

**PALEOECOLOGY AND EVOLUTIONARY TRENDS
IN GYPIDULID BRACHIOPODS**

A Thesis Submitted
to the Temple University Graduate Board

in Partial Fulfillment
of the Requirement for the Degree

MASTER OF ARTS

by

Joseph H. Makurath

April 1972

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Acknowledgements

The field of research was proposed by Dr. E. J. Anderson, thesis advisor, whose constant encouragement and guidance are gratefully acknowledged. In addition, Dr. Anderson generously provided samples of G. coeymanensis used in this study. The critical reading of the manuscript by Dr. P. W. Goodwin and Dr. G. Méyer, and their many helpful suggestions are much appreciated.

Financial aid was provided by the Geology Department of Temple University in the form of teaching and research assistantships. Financial support for field work during the summer of 1971 was provided by a Sigma Xi Grant-in-Aid-of-Research.

Abstract

The distribution of gypidulid brachiopods in Siluro-Devonian carbonates of the Appalachian basin is strictly limited by gypidulid specializations for poorly sorted sand substrates, normal salinity and good circulation. Gypidulid occurrences are limited to open shelf near wave base sands which are closely associated with transgressive barrier systems. Regressive phases of carbonate deposition lack suitable substrates for gypidulid habitation.

Progressive adaptive morphologic change in gypidulid spondylium/beak shape parallels progressive decrease in restriction of the gypidulid environment. Canonical analysis and comparisons of mean shape ratios, reduced major axes and allometric curves are used to statistically define variation in spondylium shape and size in three successive populations of gypidulids. Statistical tests indicate significant differences in spondylium/beak shape and size between species. Persistence of significant change in growth (allometric) curves through time indicates genetic change in successive populations.

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Introduction

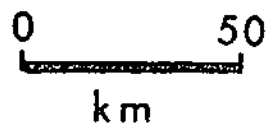
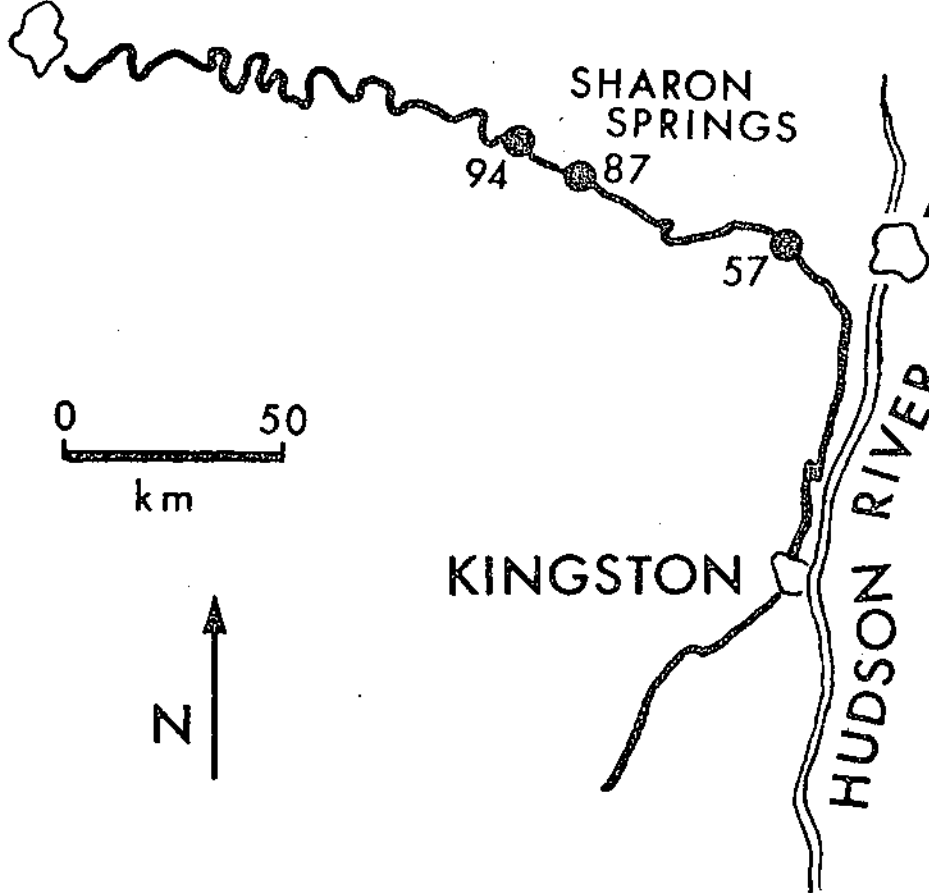
This study analyzes and interprets morphologic variation of the spondylium duplex among samples of two species of gypidulid brachiopods within an evolving phylogenetic sequence. The paleoenvironment of earlier, Silurian species of Gypidula is interpreted from its stratigraphic and lithologic distribution.

Anderson (1970) has demonstrated progressive change in shape of the spondylium through three successive populations of the later, Devonian, species Gypidula coeymanensis from the Coeymans Formation (fig. 1) of New York State. This progressive variation is described as an adaptive change in shape of the spondylium which increases the area of muscle attachments for a shell of given length. This change in shape is correlated with (but not necessarily causally related to) evolution of the gypidulid environment. Because of the persistence of this change in shape throughout Coeymans time, it is suggested to be evolutionary (genetic).

In this study, variation of the spondylium is analyzed in a sample of G. prognostica from the Silurian Keyser Formation and compared with variation in two samples of G. coeymanensis. The samples of G. coeymanensis were provided by Dr. E. J. Anderson and were among those used in his Devonian study.

Figure 1 - Outcrop belt of the Coeymans Formation:
The outcrop follows the Mohawk and Hud-
son river valleys.

SYRACUSE



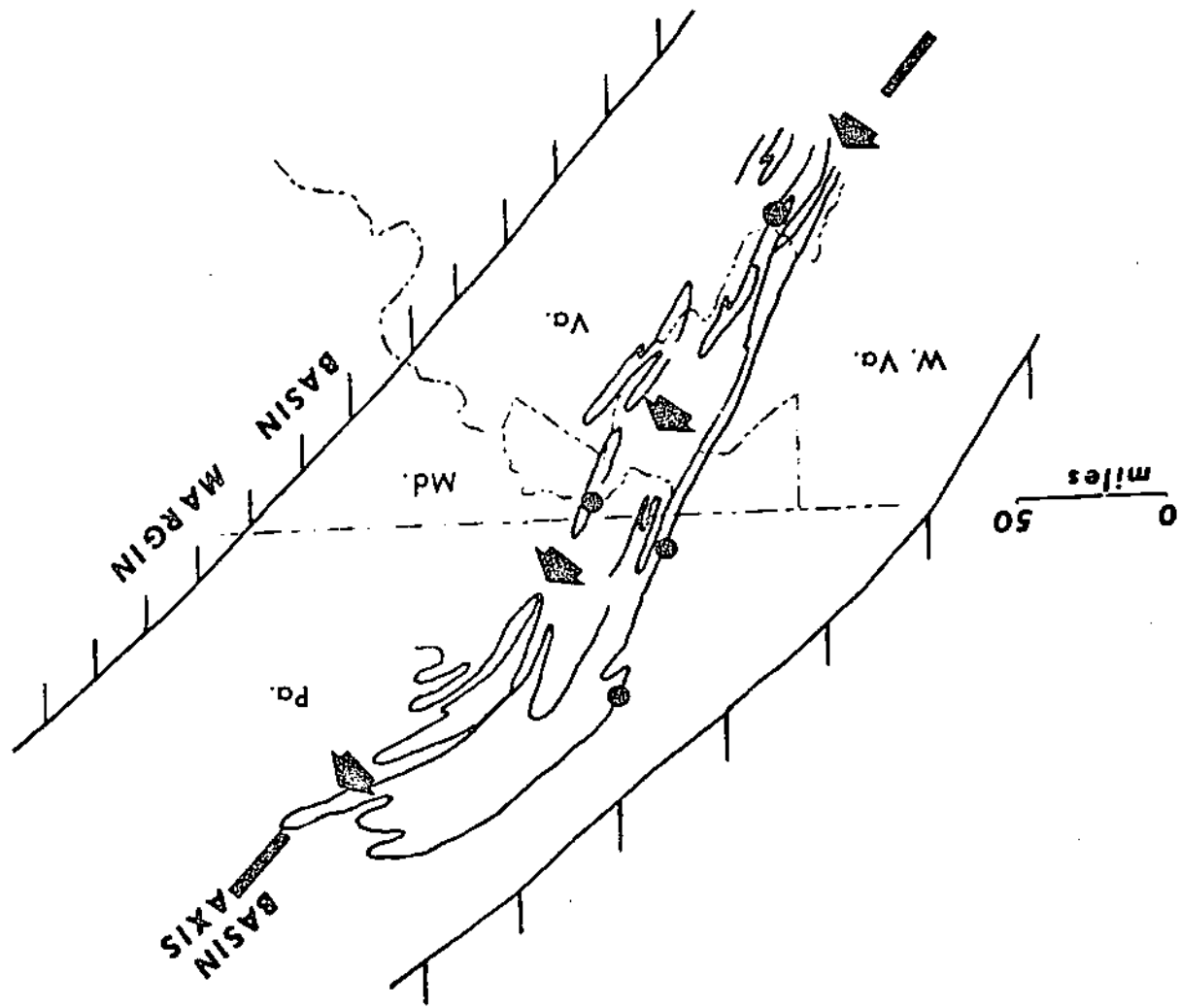
Sampling

Samples of G. prognostica were taken from two exposures of the same stratigraphic horizon of the Upper Silurian Keyser Formation (fig. 2). Fifty-one individuals were taken from the exposure at Hyndman, Pa. (Bowen, 1967, locality 5). At this locality, gypidulids preserved in life position were collected from the same horizon. Eleven individuals were taken from the same stratigraphic horizon at Warm Springs, Va. (Swartz, 1929). The two samples were found to be described by the same reduced major axis and were therefore combined and treated as one sample. The size of individuals in the total sample is approximately normally distributed. At each sampling locality bulk samples of rock were collected and all possible specimens were removed from each large block.

