GROWTH, MORPHOLOGY, HABIT AND HABITAT OF SELECTED
BRACHIOPOD AND MOLLUSC SPECIES FROM THE MEADE PEAK
MEMBER OF THE PHOSPHORIA FORMATION, PERMIAN, NORTHEASTERN
UTAH - SOUTHEASTERN IDAHO - SOUTHWESTERN WYOMING

by

Scott Lewis Russell

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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in

Geology

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Very special thanks go to my wife Karen. She assisted in collecting fossils in Montpelier Canyon, proofread the manuscript, and provided financial, as well as moral, support. Without her love and devotion, this study never would have been possible.

Scott Lewis Russell
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ABSTRACT

Growth, Morphology, Habit and Habitat of Selected Brachiopod and Mollusc Species from the Meade Peak Member of the Phosphoria Formation, Permian, Northeastern Utah - Southeastern Idaho - Southwestern Wyoming

by

Scott Lewis Russell, Master of Science
Utah State University, 1980

Major Professor: Dr. Richard R. Alexander
Department: Geology

The Permian Meade Peak Member of the Phosphoria Formation was examined at four localities in this investigation. Fossils were collected at each locality. The four collecting localities visited in this investigation are: Brazier Canyon, Utah, Montpelier Canyon, Idaho, Coal Canyon, Wyoming, and Cokeville, Wyoming.

The environment of deposition of the Meade Peak Member in the study area is inferred to have been an outer shelf or basin characterized by moderately deep and quiet water. This has aided reconstruction of life-habits, population dynamics, and growth characteristics of the examined species.

The articulate brachiopod Leiorhynchoidea weksi is inferred to have attached itself to the substrate by means
of a pedicle. The observed variability in the sulcus of this species is assumed to have been influenced by intra-specific competition, which may reflect partitioning of nutrient resources at different levels in the water above the substrate.

The articulate brachiopod *Lissochonetes ostiolatus* probably assumed an unattached existence, lying free on the substrate. Several population samples exhibited stunted growth relative to the *L. ostiolatus* population sample from Montpelier Canyon. Two environmental variants possibly contributed to the inhibition of growth. These are negative Eh, inferred from the associated organic matter in the lithologies, and competition for space.

*Lingula carbonaria*, an inarticulate brachiopod, is thought to have had an infaunal mode of life. A population sample of *L. carbonaria* from Cokeville exhibits substantially larger morphologic mean sizes than two other population samples. These differences can be explained by the fact the sandy lithology from which the larger collection was taken was associated with conditions which facilitated growth. Also, availability of phosphate, inferred from the $P_2O_5$ content of the lithology, probably accelerated growth because inarticulates utilize calcium phosphate as shell material.

*Orbiculoidea missouriensis* is an inarticulate brachiopod. It is inferred to have been attached to the substrate by a pedicle. Of the three population samples of *O. missouriensis*
analyzed, the sample from Brazier Canyon displays larger morphologic mean sizes. This is interpreted as indicating that reducing conditions, inferred from associated organic matter, were milder in that environment.

The gastropod *Babylonites ferrieri* displays a low, expanded form, and is thought to have crawled over the surface of the sediment. The food source of this gastropod is not known, but may have been algae, carrion, detritus, or soft-bodied invertebrates.

Two bivalves collected are assumed to have been shallow burrowing, labial palp feeders. Both *Nuculopsis montpelierensis* and *Polidevicia obesa* represent this mode of life. Of the two population samples of *P. obesa* examined, the one from Cokeville displays larger morphologic means. The environmental stimuli proposed for this difference is competition and an inferred softer substrate in the Montpelier assemblage.

The bivalve *Edmondia phosphatica* is inferred to have been a shallow burrowing, siphonate species.

*Streblochondria montpelierensis* and *Aviculopecten phosphaticus* are bivalves related to modern pectenoids. *S. montpelierensis* is assumed to have been unattached, living epifaunally, and capable of swimming movement. *A. phosphaticus* is inferred to have been a byssally attached epifaunal bivalve.

The environmental factors influencing the morphologic variation are also inferred to have affected size-frequency
distributions and survivorship curves. The effects of reducing conditions have resulted in higher juvenile mortality and/or inhibited growth. Coarser substrates have yielded population samples that exhibit negatively skewed distributions, whereas finer-grained substrates have yielded positively skewed distributions.

Growth curves constructed for each population sample generally show a decline in growth rate with age. Some linear trends are noted.

Growth lines were used to infer an approximate life span for each species. Conservative approximations of the life spans of the examined species are: *L. weels*, 9 years; *L. ostiolatus*, 5 years; *L. carbonaria*, 8 years; *A. phosphaticus*, 4 years; *O. missouriensis*, 2.3 years; *P. obesa*, 5 years; and *B. ferrieri*, 3.4 years.

(155 pages)
INTRODUCTION

Objective

This investigation was undertaken to reconstruct the habit, habitat, population dynamics, and growth patterns of selected abundant species of brachiopods and molluscs found within the limestones, shales, and siltstones of the Meade Peak Member of the Phosphoria Formation. Morphometric and demographic analysis of species, coupled with geochemical and petrofabric analysis of associated lithologies, facilitate interpretation of functional morphology and survivorship.

The results of field and laboratory data provide the basis for reconstructing environmental influences on morphologic variation, population dynamics, and growth rates. Inferences drawn from the lithologic and skeletal data include substrate texture and stability, bathymetric position, current intensity, redox potential of the environment, and efficiency in the utilization of calcium carbonate by the accretionary skeletonized species.

Collecting Localities

The Meade Peak Member of the Phosphoria Formation was examined at four locations in northeastern Utah, southeastern Idaho, and southwestern Wyoming. These locations
include Brazier Canyon, Utah (Figure 1), Montpelier Canyon, Idaho, Coal Canyon, Wyoming, and Cokeville, Wyoming (Figure 2). Collections of brachiopods and molluscs, as well as samples of lithologies associated with the fossil collections, were taken from each of these localities.

Brazier Canyon is located in the Rex Peak Quadrangle, Rich County, Utah. This canyon lies within the Crawford Mountains which are part of a large, north by northeast trending syncline. The canyon is accessible by an improved road which is approximately 2.0 kilometers north of Randolph, Utah along Utah State Highway 16 (Figure 3). The Phosphoria Formation crops out along both sides of the road in the canyon in NE. 1/4, NW. 1/4, SE. 1/4 section 18, T. 11 N., R. 8 E. It is in this area, on the north side of the road, that fossils were collected and lithologies sampled (Figure 4).

Montpelier Canyon, located in the Preuss Range east of Montpelier, Idaho, is situated within the Montpelier Canyon Quadrangle. Here the Phosphoria Formation, exposed in what is known as the Waterloo claim, crops out in section 6, T. 13 S., R. 45 E. (Figure 5). Collections were obtained from SE. 1/4, NW. 1/4, SW. 1/4 section 6, T. 13 S., R. 45 E. Access to the area is by an unimproved road which leads south to the county gun range from U. S. Highway 89. Here fossil populations and the associated lithology were sampled on the west slope of the mountain in debris blocks of "Cap" limestone (Figure 6).
Figure 1. Brachiopod and mollusc collecting locality in the Permian Meade Peak Member of the Phosphoria Formation, Brazier Canyon, Utah.
Figure 2. Brachiopod and mollusc collecting localities in the Permian Meade Peak Member of the Phosphoria Formation in Idaho and Wyoming.
Figure 3. Brazier Canyon, Utah: view east.
Figure 4. Brazier Canyon, Utah collecting site. The Meade Peak Member of the Phosphoria Formation crops out just north of the road: view northeast.
Figure 5. Outcrop of the Meade Peak Member of the Phosphoria Formation at Montpelier Canyon, Idaho: view south.
Figure 6. Montpelier Canyon, Idaho collecting site showing scattered debris blocks of "Cap" limestone from which collections of fossils were taken: view north.
Collections from Coal Canyon, Wyoming were taken from SW. ¼, NW. ¼, NE. ¼ section 7, T. 26 N., R. 119 W. This canyon is situated very near the Idaho-Wyoming border in the Sublette Range, south of Raymond Canyon (Figure 7). Access to the collecting site is by unimproved road east from U. S. Highway 89. Outcrops of the Phosphoria Formation are present near the mouth of the canyon between elevations of 7000 and 7320 feet, and are accessible only on foot. Most of these outcrops are poorly exposed due to weathering and the steep westerly dip of the strata (Figure 8).

The fourth area, Cokeville, Wyoming, is located in the Cokeville Quadrangle. In this location the Phosphoria Formation crops out on the east limb of a north-south trending anticline (Figure 9). This tightly folded anticline is situated immediately east of Cokeville, and is labeled on the quadrangle as Rocky Point. Vehicular access to the collection site is good. U. S. Highway 89, which passes through Cokeville, is intersected by an unimproved dirt road approximately 1.2 kilometers north of town. This road extends eastward along the exposed base of the anticline. Fossils were taken from the east limb of the anticline in NW. ¼, SE. ¼, SW. ¼ section 33, T. 25 N., R. 119 W. The collection site is the trench extending above an old mine shaft, approximately 73 meters above the road (Figure 10).
Figure 7. Coal Canyon, Wyoming: view east.
Figure 8. Coal Canyon, Wyoming collecting site (dashed): view north.
Figure 9. North-south trending anticline near Cokeville, Wyoming. Collecting site is situated on the east limb: view north.
Figure 10. Mine trench on the east limb of the anticline near Cokeville, Wyoming where fossil collections were taken. Outcrops of the Meade Peak Member of the Phosphoria Formation are well exposed: view north.
Procedure

Each of the fossil collections in this study were taken in a detailed uniform manner to insure random sampling. Care was taken not to exclude the juvenile portion of the population from the samples. It was necessary to vary the sampling technique with the different lithologies. In some lithologies it was possible to collect population samples of weathered-free fossils. In other areas fossils from talus debris were collected. In many lithologies it was necessary to extract samples from in-place bedrock. Samples were collected only from homogeneous strata, thinly bedded where possible, in order to minimize the number of generations aggregated and to maximize the uniformity of environments occupied.

In the Montpelier Canyon area it was possible to map orientations of fossils exposed on a portion of a bedding plane. Such mapping was not possible in the other collecting localities due to intense weathering of the rocks and lack of exposures. At the Cokeville collecting locality the stratigraphic section was measured. At the other localities the section had been measured previously and described in the published literature (Sheldon and others, 1954; Smith and others, 1952; Girty, 1910).

Laboratory work included: 1) measurement of various morphologic dimensions of the collected specimens; 2) graphic representation of the size-frequency distribution and
survivorship curve for each population sample; 3) graphic representation of the growth-increment pattern of selected specimens characteristic of population samples; 4) chemical analysis of each of the associated lithologies for content of $P_2O_5$ and organic matter; 5) graphic representation of the compass orientation of the fossils mapped on a bedding plane, and statistical analysis for randomness of orientations.

**Previous Work**

Early work on the Phosphoria Formation was done by Weeks and Ferrier (1907). Their work concentrated on the general geology and stratigraphy of the phosphate deposits in the western United States. Richards and Mansfield (1912) originally named the Phosphoria Formation and designated the type locality as Phosphoria Gulch, Idaho.

Much of the available information concerning the Phosphoria Formation is based on research done in connection with the development of economic phosphate deposits in the western United States. Regional studies concerning these deposits were initiated by the U. S. Geological Survey after World War II (Sheldon and others, 1967:1).

Detailed stratigraphic sections of the four localities discussed in this study are given in several U. S. Geological Survey Circulars (McKelvey, Armstrong and others, 1953; McKelvey, Smith and others, 1953; Sheldon and others, 1953; Smith and others, 1952). These circulars
contain detailed information on lithologies, thicknesses, and chemical analyses.

The history and current system of nomenclature of the Phosphoria Formation has been described by McKelvey and others (1956, 1959). These investigators recognized and named six members in the formation, and included detailed stratigraphic sections from the type locality of each. The studies also contain the current age assignment of the formation.

Sheldon (1963) described the physical stratigraphy and petrography of Permian rocks from western Wyoming. In 1967, Sheldon and others published a study on the paleogeography and sedimentation of the Phosphoria Formation. This last report concentrated on facies relationships, paleogeographic environments, and chemical environments.

Only five papers describe or illustrate the more common elements of the Permian invertebrate fauna of the study area involved. Girty (1910) published the earliest paleontological study on the Phosphoria Formation. His descriptions and identifications of fossils are based mostly on those obtained from the "Cap" limestone of the Meade Peak Member of the Phosphoria Formation in Montpelier Canyon, Idaho. Girty also included descriptions and illustrations of specimens from Cokeville and Thomas Fork, Wyoming. Boutwell (1912) and Mansfield (1927) provided illustrations of a limited number of Girty's collections from the Park City district, Utah and have described a few
species from the study area. Branson (1930) described a large Phosphoria fauna based primarily on collections from the Wind River and Owl Creek mountains in west-central Wyoming. His publication contained a more extensive list of Phosphoria species than that of Girty (1910). In 1963 Ciriacks published a study of the bivalve fauna in Utah, Idaho, Wyoming, and Montana. His work included excellent descriptions and illustrations of specimens from the Permian Phosphoria Formation, as well as Triassic specimens.

In 1963 Yochelson published a short paper on the paleoecology of the Phosphoria Formation. His article inferred a basinal setting for the black shales and cherts of the formation and the associated faunal assemblages of the environment. Later, in 1968, Yochelson produced a more extensive study on the paleoecology and biostratigraphy of the Permian age rocks of Utah, Idaho, and Wyoming. This work included a detailed interpretation of the paleoecologic implications of the Phosphoria faunas. Yochelson listed species, recorded their stratigraphic ranges, and organized their lithologic associations.
STRATIGRAPHY

The Phosphoria Formation of Permian age was named based on stratigraphic exposures in Phosphoria Gulch located in Bear Lake County, Idaho (Richards and Mansfield, 1912:684). This locality is still representative of the formation as it is presently known (McKelvey and others, 1959:20). In the area of the type locality the Phosphoria ranges in thickness from 76 to 137 meters. The dominant lithologies contained within the formation are dark chert, phosphatic and carbonaceous mudstone, phosphorite, cherty mudstone, and minor amounts of dark limestone (McKelvey and others, 1959:20).

The formation in the vicinity of the type locality is underlain by the Grandeur tongue of the Park City Formation, and overlain by the Dinwoody Formation of Triassic age. The lower boundary of the Phosphoria Formation has been placed at the base of a thin phosphorite bed which contains abundant fish scales, and overlies the Permian Park City Formation. The upper boundary is rarely exposed, but has been placed at the top of a nodular phosphorite which contains casts of what McKelvey and others (1959:20) have described as sponge spicules.

The Phosphoria Formation is divided into six members, four of which are recognizable at the type locality of
Phosphoria Gulch. In stratigraphic succession, these members are: the Lower Chert Member, the Meade Peak Phosphatic Shale Member, The Rex Chert Member, The Cherty Shale Member, the Retort Phosphatic Shale Member, and the Tosi Chert Member (Sheldon, 1963:74). This investigation is concerned only with the Meade Peak Phosphatic Shale Member.

McKelvey and others (1959:22) applied the name Meade Peak Phosphatic Shale Member of the Phosphoria Formation to the Phosphatic Shale Member of Richards and Mansfield (1912:683). The name is derived from Meade Peak, which is the highest point on Snowdrift Mountain. This peak is about 4 kilometers south of Phosphoria Gulch.

The Meade Peak Phosphatic Shale Member, in its type locality, is composed commonly of dark, carbonaceous phosphatic and argillaceous rocks (McKelvey and others, 1959:22). The wide variety of rock types indicates that the environment of deposition was not homogeneous.

Age assignment of the Meade Peak Phosphatic Shale Member has been based dominantly on regional faunal correlation. The cephalopods found in the Meade Peak Member have most frequently been used for age determination of this member (McKelvey and others, 1959:39). Miller and Cline (1934:283) originally considered the cephalopods indicative of mid-Permian Wordian age. McKelvey and others (1959:39) also asserted that certain species of the genus Psuedogastrioceras found within the Meade Peak Member are abundant only in beds of Wordian age in the United States.
Later workers have revised this correlation and considered the associated cephalopods to be indicative of a Leonardian age (Yochelson, 1968:622). The problem of age of the Meade Peak Member is still unresolved, but collectively the above-cited evidence suggests a late Leonardian-early Wordian age.

