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DISTRIBUTION AND DIVERSITY OF OSTRACODE ASSEMBLAGES FROM THE HAMLIN SHALE AND THE AMERICUS LIMESTONE (PERMIAN, WOLFCAMPIAN) IN NORTHEASTERN KANSAS[1]

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ABSTRACT

Patterns of distribution and diversity of assemblages of Ostracoda in the uppermost Hamlin Shale (Admire Group, Wolfcampian, Permian) and the Americus Limestone (Council Grove Group, Wolfcampian, Permian) in northeastern Kansas can be attributed to temporal and geographic changes in the environments of deposition of the host strata. Four lithofacies within the uppermost Hamlin Shale have been recognized: lagoonal, carbonate mudflat, intertidal shoal and beach, and nonmarine. Four lithofacies are recognized in the Americus Limestone: tidal mudflat, lagoonal, carbonate shoal, and basinal. The uppermost Hamlin Shale and the Americus Limestone are separated by a distinctive unit, the Hamlin-Americus transition bed, a regolith developed during brief emergence.

Cluster analysis, nonmetric multidimensional scaling, and computation of indices of species diversity define the following eight ostracode biotopes: 1) nonmarine and nearshore areas of the Hamlin Shale, marked by the presumed nonmarine and brackish-water ostracode *Carbonita inflata;* 2) carbonate shoal of the Americus Limestone, with *Bairdia beedei, Hollinella (Hollinella) bassleri,* and *Carbonita inflata;* 3) lagoons and tidal mudflats of the Hamlin Shale, characterized by *Paraparchites humerosus;* 4) lagoons of the Americus Limestone, also characterized by *Paraparchites humerosus* and by *Bairdia beedei;* 5) mixed quiet-water and shoal areas of the Americus Limestone, with abundant *Sulcella sulcata* and fewer *Jonesina bolliaformis?, Paraparchites humerosus,* and *Bairdia beedei;* 6) carbonate shoals of the Americus Limestone, with abundant *Bairdia beedei* along with *Hollinella (Hollinella) bassleri, Monoceratina lewisi,* and *Cavellina nebrascensis;* 7) tidal flats

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and shoals of the Americus Limestone, marked by *Carbonita inflata, Bairdia beedei,* and *Amphissites centronotus;* 8) quiet-water basin of the Americus Limestone, with *Geisina* cf. *G. gregaria.*

Four ostracode assemblages are recognized: 1) *Amphissites centronotus,* a nearshore marine assemblage present in both the Hamlin and Americus members; 2) *Bairdia beedei,* a normal-marine assemblage present in much of the Americus Limestone; 3) *Paraparchites humerosus,* an assemblage characteristic of lagoonal biotopes in both the Hamlin and Americus; and 4) *Carbonita,* an assemblage characteristic of the nonmarine and nearshore marine strata of the Hamlin Shale.

Highest indices of species diversity are from assemblages of the lagoonal, carbonate-shoal, and tidal-mudflat lithofacies of the Americus. In the Hamlin, the indices of diversity are markedly lower, characteristic of nearshore and nonmarine depositional environments.

INTRODUCTION

Pennsylvanian and Lower Permian strata of the Midcontinent have presented an enigma to geologists who have sought to understand their environments of deposition and the paleoecology of the assemblages of fossils they contain. The epeiric seas in which these rocks were deposited have no modern analogs. The difficulties are compounded, moreover, by the nearly north-to-south outcrop belt in Kansas, which closely parallels depositional strike, precluding study of onshore-to-offshore transects in most areas. Samples from the subsurface are available for some areas, but they cannot be studied by the same methods as outcrops. Mixing of cuttings from many beds and loss of sedimentary structures limit the usefulness of well cuttings. Cores are few, and cores of shales and mudstone that are likely to yield assemblages of microfossils are especially rare and usually incomplete. In addition to these problems, which pertain to the study of subsurface samples in general, the gentle westward dip of the strata in Kansas has resulted in a broad area west of the outcrop belt but east of the area of extensive exploration for hydrocarbons from which few well data are available.

In spite of these difficulties, paleoenvironments along the outcrop belt in eastern Kansas may be readily studied. Outcrops are common, fine-scale lithostratigraphic correlation is possible, fossils are generally abundant, and assemblages of fossils are often diverse and well preserved. Shales and mudstones that yield abundant microfossils are commonly interbedded at intervals of a few meters with marine limestones, the lithologies of which are readily interpreted paleoenvironmentally.

In a few areas of Kansas, however, the outcrop belt is broad, and transects perpendicular to the ancient shoreline may be sampled. Study of such areas in detail can provide the basis for more thorough understanding of environments of deposition and paleoecology of fossil assemblages in narrower parts of the outcrop belt. One such area is along the crest of the Nemaha anticline in northeastern Kansas (Fig. 1). The purpose of our study is to determine the distribution and diversity of assemblages of Ostracoda from two rock units that crop out there, the uppermost Hamlin Shale Member of the Janesville Shale and the Americus Limestone Member of the Foraker Limestone, which together comprise a section about two meters thick. Changes in stratigraphic and geographic distributions of assemblages of ostracodes are related to changes in inferred environments of deposition within the outcorp belt around the surface expression of the Nemaha anticline.

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METHODS OF STUDY

The uppermost Hamlin Shale and the Americus Limestone were studied at 20 localities (Fig. 1; see also Peterson, 1978, Appendix F). At each locality, the upper meter to half meter of the Hamlin and the entire Americus were measured and described. Carbonate units were sampled for petrographic study to help determine the environments of deposition of adjacent shale beds. Numbers of the samples from each locality are given in Appendix 1.

The Ostracoda in the samples were identified to species and counted, and the counts

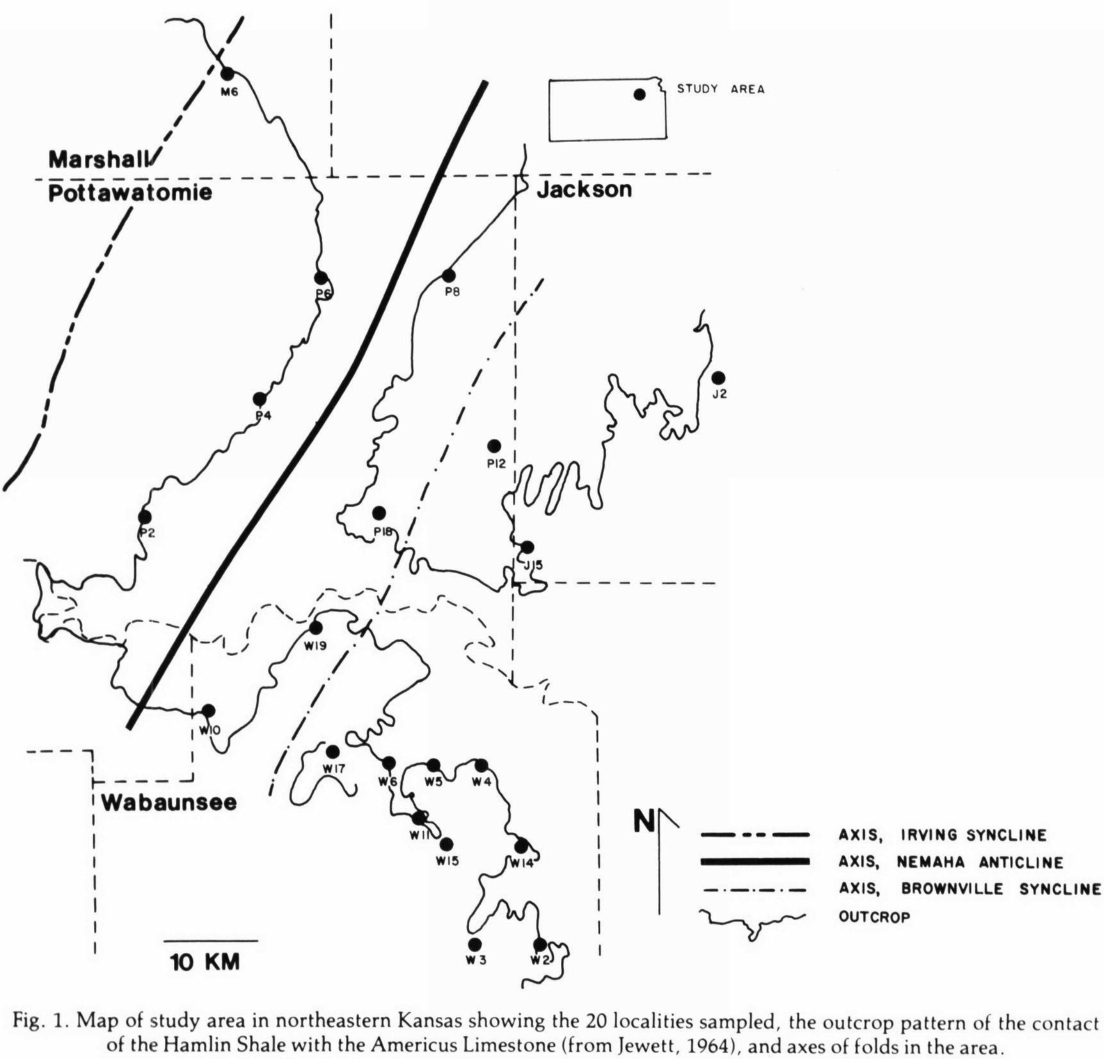

Fig. 1. Map of study area in northeastern Kansas showing the 20 localities sampled, the outcrop pattern of the contact of the Hamlin Shale with the Americus Limestone (from Jewett, 1964), and axes of folds in the area.

were compiled into a data matrix with 67 species and 81 samples. The size of the data matrix was reduced by eliminating species present in fewer than five samples (Kaesler, Mulvany, & Kornicker, 1977). The reduction of the data matrix in this fashion resulted in the deletion of 28 species of ostracodes, most of which were rare even within the few samples in which they occurred. It did not eliminate any samples.

These data were analyzed with a variety of quantitative procedures to define biotopes and assemblages. First, the data were converted to proportions of each species in each sample. The proportions were transformed using an arcsine transformation, and Q- and R-mode matrices of correlation coefficients were computed. Cluster analysis in the Q-mode arranged samples into biotopes; R-mode cluster analysis arranged species into assemblages on the basis of their distribution and abundance.

To examine further the similarities between samples, nonmetric multidimensional scaling was used (Kruskal, 1964a, 1964b), an ordination technique that has been little used in paleontology (Whittington & Hughes, 1972; Rowell, McBride, & Palmer, 1973). In an empirical comparison of principal component analysis, principal coordinate analysis, and nonmetric multidimensional scaling, Rohlf (1972) found that nonmetric multidimensional scaling typically produced a better representation of the data in the reduced space, as measured by the correlation between the distances in the reduced space and the original distances. He recommended use of nonmetric multidimensional scaling unless the number of samples in the matrix is large. Here, nonmetric multidimensional scaling was computed in two and three dimensions using the reduced ostracode data matrix.

As a further means of examining assemblages, indices of species diversity were computed using Brillouin's (1962) equation from information theory. This equation is preferred over many other available indices (see Utez, 1974) because it gives the actual diversity of a fully censused sample rather than an estimate (Pielou, 1969, 1975, 1977; Kaesler & Herricks, 1977). Diversities were computed from the original, unreduced data matrix using programs by Kaesler and Mulvany (1976a, 1976b) with subsamples of 25 and 100 individuals each replicated randomly 25 times.

All computations were done on the Honeywell 66/60 at The Kansas University Academic Computer Center using the Numerical Taxonomy System (NYSYS) package of statistical computer programs developed by F.J. Rohlf and his associates. All specimens have been deposited with the University of Kansas Museum of Invertebrate Paleontology as numbers 1,054,398 to 1,073,618.

