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PALEOECOLOGICAL NOTES ON THE FAUNA OF THE SHUMWAY LIMESTONE (MATTOON FORMATION, UPPER PENNSYLVANIAN) OF ILLINOIS

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Abstract: The fauna of the Shumway limestone including 21 brachiopod species, 20 pelecypod species, 14 gastropod species, 1 scaphopod species, 16 cephalopod species, 2 cnidarians, a trilobite, crinoid columnals, unidentified bryozoans and fragments of vertebrates is listed. Vertical preservation of nautiloids suggest that water depth was less than 10 m while the presence of 21 genera of brachiopods would suggest a depth greater than 20 m. The use of brachiopod diversity which may be related to environmental complexity as well as depth is not wise unless some independent means of confirmation is used. The contained fauna of the unit suggests that the depositional environment was shallow, quiet water over a limey mud bottom that supported a growth of submerged plants.

INTRODUCTION

Community analysis of Paleozoic marine faunas has been approached from two conceptual frameworks. Johnson (1960, 1962, 1964) defined communities on the basis of mutually associated species. Johnson (1962) showed that 19 groups of mutually associated species exist based on analysis of 152 fossil collections (see Wanless, 1958) from the Middle Pennsylvanian of western Illinois. These groups could be further grouped into three basic associations which were significantly correlated with particular lithologies as follows: the Chonetina association (upper limestones-calcareous shales), the Gastropod association (calcareous shales-upper limestones) and the Orbiculoidea association (black fissile shales). Watkins (1974) and Gilliam and Schram (1975) describe and name other Pennsylvanian associations. Gilliam and Schram's (1975) Kozlowskia-Neospirifer community is an unnecessary name since it is identical in nearly all respects to Johnson's (1962) Group I, a part of the Chonetina association. Watkins' (1974) associations are less directly comparable to Johnson's since the methods of analysis differed, the time span studied differed and faunal differences exist between Pacific and Mid-Continent sites.

Another significant method of community analysis is based on trophic level analysis (Turpaeva, 1953). Several workers (Walker and Laporte, 1970; Rhoads et al., 1972; Walker, 1972; Walker and Bambach, 1974 among

others) have modified Turpaeva's (1953) methods and applied them to fossil marine benthic communities. Studies of this nature not only point out that associations of species exist but also attempt to interpret ecological interactions of individual members of the fauna and evolutionary dynamics of marine benthic communities.

This paper presents a faunal list from the Shumway limestone. Paleoecological inferences are based on this fauna. Evidence that the use of brachiopod diversity as an estimate of depth may not be completely reliable is presented.

MATERIAL AND METHODS

Samples of megafossils were collected for identification. Collections were made over a period of 12 years. Specimens are in the private collection of the author and in the Field Museum of Natural History, Chicago (mostly nautiloids). Identifications are based on literature and comparisons with specimens in the collections of Illinois State University and the Wanless collections at the Illinois Geological Survey. Comparisons to other faunas are based on the species level where possible and the generic level in some cases. In all cases generic level taxonomy follows that given in appropriate sections of the Treatise on Invertebrate Paleontology (R. C. Moore, ed.). The Shumway limestone is a very hard micritic limestone that makes quantitative sampling very difficult. Consequently relative abundances are subjectively measured based on 12 years of experience with the fauna. Abundant species (A) are those that are likely to be found in nearly any piece of limestone that has a surface area of 20 square inches. Common species (C) are those that may be collected on every visit to the unit. Rare species (R) are those that are seldom encountered. Species represented by only one specimen are recorded as unique (U). Although microfossils are present, they are not considered in this report.

Johnson (1962) pointed out that random sampling to determine relative abundances of taxa may not be adequate for paleoecological studies. Rare species which may be important ecological indicators may be overlooked. Sight collecting while possibly providing a more complete sample of the fauna does not give an objective measure of the relative abundance of various members of the fauna. Sight collections may also reflect the individual biases of the collector. Collections from the Shumway limestone that this report is based on are biased in that the collection of nautiloid cephalopods is a primary objective of the author's studies. But since the nautiloid fauna is not used for any ecological inferences except for water depth, the effect should be unimportant.

