Universidade do Estado do Rio de Janeiro
Centro Biomédico
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Rodrigo Tinoco Figueroa

Redescription of *Brazilichthys macrognathus* Cox & Hutchinson, 1991 (Actinopterygii) and a new coelacanth for the Permian (Cisuralian) Pedra de Fogo Formation, Brazil

Rio de Janeiro
2019

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Dissertação apresentada, como requisito parcial para obtenção do título de Mestre, ao Programa de Pós-graduação em Ecologia e Evolução, da Universidade do Estado do Rio de Janeiro.

Orientadora: Prof.ª Dra. Valéria Gallo
Coorientador: Prof. Dr. Matthew Friedman

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Rio de Janeiro
2019

DEDICATION

To all brazilian scientists, that still love and believe in the science of our country, for all effort, dedication and resilience to teach, research and fight for what is right. The trail toward a better country is guided by our scientists and teachers.

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Science is the most exiting and sustained enterprise of discovery in the history of our species. It is the great adventure of our time.

Michael Crichthon

ABSTRACT

FIGUEROA, R.T. *Redescription of Brazilichthys macrognathus Cox & Hutchinson, 1991 (Actinopterygii) and a new coelacanth for the Permian (Cisuralian) Pedra de Fogo Formation, Braz*il. 2019. 204f. Dissertação (Mestrado em Ecologia e Evolução). Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, 2019.

The Pedra de Fogo Formation represents the Lower Permian, Cisuralian, interval of the Parnaíba Basin, extending through the states of Piauí, Maranhão and Tocantíns. Despite its considerably diverse vertebrate fauna, there are few studies regarding its bony fishes. Most of the studies focus on the chondrichthyan and tetrapod faunas. Several bony fish groups are known for this formation, including actinopterygians, lungfishes and coelacanths, normaly based on fragmentary and poorly preserved specimens. The only partially articulated osteichthyan formally described is Brazilichthys macrognathus, but only superficially described. The osteichthyans from the upper Paleozoic are poorly known for western Gondwana, being few species described on the basis of articulated specimens. This leads to the negligence of these South American taxa on large phylogenetic analysis for Actinopterygii and Sarcopterygii. Here I redescribe Brazilichths, as well as describing a new coelacanth genus from the same locality, using new data of microcomputed tomography, as well as their phylogenetic position based on parsimony and Bayesian analyses. The data presented herein highlights the fossiliferous potential of the Pedra de Fogo Formation, due to the presence of well-preserved and partially articulated three-dimensional specimens. In addition, the phylogenetic position of the two taxa indicate a mixture of derived and primitive traits for the Permian, suggesting that novel evolutionary traits were emerging during the Permian. This reinforces the need of detailed studies regarding the South American Paleozoic paleoichthyofauna, which could shead light on important questions about the diversification and evolution of bony fishes during the late Paleozoic.

Keywords: Actinopterygii. Sarcopterygii. Permian. Parnaíba Basin.

RESUMO

FIGUEROA, R.T. *Redescrição de Brazilichthys macrognathus Cox & Hutchinson, 1991 (Actinopterygii) e um novo celacanto para o Permiano (Cisuraliano), Formação Pedra de Fogo,* Brasil. 2019. 204f. Dissertação (Mestrado em Ecologia e Evolução). Instituto de Biologia Roberto Alcantara Gomes, Universidade do Estado do Rio de Janeiro, 2019.

A Formação Pedra de Fogo representa o Permiano Inferior, Cisuraliano, da Bacia do Parnaíba, estendendo-se pelos estados do Piauí, Maranhão e Tocantins. Apesar de possuir uma fauna consideravelmente diversa em vertebrados, poucos são os estudos que lidam com fósseis de osteíctes, sendo a maioria deles voltada para condrictes e tetrápodes. São conhecidos diversos grupos de osteíctes para esta formação, incluindo actinopterígios, peixes pulmonados e celacantos, normalmente em precário estado de conservação e articulação. O único osteícte parcialmente articulado e formalmente descrito até o momento de forma superficial é o actinoterígio *Brazilichthys macrognathus*. Os osteíctes do Paleozoico superior são pouco conhecidos no Gondwana Oriental, sendo raras as espécies descritas com base em espécimes articulados. Isso leva os táxons sul-americanos a serem negligenciados em análises filogenéticas robustas, tanto para Actinopterygii quanto para Sarcopterygii. Neste trabalho, realizo a redescrição de *Brazilichthys*, bem como a descrição de um novo gênero de celacanto proveniente da mesma localidade, com base em dados inéditos de microtomografia computadorizada. Além disso, verifiquei o posicionamento filogenético das mesmas por meio de análise de parcimônia e bayesiana. Os dados aqui apresentados demonstram grande potencial fossilífero para a Formação Pedra de Fogo, com a presença de espécimes parcialmente articulados e bem preservados em três dimensões. Além disso, o posicionamento filogenético das duas espécies indica uma mistura de estados de caráter primitivos e derivados para o Permiano, sugerindo que importantes feições evolutivas teriam surgido no início do Permiano. Isso reforça a necessidade de estudos detalhados acerca da paleoictiofana do Paleozoico da América do Sul, podendo resolver questões importantes sobre evolução e diversificação de grandes grupos de peixes ósseos durante o final do Paleozoico.

Palavras chave: Actinopterygii. Sarcopterygii. Permiano. Bacia do Parnaíba.

LIST OF FIGURES

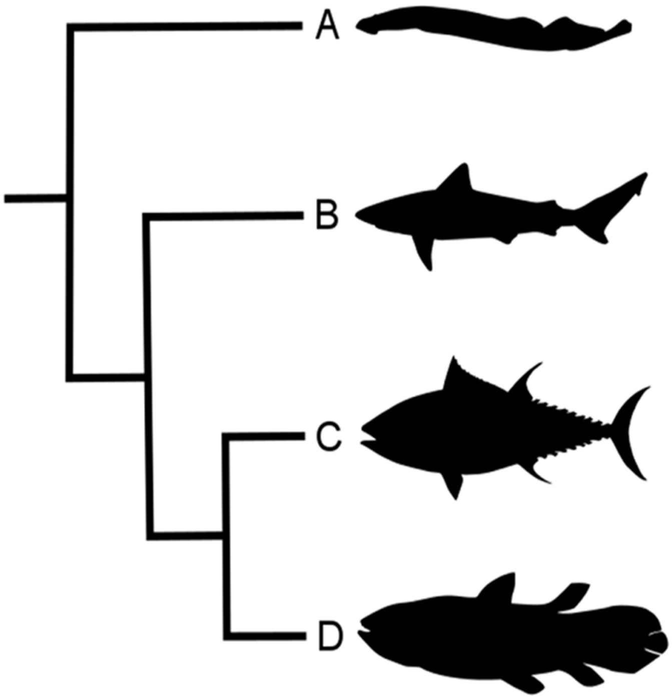
CONTENTS

GENERAL INTRODUCTION

Taxonomy and Systematics

The osteichthyan fishes are an extremely diverse group of vertebrates, including about 35.000 fish species (ESCHMEYER; FRICKLE, 2016; NELSON *et al*., 2016). It is divided in two clades: Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes and tetrapods). Actinopterygii include most species conventionally thought of as fishes, with diversity concentrated within teleosts (around 30.000 according to NELSON *et al*., 2016). Considering only recent groups, Osteichthyes is sister taxon of Chondrichthyes, with these two clades comprising the gnathostome crown group (Figure 1).

Figure 1 – Simplified cladogram of living vertebrates.



Caption: A, "Agnatha" (*Petromyzon*); B, Chondrichthyes (*Carcharhinus*); C, Actinopterygii (*Thunnus*); D, Sarcopterygii (*Latimeria*) based in Nelson *et al*. (2016).
Source: The author, 2017

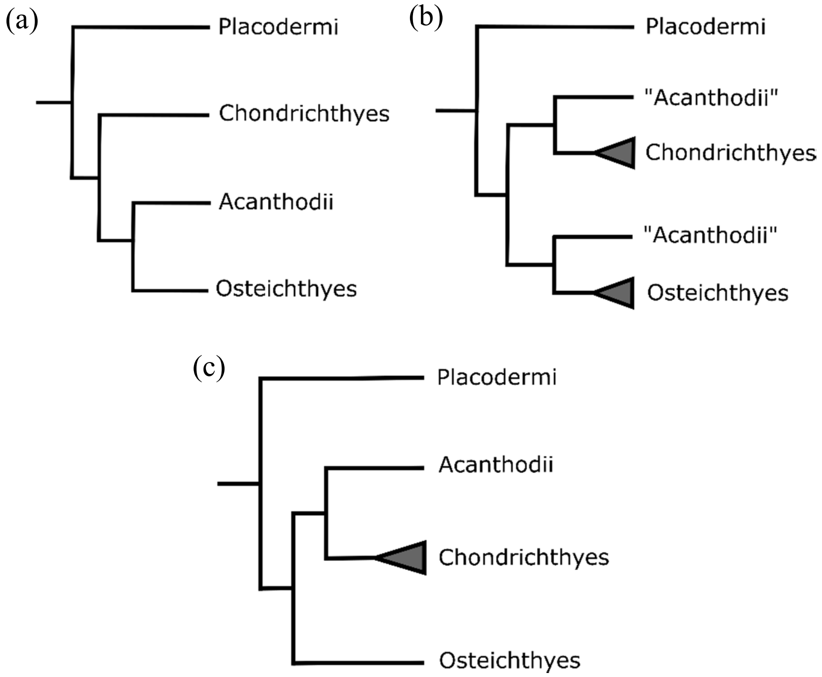
Besides these modern gnathostome clades, there are two extinct groups that are known from the Paleozoic fossil record: Placodermi and Acanthodii. The position of these assemblages relative to living gnathostome clades is still on debate but there is agreement that placoderms must be a grade of stem gnathostomes (BRAZEAU, 2009; BRAZEAU, 2012; BRAZEAU;

FRIEDMAN, 2014). Placodermi are considered stem gnathostomes in most analysis (see BRAZEAU AND FRIEDMAN, 2014), therefore they would be placed between nodes A and B of Figure 1. Cladistic analyses suggest that placoderms are not monophyletic, but rather a grade of primitive jawed vertebrates (ZHU et al., 2013; BRAZEAU; FRIEDMAN, 2015).

Acanthodii are the focus of active phylogenetic debate, with important changes occurring only recently (BRAZEAU; FRIEDMAN, 2015; GILES *et al.*, 2015a). Pioneering analyses considered acanthodians the sister group of osteichthyans, forming the clade Teleostomi (MILES, 1965), and subsequent analyses accepted this proposal (HANKE; WILSON, 2004). However, Pearson (1982) proposed the term 'Osteichthyomorpha' to unite acanthodians and osteichthyans, because the clade Teleostomi was originally proposed to unite actinopterygians and the 'crossopterygians' to the exclusion of acanthodians and dipnoans. Either way, the advance on phylogenetical research and the discovery of new fossils drastically questioned this monophyly, with the proposal that acanthodians would be a paraphyletic assemblage including stem chondrichthyans (*e.g. Climatius* and *Ptomacanthus*) and stem osteichthyans (*e.g. Acanthodes*) (FRIEDMAN; BRAZEAU, 2010; DAVIS *et al.*, 2012; BRAZEAU; FRIEDMAN, 2014). However, *Acanthodes* recently has been placed as stem chondrichthyan together with all remaining acanthodians (ZHU et al., 2013; GILES et al., 2015a; BRAZEAU; FRIEDMAN, 2015). This substantially changes the view of the origin and diversification of modern lineages and dissolves Teleostomi (Figure 2).

By placing acanthodians as total-group chondrichthyans, these studies indicate that the macromeric dermal skeleton of osteichthyans would be synplesiomorphic to gnathostomes, being present in stem taxa as *Entelognathus primordialis* (Zhu *et al.*, 2013) and *Janusiscus schultzei* (GILES *et al.*, 2015a). As stated by Giles *et al.* (2015a), this implies that some Siluro-Devonian osteichthyans described by fragmentary and incomplete material (e.g. *Andreolepis*) could be better classified as stem gnathostomes or stem chondrichthyans, representing the ancestral macromeric condition of the dermal skeleton. This changes the listed synapomorphies of Friedman and Brazeu (2010) for Osteichthyes, due to the new positioning of *Acanthodes* on the chondrichthyan stem and the discovery of placoderms with characteristics previously regarded to be exclusive of osteichthyans (ZHU *et al.*, 2013; GILES *et al.*, 2015a).

Figure 2 – Phylogenetic hypothesis for Gnathostomata.



Caption: (a) – Classical hypothesis of sister group of Acanthodii and Osteichthyes forming the clade Teleostomi (following Miles, 1965); (b) – Hypothesis of paraphyletic arrays for Acanthodii on the stem lineage of Chondrichthyes and Osteichthyes (see Brazeau and Friedman, 2014); (c) – hypothesis of Acanthodii as stem Chondrichthyes (see Giles *et al*., 2015a).
Source: The author, 2018.

Some of the shared characters of osteichthyans and the stem gnathostome *Janusiscus*, are, according to Giles *et al*. (2015a): (1) a rectilinear pattern of the skull roof bones bearing vermiform ornamentation; (2) partially buried sensory canals; (3) endolymphatic ducts opening posterior to the dermal skull roof; and (4) hyomandibular branch of the facial nerve exiting into the jugal canal. On the other hand, Giles *et al.* (2015a) also noticed that other features of *Janusiscus* are plesiomorphies present in stem chondrichthyans or stem gnathostomes: (5) flat-based braincase; (6) weakly developed basipterygoid processes; (7) absence of vestibular fontanelles; (8) lack of a ventral canial fissure; (9) the absence of paired openings for the internal carotids; and (10) the subcranial ridge flanking the ventrolateral angle of the braincase. Interestingly, character 9 is also present in *Acanthodes* and character 10 is comparable to the found in *Doliodus* (see Giles *et al*., 2015a).

Despite the enormous diversity of Osteichthyes, both in the modern fauna and in the fossil record, the evolution and diversification of their lineages, especially Actinopterygii, remain poorly known (FRIEDMAN, 2015; LU *et al*., 2016). Regarding Sarcopterygii, recent finds, especially those from China, continue to elucidate key characters of its early history, during the Siluro-Devonian (*e.g.* ZHU *et al*., 2009).

Both molecular and morphological data place divergence of the two osteichthyan lineages occurred in the Silurian (HURLEY *et al*., 2007; NEAR *et al*., 2012; LU *et al*., 2016). However, the first unequivocal record of actinopterygians is only from the Lower and Middle Devonian (*i.e. Meemannia* and *Cheirolepis*) (FRIEDMAN, 2015; LU *et al.*, 2016), contrasting with the oldest sarcopterygians, from the late Silurian (*e.g. Psarolepis* and *Guiyu*) (YU, 1998; ZHU *et al*., 2009). Nonetheless, Clement et al. (2018) show that these Silurian taxa might represent stem osteichthyans rather than sarcopterygians.

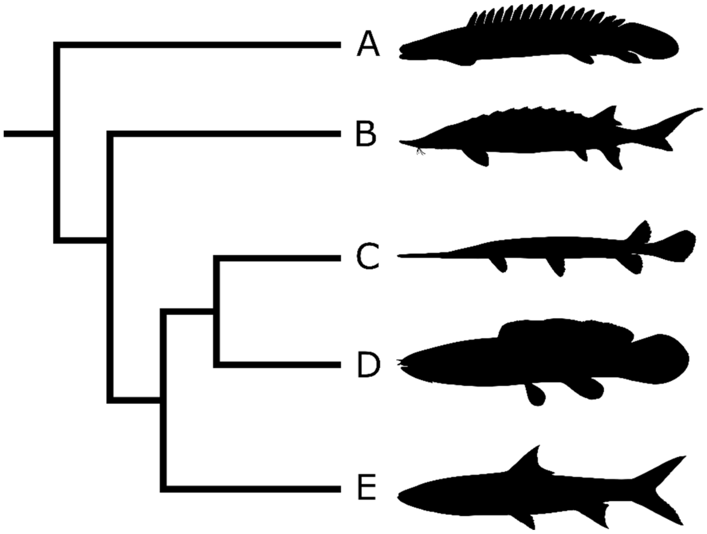
Late Silurian fossils commonly associated with actinopterygians are isolated bone fragments and scales, which lack enough diagnostic features justifying an actinopterygian placement (FRIEDMAN, 2015). Better-known taxa like *Dialipina* and *Ligulalepis* were once considered actinopterygians, but are now commonly interpreted as stem osteichthyans due to the lack of derived features common to both actinopterygians and sarcopterygians (*e.g.* FRIEDMAN, 2007; BRAZEAU, 2009; DAVIS *et al*., 2012; FRIEDMAN, 2015). However, other studies obtained different phylogenetic affinities for these taxa, with *Dialipina* as stem actinopterygian and *Ligulalepis* as stem osteichthyan (*e.g.* GILES *et al*., 2015b) or both as stem actinopterygians (*e.g.* ZHU et al., 2006).

Actinopterygii

Actinopterygii are the most successful lineage and the most diversified among osteichthyans, with around 30.000 living species (NELSON *et al*., 2016). This clade also possess a rich fossil record since the Middle Devonian (FRIEDMAN; BRAZEAU, 2010; SALLAN, 2014; FRIEDMAN, 2015). However, despite this rich evolutionary history and availability of morphological data through time, their origin and patterns of early diversification remains obscure. The positioning of Paleozoic fossil taxa in relation to modern clades is a major area of uncertainty (MICKLE, 2009; SALLAN, 2014; FRIEDMAN, 2015).

The modern lineages of Actinopterygii are: Cladistia, Chondrostei, Holostei (Gynglimodi + Halecomorpha) and Teleostei (Figure 3). Holostei was resurrected by Grande (2010) and was considered as valid in subsequent analyses (BENTACUR-R et al., 2017). The relationship of the previously mentioned clades are well supported by morphological and molecular data (e.g. NEAR *et al*., 2012; BETANCUR-R *et al*., 2017), however the modern phylogenetic hypothesis for actinopterygian clades is result of discussions of the last two centuries concerning fossil and recent taxa.

Figure 3 – Simplified phylogenetic hypothesis for the main living lineages of actinopterygian fishes.

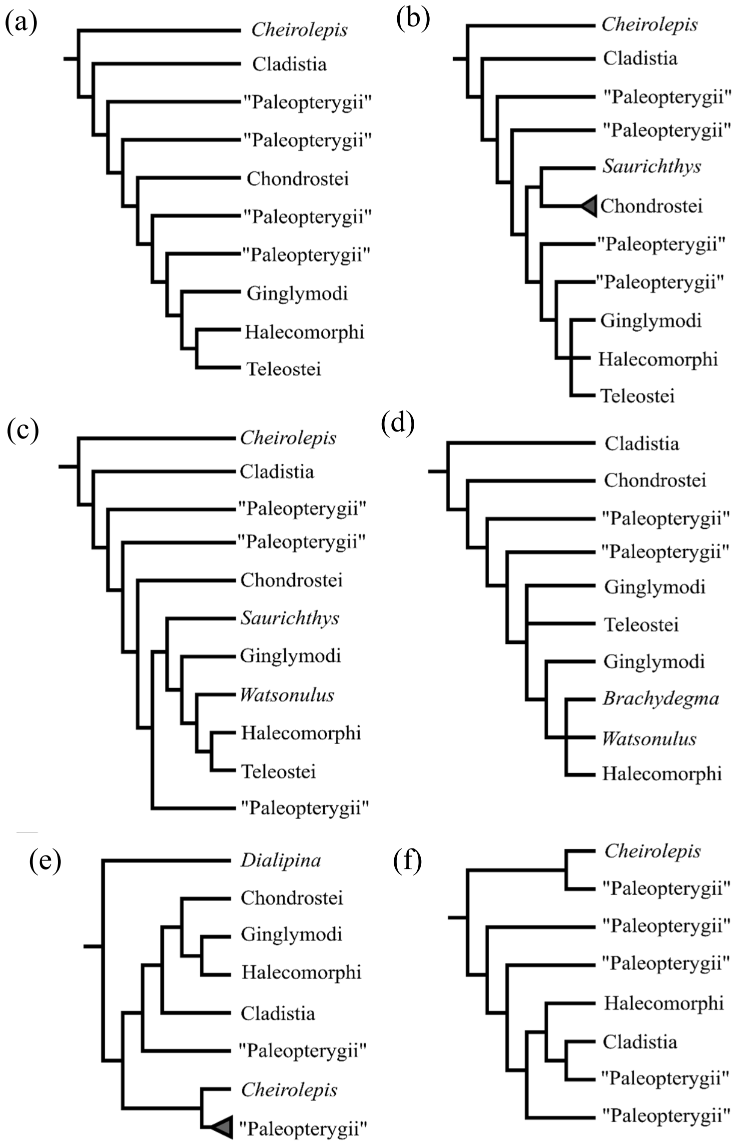


Caption: A: Cladistia (*Polypterus*); B: Chondrostei (*Acipenser*); C: Gynglimodi (*Lepisosteus*); D: Halecomorphi (*Amia*); E: Teleostei (*Elops*).

Source: The author, 2018.

‘Palaeoniscoids’ are an artificial group of early actinoptergyians that encompasses the majority of the Paleozoic taxa together with some Mesozoic species (SALLAN, 2014). It is unclear how components of the ‘palaeoniscoid’ assemblage relate to known actinopterygian lineages: Cladistia, Chondrostei, Holostei and Teleostei (GARDINER *et al.*, 2005; SALLAN, 2014) (Figure 4). ‘Palaeoniscoids’ are generally considered paraphyletic (*e.g.* GARDINER *et al.*, 2005; FRIEDMAN, 2015); however, some studies still recover them as a monophyletic group (*e.g.* MICKLE*,* 2012). Herein the term “Paleopterygii” is adopted to refer to those fishes normally referred as ‘paleoniscoids’. McCune and Schaeffer (1986) firstly used the term paleopterygian, but not implying monophyly, and therefore this is the best term to design these early actinopterygians, as explained by Figueiredo and Gallo (2006) and Friedman and Giles (2016).

Figure 4 – Phylogenetic hypothesis for “Paleopterygii” in relation to living lineages presented by Sallan (2014).



Caption: (a) – Gardiner (1984); (b) – Gardiner and Schaeffer (1989); (c) – Coates (1999); (d) – Hurley *et al*. (2007); (e) – Cloutier and Arratia (2004); (f) – Mickle *et al.* (2009).
Source: The author, 2018.

These divergent phylogenetic hypotheses show that the stem lineages of recent clades with Paleozoic origin are obscure and paleopterygians bear in many cases plesiomorphic morphologies which turns difficult to place some of these fossils in relation to living lineages. The monophyletic ‘Palaeoniscoids’ proposed recently by Mickle (2012) is weakly supported by other phylogenetic analysis (e.g. XU *et al*., 2014; GILES et al,. 2017). However, all the previously mentioned works have the same bias, that is, they do not include equally numerous taxa for the late Paleozoic or do not take on account recent taxa. Future analyses must broadly sample Paleozoic, Mesozoic, and Cenozoic taxa in order to address these problems (SALLAN, 2014; FRIEDMAN, 2015).

1. Cladistia

Cladistia comprises the living *Polypterus*, *Erpetoichthys* and their fossil relatives (DAGET *et al*., 2001; NELSON *et al*. 2016) The phylogenetic position of the polypteriforms (= Cladistia) is problematic and has been topic for discussion since the very first analysis (see SALLAN, 2014). Cladistia is considered the living sister group to the remaining actinopterygians, however they present several characters that could be autapomorphies (NELSON *et al*., 2016) and the primitive characters are restricted to the ganoid scales and enclosure of the dorsal aorta within the basicranium (FRIEDMAN, 2015).

Until recently, another problem concerning Cladistia was the lack of Paleozoic and early Mesozoic taxa. Some clades as, for example, the tarrasiids from the Carboniferous were considered closely related to *Polypterus* (TAVERNE, 1996), however, further work could not add significant data to this hypothesis and Lund and Poplin (2002) obtained tarrasiids as sister group of *Cheirolepis* and other paleopterygians rather than *Polypterus* that fell as the sister group to all remaining actinopterygians. This problem was partially resolved by Giles et al. (2017) phylogenetic analysis that recovered scanilepiforms as stem cladistians, filling the long gap on the evolutionary history of polypterids.

The features that unite scanilepiforms to crown Cladistia are, following Giles et al. (2017): (1) premaxilla contributes to orbital margin; (2) junction between supraorbital and infraorbital canals; (3) two pairs of extrascapulars; (4) multiple rami of infraorbital canal in jugal; (5) one or two supraorbitals; (6) one or two supraorbitals; (7) coronoid process contributed only by prearticular; (8) lateral process of ectopterygoid; (9) lateral gulars extend most of the lower jaw length; (10) broad interorbital septum; (11) optic foramen ventrally positioned; (12) four ceratobranchials; (13) dorsal caudal fulcra absent. Therefore, as noticed by Giles et al. (2017), some of the primitive features of crown cladistians are more probably caused by character reversal during the crown group divergence later during the Mesozoic.

Another group of fishes that was considered to be related to *Polypterus* by Lund (2000) are the Carboniferous Guildayichthyformes. However, Cloutier and Arratia (2004) regarded the Guildayichthyformes as more closely related to the tarrasiids. Either way, if we consider the hypothesis of Taverne (1996) as true, the relation regarded by Cloutier and Arratia (2004) does not dismiss a cladistian affinity for the Guildayichthyformes. However, Giles et al. (2017) recovered Discoserra (and guildaicthyform) as part of the neopterygian stem.

The late Mesozoic records of possible cladistian fishes is far more scarce, with a few disarticulated remains from the Upper Cretaceous (*e.g.* GAYET; MEUNIER, 1992; GAYET *et al.*, 2002)) and the articulated fish *Serenoichthys kemkemensis*, also from the Late Cretaceous (Dutheil, 1999). The Cenozoic record of *Polypterus,* although sparse, is well supported by the Miocene *Polypterus faraou* represented by an articulated and partially complete specimen (OTERO *et al*., 2006).

2. Chondrostei

Chondrosteans include the living genera *Acipenser, Huso, Scaphirhynchus, Pseudoscaphirhynchus, Psephurus gladius* and *Polyodon* of the order Acipenseriformes, together with Paleozoic, Mesozoic and Cenozoic taxa. Some authors used to classify the majority of the paleopterygians as belonging to Chondrostei, within the order Palaeonisciformes (see CLOUTIER; ARRATIA, 2004). However, recent studies consider the paleopterygians to be spread between cladistian, chondrostean, holostean and either teleostean lineages (see SALLAN, 2014).

The modern Chondrostei exhibit several derived traits that distinguish the recent species from other clades, as listed by Nelson *et al.* (2016) based on Grande and Bemis (1996): (1) Palatoquadrate with anterior symphysis; (2) gill arches confined to first two hypobranchials and upper part of the first arch; (3) interhyal hypertrophied; preopercular canal in a series of ossicles; and (4) mandibular canal short or absent; body scaling reduced to tiny isolated elements.

Some early Mesozoic actinopterygians (*e.g. Birgeria* and *Saurichthys*) are frequently considered as stem chondrosteans (GARDINER; SCHAEFFER, 1989; GARDINER *et al*., 2005; FRIEDMAN, 2015), but have also been as more closely related to neopterygians (COATES, 1999). However, Paleozoic remains of birgeriids are dubious (ROMANO; BRINKMANN, 2009). Furthermore, Lu *et al.* (2005) described one partially complete fish from the Permian of China (*Eochondrosteus sinensis*) that due to the fan-shaped subopercle and the reduced scale was attributed to the Acipenseriformes, being similar to *Birgeria* and *Chondrosteus*. Therefore, the chondrostean origin was probably during the Pennsylvanian or the lower Permian and several poorly known paleopterygians might be aligned with this clade in the future.

The positioning of this and other possible chondrostean fossil taxa are uncertain and just a complete revision including Recent, Mesozoic and Paleozoic taxa will help solving the interpretation biases. As mentioned above, *Saurichthys* and *Birgeria* are considered closely related to Acipenseriformes, and this is recovered in Rieppel (1992) where *Saurichthys*, *Birgeria* and Acipenseriformes form a trichotomy. In addition, Bemis *et al*. (1997) recover *Birgeria* as stem Acipenseriformes, and this clade is included in a trichotomy with *Saurichthys* and neopterygians. In this analysis, *Chondrosteus*, *Pelpiaosteus* and *Stichopterus* are recoverd as part of Acipenseriformes. Hilton *et al*. (2011) placed *Boreosomus* and *Birgeria* at the stem of the cladogram while *Chondrosteus* is recovered as a stem Acipenseriformes. However, this analysis does not include *Saurichthys* and other fossil taxa possibly related to Chondrostei that are important for understanding the chondrostean stem.

Considering *Birgeria* as a stem chondrostean, the synapomorphies of Chondrostei would be, according to Bemis *et al*. (1997): (1) Reduction of the opercle; (2) Elongate posterior expansion of parasphenoid; (3) Body scaling reduced to tiny isolated elements, or absent; (4) Palatoquadrate with an anterior symphysis; (5) Palatoquadrate with broad autopalatine portion, palatoquadrate bridge, and quadrate flange; (6) Presence of a triradiate quadratojugal bone; (7) Gill-arch dentition confined to first two hypobranchials and upper part of first arch; (8) subopercle possesses an anterior process; (9) Preopercular canal in a series of ossicles, mandibular canal short or absent; (10) Infraorbital sensory canal in a series of ossicles; (11) Loss of Premaxilla and maxillary bones. Regarding these, the characters 1-3 are the ones that are shared by *Birgeria* and Acipenseriformes (BEMIS *et al*., 1997).

3. Holostei

The holosteans comprise the Ginglymodi and Halecomorphi and was considered as a valid clade by Grande (2010) after many years of being dismissed by ichthyologists, it is now supported by both morphological and molecular data (e.g. Patterson, 1973; Bemis *et al*., 1997; Cloutier and Arratia, 2004). The characters observed by Grande (2010) that unite the holosteans are: (1) The posterior extent of the median rostral is reduced in adult individuals and is little more than a simple tube at the anterior snout with no internasal lamella; (2) Presence of a tube-like canal bearing anterior arm on the antorbital; (3) Two vertebral centra fused inot the occipital condyle of adults; (4) Loss of pterotic; (5) Paired vomer in adults; (6) Presence of a suprangular; (7) Presence of both paired and median neural spines in the caudal region; (8) Caudal fin normally with all principal rays branched; (9) Presence of fringing fulcra on the upper and lower margins of the caudal fin; (10) Presence of anterior and posterior clavicle elements; (11) Four hypobranchials; (12) Premaxillae are immovably attached to the braincase by means of a long process tightly sutured to the frontals; (13) The anterior portion of the premaxilla lines the nasal pit and is pierced by the olfactory foramen; (14) Sphenotic has a dermal component.

The clade Halecomorphi includes the living bowfin (*Amia calva*) and its fossil relatives and is now considered the sister group of Ginglymodi after Grande (2010) resurrection of the Holostei. Lopez-Arbarello and Sferco (2018) recovered Halecomorphi as supported by the following characters: (1) sensory canal in maxilla; (2) longitudinal articulation of the scales of the body; (3) symplectic participates directly in the jow joint; (4) the largest circumorbital bone is the jugal or the lachrymal, both with similar size; (5) opercle ornamented with well-defined tubercles.

Ginglymodi includes the living gars (Lepisosteiformes) and several fossils that extend from the Late Paleozoic to the Cenozoic. The Lepisosteiformes comprise two families, one extinct (Obaichthyidae), comprissing two genera (*Obaichthys* and *Dentilepisosteus*) and one extant (Lepisosteidae), which comprise seven living species of two genera, *Lepisosteus* and *Atractosteus*, and two extinct genera (*Cuneatus* and *Masillosteus*) (GRANDE, 2010; NELSON *et al*., 2016). Grande's (2010) definition of Ginglymodi also include two extinct orders, the Semionotiformes and the Macrosemiiformes.

The ginglymodians were recently studied by Lopez-Arbarello (2012), with special reference to semionotiforms, which contributes to the monophyly of Ginglymodi and also rearrange several of these taxa. It shows that the Semionotiforms were used as "catch-all" group for poorly understood basal neopterygians and that some of proposed semionotids (*Lepidotes*, *Scheenstia*, *Araripelepidotes* and *Pliodetes*) could be more closely related to lepisosteids.

Lopez-Arbarello and Sferco (2018) phylogenetic analysis recovered Lepisosteiformes and Semionotiformes as monophyletic lineages within Ginglymodi, and also recovered a monophyletic Lepidoteidae within Lepisosteiformes. Considering this phylogenetic analysis, the synapomorphies of Ginglymodi are: (1) Splint-like quadratojugal; (2) Anterior infraorbital bone; (3) ectopterygoid approximately crescent shape, convex dorsally, concave ventrally; (4) antorbital bone excluded from the margin of the orbit; (5) subopercle less than half the depth of the opercle; and (6) absence of gulars.

4. Teleostei

The teleosteans are the most diverse lineage of actinopterygians, and comprise most of the living taxa, together with fossils that extend from the middle-late Triassic.
Acording to Arratia (2015) Teleosteomorpha is supported by the following characters: (1) An autosphenotic lacking a small dermal component; (2) the absence of a tube-like canal bearing the anterior arm of the antorbital bone; (3) absence of two vertebral centra fused into the occipital condyle in adults; (4) and each hypural normally articulated with a few caudal rays, with further transformations in some groups. Arratia (2015) considers the synapomorphies 1-3 because they are also found on holosteans.

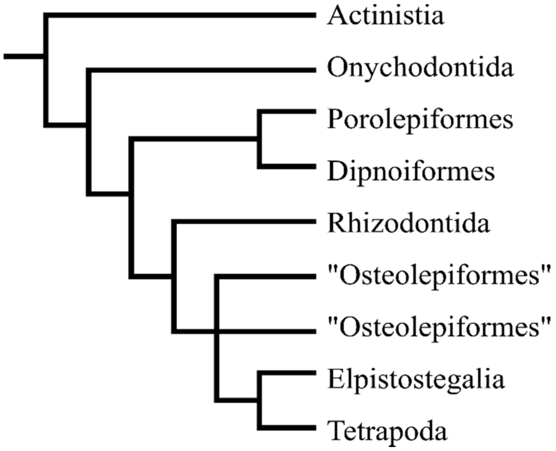
The oldest known stem teleost is *Prohalecites* from the Middle Triassic (Ladinian) and Arratia (2015) states that the group including Prohalecites and all other teleosts is supported by the ascending process on premaxillae.

Sarcopterygii

The Sarcopterygii, as previously mentioned, are the sister taxa of the Actinopterygii forming Osteichthyes. There are several lineages of sarcopterygian fishes that existed during the Paleozoic and Mesozoic, including osteolepiforms, onichodontiforms, porolepiforms, and rhizodonts. However, just coelacanths and dipnoans are still living (NELSON *et al.*, 2016). It is important to address that sarcopterygians just form a natural group with the inclusion of tetrapods (Zhu & Yu, 2002; Johanson, 2004; Daeschler *et al.*, 2006).

Unfortunately, the interrelationships of these fossil groups are poorly known. As noticed by Cloutier and Ahlberg (1995) the positioning of some of the extinct lineages (e.g. Onychodotiformes) are problematic. Cloutier and Ahlberg (1995) recovered Actinistia as sister group to all remaining crown sarcopterygians, Dipnoiformes as sister group of Porolepiformes, and Osteolepiformes forming a paraphyletic array in a polytomy with the clade Elpistostegalia + Tetrapoda (Figure 5). However, the status of Actinistia as sister group of all crown sarcopterygians is weak supported in this analysis and other classical hypothesis put either Onychodontida + Actinistia or Onychodontida as the sister group of all remaining crown sarcopterygii (FOREY, 1998). Zhu and Yu (2004) studied the evolutionary patterns of the lower jaw among sarcopterygians and noticed that the unresolved lineages and lack of more fossils turns difficult to clarify the evolution and character transitions among actinistians and onychodonts.

Figure 5 – Phylogenetic hypothesis for Sarcopterygii.



Source: CLOUTIER; AHLBERG, 1995

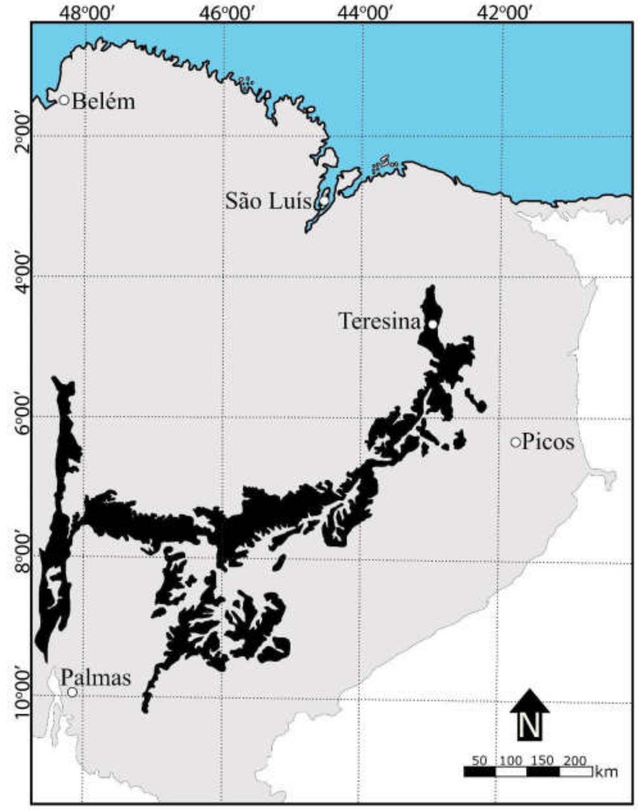
Sarcopterygii is well supported as a monophyletic group (ZHU; YU, 2002; FRIEDMAN; BLOM, 2006; QIAO; ZHU, 2010; GILES *et al*., 2015b). Friedman & Brazeau (2010) listed the characters that could place a fossil within the total group Sarcopterygii: (1) trigeminal nerve exits anteriorly to jugal canal; (2) Y-shaped supraotic recess; (3) endoskeletal urohyal; (4) broad, often bipartite hyomandibular articulation straddling jugal canal; (5) ventral articulation between base of final gill arch and penultimate arch; (6) pectoral and pelvic fins monobasal; (7) buried generations of enamel/odontotes absent from scales and dermal bones (tissue resorption).

The actinistians are well known from Devonian to recent, with a lack of Cenozoic records, with the reappearance of the clade in recent times with *Latimeria chalumnae* discovery in the coast of South Africa (SMITH, 1939). More recently, Pouyaud *et al*. (1999) described a new species of *Latimeria*, with a population living in Indonesia with different morphological and genetic features from that of *Latimeria chalumnae*, therefore they erected a new species, *L. menadoensis*, for this population.

Geological context

The Pedra de Fogo Formation (PFF) is located on the Parnaíba Basin (Figure 6), one of the principal intracratonic basins of the Brazilian territory, together with the Paraná and Amazonas basins. This formation extends through the west border of Piauí state, east border of Maranhão state, and is also present in part of Tocantins state (SANTOS; CARVALHO, 2009). Plummer (1946) gave the first report of this formation and provided a stratigraphic section. The formation was originally defined to include remains of *Psaronius* in the state of Maranhão.

Figure 6 - Scheme of the Pedra de Fogo Formation outcrops.



Caption: Black: Pedra de Fogo Formation; Light Grey: Parnaíba Basin: White.
Source: The author, 2019.

The lithology of the PFF can be divided in three members: the inferior (basal silex member) which includes intercalated siltstones and dolomite beds with concretions and siliceous horizons; the middle member characterized by fine-grained sandstones in cross stratification intercalated by siltstones, shales and carbonatic beds with small siliceous concretions; and the upper member (Trisidela member) where sandstones, siltstones, shales and carbonate beds are intercalated (SANTOS; CARVALHO, 2009). Each level of the Pedra de Fogo Formation is characterized by the presence of a cyclic sedimentation (AGUIAR, 1971).

The age of the PFF and its overlaying Motuca Formation were highly discussed in the past (ARAÚJO, 2015) and great changes have been done since the original proposal, which stated an upper Permian age (PLUMMER, 1946). Now it is known that the PFF comprehends the lower Permian (Cisuralian) of the Late Carboniferous-Early Triassic sequence of the Parnaíba Basin. The PFF is intermediate in position within this sequence, overlaying the Piauí Formation and is overlaid by the Motuca Formation (VAZ *et al*., 2007).

The paleobiota of the PFF is principally composed of vertebrate remains and plant material, normally isolated and disarticulated. However, partially articulated materials are found, including the specimens studied here. Stromatolites are also present in this formation (CISNEROS *et al*., 2015; IANNUZZI et al., 2018).

The chondrichthyans are the most diverse among the vertebrates of this formation. The first study of the paleoichthyofauna of this formation done by Silva-Santos (1946) indicated the presence of two new elasmobranch species. The ctenacanthid "*Ctenacanthus*" *maranhesis*, which was renamed as *Sphenacanthus maranhensis* after Maisey's (1981, 1982 and 1984) revision of those genera, and "*Pleuracanthus*" *albuquerquei*, which was later assigned to *Xenacanthus* by Richter (1985) and then to the new genus *Taquaralodus* by Chahud & Petri (2010).

Other chondrichthyans were described in the following years: the petalodont *Itapyrodus punctatus* and the eugeneodontid *Anisopleurodontis pricei* (SILVA-SANTOS, 1990; 1994); fragmentary cladodont teeth associated with the genus *Glikmanius* (CISNEROS *et al*., 2015). Recently, three new species for the PFF were described by Figueroa and Gallo (2017) based on isolated fin spines, two of them showing affinities to Sphenacanthidae (*Rubencanthus diplotuberculatus* and *Sphenacanthus ignis*) and one of the family Heslerodidae (*Bythiacanthus lopesi*), following the proposal of this family to *Bythiacanthus* made by Maisey (2010).

Little is known about the bony fishes of PFF, because few specimens preserve diagnostic features. The only named species is the actinopterygian *Brazilichthys macrognathus*, which is redescribed here. Isolated and fragmented coelacanth remains are also known, showing affinities with *Spermatodus* (SILVA-SANTOS, 1989) and *Rhabdoderma* (WEISS; GARCIA, 2005). Dipnoans are poorly known from the PFF, but Silva-Santos (1990) mentioned tooth plates he associated with Lepidosirenidae, Sagenodontidae and Ceratodontidae (TOLEDO; BERTINI, 2005). Cisneros *et al*. (2015) reported tooth plates and isolated scales.

Price (1948) made the first report of tetrapods for the PFF in his description of the temnospondyl *Prionosuchus plummeri*, did the first report of tetrapods for the PFF. Cox & Hutchinson (1991) then described new material of this species. Cisneros *et al*. (2015) described new temnospondyl species: *Timonya anneae* and *Procuhy nazarensis* (Dvinosauria), together with an undetermined rhinesuchid (Stereospondyli). Therefore, the tetrapod fauna of the PFF is showing the same pattern observed for the paleoichthyofauna, of a great diversity of taxa being recently described.

The paleoflora is composed mainly by *Psaronius brasiliensis*, *Arthropitys cacundensis* and *Teresinoxylon euzebioi*, besides undetermined gymnosperms (CALDAS *et al*., 1989; SANTOS; CARVALHO, 2009; CONCEIÇÃO *et al*., 2016).

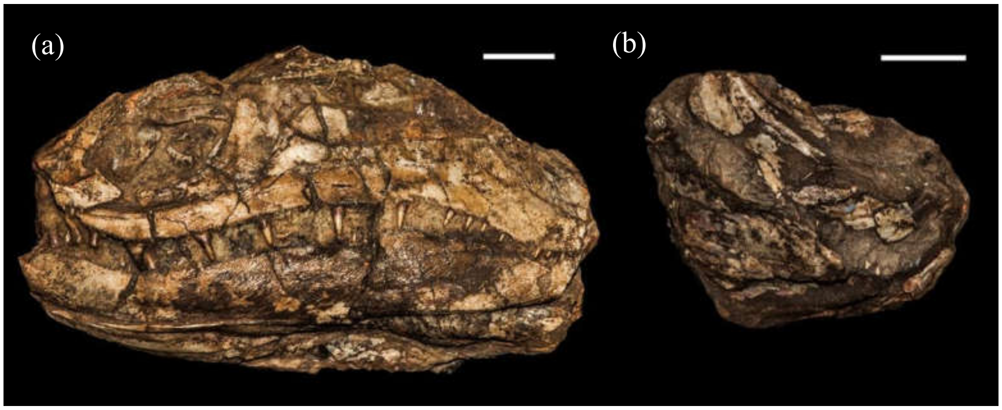
MATERIAL AND METHODS

The analysed material consists of two samples, housed at the collection of the Museu de Ciências da Terra (MCT), of the Departamento Nacional de Produção Mineral (DNPM), on behalf of the Centro de Pesquisas de Recursos Minerais (CPRM).

Both samples were in the same box and catalogued under the same collection number (DGM 1061-P) (Figure 7). The material comprises the partially complete skull of *Brazilichthys macrognathus* (Figure 7A) and partially articulated and unidentified bones (Figure 7B).

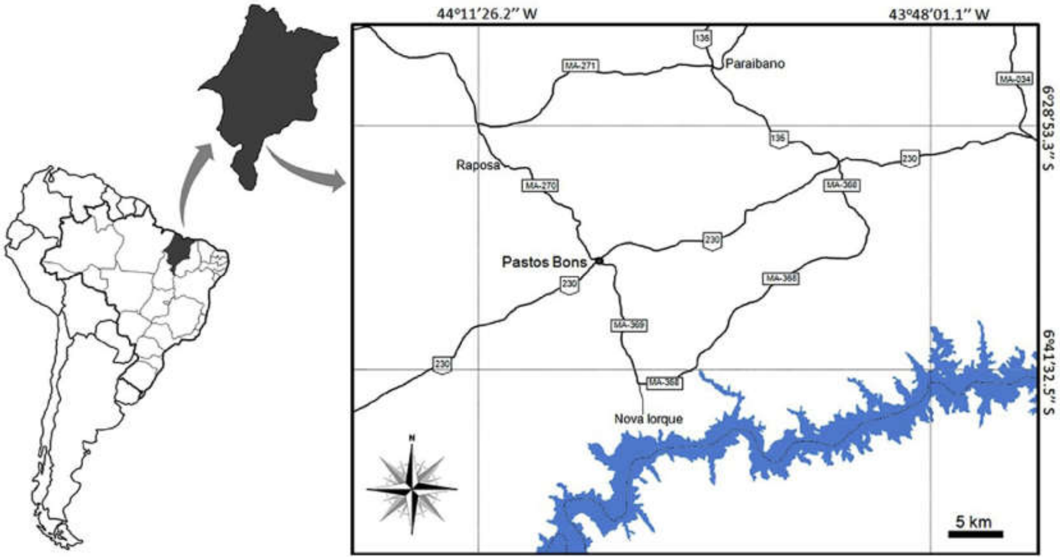
The specimens were collected by the late paleontologist Llewellyn Ivor Price in the "Pastos Bons" locality, on the road to the city of Nova Iorque, state of Maranhão (Figure 8).

Figure 7 – Studied specimens.



Caption: A, holotype of *Brazilichthys macrognathus*; B, Actinistia Indet. Scale bar = 10 mm.
Source: The author, 2019.

Figure 8 – Schematic map of the Pastos Bons Locality from the Pedra de Fogo Formation showing the neighborhood cities, with special reference to Pastos Bons and Nova Iorque.



Source: Adapted from Figueroa and Gallo, 2017.

Tomography

Computed microtomography (µCT) of both samples was conducted at the Laboratório de Instrumentação Nuclear, of the Instituto Alberto Luiz Coimbra de Pós-graduação e Pesquisa de Engenharia (COPPE), located on the Centro de Tecnologia (CT) of the Universidade Federal do Rio de Janeiro (UFRJ)., using a SkyScan 1173 scanner.

A current of 61 µA and a voltage of 130 kV were used for the scans of both specimens. This provided the optimal contrast and penetration possible within the range of X-ray powers possible for the scanner. A copper filter was used.

Resulting X-ray projections were processed in NRecon 1.6.9.4 producing a tomogram stack.

The segmentation was completed in Spiersedit 2.20, using bmp. files of the slices. Downsampling (by 50% in x, y, and z axes) of the data was done to speed the construction of the 3D model, without any conspicuous loss of detail. The slices were then processed manually, to identify each structure of both specimens and obtain a better 3D final model.

After the segmentation, the 3D model was visualized using Spiersview 2.20. Minor modifications such as smoothing and brightness were also made with this software, along with removal of 'islands' of sediment or unidentifiable bone fragments.

Photography and Illustration

Specimens were photographed using a Nikon D3100 digital SLR camera with AF-S Nikkor 18-55mm f/3.5-5.6G ED and AF-S Micro Nikkor 105mm 1:2.8 G ED lenses. Interpretive drawings were made using Inkscape and Adobe Photoshop CS6 using these photos and the 3D models.

Phylogenetic analysis

1. Parsimony:

The anatomical characters of *Brazilichthys macrognathus* were added to the matrix of Giles et al. (2017). An equally weighted parsimony analysis was conducted using the software TNT using the algorithm New Technology Search, with five initial additional sequences and minimum branch length equal to one.

The anatomical characters of Actinistia gen. et sp. nov. were added to the matrix of Cavin et al. (2017) for our phylogenetic analysis of coelacanth taxa. New characters were added to this matrix so that the analyzed specimen could be the accurately placed on the phylogenetic analysis as well as testing for uninvestigated character evolution. The resulting data was exported to TNT software where an equally weighted parsimony analysis was conducted using the New Technology Search Algorithm.

2. Bayesian:

The Bayesian analysis was conducted on MrBayes 3.2.5 (RONQUIST et al., 2012) using the Metropolitan Coupled Markov Chain Algorithm – MCMC for discrete morphological data (WRIGHT; HILLIS, 2014). Character coding was set to “variable” and a gamma distribution was incorporated. The number of substitution types was set to “nst2”, which mean that all transitions have potentially different rates. Specific differences between the analysis of *Brazilichthys* and the new coelacanth are described respectively on each chapter.

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1 REVISION OF *BRAZILICHTHYS MACROGNATHUS* (ACTINOPTERYGII)

(Manuscript: FIGUEROA, R.T.; FRIEDMAN, M.; GALLO, V. Cranial anatomy of the Permian predatory actinopterygian *Brazilichthys macrognathus.* (*Submitted to Journal of Vertebrate Paleontology*).

Abstract

Brazilichthys macrognathus is the only named actinopterygian from the Paleozoic sediments of the Pedra de Fogo Formation (Permian, Cisuralian) of northeastern Brazil, where it is represented by a single three-dimensionally preserved by incompletely described skull. We used X-ray computed microtomography (μ-CT) to better document its anatomy and phylogenetic affinities. μ-CT reveals parts of the internal skeleton including the palatoquadrate, parasphenoid, and branchial apparatus. Our results show that some bones were misidentified in the original description (e.g. dermosphenotic as sclerotic ring fragment). These reinterpretations, together with new data on significant features previously concealed by matrix, permitted us to position this taxon on a phylogenetic analysis of Paleozoic actinopterygians. A maximum parsimony analysis of anatomical data put *Brazilichthys* as a stem actinopterygian, crownward of all Devonian species. This placement is supported by the absence of a dermosphenotic posterior ramus and the presence of opercular process of the hyomandibula. We therefore reject previous interpretations of *Brazilichthys* as a relative of Birgeriidae, a Triassic group consistently placed within the actinopterygian crown. *Brazilichthys* is more similar to genera such as the Triassic *Pteronisculus* based on parasphenoid morphology and arrangement of the circumorbital series. It also bears distinct extralateral gulars as in the Carboniferous *Wendyichthys* and *Beagiascus*. The morphology of *Brazilichthys* and our phylogenetic analysis indicate that despite its considerable similarities to other Permo-Carboniferous taxa, it is sufficiently distinctive to be retained in its own family (Brazilichthyidae), as originally proposed.

Key-words: Actinopterygii. Systematics. Paleopterygii. Evolutiono. Morphology.

Resumo

Brazilichthys macrognathus é a única espécie de actinopterígio formalmente descrita para a Formação Pedra de Fogo (Permiano, Cisuraliano) do Nordeste do Brasil, sendo representada por um único crânio tridimensional e incompletamente descrito. Usamos aqui microtomografia computadorizada de raios-X (µCT) para melhor documentar sua anatomia e relações filogenéticas. µCT revela partes do endoesqueleto incluindo palatoquadrado, paraesfenóide e aparato branquial. Nossos resultados demonstram que alguns ossos foram errôneamente interpretados na descrição orginal (e.g. dermoesfenótico como um fragmento do anel esclerótico). Essas reinterpretações, juntamente com novos dados de características significativas previamente inacessíveis nos permitiram posicionar esse táxon em uma análise filogenética para actinopterígios do Paleozoico. A análise de parcimônia dos caracteres anatômicos posiciona *Brazilichthys* como um actinopterígio basal, mais apical que todas as espécies do Devoniano. Esse posicionamento é suportado pela ausência de ramo posterior no dermoesfenótico e a presence de processo opercular na hiomandíbula. Nós, portanto, rejeitamos a interpretação prévia de *Brazilichthys* sendo relacionado à Birgeriidae, um grupo do Triássico consistentemente posicionado no grupo apical de actinopterígios. *Brazilichthys* é mais similar a generos como *Pteronisculus* por conta da morfologia do paraesfenóide e arranjo da série circumorbital. Também possui placas gulares extralaterais como nos táxons do Carbonífero *Wendyichthys* e *Beagiascus*. A morfologia de *Brazilichthys* e análise filogenética indicam que apesar de similaridades similares a outros táxons do Permo-Carbonífero, é suficientemente distinto para ser posicionado em sua própria família (Brazilichthyidae), como proposto originalmente.

Palavras-chave: Actinopterygii. Sistemática. Paleopterygii. Evolução. Morfologia.

