

Axelrodichthys araripensis Maisey, 1986 Revisited.

[names of the authors deleted to maintain the integrity of the review process]

Axelrodichthys araripensis Maisey, 1986 Revisited.

Axelrodichthys is a genus of fossil coelacanth of the family Mawsoniidae with a wide spatial and temporal range, spanning from the Aptian/Albian of Brazil to the Campanian of France. In light of new discoveries in recent years a renewed interest in *Axelrodichthys* has emerged. Here we offer new insights on the type species, *A. araripensis*, based on a complete new description of all its morphological characters and a comparative study of several other Mawsoniidae. A relatively large sample composed of 113 specimens of *A. araripensis* and associated Mawsoniidae species was observed; ~~deposited in twelve institutions based on four different countries~~. Among the newly observed features are the broad aspect of premaxillae supporting the anterior opening of the rostral organ; a unique pattern of skull roof ornamentation; the basioccipital; ~~with never discussed before blood vessel passages~~; a passage of nerves in the prootic; the passage for the superior ophthalmic nerve; ~~the scapulocoracoid~~; the anocleithrum; and ~~the~~ ossified zygial plates. Observation of two juvenile specimens in different growth stages allowed for the inference of negative allometric growth in the epicaudal lobe. Morphological comparisons pointed out that *M. lavocati* is more closely associated with the *Axelrodichthys* than with *Mawsonia*, therefore we included it in the *Axelrodichthys* genus as *A. lavocati*. ~~Some anatomical features of *Axelrodichthys* suggest that the genus is more closely related to basal mawsoniids than the sister genus *Mawsonia*.~~

Keywords:-*Axelrodichthys araripensis*; *Axelrodichthys lavocati*; coelacanths; anatomical review; gondwanian mawsoniids. ~~coelacanth;~~

Comentado [LF1]: Upon new observation I have changed this entry. The openings were located on the posterior wing of the prootic (next to the basioccipital). I adjusted the figures and text accordingly.

Comentado [LF2]: Reviewer 2: As this character has a really conservative shape in comparison to other coelacanths and in the interest of keeping the discussion more succinct we opted to remove from the abstract and not add it to the discussion.

Axelrodichthys araripensis; anatomical review; *Mawsonia*; gondwanian mawsoniids.

1: Introduction

~~Few groups of fishes have received the attention of the scientific community and the general public alike as coelacanths (Sarcopterygii: Actinistia). Especially since the discovery of a current living species in the South African coast in 1939 (Smith 1939), even though the group has being known in the fossil record for about a hundred years prior to that event (Agassiz 1839). Paragraph: use this for the first paragraph in a section, or to continue after an extract.~~

Comentado [LF3]: Reviewer 2: This part was removed to increase text fluency.

The Mawsoniidae ~~constitute is~~ a family of fossil coelacanths of singular importance, being the predominant Actinistia family in the Mesozoic of Gondwana. This group, found mostly in continental deposits, hold some of the largest recorded species of coelacanth (Dutel et al. 2012) like *Mawsonia gigas* ~~A. S.~~ Woodward (1907) and *Axelrodichthys araripensis* ~~J.~~ Maisey (1986), both from ~~Brazilian Cretaceous~~ Cretaceous of Brazil. The family was ~~established-named~~ by Shultze (1993) based on a number of morphological characters (*i.e.* presence of ossified ribs, ornament of the dermatocranium usually rugose, spiracular and suboperculum usually absent, reduction or loss of supratemporal descending process). ~~There are six genera of Mawsoniidae whose positioning on the family are well accepted: Chinlea B. Schaeffer (1967), Parnaibaia Y. Yabumoto (2008), Trachymetopon E. Hennig (1951), Axelrodichthys J. Maisey (1986) e Mawsonia A. S. Woodward (1907). According Dutel, Herbin & Clément (2015) the phylogenetic relationships of these genera are as following: (Diplurus + (Chinlea + Parnaibaia + (Trachymetopon + (Axelrodichthys +~~

54 *Mawsonia*))). Other genera present characters that suggest affinities with the
 55 Mawsoniidae but require further supporting evidence (Forey 1998; Gallo da Silva et al.
 56 2010); *Lualaba* P. Saint-Seine (1955); *Alcoveria* L. L. Beltan (1972); *Garnbergia* M.
 57 Martin, S. Wenz (1984); *Indocelacanthus* S. L. Jain (1974) and *Libys* G. V. Münster
 58 (1842).
 59 *Axelrodichthys* is a genus of wide spatial and temporal distribution. The type
 60 species *A. araripensis* Maisey (1986), 1986 was described from fossils of the
 61 Aptian/Albian of north-eastern Brazil. Recently the interest in *Axelrodichthys* has
 62 resurfaced with new accounts from Kem Kem Beds, ?Cenomanian of Morocco (Cavin
 63 and Forey 2004); Ankazomihaboka sandstones, Cenomanian of Madagascar (Gottfried
 64 et al. 2004), and from a lower Campanian site in Southern France, (Ventabren
 65 motorway. The latter turned out to be a new species, *A. megadromus* L. Cavin, X.
 66 Valentin & G. Garcia et al. (2016); and constitutes the latest occurrence of a
 67 mawsoniids worldwide (Cavin et al. 2016). Another species of the genus, *A. maiseyi* M.
 68 S. S. de Carvalho, V. Gallo & H. R. S. Santos de Carvalho et. al. (2013), another species
 69 of the genus was discovered in the Grajaú Basin (Aptian of Brazil).

70 The renewed interest in *Axelrodichthys* follows a general trend that seeing trend
 71 seen in coelacanth studies in recent years, where several new Mesozoic actinistians have
 72 been discovered or re-described. That prompted us to revisit the type species of the
 73 genus, *A. araripensis*, and contrast it with other species of the Gondwanian branch of
 74 the family Mawsoniidae.

77 2: Objectives

78 The present work aims to revisit *A. araripensis* under a broad perspective,

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through a completely new morphological description and comparisons with [other](#)
[phylogenetically](#) associated Mawsoniidae genera. That will serve to both uncover
previously undescribed features and as a review of the accumulated data present to date
in the literature.

32: Material and Methods

Knowledge of coelacanths have been mostly acquired through fragmentary remains
(Arratia & Schultze, 2015). A relatively large sample can provide a more complete
picture of the anatomical features of the species as a whole ([see](#) ~~(de~~ Carvalho and Maiséy
2008 [for a similar approach on the genus Mawsonia](#)). We have gathered a sample of 59
specimens of *A. araripensis* and 55 additional exemplars of other mawsonids belonging
to eight different species: *A. maiséyi*, *Chinlea sorenseni* [Schaeffer](#) (1967), *Parnaíbaia*-
maranhoensis [Yabumoto](#) (2008), *M. gigas*, *M. minor* ~~A. S.~~ Woodward (1908), *M.*
lavocati ~~N.~~ Tabaste (1963), *M. tegamensis* ~~S.~~ Wenz (1975); *M. brasiliensis* ~~Y.~~
Yabumoto (2002) and *Lualabaia*-*lerichei* [Saint-Seine](#) (1955). The whole sample is
formed by a total of 113 specimens. See the complete list of fossil specimens in the
Supplementary Material, which also contain supplementary figures that will be
referenced in the text. ~~We strongly recommend the reader to study them as well. We~~
~~strongly recommend the reader to study them as well.~~

All but two specimens were personally ~~observed, and~~ [observed and](#)
photographed. Measurements were made using the software Fiji (Schindelin et al.
2012).

Scaled photographs in high resolution of the holotypes of *M. tegamensis* (GDF 401) and
L. lerichei (MRAC R.G.10.046) were granted to us by the Muséum National d'Histoire

103 Naturelle (Paris, France) and the Museum Royale l'Afrique Centrale (Tervuren,
104 Belgium) respectively.

106 **32.1: Institutional abbreviations**

107 The specimens examined were deposited in thirteen different institutions listed below:

- 108 • UERJ-PMB, Universidade do Estado do Rio de Janeiro (UERJ), ~~(UERJ), Rio de~~
109 ~~Janeiro, Brazil;~~
- 110 • UFRJ-DG, Universidade Federal do Rio de Janeiro (UFRJ), ~~(UFRJ), Rio de Janeiro,~~
111 ~~Brazil;~~
- 112 • MN, Museu Nacional, ~~(Rio de Janeiro, Brazil)~~
- 113 • DGM-DNPM, Divisão de Geologia e Mineralogia do Departamento Nacional de
114 Produção Mineral, ~~(DGM-DNPM), Rio de Janeiro, Brazil;~~
- 115 • MSPC, Universidade Regional do Cariri (URCA; Crato, Brazil), ~~(MSPC),~~
- 116 • AMNH, American Museum of Natural History (AMNH), ~~(AMNH), New York, United~~
117 ~~States of America;~~
- 118 • FMNH, Field Museum of Natural History (FMNH), ~~(FMNH), Chicago, United States;~~
- 119 • NHUK PV.P, Natural History Museum (London, England), ~~(NHUK PV.P),~~
- 120 • KMNH VP, Kitakyushu Museum of Natural History and Human History
121 (Kitakyushu, Japan), ~~(KMNH), Kitakyushu, Japan;~~
- 122 • AMF, Aquamarine Fukushima (Fukushima, Japan), ~~(AMF);~~
- 123 • NSM-PV, National Museum of Nature and Science (NSM-PV), Tokyo, Japan), ~~(NSM-PV),~~
- 124 • MNH.F.GDF, ~~(MNH.F.GDF), and~~ Muséum National d'Histoire Naturelle (Paris, France), ~~(MNH.F.GDF),~~
125 ~~Paris, France (MNH.F); Muséum National d'Histoire Naturelle (Paris, France).~~
- 126 • ~~(MNH.F); Muséum National d'Histoire Naturelle (Paris, France).~~
- 127 • MRAC R.G., Museum Royale l'Afrique Centrale (Tervuren, Belgium), ~~(MRAC R.G.),~~

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43: Systematic palaeontology

Sarcopterygii Romer, 1955

Actinistia Cope, 1871

Coelacanthiformes Huxley, 1861

Latimeroidei Schultze, 1993

Mawsoniidae Schultze, 1993

Axelrodichthys Maisey, 1986

Diagnosis (emended from Maisey, 1986): Coelacanth reaching estimated lengths of 1-2 m. Roofing bones of skull and angular with rugose ornament, particularly in the supraorbitals and tectals; operculum and gular plates ornamented with numerous fine radiating striae; parietonasal moiety of skull roof 2.5 – 3 times longer than otico-occipital part, and at least 3 times as long as broad; postparietal moiety with large parietals and postparietals, plus three extrascapulars integrated as part of the skull roof; postorbital extends as far in front of intracranial joint as behind; lachrymojugal semicircular, not elongated anteriorly and not reaching lateral rostral; antotic process of the basisphenoid short and robust; foramina for VII and jugular vein extremely small, jugular canal reduced or closed; scales ornamented with narrow, sometimes interrupted ridges; lung strongly ossified.

Type species *Axelrodichthys araripensis*

Holotype: AMNH 11759

Diagnosis (emended from (Maisey 1986)): Meristic data of the fin rays as follows: D1 = 9-10, ~~;~~ D2 = 10, ~~;~~ P = 12-15, ~~;~~ V = 17-18, A = 19, ~~;~~ C = ~~17-18 in the upper lobe, 15-16 in the lower lobe~~ ~~15/15~~; gular plate relatively short, less than 75% of the jaw length; ornament of the skull roof marked by small rounded ~~excavations~~ cavities, which are

concentrated mainly on the marginal bones of the skull roof; anterior opening of the rostral organ contained within the premaxillae; median extrascapular leaf shaped; ventral swelling of the pterygoid present; ~~shagreen pattern located on the lateral wall of the pterygoid~~; parasphenoid toothed surface ending in a simple triangular outline; ~~sphenoid condyles oblique in relation to the longitudinal axis of the ethmosphenoid shield~~; presence of a ventrally oriented bulge on the main body of the base of the second dorsal fin.

