

Taxonomic Note

Resolving the identity of *Platylithophycus*, an enigmatic fossil from the Niobrara Chalk (Upper Cretaceous, Coniacian–Campanian)

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Abstract.—Misidentified fossils are common in paleontology, but *Platylithophycus* has undergone a particularly problematic series of descriptions. The holotype of *P. cretaceus* comes from the Upper Cretaceous Niobrara Chalk of Kansas, and was first described as a calcareous green alga, based on the surface texture of the specimen. Later, *Platylithophycus* was re-identified as a sepiid cephalopod, based partly on a comparison of microstructure between *P. cretaceus* and the pen of modern squids. *Platylithophycus* then became part of the University of Nebraska teaching collection, where, according to paleontological legend, an undergraduate student suggested that the fossil's tessellated surface looked a lot like shark cartilage. However, that interpretation has not been formally proposed until now. This work re-describes the holotype of *Platylithophycus cretaceus* as part of the branchial endoskeleton of an elasmobranch, based on both gross morphology and ultrastructure, including recognizable tessellated cartilage with intertesseral pores and joints.

Introduction

The Upper Cretaceous (Coniacian–Campanian) Niobrara Chalk of Kansas is a famed source of well-preserved vertebrate fossils, and is likely the “most-diverse and best-known Mesozoic fish assemblage in North America” (Wilson and Bruner, 2004, p. 583; Shimada and Fielitz, 2006). As the Farallon Plate was subducted under the North American Plate, in the channel known as the Western Interior Seaway, the Niobrara Chalk was deposited as part of the Niobrara cyclothem; it represents the farthest extent of Western Interior Seaway depositional events. The Western Interior Seaway served as a throughway for marine organisms, resulting in a diverse fossil fauna. Abundant macroinvertebrates (cephalopods, bivalves, ammonoids, and crinoids) are present in the Niobrara Chalk, as are invertebrate trace fossils (Frey, 1972). Vertebrate diversity of the Niobrara Chalk is comprised of bony fishes (Stewart, 1999; Shimada and Fielitz, 2006) cartilaginous fishes (Stewart, 1978; Shimada, 1996), and tetrapods (sea turtles [Matzke, 2007], plesiosaurs, mosasaurs [Everhart, 2001, 2002], pterosaurs [Bennett, 2000], and avian and non-avian dinosaurs [Carpenter et al., 1995]). The fish fauna includes isolated teeth, denticles, and body fossils of numerous taxa (Shimada and Fielitz, 2006), including holocephalans (*Edaphodon*, Callorhynchidae), elasmobranchs (Ptychodontidae, Mitsukurinidae, Odontaspidae, Cretoxyrhinidae, Anacoracidae), batoids (*Cretomanta*, Rhinobatidae), and bony fishes (actinopterygians [Pycnodontiformes, Semionotiformes, and many members of the teleost stem and crown], as well as sarcopterygians [Coelacanthiformes]).

The depositional environment of the layers that yielded *Platylithophycus* may have been hypersaline, and likely

represented a circalittoral zone, as is the case with most marine chalks (Frey, 1972). The depositional environment of the Smoky Hill Member of the Niobrara Chalk has been well reviewed, but the formation is otherwise not thoroughly catalogued or integrated, partly because it is mostly exposed as a series of discontinuities (Hattin, 1982). Hattin (1982) described a depositional environment with poorly oxygenated benthic zones, and a paleoenvironment in which epibenthic communities were highly diverse and nearly all benthic invertebrate taxa were suspension feeders.

Platylithophycus has been ascribed to two different phyla over the past 70 years, first deemed a green alga, and later re-described as a cephalopod. Johnson and Howell (1948) were the first to describe *Platylithophycus* and compared the texture of the slab with that of calcareous green algae, such as *Codium*. They described two parts of a “plant”: (1) surfaces covered with hexagonal plates, and (2) supposedly calcium carbonate-covered thread-like filaments (Johnson and Howell, 1948, fig. 1). They struggled to determine how these two parts were related to one another—they proposed the hexagonal, tessellated structures might have been protoplasmic objects produced inside cells, rather than representing an external surface of the “plant.” They called the tessellated surfaces “fronds,” and described filaments so dense that they lay matted both beneath and on top of the fronds (Johnson and Howell, 1948).

The focus of Miller and Walker's (1968) work was to describe two new teuthid cephalopods from the Niobrara Formation, but they also included a revision of *Platylithophycus*. Their experience with cephalopod fossils led them to compare *Platylithophycus* with a sepiid (cuttlefish), based primarily on its textural similarities to cuttlebone. However, they did not confirm

