[AMERICAN JOURNAL OF SCIENCE, VOL. 271, OCTOBER, 1971, P. 227-251]

LIFE HABITS OF DIMINUTIVE BIVALVE MOLLUSCS IN THE MAQUOKETA FORMATION (UPPER ORDOVICIAN)

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ABSTRACT. The benthic invertebrate fauna of the basal Maquoketa Formation (Upper Ordovician) in eastern Iowa and northwestern Illinois has provided a near-classic example of a dwarfed or stunted faunal assemblage. Termed the Depauperate Zone or fauna by Ladd (ms, 1929), it consists of a low to moderately diverse assemblage of small-sized gastropods, scaphopods, bivalve molluscs, and linguloid brachiopods. Two species of nuculoid bivalve molluscs, *Palaeoneilo? fecunda* (Hall) and *Nuculites neglectus* (Hall), which dominate the faunal assemblage at many localities, have been extensively sampled for the first time in order to determine the possible causes for the apparent small size of the individuals.

Size-frequency distributions, survivorship curves, and size comparisons with congeneric Paleozoic species emphasize the fact that the individual nuculoids in the basal Maquoketa beds are indeed small. Perhaps more importantly, they represent mature populations, as there is no evidence of selective preservation of smaller-sized individuals. An environmental interpretation of the basal Maquoketa fauna and its sedimentological and stratigraphic setting indicates that the faunal assemblage was preserved where it was living. Post-mortem transportation of shells was negligible, and the phosphate-rich carbonate substratum was highly reworked biogenically.

Attempts to recognize the factors producing small individuals are normally equivocal, because similar environmental conditions have different effects on different taxa. Of all the physical, chemical, and biological factors previously suggested as causes of dwarfing or stunting, it appears that oxygen deficiency, abnormal salinity, and a deficient food supply have been considered the most crucial. We believe that stress conditions related to fluidity of the substratum, oxygen deficiency, and/or abnormal salinities probably limited the general type of invertebrates that could inhabit the basal Maquoketa environment, but that an abundant food resource rather than a deficient one was a major selective factor that caused the small size of the individual nuculoid bivalves. We suggest that a major portion of the depauperate fauna is composed of paedomorphic, rather than stunted, individuals, which had undergone selection for early maturity and high fecundity in a high-stress environmental setting.

INTRODUCTION

The present study is concerned with the life habits of small-sized nuculoid bivalve molluscs that occur in the basal beds of the Maquoketa Formation (Upper Ordovician) of eastern Iowa and northwestern Illinois. These beds were termed the Depauperate Bed or Zone by Ladd (ms, 1929); the small size of the individuals constituting the fauna has provided subsequent investigators (see especially Tasch, 1953; Hallam, 1965) with an example of a stunted or dwarfed assemblage. The fauna has never before been sampled extensively, however, and this is the first study to propose an environmental reconstruction and a detailed investigation of the autecology of a major faunal component.

Faunal assemblages composed of what appear to be abnormally small-sized individuals are common throughout the fossil record and are reported from a number of Recent environments (see especially Segerstrale, 1957; Ladd, Hedgpeth, and Post, 1957). Hallam (1965, p. 151), however, has cautioned one cannot readily determine what factors have produced

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the small individuals because similar environmental conditions affect different taxa differently. Of all the physical, chemical, and biological factors suggested as causes of dwarfing or stunting, it seems that oxygen deficiency, abnormal salinity, and a deficient food supply may be the most crucial. We believe that an abundant food resource rather than a deficient one was a major selective factor that caused the small size of the individual nuculoids in the basal Maquoketa beds. Through bulk sampling and subsequent analyses of growth-mortality curves, and through the investigation of faunal differences in size, density, and life habits throughout the basal Maquoketa, we feel that a major portion of the depauperate fauna is composed of paedomorphic, rather than stunted or dwarfed, individuals. Selection for early maturation and high fecundity enhanced survival in a high-stress or immature environment.

Most previous investigations of stunting in the fossil record have failed to consider rigorous criteria for establishing the maturity of the species under study, and the environmental settings have not been analyzed from the standpoint of the stability and maturity of the marine ecosystem in question. In this investigation we have attempted to bring into concert interpretations of the environmental setting from: (A) stratigraphic and sedimentological results (see especially Bromberger, ms), (B) a review of the probable ecological requirements of the total faunal assemblage (see Ladd, ms, 1929; Ojakangas, ms; Bretsky and Bermingham, 1970), and (C) a more detailed study of the life habits and autecology of two species of nuculoid bivalve molluscs, *Palaeoneilo? fecunda* (Hall) and *Nuculites neglectus* (Hall).

Stratigraphy.—Maquoketa strata are exposed along a narrow northwest to southeast band of the Driftless Area in Iowa and Illinois (fig. 1). The basal Maquoketa is distinctive lithologically and is composed of a highly phosphatic (hydroxylapatite) and ferruginous carbonate (mostly dolomitic); the phosphate occurs as pellets, nodules, and oolites (pl. 1, figs. A to C). The basal Maquoketa beds vary from a few centimeters to 60 cm thick in eastern Iowa and disappear near the Iowa-Minnesota border. These basal phosphatic beds appear to be entirely reworked, most likely biogenically. The phosphate nodules are larger near the lower contact with the Galena Formation where they encrust and partially infill a dolomitic bed in an apparently unconformable relationship (see fig. 2). At six localities (fig. 1, A-505, A-508, A-514, A-516, A-517, and A-521) a lithology similar to the basal beds occurs higher in the section, being separated from the basal beds by non-phosphatic ferruginous shales and shaly dolomites. Similar phosphatic beds have been identified also in the subsurface and in outcrop at other stratigraphic levels within the Maquoketa Formation in eastern Missouri, Illinois, and Indiana, and in the Upper Ordovician rocks of Michigan, Ohio, Kentucky, Arkansas, and Oklahoma. The reader is referred to Johnson (ms), DuBois (1945), Gutstadt (1954, 1958), Agnew (1955), and Templeton and Willman (1963) for detailed stratigraphic analyses of these phosphate-rich Upper Ordovician beds.

General environmental setting of the basal Maquoketa.—Studies of the basal Maquoketa beds by Bromberger (ms) and Bretsky and Bermingham (1970) have shown that the substratum was probably a soft and gently undulating, organically-rich carbonate mud, undergoing penecontemporaneous replacement by dolomite and phosphate. Eastern Iowa and northwestern Illinois were part of a regionally shallow epeiric sea, situated in a tropical or sub-tropical climatic belt. The environment was probably a warm-water one; this interpretation is derived from the paleomagnetic and paleoclimatic studies of Opdyke (1962), Ma (1962), and Fell (1968), who have delineated an Ordovician paleoequator within 10 to 15 degrees of the area of Maquoketa exposures.

The fauna of the basal beds is of low to moderate diversity and is characteristically dominated by large numbers of a few species: *Palaeoneilo? fecunda* and *Nuculites neglectus*, infaunal deposit-feeding bivalve molluscs; *Plagioglypta*, an infaunal deposit-feeding scaphopod; *Liospira*, an epifaunal detritus-feeding archaeogastropod; *Septemchiton*, an epifaunal (?) detritus-feeding polyplacophoran; and *Leptobolus*, an infaunal and/or epifaunal (?) suspension-feeding inarticulate brachiopod (see Ladd, ms, 1929; Johnson, ms; Ojakangas, ms; and Bretsky and Bermingham, 1970, for a more detailed discussion of the basal Maquoketa fauna). This fossil assemblage is dominantly molluscan and characteristically infaunal, and the geographic distribution of taxa was probably patchy at any one time during the deposition of the basal beds. The faunal composition, density, and diversity of the assemblage emphasize a relatively shallow-water, perhaps nearshore, environmental setting (Bretsky, 1968). Bretsky and Bermingham (1970) have proposed that there may have been local concentrations of algae. The algal stands could have contributed to the high organic content of the sediment, and, in addition, provided attachment and grazing sites for chitons and pleurotomarid gastropods, and served as a holdfast for the linguloid brachiopods. Articulate brachiopods are rare in these basal Maquoketa beds. Their scarcity may reflect severe limitations in sites for the settling and metamorphosis of articulate brachiopod larvae. To the north and west of the area under investigation, the basal Maquoketa is a fossiliferous limestone and dolomite, low in organic content and in phosphate, and it is here that articulate brachiopods are quite common, presumably having located a suitably firm or hard shell bottom (see Agnew, 1955; Bayer, ms; Bretsky, in preparation).

Nuculoid densities, incorporating counts of *Palaeoneilo? fecunda, Nuculites neglectus, Palaeoconcha obliqua* (Hall), *Palaeoconcha? hamburgensis* (Walcott), *Praenucula* spp., *"Ctenodonta" pulchella* Ulrich, and *"Ctenodonta" albertina* Ulrich, were computed for twelve localities (see fig. 3) and show that there is generally a decrease in density from the southeast to the northwest; this decrease coincides with the increase in the carbonate/phosphate ratio. The cause of this density pattern is unknown, but it is possible that epeiric surface currents controlled the distribution of phyto- and zooplankton, as did the equatorial current and counter-current patterns that heavily influenced the distribution of the

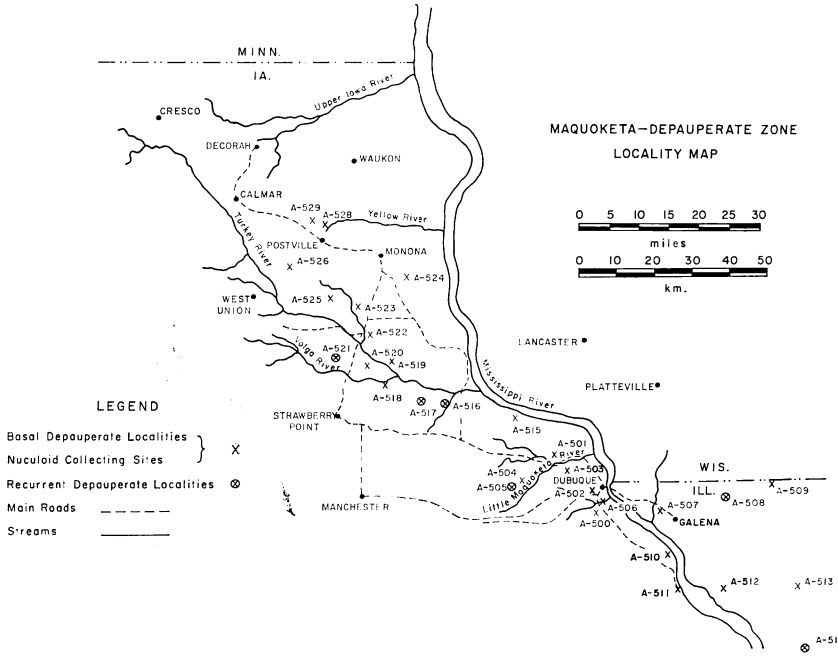

Fig. 1. Locality map. Numerals refer to exposures of the basal Maquoketa depauperate bed and collecting sites of nuculoid bivalve molluscs. Circles indicate exposures of the recurrent depauperate bed or beds.