STRATIGRAPHY AND DEPOSITIONAL ENVIRONMENTS

Uppermost Hamlin Shale.—The Hamlin Shale Member is the upper member of the Janesville Shale (Fig. 2). In Kansas it ranges in thickness from 10 to 15 m (Zeller, 1968). It is overlain by the Americus Limestone Member of the Foraker Limestone and underlain by the Five Point Limestone Member of the Janesville Shale. The Hamlin Shale was named by Moore, Elias, and Newell (1934), who designated no type locality. Mudge and Yochelson (1962) discussed the stratigraphy and lithology of the Hamlin along its outcrop belt in Kansas and found that it averages about 14 m in thickness in northern Kansas and is maroon to gray green in its lower part and gray to gray green with some maroon in its upper part. Beds of sandy shale and sandstone are present locally, and Mudge (1956, p. 674) reported these beds as filling channels, some as deep as 3 m. Mudge and Yochelson also noted that beds of limestone are distributed throughout the member, the most prominent of these being the Houchen Creek limestone bed (Mudge & Yochelson, 1962, p. 28). They also noted the presence of a persistent limonite-impregnated calcarenite bed at the very top of the Hamlin. This bed, the significance of which is discussed below, ranges in thickness from a featheredge in northern Pottawatomie County to about 30 cm in cen-

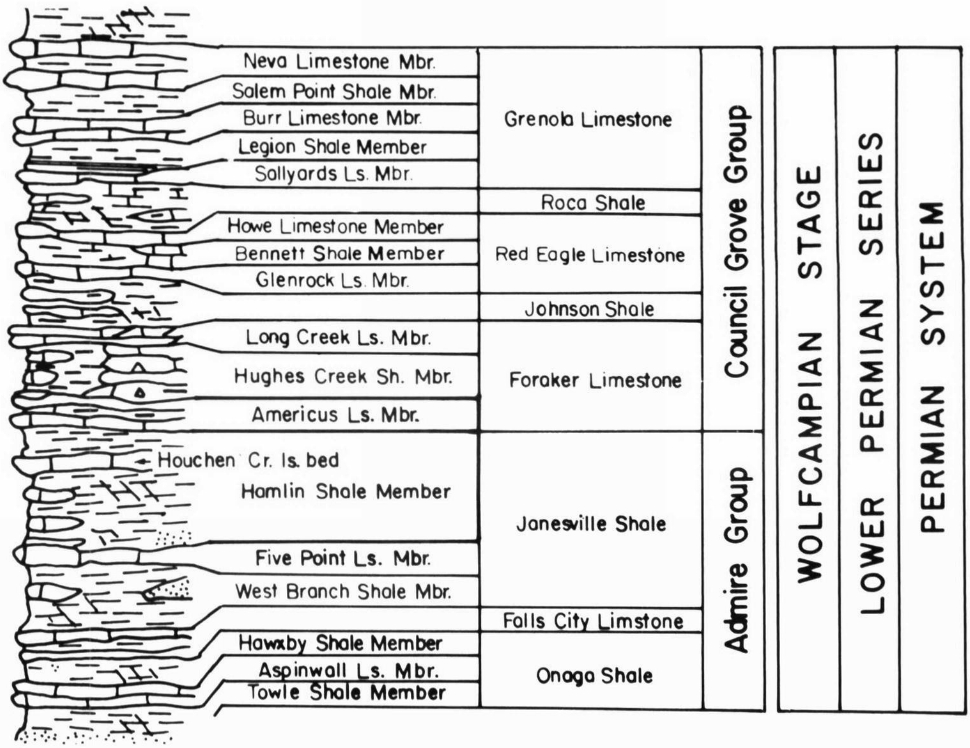

Fig. 2. Stratigraphic section of part of the Lower Permian (Wolfcampian) in Kansas (after Zeller, 1968).

tral Cowley County. They judged that this bed is transitional with the overlying Americus Limestone and that its lower contact is distinct except where it locally overlies massive, tan, silty shales of the Hamlin. Several other investigators have studied the Hamlin (Walters, 1953, 1954; Mudge & Burton, 1959; Scott, Foster, & Crumpton, 1959; and Johnson & Adkison, 1967), but only general aspects of the stratigraphy have been presented. A study by W.L. Fisher (1980, personal communication) provides the only detailed discussion of the Hamlin Shale. It should be emphasized, however, that Fisher's work, like the present study, was restricted primarily to the uppermost 1 to 1.5 m of the Hamlin Shale.

Within the study area, the Hamlin Shale is remarkably variable. The typical lithology is a blocky, somewhat silty, hard, gray-green shale. In the uppermost meter, this shale is interbedded with or overlain by a variety of other rock types. The Hamlin can be divided into four lithofacies: intertidal shoal and beach carbonates, mudflat carbonates, lagoonal shales and mudstones, and nonmarine possibly fluvial conglomeratic claystones and mudstones.

The intertidal shoal and beach carbonates and mudflat carbonates are present in two principal areas (Fig. 3). One area occupies central and western Jackson County, and the other area lies along the western margin of the nonmarine lithofacies in central Wabaunsee County and southern Pottawatomie County. These rocks were formed on intertidal and supratidal carbonate mudflats flanking shallow embayments in the southwestern and southeastern margins of a low land mass. In eastern and central Wabaunsee County, these carbonate rocks are present in an areally restricted tract approximately 3 km wide and 15 km long, trending west-northwest. A variety of lithologies is present including algal stromatolitic lime boundstone (localities W14, W11, W6), creamy white fenestral stromatolitic ostracode lime boundstone (locality W11), and brecciated, possibly desiccated, lime wackestone to lime mudstone. Similar rocks in north-central Wabaunsee, southern Pottawatomie, and western Jackson counties were formed in a similar environment. A notable exception is an embayed hypersaline lagoon or tidal pool at locality P2, indicated by an ostracode algal lime mudstone with desiccation fractures partially filled with gypsum. W.L. Fisher (1980, personal communication) postulated a carbonate beach or shoal in central Jackson County indicated by interbedded pelleted lime mudstones and ostracode

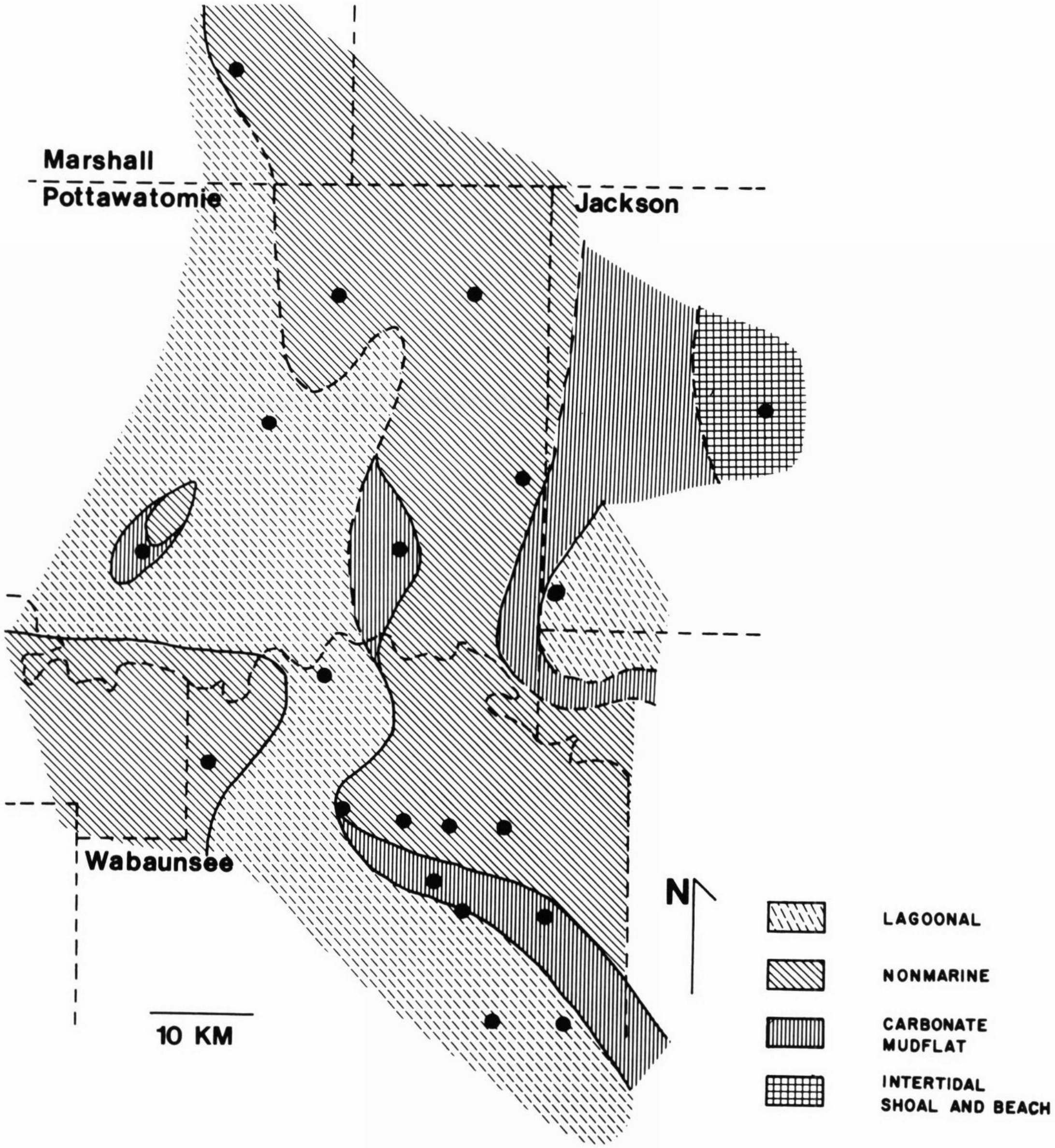

Fig. 3. Inferred distribution of lithofacies in the uppermost Hamlin Shale; dots represent localities sampled. Not all outcrops studied were sampled, resulting in apparent lack of control of extent of some lithofacies. See Figure 1 for locality numbers.

pellet lime packstones to grainstones. Some of these rocks, especially at locality J2, contain abundant ooids and exhibit low-angle cross stratification. They also contain ostracode carapaces, fragments of phylloid algae, bivalves, and gastropods, a fauna indicative of shallow water near an area of shoaling.

Shales and mudstones inferred to have been deposited in lagoons (Fig. 3) are more widely distributed than the carbonate lithologies and are composed of either calcareous, silty, gray-brown, laminated shales with scattered coal fragments and rare plant debris or olive-green to yellow-green mudstones. The lagoonal rocks are thickest in central and southern Wabaunsee County, where they make up all of the uppermost Hamlin Shale (localities W2′, W3, W15). Sediment was apparently deposited in a shallow, brackish-water lagoon that either contained or was surrounded by abundant plant growth. The finely laminated shale indicates quiet water and also implies restricted circulation and lack of bioturbation. The carbonate lithologies at locality W11, which are overlain by about 10 cm of lagoonal shale, probably represent the margin of the lagoon. Lagoonal mudstone in northern Wabaunsee County (locality W19) and central Pottawatomie County (locality P4) is olive green to yellow green and is interbedded with and overlies the carbonate and nonmarine lithologies of the uppermost Hamlin, indicating that as Hamlin deposition ceased the brackish-water lagoons expanded, overstepping the other depositional environments.

The nonmarine lithologies in the uppermost Hamlin Shale display the greatest areal and stratigraphic distribution (Fig. 3). They also show such complex and subtle stratigraphic relationships that a precise interpretation of their origin is impossible. These highly calcareous, silty, conglomeratic claystones and mudstones were deposited in nonmarine environments landward of coeval lagoonal and tidal mudflat environments. The absence of a demonstrably marine fauna and the presence of calichelike nodules are evidence for this interpretation. In addition, a subaerial weathering profile at locality P8 and a probable channel fill with clayey, sandy siltstone occur within the top 1.5 m of the Hamlin at the east end of locality W4. The gray-green blocky shale, the typical Hamlin lithology, is interpreted as resulting from deposition in fluvial and adjacent environments on low land.

Hamlin-Americus Transition Bed.—The Hamlin-Americus transition bed is present everywhere within the study area except central Jackson County. This bed, which separates the Hamlin Shale from the Americus Limestone, is a highly altered, poorly indurated, calcareous unit with a granular or sandy texture. Mudge (1956) described it as a calcarenite with the appearance of a fine-grained sandstone, and Mudge and Yochelson (1962, p. 27) described it as a limonite-impregnated calcarenite comprising angular calcium carbonate fragments 0.12 to 0.25 mm in size and containing ostracodes. W. L. Fisher (1980, pers. commun.) has discussed the bed in more detail, pointing out its mixed lithology including sand-sized grains of clay enclosed in an altered and porous calcareous matrix, pure claystone, carbonate intraclast-lithoclast grainstone, carbonate intraclast conglomerate, and various admixtures of the above lithologies. Some plant debris is also present. The basal contact is typically sharp, but local interfingering with underlying lithologies has been observed, and the upper contact of the bed is gradational into the basal Americus Limestone.

