THE FIRST OCCURRENCE OF VERTEBRATES, REPRESENTED BY THE PALEOZOIC SHARKS *PETRODUS*, *LISTRACANTHUS*, *CLADODUS*, AND *CRANODUS*(?) FROM THE PENNSYLVANIAN-PERMIAN MINNELUSA FORMATION NEAR PIEDMONT, SOUTH DAKOTA

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ABSTRACT

The sharks *Listracanthus*, *Petrodus*, *Cladodus*, and other chondrichthyian remains in the Pennsylvanian to Permian Minnelusa Formation of South Dakota represent the first reported vertebrate remains from this formation. A site in Little Elk Creek Canyon has yielded over 100 fragments and complete *Petrodus* denticles, two *Listracanthus* spines, and several complete and/or fragmentary teeth of associated sharks.

The environment of the main fossil-bearing unit is a lagoon, with associated sabkha-type environments also being represented at the site.

The conodont genus *Idiognathodus* in the same layer as the most prolific *Petrodus*-bearing bed establishes the age of this portion of the Minnelusa Formation as Desmoinesian to Missourian.

PREVIOUS WORK

M'Coy first described the type specimen *Petrodus patelliformis* in 1848. Although his description was based on a European occurrence, several North American finds have also been described. *Petrodus* denticles have also been found in Arkansas (Zangerl, 1981), Illinois (Newberry and Worthen, 1866), Indiana (Zangerl and Richardson, 1963), Iowa (Case, 1982), Kansas (Chorn and Reavis, 1978), and Oklahoma (Morgan 1924, Stovall, 1945, Branson, 1965). Woodward (1903) reported several European specimens, most notably from England and Moscow.

Worthen (1870) and Woodward (1903) described the fish spine *Listracanthus*, and Chorn and Reavis (1978) suggested a relationship between *Petrodus* and *Listracanthus*. Case (1982) mentioned *Listracanthus* occurrences in Illinois, Iowa, and Nebraska.

Eaton (1962) and Zidek (1973) described the dentition of associated Edestid and Cladodont sharks.

Ward (1979) studied the sedimentology of the Minnelusa Formation in Dark Canyon, Rapid City, and Motes (1984) studied the Minnelusa in Wyoming. The Little Elk Creek Canyon area itself was studied in a 1963 thesis by Wilshusen.

Jennings (1959) provided the most comprehensive study of Minnelusa Formation conodonts. *Gondollela*, *Idiognathodus*, and *Streptognathodus* were all discussed in his paper. To this point in time, there have been no reported occurrences of vertebrates in the Minnelusa Formation.

DESCRIPTION OF LITTLE ELK CREEK MINNELUSA FORMATION

The great complexity of the Minnelusa Formation, due to profound changes in bed thicknesses, provided problems with correlation, although some key beds were found. The spines and dermal denticles were found in only two shale layers of the area. Figure 1 shows the location of Little Elk Creek Canyon.

The *Petrodus* I bed is located approximately one foot above the lower, covered portion of the section. The gray shale is platy and hard on fresh surfaces but is rather soft on weathered portions. It is located between two layers of dolomite and has yielded few fossil denticles.

Petrodus II is found about 2.5' above the *Petrodus* I bed. The upper and lower contacts of *Petrodus* II are very wavy and irregular. A light green shale underlies a gray-black shale, with the green shale measuring about .5" to 1.0" thick and the black shale being about 4.5" to 6" in thickness. The shale layers are slightly calcareous, blocky, and somewhat soft. *Petrodus* denticles have been found in low spots at the lower contact with the dolomite, and both denticles and spines have been found at the interface of the black and green shale units. Since this is the case, it appears that both a lag deposit and an undisturbed deposition of denticles are present at the site. A lag deposit, in this case, may represent the unconformity between the Atokan and Desmoinesian Stages of the Minnelusa Formation (Gries and Martin, 1985). The occurrence of an olive-green shale due to sulfides represents a highly poisonous environment at the Garrard Quarry (Zangerl and Richardson, 1963). No bioturbation of the fossiliferous layers is noted at either Little Elk Creek Canyon or the Garrard Quarry.

The portion of the Minnelusa Formation above the *Petrodus* I and II beds is dominated by thick sequences of dolomites, limestones, thin shales, and sandstones. The "Red Marker" bed is thought to lie within an 84' thick covered portion, near the top of the section.

