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Revisão da ordem Polypteriformes (Actinopterygii: Cladistia): morfologia e taxonomia

Rio de Janeiro

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Tese apresentada, como requisito parcial para obtenção do título de Doutor, ao Programa de Pós-Graduação em Biociências, da Universidade do Estado do Rio de Janeiro.

Orientador: Prof. Dr. Paulo Marques Machado Brito

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Rio de Janeiro
2022

DEDICATÓRIA

À minha querida avó Nely, que partiu sendo mais uma vítima da ignorância que nos assola. Que não deixemos a ignorância nos tomar mais ninguém.

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Ao laboratório Palevoprim, à Université de Poitiers e ao Muséum national d'Histoire naturelle e seus professores e funcionários, por terem me possibilitado acesso ao material e equipamentos indispensáveis para a realização da minha tese. // Au laboratoire Palevoprim, à l’Université de Poitiers et au Muséum national d’Histoire naturelle et leurs enseignants et employés, de m’avoir permis d’accéder au matériel et aux équipements indispensables à la réalisation de ma thèse.

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Às entidades independentes que se esforçam para fazer a ciência ser mais acessível a todos, Biodiversity Heritage Library, Library Genesis, Sci-hub.

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The bones of the past will tell their tales—if you know how to speak their language.

Savra, Queen of the Golgari, personagem criada por Mark Rosewater para o jogo "Magic: the Gathering".

RESUMO

COELHO, Marcos Vinícius de Lima. *Revisão da ordem Polypteriformes (Actinopterygii: Cladistia):* morfologia e taxonomia. 2022. 148 f. Tese. (Doutorado em Biociências) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2022.

A Ordem Polypteriformes é conhecida do Triássico até o presente e representa o grupo irmão de todos os outros Actinopterygii atuais. Polypteriformes atuais são representados pela família africana Polypteridae. Os Polypteridae formam um clado monofilético composto por dois gêneros: *Polypterus*, os ‘*bichirs*’, composto por 13 espécies e monoespecífico *Erpetoichthys*, o ‘*reedfish*’. Apesar de serem estudados por mais de 200 anos, não há um consenso sobre as espécies válidas pertencentes ao grupo, nem sobre as relações filogenéticas dentro dele. A presente tese procura ajudar a elucidar algumas destas questões e é dividida em 3 *drafts*. Cada *draft* tem como objetivo i) produzir uma descrição osteológica detalhada de *Polypterus senegalus* e compará-la com a osteologia de outras 9 espécies de Polypteriformes, para tentar achar novos caracteres para melhor separar estas espécies, e depois, ajudar a elucidar as relações filogenéticas do grupo; ii) analisar a morfologia intraindividual e intraespecífica nas pínulas de *Polypterus bichir*, para entender se a variação morfológica nas pínulas de uma única espécie, a fim de determinar a sua validade como ferramenta taxonômica, para, assim, confirmar a validade dos táxons fósseis descritos com base em material isolado; e iii) analisar a ornamentação de ganoína nas escamas de diferentes regiões do corpo de *Polypterus bichir* para entender se a ornamentação de ganoína dessas escamas se mantém constante, independentemente da região corporal, e se ela pode ser utilizada para separar espécies ou grupos. Para cada *draft*, nós mostramos que i) as diferenças no rostral, lacrimal, série espiracular, região opercular e nadadeira caudal são caracteres promissores para separar as espécies atuais de Polypteridae; ii) há um padrão morfológico relacionado ao eixo antero-posterior na nadadeira dorsal. Nós também reportamos diferenças morfológicas nas pínulas de diferentes espécimes e inconsistências entre nossos resultados e os resultados de outros estudos; e iii) que os parâmetros estudados aqui são consideravelmente variáveis, não importando a região corporal, e que eles se sobrepõem aos dados para outras espécies na literatura, não sendo possível achar nenhum padrão distinto neles.

Palavras-chave: Polypteridae. Anatomia. Osteologia. Pínulas. Escamas. Delimitação de espécies. Variação morfológica. Taxonomia.

ABSTRACT

COELHO, Marcos Vinícius de Lima. *Revision of the order Polypteriformes (Actinopterygii: Cladistia):* morphology and taxonomy. 2022. 148 f. Tese. (Doutorado em Biociências) – Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro, 2022.

The order Polypteriformes is known from the Triassic to the Recent and represents the sister group of all other extant actinopterygians. Extant polypteriforms are represented by the unique African family, Polypteridae. The polypterids form a monophyletic assemblage of two nominal genera: *Polypterus*, the bichirs, with 13 species, and the monospecific *Erpetoichthys*, the reedfish. Despite being studied for over 200 years, there is still no consensus on the valid species belonging to the group and the phylogenetic relationships within it. The present thesis seeks to help elucidate some of these questions and is divided into three drafts. The drafts aim to i) produce a detailed description of the osteology of *Polypterus senegalus* and compare it with the osteology of 9 other species of Polypteriformes to try to find new characters to more clearly separate species, and later help to elucidate the phylogenetic relationships within the group; ii) analyze the intraindividual and intraspecific morphology on the pinnules of *Polypterus bichir*, to understand the morphological variation on the pinnules in a single species, to determine their validity as taxonomic tools to later assess the validity of the fossil taxa erected on isolated material; and iii) analyze the ganoin ornamentation on the scales of different body regions of *Polypterus bichir*, to understand if the ganoin tubercle ornamentation in these scales remain constant, independently of its position on the body, and can be used to separate species or groups. For each draft, we found that i) the differences on the rostral, lacrimal, spiracular series, opercular region and caudal fin are some promising features to separate the extant polypteridae species; ii) there is a pattern on the morphology related to the anteroposterior axis on the dorsal fin. We also report morphological differences on the pinnules of the different specimens and inconsistencies between our findings and previous studies; and iii) that these parameters are considerably variable, no matter the body region, and overlapping with the data for other species in the literature, thus not possible to find any distinguished pattern on them.

Keywords: Polypteridae. Anatomy. Osteology. Pinnules. Scales. Species delimitation. Morphological variation. Taxonomy.

LISTA DE ILUSTRAÇÕES

LISTA DE ABREVIATURAS E SIGLAS

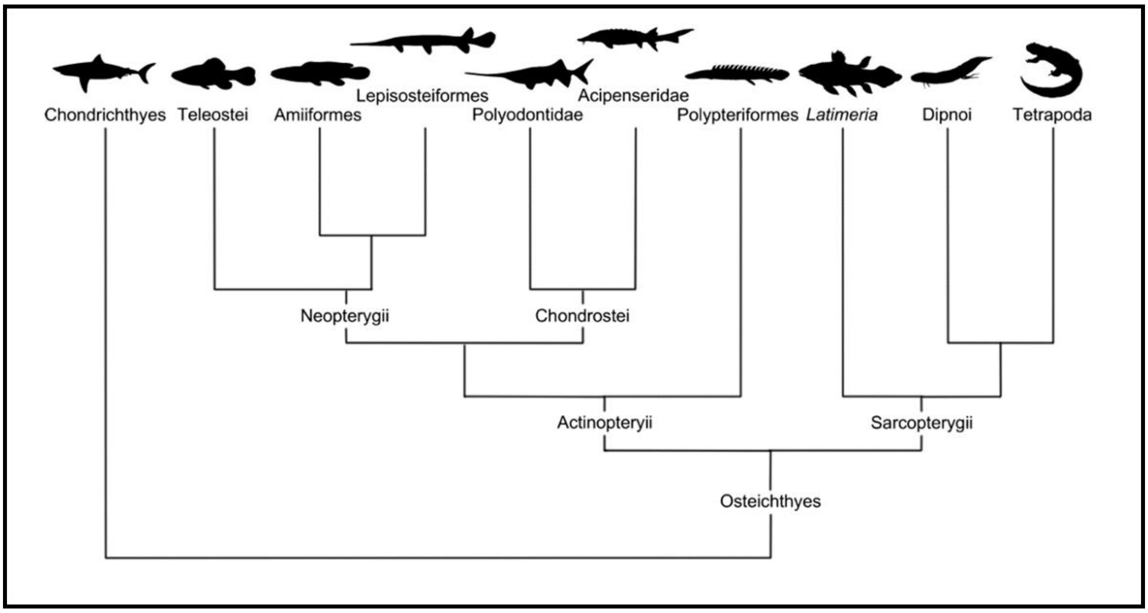
IC	Ichtyologie
MNHN	Muséum national d'Histoire naturelle
PNT	Peixes neotropicais
UERJ	Universidade do Estado do Rio de Janeiro
UP	Université de Poitiers

SUMÁRIO

INTRODUÇÃO

Os Actinopterygii, chamados de "peixes de nadadeira raiada", são caracterizados pela ausência do canal sensorial jugal, septo interorbital do neurocrânio estreito, capuz de acrodina nos dentes e múltiplas camadas sobrepostas de esmalte (ganoína) (FRIEDMAN, 2015). Este grupo possui mais de 31.000 espécies, o que consiste em aproximadamente metade da riqueza de vertebrados atuais (ESCHMEYER; FONG, 2015; NELSON *et al*., 2016). Na base deste clado está situada a ordem Polypteriformes, considerada como a mais basal, ou seja, a primeira linhagem a se diversificar entre os Actinopterygii atuais, sendo assim o grupo-irmão dos demais actinopterígios viventes (Figura 1) (GARDINER; SCHAEFFER, 1989; GARDINER *et al*., 2005; GILES *et al*., 2017; PATTERSON, 1982; VENKATESH *et al*., 1999; VENKATESH *et al*., 2001;). Esta ordem é constituída por apenas uma família, Polypteridae (NELSON *et al*., 2016; VAN DER LAAN *et al*., 2014). O primeiro exemplar de Polypteridae foi descoberto no Rio Nilo (Cairo, Egito) em 1799 durante a 'Campanha do Egito' feita pelo exército francês sob o comando de Napoleão Bonaparte (SAINT-HILAIRE, 1802; 1809). O mesmo espécime de *Polypterus bichir* só foi descrito em 1802 por Geoffroy Saint-Hilaire.

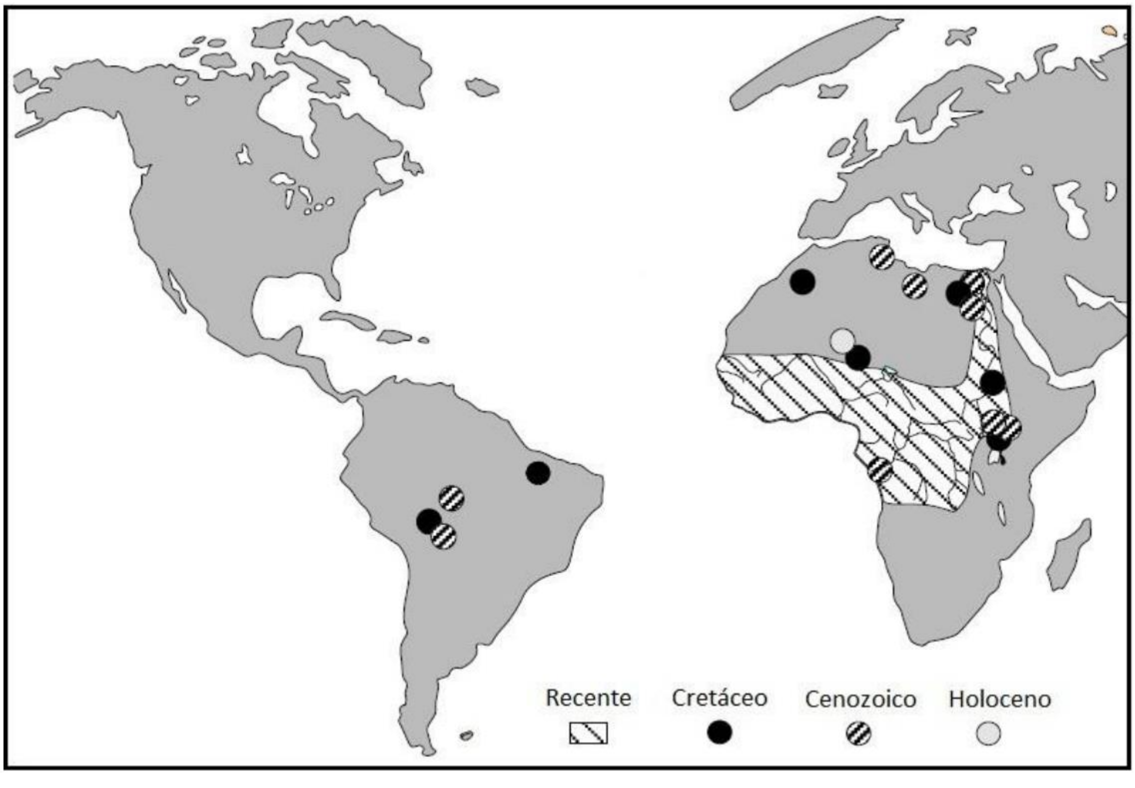
Figura 1 - Filogenia de Osteichthyes



Fonte: Adaptada de WILHELM *et al*., 2015.

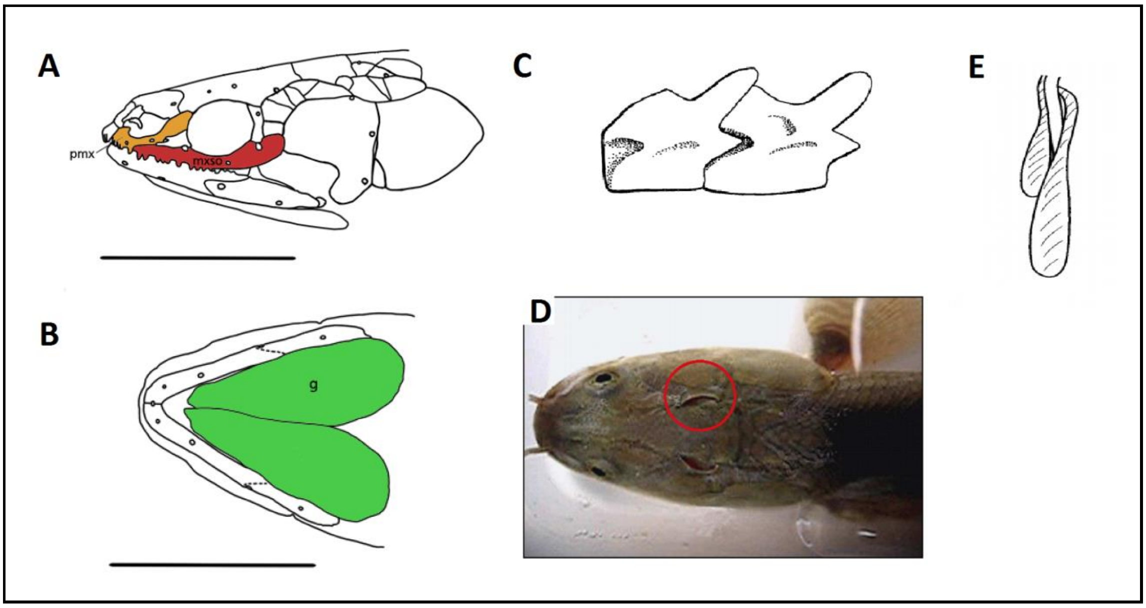
Os ‘bichir’ atuais, como são popularmente conhecidos, são encontrados exclusivamente no continente africano e se restringem à África tropical (DAGET *et al*., 2001) (Figura 2). Esta família apresenta um mosaico de características primitivas e derivadas que os destacam dos demais Actinopterygii (FRIEDMAN, 2015). Dentre as características primitivas, podem ser citadas: presença de escamas ganóides do tipo paleoniscóide (apresentando uma camada de dentina entre o osso e a placa óssea), se articulando através de uma junção ‘peg-and-socket’ (SCHULTZE, 1996); espiráculos funcionais (GRAHAM *et al*., 2014; MAGID, 1966); presença de placas gulares; pré-maxila e maxila imóveis (DAGET, 1950); e pulmão funcional (GRAHAM, 1997) (Figura 3). Já para as características derivadas, podem ser citadas: corpo alongado; nadadeira dorsal composta por 5 a 18 pínulas e quatro arcos branquiais, onde o quinto foi perdido durante a evolução do grupo (BRITZ; JOHNSON, 2003; LACÉPÈDE, 1803; NELSON *et al*., 2016; STANDEN *et al*., 2014) (Figura 4).

Figura 2 - Distribuição de Polypteriformes atuais e fósseis



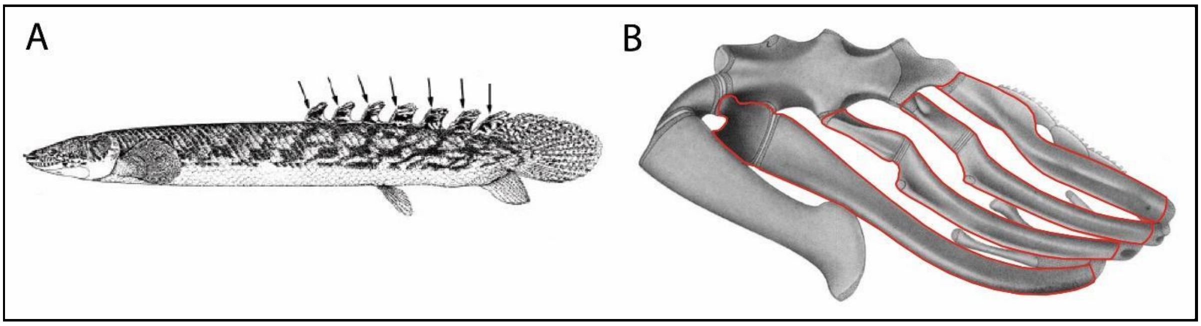
Fonte: Adaptada de DAGET *et al.*, 2001.

Figura 3 - Conjunto de caracteres primitivos presentes em Polypteriformes



Legenda: A- Vista lateral do crânio de *Polypterus sp*, destacado em laranja a pré-maxila (pmx) e em vermelho a maxila (mxso), Escala 12mm. B- Vista ventral do crânio de *Polypterus sp*, destacado em verde as placas gulares (g), Escala 12mm. C- Escamas com articulação do tipo *'peg-and-socket'* (retirado de JANVIER, 1996). D- Foto de *P. senegalus* com os espiráculos abertos em destaque (modificado de GRAHAM *et al.*, 2014). E- Esquema do pulmão de *Polypterus*, onde o lobo esquerdo é mais curto que o direito (retirado de GRAHAM, 1997).
Fonte: O autor, 2022.

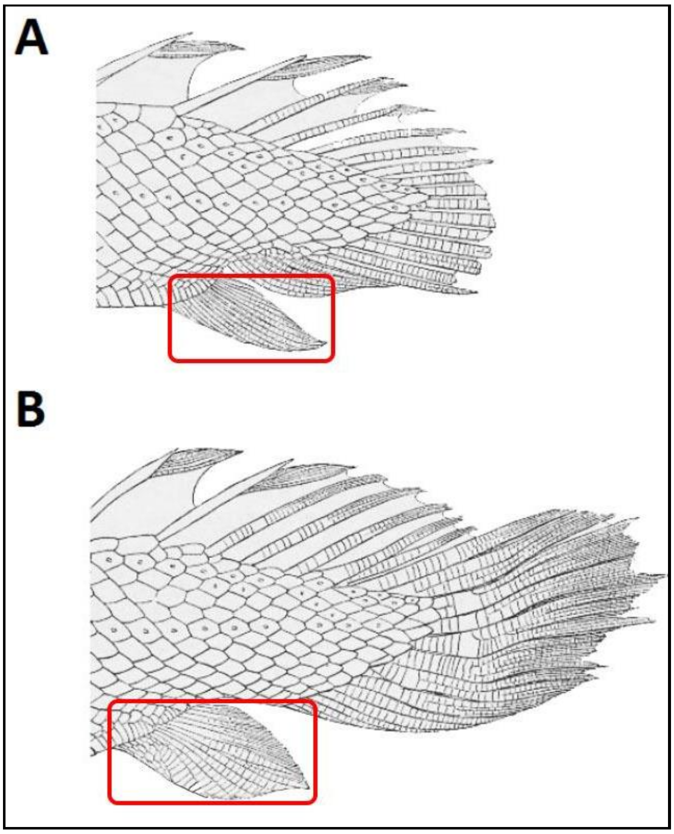
Figura 4 - Conjunto de caracteres derivados presentes em Polypteriformes



Legenda: A- Vista lateral de *Polypterus palmas*, setas indicam as pínulas (retirado de DAGET *et al.*, 2001). B- Vista ventral dos arcos branquiais direitos (contornados em vermelho) de *P. bichir* (modificado de ALLIS, 1922).
Fonte: O autor, 2022.

O grupo também apresenta outras peculiaridades como dimorfismo sexual na nadadeira anal (BOULENGER, 1907), respiração aérea (MAGID, 1966) e possibilidade de locomoção terrestre, devido à anatomia lobada das nadadeiras peitorais dos Polypteriformes (STANDEN *et al.*, 2014). Este dimorfismo da nadadeira anal possibilita a identificação do sexo dos indivíduos de forma externa, onde a nadadeira anal da fêmea é estreita e pontuda e a do macho é mais larga e arredondada (Figura 5) (BOULENGER, 1907; KOMAGATA *et al*., 1993). A nadadeira do macho pode tomar forma de taça, servindo como uma estrutura fertilizadora. Durante a reprodução o macho nada ao lado da fêmea com sua nadadeira anal dobrada na direção do ventre da fêmea, para fertilizar os ovos assim que são postos (ARNOULT, 1964; HOLDEN, 1971).

Figura 5 - Dimorfismo sexual da nadadeira anal de *P. senegalus*



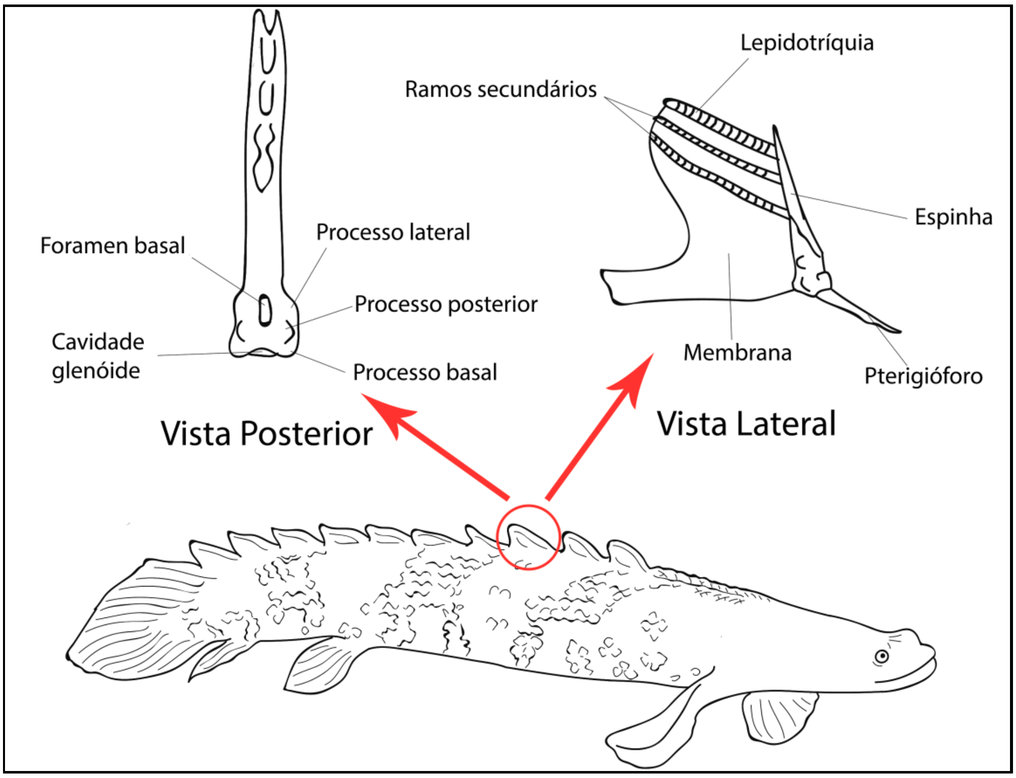
Legenda: Detalhe da nadadeira anal de dois espécimes de P. senegalus, uma fêmea (A) e um macho (B).
Fonte: Adaptada de BOULENGER, 1907.

A respiração aérea se dá, eventualmente, pela ingestão de ar pela boca e, principalmente, através de espiráculos (Figura 3-D), que são tubos presentes em pares situados no teto craniano, que se estendem até a câmara bucofaringeana, onde há a abertura da glote na porção ventral do esôfago que se comunica com os pulmões (GRAHAM *et al*., 2014; MAGID, 1966; SMET, 1966). Após passar pela glote, o ar vai para os pulmões, que são bilobados, onde o lobo direito se estende por toda cavidade abdominal, enquanto o lobo esquerdo é limitado à porção anterior da cavidade (Figura 3-E) (BRAINERD *et al*., 1989; GRAHAM, 1997; MAGID *et al*., 1970; SMET, 1966). Este mecanismo serve como alternativa a baixas concentrações de oxigênio na água ou resposta a situações de estresse (GRAHAM *et al*., 2014; MAGID, 1966).

O aspecto mais marcante da anatomia e caráter exclusivo deste grupo é a presença de pínulas formando a nadadeira dorsal. Nas diferentes espécies pode-se encontrar de 5 a 18 pínulas em um mesmo indivíduo (MORITZ; BRITZ, 2019; NELSON *et al*., 2016). De acordo com Gayet, Meunier e Werner (1997) cada pínula pode ser dividida em 3 partes (Figura 6): i) um espinho que se articula com o pterigióforo, em sua base estão os processos basal, lateral e posterior e o forâmen basal, este último é o ponto de saída do canal medular; ii) uma única lepidotriquia, fusionada em sua parte basal com o espinho, e onde sua parte distal é livre e se divide em ramos secundários; iii) uma membrana sustentada pelo espinho e pela lepidotriquia, que se estende até a porção anterior do espinho da próxima pínula. Adicionalmente, foi descrita variação morfológica intraindividual, ao longo da nadadeira dorsal, nas pínulas de 4 espécies de Polypteridae (*E. calabaricus*, *P. delhezi*, *P. endlicherii* e *P. palmas*), além de pouca ou nenhuma variação morfológica intraespecífica em espécimes de *P. delhezi* (COELHO *et al.*, 2018). O que indica que as pínulas possam ser relevantes como caráter diagnóstico (COELHO *et al.*, 2018).

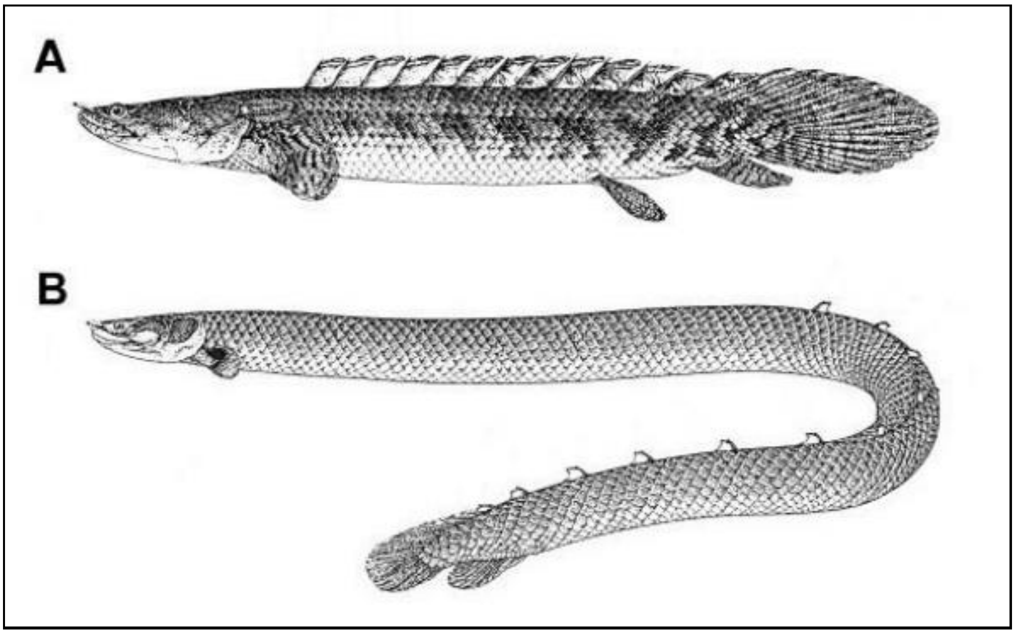
O grupo é composto por dois gêneros viventes, *Polypterus* Lacépède, 1803 e *Erpetoichthys* Smith, 1865 (Figura 7). *Polypterus* é composto por 13 espécies atuais: *P. ansorgii* Boulenger, 1910; *P. bichir* Lacépède, 1803; *P. congicus* Boulenger 1898; *P. delhezi* Boulenger, 1899; *P. endlicheri* Heckel, 1847; *P. mokelembembe* Schliewen & Schäfer, 2006; *P. ornatipinnis* Boulenger, 1902; *P. palmas* Ayres, 1850; *P. polli* Gosse, 1988; *P. retropinnis* Vaillant, 1899; *P. senegalus* Cuvier, 1829; *P. teugelsi* Britz, 2004 e *P. weeksii* Boulenger, 1898. O gênero *Erpetoichthys* é composto unicamente pela espécie *E. calabaricus* Smith, 1865.

Figura 6 - Desenho destacando as estruturas que formam uma pínula em vista lateral e posterior



Fonte: COELHO *et al.*, 2018.

Figura 7 - Vista laterais de (A) *Polypterus ansorgii* e (B) *Erpetoichthys calabaricus*



Fonte: Adaptada de DAGET *et al.*,2001.

O gênero *Erpetoichthys* pode ser diferenciado de *Polypterus* em sua morfologia externa por apresentar corpo anguiliforme, tamanho relativo do crânio menor e ausência de nadadeiras pélvicas (CLAESON *et al.*, 2007; NELSON *et al.*, 2016). Internamente, também se notam diferenças na morfologia do crânio, onde em *Erpetoichthys* estão ausentes o quadratojugal e o subopérculo (CLAESON *et al*., 2007).

O gênero *Polypterus* foi inicialmente nomeado 'Polyptère' em sua primeira descrição por Saint-Hilaire (1802), porém o nome só foi latinizado no ano seguinte (1803) por Lacépède, passando a ser considerado o nome correto frente ao Código Internacional de Nomenclatura Zoológica (ICZN).

Inicialmente, a nomenclatura de *Erpetoichthys* permaneceu confusa por algumas décadas devido a algumas descrições feitas por Smith (1865a, 1865b, 1866a, 1866b), onde ele usava o nome *Erpetoichthys*, sua escolha inicial, porém destacava a mudança de nome para *Calamoichthys*, pois acreditava que a alcunha *Erpetoichthys* já estava sendo utilizada. Jordan em 1905 discutiu que os gêneros *Erpichthys* e *Herpetoichthys*, usados para um gênero de peixes da família Blenniidae e um gênero de enguias, respectivamente, são escritos de maneira diferentes, portanto, são nomes diferentes e assim o gênero *Erpetoichthys* é um nome válido. Porém, em 1919, Jordan reconheceu *Erpetoichthys* e *Herpetoichthys* como homônimos, reconhecendo *Calamoichthys* como nome válido para o gênero. Swinney e Heppel (1982) encerraram a discussão ao reconhecer que a primeira afirmação de JORDAN estava correta sob o atual código de nomenclatura, portanto *Erpetoichthys* Smith 1865 seria o nome correto.

Recentemente, Rizzato e Bockmann (2017) reabriram esta discussão ao analisarem as primeiras publicações de Smith (1865a, 1865b, 1866a, 1866b). Eles concluíram que as primeiras publicações atribuídas a Smith, feitas em 1865, não são válidas perante o ICZN por se tratar de uma publicação em um jornal de Edimburgo (Escócia, Reino Unido) sem a intenção de ser um registro científico, e por isso, não podem ser consideradas um ato de nomenclatura válido. Sendo assim, a primeira publicação científica de Smith descrevendo a espécie nova é de 1866, e, consequentemente, a alcunha correta perante o ICZN é *Calamoichthys* Smith 1866 (RIZZATO; BOCKMANN, 2017). Alguns autores (MEUNIER; GAYET, 2020; MORITZ; BRITZ, 2019) discordam da visão de Rizzato e Bockmann (2017) e argumentam em suas publicações que a interpretação deles reside na suposta intenção de Smith utilizar sua publicação no jornal de Edimburgo para fins de divulgação e não de registro científico. Como a intenção do autor não pode ser descoberta e o nome *Erpetoichthys calabaricus* foi publicado junto com uma diagnose (SMITH 1865), este seria o nome válido. E por isso, concordam com Swinney e Heppel (1982), que o nome válido para a espécie é *Erpetoichthys calabaricus,* Smith 1865.

Histórico sistemático do grupo

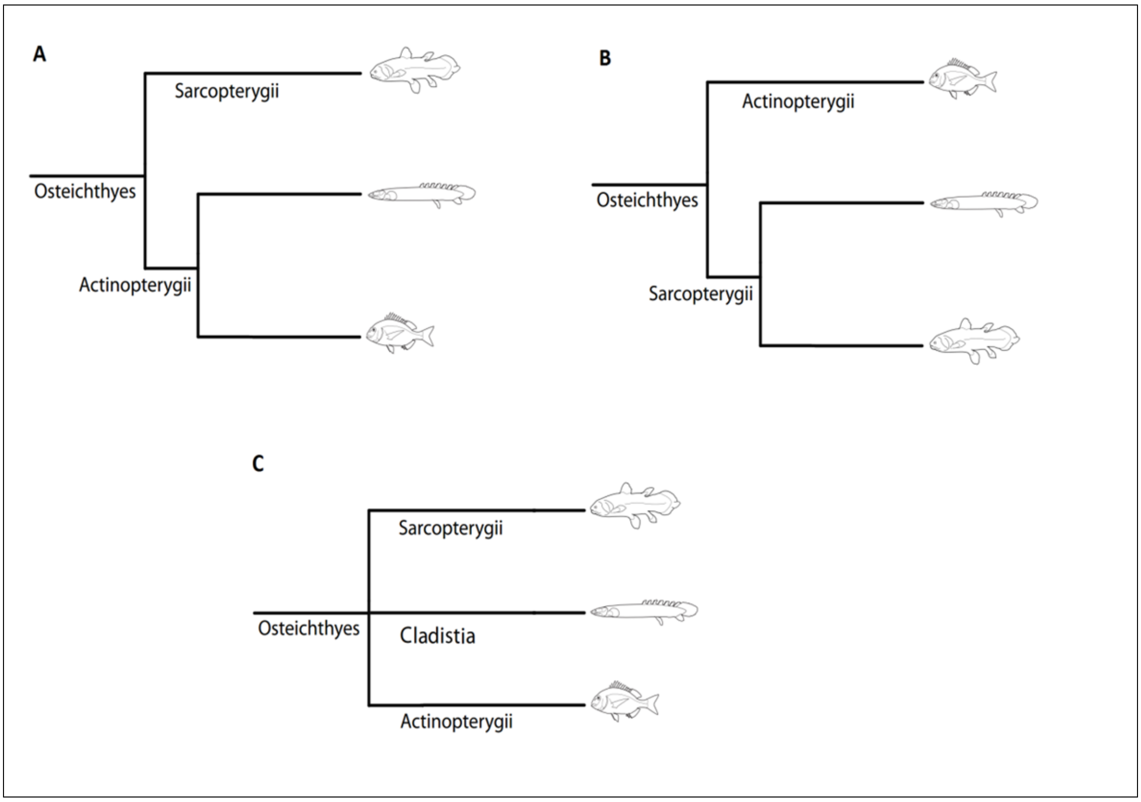
A classificação dos bichirs como pertencentes aos Actinopterygii sempre foi problemática, já que o grupo possui um mosaico de características tanto primitivas (por exemplo, pulmão e escama ganóide do tipo paleoniscóide), quanto derivadas (por exemplo, nadadeira dorsal composta por diversas pínulas), compartilhando, assim, caracteres com os Actinopterygii e Sarcopterygii.

Este mosaico fez com que diversos autores discutissem acerca de sua posição filogenética por quase 200 anos. Assim, três hipóteses podem ser identificadas: a) os Polypteriformes pertencem ao grupo Actinopterygii (PATTERSON, 1982); b) os Polypteriformes pertencem ao grupo Sarcopterygii (COPE, 1871); c) os Polypteriformes constituem um grupo distinto dos Actinopterygii e Sarcopterygii (BJERRING, 1985) (Figura 8).

Após anos de discussões e vários trabalhos publicados, foi reconhecido que os Polypteriformes pertencem aos Actinopterygii, sendo o grupo irmão dos demais táxons do grupo (i.g. Actinopteri = Chondrostei + Neopterygii) (GARDINER; SCHAFFER, 1989; GARDINER *et al.*, 2005; INOUE *et al.*, 2003; PATTERSON, 1982). Como exemplo de sinapomorfia que une o grupo, pode-se citar a presença de escamas ganóides com articulação do tipo '*peg-and-socket*' e capuz de acrodina na ponta dos dentes (PATTERSON, 1982). Além disso, o grupo se difere dos Sarcopterygii por não possuírem a nadadeira peitoral mono basal (sinapomorfia de Sarcopterygii), ou seja, a semelhança entre as nadadeiras peitorais destes grupos se dá apenas externamente (ROSEN *et al.*, 1981).

Recentemente, foram descritos espécimes representantes do grupo fóssil Scanilepiformes - *Fukangichthys* - com quatro arcos branquiais (GILES *et al.*, 2017), característica, até então, apenas encontrada em Polypteriformes (BRITZ; JOHNSON, 2003). Após análises, foi concluído que Scanilepiformes faz parte da base da linhagem dos polypterídios. Além do número de arcos branquiais, a monofilia do grupo também é suportada por sinapomorfias como ectopterigóide com processo lateral; processo coronóide da mandíbula composto apenas pelo pré-articular, septo interorbital largo, dentre outras (GILES *et al.*, 2017).

Figura 8 - Hipóteses de relacionamento entre os Osteichthyes viventes



Legenda: A - Cladistia pertencente à Actinopterygii. B - Cladistia pertencente à Sarcopterygii. C - Cladistia formando um grupo distinto de Actinopterygii e Sarcopterygii.
Fonte: Adaptada de SUZUKI *et al.*, 2010.

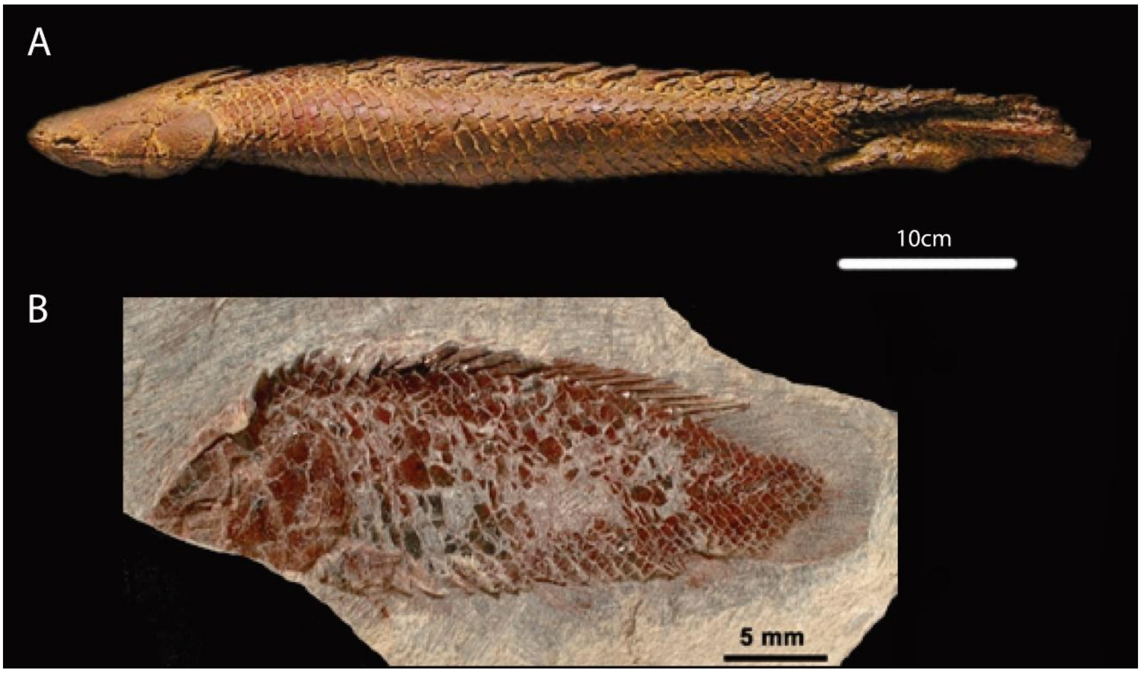
Os Scanilepiformes são um grupo amplamente distribuído do Triássico [entre 252 e 201 milhões de anos (m.a.)] (GILES *et al.*, 2017), enquanto os Polypteriformes mais antigos conhecidos são do Cretáceo Superior (?Cenomaniano; aproximadamente 100 m.a.) (DUTHEIL, 1999; GAYET *et al.*, 2002). Com isso, esses fósseis rompem a longa linhagem dos Polypteriformes, antes estimada em pelo menos 390 m.a. (Devoniano Médio) (NEAR *et al.*, 2014), o que implicava em uma lacuna de aproximadamente 290 m.a.. Apesar da diminuição dessa lacuna, a falta de polypterídios mais primitivos ainda é problemática para a elucidação da história evolutiva do grupo.

Formas fósseis

As espécies viventes são encontradas exclusivamente em água doce no continente africano, por outro lado, há fósseis no Cretáceo, Terciário e Quaternário da África e no Cretáceo e Paleoceno da América do Sul, mais precisamente Bolívia e Brasil, o que corrobora com a hipótese da origem gondwânica do grupo (Figura 2) (CANDEIRO *et al*., 2011; GAYET; MEUNIER, 1991, 1992; GAYET *et al*., 2001).

Um desafio encontrado na classificação das espécies fósseis é o fato de, em grande parte, só ser encontrado material desarticulado (por exemplo, escamas, pínulas e vértebras) (GAYET; MEUNIER, 1996; GAYET *et al*., 1997; WERNER; GAYET, 1997). Os únicos fósseis articulados quase completos são *Serenoichthys kemkemensis* (DUTHEIL, 1999) e *Polypterus faraou* (OTERO *et al*., 2006) (Figura 9). Até hoje foram descritos 9 gêneros com representantes exclusivamente fósseis, totalizando 20 espécies, além de 2 espécies fósseis atribuídas ao gênero atual *Polypterus* (DAGET *et al*., 2001; OTERO *et al*., 2006).

Figura 9 - Espécimes fósseis articulados de Polypteriformes



Legenda: Vistas laterais de (A) *Polypterus faraou* e (B) *Serenoichthys kemkemensis*.
Fonte: A - Adaptada de OTERO *et al.*, 2006; B - Adaptada de DUTHEIL, 1999.

Dentre os táxons fósseis, 6 gêneros, incluindo 17 espécies, foram descritos com base na cabeça articular de pínulas, sendo a maioria das mesmas formações e localidades (DAGET *et al*., 2001; GAYET; MEUNIER, 1996; GAYET, MEUNIER; WERNER, 1997; WERNER; GAYET, 1997). Apesar do grande número de espécies descritas dessa maneira, não havia estudo que atestasse a viabilidade desse caráter como diagnóstico de gênero e/ou espécie. Porém, recentemente, foi descrita variação morfológica individual não taxonômica em pínulas (para discussão sobre variação morfológica ver GRANDE, 2004), questionando, assim, a validade destes táxons fósseis (COELHO *et al.*, 2018).

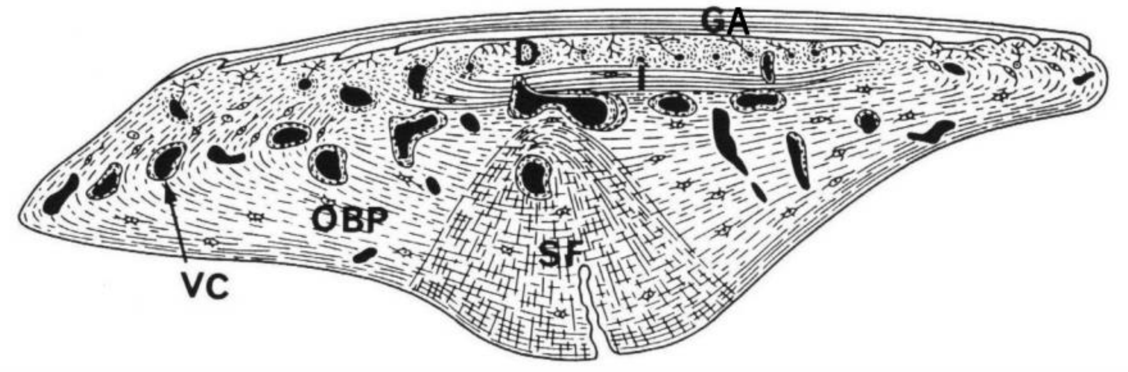
Os fósseis mais antigos já encontrados são datados do Cenomaniano, Cretáceo Superior, entre 100 e 93,9 m.a. (DUTHEIL, 1999; GAYET *et al.*, 1997; 2002; WERNER; GAYET, 1997). E os mais recentes são atribuídos ao gênero *Polypterus*, sendo *P. faraou* do final do Mioceno, aproximadamente 7 milhões de anos, e material desarticulado atribuído a *Polypterus* sp. do Paleogeno até o Pleistoceno, constituindo uma amplitude temporal de 16 a 3,6 m.a. (ARAMBOURG, 1947; OTERO *et al.*, 2006).

Apesar de somente uma pequena parte dos organismos que viveram serem preservados no registro fossilífero (NUDDS; SELDEN, 2008), a partir das espécies fósseis é possível observar parte da antiga diversidade do grupo, pois há espécimes de 30cm (*Serenoichthys kemkemensis* do Cenomaniano da Formação Kem Kem Beds, Marrocos) até 3m de comprimento (*Bawitus bartheli* do Cenomaniano da Formação Bahariya, Egito) (DUTHEIL, 1999; GRANDSTAFF *et al.*, 2012). Adicionalmente, *Serenoichthys kemkemensis* é considerado o táxon mais primitivo da ordem, pois este possui um corpo curto e robusto, que mais se assemelha à condição generalizada dentro de Actinopterygii em relação aos outros Polypteridae (DUTHEIL, 1999).

Paleoniscídios

O grupo parafilético conhecido como “peixes paleoniscídios” comporta alguns gêneros fósseis como *Cheirolepis*, *Mimia* e *Moythomasia*, e a ordem vivente Polypteriformes (GARDINER *et al.*, 2005). Este grupo é caracterizado pela presença de escamas ganóides do tipo paleoniscóide, que possuem três camadas sobrepostas compostas, respectivamente, por ganoína, dentina e uma placa basal óssea (GOODRICH, 1928) (Figura 10).

Figura 10 - Corte de uma escama de *P. senegalus*



Legenda: GA - ganoína; D - dentina; OBP - placa basal óssea; SF - fibras de sharpey; VC - canal vascular.
Fonte: Adaptada de SIRE, 1990.

Este tipo de escama se diferencia da escama ganóide do tipo lepidosteóide, onde a escama lepidosteóide apresenta a camada basal óssea diretamente recoberta por ganoína sem a camada de dentina, com exceção de táxons mais primitivos que apresentam apenas parte da camada de dentina (GOODRICH, 1907; KERR, 1952; SCHULTZE, 1996), além de não possuir os canalículos de Williamson, que são estruturas vasculares situadas perpendicularmente à placa basal óssea, presentes em peixes holósteos (Amiidae + Lepisosteiformes) (GOODRICH, 1907; SCHULTZE, 1996; SIRE; MEUNIER, 1994; THOMSON; MCCUNE, 1984).

Justificativa

Apesar de serem estudados há pouco mais de 200 anos, os Polypteriformes não possuem um consenso sobre as relações filogenéticas dentro do grupo (BOULENGER, 1909; DAGET; DESOUTTER, 1983; NEAR *et al.*, 2014; SUZUKI *et al.*, 2010), assim como um consenso sobre as espécies válidas do mesmo (GOSSE, 1988 e 1990; HANSSENS *et al.*, 1995; MORITZ; BRITZ, 2019; SUZUKI *et al.*, 2010). Por isso, se faz necessário o estudo dos caracteres anatômicos a fim de elucidar os problemas taxonômicos e propor uma hipótese de relacionamento para os táxons do grupo.

1 **OBJETIVOS**

A presente tese é apresentada em formato de artigo e seus objetivos correspondem aos objetivos de cada artigo separadamente:

a) descrever a anatomia osteológica completa de integrantes da família Polypteridae.

   Foi feita uma descrição comparativa da anatomia osteológica completa de 10 espécies de Polypteriformes, com o objetivo de encontrar caracteres para separá-las entre si.

b) analisar a variação morfológica das pínulas de *P. bichir*.

   Foi analisada as variações morfológicas intraindividual e intraespecífica nas pínulas de 5 espécimes de *P. bichir* em relação à sua posição relativa na nadadeira dorsal, com o objetivo de continuar a discussão acerca da validade das pínulas como caráter diagnóstico à nível de espécie.

c) analisar a variação morfológica na ornamentação de ganoína nas escamas de *P. bichir*.

   Foi analisada as variações morfológicas intraindividual e intraespecífica na ornamentação de ganoína nas escamas de 5 espécimes de *P. bichir*, com a finalidade de avaliar a sua utilização na identificação e separação das espécies do grupo.