Samples of G. coeymanensis were taken from the Coeymans Formation of New York State (Anderson, 1970). The first sample of seventy-nine individuals (loc. 57) was collected from the lower Coeymans near New Salem, N. Y. (Rickard, 1962, locality 57). The second sample of ninety individuals (loc. 94) was taken from the upper Coeymans at Cherry Valley, N. Y. (Rickard, 1962, locality 94). Each of these samples was found to be normally distributed in size.

The vertical stratigraphic distance between the two

Figure 2. Outcrop belt of the Keyser Formation showing the configuration of the Appalachian basin during Late Silurian time - localities shown are; Tyrone, Pa. (northernmost dot), Hyndman, Pa., Great Capacon, Md. and Warm Springs, Va. (southernmost dot) - arrows indicate the basin axis and direction of regional transgression.



Coeymans samples is estimated to be about eighty feet (Anderson, 1970). Discontinuous outcrop of Lower Devonian rocks between Pennsylvania and New York makes correlation of the Keyser sample with the later Coeymans samples difficult.

Head (1969) has used basin-wide transgressive and regressive events to correlate rocks of the Appalachian basin. From this point of view, the Keyser sample and the Coeymans samples come from rocks deposited by two successive transgressive events separated by a major regression during late Keyser time. Thus the New Creek Formation (fig. 5) represents the same transgressive event that is responsible for the deposition of the lithologically similar Coeymans Formation.

The vertical stratigraphic distance between the sampled horizon in the Keyser Formation and the base of the New Creek Formation ranges from about sixty to about one-hundred feet. Because the New Creek and Coeymans Formation represent the same time transgressive horizon (Head, 1969) it is concluded that the time interval between the Keyser sample and the earlier Coeymans sample is at least as great as that between the Coeymans samples.

It is believed that all samples represent individuals that lived near the collecting localities, however, the relative effects of mortality, current sorting and selective breakage are not known. Although measuring techniques were slightly different, this report

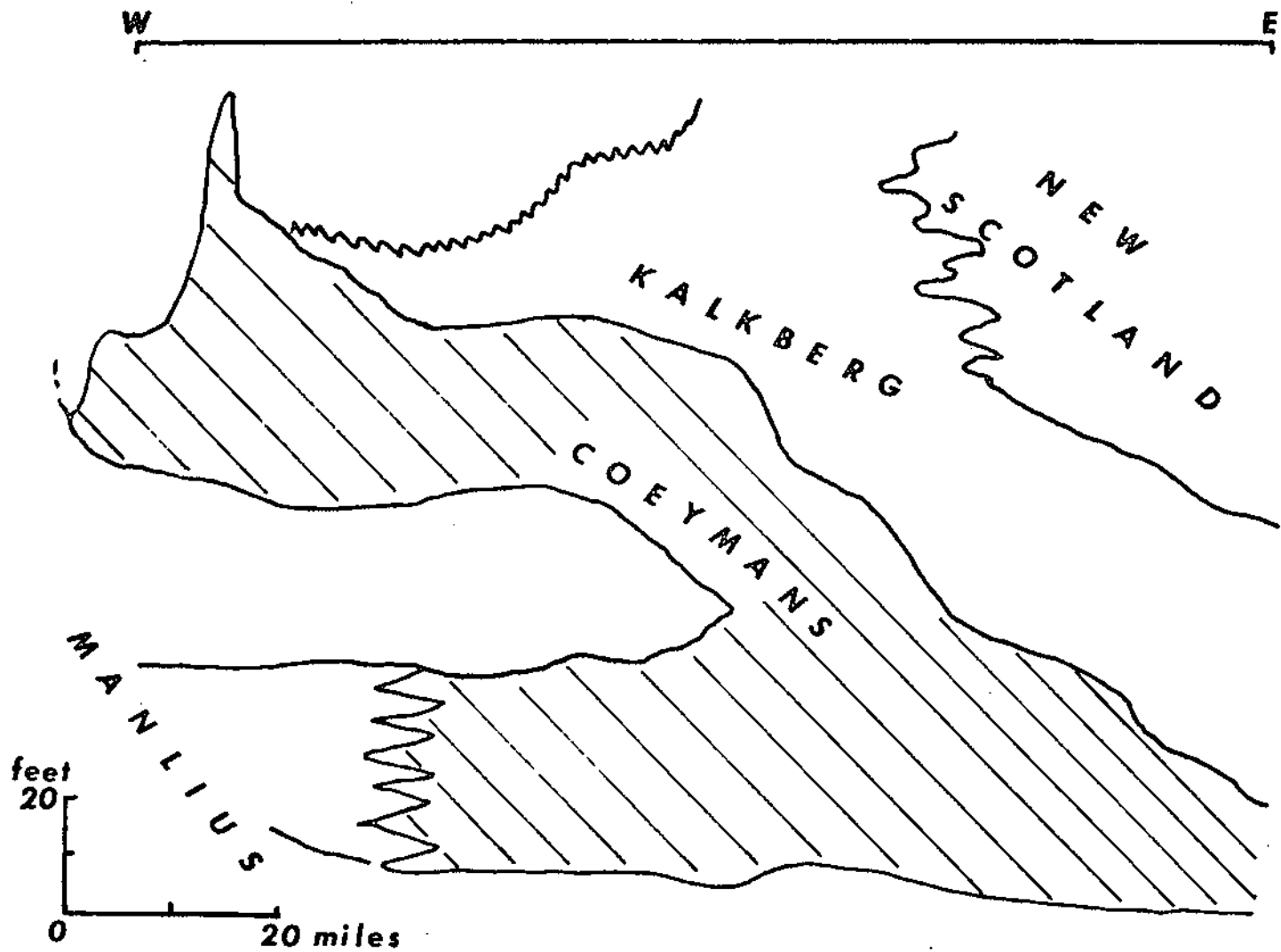
verifies the results of the previous study by Anderson (1970) on G. coeymanensis and indicates change in shape and size between G. prognostica (Keyser) and G. coeymanensis (Coeymans) which is consistent with the trends found by Anderson (1970). These differences in size and shape between species are interpreted as progressive adaptation.

Gypidulid Distribution and Paleoenvironment

The distribution of the Devonian brachiopod G. coeymanensis, Schuchert, 1913, has been shown by Anderson (1970) to be sharply limited by environment, occurring only in calcarenites representing shallow open shelf marine environments which are near or above wave base. These poorly sorted pelmatozoan-brachiopod calcarenites are current deposited and biogenically reworked, and occur consistently in the same lateral and vertical position within a sequence of lithologies which spans the Manlius, Coeymans, and Kalkberg Formations. The stratigraphic relationships of these formations have been determined by Rickard (1962), and environmental interpretations of the sequence of lithologies associated with gypidulid bearing calcarenites have been refined by Laporte (1967 and 1969), Anderson (1971a) and Epstein (1969). The resultant paleoenvironmental framework is one of transgressive migration of laterally contemporaneous environments.

The depositional environments represented by the Coeymans Formation (fig. 3) lie between offshore, deeper water environments (Kalkberg) and tidal flat and restricted subtidal environments (Manlius) onshore. On the basis of sedimentary and biogenic structures, Anderson (1971a) recognizes three environmental zones within the Coeymans in an onshore to offshore sequence. The first

Figure 3- Stratigraphic cross section of Lower Devonian rocks of New York from Syracuse (west) to Albany (east)- modified from Rickard, 1962.



is a barrier zone which evolves from an area of mud mounds and channels in early Coeymans time to patch reefs in late Coeymans time. During a mid-Coeymans progradation the barrier zone does not develop. Seaward of the barrier zone are located two shallow shelf zones, one (onshore) characterized by persistent current and wave agitation and a second (offshore) zone of regular reworking by organisms and only occasional wave and current reworking. The two shallow shelf zones remain lithologically distinct throughout Coeymans time. G. coeymanensis is found only in shelf zones offshore from barrier complexes. It is found neither within patch reefs nor in the earlier mud mound zone. Furthermore, it disappears when the lateral sequence of environments is disrupted by progradation of tidal flat sediments during middle Coeymans time. On the basis of these occurrences, Anderson (1970) concludes that G. coeymanensis exhibits specialization for normal salinity, low turbidity and firm or slowly shifting sandy substrates.

