

A PERMIAN ACTINOPTERYGIAN FROM THE MINNEKAHTA LIMESTONE OF SOUTH
DAKOTA, USA

By

Jack Reza Stack

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Geological Sciences—Master of Science

2021

ABSTRACT

A PERMIAN ACTINOPTERYGIAN FROM THE MINNEKAHTA LIMESTONE OF SOUTH DAKOTA, USA

By

Jack Reza Stack

The interrelationships and phylogenetics of extinct Paleozoic and Early Mesozoic ray-finned fishes (Actinopterygii) are obscured by a low-quality fossil record and understudy of Late Paleozoic (Permo-Carboniferous) actinopterygians. To help address this issue, I describe a new species of ray-finned fish from the late Early Permian Minnekahta Limestone of South Dakota. This taxon is represented by two specimens, Field Museum of Natural History PF 3721 and Yale Peabody Museum 18649. PF 3721 is an exceptionally well-preserved partial three-dimensional head and trunk preserving the external anatomy of and some internal elements from the skull, paired fins, and scale cover. YPM 18649 is a partially articulated, laterally compressed individual with a heavily disarticulated skull. This fish has features of the paraphyletic "paleoniscoid" group, including an immobile maxilla with a narrow suborbital process and a broad postorbital expansion, a heterocercal caudal fin, and rhombic ganoid scales. I conducted an equally weighted maximum parsimony analysis in PAUP and a Bayesian analysis with the Mkv model of morphological evolution in MrBayes with 73 other taxa and 222 characters that placed this taxon in a polytomy with other Late Paleozoic and Early Mesozoic "paleoniscoids" in the respective consensus trees. I recommend the application of parsimony and Bayesian inference techniques in tandem to the problem of early actinopterygian interrelationships to provide necessary caution and direction to future work.

This thesis is dedicated to my family and friends.

ACKNOWLEDGMENTS

This work would not have been completed without the guidance and support of Drs. Michael Gottfried, Danita Brandt, Dalton Hardisty, and Allen McNamara. Specimen and equipment access was provided by Laura Abraczinskas, Zerina Johanson, Emma Bernard, Adrienne Stroup, William Simpson, Matthew Friedman, and Donald Brinkman. I want to thank Drs. Ilja Kogan and Carlo Romano for providing crucial advice and copies of papers on Permian ray-finned fishes. I would also like to thank my friends Olivia Fitch, Brent Heerspink, Alessio Capobianco, Rodrigo Figueroa, Mingda Lyu, Brenen Wynd, Khanh To, Benjamin Brugman, Ryan Mckeeby, and every graduate student in the Earth and Environmental Sciences department for welcoming me into their community and providing advice, support, and good cheer. This degree also would not have been completed without the support of Ami McMurphy, Pamela Robinson, Elizabeth McElroy, and Judi Smelser.

I have been blessed with a loving and supportive family and group of friends. My parents, Michael Stack and Leyla Moossavi, have supported my paleontological ambitions from the start. I also want to thank Dr. Murray Borrello, my first geology professor and colleague, for his mentorship, guidance, and friendship. My sister and brother, Sara and Camran Stack, along with my cousin Marina Stack and friends Colton Morrow, Toby Santamaria, Joseph Sileo, Nicholas Beckish, Olivia Fitch, and Geeta Minocha have always been there for me, in the highest and lowest parts of these last two years.

This study includes data produced in the CTEES facility at the University of Michigan, supported by the Department of Earth & Environmental Sciences and College of Literature, Science, & the Arts. Support for this project came from a Michigan State University

Distinguished Fellowship, a Michigan State University Department of Earth and Environmental Sciences Alumni Fellowship, a Graduate Student Research Grant from the Geological Society of America, and a Rodney M. Feldmann Student Research Award from the Paleontological Society. The fossils examined in this research were collected from the ancestral, traditional, and contemporary lands of the Sioux Nation (Dakota, Lakota, Nakota, and Arapaho people) in the Black Hills of South Dakota, which are occupied in violation of the Fort Laramie Treaty of 1868.

TABLE OF CONTENTS

LIST OF TABLES	viii
LIST OF FIGURES	ix
KEY TO ABBREVIATIONS	xi
A PERMIAN ACTINOPTERYGIAN FROM THE MINNEKAHTA LIMESTONE OF SOUTH DAKOTA, USA..... 1	
1. Introduction.....	1
2. Geologic Setting	5
3. Material and Methods	8
3.1 Material	8
3.2 Assignment of Material.....	9
3.3 Photographs and Interpretative Drawings.....	10
3.4 Terminological Conventions.....	11
3.5 Anatomical Abbreviations	11
3.6 Micro-Computed Tomography	12
3.7 Systematic Comparisons	13
3.8 Phylogenetic Analysis.....	14
3.9 Institutional Abbreviations.....	16
4. Systematic Paleontology.....	16
4.1 Type Species	17
4.2 Generic Diagnosis.....	17
4.3 Derivation of Name.....	17
4.4 Diagnosis.....	17
4.5 Holotype.....	18
4.6 Referred Specimens	18
4.7 Occurrence	18
5. Description.....	19
5.1 Skull Roof.....	19
5.2 Circumorbital Bones	25
5.3 Jaws, Palate, and Dentition	28
5.4 Opercular Series and Associated Bones	33
5.5 Gulars and Branchiostegal Rays	35
5.6 Parasphenoid and Braincase	36
5.7 Shoulder Girdle.....	37
5.8 Hyoid and Branchial Arches.....	38
5.9 Paired Fins	39
5.10 Median and Caudal Fins	42
5.11 Squamation	46
6. Micro-CT	49
7. Phylogenetic Analysis.....	50

7.1 Parsimony Analysis	50
7.2 Bayesian Analysis	53
8. Discussion	55
8.1 Systematic Affinities and Comparisons.....	55
8.2 Taphonomy of PF 3721 and YPM 18649	57
8.3 Interrelationships of Early Ray-finned Fishes	61
9. Conclusions.....	65
APPENDIX.....	66
REFERENCES	188

LIST OF TABLES

Table A1.1. Summary of examined material.	67
--	----

LIST OF FIGURES

Figure 1.1. The Minnekata Limestone of South Dakota.....	6
Figure 1.2. The five pieces of PF 3721 and associated cast.	9
Figure 1.3. Cast of the skull roof of PF 3721 in dorsal view, taken from the right lateral piece..	20
Figure 1.4. Cranial elements in the left lateral piece of PF 3721, internal surface of bones preserved in lateral view.	27
Figure 1.5. Cranial elements in the right lateral piece of PF 3721, internal surface of bones preserved in lateral view.	27
Figure 1.6. Cranial elements in YPM 18649 preserved in lateral view.....	28
Figure 1.7. Left side of the medial piece of PF 3721, internal bones preserved in lateral view...	32
Figure 1.8. Right side of the medial piece of PF 3721.	33
Figure 1.9. Cranial elements in the ventral piece of PF 3721.....	36
Figure 1.10. Right pectoral fin in the ventral piece of PF 3721.....	41
Figure 1.11. Attachment of the pectoral fin to the shoulder girdle in the medial piece of PF 3721.	41
Figure 1.12. Pelvic fin in the left lateral and ventral pieces of PF 3721.....	42
Figure 1.13. Anal fin of YPM 18649.....	44
Figure 1.14. Dorsal fin of YPM 18649.....	45
Figure 1.15. Caudal fin of YPM 18649.	45
Figure 1.16. Lateral squamation in the left lateral piece of PF 3721.....	48
Figure 1.17. Abdominal squamation in the medial piece of PF 3721.....	48
Figure 1.18. 3-D model of the internal structures in the micro-CT scan of the medial piece.	49
Figure 1.19. Phylogenetic hypothesis of actinopterygian interrelationships, strict consensus tree of a maximum parsimony analysis of 222 morphological characters from Giles <i>et al.</i> (2017).	52

Figure 1.20. Phylogenetic hypothesis of actinopterygian interrelationships, maximum clade credibility tree from Bayesian analysis of 222 morphological characters from Giles <i>et al.</i> (2017).....	54
--	----

Figure 1.21. Reconstruction of <i>Concentrilepis minnekahtaensis</i> in lateral view.	55
--	----

KEY TO ABBREVIATIONS

Ab	Anal basal fulcra
Abs	Abdominal squamation
Af	Anal fin
Afr	Anal fin rays
An	Angular
Ano	Anterior nasal opening
Ao	Antorbital
Asq	Axial squamation
Br	Brachiostegeal ray
Bre	Brachial arch element
Cf	Caudal fin
Cl	Cleithrum
Cr	Coronoid
Cv	Clavicle
Dcf	Dorsal caudal lobe basal fulcra
Dcr	Dorsal caudal fin rays
Df	Dorsal fin
Dfr	Dorsal fin rays
Dh	Dermohyal
Dn	Dentary
Dp	Dermopalatine

Ds	Dermosphenotic
Endg	Endoskeletal shoulder girdle
El	Insertion for ethmopalatine ligament
Exsc1	Lateral extrascapular
Exsc2	Medial extrascapular
Ff	Fringing fulcra
FMNH	Field Museum of Natural History
Fmi	Foraman for internal mandibular branch of facial nerve
Fr	Frontal
Gpl	Gular pit line
Hbp	Hole for the basipterygoid process
Hy	Hyomandibula
It	Intertemporal
Ju	Jugal
La	Lacrima
Lg	Lateral gular
Lpr	Lateral process of palatoquadrate
Lsq	Lateral squamation
Mg	Median gular
Mk	Ossified Meckelian cartilage
Mx	Maxilla
Na	Nasal
Nc	Neurocranium

NHM	Natural History Museum
Op	Opercular
Pa	Parietal
Pcl	Post-cleithrum
Pcr	Pectoral fin rays
Pe	Pelvic fin
Pf	Pectoral Fin
Pm	Premaxilla
Po	Preopercular
Pq	Palatoquadrate
Pocl	Presupracleithrum
Pr	Prearticular
Pro	Propterygium
Psp	Parasphenoid
Pspi	Postspiracular
Pt	Post-temporal
Pvr	Pelvic fin rays
Qu	Quadrate
Quj	Quadratojugal
Ra	Radials
Ro	Rostral
Sc	Sclerotic ring
Scl	Supracleithrum

Shd	Shoulder girdle
Skr	Skull roof
Sop	Subopercular
So	Suborbital
Sq	Squamation
St	Supratemporal
Sur	Surangular
Te	Teeth
Th	Canal for the truncus hyoideomandibularis
Vcb	Ventral caudal lobe basal fulcra
Vcr	Ventral caudal lobe fin rays
Vr	Ventral ridge scale
X	Anamestic dermal element
YPM	Yale Peabody Museum of Natural History

A PERMIAN ACTINOPTERYGIAN FROM THE MINNEKAHTA LIMESTONE OF SOUTH DAKOTA, USA

1. Introduction

The interrelationships of Paleozoic and Early Mesozoic "paleoniscoids" (a paraphyletic group of early actinopterygians) and their phylogenetic placement relative to more crownward ray-finned fishes with living representatives remains highly uncertain (Sallan, 2014; Friedman, 2015). This grouping has been widely recognized as paraphyletic in several previous phylogenetic analyses of early ray-finned fishes (e.g., Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1993). Studies of Paleozoic ray-finned fishes that have attempted to address these uncertainties have been hampered by a relative scarcity of detailed data from late Paleozoic (Permo-Carboniferous) taxa (Hurley *et al.* 2007; Giles *et al.* 2017). Whereas many Devonian and Triassic ray-finned fishes have been the subject of detailed morphological and phylogenetic studies (e.g., Stensiö, 1921; Nielsen, 1942; Nielsen, 1949; Lehman, 1952; Gardiner, 1984; Swartz, 2009; Choo, 2011; Xu *et al.* 2014; Giles *et al.* 2015a; Giles *et al.* 2017; Argyriou *et al.* 2018) comparatively little work has been conducted on late Paleozoic, particularly Permian, actinopterygians (Sallan, 2014; Friedman, 2015). Consequently, the majority of late Paleozoic ray-finned fishes are not well-enough described to be included in phylogenetic analyses, and the interrelationships of those that can be included are difficult to resolve relative to their Devonian and Triassic counterparts (Sallan, 2014; Giles *et al.* 2017). In fact, many Late Paleozoic taxa are defined with generalized, non-diagnostic features (e.g., size, body shape) and are based on poorly preserved type specimens that make the construction of new diagnoses and phylogenetic analysis difficult even with careful re-examination (Sallan, 2014; Mickle, 2017). Recent reviews of the evolutionary history of ray-finned fishes agree that address these issues

will require renewed morphological and systematic study of late Paleozoic "paleoniscoids" (Friedman & Sallan, 2012; Sallan, 2014; Friedman, 2015).

Many late Paleozoic ray-finned fish fossils are laterally compressed and poorly preserved, severely limiting the information that can be obtained regarding the taxa they represent (Gardiner & Schaeffer, 1989; Friedman, 2015). The specimens that are available to study from this interval are also limited by a scarce Late-Pennsylvanian-Middle Permian marine actinopterygian fossil record (Hurley *et al.* 2007; McGowan & Smith, 2008; Romano *et al.* 2014). Therefore, detailed study of well-preserved "paleoniscoids" from understudied Late Pennsylvanian-Middle Permian marine faunas will contribute to the documented fossil record of ray-finned fishes from this interval and potentially strengthen phylogenetic analyses of early actinopterygians (e.g., Figueroa *et al.* 2019).

The focus here is on a largely unstudied assemblage of ray-finned fishes from the Minnekahta Limestone of the Black Hills of South Dakota. Ray-finned fishes from the Minnekahta Limestone were reported by Hussakof (1916), Braddock (1963, David Dunkle pers. comm.), and by Dierks & Pagnac (2010), based on material in the collections of the South Dakota School of Mines Museum of Geology (SDSM). Hussakof (1916) and Dunkle (in Braddock, 1963) offer short descriptions of isolated specimens that are not well enough preserved to be assigned to existing taxa or to justify the erection of new taxa. However, Hussakof (1916) noted the similarity of the specimens they described to the problematic taxon *Acrolepis* and Dunkle (in Braddock, 1963) compared the specimen they examined to the deep-bodied Amphi-centridae. The abstract of Dierks & Pagnac (2010) summarizes an unpublished survey of the Minnekahta Limestone material in the SDSM that notes specimens identified as "*Acrolepis*" and *Platysomus*, but they do not figure this material or provide a basis for these

identifications. Therefore, although a fauna of ray-finned fishes has been documented from the Minnekahta Limestone for over a century, no focused taxonomic work has been undertaken on this material.

In addition to the material from the SDSM, nine partially articulated specimens of actinopterygians from the Minnekahta Limestone in the collections of the Field Museum of Natural History (FMNH, on loan to MSU) and the Yale Peabody Museum of Natural History (YPM, on loan to MSU) have not been described, offering an opportunity for detailed study (list of examined material in Table A1.1). A partially articulated and three-dimensionally preserved head and trunk of a ray-finned fish (FMNH PF 3721) has a suite of anatomical features that are not typically preserved in Permian actinopterygians, including an uncrushed skull preserving lateral, dorsal, and ventral elements, endoskeletal jaw elements, the paired fins and some of their endoskeletal supports, and the scale cover. An additional specimen (YPM 18649) with similar morphology to PF 3721 contains some of the branchial arch elements, the paired fins, median fins, caudal fin, and most of the lateral squamation.

Herein I describe a new genus and species of ray-finned fish, *Concentrilepis minnekahtaensis* gen. et sp. nov., based on PF 3721 and YPM 18649. I compare *Concentrilepis* to morphologically similar Permian and Triassic ray-finned fishes using published descriptions and examination of museum specimens to establish that this material represents a new species. I then incorporate this taxon into a modified version of the phylogenetic framework of Giles *et al.* (2017) and conduct two sets of phylogenetic analyses to examine its evolutionary position relative to other Late Paleozoic and Early Mesozoic ray-finned fishes. This study improves the documented fossil record of Permian ray-finned fishes by describing a new taxon that is represented by specimens that preserve more morphological data than is typical for a Late

Paleozoic ray-finned fish. I also address the historic paucity of Permian taxa in phylogenetic analyses of ray-finned fishes by incorporating this taxon into an existing phylogenetic framework. Finally, I explore the effectiveness of applying both traditional parsimony and more novel Bayesian techniques to the phylogeny of early ray-finned fishes.

2. Geologic Setting

The Minnekahta Limestone of the Black Hills region of South Dakota is a ~2 m to ~15 m thick deposit of thinly bedded and pinkish-grey or light red, finely crystalline limestone situated between two continental redbeds, the underlying Opeche Shale and overlying Spearfish Formation (Darton, 1901; Maughan, 1964; Fahrenback & Sawyer, 2001; Benison *et al.* 2018; Fig. 1.1A). The Minnekahta Limestone was deposited during a transgressive episode of the Phosphoria seaway that flooded western South Dakota, which was situated in the eastern part of a marine basin on the western margin of the North American Craton (Fig. 1.1B; Piper & Link, 2002; Dopheide & Winniger, 2008). Benison *et al.* 2018 claim that no fish fossils have been collected from the Minnekahta Limestone *in situ* to support their argument that this formation was deposited in a saline lake environment. However, fossils of conodonts, ray-finned fishes, gastropods, and pelecypods have been reported in the literature (albeit in relatively obscure reports) from the Minnekahta Limestone (Hussakof, 1916; Darton & Paige, 1925; Braddock, 1963).

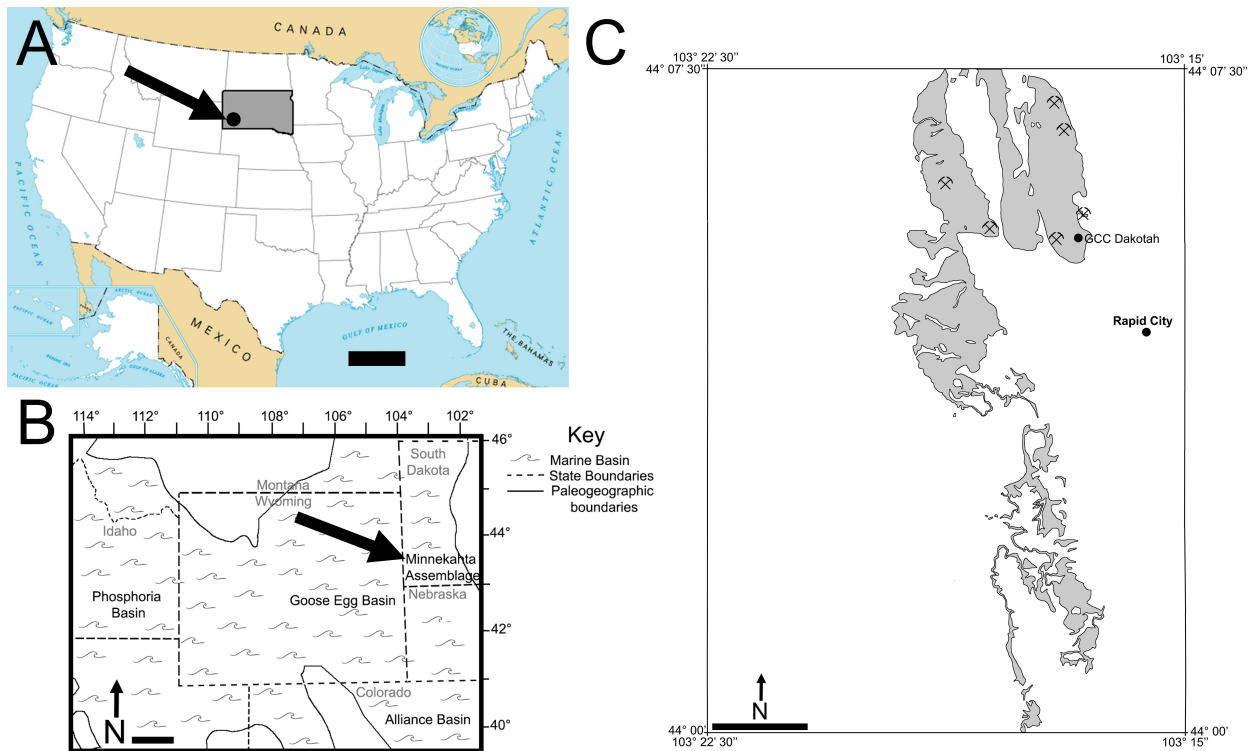


Figure 1.1. The Minnekahta Limestone of South Dakota. **A**, location of the Black Hills of South Dakota (indicated by arrow), modified from the United States National Atlas. Scale bar equal to 482 km. **B**, paleogeographic map of the northwestern United States ~260 ma, showing the location of the Minnekahta assemblage (indicated by arrow), after Piper and Link (2002, fig. 1. Scale bar equal to 100 km. **C**, outcrop belt of the Minnekahta Limestone in the Black Hills region of South Dakota. Quarries indicated by pickaxe symbol and location of a fish bearing locality (GCC Dakotah) marked. Scale bar equals 1 km.

The Minnekahta Limestone in the Black Hills is correlated to the Minnekahta Member of the Goose Egg Formation of eastern Wyoming, a carbonate spillover of the Meade Peak Phosphatic Shale Member of the Phosphoria Formation (S.E. Idaho, western and central Wyoming) (Burk & Thomas, 1956; Boyd & Maughan, 1972; Wardlaw & Collinson, 1984; Wardlaw & Collinson, 1986; Maughan, 1994; Whalen, 1996; Inden & Coalson, 1996; Piper & Link, 2002). The conodont biostratigraphy of Wardlaw & Collinson (1986) indicates a late Leonardian age, or late Early Permian (Kungurian, 283.5 $\pm$ 0.6 to 272.95 $\pm$ 0.11 ma) for the Minnekahta Limestone (Gradstein *et al.* 2012; Cohen *et al.* 2013).

The material used in this study was collected from Pennington County, South Dakota, in the area around Rapid City (Fig. 1.1C). PF 3721 and the other specimens from the FMNH are identified as being recovered from "City Quarry" and the YPM material are from the "South Dakota State Cement Plant". In the over half-century since the YPM material was collected, the South Dakota State Cement Plant was purchased by GCC Dakotah, Inc (Fig. 1.1C). I was not able to determine which quarry the FMNH specimens were collected from, but I can narrow down the locality to a handful of quarries in the Minnekahta Limestone in the Rapid City region (Fig. 1.1C). Although these specimens are identified as having been collected from the Opeche Shale, based on lithology they were collected from the Minnekahta Limestone. Although the Opeche Shale consists almost entirely of red mudstone (with some gypsum interbedded), the examined specimens are preserved in a matrix of pinkish grey, thinly bedded limestone characteristic of the Minnekahta Limestone. Hussakof (1916), Braddock (1963), and Dierks and Pagnac (2010) also described fish material of the same type from the Minnekahta Limestone. Because these specimens lack detailed geologic data, I cannot be certain of my attribution of this material to the Minnekahta Limestone. Further field research on the Minnekahta Limestone and the Opeche Shale is necessary to determine the exact geologic affinity of this fauna.

In addition to ray-finned fishes, arthropods (*Mamayocaris*), pelecypods, gastropods, and stromatolites have been reported from the Minnekahta Limestone (Darton & Page, 1925; Brooks, 1962; Braddock, 1963; Dopheide & Winniger, 2008; Dierks & Pagnac, 2010; Benison *et al.* 2018). However, only the phyllocarid crustacean *Mamayocaris* (also known from the Early Permian of Texas; Hotton *et al.* 2002) has been found in direct association with fish remains (Brooks, 1962; Clarkson, 2009; Dierks & Pagnac, 2010; pers. obs.).

3. Material and Methods

3.1 Material

This description is primarily based on PF 3721, the front half of a fish that was broken (prior to this study, likely in the process of collection) into five pieces that each preserve a distinct aspect of the individual's morphology. These pieces do not fit together perfectly, but taken together, they preserve much of the anterior portion of a medium-sized fish (estimated at approximately 12.5 cm in standard length), including the skull, pectoral and pelvic fins, and the anterior portion of the trunk. Each piece of PF 3721 has been assigned the same specimen number by the FMNH. For ease of reference, I assigned an informal name to refer to each piece in my description corresponding to the part of the fish it preserves (Fig. 1.2). The left lateral piece contains the left lateral side of the anterior portion of the fish in internal view and includes some of the skull (the snout is missing), a small portion of the left pectoral fin, a large patch of lateral squamation from the anterior portion of the trunk, and the base of the left pelvic fin. The right lateral piece is a natural mold of the right lateral side of the skull in internal view. I also used a latex cast (from the FMNH collections, creator unknown) of the right lateral piece in the description. The medial piece fits in between the left and right lateral pieces, although it does not contain the anterodorsal part of the interior of the skull. The lateral parts of the medial piece show a mixture of internal elements from the jaws and the hyoid arch, along with portions of external elements from the shoulder girdle, opercular apparatus, and skull roof. Ventrally, the medial piece preserves the underside of the skull (in part), including the branchiostegal rays, gulars, the attachment of the pectoral fins to the shoulder girdle, and the anterior abdominal squamation. The ventral piece preserves the ventral surface of the skull in dorsal view, showing the ventral aspect of the skull and the shoulder girdle in counterpart (including the cleithrum,

clavicles, gulars, and branchiostegal rays), along with the pectoral fins, a piece of the pelvic fin, and some of the abdominal squamation in counterpart. The pectoral piece preserves the part of the right pectoral fin, along with some of the associated abdominal squamation.

YPM 18649, a laterally compressed fish with a severely disarticulated skull, was also used in the description. The paired, median, and caudal fins are preserved in this specimen, along with a largely complete lateral scale cover. I did not add the outline to the edge of this specimen.

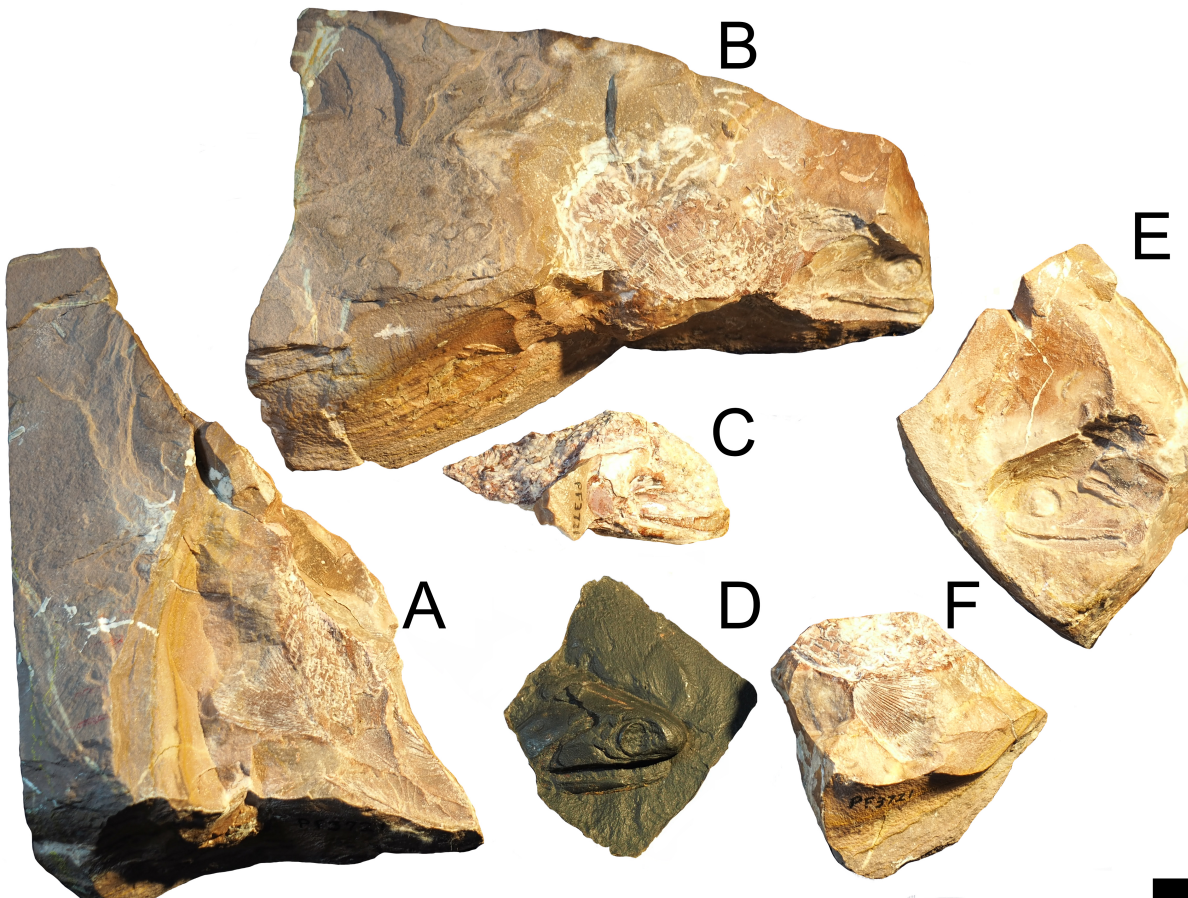


Figure 1.2. The five pieces of PF 3721 and associated cast. A, ventral piece. B, right lateral piece. C, medial piece. D, cast of right lateral piece. E, right lateral piece. F, pectoral piece. Labels are to the top right of the piece they are assigned to. Scale bar equals 1 cm.

3.2 Assignment of Material

I consider PF 3721 and YPM 18649 to be from the same taxon on the basis of the following shared features: supracleithrum with round ventral margin posterior to contact with

cleithrum, indented ventral margin of the supracleithrum at the contact with cleithrum, supracleithrum with broad middle section and pointed dorsal margin; series of small lateral scales ventral to supracleithrum (no postcleithrum); pectoral fin with thin, closely packed lepidotrichia; pectoral lepidotrichia unsegmented proximally, segmented and then branching distally; pectoral fin with fringing fulcra composed of a combination of expanded terminal segments of lepidotrichia and independent small, spiny elements; pelvic lepidotrichia broad and segmented to their base; rhomboidal, wider than tall lateral flank squamation that is dorso-ventrally compressed in the ventral region of the body; lateral scales ornamented with terraced ridges at their edges and oblique ridges at their centers; rhomboidal, dorso-ventrally compressed ventral ridge scales anterior to pelvic fin.

3.3 Photographs and Interpretative Drawings

Specimens were examined under a binocular microscope (Amscope SKU:SM-4NTP). PF 3721 and YPM 18649 were photographed with an Olympus E-M5 Mark 2 camera using a M. Zuiko Digital ED 14-150MM F4.0-5.6 II lens and a M. Zuiko ED 60mm F2.8 macro lens at the MSU Museum. The three-dimensional preservation of PF 3721 required stacks of images to be taken to capture all features in focus. Image stacks were compiled in HeliconFocus (Heliconsoft.com) and with the image stacking feature of the Olympus E-M5 Mark 2. In addition to the Minnekahta Limestone material, I examined and photographed specimens of Permian and Triassic ray-finned fishes in the collections of the Natural History Museum, London, UK (list of examined material in Appendix 1, Table A1.1).

Interpretative drawings were made in Adobe Photoshop using digital photographs of the specimens. I traced printouts of the digital specimen drawings in ink to ensure consistency in line thickness, and then used Adobe Illustrator to trace scans of the ink drawings to make final line

drawings. In the interpretative drawings dotted lines indicate inferred boundaries, dashed lines show physical breaks in the rock that run through the fossilized material, light grey infill marks areas where bone is absent, and dark grey infill marks areas where the bone is degraded to the point where reliable identification of individual elements is not possible. Color infills were added in Adobe Photoshop.

3.4 Terminological Conventions

The conventional terminology for Paleozoic actinopterygian anatomy, following Gardiner (1984), is used. Although the frontals and parietals of actinopterygians in this scheme are homologous to the parietals and postparietals of sarcopterygians, respectively (Schultze, 2008), using this standard terminology will facilitate comparisons with other descriptions of Paleozoic actinopterygians.

3.5 Anatomical Abbreviations

Ab, anal basal fulcra; **Abs**, abdominal squamation; **Af**, anal fin; **Afr**, anal fin rays; **An**, angular; **Ano**, anterior nasal opening; **Ao**, antorbital; **Asq**, axial squamation; **Br**, branchiostegal ray; **Bre**, branchial arch element; **Cf**, caudal fin; **Cl**, cleithrum; **Cr**, coronoid; **Cv**, clavicle; **Dcf**, dorsal caudal lobe basal fulcra; **Dcr**, dorsal caudal fin rays; **Df**, dorsal fin; **Dfr**, dorsal fin rays; **Dh**, dermohyal; **Dn**, dentary; **Dp**, dermopalatine; **Ds**, dermosphenotic; **En**, endoskeletal shoulder girdle; **El**, insertion for the ethmopalatine ligament; **Exsc1**, lateral extrascapular; **Exsc2**, medial extrascapular; **Ff**, fringing fulcra; **Fmi**, foramen for internal mandibular branch of facial nerve; **Fr**, frontal; **Gpl**, gular pit line; **Hbp**, hole for the basipterygoid process; **Hy**, hyomandibula; **It**, intertemporal; **Ju**, jugal; **La**, lacrimal; **Lg**, lateral gular; **Lpr**, lateral process of palatoquadrate; **Lsq**, lateral squamation; **Mg**, medial gular; **Mk**, ossified Meckelian cartilage; **Mx**, maxilla; **Na**, nasal; **Nc**, neurocranium; **Op**, opercular; **Pa**, parietal; **Pcl**, post-cleithrum; **Pcr**, pectoral fin rays;

Pe, pelvic fin; **Pf**, pectoral fin; **Pm**, premaxilla; **Po**, preopercular; **Pq**, palatoquadrate; **Pscl**, presupracleithrum; **Pr**, prearticular; **Pro**, propterygium; **Psp**, parasphenoid; **Pspi**, postspiracular; **Pt**, post-temporal; **Pvr**, pelvic fin rays; **Qj**, quadratojugal; **Qu**, quadrate; **Ra**, radials; **Ro**, rostral; **Sc**, sclerotic ring; **Scl**, supracleithrum; **Shd**, shoulder girdle; **Skr**, skull roof; **Sop**, suboperculum; **So**, suborbital; **Sq**, squamation; **St**, supratemporal; **Sur**, surangular; **Te**, teeth; **Th**, canal for the truncus hyoideomandibularis; **Vcb**, ventral caudal lobe basal fulcra; **Vcr**, ventral caudal lobe fin rays; **Vr**, ventral ridge scale; **X**, anamestic dermal element.

3.6 Micro-Computed Tomography

The medial piece of PF 3721 was μ CT scanned at the CTEES facility at the University of Michigan using a Nikon XT H 225 ST scanner. The parameters of the scan were as follows: voltage (180 kV), current (155 uA), filter (0.5 mm Cu), projections (3141, 2 frames per second), resolution (27.9 μ m) and exposure time (1000 ms). The .vgi file was imported from the scan of PF 3721 into Drishti import (Limaye, 2012) and exported as a stack of .bmp images using the save images function for segmentation. The .vgi is available in the electronic supplementary files.

I imported this stack into SPIERSalign (Smith *et al.* 2016) to be cropped to reduce image size before segmentation. I imported the cropped .bmp image stack to SPIERSedit (Smith *et al.* 2016), downsampling by 50% in the x, y, and z dimensions to improve the speed of three-dimensional (3-D) model construction. Segmentation was done with the range generation tool, with manual inspection of individual slices and correcting details with the brush tool. These slices were then used to create two 3-D models that I visualized, smoothed (Smoothing=very weak), and removed islands from (Island removal=medium) in SPIERSview (Smith *et al.* 2016). One model shows the external surface of the specimen and the other shows segmented out

internal structures (Fig. 18). I used the "Apply Multiple Steps Saving Images" command to save 500 images while rotating the model with the "Simple Autospin" command. I imported this image sequence into FIJI (Schindelin *et al.* 2012) and exported as an .avl file to produce 3-D animations of the model's external fossil and internal structures. The image in Figure 1.18 was captured in SPIERSview using the "Apply Single Step Saving Image" Command.

3.7 Systematic Comparisons

I compared the morphology of PF 3721 and YPM 18649 to 38 other species of ray-finned fishes described from the Permian and Early Triassic to determine if the Minnekahta specimens represent a new species. I chose these 38 species based on a survey of the literature and the collections of the Natural History Museum (United Kingdom, NHM; the most extensive collection of Paleozoic ray-finned fishes) to search for Late Paleozoic and Early Mesozoic ray-finned fishes with features that closely resemble PF 3721 and YPM 18649. A list of these 38 species and the diagnoses used for comparison is provided in Appendix A2. I focused my comparisons on features in established diagnoses and descriptions and verified details where possible with published photographs, drawings, and observations gathered directly from specimens (Table A1.1). I focused on taxa that are known from relatively complete remains, excluding scale-based taxa from my comparisons. When comparing PF 3721 and YPM 18649 to taxa known from multiple species, I focused on the most completely described species in the genus and those that I examined directly at the NHM (i.e., *Acrolepis sedgwicki* Agassiz, 1833, *Palaeoniscum freieslebeni* de Blainville, 1818, and *Pygopterus humboldti* Agassiz, 1833).

3.8 Phylogenetic Analysis

3.8.1 Character matrix

I expanded and modified the morphological dataset of Giles *et al.* (2017) in Mesquite version 3.61 (Maddison & Maddison, 2019) to integrate the new taxon into an existing phylogenetic framework for early actinopterygians. I modified this framework to suit our goal of determining the phylogenetic placement of the new form amongst early actinopterygians. A full list of these changes can be found in Appendix 3. In addition to coding the new taxon into this matrix, I modified the assignments for 26 taxa based on recent descriptive work (full list of changes Appendix A3.2; Argyriou *et al.* 2018; Coates & Tietjen, 2019). Previous studies with this matrix (Giles *et al.* 2017; Argyriou *et al.* 2018; Figueroa *et al.* 2019) designate the placoderm *Dicksonosteus articus* Goujet, 1975 as the outgroup and include eighteen additional non-actinopterygian taxa in the ingroup. I restricted the ingroup to ray-finned fishes to focus our analyses on actinopterygian interrelationships.

I designate the three species of the Middle Devonian actinopterygian *Cheirolepis* Agassiz, 1835 as the outgroup in the maximum parsimony analysis. I chose *Cheirolepis canadensis* as the outgroup for the Bayesian analysis because the program (MrBayes 3.2.7a; Höhna *et al.* 2016) only allows for one taxon to be set as the outgroup. Although *Cheirolepis* is 30 million years younger than the minimum divergence of actinopterygians and sarcopterygians, it is the earliest known taxon that consistently resolves as an actinopterygian (Sallan, 2014; Friedman, 2015). I did not include potential actinopterygian taxa whose position is disputed (including *Dialipina* Schultze, 1968, “*Ligulalepis*” Schultze, 1968, and *Meemania* Zhu *et al.* 2006) because resolving their position is not my aim and would require the inclusion of non-osteichthyan taxa. I also removed *Brachydegma caelatum* Dunkle, 1939 from this matrix because

a major revision of its anatomy is forthcoming (Argyriou *et al.* in prep). After these alterations, we removed 43 characters that were not parsimony-informative according to the “show character status” command in PAUP (complete list of deleted characters Appendix A3.3). The resulting character matrix contained 74 total taxa and 222 characters. The full matrix is available in NEXUS form in Appendix A4 and character assignments by taxon are available in Appendix A5.

3.8.2 Parsimony analysis

The new taxon was incorporated into an equally weighted maximum parsimony analysis in PAUP (Swofford, 2003). I used a heuristic search to find the most parsimonious trees, building a starting tree with stepwise addition and estimating the global optimal tree with tree bisection and reconnection (TBR) and 500 random addition sequences. I set Maxtrees to increase automatically, with nchuck = 10,000, and chuckscore = 1. A full log file generated by PAUP for the parsimony analysis is available in the Appendix A6. I calculated the strict consensus tree in PAUP using the most parsimonious trees found in the heuristic search. Consistency index (CI), retention index (RI), rescaled consistency index (RCI), and tree length were calculated with the tree scores function in PAUP. I calculated Bremer decay values for the nodes of the strict consensus tree (Bremer, 1994) iteratively in PAUP with abbreviated heuristic searches (Maxtrees set to increase automatically, 20 RAS, rearlimit = 200,000,000 applied to each rep), increasing the number of steps one at a time from the maximum parsimony result. I also calculated bootstrap values in PAUP using 500 replicates of a full heuristic search, with Maxtrees set to increase automatically, rearlimit=50,000,000 applied to each rep, 5 trees held at each step, with nchuck = 10,000, and chuckscore = 1.

3.8.3 Bayesian analysis

I conducted a Bayesian analysis with two independent runs of Metropolis-coupled Markov chain Monte Carlo (MCMCMC, or MC³) analyses using the MkV model for discrete morphological characters in MrBayes 3.2.7a (Lewis, 2001; Höhna *et al.* 2016). I initially set the number of iterations to 500,000 and burn-in to 25% for four independent chains per run. I ran more iterations (increasing in sets of 500,000) until the standard deviation of split frequencies was lower than 0.01 to ensure consistency amongst runs. The MC³ converged within 4,000,000 generations. I also used the “plot” command in MrBayes to examine the trend in sampled log-likelihood values from the analysis and ensure that all chains reached a stable part of the distribution. I built a consensus tree with the “sumt” command in MrBayes (burnin fraction set to 0.5) that shows nodes with posterior probability higher than 0.5 and collapses nodes with posterior probability lower than 0.5. I set the burn-in fraction to 50% when calculating consensus trees. The scripts needed to re-run this analysis can be found in Appendix A7.

3.9 Institutional Abbreviations

PF, FMNH, Field Museum of Natural History, Chicago, USA.

YPM, Yale Peabody Museum of Natural History, New Haven, USA.

NHM, P, Natural History Museum, London, UK.

4. Systematic Paleontology

Class **Osteichthyes** Huxley, 1880

Subclass **Actinopterygii** Cope, 1887

Concentrilepis gen. nov.

4.1 Type Species

Concentrilepis minnekahtaensis sp. nov.

4.2 Generic Diagnosis

As for type species.

4.3 Derivation of Name

From the Latin *concentrum* (concentric) and *lepis* (scale), for the concentric ridges that ornament the lateral scales.

4.4 Diagnosis

Fusiform body; pronounced, rounded snout; single median rostral capping snout; separate antorbital and premaxillary elements; middle part of medial suture between frontals sinuous; frontals more than twice as long as parietals and each bearing two pronounced lateral expansions; anterior lateral extension of frontal less than 1/3 of total frontal length, with a broad point fitting between the postero-medial margin of the corresponding nasal and the postero-lateral margin of the rostral; separate intertemporal and supratemporal; nasal in contact with intertemporal; anterior median process on right parietal at contact with left parietal and medial suture of frontals; small posterior lateral process on parietal articulated with posterior median notch on supratemporal; crescent-shaped dermosphenotic lacking posterior ramus; dermosphenotic in contact with nasal; three suborbitals; separate lacrimal and jugal with the lacrimal excluded from the oral margin; opercular larger and wider than subopercular; dermohyal present as a single ossification; maxilla with a broad, rectangular postorbital expansion, a straight suborbital expansion, and a round posteroventral expansion that wraps around the posterior part of the dentary; dorsal margin of maxilla straight and flat; antopercular and epiopercular absent;

single median gular and paired lateral gulars; 15 branchiostegal rays; dorsal-most branchiostegal ray more than twice as tall as preceding rays; cleithrum arched, broad ventrally, and narrow and pointed dorsally, supracleithrum with round ventral margin posterior to contact with cleithrum, indented ventral margin at contact with cleithrum, broad middle section, and pointed dorsal margin; postcleithrum absent; fringing fulcra present on all fins; all lepidotrichia lack ornament; pectoral fin broad and triangular; caudal fin strongly heterocercal and deeply forked; flank scales broader than they are tall; anterior lateral flank scales dorso-ventrally compressed ventrally; scales ornamented with straight, concentric ridges at their margins (oriented parallel to corresponding scale margin) and diagonal ridges at their centers; scales lack serration on all margins.

4.5 Holotype

PF 3721, articulated skull and partially articulated trunk with the containing rock broken into five pieces. Tail and posterior portion of the body absent.

4.6 Referred Specimens

YPM 18649 (partially articulated individual with all fins and scale cover present, skull severely disarticulated).

4.7 Occurrence

Minnekahta Limestone of GCC Dakota Inc. Quarry (formerly the South Dakota State Cement Plant) and “City Quarry” (exact location unknown) of Pennington County, South Dakota, USA. The Minnekahta Limestone was deposited in the late Early Permian (Kungurian; Wardlaw & Collinson, 1986; Gradstein *et al.* 2012).

5. Description

5.1 Skull Roof

The skull roof is preserved in both PF 3721 and YPM 18649. In YPM 18649, a large area of bone from the skull roof is present ("Skr", Fig. 1.6B), but it is not possible to distinguish individual elements. Therefore, the description of this region relies almost entirely on PF 3721. The skull roof is divided into two pieces in PF 3721. The right lateral piece contains most of the skull roof, which is preserved as a natural mold. This description of the skull roof is largely based on a latex cast of the mold of the skull roof from the right lateral piece (Fig. 1.3). Only a small, poorly preserved portion of the skull roof ("Skr", Fig. 1.4B), in which individual elements cannot be discerned, is present in the left lateral piece of PF 3721.

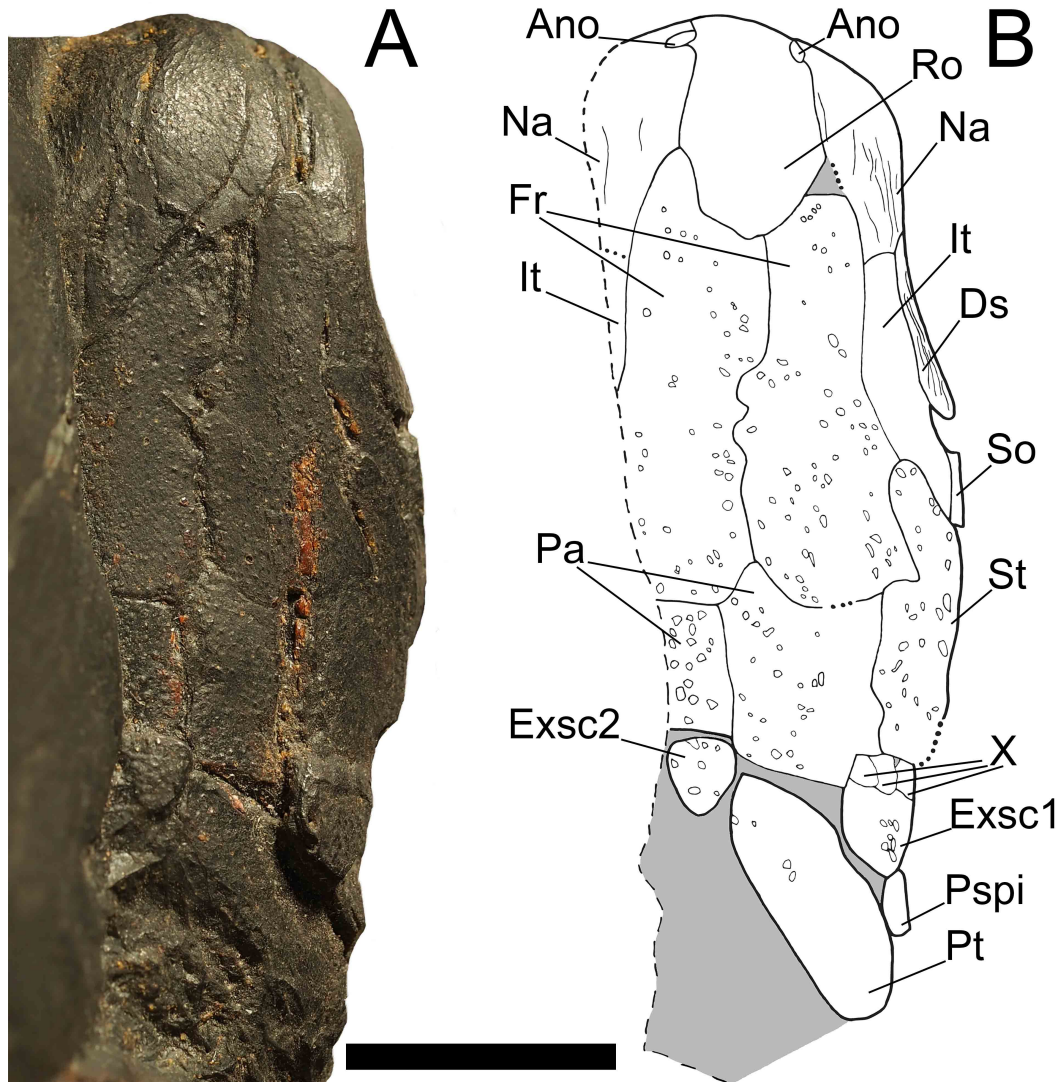


Figure 1.3. Cast of the skull roof of PF 3721 in dorsal view, taken from the right lateral piece. A, photograph. B, specimen drawing. Scale bar equals 1 cm (anterior is to the top of the page).

