p. 311–314, fig. 1.

Description

The new specimen (Fig. 1) is small, with an estimated total length of about 100 mm and an estimated length from the snout to the base of the caudal peduncle (standard length of Forey 1998: 298) of about 73 mm. Its head length is 25.6 mm. The body is bent in the middle; the body depth at the origin of the first dorsal fin is 21 mm.

The parietonasal shield is about twice the length of the postparietal shield: the length of the parietonasal shield is 15.6 mm, whereas the estimated length of the postparietal shield is about 8 mm. Both parietals are narrow. Bones of the anterior part of the parietonasal shield are preserved, but the boundary of each bone is unclear.

Supraorbitals are located alongside both parietal bones; the width of the supraorbitals is slightly narrower than that of the parietals (Fig. 1).

The postparietal shield consists of a pair each of postparietals, supratemporals, and lateral extrascapulars, and a median extrascapular bone. The postparietal is largest and is slightly longer than the lateral extrascapular, which is almost the same size as the supratemporal. The median extrascapular (Fig. 1) is a small, square bone that is about one-third the size of the lateral extrascapular.

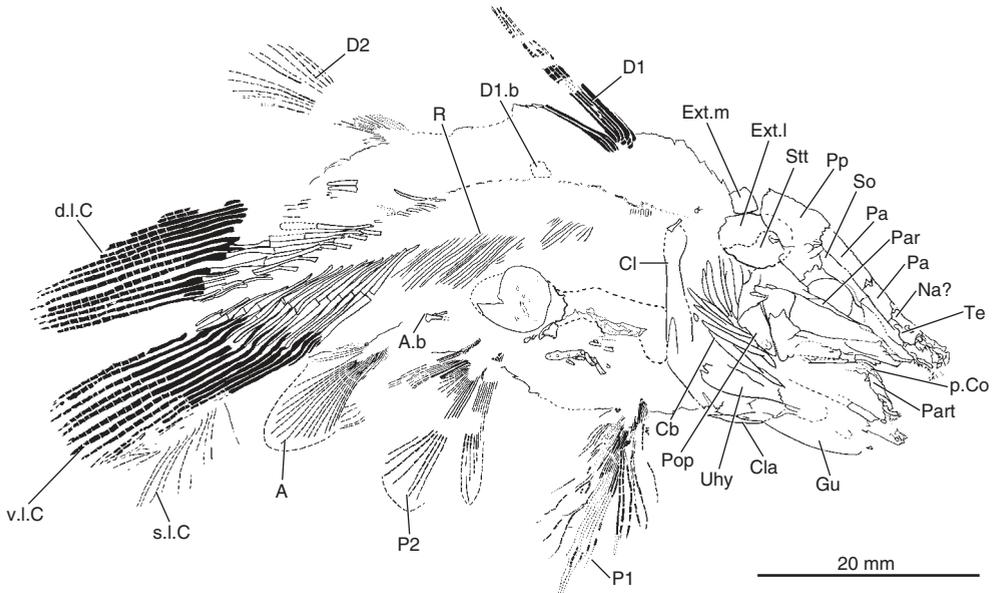
The cheek bones are not well preserved. The postorbital, lachrymojugal and squamosal are missing. The preoperculum is preserved behind the quadrate. The surface of its ventral part has ridged ornamentation.

Both lower jaws are visible. Relatively large conical teeth (Fig. 2) present at the anterior end of the snout are probably premaxillary teeth. The lower jaw is deep, with the deepest point anterior to the midpoint of the lower jaw. The anterodorsal part of the angular is preserved, but the articular cannot be seen. The principal coronoid is a long, saddle-shaped bone, which articulates with the prearticular at its anteroventral edge. Several conical teeth are preserved at the rostral or anterior end of the lower jaw (Fig. 3).

The quadrate and pterygoid are well preserved. There is a distinct, wide strut along the posterior margin of the pterygoid above the quadrate. The quadrate inclines caudally. The ventral end of the quadrate forms two condyles for the articulation of the lower jaw. The angle between the posterior margin of the quadrate and the ventral margin of the pterygoid is obtuse. Behind the premaxillary teeth, a flat bone, probably the autopalatine, is tightly articulated at its anterior end with a bone that is probably the lateral ethmoid (Fig. 2). The dermopalatines are located ventral to the autopalatine and have smaller teeth than the premaxilla. Two anterior dermopalatines can be seen. The ectopterygoid is located slightly apart from the posterior dermopalatine. The ectopterygoid teeth are almost the same size as those of the dermopalatines (Fig. 2). The metapterygoid is missing.



