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UPPER PENNSYLVANIAN), IN THE APPALACHIAN
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SYNOPSIS:. Nine Brush Creek localities in western Pennsylvania were trench sampled for the purpose of recovering the total fauna from each visible marine horizon. The 9 localities provided 61 samples that were disaggregated by the Amine 220 technique, washed, dried, and sieved into 305 individual samples. The recovered fossils are judged to have lived, died, and been preserved at each collecting site and are therefore members of fossil communities. This judgement is based on qualitative judgements of state of articulation, abrasion level, quality of preservation, and taxonomic associations.

Animals from the sieve-sample splits were viewed microscopically to determine taxonomic composition and frequencies. Raw faunal assemblage data were adjusted to reduce the frequencies to whole numbers of individuals and, secondly, to a single generation. The purpose of making a generation correction is to reflect standing crop, which in turn provides a reasonable approximation of the once-living communities.

The adjusted outcrop data were examined for faunal similarities among localities for the purpose of zoning the localities into workable groups. Two distinct faunal groups are recognized on the basis of relative water depths and distances from shore. Four shallow water and five deep water localities are inferred. The deep-water localities are characterized by low diversity molluscan faunas, whereas the shallow-water localities are characterized by high-diversity molluscan faunas.

The adjusted data were further subjected to programmed diversity and equitability tests to decipher faunal succession and community structure. The diversity and equitability data were graphed for each locality and the resultant curves compared with ecological criteria such as animal habitat preferences and feeding types. These combined types of data aided in deciphering the sea-level history of the marine event at each locality. Transgressive, stillstand, and regressive phases are deciphered, along with their corresponding opportunistic, stable-mature, and relict-mature faunas. These data also show that the faunal distribution above and below the stillstand is asymmetrical.

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INTRODUCTION

The purpose of the investigation was to apply and test modern paleo-ecological and ecological concepts and information theory in attempting to resolve the present problem. It is a segment of a long-range investigation, already in progress, by several faculty members of the Department of Earth and Planetary Sciences, University of Pittsburgh, to reconstruct and interpret the shallow benthic marine communities for all the marine events represented in the Conemaugh Group. Compari-

sons will later be made between the Conemaugh communities and contemporaneous faunas of similar lithologies in the more western basins of
Pennsylvanian age.

The problem is one of reconstructing and interpreting the shallow
benthic marine communities of the Brush Creek marine interval, Conemaugh Group (Upper Pennsylvanian) in the appalachian basin of western Pennsylvania. The Brush Creek marine event represents one of a
series of four temporally limited marine events in a succession of principally non-marine events represented in a cyclothemic sequence, the
Conemaugh Group.

GEOGRAPHIC AND STRATIGRAPHIC SETTING

The study area is that part of the Appalachian basin lying within the
Pittsburgh · Plateaus section of the Allegheny Plateaus physiographic
province. The study area lies between 79°00′ and 80°30′ west longitude
and 39°30′ and 41°00′ north latitude. It encompasses 3,960 square miles.
Nine localities in six western Pennsylvania counties (Armstrong, Indiana,
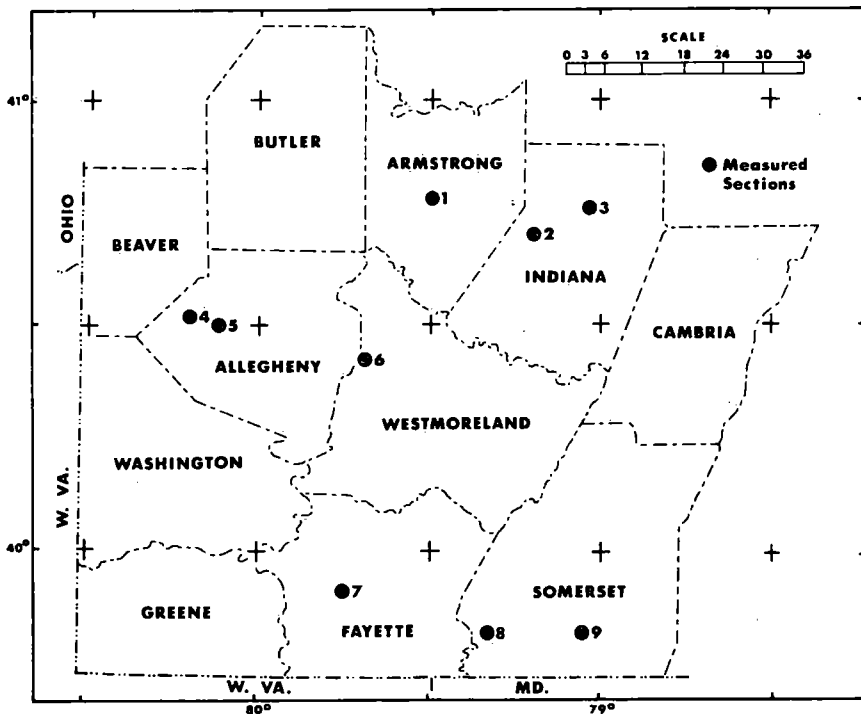
FIGURE 1.—Brush Creek locality map, western Pennsylvania.

Allegheny, Westmoreland, Fayette, and Somerset) were measured and trench sampled in this investigation (Fig. 1).

The Pennsylvanian System was named by Williams (1891) for the state of Pennsylvania in the central Appalachians, replacing the outmoded name "Coal Measures." The Pennsylvanian System is divided into the Pottsville, Allegheny, Conemaugh, and Monongahela Groups in ascending order.

The Conemaugh Series was named by Platt (1879) for the Conemaugh River valley of western Pennsylvania (Fig. 2). The Conemaugh
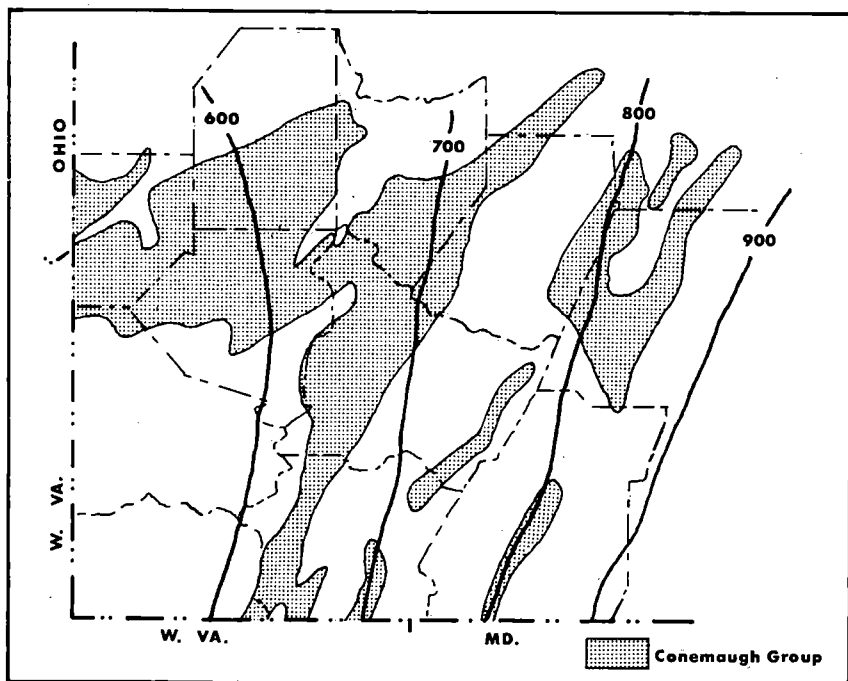
FIGURE 2.—Distribution and isopachous map of the Conemaugh group, western Pennsylvania (adapted from Branson 1962).

includes the strata from the top of the Upper Freeport coal (Upper Allegheny) to the base of the Pittsburgh Coal (Lower Monongahela). These boundaries correspond with those of the Lower Barren Coal Measures, as previously named by Rogers (1858). Flint (1965) proposed subdividing the Conemaugh Group into lower (Glenshaw) and upper (Casselman) formations for their type sections in the Glenshaw vicinity, Shaler Township, Allegheny County, and along the Casselman River in Somerset County, Pennsylvania, and Garrett County, Maryland, respectively (Fig. 3). This nomenclature is adopted for this study.

Pittsburgh coal bed

CONEMAUGH GROUP

CASSELMAN FORMATION

Marine beds lacking;
freshwater limestones
relatively abundant

Ames limestone (marine)

Woods Run limestone (marine)

Pine Creek limestone (marine)

Buffalo sandstone

Brush Creek shale ——————

Brush Creek limestone

Brush Creek shale ——————

Brush Creek coal

marine
interval

GLENSHAW FORMATION

Upper Freeport coal bed

FIGURE 3.—Subdivision of the Conemaugh group and generalized Brush Creek interval (adapted from Flint 1965).

The Brush Creek Member is the lowest of four marine units in the Glenshaw Formation and was named by I. C. White (1878) for exposures along Brush Creek, Cranberry Township, Butler County, Pennsylvania. The Brush Creek is correlated with the Kansas City Group, Missourian age, of the northern midcontinent area, based on the common occurrences of the fusulinid *Triticites ohioensis* (Moore 1944: 684).

PREVIOUS INVESTIGATIONS

Other than general faunal lists, there is a paucity of published paleontological studies of the Conemaugh Group. Mark (1912) prepared the first comprehensive taxonomic treatment of Conemaugh fossils from Ohio. Many of her identifications were documented from Raymond's (1910) preliminary faunal list of Allegheny and Conemaugh fossils in western Pennsylvania. Burke (1930) described the Ames Limestone fauna from Painter Hollow, West Virginia. The Ames fauna of the Pittsburgh Quadrangle was described by Theiss (1940). Seaman (1940, 1941, 1942) published short papers on the Ames, Pine Creek, and Brush Creek limestones and their associated faunas of western Pennsylvania. Miller and Unklesbay (1942) prepared a comprehensive faunal study of cephalopods from Conemaugh rocks of western Pennsylvania. Leighton (1947) prepared a guidebook for Pittsburgh geology in which he figured 21 Conemaugh taxa and prepared an extensive faunal list of Conemaugh invertebrates. Doney (1954) figured and described 11 Brush Creek bivalve species from the Pittsburgh area and the immediate vicinity. Lintz (1958) published on the fauna of the Ames and Brush Cre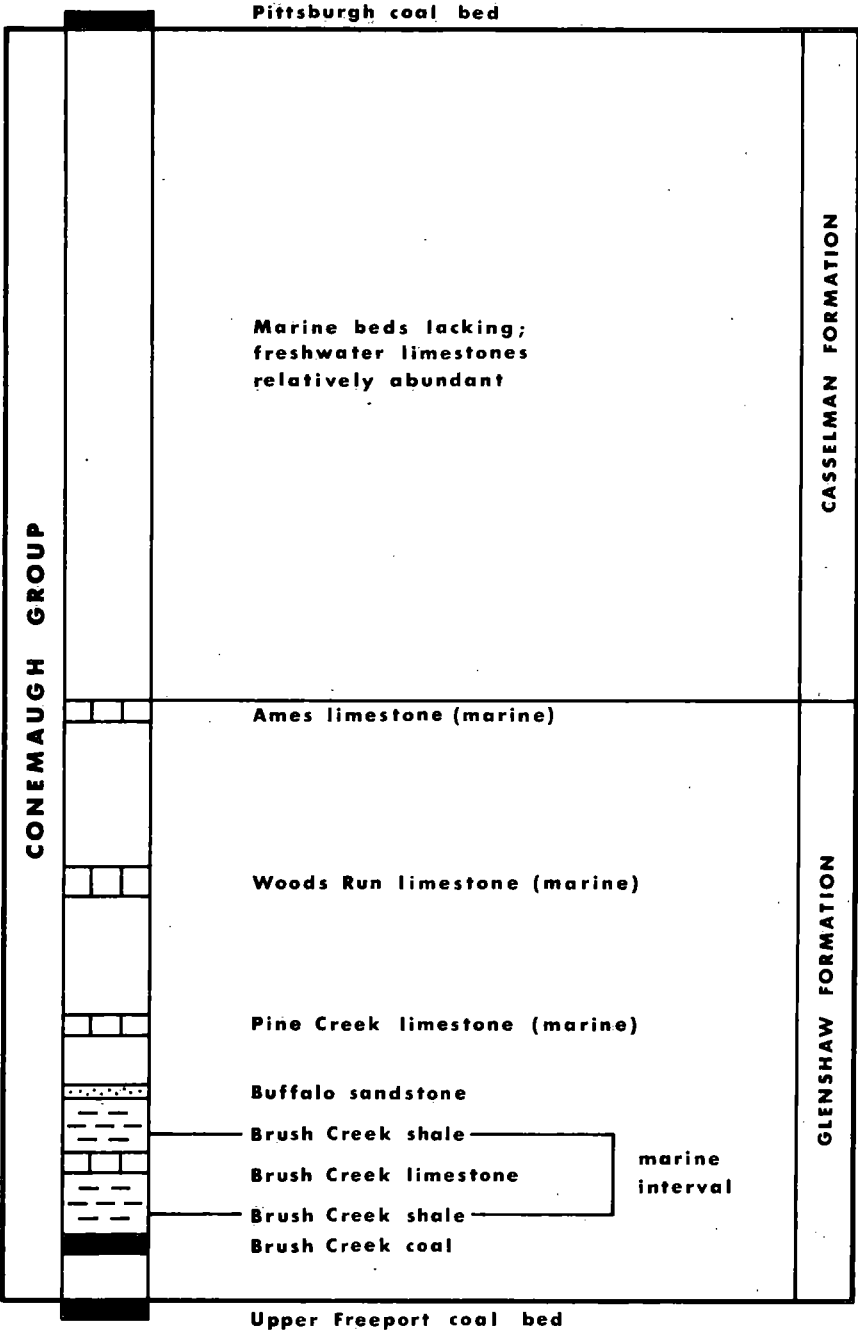ek shales of western Maryland. Murphy (1967) published one short paper on the Brush Creek bivalves from Ohio and another (1970) on the Brush Creek coiled nautiloid cephalopods from eastern Ohio and western Pennsylvania.

One of the most valuable taxonomic aids used during this study was *Pennsylvanian Brachiopods of Ohio* (Sturgeon and Hoare 1968). Hoskins' (1969) *Fossil collecting in Pennsylvania* and Wagner *et al.'s* (1970) *Geology of the Pittsburgh area* were two very general but valuable taxonomic aids.

Paleoecology, although a youthful branch of geology, is becoming an extremely valuable tool in deciphering earth history. Several recent excellent paleoenvironmental studies have been conducted that are of great aid in paleoecological reconstructions. For example, Morris (1967) prepared a very detailed and comprehensive environments-of-deposition and paleogeographic study of the Appalachian basin coal fields. Griese-

mer (1970) recognized seven faunal assemblages in the Ervine Creek
Limestone (Late Pennsylvanian) of the midcontinent region. He com-
bined both lithologic and paleontologic criteria for this reconstruction.

One of the more successful areas of paleoecological research has in-
volved the Pennsylvanian shallow marine benthic faunas. Johnson's
(1962) pioneering statistical approach to interspecific associations (often
termed fossil communities) with Pennsylvanian assemblages is an ex-
cellent work, and it is one of the most frequently cited papers among
the more recent literature. Fagerstrom (1964) described four fossil
assemblages from the Pennsylvanian of Nebraska, two of which were
named communities (fossil community and residual fossil community).
Stevens (1965, 1966, 1969, 1971) recognized communities from fossil
assemblages of the Pennsylvanian Minturn Formation in Colorado and
the Permian rocks of Nevada and Utah. Other important Pennsylvanian
studies are by Shabica (1970), West (1970), Williams (1960), and
Zangerl and Richardson (1963).

Many recent paleoecological endeavors have become quite sophisti-
cated in their approach. Cybernetics, stability, diversity, community
dynamics, and other concepts in modern ecological theory are being
tested in the fossil record. Species diversity and equitability gradients as
paleoecologic tools have been applied to carboniferous studies by Beer-
bower and Jordan (1969), Donahue and Rollins (in press), Donahue,
Rollins, and Shaak (1972), Rollins and Donahue (1971, 1972), and
West (1970).

METHODS OF INVESTIGATION

FIELD SAMPLING

The stratigraphic section at each of nine selected field localities was
measured and described. Stratigraphic descriptions were recorded for
the purpose of defining major lithologic units. The lithologic units
complement the faunal analyses in deciphering paleoenvironments in that

the environments of deposition can sometimes be interpreted from the resultant lithologies.

The sampling method selected for this study is the stratified sampling technique described by Griffiths (1967: 18). The visible marine zone (the vertical extent of macrofossils) at each locality was trench sampled from top to bottom. Individual subsamples were taken within single lithologies. In relatively thick homogeneous lithologies one foot intervals were sampled, with approximately five pounds of rock taken in each bulk sample. The entire trenched vertical marine horizon containing macrofossils was brought back to the laboratory. The reason for this form of detailed sampling is to eliminate the effect of errors or biased samples. In addition to these stratified samples, several spot samples were taken at each locality to aid in the identification of the fauna. Observations on the state of fossil preservation were recorded.

Laboratory Preparation

The bulk random samples were brought to the laboratory, and the total samples treated by the Amine 220 technique (Lund 1970: 578). The Amine 220 technique is superior to the use of either kerosene or Quaternary "O" (Geigy Chemical) for disaggregation of shales and friable limestones. It is not successful, however, in treating dense limestones. Bulk samples were left in the solution for an average of two days and were frequently agitated to keep the fines in suspension. Many samples, especially argillaceous shales and mudstones, were completely disaggregated into fossils and mud.

The disaggregate was wet sieved through U.S. Standard Sieve series numbers 2, 10, 40, 100, and 120. Numbers 2 and 10 retain the available macrobenthos, number 40 retains the meiobenthos, and numbers 100 and 120 retain much of the microbenthos (Wigley and McIntyre 1964). The disaggregate was thoroughly washed until all traces of the Amine 220 were removed. The washing process must be complete or upon drying the individual grains become cemented into a gelatinous mass.

A total of 9 localities was trench sampled, providing 61 stratified samples and 305 individual sieve fractions.

Faunal Analysis

All sieve fractions were split with a standard sample splitter until a workable quantity was reached. A workable quantity was determined from a preliminary microscopic count of the fossils from the individual sieve fractions.

Samples from each locality were analyzed, one sieve size at a time. The +40 splits were analyzed first because this size fraction contained an admixture of the larger microfossils and smaller macrofossils. The +40 splits were followed in order by the +100, +120, +10, and +2 splits. An artificial subdivision of micro-macrofossils, based on size, was established for the convenience of data accumulation and processing. All fossils retained on the number 40, and coarser, sieves were deemed macrofossils, and all those passing through the number 40 sieve, microfossils.

A stereoscopic microscope was used for identification and counts of the faunal elements, the microfossils at 40X and 100X magnification and the macrofossils at 25.6X. Whenever possible, fossils were identified to the generic level. Owing to their disarticulated state, echinoderms were identified to class. Sponge spicules, conodonts, and vertebrates, all of which were fragmentary, were identified to phylum. Bryozoans, except for two readily recognizable genera, were identified only to growth form.

