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ECOLOGY OF AN ORDOVICIAN
DEEPWATER FAUNA

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JOHN L. CISNE

Department of the Geophysical Sciences
The University of Chicago
Chicago, Illinois 60637

ABSTRACT

Beecher's Trilobite Bed in the Frankfort Shale of New York State preserves an exceptional record of the benthic macrofauna of a Late Ordovician deepwater marine environment. It has long been famous for specimens of the trilobites *Triarthrus eatoni* (Hall), *Cryptolithus bellulus* (Ulrich), *Primaspis crosotus* (Locke), and *Cornuproetus beecheri* (Ruedemann), new combination, which preserve the ventral appendages and even traces of the musculature. This fossil assemblage was accumulated when benthic animals and associated detritus were caught up and buried by a turbidity flow. Burial was indirectly the cause of mortality; and this factor, together with the abundance of already decayed organic matter in the sediment, the protection of a thickness of fine sediment, and sedimentary compaction following soon after burial, contributed to the exceptionally fine preservation of these animals in iron pyrite. As a natural census, this assemblage reveals the "preservable" benthic macrofauna as comprised of some 24 species of epifaunal and shallow infaunal organisms, chief among which were deposit-feeding trilobites (2 common species comprising 58 percent of individuals), suspension-feeding dendroid graptolites (3 species; 22 percent) and brachiopods (3 species; 9 percent). Annelids were probably abundant; large, poorly preserved specimens comprise about 6 percent of the sample. As compared with the benthic faunas of similar modern environments in deep basins on the continental borderland off southern California, this Ordovician fauna differs greatly in high-level taxonomic composition but has very much the same level of diversity in "preservable" species.

Introduction

Beecher's Trilobite Bed, a thin microturbidite bed in the Frankfort Shale near Rome, New York, preserves an exceptional record of the benthic fauna of a Late Ordovician deepwater environment. Through the years since its discovery in 1892, it has become famous for specimens of the trilobites *Triarthrus eatoni* (Hall), *Cryptolithus bellulus* (Ulrich), and *Primaspis crosotus* (Locke) which preserve the appendages and musculature. These species have become classic examples of trilobites; and the specimens themselves, so meticulously prepared by Beecher, have become standard references in studies of trilobite morphology. But aside from work on the trilobites, the entire assemblage of exceptionally preserved organisms has to date gone unstudied. The present paper investigates the entire assemblage, interprets its manner of accumulation and preservation, and interprets the ecology of the benthic fauna therein represented. This fossil assemblage takes on importance not only because fossil animals are so well preserved but also because it represents a natural census of a benthic fauna. It thus presents a rare opportunity for making approximate quantitative comparisons with modern faunas in similar types of environment.

The Frankfort Shale is a flysch sequence made up of thin beds of turbidite sand and silt alternating with thin beds of black graptolitic shale. Ruedemann (1925a, b; 1926a, b; 1935), who extensively studied the stratigraphy and paleontology of Ordovician rocks of the Utica Basin, concluded that it was deposited in deep, quiet water in the central portion of an enclosed basin. More recently, deep, enclosed basins on the continental borderland off southern California have been suggested as models for this sort of paleoenvironment (Emery, 1960; Rhoads and Morse, 1971), and for this particular paleoenvironment (Bretsky, 1969, 1970). There are many similarities in the geographic setting and sediments between the respective basins. In the Santa Barbara Basin, the most intensively studied of the modern borderland basins, sediments are comprised of turbidite silt beds alternating with beds of pelagic debris, including biogenic sediment from the plankton that may or may not have been reworked by benthic organisms before its burial (Hülsemann and Emery, 1961; Emery and Hülsemann, 1962). Likewise, in the Frankfurt Shale, thin graptolitic shale beds may or may not show evidence of biogenic reworking; and it is possible that a fluctuating oxygen sill may have determined the presence or absence of a benthic fauna, as in the Santa Barbara Basin (Emery and Hülsemann, 1962).

Beecher's Trilobite Bed was discovered in Cleveland's Glen near Rome, New York, by W. S. Valiant of Rutgers College on September 24, 1892 (Valiant, 1901, and unpublished notes). It was mined out by the summer of 1895 by C. E. Beecher of Yale University (Beecher, unpublished notes; the information that the bed was mined out came to me from C. O. Dunbar through Charles Schuchert from Beecher himself). The photograph in Figure 1 shows the outcrop on September 26, 1892 before it was altered by

FIG. 1. The locality, a photograph taken on 26 September 1892 showing W. S. Valiant ("V.") and his half-brother Sid Mitchill ("M."), and two dogs. The notations were made by Valiant himself. The "X" marks where the first of the famous specimens of *Triarthrus* with appendages was found in place. This marks the location of the Trilobite Bed.

Beecher's extensive quarrying. The "X" in Valiant's handwriting marks the spot where the first specimen of *Triarthrus* with appendages was found in place. This marks the location of the Trilobite Bed.

By various means, material from Beecher's Trilobite Bed has found its way into the collections of many museums, though mostly only in small lots. Beecher collected by far the largest amount of material from the outcrop. By July, 1895, he had assembled in Yale University's Peabody Museum of Natural History 34 barrels and 22 large boxes of rock, in addition to other smaller lots of material (Beecher, unpublished notes). He obtained his specimens for study from only a few of these parcels. The rest remained unopened at the time of his death in 1904, and most of this material has subsequently either been lost or destroyed without having been unpacked.

Most of the material remaining from Beecher's Trilobite Bed has been found and examined. This includes about 200 pounds in the Peabody Museum, Yale University, about 300 pounds in the Museum of Comparative Zoology, and about 10 pounds in the Geological Museum of Rutgers University at New Brunswick. The material at Yale — Beecher's and Raymond's published specimens, numerous other specimens just as exquisitely prepared for study, large prepared slabs, and a large amount of sorted and unsorted bulk material — was examined under hand lens and dissecting microscope in

finding, identifying, and counting specimens. The Trilobite Bed itself was examined in 20 large and small thin-sections. An X-ray study of the internal anatomy of *Triarthrus* currently in progress is incidentally making more study materials available.

Following Valiant's original field directions, I attempted to relocate Beecher's Trilobite Bed in the field in May, 1969. At the location described, I found a large, defoliated scar on the side of the ravine at Cleaveland's Glen which is likely the remains of Beecher's quarry. The outcrop was badly slumped. Nevertheless, after some digging, I found a bed of dark gray siltstone four cm thick in approximately the location expected from the photograph in Figure 1. Though in these respects the particular bed matched the description of Beecher's Trilobite Bed, it most unfortunately lacked the concentration of *Triarthrus* specimens in its basal portion. Hence it could not be conclusively identified as the Trilobite Bed itself; still, it is possible that it is. There is independent sedimentological evidence to suggest that the concentration of *Triarthrus* specimens may have been a very localized phenomenon within the particular turbidite bed. Beecher may have mined out only that portion containing the extraordinarily preserved trilobites.

BEECHER'S TRILOBITE BED

MICROSTRATIGRAPHY. As represented in museum collections, Beecher's Trilobite Bed is a layer of dark gray, graded siltstone 40 mm thick, which is characterized by an abundance of complete specimens of *Triarthrus* near its lower surface. The microstratigraphy of this and adjacent beds is illustrated in Figure 2.

The Trilobite Bed rests on a layer of black mudstone about three mm thick that in turn grades downward into another bed of graded siltstone about eight mm thick (Fig. 3a–c). The mudstone is made up of organic and pyritic material — biogenic sediment — mixed with silt. Its most obvious component is flattened, carbonized rhabdosomes of the graptoloid *Climacograptus*, which lie horizontally in random orientations. Otherwise the most common fossils in the mudstone are the brachiopods *Schizocrania* and *Camaratoecia*, the trilobites *Triarthrus* and *Cryptolithus*, and the dendroid graptolite *Inocaulis*. (Hereafter see Table 1 for specific identifications.) Burrows are common, and all recognized have been laterally directed and filled with silt from the underlying siltstone bed.