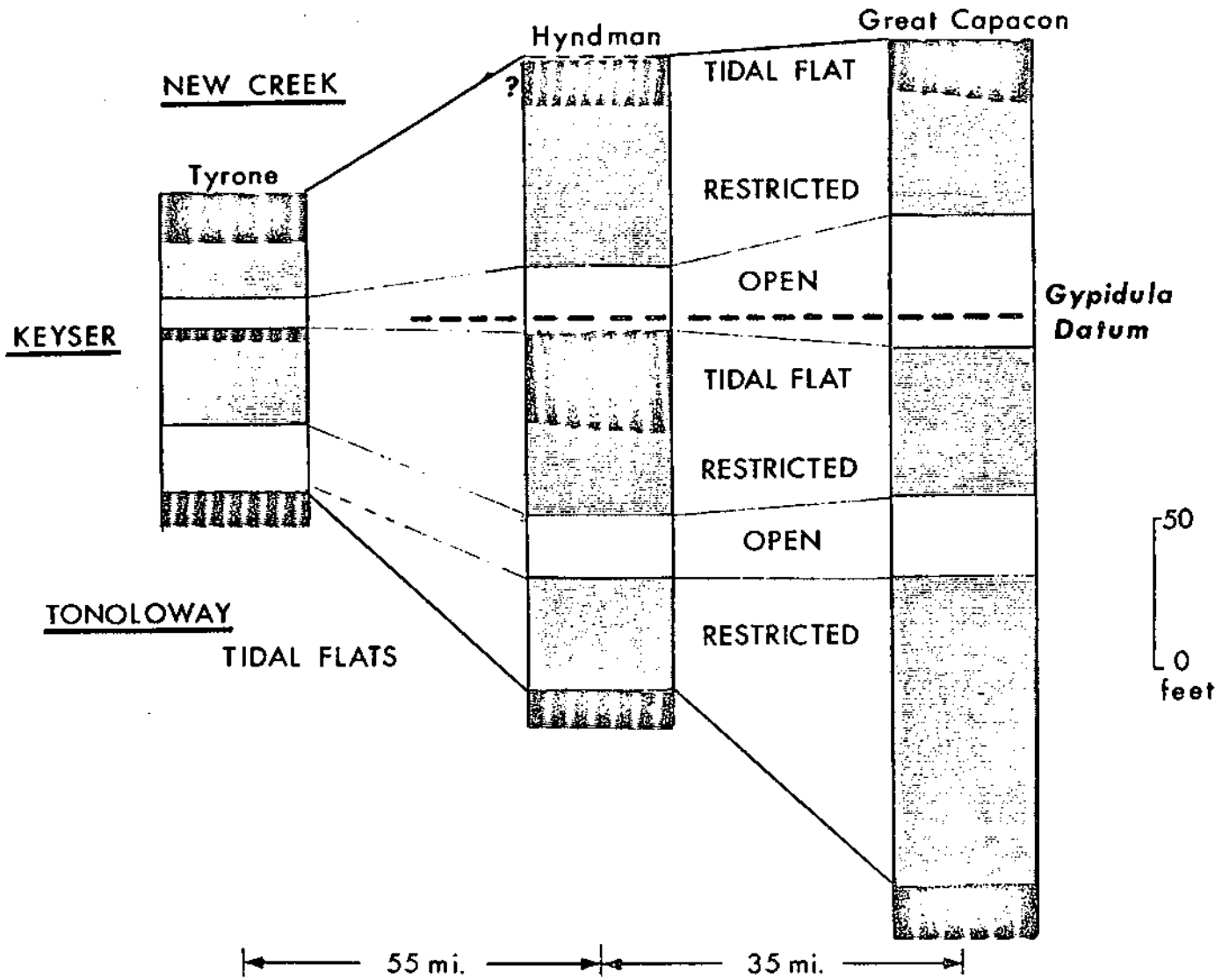
Although the detailed environmental relationships are not as well understood as those in New York State, occurrences of G. prognostica within the Keyser Formation (Silurian-Devonian) of Pennsylvania, Maryland, West Virginia and Virginia support these conclusions. The Keyser Formation represents carbonate deposition within the same basin but at an earlier time than the Coeymans Formation. Evolution of the Appalachian basin

through the Keyser-Coeymans interval is described by Head (1969) as a series of transgressive and regressive pulses which had a net effect of transgression in a northern and northeastern direction. During the course of this transgression the basin becomes progressively larger and more influenced by normal marine conditions. The basin evolves from an area of tidal flats and evaporites during pre-Keyser time to a more open epeiric sea during post-Coeymans time (Head, 1969).

The Keyser Formation (figs. 2 and 5) ranges in thickness from about two-hundred and ninety feet near Keyser, West Virginia to less than two-hundred feet over most of Pennsylvania. South of Keyser, it thins slightly to about two-hundred and fifty feet (Bowen, 1967). The lower contact of the Keyser is invariably sharp and easily recognized due to the contrast in lithologies between the top of the underlying Tonoloway Formation which is characterized by unfossiliferous, laminated and mud-cracked limestones and dolomitic limestones and the basal Keyser which is, in most cases massive and fossiliferous. The upper contact between the Keyser and the overlying New Creek Formation is easily recognized in the northern half of the outcrop belt where the upper Keyser is laminated and conformably overlain by coarse crinoidal biosparites of the New Creek. In the southern half of the outcrop belt, the upper Keyser is characterized by biointrasparites, making the contact less sharp (Bowen, 1967).

During mid-Keyser time, the Appalachian basin extended from Tennessee northeast over much of western Virginia, West Virginia, Maryland and most of central Pennsylvania. A map of the Keyser outcrop belt and a superimposed diagram indicating the configuration of the basin is shown in figure 2. The arrows are positioned along the basin axis where the formation is thickest; their direction is that of regional transgression. Lithologies exposed along this axis are generally characteristic of deeper water environments than lithologies exposed at the basin margin. The basin margin to the southeast remained in approximately the same position throughout deposition of the Keyser and served as source of clastic material which was periodically dispersed into the basin to the west. In contrast, the position of the basin margin to the northwest was highly variable during deposition of the Keyser, as this area was characterized by very low slope tidal flat and evaporite deposits of the Tonoloway and Salina Formations of western Pennsylvania (Head, 1969). The three localities in figure 2 may be used to construct a cross section of the Keyser Formation from near the northwestern basin margin (Tyrone, Pa.) through south central Pennsylvania (Hyndman) to near the basin axis in Maryland (Great Capacon). The three exposures contain the lithologic record of two major transgressive events which may be used to correlate the the sections (fig. 4). Head (1969) recognizes these

Figure 4- Stratigraphic cross section of Keyser Formation from near the western basin margin at Tyrone to near the basin axis at Great Capacon.

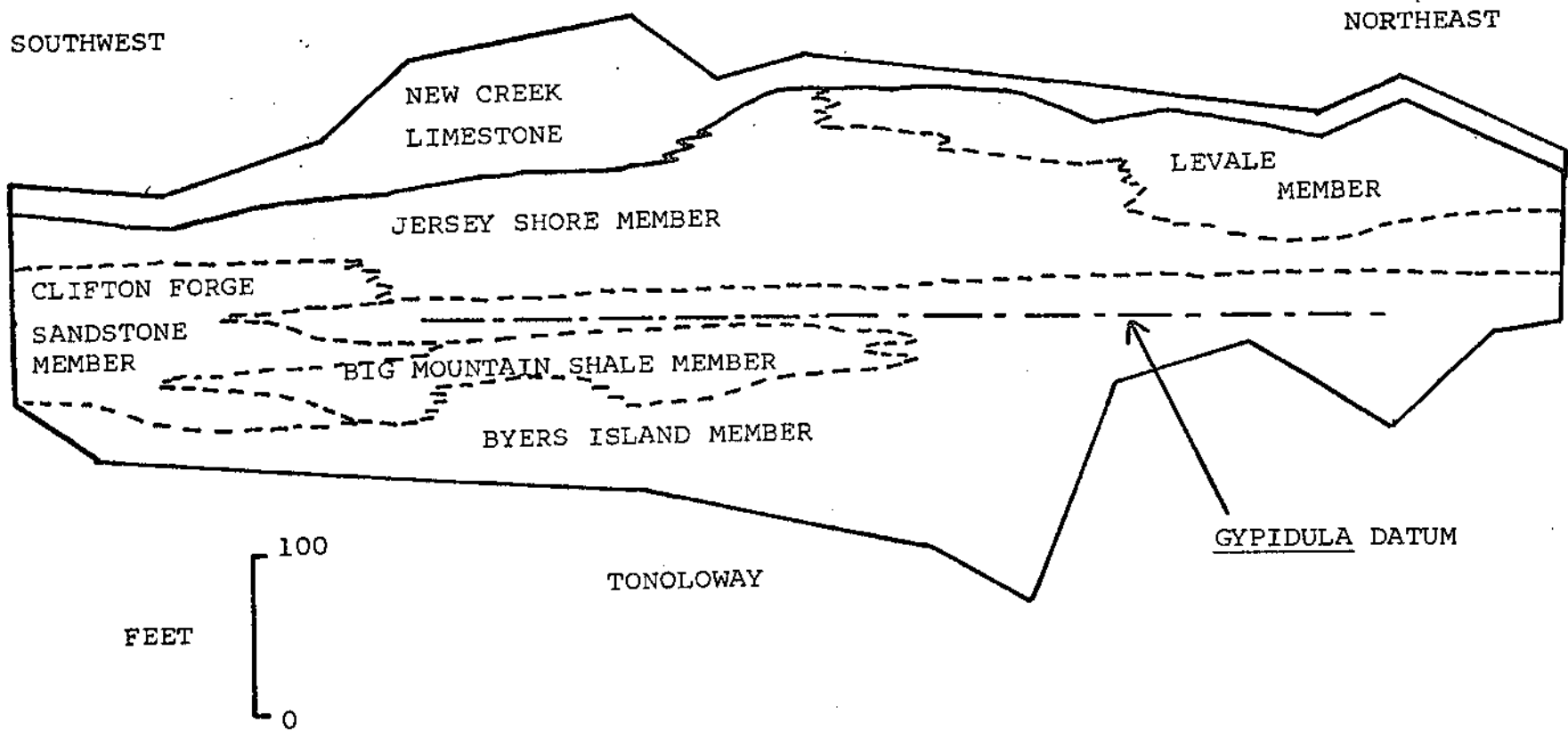


events to be basin-wide. The Gypidula Datum (fig. 4) locates the stratigraphic horizon from which the samples of G. prognostica for quantitative analysis were taken. Occurrences of G. prognostica within the Keyser are limited to a narrow vertical zone near the base of lithologies which represent open marine conditions (nodular lithofacies of Head, 1969).

Anderson (1970) has demonstrated that gypidulids are distributed parallel to the basin margin in the Coeymans Formation. Occurrences of gypidulids in the Keyser indicate the same distribution. The horizon represented by the Gypidula Datum in figure 5 is slightly time transgressive; transgression being perpendicular to depositional strike. However, the two localities from which specimens of G. prognostica were taken are separated by a distance of about one-hundred miles, however, this distance is nearly parallel to the basin margin or to depositional strike. Transgression through these areas must have been nearly synchronous. Previous investigators (Reeside, 1913; Swartz, 1929; Bowen, 1967; Head, 1969) have recognized this horizon as an approximate time plane within the Keyser Formation. For these reasons, it is concluded that the samples from the Gypidula Datum represent nearly contemporaneous populations.

