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DIVERSITY AS A TOOL TO THE PALEOECOLOGIC STUDY  
OF A PENNSYLVANIAN SHALE

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ABSTRACT

The fauna of the Stull Shale Member (Upper Pennsylvanian, Virgil Series) in southeastern Nebraska and southwestern Iowa is dominated by brachiopods. The biofacies succession is largely represented by a double recurrence of the *Crurithyris* (*Neochonetes*) Assemblages, interrupted by the *Crurithyris*-(Productoidea) Assemblages in the Middle Stull and by the *Crurithyris*-Low Diversity-Low Biomass Assemblage in the Upper Stull.

The Shannon-Wiener information function and some abiotic parameters (Rock color and lime content) have been used to interpret the paleoenvironment represented by each of these assemblages. Moderate diversity index values are present in the *Crurithyris*-(*Neochonetes*) Assemblages for the Lower Stull, a diversity consistent with the predominance of light-weight brachiopods and bivalves in relatively lime-poor sediment. High index values are revealed by the *Crurithyris*-(Productoidea) Assemblages for the Middle Stull; such diversity is indicative of optimum biotic conditions as evidenced by the prominence of heavy shelled brachiopods, particularly the so-called "quasi-infaunal" productoids (Rudwick, 1970), and bivalves in relatively limy sediments. Moderate values are again present in the lowest part and highest part of the Upper Stull by the *Crurithyris*-(*Neochonetes*) Assemblages and are consistent with the predominance of light-weight forms; these assemblages are interrupted by the *Crurithyris*-Low Diversity-Low Biomass Assemblage containing low index values characteristic of the black-colored rocks indicative of stagnant bottom conditions.

INTRODUCTION

"Species diversity," in the sense of Whittaker (1965), is a measure of the number of species with respect to the number of individuals in a sample. Such diversity for a given sample is largely controlled by the large number of rare species present, though the few dominant species actually control most of the energy flow through a community (Odum, 1971, p. 148). Species diversity has long been regarded as low in "physically controlled ecosystems (*i.e.*, subjected to strong physiochemical limiting factors) and high in biologically controlled ecosystems" (Odum, 1971, p. 148). Because of their ecologic utility, species diversity indices have been employed quite extensively in recent years, particularly for benthic Foraminifera of the Quaternary (Sen Gupta and Kilbourne, 1974; Gibson and Buzas, 1973; Buzas, 1972; Buzas and Gibson, 1969).

Other forms of diversity, however, such as measurement of the numerical percentage composition of the number of species, or "dominance diversity"

(Whittaker, 1965), have been demonstrated to be of little value for ecologic correlation (Sanders, 1968); consequently, this author has employed the species diversity measurement.

This study proposes to show that a species diversity index can be a potential paleoecologic tool even for macroinvertebrates of Pennsylvanian rocks, despite significant post-depositional shell fragmentation. The Stull