2 **MATERIAL E MÉTODOS**

2.1 **Abreviaturas osteológicas**

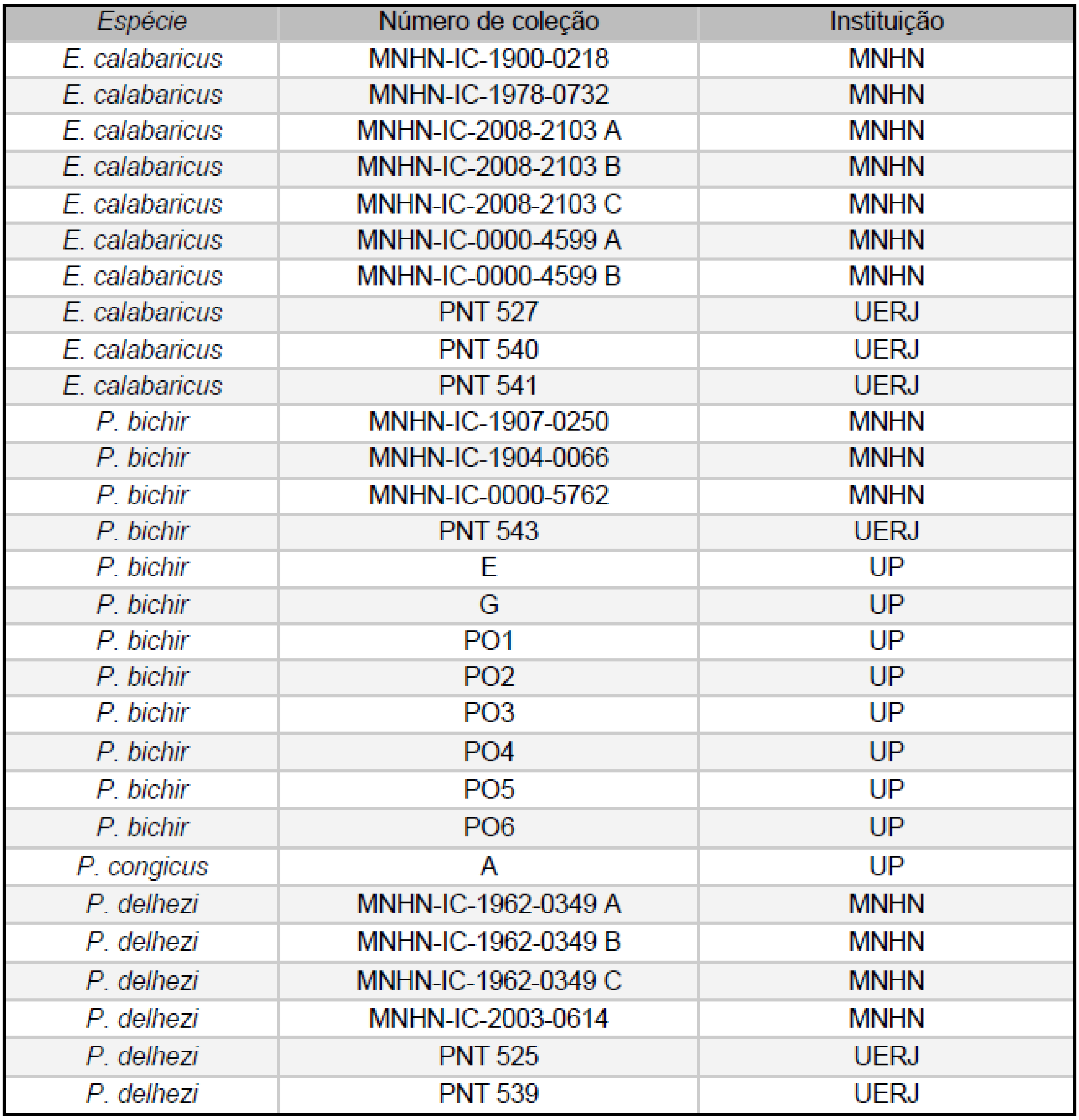
ang	angular
ar	articular
bb	basibranquial
bh	basihial
cb1-4	ceratobranquial 1-4
cha	ceratohial anterior
chp	ceratohial posterior
cl	cleitro
clv	clavícula
co1-2	coronóide 1-2
corc	coracóide
cp	placa facial
d	dentário
dhy	dermohial
dpl1-2	dermopalatino 1-2
dsp	dermosfenótico
ecp	ectopterigóide
enp	endopterigóide
epo	epiocipital
es	extraescapular
fr	frontal
g	gular
h	hiomandibular
hb1-3	hipobranquial 1-3
hh	hipohial
hyp	hipural
itst	intertemporo-supratemporal
l	lacrimal
le	lateral etimóide
m	mentomeckliano
meso	placa óssea mesopterigial
mpt	metapterigóide
mtg	metapterígio
mx	maxila
n1-3	nasal 1-3
occ	ocipital
op	opérculo
ors	orbitoesfenóide
par	prearticular
pas	paraesfenóide
pb1-2	faringobranquial 1-2
pcl	pós-cleitro
pesp	ossos pre-espiraculares
phy	parhipural
pmx	premaxila
po	pós-orbital
pop	pré-opérculo
posp	ossos pós-espiraculares
prtg	pró-pterígio
pt	pós-temporal
pu	centro pré-ural
q	quadrado
r	rostral
ra	raios proximais alongados da nadadeira peitoral
scl	supracleitro
scp	escapula
sop	subopérculo

sp	ossos espiraculares	uh	urohial
u	centro ural	vo	vômer

2.2 **Material de estudo e comparativo**

Todos os espécimes utilizados na presente tese, incluindo material de comparação, estão listados no Quadro abaixo:

Quadro - Espécimes de Polypteridae utilizados na presente tese (continua)

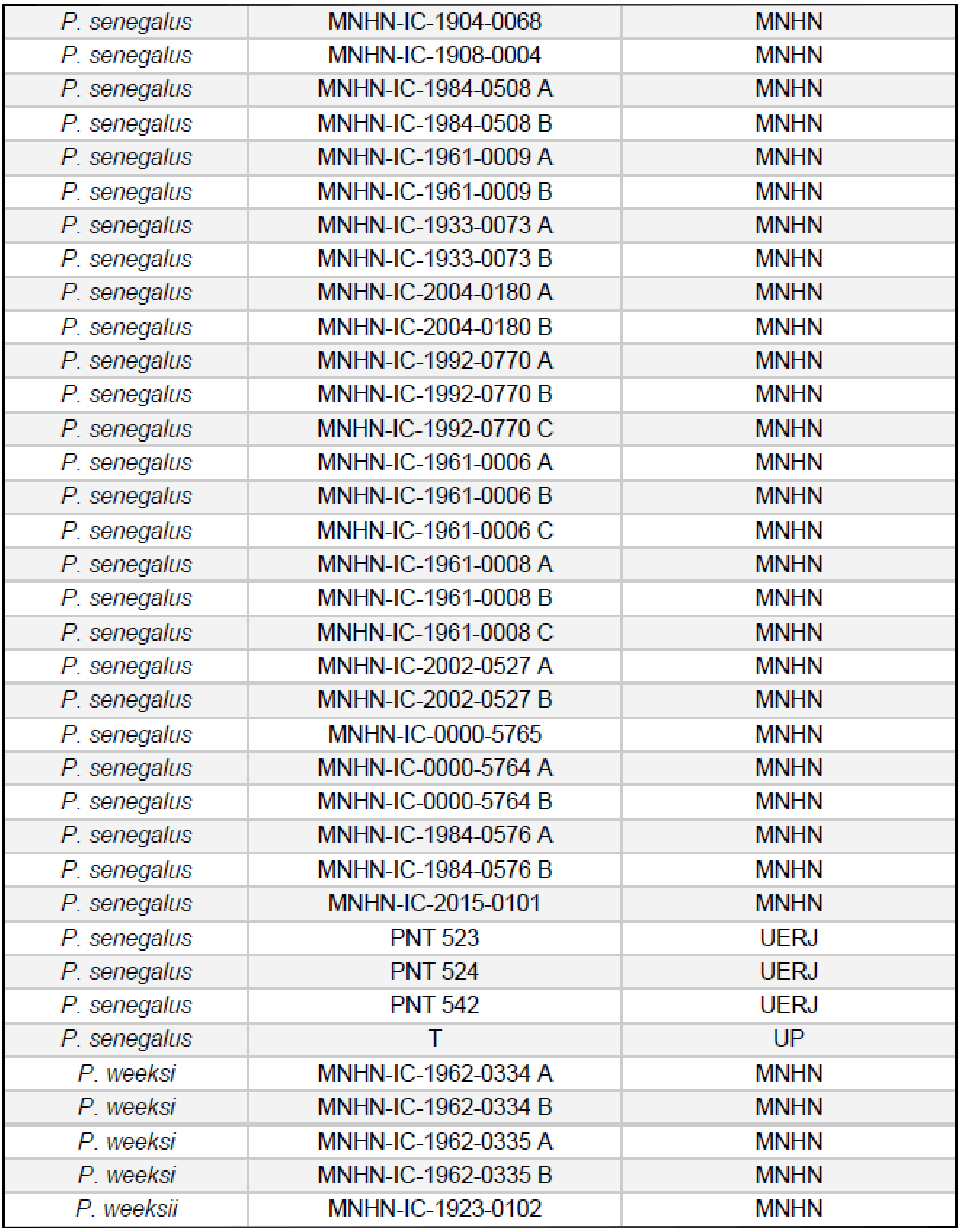


Espécie	Número de coleção	Instituição
E. calabaricus	MNHN-IC-1900-0218	MNHN
E. calabaricus	MNHN-IC-1978-0732	MNHN
E. calabaricus	MNHN-IC-2008-2103 A	MNHN
E. calabaricus	MNHN-IC-2008-2103 B	MNHN
E. calabaricus	MNHN-IC-2008-2103 C	MNHN
E. calabaricus	MNHN-IC-0000-4599 A	MNHN
E. calabaricus	MNHN-IC-0000-4599 B	MNHN
E. calabaricus	PNT 527	UERJ
E. calabaricus	PNT 540	UERJ
E. calabaricus	PNT 541	UERJ
P. bichir	MNHN-IC-1907-0250	MNHN
P. bichir	MNHN-IC-1904-0066	MNHN
P. bichir	MNHN-IC-0000-5762	MNHN
P. bichir	PNT 543	UERJ
P. bichir	E	UP
P. bichir	G	UP
P. bichir	PO1	UP
P. bichir	PO2	UP
P. bichir	PO3	UP
P. bichir	PO4	UP
P. bichir	PO5	UP
P. bichir	PO6	UP
P. congicus	A	UP
P. delhezi	MNHN-IC-1962-0349 A	MNHN
P. delhezi	MNHN-IC-1962-0349 B	MNHN
P. delhezi	MNHN-IC-1962-0349 C	MNHN
P. delhezi	MNHN-IC-2003-0614	MNHN
P. delhezi	PNT 525	UERJ
P. delhezi	PNT 539	UERJ

Quadro - Espécimes de Polypteridae utilizados na presente tese (continuação)

P. delhezi	P	UP
P. delhezi	R	UP
P. endlicherii	MNHN-IC-B-0384	MNHN
P. endlicherii	MNHN-IC-2001-2180	MNHN
P. endlicherii	MNHN-IC-1984-0392 A	MNHN
P. endlicherii	MNHN-IC-1984-0392 B	MNHN
P. endlicherii	PNT 522	UERJ
P. endlicherii	N	UP
P. mokelembembe	MNHN-IC-1886-0297	MNHN
P. mokelembembe	B	UP
P. ornatipinnis	MNHN-IC-1977-0307	MNHN
P. ornatipinnis	MNHN-IC-2009-0725 A	MNHN
P. ornatipinnis	MNHN-IC-2009-0725 B	MNHN
P. ornatipinnis	MNHN-IC-1886-0293	MNHN
P. ornatipinnis	C	UP
P. ornatipinnis	I	UP
P. ornatipinnis	M	UP
P. palmas	MNHN-IC-1940-0069	MNHN
P. palmas	MNHN-IC-1977-0308 A	MNHN
P. palmas	MNHN-IC-1977-0308 B	MNHN
P. palmas	MNHN-IC-1958-0026	MNHN
P. palmas	PNT 526	UERJ
P. polli	MNHN-IC-1900-0197	MNHN
P. polli	D	UP
P. polli	F	UP
P. polli	H	UP
P. polli	J	UP
P. polli	K	UP
P. polli	L	UP
P. polli	O	UP
P. polli	Q	UP
P. polli	S	UP
P. polli	U	UP
P. polli	V	UP
P. polli	W	UP
P. polli	X	UP
P. retropinnis	MNHN-IC-1963-0239	MNHN
P. retropinnis	MNHN-IC-1964-0253	MNHN
P. retropinnis	MNHN-IC-1930-0001 A	MNHN
P. retropinnis	MNHN-IC-1930-0001 B	MNHN
P. retropinnis	MNHN-IC-1930-0001 C	MNHN
P. retropinnis	MNHN-IC-1886-0295	MNHN

Quadro - Espécimes de Polypteridae utilizados na presente tese (conclusão)



P. senegalus	MNHN-IC-1904-0068	MNHN
P. senegalus	MNHN-IC-1908-0004	MNHN
P. senegalus	MNHN-IC-1984-0508 A	MNHN
P. senegalus	MNHN-IC-1984-0508 B	MNHN
P. senegalus	MNHN-IC-1961-0009 A	MNHN
P. senegalus	MNHN-IC-1961-0009 B	MNHN
P. senegalus	MNHN-IC-1933-0073 A	MNHN
P. senegalus	MNHN-IC-1933-0073 B	MNHN
P. senegalus	MNHN-IC-2004-0180 A	MNHN
P. senegalus	MNHN-IC-2004-0180 B	MNHN
P. senegalus	MNHN-IC-1992-0770 A	MNHN
P. senegalus	MNHN-IC-1992-0770 B	MNHN
P. senegalus	MNHN-IC-1992-0770 C	MNHN
P. senegalus	MNHN-IC-1961-0006 A	MNHN
P. senegalus	MNHN-IC-1961-0006 B	MNHN
P. senegalus	MNHN-IC-1961-0006 C	MNHN
P. senegalus	MNHN-IC-1961-0008 A	MNHN
P. senegalus	MNHN-IC-1961-0008 B	MNHN
P. senegalus	MNHN-IC-1961-0008 C	MNHN
P. senegalus	MNHN-IC-2002-0527 A	MNHN
P. senegalus	MNHN-IC-2002-0527 B	MNHN
P. senegalus	MNHN-IC-0000-5765	MNHN
P. senegalus	MNHN-IC-0000-5764 A	MNHN
P. senegalus	MNHN-IC-0000-5764 B	MNHN
P. senegalus	MNHN-IC-1984-0576 A	MNHN
P. senegalus	MNHN-IC-1984-0576 B	MNHN
P. senegalus	MNHN-IC-2015-0101	MNHN
P. senegalus	PNT 523	UERJ
P. senegalus	PNT 524	UERJ
P. senegalus	PNT 542	UERJ
P. senegalus	T	UP
P. weeksi	MNHN-IC-1962-0334 A	MNHN
P. weeksi	MNHN-IC-1962-0334 B	MNHN
P. weeksi	MNHN-IC-1962-0335 A	MNHN
P. weeksi	MNHN-IC-1962-0335 B	MNHN
P. weeksii	MNHN-IC-1923-0102	MNHN

Legenda: MNHN - Muséum national d'Histoire naturelle; UERJ - Universidade do Estado do Rio de Janeiro; UP - Université de Poitiers.

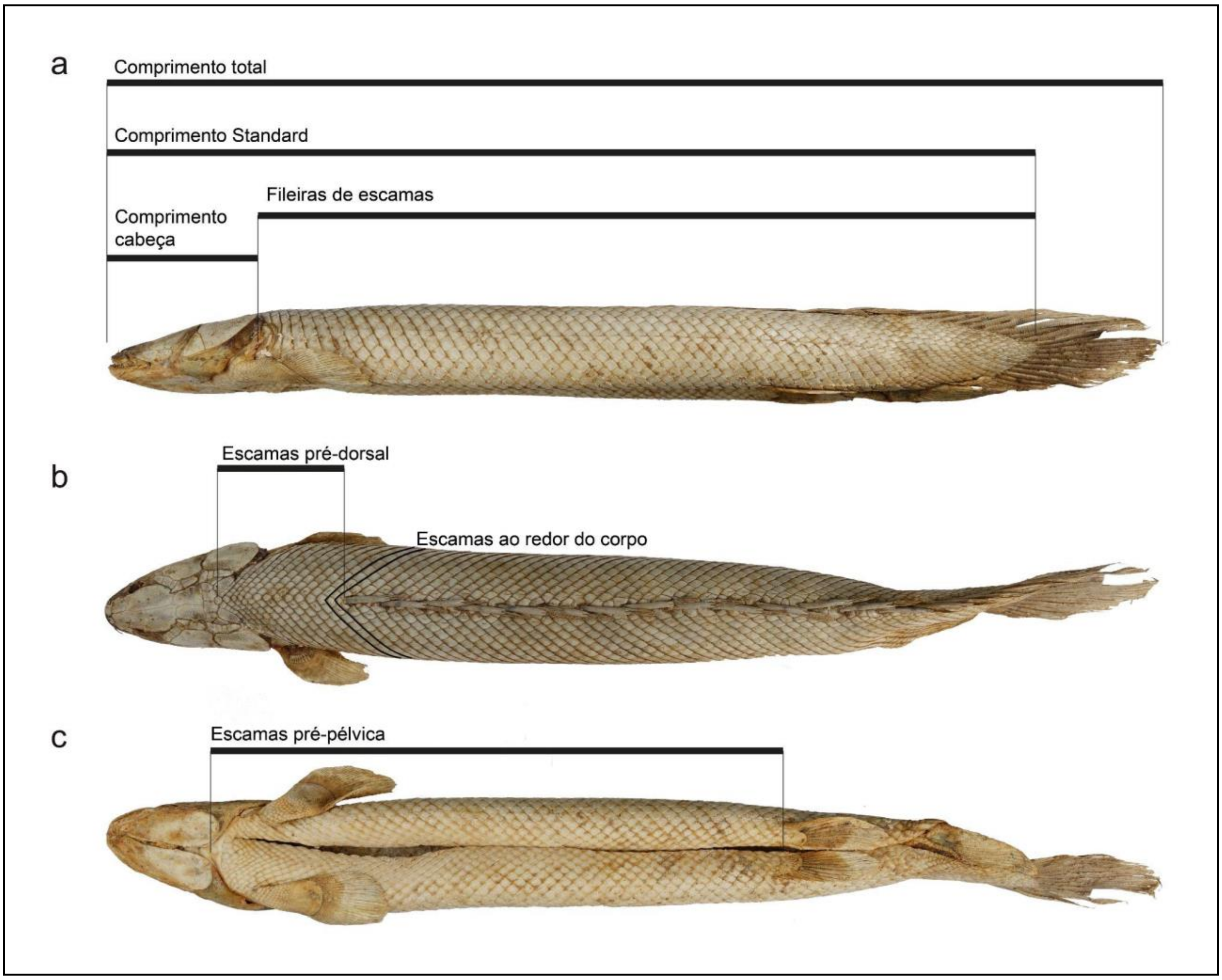
Fonte: O Autor, 2022.

2.3 **Medidas e contagens**

As medidas e contagens feitas a partir dos espécimes estudados seguem o esquema a seguir (Figura 11). Adicionalmente foram contados o número de pínulas e os números de raios das nadadeiras dorsais, pélvicas, anal e caudal. Todos esses dados podem ser encontrados no APÊNDICE.

Essas medidas e contagens seguem principalmente as utilizadas por MORITZ e BRITZ (2019) em sua recente revisão dos Polypteriformes baseada em caracteres merísticos e contínuos.

Figura 11 - Esquema das medidas e contagens feitas nos espécimes de Polypteridae



Fonte: O autor, 2022.

2.4 **Terminologia anatômica e nomenclatura osteológica**

Neste estudo foi utilizado a nomenclatura osteológica craniana presente em CLAESON *et al.* (2007) com exceção dos ossos da série espiracular, para estes foi utilizada a nomenclatura osteológica presente em OTERO *et al.* (2006). Para os elementos pós-cranianos, foi utilizada a nomenclatura presente em GRANDE (2010). Para as pínulas foi utilizada a nomenclatura de MEUNIER e GAYET (2020).

3 DESCRIPTION OF THE OSTEOLOGY OF *POLYPTERUS SENEGALUS*, WITH COMPARISONS WITH OTHER NINE POLYPTERIDAE SPECIES (Artigo submetido)

O presente capítulo está sendo preparado para publicação e, por isso, é apresentado no formato de artigo científico e é tratado como uma seção à parte da presente tese possuindo suas próprias subseções (resumo, introdução, material e métodos, resultados, discussão, conclusão e referências) e está nos moldes de formatação da revista PeerJ - Life & Environment.

Este capítulo aborda a necessidade de um maior conhecimento sobre a osteologia das espécies de Polypteridae como forma de ajudar na elucidação das relações filogenéticas do grupo. Pois, mesmo após mais de 200 anos de estudos sobre o grupo, estas ainda permanecem incertas. Isso se dá devido aos poucos trabalhos sobre essas relações filogenéticas e ao conturbado histórico taxonômico do grupo. Focando no segundo ponto e sabendo que a separação das espécies de Polypteridae atualmente é realizada com base em caracteres merísticos e contínuos que, eventualmente, se sobrepõe entre as espécies, nós analisamos a osteologia de *P. senegalus* e fazemos uma descrição comparativa com outras 9 espécies do grupo. Para isso utilizamos imagens 3D obtidas através de tomografias que, posteriormente, foram segmentadas e reconstruídas digitalmente. Nossos dados nos permitiram separar as espécies aqui estudadas da seguinte forma: *Erpetoichthys* se difere das espécies de *Polypterus*, onde *Erpetoichthys* apresenta um pós-orbital mais robusto, com uma parte dorsal maior; ausência de placas faciais; pré-opérculo com a mesma altura de seu processo ventral, que é consideravelmente maior que em *Polypterus*; opérculo triangular com limite posterior arredondado; e um ceratohial anterior mais fino. Entre as espécies de *Polypterus*, *P. bichir* e *P. endlicherii* distinguem-se das demais por sua pré-maxila mais curta (antero-posterior); maxila mais curta (antero-posterior) e mais robusta (ventral-dorsalmente); e região do neurocrânio proporcionalmente mais longa e mais baixa. Entre eles, *P. bichir* apresenta região opercular proporcionalmente maior (⅔ da cabeça) e *P. endlicherii* possui o processo ventral do pré-opérculo ligeiramente curvado para frente. *P. ornatipinnis*, *P. palmas* e *P. polli* apresentam um angular subretangular, comparativamente mais baixo que o das demais espécies. *P. palmas* apresenta uma placa facial mais robusta e subopérculo maior em comparação com *P. ornatipinnis* e *P. polli*. Estas duas últimas diferenciam-se onde *P. ornatipinnis* tem um rostral subtriangular ou subretangular e um lacrimal subretangular e *P. polli* tem um rostral losangular e um lacrimal subtriangular. *P. retropinnis* é separado de *P. delhezi* e *P. senegalus* por

apresentar o extraescapular mais lateral mais curto que termina antes do último osso pós-espiracular; um processo ventral mais robusto do pré-opérculo; e um subopérculo mais fino. *P. delhezi* apresenta um subopérculo proporcionalmente maior que *P. senegalus*; e maior contagem de ossos pós-espiraculares (3, 4 ou 5 contra 2 ou 3). Finalmente, *P. weeksii* se distingue dos demais por seu frontal com um processo antero-medial agudo que separa o par de 3 nasais, 3 pares de aberturas de canal no frontal e uma alta contagem de ossos pré-espiraculares (6 a 8), onde a duplicação desses ossos é frequente. Além das diferenças encontradas nos crânios, os elementos da nadadeira caudal parecem ser específicos, apesar de não exclusivos.

ABSTRACT

The Polypteridae is a family of freshwater African fishes that was discovered about 200 years ago and, up to date, comprises two extant genera, *Polypterus* and *Erpetoichthys*, including 14 valid species. Despite being studied for that long, the phylogenetic relationships within the group is still unclear. Two factors contribute to this i) the few works on the phylogenetic relationships of the polypteridae members and ii) the troubled taxonomic history of the polypterids. Focusing on the second issue, and knowing that, currently, the separation of all Polypteridae species is based on ranges of meristic characters that eventually overlap among the different species. The goal of this work is to produce a detailed description of the osteology of *Polypterus senegalus* and compare it with the osteology of 9 other species of Polypteriformes in order to try to find new characters to more clearly separate species, and later help to elucidate the phylogenetic relationships within the group. The differences found here are some promising characters to clearly separate the extant polypteridae species, mainly the differences on the rostral, lacrimal, spiracular series, opercular region and caudal fin.

Keywords Polypteridae, Morphological variation, Anatomy, Osteology, Taxonomy

INTRODUCTION

The Polypteridae is a family of freshwater African fishes discovered about 200 years ago during the French Campaign of Egypt, leadered by Napoleon Bonaparte (Saint-Hilaire, 1802; 1809; Lacépède, 1803). The extant representatives of the family are the two genera *Polypterus*, Lacépède 1803 and *Erpetoichthys* Smith 1865 (we agree with the arguments brought by Moritz & Britz (2019) as we follow the conclusions of Swinney & Heppell (1982) regarding the valid name for *Erpetoichthys*; see Rizzato & Bockmann (2017) for the opposite conclusion). *Polypterus* species are easily distinguished from the monotypic *Erpetoichthys*, where *Erpetoichthys* has a anguilliform body and the absence of subopercle, accessory cheek plates (=quadratojugal) and pelvic fins (Smith, 1865; 1866; Traquair, 1866; Claeson, Bemis & Hagadorn, 2007). The first specimen described belonging to the Polypteriformes was collected (1799) and described (1802) by Geoffroy Saint-Hilaire and named "Polyptére bichir". The name was later latinized by Lacépède (1803), within the norms of the ICZN, thus becoming the accepted name for the species: *Polypterus bichir*. Since its discovery, a lot of discussion has been raised concerning the group's phylogenetic position within the Osteichthyes (Cope, 1871; Patterson, 1982; Bjerring, 1985; Gardiner & Schaffer, 1989; Inoue et al., 2003; Rocco *et al*., 2004) and also about the phylogenetic relationships within the group itself (Boulenger, 1909; Daget & Desoutter, 1983; Suzuki, Brandley & Tokita, 2010; Near *et al*., 2014). Although the first discussion has been solved, and the polypterids are placed on the base of the Actinopterygii (Rosen *et al*., 1981; Patterson, 1982; Gardiner & Schaffer, 1989; Venkatesh *et al*., 1999; Venkatesh *et al*., 2001; Inoue *et al*., 2003; Gardiner *et al*., 2005), the second is not yet solved. Two factors contribute to this i) the few works on the phylogenetic relationships of the polypteridae members, where two are based on morphological characters (Boulenger, 1909; Daget & Desoutter, 1983) and other two are based on molecular data (Suzuki Suzuki, Brandley & Tokita, 2010; Near *et al*., 2014). Although, both molecular studies provided similar results, there are still some points to be solved, such as, the position of *P. retropinnis* inside the family tree (as sister taxon of others *Polypterus* species (Suzuki, Brandley & Tokita, 2010) or inside the group formed by *P. mokelembembe*, *P. ornatipinnis* and *P. weeksii* (Near *et al*., 2014)); the position of the "lower jaw" group (= *P. ansorgii*, *P. bichir*, *P. congicus* and *P. endlicherii*) inside the family tree (as sister group of other species (Suzuki Suzuki, Brandley & Tokita, 2010) or clustered with the group formed by *P. mokelembembe*, *P. ornatipinnis*, *P. retropinnis* and *P. weeksii*, where these together are sister group to the cluster formed by *P. delhezi*, *P. palmas*, *P. polli*, *P. senegalus* and *P. teugelsi* (Near *et al*., 2014)); and the general position of *P. palmas* and *P. polli*, that even though they are so similar (Gosse, 1988; Hanssens *et al*. 1995; Moritz & Britz, 2019), they are always clustered first with other species (Suzuki, Brandley & Tokita, 2010; Near *et al*., 2014); ii) the troubled taxonomic history of the polypterids (Steindachner, 1895; Poll, 1941; 1942; 1954; Gosse, 1988; Hanssens et al., 1995; Suzuki, Brandley & Tokita, 2010; Moritz & Britz, 2019), partially caused by the lack of new morphological characters besides the ones already used for the group. This observation is made on the last two descriptions of new polypterid species (Britz, 2004; Schliewen & Schäfer, 2006).

To make a better understanding on the meaning of "troubled", here, we will try to summarize the taxonomic history of each of the 13 *Polypterus* valid species (as considered by Moritz & Britz, 2019 and utilized in the present work).

Polypterus ansorgii: Described by Boulenger (1910);

Polypterus bichir: Type species for the group, described by Geoffroy Saint-Hilaire (1802). Poll (1941, 1942) attributed three subspecies for *P. bichir*: *P. bichir bichir* Geoffroy Saint-Hilaire, 1802, *P. bichir lapradei* Steindachner, 1869 and *P. bichir katangae* Poll, 1941. Moritz & Britz (2019) considered *P. bichir lapradei* and *P. bichir katangae* as junior synonyms of *P. bichir*. Additionally *P. niloticus* Shaw, 1804 was considered synonym of *P. bichir* (Swain, 1882);

Polypterus congicus: Described by Boulenger (1898). Poll (1942) considered as subspecies of *P. endlicherii* (= *P. endlicherii congicus* Boulenger 1898). Later Suzuki *et al.* (2010) reconsidered *P. congicus* as a species;

Polypterus delhezi: Described by Boulenger (1899). Poll (1954) attributed *P. delhezi* as a synonym of *P. ansorgii*;

Polypterus endlicherii: Described by Heckel (1847). Poll (1941, 1942) attributed two subspecies: *P. endlicherii endlicherii* Heckel 1849 and *P. endlicherii congicus* Boulenger 1898. Later Suzuki *et al.* (2010) reverted the changes by Poll (1941, 1942) and separate the two species;

Polypterus mokelembembe: Recently described by Schliewen & Schäfer (2006);

Polypterus ornatipinnis: Described by Boulenger (1902);

Polypterus palmas: First described by Ayres (1850). Steindachner (1895) considered *P. buettikoferi* Steindachner 1891 as a synonym of *P. palmas*. In 1954, Poll described its first subspecies *P. palmas congicus* Poll, 1954, which was considered a nomen nudum and a junior homonym of *P. congicus* by Gosse (1988). Later, Hanssens *et al*. (1995) erected three subspecies for *P. palmas*: *P. palmas palmas* Ayres, 1850, *P. palmas buettikoferi* Steindachner, 1981 and *P. palmas polli* Gosse, 1988. The changes from Hanssens *et al.* (1995) were reverted by Suzuki *et al*. (2010), which reconsidered *P. polli* at species level, and Moritz & Britz (2019), which considered *P. palmas buettikoferi* as synonym of *P. palmas*. Additionally, Gosse (1988) and Moritz & Britz (2019) considered *P. lowei* Boulenger 1911 and *P. retropinnis lowei* 1911 as a synonym and junior synonym, respectively, of *P. palmas*;

Polypterus polli: Described by Gosse (1988). Hanssens *et al.* (1995) considered a subspecies of *P. palmas*: *P. palmas polli*. Later Suzuki *et al.* (2010) put *P. polli* back at the species level;

Polypterus senegalus: Described by Cuvier (1829). Poll (1941, 1942) attributed two subspecies: *P. senegalus senegalus* Cuvier, 1829 and *P. senegalus meridionalis,* Poll 1942. Later Moritz & Britz (2019) synonymized *P. senegalus meridionalis* with *P. senegalus*. Additionally *P. arnaudii* Duméril, 1870 was considered synonym of *P. senegalus senegalus* by Poll (1941);

Polypterus retropinnis: Described by Vaillant (1899). Poll (1941, 1942) erected two subspecies for it: *P. retropinnis retropinnis* Vaillant, 1899 and *P. retropinnis lowei* 1911 (been synonymized from *P. lowei* Boulenger, 1911). Gosse (1988) reverted these changes declaring *P. lowei* Boulenger, 1911 as synonym of *P. palmas* Ayres, 1850. The type series of *P. retropinnis* used to contain two specimens of *P. mokelembembe*, which caused Schliewen & Schäfer (2006) to erect a lectotype for it;

Polypterus teugelsi: Recently described by Britz (2004);

Polypterus weeksii: Described by Boulenger (1898). Additionally *P. schoutedeni* Pellegrin 1923 was considered synonym of *P. weeksii* by Poll (1941).

Currently, The separation of all Polypteridae species is based on ranges of meristic characters that eventually overlap among the different species (Moritz & Britz, 2019). The goal of this work is to produce a detailed description of the osteology of the Senegal Bichir, *Polypterus senegalus* and compare it with the osteology of 9 other species of Polypteriformes in order to i) try to find new characters to distinguish the species; ii) later help to elucidate the phylogenetic relationships within the group; iii) and provide to the scientific community CT scan data on the extant Polypteridae species.

MATERIAL AND METHODS

Specimen information

All the specimens used in this study were borrowed from the Muséum national d'Histoire naturelle (MNHN), France, and are listed in table 1.

Morphometric and meristic characters

The measurements taken are being shown in figure 1. Additionally, were counted the number of pinnules, pectoral fin rays, pelvic fin rays, anal fin rays and caudal fin rays.

CT-Scan, 3D Reconstruction and segmentation

All the specimens utilized here were scanned on a Easytom XL Duo Tomograph (RX Solutions) in the Université de Poitiers. Each scan was done with different parameters for better resolution according to the size of the scanned animal. The voxel size ranged from 0.0185811 to 0.0529362 mm; the current ranged from 125 to 375 mA; and the energy 80 kV. All specificities of each scan can be found in the table S1 (Supp. info). Images were reconstructed and exported into 16-bit TIFF stacks using the software X-Act (RX Solutions). The stacks were pre-treated in the software Image J, being converted to 8-bit TIFF stacks. For all the specimens, segmentation and three-dimensional rendering were realized using the software Avizo 8.0 (Thermo Fisher Scientific). The number of slices of each segmentation can also be found in the table S1 (Supp. info).

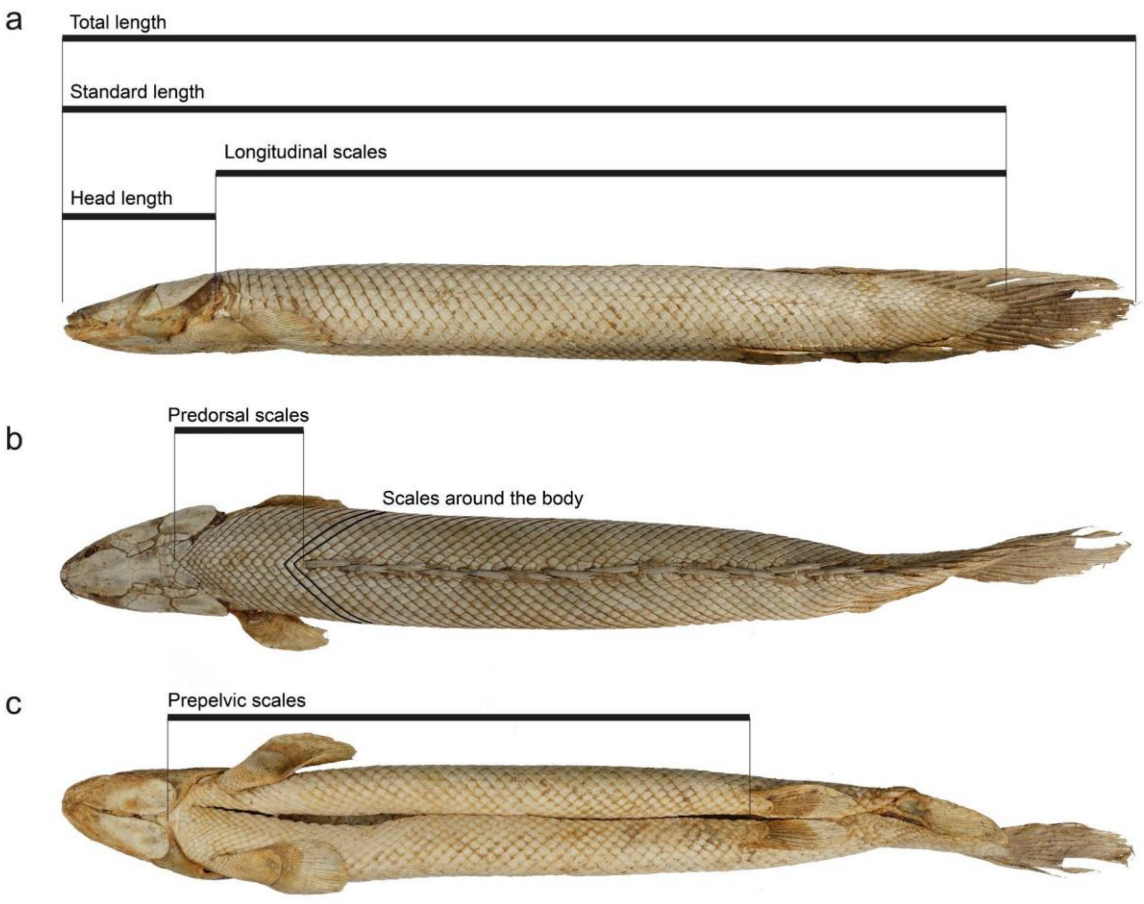


Figure 1- Lateral (a), dorsal (b) and ventral (c) views of *P. bichir* showing the measurements taken for all the specimens in this study.

Nomenclature

In the present work, we utilize the cranial osteological nomenclature presented in Claeson, Bemis & Hagadorn (2007), except for the bones of the spiracular series, for this we utilize the one in Otero *et al.* (2006). For the postcranial elements, we utilize the nomenclature presented in Grande (2010).

Osteological abbreviations

angular **ang**; anterior ceratohyal **cha**; articular **ar**; basibranchial **bb**; basihyal **bh**; ceratobranchial 1-4 **cb1-4**; cheek plate **cp**; clavicle **clv**; cleithrum **cl**; coracoid **corc**; coronoid 1-2 **co1-2**; dentary **d**; dermohyal **dhy**; dermopalatine 1-2 **dpl1-2**; dermosphenotic **dsp**; ectopterygoid **ecp**; elongate proximal radiais of pectoral fin **ra**;

endopterygoid **enp**; epioccipital **epo**; extrascapular **es**; frontal **fr**; gular **g**; hyomandibular **h**; hypobranchial 1-3 **hb1-3**; hypohyal **hh**; hypural **hyp**; intertemporo-supratemporal **itst**; lacrimal **l**; lateral ethmoid **le**; maxilla **mx**; mentomecklian **m**; mesopterygial bony plate **meso**; metapterygium **mtg**; metapterygoid **mpt**; nasal 1-3 **n1-3**; occipital **occ**; opercle **op**; orbitosphenoid **ors**; parasphenoid **pas**; parhypural **phy**; pharyngobranchials 1-2 **pb1-2**; postcleithrum **pcl**; posterior ceratohyal **chp**; postorbital **po**; postspiracular bones **posp**; posttemporal **pt**; prearticular **par**; prespiracular bones **pesp**; premaxilla **pmx**; preopercle **pop**; preural centra **pu**; propterygium **prtg**; quadrate **q**; rostral **r**; scapula **scp**; spiracular bones **sp**; subopercle **sop**; supracleithrum **scl**; ural centra **u**; urohyal **uh**; vomer **vo**.

RESULTS

Systematic classification

Actinopterygii Cope, 1887 (*sensu* Rosen *et al*., 1981).

Cladistia Cope, 1871.

Polypteriformes Bleeker, 1859.

Polypteridae Günther, 1870.

Polypterus Lacépède, 1803.

Polypterus senegalus Cuvier, 1829.

Morphometric and meristic characters

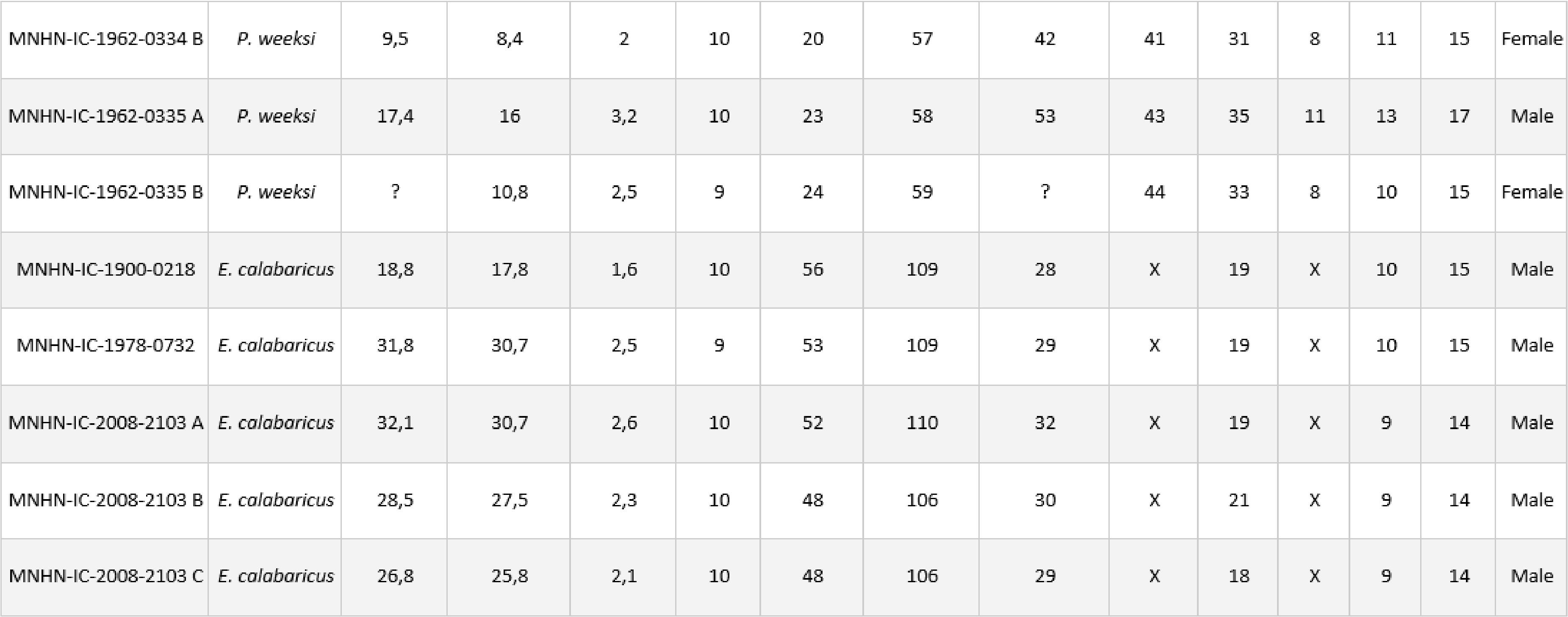
The table (Tabl. 1) below shows all measurements (Fig. 1) and meristic data in the specimens of the present study.

Collection Number	Species	Total length (cm)	Standard length (cm)	Head length (cm)	Pinnules	Predorsal scales	Longitudinal scales	Scales around the body	Prepelvic scales	Pectoral fin rays	Pelvic fin rays	Anal fin rays	Caudal fin rays	Sex
MNHN-IC-1907-0250	*P. bichir*	?	36	7,3	14	13	62	48	44	37	13	12	21	Female
MNHN-IC-1962-0349 A	*P. delhezi*	?	11,2	2,2	11	15	55	40	37	35	7	8	15	Female
MNHN-IC-1962-0349 B	*P. delhezi*	11	9,4	2,1	12	14	57	37	38	28	8	9	15	Female
MNHN-IC-1962-0349 C	*P. delhezi*	8,6	7	1,5	10	13	56	?	34	30	7	9	16	Female
MNHN-IC-2003-0614	*P. delhezi*	22,4	19,7	3,6	10	13	56	34	35	30	9	7	15	Female
MNHN-IC-B-0384	*P. endlicherii*	?	13,1	3,2	12	13	53	39	41	38	12	8	17	Female
MNHN-IC-2001-2180	*P. endlicherii*	27,3	23,3	5,2	12	13	55	39	38	39	13	8	17	Female
MNHN-IC-1977-0307	*P. ornatipinnis*	13,4	11	2,2	10	24	59	40	45	32	12	10	15	Female
MNHN-IC-2009-0725 A	*P. ornatipinnis*	24,8	23,2	4	11	24	62	42	44	32	11	10	16	Female

MNHN-IC-2009-0725 B	*P. ornatipinnis*	22,7	19,9	3,6	9	26	62	40	44	28	12	12	15	Female
MNHN-IC-1940-0069	*P. palmas*	24,5	21,4	3,4	8	26	57	37	39	34	9	13	15	Male
MNHN-IC-1977-0308 A	*P. palmas*	?	26,4	4,6	7	23	53	38	37	31	10	13	15	Male
MNHN-IC-1977-0308 B	*P. palmas*	14,5	12,5	2,5	6	27	53	38	36	32	11	11	15	Female
MNHN-IC-1958-0026	*P. palmas*	?	21,4	3,7	6	24	52	38	37	30	10	14	14	Male
MNHN-IC-1900-0197	*P. polli*	13,3	11,6	2,3	5	27	53	35	36	31	9	7	15	Female
MNHN-IC-1963-0239	*P. retropinnis*	?	25,1	3,8	8	31	58	35	43	34	7	11	14	Male
MNHN-IC-1964-0253	*P. retropinnis*	?	28,9	4,7	7	32	56	36	42	32	8	7	?	Female
MNHN-IC-1930-0001 A	*P. retropinnis*	?	7	1,4	7	32	58	32	44	29	8	11	?	Female
MNHN-IC-1930-0001 B	*P. retropinnis*	?	7	1,4	7	30	55	?	42	25	7	10	16	Female
MNHN-IC-1930-0001 C	*P. retropinnis*	?	6,8	1,4	7	30	56	?	39+	26	8	9	?	Female

MNHN-IC-1904-0068	*P. senegalus*	30,2	27,1	4,1	9	18	58	38	38	30	10	12	16	Male
MNHN-IC-1908-0004	*P. senegalus*	12	10,3	2	10	18	57	37	37	31	8	10	17	Female
MNHN-IC-1984-0508 A	*P. senegalus*	19	17	2,9	9	18	58	35	39	31	8	11	14	Female
MNHN-IC-1984-0508 B	*P. senegalus*	?	11,4	2	9	17	54	32	37	32	10	9	14	Female
MNHN-IC-1961-0009 A	*P. senegalus*	?	19,5	3,1	10	18	59	37	39	35	10	9	15	Female
MNHN-IC-1961-0009 B	*P. senegalus*	?	12,8	2,3	9	17	56	35	38	32	11	9	16	Female
MNHN-IC-1933-0073 A	*P. senegalus*	26,9	24,5	4	10	17	59	37	41	30	10	11	17	Female
MNHN-IC-1933-0073 B	*P. senegalus*	22,7	20,3	3,3	9	16	58	35	39	28	9	10	16	Female
MNHN-IC-2004-0180 A	*P. senegalus*	19,3	16,6	2,5	9	19	56	33	38	33	10	12	17	Male
MNHN-IC-2004-0180 B	*P. senegalus*	19	17	2,7	9	18	57	34	38	33	11	10	16	Female
MNHN-IC-1992-0770 A	*P. senegalus*	?	25,9	3,6	9	19	58	36	41	34	9	10	16	Male

MNHN-IC-1992-0770 B	*P. senegalus*	?	22,8	3,6	11	17	59	36	39	34	10	10	17	Male
MNHN-IC-1992-0770 C	*P. senegalus*	?	23,3	3,3	9	20	57	36	38	33	11	12	17	Female
MNHN-IC-1961-0006 A	*P. senegalus*	13,1	11,1	2	10	16	57	37	37	34	9	11	16	Male
MNHN-IC-1961-0006 B	*P. senegalus*	12,2	10,1	1,9	10	15	56	35	37	33	10	10	15	Female
MNHN-IC-1961-0006 C	*P. senegalus*	11,5	9,3	1,8	9	17	56	37	37	28	8	11	15	Male
MNHN-IC-1961-0008 A	*P. senegalus*	25,1	22,9	3,4	9	18	56	36	36	34	11	13	16	Male
MNHN-IC-1961-0008 B	*P. senegalus*	?	20,9	3,4	9	19	57	35	37	32	9	12	15	Male
MNHN-IC-1961-0008 C	*P. senegalus*	16,2	15,1	2,5	9	18	54	30	37	33	9	12	15	Female
MNHN-IC-2002-0527 A	*P. senegalus*	25,1	22,8	3,4	10	16	57	33	37	32	9	12	16	Male
MNHN-IC-2002-0527 B	*P. senegalus*	?	10,2	2	10	15	56	38	37	34	11	10	?	Female
MNHN-IC-1962-0334 A	*P. weeksi*	15,9	13,8	3,1	11	19	58	45	39	32	12	11	15	Male



MNHN-IC-1962-0334 B	*P. weeksi*	9,5	8,4	2	10	20	57	42	41	31	8	11	15	Female
MNHN-IC-1962-0335 A	*P. weeksi*	17,4	16	3,2	10	23	58	53	43	35	11	13	17	Male
MNHN-IC-1962-0335 B	*P. weeksi*	?	10,8	2,5	9	24	59	?	44	33	8	10	15	Female
MNHN-IC-1900-0218	*E. calabaricus*	18,8	17,8	1,6	10	56	109	28	X	19	X	10	15	Male
MNHN-IC-1978-0732	*E. calabaricus*	31,8	30,7	2,5	9	53	109	29	X	19	X	10	15	Male
MNHN-IC-2008-2103 A	*E. calabaricus*	32,1	30,7	2,6	10	52	110	32	X	19	X	9	14	Male
MNHN-IC-2008-2103 B	*E. calabaricus*	28,5	27,5	2,3	10	48	106	30	X	21	X	9	14	Male
MNHN-IC-2008-2103 C	*E. calabaricus*	26,8	25,8	2,1	10	48	106	29	X	18	X	9	14	Male

Table 1- Meristic and morphometric data gathered from the specimens in the present study. A ‘X’ means that a specific structure is absent on the species, thus it is not possible to take the measurement. A ‘?’ means that the structure is not well conserved on the specimen, thus it was not possible to take the measurement.

Bones of the cranial roof

The single rostral bone (Fig. 2) is found in the most anterior portion of the skull, between the pair of nasal 2 and in front of the pair of nasal 3. It presents an approximate triangular shape. The nasal 1 (Fig. 3) is a tubular bone that articulates laterally with the nasal 2, and has approximately half of its size, and that's where the infraorbital canal ends. The nasal 2 (Fig. 2) is located medially to nasal 1 and anterior to nasal 3. Nasal 2 is trapezoid and similar in size to the rostral. The nasal 3 (Fig. 2), which has an approximately quadrangular shape, is connected to the frontal through the medial suture.There is a sensory canal opening in nasal 3, through which the supraorbital canal passes, located at the lateral margin of the bone. The frontal (Fig. 2) articulates anteriorly with the nasal 3; postero-laterally with the postorbital and the dermosphenotic; and posteriorly with the intertemporo-supratemporal. The frontal is approximately rectangular in shape, measuring approximately one third of the size of the skull. The anterior margin of the frontal has a curvature where the nasal 3 articulates. In its lateral portion, the frontal forms the upper limit of the eye socket. There are two openings on the frontal, which correspond to the supraorbital canal. The dermosphenotic (Figs. 2, 7) is an elongated bone that is located dorsal to the postorbital and anteromedially to the prespiracular bones. It has a canal opening that corresponds to the optic canal, which bifurcates anterolaterally into the infraorbital canal and anteriorly into the supraorbital canal.

The intertemporo-supratemporal (Fig. 2) is posterior to the frontal and has a quadrangular shape, its size is half the size of the frontal. In its lateral portion, there is the opening of the optic canal, which passes through the entire length of the bone. The extrascapular (Fig. 2) is present in 3 pairs, sometimes there is an extra bone behind the middle extrascapulars, all posterior to the intertemporo-supratemporal, the largest being the median extrascapular, measuring 1/3 of the intertemporo-supratemporal. All bones are triangular or trapezoidal in shape. At the canal opening of the most lateral extrascapular bone, the posttemporal canal, coming from the opening of the most posterior extrascapular, bifurcates into the supratemporal canal medially and into the otic canal anteriorly. Through the openings of the medial and central extrascapulars, the supratemporal canal passes. The postorbital (Fig. 3) is a rectangular bone, located anterior to the prespiracular bones, and ventral to the frontal, forming the posterior limit of the eye socket. This bone has an infraorbital canal opening in its most dorsal portion.

Spiracular, opercular and gular series

The series of spiracular bones (Figs. 2, 3) extends from the dorsoposterior end of the maxilla to the dorsal region of the opercle. The prespiracular bones vary from 3 to 5, sometimes with different numbers of bones for each side of the skull. They present an approximate average size equal to the extrascapular bones and rectangular or square shape. The prespiracular bones are positioned dorsoposterior to the maxilla, posterior to the postorbital, lateral to the dermosphenotic, anterodorsal to the preopercle and anterior to the spiracular bones. The pair of spiracular bones (Figs. 2, 3) have an average size equal to the biggest bone of the postspiracular bones. These bones are positioned lateral to the frontal and intertemporo-supratemporal, medial to the preopercle and anterior to the postspiracular bones. Posteromedial to the last spiracular bone, a small, approximate rounded dermohyal (Fig. 2) is present. The postspiracular bones (Fig. 2, 3) are composed of 2 to 3 bones on either side. The series usually extends from the end of the intertemporo-supratemporal to the end of the posttemporal (this series may sometimes extends only to the middle of the most lateral extrascapular), and its bones have a subrectangular or subquadrangular shape. They articulate with the dorsal part of the preopercle and opercle.

The preopercle (Fig. 3) is located ventral to the spiracular bones, anterior to the opercle, and dorso-anterior to the subopercle, and is approximately the same size as the opercle. This bone has a trapezoid shape with the exception of its ventro-posterior part, where the bone has a subrectangular process, sometimes this process presents itself with a base larger than the rest of the process. Three external canal openings are associated with the preopercular canal, all situated at the posterior margin of the bone. The most ventral of these is situated in the process that this bone presents, the middle one is situated near the limit with the subopercle and the most dorsal one is situated at the limit with the spiracular bones. The subopercle (Fig. 3) is triangular in shape, sometimes with a little more narrowed dorsal part, and lies ventro-posteriorly to the preopercle and ventro-anterior to the opercle. The opercle (Fig. 3) has an approximately trapezoid shape with its posterior limit rounded and is located posterior to the preopercle. Anterior to the clavicles and medial to the mandible is the pair of gulars (Fig. 4), which measure about 3/4 of the length of the skull. The gulars are approximately triangular, narrower anteriorly and wider mid-posteriorly, and connect only in the anterior portion of their medial extent. None of the gulars touch the dentary symphysis, leaving this region exposed.

