Paludicola 5(2)65-76 May 2005

MIDDLE PENNSYLVANIAN (DESMOINESIAN) CHONDRICHTHYANS FROM THE LAKE NEOSHO SHALE MEMBER OF THE ALTAMONT LIMESTONE IN MONTGOMERY COUNTY, KANSAS

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ABSTRACT

Recent investigations into the Lake Neosho Shale Member of the Altamont Limestone (Desmoinesian, Middle Pennsylvanian) in Montgomery County, Kansas, have yielded a moderately diverse chondrichthyan assemblage. Taxa include teeth of *Caseodus eatoni, Edestus* cf. *E. heinrichi, Petalodus ohioensis*, "*Cladodus*" *occidentalis, Lagarodus angustus, Deltodus* cf. *angularis*, the finspine *Bythiacanthus* sp. and *Listracanthus hystrix* and *Petrodus patelliformis* denticles.

The Altamont Limestone represents a transgressive-regressive cycle that took place during the Middle Pennsylvanian, and the Lake Neosho Shale Member was deposited in deep water under stagnant, dysaerobic conditions during the highstand phase (maximum transgression).

INTRODUCTION

In southeastern Kansas the Altamont Limestone is divided into three members that are, from oldest to youngest, the Amoret Limestone Member (Greene and Searight, 1949; Moore, 1949: note that this unit was originally referred to as the Tina Limestone Member [see Cline, 1941]), Lake Neosho Shale Member (Jewett, 1941), and Worland Limestone Member (Greene, 1933; Cline, 1941). Jewett (1941) erected the Lake Neosho Shale Member for exposures of black, fissile, non-calcareous shale located at the southeastern end of Lake Neosho in Neosho County, Kansas. Based on invertebrate macrofossils Moore (1932, 1936) reported that the Altamont Limestone is of Desmoinesian age (Middle Pennsylvanian), and this has been confirmed through studies of conodont biostratigraphy (see Swade, 1985).

At the study area (Figure 1), the Lake Neosho Shale Member unconformably overlies the Amoret Limestone Member and is itself unconformably overlain by the Worland Limestone Member (Figure 2). The upper four meters of the Amoret Limestone Member is exposed, and consists of tan sparry limestone containing abundant brachiopods (spiriferids, terebratulids, productids), crinoid stems, and sponges (up to 0.6 m high and 0.6 m wide at the base). The contact surface with the Lake Neosho Shale Member is highly irregular and strewn with clusters of large productid brachiopods. The Lake Neosho Shale Member is approximately 0.6 m thick and contains phosphatic nodules that vary in size and shape (spherical to ovoid and up to 4 cm in diameter) that occasionally contain vertebrate fossils. The basal four meters of the Worland Limestone Member is exposed, which is a tan, fine-grained limestone with sparse brachiopods, crinoids, and chert nodules. The contact between the Worland Limestone and the Lake Neosho Shale is also highly irregular.

There are a limited number of reports of vertebrate remains from Pennsylvanian rocks of Kansas, and previous studies have thus far documented a relatively low number of chondrichthyan taxa. Those reports include the occurrence of *Petalodus* (Miller, 1957; Miller and Mann, 1958; Robb, 2003), *Holmesella quadrata* (Ørvig, 1966), *Petrodus* and *Listracanthus* (Chorn and Reavis, 1978), *Physonemus* (Chorn and Frailey, 1978), "*Cladodus*" and *Orthacanthus* (Robb, 1992). This report constitutes the first detailed account of chondrichthyan fossils from the Lake Neosho Shale Member of the Altamont Limestone, and they represent the most diverse Pennsylvanian vertebrate assemblage in Kansas.

GEOLOGIC SETTING

The Altamont Limestone was deposited during a middle Pennsylvanian transgressive-regressive cycle, and the contact between this unit and the underlying Bandera Shale represents a flooding surface that marks the lower boundary of this cycle. The Bandera Shale consists of alternating sandstone and shale beds that represent a marine-influenced, prograding siliciclastic complex that accumulated during lowstand (Brownfield et al., 1998). As sea level began to rise coastal swamps formed as freshwater ponded ahead of marine flooding, and these are preserved as a coal bed at the top of the Bandera Formation (Brownfield et al., 1998; Pope et al., 2002). Carbonate deposition eventually began as the transgression continued, resulting in the formation of the Amoret Limestone Member of the Altamont Limestone.

The overlying Lake Neosho Shale Member represents a shift from carbonate to shale deposition that was the result of a continued, possibly rapid, rise in sea level (King and Sutton, 2003). Heckel (1986) estimated that Pennsylvanian black shales of the mid-continental U.S. formed at water depths that may have exceeded 100 m during maximum transgression (highstand). As sea level rose, water depth eventually inhibited photosynthesis and carbonate-producing microorganisms ceased growing, ending carbonate deposition (Pope et al., 2002). Fine clay particles and organic debris accumulated over a long period of time, resulting in a condensed section of black shale (Heckel, 1988; Pope et al., 2002). In addition, current circulation was reduced (and may have ceased entirely) and dysaerobic conditions subsequently formed at the sea bottom (Heckel, 1988). The radioactive material that accumulated during deposition of the Lake Neosho Shale produces distinct spikes in gamma-ray logs that can be traced over large distances (Brownfield et al., 1998).