In the Keyser Formation, as in occurrences of G. coeymanensis in New York, G. prognostica is found in poor to well sorted skeletal sands. Onshore tidal flat

Figure 5. Northeast to southwest cross section of the Keyser Formation- Gypidula Datum locates the stratigraphic horizon from which samples of G. prognostica were taken.



and lagoonal muds are devoid of gypidulids as are offshore deposits of fossiliferous muds.

The section at Hyndman (fig. 6) represents a typical Keyser environmental sequence and demonstrates the succession of lithologies associated with gypidulid bearing calcarenites in the formation. At this locality basal Keyser sediments overlie the Tonoloway Formation which is characterized by laminated dolomitic limestones. These resemble sediments described by Laporte (1967) from the Manlius Formation and recent sediments described by Shinn, Ginsberg and Lloyd (1966) and Hardie and Ginsberg (1971) and are interpreted as sediments deposited in a tidal flat environment.

The basal Keyser at Hyndman comprises a sequence of bioturbated biomicrites with a restricted fauna of ostracods, very small crinoids and a few brachiopods. These are interpreted as lagoonal sediments which represent restricted subtidal, low energy environments.

Overlying these biomicrites, crinoid-brachiopod biosparudites (figs. 7 and 8) occur at Hyndman and elsewhere in the Keyser as tabular bodies which resemble the Sheet Deposit Facies of Anderson (1971a). These sediments are suggested to be the result of destruction by transgression (ravinement) of barrier bar sediments. Diversity of organisms in these sediments is higher than that found in underlying lithologies. The addition of large pelmatozoan, brachiopod and bryozoan fragments to the sediment

Figure 6 - Diagrammatic section of the exposure at Hyndman, Pa. illustrates a typical Keyser environmental sequence and indicates the distribution of G. prognostica.

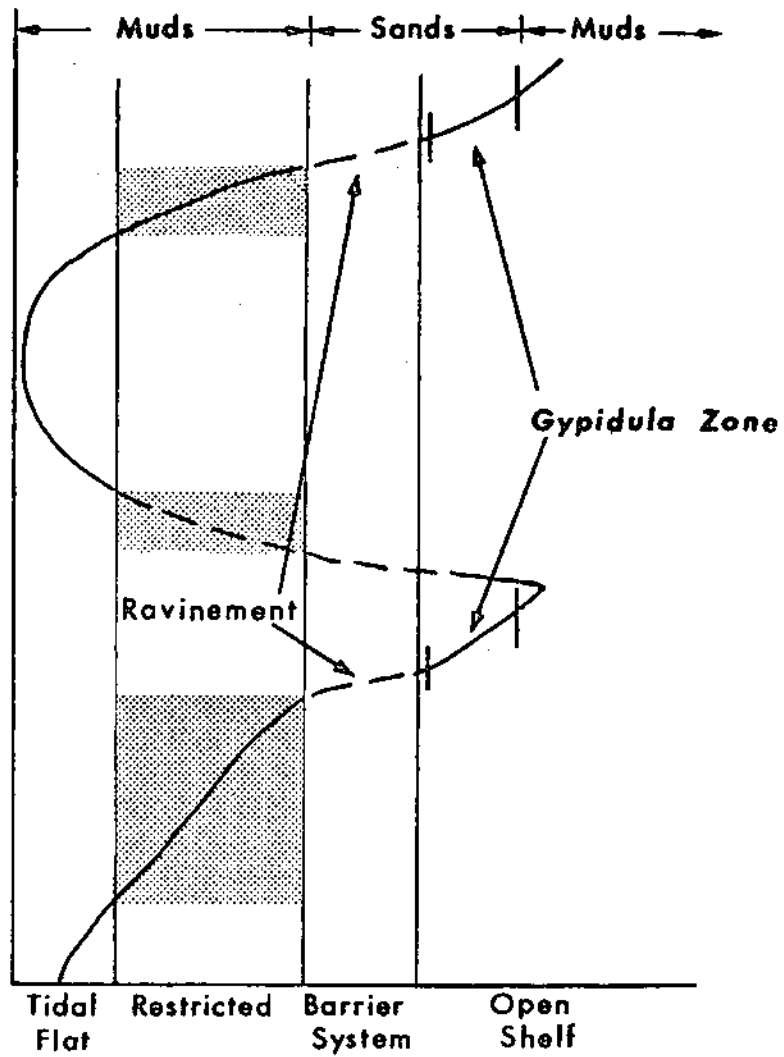
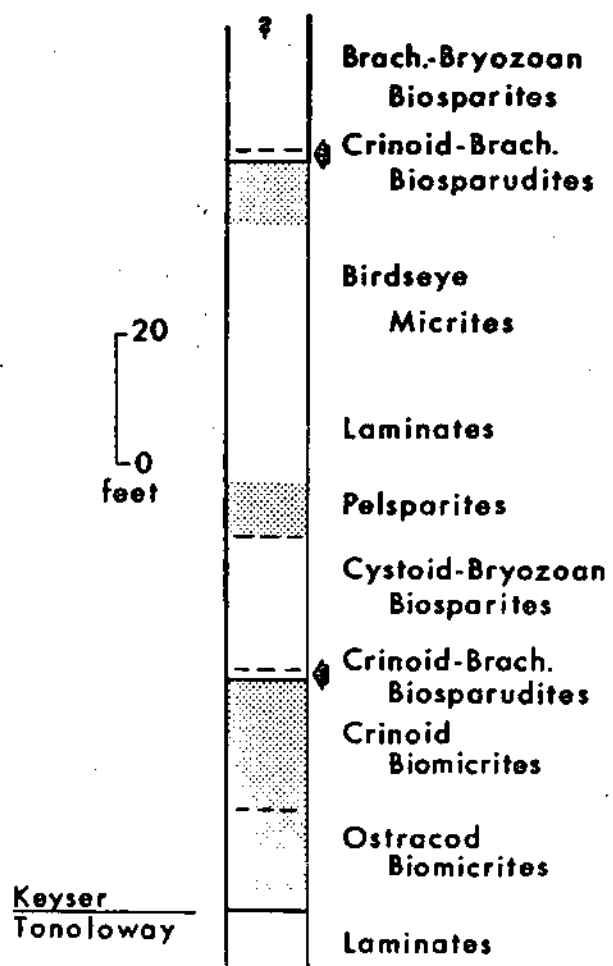
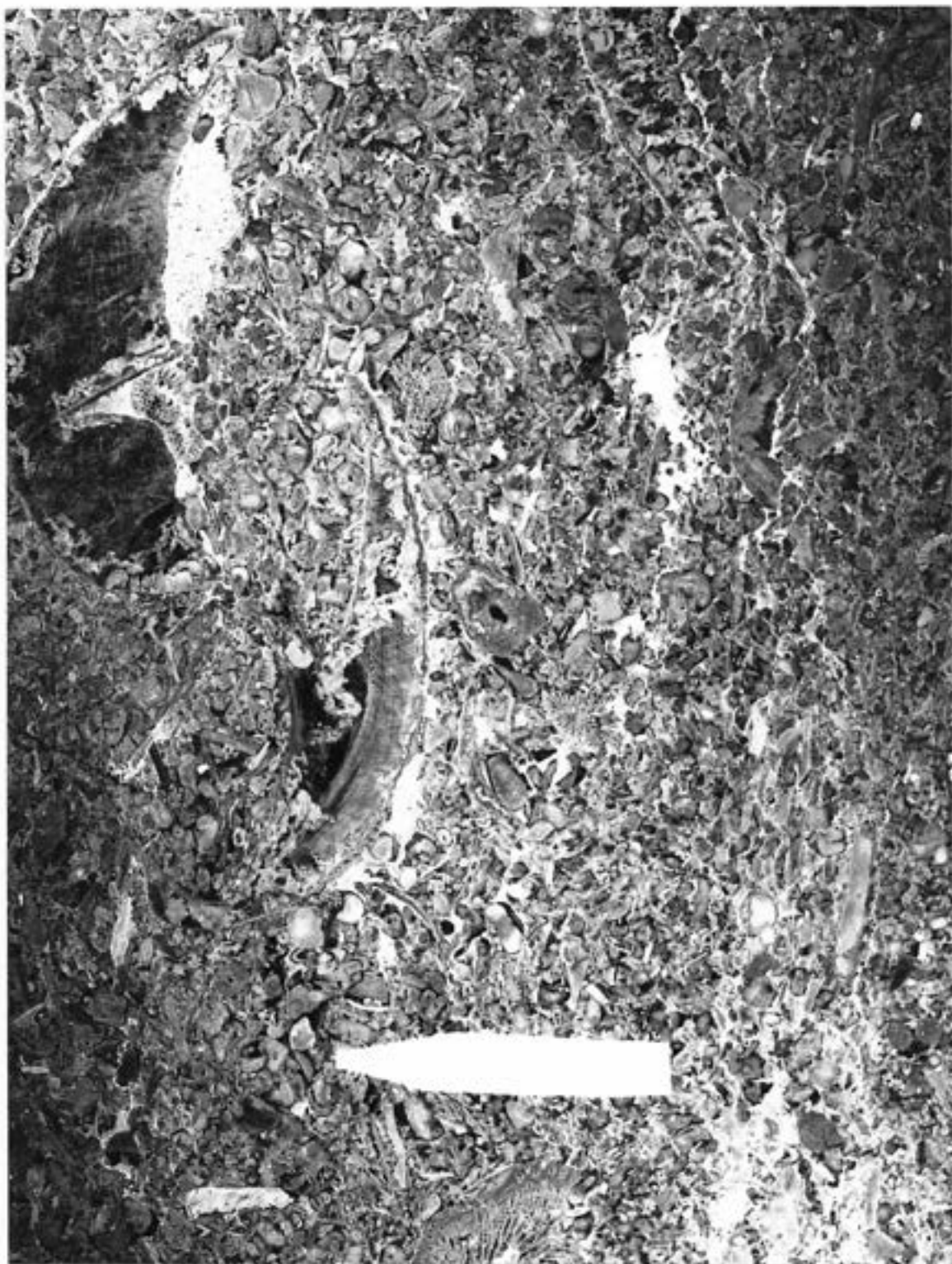


Figure 7 - A negative print of a thin section from
a crinoid-brachiopod biosparudite at
Hyndman, Pa. (Keyser Fm.) arrow= 1 cm.



