UNIVERSIDADE DE SÃO PAULO
FACULDADE DE FILOSOFIA, CIÊNCIAS E LETRAS DE RIBEIRÃO PRETO
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

A review of the anatomy of Polypteridae (Vertebrata: Cladistii)

Uma revisão da anatomia de Polypteridae (Vertebrata: Cladistii)

Pedro Pereira Rizzato

Tese apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, como parte das exigências para obtenção do título de Doutor em Ciências, obtido no Programa de Pós-Graduação em Biologia Comparada

Ribeirão Preto – SP
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Orientador: Dr. Flávio Alicino Bockmann

Ribeirão Preto – SP
2019

Rizzato, Pedro Pereira
A review of the anatomy of Polypteridae (Vertebrata: Cladistii). Ribeirão Preto, 2019.
383 p.: 107 il.; 30 cm

Tese de Doutorado, apresentada à Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto/USP. Área de concentração: Biologia Comparada.
Orientador: Bockmann, Flávio Alicino.

1. Ichthyology. 2. Comparative Anatomy. 3. Morphology. 4. Evolution. 5. Fishes.

RIZZATO, Pedro Pereira. **A review of the anatomy of Polypteridae (Vertebrata: Cladistii)**. 2019. 383 p. Tese (Doutorado em Ciências) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, SP, 2019.

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Dedico a todas as pessoas que acreditam no poder transformador, libertador e emancipador do conhecimento, e que dedicam suas vidas a produzi-lo e compartilhá-lo com toda a humanidade, indiscriminadamente.

ACKNOWLEDGEMENTS

Ao Prof. Dr. Flávio Alicino Bockmann, meu orientador e amigo, por ter aceitado me orientar no doutorado, ter confiado em mim e no meu trabalho, me dando liberdade para desenvolver o projeto e sempre me incentivando a ir além, por ter se dedicado ao projeto e dele participado ativamente, por compreender genuinamente que a formação na pós-graduação vai muito além do desenvolvimento de um projeto de pesquisa e, por isso, ter sugerido, incentivado, apoiado e defendido minha participação em diversas atividades acadêmicas que contribuíram de maneira decisiva para minha formação acadêmica e pessoal, por ter sempre lutado de maneira apaixonada e sincera, muitas vezes renunciando direitos que lhe são devidos, para aumentar a qualidade da ciência produzida pelo laboratório e pelo departamento, o que se reflete também na qualidade da ciência que é produzida no Brasil, pelo exemplo de ética científica, acadêmica, profissional e pessoal que expressa ao alinhar suas atitudes e seus discursos aos princípios que defende, dos quais compartilho, e que tive a oportunidade de testemunhar diversas vezes, pelo companheirismo e amizade que desenvolvemos ao longo desse período, e, sobretudo, por ter me ensinado que 'é preciso ter coragem pra viver'.

À banca examinadora, cuja honrosa presença e criteriosa avaliação são de grande contribuição no sentido de aprimorar o presente trabalho, em vista de seu profundo conhecimento e vasta experiência em suas respectivas áreas do conhecimento.

Ao Programa de Pós-Graduação em Biologia Comparada, seus docentes, funcionários e alunos, especialmente nas pessoas dos atuais coordenadores Dra. Tiana Kohlsdorf e Dr. Milton Groppo Jr. e da secretária Vera Cássia Cicilini de Lucca, por terem providenciado o ambiente, do qual venho desfrutando desde o meu mestrado, que permitiu minha formação científica, acadêmica e pessoal enquanto aluno de pós-graduação, e por terem permitido que eu me ausentasse pelo período de um ano para usufruto da Bolsa de Estágio em Pesquisa no Exterior e concedido extensão do prazo para depósito da Tese.

À Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), que financiou, através de uma bolsa de Doutorado e de uma Bolsa de Estágio em Pesquisa no Exterior (BEPE), os projetos de pesquisa que deram origem ao presente trabalho (proc. #2014/10849-6 e #2016-06677-0, respectivamente), bem como minha formação enquanto pesquisador ao longo dos últimos nove anos através de duas bolsas de Iniciação Científica (proc. #2009/15030-7 e #2011/06736-3) e uma bolsa de Mestrado (proc. #2011/15429-7).

À Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto da Universidade de São Paulo, por ter diponibilizado a infra-estrutura necessária para o desenvolvimento do presente trabalho.

Ao meu supervisor durante a Bolsa de Estágio em Pesquisa no Exterior, Dr. Eric J. Hilton, por ter gentilmente aceitado o convite para me supervisionar durante um ano no seu laboratório, por ter sido um excelente supervisor dando-me liberdade para desenvolver a pesquisa e confiando no meu trabalho, sempre com gentileza, paciência e atenção, por ter me convidado

e incentivado a participar de diversas experiências acadêmicas e não-acadêmicas que contribuíram de maneira fundamental para complementar minha formação acadêmica, profissional e pessoal, e por ter demonstrado, através do exemplo, o que é ser um cientista anatomista realmente e genuinamente comprometido com a Ciência e o conhecimento.

Ao Virginia Institute of Marine Sciences (VIMS) do College of William & Mary, seus pesquisadores, alunos e funcionários, por terem me recebido durante a Bolsa de Estágio em Pesquisa no Exterior, terem disponibilizado sua infra-estrutura para o desenvolvimento do projeto de pesquisa, por terem me permitido vivenciar diversas experiências acadêmicas fundamentais para complementar minha formação, e em especial à Dra. Sarah Huber, MSc. Diego Vaz, MSc. Kate Bemis, Clare e Emma, por sua atenção, paciência, carinho, por tudo que fizeram para que eu me sentisse acolhido e bem-vindo no VIMS.

Aos curadores e pesquisadores das coleções científicas que visitei ou que concederam empréstimo do material utilizado no presente trabalho: Laboratório de Ictiologia de Ribeirão Preto (LIRP): Prof. Dr. Ricardo Macedo Corrêa e Castro, Prof. Dr. Flávio Alicino Bockmann, Dr. Hertz Figueiredo dos Santos e Dr. André Esguícero; Museu de Zoologia da Universidade de São Paulo (MZUSP): Prof. Dr. Aléssio Datovo da Silva e Dr. Michel Donato Gianeti; Smithsonian Institution, National Museum of Natural History (USNM), Division of Fishes: Dr. David Johnson, Dra. Ai Nonaka, Dr. Jeff Clayton e Dr. Tom Monroe; Smithsonian Institution, National Museum of Natural History, Museum Support Center (USNM-MSC): Dra. Sandra Raredon, Dra. Kris Murphy e Dra. Diane Pitassy; Virginia Institute of Marine Sciences (VIMS): Dr. Eric Hilton, Dra. Sarah Huber; American Museum of Natural History (AMNH): Dr. Scott Schaeffer, Dra. Melanie Stiassny e Radford Arrindell; Natural History Museum (NHM): Dr. James Maclaine, Dr. Oliver Crimmen e Dr. Ralf Britz; Muséum national d'Histoire naturelle (MNHN): Dr. Patrice Pruvost, Dra. Nalani Schnell e Gabsi Zora; Cornell University Vertebrate Collections (CUMV), Dr. William E. Bemis e Dr. Casey Dillman; Natural History Collection, University of Massachussets (UMAF), Dr. Cristina Cox-Fernandes, Dr. Jeff Podos, Dr. Craig Albertson, Kate Doyle e Sally Klingener. Alguns dos espécimes depositados em coleções foram diafanizados ou corados pelos pesquisadores Dr. Aléssio Datovo, Dr. Murilo Carvalho, Dr. Peter Konstantinidis, Dr. Casey Dillman e Dr. Eric Hilton.

Aos meus *roommates* durante minhas idas ao exterior, que se tornaram grandes amigos e me fizeram me sentir em casa mesmo estando tão longe: Kristene, CJ, Kaya, Jeff Podos, Chad Walters, Dandan e Julien.

Ao Msc. Ivan Britto e à equipe do Centro de Pesquisas Global da GE, e ao Dr. Daniel Cavallari do Centro para Documentação da Biodiversidade da FFCLRP-USP, pela produção dos modelos tridimensionais de *CT-scanning*; ao Dr. André Esguícero (LIRP) pelo auxílio na preparação dos espécimes para serem escaneados; e ao Msc. Diego Vaz (VIMS) pelo auxílio com o tratamento das imagens em softwares de análise. Esta Tese de Doutorado é parte do projeto "Core-facility for conservation of scientific documentation: biological collections and high technology research in comparative morphology" (CT-INFRA), financiado pela Financiadora de Estudos e Projetos – FINEP, Ministério da Ciência, Tecnologia, Inovação e Comunicação, Governo Federal, Brasil.

À Msc. Anna Pospisilova por fornecer dados sobre a série ontogenética de *P. senegalus* produzida durante sua dissertação para ser utilizada no presente estudo, e por ter aceitado o convite de estabelecer uma parceria no desenvolvimento de um projeto de pesquisa conjunto.

Aos colegas do Laboratório de Ictiologia de Ribeirão Preto, Dr. Fernando Apone, Dr. Hertz dos Santos e Dr, André Esguícero, por terem auxiliado no planejamento e montagem do aquário do LIRP para manutenção dos espécimes estudados no presente projeto.

Ao consórcio de bibliotecas e livrarias que compõem o Biodiversity Heritage Library (BHL), uma iniciativa que tem colaborado e muito para este e outros trabalhos de pesquisa através da disponibilização de artigos clássicos sobre biodiversidade.

Ao Prof. Dr. Marco Antonio Del Lama, que me acolheu num momento de dúvida e que, com sua atenção e conselhos precisos e de forma decisiva, me manteve no caminho da Biologia, que desde então nunca mais tive dúvidas que fosse de fato o meu.

À Profa. Dra. Maria Elina Bichuette, minha orientadora durante a graduação e o mestrado, que me introduziu no campo acadêmico e ensinou os primeiros passos da pesquisa e da Ciência, e a quem serei sempre grato por todas as experiências que me permitiu ter durante minha formação sob sua supervisão.

Aos colegas ictiólogos, especialmente Murilo Pastana, Aléssio Datovo, George Mattox, Verônica Sobodian, Thiago Loboda, Osmar Santos, João Pedro Fontenelle, João Paulo Capretz, pelas discussões sobre peixes e outros tópicos menos acadêmicos.

Aos colegas do Laboratório de Ictiologia de Ribeirão Preto (LIRP), egressos, atuais e agregados, pelo auxílio em diversos momentos da realização do presente trabalho, e por possibilitarem um ambiente agradável, divertido e muito produtivo de trabalho, contribuindo de forma essencial para minha formação acadêmica e pessoal, em especial: Dr. André Esguícero, Bruno Botão, MSc. Dahyes Regasso, MSc. Davi Lee Bang, Dr. Fernando Apone, Haroldo Braga, João Pedro Trevisan, Malu Araújo, Marcela Renoldi, MSc. Mariana Bissoli, MSc. Murilo Pastana, MSc. Nathalia Rossigali, Dra. Renata Stopiglia, Otávio Otaviano, Dr. William Ruiz, Dr. Hertz dos Santos e Dr. Ricardo Castro.

A todos os meus amigos ainda não citados, em especial Lucas, Marcos e Bruno, que a nossa amizade continue resistindo à distância e ao tempo.

A todos familiares e amigos, incluindo os Martins (Vânia, Douglas, Renan, Laudy e Tasso), por terem me apoiado e acolhido com carinho em diversos momentos da minha caminhada.