Eventually the regressive phase of the cycle began, the water became shallow enough that bottom currents scoured the upper part of the Lake Neosho Shale, and carbonate deposition resumed (Worland Limestone Member). Heckel (1988; 1994) and others (Wanless and Shepard, 1936) have argued that Pennsylvanian sea level fluctuations were climate-controlled (i.e. glacio-eustacy).

SYSTEMATIC PALEONTOLOGY

Specimens discussed in this report are housed at the Fort Hays State Museum (FHSM) in Hays, Kansas. Additional fossils are located at the Bob Campbell Geology Museum (BCGM) in Clemson, South Carolina.

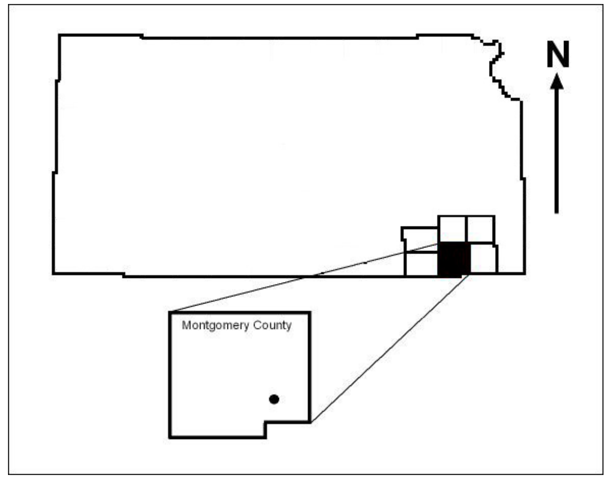

FIGURE 1. Geographic location of the Midwest Minerals quarry in Montgomery County, Kansas.

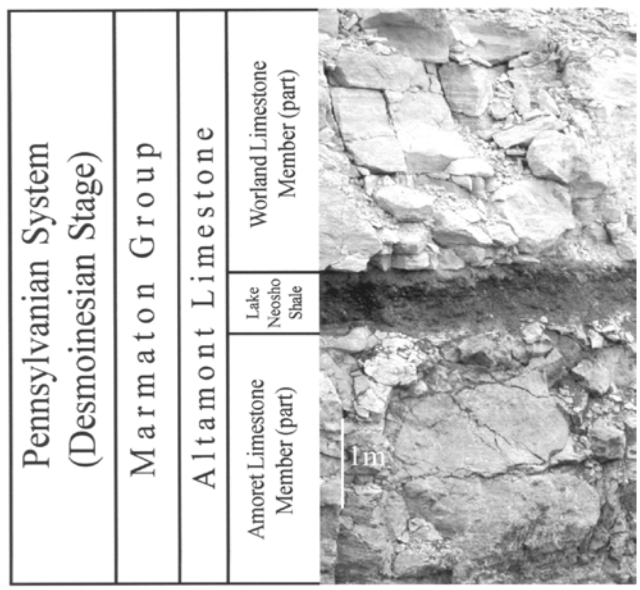

FIGURE 2. Partial stratigraphic section of the Altamont Limestone exposed at the Midwest Minerals quarry showing rock units discussed in text.

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Superfamily Ctenacanthoidea Zangerl, 1981
Family Ctenachanthidae Dean, 1909
Genus "*Cladodus*" Agassiz 1843
"*Cladodus*" *occidentalis* Leidy, 1859
(Figure 3 A, B)

Material--FHSM VP-15589 and FHSM VP-15590.

Description--Teeth consist of a tall, narrow cusp that is flanked by two pairs of lateral cusplets. The lingual face of the central cusp is very convex, whereas the labial face is moderately convex and there is a distinct medial sulcus at the base of the crown. The cutting edge is smooth and sharp along the central cusp, but it is indistinct on the lateral cusplets. Crown ornamentation consists of longitudinal ridges that are bifurcated at the crown foot and extend to the apices of the central cusp and lateral cusplets. There are two pairs of lateral cusplets, with the second being highly divergent and larger than the first. The root is wide, dorsoventrally compressed, and extended lingually past the crown. On the dorsal surface of the root, a small protuberance is located on each side of the central cusp, close to the lingual margin. There are also two protuberances on the labial margin of the root base. The basal attachment surface is weakly concave.

Discussion--The teeth in the dentition articulate to form tightly packed rows of piercing cusps. The dorsal protuberances on the root fit into the basal concavities of the succeeding teeth, and the labial crown sulcus fits tightly to the base of the lingual base of the preceding tooth (see also Ginter, 2002).

