

CHONDRICHTHYANS FROM THE PENNSYLVANIAN (DESMOINESIAN) NACO FORMATION OF CENTRAL ARIZONA

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ABSTRACT—Teeth, spines, and dermal denticles of chondrichthyans are reported from the Middle Pennsylvanian (Desmoinesian) Naco Formation of central Arizona. The most common elements are crushing teeth of the coeliodont *Deltodus angularis*, less common are teeth of *D. sublaevis*, *Venustodus leidyi*, *Lagarodus angustus*, “*Cladodus*” *occidentalis*, *Petalodus ohioensis*, *Orodus* sp., and Hybodontoidea. Fin spines of *Acondylacanthus* sp., *Amelacanthus* sp., and *Physonemus* sp., and the dermal denticle *Petrodus patelliformis* are also present. The material of *Venustodus leidyi* shows for the first time that this animal was heterodont, having arched anterior teeth with a v-shaped profile grading posteriorly into lower crescentic, and finally flattened teeth. *Lagarodus angustus* is shown to have at least three tooth morphotypes, and a new tooth arrangement is proposed in which small anterior teeth are replaced posteriorly by large crushing teeth arranged in whorls.

This fauna is similar to others in New Mexico, Colorado, and Ohio and constitutes a western extension of such faunas in North America. In addition, the presence of *Deltodus sublaevis* and *Lagarodus angustus* documents a range extension from a known European distribution, reinforcing the cosmopolitan nature of chondrichthyan faunas at this time.

INTRODUCTION

The Pennsylvanian Naco Formation of central Arizona has for many years yielded an extremely diverse invertebrate fauna, particularly from a roadside locality near Kohls Ranch (Fig. 1). The main elements of the fauna were described by Brew and Beus (1976); the crinoids by Webster and Lane (1970), Webster (1981), and Webster and Olson (1998); the edrioasteroids by Sumrall (1992); the ostracodes by Lundin and Sumrall (1999); and aspects of predation by Elliott and Bounds (1986) and Elliott and Brew (1988). Recently, sponges have been described from a locality near Pine, Arizona (Dilliard and Rigby, 2001; Fig. 1, locality 2), and work is continuing on other aspects of the invertebrate fauna. The only mention of the vertebrates was made by Elliott and Bounds (1986) who illustrated specimens identified as “*Helodus*,” “*Cladodus*,” and “*Cochliodus*,” as part of a discussion of predation on brachiopods. However, the present paper documents an extensive and hitherto unreported fauna of chondrichthyans from the Naco Formation.

Chondrichthyans experienced an explosive Paleozoic radiation that reached its zenith in the Late Mississippian (Lund, 1990; Janvier, 1996), at which time they occupied many of the ecological niches now dominated by teleosts. In addition to the elasmobranchs that normally replaced their teeth regularly, as do modern sharks (although note tooth retention in cladodonts documented by Williams, 2001), there were many Paleozoic chondrichthyans that are generally considered to have been related to modern holocephalians and in which the dentition consisted of tooth plates that enlarged and were not shed as the fish grew (Janvier, 1996; Stahl, 1999). These tooth plates usually separated from the cartilaginous jaws during post-mortem decay and are generally the only parts of the organisms preserved. Holocephalian tooth plates have been collected and classified over the last 150 years with particular efforts during the late 1800s (Newberry and Worthen, 1866; St. John and Worthen, 1875, 1883; Trautschold, 1874; de Koninck, 1878; Davis, 1883; Newberry, 1889; Woodward, 1889), but the lack of associated material has resulted in the erection of many gen-

era based solely on individual tooth shapes. In some cases these teeth have later been shown to have belonged to heterodont organisms (Patterson, 1968) and this situation was probably true for many others. There has been little work carried out on these organisms until recently due, at least in part, to the lack of articulated material and a consequent feeling that little progress could be made. As noted by Maisey (2002:188) in his review of Stahl (1999) “For well over a century, paleontologists have dusted off weird and wonderful old specimens of Paleozoic tooth plates in their collections, wondered just what kind of monster could have possessed such things, and quietly put them away again.” Despite Maisey’s comment our knowledge of these organisms has been improving rapidly in recent years with the discovery of numerous chondrichthyans with articulated tooth plates in the fossil-lagerstätte of the Bear Gulch Limestone of Montana (Lund, 1990; Lund and Grogan, 1997; Lund and Poplin, 1999) and the Pennsylvanian black shales of the Illinois and Midcontinental basins (Zangerl, 1981). Although the Naco fauna does not provide articulated material it does add to our knowledge of the distribution of such faunas in the Pennsylvanian as many of the taxa found within it also occur in Ohio (Hansen, 1986), Colorado (Itano et al., 2003; Lockley, 1984), and New Mexico (Lucas and Estep, 2000). In addition some taxa have previously been reported from Europe and Siberia underscoring the cosmopolitan nature of chondrichthyan faunas at this time.

LOCALITIES

The Kohls Ranch locality (Fig. 1) is located on both sides of State Route 260 at a point 1.7 km southwest of Kohls Ranch, Arizona (Promontory Butte 7.5’ quadrangle). Collections were made from a small outcrop southeast of the highway, from the main outcrop along the northwest of the highway, and along the disused road that starts south of it. Parts of this latter outcrop will be lost in the near future due to realignment of the road. All of the material collected here was picked from the weathered surface or from bulk samples that were processed

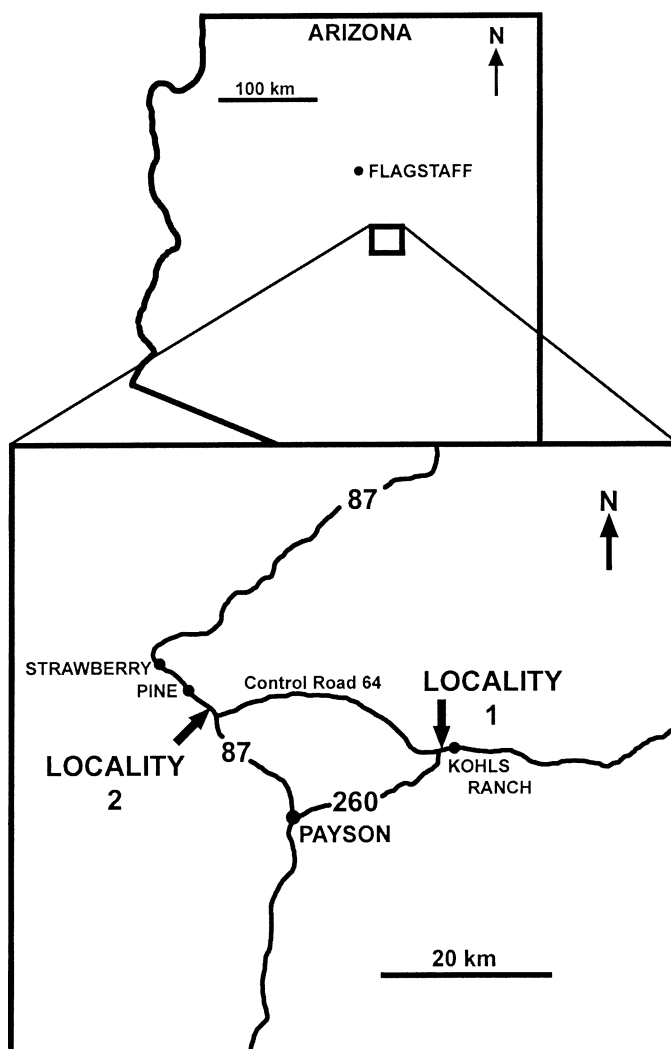


FIGURE 1. Map of central Arizona showing the localities at Pine and Kohls Ranch.

later. The Pine locality (Fig. 1) is located in road cuts and associated exposures along State Highway 87, approximately 2.5 km southeast of Pine and a few meters north of the junction with Control Road (Buckhead Mesa 7.5' quadrangle). Vertebrate material is less common here but larger elements are found in the limestone units interbedded with the purple shales.

GEOLOGY

The Naco Formation of central Arizona consists of a predominantly marine sequence of interbedded limestones and shales that grades laterally into the Supai Group of Late Pennsylvanian–Early Permian age. It was deposited during a marine transgression over a karst surface developed on the Mississippian Redwall Limestone. Brew (1970) recognized three members within the Naco Formation that were informally designated the alpha, beta, and gamma members. The lowermost, or alpha, typically consists of a basal reddish-brown cherty mudstone, siltstone, or conglomerate interpreted as a regolith formed by solution of the Redwall Limestone and followed by stratified mudstone, siltstone, and sandstone. The alpha member is gradually overlain by the beta member, which consists of richly fossiliferous resistant limestones interbedded with purple shales and siltstones. Both the Kohls Ranch and Pine localities occur

within this member. The overlying gamma member consists of a succession of reddish-brown clastics and interbedded limestones produced by the interfingering of marine units and continental margin and terrestrial redbeds of the south-eastward building Supai delta (Brew, 1970).

The invertebrate assemblage at Kohls Ranch was described by Brew and Beus (1976) as representing a fossil community that inhabited quiet marine waters no more than 15–20 m deep. They based this view on the high degree of articulation of the megafossils and their generally unworn condition. However, as noted by Lundin and Sumrall (1999), the alternating limestones and siliciclastic mudstones indicate frequent alternations from autochthonous to allochthonous deposition within this setting, and the presence of articulated crinoids (Webster, 1981), edrioasteroids (Sumrall, 1992), and echinoids (pers. obs.) suggests that there were periods of rapid burial, perhaps during storm events. The condition of the bone material described here supports this view, as in all the Naco localities it shows a high degree of abrasion even to the stage of polished bone pebbles, in contrast to the unabraded invertebrate fauna. It seems probable that the vertebrates have a different taphonomic history from the invertebrates and that they may have been transported during storm events from more near-shore environments in which they had undergone abrasion in more turbulent conditions.

The two localities appear to be coeval based on their stratigraphic relationships and the included invertebrates. Brew and Beus (1976) used the presence of fusulinids to show that the Beta member can be dated to the early part of the Desmoinesian (*Wedekindella euthysepta* Subzone). This date is consistent with the ostracode fauna identified by Lundin and Sumrall (1999) and with the described invertebrate megafauna.

MATERIALS AND METHODS

The material described here was mainly collected from surface exposures after it had already weathered free from the matrix. Collections were initially accumulated as part of regular visits by NAU Geology Department paleontology classes starting in the early 1980s and subsequently from more targeted collecting, particularly by one of the junior authors (TJO). Little or no preparation was required for most of the material but some of the larger specimens from the Pine locality were etched free from matrix using 10% acetic acid, in some cases after reversal on plastic. Specimens were strengthened and preserved using a solution of Acryloid B-72 in acetone. All the specimens are deposited in the collections of the Museum of Northern Arizona (MNA).