À Camila, que esteve comigo desde o início da minha trajetória enquanto biólogo, nas horas difíceis e principalmente nos momentos mais felizes, e por ter compartilhado comigo a paixão pela vida e a natureza e o amor genuíno e sincero por educar, onde quer que estivermos.

Aos meus sobrinhos, Lucca e João Roberto, por quem espero contribuir para deixar um mundo melhor.

À minha avó, Anna Maria Pereira, que sempre dedicou seu tempo, carinho e amor para a minha criação e educação, e a quem jamais serei capaz de retribuir, por tudo que fez e tem feito por mim.

Aos meus pais, Silvia e Roberto, por terem feito todo o possível para permitir que eu trilhasse meu próprio caminho e perseguisse meus sonhos. Amo vocês.

Agradeço, por fim, à Universidade Pública, onde me formei desde a Graduação até o Doutorado, e à qual devo a maioria absoluta dos conhecimentos que adquiri e das experiências acadêmicas, profissionais e pessoais que vivi no decurso de minha formação. Que a luta pela democratização do acesso ao conhecimento, do qual a Universidade Pública é parte integrante, estratégica e fundamental, não ceda aos interesses espúrios dos que veem nela uma ameaça aos instrumentos de manutenção das desigualdades e injustiças sociais.

“ I’ay eſté nourri aux lettres dés mon enfance, & pour-cequ’on me perſuadoit que par leur moyen on pouuoit acquerir vne connoiſſance claire & aſſurée de tout ce qui eſt vtile a la vie, i’auois vn extreme deſir de les apprendre. Mais ſitoſt que i’eu acheué tout ce cours d’eſtudes, au bout duquel on a couſtume d’eſtre receu au rang des doctes, ie changay entierement d’opinion. car ie me trouuois embaraſſé de tant de doutes & d’erreurs, qu’il me ſembloit n’auoir fait autre profit en taſchant de m’inſtruire, ſinon que i’auois découuert de plus en plus mon ignorance”

René Descartes, 1637

ABSTRACT

RIZZATO, Pedro Pereira. **A review of the anatomy of Polypteridae (Vertebrata: Cladistii).** 2019. 383 p. Thesis (PhD. in Sciences) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 2019.

Polypteridae is a group of freshwater and brackish water fishes currently ocurring exclusively in tropical regions of Africa. The 14 extant species of polypterids are distributed in two genera, *Polypterus* (bichirs, 13 species) and *Calamoichthys* (the reedfish, *C. calabaricus*). The group attracts special interest of researchers due to their peculiar anatomy that combines features observed in different groups of living and extinct vertebrates with exclusive characters such as the presence of a unique type of dorsal fin. The singular combination of characteristics difficults establishing the phylogenetic position of polypterids, although they are considered nowadays the sister-group of all living ray-finned fishes, occupying a key phylogenetic position among the bony fishes. In this context, understanding in details their anatomy is crucial for understanding the evolutionary history of vertebrates as a whole and particularly of bony fishes. The present study consists of a revisionary investigation of the anatomy of polypterids, emphasizing underexplored mophological systems and complexes such as the laterosensory and musculoskeletal systems, on a holistic approach. We integrate the analysis of living specimens, specimens preserved in collections (ethanol-preserved and dry-skeleton preparations), stained and dissected specimens, radiographs, and tridimensional models generated by computadorized tomography. The analysis focuses on the Senegal Bichir, *Polypterus senegalus*, but includes several specimens of different sizes of all species of polypterids, including types of almost all of them. We include information from early ontogeny, with basis on an analysis of developmental series of *P. senegalus* and of representatives of the remaining groups of non-teleost actinopterygians (Acipenseriformes, Lepisosteiformes and Amiiformes). The study also includes an extensive revision of the literature on the anatomy and phylogenetic relationships of polypterids and other basal bony fishes. We provide several new interpretations about the anatomy of polypterids and other bony fishes, many of which are incorporated into new proposals of anatomical terminology for Actinopterygii or for Osteichthyes. We also provide a detailed analysis of the intra- and interspecific variation on the external anatomy of polypterids that will be useful in future attempts to unravel their taxonomy and phylogenetic interrelationships. The present study demonstrates that, even considering all the efforts by previous authors, there is still a lot to be known regarding the anatomy of polypterids, as well as of other basal groups of bony fishes.

Much of this information can be incorporated into phylogenetic studies in order to improve our hypotheses of evolutionary relationships between the major clades of Vertebrata, and can also provide new ideas about the anatomy and evolutionary history of vertebrates.

Keywords: Ichthyology. Comparative Anatomy. Morphology. Evolution. Fishes.

RESUMO

RIZZATO, Pedro Pereira. **Uma revisão da anatomia de Polypteridae (Vertebrata: Cladistii).** 2019. 383 p. Tese (Doutorado em Ciências) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 2019.

Polypteridae é um grupo de peixes de água doce e salobra que ocorre atualmente apenas em regiões tropicais da África. As 14 espécies viventes de polipterídeos estão distribuídas em dois gêneros, *Polypterus* (bichirs, 13 espécies) e *Calamoichthys* (o peixe-corda, *C. calabaricus*). O grupo atrai interesse especial dos pesquisadores devido à sua peculiar anatomia que combina características observadas em diferentes grupos viventes e extintos de vertebrados, com caracteres exclusivos, como a presença de um tipo único de nadadeira dorsal. Essa combinação singular de características dificulta o estabelecimento de sua posição filogenética, embora sejam considerados atualmente o grupo irmão de todos os peixes de nadadeiras raiadas viventes, ocupando uma posição filogenética chave entre os peixes ósseos. Nesse contexto, compreender em detalhes sua anatomia é fundamental para entender a história evolutiva dos vertebrados como um todo e particularmente dos peixes ósseos. O presente estudo consiste de uma revisão sobre a anatomia dos polipterídeos, enfatizando sistemas e complexos mofológicos pouco explorados, como os sistemas laterossensorial e musculoesquelético, em uma abordagem holística. Integramos a análise de espécimes vivos, espécimes preservados em coleções (preservados em etanol ou preparações secas do esqueleto), espécimes corados e dissecados, radiografias, e modelos tridimensionais gerados por tomografia computadorizada. A análise é focada no bichir do Senegal, *Polypterus senegalus*, mas inclui vários espécimes de diferentes tamanhos de todas as espécies de polipterídeos, incluindo espécimes-tipo de quase todas elas. Foram incluídas informações da ontogenia, com base em uma análise das séries de desenvolvimento de *P. senegalus* e de representantes dos demais grupos de peixes actinopterígios não-teleósteos (Acipenseriformes, Lepisosteiformes e Amiiformes). O estudo também inclui uma extensa revisão da literatura sobre a anatomia e relações filogenéticas dos polipterídeos e outros peixes ósseos basais. Várias novas interpretações sobre a anatomia dos polipterídeos e dos demais peixes ósseos são apresentadas, muitas dos quais são incorporadas em novas propostas de terminologia anatômica para Actinopterygii ou para Osteichthyes. Também é apresentada uma análise detalhada da variação intra- e interespecífica na anatomia externa dos polipterídeos, que será útil em futuras tentativas de desvendar sua taxonomia e inter-relações filogenéticas. O presente estudo demonstra que, mesmo considerando todos os esforços anteriores, ainda há muito a ser conhecido sobre a anatomia dos polipterídeos, bem como de outros grupos basais de peixes ósseos. Muitas dessas informações podem ser incorporadas em estudos filogenéticos, a fim de aperfeiçoar as hipóteses sobre as relações evolutivas entre os principais clados de Vertebrata, e também podem fornecer novas idéias sobre a anatomia e a história evolutiva dos vertebrados.

Palavras-chave: Ictiologia. Anatomia Comparada. Morfologia. Evolução. Peixes.

SUMMARY

1 INTRODUCTION

Polypteridae (Vertebrata: Cladistii: Polypteriformes) is a group of freshwater and brackish water fishes endemic to the tropical regions of Africa (Poll 1954, Gosse 1984, Berra 2007). The family includes 14 extant valid species (see ‘Material and Methods: Taxonomy’) distributed in two genera: *Polypterus* La Cepède 1803, the bichirs, including 13 species; and *Calamoichthys* Smith 1866a, a monotypic genus comprised by the reedfish or ropefish, *C. calabaricus* Smith, 1866a (*Erpetoichthys* Smith, 1866a is a junior synonym of *Calamoichthys* Smith, 1866a; Rizzato and Bockmann 2017). Some fossil material from the African continent is also atributed to Polypteridae (Dutheil 1999, 2000, Daget *et al.* 2001, Gayet *et al.* 2002, Otero *et al.* 2006, Smith *et al.* 2006, Otero *et al.* 2010, Grandstaff *et al.* 2012, Coelho *et al.* 2018), mostly including isolated scales, dorsal-fin spines, vertebrae, and fragmented skull bones (Dutheil 2000, Gayet *et al.* 2002, Otero *et al.* 2010, Giles *et al.* 2017). The scarce fossil record of polypterids also includes two articulated postcranial skeletons (†*Serenoichthys kemkemensis* Dutheil, 2000), a subcomplete, tridimensionally-preserved articulated skeleton from the Late Miocene of Chad (†*Polypterus faraou* Otero, Likius, Vignaud and Brunet, 2006), as well as fragmentary material from the Late Cretaceous of Bolívia and Brazil (Gayet and Meunier 1991, 1992) evidencing a wider distribution in the past and an origin that predates at least the separation of the South American and African continents around 110-148 million years ago.

Polypterids occur in shores and flood plains of rivers and lakes (Berra 2007). Since they have lungs and can breathe atmospheric oxygen (Magid 1967, Lechleuthner *et al.* 1989, Graham *et al.* 2013), they can be found in poorly-oxygenated water bodies such as swamps, and are even capable of making short excursions outside the water (Berra 2007, Standen *et al.* 2014, Du *et al.* 2016). They usually occupy muddy habitats at the bottom of rivers, and are carnivorous nocturnal predators feeding mostly on small aquatic vertebrates (fishes and amphibians) and invertebrates, but they can also feed on terrestrial insects (Smith 1866a, b, Harrington 1899, Berra 2007). The reedfish, *C. calabaricus*, occurs in brackish waters at the coastline near the Gulf of Guinea, in streamlets that run into the main rivers or in pools in marshy lands and swamps, and feeds mostly on aquatic and terrestrial invertebrates, especially insects (Smith 1866a, Berra 2007). Polypterids, including *C. calabaricus*, are used for human consumption in some places of Africa (Cuvier 1836-49, Smith 1866a, b).

The group was first described by the French naturalist Étienne Geoffroy Saint-Hilaire at the beginning of the XIX Century (Geoffroy Saint-Hilaire 1801, 1802, La Cepède 1803). During the famous French campaing in Egypt and Syria (Ottoman territories at the time) in 1798-1801, Napoleon Bonaparte ordered a scientific expedition of naturalists, scientists and scholars, including Geoffroy Saint-Hilaire, that resulted, among other findings and achievements, in the creation of the Institut d'Égypte, the foundation of the discipline of Egyptology, the publication of a series of volumes of the Description de l'Égypte, and the finding of the Rosetta Stone. During this expedition, Geoffroy Saint-Hilaire collected and described the first specimens of the group, and with basis on the peculiarities of the fish in comparison with other groups described so far, he decided to propose a new genus, named 'Polyptére' (in French). He proposed as diagnosis for the new genus (Geoffroy Saint-Hilaire 1802a, b) the presence of a single 'branchiostegal ray' (refering to the gular plates) and of two spiracles, and the high number of 'fins' (refering to the finlets on the segmented anterior portion of the dorsal fin, see below). His new genus would include a single species, 'Polyptére Bichir' from the Nile River. Since the author only used the names in the vernacular form, the authorship of the genus and species is attributed (*e.g.*, Fricke *et al.* 2018) to La Cepède, who included a short description of the group in the fifth volume of his Histoire Naturelle des

Poissons, accompained by the names in their latinized form: '*Polypterus bichir*' (La Cepède 1803: 340).