What is here called the "basal layer" of the Trilobite Bed is a layer of coarse, medium-gray siltstone less than a millimeter thick that grades upward into the finer, dark-gray siltstone which comprises the rest of the bed (Fig. 3a, b). The contact with the underlying mudstone is, in thin-section, sharp and undulating, the undulation corresponding to ripple marks (wave
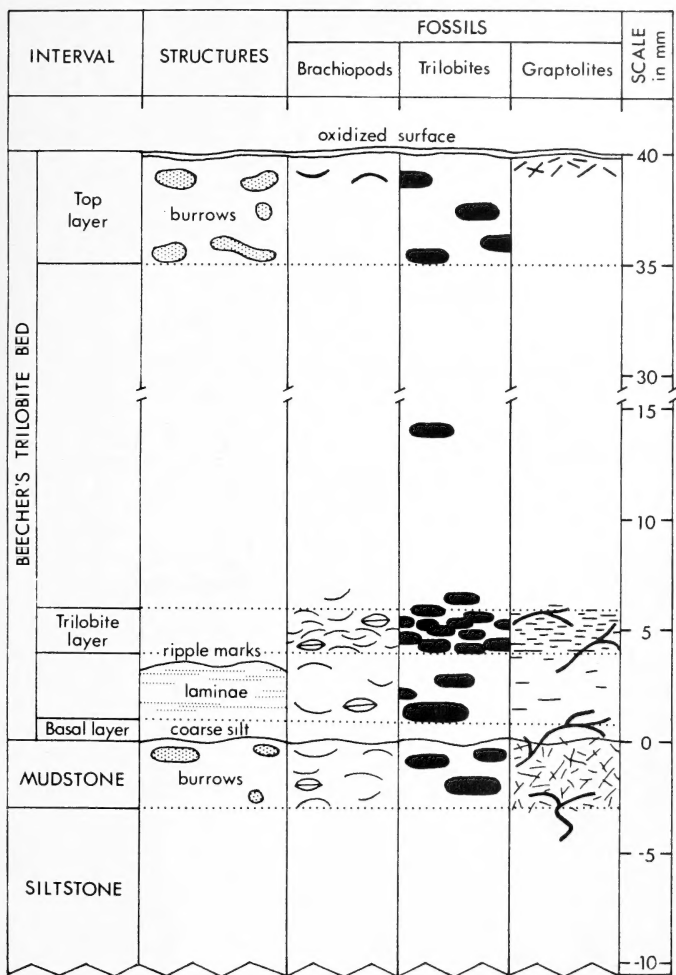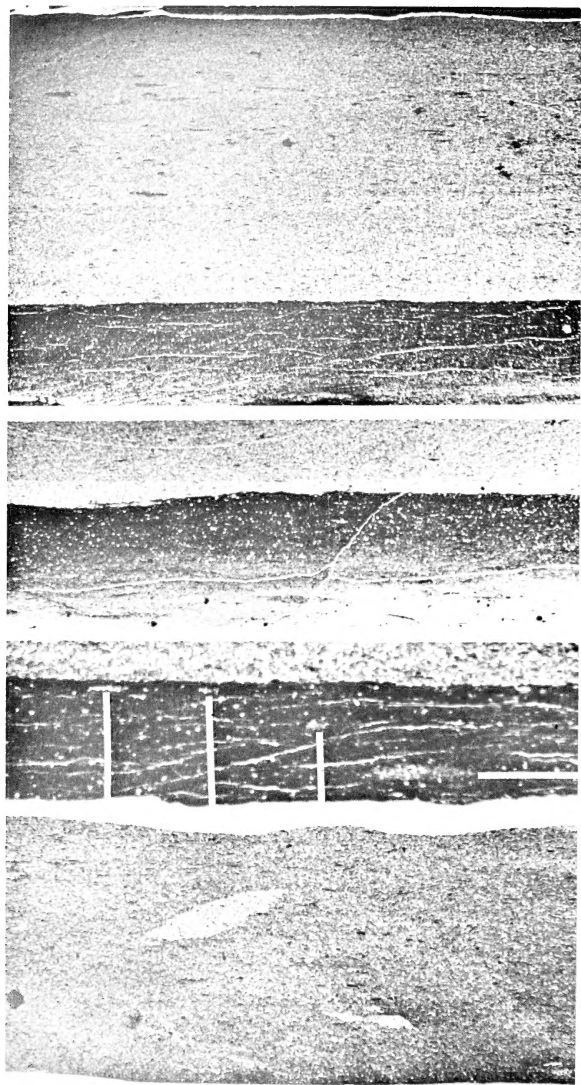
FIG. 2. Microstratigraphic section of Beecher's Trilobite Bed and associated beds.

length about 10 mm, amplitude about 0.5 mm; Fig. 3c). The grade of the bedding is continuous from this contact upward, though it is much more subtle above the basal layer. However, about three mm above the contact, symmetrical ripple marks (wave length about 20 mm, amplitude about 0.5 mm) occur. These are crossed perpendicularly to their strike by drag marks of very low relief.

Organic and pyritic material in filaments, pellets, and smaller particles colors the siltstone; this material diminishes somewhat in abundance upward from the mudstone through the Trilobite Bed. Very fine particles of this are concentrated in dark, discontinuous laminae, each only a few tenths of a millimeter thick; these occur in the first few millimeters above the basal layer (Fig. 3a, b). The maximum concentration occurs as a laterally continuous lamina about two mm thick lying between four and six mm above the contact with the mudstone (Fig. 3a). When excavated, this thin layer has a rough, slightly shiny surface, which is littered with the brachiopods, trilobites, and graptolites most common in the underlying mudstone. Macrofossils are concentrated in this layer, but are much less common in the underlying part of the Trilobite Bed and are almost absent from the next 30 mm of siltstone above it. Beecher obtained his famous trilobite specimens from this layer, which can appropriately be termed the "trilobite layer" of the Trilobite Bed.

Specimens of *Climacograptus* and *Triarthrus* in the trilobite layer lie with strong directional orientation (Fig. 4a, b). As apparent from Figure 4b, trilobites show no preference for anterior or posterior nor for dorsal or ventral orientation. No evidence has been found to support Beecher's (1894a) statement that nearly all trilobites lie with their ventral surfaces upward.

Fossils and laterally directed burrows are common in the uppermost five mm of the Trilobite Bed, and this zone will be termed the "top layer." Unlike the basal part of the bed, no directional features are apparent; and graptoloid rhabdosomes in this layer lie in random orientation.

DEPOSITION OF THE BED AND ACCUMULATION OF THE FOSSIL ASSEMBLAGE. As indicated by its graded bedding, sole markings, and internal directional features, Beecher's Trilobite Bed is a microturbidite. Its internal ripple marks and laminae are unusual features for turbidites, though they are known to occur in microturbidites such as this (Kuenen, 1953).

FIG. 3. (Opposite page.) Thin-sections of Beecher's Trilobite Bed and associated beds. A. Section showing the trilobite layer (*tl*), Laminae (*ll*), and the basal layer (*bl*) of the Trilobite Bed, and the mudstone (*ms*), and the underlying siltstone (*ss*). YPM 26881; × 6.4. B. Section more clearly showing the stratigraphic relationships of the basal layer (*bl*) to the Trilobite Bed, the mudstone (*ms*), and the underlying siltstone (*ss*). YPM 27818; × 6.5. C. Section of the mudstone in which four silt-filled burrows are indicated. YPM 27819; × 18. D. Section of the top layer of the Trilobite Bed showing one large burrow. YPM 6673c; × 5.5.

The Trilobite Bed was deposited from a turbidity current that flowed over a mud bottom that is now the mudstone underlying it. The underlying mudstone represents detritus, largely biogenic sediment from the plankton, which accumulated slowly on top of another microturbidite under quiescent conditions. It represents a zoic bottom of high organic content which, as indicated by fluid deformation of sediment around the margins of burrows, also had a high water content (Rhoads, 1970).