The systematic position of this tooth type remains in question, as specimens have variously been reported in the literature as "*Cladodus*" *occidentalis* (Newberry and Worthen, 1885; Elliott et al., 2004), "*Symmorium*" *occidentalis* (Itano et al., 2003), and *Symmorium reniform*e (Lockley, 1984; Lucas and Estep, 2002). The confusion may stem from the work of Williams (1985), in which some of the specimens he referred to *Symmorium reniforme* do not match the type specimens (Cope, 1894) because they possess dorsal and ventral root protuberances. According to Ginter (2002), teeth with such features are more appropriately referable to "*Cladodus*" *occidentalis* Leidy, 1859. However, *Cladodus* is considered a *nomen dubium* (Zangerl, 1981) because some teeth previously referred to *Cladodus* have been reassigned to several different genera. For simplicity, we follow Elliot et al. (2004) and refer our specimens to "*Cladodus*" *occidentalis.*

Order Eugeneodontida Zangerl, 1981
Family Caseodontidae Zangerl, 1981
Genus *Caseodus* Zangerl, 1981
Caseodus eatoni Zangerl, 1981
(Figure 4A-E)

Material--FHSM VP-15578 - FHSM VP-15582.

Description--FHSM VP-15578 (Figure 4A, B) is a large isolated anterior tooth that is mesodistally wide but labiolingually narrow, measuring 29 mm x 8 mm in these dimensions. The crown is low (measuring only 5.5 mm in height), asymmetrical in labial/lingual view, and rather straight with only slight sinuosity in occlusal view. The labial face is weakly convex and bears eight very large transverse protuberances. The lingual face is also convex, but transverse protuberances, located directly opposite those of the labial face, are much smaller. These protuberances combine to form indistinct cusps. The cutting edge is slightly arched, dull, and continuous along nearly the entire crown. Crown ornamentation consists of a granular texture, and there are indistinct transverse crenulations located on both sides of the cutting edge and the crown foot. The root is very thin labiolingually and it is nearly the same dimension as the crown (mesodistally).

FHSM VP-15580 is a slab of shale with an associated tooth set consisting of 45 teeth and impressions of nine others (Figure 4C). The slab was x-rayed to determine if additional teeth were obscured by matrix, but this met with limited success because of high concentrations of iron oxides and iron sulfides. The teeth have a very low, rather straight crown that is labiolingually thin and mesodistally elongated. Anterior teeth measure up to 13 mm in width, whereas posterior teeth measure as little as 4 mm. Teeth from anterior files have an indistinct cusp that is nearly centrally located, but the cusp becomes distally offset and eventually lost posteriorly. The labial crown face is convex and bears up to seven large transverse protuberances. The lingual face is also convex, but there are only indistinct bumps on the upper crown surface, directly opposite to the labial protuberances. These features combine to form small, inconspicuous cusps on the occlusal surface. The cutting edge is smooth, continuous, and may extend onto the mesial and distal margins of the crown (esp. in posterior teeth). Crown ornamentation varies considerably and consists of crenulations, short longitudinal ridges on the upper surface of the crown, small, evenly distributed tubercles and pits, or any combination of these features. Two incomplete symphyseal teeth are associated with FHSM VP-15580; one specimen preserved in transverse cross section, the other exposed in labial view (Figure 4D). The crown is U-shaped with the mesial and distal portions forming an approximately 60-degree angle. The labial face is convex with very short longitudinal ridges and a large medial protuberance. The cutting edge is smooth and continuous.

A number of tiny elements (2 mm or less) are associated with FHSM VP-15580 (Figure 4E). Although they are morphologically similar to the teeth described above (i.e. mesodistally elongated, highly crenulated), we believe these elements are too small to represent functional teeth and are likely oral denticles. In addition, remnants of cartilage are preserved (mostly impressions with isolated clusters of cartilage tesserae), and we assume that these represent jaw elements.

Discussion--Based on tooth morphology, we are confident that FHSM VP-15578 represents *Caseodus*