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54: Results

54.1: Skull roof

Like in all lineages of coelacanth the skull of *A. araripensis* is divided into two ~~shields~~moieties, anterior and posterior (Thomson 1969). In accordance with the nomenclature used by Forey (1998), the anterior and posterior ~~shields~~moieties or shields of the dermatocranium will be henceforward referred as parietonasal and postparietal respectively, while in the neurocranium the same will be referred as ethmosphenoid and otico-occipital. The proportion parietonasal/postparietal shield in *A. araripensis* ~~is about~~is between 2.5 and 3 (Maisey, 1986). The parietonasal shield is 2.5 to 3 times as long as it is broad and abruptly narrows at the level of the posterior tectals. It is strongly concave in lateral profile and ~~descends~~forms a descendent arch in relation to the postparietal shield, ~~at an angle of approximately~~ 160° (Fig. 1)

Comentado [LF5]: Upon suggestions from Reviewer 1 we are taking this information off the text. The measure in question was made on the holotype. We have made many attempts to make a morphometric study, which were unsuccessful either by lack of statistical significance or because the positioning of the fossils. In addition, given more thought on the subject we came to realize that the measurement of angle between the two shields is located at an articulation, which could complicate matter even further.

Fig. 1. Skull of a young specimen *A. araripensis* specimen in left lateral view (UERJ-PMB 434) – chemically prepared. Scale bar = 1 cm. Abbreviations: ?Cor(1-3): possible fragment of coronoids 1-3; Ang(l): left angular; Ang(r): right angular; art(r): right articular; Cor.p, principal coronoid; De(l), left dentary; Dpl, dermopalatine; L.e, lateral ethmoid; Op, operculum; pect.Gr, pectoral girdle; Po: postorbital; Pp.S, postparietal shield; Prn.S, parietonasal shield; Pro: prootic; Pt, pterygoid; Q, quadrate; rart(r), right retroarticular.

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Fig. 2. Skull roof of juvenile *A. araripensis* (AMNH 13962) – chemically prepared. (A) Right lateral view Dorsal view of the skull shield displaying dislocated right side cheek bones; (B) representation of the skull roof bones and its ornament; (CB) inferred path of the lateral line canals in the skull roof and cheek bones with information complemented from UERJ-PMB 468; FMNH PF. 12840 and MN-5734-V. Scale bar = 1 cm. Abbreviations: ant.p, anterior parietal; Ext.l, lateral extrascapular; Ext.m, medial extrascapular; io.s.c, infraorbital sensory canal; j.s.c, jugal sensory canal, Lj, lachrymojugal; Na, nasals; post.pr, posterior parietal; p.ros; posterior opening of the rostral organ; Po, postorbital; Pop, preoperculum; Pp, postparietals; So, supraorbitals; so.s.c; supraorbital sensory canal; ot.sc, otic sensory canal; Sq, squamosal; Stt, supratemporal; stt.com, supratemporal commissure; Te, tectals.

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The premaxillae are preserved on three individuals in the sample, three juveniles: KMNH PV P. 100,262 (Fig. 3A, B), NSM-PV 20382 (Fig. 3C, D) and UERJ-PMB 468 (Fig. 4); and in an adult: specimen, AMNH 12211 (Fig. S1). It presents a broad aspect

and is pierced by a large foramen (Fig. 3, Fig. 4, Fig. S1). Here we interpret it as representing the anterior opening of the rostral organ (see further information on the discussion). The premaxillae form buds outlining the anterior opening of the rostral organ (Fig. 3, Fig. 4) which makes it more evident.

Fig. 3. Snout region of two juvenile *A. araripensis*. (A) KMNH VP. 100,232. (B) NSM-PV 20382. Components of the snout and palate are ~~colored gray~~ grey shaded. Circled regions show the portion of the premaxilla bearing small teeth. (A) ~~and~~ (B) Scale Bar = 0,1 cm. (C) ~~& and~~ (D) Scale Bar = 1 cm. Abbreviations: ~~a.ross: anterior opening of the rostral organ an~~ a.ross: anterior opening of the rostral organ; ~~an, anterorbital commissure~~; Dpl, dermopalatine; ~~e, ethmoid commissure~~; Ectp, ectopterygoid; ~~Ina.l, lateral internasal; Ina.m, medial internasal~~ Ina.l, lateral internasal; Ina.m, medial internasal; ~~Ina, internasal~~ Ina, internasal; Pmx.l, left premaxillae; Pmx.r, right premaxillae; ros.oss, rostral ossicles.

Fig. 4. Left premaxilla of a juvenile *A. araripensis* ~~with displaying the~~ anterior opening of the rostral organ (UERJ-PMB 468) ~~– chemically and mechanically prepared~~. Dashed lines contour the region of interest. ~~Scale bar: (A) 1 cm~~ Scale bar = 1 cm; (B) Scale bar = 0,5 cm. Abbreviations: at, anterior transverse commissure; a.ros, anterior opening of the rostral organ; Pmx, premaxilla; Pmx.B, buds of the premaxilla.

Each premaxilla ~~has a notch on their distal extremity. When in contact with the corresponding notch of the anterior end of~~ contacts the corresponding lateral rostral ~~they~~ to delimit the anterior nostril (see details in Fig. S1, Fig. S2).

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The dispositional pattern of bones in the snout of *Axelrodichthys A. araripensis*
~~snout~~ is not much clear. KMNH VP. 100,232 (Fig. 3A) seem to have preserved two
rostral ossicles immediately behind the premaxillae, following their curved contour.
One internasal element is positioned immediately behind the rostral ossicles.

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The remainder of the parietonasal shield conforms with a dispositional bone
pattern usual for all the species of coelacanth where a central row of paired bones is
flanked by two series (one on each side) of supraorbitotectals (Fig. 2). The central row
is formed by three nasals (each successively longer then the preceding one) and two
pairs of parietals, with the second pair being only slightly longer and wider than the
first. On the flanks there are three tectals and four supraorbitals. The snout of
Axelrodichthys is marked by an abrupt narrowing at the level of the last tectal. The
sutures that separates all the bones on this shield are highly interdigitated.

The passages for the superficial ophthalmic nerve are located on their
posteroventral surface of the parietals (Fig. 5). The pair of posterior parietals meet the
basisphenoid through the pleurospenoid suture (Fig. 6).

Fig. 5. Skull of juvenile *A. araripensis* (UERJ-PMB 33) – chemically prepared. The
cheek bones on the right side of the parietonasal shield were not preserved exposing the
supraorbital canal. It also shows features of the neurocranium and nerve foramens. A
larger scale ~~version of this picture~~ photograph of this specimen can be seeing in the
supplementary material S2 (Fig. S16). Arrow points in cranial direction. Scale bar = 1
cm. Abbreviations: Bsph: basisphenoid, ot.s.c. otic sensory canal; Pro, prootic; S.opht,
superior branch of the ophthalmic nerve; V1, profundus foramen.

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Fig. 6. Posterior view of the parietonasal shield of juvenile *A. araripensis* (AMNH 11760) – chemically prepared. Notice, on the limits of the shield, the two foramina that represent the passage of the supraorbital sensory canal through the intracranial joint. The dorsum sellae can be seen pressing against the ~~foramen magnum~~ cranial cavity. ~~The sphenotic condyles that turn obliquely in relation to the longitudinal axis of the parietonasal shield (the arrows point to the direction of the turn).~~ Scale bar = 1 cm. Abbreviations: ant.pr, antotic process of the basisphenoid; Cc, cranial cavity; d.s, dorsum sellae; ~~fm, foramen magnum~~; ~~pl.sut, pleurosfenoid suture~~; post.pr, posterior parietal; post.pr-Bsph.sut, suture between the postparietal and the basisphenoid; pr.con, *processus connectens*; sph.c, ~~sphenotic~~ sphenoid condyles; so.s.c, supraorbital sensory canal.

The postparietal shield is formed by a pair of postparietals, a pair of supratemporals and three extrascapulars (Fig. 2). In transverse section, the postparietal shield has the aspect of a dome (Fig. S3). In dorsal view the shield is in the form of a bell, with the anterior margin being convex and the posterior margin, concave (or “embayed” according to (Forey 1998). The extrascapulars are located on the posterior margin. The extrascapulars are placed in the space formed by the posterior projections of the supratemporals. Forey (1998) calls this configuration “embayed”, as opposed to other coelacanths whose posterior margins of the postparietal shields are straight. The width of this shield reaches its maximum at the level of the ~~increases continually from the most anterior point of the postparietals to the~~ most posterior point of the supratemporals, which incidentally also marks the posterior limits of the postparietal shield. The middle third ~~extrascapular~~ is “leaf” shaped (Gottfried et al. 2004) (Fig. 2)

and its prominent posterior projection aligns in lateral view with the posterior end of the supratemporal.

5.1.1: Ornament of the Skull Roof

The external surface of each dermal bone in the skull roof is **excavated** **ornamented** in ~~an a heavy and~~ intricate pattern of **heavy rugose ornament** **striae** (Fig. 2). The ~~excavations striae appear to~~ irradiate **from the centres of ossification (Forey 1998)** ~~in straight lines from the centres of ossification (Forey 1998). As farther they are from~~ ~~such point the more irregular they become, which forms a reticulate, rough pattern and~~ **form an irregular and more reticular pattern as they distance themselves from it.** Bones in the medial series of the parietonasal shield and the postparietals demonstrate a smoother area where the reticulation is restricted or non-existent. In the marginal bones (i.e. the supraorbitotectal series, the temporals and extrascapulars) ornamentation has a rougher aspect and the lines demonstrate an array of extremely irregular paths.

Scattered throughout the surface of the skull roof bones ~~are~~ are small rounded **cavities** **excavations** (Fig. 2, Fig. S4A, Fig. **S5GS6C**) (not to be confused with lateral line openings). They are more prevalent on the marginal bones like the extrascapulars and the first nasals.

5.1.2: Lateral Line Canals of the Skull Roof

The heavy ornament ~~of on~~ the dermal bones ~~in of~~ the skull **roof** makes it difficult to determine the number of pores or even the paths taken by the lateral line canals. Figure 2C presents an inferred path for the supraorbital (anterior shield) and otic (posterior shield) sensory canals based on observations made on some individuals of the sample. According to Maisey (1986) **most of** the supraorbital sensory canal is enclosed in the skull roof, being the openings restricted to the snout. **Two specimens in the**

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sample: a juvenile (KMNH VP. 100,232; Fig. 3) and an adult (AMNH 12214) presented a clear large medial pore on the internasal; in addition, UERJ-PMB 468 (Fig. 4) has a large pore in front of the anterior opening of the rostral organ. The positioning of the aforementioned pores seem to suggest that they belong to the ethmoid commissure (see Forey 1998, Fig. 3.1, Fig. 3.2); (Hensel and Balon 2001; Fig. 5) At the tip of the snout the two lines of the supraorbital sensory canal are joined together by two commissures: the anterior transverse commissure (more anterior; Fig. 4) and the antorbital commissure (more posterior; Fig. 3) (see Lund & Lund, 1985). KMNH VP 100,331 (Fig. S6S8) shows the openings-pores on the first third of the snout between the bones of the lateral and central series of the skull roof. On AMNH 11760 the passage from the supraorbital canal into the otic canal can be seeing in posterior view (Fig. 6). On UERJ-PMB 33 the same point can be observed from anterior view. The otic canal can be seeing on MN-5734-V (S2-Fig. 7Fig. S9)) where ornamentation has been worn out. A rudimentary path can be observed through the lateral surface of the left postparietal and descending into the supratemporal of the same side, from there it makes an anterior curve before it heads in the direction of the extrascapulars where it will presumably meet with the canal of-on the other side in the occipital commissure (Lund and Lund 1985).