Certain features of the Trilobite Bed itself, interpreted in the light of recent experimental investigations of turbidity currents and turbidites, make possible a rough quantitative reconstruction of the flow that deposited it.
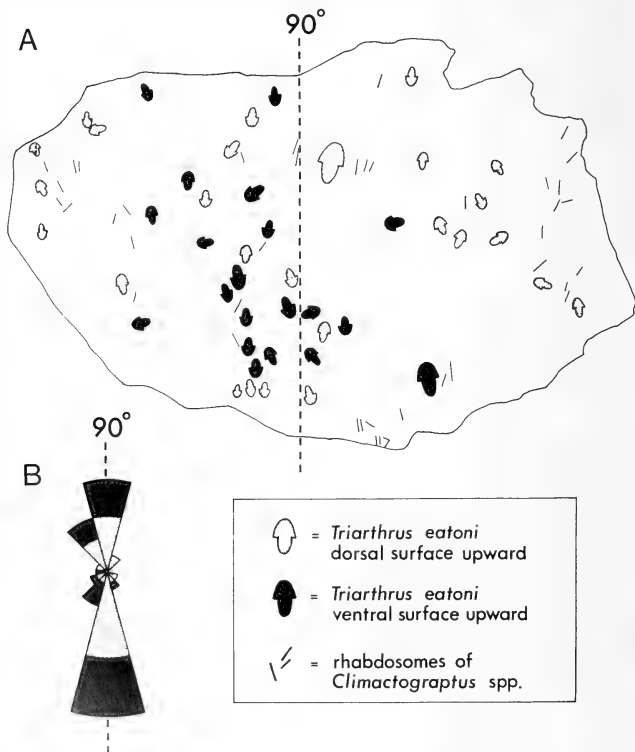

FIG. 4.   A. Stylized drawing of slab YPM 27801 showing the orientation of complete specimens of *Triarthrus eatoni* shown in outline and of rhabdosomes of *Climacograptus* spp. shown as sticks in the trilobite layer of Beecher's Trilobite Bed.   B. Current rose for the orientations of specimens of *Triarthrus*.

Prior to the onset of deposition, the flow eroded material from the surface of the mud and produced ripple marks. As estimated by Kuenen (1968), the time difference between the arrival of the flow at a point and the onset of deposition from the flow at that point should have been on the order of a minute. During deposition of the turbidite, that is, for the deposition of silt-size particles, the velocity of the current must have been approximately 10 to 20 cm per second (Kuenen, 1967). Ripple marks such as those on the surface of the mudstone and within the Trilobite Bed are associated with very high rates of deposition (Kuenen, 1953, 1967). Laminations such as those in the first few millimeters of the Trilobite Bed generally occur under conditions of decreasing current velocity and high rates of sedimentation on the order of 1 cm per minute. Under these conditions, overloading and the formation of a traction carpet may have occurred in the flow (Sanders, 1965; Kuenen, 1966a, b).

The fossil assemblage preserved in the basal portion of Beecher's Trilobite Bed was derived from the zoic mud bottom in the immediate area. The distance of transportation in all probability was negligible. This is first indicated in that the same taxa most commonly represented in the underlying mudstone are exactly those most commonly represented in the basal part of the Trilobite Bed. The turbidity flow simply caught up and buried material from the bottom over which it passed. The preservation of very delicate features in fossils and the lack of size-sorting among animals in the trilobite layer suggests that transportation was accomplished in a gentle manner, though not necessarily over a short distance. In all, the time over which transportation occurred should be approximately equal to the time interval between the arrival of the turbidity current and the onset of deposition plus the time interval necessary for the deposition of about a one centimeter thickness of turbidite, that part containing the fossil assemblage. Accepting Kuenen's estimates cited above, that time interval should have been on the order of 100 seconds. Considering that the average velocity of the flow was probably no more than 20 cm per second, the distance of transport should have been on the order of 20 m.

The concentration of fossils in the trilobite layer probably represents a localized event. Laminae such as found just above the basal layer and such as the trilobite layer itself are associated with strong, localized sorting in turbidity flows (Kuenen, 1953). This is consistent with information on the limited extent of the trilobite layer at the outcrop in Cleaveland's Glen.

Beecher (1894a) astutely inferred that the concentration of complete specimens of *Triarthrus* in the trilobite layer was the result of a mass killing. Indeed this seems to be the case for many of the benthic organisms preserved in the basal part of the Trilobite Bed. The preservation of especially delicate structures in fossils — such as the filaments of *Polyplectella,* the body of *Protoscolex*, and limbs and musculature of trilobites — strongly suggests that these animals were alive just prior to the burial event. Many of the benthic organisms in the basal portion of the Trilobite Bed are preserved complete, these including complete trilobites and dendroid graptolites and

brachiopods with the valves articulated, closed, and in place. The probable cause of mortality is the turbidity flow itself. Burial in the turbidite accounts for the killing of the various sessile organisms in the fossil assemblage though not so well for the killing of errant organisms such as trilobites. Specimens of trilobites in the trilobite layer, showing preference neither for dorsal or ventral nor for anterior or posterior orientation, appear to have been oriented parallel to the current as passive objects, like the associated graptoloid rhabdosomes, and thus appear to have been moribund when buried. Why this should be is a problem. One likely answer is temperature shock. The temperature of the turbidity flow may well have been somewhat higher than that to which the animals were acclimated; and as it passed over them, the animals might have been stunned by the sudden change in temperature. They might thus have been rendered the passive objects they appear to have been. Once buried, the decaying organic matter with which they were buried might be presumed to have rapidly elevated the hydrogen sulfide concentration of interstitial water sufficiently to have made the immediate environment anoxic so as to suffocate animals, and to have poisoned whichever animals remained alive.

Owing to these conditions of burial and death, the fossil assemblage in the basal part of Beecher's Trilobite Bed should contain the preservable benthic macrofauna that was living in the immediate area and also the debris of dead benthic and pelagic organisms. Through further examination of the fossil assemblage, many of those specimens representing living animals can be identified, and the composition of the standing crop can be roughly reconstructed.

DIAGENESIS AND PRESERVATION OF THE FOSSIL ASSEMBLAGE. Following deposition of Beecher's Trilobite Bed, quiescent conditions again prevailed, as indicated by the random orientation of graptoloid rhabdosomes in the top layer. The turbidite then formed a zoic silt bottom of high water content, as indicated by numerous burrows in the top layer which show fluid deformation of the sediment around their margins (Fig. 3d). The infauna penetrated only shallowly into the top of the bed: bioturbation extends no more than about five mm into the rock. The then recently killed organisms in the trilobite layer were protected from disturbance by a blanket of sediment at least 30 mm thick.

Compaction of the turbidite bed occurred very soon after its deposition. Beecher (1902) noted that compaction of the sediment was expressed in the appression of the ventral membrane toward the dorsal exoskeleton in certain specimens of *Triarthrus* such that the membrane bore the impress of intervening muscles. Clearly a considerable amount of compaction took place before the musculature could decompose to any great extent — probably during the first day or few days after burial. Additional evidence of compaction is found in the compression of trilobites and graptolites in both the mudstone and the microturbite. In the case of graptoloid rhabdosomes, which represent one sort of debris common to both the trilobite layer and

initially the same when buried by the turbidite, some idea may be gained of the effect of compaction on the two types of sediment. Rhabdosomes in the turbidite are pseudomorphs in pyrite, and, though somewhat flattened, are often preserved in three dimensions. However, rhabdosomes in the mudstone are carbonized films and are flattened virtually into two dimensions. Thus, whereas the mudstone was very highly compacted, the turbidite was compacted comparatively little.

Specimens in the basal part of Beecher's Trilobite Bed are generally preserved as pseudomorphs in pyrite. Specimens of *Triarthrus,* for example, have their various parts preserved either as pyrite films or as packed masses of pyrite microspheres of several tens of microns in diameter. Shells of mollusks and brachiopods are preserved as films of pyrite; little of the carbonate material remains.