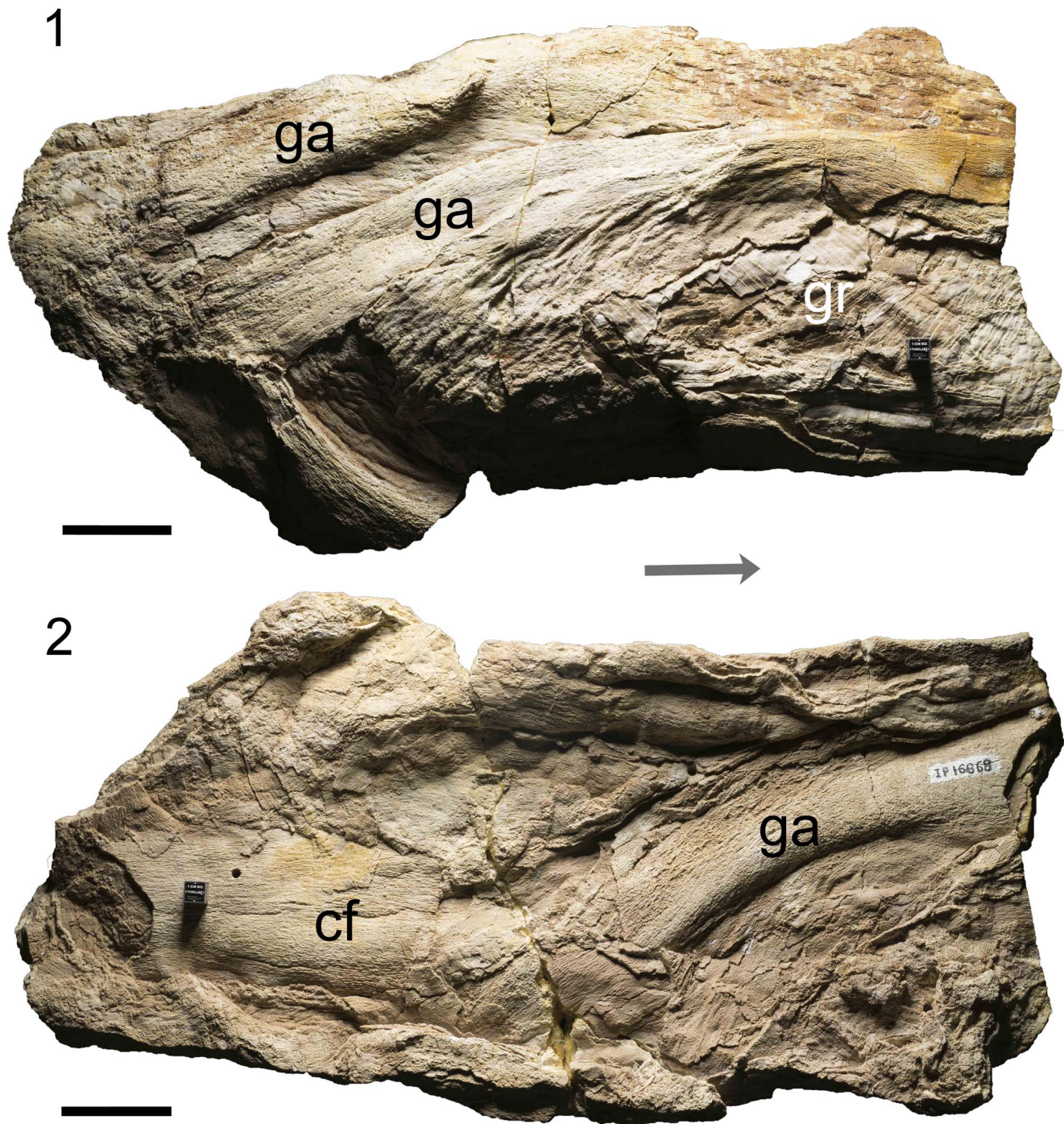


Figure 1. Holotype of *Platylithophycus cretaceus* (UNSM IP 16868), showing arc of the features interpreted here as gill arches. (1) Lateral view; (2) medial view. Abbreviations: ga = gill arches, gr = gill rakers, cf = cartilage fragments. Arrow indicates anterior, scale = 5 cm. Photo courtesy of M. Eklund.

the fossil's chemical composition to support their assertion that it was composed of aragonite. Moreover, their diagnosis ignored the "fronds" described by Johnson and Howell, and only discussed the "filaments" (Johnson and Howell, 1948; Miller and Walker, 1968). Despite describing a "septate ventral pad," and "porous pen structure," (not figured in their paper), Miller and Walker (1968, p. 183) were unable to assign *Platylithophycus* at the family level. They refuted Dr. Maxim K. Elias' unpublished observations and re-assignment to the genus *Trachyteuthis*, instead designating the original genus *Platylithophycus* to the order Sepiida, Zittel 1895.

This description made *Platylithophycus* the oldest sepiid squid then on record (Miller and Walker, 1968).

Importantly, in all these earlier studies, the hard tissue in *Platylithophycus* was assumed to be composed of calcium carbonate, although a simple test such as the application of a dilute organic (e.g., formic, acetic) acid would easily have falsified that interpretation, because these acids attack calcium carbonate but not calcium phosphate (a property that forms the basis of a widely used preparation technique in vertebrate paleontology; Toombs, 1948). When we performed this test, the fossilized tissue was unaffected.

Materials and methods

Materials.—Well-preserved gill arches and cartilage fragments (UNSM IP16868). Three small chips of the holotype (previously numbers 26071, 26072, and 26073 in Princeton University's geology collection) had been given to the American Museum of Natural History in 1982 with a note to rejoin the holotype (then residing at the Carnegie Museum). These fragments are now reunited with UNSM IP 16868.

Locality information.—No coordinates were provided at the time of this specimen's collection, so its exact position is unknown beyond the following: "Upper Cretaceous Niobrara Formation, three miles northeast of Monument Rocks, Cove County, Kansas" (Johnson and Howell, 1948, p. 632).

Methods.—Specimen was examined using a dissecting microscope, and photographed using a DinoLite handheld microscope (AnMo Electronics Corporation), and photographed under UV light (by Mike Eklund, ThinkLabz), which produced fluorescence consistent with use of some kind of sealant or epoxy treatment (not necessarily consistent with biological or geological fluorescence). Morphology of UNSM IP16868 was compared with figures and descriptions from the work of Johnson and Howell (1948) and Miller and Walker (1968). The fragments previously known as Princeton specimens 26072 and 26073 (now part of UNSM IP 16868) were imaged using scanning electron microscopy, with a Zeiss EVO 60 Variable Pressure SEM.

Repository and institutional abbreviation.—Specimen housed at the University of Nebraska State Museum (UNSM).

Systematic note.—The original species name has been emended here to agree with the gender of the genus name (Latin *phycus*, masculine noun III declension; *cretaceus*, adjective I class).