Our description of the tooth plates follows the standardized terminology suggested by Stahl (1999), following Duffin (1984) and Patterson (1992). The taxonomic groupings for the spines and denticles are highly uncertain as they are not known from articulated material, hence their assignments to higher taxa are here kept to a minimum.

SYSTEMATIC PALEONTOLOGY

- CHONDRICHTHYES Huxley, 1880
 SUBTERBRANCHIALIA Zangerl, 1979
 HOLOCEPHALI Bonaparte, 1832–41
 COCHLIODONTIFORMES Obrucsev, 1953
 COCHLIODONTIDAE Owen, 1867
DELTODUS Morris and Roberts, 1862
DELTODUS SUBLAEVIS (Agassiz, 1838)
 (Fig. 2A, B)

Material—One anterior (MNA V9390) and one posterior (MNA V9391) right mandibular tooth.

Description—This is the less common of the two species of

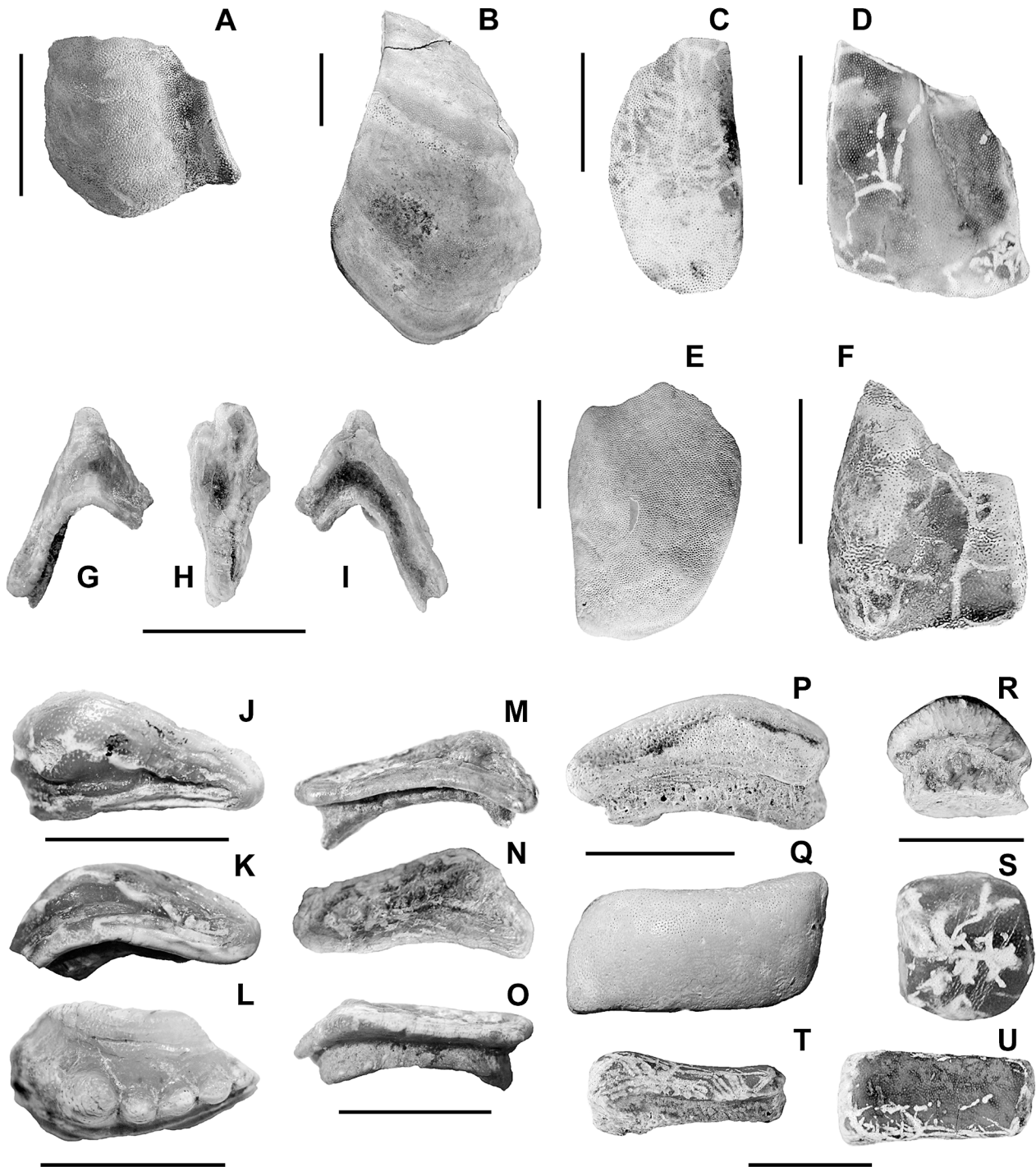


FIGURE 2. **A, B**, *Deltodus sublaevis*. **A**, right anterior mandibular tooth (MNA V9390); **B**, right posterior mandibular tooth (MNA V9391). **C–F**, *Deltodus angularis*. **C**, right anterior mandibular tooth (MNA V9392); **D, F**, right posterior mandibular teeth (MNA V9393, 9394); **E**, right upper jaw tooth (MNA V4713). **G–O**, *Venustodus leidy*. **G–I**, morphotype A (MNA V9398) in labial (**G**), lateral (**H**), and lingual (**I**) views; **J–K**, morphotype B (MNA V9400) in occlusal (**J**) and lingual (**K**) views, and (**L**) occlusal view (MNA V9401); **M–O**, morphotype C (MNA V9403) in labial (**M**), occlusal (**N**), and lingual (**O**) views. **P–U**, *Lagarodus angustus*. **P, Q**, rhomboidal morphotype (MNA V9404) in lingual (**P**) and occlusal (**Q**) views; **R, S**, square morphotype (MNA V9407) in lateral (**R**) and occlusal (**S**) views; **T, U**, rectangular morphotype (MNA V9408) in labial (**T**) and occlusal (**U**) views. Scale bars equal 1 cm (**A, B, D–I, P, Q, T, U**), 5 mm (**C, J–O, R, S**).

Deltodus in the Naco Formation. Only four specimens have been collected, two of which are so badly weathered that they were not used in the description. The two most complete specimens represent the right anterior and right posterior mandibular

teeth, missing (respectively) the anterior end and lingual margin.

The anterior mandibular tooth is of medium size, the maximum width is 14 mm, and the length is estimated to be 20 mm

as the anterior part is missing. It is roughly triangular in shape with a curved posterior margin. The crown is moderately convex in cross-section and at least 3 mm thick, with a small trough and ridge forming the lingual margin, which probably articulated with the labial edge of the posterior plate (Stahl and Hansen, 2000). Poorly developed coarse labial-lingual ridges are visible across the tooth.

The posterior mandibular tooth is large, with an estimated width of 34 mm (the lingual margin is missing) and an estimated length of 50 mm (the anterior margin is missing). The tooth is convex in cross-section and at least 8 mm thick with the crown forming a moderately high dome. The labial margin is straight and it articulated with the lingual margin of the anterior tooth. The posterior end of the tooth slants down to a rounded point near the centerline; the margin then slants anteriorly, presumably to meet the lingual edge of the tooth, which is not preserved. At least five well-developed coarse labial-lingual ridges cross the tooth. A flat wear spot near the high point of the tooth presumably formed during occlusion with the corresponding tooth of the upper jaw.

Discussion—*Deltodus sublaevis* is the type species of the genus *Deltodus*. Originally described as *Poecilodus sublaevis* by Agassiz (1838), it was removed to the new genus *Deltodus* by Morris and Roberts (1862). This new material accords well with the description of *D. sublaevis* in its shape, large size, and robust structure, and in the presence of transverse corrugations on the tooth plate surface (Stahl, 1999:fig. 66).

Stahl (1999:fig. 11B) figured a specimen of *Cochliodus contortus* (considered to be related to *Deltodus* and generally similar to it by Stahl, 1999) with a complete mandibular dentition, thus providing a clear indication of the lower jaw arrangement. The large posterior plate was oriented parallel to the long axis of the jaw ramus with the anterior end towards the jaw symphysis. Parallel to this tooth was the small anterior tooth plate whose lingual side articulated with the labial side of the posterior plate. There may have been additional plates anteriorly but these are not preserved in the articulated specimen (Stahl, 1999). The upper jaw figured by Stahl (1999:fig. 11A) contains two large posterior plates, referred to *Streblodus oblongus*, with two rows of anterior tooth whorls of *Helodus*-type placed anteriorly. The upper teeth were set more closely together than the mandibular tooth plates and would have occluded with their medial faces as is supported by the wear facet on the posterior tooth described here.

It is likely that *D. sublaevis* was durophagous with a dentition designed for crushing hard-shelled invertebrates such as those that are common in the Naco Formation (Brew and Beus, 1976). The function of the coarse ridging on the teeth is unknown, but may have kept the prey from slipping off the convex crushing surfaces. This species is very rare compared to the high numbers of *D. angularis* at this locality (less than 1% of the total). This is the first reported occurrence outside of the type locality in Ireland.

DELTODUS ANGULARIS Newberry and Worthen, 1866
(Fig. 2C–F)

Material—Right anterior mandibular tooth, one representative specimen (MNA V9392) and four additional specimens (MNA V9396); right posterior mandibular tooth, two representative specimens (MNA V9393, 9394) and six additional specimens (MNA V9395); right upper jaw tooth, one representative specimen (MNA V4713) and four additional specimens (MNA V9397).

Description—This is the most common taxon from the Kohls Ranch locality. Over 50 partial or complete teeth along with hundreds of fragments are known. Three morphs corresponding to different jaw positions are known for this species;

the mandibular tooth set consisted of a small teardrop-shaped anterior tooth with a larger, roughly triangular posterior tooth on each side, while the upper jaw contained a single large triangular tooth on each side (Stahl and Hansen, 2000).

The anterior mandibular tooth is shaped like an inverted teardrop with an accessory labial flange. The anterior point and labial flange are often missing due to weathering, however, length and width estimates indicate that these plates are generally 4–9 mm in width and 8–18 mm in length. The tooth has a convex arch in the labial-lingual axis, and broadens labially to form the flange. The flange is developed anteriorly and then is constricted until it disappears just before the posterior end of the tooth. Posteriorly, the tooth narrows to a point and presumably articulated with the anterior labial edge of the posterior mandibular tooth.

The posterior mandibular tooth is roughly triangular in shape, with a straight posterior edge. The tooth is large and more robust than the anterior tooth, with an estimated anterior-posterior length of 14–25 mm and a posterior width of 9–19 mm. The tooth has a large platform, which narrows to a point anteriorly and broadens to form most of the posterior edge. Labially adjacent to this platform is a trough, which starts near the anterior edge and broadens and shallows posteriorly, before it grades into the wide posterior edge of the platform. In some cases the labial margin of the trough forms a thickened ridge.