A



B

Fig. 1. Second specimen of coelacanth from the Nova Olinda Member of the Crato Formation in the Araripe Plateau, Brazil. **A**, *Axelrodichthys araripensis* (KMNH VP 100,262, 73 mm SL). **B**, line drawing of A. Abbreviations: **A**, anal fin; **A.b**, basal plate of anal fin; **Cb**, ceratobranchial; **Cl**, cleithrum; **Cla**, clavicle; **D1**, first dorsal fin; **D1.b**, basal plate supporting first dorsal fin; **D2**, second dorsal fin; **d.I.C**, dorsal lobe of the caudal fin in traditional terminology (= third dorsal fin of UYENO 1991); **Ext.l**, lateral extrascapular; **Ext.m**, median extrascapular; **Gu**, gular plate; **Na**, nasal bone; **P1**, pectoral fin; **P2**, pelvic fin; **Pa**, parietal bone; **Part**, prearticular; **p.Co**, principal coronoid; **Pp**, postparietal bone; **R**, rib; **s.I.C**, supplementary lobe of the caudal fin; **So**, supraorbital bone; **Stt**, supratergular; **Te**, tectal; **Uhy**, urohyal; **v.I.C**, ventral lobe of the caudal fin (= second anal fin of UYENO 1991).

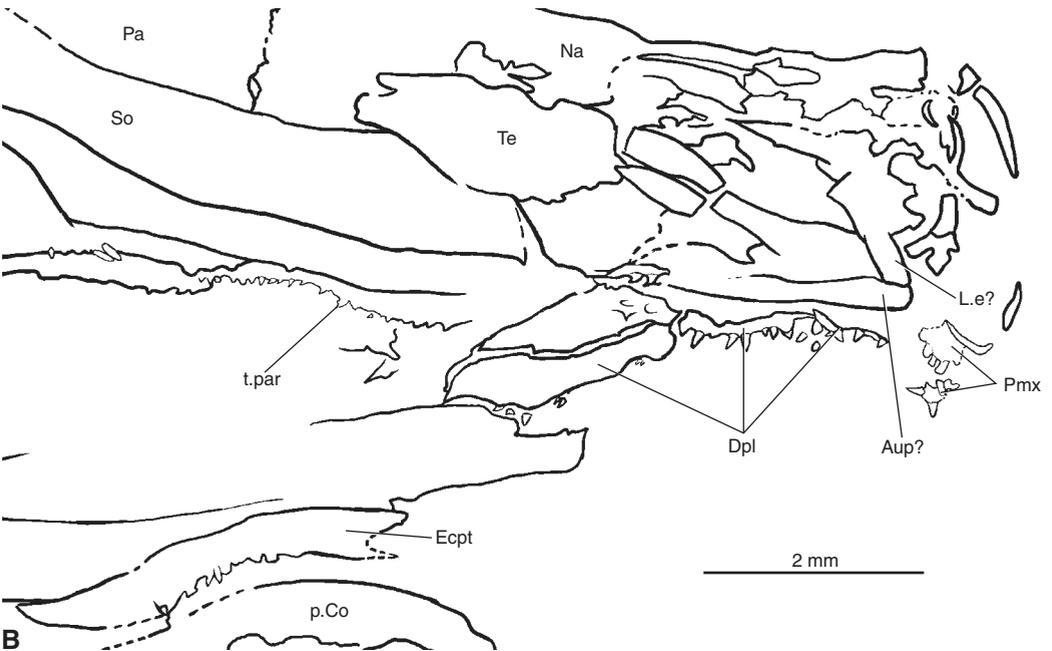


Fig. 2. *Axelrodichthys araripensis* (KMNH VP 100,262) from the Nova Olinda Member of the Crato Formation in the Araripe Plateau, Brazil. **A**, Close up of the anterior part of the head. **B**, line drawing of A. Abbreviations: **Aup**, auto-palatine; **Dpl**, dermopalatine; **Ecpt**, ectopterygoid; **L.e?**, lateral ethmoid; **Na**, nasal bone; **So**, supraorbital bone; **Pa**, parietal bone; **p.Co**, principal coronoid; **Pmx**, premaxilla; **Te**, tectal; **t.par**, teeth of parasphenoid.