Maxillar bones

The premaxilla (Fig. 3) is the most anterior bone of the maxillar, is present in pairs, has an irregular shape, presenting a medium sized anterior portion, a thin median portion and a higher and thicker posterior portion. It articulates dorso-anteriorly with the rostral, ventro-posteriorly with the lacrimal, and dorso-posteriorly with the nasal 3 and the frontal. In the premaxilla, the infraorbital canal divides into dorsal and ventral branches. The dorsal branch joins the supraorbital canal and the left and right ventral branches curve dorsomedially to merge themselves in the rostral bone. The maxilla (Fig. 3) is fused with the subinfraorbital (Pehrson, 1947; 1958), and is the longest bone in the maxillar, having the same length relative to the skull as the frontal. The maxilla is sutured to the premaxilla anteriorly and articulates with the dermopalatine and ectopterygoid ventrally ((Figs. 2, 6). The maxillar has three canal openings corresponding to the infraorbital canal: the most anterior, associated with the lacrimal; another in a central position in the maxilla; and a more posterior one, associated with the postorbital. The lacrimal (Fig. 3) is a small bone that can be found in some shapes depending on the size of its anterior and dorsal portions. The most common shapes are “L” shaped (the posterior portion is higher forming an approximate 90° degree with the anterior portion - Fig3) or subtriangular, but subretangular is also seen. The lacrimal is situated above the maxilla and is part of the anterior portion of the orbit. Posterior to the lacrimal, the dorsal limit of the maxilla is concave, thus forming the lateral base of the orbital cavity. Posterior to the maxilla, there are one or two (rarely three) cheek plates (= quadratojugal)(Fig. 3), the first cheek plate is larger, has a trapezoid shape and twice the size of the second, which has a rounded, sometimes trapezoidal, shape. The largest plate articulates posterior to the maxilla. The plates may articulate with each other.

Jaw bones

The dentary (Fig. 2) is an elongated bone and is almost the same length as the maxilla. Posteriorly, the dentary bifurcates forming a socket where the angular articulates. In the dentary there are three canal openings in its anterior limit, where the mandibular canal passes, its length is equivalent to approximately 2/3 of the jaw, and it is covered medially by the prearticular. The angular (Fig. 2) has an approximate rhombus shape and is sutured with the articular posteromedially. The mandibular canal also passes through the angular and it has an opening corresponding to this canal. The articular (Figs. 2, 5) is the most posterior bone in the jaw. Its size is equivalent to 1/3 of the angular, it has a quadrangular shape, presenting a rounded protuberance with a socket at its posterior limit, and articulates with the angular latero-posteriorly and with the quadrate dorsally (through the socket). The prearticular (Fig. 5) is the second longest bone of the jaw, being slightly smaller than the dentary, it is more narrow anteriorly, where it articulates with the dentary, and it becomes more thick in its final third. The bone also presents a dorsal process, where it articulates with the maxilla. Medial to the dentary are the mentomeckelian and coronoids 1 and 2 (co1-2) (Fig. 5). The mentomeckelian is a small rectangular bone ventral to the co1 and half its size. The co1 and co2 are small paired bones that present dentition and are articulated with each other, both subrectangular of the same size. The co2 also articulates with the prearticular in the most anterior portion of the jaw.

Bones of the palate and hyoid arch

Two pairs of dermopalatines (dpl 1-2) (Fig. 6) are located on the anterior margin of the palate, posterior to the premaxilla. The dpl 1 articulates with the vomer (Fig. 6), a small rounded bone, in its medial portion and, in its lateral portion, it articulates with the dpl 2, which articulates posteriorly with the ectopterygoid. The parasphenoid (Figs. 6, 7) is the largest element of the braincase, extending from the anterior suture of the dermopalatine to the posterior portion of the occipital, which comprises almost the entire extension of the skull. The bone is broad and covers approximately one-third of the endopterygoid. It has a rounded anterior portion (head) with a narrow base. In the middle of the extension of the bone, there are two lateral processes that narrow from the center of the bone towards its end and articulate with the hyomandibula. This process also grows dorsally, articulating with the posterior portion of the dermosphenotic. The posterior part of the parasphenoid forms a socket where part of the occipital articulates.

The quadrate (Fig. 3) is trapezoidal in shape, its length is approximately four times less than that of the endopterygoid, and it articulates laterally with the metapterygoid. The hyomandibula (Fig. 6) is “L” shaped and twice as large as the quadrate. It articulates anteriorly with the quadrate and the metapterygoid, laterally with the preopercle, posteriorly with the opercle and dorsally with the dermohyal. The endopterygoid (Fig. 6) is situated behind the head of the parasphenoid and its lateral portion is approximately triangular in shape, with the posterior side slightly curved. Its size corresponds to approximately one third of the size of the parasphenoid. The ectopterygoid (Fig. 6) has a subrectangular shape and length equivalent to the endopterygoid. the endopterygoid presents a small process on its laterodistal part that articulates with the maxilla. Additionally, its most anterior part articulates with the dermopalatine 2, its lateroproximial portion articulates with the endopterygoid, and its most posterior end with the metapterygoid. The metapterygoid (Fig. 6) has an elongated, approximately rhombus shape and is situated posterior to the ectopterygoid, lateral to the posterior portion of the endopterygoid, medial to the quadrate and anterior to the hyomandibula.

Endocranium and Neurocranium bones

The lateral ethmoid (Fig. 7) is a paired thin rounded bone one-third the size of the orbitosphenoid that articulates anteriorly with the premaxilla, dorsally with the frontal and posteriorly with the orbitosphenoid. The orbitosphenoid (Fig. 7) is approximate rectangular in shape and its anterior portion is oriented more laterally, where it articulates with the lateral ethmoid, The bone also articulates with the parasphenoid ventrally and with the frontal and the dermosphenotic dorsally. The epioccipital (Figs. 6, 7) bone presents a irregular shape, its anterior half is wider and subtriangular in shape, while the posterior half is thinner and elongated. This bone articulates anteriorly with the parasphenoid, dorsally with the intertemporo-supratemporal, and posteriorly with the occipital. The occipital (Figs. 6, 7) is the most posterior bone of the skull of Polypterus, it has a triangular shape and the same length as the epioccipital. It articulates in the final portion of the parasphenoid and anterior to the first vertebra.

Branchial arches

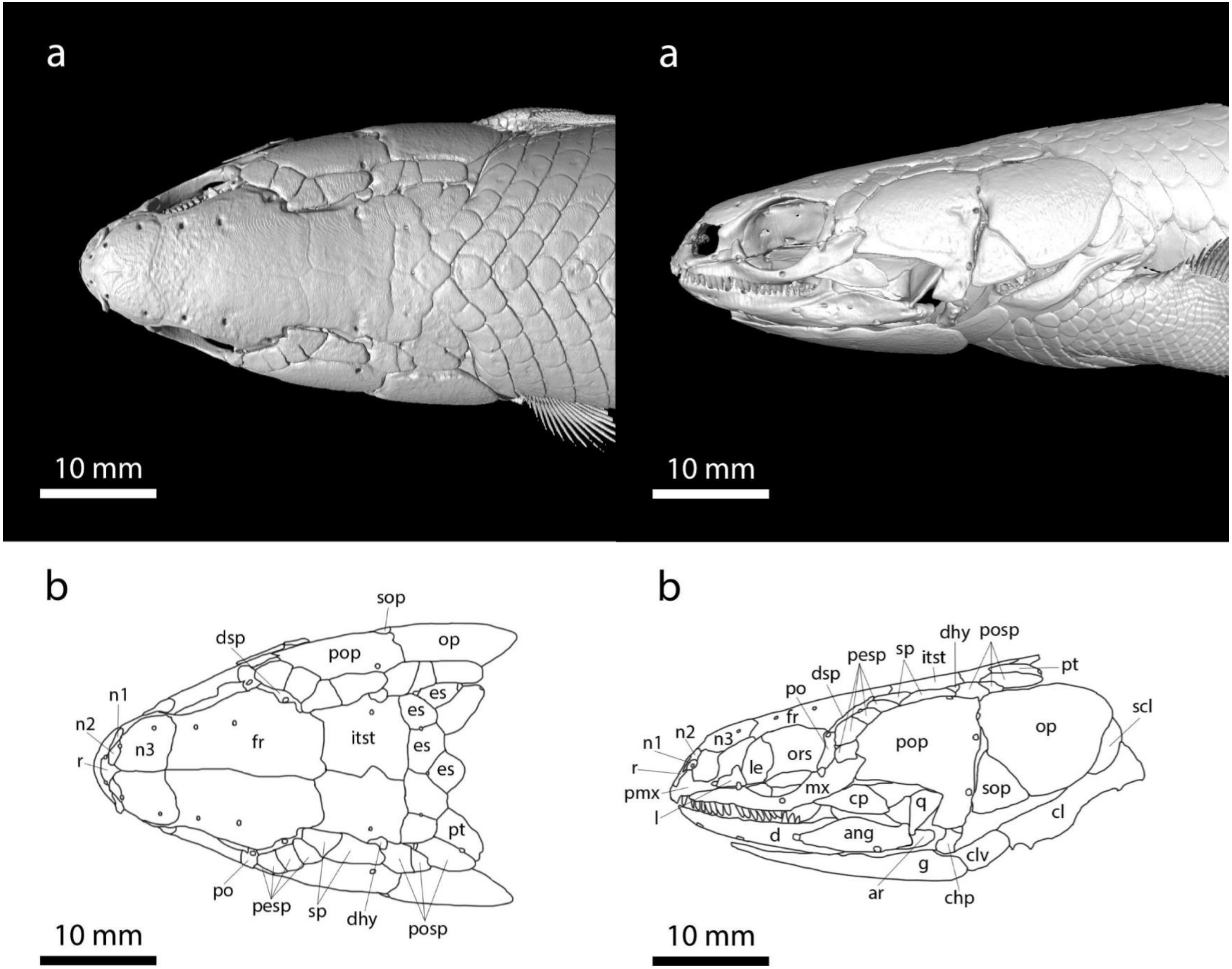
Polypterus senegalus has four branchial arches (hypobranchials + ceratobranchials, (Fig. 8). The most posterior gill arch is homologous to the 4th arch of other fish, where the 5th arch is absent in Polypteridae (Britz & Johnson, 2003). The hypobranchials articulates with the basibranchial. The ceratobranchials 1, 2 and 3 are associated with hypobranchials 1, 2 and 3 (hb 1-3), respectively. The rounded hypohyals are located at the anterior end of the basibranchial, articulating ventrolaterally with the anterior ceratohyal (cha) (Fig. 8). The basibranchial has an approximately rectangular shape, where it is wider laterally. It presents numerous tooth patches on each side, which are concentrated at the lateral edges. Hypobranchial 1 is short, broad and rounded distally, where it articulates with Ceratobranchial 1, and is narrower proximally, where it articulates with basibranchial. The hypobranchials 2 and 3 are thinner and more elongated, and are approximately equal in length. The hypobranchials and the ceratobranchials present tooth patches on their surfaces. Ceratobranchial 1 is the longest of the four ceratobranchials. The cb1 is wider anteriorly, where it articulates with the hb1, and thinner posteriorly, where it articulates with the pharyngobranchials through the epibranchial cartilage. Two small pharyngobranchials (Fig. 8) are present distal to the epibranchial cartilage. Ceratobranchial 2 is shorter than cb-1 and bigger than cb-3. Cb 4 is longer than cb2 and cb3 and articulates directly with the basibranchial. Situated underneath the anterior part of the basibranchials is a pair of basihyals approximately one-third the length of the anterior ceratohyal, subtriangular in shape. Centered below the basibranchial, there is a thin, "Y" shaped urohyal. The anterior ceratohyal is thick and long, with a broad posterior end. The proximal end of the cha is parallel to the lateral surface of the hypohyal. Posterior and perpendicular to the anterior ceratohyal is the posterior ceratohyal, a cylindrical bone with a length equivalent to 1/3 of the anterior ceratohyal.

Pectoral fin

The dorsalmost element of the pectoral fin is the posttemporal bone (Fig. 2), a somewhat rectangular bone with rounded edges that articulates anteriorly with the extrascapular series and dorsally on the supracleithrum. The posttemporal bears the posttemporal canal that connects the lateral line with the skull. The supracleithrum (Fig. 9) also has an approximate rectangular shape and articulates dorsally with the cleithrum and the postcleithrum. The two postcleithrum (Fig. 9) also articulate with the cleithrum, one presents a rounded and elongate shape, while the other presents a triangular shape, both sizes are approximately 1/3 of the supracleithrum size. The cleithrum (Fig. 9) is the biggest bone of the pectoral fin, about two times the supracleithrum size, has a rectangular and curved shape and also articulates ventrally with the clavicle and anteriorly with the scapula and the coracoid. The clavicle (Fig. 4) is as big as the cleithrum, has a triangular shape and articulates anteriorly with the gular. The scapula is a small bone, about half the size of the coracoid, that presents an approximate trapezoidal shape.The coracoid presents a trapezoidal shape. The scapula and the coracoid form the pectoral girdle and articulate with the propterygium and the metapterygium (Fig. 9). These last are two elongate bones, where the metapterygium is twice the size of the propterygium, that articulate with each other on their anteriormost parts. Both articulate with the mesopterygial bony plate (Fig. 9), where the propterygium articulates dorsally and the metapterygium ventrally. The mesopterygial bony plate presents a round shape. Posterior to the propterygium, mesopterygial bony plate and metapterygium are the elongate proximal radials of pectoral fin (Fig. 9), which are numerous small cylindrical bones that articulate with the numerous lepidotrichia.

Caudal fin

The caudal fin (Fig. 10) presents 5 ural centra (u1-u5), where the u5 is the posteriormost element of the vertebral column. The u1 is slightly smaller than the preural centrum 1. These vertebrae decrease in size in an anterior-posterior gradient, where the last one (u5) is the smallest of the ural centra. Each ural centrum has its corresponding hypural, which are long hemal spines positioned ventral on the centra, oriented ventroposteriorly and supporting the caudal fin rays. Anterior to the ural centra, are the preural centra. These vertebrae differentiate themselves from the ural centra by the presence of parhypurals, which are hemal spines where the caudal artery is surrounded by hemal arches (Nybelin, 1977; Schultze & Arratia, 2013). There are 7 preural centra (pu1-pu7), each of them associated to a long, “Y” shaped parhypural oriented ventroposteriorly. The preural centra, counted posterior-anteriorly (*i.e*. the pu7 is the most anterior vertebrae of the preural centra), goes until the anterior part of the anal fin.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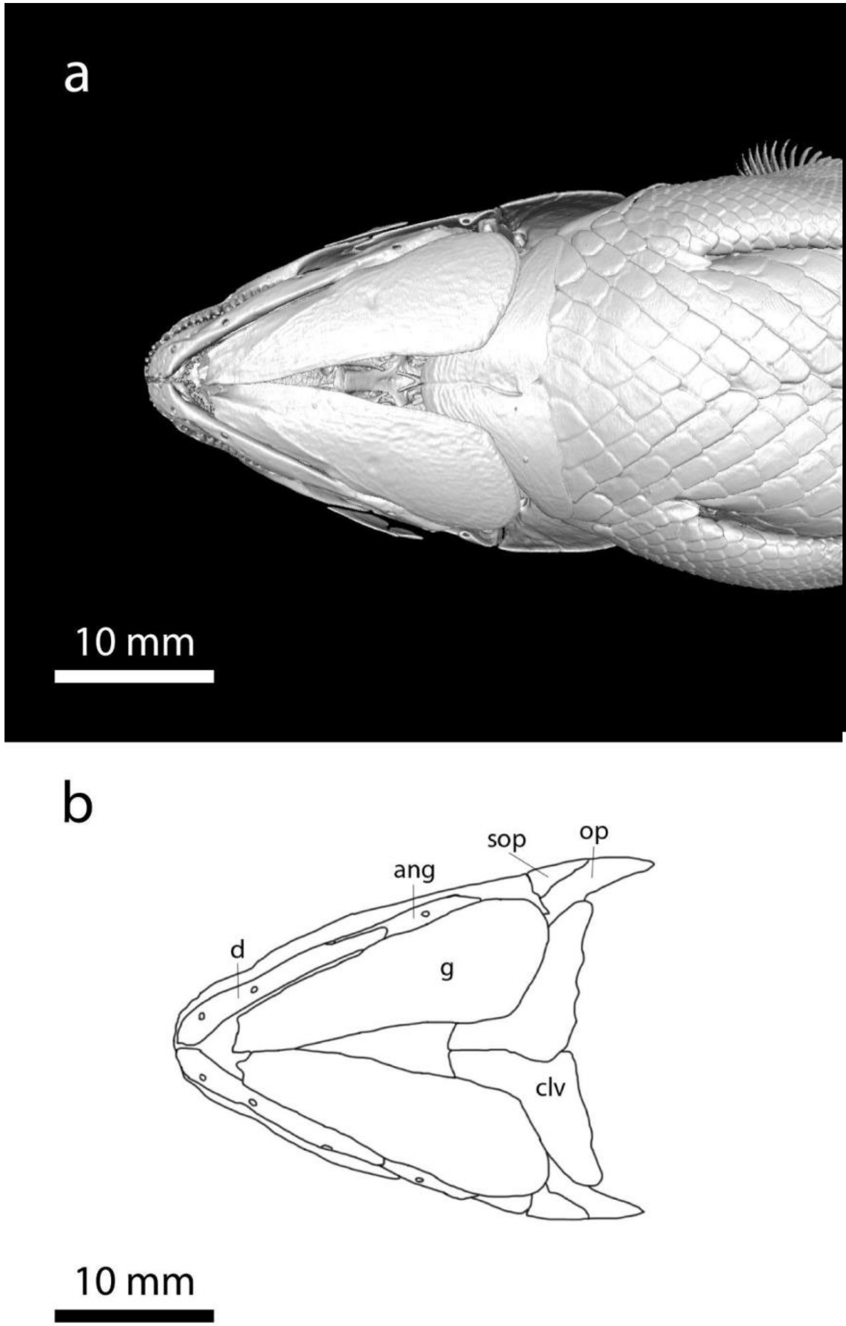
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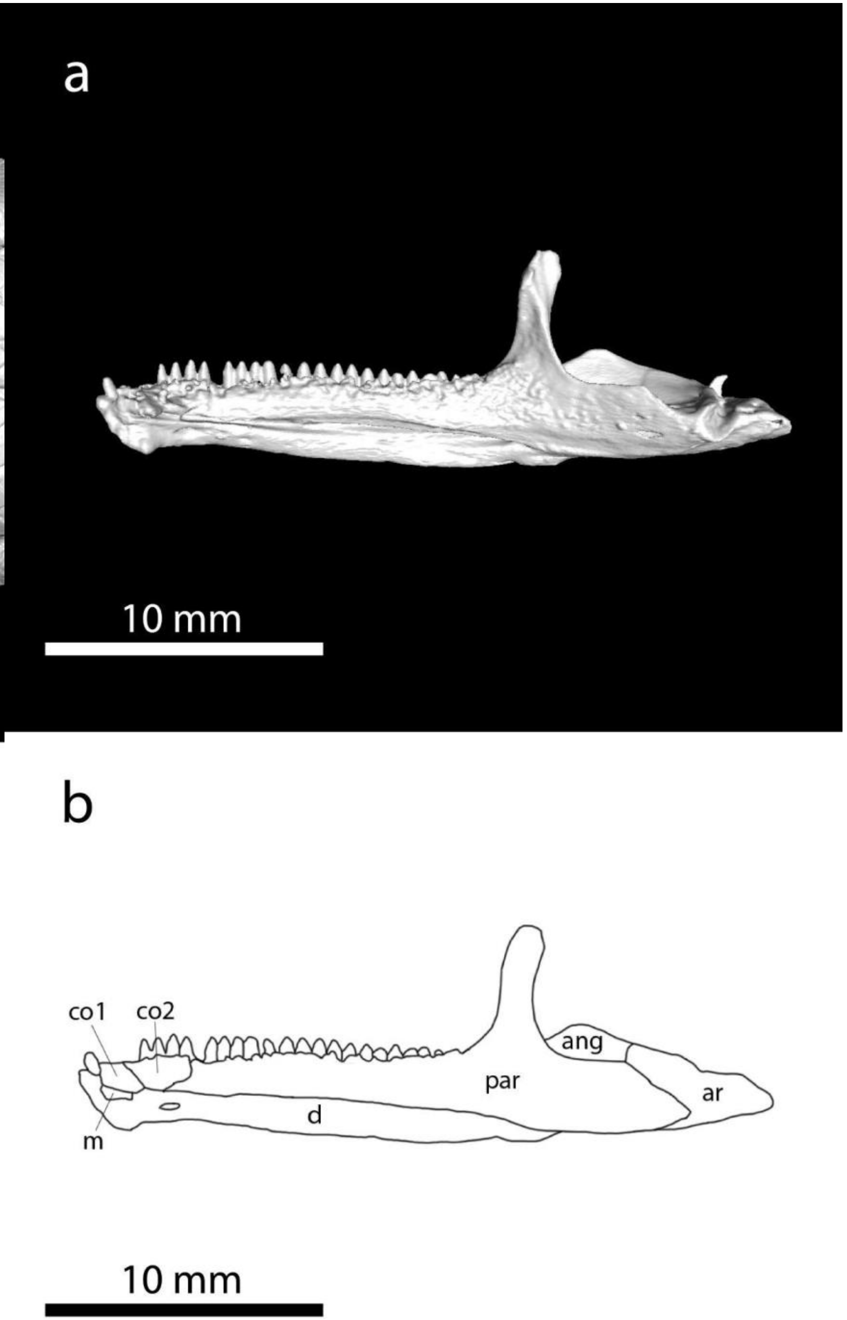
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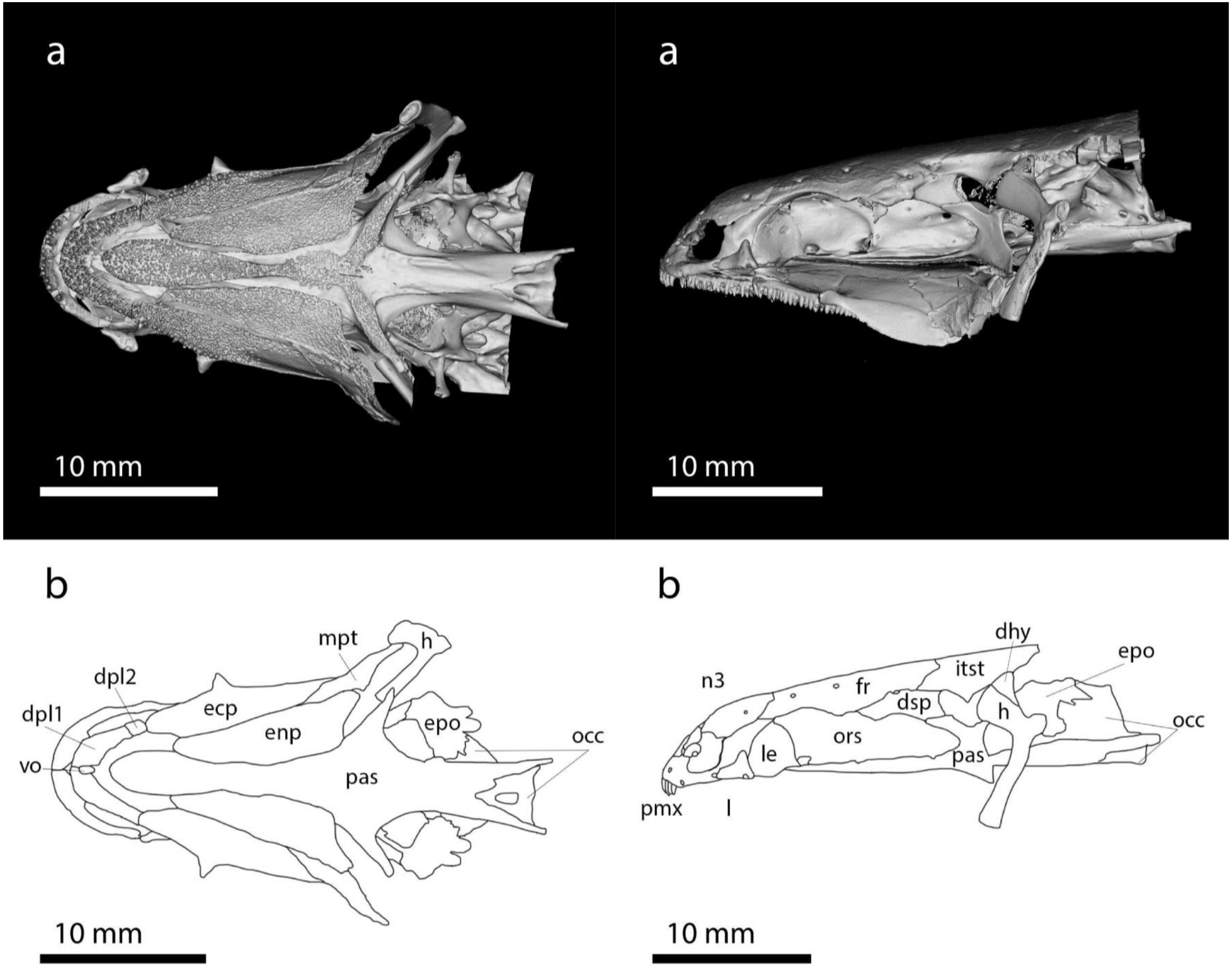
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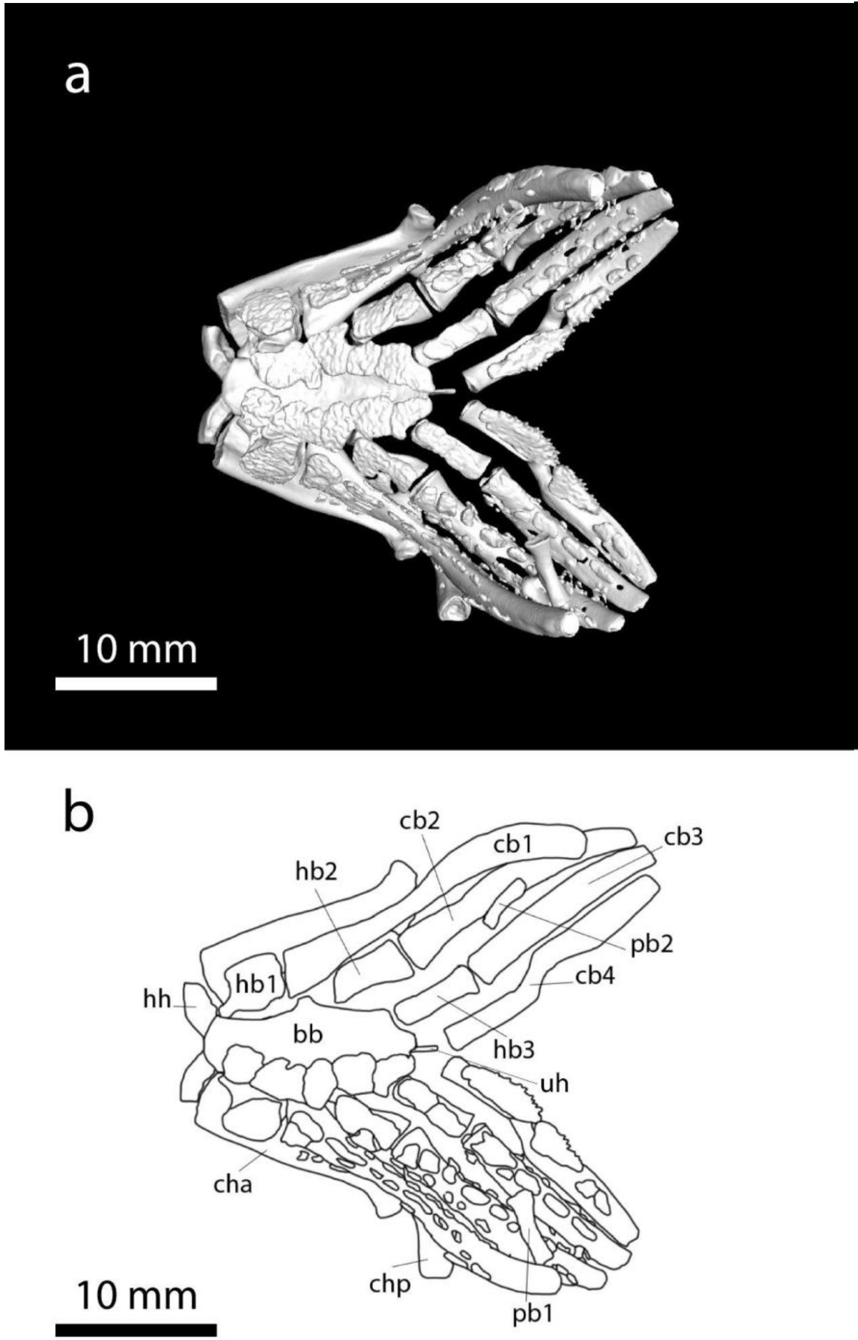
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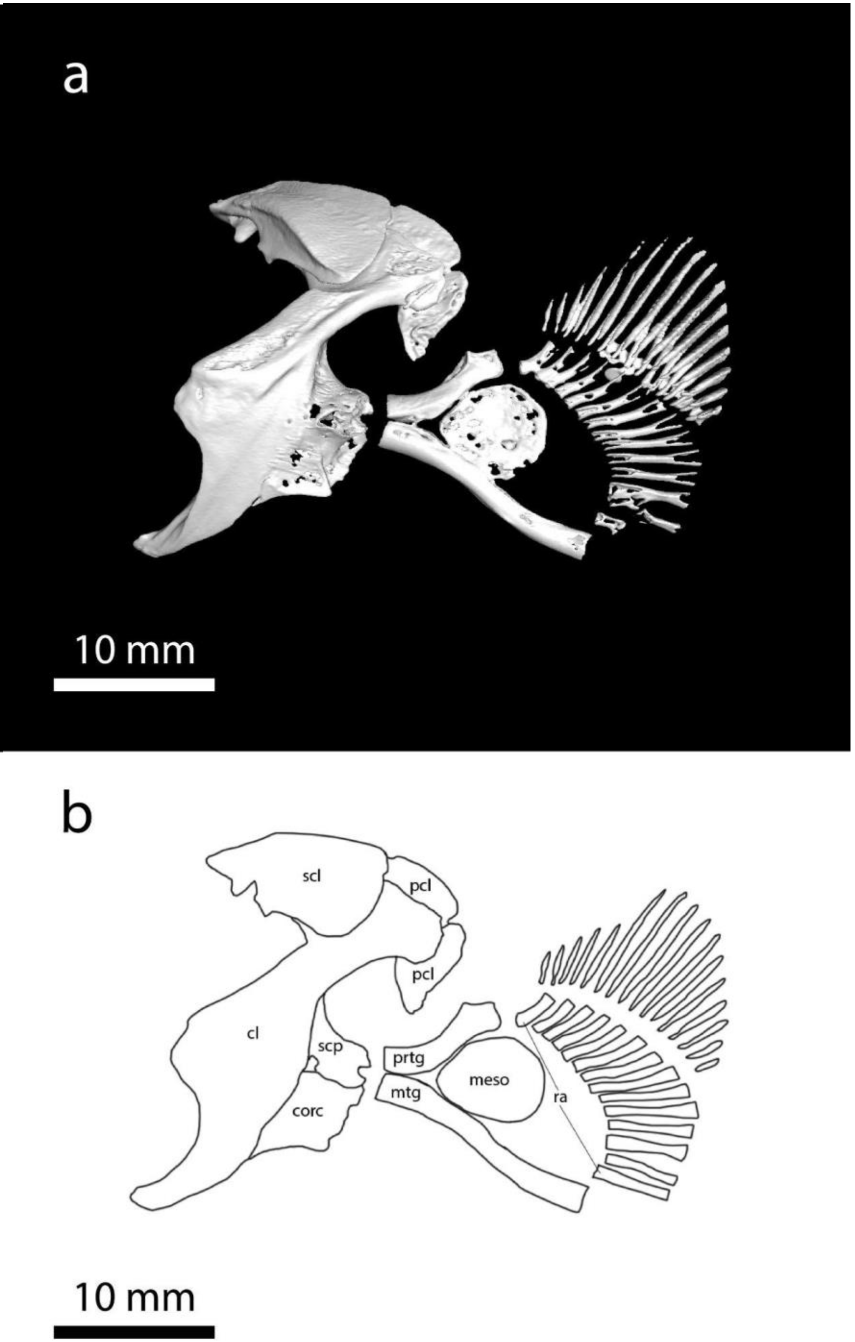
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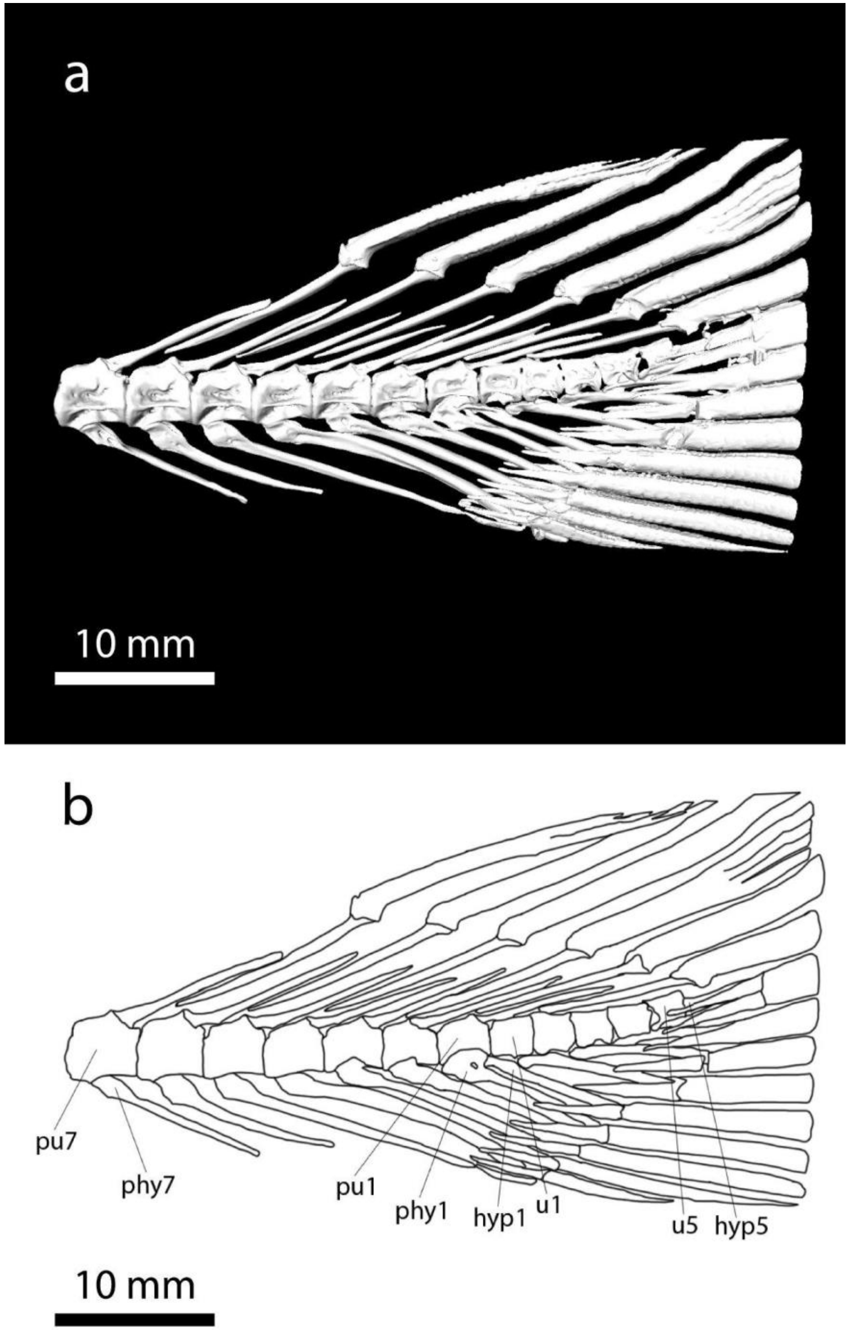
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Figure 2- 3D model (a) and drawing (b) of the dorsal view of the head of *P. senegalus* (MNHN-IC-2002-0527). Abbreviations on page 37. Scale = 10mm.

Figure 3- 3D model (a) and drawing (b) of the lateral left view of the head of *P. senegalus* (MNHN-IC-2002-0527). Abbreviations on page 37. Scale = 10mm.

Figure 4- 3D model (a) and drawing (b) of the ventral view of the head of *P. senegalus* (MNHN-IC-2002-0527). Abbreviations on page 37. Scale = 10mm.

Figure 5- 3D model (a) and drawing (b) of the lateral left view of the right lower jaw of *P. senegalus* (MNHN-IC-1904-0068). Abbreviations on page 37. Scale = 10mm.

Figure 6- 3D model (a) and drawing (b) of the ventral view of the palate region of *P. senegalus* (MNHN-IC-2002-0527). Abbreviations on page 37. Scale = 10mm.

Figure 7- 3D model (a) and drawing (b) of the lateral left view of the neurocranium region of *P. senegalus* (MNHN-IC-2002-0527). Abbreviations on page 37. Scale = 10mm.

Figure 8- 3D model (a) and drawing (b) of the dorsal view of the branchial arches of *P. senegalus* (MNHN-IC-1904-0068). Abbreviations on page 37. Scale = 10mm.

Figure 9- 3D model (a) and drawing (b) of the lateral left view of the left pectoral fin of *P. senegalus* (MNHN-IC-1904-0068). Abbreviations on page 37. Scale = 10mm.

Figure 10- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. senegalus* (MNHN-IC-1904-0068). Abbreviations on page 37. Scale = 10mm.

DISCUSSION

Osteology Comparison

Some morphological differences were observed among the species of Polypteridae analyzed in the present work. Here, we took the osteology description of *P. senegalus* as reference for the comparisons with the other species.

The rostral bone of *P. delhezi*, *P. endlicherii*, *P. palmas*, *P. retropinnis* and *E. calabaricus* (Figs. 12, 13, 15, 17, 19) are equal in shape and relative position to those observed in *P. senegalus*. Also *P. palmas* (Fig. 15) may present the rostral with a rounded dorsal portion. The rostral of *P. bichir* (Fig. 11) has the same shape of *P. senegalus*, but the bone ends between the middle of the pair of nasal 3. *P. ornatipinnis* (Fig. 14) may present the same as *P. bichir* or a rostral with rectangular shape, separating the nasal 3 completely, the last one is also seen in *P. weeksii* (Fig. 18). *P. polli* (Fig. 16) presents it with a rhombus shape, in the same relative position as *P. bichir*. The pair of nasal 2 of all species (Fig. 47) studied here is similar to the ones in *P. senegalus*. Additionally, *P. ornatipinnis* (Fig. 14) may present these bones in trapezoidal shape and *P. palmas* (Fig. 15) may present these bones relatively thinner laterally than in other species. The pair of nasal 3 of all species studied here is similar to the ones in *P. senegalus*, except for *P. ornatipinnis* and *P. weeksii* (Figs. 14, 18), where they do not articulate medially with each other, and *P. palmas* (Fig. 15), where the bone may present an acute anterior process. It seems that the disconnection between the pair of nasal 3, as seen in *P. ornatipinnis* and *P. weeksii*, is a juvenile state that these species maintain during adulthood (Poll, 1941; 1942; Grande 2010; Rizzato et al., 2020).

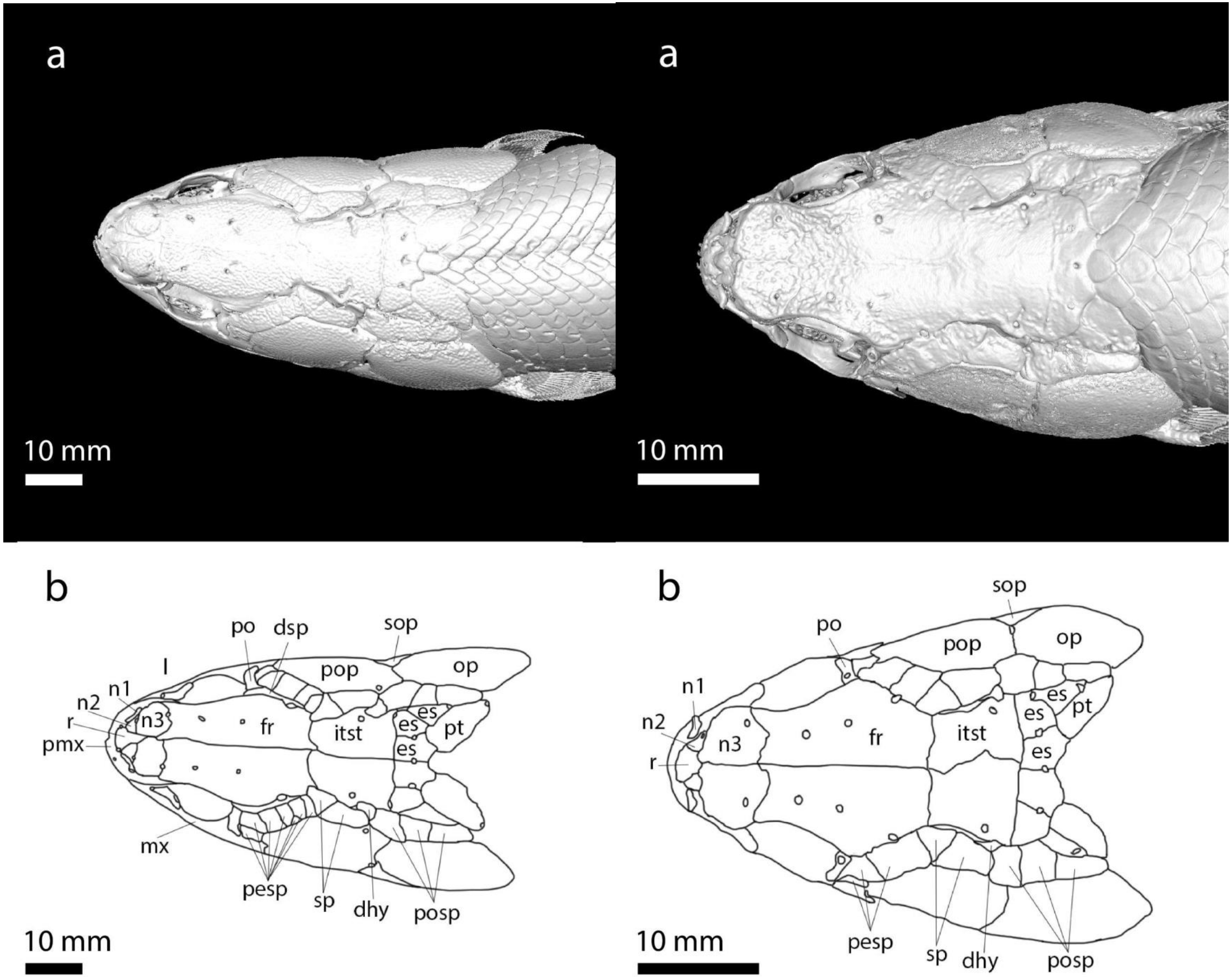
The frontal of *P. ornatipinnis*, *P. polli* and *P. weeksii* (Figs. 14, 16, 18) are slightly different than in the other species, where it presents an acute anterior-medial process that goes between the pair of nasal 3. In *P. weeksii* (Fig. 18) It also presents an extra pair of canal openings in medial position. *P. senegalus* is the only species seen here with a 7th extrascapular (Fig. 2). The extrascapular of *P. bichir*, *P. delhezi*, *P. endlicherii*, *P. ornatipinnis* (*P. ornatipinnis* of Grande (2010) has a 7th extrascapular, but not as seen in *P. senegalus* here), *P. weeksii* and *E. calabaricus* (Figs. 11, 12, 13, 14, 18, 19) is the same as in *P. senegalus* (3 pairs). On the other hand, *P. palmas*, *P. polli* and *P. retropinnis* (Figs. 15, 16, 17) present a shorter most lateral extrascapular, which causes the spiracular series to end far behind the extrascapular. All polypteridae species present in this study presented the following bones of the skull roof with the same shape and relative position as observed in *P. senegalus*: Nasal 1, dermosphenotic and intertemporo-supratemporal (Fig. 47).

The postorbital of all *Polypterus* species studied here present the same morphology, while *E. calabaricus* (Figs. 28, 48) presents a postorbital with a dorsal portion larger than its ventral part. The prespiracular bones showed a lot of variation through the species in this study and the number of bones of each side of the head may vary in a single specimen. *P. bichir* (Figs. 11, 20) presented 5 or 7 of these bones

(According to Poll (1941) the species may present 4 to 6 of these bones; Allis (1922) shows a *P. bichir* with 6 and 7 of these); *P. endlicherii* (Figs. 13, 22) presented 5 bones for this series; *P. delhezi* and *P. palmas* (Figs. 12, 15, 21, 24) presented 3 to 4. *P. delhezi* may present 2 to 5 in Poll's (1941) observations and *P. palmas* also 2, according to Poll(1942). *P. ornatipinnis* and *E. calabaricus* 3 to 6 (Figs. 14, 19, 23, 28), where some may be doubled (Poll (1941) also observed the occurrence of 7 prespiracular bones in *P. ornatipinnis*); *P. polli* (Figs.16, 25) 2 or 4 (probably the species may present 3 of this bones, but it was not observed here); *P. retropinnis* 4 or 5 (Figs. 17, 26)(also 3, according to Poll (1942)), where doubling may be present; and *P. weeksii* 6 to 8 (Figs. 18, 27), where doubling may also be present. On Poll's (1941; 1942) observations, he stated that the doubling of these bones is more common in *P. weeksii* than in other species he analyzed, which presented 4 to 8 prespiracular bones. For the postspiracular bones, they also presented some variation, including on each side of the skull in a single specimen. *P. bichir* (Figs. 11, 20) presented 3 postspiracular bones (It may present 4, according to Poll (1941)); *P. endlicherii* (Figs. 13, 22) presented 4 of these bones; *P. ornatipinnis*, *P. polli*, *P. retropinnis* and *P. weeksii* presented 3 or 4 (Figs. 14, 16, 17, 18, 23, 25, 26, 27)(*P. ornatipinnis* may present 2 of these (Poll, 1941)); *P. delhezi* and *P. palmas* 3 to 5 (Figs. 21, 24)(Only 3 and 4, according to Poll (1942)); and *E. calabaricus* (Figs. 19, 28) 4 or 5 of postspiracular bones. The spiracular bones and the dermohyal are the same for all the species in the present work (Fig. 48)(same as Allis, 1922; Poll, 1941; 1942; Jollie, 1984; Bartsch, 1997).

The opercle region showed great variation throughout the species observed here. In *P. bichir* (Fig. 20), the bones of the opercular region are proportionally bigger (⅔ of the head) than the ones in *P. senegalus* (Allis, 1922). *P. delhezi* (Fig. 21) presents a larger ventral process of the preopercle when compared with *P. senegalus*, a proportionally bigger subopercle and smaller opercle. *P. endlicherri* (Fig. 22) has the preopercle and the opercle proportionally shorter and the ventral process of the preopercle slightly curved forward. *P. ornatipinnis* and *P. weeksii* (Figs. 23, 27) present an anterior process of the preopercle more prominent forward; a bigger ventral process of the preopercle, of the same size as the body of the bone; and a subopercle proportionally smaller. *P. palmas* (Fig. 24) has a shorter and larger ventral process of the preopercle and a smaller subopercle. *P. retropinnis* (Fig. 26) presents a ventral process of the preopercle shorter and larger (as *P. palmas*) and a thinner subopercle, thus a larger opercle. *E. calabaricus* (Fig. 28) has a preopercle with the same height as its ventral process, which is larger than in *P. senegalus*, and the opercle is triangular with a rounded posterior limit (Claeson, Bemis & Hagadorn, 2007). It is broadly known that the subopercle is absent in *E. calabaricus* (Smith, 1866; Traquair, 1870; Jollie, 1984; Claeson, Bemis & Hagadorn, 2007; Moritz & Britz, 2019), but we observed what seems to be a subopercle in two specimens of *E. calabaricus* (MNHN-IC-1978-0732 and MNHN-IC-2008-2103A). The observed bones were present in just one side of the head, were triangular shaped and occupied the same relative position as the subopercle in *Polypterus*. The only register of a similar bone is made by Claeson, Bemis & Hagadorn (2007, p. 1028-1029), where they claim that "a definitive subopercle is absent in all specimens of *Erpetoichthys calabaricus* examined. There is, however, in specimen MNHC F20004, a small bone antero-ventral to the opercle. This bone is long, narrow, and is approximately one-third the width of the opercle. This bone and the opercle do not suture to one another, though they are clearly associated.”.