Berner (1970, 1971) has described a process by which sedimentary pyrite with these characteristics is formed in similar marine sediments. Oxygen is removed from interstitial water very soon after burial, and bacterial degradation of organic matter begins to produce hydrogen sulfide. This in turn reacts immediately with iron in the sediment to yield ferrous sulfide. In those instances described by Berner (1970), this reaction was complete within about two days. Those parts of the trilobites ultimately preserved as pyrite would first have been preserved in this iron sulfide. The high rate of reaction, consistent with the preservation of the musculature in trilobites, suggests that the initial chemical changes in fossilization were complete within days after burial and that they proceeded concurrently with sedimentary compaction. Berner (1970) found that ferrous sufide was converted to pyrite over a period of years through reaction with elemental sulfur.

Pyrite formation was particularly favored in the preservation of organisms in the Trilobite Bed. Pyrite forms as a result of reaction of dissolved hydrogen sulfide with iron minerals, and the two major sources of this are bacterial sulfate reduction and decomposition of organic sulfur compounds derived from dead organisms (Berner, 1971). Though dissolved sulfate is usually by far the more important source (Berner, 1971), the abundance of decomposing organic matter in the Trilobite Bed and the underlying mudstone suggests that it was an important source in the present instance, especially in view of the strong association of pyrite with dead organisms manifested in the extraordinarily preserved fossils. Hydrogen sulfide presumably was given off by the decomposing carcasses; and spheres of pyrite up to a millimeter in diameter found in the area immediately around complete, thoroughly pyritized specimens of trilobites and graptolites may represent the infillings of bubbles, as has been found in a number of similarly formed fossils (Zangerl and Richardson, 1963; Zangerl, et al., 1969; Zangerl, 1971). Of the factors limiting pyrite formation, Berner (1970, 1971) found the concentration of decomposable organic matter to be the most important. In the case of the Trilobite Bed, organic detritus was initially present in great abundance; the underlying mudstone was a concentration of such material in proximity to trilobites and other organisms in the trilobite

layer. This is probably one important factor contributing to the exceptional preservation of the fauna. Compaction soon after burial is probably another important factor. As water was lost upward through the sediment, the net flow upward through the sediment would have brought a continuing supply of iron and hydrogen sulfide from the mudstone to the decaying animals in the trilobite layer.

PRESERVATION OF TRILOBITES. Trilobite specimens fall into two categories: complete and thoroughly pyritized specimens very often preserving the limbs, and a variety of partially articulated, disarticulated, and broken exoskeletal pieces that are thinner and less thoroughly pyritized and often have a whitish rather than golden cast to them. The former type, found in almost 99 percent of the specimens, most probably represents animals alive just prior to the burial event. The latter type probably represents remains of exuviae and dead, disarticulated individuals.

Specimens of the former type have been variously deformed in compaction. Living specimens of *Triarthrus* probably carried their limbs at a small angle below the horizontal and away from the dorsal exoskeleton. Yet in all specimens, the appendages, including their endites, are appressed toward the dorsal exoskeleton and are bent upward around its edges as much as 20° from the horizontal. This effect of compaction has scarcely been taken into account in morphological reconstructions of the trilobite. Although Beecher was aware of the compaction effect generally, at least by 1902, he did not take it into account in his earlier reconstructions. Two of these (Beecher, 1894a, 1895a) show the thoracic exites bent around the pleurae. In nearly all cases, the trilobite is arrayed in a very nearly horizontal plane such that displacement of the appendages in compaction was in a vertical direction. Their essential relationship to the body has been maintained. However, in the few specimens that rest oblique to the bedding, compaction has resulted in a systematic lateral displacement of the entire set of limbs with respect to the body. This has important consequences for reconstruction of the morphological mechanisms of locomotion and feeding.

RECONSTRUCTION OF THE BENTHIC FAUNA

THE FOSSIL ASSEMBLAGE. Two discrete fossil assemblages are represented in Beecher's Trilobite Bed and the underlying mudstone: that preserved in the mudstone and the first few millimeters of the microturbidite, which is to be termed the "mud assemblage," and that preserved in the top layer, which is to be termed the "silt assemblage." It is the mud assemblage that is of primary interest. The composition of both assemblages as ascertained from the 200-odd· pounds of rock in the Peabody Museum of Natural History, Yale University (YPM), is given in Table 1. The samples have undoubtedly incurred biases in earlier sorting of the collection and in preferential prepara-

tion of certain trilobite specimens, but examination of the far larger amount of unsorted bulk material should tend to correct such biases.

TABLE 1. Composition of fossil assemblages given for individual taxonomic groups as a percentage of the total number of specimens (individual pieces, colonies or individuals as appropriate to the species) and of the total number of specimens of benthic groups. The mud assemblage is the fossil content of the first few millimeters of Beecher's Trilobite Bed and the underlying mudstone (total = 1547; benthic total = 1055), and the silt assemblage is the fossil content of the top layer of the Trilobite Bed (total = 87; benthic total = 60).

Taxonomic Group	Mud Assemblage		Silt Assemblage	
	total	benthic	total	benthic
Porifera				
Polyplectella mira Ruedemann	1	2	0	0
favositid	+	+	0	0
Ectoprocta				
Arthrostylus tenuis (James)	1	1	1	2 −
Brachiopoda	15 +	9 −	4 +	5
Inarticulata	12	4	2 +	2 −
Leptobolus insignis (Hall)	2 −	3	0	0
Lingula? procne Billings	1 −	1	1	2 −
Orbiculoidea tenuistriata Ulrich	1	0	0	0
Schizocrania filosa (Hall)	8 −	0	1	0
Trematis sp.	1	0	1	0
Articulata				
Camaratoecia? humilis Ruedemann	3	5 −	2	3 +
Orthid	+	+	0	0
Annelida	4 +	6	3 +	5
Protoscolex spp. (2)	4	6 −	3 +	5
Serpulites sp.	+	+	0	0
Arthropoda	45	62 −	58	83
Trilobita	42	54 +	55	78
Triarthrus eatoni (Hall)	36	50 −	6	8 +
Holaspides	28	41	3 +	5
Meraspides	6 −	8 +	2	3 +
Protaspides	2	0	0	0
Cryptolithus bellulus (Ulrich)	5 +	8	27	38
Holaspides	1	1 +	15	22
Meraspides	4 +	6 +	12	17 −
Cornuproetus beecheri (Ruedemann)	+	+	22	32
Holaspides	+	+	21	30
Meraspides	+	+	1	2 −
Protaspides	+	0	0	0

TABLE 1 continued

Taxonomic Group	Mud Assemblage		Silt Assemblage	
	total	benthic	total	benthic
Primaspis crosotus (Locke)	+	(?)	1	2 −
Holaspides	0	0	1	2 −
Meraspides	+	(?)	0	0
Ostracoda	2	3	3 +	5
Aparchites sp.	1	2 −	1	2 −
Primitia sp.	+	+	2 +	3 +
unidentified	1 −	1	0	0
Cirripedia?				
Lepidocoleus jamesi				
(Hall & Whitfield)	1	0	0	0
Archeostraca				
Ceratiocaris sp.	+	+	0	0
Bivalvia	+	+	0	0
Pterinea sp.	+	+	0	0
Rhytimya sp.	+	+	0	0
Echinodermata	0	0	5 −	7 −
crinoid	0	0	2 +	3 +
asteroid				
Mesopaleaster? lanceolatus	0	0	2 +	3 +
Schuchert				
Graptolithina	35 −	22	30 −	0
Dendroidea	15	22	0	0
Inocaulis arborescens Ruedemann	11	16	0	0
Mastigograptus spp. (2)	4	6	0	0
Graptoloidea				
Climacograptus spp.	19	0	30	0
Problematica (2 spp.)	+	+	0	0

A total of 32 species are represented in the two fossil assemblages together, 30 occur in the mud assemblage, and 17 occur in the silt assemblage. Nearly all the species known from the Frankfort Shale are represented, including a few reported here for the first time. All but two species of Problematica and the favositid sponge are figured by Ruedemann (1925b, 1926b).