The amazement for these fishes is evident even from those early descriptions. They are described, for example, as 'a species almost entirely different from its analogues, and, so to speak, a stranger in the midst of its own family; it is doubtless a new consideration for natural history, and worthy of the attention of physiologists' (Geoffroy Saint-Hilaire 1802b, translated from French). A few years later, in his work Histoire naturelle des poissons du Nil, Geoffroy Saint-Hilaire (1809: 4, translated from French) passionately wrote: 'if I had discovered only this species in Egypt, it would already be worth the penalties that a journey of such a long course usually entails: for I do not know a more singular animal, more worthy of the attention of naturalists, and which, showing how much nature can deviate from its ordinary types, is more likely to enlarge the sphere of our ideas on organization'. Since then, polypterids have atracted the attention and special interest of some of the most eminent and renowned vertebrate anatomists, including names such as Louis Agassiz, Thomas Huxley, Ramsay Traquair, Edward P. Allis, Edwin S. Goodrich and Malcolm Jollie.

The special interest in polypterids is explained mainly by their peculiar anatomy that combines features shared with diferent groups, living and extinct, of Gnathostomata – *e.g.*, muscular and rotational pectoral fins, external gills in larvae, and paired ventral lungs with living lobe-finned fishes (Sarcopterygii); paired gular plates with *Latimeria* (Sarcopterygii: Actinistia) and some of the extinct †Osteolepiformes (Sarcopterygii); ganoid scales with gars (Actinopterygii: Lepisosteiformes) and the extinct †"Palaeonisciformes" (Actinopterygii); spiracle with chondrostreans (Actinopterygii: Acipenseriformes), fossil actinopterygians, and cartilaginous fishes (Chondrichthyes) – with characters exclusive of the group, the most conspicuous of which is the presence of a unique type of dorsal fin, segmented anteriorly, bearing a series of spines, and supported by an also unique type of rays. This singular combination of characteristics difficults establishing the phylogenetic position and evolutionary relationships of the group (Suzuki *et al.* 2010, Sallan 2014), in addition to its poor and fragmentary fossil record, not extending beyond the Middle Cretaceous (Dutheil 2000, Gayet *et al.* 2002, Giles *et al.* 2017), and the relatively outdated anatomic descriptions of some of its few representatives (Claeson *et al.* 2007, Near *et al.* 2013).

Consequently, Polypteridae is one of the fish groups of whose ideas of phylogenetic position changed the most through time (Lauder and Liem 1983, Claeson *et al.* 2007, Sallan 2014; see 'Phylogenetic remarks'). Before the advent of cladistics, polypterids were alternatively grouped with representatives of each of the two main lineages of bony fishes, the ray-finned fishes, Actinopterygii (*e.g.*, Müller 1846a, b, Goodrich 1901, 1908, 1909, 1928, Daget 1950) and the lobe-finned fishes, Sarcopterygii (*e.g.*, Huxley 1861, Cope 1871, 1877, 1887, Woodward 1891, Jarvik 1942, 1947). Other authors argued that polypterids should be considered as the sole member of a group of their own, named Brachiopterygii or Cladistii/Cladistia (Stensiö 1921, 1932, Jessen 1973, Jarvik 1980, Bjerring 1985a, b, 1986). The latter view somehow influenced recent classifications, *e.g.*, Betancur-R *et al.* (2017) and van der Laan *et al.* (2018), in which polypterids are included in a group, named Cladistia or Cladistii, respectively, of the same taxonomic rank (Class) of the group including the remaining actinopterygians (in Actinopteri).

After the advent of cladistics (Hennig 1950, 1965, 1999), the hypothesis of polypterids as more closely related to actinopterygians became prevalent, especially after the influential work of Patterson (1982). In phylogenies based on morphological data, polypterids are considered the living sister-group to all remaining extant ray-finned fishes, or at least one of the earliest-diverging lineages of Actinopterygii when fossils are included (*e.g.*, Rosen *et al.* 1981, Patterson 1982, Lauder and Liem 1983, Gardiner 1984, Gardiner and Schaeffer 1989, Coates 1999, Cloutier and Arratia 2004, Hurley *et al.* 2007, Xu *et al.* 2014, Friedman 2015).

Phylogenies based on molecular data suggest different positions for the group, but most converge to the same topology supported by morphological data (*e.g.*, Noack *et al.* 1996, Venkatesh *et al.* 2001, Inoue *et al.* 2003, 2005, 2009, 2010, Kikugawa *et al.* 2004, Azuma *et al.* 2008, Alfaro *et al.* 2009, Santini *et al.* 2009, Setiamarga *et al.* 2009, Near *et al.* 2012, Chen *et al.* 2012, Betancur-R *et al.* 2013, Broughton *et al.* 2013, Faircloth *et al.* 2013, Betancur-R *et al.* 2017, Hughes *et al.* 2018). Recently, Giles *et al.* (2017) suggested that polypterids are related to †Scanilepiformes, a group of fossil palaeonisciform fishes widely distributed throughout the Triassic, reinforcing the hypothesis of polypterids as the living sister-group to the clade formed by all remaining extant actinopterygians (see ‘Phylogenetic remarks’, below).

Considering, therefore, on one hand the peculiar anatomy of polypterids, in terms of the unique combination of characteristics shared with different groups of fishes with characters that are exclusive of the group, and on the other hand their key phylogenetic position in relation to the remaining bony fishes, especially the actinopterygians, it becomes justified and of great interest a detailed anatomic study of the group, in order to generate data that contributes for a better understanding of the morphological diversity and evolution at the base of the vertebrate tree. This study will not only contribute for revisiting and producing more robust hypotheses of phylogenetic relationships between the main lineages of bony fishes, but will also offer the opportunity to map the evolution of the anatomy of these groups in order to establish the set of characters present in the common ancestor of Actinopterygii and Sarcopterygii. Additionally, a more detailed understanding of their anatomy, especially the intra- and interspecific variability of the characters, may also contribute for a better definition of the taxonomy of the group, that remains controversial (see “Material and Methods: Taxonomy’), and for identifying characters with potential phylogenetic signal for unraveling the internal relationships between polypterids.

Since their discovery, polypterids have been the focus of several morphological studies thoughout the years. Classic studies include descriptions, with different levels of detail, of the skeleton (*e.g.*, Agassiz 1833-44, Traquair 1870, Bridge 1888, Gegenbaur 1895, Allis 1900b, 1919a, Bamford 1913, Moy-Thomas 1933, Haines 1937, Pehrson 1947, 1958, Daget *et al.* 1964, Jessen 1969, Jollie 1984b), musculature (*e.g.*, Luther 1913, Schmalhausen 1913, Edgeworth 1929, 1935, Jessen 1969, 1972, Wiley 1979), nervous system (Thomopoulos 1951, Pickford and Atz 1957, Lagios 1968, Pfeiffer 1968, 1969), laterosensory system (Collinge 1893, Allis 1900a, Thomopoulos 1970, Jorgensen 1982), respiratory and circulatory systems (Hyrtl 1852, 1870, Boas 1880, Budgett 1901, Allis 1908, DeSmet 1966, 1969), and urogenital system (Hyrtl 1854, Budgett 1901), as well as studies involving an integrated description of different anatomical complexes (Müller 1846a, b, Leydig 1854, Van Wijhe 1882, Pollard 1892, Allis 1922, Sewertzoff 1924, Purser 1951). Many studies also incorporated information from development (*e.g.*, Kerr 1907, Lehn 1918, Sewertzoff 1924, Moy-Thomas 1933, Pehrson 1947, 1958, Daget *et al.* 1964, Lagios 1968).

Despite all these efforts to describe the anatomy of the group and to understand it on a phylogenetic context, recent studies, especially using new techniques and technologies of morphological investigation such as differential staining methods and the CT-scanning (Claeson *et al.* 2007, Claeson and Hagadorn 2008, Noda *et al.* 2017, Giles *et al.* 2017), have demonstrated that there is still much to be known. Underexplored anatomical complexes have been investigated (*e.g.*, Wilhelm *et al.* 2015, Molnar *et al.* 2016), and previous interpretations regarding polypterid anatomy have been revisited (Britz and Bartsch 2003; Britz and Johnson 2003, 2010a; Carvalho *et al.* 2013). Even after years of morphological studies including polypterids, these approaches have led to new interpretations about some aspects of the anatomy of the group and, as a consequence, of the morphological evolution of gnathostomes as a whole (Carvalho *et al.* 2013; Graham 2013; Durán *et al.* 2014, Tatsumi *et al*. 2016).

Many authors even pointed out that the group represents an emerging model for studies regarding the evolution of not only actinopterygians or bony fishes, but of vertebrates as a whole (Takeuchi *et al.* 2009, Braasch *et al.* 2015, Standen *et al.* 2014). In fact, polypterid development has been investigated using molecular evo-devo approaches, and has provided new insights about the evolution of many aspects of vertebrate anatomy (*e.g.*, Tatsumi *et al.* 2016, Minarik *et al.* 2017). Finally, recent years have demonstrated that the area of systematic morphology of fishes remains extremely relevant even considering the advances of studies using molecular data. There are nowadays clear signs of a revival of morphological systematic studies, impelled inclusively by new technological and methodological possibilities (Hilton *et al.* 2015, Friedman 2015).

Considering all these factors, the present study investigates in details the anatomy of polypterids in a comparative approach with other gnathostomes, aiming to review previous intepretations regarding their anatomy and to produce an updated reference material for the group. The study also aims to generate data that will contribute to discussions about the evolutionary relationships between the major clades of bony fishes and, ultimately, about the main cladogenetic event on the evolutionary history of vertebrates that originated Actinopterygii on one side, and Sarcopterygii on the other.

The study is focused on the Senegal Bichir, *Polypterus senegalus* Cuvier, 1829, the most common, widespread, easily identifiable and frequently studied polypterid species, but provides, whenever possible, comparisons with other species of Polypteridae, especially *Calamoichthys calabaricus*. We emphasize aspects of their external anatomy (morphometry and meristics), laterosensory system and bones associated, and musculature, discussing the main implications of our findings for each of the morphological complexes and structures analyzed. Other aspects of their anatomy are also mentioned. At the end, we provide a general discussion about the phylogenetic implications of the main findings of the present study.

2 MATERIAL AND METHODS

2.1 Taxonomy. Fricke *et al.* (2018) recognize 12 extant valid species of polypterids:

1. *Calamoichthys calabaricus* Smith, 1866a;
2. *Polypterus ansorgii* Boulenger, 1910;
3. *Polypterus bichir* La Cepède, 1803;
4. *Polypterus delhezi* Boulenger, 1899;
5. *Polypterus endlicherii* Heckel, 1847;
6. *Polypterus mokelembembe* Schliewen and Schäfer, 2006;
7. *Polypterus ornatipinnis* Boulenger, 1902;
8. *Polypterus palmas* Ayres, 1850;
9. *Polypterus retropinnis* Vaillant, 1886;
10. *Polypterus senegalus* Cuvier, 1829;
11. *Polypterus teugelsi* Britz, 2004; and
12. *Polypterus weeksii* Boulenger, 1898.