Systematic paleontology

Class Chondrichthyes Huxley 1880
 Subclass Elasmobranchii Bonaparte 1838
 Elasmobranchii incertae sedis
 Genus *Platylithophycus* Johnson and Howell, 1948

Platylithophycus cretaceus (Johnson and Howell, 1948)
 Figures 1–3, 4.1, 5, 6, 7.1, 7.3

- 1948 *Platylithophycus cretaceum* Johnson and Howell, p. 632, pl. 93, figs. 1, 2.
 1968 *Platylithophycus cretaceum*; Miller and Walker, p. 181, pls. 2, 3.

Holotype.—Gill arches and associated cartilage fragments (UNSM IP 16868) from the Niobrara Chalk, Kansas (Johnson and Howell, 1948, pl. 93, figs. 1, 2).

Diagnosis.—Cartilaginous gill arches of a large chondrichthyan fish, embedded in chalk matrix. Calcified cartilage of the gill arches possesses a filamentous appearance (Fig. 2), while



Figure 2. Holotype of *Platylithophycus cretaceus* (UNSM IP 16868), detail of mineralized cartilage on surface of features interpreted as gill arches, scale = 1 cm. Photo courtesy of M. Eklund.



Figure 3. Holotype of *Platylithophycus cretaceus* (UNSM IP 16868), detail of features interpreted here as gill rakers, scale = 1 cm. Photo courtesy of M. Eklund.

the cartilage present on gill rakers (Fig. 3) is tessellated ("canaliculate" according to Miller and Walker, 1968).

Occurrence.—Upper Cretaceous Niobrara Chalk, 3 miles northeast of Monument Rocks, Cove County, Kansas (Johnson and Howell, 1948).

Description.—The specimen is 48 cm in length and 24 cm across at its widest point. Gill arch elements are all fairly stout

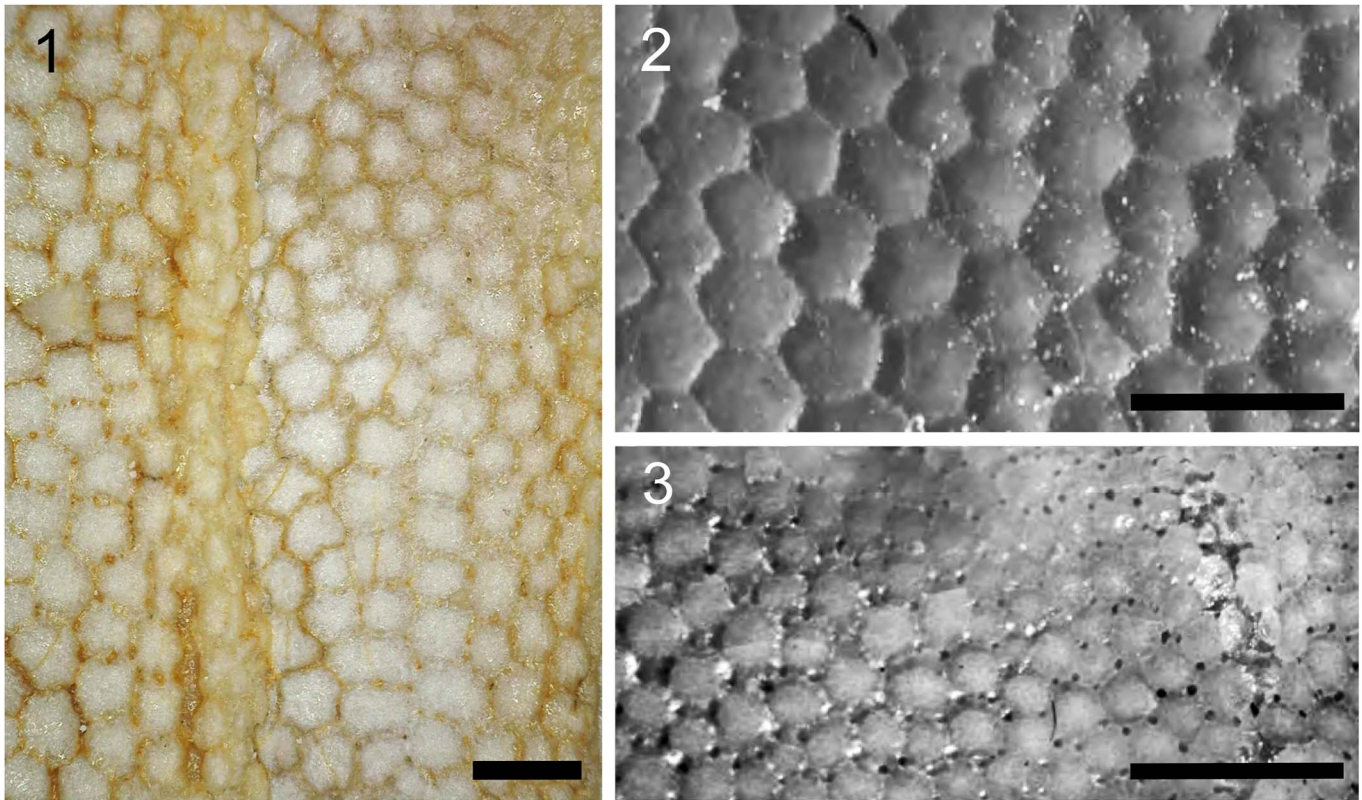


Figure 4. Comparison of (1) *Platyolithophycus* (UNSM IP 16868) tesserae with cartilage tesserae of (2) extinct *Libanopristis* (AMNH FF 3705) and (3) extant *Rhizoprionodon* (AMNH FF 21652); (2) and (3) are modified from Maisey 2013; scale = 1 mm.

and flattened in shape, which may be a result of taphonomic distortion (Fig. 1). The exposed elements are considered to represent the actual gill-bearing parts of branchial arches (i.e., ceratobranchials and/or epibranchials). More ventral (basio-, hypo-) and dorsal (pharyngo-) elements could not be recognized. Gill rakers are present beneath the elements identified here as ceratobranchials, and are tessellated differently from the skeletal cartilage (Fig. 3).