The Hamlin-Americus transition bed marks a disconformity between the Hamlin Shale and the Americus Limestone, and its lithologies are interpreted as representing a regolith developed on a briefly emergent Nemaha anticline following the end of Hamlin deposition. The generally sharp lower contact with only local interfingering of lithologies of the transition bed with a variety of uppermost Hamlin lithologies suggest a disconformable contact between the Hamlin Shale and the Americus Limestone. The dominant lithology, conglomeratic clay grainstone, is interpreted as sheetwash deposits developed on a broad erosional surface. The interfingering of the bed with underlying lithologies occurred as the lagoons present at the close of Hamlin deposition expanded, causing the lagoonal and marsh sediments to interfinger with the regolithic material developed along the margins of the lagoons. Similarity of ostracode assemblages of this and subjacent beds supports this interpretation.

Americus Limestone.—The Americus Limestone is well exposed throughout the study area and in a north-south outcrop belt across eastern Kansas (Mudge & Yochelson, 1962). It was named by Kirk (1896) for exposures near the town of Americus in Lyon County, Kansas. In general, it consists of two limestone beds separated by shale of variable thickness and lithology. The member averages about 1.2 m in thickness in the northern part of its outcrop belt and about 3.6 m in southern Kansas. Details of the stratigraphy of the Americus Limestone Member were given by Mudge and Burton (1959), Garber (1962), Mudge and Yochelson (1962), Harbaugh and Demirmen (1964), Johnson and Adkison (1967), and W. L. Fisher (1980, pers. commun.)

Within our study area, the lithology of the lower Americus beds is variable, whereas the uppermost limestone bed is monotonously constant. Except in extreme east-central Pottawatomie County and west-central Jackson County, the basal bed of the Americus is a limestone, which ranges in thickness from a few centimeters in the north to nearly a meter in the south and southwest. This bed is characterized by a wide variety of carbonate lithologies: algal-laminated lime boundstone at the base, foraminiferal coated-grain lime wackestone to packstone, and skeletal lime packstone containing silt-sized quartz grains.

A variable shale bed is present between the two limestone units or, where the basal limestone is absent, forms the basal unit. This shale thins to less than 1 cm in the east and northeast and thickens to about a half meter in the south, west, and northwest. In the southern portion of the study area, it comprises interlaminated gray, gray-green, black, and yellow-tan shales that are complexly intergraded. To the north, however, it is differentiated into distinct beds of black shale with the inarticulate brachiopod *Orbiculoidea;* finely laminated gray, green, and brown shale; and fossiliferous calcareous gray shale, which is laterally equivalent to the upper part of the lower limestone unit. These shale beds are generally less than 20 cm thick and are complexly interbedded except where black shale is present.

The overlying limestone unit is a resistant, massive, brachiopod-echinoderm lime packstone to wackestone that is a laterally persistent ledge-former throughout the study area. It has a sharp contact with units above and is conformable with units below. The basal surface of the bed is characterized by burrow structures. The bed thins toward the north from north-central Wabaunsee County, where it attains a maximum thickness of approximately 50 cm.

For ease of presentation, in the following discussion of the paleoenvironmental framework of the Americus Limestone, two informal units are designated, the lower Americus interval and the upper Americus limestone bed.

The lower Americus interval includes all strata between the top of the Hamlin-Americus transition bed and the base of the upper Americus limestone bed. These shale and limestone beds intertongue and intergrade laterally and represent a variety of shallow subtidal to intertidal marine environments. These strata represent a transgressive sequence deposited on the unconformable surface represented by the Hamlin-Americus transition bed.

Four lithofacies are recognized within the study area. These have a general northwesterly trend and are, from northeast to southwest: tidal-mudflat, lagoon, carbonate-shoal, and basinal facies (Fig. 4). Except in the easternmost part of the study area, the basal part of the lower Americus interval is an algal-stromatolitic limestone. This lithology underlies nearly all the above lithofacies, and the contained algal stromatolites had a profound effect on the subsequent development of lower Americus lithofacies. The stromatolitic unit was deposited in supratidal, intertidal, and shallow subtidal environments and shows reworking of the transition bed and the algal stromatolite as the Americus sea transgressed across the area. The transgression removed much of the supratidal sediment and incorporated it into the preserved intertidal and shallow subtidal sediments of the lower Americus interval.

The carbonate-shoal lithofacies of the lower Americus interval occupies the largest

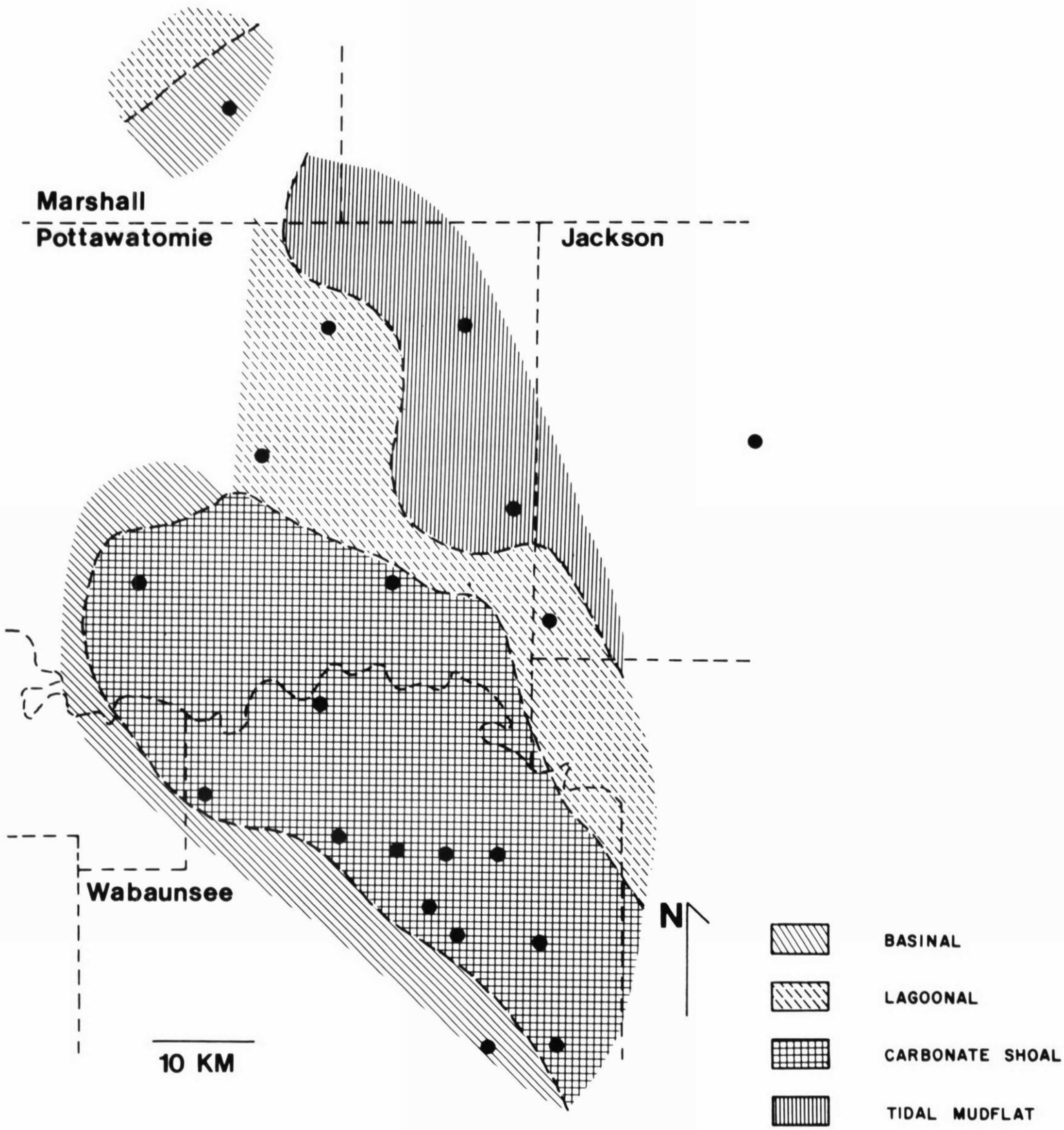

Fig. 4. Inferred distribution of lithofacies in the lower Americus interval; dots represent localities sampled. Not all outcrops studied were sampled, resulting in apparent lack of control of extent of some lithofacies. See Figure 1 for locality numbers.

area (Fig. 4). It lies in a northwesterly trending belt in Wabaunsee and south-central Pottawatomie counties. The shoal lithologies consist of intraclast skeletal lime packstone with burrowed molluscan lime packstone to wackestone toward the top of the shoal. The latter may be equivalent to the dark-gray fossiliferous calcareous shale that also occurs within this lithofacies belt. This shale formed either in ponded areas of quiet water within the shoal or as basinal facies onlapping the carbonate shoal as the Americus transgression proceeded. The shale thickens toward the basinal and lagoonal lithofacies tracts with concomitant thinning of the shoal carbonate lithologies in the same direction.

The carbonate-shoal lithofacies grades northeastward into the shales and coated-grain, intraclast skeletal lime packstones to grainstones of the lagoonal lithofacies. This is an areally restricted, relatively narrow tract that occurs in southwestern Jackson County, in eastern and central Pottawatomie County, and in an isolated area in southeastern Marshall County (Fig. 4). Within this tract, the entire Lower Americus interval thins and contains proportionately more shale. The carbonate rocks of this lithofacies are thin, intraclast and molluscan coated-grain lime packstones to grainstones. Many of the grains have been coated by the algal-forminiferal consortium *Osagia,* which typifies the sediments deposited in the lagoonal lithofacies. Several shale lithologies are present including black shales containing the inarticulate brachiopod *Orbiculoidea;* abundantly fossiliferous, calcareous, gray to tan shale; and gray-green shale with crinoids, brachiopods, and bivalves.

Easternmost is the tidal mudflat lithofacies, present in western Jackson County and eastern Pottawatomie County (Fig. 4). This is the thinnest lithofacies, and it contains a large amount of shale relative to carbonate rock. The few carbonate rocks present are dominated by algal stromatolites containing pustular or tufted crusts or *Ottonosia* colonies directly overlying or encased in a thin calcareous shale just a few centimeters above the transition bed. W. L. Fisher (pers. commun.) has compared these rocks to those in the high intertidal to supratidal mudflats of Shark Bay, Western Australia (Logan, Hoffman, & Gebelein, 1974).

As a result of continued transgression of the Americus sea, shales of the lagoonal lithofacies overstep the tidal-mudflat lithofacies, and the shales of the basinal lithofacies cap both the carbonate-shoal lithofacies and the lagoonal lithofacies. The shales of the lagoonal lithofacies are gray, laminated to somewhat fissile, and contain a diverse fauna of brachiopods, mollusks, echinoderms, ostracodes, foraminifers, and conodonts. The basinal lithofacies generally lies to the west of the carbonate-shoal lithofacies (Fig. 4). It is marked by an increase in the amount of shale and an increase in the thickness of the entire lower Americus interval, especially in southeastern Marshall and southeastern Wabaunsee counties. The shales in these areas are dark brown to black, sparsely fossiliferous (foraminifers and conodonts being the most abundant fossils), and finely laminated, probably indicating deposition in undisturbed, perhaps deeper, quiet-water environments.

The upper Americus limestone bed, a unit of nearly constant thickness and lithology throughout much of its outcrop belt across Kansas, has been the subject of several detailed studies. Harbaugh and Demirmen (1964), who termed this unit the "main ledge" of the Americus in reference to its distinctive ledge-forming outcrop habit, studied the Americus at 27 Kansas localities, five of which are within our study area. After detailed petrographic and chemical analyses of many samples, they computed a factor analysis in order to recognize depositional regimes. They concluded that the portion of the main ledge that lies within our study area was deposited as a single unit relatively far from shore (Harbaugh & Demirmen, 1964, p. 31).

