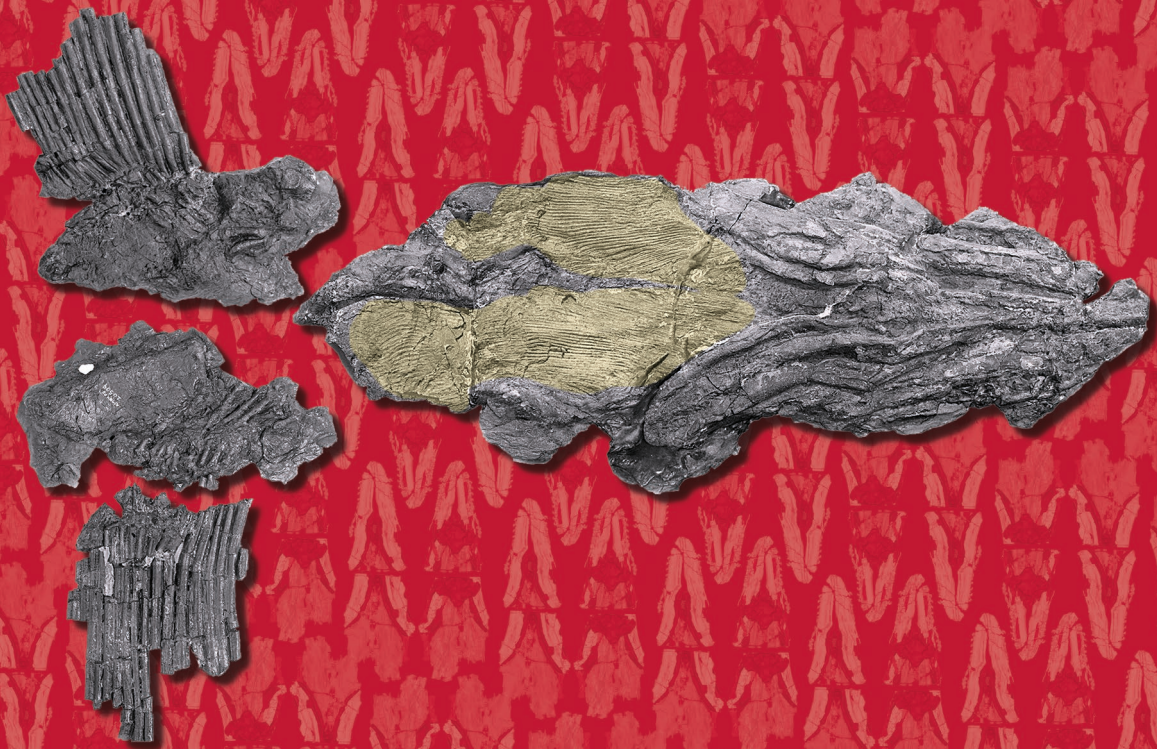# A new operculate symmoriiform chondrichthyan from the Late Mississippian Fayetteville Shale (Arkansas, United States)

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A new operculate symmoriiform chondrichthyan from the Late Mississippian Fayetteville Shale (Arkansas, United States)

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ABSTRACT

We describe a new genus of symmoriiform chondrichthyan from the Late Mississippian Fayetteville Shale of Arkansas, USA and include this fossil in a phylogenetic analysis of chondrichthyans. This taxon possesses elongate cartilaginous rays extending from the gill arches, forming an operculate structure that covers at least two of the branchial arches farther posteriorly. Although presence of a 'hyoid operculum' has been postulated in at least two unrelated Paleozoic sharks (e.g., *Triodus*, *Tristychius*), subsequent investigations failed to corroborate those claims. The new fossil therefore provides the first evidence of an endoskeletal operculum formed by elongate, fused pharyngeal arch rays in a chondrichthyan.

KEY WORDS
Chondrichthyes,
Symmoriiformes,
operculum,
CT scanning,
phylogeny,
new genus,
new species.

RÉSUMÉ
Un nouveau chondrichtyen symmoriiforme operculé du Mississippien supérieur Fayetteville Shale (Arkansas, États-Unis).
Nous décrivons un nouveau genre de chondrichtyen symmoriiforme des schistes Fayetteville du Mississippien supérieur de l'Arkansas, aux États-Unis, et incluons ce fossile dans une analyse phylogénétique des chondrichthyens. Ce poisson possède des rayons cartilagineux allongés s'étendant des arcs branchiaux, formant une structure operculaire qui couvre au moins deux des arcs branchiaux plus en arrière. Bien que la présence d'un «opercule hyoïde» ait été inféré chez au moins deux requins paléozoïques non apparentés (par exemple, *Triodus*, *Tristychius*), des études ultérieures n'ont pas permis de corroborer ces affirmations. Le nouveau fossile fournit donc la première preuve d'un opercule endosquelettique formé par des rayons pharyngiens allongés et fusionnés chez un chondrichthyen.

INTRODUCTION

Modern crown chondrichthyans include two distinct lineages (Elasmobranchii, including sharks and rays, and Holocephali, including chimaeroids), which share a common ancestor with the paraphyletic acanthodians and collectively represent the collateral sister group of modern bony jawed vertebrates (osteichthyans) (Zhu *et al.* 2013; Giles *et al.* 2015; Dearden *et al.* 2019). The divergence of elasmobranchs and holocephalans can be traced back to the Late Devonian (Coates *et al.* 2017, 2018), but the evolutionary relationships of many Paleozoic shark-like fishes to the chondrichthyan crown remain uncertain (Grogan *et al.* 2012; Coates *et al.* 2017; Maisey *et al.* 2019). One group whose position is especially controversial is the order Symmoriiformes (including *Symmorium* Cope, 1893, *Cobelodus* Zangerl, 1973, *Ozarcus* Pradel, Maisey, Tafforeau, Mapes & Mallatt, 2014, *Kawichthys* Pradel, Tafforeau, Maisey & Janvier, 2011, *Maghriboselache* Klug, Coates, Frey, Greif, Jobbins, Pohle, Lagnaoui, Bel Haouz & Ginter, 2023, and *Dwykaselachus* Oelofsen, 1986, and more eccentric spine-bearing forms, such as *Stethacanthus* Newberry, 1890*, Falcatus* Lund, 1985*, Damocles* Lund, 1986*,* and *Akmonistion* Coates & Sequeira, 2001) (Lund 1985, 1986; Coates & Sequeira 1998, 2001; Pradel *et al.* 2011, 2014; Coates *et al.* 2017; Klug *et al.* 2023). Some analyses have placed symmoriiforms below the divergence of holocephalans and elasmobranchs (i.e., excluding them from the chondrichthyan crown) (Pradel *et al.* 2011), whereas other studies have allied them with holocephalans, thus placing symmoriiforms within the chondrichthyan crown (Janvier 1996; Coates & Sequeira 2001; Coates *et al.* 2017). Renewed support for a holocephalan-symmoriiform relationship emerged several years ago from a study of cranial morphology in *Dwykaselachus*, the youngest symmoriiform known from endoskeletal fossil remains, from the Permian of South Africa (Coates *et al.* 2017). This relationship was also recently supported as part of a study of the gill skeleton, jaws, cranium, scales, and teeth of *Gladbachus* Heidtke & Krätschmer, 2001 (Coates *et al.* 2018), and from an analysis including the Late Devonian *Ferromirum* Frey, Coates, Tietjen, Rücklin & Klug, 2020 (Frey *et al.* 2020).

Here, we introduce a previously undescribed symmoriiform from the Late Mississippian Fayetteville Shale of Arkansas, which has a unique operculum-like structure, but also has a symmoriiform-like basicranium, jaws, and teeth. The basicranium is only partially preserved, and the gill arches are disarticulated, but these gill arches are associated with elongate endoskeletal rays forming a gill cover.

Chondrichthyan paleontology is continually challenged by the rarity of cartilage in the fossil record. However, when cartilage is preserved, it provides a great deal of information about early chondrichthyan anatomy, evolution (Brazeau 2009; Maisey *et al.* 2019), life history strategies and reproductive structures (Lund 1982; Capetta 1987; Stumpf *et al.* 2021), and phylogenetics (Brazeau 2009; Davis *et al.* 2012; Coates *et al.* 2017). The Fayetteville Shale of northwestern Arkansas is beginning to yield remarkably preserved fossil cartilage, with implications for our understanding of Late Mississippian chondrichthyan evolution (Lund & Mapes 1984; Maisey 2007; Pradel *et al.* 2014; Bronson *et al.* 2018).

The exceptionally preserved chondrichthyans of the Fayetteville Shale represent just one aspect of its biodiversity. The formation is perhaps best known for its oil-bearing black shales, which have been well known to geologists for many years (Meeks 1997; Murthy *et al.* 2004; Alase 2012). However, the formation is also famous for its fossil plants (Dunn 2002; Dunn *et al.* 2002, 2003, 2006), whose abundance and good preservation enabled a reconstruction of the formation's wetland ecosystem (Dunn 2002, 2003; Dunn *et al.* 2006), and for its diverse cephalopod assemblages (Girty 1910; Gordon Jr *et al.* 1969), which provide evidence of the formation's marine ecosystems. The preservation of these cephalopods, including evidence of mass mortality events, is informative for reconstructing the depositional environment of the formation (Meeks 1997), which was likely characterized by rapid burial events and transgression-regression cycles which resulted in preferential preservation of cartilage, and simultaneous degradation of shell and bone (Bronson *et al.* unpublished data).