At the collection localities of this report the Meade Peak Member of the Phosphoria Formation is dominated by calcareous siltstones, mudstones, and phosphorites. The Meade Peak Member varies in thickness between collecting localities, but rarely exceeds more than 60 meters.

At all of the localities visited the Meade Peak Member was conformably underlain by the Pennsylvanian Wells Formation, and conformably overlain by the Rex Chert Member of the Phosphoria Formation. Only one stratigraphic section was measured in the field. This section was at the Cokeville, Wyoming locality (Figure 11d). Generalized stratigraphic sections obtained from the literature for the other three localities are also presented in Figure 11a, b, and c.

The variety and frequency of alternation of rock types in the Meade Peak Member, shown in these short vertical sequences reflect the geologically rapid changes in depositional environment characteristic of this member. Exposures of this member are usually extremely weathered, and in many areas bedrock is covered by weathering products. The best exposures, and those utilized in this
study, are man-made, i.e., created by trenching and mining activity.
Figure 11. Stratigraphic sections of the Permian Meade Peak Member of the Phosphoria Formation at the study localities. Numbers adjacent to beds indicate the position of fossil collections within each section and the lithologic number referred to in this report. a. Coal Canyon, Wyoming (Sheldon and others, 1954:3). b. Montpelier Canyon, Idaho (Girty, 1910:15). c. Brazier Canyon, Utah (Smith and others, 1952:2). d. Cokeville, Wyoming section measured in this investigation.
LITHOLOGY

Lithologic Description and Faunal Content

Many different lithologies are found in the Meade Peak Member of the Phosphoria Formation at the localities in this study. It is not within the scope of this report to describe all of these lithologies. The lithologies discussed and described in this section are those which are associated with the various fossil collections made in the field. The lithologies were sampled for description only if they contained abundant, identifiable fossils.

The following descriptions and the associated fauna of each lithology are keyed with a lithologic number. These numbers will aid in referring to a particular bed from which a fossil collection was taken, and will be used for future reference in this study. Table 1 gives a summary of lithologies, associated fauna, location, and results of chemical analyses. In this report the Munsell color system is used in connection with lithologic descriptions.

Brazier Canyon, Utah locality

Two different lithologies were found in Brazier Canyon which contain abundant, collectable fossils. Each of these beds is dominated by a single species. Other faunal elements are rare.
Table 1. Key for lithologies associated with brachiopod and mollusc collections.

<table>
<thead>
<tr>
<th>Collecting Locality</th>
<th>Lithologic Number</th>
<th>% Organic</th>
<th>% P₂O₅</th>
<th>Lithologic Description</th>
<th>Collected Fauna</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brazier Canyon, Utah</td>
<td>1</td>
<td>0.42</td>
<td>0.46</td>
<td>Brownish grey (5YR2/1) calcareous mudstone</td>
<td>Lissochonetes ostiolatus</td>
</tr>
<tr>
<td>Brazier Canyon, Utah</td>
<td>2</td>
<td>0.35</td>
<td>0.20</td>
<td>Pale yellowish brown (10YR6/2), sandy siltstone</td>
<td>Orbiculoidea missouriensis</td>
</tr>
<tr>
<td>Montpelier Canyon, Idaho</td>
<td>3</td>
<td>0</td>
<td>4.83</td>
<td>Greyish black (N2) micritic limestone</td>
<td>Bablyonites ferrieri</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Leio rhynchoidea wekbi</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lissochonetes ostiolatus</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Polidevcia obesa</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Nuculopsis montpelierensis</td>
</tr>
<tr>
<td>Coal Canyon, Wyoming</td>
<td>4</td>
<td>1.30</td>
<td>0.38</td>
<td>Pale yellowish brown (10YR6/2) siltstone</td>
<td>Orbiculoidea missouriensis</td>
</tr>
<tr>
<td>Coal Canyon, Wyoming</td>
<td>5</td>
<td>0.54</td>
<td>0.81</td>
<td>Dark yellowish brown (10YR4/2), calcareous mudstone</td>
<td>Lissochonetes ostiolatus</td>
</tr>
<tr>
<td>Coal Canyon, Wyoming</td>
<td>6</td>
<td>0.49</td>
<td>0.21</td>
<td>Medium grey (N5) calcareous siltstone</td>
<td>Orbiculoidea missouriensis</td>
</tr>
<tr>
<td>Coal Canyon, Wyoming</td>
<td>7</td>
<td>0.59</td>
<td>0.29</td>
<td>Pale brown (5YR5/2) siltstone</td>
<td>Lingula carbonaria</td>
</tr>
<tr>
<td>Collecting Locality</td>
<td>Lithologic Number</td>
<td>% Organic</td>
<td>% P$<em>{2}O</em>{5}$</td>
<td>Lithologic Description</td>
<td>Collected Fauna</td>
</tr>
<tr>
<td>---------------------------</td>
<td>-------------------</td>
<td>-----------</td>
<td>----------------</td>
<td>----------------------------------------------------------------------------------------</td>
<td>----------------------------------------------------</td>
</tr>
<tr>
<td>Cokeville, Wyoming</td>
<td>8</td>
<td>0.27</td>
<td>0.37</td>
<td>Pale yellowish brown (10YR6/2), calcareous siltstone</td>
<td>Streblocodonida montpelierensis Aviculopecten phosphaticus Polidevicia obesa Edmondia phosphatica</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>0.43</td>
<td>1.01</td>
<td>Pale yellowish brown (10YR6/2), very fine-grained sandstone</td>
<td>Lingula carbonaria</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>0.56</td>
<td>0.49</td>
<td>Brownish grey (5YR2/1), shaly mudstone</td>
<td>Lissochonetes ostiolatus</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>1.22</td>
<td>0.42</td>
<td>Dark yellowish brown (10YR4/2) shale</td>
<td>Lingula carbonaria</td>
</tr>
</tbody>
</table>
Lithology 1 (Table 1) at this locality can be described as a brownish grey (5YR2/1), calcareous mudstone. This bed is approximately 0.5 meters thick. In this lithology only *Lissochonetes ostiolatus* was found in abundance and collected.

Lithology 2 (Table 1) from Brazier Canyon is a pale yellowish brown (10YR6/2), sandy siltstone. This lithology contains only *Orbiculoides missouriensis*. No other fossils were found associated with this species in this lithology.

**Montpelier Canyon, Idaho locality**

Only one lithology was sampled in the Montpelier Canyon, Idaho locality. This bed is known as the "Cap" limestone (Yochelson, 1968:574; Girty, 1910:15), and shall be referred to in this report as lithology 3 (Table 1). This rock unit can be described as a greyish black (N2), micritic limestone. It is extremely fossiliferous. The calcified volume of fossils in this bed, determined from several large blocks, accounts for an average of 12 percent of the total rock volume. Lithology 3 is generally about 0.5 meters thick.

From this lithology Girty (1910:16) compiled a list of 26 species. I collected only the five most abundant species from lithology 3: *Babylonites ferrieri, Leirohynchoidea wekksi, Lissochonetes ostiolatus, Polideucia obesa*, and *Nuculopsis montpelierensis*. 
Coal Canyon, Wyoming locality

The Coal Canyon, Wyoming collecting locality includes four different lithologies which contain abundant fossils. Similar to the Brazier Canyon area, these lithologies are each dominated by a single species. Other taxa are present in most of these beds, but are very rare.

Lithology 4 (Table 1) from this area is a pale yellowish brown (10YR6/2) siltstone. This lithology corresponds to bed 11 from the stratigraphic section described by Girty (1910:18). This siltstone is dominated by *Orbiculoidea missouriensis* and numerous specimens of this species were collected.

Lithology 5 (Table 1) from Coal Canyon consists of dark yellowish brown (10YR4/2), calcareous mudstone. This unit is described by Girty (1910:18) as bed 14 from his stratigraphic section in the canyon. *Lissochonetes ostiolatus* was collected from this lithology.

Lithology 6 (Table 1) is a medium grey (N5), calcareous siltstone. It is bed 16 in the stratigraphic section by Girty (1910:18). *Orbiculoidea missouriensis* was the only species found and collected in lithology 6.

Lithology 7 (Table 1) is a pale brown (5YR5/2) siltstone from which *Lingula carbonaria* was collected. No other faunal elements were detected in this lithology.

Cokeville, Wyoming locality

The rapid changes of lithology at the Cokeville,
Wyoming site are shown in the illustration of the measured section (Figure 11d). Here fossil collections were taken from four different lithologies. The lithologies in this locality are revealed in a north-south trending trench resulting from local mining activity.

The bed containing the most diverse fauna from the Cokeville locality is lithology 8 (Table 1). This bed is a pale yellowish brown (10YR6/2), calcareous siltstone which is 0.6 meters thick. Most of the fauna preserved in this lithology are relatively abundant. Fossil collections from lithology 8 yielded specimens of *Strebelochondria montpelierensis*, *Aviculopecten phosphaticus*, *Polidevicea obesa*, and *Edmondia phosphatica*.

Lithology 9 (Table 1) from Cokeville is a pale yellowish brown (10YR6/2), very fine-grained sandstone. This was the coarsest-grained lithology encountered and contains only *Lingula carbonaria*. This bed is 0.76 meters thick.

*Lissochonetes ostiolatus* was collected at this locality from lithology 10 (Table 1), a brownish grey (5YR2/1), shaly mudstone. The fossil specimens taken from this lithology are not as well-preserved as those from other lithologies.

Lithology 11 is a dark yellowish brown (10YR4/2) shale. This shale contains numerous, well-preserved specimens of *Lingula carbonaria*.
Chemical Analyses

Each of the discussed lithologies was subjected to chemical analysis for the determination of $P_2O_5$ content and content of organic matter. These analyses supply information pertinent to a consideration of organismal adaptations to phosphatic substrates and reducing conditions. The following is a description of the procedure used in the chemical work and the results of the analyses.

$P_2O_5$ analysis

Samples of matrix surrounding the collected fossils were taken for the determination of $P_2O_5$ content. Each of the lithologic samples was powdered and sieved (150 mesh) in order to speed dissolution. Approximately 0.1000 grams of each sample was weighed out on an analytical balance and placed in platinum crucibles. Five milliliters of HNO$_3$ were added to remove carbonate and oxidize organic matter. The crucibles were fumed to dryness on a hot plate. Ten milliliters of HF and five milliliters of H$_2$SO$_4$ were added and the crucibles again fumed to dryness. This procedure was done to remove the silica in the samples and to put the phosphate into solution. The remaining residue was loosened with three milliliters of H$_2$SO$_4$, and filtered. The filtrate was retained and diluted to 100 milliliters. Ten milliliters of each remaining solution was mixed with ten milliliters of standard phosphate reagent. Colorimetric procedure was followed to determine the total percent
$P_2O_5$ contained in each sample. An andesite analyzed by the labs of the U. S. Geological Survey was run as a standard to determine the accuracy of the procedure. The results of the analyzed standard match the published results within 0.01 percent. The results of the analyses are presented in Table 1.

The analyses show that most of the lithologies have a low $P_2O_5$ content. The highest percentage (4.83%) is found in lithology 3, but none of the lithologies can be considered phosphatic in terms of the 7.8 percent $P_2O_5$ minimum value boundary set by McKelvey, Davidson and others (1953:4).

Organic matter analysis

The previously powdered samples were used for the determination of the percentage of organic matter present in each lithology. Approximately 1.0000 grams of each lithology was weighed in a beaker on an analytical balance. Eight milliliters of thirty percent $H_2O_2$ were added to the beakers and the oxidation of organic matter was allowed to progress for 24 hours. Tall beakers were used because bubbling and splattering resulted from the reaction. The residual samples were dried in an oven, and the beakers weighed. The resulting weight loss was interpreted as the total weight percent organic matter in the sample. Experimental accuracy in this analysis is not known, but the results do give some indication of the relative organic
matter content of compared lithologies. The results are presented in Table 1.

This procedure shows that most of the lithologies have a relatively high content of organic matter. The only sample which shows no organic content is lithology 3. Interestingly, this lithology exhibits the highest P$_2$O$_5$ content. X-ray patterns reveal that no iron sulfides are present in lithology 3.
PALEOGEOGRAPHY AND PALEOCURRENTS

Paleogeographic reconstruction of North America shows that the shallow seas which had covered most of the continent throughout much of the Paleozoic had retreated to the margins of the continent by Permian time (Scotese and others, 1979:223). Bambach and others (1980:36) showed that a narrow embayment of the open ocean extended southward from Canada in Permian time, covering much of the western United States. Those areas covered by this Permian embayment now include western Wyoming, western Montana, Idaho, northeastern Utah, eastern Nevada, and portions of western Colorado. This body of water is referred to as the Phosphoria Sea. The diverse lithologies of the Phosphoria Formation are the result of the various sedimentary environments within the Phosphoria Sea.

The Phosphoria embayment was bounded on the north by low-lying land area in Montana, and by the ancestral Uncompahgre and Front Range uplifts to the south (Sheldon and others, 1967:6). Ziegler and others (1979:492) indicated that the western limits of the sea were bounded by andesitic volcanic rocks in western Nevada, Oregon, and Washington.

The relative depths of the sea can be inferred from sediment types, deposit thickness, sedimentary structures,
and chemical content. The thickest Phosphoria deposits are found in northeastern Utah and southeastern Idaho. Scotese and others (1979:273) graphically depicted the Phosphoria Sea as deepest in Utah and Idaho. Rocks from this area consist mainly of thinly laminated mudstones, micritic limestones, and cherts. Sheldon (1963:145) indicated that reducing conditions were present in these deeper areas, as evidenced by the presence of organic matter preserved in the rocks. The rocks deposited in Utah and Idaho lack structures, such as ripple marks or cross-laminae, which would indicate current activity. Bioturbation structures, which could suggest the destruction of sedimentary structures, are not noted in the literature and were not seen in the field.

Facies relationships show that the Phosphoria Sea was progressively shallower toward the east. The sediments coarsen to sand-sized particles eastward, and at the farthest eastern boundary evaporites are present (Sheldon and others, 1967:7). The evidence indicates a basin shallowing shoreward to the east.

Water currents over the general area probably included upwelling on the outer shelf areas and wave-generated currents in the shallow portions. No direct evidence of upwelling can be found in the Phosphoria lithologies, but modern theories of phosphorite formation invoke upwelling. Most Holocene phosphorite deposits are situated in areas of oceanic upwelling, such as the sea floors off the coasts
of Peru and South Africa (Parker and Siesser, 1972; Manheim and others, 1975). Wave-generated currents in the shallow areas of the sea are inferred to have had a southerly movement based on elongate sandstone bodies extending southward from Montana (Sheldon, 1963:145; Sheldon and others, 1967:7).

Bambach and others (1980:27) indicated that the prevailing wind direction during this time is considered to have been south to southwesterly. This inference is based on an idealized construction of climatic conditions as a function of latitude and geographic configuration.

The climate of this region during Permian time was probably warm and arid. The presence of gypsum and halite along the eastern limits of the Phosphoria Sea indicate that evaporation must have exceeded precipitation. Ziegler and others (1979:493) maintained that the rise of mountains along the contact of Gondwana and Laurussia blocked the moist equatorial easterlies. This resulted in an intense rain shadow effect creating very dry conditions in North America. The warm temperatures were a result of the paleo-latitudinal position of the area during this time. Bambach and others (1980:36) showed that the area in question was near 10° north paleolatitude.

The lithologies collected and described in this study support many of the previous conclusions. Rock samples taken during field work are dominated by mudstones and siltstones containing substantial amounts of organic
matter. Fossils collected are predominantly articulated and show no signs of abrasion or fragmentation. Sedimentary structures, such as cross-laminae or ripple marks, were absent in the associated lithologies. This evidence supports the conclusion that the depositional environment of the study area was located in the outer shelf to basinward region of the Phosphoria Sea, away from strong current activity.

