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Tritor vascular tubules in a holocephalan tooth plate (*Ischyodus* sp.) from the Cretaceous of Mississippi, USA

MARK A. S. MCMENAMIN* & DOUGLAS FLEURY
Department of Geology and Geography, Mount Holyoke College, South Hadley, Massachusetts 01075, USA
mmcmenam@mtholyoke.edu; https://orcid.org/0000-0002-3764-0963
dfleury@mtholyoke.edu; https://orcid.org/0009-0001-5059-8851
**Corresponding author*

Abstract

A fossil chimaeroid tooth plate (*Ischyodus* sp.) from the Cretaceous of Frankstown, Mississippi shows exceptional preservation of tritor microstructure. Diagenetic loss of the petrodentine/whitlockin in this specimen has revealed the ultrastructure of the vascular tubule networks of tritor interior structure. The observation that vascular tubes running through the hard tissues of chimaeroid tritors host odontoblast cells supports the hypothesis of an odontoblastic origin for chimaeroid tritor tissue.

Keywords: chimaeroids, holocephalans, tritor, pleromin, whitlokin, Cretaceous, Mississippi, *Ischyodus*

Introduction

Chimaeroids (ratfish or elephantfish) are a distinctive group of cartilaginous, oviparous holocephalan fishes that range from the Late Triassic (Carnian–Norian) to Recent (Ward & Duffin, 1989; Didier, 1995; Duffin, 1996; Hoganson & Erickson, 2005). They represent a late Palaeozoic lineage that diversified into deep marine habitats. Chimaeroids swim primarily by means of enlarged, wing-shaped pectoral fins. Holocephalan body length reached more than 3 m in the Cretaceous Antarctic species *Edaphodon snowhillensis* (Gouiric-Cavalli *et al.*, 2015).

Chimaeroids have been reported from the Upper Cretaceous of the south-eastern USA from New Jersey to Mississippi, USA (Hussakov, 1912; Case, 1978; Manning & Dockery, 1992; Manning, 2006; Cicimurri, 2010). *Ischyodus* has been reported from the Cretaceous of the western USA (Hoganson & Erickson, 2005; Johnson-Ransom *et al.*, 2018). The fossil record of chimaeroids from the eastern USA continues into the Cenozoic (Cicimurri & Ebersole, 2015) but with evidence of faunal turnover at the end-Cretaceous extinction event (Hoganson & Erickson, 2005).

Chimaeroids have statodont dentition and thus do not replace teeth. Chimaeroids in fact lack teeth, but instead have sclerophagous/durophagous plates for crushing prey. These plates consist of elongate pads called tritors. Tritor plates are largely composed of pleromin/whitlockin ensconced in whitlockite-poor trabecular dentine (ranging from osteodentine to denser sclerotic osteodentine). The high magnesium content of whitlockin causes it to be diagenetically unstable, so that, ironically, the hardest tissue was the first to disappear. The preservation observed here shows the ultrastructure of the tubule networks of tritor interior structure, with the vascular tube in the center, comparable to that of the modern chimaeroid *Harriotta raleighana*. As the vascular tubes were the site of residence of odontoblast cells, this suggests an odontoblastic as opposed to an osteoblastic origin for chimaeroid tritor tissue.

Chimaeroids are remarkable for their unusual jaws, consisting of three pairs of crushing plates (vomerine, palatine and mandibular; Stahl & Parris, 2004). In a unique development in the animal kingdom, the plates are largely composed of a material called whitlockite-rich dentine (pleromin or whitlockin) ensconced in whitlockite-poor trabecular dentine (ranging from osteodentine to denser sclerotic osteodentine) to form the tritor plate (Smith *et al.*, 2019; Johanson *et al.*, 2021). This unusual dentition can be traced back at least to Early Jurassic (Duffin, 1984). Pleromin/whitlockin is a phosphorus and calcium-bearing biomineralized tissue (Ishiyama *et al.*, 1991) with a composition similar to that of the mineral whitlockite ($Ca_9(MgFe)(PO_4)_6PO_3OH$).