A median shield-like rostral ("Ro", Fig. 1.3B and 1.4B) forms the anteriormost portion of the skull roof. The rostral is flanked by the nasals, contacted posteriorly by the frontals, and contacted anteroventrally by the premaxillae. The rostral curves to form the anteriormost portion of the protruding, rounded snout. Paired nasal openings ("Ano", Fig. 1.3B) are present at the contacts of the rostral with the nasals at the tip of the snout. The anterior margin of the rostral is broad, with a distinct medial indentation where it contacts the premaxillae. The lateral parts of

this margin are pointed, curving outwards around the anterior part of the nasal opening. The lateral margins of the rostral are concave where they form the medial portion of the anterior nasal openings. The lateral margins of the rostral curve medially and form long, convex margins that make up approximately half of the total length of the bone where it curves over the apex of the snout. Posteriorly, at the contact with the anterior portion of the frontals, the lateral margins curve medially to a greater degree and meet at the midline of the skull. A break in the right lateral piece created a line through the rostral that could be misinterpreted as a suture, but it is clear from close examination that the rostral is a single medial element. There is no apparent ornamentation on the posterior portion of the rostral, but some thin, oblique ganoine ridges are present on the anterior portion that houses the nasal openings.

A pair of nasals ("Na", Fig. 1.3B and 1.4B) form the lateral portions of the anterior part of the skull roof. The nasals are broad, curved bones that, along with the rostral, form a protruding snout. The nasals extend from the midpoint of the snout anteroventrally to the midpoint of the orbit. They have a broad, curved anterior margin contacting the paired premaxillae. The concave lateral margin of the nasal forms the anterodorsal part of the orbit. The nasals also have laterally slanted medial margins contacting the rostral. The anterior portion of the medial margins of the nasals bear notches for the anterior nasal openings ("Ano", Fig. 1.3B). The posterior margin of each nasal has a curved, concave medial embayment that the lateral part of the anterior margin of the corresponding frontal fits into. The posterior margins of the nasals are slightly concave, contacting the intertemporal posteriorly and the dermosphenotic laterally. The nasals are ornamented with thin, longitudinal ganoine ridges posteriorly and sparse tubercles and branching ganoine ridges anteriorly.

The frontals ("Fr", Fig. 1.3B; "Fr?", Fig. 1.7B) are long, anteriorly pointed bones that are the largest elements in the skull roof, approximately twice the length of the parietals. The lateral part of the anterior margin of each frontal is extended and curved into a broad point that fits between the postero-medial margin of the corresponding nasal and the postero-lateral margin of the rostral. The lateral margin of each frontal is straight anteriorly but posteriorly bearing two pointed, posteriorly curved lateral expansions. The most posterior lateral expansion is more pronounced than the most anterior lateral expansion and fits into an embayment in the median margin of the supratemporal. The frontals contact the intertemporal anterolaterally and the supratemporal posterolaterally. The medial margin of the frontals is straight posteriorly and anteriorly but is sinuous (although not interdigitating) medially. The posterior margins of the frontals are broad and convex, contacting the parietals medially and the supratemporals laterally. The medial part of the posterior margins of the frontals is curved inward where the anteromedial process of the right parietal fits between them. The frontals are sparsely ornamented with small tubercles that are denser on the posterior part of the elements.

The parietals ("Pa", Fig. 1.3B) are subrectangular bones that are approximately half the length of the frontals. Although the lateral portion of the left parietal is not preserved, it is clear that the left and right parietals are not equivalent in shape. The right parietal bears a pointed anteromedial process that extends between the posterior part of the medial contact of the frontals. The left parietal lacks an anteromedial process. The medial portion of the anterior margin of the left parietal is straight, while its lateral portion is not preserved. The lateral portion of the anterior margin of the right parietal is concave, curving around the posterior margin of the right frontal. The medial margin between the parietals is roughly straight. The right parietal contacts the supratemporal laterally at a broad, concave margin with a small posterior lateral process that fits

into a posterior median notch on the supratemporal. The parietals are ornamented with small to medium-sized tubercles, which are more numerous on the left parietal.

A series of three small anamestic dermal elements sit anterior to the lateral extrascapular in the right lateral piece and its cast ("X", Fig. 1.3B). These partially overlapping elements are longer than they are wide and do not have a uniform shape. The medial-most element is oblong and teardrop-shaped, the central element is sub-rectangular, and the most lateral element is nearly trapezoidal. These elements and the lateral extrascapular are deeper into the rock relative to the other skull roof elements. Similar ossifications have been observed in the corresponding region of the skull of *Pteronisculus stensioi* (Nielsen, 1942; fig. 19), *Pteronisculus macropterus* (Lehman, 1952; fig. 26), *Pteronisculus arambourgi* (Lehman, 1952; fig. 25), *Oxygnathus ornatus* (Watson, 1925; fig. 30), *Acrolepis sedgwicki* (Aldinger, 1937; fig. 4 after Westoll, 1934 unpublished), *Acropholis stensioi* (Aldinger, 1937; fig. 5), and *Plegmolepis kochi* (Aldinger, 1937; fig. 17). Additionally, I observed these elements in a specimen of *Pteronisculus cicatrosus* (P. 16297-8; pers. obs.). These elements in PF 3721 most closely resemble those in *Pteronisculus macropterus* (Lehman, 1952; fig. 26).

Two small extrascapulars ("Exsc1" and "Exsc2", Fig. 1.3B and 1.5B) are located posterior to the parietals and anterior to the post-temporal (visible in the right lateral piece and cast). These bones are distinct from each other in size and are separated, indicating that there are distinct pairs of medial and lateral extrascapulars. The medial extrascapular ("Exsc2", Fig. 1.3B and 1.5B) is between the posterior margin of the left parietal and the anterior part of the medial margin of the post-temporal. The medial extrascapular is ornamented with small tubercles and has a convex, rounded anterior edge and lateral margins that curve to form a bluntly pointed posterior edge. The lateral extrascapular ("Exsc 1", Fig. 1.3B and 1.5B) is larger and wider than

the medial extrascapular but is similar in shape. It contacts the parietal anteromedially, the post-temporal posteromedially, the anamestic dermal elements anteriorly, and the postspiracular (of Nielsen, 1942) posterolaterally. The lateral extrascapular has a broad, curved, convex anterior margin with sloping lateral margins that extend posteriorly to a blunt point. The lateral extrascapular is ornamented with small tubercles.

A single post-temporal is preserved in the cast of the right lateral piece and in YPM 18649 ("Pt", Fig. 1.3B, 1.5B, and 1.6B). The post-temporal is an oval-shaped bone that extends posterolaterally from the parietals. The anterior margin is long and slightly convex, contacting the parietal anterodorsally, the lateral extrascapular anteriorly, and the postspiracular and supracleithrum anteroventrally. The medial margin is short and slightly concave, sitting underneath the medial extrascapular. The post-temporal broadens laterally, giving it a blade-like shape. The dorsal part of this element is ornamented with sparse tubercles in PF 3721 and its ventral part is ornamented with evenly spaced, thick, and short bony ridges in YPM 18649.

The intertemporal ("It", Fig. 1.3B) is a narrow, boomerang-shaped bone between the posterodorsal part of the orbit and the anterior portion of the frontal and is only observable in the cast of the right lateral piece. It is divided into a straight anterior portion and a curved, blade-like posterior portion. The anterior margin of this bone is convex and curved, contacting the nasal. The concave, deeply curved lateral margin of the intertemporal runs along the dorsal margin of the dermosphenotic, with a short region posteriorly without a visible contact. The medial margin of the intertemporal contacts the frontal anteriorly and the supratemporal posteriorly. The more anterior lateral expansion of the frontal curves around the medial part of the intertemporal.

The supratemporal ("St", Fig. 1.3B) is larger than the intertemporal and is only observable in the cast of the right lateral piece. The narrow anterior portion of this bone curves

around the posterior lateral expansion of the frontal. The supratemporal expands posteriorly into a broader, roughly rectangular portion that narrows slightly at its most posterior extent. The supratemporal contacts the intertemporal anteriorly and anteroventrally, the most dorsal suborbital laterally, and the anamestic dermal elements posteriorly. The supratemporal also contacts the parietal medially along a margin bearing a posterior notch that fits around the small posterior lateral process of the parietal. The supratemporal is ornamented with small, sparse tubercles.

5.2 Circumorbital Bones

The bones surrounding the orbit are preserved in the right and left lateral piece, and in the cast of the right lateral piece. The circumorbital bones are not preserved in YPM 18649. The posterior, dorsal, and ventral parts of the sclerotic ring ("Sc", Fig. 1.5B) are preserved in the right lateral piece. Elements associated with the orbit include (clockwise from the top, with anterior to the right) the nasal, antorbital, lacrimal, jugal, suborbital, and dermosphenotic. As noted in the description of the skull roof, the lateral margin of the nasal forms the anterodorsal margin of the orbit ("Na", Fig. 1.3B and 1.4B). A small portion of the anteroventral region of the orbit is built from the broad, concave lateral margin of the antorbital, which is a small, rhomboidal bone visible in the cast of the right lateral piece. The antorbital's dorsal margin contacts the lateral part of the ventral margin of the nasal, its straight medial margin contacts the posterolateral part of the premaxilla, and its short, rounded posterior margin contacts the lacrimal. The antorbital bears small ridges with tubercles.

The posterior segment of a long, thin lacrimal ("La", Fig. 1.5B) sits directly anterior to the jugal and dorsal to the infraorbital expansion of the maxilla in the right and left lateral pieces. The anterior segment of this element is broken off in the right lateral piece but is preserved but

not visible laterally in the left lateral piece. It is necessary to look down into the region of the orbit that is behind the maxilla (technically lateral to) to see the lacrimal. The lacrimal is straight posteriorly, and then curves dorsally in its anterior portion. This element has a rounded posterior margin, a convex dorsal margin, and a curved ventral margin. The anterior margin is not preserved. The lacrimal is excluded from the oral margin by the maxilla. A large, thick, crescent-shaped jugal ("Ju", Fig. 1.4B and 1.5B) is posterior to the lacrimal. The concave anterodorsal margin of this element forms the posterior-ventral margin of the orbit. The posterior section of the jugal is broad and thick, narrowing anteriorly into a blunt concave margin that contacts the lacrimal anteriorly. The jugal also contacts the anterior and posterior-most suborbitals dorsally, and the maxilla posteriorly and ventrally. The jugal is ornamented with thick tubercles.

The dermosphenotic ("Ds", Fig. 1.3B, 1.4B, and 1.5B) is a crescent-shaped element forming the postero-dorsal part of the orbit. The convex medial margin of the dermosphenotic contacts the intertemporal, while its narrow posterior margin contacts the anterior-most suborbital ventrally and the intertemporal dorsally. The dermosphenotic narrows anteriorly into a sharp point that contacts the nasal dorsally. The dermosphenotic is ornamented with small, longitudinal ganoine ridges dorsally, along with sparse tubercles laterally.

Three suborbitals ("So", Fig. 1.4B and 1.5B) are partially preserved in the right and left lateral piece. A suborbital is at the anterior-dorsal margin of the jugal and has a dorsal margin contacting the dermosphenotic in both the right and left lateral piece. This suborbital is best preserved as an impression in the right lateral piece, which shows that it is a rounded, slightly oval-shaped bone. A second long, thin, curved suborbital is preserved as an impression in the right lateral piece and sits between the first suborbital and a third, broader suborbital that is partially preserved in the left lateral piece. The posterior most suborbital has a broken anterior

margin, but contacts the jugal anteroventrally, the maxilla posteroventrally, and the preopercular posteriorly. A few tubercles are visible on the anterior most suborbital in the right lateral piece, and oblong ganoine ridges and tubercles are present on the posterior most suborbital.

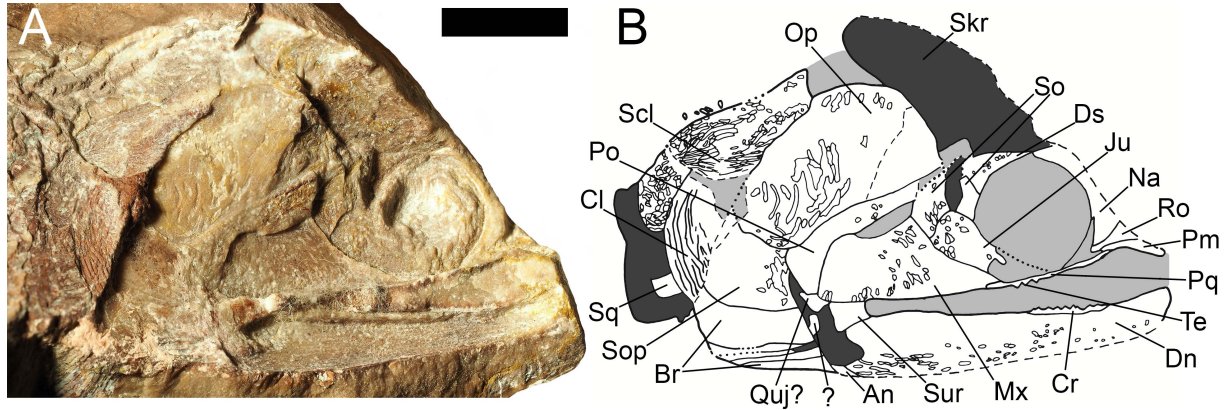


Figure 1.4. Cranial elements in the left lateral piece of PF 3721, internal surface of bones preserved in lateral view. A, photograph. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

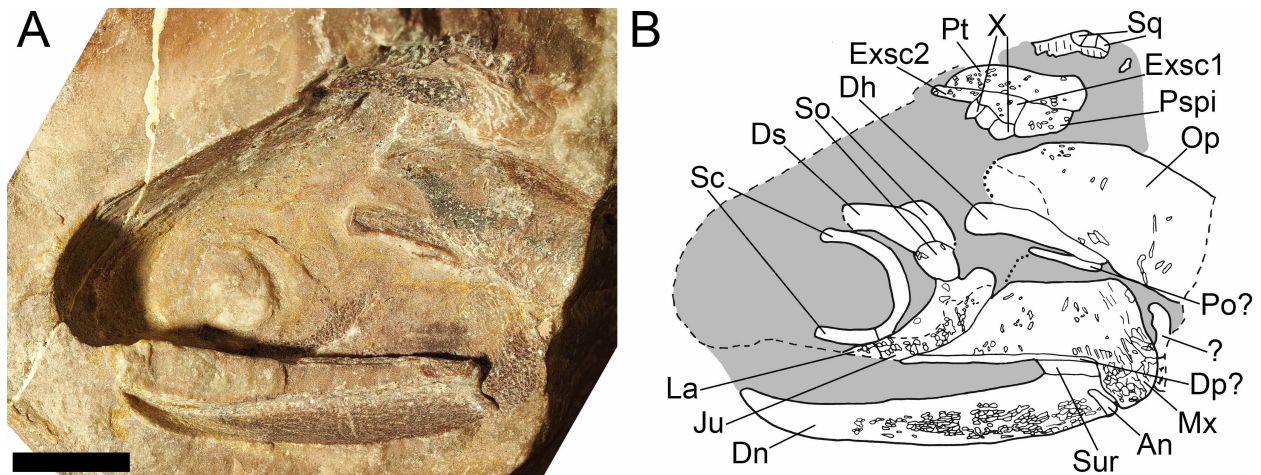


Figure 1.5. Cranial elements in the right lateral piece of PF 3721, internal surface of bones preserved in lateral view. A, photograph. B, specimen drawing. Scale bar equals 1 cm (anterior is to the left).

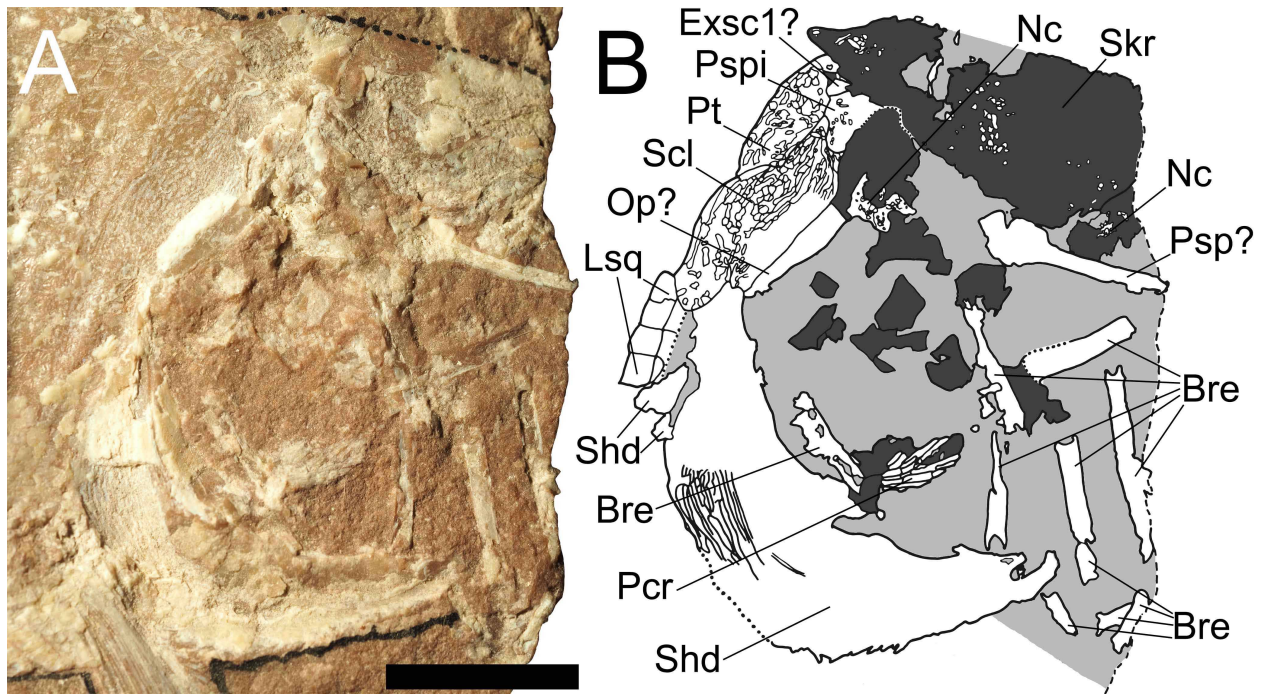


Figure 1.6. Cranial elements in YPM 18649 preserved in lateral view. A, photograph. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

5.3 Jaws, Palate, and Dentition

The maxillae ("Mx", Fig. 1.4B and 1.5B) are present in the left lateral and right lateral pieces. The maxilla has a shape typical for a Paleozoic actinopterygian, with an expanded and somewhat rectangular postorbital area that leads into a narrow anterior suborbital expansion. The long, thin suborbital expansion contacts the premaxilla anteriorly. The suborbital expansion of the maxilla is not easily observed in lateral view because it is covered by a broken portion of the palatoquadrate in the left lateral piece. The right and left lateral pieces are preserved so that the anterior part of the maxilla, lacrimal, and the premaxilla are in deep recesses in the rock that cannot be observed in lateral view. It is necessary to look down into the specimens to see the entirety of lacrimal, maxilla, and premaxilla in both pieces. The postorbital portion of the maxilla has a long, concavely curved anterodorsal margin contacting the jugal anteriorly and the ventral-most suborbital posteriorly. The dorsal margin of the maxilla is slightly convex, contacting the

preopercular posteriorly. The posterior margin of the maxilla contacts the preopercular and has a distinct rounded posteroventral expansion that externally overlaps the dorsal part of the posterior end of the dentary. The ventral margin of the maxilla is relatively straight where it forms the dorsal margin of the mouth, until its most posterior point, where it curves ventrally, forming the anterior part of the posteroventral process of the maxilla. The maxilla is ornamented with coarse ganoine tubercles and some short ridges.

The premaxillae ("Pm", Fig. 1.4B) form the ventral-most part of the snout and the anterior section of the gape. The left and right premaxillae are partially preserved in the left and right lateral pieces, but their morphology is most easily observed in the cast of the right lateral piece. The right premaxilla is broad and roughly rectangular anteriorly and narrows to a point that fits between a dorsal contact with the antorbital and a ventral contact with the anterior part of the maxilla posteriorly. The premaxilla has a straight dorsal margin that contacts the nasal posteriorly, the rostral anteriorly, and a curved, slightly concave ventral margin that forms the anterior part of the gape. The anterior margin of the maxilla contacts the premaxilla. It cannot be determined if teeth or ornamentation are present on the premaxilla.

The palatoquadrate complex ("Pq", Fig. 1.4B, 1.7B, and 1.8B) is visible on the left lateral piece, and the left and right sides of the medial piece. The palatoquadrate is ossified as a single element, suggesting that PF 3721 is an adult individual (as has been observed in larger specimens of *Pteronisculus* White, 1933, *Australosomus* Nielsen, 1949, and *Mimipiscus* Gardiner & Bartram, 1977 that are thought to represent adults (Nielsen, 1942; Nielsen, 1949; Gardiner, 1984). The palatoquadrate is roughly rectangular and broad posteriorly and narrows to a blunt point anteriorly. The dorsal margin is largely straight, but curves ventrally at its most posterior point and is concave anteriorly. A prominent lateral process is visible on the right lateral side of

the palatoquadrate in the medial piece ("Lpr", Fig. 1.8B). The ventral margin of the palatoquadrate is lined with short, rounded teeth ("Te", Fig. 1.4B, 1.7B, and 1.8B), some of which are attached to long, thin dermopalatines ("Dp", Fig. 1.8B) that are fused to the palatine portion of the palatoquadrate. A small groove that may be an insertion for the ethmopalatine ligament ("El", Fig. 1.8B) is visible on the dorsal margin of the palatoquadrate on the right side of the medial piece. An opening is present where the palatoquadrate narrows on the right side of the medial piece, approximately where the attachment area for the basipterygoid process ("Hbp?", Fig. 1.8B) would be expected. However, it is not clear if this is a biological feature or a break in the specimen (as suggested by the disarticulated pieces of bone that surround it). The posterior part of the palatoquadrate is covered by a broad quadrate ("Qu", Fig. 1.7B and 1.8B) in both the left and right sides of the medial piece. The quadrate is best preserved (although it is still incomplete) on the right side of the medial piece, where it curves around an element tentatively identified as a surangular ("Sur", Fig. 1.8B) ventrally. A groove ("Fmi?", Fig. 1.8B) running through the quadrate and a region of unidentified bone may be the foramen for the internal mandibular branch of the facial nerve.

The dentaries ("Dn", Fig. 1.4B, 1.5B, 1.7B, 1.8B, and 1.9B) are preserved in the left lateral, right lateral, ventral, and medial pieces. The ventral position of the dentary in the left and right lateral pieces shows that the mouth is partially open in PF 3721. Each dentary is a long, curved bone that is deepened posteriorly and narrows anteriorly into a dorsally reflexed point. Ventrally, the dentaries are contacted by the branchiostegal rays, a pair of lateral gulars, and the median gular. Fragments of surangulars are visible at the postero-dorsal margin of the dentary in the left lateral piece, the right side of the medial piece, and the right lateral piece ("Sur", Fig. 1.4B, 1.5B, and 1.8B). Small, curved angulars are visible at the postero-ventral part of the

dentary in the right lateral and left lateral pieces ("An", Fig. 1.4B and 1.5B). Several medial endoskeletal elements from the lower jaw are visible in both the right and left side of the medial piece. The endoskeletal elements of the lower jaw are best preserved on the left side of the medial piece. Small, short, triangular teeth are set into long, thin coronoids ("Cr", Fig. 1.7B and 1.8B) along the dorsal margin of the lower jaw on both the left and right side of the medial piece. A tooth-bearing coronoid is also visible in the left lateral piece ("Cr", Fig. 1.4B). Sutures between individual coronoids are only visible on the left lateral side of the medial piece. A thin sheet of slightly concave bone is ventral to the coronoids on the left lateral side of the medial piece. Two long, thin elements are visible in this sheet, the dorsal of which is a prearticular ("Pr", Fig. 1.7B) and the ventral element is ossified Meckelian cartilage ("Mk", Fig. 1.7B). These elements are bordered anteriorly and posteriorly by regions of bone that cannot be identified.

A



B

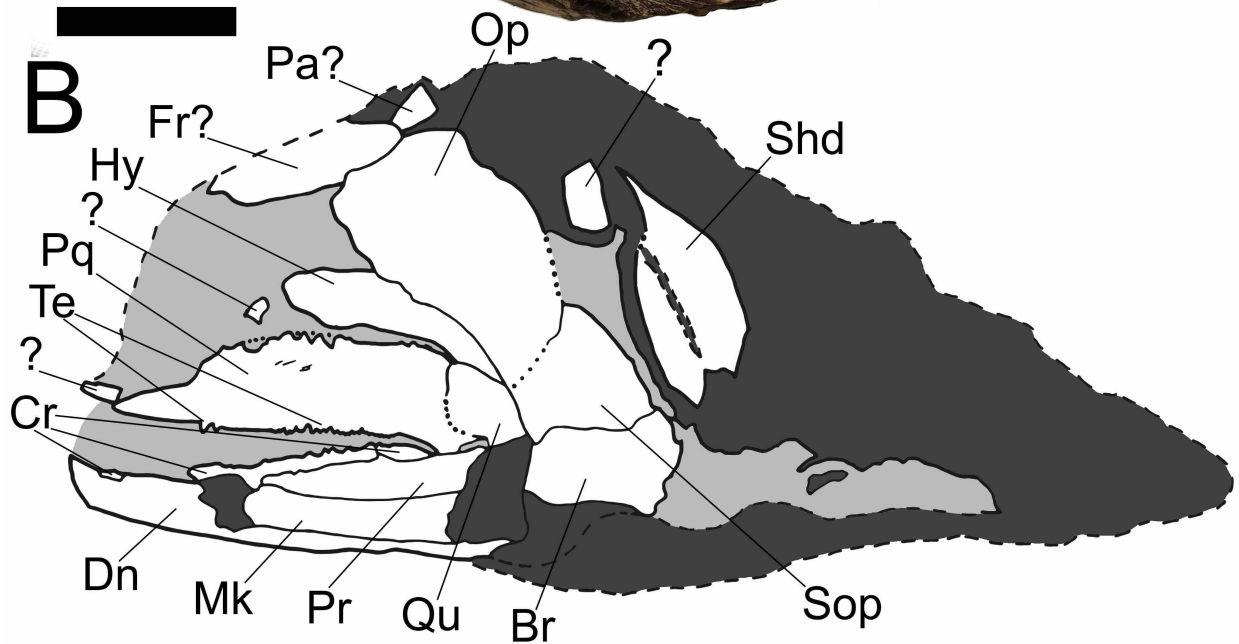


Figure 1.7. Left side of the medial piece of PF 3721, internal bones preserved in lateral view. **A**, specimen photo. **B**, specimen drawing. Scale bar equals 1 cm (anterior is to the left).

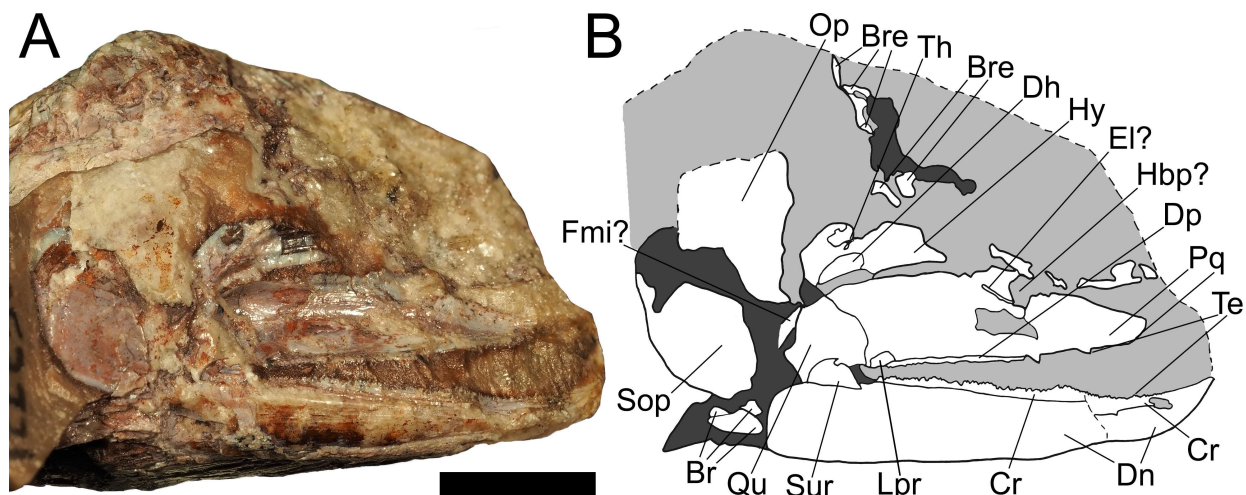


Figure 1.8. Right side of the medial piece of PF 3721. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

5.4 Opercular Series and Associated Bones

The opercular apparatus and associated elements are largely absent in YPM 18649. The preopercular ("Po", Fig. 1.4B; "Po?", Fig. 1.5B) is preserved in both the left and right lateral pieces. Only the ventral portion of the preopercular is preserved in the left lateral piece, showing that the ventral limb of this element is thin and slants sharply over the dorsal margin of the maxilla. An indistinct impression of the dorsal limb of the preopercular and a small bone fragment that is possibly from the preopercular are also present in the right lateral piece but provide little anatomical information. The dorsoposterior margin of the preopercular contacts the opercular and dermohyal. The opercular ("Op", Fig. 1.4B, 1.5B, 1.7B, 1.8B; "Op?", Fig. 1.6B) is well preserved in the left lateral piece, the left and right side of the medial piece, and is partially preserved in the right lateral piece. It is a tall, oblique, rounded bone with a straight, anteriorly inclined, narrow ventral margin contacting the subopercular. The opercular expands and broadens dorsally from its ventral margin and is contacted anteroventrally by the preopercular, anterodorsally by the dermohyal along a curved, convex anterior margin, and posterodorsally by the supracleithrum. The dorsal and posterior margins of the opercular are broad, convex, and

curved, the ventral margin is short and slightly curved, and the anterior margin is concave and arched.

The subopercular ("Sop", Fig. 1.4B, 1.7B, and 1.8B) is a short, stout bone sitting directly ventral to the opercular and posterior to the jaws in the left lateral piece and both sides of the medial piece. The subopercular has an anteriorly inclined, short dorsal margin contacting the opercular, and then expands ventrally to a curved ventral margin contacting the anterior-most branchiostegal ray. The subopercular contacts the preopercular anterodorsally. Other than its contact with the preopercular, its anterior extent cannot be discerned because the area of the skull directly posterior to the jaws is not well-preserved. Some filled in canals, which likely housed blood vessels, are present on the anterior portion of the subopercular in the left lateral piece.

The dermohyal ("Dh", Fig. 1.5B and 1.8B) is preserved in the right lateral piece (and its cast) and the right side of the medial piece. The right lateral piece preserves the internal surface of the medial part of the dermohyal, showing that it is a narrow, slightly curved, anteriorly inclined bone with a round anterior margin, and that it thins ventrally into a pointed ventral margin. The dermohyal is anterior and slightly medial to the opercular. The right side of the medial piece also has a small piece of the dermohyal that is fused to the hyomandibular. A small, roughly triangular postspiracular ("Pspi", Fig. 1.3B, 1.5B, and 1.6B) is present in the right lateral piece, its cast, and YPM 18649, nestled between the dorsal part of the posterior margin of the opercular and the ventral part of the anterior margin of the post-temporal. This element is broad anteriorly and narrows to a blunt point posteriorly. Although there is a small space anterior to the opercular in the right lateral piece of PF 3721 that superficially resembles an antopercular, close examination suggests that it is a section of the opercular that has broken off. There is no suture that would indicate a separate element anterior to the opercular in this piece, and the more

complete opercular from the left side of the medial piece does not have a separate antopercular or a space for a separate element ("Op", Fig. 1.7B). Therefore, it is likely that this taxon lacked an antopercular.

5.5 Gulars and Branchiostegal Rays

The gulars and branchiostegal rays are well preserved on the underside of the skull in the ventral (counterpart) and medial (part) pieces (not preserved in YPM 18649). PF 3721 has a single median gular ("Mg", Fig. 1.9B), which is an ovoid bone with a pointed anterior margin. The median gular is broad and triangular anteriorly and has long, curved lateral margins that meet posteriorly. Evenly distributed pore-like structures visible on the internal surface of the median gular are the bases of tubercles that ornament the external surface of the element. Two lateral gulars ("Lg", Fig. 1.9B) sit on either side of the median gular and anterior to the branchiostegal rays. Each lateral gular, which are larger and broader than the median gular, has a pointed anterior margin from which they expand posteriorly into broad, roughly triangular bones. The medial margins of these bones extend farther posteriorly than their lateral margins, meaning that their broad posterior margins are sharply inclined. Each lateral gular also has ornamentation like that of the median gular. Small gular pit lines ("Gpl", Fig. 1.9B) are visible on the lateral gulars. Each lateral gular is contacted posteriorly by the corresponding paired set of the branchiostegal rays.

The branchiostegal rays ("Br", Fig. 1.4B, 1.7B, 1.8B, and 1.9B) are a paired series of curved, narrow bones that extend posterior to the lateral gulars, curving around the back of the dentary and ending at the base of the subopercular. Each of these narrow, blade-like bones has a short lateral margin and expands medially to form a broader, curved medial margin. The most anterior branchiostegal ray is straight and almost rectangular. The branchiostegals curve and

shorten as they extend around the posterior part of the dentary. The first four branchiostegal rays visible in the lateral part of the skull are thin and straight, while the final branchiostegal ray is more than twice as tall as the preceding element. There are approximately fifteen pairs of branchiostegal rays. Of these elements, eleven pairs are visible in the series on the ventral side of the skull, and an additional 4 pairs sit beneath the subopercular. The anterior branchiostegal rays are ornamented with the bases of tubercles. This ornament is much sparser in the posterior branchiostegal rays.

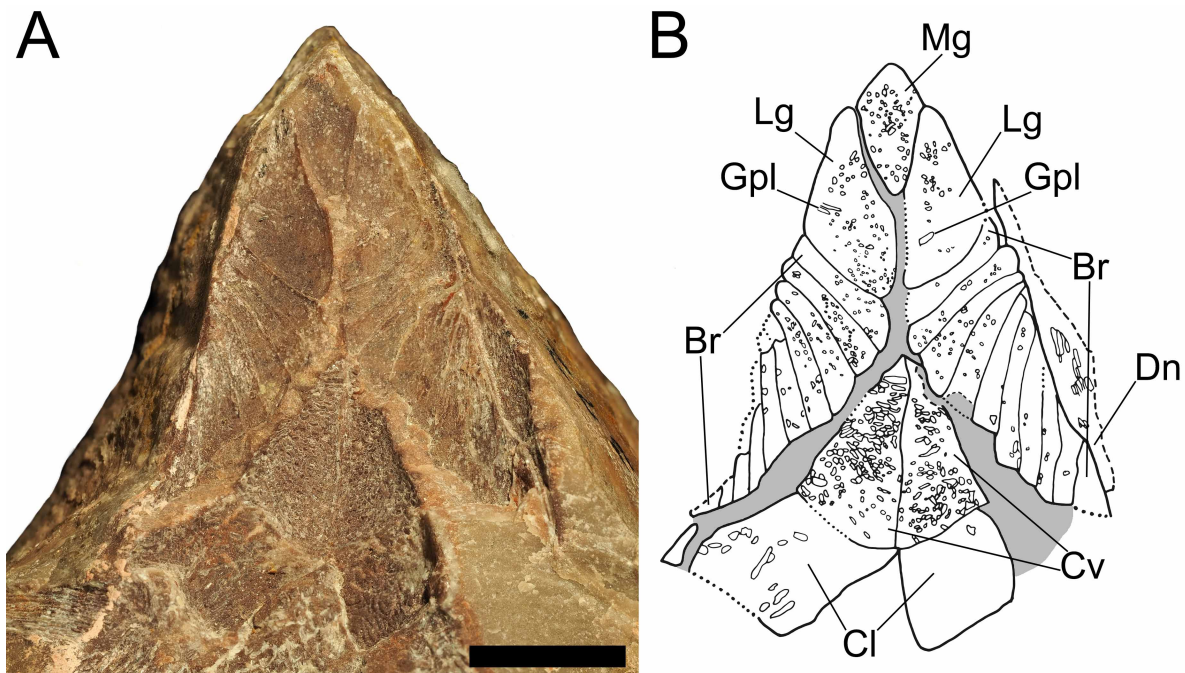


Figure 1.9. Cranial elements in the ventral piece of PF 3721. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the top of the page).

5.6 Parasphenoid and Braincase

In YPM 18649, a long element ventral to the skull roof that is broad and rounded posteriorly with a narrow anterior stalk is likely the parasphenoid ("Psp?", Fig. 1.6B). This identification is uncertain because this element is disarticulated and the surrounding elements are not well-preserved. The parasphenoid is not preserved in PF 3721. Two small pockets in the dorsal region of the skull of YPM 18649 show thin pieces of cancellous bone that are likely from

the internal part of the neurocranium ("Nc", Fig. 1.6B), but no identifiable neurocranial features are preserved.

5.7 Shoulder Girdle

A large arch of bone that forms the posterior and ventral part of the skull of YPM 18649 likely includes both the cleithrum and clavicles, but I am not able to clearly distinguish the suture between these elements ("Shd", Fig. 1.6B). The supracleithrum ("Scl", Fig. 1.4B and 1.6B), however, can be distinguished in both YPM 18649 and the left lateral piece of PF 3721. This element is a thick, curved bone posterior to the opercular that contacts the dorsal margin of the cleithrum anteroventrally and lateral flank scales ("Lsq", Fig. 1.6B) posteroventrally. The ventral margin of the supracleithrum is broad and rounded, while its dorsal margin is pointed. Although roughly crescent-shaped, the supracleithrum has a strongly indented ventral margin where it contacts the cleithrum and a rounded ventral margin posterior to its contact with the cleithrum. Additionally, the dorsal part of the posterior margin of this element is curved inward and around the ventral margin of the post-temporal.

The cleithrum ("Cl", Fig. 1.4B, 1.9B, 1.11B, and 1.17B; "Shd", Fig. 1.6B and 1.7B) is partially preserved in the left lateral piece, the ventral and left lateral side of the medial piece, and the ventral piece. Although its ventral margin cannot be distinguished in YPM 18649, its dorsal margin is identifiable. The cleithrum is a tall, arched bone with a broad base that thins dorsally into a sharp apex where it contacts the supracleithrum. The ventral portion of the cleithrum is broad and approximately rectangular where it contacts the clavicles anteriorly and where the pectoral fin attaches posteriorly (see paired fin section for a description of the pectoral fin attachment).

The clavicles ("Cv", Fig. 1.9B) are well-preserved on the ventral side of the medial (in part) and ventral (in counterpart) pieces. They are a pair of stout, roughly triangular bones that sit between the branchiostegal rays and are each attached to the respective ventral part of the right and left cleithrum. Each clavicle has a pointed apex, and expands posteriorly into a broad, convex posterior margin that attaches to its respective cleithrum. The clavicles are jointed at a straight medial margin, and are ornamented with short, staggered, curved ridges that grade into smaller, denser tubercles posteriorly.

5.8 Hyoid and Branchial Arches

Both the left and right hyomandibulae are preserved on the right and left lateral sides of the medial piece ("Hy", Fig. 1.7B and 1.8B). Only the dorsal limb of the hyomandibula is visible on the right lateral side of the medial piece, while more of the ventral part of this element is visible on the left lateral side. The hyomandibula is a curved, arching bone with a broad, rounded anterior margin, a concave ventral margin, and a convex dorsal margin. The dorsal limb of the hyomandibula is spatulate and broad. A piece of the dermohyal is fused to the dorsal limb of the hyomandibula visible on the right side of the medial piece (see section on opercular series and associated bones for a description of the dermohyal). There is a small opening for the canal for the truncus hyoideomandibularis directly above the dermohyal on the right side of the medial piece ("Th", Fig. 1.8B). The hyomandibula is dorsal to the palatoquadrate, medial to and nestled under the opercular, and medial to the quadrate. There is not a pronounced opercular process on the hyomandibula, but the dorsal margin is not well-preserved on either side of the medial piece.

Although the skull is severely disarticulated in YPM 18649 (with most of the elements absent), several disarticulated, bar-shaped elements of varying size that match the typical morphology of branchial arches in early actinopterygians are present ("Bre", Fig 1.6B). These

include five long, thin elements oriented dorso-ventrally, and four considerably shorter elements in the ventral part of the skull that lack a consistent orientation. A larger, thicker element with its long end oriented anteriorly is also present. Five similar elements are on the right lateral side of the medial piece of PF 3721 (“Bre” and “Bre?”, Fig. 1.8B). Because these elements are incomplete and disarticulated, they are not assigned more specific identifications.

5.9 Paired Fins

Both the right and left pectoral fins are preserved in PF 3721 and in YPM 18649 (“Pcr”, Fig. 1.6B). The complete right pectoral fin of PF 3721 is extended out from the body and is preserved in the pectoral and medial piece (in part) and the ventral piece (in counterpart; Fig. 1.10). The left pectoral fin of PF 3721 is represented by broken patches of fin rays from its base in the medial, ventral, and left lateral pieces. The pectoral fin is ventrally inserted, broad, and roughly triangular, with a distinct peak in its anterior half, a dip in its medial section, and a smaller posterior peak. The leading edge of this fin has small fringing fulcra (“Ff”, Fig. 1.10B). The lepidotrichia (“Pcr”, Fig. 1.10B) are long, thin, and closely packed, and are segmented and branching distally. Segmentation begins closer to the base of the fin in the more posterior lepidotrichia. There are approximately 30 principal pectoral fin rays.

The medial piece preserves the attachment of both pectoral fins to the shoulder girdle (Fig. 1.11). The attachment area of the right pectoral fin preserves a partial curved endoskeletal shoulder girdle (“Endg”, Fig. 1.11B) with attached radials. The endoskeletal shoulder girdle is broken and has a large, irregular hole in its anterior region that is likely the result of decay or breakage post-fossilization. Seven long, thin radials (“Ra”, Fig. 1.11B) are attached to the endoskeletal shoulder girdle directly, while seven others are visible but are not connected to the shoulder girdle. Two additional round, thick propterygia (“Pro”, Fig. 1.11B) are attached to the

endoskeletal shoulder girdle. The medial of these two elements is more than twice the length of the more lateral element. The lateral margin of the more medial propterygium wraps around the lateral propterygium, which is circular.

The left pelvic fin is split between the left lateral and ventral piece in PF 3721, with the proximal part of the anterior portion of this fin missing. The pelvic fin is also preserved in YPM 18649, with the morphology of the lepidotrichia not as well-preserved as in PF 3721. The distal part of the anterior portion is long, thin, curved, and triangular, indicating that the peak of the pelvic fin is in its anterior half. The pelvic fin lepidotrichia ("Pvr", Fig. 1.12B) are thicker than those in the pectoral fin and are segmented to their bases. The pelvic fin is inserted ventrally along the abdomen, approximately midway between the pectoral and anal fins. Small fringing fulcra ("Ff", Fig. 1.12B) are situated on the anterior edge of this fin. In addition to these distal elements, several pelvic radials ("Ra", Fig. 1.12B) from the posterior part of the fin are preserved. These are larger and more triangular than the lepidotrichia that are fused to them ventrally. A pair of round, oval-shaped pelvic basal fulcra are also present anterior to the pelvic fin in YPM 18649.