Fine-grained lithologies, organic content, and facies relationships suggest a moderately deep water environment for the Meade Peak Member of the Phosphoria Formation. Yochelson (1968:614) pointed out that no precise depth figures can be given, but postulated a depth range of 60 to 100 meters for the Meade Peak Member.

An orientation study was done on a portion of a bedding plane of lithology 3 (Plate 1). Fossil specimens preserved on this bedding plane show no preferred compass orientation when plotted graphically (Figure 12) and analyzed statistically (Table 2). Furthermore, most of the fossils are preserved in life orientation (Plate 1) suggesting little post-mortem disturbance of shells. Random fossil orientation and preservation of life orientation support the suggestion that this habitat was situated in quiet water, probably below effective wave base.
Figure 12. Rose diagram of brachiopod and mollusc orientations from the mapped bedding plane of lithology 3 (Plate 1). The arrow indicates the resultant vector (155.7°). A-B shows the angular deviation (79.8°). The associated numbers and dashes indicate the radii of successive units. Black = brachiopods; stippled = molluscs.
Table 2. Test for goodness of fit for circular data from the orientations of brachiopods and molluscs obtained from the mapped bedding plane of lithology 3.

The statistical test is:

\[ x^2 = \sum_{i=1}^{n} \frac{(O_i - E_i)^2}{E_i} \]

where \( O_i \) is the observed number of individuals in a sector and \( E_i \) is the expected number in the same sector, determined by the total number of observations divided by the number of sectors. The null hypothesis is that the orientation is completely random.

\[ E_i = \frac{79}{4} = 19.75 \]

<table>
<thead>
<tr>
<th>Quadrant</th>
<th>( (O - E)^2 / E )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( (20 - 19.75)^2 / 19.75 = 0.003 )</td>
</tr>
<tr>
<td>2</td>
<td>( (19 - 19.75)^2 / 19.75 = 0.029 )</td>
</tr>
<tr>
<td>3</td>
<td>( (23 - 19.75)^2 / 19.75 = 0.535 )</td>
</tr>
<tr>
<td>4</td>
<td>( (17 - 19.75)^2 / 19.75 = 0.383 )</td>
</tr>
</tbody>
</table>

\[ \sum = 0.950 \]

For three degrees of freedom the critical value of \( x^2 \) at \( \alpha = 0.05 \) is 7.814. The calculated value of 0.950 does not exceed the critical value. This means that the orientational distribution may be considered to be random.
ANALYZED TAXA

General Statement

A total of ten different species have been selected for morphometric and demographic analysis in this study. These species were chosen for use on the basis of 1) the excellent preservational state of the specimens for the purpose of detailed measurement of morphologic dimensions and growth increments, and 2) the abundance of specimens for reconstruction of population dynamics. The fact that the collections are limited to brachiopods and molluscs is not a product of preservation, but a characteristic of the Meade Peak Member of the Phosphoria Formation.

Pertinent paleontologic literature which describes or lists the species selected for study includes Girty (1910), Branson (1930), Yochelson (1956), and Ciriacks (1963). A recent publication by Wardlaw (1978) lists the brachiopod species identified from the various collections of the U. S. Geological Survey from the Phosphoria Formation.

Description of Taxa

*Leiorhynchoidea wekksi* (Figure 13, 1 - 3) is an articulate brachiopod belonging to the family Camarotoechidae. This brachiopod was collected in abundance from lithology 3. Its presence elsewhere within the study area is rare.
Figure 13. Articulate and inarticulate brachiopods from the Meade Peak Member of the Phosphoria Formation. 1 – 3 Leiorhynchoidea weeksi from lithology 3 (pedicle view). 4 – 6 Lissochonetes ostiolatus from lithology 3 (pedicle view). 7 – 9 Lingula carbonaria from lithology 9. 10 – 12 Orbiculoidea missouriensis from lithology 6; 10 is a brachial valve, 11 and 12 are pedicle valves. Illustrations of specimens are actual size.
The original assignment of *L. weeksi* was to the genus *Pugnax* (Girty, 1910:31). Yochelson (1968:583) assigned this species to the genus *Leiorhynchus*, but the most recent update by Wardlaw (1978) placed the species in the genus *Leiorhynchoidea*. The specimens of *Leiorhynchoidea weeksi* collected can be described as subtriangular to subovate. The sulcus is generally well developed and bears from one to four plicae. The foramen is apparently triangular and open (Girty, 1910:31). In juvenile specimens the shell is broadly ovate, and flattened, and the sulcus may be very faint to absent. The pedicle valve in all specimens is of lower convexity than the brachial valve.

*Lissochonetes ostiolatus* (Figure 13, 4 - 6) is an articulate brachiopod belonging to the family Chonetidae. Specimens of this species were collected from lithologies in all four study locations. This species seemed to be the most ubiquitous of all those recovered. The species *L. ostiolatus* was originally assigned to the genus *Chonetes* by Girty (1910:25), but Branson (1948:398) reassigned the species to *Lissochonetes*. The shell of this brachiopod has been described as subquadrate, the width being greater than the length (Girty, 1910:25). Generally the side margins of the shell are nearly parallel, but often the sides tend to converge toward the anterior margin. Along the hinge, on either side of the beak, are five or six spines. These spines are not particularly evident in specimens from lithologies 3 and 10.
*Lingula carbonaria* (Figure 13, 7 - 9) is a brachiopod of the class *Inarticulata*, and a member of the family *Lingulidae*. This species was collected at only two of the four localities. It is most abundant in lithology 11. *L. carbonaria* was first described from the Phosphoria Formation by Girty (1910:21). The shell length is generally about 1.5 times the width, although several specimens were obtained which were nearly equidimensional. The sides are approximately parallel, rounding into the anterior and posterior margins. The valve convexity is marked in many specimens, but is often altered and flattened by compaction.

*Orbiculoides missouriensis* (Figure 13, 10 - 12) is an inarticulate brachiopod belonging to the family Discinidae. This species was found in abundance only at the Coal Canyon and Brazier Canyon localities. Its presence was also noted at the Cokeville site, but it was rare. *O. missouriensis* was first assigned to the genus *Lingulidiscina* by Girty (1910:22). Branson (1930:25) initially retained this identification, but in a later work (1948:439) reassigned *L. missouriensis* to the genus *Orbiculoides*. *Orbiculoides missouriensis* is the designation currently accepted by Wardlaw (1978). The shell of *O. missouriensis* can be described as small, low, and cone-shaped, with the beak offset toward the posterior. The brachial valve is conical, but the pedicle valve is flattened. A slit-like opening near the posterior portion of the pedicle valve reveals the location of the pedicle. The shell is covered with fine, concentric
growth lines which are more pronounced on the pedicle valve.  

*Babylonites ferrieri* (Figure 14, 1 - 3) is a mollusc belonging to the class Gastropoda, and to the family Omphalotrochidae. *B. ferrieri* was found only in lithology 3 within the study area and seemed to dominate the assembly. Another gastropod, *Babylonites conoides*, was associated with *B. ferrieri* in this lithology, but very few specimens were encountered during collecting. *B. ferrieri* was originally placed in the genus Omphalotrochus by Girty (1910: 48). Yochelson (1956:202) reassigned this species to the genus *Babylonites* on the basis of morphologic differences, and it retains this generic assignment. This species can be described as trochoform, with a distinctly triangular whorl section (Yochelson, 1956:202). The shell is somewhat flattened with a low spire. The diameter of the last whorl is about twice the height. The number of whorls in the adult is generally four. The profile of the upper whorl surface is gently arched, and the upper and basal whorl surfaces are in contact (Yochelson, 1956:202). The shell is ornamented with fine, regular growth lines which become overlapped near the aperture in larger specimens.  

*Nuculopsis montpelierensis* (Figure 14, 4 - 6) is a mollusc belonging to the class Bivalva, and the family Nuculidae. This bivalve is not extremely abundant in the study area, being found only in lithology 3. Originally described by Girty (1910:38) as a species of *Nucula*, this species was reassigned to the genus *Nuculopsis* in a comprehen-
Figure 14. Gastropods and bivalves from the Meade Peak Member of the Phosphoria Formation. 1 - 3 Babylonites ferrieri from lithology 3. 4 - 6 Nuculopsis montpelierensis from lithology 3. 7 - 9 Polidevca obesa from lithology 3. Illustrations of specimens are actual size.
sive study done by Ciriacks (1963:40). Ciriacks described the shell as having rounded umbonal ridges which define highly inclined slopes between the central portion of the shell and the dorsolateral margins. The surface is marked by fine, concentric growth lines. The dorso-ventral length in this species is generally about equal to the width.

*Polidevcia obesa* (Figure 14, 7 - 9) is a mollusc of the class Bivalva, and a member of the family Nuculanidae. This bivalve is found only at two of the study locations. Ciriacks (1963:42) indicated that the geographic distribution of this species is generally restricted within the Meade Peak Member. *P. obesa* was first assigned by Girty (1910:40) to the genus *Leda*. In ciriacks (1963:42), detailed study of this bivalve species was accompanied by reassignment to the genus *Polidevcia*. The shell of *P. obesa* is distinctly elongate, narrowing toward the posterior margin. Girty (1910:41) characterized this species as having flattened sides, umbonal ridges very close to the upper outline, and a very broad escutcheon. The shell exhibits narrow, regularly spaced, concentric growth lines.

*Edmondia phosphatica* (Figure 15, 1 - 3) is a mollusc of the class Bivalva, and a member of the family Edmondiidae. The distribution of this species is limited to lithology 8 in this study. In this lithology it coexists with three other species of bivalves which are equally abundant. *E. phosphatica* was first described by Girty (1910:36). The shell of *E. phosphatica* is generally subquadrate, but shorter
Figure 15. Bivalves from the Meade Peak Member of the Phosphoria Formation. 1 - 3 Edmondia phosphatica from lithology 8. 4 - 6 Streblochondria montpelierensis from lithology 8. 7 - 8 Aviculopecten phosphaticus from lithology 8. Illustrations of specimens are actual size.
along the dorso-ventral axis. The relatively prominent post-umbonal ridge is characteristic of this species (Ciriacks, 1963:74). The shell displays closely spaced concentric growth lines which generally are not well preserved.

*Streblochondria montpelierensis* (Figure 15, 4 - 6) is a bivalve belonging to the family Aviculopectinidae. This species is found only in lithology 8 within the boundaries of this investigation, but Yochelson (1968:587) indicated that it is abundant in other localities. This bivalve, first described by Girty (1910:42) as *Aviculopecten montpelierensis*, was assigned to the genus *Streblochondria* by Ciriacks (1963:55). *S. montpelierensis* can be described as subcircular, with very smooth valves. The shell displays a small, right anterior auricle when preservation permits. However, this portion is generally broken or not preserved. This species is most often acine, but slightly prosocline individuals were noted during collecting activities.

*Aviculopecten phosphaticus* (Figure 15, 7 - 8) is the final species collected in the study area. This bivalve is a member of the family Aviculopectinidae. Specimens of *A. phosphaticus* were collected only from lithology 8 within the study area. Its distribution elsewhere was not noted. Girty (1910:43) described this bivalve as small, subquadrate, and slightly wider along the posterior-anterior axis. The shell ranges from acine in juveniles, to strongly prosocline in larger specimens. The auricular sulcus is
generally well developed. The shell ornamentation consists of faintly developed radiating costae, and concentric growth lines. Ciriacks (1963:46) indicated that the right valve of *A. phosphaticus* exhibits up to about 10 hinge spines, which attain a length of more than 4 millimeters. Specimens of this species that I collected display from 5 to 9 hinge spines, which do not exceed 4 millimeters in length.
MORPHOLOGIC VARIABILITY AND MODE OF LIFE OF SELECTED SPECIES

General Statement

The morphologic variability found within a particular species is the result of the genetic constitution of the population and/or morphologic adjustments to environmental variants. The gene pool possessed by a population is distinctive, and is the source of variation in functional responses elicited in genotypes (Valentine, 1973:254). Morphologic response to environmental stimuli, however, is the result of phenotypic variation and is closely associated with the mode of life of an organism. Invertebrates tend to produce phenotypes that are best adapted to their particular mode of life and environment.

The genetic character of a fossil population cannot be reconstructed. However, morphologic adaptations to the environment are phenotypic in nature and can be assessed. The expression of intraspecific variation, in response to environmental gradients, can be most easily interpreted when the variation in shape or dimension of a fossil skeleton can be directly measured, compared with other populations, and related to an adaptive function for a habit and habitat (Valentine, 1973:255).

Several physical conditions may affect the morphology
of marine invertebrates, and are deemed important in this study. Hallam (1965:138) noted that the character of the substrate is very important in controlling the distribution and growth of individual species. Soft substrates may limit of influence the size of benthic organisms. If the substrate is fine-grained an organism may sink if the stress applied is greater than the bearing capacity of the sediment (Thayer, 1975a:178). These circumstances would make it advantageous for organisms with a benthic mode of life to adapt their shapes and sizes to soft, fine-grained substrates.

Food supply is another important factor which influences morphology. If the supply of nutrients is low then growth will be correspondingly reduced. The supply of food can be controlled either by lack of source or by the absence of a transporting current. Many organisms are able to adapt morphologically to be more efficient in collecting food under quiet water conditions. Hallam (1965:134) indicated that the capacity to feed, influenced by seasonal conditions, storms, or sediment fouling of the feeding mechanism, may be more important than the actual supply of nutrients.

Competition and population density also stimulate adjustments in skeletal morphology. High population densities can affect morphology because of the relatively intense competition for the same resources. Alexander (1976) argued that intraspecific competition among articu-
late brachiopod associates may be minimized by morphologic divergence or character displacement.

A deficiency in the dissolved oxygen content of marine water can have an inhibiting effect on the growth of an organism. Rhoads and Morse (1971) have found that heavily calcified taxa are largely limited to well-oxygenated water, and that greater calcium carbonate efficiency is found in areas of oxygen deficiency where the cost of producing shell material is high.

Other environmental conditions such as salinity, wave and current agitation, and temperature can be important factors in the regulation of skeletal form (Hallam, 1965), but are not considered important in the analysis of the fossil assemblages in this report. The reason for this is that the fossil samples collected are inferred to have inhabited moderately deep water based on evidence of fine-grained lithologies, lack of sedimentary structures indicative of turbulence, organic matter contained in the lithologies, and regional facies relationships. At the moderate depths inferred, current action would be infrequent (except for turbidity currents), temperatures would remain relatively constant, and salinity would not fluctuate. As a result, these three variables are suspected to have had little effect on morphologic variability within or among fossil populations sampled.

Closely interrelated with the intraspecific variability of a particular species is the mode of life. The
life-habit of a particular species brings it into contact with its environment in a distinctive manner. Because environmental fluctuations are the dominant stimulus for phenotypic variation, the mode of life of an individual may greatly influence the type of adaptive, morphologic plasticity genetically engineered into the skeletal form.

Invertebrate fossils are commonly interpreted as occupying the same ecological niche as closely related living species. This assumption is based on the premise that because a fossil is morphologically similar to, or phyletically related to, a species for which ecological information is available, it should share the same mode of life and environmental responses. This assumption is not always true. Park (1968) examined the paleoecology of six subgenera of the bivalve *Venericardia* from Cenozoic strata of the Atlantic and Gulf coasts of North America to see if significant changes in ecology could be detected through time. His study showed that some, but not all, of the subgenera examined exhibited a change in characteristic habitat. One example is that of *Cyclocardia*. This genus was restricted to a shallow, inner-shelf environment in fossil samples, but was found in deeper water environments in living samples (Park, 1968:978).

The range of physical tolerances and functions, inferred from modern species, does indicate the general ecological realm that individuals of a fossil species may have inhabited, and thus becomes very useful in the inter-
pretation of past modes of life. Even though a few closely related living species do exhibit different modes of life than their fossil relatives, the method of interpreting the paleoecology of fossil species from the ecology of directly, or closely related modern forms is valid (Yochelson, 1968:577).

In making paleoecological interpretations from fossil species with no closely related living representatives, it is necessary to evaluate the preserved skeletal morphology. Many functions are reflected in external morphologies. The functional information not found in the skeletal form must be inferred empirically by matching paleoenvironmental patterns with individuals (Valentine, 1973:209).