1.1 Introduction

The late Paleozoic is an important episode of actinopterygian evolution, representing a bridge from low-disparity and low-diversity ray-finned fish faunas of the Devonian to the emergence of the earliest teleosts in the Triassic (SALLAN, 2014; FRIEDMAN, 2015). This Permo-Carboniferous interval is marked by substantial innovation in skull and body morphology (SALLAN; FRIEDMAN, 2011), as well as the possible origin of the crown radiation and divergence of the cladistian, chondrostean, and neopterygian total groups (GILES et al., 2017). Despite its clear signficance, the Permo-Carboniferous remains a poorly known interval in the fossil record of fishes. Despite relatively abundant actinopterygian fossils during some parts of the late Paleozoic, their taxonomy is confused and relatively few species are known in detail. Consequently, fossil fishes of Carboniferous and Permian age are among the least stable taxa in analyses of actinopterygian interrelationships (GILES et al., 2017). Compounding these issues, the known Permo-Carboniferous record shows a strong geographic collecting and research bias toward northern landmasses, with the best known actinopterygian faunas of this age deriving from North American (Mississippian: Bear Gulch; Pennsylvanian: Mazon Creek, Linton, Kinney Brick Quarry; Schultze and BARDACK, 1987; KUES; LUCAS, 1992; HANSEN, 1996; POPLIN; LUND, 2002) and European (Mississippian: Foulden, Wardie, Bearsden; Pennsylvanian: Bohemian Massif; Permian: East Greenland, Zechstein; ALDINGER, 1937; GARDINER, 1985; HAUBOLD; SCHAUMBERG, 1985; COATES, 1998; ŠTAMBERG, 2013) localities. While a handful of productive localities are known from southern continents, these have generally been the subject of broad faunal overviews (e.g. Witteburg Group of South Africa; GARDINER, 1969) or detailed descriptions of only single constituent taxa (e.g. *Ebenaqua* from Rangal Coal Measures of Blackwater, Australia; CAMPBELL; PHUOC, 1983).

Brazilian deposits yield the vast majority of Permo-Carboniferous actinopterygians known from South America (CIONE et al., 2010), with only a handful of examples known from elsewhere, mostly based on poorly preserved specimens (e.g. BELTAN, 1978; this material is now considered lost, pers. comm. Piñeiro, G., April 18, 2017). Despite the relative neglect of the South American record of Paleozoic fishes, sporadic research efforts reveal substantial assortment of Permian actinopterygians from Brazil. These span the Permian and overwhelmingly derive from deposits in the Paraná Basin of southern Brazil: the Rio do Sul (Cisuralian in age and yielding *Elonichthys gondwanus*; RICHTER et al., 1985), Campo Mourão (Cisuralian in age and yielding *Roslerichthys riomafrensis* and *Santosichthys* *mafrensis*; HAMEL, 2005; MALABARBA, 1988), Rio Bonito Formation (Guadalupian-Lopingian in age yielding *Tholonosteon santacatarinae*; RICHTER et al., 1985) Rio do Rasto (Guadalupian-Lopingian in age and yielding *Rubidus pascoalensis* and *Paranaichthys longianalis*; RICHTER, 2002; DIAS, 2012), and Corumbataí (Lopingian in age and yeilding *Tholonotus brasiliensis* and *Angatubichthys mendesi*; DUNKLE; SCHAEFFER, 1956; FIGUEIREDO; CARVALHO, 2004) formations. By contrast, *Brazilichthys macrognathus* is the only Permian actinopterygian known from the Parnaíba Basin in northeastern Brazil. *Brazilichthys* in many ways encapsulates the problems surrounding the study of Permo-Carboniferous fishes from Brazil and elsewhere. Known only from the holotype specimen, *Brazilichthys* has only been described externally (COX; HUTCHINSON, 1991). The limited data available for the genus have led to informal alignment with multiple lineages of early actinopterygians on the basis of overall resemblance: first Acrolepidae by Cox and Hutchinson (1991), and then Birgeriidae by Romano and Brinkmann (2009).

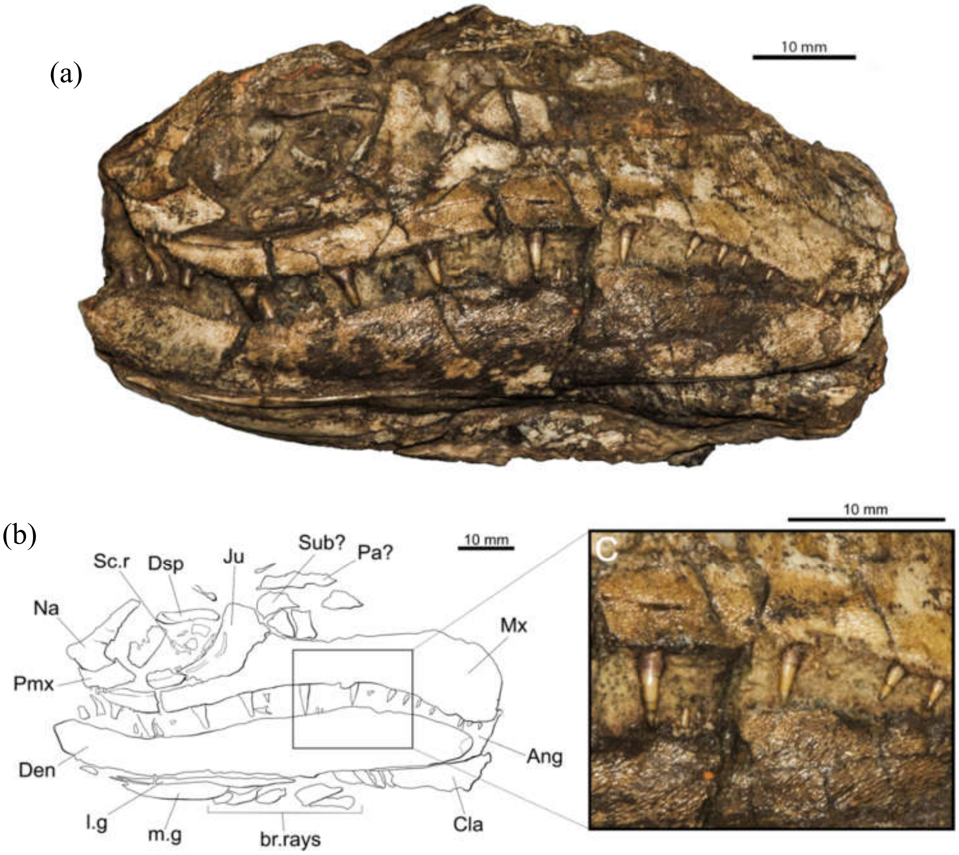
Some of the ambiguity surrounding the phylogenetic placement of many early ray-finned fishes stems from restricted anatomical description, often restricted to superficial details of the dermal skeleton. The widespread availability of micro computed tomography (μ-CT) now permits detailed examination of character-rich internal skeletal features. Application of μ-CT to previously described early actinopterygians has resulted in substantial new information for previously described taxa that has helped to refine--and in some cases substantially change--their inferred phylogenetic positions (GILES et al., 2017; ARGYRIOU et al., 2018; COATES; TIETJEN, in press; FRIEDMAN et al., in press). Here we provide a revised description of *Brazilichthys macrognathus* based on μ-CT scans of the type and only specimen. Using these new data in combination with a recently developed character matrix, we examine the phylogenetic placement of *Brazilichthys* among early actinopterygians, comparing our results to previous hypothesis regarding the actinopterygian stem. Further, we compare *Brazilichthys* to large predatory Paleozoic actinopterygians, proposing steps for future studies.

1.2 Materials and methods

1.2.1 Specimens examined

Brazilichthys macrognathus, holotype, DGM 1061-P (Figure 9).

Figure 9 – *Brazilichthys macrognathus*, DGM 1061-P, holotype, Pedra de Fogo Formation, Pastos Bons locality, state of Maranhão, Brazil.



Caption: (a) – Specimen photograph in left lateral view. (b) – Interpretive drawing. (c) – Close-up of maxilla showing fine ornament ridges and acrodin caps on teeth.
Source: The author, 2019.

1.2.2 Computed microtomography

Computed microtomography (μ-CT) of DGM 1061-P was conducted at the Laboratório de Instrumentação Nuclear, of the Instituto Alberto Luiz Coimbra de Pós-graduação e Pesquisa de Engenharia (COPPE), located in the Centro de Tecnologia (CT) of the Universidade Federal do Rio de Janeiro (UFRJ), using a SkyScan 1173 scanner.

Parameters of the scan were: current = 61 μA; voltage =130 kV; projections = 2234. A 1 mm copper filter was used and projections were processed in in the proprietary software NRecon 1.6.9.4 to produce a tomogram stack. The resolution of the scan was 35.61 μm.

Segmentation was completed in Spiersedit 2.20 (Smith et al., 2016), using tomograms saved as .bmp format. Downsampling (by 50% in x, y, and z axes) of the data was done to speed the construction of the 3D model, without any conspicuous loss of detail. The slices were then processed manually, with the resulting 3D model was initially visualized using Spiersview 2.20. More minor modifications such as smoothing and brightness were made using this software, along with removal of 'islands' of sediment or unidentifiable bone fragments. Production of final images was completed in Blender (blender.org) (GARWOOD; DUNLOP, 2014). Illustrations of the resulting renders and specimen reconstructions were completed in Inkscape (inkscape.org; HARRINGTON, 2005).

1.2.3 Phylogenetic dataset

Brazilichthys macrognathus was coded for the characters in the matrix (APPENDIX A) presented by Giles et al. (2017). *Brachydegma caelatum* was excluded from this matrix because its anatomy is under revision by M. Friedman and others, and available descriptions are not reliable. The complete matrix contains 93 taxa and 265 unweighted characters (APPENDIX B). *Brazilichthys* can be evaluated for 33% of all characters. The analysis includes several non-actinopterygian fishes, with *Dicksonosteus arcticus* set as the outgroup. In contrast to Giles et al. (2017), we did not enforce relationships among non-actinopterygian taxa. All characters were treated as unordered in both analysis.

Parsimony analysis—An equally weighted parsimony analysis was conducted using the software TNT 1.5 (GOLOBOFF et al., 2016). The New Technology search algorithm was used, with 5 initial additional sequences. Bremer support was calculated in TNT using the TBR ("tree bisection and reconnection") for all most parsimonious trees. The results where then plotted against the strict consensus tree. Nodes with Bremer support below 1 were automatically collapsed. A formatted file is provided in Supplementary Data 2 to reproduce results of the parsimony analysis.

Bayesian analysis—The Bayesian analysis was conducted on MrBayes 3.2.5 (RONQUIST et al., 2012) using the Metropolis Coupled Markov Chain Algorithm (MCMC) and the MkV model for discrete morphological data (LEWIS, 2001; WRIGHT; HILLIS, 2014). Character coding was set to "variable" and a gamma distribution was incorporated. The number of substitution types was set to "nst2", which mean that all transitions have potentially different rates. The number of generations was initially set to 500,000, with the number of generations increased until reaching a low standard deviation of split frequencies. Burn-in fraction was set to 50% of the resulting topologies. A complete script for MrBayes is given in Supplementary Data 3.

The resulting phylogram was visualized in FigTree 1.4.3 (RAMBAUT, 2018) and the tree file was exported to Mesquite (MADDISON; MADDISON, 2018) where we mapped the evolution of each character based on the likelihood algorithm (LEWIS, 2001).

1.2.4 Anatomical abbreviations

V – foramen or canal for trigeminal nerve; **Ac.Vo** - accessory vomer; **Ang** – angular; **app** – anterior process of parasphenoid; **Art** – articular; **asp** – ascending process of parasphenoid; **bpt** – basipterygoid process; **Cbr** – ceratobranchial; **Chy** – ceratohyal; **Cla** – clavicle; **Cor** – coronoid; **Den** – dentary; **Dhy** – dermohyal; **Dsp** – dermosphenotic; **e.g** – extralateral gular; **Epb** – epibranchial; **f** - foramen; **f.mand.V** – foramen for mandibular branch of trigeminal nerve; **fo.add** – fossa for adductor muscle; **f.scl** – sensory canal foramen; **h.op.** – opercular process of hyomandibula; **Hb$_1$** – first hypobranchial; **Hb** – hypobranchials; **Hh** – hypohyal; **Hy** – hyomandibula; **hy.c** - hyomandibular canal; **h.op** - opercular process of hyomandibula; **Inf** - infraorbitals; **Inf.s** – infraorbital series; **i.sc** – infraorbital sensory canal; **Ju** – jugal; **l.g** – lateral gular **m.g** – median gular **Men** – mentomeckelian; **Mx** – maxilla; **n.ao** – anterior nasal opening; **n.po** – posterior nasal opening; **Na** – nasal; **p.l** – pit-line; **Pa** – parietal; **pal.te** - palatal teeth; **Part** – prearticular; **Pmx** – premaxilla; **Pop** – preoperclum; **Pq** – palatoquadrate; **Propt** – propterygium; **Psp** - parasphenoid; **B.rays** – branchiostegal rays; **San** – surangular; **Sc.r** – sclerotic ring; **scl** – sensory canal line; **Sob** - supraorbital; **Sub** – suborbital; **spig** – spiracular groove; **Te** – teeth.

1.2.5 Terminological conventions

Following McCune and Schaeffer (1986; see also Friedman and Giles 2016), we apply the term ‘paleopterygian’ to designate the assemblage of Paleozoic ray-finned fishes of uncertain relationships to one another and modern actinopterygian clades. Our use of this term is not a suggestion that species falling within this category represent a natural group, as we explicitly seek to avoid the taxonomic connotations associated with baggage-laden terms like ‘palaeonoiscoid’ or ‘palaeonisciform’. This nomenclature is plastic and with no implication of evolutionary affinities, although it is our anticipation that groups will be extracted from this paleopterygian assemblage as their relationships to fossil and living actinopterygians are clarified with further anatomical and phylogenetic investigation.

Bone nomenclature adopted here follows the conventional terminology for actinopterygians as in Gardiner (1984). We acknowledge that the frontals and parietals of actinopterygians under this scheme are the homologues of sarcopterygian parietals and postparietals, respectively (SCHULTZE, 2008).

1.3 Results

SYSTEMATIC PALEONTOLOGY
ACTINOPTERYGII Cope, 1887
BRAZILICHTHYIDAE Cox & Hutchinson, 1991
BRAZILICHTHYS Cox & Hutchinson, 1991
BRAZILICHTHYS MACROGNATHUS Cox & Hutchinson, 1991

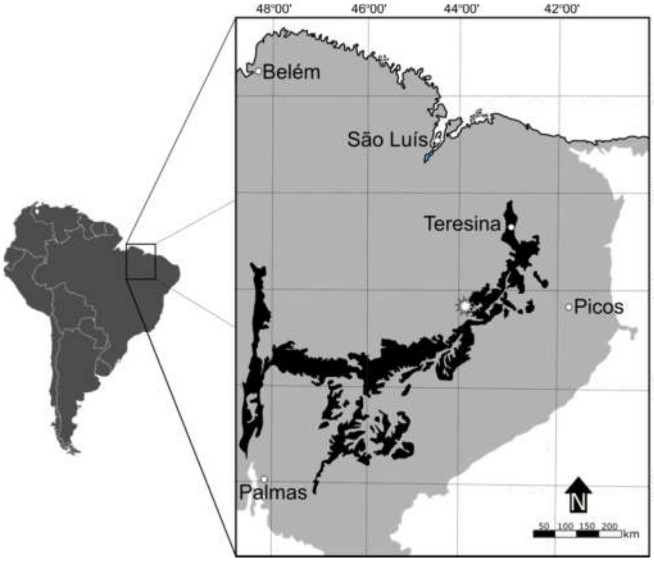
1.3.1 Type and only specimen

DGM 1061-P, incomplete skull. The specimen is housed at the paleontological collection of the Museu de Ciências da Terra (MCT), of the Departamento Nacional de Produção Mineral (DNPM), on behalf of the Centro de Pesquisas de Recursos Minerais (CPRM)

1.3.2 Type Locality and Horizon

Pedra de Fogo Formation, Pastos Bons Locality (~ 6º 40' S, 44º 04' W), between the cities of Pastos Bons and Nova Iorque, state of Maranhão, Brazil (Figure 10). The Pedra de Fogo Formation is assigned to the Artinskian-Kungurian stages of the Permian based on its palynological assemblage (IANNUZZI et al., 2018).

Figure 10 - Map showing outcrop area of the Pedra de Fogo Formation.



Caption: Black: Pedra de Fogo Formation; grey: Parnaíba Basin. Star marks the type locality of *Brazilichthys macrognathus*.
Source: Based on Santos and Carvalho (2009).

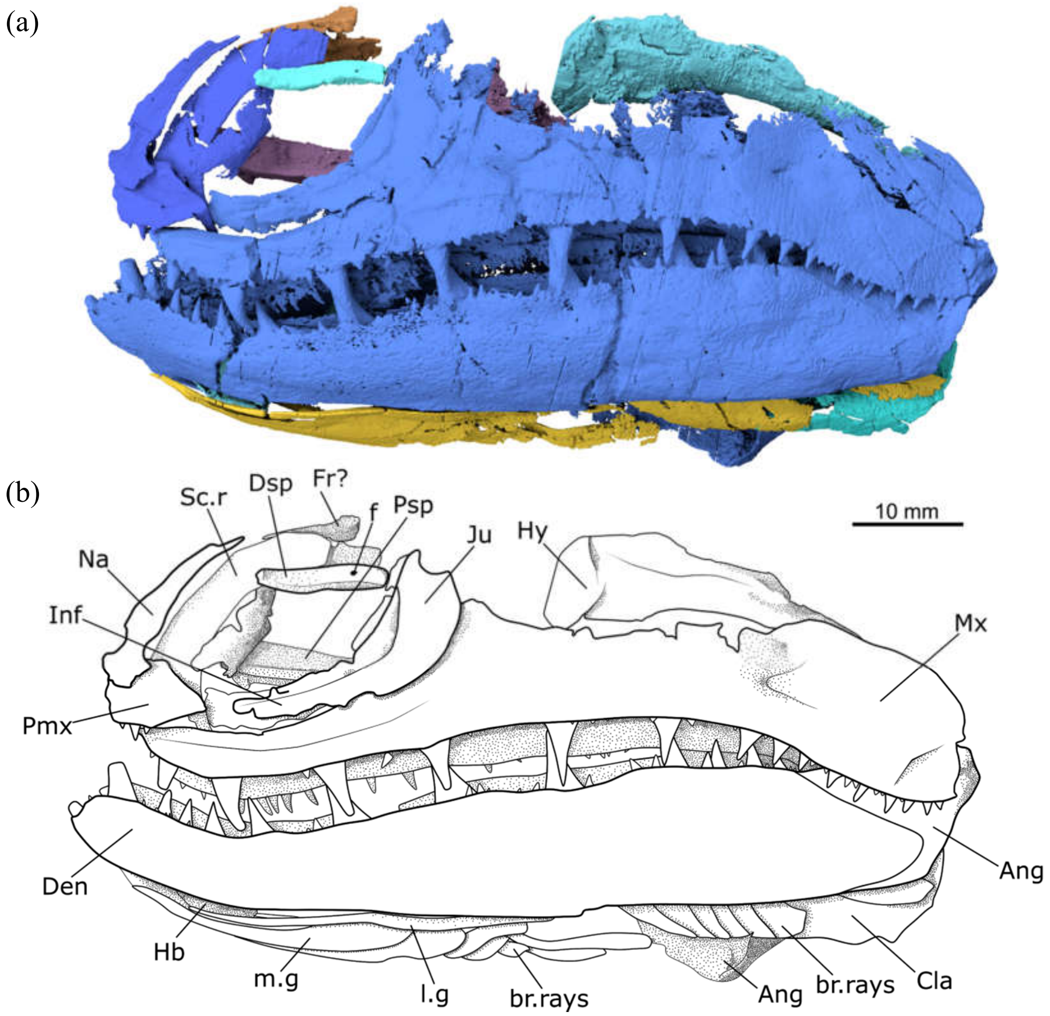
1.3.3 Emended Diagnosis

'Paleopterygian' actinopterygian distinguished by the following combination of characters: parasymphysial fangs, some of which are strongly procumbent; flexed symphysial region of the mandible in lateral view; widely spaced glenoid fossae of articular; long ellipsoidal median and lateral gulars; presence of long extralateral gulars; rod-like dermosphenotic; parasphenoid with distinct basipterygoid processes, short and rectangular ascending processes and robust anterior process, and a prominent dorsal keel on the anterior corpus.

1.3.4 Notes

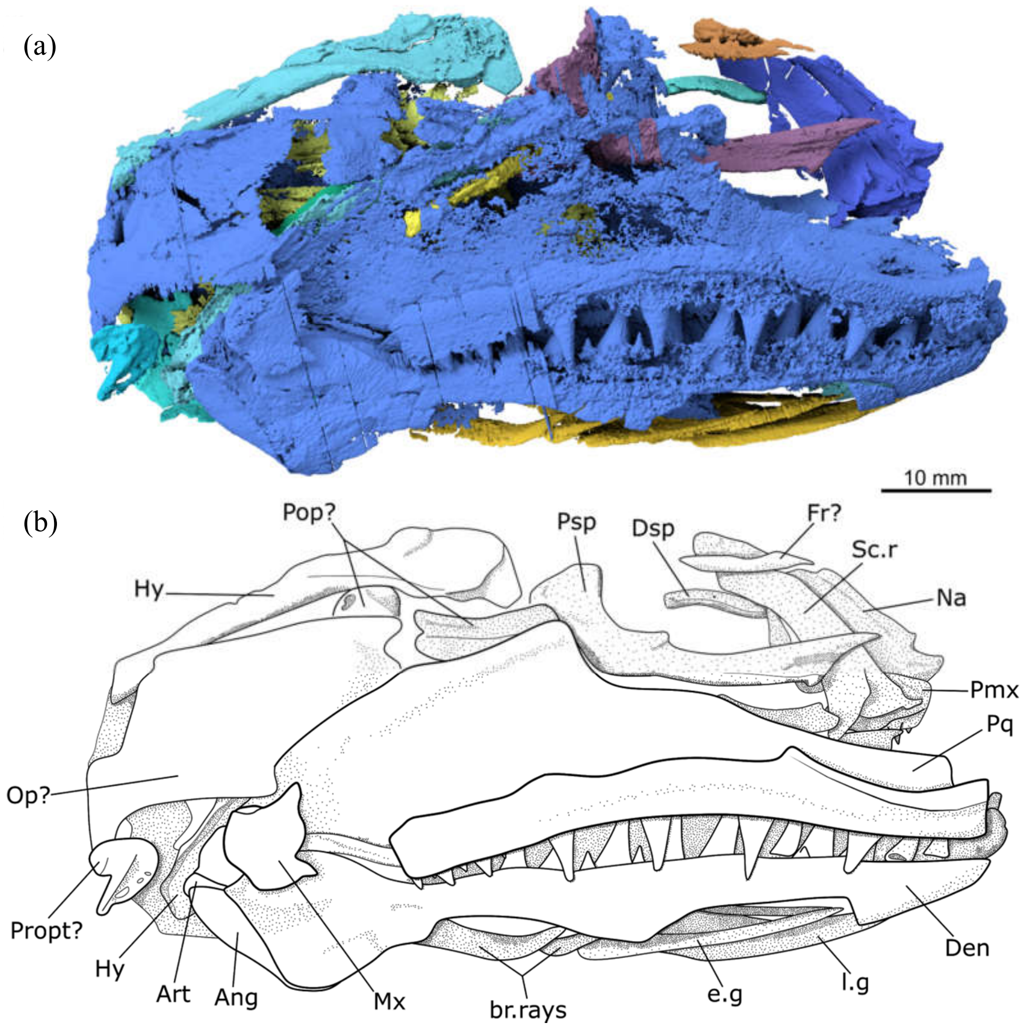
The bones originally mentioned by Cox and Hutchinson (1991) were: nasal, rostral, premaxilla, infraorbito-suborbital, infraorbital (jugal), infraorbital (lacrimal?), suborbital, maxilla, dentary, angular, clavicle, median gular, lateral gulars, branchiostegal rays, and part of the sclerotic ring. However, the holotype of *B. macrognathus* lacks the rostral bone described by Cox & Hutchinson (1991), suggesting loss or other damage in the time between their account and this redescription. Cox & Hutchinson (1991) also illustrated the delicate ornamentation of the dermal bones of the skull, which is composed of closely spaced wavy ridges.

Figure 11 – *Brazilichthys macrognathus*, DGM 1061-P, skull in left-lateral view.



Caption: (a) – Surface rendering based on μ-CT data; (b) – Interpretive drawing.
Source, The author, 2019.

Figure 12 – *Brazilichthys macrognathus*, DGM 1061-P, skull in right-lateral view.



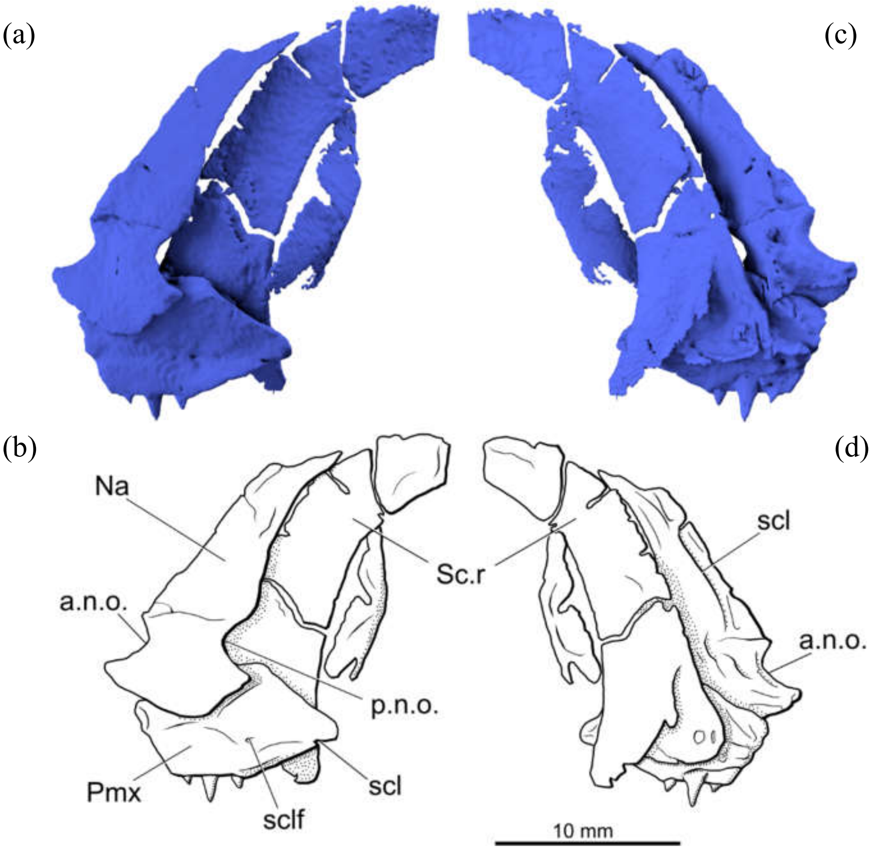
Caption: (a) – Surface rendering based on µ-CT data; (b) – Interpretive drawing.
Source: The author, 2019.

1.3.5 Description

Skull roof—The skull roof is represented only by isolated fragments visible dorsal to the circumorbital series. A small fragment dorsal to the dermosphenotic might represent part of the frontal (Figures 11, 12), but it lacks any diagnostic features (e.g. sensory canals). A posterior element above the suborbital might be part of the left parietal bone, but this too lacks any characteristic detail.

Snout region and circumorbital series—The nasal is large and bears notches for the anterior and posterior nasal openings (Figure 13). There is no obvious indication of the sensory canal externally, but it is apparent internally as a slight longitudinal groove near the anterior border of the bone. The positioning of this groove is consistent with the sensory canal line of the nasals of early actinopterygians. The anterior nasal opening would have been enclosed anteriorly by the the rostral, which is not preserved but was reported in a previous description (COX; HUTCHINSON, 1991: p. 565). The posterior nasal opening is confluent with the orbital opening.

Figure 13 - *Brazilichthys macrognathus*, DGM 1061-P, left antorbital region.



Caption: (a) – Surface rendering in external view based on μ-CT data; (b) – interpretive drawing; (c) – surface rendering in internal view based on μ-CT data; (d) – Interpretive drawing.
Source: The author, 2019.

A slender bone located inside the orbital cavity of the DGM 1061-P was originally identified as part of the sclerotic ring. However, μ-CT revealed an enclosed canal extending through half of the length of the bone, exiting by a foramen in the center of the outer surface (Figures 11, 12). Bones of the sclerotic ring are not canal bearing, indicating a different affinity than that proposed by Cox & Hutchinson (1991). Due to the peculiar path drawn by this canal and its positioning, the bone is interpreted here as the dermosphenotic. It is an elongate robust bone that contacts the nasal anteriorly, the jugal posteriorly, and probably the frontal dorsally, composing the dorsal margin of the orbit.

The sclerotic ring is partially visible superficially on the specimen. However, a large, thin element mesial to the nasal and premaxilla represents a concealed part of the sclerotic ring (Figure 13). This element is large in comparison to the orbital opening but its outline closely matches it in shape.

The rest of the circumorbital series is well preserved. The infraorbital series is composed of three infraorbitals. These are, from anterior to posterior: the lachrymal, a single infraorbital, and the jugal. The jugal is lunate and the infraorbital sensory canal line lies near its anterior border, without any evidence of posterior branching. This bone slightly overlaps the postorbital expansion of the maxilla. The infraorbital lies anterior to the jugal and bears the extension of the infraorbital sensory canal line. The lachrymal is displaced within the orbital cavity but would contact the premaxilla and the nasal anteriorly and the infraorbital posteriorly. A poorly preserved rhomboidal bone lies ventral to the jugal and the posterior expansion of the maxilla. Cox & Hutchinson (1991) interpreted it as a suborbital, an identification adopted here due to the absence of any sensory canals.

The premaxilla is a short and robust bone. Its triangular posterior border, restricted to the anterior margin of the orbit. It bears an enclosed sensory canal that exits to the surface medially by small foramina on the exposed surface of the premaxilla. It is partially overlapped posterodorsally by the nasal. We assume it would contact the (unpreserved) rostral anterodorsally. The premaxilla bears at least 3 small conical teeth.

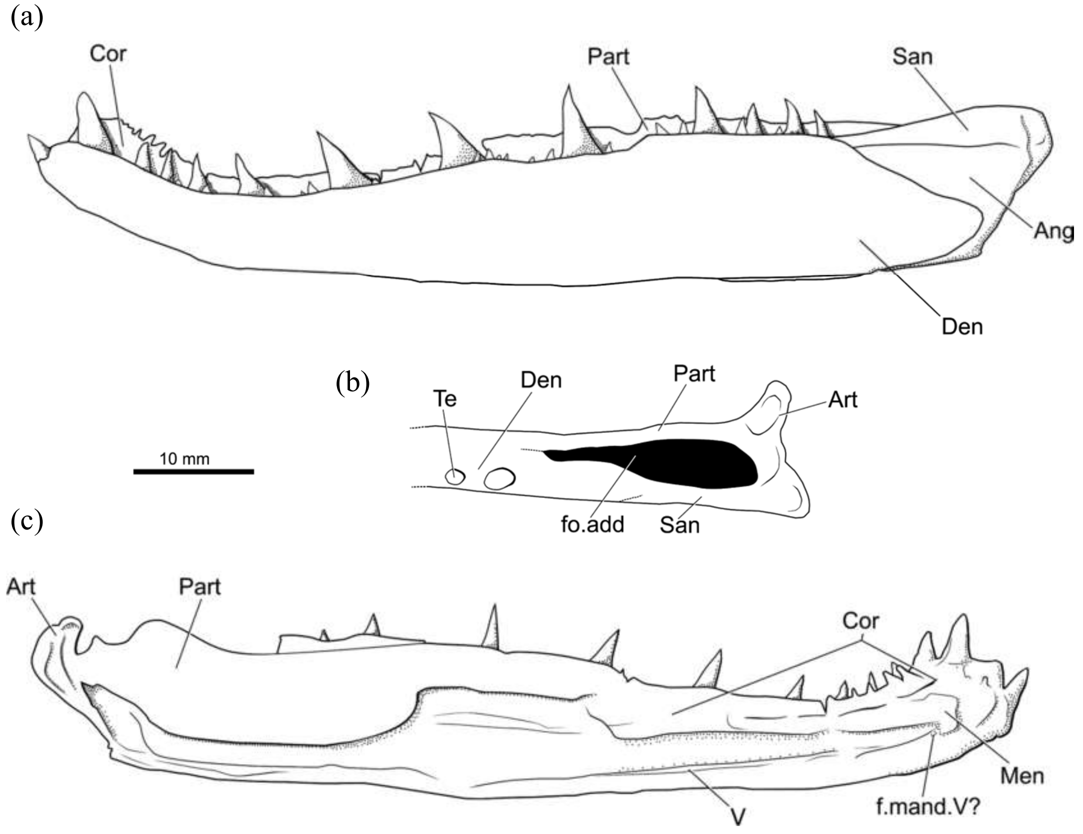
Jaws and palate—Both the dentary and the maxilla bear two series of teeth (Figures 14, 15), one inner series composed of large conical and posteriorly directed teeth and one outer series of much smaller teeth. Tooth rows extend the complete length of these bones, even on the portion of the maxilla that overlaps the dentary. The teeth in this area are anteriorly directed. The big teeth of the lingual series bear acrodin tooth caps (Figure 9).

The maxilla is the largest bone of the upper jaw. It consists of a curved suborbital arm and a large postorbital expansion. The dorsal margin of this expansion is incomplete. Roughly the upper one-third of the bone is missing with the exception of two small fragments immediately posterior to the jugal and suborbital. The ventral margin of the maxilla is ‘S’-shaped, and bears two series of teeth: large, widely spaced inner teeth and smaller, closely spaced outer teeth.

The dentary is the largest bone of the lower jaw (Figure 14a), covering almost its entire lateral surface. It bears at least 12 large conical teeth. The mandibular sensory canal extends along the ventral border of the dentary, and there is a foramen below the mentomeckelian that represents the exit of the trigeminal nerve to the inner jaw surface (Figure 14c). The ornamentation of this bone is similar to the other dermal bones of the skull, being only distinct due to the more robust ornamentation on the anterior portion of this bone. The angular and surangular represent the remaining bones on the external surface of the mandible. The angular is partially covered by the dentary but its ventral margin is visible along the posterior half of the dentary. The dentary partially overlaps the angular posteriorly, and tapers in this region. The surangular bone is poorly preserved, but represents a thin lamina dorsal to the angular and composes most of the external margin of the adductor fossa.

The jaw is only partially mineralized. The articular is ossified and rhomboidal, bearing two concave articular facets that mark the joint with the quadrate condyles (Figure 14b). A small rugose ossification on the distalmost portion of the inner surface of the dentary might be a mentomeckelian ossification (Figure 14c).

Figure 6 – Reconstruction of the left mandible of *Brazilichthys macrognathus* based on µ-CT scanning of DGM 1061-P.

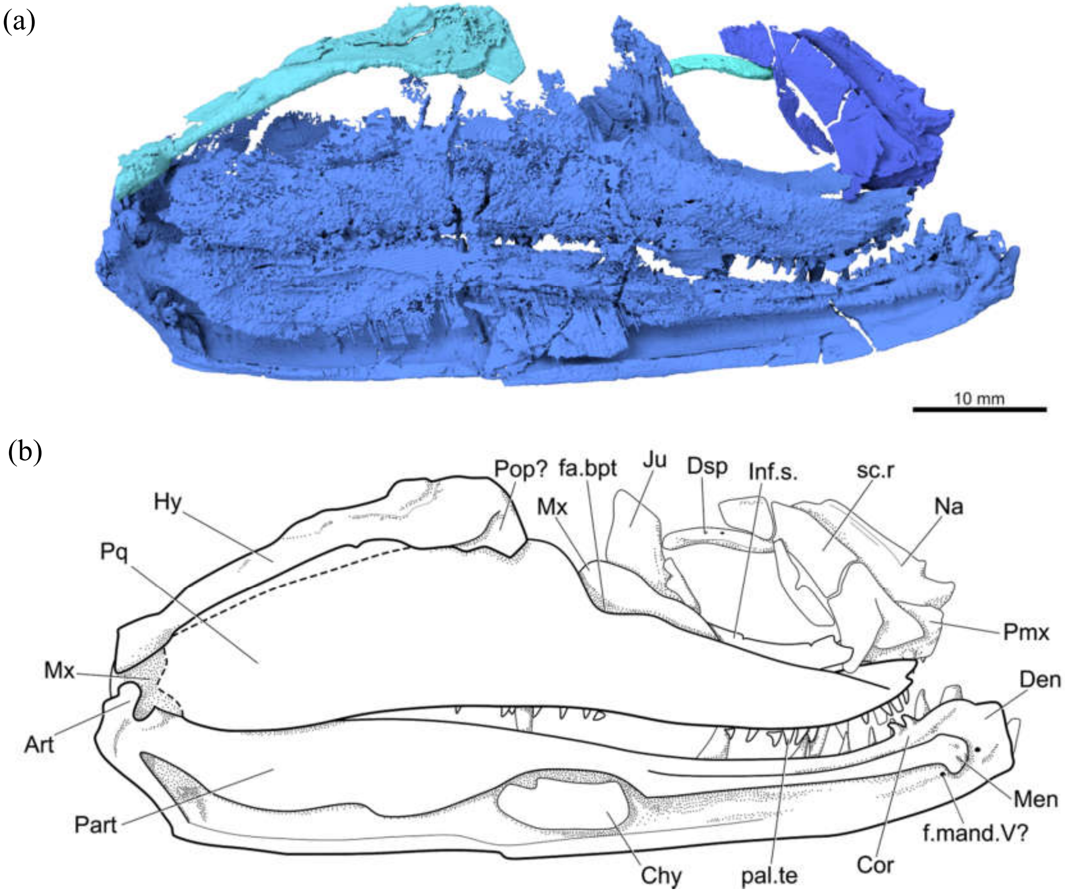


Caption: A, lateral view; B, dorsal view of articular region and adductor fossa; C, mesial view.
Source: The author, 2019.

The internal wall of the lower jaw is presumably formed by the prearticular and the coronoids (Figure 14c), although their boundaries cannot be discerned. The region interpreted as the prearticular consists of a vertical sheet of bone that forms the mesial wall of the adductor chamber and has a convex ventral margin. The anteriormost coronoids bear small conical teeth, but no teeth can be resolved more posteriorly in scans. The adductor fossa is large and triangular in dorsal view, bordered by the dentary anteriorly, the surangular and prearticular laterally and the articular posteriorly (Figure 14b).

The palatoquadrate complex is partially preserved, and divisions between constituent ossifications are not apparent. Its shape broadly mirrors that of maxilla, with an expanded posterior blade and narrow subortbital ramus. At the junction of these two regions, the dorsal margin of the palatoquadrate bears a shallow embaument marking the position of the basipterygoid articulation. This is open dorsally, rather than being an enclosed fenestra (Figure 15). One series of teeth extends along the ventral margin of the palate. These teeth are intermediate in size between those of the two dentary tooth rows. It is unclear if this tooth row is restricted to the dermopalatines or are also borne by the ectopterygoid.

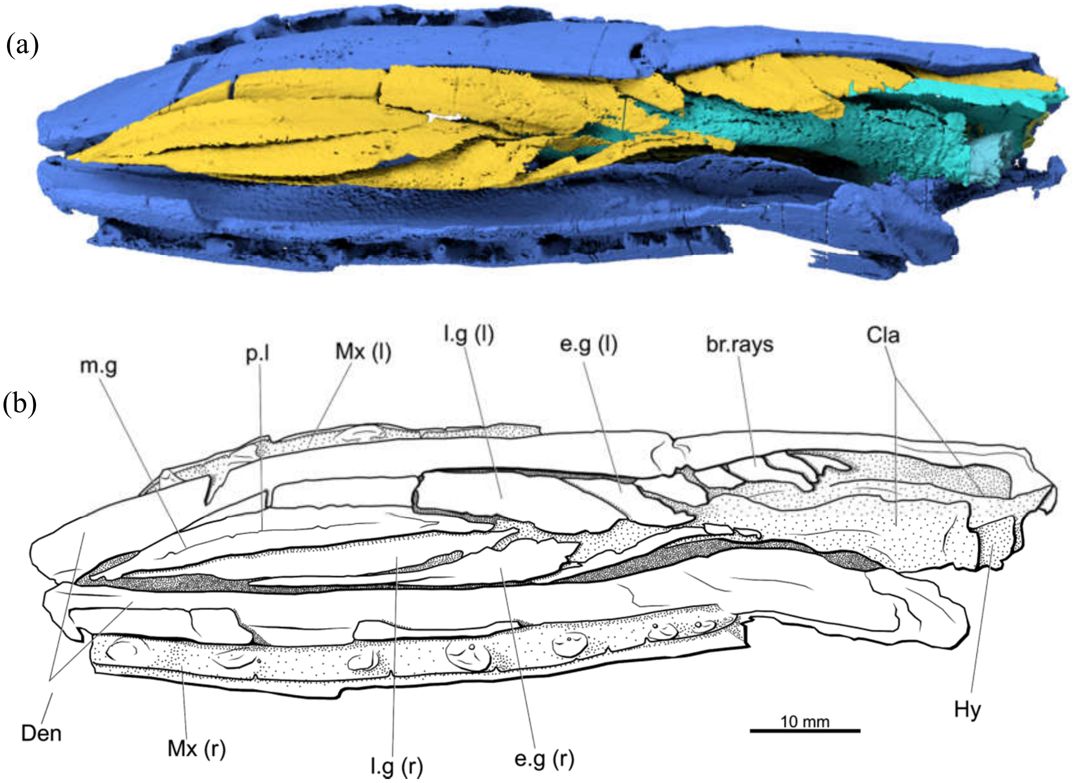
Figure 15 – *Brazilichthys macrognathus*, DGM 1061-P, left palate, lower jaw, hyomandibula, and regions of dermal skull in mesial view.



Caption: (a) – surface render based on μ-CT data; (b) – Interpretive drawing.
Source: The author, 2019.

Operculo-gular apparatus—The median gular is elongate and ellpisoidal, and bears a longitudinally oriented pit-line on the its external surface. The lateral gulars are similar in size to the median gular, but do not bear a pit-line. Both median and lateral gulars cover the anterior half of the intramandibular region (Figure 16). μCT reveals one extra pair of gulars buried within the matrix. Due to their position and shape they are herein described as extralateral gulars, laying behind the lateral gulars and extending until the first pair of branchiostegal rays (Figure 17).

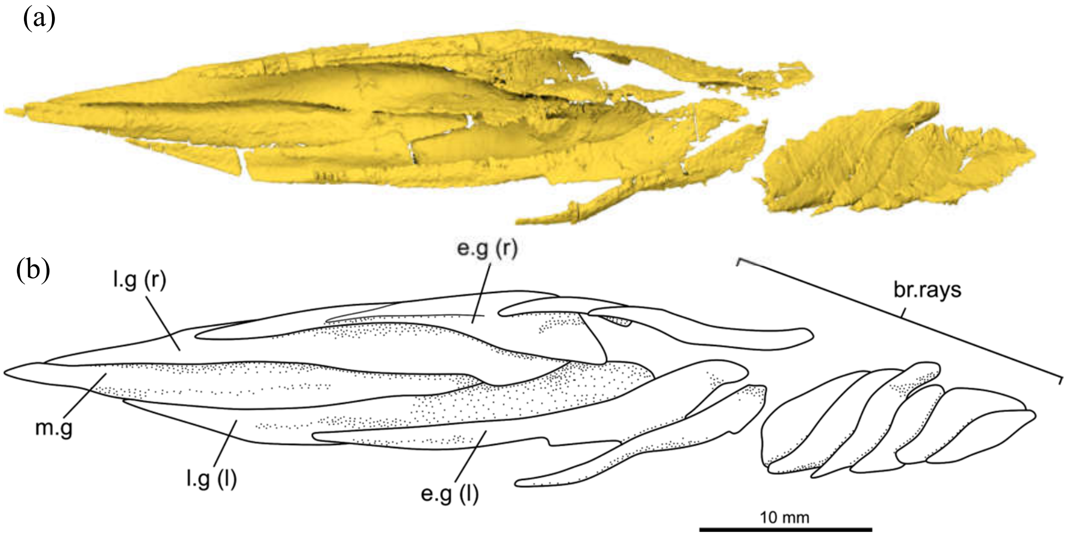
Figure 16 – *Brazilichthys macrognathus*, DGM 1061-P, ventral view of jaws and intermandibular region.



Caption: (a) – surface render based on µ-CT data; (b) – interpretive drawing.
Source: The author, 2019.

At least seven pairs of branchiostegal rays are partially preserved and visible externally. The posterior rays are partially broken, near the jaw articulation. The first pair is elongated but differs from the lateral and extralateral gulars by not being flattened. The exposed branchiostegal rays exhibit the same ornamentation pattern of other dermal bones of the skull: thin, wavy and closely arranged ridges.

Figure 17 – *Brazilichthys macrognathus*, DGM 1061-P, dorsal view of gular plates and branchiostegals.

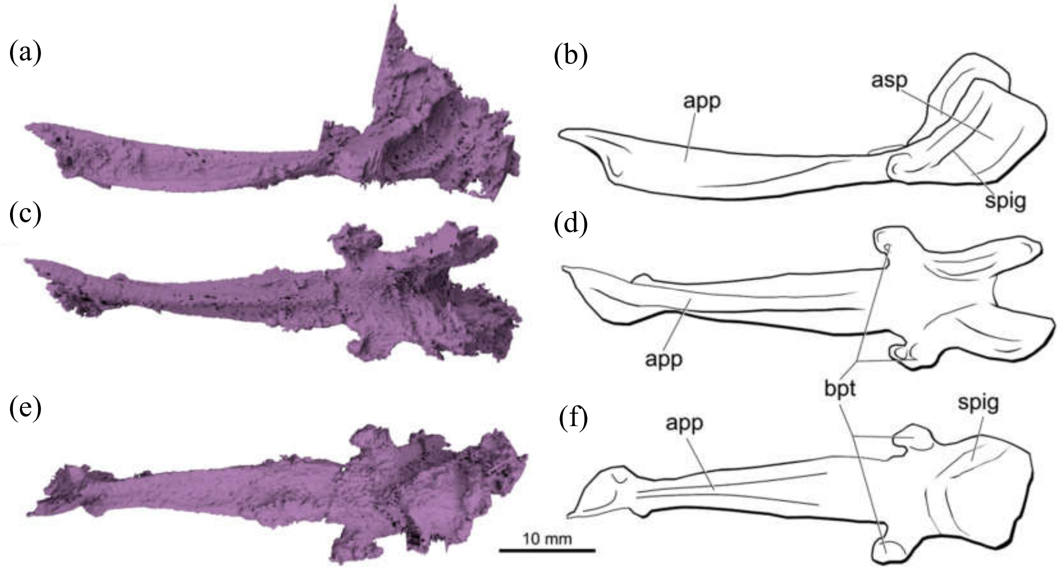


Caption: A, surface render based on µ-CT data; B, interpretive drawing.
Source: The author, 2019.

The opercular series is almost completely missing, with the exception of the left opercle, which is preserved as a thin lamina behind the palatoquadrate complex (Figure 12b). Due to the poor preservation of this element, it is impossible to provide accurate descriptions of the opercular series. Small fragments of a canal bearing overlapping the dorsal part of the palatoquadrate likely represent portions of the preoperculum, but are too incomplete to provide clear information on the bone.

Parasphenoid, braincase and associated ossifications—The parasphenoid (Figure 18) coprises a long, slender anterior corpus that is expanded anterodorsally, likely for articulation with the vomer(s) and ethmoid region of the braincase, neither of which is well preserved. The anterior process of the parasphenoid is sub-triangular in cross-section. The ventral surface of the parasphenoid is smooth, with no evidence of a buccohypophysial foramen, any dentigerous area or ornamentation. However, individual denticles are likely beyond the resolution of the scan, so it is not possible to exclude the possibility that a denticle field was present. Stout dermal basipterygoid processes emerge from the lateral margin of the parasphenoid corpus immediately anterior to the broad ascending processes. Each basipterygoid process bears a small depression near its anterior border. The ascending processes expand dorsally, terminating with a straight margin. A shallow spiracular groove extends along the external surface of the left ascending process. There is no evidence of a posterior extension of the parasphenoid behind the ascending processes.

Figure 18 – *Brazilichthys macrognathus*, DGM 1061-P, parasphenoid.

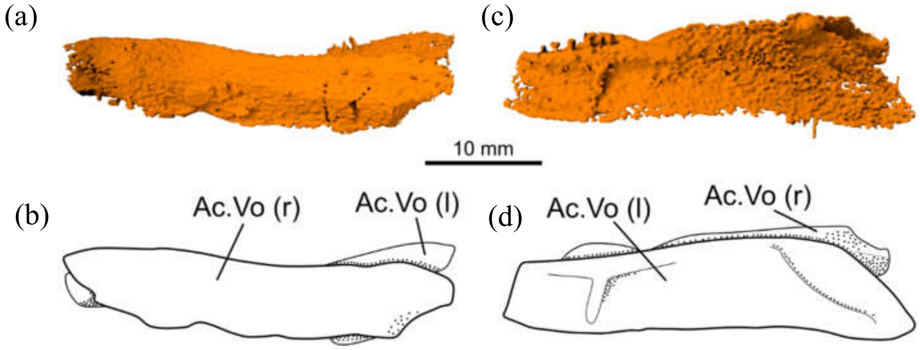


Caption: (a) – surface render in left-lateral view based on μ-CT data; (b) – interpretive drawing; (c) – surface render in dorsal view; (d) – interpretive drawing; (e) – surface render in ventral view; (f) – Interpretative drawing.
Source: The author, 2019.

Two long laminar bones preserved lateral to the parasphenoid represent accessory vomers (Figure 19). These plates contributed to the roof of the mouth in life, and would occupy the entire lateral margins of the anterior corpus of the parasphenoid. As the parasphenoid, these accessory vomers do not bear teeth large enough to be apparent in our scans. Compression of the skull resulted in a displacement of the right accessory vomer to the opposite side of the skull.

There is no trace of the neurocranium, and it is assumed to be cartilaginous due to the displacement of the branchial arches above the parasphenoid.

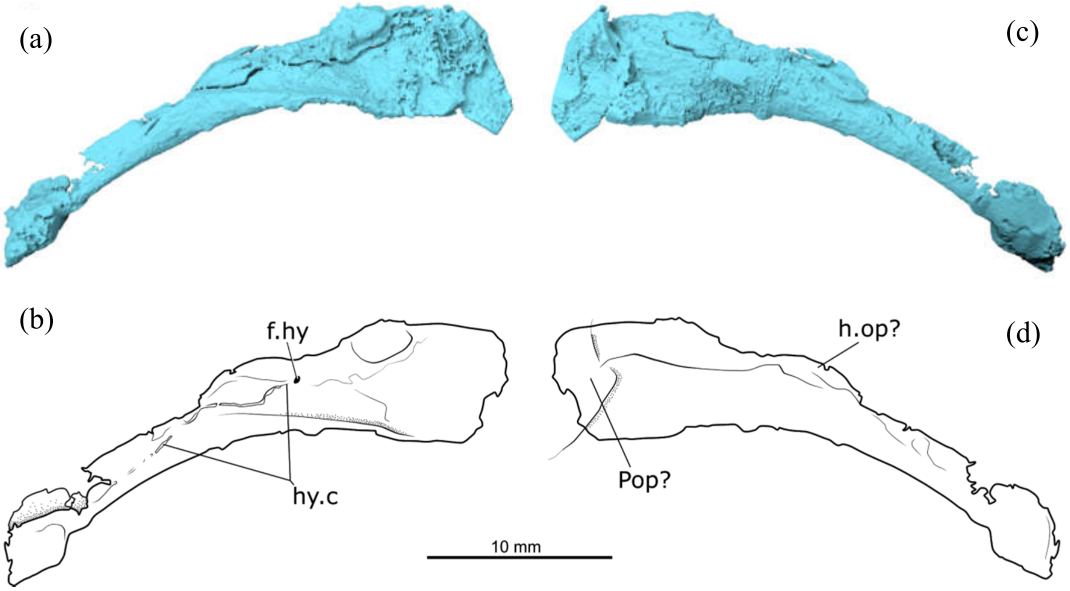
Figure 19 – *Brazilichthys macrognathus*, DGM 1061-P, accessory vomers.



Caption: (a) – surface render in right-lateral view based on µ-CT data; (b) – interpretive drawing; (c) – surface render in left-lateral view; (d) – interpretive drawing.
Source: The author, 2019.

Hyoid and branchial arches—The left hyomandibula (Figure 20) is well preserved. It is strongly reclined, and the angle between its dorsal and ventral limbs is subtle. The dorsal limb is spatulate, with a compressed and proximal region representing the articular head. By contrast, the ventral limb is more cylindrical, with a rounded cross-section. Attached to the anterodorsal portion of the hyomandibula there is a fragment of what would be the preopercle (Figure 20d), but the poor preservation of this element turns impossible its identification. The hyomandibular canal extends along the mesial surface of this element, exiting to the lateral surface by a foramen, before the expanded anterior surface of the hyomandibula. A sight dorsal expansion at the junction between the dorsal and ventral limbs of the hyomandibula represents a weakly developed opercular process. No dermohyal is preserved, and it was apparently not fused to the hyomandibula.

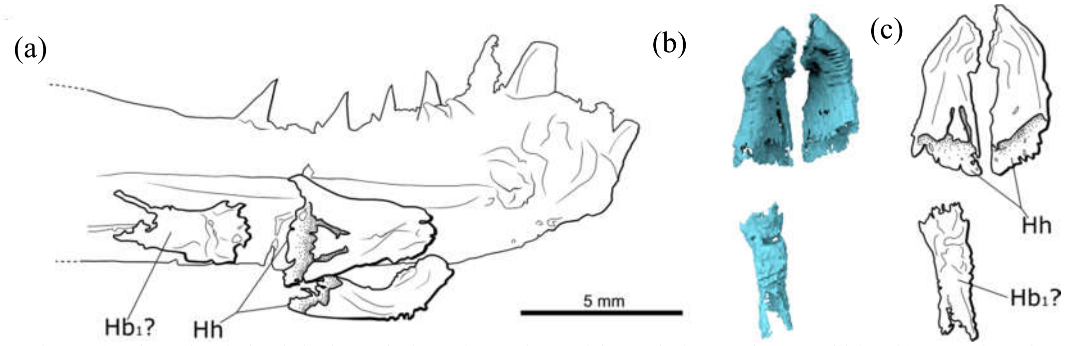
Figure 20 - *Brazilichthys macrognathus*, DGM 1061-P, left hyomandibula.