As will be seen by inspection of Table 1, relatively few taxa of brachiopods, trilobites, and graptolites contain over 90 percent of the total number of specimens in the mud assemblage. Essentially the same proportions of the numerically more abundant forms are found on large prepared slabs of the trilobite layer (YPM 27801–27804).

Because the conditions of its accumulation are unknown, and because of its much smaller size, the silt assemblage serves only for very general comparison with the mud assemblage. As shown in Table 1, it is comprised pri-

marily of trilobites and graptoloids. In contrast to the mud assemblage, echinoderms are present and dendroid graptolites are absent.

BRACHIOPODS. Brachiopods collectively are common in both assemblages. Most common in the mud assemblage is the acrotretid *Schizocrania filosa*. Elsewhere this species is often found complete with its pedicle valve cemented to various types of shells. Like the modern *Crania*, it seems to have required a hard substrate for attachment. But in the present instance, it is represented only by brachial valves. No pedicle valves have been found cemented to various shells in the fossil assemblage. Hence this particular brachiopod was evidently not part of the bottom fauna. As an explanation for its mode of occurrence, it is suggested that *Schizocrania* was epizoic on shells of pelagic organisms, and that after the death and decomposition of the brachiopod animal, the brachial valve fell to the bottom while the pedicle valve remained attached to whatever was its host. This interpretation is supported by Ruedemann's (1925b) finding of other acrotretid brachiopods complete and cemented to nautiloid shells. The similar but less common acrotretids *Orbiculoidea* and *Trematis* have the same mode of occurrence as *Schizocrania,* and probably had similar modes of life. With regard to the benthic environment, the shells of these brachiopods are interpreted simply as biogenic sediment.

The lingulids *Lingula* and *Leptobolus* and the rhynchonellid *Camaratoecia* are represented mostly by articulated valves covering a wide range in size. These brachiopods evidently belonged to the local benthos.

TRILOBITES. *Triarthrus* is abundantly represented in the mud assemblage, by approximately 550 specimens. About 60 of these represent protaspides, and all of these are exuviae. Of the remainder, almost 99 percent are complete and thoroughly pyritized specimens representing animals probably alive just prior to the burial event. The remaining few specimens consist of disarticulated exoskeletal pieces — librigenae and parts of cranidium-thorax-pygidium units. Most of these come from the underlying mudstone, where no complete and thoroughly pyritized specimens have been found. These quite probably represent exuviae; for, while somewhat scattered, these same exoskeletal units have been identified with undisturbed exuviae of other species of *Triarthrus* (Harrington and Leanza, 1957; Harrington, 1959).

In view of the manner of accumulation of the fossil assemblage, the occurrence of complete trilobite specimens, those representing actual animals, only in the microturbidite and not in the underlying mudstone is taken to indicate that these holaspides were living epifaunally near the surface of the mud in a situation such that they were caught up and then buried by the turbidity flow. Exuviae near the surface were also caught up and buried in the turbidite, but exuviae deeper in the mud were left where they were. The peculiar occurrence of exuvia of protaspides but not of the animals themselves is taken to indicate that the larval trilobites were not living on the

bottom. Rather they may well have been living in the plankton, as has often been hypothesized.

The comparative rarity of holaspid exuviae suggests that molted parts were destroyed rapidly after having been shed. If one considers that a large holaspis went through on the order of 20 molts, leaving an exuvia at each molt, it would be expected that with a theoretical "perfect" preservation, the ratio of molted exoskeletons to actual animals in the fossil assemblage would be about twenty to one. However, this ratio for postlarval specimens in the mud assemblage is roughly one to fifty. This great disparity is probably not an artifact of preservation since even tiny protaspid exuvia (belonging in this case to animals in a different age-class in the population: Cisne, in press) are present in the assemblage. The most likely explanation is that exuviae were rapidly destroyed by benthic organisms, in particular, by the trilobites themselves. Like many modern crustaceans, they may have eaten their own exuviae. It has been my observation that fresh crustacean exuviae are much more fragile that the intermolt exoskeletons of the same animals, and that the exuviae themselves decay within a matter of a few days to become even more fragile and still more subject to destruction. This may have been the case for trilobite exuviae as well.

Complete specimens of *Cryptolithus* occur together with those of *Triarthrus* in the trilobite layer, and its exoskeletal pieces representing exuviae occur in the underlying mudstone. It is fairly common in the mud assemblage and is abundant in the silt assemblage. It was an epifaunal deposit-feeder (Cisne, 1970; Bergström, 1972).

Cornuproetus is very sparsely represented in the trilobite layer by exoskeletal pieces alone, but it is commonly represented in the silt assemblage by complete specimens in addition to such pieces. It was very probably benthic, and its large eyes suggest primarily epifaunal habits.

OTHER GROUPS. Rhabdosomes of the graptoloid *Climacograptus* are abundant in both asemblages. These represent simply debris from the plankton.

As deduced from their modes of occurrence and, where appropriate, from comparison with living representatives, groups in the benthic fauna included sponges, ectoprocts, bivalves, ostracod and archeostracan crustaceans, crinoids, asteroids, and dendroid graptolites, in addition to two rare problematical forms. Of these, only dendroid graptolites are abundant. Large, poorly preserved annelids such as *Protoscolex* are not uncommon.

THE BENTHIC FAUNA. The compositions of the benthic faunas represented in the mud and silt assemblages are given in Table 1. The former, the fauna of a soft mud bottom rich in detritus, is comprised of 24 species; the latter, the fauna of a soft turbidite silt bottom, is comprised of 12 species. The most obvious differences between the two is the absence of dendroid graptolites from the silt assemblage and the absence of echinoderms from the mud assemblage.
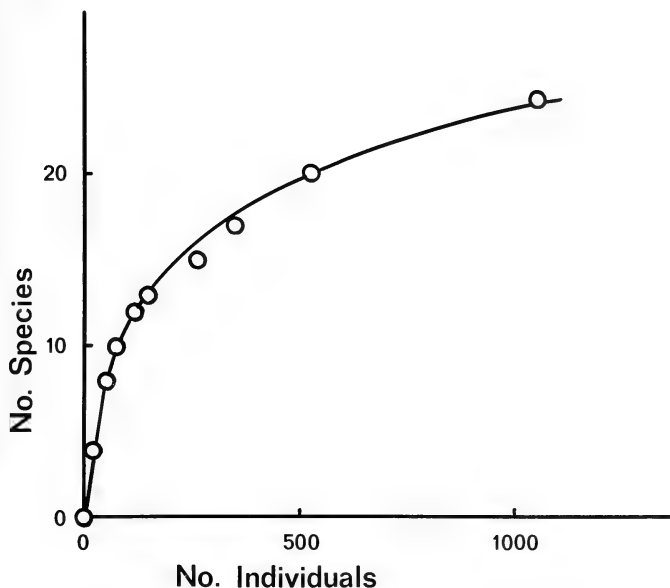
FIG. 5. Rarefaction plot for the benthic fauna in the mud assemblage.

Because the mud assemblage represents a kind of census of the more "preservable" organisms in the benthic fauna — organisms of types commonly found as fossils, and in this case, also organisms of types not commonly found as fossils — it should preserve in a rough way the relative abundance of those species. There are of course certain biases of preburial accumulation of exoskeletons (e.g. accumulation of articulated brachiopod shells together with brachiopods alive at the time of the burial event, these being indistinguishable as fossils), of sorting in the turbidity current and non-burial in the turbidite, and of differential preservation (e.g. the very probably altered proportion of trilobites to annelids in going from life to fossil assemblages). Despite its shortcomings as a "real" census such as a modern benthic dredge sample (which of course has biases all its own), the occurrence of such a census assemblage is so rare that the data deserve some analysis.