**Analysis of Morphologic Variation and Mode of Life**

The purpose of this analysis is to compare the variability of skeletal dimensions within a species and relate it to different functional responses to the environment and mode of life. In the following discussion intraspecific morphologic variability will be analyzed, and life-habits reconstructed for selected species collected from the four study localities in the Meade Peak Member of the Phosphoria Formation.

To aid in the analysis of variability the prominent dimensions of a sufficient number of fossil specimens from each population sample were assessed by direct measurement with vernier calipers. Where necessary, angular data were
determined using a protractor. The morphologic skeletal dimensions for which data were collected are defined in Figures 16 and 17, and the subsequent means and standard deviations are listed in Table 3. However, statistical comparisons of means are precluded by dissimilarities in variances and skewed size-frequency distributions.

Modes of life of the fossil species collected in this study are reconstructed from published literature on the ecology of related living species. The life-habit of fossils which have no closely related living species is based on inferences from morphology and paleoenvironment. A block diagram (Figure 18) graphically depicts the mode of life of each discussed species.

**Brachiopods**

The brachiopods as a group are generally as abundant as the molluscs in the Phosphoria Formation, but exhibit slightly less taxonomic diversity (Yochelson, 1968:582). In the area involved in this investigation the brachiopods numerically dominate the fossil collections by more than two to one over the molluscs. The specimens collected, both articulates and inarticulates, exhibit interesting trends in intraspecific variability, and represent at least three fundamentally different modes of life.

All brachiopods are ciliary suspension feeders. The feeding mechanism, the lophophore, acts as a combined pump and filter in taking nutrients out of the water (Tasch,
Figure 16. Examples of measured morphologic dimensions of brachiopods and gastropods. 

a. *L. weeksi*: 1) length, 2) width, 3) posterior angle, 4) height, 5) sulcus width, 6) sulcus height, 7) number of plicae.

b. *L. ostiatus*: 8) length, 9) width at ant.-post. midpoint, 10) hinge width, 11) convexity, 12) thickness.

c. *B. ferri*: 13) number of whorls, 14) aperture diameter, 15) height, 16) diameter of last whorl, 17) whorl expansion rate (W) = K/K', distance of generating curve from the axis of coiling (D) = (ED-R)/(ED+R), translation rate (T) = OD/ED (Graus, 1974).
Figure 17. Examples of measured morphologic dimensions of bivalves. 
a. *A. phosphaticus*: 1) length, 2) width, 3) hinge width, 4) auricular sulcus length, 5) length of spines, 6) auricular sulcus depth, 7) angle of asymmetry, 8) number of spines. 
b. *E. phosphatica*: 9) length, 10) width, 11) height.
Table 3. Numerical data for the analyzed fossil population samples depicting taxonomic name, morphologic characteristics, and corresponding lithologic number. *n* = sample size, *x* = average measurement, and *sd* = standard deviation of the measurements. Numerical data is in millimeters unless indicated otherwise.

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- indicates that data was not available.
The ciliated filaments induce a one-way circulation of water through the mantle cavity. This brings the food supply into contact with the lophophore and directs it into the digestive tract. Suchanek and Levinton (1974) examined the gut content of four genera of articulate brachiopods dredged from various depths. They found that brachiopods inhabiting shallow water primarily filter out diatoms and dinoflagellates for nutrition, but in deep water, where phytoplankton is scarce, the gut content was predominantly inorganic. This may indicate that brachiopods in deeper water alter their nutritional mode from suspension feeding to adsorption of dissolved nutrients (Suchanek and Levinton, 1974:4).

The nutritional mode of adsorbing dissolved nutrients is not assumed to have been the primary source of food for the brachiopods collected in this study. The 60 to 100 meter depths of the Phosphoria Sea, suggested by Yochelson (1968:614), probably would have permitted the filtration of diatoms and dinoflagellates settling through the water column.

Leiorhynchoidea weaksi

*L. weaksi* possesses a moderately sized pedicle opening. Because the foramen is not restricted it is very likely that this brachiopod was attached to some surface by a pedicle. Several attachment surfaces are assumed to have been available to *L. weaksi*. However, data from this
study suggest that not all of these substrates were utilized.

Living brachiopods are known to attach to other shell material or even other living brachiopods (Thayer, 1975b: 140). If such substrates were utilized by *L. weelsi*, attachment marks on associated shells would be present and preserved specimens would be found in contact with, or near, other shells. Neither of these evidences are noted in lithology 3, from which *L. weelsi* was collected. Other collected population samples exhibit no evidence of attachment marks. Plate 1 shows that specimens of *L. weelsi* are not generally preserved in extreme proximity to other shell material. This evidence suggests that pedicle attachment involved material other than neighboring shells.

Rudwick (1965:201) suggested that floating algae or other soft, organic material may have provided an epiplanktonic mode of life for some species of brachiopods. It is possible that *L. weelsi* utilized floating material for pedicle attachment. This soft, organic material would not be preserved as evidence in the fossil record. Nearly all collected specimens of this brachiopod exhibit perfect shell symmetry. This might suggest an epiplanktonic life in which a fluid medium contributed to uninhibited shell growth.

The most probable surface of attachment for *L. weelsi* was that of the sea floor. The pedicle may have been inserted into the sediment, acing as an anchor, support-
ing the shell at some angle in relation to the bottom. The pedicle adjuster muscles probably enabled this brachiopod to rotate, or elevate, the shell in response to currents and biotic factors (LaBarbera, 1977; Richardson and Watson, 1975).

Soft lime muds are the inferred substrate of lithology 3. Such soft substrate would make it necessary to maintain the commissure as far as possible above the substrate to avoid the influx of suspended sediment, and would make pedicle attachment somewhat difficult. Rudwick (1970:77) asserted that some brachiopods have adapted to life on soft substrates by possessing exceptionally long pedicles with rootlets to anchor them in place. Schumann (1969:200) cited the example of *Chlidonophora* which exhibits a pedicle divided into hair-like threads which wrap around foraminifera tests for anchorage. *L. weeksi* possibly possessed a long, perhaps branched, pedicle for insertion into the soft substrate to aid attachment and stabilization.

Richardson and Watson (1975), in their discussion of *Magadina cumingi*, have asserted that the possession of an open foramen in an articulate brachiopod cannot be equated with permanent attachment. They indicated that *M. cumingi* is free lying, but possesses a retractable pedicle which is used as an elevating device. This pedicle arrangement would be useful in soft sediments and areas of high sedimentation where readjustment of living position could aid survival. It is possible that *L. weeksi* was not permanently
tethered to the substrate, but was able to adjust its position to fluctuating levels of sediment by retracting the pedicle.

*L. weeksi* is represented in this study by a single population, found in lithology 3. In this species the morphologic characters of width and height both increase ontogenetically, and the posterior angle remains relatively constant during growth. The presence of a sulcus is not observed in specimens shorter than about 14 millimeters. Larger specimens exhibit a well developed sulcus, and show wide variation in the sulcus height, sulcus width, and the number of plicae within the central fold.

Because lithology 3 is inferred to have been located in a quiet environment, below wave base, nutrient availability may have been limited. Food supply also has been noted or inferred to decrease toward deeper, offshore water (Fursich and Hurst, 1974:880; Suchanek and Levinton, 1974:4). These circumstances would favor the development of a large sulcus, which gives maximum separation of the inhalent and exhalent currents so that previously filtered water is not refiltered and the maximum amount of food is obtained (Fursich and Hurst, 1974:888). The variation seen in the width and height of the sulcus and in the number of plicae cannot be attributed to quiet water. Selective pressure for a well-developed sulcus to increase feeding capacity would tend to reduce variability. This directional selection should have eliminated weakly sulcate
forms.

Fursich and Hurst (1974:888) correlated strong angular plicae with brachiopods inhabiting turbulent water, inferring that plications reduce the amount of opening necessary and restrict the entrance of coarse sediment. This environmental response cannot be applied to *L. weeksi* because the sediment of lithology 3 is inferred to have accumulated below effective wave base.

Variability in the sulcus and plicae can be related to competition in this environment. Alexander (1976) concluded that the variability within the sulcus is inversely related to the diversity of other associated brachiopods. *L. weeksi* is associated with only three other uncommon species of brachiopods in lithology 3. This means that intraspecific competition may have been the driving force toward sulcus variability. Because the mode of life of *L. weeksi* was one of pedicle attachment to the sea floor, nutrients existing at the level above the substrate at which this species existed may have been a limiting factor. If food was a limiting resource in this environment, then it may be possible that the variation in the sulcus and plicae number in *L. weeksi* is a response to competition. Variability in the sulcus geometry, as evidenced by the number of plicae in the central fold, may reflect the partitioning of nutrient resources through filtration of different layers of water above the substrate (Alexander, 1976:243).
*Lissochonetes ostiolatus*

*L. ostiolatus* exhibits a foramen restricted by a pseudodeltidium, which indicates atrophy and loss of the pedicle at an early age. This type of pedicle loss is characteristic of the strophomenid order of brachiopods (Tasch, 1973:296). After the pedicle atrophied, *L. ostiolatus* would have maintained the shell in living position by means of its weight, allowing the valves to subside into the substrate. The concavo-convex shell geometry probably kept the commissure very close to the sediment-water interface (Rudwick, 1970:89).

With the commissure close to the substrate, *L. ostiolatus* would have had problems of sinking into soft sediments, being covered by sedimentation, and expelling material seeping through the commissure when the valves gaped to filter water. Rudwick (1965:202, 1970:91) and Valentine (1973:196) both suggested that these brachiopods could clear the commissural area of sediment by clapping the ventral valve shut rapidly, creating a quick burst of expelled water from the mantle cavity. It is probable that *L. ostiolatus* was capable of this snapping motion. It is also possible that *L. ostiolatus*, if overturned, could right itself by this same snapping motion, and even be capable of short bursts of movement similar to some modern pectenoids (Rudwick, 1970:91).

*L. ostiolatus* characteristically possess hinge spines. The presence of these spines suggests several functional
uses. Rudwick (1970:109) asserted that the spines may have served a sensory function, particularly for short swimming bursts where they would project in the direction of motion. The spines of *L. ostiolatus* are not assessed to have served a sensory function. The spines are solid which would preclude the presence of any sensory tissue within.

Spencer (1978) analyzed the function of hinge spines in several different assemblages of *Chonetinella flemingi* and *C. alata*. He found that in lithologies representing more turbulent water the brachiopods possessed fewer hinge spines, and postulated that the spines may act as balances or stabilizers, or may be thrust into the sediment. In lithologies representing quiet, deep water he observed more hinge spines and suggested that they were used for buoyancy.

The hinge spines of *L. ostiolatus* are assumed to have been utilized for buoyancy and balance in the soft substrates of the Meade Peak Member of the Phosphoria Formation. The spines increased the bearing surface of the brachiopod. This inhibited sinking into the sediment. The spines also may have acted as balances, helping to elevate the commissure above the substrate.

Four population samples of *L. ostiolatus* were examined and compared in this study. Several notable patterns have emerged from this comparison. The measured parameters of length, width at the anterior-posterior midpoint, and hinge width all appear to have increased ontogenetically.
However, distinct differences exist in the means of these dimensions when comparing population samples. Table 3 shows that the means of the morphologic dimensions of population samples of *L. ostiolatus* from lithologies 3, 10, 1, and 5 differ appreciably. In general the collection of *L. ostiolatus* from lithology 3 exhibits the largest average dimensions. The population sample of lithology 10 displays the next largest mean sizes. The population samples from lithologies 1 and 5 are very similar and have the smallest mean skeletal dimensions.

The differences noted in these population samples are not the result of the accumulation of juvenile specimens in the assemblages with the smaller mean size. This conclusion is supported by growth-increment data in Figure 38. The growth lines of examined specimens show that growth rate was more rapid in individuals from lithology 3, whereas the population samples of lithologies 1 and 5 exhibit slower growth. Also, specimens which are assumed to be of the same age-class and have the same number of growth lines are much larger from lithology 3 than from lithologies 1 and 5. The information concerning growth lines in *L. ostiolatus* from the population sample of lithology 10 is lacking due to poor preservation.

Several environmental conditions may have interacted with the mode of life to stunt the growth of *L. ostiolatus* in lithologies 10, 1, and 5 relative to that in lithology 3. The lithologies in which these four assemblages occur
are very similar texturally; therefore substrate differences are inferred to have been negligible factors in the differentiation of growth rates among different populations.

One important fact is that lithology 3 is void of any preserved organic matter (Table 1), even though the presence of an abnormal amount of $P_2O_5$, suggestive of a negative Eh, was found. The presence of abundant infauna in lithology 3, i.e., scaphopods and nuculid bivalves, indicates that the Eh=0 line was present at some level beneath the sediment surface. This may signify that the population associated with lithology 3 was not subjected to reducing conditions. The remaining lithologies associated with *L. ostiolatus* contain detectable amounts of organic matter and supported no infauna. This may indicate an Eh=0 line very near the sediment-water interface. A low dissolved oxygen level in the environments associated with lithologies 10, 1, and 5 would have slowed metabolic processes and calcification would have been retarded (Rhoads and Morse, 1971).

Another possible factor which may have added to the inhibition of growth rate for the populations associated with lithologies 1 and 5 is the population density and competition. These two populations are typified by an extreme abundance of individuals per unit area of rock. Crowding of these free-lying brachiopods is so intense in the collected samples that a single, hand-sized rock spec-
imen may contain as many as 50 to 100 individuals, many of
which are in contact. This type of densely populated sub-
strate would point to very active competition for space,
and perhaps food and oxygen. Such limitations may have
slowed the rate of growth of individuals of *L. ostioloatus* in
lithologies 1 and 5. However, Hallam (1965:138) indicated
that the high population density may be a response to an
abundant food supply. The organic content of the lithol-
ogies seems to indicate that food was abundant and possi-
bly not a limiting resource.

The difference in convexity displayed between the
population samples of *L. ostioloatus* from lithology 3 and
those sampled from lithologies 1 and 5 is readily apparent
(Table 3). This difference may be a response to the sub-
strate on which this brachiopod lay. Thayer (1975a:185)
and Fursich and Hurst (1974:888) explained that the expan-
sion of the resting surface, or "snowshoe adaptation", is
a common response in brachiopods to soft substrates. The
expanded resting area reduces sinking and keeps the com-
missure as far above the substrate as possible. Spencer
(1978) showed that higher convexity is associated with
lithologies which represent soft, fluid substrates. The
lime muds of lithology 3 were probably softer than the
silts and muds of lithologies 1 and 5. The increased
convexity in specimens of *L. ostioloatus* from lithology 3
may reflect an adaptation to a softer, more fluid sub-
strate.
No geniculate convexity is seen in the examined population samples of *L. ostiolatus*. This probably indicates that sedimentation rates were constant in the environments of lithologies 3, 1, and 5.

One morphologic aspect of *L. ostiolatus* not noted in Table 3 is that hinge spines were well-developed on specimens from lithologies 1 and 5, and poorly-developed, if not absent, on specimens from lithologies 3 and 10. Spencer (1978) cited several examples of hinge spine development in chonetids collected from lithologies representing soft sediment and quiet water. Long hinge spines increase stabilization and buoyancy by producing a greater bearing surface (Spencer, 1978:1366). The development of hinge spines on *L. ostiolatus* from lithologies 1 and 5 is inferred to represent a buoyancy adaptation to a soft substrate. The fact that hinge spines are not well-developed on *L. ostiolatus* from lithologies 3 and 10, even though lithology 3 is inferred to have provided the softest of the compared substrates, may be the result of solution acting on the greater surface area presented by the spines.

*Lingula carbonaria*

Three population samples of *L. carbonaria* were collected in this study. Some species of *Lingula* have persisted to the present time, and life-habits of extant individuals can be studied. Pickerill (1973:146) asserted that modern lingulids are confined to shallow, tropical to subtropical
water, and are not known to occur in cold water. Hammond and Kenchington (1978) collected specimens of *Lingula tumidula* from the Queensland coast of Australia and observed a subtidal occurrence in all cases. Other species of extant lingulids are found to prefer a littoral distribution (Kenchington and Hammond, 1978:72). From this discussion it is apparent that the depth preference of modern *Lingula* is species-dependant, and may vary from subtidal to intertidal. The depth ranges for modern lingulids have been recorded from 0 to 90 meters (Pickerill, 1973:146). However, Cherns (1979) collected fossil species of *Lingula* from the Ludlow Series of the Welsh borderland and Wales which are inferred to have inhabited basins as deep as 1000 to 1500 meters. This suggests that the ecology of *Lingula* may have changed through time.