MATERIAL AND METHODS

SPECIMEN INFORMATION

AMNH FF 20509, represented by nearly complete lower jaws, dentition *in situ* in lower jaw, partial upper jaw, partial basicranium, branchial arch elements, partial pectoral girdle cartilage and fins, fin impressions, and branchial arch rays

LOCALITY INFORMATION

The specimen was collected along a series of outcrops of the Fayetteville Shale, in the bed of Cove Creek, Searcy County, Arkansas (Mapes Locality ARC-08) (Mapes 1979) beginning at the junction of Highway 65 and Cove Creek Bridge and going upstream for approximately 1 mile. The precise outcrop at which this specimen was collected, however, is unknown.

COMPUTED TOMOGRAPHY METHODS

Specimen number AMNH FF 20509 was photographed using a Canon EOS 70D SLR camera. The entire specimen except for the partial pectoral girdle and fins was then scanned at the American Museum of Natural History on a 2010 GE phoenix v|tome|x s240 high-resolution microfocus computed tomography system (General Electric, Fairfield, CT, United States), using a diamond target and 0.5 mm copper filter. This specimen was too large to be imaged as a single scan, and so the anterior and posterior ends were scanned one at a time, and each half was reconstructed and segmented as a separate image stack, producing 1 836 images for each portion, both with a voxel size of 0.13 mm.

Image stacks were reconstructed using GE phoenix datos|x and FIJI software (Schindelin *et al.* 2012). Anatomical features were segmented using Mimics software (*Materialise*, Leuven, Belgium).

COMPILATION OF MORPHOLOGICAL CHARACTER DATA

This study built upon an existing character matrix focused on fossil chondrichthyans and bony fishes (Coates *et al.* 2018; Frey *et al.* 2020). A data set of 222 morphological characters was compiled for 48 genera. Characters, taxa, and character scorings are listed in the Supplementary Material (Appendix 1). The matrix is available as a NEXUS file on MorphoBank, as project 3996, matrix 28783 (Appendix 2).

We added 32 characters to the matrix described in Frey *et al.* 2020, largely focused on the chondrichthyan chondrocranium (see Supplementary Material in Appendix 1) and removed 40 characters that were primarily focused on early osteichthyans or acanthodians and thus became phylogenetically uninformative for our set of taxa. One notable character added to the matrix is Character 39: Endoskeletal operculum absent (0) or present (1). We defined an endoskeletal operculum as a flap or cover, supported by endoskeletal hyoid rays, such as that which exists in extant holocephalans, and unlike the dermal bone opercle of bony fishes or the palatomandibular operculum of some acanthodians or the short, septate branchial arch rays of extant elasmobranchs. This character was thus marked 'present' in both this new taxon and in holocephalans.

The scoring of several characters from Coates *et al.* (2018) and Frey *et al.* (2020) was modified: In terms of coding character states in the dorsal aorta and occipital region, Coates *et al.* (2018) characterized the position of the dorsal aorta similarly between holocephalans and symmoriiforms, likely to maintain character independence. However, we chose to code this character (our Character 166) as follows: occipital region overlies paired *pre*branchial dorsal aortae (0); overlies *median* prebranchial dorsal aorta (1); overlies paired *post*branchial aortae (2). This character portrays the three conditions observed across total group Chondrichthyes. In euselachians (elasmobranchs + hybodonts) (Maisey 2012) as well as some Paleozoic chondrichthyans, the branchial skeleton is mostly posterior to the occipital region, and the prebranchial part of the aortic circuit lies below the braincase. In chimaeroids, the branchial arches are almost completely subcranial. In symmoriiformes and the modern hooktooth dogfish *Aculeola*, the occipital region overlies an undivided *median* prebranchial dorsal aorta. In xenacanths, euselachians, *Tamiobatis* Eastman, 1897, and *Cladodoides* Maisey, 2001, the occipital region overlies a *pair* of prebranchial aortae that divide posterior to the occipital region. The modern holocephalan arrangement is completely different: the occipital region overlies the postbranchial (not prebranchial) part of the aortic circuit. Extinct holocephalans with subcranial branchial arches likely had the same aortic arrangement (Pradel *et al.* 2021). Other modifications to character scorings *contra* Coates *et al.* 2018 and Frey *et al.* 2020 are noted in the Supplementary Material (Appendix 1).

METHODS FOR PHYLOGENETIC ANALYSIS

To explore the effect of parameterization on the inferred topology for this dataset, unweighted parsimony, implied weights parsimony (Goloboff *et al.* 2008a), and the Lewis Mkv model (Lewis 2001) were compared under the Akaike Information Criterion (Akaike 1974) using likelihood approximations of parsimony methods within TNT software using the "morphotestall" and "morphodoaic" scripts (Goloboff & Arias 2019). The best AIC score was obtained for the Lewis/Mkv model, which we show here alongside unweighted parsimony (the method used by Frey *et al.* 2020, to compare our results more directly to their analysis). For all analyses, we used *Cowralepis* as the outgroup.

For unweighted parsimony analysis, the data set was subjected to a new technology search in TNT software (Goloboff *et al.* 2008b) through ratchet, fusing, and drifting. Bootstrap values were generated using 1 000 replicates on this strict consensus tree, as were Bremer support values, a consistency index, and a retention index (CI and RI). Search parameters and the TNT script used in this search can be found in the Supplementary Material (Appendix 1). We used Driven search ("xmult") as the source of initial trees, the best score was found 10 times and we used 10 replications. We then used default parameters (without constraint) for Sectorial searches, 10 Ratchet iterations, one round of Tree fusing, and five Drift iterations. Finally, a round of TBR (tree bisection reconnection), with trees from RAM, was performed after the initial search.

Maximum likelihood analysis was conducted using the Mkv model in RAxML v8.2.9 (Stamatakis 2014), with five independent searches. One thousand bootstrap replicates were conducted and mapped onto the inferred topology. Likelihood analysis yielded a slightly different topology from the parsimony topology, likely at least partially because polymorphisms must be transformed to the character state "unknown" to use the Mkv in RAxML. Results of the likelihood analysis, parameters, and AIC scores used to determine model rankings, are included in the Supplementary Material (Appendix 1).

ABBREVIATIONS
Institutional abbreviations
AMNH   American Museum of Natural History, New York.

Anatomical abbreviations
add   depression potentially for adductor musculature;
c   cranium;
cb   ceratobranchials;
ch   ceratohyals;
d   denticles;
da?   possible opening for the dorsal aorta;
mc   Meckel's cartilage;
occ   occiput;
op   opercular cartilage;
ot cap   otic capsule;
pa f   pharyngeal arch fragments;
pq   palatoquadrate fragment;
t   teeth.

SYSTEMATICS

Class CHONDRICHTHYES Huxley, 1880
Order SYMMORIIFORMES Maisey, 2007
Family FALCATIDAE Zangerl, 1990

Genus *Cosmoselachus* n. gen.

urn:lsid:zoobank.org:act:AA6327F6-28D1-4F32-AFD8-4D70F8F2D56C

TYPE SPECIES. — *Cosmoselachus mehlingi* n. sp.

DIAGNOSIS. — As for type and only species.

Cosmoselachus mehlingi n. gen., n. sp.
(Figs 1-6)

urn:lsid:zoobank.org:act:4F449FFA-E9C8-4190-8478-7BCC0ADA88BA

HOLOTYPE. — Partial cranium, jaws, gill arches, partial pectoral girdle and fins, and lower teeth, AMNH FF 20509.

ETYMOLOGY. — *Cosmoselachus mehlingi* n. gen., n. sp. is named in honor of American Museum of Natural History Senior Museum Specialist Carl Mehling, nickname "Cosm", therefore "*Cosm*"-*oselachus*, in recognition of his contributions toward the acquisition and identification of numerous fossil chondrichthyans, as well as his indefatigable enthusiasm for all unusual vertebrates and many years of service to paleontology.

GEOLOGICAL RANGE. — Fayetteville Shale (Upper Mississippian, Middle Chesterian) of northwest Arkansas, United States.

TYPE LOCALITY. — River bed of Cove Creek, near the town of Leslie, Searcy County, Arkansas, United States, Middle Chesterian (Upper Mississippian), Carboniferous.

DIAGNOSIS. — Teeth small and cladodont type, with unfused bases and three lingually gently recurved cusps, set in elongate, scalloped Meckel's cartilages that house widely spaced tooth families. Denticles present between tooth families. Hyoid and branchial arches possess elongate rays, which are fused together to form a corrugated structure covering the gill openings.
The presence of ten upper and lower families of small cladodont teeth, widely spaced and housed in large alveoli, which, combined with phylogenetic analysis places the taxon within the family Falcatidae (Zangerl 1981; Ginter *et al.* 2010).
The presence of buccopharyngeal denticles that may be compound or single (insufficient resolution in CT scan to determine their type), scalloped jaw margins, and tentatively a single canal for the dorsal aorta entering the basicranium, combined with symplesiomorphic characters (such as possessing 15-18 distal fin radials and cladodont teeth, the shape of the basicranium [see Description], and elongate jaws), as well as the results of a phylogenetic analysis, place this taxon within Order Symmoriiformes (Coates & Sequeira 2001; Maisey 2007).

