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I am submitting herewith a thesis written by William C. Parker entitled "Paleoecological Significance of Population Structures and Dynamics of Selected Middle Ordovician Brachiopods." I recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Geology.

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A

PALEOECOLOGICAL SIGNIFICANCE OF POPULATION STRUCTURES AND DYNAMICS OF SELECTED MIDDLE ORDOVICIAN BRACHIOPODS

A Thesis

Presented for the

Master of Science

Degree

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ABSTRACT

The population structures and dynamics of four species of Middle Ordovician brachiopods have been studied to derive paleoecological implications. The populations used were collected from the Chickamauga rocks of Raccoon Valley and adjacent areas in Knox and Anderson counties, Tennessee. The species studied are Dinorthis holdeni, D. transversa, Sowerbyella compacta, and Rostricellula rostrata, with population sizes ranging from 458 to 191 individuals.

The populations were collected from weathered residuum and the measurements of the individuals were analyzed in terms of length X width plots, size-frequency histograms, and derived growth and survivorship/mortality rates, in the manner of Surlyk (1972) and Richards and Bambach (in press, 1975). Bulk samples and thin-sections of the associated lithologies were studied to ascertain the depositional environments. All four populations came from highly argillaceous biomicrites deposited in quiet, muddy environments.

The analysis of the size-frequency data by the methods of Sheldon (1965), Levinton and Bambach (1970), and the histogram peak method (described herein) permitted evaluation of these methods. The latter method is preferred here because of the close agreement of its results with those of the other methods, fewer a priori assumptions, and results scaled in absolute units (years).

The results can be summarized as follows: The D. holdeni and R. rostrata populations have strongly curved growth curves

while the D. transversa and S. compacta populations have more linear ones. The D. transversa and S. compacta populations show relatively low juvenile mortality, the R. rostrata population shows extremely high juvenile mortality, and the D. holdeni population shows intermediate juvenile mortality.

The analysis revealed that some aspects of population structures and dynamics, such as growth curve shape, are correlated with life habits and shell morphology. Small, pedunculate forms have strongly curved growth curves. Unattached, "floating" forms have more linear growth curves. Similar species of the same genus have growth curves differing only in older age classes.

Survivorship/mortality rates appear to reflect population response to the environment. The same species in different environments has different mortality rates. Two different species in the same environment have different mortality rates. Similar species in similar environments may have similar mortality rates or drastically different mortality rates.

Small, pedunculate forms in "muddy" environments have high mortality at lengths less than two mm due to burial and/or lophophore clogging. Species with low juvenile mortality experience increased mortality in older age classes due to the onset of reproduction or geriatric effects.

A possible correlation between high phenotypic variability, linearity of growth rate, low juvenile mortality, adaptation to physically stressed ("muddy") environments, and low species diversity communities is suggested.

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CHAPTER I

INTRODUCTION

Purpose

> And if you were to say that these shells were created, and were continually being created in such places by the nature of the spot, . . . such an opinion cannot exist in a brain of much reason, because here are the years of their growth, numbered on their shells, and there are large and small ones to be seen which could not have grown without food, and could not have fed without motion--and here they could not move.
>
> Leonardo da Vinci, 1883

Since approximately the middle of this century, earth scientists have given increasing consideration to fossils as organisms, rather than mere rock components. As a result paleontology, especially paleoecology, has flowered and borrowing many established biologic approaches has found new applications for them in the study of the fossil record. The study of population dynamics is one such approach. By 1935 (Pearl and Miner) the dynamics of bird, fish, Drosophila, and even automobile populations had been described; however, comparable studies of fossil populations have only recently begun.

It now appears that the implications of population studies extend far beyond the recognition of taxonomic parameters, the initial application of the methodology to fossil assemblages. Just as the paradigm approach to functional morphologic analysis of fossils by Rudwick (1964), among others, has provided a tool by which morphologic responses of extinct organisms to environmental

processes might be examined, population dynamics studies have revealed shorter-term environmental responses in the form of reproductive, growth, and mortality rates.

The main purpose of this study is to apply the methods of population dynamics to selected fossil brachiopod populations from the Middle Ordovician rocks of east Tennessee. The compiled data will be used to determine the paleoecologic responses, and a consideration of the probable cause and effect relationships will follow. It is hoped that this study of population dynamics and other implications derived from the data will lead to a better understanding of the total fauna and associated rocks.

Previous Investigations

In the past, size-frequency distribution studies of fossil organisms have reflected, most commonly, a predominant sedimentologic rather than paleontologic interest on the part of the author. Boucot (1953) and Fagerstrom (1964) suggested that "life assemblages" (in situ populations) should possess right-skewed size-frequency distributions with abundant small individuals, caused by presumed high infant mortality. Conversely, normally skewed and left-skewed distributions were assumed to be indicative of transported assemblages. Fagerstrom (1964) also assumed that right-skewed distributions with an absence of small individuals were indicative of "residual assemblages," from which the smaller individuals had been selectively "winnowed." However, independent criteria for determining the degree of disturbance of fossil assemblages have been proposed by Johnson (1960); and

Walker and Bambach (1971) have expressed the conviction that most fossil assemblages in fine grained sediments suffer little transportation. Furthermore, studies of recent *in situ* brachiopod and bivalve populations by Percival (1944), Rudwick (1962), Craig and Hallam (1963), Paine (1963, 1969), and others, summarized by Thayer (1975), have shown variously skewed and uni- to multimodal distributions.

Raup and Stanley (1971), Tasch (1973), and Valentine (1973) provide introductory treatments of fossil population analysis. Detailed analyses of those factors which may influence population structures are given by Kurten (1954), Olson (1957), and Craig and Oertel (1966). Surlyk (1972) and Richards and Bambach (in press, 1975) have presented excellent paleoecologic studies of the population structures and dynamics of various fossil brachiopods.

The systematics and distribution of fossil brachiopods found in Middle Ordovician rocks in east Tennessee and stratiagraphically equivalent strata elsewhere have been compiled by Cooper (1956). The more recent brachiopod volumes of the Treatise on Invertebrate Paleontology (Williams, *et al.*, 1965) contains a few revisions of Cooper's taxonomy. The Treatise volumes and Rudwick (1970) summarize recent advances in knowledge of the biology and geologic history of the brachiopods.

Geographic And Stratigraphic Setting

Fossils used in this study were collected in Raccoon Valley in northwestern Knox County and southeastern Anderson County,

Tennessee, approximately twelve miles northwest of Knoxville (Figure 1). The valley extends across the north central portion of the Powell (Station) quadrangle (T.V.A. 137-SE) with outcropping Middle Ordovician formations striking approximately N40°E, paralleling the topographic expression of the valley. Flint Ridge, underlain by the Lower Ordovician Knox (Mascot) Dolomite, and Bull Run Ridge (Haw Ridge), capped by the overthrust Lower Cambrian Rome Formation, flank the valley on the northwest and southeast, respectively (see Figure 2).

In the easternmost belts northwest of the Saltville fault, Rodgers (1953) mapped the Middle Ordovician rocks above the Knox Dolomite in ascending order either as Chickamauga Limestone, unit one; Chickamauga Limestone, unit two; and Moccasin Formation; or as lower and middle parts of the Chickamauga Limestone, undifferentiated. The latter was the case in the section of Raccoon Valley included on the Briceville Folio (Rodgers, 1953, plate 1). Although Rodgers' units were established principally on lithologic grounds with little paleontologic reference, there appears to be little question that the Raccoon Valley rocks, from which the collections were made, are faunally related to rocks mapped elsewhere along strike as Chickamauga units one and two and Moccasin.

G. A. Cooper (1956), in his comprehensive study of Middle Ordovician brachiopod faunas, employed stratigraphic terms either previously defined by B. N. Cooper and Prouty (1943) and B. N. Cooper (1945), or introduced by himself (with B. N. Cooper) in that publication. In sequential order (above the Knox Dolomite and below the Moccasin Formation) Raccoon Valley brachiopod assemblages were

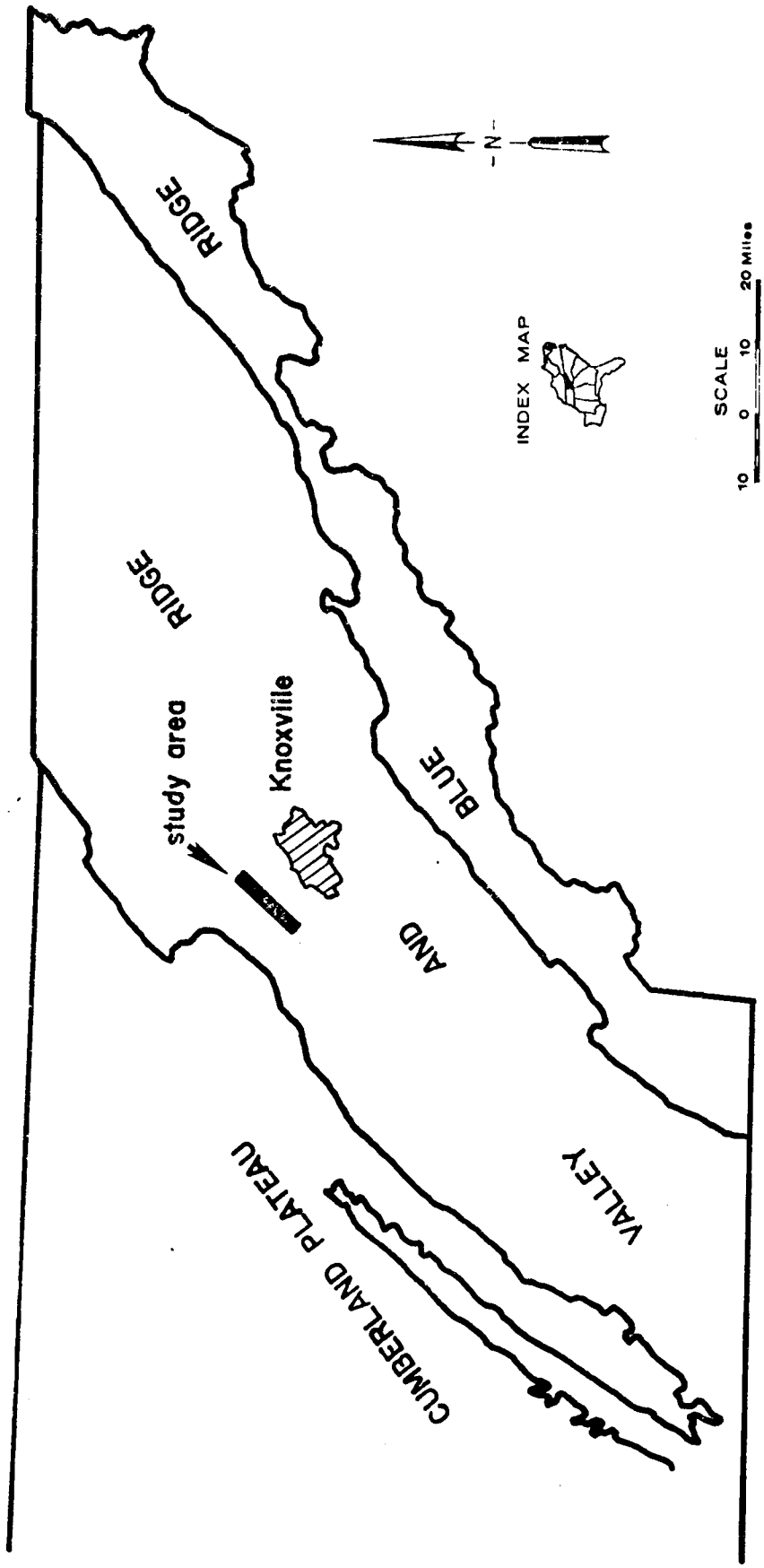
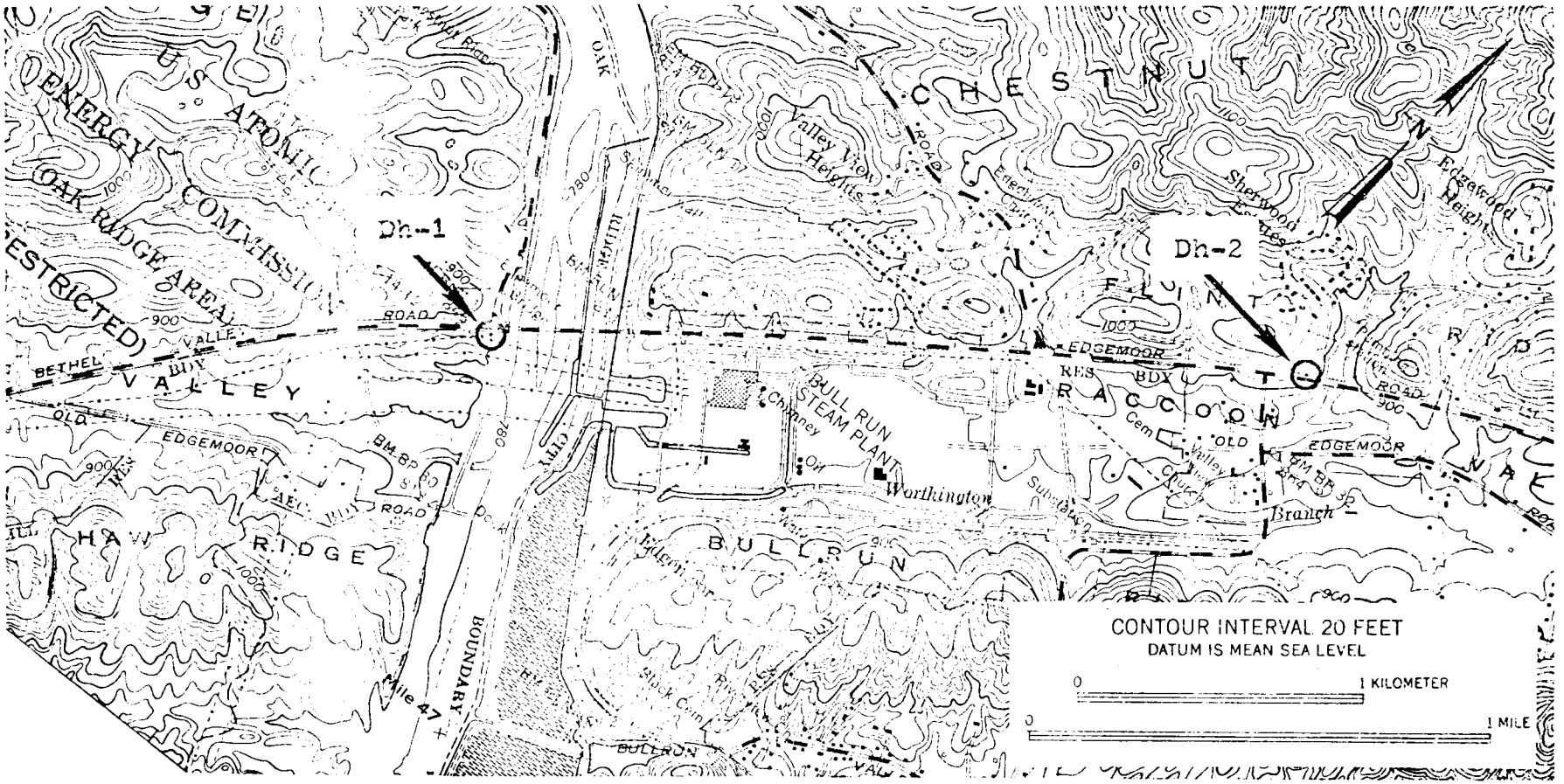


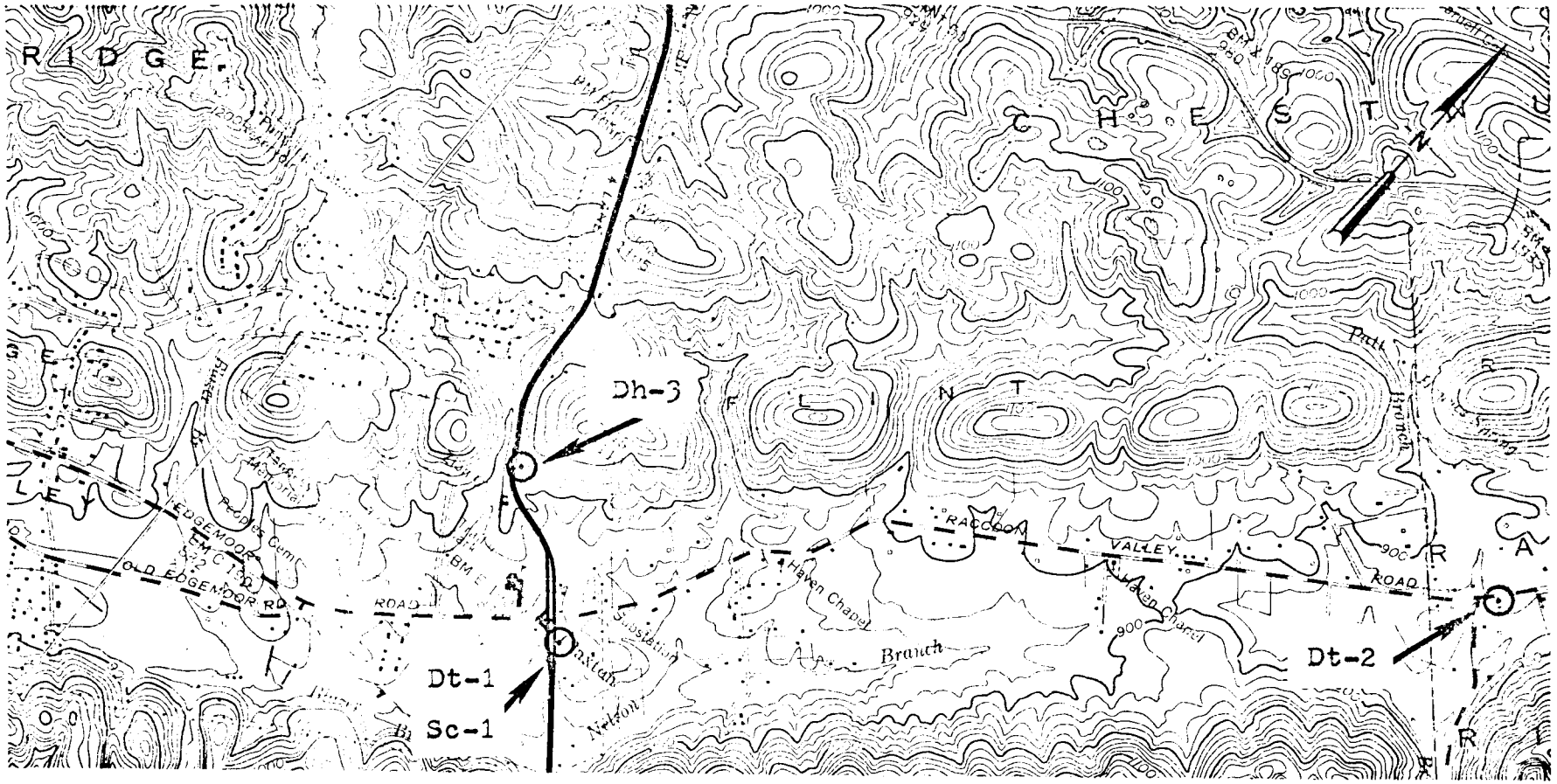
Figure 1. Location of Study Area (East Tennessee).

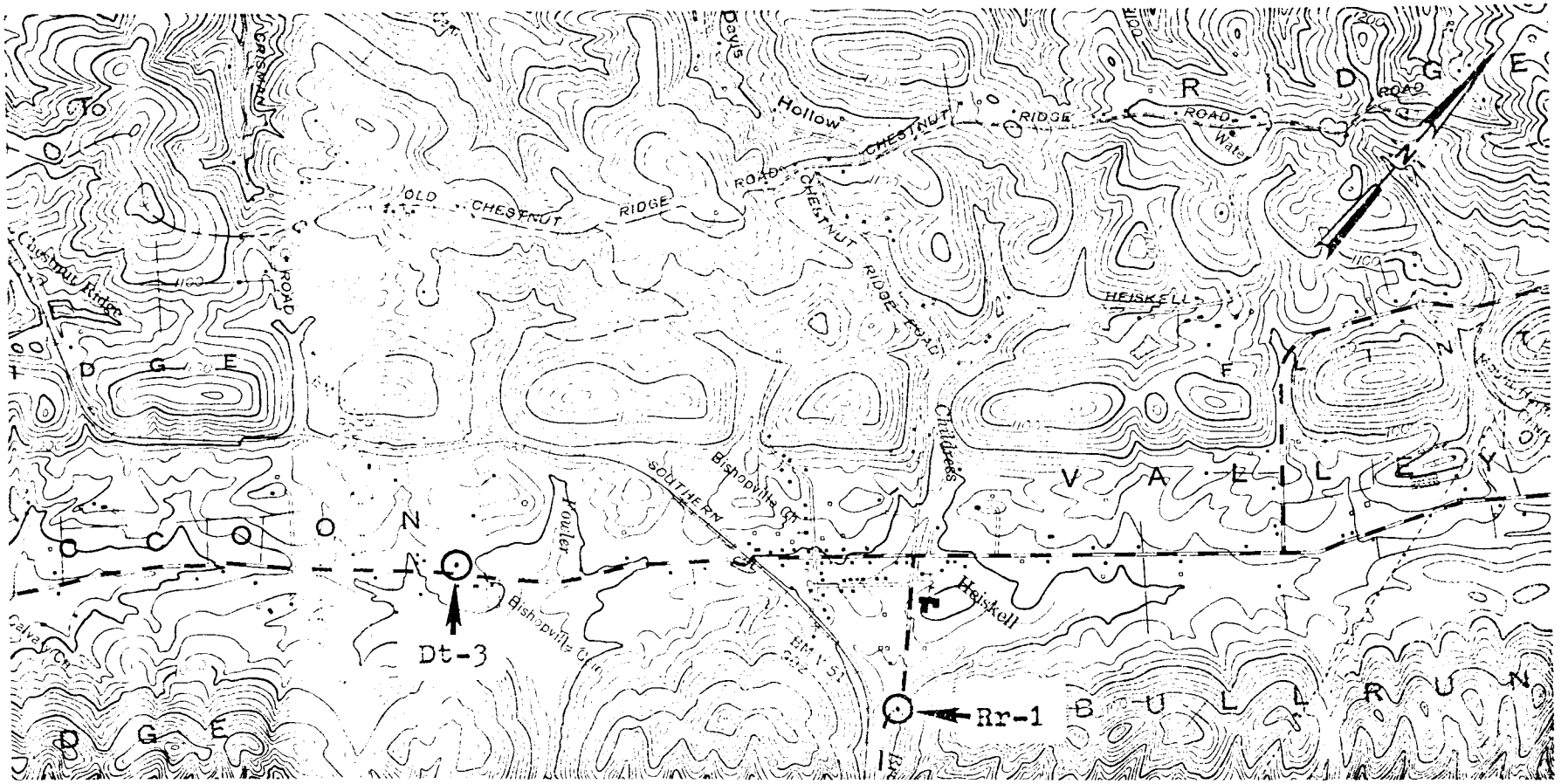


(A) south section

Figure 2. Collection Localities in a Portion of Raccoon Valley, Knox and Anderson Counties, Tennessee.