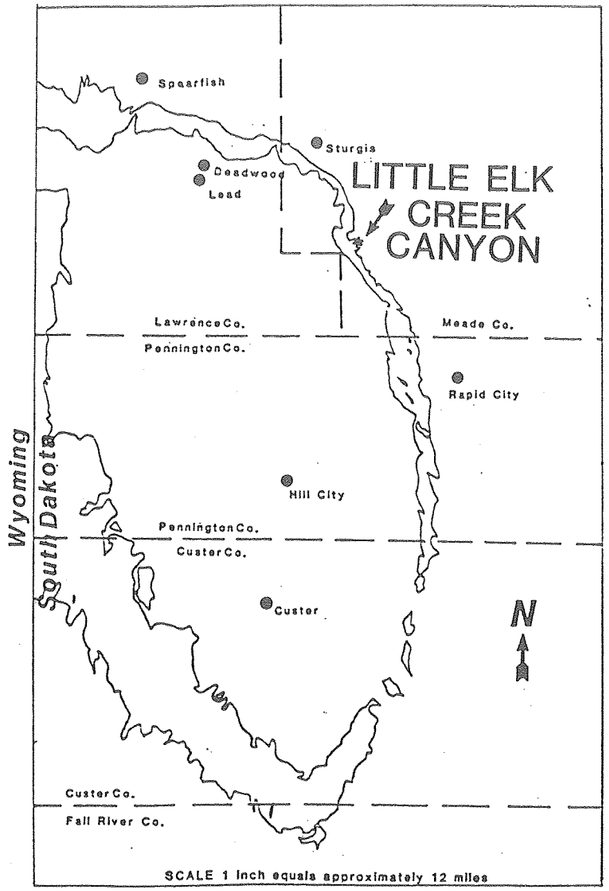

Figure 1. Map of the Black Hills showing the extent of the Minnelusa Formation outcrop (after Darton, 1951).

SYSTEMATIC PALEONTOLOGY

All materials are deposited in the Museum of Geology (SDSM) and come from locality SDSM V9215.

Chondrichthyes

Elasmobrachii

Ctenacanthiformes

Hybodontidae

Petrodus

Petrodus occidentalis Newberry and Worthen, 1866

Referred specimens -- SDSM 26051, 1 dermal denticle; SDSM 26052, 1 large dermal denticle; SDSM 26053, 125 dermal denticles.

Description

Most of the *Petrodus* denticles (Figure 2) are conical in shape, with the larger ones averaging 7 mm in height and 8-10 mm in diameter. In these dimensions, medium-sized denticles average around 4 mm high and 6 mm in diameter, and small denticles are around 2.5 mm and 4 mm respectively. The smallest complete denticle found is only 1 mm high and has a diameter of 2 mm.

A number of diverging ridges run down the sides of the denticles, with many of these forking into two or more ridges near the base. Usually, the *Petrodus* denticles are circular to semi-circular.

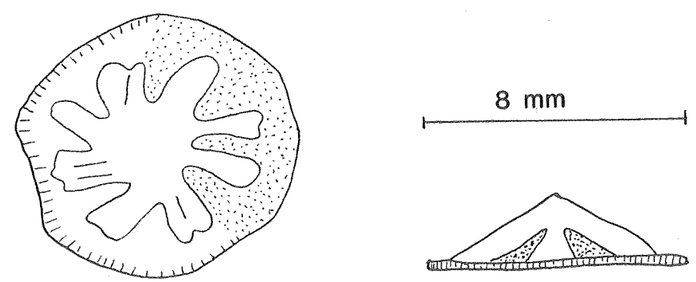

Figure 2. Typical *Petrodus occidentalis* dermal denticle (SDSM 26051).

There are a few denticles found that are domal and have rounded, smooth surfaces with very little or no ridges. The largest one of this type is 7 mm high, with a diameter of 12 mm. A slight hint of ridges can be seen near the base, but they are not fully developed in these particular specimens.

The underside of the *Petrodus* denticles differ with size. The larger ones have a concave base, while the medium to small denticles tend to have a flat or convex base. Some of the denticles have a flared base, which may have aided in the attachment of the denticle to the outer surface of the skin.

The large diversity in size and form probably relates to the different locations of the denticles on the animal's body, or may represent different stages of either the denticle's growth or the animal's growth. The possibility of different morphologies representing different animals also exists, but the ideas of different locations and growth stages seem to be more likely.