DESCRIPTION
Our description is based on the holotype AMNH FF 20509, which has been part of the Mapes Fossil Collection since the 1970s. The specimen was recognized as a chondrichthyan by Royal Mapes and brought to the attention of Rainer Zangerl in a photograph dated 1979. Since this early photograph (Supplementary Material, Fig. S1; Appendix 1) was taken, the specimen was damaged in shipping, and later experienced significant pyrite decay; it was previously a continuous slab of matrix, but now the pectoral girdle is separated from the pharyngeal region (Fig. 1). Much of the morphology is recognizable on the surface: An acuminate rostral end of elongate lower jaws, posterior to which are a collapsed set of gill arches that support elongate cartilaginous rays which extend posteriorly for most of the length of the pharynx, as well as an exceptionally preserved pair of pectoral fins with three-dimensional fin radials and impressions of the ceratotrichia and fin margins. Computed tomography reveals teeth, pharyngeal denticles, a partial basicranium, and fragments of additional branchial arches within the largely phosphatic matrix.

Teeth
AMNH FF 20509 (Fig. 1) has an apparently complete lower dentition (Figs 2, 3), with cladodont teeth that have a lingually recurved central cusp and a reniform tooth base (Fig. 3) (Ginter *et al.* 2010). No teeth from the upper jaw are identifiable in the specimen, and all teeth are hidden within the matrix and made visible only by CT scanning. Like *Ozarcus* (Pradel *et al.* 2014) and all other falcatid symmoriiforms (e.g., *Falcatus*, *Damocles* [Lund 1985, 1986; Maisey 2009])*,* the teeth are small and housed in widely-spaced "pockets," with tooth families an average of 4.4 mm apart (ranging from 1.6 to 6.42 mm apart, excluding areas where the fossil is bro-
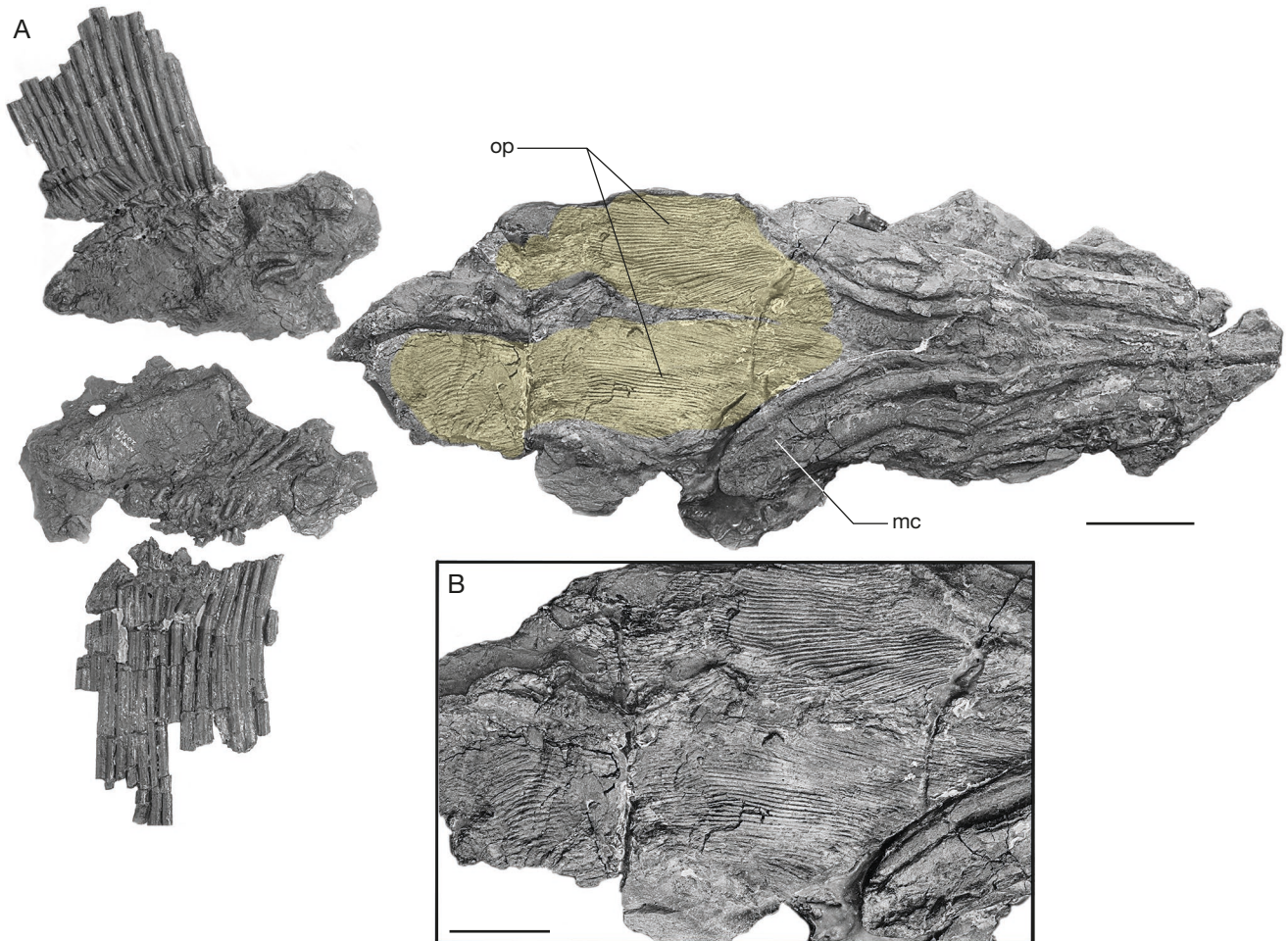
Fig. 1. — *Cosmoselachus mehlingi* n. gen., n. sp., specimen AMNH FF 20509, anterior to right: **A**, entire specimen, ventral view. Abbreviations: **mc**, Meckel's cartilage; **op**, opercular flap; **B**, detail of opercular flap. Scale bars: A, 5 cm; B, 2 cm. Photographs by Lorraine Meeker.

ken). Tooth family spacing is most regular at the middle of Meckel's cartilages; tooth families are slightly closer together at the anterior of the jaw, and spacing is difficult to determine more posteriorly, where teeth are clumped and disorganized, possibly because of taphonomic processes. The fossil has uniformly sized teeth within tooth families, indicating relatively rapid tooth replacement in a linguo-labial sequence. There are generally seven teeth per family, though this can be hard to see in rows that are less organized, and there are at least 25 tooth families (12 clear families on one side, and 13 on the other, plus a jumble of teeth at the back of that row), as well as a single symphysial tooth family (Fig. 2).

Based on the shape of the teeth, with a large central cusp and subtle lateral cusps, they were likely used for clutching prey (Ginter *et al.* 2010; Maisey *et al.* 2014). Their appearance is somewhat like that of *Symmorium* or *Cladoselache* Dean, 1894, but no features are identifiable that might warrant placement in a previously described genus (Fig. 3). Due to the scan's resolution, no basal canal opening can be identified. No large orolingual buttons are obvious, though a lingual torus is present, much like the morphology of teeth in *Cladoselache* and related taxa (Ginter *et al.* 2010).

Denticles

Denticles cover the space between tooth families (Fig. 3), and pharyngeal denticles are visible both as bumps just barely under the matrix surface, and in more detail through CT imaging (Fig. 4). The location of these denticles in the specimen, between the posterior ends of the Meckel's cartilages, indicates they are buccopharyngeal denticles. The pharyngeal denticles are difficult to see in detail in the CT scan, due to low resolution, but they are shaped like grains of rice. The denticles between tooth rows are less regular in shape. Higher resolution scanning would confirm whether or not the pharyngeal denticles are stellate (Williams 1979; Ivanov 2005), as well as determine whether they are simple or compound (as in *Akmonistion* [Coates & Sequeira 2001]). No external dermal denticles have been observed in this specimen, though they may have been lost to taphonomy or preparation early in the specimen's history.

Cartilage structure

Scan resolution was insufficient to discern many details of cartilage structure, apart from there being evidence of only single-monolayered tessellated calcified cartilage (Maisey

et al. 2021) in much of the skeleton (i.e., it seems to lack multiple-monolayer tesserae like that of forms such as *Tamiobatis*, *Cladodus* Agassiz, 1843, etc.). The tessellated layer of the hyoid and branchial rays appears to be thinner than elsewhere, suggesting that the onset of biomineralization here was delayed relative to other parts of the skeleton (the size of individual tesserae has been shown to be related to their age in *Urobatis* Garman, 1913 [Seidel *et al.* 2016]).

Visceral arches

The jaws are long and gracile, extending nearly 5 centimeters behind the posterior margin of the cranium. The mandibular joint is located posterior to the braincase, as is the case in symmoriiform taxa such as *Falcatus* and *Ozarcus*, as well as in *Notorynchus*, and xenacanths like *Orthacanthus* Agassiz, 1843 (Lund 1985; Wilga 2002; Ginter & Maisey 2007; Pradel *et al.* 2014). This is in contrast to the condition in *Tristychius* Agassiz, 1837, *Chondrenchelys* Traquair, 1888, *Iniopera* Zangerl & Case, 1973, and other Paleozoic crown-chondrichthyans with elongate otico-occipital regions, in which this joint is located anteroventral to the braincase (Coates *et al.* 2017). The Meckel's cartilages have a moderate depression along the ventral surface, running along the concave curvature of the jaw from roughly five to ten centimeters anterior to the jaw joint, which does not appear to be an artifact of taphonomy and may have housed an attachment for the adductor musculature in life (Fig. 2). A similar ventral depression is present in the jaws of *Ozarcus* (Pradel *et al.* 2014).