Materials.—University of Nebraska State Museum IP 16868.

Remarks.—*Platyolithophycus cretaceus* is founded on material that bears many similarities to the calcified cartilage of a chondrichthyan fish. Its surface structure is remarkably similar to that of tessellated cartilage (Figs. 2, 3), and the overall morphology is that of large gill arches (probably epibranchials and ceratobranchials). Structures interpreted to be gill rakers are present, medial to the gill arches (Figs. 1.1, 3). The size of these elements indicates this was a large chondrichthyan.

Results

The tiled appearance of the surface of *Platyolithophycus* is identical to the tessellated calcified cartilage of both extinct and extant chondrichthyans (Fig. 4). Tesserae are arranged with a sub-hexagonal close-packing arrangement, with individual tesserae defined by an intertesseral joint system (Fig. 5), as well as local presence of intertesseral pores between tesserae (Fig. 5.1).

When previous descriptions of *Platyolithophycus* are reinterpreted in the light of our interpretation of the structure and morphology of the holotype (Fig. 1, UNSM IP16868), several noteworthy features emerge. Johnson and Howell (1948) described a “plant consisting of many flat fronds about six inches long and half an inch wide.” The difference in texture between these structures and surrounding filamentous structures baffled these earlier workers, who wrote, “the filaments appear to have grown from both sides of the fronds and they were so numerous that, where the fronds lie flat on the bedding surface, as they do in our specimen, the filaments form an almost matted layer above and beneath them” (Johnson and Howell, 1948, p. 632). Based on our interpretation of *Platyolithophycus* as having tessellated cartilage, the “filaments” described by Johnson and Howell probably represent differentially calcified cartilaginous gill arches (Fig. 2). The filaments resemble continuous strands at low magnification (Fig. 6.1), but when examined under an electron microscope, they are composed of semi-contiguous individual tesserae, separated from neighboring tesserae by faint traces of intertesseral joints (Fig. 6.2, 6.3). This filamentous structure might initially appear unusual, but similar coalesced strands of tesserae are sometimes present in the cartilage of extant chondrichthyans (e.g., *Lamna*; Fig. 7).

Johnson and Howell’s “fronds” are reinterpreted here as the cartilage forming serial arrays of chondrichthyan gill rakers (Fig. 3). Comparison of their overall morphology with extant and fossil cartilaginous fishes indicates the fossil represents only the gill arches of the animal. No teeth are visible on the holotype specimen, although some may be hidden inside

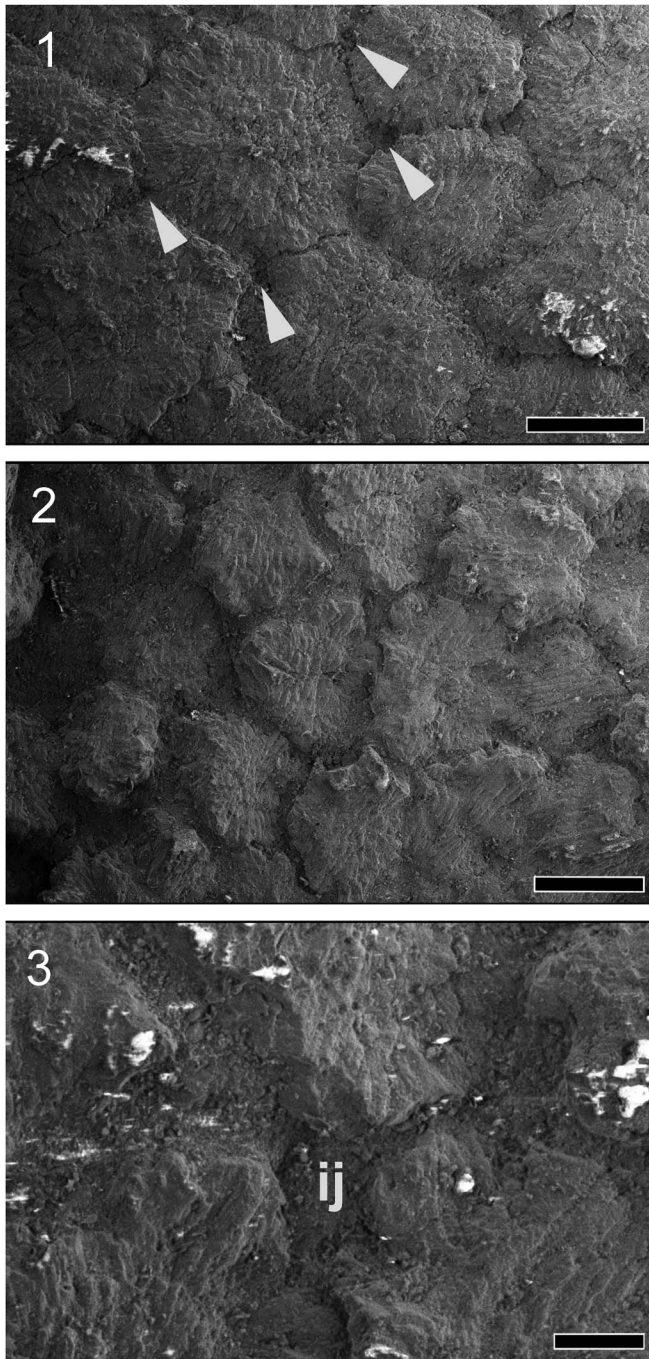


Figure 5. Scanning electron micrographs of the tessellated surface of *Platylithophycus* (UNSM IP 16868, previously Princeton specimen 26073). (1) Smooth section of undisturbed tesserae, showing intertesseral pores, marked by arrowheads, scale = 400 um; (2) tesserae of relatively uniform size, showing intertesseral joints, scale = 400 um; (3) detail of (2), magnifying the intertesseral joint area (ij), scale = 100 um.

the matrix and therefore inaccessible without CT scanning or additional preparation.