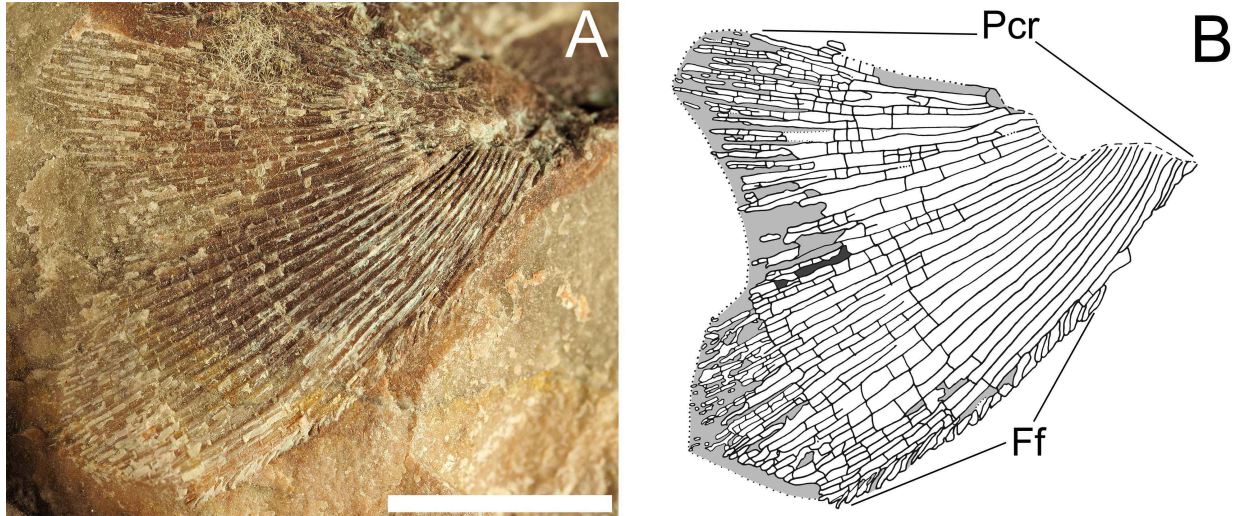


Figure 1.10. Right pectoral fin in the ventral piece of PF 3721. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

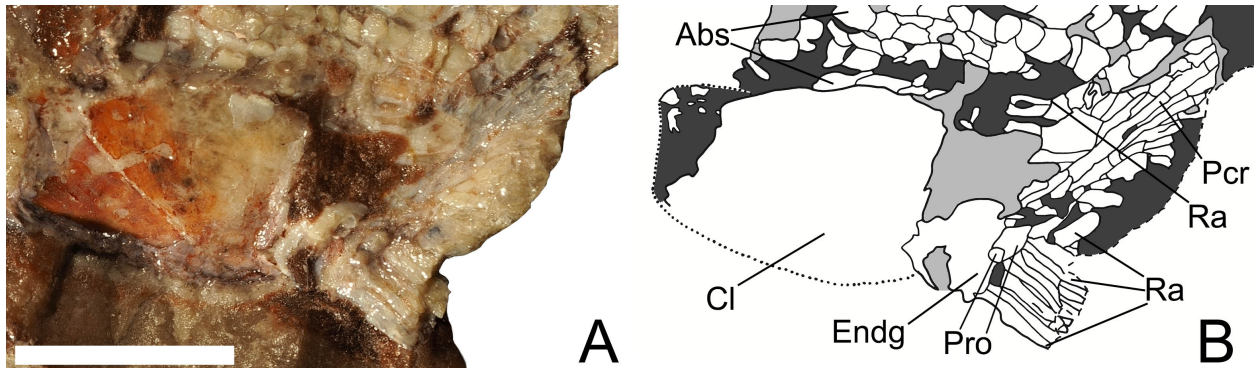


Figure 1.11. Attachment of the pectoral fin to the shoulder girdle in the medial piece of PF 3721. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the left).

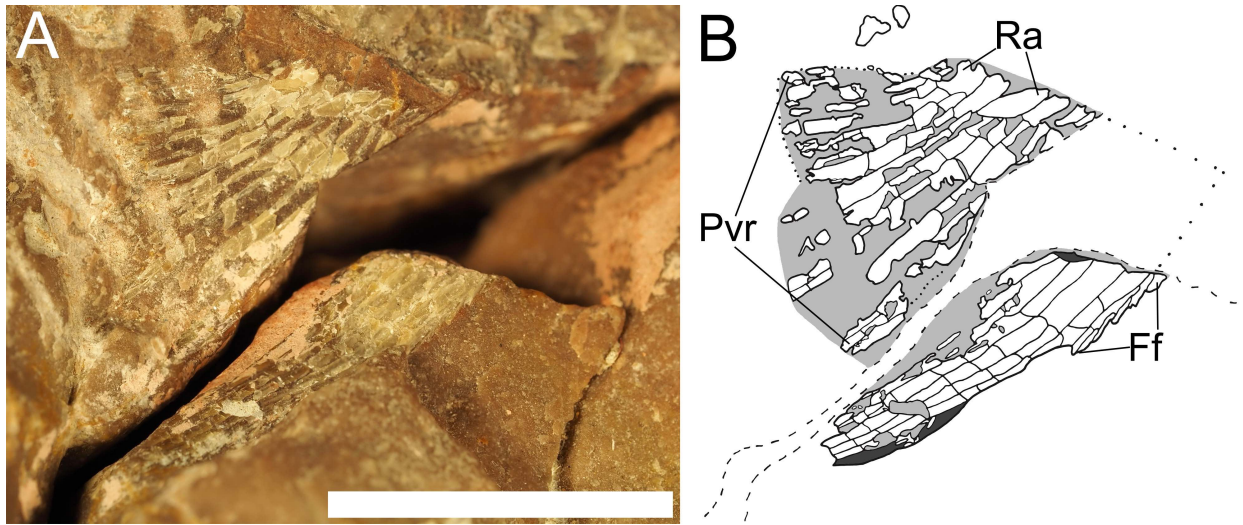


Figure 1.12. Pelvic fin in the left lateral and ventral pieces of PF 3721. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

5.10 Median and Caudal Fins

Although the posterior half of the fish is not preserved in PF 3721, the median and caudal fins are preserved in YPM 18649. The median fins are inserted posteriorly, closer to the caudal fin than the midline of the body. The anal fin is long-based, triangular, and is inserted posterior to the dorsal fin. It has a long, posteriorly curved anterior margin bearing fringing fulcra ("Ff", Fig. 1.13B), and has a peak approximately midway along the length of the fin. The anal fringing fulcra are expanded terminal segments of the anal lepidotrichia. The posterior margin is not as well-preserved as the anterior margin but is low and convex. The lepidotrichia ("Afr", Fig. 1.13B) of the anal fin are long, thin, closely packed, branch distally, and are regularly segmented to their bases. Proximally, these lepidotrichia attach to broader, thicker, rectangular radials ("Ra", Fig. 1.13B). The anal fin is preceded by a set of anal basal fulcra ("Ab", Fig. 1.13B). Anteriorly, there is a single small, diamond-shaped fulcrum whose anterior tip is between two abdominal scales and whose posterior tip is between an additional pair of fulcra. These fulcra are rhombohedral, and sit directly anterior to a large, oval-shaped fulcrum. These fulcra are ornamented with thin, lengthwise ganoine ridges. The area between this circular fulcrum and the

anterior edge of the anal fin is not well-preserved, but contains a single long, roughly oval-shaped scale (pointed anteriorly, broad and flat posteriorly) sitting directly anterior to the insertion of the anal fin that may represent an additional unpaired fulcrum. There are at least 24 anal lepidotrichia, although this is likely an undercount because the entire fin is not preserved.

The dorsal fin (Fig. 1.14) is not as well-preserved as the anal fin, with the insertion and the posterior part of the fin largely absent. The insertion of the dorsal fin is anterior to the anal fin. The dorsal fin is short and rounded with a broad base and fringing fulcra present along its anterior margin ("Ff", Fig. 1.14B). The dorsal fin lepidotrichia ("Dfr", Fig. 1.14B) are thin, closely packed, and (where adequately preserved) are branching distally and regularly segmented to their bases, where they attach to broader, rectangular radials ("Ra", Fig. 1.14B). The insertion of the dorsal fin is not well-enough preserved to determine if dorsal basal fulcra are present.

The caudal fin (Fig. 1.15) is partially preserved in YPM 18649 (with the posterior portion of the dorsal lobe largely absent), showing that it was strongly heterocercal, broad, and deeply forked. The ventral lobe of the caudal fin is long and preceded by four caudal basal fulcra ("Vcb", Fig. 1.15B; possibly four pairs, but this cannot be determined due to the laterally compressed preservation of the specimen). The ventral lobe bears long, pointed fringing fulcra ("Ff", Fig. 1.15B) formed from terminal segments of the marginal rays of the caudal fin. These preceded by three caudal basal fulcra that are visible on the ventral lobe of the caudal fin. These elements are short and triangular. The ventral lepidotrichia ("Vcr", Fig. 1.15B) are long, closely packed, branch distally, and are regularly segmented to their base. There are at least 50 caudal lepidotrichia, but the dorsal lobe of the fin is not completely preserved so this is likely an undercount. The dorsal lobe of the caudal fin bears a series of 17 pointed, wedge-shaped caudal basal fulcra ("Dcf", Fig. 1.15B) that shorten posteriorly. The anterior and posterior extents of this

fulcra are not well-preserved, so more may have been present. The lepidotrichia in the dorsal lobe of the caudal fin ("Dcr", Fig. 1.15) appear to have the same morphology as those in the ventral lobe, although a large portion of them are absent.

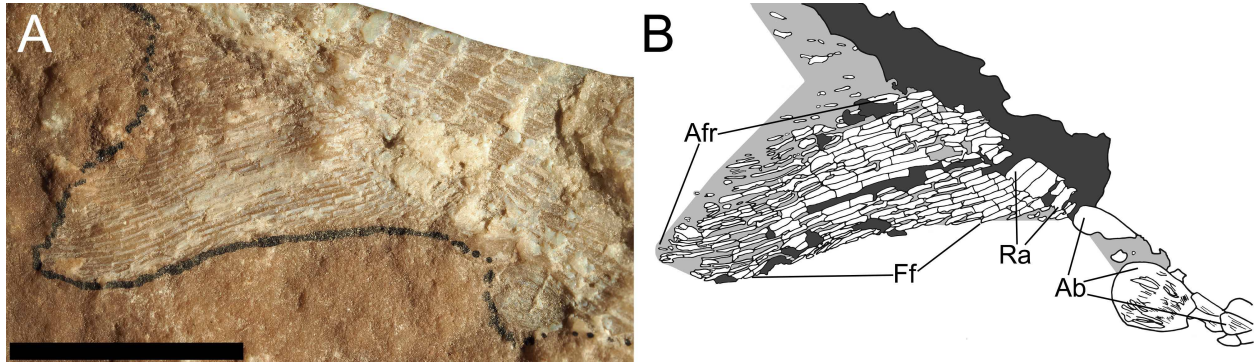


Figure 1.13. Anal fin of YPM 18649. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

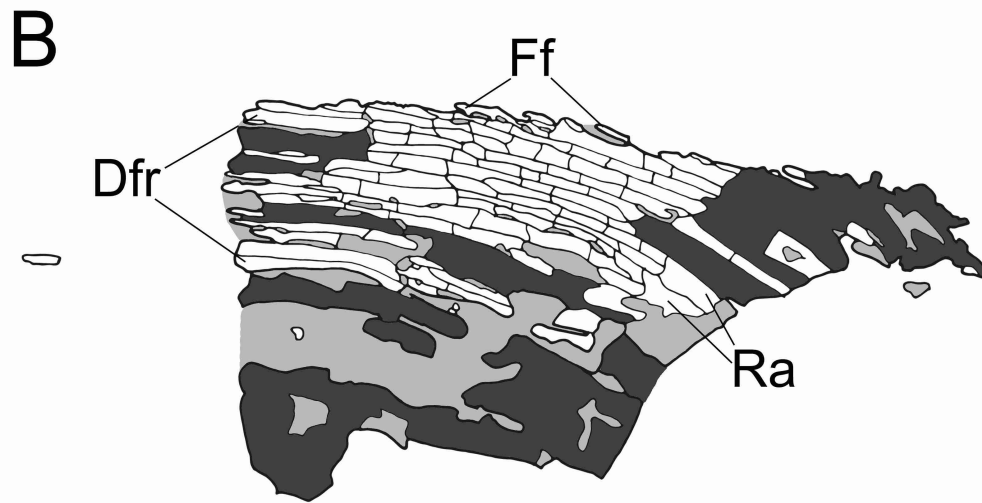


Figure 1.14. Dorsal fin of YPM 18649. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

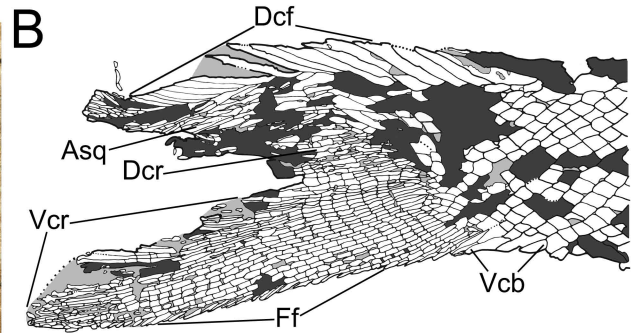
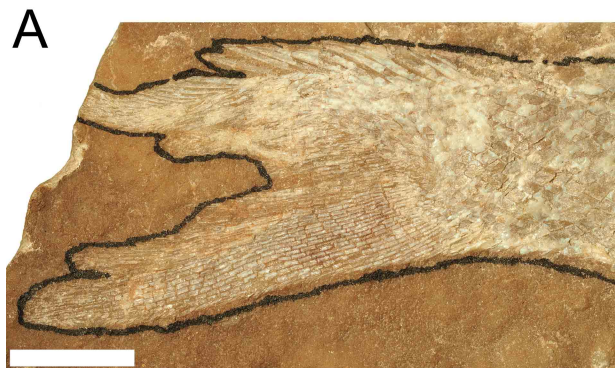


Figure 1.15. Caudal fin of YPM 18649. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

5.11 Squamation

PF 3721 partially preserves both the lateral flank scales between the pectoral and pelvic fin and the abdominal scales immediately posterior to the skull, divided between the pectoral, ventral, and medial pieces. YPM 18649 preserves almost the entirety of the lateral squamation with some of the abdominal scales visible due to the lateral compression of the specimen. The lateral line is not visible in either specimen. The scale cover in the region anterior to the insertion of the dorsal fin consists of rhombohedral scales that are longer than they are tall. The anterior margins of these scales are oriented ventrally, giving them a tilted appearance. The scales in the lateral flank region are dorsoventrally compressed in the dorsal and ventral part of the body. This pattern holds in the region between the posterior insertion of the pelvic fin and the anterior insertion of the anal fin. The scales are consistently ornamented with thin ganoine ridges. While the ridges at the edges of the scales (generally two or three, but sometimes as many as six) are straight and concentric, most of the ridges (in the center of each scale) are oblique, curved, and terraced, with their anterior ends oriented dorsally and their posterior ends oriented ventrally. The scales are more diamond-shaped at the anterior part of the nape and have lighter ornamentation. At the insertion of the dorsal fin the scales become more diamond-shaped, extending all the way to the axial squamation ("Asq", Fig. 1.15). The scales are dorsoventrally compressed both the dorsal and ventral regions of the body, although not nearly to the same degree as the ventral scales on the anterior part of the body. The ornamentation pattern on these scales is consistent with the rest of the squamation, but the ridges are less prominent. The scales on the axial lobe of the caudal fin transition from diamond-shaped to longer, thinner, pointed, and spindle-shaped scales.

A series of ventral ridge scales ("Vr", Fig. 1.16B) are present, beginning immediately posterior to the pectoral fin and extending posteriorly to the caudal basal fulcra, and interrupted by the basal fulcra of the pelvic and anal fins. Initially, the ventral ridge scales are small and round. However, they transition to longer, more rhomboidal scales approximately 1/4 of the way between the area posterior to the pectoral fin and the anterior insertion of the pelvic fin. The ventral ridge scales are ornamented with thin, ganoine ridges that are straight and terraced around the edges but are curved and oblique near the center of the scales. They are smaller in the area between the posterior insertion of the anal fin and the caudal basal fulcra. The dorsal margin of YPM 18649 is not as well-preserved as its ventral margin. However, a short section of dorsal ridge scales is visible immediately posterior to the head, which transition from being diamond-shaped anteriorly to longer, more rhomboidal scales posteriorly. These are ornamented with thin ganoine ridges.

The anterior part of the abdominal squamation is preserved in the medial, ventral, and pectoral pieces of PF 3721 ("Abs", Fig. 1.11B and 1.17B). The morphology of the abdominal squamation varies considerably depending on position. Anteriorly, the abdominal scales are smaller and more rounded than the scales elsewhere on the body, and are ornamented with curved, terraced, concentric ganoine ridges that are most easily observed in the ventral piece. Posteriorly, the abdominal scales become larger and more rhomboidal, transitioning into longer, straighter, and more regular scales.

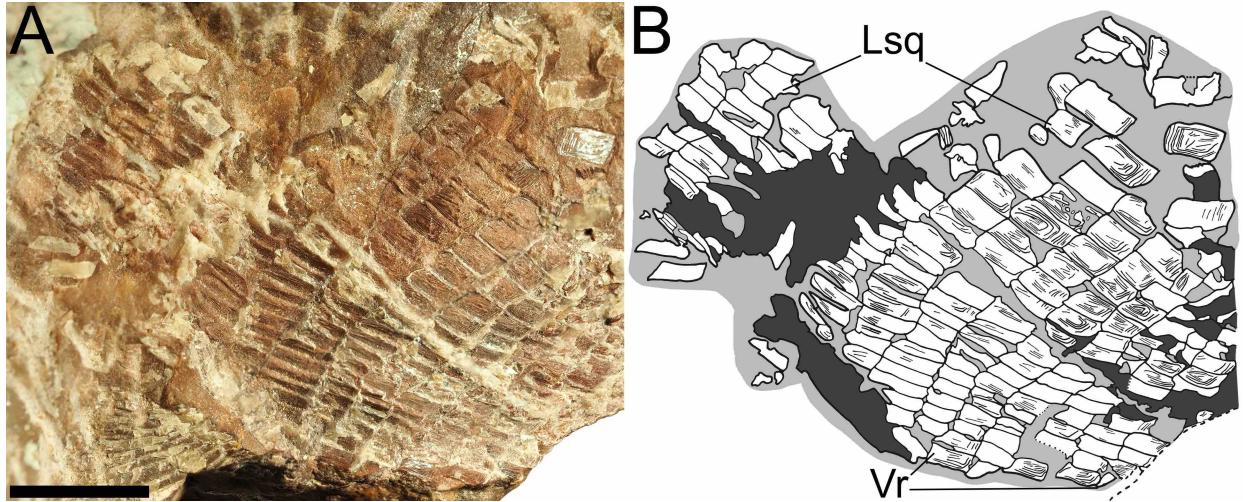


Figure 1.16. Lateral squamation in the left lateral piece of PF 3721. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the right).

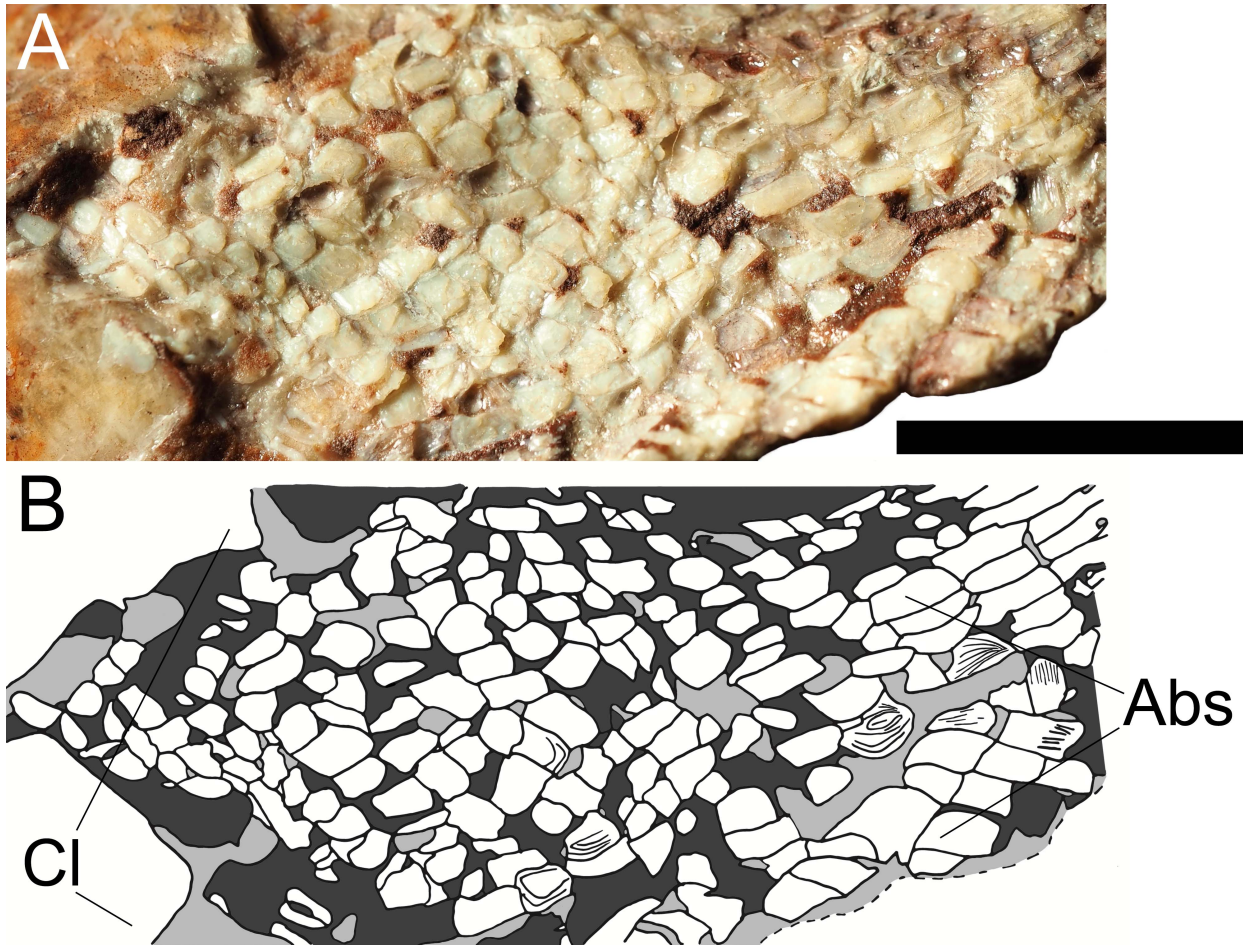


Figure 1.17. Abdominal squamation in the medial piece of PF 3721. A, specimen photo. B, specimen drawing. Scale bar equals 1 cm (anterior is to the left).

6. Micro-CT

The medial piece of PF 3721 was μ CT scanned to image internal structures. I initially examined individual slices of the μ CT data in SPIERSedit and Preview and observed internal structures with different grey values than the surrounding matrix. These structures appeared as a series of small, irregular blobs. When segmented out and visualized as a 3-D model in SPIERSview, and I found that in three dimensions these structures form a large constellation of irregular blobs and specks with no discernible anatomical structure (Fig. 1.18). These may be mineral inclusions of lower density than the surrounding calcium carbonate, but the destructive techniques necessary to analyze the chemical makeup of these structures is not possible or necessary for the goals of this study. I found no relevant anatomical data in this scan.

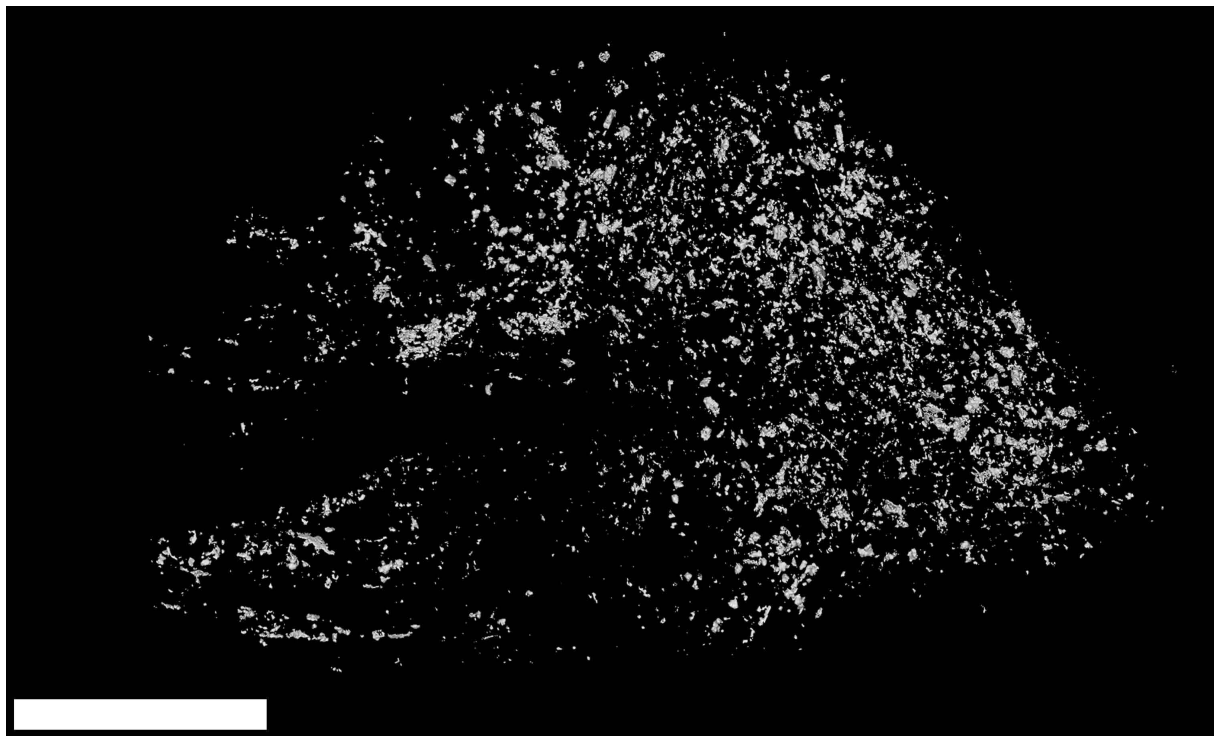


Figure 1.18. 3-D model of the internal structures in the micro-CT scan of the medial piece. Scale bar equals 1 cm (anterior is to the left).

7. Phylogenetic Analysis

7.1 Parsimony Analysis

The maximum parsimony analysis recovered 1088 equally parsimonious trees. The strict consensus of these trees has a length of 1154 steps, consistency index (CI)=0.219, retention index (RI)=0.597, and rescaled consistency index (RCI)=0.131 (Fig. 1.19). *Cheirolepis* is set as the outgroup, with a clade containing *Osorioichthys* Taverne, 1997 and *Tegeolepis* Newberry, 1888 as the earliest diverging lineage after *Cheirolepis*. Devonian actinopterygians resolve separately from a series of three unstable polytomies (Bremer support equal to 1 and bootstrap support lower than 0.5) containing most of the late Paleozoic and early Mesozoic “paleoniscoid” ray-finned fishes in the analysis (including taxa that range in age from the Carboniferous to the Triassic). *Concentrilepis* resolves on the largest and most crownward of these polytomies, which contains a set of Carboniferous and Triassic actinopterygians, including *Australosomus kochi*, *Aesopichthys erinaceus* Poplin & Lund, 2000, *Kalops monophrys* Poplin & Lund, 2002, *Beagiascus pulcherrimus* Mickle *et al.* 2009, *Pteronisculus stensioi*, *Cyranorhis bergeraci* Lund *et al.* 1997, *Wendyichthys dicksoni* Lund *et al.* 1997, and *Cosmoptychius striatus* Watson, 1928. The low phylogenetic resolution of late Paleozoic actinopterygians in this tree and the low stability of the nodes separating out the polytomies containing these fishes obscures the exact position of *Concentrilepis*.

Australosomus resolves as the sister taxon to the clade containing crown actinopterygians. In this tree, crown Actinopterygii is split between a clade showing *Birgeria* Nielsen, 1949 and *Saurichthys* Agassiz, 1834 as the sister-group to a clade containing chondrosteans and polypterids. A series of Paleozoic and Mesozoic “paleoniscoid” taxa, mostly morphologically specialized deep-bodied forms (*Platysomus superbus* Traquair, 1881,

Amphicentrum granulosum Young, 1866, *Fouldenia ischiptera* Traquair, 1881, *Styracopterus fulcratus* Traquair, 1881, *Discoserra pectinodon* Lund, 2000, *Ebenaqua ritchei* Campbell & Phouc, 1983, and *Bobasatrania groenlandica* Stensiö, 1932) branches from the neopterygian stem. The uncertain placement of *Hulettia americana* Schaeffer & Patterson, 1984, dapediids, and *Tetragonolepis semicineta* Bronn, 1830 relative to the holosteans and teleosts obscures the interrelationships of crown neopterygians in the strict consensus tree.

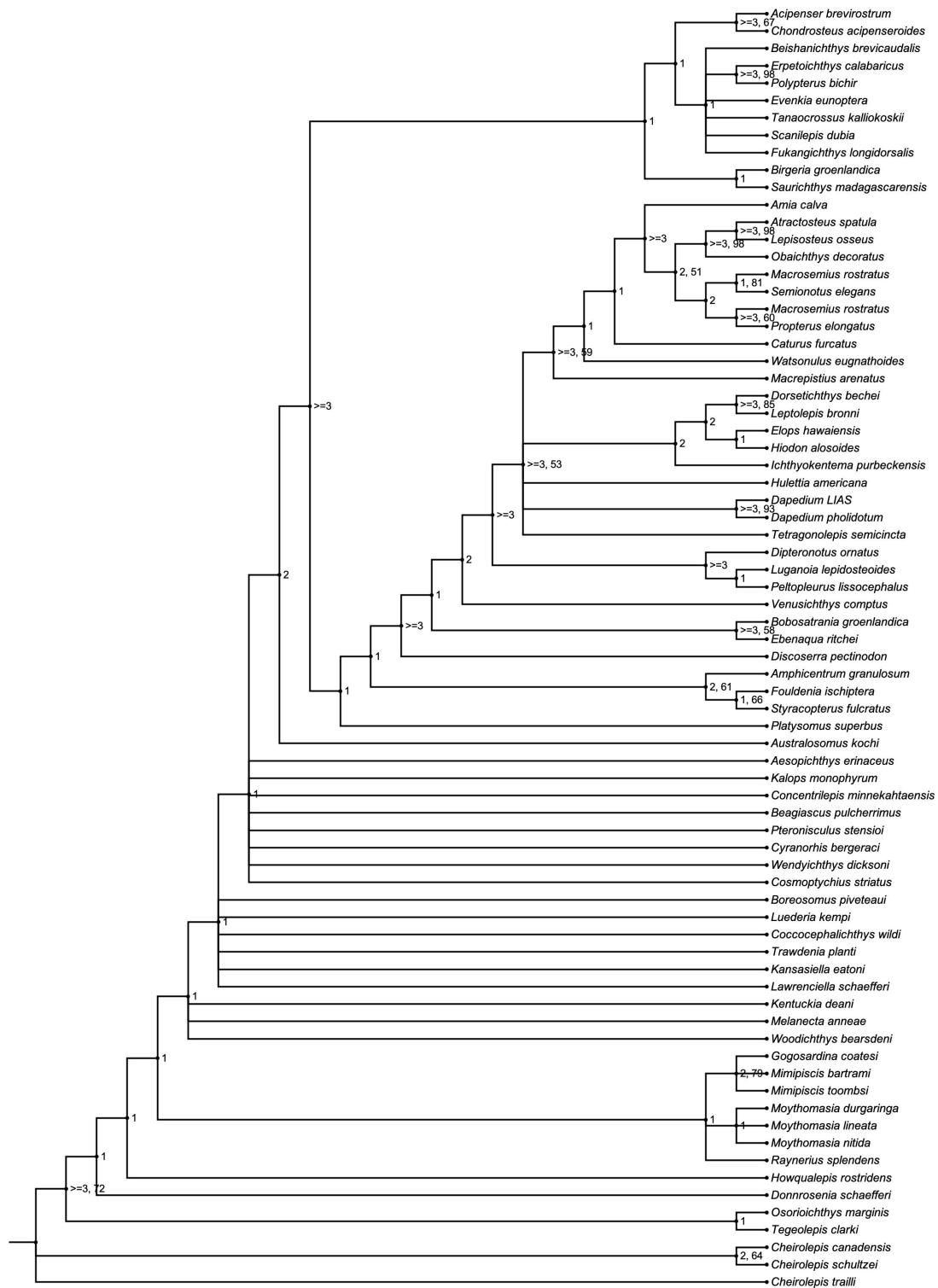


Figure 1.19. Phylogenetic hypothesis of actinopterygian interrelationships, strict consensus tree of a maximum parsimony analysis of 222 morphological characters from Giles *et al.* (2017). Tree length = 1154 steps, CI = 0.219, RI = 0.597, RCI = 0.131. Bremer support values (first value) and bootstrap support greater than 0.5 (second value) are indicated at each node.

7.2 Bayesian Analysis

The consensus tree calculated from the results of the Bayesian analysis resolves the majority of Devonian actinopterygians in a large, well-supported polytomy (posterior probability of 1) closer to the root than other Paleozoic and early Mesozoic ray-finned fishes (Fig. 1.20). *Cheirolepis trailli* Agassiz, 1835 is the first diverging lineage on a branch with a posterior probability of 1. *Melanecta* Coates, 1998 and *Kentuckia* Rayner, 1952 branch off of a strongly supported polytomy (posterior probability = 0.91) after the clade containing most of the Devonian actinopterygians, followed by a branch containing *Woodichthys* Coates, 1998 (posterior probability = 0.83).

The Bayesian consensus tree contains an enormous polytomy (posterior probability = 0.91) with many of the unresolved post-Devonian “paleoniscoids” (including *Concentrilepis*), along with the lineages that lead to the neopterygians, chondrosteans, and polypteriformes. This tree lacks the series of deep-bodied morphologically specialized “paleoniscoids” branching off along the neopterygian stem that is present in the strict consensus tree from the maximum parsimony analysis. In the Bayesian consensus tree, the clades containing these taxa fall within the large polytomy containing most of the post-Devonian “paleoniscoids”. Additionally, *Birgeria* and *Saurichthys* are not the sister group to a clade containing the chondrosteans and polypterids in the Bayesian consensus tree. Instead, these species fall within the large post-Devonian polytomy, along with the chondrostean branch and the polypterids. The placement of *Hulettia*, dapediids, and *Tetragonolepis* relative to the crown neopterygians is also unresolved.

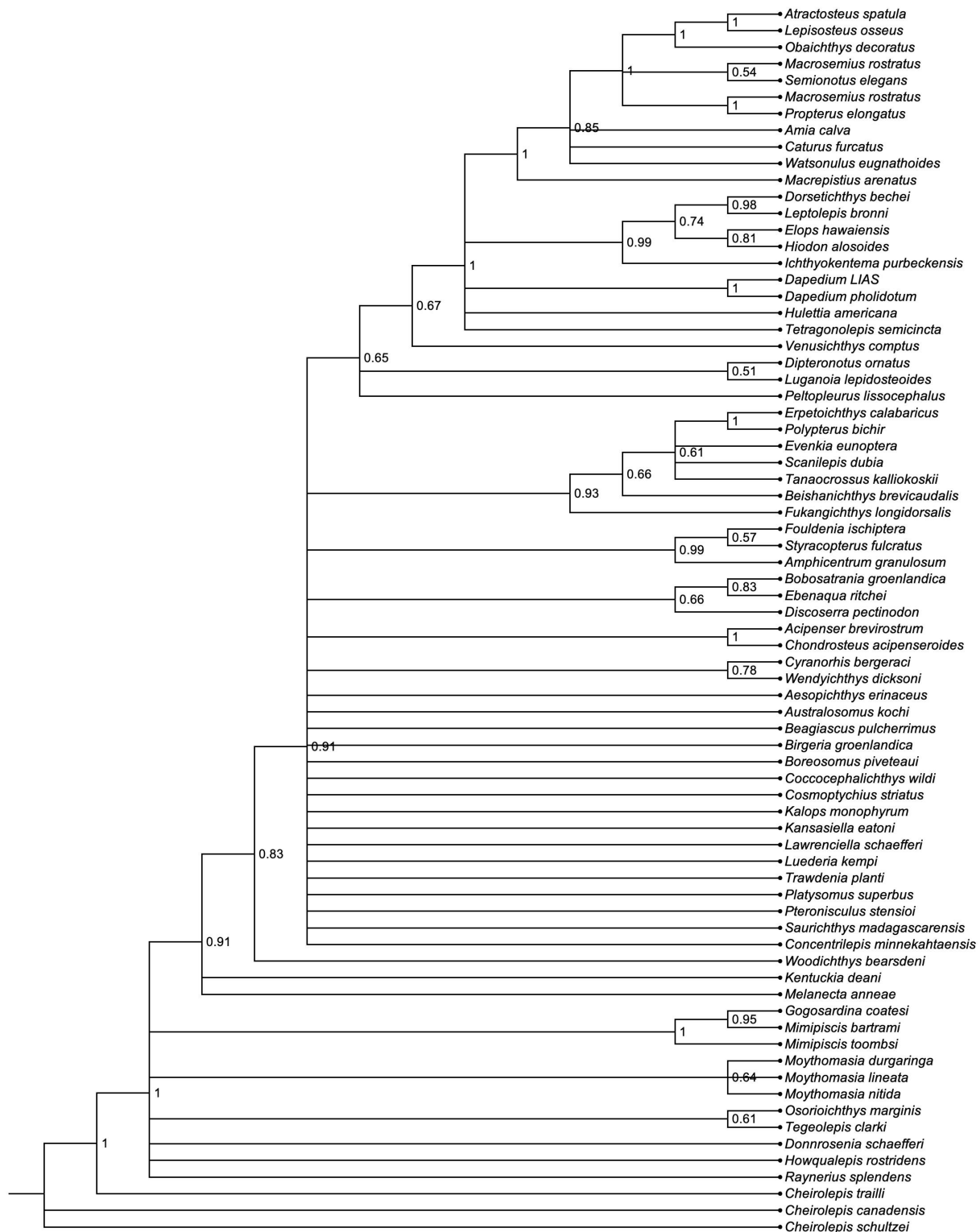


Figure 1.20. Phylogenetic hypothesis of actinopterygian interrelationships, maximum clade credibility tree from Bayesian analysis of 222 morphological characters from Giles *et al.* (2017). Posterior probabilities labeled at nodes, all nodes with posterior probability less than 0.5 are condensed to polytomies.

8. Discussion

8.1 Systematic Affinities and Comparisons

Concentrilepis falls within the non-monophyletic grouping of relatively basal actinopterygians commonly referred to as “paleoniscoids”. In the consensus trees from the parsimony and Bayesian analyses (Figures 1.19 and 1.20), *Concentrilepis* has an unresolved position amongst Carboniferous, Permian, and Triassic “paleoniscoids”. Characteristically for a “paleoniscoid” the new taxon has an immobile maxilla-palato-preopercular complex, a maxilla with broad postorbital plate and a narrow suborbital expansion, rhombic, ganoine-covered scales, and a strongly heterocercal caudal fin (Sallan, 2014; Friedman, 2015; Figure 1.21). Following below is a summary of comparisons of *Concentrilepis* to morphologically similar “paleoniscoids” from the Permian and Early Triassic, and the criteria and features I used to justify erecting a new genus and species.

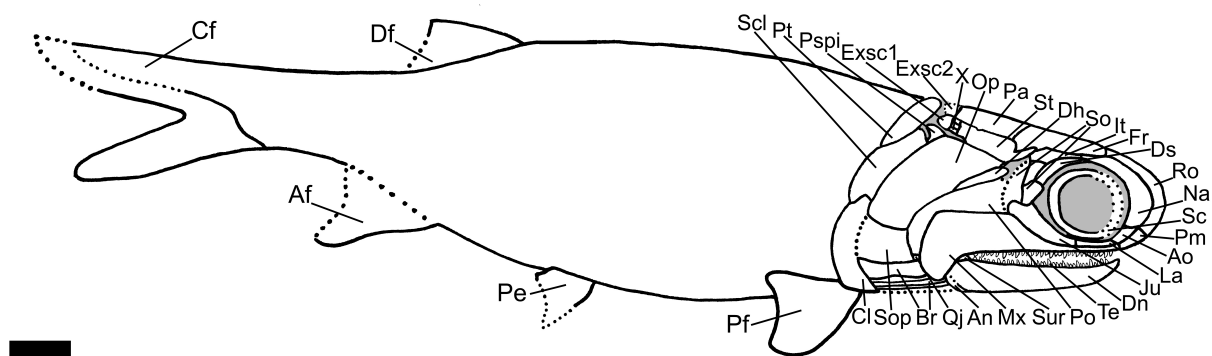


Figure 1.21. Reconstruction of *Concentrilepis minnekahtaensis* in lateral view. Scale bar equals 1 cm.

Concentrilepis most closely resembles the Late Permian-Middle Triassic genus *Pteronisculus* White, 1933 based on comparisons with the well-preserved species of this genus that are included in the diagnoses of Nielsen (1942), namely, *P. stensioi*, *P. magna*, *P. aldingeri*, *P. gunnari*, and *P. artica*, the descriptions of White (1933) and Lehman (1954), including *P.*

macropterus, *P. cicatrosus*, *P. arambourgi*, and *P. broughi*, along with *P. nielseni* (Xu *et al.* 2015). The type specimens of *P. macropterus*, *P. cicatrosus*, *P. arambourgi*, and *P. broughi* were examined at the NHM to verify details from the descriptions of White (1933) and Lehman (1954) – see Table A1.1 for list of examined material. Species of *Pteronisculus* described by Gardiner & Jubb (1975, *P. meiringi*) and Schaeffer & Magnus (1976, *P. ?laetus*) are not described in enough detail to be included in this discussion.

Although it is a geologically younger taxon, *Pteronisculus* is like *Concentrilepis* (approximately 10-15 cm in standard length, prominent snout, broad and triangular pectoral fin, triangular dorsal and anal fins, and deeply forked, heterocercal caudal fin). The large number of species included in *Pteronisculus* makes a comparison challenging because there is wide variation of certain features within the species that have been included in the genus, even when only relatively well-described species are considered. For instance, among the species considered here the number of antopercular elements varies from zero to four (Nielsen, 1942; Lehman, 1954; pers. obs.). This indicates that the current definition of *Pteronisculus* may be too broad and possibly includes multiple distinct genera. However, there are distinctive characters that are shared by all members of *Pteronisculus* as it currently stands that are absent in *Concentrilepis*.

The suborbital expansion of the maxilla in *Pteronisculus* is short, with the lacrimal (the lacrimo-maxillary of Nielsen, 1942) expanded anteriorly and bearing teeth, forming the anterior portion of the oral margin. While this is consistent where observable in available material, the infraorbital bones are not well-enough preserved in *P. aldingeri*, *P. arambourgi*, and *P. broughi* to evaluate this character (Nielsen, 1942; pers. obs.). Although *Pteronisculus* is not the only “paleoniscoid” in which the infraorbitals contribute to the oral margin (i.e., the antorbital in *Turfania taoshuyuanensis*, Liu & Ma, 1973, *Gardinerpiscis akkolhensis* Kasantseva-Selezneva,

1981, and *Kalops monophrys*, Poplin & Lund, 2002; the lacrimal in *Eigilia nielsen*, Kasantseva-Selezneva, 1981) this is a relatively uncommon feature. *Concentrilepis* (as noted in the description) has the typical ancestral “paleoniscoid” arrangement, in which the dorsal oral margin is only composed of the maxilla and premaxilla, with the lacrimal excluded from the oral margin. Another consistent character in *Pteronisculus* is that the lateral flank scales are ornamented entirely with thin, diagonal ganoine ridges (Nielsen, 1942; pers. obs.). Although the lateral flank scales of *Concentrilepis* bear diagonal ridges near their center, they also have straight, terraced ridges at their edges, unlike *Pteronisculus*. Finally, in all examined species of *Pteronisculus* besides *P. arambourgi* (pers. obs.), the posterior margins of the lateral flank scales are serrated. In contrast, the posterior margins of the scales of *Concentrilepis* are not serrated. Therefore, I found that *Pteronisculus* differs from *Concentrilepis* in the arrangement of the infraorbital bones and the morphology of the lateral squamation, strongly indicating that they are distinct genera.

8.2 Taphonomy of PF 3721 and YPM 18649

It is crucial to discuss the mode of preservation of PF 3721 and YPM 18649 to understand how the anatomical data used in this study were preserved. Because the geological data from the FMNH and YPM specimens are limited to the level of formation (not to a specific facies or section), it is not possible to know if individual specimens were collected from distinct facies. The only direct geological data available from these specimens is the micritic (fine-grained) limestone matrix they are preserved in. This indicates that the examined fish specimens were deposited in a low-energy environment (Boggs, 2009). Other inferences of the environmental processes and conditions that influenced the preservation of PF 3721 and other Minnekahta specimens is limited to features that can be observed from the skeletons of the

specimens. The decomposition of fish specimens is influenced by a wide variety of factors, including scavengers, the presence or absence of microbial mats, water depth, water temperature, substrate composition, salinity, alkalinity, and water energy (Schäfer, 1972; Elder, 1985; Weigelt, 1989; Whitmore, 2003; Hellowell & Orr, 2012). Variation in characteristics of the individual fish carcass, including the size and shape of the body, presence or absence of a swim bladder, and intestinal contents (full or empty) also influence how an animal is preserved (Schäfer, 1972; Elder, 1985; Weigelt, 1989; Whitmore, 2003). Therefore, in the absence of independent environmental information from geologic data, caution is warranted in making inferences about the environmental conditions that influenced the preservation of PF 3721 and YPM 18649.

The position of the mouth, fins, and body of individual fish carcasses have been used to make environmental inferences in past taphonomic studies of fossil and extant ray-finned fishes (Schäfer, 1972; Elder & Smith, 1984; Smith & Elder, 1985; Elder & Smith, 1988; Weigelt, 1989; Wilson & Barton, 1996; Whitmore, 2003; Barton & Wilson, 2005; Anderson & Woods, 2013). The carcass of PF 3721 shows characteristics of tetany, a severe form of postmortem muscular contraction resulting in an open mouth, expanded and stiffened fins, and/or an arched body (Elder, 1985; Smith & Elder, 1985; Barton & Wilson, 2005; Anderson & Woods, 2013). YPM 18649 does not have a preserved mouth, and the fins and body do not show evidence of tetany. Tetany has been observed in laboratory experiments in fishes killed by anoxia, rotenone (a plant based poison, Tomlin, 1997), changes in alkalinity, and changes in salinity (Elder, 1985; Smith & Elder, 1985; Whitmore, 2003). Therefore, the tetany in PF 3721 is not a definitive indicator of a particular environmental condition or mode of death. Documentation of the facies of the Minnekahta Limestone that contain fish fossil and study of their geochemistry will be necessary

to investigate if anoxic conditions or other environmental factors were present that would have contributed to tetany in PF 3721.

The pattern and degree of disarticulation in the skeletons of PF 3721 and YPM 18649 may also provide insight into the depositional environment, including events that occurred prior to their burial (such as scavenging, bloating due to gas buildup, etc.) and the amount of time that passed between their death and burial (Schäfer, 1972; Elder & Smith, 1984; Smith & Elder, 1985; Elder & Smith, 1988; Wilson & Barton, 1996; Barton & Wilson, 2005). The head and anterior portion of the trunk of PF 3721 are slightly disarticulated whereas the tail and posterior portion of the body are absent or severely disarticulated. This is the exact opposite of the pattern of disarticulation that has been observed in several assemblages of fossil ray-finned fishes, where disarticulation in the skull is more frequent than disarticulation in the scales and fins in the posterior part of the body (McGrew, 1975; Wilson & Barton, 1996; Mancuso, 2003; Barton & Wilson, 2005; Grande, 2010; Anderson & Woods, 2013). The pattern in PF 3721 is also distinct from YPM 18649 and all but one other fish specimen from the Minnekahta Limestone that was examined (PF 3712, FMNH), where carcasses have moderately to severely disarticulated scales and fins and severely disarticulated or absent skulls. This raises the question of why the skull and anterior portion of PF 3721 are slightly disarticulated, while the posterior portion of its body is absent or severely disarticulated.