STRATIGRAPHY

The Shumway limestone which is part of the Shumway Cyclothem of the Mattoon formation is made up of a lower bed and upper bed. The contact between them is relatively distinct and they are lithologically distinctive as well. The lower bed is a fine grained almost lithographic micritic limestone that when fresh is very hard. The upper bed is much more argillaceous and is very slightly bedded. All collections reported here are from the lower bed of the Shumway limestone. Kosanke et al. (1960) described the stratigraphic section containing the Shumway Cyclo-

them at the type locality which is the collecting site for the species reported here. It is located 2 mi E of Shumway, Effingham Co., Ill. (SE ¼, SE ¼, SW ¼ sec. 26, T9N, R5E, Effingham Quadrangle). The marine portion of the cyclothem closely approaches the ideal cyclothem of Weller (1957). Bed 9 of the ideal cyclothem corresponds to the lower bed of the Shumway limestone. Correlations within the Mattoon formation are unsure (Kosanke et al., 1960) but the Shumway limestone is considered to be uppermost Missourian or lowermost Virgilian and roughly correlates with the Lawrence shale or the Iatan limestone of the Mid-Continent (Kosanke et al., 1960). Occurrence of the fusulinid genus Triticites (Weller et al., 1942) supports these correlations.

THE FAUNA

The megafossils collected from the Shumway limestone are listed in Table 1. Interpretations of the life habits of Shumway limestone pelecypods and gastropods follow Kauffman (1969) and Knight et al. (1960) where possible.

DISCUSSION

Certain aspects of the fauna strongly suggest that plants were an important part of the environment. The gastropod fauna contains Euphemites, Pharkidonotus and Glabrocingulum which were almost certainly herbivorous (Knight et al., 1960). The other Archeogastropoda and Mesogastropoda may also have been herbivorous. Smaller pedunculate brachiopods (Table 1) are much more common than the larger pedunculates (Table 1). The pelecypod fauna parallels this in that smaller byssate species (Table 1) are much more common than larger byssate species (Table 1). Pteronites sp. is an exception to this as it is moderately common. However, unlike other byssate species Pteronites was probably partially infaunal (Kauffman, 1969). The relative rarity of larger byssate pelecypods and larger pedunculate brachiopods as compared to smaller species of each group suggests that suitable substrates for attachment for the larger species was rare. Rhoads et al. (1972) and Kauffman (1969) suggested that smaller byssate pelecypods may use vegetation for attachment sites. Johnson (1962) suggested that a high incidence of gastropods in association with an infauna indicates the presence of plants on a soft substrate.

If the Shumway limestone was deposited at a site of moderately heavy although possibly patchy plant growth on a relatively soft substrate then certain features of the fauna are explicable. Plants may have been strong enough to support smaller pedunculate brachiopods and byssate pelecypods but too weak to support larger pelecypods and brachiopods. Pelecypods which utilize a relatively uncoordinated swimming reaction to escape predators could be hampered by vegetation and their rarity may thus be correlated with plant growth. While plants could conceivably interfere with swimming pelecypods which are relatively uncoordinated, there is no reason to believe that it would disturb nautiloid cephalopods which utilize strong coordinated swimming movements. Cephalopods would also have the water column above any plants or bare patches between plants available to them.

Johnson (1962) noted that lophophyllid corals and Crurithyris are

TABLE 1. Feeding category, life site, abundance (Ab) and group number (Johnson, 1962) of faunal elements of the Shumway limestone.