In addition to these, other names were proposed for species of polypterids, some of which are considered synonyms of the names above: *P. niloticus* Shaw 1804, synonym of *P. bichir*; and *P. schoutedeni* Pellegrin 1923, synonym of *P. weeksii*. There are some names, however, that were proposed as distinct species, but were converted to subspecies by Poll (1941a, b, 1942), in his pivotal contributions to the study of polypterid taxonomy:

- *P. congicus* Boulenger, 1898, considered a subspecies of *P. endlicherii*;
- *P. lapradei* Steindachner, 1869, considered a subspecies of *P. bichir*;
- *P. lowei* Boulenger, 1911, considered a subspecies of *P. retropinnis*;
- *P. polli* Gosse, 1988, considered a subspecies of *P. palmas.*

In addition, Poll (1941a) proposed two new subspecies: *Polypterus bichir katangae* Poll, 1941a and *Polypterus senegalus meridionalis* Poll, 1941a.

A few years later, in a study about the zoogeography of protopterids and polypterids, Poll (1954) proposed other taxonomic interpretations: *P. delhezi* as a synonym of *P. ansorgii*, and a new subspecies, *P. palmas congicus* (proposed as a name only in Poll 1954 and Daget 1958, later described by Daget 1962). Gosse (1988) further described the later as a distinct species, *P. polli* Gosse, 1988, and considered *P. lowei* Boulenger, 1911 as a synonym of *P. palmas*.

Daget and Desoutter (1983) attempted to develop for the first time a cladistic study of polypterids with basis on morphological characters. The authors considered as operational taxonomic units the following species and subspecies: *C. calabaricus, P. ansorgii, P. bichir bichir, P. bichir katangae, P. bichir lapradei, P. endlicherii endlicherii, P. endlicherii congicus, P. delhezi, P. senegalus senegalus, P. senegalus meridionalis, P. ornatipinnis, P. palmas, P. retropinnis* and *P. weeksii.* With basis on their analysis, the authors concluded that there is no reason to elevate any of the subspecies within the *bichir-lapradei* group (*P. bichir bichir, P. bichir katangae, P. bichir lapradei, P. endlicherii endlicherii, P. endlicherii congicus*) to the level of species.

Hanssens *et al.* (1995) proposed the existence of three subspecies of *P. palmas*. They considered *P. buettikoferi* Steindachner 1891, which had been synonymized with *P. palmas* by Steindachner (1894), as a subspecies, *P. palmas buettikoferi* Steindachner, 1891, and converted *P. polli* to a subspecies, *P. palmas polli* Gosse, 1988.

In the most recent works regarding polypterid taxonomy, two extant species were described: *P. teugelsi* from the upper Cross River in Cameroon (Britz 2004) and *P. mokelembembe* from the central Congo River basin (Schliewen and Schäfer 2006). In addition, one extinct species of polypterid, †*Polypterus faraou* Otero, Likius, Vignaud and Brunet, 2006, was described from a subcomplete articulated fossil skeleton from the Late Miocene of Chad. In these works, the authors comment about the lack of resolution of the interrelationships of polypterids and stress out the need for a revisionary taxonomic study of the group.

On the first molecular phylogeny of polypterids, Suzuki *et al.* (2010) included all 12 species recognized by Fricke *et al.* (2018), including all but three (*P. bichir katangae, P. palmas palmas* and *P. senegalus meridionalis*) of the subspecies recognized, representing 15 taxa. These were *C. calabaricus, P. ansorgii, P. bichir bichir, P. bichir lapradei, P. delhezi, P. endlicherii congicus, P. endlicherii endlicherii, P. mokelembembe, P. ornatipinnis, P. palmas buettikoferi, P. palmas polli, P. retropinnis, P. senegalus senegalus, P. teugelsi* and *P. weeksii*. The authors conclude that *P. endlicherii endlicherii* and *P. endlicherii congicus* should be regarded as distinct species: *P. endlicherii* and *P. congicus*, respectively. They also considered *P. palmas buettikoferi* and *P. palmas polli* to represent distinct groups, but they did not include *P. palmas palmas* in their analysis. Their conclusion is that the current taxonomy of polypterids underestimate their genetic diversity.

Near *et al.* (2013) recognize 18 species of polypterids. They elevate all subspecies considered in Suzuki *et al.* (2010), except *P. bichir katangae*, to the level of species, and include *P. lowei* (that they describe as previously treated as a subspecies of *P. retropinnis*, but that was regarded as a synonym of *P. palmas* by Gosse 1988).

The uncertainties regarding the taxonomy of polypterids make it difficult to circumscribe operational taxonomic units and to establish comparisons between these units in a morphological study such as the present work. Despite recent contributions from molecular studies (Suzuki *et al.* 2010, Near *et al.* 2013), a detailed revisionary study of polypterid taxonomy and systematics, including robust morphological diagnoses for each species and a review about their geographical distribution, is still lacking and urgently needed.

The resolution of the taxonomy and systematics of polypterids is beyond the scope of the present study, which is focused on analyzing, reviewing and redescribing the anatomy of the representatives of the family, using *Polypterus senegalus* as the reference. As part of this investigation, we establish comparisons with other taxa within the family to describe the extent of intra- and interspecific variation on their anatomy. In the course of the present study, and as a natural consequence of this investigation, we found morphological characters that allow for distinguishing some of the taxa considered by previous studies. On the other hand, we were not able to distinguish some of the species or subspecies recognized by previous authors with basis on the morphological characters that we have analyzed (*e.g.*, *P. bichir lapradei* from *P. bichir bichir*, *P. palmas buettikoferi* from *P. palmas palmas*). It is important to remark that our analysis included type specimens of almost all the species analyzed (see “Material analyzed”, below). The present work, therefore, constitutes a valuable source of information about polypterid morphology that can be incoroporated in future taxonomical and systematic investigations of the group.

In the present work, we recognize as valid the following taxa:

1. *Calamoichthys calabaricus* Smith, 1866a;
2. *Polypterus ansorgii* Boulenger, 1910;
3. *Polypterus bichir* La Cepède, 1803;
4. *Polypterus congicus* Boulenger, 1898;
5. *Polypterus delhezi* Boulenger, 1899;
6. *Polypterus endlicherii* Heckel, 1847;
7. *Polypterus mokelembembe* Schliewen and Schäfer, 2006;
8. *Polypterus ornatipinnis* Boulenger, 1902;

9. *Polypterus palmas* Ayres, 1850;
10. *Polypterus polli* Gosse, 1988;
11. *Polypterus retropinnis* Vaillant, 1886;
12. *Polypterus senegalus* Cuvier, 1829;
13. *Polypterus teugelsi* Britz, 2004; and
14. *Polypterus weeksii* Boulenger, 1898.

The list, therefore, includes all the species considered valid by Fricke *et al.* (2018, see above), in addition to: *P. congicus,* considered by Fricke *et al.* (2018) as synonym of *P. endlicherii*, and *P. polli,* considered by Fricke *et al.* (2018) as a synonym of *P. palmas*. In addition to these, *P. buettikoferi* Steindachner, 1891, defined by Hanssens *et al.* (1995) as the subspecies *P. palmas buettikoferi,* may also represent a valid species, but the distinction from *P. palmas palmas* is more confidently based only on the color pattern. Since we were not able to precisely distinguish between these two subspecies of *P. palmas* with basis on our analyses, we prefered to maintain *P. buettikoferi* as a synonym of *P. palmas* in the present work. The same applies for the subspecies *P. bichir lapradei* Steindachner, 1869, considered by Poll (1941a, b, 1942) as a subspecies of *P. bichir*, from which we were not able to distinguish.

2.2 Material analyzed. Table 1 lists the material of Polypteridae analyzed in the present study. The material includes specimens, including types (Fig. 1), from the following collections (acronyms follow Fricke and Eschmeyer 2018):

1. AMNH: American Museum of Natural History, New York, NY, USA;
2. BMNH: Natural History Museum, London, UK;
3. CUMV: Cornell University, Vertebrate Collections, Ithaca, NY, USA;
4. LIRP: Laboratório de Ictiologia de Ribeirão Preto, Ribeirão Preto, Brazil;
5. MNHN: Muséum National d'Histoire Naturelle, Paris, France;
6. MZUSP: Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil;

7. UMAF: Natural History Collection, University of Massachussets, Amherst, MA, USA;
8. USNM: Smithsonian Institution, National Museum of Natural History, Division of Fishes, Washington, DC, USA;
9. VIMS: Virginia Institute of Marine Scienes, Gloucester Point, VA, USA.

The material analyzed includes ethanol-preserved specimens (alc), cleared and double-stained specimens (c&s), double-stained specimens for analysis of musculature (mus), and dry skeleton preparations (sk). Ethanol-preserved, c&s and mus specimens were previously fixed in 10% formalin and preserved in 70% ethanol. Cleared and double-stained specimens were prepared following the procedures described by Taylor and Van Dyke (1985). Double-stained specimens for analysis of musculature were prepared following the procedure described in Datovo and Bockmann (2010).

Tab 1. Comparative material of polypterids analyzed in the present work. N = Number of specimens. * = type specimen(s). Names in brackets are modern names of localities.

Species	Catalog Number	N	Locality
C. calabaricus	AMNH3528	3	Gambia, Gambia River
	AMNH226128	1	Aquarium
	BMNH18.22.2	2	Cameroon
	BMNH1901.3.21.2	1	Nigeria, Sapele, Niger Delta
	BMNH1969.3.26	2	Nigeria, Okhuo and Ogba River
	BMNH1983.7.25	2	Nigeria, Cross River
	LIRP4572	1	Aquarium
	LIRP10234	1	Aquarium
	LIRP13571	1	Aquarium
	LIRP13572	1	Aquarium
	LIRP14025	1	Aquarium
	MNHN0000.4599	2*	Old Calabar [Nigeria]
	MNHN1900.0218	1	Cameroon, Victoria
	MNHN1924.0226	1	West Africa
	MNHN1988.0253	1	Nigeria
	MZUSP63077	2	Aquarium
	UMAF00097	1	No data
	UMAF20002-02-598	1	No data
	UMAF20006-04-011	1	Aquarium
	UMAF20007-04-012	1	No data
	UMAF20008-04-013	1	No data
	UMAF20009-04-014	1	No data
	UMAF20010-04-015	1	Aquarium
	USNM22166	1	Old Calabar [Nigeria]
	USNM120734	1	West Africa
	USNM229749	1	Nigeria, Niger Delta
	USNM380263	12	Aquarium