All fragmentary fossils greater than 50 percent complete were counted, and the identification and frequencies were recorded on data sheets for subsequent analyses. The counting of the individual sieve size splits was stopped when a qualitative guess as to adequacy of sample size was reached. This guess was adapted from the rarefaction method arithmetic plots of Sanders (1968). If the number of species is plotted against their frequency, the curve initially parallels the ordinate because of the high frequency of new species. As fewer and fewer new species are added, the frequencies of already identified species are still increasing and the curve now asymptotically approaches the abscissa. The inflection point of the curve was used to guess the adequacy of sample size. In most cases an adequately sized sample was reached within the range of the initial sample splits but in several samples the remaining fraction had to be resplit and counted to achieve adequacy of sample size. The equitability of each split was subsequently quantitatively determined in conjunction with the diversity indices.

DATA ADJUSTMENT TO REFLECT STANDING CROP

Ager (1963: 184) provides a comment on the tenuity of reconstructing fossil communities from fossil assemblages:

"The Paleoecologist must never forget that he is studying not the living inhabitants of the village but only the bodies in the churchyard, and then only after many visits by grave robbers."

The fossil assemblage, as quarried from the outcrop, may reflect little

about its predecessor, the living community. However, by adjusting the
raw faunal assemblage data to reflect standing crop, a realistic approxi-
mation of the once living community is possible. One important condi-
tion that must be met before making these adjustments is that the as-
semblage cannot be biased by transport and mixing. Indicators of trans-
portation, such as the right-left value-sorting phenomenon, size sorting,
and abrasion were judged at the outcrops and in the washed samples
to be at a minimum. The concept of post-mortem transportation has long
been a deterrent to paleoecological reconstructions. Johnson (1972:152)
stresses this overemphasis and states that transportation is rare. He also
provides a most refreshing statement: "It is about time that paleontol-
ogists stop apologizing about this possible source of bias as there are
enough probable sources to worry about."

Recorded taxonomic frequencies must be adjusted to a common stan-
dard to enable comparison not only between the different samples within
an outcrop but among outcrops. These adjustments are necessary because
of the combined fossil and sediment weight differences of the individual
sieve sample splits. Initial frequencies were adjusted to a weight stan-
dard of 500 grams. For example, if the weight of the counted sample
(both fossils and sediment) was 1.25 grams, the individual frequencies
were increased by a factor of 400, which approximated the total that
would be found if 500 grams were initially counted.

Taxonomic frequencies in raw faunal assemblage data are strongly
biased by the various taxa that fragment or disarticulate during taphon-
omy. These biases should be compensated for before the data can
validly be subjected to statistical tests. The frequencies of fragmented
or disarticulated taxa must be reduced to a whole number of individuals.
For example, in only the rarest preservations are the radix, column, and
calyx of a crinoid preserved in an articulated state. The calyx usually
disarticulates into single crystal calcite plates that literally "cleave"
themselves out of existence. The column disarticulates into individual
columnals. Inasmuch as these columnals often are the only crinoid
remnants in an outcrop, the whole number of individuals must be de-
rived from the frequency of individual columnals. Frequencies of cri-
noid columnals, sponge spicules, echinoid spines, holothurian sclerites,
conodonts, and vertebrate fragments were reduced by a factor of 20
(Lund, pers. comm.).

Bryozoan frequencies were reduced by a factor of 6.3, based on the
ratio between the average zoarial lengths of nearly complete specimens
on slabs and those retained on the intermediate sized sieve (+40).

Ostracods average nine ecdysis stages; thus their frequencies were
reduced by a factor of nine (Kesling 1961: Q19).

Final adjustments to the taxonomic frequencies are intended to re-
duce the values to a "reflection" of standing crop (Shaak and Rollins
1972). Molluscs, which probably enjoy the longest average longevity
(five years), were selected to be the "standard bearer." This five-year
average molluscan longevity value is here defined as unity. The fre-
quencies of all remaining taxa with either longer or shorter estimated
longevity were reduced in proportion of their longevities to the average
molluscan value (Table 1). For example, most foraminifers and ostra-

TABLE 1.—SUMMARY OF LONGEVITY VALUES OF BRUSH CREEK TAXA.

Taxon	Longevity	Source
Gastropoda		
small	3 years	Comfort 1964: 82-83
large	5 years	Comfort 1964: 82-83
Bivalvia		
epifaunal	5 years	Comfort 1964: 84-85
infaunal	3 years	Comfort 1964: 84-85
Foraminifera	3 generations per year	Thorson 1971: 152
Ostracoda	3 generations per year	Thorson 1971: 152
Echinodermata		
Crinoidea	5 years	Fell and Pawson 1966: 50 Meyer (pers. comm.)
Echinoidea	5 years	Moore 1966: 75
Holothuroidea	5 years	Pawson 1966: 63
Asteroides	5 years	Feder and Christensen 1966: 109
Ophiuroidea	15 years	Fell 1966: 130
Bryozoa	5 years[1]	Ryland 1971: 82-85 Boardman and Cheetam 1969: 225
Brachiopods	4 years	Hymen 1959: 590 Rudwick 1971: 156
Trilobita	5 years[2]	Comfort 1964: 80
Porifera	12 years	Comfort 1964: 81
Coelenterata		
Anthozoa	5 years[3]	Wells (pers. comm.)

[1] Based on sexual maturity at five years.
[2] Average longevity of Malacostraca.
[3] Based on annual growth increments of 20 mm per year.

cods average three generations per year; thus their frequencies were
reduced by a factor of 15. These longevity data were compiled from
estimated values of fossils as well as recent analogs.

DIVERSITY INDICES, SPECIES DIVERSITY, AND EQUITABILITY

Diversity can vary in two ways; thus there are two different groups
of diversity indices (Donahue and Carothers 1972). One type is the

numerical percentage composition (Sanders 1968) of the various taxa in the sample. This is based on numerical dominance. If all taxa are numerically dissimilar, dominance is high and diversity low. The second variety is known as species diversity (Whittaker 1965) and is determined by the number of taxa present in the sample. The more species present in the sample, the higher the diversity. With the two types of diversity and their two types of numerical variance, it was decided to use a representative diversity index of each type.

The Simpson index (1949) is calculated from the following equation ($N =$ number of taxa per sample and $n =$ number of individuals per taxon):

$$Ds = \frac{N(N-1)}{\Sigma n\,(n-1)}$$

The observed Simpson values range from 1.00 to 6.441.

The second index used is the Shannon-Wiener information function (Lloyd and Ghelardi 1964) ($s =$ total number of species and $p_r =$ observed proportion of individuals that belong to the rth species $[r = 1, 2, \ldots, S]$):

$$H(s) = -\sum_{r=1}^{s} p_r \, \log_2 p_r$$

The calculated Shannon-Wiener values range from 0.0 to 3.030.

Donahue (pers. comm.) developed an equitability test used in this study that not only measures numerical equality or evenness of the distribution but also the adequacy of sample size: $\dfrac{\text{Simpson Index}}{\text{number of taxa}}$ where the calculated Simpson Index (D_s) for a particular sample is divided by the number of taxa in that sample. The calculated equitability values range from 1.0 to 0.064. An equitability value of 1.0 denotes a perfect equitable distribution, and decreasingly lower values reflect increased dominance. The equitability values also provide a numerical test for adequacy of sample size. The ratio between equitability and the number of taxa in each sample should approximate a value of one, omitting the decimal in the equitability value, if the sample size is adequate. Unfortunately there are no data to define the range of acceptable values in either rejecting or accepting the sample as being of statistically sound size. Because the Simpson index is affected by sample size, a ratio near a value of one suggests that the particular Simpson value used here is not overly biased by sample size.

The taxonomic frequency values were plotted for each sample from

each outcrop for total fauna, molluscs only, and without molluscs to aid in the interpretations of diversity and equitability fluctuations.

THEORETICAL FRAMEWORK

CHARACTERISTICS OF LEVEL-BOTTOM MARINE COMMUNITIES

With respect to hard parts and probability of rapid burial, the marine benthic communities are the most preservable communities of the biosphere (Johnson 1964: 120). If one accepts this premise, the level-bottom marine community concept should be relatively easy to define, but a review of the literature indicates just the opposite.

The term *biocoenose* community is applied where the importance is placed on species interdependence. This approach, however, is not applicable to modern marine communities because of the relative independence of marine level-bottom species (Speden 1966: 411). The *habitat* community approach of Newell *et al.* (1959: 200) is based on "environmental" species, or the relationship between environmental parameters and certain index taxa. A third kind of definition is based on the classical work of Petersen (1911, 1913, 1914, 1915, 1918), in which the most "characteristic" species of animals were used to designate the community. The Petersen communities are synonymous with the *organism* communities of Newell *et al.* (1959). The Petersen community is based on numerically dominant, recurring species which are designated as the standard-bearers (Thorson 1957: 467). This concept was expanded by Thorson (1955), who designated "parallel level-bottom communities." These parallel communities inhabited the same type of substrate in areas scattered geographically (Odum 1971: 340). The Petersen concept for naming communities has been adopted in this investigation.

The species compositions of communities are not fixed and bordering communities commonly integrate (Johnson 1964: 108). This inhomogeneity of communities is an argument against communities being real units. The disagreement among marine biologists as to the validity of communities being real ecological units is probably the least critical in level-bottom marine communities. Probably the most uniform place in the biosphere is the level-bottom area of the sea (Thorson 1957: 469). Johnson (1964: 108) convincingly sums up the defense: ". . . All species living today do not occur in all possible combinations in natural assemblages. Rather, we observe around us a finite number of recurring associations of species." The high recurrence rates of suites of species in modern environments, especially level-bottom marine environments, are probably not chance associations. Thus it seems reasonable to accept level-bottom communities as real or natural entities.

In a paleoecological study, the recognition of communities is not an end but only the means to an end. It is well documented that the species composition of communities is not constant, and communities also change with time. There is a natural succession during the stages of community development. Species diversity increases during the pioneering stages of succession and will peak and then decline in the climax (Margalef 1963). The concept of climax is valid; however, documentation of a climax community that would develop in an ecosystem at equilibrium is very tenuous indeed. All systems strive to reach a condition of equilibrium or environmental stability, and the principal limiting factor is time. Dunbar (1960), Margalef (1968), and Wilson (1969) provide excellent accounts of stability evolution in marine environments.

The application of the concepts of community succession and stability is difficult in recent benthic marine studies, and these difficulties are compounded when applied to the fossil record. Fortunately, the level-bottom marine communities and their related environments are relatively simple in comparison with complex systems such as rocky intertidal, reef, and terrestrial regimes. Upon recognition of the level-bottom benthic communities, it is necessary to interpret their temporal and spatial variations. These variations are reflected by variations in species diversity. Several workers have attempted to explain variations in species diversity between marine communities (e.g., Buzas and Gibson 1969, Johnson 1970, Stevens 1971). The most attractive concept at this time is the "stability-time" hypothesis of Sanders (1969). Sanders defines two end members in explaining differences between communities. At one end is the physically controlled, or "physically accommodated," community in which diversity is low, stress is high, and adaptations are controlled by the physical environment. This type of community is not resource-limited (Valentine 1971: 51). At the opposite end of the spectrum is the biologically controlled, or "biologically accommodated," community in which diversity is high, stress is low, and adaptations are controlled biologically. This type of community is resource-limited. These end-member communities parallel the immature and mature community of Margalef (1968), and perhaps the non-interactive, interactive equilibria model of Wilson (1969). Any natural or real community probably falls somewhere between these end points and is an admixture of the two. If local environmental conditions remain nearly constant, the community undergoes succession toward the state of biological accommodation. If the stresses remain low, a biologically accommodated community evolves; if the stresses remain high, a physically accommodated community develops (Johnson 1970:286).

A marine transgressive-stillstand—regressive faunal sequence can be

recognized by the presence or absence of various taxa, taxonomic associations, inferred feeding types of modes of life, sedimentologic criteria, and geochemical techniques (Stevens 1971). The transgressive phase, is marked faunally by *opportunistic* communities composed of relatively few eurytopic species living in rigorous near-shore marginal environments. The stillstand represents the time of maximum marine inundation and supports the most diverse fauna, that of the *stable-mature* communities. Both eurytopic and stenotopic species are found in this higher stability regime. The regressive phase results in a biological winnowing out of the stenotopic species, resulting in *relict-mature* communities composed of the more eurytopic components of the stable mature phase (Rollins and Donahue 1971).

Certain suites of fossils are recurrent both vertically and laterally, and adequately reflect regional shallow-benthic communities. Detailed paleoecological analyses, including species diversity, equitability, taxonomic frequencies, and feeding and habitat preferences, serve to document the similarities between the faunal successions at the different localities and warrant the naming of recurrent regional communities.

One of the greatest attributes of the "stability-time" hypothesis is that it predicts recognizable changes within marine communities. Species diversity varies directly with environmental stability (Donahue and Rollins 1972: 4) and is predictable in a transgressive-stillstand-regressive sequence.

The Brush Creek marine transgressive front provided numerous new habitats for colonization by marine organisms (Rollins and Donahue 1972: 3). The frontal environments would have been of high stress and fluctuation and would have supported only a few eurytopic species. The communities would have been opportunistic, and in the stability-time framework nearer the physically accommodated end. The species diversity values would be low with the exception of localized "chance" patches of high diversity.

As environmental stress decreased or fluctuated less and transgression continued, colonization would increase at a given locality. Stenotopic species would invade the area and physical accommodation would decrease, whereas biological accommodation would increase. Increased stability would be paralleled by diversity increases. Eventually maximum transgression would be reached and if maintained, stillstand communities would develop. The highest stability at a given locality would be reached during the stillstand, and communities would approach biological accommodation, increase in diversity, enjoy low stress environments, and, if time allowed, would continue through succession to approach equilibrium. These stillstand communities would be stable-

mature communities with both stenotopic and eurytopic species, and their successional level or maturity would be a function of time. A high diversity stillstand average for several localities would suggest a relatively lengthy period of stability and ecosystem maturity.

The regressive phase should show almost the reverse of the transgressive phase. Increasing environmental stress and fluctuations would cause a deterioration of the communities. Physical accommodation would become increasingly important as the stenotopic species are biologically winnowed out. The residual communities would be the relict-mature communities composed of the more eurytopic species left over from the degraded stable-mature communities. Theoretically, the relict-mature communities would be numerically represented by diversities intermediate between those of the transgressive and stillstand phases.

CHARACTERISTICS OF THE BRUSH CREEK DEPOSITIONAL BASIN

The Brush Creek marine depositional basin covered parts of Pennsylvania, Maryland, Ohio, Kentucky, and West Virginia. In early Brush Creek time the sea was essentially landlocked (thus brackish), with only a narrow seaway or strait that was the connection with the major midcontinent Pennsylvanian sea extending through portions of Muskingum, Guernsey, and Noble counties in Ohio. The majority of the terrigenous sediments were being shed from the southeastern bordering Appalachian highlands by a river system that built an extensive deltaic clastic edge, prograding toward the center of the basin (Morris 1967: 111).

The Brush Creek marine deposition commenced with transgression of the Brush Creek sea from the midcontinent region, through the Ohio straits, and into the Brush Creek depositional basin. Concurrently, along with the transgression, the basin (originally brackish) took on a marine aspect (Morris 1967: 2). The study area (western Pennsylvania) was that part of the basin bounded by a low delta plain to the east and the pro-delta portion of the basin to the west (Ferm, pers. comm.). Therefore the Brush Creek basin within the study area was directly influenced by both the prograding deltaic wedge and the transgressing sea.

FAUNAL SUCCESSION AND DIVERSITY

In order to avoid a cumbersome outcrop-by-outcrop treatment of faunal succession and species diversity, the taxonomic data were grouped and examined to ascertain faunal trends. Total outcrop faunal composition, stillstand composition (the samples from each locality judged to represent the stillstand), stillstand, sub-stillstand, and supra-stillstand

composition, as well as associated lithologic types are the bases for sub-
dividing the total fauna into two gross faunal groups, namely high and
low diversity molluscan faunas.

Of the nine localities studied (Fig. 1), the geographically peripheral
localities (1, 7, 8, and 9) contain high diversity molluscan faunas, where-
as the more central localities (2, 3, 4, 5, and 6) contain low diversity
molluscan faunas. Although very general in scale, this grouping is very
real and critical in the interpretation of diversity and community struc-
tures.

Taxonomic frequencies in the samples considered representative of
the stillstand average 15 molluscan taxa for the high diversity molluscan
faunas, whereas the low diversity molluscan faunas in stillstand samples
average 10 molluscan taxa (Table 2). The high diversity faunas average
62% molluscan taxa of the total number of taxa, as opposed to 46%
molluscs for the low diversity faunas. Though ubiquitous, *Astartella*
(a small rhomboidal to ovate eurytopic bivalve of the family Astartidae)
is 10 times more abundant in the high density molluscan faunas than in
the more central ones.

Total outcrop faunal compositions, although less useful than stillstand
data, show similar relationships. Molluscs average 15 taxa in the high
diversity faunas, whereas the low diversity faunas average 11 molluscan
taxa. The molluscan taxa from the high diversity faunas average 61%
of the total number of taxa, and the low diversity average is 47% mollus-
can taxa. *Astartella* is four times more abundant in the high diversity
molluscan outcrops (Table 3).

These data lead to a suggestion of relative water depth and distance
from shore for the depositional environments of these two outcrop
groups. Pennsylvanian molluscan faunas in shallow benthic communities
in Colorado increase in diversity nearshore according to Stevens (1971:
406), whereas other faunal components increase in diversity offshore.
Thus the high diversity molluscan faunas of the western Pennsylvania
Brush Creek marine unit represent marginal or shoal water localities
(Rollins and Donahue 1972).

There is also lithologic support for these conclusions. Locality 7,
near Uniontown, Pennsylvania, has its diversity peak at the position of
a sideritic ironstone layer containing a molluscan dominant fauna and
associated phylloid algae, representing an interdistributary bay facies
(Donahue, Rollins, and Shaak 1972: 8). Similarly, the remaining high
diversity molluscan localities (1, 8, and 9) have bedded ironstone no-
dules below the position of their diversity peaks. In the low diversity
molluscan outcrops the first occurrence of ironstone nodules, either
bedded or scattered upward from the base of the fossiliferous zone, is

TABLE 2.—SUMMARY OF STILLSTAND SAMPLE FREQUENCIES.

Sample	Locality								
	1	2	3	4	5	6	7	8	9
Shansiella	13445	18011	3	748	48810	0	0	0	0
Plagioglypta	9942	0	106528	0	6894	6190	10398	392	12066
Aclisina	7753	919	3272	444	3705	28378	5218	9100	284
Crinoids	1370	0	81	2271	3148	3228	0	60	981
Ornamented Ostracods	970	0	1879	1174	110	0	298	100	653
Smooth Ostracods	2891	5450	2767	5373	525	3480	5783	1656	6577
Cyclogyra	657745	243071	246744	630958	16652	179599	0	665	967639
Glabrocingulum	180720	2521	275042	19700	1399	221960	108066	7999	92502
Astartella	189335	26173	699	296	7844	312337	312337	10397	93512
Inathanopsis	54936	5304	5602	0	34012	556	8726	5193	13181
Molluscan taxa	19	10	11	10	10	12	13	13	16
Number of taxa	31	23	25	22	21	23	25	18	26
Molluscan % of taxa	61	43	44	45	48	52	52	72	61

TABLE 3.—SUMMARY OF TOTAL OUTCROP TAXONOMIC FREQUENCY AVERAGES.