Caption: (a) – surface render in mesial view based on μ-CT data; (b) – interpretive drawing; (c) – surface render in lateral view; (d) – interpretive drawing.
Source: The author, 2019.

The hypohyals (Figure 21) are well preserved, located in the distal portion of the ventral surface of the lower jaw. They are cylindrical and expand posteriorly, and curve toward one another along the midline. There is no evidence of a mineralized basibranchial.

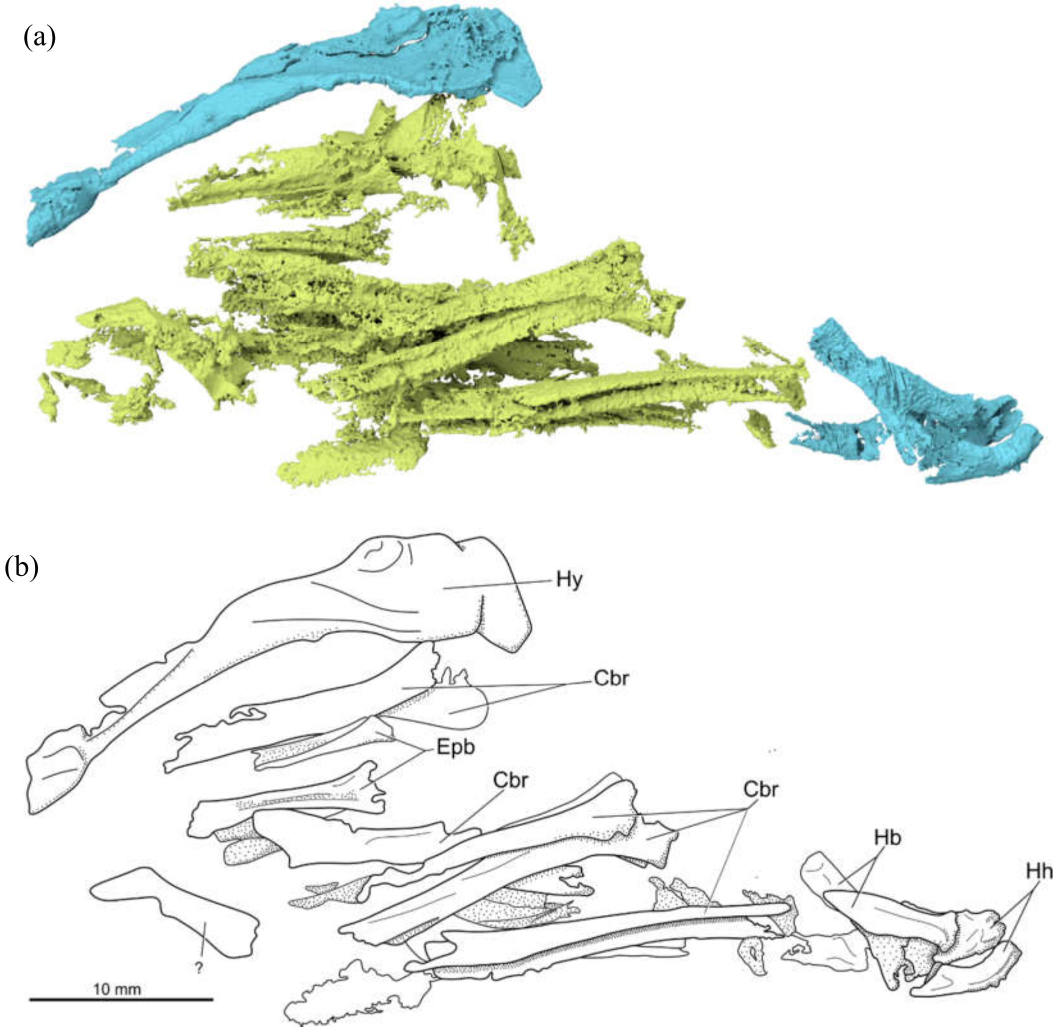
Figure 13 - *Brazilichthys macrognathus*, DGM 1061-P, portions of ventral hyoid arch.



Caption: (a) – hypohyals in right-lateral view shown in position relative to the mandible; (b) – render of ventral hyoid arch in dorsal view based on μ-CT data; (c) – interpretive drawing.
Source: The author, 2019.

Preserved components of the branchial skeleton (Figure 22) are located in the posterior half of the skull and consist of four pairs of long rods that probably represent ceratobranchials. There are two short epibranchials that do not show an evidence of developed uncinate processes. The hypobranchials are long, expanded anteriorly to for their articulation with the unpreserved basibranchial. Other smaller elements are present, but fragmentation and displacement makes identifications difficult.

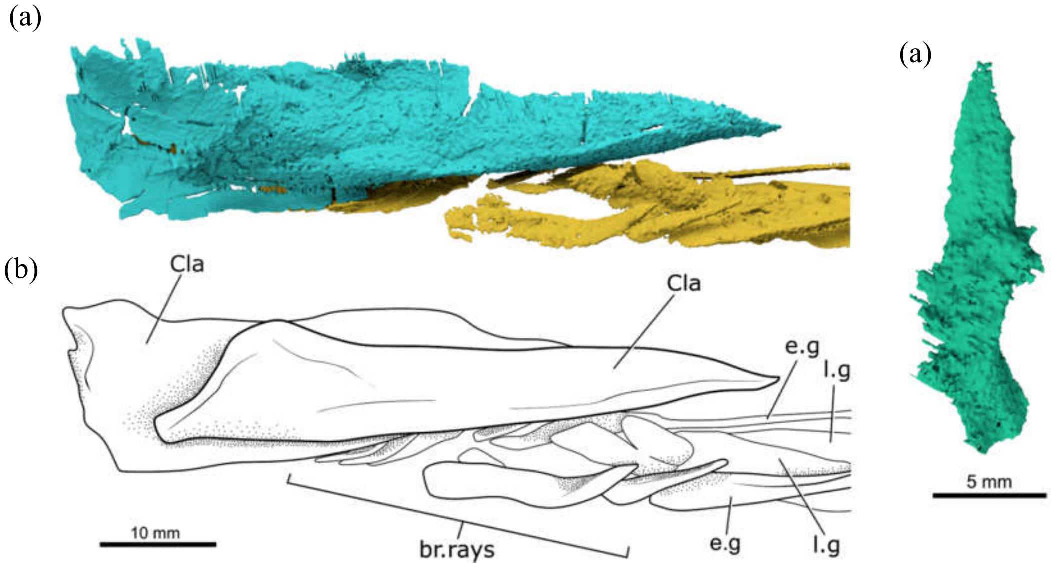
Figure 22 – *Brazilichthys macrognathus*, DGM 1061-P, hyoid and branchial arches in right-lateral view.



Caption: (a) – surface render based on μ-CT data; (b) – interpretive drawing.
Source: The author, 2019.

Shoulder girdle—The clavicles (Figure 23a-b) bound the branchial skeleton ventrally. Each clavicle has an elongated anterior ramus and terminates in a lamina with a triangular profile in dorsal view. There is a displaced, ellipsoidal bone between the branchial rays and dorsal to the clavicles that could be a poorly preserved interclavicle (Figure 23c), however it is not possible to accurately identify this bone, and therefore it was not coded as present in the phylogenetic matrix. Other components of the shoulder girdle are not preserved. However, one small rhomboid element located posteriorly to the end of the clavicles could be interpreted as the first fin rays that fused to form this rigid structure.

Figure 23 – *Brazilichthys macrognathus*, DGM 1061-P, clavicles in ventral view.



Caption: (a) – surface render based on µ-CT data; (b) – interpretive drawing. (c) – surface render of possible interclavicle.
Source: The author, 2019.

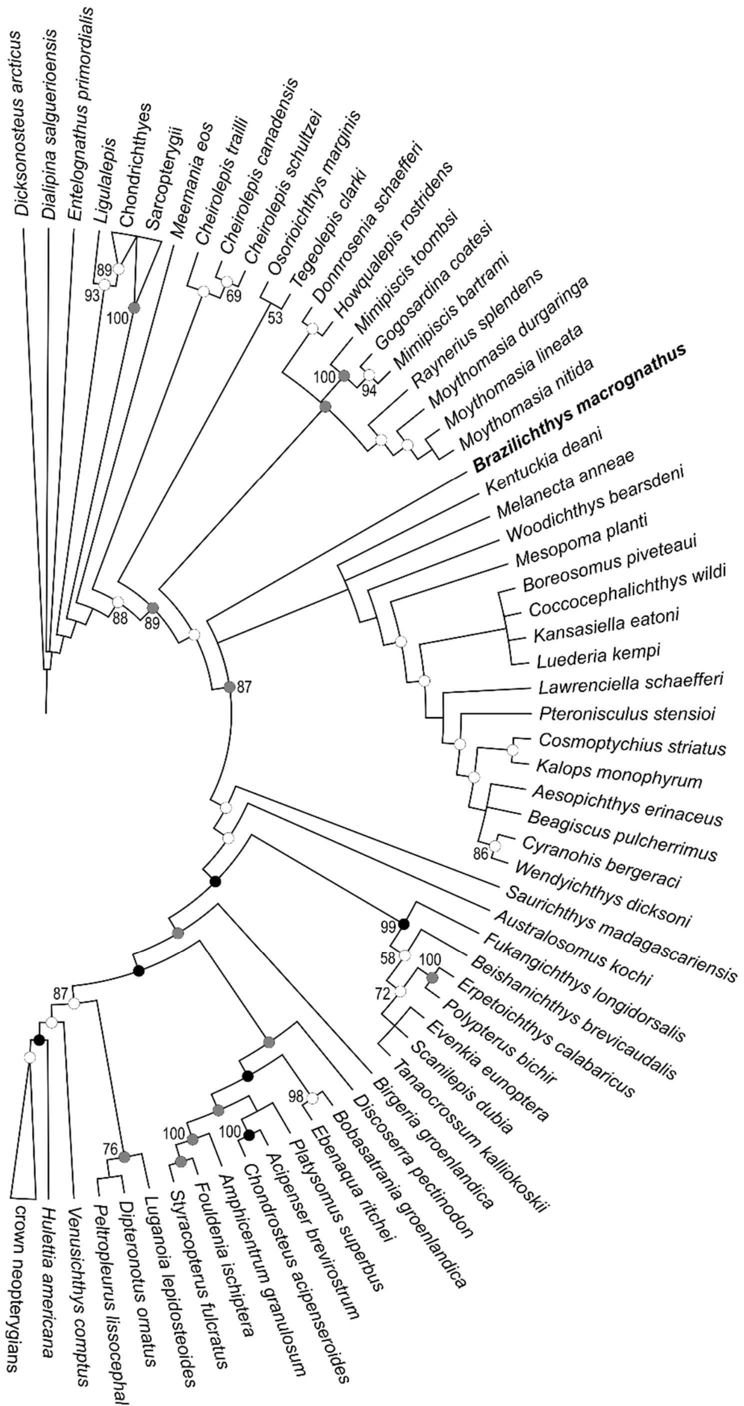
1.3.6 Phylogenetic results

Parsimony analysis—The parsimony analysis including *Brazilichthys* recovered 3 equally parsimonious trees (length = 1325 steps; consistency index: 0.22; retention index: 0.64).

The strict consensus of the 3 most parsimonious trees (Figure 24) is well resolved, showing actinopterygian, sarcopterygian and chondrichthyan clades. Devonian actinopterygians form a grade on the actinopterygian stem, with most the Middle-Late Devonian species forming a clade (Bremer decay index [BDI] = 2). *Brazilichthys* is placed crownward of all Devonian taxa, in a polytomy with two other clades (BDI = 2). The first of these includes most late Paleozoic taxa and is poorly supported (BDI = 1). The second unites *Saurichthys* and *Australosomus* with the actinopterygian crown. *Discoserra*, *Ebenaqua*, *Platysomus*, *Amphicentrum, Styracopterus* and *Fouldenia* are the most highly nested Paleozoic taxa, and are placed on the chondrostean stem (BDI = 3).

The following characters are optimized as arising along the branch below the clade including *Brazilichthys* plus all other post-Carboniferous taxa: dermopterotic carying lateral line canal between dermosphenotic and skull roof (36; 0 – 1); absence of a distinct posterior ramus of the dermosphenotic (56; 1 – 0); 91 (presence of two coronoids [1 – 3]); 136 (presence of median posterior myodome [0 – 2]); 138 (spiracle enclosed in canal [1 – 2]); 143 (presence of fossa bridgei [0 – 1]); 180 (absence of anterolaterally divergent olfactory tracts [1 – 0]); 184 (optic lobes of same width or wider than cerebellum [0 – 1]); 186 (optic tectum divided into bilateral halves [0 – 1]); 187 (presence of cerebellar corpus [0 – 1]); 193 (crus commune ventral to endocranial roof [0 – 1]); 211 (presence of opercular process of hyomandibula [0 – 1]); and 233 (absence of interclavicle [0 – 1]). However, of these synapomorphies only 56 and 211 can be assessed and are present in *Brazilichthys*. Both characters show multiple changes on the tree. Sarcopterygians have a dermosphenotic (sarcopterygian intertemporal; SCHULTZE, 2008) that lack a posterior ramus, while Devonian actinopterygians bear a distinct posterior ramus of the bone. This posterior extension is lost in the clade uniting *Brazilichthys* and all post-Devonian actinopterygians, with multiple reversals within the group (e.g. *Beagiascus*, *Wendyichthys*, *Cyranorhis*, *Birgeria*, *Bobasatrania* and some neopterygians). With respect to the hyomandibula, sarcopterygians, chondrichthyans and the earliest actinopterygians show absence of an opercular process. The node including *Brazilichthys* and all other post-Devonian is united by presence of opercular process, with reversals in *Acipenser*, *Amphicentrum*, *Birgeria*, *Chondrosteus*, and *Kalops*.

Figure 24 - Phylogenetic hypothesis of early actinopterygian interrelationships, based on maximum parsimony analysis of 265 morphological characters.



Caption: Tree length: 1326 steps; consistency index: 0.22; retention index: 0.64. Node colors represent Bremer support values: white = 1, light gray = 2, black ≥ 3. Numbers represent posterior probabilities (x 100), and are only shown for nodes found in the majority-rule consensus of the posterior distribution of trees in the Bayesian analysis.

Source: The author, 2019.

Bayesian analysis—The Bayesian analysis shows a similar result to the parsimony analysis presented above. The major differences include: the resolution of Paleozoic actinopterygians; the chondrostean stem; and the topology of the neopterygian lineages. It is interesting to notice that the well supported nodes of the parsimony analysis (BDI ≥ 3), were not recovered on the Bayesian consensus, with the exception of the cladistian total group.

Most of paleopterygian fishes are recovered within a large polytomy, but a few clades were resolved. Cladistians and chondrosteans are supported with considerably high posterior probabilities, including the stem lineages (0.99 and 0.8, respectively). However, the chondrostean stem in the Bayesian analysis is restricted to *Birgeria*, while in the parsimony it includes deep-bodied fish such as *Platysomus*, *Amphicentrum* and *Bobasatrania*. The considerably lower probability of the chondrostean total group might be due to weak support regarding the position of *Birgeria* as a stem chondrostean, which is present on the Bayesian analysis but was not encountered on the parsimony analysis. The strongest group formed (posterior probability of 1.00) is the Amphicentridae, including *Amphicentrum*, *Styracopterus* and *Fouldenia*, within the large Carboniferous-Permian polytomy, rather than a stem chondrostean lineage.

As in the parsimony analysis, *Brazilichthys* is placed crownward of all Devonian actinopterygians, within a polytomy including most late Paleozoic actinopterygians. The character state reconstruction for the consensus tree exhibits the same synapomorphies of the parsimony analysis. In addition, the likelihood of most ancestral states of the node are above 0.99, with the exception of character 91 (presence of two coronoids [1 - 3]), with a likelihood of 0.28, being the most probable ancestral state the presence of three coronoids [1 - 2] with a likelihood of 0.48. Additional synapomorphies for the node including *Brazilichthys* and all post-Devonian species were found by the likelihood ancestral state reconstruction. Of these, characters 141 (presence of dermal component of basipterygoid process [0 - 1]);173 (absence of multifid anterior margin of parasphenoid [1 - 0]); and 174 (absence of buccohypophyseal canal piercing parasphenoid [0 - 1]) are the only ones visible for *Brazilichthys*. A list of synapomorphies for the *Brazilichthys* node is available on Supplementary Data 4.

1.4 Discussion

1.4.1 Phylogenetic relationships of early actinopterygians

Although early actinopterygians have been point of discussion several times, the relationship of most paleopterygians remains unclear (COATES, 1999; GARDINER et al., 2005; GILES et al., 2017). The most recent analyses show that most Paleozoic ray-fins branch from the actinopterygian sten, with some exceptions falling within the crown. However, there is considerable inconsistency regarding these stem lineages, and their position shifts in different analyses, even with similar datasets.

The hypothesis presented herein is no exception to this, with the topology and organization of the actinopterygian tree changing considerably from Giles et al. (2017), despite the matrix being almost exactly the same (with the insertion of *Brazilichthys* and the deletion of *Brachydegma*). Both analyses show a clade including most Devonian actinopterygians crownward of *Cheirolepis*, *Tegeolepis* and *Osorioichthys*, and a subsequent clade including most post-Devonian Paleozoic actinopterygians. However, the Paleozoic and early Mesozoic clades composing the stem of crown lineages presented herein is different from Giles et al. (2017) hypothesis. The most distinct is the position of the amphicentrids, which are stem actinopterygians on Giles' analysis but recovered as part of the chondrostean stem herein. The same is true for *Discoserra*, *Ebenaqua* and *Bobasatrania*, which are here recovered as stem chondrosteans and as stem neopterygians by Giles et al. (2017).

The presence of large paleopterygian groups forming polytomies, and the low posterior probabilities of some clades, are indicatives of the poor resolution of early actinopterygian relationships, which is in agreement with the results shown by Giles et al. (2017), and indicates that future effort is needed to find evolutionary patterns among stem actinopterygian lineages, that remain obscure. The anatomical revision of neglected late Paleozoic taxa from Africa, South America and Asia might shed light on the obscure evolutionary pattern of stem actinopterygians.

1.4.2 Assessment of previous phylogenetic placements of *Brazilichthys*

The phylogenetic analyses presented herein do not support previous assumptions regarding the affinities of *Brazilichthys*. The original alignment of Brazilichthyidae to Acrolepidae is only supported by plesiomorphic characters for actinopterygians such as: long jaws, dermal bone ornamentation, multiple series of teeth on the dermal bones of the jaw. In addition, the CT-scan results do not indicate any character that could more precisely align *Brazilichthys* to Acrolepis, despite overall similarity.

The hypothesis presented by Romano and Brinkmann (2009) considers that *Brazilichthys* could be related to *Birgeria*, as well as other possible birgeriids from the Permian of China. However, the authors do not specify which characteristics could support their assumption, and do not attempt a phylogenetic analysis, due to the poor description of these taxa. The new features presented herein for *Brazilichthys* do not support Romano and Brinkmann (2009) hypothesis, which agrees with our phylogenetic analysis.

1.4.3 Possible affinities of *Brazilichthys*

The CT-scan revealed several new features of *Brazilichthys* that could help drawing up assumptions of its relationships within Actinopterygii. These features are briefly discussed below.

Parasphenoid and braincase—Although the parasphenoid of stem actinopterygians from the Devonian (e.g. *Cheirolepis*, *Moythomasia*, *Mimipiscis*) show a considerably different morphology to post-Devonian taxa, *Tegeolepis clarki* closely resembles more derived actinopterygians with developed basipterygoid processes and developed ascending processes (see GILES et al., 2015c, fig. 13). The overall morphology of the parasphenoid of *Tegeolepis* is considerably similar to *Brazilichthys*, especially concerning the shape of the anterior process and position of the basipterygoid processes. However, there are few other characters comparable between this taxa, and just a extensive revision of *Tegeolepis* could shed light on its affinities to other early ray-finned fishes.

The parasphenoid of *Brazilichthys* is distinguishable from most Carboniferous-Permian taxa by the presence of robust basipterygoid processes and rectangular ascending processes. Most late Paleozoic actinopterygians bear a triangular parasphenoid with long ascending processes and weakly developed basipterygoid processes (STAMBERG; ZAJIC, 2000). This morphology is associated with amblypterids, paramblypterids and elonichthyids (SCHINDLER, 1993; DIETZE, 2000; STAMBERG; ZAJIC, 2000), but is also similar to other taxa such as *Kansasiella* and *Woodichthys*, differing mostly by the extent of development of the basipterygoid processes (COATES, 1998). Thus, the parasphenoid of *Brazilichthys* more closely resembles *Kansasiella* and *Woodichthys*, but differs from the first two by the presence of a robust and slender anterior process that does not taper anteriorly. Cosmoptychius also bears large basypterygoid processes and squared ascending processes (SCHAEFFER, 1971) that closely resemble *Brazilichthys*.

The parasphenoid of *B. macrognathus* is similar to that of *Pteronisculus nielseni*, due to the robust anterior process that seems to have a subtriangular transversal section. The basipterygoid processes of these two species are also similar in shape and position, just varying in length (more developed in *P. nielseni*; XU et al., 2014).

Although it seems that the braincase of *Brazilichthys* would be cartilaginous, we could not confirm this assumption and therefore did not included this on our phylogenetic analysis. In addition, in most fossil species it is difficult to state if the braincase was indeed ossified (e.g. GILES; FRIEDMAN, 2014).

Extralateral gulars—The extralateral gulars are long a narrow in *B. macrognathus* and are located more posteriorly than in *Wendyichthys dicksoni* and much more elongated than in *Cyranorhis*, *Lineagruan* and *Beagiscus* (LUND; POPLIN, 1997; MICKLE *et al*., 2009). Either way, all the gular apparatus of *Brazilichthys* is significantly longer than in other Paleozoic actinopterygians. Considering that presence of extralateral gulars was assumed by Lund and Poplin (1997) to be associated with an extensive jaw opening, the long elements of *Brazilichthys* could be related to a bigger jaw opening.

Accessory vomers—*Brazilichthys* bears large accessory vomers, which are uncommon among paleopterygians, being found in *Mimipiscis*, *Moythomasia*, *Raynerius*, *Elonichthys*, *Eurynotus*, *Pteronisculus* and *Australosomus* (GARDINER, 1984; GILES et al. 2015; FRIEDMAN et al. in press). However, Gardiner (1984) considered this character to be primitive for actinopterygians. This thin element are probably prompt to disarticulation from the remaining skull, difficulting its fossilization. Therefore, this feature could be more widespread than it appears on the fossil record.

Dermosphenotic—The dermosphenotic of derived paleopterygians normally exhibit a keystone shape (GARDINER, 1989; GARDINER et al., 2005; FIGUEIREDO; GALLO, 2006; MICKLE, 2015), but in *B. macrognathus* it is tube shaped and would cover the dorsal margin of the orbit, similar to that of *Pteronisculus nielseni* and *Canobius*.

Shoulder girdle—The clavicles of lower actinopterygians are normally well-developed (GARDINER, 1984; GARDINER et al., 2005), being reduced in derived actinopterygians and lost in crown teleosts (ARRATIA, 1997; 2015). The shape and length of the clavicle of *Brazilichthys* is mostly comparable to Devonian taxa, especially *Gogosardina coatesi*, which bears large and triangular clavicles (CHOO et al., 2009), longer than other stem actinopterygians as *Raynerius splendens* and *Moythomasia* (GARDINER, 1984; CHOO, 2015; GILES et al., 2015b).

Brazilichthys macrognathus possess a displaced ossification that might be an interclavicle, due to its flattened and ellipsoid morphology. Interclavicles are present in several Devonian taxa (e.g. *Cheirolepis trailli*, *Osorioichthys marginalis*, *Raynerius splendens*, *Moythomasia durgaringa*, *Howqualepis rostridens* and *Mimipiscis tombsi*; TAVERNE, 1997; CHOO et al., 2009; GILES; FRIEDMAN, 2014; CHOO, 2015; GILES et al., 2015b; GILES et al., 2015c). Other actinopterygians also bear an interclavicle, but those are chondrosteans and their relatives (e.g. *Acipenser brevirostrum*, *Styracopterus fulcratus* and *Fouldenia ischiptera* (HILTON et al., 2011; SALLAN; COATES, 2013)). However, the lack of more diagnostic features and the displacement of this plate, it becomes impossible to draw accurate assumptions.

1.4.4 Phylogenetic position of *Brazilichthys*

The resolution of *Brazilichthys* is consistent with the observed characters of the holotype skull in comparison to other Paleozoic actinopterygians. It is positioned within a polytomy that included one clade that encompass most late Paleozoic actinopterygians and species more closely related to crown actinopterygians.

The Bayesian analysis yielded a similar result to the parsimony analysis described above, although with substantially less resolution. Major differences include: '*Ligulalepis*', a stem osteichthyan in most early vertebrate phylogenies (LU et al., 2017; CLEMENT et al., 2018), was recovered as a stem chondrichthyan. The position of Paleozoic actinopterygians in relation to crown lineages also vary between analyses. The node including the crown actinopterygians presented herein was not found on the Bayesian analysis of Giles et al. (2017), where cladistians, chondrosteans and neopterygians are part of a big polytomy including most late Paleozoic species. In addition, our Bayesian analysis resolved *Meemannia* as a stem actinopterygian, differing from Giles et al. (2017).

Alignment to Acrolepidae, as proposed by Cox and Hutchinson (1991), is only supported by plesiomorphic characters for actinopterygians (e.g. long jaws, dermal bone ornamentation, multiple series of teeth on the dermal bones of the jaw). The presence of an elongated maxilla and large teeth is too plastic to support any phylogenetic affinity, especially when dealing with large arrays of plesiomorphic species, as is the case for paleopterygians. The diagnosis of Acrolepidae is also based on plesiomorphic characters (see STAMBERG, 1991), therefore, it is not possible to securely align any species to this family before a major revision of its species.

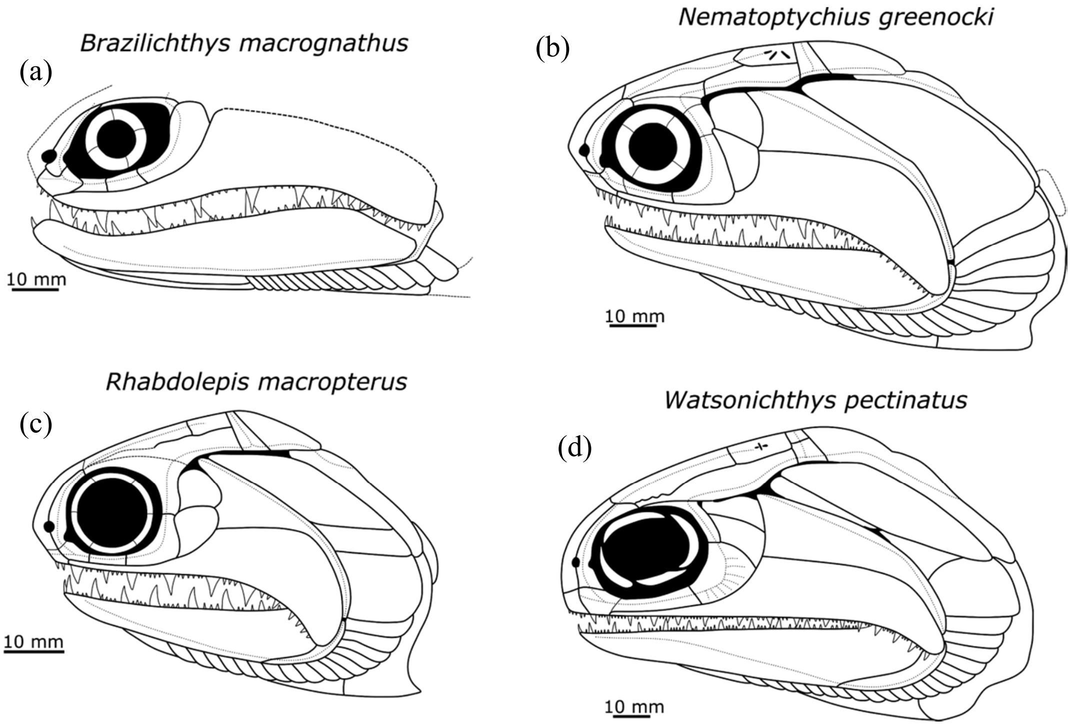
The hypothesis that *B. macrognathus* could be related to *Birgeria*, from Romano and Brinkmann (2009), is not supported by our phylogenetic analysis. The only feature that could align *B. macrognathus* to *Birgeria* would be the presence of several rows of teeth on the jaw, and well-developed and long coronoid teeth, extending towards the jaw articulation. However, these features are primitive among actinopterygians and, therefore, not sufficient to support the Romano and Brinkmann (2009) hypothesis. The possible unmineralized braincase of *Brazilichthys* could be a similar feature to chondrosteans, but the absence of a braincase on this specimen alone is not sufficient to state that the braincase was indeed unmineralized in this taxon.

Apparently, *Brazilichthys macrognathus* would be part of the grade that includes most Paleozoic actinopterygians. However, the relationships among early actinopterygians is still poorly resolved, and future work should focus on investigating new characters that might indicate possible evolutionary patterns of the actinopterygian stem. Thus, detailed revisions of poorly understood actinopterygian taxa from the late Paleozoic are substantially important for revealing new characters and evolutionary trends in the early history of ray-finned fishes.

1.4.5 Large predatorial paleopterygians

Despite the high species diversity of Carboniferous and Permian paleopterygians, the majority of the known species is composed of relatively small fishes with minute small conical teeth on their jaws (see MOY-THOMAS; DYNE, 1938; FIGUEIREDO; GALLO, 2006). However, a few species (e.g. *Nematoptychius greenocki*, *Rhabdolepis macropterus* and *Watsonichthys pectinatus*; GARDINER, 1963) show larger size (> 50 mm skull length) and comparably larger teeth (> 3 mm) that indicate a higher predatorial capacity (Figure 25). Although some of these species are closely related (GARDINER, 1963; LUND; POPLIN, 1997), the variation of the dermal bones of the skull (Figure 25) could indicate different phylogenetic affinities to these taxa.

Figure 25 - Selected predatorial actinopterygians from the late Paleozoic.



Caption: A, *Brazilichthys* reconstruction; B-D reconstructions based on Gardiner (1963).
Source: The author, 2019.

Although paleopterygians that show at least some degree of macro-predation in the Carboniferous-Permian are spread between several families (e.g. Acrolepidae, Cosmoptychiidae, Rhadinichthyidae and Pygopteridae; GARDINER, 1963) there is a considerable amount of shared characteristics that could indicate close affinities between some of these families. Unfortunately, most of these taxa is only superficially known by fragmentary and/or disarticulated remains, being difficult with the present data to include most of these in a robust phylogenetic analysis. Therefore, it is possible that predatorial adaptation evolved several times on the actinopterygian stem, but until a detailed revision of these taxa is conducted, any assumption will remain putative.

1.5 Conclusions

µCT of the holotype of the Permian actinopterygian *Brazilichthys macrognathus* from Brazil reveals considerable new anatomical information. The sclerotic ring element described by Cox and Hutchinson (1991) is reinterpreted as a dermosphenotic; the infraorbital series is composed of three bones rather than two; the rostral element originally figured is not present. In addition here we provide new anatomical data including: parasphenoid, accessory vomers, clavicles, hyoid and branchial arches, opercular series and jaw articulation that were not accessible to Cox and Hutchinson (1991)

The positioning of *Brazilichthys* rejects a close relationship with the Triassic *Birgeria* recently proposed by Romano and Brinkmann (2009). Although our analysis does not include *Acrolepis*, affinity with this genus and other putative acrolepids seems unlikely on the basis of conspicuous differences in lower jaw, parasphenoid and gular morphologies.

There are several examples of large predatorial actinopterygians during the late Paleozoic, and their affinities remain only putative. The detailed revision of these taxa might help understanding if predatorial behavior emerged only once during the paleopterygian grade or if these species show different affinities in relation to the crown. Recent studies have shown that endocranial characters might be crucial for phylogenetic studies of early actinopterygians (e.g. GILES; FRIEDMAN, 2014; GILES et al., 2015b; GILES et al., 2017; CLEMENT et al., 2018). Therefore, future work should focus on modern imaging techniques for these poorly understood taxa that could potentially reveal new important characters.

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2 A NEW COELACANTH GENUS AND SPECIES

(Manuscript under development: FIGUEROA, R.T.; FRIEDMAN, M.; GALLO, V. A new coelacanth from the early Permian (Cisuralian) of Brazil, with comments on actinistian phylogeny).

Abstract

The Pedra de Fogo Formation comprises the lower Permian (Cisuralian) interval of the Mississippian-Lower Triassic sequence of the Parnaíba Basin in Brazil. Of the vertebrates known from this formation, chondrichthyans and tetrapods are better known than bony fishes. The coelacanth record of the Pedra de Fogo Formation is restricted to isolated bone remains associated to *Spermatodus* and *Rhabdoderma*. Here we describe a new coelacanth based on a partially articulated specimen, mostly composed by skull and shoulder girdle, studied by microcomputed tomography (μCT). This specimen has a palate similar to that of Paleozoic taxa, such as *Rhabdoderma* and *Coelacanthus*, but the skull roof, lower jaw and ceratohyal share features with Mesozoic taxa, such as *Whiteia*, *Wimania* and *Coccoderma*. The unique combination of characters found in this specimen indicate it as a new species placed in a new genus. A phylogenetic analysis recovers the new species as the most crownward Paleozoic coelacanth, highlighting the importance of the osteichthyan fossil record of Brazil, which may provide important data for phylogenetic studies within the late Paleozoic. The evolutionary rate analysis indicates that as other long-living lineages, the coelacanths experienced a high morphological diversification rates early on their evolutionary history within the Devonian, with a posterior stability toward more recent ages.

Key-words: Actinistia. Permian. Parsimony. Bayesian. Evolutionary Rates.

Resumo

A Formação Pedra de Fogo representa o permiano inferior (Cisuraliano) dentro da sequência Mississipiana-Eotriássica da Bacia do Parnaíba no Brasil. Dos vertebrados que são conhecidos para esta formação, condrictes e tetrápodes são mais bem conhecidos que os peixes ósseos. O registro de celacantos da Formação Pedra de Fogo é restrito a ossos isolados associados a *Spermatodus* e *Rhabdoderma*. Aqui, descrevemos um novo celacanto com base em um espécime tridimensional parcialmente articulado, composto principalmente por porções do crânio e da cintura peitoral, acessados a partir de microtomografia computadorizada (μCT). Esse espécime possui um palato similar ao de táxons do Paleozoico, como *Rhabdoderma* e *Coelacanthus*, porém o teto craniano, mandíbula inferior e ceratohial compartilham semelhanças com táxons do Mesozoico como *Whiteia*, *Wimania* e *Coccoderma*. A combinação única de caracteres encontrada nesse espécime indica que se trata de uma nova espécie. A análise filogenética resolve o novo táxon como o táxon mais apical dentre os celacantos do Paleozoico, evidenciando a importância do registro fóssil de peixes ósseos do Brasil, que pode prover dados importantes para estudos filogenéticos com enfoque no Paleozoico tardio. A análise de taxas evolutivas indica que assim como outras linhagens viventes antigas, os celacantos tiveram altas taxas de diversificação morfológica cedo durante a sua história evolutiva durante o Devoniano, com uma posterior estabilidade em direção ao tempo recente.

Palavras-chave: Actinistia. Permiano. Parcimônia. Bayesiana. Taxas Evolutivas.

2.1 Introduction

The Brazilian Paleozoic fish record is relatively poorly known, with most assemblages represented by sparse and fragmentary material (FIGUEROA; MACHADO, 2018). However, there are several partially articulated specimens reported from the Permian of the Paraná Basin (e.g. MALABARBA, 1988; FIGUEIREDO; CARVALHO, 2004 HAMEL, 2005). By contrast, articulated remains are rare from the Parnaíba Basin, with the Permian Pedra de Fogo Formation representing the most promising candidate for yielding well preserved fish material.

Vertebrate fossils from this formation were first reported by Silva-Santos (1946). He described two new shark species (*Ctenacanthus maranhensis* and *Pleuracanthus albuquerquei*) which were subsequently reassigned to other genera (*Sphenacanthus* and *Taquaralodus*; MAISEY, 1982, 1984; CHAHUD; PETRI, 2010). Price (1948) described the gigantic temnospondyli *Prionosuchus plummeri*. Silva-Santos (1990 and 1994) described the holocephalians *Itapyrodus punctatus* and *Anisopleurodontis pricei*. Cox and Hutchinson (1991) described new material of *Prionosuchus plummeri* and also a new species of actinopterygian, *Brazilichthys macrognathus*. Recently, Cisneros et al. (2015) described the tetrapods *Timonya anneae* and *Procuhy nazarensis* (Dvinosauria), together with an undetermined rhinesuchid (Stereospondyli) while Figueroa and Gallo (2017) described three new shark species (*Rubencanthus diplotuberculatus*, *Sphenacanthus ignis* and *Bythiacanthus lopesi*), based on isolated fin spines.

Sarcopterygian fishes from the Pedra de Fogo Formation are poorly known, represented by isolated and poorly preserved bone fragments, scales and tooth plates. Material includes an isolated coelacanth basisphenoid attributed to *Spermatodus* (Silva-Santos 1989), a poorly preserved coelacanth pterygoid compared to *Rhabdoderma* (Weiss and Garcia 2005), and undescribed dipnoan toothplates putatively assigned to Lepidosirenidae, Sagenodontidae, and Ceratodontidae (SILVA-SANTOS 1990; TOLEDO; BERTINI 2005).

Although there is a vast number of analyses dealing with new coelacanth descriptions and coelacanth phylogenies in the light of these new fossil discoveries, there is few consensus on the phylogenetic position of several taxa (e.g. GENG et al., 2009; WENDRUFF; WILSON, 2012; CAVIN et al., 2013; ARRATIA; SCHULTZE, 2015). The only clade that is consistently recovered on coelacanth phylogenies is Latimerioidei, but the topology of its two families (i.e. Mawsoniidae and Latimeriidae) is considerably variable in different analysis (e.g. WENDRUFF; WILSON, 2012; ARRATIA; SCHULTZE, 2015; CAVIN et al., 2017). Other families have already been erected (e.g. Laugiidae, Whiteiidae, Sasseniidae and

Rebellatricidae) but dismissed or recovered with different topologies in subsequent phylogenies (FOREY, 1998; GENG et al., 2009; WENDRUFF; WILSON, 2012; ARRATIA; SCHULTZE, 2015).

Here we present the description of a new partially articulated and three-dimensional coelacanth skull from the Pedra de Fogo Formation, classified as a coelacanth due to palate morphology and lower jaw organization. In addition, we furnish new phylogenetic inferences for the coelacanth interrelationships under parsimony and Bayesian frameworks.

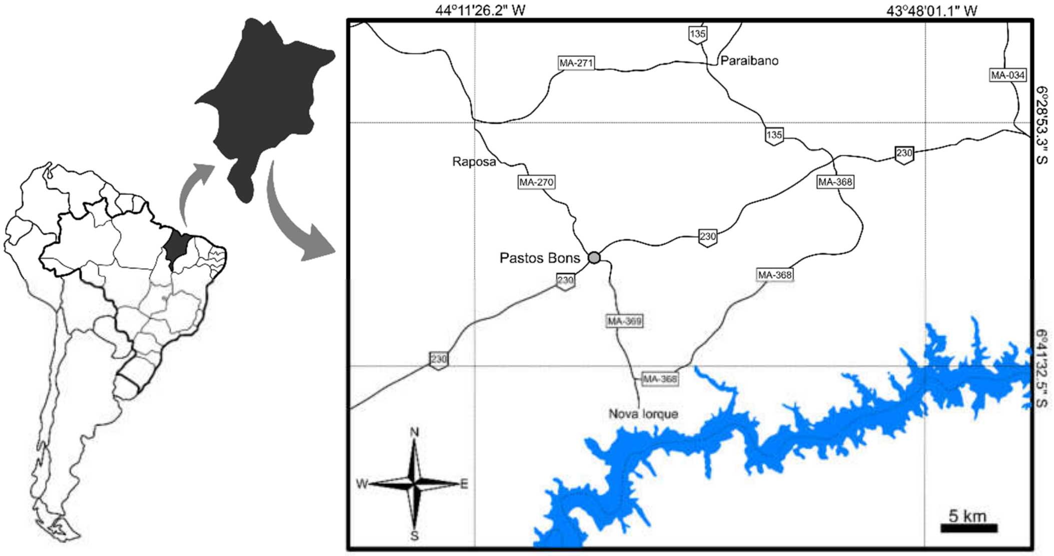
2.2 Material and methods

2.2.1 Material

The analyzed specimen is a small cluster of bones that was originally associated with the actinopterygian *Brazilichthys macrognathus* (DGM 1061-P), but are shown here to belong to a coelacanth. The specimen is deposited at the Museu de Ciências da Terra (MCT) and received the collection number MCT 1463-P.

This material was collected by Llewellyn Ivor Price in 1948 during fieldwork at the Pastos Bons locality in the state of Maranhão, near the city of Nova Iorque (Figure 26). As indicated by Figueroa and Gallo (2017), the material from this expedition deposited in the DNPM collection lacks precise stratigraphic data.

Figure 26 – Schematic map of the Pastos Bons locality of the Pedra de Fogo Formation.



Source: Adapted from Figueroa and Gallo (2017).

2.2.2 Micro computed tomography (µCT)

The µCT was conducted at the Laboratório de Instrumentação Nuclear – UFRJ using a Skyscan 1173 scanner. The following main parameters were used: current, 61 µA; voltage, 130 kV; cupper filter; projections taken at steps of 0.5 degrees of sample rotation. Resolution of the resulting scan was 23.86 µm pixel size.

2.2.3 Character matrix

Certain morphological data of the analyzed specimen was added to Cavin et al. (2017) data matrix, which is the most recent phylogenetic analysis concerning coelacanths. New characters were added to this matrix to better access the relationships of the studied specimen.

The following new characters were added to the matrix of Cavin et al. (2017):

111: Pterygoid Cristae – 0 = covered by palatoquadrate; 1 = anterodorsally directed; 2 = dorsally directed

Stem actinopterygians such as *Cheirolepis* and *Moythomasia* bear a palatoquadrate ossification (GARDINER, 1984; GILES et al., 2015), differing from that of coelacanths. The same is true for stem sarcopterygian fishes (e.g. Onychodontiformes, Porolepiformes) which bear ossifications similar to those of basal actinopterygians (ANDREWS et al., 2006). Therefore, the condition among coelacanth fishes could be considered derived, due to the presence of prominent cristae on the pterygoid. In addition, the orientation of these cristae vary among genera, with some showing anterodorsally directed cristae (e.g. *Rhabdoderma*) (FOREY, 1981) and others show dorsally oriented cristae (e.g. *Axelrodichthys*) (MAISEY, 1986; CARVALHO et al., 2013).

112: Dermopalatine teeth – 0 = absent or reduced; 1 = large

Although dermopalatine dentition is present in early osteichthyans (GARDINER, 1984), the presence of large dermopalatine fangs could be considered derived among coelacanths, due to the presence of this feature in the crown taxa *Latimeria* and the Mesozoic *Macropoma* (LAMBERS, 1996) and the absence in Middle-Late Paleozoic species such as *Diplocercides* (STENSIÖ, 1922; FOREY, 1998). Developed dermopalatine dentition is well known among actinopterygians and stem sarcopterygians. Several stem actinopterygians bear dermopalatine fangs (e.g. *Mimipiscis*; GARDINER, 1984) and the same is true for the Sarcopterygians (e.g. *Glyptolepis*; CLEMENT, 2001).

113: Supratemporals extention – 0 = terminate at the same level of the postparietals; 1 = terminate beyond posterior margin of postparietals.

The condition in most of early coelacanths (e.g. *Allenypterus*, *Diplocercides*) is that the supratemporal does not extend beyond the posterior margin of the postparietals, and therefore does not bear the path of the otic sensory canal line to the extrascapulars. Some taxa (e.g.

Coccoderma, *Libys*, *Holophagus*) show a derived condition where the supratemporal extends beyond the posterior margin of the postparietals (see FOREY, 1998).

2.2.4 Phylogenetic analysis

A parsimony analysis was conducted on TNT 1.5 software using the New Technology Search Algorithm (GOLOBOFF; CATALANO, 2016). Synapomorphies of the resulting consensus tree were mapped on TNT 1.5 and an agreement subtree was constructed from the most parsimonious trees obtained.

Bibliographical data of coelacanth chronostratigraphical distribution was obtained and used to access the temporal distribution of the coelacanth groups, as well as constructing a time-calibrated tree based on the agreement subtree.

2.2.5 Bayesian analysis

The Bayesian tip dating analysis was conducted on MrBayes 3.2.5 (RONQUIST et al., 2012a) using the Metropolitan Coupled Markov Chain Algorithm – MCMC for discrete morphological data (WRIGHT; HILLIS, 2014). Character coding was set to “variable” and a gamma distribution was incorporated.

The previously mentioned chronostratigraphical distribution of all taxa included in the analysis was used to calibrate each taxon as uniform distribution between its maximum and minimum ages. The prior probabilities distribution on branch lengths was set to “clock: fossilization”, for a birth-death prior. The speciation rate was set to exponential 20 and the extinction rate was set to “beta (1, 1)”. The “sampleprob” parameter, which is the fraction of extant species that were sampled, was set to 1, since *Latimeria*, the only living coelacanth, is sampled on our analysis. Since this work deals with fossil data, but also includes living clade data, the sample strategy was set to “fossiltip”. The type of clock was set to IGR, which uses independent-gamma rates, and assumes that the variance in branch lengths increases over time (LEPAGE et al., 2007; RONQUIST et al., 2012b), with the prior distribution set to exponential of 10. Since we calibrated the taxon ages, the “clockratepr” parameter was set to “calibrated”. Finally, the number of substitution types was set to “nst2”, which mean that all transitions have potentially different rates.

The script of the complete analysis is available on the supplementary material 2.

The resulting phylogram was analyzed on FigTree 1.4.3 and the tree file was exported to Mesquite where we mapped the evolution of each character based on the likelihood algorithm.

2.2.6 Geological Settings

The Pedra de Fogo Formation from the Parnaíba Basin is considered of Cisuralian (possibly Kungurian) age, based on biostratigraphic correlations with the Chemnitz Fossil Forest (Germany) and Irati Formation (Brazil) (RÖSLER, 2006; SANTOS et al., 2006; DIAS-BRITO et al., 2007). It is located in the northeastern region of Brazil (VAZ et al., 2007), with its sediments disposed along the frontier of Piauí and Maranhão states, and more to the west covering part of the Tocantins state (SANTOS; CARVALHO, 2009).

This formation contains three informal members (SANTOS; CARVALHO 2009): (1) an inferior basal member of interbedded siltstones and dolomites bearing concretions and siliceous horizons; (2) the middle member, characterized by fine-grained sandstones exhibiting cross stratification, intercalated by siltstones, shales and carbonates with small silica concretions; and the (3) upper member (Trisidela member) composed of intercalated sandstones, siltstones, shales and carbonatic beds.

There are also three different depositional environments within this formation (ARAÚJO et al., 2016). The lowermost portion of this formation is interpreted as a shallow marine and coastal mudflat environment. The middle portion of the formation as a deltaic, or nearshore lake, environment where there is a mixture of continental and marine taxa (FIGUEROA; GALLO, 2017), and the upper portion of the formation comprising a possible lacustrine environment dominated by continental taxa (e.g. dipnoans and temnospodyls) (CISNEROS et al., 2015). These depositional environments might correspond to some degree to the three members proposed for the formation.

2.3 Results

SYSTEMATIC PALEONTOLOGY

SARCOPTERYGII Romer, 1955
ACTINISTIA Cope, 1871
gen. et sp. nov.

2.3.1 Diagnosis

Coelacanth with jaw bearing two types of ornamentation (ridges and tubercles on the angular)*; strong association of angular bone to the plate-like prearticular; angular surface densely covered by pores; metapterygoid strongly associated to pterygoid anterodorsal margin, with developed process for articulation; large quadrate with markedly posteriorly oriented condyles; posterodorsal expansion of quadrate margin; large autopalatines; pectoral girdle with large clavicles.

* Indicates autapomorphy.

2.3.2 Description

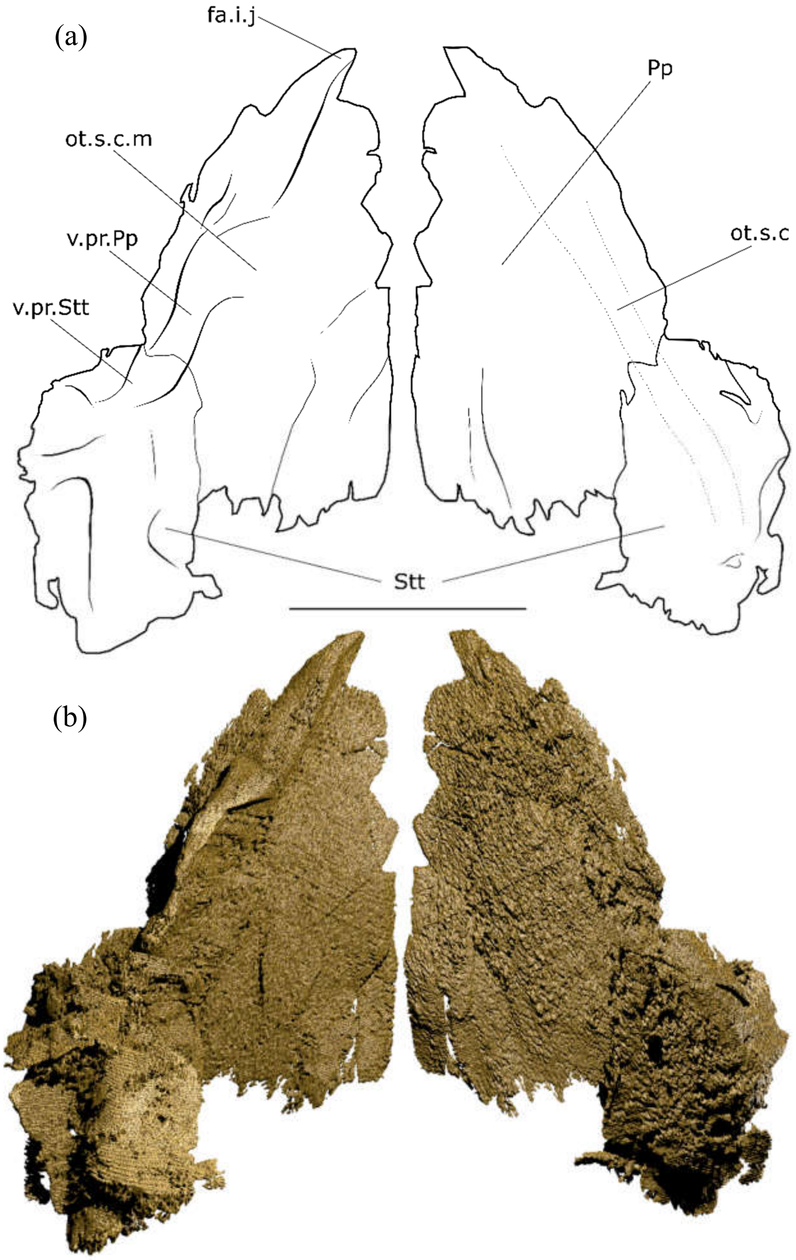
- *Skull roof:*

Only the posterior division of the skull roof is preserved, and consists of the postparietal and supratemporal (Figure 27).

The postparietal is triangular. The otic sensory canal extends along the lateral margin of this bone, exiting to the surface by a series of pores. The shape and arrangement of these pores is not clear. The ventral surface of the postparietal bears the ventral descending process at its lateral margin, which traces the path of the otic sensory canal. The postparietal bears an anterior facet for articulation of the intracranial joint.

The supratemporal is large, extending beyond the posterior margin of the postparietal. The supratemporal bears a continuation of the ventral descending process of the postparietal. It terminates medially at its outer margin, following the path of the otic sensory canal.

Figure 27 - Skull roof.



Caption: (a) – Schematic drawing in ventral (left) and dorsal (right) views of the right half of the skull roof. (b) – Digital model. **fa.i.j**: facet for intracranial joint; **ot.s.c**: otic sensory canal; **ot.s.c.m**: medial branch of otic sensory canal; **Pp**: postparietal; **Stt**: supratemporal; **v.pr.Pp**: ventral descending process of postparietal; **v.pr.Stt**: ventral descending process of supratemporal. Scale bar = 10 mm.

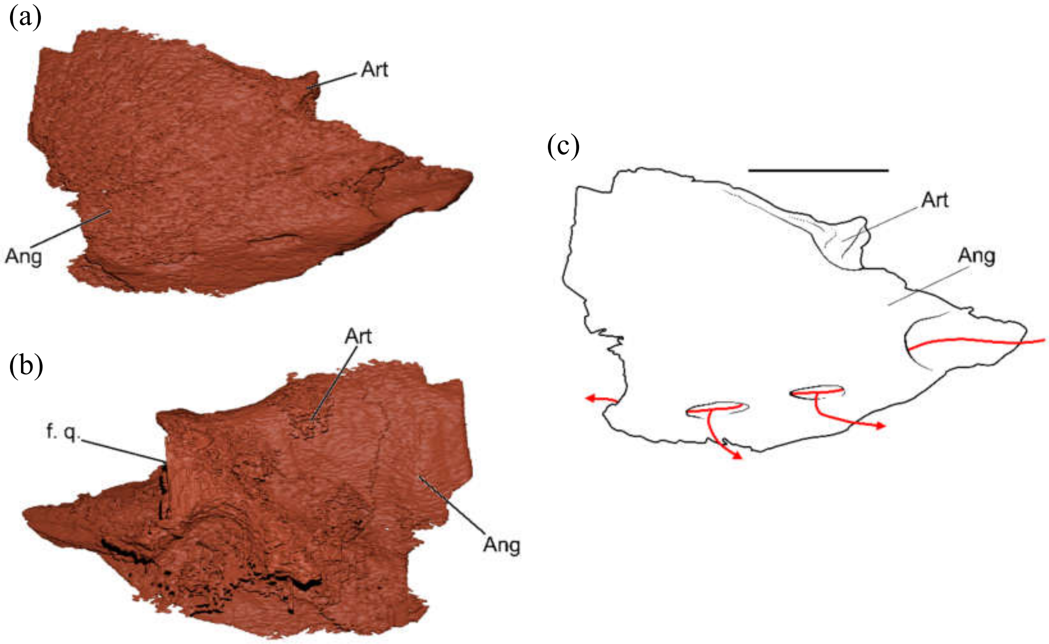
Source: The author, 2019.