A-500. Road ditch, Key West, sec. 13, T 88 N, R 2 E, Dubuque South Quadrangle, Dubuque County, Iowa.

A-501. Road ditch, Rickardsville, sec. 26, T 90 N, R 1 E, Sherrill Quadrangle, Dubuque County, Iowa.

A-502. Field, A&P Food Store, sec. 26, T 89 N, R 2 E, Dubuque South Quadrangle, Dubuque County, Iowa.

A-503. Quarry, Furnace Hollow, sec. 7, T 89 N, R 2 E, Sherrill Quadrangle, Dubuque County, Iowa.

A-504. Quarry, Twin Springs, sec. 16, T 89 N, R 1 E, Sherrill Quadrangle, Dubuque County, Iowa.

A-505. Road cut, Graf, sec. 29, T 89 N, R 1 E, Peosta Quadrangle, Dubuque County, Iowa.

A-506. Road cut, Junction 61-52, sec. 1, T 88 N, R 2 E, Dubuque South Quadrangle, Dubuque County, Iowa.

A-507. Road cut, Galena, sec. 3, T 28 N, R 1 W, Galena Quadrangle (15 min), Jo Daviess County, Ill.

A-508. Railroad cut, Scales Mound, sec. 26, T 29 N, R 2 E, Galena Quadrangle (15 min), Jo Daviess County, Ill.

A-509. Road ditch, Apple River, sec. 24, T 29 N, R 3 E, Elizabeth Quadrangle (15 min), Jo Daviess County, Ill.

A-510. Road ditch, Tete de Morte, sec. 14, T 87 N, R 4 E, Galena Quadrangle (15 min), Jackson County, Iowa.

A-511. Creek cut, Bellvue, sec. 19, T 86 N, R 5 E, Galena Quadrangle (15 min), Jackson County, Iowa.

A-512. River cut, Hanover, sec. 9, T 26 N, R 2 E, Galena Quadrangle (15 min), Jo Daviess County, Ill.

A-513. River cut, Elmoville, sec. 9, T 26 N, R 4 E, Elizabeth Quadrangle (15 min), Jo Daviess County, Ill.

A-514. Quarry, Mt. Carroll, sec. 10, T 25 N, R 4 E, Savanna Quadrangle (15 min), Carroll County, Ill.

continental margin faunas during the Late Ordovician (Williams, 1969). Perhaps bottom circulation increased toward the northwest and brought with it more nearly normal salinities and/or suitable conditions for suspension feeding, hence allowing the settlement of the normal marine articulate brachiopods. The initial establishment of a shell benthos would limit the area of potential colonization for infaunal soft-bottom species such as the nuculoid bivalve molluscs but would provide numerous settling sites for future articulate brachiopod spat. The density pattern may, however, be only apparent, having resulted from higher sedimentation rates to the northwest even though the standing crop of living animals was the same over the whole area. Dilution of the concentration of organic detritus by higher rates of inorganic sedimentation would in turn have limited phosphate formation and could also have discouraged colonization of the area by deposit-feeding nuculoids (R. Bambach, personal commun.).

Thus we believe that the sedimentological and paleontological evidence indicates that bottom currents were probably restricted to the southeast over a shallow, undulating depositional interface. Limited circulation could have been further inhibited by algal stands, which, in turn, would contribute to a continued organic build up and development of a soft, muddy substratum. Increased organic detritus and limited circulation would lead locally to oxygen-deficient toxic conditions near the sediment-water interface. Oxygen levels were reduced to such a degree in sediments of some microenvironments that sulfides were formed during the deposition of the basal beds. Deviations from normal marine salinities

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A-515. Road cut, Buena Vista, sec. 27, T 91 N, R 1 W, Cassville Quadrangle, Clayton County, Iowa.

A-516. Road ditch, Peck Creek, sec. 14, T 91 N, R 3 W, Colesburg Quadrangle, Clayton county, Iowa.

A-517. Road cut, Wayman Creek, sec. 7, T 91 N, R 3 W, Colesburg Quadrangle, Clayton County, Iowa.

A-518. Quarry, Littleport, sec. 25, T 92 N, R 5 W, Edgewood Quadrangle, Clayton County, Iowa.

A-519. Quarry, Motor, sec. 7, T 92 N, R 4 W, Littleport Quadrangle, Clayton County, Iowa.

A-520. Quarry, Osborne, sec. 9, T 92 N, R 5 W, Elkader Quadrangle, Clayton County, Iowa.

A-521. River cut, Volga, sec. 3, T 92 N, R 6 W, Volga Quadrangle, Clayton County, Iowa.

A-522. Road ditch, Elkader, sec. 14, T 93 N, R 5 W, St. Olaf Quadrangle, Clayton County, Iowa.

A-523. Quarry, North Big Springs, sec. 29, T 94 N, R 5 W, St. Olaf Quadrangle, Clayton County, Iowa.

A-524. Road cut, Froelich, SW¼ SE¼, sec. 28, T 95 N, R 4 W, La Crosse Quadrangle (1:250,000), Clayton County, Iowa.

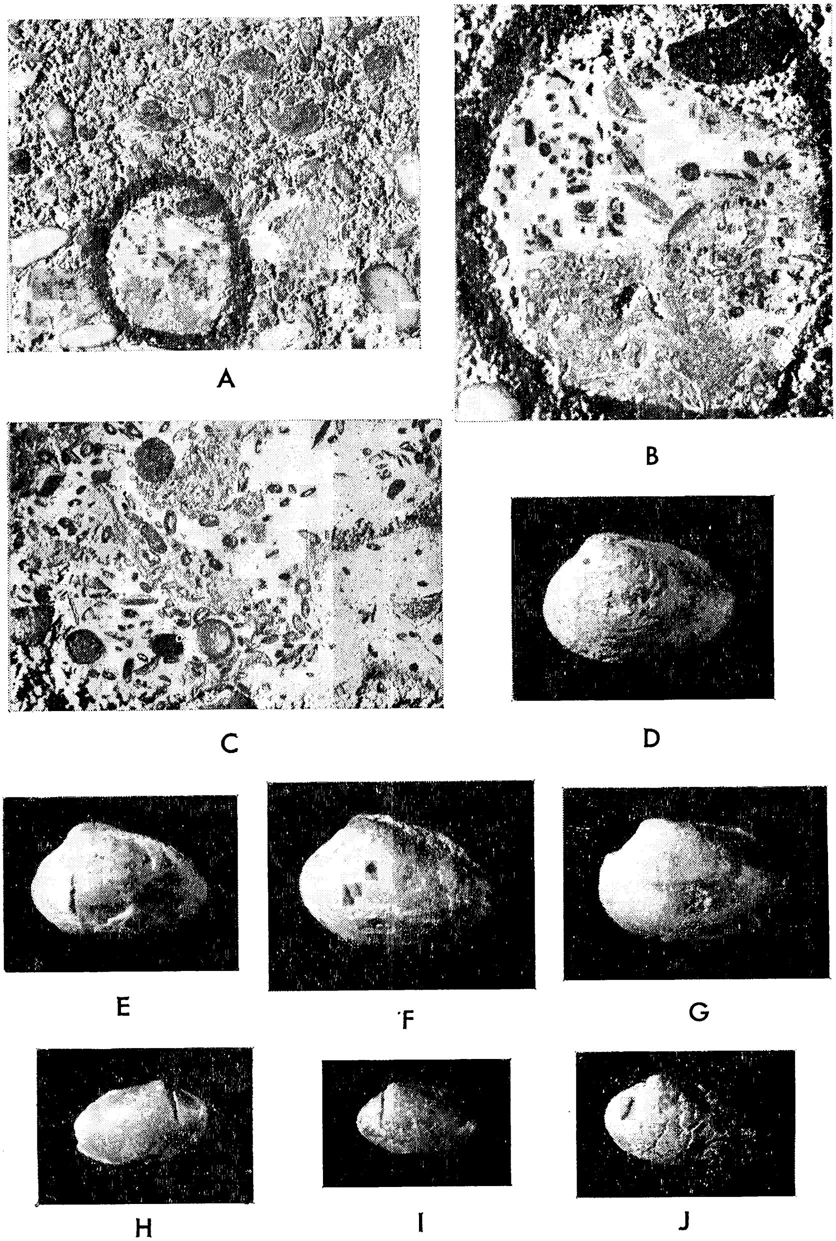
A-525. Quarry, Houg Cemetery, sec. 21, T 94 N, R 6 W, Gunder Quadrangle, Clayton County, Iowa.