Sample	Locality								
	1	2	3	4	5	6	7	8	9
Shansiella	2421	23127	3	1732	63242	789	0	29	10
Plagioglypta	985	1	33403	62	2862	4095	12294	87	13604
Aclisina	1298	4074	3269	788	2834	36727	870	14485	3618
Crinoids	764	2	361	1107	1560	655	2111	127	341
Ornamented Ostracods	209	159	353	8926	95	199	139	17	92
Smooth Ostracods	3517	3113	1136	8654	917	1523	5161	3296	3106
Cyclogyra	255826	359156	91268	608586	8175	113118	0	612	434907
Glabrocingulum	33373	1452	68000	6812	646	239608	63026	26499	11835
Astartella	36868	46811	984	10692	21971	103480	442384	13845	82243
Ianthanopsis	8623	1246	1152	161	6020	959	11103	46264	33276
Stillstand number of taxa	31	23	25	22	21	23	25	18	26
Molluscan taxa	26	15	11	15	13	17	20	21	20
Number of taxa	46	38	28	31	25	32	39	29	31
Molluscan % of taxa	57	39	39	49	52	53	51	72	65

above the position of the diversity peak; that is, in the regressive sequence (Appendix A). The significance of the bedded nodules and their relationship to the sideritic ironstone layers at Loc. 6 and the overall relationship to water depth and distance from shore is that many of the aforementioned bedded nodules contain fractures resembling desiccation cracks, further suggestive of shoal conditions (Wilson 1967: 85, Emery 1950: 220).

One other taxonomic group provides excellent supportive evidence for a shallow water origin of the high diversity molluscan samples. The ornamented ostracods may require near normal marine salinities for the precipitation of their elaborate shells (Benson 1961: Q58). Looking at total outcrop taxonomic frequency averages (Table 3), the ornamented ostracods are 17 times more abundant in the low diversity molluscan outcrops, whereas smooth ostracods are more abundant in the high diversity molluscan localities.

Such treatment of data, which was originally intended only for a general grouping of faunas from the nine localities, proves to be a surprisingly valuable paleoecological tool in this investigation. It is within the framework of low versus high diversity molluscan faunas that the individual localities are discussed with respect to species diversity and faunal succession.

HIGH DIVERSITY MOLLUSCAN FAUNAS

LOCALITY 1, KITTANNING, PENNSYLVANIA.—Eleven trench samples, excluding the limestone (1.5 ft.), were trenched in an 11 foot interval from 17-28 ft. above the Brush Creek coal. Data derived from the 11 samples show a distinct molluscan dominancy, as evidenced by the number-of-taxa curves (Fig. 4). The equitability curve shows an inverse relationship to the molluscan curve. At molluscan lows there are corresponding equitability highs, and molluscan highs are paralleled by equitability lows. This inverse relationship is explained by dominance within the molluscan fauna of the omnipresent bivalve *Astartella*.

The diversity index curves essentially parallel the equitability curve and roughly parallel the species diversity curves. These relationships, as well as the numerical values calculated for these curves, delineate the transgressive-stillstand-regressive phases of the marine event. The marine faunal stillstand is judged to occur at the position of Sample 8, 1.0-2.0 ft. above the limestone. This sample contains 31 taxa, of which 19 (61%) are molluscs. This species diversity high is paralleled by Shannon-Wiener and Simpson index highs of 2.7 and 4.3 respectively (Table 4). The equitability values for this sample (0.14) is an intermediate
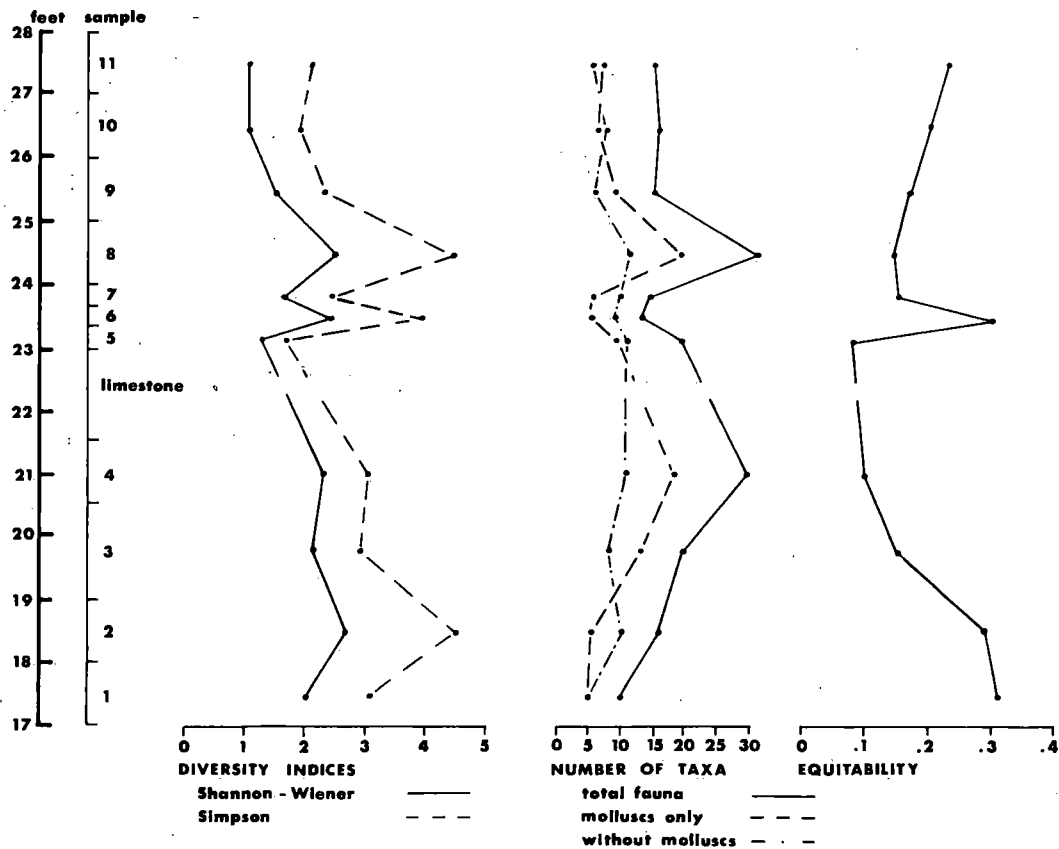
FIGURE 4.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 1, Kittaning, Pennsylvania.

value for this locality and again reflects an internal dominance within the molluscs.

There are several anomalous peaks on the curves that require an explanation. First, diversity index highs (2.6 and 4.6) occur within sample 2 (2.5-3.5 ft. below the limestone). These highs correspond to an equitability high of 0.29. The explanation is that only 16 taxa are recorded from the sample and the frequencies are evenly spread among these taxa. Thus the diversity index highs are controlled, in this case by an equitability high. This same factor controls the diversity index peaks in Sample 6. Secondly, at sample 4 there is a marked species diversity high which closely approximates the stillstand values at Sample 8. However the diversity indices are intermediate in value (2.3, 3.0) at Sample 4, and the corresponding equitability value is low (0.1). This anomalous sample probably reflects patchiness in the areal distribution of the fauna and reflects a local diversity and density high (garden or oasis) within the transgressive phase that was a "chance" find in the sampling. Such patchiness is evidently more common in both the fossil record and in modern faunas than is generally recognized (Speden 1966: 413). The assumption that this sample represents a local diversity high is further evidenced by the fact that both species diversity and diversity index values are intermediate in the subjacent and suprajacent samples. This transgressive high represents an opportunistic fauna dominated by eurytopic organisms such as *Cyclogyra* and *Glabrocingulum*.

The transgressive-regressive phases are distributed asymmetrically above and below the stillstand. The stillstand contains the stable mature fauna.

LOCALITY 7, UNIONTOWN, PENNSYLVANIA (PICCOLOMINI LOCALITY).— A report on a paleoecological investigation of this locality has been published (Donahue, Rollins, and Shaak 1972); only the salient features are mentioned here. Faunal analysis of six trenched samples taken within a three foot continuous interval suggests the following conclusions. First, species diversity, diversity indices, and equitability data (Fig. 5) suggest that the stillstand occurred within a limestone-ironstone unit and associated subjacent and suprajacent shales. Secondly, the diversity indices at the stillstand are qualitatively estimated to be 3.0 and 4.0 (Table 5), with an equitability values of 1.3. The estimates were made from hand picked specimens of the highly fossiliferous limestone-ironstone that could not be treated with the conventional laboratory techniques (a discussion of the limestone problem is found at the end of this section). Thirdly, a second diversity peak occurs within Sample 5, which is dominated by a productid-chonetid brachiopod fauna with smaller numbers of bivalves. This regressive high represents a somewhat stable relict-
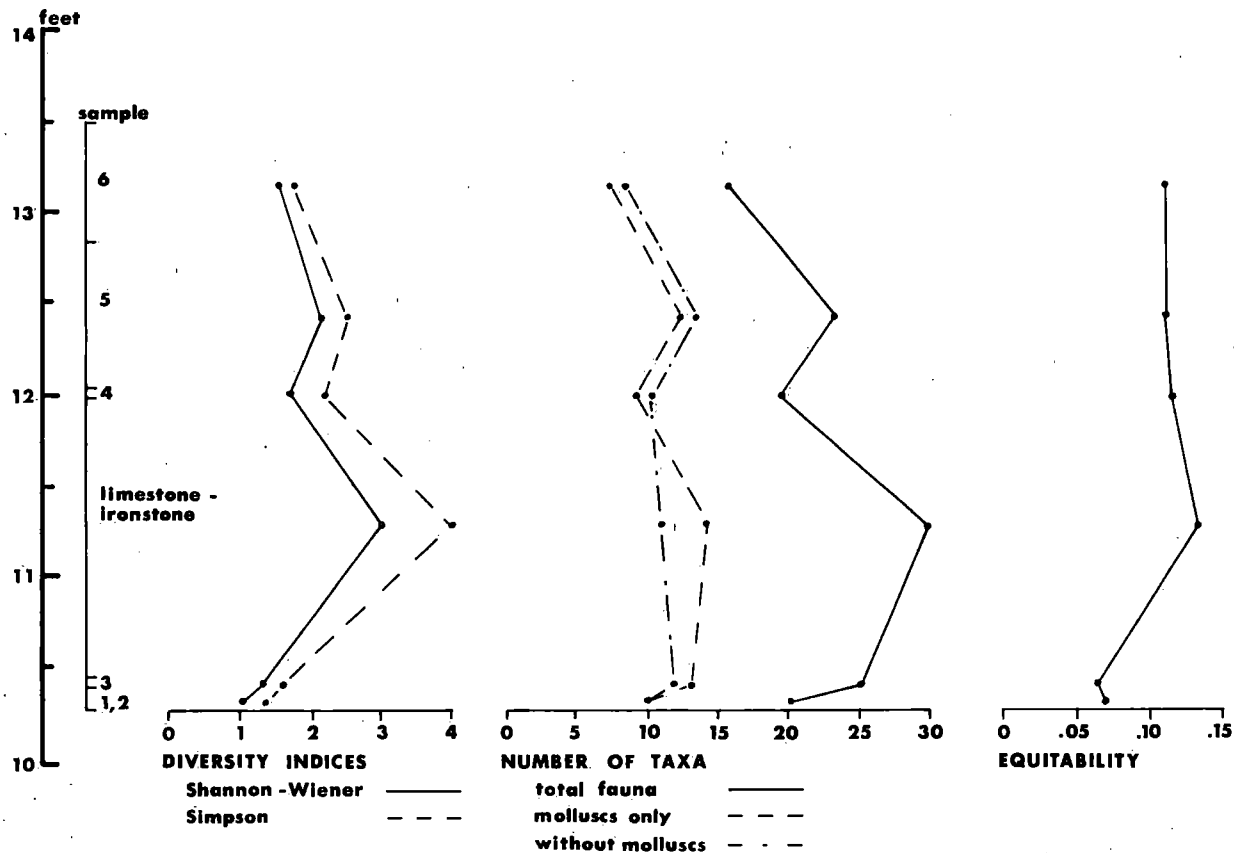
FIGURE 5.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 7 (Piccolomini locality), Uniontown, Pennsylvania.

TABLE 4.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 1, KITTANING, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equitability
11	4.0-5.0′ above limestone	14	8	6	2.04	3.16	.23
10	3.0-4.0′ above limestone	15	7	8	2.05	2.93	.20
9	2.0-3.0′ above limestone	14	8	6	1.53	2.39	.17
8	1.0-2.0′ above limestone	31	19	12	2.74	4.26	.14
7	8″-1.0′ above limestone	15	7	8	1.65	2.27	.15
6	4-8″ above limestone	13	6	7	2.48	3.94	.30
5	0-4″ above limestone	20	10	10	1.28	1.63	.08
4	0-1.0′ below limestone	30	18	12	2.29	3.04	.10
3	1.0-2.5′ below limestone	20	13	7	2.06	2.96	.15
2	2.5-3.5′ below limestone	16	6	10	2.65	4.57	.29
1	3.5-4.5′ below limestone	10	5	5	2.00	3.09	.30

[1] S-W=Shannon-Wiener
[2] S=Simpson

mature fauna dominated by the more eurytopic components left over from the stable-mature (stillstand) phase. Lastly, the faunal distribution above and below the stillstand is asymmetrical.

LOCALITY 8, URSINA, PENNSYLVANIA.—This locality is a collector's paradise for an exquisitely rich molluscan fauna. The bellerophontid gastropod *Pharkidonatus* is very abundant and, because of its large size, is the most conspicuous component of the macrofauna.

Seven trench samples were taken within a 6.5 ft. stratigraphic interval. The resultant data curves (Fig. 6) are diagnostic and again show the molluscan dominance characteristic of these shoaler localities. The stillstand phase peaks in Sample 5 at diversity index highs of 2.6 and 5.1 (Table 6). The equitability value of 0.28 for Sample 5 explains

TABLE 5.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 7, UNIONTOWN, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equitability
6	10.0-18.0″ above limestone	15	7	8	1.50	1.68	.11
5	0.5-10.0″ above limestone	23	12	11	2.10	2.54	.11
4	0-0.5″ above limestone limestone-ironstone	19	9	10	1.67	2.20	.12
3	0-0.5″ below limestone	25	13	12	1.39	1.60	.06
2,1	0.5-2.0″ below limestone	20	10	10	1.05	1.40	.07

[1] S-W=Shannon-Wiener
[2] S=Simpson

the diversity index peaks on the basis that the faunal distribution is evenly spread among the various taxa. This sample contains a stable-
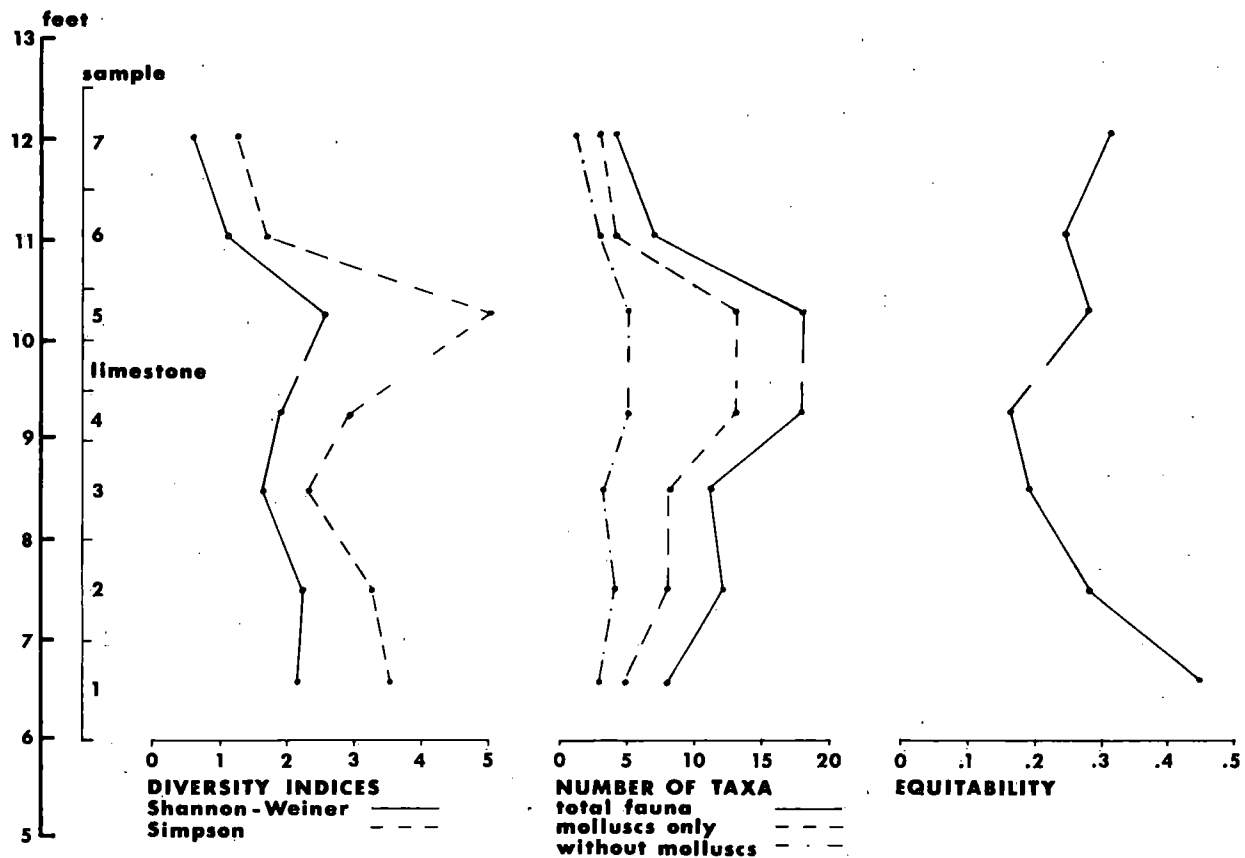
FIGURE 6.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 8, Ursina, Pennsylvania.

TABLE 6.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 8,
URSINA, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equita-bility
7	1.5-2.5' above limestone	4	3	1	0.63	1.26	.32
6	0.5-1.5' above limestone	7	4	3	1.14	1.72	.25
5	0-0.5' above limestone	18	13	5	2.57	5.07	.28
4	0-0.5' below limestone	18	13	5	1.86	2.88	.16
3	0.5-1.5' below limestone	11	8	3	1.63	2.17	.20
2	1.5-2.5' below limestone	12	8	4	2.23	3.39	.28
1	2.5-3.5' below limestone	8	5	3	2.17	3.58	.45

[1] S-W=Shannon-Wiener
[2] S=Simpson

mature fauna. The very high data curve values suggest a relatively high state of biological accommodation. There is perfect agreement between species diversity at the stillstand and Sample 4, and upon initial inspection suggests a relatively lengthy stillstand characterized by two lateral stable-mature faunas separated by a low diversity limestone facies. However the lower species diversity peaks (Sample 4) have low diversity index and equitability counterparts. This phenomenon is explained by numerical dominance of several eurytopic taxa within the faunas, and also by the fact that 8 of the 18 taxa have frequencies of 20 or less. Thus, the species diversity high of Sample 4 is interpreted as a relatively stable opportunistic faunal patch that developed in the late stages of the transgressions. This fauna perhaps gave rise directly to the stable-mature fauna of the stillstand by a decrease in the frequencies of the eurytopic components of the opportunistic fauna.