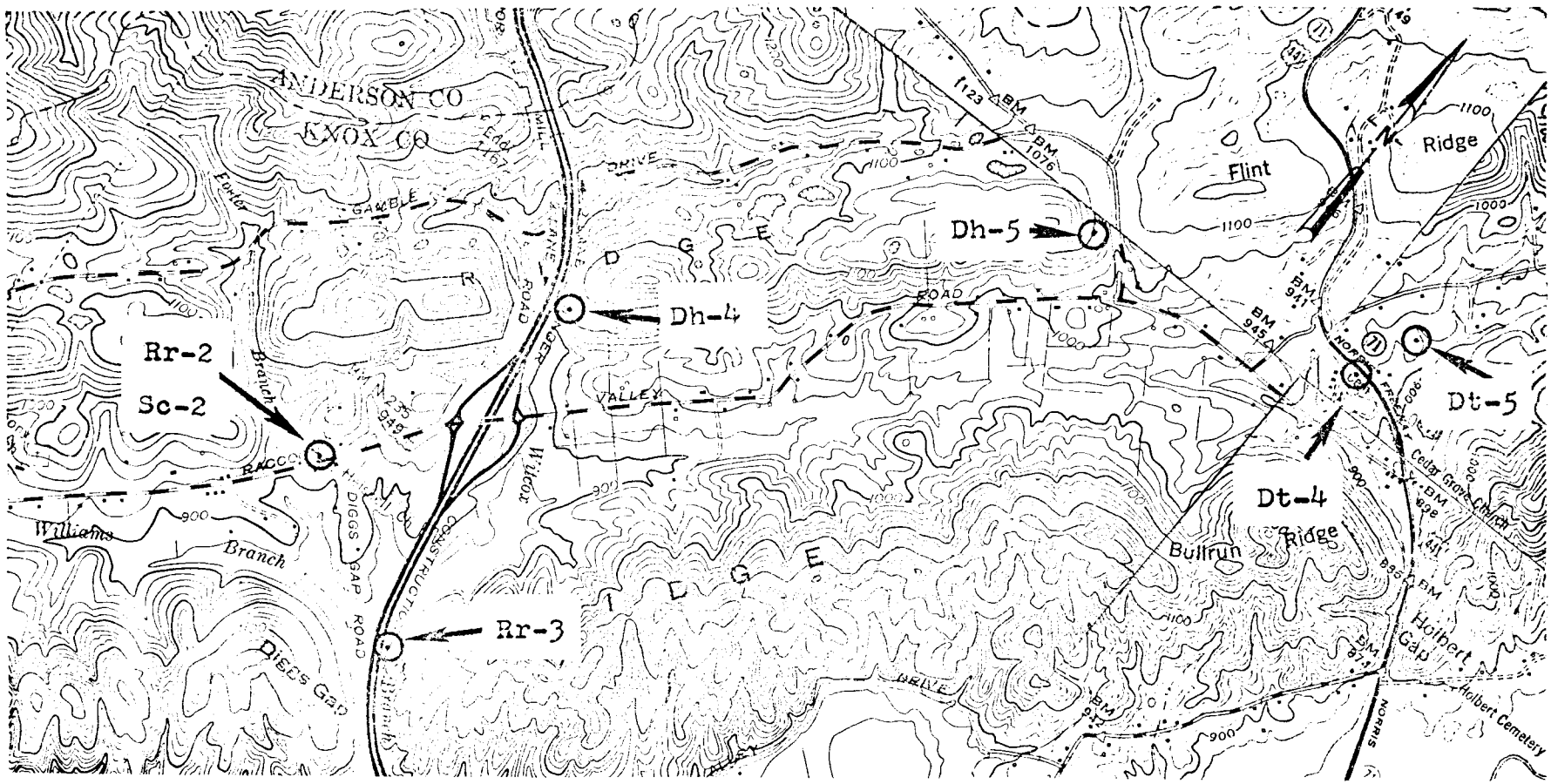
(⊙) fossil locality; (Dh) Dinorthis holdeni; (Dt) Dinorthis transversa; (Sc) Sowerbyella compacta; (Rr) Rostricellula rostrata. Topography from Big Ridge Park, Fountain City, Norris, Clinton, and Powell TVA Quadrangles.


RIDGE
CHESTNUT
Dh-3
Dt-1
Sc-1
Dt-2
OLD EDGEMOOR RD
EDGEMOOR
ROAD
RACCOON
VALLEY
ROAD
Haven Chapel
Branch
Path
Nelson
Branch
Haven Chapel
Branch
Path
Path
Path



(C) north central section

Figure 2. (continued)



(D) north section

Figure 2. (continued)

described from units named (in ascending order): Elway; Fleanor; Lincolnshire (Hogskin member); Ward Cove; Benbolt; Wardell; and Witten Formations. Cooper (1956) further regarded the brachiopod faunas of these formations as representative of the Marmor (Elway), Ashby (Fleanor, Lincolnshire), Porterfield (Ward Cove, Benbolt), and Wilderness (Wardell, Witten) stages of the standard section (see Figure 3).

Fields (1960) and, more recently, McLaughlin (1973a) have attempted to relate the stratigraphic succession in Raccoon Valley to a sequence of "biostratigraphic zones," combining lithologic and paleontologic features of the rocks. McLaughlin (1973a, p. 55) lists the chief faunal elements characterizing four "zones" beginning at the disconformable basal contact with the Knox Dolomite along the northwest side of the valley and terminating with the Copper Creek Fault contact with the Rome Formation in Bull Run Ridge on the southeast. Approximately 1700 to 2000 feet (560-660 m) of Middle Ordovician strata are exposed in this section.

The uppermost 300 feet (100 m) of the Raccoon Valley section exposed along Interstate 75 in the Diggs Gap cut through Bull Run Ridge has been described in detail by Milici and Walker (1973). Based on lithologic and paleontologic features of the rocks, these authors have proposed a model for the depositional environments represented. McLaughlin (1973a, b) has described recognizable paleoecologic associations of faunal elements in other "zones" in Raccoon Valley and has drawn attention to the provincial character of this and related faunas found northwest of the Saltville Fault.

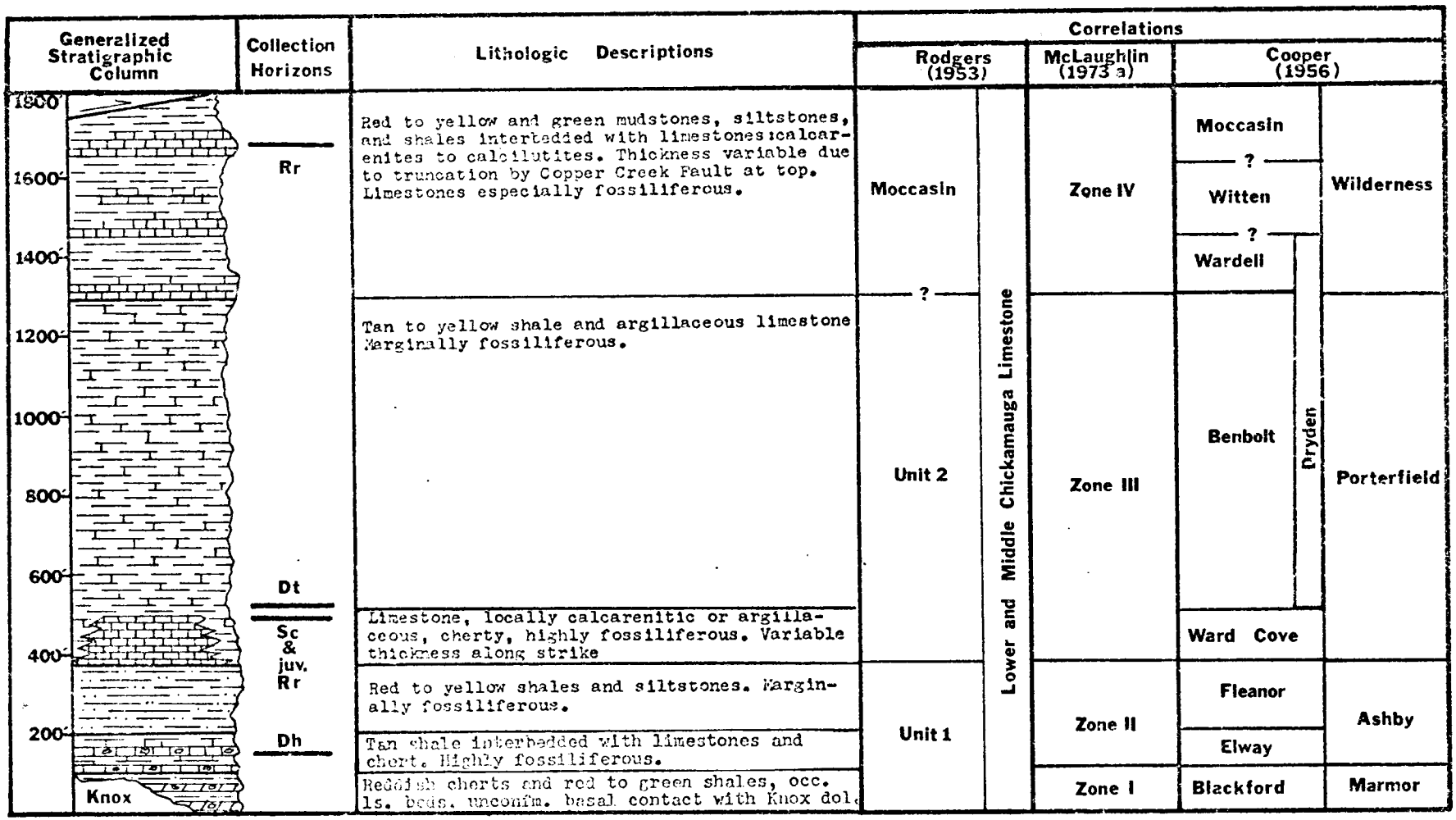


Figure 3. Generalized Stratigraphic Column, Stratigraphic Description, Location of Collection Horizons, and Stratigraphic Correlations.

(Dh) Dinorthis holdeni, (Dt) Dinorthis transversa, (Sc) Sowerbyella compacta, (Rr) Rostricellula rostrata, (juv. Rr) "Juvenile" Rostricellula rostrata.

The brachiopod species examined in the present study are confined to certain biostratigraphic units, as shown in Figure 3. The location of the collection sites used are shown in Figure 2, pages 6-9, placed stratigraphically in Figure 3, and illustrated by photographs in Plates I-III, Appendix. The locations of the collection sites are described in detail in Table 2, Appendix.

Species Descriptions

The four species considered in this thesis were described by Cooper (1956). The following section contains brief summaries of Cooper's descriptions as well as systematic revisions given in the brachiopod volume of the Treatise on Invertebrate Paleontology (Williams, et al., 1965). The faunas associated with these species in the collection horizons are given in Table 1.

Dinorthis holdeni (Willard, 1926, but recently reassigned to the genus Plaesiomys, Hall and Clarke, 1892, by Williams, et al., in the Treatise), illustrated in Plate IV, Figure 38, Appendix, is a relatively small (holotype 14.1 mm long; 18.9 mm wide; 5.7 mm thick), highly variable, convexi-concave orthid brachiopod, with the greatest width at about the middle. The lateral margins of the shell are gently rounded while the anterior margin is truncated, uniplicate to nearly straight. The surface is marked by 30 to 33 costae separated by spaces equal to their width.

In lateral profile, the pedicle valve is convex toward the posterior margin and gently concave toward the anterior margin. The brachial valve is unevenly convex with the maximum convexity

TABLE 1

ASSOCIATED FAUNA

Study Species	Degree of Association*	Associated Fauna
Dinorthis holdeni	Intimate	Brachiopods; *Rhipidomena subparallela*, *Mimella globosa*; bryozoans: 3 species trepostomes, one of which resembles *Prasopora* and forms globular colonies covering fossil debris; gastropods: 1 species; pelmatozoans: 1 species; trilobites: 3 species; burrowers.
	Extended	Same.
Dinorthis transversa	Intimate	Brachiopods: "juvenile" *Rostricellula rostrata*?; bryozoans: prasoporan; echinoderms: edrioasteroid?; burrowers.
	Extended	Same as intimate fauna plus the following material in the "channels" - bryozoa: *Stictopora*?; trilobites: 1 species; pelmatozoans: 1 species.

*"Intimate" refers to being in the same bed as the study species, "Extended" refers to being within one foot (0.3 m) stratigraphically above or below.

TABLE 1 (continued)

Study Species	Degree of Association*	Associated Fauna
Sowerbyella compacta and *Rostricellula rostrata* ("juvenile")	Intimate	Brachiopods: "juvenile" orthids and strophomenids; ostracodes: 1 species.
	Extended	Intimate fauna plus - brachiopods: *Multicostella semisulcata*, *Mimella globosa*, *Rhipidomena tennesseensis*, *Macrocoelia magna*; bryozoans: 2 species of trepostomes; pelecypods: 1 species; trilobites: 1 species; cephalopods: *Gonioceras* and *Michelinoceras*?; pelmatozoans: 1 species; *Nidulites*.
Rostricellula rostrata ("normal")	Intimate	Brachiopods: *Strophomena basilica*; bryozoans: 2 species trepostomes and *Stictopora* sp.; gastropods: 2 species, one macluritid; trilobites: 2 species; ostracodes: 2 species; cephalopods: *Michelinoceras*?.
	Extended	Same.

*"Intimate" refers to being in the same bed as the study species, "Extended" refers to being within 1 foot (0.3 m) stratigraphically above or below.

just posterior to the middle. D. holdeni is smaller and less robust than average for the genus. It has been identified from the Elway Formation of Tennessee and Virginia and the Whistle Creek Formation of Virginia. In the terminology of Rodgers (1953), the Elway Formation is included in the basal Chickamauga (unit 1) as mapped in the western belts of the Valley and Ridge of Tennessee.

Dinorthis transversa (Willard, 1942, but recently reassigned to the genus Plaesiomys, Hall and Clarke, 1892, by Williams and Wright in the Treatise), illustrated in Plate IV, Figure 39, Appendix, is a medium sized (holotype 20.6 mm long; 30.0 mm wide 7.6 mm thick), convexi-concave orthid brachiopod, with a subrectangular outline, the maximum width occurring at about the middle of the shell. The lateral margins are broadly rounded while the anterior margin is nearly straight and broadly uniplicate. The surface is multicostate with two or three generations of costae, the first bifurcation often occurring near the middle of the shell.

In lateral profile, the pedicle valve is strongly convex in the umbonal region while the anterior portion is moderately to strongly concave. The brachial valve is moderately convex with the greatest convexity at about the middle. D. transversa has been identified from the Benbolt (Chickamauga, unit 2 of Rodgers, 1953) and Sevier Formations of Tennessee, the Benbolt and Edinburg Formations of Virginia, and the Shippenburg Formation of Maryland and Pennsylvania.

In general, Dinorthis transversa is larger, more robust (especially noticeable in the larger lateral profile), and more variable in morphology than D. holdeni.

Sowerbyella compacta (Cooper, 1956), illustrated in Plate IV, Figure 40, Appendix, is a medium sized (holotype 6.9 mm long; 10.2 mm wide; 1.4 mm thick), highly variable, concavo-convex strophomenid brachiopod. The cardinal extremities are slightly acute or approximately rectangular and often auriculate. The lateral margins are indented immediately anterior to the cardinal extremities, extending nearly straight to the broadly curved anterior margin. The surface is equally costellate with approximately six or seven costellae within one millimeter, near the front margin of an adult.

In lateral profile, the pedicle valve is moderately convex, with the greatest convexity at about the middle of the shell. The brachial valve is moderately concave with the most concave portion between the umbo and the middle of the shell. S. compacta has been identified from the Benbolt Formation of Virginia and in the Dryden Formation of Tennessee (Chickamauga, unit 2 of Rodgers, 1953).

Rostricellula rostrata (Ulrich and Cooper, 1942), illustrated in Plate IV, Figure 41, Appendix, is a medium sized (holotype 14.3 mm long; 14.4 mm wide; 8.6 mm thick), triangular to subpentagonal rhynchonellid brachiopod, with the greatest width at or slightly anterior to the middle of the shell. The shell is biconvex with the brachial valve being slightly deeper than the pedicle and the beak forming approximately a right angle. Half of the anterior edge of the shell is taken up by the sulcus, which originates approximately

six millimeters anterior of the beak. The surface of the shell is costate, three to five costae occupying the sulcus. Fine radial and concentric lines cover the entire surface and produce granules where they intersect. R. rostrata has been identified from the Wardell, Dryden, Ridley, and the Pierce Formations of Tennessee and in the Wardell of Virginia.

Rostricellula rostrata apparently undergoes a great deal of morphologic change during ontogeny, based on observations compiled during the course of the present study. The sequence, as seen by this author (Plate IV, Figure 42, Appendix), begins soon after settling with the development of a 0.6 mm long, smooth, flat, oval shell, with a pedicle opening almost between the two valves. With continued growth the shell becomes biconvex and at approximately 2 mm in length, the ribs, fold and sulcus begin to appear. By this time, the pedicle opening is well restricted to the pedicle valve and the commissure has begun to develop zig-zag deflection. The atypical, almost terebratulid, shell of the early juveniles could conceivably cause taxonomic difficulties if no adult forms were available for identification.

CHAPTER II

METHODS OF ANALYSIS

Introduction

In this study, two general mathematical/graphical methods of analysis are applied to the measurement data obtained from the fossil populations. These two methods, bivariate analysis and size-frequency analysis, are outlined in this chapter, in the hope that a general discussion of the influencing factors and problems in applying the methods will aid in understanding the actual application which follows.

Bivariate Analysis

Bivariate analysis consists of comparing one parameter of size (length, width, thickness, etc.) to another, by means of a graphical display (Figure 4). Such a display can be affected by several factors. Selective destruction of certain features, such as compaction which primarily affects thickness or breakage of fragile hinge extensions, may influence the shape of the bivariate plot. Individual variation in growth will tend to spread the plot out, rather than giving a narrow line. Growth allometry will affect the trend of the distribution, giving a non-linear plot (Parkinson, 1951).

The presence of more than one species will be revealed by a badly spread distribution, possibly resolving itself into two

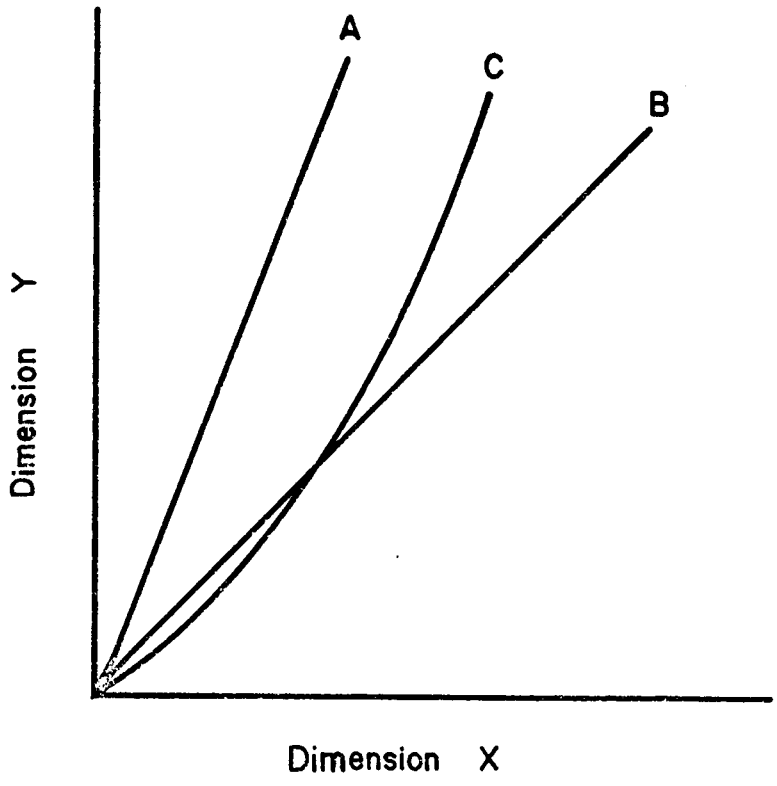


Figure 4. Example of Bivariate Analysis Comparing Dimension X to Dimension Y.

(A) linear plot with low X/Y ratio. (B) linear plot with high X/Y ratio. (C) non-linear plot with high initial X/Y ratio and low final X/Y ratio.

or more divergent distributions. Considerations of the resolution of the various plots (length X width, length X thickness, etc.) may reveal that one dimension is more representative of the size of the individual (Parkinson, 1951). If so, the more representative dimension should be selected for size-frequency considerations.

Size-Frequency Distributions

Size-frequency distributions, herein illustrated by non-cumulative size-frequency histograms, are influenced by such factors as preservation bias, collection bias, and the population dynamics of the species under study. These factors are discussed in detail below.

Preservation Bias

Preservation bias may result from selective destruction of shells during transportation, from selective sorting or "winnowing," or from selective destruction of shells in place, prior to or after burial. The presence of more easily broken or disarticulated shells within a certain size range may significantly affect the size-frequency distribution. Such a condition can be anticipated if the assemblage contains an abnormally high percentage of fragments and/or disarticulated valves from a particular part of the distribution range. Post-burial bias may be caused by the selective dissolution of smaller individuals. This process may be expected, however, to be equally effective in altering the fine detail of large as well as small individuals and whole fossils along with fragments, regardless of species.

Collection Bias

Ideally, blocks of unaltered rock should be brought to the laboratory for controlled break down and complete removal of fossil material. Such a method is practical when working with chalks and calcareous shales (Surlyk, 1972; Richards and Bambach, in press), but is not easily applicable to denser limestones. However, the warning of Fagerstrom (1964) against casual field collection is well taken, as personal experience in conducting the present study has shown. As a result, the data presented here are based on what is believed to be a reliable compromise. Collections consisted of bulk samples of weathered residuum, which lay in close proximity to the strata under study. The sample was washed and sieved in the laboratory, and all size fractions were searched for fossil material. In all but one case high fossil density made such collection possible. In the single case, the representativeness of the collection was established by other considerations, as will be discussed later.

Population Dynamics

As suggested by Craig and Oertel (1966), size-frequency distributions are influenced by such factors as recruitment, growth rate and its variation, and mortality rate. These factors combine to produce a variety of size-frequency distributions. However, as Richards and Bambach (in press) point out, if the effects of two of the factors can be isolated, the third can be deduced. A discussion of these factors follows.

Craig and Oertel (1966) divide recruitment into five major types: tropical, constant, boreal, short burst and arctic (Figure 5). Although various paleogeographic reconstructions (Spjeldnaes, 1961; Williams, 1973; among others) have placed eastern Tennessee within 20° of the Ordovician equator, one cannot, on this basis, assume tropical recruitment without reservation. Based on the study of reproductive periodicity in modern abyssal invertebrates, Schoener (1968) has shown that recruitment of marine organisms is not necessarily controlled by the environment. Other factors related to the internal biology of the organisms, such as internal "clocks" or biochemical signals, may induce periodicity.

The determination of the growth rate of a fossilized organism requires some method of relating size of the organism to its age. Levinton and Bambach (1970) have provided a formula which they demonstrate can be used to approximate the growth of five modern pelecypods selected at random from the data presented by Hallam (1967). The formula is $D = s \ln (T + 1)$, where D is some measurement of size reflective of growth (usually length), T is age of the organism as a percentage of the maximum age obtainable, s is a constant and ln indicates the log to the base e. The growth rate model represented by this formula shows high juvenile growth followed by a logarithmic decrease in growth rate toward maximum age (and size). Hallam (1972), while cautioning that the details of growth are probably more complex than implied by the Levinton-Bambach model, has supported the formula as useful.