A-526. Stream cut, Clermont, sec. 21, T 95 N, R 7 W, Decorah Quadrangle (30 min), Fayette County, Iowa.

A-528. Road cut, Postville, sec. 16, T 96 N, R 6 W, Decorah Quadrangle (30 min), Allamakee County, Iowa.

A-529. Road cut, Yellow River, sec. 13, T 96 N, R 7 W, Decorah Quadrangle (30 min), Winneshiek County, Iowa.

PLATE 1



also would be expected in the shallow, poorly circulating, warm waters. Therefore, these conditions, along with a soft substratum, would discourage a sessile benthonic life habit and furthermore would drastically limit the kinds of species attempting to occupy such an area of the epeiric sea floor.

Phosphate, which is characteristic of the basal beds, could have resulted from the accumulation of organic matter either through the development of extensive algal stands or through high planktonic productivity. The warm, shallow-water region experienced little terrigenous clastic sedimentation but received large amounts of organic detritus that could have provided an environment of phosphate precipitation, given the optimal P_{CO_2} and pH. The concentration of phosphates in the basal Maquoketa beds likely affected the penecontemporaneous replacement of carbonate mud and shells at or near the sediment-water interface, whereas direct interstitial precipitation of phosphate may have been locally important (Bromberger, ms). The reader is referred to Bushinskii (1964), Sheldon (1964), Bromley (1967), McKelvey (1967), D'Anglejan (1967, 1968), Kolodny (1969), and especially Tooms, Summerhayes, and Cronan (1969) for further discussion of Recent and fossil phosphate formation.

A Basal Maquoketa Life Assemblage.—The fossil assemblage of the basal Maquoketa appears from all available sedimentological and paleontological evidence to have been preserved where it was living. This interpretation is contrary to that of some previous investigators (see especially Tasch, 1953; Bromberger, ms) who have placed a great deal of emphasis on current and wave activity to account for a presumably transported and winnowed assemblage. A high degree of physical reworking was thought necessary to explain the unusually small-sized faunas of the basal Maquoketa beds. The shells, however, are rarely broken or abraded, and there is a high degree of articulation, especially in the nuculoid bivalves. Furthermore, growth or disturbance lines and other surface sculpture are often well preserved. The remarkable degree of detailed preservation of the Maquoketa nuculoid bivalves, and the fact that there is a marked discrepancy between the size-frequency distributions of *Nuculites neglectus* and the total sediment size-frequency histograms at the Mt. Carroll lo-

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PLATE 1

A.-B. Locality A-503 (Furnace Hollow, Iowa). A. Rock section of basal Maquoketa showing phosphate nodules, ×2; B. enlargement of circled nodule with inclusions of small shells, ×5.5.

C. Locality A-503 (Furnace Hollow, Iowa), portion of an elongate phosphate nodule with shell inclusions, ×4.5.

D. to G. *Palaeoneilo? fecunda* (Hall). D. Northwestern University Paleontological Collection #1350, Locality A-500 (Key West, Iowa), ×4; E. N.U.P.C. 1351, Locality A-507 (Galena, Illinois), ×3; F. N.U.P.C. 1352, Locality A-500 (Key West, Iowa), ×3; G. N.U.P.C. 1353, Locality A-500 (Key West, Iowa), ×3.

H. to J. *Nuculites neglectus* (Hall). H. N.U.P.C. 1354, Locality A-514 (Mt. Carroll, Illinois), ×3; I. N.U.P.C. 1355, Locality A-514 (Mt. Carroll, Illinois), ×3; J. N.U.P.C. 1356, Locality A-514 (Mt. Carroll, Illinois), ×3.

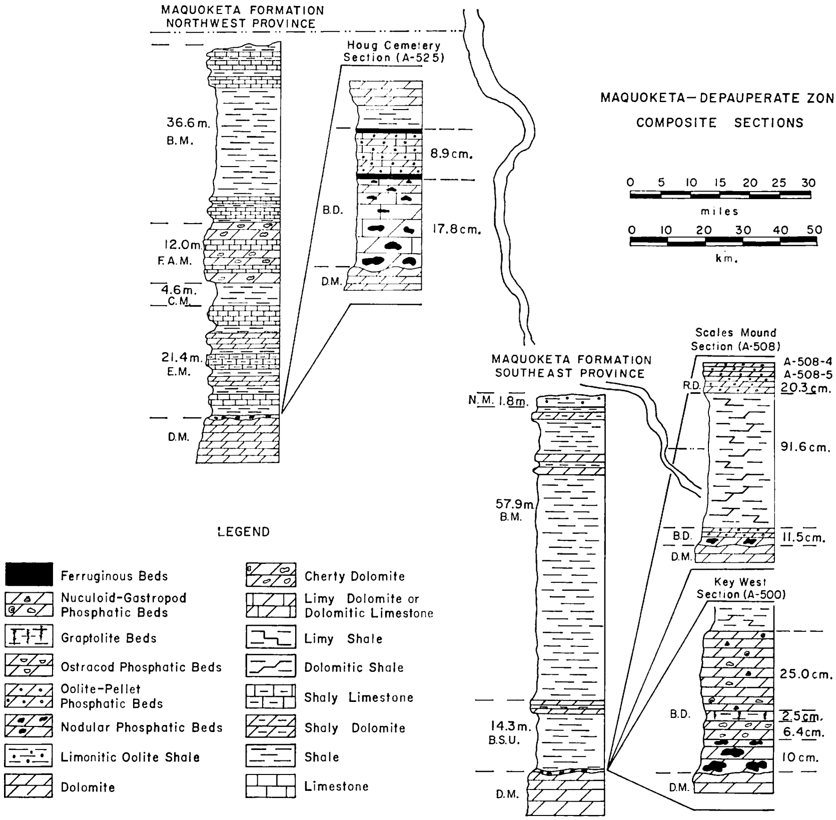

Fig. 2. Composite stratigraphic sections. The columnar section of the Maquoketa Formation in the southeast province is adapted from a subsurface drilling log (SW$\frac{1}{4}$ Dubuque South Quad., Dubuque County, Iowa, near loc. A-500; see Brown and Whitlow, 1960, p. 82). The columnar section of the Maquoketa Formation in the northwest province is adapted from a composite section given by Calvin (1906, p. 97-98; see also Savage, 1905, p. 484-486) from scattered outcrops in Fayette and Winneshiek Counties, Iowa, near our localities A-526 and A-529.

N.M.—Neda Member; B.M.—Brainard Member; F.A.M.—Fort Atkinson Member; C.M.—Clermont Member; E.M.—Elgin Member; B.S.U.—Brown Shaly Unit; R.D.—Recurrent Depauperate Zone; B.D.—Basal Depauperate Zone; D.M.—Dubuque Member (Galena Formation).

cality (see fig. 1, A-514), testifies only to mild, if indeed any, physical reworking.

Although the majority of individuals from the basal Maquoketa beds are 1 to 5 mm in their greatest dimension, some orthoconic cephalopods, inarticulate brachiopods, and the few articulate brachiopods are several centimeters long. Measurements of orthoconic cephalopods up to 10 cm in length from the basal beds indicate a wide range in the size of the faunal assemblage. Furthermore, the phosphatic nodules that are common in the basal beds show a similar large range of sizes, from oolites less than 250 mu in diameter to phosphatic nodules greater than 10 cm in diameter. In fact, the phosphate in many cases appears to take the form of internal and composite molds of valves and tests, and the "nodules" which are not of obvious organic origin show little appearance of abrasion or rounding. Also, there are no primary sedimentary structures in the basal beds characteristic of current activity.

All the sedimentological and paleontological factors listed above, in addition to the broad areal exposures of the basal Maquoketa beds, point up the fact that this fauna was preserved where it was living, with physical reworking occurring only in very localized situations. Finally, Bretsky and Bermingham (1970) have shown that the fauna of the basal Maquoketa is not unique but rather is quite similar in composition and environmental setting to assemblages of later Paleozoic ages.

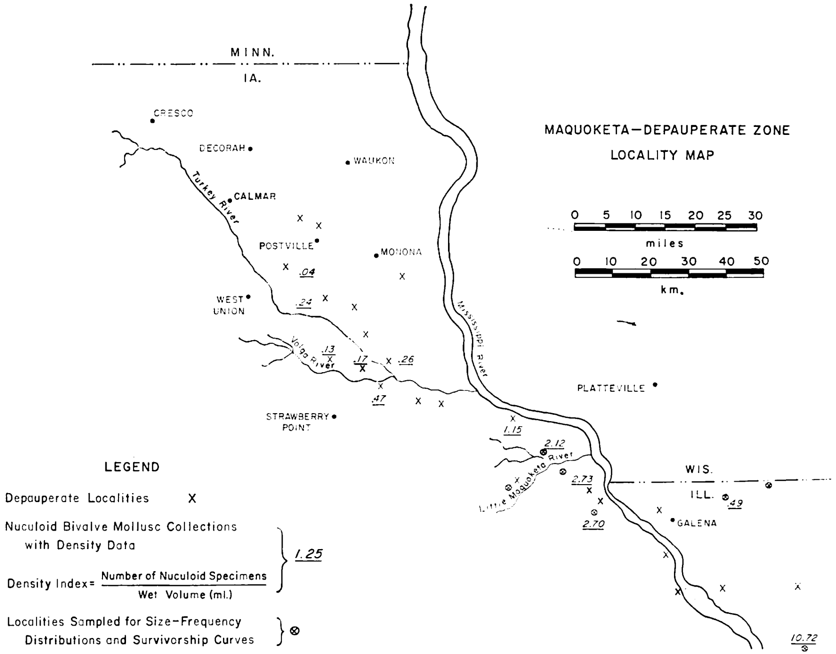

Fig. 3. Locality map. Numerals refer to nuculoid densities from selected localities of the basal Maquoketa depauperate beds. Circles are those localities sampled for size-frequency distributions and survivorship curves of *Palaeoneilo*? *fecunda* and/or *Nuculites neglectus*. Densities were computed from 12 localities where stratigraphic position was clearly determined and where the sediment could be completely disaggregated. The measurement is the number of nuculoids collected on sieves larger than 250 mu divided by the volume of water (ml) displaced by the sample. The densities recorded represent maximum values at those localities where several samples were taken from the basal beds.