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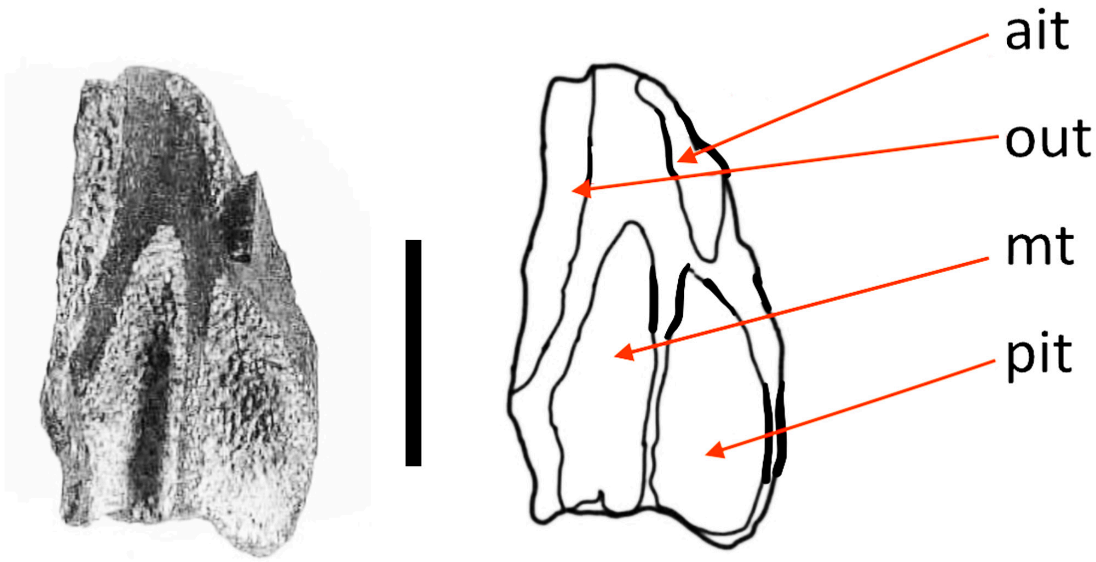

FIGURE 1. *Ischyodus* sp. (specimen number Fleury 1991-04-26 A [MMNS VP-12190]). Right palatine tooth plate, occlusal surface. Abbreviations: ait, antero-inner tritor; mt, median tritor, out, outer tritor; pit, postero-inner tritor. Scale bar = 1 cm.

Hypermineralization with pleromin of the raised tritors of tooth plates is characteristic of chimaeroid fishes. The hypermineralized dentine of tooth plate tritors and tritor ovoids form a rectilinear grid when revealed by density dissected micro-CT mapping (Smith *et al*., 2019). Plates consist primarily of dentine, with bone-like trabecular dentine (‘osteodentine’) transitioning to more heavily mineralized dentine (‘sclerotic osteodentine’) near the occlusal surfaces (Smith *et al*., 2019).

Whether or not the trabecular hypermineralized dentine is odontoblastic in origin (Smith *et al*., 2019) or osteoblastic in origin (Ishiyama & Sasagawa, 1984) is controversial. However, the fact that the vascular tubes running through the hard tissues of chimaeroid tritors host odontoblast cells (Moya Meredith Smith, personal communication) supports the hypothesis of an odontoblastic origin for chimaeroid tritor tissue.