Discussion

Endoskeletal tessellated calcified cartilage is considered a synapomorphy of conventionally defined chondrichthyans, within the total group Chondrichthyes (including acanthodian

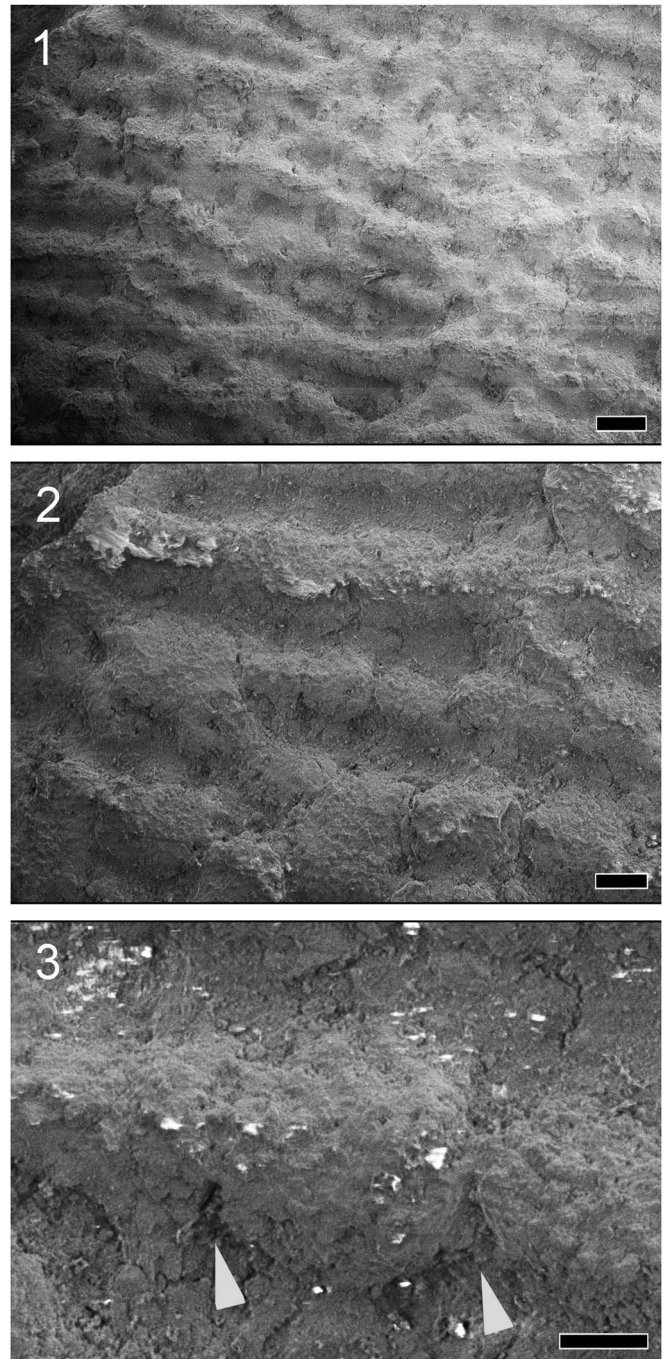


Figure 6. Scanning electron micrographs showing the thread-like “filaments” of *Platylithophycus* (UNSM IP 16868, previously Princeton specimen 26072) previously considered part of a sepiid cuttlebone or a calcareous green alga, but here shown to be composed of tessellated cartilage, by a series of increasingly magnified images of a region of the cartilage. (1) Filaments appear uniform at higher magnification, scale = 400 um; (2) filaments are revealed to be made up of tesserae, scale = 200 um; (3) detail of individual tesserae, intertesseral joints marked by arrowheads, scale = 100 um.

fishes that lack this hard tissue; Zhu et al., 2013). Thus, presence of this unique endoskeletal tissue in *Platylithophycus* is a hallmark feature of many chondrichthyans. Although the basic structure of tessellated calcified cartilage is highly conserved among these forms, the arrangement and density of individual tesserae, and the depth of calcification within the cartilaginous

