A Case Study in Paleoecology From the Mississippian of Missouri, With a Focus on Chondrichthyan Teeth

Lisa B. Whitenack
Department of Geology, University of Illinois at Urbana-Champaign, Urbana, IL 61801
(Current address: Department of Biology, University of South Florida, Tampa, FL 33620)

Dana R. Elliot
Department of Biology, Central Methodist College, Fayette, MO 65248

J.P. Brandenburg
Department of Geological Sciences, Michigan State University, East Lansing, MI 48825

Abstract: A suite of fossils collected from the Warsaw Formation (Mississippian) of Missouri includes brachiopods, bryozoans, cnidarians, poriferans, echinoderms, and chondrichthyan teeth. The chondrichthyan fauna includes *Helodus*, *Leiodus*, *Orodus*, *Chomatodus*, *Polyrhizodus*, Xenacanthidae, and Cochliodontidae. Specimens of a questionable nature were also recovered, including several teeth belonging to the form taxon '*Cladodus*' and an unknown tooth. The Warsaw fauna is usually described as a typical Mississippian suspension-feeder benthic community; adding the chondrichthyan fauna provides a more comprehensive picture of the nektonic component of this ecosystem.

Key Words: Chondrichthyes, Warsaw, Mississippian, paleoecology

Introduction

Considerable attention has been paid to the geology and fossil invertebrates of the Mississippian strata of Missouri (e.g. Miller and Collinson, 1951; Spreng and Howe, 1963; Hays, J.B., 1964; Thompson and Fellows, 1969; McKay and Fraunfelter, 1982; Brezinski, D.K., 1986; King, 1986; Thompson, 1986; Carter, 1988; Work et al., 1988; Ausich and Kammer, 1990; Blake and Elliott, in press). However, the vertebrate fauna has been largely ignored. Much of the chondrichthyan material consists of isolated teeth and spines, due to the poor preservation potential of a cartilage. Fragmentary preservation and heterodonty makes identification difficult, but the rich diversity and ecological significance of chondrichthyan fossils makes their study worthy of a greater effort. The present work demonstrates that many of these isolated teeth can be readily identified and included in paleoecological analyses.

Geological Setting

Fossils were collected from surface debris along the Missouri River near Lisbon, Missouri (Howard County, Glassgow, quadrangle, T50N, R18W, Sec. 35). The Mississippian Keokuk and Warsaw Formations are composed mostly of gray fossiliferous limestones interbedded with gray shale and white to gray chert (Thompson, 1986). The boundary between these two sites, both lithographically and biologically, is unclear and has been discussed in a number of papers (Kammer et al., 1989, 1990; Hirt, 1991). Though the locality that the fossils were collected from was previously described as part of the Keokuk Formation (Spreng and Howe, 1963), the presence of *Pentremites conoideus* indicates that this locality is the Warsaw Formation (Waters et al., 1985). Currently, the lithology of the Keokuk and Warsaw Formations is being reexamined (pers. communication, B. Witzke, 1999), and hopefully those studies will yield data that will further support the identification of this locality.

Invertebrate Fauna

The invertebrate fauna is extremely rich and abundant and reflects a typical benthic suspension-feeding community (Table 1). The phylum Porifera is represented solely by disarticuled spicules scattered throughout the rock. Both rugose and tabulate corals (Cnidaria) are present. The Echinodermata are represented by a number of groups: Crinoidea, represented by articulated calyxes and disarticulated columnals and brachials; Blastoidea, represented by columnals and calyxes, especially those of *Pentremites conoideus*; Echinoidea, represented by disarticulated interambulacral plates as well as several largely intact specimens; and Asteroidea, represented by one nearly complete specimen, as well as disarticulated dorsal plates from the same species.

Two identifiable orders of Brachiopoda are present: Spiriferida and Rhynchonellida. From these, two genera from each order could be identified: *Athyris* and *Spirifer*, and *Camartoechia* and *Rynchonella*. The brachiopods showed the most distortion of all

Table 1.