The visceral arches are partially preserved, but the branchial elements have collapsed. The flattened condition of the branchial arches makes it difficult to identify individual elements with certainty, though components of at least three pharyngeal arches are recognizable (Fig. 2). Each of these three pharyngeal arches is represented by paired ventral (ceratal) elements (Fig. 2). The dorsal (epal) elements of the pharyngeal arches are mostly absent, though the dorsal portion of the mandibular arch is preserved as a small remnant that is likely part of the palatoquadrate. A single basihyal may be present based on an irregular chunk of cartilage present in the correct location; however, its identity as a basihyal is uncertain because it is poorly preserved, and as such is not rendered in the reconstruction in Fig. 2. Two pairs of ceratobranchials are preserved, presumably representing the first and second branchial arches, with a fragment of a third arch just posterior to them. The ceratohyals (Fig. 2B) have a slight flange or ridge on their ventromedial edge; however, the ceratobranchials do not have a similar flange and are more rounded in cross section than the flattened ceratohyals.

Gill cover

One unique feature of AMNH FF 20509 is a structure interpreted as an operculum, which extends posteriorly from the level of the hyoid and first branchial arch. The hyoid rays extend to almost the same point as the rays from the first branchial arch. Though the gill arches are collapsed so we cannot confirm that the hyoid and first branchial arch rays covered all the posterior successive gill slits in life, the rays are certainly long enough to close off all the gill openings. The cartilaginous opercular rays attached to the hyoid arch appear to have a ventral and at least partly dorsal component (Fig. 5). Possibly because of weathering, or events post-preparation, the rays lift off from the rest of the specimen in cohesive layers. The flaps formed by the cartilaginous rays have a corrugated appearance, indicating the rays are more adhered to one another than they are to any other part of the specimen, unlike the hyoid rays of other chondrichthyans. A similar adherence of other small structures (denticles, cartilaginous fin radials) is not observed in the specimen, so we interpret the adherence of these hyoid rays as a true feature of the fossil rather than purely a taphonomic artifact. This close adhesion of adjacent rays is visible directly on the surface of the fossil and is consistent in tomographic sections. At least two other branchial arches possess thin and elongate rays, which do not seem to be fused together quite so closely as the rays from the hyoid arch, but they do appear to be fused as they also produce a corrugated appearance. It is difficult to determine the length of the branchial rays from the oblique sectional view provided by CT scans, but the hyoid arch rays are over 10 cm long, covering much of branchial opercular rays and therefore likely covering the branchial openings in life.

Fins

Two pectoral fins and partial pectoral girdle cartilages are preserved with the specimen (Supplementary Material, Fig. S1; Appendix 1); however, they are no longer articulated with the rest of the specimen and were not CT scanned alongside the cranial skeleton. The connection between the fins and cartilages is degraded due to pyrite decay, leaving little preserved of the pectoral cartilages, however the preservation of the fin radials is exceptional; they are three dimensionally preserved without any evidence of becoming crushed taphonomically. Joints appear to be present between the proximal and distal radials (Supplementary Material, Fig. S2; Appendix 1). Impressions of the fins are also preserved, including impressions of ceratotrichia (Supplementary Material, Fig. S1; Appendix 1). Length of the fin impressions indicates the fins were at least 24 cm in length. In this specimen, there are 15-18 distal fin radials (differing from right to left, due to preservation), with no interradials (smaller, sometimes distally forked elements found between fin radials). Among Paleozoic chondrichthyans, only *Cladoselache* is known to have interradials (Maisey 1989).

Partial basicranium

The most posterior portion of the cranium is partially preserved, and it is not dramatically crushed by taphonomic processes (Figs 2; 6). However, little information can be inferred about the structure and size of the orbits, or about the internal structure of the braincase. Compared with the braincase of '*Cobelodus*' (FMNH PF 13242, see http://zenodo.org/record/10110242), also from the Fayetteville Shale (Maisey 2007), as well as in comparison with *Phoe-*
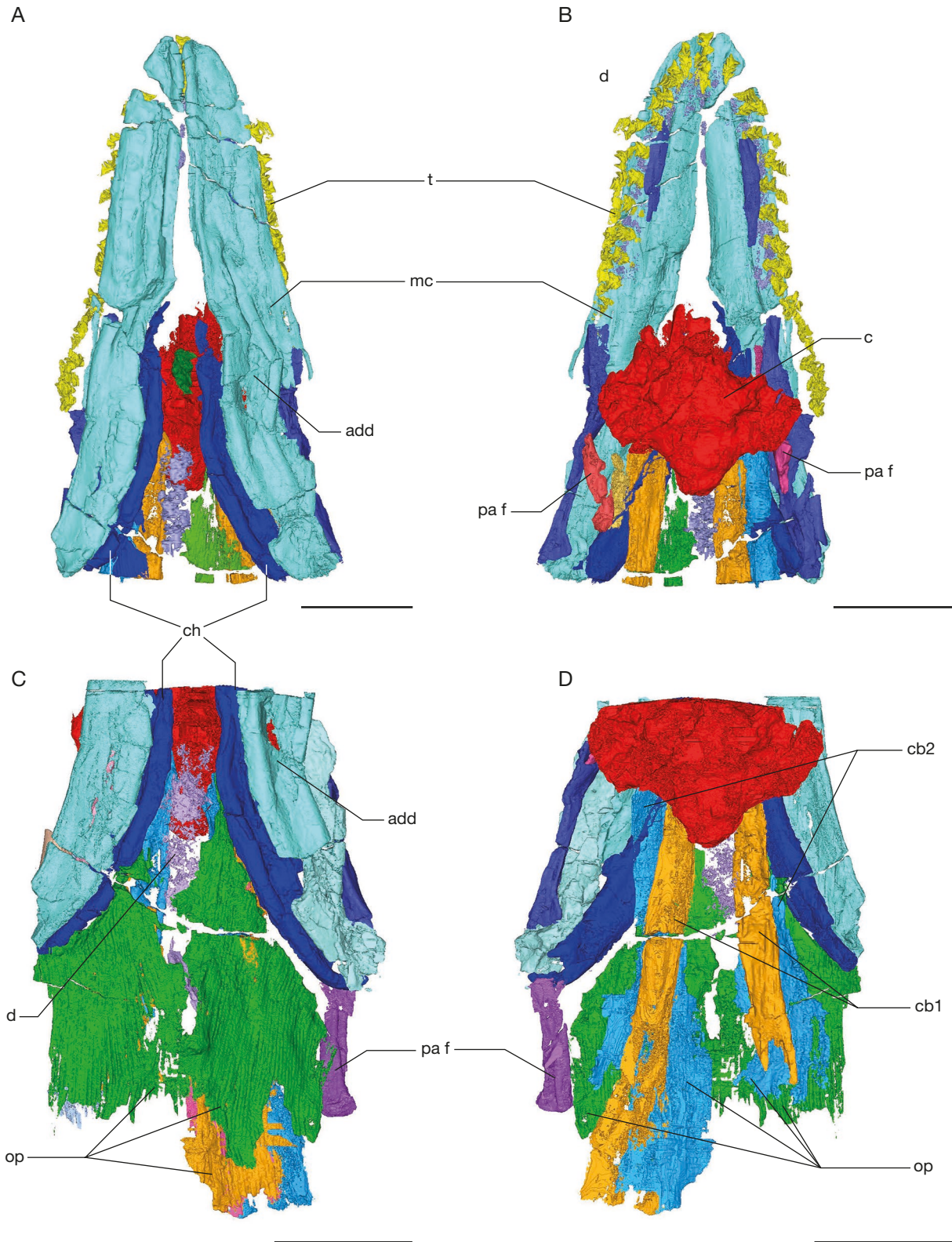
FIG. 2. — *Cosmoselachus mehlingi* n. gen., n. sp., three-dimensional renderings of specimen AMNH FF 20509, produced by computed tomographic (CT) scanning: **A**, ventral view of posterior half of specimen, anterior to top; **B**, ventral view of anterior part of the specimen, anterior to right, with opercular elements removed; **C**, dorsal view of anterior half of specimen, anterior to right. Note loss of anterior portion of cranium due to taphonomy. Abbreviations: **add**, depression potentially for adductor musculature; **c**, cranium; **cb**, ceratobranchials; **ch**, ceratohyals; **d**, denticles; **mc**, Meckel's cartilage; **op**, opercular cartilage; **pa f**, pharyngeal arch fragments; **pq**, palatoquadrate fragment; **t**, teeth. Scale bars: 5 cm.