- *Lower Jaw:*

The lower jaw is incomplete, with only parts of the angular, articular, prearticular and the principal coronoid preserved. Dentary, retroarticular, splenial, and anterior coronoids are missing.

The anterior portion of the angular is lacking (Figure 28). External ornamentation is mainly composed of well-spaced ridges, but small rounded tubercles are present near the sensory canal pores (Figure 29c) and minute small pores mark its entire surface. The mandibular sensory canal extends along the ventral margin of the bone, with two large, oval pores (Figure 28). The canal opens near the posterior edge of the bone.

Figure 28 – Angular and articular bones.



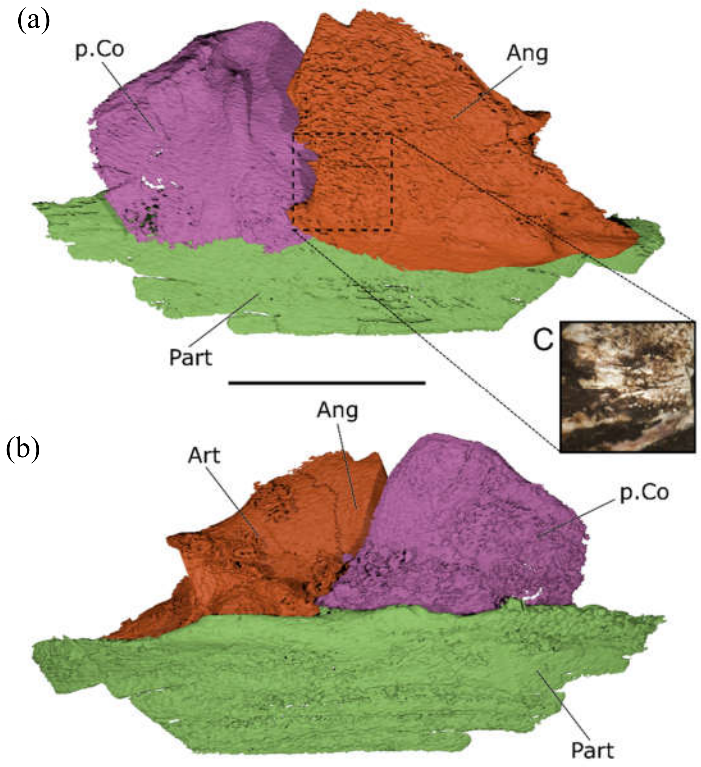
Caption: (a) – Lateral view, (b) – Mesial view, (c) – Schematic drawing showing the path of the lower jaw sensory canal line (red arrows) and the sensory canal pores. **Ang**: Angular; **Art**: Articular; **f.q.**: facet for articulation with quadrate. Scale bar = 5 mm.
Source: The author, 2019.

The articular is partially broken, but is visible in contact with the mesial surface of the angular (Figure 28), showing the facet for articulation with the quadrate. Differently from other species, the articular bone of MCT 1463-P is mostly composed of a thin bone layer, that is strongly associated to the angular.

The prearticular is missing both its anterior and posterior ends. It is considerably deeper than the angular and has a smooth surface on both sides. Anterodorsaly on its inner surface, there are series of disorganized and robust conical teeth. It bears a medial-dorsal process that join it to the angular bone. The ventral margin is thicker than the dorsal. There seems to have been a strong connection of the prearticular bone to the outer bones of the lower jaw.

The rectangular principal coronoid lies anterior to the angular, flanked on either side by the angular and prearticular (Figure 29). It bears a T-shaped process on its mediodorsal portion for the insertion of the adductor muscle. The prearticular appears relatively large in comparison to other bones of the jaw.

Figure 29 – Lower Jaw.



Caption: (a) – Digital model; (b) – Schematic drawing; (c) – detail of angular ornamentation. **Ang**: Angular; **m.s.c**: mandibular sensory canal; **Part**: Prearticular; **p.Co**: principal coronoid. Scale bar = 10 mm.
Source: The author, 2019.

- *Palate:*

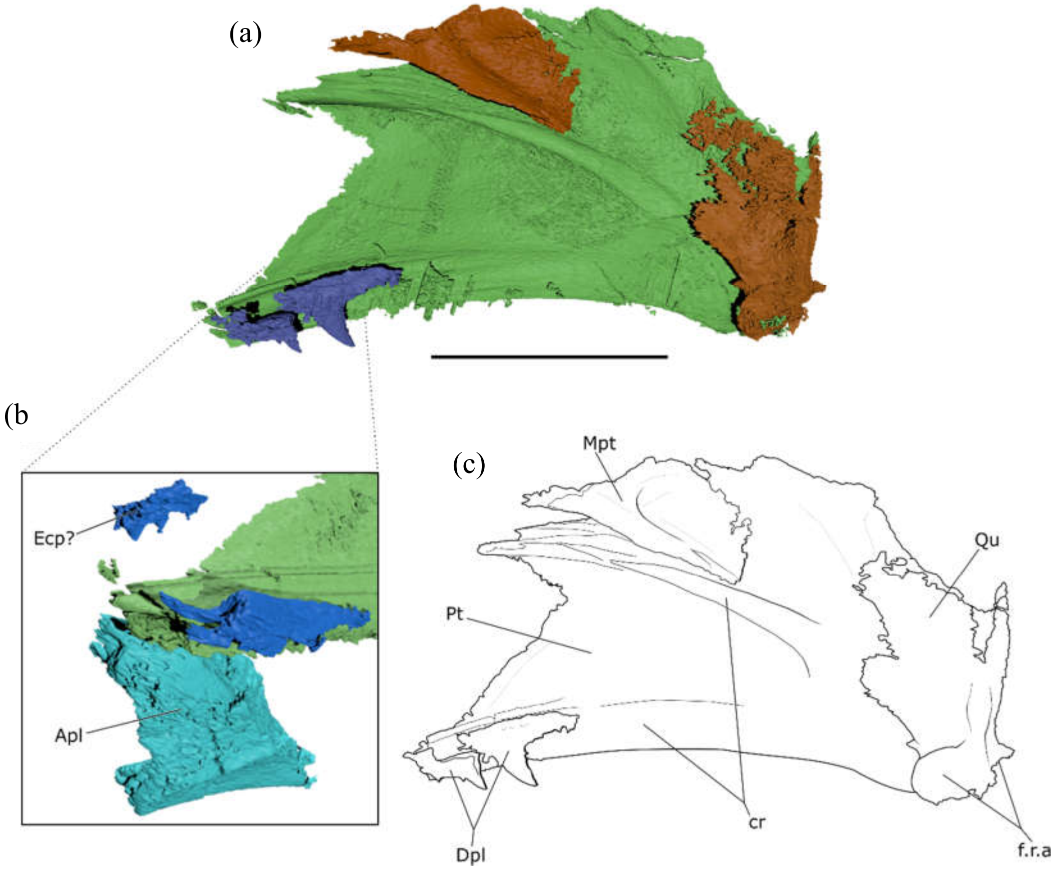
The palate is intact and well preserved (Figure 30). The triangular pterygoid bears prominent lateral ridges that extend from the posteroventral edge towards the anterior margin. Its anterior margin is incomplete. Posteroventrally it contacts the quadrate and dorsally the metapterygoid.

The quadrate is large, covering a considerable portion of the pterygoid posteriorly. The bone becomes thicker ventrally, towards the condyles for articulation with the lower jaw. It is interesting to notice that the quadrate articular facet, that would contact the articular and retroarticular, is considerably posteriorly directed. The quadrate is big and covers part of the posterior region of the pterygoid. Also, the posterodorsal border extends posteriorly beyond the margin of the pterygoid.

The metapterygoid is poorly preserved. It is only noticeable that it was attached to the anterodorsal border of the pterygoid, just above the dorsalmost ridge. It bears a delicate process for articulation with the pterygoid.

Anteroventral to the pterygoid, there are several dermal bone remains. Two dermopalatines bear prominent fangs. Some other fragments associated with the dermopalatines could be represent the ectopterygoid and parts of the coronoids of the lower jaw (Figure 30b). Also alongside the anteroventral margin of the pterygoid, there is a robust bone, apparently partially ossified, that could be interpreted as the autopalatine. If so, it would contact the ethmoid region of the braincase anteriorly.

Figure 30 – Palate.

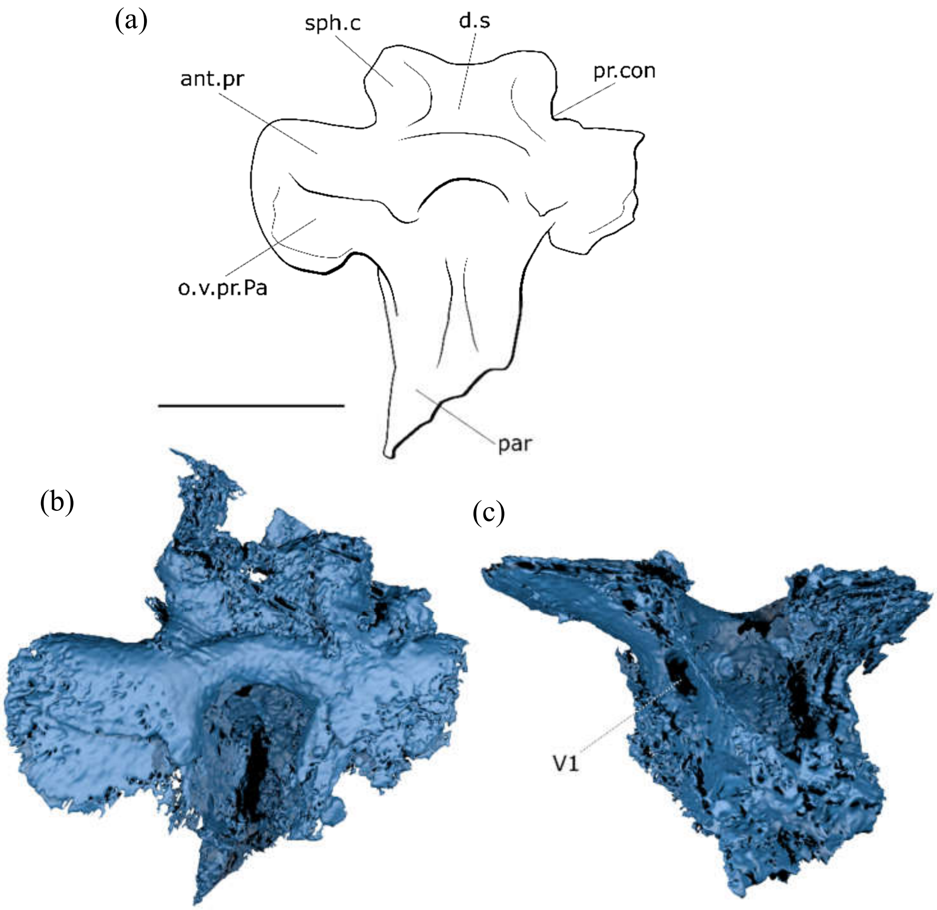


Caption: A: Digital model; B: Detail of the anterior portion in mesio-ventral view; C: Schematic drawing. **Apl**: Autopalatine; **cr**: cristae; **Dpl**: Dermopalatine; **Ecp**: Ectopterygoid; **f.r.a**: fossa for retroarticular articulation; **Mpt**: Metapterygoid; **Pt**: Pterygoid; **Qu**: Quadrate. Scale bar = 10 mm.
Source: The author, 2019.

- *Neurocranium:*

The neurocranium is poorly preserved and represented only by an incomplete basisphenoid (Figure 31). It bears large antotic processes with rounded anterior margins that extend beyond the level of profundus foramina. The sphenotic condyles are small, rounded structures on both sides of the dorsum sellae. The dorsum sellae is deep and seems to have been deeper posteriorly (Figure 31a-b). The profundus foramina are clearly visible in the anterior view of the basisphenoid (Figure 31c), but are covered by the expansions of the antotic processes in dorsal view. Ventral to the basisphenoid body, there are evidences of what would probably be the posteriormost portion of the parasphenoid, but it is too poorly preserved to allow a precise identification.

Figure 31 – Basisphenoid.



Caption: Schematic drawing of the basisphenoid in dorsal (a - b) and mesial (c) views. **ant.pr**: antotic process; **d.s**: dorsum selae; **o.v.pr.Pa**: overlap surface for descending process of postparietal; **Par**: Parasphenoid; **pr.con**: processus connectens; **sph.c**: sphenotic condyle, **V1**: profundus foramen. Scale bar = 5 mm.
Source: The author, 2019.

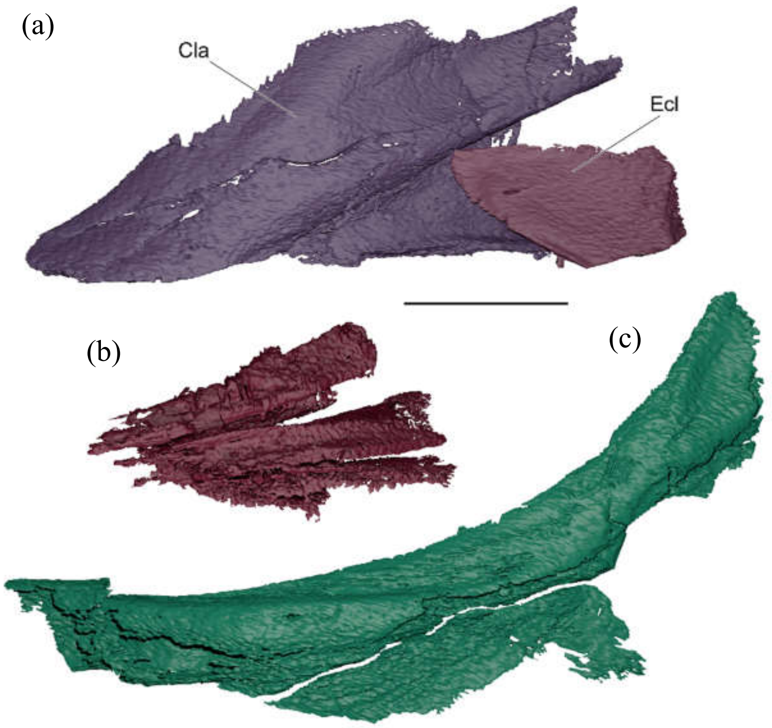
- *Shoulder Girdle:*

The clavicle is large and triangular in lateral view, with a thick dorsally oriented expansion and an articulation surface for the extracleithrum ventrally (Figure 32a). The extracleithrum is a small but robust bone (Figure 32a). It is triangular in lateral view, thickening anteriorly, with a straight lateral surface, without any sign of ornamentation.

- *Hyoid Arch:*

The branchial apparatus is poorly preserved but is noticeable between the palatal bones, where several ceratobranchial elements are visible (Figure 32b). The ceratohyal (Figure 32c) is flattened and fractured but it is identifiable for being hollow and bearing a thick proximal expansion, the lateral process. It shows little curvature posteriorly.

Figure 32 – Other elements of MCT 1463-P.

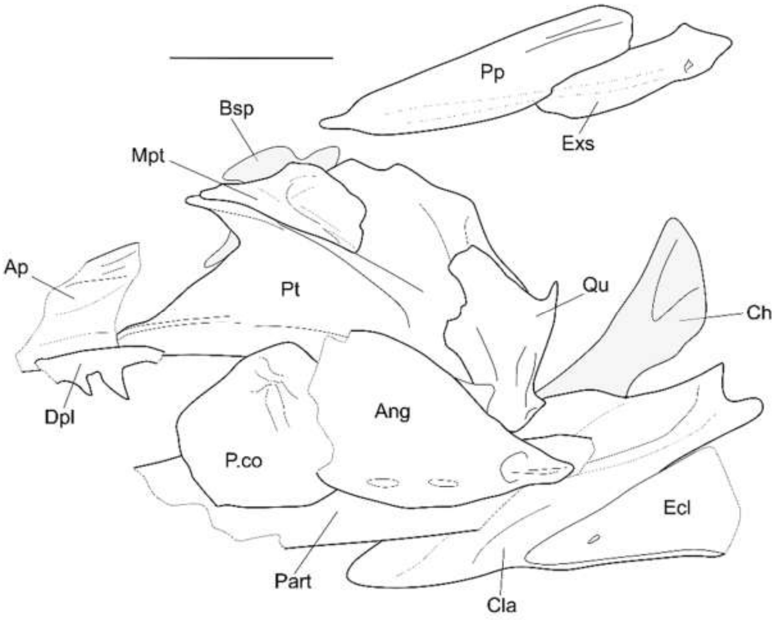


Caption: (a) – Shoulder girdle; (b) – Ceratobranchial fragments; (c) – Ceratohyal.
Cla: Clavicle, **Ecl**: Extracleithrum.
Source: The author, 2019.

2.4 Discussion

The coelacanth specimen from the Pedra de Fogo Formation (Figure 33) shows a mixture of characters that differentiate it from other Paleozoic taxa (e.g. *Spermatodus*, *Coelacanthus*, *Rhabdoderma*), and align it to Early Mesozoic taxa (e.g. *Dobrogeria*, *Wimania*, *Whiteia*). Unfortunately, the specimen preserved few diagnostic features and its phylogenetic position should be considered tentative.

Figure 33 – Interpretative drawing of the organization of the preserved bones of MCT 1463-P.



Caption: Scale bar = 10 mm. **Ang:** angular; **Ap:** autopalatine; **Bsp:** basisphenoid; **Ch:** ceratohyal; **Cla:** clavicle; **Dpl:** dermopalatines; **Exs:** extrascapular; **Mpt:** metapterygoid; **Pp:** postparietal; **Pt:** pterygoid; **Qu:** quadrate.
Source: The author, 2019.

Skull roof – Although the skull roof is an important feature for taxonomy and systematics of coelacanths (CLOUTIER, 1991; FOREY, 1998; ZHU et al., 2012), it shows considerable variation among them (see SCHAEFFER, 1952; FOREY, 1998).

In several coelacanth genus (e.g. *Diplocercides*, *Spermatodus*, *Diplurus*) the supratemporal ends at the same level of the postparietal (STENSIÖ, 1922; WESTOLL, 1939; SCHAEFFER, 1952; FOREY, 1998), but some others exhibit the apomorphic state, where these paired bone extend beyond the posterior margin of the postparietals, contacting the extrascapulars laterally (e.g. *Coelacanthus*, *Lybis*, *Latimeria*, *Mawsonia*, *Dobrogeria*; MOY-

THOMAS; WESTOLL, 1935; FOREY, 1998; CARVALHO; MAISEY, 2008; CAVIN; GRĂDINARU, 2014). *MCT 1463-P* bears the apomorphic condition, with the supratemporals extending far beyond the posterior margin of the postparietals. Due to the position of the sensory canals in both, postparietal and supratemporal, and the expanded ventral processes of these bones, the skull roof of MCT 1463-P most closely resembles that of *Dobrogeria*.

The ventral processes of the skull roof are also important diagnostic features. Most of the Devonian species lack these ventral processes (FOREY, 1998), indicating the primitive condition among coelacanths. Regarding MCT 1463-P, the presence of well-developed ventral processes on the postparietal and supratemporal closely resembles other late Paleozoic and early Mesozoic species (e.g. *Spermatodus*, *Whiteia*, *Dobrogeria*).

Lower Jaw – Mandibular morphology is conservative among coelacanths (Forey, 1998), but some interesting aspects are worth mentioning.

The ornamentation and sensory canal pores of the angular show pronounced variation in coelacanths. However, the patterns of variation between species are considerably unknown, with few indicatives of polarity. Most stem osteichthyans, early actinopterygians and sarcopterygians normally bear jaw bones with elongated tubercles or ridge ornamentation (FOREY, 1998). This indicates that the primitive condition for coelacanths would be the same, and the data on Devonian coelacanths agrees with this polarity hypothesis (STENSIO, 1922; CLOUTIER, 1996; FOREY, 1998; SZREK, 2007). The Carboniferous taxa *Rhabdoderma,* exhibit an ornamentation composed of closely spaced thin ridges (FOREY, 1981). Permian and Mesozoic taxa show considerable variation, but most taxa bear the putative apomorphic state, composed of turculate ornamentation (e.g. *Laugia*, *Spermatodus*, *Whiteia*; MOY-THOMAS, 1935; WESTOLL, 1939; FOREY, 1998). Other late Paleozoic and early Mesozoic species bear ornamentation formed by ridges (e.g. *Caridosuctor*, *Allenypterus*; LUND; LUND, 1984; FOREY, 1998), or lack ornamentation (e.g. *Coelacanthus*; MOY-THOMAS; WESTOLL, 1935; FOREY, 1998). This contrast with MCT 1463-P, where both ridges and tubercles are found, sparsely distributed ridges dorsally and small tubercles surrounding the sensory canal pores. Apparently, MCT 1463-P is the only coelacanth species that bear both ornaments.

The sensory canal pores can be small and numerous (*Laugia*, *Sassenia*, *Macropoma*, Rhabdoderma; FOREY, 1981; LAMBERS, 1996; FOREY, 1998), small but few (*Allenypterus*, *Axelrodichthys maiseyi*, *Caridosuctor*, *Ticinepomis*; LUND; LUND, 1984; FOREY, 1998; CARVALHO et al., 2013; CAVIN et al., 2013), large elongated (*Axelrodichthys araripensis, Coccoderma*, *Whiteia woodwardi*, *W. nielseni*; MOY-THOMAS, 1935; MAISEY, 1986;

FOREY, 1998), and large rounded (*Diplurus*, *Whiteia tuberculata*; SCHAEFFER, 1952; FOREY, 1998). The condition in MCT 1463-P is “large elongated” exhibiting a rectangular shape in lateral view, closely resembling the angular sensory canal pores of *Coccoderma*. However, there is considerable variation of the shape and number of these pores between species of the same genus. For example, as above mentioned, some species of *Whiteia* and *Axelrodichthys* exhibit large elongated pores while other bears rounded pores (see FOREY, 1998). Therefore, the shape and number of mandibular sensory canal pores is probably highly homoplastic and of limited use in reconstructing higher-level coelacanth relationships.

The shape of the principal coronoid appears to be uninformative for coelacanths, showing substantial variation in closely related species (see FOREY, 1998). Therefore, this ossification might be more useful for differentiating taxa rather than establishing coelacanth interrelationships. This assumption can be also true for the previously mentioned angular and the mandibular sensory canal pores.

The ornamentation of the bones of the lower jaw is commonly used as a taxonomically informative character in coelacanths (e.g. ECHOLS, 1963; FOREY et al., 2000; CLEMENT, 2005). The condition in MCT 1463-P differs from that of other coelacanth species, with two types of ornamentation (ridges, tubercles) present on its angular bone.

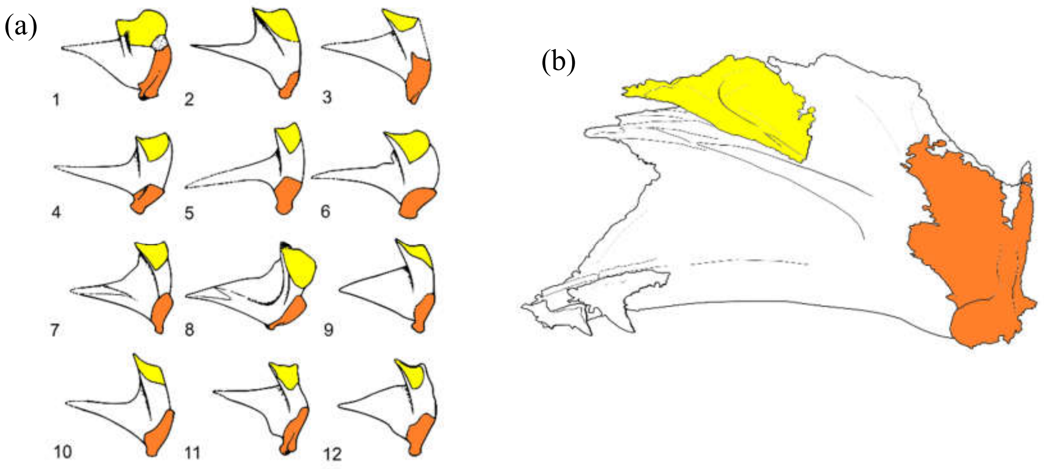
The prearticular bone is large among coelacanths, being the main component of the mesial surface of the lower jaw, bordering the meckelian. The prearticular commonly bears tiny villiform teeth sometimes forming a shagreen-like structure. However, due to the resolution of the CT-scan, it is impossible to ensure that this element lacked teeth, as the previously illustrated models show.

The surface of the prearticular that is directed to the meckelian and the outer dermal bones of the lower jaw is poorly described in the literature, probably because of its firm attachment to the angular. On MCT 1463-P, the surface of the prearticular bears a small process that contacts the inner surface of the angular bone. Although this character is poorly understood for other coelacanths, a similar structure is found in some species (e.g. *Axelrodichthys araripensis*, *Mawsonia gigas*), evidenced by the presence of a contact surface on the mesial surface of the angular (MAISEY, 1986 fig. 24C-D; FOREY, 1998 fig. 5.11A).

The other bones that compose the lower jaw of coelacanths are missing from the analyzed specimen. Therefore, the taxonomical and phylogenetic information regarding these elements is unknown for MCT 1463-P.

Palate – The large pterygoid occupies a significative portion of the entire fossil. However, the amount of relevant information on palatal bones is uncertain, and due to the low variation between species it is frequently just briefly described (Forey, 1998), but described in detail when in exceptional preservation or when there are few other preserved structures (e.g. SCHAEFFER, 1952; DUTEL et al., 2014). There seems to be significant variation between genera to assume that it has some diagnostic value (SCHAEFFER; GREGORY, 1961) (Figure 34), but the amount of missing data in several species turns difficult to understand possible synapomorphies regarding these ossifications.

Figure 34 – Comparison of coelacanth palate morphology.



Caption: Orange: quadrate; Yellow: metapterygoid. (a) – Coelacanth palates adapted from Schaeffer and Gregory (1961), 1: *Nesides schimidti*; 2: *Rhabdoderma elegans*; 3: *Coelacanthus granulatus*; 4: *Axelia robusta*; 5: *Mylacanthus lobatus*; 6: *Wimania sinuosa*; 7: *Whitea woodwardi*; 8: *Diplurus newarki*; 9: *Undina acutidens*; 10: *Coccoderma nudum*; 11: *Macropoma mantelli*; 12: *Latimeria chalumnae*. (b) – MCT 1463-P.
Source: The author, 2019.

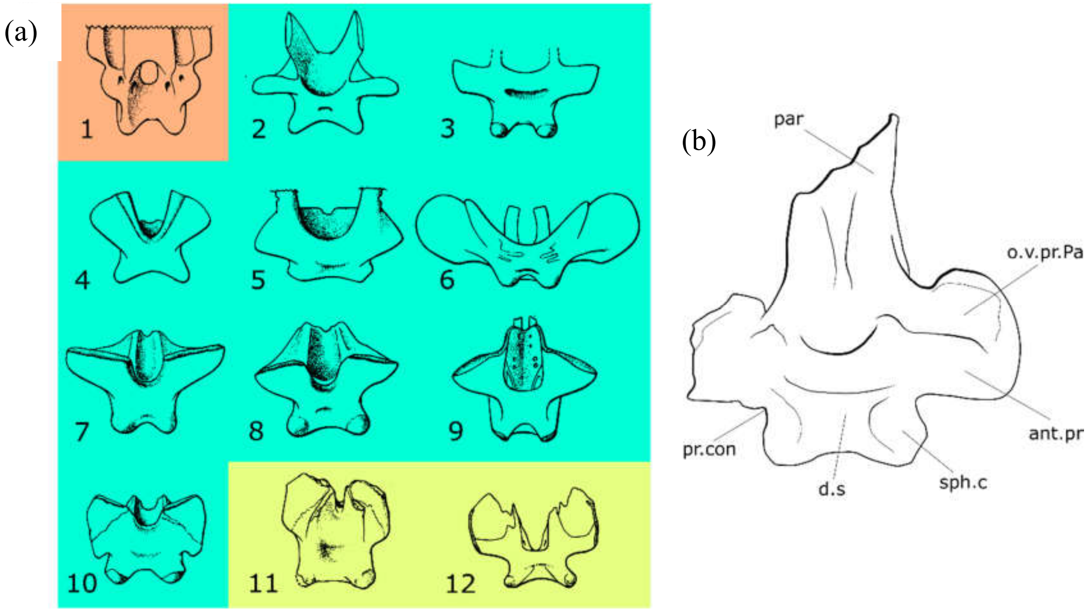
The quadrate joint is composed of double condyle that articulates anteriorly with the articular and posteriorly with the retroarticular (FOREY, 1998; DUTEL et al., 2013). On most coelacanths, these condyles are slightly anteriorly directed, but MCT 1463-P show a posterior orientation of this articulation, in relation to the pterygoid body. The glenoid portion of the lower jaw of MCT 1463-P is poorly preserved; therefore, it is impossible to ensure that the posterior orientation of the quadrate condyles in this species is indeed related to its anatomy or if taphonomical processes caused it. However, if this condition is true, it might have lead to an increase in the angle of the jaw opening.

Dermopalatine fangs are uncommon among coelacanths, and are present in Mesozoic and Recent taxa such as *Macropoma* and *Latimeria* (LAMBERS, 1996; FOREY, 1998; DUTEL et al., 2013). Moy-Thomas (1937) illustrated large dermopalatine fangs for *Rhabdoderma elegans*, but these were not mentioned in Forey's (1981) redscription. As noted by Forey (1998), the dermopalatines are weakly associated with the palate, and therefore are often missing from fossil specimens.

The ectoperygoid of coelacanths is also know to bear teeth, and bone fragments bearing small conical teeth are probably displaced fragments of the ectopterygoids. The ectopterygoid dentition is variable among coelacanth species, from large and numerous teeth as in *Swenzia* to small and few teeth as in *Coelacanthus* (MOY-THOMAS; WESTOLL, 1935; CLEMENT, 2005).

Neurocranium – The basisphenoid is commonly used for comparison of coelacanths (SCHAEFFER; GREGORY, 1961; DEESRI et al., 2018), and has clear diagnostic value. Variations among coelacanth basisphenoids include but are not restricted to: the shape of the antotic processes, the thickness of the corpus, and the shape and extension of the lateral lamina. Three morphotypes were distinguished by Schaeffer and Gregory (1961) based on these characteristics (Figure 35a). The first morphotype (Figure 35a$_{1}$) includes coelacanths where the basisphenoid is part of the highly ossified moiety of the braincase, a dorsum sellae is not differentiated, and the canals for the profundus and the superficial ophthalmic nerves are closely associated. The second morphotype (Figure 35a$_{2\text{-}10}$) includes several Paleozoic and Mesozoic species that share mostly triangular antotic processes and the shape of the pleurosphenoid ossification (bar-like or plate-like). The third morphotype (Figure 35a$_{11\text{-}12}$) includes species with nearly rectangular antotic processes, with an extensive overlap area for the pleurosphenoid. Considering these morphotypes, MCT 1463-P closely resembles the species from the third morphotype, especially because of a large overlapping area for the pleurosphenoid.

Figure 35 – Comparison of coelacanth basisphenoids in dorsal view.



Caption: (a) – Coelacanth basisphenoids adapted from Schaeffer and Gregory (1961): 1, *Nesides schmidti*; 2, *Rhabdoderma elegans*; 3, *Coelacanthus granulatus*; 4, *Wimania sinuosa*; 5, *Axelia robusta*; 6, *Diplurus newarki*; 7, *Coccoderma suevicum*; 8, *Undina cirinensis*; 9, *Macropoma praecursor*; 10, *Spermatodus pustulosus*; 11, *Moenkopia wellesi*; 12, *Latimeria chalumnae*. (b) – MCT 1463-P (captions are listed in figure 6A). Colors represent morphotypes of Schaeffer and Gregory (1961): Blue = M. one; Green = M. two and Yellow = M. three.

Source: The author, 2019.

Although the basisphenoid morphotypes of Schaeffer and Gregory (1961) are easily recognizable, there seems to be no relation between these morphotypes and coelacanth clades recovered in phylogenies, even though the first morphotype appears to be exclusive of Middle Paleozoic species (e.g. *Diplocercides*). The phylogenetic information regarding the basisphenoid is therefore more relevant when dealt as separate characters, as in most recent studies (e.g. CAVIN et al., 2017).

Hyoid and Branchial elements – These structures are too poorly preserved to allow any phylogenetic inference for MCT 1463-P. However the ceratobranchials of coelacanths sometimes bear small tooth plates as in *Rhabdoderma*, *Undina*, *Axelrodichthys* (FOREY, 1981; 1998; FOREY et al., 1985). Tooth plates are also present in the Upper Triassic mawsoniid recently described by Deesri et al. (2018). These elements seem to be smooth on MCT 1463-P, however, due to the CT-scan resolution, it is impossible to ensure that there were no tooth plates. Therefore, no phylogenetic inference can be done regarding these structures.

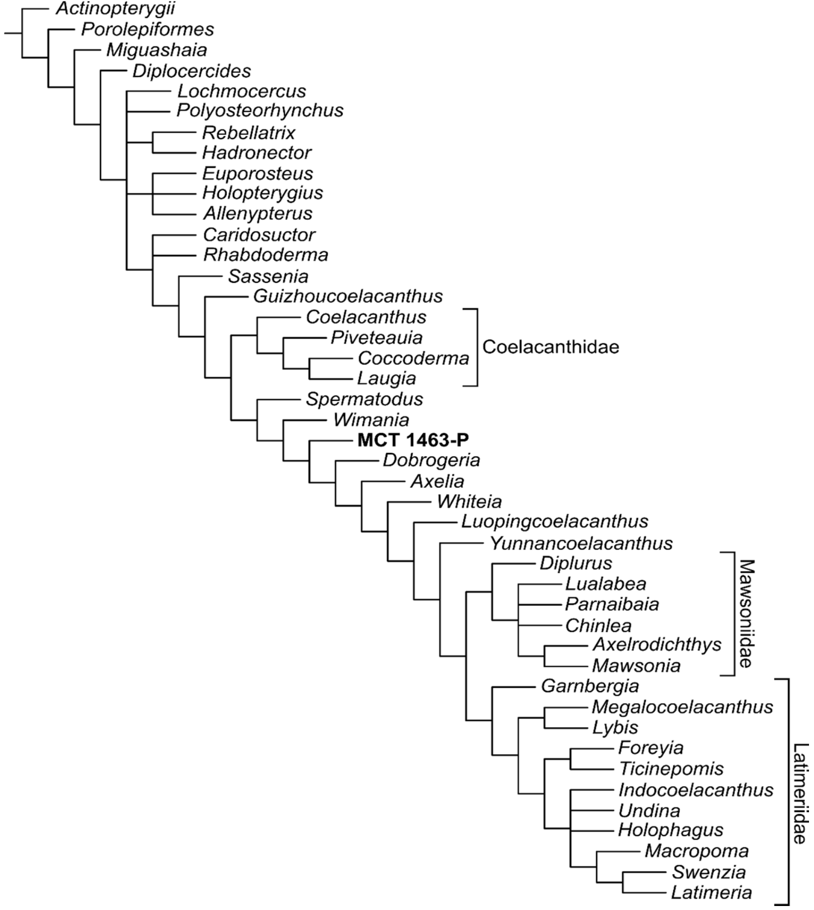
Shoulder girdle and postcranium – There are few elements of the shoulder girdle and apparently no evidence of postcranial elements in MCT 1463-P. The presence of an extracleithrum is considered a coelacanth synapomorphy (FOREY, 1998; FRIEDMAN;

COATES, 2006; ARRATIA; SCHULTZE, 2015). The clearest element is the large clavicle that differs meaningly from other coelacanths, due to the large proportion in relation to other skull elements. The clavicles are normally slender in taxa crownward of *Miguashaia* (CLOUTIER, 1996; FOREY et al., 2000; FRIEDMAN; COATES, 2006), and therefore the presence of a large clavicle in a Permian coelacanth is unusual. The only other preserved element of the shoulder girdle of MCT 1463-P is the robust extracleithrum that closely resembles early taxa such as *Miguashaia* (see FOREY et al., 2000 fig. 5).

2.4.1 Phylogenetic position

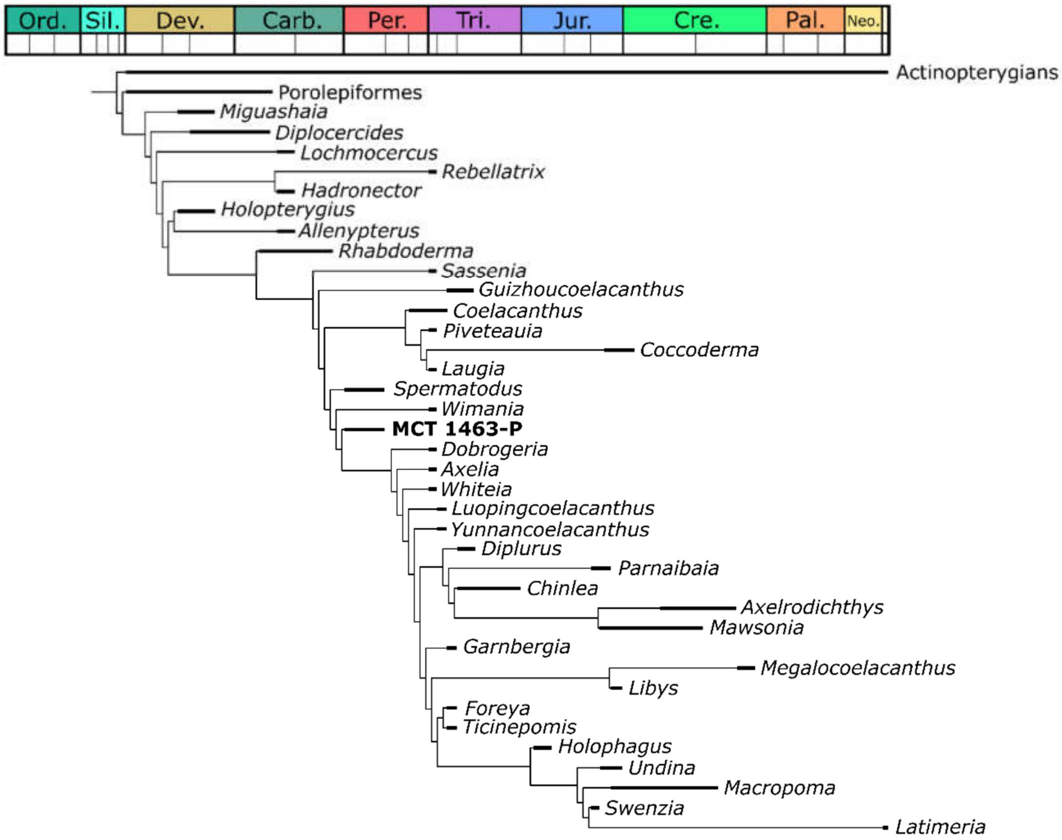
The analysis yielded four equally parsimonious trees, and the strict consensus is shown in figure 36. To deal with problematic taxa, or taxa with few diagnostic features, we performed the agreement subtree of the four most parsimonious trees. The resulting tree includes 39 taxa (Figure 36) and resolved polytomies of the strict consensus.

Figure 36 - Strict consensus of the four most parsimonious trees using the New Technology Algorithm of TNT.



Caption: Tree length: 335 steps; consistency index: 0.37; retention index: 0.66.
Source: The author, 2019.

Figure 37 - Agreement subtree (39 taxa) of the coelacanth strict consensus (including four new characters) using New Technology Search on TNT, calibrated with timescale.



Source: The author, 2019.

The analysis including the three new characters recovered MCT 1463-P as a crown coelacanth, crownward of *Spermatodus* and *Wimania* (Figures 36, 37). The node including MCT 1463-P and all crownward taxa is supported by only one synapomorphy (13 [0-1]) (i.e. presence of a descending process on the postparietal). However, this clade shows a reversal of this character in *Whitea* (13 [1-0]), and a possible convergence in *Piveteauia* (13 [0-1]). The only autapomorphy of MCT 1463-P was the presence of ridge and tubercle ornamentation on the lower jaw bones (62 [1-2]). However, the detailed description indicates that the presence of a posterodorsal expansion of the quadrate margin might be unique among coelacanths, therefore a another putative autapomorphy of MCT 1463-P.

The Mesozoic coelacanth families (Mawsoniidae and Latimeriidae) were recovered in our analysis (Fig. 10), with a similar topology to most recent studies (e.g. WEN et al., 2013; DUTEL et al., 2015; CAVIN et al., 2017).

Mawsoniidae is supported by the absence of supratemporal descending process (14 [1-0]), coronoid opposite to the posterior end of the dentary (56 [1-0]), and presence of ossified ribs (92 [0-1]). The first character is almost exclusive of Mawsoniidae, being shared only with the stem *Diplocercides*. The coronoid character is more plastic, being shared with most stem lineages (*Diplocercides*, *Lochmocercus*, *Polyosteorhynchus* and *Holopterygius*) and *Laugia*. The only exclusive character of mawsoniids is the presence of ossified ribs.

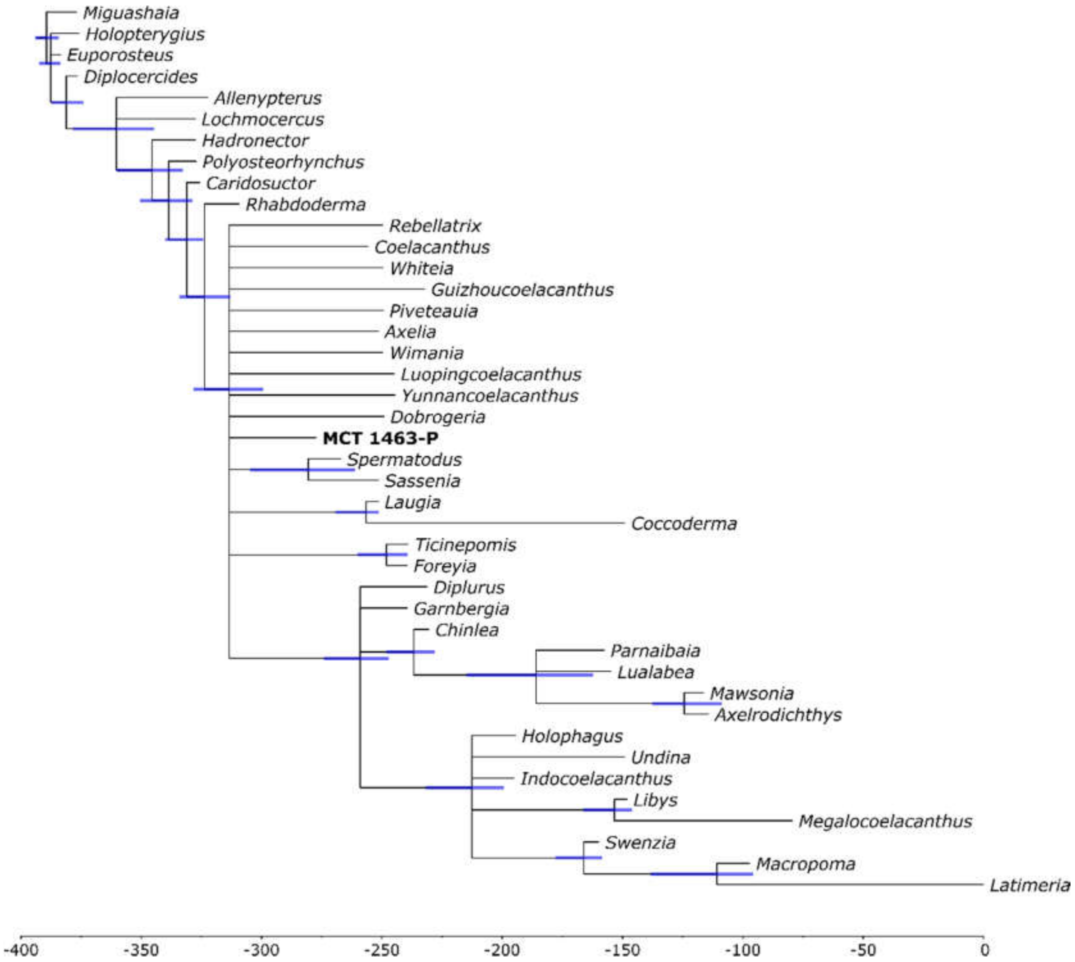
Latimeriidae is supported by the absence of differentiation in scale ornamentation (104 [1-0]) and the supratemporals extending beyond posterior margin of postparietals (113 [0-1]). This last character is also present in taxa crownward of *Rhabdoderma*; however, it would have been lost in Latimerioidei and reverted in Latimeriidae to the apomorphic state. Also, the apomorphic state is found in crown mawsoniids (e.g. *Mawsonia* and *Axelrodichthys*). Therefore, a more detailed investigation of this character is needed to identify more robust phylogenetic patterns.

The family Coelacanthidae was recovered, but also including the previously recognized family Laugidae. Cloutier (1991) had already mentioned the relationships between *Coelacanthus* and *Laugia*, supported by the reduction of the premaxilla dorsal lamina, parietal bigger than most-posterior postparietals, triangular squamosal, and the jugal canal running along the ventral margin of the squamosal. However, the node Coelacanthidae included *Coelacanthus*, *Laugia* and all crownward taxa included in Cloutier's analysis. Herein, this family is supported by the absence of the dorsal lamina of the premaxilla and the asymmetrical caudal lobes. The first character (5 [0-1]) is also uniting Latimerioidei taxa, and might be a crown coelacanth synapomorphy, but it was herein obtained as independent acquisition in Coelacanthidae and Latimeirioidei. The second character (97 [0-1]) is present in other Paleozoic species (i.e. *Polyosteorhynchus*, *Holopterygius*, *Allenypterus*, *Caridosuctor*).

2.4.2 Bayesian analysis

The Bayesian analysis topology was considerably different from the parsimony analysis, and several relations were not resolved (Figure 37). *Miguashaia* was recovered as the sister group to all remaining coelacanths, starting with *Holopterygius* and *Euporosteus*. Most of the Paleozoic coelacanths where recovered within polytomies, with *Lochmocercus* and other mid-Paleozoic species crownward of *Diplocercides*. The Permian and Mesozoic species were recovered within a big polytomy including MCT 1463-P, and four distinct clades were obtained (*Spermatodus* + *Sassenia*), (*Laugia* + *Coccoderma*), (*Ticinepomis* + *Foreyia*) and (Latimerioidei).

Figure 37 - Result of the Bayesian analysis with fossil tip-dating dates of divergence.



Caption: Node Bars represent the deviation of age estimation of the respective nodes. Branch length represents number of character acquisition/modifications. Scale bar in million years.

Source: The author, 2019.

The main difference from the parsimony analysis is on the sister relationship of *Spermatodus* + *Sassenia*, and *Macropoma* + *Latimeria*. The first clade is not supported by the unique acquisition of any character, but by the independent acquisition of two characters shared with other groups (i.e. 23 [0-2] (prob = 0.89) supraorbital sensory canal opening through many tiny pores; 34 [0-1] (prob = 0.94) squamosal extending behind postorbital to reach the skull roof). The clade uniting *Macropoma* and *Latimeria* is supported by one synapomorphy (51 [0-1] (prob = 0.68) absence of contact between the lachrymojugal and the preorbital or tectal-supraorbital series).

The polytomy containing Permian and crownward taxa is supported by 3 unambiguous synapomorphies (i.e. 5 [0-1] (prob = 0.98) fragmented premaxilla; 6 [0-1] (prob = 0.86) anterior opening of rostral organ within separated rostral ossicles; 111 [1-2] (prob = 0.73) dorsally directed pterygoid cristae). Two other synapomorphies are shared with other taxa with independent acquisition (i.e. 21 [0-1] (prob = 0.99) otic canal in supratemporal; 48 [0-1] (prob = 0.99) pit lines failing to mark cheek bones). Character 21 [0-1] is shared with *Polyosteorhynchus* and *Lochmocercus* while character 48 [0-1] is shared with *Allenypterus*.

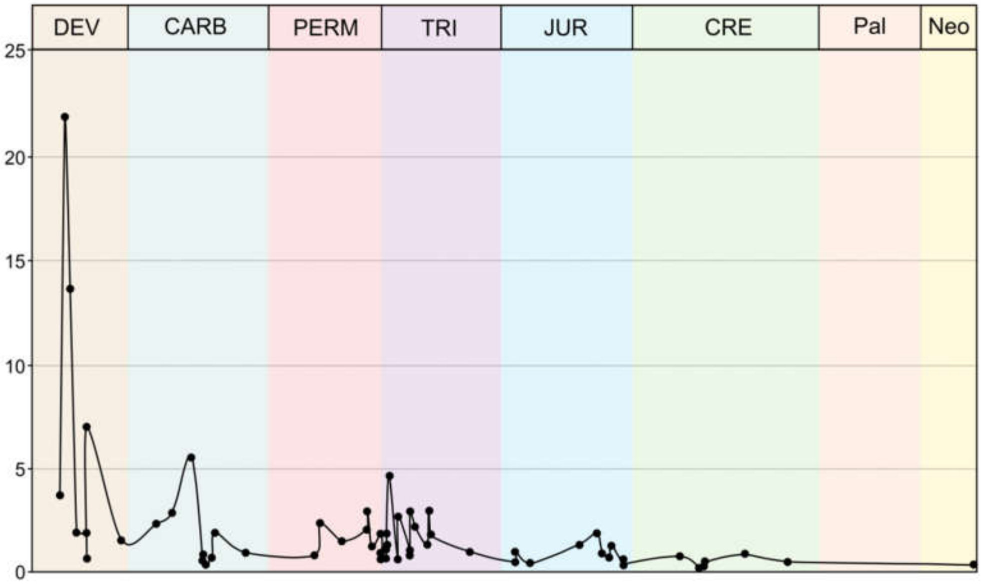
Latimerioidei is supported by three unambiguous synapomorphies (i.e. 9 [0-1] (prob = 0.6) more than 10 supraorbitals/tectals; 76 [0-1] (prob = 0.99) presence of supraoccipital; and 92 [0-1] (prob = 0.68) presence of ossified ribs). This last character (92) is considered as a mawsoniid synapomorphy (e.g. SCHULTZE, 1993; FOREY, 1998), but since the family Mawsoniidae on our analysis does not include *Diplurus* (as in Wendruff and Wilson (2012), where *Diplurus* is sister taxon to *Libys* and this clade is sister group of Latimeriidae into Latimerioidei). *Diplurus* was herein recovered within the Latimerioidei polytomy, and the likelihood algorithm optimized it as a Latimerioidei character present on the recovered Mawsoniidae and *Diplurus* separately.

Other three characters were optimized as Latimerioidei synapomorphies but are present in other taxa: 27 [0-1] (prob = 0.5) unornamented parietals and postparietals, also present in *Coelacanthus*; 35 [0-1] (prob = 0.99) lachrymojugal expanded anteriorly, also present on *Yunnancoelacanthus* and *Dobrogeria*; and 52 [1-0] (prob = 0.99) absence of sclerotic ossicles, which is shared with *Ticinepomis* + *Foreyia*.

The divergence age estimation indicate that Actinistia would have emerged during the Early Devonian, which agrees with the oldest known coelacanth fossils (FRIEDMAN, 2007). The Latimerioidei emerged during the Permo-Triassic boundary, around 250 million years ago, and its families, Latimeriidae and Mawsoniidae, diverged almost at the same time, around the Triassic-Jurassic boundary (Fig. 12). This might indicate that the great faunal collapse during the Permian extinction, and the following recovery during the Triassic, could have favored the emergence of several coelacanth lineages.

The rate calculation indicates high evolutionary rates (i.e. acquisition of new characters along the branches) during the early history of coelacanths within the early-middle Devonian (Figure 39). After the Devonian the rate stabilizes, remaining considerably low, with two major diversification events during the mid-Carboniferous and the Permo-Triassic bondary. This is consistent with other rate estimation for large and early diverged groups of vertebrates with living representants (e.g. dipnoan fishes; LLOYD et al., 2011). This is consistent with the “push to the past” effect of lineage evolution across time, where clades that survived a substantial timespan are likely to have experienced high rates of morphological evolution early on their history (BUDD; MANN, 2018).

Figure 39 – Evolutionary rate estimation for coelacanth fishes based on the Bayesian analysis results. Evolutionary rates of nodes and tips of the consensus tree plotted against the stratigraphic timescale.



Source: The author, 2019.

2.5 Conclusions

MCT 1463-P is the first three-dimensional and partially articulated coelacanth from the Paleozoic of Brazil to be described in detail. It is distinguished as a new taxon on the basis of the presence of a posterodorsal expansion of the quadrate, posteriorly oriented facets for quadrate articulation, highly associated articular and prearticular, and presence of a articulation process of the metapterygoid to attach to the pterygoid surface. Phylogenetic analysis recovered it the most crownward Paleozoic coelacanth (Fig. 11).

Our parsimony analysis recovered a relationship between *Coelacanthus* to laugiids (*Ticinepomis*, *Laugia* and *Coccoderma*), differing from most phylogenetic analyses where *Coelacanthus* is recovered as part of the paraphyletic lineage including most late Paleozoic and early Mesozoic taxa.

By adding new morphological characters to the phylogenetic analysis of coelacanths, we obtained the common relationships between mawsoniids and latimeriids. However, one of the new analyzed characters (supratemporals extending beyond the posterior margin of postparietals) might have brought light to a new synapomorphy for latimeriids, emerged from a character reversal of the latimerioidei plesiomorphic state, which in turns is a reversal from the apomorphic late Paleozoic condition.