Modern species of *Lingula* prefer a sand-sized substrate (Paine, 1970:24; Kenchington and Hammond, 1978:72). The fact that *L. carbonaria* is generally associated with fine-grained lithologies in this study seems to contradict the expected concentration in coarser-grained lithologies. Paine (1970:30) postulated that the habitat of *Lingula* has not changed, but that the probability of preservation in shallow-water sediments is low and has biased the paleontologic record in favor of occurrences in fine-grained lithologies. Nevertheless, Cherns (1979) has presented evidence of fossilized deep-water species which may have preferred softer substrates.
*Lingula carbonaria*, unlike the other brachiopods discussed in this report, was a member of the infauna. The parallel-sided shell form of this species is characteristic of those lingulids known to be burrowers (Rudwick, 1970:95). Living species of *Lingula* employ an infaunal burrowing mode of life. Thayer and Steele-Petrovic (1975) observed the burrowing process of the lingulid brachiopod *Glottidia pyramidata* and noted that the pedicle props up the posterior portion of the shell so that the anterior end is in contact with the sediment. The animal enters the substrate anterior end first by complex motions of the valves. These motions include oscillatory rotation of the valves out of phase with each other, rotary motion, sliding motion, and gaping. Since the brachiopod must right itself, a u-shaped burrow is produced so that an anterior-up feeding position is assumed, with the pedicle extending downward into the burrow (Thayer and Steele-Petrovic, 1975:213).

Similar to the agile motion of *Glottidia* observed by Thayer and Steele-Petrovic (1975), *L. carbonaria* was probably able to adjust its position in the burrow. The motion in the burrow, once a life position was attained, is assumed to have included rotation, and movement up and down in response to food and predators (Rudwick, 1965:200).

Some morphologic differences are found in the three populations of *L. carbonaria* sampled in this investigation. Table 3 shows that the population samples of *L. carbonaria* from lithologies 9, 7, and 11 all differ substantially in
mean lengths and widths.

The assemblage of *L. carbonaria* from lithology 9 displays the largest mean values among the morphologic dimensions, as shown in Table 3. The next largest mean morphologic sizes are exhibited by the population sample of lithology 7, and the smallest are shown by the population sample of lithology 11. These size variations are not the result of juvenile accumulations in the smaller-sized assemblages, as evidenced by the growth-line analysis in Figure 39. The population sample from lithology 9 shows a much greater rate of growth than the others, and individuals of each inferred age-class of this sample are larger than the same age-classes of the other population samples. Because differences in age structure do not account for the different mean sizes of the population samples, environmental factors which affected the individuals must be the major influence differentiating mean sizes of the populations.

The inferred substrates of the environments of lithologies 9, 7, and 11 differ considerably. They were probably a large factor in size-variation among population samples of this brachiopod. Lithology 9 is a fine-grained sandstone which was formerly a sandy substrate. Because modern lingulids have been shown to prefer coarser bottoms, lithology 9 is inferred to have provided improved growing conditions for the associated population of *L. carbonaria*. These conditions would make growth parameters, on the
average, larger than the other populations of *L. carbonaria*. Lithology 7 is a siltstone which would have made a finer, and perhaps less firm, substrate than lithology 9. Paine (1970:27) indicated that lingulids as adults are excellent burrowers, but much less efficient in the immediate post-larval stages. In environments of fine particle size, juveniles may become buried, foul the lophophore filtration system, and be suffocated. Increased energy expenditure for cleansing the filtration system, and decreased feeding time, would have resulted in reduced growth rate. The population sample from lithology 11 existed on a muddy bottom, as evidenced by the shale matrix. This substrate would have aggravated the problems discussed for lithology 7 and retarded growth further. This pattern shows that the size-variation seen among the three population samples of *L. carbonaria* can in part be explained as the result of textural differences in substrate.

Another factor also may have influenced the observed differences in mean size among the population samples. Each of the lithologies associated with *L. carbonaria* shows a substantial content of organic matter (Table 1). The presence of organic matter indicates that reducing conditions were prevalent. The fact that *L. carbonaria* was an infaunal inhabitant indicates that the Eh=0 line existed at some level below the sediment-water interface, perhaps very near the burrowing level of some populations. Because morphologic means are smaller in *L. carbonaria* samples from
lithologies 7 and 11, reducing conditions may have existed near the burrowing level. The associated decrease in dissolved oxygen would have further retarded growth, thereby accounting for the observed size reduction.

One other possible correlation exists between the morphologic size-variation in the *L. carbonaria* population samples and the chemical content of the associated lithologies. Lithology 9 is found to contain 1.01% $P_2O_5$, whereas the other two lithologies contain less than half as much (Table 1). Because the shell material of linguids is calcium phosphate with occasional layers of organic matter, phosphate diffusion in the associated water is an important factor in growth and development (Pickerill, 1973:52). It is postulated that the greater phosphate content in the sediment and water surrounding those individuals from lithology 9 contributed to a more rapid growth rate. The growth rate of *L. carbonaria* from lithologies 7 and 11 may have been correspondingly diminished as a result of less phosphate available for shell construction.

*Oribiculoidea missouriensis*

*O. missouriensis* had a completely different life-habit than the inarticulate *Lingula carbonaria*. A small, slit-like opening in the subcentral area of the pedicle valve indicates the point of protrusion of the pedicle. *O. missouriensis* was a member of the epifauna, probably attached to the substrate by its pedicle. The pedicle is
assumed to have been relatively short for support of the valves off of the substrate. This kept the shell very near to the sediment-water interface.

The shell of *O. missouriensis* is small, round, and flattened. It is difficult to visualize such a flat shell remaining on the substrate without being buried by sediment. The small size and inferred shortness of the pedicle would mean that the commissure of this species would only have been a few millimeters above the sediment surface, if not completely touching the sediment. Yochelson (1968: 583) suggested the possibility that *O. missouriensis* could have led a planktonic existence, but in the absence of any seaweed remains it is impossible to substantiate. Alternatively, *O. missouriensis* may have been attached to the bottom, but was restricted to firm substrates and areas of low sedimentation.

Population samples of *O. missouriensis* collected from three different localities display appreciable differences in the morphologic means (Table 3). The population sample from lithology 2 differs greatly from those of lithologies 4 and 6 in both length and width (Table 3). In this comparison, the possibility is small that the differences in morphology are related to a greater accumulation of immature specimens, resulting from environmental factors which reduced life expectancy, in lithologies 4 and 6. Growth-increment data (Figure 40) show a much greater growth rate and a larger size per number of growth lines for individ-
uals from lithology 2. Consequently, environmental conditions are invoked to account for size differential.

As an inarticulate brachiopod, *O. missouriensis* possessed a chitinophosphatic shell. The fact that phosphate is important in shell deposition may have been a factor in morphologic size-variation among population samples (Pick-erill, 1973:52; Yochelson, 1968:583). Table 1 shows that the $P_2O_5$ percentages contained in lithologies 2, 4, and 6 are very similar. This may indicate that phosphate content in the water surrounding these three populations did not differ greatly among environments. It is assumed that phosphate diffusion in the associated marine water was not an important factor influencing differences in growth rates among population samples.

All three lithologies from which *O. missouriensis* was collected are siltstones. This means that textural differences in substrate can be eliminated as a factor which differentiated growth rates.

The lithologies associated with the population samples of *O. missouriensis* all contain substantial amounts of organic matter (Table 1). The dysaerobic nature of the substrates, inferred from organic content, is probably the largest single cause of morphologic size differences. These three assemblages are not associated with any infaunal inhabitants, indicating that the $Eh=0$ line probably existed very near, or just below, the sediment-water interface. Because specimens of *O. missouriensis* collected from
lithology 2 display a more rapid growth rate and a larger average size (Table 3), the geochemical conditions are inferred to have been comparatively less reducing and exerted less physiological stress than in the other two lithologies. The inhibited size in individuals from lithologies 4 and 6 is interpreted as a morphologic response to less dissolved oxygen. Schopf and others (1971) have shown that smaller organisms use less oxygen.

Molluscs

Only two classes of molluscs were sufficiently abundant and well preserved to warrant collection. These are the gastropods and the bivalves. The bivalves formed the largest single class, both in numbers and in taxonomic diversity. The gastropods were dominant in only one collecting locality. The representatives of these two classes exhibit important trends in morphologic variation, and possessed several distinct modes of life.

Babylonites ferrieri

*B. ferrieri*, from lithology 3, is the only gastropod population represented in this investigation. *B. ferrieri* is inferred to have been part of the vagile epifauna. The low, broad, helically-shaped shell would have made living partly or wholly buried in muddy substrates virtually impossible because of the drag which would have resulted. Among living gastropods, only smooth, sculptureless, elongate shells, such as the shell form of the family Olividae,
are adapted for a burrowing mode of life (Graus, 1974:312). The shell of *B. ferrieri* would have been ideal for movement on top of the substrate because it would rest stably on the surface. Graus (1974:313) asserted that gastropods with a broad, tripod-like shell form will fall back to their living position when rotated up to 90°.

Living marine gastropods exhibit several different feeding habits. Cox (1960:87) reviewed the feeding modes of several living gastropods. He included carnivorous gastropods which feed on the living flesh of other organisms, often by boring holes in the shell; carrion feeders; browsers which feed on seaweed and lichens; deposit feeders which collect detritus of organic origin; and ciliary feeders which feed on finely sifted bottom sediment.

It seems unlikely that *B. ferrieri* was a ciliary feeder. Cox (1960:87) indicated that this feeding mode has only been demonstrated in fresh water species of gastropods.

No bore holes were found in the fauna associated with *B. ferrieri*. This suggests that the radula was not used as a boring tool to feed on shelled invertebrates. However, it is possible that *B. ferrieri* may have fed on soft-bodied, living organisms such as worms.

Many overturned shells are noted on the mapped bedding plane of lithology 3 (Plate 1). This overturning may have resulted in part from *B. ferrieri* slowly crawling over the substrate. The abundant infauna of this lithology may
have also added to this shell-overturning. If *B. ferrieri* did participate in this overturning, it may have been in the search for food. This may indicate that this gastropod fed on carrion, overturning dead organisms. It also could indicate a possible grazing habit. The shell-overturning may have been the result of a search for decayed organic debris, if *B. ferrieri* were a detritus feeder.

Valentine (1973:459) generalized that Paleozoic marine gastropods were mainly browsers and detritus feeders. Nevertheless, no definite feeding habit can be presented for *B. ferrieri* at this time. Perhaps a detailed search for radula remains in lithology 3 could lend more evidence for the solution of this problem.

For *B. ferrieri* the measured height, aperture diameter, and number of whorls all increase with size. The distance of the generating curve from the axis of coiling (D) and the translation rate (T) both remain relatively constant for this species. The whorl expansion rate (W) displays a wide range of variability (Table 3).

Graus (1974:305) indicated that a gastropod with a very low translation rate and a high whorl expansion rate, such as *B. ferrieri*, is characteristic of species which are efficient in the utilization of calcium carbonate. The low-spired (T=0.91), expanded (W=3.61) form of *B. ferrieri* could be explained as a morphologic adaptation to an oxygen-depleted environment above the phosphate-rich substrate of lithology 3. However, abundant infauna in this
lithology suggest that reducing conditions were present at some depth within the substrate. An aerobic habitat indicates that the form of this gastropod was genetically programmed and adapted for reasons other than merely calcium carbonate efficiency.

_Nuculopsis montpelierensis_

_N. montpelierensis_ is a small bivalve species which is represented in this study by only one population sample. All of the skeletal dimensions measured for this species appear to have increased ontogenetically. The mode of life of _N. montpelierensis_ is important and should be discussed.

_N. montpelierensis_ probably is best represented by living species of _Nucula_. This extant relative is a member of a group of bivalves known as the prosobranchs, which are characterized by the most primitive of paired gill structures (Moore and others, 1952:409). There is so little difference in shell morphology between fossil forms and living forms of _Nucula_ that similarity of soft parts and living habitat is inferred (Yochelson, 1968:586).

For modern forms of _Nucula_, Cox (1969:6) stated that "...the shell is buried so shallowly that it is possible for the inhalent current to be drawn in between the more deeply buried posterior margins, by repeated extrusions of water expelled from the mantle cavity." This indicates that _N. montpelierensis_ may have been a very shallow burrower.
Burrowing in living *Nucula* takes place by a seesaw rocking motion, slicing into the sediment with short rocking bursts. *N. montpelierensis* probably burrowed at a steep angle, but the final life orientation was different. At the end of the burrowing process, *N. montpelierensis* is assumed to have reoriented the shell so that the commissure was vertical and the anterior-dorsal margin approximately horizontal (Stanley, 1970:117).

*N. montpelierensis* is inferred to have been a deposit-feeder, collecting food from the sediment by proboscide extensions of the labial palps. Kauffman (1969:165) explained that prosobranchs, as members of the infauna, search for food by moving horizontally through the substrate, extracting organic matter. The larger particles of sediment were probably sorted out on the labial palps, while the smaller particles passed through the alimentary tract (Wilbur and Yonge, 1964:37).

Stanley (1970:115) found the modern *Nucula* prefers to inhabit muddy substrates. This habitat preference is supported by the lithology in which *N. montpelierensis* was collected (lithology3).

*Polidencia obesa*

The mode of life of *P. obesa* is assumed to have been very similar to that described for *Nuculopsis montpelierensis*. Yochelson (1968:586) asserted that *P. obesa* was also a prosobranch, and gathered nutrients infaunally by means of
labial palps. The only difference that can be noted between the two prosobranchs described in this study is that the living position of *P. obesa* probably was slightly different than that of *N. montpelierensis*. Stanley (1970:48) indicated that very few elongate bivalves rotate from their burrowing orientation to a different life position. The elongate *P. obesa* probably retained an angular orientation within the substrate, with the commissure vertical and the anterior-posterior axis at some angle with respect to the sediment surface.

*P. obesa* was collected from two different populations during this investigation, and so comparisons between them are possible. Although length, width, and height increased with size for this bivalve, a difference in the mean sizes of length and width is noted between the assemblages of *P. obesa* from lithologies 3 and 8 (Table 3). Lithology 8 yields larger specimens on the average. The possibility exists that the differences in mean length and width may be due to the accumulation of smaller individuals in lithology 3 as a result of juvenile mortality. Comparisons of growth increment do not substantiate differences in age structure of the populations because growth lines are not well preserved in specimens from lithology 8. Assuming that the populations had comparable life spans, growth has been stunted in *P. obesa* in lithology 3. If growth has been stunted on the substrate that became lithology 3, several environmental factors may have interacted with the
mode of life.

The substrate texture inferred for lithology 3 is soft lime mud, and growth retardation of *P. obesa* inhabitants may have resulted from this. Hallam (1965:138) suggested that fine muds may clog the feeding mechanism of burrowers, thereby inhibiting growth because of reduced feeding time and excess energy expenditure for cleansing the filtration system. The siltier nature of lithology 8 may have minimized energy lost in formation of pseudo-faecies, and thereby permitted *P. obesa* to attain larger size.

Food availability also may have played a substantial role. As previously noted, the quiet water environments of these two lithologies may have limited the supply of food. Levinton and Bambach (1975) asserted that when food becomes a limiting factor, competition may generate a distinct stratification in feeding depth in deposit-feeders so that they utilize different layers of available resources. The fact that *P. obesa* is associated with another labial palp feeder in lithology 3 may indicate that competition for food made that resource a limiting factor.

*Edmondia phosphatica*

*E. phosphatica* is represented in this investigation by only one population, collected in lithology 8. The measured dimensions of length, width, and height are found to
increase with size in this bivalve species. Because the distribution is limited, *E. phosphatica* cannot be assessed in terms of morphologic variation between habitats. This bivalve does have a mode of life distinct from that of the other bivalves examined, and discussion will be restricted to that.