The petrographic and quantitative study by W. L. Fisher (1980, pers. commun.) provides still more detailed information about the upper Americus bed. In our study area the upper Americus bed is from about 19 to 50 cm thick and has two intergrading lithologies. The lower part of the bed is a brachiopod, echinoderm lime packstone to wackestone in which trilobite remains are common in many places. Toward the top of the unit the predominant lithology is an echinoderm, bryozoan, brachiopod, fusulinid lime packstone. Diagnostic fossils near the top of the bed are fusulinids, which are rare in the lower part of the unit. Throughout the unit, sorting of fossils is generally poor to fair with much highly abraded, fragmental, and hence generally unidentifiable fossil debris. Glauconite and phosphatic grains, possibly the remains of fish, are scattered throughout the bed.

OSTRACODE BIOTOPES

Q-mode cluster analysis of the reduced ostracode data matrix grouped samples into eight more-or-less clearly defined ostracode biotopes (Fig. 5), areas "of relatively uniform environmental conditions evidenced by a particular fauna found in the area and presumably adapted to environmental conditions existing there" (Kaesler, 1966, p. 3). Samples in each of the biotopes have several aspects in common besides their obvious faunal similarities: lithology, stratigraphic position, and geographic position within the inferred paleoenvironmental framework.

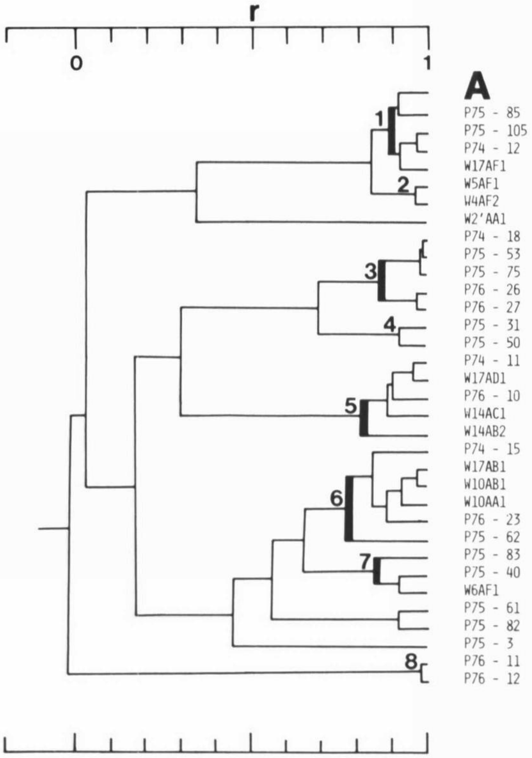

Fig. 5. Dendrogram from Q-mode cluster analysis (UPGMA) of the reduced ostracode matrix using the product-moment correlation coefficient; cophenetic correlation coefficient=0.953. The eight biotopes are numbered and shown by a heavy bar at the appropriate level of similarity.

Distributions of ostracodes and the inferred environments of deposition are correlated, but for several reasons these correlations are rarely high. The underlying cause is that many of the assemblages appear to be mixed marine and nonmarine faunas. One reason for the mixing of faunas lies with the sample design. If sampling was on a coarser scale than changes of the fauna from marine to nonmarine, it is likely that the changes will go undetected. Instead, groupings of samples or species would occur that are difficult to relate to the paleoenvironments inferred from sedimentological evidence. Such a coarse sample design would yield composite samples that are, in effect, time averaged and thus not suitable for precise paleoenvironmental inference. Although our samples were taken in 10-cm-thick blocks, it is possible that the changes in the faunas were on a scale of centimeters rather than tens of centimeters. Successional changes in assemblages of some Pennsylvanian ostracodes occurred on a scale of centimeters (Peterson, Kaesler, & Walsh, 1976; Peterson & Kaesler, in ms), suggesting that careful sample design is necessary to avoid operator-induced time averaging. The beds we studied did not lend themselves to fine-scale sampling, and some details of the paleoecology may have been obscured.

Another possible reason for the apparent mixing of marine and nonmarine species may be that some species were transported from other environments. Given the variety and proximity of terrestrial and nearshore, shallow, potentially high-energy marine environments, it is not unreasonable to expect that some mixing took place. Terrestrial environments may have contributed nonmarine species such as *Carbonita inflata* to nearshore, shallow-marine deposits that normally contain predominately marine species. Examination of the inferred lithofacies patterns of both the Hamlin and the Americus (Figs. 3, 4) shows that areas of potential mixing occur throughout the study area.

A third reason may lie with the ostracodes themselves. For example, *Carbonita inflata*, generally considered to be a nonmarine species, is one of the most common species in our collections. It is, however, common in samples from strata inferred to have been deposited in marginal-marine environments. Perhaps *C. inflata* was more eurytopic than has been assumed previously (Pollard, 1966; Anderson, 1970; Sohn, 1975) and was tolerant of brackish-water environments.

Biotope 1 (Hamlin Shale).—This biotope, which forms the largest cluster in the dendrogram (Fig. 5), includes 53 samples (see Appendix 1 for localities). The cluster is situated in the uppermost portion of the dendrogram and is represented by the large block letter "A" and the four samples immediately below it. The letter "A" represents 49 samples that have correlation coefficients with each other equal to or greater than 0.98.

The samples of this biotope are from the Hamlin Shale and the Hamlin-Americus transition bed along with two samples of shale from the Americus Limestone. The high similarities of samples in the cluster are due primarily to the dominance of several species of *Carbonita*. These are the only ostracodes present in many samples, where they are accompanied by charophytes, microgastropods, and possible worm tubes. In some samples, a small number of foraminifers is also present. These faunas, which typify the Hamlin Shale, are from dark-gray and brown to olive-green, blocky to somewhat fissile shale beds, a

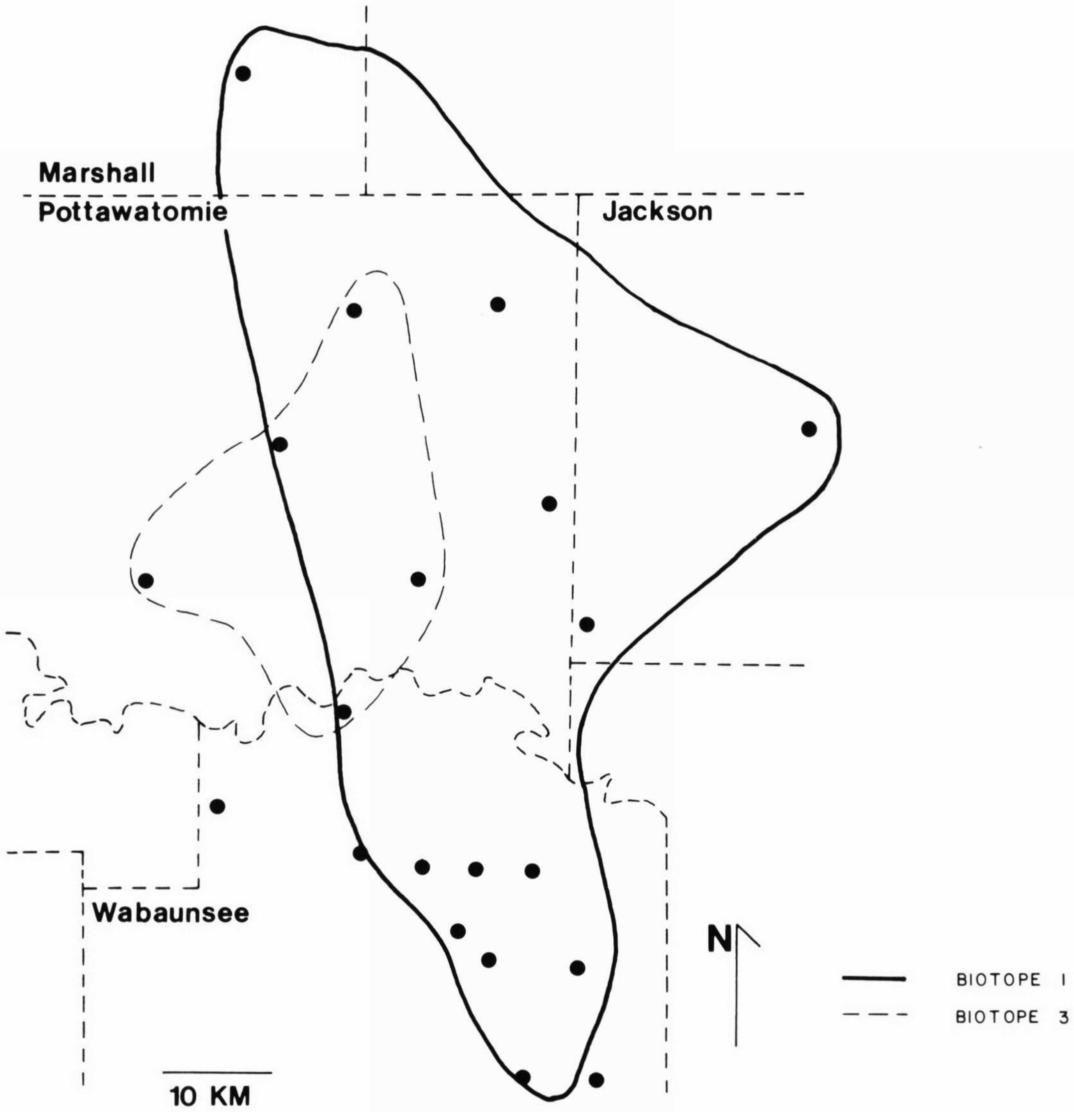

Fig. 6. Distribution of the two ostracode biotopes of the uppermost Hamlin Shale. See Figure 1 for locality numbers.

marked contrast in lithology to Sample Group 3, the other Hamlin Shale biotope.

The areal distribution of this biotope (Fig. 6) encompasses several nearshore marine environments, including tidal flats, shoals, and lagoonal environments, as well as nonmarine ones (Fig. 3). *Carbonita inflata* and several other species of *Carbonita* are the dominant ostracodes in this biotope; all have been interpreted as nonmarine species (Pollard, 1966; Sohn, 1975). In these beds, however, they occur in association with such lagoonal and nearshore ostracodes as *Paraparchites humerosus, Sulcella sulcata,* some species of *Bairdia, Amphissites centronotus,* and *Hollinella (Hollinella) bassleri,* suggesting that they may have been tolerant of brackish water.

The common association of *Carbonita* with charophytes, however, suggests nonmarine conditions. Lane (1964) noted that modern charophytes are found principally in fresh water but that some are tolerant of brackish waters. "The assumption is made that the early Permian charophytes . . . lived in fresh water, although it is certainly a possibility that the oogonia might have been carried out into saline waters before deposition" (Lane, 1964, p. 15). Such a situation can also be envisioned for the Hamlin charophytes, which, together with ostracode carapaces, may have been transported into nearshore environments by streams flowing from nearby land. *Carbonita inflata* shows a range of relative abundances in this biotope that is highest in the nonmarine part and decreases somewhat toward the nearshore part (Fig. 7). Whether this indicates transportation of empty carapaces from preferred environments or reduced populations of living ostracodes in less favorable environments cannot be determined from our data.

The occurrence of two samples from the Americus Limestone (P75-41 and P75-101) within this sample group is due to the abundance of *Carbonita inflata.* P75-101 is from locality W15, which is located on the basinward margin of the carbonate shoal that was present during deposition of the lower Americus interval (Fig. 4). The assemblage in this sample is anomalous, and its significance is not clear. *Carbonita inflata* was abundant in sample P75-41 from locality J2 because the sample was deposited very near shore on a tidal mudflat (Fig. 4). The presence of *Bairdia beedei, Hollinella (Hollinella) bassleri, Cryptobairdia seminalis,* and *Amphissites centronotus* suggests that a normal-marine environment was close. Thus, the mixed nonmarine-marine character of this assemblage probably indicates the influence of tidal and wave action on these nearshore environments.