The single upper-jaw tooth is large and broad, being 8–23 mm wide and 15–31 mm long. The outline of the tooth is that of a broad, rounded triangle with anterior, posterior, and labial vertices. The labial side is longest and the posterior lingual side shortest. The labial side consists of a large anterior-posterior ridge that broadens lingually and slightly posteriorly. The tooth has an airfoil cross-section, being thickest on the labial edge and thinning lingually.

Discussion—Newberry and Worthen described *Deltodus angularis* and *Sandalodus carbonarius* in 1866. Woodward (1889) synonymized the two taxa, identifying *S. carbonarius* as the upper jaw tooth plate of *D. angularis*. Although Eastman (1903) disagreed with the synonymy, Stahl and Hansen (2000) support it, as do the current authors.

Stahl and Hansen (2000) described an associated dentition of *Deltodus angularis* from the Upper Carboniferous of Ohio. In the lower jaw, two tooth plates are positioned on either side of the symphysis. The anterior plate is small and teardrop shaped with the margins narrowing posteriorly. Behind this tooth is a large triangular plate that formed the main lower crushing surface and has a large ridge and trough that occluded with the upper jaw tooth plate. In the upper jaw was a single, large, triangular plate with a well-developed labial ridge that occluded with the trough in the posterior mandibular plate. This arrangement fits with hypothesized cochliodont tooth plate arrangements (Patterson, 1968) and also with known jaws that show elongated closely set upper tooth plates occluding with more broad, triangular, and convex mandibular plates. This also fits with the relative numbers of tooth plate morphotypes found in this collection.

This species has been reported from a number of U.S. localities including Illinois (Newberry and Worthen, 1866), Ohio (Stahl and Hansen, 2000), West Virginia (Lund et al., 1979), and Colorado (Lockley, 1984).

COCHLIODONTIDAE incertae sedis Owen, 1867
VENUSTODUS St. John and Worthen, 1875
VENUSTODUS LEIDYI St. John and Worthen, 1875
(Fig. 2J–O)

Venustodus argutus St. John and Worthen, 1875

Revised Diagnosis—Crown platform-like with prominent

lingually imbricated basal ridge; cusps stout and conical; median cusp most prominent; crown nearly horizontal or strongly arched with a V-shaped profile; crown covered with thick enameloid; tooth base short, restricted and platform-like. Three morphotypes recognized: A consists of teeth that are highly arched and V-shaped in profile with well-developed central cusp; B is moderately arched and crescentic in occlusal view with moderately developed central cusp; C consists of teeth that are small, highly asymmetric, weakly arched in profile, and with central cusp poorly developed.

Material—Two specimens of morphotype A (MNA V9398, 9399); two specimens of morphotype B (MNA V9400, 9401) and three additional specimens (MNA V9402); and one specimen of morphotype C (MNA V9403).

Description—Three basic morphotypes of this species exist but the range of variation of each allows a continuum of morphologies to be seen between them showing that they all belong to the same species. We consider that Morphotype A was probably in an anterior position in the jaw, Morphotype B was medial, and Morphotype C was situated in the posterior portion of the jaw.

The teeth of Morphotype A are symmetrical and sharply arched with a V-shaped profile. The crown is gently convex labial-lingually with a prominent central cusp. When complete, the crown forms an asymmetric, rounded cone. There is a moderately well-developed boss on the lingual side of the cusp. A well-developed flange is present below the cusp on the labial edge of the crown. This flange articulated with the next anterior adjacent tooth. A basal ridge with two-to-three sinuous imbrications forms the margin of the crown.

The tooth base is abruptly constricted below the crown, and then broadens ventrally to match the crown width. The ventral base extends away from the crown on the lingual side. This gives the appearance of a channel between the crown and the base when the tooth is viewed lingually. The channel articulates with the labial flange of the lingually adjacent tooth in the tooth whorl. On the labial side of the tooth, the ventral part of the base extends towards the crown, almost meeting it on the labial edge. No foramina are observed anywhere on the tooth. Only one complete and one almost complete specimen is available; they are 11–12 mm in labial-lingual width, 3.5–6 mm in anterior-posterior length, and 7.5–12 mm in height.

Morphotype B is a transitional morph between the anterior Morphotype A and posterior Morphotype C. It is crescentic in occlusal view, gently arched in profile and slightly asymmetric. The crown is gently convex with a moderately well developed central cusp. This cusp is not as conical as Morphotype A, and is more globular in shape. The lingual boss is poorly developed, as is the labial flange. The basal ridge seen in Morphotype A is still well developed, but the two to three imbrications are less apparent and not nearly as sinuous. The expression of the imbrications varies from poor to moderate, and may depend on the tooth position within the jaw.

The base of the tooth is poorly developed labially and slopes linguo-ventrally to form a lingual channel below the crown, although this channel is not as well developed as in Morphotype A. The length ranges from 4–5 mm; width from 8–10 mm; and height from 3–4 mm.

Only one complete tooth of Morphotype C is known. This tooth type is highly asymmetric, with one side being three times as long as the other. The long side is relatively flat, while the short side that curves down from the central cusp is low and poorly developed. In line with the central cusp are six smaller but well-developed lateral cusps on the long side and one lateral cusp on the short side. No boss or flange is observed on either side of the central cusp. The basal ridge around the crown edge has three to five parallel imbrications.

The tooth base is well-developed and about two-thirds the

thickness of the crown. It forms a small platform on the anterior edge of the tooth, presumably forming an insertion point for the previous tooth. The ventral face of the base is parallel with the crown, but flares out ventrally at the end of either side of the tooth.

Discussion—*Venustodus* is one of the most poorly known Carboniferous chondrichthyans and its phylogenetic placement is uncertain. It most closely resembles *Lophodus*, and Stahl (1999) has placed it in *Cochliodontidae incertae sedis*, a placement that we follow.

A number of species of *Venustodus* were named by St. John and Worthen (1875) for isolated teeth of similar appearance from the Carboniferous limestones of Missouri, Iowa, Illinois, and Indiana, USA. In particular they described *V. leidy* and documented the presence of two morphotypes equivalent to our morphotypes A and B (St. John and Worthen, 1875). The collection of *Venustodus leidy* teeth from the Naco Formation includes both forms gradational between the described morphotypes and material of a third morphotype indicating that only one heterodont species is present.

Based on the arrangement in other holocephalian teeth such as *Helodus* (Stahl, 1999:fig. 8), *Venustodus* teeth were most likely arranged in tooth whorls. The labial edge bears a flange that would have articulated with the lingual groove on the preceding tooth in the whorl. The large, symmetrical teeth with large central cusps are similar to the holotype of *V. leidy*. These were probably developed for gripping and most likely occupied anterior tooth rows. Whorls farther back had more crescentic teeth with larger lateral cusps and a lower arch in profile while the most posterior whorls had highly asymmetric flat teeth, with poorly developed cusps.

Thus, several trends are noticed in the different tooth morphs as one moves posteriorly in the jaw. Labio-lingual asymmetry increases, the height of the crown decreases, and the development of lateral cusps decreases. The “tongue and groove” system becomes less developed, as does the size of the base in relation to the crown.

Presumably the heterodonty observed is due to tooth function; clearly the large hooked central cusps of the anterior tooth whorls suggest an adaptation for grasping prey. Most likely, these animals were grasping prey with their front teeth and crushing them with the posterior teeth, but the type of prey remains unknown.

The distribution of *Venustodus leidy* ranges from Missouri, Iowa, and Illinois (St. John and Worthen, 1875), to Ohio (Hansen, 1986), and Montana (Lund, 1990). This suggests a wide continental distribution for the taxon in North America.

PSAMMODONTIFORMES Obruche, 1953
PSAMMODONTIDAE incertae sedis de Koninck, 1878
LAGARODUS ANGUSTUS (Romanovsky, 1864)
(Figs. 2P–U, 3)

Revised Diagnosis—A psammodont chondrichthyan in which the tooth plates are rectangular, smooth-surfaced, and finely punctate with a crown and base of almost equal thickness. Three morphotypes are recognized: a rectangular morph in which one end is raised into a high gibbous prominence and then downturned; a more rhomboidal morph with no gibbous prominence; and a smaller morph in which the crown is square in outline.

Material—Four specimens of the rhomboidal morphotype (MNA V4715, 9404–9406); one specimen of the square morphotype (MNA V9407); one specimen of the rectangular morphotype (MNA V9408) and two additional specimens (MNA V9409).

Description—Three morphotypes are recognized here although only two have previously been referred to the species