*E. phosphatica* has no closely related extant bivalve species, and so inferences concerning the life habit are only speculative. *E. phosphatica* is assumed to have been a burrowing bivalve based on its elongate, compressed form. Stanley (1970:73) indicated that the pallial sinus can be used as a crude estimator of the depth of burrowing. No internal characteristics are known from *E. phosphatica* due to poor preservation, but the bivalve is conjectured to have been a siphonate shallow burrower.

The food of *E. phosphatica* probably consisted of phytoplankton and suspended organic matter drawn into the digestive system by means of the siphons. The particulate matter was then filtered out.

*Lutricia montpelierensis*

*S. montpelierensis* was collected only from lithology 8 in this study. The measured morphologic dimensions of length, width, hinge width, auricular sulcus length, and auricular sulcus depth increased with size in this species. The average values of these dimensions are listed in Table 3. Only the mode of life of this species will be discussed
because other population samples of *S. montpelierensis* are not available for morphologic comparisons.

Yochelson (1968:587) indicated that the life-habit of *S. montpelierensis* is best represented by living members of the Superfamily Pectinacea. Many members of this superfamily live unattached, lying free on the sea bottom. Kauffman (1969:160) explained that free-living pectenoids inhabit a variety of environments ranging from shallow, current-swept areas, to abyssal depths. This depth range implies a variety of inhabitable substrates for bivalves with this mode of life.

*S. montpelierensis* is inferred to have been a free-living, epifaunal bivalve. This assumption is based on the fact that this bivalve species is almost always disc-shaped, and symmetrically disposed about the length axis. Kauffman (1969:160) indicated that this rounded type of shell-form is characteristic of free-living bivalves. Another morphologic feature which supports this assumption is the poorly developed anterior auricle of *S. montpelierensis*. Stanley (1970:41) suggested that unattached pectenoids have no need for an elongate anterior auricle, which is developed for byssal attachment.

Extant free-living pectenoids are noted for their ability to actively swim for short periods of time. Kauffman (1969:160) indicated that swimming is effected by rapid clapping of the valves, accompanied by forceful ejection of water from within the shell. The disc-shaped
shell of *S. montpelierensis* would have been well adapted to a swimming habit since the symmetry would have maintained balance while gliding through the water in short bursts. Yochelson (1968:587) noted that *S. montpelierensis* has a thin shell which might have easily been broken by clapping motions for swimming. However, Stanley (1970:40) asserted that thin shells require little lift for swimming. Based on this discussion, it is likely that *S. montpelierensis* was capable of short periods of swimming movement.

Ciriacks (1963:55) commented that the right valve of *S. montpelierensis* is less convex than the left valve. Most swimming pectenoids possess a lower valve more convex than the upper valve to aid in elevation of the commissure above the sediment for feeding (Stanley, 1970:39).

*Aviculopincten phosphaticus*

The bivalve species *A. phosphaticus* was found as a single population in this study and was collected from lithology 8. All of the morphologic dimensions measured for this species (Table 3), except for the number of spines, increase with size. The number of spines possessed by a specimen ranges from 5 to 9 and is not size-dependent. The spine development seen in this bivalve is not known in any other species of pectenoids (Ciriacks, 1963:46). The spine development seems to be closely related to the mode of life of *A. phosphaticus*.

The life-habit of *A. phosphaticus* is noted by Yochel-
son (1968:587) to be best represented by some modern pectenoids. One mode of life of the pectenoids, that of free-living epifauna, has been discussed for *S. montpelieri-

ensis*. *A. phosphaticus* is thought to represent a different mode of life than that of *S. montpelieriensis*. Some members of the Superfamily Pectinacea exhibit epifaunal byssal attachment. Kauffman (1969:144) suggested that byssally attached pectenoids are characterized by moderately to strongly prosocline shells, with a well-developed anterior auricle. The development of asymmetry would be the result of byssal attachment from the auricular sulcus. Table 3 shows that *A. phosphaticus* exhibits a moderately high angle of asymmetry. The angle of asymmetry (Figure 17) is defined as the angle between a line extended from the beak, perpendicular to the hinge axis, and a line extended from the beak through the midpoint of the shell width. The angle of asymmetry would support the assumption that this species of bivalve lived epifaunally, attached by a byssus. The depth of the auricular sulcus (Table 3), which is related to the elongation of the anterior auricle, is also well-developed and suggests byssal attachment (Stanley, 1970:30). *A. phosphaticus* probably attached the byssus to partially buried shells, grasses, or kelp for stabilization.

An epiplanktonic existence may have been possible for *A. phosphaticus*. Stanley (1970:30) indicated that modern *Pteria* lives above the sea floor, attaching the byssus to
kelp and grasses. This mode of life would have favored survival of *A. phosphaticus* by removing the influence of a soft substrate. However, the size-frequency histogram constructed for *A. phosphaticus* (Figure 37) is highly positively skewed. This suggests that this species was highly influenced by the soft sediments of lithology 8. A byssally attached mode of life on the sea floor seems more likely for *A. phosphaticus*.

Stanley (1970:130) indicated that modern *Mytilus edulis*, a mussel, is able to release its byssus and move about, to a limited extent, by means of the foot. The presence of hinge spines on *A. phosphaticus* is highly suggestive of immobility. This fossil pectenoid is inferred to have been permanently attached. If the byssus happened to fail, this bivalve probably could secrete a new one.

Kauffman (1969:145) commented that many byssate forms are able to retract the byssus in response to predators. *A. phosphaticus* may have been able to retract the byssus, pulling the shell tightly to the substrate for protection.

Ciriacks (1963:46) noted that the hinge spines on *A. phosphaticus* may have been utilized for attachment in some way, but he was not specific about the exact function. I would interpret the function of the hinge spines in two ways. First, if *A. phosphaticus* lay on the soft sediment, with the byssus attached to something nearby, the hinge spines may have acted as balancers to keep the
commissure elevated above the silty substrate inferred for lithology 8. In this function they also would have increased the surface area of the bivalve and deterred sinking. The second functional possibility of the hinge spines is that of maintaining the commissure completely above the substrate. If *A. phosphaticus* were byssally attached to living plants or other material, with the spines projecting downward into the sediment, the valves could have been propped up on the hinge. This orientation would have helped eliminate sediment fouling of the filtration system.
Figure 18. Composite block diagram depicting the living position inferred for each of the selected species discussed in this study. a = Leiorhynchochaidea weaksi, b = Lissochonetes ostiolatus, c = Lingula carbonaria, d = Orbiculoidea missouriensis, e = Babylonites ferrieri, f = Nuculopsis montpelierensis, g = Polidevicia obesa, h = Streblocordia montpelierensis, i = Aviculopecten phosphaticus, and j = Edmondia phosphatica.
RECONSTRUCTION OF POPULATION DYNAMICS

General Statement

Size-frequency histograms and survivorship curves are useful tools in determining mortality and growth patterns in fossil populations. In using fossils several difficulties are encountered in an attempt to reconstruct the population dynamics of a species accurately. Those factors which may distort the reconstruction of the population structure are collection failure, solution, current transport, and lack of age-size correlation.

The human factor plays a large role in obtaining an unbiased sample of the population. Even with meticulous collecting methods, small individuals are more likely to be overlooked than larger ones. The absence of juveniles may therefore be the result of collection failure (Thayer, 1975b:145). The collections used in this study include juveniles to adults of each species. The smallest specimens of any species measured 0.5 millimeters. Nevertheless, the size-frequency distributions did exhibit a deficiency of juveniles for many species. Collecting failure is a possibility, but care was taken in the field to locate and recover the juvenile portion of the population. The presence of very tiny specimens in the collections tends to support the contention that the collecting pro-
procedure was unbiased.

Loss of skeletal material by solution may differentially destroy the smaller, more fragile shells (Valentine, 1973:238). This size-related bias may play an important role in altering population information. Peterson (1976:140) has shown that calcareous shells buried in shallow lagoons are highly affected by solution, particularly those shells which are smaller or more porous. However, Rhoads and Morse (1971:423) suggested that complete or partial preservation of calcareous shells indicates that solution is not totally effective in dysaerobic or anaerobic environments. Solution is not considered a major factor affecting the population samples collected from the Phosphoria lithologies. The association of fossil collections with lithologies that contain organic matter would support the conclusion of Rhoads and Morse (1971).

Current transport is considered by many to be an important agent in the alteration of size-frequency distributions. Boucot (1953:29) pointed out that wave and current activity will tend to remove smaller shells from the assemblage when the velocity of the surrounding water reaches the minimum velocity required for shell transport. Transporting agents normally move small skeletons more easily than large ones. This may have biased the fossil record in favor of large individuals (Valentine, 1973:238). Hallam (1967:31) disputed this point of view. In studies conducted by Hallam a population of a larger-sized species
was found deficient in juveniles in a current-swept environment, whereas an associated population of smaller-sized species had retained numerous juvenile shells. If the juveniles of the larger species were removed by selective winnowing, the smaller species should have been affected also. From this example it is not clear to what extent current transport and winnowing have altered fossil populations.

The populations sampled in this investigation show no evidence of being modified by transport. Specimens exhibit no signs of abrasion, and fossils such as *Lissocidaris ostiolatus* and *Aviculopecten phosphaticus* retain their hinge spines intact. A great majority of the shells are articulated and unbroken indicating no transport (Boucot, 1953:32). The only individuals which are commonly disarticulated are the inarticulate brachiopods. This phenomenon among the inarticulates is not necessarily an indication of current activity, but rather a lack of hinge teeth and sockets. Also, a majority of the specimens in lithology 3 are preserved in an inferred life-orientation (Plate 1). For the populations considered in this report, the evidence suggests that the assemblages are essentially unwinnowed by current activity.

Another problem which may affect the interpretation of size-frequency distributions is lack of correlation between size of an individual and age. In constructing a size-frequency histogram, or a survivorship curve, the
size of an individual is assumed to reflect its relative age. This assumption is not always true. Thayer (1977) demonstrated that not all members of a population, which are of the same age, are of the same size. Variation in size at a given age is the result of both genetic and environmental factors. Consequently, a given size-class may include several age-classes; a consideration that complicates interpretations of size-frequency distributions. Nevertheless, size is often curvilinearly related to, and may be used to approximate, the age distribution in fossil populations.

Craig and Oertel (1966:349) indicated that size-frequency distributions in populations not subjected to post-mortem perturbations are controlled by four factors: growth rate and its variation, mortality rate, recruitment, and periodic cessation of growth. In the reconstruction of fossil population dynamics only mortality rate interacting with growth rate, and perhaps recruitment, can be analyzed.

The shape of the size-frequency histogram is highly influenced by mortality patterns. Craig and Oertel (1966:349) noted that with constant mortality, decreasing growth produces a negatively skewed distribution because older age classes are concentrated in a few size classes. In the case of constant growth, decreasing mortality produces positive skewness, while increasing mortality leads to negative skewness. Hallam (1972:72) indicated that moder-
ately positively skewed size-frequency distributions are more common than those which are strongly positively skewed. He also suggested that normal distributions are unusual, and negatively skewed distributions highly exceptional.

Craig and Oertel (1966) recognized five major types of recruitment: constant, tropical, boreal, arctic, and single burst. Reconstruction of Permian paleogeography (Ziegler and others, 1979:492; Scotese and others, 1979: 273; Bambach and others, 1980:36) places the depositional environment of the Phosphoria Formation within 10° north of the equator. The warm climates of this area are assumed to have produced tropical recruitment, wherein recruitment occurred throughout the year with a maximum during the winter months.

Survivorship curves constructed from size-frequency distributions are used in this study in determining mortality patterns. The slope of the curve is proportional to the mortality rate, and variations in the curve give clues to the overall pattern (Richards and Bambach, 1975: 78). The fossil assemblages in this study are thought to have resulted from time-averaged mortality operating on numerous generations, rather than instantaneous exterminations ("census mortality"), and so give a good representation of population structure.

Analysis of the size-frequency histograms in this study includes examination of skewness. The formula used
to determine skewness is from Inman (1952:133):

\[(\text{mean} - \text{median}) / \frac{1}{2}(84^{\text{th}} \text{ percentile} - 16^{\text{th}} \text{ percentile})\]

**Size-Frequency Histograms and Survivorship Curves**

The population sample of the articulate brachiopod *Leiorychhoidea weeksi* from lithology 3 exhibits a moderately negatively skewed, unimodal distribution from the constructed size-frequency histogram (Figure 19a). This type of distribution, showing a rarity of small specimens, is indicative of high juvenile growth rate and/or mortality rate increasing with age (Hallam, 1972:72). The survivorship curve (Figure 19b) also shows a very low death rate in juvenile to moderately-sized specimens, with a sharp increase in mortality rate at about 67 percent of maximum size. The curve probably reflects a constantly increasing mortality rate with increasing age of the individuals (Craig and Oertel, 1966:321).

The population sample of the gastropod *Bablyonites ferrieri* (Figure 20), also from lithology 3, has a size-frequency distribution and survivorship curve similar to that of *L. weeksi*. The histogram is moderately negatively skewed. The deficiency of juveniles indicates rapid initial growth and/or mortality increasing from youth to old age. The survivorship curve shows a very low mortality rate to about 59 percent of maximum size. At this point the death rate increased.

The deficiency of juveniles in both of these popu-
Figure 19. a. Size-frequency distribution for the population sample of Leiorthynchoidea weksi from lithology 3. The skewness = -0.23. n = sample size, $\bar{x}$ = average length, and $sd$ = standard deviation. b. Survivorship curve for this population sample.
Figure 20.  a. Size-frequency distribution for the population sample of Babylonites ferrieri from lithology 3. The skewness = -0.18. n = sample size, $\bar{x}$ = average diameter, and sd = standard deviation. b. Survivorship curve for this population sample.
lations has been explained by Yochelson (1968:589) as the result of current winnowing, and lag accumulation of larger specimens. This explanation cannot be accepted on the basis of lack of fossil orientation by currents (Figure 12), the occurrence of many individuals in assumed life position (Plate 1), and the recovery of smaller specimens of other species. Size-frequency histograms which have skewed distributions do not necessarily indicate winnowing (Craig and Hallam, 1963:745). A more likely cause for the deficiency of juveniles is local absence of recruitment, or patchy recruitment (Thayer, 1975b). Also, because growth was rapid in the early stages of life, animals dying at an early age would tend to be spread through several size classes, while slower growth in the later stages of life would tend to crowd several ages into a single size class (Craig and Hallam, 1963:746). Rudwick (1965:209) indicated that high juvenile mortality rates may occur in the larval stage or at spatfall if large numbers of small shells are not found. This implies that once an individual had survived the larval stage it had a good chance of surviving to maturity. Environmental conditions in this lithology must have been relatively favorable to maintain juvenile survival.

The only population sample of the bivalve *Nuculopsis montpelierensis* included in this study is also from lithology 3 (Figure 21). The size-frequency distribution for the sample of this species is slightly negatively skewed,
Figure 21. a. Size-frequency distribution for the population sample of *Nuculopsis montpelierensis* from lithology 3. The skewness = -0.06. $n =$ sample size, $\bar{x} =$ average length, and $sd =$ standard deviation. b. Survivorship curve for this population sample.
indicating a low juvenile mortality and/or rapid initial growth rate. The survivorship curve shows a slightly higher mortality rate in younger specimens than that of B. ferrieri and L. weaksi from the same lithology, but still indicates a constantly increasing mortality with age.

The inferred slightly higher juvenile mortality for N. montpelierensis, than that of the previously mentioned species from the same lithology, may be due to the infaunal nature of this bivalve. The lime muds inferred for lithology 3 probably caused fouling problems in the juvenile filtration system of infaunal bivalves which would not generally affect epifaunal suspension feeders, such as brachiopods, to the same degree (Steele-Petrovic, 1975).

The Lissochonetes ostiolatus population samples in this study exhibited size-frequency distributions which ranged from very slightly negatively skewed to moderately positively skewed. The size-frequency histogram of the population sample from lithology 3 (Figure 22) is slightly negatively skewed. This graph indicates low to moderate juvenile mortality rate coupled with an initially moderate growth rate. The survivorship curve shows that mortality increased with age.