Identity	Feeding category	Life site	Ab	Group	Remarks
Brachiopoda					
Cancrinella boonensis (Swallow)	suspension	epifaunal	C	-	productid
Neochonetes granulifer (Owen)	suspension	epifaunal	A	I	productid
Linoproductus prattenianus Dunbar & Condra	suspension	epifaunal	C	VIII	productid
Reticulatia huecoensis (King)	suspension	epifaunal	C	I	productid
Echinaria sp.	suspension	epifaunal	C	I	productid
Retaria lasallensis (McChesney)	suspension	epifaunal	A	I	productid
Juresania symmetrica (McChesney)	suspension	epifaunal	R	IX	productid
Kozlowskia splendens (Norwood & Pratten)	suspension	epifaunal	A	I	productid
Lissochonetes geinitzianus (Waagen)	suspension	epifaunal	A	XIV	productid
Derbyia crassa (Meek & Hayden)	suspension	epifaunal	C	I	free lying
Derbyoides nebrascensis Dunbar & Condra	suspension	epifaunal	C	-	free lying
Punctospirifer kentuckyensis (Shumard)	suspension	epifaunal	C	I	free lying-pedunculate
Neospirifer triplicatus (Hall)	suspension	epifaunal	C	I	free lying-pedunculate
Composita subtilita (Hall)	suspension	epifaunal	R	I	large pedunculate
Enteletes hemiplicatus (Hall)	suspension	epifaunal	R	-	large pedunculate
Cleiothyridina atrypoides (Girty)	suspension	epifaunal	C	I	small pedunculate
Phricodothyris perplexa (McChesney)	suspension	epifaunal	R	VII	small pedunculate
Wellerella osagensis (Swallow)	suspension	epifaunal	C	IX	small pedunculate
Rhipidomella carbonaria (Swallow)	suspension	epifaunal	C	-	small pedunculate
Hustedia marmoni (Marcou)	suspension	epifaunal	C	II	small pedunculate
Pelecypoda					
Wilkingia costatum (Meek & Worthen)	deposit	infaunal	C	XIV	
Palaeoneilo taffiana (Girty)	deposit	infaunal	C	-	
Nuculopsis girtyi Schenck	deposit	infaunal	C	II	
Astartella compacta Girty	suspension	epifaunal	C	II	free lying?
Placunopsis carbonaria	suspension	epifaunal	R	-	byssate?
Monopteria longa (Geinitz)	suspension	epifaunal	R	-	byssate
Edmondia ovata Meek & Worthen	deposit	infaunal	R	-	

TABLE 1 continued.

Identity	Feeding category	Life site	Ab	Group	Remarks
Palaeolima retifer (Shumard)	suspension	epifaunal	C	III	small byssate
P. equistriata (Boebe)	suspension	epifaunal	C	III	small byssate
Fasciculiconcha knighti Newell	suspension	epifaunal	R	-	large swimmer or byssate
Phestia bellistriatus (Stevens)	deposit	infaunal	R	XIII	
Parallelodon sangamonensis (Worthen)	suspension	epifaunal	R	XV	large byssate
P. obsoletus (Meek)	suspension	epifaunal	R	XV	large byssate
Schizodus sp.	suspension	epifaunal ?	R	-	byssate ?
Solemya trapezoides Meek	deposit	infaunal	R	III	
Volsellina subelliptica (Meek)	suspension	epifaunal	C	-	small byssate
Acanthopecten carboniferus (Stevens)	suspension	epifaunal	U	-	swimmer or byssate
Pteronites sp.	suspension	infaunal	C	-	byssate ?
Pernopecten ohioensis (Newell)	suspension	epifaunal	R	VIII	swimmer ?
Modiomorpha sp.	suspension	epifaunal	C	-	byssate
Gastropoda					
Euphemites carbonarius (Cox)	browser	epifaunal	R	II	
Glabrocingulum grayvillense (Worthen & Pratten)	browser	epifaunal	C	II	
Pharkidonotus percarinatus (Conrad)	browser	epifaunal	C	II	
Straparolus subquadratus Meek & Worthen	browser	epifaunal	C	XVI	
Trepospira depressa (Cox)	browser	epifaunal	R	VI	
Worthenia tabulata (Conrad)	browser	epifaunal	C	-	
Bellerophon stevensianus McChesney	browser	epifaunal	R	-	
Shansiella sp.	browser	epifaunal	R	-	
Lepetopsis sp.	suspension	epifaunal	U	-	
Ianthinopsis brevis (White)	? predator	epifaunal	R	II	
I. paludinaeformis (Hall)	? predator	epifaunal	C	II	
I. primogenius (Conrad)	? predator	epifaunal	C	II	
Meekospira sp.	? predator	epifaunal	R	VI	
Stephanozyga sp.	? predator	epifaunal	R	-	