Biotope 2 (Americus Limestone).—This biotope contains only two samples, one from locality W4 and one from locality W5 (Fig. 5), both located in the southeastern portion of the carbonate shoal (Fig. 4). The samples are closely similar to those in sample group 1, and both contain about 40 percent *Carbonita inflata.* Normal-marine species are also present, including *Bairdia beedei, Paraparchites humerosus, Cryptobairdia seminalis,* and *Hollinella (Hollinella) bassleri,* suggesting mixing of marine and nonmarine species.

The isolated sample W2′AA1 just below sample group 2 in Figure 5 has a fairly diverse ostracode fauna, but no single species is dominant. The sample does not seem to be strikingly different from other samples from the Americus, and the significance of its low similarity to other samples is not clear.

Biotope 3 (Hamlin Shale).—This biotope comprises five samples, all of which are from the Hamlin Shale or the Hamlin-Americus transition bed (Fig. 5). The biotope encompasses five localities, W19, P2, P4, P6, and P18 (Fig. 6) and is located in the west-central part of the study area. It is of limited areal extent compared to biotope 1 and contains a markedly different fauna that includes several species of ostracodes along with foraminifers, conodonts, brachiopod shell debris, bryozoans, holothurian sclerites, and rare charophytes. Although *Carbonita* is present, it is generally rare. The predominant ostracode species is *Paraparchites humerosus,* with *Sulcella sulcata, Jonesina bolliaformis?,* and *Kindlella* sp. of subsidiary importance. Other common species include *Bairdia beedei, Bairdia acuminata, Cavellina nebrascensis, Hollinella (Hollinella) bassleri,* and *Pseudobythocypris pediformis.*

The lithology of these samples is markedly different from that of biotope 1. Excluding

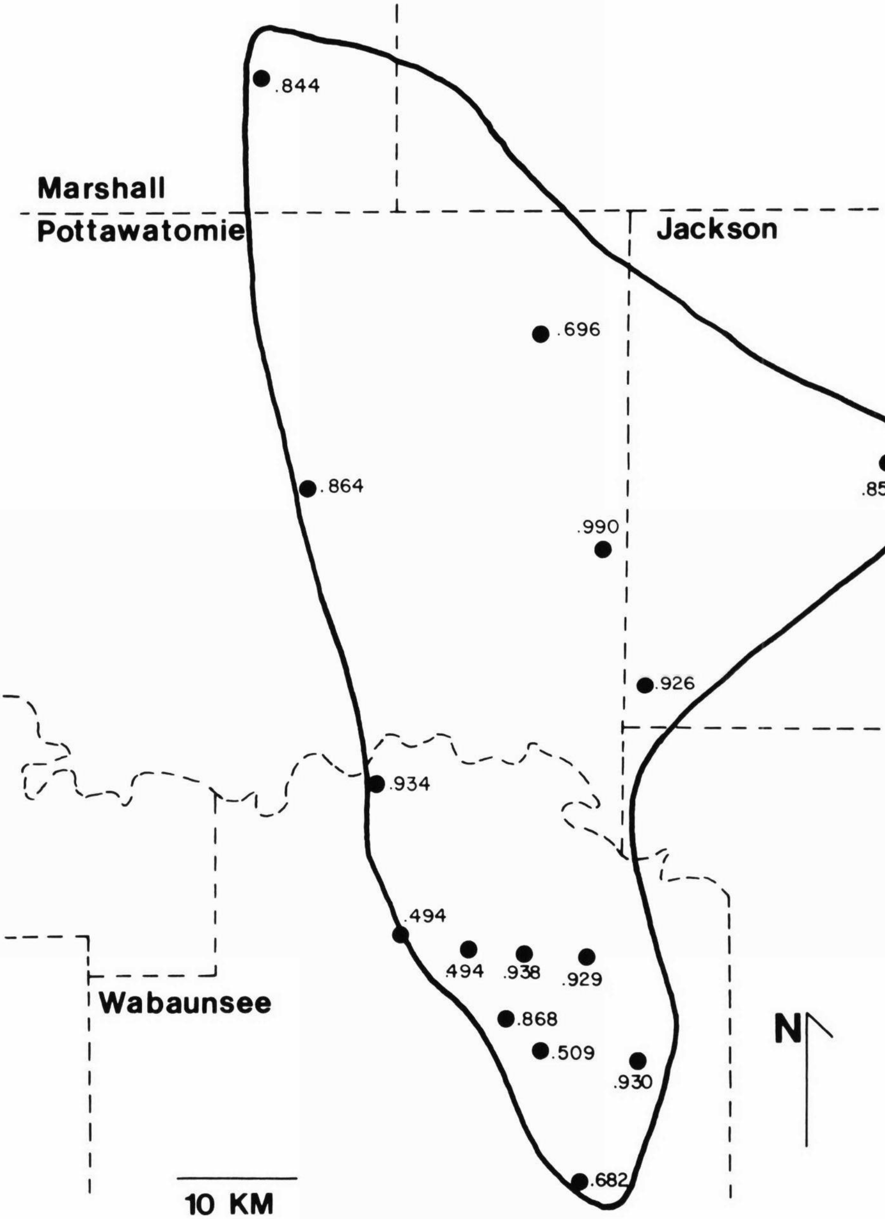

Fig. 7. Proportions of *Carbonita inflata* in assemblages of biotope 1 of the uppermost Hamlin Shale. See Figure 1 for locality numbers.

samples from the Hamlin-Americus transition bed, P74-18 and P75-53, the group includes samples only from tan to yellow-brown, fissile, calcareous shale from the top of the Hamlin Shale. Samples from biotope 1, on the other hand, were from throughout the Hamlin. Thus, the separation of this sample group from the other Hamlin samples results from a different faunal composition that reflects differing lithology and stratigraphic position.

Areal distribution suggests that this is a lagoonal biotope and that the dominant ostracode species thrived in quiet, normal-marine to somewhat brackish water. Such normal-marine species as *Bairdia beedei* and *Hollinella (Hollinella) bassleri* indicate that circulation between the lagoon and open-marine environments was not highly restricted and that the water of the lagoon may have been of nearly normal-marine salinity.

Biotope 4 (Americus Limestone).—This group includes only two samples, both from the Americus Limestone: P75-31 from locality J15 and P75-50 from locality P18. Both samples are from dark gray, somewhat fissile, calcareous shale.

Ostracodes and foraminifers are the most abundant fossils, with conodonts, echinoderms, brachiopods, and bryozoans being of lesser importance. The ostracode fauna is clearly dominated by *Paraparchites humerosus,* hence the similarity to sample group 3. The abundance of *Bairdia beedei* in both samples is the primary reason for their separation from those in sample group 3.

The relative abundance of *Paraparchites humerosus* and the areal distribution of this biotope (Fig. 6) and its host strata suggest that this is a lagoonal biotope. The presence of *Bairdia beedei* and several other species of *Bairdia,* all marine species, indicates that this biotope occupied a nearly normal-marine part of the lagoon. The southern margin of the biotope, in fact, overlaps the carbonate-shoal lithofacies tract in the vicinity of locality P18 (Fig. 4). *Bairdia beedei* is the dominant ostracode in the carbonate shoal (see below), and its occurrence in these samples suggests that this biotope was located toward the seaward margin of the Americus lagoon.

Biotope 5 (Americus Limestone).—This group of five samples is one of three from the carbonate shoal in the lower Americus interval. Two samples (P74-11 and W17AD1) are from the same bed at the same locality. Another, P76-10 from locality M6, is from the basinal portion of the lower Americus interval. The other two samples, W14AB2 and W14AC1, are from a dark-gray, somewhat fissile shale located between the two limestone beds of the Americus at locality W14. The ostracode fauna is characterized by abundant *Sulcella sulcata.* Other less common ostracodes found in all the samples are *Jonesina bolliaformis?, Paraparchites humerosus, Bairdia beedei, Pseudobythocypris pediformis,* and *Basslerella firma.*

Some of the samples are from the southern margin of the carbonate shoal, and one is from an isolated area in southeastern Marshall County. The fauna is similar to those of sample groups 3 and 4 and suggests a lagoon or other quiet-water environment. The location of this biotope near the margin of the carbonate shoal and the isolated basinal occurrence in Marshall County suggest that the margin of the shoal was not static. Use of the term "basinal" in discussing this biotope may be misleading. The area, characterized by dark-gray, finely laminated to somewhat fissile shales, was inferred by W.L. Fisher (1980, personal communication) to be basinal but may, in fact, be merely an area of quiet water not much deeper than adjacent environments. Certainly it was farther offshore than other environments of the lower Americus interval.

Samples P74-11 and W17AD1, from a thin, yellow-brown calcareous shale immediately above the basal algal stromatolite unit at locality W17, contain abundant *Sulcella sulcata* associated with the encrusting foraminifers *Ammovertella* and *Minammodytes.* Only at locality W17 does a thin shale immediately overlie the basal algal stromatolite. This and the similarity of the ostracode assemblage to those from the quiet-water assemblages suggest that this shale and its associated fauna were deposited in quiet-water ponds in the algal-stromatolite-shoal complex of the lower Americus interval.

Biotope 6 (Americus Limestone).—Figure 8 shows the areal distribution of this biotope at five localities in north-central Wabaunsee and southern and central Pottawatomie counties, occopying the central and western part of the carbonate shoal (Fig. 4). Sample P75-62 (locality P4) from the lagoonal lithofacies belt is also included. It was the last to join the cluster and shows fairly high similarities to samples in some of the previous clusters. Locality P4 is just to the north of the inferred boundary of the carbonate shoal, and it is likely that the boundary between the two depositional environments was gradational.

Bairdia beedei predominates in these samples, comprising from 29 to 65 percent.

Other common species include *Hollinella (Hollinella) bassleri, Monoceratina lewisi, Cavellina nebrascensis, Pseudobythocypris pediformis,* and *Basslerella firma.* This is one of the most common assemblages and indicates a normal-marine environment. The occurrence of this fauna in many samples from the carbonate shoal suggests that these species may have lived in high-energy conditions. The thick carapaces of such species as *Bairdia beedei* and *Hollinella (Hollinella) bassleri* may be adaptations to such conditions. The presence of *Cavellina nebrascensis,* a pioneering species in other areas of the Midcontinent (Peterson & Kaesler, in ms.), is not surprising, as the carbonate shoal was probably an area of high environmental stress. Eurytopic species would have greater likelihood of survival under such conditions.