Comentado [LF6]: Reviewer 1: The Lund & Lund, 1985 reference was a little obscure. The figure depicting the commissures and names (Fig. 74) was in fact referring to an idealized osteichthyan and not precisely a coelacanth. So, we reviewed it.

54.2: Cheek Bones and Operculum

The cheek bones of *A. araripensis* are sparse. In the absence of a preorbital, a deeply curved lachrymojugal comes in direct contact with the skull roof between the third tectal and the first supraorbital (Fig. 2, Fig. S5HS7). The anterior extremity of the lachrymojugal is expanded and bifurcates forming the posterior opening of the rostral organ. It reaches its lowest point, directly under the suture between the third and fourth

supraorbitals. The posterior extremity of the lachrymojugal contacts (but is not sutured to) the ventral portion of the postorbital.

The postorbital is large and irregularly shaped (Fig. 1, Fig. 2, Fig. S5H-S7). It is excavated anteriorly forming the posterior wall-margin of the orbit, and dorsally to accommodate the skull roof (Fig. S8-S10). The anteroventral corner forms a small projection above the posterior portion of the lachrymojugal (Fig. 2). ~~The postorbital is~~ positioned directly under the intracranial joint with its anterior edge located in the parietonasal portion of the skull and its posterior edge in the otico-occipital portion.

~~Two small bones rest underneath the postorbital: the triangular. There are two small cheek bones located beneath the postorbital and above the lachrymojugal: the squamosal (Fig. 2, Fig. S5H-S7) and the preoperculum (Fig. 2, Fig. S8-S10), which looks roughly rectangular with rounded corners.~~

The operculum ~~is the largest bone on the cheek~~ is large and has a rounded posterior edge (Fig. 1, Fig. S5, Fig. S6, Fig. S7A,H). ~~It has an anteriorly inclined main axis that goes from the level of the posterior edge of the otico-occipital shield to the level of the base of the principal coronoid in the mandible. Its articular surface is accommodated on the skull roof by the supratemporal (Fig. S5H). In A. araripensis the posterior edge of the operculum in is rounded. It comes in contact with the skull roof at the lateral edge of the supratemporal.~~

5.2.1: Ornament of the Cheek bones

Ornament on the ~~Cheek-check Bones bones~~ is coarse (Fig. 2). Most of it is composed of rounded ~~cavitiesexcavations~~ a little deeper than the ones show on the skull roof.

Comentado [LF7]: Reviewer 1: Legend and figure modified.

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~~The Operculum is an exception.~~ The ornament in the surface of the operculum
however on its surface is characterized by very fine radiating straight striae, departing
from the centre of ossification near ~~the articular surface~~the contact point between the
operculum and the skull roof (Fig. ~~S9S11~~). Some individuals show areas in the
operculum with rough reticulated ornamentation but, like in the medial bones of the
parietonasal shield, they are either restricted to the margins of the operculum or simply
non-existing.

~~5.2.2: Lateral Line Canals of the Cheek Bones~~

The jugal sensory canal runs through out the extension of the lachrymojugal
(Lund and Lund 1985; Forey 1998), with pores opening on its ventral edges (Fig. 2C).

Specimen FMNH PF. 12840 displays a series of small pores running through the
centre of the squamosal as part of the infraorbital sensory canal thus helping composed
the inferred path represented in Fig. 2C.

~~According to Forey's matrix (Forey 1998) the infraorbital sensory canal runs through
the centre of the postorbital (character 21 — coding 0).~~

~~5.3: Lower Jaw and Gular Plates~~

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Comentado [LF8]: Reviewer 1: Sentence removed as it was just a quotation and ultimately judged unnecessary.

The lower jaw is formed by a complex set of ~~structures-bones~~ (Fig. 1, ~~Fig. 7~~, Fig. ~~S5HS7~~).

Three bones form the main structure of the anterior extremity of the lower jaw: the dentary (Fig. 1, Fig. ~~S5HS5C~~, Fig. ~~S7~~), the mentomeckelian (~~Fig. 7~~) and the splenial (Fig. ~~S5B~~). The latter can only be seen from a ventral perspective. The dentary is the largest ~~one with a more elaborate form. one of the three, with a more elaborate shape.~~ It has an anterior hook shape process and a bifurcated posterior end. The inferior projection of the bifurcation ~~is the longer one. It~~ is involved by the anterior extremity of the ~~-angularprearticular beneath the angular. The superior extremity embraced by the coronoid 4 (Fig. S5H,C). Between the projections a deep space is formedThe space between the projections would. In life that would be in life be~~ covered by the tissue of the pseudomaxillary fold (Forey 1998; Cupello et al. 2016).

Comentado [LF9]: Reviewers 1 & 2: This picture has been adjusted. On the supplementary material.

Comentado [LF10]: Reviewer 2: Text excluded to increase fluidity.

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~~Fig. 7. Lower jaw of *A. araripensis* (FMNH PF. 10706). (A) Structure in medial view. (B) Schematic representation with the bones of the medial side and components of the glenoid fossa featured in gray. The prearticular is subdivided into three sections for better understanding of its form (see text for clarification). Scale bar = 5 cm. Legend: art, articular; Cor.4, coronoid 4; Cor.p, principal coronoid; Glen.f, glenoid fossa; Part, prearticular; rart, retroarticular.~~

The mentomeckelian is in a medial position in relation to the dentary (~~Fig 7~~). It is a flat bone that curves medially accompanying the curvature of the dentary hook process.

There are three small rounded plates (~~Fig. S5D~~) resting above the region of suture between the mentomeckelian and the dentary. ~~Such platesThey~~ are covered with small teeth. ~~and~~ Forey (1998) considers ~~the possibility of those teeth being them to the~~

homologous equivalent of the coronoids 1, 2 and 3. The specimen UERJ-PMB 473 displays fragments of these plates (Fig. S5D).

Comentado [LF11]: Reviewer 1: Actually, these teeth are described by Forey as being needle-like (See Forey, 1998; page 154, 2nd paragraph.) the ones with striation are in the walls of the prearticular and coronoid 4.

Comentado [LF12]: Reviewer 2: Text excluded to increase fluidity.

The splenial is positioned in the space underneath the dentary and the mentomeckelian (Fig. S5C). Its longitudinal length is equivalent to that of the dentary. It is dorsoventrally flattened with a rounded anterior extremity and a narrow posterior one.

Two bones placed parallel to each other compose the main body of the lower jaw. The angular on the lateral side (Fig. 1, Fig. S5A, ~~H Fig. S7~~) and the prearticular on the medial side (~~Fig. 7~~). The angular is slightly concave in its ventral edge. The anterior end is bifurcated and, as stated above, embraces the ventral tip of the dentary (Fig. S5HS7). It has a high coronoid eminence with an anteriorly turned process (Fig. 1, Fig. S4B, Fig. S5HS7), which is located before its anterior half. At that point the principal coronoid is sutured to the lower jaw. The prearticular has a dagger like anterior end above which the coronoid 4 is positioned, and is more elevated on its posterior portion (see (Forey 1998), Fig 5.10E).

The coronoid 4 is located dorsallyanteriorly to the prearticular, and is sutured to it by its ventral and posterior edges (Fig. 7, Fig. 8). The medial surface of both are covered in small conical teeth with radiating striae (Forey 1998). The coronoid 4 resembles a knife's blade, pointing out towards the anterior end of the lower jaw. Its posterior also has a dagger-like anterior portion with its posterior extremity is being rectangular and fits-fitting in the space formed by the prearticular (Fig. 8).

For better explaining the complex form of the prearticular, we divided it into three sequential parts (Fig. 7B). The anterior end is triangular, shaped like dagger. The following section consists of a straight plateau that proceeds to the level of the posterior

end of the base of the principal coronoid. The last section is a descending curve

accompanying the contour of the angular to the point of formation of the glenoid fossa.

Comentado [LF13]: Reviewer 2: Portion removed to improve fluidity.

The morphology of the principal coronoid (Fig. 1, ~~Fig. 7~~, Fig. S5HS7) is a very peculiar feature of the *Mawsonia*/*Axelrodichthys* complex (Cloutier 1991; Forey 1998). It is saddle shaped displaying a cranial and a caudal process. The first extends above the dorsal edge of the coronoid 4 and overlaps the anterior end of the angular. The latter extends dorsally in a diagonal path and has a small bone fold formed underneath it (Fig. S8).

~~The coronoid 4 overlaps the prearticular and it is laterally flattened, also shaped like a dagger (Fig. 7).~~

The angular and the prearticular provide the floor for the glenoid fossa (point of articulation with the palate), which is formed by two ~~additional~~ small ~~bone~~ ~~additional~~s, longitudinally aligned ~~bones~~: the articular and the retroarticular (~~Fig. 7~~). The articular has a roughly rounded shape with an articular facet on its posterior side. The retroarticular is conical, with its articular facet on the anterior end. It is marked by longitudinally running striae.

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According to Schultze (Schultze et al. 2010) coelacanth's gular plates are rarely well described. *A. araripensis* has a pair of robust gular plates (Fig. S5A, ~~H Fig. S7~~, Fig. S11). The medial edge of each one is straight which allow them to meet one another at midline (~~Fig. 10~~). Their lateral edges give them a somewhat oval, albeit slightly irregular shape. The anterior extremity of the individual plates is broad and round while the posterior one is narrow. The widest portion of the ~~shape set formed by the plates~~ is transversely aligned with the coronoid eminence in the lower jaw. The plates are slightly smaller than the lower jaw. ~~The plates run through the hole extension of the~~

lower jaw and their posterior extremities align with the posterior extremities of the retroarticular on their respective side.

5.3.1: Ornament of the Lower Jaw and Gular Plates

The ornament of the angular consist of straight striae irradiating from the centre of ossification on the medial wall the angular (Fig. 1, Fig. S4B, Fig. S10S13). The centre of irradiation represents also centre of ossification which in the angular is straight in ossification, which is located in front of the glenoid fossa. On the gular plates faint lines of ornament depart from the medial surface heading outwards (Fig. S11S13).

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5.3.2: Lateral Line Canals of the Lower Jaw and Gular Plates

The configuration of the mandibular sensory canal in the lower jaw is rather simple. The only canal running through the Lower Jaw it connects with the preopercular sensory canal by the pore located at the posterior end of the retroarticular (Fig. S5HS7).

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In *Latimeria chalumnae* (Smith (1939) This this pore also serves as an entry for the internal mandibular ramus of the facial nerve (Millot and Anthony 1958; Forey 1998). The canal passes along the lower jaw inside the angular opening through a series of four large pores on its the-ventrolateral side (Fig. S10S12).

Código de campo alterado

Continuing its path along the lower jaw, the mandibular sensory canal passes through the splenial heading to the dentary, which represents its anteriormost extremity. On the splenial, it opens through what it seems to be a set of at least four pores (Fig. S5B). On the dentary, the canal opens through only one pore, not aligned with the ones on the splenial. It is located on a bulge that marks the point on which the dentary starts to curve medially to forming its hook (Fig. S5FS6B, HFig. S7).

Pit lines were reported before in the gular plates of other species of coelacanth
(Milot and Anthony 1958; Forey 1998; Gess and Coates 2015) but none were observed
in the present study.

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5.4.4: Palatoquadrate

The palate of coelacanth is a very distinctive structure. In general, it is laterally flat
with a triangular shape (Cloutier 1991). Peculiarities such as the proportion of length
and height can reflect differences in skull proportions of different groups of coelacanth
providing distinction perhaps at genus level (Forey 1998). In the case of *A. araripensis*
the ratio between length and height is 1.3 (Fig. 8).

Fig. 8. Right palate of *A. araripensis* (NHMUK PV P. 62347). (A) & (B) medial view.
Arrow indicates the ventral swell of the pterygoid; (C) & (D) lateral view. Dotted
pattern represents a shagreen pattern (see text for clarification). Scale bar = 1 cm.
Abbreviations: Aup, autopalatine; gr.Pt, groove of the pterygoid; Mtp, metapterygoid;
Pt, pterygoid; Q, quadrate; v.rm.Pt, vertical ramus of the pterygoid.