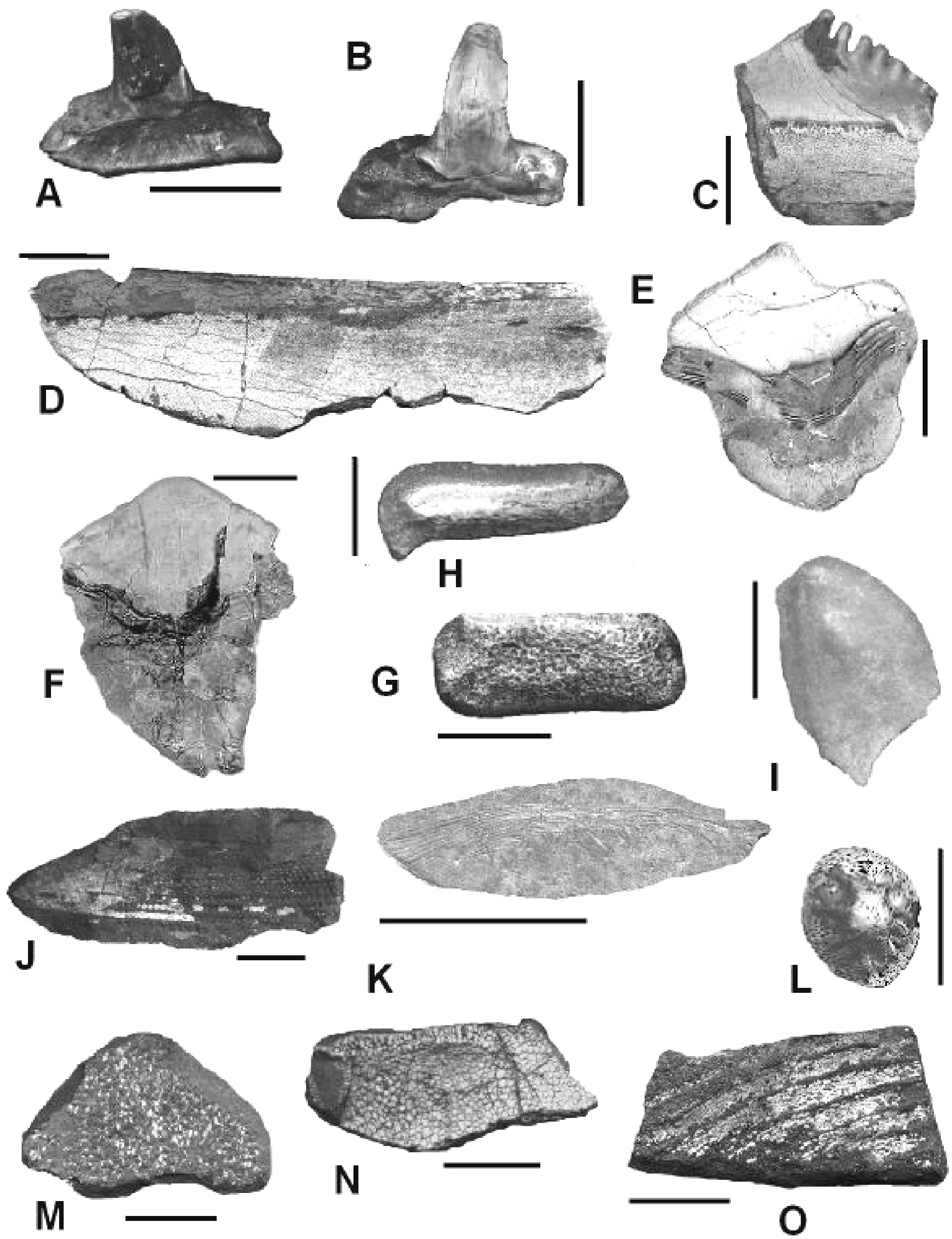

FIGURE 3. A, B, "*Cladodus*" *occidentalis* (FHSM VP-15589), A, lingual view, B, labial view. C, D, *Edestus* cf. *heinrichi* (FHSM VP-15583), C, incomplete tooth in lateral view, D, (FHSM VP-15584) incomplete tooth root in lateral view. E, F, *Petalodus ohioensis*, E, (FHSM VP-15587) ventral view, F, *P. ohioensis* (FHSM VP- 15588) ventral view. G, H, *Lagarodus angustus*, (FHSM VP-15591), G, aboral view, H, labial (?) view. I, *Deltodus* cf. *angularis*, (FHSM VP-15592), oral view. J, *Bythiacanthus* sp., (FHSM VP-15628) partial finspine (distal end left). K, *Listracanthus hystrix*, (FHSM VP-15609) lateral view of spine. L, M, *Petrodus patelliformis* (FHSM VP-15625), L, dermal denticle in apical view, M, shagreen; (FHSM VP-15617). N, elasmobranch cartilage fragment, (FHSM VP-15594). O, elasmobranch fin radials, (FHSM VP-15627). Scale bars = 10 mm.

eatoni. However, one could argue that the remainder of the specimens represent *C. basalis*. Zangerl (1981) has noted that the two species occur together in the Desmoinesian Mecca Quarry Shale of Illinois, and that they are indistinguishable based on postcranial remains.

Although the anterior and lateral teeth of FHSM VP-15580 have weakly developed lingual protuberances reminiscent of *C. basalis*, they are heavily ornamented as in *C. eatoni*. Zangerl (1981) has stated that the teeth of both species were highly variable, with the ornamentation of *C. basalis* approaching that of some examples of *C. eatoni*. Symphyseal teeth of *C. basalis* have been reported as having a 90-degree angle, whereas those of *C. eatoni* have an angle of approximately 60-degrees (Zangerl, 1981). In this respect, the symphyseal tooth in our sample (Figure 4D) compares closely to that of *C. eatoni*. We believe that all of the teeth in our sample represent *C. eatoni*, with FHSM VP-15578 being diagnostic of an adult specimen, whereas the remaining specimens are regarded as those of juvenile's basis of tooth size.

Family Edestidae Jaekel, 1889
Genus *Edestus* Leidy 1855
Edestus cf. *E. heinrichi* (Newberry and Worthen, 1870)
(Figure 3C, D)

Material--FHSM VP-15583 - FHSM VP-15586.

Description--FHSM VP-15583 (Figure 3C) represents a large fragment of a symphyseal tooth. The specimen consists of an incomplete triangular crown measuring 24 mm wide x 25 mm high. The labiolingual cutting edge is coarsely serrated, and the serrae are compound. The mesial and distal faces are smooth and very weakly convex.