Biotope 7 (Americus Limestone).—This

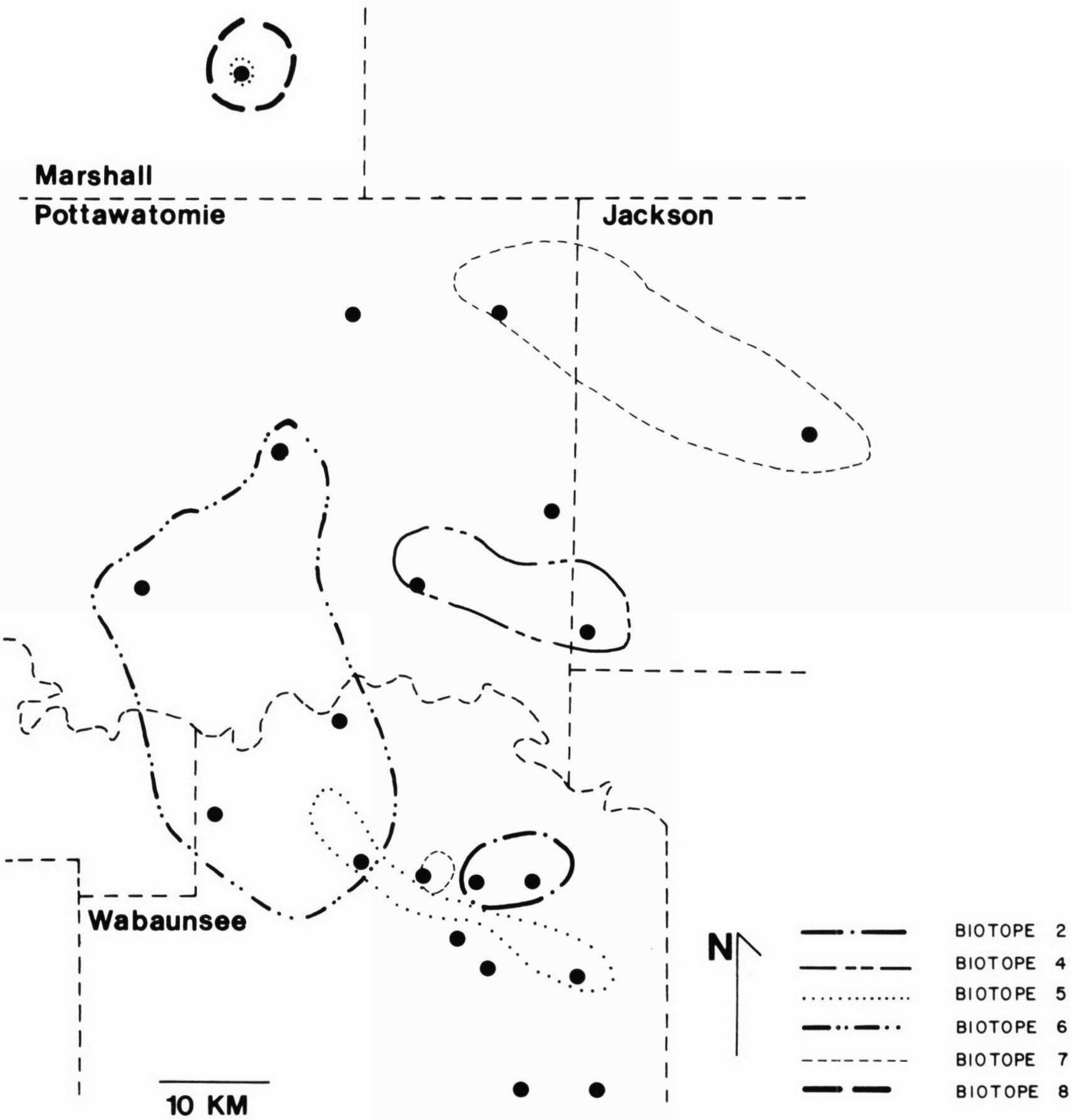

Fig. 8. Distribution of the six ostracode biotopes of the lower interval of the Americus Limestone. See Figure 1 for locality numbers.

group has just three samples from two widely separated areas (Figs. 5, 8). Samples P75-40 and P75-83 are from localities J2 and P8, respectively, which lie well within the tidal-mudflat lithofacies. The other sample, W6AF1, from locality W6, however, is from the carbonate shoal lithofacies tract.

Sample P75-83 is from the calcareous shale bed that is equivalent to the entire lower Americus interval at locality P8 and contains a fauna dominated by *Bairdia beedei* and *Carbonita inflata*. Less abundant species are *Hollinella (Hollinella) bassleri* and *Paraparchites humerosus*. Sample P75-40 is similar but also contains abundant *Amphissites centronotus* and *Bairdia acuminata*. Sample W6AF1, on the other hand, is clearly dominated by *Bairdia beedei*, *Carbonita inflata*, and *Paraparchites humerosus* with the other, previously mentioned species being of lesser importance. The association of *Carbonita inflata* and *Bairdia beedei* makes the assemblage from this biotope unique and causes the samples to cluster separately from the other Americus samples.

Specimens of *Carbonita inflata* in these samples were probably transported from nearby nonmarine environments, but *C. inflata* may have been tolerant of salinity conditions on the tidal flat and may even have thrived there.

Biotope 8 (Americus Limestone).—This biotope includes two samples of black, finely laminated shale from between the two limestone beds of the Americus Limestone at locality M6 (Figs. 5, 8). Conodonts are the most abundant fossils in these samples, ostracodes are uncommon, and a few foraminifers and fragments of inarticulate brachiopods are present. The ostracode fauna has low diversity. The most abundant species, *Geisina* cf. *G. gregaria*, is thought to have been a brackish-water, probably euryhaline species. In the British Coal Measures *Geisina* is commonly associated with abundant plant debris in carbonaceous shales. Pollard (1966, p. 676) believed it may have fed on floating or detrital plant material and had a mode of life similar to that of the modern *Cypridopsis*. The abundance of this species in organically rich, black shales of the Americus suggests a similar mode of life.

This biotope lies in that part of the lower Americus lithofacies pattern inferred by W.L. Fisher (1980, personal communication) to be basinal. The finely laminated shale and abundant organic material indicate quiet-water deposition, slow sedimentation, little bioturbation, and restricted circulation. Depth of water, however, cannot be determined from our data, and rather than being basinal this biotope may simply have been farther offshore than contemporary environments.

OSTRACODE ASSEMBLAGES

R-mode cluster analysis of the reduced ostracode data matrix formed four ostracode assemblages, with nine species left unclustered (Fig. 9). Correlations within and between clusters show the overall low similarities of distributions and abundances among species. Species in each assemblage are also similar in stratigraphic position, and lithology in which they are found. The following discussion summarizes the most important aspects of each assemblage, relates assemblages to inferred paleoenvironments, and demonstrates some causes of the low similarities of distribution and abundance of species.

A. Amphissites centronotus *Assemblage.*—This assemblage includes five species that are generally most abundant in shales of the Americus Limestone: *Amphissites centronotus*, *Shleesha pinquis*, *Fabalicypris acetelata*, *Bairdia acuminata*, and *Orthobairdia texana*. They are not restricted to the Americus, however, and are also fairly abundant in some samples from the uppermost Hamlin Shale. The species are all marine, and the relative proportion of samples in which all were found is highest in the lagoonal and tidal-mudflat lithofacies of the lower Americus except for *B. acuminata* (Table 1), suggesting that this is a nearshore assemblage.

These five species represent two orders of

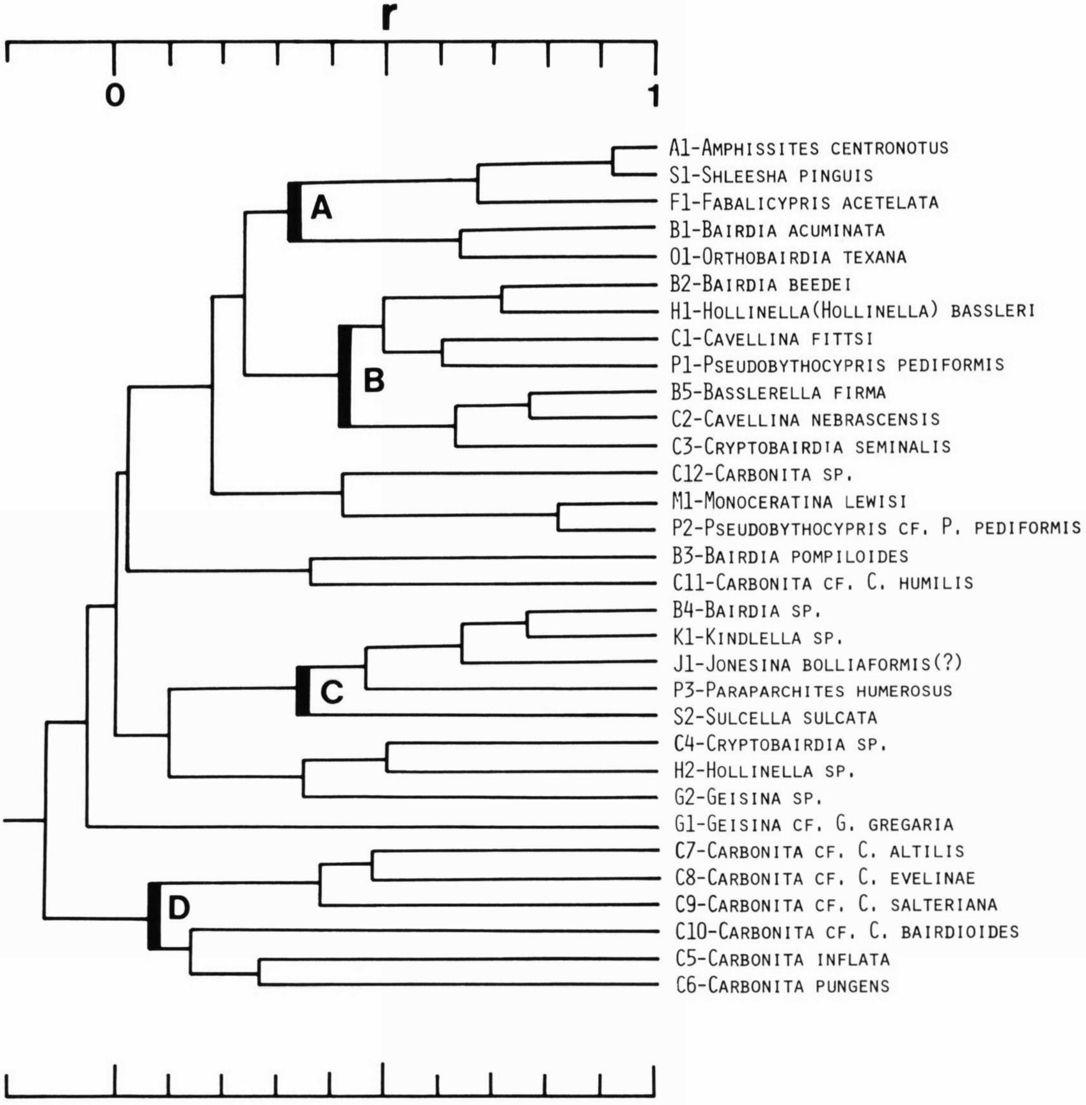

Fig. 9. Dendrogram from R-mode cluster analysis (UPGMA) of the reduced ostracode data matrix using the product-moment correlation coefficient; cophenetic correlation coefficient = 0.847. The four assemblages are designated A to D and marked by a heavy bar at the appropriate level of similarity.

Ostracoda. *Amphissites centronotus* and *Shleesha pinquis* are palaeocopids of the family Amphissitidae (Knight, 1928; Moore, 1961; Sohn, 1961), and *Fabalicypris acetelata, Bairdia acuminata,* and *Orthobairdia texana* are podocopids of the family Bairdiidae (Sars, 1887; Sohn, 1960; Moore, 1961). The clustering of species from the same families suggests similar paleoecological requirements at the family level, supporting the suggestion that some palaeocopid families were environmentally restricted during the late Paleozoic (Kaesler, Peterson, & Brondos, 1977).

B. Bairdia beedei *Assemblage.*—The seven species in this cluster include some abundant and easily recognized species (Fig. 9), one of which, *Bairdia beedei,* is the most abundant in the study (Peterson, 1978). *B. beedei* is nearly ubiquitous (Table 1). It is the species most consistently present in three of the four

Table 1. Proportions of Samples from Each Lithofacies of the Lower Americus Interval Containing Major Ostracode Species.

Species	Carbonate shoal	Lagoonal	Tidal mudflat	Basinal
Amphissites centronotus	0.62	1.00	1.00	0.00
Shleesha pinquis	0.62	1.00	0.66	0.00
Fabalicypris acetelata	0.62	1.00	1.00	0.00
Bairdia acuminata	0.46	0.25	0.33	0.00
Orthobairdia texana	0.69	0.75	1.00	0.33
Bairdia beedei	1.00	1.00	1.00	0.33
Hollinella (Hollinella) bassleri	0.85	1.00	1.00	0.33
Cavellina fittsi	0.54	0.00	0.66	0.00
Pseudobythocypris pediformis	0.62	0.25	0.00	0.66
Basslerella firma	0.85	1.00	0.33	0.33
Cavellina nebrascensis	0.92	1.00	0.33	0.33
Cryptobairdia seminalis	0.46	0.75	0.66	0.00
Monoceratina lewisi	0.85	1.00	1.00	0.00
Pseudobythocypris cf. *P. pediformis*	0.15	0.75	0.33	0.00

Americus lithofacies tracts, suggesting that it was eurytopic and that, unlike *Amphissites centronotus* or *Carbonita inflata*, it is not characteristic of a single environment. The close association of *Hollinella (Hollinella) bassleri* with *B. beedei* suggests a similar paleoecology for this morphologically striking upper Paleozoic species. The two species of *Cavellina*, *C. nebrascensis* and *C. fittsi*, are similarly judged to have been eurytopic.