The assemblage probably contains most of the "preservable" species in the local benthos. A rarefaction plot (Fig. 5) — a plot of the number of species expected in hypothetical smaller samples drawn from the total sample —

tends to level off for samples a third to half the size of the total (See Sanders, 1968, for an explanation of the method). Extrapolating, perhaps half a dozen very rare species (or at least species very rarely preserved) would be expected to appear in the sample if it were trebled or quadrupled in size. Few more would be expected if the sample size were increased indefinitely.

The diversity of the benthic fauna of the mud assemblage as calculated from the Shannon-Weaver information measure (See, for example, Pielou, 1969, for explanation) is 2.65 bits. For comparison, the Shannon-Weaver diversity of benthos in the silt assemblage is 2.48 bits.

BENTHIC ECOLOGY

The benthos of the mud and silt assemblages was comprised of epifaunal and shallow infaunal organisms. The depth of biogenic reworking in the mudstone underlying the Trilobite Bed is only about three mm; and in the top layer of the Trilobite Bed, it is about five mm. Though the surface of the mudstone was scoured by the turbidity current, and though the apparent depth of reworking in both the mudstone and siltstone has undoubtedly been reduced by sedimentary compaction, it is still apparent that benthic animals penetrated no more than a few millimeters into the sediment.

The fauna of the mud assemblage is dominated by deposit-feeders — the arthropods and annelids, which together comprise nearly 70 percent of the individual specimens in the fossil benthic fauna. In rank order of abundance, the species alternate as to feeding type. *Triarthrus* (50 percent of specimens; the dominant species) was an epifaunal deposit-feeder. (See Appendix II.) *Inocaulis* (16 percent) was a high-level suspension-feeder. *Cryptolithus* (8 percent) was an epifaunal deposit feeder. (See Appendix II.) *Mastigograptus* spp. (6 percent) were low-level suspension-feeders. *Protoscolex* spp. (6 percent) were probably infaunal deposit-feeders.

The source of food to this benthic fauna was probably the rain of detritus from the plankton. The most obvious fraction of this is the great number of graptoloid rhabdosomes in the mudstone underlying the Trilobite Bed. These are often found broken and torn up as if partially consumed. Ruedemann (1925a) first noticed this in many instances. For the benthic fauna of the silt assemblage, however, finely particulate food material contained in the turbidite itself was likely the most important source. *Cryptolithus*, the most abundant species in that assemblage, is peculiarly adapted for size-selective feeding on such material (Cisne, 1970).

COMPARATIVE BENTHIC ECOLOGY.   With regard to the evolution of communities, it is interesting to compare this Ordovician fauna with modern ones in similar types of environment. The general similarity of the benthic environment of the Frankfort Shale of the Utica Basin to the benthic environments

in the basins on the continental borderland off southern California has been pointed out in the Introduction. These modern benthic faunas have been extensively studied by Hartman (1955) and Hartman and Barnard (1958, 1960). Their data, collected from a large number of samples taken with an orange peel grab, are here used for the comparison.

In numerical abundance, the Recent benthic faunas are dominated by small polychaetes which would not be expected to fossilize. A similar situation likely obtained in the Ordovician faunas in question. Whatever comparisons are to be made between them concerning "preservable" species are necessarily based on a numerically small fraction of the total fauna.

Many of the same groups preserved in the two Ordovician assemblages are found in the modern faunas: sponges, ectoprocts, brachiopods, annelids, arthropods, bivalves, echinoderms, and chordates. The phyla are the same but very often the classes and orders are different. Trilobites, for example, are seemingly replaced by malacostracan crustaceans. But there is no obvious parallel for dendroid graptolites in the modern benthic faunas; nor is there a parallel for graptoloid rhabdosomes in the modern sediments.

The diversity in "preservable" species is comparable between the Ordovician and modern benthic faunas. For the modern faunas, these are species that might be expected to be found as fossils if preserved as were fossils in the mud assemblage. Species diversity in continental borderland basins is quite variable from basin to basin and is controlled importantly by the concentration of dissolved oxygen in bottom waters (Hartman and Barnard, 1958; Emery and Hülsemann, 1962). Values for the basins investigated are: Santa Barbara (19 species), San Pedro (53), Santa Monica (11), Santa Catalina (47), Santa Cruz (27), San Nicolas (34), Tanner (25), West Cortes (8), San Clemente (19), East Cortes (8), Long (19), Velero (3), and San Diego Trough (5; very sparsely sampled). These diversity levels are comparable to the 24 species in the benthic fauna of the mud assemblage, which include almost all of the benthic species known from the Frankfort Shale.

By another means of measuring faunal diversity, the Shannon-Weaver information index, the levels for preservable species are comparable between the Ordovician and modern faunas. It is important to note that this index is essentially independent of sample size, as the modern samples considered are individually smaller than the sample represented in the mud assemblage. Among the 18 samples containing more than 5 preservable species reported from the San Pedro Basin, that basin most extensively sampled, diversity averages about 2.50 bits. This is quite close to the values of 2.65 and 2.48 bits for the benthic faunas of the mud and silt assemblages, respectively.

This similarity in diversity conflicts with Valentine's (1970) estimate that species diversity was, by and large, more than an order of magnitude lower in the Paleozoic than it is at present. A difference so large as that would seem to be outside the range of error for the present estimate. Of course the present findings relate only to within-habitat diversity in an environment which, in its rigors, may be severely limiting on diversity at present, as in the past.

The present result suggests that, despite differences in taxonomic composition, the Ordovician and the Recent benthic faunas in question have a similar niche structuring. That is, there is no great difference in the degree of ecological specialization among the constituents of the faunas.

APPENDIX I: SYSTEMATIC REVIEW OF TRILOBITES

Over the years, there has been much confusion in the literature concerning the identifications of the trilobites in Beecher's Trilobite Bed. In view of their importance in the study of trilobite morphology, it is important that they be clarified. It is this which the following synonymies and discussions are intended to do.

Triarthrus eatoni (Hall)

Triarthrus Beckii Green: Matthew, 1893; Valiant, 1901.

Triarthrus Becki Green: Beecher, 1893a,b, 1894a,b, 1895a,c, 1896, 1902.

Triarthrus becki Green: Walcott, 1894, 1918, 1921; Raymond, 1920.

Triarthrus eatoni (Hall): Ruedemann, 1925a,b, 1926b; Størmer, 1933, 1939, 1942, 1944, 1951; Harrington, et al., 1959.

REMARKS. This identification has further been confirmed by D. S. Thompson (personal communications, 1967, 1969), who is presently completing his doctoral dissertation, "A Biometrical Study of the Genus *Triarthrus*," for Syracuse University.

The protaspides ascribed to this species by Beecher (1893a) does indeed belong to this species, contrary to the assertion of Whittington (1957). As will be discussed elsewhere (Cisne, in press), the protaspides are related to the holaspides by a graded series of meraspides.

Cornuproetus beecheri (Ruedemann), new combination

Proetus parviusculus Hall: Beecher, 1895c; Valiant, 1901.

Proetus beecheri Ruedemann, 1926b: Ruedemann, 1925a, 1926b.

DISCUSSION. This proetid has a medium-sized glabella and a rather wide anterior border not encroached upon by the glabella and lacks differentiated occipital lobes. It is therefore referred to the Cornuproetinae, not the Proetinae, within the Proetidae. Because of its similarity to *Cornuproetus (Cornuproetus) cornutus* (Goldfuss), the type-species of the type-genus, it is referred to this genus, but without subgeneric distinction.

Cryptolithus bellulus (Ulrich)

Trinucleus concentricus Eaton: Beecher, 1895b,c; Valiant, 1901.

Cryptolithus tesselatus Green: Raymond, 1920; Størmer, 1939; Harrington, et al., 1959; Bergström, 1972.