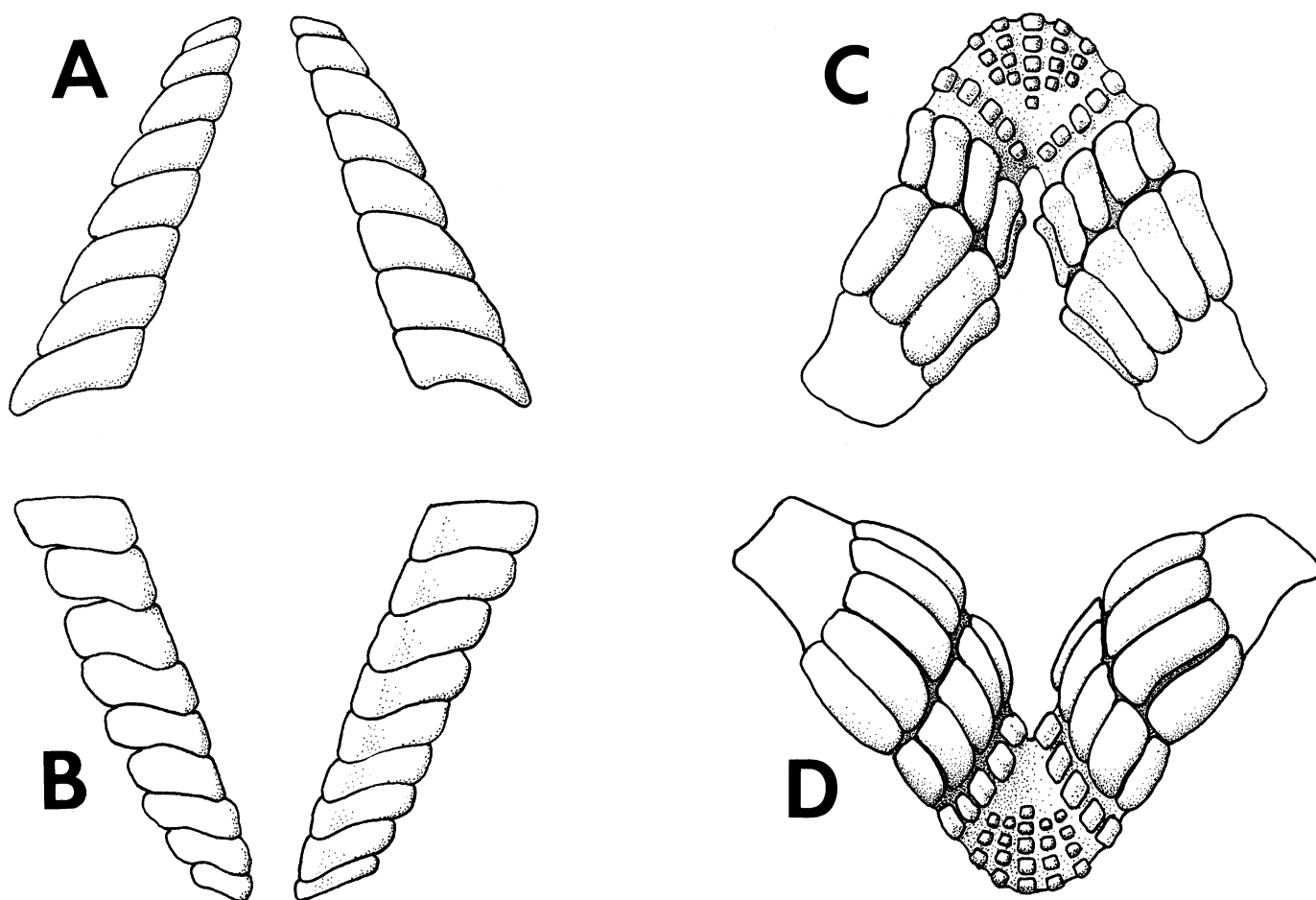


FIGURE 3. Postulated arrangements of the dentition in *Lagarodus angustus*. A, upper, and B, mandibular dentitions after Hansen (1986); C, upper, and D, mandibular dentitions proposed here. No scale.

(Hansen, 1986). Two are large with rectangular and rhomboidal outlines, while the third is roughly square in outline. The first two morphotypes are equally abundant at the Kohl Ranch locality and the third is slightly scarcer, while the sole representative at Pine is a large rhomboidal example (MNA V9406).

The rectangular morphotype has the lowest lateral side of the crown at a slight angle to the nearly parallel labial and lingual margins. The coronal surface rises slightly on the presumed posterolateral side, then dips slightly, and finally rises steeply to form a high gibbous prominence. The crown then slopes sharply to form an almost vertical edge on the presumed anteromedial side of the tooth. The labial and lingual sides of the crown converge to form a spur on the ventral part of the presumed anteromedial side. The thickness of the tooth base is nearly equal to that of the crown. Large foramina form a row on the presumed lingual side of the base while smaller foramina are randomly spread over both sides. The teeth range from 6.5–8 mm in length; 5–7 mm in height; and 13–18 mm in width.

The rhomboidal teeth are generally slightly longer than their rectangular counterparts and have a gently arching oral surface caused by a slight labial-lingual twist. Unlike the rectangular form, there is no gibbous prominence and the crown does not slope sharply over the edge. The base is nearly as thick as the crown, and the distribution of the foramina is the same as that for the rectangular morphotype. The teeth range from 6–9 mm in length; 5–11 mm in height; and 13–22.5 mm in width.

A third morphotype is here referred to *L. angustus*. This is

square and has a central ridge on the crown that might have been oriented antero-posteriorly. The base is slightly thicker than the crown and no foramina are observed. The width of the base is slightly restricted with respect to the crown. This morphotype is 4–7 mm in width; 5–6 mm in length; and 4–5 mm in height. Its presumed position is near the symphysis of the jaw.

Discussion—*Lagarodus angustus* was originally described by Romanowsky (1864) from the Lower and Middle Carboniferous of Russia. Examples have also been reported from the Appalachian Basin of Ohio (Hansen, 1986), the Minturn Formation of Colorado (Lockley, 1984), and the Flechado Formation of New Mexico (Zidek and Keitzke, 1993). The teeth from the Naco Formation are identical to these teeth, suggesting a broad global distribution for *Lagarodus*.

No articulated material is known for *L. angustus*, so any reconstruction of the dentition is necessarily speculative. De Koninck (1878) and Davis (1883) suggested that the teeth formed a “pavement” across the jaw in other psammodonts, but reconstructed *L. angustus* as having a double row of rectangular teeth along each ramus with a border of narrow teeth similar to the rhomboidal morph.

Hansen (1986) suggested instead that the teeth were arranged in a single posteriorly broadening row along the ramus (Fig. 3A, B). He proposed that the rectangular teeth were located in the lower jaw and the rhomboidal teeth were located in the

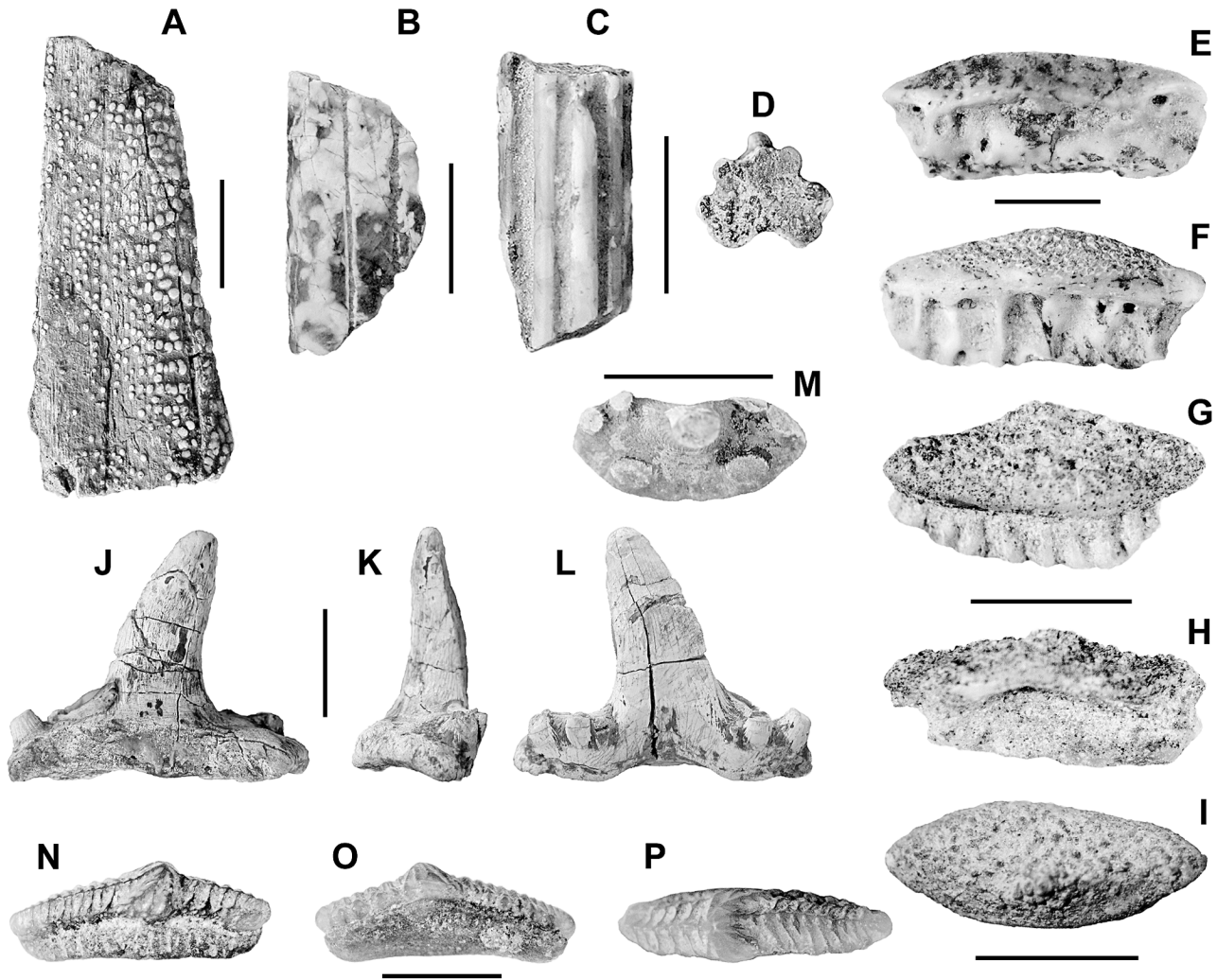


FIGURE 4. A, *Physonemus* sp., fin spine (MNA V9410). B, *Amelacanthus* sp. fin spine (MNA V9412). C, D, *Acondylacanthus* sp., fin spine (MNA V9411). E–I, Hybodontoidea teeth. E, F, MNA V9414 in lingual (E) and labial (F) views; G–I, MNA V9415 in labial (G), lingual (H), and occlusal (I) views. J–M, “*Cladodus*” *occidentalis* teeth. J–L, MNA V4714 in lingual (J), lateral (K), and labial (L) views; M, MNA V9416 showing occlusal view of tooth base. N–P, *Orodus* sp. tooth, MNA V9418 in labial (N), lingual (O), and occlusal (P) views. Scale bars equal 1 cm (A, J–M), 5 mm (B–D), 1 mm (E–I, N–P).

upper jaw. In this arrangement the more concave lower teeth would occlude effectively with the more convex upper teeth.

We disagree with Hansen in his interpretation of the occlusion of the two tooth morphologies, as commonly in these holocephalians the lower teeth are more convex suggesting that in this taxon it is more likely that the rhomboidal teeth formed the mandibular dentition. We also suggest that the teeth were not arranged in a single row along the ramus of the jaw but were instead arranged in one or two whorls on the posterior part of each ramus while the third morph was most likely located in the anterior portion of the jaw (Fig. 3C, D). This reconstruction is more consistent with the jaw morphology of other holocephalians and chondrichthyans as a whole and similar to that found now in the modern Port Jackson shark, *Heterodontus philipi*, in which numerous small sharp teeth at the front of the jaw grade posteriorly into larger blunter teeth. This arrangement is also reminiscent of that seen in hybodonts such as *Hamiltonichthys* (Maisey, 1989) in which the anterior and anterolateral tooth families become progressively larger posteriorly and are then succeeded by noticeably larger teeth that form the most

posterior families. The small square anterior teeth of *L. angustus* would have functioned as nipping and grasping teeth, while the larger posterior rectangular and rhomboidal teeth would have been effective in crushing prey. *Heterodontus* is a relatively unselective feeder but is known to eat crustaceans, molluscs, polychaetes, fish, and sea urchins (Smith, 1942; McLaughlin and O’Gower, 1971; Compagno, 1984). A broad range of potential prey items is present in the Naco Formation, and *L. angustus* may have had a similar feeding strategy to *Heterodontus*.