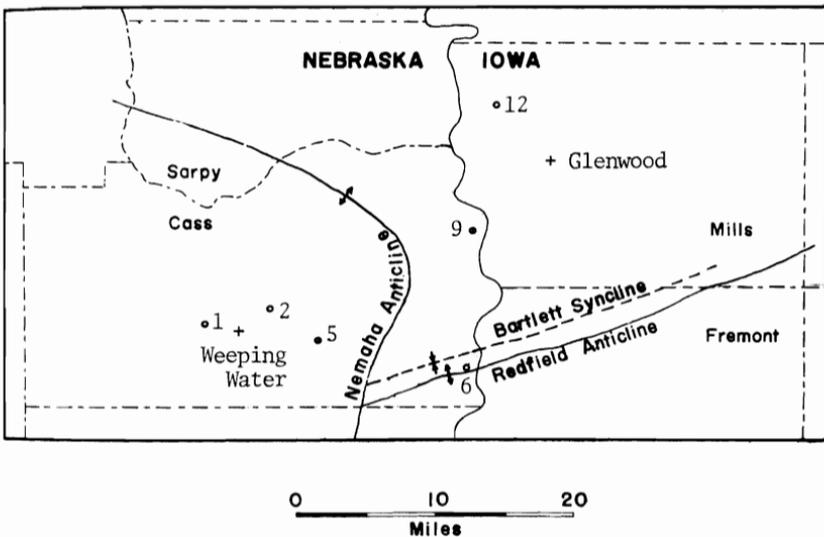
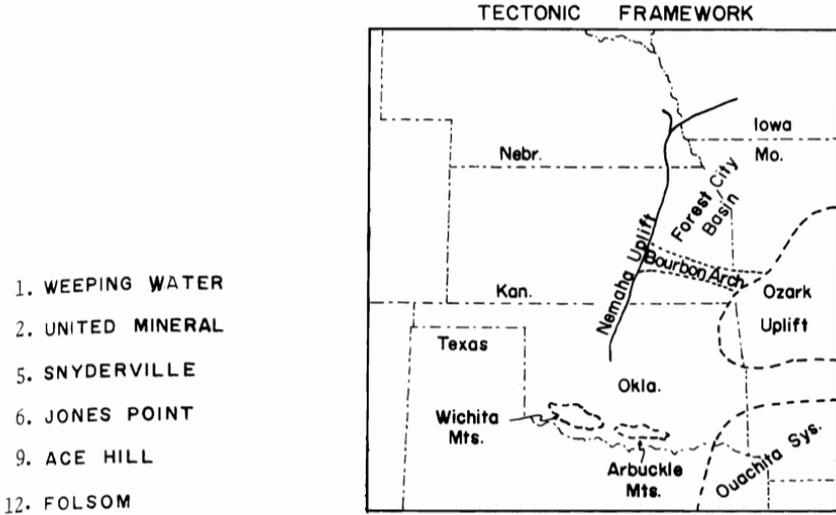


Figure 1 Location of Measured Sections and Major Structures

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Shale was, thus, chosen because of its high fossil content and brachiopod diversity.

The Stull Shale is the uppermost member of the Kanwaka Formation, Shawnee Group, Virgil Series, Upper Pennsylvanian. The Stull crops out along a northeast-southwest trending belt extending from northeastern Kansas into northwestern Missouri and southwestern Iowa, and finally terminating in southeastern Nebraska. It was studied at six localities running transverse to the Nemaha Anticline and north of the Redfield Anticline, in the northern part of the Forest City Basin, extending from near Glenwood, Iowa to Weeping Water, Nebraska (Fig. 1).

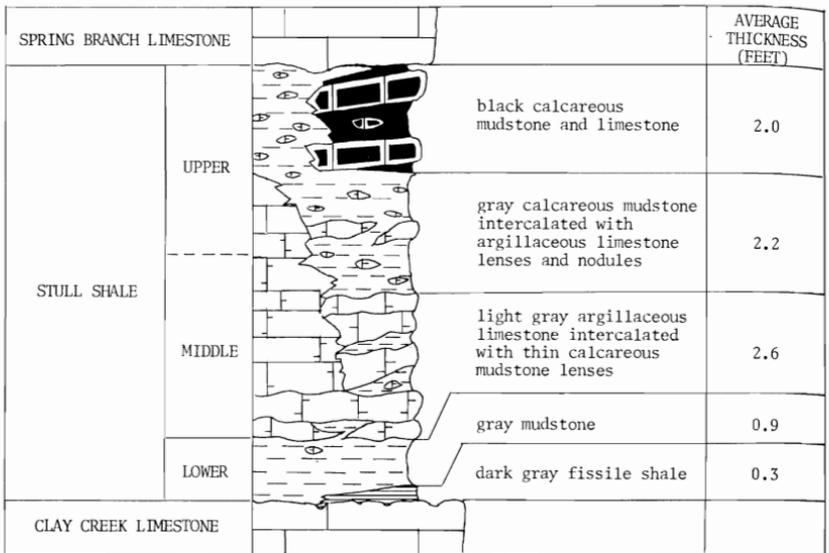


Figure 2 Stratigraphic Section of the Stull Shale (Generalized from Plate 1 of Jacobs, 1973)

Lithologically, the Stull consists of a variety of limestones and mudstones (Fig. 2) deposited in quiet shallow waters (Jacobs, 1973).