Locality	Nuculoid density index	Locality	Nuculoid density index
A-500	2.70	A-518	0.47
A-501	2.12	A-519	0.26
A-503	2.73	A-520	0.17
A-508	0.49	A-521	0.13
A-514	10.72	A-525	0.24
A-515	1.15	A-526	0.04

GROWTH-MORTALITY OF *Palaeoneilo*? AND *Nuculites*

Size-frequency distributions and survivorship curves.—Size-frequency histograms have been used commonly to interpret growth, mortality, and seasonal recruitment of living and fossil invertebrate populations. Numerous previous investigations have discussed in detail the significance of size-frequency distributions in the deciphering of environmental settings. The reader is referred to the studies of Olson (1957), Hallam (1961, 1967), Craig and Hallam (1963), Craig and Oertel (1966), Craig (1967), Paine (1969), Schmidt and Warme (1969), and Levinton and Bambach (1970, and references therein).

In our study, bulk samples were collected from the basal Maquoketa and disaggregated in a solution of dilute hydrogen peroxide heated to approximately 200°C for a period of about 30 minutes. All nuculoid bivalve molluscs larger than 250 mu were picked from the dried and sieved disaggregated samples of known volume; these nuculoid bivalves were then sorted, identified (after Ulrich, 1897; McAlester, 1968, 1969), and measured. *Palaeoneilo*? *fecunda* (Hall) and *Nuculites neglectus* (Hall) are the most abundant nuculoid bivalves, although there appear to be at least five other nuculoid taxa in the basal Maquoketa collections (J. Snyder, in preparation). Size-frequency histograms were compiled (U.C.L.A. Biometrics Program BMD05D) using data collected from localities where stratigraphic positions were clearly recognizable and selected samples contained more than 50 specimens of *Nuculites* and/or *Palaeoneilo*? (see figs. 1 and 3).

Because of the overall lithologic continuity of the basal Maquoketa, the lack of primary sedimentary structures, and the homogeneous and reworked nature of the rock, it is believed that environmental conditions remained reasonably constant throughout the deposition and subsequent biogenic reworking of the entire basal Maquoketa. Hence, environmental influences that could significantly vary in their effects on the size-frequency distributions are thought to have been constant for all generations in each sample. Simply enough, there is no sedimentological or faunal evidence that might indicate mass mortalities or any other catastrophic event leading to the total extinction of one generation at a specific point in time during the deposition of the basal Maquoketa. The fossils are found throughout the reworked rock, and there are no high concentrations of valves on any one bedding plane. Thus, like Levinton and Bambach (1970), we shall assume that the size-frequency distributions from collections at any one exposure of the basal beds are representative of the relative number of nuculoid bivalves typifying each size interval at any one instant in time during deposition.

Since size-frequency histograms incorporate both growth and mortality variables, to further aid in the interpretation of the life habits and environmental setting of *Nuculites* and *Palaeoneilo*? we constructed survivorship curves based on the growth-rate relationship for bivalve molluscs derived by Levinton and Bambach (1970, p. 99):

$$D = s \ln (T + 1)$$

where D is size, T is time, and s is a constant. Again, the reader is referred to other studies by Schmidt and Warme (1969), Kaesler and Fisher (1969), Craig and Hallam (1963), and Hallam (1967) for detailed discussions of the significance of survivorship curves in the interpretation of environmental settings. Hallam (1967, p. 32) has shown that although bivalve molluscs show continual growth, sometimes it is distinctly non-linear and can be a constantly decreasing logarithmic function of time. Although it should be stressed that not all bivalve growth is logarithmically decreasing, the relationship above appears to be a realistic first approximation. Acceptance of the log transformation of growth permits an interpretation of the size-frequency distributions of the basal Maquoketa bivalves in terms of mortality only or the number of individuals dying per interval of time.

In the present study size has been reduced to a percentage, the largest shell size in each sample represents 100 percent growth for that particular population. Size-frequency distributions that contain a large shell three or more size classes above its nearest neighbor are truncated at the right tail. The inclusion of the extreme-value specimens would result in marked, but spurious, changes in the slope of the survivorship curves, especially misleading in the smaller samples.

Measurements on Palaeoneilo? fecunda (Hall).—*Palaeoneilo? fecunda* (Hall) is a small-sized, posteriorly elongate nuculoid bivalve mollusc. It is moderately inflated, thick-shelled, and of variable shape (pl. 1, figs. D-G). The generic assignment of this species is tentative; the shell possessing characteristics of both *Palaeoneilo* and *Tancrediopsis*. Hence, *Palaeoneilo? fecunda* likely belongs to a genus as yet undescribed and therefore must be classified as *nomen inquirendum*. Well-preserved articulated valves are common in the basal Maquoketa where the calcium carbonate shell has been replaced by hydroxylapatite (see Bretsky and Bermingham, 1970).

Total length, height, and anterior length histograms for *P.? fecunda* at the Mt. Carroll exposure (fig. 1, loc. A-514) show positively-skewed, approximately log-normal, size-frequency distributions (fig. 4). Differences in the shape of the histograms among the three parameters perhaps reflect allometric growth, measurement error, or both. Because of the large number of specimens, however, the Mt. Carroll histograms exhibit what may be interpreted as secondary and tertiary peakings, especially in height. These peaks may represent: (1) a seasonal slowdown in growth, a situation that could complicate the assumed logarithmic relationship between growth and size, (2) an increase in mortality during one part of the year, (3) periodic or seasonal recuitment of spat, or (4) some combination of these three conditions.

Size-frequency distributions for *P.? fecunda* taken from one of the horizons of the recurrent Maquoketa depauperate beds at the Scales Mound, Illinois exposure (fig. 1, A-508; and fig. 2, southeast columnar section, A-508-5) exhibit a more pronounced positive skewness (fig. 5) than do those from Mt. Carroll. Furthermore, any indication of secondary

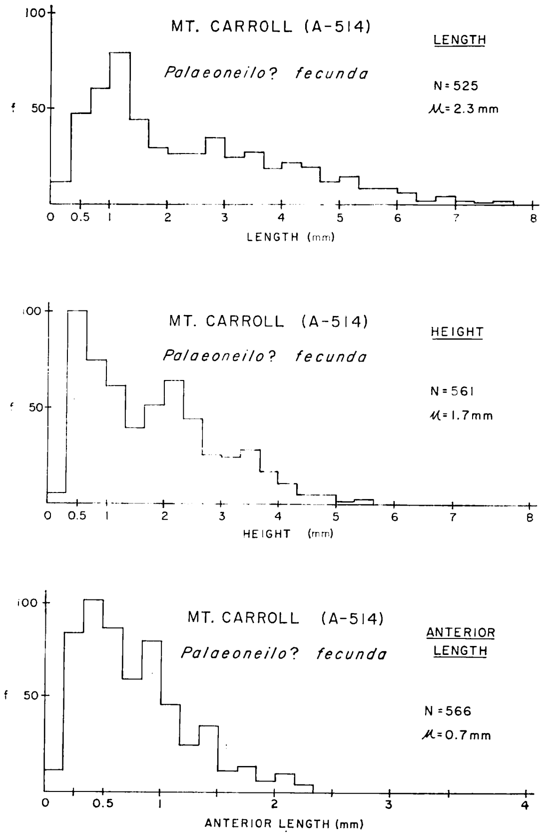

Fig. 4. Size-frequency distributions of length, height, and anterior length of *Palaeoneilo? fecunda* at Mt. Carroll, Ill. (A-514).

and tertiary peaking is absent or very poorly defined in this Scales Mound collection; this may be a direct result of a smaller sample size, as the collection from Scales Mound has only about half as many individuals as those from Mt. Carroll.

Survivorship curves drawn from the size-frequency distributions of *P.? fecunda* at Mt. Carroll (A-514) describe nearly linear mortality rates (fig. 6). The very slight perturbations in slope in the upper part of the curves may reflect the secondary peaks in the histograms (fig. 4). Changes in the slope in the lower parts are more likely a function of the small number of specimens in the larger size intervals; the lower half of the survivorship curve represents less than 4 percent of the total population. Survivorship curves from the fifth horizon of the recurrent depauperate beds at Scales Mound (fig. 7, A-508-5) are initially steeper for all parameters than those from Mt. Carroll (fig. 6), and they are noticeably sigmoidal in over-all shape, probably indicative of non-linear mortality.

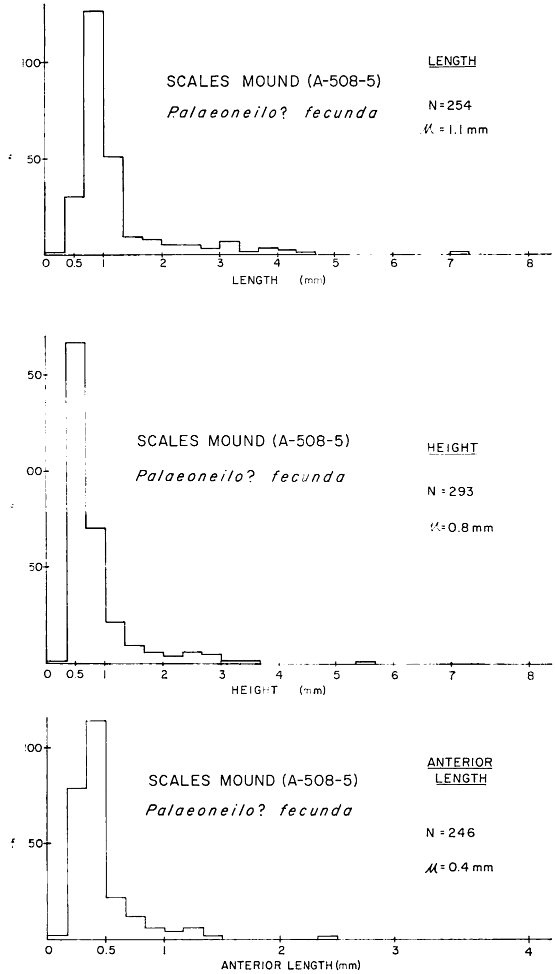

Fig. 5. Size-frequency distributions of length, height, and anterior length of *Palaeoneilo? fecunda* at the fifth horizon at Scales Mound, Ill. (A-508-5).