Figure 8 - A negative print of crinoid-brachiopod
biosparudite sampled near McDowell, Va.
arrow = 1 cm. Keyser Fm.



indicates more open marine conditions. The absence of mud strengthens the interpretation that these sediments represent above wave base shallow shelf environments.

A distinct cystoid-bryozoan community occurs above the biosparudites. Accompanying this community is a diverse assemblage of brachiopods (table 1) resembling the Zygospira-Hebertella Community of Bretsky (1970). This assemblage and the accompanying sediments are consistent with a near wave base environment of deposition. Preservation of cystoid calices by rapid influxes of terrigenous clay indicate that turbidity and sedimentation rates must have fluctuated widely. This may explain the absence of gypidulids from the base of this horizon and from the underlying biosparudites at Hyndman although gypidulids do occur at these positions elsewhere in the Keyser where large quantities of mud are absent.

Above the cystoid-bryozoan community, the sediments indicate regression and shallowing of the basin. As brachiopod diversity decreases (table 1), the abundance of crinoids and bryozoans declines. A sequence of pelsparites, interbedded pelsparites and laminites indicates very shallow subtidal, intertidal and tidal flat environments (Laporte, 1969). Birdseye micrites stratigraphically above these sediments are typical of tidal flat environments (Laporte, 1967).

Above the birdseye muds, crinoid-brachiopod-bryozoan biosparudites reoccur, indicating renewed trans-

Table 1

Twenty-five feet of the lower Keyser at Hyndman, Pa. (from 35 to 60 feet in figure 6), divide into five units of five feet each yielded the following brachiopods (listed in ascending order):

Unit 1

<u>Cupularostrum convexorus</u>	rhynchonellid
<u>Atrypa reticularis</u>	atrypid
<u>Mechaeraria whittingtoni</u>	rhynch.
<u>Dolerorthis marylandica</u>	orthid
<u>Cupularostrum gordonii</u>	rhynch.
<u>C. lichfieldensis</u>	"
<u>Rhynchotreta hancockensis</u>	"
<u>Dalejina emarginata</u>	orthid
<u>Nucleospira ventricosta</u>	spiriferid

Unit 2

<u>D. emarginata</u>	orthid
<u>M. whittingtoni</u>	rhynch.
<u>Eccentricosta jerseyensis</u>	chonetid
<u>Leptostrophia bipartita</u>	strophomenid
<u>N. ventricosta</u>	spiriferid

Unit 3

<u>A. reticularis</u>	atrypid
<u>E. jerseyensis</u>	chonetid
<u>D. emarginata</u>	orthid

Table 1 (cont'd.)

Unit 4

A. reticularis

atrypid

C. convexorus

rhynch.

E. jerseyensis

chonetid

Unit 5

E. jerseyensis

chonetid

gastropods

gression and a possible ravinement. Restricted sub-tidal lagoonal environments are absent from the section at this point, and may have been destroyed by reworking during transgression.

G. prognostica occurs in abundance in the brachiopod-bryozoan biosparites (fig. 9) which immediately overlies the biosparudites. Here, as elsewhere in the formation, the gypidulids are in association with atrypid, strophomenid and spiriferid brachiopods, as well as a diverse assemblage of bryozoans and crinoids. These sediments resemble gypidulid-bearing calcarenites found at Warm Springs, Va. (fig. 10) and Keyser, W. Va. (fig. 11). This assemblage is similar to the Pentamerus Community described by Zeigler, et al (1968). Anderson (1971b) interprets the Pentamerus Community as an assemblage which occupies shallow open shelf environments near and above wave base.

Summarizing the sequence of lithologies at Hyndman (fig. 6) it may be seen that gypidulids occur only in skeletal sands which are offshore from barrier systems during transgression. They do not occur in muds or where sedimentation rates are high. During regressive phases the barrier biosparudites are absent as are gypidulids. This is suggested to be due to filling of onshore low energy zones in progradation (Anderson, 1971b).

Barrier systems seem a necessary requirement for gypidulids for two reasons. First, they serve as protec-

Figure 9 - Negative print of brachiopod-deltmato-
zoan biosparite from the Keyser Fm. at
Hyndman, Pa. Note *gyphidula* valves and
poor sorting. arrow = 1 cm.

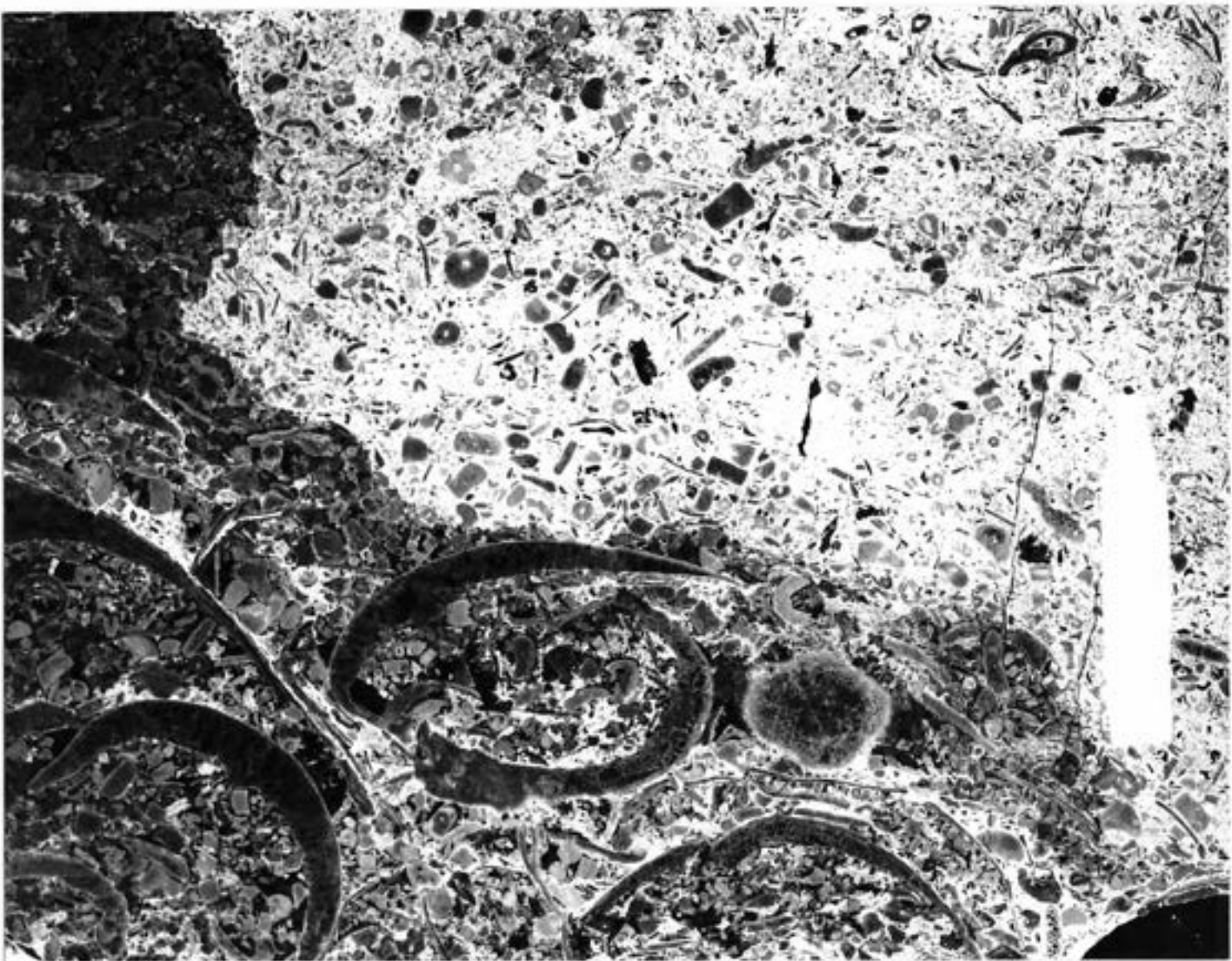


Figure 10 - Negative print of poorly sorted, gy-
pidulid-bearing calcarenite from the
Keyser Fm. at Warm Springs, Va. Note
similarity with figure 11. arrow = 1 cm.