Fig. 3. — **A**, Tooth families of *Cosmoselachus* n. gen. on the Meckel's cartilages, with denticles between tooth families. Teeth make contact but have no fused bases, dorsal oblique labial view; **B**, detail of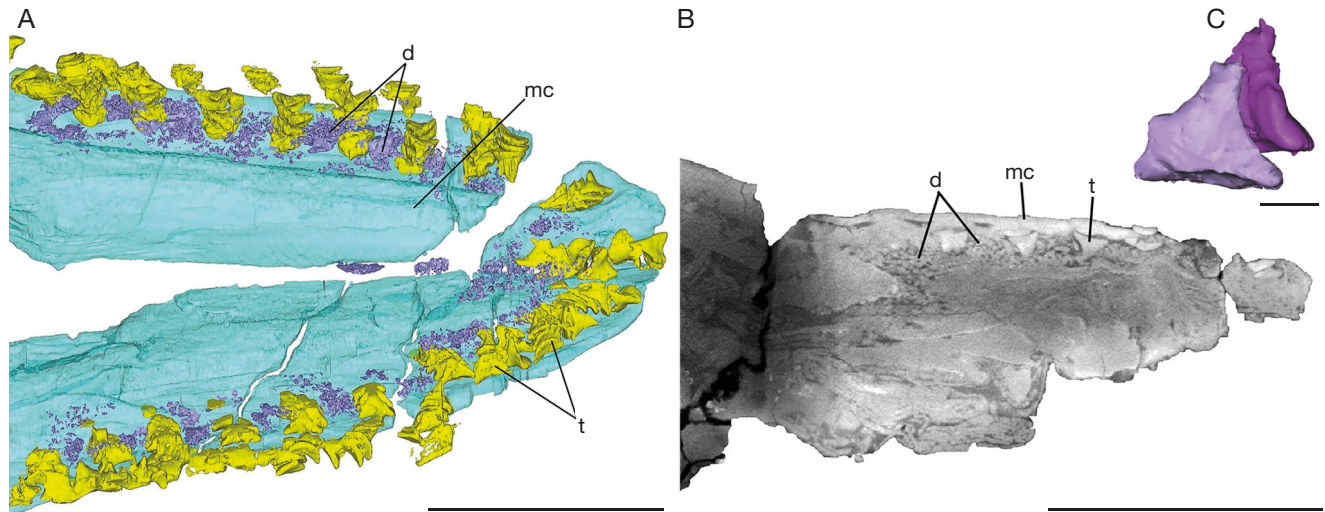 tooth batteries in axial section, anterior to right, showing denticles between each tooth family, on the scalloped Meckel's cartilage. Abbreviations: **d**, denticles; **mc**, Meckel's cartilage; **t**, teeth. Scale bars: A, B, 4 cm; C, 2 mm.

bodus saidselachus (Frey, 2019), this specimen has a more elongate, more tapered occipital region, terminating in a rounded occipital surface. Unlike '*Cobelodus*' or *Maiseyacanthus* Bronson, 2021 (Bronson 2021), the dorsal surface of the cranium is not domed; unfortunately, this region is so degraded that no precerebral fontanelle can be discerned. There is no evidence of subcranial ridges or a spiracular groove, the lateral commissure appears chondrified, and there is no evidence of a subotic occipital fossa. A crack runs through the right ventral side of the cranium just anterolateral to the hypotic lamina; however, this opening is an artifact of taphonomy. There appears to be a single opening or canal for the dorsal aorta (Fig. 6), but due to the resolution of the scan, it is challenging to reconstruct any smaller foramina.

PHYLOGENETIC RESULTS

We recovered eight most parsimonious trees from the parsimony analysis, with a tree score of 547. The Consistency Index for these trees was 0.444 and the Retention Index was 0.721.

Symmoriiform chondrichthyans grouped together in all eight most parsimonious trees, and *Cosmoselachus* n. gen. fell within the symmoriiform group in all most parsimonious trees. The analysis also recovered a monophyletic group of holocephalans separate from the symmoriiforms in all most parsimonious trees (Fig. 7). In contrast, maximum likelihood inference produced a tree in which symmoriiforms form a paraphyletic group, to which the holocephalans are sister, inclusive of the new taxon *Cosmoselachus* n. gen. (see Supplementary Material, Appendix 1).

Acanthodians were consistently recovered as paraphyletic to conventionally defined chondrichthyans, consistent with other recent analyses. In all most parsimonious trees, *Doliodus* Traquair, 1893 is nested within chondrichthyans. In previous studies, excluding the Fayetteville Shale chondrichthyans,

Doliodus alternately comes out nested among taxa that have traditionally been classified as acanthodians, or toward the base of conventionally defined chondrichthyans (Maisey *et al.* 2017).

DISCUSSION

DENTITION

Symmoriiform teeth are distinctive, having a biconvex median cusp and a shallow basolabial projection that is generally the same width or less than the width of the median cusp (Ginter *et al.* 2010). Some symmoriiform teeth have a basolabial depression, and an orolingual button is present, though sometimes divided by a large foramen to the basal nutritive canal. In symmoriiforms, the lateral and medial cusps are structurally separated with no histological connection between the dentine of adjacent cusps (Sequeira & Coates 2000).

Scanning resolution and the density of the specimen make it difficult to discern detailed morphology of the teeth, but, based on the morphology visible from the CT scan (Figs 3, 4), tiny lateral cusps are present and are not deeply separated from the central cusp. The small height of these lateral cusps distinguishes *Cosmoselachus* n. gen. from *Stethacanthus*, *Cladoselache*, *Symmorium*, and *Akmonistion* (Coates & Sequeira 2001). The teeth are also unlike those of *Denaea* Pruvost, 1922, *Damocles,* and *Falcatus*, which all have narrow median cusps (Ginter *et al.* 2010), while *Cosmoselachus* n. gen. appears to have a much thicker median cusp (Fig. 3).

The teeth are convex lingually, similar to the condition in *Symmorium* (Ginter *et al.* 2010). However, *Symmorium* typically has five cusps, but at the low resolution of this scan, it would be unlikely or impossible to see the smallest lateral cusps of a *Symmorium*-like tooth, if they were present. Further mechanical preparation of this specimen, or additional CT scanning specifically targeting the oral region of the fossil would show more detail in the teeth.
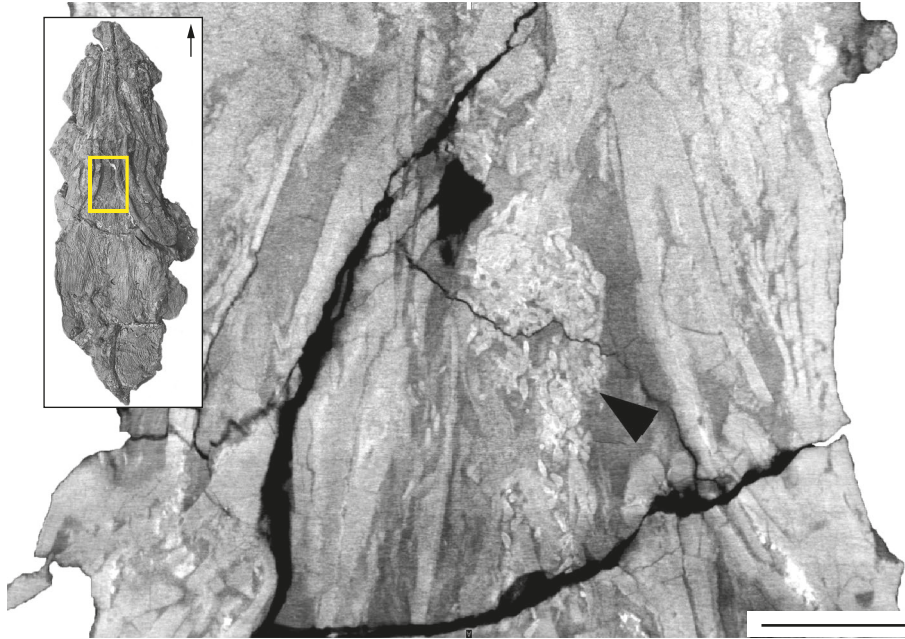
Fɪɢ. 4. — *Cosmoselachus mehlingi* n. gen., n. sp., specimen AMNH FF 20509, pharyngeal denticles (**arrowhead**) revealed by CT scanning. Anterior to top, ventral view in frontal section. Scale bar: 2 cm.

The wide spacing of tooth families in *Cosmoselachus* n. gen. is somewhat like the condition in *Symmorium* as well as in the extant frilled shark (*Chlamydoselachus* Garman, 1884), and the denticles between tooth rows are reminiscent of the arrangement in *Chlamydoselachus* (Smith 1937). Rapid tooth replacement is interpreted from the uniform size of teeth within each tooth family, and from equidistant spacing between tooth families (i.e., tooth families do not become closer together as the shark grows). However, in some living sharks (for example *Carcharhinus leucas* (Müller & Henle, 1839)) tooth size only increases drastically across tooth families when the animals are very young, and size differences are more minimal as growth slows at maturity (Maisey *et al.* 2014). Multiple teeth in each tooth row were probably functional simultaneously, as was the case in many Paleozoic sharks.