The higher frequency of disarticulation in the skulls of assemblages of fossil and extant ray-finned fishes indicates that when whole carcasses are subjected to similar conditions, the skull tends to disarticulate more rapidly than the rest of the body (McGrew, 1975; Elder & Smith, 1984; Weigelt, 1989; Wilson & Barton, 1996; Barton & Wilson, 2005; Grande, 2010; Anderson & Woods, 2013). In laboratory experiments, the lower jaw and opercular elements are the first

parts of the body to disarticulate (Elder, 1985). An exception to this is when there is enough gas build-up in the gastric tract of an individual to rupture the abdomen, causing the abdominal scales and ribs to be the first elements to disarticulate (Elder, 1985; Whitmore, 2003). The anterior part of the abdomen of PF 3721 is not ruptured, indicating that the carcass did not build up enough gas from decomposition to burst. Even in the absence of rupturing from gas buildup, fish carcasses that float to the surface for an extended period (due to gas buildup) will disintegrate over time (depending on water temperature and amount of gas build up) into several pieces, which are shed and sink to the bottom (Whitmore, 2003; Hellowell & Orr, 2012). This indicates that the carcass of PF 3721 may have resurfaced after sinking due to gas buildup and disintegrated as it decayed, breaking the animal into an anterior (PF 3721) and posterior piece (lost to history). However, the articulated lower jaw and opercular elements of PF 3721 strongly suggest that the carcass of this individual did not resurface for an extended period. A more likely explanation is that the entire carcass sank and did not resurface, and that the anterior portion of the animal was buried or protected from decomposition in a way that the tail was not (such as by a microbial mat, as was observed in experiments on modern fishes by Whitmore, 2003). Finally, it is also possible that the posterior half of the animal was lost to a scavenger or predator prior to the anterior end of the carcass sinking to the bottom and being buried. None of these explanations can be ruled out based on the specimen alone. Further study of the taphonomy of the fishes from the Minnekahta Limestone, along with work to determine if microbial mats or large predators of fishes were present in this environment, will be necessary to make a more definitive conclusion on the process that created the pattern of disarticulation in PF 3721.

The three-dimensional preservation of the skull of PF 3721 provided much of the data used in this study. In contrast to all but one other actinopterygian specimen examined from the

Minnekahta Limestone (PF 3712, FMNH), PF 3721 is not laterally compressed. The skull of the individual in PF 3721 may be three dimensionally preserved because its body is twisted around and on top of a lithological irregularity in the encasing limestone. Whereas most of the specimen is composed of a dark red/purple matrix, the body of PF 3721 is curved around and on top of a pinkish mound inside the rock that prevented the animal from being laterally compressed. The color contrast between the mound and the surrounding matrix suggests a compositional difference, but destructive chemical analysis is not permitted with PF 3721. The bending of the animal may be the result of tetany, the body bending from currents (as was observed in gar by Weigelt, 1989), or the midsection floated higher in the water than the head and tail due to gas buildup prior to the individual's burial (as observed by Whitmore, 2003). However, it is not possible to rule out any of these possible mechanisms with the information at hand. Therefore, the precise reason for the three-dimensional preservation of PF 3721 is not clear from the specimen itself.

8.3 Interrelationships of Early Ray-finned Fishes

The inclusion of a novel ray-finned fish from an under-documented segment of the actinopterygian fossil record (along with other alterations to the framework of Giles *et al.* 2017) does have some implications for our understanding of the phylogeny of this group. The framework of Giles *et al.* 2017 and more recent studies that analyzed an altered version of this framework (Argyriou *et al.* 2018; Latimer & Giles, 2018; Figueroa *et al.* 2019) have yielded several patterns that are consistent with the results of this current analysis. First, Devonian actinopterygians form a clade separate from post-Devonian taxa in the consensus trees from both the Bayesian and maximum parsimony analyses, including post-Devonian “paleoniscoids” and those groups with extant representatives. Additionally, the scanilepiforms are resolved as stem

polypterids in both sets of analyses, as was first recognized by Giles *et al.* (2017). Therefore, the results presented here reinforce the hypothesis of Giles *et al.* (2017) that most Paleozoic taxa fall on the actinopterygian stem.

The position of and resolution within several groups differs considerably between the consensus of the parsimony and Bayesian analyses. Carboniferous, Permian, and Triassic "paleoniscoids" are placed into several distinct branches in the parsimony consensus tree but are in a single massive polytomy in the Bayesian consensus tree. Deep-bodied Paleozoic lineages that fall along the neopterygian stem in the parsimony consensus tree, a pattern that has consistently emerged in previous parsimony analyses of early actinopterygians (Giles *et al.* 2017; Argyriou *et al.* 2018; Figueroa *et al.* 2019), are also placed into the enormous polytomy in the Bayesian consensus tree with late Paleozoic and early Mesozoic "paleoniscoids". Finally, acipenseriformes are placed as the sister group to the polypterids and scanilepiformes, with *Birgeria* and *Saurichthys* as a sister group to this clade in the consensus of the parsimony results. The placement of Acipenseriformes, *Birgeria*, and *Saurichthys* is unresolved in the Bayesian consensus tree, causing these lineages to be placed in the massive polytomy containing late Paleozoic and early Mesozoic "paleoniscoids". Overall, the consensus tree of the parsimony results has much higher resolution than the Bayesian consensus tree.

I consider arrangements that are present in the parsimony consensus tree but are lost in the Bayesian consensus tree to be unreliable. Studies that have compared the accuracy of Bayesian and parsimony techniques in estimating a non-empirical topology (set by researchers) from simulated datasets have consistently found that Bayesian methods find correct arrangements more often than parsimony, include incorrect arrangements less often, and assign higher support values to correct arrangements (Wright & Hillis, 2014; Puttick *et al.* 2017;

O'Reilly *et al.* 2018; Puttick *et al.* 2018). The difference in accuracy between these techniques has also been found to become larger as simulated datasets are more incomplete and contain higher levels of homoplasy and holds even when taxon assignments are simulated randomly (Wright & Hillis, 2014; Puttick *et al.* 2017; O'Reilly *et al.* 2018; Puttick *et al.* 2018). Therefore, further study of the species that vary in position between the consensus trees, many of which are represented by well-preserved but understudied material (e.g., *Platysomus*, *Bobasatrania*; pers. obs.), is necessary to resolve the discrepancies between the results of these analyses and improve the resolution of future Bayesian consensus trees.

Comparison of the parsimony and Bayesian results highlights the advantages of applying these techniques to early actinopterygian phylogenetics in tandem. Bayesian techniques provide a statistical basis for evaluating proposed topological arrangements in the results of parsimony analyses, which creates necessary caution where there is disagreement between consensus trees. However, the incompleteness of the phylogenetic framework for late Paleozoic and early Mesozoic “paleoniscoids” also led to the highly unresolved results from my Bayesian analysis. A tree with a single massive polytomy containing most of the taxa of interest, such as the Bayesian consensus tree in this study (Fig. 1.20), provides precious little in the way of direction for future research on its own. Although the obvious solution is to improve the amount and quality of data from the unresolved taxa of interest, detailed descriptive studies of early actinopterygians require a great deal of the time and effort of researchers to complete. Additionally, many of the included taxa are known from poorly preserved or incomplete material, making the construction of a complete framework impossible. The arrangements found in our parsimony strict consensus tree that have a low posterior probability, such as the inclusion of deep-bodied “paleoniscoid” lineages along the neopterygian stem in this study (Fig. 1.19), provide direction for the focus of

future time and effort of researchers. Without the low-probability arrangements from the parsimony analysis, which are also shown to be worthy of caution by measures of support and stability traditionally applied in parsimony, I would be unable to provide focused direction for future research from our phylogenetic analyses. Therefore, my application of parsimony and Bayesian inference techniques to early actinopterygian interrelationships provided focused direction for future research and introduced necessary caution during evaluation of our phylogenetic results. As datasets become more complete with continued descriptive efforts and more nuanced models of morphological evolution are developed, it may be more effective to apply Bayesian techniques alone. However, for the time being, I recommend that both Bayesian and parsimony techniques be applied to analyses of early actinopterygian phylogenetics.

The addition of a novel Permian taxon and the restriction of the analysis to ray-finned fishes did not substantially alter the results of my analyses relative to previous studies of actinopterygian interrelationships with the same underlying framework (Giles *et al.* 2017; Latimer & Giles 2018; Argyriou *et al.* 2018; Figueroa *et al.* 2019). This includes a lack of resolution amongst post-Devonian “paleoniscoids”, resulting in a large portion of the taxa falling on polytomies. The fact that I was unable to resolve the position of a novel taxon that is known from relatively complete material highlights the need to improve the available phylogenetic framework for early actinopterygians. This will require gathering more data for phylogenetic analysis by describing more novel taxa from historically underrepresented intervals (such as the Pennsylvanian-Middle Permian; Friedman & Sallan, 2012), re-describing species that have only been briefly documented, and continuing to apply micro-computed tomography to image internal skeletal structures (Friedman, 2015). In addition to making the existing framework more complete, novel data can be used to identify new characters that may improve the ability of

inference techniques to parse out the relationships of the “paleoniscoids”. Dedicated study of the fit of novel Bayesian model configurations for morphological data may also increase the accuracy of future phylogenetic analyses of Paleozoic and Mesozoic actinopterygians.

Strengthening our understanding of the phylogeny and evolution of late Paleozoic and early Mesozoic actinopterygians will be essential for reconstructing the cause and pattern of the series of diversification events in the Triassic that established the dominance of modern groups of actinopterygians in aquatic ecosystems (Friedman & Sallan, 2012; Tintori *et al.* 2014; Romano *et al.* 2014).

9. Conclusions

A new species of "paleoniscoid" ray-finned fish, *Concentrilepis minnekahtaensis*, is described from the Early Permian Minnekahta Limestone of the Black Hills of South Dakota. Although this species is represented by two well-preserved specimens (PF 3721 and YPM 18649), neither a parsimony and Bayesian analysis was able to infer the phylogenetic position of this species among an unresolved assemblage of late Paleozoic and early Mesozoic "paleoniscoids". These results indicate that resolving the late Paleozoic and early Mesozoic evolutionary history of actinopterygians will require revising the available phylogenetic framework for these animals and methods applied to it.

APPENDIX

Table A1.1. Summary of examined material.

Institution	Specimen Number	Taxon
NHM	15400	<i>Acrolepis sedgwicki</i>
NHM	43434	<i>Acrolepis sedgwicki</i>
NHM	15411	<i>Acrolepis sedgwicki</i>
NHM	P. 15096	“ <i>Elonichthys macropterus</i> ”
NHM	P. 3425c	<i>Palaeoniscum freiselebeni</i>
NHM	P. 3425a	<i>Palaeoniscum freiselebeni</i>
NHM	P. 354	<i>Palaeoniscum freiselebeni</i>
NHM	P. 17651	<i>Palaeoniscum freiselebeni</i>
NHM	P. 3425a	<i>Palaeoniscum freiselebeni</i>
NHM	P. 1029b	<i>Palaeoniscum freiselebeni</i>
NHM	8049	<i>Palaeoniscum freiselebeni</i>
NHM	39251	<i>Palaeoniscum freiselebeni</i>
NHM	P. 3476-7	<i>Palaeoniscum freiselebeni</i>
NHM	P. 5139	<i>Palaeoniscum freiselebeni</i>
NHM	P. 1029a	<i>Palaeoniscum freiselebeni</i>
NHM	P. 39971	<i>Palaeoniscum freiselebeni</i>
NHM	P. 3476-7	<i>Palaeoniscum freiselebeni</i>
NHM	19945	<i>Palaeoniscum freiselebeni</i>
NHM	P. 3474	<i>Palaeoniscum freiselebeni</i>
NHM	P. 18071	“ <i>Palaeoniscum antipodeous</i> ”
NHM	35530	<i>Platysomus gibbosus</i>

Table A1.1. (cont'd)

NHM	39160	<i>Platysomus gibbosus</i>
NHM	P. 16284-5	<i>Pteronisculus macropterus</i>
NHM	P.16282-3 (type)	<i>Pteronisculus macropterus</i>
NHM	P. 16273-4	<i>Pteronisculus macropterus</i>
NHM	P. 19508-9	<i>Pteronisculus macropterus</i>
NHM	P. 16297-8	<i>Pteronisculus macropterus</i>
NHM	P. 63969	<i>Pteronisculus</i> sp.
NHM	P. 16292	<i>Pteronisculus</i> sp.:
NHM	P.16300-1 (type)	<i>Pteronisculus cicatrosus</i>
NHM	P. 16297-8	<i>Pteronisculus cicatrosus</i>
NHM	P. 16299	<i>Pteronisculus cicatrosus</i>
NHM	P. 19502-3 (type)	<i>Pteronisculus broughi</i>
NHM	P. 16293-4 (type)	<i>Pteronisculus arambourgi</i>
NHM	P. 3414a	<i>Pygopterus humboldti</i>
NHM	18509	<i>Pygopterus humboldti</i>
NHM	P. 27408	<i>Pygopterus humboldti</i>
NHM	P. 58956	<i>Pygopterus humboldti</i>
NHM	14371	<i>Pygopterus humboldti</i>
NHM	P. 3414	<i>Pygopterus humboldti</i>
NHM	P. 833	<i>Pygopterus humboldti</i>
NHM	43267	<i>Pygopterus humboldti</i>
NHM	P. 3408	<i>Pygopterus humboldti</i>

Table A1.1. (cont'd)

NHM	36058	<i>Pygopterus humboldti</i>
NHM	P. 58956	<i>Pygopterus humboldti</i>
NHM	39698	<i>Pygopterus humboldti</i>
NHM	P. 27408	<i>Pygopterus humboldti</i>
NHM	P. 58546 (cast of type)	<i>Turfania taoshuyuanensis</i>
NHM	32576	<i>Rhabdolepis saarbrueckensis</i>
NHM	Two unnumbered specimens in Cabinet 11, drawer H5	<i>Meisenheimichthys</i>
YPM	18649	<i>Concentrilepis minnekahtaensis</i>
YPM	13592	Unidentified
YPM	18127	Unidentified
YPM	18650	Unidentified
FMNH	PF 3712	Unidentified
FMNH	PF 3721	<i>Concentrilepis minnekahtaensis</i>
FMNH	P 25772	Unidentified
FMNH	PF 3714	Unidentified

A2 Summary of systematic comparisons

Acrolepis (Agassiz, 1833)

Notes.

Diagnoses from Aldinger (1937) and Štamberg (2013).

Features distinguishing from PF 3721 and YPM 18649.

Uniform cranial ornament of short and thick ganoine ridges, giving the bones a pebbled appearance; dentary very broad and thick, diamond-shaped scales with thick, branching, curving, and lengthwise ganoine ridges; opercular narrower than subopercular. There are additional features from the diagnosis of Aldinger (1937) that would distinguish *Acrolepis* from PF 3721 and YPM 18649 (shape of the frontals and intertemporal, a possible antopercular, and the presence of a postcleithrum), but because these are not noted in Štamberg's (2013) diagnosis of the genus I exclude them here.

Acropholis stensioei (Aldinger, 1937)

Notes.

Diagnosis from Aldinger (1937).

Features distinguishing from PF 3721 and YPM 18649.

Opercular narrow and smaller than the subopercular; seven to eight extrascapular elements; 15 antopercular elements; ventral caudal fin and dorsal fin lepidotrichia ornamented with thin diagonal ganoine ridges; lateral flank scales taller than they are wide and ornamented entirely with diagonal ganoine ridges.

Amblypterus (Agassiz, 1833)

Notes.

Diagnosis from Dietze (2000).

Features distinguishing from PF 3721 and YPM 18649.

Frontals with single lateral expansion and without anterior lateral extensions; two suborbitals; ten branchiostegal rays; dorsal-most branchiostegal ray of similar size to preceding ray; pectoral fin small and rectangular.

Angatubichthys mendesi (Figueiredo & Carvalho, 2004):

Notes.

Diagnosis from Figueiredo & Carvalho (2004).

Features distinguishing from PF 3721 and YPM 18649.

Snout capped by large median rostral and smaller anterior postrostral; fused rostromaxilloantorbital; frontals with straight lateral margins (lacking lateral expansions); fused dermopterotic; dermosphenotic does not contact nasal; opercular shorter than subopercular; six brachistegal rays; lateral squamation without ornament.

Avamia malovetskajae (Kazantseva-Selezneva, 1981):

Notes.

Diagnosis from Kazantseva-Selezneva (1981).

Features distinguishing from PF 3721 and YPM 18649.

Pectoral fin spine present; anterior lateral scales taller than wide.

Bethesdaichthys kitchingi (Bender, 2001):

Notes. Diagnosis from Bender (2001).

Features distinguishing from PF 3721 and YPM 18649.

Short, flat snout; frontals with straight lateral margins and a straight median suture; fused dermopterotic; maxilla with extremely tall, square postorbital expansion; four suborbitals; nine branchiostegal rays; dorsal-most branchiostegal ray of similar size to preceding ray; lateral squamation ornamented with series of oblique ridges.

Boreolepis jenseni (Aldinger, 1937):

Notes.

Diagnosis from Aldinger (1937).

Features distinguishing from PF 3721 and YPM 18649.

Frontals lack dual lateral expansions; maxilla curved and boomerang shaped, with a short, rounded postorbital expansion and a dorsally curved and broad suborbital expansion; dentary taller posteriorly than anteriorly, with a distinct dorsal, convex curve in its posterior half, and sloping anteriorly; dentary without a reflexed distal tip; right parietal larger than left parietal; right parietal with a large, pointed, trident-shaped median process fitting between the frontals and two shorter lateral processes.

Cylindrichthys macropterus (Kasantseva-Selezneva, 1981):

Notes.

Diagnosis from Kasantseva-Selezneva (1981).

Features distinguishing from PF 3721 and YPM 18649.

Lateral margin of frontal does not interlock with intemporal or supratemporal elements; two suborbitals; maxilla lacks prominent postero-ventral corner; dorsal-most branchiostegal ray is similar in size to preceding ray; epipraeopercular present; antopercular present; extremely long pectoral fin; single pair of anal basal fulcra.

Eigilia nielsenii (Kasantseva-Selezneva, 1981):

Notes.

Diagnosis from Kasantseva-Selezneva (1981).

Features distinguishing from PF 3721 and YPM 18649.

Lacrima contributes to oral margin; antopercular present; dorsal-most branchiostegal ray is similar in size to preceding ray; scales ornamented with curving, diagonal ridges; scales with serrated posterior margins.

Eurylepidoides socialis (Case, 1935)

Notes.

This species has only been described in a brief note, which did not have a diagnosis, specimen drawings, or photographs. A re-description is needed, so I can only make a limited comparison here based on the description and reconstruction from Case (1935).

Features distinguishing from PF 3721 and YPM 18649.

Posterior expansion of maxilla curved and roughly S-shaped; opercular smaller than subopercular; dorsal-most branchiostegal ray equal in size to preceding element; second row of anterior lateral scales extremely tall.

Gardinerpiscis akkolkensis (Kazantseva-Selezneva, 1981)

Notes.

Updated name and English diagnosis from Romano & Kogan (2015). This comparison is based on their diagnosis and the reconstruction of the skull from Kazantseva-Selezneva (1981; fig. 57).

Features distinguishing from PF 3721 and YPM 18649.

Antorbital contributing to oral margin; postorbital with long posterior ramus reaching the dermohyal; antopercular and epipraeopercular present.

Ignorichthys bohemicus (Štamberg, 2016)

Notes.

Diagnosis from Štamberg (2016).

Features distinguishing from PF 3721 and YPM 18649.

Lateral margins of frontals do not interlock with dermopterotic; fused dermopterotic; maxilla crescent-shaped with curved postorbital expansion; scales with one or two large spines oriented postero-ventrally.

Inichthys gorelovae (Kazantseva-Selezneva, 1979)

Notes.

Diagnosis from Kazantseva-Selezneva (1979).

Features distinguishing from PF 3721.

Epipraeopercular present; scales ornamented with short, sparse ridges running diagonally; posterior margins of scales serrated.

Isadia suchonensis (Minich, 1990)

Notes.

We use the diagnosis of this genus from Minikh & Minikh (2009) that was translated into English by Bakaev *et al.* (2020).

Features distinguishing from PF 3721 and YPM 18649.

Dorsal margin of the maxilla convex; scales ornamented with short, thick, parallel ridges running anteriorly-posteriorly; posterior margins of scales serrated.

Karaunguria kleimani (Kazantseva-Selezneva, 1981)

Notes.

Translated diagnosis from Kazantseva-Selezneva (1981).

Features distinguishing from PF 3721 and YPM 18649.

Approximately 0.5 m in length; antorbital contributes to the oral margin; epipraeopercular and antopercular present; 16-17 branchiostegal rays; postcleithrum present.

Kasanilepis chupaevensis (Minich, 1996)

Notes.

Diagnosis from Minikh & Minikh (2009), translated into English by Bakaev *et al.* (2020).

Featured distinguishing from PF 3721 and YPM 18649.

Maxilla with tall, roughly square postorbital expansion; opercular narrower than subopercular; anterior lateral scales taller than wide; anterior lateral scales lack ornament.

Korutichthys korutensis (Kazantseva-Selezneva, 1981)

Notes.

Diagnosis from Kazantseva-Selezneva (1981).

Featured distinguishing from PF 3721 and YPM 18649.

Pelvic fin thoracic; anterior lateral scales taller than wide; anterior lateral scales ornamented with a series of oblique ridges.

Khantausia tshuiliensis (Prokofiev, 2005)

Notes.

Diagnosis from Prokofiev (2005).

Features distinguishing from PF 3721 and YPM 18649.

Frontals with smooth lateral margins and a straight medial suture; parietals without anterior median process; fused dermopterotic; maxilla with arched, curved dorsal margin; ossified dermohyal absent; lateral scales ornamented with irregular, oblique to horizontal ridges; lateral scales with weak posterior serration; ventral ridge scales absent.

Kichkassia furcae (Minich, 1990)

Notes.

Diagnosis from Minikh & Minikh (2009) that was translated into English by Bakaev *et al.* (2020).

Features distinguishing from PF 3721 and YPM 18649.

Frontals with straight lateral margins; fused dermopterotic; maxilla with short, rounded postorbital expansion; opercular nearly equal in size to subopercular; scales taller than wide in anterior lateral region; lateral squamation with serrated posterior margins.

Kompasia delaharpei (Bender, 2002)

Notes.

Diagnosis from Bender (2002).

Features distinguishing from PF 3721 and YPM 18649.

Frontals without dual lateral extensions; fused dermopterotic; dorsal margin of maxilla not flat, but with a high point in its anterior half (roughly triangular); opercular rectangular and slightly shorter and narrower than the subopercular; ten branchiostegal rays; dorsal-most branchiostegal ray similar in height to preceding ray; anterior lateral scales taller than wide; lateral scale ornament (except for axial squamation) consists two or three parallel grooves along the posterior and ventral margin.

Lapkosubia uranensis (Minich, 1990)

Notes.

Diagnosis from Minikh & Minikh (1990) that was translated into English by Bakaev *et al.* (2020).

Features distinguishing from PF 3721 and YPM 18649.

Lateral margins of frontals are straight; parietals with sinuous lateral margins; fused dermopterotic; serrated posterior margin of supracleithrum; anterior lateral scales ornamented

with parallel ridges running anteriorly-posteriorly; scales with pronounced anterodorsal corner; scales with serrated posterior margins.

Lawnia taylorensis (Wilson, 1953)

Notes.

Diagnosis from Wilson (1953), additional information gathered from Dalquest & Kocurko (1988).

Features distinguishing from PF 3721 and YPM 18649.

Frontals lack dual lateral expansions (smooth and straight lateral margins); frontals have straight median suture; right parietal lacks anterior median process; postorbital expansion of maxilla short and rounded; postcleithrum present.

Muensterichthys buergeri (Schaumberg, 1989)

Notes.

Diagnosis from Schaumberg (1989).

Features distinguishing from PF 3721 and YPM 18649.

Postcleithrum present, 13 branchiostegal rays; lateral scales ornamented with diagonal ridges.

Neuburgella cognominis (Kazantseva-Selezneva, 1981)

Notes.

Diagnosis from Kazantseva-Selezneva (1981).

Features distinguishing from PF 3721 and YPM 18649.

Antorbital contributes to oral margin; antopercular present; epipraeopercular present.

Palaeoniscum freiselebeni (Blainville, 1818)

Notes.

Diagnosis from Aldinger (1937; from Westoll, 1934, unpublished).

Features distinguishing from PF 3721 and YPM 18649.

Lateral margin of frontal is straight (lacks dual lateral expansions); anterior lateral expansion of frontal long (approximately 1/3 of element length), thin, and sharply pointed; intertemporal and nasal are not in contact; dermosphenotic separated from nasal by series of “supraorbital” bones; anterior lateral scales taller than they are wide; squamation largely lacking ornament (some scales have short, thick tubercles or diagonal ridges, but most lack ornament); postcleithrum present; dorsal-most branchiostegal ray of similar size to preceding ray.

Paramblypterus (Sauvage, 1888)

Notes.

Diagnosis from Dietze (2000) for this comparison, which is primarily based on *P. decorus*, *P. gelberti*, and *P. duvernoyi*.

Features distinguishing from PF 3721 and YPM 18649.

Nasal split into two elements on each side of the skull (four total nasals); frontals with straight medial suture and a deep indentation in the lateral margin; series of ossifications between the preopercular and the opercular (dermohyal not present as a single ossification); at least seven suborbitals; seven to nine branchiostegal rays; dorsal-most branchiostegal ray is of similar size to preceding ray; postcleithrum present; pectoral fin small and rectangular; caudal fin with hypochordal lobe; posterior margin of scales serrated; little ornamentation on scales.

Plegmolepis kochi (Aldinger, 1937)

Notes.

Diagnosis from Aldinger (1937).

Features distinguishing from PF 3721 and YPM 18649.

Multiple antopercula; opercular shorter and smaller than subopercular; three postcleithra; posterior margin of rostral trident-like, with three points (the medial point being the largest); interdigitating margin between frontals; anterior lateral scales broader than tall; no dorso-ventral compression of flank scales ventrally.

Progyrolepis (Fritsch, 1895)

Notes.

I base this comparison on the best-known European species *Progyrolepis heyleri* (Poplin, 1999), relying on recent descriptive work and a revised generic diagnosis from Štamberg (2018).

Progyrolepis tricessimalaris (Dunkle, 1946), from the Early Permian of Texas, is not known from complete enough material for a detailed comparison.

Features distinguishing from PF 3721 and YPM 18649.

Lateral margins of frontals straight; fused dermopterotic; dermosphenotic with posterior ramus; scales ornamented with long, thin, slightly oblique ridges that run the entire length of the scale; dorsal-most branchiostegal ray is of similar size to preceding ray.

Pteronisculus (White, 1933)

Notes.

Pteronisculus is a large genus (eleven species, Xu *et al.* 2015). I focus on the well-preserved species of this genus that are included in the diagnosis of Nielsen (1942; *P. stensioi*, *P. magna*, *P. aldingeri*, *P. gunnari*, *P. artica*), the descriptions of White (1933) and Lehman (1954; *P. macropterus*, *P. cicatrosus*, *P. arambourgi*, *P. broughi*), and *P. nielseni* (Xu *et al.* 2015). Species of *Pteronisculus* described by Gardiner & Jubb (1975, *P. meiringi*) and Schaeffer & Magnus (1976, *P. ?laetus*) have not been described in enough detail to be included in this discussion.

Features distinguishing from PF 3721 and YPM 18649.

The suborbital expansion of the maxilla is short, with the lacrimal (the lacrimo-maxillary of Nielsen, 1942) expanded anteriorly and bearing teeth, forming the anterior portion of the oral margin; lateral flank scales are ornamented entirely with thin, diagonal ganoine ridges; posterior margins of the lateral flank scales serrated.

Pygopterus (Agassiz, 1833)

Notes.

Diagnosis from Aldinger (1937; from Westoll, 1934 unpublished), which is based on *P. humboldti*, *P. de geeri*, *P. crecelii* (?), *P. nielseni*, and *P. gleerupi*. We were only able to examine specimens and photographs of *P. humboldti* and *P. nielseni*, therefore our comparisons focus on features I observed in these species.

Features distinguishing from PF 3721 and YPM 18649.

Opercular narrower than subopercular; hyomandibular not pierced by the canal for the truncus hyoideomandibularis facialis; anterior lateral flank scales rhombohedral, taller than they are

wide, and with a large, pointed tip at their anterodorsal corner; lateral flank scale ornamentation consists of diagonal, crooked ridges of ganoine; ventral anterior lateral scales diamond shaped.

***Roslerichthys riomafrensis* (Hamel, 2005)**

Notes.

Diagnosis from Hamel (2005).

Features distinguishing from PF 3721 and YPM 18649.

Frontals without lateral expansions; fused dermopterotic; dermosphenotic with posterior ramus; arched, crescent-shaped maxilla with a pointed dorsal margin; antopercular present; postcleithrum present; dorsal-most branchiostegal ray similar in size to preceding ray, anterior lateral scales taller than wide.

***Santosichthys mafrensis* (Malabarba, 1988)**

Notes.

Diagnosis from Malabarba (1988).

Features distinguishing from PF 3721 and YPM 18649.

Short snout; frontal with single lateral extension on each side; parietals rectangular, lacking an anterior median process; fused dermopterotic; dermosphenotic separated from nasal by “supraorbital”; jugal split into two infraorbital elements (in addition to lacrimal); postcleithrum present; dorsal-most branchiostegal ray is of similar size to preceding ray; scales ornamented with ten antero-posteriorly oriented ridges; posterior margin of scales serrated.

Strelnia (Minich, 2009)

Notes.

Diagnosis from Minikh & Minikh (2009) that was translated into English by Bakaev *et al.* (2020).

Features distinguishing from PF 3721 and YPM 18649.

Postcleithrum present; scales ornamented with thin, curving, and oblique ridges; anterior lateral scales taller than wide; scales with serrated posterior and ventral margins.

Tchekardichthys sharovi (Prokofiev, 2005)

Notes.

Diagnosis from Prokofiev (2005).

Features distinguishing from PF 3721 and YPM 18649.

Frontals lack anterior lateral extensions and do not interlock with temporal bones; fused dermopterotic present; parietals lack anterior median process; anterior lateral scales ornamented with diagonal ridges.

Tholonotus braziliensis (Dunkle & Schaeffer, 1956)

Notes.

Diagnosis from Dunkle & Schaeffer (1956).

Features distinguishing from PF 3721 and YPM 18649.

Snout flat, without pronounced rostrum; frontals with straight lateral margins; two suborbitals; opercular narrower than subopercular; dorsal and anal fin rays ornamented with ganoine striations.

Turfania taoshuyuanensis (Liu & Ma, 1973)

Notes.

Diagnosis from Liu & Ma (1973).

Features distinguishing from PF 3721 and YPM 18649.

Parietals without anterior median process; frontals do not interlock with temporal bones (lack dual lateral extensions); fused dermopterotic; antorbital contributes to the oral margin; anterior lateral scales taller than wide.

Toyemia (Minich & Minich, 1990)

Notes.

We use the diagnosis of this genus from Minikh & Minikh (2009) that was translated into English by Bakaev *et al.* (2020).

Features distinguishing from PF 3721 and YPM 18649.

Fulcral scales absent; scales with prominent anterodorsal corners.

Varialepis bergi (Minich, 1990)

Notes.

Diagnosis from Minikh & Minikh (2009) that was translated into English by Bakaev *et al.* (2020).

Features distinguishing from PF 3721 and YPM 18649.

Lateral margins of frontals with one small lateral expansion; maxilla with narrow postorbital expansion; opercular narrower than subopercular; dorsal-most branchiostegal ray of similar size to preceding ray; nine branchiostegal rays; extremely long-based pelvic fin.

A3 Alterations made to the phylogenetic character matrix of Giles *et al.* (2017)

A3.1 List of taxa removed from the matrix of Giles *et al.* (2017).

Acanthodes bronni, *Cladodoides wildungensis*, *Dialipina salguerioensis*, *Dicksonosteus articus*,
Diplocercides kayseri, *Entelognathus primordialis*, *Eusthenopteron foordi*, *Gogonasus*
andrewsae, *Ligulalepis*, *Meemannia eos*, *Ozarcus mapesae*, *Porolepis* sp. *Psarolepis romeri*,
Styloichthys changae.

A3.2 List of modified character state assignments from Giles *et al.* (2017).

Acipenser brevirostrum

C.110: 2 → -

C.127: 1 → 0

C.138: 0 → 1

C.191: ? → 1

C.192: ? → 0

C.193: ? → 1

C.194: ? → 0

C.195: 0 → -

C.200: 1 → 0

C.201: - → 1

C.202: - → 0

C.204: - → 0

C.208: 0 → 1

Amia calva

C.155: $0 \rightarrow 2$

C.171: $2 \rightarrow 3$

Amphicentrum granulosum

C.71: $1 \rightarrow 0$

C.152: $1 \rightarrow ?$

Atractosteus spatula

C.155: $- \rightarrow 2$

C.171: $2 \rightarrow 3$

C.182: $? \rightarrow 1$

Birgeria groenlandica

C.3: $0 \rightarrow 1$

C.4: $0 \rightarrow -$

C.5: $1 \rightarrow -$

C.7: $0 \rightarrow -$

C.9: $0 \rightarrow -$

C.10: $0 \rightarrow -$

C.11: $1 \rightarrow -$

C.12: $0 \rightarrow -$

C.46: $0 \rightarrow 1$

C.63: $0 \rightarrow 1$

C.64: $- \rightarrow ?$

C.65: $- \rightarrow 1$

C.69: $0 \rightarrow 1$

C.96: $- \rightarrow ?$

C.99: $2 \rightarrow 0$

C.110: $1 \rightarrow ?$

C.155: $? \rightarrow 2$

C.179: $1 \rightarrow ?$

C.200: $1 \rightarrow 0$

C.202: $? \rightarrow 0$

C.204: $? \rightarrow 0$

C.212: $0 \rightarrow ?$

C.236: $- \rightarrow ?$

C.235: $0 \rightarrow ?$

Boreosomus piveteaui

C.183: $1 \rightarrow ?$

C.223: $0 \rightarrow ?$

Chondrosteus acipenseroides

C.27: $1 \rightarrow 0$

C.51: $1 \rightarrow 0$

C.139: $0 \rightarrow ?$

C.140: $0 \rightarrow ?$

Elops hawaiiensis

C.156: $1 \rightarrow 2$

Fouldenia ischiptera

C.42: $? \rightarrow 1$

Fukangichthys longidorsalis

C.214: $0 \rightarrow 1$

Hulettia americana

C.156: $1 \rightarrow 2$

C.171: $1 \rightarrow 2$

Ichthyokentema purbeckensis

C.156: $1 \rightarrow 2$

Lepisosteus osseus

C.156: $1 \rightarrow 2$

C.171: $2 \rightarrow 3$

C.182: $? \rightarrow 1$

Leptolepis bronni

C.152: $1 \rightarrow 0$

C.156: $1 \rightarrow 2$

Luederia kemp

C.182: $? \rightarrow 0$

Luganoia lepidosteoides

C.51: $0 \rightarrow 1$

C.52: $- \rightarrow 0$

Melanecta annae

C.36: $1 \rightarrow ?$

Trawdenia planti

C.182: $? \rightarrow 0$

C.226: $? \rightarrow 1$

C.227: $? \rightarrow 0$

C.229: $? \rightarrow 1$

C.230: $0 \rightarrow 2$

C.232: $? \rightarrow 0$

C.234: $? \rightarrow 1$

Obaichthys decoratus

C.155: - $\rightarrow$ 2

Peltopleurus lissocephalus

C.68: 0 $\rightarrow$ 1

C.231: 1 $\rightarrow$?

C.257: 0 $\rightarrow$ 1

Polypterus bichir

C.151: ? $\rightarrow$ 1

C.152: ? $\rightarrow$ 0

C.153: ? $\rightarrow$ 0

C.154: ? $\rightarrow$ 1

C.155: ? $\rightarrow$ 1

Saurichthys madagascariensis

C.14: 1 $\rightarrow$?

C.20: 0 $\rightarrow$ -

C.21: 0 $\rightarrow$ -

C.61: 0 $\rightarrow$?

C.63: 1 $\rightarrow$?

C.64: 0 $\rightarrow$?

C.100: 0 $\rightarrow$?

C.110: $- \rightarrow 2$

C.111: $1 \rightarrow 0$

C.112: $- \rightarrow 0$

C.113: $- \rightarrow 0$

C.130: $0 \rightarrow ?$

C.135: $? \rightarrow 1$

C.141: $0 \rightarrow -$

C.171: $2 \rightarrow 3$

C.186: $1 \rightarrow ?$

C.232: $0 \rightarrow ?$

C.234: $1 \rightarrow 0$

Semionotus elegans

C.171: $1 \rightarrow ?$

Watsonulus eugnathoides

C.111: $1 \rightarrow 0$

C.155: $- \rightarrow 2$

A3.3 List of parsimony uninformative characters removed from the matrix from Giles *et al.* (2017).

C.1: Large dermal plates.

C.2: Sensory lines.

C.16: Pores for rostral organ.

C.92: Posterior coronoid.

C.125: Palatal opening surrounded by premaxilla, maxilla, dermopalatine and vomer (choana).

C.132: Eye stalk or unfinished area for similar structure.

C.136: Basicranial fenestra.

C.140: Basispterygoid process with vertically oriented component.

C.147: Accessory fenestration in otic capsule.

C.154: Bifurcation of dorsal aorta.

C.159: Epioccipital.

C.170: *[G117] Parasphenoid.

C.187: Cerebellar corpus.

C.198: Enamel.

C.199: Enamel layers.

C.200: Scales on body.

C.207: Lepidotrichia.

C.215: Interhyal.

C.218: Hypohyal.

C.220: Gill arches.

C.244: Pelvic fins.

A4 Full phylogenetic matrix in Nexus format, modified from Giles *et al.* (2017)

#NEXUS

[written Mon May 17 13:14:20 EDT 2021 by Mesquite version 3.61 (build 927) at Jacks-MacBook-Pro-3.local/35.20.140.55]

BEGIN TAXA;

TITLE Taxa;

DIMENSIONS NTAX=74;

TAXLABELS

Acipenser_brevirostrum Aesopichthys_erinaceus Amia_calva
Amphicentrum_granulosum_ Atractosteus_spatula Australosomus_kochi
Beagiascus_pulcherrimus Beishanichthys_brevicaudalis Birgeria_groenlandica
Bobosatrana_groenlandica Boreosomus_piveteau Caturus_furcatus Cheirolepis_canadensis
Cheirolepis_schultzei Cheirolepis_trailli Chondrosteus_acipenseroides
Coccocephalichthys_wildi Cosmoptychius_striatus Cyranorhis_bergeraci Dapedium_LIAS
Dapedium_pholidotum Dipteronotus_ornatus Discoserra_pectinodon Donnrosenia_schaefferi
Dorsetichthys_bechei_ Ebonaqua_ritchei Elops_hawaiiensis Erpetoichthys_calabaricus
Evenkia_eunoptera Fouldenia_ischiptera Fukangichthys_longidorsalis Gogosardina_coatesi
Hiodon_alosoides Howqualepis_rostridens Huletia_americana Ichthyokentema_purbeckensis
Kalops_monophyrum Kansasiella_eatoni_ Kentuckia_deani Lawrenciella_schaefferi
Lepisosteus_osseus Leptolepis_bronni Luederia_kempi Luganoia_lepidosteoides
Macrepistius_arenatus Macrosemimimus_lennieri Macrosemius_rostratus Melanecta_anneae
Trawdenia_planti Mimipiscis_bartrami Mimipiscis_toombsi Moythomasia_durgaringa

Moythomasia_lineata Moythomasia_nitida Obaichthys_decoratus Osorioichthys_marginis
Peltopleurus_lissocephalus Platysomus_superbus Polypterus_bichir Propterus_elongatus
Pteronisculus_stensioi Raynerius_splendens Saurichthys_madagascarensis Scanilepis_dubia
Semionotus_elegans Styracopterus_fulcratus Tanaocrossus_kalliokoskii Tegeolepis_clarki
Tetragonolepis_semicincta Venusichthys_comptus Watsonulus_eugnathoides
Wendyichthys_dicksoni Woodichthys_bearsdeni Concentrilepis_minnekahtaensis
;

END;

BEGIN CHARACTERS;

TITLE 'Matrix in file "Supplementary Data 1.txt";

DIMENSIONS NCHAR=222;

FORMAT DATATYPE = STANDARD RESPECTCASE GAP = - MISSING = ?