The limestone unit subjacent to the stillstand position is a transgressive limestone. A qualitative analysis indicates that its fauna is quite low in diversity and probably represents a restricted environment in which a limy mud was deposited under brackish conditions.

The faunal succession is markedly asymmetrical above and below the stillstand. The high diversity index values at the stillstand suggest a relatively high level of biological accommodation.

LOCALITY 9, GLADE CITY, PENNSYLVANIA.—This locality is unique in two aspects. First, two limestones are exposed in the sequence. The upper limestone is clearly of channel origin, and it occures as a lens-shaped body that grades laterally in two directions into bedded ironstone nodules. The channel is 5 feet wide and 0.5 feet in maximum thickness. Lithologically, the limestone is very dense, very black, and nearly devoid of fossils. This limestone perhaps was deposited as a black mud in a restricted abandoned channel on the lower part of a delta plain. Second,

the number of taxa curves graphically indicate the faunal succession (Fig. 7).

Eight trench samples were taken within a 7.5 foot stratigraphic interval. The resultant species diversity curves unquestionably pinpoint the marine stillstand. Molluscs again control the faunal succession, as shown by the parallelism of the total fauna and mollusc curves and the opposite relationship between the mollusc and non-mollusc curves. The diversity index curves are rather nondescript and, used alone, are misleading. The stillstand occurs within Sample 5. The diversity index curves show a slight inflection at the stillstand, which is in agreement with a low equitability value. These low values at the stillstand are explained by an uneven taxonomic frequency spread caused by the dominance of *Cyclogyra,* a planispiral foraminifer of the family Fischerinidae, and *Tolypammina,* a tubular encrusting foraminifer of the family Ammodiscidae.

There is a diversity index high and corresponding equitability high at the Sample 2 position, which is readily explained by the presence of only seven taxa that are evenly distributed. This equitable frequency distribution among the seven taxa pumps up the diversity indices regardless of the number of taxa present (Table 7).

TABLE 7.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 9, GLADE CITY, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equitability
8	2.5-3.5′ above limestone	6	4	2	1.42	2.21	.37
7	1.5-2.5′ above limestone	16	7	9	2.05	2.81	.18
6	10.0-14.0″ above limestone	24	13	11	2.05	2.63	.11
5	5.0-10.0″ above limestone	26	16	10	2.31	2.84	.11
4	0-5.0″ above limestone	23	13	10	2.06	2.43	.11
3	0-1.0′ below limestone	9	4	5	1.67	2.38	.27
2	1.0-2.0′ below limestone	7	4	3	1.99	3.30	.47
1	2.0-3.0′ below limestone	5	3	2	1.04	1.96	.39

[1] S-W=Shannon-Wiener
[2] S=Simpson

The faunal succession is markedly asymmetrical with a gradual transgressive phase composed of a few eurytopic taxa, peaking at the stillstand, and degrading relatively rapidly in the regressive phase.

Qualitatively, the limestone is of low diversity and probably was deposited in a brackish restricted environment. The limestone was formed during transgression.
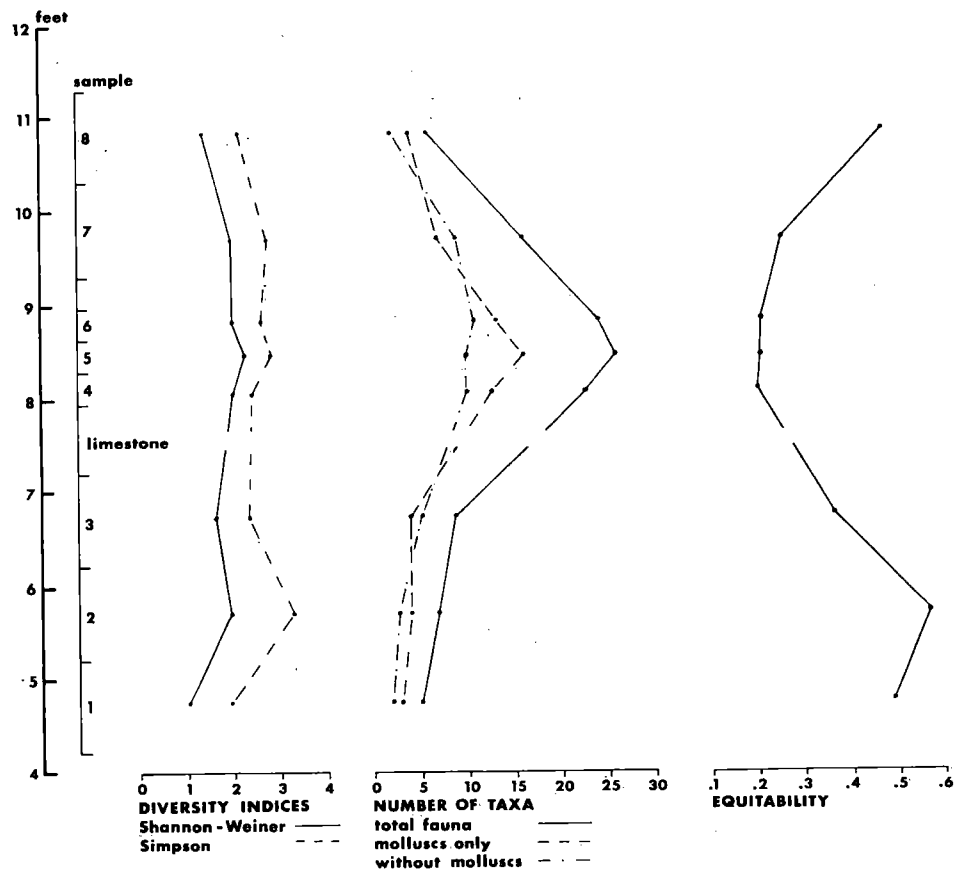
FIGURE 7.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 9, Glade City, Pennsylvania.
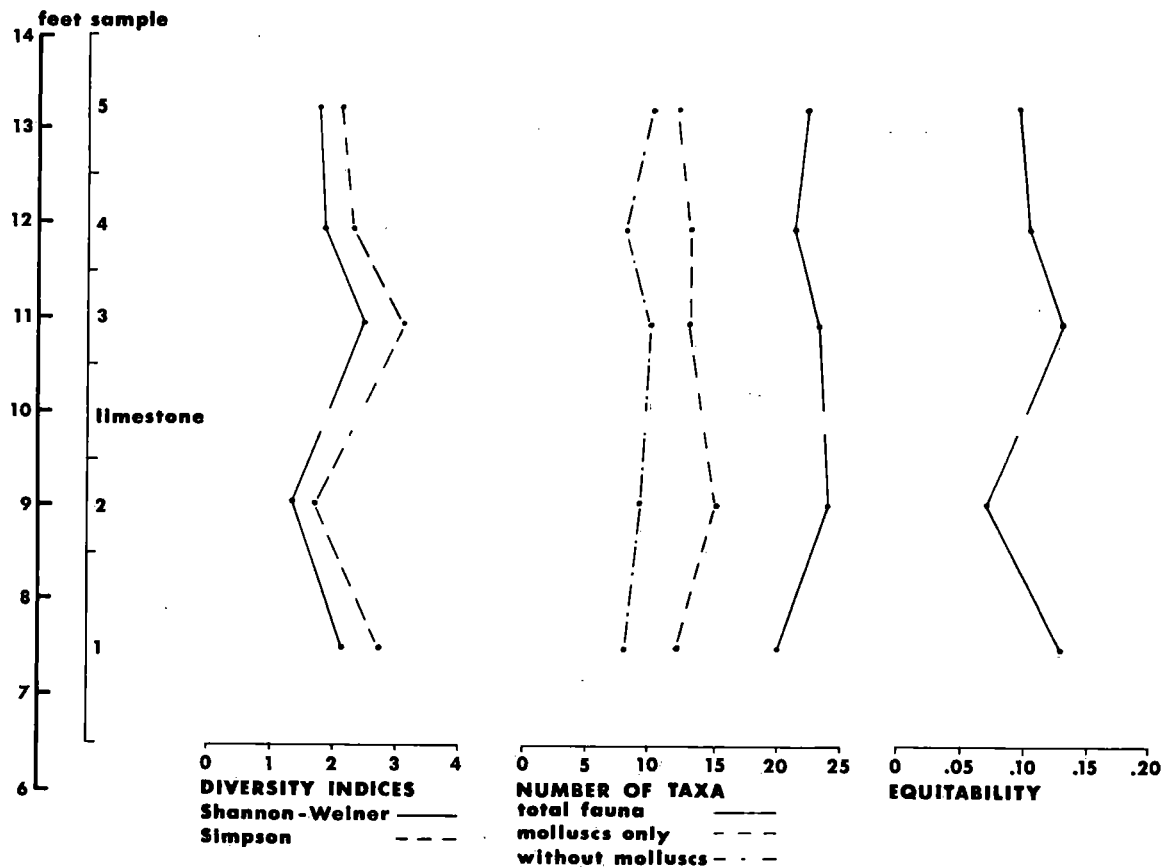
FIGURE 8.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 2, Shelocta, Pennsylvania.

Low Diversity Molluscan Faunas

LOCALITY 2, SHELOCTA, PENNSYLVANIA.—Brant (1971) presented a very detailed interpretation of the faunal succession of this locality. He used species diversity, equitability, and geochemical data for the purpose of zoning the section into communities. Brant defined 12 zones, of which zones 1 through 6 were classified as transgressive and zones 11 and 12 regressive. He did not indicate the position of the stillstand, but stated: "the position of the stillstand in this section does not appear meaningful" (Brant 1971:72).

Although the data curves for this locality (Fig. 8) are relatively flat, two diversity index highs are shown. These curves have a near-perfect fit with the equitability curve which, is explained by an "even-ness" of spread of the frequencies within the various taxa for the highs and a dominance factor for the lows.

The stillstand is judged to occur within Sample 3. Molluscs comprise 43 percent of the total number of taxa. Absolute high diversity index values of 2.5 and 3.1 also occur within this sample (Table 8).

TABLE 8.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 2, SHELOCTA, PENNSYLVANIA.

Sample. Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equita-bility
5	2.0-3.5′ above limestone	22	10	12	1.78	2.09	.095
4	1.0-2.0′ above limestone	21	8	13	1.83	2.29	.11
3	0-1.0′ above limestone	23	10	13	2.46	3.13	.14
2	0-1.0′ below limestone	24	9	15	1.39	1.70	.07
1.	1.0-3.0′ below limestone	20	8	12	2.16	2.76	.14

[1] S-W=Shannon-Wiener
[2] S=Simpson.

The diversity high at Sample 1 may represent a transgressive or opportunistic faunal patch that is controlled by eurytopic non-molluscs, including 10 taxa (50 percent) of foraminifers. Although surprisingly mature for an opportunistic fauna, Sample 1 does not reach the successional maturity of Sample 3 (stillstand).

These observations indicate that diversity index data alone can be misleading. The refinement of the raw faunal assemblage data of the "reflection" of standing crop provides the basis for the interpretation of this outcrop.

The limestone is qualitatively judged to be of low diversity, containing *Kegelites* (an amphissitid ostracod with a pitted shell) and chonetid brachiopods. Brant (1971: 52) gave a Shannon-Wiener average index for the limestone of 1.25, which is in agreement with a quali-
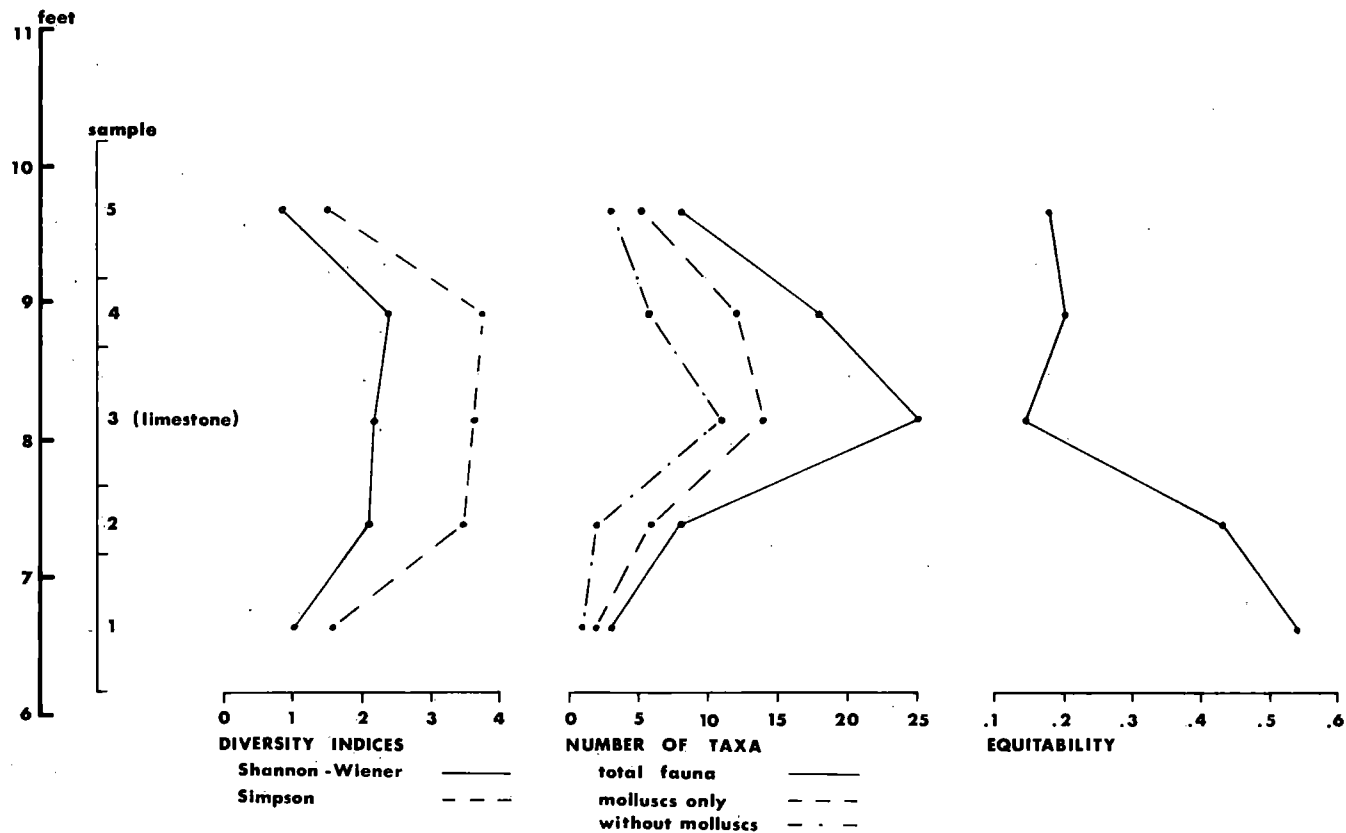
FIGURE 9.—Summary of sample locations, diversity indices, number of ttaxa, and equitability for Locality 3, Barton, Pennsylvania.

tative guess of low diversity in this study. However, he claimed that the limestone is diagenetic (secondary) in origin (Brant 1971: 9), based on its variable thickness and the localized gradational contact with the subjacent and suprajacent shales. This interpretation is in disagreement with that of the present study. The Brush Creek limestone is laterally persistent and in several localities (3 and 7) contains a stable mature fauna. Local lithologic variations, such as those at this locality, reflect different limestone lithotopes within the various limestone facies. The limestone at this locality is interpreted as a transgressive limestone deposited in a marginal but restricted environment. The restricted nature is evidenced by the absence of stenotopic organisms.

The transgressive-regressive phases are asymmetrically distributed above and below the stillstand.

LOCALITY 3, BARTON, PENNSYLVANIA.—Five trench samples were taken within a 7.5 foot stratigraphic interval. The diversity index curves (Fig. 9) for this locality are controlled by extreme fluctuations in equitability. The stillstand is judged to occur within Sample 3, the limestone unit, as evidenced by the species diversity curves. The lack of agreement between the diversity index curves and species diversity curves at the level of the stillstand is explained by the corresponding equitability low (0.15). This equitability low is a function of dominance by two taxa, *Cyclogyra* and *Glabrocingulum* (the latter a small pleurotomariacean gastropod). The stillstand, or stable-mature, fauna represents a relatively short stillstand duration, as evidenced by the lack of an inflection in the diversity index curves. The stillstand fauna failed to reach a high level of ecosystem maturity or biological accommodation even though the number of taxa increased to an absolute high of 25 (Table 9).

TABLE 9.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 3, BARTON, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equitability
5	0.5-1.5′ above limestone	8	3	5	0.86	1.43	.18
4	0-0.5′ above limestone	18	6	12	2.37	3.73	.21
3	limestone	25	11	14	2.18	3.65	.15
2	0-0.5′ below limestone	8	2	6	2.09	3.50	.44
1	0.5-1.5′ below limestone	3	1	2	1.00	1.63	.54

[1] S-W=Shannon-Wiener
[2] S=Simpson

Because it contains a stable-mature fauna, the limestone at this locality is unique. Lithologically the limestone is very argillaceous and poorly cemented, thus very friable. The fossils are exquisitely preserved

and readily removed from the matrix by the Amine 220 technique. This particular limestone perhaps represents a true pro-delta basinal organic limestone with minor but continuous terrigenous influx. The terrigenous fraction is probably the cause of the friable nature of the limestone and perhaps was the limiting factor in the low level of biological accommodation.

The transgressive-regressive phases are distributed asymmetrically around the stillstand, with a relatively rapid transgressive faunal bloom peaking at the stillstand. The regressive phase is less pronounced, with a gradual biological winnowing of the stenotopic components of the weakly developed stable-mature fauna.

LOCALITY 4, SEWICKLEY, PENNSYLVANIA.—Six trench samples were taken within a 5.5 ft. interval, including the lower 0.5 ft. of the 1.5 ft. thick limestone unit (Table 10). The resultant data and associated

TABLE 10.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 4, SEWICKLEY, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equitability
6	1.0-2.0′ above limestone	14	7	7	1.12	1.68	.12
5	0.5-1.0′ above limestone	22	10	12	1.25	1.64	.07
4	0-0.5′ above limestone	17	5	12	1.20	1.58	.09
3	lower 0.5′ of limestone	19	10	9	1.10	1.59	.08
2	0-1.0′ below limestone	19	11	8	0.86	1.33	.07
1	1.0-2.0′ below limestone	19	10	9	1.45	1.79	.09

[1] S-W=Shannon-Wiener
[2] S=Simpson

diversity curves (Fig. 10) at first appearance were rather non-descript and difficult to interpret. However several subtle faunal trends provided an insight into the faunal succession.

The values along all of the data curves are quite low compared with the other localities. The equitability scale has been exaggerated to show inflections that normally would be masked at a more reduced scale. The diversity index curves deviate only slightly from a straight line owing to a marked dominance in all samples by two foraminifer genera, Cyclogyra and Tolypammina.