Bairdia beedei is most abundant in the carbonate shoal lithofacies tract of the lower Americus interval, a high-energy marine environment. A strikingly similar species grouping was found by cluster analysis of data from the Virgilian Beil Limestone Member of the Lecompton Limestone in northeastern Kansas, a regressive marine unit (Brondos & Kaesler, 1976). Specifically, *Bairdia beedei*, *Pseudobythocypris pediformis*, *Basslerella firma* (*B.* sp. of Beil study), *Cavellina nebrascensis*, and species of both *Hollinella* and *Cryptobairdia* are common to both species groups. This assemblage occurs in the upper portion of the Beil Limestone, where the ostracode fauna responded to fluctuating environmental conditions and ". . . was adapted to shallower water with intervals of increased influx of terrigenous sediments and probably greater turbidity" (Brondos & Kaesler, 1976, p. 229). The similarity of assemblages from the Beil Limestone and the Americus carbonate shoal suggests similar environmental conditions. Both the upper Beil and the lower Americus carbonate shoal lithofacies have a relatively greater amount of terrigenous material than underlying strata, probably due to increased turbidity; and in both units the amount of shale increases upward.

C. Paraparchites humerosus *Assemblage.*—This assemblage, characteristic of the lagoonal biotopes in both the Hamlin Shale and the Americus Limestone, includes five species (Fig. 9): *Paraparchites humerosus*, which is dominant, *Bairdia* sp., *Kindlella* sp., *Jonesina bolliaformis?*, and *Sulcella sulcata*. Samples of this assemblage also commonly include species of *Cavellina*, *Hollinella*, and *Pseudobythocypris*, which are not as abundant as *P. humerosus*, especially in the lagoonal biotope of the lower Americus interval.

Some samples with this assemblage also include species of nonmarine, possibly brackish-water *Carbonita*, although in most instances individuals are rare. Most such samples are from the lagoonal lithofacies of the Hamlin Shale. The *Paraparchites humerosus* assemblage appears to be characteristic of the lagoonal lithofacies of both the Hamlin Shale and the Americus Limestone, which was deposited in quiet, normal-marine to somewhat brackish waters in the central portions of the study area. Further study of the ostracode faunas from units stratigraphically above and below the Hamlin-Americus interval is necessary to determine if this assemblage is characteristic of similar environments in other upper Paleozoic strata in the Midcontinent.

D. Carbonita *Assemblage.*—The *Carbonita* assemblage contains six species of *Carbonita* and is dominated by *C. inflata* (Fig. 9). Other species of *Carbonita*—*C.* cf. *C. humilis* and *Carbonita* sp.—clustered elsewhere in Figure 9 and are rare.

This assemblage is characteristic of the nonmarine and nearshore marine strata of the Hamlin Shale. As discussed, species of *Carbonita* are considered to be nonmarine (Pollard, 1966; Sohn, 1975), but the distribution of species of *Carbonita* and other genera suggests that not all species were restricted to nonmarine environments.

Similarities among species of this cluster are less than 0.5 because in most samples only one or two species occur together in abundance, and other species, if present, are represented by only a few individuals. Niches of the different species of *Carbonita* must have differed, but the nature of the differences are unknown.

Ordination.—The overall low similarities of distribution and abundance of species make the recognition of assemblages difficult and make paleoecological inferences drawn from the cluster analysis somewhat suspect. Several species join earlier-formed clusters only at very low levels of similarity. *Geisina* cf. *G. gregaria,* for example, joins a cluster composed of assemblages A, B, and C at a level less than zero. Several other species, for example *Bairdia pompilioides* and *Carbonita* cf. *C. humilis,* cluster at such a low level of similarity that they are not readily interpretable.

The lack of tight clusters and the overall low similarity among the species is also shown by R-mode ordination with nonmetric multidimensional scaling of the reduced ostracode data matrix (Fig. 10). No distinct groups of species are seen, but a pattern of arrangement of species is recognizable. On the left side of the diagram, *Carbonita inflata* (C5) is isolated from the 31 other species. On the far right, *Bairdia beedei* (B2) and *Hollinella (Hollinella) bassleri* (H1) are shown. The ordination represents a gradation from predominantly nonmarine species on the left, represented by *C. inflata,* to predominantly marine species on the right, represented by *B. beedei* and *H. bassleri.* Of course, exceptions occur; for example, *Cavellina fittsi* (C1) and *Cavellina nebrascensis* (C2) are marine species but occur closest to the presumed nomarine species *Carbonita pungens* (C6) and *Carbonita* cf. *C. evelinae* (C8). Species of *Cavellina* are thought to be eurytopic, pioneering species and may have been the first marine ostracodes to populate areas newly innundated by the Americus sea.

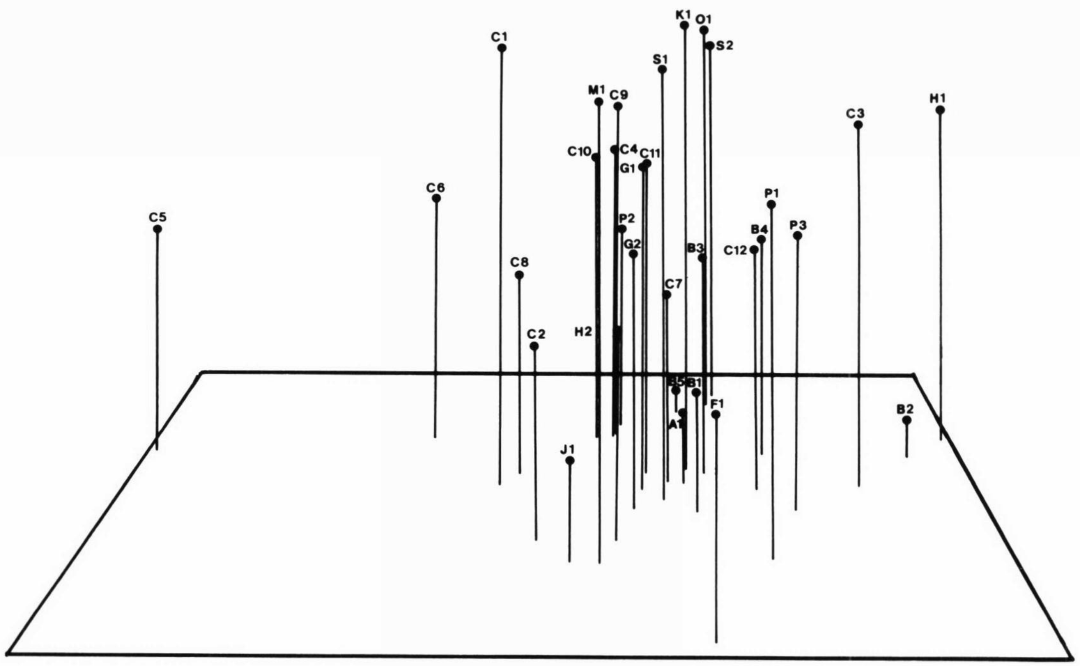

Fig. 10. Three-dimensional nonmetric multidimensional scaling of the 32 ostracode species used in the R-mode cluster analysis. Species designation given in Figure 9; stress=0.749.

OSTRACODE SPECIES DIVERSITY

An index of species diversity is a statistic that combines the number of species in a sample and the distribution of individuals among species (Pielou, 1969, p. 222). The species diversities of the ostracode assemblages from each sample were computed with Brillouin's (1962) equation from information theory (Appendix 2). Numerous biological and paleontological studies have demonstrated the usefulness of indices of species diversity to express aspects of community structure that are not brought out by other means of comparison, such as cluster analysis and ordination (e.g., Buzas & Gibson, 1969; Hazel, 1975; Pielou, 1975; Brondos & Kaesler, 1976; Kaesler & Mulvaney, 1977; Kaesler & Herricks, 1977; Haack & Kaesler, 1980). The use of indices of species diversity, however, is replete with difficulties, most of which stem from misapplication of the equations, failure to recognize the assumptions inherent in the various indices, and overinterpretation of the results (Hurlbert, 1971; Hedgpeth, 1973; Peet, 1974; Pielou, 1969, 1975, 1977).

Most authors have called upon the stability-time hypothesis (Hessler & Sanders, 1967; Sanders, 1969; Slobodkin & Sanders, 1969) to explain relatively low species diversities from environments of high physical stress and unpredictable conditions and high diversities from environments of less physical stress and greater predictability. Within the framework of evolutionary time the more stable environments are hypothesized to promote biological accommodation, greater specialization, and less interaction among organisms, resulting in higher species diversity. In a paleontological study, however, variability in species diversity cannot be explained by the stability-time hypothesis alone. Time averaging, the taphonomic overprint, and differential longevities often make it impossible to explain differences in species diversity. Moreover, as Buzas (1972) pointed out, difficulty may stem from the fact that although the diversity of the community or a subset of it may be quantified, the variables with which one hopes to explain the patterns of species diversity are poorly understood.

The characteristic pattern of species diversity of assemblages from the Hamlin-Americus interval is that the most diverse assemblages are from marine strata (Table 2). Assemblages with the highest diversities are from the carbonate-shoal, lagoonal, and tidal-mudflat lithofacies of the Americus Limestone, most with diversities above 1.0. Assemblages from the Hamlin Shale, in comparison, have diversities less than 0.9 with mean diversities less than 0.5 (Table 2). Brondos and Kaesler (1976) found a similar trend among assemblages of the regressive Beil Limestone, and Elofson (1941) and Benson (1959) found only a few Holocene ostracode species able to thrive in fluctuating nearshore environments.

Table 2. Mean Diversities of Ostracode Assemblages from Each Lithofacies of the Uppermost Hamlin Shale and the Americus Limestone. (Number of samples, n; standard deviation for each lithofacies, SD; computations based on means of 25 randomly replicated subsamples of size 100.)

Lithofacies	H	n	SD
Americus Limestone			
Carbonate shoal	1.611	14	0.399
Lagoonal	1.882	4	0.110
Tidal mudflat	1.690	4	0.207
Basinal	0.750	2	0.615
Uppermost Hamlin Shale			
Lagoonal	0.479	22	0.442
Tidal mudflat	0.371	8	0.128
Intertidal shoal and beach	0.394	3	0.039
Nonmarine	0.485	8	0.358

The most consistently high species diversities are in the lagoonal lithofacies of the Americus interval, suggesting an environment more favorable to ostracodes, perhaps due to greater stability of the substrate as a result of somewhat greater depth or reduced wave and current action. In a study of Holocene ostracodes of the continental shelf off Cape Hatteras, Hazel (1975, p. 741) found that diversity increases with depth, a trend he attributed to turbulence and turbidity in shallow nearshore environments.

Two other aspects of the species diversity of the Americus ostracodes are evident from Table 2. First, in samples from the tidal mudflat lithofacies, species diversities appear to be anomalously high if decreased diversity is expected with shoaling and greater environmental instability. An explanation is that the boundary between the lagoonal and tidal-mudflat lithofacies fluctuated. Samples from near the boundary may thus contain species from both environments because of time averaging, producing erroneously high species diversities. Second, species diversities of assemblages from the basinal lithofacies of the Americus interval are variable, perhaps due to preservational bias or postmortem transportation. The small number of samples from the basinal lithofacies precludes assessment of this variability.

The effect of proximal nonmarine environments on species diversity is shown by the diversities of assemblages from the lagoonal lithofacies of the uppermost Hamlin, in which mean diversities are markedly less than those from the Americus lagoonal lithofacies (Table 2). Although both of these lithofacies have similar assemblages, there is no compelling reason to expect their species diversities to be comparable. The Hamlin lagoonal lithofacies is restricted on its western and eastern sides by nonmarine lithofacies (Fig. 3). Communication with open marine environments was probably severely limited, resulting in stagnation of the lagoonal waters, increased accumulation of organic debris, and a highly stressed environment habitable by only eurytopic species. Such conditions would promote lower species diversity.

Table 3. Special Diversities of Ostracode Assemblages from the Hamlin-Americus Transition Bed. (Indices given for means of 25 randomly replicated subsamples of sizes 25 and 100.)

Sample	Locality No.	H (n=100)	H (n=25)
P74-5	W6	0.394	0.276
P74-12	W17	1.229	1.045
P74-18	W19	1.040	0.779
P75-6	W11	0.273	0.163
P75-53	P18	1.151	0.902
P75-65	P4	---*	1.061
P75-66	P4	0.367	0.193
P75-104	W15	0.435	0.300
W4CLBD	W4	0.543	0.413
W5AL1	W5	0.212	0.131
W6B10CL	W6	0.313	0.264
W14AD1	W14	0.621	0.529
W17AE1	W17	0.967	0.800

*Sample of less than 100 specimens.