OROPHARYNGEAL DENTICLES AND SIGNIFICANCE OF THEIR PRESENCE BETWEEN TOOTH ROWS

The presence of oropharyngeal denticles between tooth rows in *Cosmoselachus* n. gen. is unique among symmoriiforms and is uncommon among chondrichthyans in general. Chondrichthyan teeth grow from tooth anlagen, formed at intervals along the dental lamina (a thickened band of epithelial tissue (Smith *et al.* 2009). As they mature, the teeth migrate forward to the biting edge of the jaws from the mucosal fold, where they function in feeding and then are typically shed (with some exceptions, e.g. *Ctenacanthus* Agassiz, 1837 and *Dracopristis* Hodnett, Grogan, Lund, Lucas, Suazo, Elliott & Pruitt, 2021 [Williams 2001; Hodnett *et al.* 2012; Hodnett & Lucas 2015]). *Ctenacanthus* has denticles between tooth

rows, identified as dermal denticles by Williams (2001). However, in *Ctenacanthus*, many teeth were apparently not shed when they left the functional position. The replaced teeth in *Ctenacanthus* are therefore only among dermal denticles because the teeth migrated onto the skin surface, rather than the dermal denticles actually growing between the teeth (Hodnett *et al.* 2012). It is unlikely that the denticles between tooth rows in *Cosmoselachus* n. gen. represent body scales like the condition in *Ctenacanthus*, because symmoriiforms generally lack body scales, though some possess head and fin spines, specialized branchial denticles (*Stemmatias* Hay, 1899) (Coates & Sequeira 2001; Williams 2001), or specialized ring-like lateral line denticles on the head (which are not visible in the scan of this specimen) (Maisey 2009).

The presence of oropharyngeal denticles between tooth batteries is perhaps most similar to the condition in *Chlamydoselachus*, a taxon with significant intraspecific variation in the number and size of tooth families (Gudger & Smith 1933: fig. 15). At the corner of the mouth in some *Chlamydoselachus* specimens, the teeth and scales appear to intergrade (Smith 1937). Tooth families in *Chlamydoselachus* are separated by skin studded with dermal denticles, which may indicate that each tooth family has its own dental lamina, instead of the continuous dental lamina seen in other chondrichthyans (Allis Jr. 1923; Reif 1973). However, in embryonic *Chlamydoselachus*, the dental lamina appears to be continuous (Reif 1978 and personal observation).

VISCERAL ARCHES

The gill arches of many Paleozoic sharks were probably poorly calcified and thus rarely preserved, though the
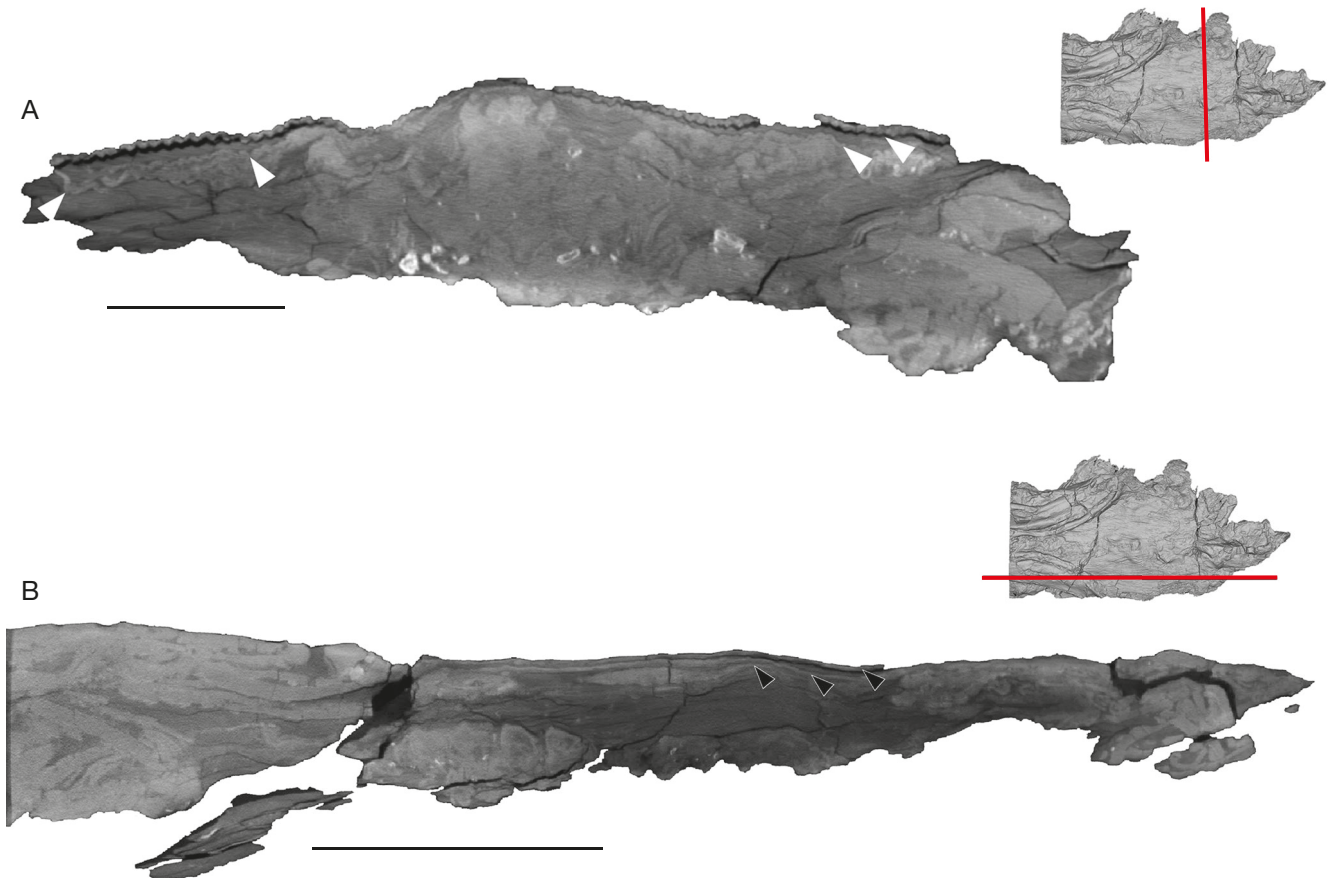
Fɪɢ. 5. — *Cosmoselachus mehlingi* n. gen., n. sp., specimen AMNH FF 20509: **A**, cross section through the posterior half of the specimen, at the point indicated by the inset 3D reconstruction, showing multilayered opercular structure made of cartilaginous branchial rays, fused to one another. Layer of rays from the first branchial arch (behind the hyoid arch) indicated by the **second-from-left arrowhead**. The **right-most arrowhead** marks the second row of pharyngeal rays (first branchial arch); another layer (second branchial arch) can be found just beneath it (**second arrowhead from the right**). Hyoid operculum appears to fold at the arrowhead furthest to the left; **B**, longitudinal section of posterior half of AMNH FF 20509 showing hyoid operculum (**right-most arrowhead**) and additional elongate branchial rays (left two arrowheads). Anterior to left, slice location within the specimen indicated by 3D reconstruction in the upper right corner. Scale bars: 5 cm.

mandibular arch cartilages are generally better preserved but crushed flat. The long, gracile jaws of *Cosmoselachus* n. gen. are similar to the mandibular arch morphology in *Cobelodus* (Zangerl & Williams 1975). The depressions present on the ventral surface of the Meckel's cartilages (as described above, this could have been an attachment for the adductor musculature) are interesting, because the attachments of the adductor musculature are quite different between extant elasmobranchs and holocephalans and because these depressions have not been described in *Cobelodus*. In modern holocephalans, the adductor muscles do not attach to the ventral surface of the Meckel's cartilage, but in living elasmobranchs, they do (Dearden *et al.* 2021).

OPERCULATE STRUCTURE

As in modern elasmobranchs, gill rays in the new fossil also extend from some (perhaps all) arches behind the hyoid (in analogous fashion to those in the modern frilled shark *Chlamydoselachus*) (Allis Jr. 1923). However, unlike the hyoid rays of all described adult elasmobranchs and holocephalans, the cartilaginous rays extending from the hyoid and at least one branchial arch in this fossil appear to be fused to one another for their entire length, forming continuous corrugated surfaces that may have functioned in sealing the gill openings. Given the high quality of cartilage preservation, we do not interpret this fusion as a taphonomic artifact. However, if our interpretation were incorrect and the fused appearance were indeed wholly taphonomic, the rays are still small in diameter, numerous, and densely packed compared to the condition in holocephalans or long-branchial-rayed sharks such as *Tristychius*. If separate in life, the rays would be connected by skin and connective tissue as in the gill clefts of living elasmobranchs and could still seal the branchial chamber during respiratory cycles.

Modern sharks and rays do not have endoskeletal opercula. Instead, the cartilaginous rays that may extend from elasmobranch gill arches are 'septate' – short, but coming from each gill arch, to support the interbranchial septa between gill slits. Holocephalans, on the other hand, have elongate hyoid rays (with no rays on other gill arches) (Didier 1995) that form the endoskeletal support for the operculum (Gillis *et al.* 2011). However these rays are only proximally joined (Didier 1995; Pradel *et al.* 2013).
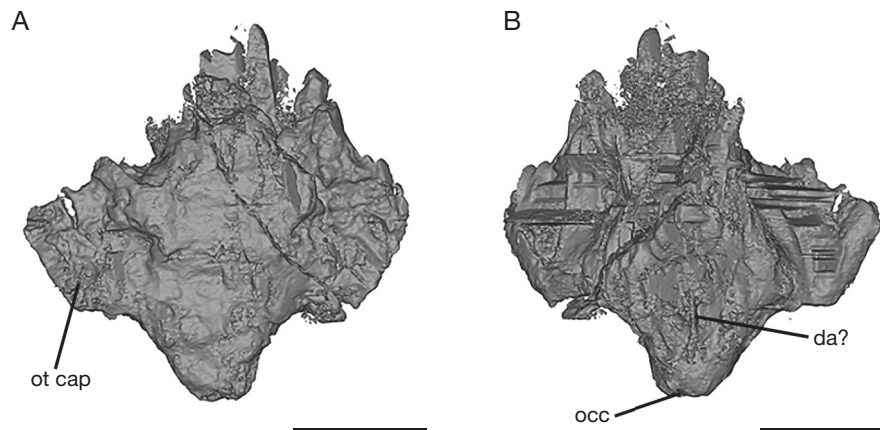
FIG. 6. — *Cosmoselachus mehlingi* n. gen., n. sp., partial basicranium of specimen AMNH FF 20509: **A**, dorsal view; **B**, ventral view. Anterior to top. Abbreviations: **da?**, possible opening for the dorsal aorta; **occ**, occiput; **ot cap**, otic capsule. Scale bar: 3 cm.