The evolutionary rate estimation is in agreement with previous work that states that long-living lineages are expected to have high diversification rates early on their evolutionary history, followed by lower and more stable rates towards recent times. However, the analysis show two minor diversification events within the Carboniferous and the Permo-Triassic boundary that deserve more detailed studies.

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3 GENERAL CONCLUSIONS

The Pedra de Fogo Formation show a considerable potential for paleontological studies regarding fish diversity and evolutionary patterns. Although articulated specimens are considerably rare for this formation, the presence of three-dimensional fossils and the considerable high contrast between the bone and matrix densities allow detailed studies of osteichthyan anatomy. However, superficial description of these remains do not support robust phylogenetic analysis, and therefore virtual visualization processes as μ-CT should be the key for gathering possible diagnostical characters for these remains.

Although both *Brazilichthys* and the new coelacanth are substantially incomplete, and lack important diagnostic features several important characters are preserved, which allowed the phylogenetic analysis presented herein. Both show a considerable mixture of derived and primitive traits for Permian taxa, indicating that important evolutionary inovations might have taken place in poorly studied localities within western Gondwana. Thus, reinforcing the need of detailed anatomical studies with an evolutionary background of several South American Paleozoic taxa that when incorporated will provide substantial framework for macroevolutionary studies.

APPENDIX A - Character list Giles et al. 2017

1 – Large dermal plates

0 = absent

1 = presente

2 – Sensory lines

0 = present as open grooves

1 = pass through canals

3 – Premaxillae as distinct ossification

0 = present

1 = absent

4 – Premaxillae, contact at midline

0 = present

1 = absent

5 – Premaxillae fused at midline

0 = absent

1 = present

6 – Premaxillae

0 = reaches or extends past anterior margin of the orbit

1 = confined to region anterior to orbit

7 – Premaxillae contributes to orbital margin

0 = absent

1 = present

8 – Teeth on premaxillae

0 = present

1 = absent

9 – Mobile premaxillae

0 = absent

1 = present

10 – Olfactory nerve pierces premaxillae

0 = absent

1 = present

11 – Nasal process of premaxillae

0 = absent

1 = short

2 = long (reaches skull roof)

12 – Sensory canal on premaxillae

0 = present

1 = absent

13 – Postrostrals (element(s) immediately anterior to frontals but not in contact with premaxillae)

0 = present

1 = absent

14 – Single median dermal bone capping snout

0 = absent

1 = present

15 – Median rostral

0 = plate-like

1 = tube-like

16 – Pores for rostral organ

0 = present

1 = absent

17 - Nasal bone as single consolidated ossification (i.e. bone(s) carrying supraorbital canal between premaxilla and anterior margin of frontals)

0 = absent

1 = present

18 – Contact of nasals on midline

0 = separated by dermal bones

1 = contacted or separated by gap unfilled by bone

19 - Nasal contributes to orbital margin

0 = absent

1 = present

20 - Mesial margin of (anterior) nasal

0 = not notched

1 = notched

21 - Posterior nostril in complete communication with orbital fenestra

0 = absent

1 = present

22 - Posterior nostril - contribution to margin by premaxillae

0 = absent

1 = present

23 - Tectals (sensu Cloutier & Ahlberg 1996, not counting the posterior tectal of Jarvik)

0 = absent

1 = present

24 – Dermal intracranial joint

0 = absent

1 = present

25 - Pineal foramen

0 = present

1 = absent

26 - Pineal eminence

0 = absent

1 = present

27 - Shape of parietals (sarcopterygian postparietals)

0 = rectangular, with long axis parallel to midline

1 = quadrate

28 - Relative lengths of frontals and parietals (sarcopterygian parietals and postparietals)

0 = frontal shorter than parietal

1 = frontal approximately equal to parietal

2 = frontal longer than parietal

29 - Frontals broad posteriorly and tapering anteriorly

0 = absent

1 = present

30 - Anterior pit line

0 = absent

1 = present

31 - Otic canal extends through parietals

0 =absent

1 = present

32 - Junction between supraorbital and infraorbital canals

0 = absent

1 = present

33 - Anterior branch of infraorbital sensory canal

0 = absent

1 = present

34 - Tabular

0 = present

1 = absent

35 - Tabular pit line

0 = absent

1 = present

36 - Number of bones carrying otic portion of lateral line canal between dermosphenotic and posterior edge of skull roof

0 = at least two (i.e. intertemporal and supratemporal)

1 = one (i.e. dermopterotic)

37 - Intertemporal - relative length

0 = shorter than supratemporal

1 = of similar length of supratemporal

2 = longer than supratemporal

38 - Intertemporal - contact with supratemporal anterior to that between frontal and parietal

0 = absent

1 = present

39 - Intertemporal contacts nasal

0 = absent

1 = present

40 - Supratemporal - narrow anterolateral flange forming ventral margin of spiracular opening

0 = absent

1 = present

41 - Parietal fused to dermopterotic

0 = absent

1 = present

42 - Bone carrying otic portion of lateral line canal extends past posterior margin of parietals

0 = absent
1 = present

43 - Number of paired extrascapulars

0 = one pair
1 = two pairs
2 = three or more pairs

44 - Extrascapular reaches lateral edge of skull roof

0 = absent
1 = present

45 - Single median extrascapular

0 = present
1 = absent

46 - Extrascapulae contact each other at midline

0 = absent
1 = present

47 - Medially-directed branch of sensory canal in extrascapulae

0 = present
1 = absent

48 - Extratemporal

0 = absent
1 = present

49 - Antorbital bone

0 = absent
1 = present

50 - Tube-like canal bearing anterior arm of antorbital

0 = absent
1 = present

51 - Infraorbitals

0 = one
1 = two
2 = more than two

52 - Anterior expansion of lacrimal

0 = absent

1 = present

53 - Notch in anterior margin of jugal

0 = absent

1 = present

54 - Suborbitals (non-canal bearing ossifications separating jugal and maxilla)

0 = absent

1 = one

2 = two

3 = three or more

55 - Multiple rami of infraorbital canal in jugal

0 = absent

1 = present

56 - Dermosphenotic with distinct posterior ramus

0 = absent

1 = present

57 - Dermosphenotic- contact with frontals blocked by intertemporal or dermopterotic

0 = absent

1 = present

58 - Supraorbital

0 = absent

1 = one or two

2 = three or more

59 - Anterior-most infraorbital anterior to orbit (i.e. does not contribute to orbital margin)

0 = absent

1 = present

60 - Three or more lachrymals

0 = absent

1 = present

61 - Circumorbital ring

0 = supraorbitals do not contact infraorbitals at the anterior rim of the orbit

1 = supraorbitals contact infraorbitals, closing the orbit

62 - Jugal canal

0 = absent

1 = present

63 - Dermohyal

0 = absent

1 = present

64 – Head of dermohyal projects above dorsal margin of operculum

0 = absent

1 = present

65 - Dermohyal

0 = fused to hyomandibular

1 = separate from hyomandibular

66 - Complete enclosure of spiracle by bones bearing otic and infraorbital canals

0 = absent

1 = present

67 - Maxilla

0 = absent

1 = present

68 - Expanded dorsal lamina of maxilla

0 = absent

1 = present

69 - Contribution by maxilla to posterior margin of cheek

0 = absent

1 = present

70 - Sensory canal/pit line associated with maxilla

0 = absent

1 = present

71 - Teeth on maxilla

0 = present

1 = absent

72 - Mobile maxilla in cheek

0 = absent

1 = present

73 - Peg-like anterior process of maxilla

0 = absent

1 = present

74 - Posterior maxillary notch

0 = absent

1 = present

75 - Supramaxilla

0 = absent

1 = one

2 = two

76 - Course of mandibular canal

0 = traces ventral margin of jaw along entire length

1 = arches dorsally in anterior half of jaw

77 - Mandibular canal reaches anterior margin of mandible

0 = present

1 = absent

78 - Mandibular canal

0 = primarily carried by infradentaries

1 = primarily carried by dentary

79 - Relative length of dentary

0 = long (constitute most of the length of the lower jaw)

1 = short (constitute less than half of lower jaw)

80 - Teeth on dentary

0 = present

1 = absent

81 - Dentary with conspicuously reflexed distal tip

0 = absent

1 = present

82 - Enlarged series of parasymphysial teeth on dentary

0 = absent

1 = present

83 - Facet for parasymphysial tooth-whorl on anterior dentary

1 = present

0 = absent

84 - Teeth of outer dental arcade

0 = several rows of disorganized teeth

1 = two rows, with large teeth lingually and small teeth labially
2 = single row of teeth

85 - Jaw margins overlain by lateral lamina

0 = absent
1 = present

86 - Acrodin caps on teeth

0 = absent
1 = present

87 - Plicidentine

0 = absent
1 = present

88 - Ossification of mentomeckelian region

0 = present
1 = absent

89 - Number of infradentaries

0 = more than two
1 = two (angular and surangular)
2 = one (angular only)

90 - Coronoids (sensu stricto, excluding parasymphysial tooth whorl or anterior coronoid)

0 = present
1 = absent

91 – Number of coronoids

0 = five
1 = four
2 = three
3 = two
4 = one

92 - Posterior coronoid

0 = morphologically similar to anterior coronoids
1 = expanded

93 - Coronoid process of lower jaw

0 = absent
1 = present

94 - Coronoid process contributed to by

0 = prearticular only
1 = surangular only
2 = dentary plus postdentary bones
3 = angular only

95 - Leptolepid notch

0 = absent
1 = present

96 - Symplectic involvement in jaw joint

0 = absent
1 = present

97 - Retroarticular process

0 = present
1 = absent

98 - Palatal bite

0 = absent
1 = present

99 - Palatal articulation with basipterygoid process

0 = articulation not obvious
1 = via basipterygoid fenestra
2 = via metapterygoid process/notch

100 - Palatoquadrate ossifications

0 = comineralized
1 = separate ossification centers

101 - Lateral process of ectopterygoid

0 = absent
1 = present

102 - Palatoquadrate symphysis

0 = absent
1 = present

103 - Dorsal margin of palate

0 = high posterior extension
1 = flat dorsal margin

104 - Metapterygoid posterior to quadrate

0 = absent
1 = present

105 - Number of dermopalatines

0 = multiple
1 = single

106 – Prearticular

0 = present
1 = absent

107 - Vomers

0 = paired
1 = single

108 - Vomer sutured to parasphenoid

0 = absent
1 = present

109 - Accessory operculum

0 = absent
1 = present

110 - Operculum - relative size

0 = at least twice as high as suboperculum
1 = subequal
2 = smaller than suboperculum

111 – Subopercle

0 = present
1 = absent

112 - Anterodorsal process of suboperculum

0 = absent
1 = present

113 - Anteroventral process of suboperculum

0 = absent
1 = present

114 - Number of cheek bones bearing pre-opercular canal posterior to jugal

0 = one
1 = multiple
2 = series of small ossicles

115 - Preoperculum orientation

0 = prounounced dorsal limb

1= vertical

2 = pronounced ventral limb

116 - Junction between preopercular and more anterior cheek bones

0 = Infraorbitals (including jugal) or suborbitals suture with or abut preopercular

1 = Infraorbitals (including jugals) and suborbitals broadly overlap preopercular

117 - Posterior border of preopeculum notched ventrally

0 = absent

1 = present

118 - Interopercle

0 = absent

1 = present

119 - Branchiostegal rays - dorsal-most in series

0 = of similar depth to adjacent branchiostegal ray

1 = deeper than adjacent branchiostegal ray

120 - Lateral gulars

0 = present

1 = absent

121 - Lateral gulars

0 = extending most of the length of the lower jaw

1 = restricted to the anterior third of the lower jaw (no longer than the width of three branchiostegals)

122 - Median gular

0 = absent

1 = present

123 - Relative length of median gular

0 = much shorter than jaw length

1 = more than half of jaw length

124 - Fenestra ventrolateralis

0 = absent

1 = present

125 - Palatal opening surrounded by premaxilla, maxilla, dermopalatine and vomer (choana)

0 = absent
1 = present

126 - Internasal cavity

0 = absent
1 = present

127 - Interorbital septum

0 = broad
1 = narrow

128 - Optic foramen

0 = dorsally positioned
1 = ventrally positioned (i.e. abuts parasphenoid)

129 - Pronounced median anterior crista on dorsal surface of braincase

0 = absent
1 = present

130 - Expanded anterior dorsal fontanelle

0 = absent
1 = present

131 - Endoskeletal intracranial joint

0 = absent
1 = present

132 - Eye stalk or unfinished area for similar structure

0 = absent
1 = present

133 - Roof of posterior myodome perforated by palatine branch of facial nerve (VII)

0 = absent
1 = present

134 - Foramen for abducens nerve (VI) dorsally positioned (level with optic foramen (II))

0 = absent
1 = present

135 - Anterodorsal myodome

0 = paired
1 = single
2 = absent

136 - Posterior myodome

0 = absent
1 = paired
2 = median

137 - Basicranial fenestra

0 = absent
1 = present

138 - Spiracle

0 = open
1 = partial closure or spiracular bar
2 = complete enclosure in canal

139 - Basipterygoid process

0 = present
1 = absent

140 - Basipterygoid process with vertically oriented component

0 = absent
1 = present

141 - Dermal component to basipterygoid process

0 = absent
1 = present

142 - Hyoid facet

0 = directed posteroventrally
1 = horizontal

143 - Fossa bridgei

0 = absent
1 = present

144 - Posttemporal fossae

0 = absent
1 = present

145 - Vestibular fontanelle

0 = absent
1 = present

146 - Ventral cranial fissure and vestibular fontanelle

0 = separated by bridge of bone

1 = confluent

147 - Accessory fenestration in otic capsule

0 = absent

1 = present

148 - Otoccipital fissure

0 = absent

1 = present

149 - Median projection overhanging posterior part of posterior dorsal fontanelle

0 = absent

1 = present

150 - Median projection overhanging anterior part of posterior dorsal fontanelle

0 = absent

1 = present

151 - Dorsal aorta

0 = open in groove

1 = canal notched posteriorly

2 = completely enclosed in canal

152 - Dorsal aorta pierced by canal/s for exit of eff.a.2

0 = absent

1 = present

153 - Dorsal aorta pierced by canal/s for exit of eff.a.1

0 = absent

1 = present

154 - Bifurcation of dorsal aorta

0 = posterior to occiput

1 = anterior to occiput

155 - Birfurcation of dorsal aorta into lateral dorsal aortae

0 = open

1 = enclosed in canal

156 - Braincase ossifications differentiated

0 = absent

1 = present

157 - Basisphenoid

0 = present

1 = absent or very reduced

158 - Opisthotic-pterotic relationship

0 = opisthotic larger than subotic

1 = opisthotic and pterotic equal in size

159 - Epioccipital

0 = present

1 = absent

160 - Forward extension of the exoccipital around the vagus nerve

0 = absent

1 = present

161 - Spenotic with small dermal component

0 = absent

1 = present

162 – Pterotic

0 = present

1 = absent

163 - Opisthotic bone

0 = present

1 = absent

164 – Intercalar

0 = present

1 = absent

165 - Supraoccipital bone

0 = absent

1 = present

166 - Membranous outgrowth of intercalar

0 = absent

1 = present

167 - Post-temporal fossa

0 = absent

1 = present

168 - Sub-temporal fossa

0 = absent

1 = present

169 - Dilatator fossa

0 = absent

1 = present

170 - Parasphenoid

0 = absent

1 = present

171 - Parasphenoid

0 = terminates at/anterior to ventral otic fissure

1 = extends across ventral otic fissure

2 = extends to basioccipital

172 - Ascending process of the parasphenoid

0 = absent

1 = present

173 - Parasphenoid with multifid anterior margin

0 = absent

1 = present

174 - Buccohypophyseal canal pierces parasphenoid

0 = present

1 = absent

175 - Parasphenoid teeth

0 = small

1 = large

2 = absent

176 - Parasphenoid pierced by internal carotid artery

0 = absent

1 = present

177 - Parasphenoid pierced by efferent pseudobranchial artery

0 = absent

1 = present

178 - Aortic notch in parasphenoid

0 = absent

1 = present

179 - Parabasal canal

0 = present

1 = absent

180 - Anterolaterally divergent olfactory tracts

0 = absent

1 = present

181 - Elongate olfactory tract(s)

0 = absent

1 = present

182 - Olfactory nerves carried in a single tract

0 = present

1 = absent

183 - Hypophyseal chamber

0 = projects posteroventrally

1 = projects ventrally or anteroventrally

184 - Optic lobes

0 = narrower than cerebellum

1 = same width or wider than cerebellum

185 - Optic lobes

0 = smaller than telencephalon

1 = larger than telencephalon

186 = Optic tectum divided into bilateral halves

0 = absent

1 = present

187 - Cerebellar corpus

0 = absent

1 = present

188 - Cerebellar corpus

0 = divided bilaterally

1 = undivided

189 - Position of cerebellar corpus

0 = enters fourth ventricle

1 = arches above fourth ventricle

190 - Cerebellar corpus with median anteriorly projecting portion

0 = absent

1 = present

191 - Horizontal semicircular canal

0 = joins vestibular region dorsal to ampulla for the posterior semicircular canal

1 = joins vestibular region level with ampulla for the posterior semicircular canal

192 - Junction between ampulla of posterior semicircular canal and cranial cavity

0 = separated by short length of canal

1 = confluent

193 - Crus commune of anterior and posterior semicircular canal

0 = dorsal to endocranial roof

1 = ventral to endocranial roof

194 - Lateral cranial canal

0 = absent

1 = present

195 - Lateral cranial canal connects to cranial cavity anteriorly

0 = absent

1 = present

196 - Enameloid on dermal bones and scales

0 = absent

1 = present

197 - Extensive pore-canal network

0 = absent

1 = present

198 – Enamel

0 = single-layered

1 = multi-layered

199 - Enamel layers

0 = applied directly to one another

1 = separated by layers of dentine

200 - Scales on body

0 = present

1 = absent

201 - Scales

0 = micromeric

1 = macromeric

202 - Scales with ‘peg and socket articulation'

0 = absent
1 = present

203 - Peg on rhomboid scale

0 = narrow
1 = broad

204 - Anterodorsal process on scale

0 = absent
1 = present

205 - Scales with well-developed pores on surface

0 = absent
1 = present

206 - Small scales below dorsal fin

0 = absent
1 = present

207 - Lepidotrichia

0 = absent
1 = present

208 - Fringing fulcra

0 = absent
1 = present

209 - Double headed hyomandibular

0 = absent
1 = present

210 - Perforate hyomandibula

0 = absent
1 = present

211 - Opercular process

0 = absent
1 = present

212 - Ceratohyal

0 = single ossification
1 = two ossifications

213 - Anterior ossification of ceratohyal

0 = no medial constriction

1 = medial constriction (hourglass-shaped)

214 - Anterior ceratohyal

0 = no groove

1 = groove for afferent hyoidean artery

215 - Interhyal

0 = absent

1 = present

216 - Symplectic

0 = absent

1 = present

217 - Symplectic shape

0 = tube/splint like

1 = hatchet

2 = l-shaped

218 - Hypohyal

0 = absent

1 = present

219 - Basihyal

0 = absent

1 = present

220 - Gill arches

0 = largely restricted to area under braincase

1 = extend far posterior to braincase

221 - Number of ceratobranchials

0 = five

1 = four

222 - Number of hypobranchials

0 = three

1 = four

223 - Uncinate processes on epibranchials

0 = absent

1 = present

224 - Endoskeletal urohyal

0 = absent

1 = present

225 - Urohyal formed as a tendon bone of the sternohyoideus muscle

0 = absent

1 = present

226 - Presupracleithrum

0 = absent

1 = present

227 - Presupracleithrum

0 = single

1 = multiple

228 - Dorsal margin of cleithrum

0 = pointed

1 = broad and rounded

229 - Medial wing on cleithrum

0 = absent

1 = present

230 - Anocleithrum

0 = bone developed as postcleithrum

1 = bone developed as anocleithrum sensu stricto

2 = bone absent

231 - Clavicle

0 = present as a broad plate

1 = much reduced or absent

232 - Serrated organ

0 = absent

1 = present

233 - Interclavicle

0 = present

1 = absent

234 - Triradiate scapulocoracoid

0 = absent

1 = present

235 - Perforate propterygium

0 = absent

1 = present

236 - Anterior rays embrace propterygium

0 = absent

1 = present

2 = fused

237 – Propterygium fused to first ray

0 = absent

1 = present

238 - Pectoral fin endoskeleton

0 = extends far beyond body wall (fins lobate)

1 = barely extends beyond body wall (fins not lobate)

239 - Pectoral fin radials

0 = unjointed

1 = jointed

240 - Fin articulation

0 = monobasal

1 = polybasal

241 - Pectoral fin-ray segmentation

0 = roughly even segmentation to fin base

1 = proximal segments elongate with terminal segmentation

2 = no significant segmentation on pectoral fin

3 = terminal segments elongate with proximal segmentation

242 - Pectoral fin

0 = leaf-like

1 = not leaf-like

243 - Paired fin spines

0 = absent

1 = present

244 - Pelvic fins

0 = absent

1 = present

245 - Pelvic fin insertion

0 = shorter than fin depth (short based)

1 = longer than fin depth (long based)

246 - Basal scutes on fins

0 = absent

1 = present

247 - Dorsal scutes anterior to dorsal fin

0 = absent

1 = few limited to region immediately anterior to fin (basal fulcra only)

2 = many, extending to posterior of skull roof (complete set of dorsal ridge scales)

248 - Ventral scutes between hypochordal lobe of caudal fin and anal fin

0 = absent

1 = present

249 - **Ventral scutes anterior to anal fin**

0 = absent

1 = present

250 - Dorsal fin(s)

0 = two

1 = one

251 - Relative positions of anal and (second) dorsal fin

0 = anal shifted anteriorly relative to dorsal

1 = fins opposite one another

2 = anal shifted posteriorly relative to dorsal

252 - Median fins (except caudal fin)

0 = rays more numerous than radials

1 = rays and radials equal

253 - Proximal and middle radials of dorsal fin

0 = proximal and middle radials of similar size

1 = proximal radials substantially enlarged

254 - Posteriormost proximal radial of dorsal fin

0 = enlarged plate

1 = smaller than more anterior radials

255 - Epichordal lobe of caudal fin

0 = present

1 = absent

256 - Fulcra along dorsal ridge of caudal fin

0 = absent

1 = present

257 - Caudal fin geometry

0 = long chordal lobe

1 = short chordal lobe

258 - Posterior margin of caudal fin

0 = forked

1 = unforked

259 - Diplospondyly in mid-caudal region

0 = absent

1 = present

260 - Median neural spines in caudal region

0 = absent

1 = present

261 - Uroneural

0 = absent

1 = present

262 - Division of hypurals into dorsal and ventral groups

0 = absent

1 = present

263 - Number of caudal lepidotrichs borne per hypural

0 = multiple

1 = single

264 - Opistocoelous vertebrae

0 = absent

1 = present

265 - Ossified ribs

0 = present

1 = absent

APPENDIX B - Matrix *Brazilichthys macrognathus*

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Acanthodes bronni	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Acipenser brevirostrum	1	1	1	-	-	-	-	-	-	-	-	-	0	0
Aesopichthys erinaceus	1	1	0	1	-	0	0	0	0	0	0	1	1	1
Amia calva	1	1	0	1	-	1	0	0	0	1	2	0	1	0
Amphicentrum granulosum	1	1	0	0	0	1	0	1	0	0	0	?	1	1
Atractosteus spatula	1	1	0	0	0	1	0	0	-	1	2	0	1	0
Australosomus kochi	1	1	1	?	?	?	?	?	-	?	?	-	?	?
Beagiascus pulcherrimus	1	1	0	0	0	0	0	0	0	0	0	1	1	1
Beishanichthys brevicaudalis	1	1	0	0	?	0	1	0	0	0	?	0	1	1
Birgeria groenlandica	1	1	0	0	1	1	0	0	0	0	1	0	1	1
Bobosatrania groenlandica	1	1	1	-	-	-	-	1	-	-	-	-	0	0
Boreosomus piveteaui	1	1	0	0	1	0	1	1	0	0	0	0	1	1
Brazilichthys macrognathus	1	1	0	?	0	0	1	0	0	0	0	0	?	?
Caturus furcatus	1	1	0	0	0	1	0	0	0	1	?	1	1	0
Cheirolepis canadensis	1	1	0	?	0	1	-	0	0	0	0	0	0	0
Cheirolepis schultzei	1	1	0	0	0	0	0	0	0	0	0	?	0	0
Cheirolepis trailli	1	1	0	0	0	0	1	0	0	0	0	0	0	0
Chondrosteus acipenseroides	1	1	1	-	-	-	-	-	-	-	-	-	1	?
Cladodoides wildungensis	0	?	-	?	-	?	?	-	-	-	-	-	?	?
Coccocephalichthys wildi	1	1	?	?	?	?	0	?	?	?	?	?	1	1
Cosmoptychius striatus	1	1	0	?	?	1	0	0	0	?	0	0	?	1
Cyranorhis bergeraci	1	1	1	-	-	-	-	-	-	-	-	-	1	1
Dapedium LIAS	1	1	0	0	1	1	0	0	0	0	1	?	1	1
Dapedium pholidotum	1	1	0	0	1	1	0	0	0	0	1	1	1	1
Dialipina salguerioensis	1	0	0	?	?	?	1	0	0	0	?	?	0	1
Dicksonosteus arcticus	1	0	0	?	?	1	-	0	0	0	0	0	0	1
Diplocercides kayseri	1	1	0	?	0	1	-	0	0	0	?	?	0	0
Dipteronotus ornatus	1	1	0	?	?	1	0	0	0	0	?	?	1	1
Discoserra pectinodon	1	1	0	0	0	0	1	0	0	0	0	1	0	1
Donnrosenia schaefferi	1	1	0	?	0	0	1	?	0	0	0	0	1	1
Dorsetichthys bechei	1	1	0	?	0	1	0	0	1	0	0	?	1	1
Ebenaqua ritchei	1	1	1	-	-	-	-	1	-	-	-	-	1	1
Elops hawaiensis	1	1	0	1	-	1	0	0	1	0	2	1	1	1
Entelognathus primordialis	1	0	0	?	?	1	-	1	0	0	0	1	0	1
Erpetoichthys calabaricus	1	1	0	1	-	1	1	0	0	0	0	0	1	0
Eusthenopteron foordi	1	1	0	0	0	1	-	0	0	0	0	0	0	0
Evenkia eunoptera	1	1	0	?	0	0	1	0	0	0	0	0	0	0
Fouldenia ischiptera	1	1	0	0	0	1	0	1	0	0	0	?	1	1
Fukangichthys longidorsalis	1	1	0	0	0	?	1	0	0	0	?	?	1	1
Glyptolepis groenlandica	1	1	0	?	-	1	-	0	0	0	0	?	?	?
Gogonasus andrewsae	1	1	0	0	-	1	-	0	0	0	0	?	0	0
Gogosardina coatesi	1	1	0	0	0	0	1	0	0	0	0	0	0	1
Guiyu oneiros	1	?	0	1	-	0	0	0	0	0	0	1	0	0
Hiodon alosoides	1	1	0	0	0	1	0	0	1	0	0	1	1	1
Howqualepis rostridens	1	1	0	1	-	0	1	0	0	0	0	0	1	1
Hulettia americana	1	1	0	0	0	1	0	0	0	0	1	1	1	1

Ichthyokentema purbeckensis	1	1	0	1	-	1	0	0	1	0	0	1	1	1
Kalops monophyrum	1	1	0	0	0	1	0	0	0	0	?	1	1	1
Kansasiella eatoni	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Kentuckia deani	1	1	0	?	0	0	1	0	0	0	0	0	0	1
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	1	1	0	0	0	1	0	0	-	1	2	0	1	0
Leptolepis bronni	1	1	0	0	0	1	0	0	1	0	1	1	1	1
Ligulalepis	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	0	?	?	?	?	?	0	?	?	?	?	?
Luganoia lepidosteoides	1	1	0	0	1	1	0	0	0	0	1	0	1	1
Macrepistius arenatus	1	1	0	?	?	1	0	0	0	1	?	?	1	0
Macrosemimimus lennieri	1	1	0	0	0	1	0	0	0	?	?	?	1	1
Macrosemius rostratus	1	1	0	0	0	1	0	0	0	1	2	1	1	0
Meemannia eos	1	1	?	?	?	?	?	?	?	?	?	?	0	?
Melanecta anneae	1	1	0	1	-	0	1	0	0	0	?	0	1	1
Mesopoma planti	1	1	0	?	0	0	1	?	0	0	?	?	1	1
Miguashaia bureaui	1	1	0	0	0	1	-	0	0	0	0	0	1	0
Mimipiscis bartrami	1	1	0	0	0	0	1	0	0	0	0	0	0	1
Mimipiscis toombsi	1	1	0	0	0	0	1	0	0	0	0	0	1	1
Moythomasia durgaringa	1	1	0	1	-	0	1	0	0	0	?	0	1	1
Moythomasia lineata	1	1	0	0	0	0	1	1	0	0	0	1	1	1
Moythomasia nitida	1	1	0	0	0	1	1	0	0	0	0	1	1	1
Obaichthys decoratus	1	1	0	?	0	1	0	0	0	?	2	0	1	0
Onychodus jandemarrai	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Osorioichthys marginis	1	1	0	0	0	0	1	0	0	0	?	0	1	1
Osteolepis macrolepidotus	1	1	0	0	1	1	-	0	0	0	-	0	0	0
Ozarcus mapesae	0	?	-	?	-	?	?	-	-	-	-	-	?	?
Peltopleurus lissocephalus	1	1	0	?	0	0	1	1	0	0	0	1	1	1
Platysomus superbus	1	1	1	-	-	1	0	?	-	-	-	-	0	1
Polypterus bichir	1	1	0	0	0	1	1	0	0	0	0	0	1	0
Porolepis sp.	1	1	0	0	1	0	0	0	0	0	-	0	0	0
Propterus elongatus	1	1	0	0	0	1	0	0	?	?	?	1	1	0
Psarolepis romeri	1	1	0	1	-	1	-	0	0	0	?	0	?	?
Pteronisculus stensioi	1	1	0	0	0	0	1	0	0	0	0	1	1	1
Raynerius splendens	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Saurichthys madagascarensis	1	1	1	-	-	0	0	0	-	-	-	-	1	1
Scanilepis dubia	1	1	0	?	?	0	1	0	?	?	?	?	1	1
Semionotus elegans	1	1	0	0	0	1	0	0	0	1	2	1	1	-
Styloichthys changae	1	?	?	?	-	?	?	?	?	0	?	?	?	?
Styracopterus fulcratus	1	1	1	-	-	1	0	1	-	-	-	-	1	1
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	1	1	0	0	0	0	0	0	?	0	?	0	1	1
Tetragonolepis semicincta	1	1	0	0	0	1	0	0	0	0	1	0	1	1
Venusichthys comptus	1	1	0	0	0	1	0	0	0	0	0	1	1	1
Watsonulus eugnathoides	1	1	0	0	0	0	0	0	1	1	1	1	1	-
Wendyichthys dicksoni	1	1	1	-	-	-	-	-	-	-	-	-	1	1
Woodichthys bearsdeni	1	1	0	0	0	0	1	0	0	0	?	0	1	1

	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Acanthodes bronni	?	?	-	?	?	?	?	?	0	?	-	?	?	?

Acipenser brevirostrum	0	0	0	0	-	1	-	?	0	1	0	0	0	0
Aesopichthys erinaceus	0	1	0	1	1	1	0	0	0	1	0	1	2	0
Amia calva	0	1	1	0	0	0	0	0	0	1	0	1	2	0
Amphicentrum granulosum	?	1	0	1	1	?	0	0	0	1	-	0	2	0
Atractosteus spatula	0	1	1	0	0	0	0	0	0	1	0	1	2	0
Australosomus kochi	?	?	0	?	?	?	?	?	0	1	0	0	2	0
Beagiascus pulcherrimus	0	1	0	1	1	1	0	0	0	1	0	1	2	0
Beishanichthys brevicaudalis	0	1	0	1	1	1	0	0	0	1	0	1	2	0
Birgeria groenlandica	0	1	0	1	1	0	0	0	0	1	0	?	2	0
Bobosatrania groenlandica	0	1	0	1	1	1	-	0	0	1	0	1	2	0
Boreosomus piveteaui	0	1	1	1	1	1	0	?	0	1	0	0	2	0
Brazilichthys macrognathus	?	1	0	1	1	1	0	?	0	?	?	?	?	?
Caturus furcatus	0	1	1	0	0	0	0	0	0	1	0	1	2	0
Cheirolepis canadensis	0	0	0	0	?	?	0	1	0	0/1	0	0	1	0
Cheirolepis schultzei	0	0	0	0	0	?	0	1	0	1	0	0	2	0
Cheirolepis trailli	0	0	0	0	1	0	0	1	0	0/1	0	0	1	0
Chondrosteus acipenseroides	?	?	?	?	?	?	-	?	0	1	0	1	2	0
Cladodoides wildungensis	?	?	-	-	?	?	?	?	-	?	-	?	?	-
Coccocephalichthys wildi	0	1	0	1	0	1	0	?	0	1	0	0	2	0
Cosmoptychius striatus	0	1	0	1	1	1	0	0	0	1	0	1	2	?
Cyranorhis bergeraci	0	1	0	1	1	1	-	0	0	1	0	1	2	0
Dapedium LIAS	0	1	1	0	?	0	0	0	0	1	0	-	-	-
Dapedium pholidotum	0	1	1	0	1	0	0	0	0	1	0	-	-	-
Dialipina salguerioensis	0	?	0	?	?	?	?	?	0	1	0	1	2	1
Dicksonosteus arcticus	0	?	?	?	?	?	?	?	0	0	-	0	0	0
Diplocercides kayseri	1	0	?	?	0	0	0	1	1	1	0	0	0	0
Dipteronotus ornatus	0	1	0	0	1	0	?	?	0	1	0	1	2	0
Discoserra pectinodon	0	1	0	1	1	1	0	0	0	1	0	1	2	0
Donnrosenia schaefferi	0	1	0	1	1	1	0	0	0	0	-	0	1	0
Dorsetichthys bechei	0	1	0	1	0	0	0	0	0	1	0	1	2	1
Ebenaqua ritchei	0	1	0	1	0	1	-	0	0	1	0	1	2	0
Elops hawaiensis	0	1	0	0	0	0	0	0	0	1	0	1	2	1
Entelognathus primordialis	0	?	?	0	?	?	?	?	0	1	0	0	?	0
Erpetoichthys calabaricus	0	0	0	0	0	1	0	0	0	1	0	0	2	0
Eusthenopteron foordi	0	0	0	0	0	0	1	1	1	0	-	0	1	0
Evenkia eunoptera	0	0	?	0	1	?	0	0	0	1	0	1	2	0
Fouldenia ischiptera	0	1	0	1	0	?	0	0	0	1	0	1	1	0
Fukangichthys longidorsalis	0	1	?	1	1	1	?	0	0	1	0	1	2	0
Glyptolepis groenlandica	0	?	0	0	?	0	1	1	1	1	1	0	0	0
Gogonasus andrewsae	0	0	0	0	0	0	1	1	1	0	-	0	0	0
Gogosardina coatesi	0	1	0	1	1	1	1	0	0	0	-	0	1	0
Guiyu oneiros	0	0	0	0	0	0	0	1	1	0	-	0	0	0
Hiodon alosoides	0	1	1	0	0	0	0	0	0	1	0	1	2	0
Howqualepis rostridens	0	1	0	1	1	1	1	0	0	0	-	1	2	0
Hulettia americana	0	1	0	0	0	0	0	0	0	1	0	?	2	0
Ichthyokentema purbeckensis	0	1	1	0	1	0	0	0	0	1	0	0	2	0
Kalops monophyrum	0	1	0	1	1	1	0	0	0	1	-	1	2	1
Kansasiella eatoni	?	?	?	?	?	?	?	?	0	0	0	0	2	0
Kentuckia deani	0	1	0	1	1	1	0	0	0	0/1	0	0	2	0
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	0	?	?	?	?	?

Lepisosteus osseus	0	0	1	0	1	0	0	0	0	1	0	0	2	0
Leptolepis bronni	0	1	0	0	?	?	0	0	0	1	0	1	2	1
Ligulalepis	?	1	?	1	?	?	?	0	0	?	?	0	0	0
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	0	1	0	0	0	?	?	0	0	1	1	-	-	1
Macrepistius arenatus	?	?	?	0	?	0	?	0	0	1	0	1	2	0
Macrosemimimus lennieri	0	1	1	0	?	0	0	0	0	1	0	1	2	0
Macrosemius rostratus	0	1	?	0	0	?	0	0	0	1	0	1	2	1
Meemannia eos	?	?	?	?	?	?	?	?	0	0/1	0	0	2	0
Melanecta anneae	0	1	0	1	1	1	0	0	0	1	0	0	2	?
Mesopoma planti	0	1	0	1	1	1	0	?	0	1	0	1	2	0
Miguashaia bureaui	1	0	1	0	0	0	0	0	1	1	0	0	0	0
Mimipiscis bartrami	0	1	0	1	1	1	0	0	0	0	-	0	1	0
Mimipiscis toombsi	0	1	0	1	1	1	1	0	0	0	-	0	2	0
Moythomasia durgaringa	0	1	0	1	1	1	0	0	0	0	-	1	2	0
Moythomasia lineata	0	1	0	1	1	1	0	0	0	0	-	0	2	0
Moythomasia nitida	0	1	0	1	1	1	0	0	0	0	-	0	2	0
Obaichthys decoratus	0	?	?	0	?	?	?	0	0	1	0	0	2	0
Onychodus jandemarrai	0	0	0	0	1	0	0	1	1	1	0	0	0	0
Osorioichthys marginis	0	1	0	1	1	0	1	0	0	1	0	0	1	1
Osteolepis macrolepidotus	0	0	?	-	0	0	1	1	1	0	-	0	0	0
Ozarcus mapesae	?	?	-	-	?	?	?	?	?	?	?	?	?	-
Peltopleurus lissocephalus	0	1	0	1	1	0	0	0	0	1	0	1	2	0
Platysomus superbus	0	1	0	1	1	1	-	0	0	1	0	1	2	0
Polypterus bichir	0	0	0	0	0	1	0	0	0	1	0	0	2	0
Porolepis sp.	0	?	?	-	?	0	1	1	1	1	1	0	0	0
Propterus elongatus	?	1	1	0	0	?	0	0	?	1	0	0	2	1
Psarolepis romeri	0	?	?	?	0	0	1	?	1	0	-	1	2	0
Pteronisculus stensioi	?	1	0	1	1	1	0	?	0	1	0	1	2	0
Raynerius splendens	?	?	?	1	?	?	?	?	0	0	-	0	1	?
Saurichthys madagascarensis	0	1	0	1	0	0	-	0	0	?	-	0	2	1
Scanilepis dubia	?	1	?	0	?	?	?	0	0	1	0	0	0	0
Semionotus elegans	-	1	1	0	1	0	0	0	0	1	0	1	2	0
Styloichthys changae	?	?	0	?	?	?	?	?	?	0	-	0	?	0
Styracopterus fulcratus	0	1	0	1	0	?	-	0	0	1	0	1	2	0
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	0	1	0	1	?	?	?	0	0	1	0	0	1	0
Tetragonolepis semicincta	0	1	0	0	1	0	0	0	0	1	0	0	2	0
Venusichthys comptus	0	1	0	1	1	0	0	0	0	1	0	1	2	1
Watsonulus eugnathoides	-	1	0	0	0	0	0	0	0	1	0	1	2	0
Wendyichthys dicksoni	0	1	0	1	1	?	-	0	0	1	0	1	2	0
Woodichthys bearsdeni	0	1	0	1	1	1	0	0	0	1	0	1	2	0

	31	32	33	34	35	36	37	38	39	40	41	42	43	44
Acanthodes bronni	?	0	1	?	-	?	?	?	?	?	?	-	?	?
Acipenser brevirostrum	0	1	0	1	-	1	-	-	-	-	0	0	1	1
Aesopichthys erinaceus	0	0	0	1	-	0	0	1	1	0	-	1	1	1
Amia calva	0	1	0	1	-	1	-	-	-	-	0	0	0	1
Amphicentrum granulosum	0	0	0	1	-	1	-	-	-	-	0	1	?	1
Atractosteus spatula	0	1	1	1	-	1	-	-	-	-	0	1	2	1

Australosomus kochi	0	0	0	1	-	1	-	-	-	-	0	1	0	1
Beagiascus pulcherrimus	0	0	0	1	-	0	0	1	1	0	-	0	2	1
Beishanichthys brevicaudalis	0	?	?	1	-	1	-	-	-	-	0	0	1	1
Birgeria groenlandica	0	0	0	1	-	1	-	-	-	-	0	1	0	0
Bobosatrania groenlandica	0	0	0/1	1	-	1	-	-	-	-	0	?	0	0
Boreosomus piveteaui	0	0	1	1	-	1	-	-	-	-	0	1	1	0
Brazilichthys macrognathus	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Caturus furcatus	0	1	1	0	-	1	-	-	-	-	0	0	0	1
Cheirolepis canadensis	0	0	0	1	-	0	0	0	-	0	-	1	0	0
Cheirolepis schultzei	0	0	?	1	-	1	-	-	-	0	0	1	0	1
Cheirolepis trailli	0	0	0	1	-	0	0	0	0	0	-	1	0	0
Chondrosteus acipenseroides	?	?	?	1	-	1	-	-	-	-	0	?	2	?
Cladodoides wildungensis	?	?	?	?	-	?	?	?	?	?	-	-	?	?
Coccocephalichthys wildi	0	0	1	1	-	1	-	-	-	-	0	0	1	1
Cosmoptychius striatus	0	0	0	1	-	1	-	-	-	-	?	0	?	1
Cyranorhis bergeraci	0	0	0	1	-	0	0	1	0	0	-	1	1	1
Dapedium LIAS	-	?	?	-	-	-	-	-	-	-	1	-	1	1
Dapedium pholidotum	-	0	1	-	-	-	-	-	-	-	1	-	2	1
Dialipina salguerioensis	0	0	0	1	-	1	-	-	-	-	0	0	?	?
Dicksonosteus arcticus	0	?	0	?	?	1	?	?	?	?	?	0	0	1
Diplocercides kayseri	0	0	0	1	-	1	-	-	-	-	0	?	0	1
Dipteronotus ornatus	0	0	0	?	?	1	-	-	-	-	?	0	?	?
Discoserra pectinodon	0	0	0	0	-	1	-	-	-	-	0	0	2	1
Donnrosenia schaefferi	0	0	0	1	-	0	0	1	0	0	-	1	0	1
Dorsetichthys bechei	0	?	1	1	-	1	-	-	-	-	0	0	0	1
Ebenaqua ritchei	0	0	0	1	-	1	-	-	-	-	0	0	1	0
Elops hawaiensis	0	1	1	1	-	1	-	-	-	-	0	0	0	1
Entelognathus primordialis	?	-	0	?	?	?	?	?	?	?	?	0	0	1
Erpetoichthys calabaricus	1	1	0	1	-	-	-	-	-	-	-	-	2	1
Eusthenopteron foordi	0	1	0	0	1	0	0	0	0	0	-	0	0	1
Evenkia eunoptera	1	1	1	1	-	-	-	-	-	-	-	-	?	1
Fouldenia ischiptera	?	?	?	1	-	1	-	-	-	-	0	?	0	1
Fukangichthys longidorsalis	0	1	0	1	-	1	-	-	-	-	0	1	1	0
Glyptolepis groenlandica	1	1	0	0	1	0	-	-	-	0	-	0	0	1
Gogonasus andrewsae	0	1	0	0	1	0	0	0	0	0	-	0	0	1
Gogosardina coatesi	0	0	?	1	-	0	0	1	0	?	-	1	?	?
Guiyu oneiros	0	0	0	0	0	0	1	0	0	0	-	0	0	1
Hiodon alosoides	0	0	1	1	-	1	-	-	-	-	1	0	0	1
Howqualepis rostridens	0	0	0	1	-	0	0	1	0	0	-	1	0	1
Hulettia americana	0	0	0	1	-	1	-	-	-	-	0	0	0	1
Ichthyokentema purbeckensis	0	0	0	1	-	1	-	-	-	-	0	0	0	1
Kalops monophyrum	0	0	0	1	-	1	-	-	-	-	0	0	0	1
Kansasiella eatoni	0	0	?	1	-	1	-	-	-	-	0	?	?	?
Kentuckia deani	0	0	0	1	-	?	-	-	?	-	?	1	0	1
Lawrenciella schaefferi	?	?	?	?	-	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	0	1	1	1	-	1	-	-	-	-	0	0	2	1
Leptolepis bronni	0	0	1	1	-	1	-	-	-	-	0	0	0	1
Ligulalepis	0	?	0	1	?	0	0	0	0	0	-	0	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	-	0	0	0	?	1	-	-	-	-	1	-	1	1

Macrepistius arenatus	?	?	?	1	-	0	0	0	0	0	-	1	0	1
Macrosemimimus lennieri	0	?	?	?	-	1	-	-	-	-	0	0	0	1
Macrosemius rostratus	0	?	1	1	-	1	-	-	-	-	0	0	0	1
Meemannia eos	0	?	?	1	-	1	-	-	-	-	0	1	?	0
Melanecta anneae	0	0	0	1	-	1	-	-	-	-	0	?	?	?
Mesopoma planti	0	?	?	1	-	1	-	-	-	-	0	0	1	?
Miguashaia bureaui	0	0	0	0	0	0	1	0	0	0	-	?	0	1
Mimipiscis bartrami	0	0	1	1	-	0	0	0	0	1	-	1	0	1
Mimipiscis toombsi	0	0	1	1	-	0	0	0	0	1	-	1	0	1
Moythomasia durgaringa	0	0	1	1	-	0	0	0	1	0	-	1	1	0
Moythomasia lineata	0	?	?	1	-	0	0	0	0	0	-	1	1	0
Moythomasia nitida	0	0	0	1	-	0	0	0	0	0	-	1	1	1
Obaichthys decoratus	0	?	?	1	-	1	-	-	-	-	0	0	1	1
Onychodus jandemarrai	0	?	0	0	1	1	-	-	-	0	0	0	0	1
Osorioichthys marginis	0	?	0	1	-	0	0	0	0	0	-	?	1	0
Osteolepis macrolepidotus	0	1	0	0	1	0	0	0	0	0	-	0	0	1
Ozarcus mapesae	?	?	?	?	?	?	?	?	?	?	-	-	?	?
Peltopleurus lissocephalus	0	0	0	1	-	1	-	-	-	-	0	0	0	1
Platysomus superbus	0	0	0	1	-	1	-	-	-	-	0	0	1	1
Polypterus bichir	1	1	0	1	-	-	-	-	-	-	-	-	2	1
Porolepis sp.	1	1	0	0	1	0	-	-	-	0	-	0	0	1
Propterus elongatus	0	1	0	1	-	1	-	-	-	-	0	0	?	?
Psarolepis romeri	0	0	?	?	?	?	?	?	?	?	?	0	?	?
Pteronisculus stensioi	0	0	0	1	-	1	-	-	-	-	0	1	1	1
Raynerius splendens	0	0	0	1	-	0	0	0	?	?	-	?	1	1
Saurichthys madagascarensis	0	?	?	1	-	1	-	-	-	-	0	?	0	0
Scanilepis dubia	?	?	?	1	-	1	-	-	-	-	0	1	1	1
Semionotus elegans	0	?	1	1	-	1	-	-	-	-	0	0	0	1
Styloichthys changae	0	0	?	0	?	?	?	?	?	?	?	0	?	?
Styracopterus fulcratus	?	?	?	1	-	1	-	-	-	-	0	1	0	1
Tanaocrossus kalliokoskii	?	?	?	?	?	1	?	?	?	?	?	?	1	?
Tegeolepis clarki	0	0	0	1	-	0	0	0	0	0	-	1	1	0
Tetragonolepis semicincta	0	0	1	1	-	1	-	-	-	-	0	0	0	1
Venusichthys comptus	0	?	?	1	-	1	-	-	-	-	0	0	0	1
Watsonulus eugnathoides	0	0	1	1	-	1	-	-	-	-	0	0	0	1
Wendyichthys dicksoni	0	0	0	1	-	0	0	1	1	0	-	1	1	1
Woodichthys bearsdeni	0	0	0	1	-	0	0	1	0	0	-	1	1	1

	46	47	48	49	50	51	52	53	54	55	56	57	58	59
Acanthodes bronni	?	?	-	?	?	?	?	?	?	?	?	?	?	?
Acipenser brevirostrum	-	0	0	?	?	1	-	0	0	1	0	0	1	-
Aesopichthys erinaceus	1	0	0	1	0	1	-	-	1	1	0	1	0	0
Amia calva	1	0	0	1	1	0	0	0	0	1	1	0	0	0
Amphicentrum granulosum	?	0	0	0	-	1	1	0	0	0	0	0	0	0
Atractosteus spatula	1	0	0	1	1	2	-	-	3	-	1	0	1	1
Australosomus kochi	0	0	0	?	?	0	-	0	0	1	-	-	0	-
Beagiascus pulcherrimus	-	?	0	1	0	1	0	0	3	1	1	1	0	0
Beishanichthys brevicaudalis	?	0	0	0	-	1	0	0	2	1	0	0	2	0
Birgeria groenlandica	0	0	0	1	0	2	0	0	3	0	1	0	2	0
Bobosatrania groenlandica	1	0	0	0	-	2	1	0	0	0	1	0	0	0

Boreosomus piveteaui	-	0	0	0	-	2	0	0	3	1	0	0	0	0
Brazilichthys macrognathus	?	?	?	0	?	2	0	1	?	0	0	?	0	0
Caturus furcatus	1	0	0	1	1	2	1	0	2	?	0	1	2	0
Cheirolepis canadensis	1	0	0	0	-	1	0	1	0	0	1	0	0	0
Cheirolepis schultzei	1	?	0	0	-	1	0	1	0	0	1	0	0	0
Cheirolepis trailli	0	0	0	0	-	1	0	1	0	0	1	0	0	0
Chondrosteus acipenseroides	-	?	0	?	?	1	?	0	?	?	0	0	?	?
Cladodoides wildungensis	?	?	-	?	-	?	?	?	-	?	?	?	-	-
Coccocephalichthys wildi	-	0	0	1	1	2	0	0	0	?	0	0	1	0
Cosmoptychius striatus	?	0	0	1	0	1	0	0	2	1	0	0	0	0
Cyranorhis bergeraci	1	0	0	1	0	1	0	0	2	1	1	0	0	0
Dapedium LIAS	1	0	0	1	0	2	-	-	3	-	0	-	1	0
Dapedium pholidotum	1	0	-	1	0	2	-	-	3	-	0	-	2	0
Dialipina salguerioensis	?	?	?	?	?	?	1	0	3	?	0	0	?	?
Dicksonosteus arcticus	-	1	?	?	?	1	0	0	0	0	?	?	0	?
Diplocercides kayseri	-	0	?	?	?	1	0	0	?	0	?	?	?	0
Dipteronotus ornatus	?	?	?	1	?	0	-	0	0	?	?	?	1	-
Discoserra pectinodon	0	0	0	0	-	2	0	0	3	0	0	1	1	0
Donnrosenia schaefferi	1	?	0	0	-	?	?	?	0	?	1	0	0	0
Dorsetichthys bechei	0	0	0	1	0	2	1	0	1	1	1	0	1	0
Ebenaqua ritchei	1	0	0	0	-	2	?	0	0	0	0	0	0	0
Elops hawaiensis	1	0	0	1	0	2	1	0	0	0	0	0	1	0
Entelognathus primordialis	-	?	?	?	?	1	0	0	0	0	?	?	0	?
Erpetoichthys calabaricus	1	0	0	0	-	1	0	0	3	0	0	0	0	0
Eusthenopteron foordi	-	0	0	0	-	1	0	0	0	0	0	1	1	0
Evenkia eunoptera	?	0	0	0	?	2	0	0	2	?	0	0	2	0
Fouldenia ischiptera	1	?	0	0	-	1	0	0	0	?	0	0	0	0
Fukangichthys longidorsalis	1	?	0	?	?	?	?	0	3	1	0	0	2	0
Glyptolepis groenlandica	-	0	1	0	-	1	1	0	0	0	0	0	0	0
Gogonasus andrewsae	-	0	?	0	-	1	0	0	0	0	0	1	?	0
Gogosardina coatesi	?	?	0	0	-	?	?	0	0	0	?	0	?	0
Guiyu oneiros	-	1	1	0	-	1	0	0	0	0	0	0	1	0
Hiodon alosoides	0	0	0	0	-	2	0	0	0	0	0	0	0	0
Howqualepis rostridens	1	?	0	0	-	1	1	0	0	0	1	0	0	0
Hulettia americana	1	0	0	1	0	2	-	0	3	1	0	0	2	0
Ichthyokentema purbeckensis	0	0	0	1	0	2	1	0	1	1	0	1	2	0
Kalops monophyrum	-	0	0	1	0	2	0	0	3	0	0	0	2	0
Kansasiella eatoni	?	?	0	?	?	?	?	?	?	?	?	0	?	?
Kentuckia deani	1	0	0	0	-	?	?	0	0	0	?	0	0	0
Lawrenciella schaefferi	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	1	0	0	1	1	2	-	0	3	1	0	0	1	1
Leptolepis bronni	-	0	0	0	-	2	-	0	1	1	1	0	1	0
Ligulalepis	?	?	0	?	?	?	?	?	?	?	0	0	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	1	-	0	0	-	0	-	0	2	0	0	1	2	0
Macrepistius arenatus	1	?	0	1	1	2	-	0	3	?	0	1	2	0
Macrosemimimus lennieri	-	?	0	1	1	2	-	?	1	0	0	1	2	1
Macrosemius rostratus	0	1	0	1	1	2	-	-	0	-	0	0	0	0
Meemannia eos	?	?	?	?	?	?	?	?	?	?	0	0	?	?
Melanecta anneae	?	?	0	0	-	1	?	0	?	0	?	0	0	0