### METHODS

The brachiopod genera (almost all of which are monospecific in the Stull Shale of Nebraska and Iowa such as to justify their substitution for species) from the Stull Shale were measured for diversity employing the Shannon-Wiener information function. This function has been used in several forms (see Margalef, 1957; Brillouin, 1964; Pielou, 1966), but the most common form is that employed by Gibson and Buzas (1973), which "measures the

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average diversity per individual.” The formula is given as

$$H(S) = -\sum p_i (\ln p_i)$$

where  $p_i$  is the proportion of individuals belonging to the  $i$ th species, and  $S$  is the number of species.

The main advantages of this diversity measure are that it accounts for the number of species and their proportions regardless of any particular mathematical model and also minimizes the difficulties of comparing diversity in different sized samples (Gibson and Buzas, 1973, p. 218, 220).

The  $H(S)$  value is largely determined by the proportions of the common species, while abundant and rare species contribute less to the value. A maximum diversity is achieved when all species ( $S$ ) are equally distributed in abundance (Gibson and Buzas, 1973).

Three diversity curves are shown in the graphs of Figure 3: The data for Diversity (A) is derived from areal shale analysis, Diversity (B) from bulk shale analysis, and Diversity (C) from acetate peel analysis of limestones (Jacobs, 1973, p. 116-119). The information function values represented by these curves can be arbitrarily designated as low for values ranging from 0.00 to 0.60, moderate for values ranging from 0.70 to 1.25, and high for those ranging from 1.40 to 1.80.

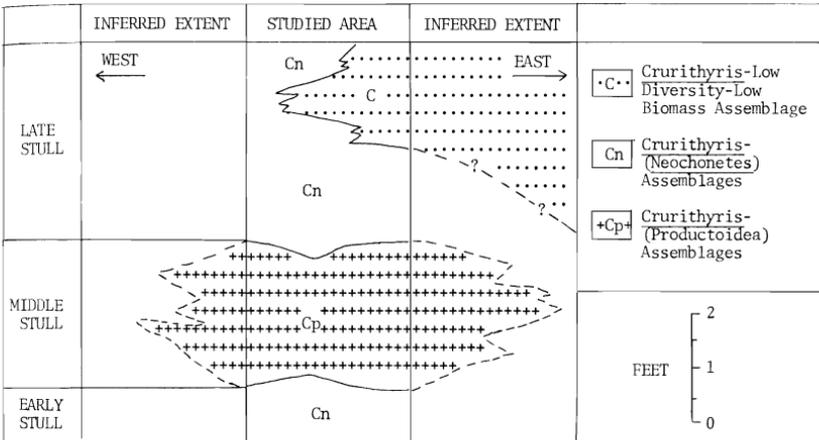


Figure 3: Paleoenvironmental-Diversity Correlation for the Stull Shale

For paleoenvironmental correlation, lime content and color value of the rocks were estimated from hand specimen examination of the structure of the rock samples (Jacobs, 1973, p. 28); color value of dry rock samples was estimated using a standard Munsell Soil Color Chart (1954).

## BIOFACIES SUCCESSION

The time divisions (early, middle, and late) of the Stull have been arbitrarily assigned from lithofacies and biofacies data (Jacobs, 1973).

The Stull fauna, which is dominated by brachiopods, is largely represented by the double recurrence of the *Crurithyris*-(*Neochonetes*) Assemblages yielding moderate diversities. These assemblages are interrupted first during the Middle Stull by the *Crurithyris*-(*Productoidea*) Assemblages revealing high diversities and again during Late Stull by the *Crurithyris*-Low Diversity-Low Biomass Assemblage (Fig. 4).