The gular plates of *P. bichir*, *P. palmas* and *P. retropinnis* (Figs. 29, 33, 35) are like the ones of *P. senegalus*. Additionally, in *P. palmas* (Fig. 33) were also observed the gulars touching each other along their entire length, as observed in *P. polli* (Fig. 34). In *P. endlicherii* (Fig. 31), the gulars just touch each other anteriorly, in a small part or they touch each other along their anterior half. *P. ornatipinnis* (Fig. 32) may also present the gulars touching themselves along their anterior half, as in *P. delhezi* and *P. weeksii* (Figs. 30, 36). *P. delhezi* and *P. weeksii* may also present the gulars separated, as in *E. calabaricus* (Fig. 37).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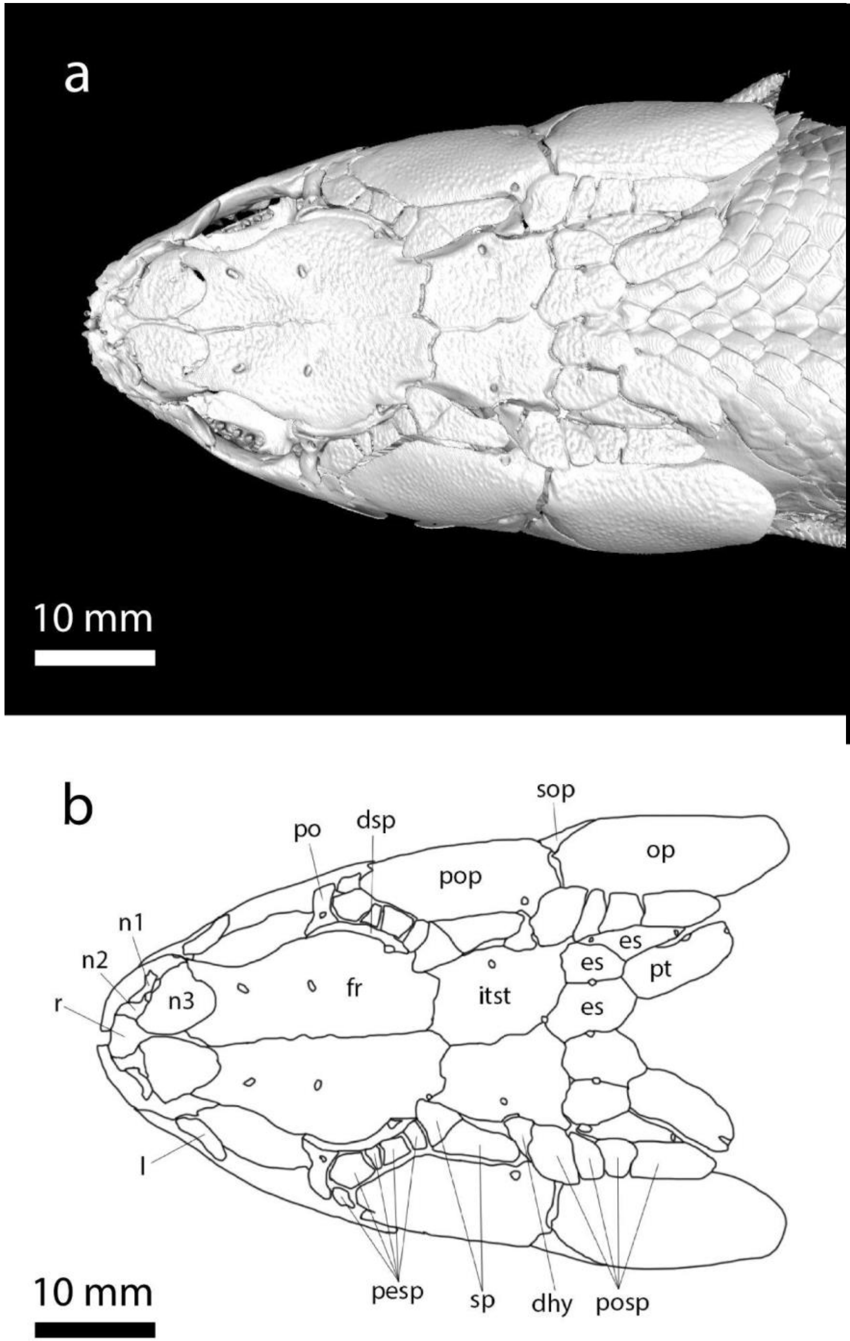
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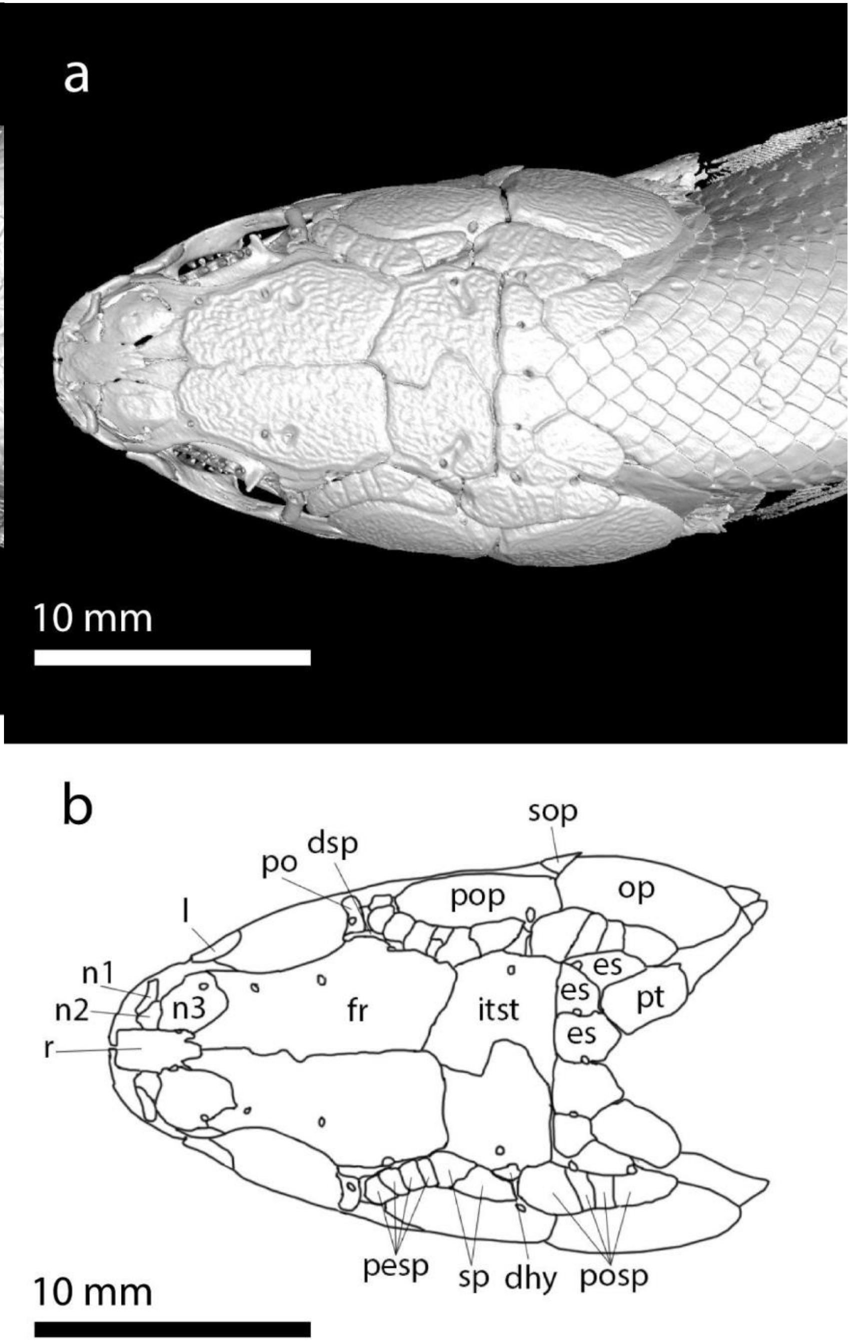
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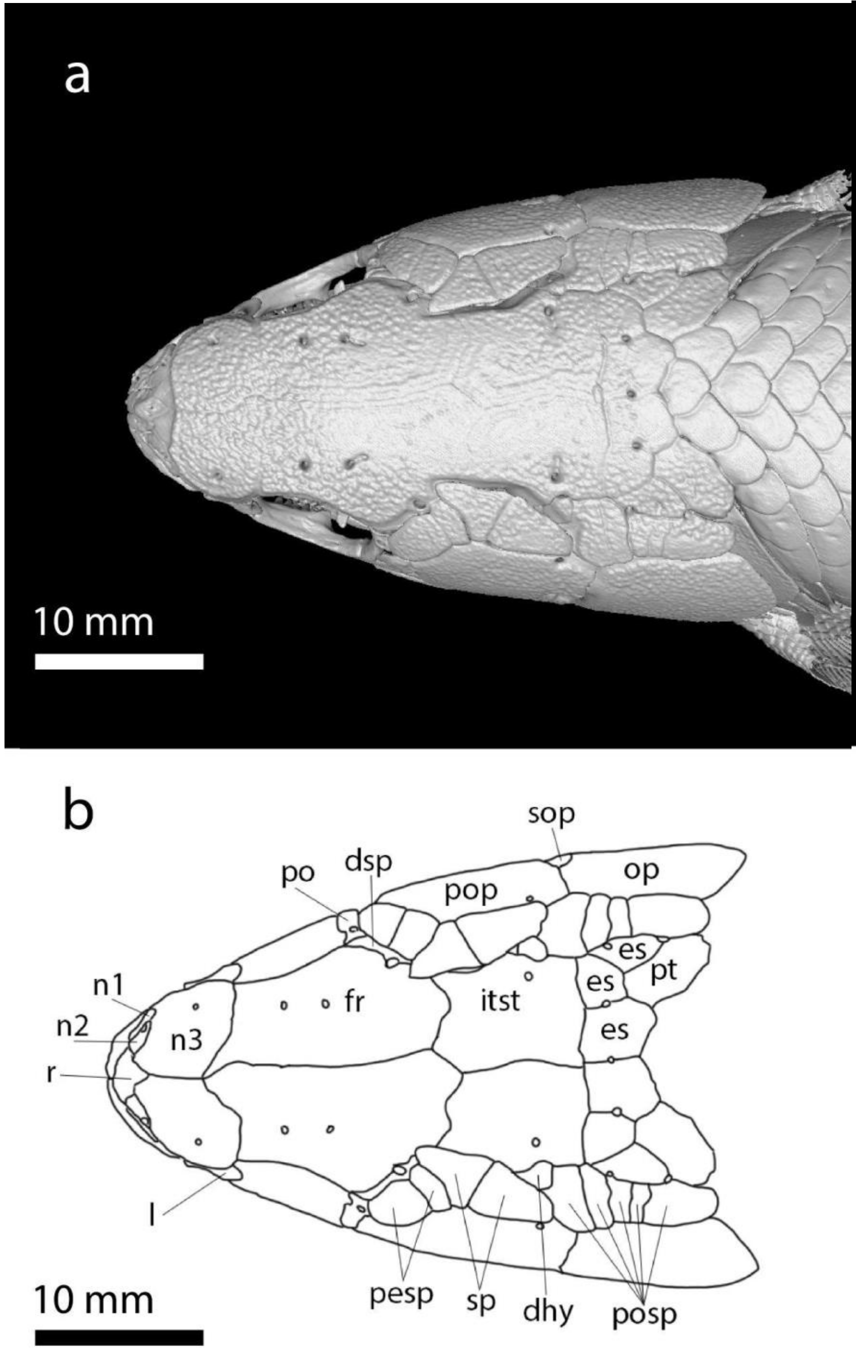
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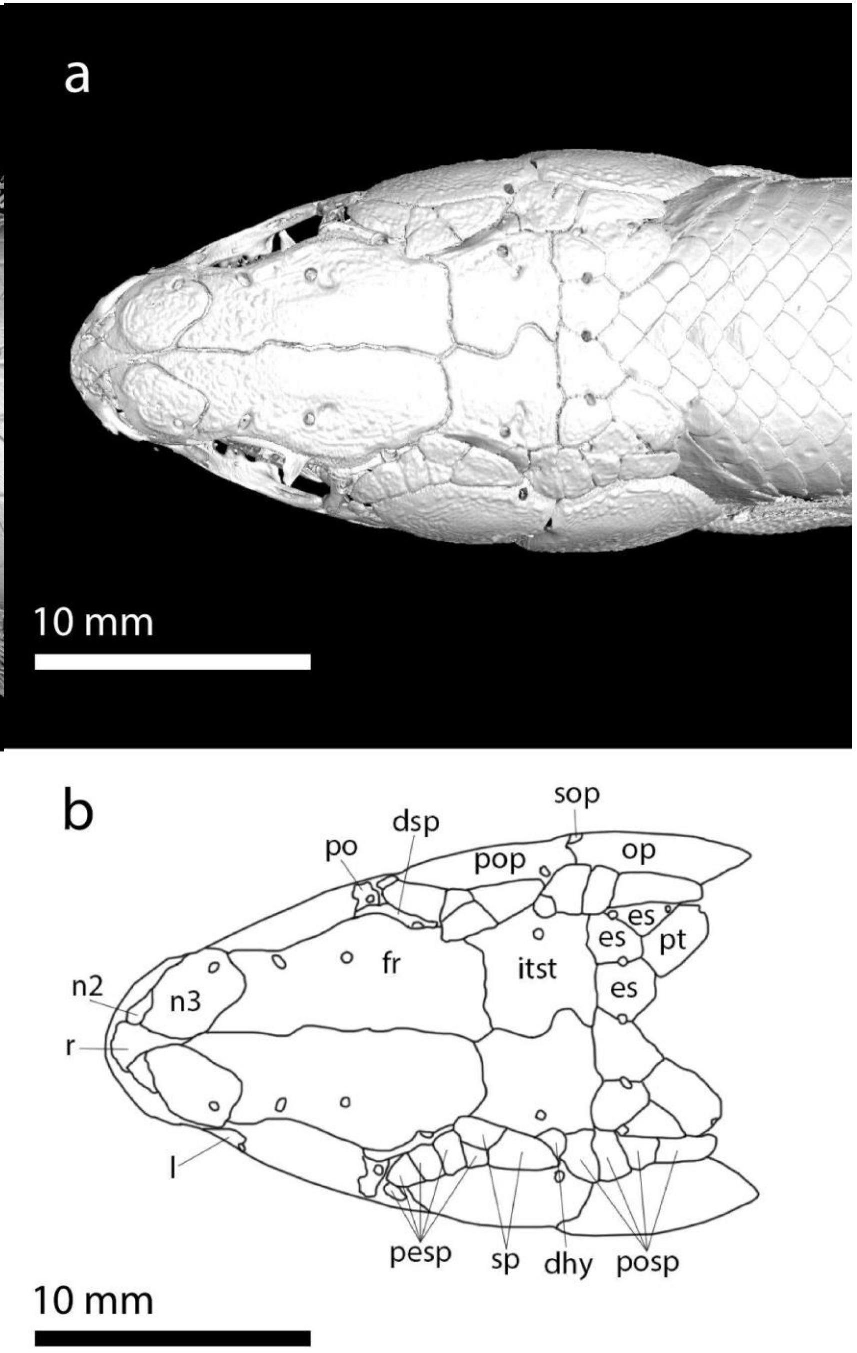
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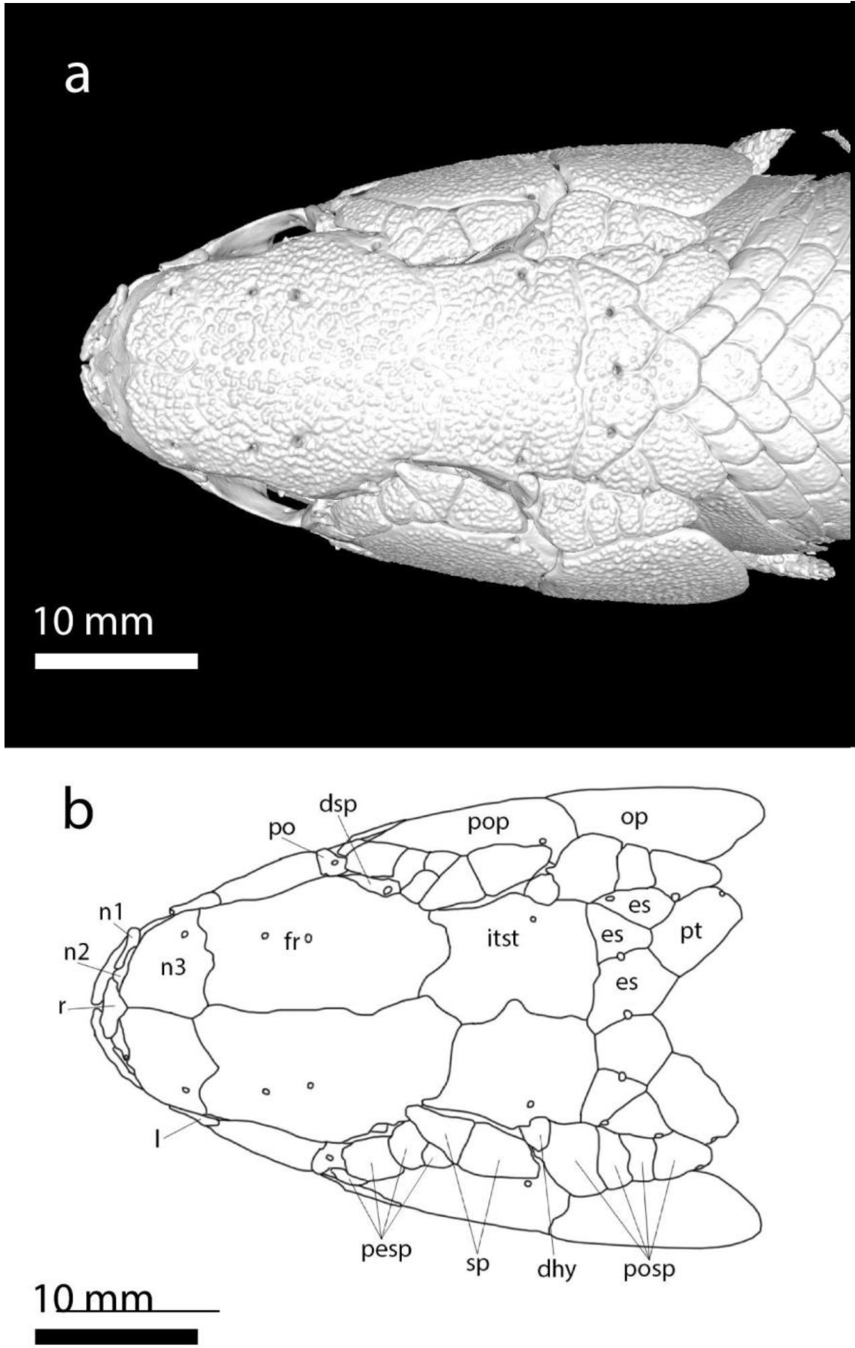
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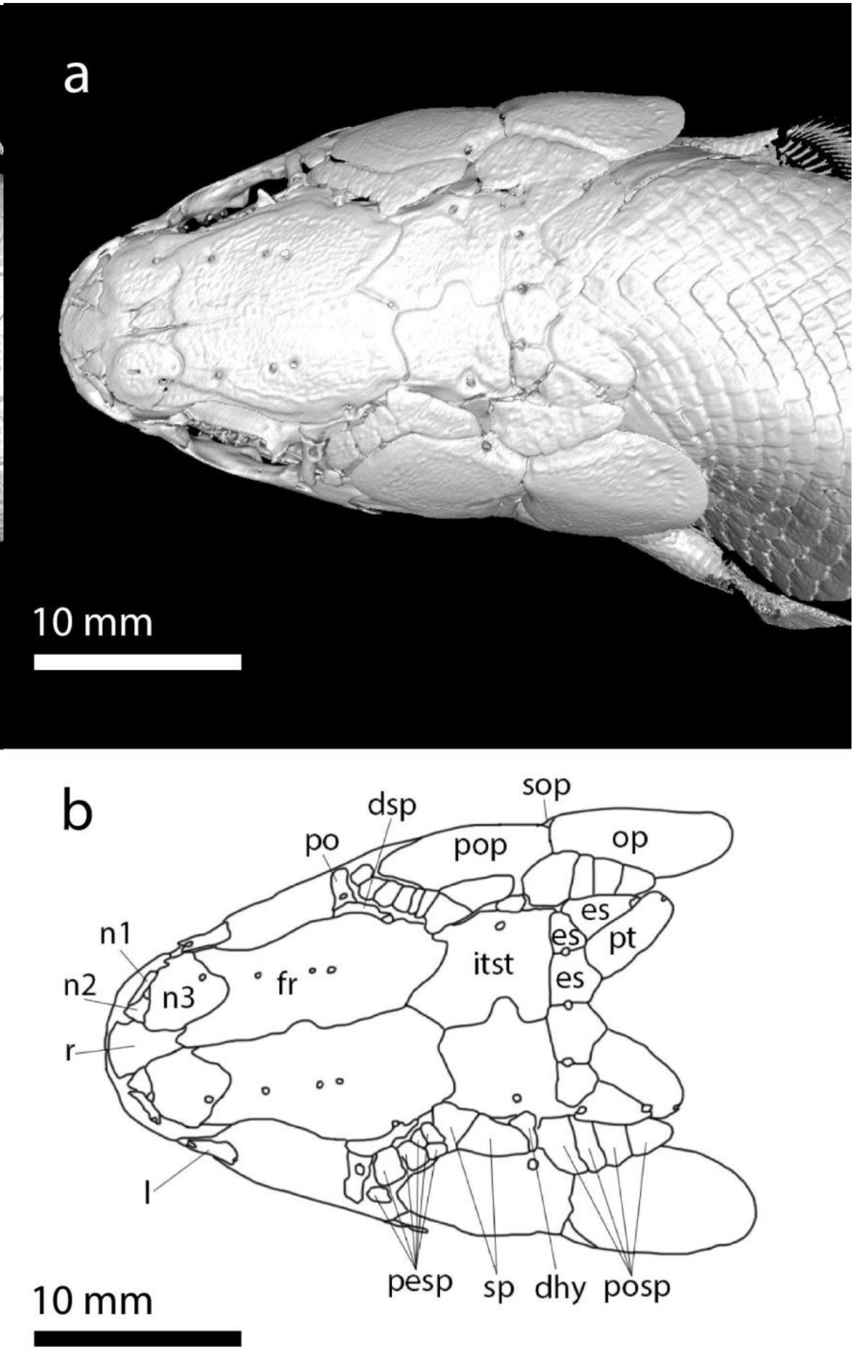
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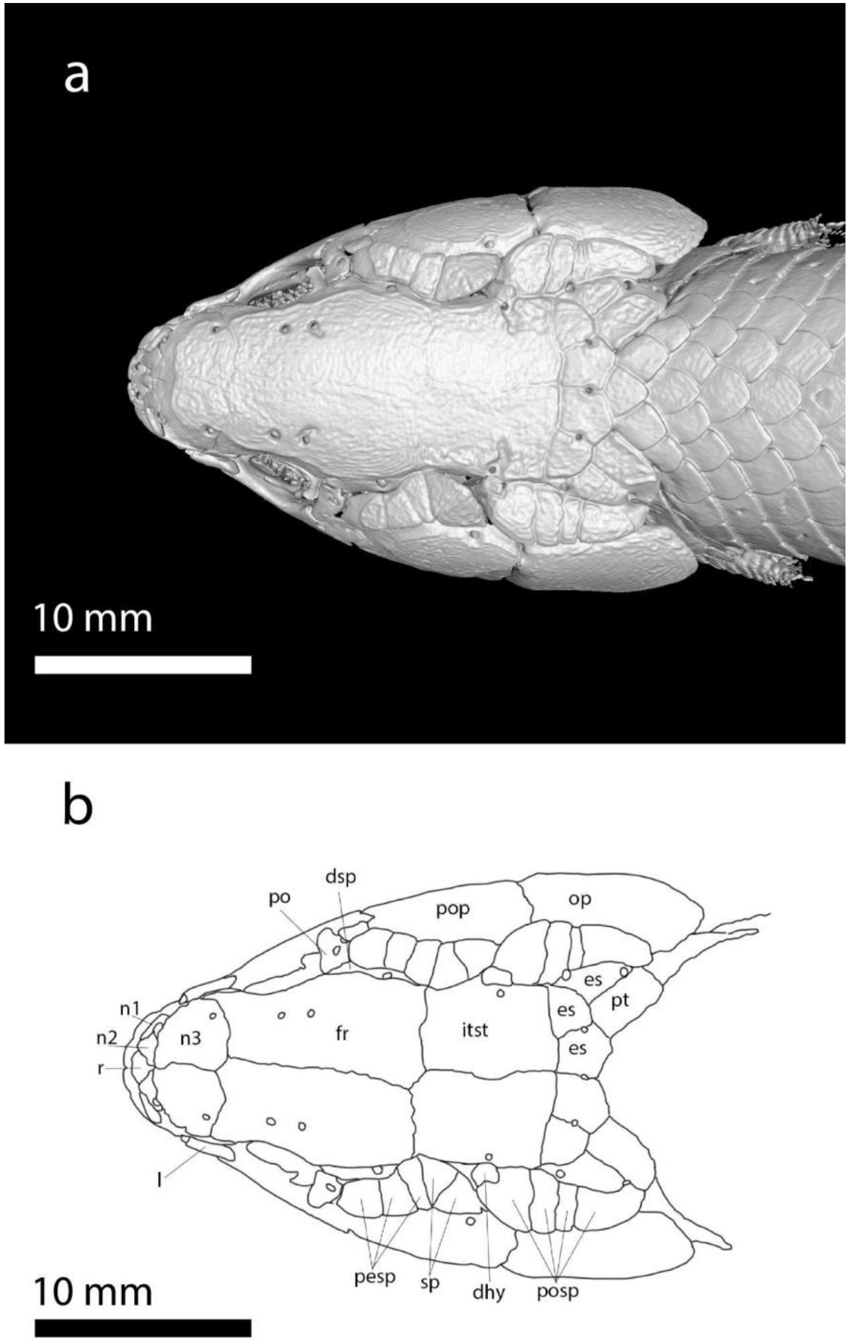
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Figure 11- 3D model (a) and drawing (b) of the dorsal view of the head of *P. bichir* (MNHN-IC-1907-0250). Abbreviations on page 37. Scale = 10mm.

Figure 12- 3D model (a) and drawing (b) of the dorsal view of the head of *P. delhezi* (MNHN-IC-2003-0614). Abbreviations on page 37. Scale = 10mm.

Figure 13- 3D model (a) and drawing (b) of the dorsal view of the head of *P. endlicherii* (MNHN-IC-2001-2180). Abbreviations on page 37. Scale = 10mm.

Figure 14- 3D model (a) and drawing (b) of the dorsal view of the head of *P. ornatipinnis* (MNHN-IC-1977-0307). Abbreviations on page 37. Scale = 10mm.

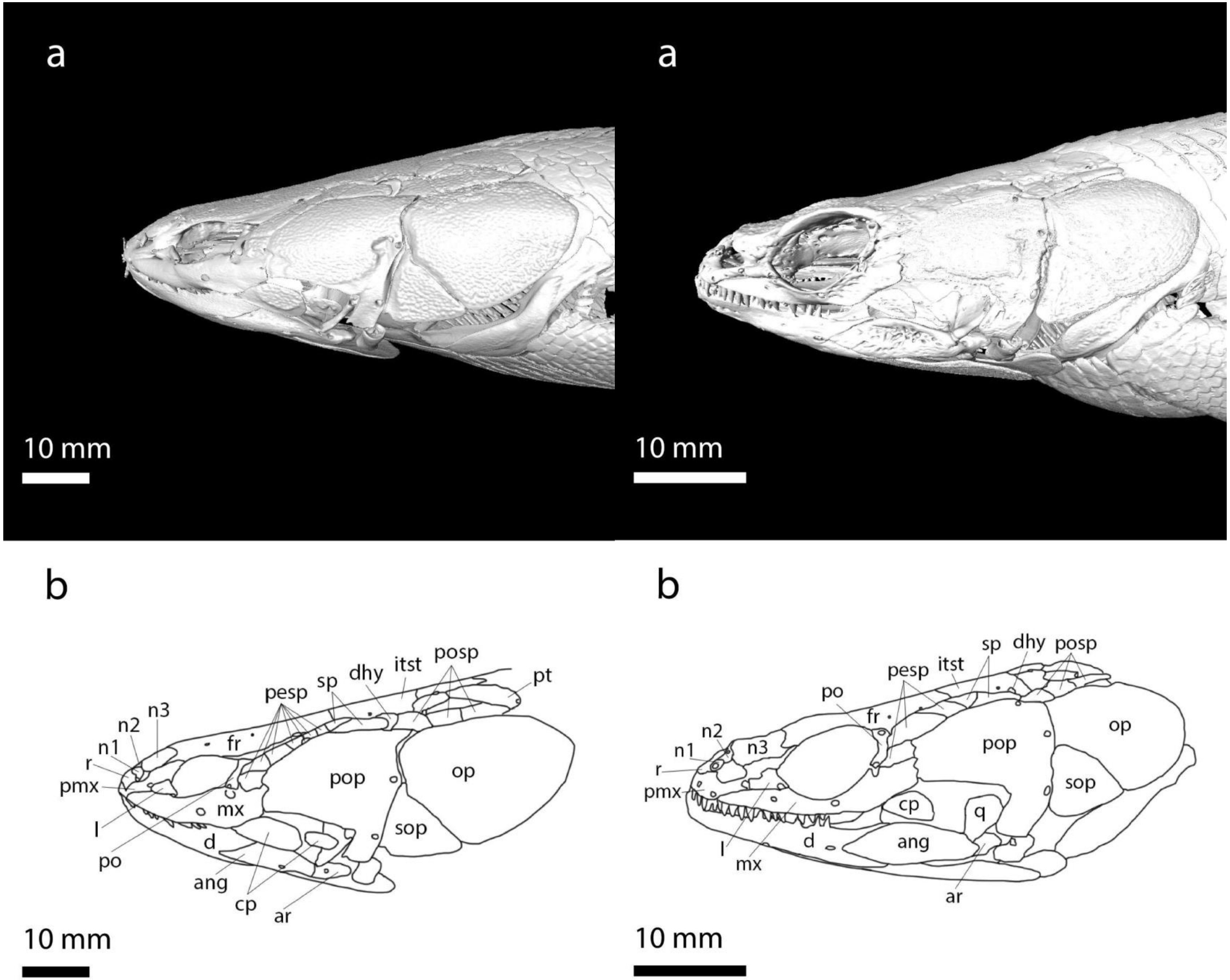
Figure 15- 3D model (a) and drawing (b) of the dorsal view of the head of *P. palmas* (MNHN-IC-1958-0026). Abbreviations on page 37. Scale = 10mm.

Figure 16- 3D model (a) and drawing (b) of the dorsal view of the head of *P. polli* (MNHN-IC-1900-0197). Abbreviations on page 37. Scale = 10mm.

Figure 17- 3D model (a) and drawing (b) of the dorsal view of the head of *P. retropinnis* (MNHN-IC-1963-0239). Abbreviations on page 37. Scale = 10mm.

Figure 18- 3D model (a) and drawing (b) of the dorsal view of the head of *P. weeksii* (MNHN-IC-1962-0334). Abbreviations on page 37. Scale = 10mm.

Figure 19- 3D model (a) and drawing (b) of the dorsal view of the head of *E. calabaricus* (MNHN-IC-1978-0732). Abbreviations on page 37. Scale = 10mm.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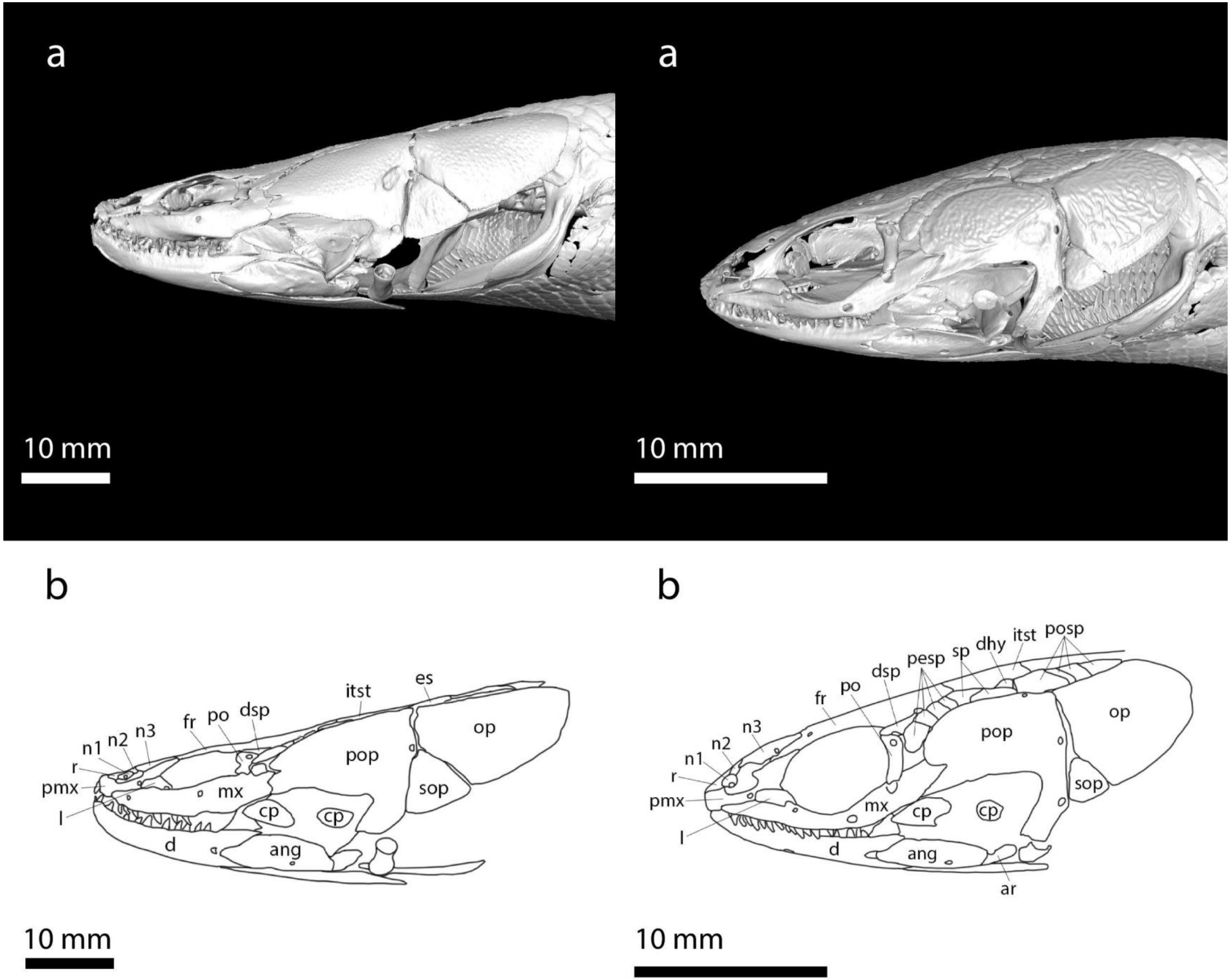
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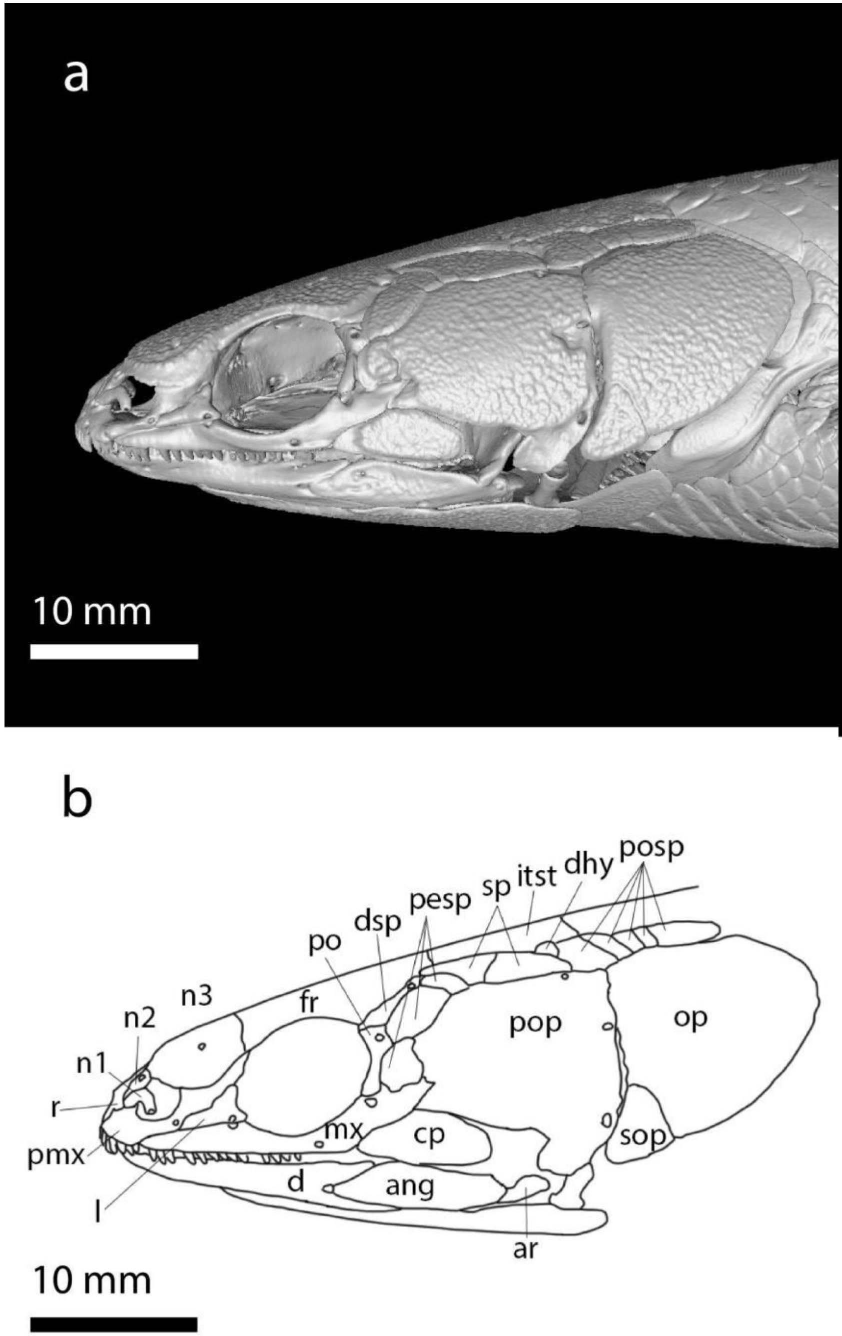
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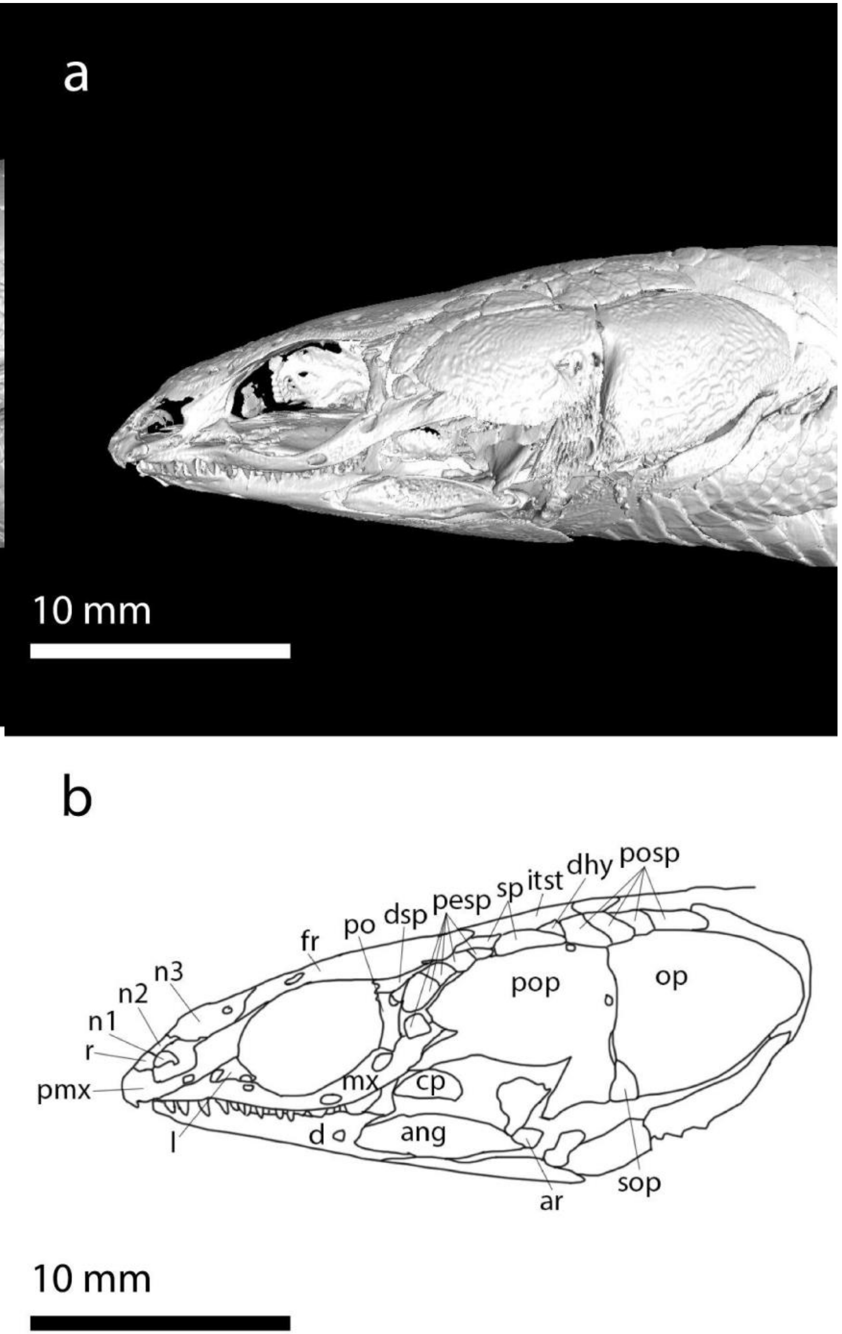
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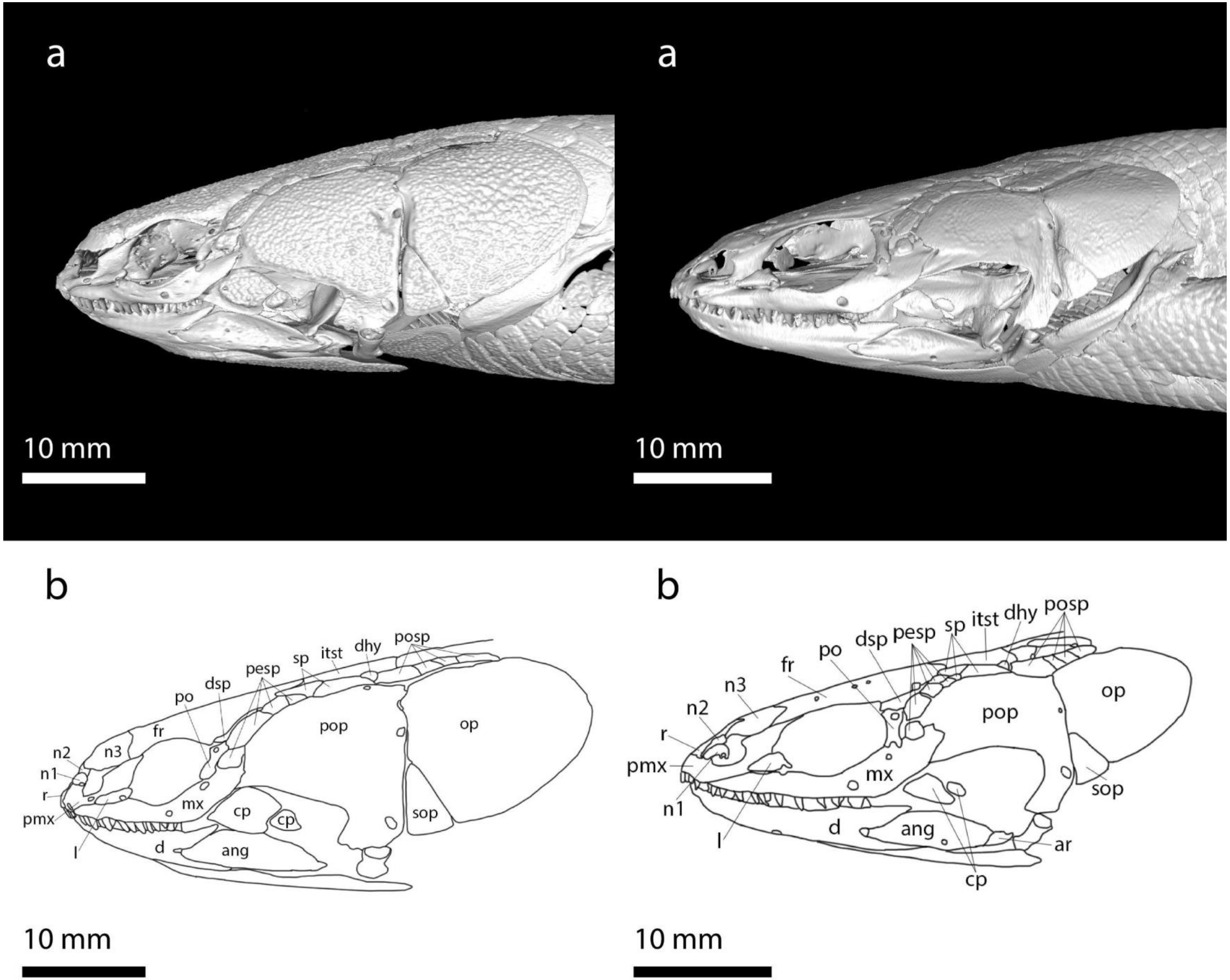
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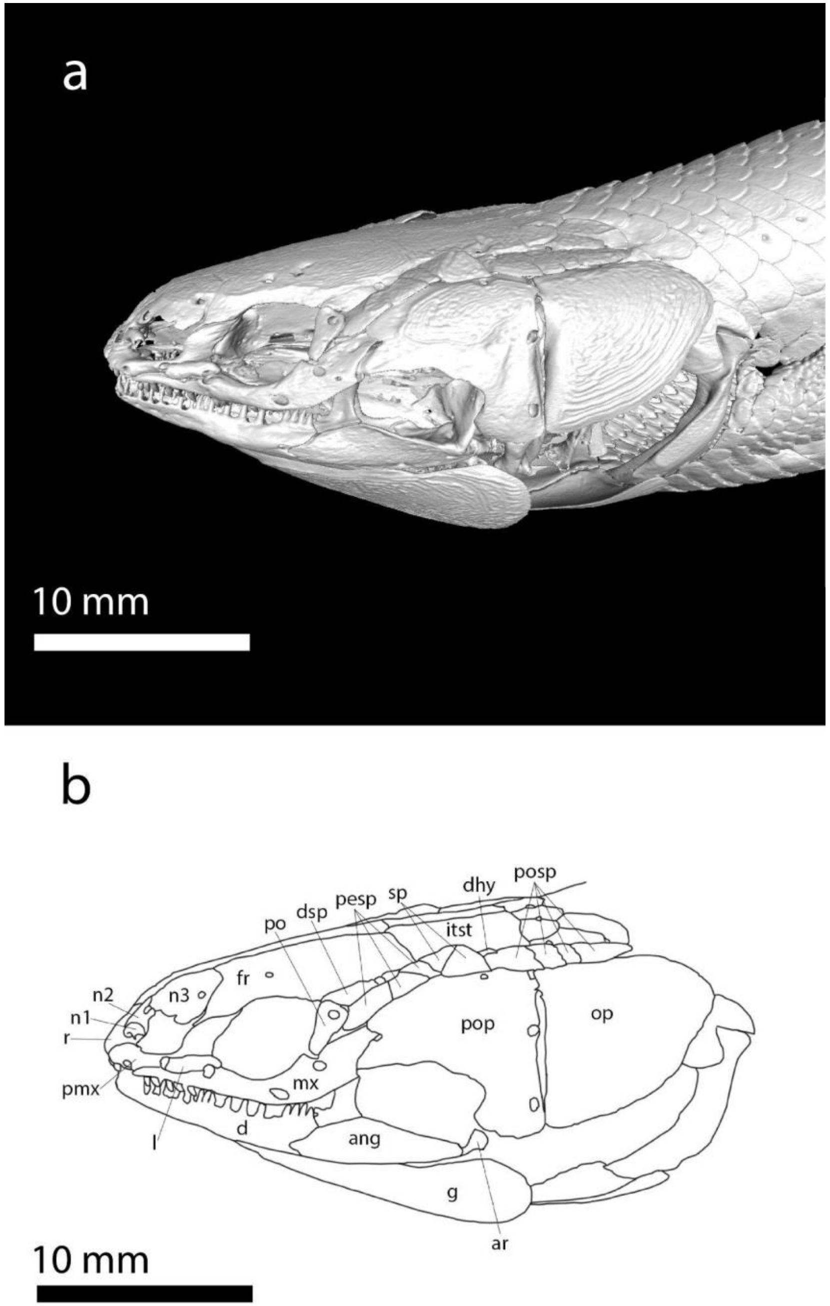
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Figure 20- 3D model (a) and drawing (b) of the lateral left view of the head of *P. bichir* (MNHN-IC-1907-0250). Abbreviations on page 37. Scale = 10mm.

Figure 21- 3D model (a) and drawing (b) of the lateral left view of the head of *P. delhezi* (MNHN-IC-2003-0614). Abbreviations on page 37. Scale = 10mm.

Figure 22- 3D model (a) and drawing (b) of the lateral left view of the head of *P. endlicherii* (MNHN-IC-2001-2180). Abbreviations on page 37. Scale = 10mm.

Figure 23- 3D model (a) and drawing (b) of the lateral left view of the head of *P. ornatipinnis* (MNHN-IC-1977-0307). Abbreviations on page 37. Scale = 10mm.

Figure 24- 3D model (a) and drawing (b) of the lateral left view of the head of *P. palmas* (MNHN-IC-1958-0026). Abbreviations on page 37. Scale = 10mm.

Figure 25- 3D model (a) and drawing (b) of the lateral left view of the head of *P. polli* (MNHN-IC-1900-0197). Abbreviations on page 37. Scale = 10mm.

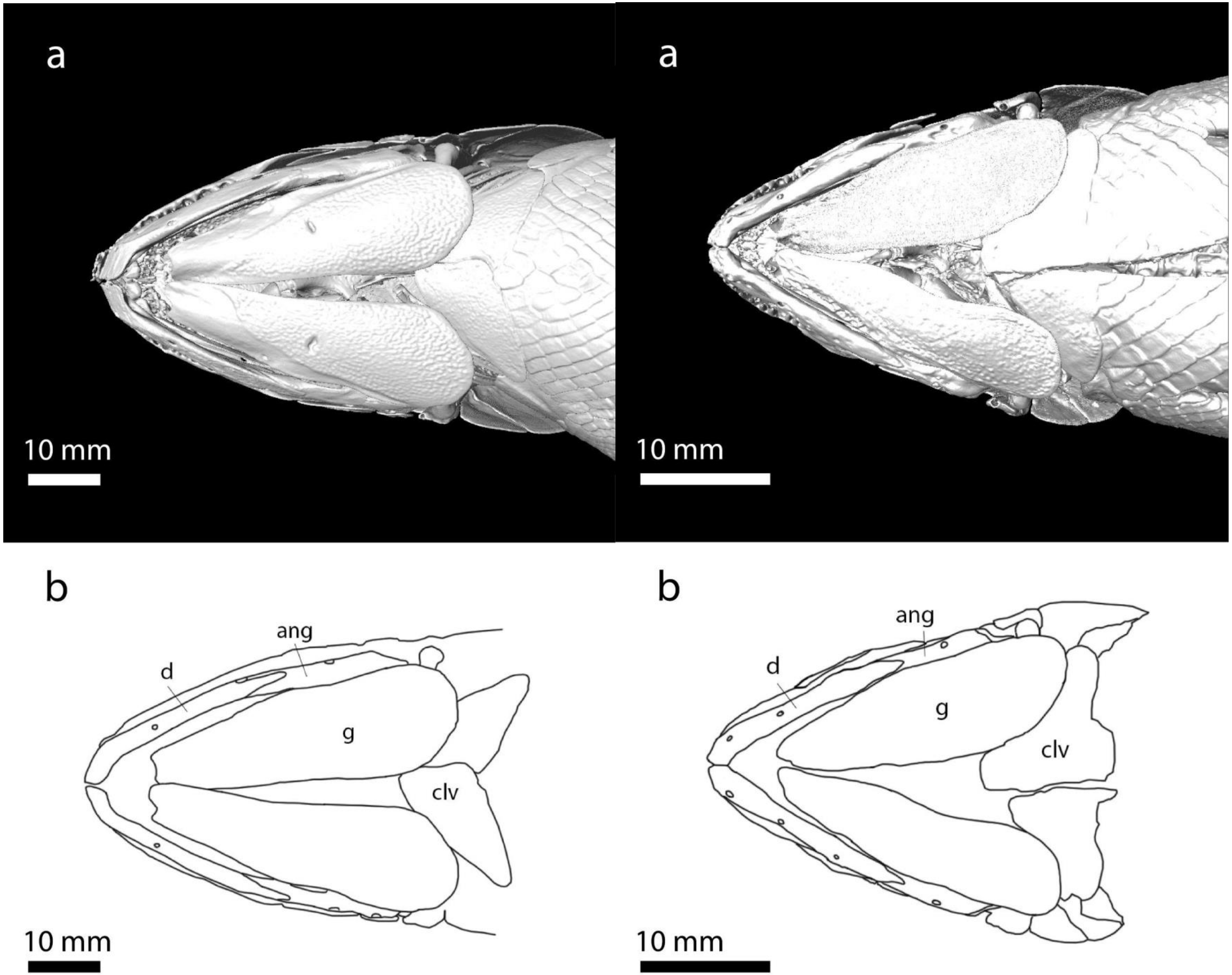
Figure 26- 3D model (a) and drawing (b) of the lateral left view of the head of *P. retropinnis* (MNHN-IC-1963-0239). Abbreviations on page 37. Scale = 10mm.

Figure 27- 3D model (a) and drawing (b) of the lateral left view of the head of *P. weeksii* (MNHN-IC-1962-0334). Abbreviations on page 37. Scale = 10mm.

Figure 28- 3D model (a) and drawing (b) of the lateral left view of the head of *E. calabaricus* (MNHN-IC-1978-0732). Abbreviations on page 37. Scale = 10mm.