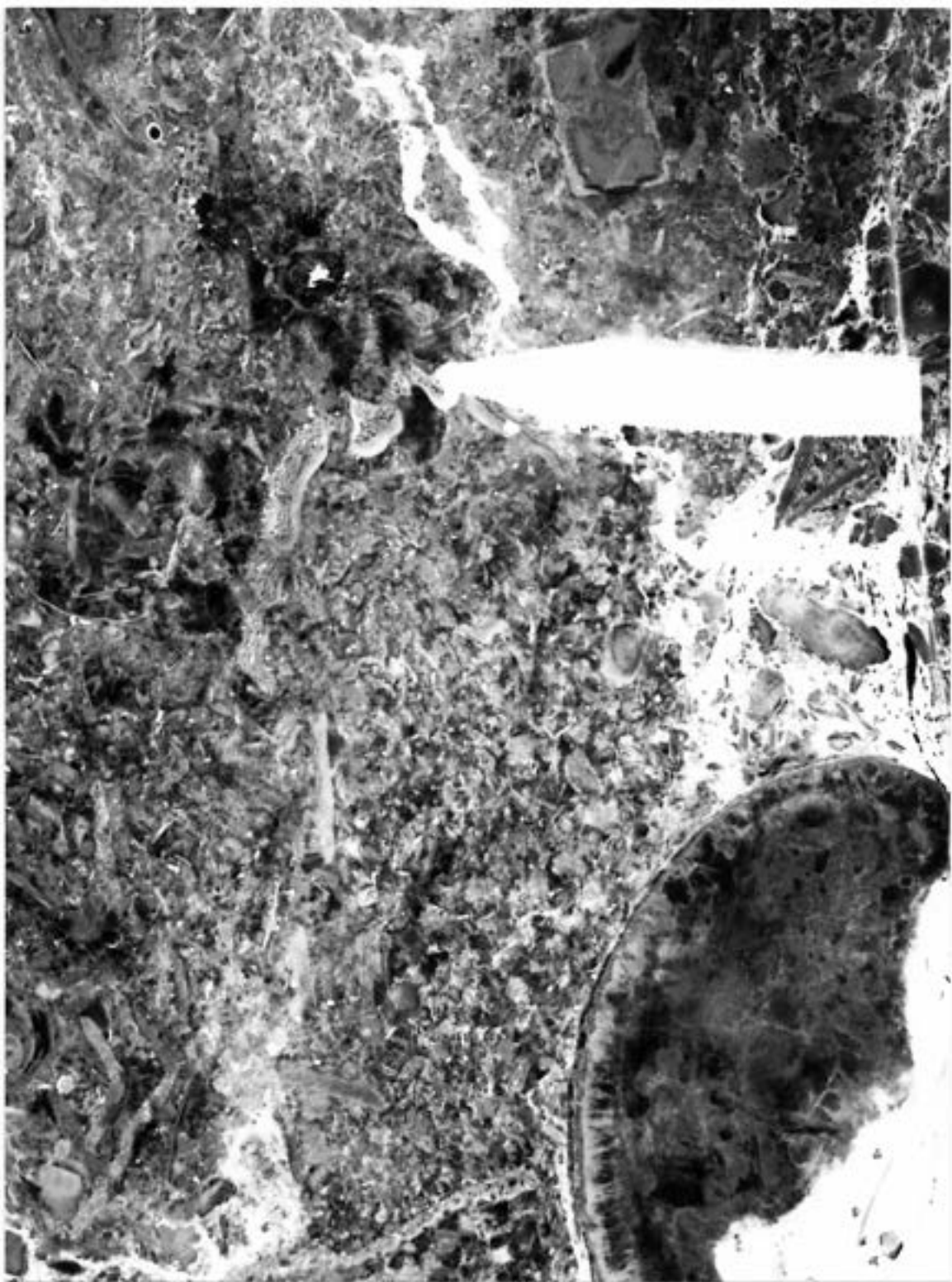
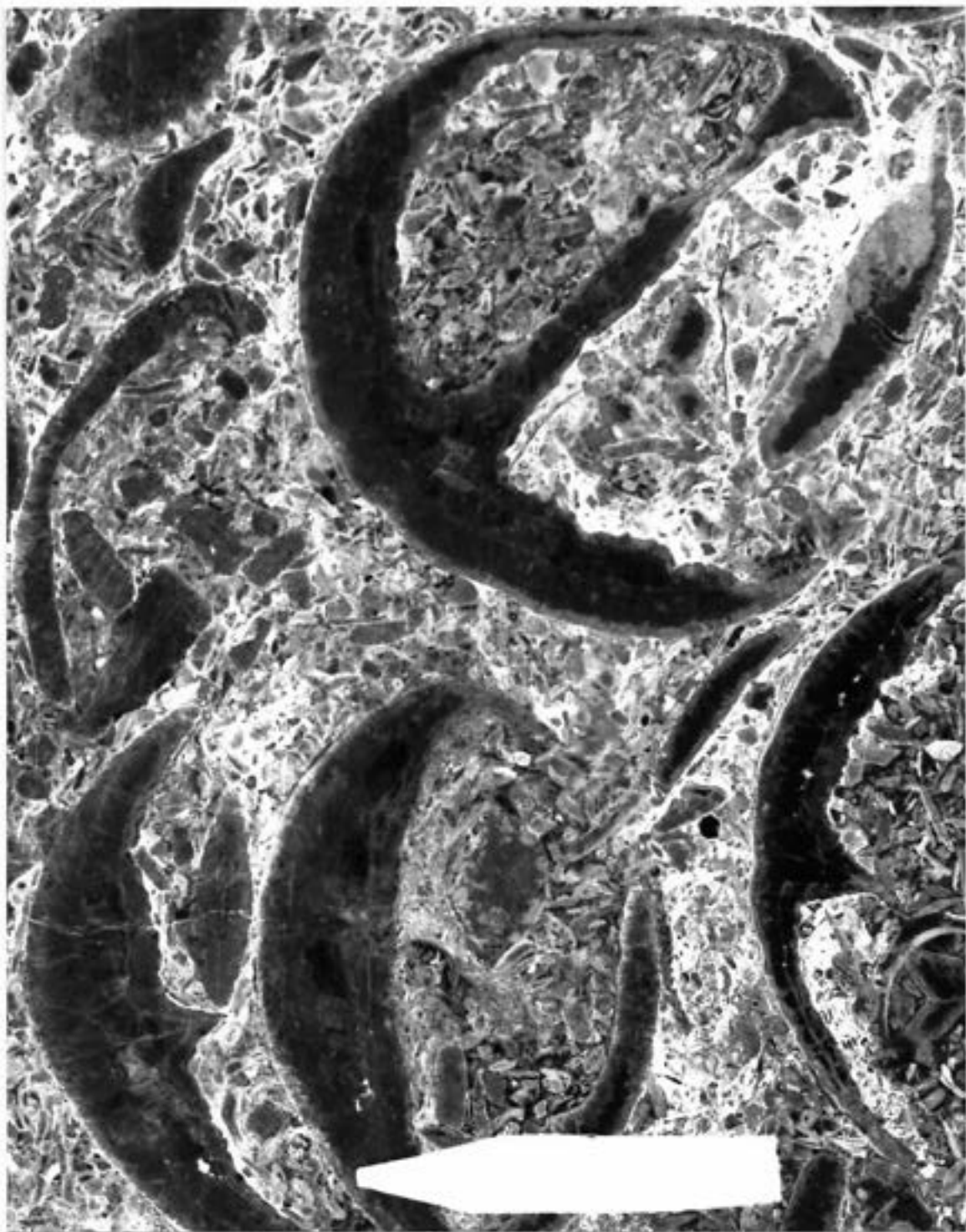


Figure 11 - Negative print of biosparite with abundant G. prognostica from Keyser Fm. at Keyser, W. Va. Note thick pedicle valve. arrow = 1 cm.



tion from fluctuating salinities of onshore lagoonal environments. Second, transgressive reworking of barrier sediments provides an ideal (second cycle) substrate for colonization by gypidulids.

An important key to interpreting the gypidulid environmental position is provided by the occurrence of gypidulid assemblages preserved in life position (Makurath and Anderson, 1972). These occur in the upper Coeymans Formation at Sharon Springs, N. Y. and in the middle of the Keyser Formation at Hyndman, Pa. The gypidulids in both cases appear to live unattached in an umbo-down position on poorly sorted skeletal sand substrates. There is no evidence of a pedicle opening which suggests that the pedicle may never have functioned or may have atrophied in adult forms. This beak-down position is promoted by weighting due to extreme thickening of the pedicle valve in the beak region, and possibly a tendency of the organisms to live in clusters so that individuals are in lateral contact. The stratigraphic occurrence of these assemblages places the gypidulid environment offshore from barrier complexes (patch reefs or pelletal mud shoals in Coeymans time, barrier bars or mud shoals in the Keyser occurrence) but onshore from open shelf fossiliferous silts and muds (fig. 6).

It is concluded that G. prognostica occupied a specific environmental locus within a specific lateral sequence of environments which only develops during

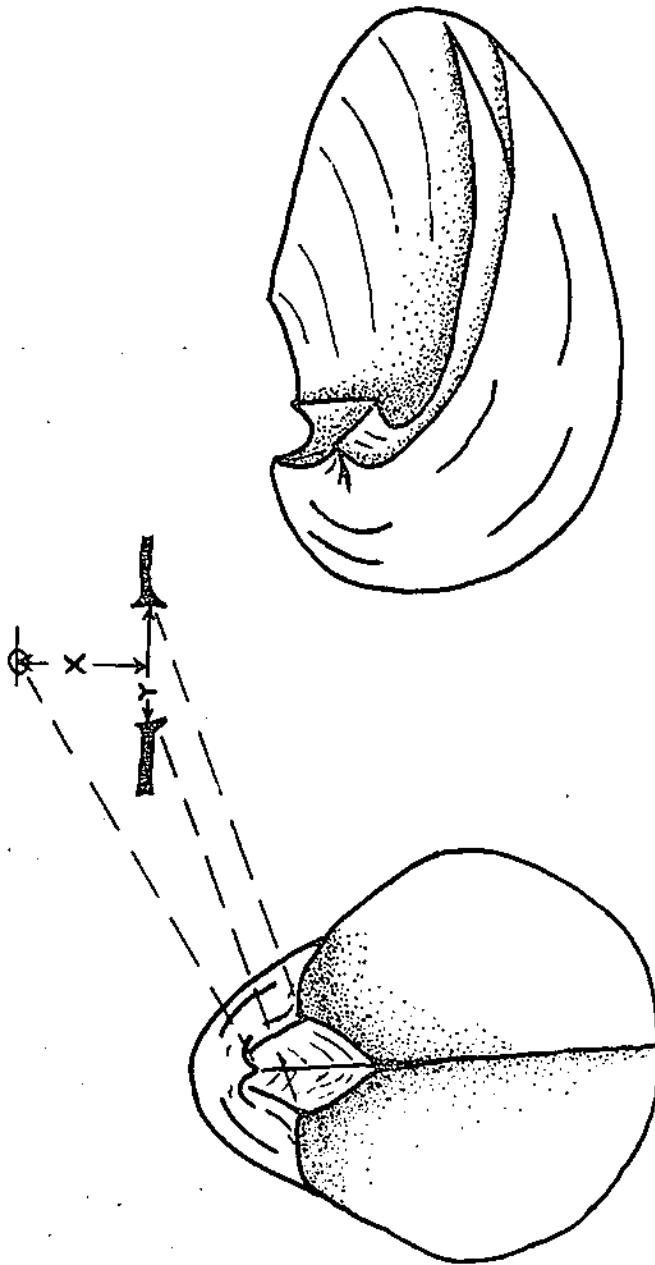
transgression. G. prognostica, like G. coeymanensis, exhibits specialization for normal salinity, good circulation, moderate to low turbidity and firm or very gently shifting sandy substrates.