The successional interpretation is derived for this locality from data other than the diversity index curves. The key to the interpretation is in the inverse relationship between the molluscs and non-molluscs in the number of taxa or species diversity curves (Fig. 10). Going up-section, the number of molluscan taxa is greater than the number of non-molluscan taxa. Within the limestone the two curves intersect and the
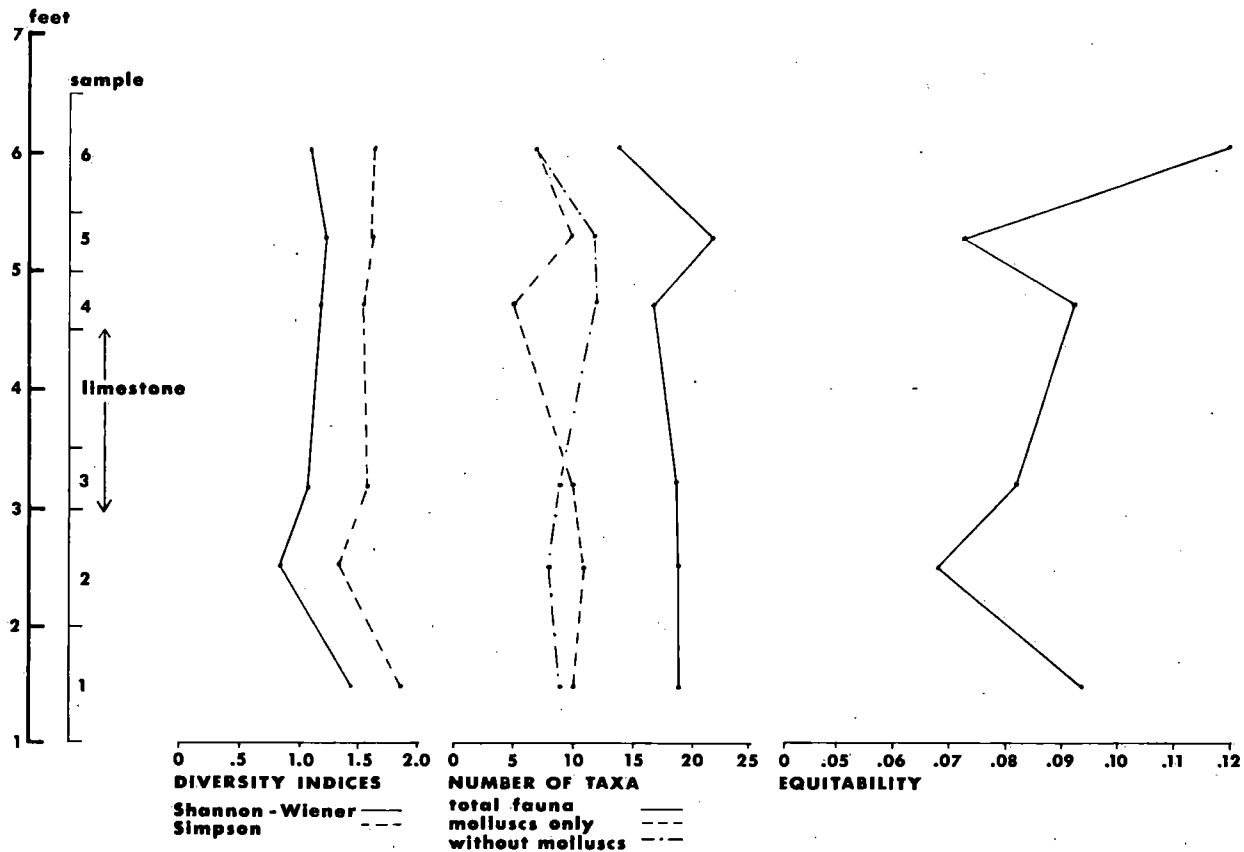
FIGURE 10.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 4, Sewickley, Pennsylvania.

non-molluscan taxa become dominant, suggestive of an increase in water depth (Stevens 1971). A molluscan low and a non-molluscan high are reached within Sample 4. This probably represents the maximum transgression (thus deepest water) at this locality. These data correspond to an equitability high of .09. The foraminiferal dominance is still paramount; however Sample 4 is more equitable than the subjacent and suprajacent samples. The ornamented ostracods and the crinoids reach an absolute high for the outcrop within Sample 4. *Astartella* reaches an absolute low in this sample. This is all suggestive of deeper water. Thus, the stillstand is judged to have occurred within Sample 4, based on relative water depths.

On visual inspection only, the species diversity curves would indicate that the stillstand occurred within Sample 5. The key to this interpretation is again the mollusc and non-mollusc relationship. The molluscs reach a taxonomic frequency low within Sample 4 and increase from 5 to 10 taxa (Table 10) at Sample 5. The non-molluscan number of taxa remains unchanged from Sample 4 to 5 (12 taxa). This phenomenon reflects a molluscan diversity pumping resulting from shoaling effects. Even though five molluscan taxa are added to the fauna, their frequencies are so low that with the increase of the dominant foraminifers (because of shoaling) the equitability value decreases drastically. The reduction of ornamented ostracods by a factor of five and the threefold increase of *Astartella* are further suggestive of shoaling conditions (Fig. 10). Thus Sample 5 reflects a very diverse relict-mature fauna.

There is an alternative explanation for the increase in the number of taxa within Sample 5. The fauna of Sample 5 may reflect an ecotone or a transition between two communities. The increase in the number of taxa from Sample 4 to 5 is entirely molluscan. This increase might be explained by the "edge effect" (Odum 1971: 1957) in which there is often a greater faunal diversity and density in the ecotone than in the adjoining communities. This edge effect may represent the junction zone between the early relict-mature fauna and an adjacent shoal water molluscan fauna. Unfortunately, this concept cannot be documented with the data available from this investigation.

There is another peculiar attribute of this locality that warrants an explanation. The lower .75 ft. of limestone is so poorly consolidated and friable that the fossils were removed from the matrix with ease and treated with the standard data recovery techniques. The upper .75 ft. of limestone is argillaceous, but less friable and more highly consolidated than the lower .75 ft. This suggests increased terrigenous influx during the deposition of the upper segment of the lime, and might explain the decrease in the number of molluscs through the limestone, peaking at a

low in Sample 4. The increased terrigenous influx would have affected the various feeding types (esp. filter feeders) and could have caused a decline in the number of taxa (Purdy 1964: 243). However the maximum density of the crinoids and fenestrate ectoprocts within this sample negates any strong sedimentologic influence.

The distribution of the transgressive-regressive phases around the stillstand is asymmetrical within the confines of the sampling design. Unfortunately the initial taxonomic buildup of the transgressive phase is lower in the section than the sampled interval. The highest and lowest samples have relatively high equitability values, as is common in early transgressive and late regressive phases.

LOCALITY 5, GLENSHAW, PENNSYLVANIA.—This locality is unique because it shows an extremely rapid transgression to the stillstand from non-marine, or near non-marine conditions within a stratigraphic interval of only 13 inches (Fig. 11). Six trench samples were taken within a 6.0 ft. stratigraphic interval. The basal unit of the sequence is a massive black mudstone at least 10 ft. thick (the basal coal is not exposed), which is capped by a six-inch bed of limestone. The sample interval extended two feet into the mudstone. Only two taxa of ostracods (one smooth and one ornamented) were recovered from the matrix. A second outcrop several hundred yards to the southwest also is barren of fossils below the limestone and lithologically is composed of interbedded shale and ironstone nodules. The black mudstone represents a restricted environment at the extreme end of the physical accommodation and member of Sanders' stability-time hypothesis. The physiological stress conditions were so great that the resultant environments were beyond the adaptive means of most marine animal taxa.

The marine transgression was initiated with the deposition of the limestone which, on a qualitative inspection, is very low in diversity. The diversity index and species diversity curves peak within Sample 3 (Fig. 11), indicating the stillstand. The stillstand peak occurs within 13 inches of stratigraphic section; thus the transgression was nearly instantaneous geologically. The high diversity index value of 6.0 for the Simpson equation is a result of the rapid increase in the number of taxa from 1 in Sample 2 to 21 in Sample 3 (Table 11). These peaks correspond to an intermediate equitability value of 0.28, which is intermediate because of dominance by *Shansiella*, a large turbiniform pleurotomariacean gastropod.

The species diversity curves show a second inflection (Sample 5) in the regressive or relict-mature fauna. The mollusc and non-mollusc curves are nearly parallel through Sample 4, but in Sample 5 the curves
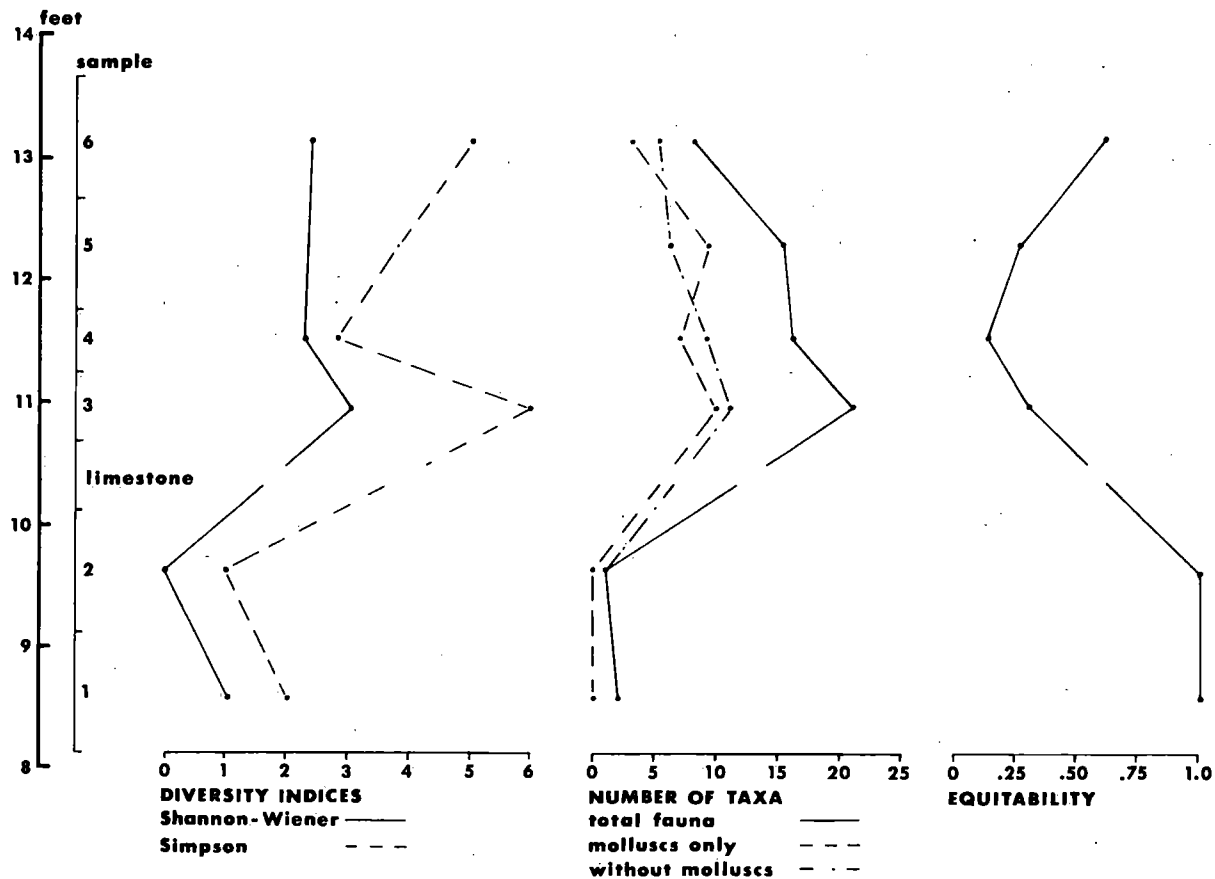
FIGURE 11.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 5, Glenshaw, Pennsylvania.

TABLE 11.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 5, GLENSHAW, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equita-bility
6	2.0-3.0′ above limestone	8	3	5	2.39	4.91	.61
5	1.0-2.0′ above limestone	15	9	6	2.26	3.86	.26
4	0.5-1.0′ above limestone	16	7	9	2.29	2.80	.18
3	0-0.5′ above limestone	21	10	11	3.03	5.96	.28
2	0-1.0′ below limestone	1	0	1	0.00	1.00	1.00
1	1.0-2.0′ below limestone	2	0	2	1.00	2.00	1.00

[1] S-W=Shannon-Wiener
[2] S=Simpson

have reversed position, with the molluscs becoming dominant with respect to the number of taxa for the first time in the sequence. This molluscan increase corresponds to an increase in equitability and diversity index values, especially the Simpson function.

An abnormally high Simpson index of 4.9 occurs in Sample 6, late in the regressive phase or relict mature fauna. This peak is not controlled by the number of taxa, but by an equitability high (.51) that reflects an even distribution of the frequencies within the eight recorded taxa.

The distribution of the transgressive-regressive sequence around the stillstand is markedly asymmetrical, with a rapid transgressive phase and an accompanying rapid buildup of the opportunistic fauna. The regressive phase was more irregular than the transgressive phase. The stillstand and accompanying stable-mature fauna was relatively shortlived, as the number of taxa increased, peaked, and decreased within a seven-inch stratigraphic interval.

The lack of agreement between the lower portion of the diversity index curves and the equitability curve warrants an explanation. Samples 1 and 2 have a value of 1.0 perfect equitability. However, the corresponding diversity index values of the Shannon-Wiener value is 0.0, compared with the perfect equitability of 1.0. The Shannon-Wiener function is strongly influenced by equitability, and in this case the diversity index should be high. However a perfectly equitable distribution (one taxon) represents a totally inequitable distribution in the Shannon-Wiener function because of total (100 percent) dominance. Thus, because of total dominance, the Shannon-Wiener index is zero. The corresponding Simpson value is 1.0 which, except for infinity, is the lowest calculable value for the equation, again because of total dominance.

LOCALITY 6, MURRYSVILLE, PENNSYLVANIA.—Six trench samples were taken within a 5.5 ft. stratigraphic interval. The diversity index curves
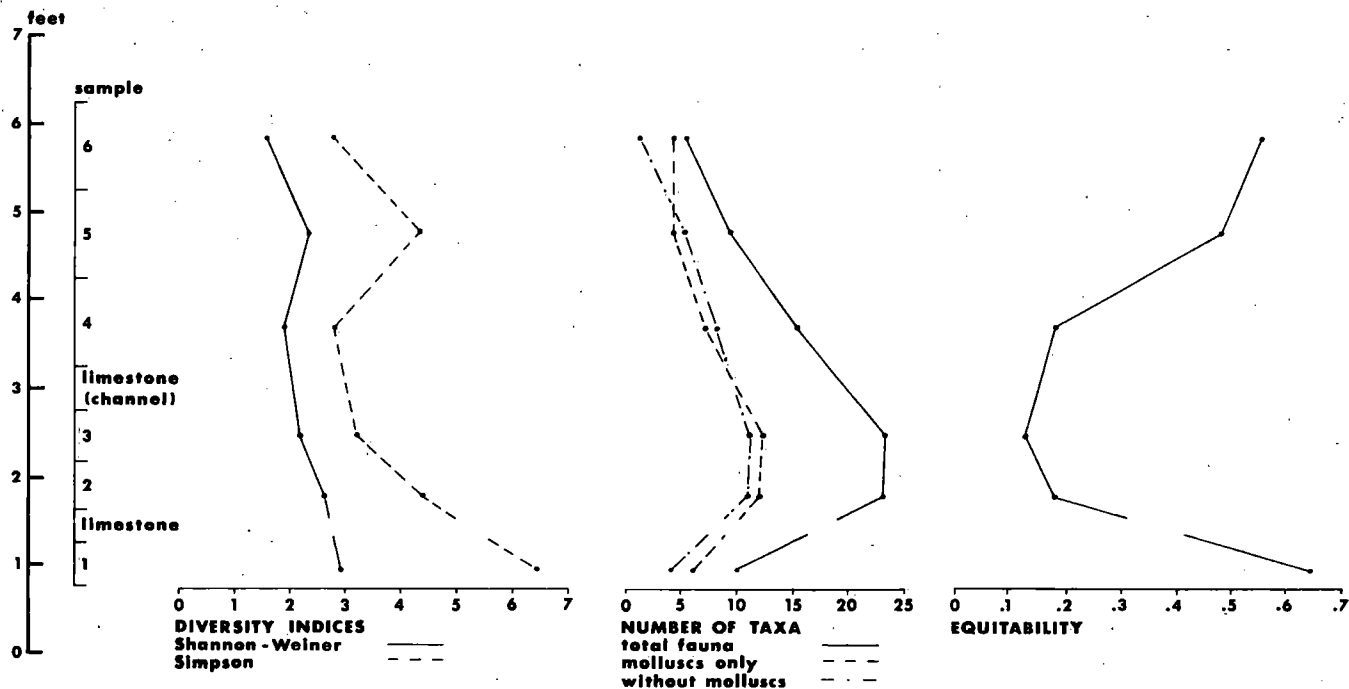
FIGURE 12.—Summary of sample locations, diversity indices, number of taxa, and equitability for Locality 6, Murrysville, Pennsylvania.

TABLE 12.—SUMMARY OF DIVERSITY AND EQUITABILITY VALUES FOR LOCALITY 6, MURRYSVILLE, PENNSYLVANIA.

Sample Number	Interval	Number of Taxa	Molluscs Only	Without Molluscs	S-W[1] Diversity	S[2] Diversity	Equitability
6	2.0-3.0' above limestone[3]	5	4	1	1.55	2.77	.55
5	1.0-2.0' above limestone	9	4	5	2.35	4.36	.49
4	0-1.0' above limestone	15	7	8	1.93	2.84	.19
3	0-7.5" below limestone	23	12	11	2.16	3.21	.14
2	7.5-15" below limestone	23	12	11	2.62	4.62	.19
1	21.0-27.0" below limestone	10	6	4	2.91	6.44	.64

[1] S-W=Shannon-Wiener
[2] S=Simpson
[3] =datum-channel limestone

(Fig. 12) alone are meaningless in the interpretation of species diversity and faunal succession. The diversity index curves peak in two samples (1 and 5), both of which are relatively equitable samples representing no marked dominance by any one taxon. Sample 1 is represented by 10 taxa, with a very high Simpson index of 6.4 (Table 12). As previously explained, the equitability factor is derived by diving the Simpson index (6.4) by the number of taxa (10), resulting in an equitability index of .64. The equitability value for this sample is an excellent guide in the understanding and interpretation of diversity-equitability data in general. Knowing what the equitability value represents allows one to look objectively at the diversity values. The Simpson index of 6.4 is controlled either by number of taxa (species diversity) or equitability. Also, the question of adequacy of sample size must be taken into consideration. The data from Sample 1 clearly define this relationship. If the Simpson index is compared with the equitability value (6.4 versus 0.64) within the framework of sample size adequacy test as described earlier, the values minus decimal are equal (in this case to five digits). If the sample-size test is valid, this sample is adequate, removing the question of incomplete data retrieval. Knowing that the sample size is adequate, the diversity index curves can be interpreted. Sample 1 contains only 10 taxa, thus the diversity index value is not controlled by the number of taxa but by the evenness of spread of the frequencies within the 10 taxa. Again, the high equitability value of Sample 1 controls the high diversity index value. An almost identical condition occurs within Sample 5, where the diversity index peak is a function of high equitability rather than the number of taxa.