FHSM VP-15586 is a small incomplete symphyseal tooth measuring 45 mm in total length and 23 mm in crown height (as preserved). The crown morphology is similar to FHSM VP-15583, but the preserved root is low and elongated lingually. FHSM VP-15584 (Figure 3D) and 15585 consist of root fragments. These are V-shaped in transverse cross-section.

Discussion--*Edestus* is an uncommon component of the Lake Neosho Shale Member chondrichthyan assemblage. Although incomplete, our specimens compare favorably to those described by Newberry and Worthen (1870) as *E. heinrichsi*. Note that the species name is spelled as *heinrichi*, as the taxon was originally named in honor of a Mr. Heinrich (Zangerl, 1981; Zangerl and Jeremiah, 2004). It is possible that our specimens could be referable to other species, but as Zangerl and Jeremiah (2004) have pointed out, these species are based on isolated specimens that may merely be form genera.

The teeth of *Edestus* form a whorl with the root of one tooth fitting into a furrow in the preceding tooth root. The base of the labial cutting edge of the crown slightly overlaps the lingual cutting edge of the preceding tooth. The tooth bases are not fused but attached to each other via connective tissue, and the anterior-most teeth are shed at intervals, with new teeth being formed at the lingual end of the whorl (Zangerl, 1981).

Order Petalodontia Zangerl 1981
Family Petalodontidae Newberry and Worthen 1866
Genus *Petalodus* Owen 1845
Petalodus ohioensis Safford 1853
(Figure 3E, F).

Material--FHSM VP-15587 and FHSM VP-15588.

Description--*Petalodus* teeth are characterized by having short, spade-like crowns. The tooth root is linguiform and is typically 2 to 4 times longer than the crown. The crown is mesodistally wide with a convex, crescent-shaped cutting edge.

FHSM VP-15588 (Figure 3E) is a small tooth embedded in matrix. It measures 11 mm wide x 12 mm high. The specimen is exposed in transverse cross-section and shows that the lower portion of the crown and the root are formed from trabecular dentine, whereas a wedge of orthodentine forms the upper part of the crown (see Zangeri et al., 1993). The inner (lingual) surface of the orthodentine has the relief of a waffle iron, being wavy in cross section (Zangerl, 1981). Radinsky (1961) considers this feature unique to the petalodonts.

Other specimens collected from the Lake Neosho Shale Member represent crown fragments of larger teeth. These show that the crown is thick basally but thins apically to a rather narrow transverse cutting edge. The labial face is weakly convex, whereas the lingual face is nearly straight or weakly concave. Crown ornamentation consists of a series of imbricated ridges located at the labial and lingual crown foot.

FHSM VP-15587 (Figure 3F) is a tooth that was recovered from the underlying Amoret Limestone Member and is included here because of its completeness. It is much larger than the Lake Neosho Shale Member specimens measuring 5.1 cm high x 4 cm wide (as preserved in matrix), and currently represents the only elasmobranch fossil reported from the Amoret Limestone Member.

Discussion--Teeth of *Petalodus* are often the most common chondrichthyan fossils reported from the Pennsylvanian and Permian rocks of eastern Kansas