The premaxilla in *P. delhezi*, *P. ornatipinnis*, *P. palmas*, *P. retropinnis*, *P. weeksii* and *E. calabaricus* (Figs. 21, 23, 24, 26, 27, 28) are similar to the premaxilla observed in *P. senegalus*. *P. bichir* and *P. endlicherii* (Figs. 20, 22) present a premaxilla that is shorter antero-posteriorly. *P. polli* (Fig. 25) presents a premaxilla with its posterior portion proportionally larger than in the other species. The maxilla of *P. senegalus* is similar to the ones of *P. delhezi*, *P. ornatipinnis*, *P. palmas*, *P. polli*, *P. retropinnis*, *P. weeksii* and *E. calabaricus* (Figs. 21, 23, 24, 25, 26, 27, 28). *P. weeksii* also may present a maxilla with a thicker posterior portion. *P. bichir* and *P. endlicherii* (Figs. 20, 22) present a shorter (antero-posteriorly) and thicker (ventral-dorsally) maxilla than the other species. Three shapes were observed for the lacrimal of *P. senegalus*: L-shaped, subtriangular and subrectangular. *P. bichir*, *P. endlicherii* and *P. polli* (Figs. 20, 22, 25) present the lacrimal in a subtriangular shape (Allis (1922) shows the same for *P. bichir*). *P. delhezi* (Fig. 21) shows both subrectangular or "L" shaped. *P. ornatipinnis*, *P. retropinnis* and *E. calabaricus* (Figs. 23, 26, 28) present a subrectangular lacrimal. *P. palmas* (Fig. 24) a subtriangular or "L" shaped bone. And *P. weeksii* (Fig. 27) has the same bone subtriangular or subrectangular. As observed here, the cheek plates of the species present in this study follow some pattern, where the first cheek plate is always bigger than the following ones. Also it is difficult to distinguish the shapes between triangular or trapezoidal due to the usually rounded edges of the bones. *P. delhezi*, *P. endlicherii, P. palmas*, *P. polli*, *P. retropinnis* and *P. weeksii* (Figs. 21, 22, 24, 25, 26, 27) may present just one trapezoidal (or triangular) cheek plate. Additionally, the bone of *P. palmas* and *P. retropinnis* (Figs. 24, 26) is bigger compared with the same bone of the other species. *P. bichir*, *P. ornatipinnis*, *P. retropinnis* and *P. weeksii* (Figs. 20, 23, 26, 27) may present the first plate bigger and trapezoidal (or triangular) and the second smaller and rounded. *P. endlicherii* and *P. retropinnis* (Figs. 22, 26) may present the first plate trapezoidal (or triangular) and the second subrectangular. These bones in *P. retropinnis* are relatively bigger than the ones in *P. endlicherii*. *P. ornatipinnis* also may present the first and second bones trapezoidal (or triangular), a third rounded bone and sometimes even a fourth rounded cheek plate. These bones are absent in *E. calabaricus* (Fig. 28).

The angular of *P. bichir*, *P. delhezi*, *P. endlicherii*, *P. retropinnis*, *P. weeksii* and *E. calabaricus* (Figs. 20, 21, 22, 26, 27, 28) are the same as in *P. senegalus*. *P. ornatipinnis*, *P. palmas* and *P. polli* (Figs. 23, 24, 25) present a subrectangular, comparatively lower angular. All polypteridae species present in this study presented the following jaw bones with the same shape and relative position as observed in *P. senegalus*: dentary, mentomeckelian, coronoid 1 and 2, articular and prearticular (same in Allis, 1922; Jollie, 1984;Claeson, Bemis & Hagadorn, 2007; Grande, 2010.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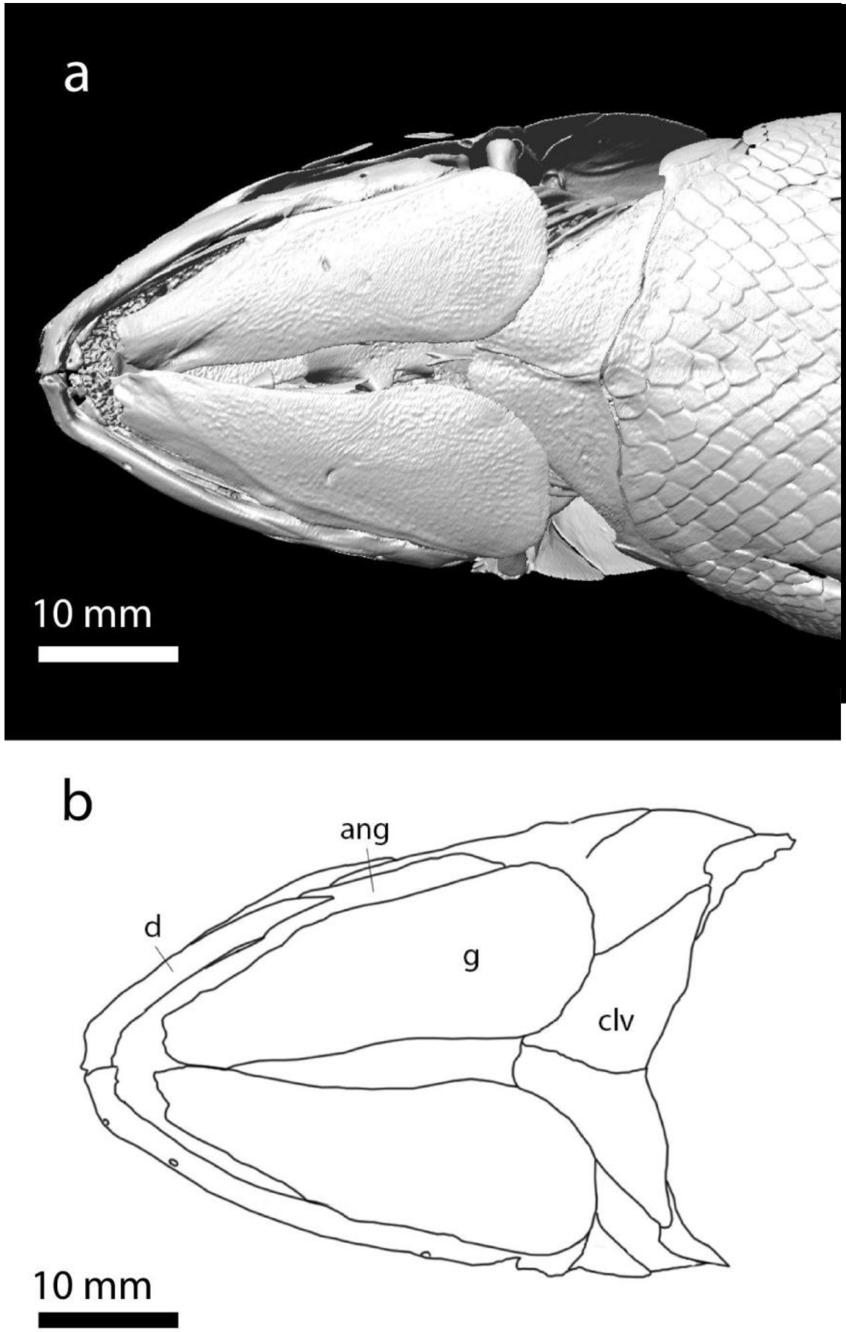
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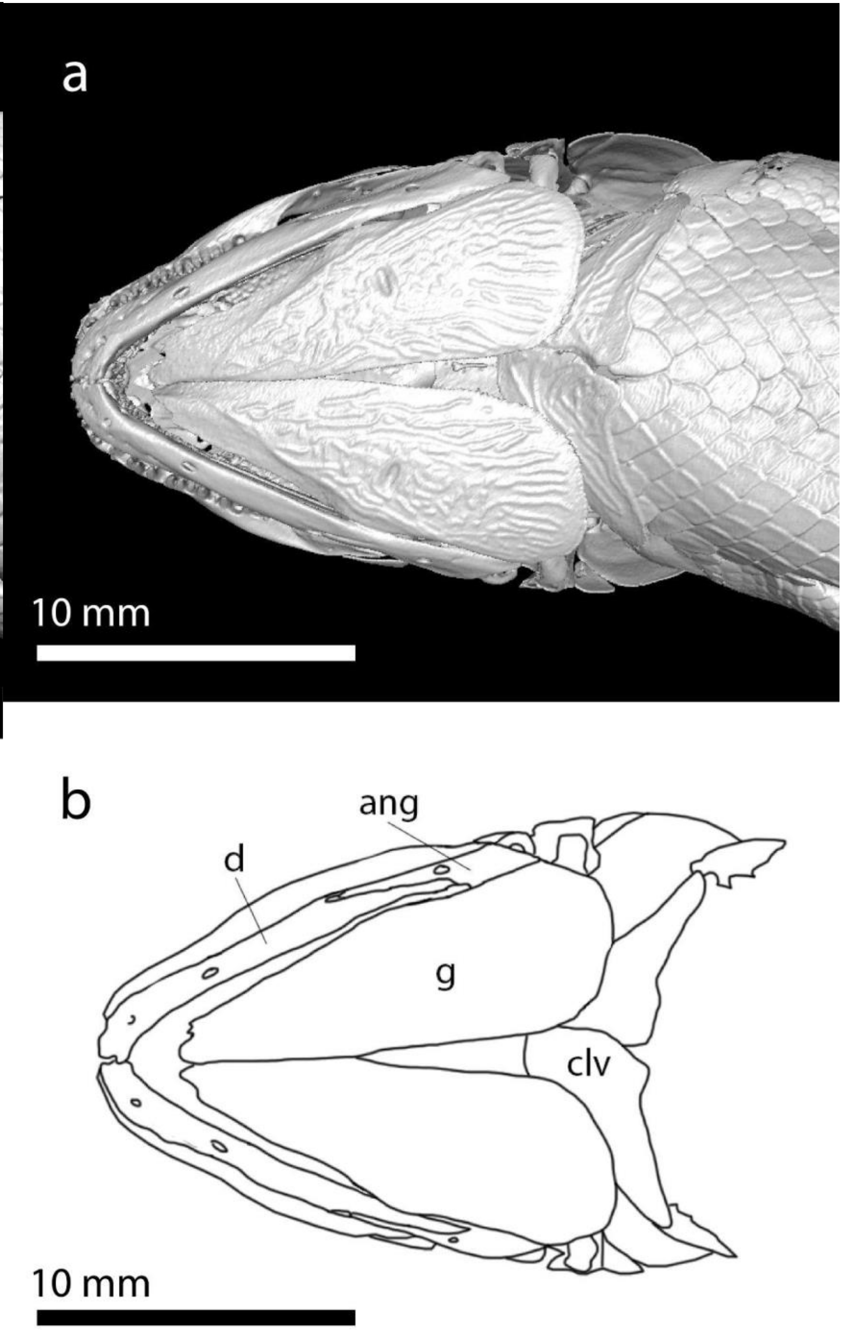
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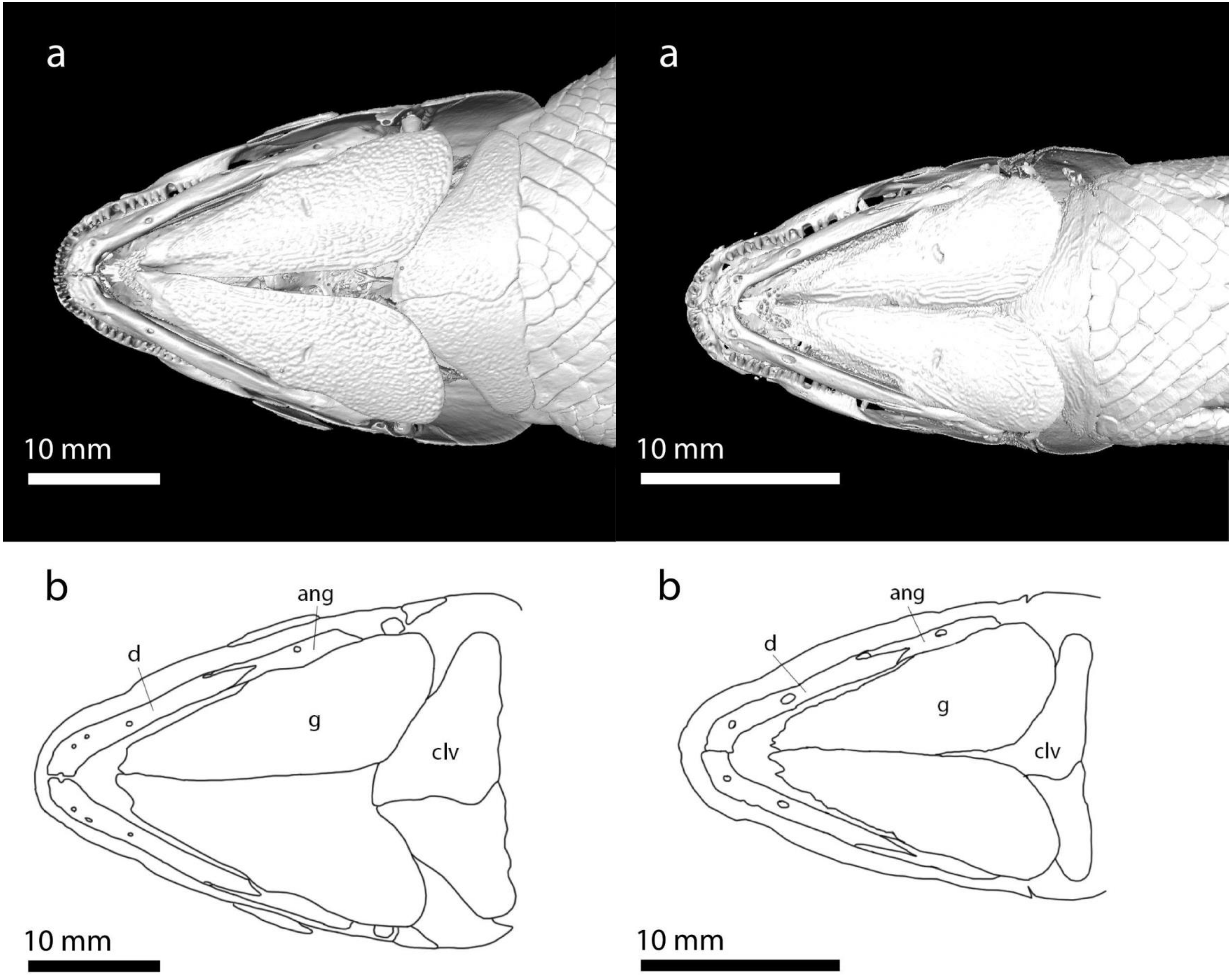
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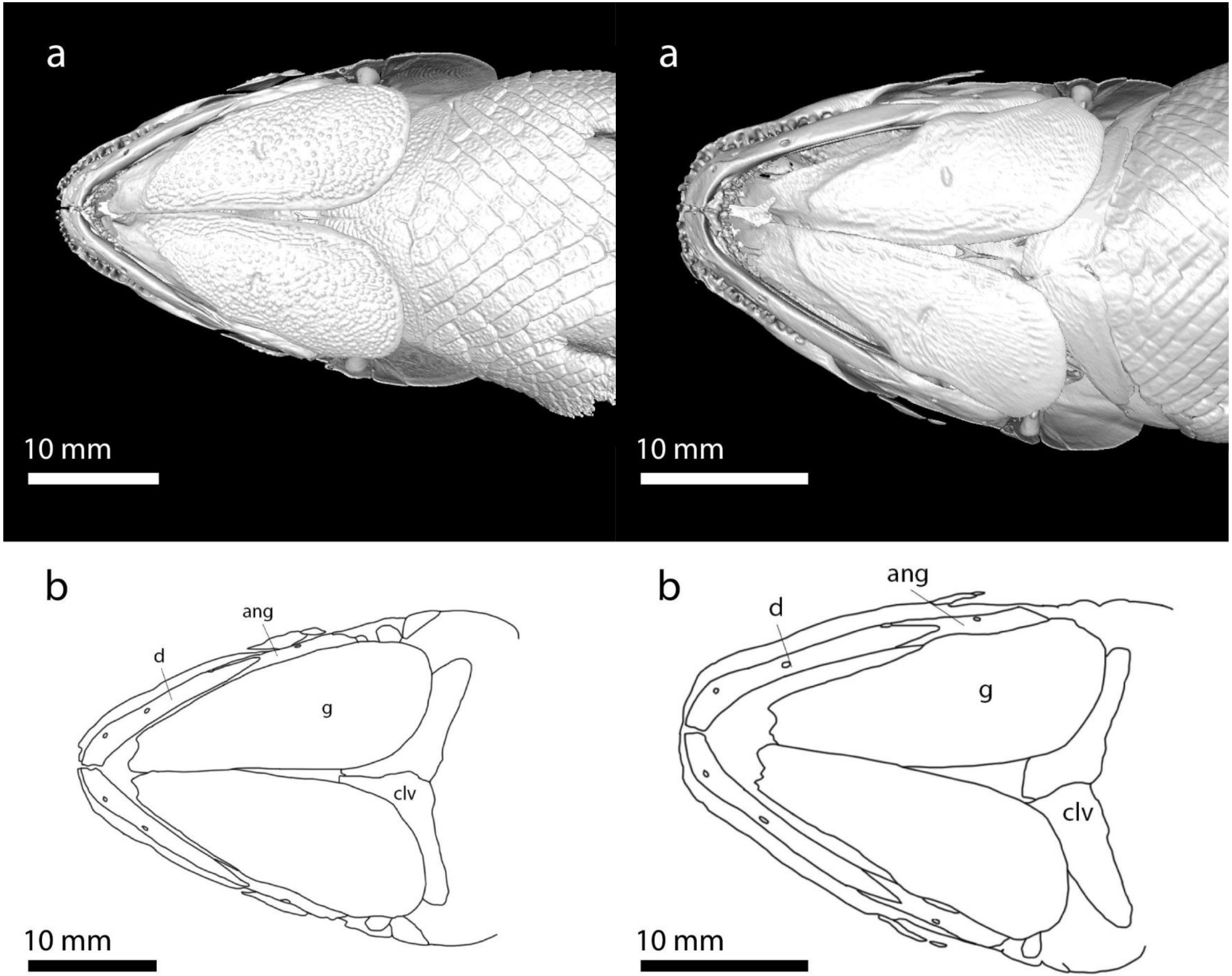
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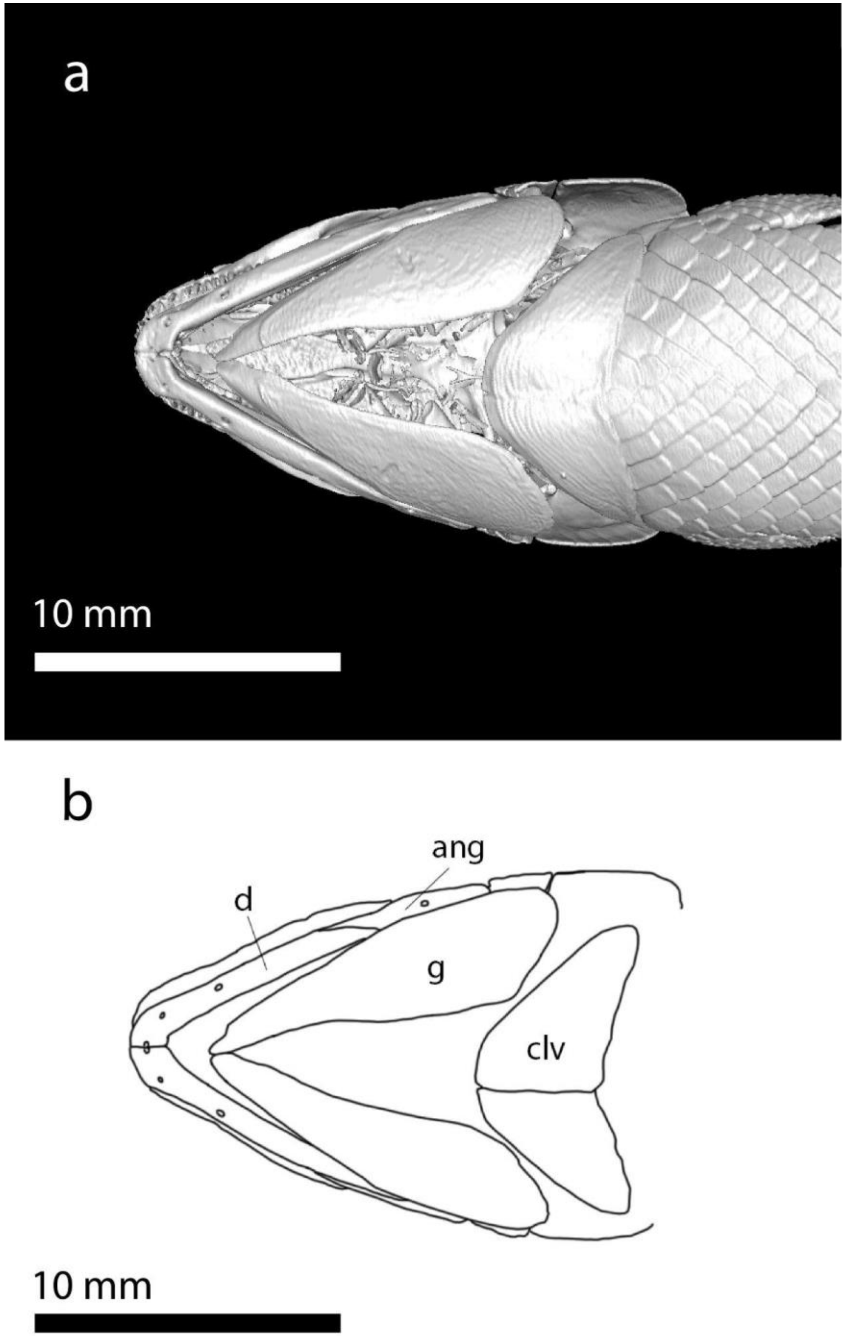
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Figure 29- 3D model (a) and drawing (b) of the ventral view of the head of *P. bichir* (MNHN-IC-1907-0250). Abbreviations on page 37. Scale = 10mm.

Figure 30- 3D model (a) and drawing (b) of the ventral view of the head of *P. delhezi* (MNHN-IC-2003-0614). Abbreviations on page 37. Scale = 10mm.

Figure 31- 3D model (a) and drawing (b) of the ventral view of the head of *P. endlicherii* (MNHN-IC-2001-2180). Abbreviations on page 37. Scale = 10mm.

Figure 32- 3D model (a) and drawing (b) of the ventral view of the head of *P. ornatipinnis* (MNHN-IC-1977-0307). Abbreviations on page 37. Scale = 10mm.

Figure 33- 3D model (a) and drawing (b) of the ventral view of the head of *P. palmas* (MNHN-IC-1958-0026). Abbreviations on page 37. Scale = 10mm.

Figure 34- 3D model (a) and drawing (b) of the ventral view of the head of *P. polli* (MNHN-IC-1900-0197). Abbreviations on page 37. Scale = 10mm.

Figure 35- 3D model (a) and drawing (b) of the ventral view of the head of *P. retropinnis* (MNHN-IC-1963-0239). Abbreviations on page 37. Scale = 10mm.

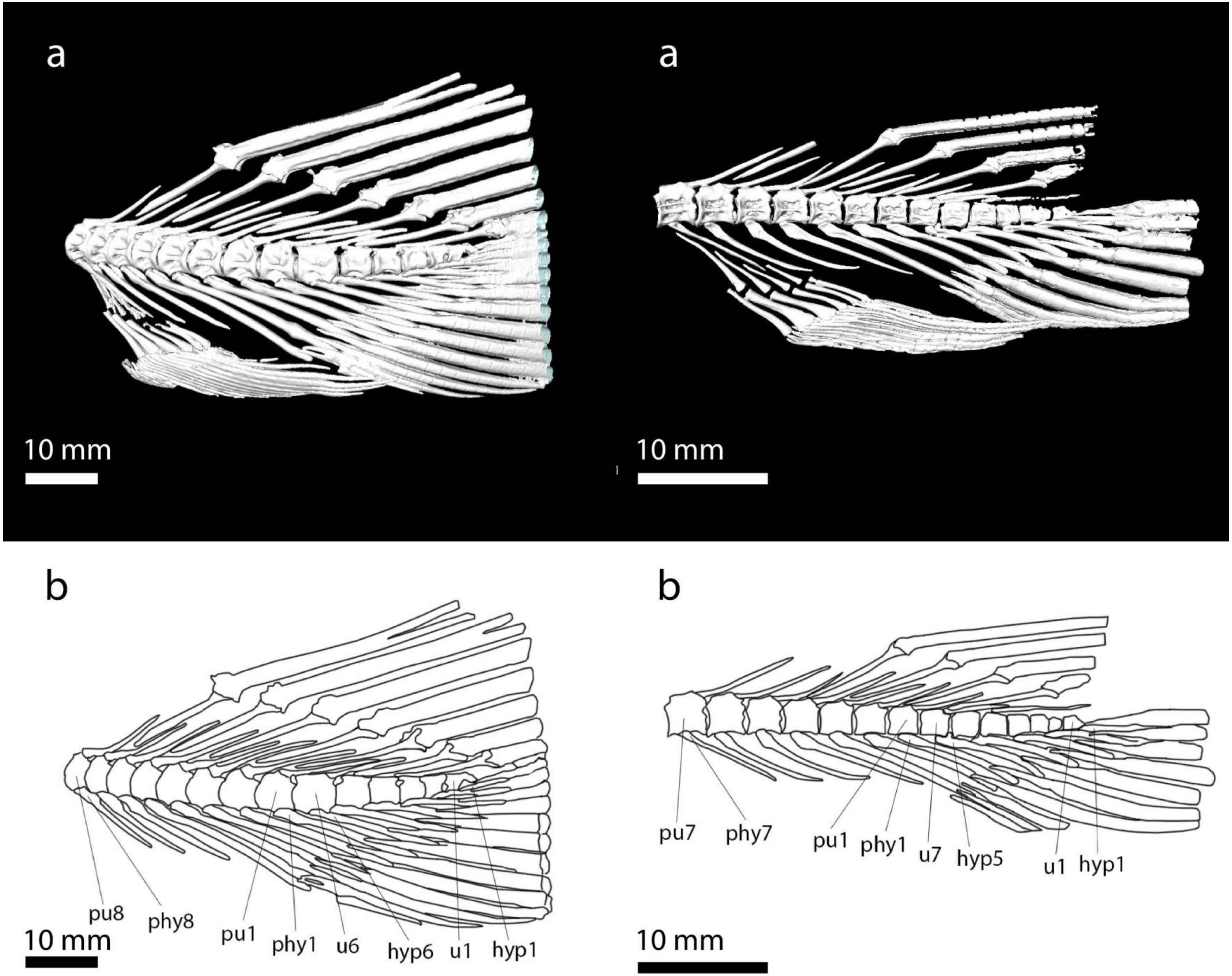
Figure 36- 3D model (a) and drawing (b) of the ventral view of the head of *P. weeksii* (MNHN-IC-1962-0334). Abbreviations on page 37. Scale = 10mm.

Figure 37- 3D model (a) and drawing (b) of the ventral view of the head of *E. calabaricus* (MNHN-IC-2008-2103). Abbreviations on page 37. Scale = 10mm.

The neurocranium of *P. bichir* and *P. endlicherii* are proportionally longer and lower than for the rest of the species studied here. This is clearly correlated with the shape of the respectives skulls, which are also longer and lower. Allis (1922) also noted this difference in the Polypteridae species. In the pictures of Allis (1922) it is possible to observe the lateral ethmoid divided in 2 or 3 bones, which contrasts with his own description, that states only one lateral ethmoid (same state as observed here).

All polypteridae species present in this study presented the same shape and relative position for the bones of the palate, hyoid arch, endocranium, branchial arches and pectoral fin as observed in *P. senegalus* (Figs. 6, 8, 9). With the exception that the anterior ceratohyal in *Polypterus* is more robust than the one in *Erpetoichthys* (Claeson, Bemis & Hagadorn, 2007). Our findings on the palate of *E. calabaricus* differs from the description given by Claeson, Bemis & Hagadorn (2007) on the parasphenoid and endopterygoid. We found the same morphology for these bones in comparison with *Polypterus*. However, Claeson, Bemis & Hagadorn (2007) described a wider parasphenoid neck for *Erpetoichthys* than in *Polypterus*, and a rectangular shape for the endopterygoid rather than the more triangular shape seen here. Our data are in accordance with those given by Traquair (1866), Goodrich (1909), Allis (1922), Jollie (1984), Geraudie (1988), Claeson, Bemis & Hagadorn (2007)(partially) and Grande (2010).

The caudal fin of each species studied here differentiates itself from the others on the number of its elements (e.g. ural centrum, hypural, preural centrum and parhypural)(Fig. 50). *Polypterus bichir* (Fig. 38) presents 6 ural centra and hypurals, and 8 preural centra and parhypurals. *Polypterus delhezi* (Fig. 39) 7 ural centra, 5 hypurals, and 7 preural centra and parhypurals. *Polypterus endlicherii* (Fig. 40) 3 ural centra, 4 hypurals, and 6 preural centra and parhypurals. *Polypterus ornatipinnis* (Fig. 41) 4 ural centra and 5 hypurals, and 6 preural centra and parhypurals. The *Polypterus ornatipinnis* studied by Grande (2010) presented 5 ural centra, and the one by Gemballa (2004) 4 hypurals. *Polypterus palmas* (Fig. 42) 5 ural centra and hypurals, and 5 preural centra and parhypurals. *Polypterus polli* (Fig. 43) 5 ural centra and 4 hypurals, and 6 preural centra and parhypurals. *Polypterus retropinnis* (Fig. 44) 7 ural centra, 6 hypurals, and 4 preural centra and parhypurals. *Polypterus weeksii* (Fig. 45) 6 or 5 ural centra and 5 hypurals, and 7 preural centra and parhypurals (same as *P. senegalus*). *Erpetoichthys calabaricus* (Fig. 46) 5 ural centra and hypurals, and 4 ural centra and parhypurals. Here, We found more variation in the caudal fin of *Polypterus* species than Bartsch & Gemballa (1992) and Gemballa (2004), that observed 4 or 5 ural centra and 3 or 4 hypurals.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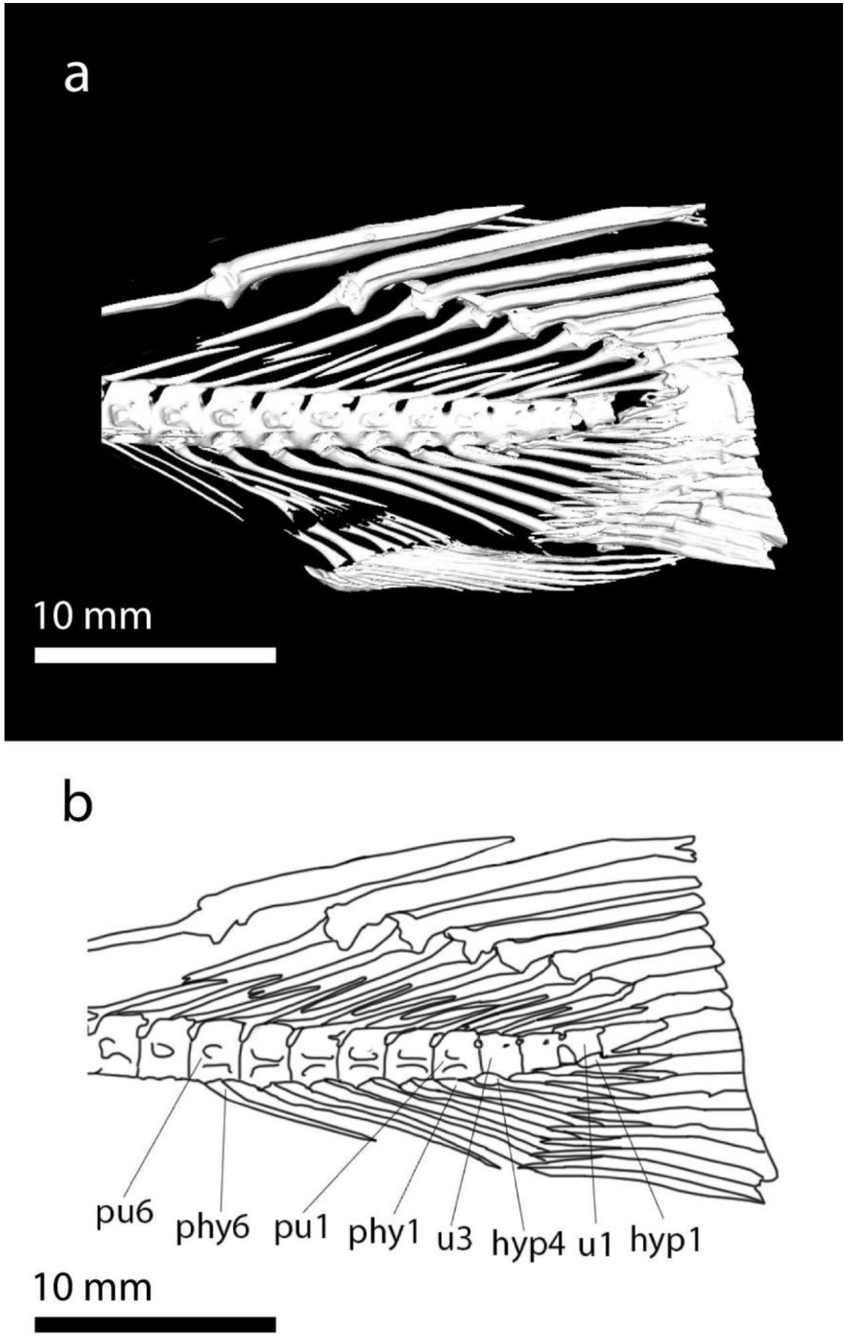
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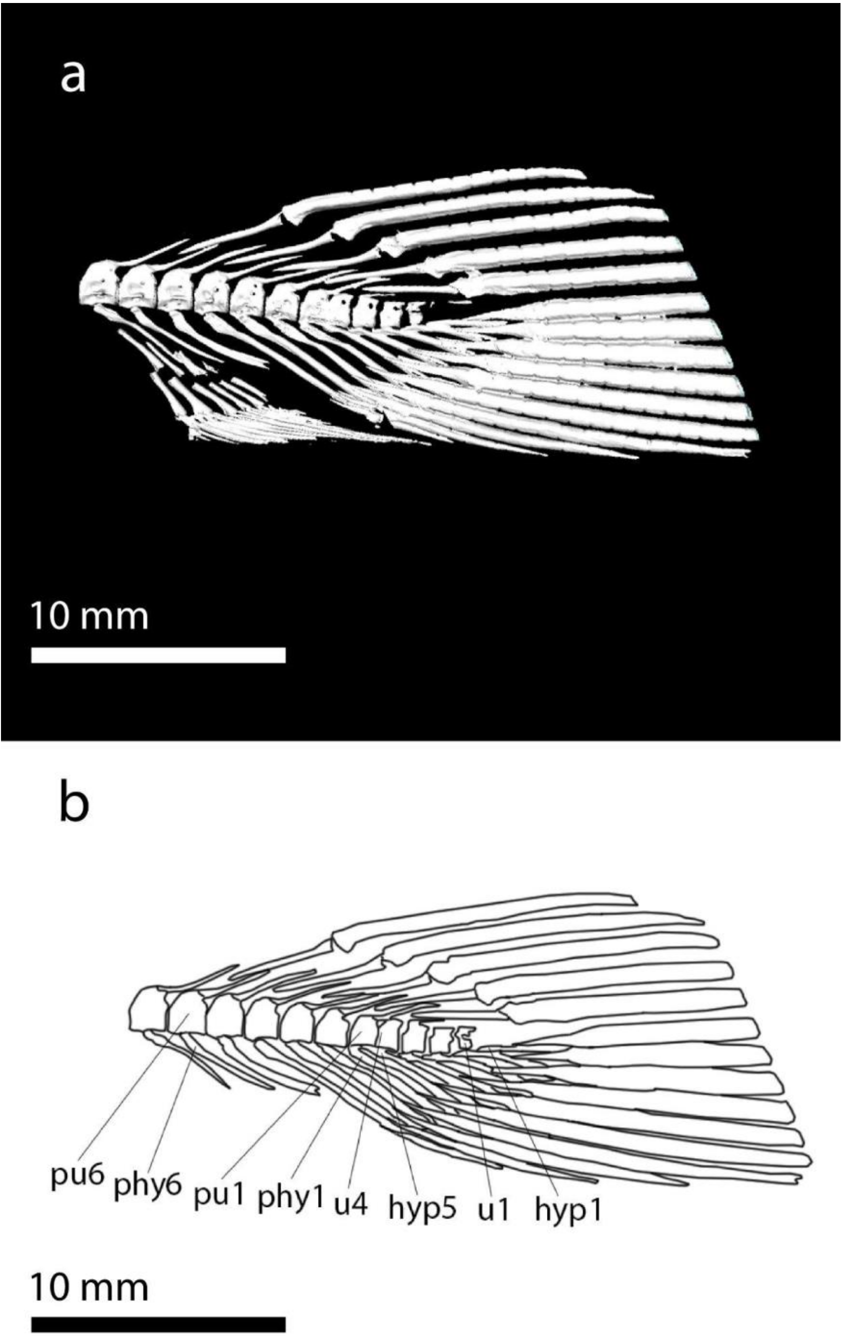
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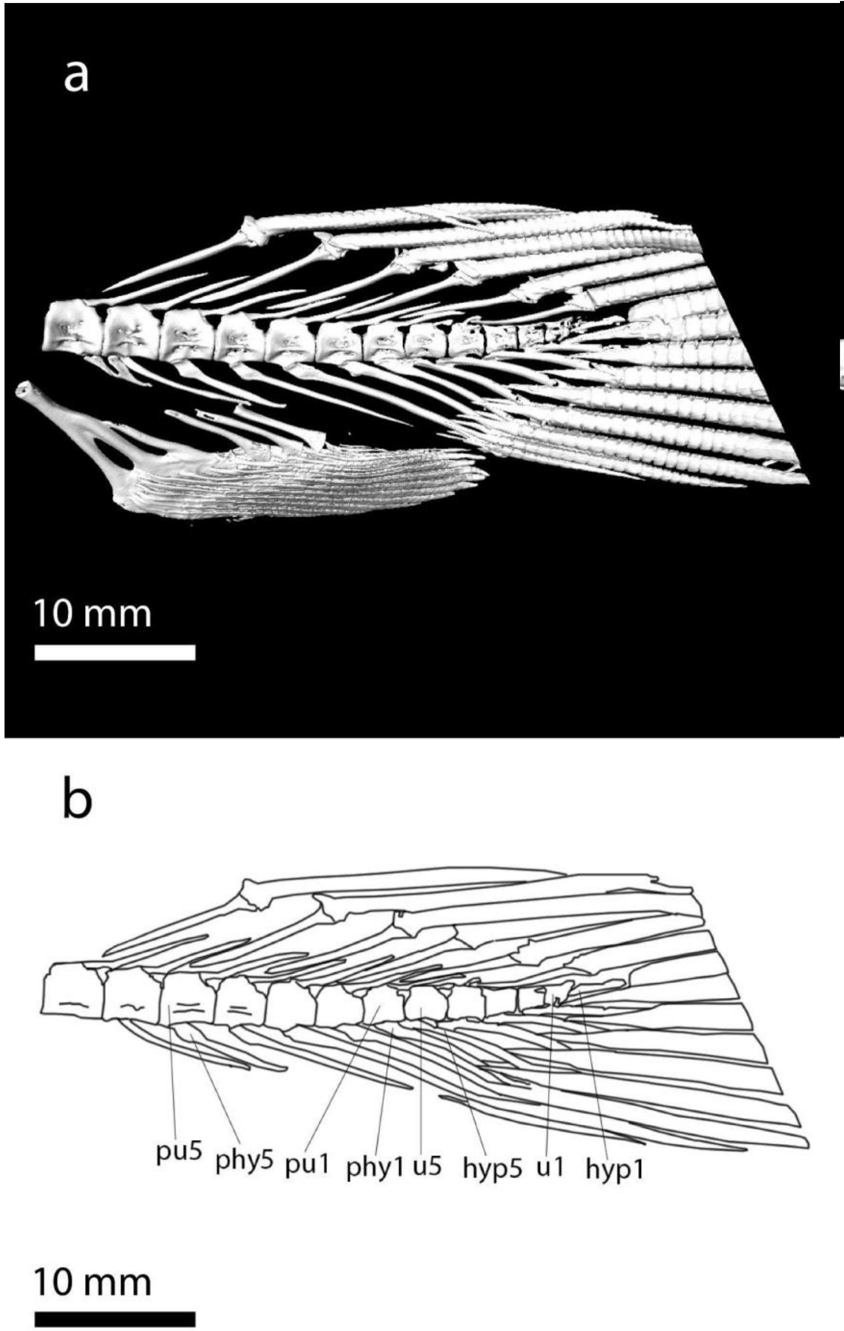
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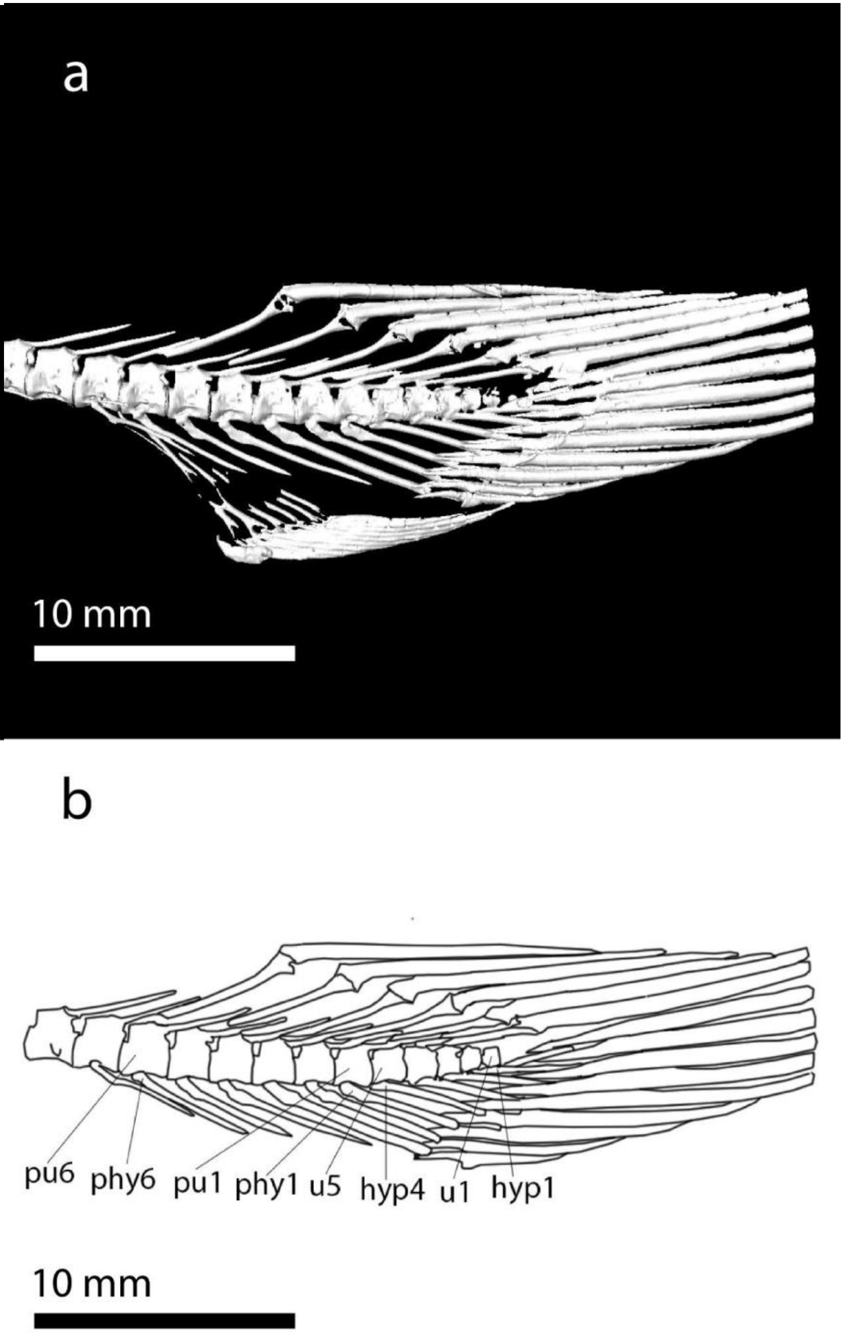
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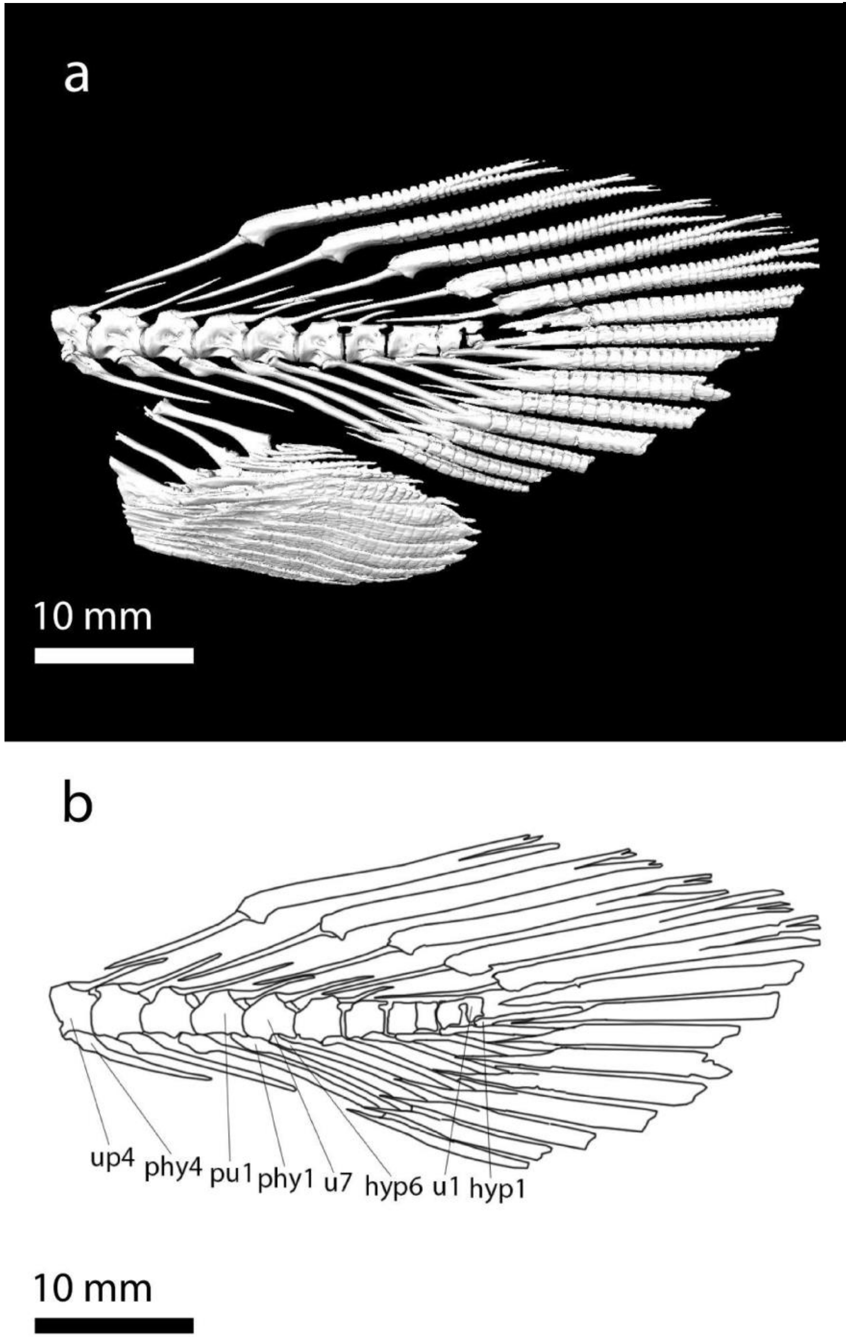
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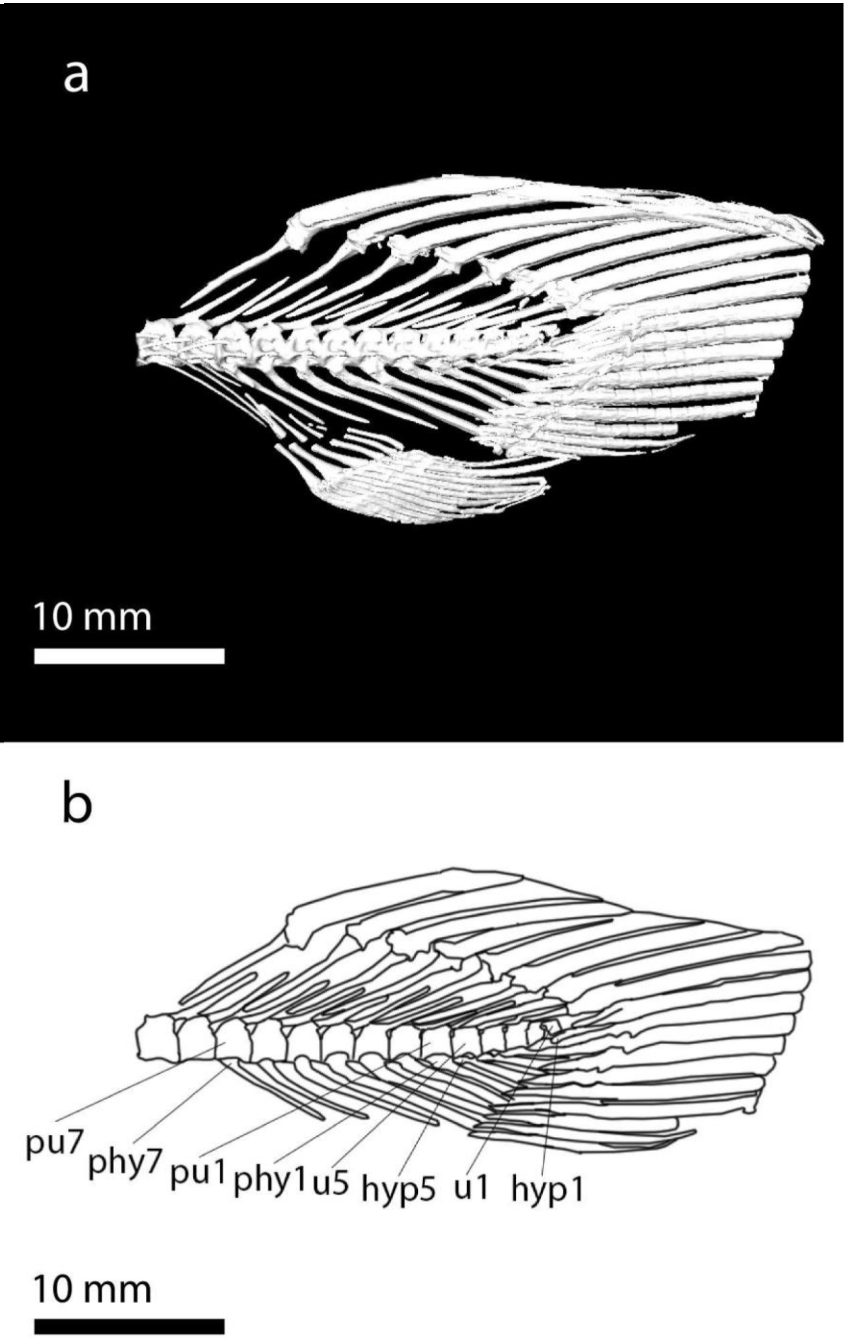
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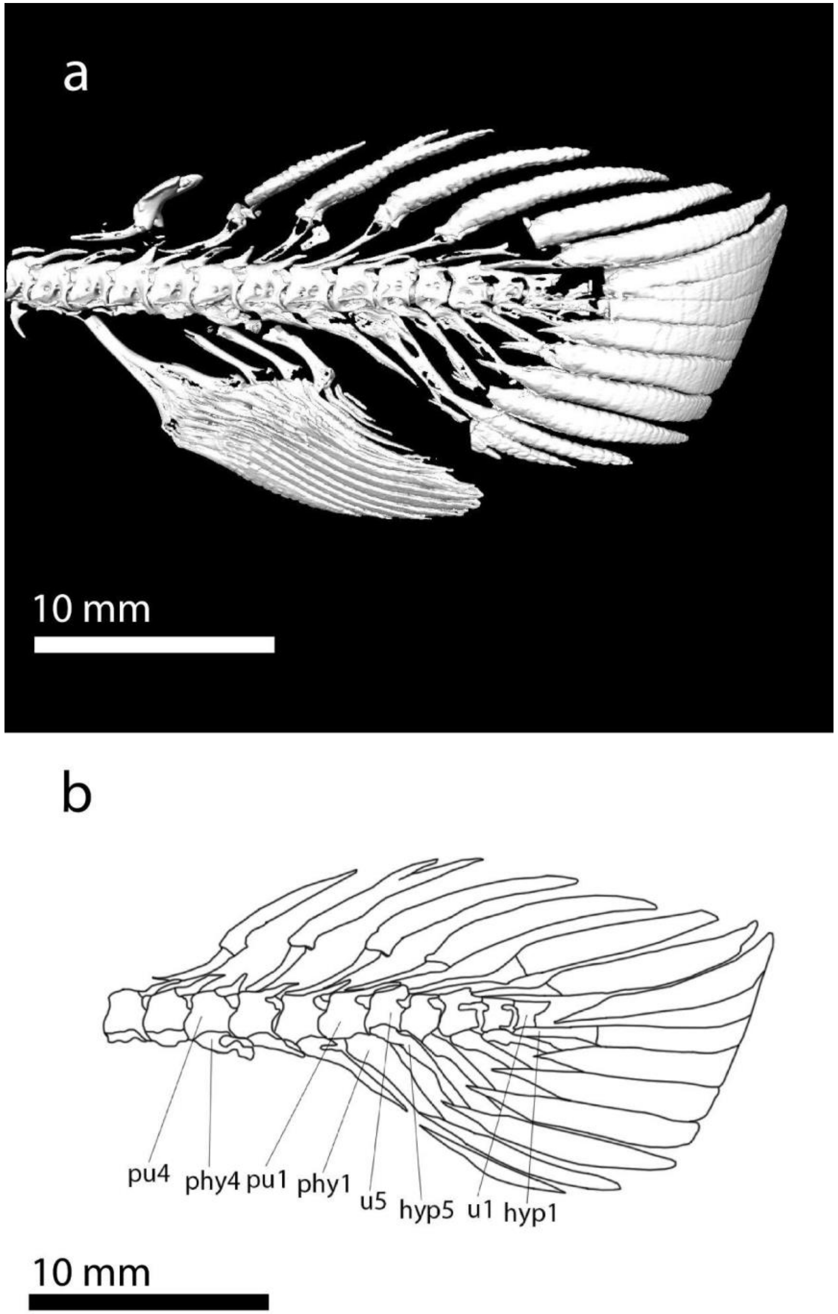
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Figure 38- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. bichir* (MNHN-IC-1907-0250). Abbreviations on page 37. Scale = 10mm.