Mesopoma planti	?	?	0	0	-	?	0	?	1	?	0/1	0	0	0
Miguashaia bureaui	-	0	0	1	?	1	?	0	0	0	0	1	1	0
Mimipiscis bartrami	1	0	0	0	-	1	0	0	0	0	1	0	0	0
Mimipiscis toombsi	1	0	0	0	-	1	0	0	0	0	1	0	0	0
Moythomasia durgaringa	?	1	0	0	-	1	1	1	0	0	1	1	0	0
Moythomasia lineata	?	1	0	0	-	1	0	0	0	1	1	0	0	0
Moythomasia nitida	1	1	0	0	-	1	1	0	2	0	1	0	0	0
Obaichthys decoratus	0	?	0	?	?	2	-	-	3	-	0	?	1	1
Onychodus jandemarrai	-	0	1	0	-	1	1	0	0	0	0	-	1	0
Osorioichthys marginis	0	0	0	0	-	1	0	0	1	0	1	0	0	0
Osteolepis macrolepidotus	-	0	1	0	-	1	0	0	0	0	0	1	0	0
Ozarcus mapesae	?	?	?	?	-	?	?	?	-	?	?	?	-	-
Peltopleurus lissocephalus	-	0	0	0	-	1	0	0	2	0	0	0	2	0
Platysomus superbus	1	0	0	0	-	1	0	0	0	0	0	0	0	0
Polypterus bichir	1	0	0	0	-	1	0	0	3	0	0	0	0	-
Porolepis sp.	-	0	1	0	-	1	0	0	0	0	0	0	0	0
Propterus elongatus	?	1	?	1	1	2	-	-	0	-	0	0	2	0
Psarolepis romeri	-	?	?	0	-	?	?	?	?	?	?	?	?	0
Pteronisculus stensioi	0	0	0	1	0	2	0	0	2	1	0	0	0	0
Raynerius splendens	?	0	0	?	?	?	?	1	0	0	1	?	?	?
Saurichthys madagascarensis	1	?	0	0	-	?	0	?	1	?	0	0	1	0
Scanilepis dubia	?	?	0	?	?	1	?	0	3	1	0	-	2	0
Semionotus elegans	1	0	0	1	1	2	-	0	1	0	0	0	2	1
Styloichthys changae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Styracopterus fulcratus	1	?	0	0	-	1	0	0	0	?	0	0	0	0
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	?	?	0	1	1	?	0	0	0	0	1	0	0	0
Tetragonolepis semicincta	0	0	0	1	0	2	1	0	3	0	0	1	1	0
Venusichthys comptus	?	0	0	1	0	2	-	0	3	0	0	0	0	0
Watsonulus eugnathoides	1	0	0	1	1	2	1	0	0	0	1	0	1	0
Wendyichthys dicksoni	1	0	0	1	1	1	1	0	2	1	1	1	0	0
Woodichthys bearsdeni	?	0	0	0	-	1	0	0	0	1	0	0	0	0

	61	62	63	64	65	66	67	68	69	70	71	72	73	74
Acanthodes bronni	?	1	?	?	?	?	?	?	?	?	?	?	?	?
Acipenser brevirostrum	0	0	0	-	-	0	0	-	-	-	-	-	-	-
Aesopichthys erinaceus	-	0	1	1	1	0	1	0	0	0	0	0	0	0
Amia calva	-	1	0	-	-	0	1	0	0	0	0	1	1	1
Amphicentrum granulosum	-	0	0	-	-	1	1	1	0	0	1	0	0	0
Atractosteus spatula	1	0	1	1	1	0	1	0	0	1	0	0	1	0
Australosomus kochi	-	0	1	0	1	1	1	1	0	0	0	0	0	0
Beagiascus pulcherrimus	-	?	1	0	?	?	1	1	1	?	0	0	0	0
Beishanichthys brevicaudalis	0	0	1	0	1	?	1	1	0	0	0	0	0	0
Birgeria groenlandica	0	0	0	-	-	0	1	1	0	0	0	0	0	0
Bobosatrania groenlandica	-	0	0	-	-	0	1	0	0	0	1	1	0	0
Boreosomus piveteaui	-	1	1	0	1	0	1	1	1	1	0	0	0	0
Brazilichthys macrognathus	?	0	?	?	?	?	1	1	1	1	0	0	0	0
Caturus furcatus	1	1	0	-	-	0	1	0	0	0	0	1	1	1
Cheirolepis canadensis	-	0	1	0	?	1	1	1	1	1	0	0	0	0
Cheirolepis schultzei	-	0	1	0	?	1	1	1	1	?	0	0	0	0

Cheirolepis trailli	-	0	1	1	0	1	1	1	1	?	0	0	0	0
Chondrosteus acipenseroides	?	?	0	-	-	0	0	-	-	-	-	-	-	-
Cladodoides wildungensis	-	?	?	?	?	?	-	?	?	?	-	-	-	-
Coccocephalichthys wildi	0	1	?	0	?	0	1	1	1	?	0	0	?	0
Cosmoptychius striatus	-	0	1	0	?	0	1	1	1	0	0	0	0	0
Cyranorhis bergeraci	-	0	1	0	1	0	1	1	1	0	0	0	0	0
Dapedium LIAS	0	?	0	-	-	0	1	0	0	0	0	1	1	0
Dapedium pholidotum	0	1	0	-	-	0	1	0	0	0	0	1	?	0
Dialipina salguerioensis	?	?	?	?	?	1	1	0	?	?	0	0	?	?
Dicksonosteus arcticus	-	?	0	?	?	?	0	-	-	-	-	-	-	-
Diplocercides kayseri	?	1	0	-	-	0	0	?	-	-	-	-	-	-
Dipteronotus ornatus	1	?	?	?	?	?	1	0	0	0	0	0	0	0
Discoserra pectinodon	0	0	0	-	-	0	1	0	0	0	0	?	0	0
Donnrosenia schaefferi	-	0	?	0	?	1	1	1	1	?	0	0	0	0
Dorsetichthys bechei	0	0	0	-	-	?	1	0	1	0	0	1	1	0
Ebenaqua ritchei	-	0	0	-	-	0	1	0	0	0	1	1	?	0
Elops hawaiensis	0	1	0	-	-	1	1	0	1	0	0	1	1	0
Entelognathus primordialis	-	1	0	?	?	?	1	0	0	1	1	0	0	0
Erpetoichthys calabaricus	-	0	1	0	1	0	1	1	0	1	0	0	0	0
Eusthenopteron foordi	1	1	0	-	-	0	1	0	0	0	0	0	0	0
Evenkia eunoptera	0	0	1	1	?	0	1	1	0	0	0	0	0	0
Fouldenia ischiptera	-	?	1	0	1	?	1	1	1	?	0	0	0	0
Fukangichthys longidorsalis	0	?	1	0	1	0	1	1	1	0	0	0	0	0
Glyptolepis groenlandica	-	1	0	-	-	0	1	0	0	0	?	0	?	?
Gogonasus andrewsae	?	1	0	-	-	0	1	0	0	0	0	0	0	0
Gogosardina coatesi	?	0	1	0	0	?	1	1	1	1	0	0	0	0
Guiyu oneiros	1	0	0	-	-	0	1	1	1	1	0	0	0	0
Hiodon alosoides	-	0	0	-	-	-	1	0	0	1	0	1	1	0
Howqualepis rostridens	-	0	1	0	0	1	1	1	1	?	0	0	0	0
Hulettia americana	0	0	0	-	-	0	1	0	0	0	0	1	1	0
Ichthyokentema purbeckensis	0	1	0	-	-	0	1	0	0	0	0	1	1	0
Kalops monophyrum	0	0	1	0	1	0	1	1	1	0	0	0	0	0
Kansasiella eatoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kentuckia deani	-	?	1	0	?	?	1	1	1	?	0	0	?	0
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	1	0	1	1	0	0	1	0	0	0	0	0	1	0
Leptolepis bronni	0	0	0	-	-	?	1	0	0	0	1	1	1	0
Ligulalepis	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Luganoia lepidosteoides	0	?	1	0	1	0	1	0	0	1	0	?	0	0
Macrepistius arenatus	1	?	0	-	-	?	1	0	0	?	0	1	?	0
Macrosemimimus lennieri	1	?	0	-	-	0	1	0	0	?	0	1	1	0
Macrosemius rostratus	-	?	0	-	-	0	1	0	1	0	0	1	1	0
Meemannia eos	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Melanecta anneae	-	0	?	0	?	1	1	1	1	?	0	0	0	0
Mesopoma planti	-	?	1	?	1	0	1	1	1	?	?	0	0	0
Miguashaia bureaui	0	1	0	-	-	0	0	?	-	-	-	-	-	-
Mimipiscis bartrami	-	0	1	0	0	1	1	1	1	1	0	0	0	0
Mimipiscis toombsi	-	0	1	0	0	1	1	1	1	1	0	0	0	0
Moythomasia durgaringa	-	0	1	0	0	1	1	1	1	1	0	0	0	0

Moythomasia lineata	-	0	1	0	?	1	1	1	1	?	0	0	0	0
Moythomasia nitida	-	0	1	0	0	1	1	1	1	?	0	0	0	0
Obaichthys decoratus	1	?	0	-	-	?	1	0	0	0	0	1	1	0
Onychodus jandemarrai	1	1	1	0	1	0	1	1	1	1	0	0	0	0
Osorioichthys marginis	-	0	1	0	?	1	1	1	1	?	0	0	?	0
Osteolepis macrolepidotus	-	?	0	-	-	0	1	0	0	0	0	0	0	0
Ozarcus mapesae	-	?	?	?	?	?	-	?	?	?	-	-	-	-
Peltopleurus lissocephalus	1	0	1	0	?	0	1	0	0	0	1	0	0	0
Platysomus superbus	-	0	0	-	-	0	1	1	1	0	?	0	0	0
Polypterus bichir	-	0	1	0	1	0	1	1	0	1	0	0	0	0
Porolepis sp.	-	1	0	-	-	0	1	0	0	0	0	0	0	0
Propterus elongatus	0	?	0	-	-	0	1	0	1	0	0	1	1	0
Psarolepis romeri	?	0	?	-	-	?	?	1	1	1	0	0	0	0
Pteronisculus stensioi	-	0	1	0	?	0	?	1	1	1	0	0	0	0
Raynerius splendens	?	?	1	1	0	1	1	1	1	?	0	0	0	0
Saurichthys madagascarensis	0	0	1	0	?	0	1	1	1	0	0	0	0	0
Scanilepis dubia	0	?	1	0	?	0	1	1	1	?	0	0	?	0
Semionotus elegans	1	?	0	-	-	0	1	0	0	0	0	0	1	0
Styloichthys changae	?	?	?	?	?	0	1	0	0	0	0	0	0	0
Styracopterus fulcratus	-	?	1	0	1	?	1	1	1	?	0	0	0	0
Tanaocrossus kalliokoskii	?	?	?	?	?	?	1	1	?	?	?	?	?	?
Tegeolepis clarki	-	0	?	?	?	?	1	1	1	?	0	0	?	0
Tetragonolepis semicincta	0	0	0	-	-	0	1	0	0	0	0	1	1	0
Venusichthys comptus	0	0	0	-	-	0	1	0	1	0	0	0	0	0
Watsonulus eugnathoides	1	0	0	-	-	0	1	0	1	0	0	1	1	1
Wendyichthys dicksoni	-	1	1	0	?	0	1	1	1	?	0	0	0	0
Woodichthys bearsdeni	-	0	1	0	?	1	1	1	1	?	0	0	0	0

	76	77	78	79	80	81	82	83	84	85	86	87	88	89
Acanthodes bronni	?	?	?	?	?	?	?	?	?	-	?	?	?	?
Acipenser brevirostrum	-	-	-	0	1	0	-	-	-	0	-	?	0	-
Aesopichthys erinaceus	0	0	1	0	0	0	0	1	2	0	?	?	?	2
Amia calva	0	0	1	0	0	0	0	1	2	0	1	?	1	1
Amphicentrum granulosum	0	?	1	0	1	0	-	-	-	1	-	?	?	2
Atractosteus spatula	0	0	1	0	0	0	0	1	1	0	0	1	1	1
Australosomus kochi	1	0	1	0	0	0	0	1	2	0	?	?	0	1
Beagiascus pulcherrimus	?	?	?	0	0	0	0	1	1	0	1	?	?	?
Beishanichthys brevicaudalis	0	?	1	0	0	0	0	1	2	0	1	?	?	2
Birgeria groenlandica	0	0	1	0	0	0	0	1	1	0	1	?	0	1
Bobosatrania groenlandica	0	0	1	0	1	0	-	-	-	0	-	?	?	2
Boreosomus piveteaui	?	0	1	0	0	0	0	1	1	0	?	0	0	1
Brazilichthys macrognathus	0	0	1	0	0	1	0	1	1	0	1	?	0	1
Caturus furcatus	?	?	?	0	0	0	0	1	2	0	?	?	0	1
Cheirolepis canadensis	1	0	1	0	0	0	0	1	1	0	0	?	?	1
Cheirolepis schultzei	1	0	1	0	0	0	0	1	?	0	0	?	?	?
Cheirolepis trailli	1	0	1	0	0	0	0	1	1	0	0	?	?	1
Chondrosteus acipenseroides	?	0	1	0	1	0	-	-	-	0	-	?	0	?
Cladodoides wildungensis	?	?	?	?	-	?	1	?	?	-	0	0	?	?
Coccocephalichthys wildi	?	?	1	0	0	0	0	1	1	0	1	?	?	1
Cosmoptychius striatus	1	?	1	0	0	0	0	?	1	0	?	?	?	2

Cyranorhis bergeraci	0	?	1	0	0	0	0	1	2	0	?	?	?	?
Dapedium LIAS	?	?	1	1	0	0	0	1	2	0	?	?	0	?
Dapedium pholidotum	0	0	1	1	0	0	0	1	2	0	?	?	?	1
Dialipina salguerioensis	?	?	?	0	0	?	0	1	0	0	0	?	?	0
Dicksonosteus arcticus	?	?	?	?	?	?	?	?	?	0	?	?	?	?
Diplocercides kayseri	0	0	0	1	0	?	?	?	0	0	?	1	0	1
Dipteronotus ornatus	0	0	1	0	0	0	0	1	2	0	1	?	?	?
Discoserra pectinodon	0	0	1	0	0	0	0	1	2	0	?	?	?	2
Donnrosenia schaefferi	1	1	1	0	0	0	0	1	1	0	?	?	?	1
Dorsetichthys bechei	0	0	1	0	0	0	0	1	2	0	?	?	?	1
Ebenaqua ritchei	0	?	?	0	1	0	-	-	-	0	-	?	?	2
Elops hawaiensis	0	0	1	0	0	0	0	1	0	0	1	0	0	2
Entelognathus primordialis	0	?	0	0	1	0	0	1	?	0	?	-	?	0
Erpetoichthys calabaricus	0	0	1	0	0	0	0	1	2	0	?	0	0	2
Eusthenopteron foordi	0	0	0	0	0	0	0	1	1	0	0	0	0	0
Evenkia eunoptera	?	?	?	?	0	?	?	?	2	0	?	?	?	1
Fouldenia ischiptera	0	?	1	0	1	0	0	1	2	1	?	?	?	2
Fukangichthys longidorsalis	?	?	?	0	0	0	0	1	2	0	1	0	0	1
Glyptolepis groenlandica	?	0	0	0	0	?	1	0	?	0	?	1	?	?
Gogonasus andrewsae	0	0	0	0	0	1	1	0	2	0	?	0	0	0
Gogosardina coatesi	0	1	1	0	0	0	0	1	1	0	1	?	0	2
Guiyu oneiros	0	?	0	0	0	1	1	0	1	0	0	?	0	?
Hiodon alosoides	0	1	1	0	0	0	0	1	2	0	0	?	0	2
Howqualepis rostridens	0	0	1	0	0	1	1	1	1	0	?	?	1	1
Hulettia americana	0	?	1	0	0	?	0	1	2	0	?	?	?	1
Ichthyokentema purbeckensis	0	0	1	0	0	0	0	1	2	0	?	?	0	2
Kalops monophyrum	?	0	1	0	0	0	0	1	1	0	?	?	?	2
Kansasiella eatoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kentuckia deani	0	?	1	0	0	0	0	1	1	?	?	?	0	2
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	0	1	1	0	0	0	0	1	1	0	0	1	1	1
Leptolepis bronni	0	0	1	0	0	0	0	1	2	0	?	?	?	2
Ligulalepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	?	?	?	?	?	?	1	?	?	?	?	?
Luganoia lepidosteoides	0	0	1	0	0	0	0	1	2	0	1	?	0	2
Macrepistius arenatus	?	?	?	0	0	0	0	1	2	0	?	?	?	1
Macrosemimimus lennieri	?	?	?	0	0	0	0	1	2	0	?	?	?	1
Macrosemius rostratus	0	?	1	0	0	0	0	1	2	0	?	?	0	1
Meemannia eos	?	?	?	0	0	0	0	1	1	?	?	?	0	?
Melanecta anneae	?	?	1	0	0	0	0	1	?	0	?	?	?	?
Mesopoma planti	?	?	1	0	0	0	0	1	?	0	?	?	?	?
Miguashaia bureaui	0	0	0	1	0	0	0	1	2	0	?	0	0	2
Mimipiscis bartrami	0	1	1	0	0	0	0	1	1	0	1	0	0	2
Mimipiscis toombsi	0	1	1	0	0	0	0	1	1	0	1	0	0	2
Moythomasia durgaringa	0	0	1	0	0	0	0	1	1	0	1	0	0	1
Moythomasia lineata	1	0	1	0	0	0	0	1	1	0	?	?	?	1
Moythomasia nitida	1	0	1	0	0	0	0	1	1	0	?	?	?	1
Obaichthys decoratus	?	?	?	0	0	?	?	?	2	0	1	0	1	1
Onychodus jandemarrai	0	0	0	0	0	0	1	0	1	0	0	0	?	0
Osorioichthys marginis	1	0	1	0	0	0	0	1	1	0	?	?	?	1

Osteolepis macrolepidotus	0	0	0	0	0	0	0	1	?	0	0	?	?	?
Ozarcus mapesae	?	?	?	?	-	?	1	?	?	-	?	?	?	?
Peltopleurus lissocephalus	0	?	1	0	0	0	0	1	2	0	1	?	?	?
Platysomus superbus	0	0	1	0	?	0	0	1	2	?	?	?	?	2
Polypterus bichir	0	0	1	0	0	0	0	1	2	0	1	0	0	2
Porolepis sp.	0	0	?	0	0	0	1	0	2	0	0	1	?	?
Propterus elongatus	0	?	1	0	0	0	0	1	2	0	?	?	?	?
Psarolepis romeri	0	0	0	0	0	1	1	0	1	0	0	1	0	0
Pteronisculus stensioi	1	0	1	0	0	0	0	1	1	0	?	0	0	1
Raynerius splendens	0	0	1	0	0	0	0	1	1	0	1	0	0	1
Saurichthys madagascarensis	0	?	1	0	0	0	0	1	2	0	1	?	0	1
Scanilepis dubia	?	?	?	0	0	?	?	?	2	0	?	?	?	?
Semionotus elegans	0	0	1	0	0	0	0	1	2	0	1	0	?	1
Styloichthys changae	?	0	0	1	0	?	?	?	2	0	0	?	?	?
Styracopterus fulcratus	0	?	1	0	1	0	0	1	2	1	1	?	?	2
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	0	?	1	0	0	1	0	1	1	0	?	?	1	1
Tetragonolepis semicincta	0	?	1	0	0	0	0	1	2	0	?	?	?	1
Venusichthys comptus	0	0	1	0	0	0	0	1	2	0	?	?	?	?
Watsonulus eugnathoides	0	0	1	0	0	0	0	1	2	0	?	?	0	1
Wendyichthys dicksoni	0	0	1	0	0	0	0	1	2	0	?	?	0	?
Woodichthys bearsdeni	0	0	1	0	0	0	0	1	1	0	?	?	?	1

	91	92	93	94	95	96	97	98	99	100	101	102	103	104
Acanthodes bronni	?	?	0	-	?	-	?	0	2	1	?	0	0	0
Acipenser brevirostrum	-	-	0	-	0	-	1	0	0	1	0	1	1	-
Aesopichthys erinaceus	?	?	1	2	0	?	1	?	?	?	?	?	?	?
Amia calva	1	0	1	2	0	1	1	0	0	1	?	0	1	0
Amphicentrum granulosum	?	-	0	-	0	-	?	1	2	0	0	0	1	0
Atractosteus spatula	2	0	1	2	0	0	1	0	0	1	0	0	1	1
Australosomus kochi	-	-	0	-	0	-	1	0	2	0	0	0	0	0
Beagiascus pulcherrimus	?	?	?	-	0	?	1	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	?	?	1	?	0	?	?	?	?	?	?	?	?	?
Birgeria groenlandica	?	?	1	1	0	-	1	0	2	1	0	0	0	0
Bobosatrania groenlandica	?	?	0	-	?	-	?	0	?	?	?	0	?	0
Boreosomus piveteaui	3	0	0	-	0	-	1	0	2	0	0	0	0	1
Brazilichthys macrognathus	?	0	?	?	0	?	?	0	?	0	?	?	0	?
Caturus furcatus	3	0	1	2	0	1	1	0	2	1	0	0	1	?
Cheirolepis canadensis	?	0	0	-	0	?	?	?	?	?	?	?	?	?
Cheirolepis schultzei	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Cheirolepis trailli	1	0	0	-	0	-	1	0	1	0	0	0	0	0
Chondrosteus acipenseroides	-	-	?	?	0	-	?	0	?	?	?	1	?	?
Cladodoides wildungensis	?	?	0	-	-	-	?	0	?	0	-	0	?	-
Coccocephalichthys wildi	?	?	1	1	0	?	1	0	1	0	?	0	0	0
Cosmoptychius striatus	?	?	?	?	?	?	1	0	2	0	?	?	?	?
Cyranorhis bergeraci	?	?	?	?	0	?	?	?	2	0	?	?	?	?
Dapedium LIAS	?	0	1	?	0	?	?	?	?	?	?	0	?	?
Dapedium pholidotum	?	0	?	?	0	?	?	0	?	0	?	?	?	?
Dialipina salguerioensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	?	?	?	?	?	?	?	0	0	0	-	0	0	?

Diplocercides kayseri	?	1	1	3	0	1	0	0	2	1	?	0	0	0
Dipteronotus ornatus	?	?	?	?	0	?	?	0	?	1	?	?	?	?
Discoserra pectinodon	?	?	0	-	0	-	1	0	?	1	?	?	?	0
Donnrosenia schaefferi	?	?	0	-	0	-	?	?	?	?	?	?	?	?
Dorsetichthys bechei	?	?	?	2	1	0	?	0	?	1	?	0	?	?
Ebenaqua ritchei	?	0	0	-	0	?	1	0	?	?	?	?	?	?
Elops hawaiensis	-	-	1	2	0	0	?	0	2	1	0	0	1	0
Entelognathus primordialis	?	-	0	-	0	-	?	0	0	0	-	0	?	?
Erpetoichthys calabaricus	3	0	1	0	0	-	1	0	0	1	1	0	1	0
Eusthenopteron foordi	2	0	0	-	0	-	1	0	2	0	0	0	0	-
Evenkia eunoptera	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Fouldenia ischiptera	?	?	0	-	0	?	?	1	?	0	?	?	?	?
Fukangichthys longidorsalis	?	?	1	0	0	?	1	0	0	1	1	0	1	0
Glyptolepis groenlandica	2	?	0	-	0	-	0	0	2	0	0	0	0	-
Gogonasus andrewsae	2	0	0	-	0	?	1	0	2	0	?	0	0	-
Gogosardina coatesi	?	0	0	-	0	-	1	0	1	0	?	0	0	0
Guiyu oneiros	0	0	0	-	0	-	1	?	?	?	?	0	?	?
Hiodon alosoides	-	-	1	2	0	0	1	0	0	1	?	0	1	0
Howqualepis rostridens	?	0	0	-	0	-	1	0	1	0	0	0	0	0
Hulettia americana	?	?	1	2	0	0	?	0	2	1	0	0	1	0
Ichthyokentema purbeckensis	4	-	1	2	1	0	1	0	2	1	0	0	0	0
Kalops monophyrum	?	0	?	?	0	?	?	?	?	?	?	?	?	?
Kansasiella eatoni	?	?	?	?	0	?	?	?	1	?	?	?	?	?
Kentuckia deani	?	?	?	?	0	-	?	0	1	0	?	0	0	0
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	3	0	1	2	0	0	1	0	0	1	0	0	1	1
Leptolepis bronni	?	?	1	2	1	?	?	0	2	1	0	0	1	0
Ligulalepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	?	?	?	?	0	?	?	0	?	1	?	0	1	?
Macrepistius arenatus	?	?	1	?	0	?	?	?	?	?	?	?	?	?
Macrosemimimus lennieri	?	?	?	?	0	0	1	0	?	1	0	0	0	0
Macrosemius rostratus	4	0	1	2	0	?	1	0	0	1	?	0	0	0
Meemannia eos	?	0	0	-	0	-	1	?	?	?	?	?	?	?
Melanecta anneae	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Mesopoma planti	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Miguashaia bureaui	?	1	1	3	-	1	0	0	?	?	?	?	?	?
Mimipiscis bartrami	?	0	0	-	0	-	?	0	1	0	0	0	0	0
Mimipiscis toombsi	1	0	0	-	0	-	1	0	1	0	0	0	0	0
Moythomasia durgaringa	1	0	0	-	0	-	1	0	1	0	0	0	0	0
Moythomasia lineata	?	?	0	-	0	?	1	?	?	?	?	?	?	?
Moythomasia nitida	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Obaichthys decoratus	?	?	1	2	0	0	1	0	?	1	0	0	?	1
Onychodus jandemarrai	1	0	0	-	?	-	1	0	0	-	0	0	0	?
Osorioichthys marginis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Osteolepis macrolepidotus	2	0	0	-	0	-	?	0	?	?	?	0	?	?
Ozarcus mapesae	?	?	?	-	-	-	?	0	?	0	-	0	0	?
Peltopleurus lissocephalus	?	?	?	?	0	?	?	0	?	?	?	?	?	?
Platysomus superbus	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Polypterus bichir	3	0	1	0	0	-	1	0	0	1	1	0	1	0

Porolepis sp.	2	0	0	-	0	-	?	0	0	0	?	0	0	-
Propterus elongatus	?	?	?	?	0	?	?	0	?	1	?	0	?	0
Psarolepis romeri	0	0	0	-	?	?	1	?	?	?	?	0	?	?
Pteronisculus stensioi	2	0	0	-	0	-	1	0	2	0	0	0	0	0
Raynerius splendens	?	0	0	-	0	-	1	0	1	0	0	0	0	0
Saurichthys madagascarensis	?	?	?	?	0	?	1	0	0	0	0	0	0	0
Scanilepis dubia	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Semionotus elegans	?	0	1	2	0	0	1	0	?	1	?	0	?	0
Styloichthys changae	?	?	0	-	0	1	0	?	?	?	?	0	?	?
Styracopterus fulcratus	?	?	0	-	0	?	?	1	?	?	?	?	?	?
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Tetragonolepis semicincta	4	-	?	?	0	0	1	0	?	1	0	0	1	0
Venusichthys comptus	?	?	?	?	0	?	?	0	?	?	?	?	?	?
Watsonulus eugnathoides	2	0	1	2	0	1	1	0	2	1	?	0	1	0
Wendyichthys dicksoni	?	?	0	-	0	?	?	?	2	?	?	?	?	?
Woodichthys bearsdeni	?	?	0	-	0	?	?	0	0	0	?	0	0	0

	106	107	108	109	110	111	112	113	114	115	116	117	118	119
Acanthodes bronni	-	?	-	?	?	?	?	-	?	-	-	?	?	0
Acipenser brevirostrum	1	1	0	0	2	0	0	0	2	-	-	-	0	1
Aesopichthys erinaceus	?	?	?	0	1	0	0	1	0	1	0	0	0	1
Amia calva	0	0	1	0	0	0	1	0	0	2	1	0	1	0
Amphicentrum granulosum	?	?	?	0	2	0	0	1	0	1	0	0	0	0
Atractosteus spatula	0	0	1	0	1	0	1	0	0	2	1	0	0	1
Australosomus kochi	0	0	0	0	1	0	0	0	0	1	0	0	0	0
Beagiascus pulcherrimus	?	?	?	1	1	0	0	0	0	0	0	0	0	1
Beishanichthys brevicaudalis	?	?	?	0	1	0	0	0	0	0	0	0	0	0
Birgeria groenlandica	0	-	-	0	1	0	0	0	0	0	0	0	0	0
Bobosatrania groenlandica	?	?	?	0	-	1	-	-	1	1	0	0	0	-
Boreosomus piveteaui	1	0	0	0	1	0	0	0	0	1	0	0	0	1
Brazilichthys macrognathus	0	?	?	?	?	?	?	?	?	?	?	?	?	0
Caturus furcatus	0	0	1	0	0	0	1	0	0	2	1	0	?	1
Cheirolepis canadensis	?	?	?	1	0	0	0	0	0	0	0	0	0	0
Cheirolepis schultzei	0	?	?	1	0	0	0	0	0	0	0	0	0	0
Cheirolepis trailli	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Chondrosteus acipenseroides	0	?	?	0	2	0	0	0	?	?	-	?	?	0
Cladodoides wildungensis	-	-	-	?	?	-	?	-	-	-	?	-	-	?
Coccocephalichthys wildi	0	?	0	?	1	0	1	?	0	0	0	0	0	?
Cosmoptychius striatus	?	?	?	1	0	0	0	0	0	0	0	0	0	1
Cyranorhis bergeraci	?	?	?	0	0	0	0	0	0	0	0	0	0	0
Dapedium LIAS	0	?	?	0	1	0	1	0	0	2	1	0	1	0
Dapedium pholidotum	0	?	1	0	1	0	0	0	0	2	1	0	1	0
Dialipina salguerioensis	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Dicksonosteus arcticus	?	-	-	0	?	?	?	?	0	?	?	?	?	?
Diplocercides kayseri	0	?	0	0	0	0	?	0	1	0	0	0	0	-
Dipteronotus ornatus	?	?	?	?	1	0	0	0	0	1	0	0	0	?
Discoserra pectinodon	0	?	?	0	-	1	-	-	1	2	0	0	0	0
Donnrosenia schaefferi	?	?	?	1	0	0	1	0	0	0	?	0	0	0
Dorsetichthys bechei	1	1	?	0	1	0	0	0	0	2	1	0	1	?

Ebenaqua ritchei	?	?	?	0	0	0	0	0	1	1	0	0	0	-
Elops hawaiensis	1	1	1	0	0	0	0	1	0	2	1	0	1	0
Entelognathus primordialis	-	-	-	0	?	?	?	?	0	?	-	0	?	?
Erpetoichthys calabaricus	0	1	0	0	-	1	-	-	0	0	0	0	0	-
Eusthenopteron foordi	0	0	0	0	1	0	0	0	1	0	0	0	0	-
Evenkia eunoptera	?	?	?	1	1	0	0	1	0	0	0	0	0	0
Fouldenia ischiptera	?	?	?	0	1	0	0	1	0	0	0	0	0	0
Fukangichthys longidorsalis	0	1	0	0	1	0	0	0	0	0	0	0	0	0
Glyptolepis groenlandica	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Gogonasus andrewsae	0	0	0	0	1	0	0	0	1	0	0	0	0	?
Gogosardina coatesi	0	?	0	0	1	0	1	0	0	0	0	0	0	0
Guiyu oneiros	?	0	0	0	0	0	1	0	0	0	0	0	0	0
Hiodon alosoides	1	1	0	0	0	0	0	0	0	2	1	0	0	0
Howqualepis rostridens	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Hulettia americana	?	1	?	0	0	0	1	0	0	2	1	0	1	0
Ichthyokentema purbeckensis	?	1	1	0	0	0	1	0	0	2	1	0	1	0
Kalops monophyrum	?	?	?	0	0	0	0	1	0	0	0	0	0	1
Kansasiella eatoni	?	?	0	?	?	?	?	?	?	0	0	0	?	?
Kentuckia deani	0	?	?	1	0	0	0	0	0	0	0	0	0	0
Lawrenciella schaefferi	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	0	0	1	0	1	0	1	0	0	2	1	0	0	1
Leptolepis bronni	1	1	?	0	1	0	0	0	0	2	1	0	1	0
Ligulalepis	?	?	-	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	?	1	1	0	1	0	0	0	0	2	0	0	0	0
Macrepistius arenatus	?	0	?	0	0	0	1	0	0	2	1	0	1	0
Macrosemimimus lennieri	?	?	?	0	0	0	1	0	0	2	1	0	1	0
Macrosemius rostratus	0	0	1	0	0	0	1	0	0	2	-	1	1	0
Meemannia eos	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Melanecta anneae	?	?	?	0	1	0	0	0	0	0	0	0	0	?
Mesopoma planti	?	?	?	0	1	0	0	0	0	0	0	0	0	1
Miguashaia bureaui	0	?	0	0	0	0	0	0	1	0	0	0	0	-
Mimipiscis bartrami	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Mimipiscis toombsi	0	0	0	0	1	0	1	0	0	0	0	0	0	0
Moythomasia durgaringa	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Moythomasia lineata	?	?	?	0	0	0	1	0	0	0	?	0	0	1
Moythomasia nitida	?	?	?	1	1	0	0	0	0	0	0	0	0	1
Obaichthys decoratus	0	0	1	0	0	0	1	0	0	2	1	0	1	0
Onychodus jandemarrai	0	-	-	0	1	0	0	0	1	0	0	0	0	-
Osorioichthys marginis	?	?	?	0	1	0	0	0	0	0	0	0	0	1
Osteolepis macrolepidotus	?	0	0	0	1	0	0	0	1	0	0	0	0	1
Ozarcus mapesae	-	-	-	?	?	-	?	-	-	-	-	-	-	?
Peltopleurus lissocephalus	?	?	?	0	1	0	0	0	0	1	0	0	0	0
Platysomus superbus	?	?	?	0	1	0	0	0	0	1	0	0	0	0
Polypterus bichir	0	1	0	0	0	0	1	0	0	0	0	0	0	-
Porolepis sp.	0	0	0	0	1	0	0	0	1	0	0	0	0	0
Propterus elongatus	?	0	?	0	0	0	1	0	0	2	-	1	0	0
Psarolepis romeri	0	0	0	0	?	0	?	?	0	0	?	0	0	?
Pteronisculus stensioi	0	0	0	1	1	0	0	0	0	0	0	0	0	0
Raynerius splendens	0	?	?	?	0	0	0	0	0	0	0	1	0	0

Saurichthys madagascarensis	?	0	0	0	-	1	-	-	0	0	0	0	0	-
Scanilepis dubia	?	?	?	1	1	0	0	?	0	0	0	0	0	0
Semionotus elegans	0	0	1	0	0	0	1	0	0	2	1	0	1	0
Styloichthys changae	0	?	0	?	?	?	?	?	0	0	0	0	?	?
Styracopterus fulcratus	?	?	?	0	2	0	0	1	0	0	0	0	0	1
Tanaocrossus kalliokoskii	?	?	?	?	1	0	0	?	?	?	?	0	0	?
Tegeolepis clarki	?	?	?	?	1	?	?	0	0	0	0	?	0	0
Tetragonolepis semicincta	?	1	?	0	0	0	1	0	0	2	1	0	1	0
Venusichthys comptus	?	?	?	0	0	0	0	0	1	1	1	0	0	0
Watsonulus eugnathoides	0	?	1	0	1	1	1	0	0	1	1	0	1	1
Wendyichthys dicksoni	?	?	?	0	0	0	0	0	0	0	0	0	0	1
Woodichthys bearsdeni	?	?	?	0	1	0	0	0	0	0	0	0	0	0

	121	122	123	124	125	126	127	128	129	130	131	132	133	134
Acanthodes bronni	?	0	-	?	?	?	?	0	0	0	0	?	?	?
Acipenser brevirostrum	-	0	-	0	-	0	1	0	0	0	0	0	-	?
Aesopichthys erinaceus	?	1	1	?	?	?	?	?	?	?	0	?	?	?
Amia calva	-	1	1	0	0	0	?	0	0	0	0	0	1	1
Amphicentrum granulosum	?	?	?	0	0	0	1	?	?	?	0	?	?	?
Atractosteus spatula	-	0	-	0	0	0	1	0	0	0	0	0	-	0
Australosomus kochi	?	1	0	0	0	0	1	0	0	1	0	0	1	0
Beagiascus pulcherrimus	1	1	0	?	?	?	?	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Birgeria groenlandica	1	1	0	0	0	0	1	0	0	?	0	0	1	0
Bobosatrania groenlandica	-	0	-	?	?	?	1	0	?	?	?	0	?	?
Boreosomus piveteaui	1	1	0	0	0	?	1	0	1	0	0	0	1	?
Brazilichthys macrognathus	0	1	1	?	?	?	1	?	?	?	?	0	?	?
Caturus furcatus	-	1	1	0	0	0	1	0	?	?	0	?	?	?
Cheirolepis canadensis	0	?	?	?	0	?	?	?	?	?	?	?	?	?
Cheirolepis schultzei	?	1	?	?	0	?	?	?	?	?	?	?	?	?
Cheirolepis trailli	0	1	0	0	0	?	0	?	?	0	0	?	?	?
Chondrosteus acipenseroides	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cladodoides wildungensis	?	?	-	?	?	0	0	0	0	0	0	1	?	0
Coccocephalichthys wildi	?	?	?	0	0	?	1	0	?	?	0	0	0	?
Cosmoptychius striatus	1	1	0	?	?	?	1	?	?	?	?	?	?	?
Cyranorhis bergeraci	1	1	0	?	?	?	?	?	?	?	?	?	?	?
Dapedium LIAS	-	1	1	?	?	?	1	0	?	0	0	0	1	?
Dapedium pholidotum	-	1	1	?	?	?	?	?	?	?	?	?	?	?
Dialipina salguerioensis	0	0	-	?	?	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	?	?	?	0	0	0	0	0	0	0	0	1	?	?
Diplocercides kayseri	0	0	-	0	?	0	0	0	?	0	1	0	?	?
Dipteronotus ornatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Discoserra pectinodon	1	0	-	?	?	?	?	0	?	?	0	0	?	?
Donnrosenia schaefferi	0	1	0	?	0	?	?	?	?	?	?	?	?	?
Dorsetichthys bechei	-	1	1	?	?	?	1	?	?	1	0	0	0	0
Ebenaqua ritchei	-	0	?	?	?	?	?	?	?	?	?	?	?	?
Elops hawaiensis	-	1	1	0	0	0	1	0	?	?	0	0	?	?
Entelognathus primordialis	0	?	?	?	?	0	?	0	?	?	0	?	?	?
Erpetoichthys calabaricus	0	0	-	0	0	0	0	1	0	0	0	0	-	0
Eusthenopteron foordi	0	1	0	1	1	0	0	0	0	0	1	0	?	?

Evenkia eunoptera	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Fouldenia ischiptera	1	1	0	?	?	?	?	?	?	?	?	?	?	?
Fukangichthys longidorsalis	0	1	0	?	?	?	0	1	?	?	?	0	?	?
Glyptolepis groenlandica	0	1	0	1	0	1	0	0	?	0	1	0	?	?
Gogonasus andrewsae	0	?	0	1	1	0	0	0	?	0	1	0	?	?
Gogosardina coatesi	0	?	0	?	0	?	?	?	?	?	?	?	?	?
Guiyu oneiros	0	1	0	0	0	1	0	?	?	?	1	?	?	?
Hiodon alosoides	-	0	-	0	0	0	?	?	0	0	0	0	1	1
Howqualepis rostridens	0	1	0	?	0	?	?	?	?	?	?	?	?	?
Hulettia americana	-	0	-	?	?	?	?	?	?	?	0	?	?	?
Ichthyokentema purbeckensis	-	1	1	0	0	0	1	0	?	?	0	0	1	0
Kalops monophyrum	1	1	0	?	?	?	?	?	?	?	?	?	?	?
Kansasiella eatoni	?	?	?	0	?	?	1	0	1	1	0	0	1	1
Kentuckia deani	1	1	?	0	0	?	1	0	0	1	0	0	?	1
Lawrenciella schaefferi	?	?	?	0	?	?	1	0	1	1	0	0	1	0
Lepisosteus osseus	-	0	-	?	?	?	?	0	?	?	?	?	?	?
Leptolepis bronni	-	1	1	?	?	?	1	0	?	?	0	0	1	0
Ligulalepis	?	?	?	?	?	?	0	0	?	0	0	1	0	?
Luederia kempi	?	?	?	0	?	?	1	0	?	1	0	0	?	?
Luganoia lepidosteoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrepistius arenatus	?	?	?	?	?	?	1	0	?	?	0	0	1	0
Macrosemimimus lennieri	?	?	?	?	?	?	?	0	?	?	0	0	?	?
Macrosemius rostratus	-	0	-	?	?	?	?	?	?	?	0	?	?	?
Meemannia eos	?	?	?	?	?	?	0	?	?	?	0	?	?	?
Melanecta anneae	?	?	?	?	0	?	?	?	?	?	?	?	?	?
Mesopoma planti	?	?	?	?	0	?	?	0	?	?	?	?	?	?
Miguashaia bureaui	0	0	-	?	?	?	?	?	?	?	?	?	?	?
Mimipiscis bartrami	0	1	0	0	0	?	1	0	?	0	0	?	0	0
Mimipiscis toombsi	0	1	0	0	0	?	1	0	?	0	0	0	0	0
Moythomasia durgaringa	0	1	0	0	0	?	1	0	?	0	0	0	1	1
Moythomasia lineata	0	1	0	?	?	?	?	?	?	?	?	?	?	?
Moythomasia nitida	1	1	0	?	?	?	?	?	?	?	?	?	?	?
Obaichthys decoratus	-	0	-	?	?	?	?	?	?	?	0	?	?	?
Onychodus jandemarrai	0	0	-	?	?	1	0	0	?	0	1	0	?	?
Osorioichthys marginis	0	1	0	?	0	?	?	0	?	?	?	0	?	?
Osteolepis macrolepidotus	0	1	0	1	?	?	?	0	?	0	1	?	?	?
Ozarcus mapesae	?	?	-	?	?	0	0	0	0	0	0	1	?	?
Peltopleurus lissocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platysomus superbus	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Polypterus bichir	0	0	-	0	0	0	0	1	?	?	0	0	-	0
Porolepis sp.	0	1	0	1	0	1	0	0	?	?	1	0	?	?
Propterus elongatus	-	0	-	?	?	?	?	?	?	?	?	?	?	?
Psarolepis romeri	?	?	?	0	0	1	0	0	?	?	1	1	?	?
Pteronisculus stensioi	1	1	0	0	0	?	1	0	?	1	0	0	1	1
Raynerius splendens	0	1	1	?	?	0	1	0	0	0	0	0	?	?
Saurichthys madagascarensis	-	0	-	0	0	0	1	0	?	0	0	0	?	?
Scanilepis dubia	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Semionotus elegans	-	0	-	?	?	?	?	?	?	?	?	?	?	?
Styloichthys changae	?	?	?	1	?	1	0	0	?	?	1	1	?	?
Styracopterus fulcratus	1	1	0	?	?	?	?	?	?	?	?	?	?	?

Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	1	1	0	?	0	?	?	?	?	?	?	?	?	?
Tetragonolepis semicincta	-	1	1	?	0	?	1	0	?	?	0	0	?	?
Venusichthys comptus	-	1	?	?	?	?	?	?	?	?	?	?	?	?
Watsonulus eugnathoides	-	1	1	0	0	0	1	?	?	0	0	0	1	1
Wendyichthys dicksoni	1	1	0	?	0	?	?	?	?	?	?	0	?	?
Woodichthys bearsdeni	1	0	?	?	0	?	?	?	?	?	0	?	?	?

	136	137	138	139	140	141	142	143	144	145	146	147	148	149
Acanthodes bronni	?	0	0	0	0	0	0	0	0	?	?	?	1	0
Acipenser brevirostrum	0	0	2	0	-	-	0	1	0	0	-	-	0	-
Aesopichthys erinaceus	?	?	2	?	?	?	?	?	?	?	?	?	1	?
Amia calva	2	0	2	1	-	-	1	1	0	0	-	0	0	-
Amphicentrum granulosum	2	0	?	0	0	1	0	?	?	0	-	0	0	?
Atractosteus spatula	2	0	2	0	0	1	1	1	0	0	-	0	0	-
Australosomus kochi	2	0	2	1	-	-	?	1	0	1	1	0	1	0
Beagiascus pulcherrimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Birgeria groenlandica	2	0	2	?	-	-	0	1	0	?	?	?	1	-
Bobosatrania groenlandica	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Boreosomus piveteaui	2	0	2	0	0	1	0	1	0	1	0	0	1	0/1
Brazilichthys macrognathus	?	?	?	0	0	1	?	?	?	?	?	?	?	?
Caturus furcatus	?	0	2	1	-	-	1	?	?	0	-	0	0	?
Cheirolepis canadensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis schultzei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis trailli	?	0	1	0	0	0	0	0	0	1	0	0	1	?
Chondrosteus acipenseroides	?	?	?	0	0	0	?	?	?	?	?	?	?	?
Cladodoides wildungensis	0	0	0	1	0	-	0	0	0	0	-	0	1	0
Coccocephalichthys wildi	2	0	2	0	0	0	0	?	0	1	0	0	1	?
Cosmoptychius striatus	?	0	?	0	0	1	?	?	?	1	1	0	1	?
Cyranorhis bergeraci	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dapedium LIAS	2	0	?	0	0	1	1	1	0	0	-	0	0	?
Dapedium pholidotum	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Dialipina salguerioensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	?	?	0	?	?	?	0	0	0	0	-	0	0	?
Diplocercides kayseri	0	1	0	0	0	0	0	0	1	0	-	1	0	?
Dipteronotus ornatus	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Discoserra pectinodon	2	?	2	?	-	-	1	1	?	0	-	0	?	?
Donnrosenia schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetichthys bechei	2	0	2	0	0	1	1	1	0	1	0	0	1	?
Ebenaqua ritchei	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Elops hawaiensis	2	0	0	0	-	-	1	1	0	0	-	0	0	-
Entelognathus primordialis	?	0	?	?	?	?	0	?	0	0	-	?	0	?
Erpetoichthys calabaricus	0	0	1	1	-	-	0	0	0	1	-	0	0	-
Eusthenopteron foordi	0	1	0	0	1	0	0	0	1	1	0	0	1	-
Evenkia eunoptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fouldenia ischiptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fukangichthys longidorsalis	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Glyptolepis groenlandica	0	1	0	?	1	?	0	0	1	?	?	?	?	?
Gogonasus andrewsae	0	1	0	0	1	0	0	0	?	1	0	0	1	-

Gogosardina coatesi	?	?	?	0	0	0	?	?	?	?	?	?	?	?
Guiyu oneiros	?	?	?	0	?	0	0	?	?	?	?	?	?	?
Hiodon alosoides	2	0	1	0	-	0	1	1	0	0	-	0	0	-
Howqualepis rostridens	?	?	1	0	0	0	?	?	?	1	0	?	?	?
Hulettia americana	?	0	2	0	?	1	1	?	?	?	-	0	1	?
Ichthyokentema purbeckensis	2	0	?	0	0	1	1	1	0	0	-	0	0	-
Kalops monophyrum	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Kansasiella eatoni	2	?	2	0	0	1	0	1	0	1	0	0	1	1
Kentuckia deani	1	0	2	0	0	1	0	1	0	1	1	0	1	0
Lawrenciella schaefferi	2	0	2	0	0	1	0	1	0	1	0	0	1	1
Lepisosteus osseus	2	0	2	0	0	1	1	1	0	1	-	0	0	-
Leptolepis bronni	2	?	?	0	0	1	1	?	?	0	-	0	0	-
Ligulalepis	0	?	0	0	0	?	0	?	0	1	?	0	1	?
Luederia kempi	2	0	2	0	0	1	0	1	0	1	0	0	1	0
Luganoia lepidosteoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrepistius arenatus	2	0	?	0	0	1	1	?	0	0	-	0	0	?
Macrosemimimus lennieri	2	0	2	0	0	1	?	?	?	0	-	0	0	?
Macrosemius rostratus	2	?	?	0	0	1	1	?	?	0	-	0	0	?
Meemannia eos	?	?	1	?	?	?	0	0	0	?	?	?	1	?
Melanecta anneae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesopoma planti	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miguashaia bureaui	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mimipiscis bartrami	0	0	1	0	0	0	0	0	0	1	0	0	1	?
Mimipiscis toombsi	0	0	1	0	0	0	0	0	0	1	0	0	1	0
Moythomasia durgaringa	1	0	1	0	0	0	0	0	0	1	0	0	1	0
Moythomasia lineata	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Moythomasia nitida	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Obaichthys decoratus	?	?	?	0	0	1	?	?	?	0	-	0	0	?
Onychodus jandemarrai	0	?	?	0	0	0	?	?	0	1	?	1	1	?
Osorioichthys marginis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Osteolepis macrolepidotus	?	?	?	?	?	?	0	?	1	?	?	?	?	?
Ozarcus mapesae	0	0	0	1	?	?	0	?	0	0	-	0	1	?
Peltopleurus lissocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platysomus superbus	?	?	?	0	?	1	?	?	?	?	?	?	?	?
Polypterus bichir	0	0	1	1	-	-	0	0	0	1	-	0	0	?
Porolepis sp.	0	1	0	0	0	0	0	0	?	1	0	?	?	?
Propterus elongatus	?	?	?	0	?	1	?	?	?	?	?	?	?	?
Psarolepis romeri	0	?	1	0	0	0	0	?	?	?	?	0	1	?
Pteronisculus stensioi	2	0	2	0	0	1	0	1	0	1	1	0	1	0
Raynerius splendens	1	0	1	0	0	0	0	0	0	1	0	0	1	0
Saurichthys madagascarensis	2	0	2	1	-	0	?	1	0	0	-	0	0	?
Scanilepis dubia	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Semionotus elegans	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Styloichthys changae	0	1	0	0	0	0	0	?	?	0	-	1	?	?
Styracopterus fulcratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tetragonolepis semicincta	?	?	2	0	0	1	1	?	?	0	-	0	0	?
Venusichthys comptus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watsonulus eugnathoides	2	0	2	0	0	1	1	?	?	1	1	0	1	-

Wendyichthys dicksoni	2	?	?	?	?	0	?	?	?	1	?	?	1	?
Woodichthys bearsdeni	?	0	?	0	?	1	0	?	?	1	0	0	1	?