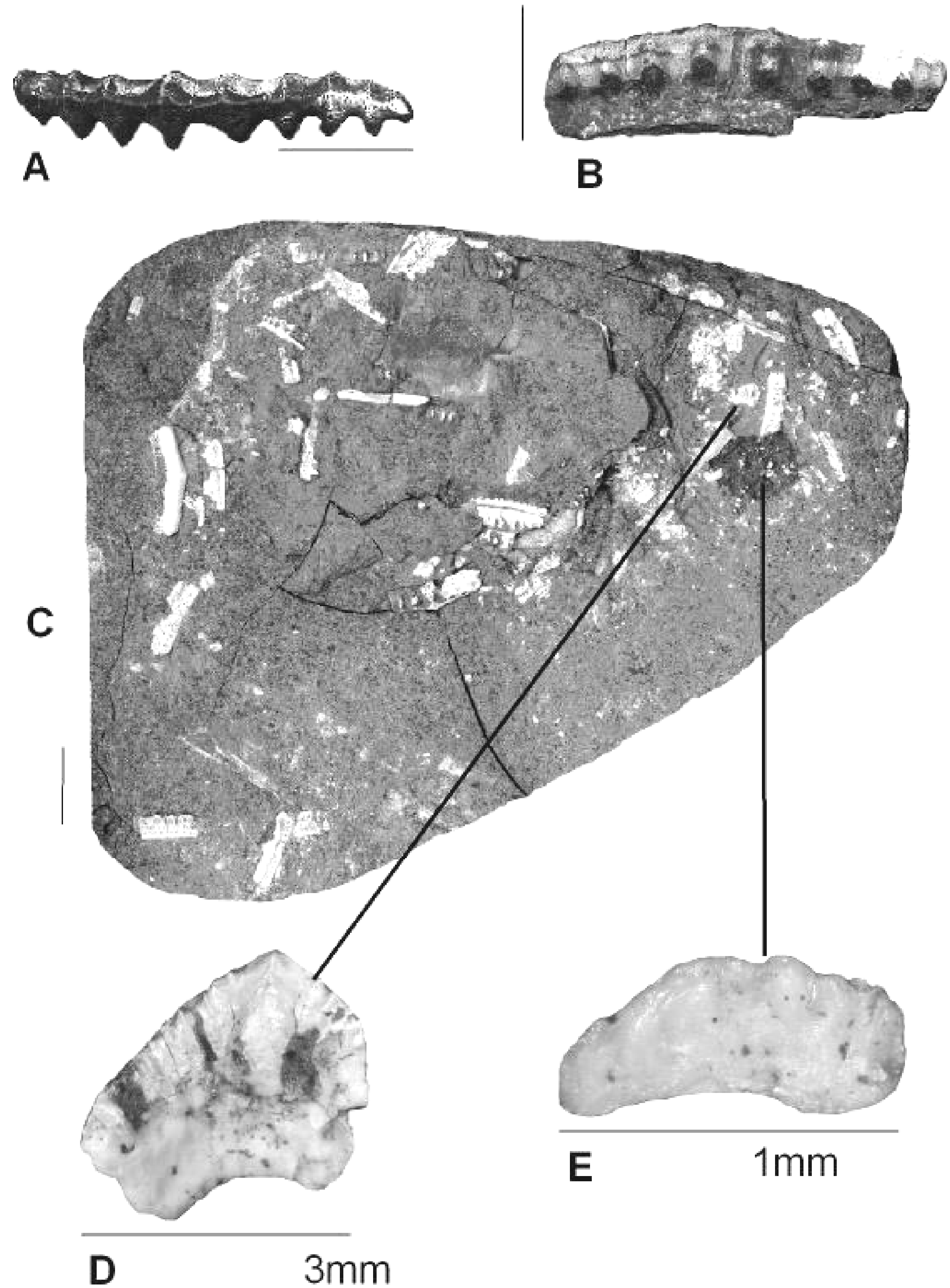

FIGURE 4. A, B, *Caseodus eatoni*, (FHSM VP-15578), A, occlusal view (labial at bottom), B, labial view. C, *Caseodus eatoni*, (FHSM VP-15580) close-up view of associated tooth set. D, labial view of symphyseal tooth from (FHSM VP-15580). E, oral denticle from (FHSM VP- 15580). Scale bars = 10 mm for A and B. For C = 20 mm.

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(Leidy, 1859; Miller, 1957; Miller and Mann, 1958; Chorn and Conley, 1978; Robb, 2003). Although associated tooth sets have not been found in Kansas, complete dentitions from other petalodonts have been described (Lund, 1977, 1983, 1989). The body shape of petalodonts appears to have varied, with some taxa having laterally compressed bodies (active, free-swimming; see Lund, 1989), and others having a more batoid-like, dorsoventrally compressed body (bottom dwelling; see Zangerl, 1981). Petalodonts appear to have been opportunistic feeders as stomach residues from one species included brachiopods, crinoids, foraminifera, and crustaceans (Malzahn, 1968).

Subclass Subterbranchialia Zangerl, 1979
Order Psammodontiformes Orbruchev, 1953
Family Psammodontidae De Koninck, 1878
Genus *Lagarodus* Jaekel, 1898
Lagarodus angustus (Romanovsky, 1864)
(Figure 3G, H)

Material--FHSM VP-15591.

Description--FHSM VP-15591 (Figure 3G) is a rectangular tooth plate measuring 22 mm long x 8.5 mm wide. The crown is rather thick and one end of the tooth is distinctly swollen. The margin of this side is also down turned (Figure 3H). The oral surface of the crown is smooth except for fine, closely spaced punctae that represent the intersection of the vascular canals of the orthotrabeculine with the occlusal surface.

Discussion--Romanovsky (1864) originally reported *Psammodus angustus* from Mississippian rocks of Russia, but Jaekel (1898) later synonymized the species with *Lagarodus*. In North America, *Lagarodus angustus* has been reported from Pennsylvanian rocks in Colorado (Lockley, 1984; Itano et al., 2003), New Mexico (Zidek and Keitzke, 1993), Arizona (Elliott et al., 2004) and Ohio (Hansen, 1986). FHSM VP-15591 represents the first occurrence of the taxon from Kansas.

Order Cochlidontiformes Obruchev, 1953
Family Cochliodontidae Owen, 1867
Genus *Deltodus* Morris and Roberts, 1862
Deltodus cf. *angularis* Newberry and Worthen, 1866
(Figure 3I)

Material--FHSM VP-15592

Description--FHSM VP-15592 is an isolated ovoid tooth plate measuring 22 mm long x 15 mm wide. The tooth plate is broad and relatively flat, and the occlusal surface is smooth, finely punctuate, and weakly convex. A blunt ridge runs along the midline of the tooth from the lingual to labial edge with a small bump near the mesial end. Whereas the mesial end is pointed, the distal end is rounded. The root is composed of trabecular dentine, and the aboral surface of the tooth plate is slightly concave.