	VIMS7366	1	Aquarium
	VIMSuncat.	1	No data
Total	29	47	12 wild caught, 11 aquarium, 6 no data
P. ansorgii	BMNH1910.9.13.4	1*	Guinea Bissau, Corbal River
Total	1	1	1 wild caugth
P. bichir	AMNH3017	2	No data
	BMNH1850.7.29.1	1	Egypt
	BMNH1900.6.28.1	1	Saint Louis, Senegal
	BMNH1901.7.17.1	1	Gambia
	BMNH1907.12.2.117	1	Egypt, New Cairo City
	BMNH1907.12.2.118	1	[Soudan,] White Nile, Kawa [Al Kawa]
	BMNH1907.12.2.119	3	Soz-abu-Suma [sic], White Nile
	BMNH1907.12.2.123	2	Gharb-el-Aish, White Nile
	BMNH1907.12.2.125	11	[South Sudan,] Fashoda [Kodok], White Nile
	BMNH1913.12.5.1	1	Nigeria, Anambra River
	BMNH1928.7.3.1	1	Nigeria, Kiyawa River
	CUMV94494	1	Ethiopia, Gambella, Baro River
	CUMV94496	1	Ethiopia, Gambella, Baro River
	LIRP13552	1	Aquarium
	LIRP13553	1	Aquarium
	LIRP14022	1	Aquarium
	LIRP14023	1	Aquarium
	LIRP14024	1	Aquarium
	MNHN0000-5761	1*	Egypt
	MNHN0000-5806	1*	Egypt
	MNHN1897-0126	1	Zaire [Democ. Rep. of the Congo]
	MNHN1925-0172	1	Niger
	MNHN1959-0390	1	Cameroon
	UMAF11341	1	No data
	USNM26093	1	No data
	USNM49135	1	Nile River
	USNM88904	1	Soudan, Umbarbit [sic]
	USNM110205	1	Upper Congo River
	USNM263337	1	No data
	USNM439328	1	Mauritania, Garak
Total	30	44	21 wild caught, 5 aquarium, 4 no data
P. congicus	AMNH5919	3	Democ. Rep. Congo, Lulaba River and Congo River confl.
	AMNH5920	3	Democ. Rep. Congo, Dungu River, Uele R.-Ubangi River
	AMNH49736	1	Congo, Congo River
	AMNH236756	1	Republic of the Congo, Fimi River at Kasai River confl.
	AMNH236783	1	Democ. Rep. of the Congo, Fimi River at Kasai River confl.
	AMNH243510	1	Democ. Republic of the Congo, Bulu, Congo River
	AMNH246152	1	Democ. Republic of the Congo, Kinshasa
	AMNH259442	1	Republic of the Congo, Malebo Pool
	AMNH268569	1	Democ. Republic of the Congo, Muwawa, Kwango River
	AMNH268570	1	Democ. Republic of the Congo, Kinguzi, Kwango River
	BMNH1897.9.30.28	1*	D. R. Congo, Stanley [Boyoma] Falls, Zaire [Congo] River
	BMNH1936.6.15.18	1	Lake Tanganyika
	BMNH99.2.20.33	1	[Democ. Rep. Congo], New Antwerp [Makanza], Congo R.
	MNHN1919-0074	1	Grilingui [sic]
	MNHN2003-0623	1	No data.
	USNM151066	1	Democ. Rep. Congo, Yakoma, Ubangi River
Total	16	20	15 wild caught, 1 no data
P. delhezi	AMNH31013	1	Aquarium
	AMNH236730	1	Repub. of the Congo, Malebo Pool, Congo River
	AMNH236788	1	Democ. Republic of the Congo, Kasai River confluence
	AMNH236800	1	Democ. Republic of the Congo, Kasai River estuary
	AMNH236817	1	Democ. Republic of the Congo, Kasai River
	AMNH240172	1	Republic of the Congo, Likouala-aux-Herbes River
	AMNH246151	1	Democ. Republic of the Congo, Petro Congo

	BMNH1899.2.20.17	1*	Democ. Republic of the Congo, New Antwerp [Makanza]
	BMNH1975.8.151:67	1	Congo, Zaire [Congo] River
	LIRP13554	1	Aquarium
	LIRP13555	1	Aquarium
	LIRP13556	1	Aquarium
	LIRP13557	1	Aquarium
	LIRP13558	1	Aquarium
	USNM191616	10	Zaire [Democ. Republic of the Congo], Lake Tanganyika
	VIMS12635	1	Aquarium
	VIMS13573	1	Congo, Stanley Pool [Malebo Lake]
Total	17	26	10 wild caught, 7 aquarium
P. endlicherii	AMNH215310	1	Nigeria, Taraba River
	AMNH226568	3	Benin, Porga, Pendjari River
	AMNH230738	2	Central African Republic, Bamingui River
	AMNH238742	7	Guinea, Niger River, Wodonkobila
	BMNH1907.12.2.138	1	[Soudan,] White Nile, Near Kawa [Al Kawa]
	BMNH1907.12.2.141	1	White Nile, mouth of Lala No [sic]
	BMNH1907.12.2.143	2	Shederah [sic], White Nile
	BMNH1913.12.5.2-3	2	[Nigeria,] Anambra River, Lower Niger
	BMNH1934.8.31.1	1	Ghana, Ejura, Ashanti Forest
	MNHN1986-0551	3	Guinea, Milo
	USNM302492	1	Ghana, Volta River
	USNM339728	1	Nigeria, Taraba River
Total	12	25	12 wild caught
P. mokelembembe	AMNH225160	2	Democ. Republic of the Congo, Mai-Ndombe River
	AMNH257820	1	Democ. Republic of the Congo, Mai-Ndombe River
	AMNH259287	1	Democ. Republic of the Congo, Mai-Ndombe River
	BMNH1907.12.3.4	1*	Republic of the Congo, Alima River
	MNHN1886.0297	1*	Congo
	UMAF11354	2	No data
Total	6	8	5 wild caught, 1 no data
P. ornatipinnis	AMNH5921	1	Democ. Republic of the Congo, Faradje
	AMNH5925	1	Democ. Republic of the Congo, Faradje
	AMNH236685	1	Republic of the Congo, Mbouono, Congo River
	AMNH236741	3/5	Republic of the Congo, Mbouono, Congo River
	AMNH240173	2/5	Republic of the Congo, Mbouono, Congo River
	AMNH245183	1	Republic of the Congo, Sangha River
	AMNH250009	1	Democ. Republic of the Congo, Congo River
	AMNH268571	1	Democ. Republic of the Congo, Kwango River
	BMNH1901.12.21.1	1*	Democ. Rep. of the Congo, Monsembé, Upper Congo River
	BMNH1919.9.10.2	1	Democ. Republic of the Congo, Lindi River
	LIRP10235	1	Aquarium
	LIRP13559	1	Aquarium
	LIRP13560	1	Aquarium
	LIRP13561	1	Aquarium
	LIRP13562	1	Aquarium
	LIRP13563	1	Aquarium
	LIRP13564	1	Aquarium
	UMAF20791-03-044	1	No data
	USNM44817	2	Kintanni, Congo [sic]
	USNM164514	1	Aquarium
	USNM292251	1	Central African Republic, Kotto River
	VIMS34420	1	Aquarium
Total	22	26	12 wild caught, 9 aquarium, 1 no data
P. palmas	AMNH257038	1	Guinea
	AMNH263186	1	Liberia, Sinoe, Gblanee Creek
	AMNH263204	1	Liberia, Sinoe, Nee Creek
	AMNH263236	1	Liberia, Sinoe, Gblanee Creek
	AMNH263238	2	Liberia, Sinoe, Neeplue Creek
	AMNH263259	4	Liberia, Sinoe, Kafron Creek

	BMNH1910.11.28.1-2	2	Guinea Bissau, Tchituti, Corbal River
	BMNH1911.5.31.1-4	4	Liberia
	BMNH1969.11.19:7	1	Liberia, Grand Gedeh County
	BMNH1975.8.15.68	3	Sierra Leone
	MNHN1963-0239	1	Ivory Coast
	MNHN2000-5133	1	Guinea
	MNHN2002-0790	1	Guinea
	USNM118747	2	Liberia, Bendaja
	USNM118748	1	Liberia, Gibi Mountain
	USNM193865	2	Liberia, Brewerville, Brewer's Creek
	VIMS7648	1	Aquarium
Total	17	29	16 wild caught, 1 aquarium
P. polli	AMNH5926	1	Democ. Rep. of the Congo, near Coquilhatville [Mbandaka]
	AMNH55502	1	Democ. Repub. of the Congo, near Stanleyville [Kisangani]
	AMNH55503	1	Democ. Repub. of the Congo, near Stanleyville [Kisangani]
	AMNH236742	1	Republic of the Congo, Congo River
	AMNH240171	1	Republic of the Congo, Kintele Market
	AMNH240174	1	Republic of the Congo, Brazzaville, Lekoli River
	AMNH245184	1	Republic of the Congo, Libongo, Sangha River
	AMNH246015	1	Democ. Republic of the Congo, Kinsasha
	AMNH246161	1	Democ. Republic of the Congo, Kinsasha
	AMNH263328	2	Democ. Republic of the Congo, Boma region, Congo river
	BMNH1899.6.27.2	1	Democ. Republic of the Congo, Upper Congo River
	BMNH1901.12.21.3	1	Democ. Rep. of the Congo, Monsembé, Upper Congo River
	MNHN2003-0622	1	No data
	UMAFunid.	1	No data
	UMAFunid.	2	No data
	USNM302509	2	Africa
	USNM374495	3	Aquarium
Total	17	22	13 wild caught, 1 aquarium, 3 no data
P. retropinnis	AMNH211415	1	Gabon, Mopia, Upper Ogooué River
	AMNH227672	1	Central African Republic, Lossi Creek, Sangha River
	AMNH237715	1	Democ. Republic of the Congo, Kinshasha, Congo River
	AMNH240175	1	Republic of the Congo, Brazzaville, Odzala National Forest
	AMNH241931	1	Democ. Republic of the Congo, Salonga River
	AMNH244078	1	Democ. Republic of the Congo, Salonga National Park
	AMNH252199	4	Democ. Republic of the Congo, Salonga National Park
	AMNH252299	1	Democ. Republic of the Congo, Salonga National Park
	AMNH253874	2	Republic of the Congo, Djoulou River
	AMNH256452	3	Republic of the Congo, Lékoumou Region
	AMNH260339	3	Central African Republic, Dzanga-Sangha Protected Area
	MNHN1886-0295	1*	Congo
Total	12	20	12 wild caught
P. senegalus	AMNH32806	1	Kenya, Mombasa
	AMNH228515	1	Central African Republic, Bamingui river
	AMNH230739	1	Central African Republic, Bamingui river
	AMNH236205	1	Kenya, Butialoa [sic] Lagoon
	BMNH1908.1.20.1-3	3	Ethiopia, Lake Rudolf [Turkana]
	LIRP4573	1	Aquarium
	LIRP7426	2	Aquarium
	LIRP10236	1	Ethiopia, Alwero [Alero] River
	LIRP10920	1	Aquarium
	LIRP13545	1	Aquarium
	LIRP13546	1	Aquarium
	LIRP13547	1	Aquarium
	LIRP13548	1	Aquarium
	LIRP13549	1	Aquarium
	LIRP13550	1	Aquarium
	LIRP13551	1	Aquarium
	LIRP14021	1	Aquarium