ELASMOBRANCHII Bonaparte, 1838
Order, Family indeterminate
ACONDYLACANTHUS St. John and Worthen, 1875
ACONDYLACANTHUS sp.
(Fig. 4C, D)

Material—One spine fragment, MNA V9411.

Description—The spine fragment is 8 mm long and has a maximum width of 4 mm. It is sub-triangular in cross-section

with a concave posterior margin and coarse parallel longitudinal ribs that are semi-circular in cross-section, smooth, and 1 mm wide. A single rib forms the anterior margin of the spine with three ribs on the lateral faces. Although weathered the remains of a single row of denticles can be seen along the right and left posterolateral margins.

Discussion—This specimen, although fragmentary, is readily identifiable as *Acondylacanthus* because of its smooth parallel semi-circular ribbing and cross-sectional shape. The sub-triangular shape in cross-section indicates it is not *A. nuperus*, which has an elliptical cross-section. *Acondylacanthus* is known from Ohio (Hansen, 1986, 1996), Iowa (St. John and Worthen, 1875), and Colorado (Itano et al., 2003).

AMELACANTHUS Maisey, 1982
AMELACANTHUS sp.
(Fig. 4B)

Material—One spine fragment (MNA V9412) and three additional fragments (MNA V9413).

Description—Several small fragments of fin spine show a distinctive ornament. The two largest fragments are about 10 mm long, triangular in cross section, and come from the anterior edge of spines. The anterior edge is formed of a single smooth, rounded, enameled ridge 3 mm wide, and flanked by two similar ridges separated by very narrow grooves. The margin of the central ridge is finely crenulate but in the lateral ridges the margins become more irregular and more coarsely crenulate.

Discussion—Although these fragments are extremely small the characteristic smooth ribs surfaced by a thick, shiny outer enameloid layer indicate that they belong to *Amelacanthus*. This genus was described by Maisey (1982) to include four species of spines from the British Lower Carboniferous. Subsequently a specimen was identified from the Pennsylvanian of Nebraska (Maisey, 1983) where it was associated with spines of *Acondylacanthus*, *Bythiacanthus*, and “*Physonemus*.” The species are separated based on the number and size of the ribs and the pattern of bifurcation but as the fragments described here are too small to show those features it is not possible to identify them to species. Although the affinities of the genus are unknown Maisey (1982) has noted that the presence of a thick enameloid layer and concave posterior wall suggests an affinity with neoselachians.

PHYSONEMUS McCoy, 1848
PHYSONEMUS sp.
(Fig. 4A)

Material—One partial fin spine, MNA V9410.

Description—One large spine fragment is known from the Pine locality. The few poorly preserved spine fragments from Kohls Ranch cannot be reliably referred to *Physonemus*, and are thus not used in this description.

The spine fragment is 42 mm long, the proximal and distal ends both being broken, and gradually narrows distally from 19 to 13 mm wide. It is slightly curved, the anterior margin being concave the posterior convex. It is most probably part of a dorsal fin spine. The specimen was clearly laterally compressed originally and is wedge-shaped in cross-section, with the thicker edge being the anterior edge of the spine; both the anterior and posterior edges are rounded. The surface is covered with small, irregularly spaced tubercles that are generally round or ellipsoid, with smooth rounded tops and finely crenulate margins. They increase in diameter anteriorly from about 0.2 mm on the posterior margin to 1 mm × 3 mm on the anterior margin. They also show an increasing tendency to become elliptical and to amalgamate towards the anterior margin, which is entirely covered by large amalgamated tubercles.

Discussion—The form genus *Physonemus* includes bilaterally symmetrical, forward-curving spines ornamented with tubercles. They are not known to occur with more complete remains so their affinities remain obscure. It has been reported from the Minturn Formation (Itano et al., 2003), where it is found with *Acondylacanthus*, *Bythiacanthus*, and *Ctenacanthus*, and from Nebraska (Maisey, 1983), where it is associated with *Acondylacanthus*, *Bythiacanthus*, and *Amelacanthus*.

It is not possible to refer this specimen to a particular species because it is incomplete and weathered. However, it shows most similarity to *Physonemus mirabilis* St. John and Worthen, 1875.

HYBODONTOIDEA Zangerl, 1981
(Fig. 4E–I)

Material—Two teeth (MNA V9414, 9415).

Description—Only two specimens of this tooth type are known from the Naco Formation. The crown forms a low triangle and is covered with small irregular tubercles. It extends further ventrally on the labial side than the lingual side. In occlusal view, the crown is an elongate ellipsoid.

The base is rectangular in shape and its width is constricted labio-lingually. On the labial side there are eight to ten large well-developed dorso-ventral ridges. Between some of these ridges there are large foramina. On the lingual side the base is concave and smooth with no ridges and large irregularly spaced foramina.

Discussion—These specimens are identifiable as hybodonts because of the large ridges, depressions, and foramina on the labial side of the base. It is unclear as to whether the ornamented surface of the crown is a diagnostic feature of these teeth.

Although hybodonts are primarily Mesozoic sharks, they are present in the Paleozoic and Zangerl (1981) suggests an origin as early as the Middle Devonian. However, Paleozoic remains are generally fragmentary, enigmatic, and poorly studied, which prevents a more detailed taxonomic placement of these specimens. Hansen (1986) described several Pennsylvanian hybodonts from Ohio, but none match the morphology of the specimens described here. Indeterminate hybodonts have been noted from several Pennsylvanian (Missourian–Virgilian) localities in Kansas (Schultze and Chorn, 1988), and *Hamiltonichthys mapei* has been described from complete material making it one of the best-known Paleozoic hybodonts (Maisey, 1989), however, none of these teeth are similar to the material described here. Rees and Underwood (2002) reviewed the taxonomic status of the hybodont *Lissodus*, and concluded that Paleozoic teeth formerly referred to this taxon represent two unnamed genera of hybodonts distinct from *Lissodus*. Based on Rees and Underwood’s descriptions, the Naco hybodonts probably do not belong to either of these taxa, but the rather brief description and lack of illustration of the teeth precludes a definitive taxonomic conclusion.

SYMMORIIDA Zangerl, 1981
?SYMMORIIDAE Dean, 1909
“*CLADODUS*” *OCCIDENTALIS* Leidy, 1859
(Fig. 4J–M)

Material—Two teeth (MNA V4714, 9416) and four additional specimens (MNA V9417).

Description—The description of this taxon is mostly based on a large, nearly complete tooth (MNA V4714), with additional information from a large incomplete base, and several small nearly complete teeth. The width of the base in these specimens ranges from 5 mm to 40 mm.

Characteristically the teeth have five cusps; a large central cusp flanked on either side by two lateral cusps. An additional pair of small lateral cusps may sometimes be present adjacent

to the central cusp. The central cusp is broad at its base, tapers to a point, and is never taller than the base is wide. In lateral view, the central cusp is somewhat compressed and exhibits a small but noticeable sigmoid flexure. This cusp is somewhat flatter on the labial side partly owing to the invasion of a shallow sulcus from the base. Two longitudinal carinae clearly demarcate the labial and lingual faces of the cusp. Fine longitudinal ridges cover the surface of the central cusp as well as the lateral cusps. The lateral cusps are conical, with the outer cusp being slightly larger than the inner cusp. Lateral cusps are rarely completely preserved in this collection but one partial tooth with a base width of 30 mm bears a complete inner lateral cusp 5 mm high.

The tooth base is reniform in shape and dorso-ventrally flattened. The cusps are in line on the labial side of the base and the portion of the base lingual to the cusps is broad and slightly convex. Two large knoblike bosses are present on the base lingual to the lateral cusps on either side. Presumably they articulated with the two baso-labial bosses that are present on either side of the central cusp on the next tooth in the tooth row. Several large foramina penetrate the base on the lingual edge while a few small foramina are present on the labial edge of the base.

Discussion—Cope (1893, 1894) described *Symmorium reniforme* from a partial skeleton from the Middle Pennsylvanian Mecca Quarry Shale of Illinois. Williams (1985) redescribed the species and referred a number of teeth and partial skeletons to the taxon. Many workers have since used the description as a guide for identification of similar teeth around the world; however, Ginter (1998) has pointed out that the holotype of *Symmorium reniforme* differs significantly from the material described by Williams (1985). Most apparent is that the holotype lacks the two large knob-like bosses on the lingual side of the base as well as the two baso-labial bosses. According to Ginter (1998), specimens with the bosses belong to "*Cladodus*" *occidentalis* Leidy, 1859. It is unclear whether this species should be retained under *Symmorium* or placed in a new genus, so we follow Ginter (1998) in retaining Leidy's binomial here.

The teeth of "*C.*" *occidentalis* were arranged in successional whorls along the rami, much as in modern sharks and the teeth articulated with each other by way of two knoblike basolabial bosses that rested on two knobs on the lingual base of the next tooth. Williams (2001) has demonstrated that the cladodonts retained teeth by migration into pockets beneath the skin on the outside of the head once they were no longer functional. In his view this was a primitive feature that was lost later during the development of a more efficient cutting mechanism.

The teeth are designed for grasping and holding prey. The main cusp would penetrate the prey's flesh and inflict injury, while the lateral cusps helped hold the prey; the sigmoid curve of the main cusp was another feature designed to keep the prey firmly in the jaws. Williams (2001) has noted that the cladodonts compare favorably to the modern sand tiger, *Carcharias taurus*, a grasper and swallower that feeds primarily on bony fishes with occasional squids, crabs, and lobsters. Mapes and Hansen (1984) suggested that a tooth with a central cusp 21 mm high could have belonged to an animal 2.5 meters long. The largest teeth from the Naco Formation have an estimated cusp height of 28 mm suggesting an animal 3.3 meters in length and thus making "*C.*" *occidentalis* possibly the largest predator of its day. It most likely was an opportunistic feeder that preyed upon a wide range of fish and invertebrates. Mapes and Hansen (1984) report an example of a cephalopod with bite marks that correspond to "*C.*" *occidentalis* teeth indicating that cephalopods may have formed part of the diet of this animal.

"*Cladodus*" *occidentalis* has a global distribution throughout the Pennsylvanian. In the U.S. it is known from the Pennsylvanian of Ohio (Hansen, 1986), Illinois (Williams, 1985), and

Colorado (Lockley, 1984). Elsewhere in the world "*C.*" *occidentalis* has been reported from Russia (Trautschold, 1874; Ob-ruchev, 1967) and Greenland (Bendix-Almgreen, 1975).