Discussion--The high degree of morphological variation of cochliodont tooth plates has led to disagreement among investigators concerning the identification of specimens and their placement within the dentition (Stahl, 1999). In addition, Branson (1905) noted the difficulty in distinguishing tooth plates of *Sandalodus* and *Deltodus*, and original identifications of some specimens were later switched between the two (Newberry and Worthen, 1866; St. John and Worthen, 1883). Woodward (1889) and Stahl and Hansen (2000) have recognized at least some tooth plates referred to *Sandalodus* are part of the dentition of *Deltodus*. Although FHSM VP-15592 is similar to tooth plates traditionally assigned to *Sandalodu*s, we assign the specimen to *Deltodus* and believe it compares favorably with *D. angularis* (see also Elliott et al., 2004).

Without the aid of associated tooth sets, it is difficult to distinguish teeth of the upper jaw from those of the lower jaw. Newberry and Worthen (1866) did not differentiate teeth as being from being either the upper or the lower jaws. However, Woodward (1889) reiterated the notion of separating the tooth plates into two varieties: the “Triangular Variety” representing teeth of the upper jaw, and the “Incurved Rounded Variety” being teeth from the lower jaw (see Stahl, 1999 and Stahl and Hansen, 2000). As preserved, FHSM-VP 15592 appears to represent the latter variety, and the specimen is significant because it is the first occurrence of the genus in Kansas.

Order, Family indeterminate
Genus *Bythiacanthus* St. John and Worthen, 1875
Bythiacanthus sp.
(Figure 3J)

Material--FHSM VP-15628.

Description--As preserved, FHSM VP-15628 measures 71 mm long x 13 mm at its widest (the spine tapers apically). Ornamentation consists of 11 closely spaced, parallel rows of small enameloid-covered nodes. These nodes bear fine radiating ridges. Although the specimen predominantly consists of actual spine, some of the morphology discussed above is represented by natural molds in the matrix where the spine has weathered away.

Discussion--St. John and Worthen (1875) originally attributed Paleozoic chondrichthyan finspines of similar morphology to *Bythiacanthus*. In his revision of Paleozoic finspines, Maisey (1982) referred material recovered from Mississippian rocks to eight species of *Bythiacanthus*, and Itano et al. (2003) recently reported the taxon from the middle Pennsylvanian of Colorado. Unfortunately, our specimen is too fragmentary to make a specific identification; however, it is the first occurrence of the genus in Kansas.

Genus *Listracanthus* Newberry and Worthen, 1870
Listrocanthus hystrix Newberry and Worthen, 1870
(Figure 3K)

Material--FHSM VP-155609 - FHSM VP-155616; BCGM 6619.

Description--The specimens consist of a narrow, bar-like base supporting a very thin (laterally compressed) spine. The spine itself is composed of up to 16 long parallel rods that are very closely spaced. The spines curve posteriorly, and the posterior edge often appears frayed. Spines reach a height of 40 mm and a basal length of 11 mm.

Discussion--*Listracanthus* spines have been found in association with *Petrodus* denticles, suggesting that both belonged to the same shark (Bradley, 1870; Chorn and Reavis, 1978). However, Zangerl (1981) believed the remains occurred on separate taxa. We have recovered a portion of shale with associated *Listracanthus* and *Petrodus* (FHSM VP-15629), and a *Listracanthus* spine is associated with FHSM VP-15580 (*Caseodus*_partial dentition). Unfortunately, our specimens do not elucidate the relationships between these remains.

Genus *Petrodus* M'Coy 1848
Petrodus patelliformis M'Coy, 1848
(Figure 3L, M)

Material--FHSM VP-15617 - FHSM VP-15626, BCGM 6617 and BCGM 6618.

Description--These dermal denticles have a circular or oval outline in dorsal/ventral view, and may be conical or rounded in saggital cross section (Figure 3L). Smaller specimens bear coarse radiating ridges that bifurcate basally, whereas larger specimens have massive ridges that are restricted to the lower half. The base of the denticles extends a short distance outward from the main body, and the basal attachment surface may be flat, weakly convex, or weakly concave.

Discussion--We have recovered sections of *Petrodus* shagreen (Figure 3M) consisting of masses of tiny (0.25 mm) denticles (FHSM VP-15624, FHSM VP-15625). These denticles differ from those described above in that they are taller (relative to their size) and curve posteriorly. This denticle morphotype is identical to specimens described by Corn and Reavis (1978). A fragment of shagreen (FHSM VP-15625) is associated with impressions of the larger denticles, indicating these were embedded within the mass of tiny denticles.

Petrodus is a rather ubiquitous fossil in Paleozoic rocks of the mid-continent of North America, having been found in Kansas (Chorn and Reavis, 1978) Colorado (Itano et al., 2003), South Dakota (Cicimurri and Fahrenbach, 2002), New Mexico (Lucas and Estep, 2002), Oklahoma (Zidek, 1973), and Indiana (Zangerl and Richardson, 1963). *Petrodus patelliformis* was originally described by M'Coy (1848) from specimens collected in Derbyshire England. He originally believed these specimens represented teeth in the dentition of a shark, but Zangerl and Richardson (1963) concluded that *Petrodus* was a type of denticle. This interpretation was supported by Chorn and Reavis (1978), and subsequent authors have followed this scheme (Cicimurri and Fahrenbach, 2002; Lucas and Estep, 2002; Itano et al., 2003).