Sample 1 was taken through a six-inch carbonaceous shale interval between the basal coal and the overlaying limestone (Appendix A). There is no non-marine sequence on top of the coal as 10 taxa were accounted for within this basal sample. The overlying limestone is quantitatively low in diversity and represents a transgressive limestone.

The stillstand occurs within Sample 2, a 7.5 inch interval immediately suprajacent to the limestone. Samples 2 and 3 have identical number of taxa values, and trends in the faunal succession. Sample 2 has a higher equitability value and correspondingly higher diversity index values than does Sample 3. Sample 2 has a more equitable frequency distribution among its taxa than Sample 3, which fits better within the definition of a stable-mature fauna. If Sample 2 represents a stillstand and Sample 3 an early regressive phase, Sample 3 should reflect shoaling trends. This is the case, especially in faunal composition. One of the more reliable shoal-water indicators is *Astartella*, which increases by a factor of 14 (36,115 to 489,365) from Sample 2 to Sample 3. Of 19 molluscan taxa recognized from Samples 2 and 3, eight taxa are common to the two samples. Six of these taxa increase in frequency in Sample 3; a further suggestion of shoaling conditions, or initiation of the regressive phase.

The number-of-taxa curves graphically depict the asymmetrical distribution of the transgressive-regressive phases around the stillstand. The transgressive phase was of relatively short duration, with a rapid buildup of the opportunistic fauna. The stillstand was achieved in Sample 2, with the accompanying degradation of the stable-mature fauna quite regular with respect to the transgressive phase.

A channel limestone is exposed at this locality (Appendix A), which on general inspection is devoid of fossils. Although very interesting with respect to sedimentation and depositional environments, the channeling removed six inches of the regressive phase deposits and associated fossils from the section. The channel has masked another important relationship in which there is a reversal in the number-of-taxa-curves from a molluscan to a non-molluscan dominance within Samples 4 and 5. With shoaling conditions resulting from regression of the sea, the molluscs should remain dominant with respect to the number of taxa. This non-molluscan dominance is only of the order of one taxon in each of the two samples and is judged to be relatively insignificant as the trend reverts to a molluscan dominance in the highest sample (Sample 6).

THE LIMESTONE PROBLEM

All nine outcrops were trench sampled, and the total samples were broken down by the Amine 220 technique. All of the washed residues were split with a standard sample splitter. Thus, from outcrop to microscope, these data are sound with respect to randomness. Every fossil within the samples had a chance of being identified and included in the frequency counts.

The limestone members of the Brush Creek interval present a worrisome drawback to an otherwise credible data recovery system. The

limestones are not amenable to the Amine 220 technique. Several lime-
stone samples were reduced in a jaw crusher and subsequently treated
with the Amine 220 technique, but the sample pieces fractured across
fossils and only fossil fragments were recovered in the washed residues.
Possible alternatives to the system are qualitative analysis of either
whole-hand samples or polished slabs. Some hand samples have whole
fossils standing out in positive relief, which allows taxonomic identifica-
tion but cannot provide adequate frequency data. Polished sections
record all taxa in contact with the plane of the cut. Unfortunately the
fossils may have any orientation with respect to the plane, thus taxo-
nomic identifications are most difficult and very time consuming.

The limestone problem was alleviated somewhat by comparison of
the various limestone lithologies. Seven of the nine localities have well
consolidated limestones that are unbreakable by the Amine technique.
The remaining two localities (Loc. 3, Barton, Pennsylvania; and Loc. 4,
Sewickley, Pennsylvania) have poorly consolidated, friable limestones
from which the fossils were readily retrieved. The entire limestone unit
from the Barton locality was broken down and quantitatively is judged
to represent the stillstand. The lower 0.5 ft. interval of the 1.5 ft. lime-
stone from the Sewickley locality broke down and quantitatively is in-
termediate in values between those of the subjacent and suprajacent
samples within the transgressive phase. The limestones at the remaining
localities, with the exception of the ironstone-limestone horizon at the
Uniontown locality, are well consolidated and judged qualitatively to be
of low diversity. The ironstone-limestone interval at the Uniontown
locality is inferred to represent the standstill on the basis of a subjective
quantitative analysis of the well preserved and very rich molluscan fauna
that was retrieved from well-weathered float samples. Also, the esti-
mated diversity index and number of taxa values are substantially greater
than in the sub- and suprajacent samples. Thus there appears to be a
trend within the limestones, whether real or diagenetic, of an increase
in diversity with a decrease in the level of consolidation.

A second trend is perhaps more obvious. The limestone unit at two
of the nine localities is judged to contain the stable-mature fauna, repre-
sentative of the marine stillstand. The limestone unit at the remaining
seven localities is judged to contain a segment of the opportunistic fauna,
representative of the transgressive phase. At no locality studied in this
investigation does the limestone occur above the stillstand position. Two
of the localities have the limestone unit between two quantitatively
analyzed samples within the transgressive phase and qualitatively show
corresponding intermediate number of taxa and diversity index values.
The remaining seven localities have the limestone subjacent to the still-

stand samples and qualitatively appear to be in accord with the predicted intermediate values.

These two trends, though subjective, are considered clear enough as to not invalidate the placement of the stillstand at the seven localities where well-consolidated limestones occur.

COMMUNITY STRUCTURE

GENERAL STATEMENT

One of the most consistent features of shallow benthic marine environments is the recurrence of a particular taxon or taxonomic assemblage. These ubiquitous taxa may be numerically dominant and may reflect some observable physical environmental parameter. If these ubiquitous, numerically dominant, and environmentally sensitive taxa are found in association with other commonly recurrent species or taxonomic groups, the definition of a fossil community is met. This definition is in accord with the organism and habitat communities of Newell *et al.* (1959) and the marine level-bottom communities within the framework of marine biology (Bretsky 1969: 46).

The recurrence of species or taxonomic groups is explained by interspecific associations, similar responses to the physical environment, or chance (Johnson 1964: 128). The chance associations are probably minimal in level-bottom communities and most commonly are found among transient species (planktonic or nektonic) that are relatively unimportant at the organizational level of any particular benthic community. It is commonly accepted that benthic species are quite independent, and the resultant communities are associations of species living together in harmony with the physical environment. The simple organizational level of shallow benthic communities is more amenable to a community structure analysis than the more diverse communities, such as coral reef and rocky intertidal regimes.

The most common community analysis tools have been correlation coefficients and factor analysis of a data matrix. A data matrix (Appendix B) was prepared for this study to show either presence or absence of each recognized taxon at all nine localities. Surprisingly, only eight taxa (Table 13) were found to be ubiquitous within the study area. The faunal succession was traced through the transgressive-stillstand-regressive phases, and a relationship between these phases and the community structure seemed more logical than taxonomic groupings based on numerical dominance. Thus the transgressive, stillstand, and regressive sample-adjusted frequencies were averaged for the eight ubi-

TABLE 13.—SUMMARY OF TRANGRESSIVE-STILLSTAND-REGRESSIVE SAMPLE FREQUENCY
AVERAGES FOR TAXA COSMOPOLITAN TO THE STUDY AREA.

Taxa	Transgressive[1]	Stillstand[2]	Regressive[3]
Ostracods (smooth)	3954	3834	2882
Ostracods (ornamented)	98	600	389
Astartella	90507	75190	85065
Glabrocingulum	21904	92502	63829
Ianthanopsis	17040	13181	2189
Aclisina	5714	6564	8968
Plagioglypta	1679	16934	8673
Crinoids	847	1238	423

[1] Transgressive values are based on an average of 28 transgressive samples.
[2] Stillstand values are based on an average of 9 stillstand samples.
[3] Regressive values are based on an average of 24 regressive samples.

quitous taxa to ascertain community trends in parallel with the faunal
succession.   If the marine interval can be divided into transgressive,
stillstand, and regressive phases, the corresponding taxa should be sub-
divisible into transgressive, stillstand, and regressive communities.   The
frequency averages for the eight ubiquitous taxa adequately support this
premise.

Astartella-Ianthanopsis COMMUNITY

    Astartella and *Ianthanopsis* are selected to serve as name bearers for
the transgressive or opportunistic community.   *Astartella* is a small eury-
topic crassatellacean bivalve that was an infaunal non-siphonate suspen-
sion feeder.   It is classified as a "filterer-A" within the framework of the
Russian classificatory scheme for marine benthic invertebrates ('Turpaeva
1957: 137).   The successional trend of *Astartella* (Table 13) is quite
unique because it peaks numerically within the transgressive phase,
decreases in the stillstand, and increases within the regressive phase.
The frequency low within the stillstand phase is predictable because of
the shallow water preference of this species.   Its regressive bloom ap-
proaches, but does not reach, the numerical dominance developed within
the transgressive phase.   These marine stage frequencies of *Astartella*
lead one to speculate on the successional maturity of the stillstand or
stable-mature fauna for the study area as a whole.   Although the still-
stand frequencies are reduced, they are still relatively high.   The still-
stand values for *Astartella*, as well as any eurytopic organism, would
continue to be reduced with more pronounced biological accommodation
(Levinton 1970).   However the modest frequency deduction in the still-
stand phase suggests a relatively low level of community maturity and
an accompanying low level of biological accommodation.   In terms of the
stability-time hypothesis, this trend is also suggestive of an average short
stillstand duration.

Ianthanopsis, the second name bearer of the opportunistic com- munity, was a globular to high-spired fusiform gastropod of the family Subulitidae. It was an epifaunal vagrant browser and deposit feeder of the "collector" group of marine benthic invertebrates (Turpaeva 1957). This taxon peaks numerically within the transgressive or oppor- tunistic phase and reaches a low within the regressive or relict-mature phase (Table 13). Thus, *Ianthanopsis* is a eurytopic component of the community, and after transgressive bloom never again regained its nu- merical dominance. The trend of *Ianthanopsis* clearly delimits this species as opportunistic, even more so than *Astartella.* Further suggestive of a natural transgressive community among the ubiquitous taxa are the unornamented ostracods, which also peak numerically within the trans- gressive phase and decline through the stillstand and regressive phases.

The *Astartella-Ianthanopsis* community is dominated by epifaunal and infaunal vagrant deposit feeding organisms ("collectors" of the Tur- paeva classification). This mode of life dominance in conjunction with the paucity of sessile benthonic filterers ("filterers A and B" of Tur- paeva), such as crinoids and bryozoans, is suggestive of an unstable substrate in a high energy regime in shoal water environments. These conditions are predictable for the opportunistic community as the fauna is the product of the extremes of physical accommodation.

Glabrocingulum-Plagioglypta COMMUNITY

Glabrocingulum is a turbiniform, gradate to conically-spired gas- tropod of the family Eotomariidae. *Plagioglypta* is a scaphopod of the family Dentaliidae marked by distinct circular wrinkles generally throughout the shell. These two genera are selected as standard bearers for the stable-mature, or stillstand community because of their cosmo- politan nature and their frequency trends through the faunal succession.

Glabrocingulum was a eurytopic vagrant epifaunal browser and de- posit feeder of the "collector" benthic group of Turpaeva. The eurytopic nature of this taxon is out of phase with the stable mature concept of community succession. The eurytopic components theoretically are re- duced in frequency, if not entirely removed, as the fauna trends toward biological accommodation. With increasing biological accommodation, the stenotopic components trend toward a state of equilibrium. If the succession goes unchecked as a result of environmental stability over a lengthy stillstand, the opportunistic species would be relatively rare (Levinton 1970: 69). However, because of the relatively low level of successional maturity and relatively short duration of the stillstand, the stenotopic organisms did not have enough time to develop a dominance over the eurytopic organisms. Deeper water conditions and increased

substrate stability provided suitable habitats for the stenotopic organism blooms, thus pumping up the diversity of the fauna but without exclusion of the eurytopic components. It is quite possible for an explosive opportunist to numerically peak within the stillstand or stable-mature fauna if the limiting factor of that phase is temporal brevity.

Glabrocingulum peaks numerically within the stable-mature phase and tails off in the relict-mature phase to a level intermediate between the transgressive and stillstand phases (Table 13). The intermediate regressive value further supports the contention that *Glabrocingulum* is eurytopic.

Plagioglypta was a sublittoral benthic infaunal animal ("collector"), living partly embedded in the substrate with only the posterior extremity projecting into the water (Ludbrook 1960: 137). Because of its restriction to keep (sublittoral) water, it is an excellent stillstand indicator. The frequency trend of *Plagioglypta* through the faunal succession is similar to that of *Glabrocingulum,* because its peak is within the stillstand and the regressive average is intermediate in value (Table 13). However the transgressive frequency is increased by 100 percent in the stillstand, whereas the regressive frequency is reduced 50 percent from that of the stillstand. This pronounced stillstand frequency peaking is a further indication of the stenotopic nature of this animal.

There currently is marked controversy as to the exact biological affinity of *Plagioglypta.* The large forms (+10 or coarser) probably are true scaphopods. The smaller forms, many of which pass through a number 100 sieve, may represent polychaete worm tubes. However the characteristic concentrically wrinkled shell is discernible on all size specimens. Regardless of their biological affinity they are recognizable, and their frequency trends place them within the stillstand or stable-mature fauna.

Further supportive of a stillstand community is the frequency trend of the ornamented ostracods. The frequency averages of the ornamented ostracods peak within the stillstand, with the transgressive and regressive frequency averaging significantly lower (Table 13). Additional support is provided by crinoid frequencies, which also peak within the stillstand.

The successional maturity of the *Glabrocingulum-Plagioglypta* community is quite low, as evidenced by the abundance of eurytopic components. Increased water depth and near-normal marine conditions existed, even if only temporarily. The *Glabrocingulum-Plagioglypta* community is dominated by epifaunal deposit feeders of the "collector" group, as is the case of the transgressive *Astartella-Ianthanopsis* community. The most notable changes are in the sessile benthonic suspen-

sion feeders. The crinoids, ramose and fenestrate bryozoans, and brachiopods reach their frequency peaks within this community. Environmentally, this community is farthest from shore, in the deepest water (with reference to the study area), and in a low terrigenous influx regime as is required by the sessile benthonic suspension feeders ("Filterers" A and B). The substrate is more stable than in the transgressive environments, as evidenced by the marked increase in the rooted and cemented benthos.

Aclisina COMMUNITY

The *Aclisina* community represents the regressive phase and the corresponding relict-mature fauna. *Aclisina* is a high-spired snail with distinct spiral ornamentation of the family Murchisoniidae. It was probably eurytopic, as evidenced by the similar frequencies throughout the marine event. However the frequencies increase gradually through the transgressive and stillstand phases and peak within the regressive phase (Table 13). *Aclisina* is selected as name bearer for the relict mature community because it is cosmopolitan to the study area and is the only taxon of the cosmopolitan taxa that has its frequency peak within the regressive phase.

The *Aclisina* community is the highest stratigraphically (thus youngest) of the three laterally persistent benthic communities within the bounds of the study area.

Environmentally, the *Aclisina* community is interpreted as indicating a return nearer to shore and shoal water conditions. It is the relict-mature communty of the regressive phase, composed of the more eurytopic components left over from the *Glabrocingulum-Plagioglypta* stillstand community. The stenotopic components are biologically winnowed from the fauna during the entirety of the regressive phase. Thus the environment shifts from a low level of biological accommodation to pronounced physical accommodation. The opportunistic community is the product of aggradation, whereas the relict mature community is the product of degradation. The stable-mature community was marked by deeper water, offshore environments, and a decrease in terrigenous influx that allowed the more stenotopic sessile suspension feeders (crinoids and bryozoans) to increase in density. This process is reversed in the regressive phase. The only noticeable differences between the transgressive and regressive phases are in the vagaries of the faunal succession. The explosive opportunists such as *Astartella* and *Ianthanopsis* never regain their prominence in the regressive phase.

Rhombopora-Septopora COMMUNITY

The cosmopolitan communities are easily recognized and can be readily documented. However, one laterally restricted unique faunal association occurs within the study area and warrants discussion. The use of community in this instance is a convenient abstraction. Although this restricted faunal assemblage is a real three dimensional unit, it is a small scale one that cannot be recognized on a basin-wide level.

The marine transgressive phase at Loc. 4, Sewickley, Pennsylvania, yielded an exquisite bryozoan fauna composed of the genera *Septopora* and *Rhombopora*. *Septopora* is a very distinctive cryptostomatous bryozoan of the family Acanthocladiidae. The genus is recognized by its distinctive branch-bifurcation network and associated dissepiments. Also, each branch is divided by a medial carina separating the laterally adjacent zooecial rows. *Rhombopora* is a rhabdomesid cryptosome found as ramose zoarial fragments displaying irregularly spaced bifurcations. The most striking structures are large blunt spines that are the surficial expressions of megacanthopores (Huffman 1970: 675).

The *Rhombopora-Septopora* community developed within the transgressive or opportunistic phase, culminating in the limestone subjacent to the stillstand sample. This community represents the highest bryozoan density within the study area. The locality itself is classified in the low diversity molluscan group of localities characterized by offshore, deeper water environments. Macroscopically the community is dominated by bryozoans, which occur as thick mats exposed on shale and limestone bedding planes. However, microscopically the community is numerically dominated by chonetid brachiopods, agglutinated forams, and pleurotomariacean and bellerophontacean snails. The community perhaps developed in a bryozoan garden or biostrome; thus the actual find was by chance, as the community probably represents just an areal patch. The community formed offshore in relatively deep water. The bryozoans are classified as "Filterers B" in the Turpaeva classificatory scheme and require deep offshore turbid waters under conditions of low terrigenous influx on a moderately stable substrate. The bedding plane occurrence of the bryozoans perhaps represents alternating periods of silting and quiescence.

DIVERSITY INDICES AS PALEOECOLOGIC TOOLS

GENERAL STATEMENT

Paleoecological and ecological research in recent years has shown a trend toward quantification of data. This quantification is applicable

to animal communities because of their inherent feature of diversity. Because animal diversity can be quantified, critical community features such as structure, stability, and evolution can be synthesized. One of the more informative methods of quantification is the derivation of numerical species diversity.

COMPARISON OF THE SHANNON-WIENER AND SIMPSON DIVERSITY FUNCTIONS

The Shannon-Wiener information function is sensitive to both the number of taxa present and the degree of evenness by which the number of individuals are distributed among the taxa. Stable values are rapidly reached and maintained when a population size of about 200 individuals for high stress environments and about 400 individuals for low stress environments per sample is achieved (Sanders 1968: 279). With the recovery methods used in this investigation, minimum frequencies in most samples have been greatly exceeded. Therefore within the framework of this investigation the Shannon-Wiener function is relatively sample-size independent. There is, however, a very strong influence resulting from the evenness of spread of the individials among the various taxa.

The Simpson function is markedly influenced by sample size and less by the evenness of spread of the individuals among the various taxa. As more individuals are added to the samples, there is a corresponding increase in diversity values. This relationship stems from the fact that individuals are added at a constant arithmetic rate, whereas taxa are added at a decreasing logarithmic rate.