Quantitative Analysis of Gypidulid Samples

The spondylium in pentamerid brachiopods serves as the attachment for all muscles of the pedicle valve (Amsden and Biernat, 1965). This structure is therefore of considerable functional importance. Change in shape of the spondylium should reflect parallel change in either the size and/or configuration of the muscles which open and close the valves. Spondylium shape is also related to the general shape of beak; narrow beaks are associated with narrow spondylia. For these reasons, as well as infrequent preservation of complete valves, two dimensions associated with the spondylium (fig. 12) were chosen as suitable variables: the distance between hinge teeth (spondylium width); and the distance from the tip of the beak to the center of a line connecting hinge teeth (beak length). These dimensions are also related to the shape of the pedicle valve in that significant changes in general valve shape would necessitate parallel changes in the shape of the spondylium and beak.

For all three samples, rocks were collected in bulk quantities and the brachiopods broken out using a rock splitter. Each specimen was then ground so that a single plane intersected the hinge teeth and the tip of the beak. The measures of length (beak) and width (spondylium) were made using a microscope fitted with a mechanical stage. Values were recorded to the nearest 0.1 mm.

Figure 12 - Gypidulid pedicle valve- X and Y are
variables used in quantitative analysis



Measurements of length (X) and width (Y) were analysed by a number of statistical procedures: comparison of reduced major axes; comparison of mean ratios ($W = Y/X$) by t-tests; comparison of allometric curves; and discriminant function analysis. A summary of the statistical parameters used in these analyses is found in Table 2; variables are defined in appendix 1.

TABLE 2

VARIABLE	KEMSER	LOC. 57	LOC. 94
ΣY	165.2	334.2	366.0
\bar{Y}	2.67	4.23	4.07
S_Y	.89	.98	1.09
$\Sigma(Y^2)$	488.5	1489	1597
ΣX	146	274	281
\bar{X}	2.36	3.46	3.12
S_X	.76	.65	.54
$\Sigma(X^2)$	379	979	913
$\Sigma(Y/X)$	70.6	96.5	116.1
(Y/X)	1.14	1.22	1.29
$S_{Y/X}$.05	.17	.17
$\Sigma(Y/X)^2$	81.8	119.9	152.6
\bar{Y}	62	79	90
a	1.17	1.51	2.02
b	-.09	-.09	-1.96
S_a	.057	.094	.105
S_{XY}	.92	.83	.87
$\Sigma \log Y$	25.47	48.49	53.29
$\Sigma (\log Y)^2$	11.64	30.68	32.96
$\Sigma \log X$	21.71	42.03	43.68
$\Sigma (\log X)^2$	8.82	22.89	21.98

TABLE 2 (cont'd.)

VARIABLE	KEYSER	LOC. 57	LOC. 94
ΣXY	426.9	1197.8	1196.9
$s_{\log X}$.141	.082	.093
$s_{\log Y}$.139	.108	.126
$\Sigma(\log X \log Y)$	9.94	26.39	26.81
$r_{\log X \log Y}$.852	.849	.901
k	.985	1.317	1.355
B	1.16	.82	.86

Comparison of Mean Ratios

To test the hypothesis that two sample means are equal when samples are small relative to the populations and when population variances are not known, the t distribution is used (Chou, 1969, p. 398). The value of t gives the probability that the observed difference between means, or a greater difference, would be observed if the samples were taken from the same population. It assumes that the samples are normally distributed. Values of W for each sample were tested using the χ^2 test for normality and were found to be normally distributed in each case. In each of the following tests the null hypothesis states that the mean ratios are equal. To reject the null hypothesis with 95% confidence requires a value of t which is greater than or equal to 1.96.

$$1) \text{ Keyser : loc. 57} \quad H_0 : W_K = W_{57}$$

$$t = 3.59 \quad H_a : W_K \neq W_{57}$$

$$2) \text{ Keyser : loc. 94} \quad H_0 : W_K = W_{94}$$

$$t = 6.77 \quad H_a : W_K \neq W_{94}$$

$$3) \text{ loc. 57 : loc. 94} \quad H_0 : W_{57} = W_{94}$$

$$t = 2.62 \quad H_a : W_{57} \neq W_{94}$$

In every case the null hypothesis is rejected with 99% confidence and the alternative hypothesis is accepted.

Less than one percent of the time would the ratios differ as much if they were taken from the same population.

The values of the mean ratios and the significance of the difference between them indicate a progressive change in shape from the Keyser sample to the late Coeymans sample. G. prognostica, however, is recognized to be generally smaller than G. coeymanensis (Bowen, 1967). Gould (1966) has pointed out the interdependence of size and shape changes, indicating that increasing the size of an animal often requires a change in proportions. For this reason, the three samples were further compared in terms of two measures of relative growth; the reduced major axis and the allometric curve.

Comparison of Reduced Major Axes

When a reduced major axis (Imbrie, 1956 and Hayami and Matsukuma, 1970) calculated for a population has a y-axis intercept which is significantly different from zero, it may serve as a measure of allometric growth (Gould, 1966). Isometric growth is a special case of the allometric equation ($Y = BX^k$) in which the value of the exponent (k) is equal to zero and the axis intersects the origin. In isometric growth, proportions do not change as size increases.

Reduced major axes were calculated for each sample and the slopes of these lines compared using a Z test (Imbrie, 1956). The statistic Z gives a measure of the significance of a difference in slope.

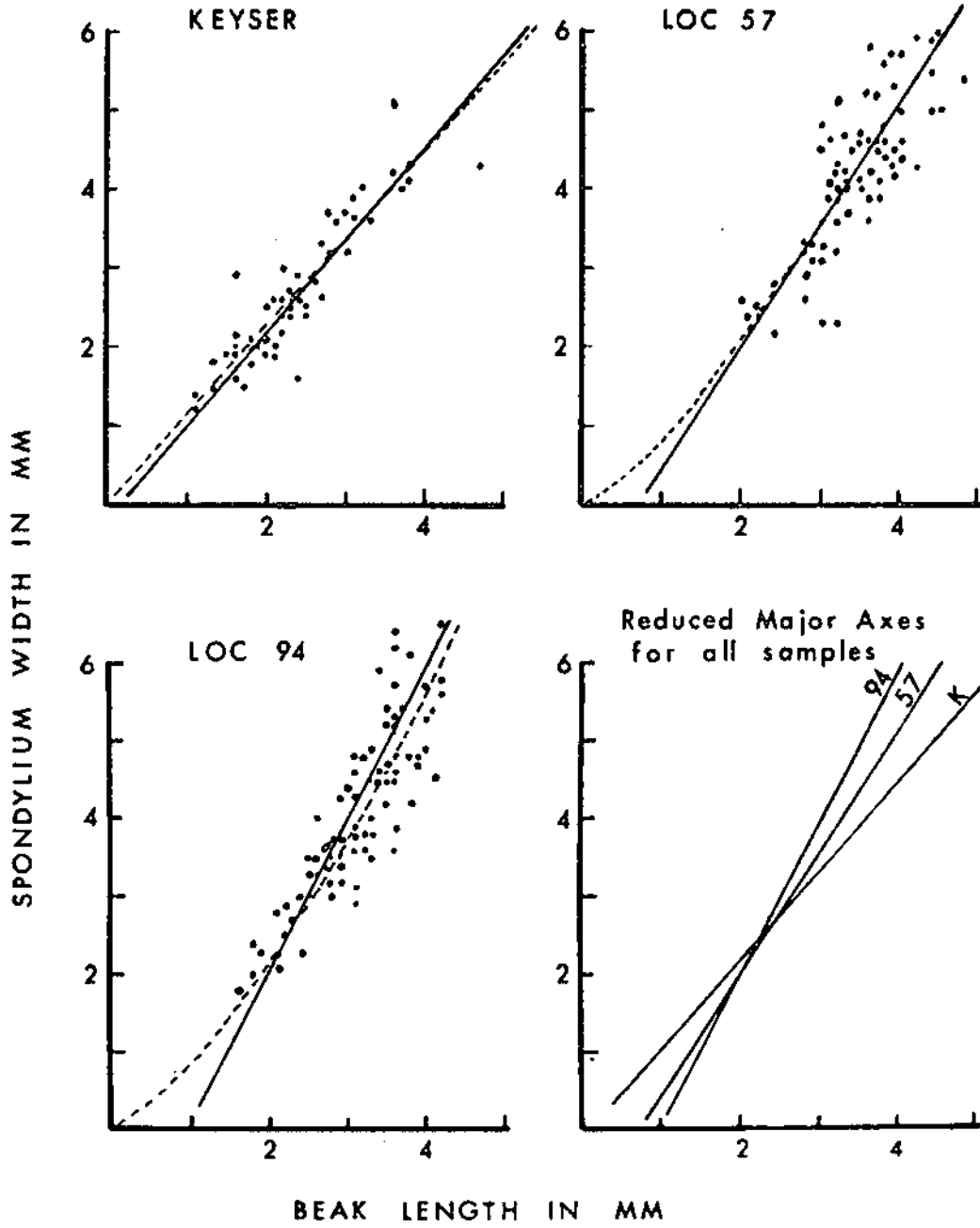
In each of the following tests the null hypothesis states that the slopes of the reduced major axes are equal. To reject this hypothesis with 95% confidence Z must be greater than 1.96.