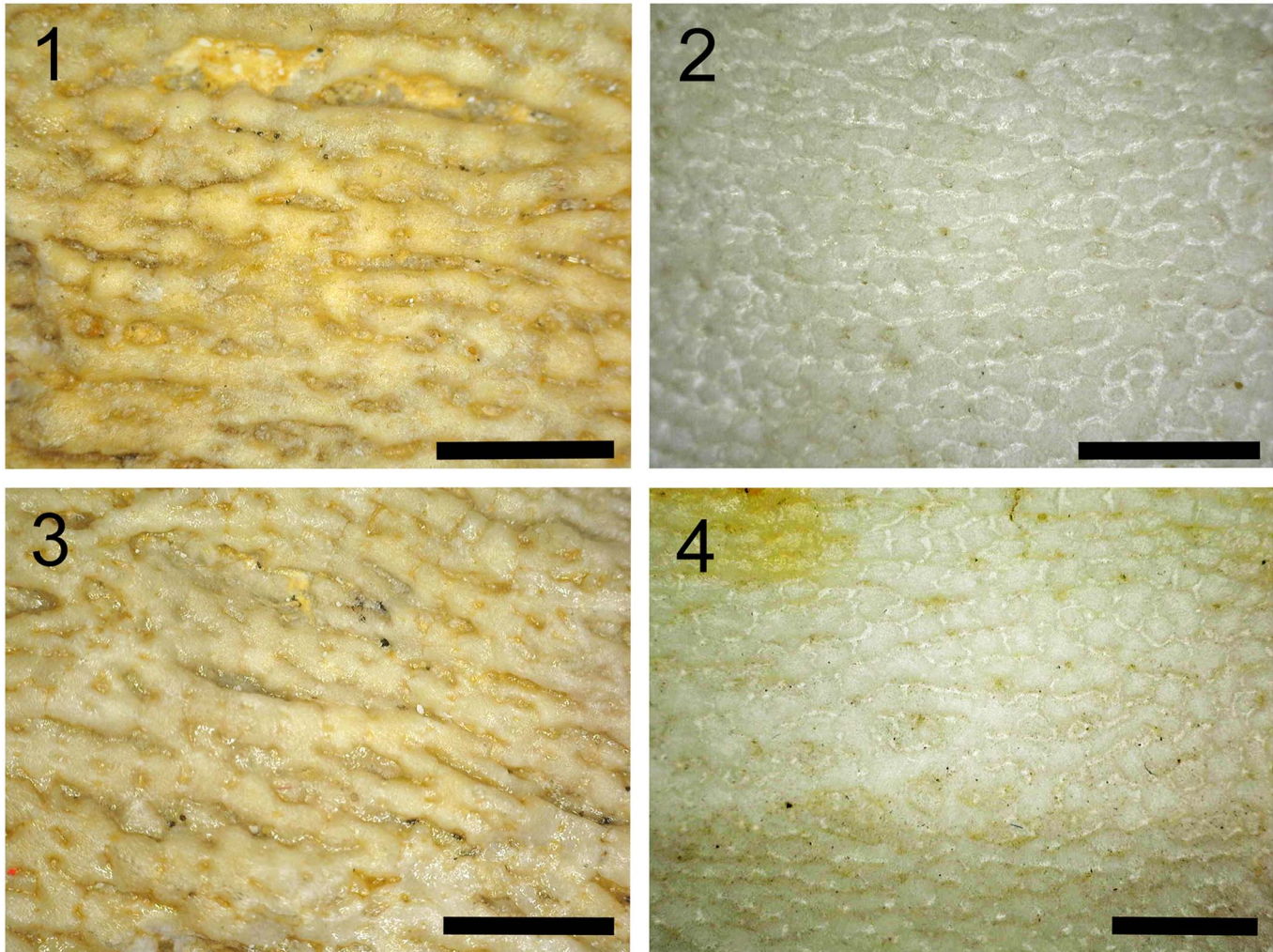


Figure 7. Surface of (1, 3) UNSM IP 16868, showing threadlike aggregations of tesserae on the surface of a gill arch in *Platylithophycus*, compared with (2, 4) a similar threadlike appearance of cartilage on the surface of the cranium in the extant mackerel shark (*Lamna*, AMNH FF 20426), scale = 2 mm.

endoskeleton varies among taxa and even across different parts of the skeleton in a single individual (Dean, 2011; Maisey, 2013). Anecdotal evidence exists for a diversity of tesseral configurations, but these have been poorly documented in the literature, and a review of these is beyond the scope of this paper. Our observations nevertheless demonstrate that *Platylithophycus* is founded on parts of a chondrichthyan whose cartilage exhibits at least two types of tesseral morphology that can be recognized in modern elasmobranchs. Only recently has much attention been devoted to resolving the development of tesserae in extant chondrichthyans (Seidel et al., 2016), the regulation of the mineralization process, and the effects of environment on calcification (Dean et al., 2015), but it seems likely that the tessellated calcification in *Platylithophycus* developed in identical manner to extant elasmobranchs.

While it is possible to diagnose *Platylithophycus cretaceus* on the basis of its unusual and potentially apomorphic gill raker morphology, the lack of features such as teeth in the holotype specimen mean that this taxon can only be classified as Elasmobranchii incertae sedis, pending the future discovery of more complete remains, which might provide clues as to its identity or possible synonymy with another large Niobrara Chalk elasmobranch.

Several large, predatory lamniform sharks have been described from the Niobrara Chalk, including *Cretoxyrhina* (Shimada, 1997a, b), *Scapanorhynchus* (Hamm and Shimada, 2002), and *Cretolamna* (Shimada, 2007), and it is possible that *Platylithophycus* belongs to one of these previously described taxa, although modern predatory lamniform sharks do not have densely arranged cartilaginous gill rakers like those of *Platylithophycus*. Dense arrays of gill rakers are found in modern filter-feeding elasmobranchs, including the whale shark (*Rhincodon typus*, order Orectolobiformes), basking shark (*Cetorhinus maximus*, order Lamniformes), megamouth shark (*Megachasma pelagios*, order Lamniformes), and rays (*Manta*, *Mobula*, order Myliobatiformes). However, extant filter feeding sharks do not have the type of gill raker structure observed in *Platylithophycus*; instead, the rakers consist either of elongate modified denticles as in *Megachasma* (Paig-Tran and Summers, 2013, fig. 14), have denticles covering their surface of cartilage as in *Cetorhinus* (Paig-Tran and Summers, 2013, fig. 15), or are entirely cartilaginous elements arranged into filtering pads as in *Rhincodon* (Matthews, 1950; Motta et al., 2010; Paig-Tran and Summers, 2013, fig. 13). Additionally, the filtering pads of *Rhincodon* are characterized by

a reticulated mesh structure that was not observed in *Platylithophycus*. Nevertheless, large, filter-feeding rays such as *Manta* and *Mobula* have densely packed, cartilaginous gill rakers (Paig-Tran and Summers, 2013, figs. 5, 6), somewhat like those observed in *Platylithophycus*. A thorough review of the gill structures in filter-feeding chondrichthyans, including images to which we compared *Platylithophycus*, was presented by Paig-Tran and Summers (2013). Paig-Tran et al. (2013) provided a detailed comparison of filter pads in devil rays, at both microscopic and macroscopic scales.