The remaining population samples of L. ostiolatus are taken from lithologies which contain substantial amounts of organic matter (Table 1). The presence of organic matter is an excellent indicator that reducing conditions persisted to varying degrees in the habitats of these
Figure 22. a. Size-frequency distribution for the population sample of *Lissochonetes ostiolatus* from lithology 3. The skewness = -0.09. n = sample size, \( \bar{x} \) = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
populations (Blatt and others, 1972:392). The effect of this type of environment is assumed to have caused a greater juvenile mortality rate than in the population associated with lithology 3. In lithology 3 organic matter is not detected and an abundant infauna is present, suggesting oxidizing conditions to some sediment depth. Size-frequency distributions of population samples from lithologies 1, 5, and 10 (Figures 23, 24, and 25) indicate low to moderate mortality among juveniles and/or a moderate to low initial growth rate. The survivorship curves also point to a low to moderate juvenile mortality rate that increased with age.

Population samples of *Lingula carbonaria* were taken from lithologies 7, 9, and 11. These lithologies all contain organic matter from which I infer reducing conditions in the depositional environments. The size-frequency distributions of these population samples vary from highly negatively skewed to moderately positively skewed, and so factors other than reducing conditions must have existed to explain the extreme differences in population dynamics.

The *L. carbonaria* population sample from lithology 9 (Figure 26) shows a highly negatively skewed size-frequency histogram. A distinct absence of juveniles indicates low initial mortality and/or high initial growth rate. The survivorship curve shows low juvenile mortality which constantly increased with age, with a sharp break to a
Figure 23. a. Size-frequency distribution for the population sample of *Lissochonetes ostiolatus* from lithology 1. The skewness = + 0.17. n = sample size, x̄ = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
Figure 24. a. Size-frequency distribution for the population sample of *Lissochonetes ostiolatus* from lithology 5. The skewness = + 0.16. \( n \) = sample size, \( \bar{x} \) = average length, and \( sd \) = standard deviation. b. Survivorship curve for this population sample.
Figure 25. a. Size-frequency distribution for the population sample of Lissochonetes ostiolatus from lithology 10. The skewness = + 0.02. n = sample size, x = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
Figure 26. a. Size-frequency distribution for the population sample of *Lingula carbonaria* from lithology 9. The skewness = -0.24. *n* = sample size, *x* = average length, and *sd* = standard deviation. b. Survivorship curve for this population sample.
higher mortality rate at approximately 52 percent of the maximum size.

The population sample of *L. carbonaria* from lithology 7 (Figure 27) is nearly normally distributed. This histogram shows that the population had moderate to low juvenile mortality and/or moderate initial growth rate. The survivorship curve indicates a low juvenile mortality rate and a constant increase in mortality rate with age.

The population sample of *L. carbonaria* from lithology 11 (Figure 28) has a moderately positively skewed size-frequency distribution. This histogram indicates that the population had a moderately high juvenile mortality rate and/or low initial growth rate. The survivorship curve shows a constant increase in mortality rate with age, changing at about 20 percent of the maximum size to constant mortality.

The variations in size-frequency distributions of these three *L. carbonaria* population samples can be attributed to substrate differences. As discussed previously, *L. carbonaria* had an infaunal burrowing habit and preferred coarser substrates. The high negative skewness of the population sample from lithology 9, which is a sandstone, is the result of a coarser, more preferable substrate. Lithology 7 is a siltstone, and the softer silty nature of the inferred substrate probably caused problems for juveniles attempting to burrow and keep sediment from fouling the lophophore (Paine, 1970:27). The population sample of
Figure 27. a. Size-frequency distribution for the population sample of *Lingula carbonaria* from lithology 7. The skewness = -0.01. n = sample size, \( \bar{x} \) = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
Figure 28. a. Size-frequency distribution for the population sample of *Lingula carbonaria* from lithology 11. The skewness = + 0.17. n = sample size, $\bar{x}$ = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
*L. carbonaria* from lithology 11 inhabited an even softer bottom, as evidenced by the shale matrix, which caused even higher juvenile mortality and growth inhibition due to burrow collapse and sediment fouling of the lophophore. Similar patterns in population structure were attributed to substrate texture by Richards and Bambach (1975) in their study of brachiopods from the Upper Ordovician Richmond Group of Indiana and Ohio.

The $P_2O_5$ content may have contributed to the differences in size-frequency distributions between lithology 9 and lithologies 7 and 11. Lithology 9 contains a higher percentage of $P_2O_5$ (Table 1) than the other two lithologies, and a greater amount of phosphate in the associated marine water is inferred. Pickerill (1973:52) indicated that phosphate is an essential shell-building material in inarticulate brachiopods. Because the population sample of lithology 9 exhibited the lowest juvenile mortality and/or most rapid growth rate, a strong correlation is drawn between the higher phosphate content of the environment and accelerated growth and survival.

Size-frequency histograms and survivorship curves were constructed for three different population samples of *Orobiculoidea missouriensis*. All of the population samples show very similar distribution patterns. *O. missouriensis* from lithologies 4, 6, and 1 (Figures 29, 30, and 31) exhibit nearly normal distributions. The populations are inferred to have been characterized by moderate to low
Figure 29. a. Size-frequency distribution for the population sample of *Orbiculoides missouriensis* from lithology 4. The skewness = -0.13. n = sample size, \( \bar{x} \) = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
Figure 30. a. Size-frequency distribution for the population sample of Orbiculoidea missouriensis from lithology 6. The skewness = - 0.06. n = sample size, x = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
Figure 31. a. Size-frequency distribution for the population sample of *Orbiculoidea missouriensis* from lithology 1. The skewness = -0.06. \( n = \) sample size, \( \bar{x} = \) average length, and \( \text{sd} = \) standard deviation. b. Survivorship curve for this population sample.
juvenile mortality and/or moderate initial growth rate. The survivorship curves indicate constantly increasing mortality rate with age.

The size-frequency distribution resemblance of these three population samples of *O. missouriensis* is striking. The inferred similarity in environment, i.e., inferred substrate texture from lithology (Table 1), P₂O₅ content (Table 1), and content of organic matter probably resulted in environmental pressures that similarly influenced population demography.

Two different population samples of *Polidevcia obesa* were analyzed to determine population dynamics. The distributions of the size-frequency histograms are very similar, as are the survivorship curves, but some differences can be detected. *P. obesa* from lithologies 8 and 3 (Figures 32 and 33) both exhibit size-frequency distributions that are nearly normally distributed. The rarity of juveniles in both population samples implies moderate to low juvenile mortality rate and/or moderate initial growth rate. Both survivorship curves show low initial mortality rates which increased constantly with age. Nevertheless, a notable difference can be seen in the juvenile portion of the graphs. The population sample from lithology 8 shows a distinct absence of specimens up to about 4 millimeters and a slight negative skewness, whereas the population sample of *P. obesa* from lithology 3 contains specimens of smaller size intervals and displays slight positive
Figure 32. a. Size-frequency distribution for the population sample of Polidevicia obesa from lithology 8. The skewness = -0.01. n = sample size, \( \bar{x} \) = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
Figure 33. a. Size-frequency distribution for the population sample of *Polidevicia obesa* from lithology 3. The skewness = +0.08. n = sample size, \( \bar{x} \) = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
skewness. If this is not an artifact of collecting procedure, it means that the population of *P. obesa* from lithology 3 had a slightly higher mortality rate and/or slower growth rate among juveniles than the population from lithology 8.

The explanation for this difference is presumed to be related to substrate texture. *P. obesa* from lithology 3 had to cope with the inferred lime muds in that environment. A study of turbidity tolerance by Steele-Petrovic (1975) suggested that bivalves are relatively intolerant of turbid water. Fouling of the gills and internal organs with mud, because of the infaunal, burrowing mode of life, probably led to higher juvenile mortality and/or greater inhibition of growth than in lithology 8, which had an inferred coarser silty bottom.

The population sample of *Streblochondria montpelierensis* analyzed in this study is from lithology 8 (Figure 34). The size-frequency distribution of this species is slightly positively skewed, indicating moderate juvenile mortality rate and/or moderate initial growth rate. The survivorship curve is somewhat compressed, with mortality rate increasing dramatically at 8 percent of the maximum size. The population sample exhibits constantly increasing mortality with age.

The moderate mortality rate and/or moderate initial growth rate seen in this population sample of *S. montpelierensis* may indicate the effects of the environment inferred
Figure 34. a. Size-frequency distribution for the population sample of *Strelochondria montpelierensis* from lithology 8. The skewness = + 0.07. n = sample size, $\bar{x}$ = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
for lithology 8. The siltstone lithology (Table 1) suggests that the silty nature of the original substrate may have induced fouling of the filtration system in this species. The lithology also exhibits a substantial organic content, and inferred reducing conditions also may have increased mortality or inhibited growth. The suggested swimming habit of this bivalve probably aided in removing fine sediment from the mantle cavity by clapping the valves shut rapidly. This activity is assumed to have been the main factor in maintaining a lower juvenile mortality rate and/or more rapid growth rate for this epifaunal bivalve than that seen in the succeeding discussion of *Aviculopecten phosphaticus*, from the same lithology.

The *Aviculopecten phosphaticus* population sample in this report is also taken from lithology 8, and exhibits a highly positively skewed size-frequency distribution (Figure 35). The survivorship curve shows a constant increase in mortality rate with age. The inferred reason for the high juvenile mortality rate and/or retarded growth rate in *A. phosphaticus* is the same as that for *S. montpelieriensis*, namely a physically fouling substrate and reducing conditions. The high degree of positive skewness seen in the distribution is probably the result of the attached epifaunal nature of this bivalve. Permanent attachment would leave no escape from the clogging nature of a turbid environment with a moderate rate of sediment accumulation.

*Edmondia phosphatica* taken from lithology 8 displays a
Figure 35. a. Size-frequency distribution for the population sample of *Aviculopecten phosphaticus* from lithology 8. The skewness = + 0.23. $n =$ sample size, $\bar{x} =$ average length, and $sd =$ standard deviation. b. Survivorship curve for this population sample.
nearly normally distributed size-frequency distribution, and only slight positive skewness is reflected in the histogram (Figure 36). This distribution is inferred to indicate moderate juvenile mortality and/or moderate initial growth rate in this population sample. The survivorship curve does not show an increase in mortality until about 18 percent of the maximum size, but indicates that mortality rate increased from youth to old age.
Figure 36. a. Size-frequency distribution for the population sample of *Edmondia phosphatica* from lithology 8. The skewness = + 0.03. n = sample size, $\bar{x}$ = average length, and sd = standard deviation. b. Survivorship curve for this population sample.
GROWTH INCREMENTATION

General Statement

Variations in rates of accretionary growth often result in growth rings in shell-bearing invertebrates. When formed at regular time intervals, these growth lines can be useful in determining the age at death and growth patterns of organisms. The method of counting and measuring the spacing of growth rings in the analysis of fossils is particularly useful for making age and growth inferences, because living representatives are rarely available.

By studying growth-increment patterns, it is possible to distinguish several depositional rhythms. A number of conditions bring about the formation of growth rings. Rhoads and Pannella (1970) have summarized the various physiologic and environmental factors which are recorded in the hard part morphology of shell-secreting organisms. They have noted that growth increments will form in response to seasonality in the environment. The effect of seasonal temperature changes results in the formation of large increments during the summer and narrow increments in the winter. This cycle of alternating rapid and slow growth results in the formation of annual growth rings. This cycle of winter and summer growth need not be totally dependant upon temperature. Wilbur and Yonge
(1964:232) noted that the seasonal availability of phytoplankton may also be an important limiting factor causing a retardation or cessation of growth in the winter.

Several other factors contribute to growth ring formation. Physical disturbances, such as storms and predator attacks, will cause depositional breaks followed by rapid recovery, whereas spawning induces skeletal depositional breaks followed by slow recovery (Rhoads and Pannella, 1970:146). Tidal cycles are expressed by increments which display a 15 to 30 day periodicity. And finally, daily, or circadian, growth increments may be present as alternating light and dark bands (Valentine, 1973:175). Daily increments are only readily discernable on a microscopic level.

From this discussion it can be seen that growth incrementation results from several factors, and a single shell may possess rings stimulated by more than one of these factors. Overprinting of episodic disturbance rings with seasonal growth rings may pose a problem. Episodic growth checks cannot always be distinguished from seasonal growth increments and may complicate age determination and growth-pattern analysis (Valentine, 1973:176). Also, molluscs, under conditions of low oxygen tension, will utilize the calcium from their own shell as a metabolite, causing resorbtion of the shell material (Rhoads and Morse, 1971:424). This may obliterate growth increments already secreted. Another problem in the study of growth rings is
that an organism may skip days without secretion of growth increments, particularly as the organism ages. Hall and others (1974:60) asserted that in older specimens of the bivalve *Tivela stultorum*, daily increments are present for only one out of every two or three days. In the absence of other means, growth increments may be successfully used if the previous problems are recognized and corrected for where possible. Hallam (1967:31) noted that the reliability of using growth increments for age and growth determination has been demonstrated by direct observation by many workers.

Growth curves may be constructed by using regularly formed growth rings. When the length of the growth axis of a fossil specimen is plotted along the abscissa of a graph, and the successive growth increments are plotted along the ordinate, several growth patterns are possible. A concave upward curve indicates that accretionary growth decreases with age. This is probably the most common type of curve among skeletal invertebrates. A straight curve shows constant growth from youth to maturity. An s-shaped, or sigmoidal growth curve shows slow juvenile growth rate changing to more rapid growth and then decreasing in older stages (Wilbur and Yonge, 1964:226). The final growth-type possible is constantly increasing, which is characterized by a concave downward curve. Valentine (1973:242) commented that continuously increasing growth rate is not known to occur in nature.
The life span of fossil organisms which bear growth increments of uniform width can also be established. The use of rings as age indicators necessitates the recognition of increment type. If an organism is characterized by tidal rings they will occur either monthly or semi-monthly, and each year will be marked by 12 or 24 increments. If the growth rings are formed seasonally, such as during winter, age in years can be determined by a direct count. The life span of living related species is useful in the assessment of growth increments.

Growth-Pattern Analysis

Brachiopod and mollusc populations collected during this study were subjected to growth-pattern analysis by using those specimens which display prominent, measurable growth increments. Several population samples were not included in this analysis because of poorly preserved incrementation, or complete lack of it. The distance between growth lines was measured with vernier calipers on a sufficient number of individuals from a population sample, and plotted cumulatively on a graph against the corresponding growth increment number. In those cases in which the growth lines were too closely spaced for accurate measurement, the total number of growth increments were counted and plotted against the total length of the individual. The graphs are the basis for making inferences about the nature of growth within a population or
species.

The study of growth patterns in brachiopods and molluscs has generally shown that a gradual decline in the rate of growth occurs from youth to maturity (Hallam; 1972:64; Rudwick, 1965:209). This means that growth does not cease with maturity, but continues at a declining rate in these organisms. Variations from this continual decrease may be due to seasonal or environmental effects.

The growth incrementation of four specimens of Leiosechynchoidea weeksi from lithology 3 was measured and plotted (Figure 37). These growth-curves show a characteristic decline in growth with age. It is important to note that all specimens exhibit a marked decrease of accretionary growth rate following the initial increment. Thayer (1975b:143) found that sexual maturity is attained in modern brachiopods at an age of about one year. If sexual maturity was reached during the second year of life of *L. weksi*, the decrease in growth increment width from the first to the second year can be attributed to gametogenesis. A slight upsurge in growth is seen in two specimens after the eighth growth increment. This increase could be the result of a minor environmental fluctuation.