Survey of individuals (N=242)

	Number of Individuals	Percentage of Total Fauna
Brachiopoda	93	38.430
Rugosa	94	38.843
Blastoidea	29	11.983
Crinoidea	25	10.331
Gastropoda	1	0.413

the invertebrate specimens. A number of the *Athyris* specimens were compressed dorso-ventrally, the *Spirifer* specimens were fragmentary, and the rynchonellids were compressed and appeared to be rolled into a ball. For this reason, identification to the species level could not be made.

The most readily identified and most abundant invertebrate fossils are those of the Bryozoa. Bryozoans occurred either as fragmented pieces or as encrusters on other organisms. Three orders were identified: Fenestrata, Cystoporata, and Treptostomata. The fenestrates are the most diverse and abundant, including *Fenestella*, *Ptylopora*, *Hemitrypa*, *Archimedes*, and *Polypora*. The cystoporates include *Actinotrypoa*, *Meekopora*, and *Dichotrypa*; the treptostomes are represented by *Leioclima* and *Tabulopora*.

Vertebrate Fauna

The vertebrate fauna, while almost entirely chondrichthyan, is still very diverse. All specimens are single teeth found disassociated from the jaw. The Chondrichthyes are represented by two subclasses: Holocephali and Elasmobranchii. The holocephalans from this suite include *Helodus* (Heliodontidae), *Chitonodus* (Chochliodontidae), and two flat tooth plates that are likely chochliodonts (Figure 1). The elasmobranchs include *Chomatodus* (Petalodontidae), *Polyrhizodus* (Petalodontidae), *Orodus* (Orodontidae), *Leiodus* (Orodontidae), and a xenacanth tooth (Xenacanthidae) (Figure 2).

There are several specimens of questionable nature. One is a single tooth that measures approximately 3.5 mm along the cusp (Figure 3). It is unlikely that it is chondrichthyan, for it appears to be composed of a different material and has a morphology that is not like typical Paleozoic chondrichthyan teeth. The other questionable specimens belong to the form taxon '*Cladodus*' (Figure 4). Teeth assigned to this form taxon generally have one large median cusp and several small accessory cusps on a wide flat base (Zangerl, 1981). Because these teeth were found disassociated from the jaw, a more specific identification cannot be made.

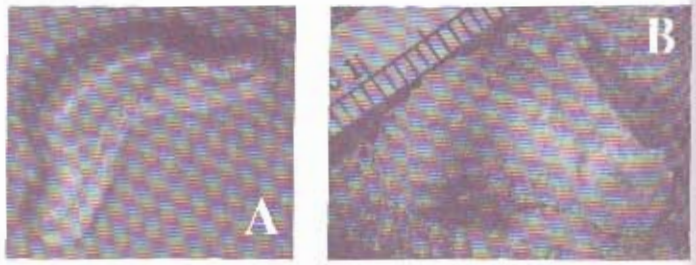

Figure 1. Holocephalii specimens- (A) *Helodus* (B) *Chitonodus*

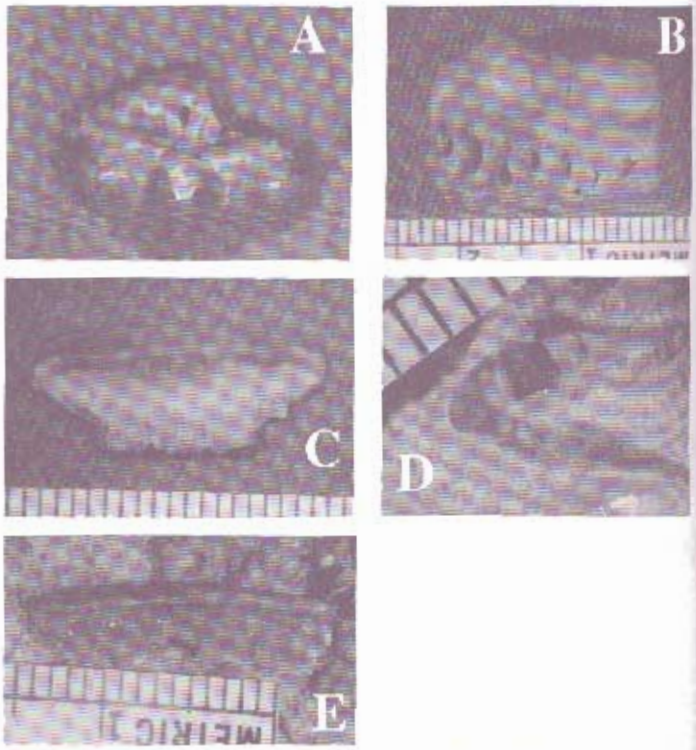

Figure 2. Elasmobranchii specimens- (A) *Leiodus* (B) *Orodus* (C) *Polyrhizodus* (D) Xenicanthidae (E) *Chomatodus*