Measurements on Nuculites neglectus *(Hall).—Nuculites neglectus* (Hall) is a small-sized, posteriorly elongate nuculoid bivalve compressed to moderately inflated, thin-shelled, and of variable shape (pl. 1, figs. H-J). As was the case for *Palaeoneilo? fecunda,* the *Nuculites* valves are commonly articulated and replaced by hydroxylapatite. Size-frequency distributions of *Nuculites neglectus* from Mt. Carroll (fig. 8, A-514), and Scales Mound (fig. 9, A-508-5) again appear to describe log-normal distributions for all three measured parameters. As was the case for *Palaeoneilo? fecunda,* secondary and tertiary peaks in the histograms can be interpreted only from the Mt. Carroll samples and, as before, may be a result of having greater numbers of specimens from the Mt. Carroll exposure.

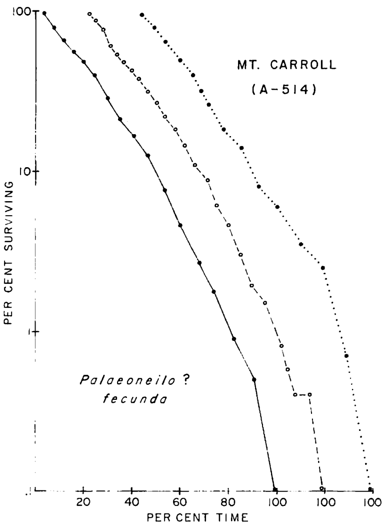

Fig. 6

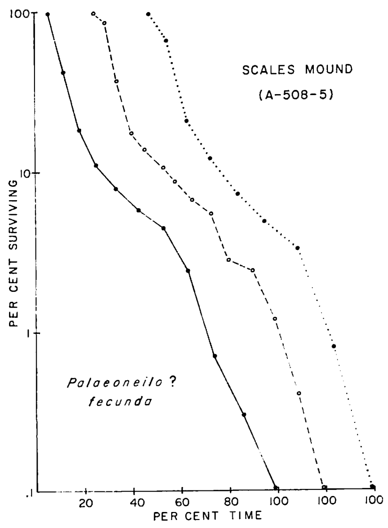

Fig. 7

Fig. 6. Survivorship curves for height (solid line), total length (dash), and anterior length (dot) of *Palaeoneilo? fecunda* at Mt. Carroll, Ill. (A-514).

Fig. 7. Survivorship curves for height (solid line), total length (dash), and anterior length (dot) of *Palaeoneilo? fecunda* at the fifth horizon at Scales Mound, Ill. (A-508-5).

Neglecting minor shape changes in the survivorship curves for *N. neglectus* at Mt. Carroll (fig. 10, A-514), there is an apparent linearity. This, however, is not the case for *N. neglectus* at Scales Mound (A-508-5), where the survivorship curves (fig. 11) have well-defined sigmoidal shapes. Interpretations based on previously discussed growth assumptions suggest that in the latter instance there is a high juvenile, low adult, and high old-age mortality rate.

DISCUSSION

Life habits of Palaeoneilo? fecunda *and* Nuculites neglectus.—*Palaeoneilo? fecunda* was most likely an infaunal siphonate, palp-proboscide deposit feeder (fig. 12) and presumably was morphologically and autecologically similar to either *Yoldia* or *Malletia,* both modern burrowing nuculanaceans. Yonge (1939), Sanders (1956, 1960), Rhoads (1963), and Stanley (ms) describe nuculanaceans as being actively burrowing deposit feeders which live with the shell's long axis at a moderate to high angle to the horizontal. The basal Maquoketa specimens probably lived several millimeters below the sediment-water interface and moved laterally during times of feeding. Like *P.? fecunda, Nuculites* presumably was an infaunal siphonate form (see also fig. 12), closely related to the modern nuculanacean *Yoldia* in basic life habit. However, because *N. neglectus* is more elongated than *Palaeoneilo?*, it probably lived at greater depth, with its posterior tip perhaps somewhat more than one centimeter below the sediment-water interface.

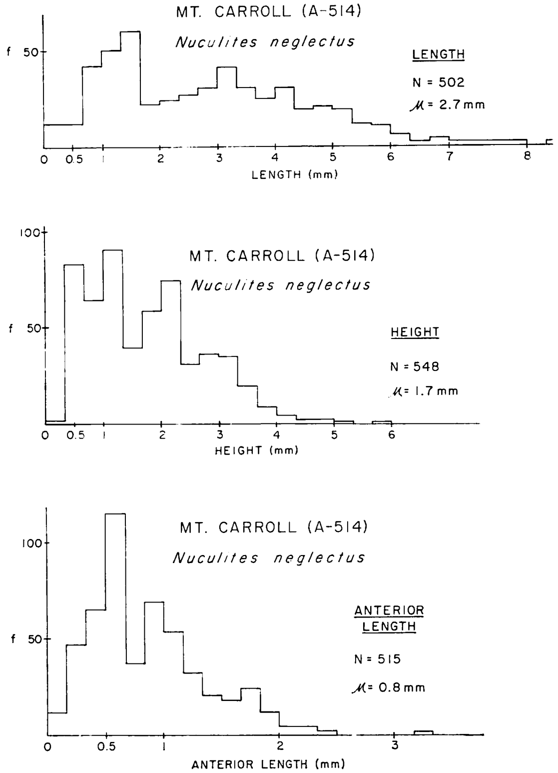

Fig. 8. Size-frequency distributions of length, height, and anterior length of *Nuculites neglectus* at Mt. Carroll, Ill. (A-514).

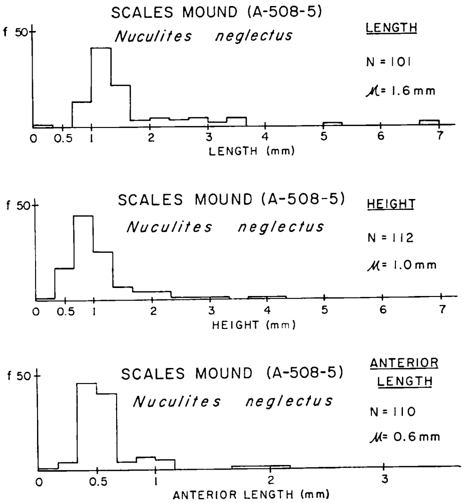

Fig. 9. Size-frequency distributions of length, height, and anterior length of *Nuculites neglectus* at the fifth horizon at Scales Mound, Ill. (A-508-5).

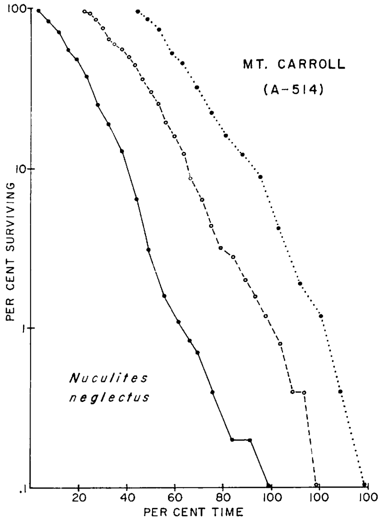

Fig. 10

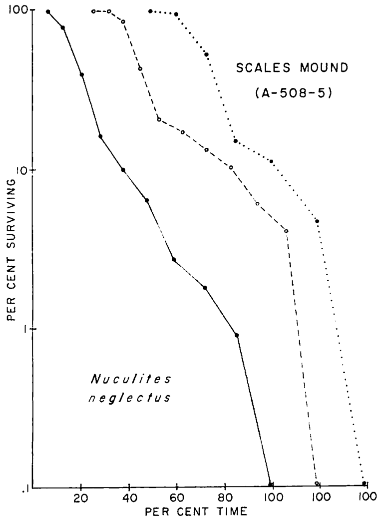

Fig. 11

Fig. 10. Survivorship curves for height (solid line), total length (dash), and anterior length (dot) of *Nuculites neglectus* at Mt. Carroll, Ill. (A-514).

Fig. 11. Survivorship curves for height (solid line), total length (dash), and anterior length (dot) of *Nuculites neglectus* at the fifth horizon at Scales Mound, Ill. (A-508-5).

Differences in the size-frequency distributions or the slope of survivorship curves of *Palaeoneilo*? *fecunda* and *Nuculites neglectus* most likely are reflections of varying life habits and life histories within or between localities (see Hallam, 1961; Levinton and Bambach, 1970). If the death assemblages of the basal Maquoketa beds accurately reflect the life assemblages, as we believe they do, there is scope for a more thorough examination of the population densities, which should be controlled by the combination of physical and biotic environmental components at each locality. In the basal Maquoketa beds extensive biogenic reworking and the formation of numerous fecal pellets by the nuculoid bivalves would be expected in an organically-rich muddy carbonate substratum. The reworking apparently took place in the absence of strong bottom currents and should have resulted in a physically unstable, highly fluid substratum. This type of "soupy", turbid sediment-water interface, perhaps less than a centimeter thick, would be underlain by more cohesive muds of lower fluidity (see Levinton and Bambach, 1970) for examples from Recent environments).