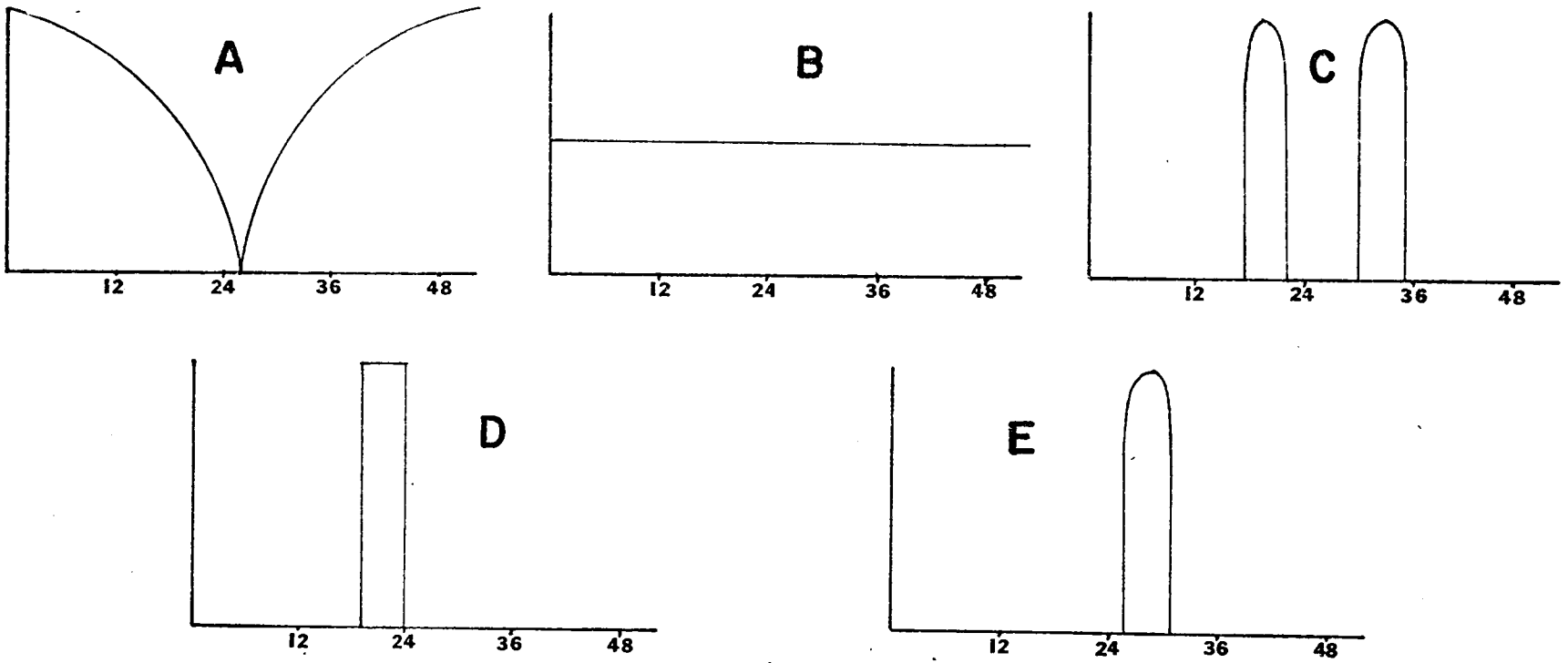


Figure 5. Diagrams Illustrating Types of Marine Recruitment.

(A) tropical, (B) constant, (C) boreal, the distance between the peaks being inversely proportional to the latitude, (D) single burst, (E) high arctic. The ordinate represents the relative number of individuals recruited and the abscissa represents the week number in a representative year. After Craig and Oertel (1966).

Paine, working with the recent brachiopods Glottidia pyramidata (1963) and Terebratalia transversa (1969), also found decreasing growth rates. Intuitively, however, it is obvious to the present author that organisms do not always adhere to mathematical formulae. By accepting the Levinton-Bambach model without qualification or reservation, important features of the data may be overlooked.

Sheldon (1965) presents an alternative to the Levinton-Bambach method when the size-frequency distribution is multimodal. Sheldon reasons that the multimodality is due to regular annual fluctuations in one, or all three previously mentioned factors of population dynamics. Since growth rate is generally assumed to decrease with age, and variation in growth rate might be expected to cause constructive and destructive interference between later modal peaks, only the first two major peaks may be judged "real." With the above assumptions, the size at a given time (L_t) is plotted against the size a year later (L_{t+1}) (see Figure 6). At maximum size (L_∞), l_t is equal to L_{t+1}.

Given the size-frequency distribution (Figure 6, A), one first plots a point using the value of the first mode as the coordinate on the l_t axis and the value of the second mode as the coordinate on the L_{t+1} axis (Figure 6, B). A second point is plotted using the maximum size of 98% of the population as the value on both axes. These two points are connected with a straight line and the line is segmented by using each L_{t+1} value as a new L_t value. The growth model thus produced (Figure 6, C) is similar to the Levinton-Bambach model, but is more reflective of the data. Earlier, Walford (1946) discovered

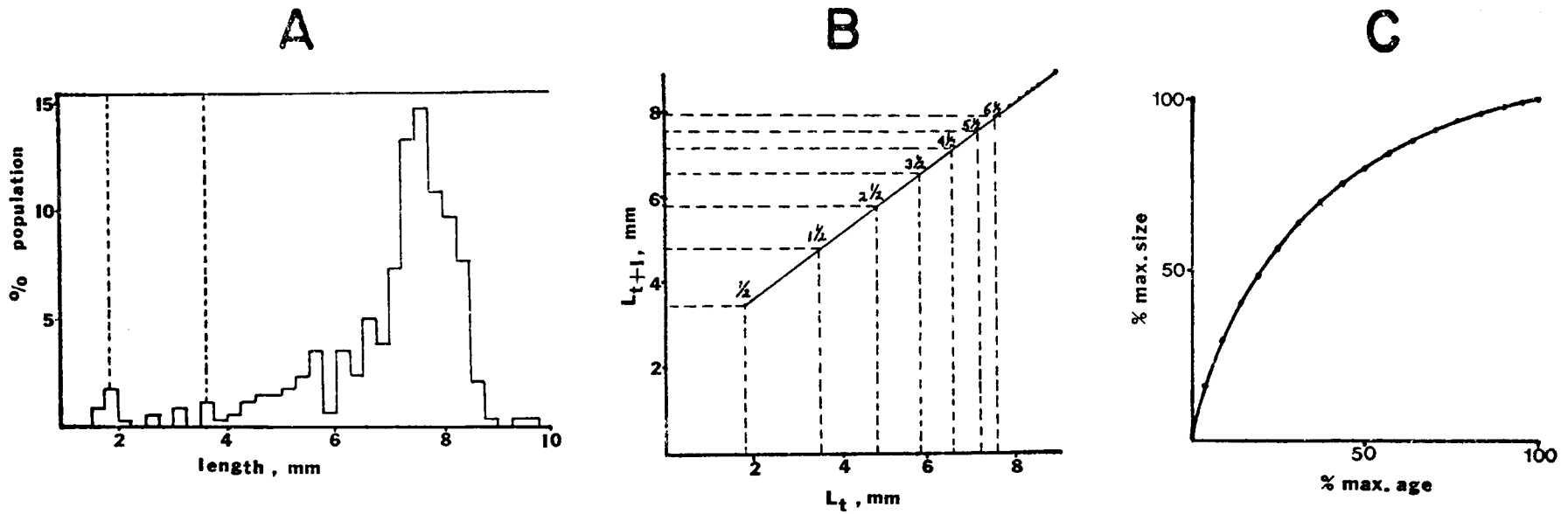


Figure 6. Method of Determining Growth Rate Used by Sheldon (1965).

(A) size-frequency histogram showing first two major modal peaks, (B) length at time t (L_t) plotted against length at time t plus one year (L_{t+1}) to determine yearly growth increments, (C) growth curve.

that a similar model approximates the growth curves of many shell fish species.

A second alternative to the Levinton-Bambach method when dealing with multimodal distributions is to consider all well defined size-frequency peaks to be "real" and to represent yearly growth (similar to the method used by Craig and Hallam, 1963). This procedure is called the histogram peak method in this study.

All three methods have advantages and disadvantages. The Levinton-Bambach (1970) method gives results scaled in relative age (percentage of maximum age), not years, and allows no comparison of growth rates between populations. The methods of both Levinton-Bambach (1970) and Sheldon (1965) require a priori assumptions about the nature of growth and ignore a large portion of the data available. The histogram peak method requires assumptions about the causes of polymodality. In order to compare the methods themselves, as well as aid comparison with the work of others, the growth rates of each species examined in the present study were computed using each of the three methods.

One method of growth rate determination pioneered by Craig and Hallam (1963) is growth line analysis. When a population is considered statistically and the lengths to major halts in growth form a multimodal distribution, it can be assumed that the interval between the modes represents the growth during the interval of time represented by the period of the causal factor. In Craig and Hallam's example the major growth halts are assumed to have been caused by winter storms; thus the interval represents the yearly growth rate.

Clark (1974) presented an excellent discussion of possible causal factors and their associated periods. He concluded (p. 77)

> . . . growth lines are not yet well enough understood to be interpreted with complete confidence. They are complex phenomena, and research on their environmental relationships is still in its infancy.

In the present study, growth line data, where available, were compared with the growth rates determined by other methods.

Deevey (1947) described three generalized mortality patterns among organisms: (1) increasing mortality, (2) constant mortality, and (3) decreasing mortality (Figure 7). It is apparent that invertebrates must experience high mortality early in life inasmuch as the thousands to millions of larvae characteristically produced each year by these organisms fail to survive to maturity; otherwise the oceans would be saturated with life. Thorson (1950) supported the contention of high larval mortality. But, what degree of this high mortality is contained within unfossilizable larval stages and thus outside the realm of fossil population studies is a major question.

It is suggested here that fossilizable mortality curves generally fall between models (1) and (2) of Figure 7, this portion of the curve representing the lower half of a sigmoidal curve (as indicated by the dashed curve in Figure 7). When survivorship curves depicting the percentage of individuals surviving per unit age are displayed in a semi-log plot, constant mortality is a straight line; the steeper the slope of the line, the higher the mortality. Since the survivorship curves are dependent upon the growth rates, three curves have been plotted for each species in the present study, each based on one growth model.

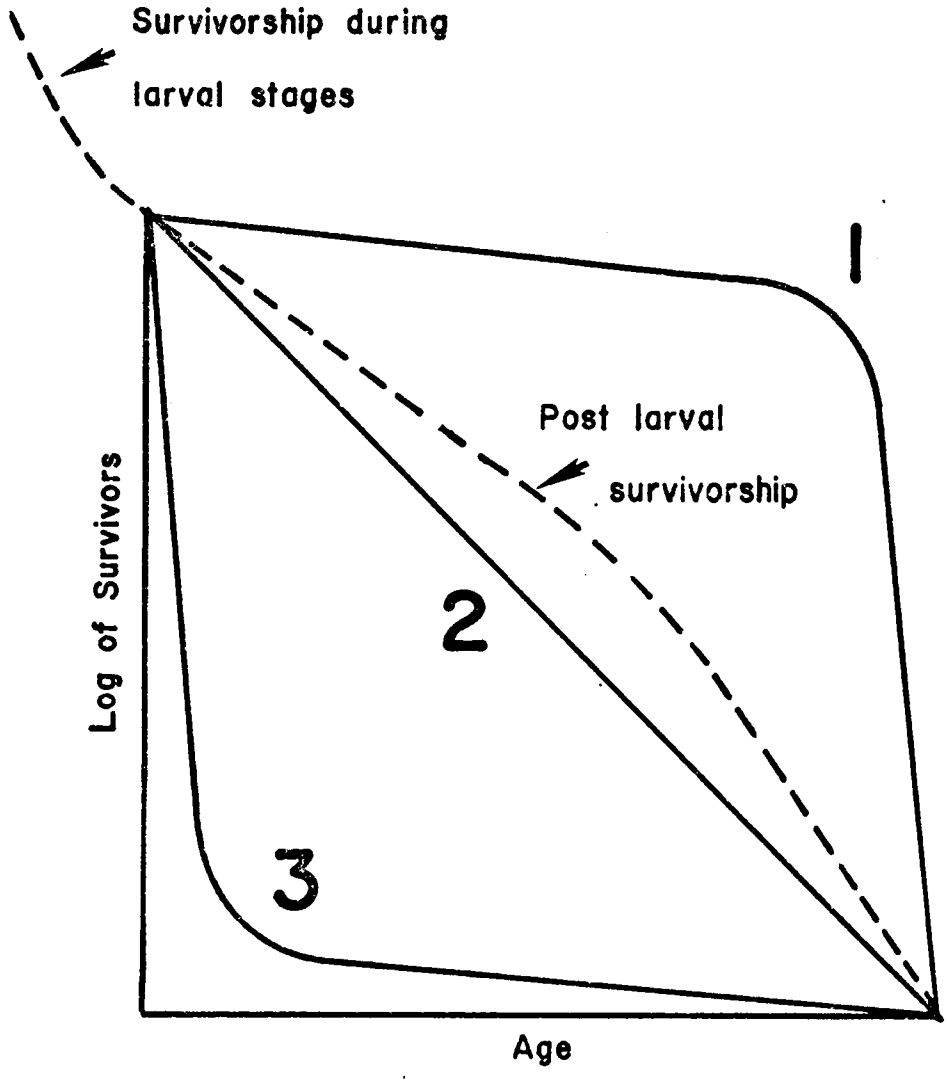


Figure 7. General Mortality Rates, After Deevey (1947).

(1) increasing mortality, (2) constant mortality, (3) decreasing mortality. The dashed line indicates a possible mortality curve.

CHAPTER III

PRESENTATION AND REDUCTION OF DATA

Introduction

Since population structures and dynamics can be affected by various non-biologic factors, it is important to consider the degree to which these factors have altered the data. Therefore, the first two sections of this chapter consider those aspects of the data and data retrieval which might affect the validity of the later analyses.

Environmental Descriptions

It is necessary to consider the environments represented by the fossil-bearing strata of this study, not only to estimate the amount of transportation and/or exposure which has affected the assemblage, but also to determine the types of environments in which the organisms lived. Johnson (1960) presented eleven criteria which can be used to approximate the affects of transportation and exposure on a fossil assemblage and thus determine how closely the thanatocoenose resembles the biocoenose. These factors are faunal composition, morphologic composition, density of fossils, size-frequency distribution of fossils, disassociation of hard parts, fragmentation of remains, surface condition of fossils, chemical and mineralogical composition of hard parts, orientation of fossils, dispersion of fossils, and texture and structure of the sedimentary aggregate. These criteria

were applied to the rocks containing the fossils under study both megascopically in the field and laboratory and microscopically by means of 2 in. x 3 in. (5 cm x 7.5 cm) thin-sections. Results of these studies indicate minimal effects on these particular fossils due to transportation or exposure. Only those criteria involving points pertinent to this discussion are considered in the following paragraphs.

Johnson (1960, p. 1081) stated that an undisturbed assemblage should show a size-frequency distribution approximating that of a living population. Because one purpose of this study is to investigate the factors influencing size-frequency distribution, to use the distribution to determine the degree of disturbance of the assemblage would involve circular reasoning.

The faunal compositions of the collection horizons are shown in Table 1 (p. 13). It should be pointed out that the species under study have a much higher specimen density within the collection horizons than do the elements of the associated fauna. This is considered to be a reflection of normal patchy distribution of organisms within a community. No faunal elements indicating distinctly different environments were found in conjunction with the brachiopods in the present study.

Detailed lithologic descriptions of the involved strata are given in Table 3, Appendix. One generalization possible is that most if not all of the lithologies were derived from very muddy sediments. This has posed a collection problem because such lithologies have tended to weather faster than the surrounding rocks, making it

difficult to obtain samples suitable for thin-sectioning. This is especially true of the Sowerbyella compacta and Rostricellula rostrata collection horizon. The author has been able to obtain thin-sections of the rock immediately above and below the horizon producing the most shells, but none from the horizon itself.

Both the Dinorthis holdeni and D. transversa strata were initially highly argillaceous biomicrites weathering to calcareous shales and containing moderately distinct burrows indicating that the sediment had a relatively low water content and was probably firm at the time of burrowing (Walker, 1974). Both the D. holdeni and D. transversa horizons exist in a body of strata of the same general lithology, probably representing rather extensive subtidal mudflats. Associated with the D. transversa horizon at localities Dt-1 and Dt-4 (see Figure 2, pp. 6-9) are lenses of coarse calcarenite composed of fossil debris, probably representing channels in the mudflat.

The Sowerbyella compacta and Rostricellula rostrata horizon appears to be a highly argillaceous biomicrite also with mud content comparable to the strata noted above. The horizon is bounded by rocks of considerably lower mud content which are interpreted as brachiopod-bryozoan biogenic mounds and channel fill. The rocks bearing the species under study are thought to represent restricted mudflats surrounding and in the midst of the mounds and channels.

Collection and Measurement Techniques

The sample populations of Dinorthis holdeni, Sowerbyella compacta, and Rostricellula rostrata were collected in the

following manner. Approximately 0.5 to 0.25 cubic meters of weathered residuum were collected from close proximity to the parent lithology. This residuum was taken to the laboratory for washing and wet seiving into three size fractions; smaller than 1.65 mm. (-0.75Ø), 1.65 mm. (-0.75Ø) to 5.66 mm. (-2.5Ø), and larger than 5.66 mm. (-2.5Ø). All fossil material was removed from each size fraction and carefully sorted into species.

As previously mentioned, the fossil density of the Dinorthis transversa horizon is too low to permit the above collection method. Therefore, the residuum at the D. transversa collection sites was carefully picked free of all fossil material, without the benefit of laboratory preparation. This method is obviously susceptible to collection bias; however, the author believes that the careful on site examination of the residuum gave a sufficiently reliable population for this study. The size distribution of the articulated shells seen in thin sections of the parent lithology is comparable to that of the population collected from the residuum. Also, shell fragments far smaller than the smallest articulated shell were retrieved from the residuum indicating that, had smaller articulated shells been present, they would have been seen.

Each articulated specimen of the species under study was numbered, measured, and its condition noted. Measurements, illustrated in Figure 8, were made on all specimens according to the following definitions: length, the largest anterior-posterior dimension of the shell; width, the largest dimension parallel to the hinge line; thickness, the largest dimension perpendicular to the plane

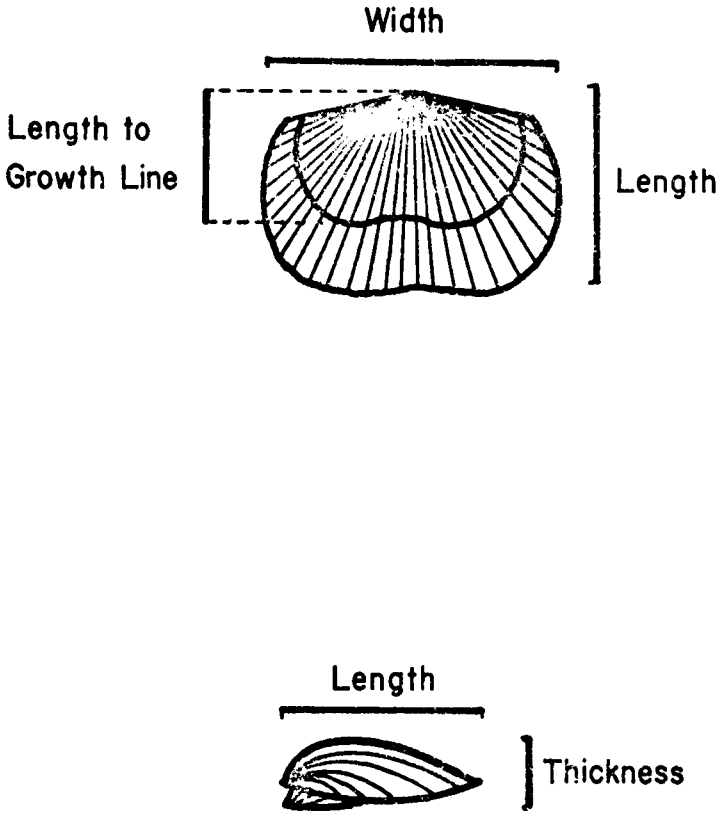


Figure 8. Dimensions Measured.

of commissure. Where applicable, the length from the furthest posterior portion of the shell to the major growth lines was measured parallel to the anterior-posterior line. The growth line measurements were made on the "flattest" valve--the valve most closely paralleling the plane of commissure--in order to facilitate direct comparison with length, a dimension within the plane of commissure. Measurements were made with micrometer calipers to an accuracy of $\pm$0.01 mm.

The data derived from these measurements were analyzed by the University of Tennessee Computing Center IBM 360 computer through two programs. Program BMD05D, from the Health Sciences Computing Facility, UCLA, was used to produce three bivariate plots (length X width, length X thickness, and width X thickness), three size-frequency histograms (length, width, and thickness) and, where applicable, a length to major growth line histogram. A second program, obtained from Dr. Peter Richards of Oberlin College, was used to apply the Levinton-Bambach growth model and determine the derived survivorship/ mortality curve.

Bivariate Analysis

Three bivariate plots (length X width, length X thickness, and width X thickness) were executed for each population. These graphs consistently revealed better resolution in the length X width plot; and it is believed that this is caused by the following factors. The sediments containing the fossils are highly argillaceous and therefore subject to some compaction. Because the forms dealt with tend to lie, after death, with the plane of commissure parallel

to bedding, thickness may be considerably affected. Such effects were obvious in crushed shells, and these specimens were not measured. However, the small increase in thickness of the shell with age (as compared with the other dimensions) and the possibility of slight compression of thickness, without breakage, reduce the reliability of this measurement. Therefore, only the length X width plots are included here (Figures 9 through 12). In the figures, N indicates the size of the population.

In each population, the superior resolution of those bivariate plots containing length indicates that length is a more reliable index of size than width. This is due, in part, to the fragile nature of the lateral margins of some species (Dinorthis holdeni, D. transversa, and especially Sowerbyella compacta) and, in others (Rostricellula rostrata), due to small increase in width with age (at least for the age range considered here). Thus, length was chosen as the dimension most representative of size and growth for the size-frequency analyses. When shell morphology and preservation conditions permit, the author heartily recommends Parkinson's (1951, p. 211 and his Figure 8) method of determining the most representative dimension through a comparison of the log of a dimension with the log of relative volume.

All of the plots available for each species, regardless of resolution, revealed nothing to suggest that any of the populations include more than one species. Nor did any of the plots reveal considerable non-linear growth. Because the population of Rostricellula rostrata presented in this paper is apparently restricted to juvenile

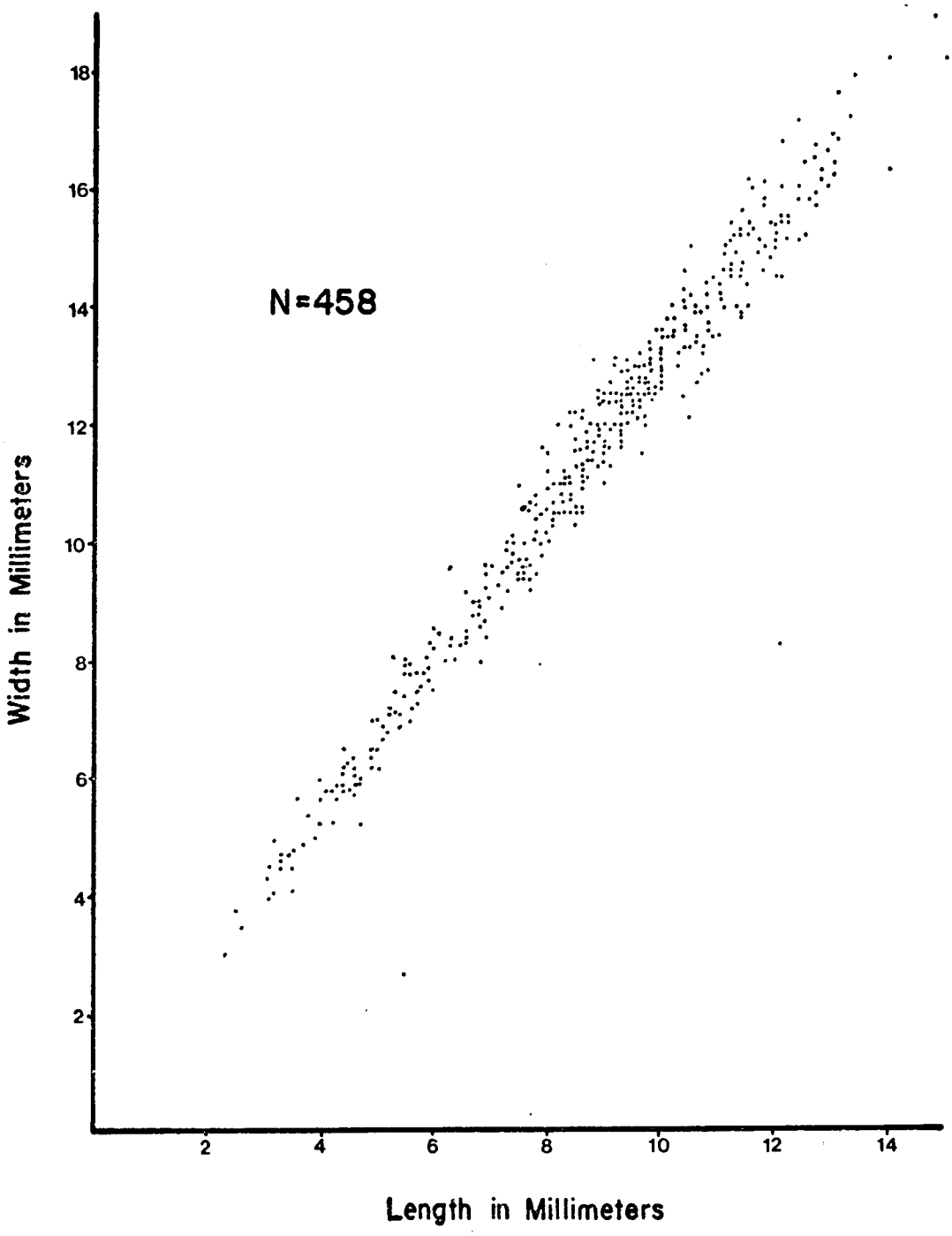


Figure 9. Length X Width Plot of Dinorthis holdeni.