SYMBOLS = " 0 1 2 3 4";

CHARSTATELABELS

1 Premaxilla_as_distinct_ossification_ / present_absent_,

2 '[CH 1; G3] Premaxillae, contact at midline' / present absent,

3 Premaxilla_fused_at_midline / absent present,

4 '[G 4] Premaxilla' / Reaches_or_extends_past_anterior_margin_of_orbit

Confined_to_region_anterior_to_orbit,

5 '[G 5] Premaxilla contributes to orbital margin' / absent present,

- 6 Teeth_on_premaxillae / present absent,
- 7 Mobile_premaxilla / absent present,
- 8 Olfactory_nerve_pierces_premaxilla / absent present,
- 9 Nasal_process_of_premaxilla / absent short 'long, reaches skull roof',
- 10 Sensory_canal_on_premaxilla / present_ absent_,
- 11 '[CH 3; G 6] Postrostrals (element[s] immediately anterior to frontals but not in contact with premaxillae)' / present absent,
- 12 '[CH 4; G 7] Single median dermal bone capping snout' / absent present,
- 13 Median_rostral / 'plate-like' 'tube-like',
- 14 '[CH 8; G 10] Nasal bone as single consolidated ossification (i.e. bone(s) carrying supraorbital canal between premaxilla and anterior margin of frontals)' / absent present,
- 15 Contact_of_nasals_on_midline / separated_by_dermal_bones contacting_or_separated_by_gap_unfilled_by_bone,
- 16 Nasal_contributes_to_orbital_margin / absent present,
- 17 '[CH 57; G 11] Mesial margin of (anterior) nasal' / not_notched notched,
- 18 '[CH 6; G12] Posterior nostril in complete communication with orbital fenestra' / absent present,
- 19 '[CH 7; G 13] Posterior nostril ñ contribution to margin by premaxillae' / absent present,
- 20 '[G 14] Tectals (sensu Cloutier & Ahlberg 1996, not counting the posterior tectal of Jarvik)' / absent present,
- 21 '[CH 9; G 15] Pineal foramen' / present absent,

- 22 '[CH 10; G17] Shape of parietals (sarcopterygian postparietals): ' /
'rectangular, with long axis parallel to midline' quadrate,
- 23 '[CH 11; G 18] Relative lengths of frontals and parietals (sarcopterygian parietals and postparietals)' / frontal_shorter_than_parietal
frontal_approximately_equal_to_parietal_ frontal_longer_than_parietal,
- 24 Frontals_broad_posteriorly_and_tapering_anteriorly / absent present,
- 25 '[G 19] Anterior pit line' / absent present,
- 26 '[G 20] Otic canal extends through parietals' / absent present,
- 27 Junction_between_supraorbital_and_infraorbital_canals / absent present,
- 28 Anterior_branch_of_infraorbital_sensory_canal_ / absent present,
- 29 '[G 21] Tabular' / present absent,
- 30 '[CH 64; G 28] Number of bones carrying otic portion of lateral line canal between dermosphenotic and posterior edge of skull roof. ' / 'at least two (i.e. intertemporal and supratemporal)' 'one (i.e. dermopterotic)',
- 31 '[CH 13; G 24] Intertemporal ñ contact with supratemporal anterior to that between frontal and parietal' / absent present,
- 32 '[G 27] Intertemporal contacts nasal' / absent present,
- 33 '[CH 69; G 29] Supratemporal ñ narrow anterolateral flange forming ventral margin of spiracular opening' / absent present,
- 34 Parietal_fused_to_dermopterotic / absent present,
- 35
Bone_carrying_otic_portion_of_lateral_line_canal_extends_past_posterior_margin_of_parietals
/ absent present,

- 36 '[CH 15; G 30] Number of paired extrascapulars' / one_pair two_pairs
three_or_more_pairs,
- 37 '[G 31] Extrascapular reaches lateral edge of skull roof' / absent_present_,
- 38 '[CH 71; G 32] Single median extrascapular' / present absent,
- 39 '[G 33] Extrascapulae contact each other at midline' / absent present,
- 40 '[CH 70; G 34] Medially-directed branch of sensory canal in extrascapulae' /
present absent,
- 41 '[CH 59; G 38] Antorbital bone' / absent present,
- 42 'Tube-like canal bearing anterior arm of antorbital:' / absent present,
- 43 '[CH 61; G 39] Infraorbitals' / one two more_than_two,
- 44 '[CH 16; G 40] Anterior expansion of lacrimal' / absent present,
- 45 '[CH 17; G 41] Notch in anterior margin of jugal' / absent present,
- 46 '[CH 18; G 42] Suborbitals (non-canal bearing ossifications separating jugal
and maxilla)' / absent one two three_or_more,
- 47 '[G 43] Multiple rami of infraorbital canal in jugal' / absent present,
- 48 '[CH 54; G 25] Dermosphenotic with distinct posterior ramus' / absent present,
- 49 '[CH 14; G 26] Dermosphenotic ñ contact with frontals blocked by
intertemporal or dermopterotic' / absent present,
- 50 Supraorbital / absent one_or_two_three_or_more,
- 51 'Anterior-most infraorbital anterior to orbit (i.e. does not contribute to orbital
margin)' / absent present,
- 52 Three_or_more_lachrymals / absent present,

53 Circumorbital_ring_ /

Supraorbitals_do_not_contact_infraorbitals_at_the_anterior_rim_of_the_orbit. 'Supraorbitals contact infraorbitals, closing the orbit.',

54 '[CH 62; G 44] Jugal canal' / absent present,

55 '[CH 53; G 45] Dermohyal' / absent present,

56 '[G 46] Head of dermohyal projects above dorsal margin of operculum' /

absent present,

57 '[G 47] Dermohyal' / fused_to_hyomandibular separate_from_hyomandibular,

58 '[G 49] Complete enclosure of spiracle by bones bearing otic and infraorbital canals' / absent_present_,

59 '[G 57] Maxilla' / absent present,

60 '[G 58] Expanded dorsal lamina of maxilla' / absent_present_,

61 '[G 60] Contribution by maxilla to posterior margin of cheek' / absent present,

62 '[G 61] Sensory canal/pit line associated with maxilla' / absent present,

63 Teeth_on_maxilla / present absent,

64 Mobile_maxilla_in_cheek / absent present,

65 'Peg-like anterior process of maxilla' / absent present,

66 Posterior_maxillary_notch_ / absent present,

67 Supramaxilla / absent one two,

68 '[CH 21; G 63] Course of mandibular canal' /

traces_ventral_margin_of_jaw_along_entire_length_arches_dorsally_in_anterior_half_of_jaw_,

69 '[G 64] Mandibular canal reaches anterior margin of mandible' / present

absent,

- 70 '[G 66] Relative length of dentary' / 'long (constitutes most of the length of the lower jaw)' 'short (constitutes less than half of jaw length)',
- 71 Teeth_on_dentary / present absent,
- 72 '[CH 22; G 67] Dentary with conspicuously reflexed distal tip' / absent_
present_,
- 73 '[G 70] Teeth of outer dental arcade' / several_rows_of_disorganized_teeth_
'two rows, with large teeth lingually and small teeth labially' single_row_of_teeth,
- 74 Jaw_margins_overlain_by_lateral_lamina / absent_present_,
- 75 '[CH 25; G 71] Acrodin caps on teeth' / absent_present_,
- 76 Plicidentine / absent present,
- 77 '[CH 27; G 73] Ossification of mentomeckelian region:' / present_absent_,
- 78 '[CH 23; G 76] Number of infradentaries' / more_than_two_ 'two (angular and surangular)' 'one (angular only)',
- 79 '[G 74] Coronoids (sensu stricto, excluding parasymphysial tooth whorl or anterior coronoid)' / present_absent_,
- 80 '[G 75] Number of coronoids' / five___ four_or_more three two one,
- 81 '[G 78] Coronoid process of lower jaw' / absent present,
- 82 Coronoid_process_contributed_to_by / prearticular_only surangular_only
dentary_plus_postdentary_bones angular_only,
- 83 Leptolepid_notch / absent present,
- 84 Symplectic_involvement_in_jaw_joint / absent present,
- 85 Palatal_bite / absent_present_,

86 '[G 82] Palatal articulation with basipterygoid process' /
 articulation_not_obvious_via_basipterygoid_fenestra 'via metapterygoid process/notch',

87 Palatoquadrate_ossifications / comineralized separate_ossification_centers,

88 Lateral_process_of_ectopterygoid / absent_present_,

89 Palatoquadrate_symphysis_hf30_ / absent present,

90 Dorsal_margin_of_palate / high_posterior_extension flat_dorsal_margin,

91 Metapterygoid_posterior_to_quadrate / absent present,

92 '[G 81] Number of dermopalatines' / multiple single,

93 Prearticular / present absent,

94 Vomers / paired single,

95 Vomer_sutured_to_parasphenoid / absent present,

96 '[CH 19; G 50] Accessory operculum' / _absent present_,

97 '[CH 67; G 51] Operculum - relative size ' /
 at_least_twice_as_high_as_suboperculum subequal smaller_than_suboperculum,

98 Subopercle / present absent,

99 '[CH 68; G 52] Anterodorsal process of suboperculum' / absent_present_,

100 Anteroventral_process_of_suboperculum / absent present,

101 '[G 62] Number of cheek bones bearing pre-opercular canal posterior to jugal'
 / one multiple series_of_small_ossicles,

102 Preoperculum_orientation / pronounced_dorsal_limb_vertical_
 pronounced_ventral_limb_,

- 103 Junction_between_preopercular_and_more_anterior_cheek_bones /
'Infraorbitals (including jugal) or suborbitals suture with or abut preopercular' 'Infraorbitals
(including jugals) and suborbitals broadly overlap preopercular',
- 104 Posterior_border_of_preoperculum_notched_ventrally_ / absent present,
- 105 Interopercle / absent present,
- 106 '[CH 72; G 53] Branchiostegal rays - dorsal-most in series' /
of_similar_depth_to_adjacent_branchiostegal_ray_deeper_than_adjacent_branchiostegal_ray__,
- 107 Lateral_gulars / present absent,
- 108 '[CH 20; G 54] Lateral gulars' /
extending_most_of_the_length_of_the_lower_jaw_'restricted to the anterior third of the lower
jaw (no longer than the width of three branchiostegals) ',
- 109 '[G 55] Median gular ' / absent_present_,
- 110 '[G 86] Interorbital septum' / broad_narrow_,
- 111 Optic_foramen / dorsally_positioned_'ventrally positioned (i.e. abuts
parasphenoid) ',
- 112 '[G 87] Pronounced median anterior crista on dorsal surface of braincase' /
absent_present_,
- 113 '[G 88] Expanded anterior dorsal fontanelle ' / absent present,
- 114 '[G 91] Roof of posterior myodome perforated by palatine branch of facial
nerve (VII)' / absent_present_,
- 115 '[G 92] Foramen for abducens nerve (VI) dorsally positioned (level with optic
foramen (II))' / absent_present_,
- 116 '[G 93] Anterodorsal myodome' / paired_single_absent,

117 '[G 94] Posterior myodome' / absent paired median,

118 '[G 98] Endoskeletal spiracular canal' / open
partial_closure_of_spiracular_bar complete_enclosure_in_canal_,

119 '[G 100] Basipterygoid process' / present_absent_,

120 '[G 103] Dermal component to basipterygoid process' / absent_present_,

121 Hyoid_facet / directed_posteroventrally horizontal,

122 '[G 104] Fossa bridgei' / absent_present_,

123 '[G 106] Vestibular fontanelle' / absent_present_,

124 '[G 107] Ventral cranial fissure and vestibular fontanelle' /
separated_by_bridge_of_bone_confluent_,

125 '[G 109] Otoccipital fissure' / absent_present_,

126 '[G 110] Median projection overhanging posterior part of posterior dorsal
fontanelle' / absent_present_,

127 '[G 111] Median projection overhanging anterior part of posterior dorsal
fontanelle' / absent_present_,

128 '[G 112] Dorsal aorta' / open_in_groove_canal_notched_posteriorly
completely_enclosed_in_canal_,

129 '[G 113] Dorsal aorta pierced by canal/s for exit of eff.a.2' / absent present,

130 '[G 114] Dorsal aorta pierced by canal/s for exit of eff.a.1' / absent present,

131 '[G 116] Bifurcation of dorsal aorta into lateral dorsal aortae' / open_
enclosed_in_canal_,

132 Braincase_ossifications_differentiated / absent present,

133 Basisphenoid / present absent_or_very_reduced,

134 'Opisthotic-pterotic relationship' / opisthotic_larger_than_subotic
opisthotic_and_pterotic_equal_in_size,

135 Forward_extension_of_the_exoccipital_around_the_vagus_nerve / absent
present,

136 Sphenotic_with_small_dermal_component / absent present,

137 Pterotic / present absent,

138 Opisthotic_bone / present absent,

139 Intercalar / present absent,

140 Supraoccipital_bone / absent present,

141 Membranous_outgrowth_of_intercalar / absent_present_,

142 'Post-temporal fossa' / absent present,

143 'Sub-temporal fossa' / absent present,

144 Dilator_fossa / absent present,

145 '[G 118] Parasphenoid' / 'terminates at/anterior to ventral otic fissure '
extends_across_ventral_otic_fissure_extends_to_basioccipital_,

146 '[CH 28; G 120] Ascending process of the parasphenoid' / absent_present,

147 '[CH 29; G 121] Parasphenoid with multifid anterior margin' / absent_
present_,

148 '[G 124] Buccohypophyseal canal pierces parasphenoid' / present_absent_,

149 Parasphenoid_teeth / small large absent,

150 Parasphenoid_pierced_by_internal_carotid_artery / absent present,

151 Parasphenoid_pierced_by_efferent_pseudobranchial_artery / absent present,

152 Aortic_notch_in_parasphenoid / absent_present_,

153 Parabasal_canal_ / present absent,

154 '[G 125] Anterolaterally divergent olfactory tracts' / absent_present_,

155 '[G 126] Elongate olfactory tract(s)' / absent_present_,

156 '[G 127] Olfactory nerves carried in a single tract' / present_absent_,

157 '[G 128] Hypophyseal chamber' / projects_posteroventrally_
projects_ventrally_or_anteroventrally,

158 '[G 129] Optic lobes' / narrower_than_cerebellum_
same_width_or_wider_than_cerebellum_,

159 Optic_lobes / smaller_than_telencephalon larger_than_telencephalon,

160 '[G 130] Optic tectum divided into bilateral halves' / absent_present_,

161 Cerebellar_corpus / divided_bilaterally undivided_,

162 Position_of_cerebellar_corpus / _enters_fourth_ventricle
arches_above_fourth_ventricle,

163 Cerebellar_corpus_with_median_anteriorly_projecting_portion / absent
present,

164 '[G 132] Horizontal semicircular canal' /
joins_vestibular_region_dorsal_to_ampulla_for_the_posterior_semicircular_canal_
joins_vestibular_region_level_with_ampulla_for_the_posterior_semicircular_canal_,

165 '[G 133] Junction between ampulla of posterior semicircular canal and cranial
cavity' / separated_by_short_length_of_canal__confluent_,

166 '[G 134] Crus commune of anterior and posterior semicircular canal' /
dorsal_to_endocranial_roof_ventral_to_endocranial_roof_,

167 '[G 135] Lateral cranial canal' / absent_present_,

168 Lateral_cranial_canal_connects_to_cranial_cavity_anteriorly / absent
present,

169 '[CH 30 in part; G 147] Enameloid on dermal bones and scales' / absent_
present_,

170 '[G 148] Extensive pore-canal network' / absent present_,

171 '[G 151] Scales' / micromeric macromeric,

172 '[CH 32 in part; G 152] Scales with ěpeg and socket articulation"' / absent_
present_,

173 '[CH 33; G 154] Anterodorsal process on scale' / absent_ present_,

174 '[CH 35; G 155] Scales with well developed pores on surface' / absent_
present_,

175 Small_scales_below_dorsal_fin / absent present,

176 '[CH 37; G 159] Fringing fulcra' / absent_ present_,

177 '[G 140] Perforate hyomandibula' / absent_ present_,

178 '[G 141] Opercular process' / absent present,

179 '[G 136] Ceratohyal' / single_ossification two_ossifications_,

180 '[G 137] Anterior ossification of ceratohyal' / no_medial_constriction 'medial
constriction (hourglass-shaped)',

181 '[G 138] Anterior ceratohyal' / no_groove_
groove_for_afferent_hyoidean_artery_,

182 Symplectic / absent present,

183 Symplectic_shape_c68 / 'tube/splint like' hatchet 'l-shaped',

184 '[G 143] Basihyal' / absent present,

185 Number_of_ceratobranchials / five_four_,
 186 Number_of_hypobranchials / three four,
 187 Uncinate_processes_on_epibranchials / absent present,
 188 Urohyal_formed_as_a_tendon_bone_of_the_sternohyoideus_muscle / absent
 present,
 189 '[CH 39; G 162] Presupracleithrum' / absent_present_,
 190 Presupracleithrum_ / single multiple,
 191 Medial_wing_on_cleithrum / absent present,
 192 '[G 161] Anocleithrum' / bone_developed_as_postcleithrum
 bone_developed_as_anocleithrum_sensu_stricto bone_absent,
 193 Clavicle / present_as_a_broad_plate much_reduced_or_absent_,
 194 Serrated_organ / absent present,
 195 Interclavicle / present absent,
 196 '[CH 40; G 167] Triradiate scapulocoracoid' / absent_present_,
 197 '[G 163] Perforate propterygium' / absent_present_,
 198 '[CH 41; G 164] Anterior rays embrace propterygium' / absent_present_
 fused,
 199 Propterygium_fused_to_first_ray / absent present,
 200 '[CH 43; G 168] Pectoral fin endoskeleton' / 'extends far beyond body wall
 (fins lobate) ' 'barely extends beyond body wall (fins not lobate) ',
 201 '[G 166] Pectoral fin radials' / unjointed_jointed_,
 202 '[CH 44; G 171] Pectoral fin-ray segmentation' /
 roughly_even_segmentation_to_fin_base_

proximal_segments_elongate_with_terminal_segmentation_

no_significant_segmentation_on_pectoral_fin_

terminal_segments_elongate_with_proximal_segmentation,

203 '[CH 45; G 174] Pelvic fin insertion' / 'shorter than fin depth (short based) '
'longer than fin depth (long based) ',

204 '[G 177] Basal scutes on fins' / absent present,

205 '[CH 48; G 178] Dorsal scutes anterior to dorsal fin' / absent_ 'few limited to
region immediately anterior to fin (basal fulcra only)' 'many, extending to posterior of skull roof
(complete set of dorsal ridge scales)',

206 '[CH 49; G 179] Ventral scutes between hypochordal lobe of caudal fin and
anal fin' / absent_ present_,

207 '[CH 50; G 180] Ventral scutes anterior to anal fin' / absent_ present_,

208 '[CH 51; G 182] Relative positions of anal and (second) dorsal fin' /
anal_shifted_anteriorly_relative_to_dorsal_fins_opposite_one_another_
anal_shifted_posteriorly_relative_to_dorsal,

209 'Median fins (except caudal fin)' / rays_more_numerous_than_radials_
rays_andradials_equal,

210 Proximal_and_middle_radials_of_dorsal_fin /
proximal_and_middle_radials_of_similar_size proximal_radials_substantially_enlarged,

211 Posteriormost_proximal_radial_of_dorsal_fin / enlarged_plate
smaller_than_more_anterior_radials,

212 '[CH 46; G 175] Epichordal lobe of caudal fin' / present_ absent_,

213 '[CH 47; G 176] Fulcra along dorsal ridge of caudal fin' / absent_ present_,

- 214 Caudal_fin_geometry / long_chordal_lobe short_chordal_lobe,
 215 Posterior_margin_of_caudal_fin / forked unforked,
 216 'Diplospondyly in mid-caudal region' / absent present,
 217 Median_neural_spines_in_caudal_region / absent present,
 218 Uroneural / absent present,
 219 Division_of_hypurals_into_dorsal_and_ventral_groups / absent present,
 220 Number_of_caudal_lepidotrichs_borne_per_hypural / multiple single,
 221 Opistocoelous_vertebrae / _absent present_,
 222 Ossified_ribs / present absent ;

MATRIX

Acipenser_brevirostrum 1-----00?000-1-?1000-01011---00110-0??1-001001--
 000--00-----010-0-?0-1-0-0-001011-11100-0002---011-00000-?2021-010-0--0---10?00?010-
 00021112001110100001011010---100001001100-000000-
 00000101?10001211200011000100001
 Aesopichthys_erinaceus 01-000000111010111001120?00010110-111110101--
 1101000-
 0111010000000000000020???2??120????????????010010100010?1????????2??????1?????00---
 -----????????????????????????????11100111????????10?00?????0?0002102???0100??????
 Amia_calva 01-100012010011000001120101011---0001110110000110000-
 10--010000111100000201?11011201001?0100001000100210101-1?000111221-110-0--0--211-
 011100110131110001000111011110010-0010--?01110011001100-
 00111001010100000211110111100100

Amphicentrum_granulosum_ 000101000?1101011?001020?00011---01?1??00-
1100000000-00--11100000000?010-1-??20?0-0-1200010????020010100000??1??????2?010?0-
0??2?01????0?????1?01100?001????????????????????10??0?????0-
??0????????????????????0?????????

Atractosteus_spatula 000100-12010111000001120101111---0121110112--3-
101111011101001001000000010011102120000100110001010100210011-01000-022201110-0-
-0---11-110110-101311100010??1????????????101100011111012001100-
1011100100010000011111110100110

Australosomus_kochi 1?????-??-??0?0?????1020100011---0101100??0-001--0---
010111100000001000020??011-0-0-0200000?000010000100000?11001102221-
?111100200001-----0?10101200000111110???1110-??111001110010-000100-
0000110?0001000000010??100100001

Beigiascus_pulcherrimus 000000000111010111001120100010110-0210-
?101003111000-?10??111?00000?0000101?????-
0?????????????11000000001011??
???111001?????????????11?00??????1?20011?1????100???????

Beishanichthys_brevicaudalis 00?01000?011010111001120?0??11---00111?00-
100210020?00101?1100000000?000201??2??1?0?????????????0100000000000?????????????
??1110?0?????0-?????0-
?0?????????1000002???1011???????

Birgeria_groenlandica 1--1-0----11010110001?20100011---
0100110102003010200001?1011100000000000101?01??110?001000000--

0?000000000011100?10?22?-01??1--??210--0??-
00021012001?????????????0??10000100?0?0-0?0?00-020010??-00300000200011000100001
Bobosatrana_groenlandica 1----1----00010111-01120?00{0 1}11---0?001100-
2100010000-00--010001100000010-0-??2??0-?-0??0?0????0-1--11000-?-
010??????0????????????1??????????21?2????????????????????11?01?10100-?????0-
001??????000101210?1100?????1
Boreosomus_piveteaui 0010110000110111110?1020100111---01100-00-
2003100000-11010111100000?000010?001030-0-
020000101000100001000101110101?1220101101{0 1}{0 1}211000-----
000010101000010?111100??110??1110010111?0-?????0-
020011??0?100010200?01000000?01
Caturus_furcatus 00010001?110111000001120001101---
0001110112102?01200110--0100001111?00020??01031201021001?001000100210?11-
110?????21-1?0-
0?????10?00110011??211100000????????????11?????011110011???1?100??1?0?????0000
021111110?100000
Cheirolepis_canadensis 0?01-00000000000?01{0 1}010?000100-0-1001100-
1010010000-010?111110000010000100??10?0-
0???????????1000000000000????????????????????????????00?????????????????
??000?01????????????0-?00???00010101010??0101??????
Cheirolepis_schultzei 000000000?0000000?011020?00?11--0010111?0-
1010010000-

010?1111?0000010000?00?????0?????????0??100000000000?1?????????????????????
?????????????0?????????????????????000??1?????????????????00?????0?0?0???????????????????

Cheirolepis_trailli 00001000000000001001{0 1}010100010000-1001000-
1010010000-01101111?0000010000100??1010-0-
01000000000100000000000010??0???10000101?00---00-----
000000000000111????????????11011?0100???0-????10000000010000101110???0100??00??1

Chondrosteus_acipenseroides 1-----1??????-?1020????11---0?2?0-
???0?0?00?????0--00-----?0010-0-?0?1-??0-0???1??10??02000??-
??0?????????????0?????????????????????211?20011?????????????-----?0000100?????0-
?0?????????2?0000???110??0000?1

Coccocephalichthys_wildi ???0?????11?101010?1020100111---00110-
0112000?0010?01?0?0111?00?00??000101??1??110?010?00000?0?101?00000????10??0?0220
00?101??210100-----
0?0010100000????????????????1?????1???0???????0?????????????????????????????

Cosmoptychius_striatus 0??1000?00?101011100112??000011---
?0?1??0101002100000-
010?01110000001?00010??2?????020???????10000000001?111???????01??111??1111?0?
00???????01?1?0000????????????1???111001?????????????0-
?000???0111101002???1100???0??

Cyranorhis_bergeraci 1-----11010111-01120100010100-
111110101002110000-
010101110000000?00020?????????0??20???????00000000000011?????????????????????

????????????????????????????????111001?1????????10?0?1????1?1001012???0100?????
??

Dapedium_LIAS 001100001?110110?0001---0-??-----1-11110102--3-0-
1000?0--0100001101??10020?0?0?1?0?????0?00?010100210101-110?01?12?01110-
0??2???0-----

11121?????1?011111????11011?11?0?1?1????????10?01?1?????20????????1?1??????0

Dapedium_pholidotum 001100001111011010001---?-01-----1-21110102--3-0-
200010--0100001?010010020???1????0?0?0?????0?1010000210101-
1??????????1?????????0-----

????????????????????????????11?001????????????10?01?1??????0021121??1111???????

Dipteronotus_ornatus 0??10000??11010010?1120?000?1---?0?????1?0-00???1--
1?????10000000000000201???1???0?0?1?????????100001000?1?????????????1?????????????
0?????????1101200????????????????????1?0?1?????????????2?????????002?12????110?100
???

Discoserra_pectinodon 000010000101010111001120?00001---00211000-
2003001100000--010000?0000000020???20?0-0-0?1???0?0?0-1--120000010?0???022?-110-
???????0-----1??21?0?0????????????????????11?0111?0000-
?????11??1?1???00?0020120001111?10???1

Donnrosenia_schaefferi 0?001?000011010111000010100010100-10111?0-
???0?10000-0?0?1111?000001100010???1?0-0-
???????????1001000?000001???
111001?????0-????????00?????1?1101011????1?????????

Dorsetichthys_bechei_ 0?0100100?1101010000112110?111---
0001100102101110100000--?1010011020000020???1???2100?1?0???11?0100002101??-
11??1000220111101??0???1010000011111210001111?10?11????11111??11?0??11???1???1?
0-?0??????10?2000002???11101111000

Ebenaqua_ritchei 1----1----11010101-01120?00011---00101100-2?00000000-
00--0100011?000?010-0-??20?0-0?0?????????0000011000-0-
0?????????1??11?00???01????????11?21?
???????2002111??11101???????

Elops_hawaiensis 01-100102111010000001121001111---
0001110102100000100010--1101001102000000010021-120002100101111000010210101-
110?????200-110-0--0---21?100101111120010101????????????????0-0000-001111110100010-
00101001110000000211111100100000

Erpetoichthys_calabaricus 01-11000001000000100102011101-----211100-
1003000000-010101101000000000020?00203100-001101000100-1--00000-0000100-00011-
001-0--200110??0?00000002101000101010101000011?010111000010000-011010-
00001???0??-????-?111?11????1?0

Evenkia_eunoptera 0?0010000000?0?01?00112001111-----
?1?00?2002?002000011?0110000000???0?20???1????0????????????1100100000000?????????
??11?010????????????10?????????0?00
00?12???100???????

Fouldenia_ischiptera 000101000?1101010?001110????11---010111?0-
1000?00000-?101?111?000000?01021???20?0-

0?1?0???????01001000000011????????????????????????????????????0?????????????
???111001????????????0-?00?0??10000002111???0100???????

Fukangichthys_longidorsalis 000?1000??1101?111?01120?01011---
011011?????0310020?0?1010111000000?000201001??100?001101000100100000000000101?
???????1????????????????????????100000?0???????????????????11?001010010-
?1?1???00?????????1000002???011???????

Gogosardina_coatesi 000010000001010111100010100?1010?-1?????0-
??000?0?0??0100?11110000001000101?020?0-0-
010?00000?00101000000000?0????????00???????100?0????????????00?0000?????????????
???111001100??0-?0????-00001????1?1002102????10??000??0

Hiodon_alosoides 000100100111011000001120100111---10011000-
2000000000-00---10010110001000200?021-1200001?0101110000000210001-
0??0011?2100110-0--0---11-10010111?1210110010?????????1110-0010-0001111010100110-
00101001110110000111110100111000

Howqualepis_rostridens 01-010000011010111100120100010100-10111?0-
1100010000-01001111?000000000110??110?0-0-
0100000000000010000000001????????100??10???0---?0??-
????????011000000?????????????????111001?0???0-
?????1000000??10001101111???0100?000???

Hulettia_americana 000100001111110000001?20100011---0001110102-
03100200000--01000011000?00?20???10?120002100100?1?000100210101-0?????????2011??-
1??0---200?000000?0?211011100?????????????????1?11?00111110100??100-
?0101???????00101211110101000000

Ichthyokentema_purbeckensis 01-100100111011010001020100011---
0001100102101101200010--01000011010000020??0204121002100001?11000100210101-
110??10?2?01110-0--0--?2111?0001111121001100????????????????101110?1??10110?????0-
001011???10?00101?1??1110?11??00

Kalops_monophyrum 00010000?111010111001121100011---00010-
0102003000200001010111000000?000010???20???0????????????00001000001011???????????1
????????????0?-----
????1????????????????????????111001?0?????????10?00?1???0?0002112???0100???????

Kansasiella_eatoni_ ??????????????????0020100?11---
0?????????????0?????????????????????????????????0?1?????????0?????000?????101111122
0101101101111100?00000?000010100000010011110?11110???????????11?????????????????
???????????????????????

Kentuckia_deani 0?001000000101011100{0 1}02010001?-?-?1011100-
??000?000?-?10??111?00?000?0001???02????0-
010?00000??100000000000111001?1112010111100110000-----
00001?0000?0010011?00?111101????0??11???0-????????????????????????????????????

Lawrenciella_schaefferi
??
???????0???????????????101110022010110111110100-----
00001?100000010011?10011110??

Lepisosteus_osseus 000100-12010101010001020101111---0021110112-
031001111011001000001000100010011103120000100110001010100210011-
0?0????22201111-0--0---21-110110-

001301100010001110111101110111110011111012001100-

1011100100010000001111110100110

Leptolepis_bronni 0001001011110100?001121100111---00010-00-2-

01110100000--?1000111020000020???2??121?0210010?11?010000210101-110??10?2?011?0-

0--201?20?00000111??2101?1111??1?????????11?????00111111?0???10-

?0111???1?0100000211011100111000

Luederia_kempi

0????0??0?????????1??????????????

??????0??????????????10?1???2201011010?211100--?-----

0??11???000??10??

Luganoia_lepidosteoides 001100001011-1000?01--11-0001---1-1111-0-

100200120?0?101010010?00000000201?02????0?0?1?01???11010000200001????????????????

????????????0?????????0????????????????????????1110??1101????????0-

?21?001?1010000021??1111???????

Macrepistius_arenatus 0??10001??10???0?0?01120????10000-10111?112-

03?012001?0--?100?01?0???00020???1??1?0? ??????????0?00010021010???10??1012?011?0-

0?????101010000111121?121001????????????????101??0?1???????-???0-

?1????????????????????1110???????

Macrosemimimus_lennieri 0001000???111110?0001120?0???1---00010-?112-

?10012111?0--0100?01100??00020???10???000?10000???00010021010???0?????2201?0-

0??0--?11-101110-11?2110?0?10????????????10??11?001????10?????0-

?01?1???1??000002???????????????

Macrosemius_rostratus 000100012110?1?00?00112100?111---0001101112--0-
00001-?0--01010011000?00020??0104120?001?00000010001002-1101-0???????2?011?0-
0?????11-10011?-1?0211??00???????????????1???11?0?11111?????100-
1?101000??0100?10211111110?00?00

Melanecta_anneae 01-01000?01101011100102?10001?---0?????0-
1?0?0?0000-
0?0?1111?00000?0000?0???????0???????????0100000000?????????????????????????
????????????????????????????????0??0?1???????????0-?00?????1?1101112???1100??????

Trawdenia_planti 0?001?00??110101110?112010??11---001?1??0-?0?1?{0
1}0000-
?1?10111??0000?0000?0???????0???????????010000000010??0????1????????????????0???
????????????????001110001?1?0??111001??011???????101200?101???1001111???0000???
???

Mimipiscis_bartrami 000010000001010111000010100110001-1011100-
1000010000-01001111100000010001010020?0-0-
010000000000101000000000110?000?010000101??200000-----0000010000-
0?11?????????1???111001??0010-10100100000??1?01010021120?0?1000000?01

Mimipiscis_toombsi 000010000011010111100020100110001-1011100-
1000010000-0100111110000001000101002010-0-
010000000000101000000000110?000001000010100200{0 1}00-----0000010000-01110010--
-1001010111001100010-101001000000111010?0021110?011000000?01

Moythomasia_durgaringa 01-01000?011010111000120100110010-110??10-
1110011000-0100111110000000000101001010-0-

010000000000101000000100110?011011000010100100000-----

000011000000??1?????????1?1?111101100010-

101001000000111?1?10021110??11?00100?01

Moythomasia_lineata 00001100011101011100002010??10000-1101?10-

1000110000-010?1111?000001000010???1??0-

0????????????0001000?001001??

101110?1????????????10?00??11??100002102???11?0???????

Moythomasia_nitida 000110000111010111000020100010000-1111110-

1102010000-

01001111?000001000010???1????0?????????????11000000001011????????????????????

?????????????????????????????????1?1111?1????????????10?00?????01?1002111???1100?????

?0

Obaichthys_decoratus 0?01000?2010???0???01020?0?11---001110???2--3-

0?1111?0--?100001100?00?2010110?12000?100?1?001000100210101-0?????????01??0-0??0-

-21?-11?110-???20110??1?????????????????1110011?11012???1?0-

10011?0?0001000001?????1?01?0?10

Osorioichthys_marginis 00001000?01101011010101110?010000-?101000-

1001010000-

010?1111?00?001000010???1?????????????????01000000001001?0????0?????????????????

?????????????????11?????????????111001?????????????0-

?00?0?110001?02?????????????????

Peltopleurus_lissocephalus 0?0011000111010110001120100011---00010-00-

10020002001010?01100100000?000201???0???0?0?????????010000100001?????????????????

?????????0????????????????????????????????1?0?1???????-??0-

02??1???1?1000012???1010???????

Platysomus_superbus 1--10?---01010111-01120100011---00111100-
1000000000-00--

01110?0000000?02???2???0??????????0100001000001????????01?????????????????
???2100?001????????????????1110?1??????????0-?00?????0?0000002???110???????

Polypterus_bichir 00011000001000000100102011101-----211100-10030000---
010101101000000000020100203100-001101000100001000000-00001??-00011-001-
0??100?10??0?000000021010001?1010101000?????10111000010000-011010-
00001000000000000201110110100100

Propterus_elongatus 000100???11011100?001021101011---00????1112--0-
002010?0--01010011000?00020???????0?0?1?0?0?0?0001002-1001-
0?????????01???????????????0????????????????????????????????11???1??11?0?????0-
0?0110?0?0100???2?111110?1??100

Pteronisculus_stensioi 0000100001110101110?1120100010---
0111100102002100000-010?0?111000001000010?001020-0-
020000000001100000000001110?111022010111101210100-----
000010100000111111110011110??111001110110-
1010010000011?101?000111200001000000?01

Raynerius_splendens ??????????????1????001?1000100??-
?111?0????1001??????1101111?0000?000001010010?0-0-
010000000???00000001000011000???11000010100100000-----
00000?000000???0010???100101?1111??100010-10100100?000????????????????????

Saurichthys_madagascarensis 1--000----1?-101---0?02100??11---0?0011?0-
?0?1?00100?0???01110000000?000201?01???0?00?0000?000200000000-1-010?0??1221-
?10-0?????0-----??031?00??0011011??????????100001??????????0-
020?10?100010021110111111??0??1

Scanilepis_dubia 0??010????11?1?0???010001???11---01111????1?0310-
20?0?10?0111?00?00?00?20???????0????????????1100?00000000????????????????????
????????????????????????????????????10111010????????????0-
????????????00???2???0????????

Semionotus_elegans 00010001211-11101000112000?111---0001110112-
010002111?0--0100000101000002010?10?12000?1?0?00001000100210101-
0???????????1???????????1?1?111?-??1?1100001????????????????101???0111?1010101100-
10111000??0100201211111110100100

Styracopterus_fulcratus 1--101----1101010?-01120????11---010111?0-1000?00000-
?101?111?000000?010211??20?0-
0?1?????????02001000001011????????????????????????????????0?????????????
???111001?1?????????0-?00?0???0?2002112???0100???????

Tanaocrossus_kalliokoskii
????????????????????????????1????1????????????????????11?????0????????????????
????????100???00??1?
010????????????????????0???????1?11??????

Tegeolepis_clarki 000000?0?0110101???01010?00010000-
1101??11?000010000-

0????111?00?000?00110??11????0????????????1??0000?00011?????????????????????
????????100?00?????????????????011??000?????????????????0?1?00101????1?????????0

Tetragonolepis_semicincta 000100001011010010001020?00111---
0001100102103001100000--01000011000?00020???104??000?100101?1?000100210101-
110?????2011?0-0?????0?????????????1??211?0?????????????????11?00111?1011?????0-
00101?1101010020121111111?100000

Venusichthys_comptus 000100000111010110001121?0??11---00011?0102-
03000000000--0101000000000020???????0?0?????????000001110001-
1??111001?????????????0-
?01?1????1?1000002???1100???????

Watsonulus_eugnathoides 00000011111-110000001120000111---
0001010112100010100100--01010011110000020??01021201021?01010?1010100110110-
11??011122011?111--0--
21010100000111210100000????????????10??1??0??11101100????10020?11???1?2000002?-
?1110??00?00

Wendyichthys_dicksoni 1-----1101011?-01120100010110-
111110111102111000-110?0111?000000000020??0???0-
0??2?????????00000000001011???????2??0??1?1?????????????????01?????????????????
???1??101????????????{0 1}-?00?1????1?0001012???1100???????

Woodichthys_bearsdeni 00001000?011010111001120100010100-1111?00-
1000100000-010?1111?000000000010???1??0-
0?000?0000???01000000000010?????????010?101??110100-----
0000100?0000????????????????111101?????????????0-?00???1101?1001112???1100???????

```

Concentrilepis_minnekahtaensis 01010?0?0?1101011??01021????1011?-
?11???102003?01010-
?100?111?00000??0?1???0010?110???01?10?0??00000?0?001011????????????????????
????????????????????????????????11101110?????????10?2001??20?1101?1120??1110????
??

;

END;

BEGIN ASSUMPTIONS;

    OPTIONS DEFTYPE = UNORD POLYTCOUNT = MINSTEPS;

    TYPESET * UNTITLED  = unord: 1- 77 79 81- 127 129- 144 146- 201 203- 204 206-
207 209- 222, ord: 78 80 128 145 202-208\3;

    TYPESET default  = unord: 1- 77 79 81- 127 129- 144 146- 201 203- 204 206- 207 209- 222,
ord: 78 80 128 145 202-208\3;

END;

BEGIN NOTES;

    TEXT TAXON = 1 TEXT = Histo?;

    TEXT TAXON = 3 TEXT = Only_dermal_skull_coded_;

    TEXT TAXON = 28 TEXT = 'Dpt/it/stBraincaseBrainLabyrinthHistologyFins';

```

TEXT TAXON = 31 TEXT = Code_from_scan;

TEXT TAXON = 41 TEXT = Histology;

TEXT TAXON = 59 TEXT = 'Dpt/it/stAortaLabyrinthHistology';

TEXT CHARACTER = 1 TEXT = 'Hurley et al. 2007; Xu et al. 2014. Typically, the premaxilla is a short, paired or median bone that contributes to the orbital margin anterior to the maxilla. However, considerable variation is present, and we have attempted to consistently code this variation as laid out here and in the following character descriptions. A premaxilla may be completely absent (e.g. *Acipenser*, *Cyranorhis*) or dorsally expanded into a midline bone (possibly fused with the rostral; e.g. *Bobasatrania*, *Styracopterus*). These two latter states are coded as ?1? here. ';

TEXT TAXON = 21 CHARACTER = 1 TEXT = 'Typically, the premaxilla i ';

TEXT CHARACTER = 2 TEXT = 'Cloutier & Ahlberg, 1996; Taverne, 1997; SchultzeCloutier & Ahlberg, 1996; Taverne, 1997; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Choo, 2011. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*). The premaxillae in *Mansfieldiscus* (Long, 1988) are thought to have contacted at the midline but have not been observed, and so the coding for this taxon is conservatively changed from "0" to 1. The snout is not preserved in *Novagonatodus* (Long, 1988; Holland et al., 2007), so the coding is changed from 1 to 1. Although a median dentigerous "rostral" is

preserved in *Luederia* (Schaeffer & Dalquest, 1978), the lack of associated bones means its identity is uncertain, and it may well represent fused premaxillae. This taxon is conservatively coded 0. The premaxilla is absent in *Wendichthys* (Lund & Poplin, 1997), so the coding is revised from "0" to "-". The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT TAXON = 9 CHARACTER = 2 TEXT = fused_into_one_;

TEXT TAXON = 20 CHARACTER = 2 TEXT = fused;

TEXT TAXON = 21 CHARACTER = 2 TEXT = fused;

TEXT CHARACTER = 3 TEXT = 'Xu et al., 2012; Xu et al., 2015; Xu & Zhao, 2016. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*).';

TEXT CHARACTER = 4 TEXT = 'Friedman, 2007; Giles et al., 2015b. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*) and in taxa where the premaxillae do not contact at the midline. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 5 TEXT = 'Cloutier & Ahlberg, 1996; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. Coded as inapplicable in taxa lacking any ossification in the

position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*), where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*), and where the premaxilla is restricted anterior to the orbit. The coding for *Moythomasia lineata* is revised to "1" (Choo, 2015).';

TEXT CHARACTER = 6 TEXT = 'Cloutier & Arratia 2004, Xu et al. 2014. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*).';

TEXT CHARACTER = 7 TEXT = 'Arratia 1999; Cavin & Suteethorn 2006; Hurley et al. 2007. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*).';

TEXT CHARACTER = 8 TEXT = 'Grande 2010; Xu et al., 2015; Xu & Shen, 2015; Xu & Zhao, 2016. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*).';

TEXT CHARACTER = 9 TEXT = 'Gardiner & Schaeffer 1989; Gardiner et al. 1996; Gardiner et al. 2005; Cavin & Suteethorn 2006; Hurley et al. 2007; Grande 2010; Lopez-Arbarello 2011; Xu & Wu 2012; Xu et al. 2014; Xu & Shen, 2015; Xu & Zhao, 2016 Xu & Zhao,

2015; Xu & Zhao, 2015. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*).';

TEXT CHARACTER = 10 TEXT = 'New character. Coded as inapplicable in taxa lacking any ossification in the position typically occupied by the premaxilla (e.g. *Acipenser*, *Cyranorhis*) and where the premaxilla appears fused with the rostral (e.g. *Bobasatrania*, *Styracopterus*).';

TEXT CHARACTER = 11 TEXT = 'Cloutier & Ahlberg, 1996; Taverne, 1997; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. Choo's (2011) codes for this character appear reversed. ';

TEXT CHARACTER = 12 TEXT = 'Gardiner & Schaeffer, 1989; Taverne, 1997; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011.';

TEXT TAXON = 71 CHARACTER = 12 TEXT = bone_absent_so_inapplicable_;

TEXT CHARACTER = 13 TEXT = 'Gardiner et al. 1996; Hurley et al. 2007. ';

TEXT CHARACTER = 14 TEXT = 'Taverne, 1997; Schultze & Cumbaa, 2001; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. ';

TEXT CHARACTER = 16 TEXT = 'Xu & Wu 2012; Xu et al. 2014; Xu & Zhao, 2016.
';

TEXT CHARACTER = 17 TEXT = 'Lund et al., 1995; Ahlberg & Johanson, 1998; Ahlberg et al., 2000; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Zhu & Ahlberg, 2004; Daeschler et al., 2006; Long et al., 2006; Zhu et al., 2006; Zhu et al., 2009; Choo, 2011. The nasal is poorly preserved in *Cheirolepis canadensis* (Pearson & Westoll, 1979; Arratia & Cloutier, 1996), and coding for this taxon is revised from 0 to 1. The position of the nostrils is not clear in *Tegeolepis*, and the coding for this taxon is revised from "1" to "?".';

TEXT CHARACTER = 18 TEXT = 'Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. The position of the nostrils is not clear in *Tegeolepis*, and the coding for this taxon is revised from "0" to "?".';

TEXT CHARACTER = 19 TEXT = 'Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. The coding for *Howqualepis rostridens* (Long, 1988) and *Gogosardina* (Choo et al., 2009) is revised from 0 to 1. The premaxilla is not preserved in *Novagonatodus* (Long, 1988; Holland et al., 2007), so the coding is changed from 0 to 1. The premaxilla is absent in *Wendichthys* (Lund & Poplin, 1997), so the coding is revised from "0" to "-". The position of the nostrils is not clear in *Tegeolepis*, and the coding for this taxon is revised from "0" to "?". The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015)."?".';

TEXT CHARACTER = 20 TEXT = 'Lund et al., 1995; Cloutier & Ahlberg, 1996; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Swartz, 2009; Zhu et al., 2009; Zhu et al., 2013. ';

TEXT CHARACTER = 21 TEXT = 'Cloutier & Ahlberg, 1996; Taverne, 1997; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu & Yu, 2002; Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Brazeau, 2009; Swartz, 2009; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015b. A pineal foramen is variably present in *Cheirolepis canadensis* (Pearson & Westoll, 1979; Arratia & Cloutier, 1996), *C. trailli* (Pearson & Westoll, 1979), *Kentuckia deani* (Rayner, 1951) and *Meemannia* (Zhu et al., 2010), and these taxa are coded "0/1" to reflect this polymorphism. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 22 TEXT = 'Dietze, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. The coding for *Cuneognathus* (Friedman & Blom, 2006), *Kentuckia hlavini* (Dunkle, 1964) and *Stegotrachelus* (Swartz, 2009) is revised from 01 to 11. The coding for *Melanecta* (Coates, 1998) is revised from 11 to 01. *Wendichthys* (Lund & Poplin, 1997) was erroneously coded by Choo (2011) as state 21, for which there is no description, and is recoded here as 11. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT TAXON = 6 CHARACTER = 22 TEXT =
two_pairs..._but_together_they_are_rectangular_;

TEXT TAXON = 9 CHARACTER = 22 TEXT = '"l" shaped...';

TEXT CHARACTER = 23 TEXT = 'Lund et al., 1995; Taverne, 1997; Dietze, 2000; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Lopez-Arbarello, 2011; Xu et al., 2014. The coding for *Mimipiscis toombsi* (Gardiner, 1984; Choo, 2011) is changed from ě1í to ě2í. The coding for *Moythomasia lineata* is revised to "2" (Choo, 2015).';

TEXT CHARACTER = 24 TEXT = 'Arratia 1999; Lopez-Arbarello 2011. ';

TEXT CHARACTER = 25 TEXT = 'Giles et al., 2015b. Although not figured, an anterior pit line is described for *Miguashaia* (Cloutier 1996).';

TEXT CHARACTER = 26 TEXT = 'Giles et al., 2015b.';

TEXT CHARACTER = 27 TEXT = 'New character. The supraorbital canal may terminate in the frontal/parietal, or it may become confluent with the infraorbital canal. The exact position of this junction is highly variable, and typically occurs in the region of the frontal, dermosphenotic, dermopterotic. ';

TEXT CHARACTER = 28 TEXT = 'New character. In some taxa (e.g. *Dapedium*), the infraorbital canal continues anteriorly above the orbit a short way.';

TEXT CHARACTER = 29 TEXT = 'Lund et al., 1995; Cloutier & Ahlberg, 1996; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Cloutier & Arratia, 2004; Long et al., 2008; Swartz, 2009. ';

TEXT CHARACTER = 30 TEXT = 'Gardiner & Schaeffer 1989; Cloutier & Arratia, 2004; Hurley et al. 2007; Choo, 2011; Xu & Zhao, 2016. This character is reformulated from Choo's character "Dermopterotic: present/absent". Rather than designating bones as an intertemporal (or supratemporal or dermosphenotic) a priori, we consider the number of bones carrying the otic portion of the lateral line canal between the dermosphenotic and the posterior edge of the skull roof. Where two bones are present, these are treated as the intertemporal and supratemporal; where only one is present, this is treated as the dermopterotic. Anamestic bones between the dermosphenotic and frontal are not included in this count. The coding in *Melanecta* (Coates, 1998) has been revised from "0" to "1". The coding in *Moythomasia nitida* (Jessen, 1968) has been revised from "1" to "0". The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015). ';

TEXT CHARACTER = 31 TEXT = 'Friedman & Blom, 2006; Choo, 2011. Coded as inapplicable in taxa with a dermopterotic. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015). ';

TEXT CHARACTER = 32 TEXT = 'Xu & Gao, 2011; Xu et al., 2014. Coded as inapplicable in taxa with a dermopterotic. ';

TEXT CHARACTER = 33 TEXT = 'Choo, 2011. Coded as inapplicable in taxa with a dermopterotic. The coding for *Mimipiscis bartrami* and *M. toomsi* (Gardiner, 1984; Choo, 2011) is revised from $\ddot{e}0\acute{i}$ to $\ddot{e}1\acute{i}$. The coding for *Moythomasia durgaringa* (Gardiner, 1984) and *Moy. nitida* (Jessen, 1968) is revised from $\ddot{e}1\acute{i}$ to $\ddot{e}0\acute{i}$. The position of the spiracular space in *Stegotrachelus* is uncertain, so this taxon is coded as $\ddot{e}?\acute{i}$. The posterior and ventral borders of the supratemporal are poorly preserved in *Krasnoyarichthys* (Prokofiev, 2002), so the coding is changed from $\ddot{e}0\acute{i}$ to $\ddot{e}?\acute{i}$. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 34 TEXT = 'Xu & Gao 2011; Xu et al. 2014. Coded as inapplicable in taxa with a separate intertemporal and supertemporal, and in taxa lacking these bones entirely.';

TEXT CHARACTER = 36 TEXT = 'Gardiner & Schaeffer, 1989; Lund et al., 1995; Cloutier & Ahlberg, 1996; Coates, 1998; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Lopez-Arbarello 2011; Zhu et al., 2013; Xu et al., 2015; Xu & Zhao, 2016. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT TAXON = 63 CHARACTER = 36 TEXT = 'polymorphic - 0/1';

TEXT CHARACTER = 37 TEXT = 'Giles et al., 2015b. The skull roof of *Moythomasia* as shown in Fig. 103 (Gardiner, 1984) is a restoration (see also Choo 2015: fig. 13). The only

skull roof directly figured by Gardiner does not preserve the extrascapulars in situ (fig. 83). However, in specimens viewed by us, as well as in published photos of articulated material (e.g. Choo 2015: fig 8), the lateral extrascapular of *M. durgaringa* is clearly excluded from the lateral margin of the skull roof. The extrascapular in *Cuneognathus* is incomplete laterally. However, the extensive posterolateral extension of the supratemporal (Friedman & Blom, 2006: fig. 3) makes it unlikely that the extrascapular would have reached the lateral edge of the skull roof, and as such this character is coded '0'. This convention is also followed for *Tegeolepis* (Dunkle, 1964), and *Meemannia* (Zhu et al., 2006). The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 38 TEXT = 'Dietze, 2000; Cloutier & Arratia, 2004; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. The coding in *Mimipiscis bartrami*, *M. toombsi* (Gardiner, 1984; Choo, 2011), *Stegotrachelus* (Swartz, 2009), *Cheirolepis canadensis* (Arratia & Cloutier, 1996), *C. schultzei* (Arratia & Cloutier, 2004), *C. trailli* (Pearson & Westoll, 1979), *Donnrosenia* (Long et al., 2008), *Howqualepis* (Long, 1988), *Mansfieldiscus* (Long, 1988) and *Woodichthys* (Coates, 1998) is revised from '0' to '1'. The extrascapulars are not preserved in *Gogosardina* (Choo et al., 2009) and *Melanecta* (Coates, 1998), and the coding for these taxa is revised from '0' to '?'. The median extrascapular in *Coccocephalichthys* has an anterior and posterior series, as well as being paired about the midline, and is coded as '0' here. The coding for *Moythomasia lineata* is revised to "1" (Choo, 2015).';

TEXT CHARACTER = 39 TEXT = 'Giles et al., 2015b. inapplicable for taxa that possess a median extrascapular, as it is logically impossible for the lateral extrascapulae to meet in the midline. It is unclear whether the extrascapulae met at the midline in *Moythomasia durgaringa* (Gardiner, 1984) or *Cuneognathus* (Friedman & Blom, 2006), so these taxa are coded "?"!;

TEXT CHARACTER = 40 TEXT = 'Choo, 2011. The codings for *Mimipiscis bartrami*, *M. toombsi* (Gardiner, 1984; Choo, 2011), *Osorioichthys* (Taverne, 1997), *Cheirolepis canadensis* (Arratia & Cloutier, 1996), *C. trailli* (Pearson & Westoll, 1979), *Mansfieldiscus* (Long, 1988), *Woodichthys* (Coates, 1998) and *Wendichthys* (Lund & Poplin, 1997) are revised from 1 to 0. Although often figured as present in reconstructions, it is unclear whether these canals were present in *Howqualepis rostridens* (Long, 1988), *Cuneognathus* (Friedman & Blom, 2006), *Donnrosenia* (Long et al., 2008), *Kentuckia hlavini* (Dunkle, 1964), *Limnomis* (Daeschler, 2000), *Stegotrachelus* (Swartz, 2009) and *Krasnoyarichthys* (Prokofiev, 2002), and the coding for these taxa is revised from 1 to 0. The coding for *Moythomasia lineata* is revised to "1" (Choo, 2015).!;