This soft, muddy benthic regime would probably be an ideal habitat for infaunal deposit feeders, whereas epifaunal and infaunal suspension feeders would be selected against. Furthermore, the degree of fluidity and/or the levels of oxygen and salinity in or immediately above the substratum probably placed severe demands on even stenotopic species (see Theede and others, 1969, for a discussion of tolerance to oxygen deficiency and hydrogen sulfide in Recent invertebrates). Although the differences

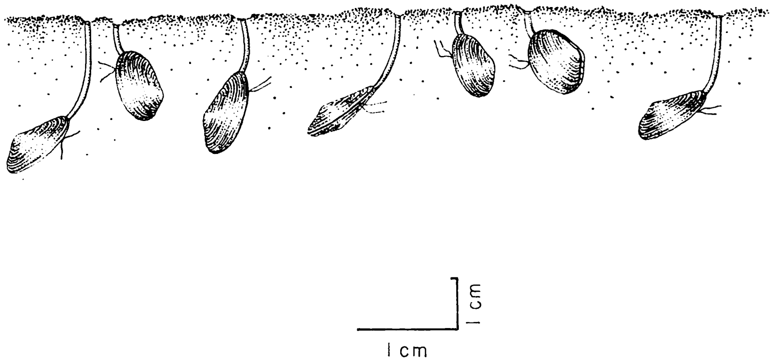

Fig. 12 A reconstruction of the life habits of *Palaeoneilo? fecunda* and *Nuculites neglectus* in the basal Maquoketa sediment. *Nuculites* is more elongate and deeper burrowing.

in sediment size, mineralogy, and chemical composition at the various basal Maquoketa exposures are slight, there appear to be pronounced dissimilarities in the survivorship curves of *Palaeoneilo? fecunda* and *Nuculites neglectus* especially between localities, which may be the result of fluidity, oxygen, and/or salinity variations. Minor variations in these parameters, while they may have exerted quite a strong selective pressure, are difficult to document in the fossil record.

Juvenile mortality rates, as exhibited in survivorship curves of *Palaeoneilo? and Nuculites* at Scales Mound (figs. 7 and 11, loc. A-508-5) are higher than those at Mt. Carroll (figs. 6 and 10, loc. A-514) perhaps reflecting a less favorable site for the settlement and early development of nuculoid spat at Scales Mound. A more highly fluid and turbid substratum at Scales Mound would cause increased clogging of ctenidia and would provide a possible explanation of the increased juvenile mortality. Nuculanacean spat which were able to survive in the more turbid regime at Scales Mound would subsequently become lodged in a more cohesive sediment below the high turbidity layer and would presumably experience a decreased mortality rate after reaching a critical size. Furthermore, *N. neglectus,* presumably a deeper burrowing form than *Palaeoneilo?* (see fig. 12), would have had a selective advantage in establishing itself in the more cohesive sediment and hence also would exhibit greater fitness in the more mature stages. *P.? fecunda* does exhibit significantly higher juvenile mortality than *N. neglectus* at Scales Mound and also has a higher mortality in presumably more mature individuals, as seen in the steeper slopes of the middle part of the survivorship curves for total length and anterior length (figs. 7 and 11). Both species apparently have increased mortality rates in the gerontic stages, resulting in the characteristic sigmoidal curves (that is, high-low-high mortality). Turbidity and/or fluidity at the sediment-water interface may have been of lesser importance at Mt. Carroll (A-514), because the initial slopes of survivorship curves for both species are more gentle, indicating lower juvenile mortality rates.

Another interspecific selection factor to consider, particularly in juvenile nuculoids, involves the degree of ctenidial activity in the gathering of potential food particles (suspension feeding), in addition to the normal palp-proboscide deposit feeding. Stasek (1965) reported that *Yoldia ensifera,* a modern burrowing nuculanacean, employed a ctenidial filter-feeding mechanism in food collection, although the details of the feeding are unknown. In a highly turbid regime, the deposit-feeding nuculoid utilizing the least amount of suspension feeding would likely have a selective advantage. Hence this may play some role in the increased survival of *Nuculites neglectus* in both juvenile and mature stages of growth at Scales Mound.

Nuculoid paedomorphosis.—Table 1 and figures 13 and 14 emphasize the fact that *Nuculites neglectus* in the basal Maquoketa beds is significantly smaller than other Lower Paleozoic congeneric populations. Selective preservation alone cannot account for the small size of the nuculoids

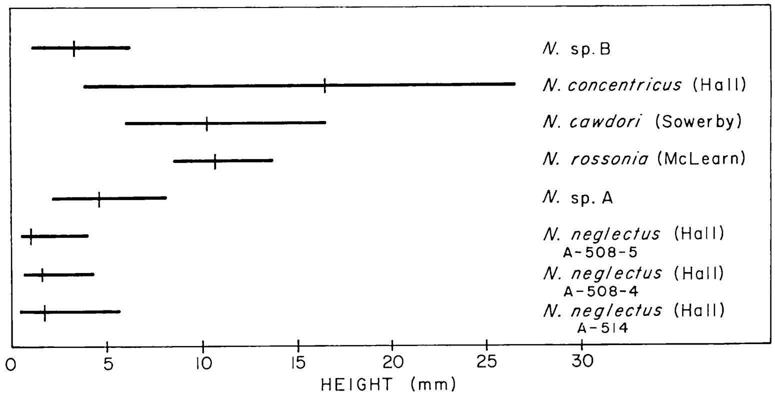

Fig. 13. A comparison of means, maximum and minimum ranges for height of some lower Paleozoic species of *Nuculites.* See also table 1 for references.

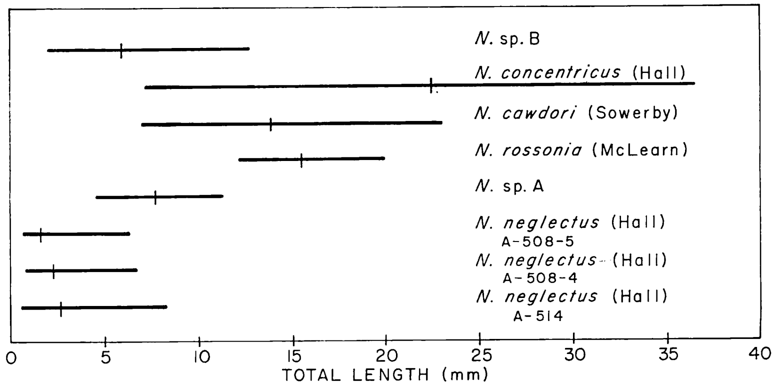

Fig. 14. A comparison of means, maximum and minimum ranges for length of some lower Paleozoic species of *Nuculites.* See also table 1 for references.

in the basal Maquoketa beds, and recourse to any such explanation fails on sedimentological and paleontological grounds. The shells are articulated and extremely well preserved, albeit replaced by phosphate. Appeal to rigorous current segregation, selective diagenetic solution, or fragmentation of the large shells by wave action or predators is inconsistent with the occurrence and preservational appearance of *P.? fecunda* and *N. neglectus* individuals, while size-frequency distributions of both species rule out mass juvenile mortality as a cause of the small size.

A more probable explanation for the small size of the individuals may be that the basal Maquoketa environmental setting is a good example of a physically unstable, immature ecosystem, *sensu* Margalef (1963). The primary productivity-biomass ratio, which is a measure of the flow or loss of energy, appears to have been very high. This conclusion is based simply on the accumulation of organic matter. The physical environment, including levels of fluidity, oxygen, and salinity, probably was not regular or predictable but quite rigorous. The shallow, warm waters of the basal Maquoketa sea were a high-stress environmental situation which favored the type of species population termed *opportunistic* (see Levinton, 1970), or *r*-strategists (see MacArthur and Wilson, 1967, p. 149). The *r*-strategists (from *r*, the intrinsic rate of natural increase) exhibit selection for early maturation and possess maximum rates of potential increase in an environment with unlimited resources. Their decreased survival rates and over-all inefficiency at utilizing the plentiful

SIZES OF LOWER PALEOZOIC SPECIES OF *NUCULITES*
TABLE I

	Means			N	AGE STATIGRAPHIC POSITION LOCALITY
	LENGTH (mm)	HEIGHT (mm)	ANTERIOR LENGTH (mm)	Specimens	
N. neglectus (Hall) A-514	2.7			502	Upper Ordovician Maquoketa Formation NW Illinois
		1.7		548	
			0.8	515	
N. neglectus (Hall) A-508-4	2.3			109	Upper Ordovician Maquoketa Formation NW Illinois
		1.6		112	
			0.8	111	
N. neglectus (Hall) A-508-5	1.6			101	Upper Ordovician Maquoketa Formation NW Illinois
		1.0		112	
			0.6	110	
N. sp. A (Bambach, 1969, p.284)	7.7	4.6		24	Silurian–Devonian Arisaig Group Nova Scotia
N. rossonia (McLearn) (Bambach, 1969, p.287)	15.5	10.7		17	Silurian–Devonian Arisaig Group Nova Scotia
N. cawdori (Sowerby) (Bambach, 1969, p.290)	13.9	10.3		137	Silurian–Devonian Arisaig Group Nova Scotia
N. concentricus (Hall) (Bambach, 1969, p.294)	22.5	16.5		135	Silurian–Devonian Arisaig Group Nova Scotia
N. sp. B (P. Richards, pers. comm.)	6.0			70	Upper Ordovician Tanners Creek Fm. Indiana
		3.3		61	

resources is outweighed by their intrinsically high rate of propagation (see especially Margalef, 1963; Gadgil and Bossert, 1970). Hence, given rigorous environmental conditions, the species selected would be those that would mature the earliest and have the highest productivity. Those few most successful species would flourish at the expense of all the others, dominate the environment, and drastically lower the faunal diversity. This appears to be the case at the Mt. Carroll and Scales Mound localities, where *Palaeoneilo*? *fecunda* and *Nuculites neglectus* are very abundant in faunal assemblages of low diversity.