	151	152	153	154	155	156	157	158	159	160	161	162	163	164
Acanthodes bronni	0	-	-	0	-	?	0	?	?	?	?	?	?	?
Acipenser brevirostrum	0	-	-	1	-	1	0	?	1	0	0	?	0	1
Aesopichthys erinaceus	?	?	?	?	?	0	0	-	-	-	-	-	-	-
Amia calva	0	-	-	1	-	1	1	-	0	0	1	1	1	0
Amphicentrum granulosum	2	1	0	1	1	?	?	?	?	?	0	?	?	?
Atractosteus spatula	0	-	-	1	-	1	1	-	0	1	1	0	1	1
Australosomus kochi	2	0	0	1	0	0	1	-	-	-	-	-	-	-
Beagiascus pulcherrimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Birgeria groenlandica	?	?	?	1	?	1	0	-	?	-	0	?	?	?
Bobosatrania groenlandica	?	?	?	?	?	?	1	?	?	?	?	?	?	?
Boreosomus piveteaui	2	1	1	1	0	0	0	-	-	-	-	-	-	-
Brazilichthys macrognathus	?	?	?	?	?	0	1	?	?	?	?	?	?	?
Caturus furcatus	?	?	?	?	?	1	0	?	0	0	0	1	1	0
Cheirolepis canadensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis schultzei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis trailli	0	-	-	1	-	0	0	-	-	-	-	-	-	-
Chondrosteus acipenseroides	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cladodoides wildungensis	-	-	-	0	-	0	0	-	-	-	-	-	-	-
Coccocephalichthys wildi	2	1	0	1	1	0	0	-	-	-	-	-	-	-
Cosmoptychius striatus	1	1	1	1	1	?	0	?	?	0	0	?	?	?
Cyranorhis bergeraci	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dapedium LIAS	2	?	?	1	?	0	-	-	-	-	-	-	-	-
Dapedium pholidotum	?	?	?	?	?	0	-	-	-	-	-	-	-	-
Dialipina salguerioensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	0	-	-	0	?	0	0	?	?	?	?	?	?	?
Diplocercides kayseri	0	-	-	1	-	0	0	-	-	-	-	-	-	-
Dipteronotus ornatus	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Discoserra pectinodon	?	?	?	?	?	0	-	-	-	-	-	-	-	-
Donnrosenia schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetichthys bechei	0	?	?	?	?	1	0	1	0	0	0	0	0	0
Ebenaqua ritchei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Elops hawaiensis	0	-	-	1	-	1	1	?	0	1	0	0	1	0
Entelognathus primordialis	0	?	?	0	-	0	0	-	-	-	-	-	-	-
Erpetoichthys calabaricus	2	0	0	1	1	1	0	?	?	?	0	?	0	0
Eusthenopteron foordi	0	-	-	1	-	0	0	-	-	-	-	-	-	-
Evenkia eunoptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fouldenia ischiptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fukangichthys longidorsalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Glyptolepis groenlandica	?	?	?	?	?	0	0	-	-	-	-	-	-	-
Gogonasus andrewsae	0	-	-	1	-	0	0	-	-	-	-	-	-	-
Gogosardina coatesi	1	0	0	1	?	?	0	?	?	?	?	?	?	?
Guiyu oneiros	?	?	?	?	?	?	0	?	?	?	-	?	?	?
Hiodon alosoides	0	-	-	-	-	1	1	-	0	1	0	0	1	0
Howqualepis rostridens	0	-	-	1	-	?	0	?	?	?	-	?	?	?
Hulettia americana	0	-	-	1	-	1	0	0	0	?	0	0	0	0

Ichthyokentema purbeckensis	0	-	-	1	?	1	1	1	0	1	?	0	0	0
Kalops monophyrum	?	?	?	?	?	0	?	-	-	-	-	-	-	-
Kansasiella eatoni	1	1	1	1	1	1	0	0	-	?	0	0	0	0
Kentuckia deani	1	1	0	1	0	0	0	-	-	-	-	-	-	-
Lawrenciella schaefferi	1	1	0	1	1	0	0	-	-	-	-	-	-	-
Lepisosteus osseus	0	-	-	1	-	1	1	-	0	1	1	0	1	1
Leptolepis bronni	2	1	1	1	?	1	0	?	?	0	0	0	0	0
Ligulalepis	?	?	?	?	?	0	0	-	-	-	-	-	-	-
Luederia kempi	2	1	1	?	1	0	0	-	-	-	?	-	-	-
Luganoia lepidosteoides	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Macrepistius arenatus	?	?	?	?	?	1	0	1	0	0	1	0	0	0
Macrosemimimus lennieri	0	-	-	1	?	1	1	-	0	1	0	1	1	1
Macrosemius rostratus	?	?	?	?	?	1	1	-	0	1	0	0	1	1
Meemannia eos	?	?	?	?	?	0	?	-	-	-	-	-	-	-
Melanecta anneae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesopoma planti	?	?	?	?	?	?	0	?	?	?	?	?	?	?
Miguashaia bureaui	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mimipiscis bartrami	2	0	0	1	0	0	0	-	-	-	-	-	-	-
Mimipiscis toombsi	2	0	0	1	0/1	0	0	-	-	-	-	-	-	-
Moythomasia durgaringa	1	0	0	1	0	0	0	-	-	-	-	-	-	-
Moythomasia lineata	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Moythomasia nitida	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Obaichthys decoratus	0	-	-	1	-	1	?	-	?	1	1	?	1	1
Onychodus jandemarrai	?	?	?	1	?	?	0	?	?	?	?	?	?	?
Osorioichthys marginis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Osteolepis macrolepidotus	?	?	?	?	?	0	0	-	-	-	-	-	-	-
Ozarcus mapesae	-	-	-	0	-	0	0	-	-	-	-	-	-	-
Peltopleurus lissocephalus	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Platysomus superbus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polypterus bichir	?	?	?	?	?	1	0	?	?	?	0	?	0	0
Porolepis sp.	0	-	-	1	-	0	0	-	-	-	-	-	-	-
Propterus elongatus	?	?	?	?	?	?	?	?	?	?	0	?	?	?
Psarolepis romeri	?	?	?	?	?	0	0	-	-	-	-	-	-	-
Pteronisculus stensioi	2	1	0	1	1	0	0	-	-	-	-	-	-	-
Raynerius splendens	1	0	0	1	0	0	0	-	-	-	-	-	-	-
Saurichthys madagascarensis	?	?	?	?	?	0	-	-	-	-	-	-	-	-
Scanilepis dubia	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Semionotus elegans	?	?	?	?	?	1	?	?	0	1	?	1	1	1
Styloichthys changae	0	-	-	1	-	0	0	-	-	-	-	-	-	-
Styracopterus fulcratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tetragonolepis semicincta	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Venusichthys comptus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watsonulus eugnathoides	0	-	-	1	-	1	0	1	0	0	1	0	0	0
Wendyichthys dicksoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Woodichthys bearsdeni	1	1	0	1	1	0	0	-	-	-	-	-	-	-

	166	167	168	169	170	171	172	173	174	175	176	177	178	179
Acanthodes bronni	?	0	0	0	0	-	-	-	-	-	-	-	-	1

Acipenser brevirostrum	-	0	0	0	1	2	1	1	1	2	0	0	1	1
Aesopichthys erinaceus	-	?	?	?	?	?	?	?	?	?	?	?	?	?
Amia calva	1	1	0	1	1	2	1	1	1	0	0	0	1	0
Amphicentrum granulosum	?	1	?	0	1	1	1	0	0	?	0	0	1	?
Atractosteus spatula	-	1	0	1	1	2	1	1	1	0	0	0	1	0
Australosomus kochi	-	0	?	1	1	0	1	0	1	2	0	0	0	0
Beagiascus pulcherrimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Birgeria groenlandica	-	0	0	0	1	2	1	0	1	2	0	0	1	1
Bobosatrania groenlandica	?	?	?	?	1	2	1	?	?	2	?	?	?	?
Boreosomus piveteaui	-	0	0	0	1	0	1	0	1	0	1	0	0	0
Brazilichthys macrognathus	?	?	?	?	1	0	1	0	1	2	0	?	0	?
Caturus furcatus	1	1	?	?	1	2	1	1	1	0	0	0	0	0
Cheirolepis canadensis	?	?	?	?	1	?	0	0	?	?	?	?	?	?
Cheirolepis schultzei	?	?	?	?	1	?	?	?	?	0	?	?	?	?
Cheirolepis trailli	-	0	0	0	1	0	0	0	0	0	0	0	0	0
Chondrosteus acipenseroides	?	?	?	?	1	2	1	1	?	2	0	0	1	1
Cladodoides wildungensis	-	0	0	0	0	-	-	-	-	-	-	-	-	1
Coccocephalichthys wildi	-	0	?	0	1	0	1	0	1	0	0	0	0	0
Cosmoptychius striatus	?	?	?	?	1	0	1	?	1	?	0	0	0	0
Cyranorhis bergeraci	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dapedium LIAS	-	1	1	1	1	2	1	?	?	?	?	?	1	?
Dapedium pholidotum	-	?	?	?	?	?	?	?	?	?	?	?	?	?
Dialipina salguerioensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	?	0	0	0	1	0	0	0	0	0	0	0	0	?
Diplocercides kayseri	-	0	0	0	1	0	0	0	0	0	0	0	0	?
Dipteronotus ornatus	?	?	?	?	1	1	1	0	1	2	0	0	?	?
Discoserra pectinodon	-	1	?	?	1	2	1	?	0	?	0	?	?	?
Donnrosenia schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetichthys bechei	1	1	1	1	1	2	1	0	0	0	1	1	1	1
Ebenaqua ritchei	?	?	?	?	1	?	1	?	?	?	?	?	?	?
Elops hawaiensis	1	1	1	1	1	2	0	0	1	0	1	0	1	?
Entelognathus primordialis	-	0	0	0	?	-	-	-	-	?	-	-	?	0
Erpetoichthys calabaricus	0	0	0	0	1	2	1	0	1	0	0	0	1	0
Eusthenopteron foordi	-	0	0	0	1	0	0	0	0	0	0	0	0	1
Evenkia eunoptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fouldenia ischiptera	?	?	?	?	1	?	?	?	?	?	?	?	?	0
Fukangichthys longidorsalis	?	?	?	?	1	?	1	0	0	0	0	0	?	0
Glyptolepis groenlandica	-	0	0	0	1	0	0	0	0	0	0	0	0	0
Gogonasus andrewsae	-	0	0	0	1	0	0	0	1	0	0	0	0	?
Gogosardina coatesi	?	?	?	?	1	0	0	?	?	0	0	0	0	?
Guiyu oneiros	-	?	?	?	1	0	0	0	0	0	0	0	0	?
Hiodon alosoides	1	1	?	1	1	2	1	0	1	1	0	0	1	0
Howqualepis rostridens	?	?	?	?	1	0	1	1	0	0	0	0	0	0
Hulettia americana	0	?	0	?	1	1	1	1	0	1	1	1	0	0
Ichthyokentema purbeckensis	1	1	1	1	1	2	1	0	0	1	1	0	0	?
Kalops monophyrum	-	?	?	?	?	?	1	?	?	?	?	?	?	?
Kansasiella eatoni	?	0	0	0	1	0	1	0	1	0	0	0	0	0
Kentuckia deani	-	0	0	0	1	0	1	?	0	0	0	0	?	0
Lawrenciella schaefferi	-	0	0	0	1	0	1	?	1	0	0	0	0	0

Lepisosteus osseus	-	0	0	1	1	2	0	1	1	0	0	0	1	0
Leptolepis bronni	1	1	?	?	1	2	1	0	1	?	1	1	1	1
Ligulalepis	-	0	0	0	0	-	-	-	-	-	-	-	-	1
Luederia kempi	-	0	?	?	1	1	1	?	?	?	0	0	0	?
Luganoia lepidosteoides	?	?	?	?	1	?	?	0	?	?	?	?	?	?
Macrepistius arenatus	1	1	1	1	1	2	1	?	1	2	1	0	0	1
Macrosemimimus lennieri	-	1	1	?	1	2	1	1	0	?	0	?	1	0
Macrosemius rostratus	-	1	?	0	1	2	1	1	?	?	0	0	?	?
Meemannia eos	-	0	0	0	?	?	?	?	?	?	?	?	?	?
Melanecta anneae	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Mesopoma planti	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Miguashaia bureaui	?	?	?	?	1	?	0	?	0	?	?	?	?	0
Mimipiscis bartrami	-	0	0	0	1	0	0	1	0	0	0	0	-	0
Mimipiscis toombsi	-	0	0	0	1	0	0	1	0	0	0	0	-	0
Moythomasia durgaringa	-	0	0	0	1	0	1	1	0	0	0	0	0	0
Moythomasia lineata	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Moythomasia nitida	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Obaichthys decoratus	-	?	?	?	1	2	0	1	1	0	?	?	1	?
Onychodus jandemarrai	?	?	?	?	1	0	0	0	0	0	0	0	0	0
Osorioichthys marginis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Osteolepis macrolepidotus	-	0	0	0	?	?	?	?	?	?	?	?	0	?
Ozarcus mapesae	-	0	0	0	0	-	-	-	-	-	-	-	-	1
Peltopleurus lissocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platysomus superbus	?	?	?	?	1	2	1	0	0	?	0	0	1	?
Polypterus bichir	0	0	0	0	1	2	1	0	1	0	0	0	1	?
Porolepis sp.	-	0	0	0	1	0	0	0	0	1	0	0	0	?
Propterus elongatus	?	?	?	?	1	?	?	?	?	?	?	?	?	?
Psarolepis romeri	-	0	0	0	1	0	0	0	0	0	0	0	0	?
Pteronisculus stensioi	-	0	0	0	1	0	1	0	1	0	0	0	0	0
Raynerius splendens	-	0	0	0	1	0	0	?	0	0	0	0	0	0
Saurichthys madagascarensis	-	?	?	0	1	2	1	?	0	0	?	?	?	0
Scanilepis dubia	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Semionotus elegans	-	?	?	1	1	1	1	1	0	0	0	0	1	?
Styloichthys changae	-	0	0	0	1	0	0	0	0	0	0	0	0	?
Styracopterus fulcratus	?	?	?	?	1	?	?	?	?	?	?	?	?	0
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	?	?	?	?	1	?	1	0	0	?	0	0	?	?
Tetragonolepis semicincta	?	?	?	?	1	?	1	?	?	2	1	1	?	0
Venusichthys comptus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watsonulus eugnathoides	0	1	1	1	1	2	1	0	1	0	0	0	0	0
Wendyichthys dicksoni	?	?	?	?	1	0	1	?	?	?	?	?	?	?
Woodichthys bearsdeni	-	0	0	0	1	0	1	0	0	?	0	0	0	0

	181	182	183	184	185	186	187	188	189	190	191	192	193	194
Acanthodes bronni	?	?	?	?	?	?	?	?	?	?	0	1	?	0
Acipenser brevirostrum	0	1	0	0	0	0	1	1	0	1	?	?	?	?
Aesopichthys erinaceus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Amia calva	0	1	1	1	0	1	1	1	1	1	0	0	1	0
Amphicentrum granulosum	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Atractosteus spatula	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Australosomus kochi	1	1	1	1	1	0	?	?	?	?	1	1	1	0
Beagiascus pulcherrimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Birgeria groenlandica	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Bobosatrania groenlandica	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Boreosomus piveteaui	1	0	1	1	1	1	1	1	0	0	?	?	1	1
Brazilichthys macrognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caturus furcatus	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Cheirolepis canadensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis schultzei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis trailli	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Chondrosteus acipenseroides	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cladodoides wildungensis	0	1	0	0	0	0	0	-	-	-	0	1	0	0
Coccocephalichthys wildi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cosmoptychius striatus	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Cyranorhis bergeraci	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dapedium LIAS	1	1	1	1	1	?	?	?	?	?	1	1	0	1
Dapedium pholidotum	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dialipina salguerioensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	0	1	?	?	?	0	0	?	?	?	?	?	?	0
Diplocercides kayseri	1	1	?	0	?	?	?	?	?	?	?	?	?	?
Dipteronotus ornatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Discoserra pectinodon	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Donnrosenia schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dorsetichthys bechei	1	0	?	1	1	?	?	?	?	?	1	1	1	1
Ebenaqua ritchei	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Elops hawaiensis	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Entelognathus primordialis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Erpetoichthys calabaricus	0	1	0	1	0	1	1	0	0	0	0	1	1	?
Eusthenopteron foordi	1	1	1	0	0	0	0	-	-	-	1	1	0	0
Evenkia eunoptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fouldenia ischiptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fukangichthys longidorsalis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Glyptolepis groenlandica	1	1	1	0	0	0	?	-	-	-	?	?	?	?
Gogonasus andrewsae	1	1	1	0	0	0	0	-	-	-	1	?	0	0
Gogosardina coatesi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Guiyu oneiros	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hiodon alosoides	?	?	?	?	?	?	?	?	?	?	1	1	1	0
Howqualepis rostridens	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Hulettia americana	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ichthyokentema purbeckensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kalops monophyrum	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kansasiella eatoni	1	0	0	1	1	1	1	1	0	?	1	1	1	1
Kentuckia deani	1	0	0	1	1	?	1	0	0	?	1	1	1	1
Lawrenciella schaefferi	1	0	0	1	1	?	1	1	0	0	1	1	1	1
Lepisosteus osseus	0	1	1	1	0	1	1	1	1	1	0	1	1	1
Leptolepis bronni	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Ligulalepis	0	1	?	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Macrepistius arenatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrosemimimus lennieri	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Macrosemius rostratus	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Meemannia eos	?	?	?	?	?	0	0	-	-	-	0	?	0	1
Melanecta anneae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesopoma planti	?	?	0	1	1	1	1	0	0	0	1	?	1	?
Miguashaia bureaui	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mimipiscis bartrami	1	1	?	?	?	?	?	?	?	?	?	?	?	1
Mimipiscis toombsi	1	1	0	0	1	0	0	-	-	-	1	0	0	1
Moythomasia durgaringa	?	1	?	?	?	?	?	?	?	?	?	?	?	1
Moythomasia lineata	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Moythomasia nitida	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Obaichthys decoratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Onychodus jandemarrai	?	?	?	?	?	?	?	?	?	?	1	1	?	?
Osorioichthys marginis	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Osteolepis macrolepidotus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ozarcus mapesae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Peltopleurus lissocephalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Platysomus superbus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polypterus bichir	0	1	0	1	0	1	1	0	0	0	?	?	?	?
Porolepis sp.	1	1	?	0	0	0	?	-	-	-	?	?	?	?
Propterus elongatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Psarolepis romeri	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pteronisculus stensioi	1	1	1	1	1	1	1	1	0	0	1	1	1	1
Raynerius splendens	?	?	0	0	1	0	?	?	?	?	1	0	0	1
Saurichthys madagascarensis	1	1	0	1	1	1	?	?	?	?	?	?	?	?
Scanilepis dubia	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Semionotus elegans	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Styloichthys changae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Styracopterus fulcratus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tetragonolepis semicincta	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Venusichthys comptus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watsonulus eugnathoides	?	?	?	?	?	?	?	?	?	?	?	?	?	1
Wendyichthys dicksoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Woodichthys bearsdeni	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	196	197	198	199	200	201	202	203	204	205	206	207	208	209
Acanthodes bronni	0	0	-	-	0	0	0	-	-	-	?	0	0	0
Acipenser brevirostrum	-	-	-	-	1	-	-	-	-	-	0	1	0	0
Aesopichthys erinaceus	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Amia calva	0	0	-	-	0	1	0	-	-	-	?	1	0	0
Amphicentrum granulosum	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Atractosteus spatula	1	0	1	?	0	1	1	0	0	0	0	1	1	0
Australosomus kochi	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Beagiascus pulcherrimus	?	?	?	?	0	1	1	?	1	0	0	1	1	?
Beishanichthys brevicaudalis	?	?	?	?	0	1	1	0	1	0	?	1	0	?
Birgeria groenlandica	?	?	?	?	1	1	?	?	?	0	0	1	1	0
Bobosatrania groenlandica	?	?	?	?	0	1	1	?	?	?	0	1	1	0

Boreosomus piveteaui	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Brazilichthys macrognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Caturus furcatus	?	?	?	?	?	?	?	?	?	?	0	1	1	0
Cheirolepis canadensis	?	?	?	?	0	0	0	-	0	?	0	1	1	?
Cheirolepis schultzei	?	?	?	?	0	0	0	-	0	?	?	1	1	?
Cheirolepis trailli	1	1	1	0	0	0	1	0	1	?	0	1	1	0
Chondrosteus acipenseroides	-	-	-	-	1	-	-	-	-	-	?	1	0	0
Cladodoides wildungensis	?	?	?	?	0	0	?	?	?	?	?	?	?	0
Coccocephalichthys wildi	?	?	?	?	0	1	?	?	?	?	?	?	?	0
Cosmoptychius striatus	?	?	?	?	0	1	1	0	1	0	0	1	1	?
Cyranorhis bergeraci	?	?	?	?	0	1	1	?	1	0	0	1	1	0
Dapedium LIAS	?	?	?	?	0	1	1	?	?	0	?	1	1	0
Dapedium pholidotum	?	?	?	?	0	1	1	?	?	0	0	1	1	?
Dialipina salguerioensis	1	?	?	?	0	1	1	0	1	0	?	1	0	?
Dicksonosteus arcticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diplocercides kayseri	?	?	?	?	0	1	-	-	-	0	?	?	?	1
Dipteronotus ornatus	?	?	?	?	0	1	?	0	?	0	?	1	1	?
Discoserra pectinodon	?	?	?	?	0	1	1	0	?	0	1	1	1	0
Donnrosenia schaefferi	?	?	?	?	0	1	1	0	1	0	0	1	1	?
Dorsetichthys bechei	?	?	?	?	0	1	1	0	?	0	?	1	?	0
Ebenaqua ritchei	?	?	?	?	0	1	1	?	?	0	0	1	?	?
Elops hawaiensis	0	0	-	-	0	0	0	-	-	0	0	1	1	0
Entelognathus primordialis	?	?	?	?	0	?	?	?	?	?	0	?	?	0
Erpetoichthys calabaricus	1	0	?	?	0	1	1	0	1	0	0	1	0	0
Eusthenopteron foordi	0	0	-	-	0	1	0	-	-	0	0	1	0	1
Evenkia eunoptera	?	?	?	?	0	1	1	?	?	0	1	1	0	?
Fouldenia ischiptera	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Fukangichthys longidorsalis	?	?	?	?	0	1	1	?	?	0	0	1	1	0
Glyptolepis groenlandica	?	?	?	?	0	1	-	-	0	0	?	1	0	1
Gogonasus andrewsae	1	1	0	-	0	1	0	-	0	0	?	1	?	1
Gogosardina coatesi	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Guiyu oneiros	1	?	1	1	0	1	1	1	1	0	0	1	?	?
Hiodon alosoides	0	0	-	-	0	1	0	-	-	0	0	1	0	1
Howqualepis rostridens	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Hulettia americana	1	?	?	-	0	1	1	0	?	0	0	1	1	0
Ichthyokentema purbeckensis	1	0	0	-	0	1	1	0	1	0	?	1	1	0
Kalops monophyrum	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Kansasiella eatoni	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Kentuckia deani	1	?	?	?	?	?	?	?	?	0	?	?	?	0
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Lepisosteus osseus	1	1	1	0	0	1	1	0	1	0	0	1	1	0
Leptolepis bronni	?	?	?	?	?	?	?	?	?	?	0	1	0	0
Ligulalepis	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Luganoia lepidosteoides	?	?	?	?	0	1	1	0	1	0	?	1	?	0
Macrepistius arenatus	1	0	?	?	0	1	?	?	?	0	?	1	1	?
Macrosemimimus lennieri	?	?	?	?	0	1	1	?	?	0	0	1	1	?
Macrosemius rostratus	?	?	?	?	0	1	1	?	?	0	?	1	1	0
Meemannia eos	1	1	1	1	?	?	?	?	?	?	?	?	?	?
Melanecta anneae	?	?	?	?	0	0	?	?	?	0	?	1	1	?

Mesopoma planti	?	?	?	?	0	1	1	0	1	0	0	1	1	?
Miguashaia bureaui	1	0	?	?	0	1	-	-	-	0	0	1	0	?
Mimipiscis bartrami	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Mimipiscis toombsi	1	0	1	0	0	1	1	0	1	0	0	1	1	0
Moythomasia durgaringa	1	?	1	0	0	1	1	0	1	1	0	1	1	0
Moythomasia lineata	1	0	1	0	0	1	1	0	1	0	?	1	1	?
Moythomasia nitida	1	?	1	0	0	1	1	0	1	1	?	1	1	?
Obaichthys decoratus	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Onychodus jandemarrai	0	0	-	-	0	1	-	-	-	0	0	1	0	0
Osorioichthys marginis	?	?	?	?	0	1	1	0	1	0	0	1	1	?
Osteolepis macrolepidotus	?	?	?	?	0	1	0	1	0	1	?	1	0	1
Ozarcus mapesae	?	?	?	?	?	?	?	?	?	?	?	?	?	0
Peltopleurus lissocephalus	?	?	?	?	0	1	?	?	?	0	?	1	1	?
Platysomus superbus	?	?	?	?	0	1	1	0	1	0	?	1	1	?
Polypterus bichir	1	0	1	0	0	1	1	0	1	0	0	1	0	0
Porolepis sp.	1	1	0	-	0	1	1	1	0	1	0	1	0	1
Propterus elongatus	?	?	?	?	0	1	1	?	?	?	?	1	1	?
Psarolepis romeri	1	1	1	1	0	1	1	1	1	1	?	?	?	?
Pteronisculus stensioi	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Raynerius splendens	1	?	?	?	0	1	1	0	1	1	?	?	?	0
Saurichthys madagascarensis	?	?	?	?	0	1	0	-	0	0	0	1	1	?
Scanilepis dubia	1	0	1	0	0	1	1	0	1	0	1	1	0	?
Semionotus elegans	1	0	1	0	0	1	?	?	?	?	0	1	1	0
Styloichthys changae	1	1	1	1	?	?	?	?	?	?	?	?	?	1
Styracopterus fulcratus	?	?	?	?	0	1	1	0	1	0	0	1	1	0
Tanaocrossus kalliokoskii	?	?	?	?	?	?	1	?	?	0	1	1	0	?
Tegeolepis clarki	?	?	?	?	0	0	1	0	1	?	?	?	0	?
Tetragonolepis semicincta	?	?	?	?	0	1	1	?	?	0	0	1	1	0
Venusichthys comptus	?	?	?	?	0	1	1	?	1	0	0	1	1	?
Watsonulus eugnathoides	?	?	?	?	0	1	?	?	?	0	?	1	?	0
Wendyichthys dicksoni	?	?	?	?	0	1	?	?	?	1	0	1	1	?
Woodichthys bearsdeni	?	?	?	?	0	1	1	0	1	1	0	1	1	0

	211	212	213	214	215	216	217	218	219	220	221	222	223	224
Acanthodes bronni	0	1	0	?	?	0	-	?	?	1	0	1	0	?
Acipenser brevirostrum	0	1	1	0	1	0	-	1	0	1	0	0	0	0
Aesopichthys erinaceus	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Amia calva	1	1	0	0	1	1	1	1	0	1	0	1	1	0
Amphicentrum granulosum	0	?	?	?	?	0	?	?	?	?	?	?	?	?
Atractosteus spatula	1	1	1	0	1	1	2	1	0	1	0	1	1	0
Australosomus kochi	1	0	0	1	1	0	-	1	0	1	0	0	1	0
Beagiascus pulcherrimus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	?	?	?	?	?	0	-	?	?	?	?	?	?	?
Birgeria groenlandica	0	0	0	?	1	0	-	1	0	1	?	0	?	0
Bobosatrania groenlandica	1	0	1	0	?	0	-	1	?	?	?	?	?	?
Boreosomus piveteaui	1	1	1	?	1	0	-	1	?	1	?	?	0	0
Brazilichthys macrognathus	1	?	?	?	?	?	?	1	?	1	1	?	?	?
Caturus furcatus	1	1	0	0	1	1	1	?	?	1	?	?	1	?
Cheirolepis canadensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis schultzei	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Cheirolepis trailli	0	?	?	?	?	0	-	?	?	?	?	?	?	?
Chondrosteus acipenseroides	0	0	1	0	?	0	?	?	?	?	?	?	?	?
Cladodoides wildungensis	?	?	?	?	?	0	-	?	?	?	?	?	?	?
Coccocephalichthys wildi	1	?	?	?	?	0	?	?	?	?	?	?	?	?
Cosmoptychius striatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cyranorhis bergeraci	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Dapedium LIAS	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Dapedium pholidotum	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dialipina salguerioensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diplocercides kayseri	?	?	?	?	?	1	0	?	?	?	?	?	?	?
Dipteronotus ornatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Discoserra pectinodon	?	0	0	0	1	0	-	?	?	?	?	?	?	?
Donnrosenia schaefferi	?	?	?	?	?	0	-	?	?	?	?	?	?	?
Dorsetichthys bechei	1	?	?	?	?	1	?	?	?	?	?	?	1	?
Ebenaqua ritchei	?	0	1	?	?	?	?	?	?	?	?	?	?	?
Elops hawaiensis	1	1	1	1	?	1	0	?	1	1	0	0	0	?
Entelognathus primordialis	?	?	?	?	?	0	-	?	?	0	-	?	?	?
Erpetoichthys calabaricus	1	0	0	0	1	0	-	1	0	1	1	1	0	0
Eusthenopteron foordi	0	1	0	1	1	0	-	1	0	0	0	1	0	1
Evenkia eunoptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fouldenia ischiptera	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Fukangichthys longidorsalis	1	0	0	0	?	0	-	?	?	1	1	?	1	?
Glyptolepis groenlandica	?	?	0	?	1	0	-	1	0	0	1	1	?	1
Gogonasus andrewsae	0	?	0	1	?	?	?	1	1	0	0	?	?	1
Gogosardina coatesi	0	0	?	?	1	0	-	1	?	1	0	?	?	?
Guiyu oneiros	?	?	?	?	?	0	-	?	?	?	?	?	?	?
Hiodon alosoides	1	1	1	0	1	1	0	1	1	1	0	0	1	0
Howqualepis rostridens	0	?	?	?	?	0	-	?	?	?	?	?	?	?
Hulettia americana	1	1	1	0	0	1	0	1	0	?	?	?	1	?
Ichthyokentema purbeckensis	?	1	0	1	?	1	0	?	?	?	?	?	?	?
Kalops monophyrum	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Kansasiella eatoni	?	?	1	1	?	?	?	?	?	?	?	?	?	?
Kentuckia deani	1	?	?	?	?	0	-	?	?	?	?	?	?	?
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	1	1	1	0	1	1	2	1	0	1	0	1	1	0
Leptolepis bronni	1	1	1	1	1	1	?	1	0	1	?	?	?	1
Ligulalepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	1	0	1	?	?	?	?	?	?	?	?	?	?	?
Macrepistius arenatus	?	?	?	?	?	?	?	?	?	?	-	?	?	?
Macrosemimimus lennieri	?	?	?	?	?	1	0	?	?	?	?	?	?	?
Macrosemius rostratus	1	1	1	?	1	?	?	1	?	?	?	?	1	?
Meemannia eos	?	?	?	?	?	0	-	?	?	?	?	?	?	?
Melanecta anneae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Mesopoma planti	?	0	1	1	?	?	?	?	?	?	?	?	?	?
Miguashaia bureaui	?	?	?	?	?	1	0	?	?	?	?	?	?	?
Mimipiscis bartrami	?	0	0	1	1	0	-	1	1	1	0	1	0	0
Mimipiscis toombsi	0	0	0	1	1	0	-	1	1	1	0	1	0	0
Moythomasia durgaringa	0	0	0	1	1	0	-	1	1	1	0	1	0	0

Moythomasia lineata	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Moythomasia nitida	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Obaichthys decoratus	?	1	1	0	?	1	2	?	?	1	?	?	1	?
Onychodus jandemarrai	0	0	1	0	1	0	-	1	0	?	?	0	0	?
Osorioichthys marginis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Osteolepis macrolepidotus	?	?	?	?	?	0	-	?	?	?	?	?	?	?
Ozarcus mapesae	0	0	0	0	0	0	-	1	0	1	0	0	0	0
Peltopleurus lissocephalus	?	?	?	?	?	?	?	?	?	?	-	?	?	?
Platysomus superbus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polypterus bichir	1	0	0	0	1	0	-	1	0	1	1	1	0	0
Porolepis sp.	0	0	0	0	1	0	-	?	0	0	?	?	?	1
Propterus elongatus	?	1	1	?	?	?	0	1	?	?	?	?	?	?
Psarolepis romeri	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Pteronisculus stensioi	1	0	1	1	1	0	-	1	1	1	0	1	0	0
Raynerius splendens	0	0	0	1	?	0	-	1	1	1	0	1	0	0
Saurichthys madagascarensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Scanilepis dubia	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Semionotus elegans	1	?	1	0	1	1	0	1	1	1	0	1	1	0
Styloichthys changae	?	?	?	?	?	1	?	?	?	?	?	?	?	?
Styracopterus fulcratus	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Tetragonolepis semicincta	1	?	1	0	1	1	1	1	?	?	?	?	?	?
Venusichthys comptus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Watsonulus eugnathoides	1	1	0	1	?	1	0	1	0	1	?	?	?	0
Wendyichthys dicksoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Woodichthys bearsdeni	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	226	227	228	229	230	231	232	233	234	235	236	237	238	239
Acanthodes bronni	-	?	?	-	?	?	?	?	0	0	0	0	1	0
Acipenser brevirostrum	0	-	0	0	0	0	0	0	1	0	1	?	1	0
Aesopichthys erinaceus	1	0	0	?	0	0	?	?	?	?	?	?	0	?
Amia calva	0	-	0	0	0	1	1	1	0	0	1	0	1	0
Amphicentrum granulosum	0	-	0	?	?	0	?	?	?	?	?	?	?	?
Atractosteus spatula	0	-	0	1	0	1	1	1	0	0	1	0	0	0
Australosomus kochi	0	-	0	0	0	0	0	1	1	0	?	0	0	0
Beagiascus pulcherrimus	1	1	0	?	0	0	?	?	?	?	?	?	1	?
Beishanichthys brevicaudalis	0	-	0	?	0	?	?	?	?	?	?	?	?	?
Birgeria groenlandica	0	-	0	0	2	0	0	1	0	0	-	-	0	0
Bobosatrania groenlandica	0	-	0	0	0	1	?	?	?	?	?	?	?	?
Boreosomus piveteaui	0	-	?	0	2	0	0	1	1	?	?	?	0	?
Brazilichthys macrognathus	?	?	?	?	?	0	?	?	?	1	?	?	?	?
Caturus furcatus	1	0	0	0	?	?	1	?	0	?	?	?	?	?
Cheirolepis canadensis	0	-	0	?	0	0	?	?	?	?	0	0	0	1
Cheirolepis schultzei	?	?	0	?	0	0	?	?	?	?	?	?	0	?
Cheirolepis trailli	1	0	0	0	0	0	0	0	0	0	1	0	0	0
Chondrosteus acipenseroides	0	-	0	?	0	?	?	?	?	?	?	?	?	?
Cladodoides wildungensis	-	-	?	-	?	-	-	-	?	?	?	?	?	?
Coccocephalichthys wildi	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Cosmoptychius striatus	0	-	0	?	0	0	0	?	?	?	?	0	1	1

Cyranorhis bergeraci	1	0	0	?	?	0	?	1	?	?	?	?	1	?
Dapedium LIAS	1	0	0	?	0	1	?	1	?	?	?	?	?	?
Dapedium pholidotum	1	0	?	?	0	1	?	1	?	?	?	?	?	?
Dialipina salguerioensis	?	?	0	?	0	?	?	?	?	?	?	?	?	?
Dicksonosteus arcticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diplocercides kayseri	?	?	?	0	?	?	?	?	?	?	?	?	?	?
Dipteronotus ornatus	?	?	0	?	2	?	?	?	?	?	?	?	?	?
Discoserra pectinodon	1	1	0	?	?	1	?	1	?	?	?	0	0	?
Donnrosenia schaefferi	?	?	0	?	0	0	?	?	?	?	?	?	1	?
Dorsetichthys bechei	0	-	0	?	0	?	?	?	?	?	?	1	0	?
Ebenaqua ritchei	1	1	?	?	2	1	?	?	?	?	?	?	?	?
Elops hawaiensis	0	-	0	0	0	1	0	1	0	0	1	1	1	0
Entelognathus primordialis	0	-	?	?	0	0	0	0	?	?	?	?	?	?
Erpetoichthys calabaricus	0	-	0	0	0	0	0	1	?	?	?	?	0	?
Eusthenopteron foordi	0	-	1	0	1	0	0	0	1	-	-	-	0	0
Evenkia eunoptera	1	0	0	?	?	?	?	?	?	?	?	?	0	?
Fouldenia ischiptera	0	-	0	?	0	0	?	0	?	?	1	0	0	0
Fukangichthys longidorsalis	?	?	0	0	0	?	?	?	?	?	?	?	?	?
Glyptolepis groenlandica	0	-	1	0	?	0	0	?	0	?	?	?	0	1
Gogonasus andrewsae	0	-	?	?	?	0	0	0	1	-	-	-	0	0
Gogosardina coatesi	?	-	0	0	0	0	0	1	?	?	?	?	1	?
Guiyu oneiros	1	0	0	?	?	0	?	?	?	?	?	?	?	?
Hiodon alosoides	0	-	0	0	0	1	0	1	0	0	1	1	1	0
Howqualepis rostridens	1	0	0	0	0	0	0	0	?	?	1	0	0	0
Hulettia americana	0	-	0	?	0	1	0	1	?	?	?	?	?	?
Ichthyokentema purbeckensis	0	-	0	0	0	1	0	1	1	?	?	?	1	0
Kalops monophyrum	1	0	0	?	0	0	?	1	?	?	?	?	0	?
Kansasiella eatoni	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Kentuckia deani	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	0	-	0	1	0	1	1	1	0	0	1	0	0	0
Leptolepis bronni	0	-	0	?	0	1	1	1	?	?	?	1	?	0
Ligulalepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	0	-	0	?	2	1	?	?	0	0	1	?	1	0
Macrepistius arenatus	0	-	0	?	?	1	?	?	?	?	?	?	?	?
Macrosemimimus lennieri	0	-	0	?	0	1	?	1	?	?	?	?	1	?
Macrosemius rostratus	0	-	0	1	?	1	0	1	0	0	0	?	?	0
Meemannia eos	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Melanecta anneae	0	-	0	?	0	0	?	?	?	?	?	?	1	?
Mesopoma planti	?	?	0	?	0	0	?	?	?	?	?	?	?	?
Miguashaia bureaui	0	-	0	0	1	0	?	1	?	?	?	?	0	?
Mimipiscis bartrami	1	0	0	0	0	0	0	?	?	1	?	0	1	0
Mimipiscis toombsi	1	0	0	0	0	0	0	0	1	1	1	0	1	0
Moythomasia durgaringa	1	0	0	0	0	0	0	0	1	1	1	?	1	?
Moythomasia lineata	1	0	0	?	0	0	?	?	1	1	?	?	1	0
Moythomasia nitida	1	0	0	?	0	0	?	?	?	?	?	0	1	?
Obaichthys decoratus	0	-	0	1	0	0	1	1	?	0	?	0	0	0
Onychodus jandemarrai	1	0	1	0	1	0	0	1	0	-	-	-	0	?
Osorioichthys marginis	0	-	0	?	0	0	?	0	?	1	1	0	0	0

Osteolepis macrolepidotus	0	-	1	?	1	0	?	?	?	?	?	?	0	?
Ozarcus mapesae	?	-	?	-	?	-	-	-	?	?	?	?	?	?
Peltopleurus lissocephalus	0	-	0	0	2	1	?	1	?	?	?	?	1	?
Platysomus superbus	0	-	0	?	0	0	?	?	?	?	?	?	0	?
Polypterus bichir	0	-	0	0	0	0	0	1	0	0	0	0	0	0
Porolepis sp.	0	-	1	0	1	0	?	?	0	?	?	?	0	?
Propterus elongatus	0	-	0	0	?	0	1	1	0	?	?	0	?	0
Psarolepis romeri	?	?	?	0	?	0	?	?	0	?	?	?	?	?
Pteronisculus stensioi	1	0	0	0	0	0	0	1	1	?	1	0	1	?
Raynerius splendens	1	0	0	0	?	0	0	0	?	?	?	?	?	?
Saurichthys madagascarensis	0	-	0	0	2	0	0	1	1	?	1	0	0	0
Scanilepis dubia	0	-	0	?	?	?	?	?	?	?	?	?	?	?
Semionotus elegans	0	-	0	1	0	1	1	1	0	0	0	?	?	0
Styloichthys changae	?	?	0	0	?	?	?	?	1	?	?	?	?	?
Styracopterus fulcratus	0	-	0	?	0	0	?	0	?	?	?	?	0	?
Tanaocrossus kalliokoskii	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	?	?	0	?	?	?	?	?	?	?	?	?	0	?
Tetragonolepis semicincta	0	-	0	0	0	1	0	1	?	1	1	0	1	0
Venusichthys comptus	0	-	0	?	0	1	?	1	?	?	?	?	1	?
Watsonulus eugnathoides	1	0	0	0	2	0	?	1	1	?	?	?	1	?
Wendyichthys dicksoni	0/1	-	0	?	0	0	?	1	?	?	?	?	1	?
Woodichthys bearsdeni	0	-	0	?	0	0	?	?	?	1	1	0	1	?

	241	242	243	244	245	246	247	248	249	250	251	252	253	254
Acanthodes bronni	?	1	1	1	0	0	0	0	0	0	2	?	?	?
Acipenser brevirostrum	0	1	1	1	0	1	2	1	1	1	2	0	0	0
Aesopichthys erinaceus	0	1	0	1	0	0	2	1	0	1	2	?	?	?
Amia calva	1	1	0	1	0	0	0	0	0	1	2	1	1	1
Amphicentrum granulosum	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Atractosteus spatula	1	1	0	1	0	0	0	0	0	?	1	1	1	1
Australosomus kochi	1	1	0	1	0	0	0	0	0	1	0	0	1	0
Beagiascus pulcherrimus	2	1	0	1	0	0	1	1	?	1	1	?	?	?
Beishanichthys brevicaudalis	1	1	0	1	0	0	0	0	0	1	2	?	?	?
Birgeria groenlandica	3	1	0	1	0	0	0	0	0	1	2	0	0	0
Bobosatrania groenlandica	0	?	0	1	0	0	1	0	1	1	2	1	0	?
Boreosomus piveteaui	1	?	0	1	0	0	0	1	0	1	2	0	0	?
Brazilichthys macrognathus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Caturus furcatus	?	?	0	1	0	0	0	0	0	1	2	1	1	1
Cheirolepis canadensis	0	1	0	1	1	0	1	0	1	1	0	?	?	?
Cheirolepis schultzei	0	1	0	?	?	0	?	?	?	?	?	?	?	?
Cheirolepis trailli	0	1	0	1	1	0	1	1	1	1	0	?	?	?
Chondrosteus acipenseroides	2	1	0	1	?	0	0	0	0	1	?	?	?	?
Cladodoides wildungensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Coccocephalichthys wildi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Cosmoptychius striatus	1	0	0	1	1	0	1	0	0	1	2	?	?	?
Cyranorhis bergeraci	1	1	0	1	0	0	1	0	1	1	2	?	?	?
Dapedium LIAS	2	1	0	1	0	?	?	?	?	?	?	?	?	?
Dapedium pholidotum	?	1	0	1	0	0	2	1	1	1	2	1	?	?
Dialipina salguerioensis	?	?	0	1	1	0	?	0	0	0	1	?	?	?
Dicksonosteus arcticus	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Diplocercides kayseri	?	1	0	?	?	0	?	?	?	?	?	?	?	?
Dipteronotus ornatus	?	?	0	1	0	0	2	?	1	1	2	?	?	?
Discoserra pectinodon	?	1	0	1	0	0	2	0	1	1	2	0	0	0
Donnrosenia schaefferi	1	1	0	1	1	0	1	0	1	1	1	?	?	?
Dorsetichthys bechei	2	1	0	1	0	0	0	0	0	1	2	?	?	?
Ebenaqua ritchei	2	1	0	1	0	0	2	1	1	1	1	?	?	1
Elops hawaiensis	0	1	0	1	0	0	0	0	0	1	2	1	1	1
Entelognathus primordialis	?	1	1	?	?	?	?	?	?	?	?	?	?	?
Erpetoichthys calabaricus	?	1	0	0	-	?	?	?	?	1	-	?	1	1
Eusthenopteron foordi	0	1	0	1	0	1	0	0	0	0	2	0	0	0
Evenkia eunoptera	0	1	0	1	0	0	0	?	1	1	2	?	?	?
Fouldenia ischiptera	0	1	0	1	0	0	2	1	1	1	1	?	?	?
Fukangichthys longidorsalis	1	1	0	1	0	0	0	0	0	1	2	?	?	?
Glyptolepis groenlandica	?	0	0	?	?	0	0	0	?	0	?	?	?	?
Gogonasus andrewsae	?	1	?	?	?	1	?	?	?	?	?	?	?	?
Gogosardina coatesi	1	1	0	1	0	0	2	1	0	1	2	?	?	?
Guiyu oneiros	?	?	1	1	0	0	1	1	1	0	1	?	?	?
Hiodon alosoides	1	1	0	1	1	0	0	0	0	1	1	1	1	1
Howqualepis rostridens	1	1	0	1	1	0	1	1	1	1	1	?	?	?
Hulettia americana	?	1	0	1	0	0	1	0	1	1	2	1	1	1
Ichthyokentema purbeckensis	?	1	0	1	0	0	1	0	1	1	?	1	?	?
Kalops monophyrum	0	1	0	1	0	0	2	1	1	1	2	?	?	?
Kansasiella eatoni	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Kentuckia deani	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	1	1	0	1	0	0	0	0	0	1	0	1	1	1
Leptolepis bronni	1	1	0	1	0	0	0	0	0	1	2	1	1	0
Ligulalepis	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	1	1	0	1	0	0	0	0	0	1	2	1	?	?
Macrepistius arenatus	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Macrosemimimus lennieri	?	1	0	1	0	0	0	0	0	1	2	?	?	?
Macrosemius rostratus	1	?	0	1	0	0	?	1	0	1	2	1	1	1
Meemannia eos	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Melanecta anneae	1	1	0	1	1	0	1	1	1	1	2	?	?	?
Mesopoma planti	1	1	0	1	0	0	1	1	1	1	1	?	?	?
Miguashaia bureaui	0	1	0	1	?	0	0	0	0	0	1	?	?	?
Mimipiscis bartrami	1	1	0	1	0	0	2	1	1	1	2	0	?	0
Mimipiscis toombsi	?	1	0	1	0	0	2	1	1	1	1	0	?	0
Moythomasia durgaringa	1	1	0	1	0	0	2	1	1	1	1	0	?	?
Moythomasia lineata	0	1	0	?	0	0	2	1	0	1	2	?	?	?
Moythomasia nitida	1	1	0	1	0	0	2	1	1	1	1	?	?	?
Obaichthys decoratus	1	1	0	1	0	0	0	0	0	1	1	?	?	?
Onychodus jandemarrai	?	?	0	1	?	0	0	0	0	0	2	0	?	?
Osorioichthys marginis	1	1	0	?	?	0	2	?	?	?	?	?	?	?
Osteolepis macrolepidotus	0	1	0	1	0	1	0	0	0	0	2	?	?	?
Ozarcus mapesae	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Peltopleurus lissocephalus	1	1	0	1	0	0	0	0	1	1	2	?	?	?
Platysomus superbus	0	?	0	1	0	0	0	0	0	1	2	?	?	?
Polypterus bichir	0	1	0	1	0	0	0	0	0	1	2	0	1	1

Porolepis sp.	?	0	0	1	0	?	0	0	0	0	1	?	?	?
Propterus elongatus	1	?	0	1	0	0	?	?	?	0	2	?	1	1
Psarolepis romeri	?	?	1	?	?	?	?	?	?	?	?	?	?	?
Pteronisculus stensioi	0	1	0	1	0	0	1	1	1	1	2	0	0	0
Raynerius splendens	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Saurichthys madagascarensis	1	1	0	1	0	0	2	1	1	1	1	0	1	1
Scanilepis dubia	?	?	0	1	0	0	?	?	?	1	2	?	?	?
Semionotus elegans	1	1	0	1	0	0	2	0	1	1	2	1	1	1
Styloichthys changae	?	?	0	?	?	?	?	?	?	?	?	?	?	?
Styracopterus fulcratus	2	1	0	1	0	0	2	1	1	1	2	?	?	?
Tanaocrossus kalliokoskii	?	?	?	1	0	?	?	?	?	?	?	?	?	?
Tegeolepis clarki	1	1	0	?	?	0	0	1	0	1	1	?	?	?
Tetragonolepis semicincta	1	1	0	1	0	0	2	0	1	1	2	1	1	1
Venusichthys comptus	1	1	0	1	0	0	0	0	0	1	2	?	?	?
Watsonulus eugnathoides	2	1	0	1	0	0	0	0	0	1	2	?	-	?
Wendyichthys dicksoni	0	1	0	1	0	0	1	0	1	1	2	?	?	?
Woodichthys bearsdeni	1	1	0	1	0	0	1	1	1	1	2	?	?	?

	255	256	257	258	259	260	261	262	263	264	265
Acanthodes bronni	?	0	0	?	?	?	?	?	-	?	-
Acipenser brevirostrum	1	1	0	0	0	1	0	0	0	0	1
Aesopichthys erinaceus	0	1	0	0	?	?	?	?	?	?	?
Amia calva	1	0	1	1	1	1	0	0	1	0	0
Amphicentrum granulosum	?	?	0	?	?	?	?	?	?	?	?
Atractosteus spatula	1	1	1	1	0	1	0	0	1	1	0
Australosomus kochi	?	?	1	0	0	1	0	0	0	0	1
Beagiascus pulcherrimus	?	1	0	0	?	?	?	?	?	?	?
Beishanichthys brevicaudalis	1	0	1	1	?	?	?	?	?	?	?
Birgeria groenlandica	1	1	0	0	0	1	0	0	0	0	1
Bobosatrania groenlandica	1	1	0	0	?	?	?	?	?	?	1
Boreosomus piveteaui	0	1	0	0	0	0	0	0	?	0	1
Brazilichthys macrognathus	?	?	?	?	?	?	?	?	?	?	?
Caturus furcatus	1	1	1	0	?	1	0	0	0	0	0
Cheirolepis canadensis	0	1	0	1	?	?	?	?	?	?	?
Cheirolepis schultzei	?	?	?	?	?	?	?	?	?	?	?
Cheirolepis trailli	0	1	0	0	?	?	0	0	?	?	1
Chondrosteus acipenseroides	1	1	0	?	?	0	0	0	0	?	1
Cladodoides wildungensis	?	?	?	?	?	?	?	?	?	?	-
Coccocephalichthys wildi	?	?	?	?	?	?	?	?	?	?	?
Cosmoptychius striatus	1	1	0	0	?	?	?	?	0	?	?
Cyranorhis bergeraci	0	1	0	0	?	?	?	?	?	?	?
Dapedium LIAS	1	?	1	?	?	?	?	?	?	?	0
Dapedium pholidotum	1	1	1	1	?	?	?	?	?	?	?
Dialipina salguerioensis	0	?	?	1	?	?	?	?	?	?	?
Dicksonosteus arcticus	?	?	?	?	?	?	?	?	?	?	?
Diplocercides kayseri	?	?	1	?	?	?	?	?	?	?	?
Dipteronotus ornatus	?	1	1	0	?	1	0	0	?	?	?
Discoserra pectinodon	1	1	1	1	?	1	0	?	?	?	1
Donnrosenia schaefferi	?	1	?	?	?	?	?	?	?	?	?
Dorsetichthys bechei	1	1	1	0	1	1	1	1	0	0	0

Ebenaqua ritchei	1	1	0	1	?	?	?	?	?	?	?
Elops hawaiensis	1	1	1	0	0	1	0	0	0	0	0
Entelognathus primordialis	?	?	?	1	?	?	?	?	?	?	?
Erpetoichthys calabaricus	1	?	1	1	?	?	?	?	1	?	0
Eusthenopteron foordi	0	0	1	1	0	1	0	0	0	0	0
Evenkia eunoptera	1	0	0	?	?	?	?	?	?	?	?
Fouldenia ischiptera	0	1	0	0	?	?	?	?	?	?	?
Fukangichthys longidorsalis	?	0	1	1	?	?	?	?	?	?	?
Glyptolepis groenlandica	0	0	0	1	?	?	?	?	?	?	1
Gogonasus andrewsae	0	?	?	1	?	?	?	?	?	?	?
Gogosardina coatesi	?	1	0	?	?	0	0	0	?	?	0
Guiyu oneiros	?	?	?	?	?	?	?	?	?	?	?
Hiodon alosoides	1	0	1	0	0	1	1	1	0	0	0
Howqualepis rostridens	0	1	0	0	?	0	0	0	?	?	?
Hulettia americana	1	0	1	0	1	0	0	0	0	0	0
Ichthyokentema purbeckensis	1	1	1	0	?	1	1	?	?	0	0
Kalops monophyrum	0	1	0	0	?	?	?	?	?	?	?
Kansasiella eatoni	?	?	?	?	?	?	?	?	?	?	?
Kentuckia deani	?	?	?	?	?	?	?	?	?	?	?
Lawrenciella schaefferi	?	?	?	?	?	?	?	?	?	?	?
Lepisosteus osseus	1	1	1	1	0	1	0	0	1	1	0
Leptolepis bronni	1	1	1	0	0	1	1	1	0	0	0
Ligulalepis	?	?	?	?	?	?	?	?	?	?	?
Luederia kempi	?	?	?	?	?	?	?	?	?	?	?
Luganoia lepidosteoides	1	1	1	1	?	?	?	?	?	?	?
Macrepistius arenatus	1	1	1	0	?	?	?	?	?	?	?
Macrosemimimus lennieri	?	?	?	?	?	?	?	?	?	?	?
Macrosemius rostratus	1	1	1	1	0	?	0	0	?	0	0
Meemannia eos	?	?	?	?	?	?	?	?	?	?	?
Melanecta anneae	1	1	0	0	?	?	?	?	?	?	?
Mesopoma planti	?	0	0	0	?	?	?	?	?	?	?
Miguashaia bureaui	0	0	0	1	?	?	?	?	0	?	1
Mimipiscis bartrami	?	1	0	0	0	0	0	0	?	0	1
Mimipiscis toombsi	1	1	0	0	0	0	0	0	?	0	1
Moythomasia durgaringa	1	1	?	0	0	1	0	0	?	0	1
Moythomasia lineata	1	1	?	0	?	?	?	?	?	?	?
Moythomasia nitida	1	1	0	0	?	?	?	?	?	?	0
Obaichthys decoratus	?	?	1	?	0	1	?	0	?	1	0
Onychodus jandemarrai	0	0	1	1	0	?	?	?	?	0	1
Osorioichthys marginis	?	?	?	?	?	?	?	?	?	?	?
Osteolepis macrolepidotus	0	0	0	1	?	?	?	?	0	?	1
Ozarcus mapesae	?	?	?	?	?	?	?	?	?	?	-
Peltopleurus lissocephalus	1	0	0	0	?	?	?	?	?	?	?
Platysomus superbus	1	1	0	?	?	?	?	?	?	?	?
Polypterus bichir	1	0	1	1	0	1	0	0	1	0	0
Porolepis sp.	1	0	0	?	?	?	?	?	?	?	?
Propterus elongatus	1	1	1	0	?	1	?	?	1	0	0
Psarolepis romeri	?	?	?	?	?	?	?	?	?	?	?
Pteronisculus stensioi	0	1	0	0	0	0	0	0	?	0	1
Raynerius splendens	?	?	?	?	?	?	?	?	?	?	?

Saurichthys madagascarensis	1	1	1	1	?	?	?	0	?	?	1
Scanilepis dubia	?	0	?	?	?	?	?	?	?	?	?
Semionotus elegans	1	1	1	1	0	1	0	0	1	0	0
Styloichthys changae	?	?	?	?	?	?	?	?	?	?	?
Styracopterus fulcratus	0	1	0	0	?	?	?	?	?	?	?
Tanaocrossus kalliokoskii	1	?	1	1	?	?	?	?	?	?	?
Tegeolepis clarki	?	1	?	?	?	?	?	?	?	?	0
Tetragonolepis semicincta	1	1	1	1	?	1	0	0	0	0	0
Venusichthys comptus	1	1	0	0	?	?	?	?	?	?	?
Watsonulus eugnathoides	1	1	1	0	?	?	0	0	?	0	0
Wendyichthys dicksoni	1	1	0	0	?	?	?	?	?	?	?
Woodichthys bearsdeni	1	1	0	0	?	?	?	?	?	?	?