The composition of the palate is relatively simple with the pterygoid being the main
component and all the other bones attached to it (see Maisey 1986, Fig. 10; Forey
1998; Fig. 7.1F). The pterygoid

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The anterior extremity of the palate is formed by the autopalatine (Fig. 8). It is shaped
like a boat sail with the anterior border convex and the posterior concave. The
autopalatine fits in a shallow ventrolateral fossa formed on the lateral ethmoid.

Following the autopalatine is the pterygoid (Fig. 8). This dermal bone is the main
structure of the palate, on which all the other components are attached. It is a thin
triangular bone. Anteriorly, on its medial surface, the pterygoid is marked with a groove

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485 ~~where the parasphenoid fits. Pis a triangular dermal bone that anteriorly it forms~~ has a
486 thick vertical ramus ~~on its posterior side that supportssupporting~~ the metapterygoid on
487 the dorsal end and the quadrate on the ventral ~~oneend~~. The ventral border of the
488 pterygoid possesses a swelling right in front of the quadrate (Fig. 8, Fig. S12S14),
489 considered by (Dutel et al. (2012) to be of phylogenetic importance. The ~~lateral-internal~~
490 wall of the pterygoid is marked by small rounded protrusions in a shagreen pattern (~~Fig.~~
491 ~~8C,D~~). It is shown in detail in the supplementary material (Fig. S13S15).

Comentado [LF14]: Reviewer 2: The text has been removed to improve fluency.

492 Dermal ossifications can also be found in the palate underneath the autopalatine
493 and the metapterygoid in the form of three thin strips of tooth bearing bones ~~in~~
494 ~~longitudinal-alignment~~longitudinally aligned: the dermopalatines (~~anterioranteriorly~~)
495 and the ectopterygoid (~~posteriorly~~) (Fig. 1, Fig. 3). They bear small and conical teeth,
496 similar ~~to~~ the ones present in the premaxillae.

Código de campo alterado

497 The metapterygoid (~~Fig. 8~~) is ~~a an upside-down~~triangle ~~with its biggest side~~
498 ~~turned dorsally~~ that connects to the dorsal extremity of the pterygoid via an
499 interdigitated suture. ~~It articulates with the antotic prosses of the basisphenoid (see~~
500 ~~section below). The dorsal surface of the metapterygoid is flat and saddle-shaped~~
501 ~~forming the articular surface for the skull roof (Fig. S8), anterior to the antotic process~~
502 ~~of the basisphenoid (see neurocranium section below).~~

503 The quadrate (~~Fig. 8~~) has a columnar body that ~~intersects-articulates~~ with the
504 mandible via the glenoid fossa, described in the previous section. The arrange~~ment~~ of
505 the articular facets of the articular and retroarticular make the central axis of the
506 quadrate be twisted in a way that its anterior condyle is placed in a medial position
507 relative to the posterior one.

508

54.5: Neurocranium

The components of the neurocranium (Fig. 5, Figs. ~~S14S16-S1619~~) are a sparsely ossified combination of single and paired elements.

The anteriormost components of the neurocranium are the lateral ethmoids (Fig. ~~S5HS7~~, Fig. ~~S14S16, S17-Fig-14~~), which form the floor and lateral walls of the nasal cavities (~~Fig. S14~~). Furthermore, ~~as discussed in the palate section~~, the lateral ethmoids house the autopalatine on their posterior extremity, the ventrolateral fossa.

The parasphenoid is placed posteriorly to the lateral ethmoids (Fig. ~~S14S16~~, Fig. ~~45S17~~); which connects them to the basisphenoid at the posterior end of the ~~otic-ethmosphenoid shield-occipital shield~~ (Fig. 5, ~~Fig. S14~~, Fig. ~~S16S17~~). It is a dorsoventrally flat structure that maintain roughly the same width throughout its entire length. The anterior half of its ventral surface is covered with small teeth in a pattern that culminates in a small triangle on its posterior end (Fig. ~~S15S17~~). *A. araripensis* does not possess an ascending lamina anteriorly on the parasphenoid.

The basisphenoid (Fig. 6, Fig. ~~S14S16, S18~~) is a large single ossification with a complex shape, located on the posterior side of the ethmosphenoid shield. The ~~foramen magnum~~cranial cavity divides it into two branches that contacts the skull roof. Anteriorly each branch yields an antotic process (Fig. S15), a projection perpendicular to the main axis of the ethmosphenoid shield that articulates with the ~~otic portion of the otic-occipital shield with the palate via the dorsal surface of the metapterygoid (see palate section above)~~. On its ventral side, the antotic process bears strong ridges (Fig. ~~S15S17~~), ~~evidence markings~~ of its cartilage capping. On the dorsolateral surface of the basisphenoid (anterior to the antotic process) there is a groove that leads to the profundus foramen, which services as a passage of the ophthalmic nerve (V1) in L.

533 *chalumnae* (Forey 1998) (Fig. S16S18). On each side the basisphenoid contacts the
534 skull roof through the pleurospenoid suture posterior parietal (Fig. 6). ~~The sutures that~~
535 ~~unites both bones are very interdigitated~~ In posterior view the sutures are curved
536 downwards, resembling cups that hold the ventral side of the posterior parietals. The
537 superficial ophthalmic nerve passes along the parietonasal shield above the
538 basisphenoid, right underneath the supraotic sensory canal (Fig. S16S18).

539 The *processus connectens* are located on the ~~ventral-posteroventral~~ portion of
540 the basisphenoid (Fig. 6, Fig. S14S16, Fig. S15S18, Fig. S16, Fig. S19). ~~They form-~~
541 ~~They are “C” shaped structures that form~~ the “track” part of a “track and groove” ~~form~~
542 ~~type~~ of articulation between the two shields of the skull (Maisey 1986; Forey 1998;
543 Dutel, Herbin, Clément, et al. 2015). (Maisey 1986; Forey 1998; Dutel et al. 2015).
544 ~~Their posterior extremity end in two small oval sphenoid condyles that meet right above~~
545 ~~the notocordal pit and articulate with the anazigal. The processus connectens are well~~
546 ~~developed in A. araripensis and end in two oval sphenotic condyles that turn obliquely~~
547 ~~in relation to the longitudinal axis of the parietonasal shield (Fig. 6).~~

548 The largest ossification in the otico-occipital ~~portion shield~~ of the neurocranium
549 is the prootic (Fig. 5, Fig. S15S17). ~~It develops into two separate ossifications that Each~~
550 ~~side~~ descends in continuity to the respective postparietals descending lamina (see
551 Maisey, 1986; Fig. 19) forming the lateral walls of the cranial cavity. The prootic
552 projects forwards into the otic shelves (Fig. S17, Fig. S19) which in turn embrace
553 the *processus connectens* and form the “groove” for it to run in the intracranial
554 articulation. Posteriorly the prootic develops into a posterior wing that expands laterally
555 to make space for the labyrinth cavity internally. The lateral wall of the posterior wing
556 of the prootic develops into a prominent facet for the hyomandibular (Fig. 7, Fig.

Comentado [LF15]: Reviewer 2: This is a reference to your commentary. It is made exclusive that any inference to soft tissue derives from comparisons with the *L. chalumnae*.

557 ~~S17S19~~. Specimen UERJ-PMB 471 presents on its posterior wing of the prootic two
558 small foramens (Fig. 7).

559
560 Fig. 7. Isolated cranial bones of juvenile *A. araripensis* showing the basioccipital ~~and~~
561 ~~attached to the~~ posterior wing of the prootic; ~~and a~~ posterior catazygal (UERJ-PMB
562 471) - chemically prepared. (A) and (B) Notice the indication of two foramens (pointed
563 by arrows) on the posterior wing of the prootic. The posterior catazygal is dislocated,
564 found beneath the basioccipital. Scale bar = 1 cm. (C) and (D) NHMUK PV P. 62347 -
565 chemically prepared. Anterior catazygal of *A. araripensis* also displaced from its natural
566 position. Scale bar = 1 cm. Abbreviations: Boc, basioccipital; Cat.a, anterior catazygal;
567 Cat.p; posterior catazygal; pw.pro (l), posterior wing of the prootic (left).

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568
569 The notochord is persistent in ~~extant~~ coelacanth ~~genus~~ *L. chalumnae* -(Millot and
570 Anthony 1958) ~~and is presumably present on fossil coelacanths~~. It passes through the
571 oto-occipital ~~shield-moiety of the skull~~ and rests in a space ~~between-below~~ the two
572 ~~sphenotiesphenoid~~ condyles in a region known as the notochordal pit, ~~which is clear in~~
573 *A. araripensis* (Fig. ~~S16S19~~, see also Maisey (1986)).

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574 ~~The Following in caudal direction it passes through a~~ “U” shaped basioccipital
575 (Fig. ~~97~~, Fig. ~~S15S17~~, Fig. ~~S17S19~~) is located posteriorly to the notochordal pit. This
576 structure was never described before for ~~the genus~~ *Axelrodichthys* *A. araripensis*,
577 although its ~~general shape~~ seems rather ordinary ~~in shape compared to other coelacanths~~
578 (Forey 1998; Cavin et al. 2013; Dutel et al. 2015). It connects to the neurocranium via
579 an interdigitated suture with the posterior wing of the prootic (Fig. S17).

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Comentado [LF16]: Reviewer 1: I change from “*Axelrodichthys*” to “*A. araripensis*” and elaborated in the discussion

There is a foramen on the lateral of the basioccipital arch (Fig. 9A, B) whose purpose will be elaborated in the discussion. On its way to the base of the tail, the notochord

The notochordal canal is flanked by the anazygals and catazygals. The posterior catazygal can be seen on Fig. 7, is flanked at least by two isolated pieces of ossification: the catazygals. The anterior (Figs 16 C, D) and the posterior (Fig. 16 A, B).

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~~Fig. 97. (A) and (B) UERJ-PMB 471—chemically prepared. Basioccipital and posterior catazygal of *A. araripensis*. On this set of disarticulated bones, the posterior catazygal plate is dislocated, found beneath the basioccipital. Scale bar = 1 cm. (C) and (D) NHMUK PV P. 62347—chemically prepared. Anterior catazygal of *A. araripensis* also displaced from its natural position. Scale bar = 1 cm. Abbreviations: Boc, basioccipital; Cat.a, anterior catazygal; Cat.p, posterior catazygal; pw.pro (l), posterior wing of the prootic (left).~~

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No exoccipital was found, however the supraoccipital can be seeing on AMNH 14026. It has the shape of a butterfly, with two round wing-like expansions protruding from the central point.

5.4.6: Hyobranchial apparatus

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Most of the upper elements of the branchial series in *coelacanths* *L. chalumnae*, such as the pharingobranchials and epibranchials do not ossify (Millot and Anthony 1958). Therefore, in fossil coelacanths most of what is left of the gill arches are disarticulated ceratobranchials (Forey 1998) such as the ones seen on NMHUK PV P. 62347 (Fig. S14S16). There are five arches, each with a central canal

Formatado: Fonte: Itálico

604 ~~groove on the posterior side~~ for their respective afferent branchial artery ~~running~~
605 ~~posteriorly, throughout all their longitudinal length~~ (Fig. ~~S12BS14B~~).