TABLE 1 continued.

Identity	Feeding category	Life site	Ab	Group	Remarks
Scaphopoda					
Prodentalium sp.	suspension	infaunal	U	XII	
Cephalopoda					
Mooreoceras sp.	predator	nektobenthos	C	-	
Brachycycloceras dilatatum (Meek & Worthen)	predator	nektobenthos	R	-	
B. normale Miller, Dunbar & Condra	predator	nektobenthos	R	-	
Tainoceras monilifer Miller, Dunbar & Condra	predator	nektobenthos	C	-	vertically entombed
T. sexlineatum Tucker	predator	nektobenthos	R	-	
Cooperoceras sp.	predator	nektobenthos	U	-	
Metacoceras copei Tucker	predator	nektobenthos	C	IX	vertically entombed
M. mochesneyi Murphy	predator	nektobenthos	U	IX	
Domatoceras wortheni Tucker	predator	nektobenthos	C	-	vertically entombed
D. mattoonensis Tucker	predator	nektobenthos	R	-	vertically entombed
Stearoceras involutum Tucker	predator	nektobenthos	U	-	
Solenochilus shumwayense Tucker	predator	nektobenthos	C	-	vertically entombed
Liroceras liratum (Girty)	predator	nektobenthos	C	-	vertically entombed
Ephippioceras moinellae Tucker	predator	nektobenthos	R	-	vertically entombed
Goniloboceras sp.	? predator	nektobenthos	R	-	
Eosasinites sp.	? predator	nektobenthos	R	-	
Other fossils					
Echinodermata-crinoid columnals	suspension	epifaunal	R	I	
Cnidaria					
Lophophyllidium proliferum (McChesney)	predator	epifaunal	R	XII	
Paraconularia sp.	? predator	epifaunal	R	-	
Bryozoa					
encrusting form or forms	suspension	epifaunal	R	-	
upright ramose form or forms	suspension	epifaunal	R	-	
Arthropoda-Ameura sp.	deposit	epifaunal	R	-	
Annelida-Serpulopsis sp.	suspension	epifaunal	A	XVII	

Rare vertebrate teeth fragments (chondrichthine) and rare stems and logs of woody plants present as well.

negatively correlated. He suggested that this may reflect different substrate prferences. At Shumway, lophophyllids are rare while Crurithyris is a common fossil. It may be that lophophyllids are not successful in areas with abundant plant growth. Vegetation could cause sediments to settle out of suspension by slowing water movements. Heavier sedimentation may be detrimental to corals, bryozoans and crinoids whose feeding structures are exposed than for brachiopods whose lophophore is enclosed by the shell. The rarity of crinoids, bryozoans and corals may also be due to the soft substratum which is indicated by the common productid brachiopods and the number of infaunal pelecypods.