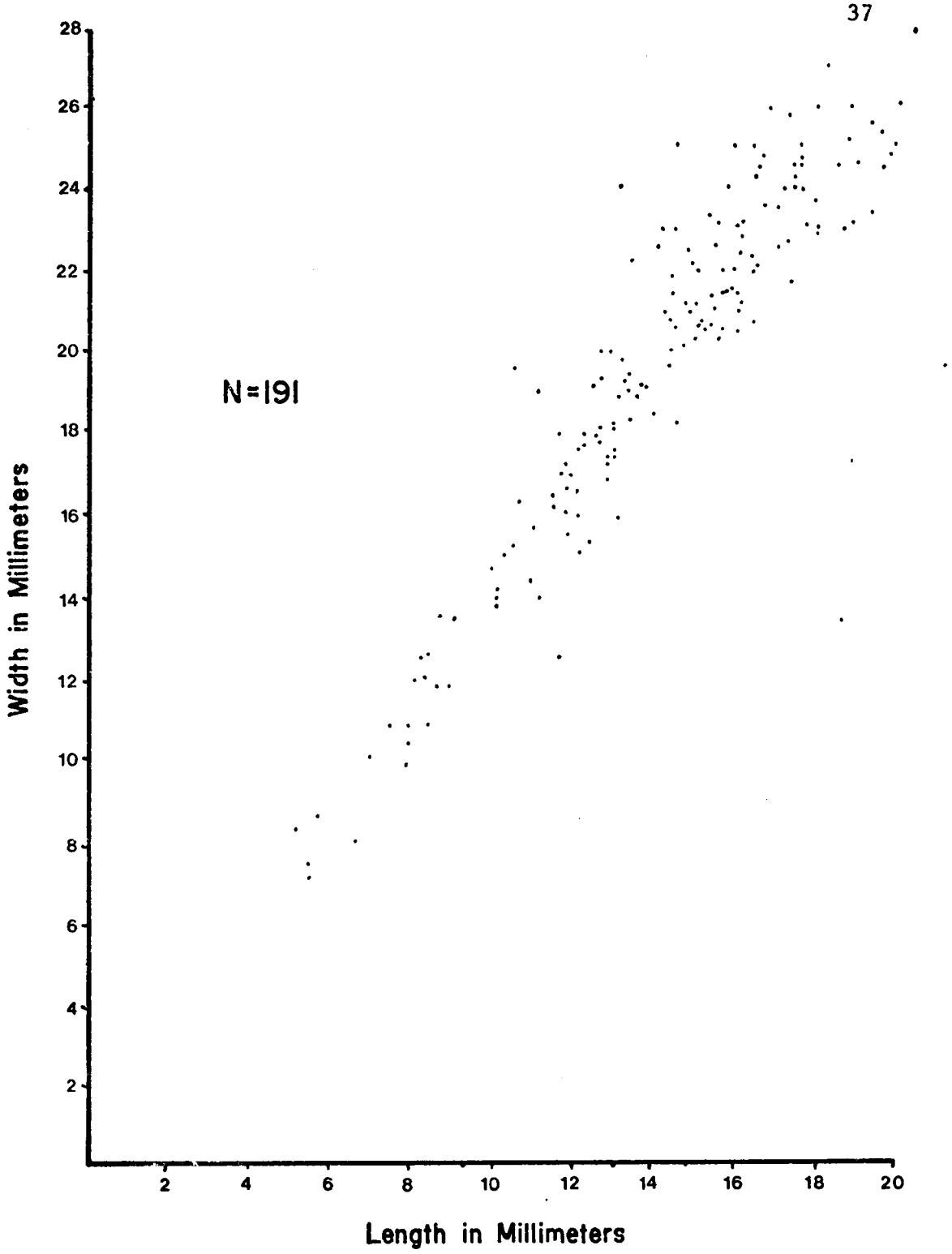


Figure 10. Length X Width Plot of Dinorthis transversa.

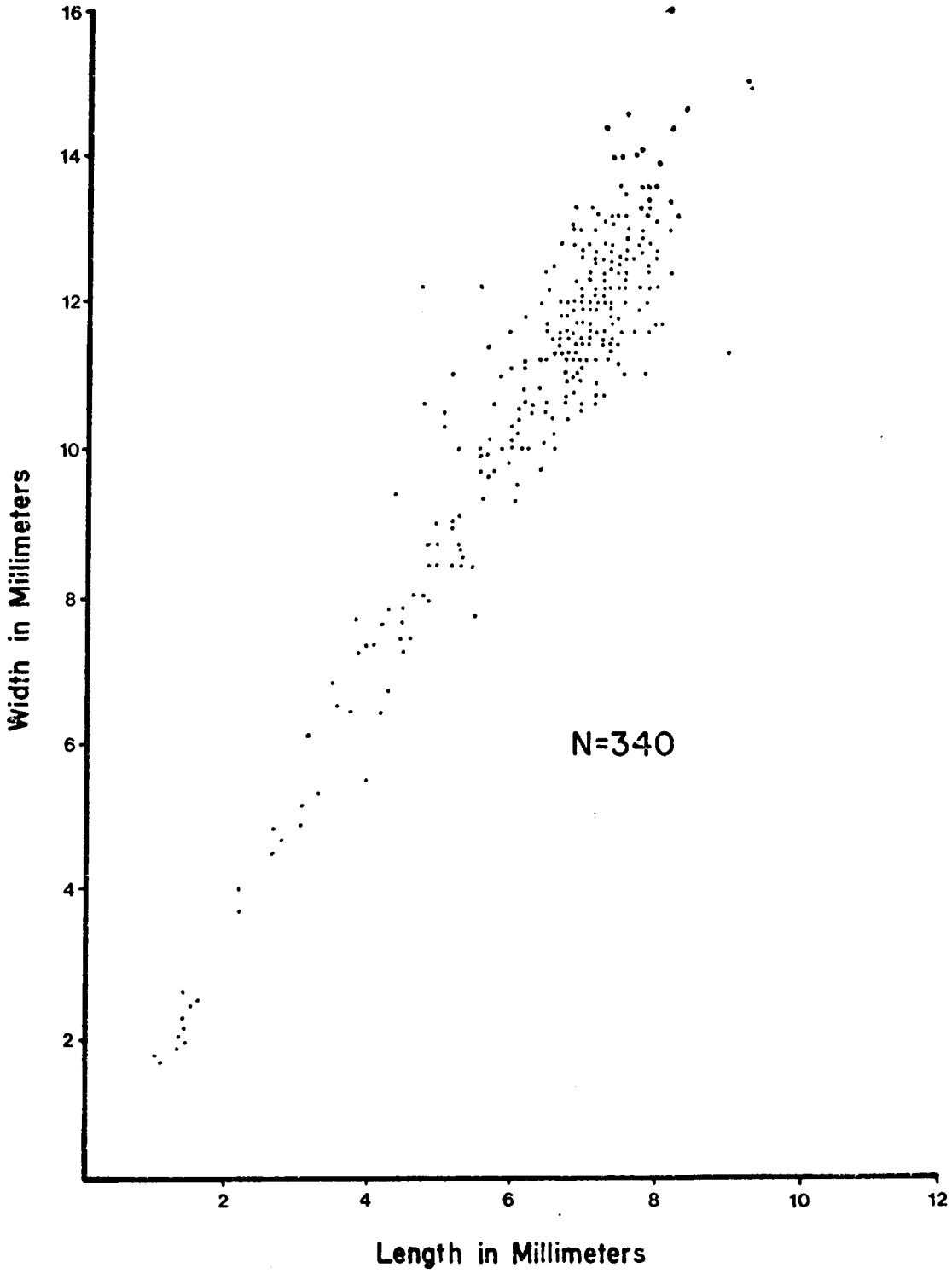


Figure 11. Length X Width Plot of Sowerbyella compacta.

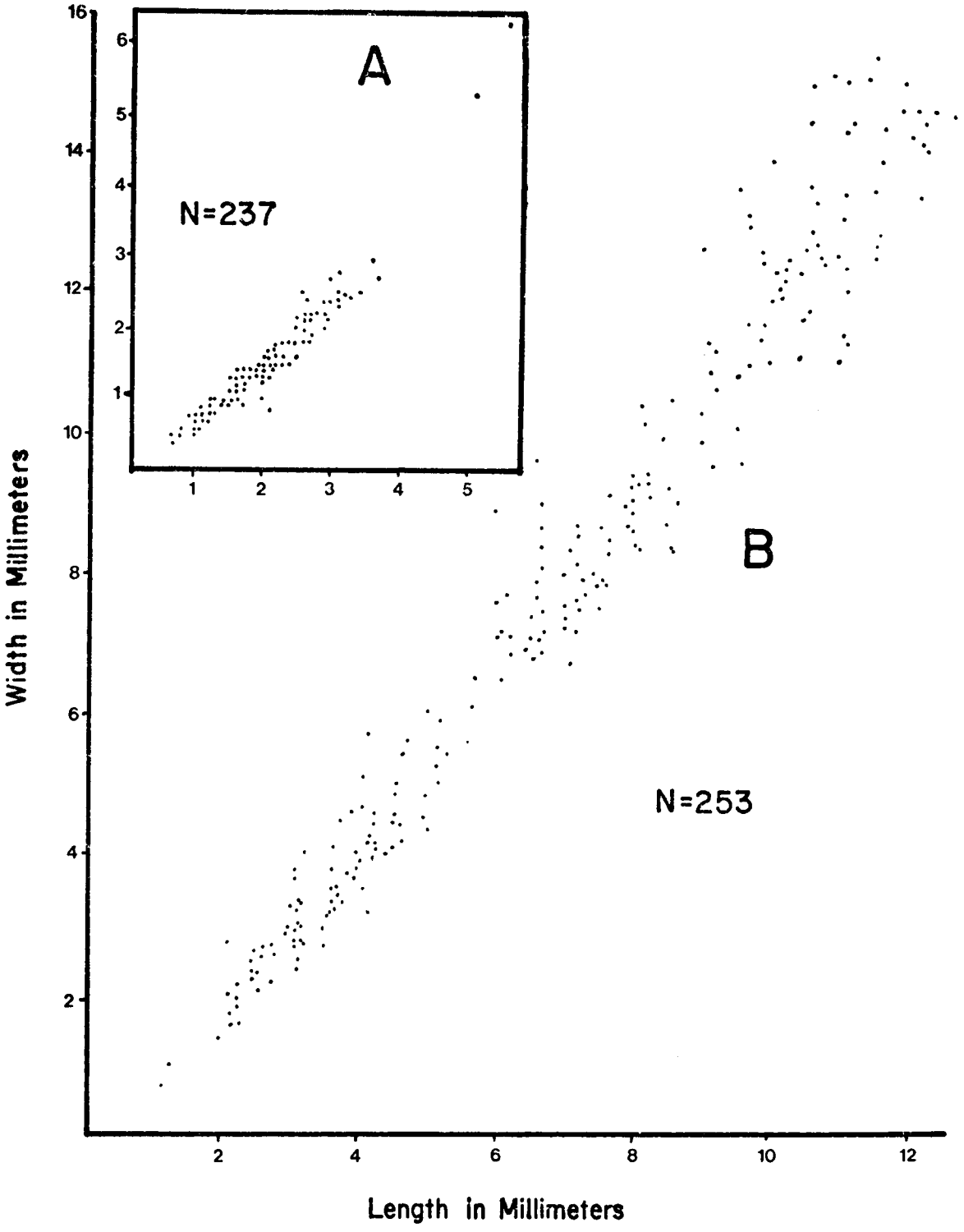


Figure 12. Length X Width Plots of Rostricellula rostrata.

(A) "juvenile" population, (B) population from Walker and Parker, in preparation, 1975.

specimens, a population of R. rostrata, described by Walker and Parker (in preparation, 1975) and Walker and Alberstadt (in press, 1975) is included for comparison. This population was collected at I-75 and Diggs Gap in Raccoon Valley (Rr-3 on Figure 2D, p. 9) from bed one of the "Moccasin" beds as described by Milici and Walker (1973, p. 155). Comparison of these Rostricellula populations reveals an apparent change in slope of the length X width graph at approximately three millimeters in length, showing a higher length/width ratio in early life. A sample of R. rostrata collected from the aforementioned "Moccasin" beds and described by Parker (1973, unpublished) reveals this same slope change within a single population.

Although no indices of resolution are presented, it is obvious that some populations, notably Dinorthis holdeni and the "juvenile" Rostricellula rostrata, are less spread than the others. The lack of resolution in Sowerbyella compacta may be explained, in part, by the fragile nature of the shell. However, this will not suffice for Dinorthis, where D. transversa is more robust than D. holdeni. It is assumed that some of this "spread" may be due to phenetic variability, previously demonstrated for some Middle Ordovician strophomenid brachiopods (Bretsky and Bretsky, 1975). Also, in the case of R. rostrata, competition for settling space and the resultant crowding (the effects of which may be seen in the marked asymmetry of some mature specimens) may explain the pronounced decrease in resolution of the mature section of the population's graph.

Size-Frequency Analysis

The length based size-frequency histograms are shown in Figures 13 through 16. With each histogram there are several possible levels of interpretation. Two levels of interpretation are presented in this paper, although the quality of the data may be such that deeper levels are possible. In the cases of the multimodal populations, the histograms were plotted at various sizes below the final size to ascertain if the distribution would change significantly with increasing population size. Because no significant changes were noted, the population sizes are considered sufficient for this study.

The first level of interpretation considers the skew of each distribution. Three of the populations (Dinorthis holdeni, D. transversa, and Sowerbyella compacta) have a negative skew, S. compacta having the most pronounced skew and D. holdeni being almost normally distributed. Both populations of Rostricellula rostrata are positively skewed, the "normal" population considerably less than the juvenile one. Positive skews are generally indicative of high juvenile mortality and negative skews, of low juvenile mortality. More refined estimates of mortality rates are discussed in a later section.

The second level of interpretation involves the recognition of major modes or "peaks" of size-frequency distribution. All of the populations, except the juvenile Rostricellula rostrata, appear multimodal. The choice of modal peaks is one of the most subjective aspects of this type of study, since it requires the recognition,

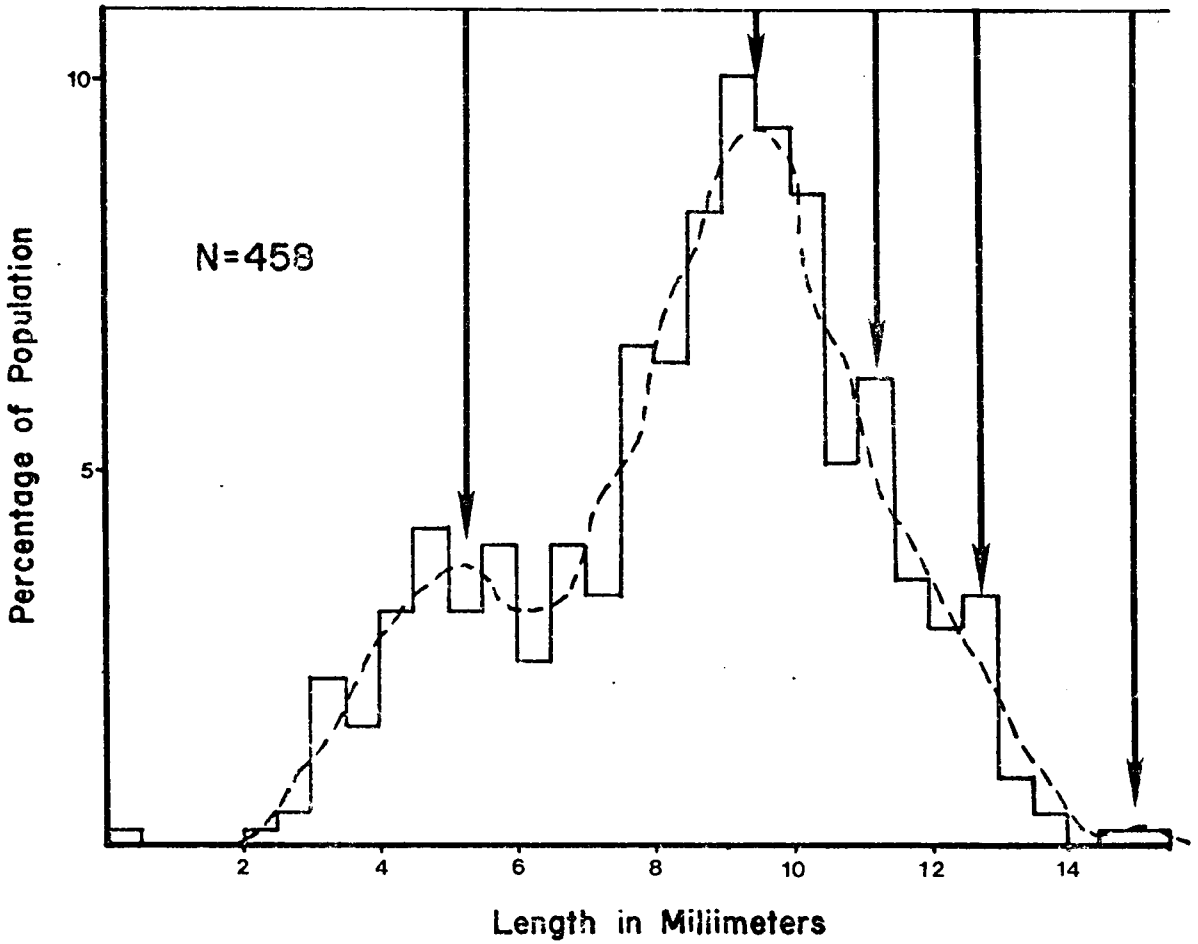


Figure 13. Length Based Size-Frequency Histogram of Dinorthis holdeni.

The dashed line is a three column moving average of the histogram and the arrows indicate the major modal peaks recognized.

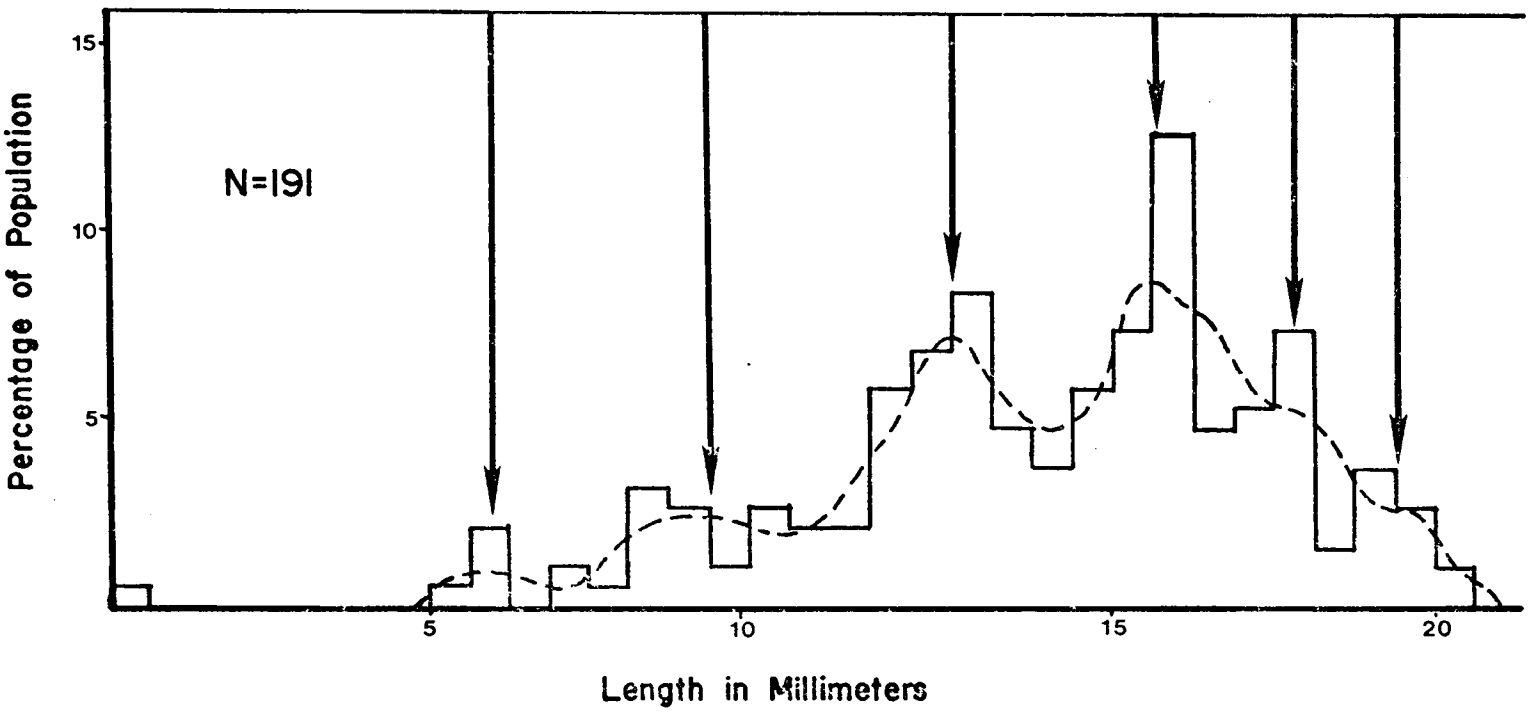


Figure 14. Length Based Size-Frequency Histogram of Dinorthis transversa.

The dashed line is a three column moving average of the histogram and the arrows indicate the major modal peaks recognized.

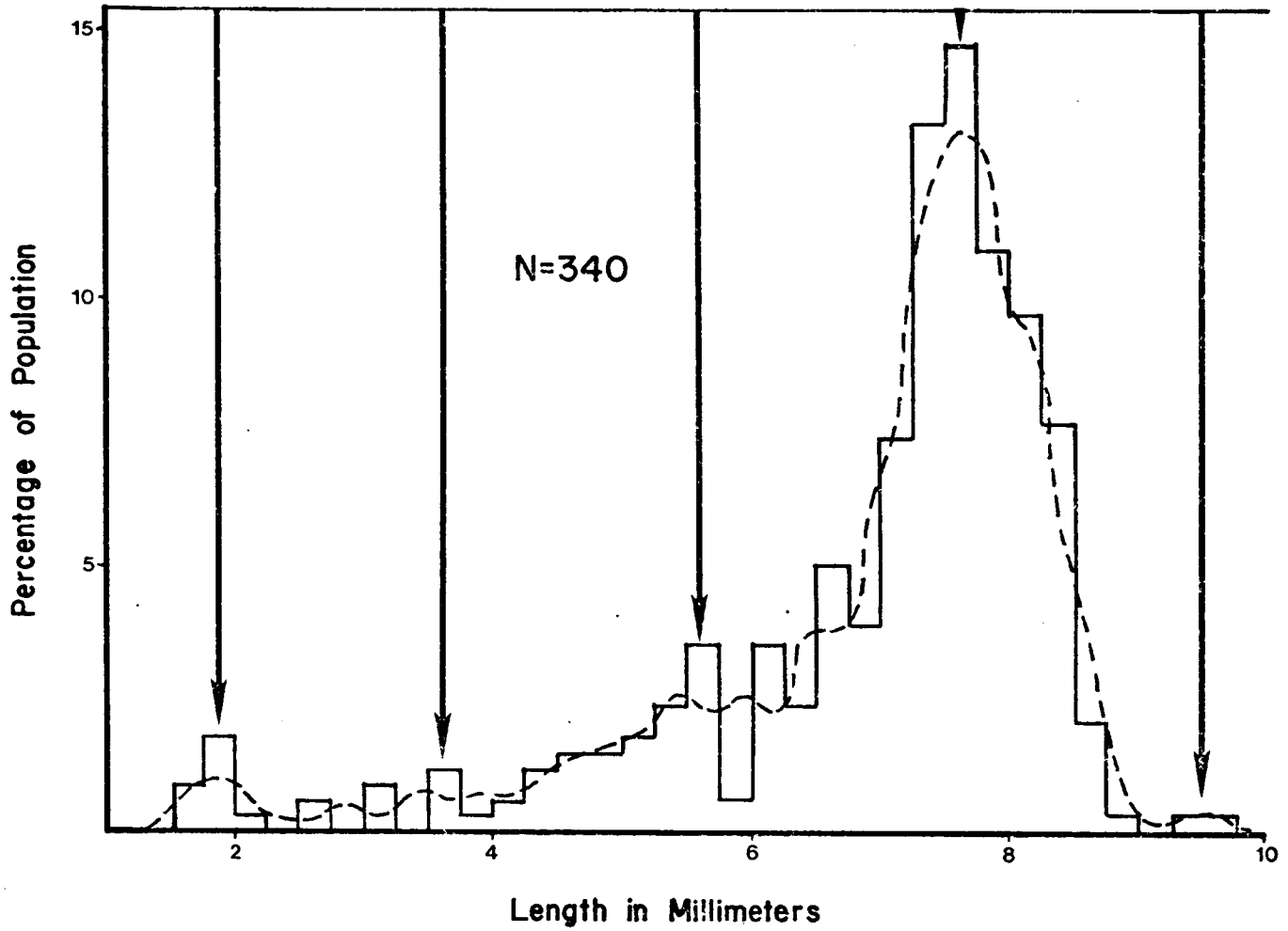


Figure 15. Length Based Size-Frequency Histogram of Sowerbyella compacta.