DISCUSSION

Among the other chondrichthyan remains recovered during this study are several fragments of cartilage (Figure 3N). These specimens consist of irregular pieces composed of very small (< 0.25 mm) calcified cartilage tesserae (FHSM VP-15594, FHSM VP-15595, FHSM VP-15596). The cartilage fragments were not associated with teeth, and we cannot be sure if the fragments represent pieces of jaw or postcranial elements (i.e. scapular bar, pelvic bar). Two isolated fin radials (FHSM VP-15593 and 15597) were also recovered during this study. They are incomplete fins composed of closely spaced, parallel rows of unsegmented cartilage rods (formed from small-calcified cartilage tesserae). Of these two specimens, FHSM VP-15593 (Figure 3-O) represents the distal portion of a fin radial and indicates that the proximal end of each cartilage rod was pointed.

Remains of other macrovertebrate taxa are rare in the Lake Neosho Shale Member at the Coffeyville quarry, with only one specimen, a paleoniscid fish (FHSM VP-15598) being collected. Conodonts, on the other hand, were found to be common and are associated with several of the specimens we collected (i.e. FHSM VP-15580). Only one inarticulate brachiopod taxon, *Orbiculoidea missouriensis* (FHSM IP-1459), and some plant material referable to *Calamites* (FHSM PB-590) and *Cordaites* were observed during our investigation.

CONCLUSION

Significance--The vertebrate fossils recovered from the Lake Neosho Shale Member of the Altamont Limestone consist almost exclusively of elasmobranch and holocephalian remains, and our report is the first detailed documentation of chondrichthyans from this lithostratigraphic unit. These fossils also constitute the most complete Pennsylvanian chondrichthyan assemblage thus far recovered from Kansas. Of the nine taxa discussed, *Deltodus, Lagarodus, Caseodus, Edestus,* and *Bythiacanthus* are new records for the state. The chondrichthyan assemblage recovered from the Lake Neosho Shale is at least partially similar to faunas reported from temporally equivalent rocks in Indiana (Zangerl and Richardson, 1963), New Mexico (Lucas and Estep, 2002), Arizona (Elliott et al., 2004), South Dakota (Cicimurri and Fahrenbach, 2001), and Colorado (Itano et al., 2003). We believe that the chondrichthyan fauna of the Lake Neosho Shale Member is incomplete due to the relatively small area of outcroppings prospected, and the possible collecting bias towards larger fossil remains.

Depositional Environment--An alternative hypothesis for Lake Neosho Shale deposition is that, as has been interpreted for some black shales of Indiana (Zangerl and Richardson, 1963), sediment was deposited in a near shore, shallow water, lagoonal environment. A low-salinity, low-oxygen lagoonal environment could contain a depauperate benthic invertebrate community. However, the lateral extent of the Lake Neosho Shale Member is too great to represent a lagoonal environment (Pope et al., 2002; King and Sutton, 2003), and at least thin beds representing short intervals of more normal marine conditions should be preserved (see Zangerl and Richardson, 1963). We favor the interpretation that the Lake Neosho Shale was deposited in deep water under stagnant, dysaerobic conditions.

Supporting this hypothesis, Kidder (1985) suggested that phosphate nodules in Pennsylvanian black shales formed in poorly oxygenated sediment in areas where upwelling occurred higher in the water column. We collected several phosphate nodules, and we believe that, at least in some instances, vertebrate remains acted as a nucleus for phosphate precipitation. Low-oxygen bottom water, coupled with upwelling higher in the water column, would explain the paucity of benthic invertebrates and the occurrence of the remains of presumably pelagic, free-swimming vertebrates. We observed invertebrate feeding traces in the Lake Neosho Shale, and we attribute disarticulated, associated tooth sets of chondrichthyans (and occasional paired conodont elements) to bioturbation rather than current circulation. We also argue that remains of *Calamites* and *Cordaites* originated from a bordering coal swamp, but that the fragments floated out to deeper water (a hypothesis proposed for dinosaur carcasses that have been found in Cretaceous marine rocks; see Carpenter et al., 1995; Hamm and Everhart, 2001).

ACKNOWLEDGMENTS

We would like to thank R. Benefield, A. Armstrong and B. Dunn for donating valuable specimens studied in this report. The senior author would like to thank L. Skelton (Kansas Geological Survey, Wichita, KS) for discussions on the geology of Kansas. We would also like to thank S. Sloan (Midwest Minerals, Pittsburg, KS) for granting us access to the Coffeyville Quarry and R. Zakrzewski (FHSM) for curating the specimens studied. This project also benefited from discussions with N. King (Lake Neosho Shale stratigraphy) and M. Ginter (cladodont shark taxonomy). The editorial suggestions of two anonymous reviewers improved an earlier version of this manuscript. Lastly, thanks to J. Massare for her efforts in putting vol. 5 of Paludicola together.

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