ORODONTIDA Zangerl, 1981
 ORODONTIDAE de Koninck, 1878
ORODUS Agassiz, 1838
ORODUS sp.
 (Fig. 4N–P)

Material—Two teeth (MNA V9418, 9419)

Description—The tooth is relatively stout and crested and is gently arched in profile. An occlusal crest delineates the labial and lingual faces of the crown and both are ridged. There is a large central cusp and one side of the tooth is slightly longer than the other. There are ten ridges on the longer side of the tooth and seven on the shorter side. The crown extends further ventrally on the labial side than on the lingual side.

The base is gently convex and has a height equal to that of the crown. The width of the base is slightly less than that of the crown in labial or lingual view. The labial side of the base has 15 poorly developed dorso-ventral ridges with no foramina visible. Small foramina are randomly spaced on the lingual side.

Discussion—These specimens match well with the descriptions and figures of *Orodus* by Zangerl (1981), however, their specific affinities are unclear. The morphology most closely resembles the descriptions of *O. cinctus* and *O. greggi*.

Complete specimens of orodontid sharks from the Mecca and Logan Quarry shales show that they lacked spines (Zangerl, 1981). However, teeth referred to *Orodus* have been found in association with hybodont spines (Hlavin, 1972; Zangerl, 1981). Thus it is likely that *Orodus* sensu lato represents a polyphyletic assemblage of convergently similar tooth morphologies.

PETALODONTIDA Zangerl, 1981
 PETALODONTIDAE Newberry and Worthen, 1866
PETALODUS Owen, 1840
PETALODUS OHIOENSIS Safford, 1853
 (Fig. 5A–D)

Material—Three teeth (MNA V9420–9422).

Description—The collection includes several large, nearly complete specimens from the Pine locality whereas specimens from Kohls Ranch are limited to crown fragments. This description is based on three complete or nearly complete teeth from the Pine locality that represent three different tooth positions within the jaw. It is unclear as to whether these teeth belong to the upper or lower jaw.

The first is a large symmetrical tooth from at or near the symphysis of the jaw (Fig. 5A, B). It is 51 mm wide at the base of the crown and 55 mm long from the tip of the crown to the tip of the base. The tooth has a sigmoid flexure in profile. The crown is broad and triangular with basally curved extremities and is convex on the labial side and concave on the lingual side. The tip of the crown has a slightly steeper slope than the rest of the cusp and although not serrated the crown has fine grooves extending 5 mm down from the edge. At the base of the crown on both the lingual and labial surfaces there is a band of six imbricated and sharp-crested ridges. The root is slightly longer than the crown. It is triangular in shape and comes to a rounded point at the base. It is more concave labially and convex lingually and bears a small number of foramina on the surface close to the base of the crown.

The second tooth (Fig. 5C) was probably situated more posteriorly in the jaw. The crown is almost identical in its proportions to that of the anterior tooth, except that it is slightly broader whereas the root differs by being highly asymmetric. A row

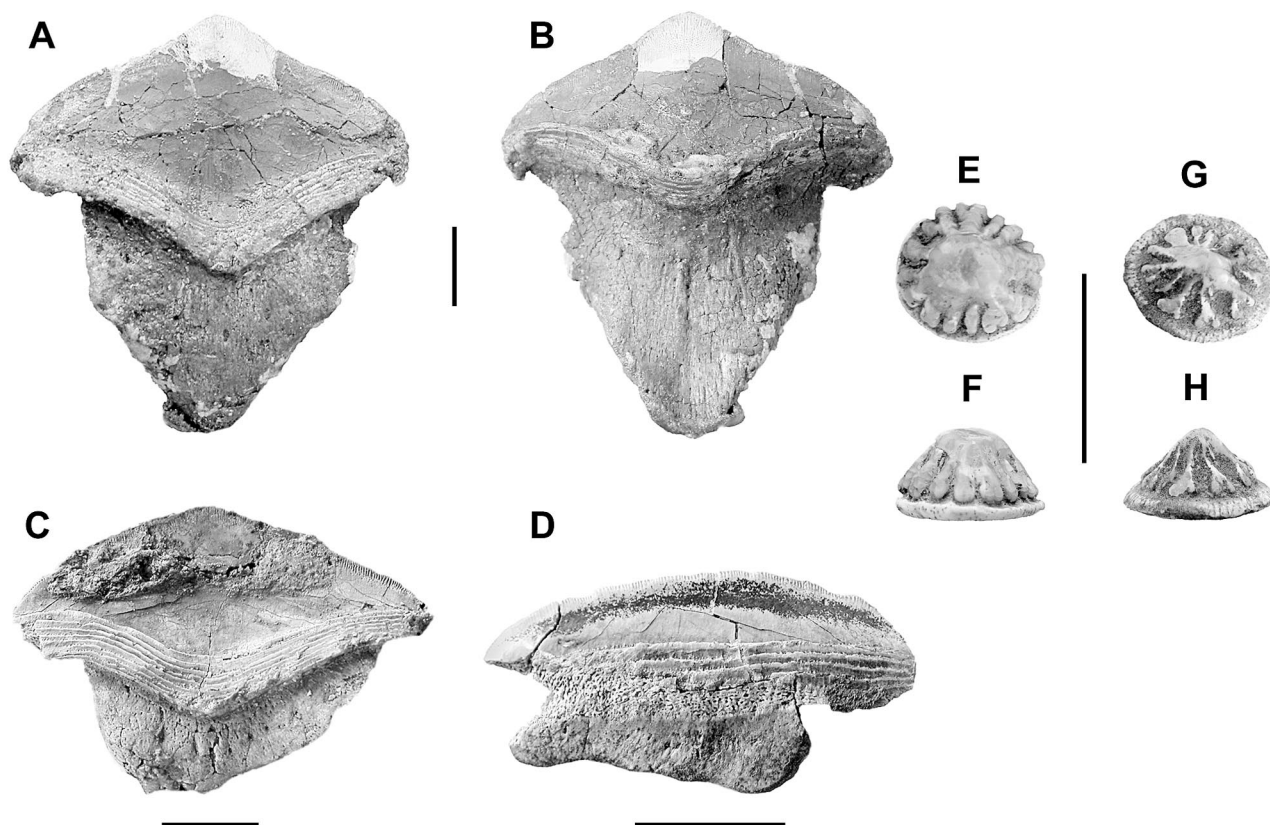


FIGURE 5. A–D, *Petalodus ohioensis*. A, B, anterior tooth (MNA V9420) in lingual (A) and labial (B) views; C, lateral tooth (MNA V9421) in lingual view; D, posterior tooth (MNA V9422) in lingual view. E–H, *Petrodus patelliformis*. Dermal denticles (MNA V 9423, 9424) in dorsal (E, G) and lateral (F, H) views. Scale bars equal 1 cm.

of large foramina is present midway on the root and a large number of small foramina are present near the crown.

The third tooth (Fig. 5D) likely occupied the most posterior tooth position. Both the crown and base are asymmetric with the whole tooth being mushroom-shaped in outline. The crown is low and arched and has a flat base that is 26 mm wide. The grooves on the edge of the cusp are very reduced, being less than 1 mm long. Five imbricating ridges are present at the base of the crown, although they are less developed than in the other teeth. The crown overhangs the root more on one side than the other and much more extensively than on the other teeth. The root is roughly rectangular, with a height of 5–6 mm on either side of the midline of the tooth and a length of 18 mm.

Discussion—Petalodont teeth are some of the most distinctive Carboniferous chondrichthyan tooth types and form a ubiquitous part of many Pennsylvanian marine faunas. *Petalodus ohioensis* was named by Safford (1853) for a tooth from near Cambridge, Ohio, and it is now known also from Europe. These large, broad teeth belonged to equally unusual animals and recent discoveries in the Bear Gulch Limestone (Lund, 1977, 1983, 1989) have helped to improve our understanding of their morphology.

Reconstruction of the dentition of petalodonts remained speculative at best until the discovery of articulated specimens from the Mississippian Bear Gulch Limestone of Montana (Lund, 1983, 1989). Although nearly all of the specimens are belantseid petalodonts they at least provide a guide for the reconstruction of dentitions in related taxa. All of the taxa show several common trends: size decreasing towards the posterior of the jaw; gradual morphological change in size and symmetry

towards the posterior of the jaw; and only one functional tooth in each tooth row with successional teeth being much smaller (Lund, 1989). The one articulated petalodontid dentition from Bear Gulch, a specimen of *Polyrhizodus digitatus*, is slightly disarticulated, but shows the same general trends (Lund, 1983).

These articulated taxa can be used as a guide for reconstructing the dentition of *Petalodus ohioensis*. Hansen (1986) suggested a reconstruction of the jaw based on a large collection of isolated teeth from Ohio. It matches with the patterns seen in the Bear Gulch specimens and we agree with it here, although we point out that it is impossible to determine whether certain teeth belong to the upper or lower jaw. The Bear Gulch specimens suggest that there was one large symphyseal tooth in the upper jaw and two in the bottom. The largest and most symmetrical teeth were located near the symphysis of the jaw, and size decreased posteriorly. The teeth also become more asymmetric towards the posterior of the jaw, especially in regard to the shape of the base.

The unique tooth morphology of *Petalodus ohioensis* indicates a very specialized lifestyle. The large occlusal surface and shearing ridges on the lingual side of the tooth suggest adaptations for biting and slicing soft tissue. Hansen and Mapes (1990) described a cephalopod that appears to have been bitten by a petalodont, however, while the morphology of the bite marks seems to fit the dentition of *Petalodus*, other predators cannot be ruled out. Certainly, *Petalodus* may have preyed upon cephalopods, but they may not have made up a large portion of its diet.

The distribution of *Petalodus ohioensis* is widespread. Beyond localities in Ohio (Safford, 1853; Hansen, 1986), it has

been reported from Colorado (Lockley, 1984; Itano et al., 2003), New Mexico (Lucas and Estep, 2000), Italy (Dalla Vecchia, 1988; Sirna et al., 1994), and Slovenia (Ramovs, 1997).

ELASMOBRANCHII incertae sedis Bonaparte, 1838
PETRODUS McCoy, 1848
PETRODUS PATELLIFORMIS McCoy, 1848
 (Fig. 5E–H)

Material—Two specimens (MNA V9423, 9424) and five additional specimens (MNA V9425).

Description—Numerous specimens of partial and complete dermal denticles from this genus have been recovered from the Kohls Ranch locality. They range in diameter from 2 mm to 5 mm and are circular to slightly oval with a height of 3–5 mm.

The denticles are conical with a flat base and rounded apex from which 10–20 ridges radiate to the base. The width of the ridges increases towards the base and about 30% of the ridges bifurcate midway down the denticle. The base is slightly concave in ventral view and projects as a narrow flange around the circumference of the denticle.