The dashed line is a three column moving average of the histogram and the arrows indicate the major modal peaks recognized.

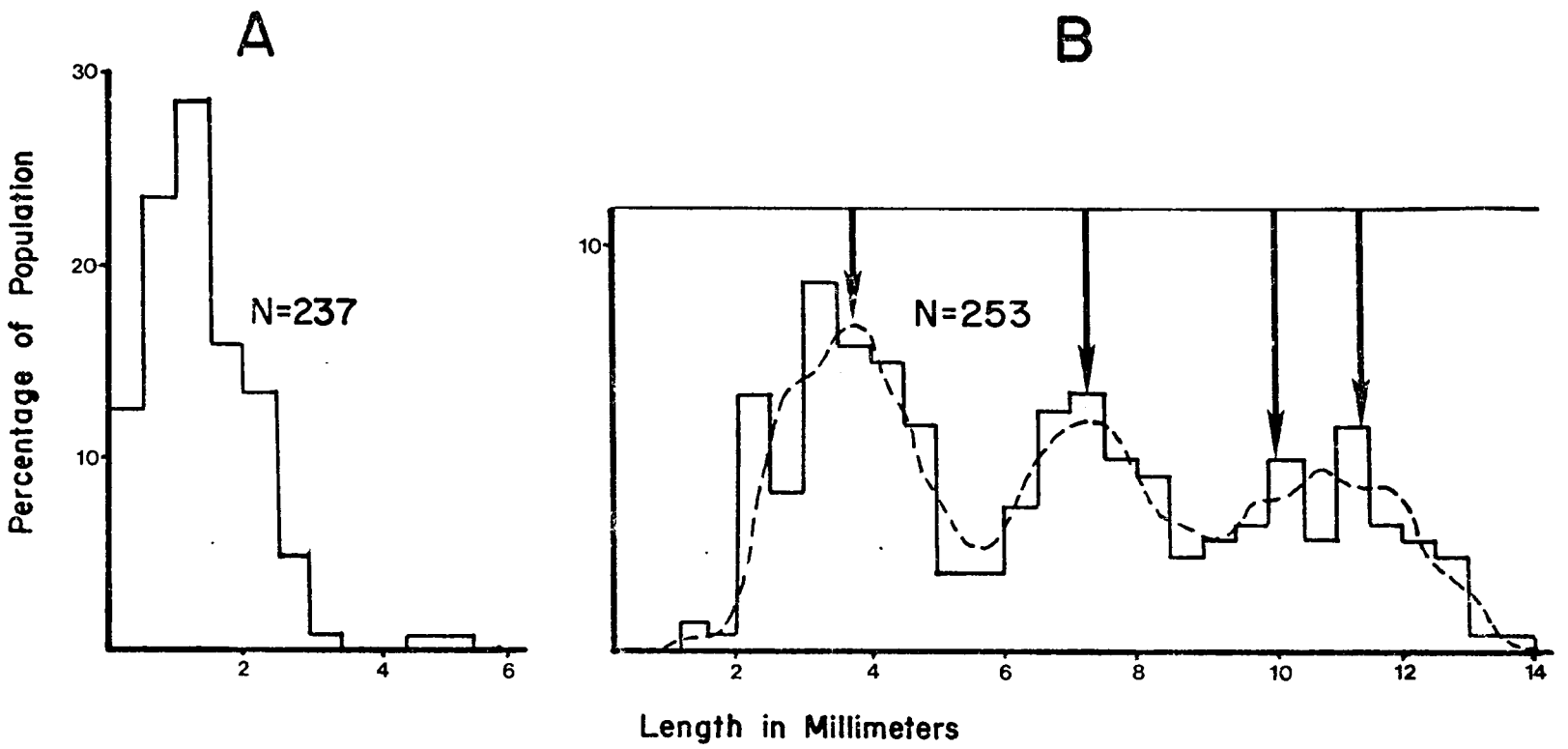


Figure 16. Length Based Size-Frequency Histograms of Rostricellula rostrata.

The dashed line is a three column moving average of the histogram and the arrows indicate the major modal peaks recognized. (A) "juvenile" population, (B) population described by Walker and Parker, in preparation, 1975.

often almost intuitive, of "real" peaks among the "noise" and interference of possible lower order peaks.

Four major modes for the Rostricellula rostrata population, five major modes for the Dinorthis holdeni and Sowerbyella compacta populations, and six major modes for the D. transversa population were recognized, as shown by the arrows in the figures, using the histogram peaks in conjunction with a three column moving average of the histogram data. The significance of these features will be discussed in the section on growth rates.

The factors affecting size-frequency distributions have been enumerated previously (Chapter II). Preservation and collection biases have been considered in the environmental analysis and collection methods sections, respectively; and the author believes that the effects of these non-biologic factors have been minimal.

The distinct polymodality of the size-frequency histograms of the species indicates periodic recruitment. As shown by Craig and Oertel (1966, pp. 325-326), polymodality will result only if periodic recruitment is coupled with periodic mortality and/or periodic decreases in growth rate. The discrete nature of the size-frequency histogram peaks (especially for Sowerbyella compacta and Rostricellula rostrata) indicates a distinct periodic recruitment with recruitment bursts being well separated in time. The timing of these bursts can not be deduced from the evidence; however, the recruitment may very well have been similar to Craig and Oertel's (1966) tropic recruitment (Figure 5, p. 23, this paper), as assumed by Richards and Bambach (in press, 1975) for their material.

With the above assumptions in mind, it is now possible to consider the factors of growth rate and survivorship/mortality rate.

Growth Rates

Growth rates determined for the four species are shown in Figures 17 through 20. As suggested by Surlyk (1972), the graphs for each population are scaled in percentages of total length (ordinate) and total age (abscissa) to facilitate comparison of growth rates between populations as well as between methods of determining growth rate within a population (note that the Levinton-Bambach formula can not determine growth rate in absolute units). The theoretical advantages and disadvantages of each method have been discussed previously (p. 26). The theoretical advantage of reduced a priori assumptions about the nature of growth rates inherent in the histogram peak method is enhanced by the relatively close agreement of the histogram peak growth rates with those predicted by the Levinton-Bambach (1970) and Sheldon (1965) methods. Thus, although the survivorship/mortality rates determined by all three methods will be presented for purposes of comparison, the histogram peak growth rates and derived survivorship/mortality rates are considered most representative.

The Levinton-Bambach (1966) model abstracts maximum size from the size-frequency data, and size in the graphs is expressed as a percentage of maximum size. Therefore, the growth curve determined by the Levinton-Bambach method is the same in all graphs and may be used as a reference curve.

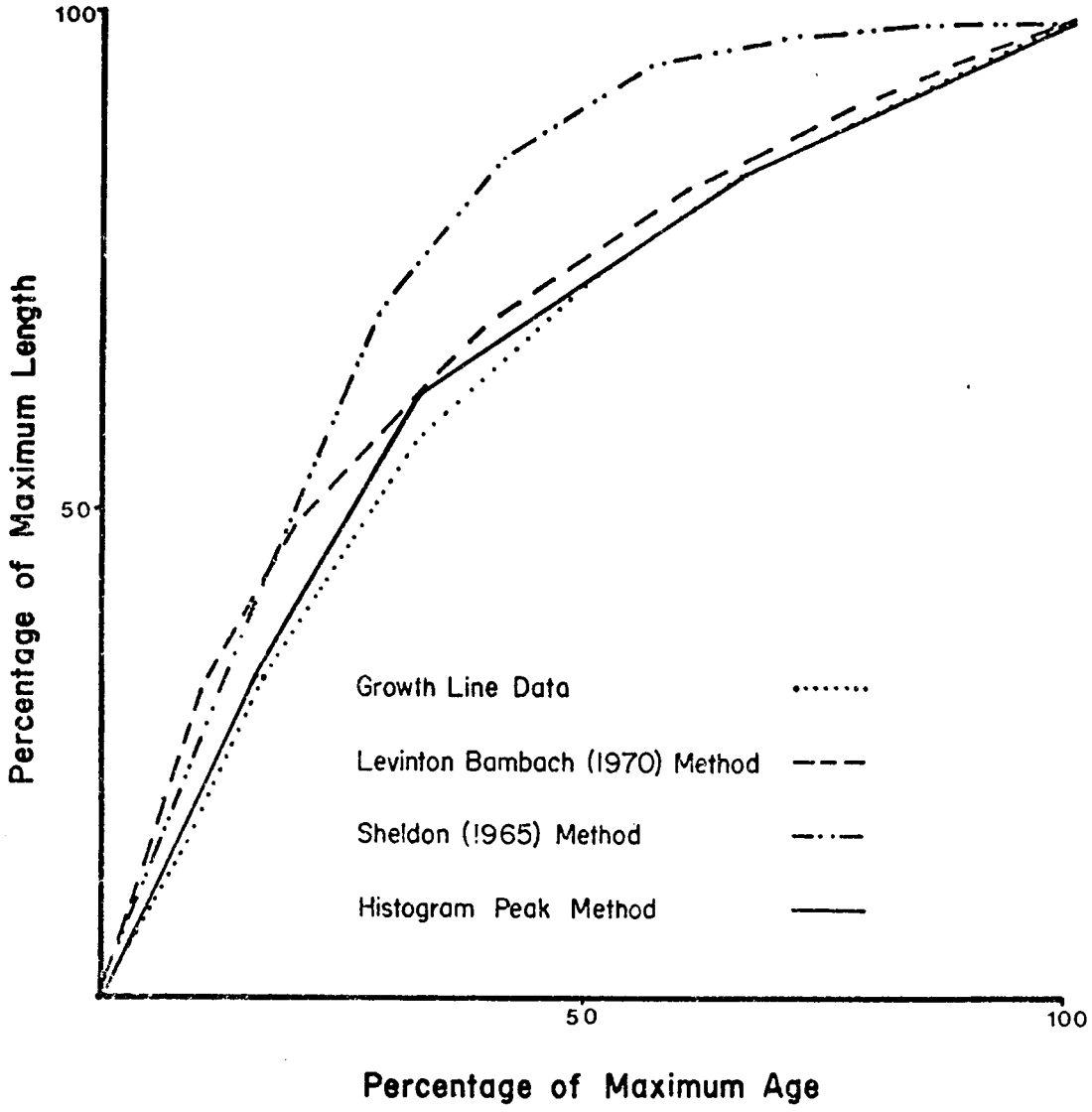


Figure 17. Growth Rates for Dinorthis holdeni.

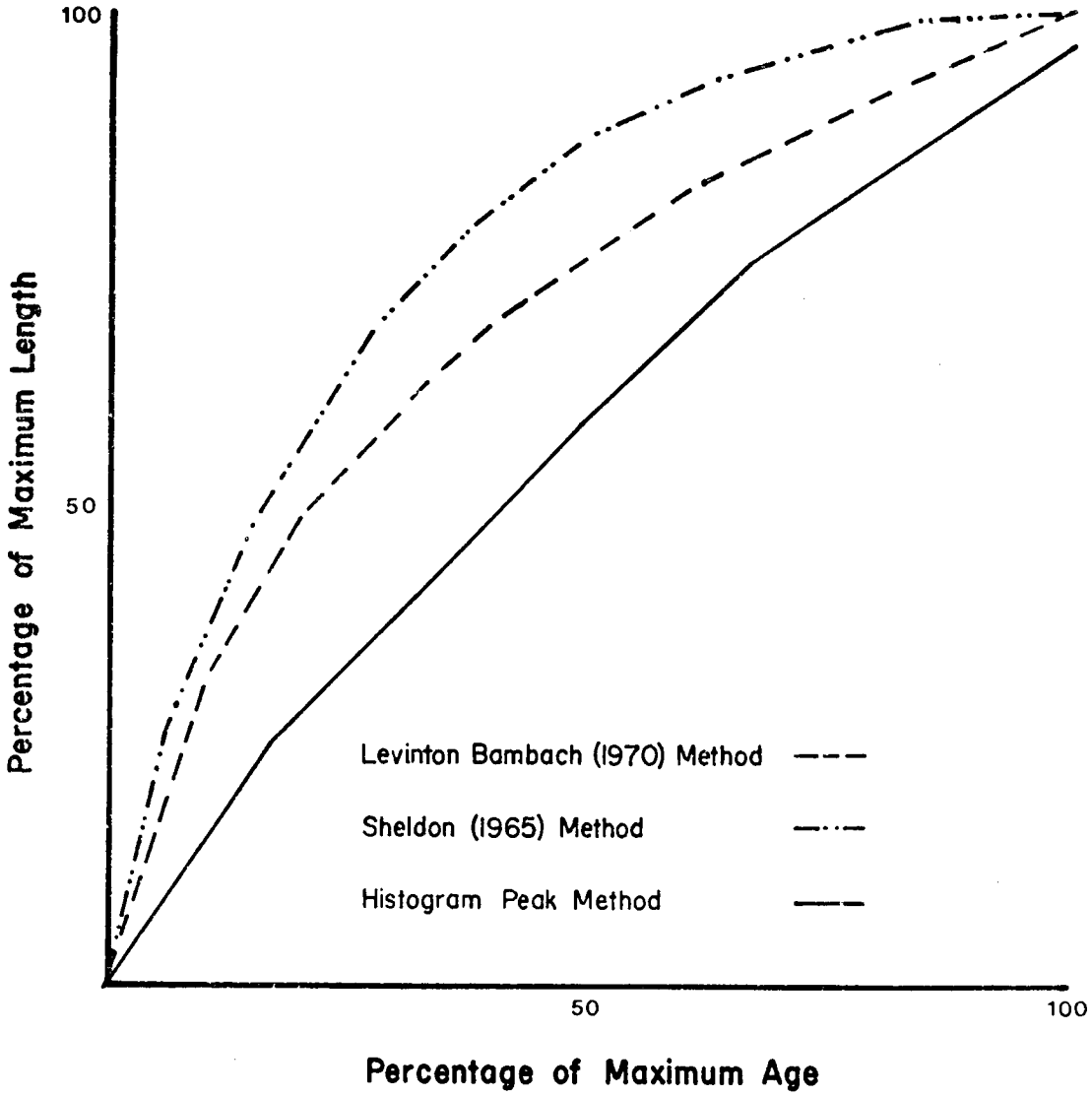


Figure 18. Growth Rates for Dinorthis transversa.

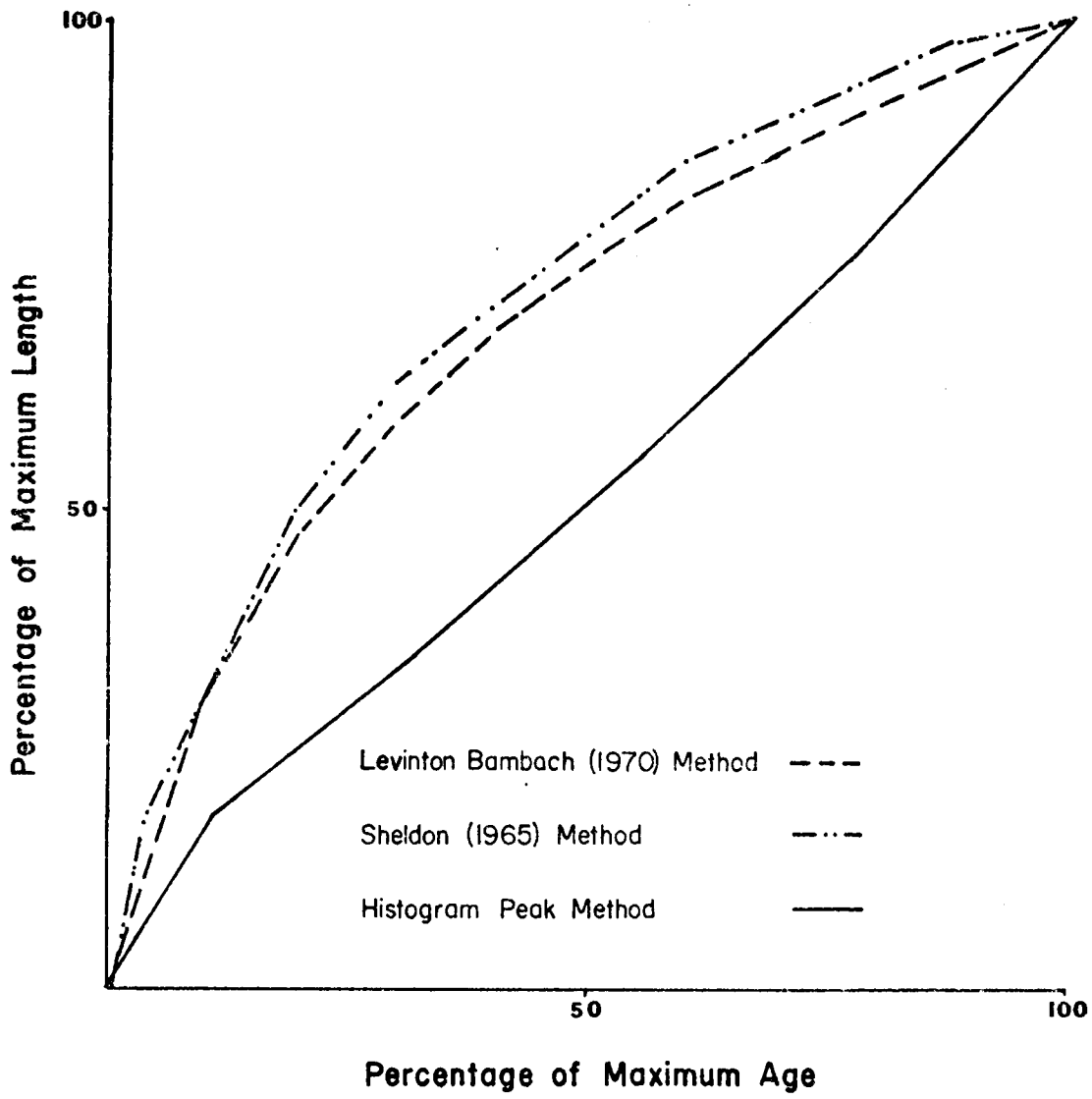


Figure 19. Growth Rates for Sowerbyella compacta.

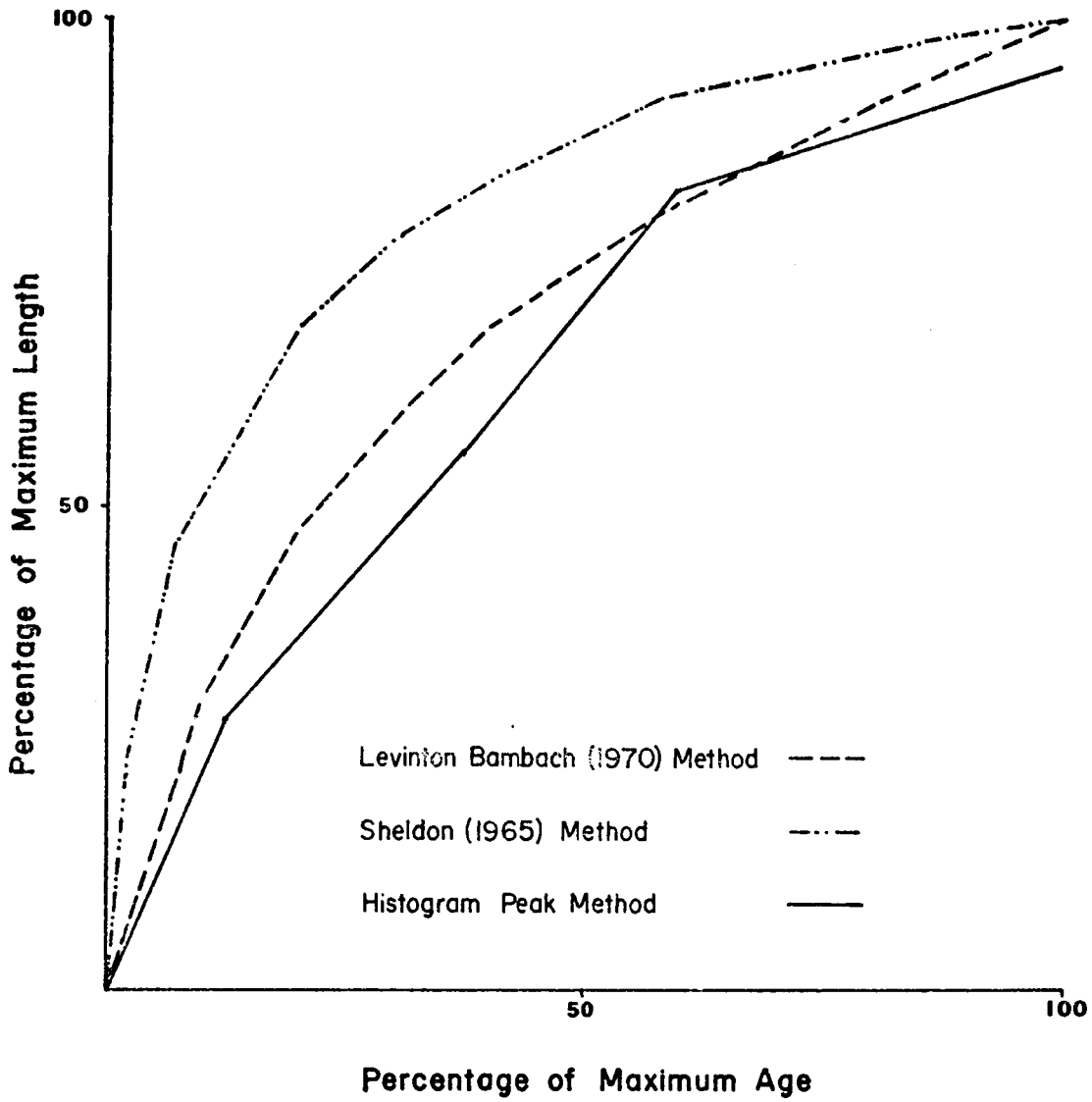


Figure 20. Growth Rates for Rostricellula rostrata.

Utilizing the first two size-frequency peaks as recognized from the histograms, a second growth curve was constructed for each population according to the method of Sheldon (1965). These growth curves display a consistently higher juvenile growth rate than the Levinton-Bambach model, approaching the latter only in the case of Sowerbyella compacta.

A third growth curve was computed for each population using all of the peaks recognized in the size-frequency histograms. The age at the first peak, whether one or one half year, was determined purely on the basis of which would produce the smoothest curve. This perhaps arbitrary decision does not affect the rest of the curves. These curves range from almost linear, in the case of Sowerbyella compacta, to surprisingly similar to the Levinton-Bambach model, as in the case of Dinorthis holdeni.

Growth line data was available for three species, Dinorthis holdeni, D. transversa, and Sowerbyella compacta. Only in D. holdeni, however, did the length to growth line size-frequency histogram (Figure 21) display sufficient polymodality to allow a comparison with the previously established growth rates. The growth line derived growth rate is compared to the other D. holdeni growth rates in Figure 17, p. 48. Note that this growth rate is quite similar to the one determined from the size-frequency peaks.