TEXT CHARACTER = 41 TEXT = 'Gardiner & Schaeffer 1989; Lund et al. 2000; Cloutier & Arratia, 2004; Hurley et al. 2007; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).H07: *Discoserra* has a large plate at the anterior of the infraorbital series, the antorbital or infraorbital identity of which is uncertain because the sensory canal pattern is unclear (a dorsally directed branch would indicate antorbital affinity). It is interpreted here as the anteriormost infraorbital (lachrymal) (figure 2a, la).!;

TEXT CHARACTER = 42 TEXT = 'Grande 2010; Xu & Wu 2012; Xu et al. 2014; Xu & Shen, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 43 TEXT = 'Cloutier & Arratia, 2004; Gardiner et al., 2005; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. Choo's (2011) codes for this character appear reversed. The coding for Gogosardina (Choo et al., 2009) is revised from "0" to "?". The coding for Limnomis (Daeschler, 2000) is revised from "?" to "0". The coding for Tegeolepis (Dunkle & Schaeffer, 1973) is revised from "0" to "?". The coding for Moythomasia lineata is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 44 TEXT = 'Taverne, 1997; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The coding for Melanecta (Coates, 1998) is revised from 001 to 01. The coding for Miguashaia (Cloutier, 1996) is revised from "1" to "?". The coding for Novagonatodus (Long, 1988; Holland et al., 2007) and Onychodus (Andrews et al., 2006) is revised from 01 to 11. The coding for Tegeolepis (Dunkle & Schaeffer, 1973) is revised from "1" to "0". The coding for Wendichthys (Lund & Poplin, 1997) is revised from "0" to "1".';

TEXT CHARACTER = 45 TEXT = 'Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. Although the jugal of Moythomasia durgaringa is only faintly notched in its reconstruction (Gardiner, 1984: fig. 103), the notch is clearly visible on the medial face (Gardiner, 1984: fig. 73). As such the coding is revised from 001 to 11. The coding in Cuneognathus (Friedman & Blom, 2006) is revised

from 01 to 1. The coding in *Novagonatodus* (Long, 1988; Holland et al., 2007) is changed from 1 to 0. The coding in *Wendichthys* (Lund & Poplin, 1997) is revised from "1" to "0". The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 46 TEXT = 'Gardiner & Schaeffer 1989; Taverne, 1997; Schultze & Cumbaa, 2001; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011; Lopez-Arbarello 2011; Xu & Gao 2011; Xu et al., 2015; Xu & Zhao, 2016 Xu & Zhao, 2015.';

TEXT TAXON = 26 CHARACTER = 46 TEXT = coded_separately._;

TEXT CHARACTER = 47 TEXT = 'Giles et al., 2015b. Multiple branches radiate from the infraorbital canal in the jugal of many Carboniferous actinopterygians.';

TEXT CHARACTER = 48 TEXT = 'Gardiner & Schaeffer, 1989; Coates, 1998; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Long et al., 2008; Zhu et al., 2009; Choo, 2011; Xu & Zhao, 2015. The dermosphenotic of *Moythomasia* illustrated by (Gardiner 1984, fig 69) lacks a posterior limb, but this is from a small individual and most likely reflects ontogenetic variability, with a posterior limb being developed in larger individuals (B. Choo, pers. comm.; Choo 2015: fig. 8). The shape of the dermosphenotic in *Cuneognathus* (Friedman & Blom, 2006) is inferred, and the coding is thus revised from 1 to 1. The coding in *Melanecta* (Coates, 1998) is revised from 0 to 1. The posterior limb of the dermosphenotic is variably developed in *Mesopoma* (Coates, 1999), so this taxon is scored "0/1" to reflect this polymorphism.';

TEXT TAXON = 6 CHARACTER = 48 TEXT = no_distinct_dsphen;

TEXT CHARACTER = 49 TEXT = 'Friedman & Blom, 2006; Choo, 2011. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 50 TEXT = 'Gardiner & Schaeffer 1989; Hurley et al. 2007; Xu & Gao 2011; Xu et al. 2014; Xu et al., 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 51 TEXT = 'Cavin & Suteethorn 2006; Lopez-Arbarello 2011.';

TEXT CHARACTER = 52 TEXT = 'Grande 2010; Xu & Wu 2012; Xu et al. 2014, 2015; Xu & Zhao, 2016. The first lachrymal is regarded here as the anteriormost canal-bearing bone that contributes to orbital margin.';

TEXT CHARACTER = 53 TEXT = 'Wiley 1976; Lopez-Arbarello 2010.';

TEXT CHARACTER = 54 TEXT = 'Patterson, 1982; Lauder & Liem, 1983; Gardiner, 1984; Cloutier & Arratia, 2004; Brazeau, 2009; Friedman & Brazeau, 2010; Choo, 2011; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015b. Choo's (2011) codes may be reversed for this character, but it is unclear. The coding for *Cuneognathus* (Friedman & Blom, 2006), *Kentuckia hlavini*, *Krasnoyarichthys* and *Limnomis* is revised from "1" to "?". The coding for *Donnrosenia*, *Gogosardina*, *Howqualepis*, *Masnfieldiscus*, *Melanecta*, *Mimipiscis bartrami*, *M. toombsi*, *Moythomasia durgaringa*, *Moy. nitida*, *Novagonatodus*, *Stegotrachelus* and *Woodichthys* is revised from "1" to "0". The coding for *Onychodus* is revised from "0" to "1". The coding for

Miguashaia is revised from "-" to "1". The coding for Moythomasia lineata is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 55 TEXT = 'Patterson, 1982; Gardiner & Schaeffer, 1989; Lund et al., 1995; Cloutier & Ahlberg, 1996; Coates, 1998; Dietze, 2000; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014; 2015; Xu & Zhao, 2016. This region of the cheek is missing in Coccocephalichthys (Poplin, 1974; Poplin & Vèran, 1996), and was presumably removed by Watson (1925) when he first described the specimen. It is unclear from the surviving cast whether a dermohyal and/or accessory operculum were present, and as such this taxon is coded as "?". The presence of a dermohyal is only inferred in Donnrosenia (Long et al., 2008), and the coding for this taxon is revised from "1" to "?".';

TEXT CHARACTER = 56 TEXT = 'Giles et al., 2015b. The dermohyal is not preserved in Melanecta (Coates, 1998), but it is clear from the surrounding bones that it would not have projected above the dorsal surface of the operculum.';

TEXT CHARACTER = 57 TEXT = 'Gardiner et al., 2005; Coates, 1999; Xu & Gao, 2011; Xu et al., 2014. The relevant part of the cheek is not preserved in Donnrosenia (Long et al., 2008), so the coding for this taxon is changed from "1" to "?".';

TEXT CHARACTER = 58 TEXT = 'Friedman, 2007; Zhu et al., 2009. The position of the spiracular space in *Stegotrachelus* (Swartz, 2009) is uncertain, so this taxon is coded as "?". The coding for *Moythomasia lineata* is revised to "1" (Choo, 2015).';

TEXT CHARACTER = 59 TEXT = 'Zhu & Yu, 2002; Friedman, 2007; Xu et al., 2014, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 60 TEXT = 'Lund et al., 1995; Lund, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015b. ';

TEXT CHARACTER = 61 TEXT = 'Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015b. ';

TEXT CHARACTER = 62 TEXT = 'Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013.';

TEXT CHARACTER = 63 TEXT = 'Cloutier & Arratia, 2004; Lopez-Arbarello 2011; Xu et al. 2014; Xu et al. 2014, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 64 TEXT = 'Gardiner & Schaeffer 1989; Gardiner et al. 1996; Gardiner et al. 2005; Coates 1999; Hurley et al. 2007; Xu & Gao 2011; Xu et al. 2014, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 65 TEXT = 'Grande 2010; Xu & Wu 2012; Xu et al. 2014. ';

TEXT CHARACTER = 66 TEXT = 'Grande & Bemis 1998; Xu & Wu 2012; Xu et al. 2014, 2015. Arratia 2013; Xu & Zhao, 2016.';

TEXT CHARACTER = 67 TEXT = 'Gardiner & Schaeffer 1989; Gardiner et al. 1996; Gardiner et al. 2005; Coates 1999; Hurley et al. 2007; Xu & Gao 2011; Xu et al. 2014, 2015; Xu & Shen, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 68 TEXT = 'Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 69 TEXT = 'Giles et al., 2015b. The mandibular canal is reconstructed as reaching the anterior margin of the dentary in *Cuneognathus* (Friedman & Blom, 2006), but specimen photos appear to show it leaving through the dorsal margin. As such, this taxon is coded "1" for this character. ';

TEXT CHARACTER = 70 TEXT = 'Ahlberg & Johanson, 1998; Zhu et al., 2001; Zhu & Yu, 2002; Zhu & Ahlberg, 2004; Friedman, 2007; Zhu et al., 2009.';

TEXT CHARACTER = 71 TEXT = 'Cloutier & Arratia 2004, Xu et al. 2014. ';

TEXT TAXON = 74 CHARACTER = 71 TEXT = '0^n';

TEXT CHARACTER = 72 TEXT = 'Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The anterior extent of the dentary is not preserved in *Limnomis* (Daeschler, 2000), so the coding for this taxon is revised from "1" to "?". ';

TEXT CHARACTER = 73 TEXT = 'Friedman, 2007. Coates (1998) states that the maxilla of *Melanecta* bears large teeth interspersed with smaller teeth, but it is unclear how these teeth are arranged. As such, this taxon is coded "?". ';

TEXT CHARACTER = 74 TEXT = 'New character. In *Styracopterus*, *Fouldenia* and *Amphicentrum*, a lateral lamina of bone obscures the maxillary dentition (Sallan & Coates 2013).';

TEXT CHARACTER = 75 TEXT = 'Patterson, 1982; Gardiner, 1984; Maisey, 1986; Gardiner & Schaeffer, 1989; Cloutier & Ahlberg, 1996; Taverne, 1997; Coates, 1999; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Zhu et al., 2009; Friedman & Brazeau, 2010; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015b. The presence of acrodin in *Limnomis* (Daeschler, 2000), *Mansfieldiscus* (Long, 1988), *Melanecta* (Coates, 1998) and

Woodichthys (Coates, 1998) is uncertain, and the coding for these taxa is revised from "1" to "?";

TEXT CHARACTER = 76 TEXT = 'Zhu & Yu 2002; Friedman 2007; Lopez-Arbarello 2011.';

TEXT CHARACTER = 77 TEXT = 'Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Grande 2010; Choo, 2011; Xu et al., 2014.';

TEXT TAXON = 3 CHARACTER = 77 TEXT = nb_three_ossifications;

TEXT TAXON = 41 CHARACTER = 77 TEXT = nb_two_ossifications;

TEXT CHARACTER = 78 TEXT = 'Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. The coding for Kentuckia hlavini (Dunkle, 1964) and Guiyu (Zhu et al., 2009) is revised from "0" to "?". The coding for Limnomis (Daeschler, 2000) and Stegotrachelus (Swartz, 2009) is revised from "1" to "?". The coding in Mansfieldiscus (Long, 1988) is revised from "0" to "2". The coding for Moythomasia lineata is revised to "1" (Choo, 2015).H07:';

TEXT CHARACTER = 79 TEXT = 'Schultze and Cumbaa, 2001; Zhu and Schultze, 2001; Zhu et al., 2001; Zhu and Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009.';

TEXT CHARACTER = 80 TEXT = 'Ahlberg & Clack, 1998; Daeschler et al., 2006; Long et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Giles et al., 2015b. A

single specimen of *Pteronisculus stensioi* has at least five or six coronoids anterior to the prearticular region. However, these appear to correspond to the three coronoids present in most specimens, so the taxon is coded here as "2". Two coronoids are reported in *Boreosomus* (Nielsen, 1942).';

TEXT TAXON = 4 CHARACTER = 80 TEXT = fused;

TEXT TAXON = 71 CHARACTER = 80 TEXT =

Hmm._The_one_figured_in_G&B_only_has_two._;

TEXT CHARACTER = 81 TEXT = 'Gardiner & Schaeffer 1989; Zhu & Yu, 2002; Friedman, 2007; Friedman, 2007; Xu & Gao 2011; Xu et al. 2014, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 82 TEXT = Modified_from_Gardiner_et_al._2005._;

TEXT CHARACTER = 83 TEXT =
Arratia_2013._A_distinct_notch_in_the_posterior_margin_of_the_dentary_is_seen_in_taxa_such_as_Leptolepis._;

TEXT CHARACTER = 84 TEXT = 'Grande & Bemis 1998; Grande 2010; Xu & Wu 2012; Xu et al. 2014, 2015; Lopez-Arbarelo 2011; Xu & Zhao, 2016.';

TEXT CHARACTER = 86 TEXT = 'Revised from Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015b. This character is expanded from previous formulations, which only considered whether a

basipterygoid fenestra was absent or present. Where a basipterygoid process is absent, the dorsal margin of the palate may be flat, or the metapterygoid may bear a distinct notch. ';

TEXT TAXON = 6 CHARACTER = 86 TEXT = mpt_proc;

TEXT CHARACTER = 88 TEXT = New_character._;

TEXT CHARACTER = 89 TEXT = 'This character captures whether the palatoquadrates contact at the midline. ^n';

TEXT CHARACTER = 92 TEXT = 'Friedman, 2007.';

TEXT CHARACTER = 94 TEXT = 'Lopez-Arbarello 2011; Arratia 2013; Xu & Wu, 2012; Xu & Zhao, 2016.';

TEXT TAXON = 21 CHARACTER = 94 TEXT = paired_and_median_vomers;

TEXT TAXON = 33 CHARACTER = 94 TEXT = vomers_fuse_ontogenetically;

TEXT TAXON = 71 CHARACTER = 94 TEXT =
sutured_to_parasphenoid._Check_in_Grande_&_Bemis._;

TEXT CHARACTER = 95 TEXT = Hurley_et_al._2007.;

TEXT CHARACTER = 96 TEXT = 'Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009. This region of the cheek was removed in *Coccocephalichthys* (Poplin, 1974; Poplin & Vèran, 1996), presumably by Watson

(1925) when he first described the specimen. It is unclear from the surviving cast whether a dermohyal and/or accessory operculum were present, and as such this taxon is coded as '0';

TEXT CHARACTER = 97 TEXT = 'Modified from Lund et al., 1995; Lund, 2000; Lund & Poplin, 2002; Cloutier & Arratia, 2004; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2015; Xu & Zhao, 2016Xu & Zhao, 2015. . The coding in *Osorioichthys* (Taverne, 1997), *Mansfieldiscus* (Long, 1988), *Melanecta* (Coates, 1988), *Moythomasia nitida* (Jessen, 1968), *Novagonatodus* (Long, 1988; Holland et al., 2007), *Woodichthys* (Coates, 1998), *Cuneognathus* (Friedman & Blom, 1906) and *Krasnoyarchichthys* (Prokofiev, 2002) is revised from '0' to '1'. The coding in *Howqualepis* (Long, 1988), *Donnrosenia* (Long et al., 2008) and *Limnomis* (Daeschler, 2000) is revised from '1' to '0';

TEXT CHARACTER = 98 TEXT = Xu_et_al._2014._;

TEXT TAXON = 9 CHARACTER = 98 TEXT = multiple_suboperc;

TEXT CHARACTER = 99 TEXT = 'Long et al., 2008; Choo, 2011; Lopez-Arbarello 2011. The coding in *Howqualepis* (Long, 1988) and *Donnrosenia* (Long et al., 2008) is changed from "0" to "1". The anterodorsal process is described as well developed in *Gogosardina* (Choo et al., 2009), and the coding for this taxon is revised from "?" to "1". An anterodorsal process is also present in "semionotiforms". Although these processes do not appear to be homologous they are coded within the character. ';

TEXT CHARACTER = 101 TEXT = 'Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013; Xu & Zhao, 2016. ';

TEXT TAXON = 1 CHARACTER = 101 TEXT = lots_of_small_ossicles...;

TEXT TAXON = 21 CHARACTER = 101 TEXT = loads!_suborbs_carry_it...;

TEXT CHARACTER = 102 TEXT = 'Modified from Gardiner et al., 2005; Swartz 2009. This character is reformulated from its original (compound) formulation, which considered both maxilla and preoperculum shape. Primitively in actinopterygians the preoperculum is wholly or partially developed dorsal to the maxilla as an anterodorsal-posteroventrally oriented bone, either with (e.g. *Mimipiscis*, *Moythomasia*) or without (e.g. *Cheirolepis*) a dorsoventrally oriented limb. The preoperculum may also be near-vertical, with no distinct anterodorsal or anteroventral extensions (e.g. *Boreosomus*, *Peltopleurus*), or developed as an anteroventral-posterodorsally-directed bone largely ventral to the maxilla (e.g. *Discoserra*, *Propterus*).';

TEXT CHARACTER = 103 TEXT = 'Modified from Lopez-Arbarello 2011.';

TEXT CHARACTER = 104 TEXT = 'Lopez-Arbarello 2011. ';

TEXT CHARACTER = 105 TEXT = 'Gardiner & Schaeffer 1989; Xu & Gao 2011; Xu et al. 2014, 2015. Gardiner & Schaeffer 1989; Olsen & McCune 1991; Gardiner et al. 1996; Gardiner et al. 2005; Cavin & Suteethorn 2006; Hurley et al. 2007; Lopez-Arbarello 2011; Xu & Zhao, 2016. ';

TEXT CHARACTER = 106 TEXT = 'Lund et al., 1995; Cloutier & Arratia, 2004; Choo, 2011. The coding for *Mimipiscis bartrami*, *M. toombsi* (Gardiner, 1984, Choo, 2011), *Stegotrachelus* (Swartz, 2009), *Cheirolepis canadensis* (Arratia & Cloutier, 1996), *C. schulzei* (Arratia & Cloutier, 2004), *C. trailli* (Pearson & Westoll, 1979) *Donnrosenia* (Long et al., 2008), *Gogosardina* (Choo et al., 2009), *Howqualepis rostridens* (Long, 1988), *Novagonatodus* (Long, 1988; Holland et al., 2007), *Mansfieldiscus* (Long, 1988) and *Woodichthys* (Coates, 1998) is revised from $\bar{e}l\acute{i}$ to $\bar{e}0i$. The coding for *Cuneognathus* (Friedman & Blom, 2006), *Kentuckia hlavini* (Dunkle, 1964) and *Melanecta* (Coates, 1998) is revised from $\bar{e}l\acute{i}$ to $\bar{e}^?i$. The coding for *Krasnoyarichthys* (Prokofiev, 2002) is changed from $\bar{e}^?i$ to $\bar{e}l\acute{i}$.';

TEXT TAXON = 74 CHARACTER = 106 TEXT = 0;

TEXT CHARACTER = 107 TEXT = 'Xu et al., 2014. ';

TEXT CHARACTER = 108 TEXT = 'Gardiner & Schaeffer, 1989; Cloutier & Ahlberg, 1996; Taverne, 1997; Lund & Poplin, 1997; Coates, 1999; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Brazeau, 2009; Xu & Gao, 2011; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015b. The coding for *Mansfieldiscus* (Long, 1988) is revised from $\bar{e}^?i$ to $\bar{e}l\acute{i}$. The condition in *Boreosomus* (Nielsen, 1942) is unique: instead of lateral gulars flanking a median gular, there appears to be a second median gular. This may well represent a fusion of the two, longer lateral gulars, is coded as such. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 109 TEXT = 'Lund et al., 1995; Cloutier & Ahlberg, 1996; Coates, 1999; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014, 2015; Giles et al., 2015b; Xu & Zhao, 2015. Pearson & Westoll (1979: p. 365) state that a median gular is not known in *Cheirolepis canadensis*. Although a median gular is reconstructed by Cloutier & Arratia (1996: fig. 7), this bone is not present in any specimen photos and is not mentioned in the text. As such, this taxon is coded as '?';

TEXT CHARACTER = 110 TEXT = 'Friedman, 2007; Zhu et al., 2009; Brazeau, 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015b. *Cheirolepis trailli* is coded "0" (Giles et al., 2015a). ';

TEXT CHARACTER = 111 TEXT = 'New character. ðPrimitively in actinoptes, the optic nerve exits the cranial cavity into the orbit through paired foramina approximately halfway up the orbital wall. In many Carboniferous and younger taxa, much of the orbital wall is unossified (the optic fenestra). The optic nerves may exit through openings just posterior to (e.g. *Pteronisculus*) or confluent with (e.g. *Pholidophorus*) the optic fenestra. In polypterids and *Fukangichthys*, the optic nerve exits ventrally through paired foramina that abut the parasphenoid.';

TEXT CHARACTER = 112 TEXT = 'Giles et al., 2015b. Carboniferous and younger actinoptes such as *Lawrenciella* (Hamel & Poplin, 2008) have a median crista anterior to the anterior dorsal fontanelle upon which the skull roof sits.';

TEXT CHARACTER = 113 TEXT = 'Giles et al., 2015b. The anterior dorsal fontanelle of many Carboniferous and younger actinoptes is greatly expanded, in contrast to the smaller fontanelle of Devonian taxa such as *Mimipiscis* (Gardiner, 1984).';

TEXT CHARACTER = 114 TEXT = 'Coates, 1999. ';

TEXT CHARACTER = 115 TEXT = 'Coates, 1999.';

TEXT CHARACTER = 116 TEXT = 'Coates, 1999; Gardiner et al. 1996; Hurley et al. 2007; Xu & Gao, 2011; Xu et al., 2014, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 117 TEXT = 'Modified from Coates, 1999; Xu et al., 2014. Wiley 1976; Gardiner, 1984; Gardiner & Schaeffer, 1989; Gardiner et al. 1996; Hurley et al. 2007; Lopez-Arbarello 2011; Xu & Gao, 2011; Xu et al. 2014, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 118 TEXT = 'Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999; Gardiner et al., 2005; Xu & Gao, 2011; Xu et al., 2014. Taxa that lack a groove on the lateral commissure are coded as inapplicable for this

character. . Following Xu et al. (2014), the spiracle in *Moythomasia durgaringa* is coded "1".
Cheirolepis trailli is coded "0" (Giles et al., 2015a). ';

TEXT CHARACTER = 119 TEXT = 'Gardiner et al., 2005; Xu & Gao, 2011; Xu et al., 2014, 2015; Xu & Zhao, 2016.);

TEXT CHARACTER = 120 TEXT = 'Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates ,1999.';

TEXT CHARACTER = 121 TEXT = 'Gardiner et al. 2005; Gardiner et al. 1996; Hurley et al. 2007; Xu & Gao 2011; Xu et al. 2015. ';

TEXT CHARACTER = 122 TEXT = 'Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999; Xu & Gao, 2011; Xu et al., 2014. *Cheirolepis trailli* is coded "0" (Giles et al., 2015a). ';

TEXT CHARACTER = 123 TEXT = 'Friedman, 2007; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles et al., 2015b. *Cheirolepis trailli* is coded "1" (Giles et al., 2015a). ';

TEXT CHARACTER = 124 TEXT = 'Coates, 1999. We follow Coates (1999) in coding *Howqualepis* as "0" on the basis of Long 1988 fig. 16 and AMF65495 (pers. obs. S.G.), rather

than the braincase reconstruction (Long, 1988: fig. 18). *Cheirolepis trailli* is coded "0" (Giles et al., 2015a). ';

TEXT CHARACTER = 125 TEXT = 'Friedman, 2007; Brazeau, 2009; Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015b. *Cheirolepis trailli* is coded "1" (Giles et al., 2015a). ';

TEXT TAXON = 71 CHARACTER = 125 TEXT = check_this_coding..._;

TEXT CHARACTER = 126 TEXT = 'Giles et al., 2015b. Variable in *Boreosomus*: the posterior dorsal fontanelle is closed in the specimen figured in Nielsen (1942: plate 25F), but developed in the specimen figured in plate 28. This taxon is coded 0/1 to reflect this polymorphism. ';

TEXT CHARACTER = 127 TEXT = 'Giles et al., 2015b. This projection is somewhat reduced in *Pteronisculus* (Nielsen, 1942), but is coded "1" here. Variable in *Boreosomus*: the posterior dorsal fontanelle is closed in the specimen figured in Nielsen 1942 plate 25F, but developed in the specimen figured in plate 28. This taxon is coded 0/1 to reflect this polymorphism. *Cheirolepis trailli* is coded "0" (2015a). ';

TEXT CHARACTER = 128 TEXT = 'Coates & Sequeira, 1998; Coates & Sequeira, 2001a, b; Coates, 1999; Friedman, 2007; Zhu et al., 2009; Friedman & Brazeau, 2010; Zhu et al., 2013; Giles et al., 2015b. This character is coded as inapplicable in taxa that lack a canal for the dorsal aorta. *Cheirolepis trailli* is coded "0" (Giles et al., 2015a). The aortic canal of *Moythomasia* is not figured by Gardiner (1984), but a clear posterior notch in the aortic canal

can be seen in Long & Trinajstić (2010:fig 5b). The neurocranium of *Gogosardina* is not yet described, but this character can be coded on the basis of Choo et al. (2009: fig. 9). ';

TEXT TAXON = 25 CHARACTER = 128 TEXT = 'Rayner says canal, Paterson says no canal...';

TEXT TAXON = 43 CHARACTER = 128 TEXT = Draw_in_notebook!;

TEXT CHARACTER = 129 TEXT = 'Giles et al., 2015b. In *Mimipiscis bartrami* and *M. toombsi*, a groove for one of the efferent branchial arteries branches off from the lateral dorsal aorta immediately before the articular area for the first infrapharyngobranchial. However, it is uncertain which, so both taxa coded as "?" for these characters. The neurocranium of *Gogosardina* is not yet described, but this character can be coded on the basis of Choo et al. (2009: fig. 9). ';

TEXT CHARACTER = 130 TEXT = 'Giles et al., 2015b. In *Mimipiscis bartrami* and *M. toombsi*, a groove for one of the efferent branchial arteries branches off from the lateral dorsal aorta immediately before the articular area for the first infrapharyngobranchial. However, it is uncertain which, so both taxa coded as "?" for these characters. The neurocranium of *Gogosardina* is not yet described, but this character can be coded on the basis of Choo et al. (2009: fig. 9). ';

TEXT CHARACTER = 131 TEXT = 'Coates, 1999. This character is coded as inapplicable in taxa that lack a canal for the dorsal aorta. In *Mimipiscis toombsi*, the bifurcation point of the dorsal aorta can be open (Giles & Friedman, 2014: fig. 2) or closed (Gardiner 1984:

fig. 15). This taxon is coded "0/1" to reflect this polymorphism. The aortic canal of Moythomasia is not figured by Gardiner (1984), but the bifurcation into the lateral dorsal aortae can be seen in Long & Trinajstić (2010:fig 5b).';

TEXT CHARACTER = 132 TEXT = New_character._;

TEXT CHARACTER = 133 TEXT = 'Wiley 1976; Lopez-Arbarelo 2011. ';

TEXT CHARACTER = 134 TEXT = 'Gardiner et al. 1996; Hurley et al. 2007. This character can only be coded when separate braincase ossifications can be identified. ';

TEXT CHARACTER = 135 TEXT = 'Olsen & McCune 1991; Gardiner et al. 1996; Cavin & Suteethorn 2006; Hurley et al. 2007; Lopez-Arbarelo 2011. This character can only be coded when separate braincase ossifications can be identified. ';

TEXT CHARACTER = 136 TEXT = 'Grande 2010; Lopez-Arbarelo 2011; Xu & Wu 2012; Xu et al. 2014, 2015; Arratia 2013; Xu & Zhao, 2016. This character can only be coded when separate braincase ossifications can be identified. ';

TEXT CHARACTER = 137 TEXT = 'Gardiner et al. 1996; Grande & Bemis, 1998; Hurley et al. 2007; Xu et al. 2014; Xu & Shen, 2015; Xu & Zhao, 2016. This character can only be coded when separate braincase ossifications can be identified. ';

TEXT CHARACTER = 138 TEXT = 'Wiley 1976; Cavin & Suteethorn 2006; Hurley et al. 2007; Grande 2010; Lopez-Arbarello 2011; Xu et al., 2014, 2015; Xu & Zhao, 2016. This character can only be coded when separate braincase ossifications can be identified.) ';

TEXT CHARACTER = 139 TEXT = 'Olsen 1994; Gardiner et al. 1996; Lopez-Arbarello 2011; Xu et al. 2014; Xu & Shen, 2015; Xu & Zhao, 2016. This character can only be coded when separate braincase ossifications can be identified. ';

TEXT CHARACTER = 140 TEXT = 'Grande 2010; Xu et al. 2014, 2015; Xu & Zhao, 2016. This character can only be coded when separate braincase ossifications can be identified. ';

TEXT CHARACTER = 141 TEXT = 'Gardiner et al. 1996; Hurley et al. 2007. This character can only be coded when separate braincase ossifications can be identified. ';

TEXT CHARACTER = 142 TEXT = 'Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Hurley et al. 2007; Lopez-Arbarello 2011; Xu & Gao, 2011; Xu et al. 2014, 2015; Xu & Zhao, 2016. ';

TEXT CHARACTER = 143 TEXT = 'Gardiner, 1984; Gardiner & Schaeffer, 1989; Gardiner et al. 1996; Hurley et al. 2007; Xu & Gao, 2011; Xu et al. 2014, 2015; Xu & Zhao, 2016.) ';

TEXT CHARACTER = 144 TEXT = 'Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Gardiner et al. 1996; Hurley et al. 2007; Xu & Gao, 2011; Xu et al. 2014, 2015; Xu & Zhao, 2016.)';

TEXT TAXON = 23 CHARACTER = 144 TEXT =
Unclear_where_hmd_articulates_so_not_sure._Also_why_foramen?;

TEXT CHARACTER = 145 TEXT = 'Coates, 1999; Zhu & Yu, 2002; Gardiner et al., 2005; Friedman, 2007, Xu & Gao, 2011; Xu et al., 2014, 2015; Xu & Zhao, 2016. Cheirolepis trailli is coded "0" (Giles et al., 2015a).';

TEXT CHARACTER = 146 TEXT = 'Patterson, 1982; Coates, 1999; Dietze, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015b. The coding in Wendichthys (Lund & Poplin, 1997) is revised from "?" to "1".';

TEXT CHARACTER = 147 TEXT = 'Friedman & Blom, 2006; Friedman, 2007; Zhu et al., 2009; Choo, 2011; Zhu et al., 2013; Giles et al., 2015b. ';

TEXT CHARACTER = 148 TEXT = 'Giles et al., 2015b. The buccohypophyseal canal typically enters the dorsal surface of the parasphenoid, but whether it exits via the ventral surface is more variable, and this distribution is captured by this character. ';

TEXT TAXON = 4 CHARACTER = 148 TEXT = 'nb median myodome means this is not trye bhc, but mmaybe an anterior extension';

TEXT CHARACTER = 149 TEXT = Arratia_2013._;

TEXT CHARACTER = 150 TEXT = 'Gardiner et al. 1996; Hurley et al. 2007; Xu & Wu, 2012; Xu et al., 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 151 TEXT = 'Gardiner et al. 1996; Hurley et al. 2007; Xu & Wu, 2012; Xu et al., 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 152 TEXT = Modified_from_Gardiner_et_al._2005._;

TEXT CHARACTER = 153 TEXT = 'Xu and Gao 2011; Xu et al. 2014.';

TEXT CHARACTER = 154 TEXT = 'Coates, 1999; Giles & Friedman, 2014. Cheirolepis trailli is coded "1" (Giles et al., 2015a). ';

TEXT CHARACTER = 155 TEXT = 'Brazeau, 2009; Friedman & Brazeau 2010; Davis et al., 2012; Zhu et al., 2013; Brazeau & Friedman, 2014; Giles & Friedman, 2014; Giles et al., 2015b. Cheirolepis trailli is coded "0" (Giles et al., 2015a). The olfactory tracts of Osorioichthys are elongate (pers. obs. unpubl. scan data S.G.).';

TEXT CHARACTER = 156 TEXT = 'Coates, 1999; Giles & Friedman, 2014.

Cheirolepis trailli is coded "1" (Giles et al., 2015a). The olfactory nerves are carried in separate tracts in *Osorioichthys* (pers. obs. unpubl. scan data S.G.);

TEXT CHARACTER = 157 TEXT = 'Coates, 1999; Xu & Gao, 2011; Xu et al., 2014. ';

TEXT CHARACTER = 158 TEXT = 'Giles & Friedman, 2014.';

TEXT CHARACTER = 159 TEXT = 'Coates 1999; Hurley et al. 2007; Xu et al. 2014.
';

TEXT CHARACTER = 160 TEXT = 'Coates, 1999. ';

TEXT CHARACTER = 161 TEXT = 'Coates 1999; Hurley et al. 2007; Xu & Gao 2011;
Xu et al. 2014. ';

TEXT CHARACTER = 162 TEXT = 'Coates 1999; Hurley et al. 2007; Xu & Gao 2011;
Xu et al. 2014. ';

TEXT CHARACTER = 163 TEXT = 'Coates 1999; Hurley et al. 2007; Xu & Gao 2011;
Xu et al. 2014. ';

TEXT CHARACTER = 164 TEXT = 'Davis et al., 2012; Zhu et al., 2013; Giles & Friedman, 2014; Giles et al., 2015b. ';

TEXT CHARACTER = 165 TEXT = 'Giles et al., 2015b. In certain primitive actinopts, such as *Mimipiscis* (Giles and Friedman, 2014), a short length of canal lies between the posterior ampulla and the remainder of the labyrinth.';

TEXT CHARACTER = 166 TEXT = 'Giles & Friedman, 2014. ';

TEXT CHARACTER = 167 TEXT = 'Gardiner, 1984; Gardiner & Schaeffer, 1989; Coates, 1999; Cloutier & Arratia, 2004; Gardiner et al., 2005; Zhu et al., 2006; Zhu et al., 2009; Zhu et al., 2013; Giles & Friedman, 2014; Xu et al., 2014; Giles et al., 2015b. The presence of a lateral cranial canal in *Ligulalepis* and *Psarolepis* is uncertain, but its presence in *Meemannia* is confirmed following Lu et al. (2016). *Erpetoichthys* is conservatively coded as "?". ';

TEXT CHARACTER = 168 TEXT = New_character._;

TEXT CHARACTER = 169 TEXT = 'Characters 147-150 form part of an atomisation of the compound characters "ganoine" (typically defined as a single or multilayer enamel covering) and "cosmine" (typically defined as a single layer of enamel with a well defined pore canal network) (e.g. Cloutier & Ahlberg, 1996; Ahlberg & Johanson, 1998; Zhu & Ahlberg, 2004; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Daeschler et al., 2006; Long et al., 2006; Zhu et al., 2006; Zhu et al., 2009; Davis et al., 2012;

Zhu et al., 2013). A similar approach to atomization was taken by Friedman (2007), Brazeau & Friedman (2010) and Giles et al. (2015b). As detailed histological investigations have not been carried out for the majority of early actinopterygians (rather, they have simply been described as being covered in/bearing ridges of ganoine), many of these characters cannot be coded for a number of taxa. Histological data are only known for specimens of *Mimipiscis toombsi* (Gardiner, 1984; Choo, 2011), so this and the following characters are coded "?" for *Mimipiscis bartrami* (Gardiner, 1984; Choo, 2011). ';

TEXT CHARACTER = 170 TEXT = 'See notes above for c. 147. *C. trailli* is coded "1" following Lu et al. 2016. ';

TEXT CHARACTER = 171 TEXT = 'Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011. ';

TEXT CHARACTER = 172 TEXT = 'Maisey, 1986; Gardiner & Schaeffer, 1989; Cloutier & Ahlberg, 1996; Coates, 1999; Dietze, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Brazeau, 2009; Swartz, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Lopez-Arbarelo 2011; Xu & Gao, 2011; Choo, 2011; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015b; Xu & Zhao, 2016. This character is coded only for taxa that possess rhombic scales. The coding for *Kentuckia hlavini* (Dunkle, 1964) is revised from 01 to 0i, and the coding for *Limnomis* (Daeschler, 2000) from 0i to 1i. The coding for *Cheirolepis trailli* (Giles et al., 2015a) is revised from 0i to 1i. ';

TEXT CHARACTER = 173 TEXT = 'Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Zhu et al., 2013; Giles et al., 2015b. The coding for *Limnomis* (Daeschler, 2000) and *Cheirolepis trailli* (Giles et al., 2015a) is revised from "0" to "1".';

TEXT CHARACTER = 174 TEXT = 'Friedman & Blom 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu et al., 2014. Scale crowns of *Cheirolepis schultzei* (Arratia & Cloutier, 2004) are not preserved, so this and the following scale characters are coded as "?". The coding for *Donnrosenia* (Long et al., 2008) is revised from "1" to "0". Scales from the posterior half of the flank in *Wendichthys* bear pores on the enamel surface, whereas those from the anterior part of the flank lack these pores (Lund & Poplin, 1997: fig. 6). This taxon is scored "1".';

TEXT CHARACTER = 175 TEXT = New_character._;

TEXT TAXON = 49 CHARACTER = 175 TEXT = check;

TEXT CHARACTER = 176 TEXT = 'Patterson, 1982; Gardiner & Schaeffer, 1989; Coates, 1999; Dietze, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Zhu et al., 2013; Xu et al., 2014, 2015; Xu & Zhao, 2016.';

TEXT CHARACTER = 177 TEXT = 'Friedman, 2007; Zhu et al., 2009; Friedman & Brazeau, 2010; Xu & Gao, 2011; Zhu et al., 2013; Brazeau & Friedman, 2014; Xu et al., 2014, 2015; Xu & Zhao, 2016 Xu et al., 2014; Xu & Zhao, 2015. Although Long (1988: p.24) mentions the presence of a depression for the hyomandibular nerve in *Howqualepis*, it is unclear whether this perforated the hyomandibula. This taxon is conservatively coded as "?". *Cheirolepis trailli* is coded "0" (Giles et al., 2015a). Following Friedman (2007), we code *Onychodus* as "0". ';

TEXT CHARACTER = 178 TEXT = 'Gardiner & Schaeffer, 1989.';

TEXT CHARACTER = 179 TEXT = 'Gardiner et al., 2005; Xu & Gao, 2011; Xu et al., 2014. ';

TEXT CHARACTER = 180 TEXT = 'Revised from Coates, 1999. The character captures whether the ceratohyal (or the anterior ossification if an anterior and posterior ceratohyal are present) is medially constricted (hourglass-shaped) or plate-like in lateral view. ';

TEXT CHARACTER = 181 TEXT = 'Coates, 1999. The groove for the afferent hyoidean artery in the ceratohyal of *Gogosardina* is visible in Choo 2009 (fig 6). ';

TEXT CHARACTER = 182 TEXT = 'Gardiner 1984; Gardiner & Schaeffer 1989; Coates 1999; Hurley et al. 2007; Hurley et al. 2007; Xu & Zhao, 2016. Xu & Zhao, 2015 . The general actinopterygian condition of the hyoid arch seems to comprise four ossifications:

hyomandibula, ceratohyal (which may be one or two bones), hypohyal, and an intermediate bone between the hyomandibula and ceratohyal termed, variably, the interhyal or symplectic. In some actinoptes (e.g. *Amia*, *Lepisosteus*, *Hiodon*, *Dorsetichthys*, *Macrosemionotus*, etc), a second intermediate cartilage is present. The history attached to naming these terms is very complex (see Paterson 1973, Patterson 1982, Vèran 1988, Gardiner et al. 1996, etc), and we have tried here to apply a simple, consistent approach. The ossification that forms an intermediary between the hyomandibula and ceratohyal is termed the interhyal. This is primitively present (and in contact with the quadrate), and may be very reduced (e.g. *Watsonulus*, *Elops*), or entirely cartilaginous (e.g. *Amia*, *Lepisosteus*) in more derived actinoptes. The ossification that contacts the hyomandibula (and typically the quadrate), but does not articulate with the ceratohyal, is termed the symplectic. This element may brace the quadrate, and in *Watsonulus*, *Caturus* and *Amia* additionally articulates with the lower jaw. We follow Grande (2010) in identifying the 'symplectic' of *Acipenser* as the posterior ceratohyal. Vèran (1988) identified a second intermediate ossification in the hyoid arch in a number of 'palaeoniscids', which she termed a symplectic. This identification has been disputed on the basis of position (e.g. Gardiner et al. 1996). We have seen no evidence (either through visual examination or CT scanning) for a second intermediate hyoid ossification in any specimens of *Boreosomus* or *Pteronisculus*. From examination of *Coccocephalichthys*, we identify the 'symplectic' of Vèran to be the interhyal and the 'interhyal' of Vèran to correspond to the articular. This casts doubt on the presence of a second element, and we have therefore coded *Boreosomus*, *Pteronisculus* and *Coccocephalichthys* as '0?';

TEXT CHARACTER = 184 TEXT = 'Davis et al., 2012; Zhu et al., 2013; Giles et al., 2015b.';

TEXT CHARACTER = 185 TEXT = New_character._;

TEXT TAXON = 9 CHARACTER = 185 TEXT = 'Poorly preserved: only know first three arches';

TEXT CHARACTER = 186 TEXT = 'Grande, 2010; Xu & Wu, 2012; Xu et al., 2014, 2015; Xu & Zhao, 2016. ';

TEXT CHARACTER = 187 TEXT = 'Coates, 1999; Xu & Gao, 2011; Xu et al., 2014, 2015; Xu & Zhao, 2016. An uncinat process is a dorsally-directed extension on the epibranchial that articulates with the pharyngobranchial skeleton. ';

TEXT CHARACTER = 188 TEXT = Arratia_2013.;

TEXT CHARACTER = 189 TEXT = 'Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Lund & Poplin, 2002; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Gardiner et al., 2005; Friedman & Blom, 2006; Zhu et al., 2006; Friedman, 2007; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. Presence of a presupracleithrum is only inferred in *Donnrosenia* (Long et al., 2008), *Gogosardina* (Choo et al., 2009) and *Kentuckia hlavini* (Dunkle, 1964), and the coding for these taxa is revised from 011

to 0. Similarly, absence is inferred in *Krasnoyarchichthys* (Prokofiev, 2002) and *Novagonatodus* (Long, 1988; Holland et al., 2007), and the coding is thus changed from "0" to "?". An elongate bone termed the "anocleithrum" is variably present in *Wendichthys* (Lund & Poplin, 1997) in the position occupied by the presupracleithrum in other taxa. We regard this as a positional homologue, and code the taxon "0/1" to reflect this polymorphism. Coded as "?" in *C. trailli* following arguments in Friedman & Blom (2006). The coding is revised to "0" in *Osorioichthys* (Taverne, 1997). The coding for *Moythomasia lineata* is revised to "1" (Choo, 2015).';

TEXT CHARACTER = 190 TEXT = Xu_et_al._2014._;

TEXT CHARACTER = 191 TEXT = Cavin_&_Suteethorn_2006.;

TEXT CHARACTER = 192 TEXT = 'Gardiner & Schaeffer, 1989; Lund et al., 1995; Cloutier & Ahlberg, 1996; Dietze, 2000; Poplin & Lund, 2000; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Cloutier & Arratia, 2004; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Zhu et al., 2013.';

TEXT CHARACTER = 193 TEXT = 'Coates 1999; Xu & Gao 2011; Xu et al. 2014; Xu & Zhao, 2016.';

TEXT CHARACTER = 194 TEXT = 'Arratia 2013. The serrated organ (or appendage) is a small, elongate element, typically ornamented with serrated ridges, present near the anterior margin of the cleithrum. ';

TEXT CHARACTER = 195 TEXT = 'Cloutier & Arratia, 2004; Xu et al., 2014. ';

TEXT CHARACTER = 196 TEXT = 'Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Friedman, 2007; Zhu et al., 2009; Xu & Gao, 2011; Zhu et al., 2013; Xu et al., 2014. The endoskeletal shoulder girdle is only described for *Mimipiscis toombsi*, so the coding for this character is revised from "?" for *M. bartrami* (Gardiner, 1984; Choo, 2011). The precise morphology of the scapulocoracoid is not known for *Cheirolepis canadensis* (Arratia & Cloutier, 1996) or *Gogosardina* (Choo et al., 2009), and as such the coding for these taxa is changed from 0 to 1. *Cheirolepis trailli* is coded 0 (Giles et al., 2015a). ';

TEXT CHARACTER = 197 TEXT = 'Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Rosen, 1989; Taverne, 1997; Coates, 1999; Zhu & Schultze, 2001; Zhu et al., 2001; Zhu & Yu, 2002; Zhu et al., 2006; Brazeau, 2009; Zhu et al., 2009; Friedman & Brazeau, 2010; Xu & Gao, 2011; Davis et al., 2012; Zhu et al., 2013; Xu et al., 2014; Giles et al., 2015b. ';

TEXT CHARACTER = 198 TEXT = 'Patterson, 1982; Gardiner, 1984; Gardiner & Schaeffer, 1989; Taverne, 1997; Coates, 1999; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011; Xu & Gao, 2011. The radials are only described for *Mimipiscis toombsi*, so the coding for this character is revised from 1 to 0 for *M. bartrami* (Choo, 2011). The radials are not described in *Gogosardina* (Choo et al., 2009), so the coding is changed from 1 to 0. ';

TEXT CHARACTER = 200 TEXT = 'Taverne, 1997; Coates, 1999; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Xu & Gao, 2011; Xu et al., 2014. The pectoral fin of *Cuneognathus* (Friedman & Blom, 2006) and *Kentuckia hlavini* (Dunkle, 1964) is unknown, and so the coding is revised from 0 to 1';

TEXT CHARACTER = 201 TEXT = 'Zhu & Yu, 2002; Friedman, 2007. Two series of pectoral fin radials are described (but not figured) for *Cheirolepis candensis* (Arratia & Cloutier, 2004). Although we consider this arrangement to be unlikely, for now this taxon is coded "1". Although Swartz (2009) describes a series of endoskeletal radials in *Stegotrachelus*, the elements figured in fig. 17 have a scale-like morphology and appear to be made of dermal bone. As such, this taxon is coded "?".';

TEXT CHARACTER = 202 TEXT = 'Coates, 1999; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011; Xu & Gao, 2011; Xu et al., 2014. The pectoral fin in *Kentuckia hlavini* (Dunkle, 1964) is not preserved, so the coding for this taxon is revised from 0 to 1. The coding for *Osorioichthys* (Taverne, 1997) is revised from "0" to "1". The segmentation of the pectoral fin is not described for *Limnomis* (Daeschler, 2000), so the coding for this taxon is revised from "0" to "?".';

TEXT CHARACTER = 203 TEXT = 'Gardiner & Schaeffer, 1989; Coates, 1998; Coates, 1999; Lund, 2000; Schultze & Cumbaa, 2001; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Zhu et al., 2006; Long et al., 2008; Swartz, 2009; Zhu et al., 2009; Choo, 2011; Xu

et al., 2014. The pelvic fin is incomplete in *Novagonatodus* (Long, 1988; Holland et al., 2007), so this taxon is coded "?". The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 204 TEXT = 'Friedman, 2007; Zhu & Yu, 2002. ';

TEXT CHARACTER = 205 TEXT = 'Lund, 2000; Poplin & Lund, 2000; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. Choo's (2011) codes for this character appear reversed. ';