Discussion—The dermal denticle genus *Petrodus* is a common Paleozoic chondrichthyan denticle fossil, however, its taxonomic placement is still unknown. A partial skeleton of *Moyacanthus thomasi* attributed by Zangerl (1981) to the Hybodontoida, has been found associated with *Petrodus* denticles (Moy-Thomas, 1935; Zangerl, 1981). However Zangerl (1981) noted that *Petrodus* denticles are ubiquitous in Carboniferous deposits containing chondrichthyan remains and has preferentially allied *Petrodus* with the tooth genus *Carcharopsis* based on associated remains from Arkansas. It has also been noted (Chorn and Reavis, 1978) that there is an association between *Petrodus* and another denticle, *Listracanthus*, suggesting that they might have occurred on the same animal. Given their wide distribution and association with different teeth and denticles it is most likely that the denticles recognized as *Petrodus* occurred on a number of different shark genera.

Petrodus patelliformis was originally named from specimens collected from Derbyshire (U.K.) (McCoy, 1848) and is well represented in the Pennsylvanian limestones of Europe (Ford, 1964). Within the U.S. its localities include Indiana (Zangerl, 1981), Ohio (Hansen, 1986), Arkansas (Zangerl, 1981), Oklahoma (Stovall, 1945), Colorado (Lockley, 1984; Itano et al., 2003), and New Mexico (Lucas and Estep, 2000).

DISCUSSION

The published record of Pennsylvanian chondrichthyans from the western U.S.A. is poor, although recent reports from New Mexico (Lucas and Estep, 2000), and Colorado (Itano et al., 2003) indicate that this may now be improving. This is the first report of such a fauna from Arizona and constitutes a westward extension of the range of such faunas. This is also a particularly diverse fauna, with eleven taxa recognized.

Comparison with the New Mexico and Colorado assemblages indicates moderate to high homogeneity between the faunas. The Minturn and Naco assemblages both contain *Deltodus angularis*, “*Cladodus*” *occidentalis*, *Lagarodus angustus*, *Physonemus*, *Acondylacanthus*, *Petalodus ohioensis*, and *Petrodus* (Lockley, 1984; Itano et al., 2003). However, the Minturn contains a much larger diversity of fin spine taxa (Itano et al., 2003). This is not necessarily due to actual differences in faunal composition, but may be due to selective taphonomic sorting in both assemblages. The New Mexico assemblage from the Gray Mesa Formation (Lucas and Estep, 2000) has in common with the Naco fauna “*Cladodus*” *occidentalis*, *Petalodus ohioensis*, and *Petrodus*, but differs in having *Agassizodus varibilis*, a species thus far absent in the Naco Formation. conspicuously absent from both New Mexico and Colorado is a

range of smaller taxa including *Venustodus leidy*, *Orodus* spp., and hybodonts. This may be a sampling artifact, or it could represent differences in taphonomy, environment, and/or actual faunal composition.

Pennsylvanian localities within Ohio provide the most similarity with the Naco assemblage. Taxa represented in both assemblages include *Deltodus angularis*, *Venustodus leidy*, *Lagarodus angustus*, “*Cladodus*” *occidentalis*, *Orodus*, *Acondylacanthus*, *Physonemus*, *Petalodus ohioensis*, and *Petrodus* (Hansen, 1986). Hybodonts are also known from Ohio, but they do not match the morphology of those from the Naco (Hansen, 1986). Hansen (1986) also reported an extensive chondrichthyan microfauna from Ohio that at present is not represented in the Naco Formation.

Isolated occurrences of other taxa from the Naco Formation are known throughout the world. This is the first recorded occurrence of *Deltodus sublaevis* from outside Ireland, and represents a large range extension. *Acondylacanthus* is also known from Iowa (St. John and Worthen, 1875), and *Petalodus ohioensis* has been reported from both Italy (Dalla Vecchia, 1988) and Slovenia (Ramovs, 1997). *Orodus* is well known from the Meca and Logan Quarries in Illinois (Zangerl, 1981).

One of the most significant range extensions is that for *Lagarodus angustus*, which was previously recorded in Belgium (de Koninck, 1878), Russia (Obruchev, 1967), and Greenland (Bendix-Almgreen, 1975). Although its presence has been reported from Colorado (Lockley, 1984), and Ohio (Hansen, 1986) this is the first detailed description of this chondrichthyan from North America. *Venustodus* is known from North America, Ireland, and England (Stahl, 1999). The wide distribution of some of these species is probably related to the formation of Pangaea which had taken place by the late Pennsylvanian (Li et al., 1993) and resulted in the connection of the shallow marine environments inhabited by these organisms.

Shark dentition can be used to infer feeding habits and this fauna shows a preponderance of flat-crowned teeth that suggest adaptation for crushing hard-shelled invertebrates, although there is no direct evidence as crushed shell fragments resulting from shark predation would not be distinguishable from those fragmented by other means. Elliott and Bounds (1986) attributed unrepaired crushing features in brachiopods to the effects of post-mortem compression (contra Alexander, 1981), and Elliott and Brew (1988) demonstrated that bite marks in a specimen of *Linoproductus prattenianus* had been caused by a nautiloid. Although forms such as “*Cladodus*” *occidentalis* and *Petalodus ohioensis* appear to have teeth adapted for gripping and slicing softer tissues, work by Hansen and Mapes (1990) and Mapes and Hansen (1984) implicates them in attacks on hard-shelled cephalopods. This probably reflects a broad spectrum of feeding habits and a considerable degree of opportunistic feeding behavior.

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LITERATURE CITED

- Agassiz, L. 1833–1843. *Recherches sur les Poissons fossiles*. Neuchatel and Soleure, 390 pp.
- Alexander, R. 1981. Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulates. *Journal of Paleontology* 55:192–203.
- Bendix-Almgreen, S. E. 1975. Fossil fishes from the marine late Palaeozoic of Holmland-Amdrupland, North East Greenland. *Meddelelser om Gronland* 195(9):1–38.
- Bonaparte, C. L. 1832–41. A new systematic arrangement of vertebrated animals. *Transactions of the Linnean Society of London* XVIII:247–304.
- Bonaparte, C. L. 1838. Synopsis vertebratorum systematis. *Nuovi Annali di Scienze naturali Bologna* II:105–133.
- Brew, D. C. 1970. The Naco Formation (Pennsylvanian) in central Arizona. *Plateau* 42:126–138.
- Brew, D. C., and S. S. Beus. 1976. A Middle Pennsylvanian fauna from the Naco Formation near Kohl Ranch Central Arizona. *Journal of Paleontology* 50:888–906.
- Chorn, J., and E. A. Reavis. 1978. Affinities of the chondrichthyan organ-genera *Listracanthus* and *Petrodus*. *The University of Kansas Paleontological Contributions* 89:4–9.
- Compagno, L. J. V. 1984. *FAO Species Catalogue, Vol. 4. Sharks of the World. Part I. Hexanchiformes to Lamniformes*. *FAO Fisheries Synopsis* 4:1–249.
- Cope, E. D. 1893. On *Symmorium* and the position of the cladodont sharks. *American Naturalist* 27:999–1001.
- Cope, E. D. 1894. New and little known Paleozoic and Mesozoic fishes. *Journal of the Academy of Natural Sciences, Philadelphia* (2):9:427–448.
- Dalla Vecchia, F. M. 1988. First record of a petalodont (*Petalodus ohioensis* Safford, 1853) from the Alps. *Gortania-Atti del Museo Friulano di Storia Naturale* 9:47–56.
- Davis, J. W. 1883. On the fossil fishes of the Carboniferous Limestone Series of Great Britain. *Transactions of the Royal Society of Dublin* 2:327–548.
- Dean, B. 1909. Studies on fossil fishes (sharks, chimaeroids and arthrodires). *Memoirs of the American Museum of Natural History* V(9):211–287.
- de Koninck, L. G. 1878. Faune Calcaire Carbonifere de la Belgique. *Annales du Musée Royal d'Histoire Naturelle de Belgique* 2:1–152.
- Dilliard, K. A., and J. K. Rigby. 2001. The New Demosponges, *Chaunactis olsoni* and *Haplition nacoense*, and associated sponges from the Pennsylvanian Naco Formation, Central Arizona. *Brigham Young University Geology Studies* 46:1–11.
- Duffin, C. J. 1984. A new myriacanthid holocephalan from the Sinemurian (Lower Jurassic) of Belgium. *Zoological Journal of the Linnean Society* 82:55–71.
- Eastman, C. R. 1903. Carboniferous fishes from the Central Western states. *Bulletin of the Museum of Comparative Zoology* 39:163–326.
- Elliott, D. K., and S. D. Bounds. 1986. Causes of damage to brachiopods from the Middle Pennsylvanian Naco Formation, central Arizona. *Lethaia* 20:327–335.
- Elliott, D. K., and D. C. Brew. 1988. Cephalopod predation on a Desmoinesian brachiopod from the Naco Formation, central Arizona. *Journal of Paleontology* 62:145–147.
- Ford, T. D. 1964. A new fish bed in the Carboniferous Limestone of Derbyshire. *The Mercian Geologist* 1:3–9.
- Ginter, M. 1998. Taxonomic problems with Carboniferous “cladodont-level” sharks’ teeth; pp. 14–16 in M. Ginter and M. V. H. Wilson (eds.), *Ichthyolith Issues Special Publication* 4.
- Hansen, M. C. 1986. Microscopic chondrichthyan remains from Pennsylvanian marine rocks of Ohio and adjacent areas. Unpublished Ph.D. dissertation, Ohio State University, Columbus, 536 pp.
- Hansen, M. C. 1996. Phylum Chordata-Vertebrate Fossils; pp. 288–369 in R. M. Feldmann and M. Hackathorn (eds.), *Fossils of Ohio*. Ohio Division of Geological Survey Bulletin 70, Columbus, Ohio.
- Hansen, M. C., and R. H. Mapes. 1990. A predator-prey relationship between sharks and cephalopods in the late Paleozoic; pp. 189–192 in A. J. Boucot (ed.), *Evolutionary Paleobiology of Behavior and Coevolution*. Elsevier, New York.
- Hlavina, W. J. 1972. New associations of fossil sharks from the Cleveland Shale, Upper Devonian (Famenian). *Geological Society of America, Abstracts* 4:1, 21.
- Huxley, T. 1880. *A Manual of the Anatomy of the Vertebrated Animals*. D. Appleton & Company, New York, 431 pp.
- Itano, W. M., K. J. Houk, and M. J. Lockley. 2003. *Ctenacanthus* and other chondrichthyan spines and denticles from the Minturn Formation (Pennsylvanian) of Colorado. *Journal of Paleontology* 77:524–535.
- Janvier, P. 1996. *Early Vertebrates*. Clarendon Press, Oxford, 393 pp.
- Leidy, J. 1859. Description of *Xystracanthus arcuatus* and *Cladodus occidentalis*. *Proceedings of the Academy of Natural Sciences of Philadelphia* (unnumbered volume): 3.
- Li, Z. X., C. McA. Powell, and A. Trench. 1993. Paleozoic global reconstructions; pp. 25–53 in J. Long (ed.), *Palaeozoic Vertebrate Biostratigraphy and Biogeography*. Johns Hopkins, Baltimore.
- Lockley, M. G. 1984. Pennsylvanian predators: a preliminary report on some Carboniferous shark remains from Colorado. *University of Colorado at Denver Geology Department Magazine* 3:18–22.
- Lucas, S. G., and J. W. Estep. 2000. Pennsylvanian selachians from the Cerros de Amado, central New Mexico; pp. 21–27 in S. G. Lucas (ed.), *New Mexico's Fossil Record 2*. New Mexico Museum of Natural History and Science Bulletin 16.
- Lund, R. 1977. A new petalodont (Chondrichthyes, Bradydonti) from the Upper Mississippian of Montana. *Annals of Carnegie Museum* 46:129–155.
- Lund, R. 1983. On a dentition of *Polyrhizodus* (Chondrichthyes, Petalodontiformes) from the Namurian Bear Gulch Limestone of Montana. *Journal of Vertebrate Paleontology* 3:1–6.
- Lund, R. 1989. New petalodonts (Chondrichthyes) from the Upper Mississippian Bear Gulch Limestone (Namurian E2b) of Montana. *Journal of Vertebrate Paleontology* 9:350–368.
- Lund, R. 1990. Chondrichthyan life history styles as revealed by the 320 million years old Mississippian of Montana. *Environmental Biology of Fishes* 27:1–19.
- Lund, R., and E. D. Grogan. 1997. Relationships of the Chimaeriformes and the basal radiation of the Chondrichthyes. *Reviews of Fish Biology and Fisheries* 7:1–59.
- Lund, R., and C. Poplin. 1999. Fish diversity of the Bear Gulch Limestone, Namurian, Lower Carboniferous of Montana, USA. *Geobios* 32:285–295.
- Lund, R., E. R. Garton, and D. B. Weishampel. 1979. Fossil vertebrates of the Pennsylvanian system of West Virginia; pp. 105–107 in K. J. Englund (ed.), *Proposed Pennsylvanian System Stratotype, Virginia and West Virginia*. AGI Selected Guidebook Series 1.
- Lundin, R. F., and C. D. Sumrall. 1999. Ostracodes from the Naco Formation (Upper Carboniferous) at the Kohl Ranch locality, central Arizona. *Journal of Paleontology* 73:454–460.
- Mapes, R. H., and M. C. Hansen. 1984. Pennsylvanian shark-cephalopod predation; a case study. *Lethaia* 17:175–183.
- Maisey, J. G. 1982. Studies on the Paleozoic selachian genus *Ctenacanthus* Agassiz. No. 2. *Bythiacanthus* St. John and Worthen, *Ame-lacanthus*, new genus, *Eunemacanthus* St. John and Worthen, *Sphenacanthus* Agassiz, and *Wodnika* Munster. *American Museum Novitates* 2722:1–24.
- Maisey, J. G. 1983. Some Pennsylvanian chondrichthyan spines from Nebraska. *Transactions of the Nebraska Academy of Sciences* XI:81–84.
- Maisey, J. G. 1989. *Hamiltonichthys mapesi*, g. & sp. nov. (Chondrichthyes: Elasmobranchii), from the Upper Pennsylvanian of Kansas. *American Museum Novitates* 2931:1–42.
- Maisey, J. G. 2002. Review of: *Handbook of Paleoichthyology, Vol. IV. Chondrichthyes III. Holocephali*, by B. J. Stahl. *Journal of Vertebrate Paleontology* 22:188–189.
- McCoy, F. 1848. On some new fossil fish of the Carboniferous period. *Annals and Magazine of Natural History, Including Zoology, Botany, and Geology* (2)II:1–10, 115–133.
- McLaughlin, R. H., and A. K. O’Gower. 1971. Life history and underwater studies of a heterodont shark. *Ecological Monographs* 41:271–289.
- Morris, J., and G. E. Roberts. 1862. On the Carboniferous limestone of Oreton and Farlow, Cleve Hills, Shropshire. *Quarterly Journal of the Geological Society of London* 18:94–106.
- Moy-Thomas, J. A. 1935. The structure and affinities of *Chondrenchelys problematica* Traquair. *Proceedings of the Zoological Society of London* 1935:391–403.