Figure 39- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. delhezi* (MNHN-IC-2003-0614). Abbreviations on page 37. Scale = 10mm.

Figure 40- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. endlicherii* (MNHN-IC-B-0384). Abbreviations on page 37. Scale = 10mm.

Figure 41- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. ornatipinnis* (MNHN-IC-1977-0307). Abbreviations on page 37. Scale = 10mm.

Figure 42- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. palmas* (MNHN-IC-1958-0026). Abbreviations on page 37. Scale = 10mm.

Figure 43- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. polli* (MNHN-IC-1900-0197). Abbreviations on page 37. Scale = 10mm.

Figure 44- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. retropinnis* (MNHN-IC-1963-0239). Abbreviations on page 37. Scale = 10mm.

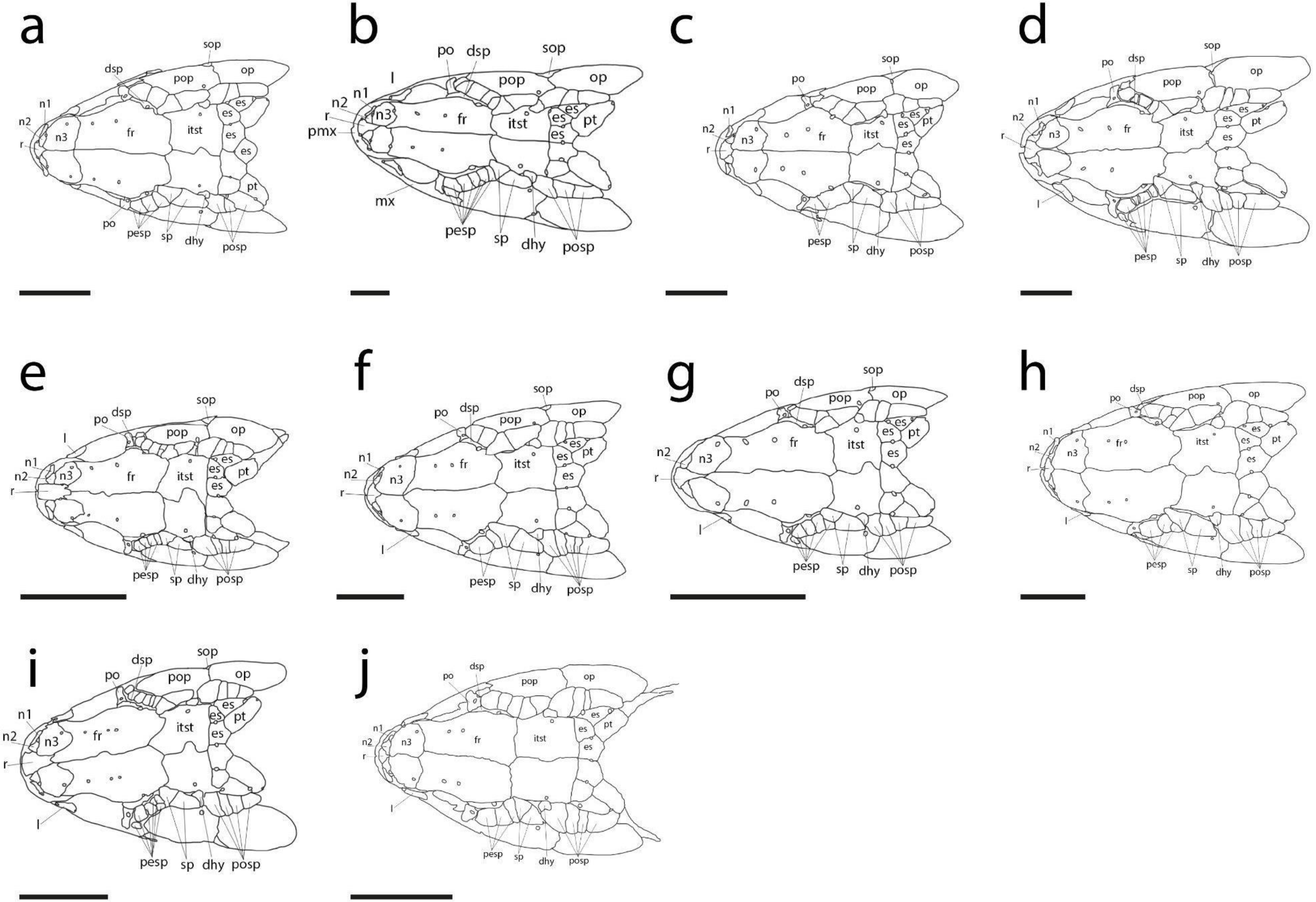
Figure 45- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *P. weeksii* (MNHN-IC-1962-0334). Abbreviations on page 37. Scale = 10mm.

Figure 46- 3D model (a) and drawing (b) of the lateral left view of the caudal fin of *E. calabaricus* (MNHN-IC-1978-0732). Abbreviations on page 37. Scale = 10mm.

Species delimitation

Due to the differences described previously here, it is possible to separate the Polypteridae species on the basis of their osteology. Besides the caudal fin differences (just described above)(Fig. 50), we can separate *Erpetoichthys* from the *Polypterus* species, where *Erpetoichthys* presents a more robust postorbital, with a larger dorsal part; absence of cheek plates; preopercle with the same height as its ventral process, which is considerably larger than in *Polypterus*; triangular opercle with a rounded posterior limit; and a thinner anterior ceratohyal (Figs. 28, 48). These observations corroborate with the ones from Traquair (1866), Jollie (1984) and Claeson, Bemis & Hagadorn (2007).

Among the *Polypterus* species, *P. bichir* and *P. endlicherii* distinguish from the others by their shorter (antero-posteriorly) premaxilla; shorter (antero-posteriorly) and thicker (ventral-dorsally) maxilla; and neurocranium region proportionally longer and lower (Figs. 20, 22, 48). Between them, *P. bichir* has an opercular region proportionally bigger (⅔ of the head) and *P. endlicherii* ventral process of the preopercle slightly curved forward (Figs. 20, 22). *P. ornatipinnis*, *P. palmas* and *P. polli* present a subrectangular, comparatively lower angular than the other species (Figs. 23, 24, 25, 48). *P. palmas* presents a more robust cheek plate and bigger subopercle compared to *P. ornatipinnis* and *P. polli* (Figs. 23, 24, 25). These two lasts differentiate themselves where *P. ornatipinnis* has a subtriangular or subrectangular rostral, that separates the pair of nasal 3, and a subrectangular lacrimal and *P. polli* has a rhombus rostral and a subtriangular lacrimal (Figs. 14, 16, 23, 25). *P. retropinnis* is separated from *P. delhezi* and *P. senegalus* by presenting a shorter most lateral extrascapular that ends before the postspiracular bones; a thicker ventral process of the preopercle; and a thinner subopercle (Figs. 2, 3, 12, 17, 21, 26, 47, 48). *P. delhezi* presents a proportionally bigger subopercle than *P. senegalus*; and a higher count of postspiracular bones (3, 4 or 5 *contra* 2 or 3) (Figs. 2, 3 12, 21). And finally, *P. weeksii* is distinguished from the others by its frontal with an acute anterior-medial process that separates the pair of nasal 3 and 3 pairs of canal openings in the frontal and a high count of prespiracular bones (6 to 8), where the doubling of these bones are frequent (Figs. 18, 27, 47, 48).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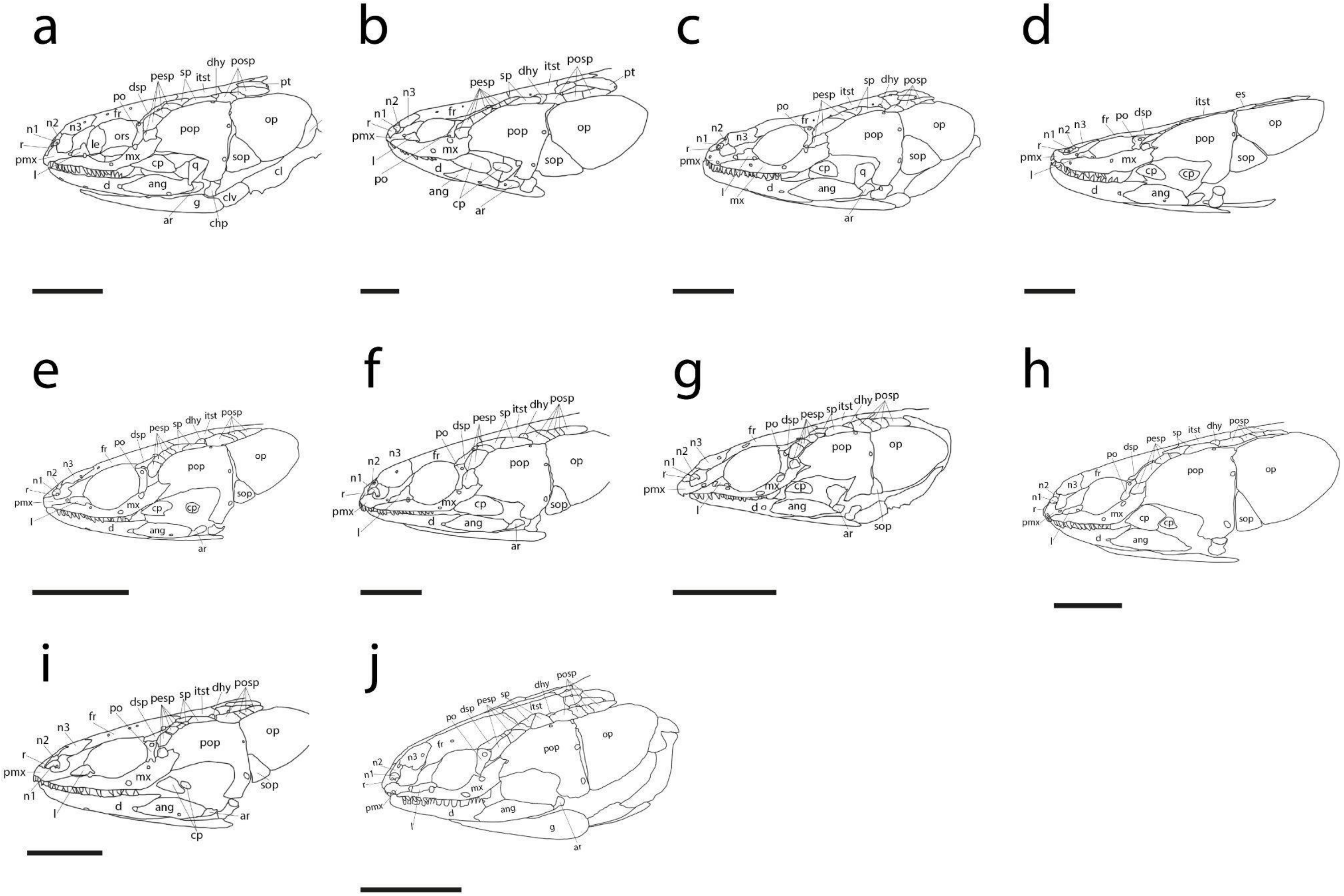
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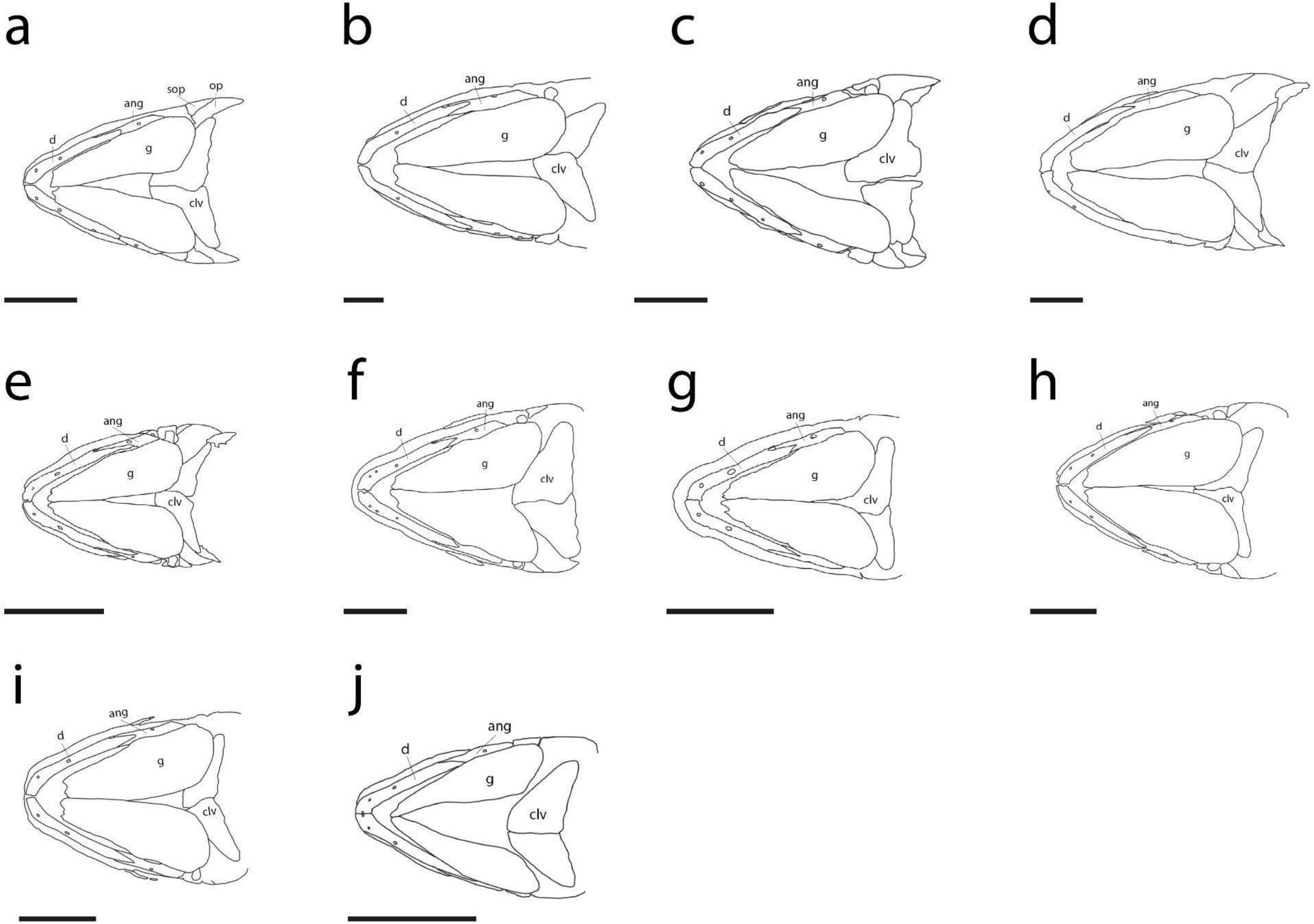
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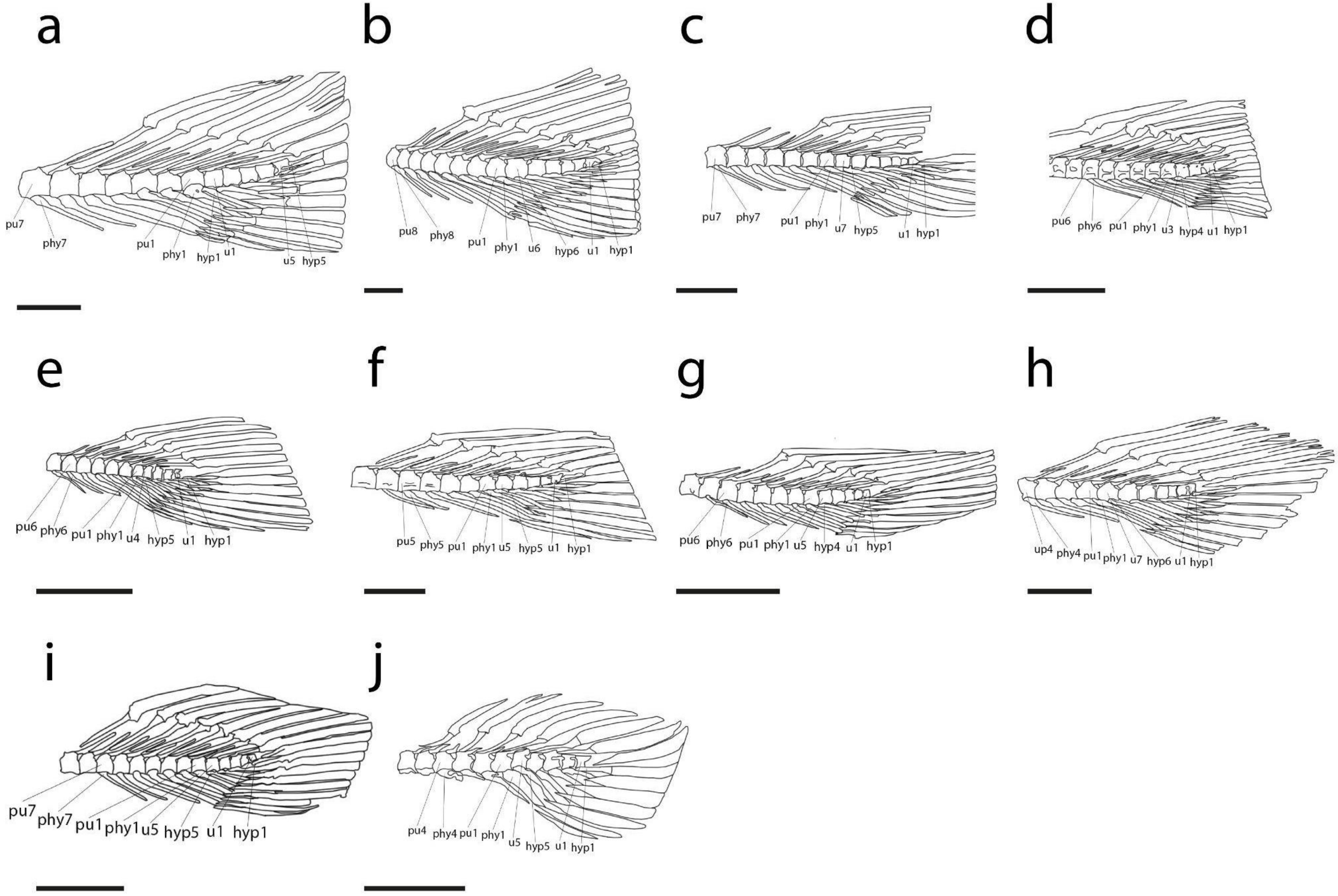
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Figure 47- Drawings of the dorsal view of the head of (a) *P. senegalus* (MNHN-IC-2002-0527); (b) *P. bichir* (MNHN-IC-1907-0250); (c) *P. delhezi* (MNHN-IC-2003-0614); (d) *P. endlicherii* (MNHN-IC-2001-2180); (e) *P. ornatipinnis* (MNHN-IC-1977-0307); (f) *P. palmas* (MNHN-IC-1958-0026); (g) *P. polli* (MNHN-IC-1900-0197); (h) *P. retropinnis* (MNHN-IC-1963-0239); (i) *P. weeksii* (MNHN-IC-1962-0334) and (j) *E. calabaricus* (MNHN-IC-1978-0732). Abbreviations on page 37. Each scale = 10mm.

Figure 48- Drawings of the lateral left view of the head of (a) *P. senegalus* (MNHN-IC-2002-0527); (b) *P. bichir* (MNHN-IC-1907-0250); (c) *P. delhezi* (MNHN-IC-2003-0614); (d) *P. endlicherii* (MNHN-IC-2001-2180); (e) *P. ornatipinnis* (MNHN-IC-1977-0307); (f) *P. palmas* (MNHN-IC-1958-0026); (g) *P. polli* (MNHN-IC-1900-0197); (h) *P. retropinnis* (MNHN-IC-1963-0239); (i) *P. weeksii* (MNHN-IC-1962-0334) and (j) *E. calabaricus* (MNHN-IC-1978-0732). Abbreviations on page 37. Each scale = 10mm.

Figure 49- Drawings of the ventral view of the head of (a) *P. senegalus* (MNHN-IC-2002-0527); (b) *P. bichir* (MNHN-IC-1907-0250); (c) *P. delhezi* (MNHN-IC-2003-0614); (d) *P. endlicherii* (MNHN-IC-2001-2180); (e) *P. ornatipinnis* (MNHN-IC-1977-0307); (f) *P. palmas* (MNHN-IC-1958-0026); (g) *P. polli* (MNHN-IC-1900-0197); (h) *P. retropinnis* (MNHN-IC-1963-0239); (i) *P. weeksii* (MNHN-IC-1962-0334) and (j) *E. calabaricus* (MNHN-IC-2008-2103). Abbreviations on page 37. Each scale = 10mm.

Figure 50- Drawings of the lateral left view of the caudal fin of (a) *P. senegalus* (MNHN-IC-1904-0068); (b) *P. bichir* (MNHN-IC-1907-0250); (c) *P. delhezi* (MNHN-IC-2003-0614); (d) *P. endlicherii* (MNHN-IC-B-0384); (e) *P. ornatipinnis* (MNHN-IC-1977-0307); (f) *P. palmas* (MNHN-IC-1958-0026); (g) *P. polli* (MNHN-IC-1900-0197); (h) *P. retropinnis* (MNHN-IC-1963-0239); (i) *P. weeksii* (MNHN-IC-1962-0334) and (j) *E. calabaricus* (MNHN-IC-1978-0732). Abbreviations on page 37. Each scale = 10mm.

CONCLUSIONS

The differences found here are some promising characters to clearly separate the extant polypteridae species, mainly the differences on the rostral, lacrimal, spiracular series, opercular region and caudal fin. Even though not exclusively specific, the number of the elements of the caudal fin seems to be efficient to distinguish species. A larger sample is needed to confirm this statement.

A study on the ontogeny of the skull of *E. calabaricus* is needed to understand the existence of a subopercle bone in this species. There is still the necessity to add the remaining species of the group (*P. ansorgii*, *P. congicus*, *P. mokelembembe* and *P. teugelsi*) to complete the dataset of this study. After that, all the data gathered will be used in a phylogenetic study of the Polypteriformes, including, if possible, fossil taxa.

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Supplemental information

Species	Collection number	Body region	Voxel Size (mm)	Current (mA)	Energy (kV)	Number of slices by axis X-Y-Z
E. calabaricus	MNHN-IC-1900-0218	Head	0.0229657	280	80	1762-1762-1141
E. calabaricus	MNHN-IC-1978-0732	Caudal	0.0212723	260	80	665-1625-715
E. calabaricus	MNHN-IC-1978-0732	Head	0.0215744	260	80	1193-1506-831
E. calabaricus	MNHN-IC-2008-2103	Head	0.0272489	340	80	1381-1207-1588
P. bichir	MNHN-IC-1907-0250	Caudal	0.052904	375	80	1000-1669-831
P. bichir	MNHN-IC-1907-0250	Head	0.0529362	350	80	1416-1650-814
P. delhezi	MNHN-IC-1962-0349	Head	0.0235219	280	80	1313-1265-1245
P. delhezi	MNHN-IC-2003-0614	Caudal	0.0282847	350	80	1003-1727-617
P. delhezi	MNHN-IC-2003-0614	Head	0.0283444	350	80	1265-1743-994
P. endlicherii	MNHN-IC-B-0384	Caudal	0.0225772	270	80	908-1769-1024
P. endlicherii	MNHN-IC-B-0384	Head	0.0226141	270	80	1092-1710-688
P. endlicherii	MNHN-IC-2001-2180	Head	0.040121	350	80	1415-1415-1528
P. ornatipinnis	MNHN-IC-1977-0307	Caudal	0.0199795	250	80	1198-1399-1661
P. ornatipinnis	MNHN-IC-1977-0307	Head	0.0200022	250	80	1292-1102-1512
P. ornatipinnis	MNHN-IC-2009-0725	Head	0.0434825	375	80	1415-1415-1469
P. palmas	MNHN-IC-1940-0069	Head	0.0326957	350	80	1331-1417-724
P. palmas	MNHN-IC-1958-0026	Caudal	0.0305572	350	80	1415-1363-1161
P. palmas	MNHN-IC-1958-0026	Head	0.0305819	350	80	1415-1625-1236

P. palmas	MNHN-IC-1977-0308	Head	0.0386968	280	80	1416-1416-1576
P. palmas	MNHN-IC-1977-0308	Head	0.0207788	250	80	1416-1416-1549
P. polli	MNHN-IC-1900-0197	Caudal	0.0253608	125	80	924-780-1641
P. polli	MNHN-IC-1900-0197	Head	0.0185811	125	80	1421-1421-1540
P. retropinnis	MNHN-IC-1964-0253	Head	0.0301797	350	80	1327-1630-900
P. retropinnis	MNHN-IC-1963-0239	Caudal	0.028309	350	80	1294-1625-605
P. retropinnis	MNHN-IC-1963-0239	Head	0.0283535	350	80	1103-1599-822
P. retropinnis	MNHN-IC-1930-0001	Head	0.0229657	280	80	1762-1762-1141
P. senegalus	MNHN-IC-1904-0068	Caudal	0.030127	350	80	1415-1624-742
P. senegalus	MNHN-IC-1904-0068	Head	0.0301838	350	80	1298-1745-1043
P. senegalus	MNHN-IC-1908-0004	Head	0.0219982	280	80	1530-1573-1229
P. senegalus	MNHN-IC-1933-0073	Head	0.0356101	350	80	1416-1626-815
P. senegalus	MNHN-IC-1961-0006	Head	0.0219982	280	80	1530-1573-1229
P. senegalus	MNHN-IC-1961-0008	Head	0.0374086	375	80	1438-1438-1591
P. senegalus	MNHN-IC-1961-0008	Head	0.0282433	350	80	1780-1780-1261
P. senegalus	MNHN-IC-1961-0009	Head	0.0282135	350	80	875-1368-1637
P. senegalus	MNHN-IC-1984-0508	Head	0.0282433	350	80	1780-1780-1261
P. senegalus	MNHN-IC-1992-0770	Head	0.0434912	375	80	1259-1184-1511
P. senegalus	MNHN-IC-2002-0527	Head	0.0282542	350	80	1426-1426-1611
P. senegalus	MNHN-IC-2002-0527	Head	0.0282433	350	80	1780-1780-1261
P. senegalus	MNHN-IC-2004-0180	Head	0.0271858	280	80	1416-1416-1525
P. weeksi	MNHN-IC-1962-0334	Caudal	0.0320799	375	80	1154-1769-900
P. weeksi	MNHN-IC-1962-0334	Head	0.0321274	375	80	1528-1552-1362
P. weeksi	MNHN-IC-1962-0335	Caudal	0.0320799	375	80	1154-1769-900
P. weeksi	MNHN-IC-1962-0335	Head	0.0321274	375	80	1528-1552-1362

Table S1 - Parameters of each CT-scan realized for this study.

4 **MORPHOLOGICAL VARIATION ON THE PINNULES OF *POLYPTERUS BICHIR* AND ITS TAXONOMIC IMPLICATIONS (Artigo submetido)**

O presente capítulo está sendo preparado para publicação e, por isso, é apresentado no formato de artigo científico e é tratado como uma seção à parte da presente tese possuindo suas próprias subseções (resumo, introdução, material e métodos, resultados, discussão, conclusão e referências) e está nos moldes de formatação da revista PeerJ - Life & Environment.

Este capítulo é uma continuação da discussão acerca da viabilidade das pínulas como ferramenta taxonômica e, consequentemente, sua implicação na validade das espécies fósseis descritas com base em pínulas isoladas. Esta discussão começou com o artigo intitulado "*Morphological variations in the dorsal fin finlets of extant polypterids raise questions about their taxonomical validity*" que foi iniciado durante minha dissertação de mestrado e finalizado e publicado durante o início da presente tese, em 2018. Aqui abordamos a variabilidade morfológica intraespecífica e intraindividual em pínulas de espécimes de *P. bichir*. Nós observamos um padrão semelhante na variação morfológica nas pínulas dos espécimes ao longo da nadadeira dorsal (eixo antero-posterior). Em todos os espécimes observados, independente do número de pínulas, pode-se observar que os processos basais tornam-se mais proeminentes e mais separados, tornando as últimas pínulas mais abertas; a cavidade glenóide se torna maior; o forâmen basal também se torna maior; e o processo mediano inicia-se menos desenvolvido e um pouco curvado para cima ou plano e torna-se mais proeminente e apresentando duas projeções orientadas para baixo. No entanto, além desse padrão, algumas diferenças entre os espécimes foram observadas: os espécimes PO2 e PO6 apresentam predominantemente a cabeça da pínula com formato geral quadrado, onde PO1, PO3 e PO5 apresentam formato predominantemente trapezoidal; todos os exemplares apresentam a cabeça da pínula mais larga que o corpo, exceto PO6, que apresenta a cabeça tão larga quanto o corpo; e todos os espécimes apresentam processos bem individualizados, exceto PO6, que apresenta processos menos individualizados (exceto os processos posteriores).

ABSTRACT

Disarticulated fossil pinnules are the majority of Polypteridae fossil taxa, consisting of six genera and 17 species. As it is important to understand the morphological variation on the pinnules in a single species, in order to determine their validity as taxonomic tools to later assess the validity of the fossil taxa erected on isolated material. Here, we analyze the intraindividual and intraspecific morphology on the pinnules of *Polypterus bichir*. We report a pattern on the morphology related to the antero-posterior axis on the dorsal fin. We also report morphological differences on the pinnules of different specimens and inconsistencies between our findings and previous studies. Until these inconsistencies are elucidated, we discourage any description based on pinnules as diagnostic characters.

Keywords Polypteridae, Pinnules, Morphological variation, Taxonomy

INTRODUCTION

The dorsal fin of all Polypteriformes are divided in numerous finlets (Lacépède, 1803; Daget *et al.*, 2001; Nelson, Grande & Wilson, 2016), each finlet is composed of a central spine (=pinnule); a lepidotrichia partially fused to the pinnule and divided in secondary rami; and a membrane connecting a finlet to the anterior part of the next finlet (Gayet, Meunier & Werner, 1997). Only found in the Polypteriformes, pinnules are the most unique and distinguished character of the group, and represent a considerable part of the known fossils of the group, usually found isolated and disarticulated (e.g. Gayet, Meunier & Levrat-Calviac, 1988; Gayet & Meunier, 1996; Gayet, Meunier & Werner, 1997; Werner & Gayet, 1997; Daget *et al*. 2001). The first isolated fossil pinnules were reported in 1988 for *Polypterus sp*. (Gayet, Meunier & Levrat-Calviac, 1988), and a lot of material is described as such in Cenozoic outcrops from Africa (e.g. Greenwood, 1951, 1972, 1973; Van Neer & Gayet, 1988; Stewart, 1994, 2001, 2003; Murray, 2000; Murray *et al*., 2010; Otero *et al*., 2009, 2010, 2015). In 1996, isolated material were reported from the Coniacian of Niger, and lastly, in 1997 more pinnules were described from the Cenomanian of Sudan and allow the description of new extinct taxa. All these fossils totalize six genera, comprising 17 species and including two *Polypterus* species (Gayet, Meunier & Levrat-Calviac, 1988; Gayet & Meunier, 1996; Gayet, Meunier & Werner, 1997; Werner & Gayet, 1997; Daget *et al*. 2001).

Since pinnules are an exclusive character of polypteriformes (Lacépède, 1803; Sewertzoff, 1924; Moritz & Britz, 2019), there is no doubt that this material belongs to the group. Even so, and despite their use to establish new taxa, the first work regarding the validity of pinnules as taxonomic units in extant fish was only published in 2018 (Coelho, Cupello & Brito, 2018). This work describes the intraindividual variation (non taxonomical) relative to the position on the dorsal fin in 5 specimens from 4 different species, and points out that it is not possible to know if the isolated material described as numerous genera and species is indeed from that many taxa, because the descriptions do not take in consideration the potential individual variation, mainly on pinnules from the same localities (Coelho, Cupello & Brito, 2018). In 2020, Meunier & Gayet described the pinnule morphology in 217 specimens from 11 extant species showed some variation on the pinnule of all extant Polypteridae species, but concluded that this variation is not enough to prevent identification and species designation. Although a large number of specimens was used for the study, the data presented by Meunier and Gayet (2020) does not allow us to understand whether the interindividual variation, observed previously, was taken into account or even questioned on their descriptions. A hint that points to the disregard of this variation is the separation of the invalid subspecies of *P. bichir*. Therefore, their results can be questioned and do not allow us to conclude completely on the utilization of isolated pinnules to identify species.

Consequently, the detailed analysis of the intraspecific variability of the morphology of the pinnules is a necessary step to be able to conclude on the use of the pinnules and/or define the framework in which these structures can be used. With this aim, we analyze here the intraindividual and intraspecific morphology of the pinnules of *Polypterus bichir*, comparing pinnules from the same relative position throughout the dorsal fin of 5 large specimens collected in Chad in july 2014 (N’Djamena fish market).

MATERIAL AND METHODS

Specimen information

The pinnules used in this study were removed from five adult specimens of *Polypterus bichir* (PO1, PO2, PO3, PO5, and PO6), ranging from 52 cm to 59 cm in standard length, collected at N’Djamena (Chad) fish Market in 2014 and housed in the collections of the Université de Poitiers.

Cleaning procedure

All pinnules were soaked in a solution of oxygenated water for at least 1 day and then they were rinsed and brushed, in order to remove soft tissues.

Microscopy

The images were obtained using an optical microscope LasX (Leica Microsystems).

Nomenclature

The anatomical nomenclature used in this study is based on Meunier & Gayet (2020) (Fig. 1).

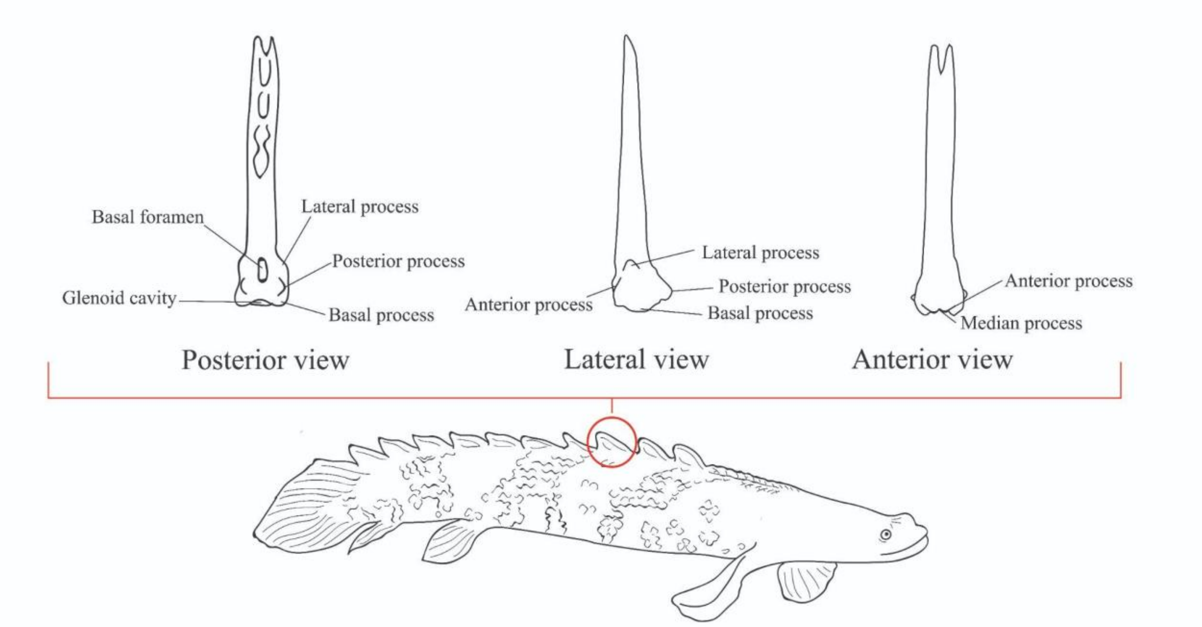

Figure 1 - Illustration of the lateral view of a *Polypterus* specimen with anatomical details on posterior, lateral and anterior views of a pinnule (Modified from Coelho, Cupello & Brito, 2018).

RESULTS

PO1 (Figs. 2, 7). The specimen had 16 pinnules with a general trapezoidal shape; head of the pinnule wider than the body, except for the 1st pinnule, which has a rectangular shape, with the body as wide as the articular head. 2nd to 6th pinnules have a more narrow distance between both basal processes, where this distance grows on the 7th to 16th pinnules. The anterior processes are little to moderate developed in all pinnules. The median processes begin less developed and little curved upwards (1st to 8th), then become a little more prominent and present two projections oriented downwards (9th to 16th). The basal processes also get more prominent towards the last pinnules (this pattern repeats itself on the other specimens). Lateral processes are little to moderate developed and absent in the last pinnule. Posterior processes are prominent in all pinnules. Basal foramen gets larger in an antero-posterior orientation. The glenoid cavity also gets larger in the antero-posterior axis, where the last pinnule is more “open” due to its position merging into the caudal fin.

PO2 (Figs. 3, 8). The specimen had 15 pinnules with a general square shape, except for the 12th, 13th, 14th and 15th that present a more trapezoidal shape; head of the pinnule wider than the body. The 1st to 13th pinnules present flat median processes (excepto for the 3rd that presents a curved process) and the 14th and 15th pinnules present two projections similar to the last pinnules of PO1. The anterior processes, lateral processes, posterior processes, basal foramen and glenoid cavity present themselves as in PO1.

PO3 (Figs. 4, 9). The specimen had 14 pinnules with a general trapezoidal shape, except for the 1st, 2nd and 3rd pinnules, which present a more square shape; the head of the pinnule is wider than the body. The specimen has less prominent median processes than PO2, where the 1st to 12th pinnules have the processes slightly curved upwards or flat; and the 13th and 14th pinnules present the two projections like PO2 and PO3. Lateral processes are little developed in all but the last pinnule, where it is absent. Anterior processes, posterior processes, basal foramen and glenoid cavity present themselves as in PO1 and PO2.

PO5 (Figs. 5, 10). The specimen had 15 pinnules with a general trapezoidal shape; the head of the pinnule is as wide as its body. The median processes on the 1st to 10th pinnules are curved upwards, then become flat on the 11th to 13th pinnules and the two last (14th and 15th) are similar to the other specimens. Lateral processes are little developed, except for the 14th and 15th pinnules, which are absent. Anterior processes, posterior processes, basal foramen and glenoid cavity present themselves as in PO1, PO2 and PO3.

PO6 (Figs. 6, 11). The specimen had 15 pinnules with a general square shape, except for the 13th, 14th and 15th pinnules, which present a more or less trapezoidal shape. Head of the pinnule is as wide as its body and presents a general rounded base. All pinnules present less individualized processes, except for the posterior processes, which are considerably proemients. The median processes are curved on the 1st to 7th, flat on the 8th to 13th and present the two projections on the 14th and 15th pinnules. The lateral processes are little developed or absent in several pinnules. The basal foramen and the glenoid cavity become larger in an antero-posterior orientation, but not as much as is observed in the other specimens. The anterior processes are similar to what is observed in other specimens.

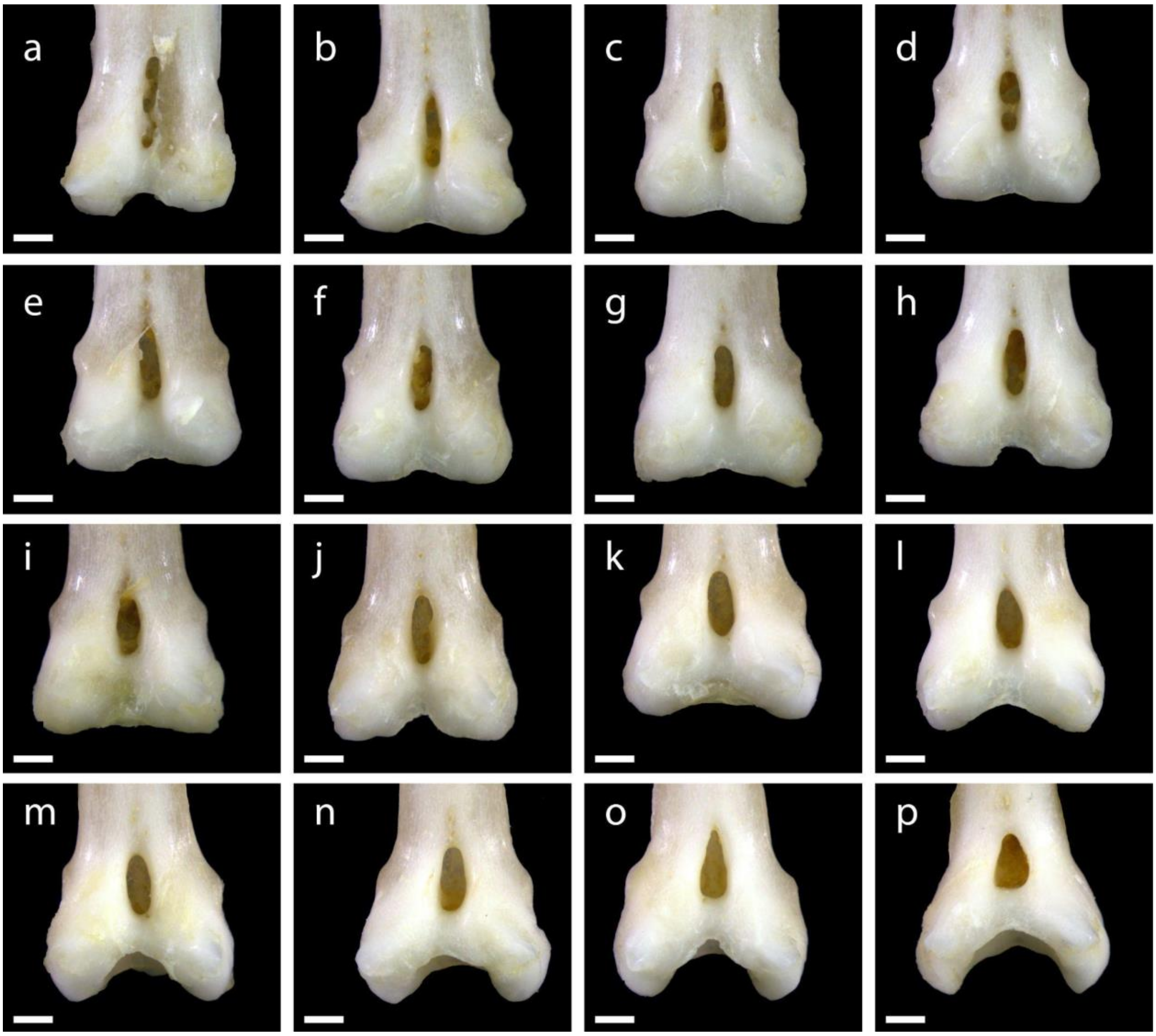

Figure 2 - SEM images of the posterior view of the pinnules of *P. bichir* PO1. (A-P) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th, 15th and 16th pinnules, respectively. Scale = 1 mm.

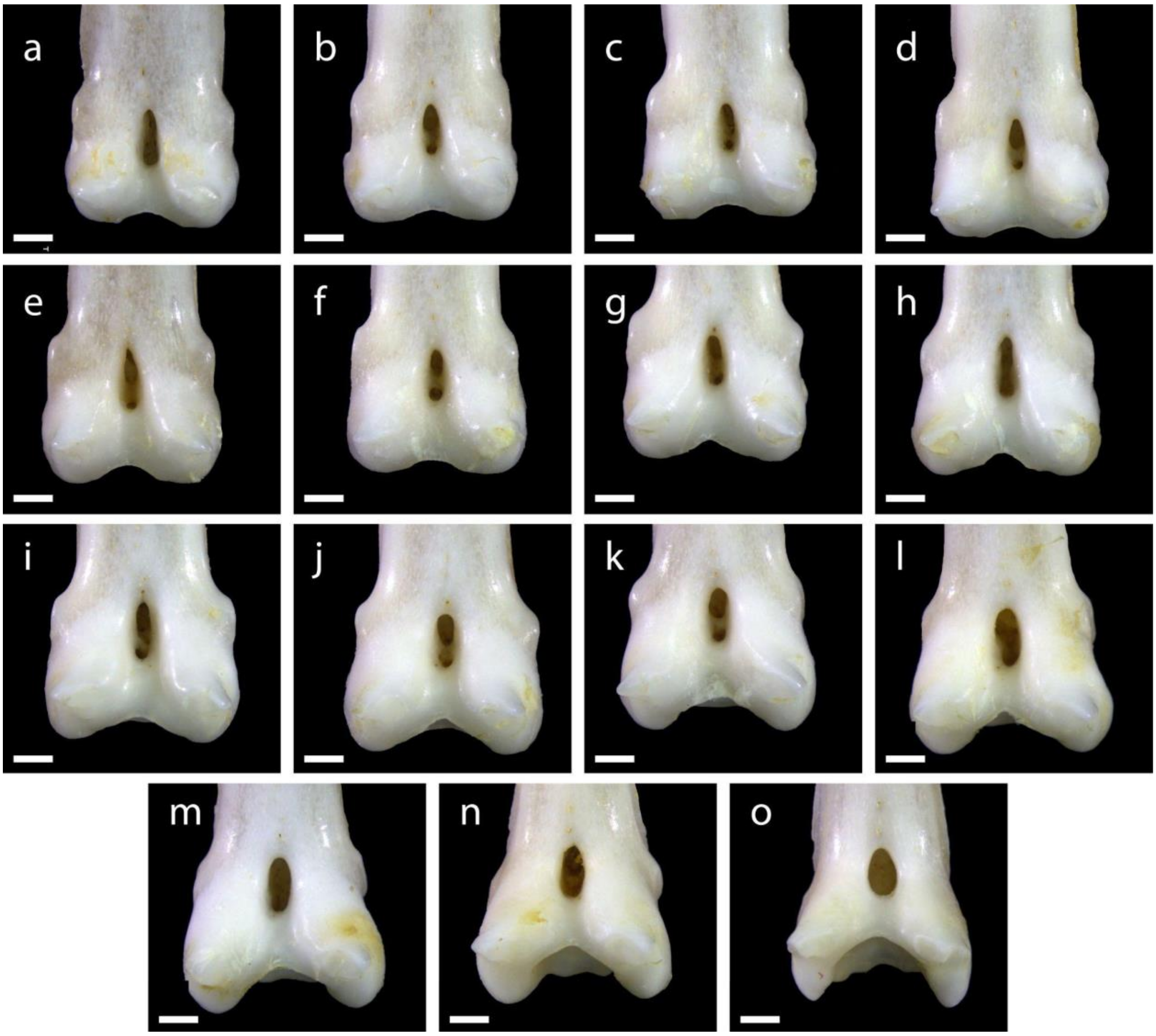

Figure 3 - SEM images of the posterior view of the pinnules of *P. bichir* PO2. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

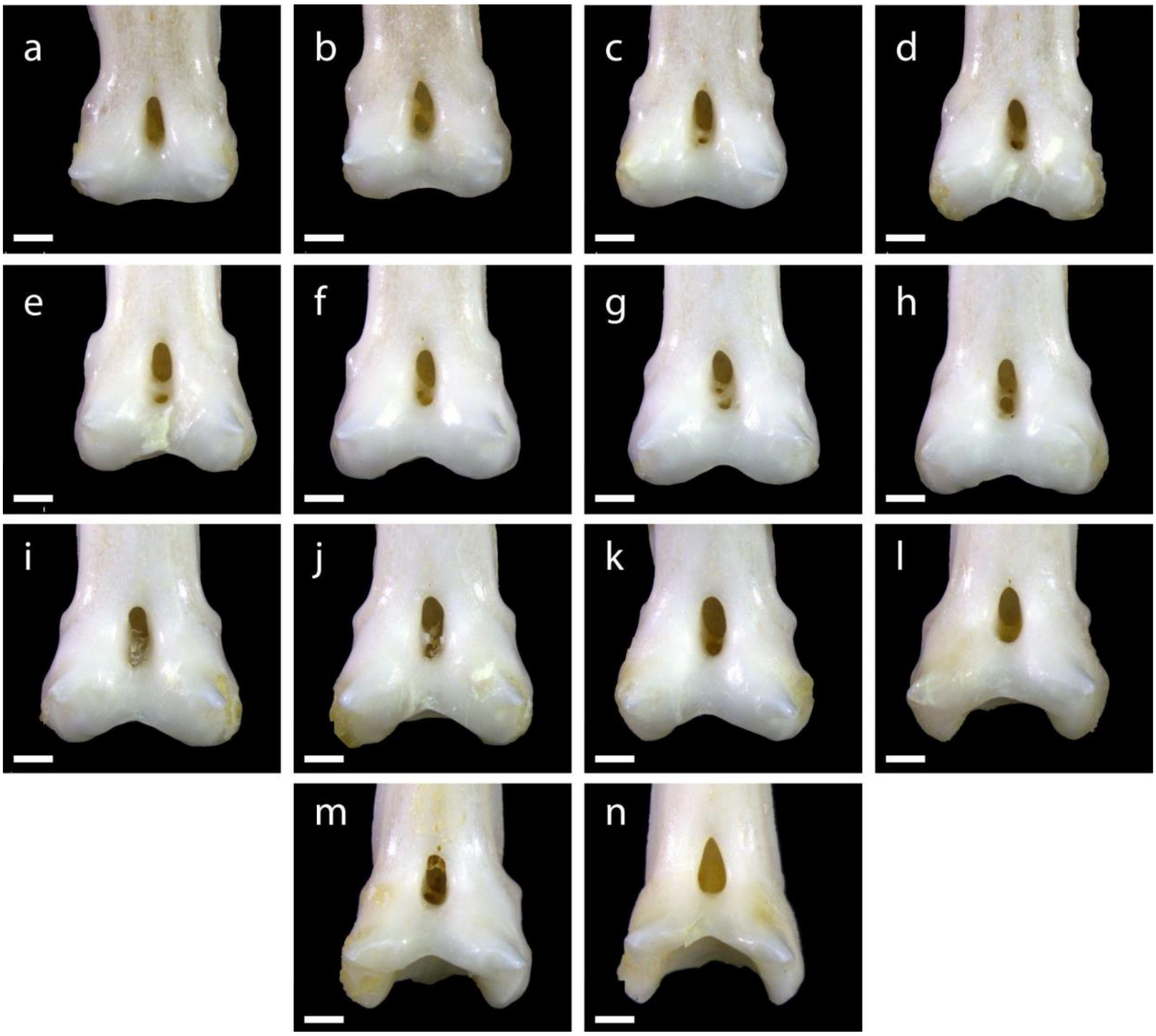

Figure 4 - SEM images of the posterior view of the pinnules of *P. bichir* PO3. (A-N) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th and 14th pinnules, respectively. Scale = 1 mm.