The operculum is not preserved. Long ceratobranchials are preserved behind the preoperculum. A bone located ventral to the ceratobranchials is probably the urohyal, which broadens posteriorly (Fig. 1). This bone is not homologous to the tendon-bone urohyal found in teleosts (see ARRATIA & SCHULTZE 1990). The cleithrum is almost straight, but the ventral end bends slightly. The pectoral fin is about 20 mm long or about 27.4 % of the estimated standard length. The pelvic fin has 16 rays, each with a length of about 14 mm, or about 19.2 % of the estimated standard length. The pelvic and pectoral fin rays are segmented.

The number of fin rays of the first dorsal fin is 10 and the length of the longest one is 19.4 mm, or about 26.6 % of the estimated standard length. About two-thirds of the distal region of first dorsal fin rays are segmented. The basal plate is not visible ventral to the dorsal fin rays, but a bone preserved between the first and the second dorsal fins is probably the basal plate. The second dorsal fin has 18 rays, which are 16.0 mm long, or about 21.9 % of the estimated standard length. The distal part of the fin rays is segmented. The basal plate of the second dorsal fin is not visible.

The dorsal lobe of the caudal fin (= third dorsal fin of UYENO 1991) has 14 rays, and the fin rays are about 23 mm long, or about 31.5 % of the estimated standard length.

There are 20 fin rays in the anal fin with a length of about 15 mm, or about 20.5 % of the estimated standard length. The anal fin rays are segmented almost entirely, except for a the short basal portion. The base of the anal fin consists of the slightly deep basal part and two cylindrical parts, which probably form the bifurcate anterior projections. The ventral lobe of the caudal fin (= second anal fin of UYENO 1991) has 14 fin rays that are almost of the same length as the fin rays of the dorsal lobe (Fig. 1).

The supplementary lobe of the caudal fin is disarticulated, but a part of this structure is preserved under the ventral lobe.

There are no ossified vertebral centra, indicating a persistent notochord. Most of the neural spines are not preserved, but their impressions are clearly seen. The anterior neural spines are ossified, extremely short, and gradually lengthen posteriad beginning at the mid point between the first and second dorsal fins. Neural spines articulating with 'supraneural' plus radial (ARRATIA et al. 2000) of the dorsal lobe of the caudal fin are long, and wide at the dorsal end. Most of the haemal spines are missing, but their impressions are visible. There are 14 haemal spines articulated with 14 interhaemals plus ventral radials (ARRATIA et al. 2000) in the ventral lobe of the caudal fin.

There are 27 very thin ribs, of which the first three are very short and the others gradually lengthen posteriad; 16 long ribs, which do not reach the ventral margin of the body, are located behind the stomach content.

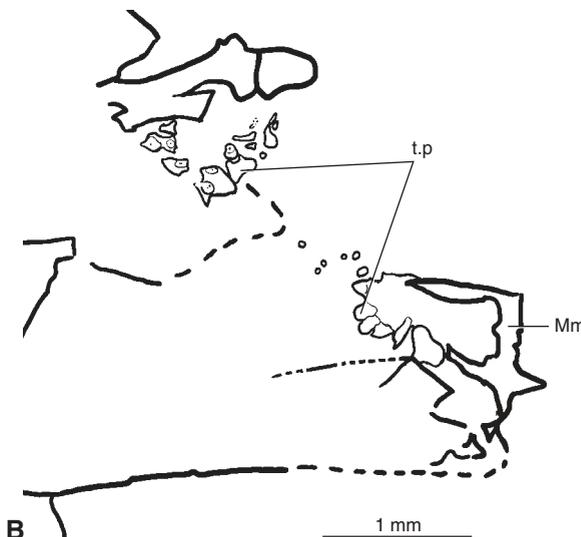


Fig. 3. *Axelrodichthys araripensis* (KMNH VP 100,262) from the Nova Olinda Member of the Crato Formation in the Araripe Plateau, Brazil. **A**, Close up of the anterior part of the lower jaw. **B**, line drawing of A. Abbreviations: **Mm**, mentomeckelian; **t.p**, tooth plate.