TEXT CHARACTER = 206 TEXT = 'Patterson, 1982; Taverne, 1997; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. The coding for *Howqualepis rostridens* (Long, 1988) and *Melanecta* (Coates, 1998) is revised from 01 to 11. ';

TEXT CHARACTER = 207 TEXT = 'Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The coding for *Gogosardina* (Choo et al., 2009) is revised from 11 to 01. *Cuneognathus* (Friedman & Blom, 2006) possesses several scutes immediately anterior to the anal fin, although it is unclear how far anteriorly they extend. As such, the coding is changed from 21 to 11. The coding in *Melanecta* (Coates, 1998) is revised from 21 to 11. Choo (2011) erroneously codes *Krasnoyarichthys* (Prokofiev, 2002) as state 21, which lacks a description; the coding is revised to 11. The coding for *Moythomasia lineata* is revised to "0" (Choo, 2015).';

TEXT CHARACTER = 208 TEXT = 'Poplin & Lund, 2000; Cloutier & Arratia, 2004; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. The coding for Stegotrachelus is revised from  11 to  21.';

TEXT CHARACTER = 209 TEXT = 'Gardiner et al., 2005; Xu & Gao, 2011; Xu et al., 2014, 2015; Xu & Zhao, 2016. ';

TEXT CHARACTER = 212 TEXT = 'Patterson, 1982; Cloutier & Ahlberg, 1996; Coates, 1999; Schultze & Cumbaa, 2001; Zhu & Schultze, 2001; Friedman & Blom, 2006; Long et al., 2008; Swartz, 2009; Choo, 2011. ';

TEXT CHARACTER = 213 TEXT = 'Patterson, 1982; Taverne, 1997; Gardiner & Schaeffer, 1989; Gardiner et al., 2005; Friedman & Blom, 2006; Long et al., 2008; Choo, 2011. Choo's (2011) codes for this character appear reversed.';

TEXT CHARACTER = 214 TEXT = 'Modified from Gardiner et al., 2005. A long chordal lobe is considered to be present when the notochord reaches the posterior margin of the caudal fin. ';

TEXT CHARACTER = 215 TEXT = 'Xu & Gao 2011; Xu et al. 2014; Xu & Zhao, 2016.';

TEXT CHARACTER = 216 TEXT = Arratia_2013.;

TEXT CHARACTER = 217 TEXT = 'Coates 1999; Hurley et al. 2007; Xu et al. 2014.';

TEXT CHARACTER = 218 TEXT = 'Pinna, 1996; Hurley et al., 2007; Xu & Wu, 2012, Xu et al., 2014; Xu & Zhao, 2016.';

TEXT CHARACTER = 219 TEXT = 'Pinna, 1996, Xu & Wu, 2012, Xu et al., 2014; Xu & Zhao, 2016.';

TEXT CHARACTER = 221 TEXT = 'Wiley, 1976; Lopez-Arbarello 2011. ';

TEXT CHARACTER = 220 STATE = 0 TEXT = single;

END;

BEGIN MESQUITECHARMODELS;

ProbModelSet * UNTITLED = 'Mk1 (est.): 1- 222;

END;

Begin MESQUITE;

MESQUITESCRIPTVERSION 2;

TITLE AUTO;

tell ProjectCoordinator;

```

timeSaved 1621271660824;

getEmployee #mesquite.minimal.ManageTaxa.ManageTaxa;

tell It;

    setID 0 8638558614273783985;

    tell It;

        setDefaultOrder 52 47 66 68 79 57 46 54 50 60 0 65 1 2 3 51 4 5
48 76 75 69 58 7 77 59 78 45 55 89 53 8 67 9 74 85 49 10 11 12 63 82 14 62 71 86 72 15 16 17
18 19 20 21 81 23 70 90 44 83 24 25 91 56 73 88 80 26 87 84 64 27 28 93;

        attachments ;

    endTell;

endTell;

getEmployee #mesquite.charMatrices.ManageCharacters.ManageCharacters;

tell It;

    setID 0 2279276808437032474;

    tell It;

        setDefaultOrder 223 2 247 3 4 207 213 246 193 231 5 6 245 8 258
192 9 10 11 12 13 15 16 217 17 18 269 268 19 26 22 25 27 174 264 28 29 30 31 32 35 191 36 37
38 39 40 23 24 175 243 244 218 41 42 43 44 46 54 55 57 58 208 177 198 199 176 60 61 63 209
64 67 272 68 222 69 73 70 71 74 241 226 202 271 78 270 237 257 259 253 77 255 221 212 47
48 203 49 273 59 274 263 219 181 50 214 51 52 82 238 83 84 87 88 89 90 92 93 95 178 96 98
99 101 102 103 104 105 106 108 240 220 210 215 190 194 195 196 197 232 170 171 172 110
111 112 113 225 250 251 233 173 114 115 116 117 118 186 119 187 188 189 121 122 123 124
248 136 137 140 141 143 144 239 146 129 130 125 126 127 216 254 132 234 200 180 227 149

```

182 256 148 183 230 201 154 150 151 249 155 153 158 161 164 165 166 167 169 184 266 267
162 163 261 185 229 204 205 206 262 224 260;

attachments ;

endTell;

mqVersion 361;

checksumv 0 3 1819193692 null getNumChars 222 numChars 222

getNumTaxa 74 numTaxa 74 short true bits 2305843009213693983 states 31

sumSquaresStatesOnly 28645.0 sumSquares -4.150517416584649E19

longCompressibleToShort false usingShortMatrix true NumFiles 1 NumMatrices 1;

mqVersion;

endTell;

getWindow;

tell It;

suppress;

setResourcesState false false 100;

setPopoutState 300;

setExplanationSize 0;

setAnnotationSize 0;

setFontIncAnnot 0;

setFontIncExp 0;

setSize 2254 1233;

setLocation 316 213;

setFont SanSerif;

```

        setFontSize 10;

        getToolPalette;

        tell It;

        endTell;

        desuppress;

    endTell;

    getEmployee #mesquite.minimal.ManageTaxa.ManageTaxa;

    tell It;

        showTaxa #8638558614273783985 #mesquite.lists.TaxonList.TaxonList;

        tell It;

            setTaxa #8638558614273783985;

            getWindow;

            tell It;

                useTargetValue off;

                setTargetValue ;

                newAssistant

            #mesquite.lists.TaxonListCurrPartition.TaxonListCurrPartition;

            setExplanationSize 30;

            setAnnotationSize 20;

            setFontIncAnnot 0;

            setFontIncExp 0;

            setSize 2154 1161;

            setLocation 316 213;

```

```

        setFont SanSerif;
        setFontSize 10;
        getToolPalette;
        tell It;
            setTool
mesquite.lists.TaxonList.TaxonListWindow.arrow;
        endTell;
        setActive;
    endTell;
    showWindow;
    getEmployee #mesquite.lists.ColorTaxon.ColorTaxon;
    tell It;
        setColor Red;
        removeColor off;
    endTell;
    getEmployee
#mesquite.lists.TaxonListAnnotPanel.TaxonListAnnotPanel;
    tell It;
        togglePanel off;
    endTell;
endTell;
endTell;

```

```

    getEmployee
#mesquite.charMatrices.BasicDataWindowCoord.BasicDataWindowCoord;

    tell It;

        showDataWindow #2279276808437032474
#mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindowMaker;

    tell It;

        getWindow;

        tell It;

            setExplanationSize 30;

            setAnnotationSize 80;

            setFontIncAnnot 0;

            setFontIncExp 0;

            setSize 2154 1101;

            setLocation 316 213;

            setFont SanSerif;

            setFontSize 10;

            getToolPalette;

            tell It;

                setTool

mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindow.ibeam;

        endTell;

        setTool

mesquite.charMatrices.BasicDataWindowMaker.BasicDataWindow.ibeam;

```

```

colorCells #mesquite.charMatrices.NoColor.NoColor;

colorRowNames

#mesquite.charMatrices.TaxonGroupColor.TaxonGroupColor;

colorColumnNames

#mesquite.charMatrices.CharGroupColor.CharGroupColor;

colorText #mesquite.charMatrices.NoColor.NoColor;

setBackground White;

toggleShowNames on;

toggleShowTaxonNames on;

toggleTight off;

toggleThinRows off;

toggleShowChanges on;

toggleSeparateLines off;

toggleShowStates on;

toggleReduceCellBorders off;

toggleAutoWCharNames on;

toggleAutoTaxonNames off;

toggleShowDefaultCharNames off;

toggleConstrainCW on;

toggleBirdsEye off;

toggleShowPaleGrid off;

toggleShowPaleCellColors off;

toggleShowPaleExcluded off;

```



```
togglePaleInapplicable on;

togglePaleMissing off;

toggleShowBoldCellText off;

toggleAllowAutosize on;

toggleColorsPanel off;

toggleDiagonal on;

setDiagonalHeight 80;

toggleLinkedScrolling on;

toggleScrollLinkedTables off;

endTell;

showWindow;

getWindow;

tell It;

    forceAutosize;

endTell;

getEmployee #mesquite.charMatrices.AlterData.AlterData;

tell It;

    toggleBySubmenus off;

endTell;

getEmployee #mesquite.charMatrices.ColorByState.ColorByState;

tell It;

    setStateLimit 9;

    toggleUniformMaximum on;
```

```

endTell;

getEmployee #mesquite.charMatrices.ColorCells.ColorCells;

tell It;

    setColor Red;

    removeColor off;

endTell;

getEmployee

#mesquite.categ.StateNamesEditor.StateNamesEditor;

tell It;

    makeWindow;

    tell It;

        setExplanationSize 30;

        setAnnotationSize 20;

        setFontIncAnnot 0;

        setFontIncExp 0;

        setSize 2154 1161;

        setLocation 316 213;

        setFont SanSerif;

        setFontSize 10;

        getToolPalette;

        tell It;

            setTool

mesquite.categ.StateNamesEditor.StateNamesWindow.ibeam;

```

```

        endTell;

        rowsAreCharacters on;

        toggleConstrainChar on;

        toggleConstrainCharNum 3;

        togglePanel off;

        toggleSummaryPanel off;

    endTell;

    showWindow;

endTell;

getEmployee #mesquite.categ.StateNamesStrip.StateNamesStrip;

tell It;

    showStrip off;

endTell;

getEmployee #mesquite.charMatrices.AnnotPanel.AnnotPanel;

tell It;

    togglePanel off;

endTell;

getEmployee

#mesquite.charMatrices.CharReferenceStrip.CharReferenceStrip;

tell It;

    showStrip off;

endTell;

```

```

        getEmployee
#mesquite.charMatrices.QuickKeySelector.QuickKeySelector;
        tell It;
            autotabOff;
        endTell;
        getEmployee
#mesquite.charMatrices.SelSummaryStrip.SelSummaryStrip;
        tell It;
            showStrip off;
        endTell;
        getEmployee
#mesquite.categ.SmallStateNamesEditor.SmallStateNamesEditor;
        tell It;
            panelOpen true;
        endTell;
    endTell;
endTell;
getEmployee #mesquite.charMatrices.ManageCharacters.ManageCharacters;
tell It;
    showCharacters #2279276808437032474
#mesquite.lists.CharacterList.CharacterList;
    tell It;
        setData 0;

```

```

getWindow;

tell It;

    useTargetValue off;

    setTargetValue ;

    newAssistant

#mesquite.lists.DefaultCharOrder.DefaultCharOrder;

    newAssistant

#mesquite.lists.CharListInclusion.CharListInclusion;

    newAssistant

#mesquite.lists.CharListPartition.CharListPartition;

    newAssistant

#mesquite.parsimony.CharListParsModels.CharListParsModels;

    setExplanationSize 30;

    setAnnotationSize 20;

    setFontIncAnnot 0;

    setFontIncExp 0;

    setSize 2154 1161;

    setLocation 316 213;

    setFont SanSerif;

    setFontSize 10;

    getToolPalette;

tell It;

```

```
                                setTool
mesquite.lists.CharacterList.CharacterListWindow.ibeam;
                                endTell;
                                endTell;
                                showWindow;
                                getEmployee
#mesquite.lists.CharListAnnotPanel.CharListAnnotPanel;
                                tell It;
                                togglePanel off;
                                endTell;
                                endTell;
                                endTell;
                                endTell;
end;
```

Taxon	1	2	3	4	5	6	7	8	99
Acipenser brevirostrum	01-----007000-1-71000-01011--00110-0771-001001-000-00-----010-0-70-1-0-0-001011-								
Aesopichthys erinaceus	1-00-000001110101110011120700010110-11110101--1101000-0111010000000000002077771207777777								
Amia calva	01-1000120100110000001120101011--0001110110000110000-10-0100001111000002017110112010017010								
Amphicentrum granulosum	000101000710101171001020700011--01717700-11000000000-11100000007010-1-772070-0-1200010								
Atractosteus spatula	0000100-1201011100000012010111--012110112-3-1011101101001001000000100110212000010011								
Australosomus kochi	177777-77-77070777771020100011-0101100770-001-0-01011100000001000207011-0-0-020000								
Beagiascus pulcherrimus	00000000011010111001120100010110-0210-7101003111000-7107117700007700010177777-077777777								
Beishanichthys brevicaudalis	007010007011010111001120707711--00111700-1002100207001017110000000070002017727717077777777								
Birgeria groenlandica	1-1-0--11010110001720100011--01001101020030102000017101110000000000101701771070010000								
Bobasatrania groenlandica	1-1--00010111-01120700011-07001100-2100100000-00-010001100000010-0-772770-7-0777070								
Boreosomus piveteau	0010110000101111107102010011--01100-00-2003100000-110101110000070000107001030-0-020000								
Caturus furcatus	000100017110111000001120001101--0001110112102701200110-0100001111770002077010312010210017								
Cheirolepis canadensis	0701-00000000000770100107000100-0-1001100-1010010000-01071111100000010000100771070-0777777777								
Cheirolepis schultzei	0000000000700000000701001020700711--001011170-1010010000-01071111700000100007007777777770777777777								
Cheirolepis trilli	000010000000000010010010100010000-1001000-1010010000-0110111170000010000100771010-0-0100000								
Chondrosteus acipenseroides	1-----17777777-71020777711--07270-777077700777777-00-----770010-0-7071-770-0777177								
Coccocephalichthys waldi	777707777771710101071020100111--00110-01120007001070170701170070077000101777171070107000								
Cosmoptychius striatus	077100070071010111001127700011--7071770101002100000-01070111000000017000107772777770207707								
Cyanorhis bergeraci	1-----11010111-01120100010100-11110101002110000-0101011000000700020777777770770277777								
Dapedium LIAS	001100001711011070001--0-77----1-11110102-3-0-100070-010000110171100207007017077777077								
Dapedium pholidotum	00110000111011010001--7-01---1-21110102-3-0-200010-010000170100100207777777707077777								
Dipteronotus ornatus	077100007711010010771120700071--7077777170-007771-177771000000000000020177777707017777								
Dissoserpa pectinodon	000010000101010111001120700001--00211000-2003001100000-0100007000000000207772070-0-0717770								
Dnrosneria schaefferi	070017000011011110000010100010100-1011170-7770710000-070711170000011000107771770-0-7777777								
Dorsetichthys bechei	070100100711010100001121107111--0001100102101110100000-7101001102000002077177772100717077								
Ebaenaqua ritchei	1--1-----11010101-01120700011--0010100-2700000000-00-010001170007010-0-772070-070777777								
Elops hawaiiensis	01-10010211010000000112100111--0001110102100000100010-1101001102000000010021-12000210010								
Erpetoichthys calabaricus	01-110000001000000100102011101--211100-1003000000-010101101000000000207002031000-0011010								
Evvenkia eunoptera	07001000000070107100112001111--7177007200200001701100000007702077717777777777777777777								
Fouldenia ischiptera	000101000711010107001110777711-01011170-1000700000-7101711170000007010217772070-0710707777								
Fugangichthys longidorsalis	000710007711017111071020701011--0110117777031002070710101100000077000201007710070011010								
Gogosaurina coatesi	000010000001011110000100701071777770-770007070770100711100000010000010702070-0-0107000								
Hiodon alosoides	0001001001101101000001120100111--10011000-2000000000-00-100101100010002007021-12000017010								
Howqualepis rostridens	01-010000001010111100102010010100-1011170-1100010000-010011170000000001107711070-0-0100000								
Hulettia americana	000100000111110000001720100011--0001110102-03100200000-0100001100070072077710712000210010								
Ichthyokentema purbeckensis	01-100100111011010001020100011--0001100102101101200010-010000110100000077020421200210000								
Kalops monophyrum	000100007711010111001121100011--00010-010200300020000101011000000700001077207707777777777								
Kansasiella eatoni	777777777777777777770020100711-0777								
Kentucky deani	07001000000010111000020100017-710711100-7700070007-7107711170000700017770277770-0107000								
Lawrenciella schaefferi	77								

182

Taxon	1	2	2
	8	9	0 1 2 2
	3456789012345678901234567890123456789012		
Acipenser brevirostrum	-000000-00000101710001211200011000100001		
Aesopichthys erinaceus	??????10700777770700021027770100777777		
Amia calva	1001100-0011100101010000021110111100100		
Amphicentrum granulosum	??????70-770777777777777777777777777777		
Atractosteus spatula	2001100-1011100100010000011111110100110		
Australosomus kochi	-000100-00001107000100000001077100100001		
Beagiascus pulcherrimus	??????1170077777771200117177771007777777		
Beishanichthys breviceaudalis	-777770-7077777777100000277710117777777		
Birgeria groenlandica	-070700-02001077-00300000200011000100001		
Bobosatrana groenlandica	-777770-00177777770001012107711007777771		
Boreosomus piveteaui	-777770-02001177707100010200701000000701		
Caturus furcatus	17771710077170777770000021111107100000		
Cheirolepis canadensis	??????70-700777000101010107770101777777		
Cheirolepis schultzei	??????77700777777070707777777777777777		
Cheirolepis trailli	-77777100000000100001011107701007700771		
Chondrosteus acipenseroides	??????70-707777777270000777711077000071		
Coccocephalichthys wildi	??????77707777777777777777777777777777		
Cosmoptychius striatus	??????70-7000777011110100277711007777077		
Cyanorhis bergeraci	??????107707177771710010127770100777777		
Dapedium LIAS	??????1070171777772077777771717777770		
Dapedium pholidotum	??????10701717777770021121771117777777		
Dipteronotus ornatus	??????777277777777777700271277771107100777		
Discoserra pectinodon	-777771177171777007700201200011117107771		
Donnrosenia schaefferi	-777777700777777171010117777177777777		
Dorsetichthys bechei	????7170-7077777710720000027771101111000		
Ebenaqua ritchei	??????71172177777720021117711017777777		
Elops hawaiiensis	0100010-00101001110000000211111100100000		
Erpetoichthys calabaricus	-011010-00001777077-7777-71117117777170		
Evenkia eunoptera	??????107777777770700007127771007777777		
Fouldenia ischiptera	??????70-7007077100000021117770100777777		
Fukangichthys longidorsalis	-7171777007777777710000027770117777777		
Gogosardina coatesi	-707777-00001777717100210277771077000770		
Hiodon alosoides	0100110-0010100111011000011110100111000		
Howqualepis rostridens	-777771000000771000110111177701007000777		
Huletia americana	00777100-7010177777700101211101010000000		
Ichthyokentema purbeckensis	0777770-00101177710700101717711107117700		
Kalops monophyrum	??????107007177770700021127770100777777		
Kansasiella eatoni	??????77777777777777777777777777777777		
Kentuckia deani	-777777777777777777777777777777777777		
Lawrenciella schaefferi	??????77777777777777777777777777777777		
Lepisosteus osseus	2001100-1011100100010000001111110100110		
Leptolepis bronni	7077710-70111777170100000211011100111000		
Luederia kempfi	??????77777777777777777777777777777777		
Luganoia lepidosteoides	??????70-7217700171010000021771111777777		
Macrepistius arenatus	??-7770-771777777777777777777777777777		
Macrosemimimus lennieri	0777770-70171777717700000277777777777777		
Macrosemius rostratus	7777100-1710100077010071021111110700700		
Melanecta anneae	??????70-700777777171011127771100777777		
Trawdenia planti	??????7101200710177710011117777000777777		
Mimipiscis bartrami	-101001000007717010100211207071000000701		
Mimipiscis toombsi	-101001000000111010700211107011000000701		
Moythomasia durgaringa	-101001000000111717100211107711700100701		
Moythomasia lineata	??????1070077117710000210277711707777777		
Moythomasia nitida	??????107007777071700211177711007777770		
Obaichthys decoratus	2777170-1001170700010000017777170170710		
Osorioichthys marginis	??????70-700707110001702777777777777777		
Peltopleurus lissocephalus	??-7770-02771777717100001277710107777777		
Platysomus superbus	??????70-7007777770700000027771107777777		
Polypterus bichir	-011010-0000100000000000201110110100100		
Propterus elongatus	0777770-07011077070100777271111107177100		
Pteroniscus stensioi	-10100100000117017000111200001000000701		
Raynerius splendens	-101001007000777777777777777777777777		
Saurichthys madagascarensis	??????70-020710710001002111011111770771		
Scanilepis dubia	??????70-777777777770077277770777777777		
Semionotus elegans	0101100-1011100077010020121111110100100		
Styracopterus fulcratus	??????70-7007077770720021127770100777777		
Tanaocrossus kalliokoskii	??????7777777777777777707777777171777777		
Tegeolepis clarki	??????777777777770717001017777777777770		
Tetragonolepis semicincta	1777770-0010171101010020121111117100000		
Venusichthys comptus	??????70-7017177771710000027771100777777		
Watsonulus eugnathoides	007777100207117771720000027-711107700700		
Wendychthys dicksoni	??????70-7007177771700010127771100777777		
	1		
Woodichthys bearsdeni	??????70-7007771101710011127771100777777		
Concetrilepis minnekahtaensis	??????107200177207110171120771110777777		

A6 Log of maximum parsimony analysis in PAUP

P A U P *

Version 4.0a (build 167) for Macintosh (X86) (built on Feb 1 2020 at 22:15:41)

Friday, July 17, 2020 at 3:37:28 PM Eastern Daylight Time

Processing of file "~/Parsimony/First Full

Run/Data/PF3721_FullMatrix_7_17_2020_MinorChanges.txt"

begins...

Data matrix has 74 taxa, 222 characters

Valid character-state symbols: 01234

Missing data identified by '?'

Gaps identified by '-'

Case significant for alphabetic character-state symbols

Character types changed:

Of 222 total characters:

7 characters are of type 'ord' (Wagner)

215 characters are of type 'unord'

All characters have equal weight

*** Skipping "NOTES" block

*** Skipping "MESQUITECHARMODELS" block

*** Skipping "MESQUITE" block

Processing of input file "PF3721_FullMatrix_7_17_2020_MinorChanges.txt" completed.

paup> Outgroup 13-15;

Outgroup status changed:

3 taxa transferred to outgroup

Total number of taxa now in outgroup = 3

Number of ingroup taxa = 71

paup> Set maxtrees=1000 increase=auto autoInc=1000;

Maxtrees reset to 1000

paup> HSearch nchuck=10000 chuckScore=1 addSeq=random nreps=500 hold=5;

Heuristic search settings:

Optimality criterion = parsimony

Character-status summary:

Of 222 total characters:

7 characters are of type 'ord' (Wagner)

215 characters are of type 'unord'

All characters have equal weight

All characters are parsimony-informative

Gaps are treated as "missing"

Multistate taxa interpreted as uncertainty

Starting tree(s) obtained via stepwise addition

Addition sequence: random

Number of replicates = 500

Starting seed = generated automatically

Number of trees held at each step = 5

Branch-swapping algorithm: tree-bisection-reconnection (TBR) with reconnection limit = 8

Steepest descent option not in effect

No more than 10000 trees of score (length) greater than or equal to 1 will be saved in each replicate

Initial 'Maxtrees' setting = 1000 (will be auto-increased by 1000)

Branches collapsed (creating polytomies) if maximum branch length is zero

'MulTrees' option in effect

No topological constraints in effect

Trees are unrooted

Heuristic search completed

Total number of rearrangements tried = 3.7375e+10

Score of best tree(s) found = 1088

Number of trees retained = 49308

Time used = 05:36:00 (CPU time = 02:46:32.0)

A7 Log of Bayesian analysis in MrBayes

#Script written by Jack Stack in August 2020

#Execute dataset

exe /Users/Hemaron/MrBayes/8_11_20_Run/Data/MrBayes1_8_10_20.nex

outgroup Cheirolepis_canadensis

lset rates=gamma coding = variable

mcmc ngen=500000

mcmc samplefreq=100

mcmc printfreq=100

sump

sumthin's burninfrac=0.5

REFERENCES

REFERENCES

- Agassiz, L.** 1834. Abgerissene Bemerkungen über fossile Fische. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 379–390.
- Agassiz, L.** 1833–1844. Recherches sur les poissons fossiles. Text (5 volumes) and Atlas (2 volumes).
- Ahlberg, P. E. & Clack, J. A.** 1998. Lower jaws, lower tetrapods - a review based on the Devonian genus *Acanthostega*. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **88**, 11–46. DOI:10.1017/S0263593300002340
- Ahlberg, P. E. & Johanson, Z.** 1998. Osteolepiforms and the ancestry of tetrapods. *Nature*, **395**, 792–794. <https://doi.org/10.1038/27421>
- Aldinger, H.** 1937. Permische Ganoidfisch aus Ostgrönland. *Meddelelser om Grønland*, **102**, 1–392.
- Alfaro, M. E., Santini, F., Brock, C., Alamillo, H., Dornberg, A., Rabosky, D. L., Carnevale, G. & Harmon, L. J.** 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 13410–13414. <https://doi.org/10.1073/pnas.0811087106>
- Allis, E. P.** 1922. The cranial anatomy of *Polypterus*, with special reference to *Polypterus bichir*. *Journal of Anatomy*, **56**, 189–294.
- Anderson, K., Woods, A.D., Min, L. & Yuan, W.** 2013. Taphonomy of Early Triassic fish fossils of the Vega-Phroso Siltstone Member of the Sulphur Mountain Formation near Wapiti Lake, British Columbia, Canada. *Journal of Palaeogeography*, **2**(4), 321–343. <https://doi.org/10.3724/SP.J.1261.2013.00034>
- Andrews, S. M., Long, J. A., Ahlberg, P. E., Barwick R., & Campbell, K.** 2006. The structure of the sarcopterygian *Onychodus jandemarra* n. sp. from Gogo, Western Australia: with a functional interpretation of the skeleton. *Transactions of the Royal Society of Edinburgh*, **96**, 197–307. DOI:10.1017/S0263593300001309
- Arnason, U., Gullberg, A. & Janke, A.** 2001. Molecular phylogenetics of gnathostome (jawed) fishes: old bones, new cartilage. *Zoologica Scripta*, **30**, 249–255. <https://doi.org/10.1046/j.1463-6409.2001.00067.x>
- Arnason, U., Gullburg, A., Janke, A., Joss, J. & Elmerot, C.** 2004. Mitogenomic analyses of deep gnathostome divergences: a fish is a fish. *Gene*, **333**, 61–70. <https://doi.org/10.1016/j.gene.2004.02.014>

- Arratia, G.** 2009. Identifying patterns of diversity of the actinopterygian fulcra. *Acta Zoologica*, Supplement, **90**, 220–235. <https://doi.org/10.1111/j.1463-6395.2008.00375.x>
- Arratia, G. & Cloutier, R.** 1996. Reassessment of the morphology of *Cheirolepis canadensis* (Actinopterygii). Pp. 165–197 in H. P. Schultze & R. Cloutier (eds). *Devonian fishes and plants of Miguasha, Quebec, Canada*. Verlag Dr. Frederich Pfeil, Munich, 374 pp.
- Bakaev, A. S., Kogan, I. & Yankevich, D. I.** 2020. On the validity of names of some Permian actinopterygians from European Russia. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, **296**(3), 305–316. <https://dSPACE.kpfu.ru/xmlui/handle/net/161726>
- Balfour F. M. & Parker, W. N.** 1882. On the structure and development of *Lepisosteus*. *Philosophical Transactions of the Royal Society, London*, **2**, 359–442.
- Barton, D. G. & Wilson, M. V.** 2005. Taphonomic variations in Eocene fish-bearing varves at Horsefly, British Columbia, reveal 10,000 years of environmental change. *Canadian Journal of Earth Sciences*, **42**(2), 137–149. <https://doi.org/10.1139/e05-001>
- Bartram, A. W. H.** 1977. The Macrosemiidae, a Mesozoic family of holostean fishes. *Bulletin of the British Museum of Natural History (Geology)*, **29**, 137–234. <http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCALGEODEBRGM7820349612>
- Bartsch, P. & Gemballa, S.** 1992. On the anatomy and development of the vertebral column and pterygiophores in *Polypterus senegalus* Cuvier, 1829 (Pisces, Polypteriformes). *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*, **122**, 497–529. <http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=4911784>
- Bartsch, P., Gemballa, S. & Piotrowski, T.** 1997. The embryonic and larval development of *Polypterus senegalus* Cuvier, 1829: its staging with reference to external and skeletal features, behaviour and locomotory habits. *Acta Zoologica, Stockholm*, **78**(4), 309–328. <https://doi.org/10.1111/j.1463-6395.1997.tb01014.x>
- Basden, A. M. & Young, G. C.** 2001. A primitive actinopterygian neurocranium from the Early Devonian of southeastern Australia. *Journal of Vertebrate Paleontology*, **21**(4), 754–766. DOI: 10.1671/0272-4634(2001)021[0754:APANFT]2.0.CO;2
- Basden, A. M., Young, G. C., Coates, M. I. & Ritchie, A.** 2000. The most primitive osteichthyan braincase? *Nature*, **403**, 185–188. <https://doi.org/10.1038/35003183>
- Bender, P.** 2001. A new actinopterygian fish species from the Late Permian Beaufort Group, South Africa. *Palaeontologia Africana* **37**, 25–40. <http://hdl.handle.net/10539/16361>
- Bender, P.** 2002. A new Late Permian ray-finned (actinopterygian) fish from the Beaufort

- Group, South Africa. *Palaeontologia Africana*, **38**, 33–47.
<http://hdl.handle.net/10539/16350>
- Berg, L. S.** 1941. Lower Triassic fishes of the Tunguska Coal basin, Yenisei, Siberia. *Izvestiya Akademii Nauk SSSR (Seriya. Biologicheskaya)*, **1941**, 458–474.
- Betancur-R, R., Broughton, R. E., Wiley, E. O., Carpenter, K., Lopez, J. A., Li, C., Holcroft, N. I., Arcila, D., Sanciang, M., Cureton, J. C., Zhang, F., Buser, T., Campbell, M. A., Ballesteros, J. A., Roa-Varon, A., Willia, S., Borden, W. C., Rowley, R., Reneau, P. C., Hough, D. J., Lu, G., Grande, T., Arratia, G. & Orti, G.** 2013. The tree of life and a new classification of bony fishes. *PLoS Currents Tree of Life*, **5**, 10.1371/currents.tol.53ba26640df0ccaee75bb165c8c26288.
- Bjerring, H. C.** 1991. Two intracranial ligaments supporting the brain of the brachiopterygian fish *Polypterus senegalus*. *Acta Zoologica, Stockholm*, **72**(1), 41–47.
<https://doi.org/10.1111/j.1463-6395.1991.tb00314.x>
- de Blainville, H.** 1818. Sur les ichthyolites ou les poissons fossiles. *Nouveau Dictionnaire d'Histoire Naturelle, appliqu'ee aux Arts, `a l'Agriculture, `a l'Economie rurale et ` domestique, `a la Medicine, etc. Nouvelle Edition*, **27**, 310–395.
- Boggs Jr. S.** 2009. *Petrology of Sedimentary Rocks*. 2nd edition. Cambridge University Press, New York, 600 pp.
- Boyd, D.W. & Maughan, E. K.** 1972. Permian-Triassic boundary in the middle Rocky Mountains. *Bulletin of Canadian Petroleum Geology*, **20**(4), 676–699.
<https://doi.org/10.35767/gscpgbull.20.4.676>
- Budgett, J. S.** 1901. On some points in the anatomy of *Polypterus*. *Transactions of the Zoological Society of London*, **15**(6), 323–338. <https://doi.org/10.1111/j.1096-3642.1901.tb00025.x>
- Bürgin, T.** 1992. Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland). *Schweizerische Paläontologische Abhandlungen*, **114**, 1–164.
- Bradley Dyne, M.** 1939. The skull of *Amphicentrum granulosum*. *Proceedings of the Zoological Society, London B*, **109**(2), 195–210. <https://doi.org/10.1111/j.1096-3642.1939.tb00713.x>
- Braddock, W. A.** 1963. Geology of the Jewel Cave SW Quadrangle Custer Country, South Dakota. Pp. 217–261 in W.A. Braddock *Geology and uranium deposits of the southern Black Hills*. Geological Survey Bulletin 1063-G. United States Government Printing Office, Washington, D.C., 267 pp.
- Brazeau, M. D.** 2009. The braincase and jaws of a Devonian ‘acanthodian’ and modern gnathostome origins. *Nature*, **457**, 305–308. <https://doi.org/10.1038/nature07436>

- Bremer, K. R.** 1994. Branch support and tree stability. *Cladistics*, **10**(3), 295–304.
<https://doi.org/10.1111/j.1096-0031.1994.tb00179.x>
- Bronn, H.** 1830. Über die muschel-versteinerungen des sud-deutschen steinsalzgebirges, welche bisher unter den namen pectines salinarius zusammenbegriffen wurden. *Jahrbuch für Mineralogie, Geognosie, Geologie, und Petrefaktenkunde*, **1**, 279–285.
- Broughton, R. E., Betancur-R, R., Li, C., Arratia, G. & Orti, G.** 2013. Multi-locus phylogenetic analyses reveals the pattern and tempo of bony fish evolution. *PLoS Currents Tree of Life* 10.1371/currents.tol.2ca8041495ffafd0c92756e75247483e).
- Brooks, H. K.** 1962. The Paleozoic Eumalacostraca of North America. *Bulletins of American Paleontology*, **44**(202), 163–338.
- Burk, C. A. & Thomas, H. D.** 1956. *The Goose Egg formation (Permo-Triassic) of eastern Wyoming*. The Geological Survey of Wyoming report of investigations 6. University of Wyoming, Laramie, 11 pp.
- Campbell, K. S. W. & Phouc, L. D.** 1983. A late Permian actinopterygian fish from Australia. *Journal of Palaeontology*, **26**, 33–70.
- Case, E. C.** 1935. A new paleoniscid fish, *Eurylepidoides socialis*, from the Permo-Carboniferous of Texas. *Contributions from the Museum of Paleontology, University of Michigan*, **4**, 275–277.
- Chang, M. M. & Miao, D. S.** 2004. An overview of Mesozoic fishes in Asia. Pp. 535–563. In G. Arratia & A. Tintori (eds.) *Mesozoic Fishes: Systematics, Paleoenvironments and Biodiversity*. Verlag Dr. Friedrich Pfeil, Munich. 576 pp.
- Chen, M., Zou, M., Yang, L. & He, S.** 2012. Basal jawed vertebrate phylogenomics using transcriptomic data from Solexa sequencing. *PLoS One* **7**, e36256.
<https://doi.org/10.1371/journal.pone.0036256>
- Choo, B.** 2011. Revision of the actinopterygian genus *Mimipiscis* (= *Mimia*) from the Upper Devonian Gogo Formation of Western Australia and the interrelationships of the early Actinopterygii. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **102**(2), 77–104. <https://doi.org/10.1017/S1755691011011029>
- Choo, B., Long, J. A. & Trinajstić, K.** 2009. A new genus and species of basal actinopterygian fish from the Upper Devonian Gogo Formation of Western Australia. *Acta Zoologica, Supplement*, **90**(1), 194–210. <https://doi.org/10.1111/j.1463-6395.2008.00370.x>
- Claeson, K., Bemis, W. E. & Hagadorn, J. W.** 2007. New interpretations of the skull of a primitive bony fish *Erpetoichthys calabaricus* (Actinopterygii: Cladistia). *Journal of Morphology*, **268**(4), 1021–1039. <https://doi.org/10.1111/j.1095-8649.2008.02007.x>

- Claeson, K. M. & Hagadorn, J. W.** 2008. The occipital region in the basal bony fish *Erpetoichthys calabaricus* (Actinopterygii: Cladistia). *Journal of Fish Biology*, **73**(4), 1075–1082. <https://doi.org/10.1111/j.1095-8649.2008.02007.x>
- Clarkson, E. N. K.** 2009. *Invertebrate paleontology and evolution*. Blackwell Science, Malden, 452 pp.
- Coates, M. I.** 1998. Actinopterygians from the Namurian of Bearsden, Scotland, with comments on early actinopterygian neurocrania. *Zoological Journal of the Linnean Society*, **122**(1-2), 27–59. <https://doi.org/10.1111/j.1096-3642.1998.tb02524.x>
- Coates, M. I.** 1999. Endocranial preservation of a Carboniferous actinopterygian from Lancashire, UK, and the interrelationships of primitive actinopterygians. *Philosophical Transactions of the Royal Society of London B*, **354**(1382), 435–462. <https://doi.org/10.1098/rstb.1999.0396>
- Coates, M. I. & Sequeira, S. E. K.** 1998. The braincase of a primitive shark. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, **89**(2), 63–85. <https://doi.org/10.1017/S026359330000701X>
- Coates, M. I. & Sequeira, S. E. K.** 2001. A new stethacanthid chondrichthyans from the Lower Carboniferous of Bearsden, Scotland. *Journal of Vertebrate Paleontology*, **21**(1), 438–459. [https://doi.org/10.1671/0272-4634\(2001\)021\[0438:ANSCFT\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2001)021[0438:ANSCFT]2.0.CO;2)
- Coates, M. I., & Tietjen, K.** 2019. ‘This strange little palaeoniscid’: a new early actinopterygian genus, and commentary on pectoral fin conditions and function. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, **109**(1-2), 15–31. <https://doi.org/10.1017/S175569101800040>
- Cohen, K. M., Finney, S. C., Gibbard, P. L. & Fan, J. X.** 2013, updated. The ICS International Chronostratigraphic Chart. *Episodes*, **36**, 199–204. [Updated at <http://www.stratigraphy.org/ICSchart/ChronostratChart2019-05.jpg>, accessed 12 August, 2019].
- Cope, E. D.** 1887. Zittel's Manual of Palaeontology. *American Naturalist*, **21**, 1014–1019.
- Daeschler, E. B., Shubin, N. H. & Jenkins, F. A.** 2006. A Devonian tetrapod-like fish and the evolution of the tetrapod body plan. *Nature*, **440**, 757–763. <https://doi.org/10.1038/nature04639>
- Daget, J.** 1950. Révision des affinités phylogénétiques des Polyptéridés. *Mémoires de l'Institut Français d'Afrique Noire*, **11**, 1–178.
- Darton, N. H., & Paige, S.** 1925. Description of the Central Black Hills quadrangle [South Dakota]: U.S. Geological Survey Geological Atlas, Folio 219.

- Davis, S. P., Finarelli, J. A. & Coates, M. I.** 2012. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature*, **486**, 247–250. <https://doi.org/10.1038/nature11080>
- Dierks, N. & Pagnac, D.** 2010. Paleozoic fish from the Minnekahta Limestone of the Black Hills. *Proceedings of the South Dakota Academy of Sciences*, **89**, 250.
- Dietze, K.** 2000. A revision of paramblypterid and amblypterid actinopterygians from Upper Carboniferous–Lower Permian lacustrine deposits of Central Europe. *Palaeontology*, **43**(5), 927–966. <https://doi.org/10.1111/1475-4983.00156>
- Dopheide, A. K., & Winniger, N. A.** 2008. A Permian stromatolite bioherm in South Dakota: Paleoenvironmental Implications. *Proceedings of the South Dakota Academy of Science*, **87**, 311–324.
- Dunkle, D. H.** 1939. A new paleoniscid fish from the Texas Permian. *American Journal of Science*, **237**(4), 262–274. <https://doi.org/10.2475/ajs.237.4.262>
- Dunkle, D. H.** 1946. A new palaeoniscoid fish from the Lower Permian of Texas. *Journal of the Washington Academy of Sciences*, **36**(12), 402–409. <https://www.jstor.org/stable/24531376>
- Dunkle, D. H. & Schaeffer, B.** 1956. Preliminary description of a paleoniscoid fish from the Late Paleozoic of Brazil, *Boletim da Faculdade de Filosofia Ciências e Letras, Universidade de São Paulo. Geologia*, **13**, 5–22.
- Elder, R. L. & Smith, G.R.** 1984. Fish taphonomy and paleoecology. *Geobios*, **17**, 287–291.
- Elder, R. L.** 1985. *Principles of aquatic taphonomy with examples from the fossil record*. Unpublished PhD thesis, University of Michigan, 336 pp.
- Fahrenback, M. D. & Sawyer, J. F.** 2001. Geologic map of the Rapid City west quadrangle, South Dakota, South Dakota Department of Environment and Natural Resources Geological Survey [http://www.sdgs.usd.edu/pubs/pdf/GQ24K-01_20060814.pdf, accessed 5 September 2019].
- Faircloth, B. C., Sorensen, L., Santini, F. & Alfaro, M. E.** 2013. A phylogenomic perspective on the radiation of ray-finned fishes based upon targeted sequencing of ultraconserved elements (UCEs). *PLoS One*, **8**, e65923. <https://doi.org/10.1371/journal.pone.0065923>
- Figueiredo, F. D. & Carvalho, B. C. M. C.** 2004. A new actinopterygian fish from the Late Permian of the Parana Basin, Southern Brazil, *Arquivos do Museu Nacional, Rio de Janeiro*, **62**, 531–547.
- Figuerola, R. T., Friedman, M., & Gallo V.** 2019. Cranial anatomy of the predatory

- actinopterygian *Brazilichthys macrognathus* from the Permian (Cisuralian) Pedra de Fogo Formation, Parnaíba Basin, Brazil. *Journal of Vertebrate Paleontology*, **39**(3), e1639722-17. <https://doi.org/10.1080/02724634.2019.1639722>
- Friedman, M.** 2007. *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *Journal of Systematic Palaeontology*, **5**(3), 289–343. <https://doi.org/10.1017/S1477201907002052>
- Friedman, M.** 2015. The early evolution of ray-finned fishes. *Palaeontology*, **58**(2), 213–228. <https://doi.org/10.1111/pala.12150>
- Friedman, M. & Blom, H.** 2006. A new actinopterygian from the Famennian of East Greenland and the interrelationships of Devonian ray-finned fishes. *Journal of Paleontology*, **80**(6), 1186–1204. [https://doi.org/10.1666/0022-3360\(2006\)80\[1186:ANAFTE\]2.0.CO;2](https://doi.org/10.1666/0022-3360(2006)80[1186:ANAFTE]2.0.CO;2)
- Friedman, M. & Brazeau, M. D.** 2010. A reappraisal of the origin and basal radiation of the Osteichthyes. *Journal of Vertebrate Paleontology*, **30**(1), 36–56. <https://doi.org/10.1080/02724630903409071>
- Fritsch (=Frič), A.** 1895. Fauna der Gaskohle und der Kalksteine der Permformation Böhmens (Volume 3). F. Rivnáč, Prague.
- Forey, P. L.** 1973. A revision of the elopiform fishes, fossil and recent (Vol. 10). British Museum (Natural History). *Bulletin of the British Museum of Natural History (Geology)*, **10**, 1–222.
- Forey, P. L.** 1980. *Latimeria*: a paradoxical fish. *Proceedings of the Royal Society of London B: Biological Sciences*, **208**(1172), 369–384. <https://doi.org/10.1098/rspb.1980.0056>
- Forey, P. L.** 1998. *History of the coelacanth fishes*. Chapman & Hall, London, 419 pp.
- Gardiner, B. G.** 1963. Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bulletin of the British Museum (Natural History): Geology*, **8**, 254–325.
- Gardiner, B. G. & Bartram, A. W. H.** 1977. The homologies of ventral cranial features in osteichthyans. Pp. 227–245 in S. M. Andrews, R. S. Miles, & A. D. Walker (eds), *Problems in Vertebrate Evolution*. Academic Press, London.
- Gardiner, B.G.** 1984. The relationships of the palaeoniscoid fishes, a review based on new specimens of *Mimia* and *Moythomasia* from the Upper Devonian of Western Australia. *Bulletin of the British Museum (Natural History): Geology*, **37**, 173–428.
- Gardiner, B. G. & Schaeffer, B.** 1989. Interrelationships of lower actinopterygian fishes. *Zoological Journal of the Linnean Society*, **97**(2), 135–187. <https://doi.org/10.1111/j.1096-3642.1989.tb00550.x>

- Gardiner, B. G., Schaeffer, B. & Masserie, J. A.** 2005. A review of lower actinopterygian phylogeny. *Zoological Journal of the Linnean Society*, **144**(4), 511–525. <https://doi.org/10.1111/j.1096-3642.2005.00181.x>
- Giebel, C. G.** 1849. Fischüberreste. Pp. 69–79 in Germar, E.F. (ed) *Versteinerungen des Steinkohlengebirges von Wettin und Löbejün im Saalkreise* 6. Schwetschke und Sohn, Halle.
- Giles, S. & Friedman, M.** 2014. Virtual reconstruction of endocast anatomy in early ray-finned fishes (Osteichthyes, Actinopterygii). *Journal of Paleontology*, **88**(4), 636–651. <https://doi.org/10.1666/13-094>.
- Giles, S., Coates, M. I., Garwood, R. J., Brazeau, M. D., Atwood, R., Johanson, Z. & Friedman, M.** 2015a. Endoskeletal structure in *Cheirolepis* (Osteichthyes, Actinopterygii), an early ray-finned fish. *Palaeontology*, **58**, 849–870. <https://doi.org/10.1111/pala.12182>.
- Giles, S., Darras, L., Clément, G., Blicek, A. & Friedman, M.** 2015b. An exceptionally preserved Late Devonian actinopterygian provides a new model for primitive cranial anatomy in ray-finned fishes. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20151485. <https://doi.org/10.1098/rspb.2015.1485>
- Giles, S., Darras, L., Clément, G., Blicek, A. & Friedman, M.** 2015c. An exceptionally preserved Late Devonian actinopterygian provides a new model for primitive cranial anatomy in ray-finned fishes. *Proceedings of the Royal Society B*, **282**(1816), 20151485. <https://doi.org/10.1098/rspb.2015.1485>
- Giles, S., Friedman, M. & Brazeau, M. D.** 2015c. Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome. *Nature*, **520**, 82–85. <https://doi.org/10.1038/nature14065>
- Goodrich, E. S.** 1908. On the systematic position of *Polypterus*. *Report of the 77th Meeting of the British Association for the Advancement of Science*, **1907**, 545–546.\
- Goodrich, E. S.** 1928. *Polypterus* a palaeoniscid. *Palaeobiologica*, **1**, 87–92.
- Goujet, D.** 1975. *Dicksonosteus*, un nouvel arthrodire du Dévonien du Spitzberg—Remarques sur le squelette viscéral des Dolichothoraci. *Colloques Internationaux du Centre National de la Recherche Scientifique*, **218**, 81–99. <http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCALGEODEBRGM7620252250>
- Gradstein, F. M., Ogg, J. G. & Schmitz, M.** (eds.). 2012. *The Geologic Time Scale 2012*, 2- volume set. Elsevier, 1176 pp.
- Grande, L.** 2010. An empirical synthetic pattern study of gars (Lepisosteiformes) and closely