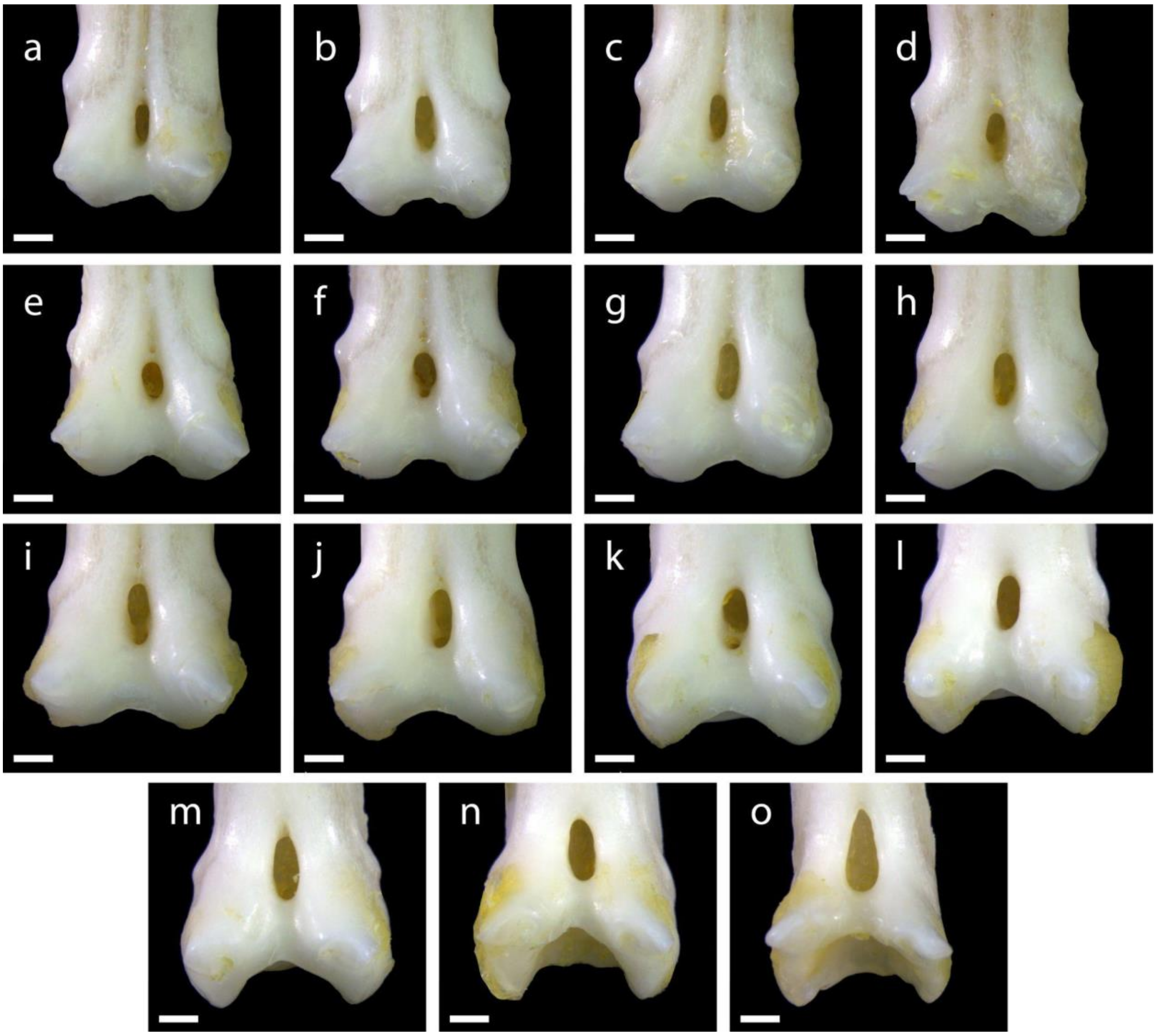

Figure 5 - SEM images of the posterior view of the pinnules of *P. bichir* PO5. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

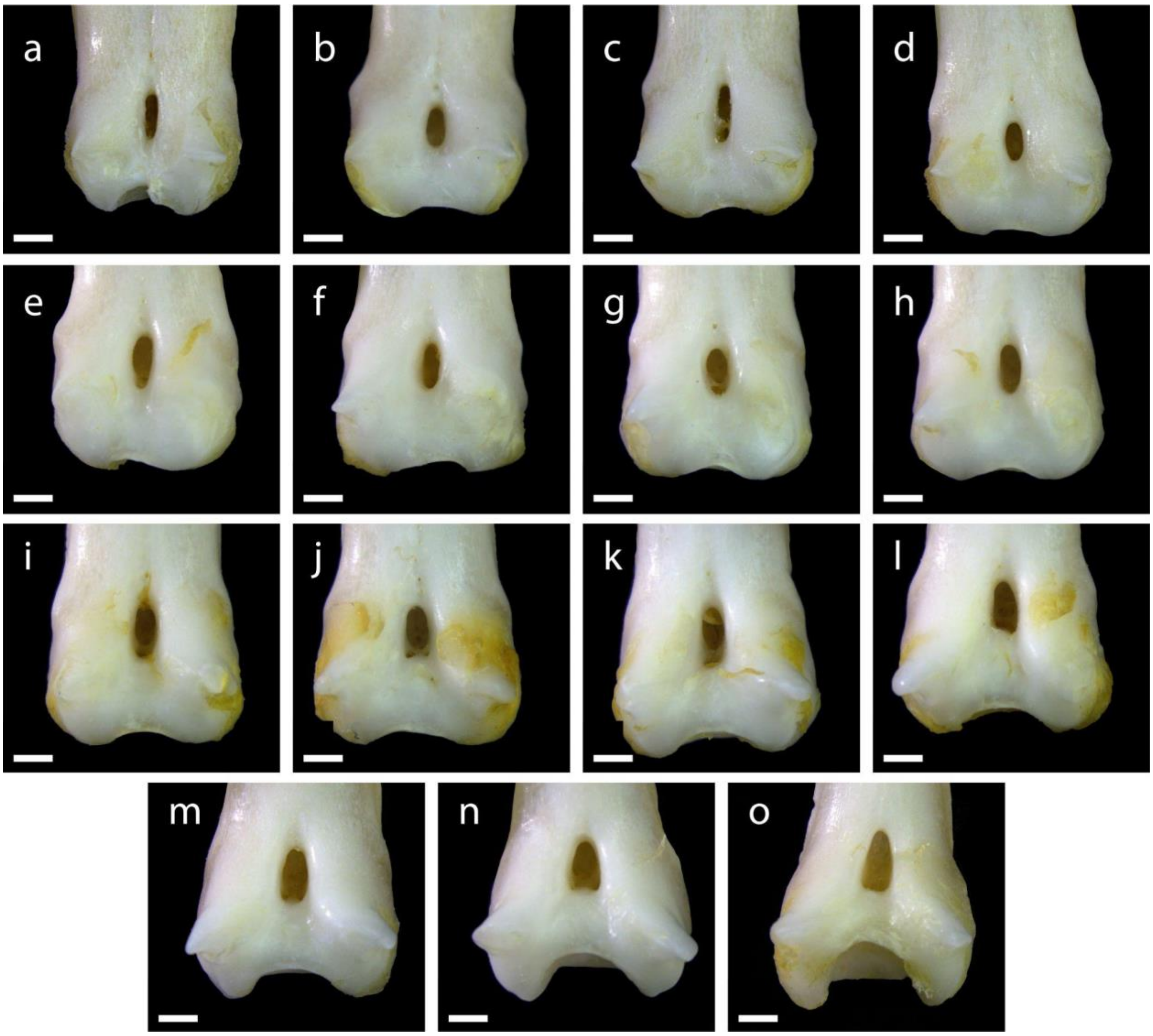

Figure 6 - SEM images of the posterior view of the pinnules of *P. bichir* PO6. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

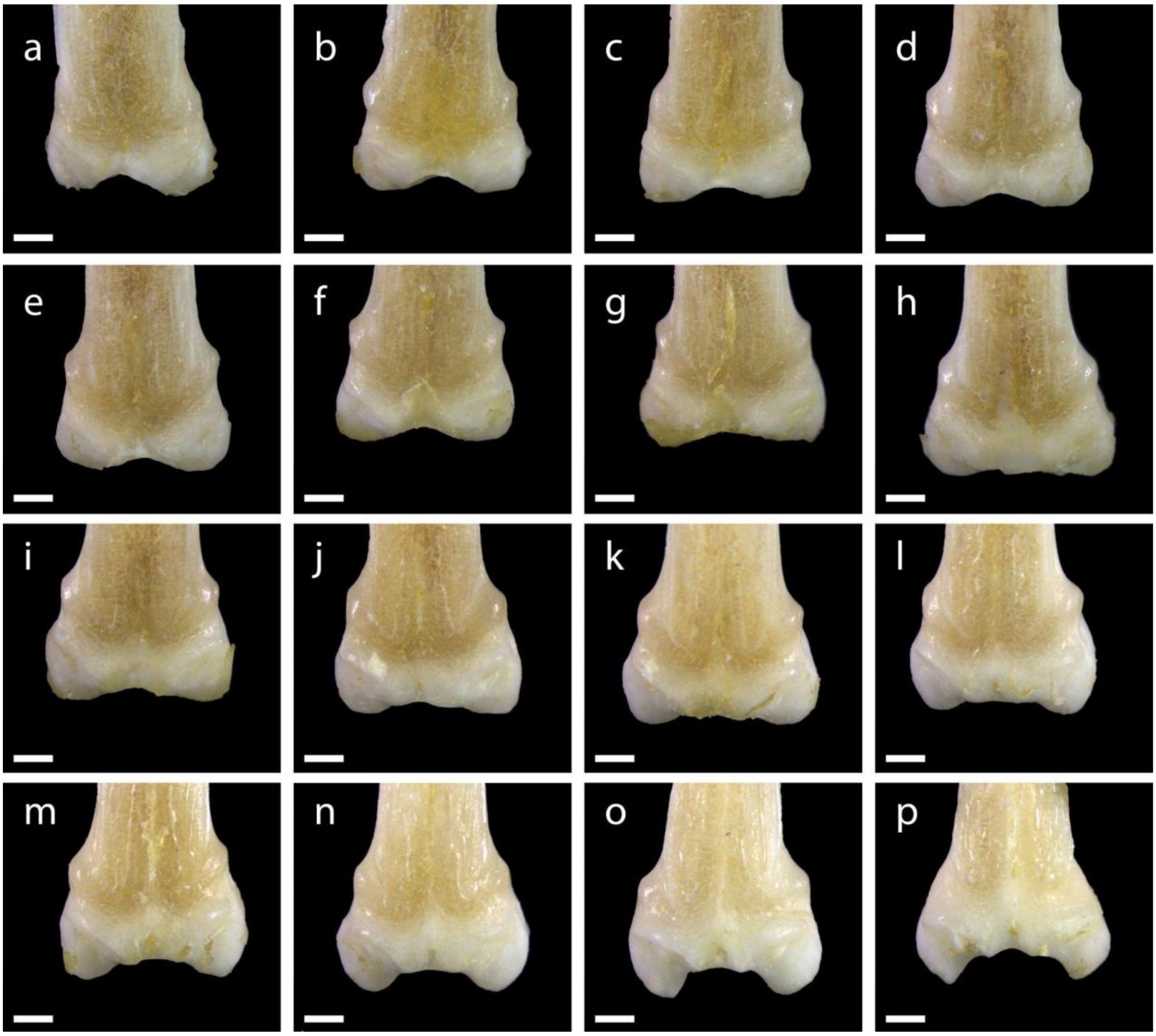

Figure 7 - SEM images of the anterior view of the pinnules of *P. bichir* PO1. (A-P) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th, 15th and 16th pinnules, respectively. Scale = 1 mm.

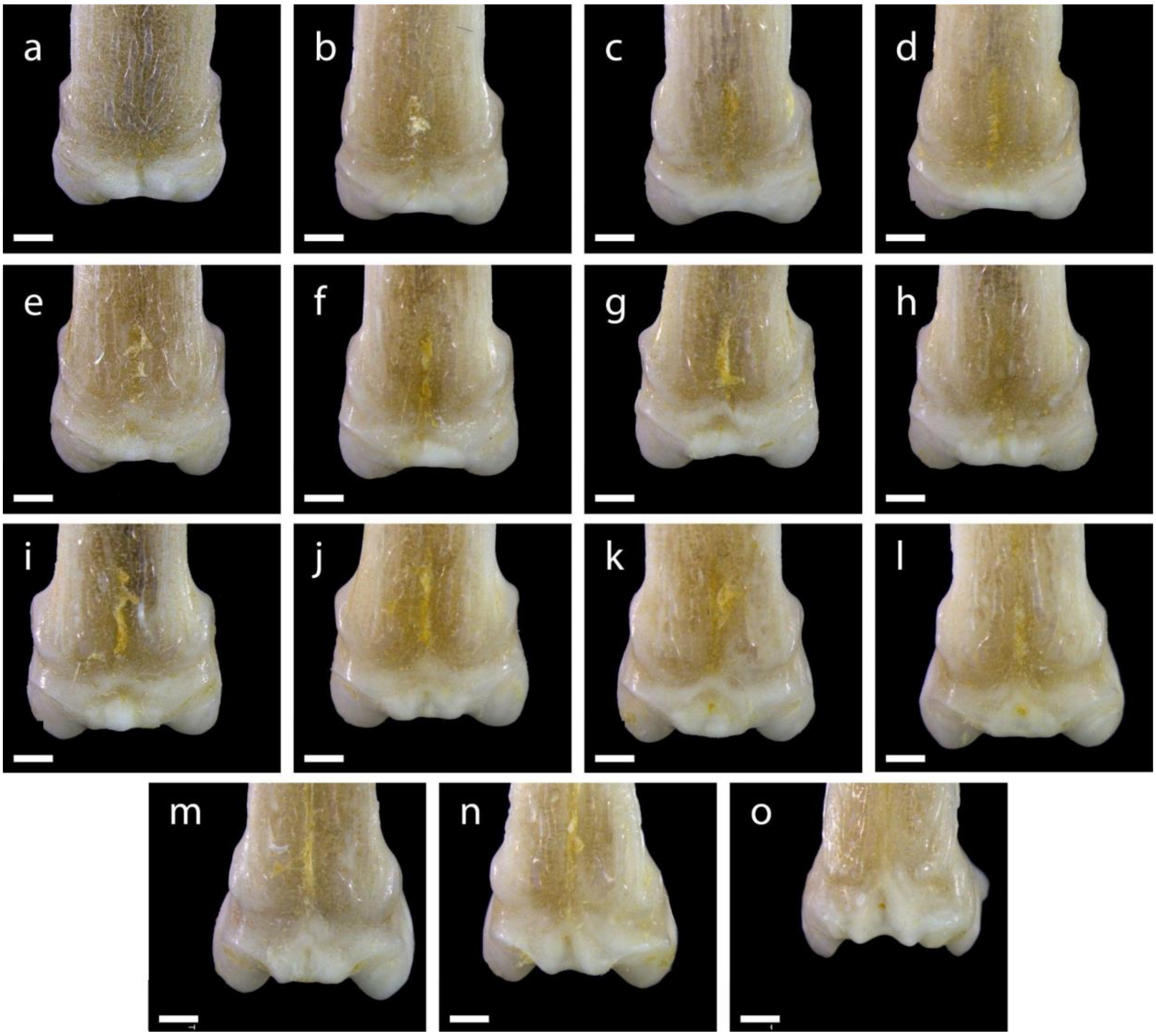

Figure 8 - SEM images of the anterior view of the pinnules of *P. bichir* PO2. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

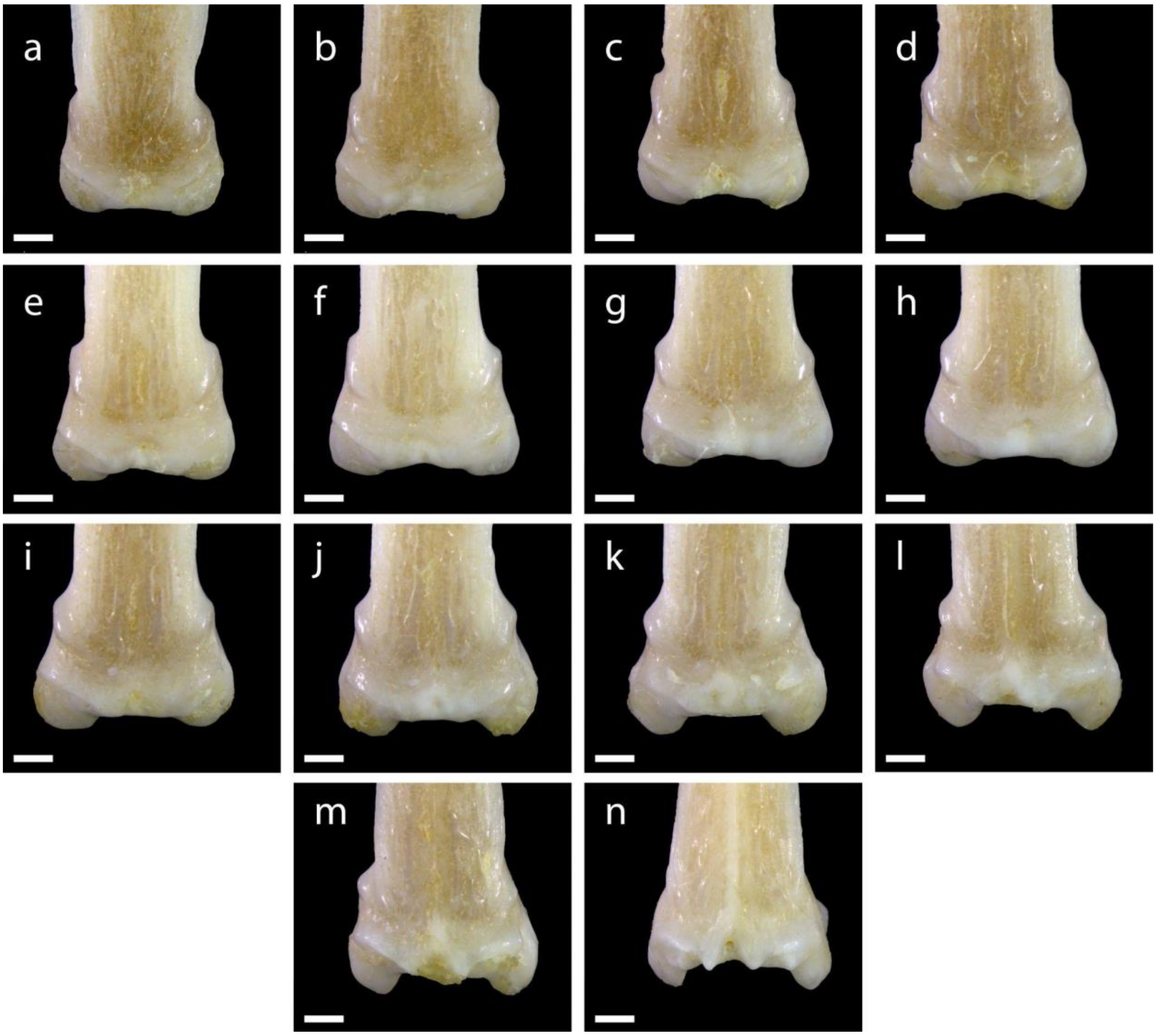

Figure 9 - SEM images of the anterior view of the pinnules of *P. bichir* PO3. (A-N) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th and 14th pinnules, respectively. Scale = 1 mm.

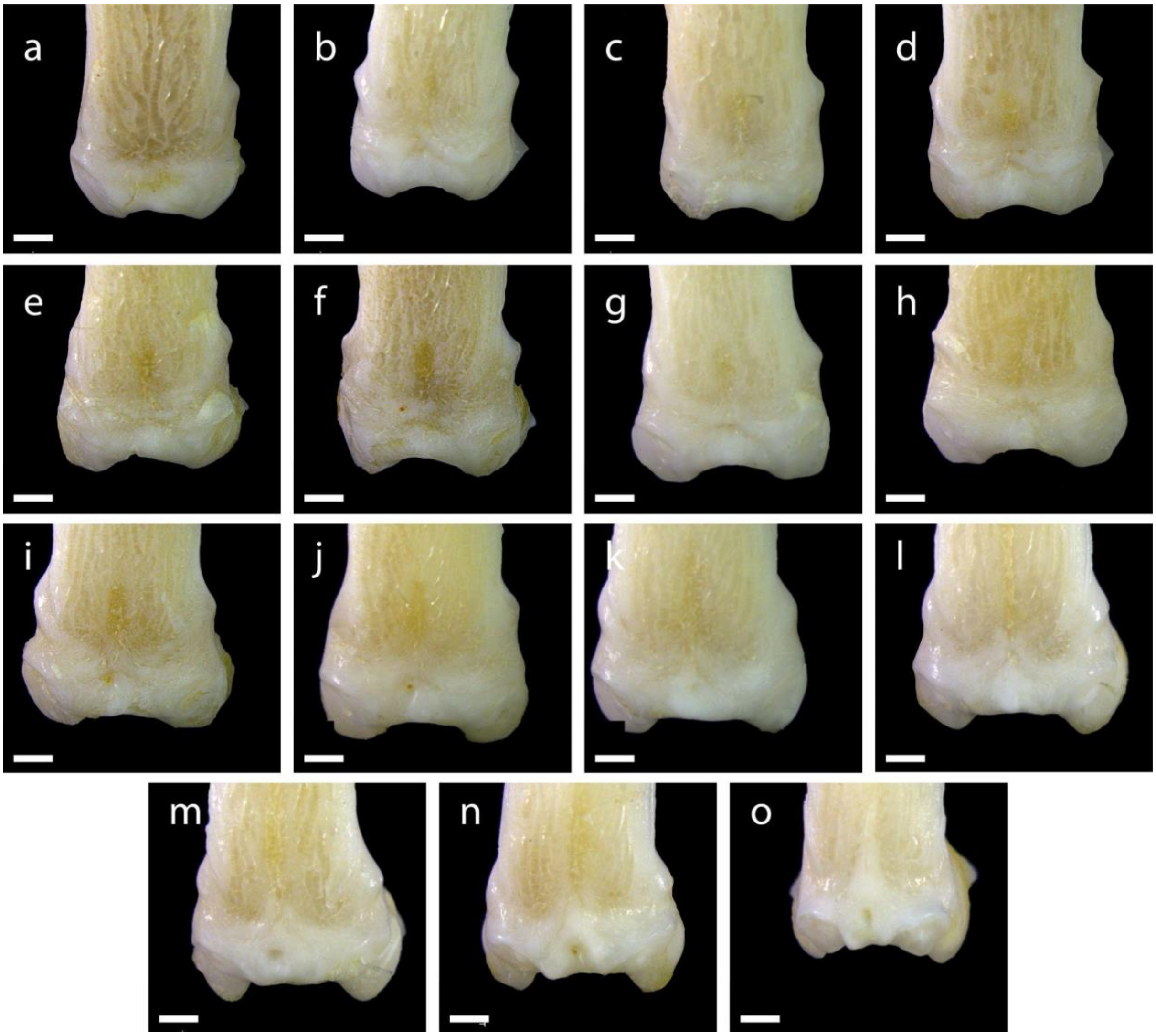

Figure 10 - SEM images of the anterior view of the pinnules of *P. bichir* PO5. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

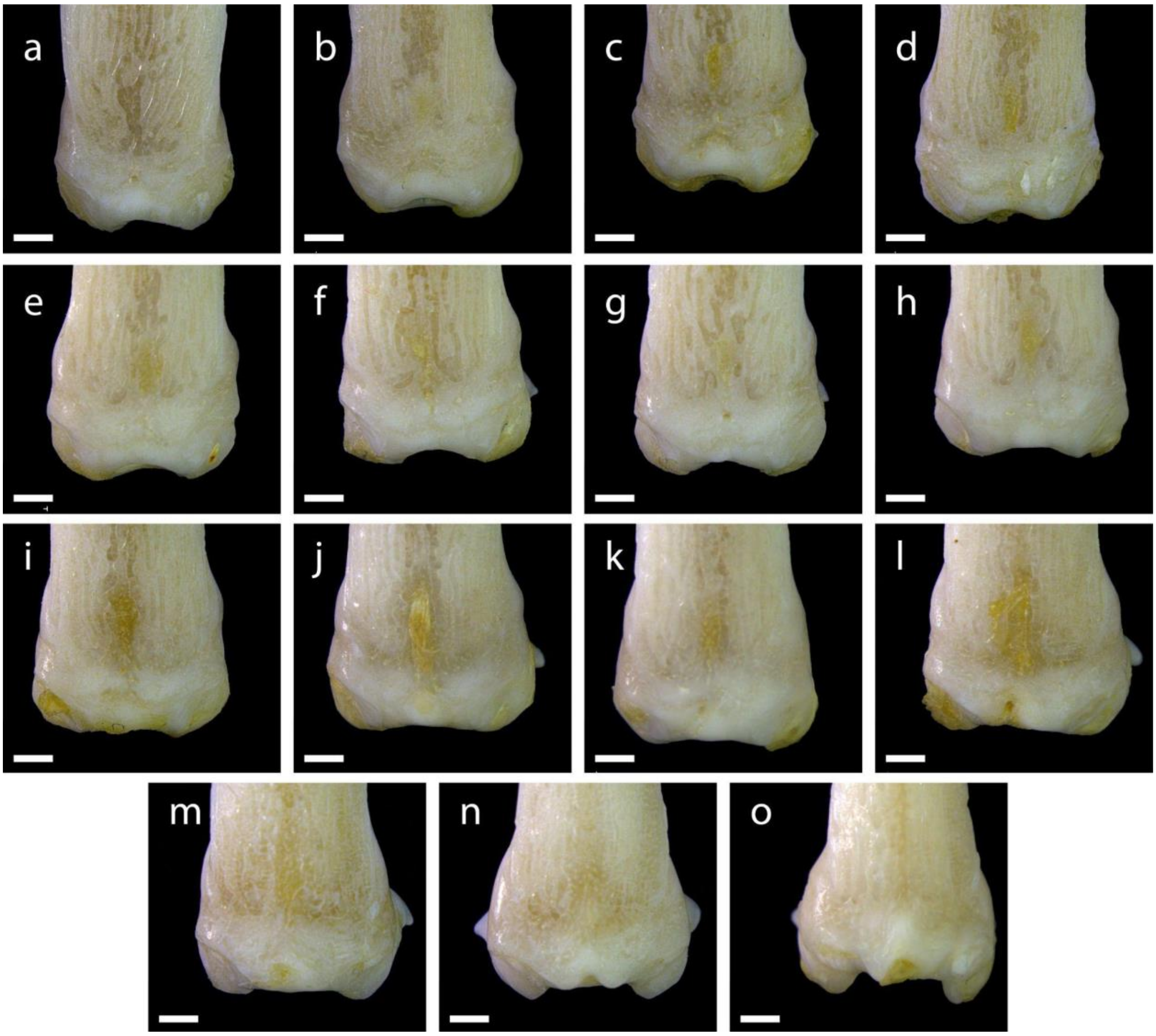

Figure 11 - SEM images of the anterior view of the pinnules of *P. bichir* PO6. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

DISCUSSION

There is a similar pattern on the changes in the pinnules of the specimens along the dorsal fin (antero-posterior orientation). In all specimens we observed, independent of the number of pinnules: i) the basal processes become more prominent and more separated, turning the last pinnules more open; ii) the glenoid cavity gets larger; iii) the basal foramen also gets larger; and iv) the median process begin less developed and a little curved upwards or flat and became more prominent and presenting two projections oriented downwards. However, besides this pattern, some differences between specimens were observed: specimens PO2 and PO6 present predominantly the head of the pinnule with a general square shape, where PO1, PO3 and PO5 present a predominantly trapezoidal shape; all specimens present the head of the pinnule wider than its body, except for PO6, which presents the head as wide as the body; and all specimens present well individualized processes, except for PO6, which presents less individualized processes (except for the posterior processes).

Features of the diagnoses for the now invalid subspecies of *P. bichir* defined by Meunier & Gayet (2020) are observed in the specimens of the present study whenever all these specimens would have belonged to the same sub-species *P. b. bichir*, notably the articular head of the spine has either a trapezoidal shape like in *P. b. bichir* or a square shape like in *P. b. katangae* and *P. b. lapradei* (Fig. 2-6). The width of the glenoid cavity, which is a diagnostic character for *P. ansorgii*, *P. bichir* and *P. endlicherii* according to Meunier & Gayet (2020), appears to be more related to the position on the dorsal fin rather to the species since the posteriormost pinnules have a wider glenoid cavity due to its position merging into the caudal fin. This pattern on the glenoid cavity can also be observed on the last pinnules of *P. delhezi* and *P. endlicherii* (Coelho, Cupello & Brito, 2018: figs. 6I, 6J,).

Finally, the ornamentation of the ganoin and dentine on the anterior face of the pinnule observed in the Chadian bichirs (Fig. 7-11) resembles more what is described for *P. weeksii* (diagnostic for the species), than what is described for *P. bichir* and its subspecies (Meunier & Gayet, 2020: fig.13). Indeed, when we consider the characters considered diagnostical in extant species in Meunier & Gayet, 2020, it appears that the shape of the head of the pinnula, the degree of individualization of the processes and the ganoin ornamentation on the anterior face of the pinnula are strongly affected by interindividual variation, while the overall shape of the processes seems more reliable, according to our observations on inter-individual variation in *P. bichir*.

CONCLUSIONS

The pinnule morphology was known to depend on the place of the pinnula, and we showed that there is also a strong interindividual variation, independently from the growth (our specimens are roughly of the same size). Moreover we show that this variation hinder or at least limits the use of certain characters for diagnosis, among which most of those used by Meunier & Gayet (2020) for extant species including *P. bichir*. Finally, these results also questioned the validity of the fossil species that were erected based on resembling characters (Gayet & Meunier, 1996; Gayet, Meunier & Werner, 1997; Werner & Gayet, 1997). It appears that in these later papers some intraindividual and intraspecific variation were interpreted as taxonomical variation (see Grande, 2004 for a discussion on the different levels of morphological variation).

In this paper, we followed a rather qualificative way to describe the pinnules, with the main aim to estimate the value of diagnostic characters that were defined so. However, we are convinced that only a quantification of the morphologies together with a systematical exploration of the intra and interindividual variation would allow to properly define diagnostical characters applicable on isolated fossil pinnules. Moreover this might allow to elucidate the probable pattern in the morphological change along the antero-posterior axis of the dorsal fin of *P. bichir* and their common traits among polypterid species.

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Supplemental Information

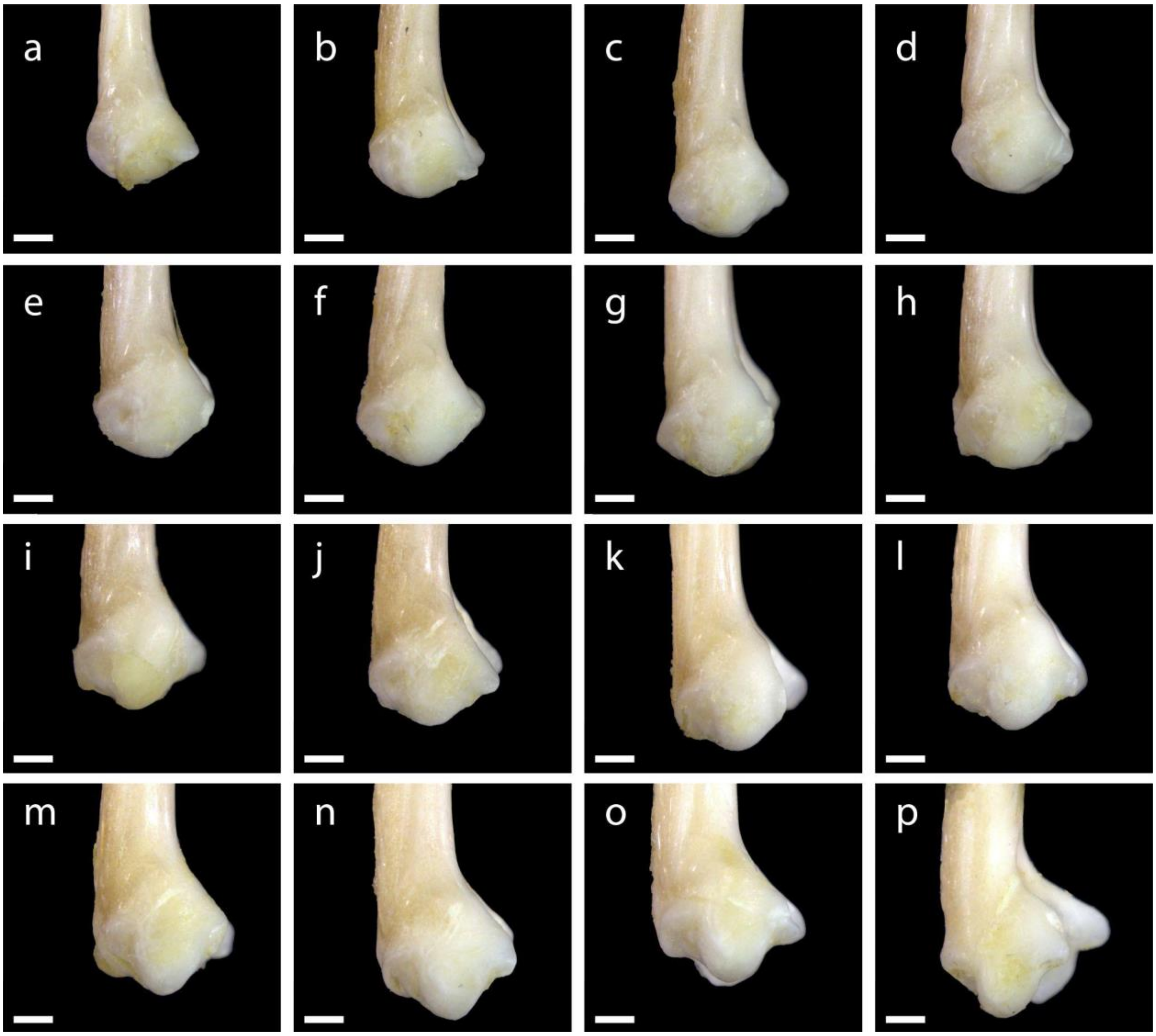

Figure S1 - SEM images of the lateral left view of the pinnules of *P. bichir* PO1. (A-P) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th, 15th and 16th pinnules, respectively. Scale = 1 mm.

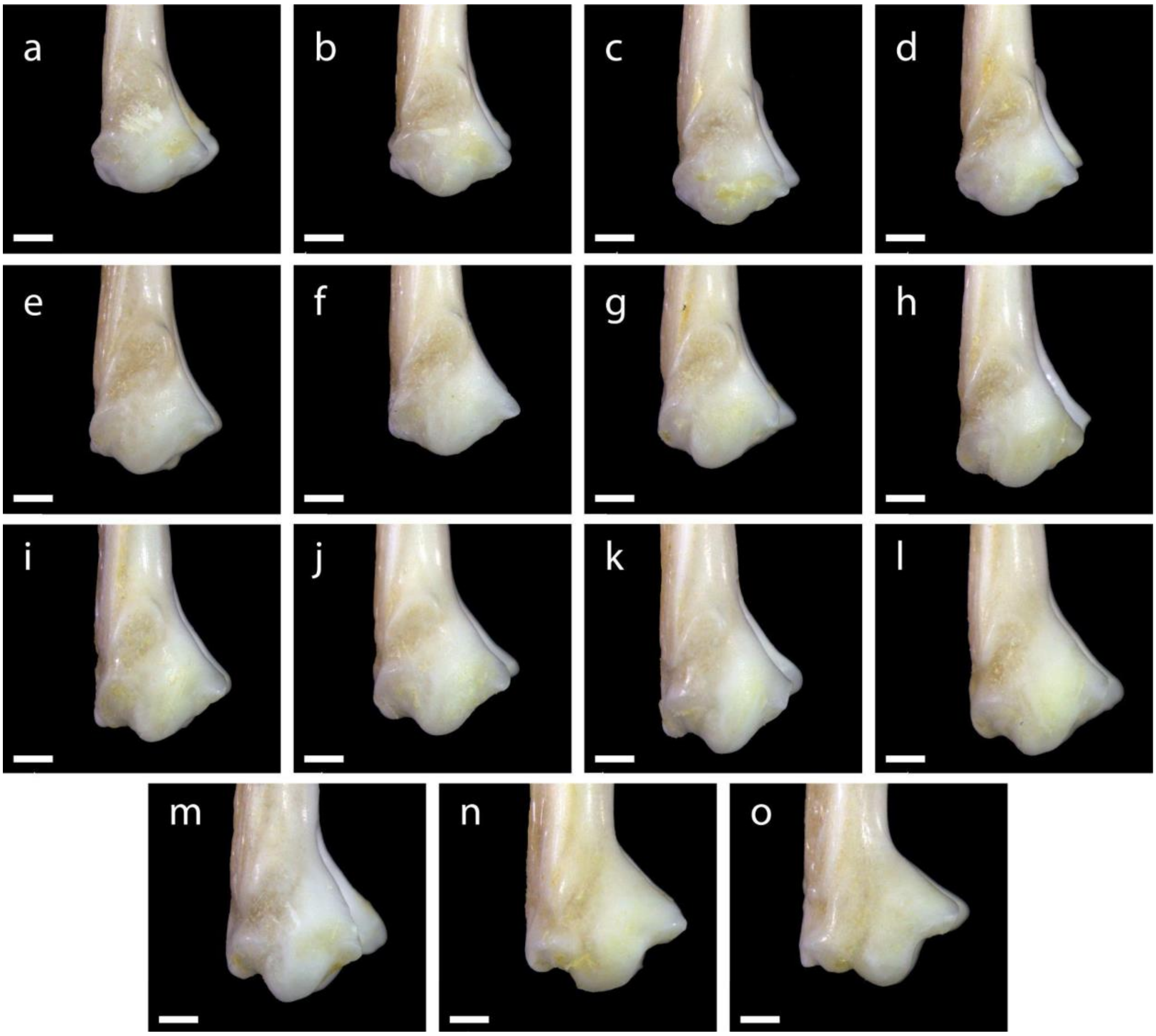

Figure S2 - SEM images of the lateral left view of the pinnules of *P. bichir* PO2. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

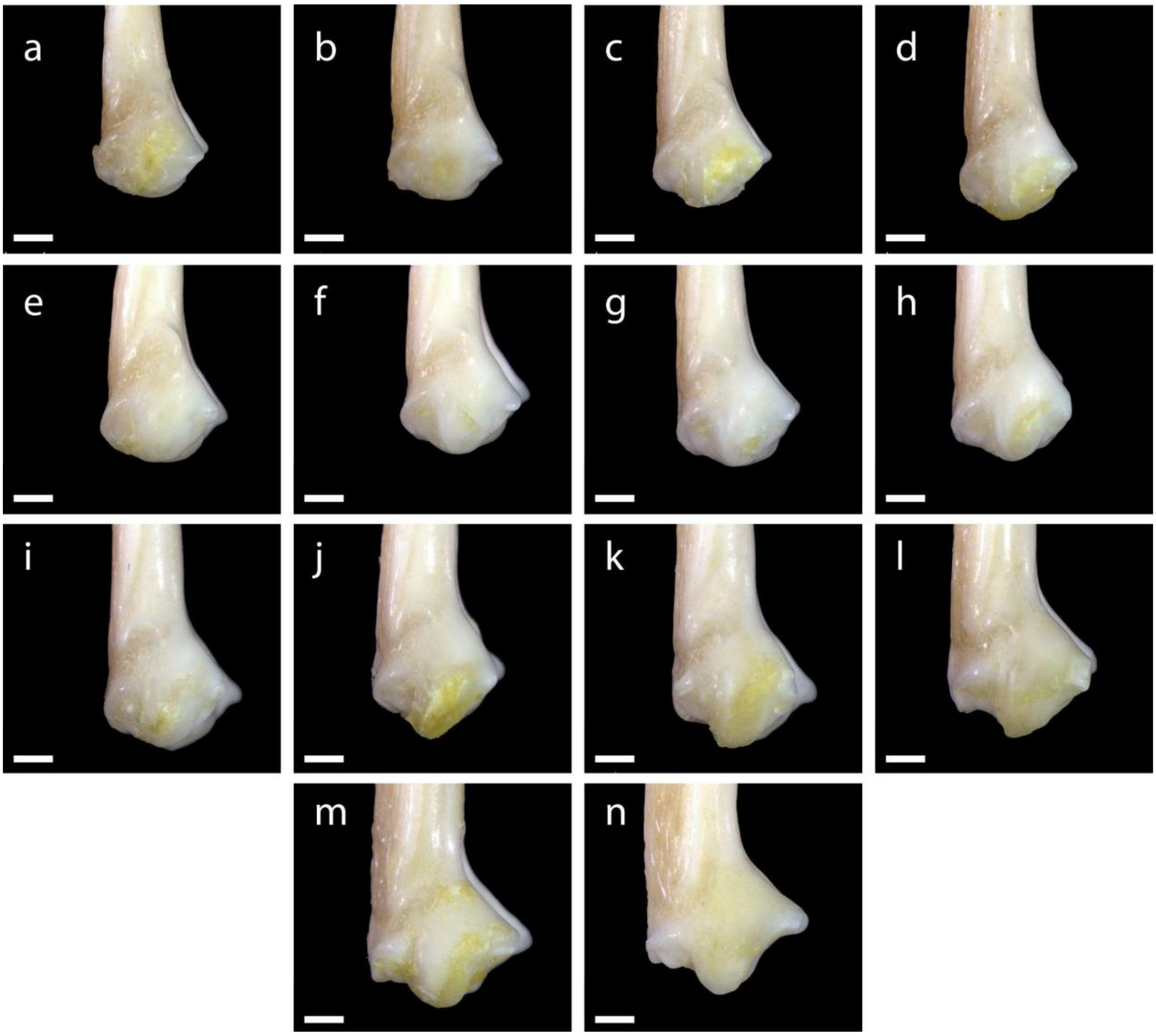

Figure S3 - SEM images of the lateral left view of the pinnules of *P. bichir* PO3. (A-N) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th and 14th pinnules, respectively. Scale = 1 mm.

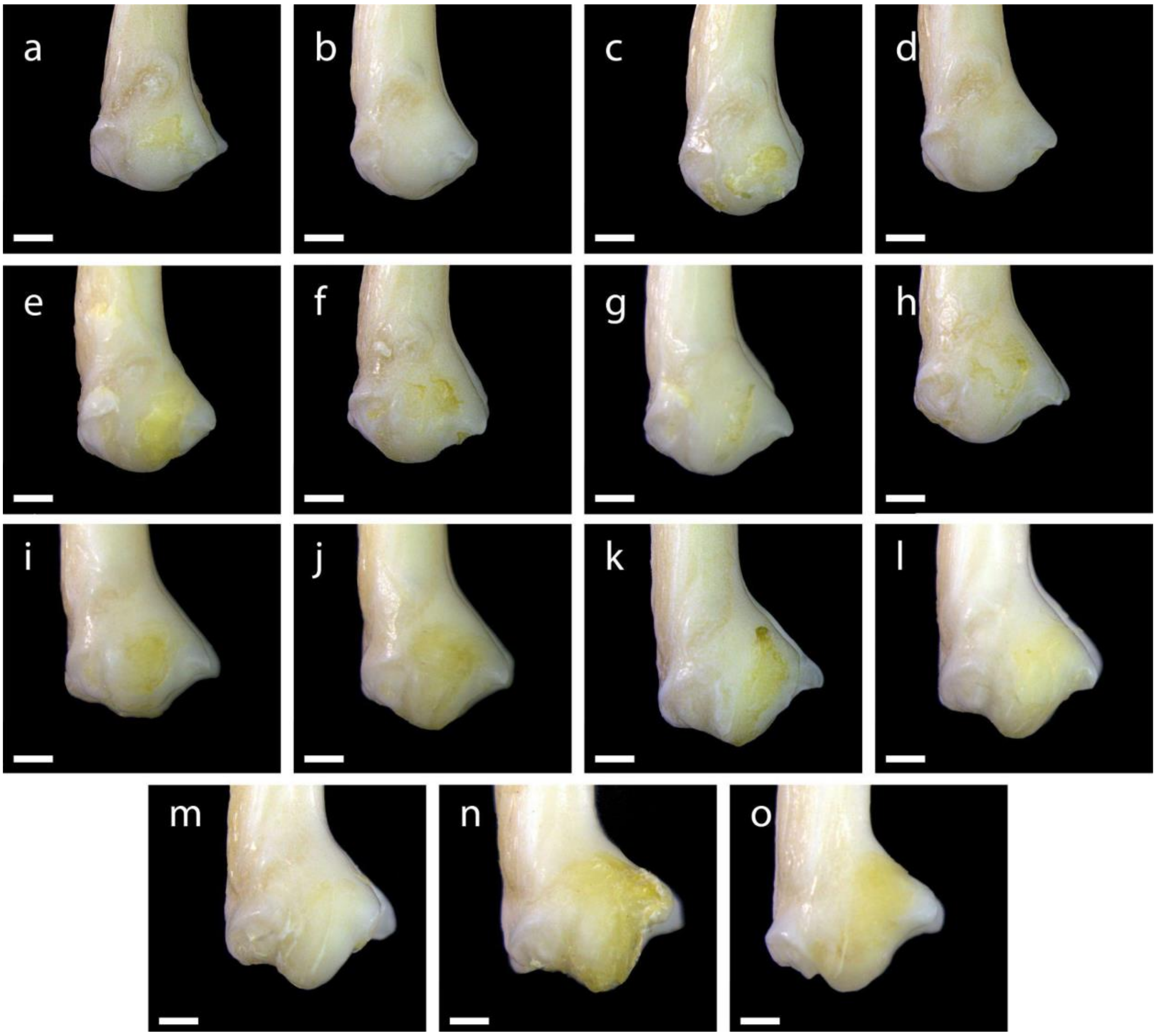

Figure S4 - SEM images of the lateral left view of the pinnules of *P. bichir* PO5. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

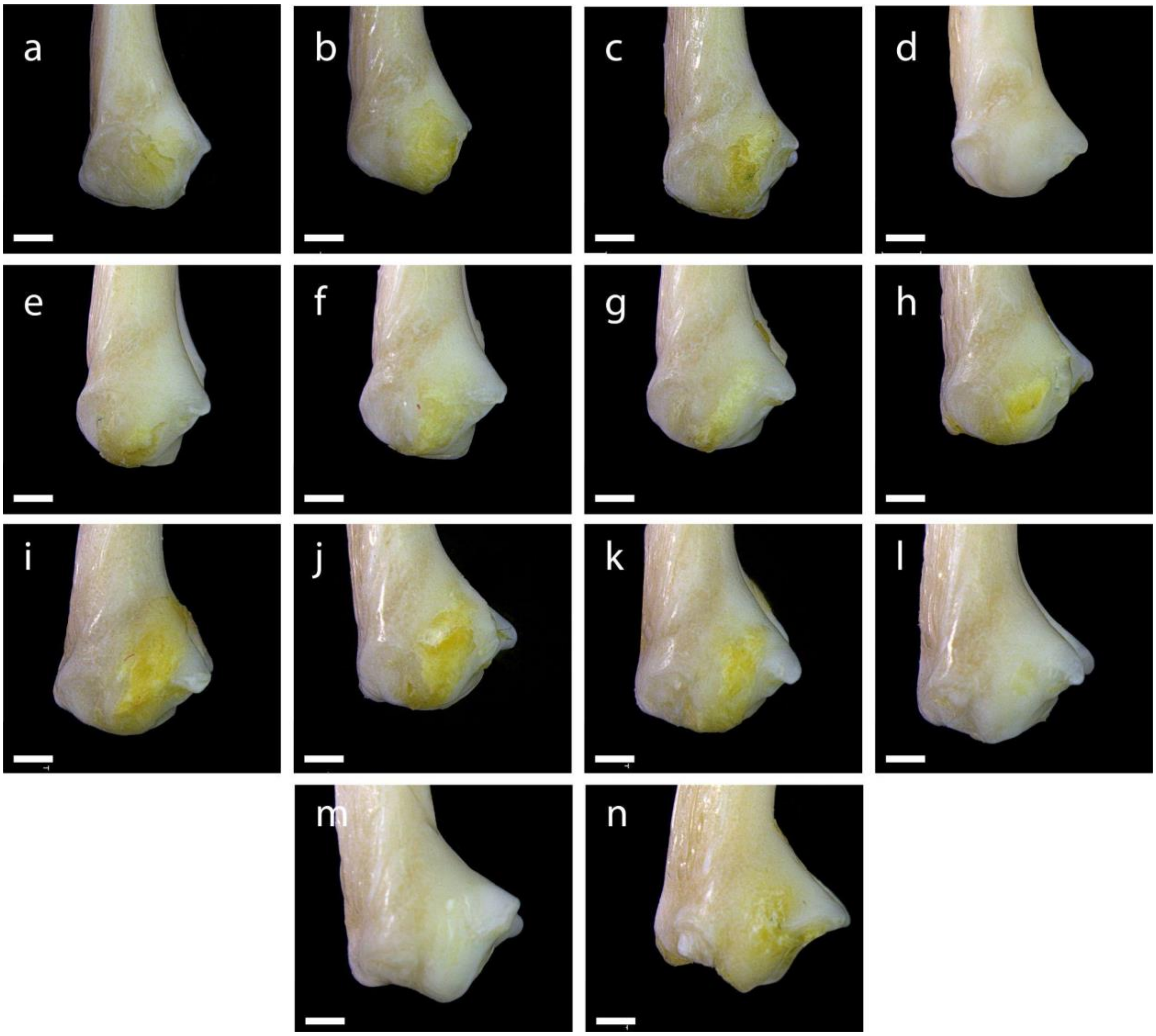

Figure S5 - SEM images of the lateral left view of the pinnules of *P. bichir* PO6. (A-O) corresponds to the 1st, 2nd, 3rd, 4th, 5th, 6th, 7th, 8th, 9th, 10th, 11th, 12th, 13th, 14th and 15th pinnules, respectively. Scale = 1 mm.

5 INTRASPECIFIC AND INTRAINDIVIDUAL VARIATIONS ON THE SCALES ORNAMENTATION IN THE EXTANT POLYPTERID *POLYPTERUS BICHIR*, CHALLENGING THEIR TAXONOMICAL IMPLICATIONS (Artigo submetido)

O presente capítulo está sendo preparado para publicação e, por isso, é apresentado no formato de artigo científico e é tratado como uma seção à parte da presente tese possuindo suas próprias subseções (resumo, introdução, material e métodos, resultados, discussão, conclusão e referências) e está nos moldes de formatação da revista PeerJ - Life & Environment.