If the growth rate remained relatively constant throughout life, one might expect periodicities in the distances between growth lines reflecting the growth between one, two, etc. periods of growth line formation. It was discovered that, when the length between

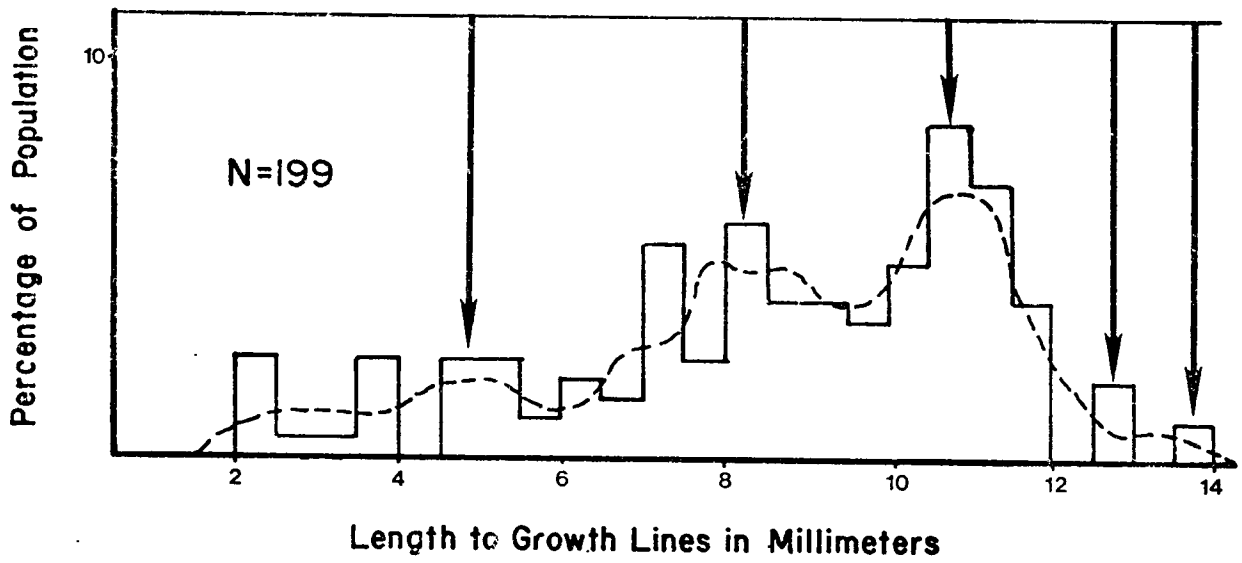


Figure 21. Growth Line Data for Dinorthis holdeni.

The dashed line is a three column moving average of the histogram and the arrows indicate the major modal peaks recognized.

successive growth lines were plotted in histogram fashion, certain periodicities (Dinorthis transversa 1.7 mm, D. holdeni 1.2 mm, and Sowerbyella compacta 0.6 mm) corresponded with the modalities (Figure 22). The implications of such periodicity are unclear at present.

Figure 23 is a comparison of the growth rates of the four species under study. All growth rates in this figure were determined using the histogram peak method and are scaled in absolute size (ordinate) and years (abscissa).

Survivorship/Mortality Rates

From the size-to-age conversion implicit in the three growth curves, three survivorship/mortality curves were constructed for each species (Figures 24 through 27). The ordinate for these graphs is a logarithmic scale of the percentage of the population surviving and the abscissa is percentage of maximum age. The three methods of determining survivorship/mortality rates yield curves which (with the possible exception of the Rostricellula rostrata population) differ from each other within reasonable limits. As predicted by the general skews of the size-frequency histograms, the Dinorthis holdeni and Rostricellula rostrata populations have increasing mortality rates. The D. transversa and Sowerbyella compacta populations have rapidly increasing mortality rates and the "juvenile" R. rostrata has an extremely high juvenile mortality rate, when compared with the other R. rostrata population. To emphasize these differences, Figure 28 was constructed with an abscissa scaled in years.

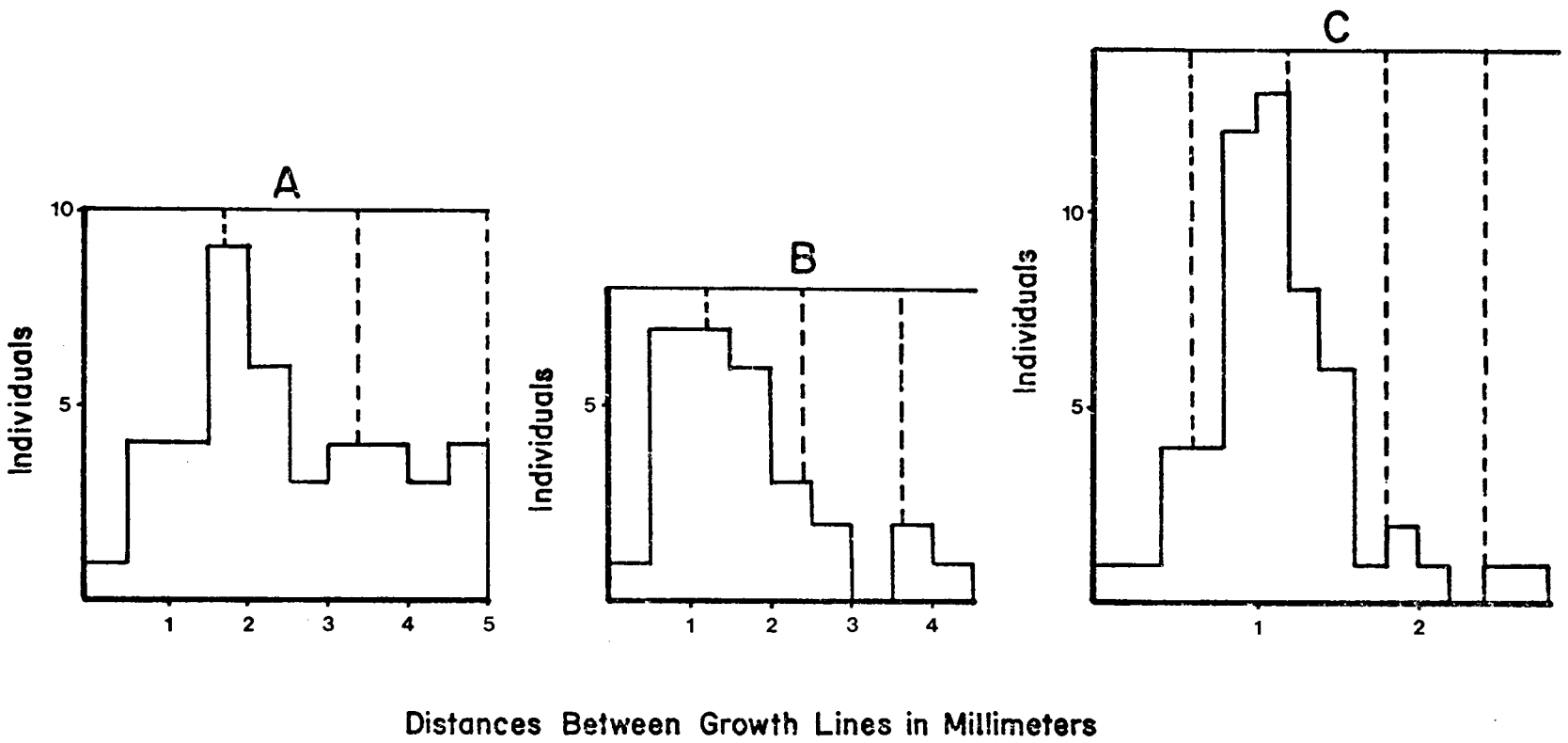


Figure 22. Distances Between Successive Growth Lines.

(A) Dinorthis holdeni, (B) Dinorthis transversa, (C) Sowerbyella compacta. The dashed lines indicate the periodicities mentioned in the text.

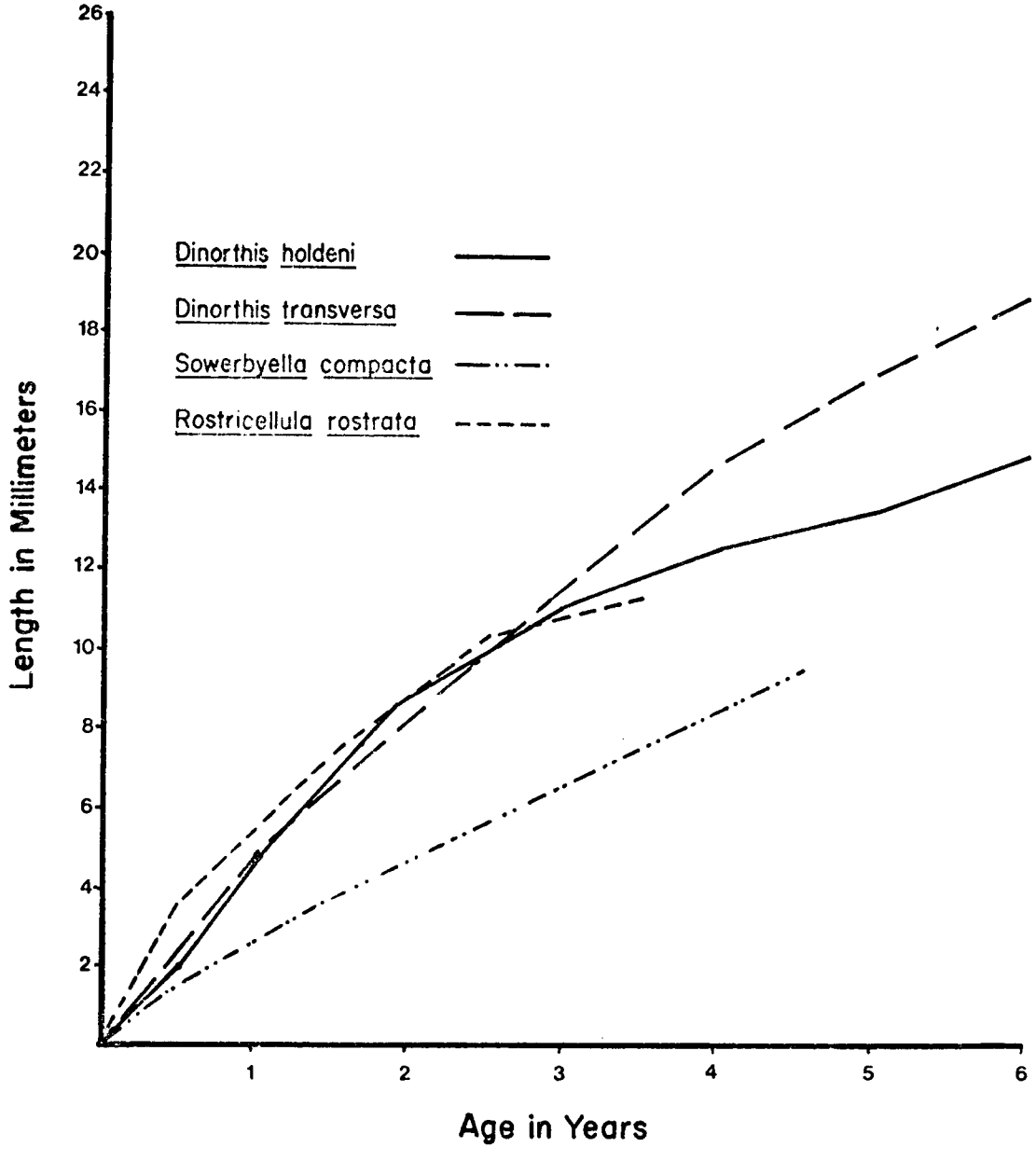


Figure 23. Comparative Growth Rates.

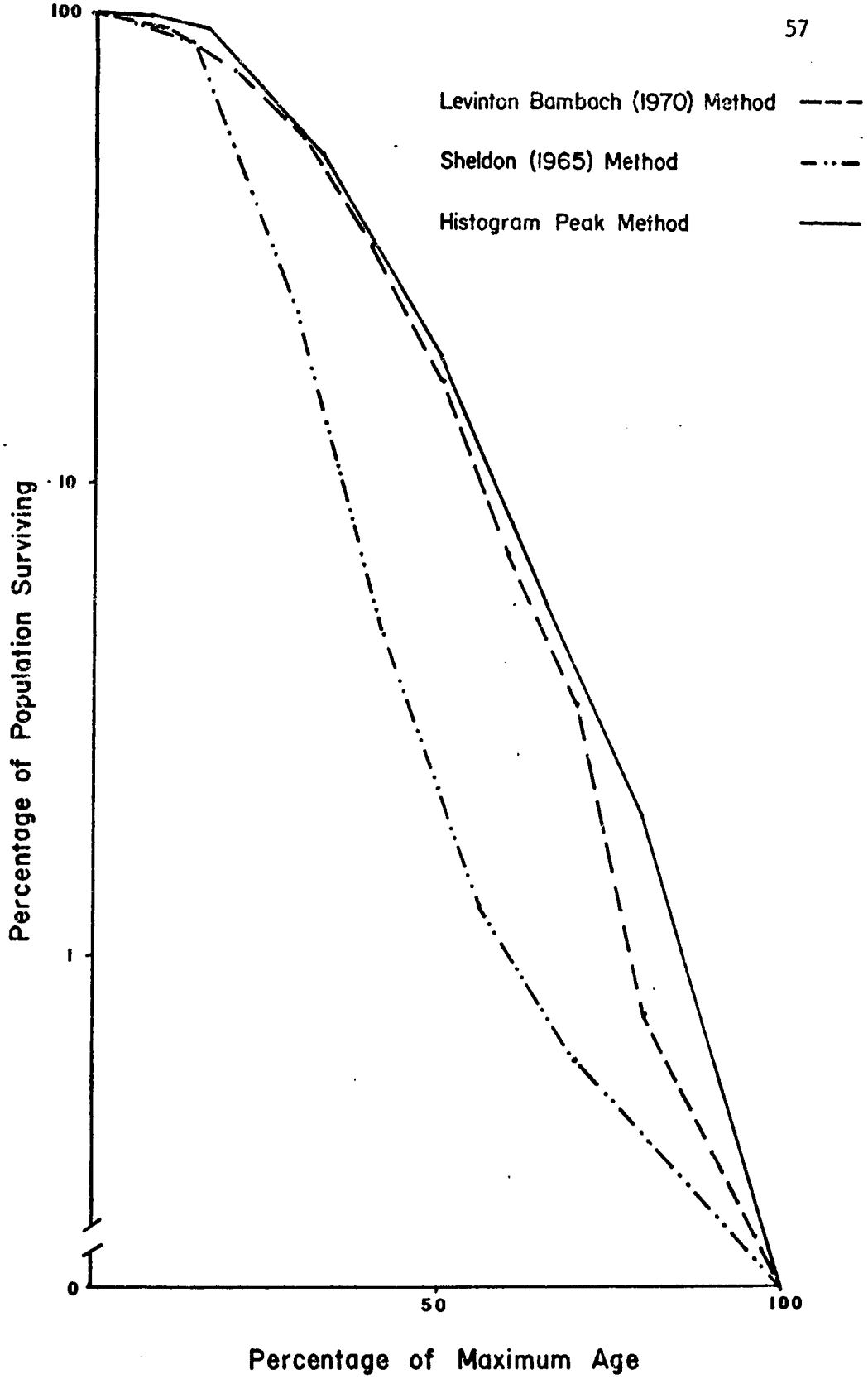


Figure 24. Survivorship/Mortality Curves for Dinorthis holdeni.

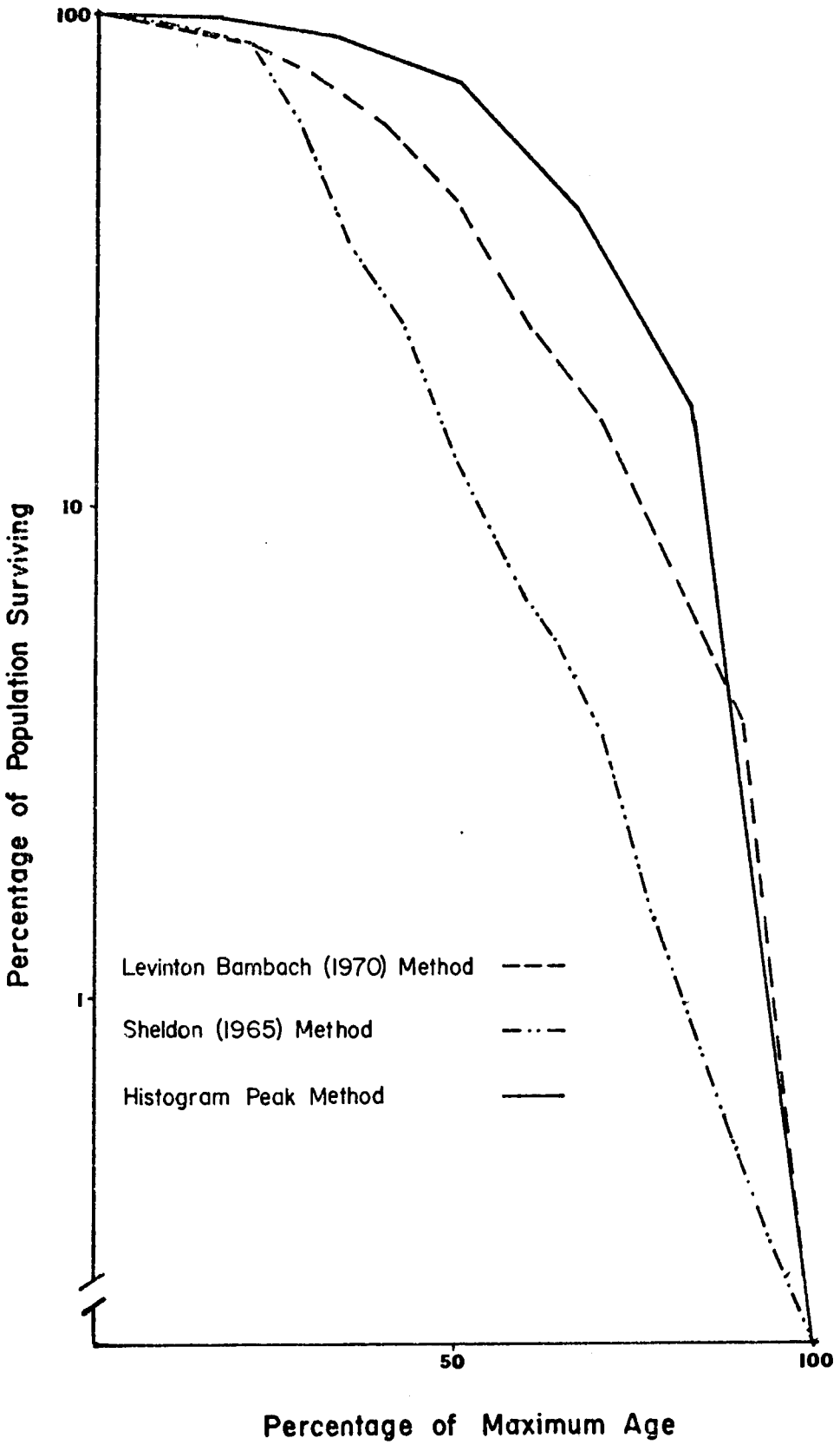


Figure 25. Survivorship/Mortality Curves for Dinorthis transversa.

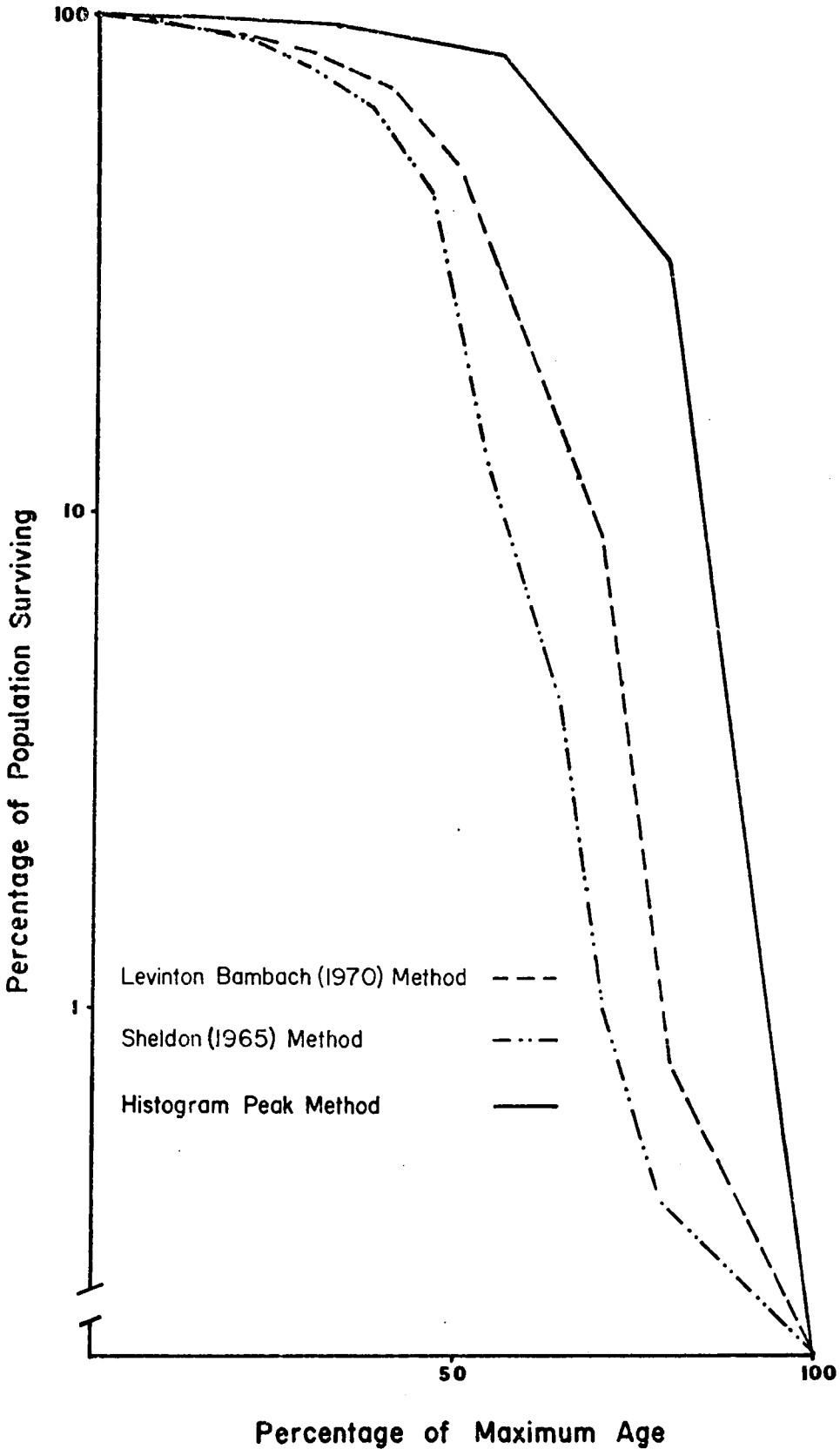


Figure 26. Survivorship/Mortality Curves for Sowerbyella compacta.