Geological setting

Late Cretaceous formations of northeastern Mississippi include the Tuscaloosa, the Eutaw, the Mooreville, the Coffee Sand, the Demopolis, the Ripley, the Prairie Bluff, and the Owl Creek Formations (Manning & Dockery, 1992). These formations largely consist of shallow marine and coastal estuarine deposits. Fossil localities occur in the basal Demopolis Formation (Late Cretaceous, middle Campanian, *ca*. 77 Ma), near its contact with the Coffee Sand, from localities near Frankstown, Mississippi. The Coffee Sand represents a deltaic deposit that was deposited in a shallow marine basin. A 60 cm thick sand bed at the base of the Demopolis Formation (the “Frankstown Sand”) is known for its abundant shark teeth (Manning & Dockery, 1992). The Frankstown Sand has also yielded chimaeroid tritors.

The specimen considered here (Figs 1–3; *Ischyodus* sp.; specimen number Fleury 1991-04-26 A [MMNS VP-12190]), is derived from the road bed on a hill south of Twenty Mile Creek, Prentiss County, Mississippi. This fossil locality, consisting of numerous fossils collected over a mile of exposed roadbed, were found (beginning in 1990) during construction of Highway 45. Fossils were obtained by washing sediment over coarse and fine screens. In spite of the abundance of fossils at this site, only a handful of chimaeroid specimens were recovered (Manning & Dockery, 1992).

Results

A fossil chimaeroid tooth plate (*Ischyodus* sp.) from the hill south of Twenty Mile Creek (Figs 1–3) shows tooth plate (tritor) microstructure in the form of superbly preserved vascular tubes that were exposed by diagenetic dissolution of the hard tissue (pleromin or whitlockin) of the tritor. The specimen described here is a right palatine tooth plate of *Ischyodus* sp. (Hoganson & Erickson, 2005; Cicimurri & Ebersole, 2015). Fig. 1 shows an antero-inner tritor, a median tritor, an outer tritor and a postero-inner tritor. This tooth plate compares closely with the specimen shown in fig. 3C of Ebersole *et al*.