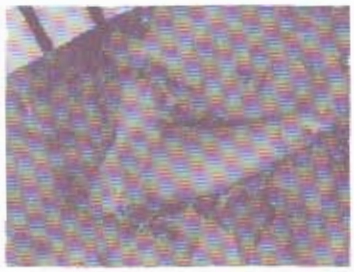

Figure 3. Unknown tooth

Figure 4. An example of '*Cladodus*'

Paleoecology

The environment these benthic invertebrates lived in was probably one of low energy currents. The fact that fenestrate bryozoans were present, for example, indicates that the energy of the currents must have been somewhat low, for many fenestrates are delicate and would be destroyed in high-energy currents. Many of the blastoid and crinoid stems are extremely thin and may not have been able to withstand high-energy currents. The presence of low energy currents in turn implies that these organisms were most likely well below wave base or in a fairly quiet shallow area. The lack of abrasion of the specimens suggests little reworking.

The flattened and fractured condition of many of the brachiopods seems to contradict this assessment. However, it is possible that the chondrichthyan fauna may be responsible. Some modern chondrichthyans with molariform or pavement-like dentitions, such as horn sharks (Heterdontiformes), bonnethead sharks (*Sphyrna tiburo*), some rays (Mylobatidae), and chimeras (Holocephali), are durophageous (Dean, 1906; Smith, 1942; Cappetta, 1987; Wilga and Motta, 2000). Similar molariform dental morphologies are found in members of the chondrichthyan fauna in this study (*Helodus, Chitonodus, Leiodus, Orodus, Polyrhizodus, Chomatodus*). There is also fossil evidence for chondrichthyan predation on brachiopods. Brachiopod fragments have been found in preserved stomach contents of *Janassa* (Petalodontidae) and *Fadenia* (Caseodontidae) (Moy-Thomas and Miles, 1971). Other authors have also suggested chondrichthyans as predators on brachiopods (Alexander, 1981; Vermeij, 1983).

Conclusion

The presence of the chondrichthyan ichthyoliths gives a better picture of what the environment of the site was during the Mississippian. When solely looking at the invertebrate fauna, only a picture of the benthic portion of the water column was obtained. By studying the chondrichthyan fauna, the nektonic community can be added to the overall picture. Predation by durophageous chondrichthyans explains the dorsoventral flattening of brachiopod shells in an environment with low energy currents. Difficulty in identifying specimens should not discourage paleoecologists from using these specimens in their analysis.

Acknowledgements

We would like to thank Daniel Blake, Brian Witzke, Robert Anstey, Danita Brandt, and Michael Gottfried for all of their help, support, and encouragement during this project.

References

Alexander, R.R., 1981. Predation scars preserved in Chesterian brachiopods: probable culprits and evolutionary consequences for the articulates. *Journal of Paleontology*. 55(1): 192-203.

Ausich, W.I. and Kammer, T.W., 1990. Systematics and phylogeny of the Late Osagean and Meramecian crinoids *Platycrinites* and *Eucladocrinus* from the Mississippian stratotype region. *Journal of Paleontology*. 64(5): 759-778.

Blake, D.B. and Elliott, D.R. in press, 2003. Ossicular homologies, systematics, and phylogenetic implications of certain North American Carboniferous asteroids (Echinodermata). *Journal ofPaleontology*.

Brezinski, D.K., 1986. Trilobites from the Keokuk Limestone (Mississippian) of Missouri. *Annals of Carnegie Museum*. 55(8): 138-143.

Cappetta, H., 1987. *Chodrichthyes II. Mesozoic and Cenozoic Elasmobranchii*. New York: Gustav Fischer Verlag. 193 p.