The small size of the individuals in the populations of *P.*? *fecunda* and *N. neglectus* might be viewed theoretically as a paedomorphic characteristic. The normal adult size is not attained, because of early maturation accompanied by a decreased life cycle length (see table 1; figs. 13 and 14), hence permitting the species, through increased fecundity of younger individuals, to survive in a rigorous and immature environmental situation. All previous explanations for the small size of the basal Maquoketa faunas, the classic "Depauperate Zone", have called upon a more direct physiologically controlled environmental stunting. Ladd (ms), Tasch (1953), Ojakangas (ms), and Bretsky and Bermingham (1970) have stressed a variety of ecological conditions such as oxygen-deficiency, hypersalinity, or unusually high concentrations of iron or phosphate in the sea water to explain a physical stunting. Paedomorphosis (or paedogenesis), implying early maturation rather than the stunting of adult forms, does not require appeal to a specific environmental parameter to slow or arrest growth rates; hence the size-frequency distributions and survivorship curves can be viewed in terms of a viable biotic selection mechanism. Furthermore, dissimilarities in a species' size-frequency distributions between localities in the basal Maquoketa beds (for example, *P.*? *fecunda* at Mt. Carroll and Scales Mound) may reflect local variance in the number of paedomorphic individuals in each population, possibly resulting from slightly different selection factors imposed by differing environmental conditions, and thus varied adaptive responses at these localities. While we have at present no direct morphological evidence for paedomorphosis (evidential strength would come from a detailed allometric study of the Maquoketa and conspecific specimens, a study that would appear to be highly improbable given these particular molluscs; or comparative counts of growth lines from the "dwarfed" and "normal"-sized conspecific populations, which would attempt to document the fact that the adults in the "dwarfed" population are truly younger, a study that would be possible given a more rigorous systematic study of Upper Ordovician nuculoids), this mechanism not only would account for the small sizes but also would be reasonably likely to occur in an immature environment, resulting from the high biotic productivity during the deposition of the basal Maquoketa beds.

Although the majority of the individuals in the basal Maquoketa are small-sized, there are some larger, seemingly normal-sized species populations. Some fairly large orthoconic cephalopods, presumably nektonic, are locally common. Furthermore, normal-sized ostracods, which possess some distinctive morphological features that might preclude a crawling or burrowing habitat (see Bretsky and Bermingham, 1970), may have been part of the nekton or plankton. Their presence may emphasize that paedomorphosis was selected for only at or near the sediment-water interface. On the other hand, there are some large infaunal linguloid brachiopods (1 cm length); perhaps these linguloid populations reflect selective factors for normal population size in areas of lower oxygen requirements or abnormal salinities. Craig (1952) found that some species of *Lingula* are adapted to a blackened and ill-smelling, oxygen-deficient, sandy-mud substratum along the coast of southern Japan, an environment hostile to most other benthic organisms. Simply enough, the overall fitness of normal-sized nuculoid bivalve individuals should be greater in less rigorous but yet somewhat marginal regimes; however, nuculoids are adapted also to the higher stress environments of the basal Maquoketa but, when compared to the larger sized individual nuculoids of other lower Paleozoic environments (see table 1), show a significant change in their responses to selection. The linguloid brachiopods in the basal Maquoketa probably occupied an environment essentially optimal for linguloids but habitable only by those nuculoids that adapted to it through paedomorphosis.

In light of the proposed biotic selection mechanism for the basal Maquoketa assemblage, we propose that other Paleozoic faunas which exhibit unusually small-sized populations may be analogous to the basal Maquoketa fauna in that they represent paedomorphic responses to high-stress, environmental selection factors. The Pennsylvanian "Dry Shale Fauna" of Kansas (Tasch, 1957) occurs in an argillaceous, limonitic sediment and contains primarily benthonic individuals (bivalves, gastropods, and brachiopods) of diminutive size. Nuculoid bivalve molluscs in this Pennsylvanian fauna, namely *"Nuculana" bellistriata, Anthraconeilopsis kansana,* and *Nuculanella piedmontia,* were thought to be composed almost exclusively of juvenile forms. Small bivalves and gastropods are dominant in faunas of the Permian Magnesian Limestone of England (Trechmann, 1913) and of the Devonian Leicester Pyrite (Tully Limestone of Loomis, 1903) and Ludlowville Formation (Fisher, 1951) of the Hamilton Group in western New York. All these strata contain large amounts of pyrite or marcasite. Furthermore, "dwarfed" bivalves and/or gastropods are present in phosphate-rich sediment of the basal beds of the Middle Ordovician Guttenberg Formation of southwestern Wisconsin (Ball, 1935) and of the Permian Phosphoria Formation of Montana (Branson, 1930). A diminutive assemblage (primarily gastropods), preserved in a white oolitic chert, also occurs in the Lower Ordovician Shakopee Formation at Cannon Falls, Minnesota (Stauffer, 1937). Most, if not all, of the above faunas may come from unstable, immature environmental situations which seem to have had restricted circulation and high organic content.

CONCLUSIONS

The basal and recurrent depauperate beds of the Maquoketa Formation (Upper Ordovician) in eastern Iowa and northwestern Illinois represent a high-stress, immature environmental setting. The substratum was predominantly a soft, gently undulating, organically-rich carbonate mud, which underwent penecontemporaneous replacement by dolomite, phosphate, and sulfides. The sediments were deposited in a regionally shallow, tropical to sub-tropical epeiric sea. Limited bottom circulation, apparently promoted by slightly irregular marine topography, the broad expanse of the epeiric sea, and local concentrations of algal stands, led to local oxygen deficiency, hypersalinity, and/or organic buildup (including P_2O_5) near the sediment-water interface. Extensive biogenic reworking and formation of fecal pellets resulted in a physically unstable, highly fluid substratum which underwent continued resuspension. A "soupy", turbid sediment-water interfacial layer perhaps less than a centimeter thick, would have been underlain by a more cohesive mud of lower fluidity.

This rigorous environmental framework would favor selection for opportunistic species, or *r*-strategists, leading to a benthic invertebrate fauna dominated by infaunal deposit-feeders. The excellent preservation and the size-frequency distributions of the nuculoid bivalve molluscs *Palaeoneilo? fecunda* and *Nuculites neglectus* in the basal Maquoketa beds point to mature populations which were preserved where they were living. Higher juvenile mortalities of both species at Scales Mound (A-508-5), as evidenced in survivorship curves, probably can be correlated with higher sediment fluidity at that site. *Nuculites neglectus,* presumably a deeper-burrowing nuculanid bivalve, was apparently slightly more fit in a highly fluid sediment regime, as shown by lower mortality rates in the middle mature stages of the survivorship curves at Scales Mound.

The diminutive size of the basal Maquoketa nuculoid populations is thought to have been a selection for paedomorphic individuals, implying early maturation, high fecundity, and accompanying decrease in life cycle length in this rigorous environment. Adaptive strategies of the nuculoids, involving paedomorphosis, would ensure survival in an immature benthic setting and would promote domination in an assemblage of low to moderate diversity.

Selection for paedomorphosis permits an explanation of small size without appealing to a specific environmental parameter that slowed or arrested growth, causing stunting. The presence of normal-sized ostracods and orthoconic cephalopods in the basal Maquoketa assemblage may indicate that paedomorphic selection pressures affected only the fauna at the sediment-water interface. Large infaunal linguloid brachiopods may have been genetically better adapted than were most other faunal constituents to lower oxygen supply and/or higher salinities. Other Paleozoic regimes which have unusually small-sized populations may also reflect assemblages responding paedomorphically to high-stress environments.

ACKNOWLEDGMENTS

We thank L. L. Sloss, Northwestern University, J. S. Levinton and S. S. Bretsky, State University of New York at Stony Brook, R. K. Bambach, Virginia Polytechnic Institute, and J. Pojeta, U. S. Geological Survey, for reading various drafts of this manuscript. S. J. Gould and A. L. McAlester provided some most helpful editorial comments. Support has come from the National Science Foundation (Biological and Medical Sciences Grant No. GB-12748 and Biological Oceanography Grant No. GA-25340).

REFERENCES

Agnew, A. F., 1955, Facies of Middle and Upper Ordovician rocks: Am. Assoc. Petroleum Geologists Bull., v. 39, p. 1703-1752.

Ball, J. R., 1935, Dwarfed gastropods in the basal Guttenberg, Southwestern Wisconsin [abs.]: Geol. Soc. America Proc., 1935, p. 384.

Bambach, R. K., ms, 1969, Bivalvia of the Siluro-Devonian Arisaig Group, Nova Scotia: Ph.D. dissert., Yale Univ., 376 p.

Bayer, T. N., ms, 1965, The Maquoketa Formation in Minnesota and an analysis of its benthonic communities: Ph.D. dissert., Univ. Minnesota, 209 p.

Branson, C. C., 1930, Paleontology and stratigraphy of the Phosphoria Formation: Missouri Univ. Studies, v. 5, 99 p.

Bretsky, P. W., 1968, Evolution of Paleozoic marine invertebrate communities: Science, v. 159, p. 1231-1233.

Bretsky, P. W., and Bermingham, J. J., 1970, Ecology of the Paleozoic scaphopod genus *Plagioglypta* with special reference to the Ordovician of eastern Iowa: Jour. Paleontology, v. 44, p. 908-924.

Bromberger, S. H., ms, 1968, Basal Maquoketa phosphatic beds: Ph.D. dissert., Univ. Iowa, 209 p.

Bromley, R. G., 1967, Marine phosphorites as depth indicators: Marine Geology, v. 5, p. 503-509.