606 Despite being stripped of the cartilage that connected all the elements of the base
607 of the ~~hyobranchial~~~~hiobranquial~~ apparatus the single basibranchial in UERJ-PMB 471
608 was preserved in close association with the ~~underlying~~ tooth plates ~~that overlap it~~ and
609 the ~~posterior~~ urohyal (Fig. ~~S18S20~~). ~~There are four plates with the two anterior ones~~
610 ~~being broader than the posterior ones (Fig. S22).~~ The basibranchial is cordiform ~~in~~
611 ~~dorsal view~~ with a notch on the posterior side that articulates with the urohyal.
612 ~~Underneath it there are four tooth bearing plates (Fig. S20).~~

613 The dorsoventrally flat urohyal is characteristic of coelacanth ~~s~~ (Forey
614 1998) ~~(Carroll 1988)~~. It is formed by three centres of ossification (Millot and Anthony
615 1958), two laterals and one central (Fig. ~~S18S20~~). It is marked by a narrowing of its
616 lateral walls dividing it into anterior and posterior parts. The posterior portion is marked
617 by a caudal “V” shaped indent. Neither the narrowing of the lateral walls ~~nor~~ the
618 posterior indent are very pronounced in *A. araripensis*.

619 The hyoid apparatus of coelacanth ~~s~~ is formed by the hyomandibular, symplectic,
620 interhyal and ceratohyal (Dutel et al. 2013). Of these elements, we could only identify
621 the ceratohyal in our sample (Fig. ~~S19S21~~). It is in fact a relatively common structure to
622 be found. It has a rod ~~like aspect~~~~shape~~, curved dorsally and is laterally compressed on
623 its posterior portion. A flat protuberance projects from its inferior edge. In life, the
624 ceratohyal would articulate with the basibranchial anteriorly and with the symplectic
625 and interhyal posteriorly.

626 627 **45.7: Pectoral Girdle and Postcranial Anatomy**

Formatado: Fonte: Negrito

The pectoral girdle is positioned just behind the operculum. The cleithrum is ~~the~~its main component ~~being of the pectoral girdle. It is~~ large and flat, ~~with an expanded ventral portion~~ (Fig. S16, Fig. S24S23).

The extracleithrum is considered to be a plesiomorphy in coelacanth (Forey 1991; Lambers 1991) (Fig. 408, Fig. S24S23). It is also a laterally flat structure and it lies in the ventral section of the pectoral girdle sutured to the cleithrum and the clavicle.

Fig. 408. Base of the pectoral fin of *A. araripensis* (UERJ-PMB 434) - ~~chemically prepared~~. The scapulocoracoid (~~grey shaded~~) is still connected to the extrascapular on its original position. Scale bar = 1 cm. Abbreviations: Cla, clavicle; Eclt, extracleithrum; Scc, scapulocoracoid.

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The clavicle (Fig. 408, Fig. S16, Fig. S24S23) is broad and thin, opening like a wing underneath the cleithrum.

The scapulocoracoid is the structure that links the pectoral girdle to the axis of the fin (Fig. 408). It is the shape of a laid down hourglass and is connected to the internal side of the extracleithrum.

The anocleithrum (Fig. S22S24) is a small component of the pectoral girdle that fits on the dorsal part of the cleithrum. In the case of *A. araripensis* the anocleithrum is simply a thin bone, laterally compressed with a sigmoid form. It has not been previously described for the *Axelrodichthys* genus.

A. araripensis is rather common in what concerns to its postcranial anatomy. It fits into the post-Devonian body plane archetype of coelacanth. The body is high with an equally deep caudal peduncle. Yet some features need to be addressed.

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One characteristic that stands out is the ossified lung (Fig. 11), (see Maissey 1986, Fig. 12). Specimens like KMNH 100,328, and the Holotype, AMNH 11759 display it as a three-chambered structure that occupy a relatively large portion of the ventral part of the body. The chambers are formed by thin layers of bone overlapped in a concentric manner (Yabumoto and Brito 2013; Cupello et al. 2015; Cupello et al. 2017) (Fig. S23).

Código de campo alterado

Código de campo alterado

Fig. 11. Midsection of *A. araripensis* (KMNH VP P. 100,328). (A) & (B) lung and pelvic bases are colored. The left pelvic base is preserved in medial view above the right (preserved in lateral view). Scale bar = 1 cm. (C) Schematic representation of the left pelvic base in medial view. Abbreviations: c (1-3), lung chambers (1 through 3); il, iliac process; isch, ischial process; l.p.b, left pelvic base; lng, lung; P.pr, pubic process; r.p.b, right pelvic base.

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The pubic pelvic fin bases girdle (Fig. 11) are not preserved in place on KMNH VP P. 100,328 (Fig. S25), suggested by the impression of the fin a few centimetres behind. The original position of the pelvic fins was possibly vertically aligned with the second dorsal fin. The internal structure of the base girdle is divided into two regions, a triangular posterior section (formed by two iliac processes and an ischial process) and an anterior one, (or pubic process). The latter is formed by two projections connected by a thin bone membrane that extends throughout their length (Fig. 11C) (Fig. 11B).

Comentado [LF17]: Reviewer 1: Actually, this is a little curious. None of the other specimens had these structures preserved. Neither the juveniles or the adults. In adults specially, such as KMNH 100,329, the holotype or the specimens figured in Maissey (1986 - Fig. 15), whose bodies are preserved as concretions, the pelvic fins are covered by external tissue. I opted to remove this information since I don't have anything of substance to offer.

The base-basal plate of the first dorsal (Fig. 12A9A, B) is a laterally flat triangle with rounded vertices. The fin rays are attached to its dorsoposterior edge. On its centre,lateral wall there are distinct areas where a central crest is formed (Fig. 9B). the bone is thicker

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Comentado [LF18]: Reviewer 1: Legend to Fig. 9 adjusted accordingly.

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Fig. 9. Base of the dorsal fins of holotype of *A. araripensis* (AMNH 11759). Right lateral view. (A) and (B) Basal plate of the first dorsal fin. Dashed circle marks the central crest. (C) and (D) Basal plate of the second dorsal fin. Arrow points to the bulge on the base of the second dorsal.. Scale Bar = 1 cm Abbreviations: apx.D2, apex on the basal plate of the second dorsal fin; b.D1, basal plate of the first dorsal fin; dp.b.D2, dorsal projection of the basal plate of the second dorsal fin; vp.b.D2, ventral projection of the basal plate of the second dorsal fin.

The apex of the basal plate second dorsal (Fig. 23C9C, D) is also laterally flat and oval. At its posterior end it is marked by the presence of a very peculiar bulge (indicated by an arrow on Fig. 12D9D). It projects two apophysis, one anterior and one ventral. separated by an angle of approximately 60° of each other.

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Comentado [LF19]: Reviewer 1: I revised this measurement, which was taken from the holotype (already fixed in the legend of the figure). The value for this specimen was 67.5°. There is one or possibly two other specimens with the base of the second dorsal preserved, both presumably adults or semi-adults: AMNH 12210: 61.3 and KMNH VP 100,331; this last one is not prepared in any form and is composed of several skeletal parts (including the parietonasal and part of the postparietal shields). The base plate that I found there can be the anal one (since the second dorsal and anal fin skeletons are mirror images of each other) and it is broken, which makes the value of the measured angle, 50.1° still more unreliable. Therefore, there is no way to test for statistical significance for variance or allometry. I opted to have this one rephrased.

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As the signature feature of the Mawsoniidae *A. araripensis* also has ossified ribs
Fig. 12. KMNH VP. 100,238. Base of the dorsal fins of *A. araripensis*. Right lateral view. (A) and (B) Base of the first dorsal fin. (C) and (D) Base of the second dorsal fin. Arrow points to the bulge on the base of the second dorsal. The value of the angle between the dorsal and ventral projections is indicated. Scale Bar = 1 cm Abbreviations: apx.D2, apex on the base of the second dorsal fin; b.D1, base of the first dorsal fin;

dp.b.D2, dorsal projection of the base of the second dorsal fin; vp.b.D2, ventral projection of the base of the second dorsal fin.

As in any typical of Mawsoniidae there are ossified ribs in *A. araripensis* (Schultze 1993). They are not easily found in the fossils. Yabumoto and Brito (2010) Yabumoto and Brito (2013) reported 27 small thin ossified ribs on the young specimen KMNH VP 100,262. Ever increasing in length from the most anterior to the most posterior (see Yabumoto and Brito 2013) Yabumoto and Brito, 2010; Fig. 1.). Fragments of the ribs can be also seen on KMNH VP 100,328 (Fig. S24).

We agree with the meristic data from According to Forey (1998) and Maisey (1986) regarding the fin rays counts are as follows: first dorsal = 9-10, second dorsal = 10, pectoral = 12-15, pelvic = 17-18, superior caudal lobe = 15, inferior caudal lobe = 15. We contribute to the meristic data with the count of the anal fin rays, 18-19.

The distal extremities of all of *A. araripensis* fin rays are divided into small articles. On the rays of the first dorsal fin, and on the rays of the superior and inferior caudal lobes each article of those articles bare a denticle that curves towards the distal end of each ray curved denticle (Fig. 13). No other fins have denticles attached. We have not identified it on the remaining fins.

Fig. 1310. Posterior end of Detail of the distal portion of the fin rays in *A. araripensis*. The rays are divided into articles, each bearing a small denticle. The two figured specimens are juveniles. (A) First dorsal fin rays of UERJ-PMB 434 - chemically prepared. (B) Superior caudal lobe fin rays of UERJ-PMB 468 - chemically prepared. (C) Inferior caudal lobe fin rays of UERJ-PMB 468. Scale bar = 0,1 cm

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Comentado [LF20]: Reviewers 1 & 2: This figure was removed.

Comentado [LF21]: Reviewers 1 & 2: We agree with Maisey (1986) account. Forey reports that the number of rays in the superior caudal and inferior caudal lobes are equal (15). It has been adjusted in the diagnosis ass well.

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721

722 The epicaudal lobe is not easily preserved and very few individuals in the sample
723 presented it. It can be seen in the two specimens shown on Fig. 1411: MSPC-287
724 (Fig. 14A11A) and KMNH VP P. 100,332 (Fig. 14B11B). MSPC-287 was described by
725 Brito & Martill (1999). It has 7 cm in total length and the epicaudal lobe is seen
726 extending far beyond the level of the superior and inferior caudal lobe rays. KMNH VP
727 P. 100,332 has only its tail preserved, however, estimating by the height of the caudal
728 peduncle it must have reached around 20 cm in total length. The posterior end of its
729 epicaudal lobe is aligned with the rays of the superior and inferior caudal lobes.

730

731 Fig. 1411. Epicaudal lobe on young individuals of *A. araripensis*. (A) MSPC-287. (B)
732 KMNH VP P. 100,332. The epicaudal lobes are marked with a dashed circle. Dashed
733 lines represent the height of the caudal peduncle. Scale bar = 1 cm.

734

735 Coelacanth scales lack cosmine and are ornamented with ridges of enameloid tissue
736 (Lund and Lund 1985; Cloutier et al. 2002; Meunier et al. 2008). The scale ornament of
737 *A. araripensis* is characterized by a slightly longer, continuous central ridge and smaller
738 ridges surrounding it (Fig. 1512). The number of ridges is variable but the presence of
739 the prominent, large central one remains constant (Yabumoto, 2008).

740

741 Fig. 1512. UERJ-PMB 472 – chemically prepared. Scale of the mid-section of *A.*
742 *araripensis*. The arrow points out to the longer central ridge. Scale bar = 0,1 cm

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65: Morphological Comparisons and Discussion

The interrelationships of *A. araripensis* and its mawsoniid peers are difficult to examine through traditional phylogenetic methods. Most of its closest relatives such as *A. megadromus*, *M. lavocati*, *A. maisey*, *M. lavocati* and *M. tegamensis*, although valid species in the taxonomic sense (see Wenz, 1975; Yabumoto & Uyeno, 2005; Cavin, Valentin & Garcia, 2016), and *Lualabaea* are known only by one or few individual specimens. If inserted into a phylogenetic matrix like for example the one created by Forey (1998), taxa such as this would result in too much missing data, which in turn would cause them to become unstable (Pol & Escapa 2009). In addition, many of the characters that seem to be relevant to mawsoniid interrelationships are not covered by Forey's matrix (see Dutel et al. 2015) (see Dutel, Herbin, & Clément 2015). Therefore, on the following discussion, we opted to focus on the particularities of Mawsoniidae interrelationships by means of anatomical comparisons only. For a more general approach on coelacanth phylogenetics we recommend the works of Dutel et al. (Dutel et al. 2015) Dutel, Herbin, & Clément (2015) and Cavin et al. (2017).