Lacking an operculum, living sharks and rays pump water over the gills by depressing and raising the floor of the buccal cavity (buccal pumping), or by opening the mouth and swimming forward (ram ventilation). Extant holocephalans have a much lower pressure system of gill ventilation, that incorporates little cranial movement, and they utilize their gill cover to prevent backflow of water into the pharyngeal cavity through the gill slits (Dean *et al.* 2012).

Among Paleozoic sharks, *Cladoselache*, *Triodus* Jordan, 1849, and *Tristychius* have been reconstructed as having elongate branchial rays; in addition, *Triodus* (as *Pleuracanthus* Agassiz, 1837) and *Tristychius* have been reconstructed as having opercula (Jaekel 1906; Dick 1978). However, in *Cladoselache* the branchial rays are somewhat elongate, but they do not form an operculum (Maisey 1989), and new observations of *Triodus* and *Tristychius* have debunked the idea that their branchial rays were a gill cover – they were actually septate (Dick 1978; Coates *et al.* 2019). These taxa do have longer branchial rays than most modern elasmobranchs, which could indicate that longer branchial rays were a condition common in the chondrichthyan stem. However, no branchial rays have been reported in *Ozarcus* (Pradel *et al.* 2014), which is exceptionally preserved, even including unique accessory cartilages between the epibranchial and ceratobranchial joints. The preservation of these tiny accessory cartilages means that the absence of branchial rays in *Ozarcus* is probably not taphonomic. An operculum has also been suggested in the euchondrocephalan *Debeerius* Grogan & Lund, 2000 (Grogan & Lund 2000)*,* as well as in the iniopterygians *Rainerichthys* Grogan & Lund, 2009 and *Papilionichthys* Grogan & Lund, 2009 (Grogan & Lund 2009).

A palatomandibular, dermal operculum is present in some acanthodians (Gillis *et al.* 2011; Dearden *et al.* 2019) covering septate gill arches. Acanthodians are stem chondrichthyans (Miles 1973; Hanke & Wilson 2006; Brazeau 2009), so therefore septate gill arch appendages are likely plesiomorphic for conventionally defined chondrichthyans, and holocephalans have undergone a reduction in the number of branchial rays (Gillis *et al.* 2011). As discussed by Dearden *et al.* (2019), a bony operculum was probably lost somewhere along the chondrichthyan stem, but it is impossible to rule out the presence of an endoskeletal operculum composed of cartilaginous rays in other species of fossil chondrichthyans – it could be that additional taxa had an operculum, but this delicate cartilaginous structure simply was not preserved.

Crown chondrichthyans represent a highly specialized monophyletic lineage that evolved from 'bony' Paleozoic ancestors (specifically, the 'acanthodian' fishes, named for their spine-bearing fins) (Brazeau 2009). Holocephalans have traditionally been considered one of the two lineages that define crown chondrichthyans. However, in several recent analyses, symmoriiform sharks were hypothesized to share a common ancestor with holocephalans (Coates *et al.* 2017, 2018; Frey *et al.* 2020), a relationship that was first alluded to two decades ago (Janvier 1996). Despite these findings, this relationship is not supported by other phylogenetic analyses (Pradel *et al.* 2011; Maisey *et al.* 2017; Brazeau *et al.* 2020). Our phylogenetic analyses specifically include the character "endoskeletal operculum", which might theoretically unite these groups, and yet AMNH FF 20509 is recovered within symmoriiforms and the symmoriiform-holocephalan relationship is not supported.

PECTORAL FINS AND GIRDLE

Symmoriiform pectoral fins tend to have long metapterygial axes, which may have allowed for increased fin mobility (Maisey 2008). Preservation makes it impossible to confirm the condition of the metapterygium, though it may be visible as a projection from the pectoral girdle (Supplementary Material, Fig. S2; Appendix 1). Jointing is apparent in the pectoral fins of *Cosmoselachus* n. gen., and it is interpreted here as a real feature of the animal, though taphonomic degradation or damage to the fossil cannot be ruled out. Within Order Symmoriiformes, the pectoral girdle is represented by sturdy scapulocoracoids, with triangular metapterygia of fused axial and basal ele-

ments and a jointed free axial whip. Among symmoriids, pectoral fins generally have 12 basal rods, but the number of axial elements is generally undefined (Zangerl 1981).

The phenomenal preservation of the fin radials speaks to the particular preservational environment of the Fayetteville Shale, which has yielded numerous well-preserved chondrichthyans in recent years, such as *Cosmoselachus* n. gen., *Carcharopsis*, and *Ozarcus* (Pradel *et al.* 2014; Bronson *et al.* 2018). The reducing depositional environment and anoxic sediments likely contributed to the preservation of these fin radials and branchial rays in three-dimensional condition. A number of symmoriiform caudal fins have been recovered from the Fayetteville Shale (Bronson *et al.* unpubl. data), though none were found in association with AMNH FF 20509.

PARTIAL BASICRANIUM

The structure interpreted here as a partial basicranium has a smaller postorbital process than many symmoriiforms, including *Cobelodus* (Maisey 2007). Additionally, its postorbital region is more acuminate than that of other symmoriiforms like *Dwykaselachus* (Coates *et al.* 2017), and does not have the domed shape or upward-angled foramen magnum of *Maiseyacanthus* (Bronson 2021). More information from a higher resolution scan could be useful, however pending the discovery of a more complete cranium, only the most general shape of the basicranium can be compared with previously described taxa.

IMPLICATIONS OF PHYLOGENETIC ANALYSES

Recent anatomical studies of *Dwykaselachus* (Coates *et al.* 2017), *Pucapampella* Janvier & Suarez-Riglos, 1986 (Maisey & Anderson 2001; Maisey *et al.* 2019), *Doliodus* (Maisey *et al.* 2017), *Gladbachus* (Coates *et al.* 2018), and *Ferromirum* (Frey *et al.* 2020) have contributed immensely to resolving early chondrichthyan relationships. The most recently published comprehensive phylogenies of early chondrichthyans support the idea that acanthodians should be categorized as stem chondrichthyans (Coates *et al.* 2018; Frey *et al.* 2020). However, contrary to our findings, these authors found that symmoriiform chondrichthyans (including *Falcatus, Ozarcus*, *Akmonistion, Kawichthys,* and *Cladoselache*) are closely aligned with holocephalans. In Coates *et al.*'s (2018) description of *Gladbachus,* this is based on comparison of orbit length to the log of otic capsule length, as well as by their phylogenetic analysis, which used 262 morphological characters with 86 taxa. Some features that traditionally defined symmoriiforms are thus repurposed as defining characters of a symmoriiform-holocephalan clade, and symmoriiforms form a monophyletic group sister to a holocephalan clade. The discrepancy between their analyses and our parsimony analysis could be the result of using slightly different sets of taxa (theirs focuses includes more acanthodians and early bony fishes than ours) or due to the adjustment of some character coding, particularly the position of the dorsal aorta and occiput relative to the branchial arches.

However, the result of our maximum likelihood analysis was a topology that did recover this symmoriiform-holocephalan clade. This could be the result of algorithmic differences between parsimony and likelihood models. An examination of the signal in the matrix using a p-distance NeighborNet in SplitsTree4 suggested that phylogenetic signal in the data more closely recalled the parsimony output than it did the likelihood output. Notably, to estimate a tree in RAxML using a Mkv analysis, the four polymorphisms in the character matrix had to be transformed to unknowns, effectively resulting in a different data matrix from the one used for our unweighted parsimony analysis.

To better understand why these results were in conflict, we used Mesquite (Maddison & Maddison 2021) to identify which traits were grouping particular clades together in both the parsimony and likelihood trees. In the likelihood tree, *Cosmoselachus* n. gen. groups with holocephalans based on characters related to the endoskeletal operculum and gill slits, and the presence of a basihyal (though this was coded as unknown in *Cosmoselachus* n. gen.). The symmoriiform-holocephalan clade recovered in the likelihood analysis is grouped together based mainly on characters for which there is a large amount of missing data (for example, presence of internal carotid arteries, absence of the trigeminofacial recess, or the direction of the palatoquadrate articulation) and on the basis of the orbit being larger than the otic capsule (though this is unknown in *Cosmoselachus* n. gen. and *Debeerius*).