Cryptolithus bellulus (Ulrich): Ruedemann, 1925a, 1926b; Whittington, 1941.

Primaspis crosotus (Locke)

Acidaspis sp.: Valiant, 1901.

Acidaspis trentonensis Walcott: Raymond, 1920; Stormer, 1939.

"Acidaspis trentonensis Hall:" Harrington, et al., 1959.

REMARKS. Beecher's photograph (Raymond, 1920, pl. 6, fig. 6) of the single holaspid specimen (YPM 243) is deceptively poor. The specimen itself is identifiable by comparison with other specimens of *Primaspis crosotus* (= *Odontopleura crosota* Locke: Whittington, 1956), which is also the only odontopleurid known from the Frankfort Shale (Ruedemann, 1925a, 1926b).

APPENDIX II: REMARKS ON THE FEEDING MECHANISMS AND
ECOLOGY OF TRILOBITES

A particular problem in interpreting the ecology of trilobites in the benthic fauna is the nature of their feeding mechanisms. Bergström (1969), in his review of trilobite limb morphology, cogently argues that trilobites like *Triarthrus* and *Cryptolithus* had a filter-feeding mechanism like that of many filter-feeding crustaceans, reviving in essence the reconstruction of Störch (1925) as opposed to the more generally accepted reconstruction of Eriksson (1935) and Størmer (1939). In particular, these trilobites probably had a trunk limb filter-feeding mechanism as found among cephalocarid, branchiopod, and leptostracan crustaceans, as opposed to a maxillary filter-feeding mechanism as found among eumalacostracan crustaceans. (See Marshall and Orr, 1960 for explanation of these terms.) These trilobites probably used this mechanism in feeding on deposited detritus much as do benthic cephalocarids, branchiopods, and leptostracans. I have summarized a functional reconstruction of *Cryptolithus* (Cisne, 1970).

There have been several morphological reconstructions of *Triarthrus* (Beecher, 1896, a synthesis of his earlier work; Walcott, 1918; Raymond, 1920; and Størmer, 1944, which included a summary of his interpretation presented in 1939); and these have confused attempts at its functional recon-

struction. Raymond's (1920) reconstruction appears best to fit the gross morphology of the specimens on the most important points. Contrary to the reconstructions of Størmer (1939, 1944), the coxae of the biramous limbs have endites. By his own admission (Størmer, 1939), these are based more on the somewhat misleading photographs published by Raymond (1920) than on thorough examination of the specimens themselves. The two specimens (YPM 216 and 219) on which he bases his argument that the coxae did not bear endites are unusual among the three dozen specimens on which Beecher and Raymond based their reconstructions in having undergone a shearing displacement transverse to the body so that the appendages do indeed fit Størmer's reconstruction, while those on the other side are just so much the more out of line with it. Thus the endites suggest a food groove along the ventral side of the thorax as found among filter-feeding crustaceans.

A controversial point of great importance is the structure and function of the cephalic endites in *Triarthrus*, the organs of a masticatory mechanism in *Triarthrus*. Beecher (1895a) and Raymond (1920) concluded that the cephalic endites were gnathobases that served in masticating food. They based their arguments on the opposition of paired endites, which closely approach one another transversely, and on the serration-like roughening on opposite edges of endites in one specimen (YPM 220), the only one in which Beecher worked them out. Inasmuch as these are the characteristic morphological features of gnathobases, the conclusion is warranted. Størmer (1951), however, dismissed this basic evidence in claiming that *Triarthrus* and trilobites categorically lacked such masticatory organs. This leads to a strange reconstruction, indeed, an organism with a means of collecting food by filter-feeding but without any apparent means of comminuting it and passing it into the mouth. In the case of filter-feeding crustaceans, it is difficult to imagine such an animal. That *Triarthrus* should have had some such masticatory mechanism makes good sense in terms of the filter-feeding mechanism adduced to it.

Cryptolithus had a similar feeding mechanism (Cisne, 1970; Bergstrom, 1972), but with the addition of the brim as a sieve filter for selecting only the finer particles from the sediment to be taken into the feeding current, as first proposed by Begg (1944).

Literature Cited

Begg, J. L., 1944. On the fringe of the *Tretaspis*. Geol. Mag. 81: 113–117.

Beecher, C. E., 1893a. A larval form of *Triarthrus*. Amer. J. Sci. (3) 46: 361–362.

—— 1893b. On the thoracic legs of *Triarthrus*. Amer. J. Sci. (3) 46: 467–470.

—— 1894a. On the mode of occurrence, structure and development of *Triarthrus becki*. Amer. Geol. 13: 38–43.

—— 1894b. The appendages of the pygidium of *Triarthrus*. Amer. J. Sci. (3) 47: 298–300.

—— 1895a. Further observations on the ventral structure of *Triarthrus*. Amer. Geol. 15: 91–100.

—— 1895b. Structure and appendages of *Trinucleus*. Amer. J. Sci. (3) 49: 307–311.

—— 1895c. The larval stages of trilobites. Amer. Geol. 16: 166–197.

—— 1896. The morphology of *Triarthrus*. Amer. J. Sci. (4) 1: 251–256.

—— 1902. The ventral integument of trilobites. Amer. J. Sci. (4) 13: 165–174.

Bergström, J., 1969. Remarks on the appendages of trilobites. Lethaia 2: 395–414.

—— 1972. Appendage morphology of the trilobite *Cryptolithus* and its implications. Lethaia 5: 85–94.

Berner, R. A., 1970. Sedimentary pyrite formation. Amer. J. Sci. 268: 1–23.

—— 1971. Principles of chemical sedimentology. McGraw-Hill, New York. 240 p.

Bretsky, P. W., 1969. Central Appalachian Late Ordovician communities. Geol. Soc. Amer. Bull. 80: 193–212.

—— 1970. Upper Ordovician ecology of the central Appalachians. Peabody Mus. Natur. Hist. (Yale Univ.), Bull. 34. 150 p.

Cisne, J. L., 1970. Feeding and trail production in a trinucleid trilobite. Geol. Soc. Amer. Abs. 2: 520.

—— in press. Life history of *Triarthrus eatoni*, an Ordovician trilobite. Ecology 54 (1).

Emery, K. O., 1960. The sea off southern california. John Wiley, New York.

Emery, K. O. and J. Hülsemann, 1962. The relationships of sediments, life and water in a marine basin. Deep-Sea Res. 8: 165–180.

Eriksson, E., 1935. Studien über die Fangapparate der Branchiopoden Bemarkungen. Zool. bedrag. f. Uppsala 15: 24–287.

Harrington, H. J., 1959. General description of the Trilobita. *In* R. C. Moore [ed.], Treatise on Invertebrate Paleontology, p. O38–O117. Geol. Soc. America and Univ. Kansas Press, Lawrence.

Harrington, H. J., and A. F. Leanza, 1957. Ordovician trilobites of Argentina. Univ. Kansas (Lawrence), Dept. Geol. Spec. Publ. 1.

Hartman, O., 1955. Quantitative survey of the benthos of San Pedro Basin, southern California. Part I. Preliminary Results. Allan Hancock Pacific Exped. 19: 1–185.

Hartman, O. and J. Barnard, 1958. The benthic fauna of the deep basins off southern California. Part I. Allan Hancock Pacific Exped. 22 (1).

——— 1960. The benthic fauna of the deep basins off southern California. Part II. Allan Hancock Pacific Exped. 22 (2).

Hülsemann, J. and K. O. Emery, 1961. Stratification of Recent sediments of Santa Barbara Basin as controlled by organisms and water character. J. Geol. 69: 279–290.

Kuenen, Ph. H., 1953. Significant features of graded bedding. Bull. Amer. Assoc. Petrol. Geol. 37: 1044–1066.

——— 1966a. Experimental turbidite lamination in a circular flume. J. Geol. 74: 523–545.

——— 1966b. Matrix of turbidites: experimental approach. Sedimentol. 7: 267–297.