APPENDIX C - Character list Cavin et al. 2017

1 - Intracranial joint margin:

0 = straight

1 = strongly interdigitate

2 - Snout bones:

0 = lying free from one another

1 = consolidated, edentulous

2 = consolidated, toothed

3 - Median rostral:

0 = single

1 = several median rostrals (internasals)

4 - Premaxillae:

0 = paired

1 = fragmented

5 - Premaxilla:

0 = with dorsal lamina

1 = without dorsal lamina

6 - Anterior opening of the rostral organ contained:

0 = within premaxilla

1 = within separated rostral ossicles

7 - Parietal:

0 = one pair

1 = two pairs

8 - Anterior and posterior pairs of parietals:

0 = of similar size

1 = of dissimilar size

9 - Number of supraorbitals/tectals:

0 = fewer than eight

1 = more than 10

10 - Preorbital:

0 = absent

1 = present

11 - Parietal descending process:

0 = absent
1 = present

12 - Intertemporal:

0 = absent
1 = present

13 - Postparietal descending process:

0 = absent
1 = present

14 - Supratemporal descending process:

0 = absent
1 = present

15 - Extrascapulars:

0 = sutured with postparietals
1 = free

16 - Extrascapulars:

0 = behind level of neurocranium
1 = forming part of the skull roof

17 - Number of extrascapulars:

0 = three
1 = five
2 = more than seven

18 - Posterior margin of the skull roof:

0 = straight
1 = embayed

19 - Supraorbital sensory canal:

0 = running through centre of ossification
1 = following sutural course

20 - Medial branch of otic canal:

0 = absent
1 = present

21 - Otic canal:

0 = joining supratemporal canal within lateral extrascapular
1 = in supratemporal

22 - Anterior branches of supratemporal commissure:

0 = absent

1 = present

23 - Supraorbital sensory canals opening through bones:

0 = as single large pores

1 = bifurcating pores

2 - many tiny pores

3 = a large, continuous groove crossed by pillars

4 = a large, continuous groove without pillars

24 - Anterior pit line:

0 = absent

1 = present

25 - Middle and posterior pit lines:

0 = within posterior half of postparietals

1 = within anterior third

26 - Pit lines:

0 = marking postparietals

1 = not marking postparietals

27 - Parietals and postparietals:

0 = ornamented with enamel-capped ridges/tubercles

1 = bones unornamented

2 = bones marked by coarse rugosities

28 - Parietals and postparietals:

0 = without raised areas

1 = with raised areas

29 - Cheek bones:

0 = sutured to one another

1 = separated from one another

30 - Spiracular (postspiracular):

0 = absent

1 = present

31 - Preoperculum:

0 = absent

1 = present

32 - Suboperculum:

0 = absent

1 = present

33 - Quadratojugal:

0 = absent

1 = present

34 - Squamosal:

0 = limited to the mid-level of cheek

1 = extending behind the postorbital to reach the skull roof

35 - Lachrymojugal:

0 = not expanded anteriorly

1 = expanded anteriorly

36 - Lachrymojugal:

0 = ending without anterior angle

1 = angled anteriorly

37 - Squamosal:

0 = large

1 = reduced to a narrow tube surrounding the jugal sensory canal only

38 - Preoperculum:

0 = large

1 = reduced to a narrow tube surrounding the preopercular canal only

39 - Preoperculum:

0 = undifferentiated

1 = developed as a posterior tube-like canal-bearing portion and an anterior blade-like portion

40 - Postorbital:

0 = simple, without anterodorsal excavation

1 = anterodorsal excavation in the postorbital

41 - Postorbital:

0 = without anterior process

1 = with anterior process

42 - Postorbital:

0 = large

1 = reduced to a narrow tube surrounding the sensory canal only

43 - Postorbital:

0 = entirely behind the level of the intracranial joint

1 = spanning the intracranial joint

44 - Infraorbital canal within the postorbital:

0 = with simple pores opening directly from the main canal

1 = anterior and posterior branches with the postorbital

45 - Infraorbital sensory canal:

0 = running through centre of postorbital

1 = running at the anterior margin of the postorbital

46 - Jugal sensory canal:

0 = simple

1 = with prominent branches

47 - Jugal canal:

0 = running through centre of bone

1 = running along the ventral margin of the squamosal

48 - Pit lines:

0 = marking cheek bones

1 = failing to mark cheek bones

49 - Ornaments upon cheek bones:

0 = absent

1 = tubercular

2 = represented as a coarse superficial rugosity

50 - Infraorbital, jugal and preopercular sensory canals:

0 = opening through many tiny pores

1 = opening through a few large pores

2 = a large, continuous groove crossed by pillars

51 - Contact between the lachrymojugal and the preorbital or tectal-supraorbital series

0 = present

1 = absent

52 - Sclerotic ossicles:

0 = absent

1 = present

53 - Retroarticular and articular:

0 = co-ossified

1 = separated

54 - Dentary teeth:

0 = fused to the dentary

1 = separated from dentary

55 - Number of anterior coronoids:

0 = Absent

1 = One

2 = Two

3 = Three

4 = Four

56 - Coronoid:

0 = opposite to the posterior end of dentary not modified

1 = modified

57 - Dentary:

0 = simple

1 = dentary hook-shaped

58 - Oral pit line:

0 = confined to angular

1 = oral pit line reaching forward to the dentary and/or the splenial

59 - Oral pit line:

0 = located at centre of ossification of angular

1 = removed from centre of ossification

60 - Subopercular branch of the mandibular sensory canal:

0 = absent

1 = present

61 - Dentary sensory pore:

0 = absent

1 = present

62 - Ornaments:

0 = ridged

1 = granular

63 - Dentary:

0 = with ornament

1 = without ornament

64 - Splenial:

0 = with ornament
1 = without ornament

65 - Dentary:

0 = without prominent lateral swelling
1 = with swelling

66 - Principal coronoid:

0 = lying free
1 = sutured to angular

67 - Coronoid fangs:

0 = absent
1 = present

68 - Prearticular and/or coronoid teeth:

0 = pointed and smooth
1 = rounded and marked with fine striations radiating from the crown
2 = pointed and marked with fine striations

69 - Orbitosphenoid and basisphenoid regions:

0 = co-ossified
1 = separate

70 - Optic foramen:

0 = enclosed by basisphenoid extending forward
1 = lying within separate interorbital ossification or cartilage

71 - Processus connectens:

0 = failing to meet parasphenoid
1 = meeting parasphenoid

72 - Basipterygoid process:

0 = absent
1 = present

73 - Antotic process:

0 = not covered by parietal descending process
1 = covered

74 - Temporal excavation:

0 = lined with bone
1 = not lined

75 - Otico-occipital:

0 = solid

1 = separated to prootic/opisthotic

76 - Supraoccipital:

0 = absent

1 = present

77 - Vestibular fontanelle:

0 = absent

1 = present

78 - Buccohypophysial canal:

0 = closed

1 = opening through parasphenoid

79 - Parasphenoid:

0 = without ascending laminae anteriorly

1 = with ascending laminae

80 - Suprapterygoid process:

0 = absent

1 = present

81 - Vomers:

0 = not meeting in the midline

1 = meeting medially

82 - Prootic:

0 = without complex suture with the basioccipital

1 = with a complex suture

83 - Superficial ophthalmic branch of anterodorsal lateral line nerve:

0 = not piercing antotic process

1 = piercing antotic process

84 - Process on braincase for articulation of infrabranchial 1:

0 = absent

1 = present

85 - Separate lateral ethmoids:

0 = absent

1 = present

86 - Separate basioccipital:

0 = absent

1 = present

87 - Dorsum sellae:

0 = small

1 = large and constricting entrance to cranial cavity anterior to the intracranial joint

88 - Extracleithrum:

0 = absent

1 = present

89 - Anocleithrum:

0 = simple

1 = forked

90 - Posterior neural and haemal spines:

0 = abutting one another

1 = not abutting

91 - Occipital neural arches:

0 = not expanded

1 = expanded

92 - Ossified ribs:

0 = absent

1 = present

93 - Diphycercal tail:

0 = absent

1 = present

94 - Fin rays:

0 = more numerous than radials

1 = equal in number

95 - Fin ray:

0 = branched

1 = unbranched

96 - Fin rays in D1:

0 = more than ten

1 = eight to nine

2 = less than eight

97 - Caudal lobes:

0 = symmetrical

1 = asymmetrical

98 - D1:

0 = without denticles

1 = with denticles

99 - Paired fin rays:

0 = not expanded

1 = expanded

100 - Pelvics:

0 = abdominal

1 = thoracic

101 - Basal plate of D1:

0 = with smooth ventral margin

1 = emarginated and accommodating the tips of adjacent neural spines

102 - D2 basal support:

0 = simple

1 = forked anteriorly

103. - Median fin rays:

0 = not expanded

1 = expanded

104 - Scale ornament:

0 = not differentiated

1 = differentiated

105 - Lateral line openings in scales:

0 = single

1 = multiple

106 - Scales:

0 = ornament of ridges or tubercles

1 = rugose

107 - Ossified bladder:

0 = absent

1 = present

108 - Pelvic bones of each side:

0 = remain separate

1 = fused in midline

109 - Ventral keel scales:

0 = absent

1 = present

110 - Ventral swelling of the palatoquadrate:

0 = absent

1 = present

111- Pterygoid cristae: (New character)

0 = absent

1 = anterodorsally directed

2 = dorsally directed

112 – Dermopalatine teeth: (New character)

0 = absent or reduced

1 = large

113 – Supratemporals extend beyond posterior margin of postparietals: (New character)

0 = absent

1 = present

APPENDIX D - Matrix Actinistia gen. et sp. nov.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Actinopterygians	?	0	0	0	0	?	0	?	?	0	0	1	0	0	0	0	?	0	0	0
Porolepiforms	0	0	1	0	0	?	0	?	?	0	0	0	0	0	0	0	0	0	0	0
Diplocercides	0	0	1	?	?	?	1	1	0	1	0	0	0	0	0	0	0	0	1	0
Rhabdoderma	1	0	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	1	1
Caridosuctor	1	0	0	0	0	0	1	1	0	1	?	0	?	?	0	0	1	0	1	1
Hadronector	0	0	1	0	0	0	1	1	?	1	?	0	?	?	0	0	0	0	1	0
Rebellatrix	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polyosteorhynchus	0	0	?	0	0	0	1	1	0	1	?	?	?	1	0	0	?	0	1	0
Allenypterus	0	?	?	?	?	?	1	0	0	1	?	0	?	?	0	0	0	0	1	0
Lochmocercus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0
Coelacanthus	0	0	?	1	1	?	1	1	0	0	1	0	0	1	0	0	1	1	?	1
Spermatodus	1	0	0	0	0	0	1	1	0	1	1	0	0	1	1	0	?	1	1	1
Whiteia	0	0	?	0	0	0	1	0	0	1	1	0	0	1	1	0	1	1	1	1
Laugia	1	?	?	0	?	?	0	?	0	1	1	0	0	1	0	0	1	0	1	1
Sassenia	1	0	?	?	?	?	1	?	0	1	1	0	0	1	0	0	?	0	1	?
Chinlea	0	0	?	0	1	?	1	0	0	0	1	0	?	?	0	0	1	1	?	1
Diplurus	0	0	0	0	1	?	1	1	1	0	1	0	1	0	1	0	2	1	1	1
Holophagus	1	0	?	0	1	?	1	1	1	0	1	0	1	1	1	0	?	1	1	1
Undina	0	0	?	0	0	?	1	1	1	0	1	0	1	1	1	0	2	1	1	?
Coccoderma	1	0	?	0	1	1	1	1	0	?	1	0	0	1	0	0	1	0	1	1
Libys	0	?	?	?	1	?	?	?	?	?	1	0	1	1	1	?	?	1	1	1
Mawsonia	1	?	?	?	?	?	1	1	0	0	1	0	1	0	0	1	1	1	?	1
Macropoma	0	2	?	0	?	1	1	1	1	0	1	0	1	1	1	0	2	1	1	1
Latimeria	0	0	1	1	1	1	1	1	1	0	1	0	1	1	1	0	2	1	1	1
Miguashaia	0	0	?	0	0	0	0	?	0	?	0	1	?	?	0	0	0	0	0	0
Axelrodichthys	1	0	0	0	1	1	1	1	0	0	1	0	1	0	0	1	1	1	1	?
Holopterygius	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Garnbergia	?	?	?	?	?	?	1	1	?	0	?	0	?	?	?	?	?	1	?	?
Parnaibaia	0	0	1	1	?	?	1	0	0	0	?	0	?	?	0	0	1	1	?	1
Swenzia	0	1	?	0	?	?	1	?	?	?	?	0	1	1	?	?	?	1	?	?
Guizhoucoelacanthus	0	0	0	0	?	?	1	0	0	1	?	0	?	?	0	0	0	1	1	1
Piveteauia	1	?	?	?	?	?	?	?	?	?	1	0	1	1	?	0	?	1	?	1
Euporosteus	0	?	1	?	?	0	1	0	?	1	0	?	0	?	1	0	?	0	?	?
Axelia	?	?	?	?	?	?	0	?	0	1	1	0	?	1	1	0	2	1	1	?
Wimania	?	?	?	?	?	?	0	?	?	?	1	0	0	1	?	?	?	?	?	?
Megalocoelacanthus	0	1	?	0	0	1	1	1	0	0	1	0	1	1	1	0	?	1	1	1
Luopingcoelacanthus	?	?	?	0	1	?	1	1	0	?	?	0	1	?	1	0	?	1	?	?
Yunnancoelacanthus	?	?	0	0	?	?	1	0	0	1	?	0	1	1	0	1	0	1	?	?
Dobrogeria	1	?	?	?	?	?	?	?	?	?	1	0	1	1	1	0	?	1	1	1
Indocoelacanthus	0	?	?	?	?	?	1	?	?	?	?	0	?	?	?	?	?	?	?	?
Lualabea	0	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Ticinepomis	0	?	?	0	?	?	1	0	?	?	1	0	?	?	?	?	?	0	?	?
Foreyia	0	0	?	?	1	1	1	0	0	1	?	0	?	?	?	?	?	?	1	?
MCT 1463-P	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?	?	?	?	?	1

	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	4
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0
Actinopterygians	0	0	2	1	1	?	0	0	0	0	1	1	1	1	?	?	?	0	0	?
Porolepiforms	0	0	2	1	0	?	0	0	0	1	1	1	1	1	?	?	0	0	0	0
Diplocercides	0	0	2	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0
Rhabdoderma	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Caridosuctor	0	0	0	0	1	0	0	0	0	1	1	1	?	?	0	0	0	0	0	0
Hadronector	0	0	1	0	1	0	0	0	0	1	1	1	0	0	?	?	0	0	0	0
Rebellatrix	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Polyosteorhynchus	1	0	1	?	?	?	0	0	0	1	1	1	?	0	0	0	0	0	0	0
Allenypterus	0	0	0	0	0	0	0	0	1	?	1	1	0	0	0	0	0	0	0	0
Lochmocercus	1	0	0	?	?	?	0	0	0	1	1	1	?	?	0	0	0	0	0	0
Coelacanthus	1	0	?	0	?	1	1	0	1	?	?	?	0	0	0	0	1	?	?	0
Spermatodus	?	0	2	0	?	1	0	0	1	?	1	1	0	1	0	0	0	0	0	0
Whiteia	1	0	0	0	1	0	0	0	1	1	1	1	0	0	0	1	0	0	0	0
Laugia	0	0	0	0	?	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sassenia	?	0	2	0	1	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0
Chinlea	1	0	?	?	?	?	2	0	1	1	1	0	0	?	1	1	0	0	0	0
Diplurus	1	0	0	0	?	1	1	0	1	1	1	0	0	0	1	0	0	0	0	0
Holophagus	1	?	2	0	?	1	0	0	1	0	1	1	0	0	1	0	0	0	0	0
Undina	1	?	2	?	?	?	0	1	1	0	1	1	0	0	?	?	0	0	0	0
Coccoderma	0	0	2	0	1	0	1	0	1	0	1	0	0	?	0	0	1	1	0	0
Libys	1	?	3	0	?	1	1	0	1	0	1	0	0	0	1	0	0	0	1	0
Mawsonia	1	0	2	0	?	1	2	0	1	0	?	0	0	0	1	0	0	1	0	0
Macropoma	1	1	2	0	?	1	0	0	1	0	1	?	0	0	1	0	0	0	1	1
Latimeria	1	1	0	0	1	0	2	1	1	1	1	1	0	0	1	0	0	0	1	1
Miguashaia	0	0	2	?	0	0	0	0	0	?	1	1	0	1	?	?	0	0	0	0
Axelrodichthys	1	0	2	0	?	1	2	0	1	0	1	0	0	0	1	0	1	1	0	0
Holopterygius	?	?	?	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Garnbergia	?	?	?	?	?	?	?	?	1	?	1	0	0	0	1	1	0	0	?	0
Parnaibaia	?	?	2	?	?	1	1	0	1	1	1	0	0	0	1	1	0	0	0	0
Swenzia	1	1	?	0	1	0	1	1	1	1	1	?	0	0	1	0	0	0	1	1
Guizhoucoelacanthus	1	0	0	0	0	0	1	0	1	?	1	?	0	0	0	1	0	0	0	0
Piveteauia	?	1	?	0	?	?	0	0	?	1	1	?	?	0	0	0	0	?	?	?
Euporosteus	0	?	0	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?
Axelia	1	0	0	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?
Wimania	?	?	?	?	?	?	?	?	1	?	0	?	?	?	0	1	0	0	0	?
Megalocoelacanthus	1	?	3	0	?	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?
Luopingcoelacanthus	?	?	?	?	?	1	0	0	1	?	1	0	0	0	0	1	0	0	0	0
Yunnancoelacanthus	?	?	?	0	0	1	0	0	1	?	1	0	?	0	1	0	0	0	0	0
Dobrogeria	1	?	?	0	?	1	0	0	1	?	?	1	?	?	1	1	?	?	?	?
Indocoelacanthus	?	?	?	?	?	?	?	?	1	?	?	?	0	0	?	?	0	0	0	0
Lualabea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ticinepomis	?	?	?	?	?	?	0	0	1	?	1	?	0	?	?	?	0	0	0	?
Foreyia	?	?	4	?	?	?	0	0	1	0	1	1	0	0	0	0	0	0	0	1
MCT 1463-P	1	0	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Actinopterygians	?	?	?	?	?	?	?	0	1	0	?	1	0	0	4	0	0	0	?	0
Porolepiforms	0	0	0	0	0	0	0	0	1	0	0	1	0	0	3	0	0	0	?	0
Diplocercides	0	0	0	0	0	0	0	0	1	0	0	1	0	0	3	0	0	1	0	0
Rhabdoderma	0	0	0	0	1	1	0	0	1	0	0	1	0	1	4	1	0	0	0	0
Caridosuctor	0	0	0	?	?	0	0	0	1	0	0	1	0	1	4	1	0	0	0	0
Hadronector	0	0	0	?	1	?	0	?	1	0	0	1	0	?	?	?	0	0	1	0
Rebellatrix	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	?
Polyosteorhynchus	0	0	0	?	1	?	0	0	1	0	0	1	0	1	?	0	0	0	1	0
Allenypterus	0	1	0	0	1	?	?	1	0	1	0	1	0	1	?	?	0	1	1	0
Lochmocercus	0	0	?	0	1	0	0	0	?	0	0	1	?	0	?	0	0	?	?	0
Coelacanthus	0	1	0	?	1	?	1	?	1	0	0	1	0	1	4	1	0	?	?	0
Spermatodus	0	0	?	?	?	?	?	0	1	0	0	1	0	1	4	1	?	0	0	0
Whiteia	0	0	0	1	1	1	0	0	1	0	0	1	1	1	4	1	1	0	1	?
Laugia	0	0	0	1	0	0	1	1	1	0	0	1	0	1	4	0	0	0	0	0
Sassenia	0	0	0	0	1	0	0	0	1	0	0	1	?	1	?	1	0	?	?	0
Chinlea	0	0	1	?	0	?	?	?	2	0	0	0	?	?	?	1	1	?	?	?
Diplurus	0	1	0	0	1	1	1	1	0	1	0	0	1	?	?	0	0	0	0	0
Holophagus	0	0	0	?	1	?	?	1	1	0	0	0	1	?	?	1	1	0	0	1
Undina	0	0	0	?	1	0	1	1	1	0	0	0	1	?	?	1	1	0	1	?
Coccoderma	0	0	0	1	0	0	1	1	0	0	0	1	?	1	4	1	0	0	0	0
Libys	0	0	0	?	1	?	?	?	0	2	?	0	?	1	4	1	1	0	0	1
Mawsonia	1	0	1	?	0	0	0	1	2	0	0	0	1	1	?	?	1	?	?	0
Macropoma	0	0	0	1	1	0	1	1	1	0	1	0	1	1	4	?	1	0	1	1
Latimeria	0	0	0	1	1	1	1	1	1	1	1	0	1	1	4	1	1	0	1	1
Miguashaia	0	0	0	0	0	0	0	?	1	0	?	1	?	0	?	?	0	0	1	?
Axelrodichthys	1	0	1	1	0	0	0	1	2	0	?	0	1	1	4	0	1	?	?	0
Holopterygius	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	0	?
Garnbergia	0	0	0	?	?	?	?	?	1	?	0	0	?	?	?	?	?	?	?	?
Parnaibaia	0	0	1	?	?	?	?	?	1	?	0	0	1	?	?	0	1	?	?	?
Swenzia	0	0	0	1	1	0	1	1	1	0	?	0	?	1	?	?	1	0	1	?
Guizhoucoelacanthus	0	0	1	0	1	?	0	0	1	0	0	0	?	?	?	?	0	0	0	?
Piveteauia	?	?	?	?	0	1	0	1	1	?	?	1	1	1	?	?	0	?	?	?
Euporosteus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Axelia	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	0	?	?	?
Wimania	0	0	?	?	?	?	0	?	?	?	0	1	?	?	?	1	0	?	?	?
Megalocoelacanthus	?	?	?	?	?	?	?	?	?	2	?	0	1	1	?	0	1	?	?	1
Luopingcoelacanthus	0	0	?	?	?	0	0	1	1	0	?	1	1	1	?	?	1	?	?	?
Yunnancoelacanthus	0	0	?	?	?	?	?	1	1	?	0	?	?	0	?	?	0	?	?	0
Dobrogeria	?	?	?	?	?	?	?	?	1	?	?	?	1	?	?	?	?	0	1	?
Indocoelacanthus	0	0	?	?	?	?	?	?	1	0	?	0	?	?	?	?	1	?	?	?
Lualabea	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	?	?	?
Ticinepomis	0	1	1	?	?	?	?	?	?	?	?	0	?	1	3	1	?	?	?	1
Foreyia	0	1	1	0	0	?	?	1	1	0	0	0	?	1	4	1	1	?	?	?
MCT 1463-P	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	1	?

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100
Actinopterygians	0	0	0	1	0	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0
Porolepiforms	0	0	0	?	0	?	0	0	0	0	0	0	0	0	0	0	?	0	0	0
Diplocercides	?	0	1	0	0	0	0	?	?	0	0	0	1	0	1	0	0	0	0	0
Rhabdoderma	?	0	0	0	1	0	1	1	0	1	0	0	1	1	1	0	0	0	0	0
Caridosuctor	?	?	?	?	?	?	?	1	0	1	?	0	1	1	1	0	1	0	0	0
Hadronector	?	?	?	?	?	?	?	1	0	1	?	0	1	1	1	0	0	0	0	0
Rebellatrix	?	?	?	?	?	?	?	1	0	1	1	0	1	1	1	0	0	0	0	0
Polyosteorhynchus	?	?	?	?	?	?	?	1	?	1	1	0	1	1	1	?	1	0	0	0
Allenypterus	?	?	?	?	?	?	?	1	0	1	0	0	1	0	1	0	1	0	0	0
Lochmocercus	?	?	?	?	?	?	?	1	0	1	?	?	1	0	1	0	0	0	0	0
Coelacanthus	?	?	?	?	?	?	?	1	0	1	0	0	1	1	1	0	1	0	0	0
Spermatodus	?	0	0	?	1	0	1	?	?	?	?	?	?	?	?	?	?	?	?	?
Whiteia	1	1	0	1	1	1	1	1	?	1	0	0	1	1	1	2	0	1	0	0
Laugia	?	0	0	0	1	0	1	1	0	1	1	0	1	1	1	1	1	0	1	1
Sassenia	?	0	0	1	1	0	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Chinlea	?	?	?	?	?	?	?	1	?	1	?	1	1	1	1	1	?	0	0	0
Diplurus	?	?	0	?	1	1	1	1	0	1	1	1	1	1	1	1	0	1	0	0
Holophagus	?	1	?	?	1	?	?	1	?	1	1	0	1	1	1	1	?	1	1	0
Undina	?	1	?	?	1	1	1	1	0	1	?	0	1	1	1	1	0	1	0	0
Coccoderma	?	?	?	?	?	?	?	1	1	1	1	0	1	1	1	0	0	0	1	1
Libys	?	?	?	?	?	?	?	1	1	1	1	0	1	1	1	1	0	1	1	0
Mawsonia	?	?	?	?	?	?	?	?	?	1	?	?	1	1	1	?	0	1	0	0
Macropoma	1	1	0	?	1	1	1	1	1	1	1	0	1	1	1	2	0	1	0	0
Latimeria	1	1	0	0	1	1	1	1	0	1	1	0	1	1	1	2	0	1	0	0
Miguashaia	?	?	?	?	?	?	?	1	?	0	?	?	0	0	0	0	?	0	0	0
Axelrodichthys	1	1	0	?	1	1	1	1	?	1	1	1	1	1	1	1	0	1	0	0
Holopterygius	0	?	?	?	?	?	?	?	?	1	0	?	0	0	1	0	1	?	1	?
Garnbergia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	0	?	?
Parnaibaia	?	?	?	?	?	?	?	1	?	1	?	1	1	1	1	1	0	1	0	0
Swenzia	?	?	?	?	?	?	?	?	?	1	?	0	1	1	?	?	0	?	?	0
Guizhoucoelacanthus	?	?	?	?	?	?	?	1	?	1	0	0	1	1	0	2	0	0	0	0
Piveteauia	?	?	?	?	?	?	?	1	?	?	1	0	?	?	1	1	1	0	0	1
Euporosteus	0	?	1	?	0	?	0	?	?	?	?	?	?	?	?	?	?	?	?	?
Axelia	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?
Wimania	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	?	?	?	?
Megalocoelacanthus	?	?	0	?	1	?	1	1	?	?	1	?	?	?	?	?	?	?	?	?
Luopingcoelacanthus	?	?	?	?	?	1	?	1	0	1	0	0	1	1	1	0	0	1	0	0
Yunnancoelacanthus	?	?	?	?	1	?	?	?	?	1	0	0	1	?	1	1	?	1	0	0
Dobrogeria	?	?	0	?	?	1	1	1	?	?	?	?	?	?	?	?	?	?	?	?
Indocoelacanthus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Lualabea	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ticinepomis	?	?	?	?	?	1	?	1	?	1	?	0	1	1	1	1	0	1	0	0
Foreyia	?	?	?	?	1	?	?	1	0	1	?	0	1	1	1	0	0	1	0	0
MCT 1463-P	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

	101	102	103	104	105	106	107	108	109	110	111	112	113
Actinopterygians	0	0	0	0	0	0	0	0	0	0	0	1	0
Porolepiforms	0	0	0	0	0	0	0	0	0	0	0	1	0
Diplocercides	?	?	0	0	0	0	?	?	?	0	1	?	0
Rhabdoderma	1	1	0	0	0	0	1	0	0	0	1	0	0
Caridosuctor	1	1	0	0	?	0	1	0	0	?	?	?	0
Hadronector	0	1	0	?	?	0	1	0	0	0	?	?	0
Rebellatrix	0	1	0	0	0	0	?	0	?	?	?	?	?
Polyosteorhynchus	1	0	0	0	?	0	1	0	0	0	?	?	0
Allenypterus	0	0	0	0	0	0	1	0	1	0	?	?	0
Lochmocercus	1	0	0	?	?	0	?	0	0	0	?	?	?
Coelacanthus	0	1	0	0	?	0	1	0	0	0	1	0	1
Spermatodus	?	?	?	0	?	0	?	?	?	?	?	1	0
Whiteia	0	1	0	0	1	0	0	0	0	0	2	?	1
Laugia	0	1	0	0	?	0	1	1	0	0	2	?	1
Sassenia	?	?	?	0	?	0	?	?	0	0	?	?	1
Chinlea	?	1	0	1	?	1	?	0	0	?	?	1	1
Diplurus	0	1	0	1	?	0	0	0	0	0	2	?	0
Holophagus	0	1	1	0	?	0	1	0	0	?	?	?	1
Undina	0	1	0	0	1	0	1	0	0	1	2	?	?
Coccoderma	0	1	0	0	1	1	1	1	0	0	2	?	1
Libys	0	1	1	0	1	0	1	0	0	1	?	?	1
Mawsonia	0	1	0	1	?	1	1	0	?	0	2	?	1
Macropoma	0	1	0	1	1	0	1	0	0	1	2	?	1
Latimeria	0	1	0	0	1	0	0	0	0	1	2	1	1
Miguashaia	?	?	0	0	0	0	?	?	0	?	1	0	0
Axelrodichthys	0	1	0	1	?	1	1	0	0	0	2	?	1
Holopterygius	?	?	?	0	0	?	?	?	1	?	?	0	?
Garnbergia	0	1	0	0	?	0	?	?	0	?	?	?	1
Parnaibaia	0	?	0	1	?	0	1	0	?	?	?	?	0
Swenzia	0	1	?	0	?	0	1	?	?	?	?	1	1
Guizhoucoelacanthus	0	1	0	0	0	1	?	?	0	?	?	?	1
Piveteauia	0	1	0	0	?	0	1	?	0	?	?	?	0
Euporosteus	?	?	?	1	?	?	?	?	1	?	?	?	?
Axelia	?	?	?	0	?	0	?	?	?	0	2	?	?
Wimania	?	?	?	0	?	0	?	?	?	0	1	?	?
Megalocoelacanthus	?	?	?	?	?	?	?	?	?	1	2	?	1
Luopingcoelacanthus	0	1	0	1	?	0	1	0	0	?	2	0	0
Yunnancoelacanthus	?	1	0	1	?	0	?	0	0	?	?	?	0
Dobrogeria	?	?	?	?	?	?	?	?	?	0	1	0	1
Indocoelacanthus	?	?	?	0	?	0	?	?	?	?	2	?	?
Lualabea	?	?	?	?	?	?	?	?	?	?	?	?	?
Ticinepomis	0	1	1	0	0	0	0	0	0	1	2	1	0
Foreyia	?	?	1	1	?	0	0	?	?	1	?	0	-
MCT 1463-P	?	?	?	?	?	?	?	?	?	0	1	1	1

APPENDIX E – Analithical abstract of the thesis (in Portuguese)

INTRODUÇÃO

Taxonomia e Sistemática

Osteichthyes é o grupo mais diverso dentre os vertebrados recentes, incluindo cerca de 35.000 espécies, com exceção de Tetrapoda (ESCHMEYER; FRICKLE, 2016; NELSON *et al.*, 2016). O grupo é dividido em dois clados: Actinopterygii (peixes de nadadeiras raiadas) e Sarcopterygii (peixes de nadadeiras lobadas + tetrápodes). Actinopterygii inclui a maioria das espécies comumente chamadas de peixes, com grande diversidade concentrada em Teleostei [cerca de 30.000 espécies (NELSON *et al.*, 2016)]. Considerando apenas grupos recentes, Osteichthyes é grupo irmão de Chondrichthyes, conjuntamente denominados Gnathostomata.

Apesar da enorme diversidade de Osteichthyes, tanto recente quanto fósseis, a evolução e diversificação de suas linhagens continuam pouco conhecidas, especialmente em Actinopterygii, (FRIEDMAN, 2015; LU *et al.*, 2016). Em relação a Sarcopterygii, achados recentes, especialmente na China, continuam a elucidar a origem de diversas linhagens durante o Siluro-Devoniano (*e.g.* ZHU *et al.*, 2009).

Tanto as análises moleculares quanto paleontológicas indicam que a divergência das duas linhagens de Osteichthyes ocorreu durante o Siluriano (HURLEY *et al.*, 2007; NEAR *et al.*, 2012; LU *et al.*, 2016). Entretanto, os registros indubitáveis de actinopterígios ocorrem apenas no Devoniano Inferior e Médio [*e.g. Meemannia* e *Cheirolepis* (FRIEDMAN, 2015; LU *et al.*, 2016)], contrastando com o registro mais antigo de sarcopterígio, no Siluriano superior [*e.g. Psarolepis* and *Guiyu* (YU, 1998; ZHU *et al.*, 2009)].

Fósseis do Siluriano associados a actinopterígios são normalmente fragmentos de ossos e escamas, que carecem de caracteres diagnósticos que justifiquem com precisão seu posicionamento dentro de Actinopterygii (FRIEDMAN, 2015). Táxons mais bem conhecidos, como *Dialipina* e *Ligulalepis*, já foram considerados actinopterígios, porém são agora relacionados à base de Osteichthyes, devido à ausência de características derivadas associadas a actinopterígios e sarcopterígios (*e.g.* FRIEDMAN, 2007; BRAZEAU, 2009).

Actinopterygii é a linhagem mais bem-sucedida e diversificada dentre os Osteichthyes viventes, com cerca de 30.000 espécies (Nelson *et al.*, 2016). Esse clado possui um rico registro fossilífero desde o Devoniano Médio (FRIEDMAN; BRAZEAU, 2010; SALLAN, 2014; FRIEDMAN, 2015). Entretanto, mesmo com essa história evolutiva rica e disponibilidade de dados morfológicos ao longo do tempo geológico, a origem e padrões de diversificação continuam obscuros, e o posicionamento de fósseis do Paleozoico em relação a linhagens viventes é uma das áreas de maior incerteza (MICKLE, 2009; SALLAN, 2014; FRIEDMAN, 2015).

As linhagens modernas de Actinopterygii incluem Cladistia, Chondrostei, Holostei (Gynglimodi + Halecomorpha) e Teleostei. Holostei foi recentemente reerguido por Grande (2010), sendo considerado válido desde então. O relacionamento dentre estas linhagens é bem suportado por análises morfológicas e moleculares (*e.g.* NELSON *et al*., 2006; NEAR *et al*., 2012; BETANCUR-R *et al*., 2017), porém a hipótese filogenética mais aceita atualmente para os actinopterígios é resultado de cerca de dois séculos de discussão sobre de táxons fósseis e viventes (SALLAN, 2014).

Diversas linhagens de peixes sarcopterígios viveram durante o Paleozoico e Mesozoico, incluindo osteolepiformes, onichodontiformes, porolepiformes e rizodontes. Contudo, apenas celacantos e dipnoicos permanecem como linhagens viventes (NELSON *et al*., 2016). É importante mencionar que os sarcopterígios formam um grupamento monofilético apenas com a inclusão de tetrápodes (ZHU; YU, 2002; JOHANSON, 2004; DAESCHLER *et al*., 2006).

O relacionamento das linhagens fósseis de Sarcopterygii permanece pouco conhecido e o posicionamento de algumas das linhagens extintas é problemático [*e.g*., Onichodontiformes (CLOUTIER; AHLBERG, 1995)]. Nesse trabalho, Cloutier e Ahlberg (1995) recuperaram Actinistia (celacantos) como grupo-irmão de todas as outras linhagens de Sarcopterygii; Dipnoiformes (peixes pulmonados) como grupo-irmão de Porolepiformes; e Osteolepiformes formando um grupamento parafilético em uma politomia com os clados Elpistostegalia + Tetrapoda. Entretanto, o *status* de Actinistia como grupo-irmão dos demais sarcopterígios é fracamente suportado nessa e em outras análises, que posicionam Onychodontida + Actinistia ou Onychodontida como o grupo-irmão dos demais sarcoterígios (CLOUTIER; AHLBERG, 1995).

Contexto Geológico

A Formação Pedra de Fogo (FPF) pertence à Bacia do Parnaíba, umas das principais bacias intracratônicas do território brasileiro, juntamente com as bacias do Paraná e Amazonas (VAZ *et al*., 2009). Essa formação abrange desde a borda oeste do Piauí, passando pela borda leste do Maranhão, até parte do Tocantins (SANTOS; CARVALHO, 2009).

A litologia da FPF pode ser dividida em três membros: Inferior (membro sílex basal), que inclui siltitos intercalados, bancos dolomíticos com concreções e horizontes silicosos; Médio, caracterizado por arenitos finos com estratificação cruzada, intercalados com siltitos, folhelhos e bancos carbonáticos com pequenas concreções silicosas; e o Superior (Membro Trisidela), apresentando arenitos, siltitos, folhelhos e bancos carbonáticos intercalados (SANTOS; CARVALHO, 2009).

A idade da FPF e da Formação Motuca, sobreposta a ela, foi amplamente discutida no passado (ARAÚJO, 2015) e grandes mudanças foram feitas, desde a hipótese original que indicava Permiano superior (PLUMMER, 1946). Atualmente, considera-se que a FPF compreende o Permiano inferior (Cisuraliano) da sequência Carbonífera-Eotriássica da Bacia do Parnaíba, aproximadamente no intervalo Artinskiano-Kunguriano. A PFF é intermediária nessa sequência às formações Piauí e Motuca (VAZ *et al*., 2009).

A paleobiota da FPF é composta principalmente por vertebrados e material vegetal, normalmente isolados e desarticulados. Contudo, espécimes parcialmente articulados são encontrados, incluindo os aqui descritos. Estromatólitos também estão presentes na unidade (CISNEROS *et al*., 2015; IANUZZI *et al*., 2018).

MATERIAL E MÉTODOS

O material analisado consiste em duas amostras depositadas na coleção de Paleovertebrados do Museu de Ciências da Terra (MCT), do Departamento Nacional de Produção Mineral (DNPM), sob os cuidados do Centro de Pesquisas de Recursos Minerais (CPRM). Ambas as amostras estavam alocadas na mesma caixa e catalogadas com igual número de tombo (DGM 1061-P). Este material compreende o crânio incompleto de *Brazilichthys macrognathus* Cox e Hutchinson, 1991 e ossos parcialmente desarticulados sem identificação, tendo sido coletado por Llewellyn Ivor Price na localidade de Pastos Bons, na estrada entre as cidades de Nova Iorque e Pastos Bons, Maranhão.

Microtomografia

Foi realizada a Microtomografia Computadorizada (µCT) de ambos os espécimes no Laboratório de Instrumentação Nuclear do Instituto de Pós-graduação e Pesquisa de Engenharia (COPPE-UFRJ), através do tomógrafo SkyScan 1173. A corrente utilizada foi de 61 µA e a voltagem 130 kV para ambas as amostras. As projeções resultantes foram processadas no *software* NRecon 1.6.9.4, produzindo o conjunto de dados tomográficos. A segmentação foi completada utilizando o Spiersedit 2.2, com arquivos bitmap das fatias. Os dados foram comprimidos em 50% nos eixos x, y e z, a fim de agilizar o processamento dos dados sem perda significativa de informação morfológica ou de proporções. As fatias foram processadas manualmente para identificar características anatômicas importantes de cada amostra e obter um melhor modelo 3D final. Após a segmentação, os dados foram visualizados em 3D no Spiersview 2.2, no qual pequenas edições foram feitas (*e.g.* brilho, retirada de pontos flutuantes e alisamento).

Análises filogenéticas

1. Parcimônia:

Os caracteres anatômicos de *Brazilichthys macrognathus* foram adicionados à matriz de Giles et al. (2017). Uma análise de parcimônia com pesos iguais para todos os caracteres foi feita utilizando-se o *software* TNT v. 1.5 (GOLOBOFF; CATALANO, 2016) e o algoritmo *New Technology Search* com cinco sequências adicionais iniciais e comprimento mínimo igual a 1.

Os caracteres anatômicos da segunda amostra foram adicionados à matriz de Cavin et al. (2017). Novos caracteres foram adicionados a esta matriz, a fim de melhor documentar a diversidade morfológica encontrada e testar hipóteses de evolução de caracteres. A matriz resultante foi analisada no TNT com os mesmo parâmetros da análise anterior.

2. Bayesiana:

A análise Bayesiana foi realizada no *software* MrBayes 3.2.5 (RONQUIST *et al*., 2012) utilizando-se o algoritmo Metropolitan Coupled Markov Chain (MCMC) para caracteres morfológicos discretos (WRIGHT; HILLIS, 2014). A codificação dos caracteres foi estabelecida como "*variable*" e as distribuições gama foram incorporadas. O número de tipos de substituições foi "*nst2*", ou seja, toda a transição potencialmente tem taxas diferentes.

Nomenclatura:

A nomenclatura osteológica seguiu Gardiner (1984) para Actinopterygii e Forey (1998) para Sarcopterygii. É importante ressaltar que ossificações consideradas homólogas podem ter nomes diferentes para os dois grandes grupos estudados (*e.g.* frontal de Actinopterygii recebe o nome de parietal em Sarcopterygii; SCHULTZE, 2008).

RESULTADOS

ACTINOPTERYGII Cope, 1887

BRAZILICHTHYIDAE Cox & Hutchinson, 1991

BRAZILICHTHYS Cox & Hutchinson, 1991

BRAZILICHTHYS MACROGNATHUS Cox & Hutchinson, 1991

Diagnose emendada

Actinopterígio paleopterígio distinguível pela seguinte combinação de caracteres: presas parasinfisianas, das quais algumas são prostadas; região sinfisiana flexionada da mandíbula inferior em vista lateral; concavidades da fossa glenoide do articular bem espaçadas; placas gulares longas e elipsóides; presença de longas placas gulares extralaterais; dermoesfenótico em forma de bastão; paraesfenóide com distintos processos basipterigóides; processos ascendentes curtos e retangulares e processo anterior robusto, com uma quilha no corpo anterior.

Descrição

Teto craniano – O teto craniano é representado por fragmentos isolados, possivelmente associados ao frontal, acima do dermoesfenótico, e parietal, acima do suborbital.

Rostro e série circum-orbital – O nasal é grande e possui entalhes para as aberturas nasais anterior e posterior. Possui também um canal sensorial visível apenas na superfície mesial deste osso. Posterodorsalmente ao nasal está o dermoesfenótico, que foi originalmente interpretado como parte do anel esclerótico, mas que por conta da presença de um canal e de uma comissura é reinterpretado aqui como dermoesfenótico. É um osso longo e robusto que contata anteriormente o nasal e posteriormente o jugal, formando a parte dorsal da órbita. Possui três ossificações infraorbitais (lacrimal, infraorbital e jugal). O jugal é lunado e o canal sensorial infraorbital passa por sua margem anterior em direção ao dermoesfenótico. O lacrimal e o infraorbital medial possuem formato retangular e estão mal preservados. Posterodorsalmente ao jugal existe uma ossificação mal preservada que é interpretada aqui como um suborbital, seguindo o proposto por Cox e Hutchinson (1991). Anterior a série infraorbital está a pré-maxila, um osso robusto que possui três dentes cônicos e a passagem do canal que conectaria o canal infraorbital ao nasal. Pequenos foramens são visíveis na superfície deste osso.

Mandíbula e Palato – Tanto a mandíbula quanto o maxilar mostram o formato típico de peixes paleopterígios. Possuem duas fileiras de dentes cônicos; uma menor externa e uma muito maior interna, onde é possível ver o capuz de acrodina. O maxilar é o maior osso do crânio, consistindo de uma expansão suborbital final e alongada e uma enorme expansão posterorbital, de formato sub-retangular. O dentário é o maior osso da mandíbula, cobrindo quase a totalidade de sua superfície lateral, sendo possível ver o canal sensorial mandibular ventralmente e uma ossificação mentomeckeliana mesialmente em seu ápice. O angular e surangular formam o restante da superfície lateral externa da mandíbula, contatando o articular internamente, formando a borda da fossa adutora, em conjunto com o pré-articular mesialmente.

O palatoquadrado está apenas parcialmente preservado, e é difícil identificar se existiriam diferentes ossificações ou uma única. Sua forma acompanha o formato da maxila. Anteriormente a sua expansão posterorbital, existe um entalhe que seria a articulação para os processos basipterigóides. Ventralmente ao palatoquadrado existe uma fileira de dentes que faria parte dos dermopalatinos.

Placas gulares – As placas gulares são visíveis ventralmente ao dentário. Externamente é possível identificar uma placa gular média impar e um par de placas gulares laterais, porém internamente existe um par de placas extralaterais, antes dos pares de raios branquiostégios. Todas as ossificações gulares são alongadas anteroposteriormente, com comprimento aproximadamente igual a metade do dentário.

Série opercular – A série opercular não foi preservada, com exceção do opérculo esquerdo que está parcialmente preservado e de fragmentos do pré-opérculo associados a hiomandíbula.

Paraesfenoide, caixa craniana e ossificações associadas – O paraesfenóiode é longo e possui um fino processo anterior que termina em uma expansão para articulação com o vômer (não preservado). Lateralmente ao corpo do paraesfenóide, existe um par de processos basipterigóides robusto e um par de processos ascendentes de formato retangular, carregando a passagem do espiráculo. Em sessão transversal, o processo anterior possui formato triangular, e sua superfície ventral é lisa, sem a presença de dentes. Lateralmente ao paraesfenóide, estariam um par de vômeres acessórios, placas finas de osso, sem dentição, que completariam o palato. Não há indícios do neurocrânio, que é então considerado cartilaginoso.

Arcos hioide e branquiais – O hiomandibular é grande e espatulado, curvando posteroventralmente em direção a articulação das mandíbulas. Este osso possui a passagem do canal hiomandibular, que se estende ao longo da superfície mesial deste osso, saindo para a superfície externa por meio de um forame. Após a expansão espatulada, existe uma leve projeção que representa o processo opercular da hiomandíbula. Não há evidências de um dermohial. Os hipiais estão localizados ventralmente ao ápice do dentário, curvando-se para contatar um ao outro medialmente. Possuem formato circular em corte transversal.

Os arcos branquiais estão mal preservados, porém é possível identificar quatro pares de longos ceratobranquiais. Existem também dois pequenos epibranquiais, que não mostram evidências de processo uncinado desenvolvido. Os hipobranquiais são longos, expandindo anteriormente para articulação com o basibranquial (não preservado).

Cintura peitoral – As clavículas são longas, porém finas, possuindo ápices triangulados, e expandindo posteriormente em direção ao cleitro (não preservado). Existe um osso desarticulado em meio aos arcos branquiais que por seu formato elipsoide poderia representar um interclavicular. Uma ossificação romboide posterior a clavícula direita poderia representar um propterígio fusionado aos primeiros raios da nadadeira.

Análise filogenética

A análise de parcimônia incluindo *Brazilichthys* encontrou três topologias igualmente parcimoniosas (L = 1325 passos; CI = 0,22; RI = 0,64). O consenso estrito é bem resolvido. Actinopterígios do Devoniano formam um grupamento parafilético na base de Actinopterygii, com a maior parte das espécies do Devoniano Médio e Superior formando um grupo monofilético (Suporte de Bremer [BDI] = 2); *Brazilichthys* está logo após os táxons do Devoniano, em uma politomia com dois outros clados (BDI = 2). O primeiro destes inclui a maioria dos táxons do final do Paleozoico, porém é fracamente suportado (BDI = 1).

A análise Bayesiana mostra um resultado muito semelhante à análise de parcimônia. As principais diferenças incluem: a resolução do posicionamento dos paleopterígios, a base de Chondrostei, e a topologia da base de Neopterygii. É interessante notar que os nós bem suportados na análise de parcimônia (BDI ≥ 3) não foram obtidos na análise Bayesiana.

Diversas sinapomorfias foram obtidas para o nó que inclui *Brazilichthys* e os demais táxons do Paleozoico superior ao Recente, porém apenas duas são visíveis em *Brazilichthys*:

- 56: Ausência de um ramo posterior diferenciado no dermoesfenótico (1 – 0);
- 211: Presença de processo opercular na hiomandíbula (0 – 1).

SARCOPTERYGII Romer, 1955

ACTINISTIA Cope, 1871

ACTINISTIA GEN. ET SP. NOV.

Diagnose:

Celacanto com mandíbula inferior apresentando dois tipos de ornamentação (estrias e tubérculos no angular)*; forte associação entre o angular e o prearticular; superfície do angular densamente coberta por poros; metapterigóide fortemente associado à margem anterodorsal do pterigoide, com processo articular bem desenvolvido; quadrado grande com côndilos posteriormente orientados; expansão posterodorsal da margem do quadrado; grandes autopalatinos; cintura peitoral com grandes clavículas.

* Indica autapomorfia.

Descrição:

Teto craniano – Apenas a porção posterior do teto craniano está preservada, e consiste em póspariental e supratemporal. O póspariental é triangular, com o canal sensorial ótico margeando o osso externamente, atingindo a superfície por meio de uma série de poros. O supratemporal é grande, estendendo além da margem posterior do póspariental. Ambos póspariental e supratemporal possuem processos descendentes que contatariam o neurocrânio.

Mandíbula – A mandíbula está incompleta, porém importantes características diagnósticas são visíveis. O angular é grande, porém sua porção anterior está faltando. Sua superfície é coberta por poros e a ornamentação é composta tanto por estrias quanto por tubérculos arredondados. Possui um grande canal sensorial mandibular, que atinge a superfície por meio de grandes foramens retangulares. O pré-articular também está parcialmente quebrado, mas seria um osso bastante longo e tabular, apresentando um processo em sua superfície externa que contataria o angular. Anteriormente em sua superfície mesial é possível ver vestígios de dentição. O articular é fortemente associado ao angular, e mostra a faceta de articulação com o quadrado. O coronóide principal possui um processo em forma de “T” mediodorsalmente em sua superfície externa, que seria a região de inserção do músculo adutor. Esse osso é relativamente grande em relação aos demais ossos da mandíbula.

Palato – O palato é a estrutura mais bem preservada do espécime. O pterigoide é triangular e possui estrias laterais que estendem da borda posteroventral em direção a margem anterior. Não há evidências de dentição em sua face mesial. Esse osso contata o quadrado posteroventralmente e o metapterigóide dorsalmente. O quadrado é grande, cobrindo uma porção considerável do pterigoide. O quadrado torna-se mais robusto ventralmente, por conta da presença dos côndilos. A borda posterior do quadrado estende além da borda do pterigoide. O metapterigóide é pequeno, mas possui um processo de articulação desenvolvido para fixar-se ao pterigoide.

Anteroventralmente ao pterigoide, existem pequenos elementos ósseos que representam parte do dermopalatino, que possui grandes dentes cônicos e outros elementos menores que poderiam ser parte do ectopterigoide e dos coronoides da mandíbula inferior. Além destes elementos, existe um grande osso endocondral que provavelmente representa parte do autopalatino.

Neurocrânio – O neurocrânio está incompleto, sendo representado apenas pelo basisfenóide. Esse osso possui grandes processos antóticos com margens anteriores arredondadas. Os côndilos esfenóticos são pequenas estruturas arredondadas em ambos os lados da *dorsum sellae*. A *dorsum sellae* é profunda e parece ter sido mais profunda posteriormente. O foramen do nervo V são evidentes em vista anterior, porém são recobertos pelas expansões dos processos antóticos dorsalmente. Ventralmente ao basisfenóide parece existir parte do que poderia ser a porção proximal do paraesfenóide.

Cintura peitoral – A clavícula é triangular e grande em vista lateral, com um uma fina expansão orientada dorsalmente, e uma superfície de articulação com o extrecleitro ventralmente. O extracleitro é um osso pequeno, porém robusto, triangular em vista lateral, afinando anteriormente, com uma face externa reta, sem sinal de ornamentação.

Arco hioide e branquial – O aparato branquial está mal preservado, porém é visível entre ambos os pterigoides, onde diversos ceratobranquiais são visíveis. O ceratohial é achatado lateralmente e possui um robusto processo lateral.

Análise filogenética:

A análise filogenética encontrou quatro topologias igualmente parcimoniosas, e o consenso estrito não apresenta politomias na área de enfoque da análise. A análise resolveu o novo táxon como o celacanto mais distal do Paleozoico, apical em relação à *Spermatodus* e *Wimania*. O nó incluindo o novo táxon e todas as espécies mais apicais é suportado por uma única sinapomorfia: Presença de processo descendente no pospariental (13: 0 – 1), que é marcadamente visível no novo táxon. A única autapomorfia do novo táxon foi a presença de ornamentação tanto por tubérculos quanto estrias. Porém, uma outra possível sinapomorfia seria a expansão da margem posterior do quadrado, que não foi incluída na análise por conta de incerteza sobre a morfologia desta ossificação em muitas espécies.

A análise Bayesiana encontrou uma topologia consideravelmente diferente do consenso estrito da análise por parcimônia, e diversas relações não foram resolvidas. A principal diferença é a presença do clado *Spermatodus* + *Sassenia* e *Macropoma* + *Latimeria.* O posicionamento do novo táxon é semelhante nas duas análises.

O cálculo das taxas evolutivas indica altas taxas (i.e. aquisição de novas características morfológicas ao longo do ramo) durante o início da história evolutiva do grupo, durante o Devoniano Médio e Superior. Após o Devoniano as taxas estabilizam consideravelmente até o tempo recente. Esse padrão é comum a linhagens antigas que ainda apresentam espécies viventes, e já foi previamente documentada para peixes pulmonados (LLOYD et al., 2011).

CONCLUSÕES

Brazilichthys macrognathus

A análise por microtomografia computadorizada de *Brazilichthys macrognathus* revela novos aspectos importantes acerca da morfologia desta espécie. O anel esclerótico descrito por Cox e Hutchinson é reinterpretado como um dermoesfenótico; a série infraorbital possui três ossificações ao invés de duas; o rostral descrito originalmente não está presente. Novas características obtidas incluem: paraesfenóide; vômeres acessórios; clavículas; e arcos hioide e branquiais.

O posicionamento de *Brazilichthys* como proximamente relacionado a Birgeria, proposto por Romano e Brinkmann (2009) não é suportado na presente análise filogenética. Embora nossa análise não inclua Acrolepis, uma afinidade com este táxon parece improvável por conta de diferenças marcantes da mandíbula, paraesfenóide e placas gulares. Por fim, é possível que paleopterígios predatórios como *Brazilichthys* e *Rhabdolepis* possam ser proximamente relacionados, porém são necessários estudos detalhados da morfologia destes outros táxons.

Actinistia gen. et sp. nov.

MCT 1463-P é o primeiro celacanto tridimensional descrito para o Paleozoico do Brasil, e possui diversas características que o diferenciam de outras espécies: presença de uma expansão da borda posterior do quadrado, côndilos do quadrado orientados posteriormente, angular e articular fortemente associados; e presença de processo para articulação do metapterigóide com o pterigoide.

A nova espécie de celacanto aqui descrita mostra uma mistura de caracteres que a diferenciam de outras espécies do Paleozoico (e.g. *Spermatodus*, *Coelacanthus*, *Rhabdoderma*), e a relacionam a espécies do Mesozoico (e.g. *Dobrogeria*, *Wimania*, *Whiteia*), sendo resolvida em ambas análises como a espécie mais apical dentre os celacantos do Paleozoico.

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