Carter, J.L., 1988. Early Mississippian brachiopods from the Glen Park Formation of Illinois and Missouri. *Bulletin of Carnegie Museum of Natural History*. 27: 82 p.

Dean, B., 1906. *Chimaeroid Fishes and Their Development*. Washington: Carnegie Institution.

Hayes, J.B., 1964. Geodes and concretions from the Mississippian Warsaw Formation, Keokuk region, Iowa, Illinois, Missouri. *Journal of Sedimentary Petrology*. 34(1): 123-133.

Hirt, D.S., 1991. Mississippian brachiopod biostratigraphy and the Osagean-Meramecian boundary in south-sentral Indiana. *Journal of Paleontology*. 65(6): 912-916.

Kammer, T.W.; Ausich, W.I. and Carter, J.L., 1989. Biostratigraphy of the Osagean-Meramecian boundary in the Mississippian stratotype region. *Geological Society of America Abstracts with Programs*. 21(6): 132.

Kammer, T.W.; Brenckle, P.L.; Carter, J.L.; Ausich, W.I., 1990. Redefinition of the Osagean-Meramecian boundary in the Mississippian stratotype region. *Palaios*. 5(5): 414-431.

King, D.T., 1986. Waulsortian-type buildups and resedimented (carbonate-turbidite) facies, Early Mississippian Burlington Shelf, central Missouri. *Journal of Sedimentary Petrology*. 56(4): 471-479.

McKay, R.H. and Fraunfelter, G., 1982. Trace fossils and environments of deposition of the Aux Vases Formation and the Joppa Member of the Ste. Genevieve Formation (Middle Mississippian) in southeastern Missouri and southern Illinois. *Transactions of the Missouri Academy of Science*. 16: 167 p.

Miller, A.K. and Collinson, C.W., 1951. Lower Mississippian ammonoids of Missouri. *Journal of Paleontology*. 37(4): 454-487.

Moy-Thomas, J.A. and Miles, R.S., 1971. *Paleozoic Fishes*. Philadelphia: W.B. Saunders Co. 259 p.

Smith, B.G., 1942. The heterodontid sharks: their natural history and the external development of *Heterodontus japonicus* based on notes and drawings of Bashford Dean. The Bashford Dean Memorial Volume: Archaic Fishes.

American Museum of Natural History. 8: 649-770.

Spreng, A.C.; Howe, W.B., 1963. Echinoid jaws from the Mississippian and Pennsylvanian of Missouri. *Journal of Paleontology*. 37(4): 931-938.

Thompson, T.L., 1986. Paleozoic Succession in Missouri. Part 4: Mississippian System. *Missouri Geological Survey Report of Investigations*. 70: 189 p.

Thompson, T.L. and Fellows, L.D., 1969. Stratigraphy and condont biostratigraphy of Kinderhookian and Osagean (lower Mississippian) rocks of southwestern Missouri and adjacent areas. *Missouri Geological Survey Report of Investigations*. 45: 263 p.

Van Tuyl, F.M., 1922. The Stratigraphy of the Mississippian Formations of Iowa. *Iowa Geological Survey Annual Reports*. 30: 33-349

Vermeij, G.J., 1983. Shell-breaking predation through time. In: Tevesz, M.J.S. and McCall, P.L. (eds.) *Biotic interactions in recent and fossil benthic communities*. New York: Plenum Press. pp. 649-669.

Waters, J.A.; Horowitz, A.S. and Marcuda, D.B., 1985. Ontogeny and phylogeny of the Carboniferous blastoid *Pentremites*. *Journal of Paleontology*. 59(3): 701-712.

Wilga, C.D. and Motta, P.J., 2000. Durophagy in sharks: feeding mechanics of the hammerhead *Sphyrna tiburo*. *Journal of Experimental Biology*. 203: 2781-2796.

Work, D.M.; Maples, R.H. and Thompson, T.L., 1988. A new prodromitid ammonoid genus from the Hannibal Shale (Lower Mississippian) of Missouri. *Journal of Paleontology*. 62(5): 772-778.

Zangerl, R., 1981. *Chondrichthyes I. Paleozoic Elasmobrachii*. New York: Gustav Fischer Verlag. 115 p.