Discussion

The first specimens of *Petrodus* described (M'Coy, 1848), were classified as *P. patelliformis*. Newberry and Worthen (1866) called the Illinois *Petrodus* remains *P. occidentalis*, although they themselves hesitated to consider the two distinct. They did, however, describe a single occurrence of *P. acutus*, which appeared to be a different morphology then that of *P. patelliformis*. Woodward (1903) also described a specimen of *P. acutus* from a carboniferous limestone, near Mjatschkowa, Moscow. The North American specimens are generally regarded as *P. occidentalis* (Zidek, 1973).

At the time, M'Coy (1848) believed that the fossil shark remains called *Petrodus* were dentition teeth. Stovall (1945) seemed to back this view, stating, "The specimens under consideration show definite signs of wear on the peak as if they had been given considerable use in the attrition of resistant matter, such as mollusks and crustaceans. They appear to show more wear than would be caused on dermal denticles by a fish accustomed to wallow on the bottom. The writer inclines to the view that these are true teeth" (Stovall, 1945, p. 722). Several of the denticles found at Little Elk Creek Canyon show such wear.

Newberry and Worthen questioned this belief as early as 1866. Later, Zangerl and Richardson (1963) and Chorn and Reavis (1978) concluded that the remains in question were dermal denticles. A large plate of shale containing a mat of densely packed *Listracanthus* spines and *Petrodus* denticles supported this notion (Chorn and Reavis, 1978).

One would assume that if *Petrodus* were indeed true dentition teeth, the denticles would have an interlocking basal area, such as seen in the Cretaceous *Ptychodus*. Stovall found a set of two attached denticles. He later found in thin section separate enamel and osteodentine layers in *Petrodus* and suggested that the denticles represent true dentition teeth.

Woodward (1903) noted a similarity between *Petrodus* and the dermal denticles at the head of *Hybodus*, and Moy-Thomas (1935) followed up on this thought.

Moy-Thomas (1935) described a partially articulated shark skeleton as *Petrodus patelliformis*, due to the fact that denticles of that name are associated with the remains. Zangerl (1981) believed "*Petrodus* denticles are, however, ubiquitous in Carboniferous deposits containing chondrichthyan remains. *Petrodus*, moreover, appears to be an entirely different kind of fish" (p. 57). Zangerl called the described specimen *Moyacanthus thomasi*.

Holocephali

Incertae Sedis

Not referred to order

Cladodus Leidy, 1859

Referred specimens -- SDSM 26054, 1 tooth base with 2 tooth fragments; SDSM 26055, 1 tooth fragment

Description

The shark *Cladodus* is represented at the site by two sets of tooth fragments and one nearly complete tooth base. The top of one specimen (SDSM 26054) shows the broken bases of three separate teeth, and tooth fragments found nearby probably belong to the same base. The base is 28 mm long, 14 mm wide, and 8 mm high. Any further classification other than *Cladodus* sp. would be useless, due to the fact that the name is merely a form genus.

Discussion

C. mortifer and *C. occidentalis* are two tooth types that have been found in the same formations as, but not necessarily associated with, *Listracanthus* and *Petrodus* (Zidek, 1973). However, Zidek believed that *C. mortifer* and *C. occidentalis* should be viewed as synonymous.

The term *Cladodus* should be looked at as a form genus only.

Cochliodontidae

?*Cranodus* Trautschold, 1879

Referred specimen -- SDSM 26056, 1 tooth.

Description

The only complete tooth found at the site is presently identified as *Cranodus zonatus* (Figure 3). The tooth is 5 mm wide and 6 mm long. Until this point in time, *C. zonatus* has not been reported in association with *Listracanthus* and *Petrodus*, so this identification remains somewhat questionable.

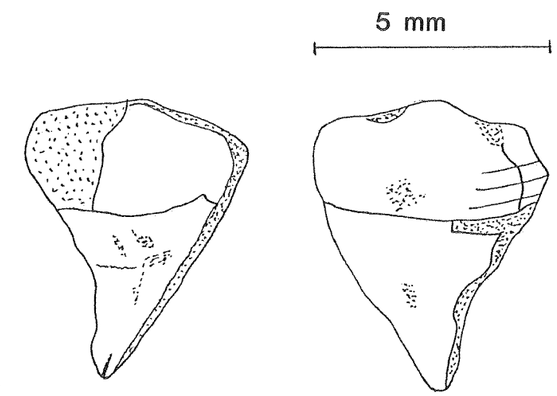

Figure 3. Unknown tooth, possibly that of *Cranodus zonatus* (SDSM 26056).