Specimens from three of the four population samples of *Lissochonetes ostiolatus* in this investigation display well-preserved growth incrementation patterns on the valve exteriors. Growth-increment patterns of individuals from
Figure 37. Graphic plot of cumulative length versus successive growth increments for selected specimens of *Leiorhynchoidea weęki* from lithology 3. All measurements taken from pedicle valves.
lithologies 1, 3, and 5 have been graphed and presented in Figure 38. All three graphs are characterized by a decrease in growth rate with age. *L. ostiolatus* representatives from lithologies 1 and 5 record a substantial growth-increment-width decrease following the initial growth increment, whereas the population samples from lithology 3 show a decrease in growth-increment-width after either the first or second growth line. This deceleration in growth rates again probably reflects the attainment of sexual maturity after the first year. The accretionary growth rate in the individuals from lithology 3 is much more rapid than the others. This indicates a more favorable environment for growth in lithology 3, particularly since reducing conditions were prevalent in lithologies 1 and 5, as evidenced by the presence of organic matter (Table 1). Crowding on the substrates of lithologies 1 and 5 probably induced competition for space and retarded calcification.

The growth patterns of *Lingula carbonaria* were measured and recorded for samples from the populations of lithologies 7, 9, and 11 (Figure 39). All of the graphs are very similar, again revealing a consistent decrease in growth with age. The decrease in successive increment width in this species is more gradual than for previously discussed species. A difference existed in relative growth rate patterns among populations of *L. carbonaria*. Specimens from lithology 9 show a much more rapid rate of growth
Figure 38. Graphic plot of cumulative length versus successive growth increments for *Lissoclonetes ostiolatus*. a. Selected specimens from lithology 3. b. Selected specimens from lithology 1. c. Selected specimens from lithology 5. All measurements taken from pedicle valves.
Figure 39. Graphic plot of cumulative length versus successive growth increments for *Lingula carbonaria*. 

a. Selected specimens from lithology 7.  

b. Selected specimens from lithology 9.  

c. Selected specimens from lithology 11.
than specimens from the other two lithologies. This difference is inferred to have been the result of three variant environmental factors. Lithology 9 is inferred to have provided a coarser substrate than the other two lithologies, based on lithologic texture (Table 1). This would have provided a more suitable substrate for the construction of burrows. Lithologies 7 and 11 are much finer-grained, posing problems of lophophore fouling and burrow maintenance. Lithology 9 also contains substantially more $P_2O_5$ (Table 1) than lithologies 7 and 11. The fact that inarticulate brachiopods utilize calcium phosphate as shell material (Pickerill, 1973:152) may indicate that the greater phosphate concentration inferred in the marine environment of lithology 9 may have contributed to accelerated growth. Each of these lithologies also contain organic matter, and the possibility is noted that reducing conditions may have been more mild in the environment of lithology 9.

The growth increments in *Oribiculoidea missouriensis* are so closely spaced that it was necessary to count the total number of growth lines on a specimen and plot it against the length of that specimen. This was done for *O. missouriensis* population samples from lithologies 2, 4, and 6 (Figure 40). The specimens representing populations from lithologies 2 and 4 display distinct concave upward curve trends, indicating a decline in growth rate with age. The population samples from lithology 6 show a distinctly
Figure 40. Graphic plot of cumulative length versus number of growth increments for Orbiculoidea missouriensis. a. Selected specimens from lithology 2. b. Selected specimens from lithology 4. c. Selected specimens from lithology 6. All measurements taken from pedicle valves.
linear growth curve. Wilbur and Yonge (1964:227) explained that linearity is probably due to early mortality of the plotted individuals. Under conditions favoring survival, a decline in growth rate would be noticeable for the specimens if they had lived longer. This is evident in the O. missouriensis population sample from lithology 6, in which the measured specimens do not exceed 12 millimeters in length, whereas in the other two population samples 12 millimeters is the approximate size at which growth begins to decline. The growth rate is faster in the representatives of O. missouriensis from lithology 2, as seen by the lower slope of the growth curve. More rapid growth may be attributed to inferred milder reducing conditions in that environment, considering that all of the lithologies contain organic matter and similar amounts of P2O5.

The growth lines exhibited by Babylonites ferrieri are very narrowly spaced and poorly preserved on some areas of the shell, so that when counting the number of increments on a specimen it was necessary to approximate the number of increments in some areas of the shell. The approximation of growth lines was accomplished by applying the spacing of growth lines which immediately preceded and succeeded the weathered or poorly preserved areas to obtain the number of growth lines in that area. The remaining well-developed growth increments were carefully counted to insure maximum accuracy. It is believed that this method provides a reliable estimate of growth increment.
numbers and that the results reflect the actual growth pattern of B. ferrieri. The approximate number of growth increments displayed by an individual was plotted against the diameter of the last whorl, and the graph is shown in Figure 41. The growth pattern of this gastropod reflects a decreasing trend with age, which is common for invertebrates. The concave-up curve is well pronounced in this particular gastropod.

A linear tendency is seen in the growth pattern of Aviculopecten phosphaticus from lithology 8 (Figure 42b). Growth rates appear very linear in the graphs for the measured specimens. Only a single individual displays a slightly decreasing growth rate with age. It is possible that a general decrease in growth rate is not observed in these specimens because of early mortality. To document this suspicion, it would be necessary to obtain additional individuals which display a greater number of growth lines than those recovered and studied.

A population sample of Polidevicia obesa from lithology 3 was subjected to growth rate study (Figure 42a). Specimens below approximately 8 millimeters in length were excluded from the study because the growth lines were not preserved. The incrementation on the selected individuals showed no definite correlation of number with size. It is possible that, if preservation had permitted the use of juveniles, a decrease in growth rate with age would have been observed. If this is the case, P. obesa reveals
Figure 41. Graphic plot of diameter of last whorl versus number of growth increments for selected specimens of *Babylonites ferrieri* from lithology 3.
Figure 42. a. Graphic plot of length versus number of growth increments for selected specimens of *Polidevnia obesa* from lithology 3. b. Graphic plot of cumulative length versus successive growth increments for selected specimens of *Aviculopecten phosphaticus* from lithology 8.
a broad variation in size with age, reflected by the points plotted on the graph. Another possibility is that the narrowly spaced incrementation on the shell is merely concentric ornamentation, which characteristically has a limited range of number of ridges for this species. The evidence is inconclusive at this point.

**Age Determination**

Counting the growth rings on the surface of the individual fossils provides an estimate of life expectancy of the various species. Because all of the population samples studied are inferred to have inhabited water of moderate depth, an environment buffered against storms and seasonal temperature fluctuations is implied. This environmental stability would have minimized stimulation of disturbance rings, so that the growth increments present should reflect annual, synodic, or daily rhythms. However, semi-annual monsoon rains, common near the equator today, may have existed within the paleogeographical area of this study. If this were the case, growth increments may have been formed twice-yearly in some species in response to food supply.

To determine the periodicity of growth increments in fossils, it is necessary to utilize current information from living representatives. The life spans of living brachiopods and molluscs provide a comparison in determination of ages for fossil species. Of course, the
duration of life of different species varies greatly, but similar sized species of the same class should have comparable life spans.

Brachiopods are known to live for 8 years or longer. Thayer (1975b:140), in his study of the population structure of brachiopods, discovered a total life span of about 8 years for the extant *Terebratalia transversa*. Rudwick (1965:209) indicated a general life expectancy of 7 to 8 years, or even longer, for brachiopods. Kenchington and Hammond (1978:70) observed that the life span of specimens of *Lingula anatina* is as much as 11 years.

Molluscs display very similar life expectancies. Cox (1969:11) explained that the average age attained by bivalves varies greatly, but generally falls within the range of 5 to 10 years. Exceptional species of bivalves, such as *Tridacna maxima*, have been observed to live 40 years or more. Cox (1960:87) contended that the life spans of gastropods are variable and species-dependent. Some species of gastropods live only one year, whereas many of the more common species generally live 5 to 7 years. A maximum age of 10 years has been recorded for modern marine gastropods (Cox, 1960:87).

The maximum number of growth increments found recorded on analyzed specimens of *Leiorhynchoidea weaksi* (Figure 37) is 9. By comparing this number with that of known life spans of extant species it can be concluded that these increments are probably annuals, and that the life
span of *L. weeksi* was approximately 9 years. This age probably represents a conservative life span estimate for this species because only a small portion of the entire population was examined.

The growth lines recorded in the shell of *Lissochonetes ostiolatus* (Figure 38) also appear to be annual, because they are few in number. Based on the maximum of 5 growth lines found in the selected specimens, the approximate life span recorded for this species is 5 years. Again, this age probably represents a conservative life span estimate for the species.

For specimens of *Lingula carbonaria* the maximum number of growth increments counted is 8 (Figure 39). These lines are assumed to have been formed annually, and so record an average life span of about 8 years. This age is comparable with that found for extant species of *Lingula*.

*Orbiculoidea missouriensis* (Figure 40) poses a slight problem in determining the kind of growth increment. A maximum of 28 growth lines was counted on one large individual. Increment numbers in the range of 20 to 25 are common. If these growth lines were formed annually, a life span of about 28 years would be indicated. If the growth increments were formed semi-annually, a life span of about 14 years would be recorded. These ages seem too lengthy in relation to the ages reported for modern inarticulate brachiopods. The small size of *O. missouriensis*, the inferred proximity of the flat shell to the substrate,
and the silty bottom sediments would have rendered long-term survival of this brachiopod unlikely. A synodic origin of the growth lines seems to be a more likely explanation. If each growth line reflects a lunar cycle, an approximate life span of 2.3 years for *O. missouriensis* is reasonable. Rudwick (1970:156) indicated that in the small lingulid *Glottidia* the average life span is estimated at 1.3 years, and in the small terebratulid *Pumilus* a life expectancy of 3 years is common. It is possible that monthly increments may have been skipped, and so a life span of 2.3 years for *O. missouriensis* would be a conservative estimate.

*Babylonites ferrieri* is the only species studied which exhibits probable daily growth increments. The growth lines are considered to have formed daily because of their presence in such great numbers. It is interesting that these daily increments are prominent, and can be seen unaided, though counting necessitates the use of a microscope. The largest number of increments recorded in those specimens examined is 1220 (Figure 41). If the increments represent daily accretion, *B. ferrieri* had an approximate life span of 3.4 years. Species exhibiting daily increments commonly skip days of shell accretion (Hall and others, 1974:60). This means that age determination based on daily growth increments may be underestimated. Therefore, the age determination for *B. ferrieri* represents a conservative life expectancy estimate.
The growth lines on *Aviculopecten phosphaticus* are faint, but observable. The maximum number of growth lines on those specimens examined is 4 (Figure 42b). Based on the life spans of extant bivalves, the increments were probably formed annually. From this analysis a life span of about 4 years is estimated for this bivalve. Four years probably represents a conservative approximation of the average life span for this species because only a small portion of the population was examined.

*Polidevicia obesa* displays very regular, narrow, sharply delimited growth increments. The number of lines expressed in the analyzed specimens suggests a monthly pattern. The maximum number of lines recorded on the collected specimens is 60 (Figure 42a). Monthly deposition of these increments would have produced individuals of *P. obesa* with a general life span of about 5 years. This life span is a minimal estimate because monthly increments may have been skipped during growth.
CONCLUSIONS

The Meade Peak Member of the Phosphoria Formation was deposited in moderately deep water. Unburrowed, organic-rich, fine-grained siltstones and shales predominate in the area of this study. Thin, parallel laminae dominate the sedimentary structures. Cross-laminae are absent. Random orientation of fossils is found on the mapped bedding plane at the Montpelier Canyon locality. Therefore, the fossil assemblages collected from in this study are inferred to be unwinnowed and untransported. The result is that analyses of morphology, size-frequency, and survivorship are assumed to be reliable indicators of the original population structure.

The modes of life of the various selected species in this study were determined from known life-habits of related extant species and from analysis of morphology. The articulate brachiopod *Leioechynoidea weeksi* is assumed to have been tethered to the sea floor by a long, perhaps branched, pedicle. It is possible that this species was not permanently attached, but was able to retract the pedicle and readjust the living position.

*Lissochonetes ostiolatus* is an articulate brachiopod which is assumed to have an unattached existence, lying free on the sea floor. A type of pectenoid-like swimming
movement was probably possible. This species characteristically possess hinge spines which are interpreted to have increased the bearing surface and prevented sinking into the sediment.

*Lingula carbonaria* is an inarticulate brachiopod which probably led an infaunal existence, making its own burrow. This species probably was able to move up and down and rotate in the burrow, by means of the pedicle, in response to food and predators.

The inarticulate brachiopod *Orbiculoides missouriensis* is assumed to have been an epifaunal inhabitant, attached to the substrate by a short pedicle. The pedicle probably elevated the shell only a few millimeters above the substrate.

The gastropod *Babylonites ferrieri* displays a low, expanded form and is thought to have crawled over the surface of the substrate in search of food. The food source of this gastropod is not known, but may have been grazed algae, carrion, detritus, or soft-bodied invertebrates.

Two bivalves in this study shared the same mode of life. *Nuculopsis montpelierensis* and *Polidevicia obesa* are assumed to have been shallow burrowing, labial palp feeders.

*Edmondia phosphatica* is a bivalve which is inferred to have been a shallow burrowing, siphonate species.

*Streblochondria montpelierensis* and *Aviculopecten phosphaticus* are both bivalves collected in this study and are related
to modern pectenoids. However, they represent two different modes of life. *S. montpelierensis* probably led an unattached existence, lying free on the sea floor. This bivalve probably was capable of short swimming bursts. *A. phosphaticus* is assumed to have been byssally attached to grasses or algae near the bottom. The spines of this species may have been utilized to increase the bearing area and deter sinking, or they may have been thrust into the sediment propping the bivalve up on the hinge.

Morphologic variation, mortality rate, and growth rate exhibited by the selected species of brachiopods and molluscs, have been modified by various environmental factors interacting with the individual life-habits. Those lithologies that contain organic matter and no infauna are inferred to have presented a slightly to strongly reducing environment to the populations involved. The oxygen depletion resulting from the negative Eh has contributed to stunted growth and high juvenile mortality rates among brachiopods and molluscs. This is reflected in the means of measured morphologic dimensions, the size-frequency histograms, and the growth curves of the population samples.

Textural substrate differences have also affected growth. Coarser, and presumably firmer, sandy or silty substrates probably were preferable for the benthic epi-fauna and infauna studied. Individuals in these substrates tend to have larger morphologic mean sizes, more rapid growth rates, and highly negatively skewed size-frequency
distributions.

The phosphate concentrations inferred in the paleoenvironment have been observed in this study to affect the growth rate and mortality rate in inarticulate brachiopods. Those lithologies containing higher concentrations of $P_2O_5$ apparently have aided shell construction and survivorship in populations of $L. carbonaria$ because they build the shell out of calcium phosphate.

Competition probably has affected morphologic variability. In the studied assemblage of *L. weksi*, competition for food has produced individuals which exhibit variable sulcus dimensions. This variability is interpreted as an effort to partition resources in the environment. Crowded substrates have resulted in stunted growth in certain assemblages of *L. ostitolatus*, which were competing for space.

Growth lines on the analyzed taxa were clearly formed at regular intervals of time, and thus reflect age and growth patterns. The growth curves constructed for each assemblage generally show a decline in growth rate with age. This pattern of growth is characteristic of modern brachiopods and molluscs in general. Some linear growth trends are present in the assemblage of *A. phosphaticus* and in one assemblage of *O. missouriensis*. These linear trends may be the result of mortality before a decline in growth was recorded.

Inferences concerning age and life span, based on
growth lines, are supported by general information on life spans of extant species of brachiopods and molluscs. The selected fossil species in this study exhibit several types of growth lines. Annual growth lines are inferred for specimens of *L. weeksi*, *L. ostiolatus*, *L. carbonaria*, and *A. phosphaticus*. General life expectancies of these species are interpreted to be: *L. weeksi*, 9 years; *L. ostiolatus*, 5 years; *L. carbonaria*, 8 years; and *A. phosphaticus*, 4 years. These are conservative life span estimates because only a small portion of each population was sampled.

Monthly growth lines are assumed for *O. missouriensis* and *P. obesa*. If this assumption is correct, *O. missouriensis* had a general life span of about 2.3 years, and *P. obesa* about 5 years. These are conservative estimates because monthly increments may have been skipped.

*B. ferrieri* exhibits what I believe are daily growth lines. The largest number of lines exhibited by an examined specimen would indicate a general life span of about 3.4 years. Organisms which exhibit daily increments commonly skip days of accretion. This means that the life span estimate for *B. ferrieri* is probably very conservative.
LITERATURE CITED