——— 1967. Emplacement of flysch-type sand bodies. Sedimentol. 9: 203–243.

——— 1968. Turbidity currents and organisms. Eclogae Geol. Helv. 61: 525–544.

Marshall, S.M., and A. P. Orr, 1960. Feeding and nutrition. *In* T. S. Waterman [ed.], The physiology of Crustacea 1: 227–258. Academic Press, New York.

Matthew, W. D., 1893. On the antennae and other appendages of *Triarthrus Beckii*. N. Y. Acad. Sci. Trans. 12: 237-241.

Pielou, E. C., 1969. An Introduction to Mathematical Ecology. Wiley-Interscience, New York.

Raymond, P. E., 1920. The appendages, anatomy, and relationships of trilobites. Conn. Acad. Arts Sci. Mem. VII.

Rhoads, D.C., 1970. Mass properties, stability, and ecology of marine muds related to burrowing activity. *In* T. P. Crimes and J. C. Harper [eds.], Trace Fossils, Geol. Jour. Spec. Publ. 3: 391–406.

Rhoads, D. C. and J. W. Morse, 1971. Evolutionary and ecologic significance of oxygen-deficient marine basins. Lethaia 4: 413–428.

Ruedemann, R., 1925a. The Utica and Lorraine Formations of New York, part I, stratigraphy. N. Y. St. Mus. Bull. 258.

——— 1925b. The Utica and Lorraine Formations of New York, part II, systematic paleontology, number 1. N. Y. St. Mus. Bull. 262.

——— 1926a. Faunal and facies differences of the Utica and Lorraine Shales. N. Y. St. Mus. Bull. 267: 61–78.

——— 1926b. The Utica and Lorraine Formations of New York, part II, systematic paleontology, number 2. N. Y. St. Mus. Bull. 272.

——— 1935. Ecology of black mud shales of eastern New York. J. Paleon. 9: 79–91.

Sanders, H. L., 1968. Marine benthic diverstiy: a comparative study. Amer. Natur. 102: 243–282.

Sanders, J. E., 1965. Primary sedimentary structures formed by turbidity currents and related resedimentation mechanisms. Soc. Econ. Paleon. Mineral. Spec. Publ. 12: 192–219.

Störch, H., 1925. Uber bau funktion der trilobitengliedmassen. Zeit. Wiss. Zool. 125: 299-356.

Størmer, L., 1933. Are trilobites related to arachnids? Amer. J. Sci., (5) 26: 147–157.

———— 1939. Studies in trilobite morphology, part I, the thoracic appendages and their phylogenetic significance. Norsk. Geol. Tidsskr. 19: 143–273.

———— 1942. Studies in trilobite morphology, part II, the larval development, the segmentation and the sutures, and their bearing on trilobite classification. Norsk. Geol. Tidsskr. 21: 49–163.

———— 1944. On the relationships and phylogeny of fossil and Recent Arachnomorpha. Vid.-Akad. Oslo Skr. 1, M.-N. kl. 1944, no. 5.

———— 1951. Studies in trilobite morphology, part III, the ventral cephalic structures with remarks on the zoological position of trilobites. Norsk. Geol. Tidsskr. 29: 108–158.

Valentine, J. W., 1970. How many marine invertebrate fossil species? A new approximation. J. Paleon. 44: 410–415.

Valiant, W. S., 1901. Appendaged trilobites. Mineral Collector 8: 105–112.

Walcott, W. D., 1894. Notes on some appendages of the trilobites. Biol. Soc. Wash. Proc. 9: 89–97.

———— 1918. Appendages of trilobites. Smith. Misc. Coll. 67 (4).

———— 1921. Notes on the structure of *Neolenus*. Smith Misc. Coll. 67 (7).

Whittington, H. B., 1941. The Trinucleidae — with special reference to North American genera and species. J. Paleon. 15: 21–41.

———— 1956. Silicified Middle Ordovician trilobites: the Odontopleuridae. Mus. Comp. Zool. Bull. 114 (5).

———— 1957. Ontogeny of *Elliptocephala, Paradoxides, Sao, Blainia,* and *Triarthrus* (Trilobita). J. Paleon. 31: 934–946.

Zangerl, R., 1971. On the geologic significance of perfectly preserved fossils. Proc. N. Amer. Paleon. Conv., part I: 1207–1222.

Zangerl, R., et al., 1969. Early diagenetic phenomena in the Fayetteville black shale (Mississippian) of Arkansas. Sediment. Geol. 3: 87–119.

Zangerl, R., and E. S. Richardson, 1963. The paleoecological history of two Pennsylvanian black shales. Fieldiana (Geology) Mem. 4.
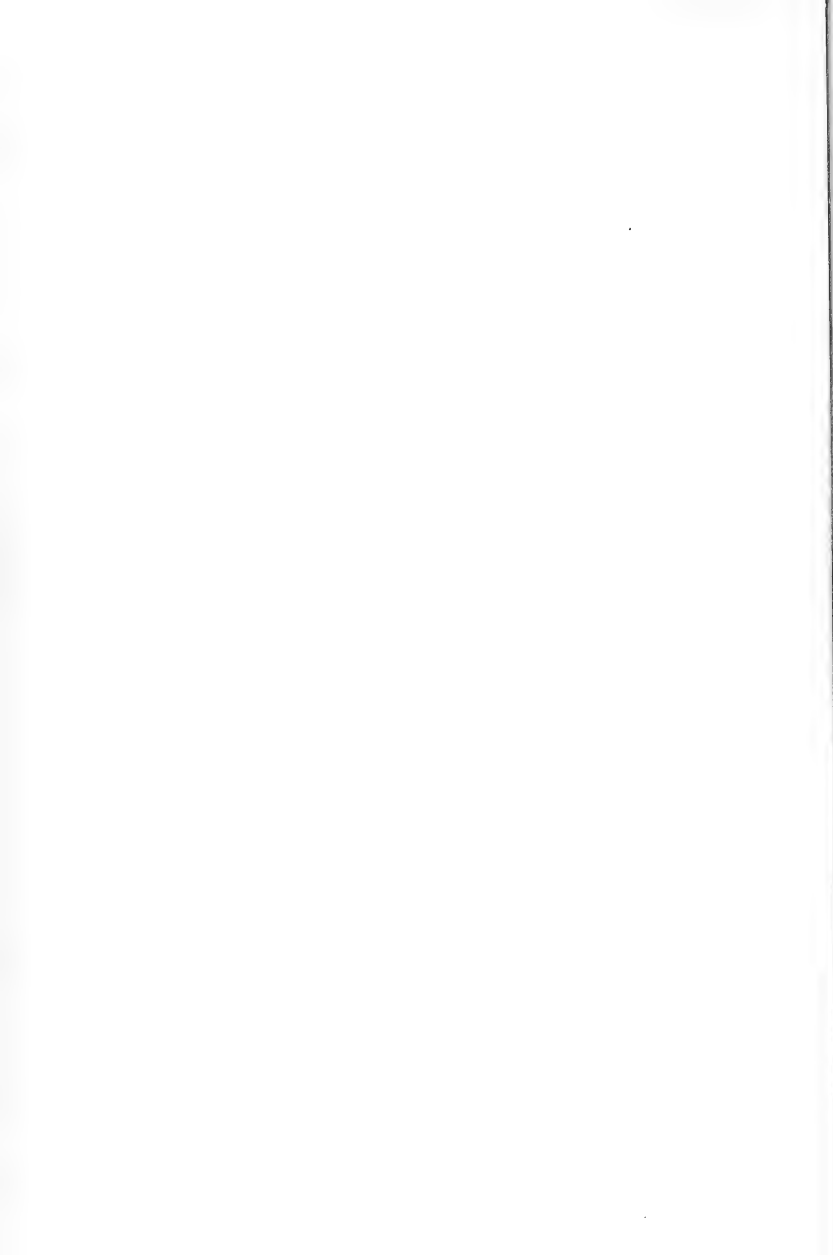
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