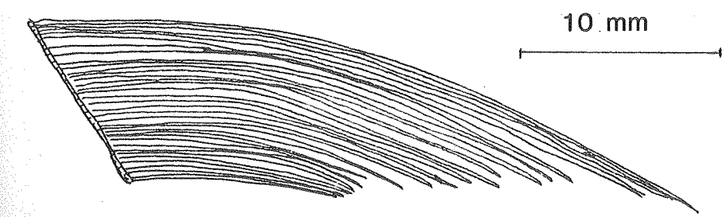

Figure 4. *Listracanthus hysterix* spine (SDSM 26057).

Menaspidae

Listracanthus

Listracanthus hystrix Newberry and Worthen, 1870

Referred specimens -- SDSM 26057, 1 spine;
SDSM 26058, 1 spine with 4 *Petrodus* dermal denticles.

Description

There are only two *Listracanthus* spines collected from the site. Both were in the green shale layer of *Petrodus* II, indicating a possible environment of zero currents, since such delicate structures could not have survived very much transport.

The specimen (SDSM 25057) in Figure 4 is 27 mm long, 9 mm wide, and about 1 mm thick. The badly damaged spine appears to have 16 parallel ribs running the length of the specimen. A number of platform-type conodonts, probably *Idiognathodus*, are associated with the spine.

The other spine (SDSM 26058) was found in association with a large number of conodonts, as well as four *Petrodus* denticles. Nineteen ribs terminate in a thin, flat base which probably provided attachment to the skin. This specimen is 1 mm in thickness, 15 mm long and 8 mm wide at the base.

Discussion

Newberry and Worthen described *Listracanthus hystrix* in 1870, and Woodward (1903) described a new species, *L. wardi*. The Woodward specimen consisted of a nodule containing at least 70 spines scattered irregularly, with a few intermingled denticles. The base of the spines was about one-fifth of the height, and the number of ridges at the base were 12 to 14.

Chorn and Reavis (1978) described a mat of *Listracanthus* spines from Kansas, with the measurements of the spines being 36 to 76 mm long, and having 8 to 11 ridges.

Both *Listracanthus* and *Petrodus* are relatively common in the Carboniferous black shales of Europe and the central United States. At many places, they are the only vertebrate remains present. Although one genus may be reported from an area that the other genus is not, the lack of one generally means the lack of the other.

Considering the size, shape, and rather frail structure of *Listracanthus*, Zangerl and Richardson (1963) believed that the

chondrichthyan bearing these spines was of a small size. They also believe that *Petrodus* was a large animal carrying a large number of denticles. If the Chorn and Reavis (1978) specimen is interpreted as a piece of shagreen, then the animal in question was of large size, and had both *Listracanthus* spines and *Petrodus* denticles.

It has been suggested, first by Bradley (1870), that the remains *Listracanthus* and *Petrodus* may represent the same animal. Woodward (1903) even classified some of the denticles as that of *Listracanthus*, and not *Petrodus*. However, Zangerl and Richardson (1963) seemed to rule out the relationship, based on the correlation between the vertical distribution of the two genera at the Mecca Quarry. The fact that Chorn and Reavis (1978) described a shagreen of both *Listracanthus* and *Petrodus* in close association should not be overlooked. However, in another find, a large concentration of *Petrodus* was discovered in the Fayetteville Shale of Arkansas, with no *Listracanthus* in association with it (Zangerl, 1981).

At Little Elk Creek, only one case of a *Listracanthus* spine and a *Petrodus* denticle appearing on the same specimen was found, so a case for either side of the argument cannot be made.

The issue of size of the animal(s) in question can also be determined by the study of gastric residues. The West Montezuma site (Zangerl and Richardson, p.196-197, 1963) produced an example of an "ill-packed gastric residue from a predator of enormous size" containing both *Listracanthus* spines and *Petrodus* denticles. At the Mecca Quarry, no definite signs of *Petrodus* were found in gastric residues. Chorn and Reavis (1978) argued that the occurrence of both *Listracanthus* and *Petrodus* in a gastric residue suggest that both remains are of a single animal. The fact that a limited number of these remains were found and only a limited number of gastric residues were found, indicates that the animal (if indeed *Listracanthus* and *Petrodus* represent the same animal) was of a medium to large size and was infrequently preyed upon.