Rare teeth from a putative manta ray relative, *Cretomanta*, have been documented from the Upper Cretaceous of northern Africa and North America, as well as from the Niobrara Formation of Saskatchewan, Canada (as *Cretomanta canadensis*, Case et al., 1990). No skeletal remains of this enigmatic taxon have been found, so it is unknown whether its branchial skeleton is like that of *Platylithophycus*.

Conclusions

Based on the tessellated structure of *Platylithophycus*, in combination with the gross morphology of the structures that we interpret as gill arches and gill rakers, *P. cretaceus* is here interpreted as a large cartilaginous fish, possibly related to extant filter-feeding rays such as *Manta* and *Mobula*. This identification potentially expands the range of morphological diversity in the Niobrara elasmobranch fauna (which includes a form that possessed *Manta*-like teeth; Case et al., 1990). However, we cannot definitively identify *P. cretaceus* beyond the level of *Elasmobranchii incertae sedis* because no name-bearing teeth or other identifiable elements such as denticles or fin spines are associated with the holotype specimen.

While we disagree with identifications of *Platylithophycus* as a plant or invertebrate, we recognize that those earlier comparisons with an alga or squid were based upon reasonable arguments given the interpretations presented. Prior researchers may simply have lacked expertise in vertebrate hard tissue ultrastructure (particularly the unique form of chondrichthyan calcified cartilage). According to paleontological legend, an undergraduate was the first to identify this fossil's chondrichthyan affinity (a student in a University of Nebraska paleontology class is said to have suggested *Platylithophycus* looked like fossil cartilage).

Paleontology is home to myriad temporarily misplaced taxa, including medullosan ferns that were once regarded as sponges (Dunn et al., 2003) and lungfish teeth misattributed to polypore fungi (Brown, 1938). Accurate identification and classification of fossils are obviously paramount criteria for estimates of clade age as well as for meaningful reconstructions of paleodiversity and paleoecology. Wilson and Bruner (2004) recommended a thorough review of Niobrara Chalk fish systematics and stratigraphy, citing uncertainties and outstanding issues with taxonomy as possible obstacles for new workers. The Niobrara Chalk is so diverse and its fossils so abundant that there may be other taxonomic puzzles besides *Platylithophycus* stowed away in teaching collections and museums around the United States, patiently awaiting fresh eyes and renewed interest.

Acknowledgments

We thank M. Gottfried, J. Kriwet, and a third anonymous reviewer for their helpful comments, which improved this manuscript. Thanks also to A. Smith and M. Hill for their management of the Microscopy and Imaging Facility (American Museum of Natural History). A. Summers (University of Washington) and M. Paig-Tran (California State University, Fullerton) provided helpful suggestions regarding the gill structure of mobulid rays. M. Eklund (ThinklabZ) produced exceptional photographs of the holotype. We are particularly grateful to G. Corner and R. Secord (University of Nebraska State Museum) and A. Gishlick (AMNH) for specimen loans, and especially to A. Prybyla (Columbia University), who flew from Nebraska to New York with this large specimen as her carry-on luggage.

References

- Bennett, S.C., 2000, Inferring Stratigraphic Position of Fossil Vertebrates from the Niobrara Chalk of Western Kansas: Kansas Geological Survey, Current Research in Earth Sciences, Bulletin 244, p. 1–26.
- Bonaparte, C.L., 1838, Synopsis vertebratorum systematis: Nuovi Annali delle Scienze Naturali Bologna, v. 2, p. 105–133.
- Brown, R.W., 1938, Two fossils misidentified as shelf fungi: Journal of the Washington Academy of Sciences, v. 28, p. 130–131.
- Carpenter, K., Dilkes, D., and Weishampel, D.B., 1995, The dinosaurs of the Niobrara Chalk Formation (Upper Cretaceous, Kansas): Journal of Vertebrate Paleontology, v. 15, p. 275–297.
- Case, G.R., Tokaryk, T.T., and Baird, D., 1990, Selachians from the Niobrara Formation of the Upper Cretaceous (Coniacian) of Carrot River, Saskatchewan, Canada: Canadian Journal of Earth Sciences, v. 27, p. 1084–1094.
- Dean, M.N., 2011, Cartilaginous Fish Skeletal Tissues, in Farrell, A.P., ed., Encyclopedia of Fish Physiology: From Genome to Environment: London, Academic Press, v. 1, p. 428–433.
- Dean, M.N., Ekstrom, L., Monsonego-Ornan, E., Ballantyne, J., Witten, P.E., Riley, C., Habraken, W., and Omelon, S., 2015, Mineral homeostasis and regulation of mineralization processes in the skeletons of sharks, rays, and relatives (Elasmobranchii): Seminars in Cell & Developmental Biology, v. 46, p. 51–67.
- Dunn, M.T., Krings, M., Mapes, G., Rothwell, G.W., Mapes, R.H., and Kequin, S., 2003, *Medullosa steinii* sp. nov., a seed fern vine from the Upper Mississippian: Review of Palaeobotany and Palynology, v. 124, p. 307–342.
- Everhart, M.J., 2001, Revisions to the biostratigraphy of the Mosasauridae (Squamata) in the Smoky Hill Chalk Member of the Niobrara Chalk (Late Cretaceous) of Kansas: Transactions of the Kansas Academy of Science, v. 104, p. 59–78.
- Everhart, M.J., 2002, New data on cranial measurements and body length of the mosasaur, *Tylosaurus nepaeolicus* (Squamata; Mosasauridae), from the Niobrara Formation of Western Kansas: Transactions of the Kansas Academy of Science, v. 105, p. 33–43.
- Frey, R.W., 1972, Paleocology and depositional environment of Fort Hays Limestone Member, Niobrara Chalk (Upper Cretaceous), West-Central Kansas: University of Kansas Paleontological Contributions, v. 58, p. 1–72.
- Hamm, S.A., and Shimada, K., 2002, Associated tooth set of the Late Cretaceous lamniform shark, *Scapanorhynchus raphiodon* (Mitsukurinidae), from the Niobrara Chalk of Western Kansas: Transactions of the Kansas Academy of Science, v. 105, p. 18–26.
- Hattin, D.E., 1982, Stratigraphy and depositional environment of Smoky Hill Chalk Member, Niobrara Chalk (Upper Cretaceous) of the type area, Western Kansas: Kansas Geological Survey Bulletin, v. 225, 108 p.
- Huxley, T.H., 1880, Manual of the Anatomy of the Vertebrated Animals: New York, D. Appleton & Co, 432 p.
- Johnson, J.H., and Howell, B.F., 1948, A new Cretaceous calcareous alga from Kansas: Journal of Paleontology, v. 22, p. 632–633.
- Maisey, J.G., 2013, The diversity of tessellated calcification in modern and extinct chondrichthyans: Revue de Paléobiologie, v. 32, p. 355–371.
- Matthews, L.H., 1950, Notes on the anatomy and biology of the basking shark (*Cetorhinus maximus* [Gunner]): Proceedings of the Zoological Society of London, v. 120, p. 535–576.