One important aspect in ~~coelacanth's evolution~~ the evolution of coelacanths that was emphasized by Forey (1998) ~~was represented by~~ are the evolutionary trends that occurred during their history. We will point them out as we progress discussing the various anatomical complexes of *A. araripensis* and comparing it with other Mawsoniidae.

One of such trends is the increase in the ratio parietonasal/postparietal shield, pointed out by Forey (1991), Cloutier (1991) and later on by Forey (1998). While in Palaeozoic coelacanths like for example *Rhabdoderma* Newberry, 1856 this ratio is practically equal to 1.0 (estimated from Forey, 1981; Fig. 2); in the Mesozoic taxon *A. araripensis* this value can be up to 2.5; ~~— 3.0~~. In this aspect, *A. araripensis* resembles

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the Triassic genus *Chinlea*, but differs from its congener *A. maysei* and the species of *Mawsonia*, all with the ratio of 1.5 between their skull shields. *Parnaíbaia maranhoensis* seems to be an offshoot of the family presenting regressive trends. Its parietonasal and postparietal shield are of similar size (Yabumoto 2008). The description of *Trachymetopon liassicum* (Hennig (1951) given by Dutel et al. (2015) Dutel, Herbin, & Clément (2015) does not make this proportion clear however, judging using by the picture of the holotype provided by the authors (Dutel et al. 2015; Fig.1) of the holotype (Dutel, Herbin, & Clément 2015, figure 1) this value was calculated to be about 1.3. Even though the skull roof of the holotype of *L. ualabaea-lerichei* was not complete (specially the anterior end of the snout and the extrascapular region), we estimate the ratio to be of at least 2,0.

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The curvature of the parietonasal shield, previously described as a marking feature of the genus *Axelrodichthys* (Fig 28) (Maisey 1986; de Carvalho et al. 2013; Yabumoto and Brito 2013), in fact it is actually shared with all genera of Mawsoniidae except *Mawsonia*, where it the shield is straight or even slightly convex. The case of *M. lavocati* is unique; the The parietonasal shield of *M. lavocati* however, in this species is curved as it is in and resembles a lot the one of *Axelrodichthys* (Fig. 4613). The affinities between *M. lavocati* and the *Axelrodichthys* genus are not restricted to this feature as we will elaborate further down the discussion. The curvature of the parietonasal shield in *A. maiseyi* is less pronounced then in *A. araripensis* (see section below). This is a trait that could not be fully understood for certain in the genera *Trachymetopon* and *Lualabaea* given the conditions of preservation of its respective specimens (Saint-Seine 1955; Dutel et al. 2015).

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Fig 1613. Parietonal-Isolated parietonal shields of *M. lavocati* and *A. araripensis* in right lateral view showing their extreme resemblance. (A) *M. lavocati* (NSM-PV-PV 20994). (B) *A. araripensis* (AMNH 11760). Scale bar = 5 cm.

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Another shared feature of the skull roof shared between *A. araripensis* and *M. lavocati* is that, in dorsal view, the parietonal shield of both abruptly narrows at the level of the last tectal (Yabumoto and Uyeno 2005).

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Three of the observed specimens, the adult AMNH 12211 (Fig. S1), the juvenile NSM-PV 20382 (Figs. 3C, D) and the juvenile UERJ-PMB 468 (Fig. 4), display what seems to be a large foramen encompassed by the premaxillae. In more primitive coelacanth this foramen represents the anterior opening of the rostral organ but as evolution progressed the premaxillae became thinner and failed to encompass this aperture (Cloutier 1991; Forey 1998). We propose that the presence of such structure on this Mesozoic genus (i.e. *A. araripensis* (a Mesozoic species)) signifies a reversal of the condition. A similar case is seen in the genus *Whiteia* Moy-Thomas (1935), 1935 (Forey 1998). Since neither of the other species in the genus (i.e. *A. maiseyi* and *A. megadromus*) had their respective premaxillae preserved we judged best to keep this particular feature as a species diagnosis instead of generalizing it for the whole genus (see diagnosis).

It is not possible to give a complete comparison of the rostral ossicles on the anteriormost extremity of the snout. The loosely nature of their attachment makes them prone to get lost during the fossilization process (Forey 1998). Therefore, the clearest assessment of these structures in our sample was made based only on one individual, KMNH 100,232 (Figs. 3A, B). The configuration of these bones in *A. araripensis* seem

similar to that given by Forey (1981; ~~fig~~Fig. 2) for *Rhabdoderma elegans* Newberry, 1856, with one median element (internasal) and two lateral ones (anterolateral rostrals in Lund and Lund, 1985). The primary difference between the two is that in *R. elegans* the internasal is anterior to the lateral ossicles whereas in *A. araripensis* the internasal appears to be posterior. Wenz (1975) describes in *M. tegamensis* a structure similar to the medial internasal of *A. araripensis* as “a small element between the anterior nasals”. Forey (1998; ~~fig~~Fig. 3.1) describes an embryo of *L. chalumnae* on which he points out the presence of two internasals aligned. The two lateral elements depart from the intersection of the internasals. It is possible that KMNH 100,232 is missing the anterior internasal and that the configuration of the rostral ossicles in both species are very similar.

All the mawsoniids have what Wenz (1975) and Saint-Seine (1955) referred to as a “classic” parietonasal shield bone disposition. ~~There are two lateral where two series of bones, (the supraorbitotectals), flanking a medial one (that containing contains the nasals and parietals).~~

A. araripensis (Maisey 1986) and *M. lavocati* (Uyeno & Yabumoto, 2005) have three pairs of nasals. All the other studied species have two, including the other species of *Mawsonia* (Schaeffer 1967; Maisey 1986; Yabumoto and Uyeno 2005; Yabumoto 2008). According to Cavin et al. (2016) *A. megadromus* also has two pairs of nasals. It should be pointed out though that the parietonasal shields of *M. brasiliensis* and the *Mawsonia* from the Araripe Basin (Brazil) ~~(referred by the one that Maisey (1986) Maisey, 1986 refers to as M. cf. gigas) (see below in this section)~~ have the snout regions broken so the counting is dubious. In *L. lerichei* Saint-Seine (1955) reports a pair of nasals but the skull where ~~it appearsthey are preserved~~ is in poor state of preservation. It seems that the nasals were not preserved in *Trachymetopon*.

The parietals are usually described as being at least twice as long as they are wide (in *A. megadromus* they are at least 3 times longer than they are wide; Cavin et al. 2016). In *A. araripensis*, the second pair is slightly wider than the first. A characteristic also reported by Yabumoto (2002) for *M. brasiliensis*. The comparative length of the second pair of parietals is a matter of discussion among specialists (Cavin et al. 2016). In *A. araripensis* the second pair is only slightly longer than the first, as it is also the case for *M. brasiliensis* (Yabumoto 2002). In *M. tegamensis* (Wenz 1975), *Parnaíbaia P. maranhoensis* (Yabumoto 2008) ~~(Yabumoto 2008)~~ and *A. megadromus* (Cavin et al. 2016) the two pairs are of similar size. And in *M. lavocati* (Cavin and Forey 2004) and *A. maiseyi* ~~(de Carvalho et al. 2013)~~ ~~(de Carvalho, Gallo and Santos, 2013)~~ the posterior pair is larger than the anterior one.

The number of elements in the supraorbitotectal series is variable among the Mawsoniidae. In fact the separation between “supraorbitals” and “tectals” is more of a conceptual understanding than a natural division (Wenz 1975). Therefore, for comparison purposes we will be counting them as a whole (for each series) instead of separating tectals and supraorbitals. *Parnaíbaia* has at least eight bones on each series (Yabumoto 2008); *Chinlea* has eleven (Schaeffer 1967); in *M. lavocati* there are six (Yabumoto and Uyeno 2005); *M. brasiliensis* has seven supraorbitals (Yabumoto 2002) (the same number is seen in AMNH 11758 – “*M. cf. gigas*”. See below). *A. araripensis* also has seven. According to Cavin et al. (2016) ~~Cavin, Valentin and Garcia (2016)~~ the supraorbitotectal series in *A. megadromus* is incomplete, but the authors believe it has less than eight bones.

As for the postparietal shield the evolutionary tendency among coelacanth was the transformation of the postparietal shield from flat, in basal coelacanth, to increasingly

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convex in more derived ones (Forey 1998)Forey (1998). The dome shaped postparietal shield of *A. araripensis* is a perfect example of such trend (Fig. S3B).

Yabumoto (2002) examined the specimen AMNH 11758 (previously described by Maisey (1986) as a *M. cf. gigas*) and interpreted it as belonging to *M. brasiliensis* given the size and position of the anterior apophysis of the postparietal. In *M. gigas* the anterior apophysis is large and more medial while in *M. brasiliensis* it is small and more lateral, close to the opening of the otic canal. Our assessment agrees with the position of Yabumoto (2002). Therefore, we will be referring to the specimen in question as *M. brasiliensis*. A comparison between several postparietal shields of different Mawsoniidae species in ventral view is shown in Fig. 1714, with the anterior apophysis of the postparietal circled on each specimen. AMNH 11758 is displayed in Fig 17B-14B and a specimen of *M. gigas* from the Natural History Museum of the of London United Kingdom is displayed in Fig 17C-14C (see the same species in dorsal view in Fig. S25S26). Notice the difference in the relative size of their respective anterior apophysis. In this aspect, *A. araripensis* resembles *M. brasiliensis* since both have small, more lateral anterior processes of the postparietal. *M. lavocati* (Fig 17D14D) is in an intermediary position in which the its apophysis are comparatively large but rests in a more medial position.

Fig. 1714. Postparietal shields of several Mawsoniidae species in ventral view. (A) *A. araripensis* (AMNH 11760); (B) *M. brasiliensis* (AMNH 11758); (C) *M. gigas* (NHMUK PV P. 10356) and (D) *M. lavocati* (NSM-PV-PV 20994). Dashed circles mark the anterior apophysis of the parietonasal shield. Scale bar = 5 cm.

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890 *Axelrodichthys*, *Mawsonia*, *Chinlea* and *Trachymetopon* all share an unusual trait
 891 amongst coelacanth, the extrascapulars are integrated to the postparietal shield
 892 covering the neurocranium (Forey 1998). This derived condition is not seeing on the
 893 ancestral Mawsoniidae genera- *Diplurus* Newberry (1878) ~~and nor in~~ *Parnaibaia*
 894 (Yabumoto 2008). *Chinlea* and *Mawsonia* have an even number of extrascapulars (*i.e.*
 895 there ~~isn't a~~ a medial element present) ~~;~~ ~~There are~~ two ~~on Mawsonia in the first~~
 896 (Maisey 1986; Yabumoto 2002) and four ~~in the latter on~~ *Chinlea* (Elliott, 1987; ~~fig~~Fig.
 897 1A). Like *Trachymetopon* (Dutel et al. 2015) *Axelrodichthys* presents an odd number of
 898 extrascapulars, three. What differentiates both genera is the shape of the middle element
 899 in the extrascapular series. In *Axelrodichthys* it is leaf shaped ~~,~~ ~~with a prominent~~
 900 ~~posterior end~~ ~~(Gottfried et al. 2004)~~ ~~(see representation on Fig.2)~~ ~~,~~ while in
 901 *Trachymetopon* it appears to be square-like (see Dutel et al., 2015b; ~~fig~~Fig. 3A). *Saint-*
 902 *Seine* (1955) describes a possible medial extrascapular in *Lualabaea* ~~,~~ ~~and~~ ~~Aan~~ isolated
 903 postparietal shield of an indeterminate *Mawsoniidae* from Morocco also has a medial
 904 extrascapular (Cavin and Forey 2004). ~~The latter was found along a parietonasal shield~~
 905 ~~of M. lavocati and there is a possibility that they belong to the same species~~ (Cavin and
 906 Forey 2004). ~~The only postparietal shield known of M. lavocati - NSM-PV 20995 (Fig.~~
 907 ~~14D) – does not have a medial extrascapular, but since it is composed of isolated parts~~
 908 ~~assembled together (see~~ ~~(Yabumoto and Uyeno 2005)~~ ~~it is possible that the medial~~
 909 ~~extrascapular~~ ~~is~~ ~~was~~ ~~simply left out or never found.~~ We consider this trait, ~~the presence~~
 910 ~~and shape of the extrascapular~~, as a diagnostic feature of *A. araripensis* and will not
 911 generalize to the whole genus since *A. megadromus* does not have this structure
 912 preserved. This matter in *A. maiseyi* is more complex and will be detailed more
 913 thoroughly on the next section.