- related species, based mostly on skeletal anatomy. The resurrection of Holostei. *American Society of Ichthyologists and Herpetologists, Special Publication*, **6**, 1–871.
- Grande, L. & Bemis, W. E.** 1998. A comprehensive phylogenetic study of amiid fishes (Amiidae) based on comparative skeletal anatomy. An empirical search for interconnected patterns of natural history. *Memoir (Society of Vertebrate Paleontology)*, **4**, 1–690.
- Griffith, J. & Patterson, C.** 1963. The structure and relationships of the Jurassic fish *Ichthyokentema purbeckensis*. *Bulletin of the British Museum of Natural History (Geology)*, **8**, 1–43.
- Hall, B. K.** 2001. John Samuel Budgett (1872–1904): In Pursuit of *Polypterus*. *BioScience*, **51**(5), 399–407. [https://doi.org/10.1641/0006-3568\(2001\)051\[0399:JSBIPO\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0399:JSBIPO]2.0.CO;2)
- Hamel, M. H.** 2005. A new lower actinopterygian from the early Permian of the Paraná Basin, Brazil, *Journal of Vertebrate Paleontology*, **25**(1), 19–26. [https://doi.org/10.1671/0272-4634\(2005\)025\[0019:ANLAFT\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0019:ANLAFT]2.0.CO;2)
- Hamel, M. H. & Poplin, C.** 2008. The braincase anatomy of *Lawrenciella schaefferi*, actinopterygian from the Upper Carboniferous of Kansas (USA). *Journal of Vertebrate Paleontology*, **28**(4), 989–1006. <https://doi.org/10.1671/0272-4634-28.4.989>
- Harrington, N. R.** 1899. The life habits of *Polypterus bichir*. *American Naturalist*, **22**, 721–728.
- Haubold, H. & Schaumberg, G.** 1985. *Die Fossilien des Kupferschiefers*. A. Ziemsen Verlag, Wittenberg, 223 pp.
- Hilton, E. J.** 2002. Osteology of the extant North American fishes of the genus *Hiodon* Lesueur, 1818 (Teleostei: Osteoglossomorpha: Hiodontiformes). *Fieldiana*, **100**, 1–142.
- Hilton, E. J. & Forey, P. L.** 2011. Redescription of *Chondrosteus acipenseroides* Egerton, 1858 (Acipenseriformes, Chondrosteidae) from the Lower Lias of Lyme Regis (Dorset, England), with comments on the evolution of sturgeon and paddlefishes. *Journal of Systematic Palaeontology*, **7**(4), 427–453. <https://doi.org/10.1017/S1477201909002740>
- Hilton, E. J., Grande, L. & Bemis, W. E.** 2011. Skeletal anatomy of the shortnose sturgeon, *Acipenser brevirostrum* Lesueur 1818, and the systematics of sturgeons (Acipenseriformes, Acipenseridae). *Fieldiana (Life and Earth Sciences)*, **3**(2A), 1–168. <https://doi.org/10.3158/2158-5520-3.1.1>
- Höhna, S., Landis, M. J., Heath, T. A., Boussau, B., Lartillot, N., Moore, B. R., Huelsenbeck, J. P. & Ronquist, F.** 2016. RevBayes: Bayesian phylogenetic inference using graphical models and an interactive model-specification language. *Systematic Biology*, **65**(4), 726–736. <https://doi.org/10.1093/sysbio/syw021>

- Holland, T.** 2014. The endocranial anatomy of *Gogonasmus andrewsae* Long, 1985 revealed through micro CT-scanning. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, **105**(1), 9–34. <https://doi.org/10.1017/S1755691014000164>
- Hotton, N., Feldmann, R. M., Hook, R. W. & Dimichele, W. A.** 2002. Crustacean-bearing continental deposits in the Petrolia Formation (Leonardian Series, Lower Permian) of north-central Texas. *Journal of Paleontology*, **76**(3), 486–494. [https://doi.org/10.1666/0022-3360\(2002\)076<0486:CBCDIT>2.0.CO;2](https://doi.org/10.1666/0022-3360(2002)076<0486:CBCDIT>2.0.CO;2)
- Hurley, I. A., Mueller, R. L., Dunn, K., Schmidt, E., Friedman, M., Ho, R. K., Prince, V. E., Yang, Z., Thomas, M. G. & Coates, M. I.** 2007. A new timescale for ray-finned fish evolution. *Proceedings of the Royal Society B*, **274**(1609), 489–498. <https://doi.org/10.1098/rspb.2006.3749>
- Hurley I. A., Mueller R. L., Dunn K. A., Schmidt E. J., Friedman M., Ho R. K., Prince V. E., Yang Z., Thomas M. G. & Coates M. I.** 2007. A new time scale for ray-finned fish evolution. *Proceedings of the Royal Society of London B: Biological Sciences*, **274**, 489–498. <https://doi.org/10.1098/rspb.2006.3749>
- Hussakof, L.** 1916. Note on a Palaeoniscoid Fish from a Permian Formation in South Dakota. *American Journal of Science*, **41**, 347–350. DOI: 10.2475/ajs.s4-41.244.347.
- Huxley, T. H.** 1861. Preliminary essay upon the systematic arrangement of the fishes of the Devonian epoch. Pp. 421–460 in *Memoirs of the Geological Survey of the United Kingdom: Figures and Descriptions Illustrative of British Organic Remains, Vol. 2: Scientific Memoirs*. Geological Survey of the United Kingdom, London.
- Inden, R. F. & E. B. Coalson.** 1996. Phosphoria Formation (Permian) cycles in the Bighorn basin, Wyoming, with emphasis on the Ervay Member. Pp. 379–404 in M. W. Longman & M. D. Sonnenfeld (eds) *Paleozoic systems of the Rocky Mountain region*. Rocky Mountain Section SEPM, Denver.
- Inoue, J. G., Miya, M., Tsukamoto, K. & Nishida, M.** 2003. Basal actinopterygian relationships: a mitogenomic perspective on the phylogeny of “ancient fish”. *Molecular Phylogenetics and Evolution*, **26**(1), 110–120. [https://doi.org/10.1016/S1055-7903\(02\)00331-7](https://doi.org/10.1016/S1055-7903(02)00331-7)
- Inoue, J. G., Kumazawa, Y., Masaki, M. & Nishida, M.** 2009. The historical biogeography of the freshwater knifefishes using mitogenomic approaches: a Mesozoic origin of the Asian notoptygerids (Actinopterygii: Osteoglossomorpha). *Molecular Phylogenetics and Evolution*, **51**, 486–499. <https://doi.org/10.1016/j.ympev.2009.01.020>
- Jain, S. L. & Robinson, P. L.** 1963. Some new specimens of the fossil fish *Lepidotes* from the English Upper Jurassic. *Proceedings of the Zoological Society of London*, **141**(1), 119–135. <https://doi.org/10.1111/j.1469-7998.1963.tb01604.x>

- Jarvik, E.** 1948. On the morphology and taxonomy of the Middle Devonian osteolepid fishes of Scotland. *Kungliga Svenska Vetenskapsakademiens Handlingar*, **25**, 1–30.
- Jarvik, E.** 1972. Middle and Upper Devonian Porolepiformes from East Greenland with special reference to *Glyptolepis groenlandica* n.sp. *Meddelelser om Grønland*, **187**, 1–295.
- Jarvik, E.** 1980. *Basic structure and evolution of vertebrates. Volume 1*. Academic Press, London, 575 pp.
- Jiang, D., Robbins, E. I., Wang, Y. & Yang, H.** 2016. Petroleum Sporopollen Assemblages and Petroleum Source Rocks. *Petrolipalynology*. Springer, Berlin Heidelberg, pp. 95–121.
- Jessen, H.** 1968. *Moythomasia nitida* Gross und *M. cf. striata* Gross, Devonische palaeonisciden aus dem oberen Plattenkalk der Bergish-Gladbach-Paffrather Mulde (Rheinisches Schiefergebirge). *Palaeontographica Abteilung A*, **128**, 87–114.
- Jessen, H. L.** 1973. Interrelationships of actinopterygians and brachyopterygians: evidence from pectoral anatomy. Pp. 227–232 in Greenwood, P. H., Miles, R. S. & Patterson, C. (eds). *Interrelationships of fishes*. Academic Press, London, 536 pp.
- Jin, F.** 2006. An overview of Triassic fishes from China. *Vert Palasiatica*, **44**, 28–42.
- Jollie, M.** 1984. Development of the head and pectoral skeleton of *Polypterus* with a note on scales (Pisces: Actinopterygii). *Journal of Zoology*, **204**(4), 469–507.
<https://doi.org/10.1111/j.1469-7998.1984.tb02382.x>
- Kazantseva-Selezneva, A. A.** 1979. A new palaeoniscoid fish from the Permian of the Kuznetsk Basin. *Paleontological Journal* **13**, 263–266.
- Kazantseva-Selezneva, A. A.** 1980. Permian Palaeonisci of Central Siberia. *Paleontological Journal*, **14**, 80–87.
- Kazantseva-Selezneva, A. A.** 1981. Late Palaeozoic Palaeonisci of East Kazakhstan [Pozdnepaleozoiskie paleoniski Vostochnogo Kazakhstana]. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, **180**, 1–140 (in Russian).
- Kerr, J. G.** 1907. The development of *Polypterus senegalus* Cuvier. Pp. 195–290. In KERR J.G. (ed). *The Work of John Samuel Budgett, Balfour Student of the University of Cambridge: Being a Collection of His Zoological Papers, together with a Biographical Sketch by A. E. Shipley, F.R.S., and Contributions by Richard Assheton, Edward J. Bles, Edward T. Browne, J. Herbert Budgett and J. Graham Kerr*. Cambridge University Press, Cambridge.
- Lambers, P. H.** 1994. The halecomorph fishes *Caturus* and *Amblysemius* in the lithographic limestone of Solnhofen (Tithonian), Bavaria. *Geobios*, **27**(1), 91–99.

[https://doi.org/10.1016/S0016-6995\(94\)80024-3](https://doi.org/10.1016/S0016-6995(94)80024-3).

- Lauder, G. V. & Liem, K. F.** 1983. The evolution and interrelationships of the actinopterygian fishes. *Bulletin of the Museum of Comparative Zoology, Harvard University*, **150**, 95–197.
- Lecointre, G., Philippe, H., Le, H. L. V. & Le Guyader, H.** 1994. How many nucleotides are required to resolve a genetic problem? The use of a new statistical method applicable to available sequences. *Molecular Phylogenetics and Evolution*, **3**(4), 292–309.
<https://doi.org/10.1006/mpev.1994.1037>
- Lehman, J. P.** 1952. Etude complementaire des Poissons de l'Eotrias de Madagascar. *K. Svenska Vetenskapsakad. Handl.*, ser. 4, bd. 2, no. 6, 201 pp.
- Lehman, J. P.** 1979. Le genre *Scanilepis* Aldinger du Rhétien de la Scanie (Suède). *Bulletin of the Geological Institution of the University of Uppsala*, **8**, 113–125. <http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=PASCALGEODEBRGM8020475834>
- Lewis, P. O.** 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic biology*, **50**(6), 913–925.
- Li, C., Lu, G. & Orti, G.** 2008. Optimal data partitioning and a test case for ray-finned fishes (Actinopterygii) based on ten nuclear loci. *Systematic Biology*, **57**(4), 519–539.
<https://doi.org/10.1080/10635150802206883>
- Li, B., Zhuang, X., Liu, X., WU, C., Zhou, J. & Ma, X.,** 2016. Mineralogical and geochemical composition of Middle Permian Lucaogou Formation in the southern Junggar Basin, China: implications for paleoenvironment, provenance, and tectonic setting. *Arabian Journal of Geosciences*, **9**, 1–16. DOI: 10.1007/s12517-015-2154-3
- Limaye, A.** 2012. Drishti: a volume exploration and presentation tool. In S. R. Stock (ed) *Developments in X-Ray Tomography VIII, Proceedings of the Society of Photo-optical Instrumentation Engineers*, **8506**, 85060X. <https://doi.org/10.1117/12.935640>
- Liu, G. B., & Shun, C. M.** 2006. A new progressive palaeoniscoid, *Mizhilepis* from the Upper Triassic in Mizhi of North Shaanxi. *Acta Palaeontological Sinica*, **45**, 514–522. [Chinese]
- Long, J. A.** 1988. New palaeoniscoid fishes from the Late Devonian and early Carboniferous of Victoria. *Memoir of the Australasian Association of Palaeontologists*, **7**, 1–64.
<http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=6632197>
- Long, J. A.** 1997. Ptyctodontid fishes (Vertebrata, Placodermi) from the Late Devonian Gogo Formation, Western Australia, with a revision of the European genus *Ctenurella* Ørvig, 1960. *Geodiversitas*, **19**(3), 515–555.

<https://sciencepress.mnhn.fr/fr/periodiques/geodiversitas/19/3/ptyctodontid-fishes-vertebrata-placodermi-late-devonian-gogo-formation-western-australia-revision-european-genus-ctenurella-orvig-1960>

- Long, J. A., Young, G. C., Holland, T., Senden, T. J. & Fitzgerald, E. M. G.** 2006. An exceptional Devonian fish from Australia sheds light on tetrapod origins. *Nature*, **444**, 199–202. <https://doi.org/10.1038/nature05243>
- Long, J. A., Choo, B. & Young, G. C.** 2008. A new basal actinopterygian from the Middle Devonian Aztec Siltstone of Antarctica. *Antarctic Science*, **20**(4), 393–412. <https://doi.org/10.1017/S0954102008001144>
- Long, J. A. & Trinajstić, K.** 2010. The Late Devonian Gogo Formation Lagerstätte of Western Australia: exceptional early vertebrate preservation and diversity. *Annual Review of Earth and Planetary Sciences*, **38**, 255–79.
- Lucas, S. G. & Johnson, S. C.** 2002. *Fukangichthys*, a Triassic fish from China. Pp. 115–119. In A. B. Heckert & S. G. Lucas (eds.) *Upper Triassic Stratigraphy and Paleontology. New Mexico Museum of Natural History and Science Bulletin*, **21**, <https://doi.org/10.1080/02724634.2014.837053>
- Lund, R. & Poplin, C.** 1997. The rhadinichthyids (paleoniscoid actinopterygians) from the Bear Gulch Limestone of Montana (USA, Lower Carboniferous). *Journal of Vertebrate Paleontology*, **17**(3), 466–486. <https://doi.org/10.1080/02724634.1997.10010996>
- Lund, R.** 2000. The new actinopterygian order Guildayichthyiformes from the Lower Carboniferous of Montana (USA). *Geodiversitas*, **22**(2), 171–206.
- Lund, R. & Poplin, C.** 2002. Cladistic analysis of the relationships of the tarrasiids (Lower Carboniferous Actinopterygians). *Journal of Vertebrate Paleontology*, **22**(3), 480–486. [https://doi.org/10.1671/0272-4634\(2002\)022\[0480:CAOTRO\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2002)022[0480:CAOTRO]2.0.CO;2)
- Lund, R., Poplin, C. & McCarthy, K.** 1995. Preliminary analysis of the interrelationships of some Paleozoic actinopterygii. *Geobios*, **28**, 215–220. [https://doi.org/10.1016/S0016-6995\(95\)80117-0](https://doi.org/10.1016/S0016-6995(95)80117-0)
- Lund, R. & Poplin, C.** 1997. The rhadinichthyids (paleoniscoid actinopterygians) from the Bear Gulch Limestone of Montana (USA, Lower Carboniferous). *Journal of Vertebrate Paleontology*, **17**(3), 466–486. <https://doi.org/10.1080/02724634.1997.10010996>
- Kogan, I. & Romano, C.** 2016. Redescription of *Saurichthys madagascariensis* Piveteau, 1945 (Actinopterygii, Early Triassic), with implications for the early saurichthyid morphotype. *Journal of Vertebrate Paleontology*, **36**(4), <https://doi.org/10.1080/02724634.2016.1151886>
- Maddison, W. P. & D. R. Maddison.** 2019. Mesquite: a modular system for

evolutionary analysis. Version 3.61. [updated at <http://www.mesquiteproject.org>, accessed 3 March 2020]

- Maisey, J. G.** 1986. Heads and tails: a chordate phylogeny. *Cladistics*, **2**(4), 201–256.
- Maisey, J. G.** 2005. Braincase of the Upper Devonian shark *Cladodoides wildungensis* (Chondrichthyes, Elasmobranchii), with observations on the braincase in early Chondrichthyans. *Bulletin of the American Museum of Natural History*, **288**, 1–103. [https://doi.org/10.1206/0003-0090\(2005\)288<0001:BOTUDS>2.0.CO;2](https://doi.org/10.1206/0003-0090(2005)288<0001:BOTUDS>2.0.CO;2)
- Malabarba, M. C. L.** 1988. A new genus and species of stem group actinopteran fish from the Lower Permian of Santa Catarina State, Brazil, *Zoological Journal of the Linnean Society*, **94**(3), 287–299. <https://doi.org/10.1111/j.1096-3642.1988.tb01197.x>
- Mancuso, A. C.** 2003. Continental fish taphonomy: a case study in the Triassic of Argentina. *Journal of South American Earth Sciences*, **16**(4), 275–286. [https://doi.org/10.1016/S0895-9811\(03\)00069-5](https://doi.org/10.1016/S0895-9811(03)00069-5)
- Mathiesen, C. & Popper, A. N.** 1987. The ultrastructure and innervation of the ear of the gar, *Lepisosteus osseus*. *Journal of Morphology*, **194**(2), 129–142. <https://doi.org/10.1002/jmor.1051940203>
- Maughan, E. K.** 1964. The Goose Egg Formation in the Laramie Range and adjacent parts of southeastern Wyoming. *US Geological Survey Professional Paper*, B53-B60.
- Mickle, K. E., Lund, R. & Grogan, E. D.** 2009. Three new palaeoniscoid fishes from the Bear Gulch Limestone (Serpukhovian, Mississippian) of Montana (USA) and the relationships of lower actinopterygians. *Geodiversitas*, **31**(3), 623–668. <https://doi.org/10.5252/g2009n3a6>
- Mickle, K.E.** 2017. The lower actinopterygian fauna from the Lower Carboniferous Albert shale formation of New Brunswick, Canada: a review of previously described taxa and a description of a new genus and species. *College of Science, Health and the Liberal Arts Faculty Papers*, **1**, 47–67. <https://jdc.jefferson.edu/jchsf/1>
- Miles, R. S.** 1973. Relationships of acanthodians. Pp. 63–103 in P. H. Greenwood, R. S. Miles, & C. Patterson (eds). *Interrelationships of fishes*. Academic Press, London, 536 pp.
- Milner, A., Spears, S. & Olsen, P.** 2008. New specimens of *Tanaocrossus* (Actinopterygii, Perleidiformes) from the Late Triassic Chinle Formation of the western United States. *Journal of Vertebrate Paleontology*, **28**(4), (Supplement): 116A. <https://www.jstor.org/stable/24523381>
- Minikh, M. G. & Minikh, A. V.** 1990. Revision of some palaeoniscids and new fishes from the Upper Permian of the East European Platform, and possibilities of using them stratigraphically [Revisija nekotorykh paleoniskov i novy'e ryby iz verkhnej permi

- Vostochno-Evropeyskoy platformy i vozmozhnosti ikh ispolzovani-ya v stratigrafii]. – Pp. 84–104 in O. I. Aleshechkin (ed): *Problems of the geology of South Urals and Lower Volga Region [Voprosy geologii Yuzhnogo Urala I Nizhnego Povo-lzh'ya]*; Saratov (SarGU Press). (Russian).
- Minikh, A. V. & Minikh, M. G.** 2009. *Ichthyofauna of the Permian of European Russia [Ikhtiofauna Permi Ev ropeyskoy Rossii]*. Nauka Publishing Centre, Saratov, 243 pp (In Russian).
- Moy-Thomas, J. A. & Bradley-Dyne, M.** 1938. XVII.—The Actinopterygian Fishes from the Lower Carboniferous of Glencartholm, Eskdale, Dumfriesshire. *Transactions of the Royal Society of Edinburgh*, **59**(2), 437–480. doi:10.1017/S0080456800009170
- Müller, J.** 1846. Über den Bau und die Grenzen der Ganoiden und über das natürliche System der Fische. *Abhandlungen der Deutschen Akademie der Wissenschaften zu Berlin*, **1845**, 119–216.
- Near, T. & Miya, M.** 2009. Ray-finned fishes (Actinopterygii). In S. B. Hedges & S. Kumar (eds). *The Timetree of Life*. Oxford University Press, Oxford, 328 pp.
- Near, T. J., Eytan, R. I., Dornberg, A., Kuhn, K. L., Moore, J. A., Davis, M. P., Wainwright, P. C., Friedman, M. & Smith, W. L.** 2012. Resolution of ray-finned fish phylogeny and timing of diversification. *Proceedings of the National Academy of Sciences of the United States of America*, **109**(34), 13698–13703. <https://doi.org/10.1073/pnas.1206625109>
- Nelson, J. S.** 1994. *Fishes of the World*. John Wiley, New York, 600 pp.
- Nelson J. S., Grande T. C. & Wilson M. V.** 2016. *Fishes of the World*. John Wiley & Sons, Hoboken, 752 pp.
- Nielsen, E.** 1942. Studies on Triassic fishes from East Greenland I. *Glaucolepis* and *Boreosomus*. *Meddelelser om Grønland*, **146**, 1–309.
- Nielsen, E.** 1949. Studies on Triassic fishes from East Greenland. II. *Australosomus* and *Birgeria*. *Meddelser om Grønland*, **146**, 1–309.
- Nieuwenhuys, R.** 1982. An overview of the organization of the brain of actinopterygian fishes. *American Zoologist*, **22**(2), 287–310. <https://doi.org/10.1093/icb/22.2.287>
- Olsen, P. E.** 1984. The skull and pectoral girdle of the parasemionotid fish *Watsonulus eugnathoides* from the early Triassic Sakamena Group of Madagascar, with comments on the relationships of the holostean fishes. *Journal of Vertebrate Paleontology*, **4**(3), 481–499. <https://doi.org/10.1080/02724634.1984.10012024>
- Olsen, P. E. & McCune, A. R.** 1991. Morphology of the *Semionotus elegans* species group

- from the Early Jurassic part of the Newark Supergroup of Eastern North America with comments on the family Semiotidae (Neopterygii). *Journal of Vertebrate Paleontology*, **11**(3), 269–292. <https://doi.org/10.1080/02724634.1991.10011398>
- Ørvig, T.** 1978. Microstructure and growth of the dermal skeleton in fossil actinopterygian fishes: *Birgeria* and *Scanilepis*. *Zoologica Scripta*, **7**(1–4), 33–56. <https://doi.org/10.1111/j.1463-6409.1978.tb00587.x>
- Patterson, C.** 1968. The caudal skeleton in Lower Liassic pholidophorid fishes. *Bulletin of the British Museum Natural History (Geology)*, **16**, 203–239. <http://pascalfrancis.inist.fr/vibad/index.php?action=getRecordDetail&idt=GEODEBRGM6820014984>
- Patterson, C.** 1973. Interrelationships of holosteans. Pp. in 233–306. P. H. Greenwood, R. S. Miles, & C. Patterson (eds). *Interrelationships of Fishes*. Academic Press, New York, 536 pp.
- Patterson, C.** 1975. The braincase of pholidophorid and leptolepid fishes, with a review of the actinopterygian braincase. *Philosophical Transactions of the Royal Society of London, Series B*, **269**(899), 275–579. <https://doi.org/10.1098/rstb.1975.0001>
- Patterson, C.** 1982. Morphology and interrelationships of primitive actinopterygian fishes. *American Zoologist*, **22**(2), 241–259. <https://doi.org/10.1093/icb/22.2.241>
- Pearson, D. M. & Westoll, T. S.** 1979. The Devonian actinopterygian *Cheirolepis* Agassiz. *Transactions of the Royal Society of Edinburgh*, **70**(13–14), 337–399. <https://doi.org/10.1017/S0080456800012850>
- Piper, D. Z., & Link, P. K.** 2002. An upwelling model for the Phosphoria sea: a Permian, ocean-margin sea in the northwest United States. *AAPG bulletin*, **86**(7), 1217–1235. <https://doi.org/10.1306/61EEDC60-173E-11D7-8645000102C1865D>
- Poplin C.** 1974. Étude de quelques Paléoniscidés pennsylvaniens du Kansas. *Cahiers de Paléontologie (Section Vertébrés)*, Paris, 151 pp.
- Poplin, C. M.** 1984. *Lawrenciella schaefferi* n. g., n. sp. (Pisces: Actinopterygii) and the use of endocranial characters in the classification of the palaeonisciformes. *Journal of Vertebrate Paleontology*, **4**(3), 413–421. <https://doi.org/10.1080/02724634.1984.10012019>
- Poplin, C. & Véran, M.** 1996. A revision of the actinopterygian fish *Coccocephalus wildi* from the Upper Carboniferous of Lancashire. *Special Papers in Palaeontology*, **52**, 7–29.
- Poplin, C. & Lund, R.** 2000. Two new deep-bodied palaeoniscoid actinopterygians from Bear Gulch (Montana, USA, Lower Carboniferous). *Journal of Vertebrate Paleontology*, **20**(3), 428–449. [https://doi.org/10.1671/0272-4634\(2000\)020\[0428:TNDDBPA\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2000)020[0428:TNDDBPA]2.0.CO;2)

- Poplin, C. M. & Lund, R.** 2002. Two Carboniferous fine-eyed palaeoniscoids (Pisces, Actinopterygii) from Bear Gulch (USA). *Journal of Paleontology*, **76**(6), 1014–1028. [https://doi.org/10.1666/0022-3360\(2002\)076<1014:TCFEPP>2.0.CO;2](https://doi.org/10.1666/0022-3360(2002)076<1014:TCFEPP>2.0.CO;2)
- Pradel, A., Maisey, J. G., Tafforeau, P., Mapes, R. H. & Mallatt, J.** 2014. A Palaeozoic shark with osteichthyan-like branchial arches. *Nature*, **509**, 608–611. <https://doi.org/10.1038/nature13195>
- Prokofiev, A. M.** 2002. First finding of an articulated actinopterygian skeleton from the Upper Devonian of Siberia and a reappraisal of the family Moythomasiidae Kazantseva, 1971 (Osteichthyes). *Palaeontological Research*, **6**, 321–327. <https://doi.org/10.2517/prpsj.6.321>
- Prokofiev, A. M.** 2005. A new genus of the family Amblypteridae (Osteichthyes: Actinopterygii) from the Lower Permian of Eastern Europe. *Paleontological Research*, **9**(1), 79–84. <https://doi.org/10.2517/prpsj.9.79>
- Puttick, M. N., O'Reilly, J. E., Tanner, A. R., Fleming, J. F., Clark, J., Holloway, L., Lozano-Fernandez, J., Parry, L. A., Tarver, J. E., Pisani, D. & Donoghue, P. C.** 2017. Uncertain-tree: discriminating among competing approaches to the phylogenetic analysis of phenotype data. *Proceedings of the Royal Society B: Biological Sciences*, **284**, p.20162290. <https://doi.org/10.1098/rspb.2016.2290>
- Puttick, M. N., O'Reilly, J. E., Pisani, D. & Donoghue, P.C.** 2018. Probabilistic methods outperform parsimony in the phylogenetic analysis of data simulated without a probabilistic model. *Palaeontology*, **62**(1), 1–17. <https://doi.org/10.1111/pala.12388>
- Qiao, T. & Zhu, M.** 2010. Cranial morphology of the Silurian sarcopterygian *Guiyu oneiros* (Gnathostomata: Osteichthyes). *Science China Earth Sciences*, **53**, 1836–1848. <https://doi.org/10.1007/s11430-010-4089-6>
- Qu, Q., Zhu, M. & Wang, W.** 2013. Scales and dermal skeletal histology of an early bony fish *Psarolepis romeri* and their bearing on the evolution of rhombic scales and hard tissues. *PLoS ONE*, **8**, e61485. <https://doi.org/10.1371/journal.pone.0061485>
- Rambaut, A.** 2014. Summarizing posterior trees: http://beast.community/summarizing_trees (accessed April 16, 2020).
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G. & Suchard, M. A.** 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, **syy032**. DOI: 10.1093/sysbio/syy032
- Rayner, D. H.** 1937. II.—On *Leptolepis bronni* Agassiz. *Journal of Natural History*, **19**, 46–74.
- Rayner, D. H.** 1952. On the cranial structure of an early palaeoniscid, *Kentuckia* gen. nov.

Transactions of the Royal Society of Edinburgh, **62**(1), 58–83.
doi:10.1017/S0080456800009248

- Romano, C. & Kogan, I.** 2015. *Gardinerpiscis* nom. nov., a replacement name for the preoccupied genus name *Gardineria* Kazantseva-Selezneva, 1981 (Actinopterygii, Osteichthyes), *Paleontological Journal*, **49**(6), 677–678.
DOI: 10.1134/S0031030115060118
- Romano, C., Koot, M. B., Kogan, I., Brayard, A., Minikh, A.V., Brinkmann, W., Bucher, H. & Kriwet, J.** 2016. Permian–Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biological Reviews*, **91**(1), 106–147. DOI: 10.1111/brv.12161
- Romer, A. S.** 1946. The early evolution of fishes. *Quarterly Review of Biology*, **21**(50), 33–69.
<https://doi.org/10.1086/408998>
- Sallan, L. C.** 2014. Major issues in the origins of ray-finned fish (Actinopterygii) biodiversity. *Biological Reviews*, **89**(4), 950–971. <https://doi.org/10.1111/brv.12086>
- Sallan, L. C. & Coates, M. I.** 2013. Styracopterid (Actinopterygii) ontogeny and the multiple origins of post-Hangenberg deep-bodied fishes. *Zoological Journal of the Linnean Society*, **169**(1), 156–199. <https://doi.org/10.1111/zoj.12054>
- Sauvage, H. E.** 1888. Etudes sur le terrain houiller de Commentry, III. Faunes ichthyologiques et entomologiques. *Bulletin de la Soci'et'e de l'Industrie Min'erale, Th'eolier*, **3**, 89–120.
- Schaeffer, B., Cope, E. D. & Hill, R. T.** 1960. The Cretaceous holostean fish *Macrepistius*. *American Museum Novitates*, **2011**, 1–18.
- Schaeffer, B.** 1967. Late Triassic fishes from the Western United States. *Bulletin of American Museum of Natural History*, **135**, 285–342. <http://hdl.handle.net/2246/1125>
- Schaeffer, B.** 1971. The braincase of the holostean fish *Macrepistius*, with comments on neurocranial ossification in the Actinopterygii. *American Museum Novitates*, **2459**, 1–34.
- Schaeffer, B.** 1973. Interrelationships of chondrosteans. Pp. 207–206 in P. H. Greenwood, R. S. Miles, & C. Patterson (eds). *Interrelationships of fishes*. Academic Press, London, 536 pp.
- Schaeffer, B. & Dalquest, W. W.** 1978. A palaeonisciform braincase from the Permian of Texas, with comments on cranial fissures and the posterior myodome. *Novitates*, **2658**, 1–15. <http://hdl.handle.net/2246/5327>
- Schaeffer, B. & Donald, N. G. M.** 1978. Redfieldiid fishes from the Triassic-Liassic Newark Supergroup of eastern North America. *Bulletin of the American Museum of Natural History*, **159**, 131–173.

- Schaeffer, B. & Patterson, C.** 1984. Jurassic fishes from the western United States, with comments on Jurassic fish distribution. *American Museum Novitates*, **2796**, 1–86. <http://hdl.handle.net/2246/5270>
- Schäfer, W.** 1972. *Ecology and Paleontology of Marine Environments*. University of Chicago Press, Chicago, 568 pp.
- Schaumburg, G.** 1989. *Muensterichthys buergeri* n. sp., ein neuer Palaeoniscoide (Actinopterygii, Pisces) aus dem permischen Kupferschiefer von Richelsdorf (Hessen, West-Deutschland). *Paläontologische Zeitschrift*, **63**(1-2), 119–131.
- Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C., Saalfeld, S., Schmid, B. & Tinevez, J. Y.** 2012. Fiji: an open-source platform for biological-image analysis. *Nature methods*, **9**(7), 676–682. <https://doi.org/10.1038/nmeth.2019>
- Schröder, K. M., López-arbarello, A. & Ebert, M.** 2012. *Macrosemimimus* gen. nov. (Actinopterygii, Semionotiformes) from the Late Jurassic of Germany, England, and France. *Journal of Vertebrate Paleontology*, **32**(3), 512–529. <https://doi.org/10.1080/02724634.2012.649626>
- Schultze, H. P.** 1968. Palaeoniscoidea-Schuppen aus dem Unterdevon Australiens und Kanadas und aus dem Mitteldevon Spitzbergens. *Bulletin of the British Museum (Natural History)*, **16**(7), 343–376.
- Schultze, H. P. & Cumbaa, S. L.** 2001. *Dialipina* and the characters of basal osteichthyans. Pp. 315–332 in P. E. Ahlberg (ed) *Major Events in Early Vertebrate Evolution*. Taylor & Francis, London. 418 pp.
- Schultze, H. P.** 2008. Nomenclature and homologization of cranial bones in actinopterygians. Pp. 23–48 in G. Arratia, H. P. Schultze, & M. V. Wilson (eds) *Mesozoic Fishes 4–Homology and Phylogeny*. Verlag Dr. Friedrich Pfeil, München.
- Selezneva, A. A.** 1985. *Evenkia* is *Polypterus* ancestor. *Paleontologicheskii Zhurnal* **19**, 71–76. [Russian]
- Smith, D. B., Bernhardt, G., Raine, N. E., Abel, R. L., Sykes, D., Ahmed, F., Pedroso, I. & Gill, R. J.** 2016. Exploring miniature insect brains using micro-CT scanning techniques. *Scientific Reports*, **6**, 21768. DOI: 10.1038/srep21768
- Štamberg, S.** 2013. Knowledge of the Carboniferous and Permian actinopterygian fishes of the Bohemian Massif-100 years after Antonín Frič. *Acta Musei Nationalis Pragae, Series B-Historia Naturalis*, **69**(3–4), 159–182. DOI 10.14446/AMNP.2013.159
- Štamberg, S.** 2016. A new actinopterygian species of *Igornichthys* Heyler, 1972 from the

- Permian of the Krkonoše Piedmont Basin (Bohemian Massif, Czech Republic), and its relationship to the actinopterygians of other European Permo-Carboniferous basins. *Geodiversitas* **38**(4), 475–488. <https://doi.org/10.5252/g2016n4a1>
- Steinke, D., Salzburger, W. & Meyer, A.** 2006. Novel relationships among ten fish model species revealed based on phylogenomic analysis using ESTs. *Journal of Molecular Evolution*, **62**, 772–784. <https://doi.org/10.1007/s00239-005-0170-8>
- Stensiö, E. A.** 1922a. Über zwei Coelacanthiden aus dem Oberdevon von Wildungen. *Palaeontologischen Zeitschrift*, **4**, 167–210.
- Stensiö E. A.** 1921. *Triassic Fishes from Spitzbergen. I.* Adolf Holzhausen, Vienna, 307 pp.
- Stensiö, E. A.** 1922b. Notes on certain crossopterygians. *Proceedings of the Zoological Society of London*, **92**(4), 1241–1271. <https://doi.org/10.1111/j.1469-7998.1922.tb07102.x>
- Stensiö, E. A.** 1932. Triassic fishes from East Greenland. *Meddelelser om Grønland*, **83**, 125–164.
- Su, D. Z.** 1978. A new Triassic palaeoniscoid fish from Fukang, Xinjiang. *Memoirs of Institute of Vertebrate Palaeontology and Palaeoanthropology, Academia Sinica*, **13**, 55–59. [Chinese]
- Sun, Z. Y., Tintori, A., Xu, Y. Z., Lombardo, C., Ni, P. G. & Jiang, D. Y.** 2016. A new non-parasemionotiform order of the Halecomorphi (Neopterygii, Actinopterygii) from the Middle Triassic of Tethys. *Journal of Systematic Palaeontology*, **15**(3), 223–240. <https://doi.org/10.1080/14772019.2016.1181679>
- Swartz, B. A.** 2009. Devonian actinopterygian phylogeny and evolution based on a redescription of *Stegotrachelus finlayi*. *Zoological Journal of the Linnean Society*, **56**(4), 750–784. <https://doi.org/10.1111/j.1096-3642.2009.00505.x>
- Swofford, D. L.** 2003. *PAUP*: Phylogenetic Analysis Using Parsimony (*And Other Methods)*. Version Sinauer Associates, Sunderland, Massachusetts.
- Swofford, D. L. & Sullivan, J.** 2009. Phylogeny inference based on parsimony and other methods using PAUP. Pp. 267–312 in P. Lemey, M. Salemi, & A-M. Vandamme (eds). *The Phylogenetic Handbook; a Practical Approach to Phylogenetic Analysis and Hypothesis Testing*. Cambridge University Press, New York.
- Sytchevskaya, E. K.** 1999. Freshwater fish fauna from the Triassic of Northern Asia. Pp. 445–468 in G. Arratia & H. P. Schultze (eds) *Mesozoic Fishes 2: Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, Munich, 604 pp.
- Taverne, L.** 1997. *Osorioichthys marginis*, “Paléonisciforme” du Famennien de Belgique, et la phylogénie de Actinoptérygiens dévoniens (Pisces). *Bulletin de l’Institut Royal des*

- Thies, D.** 1991. The osteology of the bony fish *Tetragonolepis semicincta* Bronn 1830 (Actinopterygii, †Semionotiformes) from the Early Jurassic (Lower Toarcian) of Germany. *Geologica et Palaeontologica*, **25**, 251–297.
<http://pascal-francis.inist.fr/vibad/index.php?action=getRecordDetail&idt=6485115>
- Thies, D. & Herzog, A.** 1999. New information on †*Dapedium* Leach 1822 (Actinopterygii, †Semionotiformes). 143–152 in G. Arratia & H. P. Schultze (eds) *Mesozoic Fishes 2: Systematics and Fossil Record*. Verlag Dr. Friedrich Pfeil, Munich, 604 pp.
- Thies, D. & Waschke, J.** 2015. Redescription of *Dapedium pholidotum* (Agassiz, 1832) (Actinopterygii, Neopterygii) from the Lower Jurassic Posidonia Shale, with comments on the phylogenetic position of *Dapedium* Leach, 1822, *Journal of Systematic Palaeontology*, **14**(4), 339–364. <https://doi.org/10.1080/14772019.2015.1043361>
- Tintori, A., Hitij, T., Jiang, D., Lombardo, C. & Sun, Z.** 2014. Triassic actinopterygian fishes: the recovery after the end-Permian crisis. *Integrative Zoology*, **9**(4), 394–411.
<https://doi.org/10.1111/1749-4877.12077>
- Tomlin, C. D. S.** 1997. *The Pesticide Manual, 11th ed.*; British Crop Protection Council: Farnham, Surrey.
- Traquair, R. H.** 1881. Report on the fossil fishes collected by the Geological Survey of Scotland in Eskdale and Liddesdale. Part 1. Ganoidei. *Transactions of the Royal Society of Edinburgh*, **30**, 15–71.
- Traquair, R. H.** 1877–1914. *The Ganoid Formations, Palaeontographical Society Monograph, Fishes of the 1877–1914*. British Carboniferous Palaeontographical Society, London.
- Watson, D. M. S.** 1925. The structure of certain palaeoniscids and the relationships of that group with other bony fish. *Proceedings of the Zoological Society of London*, **95**(3), 815–870.
<https://doi.org/10.1111/j.1469-7998.1925.tb07107.x>
- Watson, D. M. S.** 1928. On some points in the structure of palaeoniscid and allied fish. *Proceedings of the Zoological Society of London*, **98**(1), 49–70.
- Wardlaw, B. R. & Collinson, J. W.** 1984. Conodont paleoecology of the Permian Phosphoria Formation and related rocks of Wyoming and adjacent areas. Pp. 263–281 in D. L. Clark (ed) *Conodont biofacies and provincialism*. Geological Society of America Special Paper 196, Boulder.
- Wardlaw, B. R. & Collinson, J. W.** 1986. Paleontology and deposition of the Phosphoria Formation. *Contributions to Geology, University of Wyoming*, **24**(2), 107–142.
- Weigelt, J.** 1989. *Recent vertebrate carcasses and their paleobiological implications*. Chicago,

University of Chicago Press, 188 pp.

- Wen, W., Zhang, Q. Y., Hu, S. X., Zhou, C. Y., Xie, T., Huang, J. Y., Chen, X. Q. & Benton, M. J.** 2012. A new basal actinopterygian fish from the Anisian (Middle Triassic) of Luoping, Yunnan Province, southwest China. *Acta Palaeontologica Polonica*, **57**(1), 149–160. <https://doi.org/10.4202/app.2010.0089>
- Wenz, S.** 1968. Compléments à l'étude des poissons actinoptérygiens du Jurassique français. *Centre National de la Recherche Scientifique*, 1–276.
- Whalen, M. T.** 1996. Facies architecture of the Permian Park City Formation, Utah and Wyoming: implications for the paleogeography and oceanographic setting of western Pangea. Pp. 355–378 in M. W. Longman & M. D. Sonnenfeld, (eds) *Paleozoic systems of the Rocky Mountain region*. Rocky Mountain Section SEPM, Denver.
- White, E. I.** 1933. New Triassic Palaeoniscids from Madagascar. *Annals and Magazine of Natural History*, **11**(61), 118–128. <https://doi.org/10.1080/00222933308673632>.
- Whitmore, J. H.** 2003. *Experimental fish taphonomy with a comparison to fossil fishes*. Unpublished PhD thesis, Loma Linda University, 327 pp.
- Wilson, J. A.** 1953. Permian Vertebrates from Taylor County, Texas. *Journal of Paleontology*, **27**(3), 456–470. <https://www.jstor.org/stable/1300003>
- Wright, A. M. & Hillis, D. M.** 2014. Bayesian analysis using a simple likelihood model outperforms parsimony for estimation of phylogeny from discrete morphological data. *PLoS One*, **9**, p.e109210.
- Wright, A. M.** 2019. A systematist's guide to estimating Bayesian phylogenies from morphological data. *Insect systematics and diversity*, **3**(3), 1–14. <https://doi.org/10.1093/isd/ixz006>
- Xu, G. H. & Gao, K. Q.** 2011. A new scanilepiform from the Lower Triassic of northern Gansu Province, China, and phylogenetic relationships of non-teleostean Actinopterygii. *Zoological Journal of the Linnean Society*, **161**(3), 595–612. <https://doi.org/10.1111/j.1096-3642.2010.00645.x>
- Xu, G. H., Gao, K. Q. & Finarelli, J. A.** 2014. A revision of the Middle Triassic scanilepiform fish *Fukangichthys longidorsalis* from Xinjiang, China, with comments on the phylogeny of the Actinopteri. *Journal of Vertebrate Paleontology*, **34**(4), 747–759. <https://doi.org/10.1080/02724634.2014.837053>
- Xu, G. H., Gao, K. Q. & Coates, M. I.** 2015. Taxonomic revision of *Plesiofuro mingshuica* from the Lower Triassic of northern Gansu, China, and the relationships of early neopterygian clades. *Journal of Vertebrate Paleontology*, **35**(6), e1001515. <https://doi.org/10.1080/02724634.2014.1001515>

- Xu, G. H. & Shen, C. C.** 2015. *Panxianichthys imparilis* gen. et sp. nov., a new ionoscopiform (Halecomorphi) from the Middle Triassic of Guizhou, China. *Vertebrata Palasiatica*, **53**, 1–6.
- Xu, G. H. & Zhao, L. J.** 2016. A Middle Triassic stem-neopterygian fish from China shows remarkable secondary sexual characteristics. *Science Bulletin*, **61**(4), 338–344. <https://doi.org/10.1007/s11434-016-1007-0>
- Xu, G. H. & Zhao, L. J.** 2016. A Middle Triassic stem-neopterygian fish from China shows remarkable secondary sexual characteristics. *Scientific Bulletin*, **61**(4), 338–344. <https://doi.org/10.1007/s11434-016-1007-0>
- Young, J.** 1866. On the affinities of *Platysomus* and allied genera. *Quarterly Journal of the Geological Society of London*, **22**, 301–317. <https://doi.org/10.1111/j.1096-3642.1939.tb00713.x>
- Yu, X.** 1998. A new porolepiform-like fish, *Psarolepis romeri*, gen. et sp. nov. (Sarcopterygii, Osteichthyes) from the Lower Devonian of Yunnan, China. *Journal of Vertebrate Paleontology*, **18**(2), 261–274. <https://doi.org/10.1080/02724634.1998.10011055>
- Zhu, M., Yu, X. & Janvier, P.** 1999. A primitive fossil fish sheds light on the origin of bony fishes. *Nature*, **397**, 607–610. <https://doi.org/10.1038/17594>
- Zhu, M. & Schultze, H. P.** 2001. Interrelationships of basal osteichthyans. Pp. 289–314 in P. E. Ahlberg (ed). *Major events in early vertebrate evolution: palaeontology, phylogeny, genetics and development*. Taylor & Francis, London, 418 pp.
- Zhu, M., Yu, X. & Ahlberg, P. E.** 2001. A primitive sarcopterygian fish with an eyestalk. *Nature*, **410**, 81–84. <https://doi.org/10.1038/35065078>
- Zhu, M. & Yu, X.** 2002. A primitive fish close to the common ancestor of tetrapods and lungfish. *Nature*, **418**, 767–770. <https://doi.org/10.1038/nature00871>
- Zhu, M. & Ahlberg, P. E.** 2004. The origin of the internal nostril of tetrapods. *Nature*, **432**, 94–97. <https://doi.org/10.1038/nature02843>
- Zhu, M., Yu, X., Wang, W., Zhao, W. & Jia, L.** 2006. A primitive fish provides key characters bearing on deep osteichthyan phylogeny. *Nature*, **441**(7089), 77–80. <https://doi.org/10.1038/nature04563>
- Zhu, M., Wang, W. & Yu, X.** 2010. *Meemannia eos*, a basal sarcopterygian fish from the Lower Devonian of China—expanded description and significance. Pp. 199–214 in D. K. Elliot, J. G. Maisey, K. Yu & D. Miao (eds). *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes*. Verlag, Dr. Friedrich Pfeil, Munich, 472 pp.

- Zhu, M., Yu, X., Ahlberg, P. E., Choo, B., Lu, J., Qiao, T., Qu, Q., Zhao, W., Jia, L., Blom, H. & Zhu, Y.** 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature*, **502**, 188–193. <https://doi.org/10.1038/nature12617>
- Zhu, M., Yu, X., Wang, W., Zhao, W. & Jia, L.** 2006. A primitive fish provides key characters bearing on deep osteichthyan phylogeny. *Nature*, **441**, 77–80. <https://doi.org/10.1038/nature04563>
- Zhu, M., Zhao, W., Jia, L., Lu, J., Qiao, T. & Qu, Q.** 2009. The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature*, **458**, 469–474. <https://doi.org/10.1038/nature07855>