	LIRP15711	1	Aquarium
	MNHN0000.5765	1*	Senegal
	MNHN1961.0009	2	Haute-Volta [Burkina Faso]
	MNHN1961.0008	4	Senegal
	MNHN1961.0011	1	Sudan
	UMAF11442	1	No data
	UMAF20343	1	No data
	UMAF20600	2	No data
	UMAF20792-03-092	1	No data
	UMAFunid.	1	Aquarium
	USNM61338	1	Egypt, Fashoda [South Sudan, Kodok], White Nile
	USNM61339	1	Egypt, Tharb-el-Aish [sic]
	USNM72803	1	Sudan, Kartum, Nile River
	USNM72804	1	Sudan, Kartum, Nile River
	USNM72805	1	Sudan, Kartum, Nile River
	USNM88903	1	Sudan [South Sudan], Shambe
	USNM88905	1	Sudan [South Sudan], Shambe
	USNM89141	1	Uganda, Pakwach
	USNM224817	3	Mali, Niger River
	USNM224830	1	Mali, Niger River
	USNM229637	6	Nigeria
	USNM229760	8	Nigeria, Sokoto River
	USNM230112	6	Nigeria, Sokoto River
	USNM230130	6	Nigeria, Sokoto River
	USNM259609	4	Mauritania, Garak
	USNM292252	1	Ghana, Vakpo
	USNM299358	1	Togo, Noepe
	USNM302490	3	Togo, Kelegougan [Maritime]
	USNM302508	19	Ghana, Adawso
	USNM303215	1	Togo, Abobo [Maritime]
	USNM303216	5	Togo, Zio River
	USNM380260	1	Aquarium
	USNM395402	3	Aquarium
	VIMS12126	1	Aquarium
	VIMS35599	1	No data, C. L. Smith collection
	uncataloged	26	Developmental series, hatchery specimens
Total	53	138	31 wild caught, 16 aquarium, 1 hatchery, 5 no data
P. teugelsi	USNM303280	4*	Cameroon, Akinyam River junction with Cross River
	USNM303722	3	Cameroon, Akinyam River junction with Cross River
	USNM303773	3*	Cameroon, Mam River junction with Cross River
	USNM303799	1*	Cameroon, Cross River
	USNM303913	1*	Cameroon, Bapuo River junction with Cross River
	USNM304016	5	Cameroon, Dark Lagoon junction with Munaya River
	USNM304116	14	Cameroon, Marube River draining to Bake River
	USNM375961	5*	Cameroon, Bapuo River junction with Cross River
Total	8	36	8 wild caught
P. weeksii	AMNH236743	1	Republic of the Congo, Congo River
	AMNH244079	1	Democ. Republic of the Congo, Salonga River
	AMNH244080	1	Democ. Republic of the Congo, Luilaka River
	BMNH1898.7.9.87	1*	[Dem. Rep. of the Congo,] Monsembé, Upper Congo River
	BMNH1901.12.21.2	1	[Dem. Rep. of the Congo,] Monsembé, Upper Congo River
	MNHN1923.0102	1	Belgian Congo [Dem. Rep. of the Congo], Congo River
	MNHN1962.0334	2	Republic of the Congo, Likouala-aux-Herbes River
	MNHN1962.0335	2	Republic of the Congo, Likouala-aux-Herbes River
	MNHN2003.0621	1	No data
	CUMV89069	2	Republic of the Congo, Likouala River
	CUMV96518	2	Dem. Republic of the Congo, Lubilu River, Congo River
Total	11	15	10 wild caught, 1 no data
TOTAL	**251**	**457**	**178 wild caught, 49 aquarium, 1 hatchery, 21 no data**

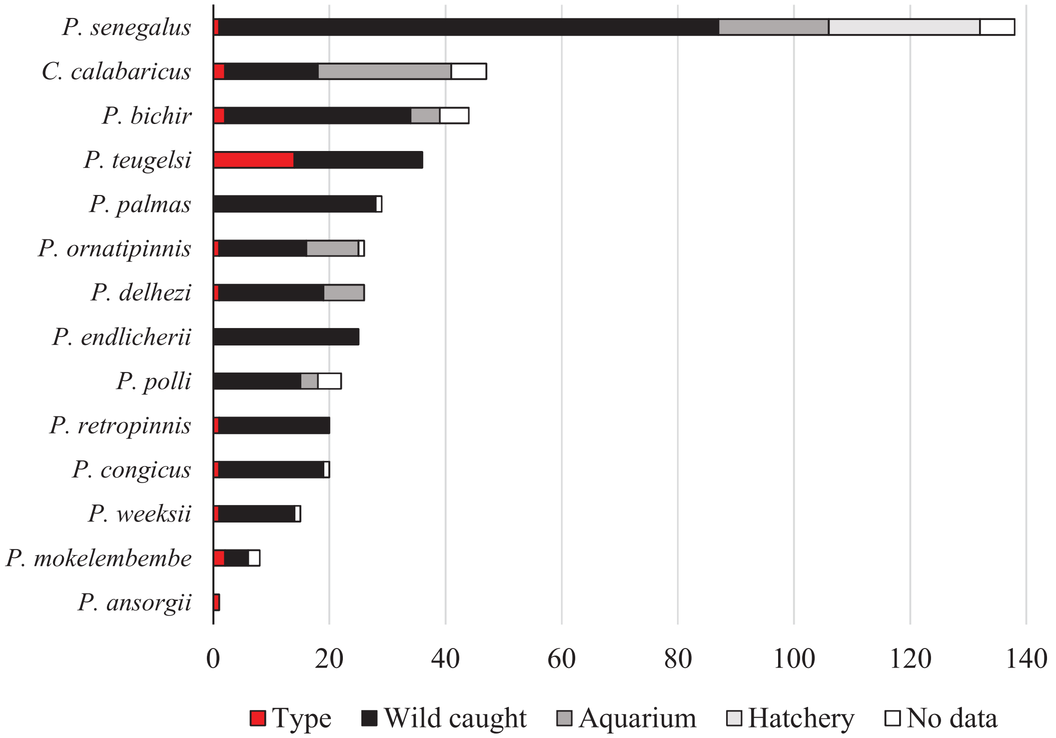

Fig. 1. Total number of specimens analyzed for each species in the present study. Species organized from largest (top) to smallest samples.

2.3 Developmental series of *Polypterus senegalus*. The material analyzed also includes an uncataloged developmental series of *P. senegalus* (Tab. 2) produced by MSc. Anna Pospisilova during her master's Dissertation project at the Department of Zoology of the Charles University in Prague. Pospsilova provided access to images of the developmental series as part of a collaboration in a study of the development of bones associated with lateral line canals in *P. senegalus* (Rizzato, Pospisilova, Hilton and Bockmann, in prep.). The rearing and staining procedures for preparation of the developmental series followed the guidelines of the institutional animal care and use committee of the Charles University in Prague for the use of embryonic material (Pospisilova 2015). The spawning took place at the Department of Zoology, Charles University in Prague, after water stimulation during the breeding season, from October to April. Fertilized eggs were collected and kept at 28 °C until the animals reached the size required. Larval specimens at appropriate size were anaesthetized by an overdose of MS-222 (Serva), fixed in 4% paraformaldehyde and stored at 4 °C. The total body size was measured after fixation as the length from the anterior tip of head to the posterior end of the caudal fin.

Tab. 2. Developmental material of *Polypterus senegalus*.

Total length (mm)	**Alcian Blue**	**Alizarin Red**
8	-	X
8.5	-	X
8.8	-	X
9	-	X
10	-	X
11	-	X
12	-	X
13	-	X
14	-	X
15	-	X
16	-	X
17	-	X
18	-	X
19	-	X
21	-	X
22	X	X
23	-	X
25	X	X
29	X	X
32	X	X
33	X	X
34	X	X
39	X	X
40	X	X
58	X	X
61	X	X

To avoid the process of decalcification by acetic acid, most stages, especially the smaller ones, were stained only with Alizarin Red. The specimens were bleached by 2% potassium hydroxide with 3% hydrogen peroxide (1:1) under a lamp. Bones were stained overnight in a solution of 8 ml 0.5% potassium hydroxide with 1 ml of stock solution of Alizarin Red (0.7 g Alizarin Red S (Sigma) and 380 ml 96% ethanol). The specimens were rinsed several times in 0.5% - 2% potassium hydroxide (according to size) and the soft tissue was cleared by an ascending series of glycerol. Samples were stored in 100% glycerol at 4 °C. Larger specimens were cleared and double-stained with Alcian Blue and Alizarin Red according to the procedures described by Taylor and Van Dyke (1985). The skulls were observed under a fluorescent stereomicroscope (Zeiss Lumar.V12) using the fluorescent filter Alexa 568 (mineralized tissue) and GFP (surrounding tissue). Images were stacked with the software AxioVision 4.0.

2.4 CT-scanning. Three-dimensional models of the head of two adult specimens of *P. senegalus* and one adult specimen of *C. calabaricus* were generated using computerized tomography technology (CT-scan). The first specimen of *P. senegalus*, LIRP 10236 (190.7 mm SL, female, Fig. 2), was scanned using a GE phoenix v|tome|x m equipment at the GE Brazil Technology Center (Rio de Janeiro, RJ, Brazil). The second specimen of *P. senegalus,* LIRP15711 (131.2 mm SL, male, Fig. 3), and the specimen of *C. calabaricus*, LIRP 10234 (190.7 mm SL, female, Fig. 4), were scanned using a GE phoenix v|tome|x s 240 equipment at the Centro para Documentação da Biodiversidade of the Biology Department of FFCLRP-USP (CBD-FFCLRP-USP, Ribeirão Preto, SP, Brazil). The second specimen of *P. senegalus*, LIRP15711, was stained with 2,5% PMA (phosphomolybdic acid) solution during 30 days prior to scanning, according to Descamps *et al.* (2014). The CT-scan data was analyzed through segmentation and virtual dissection with the softwares Amira, at VIMS, and VGStudio 3.0, at CBD-FFCLRP-USP. Images generated in the latter softwares were posteriorly edited using Adobe Photoshop© and Adobe Illustrator©.

Fig. 2. External views (left) and tridimensional models (right) of the head of an adult specimen of *Polypterus senegalus* (LIRP 10236, 190.7 mm SL, female), in lateral (top), dorsal (middle) and ventral (bottom) views. Scale bar = 1 cm.

Fig. 3. Top: tridimensional model of the head and anterior portion of body of an adult specimen of *Polypterus senegalus* (LIRP15711, 131.2 mm SL, male) stained with PMA in right dorsofrontal view. Bottom: slice (395/1000) of the same model in transversal section at about midlength of the head, showing on the left side muscles highlighted in red, brain in blue and lateral line canals in yellow.