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914 We agree with ~~the position of~~ Maissey (1986) regarding the open pores of the
915 ~~supraotic supraorbital~~ sensory canal, in that they must have been confined to the snout,
916 probably as some sort of specialization as the pores are only observed in this region
917 (Fig. ~~S6S8~~). The canal runs the entirety of its course except there are no openings for
918 most of ~~the-its~~ path. We haven't studied personally *A. megadromus* to postulate
919 anything regarding this condition. In *A. maisseyi* the preservation did not favour the
920 observation of this character.

921 An opening passage for the superior ophthalmic nerve of *A. araripensis* (Fig. 5,
922 Fig. S18) was found on a corresponding place on *M. tegamensis* (see Wenz 1975, Fig.
923 2A) and on the current coelacanth *L. chalumnae* (Forey 1998). This might represent a
924 conservative feature, if not of coelacanths, at least of Latimeroidae.

925 Lund & Lund (1985) considered the ornamentation of the dermal bones in the
926 skull roof one of the key systems that play a pivotal role on the cranial osteology of
927 coelacanths. Just as important as the lateral line system and the underlying bone
928 formations of the neurocranium. Forey (1998) distinguishes two basic types of
929 ornamentation: granular and ridged. The ornamentation on *Axelrodichthys* and
930 *Mawsonia* have been traditionally described as ridged. A series of crests and
931 depressions that intertwine in a web-like manner (Wenz 1975; Maissey 1986; Yabumoto
932 and Uyeno 2005). Saint-Seine (1955) also describes the ornamentation in *L. lerichei* as
933 a web of striae subparallel to the bone growth radiation. It appears however, that even
934 amongst the so called "ridged pattern" there is a variability to be recognized. As we
935 stated before, the marginal bones on *A. araripensis* skull are marked by small rounded
936 ~~excavations-cavities~~ as shown on UERJ-PMB 474 (Fig. S4; a young individual of
937 estimated 67 cm in total length); UERJ-PMB 473 (Fig. ~~S5S6C~~; an adult individual of
938 estimated 105 cm in total length) and yet another specimen AMNH 14026 (Fig.

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18A15A; a young individual of approximately 50 cm in total length). The same pattern of ornament present in different growth stages is important to emphasize that this is in fact a diagnostic feature that persist during different growth stages and not the by-product of ontogenetic growth. This ornament pattern is not observed in *A. megadromus* where the marginal bones (at least in the parietonasal shield) are almost devoid of ornament (Cavin et al. 2016); or in *A. maiseyi* (de Carvalho et al. 2013). Notice that even between the two-three species of *Mawsonia*, *M. gigas*, *M. brasiliensis*, and *M. tegamensis* and *M. gigas* (Fig. S. 25, Figs 18B-15B, Fig. and 18C-15C respectively and Fig. S26 respectively), the ornamentation is markedly different. In the type species (*i.e.* *M. gigas*) the ornamentation of the skull roof is composed of simple lines of depression (see Fig. 30S26, figure in in the supplementary material). In *M. tegamensis* the skull is marked by isolated excavations-vermiform cavities in a sponge like pattern. In *M. minor* (see Fig. S26S27) there appears to be a mixture of patterns with the posterior parietals and postparietals marked by lines like in *M. gigas*, and the extrascapulars with isolated excavations. The ornamentation on the skull roof of *M. lavocati* follows the general pattern of *M. brasiliensis* and *M. gigas* being however much more pronounced. Since we haven't personally observed *A. megadromus* and *T. liassicum* we will refrain from making any assertions on this matter regarding its skull roof ornament.

Fig. 1815. Depictions of the dermal skull ornament on three Mawsoniidae species of the *Mawsonia*/*Axelrodichthys* complex. (A) *A. araripensis* (AMNH 14025); (B) *M. brasiliensis* (AMNH 11758); and (C) *M. tegamensis* (MNHN F. GDF. 401). Scale bar = 1 cm.

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963 The deep curved shape of the lachrymojugal is shared by most species of *Mawsoniidae*
964 including *A. araripensis* (Schaeffer 1967; Maisey 1986; Elliott 1987; Yabumoto 2008;
965 Dutel et al. 2015) (see Fig. 4916). The exception in this case are the species of
966 *Mawsonia* on which the lachrymojugal is straight, only curving at the anterior most end
967 (Fig. 20B).

969 Fig. 4916. Comparative cheek bone features - highlighted in gray scale - of three
970 species of Mawsoniidae. (A) *M. brasiliensis*; (B) *P. maranhoensis*; and (C) *C.*
971 *sorenseni*. Scale bars = 1 cm. Abbreviations: Lj, lachrymojugal; Op, operculum; Po,
972 postorbital; Pop, preoperculum; Sq, squamosal.

974 Fig. 2017. ~~Opereulum~~ Isolated operculum and lachrymojugal of *M. lavocati*. (A) NSM-
975 PV-PV 21002, operculum. (B) NSM-PV-PV 21001, lachrymojugal. Scale bar = 5 cm.

977 The preoperculum, is present in *A. araripensis* (Forey 1998) and *Chinlea* (Schaeffer
978 1967; Elliott 1987) whereas it is absent in *Parnaibaia* (Yabumoto, 2008). The presence
979 and absence of the preoperculum in *Mawsonia* is a complex issue. Yabumoto (2002)
980 describes a preoperculum for *M. brasiliensis* as Wenz (1975) does for *M. tegamensis*. It
981 is yet to be described for *M. gigas*, *M. lavocati* or *M. minor*.

982 *M. gigas* and *M. brasiliensis* (Figs. 49A16A, B) share a specific type of
983 operculum (see NHMUK VP P. 6321 in Cupello et al., 2016; ~~fig~~Fig. 7B), with the
984 ~~posteroventral-posteripr~~ edge straight. This feature is not shared with *A. araripensis* or
985 any other species of *Mawsonia* (*ei.ge.* *M. lavocati*, Fig. 20-17 A; *M. tegamensis* and *M.*

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minor, the last two structures were observed relatively intact but not figured) on which the posteroventral-posterior edge of the operculum is curved. Notice that this is one more character that *M. lavocati* and the genus *Axelrodichthys* have in common. *Parnaibaia* (Figs. 19C16C, D), and *Chinlea* (Fig. 19E16E, F), and *Diplurus* (Schaeffer 1952) and *L. lerichei* (Fig. 21, Fig. S27S28) also have curved posteroventral edges of the operculum. With that it is reasonable to assume that the ancestral condition seems to be curved and *M. gigas* and *M. brasiliensis* display a more derived feature.

Fig. 21. Graphic representation of the right operculum (A) and right angular (B) preserved on the holotype of *L. lerichei* (MRAC R.G.10.046).

The operculum of *A. araripensis* is ornamented with thin, evenly spaced striae running close together (Fig. 1, Fig. S9). Similar to every other species of Mawsoniidae except *M. gigas* (see Fig. S28S29) on which the striae are very far apart following the pattern of other parts of its dermatocranium.

The dentary of *Mawsonia* and *Axelrodichthys* are very alike-similar (Figs. 22A18A, B),. Compare-Compare it to the dentary of *Chinlea* (Fig. 22C18C). While all are bifurcated, the region anterior to the bifurcation in *Chinlea* is much more elongated and it angles upwards. What differs the dentary of *Axelrodichthys* to that of *Mawsonia* is that in the latter the inferior extension of the bifurcation is far longer than the superior one, whereas in *Axelrodichthys* they have approximately the same length (Cupello et al. 2016). *Axelrodichthys*, *Mawsonia* and *Parnaibaia* (Forey 1998; Yabumoto 2008; Cupello et al. 2016) all bear-bare a lateral swelling process on the anterior part of the

dentary which is marked by a sensory pore. That trait is not described for *Chinlea* nor was found in *Trachymetopon* (Dutel et al. 2015) (~~Dutel et al. 2015~~).

Fig. 2218. Schematic comparative drawing of three dentaries of mawsoniids. (A) *A. araripensis* (based on UERJ-PMB 473); (B) *M. brasiliensis* (based on KMNH 100,247) and (C) *C. sorenseni* (based on AMNH 5652).

The species of the genera *Axelrodichthys*, *Lualabaea* and *Mawsonia* are distinguished from the other Mawsoniidae by possessing a high coronoid eminence. In *Mawsonia* the coronoid eminence rests halfway through the middle of the angular (Fig. 35S30) (Maisey 1986; Forey 1998) while in *Axelrodichthys* and *Lualabaea* it rests close to the anterior end of the ~~structure~~angular. There are two exceptions that must be mentioned. The first is *A. maiseyi* with a lower coronoid eminence (de Carvalho et al. 2013; see section below). The second is *M. minor* which we observed on specimen NHMUK PV P.10569 to have a coronoid eminence more anterior than the other species of the genus, being closer to *Axelrodichtys*.

Forey (Forey 1998) ~~also~~ uses the shape of the coronoid eminence, with an anteriorly directed process on the angular of *Mawsonia* as a way to differentiate between this genus and *Axelrodichthys*. As we previously described, the coronoid eminence of *A. araripensis* also possess such process (Fig. 1, Figs. S5A, Fig. S7H, Fig. S10S12). Therefore, this is not a valid diagnostic character.

The ornament of the lower jaw in *Mawsonia* is heavier than in *Axelrodichthys* (Fig. S4B). In *Mawsonia* the ridges appear to follow primarily a path parallel to the

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1032 longitudinal axis of the angular (Fig. S3029), while in *Axelrodichthys* they are radial,
1033 departing from the centre of ossification.

1034 _____
1035 _____The palates of three Mawsoniidae species are displayed on Fig. 2.319. Observe
1036 that in all of them the palate is more elongate than deep, accompanying the evolutionary
1037 trend of increase ~~in-of~~ the parietonasal shield length relative to the postparietal shield
1038 (Forey 1998). In *A. araripensis* (Fig. 23A19A) the dorsal edge of the pterygoid is
1039 relatively straight just like in *M. lavocati* (Fig. 19C), whereas in ~~*Mawsonia*~~*M.*
1040 *brasiliensis* (Fig. 19B)(~~Figs. 23B, C~~) it curves downwards. Furthermore *A. araripensis*
1041 (Fig. 23A19A) and *M. lavocati* (Fig. 23C19C) have a ventral swelling on the pterygoid,
1042 a relevant character for coelacanth phylogeny ~~-(see (Dutel et al. 2012; Dutel et al. 2014;~~
1043 ~~Cavin et al. 2017))~~(~~see Dutel et al. 2014~~). *M. brasiliensis* (Fig 23B19B) lacks such a
1044 character. ~~On the pterygoid of *Axelrodichthys* the shagreen pattern is found in the lateral~~
1045 ~~rather than the medial wall (Fig. 8, Fig. 13), contrary to what it is seeing in~~
1046 ~~*Megalocoelacanthus dobiei* Schwimmer, Stewart & Williams, 1994 (Dutel et al. 2012).~~
1047 ~~This information is not available for~~The palates of *A. maiseyi* (de Carvalho et al. 2013),
1048 ~~nor for~~and *A. megadromus* (Cavin et al. 2016) are not yet described.