- Newberry, J. S. 1889. The Paleozoic fishes of North America. United States Geological Survey Monograph 16:1–340.
- Newberry, J. S., and A. H. Worthen. 1866. Description of vertebrates. Geological Survey of Illinois 2:9–141.
- Obruchev, D. V. 1953. Studies on edestids and the works of A. P. Karpinski. U.S.S.R. Academy of Sciences, Works of the Palaeontological Institute 45:1–86.
- Obruchev, D. V. 1967. Fundamentals of Paleontology. A manual for paleontologists and geologists of the USSR, Vol. 11. Agnath, Pisces. J. A. Orlov (ed.), Israel Program for Scientific Translations. 825 pp.
- Owen, R. 1840. Odontography; or a Treatise on the Comparative Anatomy of the Teeth. Bailliere, London. 1, 1–655; 2, 1–150.
- Owen, R. 1867. On the mandible and mandibular teeth of coelodonts. Geological Magazine 4:59–63.
- Patterson, C. 1968. *Menaspis* and the bradyodonts; pp. 171–205 in T. Orvig (ed.), Current Problems of Lower Vertebrate Phylogeny. Proceedings of the 4th Nobel Symposium, Stockholm.
- Patterson, C. 1992. Interpretation of the toothplates of chimaeroid fishes. Zoological Journal of the Linnean Society 106:33–61.
- Ramovs, A. 1997. *Petalodus ohioensis* (Chondrichthyes, Upper Carboniferous) from the Karavanke Mountains, Slovenia. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 2:109–113.
- Rees, J., and C. J. Underwood. 2002. The status of the shark genus *Lissodus* Brough, 1935, and the position of the nominal *Lissodus* species within the Hybodontioidea (Selachii). Journal of Vertebrate Paleontology 22:471–479.
- Romanovsky, H. 1864. Descriptions de quelques restes de poissons fossiles trouvés dans le calcaire Carbonifère du Gouvernement de Toula. Bulletin de la Société impériale des naturalistes de Moscou 37: 157–170.
- Safford, J. M. 1853. Tooth of *Gettalodus (Petalodus) ohioensis*. American Journal of Science 16:142.
- Schultze, H.-P., and J. Chorn. 1988. The Upper Pennsylvanian vertebrate fauna of Hamilton, Kansas; pp. 147–154 in G. Mapes and R. H. Mapes (eds.), Regional Geology and Paleontology of Upper Paleozoic Hamilton Quarry Area in Southeastern Kansas. Kansas Geological Survey Guidebook 6.
- Sirna, G., F. M. Dalla Vecchia, G. Muscio, and G. Piccoli. 1994. Catalogue of Paleozoic and Mesozoic vertebrates and vertebrate localities of the Tre Venezie area (North Eastern Italy). Memorie di Scienze Geologiche Padua 46:255–281.
- Smith, B. G. 1942. The heterodontid sharks: their natural history and the external development of *Heterodontus (Cestracion) japonicus* based on notes and drawings by Bashford Dean; pp. 651–770 in E. W. Gudger (ed.), The Bashford Dean Memorial Volume—Archaic Fishes. American Museum of Natural History, New York.
- Stahl, B. J. 1999. Chondrichthyes III: Holocephali. H.-P. Schultze (ed.), Handbook of Paleoichthyology, Vol. 4. Verlag Dr. Friedrich Pfeil, München. 164 pp.
- Stahl, B. J., and M. C. Hansen. 2000. Dentition of *Deltodus angularis* (Holocephali, Coelodontidae) inferred from associated tooth plates. Copeia 4:1090–1096.
- Stovall, J. W. 1945. The occurrence of *Petrodus* in Oklahoma. American Midland Naturalist 34:720–722.
- St. John, O., and A. H. Worthen. 1875. Description of fossil fishes. Geological Survey of Illinois, Geology and Paleontology 6:245–488.
- St. John, O., and A. H. Worthen. 1883. Description of fossil fishes. Geological Survey of Illinois, Geology and Paleontology 7:55–264.
- Sumrall, C. O. 1992. *Spiraclavus nacoensis*, a new species of clavate agelacrinitid edrioasteroid from central Arizona. Journal of Paleontology 66:90–98.
- Trautschold, H. 1874. Die Kalkbrusche von Kjatschowa. Nouveau mémoires de la Société impériale des naturalistes de Moscou 13:398.
- Webster, G. D. 1981. New crinoids from the Naco Formation (Middle Pennsylvanian) of Arizona and a revision of the Family Cromyocrinidae. Journal of Paleontology 55:1176–1199.
- Webster, G. D., and N. G. Lane. 1970. Carboniferous echinoderms from the southwestern United States. Journal of Paleontology 44:276–296.
- Webster, G. D., and T. J. Olson. 1998. *Nacocrinus elliotti*, a new pachylocrinid from the Naco Formation (Pennsylvanian, Desmoinesian) of central Arizona. Journal of Paleontology 72:510–512.
- Williams, M. E. 1985. The “cladodont level” sharks of the Pennsylvanian black shales of central North America. Palaeontographica 190:83–158.
- Williams, M. E. 2001. Tooth retention in cladodont sharks: with a comparison between primitive grasping and swallowing and modern cutting and gouging feeding mechanisms. Journal of Vertebrate Paleontology 21:214–226.
- Woodward, A. S. 1889. Catalogue of the Fossil Fishes in the British Museum (Natural History). Part 1. British Museum (Natural History), London, 567 pp.
- Zangerl, R. 1979. New chondrichthyans from the Mazon Creek fauna (Pennsylvanian) of Illinois; pp. 449–500 in M. H. Nitecki (ed.), Mazon Creek Fossils. Academic Press, New York.
- Zangerl, R. 1981. Chondrichthyes I: Paleozoic Elasmobranchii. H.-P. Schultze (ed.), Handbook of Paleoichthyology, Vol. 3A. Gustav Fischer, Stuttgart, 115 pp.
- Zidek, J., and K. K. Kietzke. 1993. Pre-Permian vertebrates of New Mexico, with remarks on some Early Permian specimens; pp. 1–10 in S. G. Lucas and J. Zidek (eds.), Vertebrate Paleontology in New Mexico. New Mexico Museum of Natural History and Science, Bulletin 2.

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