Because these two diversity indices are influenced by several variables, both were used for all samples in the calculation of diversity values. A comparison of the two diversity index curves for each locality (Fig. 3 to 11) shows a remarkable closeness of fit or parallelism.

The index curves at localities 2 and 4 (Shelocta and Sewickley) are practically congruent. The remaining localities show a close parallelism between the diversity index peaks. The Simpson index values are numerically higher than the Shannon-Wiener values, and the diversity value highs for the Simpson function are markedly more peaked than the corresponding Shannon-Wiener values. This pumping up of the Simpson peaks over the Shannon-Wiener peaks leads to the conclusion that these particular samples represent an increase in the number of taxa over those from the subjacent samples. This is not always true, however. Because of the individual frequencies evenness of spread in several sample analyses, the Simpson high peaks are controlled by high equitability values. As expected, the Shannon-Wiener peaks, except under

conditions of low sample frequencies, are controlled by the equitability factor.

The number of taxa retrieved with corresponding high numerical frequencies in this investigation generally average out the differences between the Simpson and Shannon-Wiener functions. Even though inflections in the curves for the Simpson function are more pronounced than in Shannon-Wiener, the Simpson index values and curves, if used alone, are less reliable. This unreliability results from the dual influence of both equitability and taxonomic frequencies.

RESTRICTIONS IN THE USE OF DIVERSITY INDICES

A review of the data plots (Figs. 3 to 11), including the diversity index, number of taxa, and equitability curves, supports the contention that the diversity index values and curves cannot safely be used alone to define communities or their trends. The diversity index curves range from peaked to flat, and the general shape of the curves can be controlled by masked subtleties in the faunal distribution. Two very real situations that are difficult to detect are patchiness, as previously described, and faunal aggregations. Faunal aggregations are a function of sampling if these aggregates are not due to taphonomy. Two distinct vertical faunal assemblages might be grouped within a single sample. An ectone might be sampled, showing combined effects of two adjacent communities. Unfortunately these vagaries generally cannot be detected in the outcrop. A faunal aggregation or ecotone commonly will cause an inflection on the diversity index curves that could go unexplained without further investigation.

Shallow benthic marine communities, in general, are controlled by the density and diversity of the molluscs. Molluscan densities and diversities increase towards shore, whereas the remaining faunal elements increase offshore (Stevens 1971: 406). Thus the relationship of the molluscan species diversity curves to non-molluscs and total fauna quite often are as informative, or more informative, than the diversity index curves. Inflections on some diversity index curves can be interpreted by molluscan faunal changes from the subjacent sample.

A third tool, in addition to diversity index and number of taxa, is equitability. Some of the anomalous inflections on the diversity index curves, especially the Shannon-Wiener index curves, can be interpreted by inflections on the equitability curves.

Thus a careful study of the relationship among diversity index, species diversity, and equitabilty curves can provide a relatively sound interpretation of faunal succession and community structure. If the

diversity index curves were smooth, with the only inflection due to still-stand, sea level history would be easy to interpret. However the many factors that influence faunal distributions make this type of investigation very rewarding, because these factors can be reasonably interpreted by these combined techniques.

CONCLUSIONS

The classical interpretation of marine cycles places the stillstand and accompanying maximum diversity faunas at the position of the limestone unit. However this investigation shows that the limestone unit generally represents a transgressive stage. At only two places, within the limits of the study area does it occur at the stillstand position. Also, there is a marked asymmetrical faunal distribution above and below the still-stand.

Faunal successions, recurrent fossils, and suites of fossils were used to reconstruct laterally persistent fossil communities. The transgressive phase includes the *Astartella-Ianthanopsis* community, the stillstand phase supports the *Glabrocingulum-Plagioglypta* community, and the regressive phase includes the *Aclisina* community.

Communities are named for the dominant genus or genera that occur in each. The structure of each community is inferred from recent ma-rine benthic communities of similar substrates, as well as presumed habitat and feeding preferences of the extinct animals.

One localized exotic community, the *Rhombopora-Septopora* com-munity, is interpreted as a faunal garden or biostrome within the trans-gressive phase at one of the deep-water localities.

This investigation also shows that the use of a diversity index as the primary interpretive tool in a paleoecological study can be misleading. A combination of diversity indices, equitability, and faunal composition provides an excellent system for a relatively sound interpretation of not only faunal succession but also community structure.

This investigation shows that the limestones with a high terrigenous content generally are more friable than the low terrigenous limestones. Limestone terrigenous content also appears to be one of the limiting factors in the level of biological accommodation reached by the faunas recovered from limestone samples.

One of the more significant results of this investigation is the mollusc, non-mollusc relationship. Molluscan faunas increase in both density and diversity nearshore, whereas the non-molluscan faunas increase offshore. Thus, not only the faunal succession but also the relative water depths for each locality throughout the marine event can be inferred from mollusc, non-mollusc trends.

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APPENDIX A.—MEASURED SECTIONS SHOWING SAMPLING INTERVAL AT SAMPLE SITES[1]
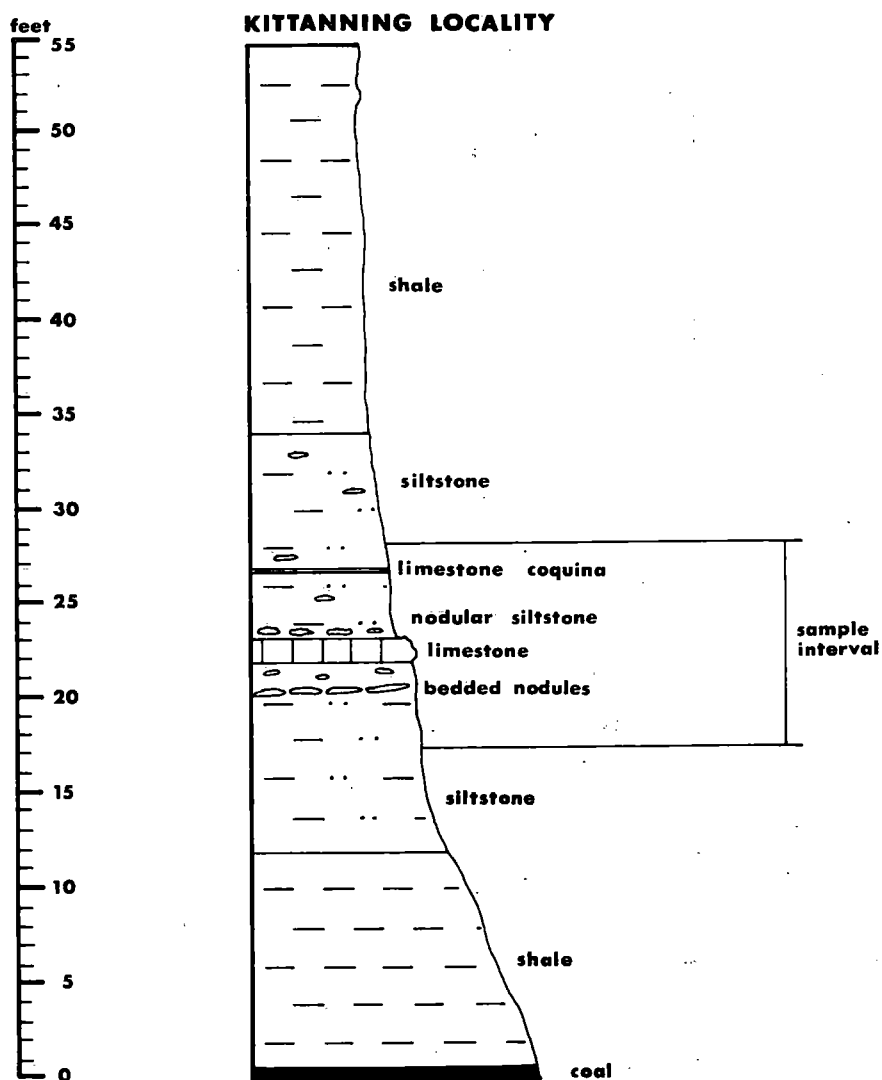
LOCALITY 1.—Stratigraphic section and sample interval at Kittaning, located along northside of U.S. 422, 0.7 mi. E. of intersection of U.S. 422 and Pa. 66N, Armstrong County (Cadet Drive-In).

[1] All localities are in Pennsylvania.
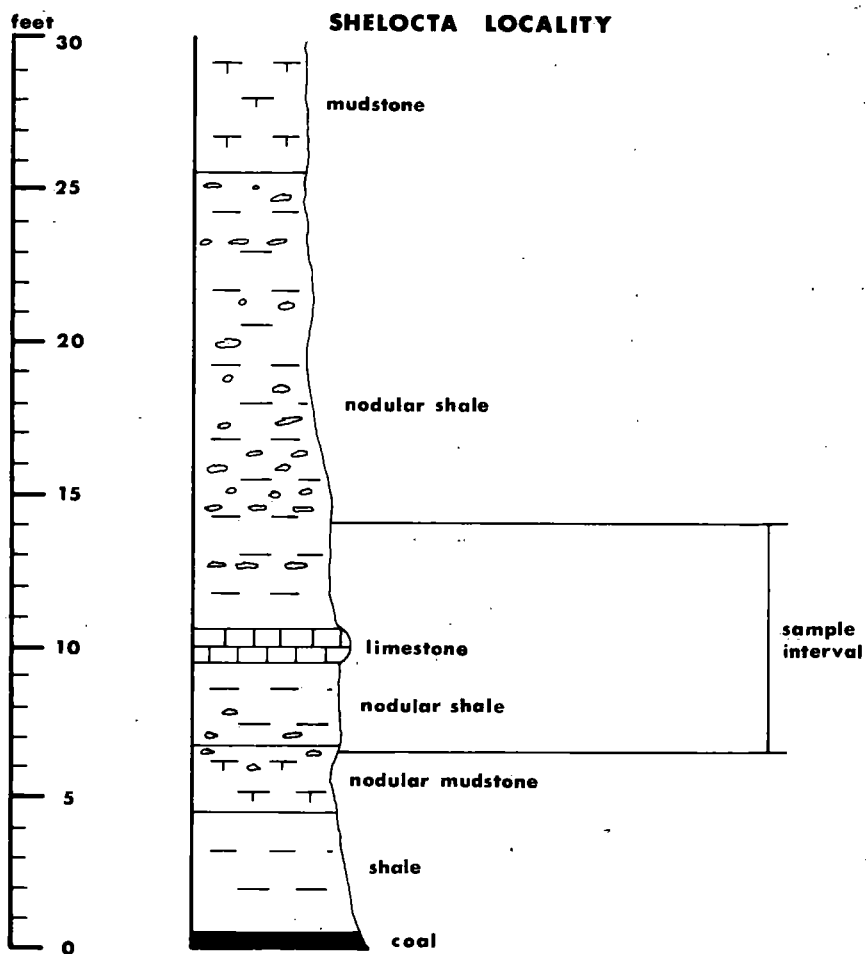
LOCALITY 2.—Stratigraphic section and sample interval at Shelocta, located along northside of U.S. 422, 0.5 mi. W. of intersection of U.S. 422 and Pa. 156, Indiana County (adapted from Brant 1971).
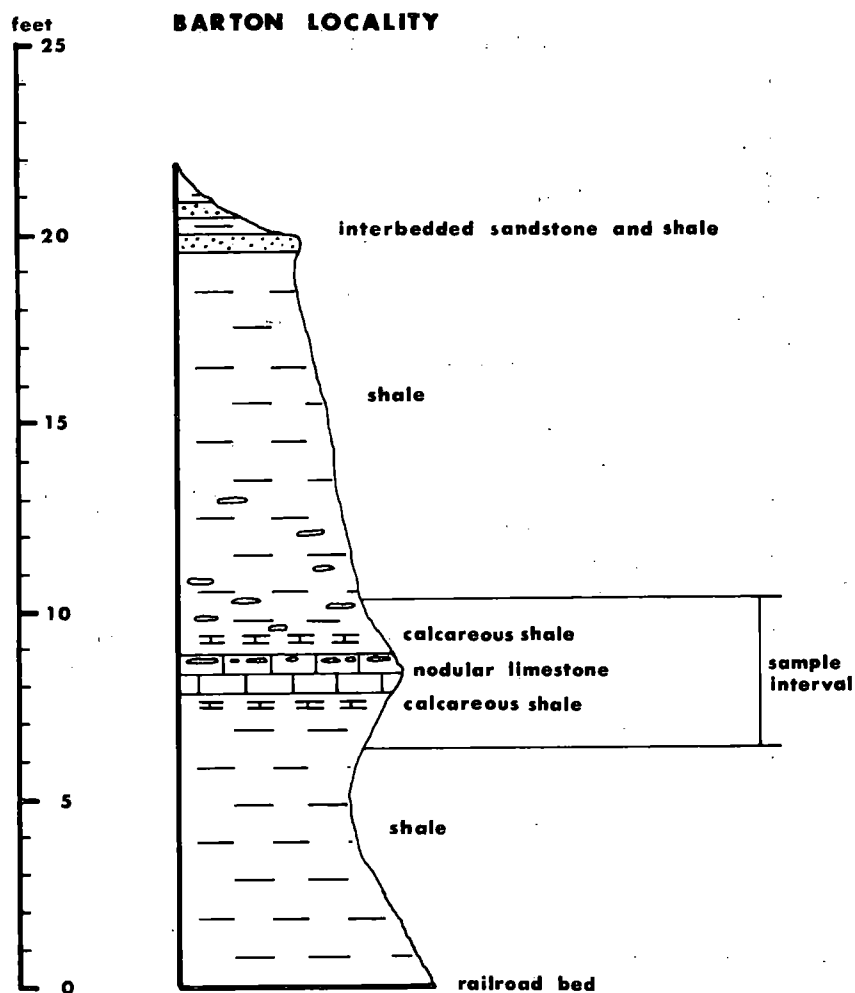
LOCALITY 3.—Stratigraphic section and sample interval at Barton, located along Baltimore and Ohio Railroad cut on eastside of U.S. 119, 1.9 mi. N. of intersection of U.S. 119 and Pa. 403 (Marion Center, Pa.), Indiana County.
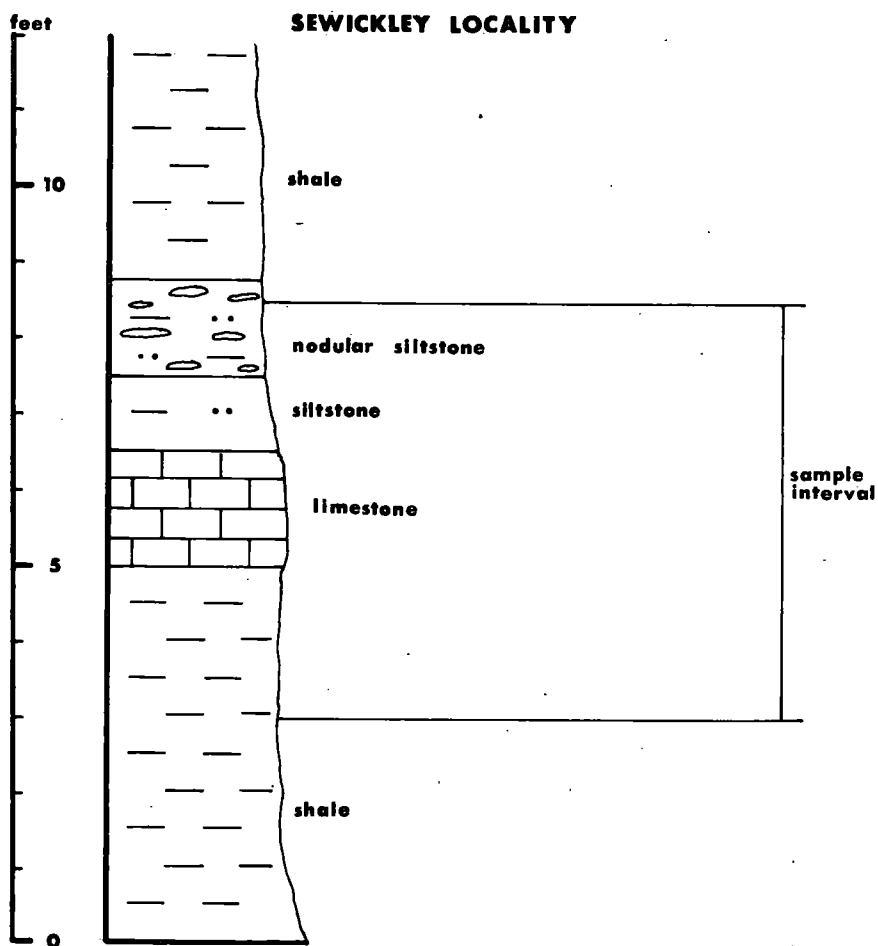
LOCALITY 4.—Stratigraphic section and sample interval near Sewickley, located at a roadcut along southside of Pa. 51, at south end of Sewickley Bridge, Allegheny County.

GLENSHAW LOCALITY

feet

- 20

shale

- 15

mudstone
nodular mudstone
limestone

sample
interval

- 10

massive mudstone

- 5

- 0
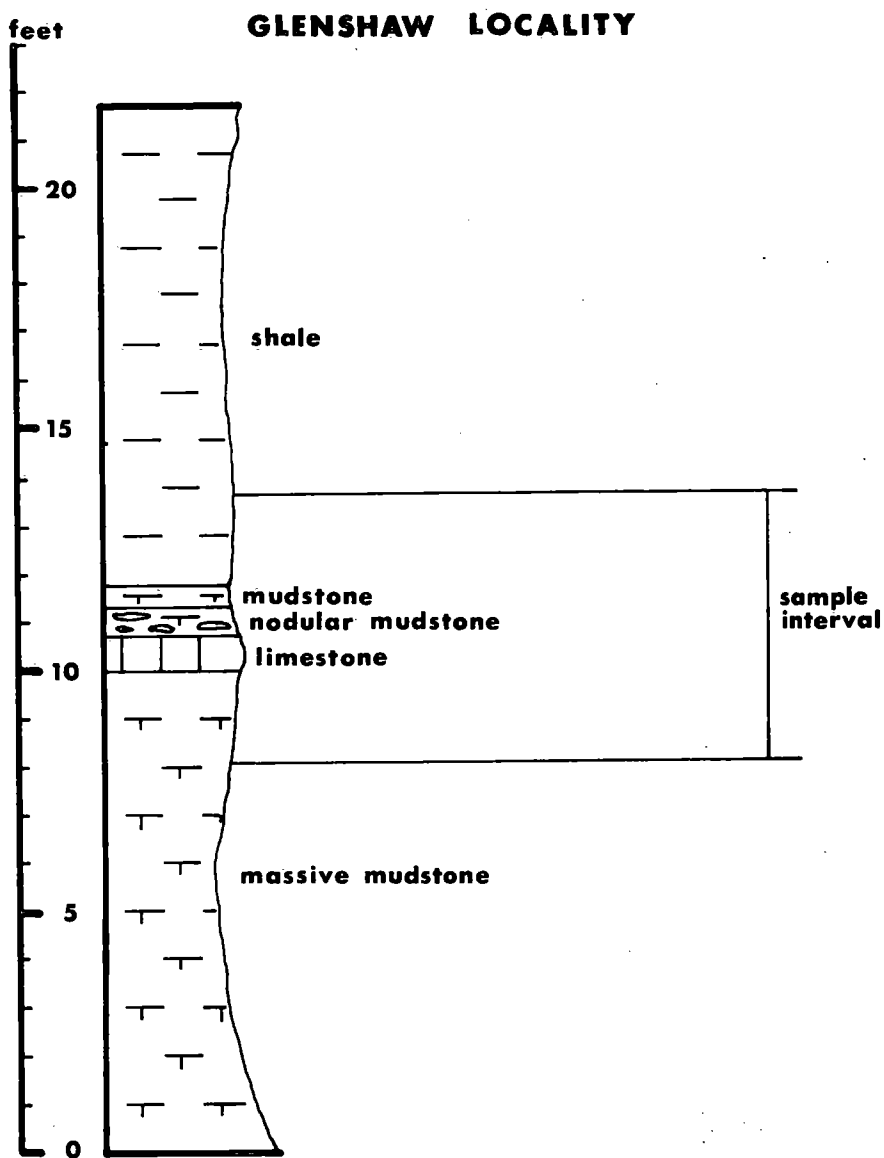
LOCALITY 5.—Stratigraphic section and sample interval at Glenshaw, located at an excavation along westside of Pa. 8, at intersection of Pa. 8 and Maple Street, Allegheny County (Glenshaw Glass Company).