1049
1050 Fig. 2319. Left palate in medial view of three species of Mawsoniidae. (A) ~~& (B)~~*A.*
1051 *araripensis* (NHMUK VP P. 62347)-); (~~EB~~) ~~& (D)~~*M. brasiliensis* (AMNH 11758)-);
1052 ~~and (DC) & (F)~~*M. lavocati* (NSM-PV-PV 21000). Scale bars = 5 cm. The arrows point
1053 to the ventral swelling of the pterygoid.

1054

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As pointed out by [Cavin et al. \(2016\)](#), ~~Cavin, Valentin & Garcia (2016)~~ one of the key differences between *A. araripensis* and *A. megadromus* is the distal end of the toothed surface covering of the parasphenoid. In *A. megadromus* it is hart shaped, and in *A. araripensis* it has a simple triangular outlining, as it is shown in Fig. [2420](#).

Fig. [2420](#). UERJ-PMB 33. Close view of the tooth covering of the parasphenoid in *A. araripensis*. Scale bar = 5 cm.

~~The two foramens present on the posterior wing of the prootic (UERJ-PMB 471, Fig. 7) have not been currently described on any other species of coelacanth. By their posteriorly oriented position we assume that they represent the passages for spinal nerves.~~

~~We previously pointed out the lateral foramens present on the basioccipital (Figs. 9A, B). There are no prior references in the literature discussing its purpose in coelacanth. In the Amiidae species *Amia calva* and *Calamopleurus cylindricus* the basioccipital lateral foramens are passages for occipital arteries (Grande and Bemis 1998). In coelacanth it might have a similar purpose.~~

There is a particular feature on the base of the second dorsal fin of *A. araripensis*: a ventrally oriented bulge located on ~~the~~ [its](#) ventral edge (Fig. [25A21A](#)), which is inexistent in *Mawsonia* (or at least the two species where the structure was available, *M. minor* and *M. brasiliensis*) (Fig. [25B21B](#)). We consider it to be a diagnostic feature of the species, but we will not extrapolate it to the remainder of the species in the genus since those were described based on cranial characters only (de Carvalho et al. 2013; Cavin et al. 2016).

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1079

1080 Fig. ~~2521~~. Schematic drawing of the second dorsal fin base. (A) *A. araripensis* (based
1081 on the holotype of the species AMNH 11759), the arrow points to the bulge on the base
1082 of the second dorsal; ~~and~~ (B) *M. minor* (based on the holotype of the species NHMUK
1083 PV P. 10567.

1084

1085 — Brito *et al.* (2010) commented on the possibility of the lung being composed of
1086 two or three chambers. Since several specimens on the sample (including the holotype)
1087 were observed with three chambers (~~see Fig 11 for an example~~) the latter proposition
1088 seems more likely.

1089 The thin bony membrane that connects the two anterior apophysis of the pubic
1090 process on the base of the pelvic fin in *A. araripensis* (~~Fig. S25~~)(~~Fig. 11C~~) is similar to
1091 what has been described for *Whiteia* Moy-Thomas (1935) (Schaeffer 1948). This
1092 condition differs from *Chinlea* according to our observations of the holotype (AMNH
1093 5652), where the apophysis seem to be separated through the first half of their length,
1094 resembling more of what is known for *Diplurus*, ~~*Coelacanthus* Agassiz (1839) and~~
1095 ~~*Rhabdoderma* (Schaeffer 1948).~~

Comentado [LF23]: Reviewer 2: This passage was removed to keep the comparisons restricted to Mawsoniidae.

1096 According to Forey (1998) there a two types of anocleithrum in coelacanth:
1097 simple and forked. This trait was included the authors phylogenetic Matrix. Our
1098 findings suggest that the one found on *A. araripensis* is simple (see Fig. S24) as it is in
1099 *Chinlea* and *Diplurus* (Forey 1998).

1100 The relative size difference of the epicaudal lobe between the two juvenile
1101 specimens of *A. araripensis*, MSPC-287 and KMNHVP VP 100,332 (Figs. ~~14A~~11A, B
1102 respectively), led us to conclude that there is indeed negative allometric growth between

the early stage represented by MSPC-287 and a later stage represented by KMNHVP P. 100,332. Although it is not as pronounced as it is in *Rhabdoderma exiguum* Eastman (1902) as reported by Schultze (1972) where the epicaudal lobe discrepancy between two displayed ontogenetic phases are much more pronounced. This was not described for other species of coelacanth.

Carvalho and Maisey (2008) and Dutel *et. al* (2012) affirm that the zygial plates of *Axelrodichthys* do not ossify. ~~We disagree b~~ We could observe ossify zygial plates as was shown on Fig. 7B,C,ased on the evidence presented here (see Figs. 9C, B).

5.1: The case of *Mawsonia lavocati*

Traits that link or somehow suggest an affinity between the species *M. lavocati* and the genus *Axelrodichthys* were pointed out by other authors, namely Cavin & Forey (2004), Cavin et al (2015) and Cavin et al (2016). Throughout the course of the discussion on the present paper we presented some of them (*i.e.* the curved parietonasal which, in dorsal view narrows at the level of the first tectal; the three pairs of nasals; the fine ornament of the operculum and its curved posterior edge and finally the ventral swelling of the pterygoid). The ventral swelling of the pterygoid is of particular importance since has been considered of phylogenetic relevant for coelacanth (see Dutel et al. 2012; Cavin et al. 2017). Moreover, there is the aforementioned possibility that a posterior parietal presenting a middle extrascapular from Morocco (MDE F36) might have belonged to a specimen of *M. lavocati* (Cavin and Forey 2004).

Cavin et al (2016) suggests that systematic statuses of several African species of Mawsoniidae be reviewed. In light of the evidence presented here we propose the inclusion of *M. lavocati* on the genus *Axelrodichthys* as *Axelrodichthys lavocati*.

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The only presumable trait of *A. lavocati* that differs from *A. araripensis* is its straight lachrymojugal (see NSM-PV 21001; Fig. 17B). *A. araripensis* has a curved lachrymojugal (Fig. 1, Fig. 2, Fig. S7). But we have to consider the fact that none of the other *Axelrodichthys* species (i.e. *A. megadromus* and *A. maiseyi* – see below) had their respective lachrymojugals described yet. The curved structure of *A. araripensis* might have been an exclusive species trait.

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6.5.2: The case of *A. maiseyi*

A. maiseyi is a relatively recent addition to the *Axelrodichthys* genus (de Carvalho et al. 2013). It comes from the Codó Formation (Grajaú Basin, North-eastern Brazil). Dated from the Aptian/Albian, the composition of the ichthyofauna of this formation is related to the Santana Formation (de Carvalho et al. 2013), in the Araripe Basin. The specimen consists of a three-dimensionally articulated and well-preserved skull in a carbonate concretion and a separate lower jaw.:-

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The authors very thoroughly pointed out differences between the newly recognized species and *A. araripensis* such as the ratio between the parietonasal and postparietal shields (1.5 versus 2.5 ~~of in A. araripensis~~); supraorbitotectal series with six elements instead of seven, the last pair of parietals being larger than the anterior ones (according to the authors in adult individuals of *A. araripensis* the second pair of parietals are smaller than the first pair. This observation ~~does~~ not concur with ~~our observations~~); a lower profile of the lower jaw, with the coronoid eminence halfway through the total length of the structure and a parietonasal shield with a

smoother curvature (so smooth in lateral profile that it can be described as straight). All these characters however, make it closer to the genus *Mawsonia* than to *Axelrodichthys*.

The authors also justify the inclusion of the specimen in the *Axelrodichthys* genus based on the following combinations of characters: ~~bone-skull~~skull bones with rugosities, gular plates with fine radiating striae, mandibular sensory canal opened by five elongated pores, antotic process of the basisphenoid short and robust. With the exception of the last two the other characters are seeing in members of both *Mawsonia* and *Axelrodichthys*.

A more problematic character that the authors present as justification for the inclusion of *A. maiseyi* in the *Axelrodichthys* genus is the presence of a third extrascapular. We examined the specimen and we offer here a different interpretation (displayed in Fig. ~~2622~~) from what is presented in ~~de Carvalho et. alde Carvalho, Gallo and Santos~~ (2013; ~~fig~~Fig. 3). Observe that in our interpretation there are only two extrascapulars and ~~r~~-where the authors point to the existence of the right lateral extrascapular there is only rock matrix. A more detailed photograph of this area can be seen in Fig. ~~S30~~S31.

Fig ~~2622~~. UFRJ-DG 220-P. Dorsal view of the holotype of *A. maiseyi*. Dotted pattern represents rock matrix. Scale bar = 5 cm. Abbreviations: Ext.l (l), left lateral extrascapular; Ext.r (r), right lateral extrascapular; Pp, postparietals; Prn.S, parietonasal shield; Stt.l, left supratemporal; Stt.r, right supratemporal.

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_____ Furthermore there are no ventral swelling on the pterygoid of *A. maisey*
(see de Carvalho, Gallo and Santos, 2013; fig. 8).

However it is important to notice that de Carvalho et al. (2013) observed the specialized
presence of pores of the supraotic sensory canal restricted to the anterior part of the
snout. Which corresponds with the observations we have made in *A. araripensis* (Fig.
S6S8).

We propose a review of this species upon the discovery of future material.

76. Conclusions:

Through the course of this study we made a complete revision of all the
~~anatomical complexes~~ skeletal complexes of *A. araripensis*. Some characters were
detailed in more depth (*e.g.* base of the pelvic fin) and others were described for the first
time: the premaxillae containing the anterior opening of the rostral organ, the particular
ornamentation of the marginal bones of the dermal skull roof, ~~the positioning of the~~
~~shagreen pattern of the pterygoid — on the external rather than the internal wall — the~~
anocleithrum, the ossified zygale plates, the prootic with nerve passages previously
undescribed on coelacanths, the basioccipital ~~with its possible arterial passages~~ and the
ventral bulge on the body of the base of the second dorsal fin. Aside from the number of
rays on the anal fin (~~18~~) ~~— (which had not been previously established)~~. This allowed
us to contribute to the pre-existing diagnosis of the genus *Axelrodichthys* and the
species *A. araripensis*.

The comparative study has shown many morphological similarities between the
genus *Axelrodichthys* and the species *M. lavocati* (*i.e.* the curved parietonasal which, in
dorsal view narrows at the level of the first tectal; the three pairs of nasals; the fine

ornament of the operculum and its curved posterior edge and finally the ventral swelling of the pterygoid). Upon this evidence we propose the inclusion of *M. lavocati* in the *Axelrodichthys* genus as *A. lavocati*, between *A. araripensis* and the other mawsoniids, has shown to be of great value in contributing to the knowledge of their evolutionary interrelationships, even if, for now, it is not possible to compare them using a phylogenetic methodology.

The following characters: curvature of the parietonasal shield, the arched form of the lachrymojugal and the curved posterior round shape of the posterolateral edge of the operculum also suggest that *Axelrodichthys* is at some level more closely related to basal Mawsoniidae (e.g. *Diplurus*, *Chinlea*, *Parnaibaia* and *Lualabaea*) than *Mawsonia*.

The height and position of the coronoid eminence in *Lualabaea* may indicate a probable connection between this genus and *Trachymetopon* and *Axelrodichthys*.

On the other hand, *Mawsonia* seems to be a rather polymorphic genus, with different species presenting a mosaic of primitive and derived features (e.g. *M. lavocati*). The evolutionary relationships of Mawsoniidae is far from being resolved. And future efforts incorporating species rather than genus in a phylogenetic matrix must be made. Future efforts at producing Mawsoniidae phylogeny must be made, incorporating species rather than genus as terminal taxa.

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1234 The images of the fossils of the Natural History Museum United Kingdom are
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1241

1242 **87: Bibliography**

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