Character development and scoring, though a process that aims for objectivity, is perpetually evolving to accommodate new data, particularly as hypotheses of homology are confirmed or debunked. In fishes, characters such as presence/absence of claspers or, indeed, presence/absence of an operculum are often, perhaps erroneously, treated as homologous traits by virtue of being scored the same way. Sonic hedgehog (*shh*) signaling maintains elongation of the branchial rays in all modern cartilaginous fishes (Gillis *et al.* 2011), however the operculum character could be scored differently: a holocephalan hyoid-only state, a chondrichthyan septate state, and a *Cosmoselachus* n. gen. state somewhere in between. Ultimately, we scored *Cosmoselachus* n. gen. and holocephalans identically for this character, in part, to test the symmoriiform-holocephalan relationship; theoretically, this shared character would support to the existence of a symmoriiform-holocephalan clade, but this is only the case in the likelihood tree, and we don't recover the symmoriiform-holocephalan group in the parsimony analysis.

Given the combination of characters present in *Cosmoselachus* n. gen.: a sharklike dentition and jaws with a holocephalan-like operculum, we expected it to be more helpful in resolving the symmoriiform-holocephalan relationship. Future studies could apply additional phylogenetic methodology to the conundrum, perhaps by using implied weighting, Bayesian methods, or alternate methods of tree estimation. However, the crux of the problem is ultimately incomplete fossil data. Careful attention to the
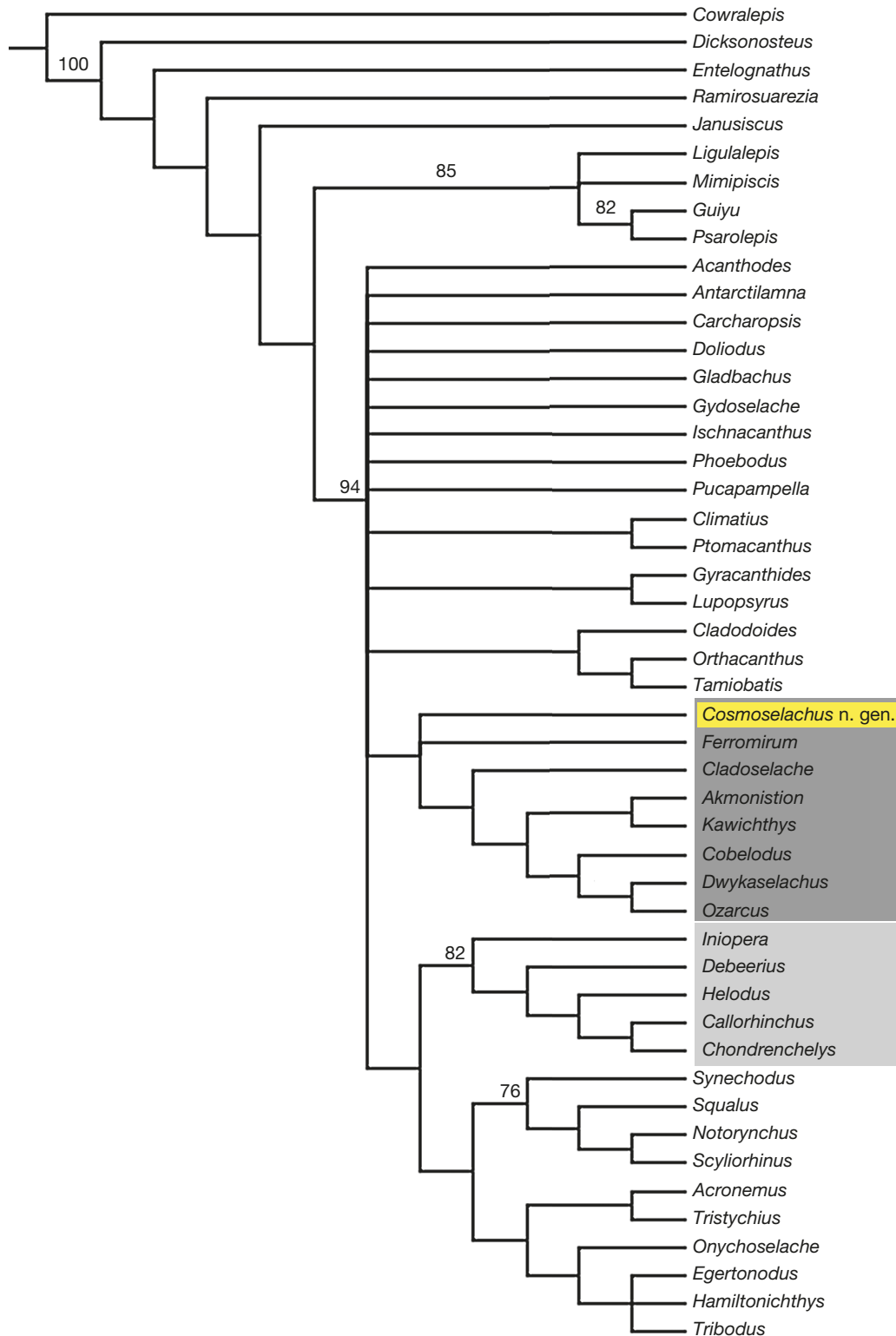
Fig. 7. — Consensus of eight most parsimonious trees. Bootstrap values are shown above branches; bootstrap values below 50 are not shown. New taxon *Cosmoselachus* n. gen. indicated by yellow highlight, holocephalan group and symmoriiform group indicated in differing shades of gray.

morphology of these fishes and subsequent adjustments to character descriptions and scorings (for example, should we be coding the *Cosmoselachus* n. gen. operculum with fused rays as the same character state as the un-fused opercular rays of holocephalans?) may better resolve the relationships of these fishes.

CONCLUSION

Cosmoselachus mehlingi n. gen., n. sp. possesses a unique operculum comprised of cartilaginous branchial rays that are fused together to form a corrugated structure extending over the gill openings. This structure differs from the operculum of holocephalans because the rays extend posteriorly from multiple gill arches (not only the hyoid), yet it also differs from the septate condition seen in elasmobranchs, because all of the endoskeletal rays in *Cosmoselachus* n. gen. are elongate. Unlike the condition in both holocephalans and elasmobranchs, the cartilaginous rays are fused to one another.

Features of the dentition and elongate Meckel's cartilages, as well as phylogenetic analysis by both parsimony and likelihood, place *Cosmoselachus* n. gen. among the symmoriiform chondrichthyans. However, phylogenetic analysis provides conflicting hypotheses of the affinity between holocephalans and other chondrichthyans (Pradel *et al.* 2011; Giles *et al.* 2015; Coates *et al.* 2018; Frey *et al.* 2020). Our results do not provide strong support for a symmoriiform-holocephalan clade, despite inclusion of an endoskeletal operculum character coded identically in both *Cosmoselachus* n. gen. and holocephalans.

Chondrichthyans represent a specialized group of fishes, at the base of which is a paraphyletic stem group of 'acanthodians' (Davis *et al.* 2012; Maisey *et al.* 2017). Some acanthodians had an operculum formed from a series of bony plates, supposedly of dermal origin (Eaton Jr. 1939), and thus these are non-homologous with the endoskeletal cartilaginous supports of the chimaeroid operculum. In developmental studies, holocephalan embryos have shown slightly elongated branchial rays, posterior to the hyoid arch (Gillis *et al.* 2011). If the structure identified here is functionally an operculum, then a hyoid operculum may have been repeatedly acquired and lost among chondrichthyans, or the operculate structure may be plesiomorphic here, due to the deep divergence between elasmobranchs and holocephalans, in which case the structure was lost in all non-operculate chondrichthyan lineages.

Cosmoselachus n. gen. is one of many exceptionally preserved chondrichthyans from the Late Mississippian Fayetteville Shale, which are gradually being described after many decades of collecting. The three-dimensional condition of its fin radials, *in situ* dentition, and preservation of thin cartilaginous structures such as the branchial rays are examples of the remarkable information available from Fayetteville Shale fishes. Continued study of fossils from this formation will likely yield more data that can improve understanding of chondrichthyan morphology and evolution.

DATA AND SOFTWARE AVAILABILITY

Surface files (.stl) of teeth, denticles, cranial fragments, jaws, and gill arch elements have been deposited in MorphoSource under the project title "*Cosmoselachus mehlingi*". An image stack (.tiff) of CT slices through AMNH FF 20509 was also deposited in MorphoSource (project 00000C478, https://www.morphosource.org/projects/00000C478).

The Nexus file (Appendix 2) of the character matrix is available on MorphoBank under matrix 28783 as part of Project 3996 ("A new operculate symmoriiform chondrichthyan from the Late Mississippian Fayetteville Shale [Arkansas, United States]"), alongside input files for the parsimony and likelihood analyses, as well as tree file output from our analyses and a tree file of the strict consensus tree. All of these can be found at http://morphobank.org/permalink/?P3996.

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APPENDICES

APPENDIX 1. — Supplementary material on *Cosmoselachus mehlingi* n. gen., n. sp.: Figures S1 to S4, Script for parsimony analysis in TNT, AIC scores for likelihood analysis, Parameters for likelihood analysis, Taxa included in phylogenetic analysis, Characters used in phylogenetic analysis and References for character descriptions and scoring. https://doi.org/10.5852/geodiversitas2024v46a4_s1

APPENDIX 2. — Chondrichthyan phylogeny including *Cosmoselachus mehlingi* n. gen., n. sp. (MorphoBank, project 3996, matrix 28783, http://morphobank.org/permalink/?P3996): https://doi.org/10.5852/geodiversitas2024v46a4_s2