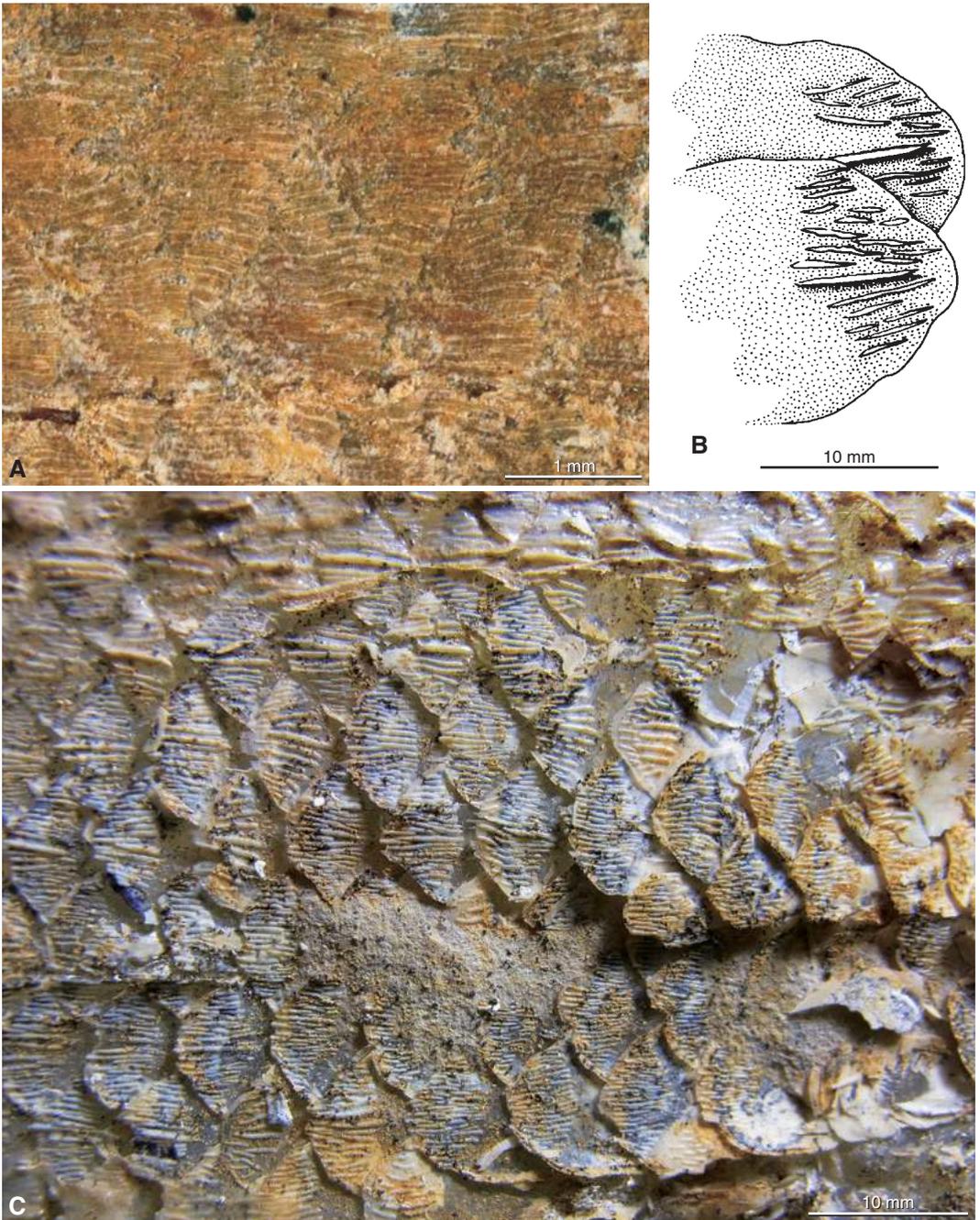


Fig. 4.

A, scale of the dorsal part between the first and second dorsal fins in the juvenile of *Axelrodichthys araripensis* (KMNH VP 100,262). **B**, scale of the posterior part of the body in the adult of *A. araripensis* (FMNH PF 11856) (from FOREY 1998). **C**, scales of the middle of the body below the first dorsal fin in the small specimen of *A. araripensis* (UERJ-PMB 79).