Indices of species diversity were also computed for ostracode assemblages from the Hamlin-Americus transition bed, where a wide range of diversity is probably the result of reworking (Table 3). Three samples from the transition bed with high diversities (P74-12, P74-18 and P75-53) are from localities W17, W19, and P18, respectively, where the transition bed overlies the marine, lagoonal lithofacies of the uppermost Hamlin. The effect of reworking of these samples is further shown by the correlation coefficients in Table 4. Except for two of the three localities noted, the proportions of ostracode species in samples of the transition bed are nearly perfectly correlated with proportions in the sample immediately underlying the transition bed. This strongly supports Fisher's (in prep.) contention that the Hamlin-Americus transition bed developed as a regolith on emergent land. The low correlations at localities W17 and W19 may be due to extensive reworking of the regolith with possible addition of taxa on the lagoonward margins of the land as the lagoon expanded just prior to inundation by the Americus sea.

Table 4. Correlation Coefficients between the Proportions of Ostracodes in Hamlin-Americus Transition Bed Samples and Samples Taken Immediately Below.

Locality	r	Locality	r
W5	1.000	W17	0.222
W11	0.994	W19	0.001
W14	0.988	P4	0.984
W15	0.904	J15	0.999

To summarize the relationships between species diversity and stratigraphy of samples, a two-dimensional Q-mode nonmetric multidimensional scaling of the 81 samples was computed and combined graphically with ostracode species diversities of each sample (Fig. 11). Plots on three planes, A, B, and C, are from the same ordination and represent the Americus Limestone, the Hamlin-Americus transition bed, and the uppermost Hamlin Shale, respectively. Each plane shows the two-dimensional scatter diagram from nonmetric multidimensional scaling of the appropriate samples. The vertical axis is species diversity. Figure 11 shows three patterns. The first is the distinct separation of samples of the

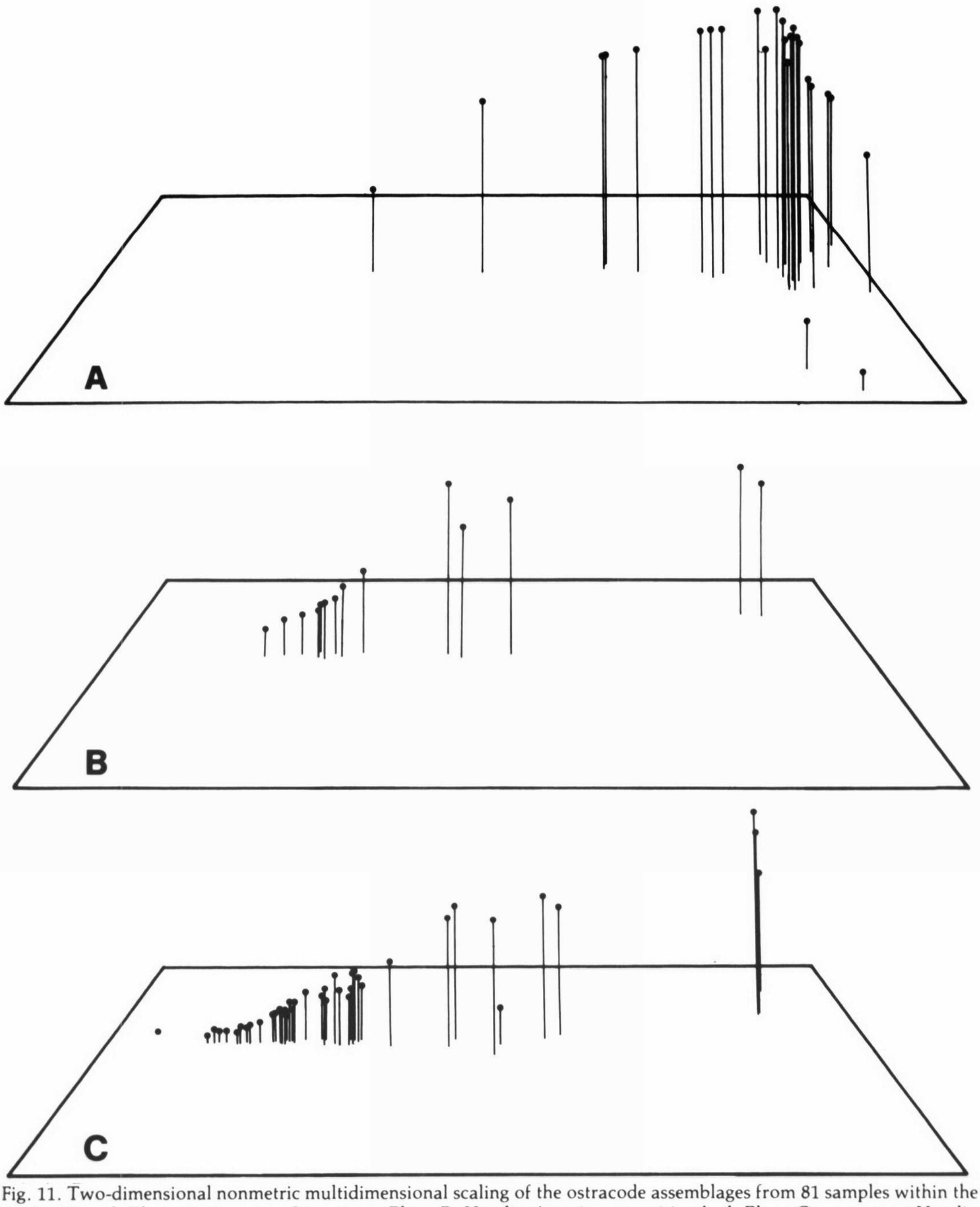

Fig. 11. Two-dimensional nonmetric multidimensional scaling of the ostracode assemblages from 81 samples within the study interval. Plane A, Americus Limestone; Plane B, Hamlin-Americus transition bed; Plane C, uppermost Hamlin Shale. The vertical axis is the species diversity of each assemblage; stress = 0.115.

Hamlin (C) from those from the Americus (A), indicating fundamental differences in assemblages of these units. Second, species diversities of the Hamlin samples are, for the most part, markedly lower than those of the Americus. Third, the transitional, regolithic character of the Hamlin-Americus transition bed is indicated by the scatter of points in plane B and by the range of diversity values of assemblages from those samples.

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APPENDICES

Appendix 1. Samples and Localities in Each Ostracode Biotope Recognized in the Hamlin Shale and the Americus Limestone of Northeastern Kansas.

(Samples with asterisk from Americus Limestone clustered with Hamlin Shale; samples with plus from Hamlin-Americus transition bed.)

Biotope (Member)	Sample no.	Locality
1 (Hamlin Shale)	P75-41*, P75-44, P75-45, P75-46	J2
	P75-25, P75-27, P75-33, P75-34, P75-37	J15
	P76-18	M6
	P75-65+, P75-66+, P75-67, P75-68, P75-69	P4
	P75-84, P75-85, P75-86	P8
	P75-118, P75-119, P75-120, P75-121, P75-122	P12
	P75-89	W3
	W4AG2, W4CLBD+	W4
	W5AG1, W5AH1, W5AI1, W5AL1+	W5
	P74-5+, W6B10CL+	W6
	P75-6+, P75-7, P75-8, P75-10, P75-11, P75-12	W11
	W14AD1+, W14AE1, W14AF1, W14AG1	W14
	P75-101*, P75-104+, P75-105, P75-108	W15
	P74-12+, W17AE1+, W17AF1, W17AJ1	W17
	P74-19, P74-20, P74-22	W19
2 (Americus Limestone)	W4AF2	W4
	W5AF1	W5
3 (Hamlin Shale)	P76-26, P76-27	P2
	P75-75	P6
	P75-53+	P18
	P74-18+	W19
4 (Americus Limestone)	P75-31	J15
	P75-50	P18

Biotope (Member)	Sample no.	Locality
5 (Americus Limestone)	P76-10	M6
	W14AB2, W14AC1	W14
	P74-11, W17AD1	W17
6 (Americus Limestone)	P76-23	P2
	P75-62	P4
	W10AA1, W10AB1	W10
	W17AB1	W17
	P74-15	W19
7 (Americus Limestone)	P75-40	J2
	P75-83	P8
	W6AF1	W6
8 (Americus Limestone)	P76-11, P76-12	M6

Appendix 2. Species Diversity of Ostracode Assemblages from Lithofacies of the Uppermost Hamlin Shale and Americus Limestone of Northeastern Kansas.

(Indices computed for randomly selected subsamples of 25 and 100 individuals, each replicated 25 times; missing values indicate samples with fewer than 100 individuals.)

Lithofacies (Member)	Sample no.	Locality	H (n=100)	H (n=25
Lagoonal (Hamlin Shale)	P74-19	W19	0.276	0.193
	P74-20	W19	0.265	0.191
	P74-22	W19	0.532	0.392
	P75-25	J15	0.074	0.036
	P75-27	J15	0.127	0.085
	P75-33	J15	0.448	0.298
	P75-34	J15	0.334	0.214
	P75-37	J15	0.068	0.086
	P75-65	P4	---	1.061
	P75-66	P4	0.367	0.193
	P75-67	P4	0.410	0.372
	P75-68	P4	0.091	0.079
	P75-69	P4	0.148	0.109
	P75-75	P6	0.909	0.743
	P75-89	W3	1.038	0.832
	P75-105	W15	1.214	1.024
	P75-108	W15	---	0.154
	P75-118	P12	0.032	0.056
	P75-119	P12	0.306	0.240
	P75-120	P12	0.316	0.270
	P75-121	P12	0.429	0.368
	P75-122	P12	0.182	0.183
	P76-26	P2	1.412	1.181
	P76-27	P2	1.576	1.294
Carbonate mudflat (Hamlin Shale)	P75-7	W11	0.397	0.317
	P75-8	W11	0.223	0.162
	P75-10	W11	0.441	0.330
	P75-11	W11	0.550	0.461
	P75-12	W11	0.557	0.443
	W14AE1	W14	0.317	0.224
	W14AF1	W14	0.257	0.193
	W14AG1	W14	0.228	0.175
Intertidal shoal and beach (Hamlin Shale)	P75-44	J2	0.402	0.337
	P75-45	J2	0.343	0.300
	P75-46	J2	0.436	0.359
Nonmarine (Hamlin Shale)	P75-84	P8	0.998	0.773
	P75-85	P8	1.055	0.869
	P75-86	P8	0.650	0.514
	P76-18	M6	0.466	0.405
	W4AG2	W4	0.269	0.240
	W5AG1	W5	0.248	0.193
	W5AH1	W5	0.116	0.130
	W17AF1	W17	---	1.013
	W17AJ1	W17	0.075	0.036
Carbonate shoal (Americus Limestone)	P74-11	W17	1.168	0.891
	W17AD1	W17	1.344	1.090
	P74-15	W19	1.933	1.493
	P75-3	W11	2.048	1.668
	P75-101	W15	0.630	0.478
	P76-23	P2	1.958	1.570
	W2′AA1	W2′	1.948	1.555
	W4AF2	W4	1.656	1.333
	W5AF1	W5	1.680	1.403
	W6AF1	W6	1.892	1.488
	W10AA1	W10	1.912	1.478
	W10AB1	W10	1.079	0.899
	W14AB2	W14	---	1.674
	W14AC1	W14	1.729	1.419
	W17AB1	W17	1.576	1.268
Lagoonal (Americus Limestone)	P75-31	J15	1.770	1.387
	P75-50	P18	1.917	1.417
	P75-61	P4	1.795	1.438
	P75-62	P4	2.047	1.589
Tidal mudflat (Americus Limestone)	P75-40	J2	1.907	1.510
	P75-41	J2	1.348	0.869
	P75-82	P8	1.755	1.384
	P75-83	P8	1.750	1.420
Basinal (Americus Limestone)	P76-10	M6	1.364	0.880
	P76-11	M6	0.135	0.126
	P76-12	M6	---	0.375