Brown, C. E., and Whitlow, J. W., 1960, Geology of the Dubuque South quadrangle, Iowa-Illinois: U. S. Geol. Survey Bull. 1123-A, p. 1-93.

Bushinskii, G. I., 1964, On shallow water origin of phosphorite sediments, *in* Van Stratten, L.M.J.U., ed., Developments in Sedimentology: New York, Elsevier, p. 62-69.

Calvin, Samuel, 1906, Geology of Winneshiek County: Iowa Geol. Survey Ann. Rept., 1905, v. 16, p. 37-146.

Craig, G. Y., 1952, A comparative study of the ecology and palaeoecology of *Lingula*: Edinburgh Geol. Soc. Trans., v. 15, p. 110-120.

——— 1967, Size-frequency distributions of living and dead populations of pelecypods from Bimini, Bahamas, B.W.I.: Jour. Geology, v. 75, p. 34-45.

Craig, G. Y., and Hallam, A., 1963, Size-frequency and growth-ring analyses of *Mytilus edulis* and *Cardium edule* and their palaeoecological significance: Palaeontology, v. 6, p. 731-750.

Craig, G. Y., and Oertel, G., 1966, Deterministic models of living and fossil populations of animals: Geol. Soc. London Quart. Jour., v. 122, p. 315-355.

D'Anglejan, B. F., 1967, Origin of marine phosphorites off Baja California, Mexico: Marine Geology, v. 5, p. 15-44.

——— 1968, Phosphate diagenesis of carbonate sediments as a mode of *in situ* formation of marine phosphorites: observations on a core from the eastern Pacific: Canadian Jour. Earth Sci., v. 5, p. 81-87.

Du Bois, E. P., 1945, Subsurface relations of the Maquoketa and "Trenton" Formations in Illinois: Illinois Geol. Survey Rept. Inv. 105, p. 7-38.

Fell, H. B., 1968, The biogeography and paleoecology of Ordovician seas, *in* Drake, E. T., ed., Evolution and Environment: New Haven, Conn., Yale Univ. Press, p. 139-162.

Fisher, D. W., 1951, Marcasite fauna in the Ludlowville formation of western New York: Jour. Paleontology, v. 25, p. 365-371.

Gadgil, M., and Bossert, W. H., 1970, Life historical consequences of natural selection: Am. Naturalist, v. 104, p. 1-24.

Gutstadt, A. M., ms, 1954, Stratigraphy of the Upper Ordovician rocks in Iowa, Illinois, and Indiana: Ph.D. dissert., Northwestern Univ., 216 p.

———— 1958, Upper Ordovician stratigraphy in eastern interior region: Am. Assoc. Petroleum Geologists Bull., v. 42, p. 513-547.

Hallam, Anthony, 1961, Brachiopod life assemblages from the Marlstone Rock-bed of Leicestershire: Palaeontology, v. 4, p. 653-659.

———— 1965, Environmental causes of stunting in living and fossil marine benthonic invertebrates: Palaeontology, v. 8, p. 132-155.

———— 1967, The interpretation of size-frequency distributions in molluscan death assemblages: Palaeontology, v. 10, p. 25-42.

Johnson, H. N., ms, 1939, The stratigraphy of the Maquoketa Shale in Missouri and adjacent parts of Illinois: M.S. thesis, Washington Univ., 185 p.

Kaesler, R. L., and Fisher, W. L., 1969, Population dynamics of *Triticites ventricosus* (Fusulinacea), Hughes Creek Shale, Kansas: Jour. Paleontology, v. 43, p. 1122-1124.

Kolodny, Y., 1969, Are marine phosphorites forming today: Nature, v. 224, p. 1017-1018.

Ladd, H. S., ms, 1925, The stratigraphy and fauna of the Maquoketa Shale of Iowa: Ph.D. dissert., Univ. Iowa, 221 p.

———— 1929, The stratigraphy and paleontology of the Maquoketa Shale of Iowa: Part I: Iowa Geol. Survey Ann. Rept., 1928, v. 34, p. 305-448.

Ladd, H. S., Hedgpeth, J. W., and Post, Rita, 1957, Environments and facies of existing bays on the central Texas coast, *in* Ladd, H. S., ed., Treatise on Marine Ecology and Paleoecology: Geol. Soc. America Mem. 67, v. 2, p. 599-639.

Levinton, J. S., 1970, The paleoecological significance of opportunistic species: Lethaia, v. 3, p. 69-78.

Levinton, J. S., and Bambach, R. K., 1970, Some ecological aspects of bivalve mortality patterns: Am. Jour. Sci., v. 268, p. 97-112.

Loomis, F. B., 1903, The dwarf fauna of the pyrite layer at the horizon of the Tully Limestone in western New York: New York State Mus. Bull. 69, p. 892-920.

Ma, T. H., 1962, A recomparison of paleomagnetic latitudes and paleogeographical latitudes deduced from growth values of reef corals: Geol. Soc. China Mem. 1, p. 75-93.

MacArthur, R. H., and Wilson, E. O., 1967, The theory of island biogeography: Princeton, N. J., Princeton Univ. Press, 203 p.

Margalef, R., 1963, On certain unifying principles in ecology: Am. Naturalist, v. 97, p. 357-374.

McAlester, A. L., 1968, Type species of Paleozoic nuculoid bivalve genera: Geol. Soc. America Mem. 105, 143 p.

———— 1969, Nuculanacea (Bivalvia), *in* Moore, R. C., Treatise on invertebrate paleontology, Pt. N, Mollusca 6: Lawrence, Kansas, Geol. Soc. America and Kansas Univ. Press, p. N231-N235.

McKelvey, V. E., 1967, Phosphate deposits: U. S. Geol. Survey Bull. 1252-D, p. 1-21.

Ojakangas, D. R., ms, 1959, Depauperate fauna from the Maquoketa Formation of Iowa and Illinois: M.S. dissert., Univ. Missouri, 107 p.

Olson, E. C., 1957, Size-frequency distributions in samples of extinct organisms: Jour. Geology, v. 65, p. 309-333.

Opdyke, N. D., 1962, Paleoclimatology and continental drift, *in* Runcorn, S. K., ed., Continental drift: New York, Academic Press, p. 41-64.

Paine, R. T., 1969, Growth and size distribution of the brachiopod *Terebratalia transversa* Sowerby: Pacific Sci., v. 23, p. 337-343.

Rhoads, D. C., 1963, Rates of sediment reworking by *Yoldia limatula* in Buzzards Bay, Massachusetts, and Long Island Sound: Jour. Sed. Petrology, v. 33, p. 723-727.

Sanders, H. L., 1956, Oceanography of Long Island Sound, 1952-1954. X. Biology of marine bottom communities: Bingham Oceanog. Colln. Bull., v. 15, p. 345-414.

———— 1960, Benthic studies in Buzzards Bay. III. The structure of the soft bottom community: Limnology and Oceanography, v. 5, p. 138-153.

Savage, T. E., 1905, Geology of Fayette County: Iowa Geol. Survey Ann. Rept., 1904, v. 15, p. 433-560.

Schmidt, R. R., and Warme, J., 1969, Population characteristics of *Protothaca staminea* (Conrad) from Mugu Lagoon, California: Veliger, v. 12, p. 193-199.

Segerstrale, S. G., 1957, Baltic Sea, *in* Hedgpeth, J. W., ed., Treatise on Marine Ecology and Paleoecology: Geol. Soc. America Mem. 67, v. 1, p. 751-800.

Sheldon, R. P., 1964, Paleolatitudinal and paleogeographic distribution of phosphorite: U. S. Geol. Survey Prof. Paper 501-C, p. C106-C113.

Stanley, S. M., ms, 1968, Relation of shell form to life habits in the Bivalvia (Mollusca): Ph.D. dissert., Yale Univ., 245 p.

Stasek, C. R., 1965, Feeding and particle-sorting in *Yoldia ensifera* (Bivalvia: Protobranchia), with notes on other nuculanids: Malacologia, v. 2, p. 349-366.

Stauffer, C. R., 1937, A diminutive fauna from the Shakopee Formation at Cannon Falls, Minn.: Jour. Paleontology, v. 11, p. 55-60.

Tasch, Paul, 1953, Causes and paleoecological significance of dwarfed fossil marine invertebrates: Jour. Paleontology, v. 27, p. 356-444.

———— 1957, Fauna and paleoecology of the Pennsylvania Dry shale of Kansas, *in* Ladd, H. S., ed., Treatise on marine ecology and paleoecology: Geol. Soc. America Mem. 67, v. 2, p. 365-406.

Templeton, J. S., and Willman, H. B., 1963, Champlainian Series (Middle Ordovician) in Illinois: Illinois Geol. Survey Bull. 89, 260 p.

Theede, H., Ponat, A., Hiroki, K., and Schlieper, C., 1969, Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulfide: Marine Biology, v. 2, p. 325-337.

Tooms, J. S., Summerhayes, C. P., and Cronan, D. S., 1969, Geochemistry of marine phosphate and manganese deposits: Oceanog. Marine Biology Ann. Rev., v. 7, p. 49-100.

Trechmann, C. T., 1913, On a mass of anhydrite in the Magnesian Limestone of Hantlepool, and on the Permian of southeastern Durham: Geol. Soc. London Quart. Jour., v. 69, p. 184-218.

Ulrich, E. O., 1897, The Lower Silurian Lamellibranchiata of Minnesota: Minnesota Geol. Nat. History Survey, 1892-1896, v. 3, pt. 2, p. 475-628.

Williams, A., 1969, Ordovician faunal provinces with reference to brachiopod distribution, *in* Wood, A., ed., The Precambrian and Lower Paleozoic rocks of Wales (symposium): Cardiff, Univ. Wales Press, p. 117-154.

Yonge, C. M., 1939, The protobranchiate Mollusca: a functional interpretation of their structure and evolution: Royal Soc. London Philos. Trans., v. 230, p. 79-147.