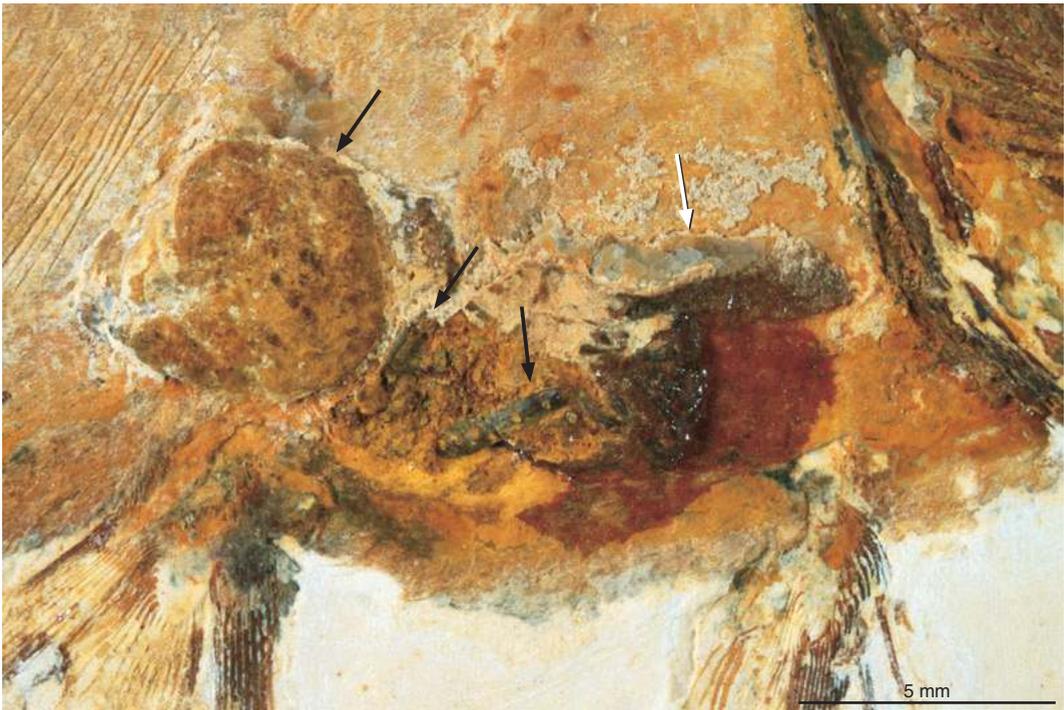


Fig. 5. Stomach contents and calcified thin plates of the lung of *Axelrodichthys araripensis* (KMNH VP 100,262). Black arrows indicate the stomach contents. The white arrow indicates the calcified thin plates of the lung.

Scales (Fig. 4A) are relatively large and exposed on the inner surface of the left side. Most of the scales show only embedded portions, but some scales show the exposed portions with minute tubercles.

Many cylindrical fragments with several pores and a spiral-shaped lump are preserved in the abdomen. These are probably stomach contents (Fig. 5). The calcified thin plates preserved above the stomach contents are probably a part of the calcified lung (Fig. 5). This organ, in adult specimens, consists of osseous blades of variable thickness separated from each other, indicating that in the living individuals, these ossified plates were probably separated by connective tissue (BRITO et al. 2010).

Discussion

The new coelacanth specimen is almost complete, and is better preserved than the first smaller specimen described from the Crato Formation, although the supplementary or accessory lobe of the tail is partially disarticulated. It is a slightly larger specimen, with an estimated total length about 100 mm (the first one, with a total length of 70 mm, was identified as *Axelrodichthys* sp. by BRITO & MARTILL 1999).

Based on the new specimen, we note two additional characteristics for the diagnosis of *Axelrodichthys* proposed by MAISEY (1986) and FOREY (1998). These are: (1) the concave dorsal margin of the parietonasal shield in lateral view and (2) the deepest point of the lower jaw located anteriorly, as the genus *Axelrodichthys* is clearly distinguished from its sister genus *Mawsonia* by these characteristics (MAISEY 1986: figs. 7, 18B, 26A; YABUMOTO 2002: fig. 3). We consider that both the new specimen and the first and smaller specimen represent juveniles of *A. araripensis*, due to the presence of the median extrascapular, the concave dorsal margins of the parietonasal shields, and the anterior position of the deepest point of the lower jaws (Fig. 1).