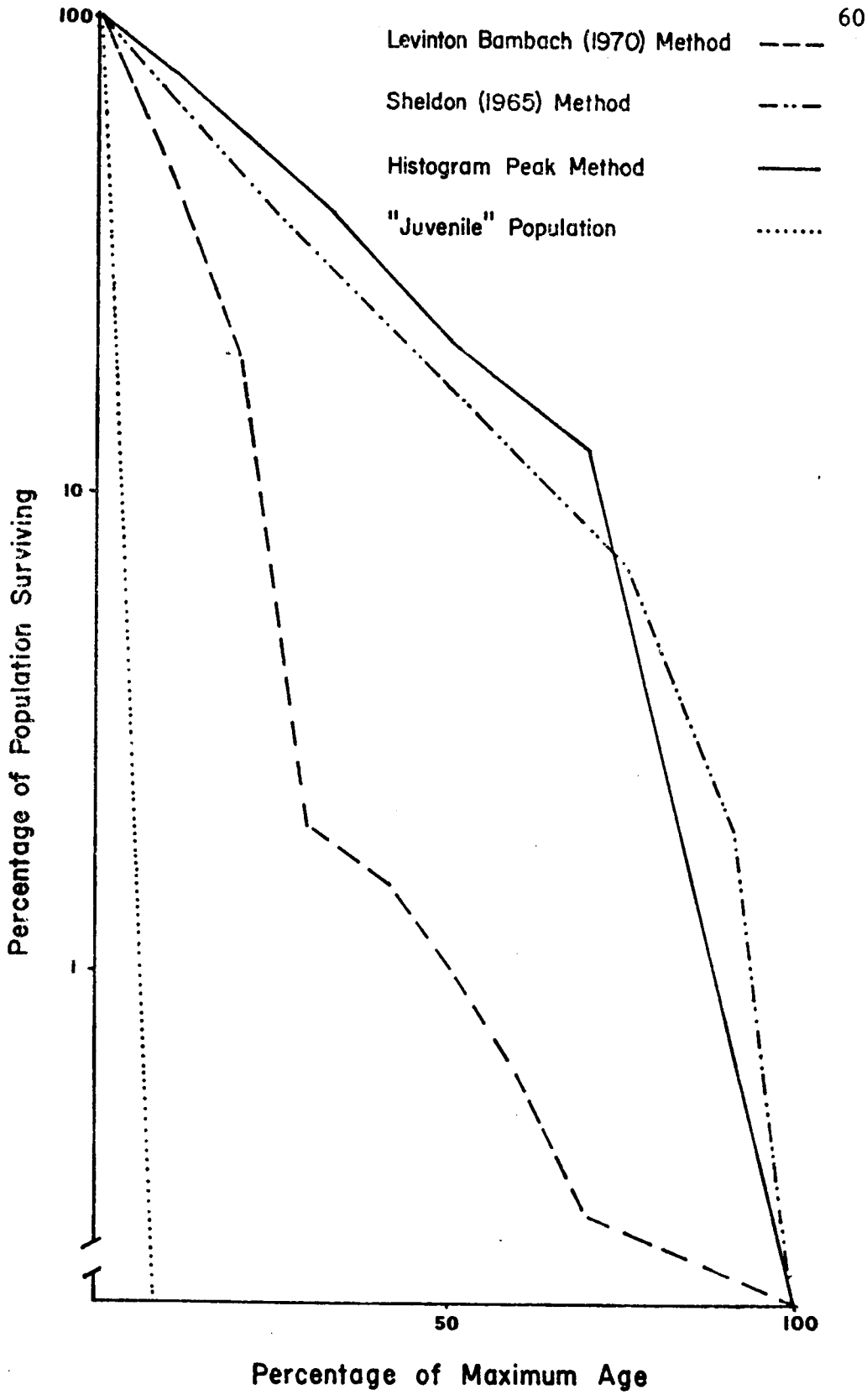


Figure 27. Survivorship/Mortality Curves for Rostricellula rostrata.

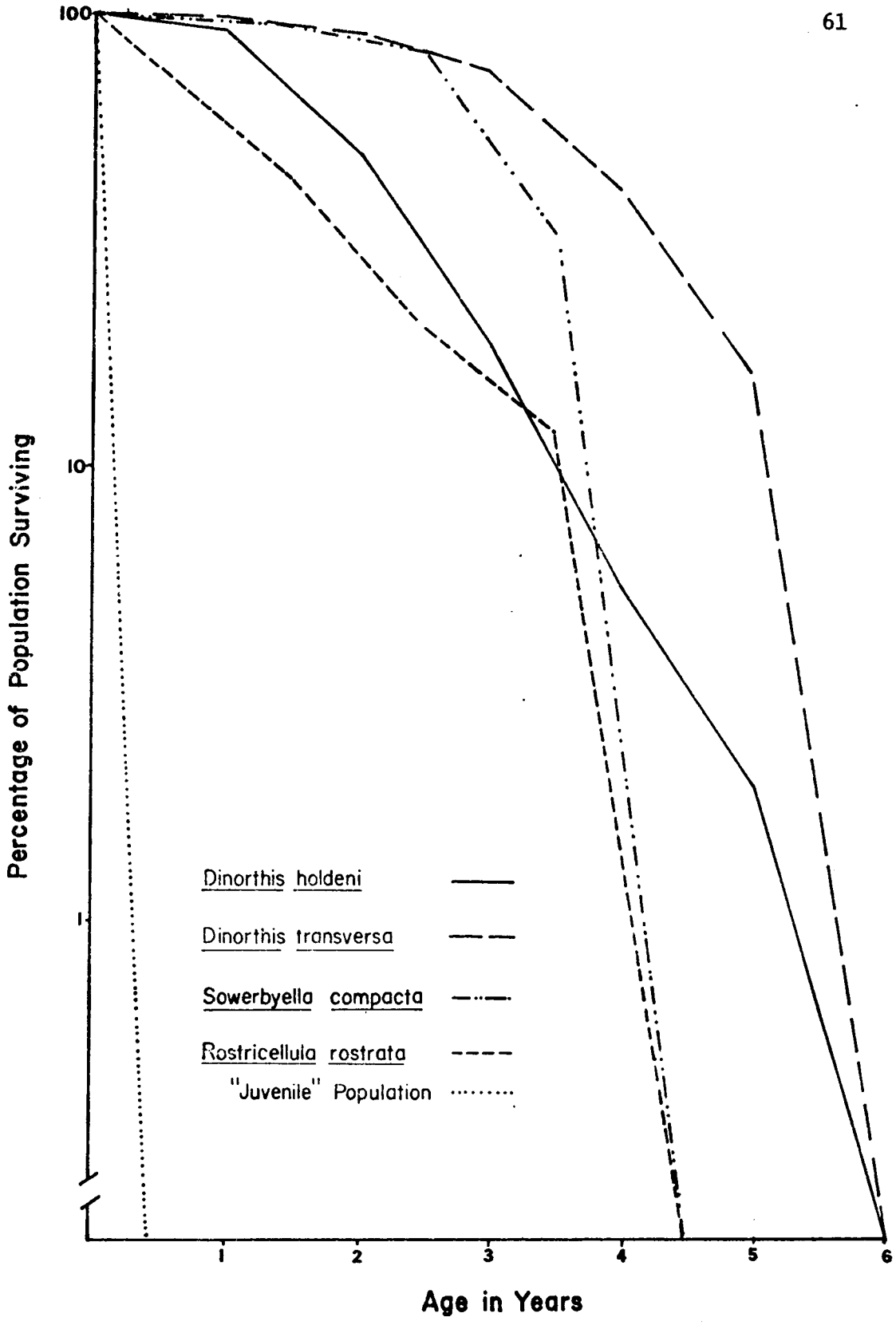


Figure 28. Comparative Survivorship/Mortality Curves.

CHAPTER IV

SUMMARY AND CONCLUSIONS

Comparison With Previous Work

The results and observations presented herein from the four populations studied agree quite well with those of Surlyk (1972) and Richards and Bambach (in press, 1975). Richards and Bambach (in press, 1975) examined eleven fossil brachiopod populations and Surlyk (1972) studied forty (only two of the forty were discussed in sufficient detail for comparison with the present investigation).

The size-frequency distributions in the two studies ranged from uni- to multimodal. However, it is possible that a large number of the unimodal distributions harbor multimodality that has been masked by excessive histogram interval width and small population size. Comparison of growth rates between the two papers is complicated by the fact that Surlyk (1972) used the method of Sheldon (1965) on growth line data, while Richards and Bambach (in press, 1975) used the Levinton-Bambach (1970) model on size-frequency data.

Surlyk (1972, p. 47) recognized a pattern relating mode of life to growth rate. Small pedunculate brachiopods, such as Gisilina gisii, have decreasing growth rates (see Surlyk, 1972, Figure 22, p. 45) which decrease rapidly, indicating a necessity to limit the time spent at small, vulnerable growth stages. Free living forms, such as Terebratulina gracilis, however, have decreasing growth

rates which do not decrease as rapidly, indicating an advantage of maximum size to such a mode of life.

Other factors than mode of life may also affect growth rate. Fursich and Hurst (1974) have presented a thought provoking analysis of brachiopod feeding efficiencies in relation to lophophore types. It is their conclusion that orthids and strophomenids had very simple lophophore types, limiting them to areas of high food availability (shallow water). Orthids and strophomenids also had a rather large feeding gape, thus making members of these groups especially susceptible to sediment inhalation. Rhynchonellids, on the other hand, are assumed to have had a slightly more efficient lophophore and morphological adaptations to reduce gape. Therefore, if one is attempting to relate mode of life, one must consider the possible effects of other factors.

Rostricellula rostrata in the present study, like Gisilina gisii, is a relatively small, pedunculate form with a rapidly decreasing growth rate (Figure 20, p. 51). Sowerbyella compacta, following the interpretations of Lamont (1934, p. 63 and elsewhere) and Rudwick (1965, p. H202), is assumed to have "floated," unattached, at the sediment-water interface. S. compacta, like Terebratulina gracilis, displays a less rapidly decreasing (almost linear) growth rate (Figure 19, p. 50). The fact that the S. compacta growth rate is less rapid, on the average, than any of the other species studied is believed to be a reflection of the poor feeding efficiency of this form, perhaps due to its rather thin lateral profile (and, hence, restricted lophophore accommodation).

In regard to survivorship/mortality rates, Surlyk (1972, p. 47) noted that plots of the free-living Terebratulina gracilis result in left-skewed size-frequency histograms. The mortality curve of this species is closely similar to that of Sowerbyella compacta and not unlike that of Dinorthis holdeni and D. transversa. Gisilina gisii, however, has a right-skewed size-frequency histogram and a mortality curve similar to the Rostricellula rostrata population and not unlike that of the "juvenile" R. rostrata population.

Richards and Bambach (in press, 1974) noted two basic patterns of mortality. In one there is high juvenile mortality, usually at a length less than two millimeters, followed by a period of decreased mortality. The other pattern has low juvenile mortality followed by increasing mortality in later life. They noticed that the populations with high juvenile mortality had inhabited "muddy bottoms" and they reasoned that the high death rate among juveniles was, according to the manuscript, due to ". . . turbidity and burial resulting from resuspension of the layer of unconsolidated sediment and fecal pellets at the sediment water interface (p. 26)." The threshold of tolerance to lophophore clogging and burial is apparently two millimeters, thus explaining the reduced mortality following the attainment of this size.

Of the four species considered in this study, only one, Rostricellula rostrata, fits the Richards and Bambach (in press, 1975) pattern of high juvenile mortality. Both populations of R. rostrata have high mortality below two millimeters in length. It is interesting to note that the length/width ratio of R. rostrata

decreases abruptly at about two millimeters in length. However, as shown by the Dinorthis holdeni, D. transversa, and Sowerbyella compacta populations, a "muddy bottom" is not the only cause of high infant mortality. These species were apparently well adapted to a muddy environment. S. compacta appears to have been adapted to "floating" at the sediment-water interface and both of the Dinorthis species to attachment to larger sediment particles in the mud with, possibly, partial burial of the beak area for further support.

Richards and Bambach (in press, 1975) note that in populations with low juvenile mortality there is an increase in mortality at approximately 10-15% of the maximum age. This increase is attributed to the onset of sexual maturity and the physiological "strain" of reproduction. Only one species in the present study, Dinorthis holdeni (Figure 17, p. 48), displays a mortality increase (approximately 25% of maximum age) which can be explained in this manner. The other species have either a gradual increase with age (D. transversa, Figure 18, p. 49) or an increase too late in life to be explained by sexual maturity (Sowerbyella compacta, Figure 19, p. 50). The reason for the increases in these taxa is assumed here to have been due to geriatric effects.

It is interesting to note that two of the species discussed by Richards and Bambach (in press, 1975) bear striking resemblance, in terms of general morphology and life habits, to two species presented here. Zygospira modesta and Holtedahlina sulcata are analogous to Rostricellula rostrata and Sowerbyella compacta,

respectively. Both of the Zygospira and Rostricellula populations have high juvenile mortality in muddy environments, while the Holtedahlina and Sowerbyella populations have low juvenile mortality under similar conditions, suggesting a correlation between similar modes of life and similar responses to an environment, despite large taxonomic differences.

Summary

In summary, it is possible to draw the following conclusions:

1. The relatively close resemblance of the results of the three growth models (Levinton-Bambach, Sheldon, and histogram methods) indicates that all three can be employed to provide useful approximations of growth and mortality rates.

2. The theoretical advantages of the histogram peak method (requiring fewer a priori assumptions about the nature of growth rates and providing derivation of age in absolute units) make it the best choice when multimodal size-frequency histograms are available.

3. Population studies, as shown by the examples presented here, demonstrate that certain aspects of the structure and dynamics of a population appear to be intimately related to life habits and associated gross shell morphology. These aspects are believed to represent the population's "strategies" employed in dealing with various environments. In this study, at least one factor seems to reflect the population's response to its environment. The following cause and effect conclusions have been reached as a result of this study.

a. The shape of the growth curve of a population appears to be related to the life habits and gross morphology of the organisms. Small, pedunculate, rostrate brachiopods, such as Rostricellula rostrata (this study) and Gisilina gisii (Surlyk, 1972), have rapidly decreasing growth rates. Unattached, "floating" brachiopods, whether relatively flat strophomenids such as Sowerbyella compacta (this study) or large, biconvex terebratulids such as Terebratulina gracilis (Surlyk, 1972), have more linear growth rates. Two similar species of the same genus, such as Dinorthis holdeni and D. transversa (this study), have growth curves differing only in the older age classes. It is felt that the effects of environment are minimal since in one case populations of Rostricellula and Sowerbyella were taken from the same environment and the populations of the species of Dinorthis were taken from similar environments.

b. The mortality rate of a population appears to reflect, in part, the responses of the population to environmental conditions. The degree and form of the responses are determined by the tolerances of the organisms, which are, in turn, influenced by such factors as morphology, life habits, environmental strategies, etc. The same species, such as Rostricellula rostrata (this study), in different environments, has different mortality rates, reflecting the tolerance of the species to unfavorable conditions (brought on, in this case, by an increase in terrigenous clay in the environment).

Two species differing in life habits and morphology, such as Sowerbyella compacta and Rostricellula rostrata (this study), in the same environment, have different mortality curves, reflecting differences in tolerances. Two species of similar life habits and morphology, such as Zygospira modesta (Richards and Bambach, in press, 1975) and Rostricellula rostrata (this study) or Holtedahlina sulcata (Richards and Bambach, in press, 1975) and Sowerbyella compacta (this study), in similar environments, may have similar mortality rates, reflecting similar environmental tolerances. However, two similar species of the same genus, such as Dinorthis holdeni and D. transversa (this study) in similar environments, may have considerably different mortality rates, reflecting different tolerances.

c. Small, pedunculate brachiopods, such as Rostricellula rostrata (this study) and Zygospira modesta (Richards and Bambach, in press, 1975), when in "muddy" environments appear to have high juvenile mortality at sizes below two millimeters due to burial and/or lophophore clogging by the mud, as suggested by Richards and Bambach (in press, 1975). In the case of one population the effect was catastrophic. The absence of such a mortality pattern in the populations of Dinorthis studied suggests that the species were capable of coping with the problem in some unidentified manner.

d. Species with low juvenile mortality, such as Dinorthis holdeni, D. transversa, and Sowerbyella compacta, have

increased mortality in the older age classes due either to the onset of sexual reproduction (Richards and Bambach, in press, 1975, p. 27) or to geriatric effects.

4. There appears to be a correlation between high phenetic variability, linearity of growth rate, low juvenile mortality, adaptation to physically stressed ("muddy") environments and low species diversity communities. Although insufficient data are presented here to support this hypothesis, the data derived from this study agree well with the work of Sanders (1968), Bretsky and Lorenz (1969) and Levinton (1970). Additional studies along the lines established here are recommended on the basis of results to date.

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APPENDIX

TABLE 2

LOCATION OF COLLECTION SITES

Collection Site	Location and Remarks
	Dinorthis holdeni
Dh-1	West end of Edgemoor Bridge, on the south side of Edgemoor Road, 3.5 mi. (5.6 km) west of Claxton, Tn., in Anderson Co. Clinton Quadrangle (T.V.A. 137-SW). Remarks: good exposure of weathered residuum with silicified specimens, but has been overcollected.
Dh-2*	North side of Edgemoor Road, 3 mi. (5 km) west of Claxton in Anderson Co., Tn. Clinton Quadrangle (T.V.A. 137-SW). Remarks: excellent exposure producing both calcified and silicified specimens. Due to relief, the enclosing shales are well exposed yielding a diverse non-brachiopod fauna preserved as impressions. This locality is the source of the D. holdeni study collection.
Dh-3	East side of Clinton Highway (U.S. 25W), on the south slope of Flint Ridge, 4.7 mi. (7 km) south of Clinton, in Anderson Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: specimens silicified and apparently associated with (secondary?) chert layers. This location was reported by Cooper (1956, p. 396).
Dh-4	East side of Interstate 75 on the south slope of Flint Ridge, approximately 0.25 mi. (0.4 km) north of Raccoon Valley Road, Knox Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: poor exposure, specimens silicified.
Dh-5	On hillside to west of Elkins Road immediately north of the intersection with Raccoon Valley Road, Knox Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: specimens silicified and associated with beds of (secondary?) chert.

TABLE 2 (continued)

Collection Site	Location and Remarks
	Dinorthis transversa
Dt-1*	In drainage ditch on the east side of Clinton Highway (U.S. 25W), 5 mi. (8 km) south of Clinton, 100 yds. (90 m) south of the intersection with Raccoon Valley Road, approximately 10 ft. (3 m) stratigraphically above Sc-1, in Anderson Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: articulated D. transversa scattered throughout rock and associated with "channels." This location supplied a few specimens to the study collection.
Dt-2	South side of Raccoon Valley Road, approximately 2 mi. (3.6 km) east of Claxton, in Knox Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: poor exposure.
Dt-3*	North side of Raccoon Valley Road, approximately 3 mi. (5 km) east of Claxton and 1 mi. (1.6 km) west of Heiskell, Knox Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: excellent exposure from which most of the study collection came.
Dt-4*	West side of Norris Freeway (U.S. 441) 14 mi. (23 km) north of Knoxville, in bank adjacent to Cedar Grove Church, Knox Co., Tn. Big Ridge Park Quadrangle (T.V.A. 146-NW). Remarks: locality once good but now over-collected. The few specimens found were included in the study collection.
Dt-5*	Approximately 500 yds. (450 km) east of Norris Freeway (U.S. 441) 14 mi. (23 km) north of Knoxville, on hillside opposite Cedar Grove Church, Knox Co., Tn. Big Ridge Park Quadrangle (T.V.A. 146-NW). Remarks: excellent exposure of D. transversa and "channels." This location is the source of a large portion of the study collection.

TABLE 2 (continued)

Collection Site	Location and Remarks
	Sowerbyella compacta
Sc-1	In drainage ditch on the east side of Clinton Highway (U.S. 25W), 5 mi. (8 km) south of Clinton, 100 yds. (90 m) south of the intersection with Raccoon Valley Road, approximately 10 ft. (3 m) stratigraphicly below Dt-1, in Anderson Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: the Sowerbyella fauna does not appear to be as well developed here as in Sc-2.
Sc-2*	North side of Raccoon Valley Road approximately 1.6 mi. (2.6 km) east of Heiskell and 100 yds. (90 m) west of Diggs Gap Road, Knox Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: several excellent exposures in the general area, the one from which the study collection was taken 30 ft. (10 m) west of an abandoned driveway. This locality was reported by Cooper (1956, p. 779).
	Rostricellula rostrata
Rr-1	East side of Old Central Pike, 0.4 mi. (0.6 km) south of Heiskell, Knox Co. Tn. Powell Station Quadrangle (T.V.A. 137-SE).
Rr-2*	North side of Raccoon Valley Road approximately 1.6 mi. (2.6 km) east of Heiskell and 100 yds. (90 m) west of Diggs Gap Road, Knox Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: the residuum from which the "juvenile" population was collected forms the bed of an abandoned driveway.
Rr-3*	East side of Interstate 75 at Diggs Gap, south of Raccoon Valley, at north end of outcrop, in Knox Co., Tn. Powell Station Quadrangle (T.V.A. 137-SE). Remarks: excellent exposure and source of comparative population.

TABLE 2 (continued)

Collection Site	Location and Remarks
	This locality was described as "bed 1" by Milici and Walker (1973, p. 154). Ecological succession involving R. rostrata at this locality described by Walker and Alberstadt (in press, 1975).

*Collection sites from which the populations in this study were taken.

TABLE 3

LITHOLOGIC DESCRIPTIONS OF COLLECTION HORIZONS

Dinorthis holdeni Beds
HIGHLY ARGILLACEOUS BIOMICRITE - Fossil content approx. 20%, composed primarily of *Dinorthis* and other brachiopods, trilobite segments, ramose trepostome bryozoans, and sponge spicules. Most brachiopods articulated and all larger fossils appear to have suffered little abrasion. Indistinct layers of fine (approx. 50-100 microns) fossil debris present. Some selective replacement of brachiopod shell material by silica.
Dinorthis transversa Beds
HIGHLY ARGILLACEOUS BIOMICRITE - Fossil content low, approx. 2%, composed of *Dinorthis* and unidentified juvenile (*Rostricellula*?) brachiopods, sponge spicules, trilobites and echinoderm fragments. All except the last category appear to be relatively in place. The fragmentary nature of the echinoderm fossils implies transportation. Relatively well defined burrows, oval in cross section with their long axis parallel to bedding, are present and appear to be filled with microspar. Thin indistinct lenses of fine (approx. 50-100 microns) fossil debris are present, although in lesser abundance than in the *D. holdeni* beds. "Channel deposits" found within the *D. transversa* beds are composed of argillaceous biomicrite with approx. 20% fossils, which include fragments of brachiopods, trilobites, cryptostome and trepostome bryozoans in both ramose and encrusting habits, ostracodes, and echinoderms. All fossil material appears somewhat abraded and few specimens are articulated. Rounded intraclasts and fecal pellets present, primarily near base. Some geopedal, spar-filled voids beneath fossil fragments. Contact with surrounding lithology sharp.
Sowerbyella compacta and "juvenile" *Rostricellula rostrata* Beds
HIGHLY ARGILLACEOUS BIOMICRITE - Fossil content approx. 10-20% composed primarily of articulated *Sowerbyella* and juvenile *Rostricellula* shells. Rocks from these beds not available for thin-sectioning. Rock immediately above and below these beds is argillaceous biomicrite, fossil content approx. 30%, composed of brachiopods (orthids, strophomenids, rhynchonellids), cryptostome and trepostome ramose bryozoans, trilobites, gastropods, ostracodes,

TABLE 3 (continued)

and echinoderms. A few rounded intraclasts are present, as well as relatively distinct burrows. The fossils are not badly abraded, but few are articulated and their arrangement is chaotic, numerous geopedal pockets of spar and microspar occurring beneath the fragments. As the distance away from the collection horizon is increased (1 foot above) the amount of spar and microspar as well as the chaotic nature of the deposits are increased.

"Normal" Rostricellula rostrata Beds*

BIOSPARITE - Fossil content 10-20%, composed primarily of brachiopods (strophomenids and rhynchonellids, the strophomenids being concentrated near the base of beds), ramose and encrusting trepostome and cryptostome bryozoans, trilobites, ostracodes, gastropods, and echinoderm fragments. Pellets and intraclasts of argillaceous micrite present. Many geopedal spar filled voids. Shells poorly sorted, generally disarticulated, but relatively unabraded. The above lithology is found interbedded with highly argillaceous micrite, which is generally unfossiliferous.