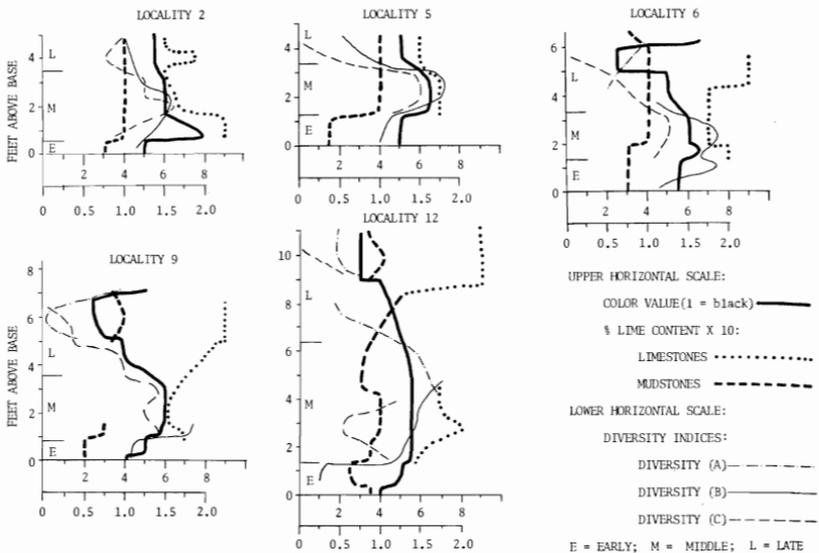


Figure 4: Biofacies Succession of the Stull Shale (Generalized from Plate 3 of Jacobs, 1973)

## PALEOECOLOGY

Upon consideration of the three paleoecologic indicators (diversity index, lime content, and color value) from Figure 3, the following paleoenvironmental inferences have been made:

Moderate diversity values characterize Early Stull time as represented by the *Crurithyris*-(*Neochonetes*) Assemblages. This diversity is consistent with the dominance of abundant, relatively small and light-weight shell forms in lime-poor, gray mudstones. The presence of small nuculoid bivalves in this environment is not surprising, since "modern nuculoid clams depend largely on deposit feeding for food gathering and live predominantly in muddy sediments" (Raup and Stanley, 1971, p. 202). By contrast, the absence of

large infaunal bivalves and scarcity of large brachiopods in this inferred "soupy" environment is probably due to their heavy bulk which would have caused them to sink into the soft mud, thereby making their feeding and respiratory mechanisms unable to function properly (Raup and Stanley, 1971, p. 204).

Middle Stull time is characterized by high diversity values for the *Crurithyris*-(Productoidea) Assemblages signifying optimum biotic conditions in light gray calcareous mudstone intercalated with argillaceous limestone lenses (Fig. 2). Consistent with this lithologic environment and high diversity is the sudden prominence of relatively large, heavy shelled brachiopods, such as *Derbyia*, *Composita*, *Neospirifer*, and particularly the so-called "quasi-faunal" productoids (Rudwick, 1970) such as *Juresania*; large infaunal bivalves include *Wilkingia* and *Edmontia*(?). This larger shell size is consistent with the argument that these forms prevailed in limy substrates hard enough to support their weight (Raup and Stanley, 1971, p. 204).

Moderate index values, however, return during early Late Stull with the recurrence of the *Crurithyris*-(*Neochonetes*) Assemblages and the corresponding predominance of light-weight shell forms in gray rocks, considerably less limy than those of the Middle Stull. These assemblages and corresponding environment reoccur a second time during latest Late Stull (Fig. 4).

These assemblages are, however, interrupted during middle Late Stull by the *Crurithyris*-Low Diversity-Low Biomass Assemblage. The low diversity, low biomass, and virtual absence of benthic organisms is consistent with the black color of the enclosing rock matrix; also present are iron sulfide nodules, the stable chemical compound commonly associated with black sediments under low Eh and low  $pS^{-2}$  (Berner, 1970; 1971); these joint occurrences strongly suggest stagnant bottom conditions, a reducing environment (Emery, 1960, p. 183), during this time. The presence of the suspension feeding brachiopod *Crurithyris*, however, in black rocks suggests an anomaly: Rudwick (1970) has proposed that brachiopods occurring in "black shale facies" of the Paleozoic avoided unfavorable conditions in the sediment by becoming "pseudo-planktonic, being attached to floating seaweed or other organic materials . . ." (Rudwick, 1970, p. 160).

## CONCLUSIONS

The Shannon-Wiener information function has been demonstrated as a workable paleoecologic tool for macrofauna of non-transported assemblages in rocks as old as the Pennsylvanian, despite the hindrance of significant shell fragmentation and disarticulation. The information function has clearly revealed distinct diversity horizons: maximum values for the fauna during Middle Stull and minimum values during Late Stull.

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