An unidentified denticle is associated with the Kansas *Listracanthus* and *Petrodus* remains (Chorn and Reavis, 1978). The author of this paper tentatively identifies the denticle as that of *Multidentodus gracilis*.

Patterson (1965) believed that *Listracanthus* should be used as a synonym for *Deltoptychius*. He concludes this upon describing the type specimen *D. armigerus* and noting *Listracanthus*-like spines and *Petrodus*-like dermal denticles on the head and body. Carroll (1988) favors the name *Deltoptychius*.

OCCURRENCE OF CONODONTS IN THE MINNELUSA FORMATION

During the washing and screening of the *Petrodus*-bearing shale samples, a large number of conodonts were recovered from the *Petrodus* II bed. No conodonts were found in the *Petrodus* I layer. The dominant types that were collected were *Idiognathodus magnificus* and *I. claviformis*. These conodonts provide an excellent means of determining the age of the Little Elk Creek site fauna.

According to one study, "Although the genus *Idiognathodus* ranges from basal Pennsylvanian to the base of the Permian, the species noted are strikingly similar to those of the Des Moines and Missouri series. . . . The presence of *Idiognathodus magnificus*, *Idiognathodus* aff. *I. claviformis*, and *Idiognathodus* aff. *I. acutus* 20 feet below the suggested Pennsylvanian-Permian boundary would suggest a Des Moines-Missouri age for these beds" (Jennings, 1959, p. 989).

No *Gondolella* forms were recognized at Little Elk Creek. Based on the presence of *I. magnificus* and *I. claviformis*, the age of the *Petrodus* II bed is determined to be Desmoinesian to Missourian.

THE PALEOECOLOGY OF PETRODUS AND LISTRACANTHUS

At Little Elk Creek, it is believed that the *Petrodus*-bearing shales represent a lagoon environment. The shale layers containing *Listracanthus* and *Petrodus* are also in close proximity to tidal mudflat facies. This would be expected if the environment were indeed that of a lagoon. The green shale that is present in the *Petrodus* II bed is typical of a reducing-type environment. The fact that some specimens have a large amount of reduced iron in contact with them may be important in proving the timing in which the reduction took place. The presence of thin, frail dermal spines must have meant that low-energy currents, or the complete lack of current, preserved the delicate *Listracanthus* remains. There is also no reason not to believe that the conodonts lived in the area at a time in which the sea was deeper. With the above information taken together, it is believed that the lagoonal interpretation is the most likely possibility.

Zangerl and Richardson (1963), Ford (1964), and Branson (1965) discussed the probable environment in which *Petrodus* and *Listracanthus* lived. All of the studies conclude that a near-shore, shallow water marine environment existed, with either low-energy or the complete absence of currents. The presence of delicate and fragile spines such as *Listracanthus*, according to Zangerl and Richardson (1963), indicate that the currents were relatively calm. Giles (1963) believed that the *Petrodus*-bearing beds of the Francis Formation of Oklahoma were of a shallow-water marine environment also.

During a period of higher sea level, the denticles of a deceased animal would have fallen to the bottom and would have been worked by the higher energy currents. This accounts for the lag deposit thought to be present at the base of the *Petrodus* II bed and the lack of *Listracanthus* in the black shale. The possibility of the denticles being washed in from another area does not appear to be likely because the majority of the specimens do not show the wear that would be expected in such a case.

SUMMARY

The occurrence of the chondrichthyians *Listracanthus* and *Petrodus* represent the first vertebrate remains found in the Minnelusa Formation of South Dakota. Along with spines and denticles, tooth fragments of *Cladodus* and a complete tooth of what may be *Cranodus* were found at Little Elk Creek Canyon. The question of the possible relationship between *Listracanthus* and *Petrodus* remains unanswered, however.

It is believed that the shale layer *Petrodus* II represents a lagoon environment, based on evidence of reducing conditions, a low-energy environment, and the association with other environments seen in the section.

Conodonts were also found at the site, with the Desmoinesian to Missourian *Idiognathodus* being the dominant genus found. Therefore, it is believed that the vast majority of the chondrichthyian remains are of the same age as the conodonts.

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