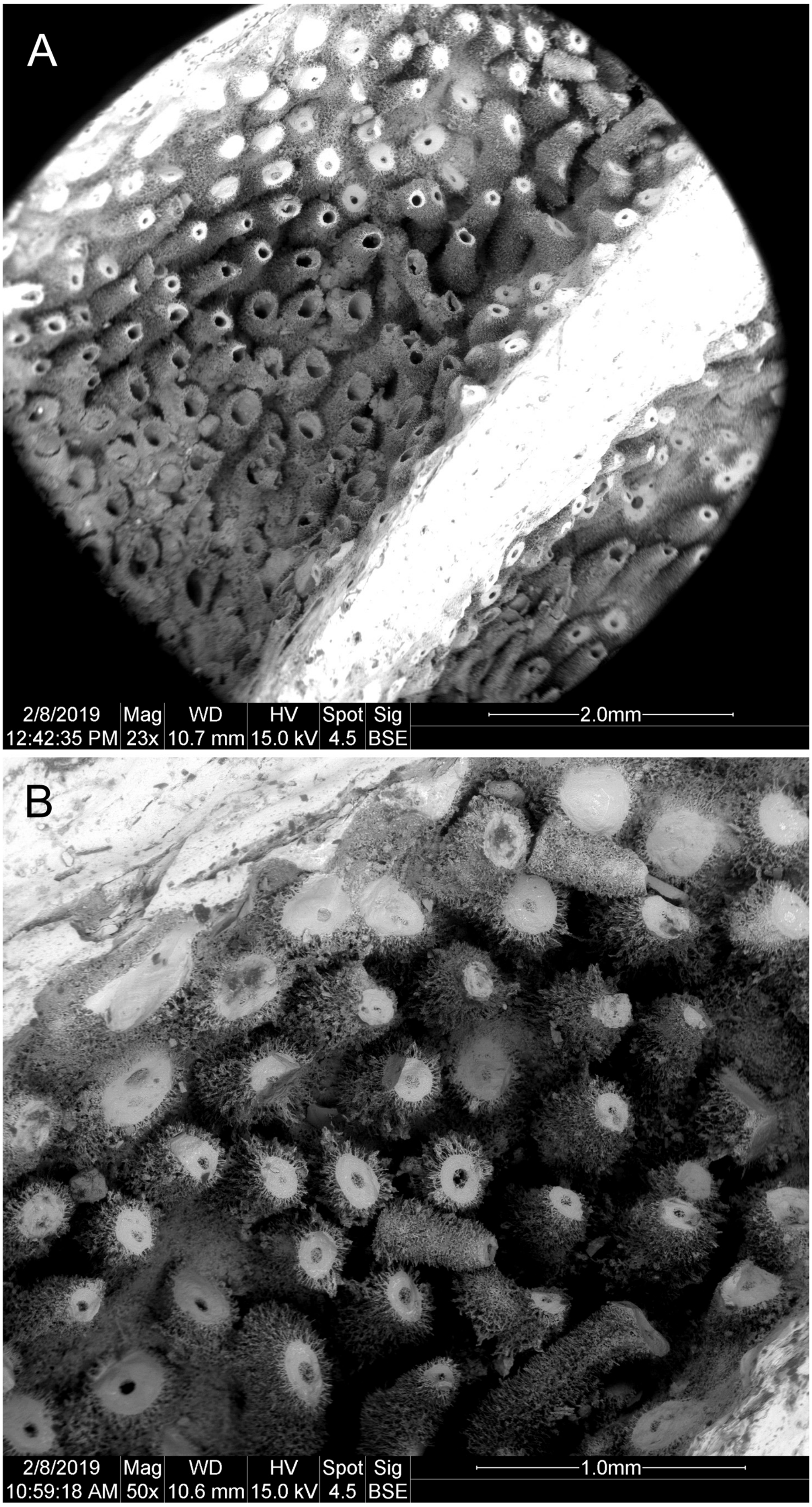

FIGURE 2. *Ischyodus* sp. Right palatine tooth plate. **A**, Details of the exposed base of a tritor pad. **B**, Detail showing starburst trabeculae on the tubes of an inner tritor. Backscattered electron images.