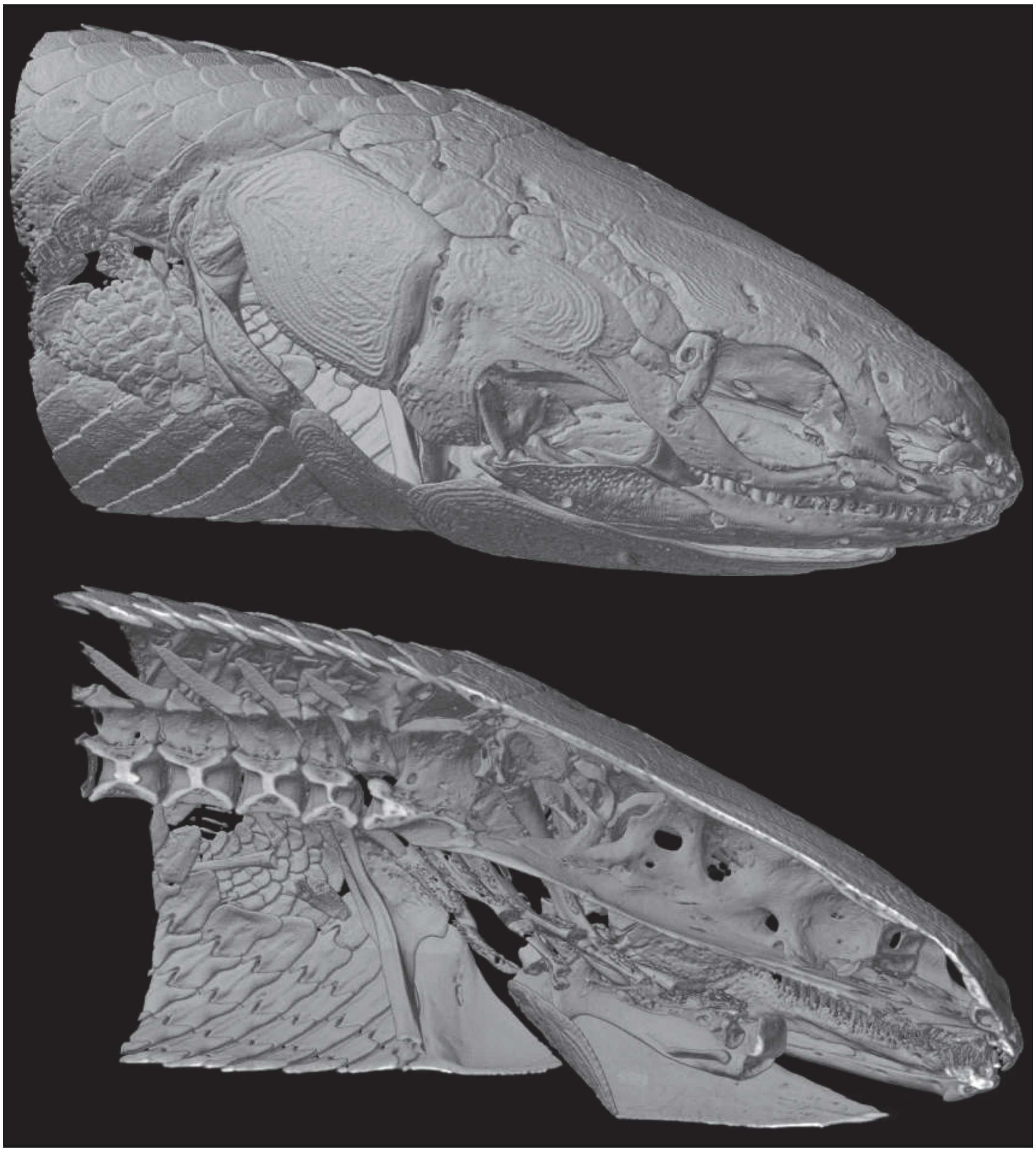

Fig. 4. Top: tridimensional model of the head and anterior portion of body of an adult specimen of *C. calabaricus* (LIRP 10234, 190.7 mm SL, female), in right dorsofrontal view. Bottom: orthoslice (335/660) of the same model in sagital section.

2.5 Morphometry and meristics. Morphometric and meristic data was collected from specimens of different sizes of all species analyzed, including type specimens of almost all species (Tab. 1). Table 3 lists the morphometric and meristic data collected, and Fig. 5 illustrates the measurements.

Tab. 3. Morphometric and meristic data collected in the present study. For illustrations of measurements, see Fig. 5.

	Abbrev.	**Description**
Morphometry		
Standard length	SL	From tip of snout to posterior margin of caudal-fin base
Head length	HL	From tip of snout to posterior margin of extrascapula
Total length	TL	From tip of snout to distal most tip of caudal fin
Pre-pelvic length	PPvL	From tip of snout to anterolateral base of pelvic fin
Pre-dorsal length	PDL	From tip of snout to anterior base of dorsal fin
Pre-pectoral fin length	PPcL	From tip of snout to posteromedial base of pectoral fin
1st dorsal spine length	DSL	From base to tip of first spinous dorsal-fin ray
Interspinal length	ISL	Distance between bases of first and second spinous dorsal-fin rays
Anal-fin base length	AFBL	Distance between anterior and posterior margins of anal-fin base
Ventral caudal length	VCL	Distance between posterior margin of anal-fin base and posterior margin of caudal-fin base
Dorsal caudal length	DCL	Distance between base of first non-spinous dorsal-fin ray and posterior margin of caudal-fin base
Pectoral base length	PcBL	Distance between anterior and posterior margins of pectoral-fin base
Pelvic base length	PvBL	Distance between anterior and posterior margins of pelvic-fin base
Pre-opercular length	POpL	From tip of snout to posterior margin of opercle
Pre-orbital length	POrL	From tip of snout to center of orbit
Interorbital width	IOrW	Width between dorsal margins of orbits
Interspiracular width	ISpW	Width between medial margins of spiracular openings
Interopercular width	IOpW	Head width at the level of the articulation of opercle
Maxilar length	MxL	From tip of snout to posterior labial fold
Mandibular length	MdL	From tip of lower jaw to posterior labial fold
Isthmus-length	IL	From tip of lower jaw to posterior margin of isthmus
Posterior head depth	PHD	Head depth at vertical through articulation of opercle
Anterior head depth	AHD	Head depth at vertical through the center of orbit
Eye diameter	ED	Horizontal diameter of orbit
Meristics		
Vertebrae	V	Total number of vertebral centra
Spinous dorsal finlets	SDF	Number of spines on dorsal fin
Non-spinous dorsal finlets	DF	Number of dorsal-fin rays devoid of spines
Caudal-fin rays	CR	-
Anal-fin rays	AR	-
Pectoral-fin rays - right	PcRR	-
Pectoral-fin rays - left	PcRL	-
Pelvic-fin rays - right	PvRR	-
Pelvic-fin rays - left	PvRL	-
Predorsal scales	PDS	Number of circumcorporal scale rows between head and anterior margin of dorsal fin
Interspinal scales	ISS	Number of circumcorporal scale rows between fisrt and second dorsal-fin spines
Circumborbital scale rows	CSR	Total number of scale rows
Scales above lateral line	SLL	Number of scales above lateral line scale (including the lateral line scale) on first complete circumcorporal row anterior to dorsal fin
Scales around body	SB	Total number of scales on first complete circumcorporal row anterior to dorsal fin

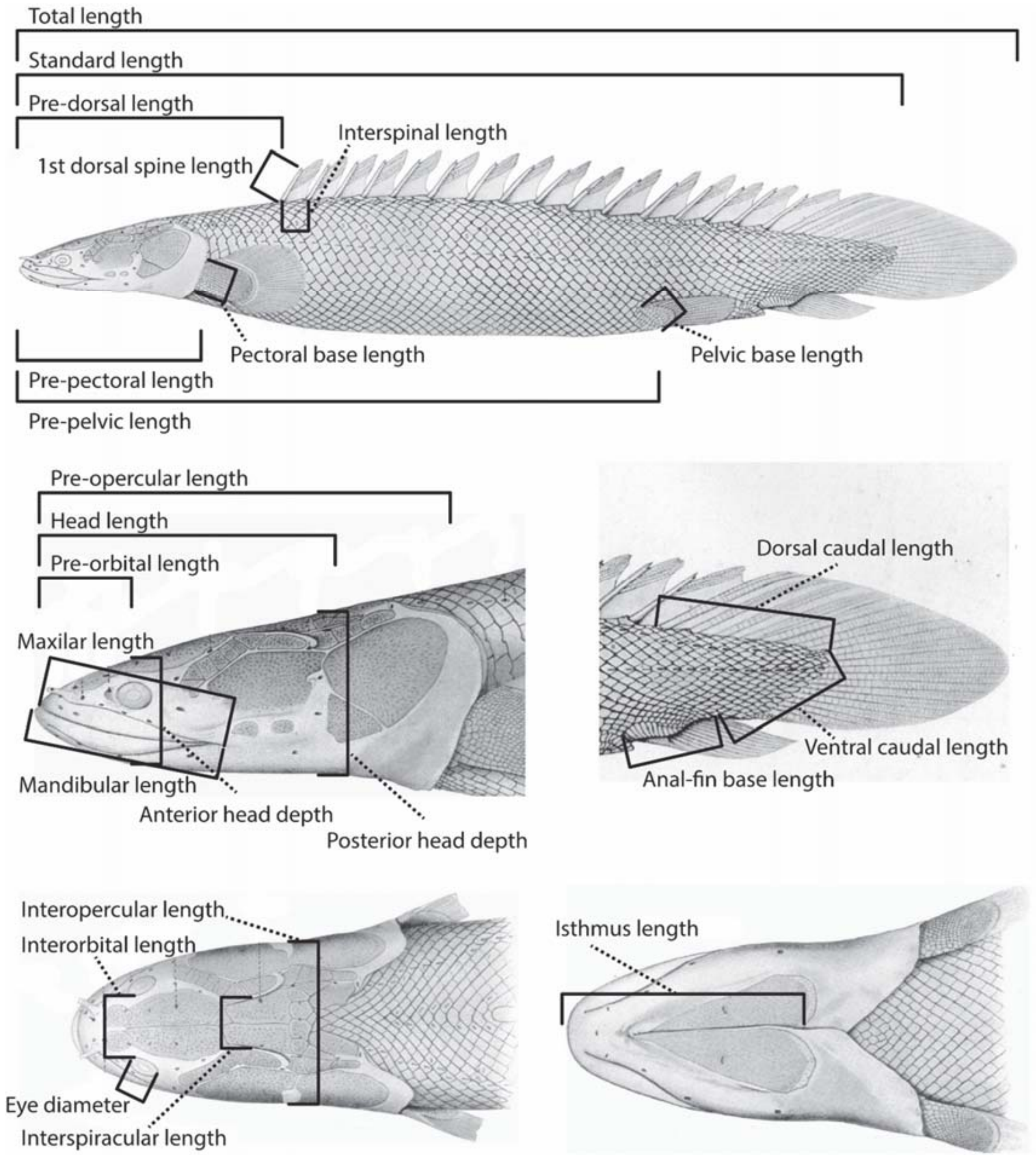

Fig. 5. Morphometric data collected from specimens of polypterids analyzed. For description, see Tab. 3. Illustrations modified from Allis (1922).

2.6 Comparative material. The comparative material is listed in Tab. 4, and includes specimens representing basal groups of Sarcopterygii (Dipnoi) and other non-teleots actinopterygians (Acipenseriformes, Lepisosteiformes and Amiiformes). Data from the remaining groups was obtained from literature.

Tab. 4. Comparative material analyzed. alc = ethanol-preserved specimen. c&s = cleared-and-stained specimen. mus = muscle dissection.