MURRYSVILLE LOCALITY

feet

10

5

0

nodular siltstone

bedded nodules

shale

limestone (channel)

siltstone

limestone

carbonaceous shale

coal
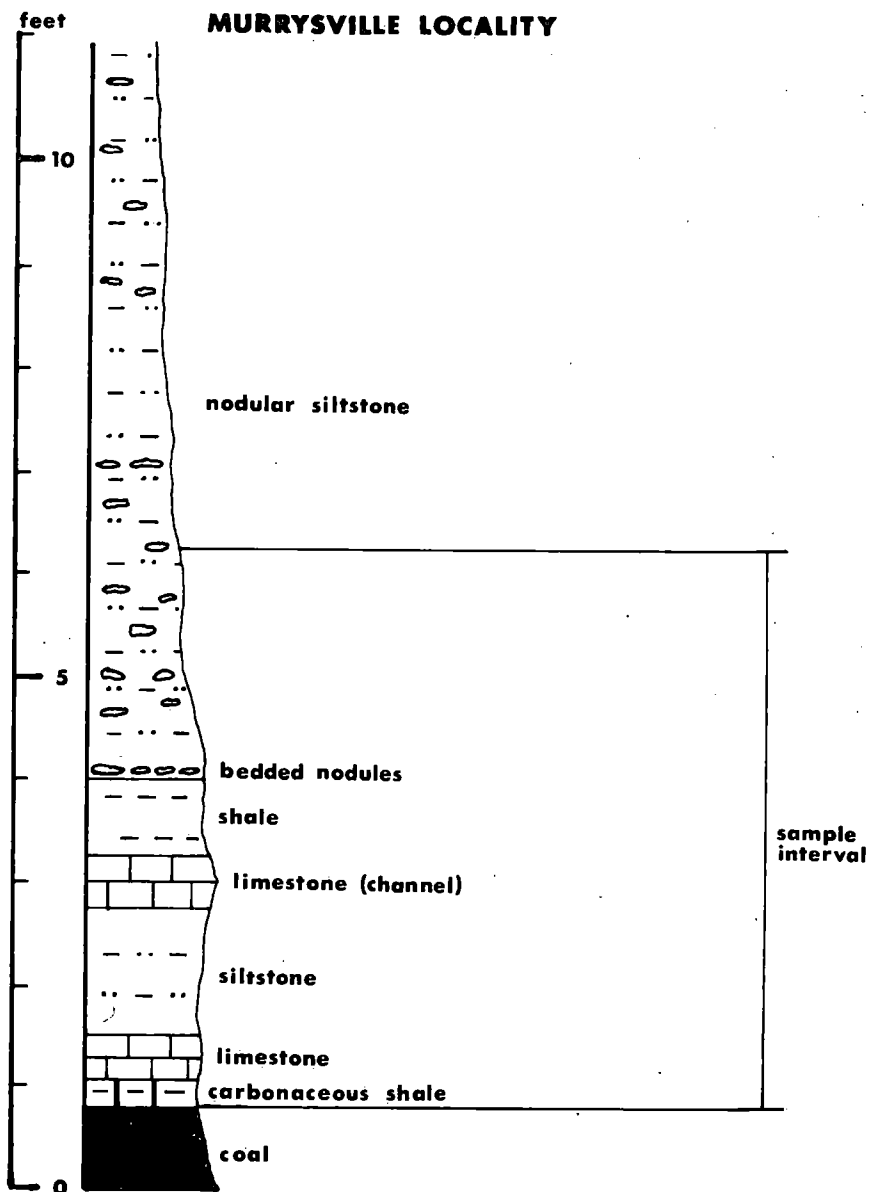
sample interval

LOCALITY 6.—Stratigraphic section and sample interval at Murrysville, located at an excavation on northside of U.S. 22, to immediate east of Allegheny-Westmoreland County line, Westmoreland County (William Penn Lumber Company).

PICCOLOMINI LOCALITY
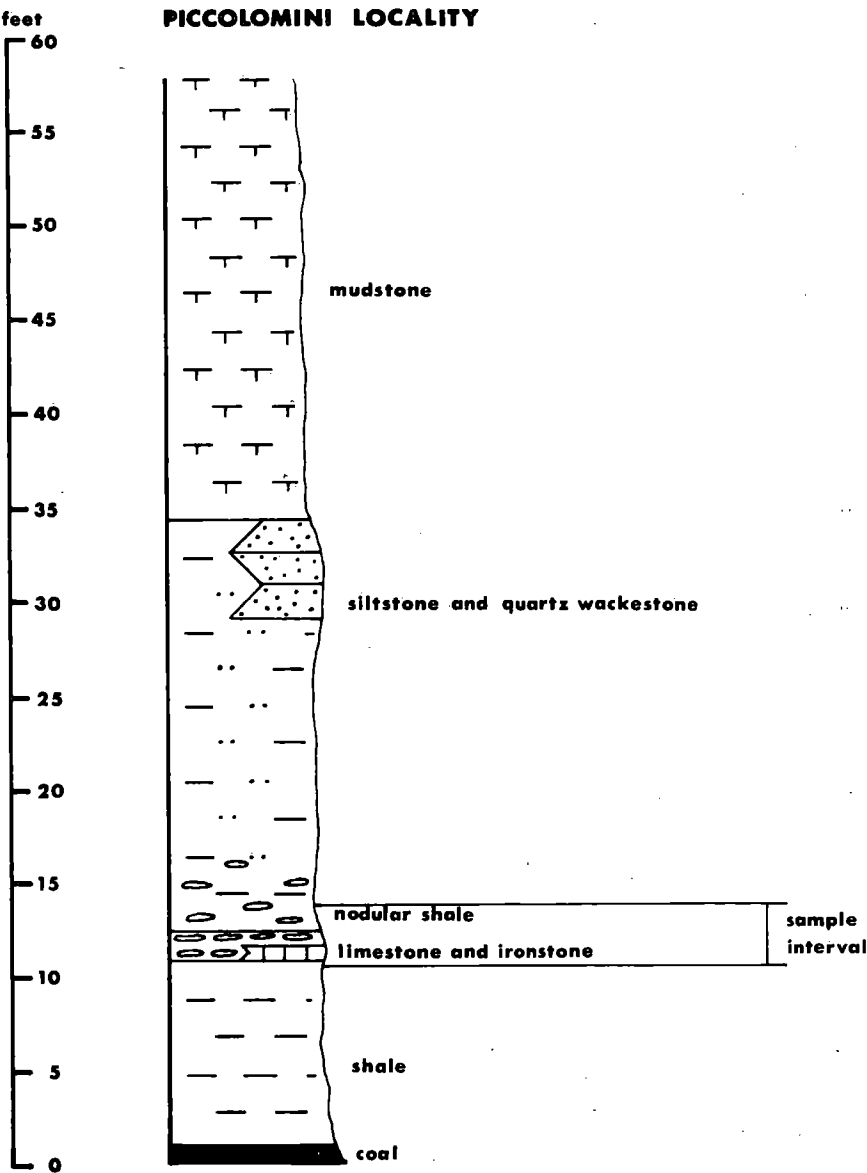
LOCALITY 7.—Stratigraphic section and sample interval near Uniontown, located at abandoned Piccolomini Brothers strip mine, on eastside of Pa. 51, 5 mi. N. of Uniontown, Fayette County.
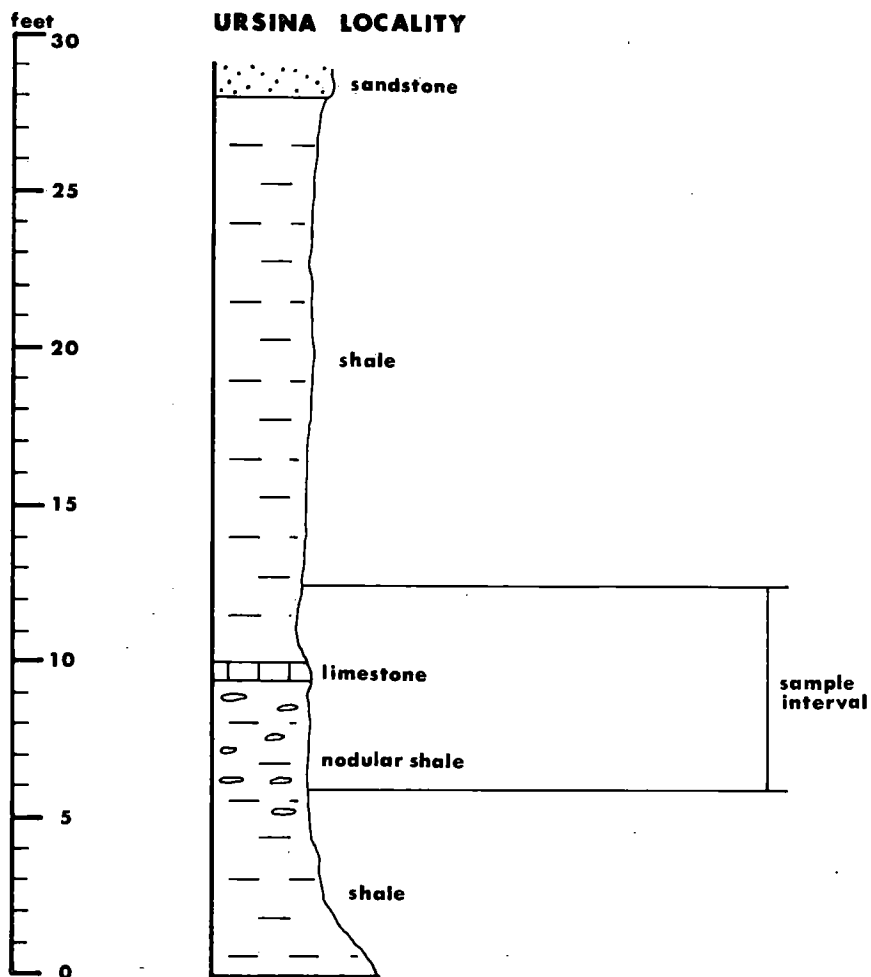
LOCALITY 8.—Stratigraphic section and sample interval near Ursina, located along westside of Jersey Church Road, 0.95 mi. N.W. of intersection of Pa. 53 and Jersey Church Road, Somerset County (adapted from Flint 1965).

GLADE CITY LOCALITY

feet

sandstone

siltstone

shale

channel limestone
nodular shale
limestone
shale
nodular siltstone

sample interval

shale

coal
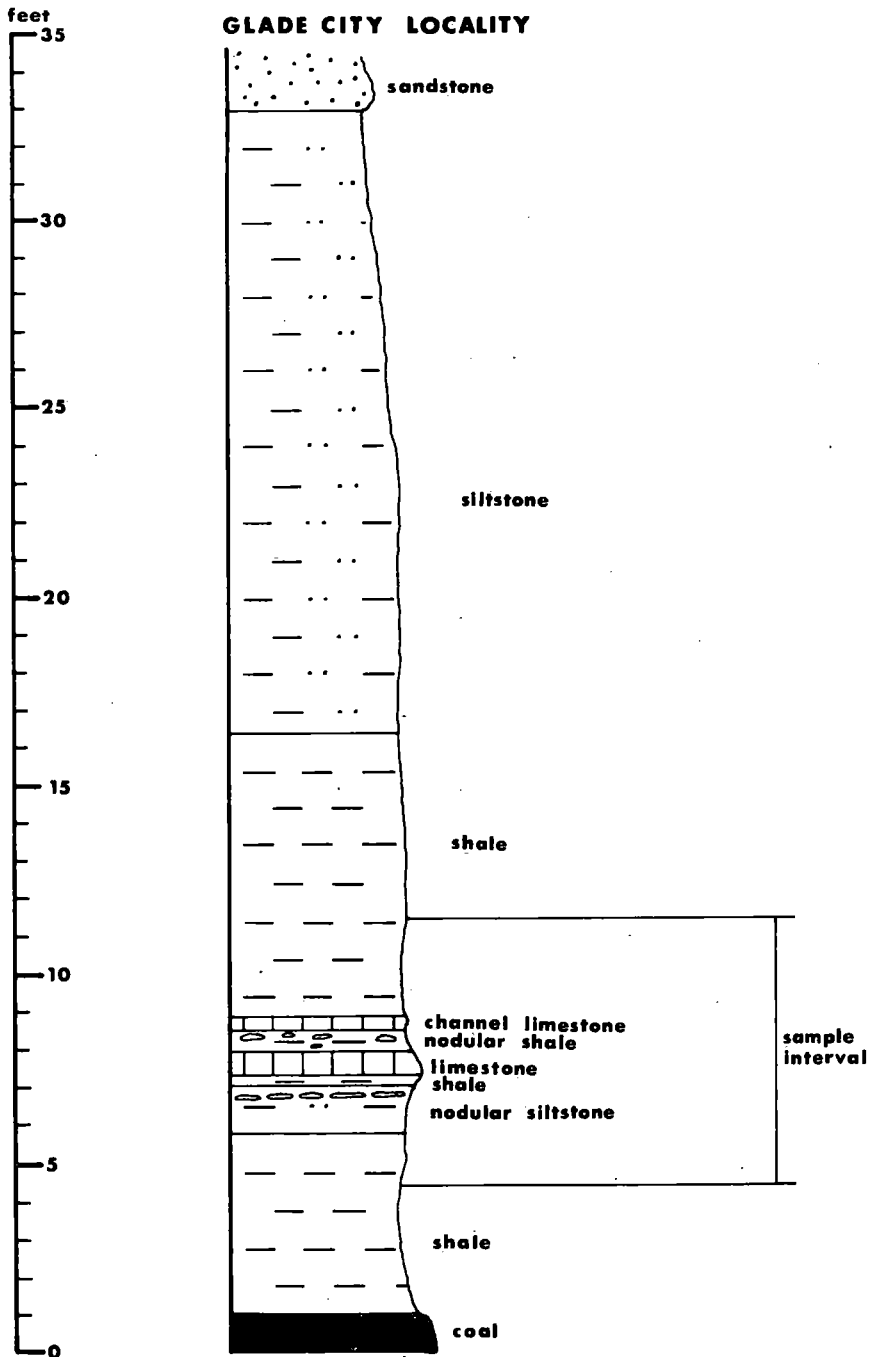
LOCALITY 9.—Stratigraphic section and sample interval at Glade City, located along northside of Western Maryland Railroad, 1.5 mi. E. of Meyersdale, Somerset County (adapted from Flint 1965).

APPENDIX B.—DATA MATRIX OF BRUSH CREEK FOSSILS.

TAXON	LOCALITY								
	1	2	3	4	5	6	7	8	9
Foraminifera									
Cyclogyra sp.	X	X	X	X	X	X		X	X
Tolipammina sp.	X	X	X	X	X	X	X		X
Ammobaculites sp.	X	X	X	X		X	X		X
Ammovertella sp.	X		X				X		X
Glomospira sp.	X		X	X	X	X	X		X
Thurammina sp.	X								
Lituotuba sp.	X		X		X		X		
Ammodiscus sp.	X				X		X		
Paleotextularia sp.	X	X	X						
Psammosphaera sp.	X		X						
Reophax sp.			X		X	X	X		
Hemigordius sp.							X		
Bigenerina sp.			X						
Hyperammina sp.			X						
lagenid			X						
Ostracods									
Healdia-Bairdia sp. (smooth)	X	X	X	X	X	X	X	X	X
Amophissitids (pitted)	X	X	X	X	X	X	X	X	X
Hollinella sp. (nodose)	X	X		X	X	X	X	X	X
Porifera									
Spicules	X						X		
Coelenterata									
Stereostylus sp.	X	X	X		X	X			
Brachiopoda									
Crurithyris sp.	X	X	X	X			X		X
Juresania sp.		X		X			X		
Neochonetes sp.	X	X	X	X		X			X
Linoproductus sp.		X				X			
Composita sp.		X							
Derbya sp.		X							
Antiquatonia sp.						X			
Bryozoa									
Ramose	X	X	X		X	X	X	X	
Fenestrate			X	X					
Septopora biserialis	X			X					
Rhombopora lepidodendroides				X					
Bivalvia									
Astartella sp.	X	X	X	X	X	X	X	X	X
Girtyana sp.	X						X		X
Nucula sp.	X					X	X		
Culunana sp.	X		X				X		X
Allorisma sp.				X		X	X	X	X
Nuculana sp.	X			X			X	X	
Naiadites sp.								X	
Aviculopecten sp.			X			X	X	X	X
Septimyalina sp.							X		
Anthraconaia sp.								X	
Gastropoda									
Glabrocingulum sp.	X	X	X	X	X	X	X	X	X
Pseudozygoplieurids	X		X	X	X		X	X	X

Appendix B.—Continued

Taxon	Locality								
	1	2	3	4	5	6	7	8	9
Ianthanopsis sp.	X	X	X	X	X	X	X	X	X
Meekospira sp.	X	X	X				X		X
Belleron sp.				X					
Pharkidonatus percarinatus							X	X	X
Euphemites sp.	X	X	X	X	X	X	X		X
Retispira sp.	X		X	X		X	X	X	X
Bulimorpha sp.	X						X	X	X
Worthenia sp.		X	X			X		X	
Shansiella sp.	X	X	X	X	X	X		X	X
Cymatospira sp.	X	X		X	X	X		X	X
Straparollus sp.	X	X	X	X	X	X			X
Trepospira sp.	X								
Aclisina sp.	X	X	X	X	X	X	X	X	X
Cephalopoda									
Pseudorthoceras sp.		X	X	X	X	X			X
Metacoceras sp.				X		X		X	
Scaphopoda									
Plagioglypta sp.	X	X	X	X	X	X	X	X	X
Dentalium sp.	X								
Echinodermata									
Echinoid debris	X	X	X	X		X	X	X	X
Crinoid columnals	X	X	X	X	X	X	X	X	X
Holothurian sclerites						X			X
Trilobita									
Ameura sp.				X					
Condodonts debris	X	X		X	X	X			X
Vertebrates debris	X		X	X		X	X		

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