The high diversity of brachiopods (21 genera) should indicate a water depth of greater than 20 m (Stevens, 1971). However, specimens of seven species of coiled nautiloids have been found vertically entombed with the venter of the living chamber oriented toward the substrate. Vertical preservation of coiled cephalopods may be taken as evidence that water depth was less than 10 m (Raup, 1973; Weaver and Chamberlain, 1976) if the cephalopod is reasonably similar morphologically to Nautilus pompilius and if the vertical orientation cannot be attributed to secondary disturbance. E. moinellae and L. liratum are reasonably similar to N. pompilius in gross shape. Neither of these species have flat venters or spines that could act as stabilizing platforms even after the phragmocone filled. There is no evidence that any of the vertically preserved nautiloids were secondarily disturbed. While it is possible that a nautiloid sinking into plants could be kept from falling over by surrounding vegetation, two things suggest that this is unlikely. If plants were not able to support larger byssate pelecypods and pedunculate brachiopods, it seems unlikely that they would be able to support even larger nautiloids. More importantly Weaver and Chamberlain (1976) showed that beyond a depth of 7 m, rapidly filling Nautilus shells sink in a horizontal orientation. Slowly filling shells may sink vertically oriented for depths as great as 600 m but will fall over within one to two days after settling due to fillage. Consequently vertical preservation should be rare beyond a depth of 10 m (Weaver and Chamberlain, 1976).

The disagreement between depth inferences based on cephalopod preservation and brachiopod diversity could be an artifact if the fauna preseved in the Shumway limestone was carried there after death. This seems unlikely for several reasons. Many of the productid brachiopods have well preserved spines. Few of the fossils show any signs of wear and benthic organisms are commonly found complete and unbroken. Only rarely are disarticulated brachiopods found. It is also possible to correlate the life habits of the pelecypods with their mode of preservation. Infaunal pelecypods are found with the valves articulated and generally closed. Epifaunal pelecypods are usually found as disarticulated valves though in smaller byssate species the valves are often found articulated but opened or disarticulated and lying near each other. Pteronites which is shallowly infaunal are usually found disarticulated but with the valves lying near each other. Micritic limestones usually form in areas where current transport is limited (Laporte, 1968). Valentine (1961), Johnson (1965) and Warme (1969) have all shown that buried dead shells reflect the organisms living in the area even in some cases where strong currents exist (Warme, 1969). Apparently then, at least the benthic fauna lived at or near the site of collection. No indications of faunal or lithological changes are present within the lower bed of the Shumway limestone which averages less than one foot thick. Consequently it is difficult

to attribute high brachiopod diversity to faunal replacements during the period that the limestone was deposited. Another possibility is that Stevens' (1971) correlation of brachiopod diversity and depth is not completely reliable.

The Shumway limestone appears to have been deposited in a complex environment with both plant growth and patches of bare, fairly soft substrate. More complex environments may provide habitats for species that in less complex environments could not coexist. One indication that this might be the case may be found in the relationship of the Shumway fauna and Johnson's (1962) associations. The Shumway fauna incorporates most elements of both the Chonetina and Gastropod associations. If these associations are correlated with substrate as Johnson (1962) implies, then it is reasonable to expect elements of both associations to be present in areas where both substrates exist. There is no reason to believe that intermediate or mixed habitats should occur at depths greater than the individual habitats. Stevens' (1971) correlation between brachiopod diversity may in some cases be appropriate but application of the hypothesis without some independent means of confirmation is not wise. Brachiopod diversity may be especially misleading where a complex environment is indicated by the pelecypod and gastropod faunas.

Trophic level analysis in the sense of Walker and Laporte (1970) and Walker and Bambach (1974) cannot be performed since no attempt was made to quantify the relative abundance of each taxon. As in other Paleozoic faunas reviewed by Walker and Laporte (1970) and Bretsky (1969) suspension feeders dominate the fauna. Like other open shelf environments (Bretsky, 1969), brachiopods are the most common and diverse suspension feeders.

SUMMARY

The Shumway limestone appears to have been deposited in shallow, quiet water. Plants were apparently an important component of the biota and may have provided attachment sites for smaller byssate pelecypods and pedunculate brachiopods and possibly provided food for certain of the gastropods. The substrate was relatively soft allowing infaunal pelecypods to inhabit the area. Bare spaces between the plants were occupied by productid brachiopods of several genera, free lying brachiopods and occassionally by larger pedunculate brachiopods and byssate pelecypods in areas where the bottom was locally firmer.

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