Este capítulo aborda a validade da utilização do padrão da ornamentação da ganoína em escamas como ferramenta de separação de espécies em Polypteriformes, pois esse padrão de ornamentação (=tubérculos) é tida como específica em diferentes táxons (Polypteriformes, Lepisosteiformes, Semionotiformes, etc.). Para tanto, analisamos essa ornamentação sob diferentes parâmetros: a distância entre tubérculos centro-a-centro; a quantidade de tubérculos por 100µm²; e a existência de alguma organização preferencial nessas escamas. Mostramos aqui que esses parâmetros são consideravelmente variáveis, não importa a região do corpo, e se sobrepõem aos dados de outras espécies na literatura. As medidas da distância centro-a-centro entre tubérculos mostraram variações significativas na mesma escama e nenhum padrão particular entre escamas de mesma posição. A menor medida foi de 4,88 µm e a maior foi de 15,8 µm. A maior diferença entre a maior e a menor medida na mesma escama foi de 9,69 µm. A densidade de tubérculos por área de 100 µm², quando observada, variou inclusive na mesma escama, a menor contagem foi de 90 tubérculos por 100 µm² de área e a maior foi de 154 tubérculos na mesma área. Além disso, para todas as áreas contadas, o número médio de tubérculos por 100 µm² foi de 115,5. Sobre a organização preferencial, o número de tubérculos em torno de um único tubérculo pode variar de quatro a oito. As disposições mais raras observadas foram com quatro e oito tubérculos ao redor de um único tubérculo. Essas disposições foram encontradas em uma e cinco escamas, respectivamente. As disposições com cinco e sete tubérculos foram encontradas em quase o mesmo número de escamas, foram encontradas em 76% e 74% das escamas analisadas, respectivamente. A disposição com seis tubérculos foi encontrada em todas as escamas analisadas.

ABSTRACT

Ganoid scales can be found in many groups, for example extant and fossil Polypteriformes and Lepisosteiformes. Some authors reported that the ganoin tubercle ornamentation in these scales remain constant for a given species, independently of its position on the body, and as such, that it could be used to separate species or at least groups of species. Here, we analyze the ganoin ornamentation on the scales from different body regions in several specimens of *Polypterus bichir*, in order to test this hypothesis. We analyzed the distance center-to-center between tubercles; counted the number of tubercles per 100 µm² area; and checked if there is any preferential organization. We show here that the distribution of the tubercles is highly variable in the same species and no matter the body region. Moreover it overlaps with the distribution described for different species in the literature. Thus, it seems not possible to find any distinguished pattern on them to be used as diagnostical feature.

Keywords: Polypteridae, Scales, Morphological variation, Taxonomy

INTRODUCTION

Ganoid scales can be found in a range of both extant and fossil non euteleost actinopterygians. They are characterized by their rhomboidal shape, the presence of connective fibers (Sharpey's fibers) and an articulation of the type 'peg-and-socket', and the presence of an enamel cover called ganoine, that is present on most of the exposed surface of the scale (e.g. Kerr, 1957; Schultze, 1996). This type of scale can be divided into two subtypes according to their histology: palaeoniscoid and lepidosteoid. Palaeoniscoid scales are found on all extant Polypteriformes and some fossil taxa, such as some pycnodonts and some pachycormids and are formed by a upper layer of ganoine, a middle layer of dentine and a lower layer of bone. On the other hand, lepidosteoid scales are found in all Lepisosteiformes and some fossil taxa, such as some semiotids and some macrosemiids and they are composed of an upper layer of ganoine and a lower layer of bone, where Canals of Williamson extend from bone layer to the ganoine layer (Goodrich, 1907; Kerr, 1957; Schultze 1996, 2016).

The main function of the scale is to provide protection from predators as a natural armor. During the evolution of fishes, scales became smaller, more numerous and thinner, what improved the animal's maneuverability and increased its speed, allowing the scale to also help with mobility, without losing its protection properties (Raschi & Tabit, 1992; Long & Nipper, 1996; Bruet *et al.*, 2008; Vernerey & Barthelat, 2014). According to Bruet *et al.* (2008), each of the layers of the *Polypterus* scale contributes to the protection role of the scale: each layer has its own particular deformation and energy dissipation mechanisms. The ganoine is a hard and stiff layer that provides load transfer across the ganoine-dentine junction and a circumferential cracking mechanism (see Bruet *et al.*, 2008 for the discussion on cracking patterns).

The dentine layer beneath the ganoine is softer, more compliant and plays a role in the dissipation of energy via plasticity. The isopedine stratified layer, with its plywood-like structure, acts on preventing crack propagation and increasing energy dissipation and fracture resistance. At last, the bone layer acts as the base of the whole structure, giving physical support and also, it is where plastic deformation takes place (Bruet *et al.*, 2008). Finally, the ganoine layer displays an ornamentation of tubercles on its surface (Sire *et al.*, 1987) which function remains unknown whenever it is hypothesized by Zylberberg *et al.* (1985) that they might have a mechanical function in the fixation between the epidermis and the scale.

So finally, it is rather easy to recognize a polypterid scales notably in the Cenozoic deposits since they display the typical palaeoniscoid organization. Indeed, these isolated scales constitute most of the polypterid fossil record. Today, polypterids are endemic in Africa, while their scales are found from the Cenomanian to the Pliocene in Africa (96-2 My), and also from the Maastrichtian to the Thanetian in South America (72-58 My) as a relic of their original Western Gondwanan distribution (e.g. Greenwood, 1974, 1984; Gayet & Meunier, 1992; Meunier & Gayet, 1996; Daget et al., 2001; Gayet *et al*., 2001; Otero *et al*., 2010; 2015). Then they were some tentatives to find a way to find a way to decipher polypterid taxa based on their ganoid cover ornamentation.

In that sense, some authors reported that the diameter and density of tubercles on the same individual remains constant no matter the scale position on the body, not even if it belongs to the lateral line (Gayet & Meunier, 1986; Gayet & Meunier, 1993; Meunier & Gayet, 1996) or is a regenerated scale (Komagata, Suzuki & Kuwabara, 1993). They also suggest that this ornamentation pattern repeats remains conservative in the polypteridae species and consequently to separate taxa at the species level by the differences on the ganoin ornamentation tubercles morphology (distance between tubercles, size of the tubercles, etc). Komagata, Suzuki & Kuwabara (1993) go even further stating that it is possible to separate the scales of males and females specimens of *Erpetoichthys calabaricus*, where females have smoother scales than males, that have bigger and stouter tubercles. However, these hypotheses were never properly tested.

With that aim, we analyze the intraspecific and intraindividual variation on the ganoin ornamentation of selected scales of 4 large specimens of *Polypterus bichir* collected in 2014 in Chad. We aim to evaluate (1) how much the ornamentation pattern is constant in each body regions in specimens from a same species, (2) how much the ornamentation pattern is constant between different body regions in a same specimen, and finally (3) how much the ornamentation pattern is constant in a same species. Finally we also compare the ornamentation observed on scales of our 4 bichirs with those presented in other species in the papers claiming the systematic potential of this ornamentation.

MATERIAL AND METHODS

Specimen information

The scales used in this study were removed from four adult specimens of *Polypterus bichir* (PO2, PO3, PO5, and PO6), ranging from 52 cm to 59 cm in standard length, collected at N'Djamena (Chad) market in 2014 and housed in the collections of the Université de Poitiers.

Scales information

The scales from each specimen were removed from the following body regions (Fig. 1), for each it one of them it was assigned a different code, as following:

D1. Dorsal central scale on the height of the end of the operculum;

D2. Dorsal central scale anterior to the first pinnule;

D3. Dorsal central scale on the height of the middle of the standard length;

D4. Dorsal central scale on the height of the middle between the pelvic and anal fins;

V1. Ventral central scale on the height of the base of the pectoral fin;

V2. Ventral central scale on the height of the middle of the standard length;

V3. Ventral central scale on the height of the middle between the pelvic and anal fins;

L1. Scale of the lateral line on the height of the end of the operculum;

L2. Scale of the lateral line on the height of the middle of the standard length;

L3. Scale of the lateral line on the height of the middle between the pelvic and anal fins;

L4. Scale of the lateral line on caudal fin;

C1. Scale of the caudal fin below the L4;

Additionally, we took some scales (PO5-L2-1, PO5-L2-2, PO5-L2-3, PO5-L2-4, PO5-L2-5, PO5-L2-6 and PO5-L2-7) surrounding the scale L2 from the specimen PO5, in order to check if there is any local pattern on these scales.

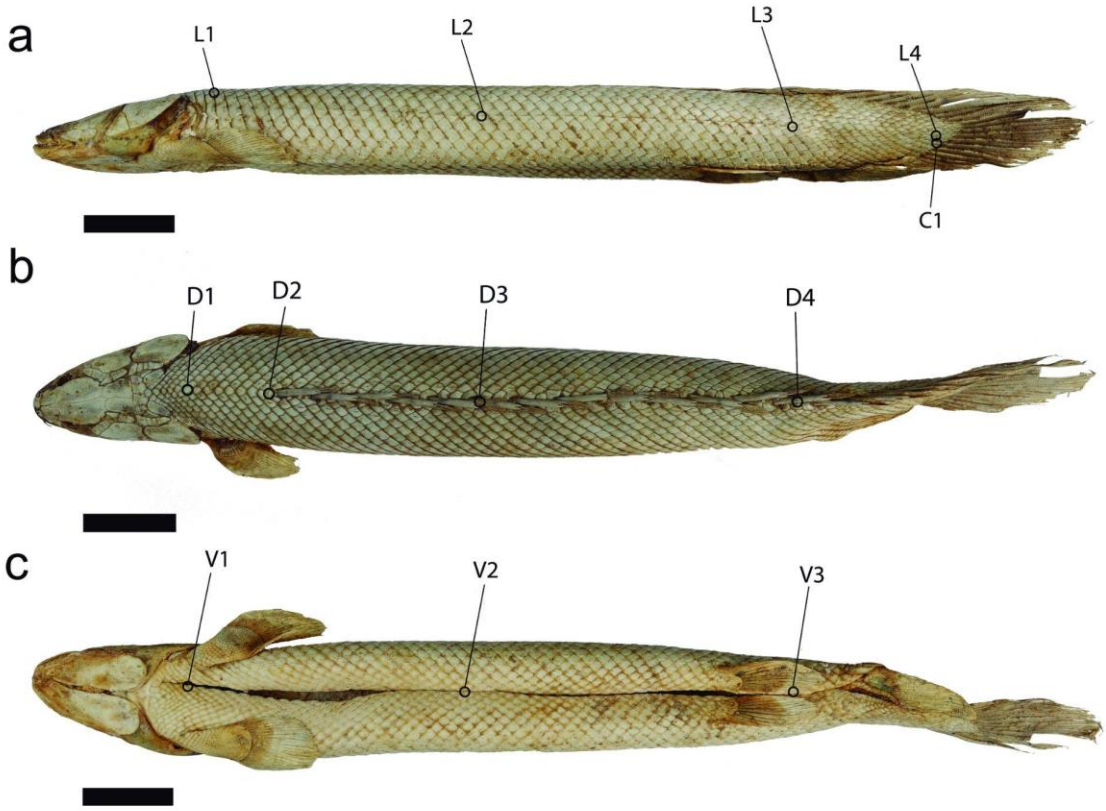

Figure 1- Images of *P. bichir* PO2 in lateral (a), dorsal (b) and ventral (c) views, showing the spots where the scales were removed. D1 = Dorsal central scale on the height of the end of the operculum; D2 = Dorsal central scale anterior to the first pinnule; D3 = Dorsal central scale on the height of the middle of the standard length; D4 = Dorsal central scale on the height of the middle between the pelvic and anal fins; V1 = Ventral central scale on the height of the base of the pectoral fin; V2 = Ventral central scale on the height of the middle of the standard length; V3 = Ventral central scale on the height of the middle between the pelvic and anal fins; L1 = Scale of the lateral line on the height of the end of the operculum; L2 = Scale of the lateral line on the height of the middle of the standard length; L3 = Scale of the lateral line on the height of the middle between the pelvic and anal fins; L4 = Scale of the lateral line on caudal fin; C1 = Scale of the caudal fin below the L4. Scale = 10cm.

Cleaning procedure

All the scales were rinsed with Hydrogen peroxide (H2O2) 3 to 4 times and brushed after each rinse.

Scanning electron microscopy

For scanning electron microscopy, the scales of *P. bichir* were high vacuum coated with tungsten in the Leica EM AC600 metallizer (Leica Microsystems). SEM images were obtained using a SEM Blockface Volumescope at ImageUP.

Measurements

The measurements were made with the assistance of the software Image J. We measured the distance center-to-center between tubercles, at least ten measurements, varying according to the condition of the scale; counted the number of tubercles per 100 µm² area, whenever possible and as much times as possible, also according to the condition of the scale; and checked if there is any preferential organization. As stated by Gayet & Meunier (1993), the diameter of the tubercle as well as the distance between tubercles remain constant in each scale of individuals of the same species. Since we cannot state where the tubercle begins, we cannot replicate their exact methodology, although, it is possible to test their results with the following methodology:

Distance between tubercles center to center = tubercle diameter + distance between tubercles

RESULTS

The measurements of the distance center-to-center between tubercles showed significant variations on the same scale and no particular pattern between scales of the same position (Fig. 2). The lowest measurement was recorded on the scale PO5-V3 of 4,88 µm and the highest measurement was recorded on the scale PO5-L2-4 of 15,8 µm. The biggest difference between the highest and the lowest measurement was also observed on the scale PO5-L2-4 of 9,69 µm.

The density of tubercles per 100 µm² area, when observed, varied even on the same scale, the lowest count was recorded on the scale PO5-L2-4 of 90 tubercles on the area and the highest count was recorded on the scale PO6-D1 of 154 tubercles on the area. Also, for all the counted areas, the average number of tubercles per 100 µm² area was 115,5.

On the preferential organization, the tubercles are disposed as seen in Figure 3. The number of tubercles around one single tubercle can vary from four to eight. The rarest dispositions that were observed were with four and eight tubercles around a single tubercle. These dispositions were found in one and five scales, respectively. The dispositions with five and seven tubercles were found in almost the same number of scales, they were found in 76% and 74% of the scales analyzed, respectively. The disposition with six tubercles was found in all the scales analyzed.

DISCUSSION

As stated above, some authors claimed that tubercles are good parameters to separate species (Gayet & Meunier, 1986; Gayet & Meunier, 1993 Meunier & Gayet, 1996). For these authors, the size and the distance between them are constant and specific for each species, which also causes the density of tubercles to be constant (Gayet & Meunier, 1986; Gayet & Meunier, 1993 Meunier & Gayet, 1996). Here we gathered these measures from the literature to show the values for each species (Tabl. 1).

Species	Tubercle diameter (µm)	Distance intertubercle (µm)	Diameter + distance (µm)	Reference
Dagetella sudamericana	3,2	5,8	9	Gayet & Meunier, 1993 / Meunier & Gayet, 1996
Erpetoichthys calabaricus	2,98	5,57	8,55	Gayet & Meunier, 1993 / Meunier & Gayet, 1996
Latinopollia suarezi	5,3	7,5	12,8	Meunier & Gayet, 1996
Polypterus bichir bichir	2,63	6,19	8,82	Gayet & Meunier, 1993 / Meunier & Gayet, 1996
Polypterus bichir lapradei	2,53	6,6	9,13	Gayet & Meunier, 1993
Polypterus delhezi	2,19	5,76	7,95	Gayet & Meunier, 1993
Polypterus endlicherii	2,54	5,87	8,41	Gayet & Meunier, 1993
Polypterus ornatipinnis	2,81	5,97	8,78	Gayet & Meunier, 1993
Polypterus palmas	3,03	6,71	9,74	Gayet & Meunier, 1993
Polypterus retropinnis	2,81	8,54	11,35	Gayet & Meunier, 1993
Polypterus senegalus	2,63	8,17	10,8	Gayet & Meunier, 1993 / Meunier & Gayet, 1996
Polypterus weeksii	2,63	7,23	9,86	Gayet & Meunier, 1993

Table 1- Values of tubercle diameter, distance intertubercle and the sum of these two values for scales of polypteridae species. Modified from Gayet & Meunier, 1993 and Meunier & Gayet 1996.

As seen in table 1, the minimum and the maximum value for the tubercle diameter + distance between tubercles, in the literature, is recorded for *Polypterus delhezi* (7,95 µm) and *Latinopollia suarezi* (12,8 µm), respectively. All these values are overlapping with our measurements on the scales of *P. bichir*, which shows that in a single species, it is possible to find a considerable variation for the distance center-to-center of tubercles. The overlap on these parameters was already mentioned by Schultze (1996) regarding the values for *Latinopollia suarezi*.

We have shown here that the parameters we have tested for the scales of *P. bichir* are considerably variable, no matter the body region, and overlapping with the data for other species in the literature - contrasting with former studies. So, based on this high variability and overlapping, it was not possible to find some distinguished pattern on these scales that made possible the separation from other species of the same group. Therefore, we strongly suggest that these parameters are not used to separate Polypteridae species.

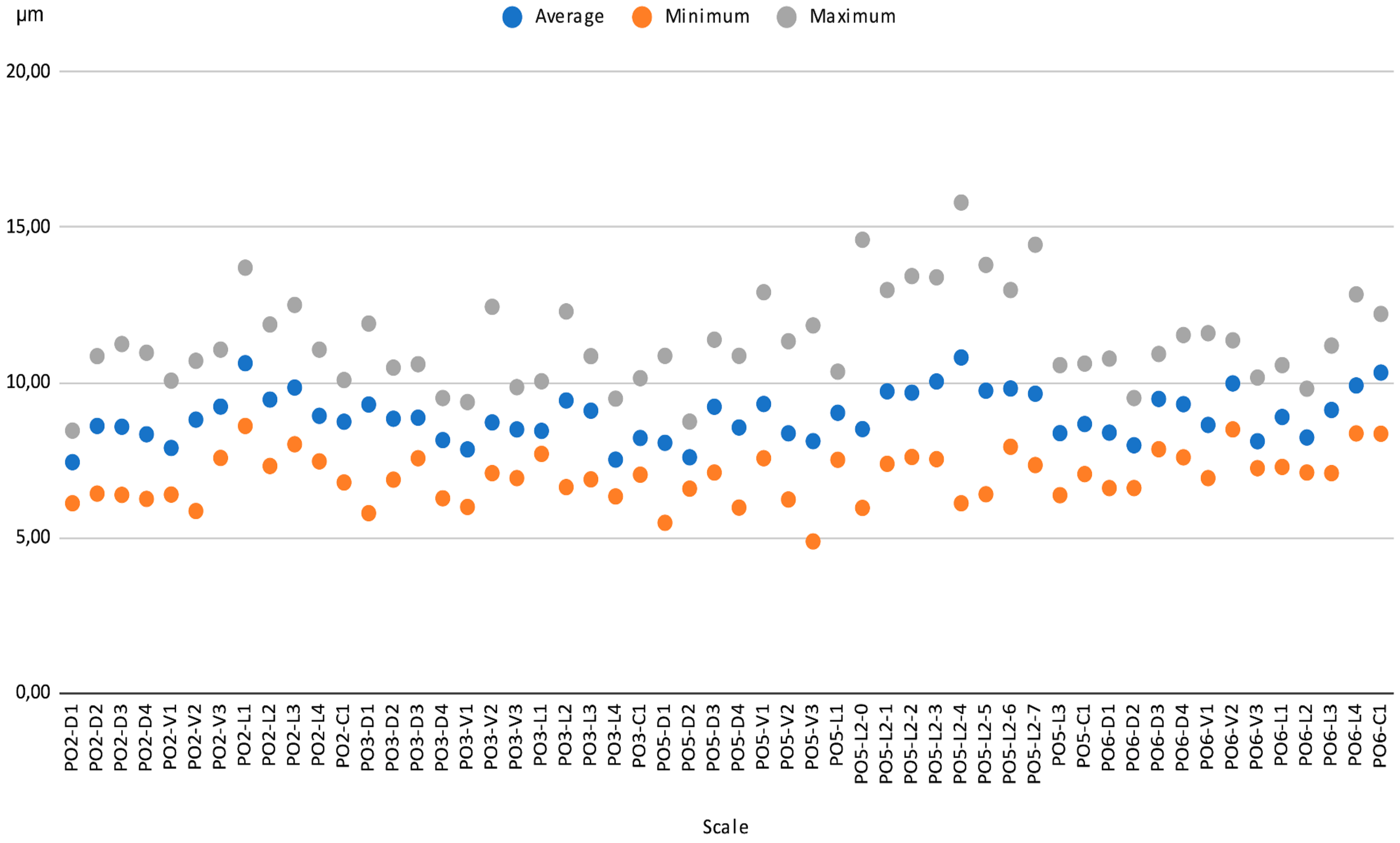
µm
● Average
● Minimum
● Maximum
20,00
15,00
10,00
5,00
0,00
PO2-D1
PO2-D2
PO2-D3
PO2-D4
PO2-V1
PO2-V2
PO2-V3
PO2-L1
PO2-L2
PO2-L3
PO2-L4
PO2-C1
PO3-D1
PO3-D2
PO3-D3
PO3-D4
PO3-V1
PO3-V2
PO3-V3
PO3-L1
PO3-L2
PO3-L3
PO3-L4
PO3-C1
PO5-D1
PO5-D2
PO5-D3
PO5-D4
PO5-V1
PO5-V2
PO5-V3
PO5-L1
PO5-L2-0
PO5-L2-1
PO5-L2-2
PO5-L2-3
PO5-L2-4
PO5-L2-5
PO5-L2-6
PO5-L2-7
PO5-L3
PO5-C1
PO6-D1
PO6-D2
PO6-D3
PO6-D4
PO6-V1
PO6-V2
PO6-V3
PO6-L1
PO6-L2
PO6-L3
PO6-L4
PO6-C1
Scale

Figure 2. Graph showing the average, minimum and maximum scores for the distance center-to-center between tubercles (µm) for each scale used in this study.

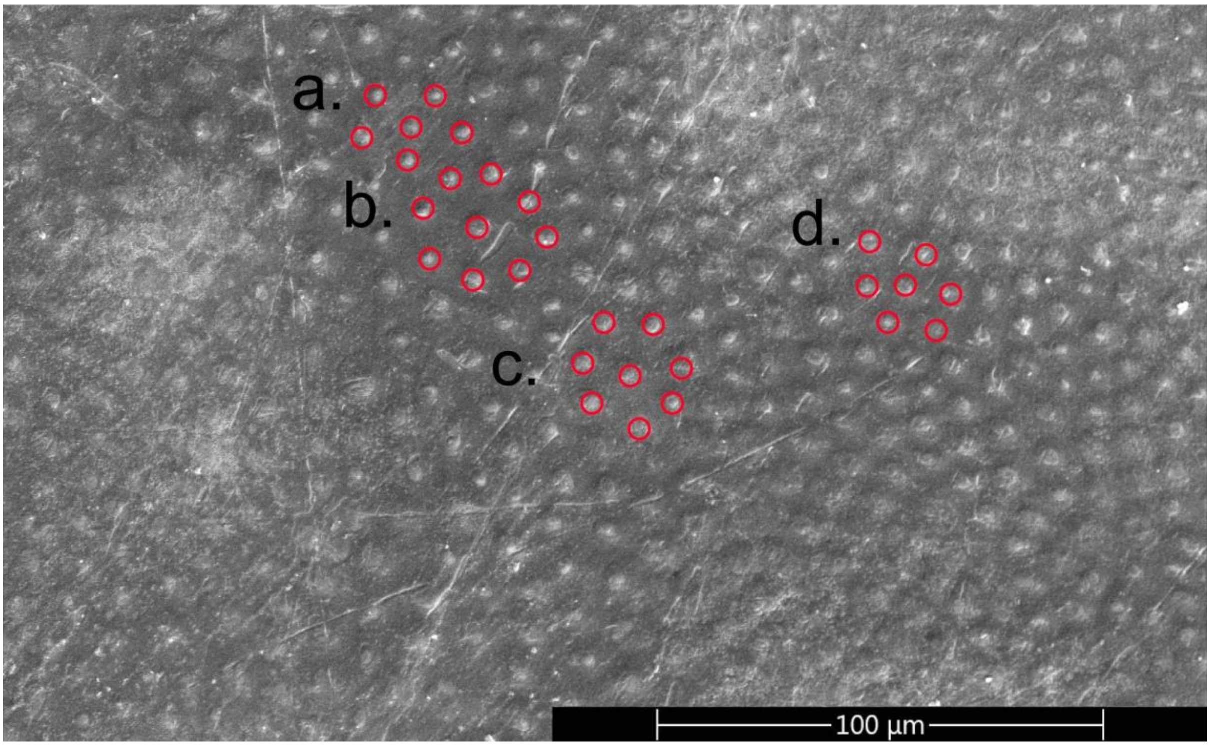

Figure 3 SEM image of a section of the scale PO5-L2-4 showing the patterns on tubercle organization. It is possible to observe five (a), six (d), seven (c) and eight (b) tubercles around one single tubercle. Scale = 100 µm.

CONCLUSIONS

As shown throughout this work, the diameter of tubercles, the distance between tubercles and the density on the scale seems not viable as a morphological tool to distinguish species of Polypteriformes. However, we should complete this preliminary work in *Polypterus bichir* with a statistical analysis of the variables distribution in each fish to definitely exclude or on the contrary identify some taxonomical value of the ganoid ornamentation pattern.

Additionally, the same statement was made for other groups of fishes (*e.g.* Lepisosteiformes and Semionotiformes) (Meunier & Gayet, 1992; Gayet & Meunier, 1993 and 2001; Gayet, Meunier, & Werner, 2002). As the present work does not regard these specific groups, further investigation is more widely needed to confirm the viability of these parameters in scales of those groups.

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6 **DISCUSSÃO GERAL**

Devido ao histórico taxonômico conturbado dos Polypteriformes (ver o capítulo 3 para descrição detalhada desse histórico) (GOSSE, 1988; HANSSENS *et al*., 1995; MORITZ; BRITZ, 2019; POLL, 1941; 1942; 1954; STEINDACHNER, 1895; SUZUKI *et al*., 2010), a presente tese teve como intuito revisar a taxonomia da ordem, baseando-se em caracteres morfológicos. Para isso, testou-se a delimitação das espécies atuais com base em sua osteologia (capítulo 3) e a empregabilidade de certos complexos anatômicos como ferramentas de distinção dessas espécies (capítulos 4 e 5).

Em relação à delimitação das espécies, foi possível distingui-las com base nas diferenças osteológicas do crânio e da nadadeira caudal. Pode-se separar as espécies aqui presentes da seguinte forma: *Erpetoichthys* se difere das espécies de *Polypterus*, onde *Erpetoichthys* apresenta um pós-orbital mais robusto, com uma parte dorsal maior; ausência de placas faciais; pré-opérculo com a mesma altura de seu processo ventral, que é consideravelmente maior que em *Polypterus*; opérculo triangular com limite posterior arredondado; e um ceratohial anterior mais fino. Entre as espécies de *Polypterus*, *P. bichir* e *P. endlicherii* distinguem-se das demais por sua pré-maxila mais curta (antero-posterior); maxila mais curta (antero-posterior) e mais robusta (ventral-dorsalmente); e região do neurocrânio proporcionalmente mais longa e mais baixa. Entre eles, *P. bichir* apresenta região opercular proporcionalmente maior (⅔ da cabeça) e *P. endlicherii* processo ventral do pré-opérculo ligeiramente curvado para frente. *P. ornatipinnis*, *P. palmas* e *P. polli* apresentam um angular subretangular, comparativamente mais baixo que o das demais espécies. *P. palmas* apresenta uma placa facial mais robusta e subopérculo maior em comparação com *P. ornatipinnis* e *P. polli*. Estas duas últimas diferenciam-se onde *P. ornatipinnis* tem um rostral subtriangular ou subretangular e um lacrimal subretangular e *P. polli* tem um rostral losangular e um lacrimal subtriangular. *P. retropinnis* é separado de *P. delhezi* e *P. senegalus* por apresentar o extraescapular mais lateral mais curto que termina antes do último osso pós-espiracular; um processo ventral mais robusto do pré-opérculo; e um subopérculo mais fino. *P. delhezi* apresenta um subopérculo proporcionalmente maior que *P. senegalus*; e maior contagem de ossos pós-espiraculares (3, 4 ou 5 contra 2 ou 3). E finalmente, *P. weeksii* se distingue dos demais por seu frontal com um processo antero-medial agudo que separa o par de 3 nasais, 3 pares de aberturas de canal no frontal e uma alta contagem de ossos pré-espiraculares (6 a 8), onde a duplicação desses ossos é frequente. Além das diferenças encontradas nos crânios, os elementos da nadadeira caudal parecem ser específicos, apesar de não exclusivos.

Nossos resultados corroboram com dados da literatura para o rostral e nasal 3 (GRANDE 2010; POLL, 1941; 1942; RIZZATO *et al*., 2020); ossos espiraculares e dermohial (ALLIS, 1922; BARTSCH, 1997; JOLLIE, 1984; POLL, 1941; 1942); região opercular (ALLIS, 1922; CLAESON et al., 2007); lacrimal (ALLIS, 1922; GRANDE, 2010); dentário, mentomeckeliano, coronóide 1 e 2, articular e pré-articular (ALLIS, 1922; CLAESON *et al*., 2007; GRANDE, 2010; JOLLIE, 1984); ossos do neurocrânio (ALLIS, 1922; GRANDE, 2010); ceratohial anterior (CLAESON *et al*., 2007); ossos do palato (ALLIS, 1922; CLAESON *et al*., 2007 (parcialmente); GERAUDIE, 1988; GOODRICH, 1909; GRANDE, 2010; JOLLIE, 1984; TRAQUAIR, 1866). Eles são complementares em relação aos ossos pré-espiraculares e pós-espiraculares (ALLIS, 1922; POLL, 1941; 1942); e elementos da nadadeira caudal (BARTSCH; GEMBALLA, 1992; GEMBALLA, 2004; GRANDE, 2010). Porém eles divergem sobre o subopérculo em *E. calabaricus* (CLAESON *et al*., 2007; JOLLIE, 1984; MORITZ; BRITZ, 2019; SMITH, 1866; TRAQUAIR, 1870); e sobre o paraesfenóide e endopterigóide em E. calabaricus (CLAESON *et al*., 2007).

Estas diferenças osteológicas apontadas aqui corroboram com a separação destas espécies através dos caracteres merísticos e contínuos apresentados por Moritz e Britz, 2019. As únicas exceções encontradas foram os espécimes MNHN-IC-1958-0026 e MNHN-IC-1977-0308 A e B de *P. palmas* que possuem a morfologia do crânio condizente com a espécie, inclusive já estavam previamente identificados assim, mas suas contagens de pínulas e escamas condizem com as apresentadas por Moritz e Britz (2019) para *P. polli*. MNHN-IC-1958-0026 apresentou 6 pínulas e 37 escamas pré-pélvicas; MNHN-IC-1977-0308 A 7 pínulas e 37 escamas pré-pélvicas e MNHN-IC-1977-0308 B 6 pínulas e 36 escamas pré-pélvicas.

As duas espécies são muito parecidas na sua morfologia externa, tanto que *P. polli* já foi considerada subespécie de *P. palmas* e essa mudança foi revertida com base em dados moleculares (HANSSENS *et al*., 1995; SUZUKI *et al*., 2010). De acordo com a revisão proposta por Moritz e Britz (2019), *P. palmas* se diferencia de *P. polli* por apresentar uma combinação no número de pínulas (7-10 *vs*. 5-8, respectivamente) e escamas pré-pélvicas (39-45 *vs*. 34-40, respectivamente). No caso de espécimes onde há a interseção do número de pínulas esperado de ambas as espécies, ou seja, 7 ou 8 pínulas, estas são distinguidas pela contagem de escamas pré-pélvicas, onde *P. palmas* apresenta 39 a 45 dessas escamas e *P. polli* 35 a 38 das mesmas (MORITZ; BRITZ, 2019 - Figura 46).

Além disso, as duas espécies não são encontradas nas mesmas localidades, *P. palmas* é encontrado no oeste africano, região da Guiné, do rio Casamance, Senegal, até a bacia Cavally, na Costa do Marfim (MORITZ; BRITZ, 2019 - Figura 43); e *P. polli* é encontrado na África central, na bacia hidrográfica do Congo, em diversas localidades (MORITZ; BRITZ, 2019 - Figura 49). Os três espécimes de *P. palmas* citados acima foram coletados em localidades típicas de *P. polli*, Camarões e República Democrática do Congo.

Como no presente estudo apenas um espécime de *P. polli* esteve disponível e levando em consideração o que foi discutido anteriormente, a divisão dessas espécies permanece confusa e requer maior atenção em trabalhos futuros.

Sobre a empregabilidade de certos complexos anatômicos como ferramentas de distinção dessas espécies, aqui foram abordadas questões sobre pínulas e escamas. Em relação às pínulas, continuamos a discussão sobre sua validade taxonômica para separar espécies. Ao analisar as pínulas de diferentes espécimes de *P. bichir*, pode-se notar um padrão semelhante na variação morfológica nas pínulas dos espécimes ao longo da nadadeira dorsal (eixo antero-posterior). Em todos os espécimes observados, independente do número de pínulas, pode-se observar que os processos basais tornam-se mais proeminentes e mais separados, tornando as últimas pínulas mais abertas; a cavidade glenóide se torna maior; o forâmen basal também se torna maior; e o processo mediano inicia-se menos desenvolvido e um pouco curvado para cima ou plano e torna-se mais proeminente e apresentando duas projeções orientadas para baixo. No entanto, além desse padrão, algumas diferenças entre os espécimes foram observadas: os espécimes PO2 e PO6 apresentam predominantemente a cabeça da pínula com formato geral quadrado, onde PO1, PO3 e PO5 apresentam formato predominantemente trapezoidal; todos os exemplares apresentam a cabeça da pínula mais larga que o corpo, exceto PO6, que apresenta a cabeça tão larga quanto o corpo; e todos os espécimes apresentam processos bem individualizados, exceto PO6, que apresenta processos menos individualizados (exceto os processos posteriores).

A largura da cavidade glenóide, que é um caráter diagnóstico para *P. ansorgii*, *P. bichir* e *P. endlicherii* de acordo com Meunier e Gayet (2020), parece estar mais relacionada à posição na nadadeira dorsal do que à espécie, pois as pínulas mais posteriores têm uma cavidade glenóide mais larga devido à sua posição fundindo-se na nadadeira caudal. Este padrão na cavidade glenóide também pode ser observado nas últimas pínulas de *P. delhezi* e *P. endlicherii* (COELHO *et al*., 2018: figs. 6I-J).

Adicionalmente, a ornamentação de ganoína e dentina na face anterior das pínulas observadas nos bichirs do Chade (Cap. 4: figs. 7-11) se assemelha mais ao descrito para *P.*

weeksii (diagnóstico para a espécie), do que ao descrito para *P. bichir* e suas subespécies (MEUNIER; GAYET, 2020: fig.13). De fato, quando consideramos os caracteres tidos como diagnósticos em espécies existentes em Meunier e Gayet (2020) verifica-se que a forma da cabeça da pínula, o grau de individualização dos processos e a ornamentação de ganoína na face anterior da pínula são fortemente afetados pela variação interindividual, enquanto a forma geral dos processos parece mais confiável, de acordo com nossas observações sobre a variação interindividual em P. bichir.

Além disso, mostramos que essa variação dificulta ou pelo menos limita o uso de certos caracteres para diagnóstico, entre os quais a maioria dos usados por Meunier e Gayet (2020) para espécies viventes, incluindo *P. bichir*. Por último, esses resultados também questionam a validade das espécies fósseis que foram descritas com base em caracteres semelhantes (GAYET; MEUNIER, 1996; GAYET *et al.*, 1997; WERNER; GAYET, 1997). Parece que nesses trabalhos algumas variações intraindividuais e intraespecíficas foram interpretadas como variação taxonômica (ver GRANDE (2004) para uma discussão sobre os diferentes níveis de variação morfológica).

Acerca da ornamentação das escamas, alguns autores afirmam que os tubérculos são bons parâmetros para separar espécies (GAYET; MEUNIER, 1986; GAYET; MEUNIER, 1993; MEUNIER; GAYET, 1996). Para esses autores, o tamanho e a distância entre eles são constantes e específicos para cada espécie, o que também faz com que a densidade dos tubérculos seja constante (GAYET; MEUNIER, 1986; GAYET; MEUNIER, 1993; MEUNIER; GAYET, 1996).

Conforme observado no capítulo 5, o valor mínimo e máximo para o diâmetro do tubérculo mais distância entre tubérculos, na literatura, é registrado para *Polypterus delhezi* (7,95 µm) e para a espécie fóssil *Latinopollia suarezi* (12,8 µm), respectivamente. Todos esses valores se sobrepõem às nossas medidas nas escamas de *P. bichir*, o que mostra que em uma única espécie é possível encontrar uma variação considerável para a distância centro-a-centro dos tubérculos. A sobreposição desses parâmetros já foi mencionada por Schultze (1996) em relação aos valores para *Latinopollia suarezi*.

Foi mostrado aqui que os parâmetros testados para as escamas de *P. bichir* são consideravelmente variáveis, independentemente da região do corpo, e se sobrepõem aos dados de outras espécies na literatura - contrastando com estudos anteriores (GAYET; MEUNIER, 1996; GAYET *et al.*, 1997; MEUNIER; GAYET, 2020; WERNER; GAYET, 1997). Assim, com base nessa alta variabilidade e sobreposição, não foi possível encontrar algum padrão diferenciado nessas escamas que possibilitasse a separação de outras espécies do mesmo grupo.

CONCLUSÃO

O presente estudo tentou contribuir para a elucidação de diferentes problemas acerca da taxonomia de Polypteridae, incluindo a definição de caracteres diagnósticos aplicáveis ao registro fóssil. Podemos resumir estas contribuições da seguinte forma: 1) As diferenças apresentadas aqui são promissoras para separar claramente as espécies de Polypteridae atuais, principalmente o rostral, lacrimal, série espiracular, região opercular e nadadeira caudal. Apesar de não ser exclusivamente específico, o número de elementos da nadadeira caudal parece ser eficiente para distinguir as espécies. Uma amostra maior é necessária para confirmar esta proposição. Um estudo da ontogenia de *E. calabaricus* é necessário para entender a existência de um possível osso subopercular nesta espécie. Ainda é necessário adicionar as demais espécies do grupo (*P. ansorgii*, *P. congicus*, *P. mokelembembe* e *P. teugelsi*) para completar o conjunto de dados deste estudo. Após, todos estes dados serão usados para se propor uma hipótese de relacionamento filogenético dos Polypteriformes, incluindo, se possível, formas fósseis. 2) Como mostrado aqui, é importante entender se os padrões morfológicos relacionados ao eixo antero-posterior da nadadeira dorsal de *P. bichir* se repetem nas outras espécies de polypterídeos ou se é algo exclusivo. Uma análise morfométrica pode ser capaz de elucidar esses padrões, que podem ser extrapolados aos fósseis isolados posteriormente. Devido às inconsistências discutidas aqui, mais investigação é necessária sobre as pínulas de todos os polypterídeos atuais, para melhor entender os diferentes tipos de variação (*i.e.* interespecífica, intraespecífica e intraindividual) neste complexo anatômico. Só então, será possível determinar: i) se é possível identificar as espécies viventes com base somente na morfologia de pínulas; ii) a validade das diagnoses propostas por Meunier & Gayet (2020); e iii) a validade dos táxons fósseis descritos com base em pínulas isoladas. 3) Como visto, a ornamentação de ganoína (*i.e.* diâmetro dos tubérculos, a distância entre tubérculos e a densidade dos tubérculos) na superfície de escamas não é viável como ferramenta morfológica de separação das espécies de Polypteriformes. Apesar deste trabalho ter uma abordagem qualitativa, é necessário completá-lo com uma análise estatística da distribuição das variáveis em cada peixe para excluir definitivamente ou identificar algum valor taxonômico do padrão de ornamentação da ganoína nessas escamas.

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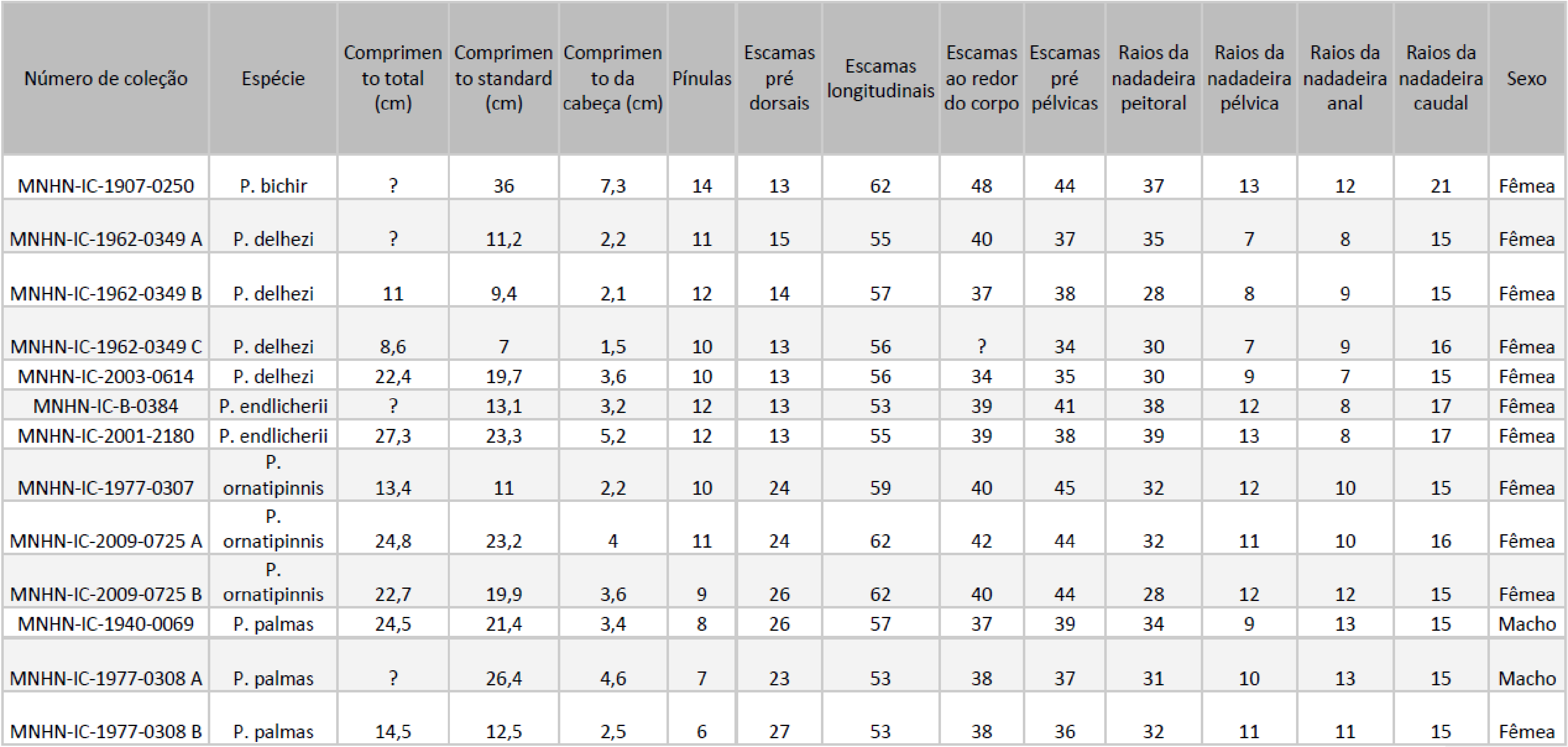
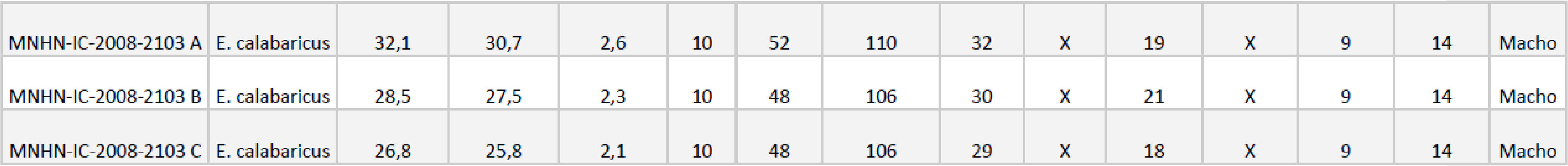
APÊNDICE – Medidas e contagens feitas nos espécimes estudados na presente tese



Número de coleção	Espécie	Comprimento total (cm)	Comprimento standard (cm)	Comprimento da cabeça (cm)	Pínulas	Escamas pré dorsais	Escamas longitudinais	Escamas ao redor do corpo	Escamas pré pélvicas	Raios da nadadeira peitoral	Raios da nadadeira pélvica	Raios da nadadeira anal	Raios da nadadeira caudal	Sexo
MNHN-IC-1907-0250	P. bichir	?	36	7,3	14	13	62	48	44	37	13	12	21	Fêmea
MNHN-IC-1962-0349 A	P. delhezi	?	11,2	2,2	11	15	55	40	37	35	7	8	15	Fêmea
MNHN-IC-1962-0349 B	P. delhezi	11	9,4	2,1	12	14	57	37	38	28	8	9	15	Fêmea
MNHN-IC-1962-0349 C	P. delhezi	8,6	7	1,5	10	13	56	?	34	30	7	9	16	Fêmea
MNHN-IC-2003-0614	P. delhezi	22,4	19,7	3,6	10	13	56	34	35	30	9	7	15	Fêmea
MNHN-IC-B-0384	P. endlicherii	?	13,1	3,2	12	13	53	39	41	38	12	8	17	Fêmea
MNHN-IC-2001-2180	P. endlicherii	27,3	23,3	5,2	12	13	55	39	38	39	13	8	17	Fêmea
MNHN-IC-1977-0307	P. ornatipinnis	13,4	11	2,2	10	24	59	40	45	32	12	10	15	Fêmea
MNHN-IC-2009-0725 A	P. ornatipinnis	24,8	23,2	4	11	24	62	42	44	32	11	10	16	Fêmea
MNHN-IC-2009-0725 B	P. ornatipinnis	22,7	19,9	3,6	9	26	62	40	44	28	12	12	15	Fêmea
MNHN-IC-1940-0069	P. palmas	24,5	21,4	3,4	8	26	57	37	39	34	9	13	15	Macho
MNHN-IC-1977-0308 A	P. palmas	?	26,4	4,6	7	23	53	38	37	31	10	13	15	Macho
MNHN-IC-1977-0308 B	P. palmas	14,5	12,5	2,5	6	27	53	38	36	32	11	11	15	Fêmea

MNHN-IC-1958-0026	P. palmas	?	21,4	3,7	6	24	52	38	37	30	10	14	14	Macho
MNHN-IC-1900-0197	P. polli	13,3	11,6	2,3	5	27	53	35	36	31	9	7	15	Fêmea
MNHN-IC-1963-0239	P. retropinnis	?	25,1	3,8	8	31	58	35	43	34	7	11	14	Macho
MNHN-IC-1964-0253	P. retropinnis	?	28,9	4,7	7	32	56	36	42	32	8	7	?	Fêmea
MNHN-IC-1930-0001 A	P. retropinnis	?	7	1,4	7	32	58	32	44	29	8	11	?	Fêmea
MNHN-IC-1930-0001 B	P. retropinnis	?	7	1,4	7	30	55	?	42	25	7	10	16	Fêmea
MNHN-IC-1930-0001 C	P. retropinnis	?	6,8	1,4	7	30	56	?	39+	26	8	9	?	Fêmea
MNHN-IC-1904-0068	P. senegalus	30,2	27,1	4,1	9	18	58	38	38	30	10	12	16	Macho
MNHN-IC-1908-0004	P. senegalus	12	10,3	2	10	18	57	37	37	31	8	10	17	Fêmea
MNHN-IC-1984-0508 A	P. senegalus	19	17	2,9	9	18	58	35	39	31	8	11	14	Fêmea
MNHN-IC-1984-0508 B	P. senegalus	?	11,4	2	9	17	54	32	37	32	10	9	14	Fêmea
MNHN-IC-1961-0009 A	P. senegalus	?	19,5	3,1	10	18	59	37	39	35	10	9	15	Fêmea
MNHN-IC-1961-0009 B	P. senegalus	?	12,8	2,3	9	17	56	35	38	32	11	9	16	Fêmea
MNHN-IC-1933-0073 A	P. senegalus	26,9	24,5	4	10	17	59	37	41	30	10	11	17	Fêmea
MNHN-IC-1933-0073 B	P. senegalus	22,7	20,3	3,3	9	16	58	35	39	28	9	10	16	Fêmea
MNHN-IC-2004-0180 A	P. senegalus	19,3	16,6	2,5	9	19	56	33	38	33	10	12	17	Macho
MNHN-IC-2004-0180 B	P. senegalus	19	17	2,7	9	18	57	34	38	33	11	10	16	Fêmea
MNHN-IC-1992-0770 A	P. senegalus	?	25,9	3,6	9	19	58	36	41	34	9	10	16	Macho

MNHN-IC-1992-0770 B	P. senegalus	?	22,8	3,6	11	17	59	36	39	34	10	10	17	Macho
MNHN-IC-1992-0770 C	P. senegalus	?	23,3	3,3	9	20	57	36	38	33	11	12	17	Fêmea
MNHN-IC-1961-0006 A	P. senegalus	13,1	11,1	2	10	16	57	37	37	34	9	11	16	Macho
MNHN-IC-1961-0006 B	P. senegalus	12,2	10,1	1,9	10	15	56	35	37	33	10	10	15	Fêmea
MNHN-IC-1961-0006 C	P. senegalus	11,5	9,3	1,8	9	17	56	37	37	28	8	11	15	Macho
MNHN-IC-1961-0008 A	P. senegalus	25,1	22,9	3,4	9	18	56	36	36	34	11	13	16	Macho
MNHN-IC-1961-0008 B	P. senegalus	?	20,9	3,4	9	19	57	35	37	32	9	12	15	Macho
MNHN-IC-1961-0008 C	P. senegalus	16,2	15,1	2,5	9	18	54	30	37	33	9	12	15	Fêmea
MNHN-IC-2002-0527 A	P. senegalus	25,1	22,8	3,4	10	16	57	33	37	32	9	12	16	Macho
MNHN-IC-2002-0527 B	P. senegalus	?	10,2	2	10	15	56	38	37	34	11	10	?	Fêmea
MNHN-IC-1962-0334 A	P. weeksi	15,9	13,8	3,1	11	19	58	45	39	32	12	11	15	Macho
MNHN-IC-1962-0334 B	P. weeksi	9,5	8,4	2	10	20	57	42	41	31	8	11	15	Fêmea
MNHN-IC-1962-0335 A	P. weeksi	17,4	16	3,2	10	23	58	53	43	35	11	13	17	Macho
MNHN-IC-1962-0335 B	P. weeksi	?	10,8	2,5	9	24	59	?	44	33	8	10	15	Fêmea
MNHN-IC-1900-0218	E. calabaricus	18,8	17,8	1,6	10	56	109	28	X	19	X	10	15	Macho
MNHN-IC-1978-0732	E. calabaricus	31,8	30,7	2,5	9	53	109	29	X	19	X	10	15	Macho



MNHN-IC-2008-2103 A	E. calabaricus	32,1	30,7	2,6	10	52	110	32	X	19	X	9	14	Macho
MNHN-IC-2008-2103 B	E. calabaricus	28,5	27,5	2,3	10	48	106	30	X	21	X	9	14	Macho
MNHN-IC-2008-2103 C	E. calabaricus	26,8	25,8	2,1	10	48	106	29	X	18	X	9	14	Macho

Legenda: ‘X’ significa que a estrutura é ausente na referida espécie. ‘?’ significa que a referida medida não pode ser feita devido ao estado de conservação do espécime.