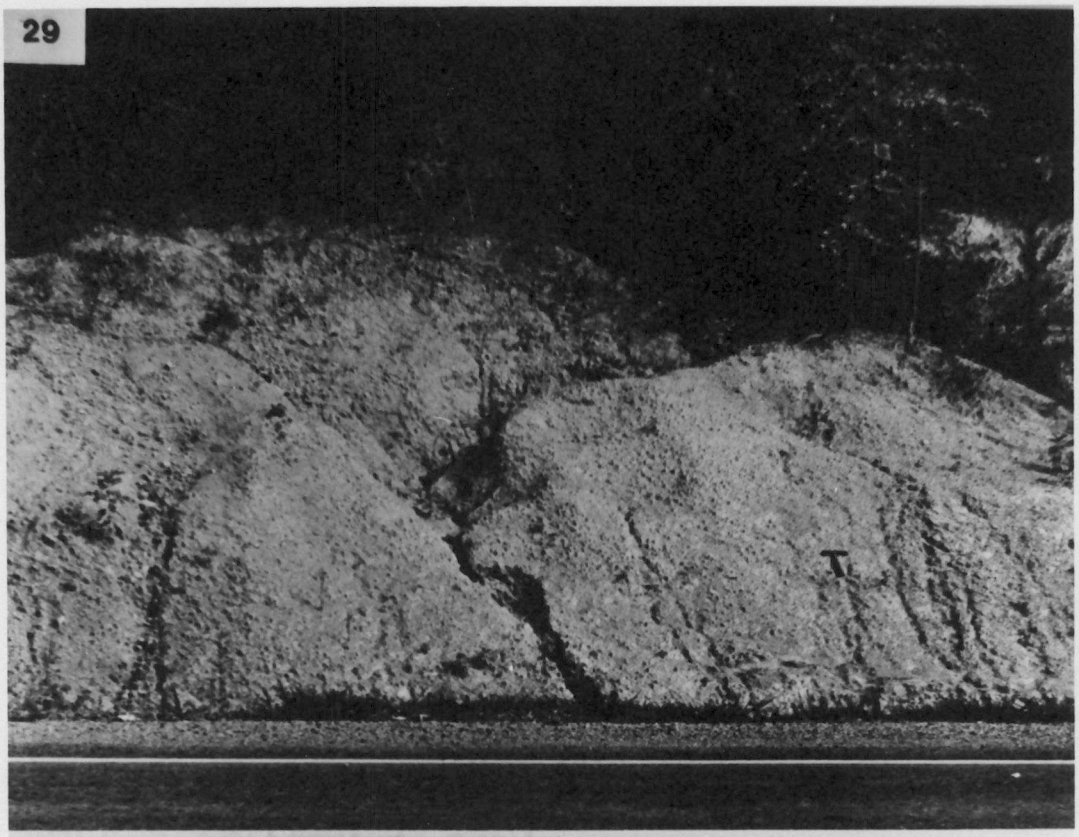
*This description abstracted, in part, from Milici and Walker, 1973.

PLATES

PLATE I. *Dinorthis holdeni* Collection Horizon, Collection Locality Dh-2.

Figure 29. Collection Locality Dh-2.
Note rock hammer for scale.

Figure 30. Close-up of Area Around Hammer in Figure 29.
The scale is six inches (15 cm) long.



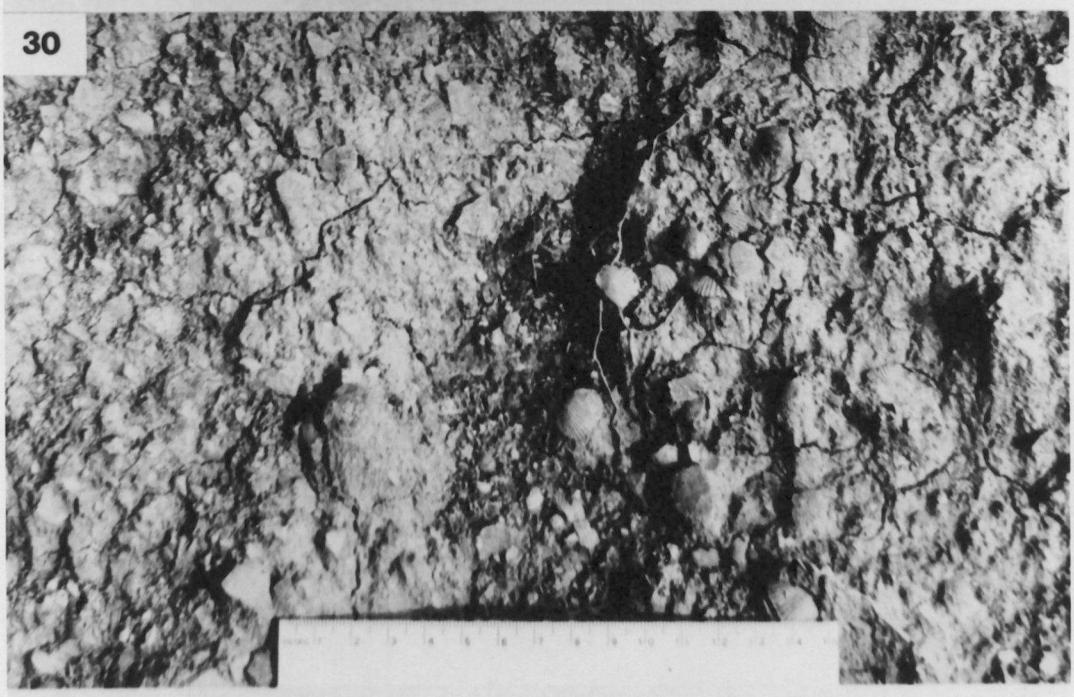


Plate I

PLATE II. Dinorthis transversa Collection Horizon, Collection Localities Dt-1 and Dt-4.

Figure 31. Collection Locality Dt-1.
Rock hammer gives scale and exact location of horizon.

Figure 32. Close-up of Area Around Hammer in Figure 31.
The scale is six inches (15 cm) long and parallel to bedding.

Figure 33. Collection Locality Dt-4.
Note rock hammer for scale.

Figure 34. Close-up of Area Around Hammer in Figure 33.
The scale is six inches (15 cm) long and parallel to bedding.



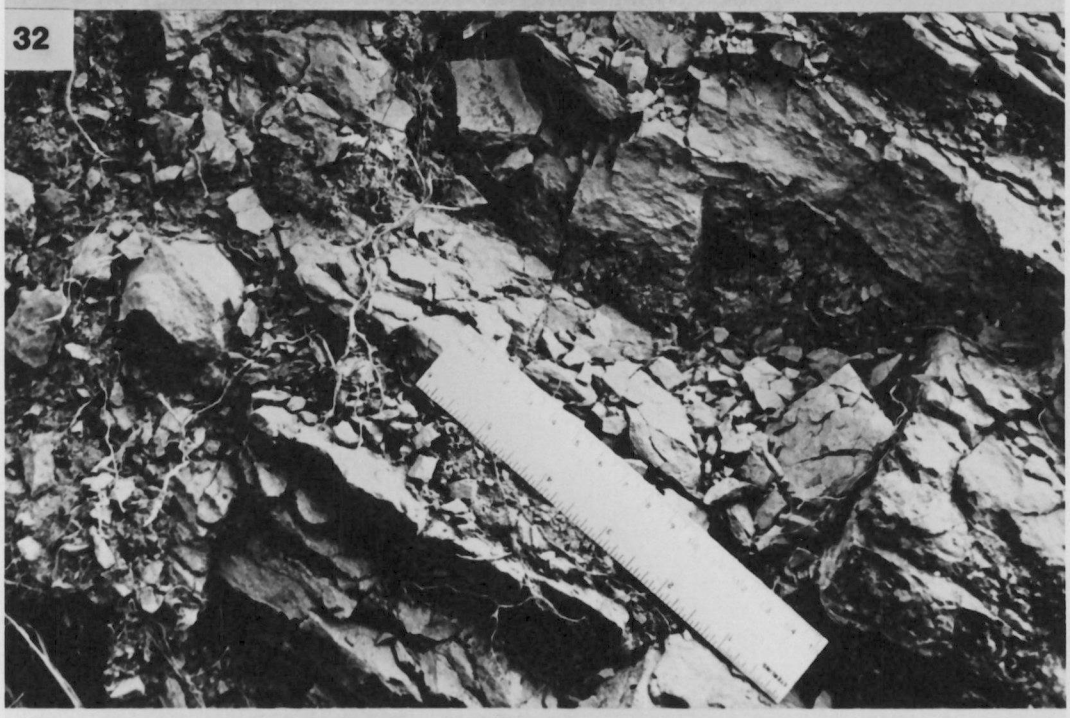


Plate II



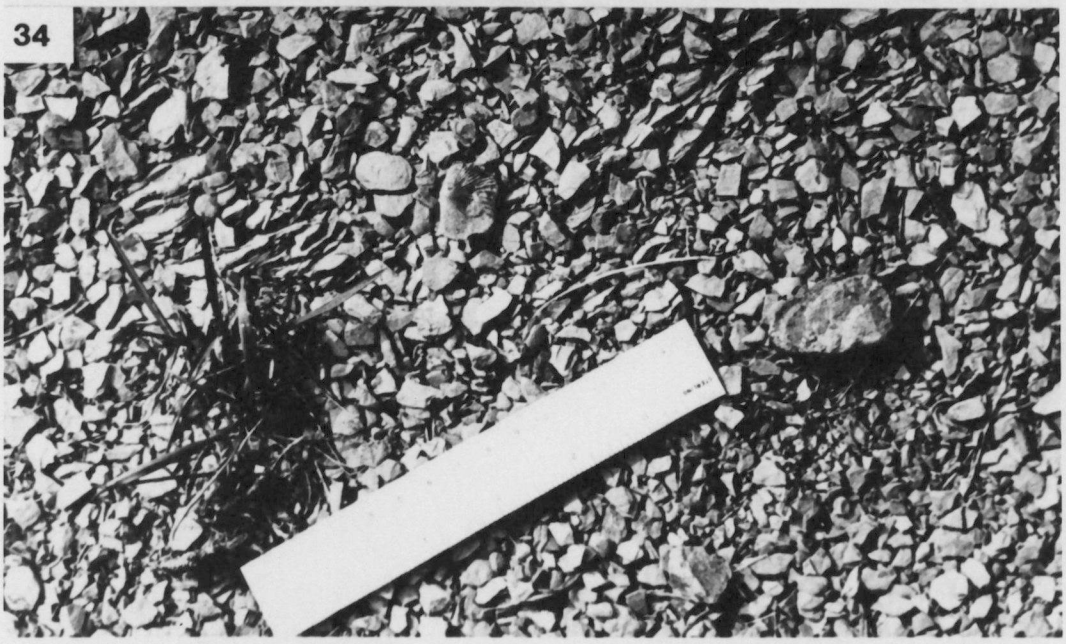


Plate II (continued)

PLATE III. Sowerbyella compacta and "Juvenile" Rostricellula rostrata Collection Horizon, Collection Localities Sc-2 and Rr-2.

Figure 35. Collection Localities Sc-2 and Rr-2.

Figure 36. Close-up of Collection Locality Sc-2. The scale is six inches (15 cm) long.

Figure 37. Close-up of Collection Locality Rr-2. The scale is six inches (15 cm) long.



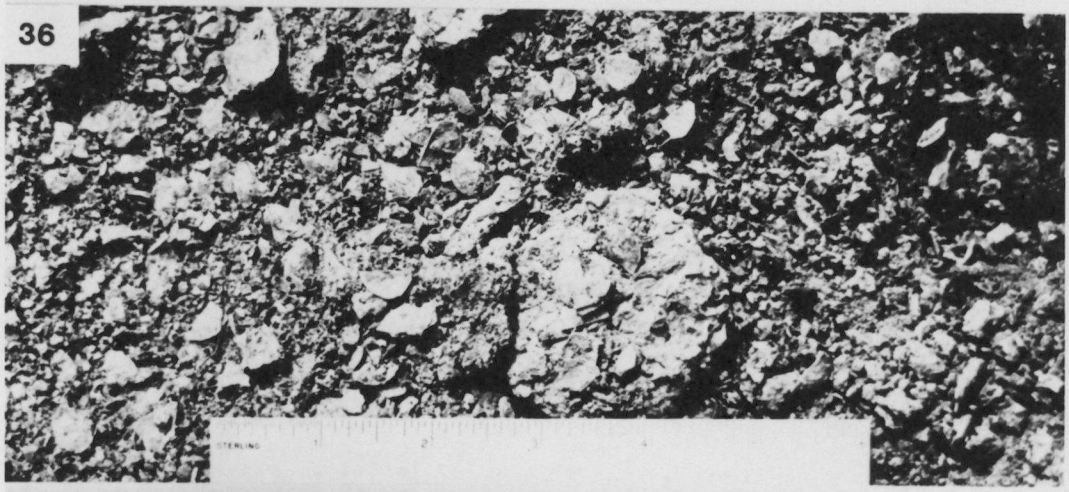




Plate III

PLATE IV. Brachiopod Species Under Study.

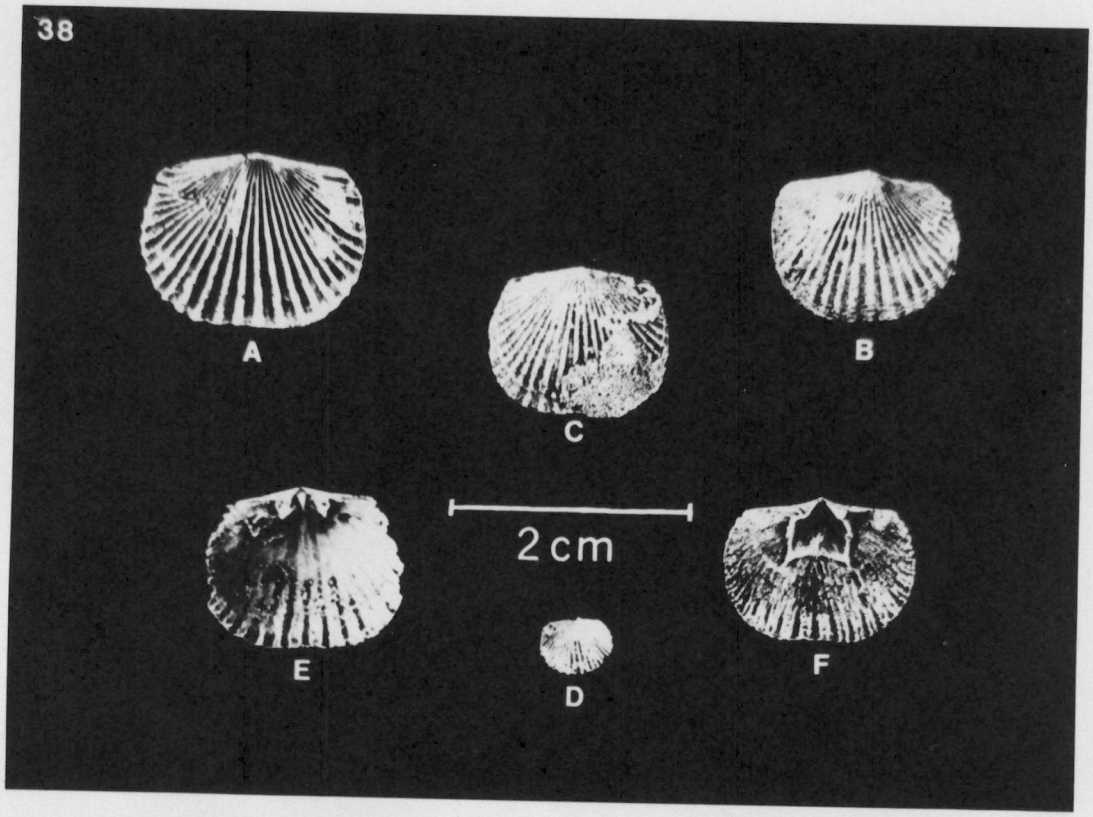
Figure 38. Dinorthis holdeni.
(A) brachial valve, exterior. (B) pedicle valve, exterior. (C) brachial valve, exterior, showing growth line and encrusting bryozoan. (D) juvenile. (E) brachial valve, interior. (F) pedicle valve, interior.

Figure 39. Dinorthis transversa.
(A) pedicle valve. (B) brachial valve. (C) brachial valve with growth lines and edrioasteroid? (D) brachial valve with growth lines and encrusting bryozoan.

Figure 40. Sowerbyella compacta.
(A) brachial valve. (B) and (C) pedicle valves.

Figure 41. Rostricellula rostrata.
(A) and (C) pedicle valves. (B), (D), and (E) brachial valves.

Figure 42. Rostricellula rostrata Juveniles.



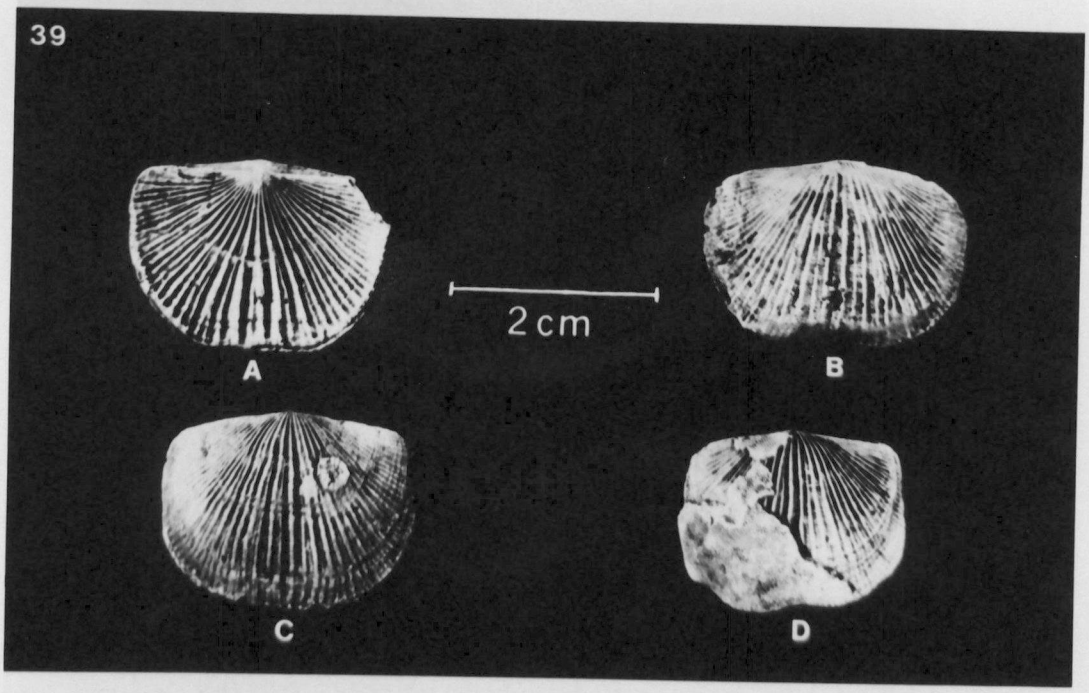
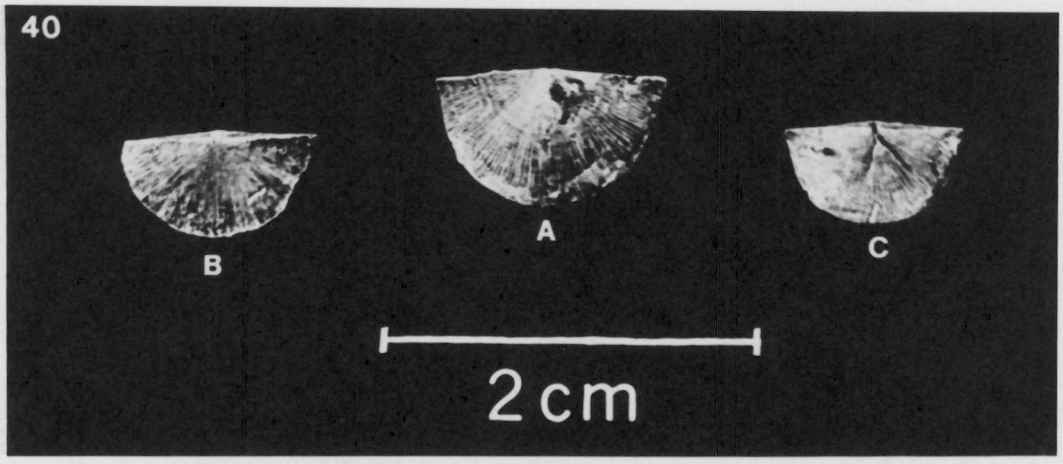
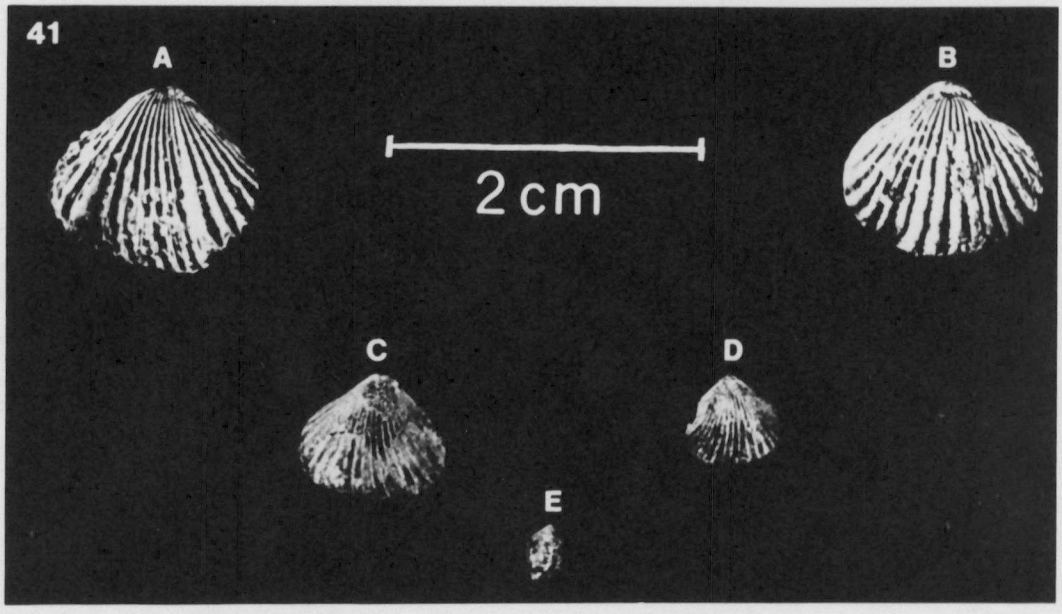


Plate IV





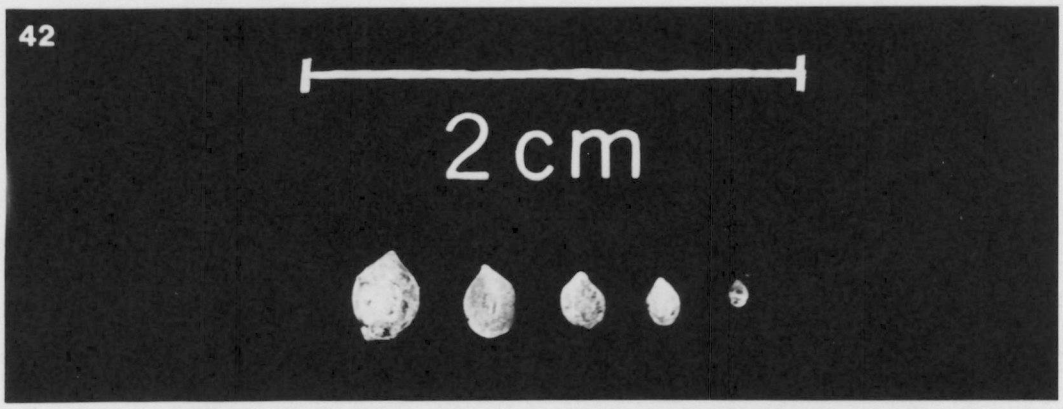


Plate IV (continued)

VITA

Born on May 25, 1952, in Knoxville, Tennessee, William Charles Parker attended primary and secondary schools in that city. After graduating first in his class from Knoxville's Central High School in June of 1970, he entered the University of Tennessee in the summer of 1970 on a National Merit Scholarship. During the course of his study, he received the W. A. Tarr award and a Schlumberger scholarship, was elected to Phi Beta Kappa and Sigma Gamma Epsilon, and served one year as Vice-President of Gamma Gamma Chapter of S.G.E. In spring of 1973 he graduated with highest honors and received a Bachelor of Arts degree in geology. His Master's study began in the fall of 1973, specializing in paleontology and paleoecology. After receiving his Master of Science degree in geology in December of 1975, he will begin work on a Doctoral degree at the University of Chicago. Bill is presently a member of Sigma Gamma Epsilon and The Palaeontological Association.