Species	Catalog Number	N	Source
Acipenseriformes			
Acipenseridae			
Acipenser fulvescens	MZUSP 48364	1 mus	
	VIMS 17717	1 c&s	USA, Tenesse Aquarium
	VIMS 35590	43 alc	USA, Tenesse Aquarium
	VIMS 35591	1 mus	USA, Tenesse Aquarium
	VIMS 35592	1 c&s	USA, Tenesse Aquarium
	VIMS 35593	3 c&s	USA, Tenesse Aquarium
Acipenser transmontanus	LIRP 9370	3 alc	-
	LIRP 9371	2 alc	-
	LIRP 9372	2 alc+1 c&s	-
	LIRP 9373	2 alc+1 c&s	-
	LIRP 9374	2 alc+1 c&s	-
	LIRP 9375	1 alc+1 c&s	-
Acipenser sp.	LIRP 4575	2 alc	USA, Hatchery
Scaphirhynchus platorhynchus	VIMS 12098	1 c&s	USA, MO, Missouri R.
Polyodontidae			
Polyodon spathula	LIRP 9639	4 alc	-
	LIRP uncat.	1 c&s	-
	VIMS 12227	26 alc	-
	VIMS 19827	3 c&s	-
	VIMS 35594	1 mus	-
Lepisosteiformes			
Lepisosteidae			
Lepisosteus platostomus	LIRP 4577	2 alc	USA, Tenessee
	USNM 54983	1 mus	-
Lepisosteus osseus	LIRP 9137	1 alc	USA, Alabama
	LIRP 9138	1 c&s	USA, Georgia
	LIRP 9140	1 alc	USA, South Carolina
	LIRP 13573	1 c&s	Aquarium
	LIRP 13574	1 c&s	Aquarium
	LIRP 13576	1 mus	Aquarium
	LIRP 13575	1 alc	Aquarium
	VIMS 13551	1 alc	USA, VA, Pamunky R.
	VIMS 31029	9 alc	USA, VA, Mattaponi R.
Amiiformes			
Amiidae			
Amia calva	LIRP 4576	2 alc	USA, Tenessee
	LIRP 9139	2 alc+1 c&s	USA, Georgia
	MZUSP 46123	5 c&s	-
	MZUSP 194454	1 c&s	-
	USNM 64338	1 mus	-
	VIMS 35717	1 mus	-
Dipnoiformes			
Lepidosirenidae			
Lepidosiren paradoxa	LIRP 1096	9 alc	Brazil, Mato Grosso
	LIRP 4391	6 alc	Brazil, Mato Grosso
Protopteridae			
Protopterus sp.	LIRP 13577	1 alc	Aquarium
	LIRP 12236	1 alc	Aquarium
	MZUSP 84530	2 alc	Benin

The comparative material also includes developmental series of species representing the main lineages of non-teleost actinopterygians – Acipenseriformes, Lepisosteiformes and Amiiformes – supplemented by larger juvenile specimens of each species (Tab. 4). The developmental series were prepared and deposited at VIMS. The series of *Acipenser fulvescens*, *Polyodon spathula* and *Scaphirhynchus albus* were prepared by C. Dillman and E. Hilton, and of *Lepisosteus osseus* and *Amia calva* were prepared by P. Rizzato and E. Hilton. Specimens of the developmental series were collected from hatcheries and preserved by direct immersion in 4% neutrally buffered paraformaldehyde at regular intervals after hatching. Once received from the hatchery, specimens were transferred to 70% ethanol for storage. Some specimens from the series were cleared and double-stained (c&s) for bone and cartilage following a modified protocol based on Dingerkus and Uhler (1977).

- *Acipenser fulvescens*: **VIMS 13577**, N = 303, developmental series representing 1-68 days post-hatch, 23/iv/2010, hatchery specimens (USFWS Warm Springs Fish Hatchery).
- *Polyodon spathula*: **VIMS 35636**, N = 184, developmental series representing 1-59 days post-hatch, 2/vi/2011, hatchery specimens (USFWS, Gavins Point National Fish Hatchery), 3/vi-1/viii/2011.
- *Scaphirhynchus albus*: **VIMS 17714**, N = 122, developmental series representing 1-59 days post-hatch, 14/vii/2011-19/ix/2011, hatchery specimens (USFWS, Gavins Point National Fish Hatchery).
- *Lepisosteus osseus*: **VIMS 13559**, N = 285, Mattaponi River, Sandy Point State Forest, King William County, VA, USA, 01-26/vi/2011, P. Konstantinidis.
- *Amia calva*: **VIMS 35596**, N = 1, Dragon Run, King and Queen County, VA, USA. **VIMS 13532**, N = 4, Nest 3, Big Bay Creek, Oneida Lake, Oswego County, NY, USA, 21/v/2010 (fixed 29/v/2010). **VIMS 34515**, N = 176, Chickahominy River, Charles City

County, VA, USA, 28/iv/2011, P. Konstantinidis. **VIMS 34527**, N = 8, Chickahominy River, Charles City County, VA, USA, 03/v/2011, P. Konstantinidis. **VIMS 34536**, N = 51, Chickahominy River, Charles City County, VA, USA, 05/v/2011, P. Konstantinidis. **VIMS 34538**, N = 42, Chickahominy River, Charles City County, VA, USA, 10/v/2011, P. Konstantinidis. **VIMS 34528**, N = 24, Chickahominy River, Charles City County, VA, USA, 03/v/2011, P. Konstantinidis. **VIMS 34521**, N = 20, Chickahominy River, Charles City County, VA, USA, 07/v/2011, P. Konstantinidis. **VIMS 17527**, N = 14, Pine Hills, sem dados de coleta. **VIMS 34525**, N = 176, Chickahominy River, Charles City County, VA, USA, 10/v/2011, P. Konstantinidis.

4 CONCLUSION

“*Good morphology lasts forever, whereas today’s matrix and the cladograms it yields will soon be superseded.*”

Colin Patterson (1998)

The present study attempted to provide a revisionary investigation of the anatomy of polypterids, in a comparative approach with representatives of the main clades of Gnathostomata, especially of Actinopterygii.

The first part of the work dealt with morphometric and meristic characters, and aimed to describe the extent of intra- and interspecific variation among polypterids, in order to provide an improved and detailed characterization of the group as a whole and of its living representatives. A differential of this study is the inclusion of several specimens of different sizes and developmental stages for each species, including types for almost all of them, and an analysis of the variation of the characters in relation to the size of the specimens. In the course of this investigation, we faced difficulties resulting from the controversial taxonomy of the group that is in urgent need of a comprehensive revision. Despite these difficulties, we were able to identify many morphometric and meristic characters that can be useful not only for distinguishing species, but also as possibly informative in terms of suggesting a closer relationship between some of them. As result, we provide many morphological characters that can be useful in future attempts to review the taxonomy and to unravel the phylogenetic relationships inside Polypteridae.

The remaining part of the study focused on the internal anatomy of polypterids, and aimed to provide a detailed review and analysis, emphasizing morphological systems and complexes that are traditionally underexplored for systematic purposes: the laterosensory system and the musculature. We adopted a holistic approach, incorporating data from ontogeny, including information from literature and the analysis of images of an ontogenetic series of *P. senegalus*, and combining information from many different anatomical systems and complexes, including bones, muscles, ligaments, nerves, lateral line and viscerae. In order to study the internal anatomy, we also combined different methodological approaches, including the analysis of cleared and double-stained specimens, double-stained and dissected specimens, radiographs, and 3D models from CT-scanning (including tissue-enhanced staining methods). In addition, we included the analysis of representatives of other groups of non-teleost actinopterygians, including developmental series of four species representing each of the main groups of Acipenseriformes (Acipenseridae and Polyodontidae) and Holostei (Lepisosteiformes and Amiiformes). The analysis of the internal anatomy also included thorough revisionary studies of the literature, especially regarding the different terminologies and homology hypotheses implicit on them. To our knowledge, this is the first time such an effort is applied for the study of the internal anatomy of polypterids.

The results of the study of the internal anatomy of polypterids are summarized as follows. We provide a detailed, thorough description of the laterosensory system, more specifically of the mechanosensory lateral line system, including the distribution of superficial and canal neuromasts in the head and trunk, their innervation by lateral line nerves (which provides the basis for identifying canal segments and lines of superficial neuromasts), and the ontogeny of the organs and canals. This decription provides the basis for comparisons with other actinopterygians, as well as with other bony fishes, and for the proposal of a standardized nomenclature for the lateral line system, especially the canals and lines of superficial neuromasts. The next step will be to provide similar descriptions of other groups of bony fishes, including sarcopterygians and basal actinopterygians, using a standardized nomenclature, and then perform a phylogenetic analysis in order to identify phylogenetically informative characters for unraveling the evolutionary relationships between the main clades of Osteognathostomata.

We also provide a detailed study of the development of bones associated with lateral line canals in *Polypterus senegalus*. This study revealed the existence of a previously neglected layer of ossifications in the skull of bony fishes associated with the laterosensory system, more specifically, with lateral line canals. The findings of this study support the hypotheses that there is a two-component pattern of development of lateral line canal bones in bony fishes, and reveal that bones associated with lateral line canals in polypterids and many other fishes are actually of a compound nature. The main consequence of these findings is realizing that many of the homology issues regarding some of the bones in the skull of fishes, especially of fossils, are actually derived from neglecting the existence of this additional, independent layer of ossifications interacting with the dermal and endochondral components. We discuss some of these homology issues regarding bones of polypterids, but there are many other issues in other groups that need to be investigated and reevaluated in the light of these new findings.

The present study also addressed long-standing issues regarding polypterid anatomy. The unique articulation of the skull with the vertebral column was studied in details, including a review of previous hypotheses regarding the identity of the basiexoccipital. We associated the peculiar anatomy of the occipital region of polypterids with the presence of a functional neck in the group, a very interesting characteristic of polypterids that have been neglected so far. We also readdressed and provided new evidences, with basis mainly on the analysis of branchial arch muscles and nerves, that the fifth arch is the one that is lacking in polypterids. The review of the branchial arch musculature also resulted in new interpretations of the identity of some muscles, notably the *adductor 4* and *levator externus 5*.

Some of the most interesting results of the present study regard the musculature of polypterids. Several new interpretations are proposed, and these interpretations lead to new hypotheses regarding the evolution of the musculature of gnathostomes as a whole. The facial musculature was thoroughly reviewed, and analyzed in a phylogenetic context with other basal representatives of the main clades of Actinopterygii, as well as in comparison with other gnathostomes. A new, standardized terminology is proposed for these muscles, and phylogenetically significant characters were identified (Datovo and Rizzato, 2018). We also redescribe the muscles on the ventral surface of the head and the hypobranchial muscles, identifying phylogenetically significant characters, including at least two conspicuous synapomorphies for Actinopterygii present in polypterids, the presence of the *interhyoideus*, and of a *coracomandibularis* attached to the branchial skeleton.

The muscles of the dorsal and caudal fin were described, and a detailed analysis of the hypotheses regarding the caudal fin evolution in vertebrates is presented. We incorporate information about the caudal fin musculature, which is usually neglected in discussions about the evolution of the caudal fin in vertebrates, and identify the main factors involved in the transformation of the plesiomorphic condition of a typically heterocercal caudal fin to the apomorphic, ‘true’ homocercal caudal fin of more derived teleosts. We also provide redescriptions and new interpretations regarding the pectoral fin muscles of polypterids. Finally, we describe for the first time the sexually dimorphic anal-fin musculature of male polypterids, which is highly modified in concert with modifications on the external anatomy and internal skeleton associated with the unique courtship behavior of the group.

In addition, we provide at the end of this work a review of previous ideas and hypotheses of the phylogenetic position of polypterids in relation to other groups of fishes. We overview the history of classification of the group in precladistic times, as well as the attempts to determine their evolutionary relationships in a cladistics paradigm. This review shows how the peculiar anatomy of the group was decisive for considering them as a very specialized lineage in relation to other bony fishes, and revealed the major influence of two authors, Goodrich and Patterson, on the interpretation of an actinopterygian affinity of polypterids. This review also highlights that, in order to provide more comprehensive and robust hypotheses of the phylogenetic position of polypterids in relation to other basal groups of bony fishes, it is crucial, in the first place, to have a detailed understanding of their anatomy, exploring a wider and more diverse set of morphological systems and complexes and adopting a holistic and comparative approach.

The present study represents, therefore, an initial effort towards this goal, and demonstrates how the integration of information from different morphological complexes and systems, from development, from an analysis of a large sample of specimens of different developmental stages and sizes, from a comparative analysis with closely-related taxa, and combining different methods and technologies for morphological investigation and a detailed and thorough historical analysis of previous interpretations of several authors, is fruitful in order to provide a better understanding of the anatomy of very specialized groups, especially those occupying key-phylogenetic positions in the phylogeny. This kind of study contributes to reevaluate of our ideas regarding the phylogenetic relationships between the groups, and to provide a more complete picture of the evolution of the anatomy of vertebrates.

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