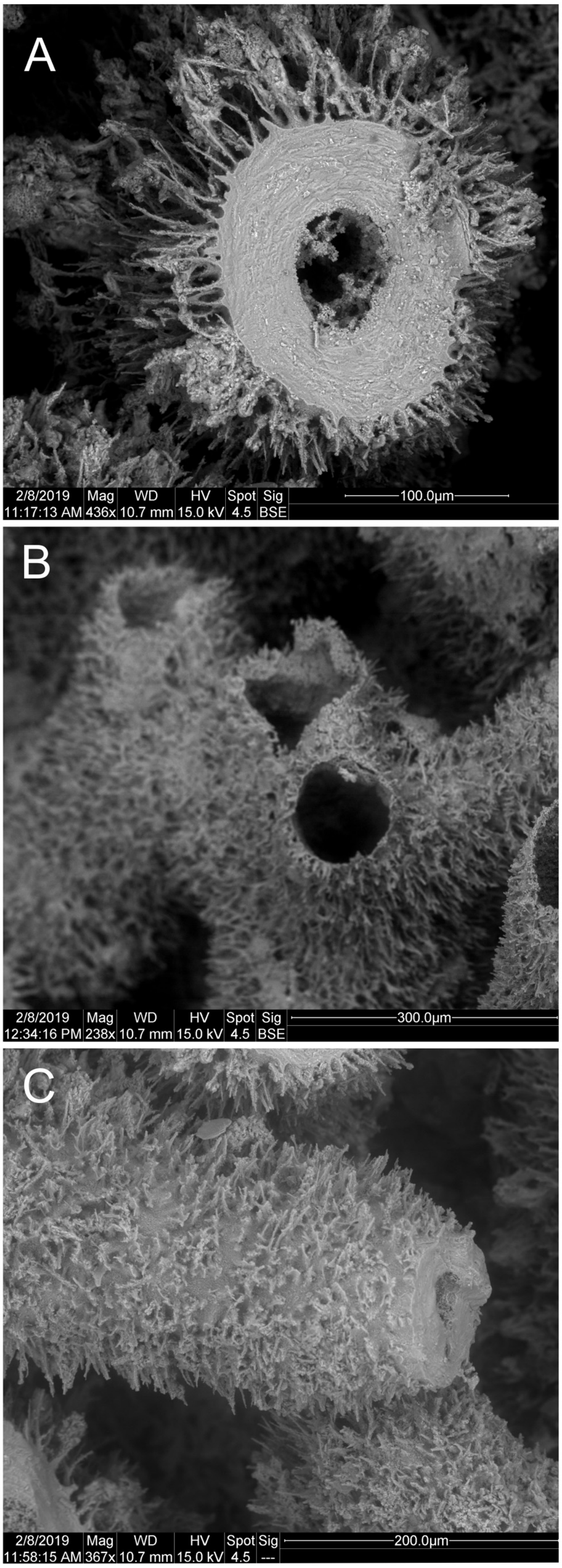

FIGURE 3. *Ischyodus* sp. Right palatine tooth plate. **A**, Detail showing starburst trabeculae on a single tube. Note how laminated cores of the tubes extend outward to join the starburst pattern. **B**, Details showing fusion of tubes. **C**, Details showing side of tubes with trabeculae oriented at an inclined angle. Backscattered electron images.

(2022), and also resembles a juvenile palatine plate that Manning & Dockery (1992, their plate 3: fig. 1) assigned to *Ischyodus bifurcatus*. The tritors in the specimen described here, unlike the specimen illustrated by that Manning & Dockery (1992), are longer and more closely spaced. This may be related to ontogenetic differences, but may also indicate a species-level characteristic trait, thus the specimen described here is assigned to *Ischyodus* sp. rather than *I. bifurcatus*.

The specimen described here preserves, in spectacular fashion, vascular tubules on the caudal inner tritor (Figs 2, 3). Fig. 2B shows starburst trabeculae on the tubes of the tritor interior. Fig. 3A shows how the laminated cores of the tubes extend outward to join the starburst pattern. The trabeculae form very roughly parallel stacks along the length of each tubule (Fig. 3C). Tubules may be fused together (Fig. 3B). These structures are identical to the tubule networks of tritor interior structure, with the vascular tube in the centre, as illustrated by Johanson *et al*. (2021) in their fig. 9f illustrating *Harriotta raleighana*. The comparison is so close that there is no doubt that this superb preservation illustrated here has revealed the ultrastructure of vascular tissues associated with tritor pleromin/whitlockite. Manning & Dockery (1992) noted the effects of dissolution on specimens of *Ischyodus bifurcatus*, but attributed this to loss of aragonite, not pleromin/whitlockin as is evidently the case.

Fig. 5 of Kemp (2001), in a petrodentine system (dipnoan tooth plates), shows a possibly homologous morphology with radiating spaces for cell processes in the circumdenteonal dentine radiating outward from the secondary denteons within interdenteonal dentine. The fact that the spaces for cell processes that radiate into the petrodentine of dipnoan tooth plates supports the hypothesis of an odontoblastic origin for lungfish teeth.

Conclusion

A fossil chimaeroid tooth plate (*Ischyodus* sp.) from the Cretaceous of Frankstown, Mississippi shows exceptional preservation of tooth plate (tritor) microstructure, displaying fossilized tubule networks that compare closely to those of the modern chimaeroid *Harriotta raleighana*. Diagenetic loss of the petrodentine/whitlockin in this Cretaceous specimen has revealed the ultrastructure of the vascular tubule networks of tritor interior structure (with vascular tube in the center), which was the place of residence of the odontoblast cells. The observation that vascular tubes running through the hard tissues of chimaeroid tritors host odontoblast cells supports the hypothesis of an odontoblastic origin for chimaeroid tritor tissue.

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