Except for the two young individuals found in the Crato Formation, all other specimens of *A. araripensis* occur in nodules from the Romualdo Member of the Santana Formation, which is slightly younger

Table 1.

Some proportional measurements of *Axelrodichthys araripensis*. Abbreviations: CP, body depth at dorsal lobe of caudal fin origin (= 3rd dorsal of UYENO 1991); HD, depth of head; HL, head length; PD1, length from snout to 1st dorsal origin; PNL, length of parietonasal shield; PPL, length of postparietal shield; SL, estimated standard length; TD, body depth.

	HL	HD	TD	CP	PD1	PNL/PPL
	/SL					
MSPC-287	0.36	0.25	0.28	0.18	0.47	2.12
KMNH VP 100,262	0.35	0.24	0.29	0.19	0.42	1.98
AMNH 11756	0.29	0.20	0.29	0.25	0.37	1.99

not previously been described in this species. The teeth at the anterior end of the lower jaws are needle-like in adults (FOREY 1998), but conical in the juvenile (Fig. 3).

The quadrate is similar to that of adults, but it is inclined caudally, whereas it is almost vertical in adults. The angle between the posterior margin and the ventral margin of the pterygoid is obtuse, but it is acute in adults. The specimen described here has relatively long fin rays. The ratio of head length to estimated standard length is larger than that of adults. The long fin rays and the large head are interpreted here as juvenile characters of this species (Table 1). Surprisingly, the lung in this specimen (Fig. 5) has the calcified thin plates of some fossil coelacanth, rather than the phosphatic mass, probably formed by collagenic fibres during life, found in the 70 mm specimen and in others.

The ornamentation of the scales of the juvenile is distinct from that of adults. The scales of the young specimen described here have minute tubercles on the exposed area (Fig. 4A). In contrast, in the adults of this species the scales are ornamented with short, irregularly spaced horizontal ridges (Fig. 4B) (see FOREY 1998: fig. 11.7). Some specimens of *Axelrodichthys* from the Santana Formation, considered as representing intermediate stages between juveniles and adults (cf. specimen UERJ-PMB 79) present a mixture of scale ornamentations, presenting both some scales with ornamentation as described here for the Crato specimen and other scales presenting the ornamentation as described by FOREY (1998) (Fig. 4C). Based on these observations, we suggest that the ornamentation of the scales changes from young to adult stages.

Differences in the ornamentation in the scales, depending on the part of the body, were observed in other coelacanth such as *Macropoma* (see FOREY 1998); however, these differences are not ontogenetic. Ontogenetic changes in the ornamentation of scales are presently unknown in other fossil species and extant coelacanth and were not observed in the mawsoniid species *Parnaibaia maranhaoensis* where specimens of different sizes are known. Therefore, this pattern of ontogenetic variation should be sought in other species, especially in other mawsoniids.

That the specimens of *Axelrodichthys* from the Crato Formation are juveniles, as well as the fact that juvenile specimens of other species also found in both the Santana and the Crato formations (e. g., *Placidichthys*, *Santanichthys*, *Cladocyclus*) (LEAL & BRITO 2004; BRITO 2000, 2007) led us to suggest some paleoecological implications relating to their reproductive biology. As BRITO (2007) mentioned, considering that the paleoenvironmental conditions of the Crato Formation are currently interpreted as lagoon-like with probable fluctuating salinities (MARTILL 1993), it is suggested that marine forms had entered the lagoon through one of the restricted links to the sea, perhaps for reproduction. The finding of young *A. araripensis* in the Crato Formation implies that this coelacanth gave birth in the lagoon and juveniles of this species remained there at least until they reached a total length of approximately 100 mm.

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than the Crato Formation. It is difficult to compare all the characters present in our specimen to adult specimens, since most of the larger specimens from the Santana Formation are incomplete, and especially because entire fin rays are not preserved. The ratio of the length of the parietonasal shield to that of the postparietal shield in the juvenile is almost the same as in adults, but the lower jaw is deeper and the head is larger than that of the adults (Table 1).

The new juvenile specimen has conical teeth on the dermopalatine and ectopterygoid (Fig. 2). These bones and teeth have

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