- Matzke, A.T., 2007, An almost complete juvenile specimen of the cheloniid turtle *Ctenochelys stenoporus* (Hay, 1905) from the Upper Cretaceous Niobrara Formation of Kansas, USA: *Palaeontology*, v. 50, p. 669–691.
- Miller, H.W., and Walker, M.V., 1968, *Echinoteuthis melanae* and *Kansasteuthis lindneri*, new genera and species of teuthids, and a sepiid from the Niobrara Formation of Kansas: *Transactions of the Kansas Academy of Science*, v. 71, p. 176–183.
- Motta, P.J., Maslanka, M., Hueter, R.E., Davis, R.L., de la Parra, R., Mulvany, S.L., Habegger, M.L., Strother, J.A., Mara, K.R., Gardiner, J.M., Tyminski, J.P., and Zeigler, L.D., 2010, Feeding anatomy, filter-feeding rate, and diet of whale sharks *Rhincodon typus* during surface ram filter feeding off the Yucatan Peninsula, Mexico: *Zoology*, v. 113, p. 199–212. Available at: <http://dx.doi.org/10.1016/j.zool.2009.12.001>.
- Paig-Tran, M.E.W., and Summers, A.P., 2013, Comparison of the structure and composition of the branchial filters in suspension feeding elasmobranchs: *Anatomical Record*, v. 297, p. 701–715.
- Paig-Tran, M.E.W., Kleintech, T., and Summers, A.P., 2013, The filter pads and filtration mechanisms of the devil rays: variation at macro and microscopic scales: *Journal of Morphology*, v. 274, p. 1026–1043. doi: 10.1002/jmor.20160.
- Seidel, R., Lyons, K., Blumer, M., Zaslansky, P., Fratzi, P., Weaver, J.C., and Dean, M.N., 2016, Ultrastructural and developmental features of the tessellated endoskeleton of elasmobranchs (sharks and rays): *Journal of Anatomy*, v. 229, p. 681–702.
- Shimada, K., 1996, Selachians from the Fort Hays Limestone Member of the Niobrara Chalk (Upper Cretaceous), Ellis County, Kansas: *Transactions of the Kansas Academy of Science*, v. 99, p. 1–15.
- Shimada, K., 1997a, Skeletal anatomy of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*, from the Niobrara Chalk in Kansas: *Journal of Vertebrate Paleontology*, v. 17, p. 642–652.
- Shimada, K., 1997b, Dentition of the Late Cretaceous lamniform shark, *Cretoxyrhina mantelli*, from the Niobrara Chalk of Kansas: *Journal of Vertebrate Paleontology*, v. 17, p. 269–279.
- Shimada, K., 2007, Skeletal and dental anatomy of lamniform shark *Cretalamna appendiculata*, from Upper Cretaceous Niobrara Chalk of Kansas: *Journal of Vertebrate Paleontology*, v. 27, p. 584–602.
- Shimada, K., and Fielitz, C., 2006, Annotated checklist of fossil fishes from the Smoky Hill Chalk of the Niobrara Chalk (Upper Cretaceous) in Kansas: *Bulletin of the New Mexico Museum of Natural History and Science*, v. 35, p. 193–213.
- Stewart, J.D., 1978, Enterospirae (fossil intestines) from the Upper Cretaceous Niobrara Formation of Western Kansas: *University of Kansas Paleontological Contributions: Fossil Fish Studies*, v. 89, p. 9–16.
- Stewart, J.D., 1999, A new genus of Saurodontidae (Teleostei: †Ichthyodectiformes) from Upper Cretaceous rocks from the Western Interior of North America, in Arratia, G., and Schultze, H.-P., eds., *Mesozoic Fishes 2—Systematics and Fossil Record*: Verlag Dr. Friedrich Pfeil: München, Germany, p. 335–360.
- Toombs, H.A., 1948, The use of acetic acid in the development of vertebrate fossils: *Museum Journal*, London, v. vol. 48, p. 54–55.
- Wilson, M.V.H., and Bruner, J.C., 2004, Mesozoic fish assemblages of North America, in Arratia, G., and Tintori, A., eds., *Mesozoic Fishes 3—Systematics, Paleoenvironments and Biodiversity*: Verlag Dr. Friedrich Pfeil: München, Germany, p. 575–595.
- Zhu, M., Yu, X., Ahlberg, P.E., Choo, B., Lu, J., Qiao, T., Qu, Q., Zhao, W., Jia, L., Blom, H., and Zhu, Y., 2013, A Silurian placoderm with osteichthyan-like marginal jaw bones: *Nature*, v. 502, p. 188–193.
- Zittel, K.A., 1895, Mollusca, in *Grundzüge der Palaeontologie (Palaeozoologie)*: München, Leipzig, Verlag von Oldenburg, p. 386–435.

Accepted 12 February 2018