- | | |
|----------------------------------|---|
| 1) Keyser : loc. 57
Z = 3.1 | $H_0 : a_K = a_{57}$
$H_a : a_K \neq a_{57}$ |
| 2) Keyser : loc. 94
Z = 7.14 | $H_0 : a_K = a_{94}$
$H_a : a_K \neq a_{94}$ |
| 3) loc. 57 : loc. 94
Z = 3.62 | $H_0 : a_{57} = a_{94}$
$H_a : a_{57} \neq a_{94}$ |

Each case shows a significant difference in slope. These differences suggest a progressive widening of the spondylium in larger individuals (fig. 13).

Figure 13 - Reduced major axes (solid lines) and allometric curves (dotted) for each sample - note that samples differ mainly in larger size ranges.

REDUCED MAJOR AXES and ALLOMETRIC CURVES



Comparison of Allometric Curves

The most frequently used measure of relative growth is the allometric equation of Huxley (1932). The geometric accretionary growth of brachiopods results in a curvilinear relation between the variables measured. This relation may be described by the equation $Y = BX^k$ where X and Y are the variables in question and k is the growth ratio characteristic of a species. B is the initial growth index which simply gives the value of Y when $X = 1$ (Huxley, 1932).

Studies of recent brachiopod populations from the Strait of Magellan (McCammon and Buchsbaum, 1967) indicate that this relation ($Y = BX^k$) accurately describes relative growth of shell length, width and thickness within a species and is relatively unaffected by environment. The predominant effect of environment is seen in relative size of individuals which accounts for over 99% of the variation between samples.

Both constants B and k for a population reflect the genetic mechanism responsible for growth of a character (Simpson, 1953, p. 29) and may be changed by selection (Kidwell, Gregory and Guilbert, 1951). Progressive changes in allometric growth relationships between gyridid populations may reflect genetic (evolutionary) changes.

The allometric equation may be calculated for each

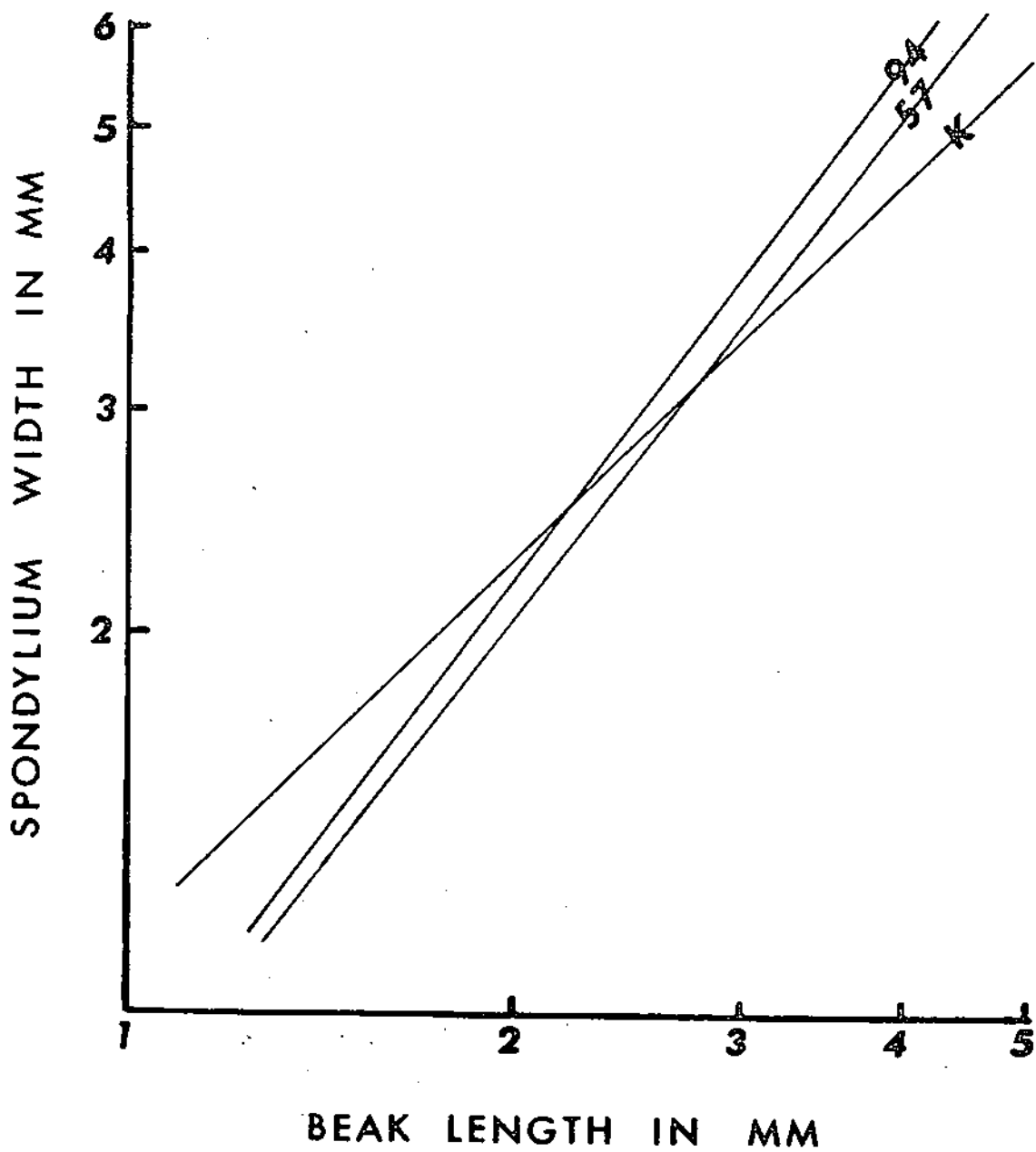
sample in the same manner as the reduced major axis, substituting logarithmic values for the original variables. This equation was calculated and the resultant curves plotted for each sample (fig. 13). It can be seen that differences between curves are most pronounced in larger individuals. Allometric curves plot as straight lines on logarithmic scales (fig. 14), and their slopes may be compared using a Z test (Hayami and Matsukuma, 1970). The null hypothesis in each case states that the slopes of the allometric lines are equal. To reject this hypothesis with 95% confidence Z must be greater than 1.96.

1) Keyser : loc. 57	$H_0 : k_K = k_{57}$
Z = 3.29	$H_a : k_K \neq k_{57}$
2) Keyser : loc. 94	$H_0 : k_K = k_{94}$
Z = 4.14	$H_a : k_K \neq k_{94}$
3) loc. 57 : loc. 94	$H_0 : k_{57} = k_{94}$
Z = .38	$H_a : k_{57} \neq k_{94}$

Significant differences in slope are observed between the sample of G. prognostica (Keyser) and each sample of G. coeymanensis (loc. 57 and 94), but not between samples of the latter. These differences in slope represent a progressive widening of the spondylium

Figure 14 - Solutions for the allometric equation
for each sample are plotted on logarithmic
scales.

ALLOMETRIC LINES



for a given length from the Keyser sample to the Coeymans samples, but no difference between the Coeymans samples. If ontogenetic allometry is approximated by measures of a large number of individuals at various growth stages (Gould, 1966), the form of the allometric equation then reveals a similar relative widening of the spondylium throughout ontogeny of each individual.

Hayami and Matsukuma (1970), in a review of methods for analysing bivariate data, provide a test using the Z statistic to determine whether the slope of the allometric line is significantly different from one. This statistically defines isometric and allometric growth for each population. Z values for both Coeymans samples indicate allometric growth, but the slope of the Keyser sample does not differ significantly from isometry. This indicates that growth of Coeymans samples is best represented by the allometric equation, while the Keyser sample is equally well represented by either a reduced major axis or an allometric curve (line).

Visual inspection of allometric curves for the three samples shows that differences in relative growth of the characters measured is most pronounced in the larger individuals of each sample. Statistical comparisons show significant differences in growth curves between populations of G. prognostica and G. coeymanensis. G. prognostica appears to grow isometrically, that is, without change in proportions with increase in size. G. coeymanensis shows change in proportions with size increase.

Discriminant Function Analysis

Treating all variables simultaneously, discriminant function analysis provides the best mathematical discrimination of predetermined groups. In addition, it gives a measure of relative importance of each original variable in distinguishing the groups. Demonstrations and discussion of this type of analysis are given by Rees (1969) and Klován and Billings (1967). The discussion in Rees' (1969) analysis of deer skull morphology uses the same computer program used in this study (Library Computer Program BMD-07M). The statistical process used in this program gives one or more linear functions (canonical variables) which maximize separation between groups while minimizing within group dispersion. This is done by considering all possible combinations of the variables (X and Y) and chooses the ones that provide maximum discrimination. In the case of gypidulid samples, the groups are predetermined on the basis of time stratigraphy.

The first step in the computer analysis evaluates each variable separately by determining the overlap between groups in both X and Y dimensions. The program provides a measure of the relative discriminatory power of each original variable. In this case the variables are of about equal importance in distinguishing the groups; restated, overlap between groups is equal in both X and Y dimensions.

The next step evaluates the variables simultaneously by comparing each individual with every other individual in each group. In the case of this comparison, the program calculated two linear discriminant functions (DF 1 and DF 2) along which separation of groups is maximized. The comparison is summarized by an F matrix with 2 and 227 degrees of freedom:

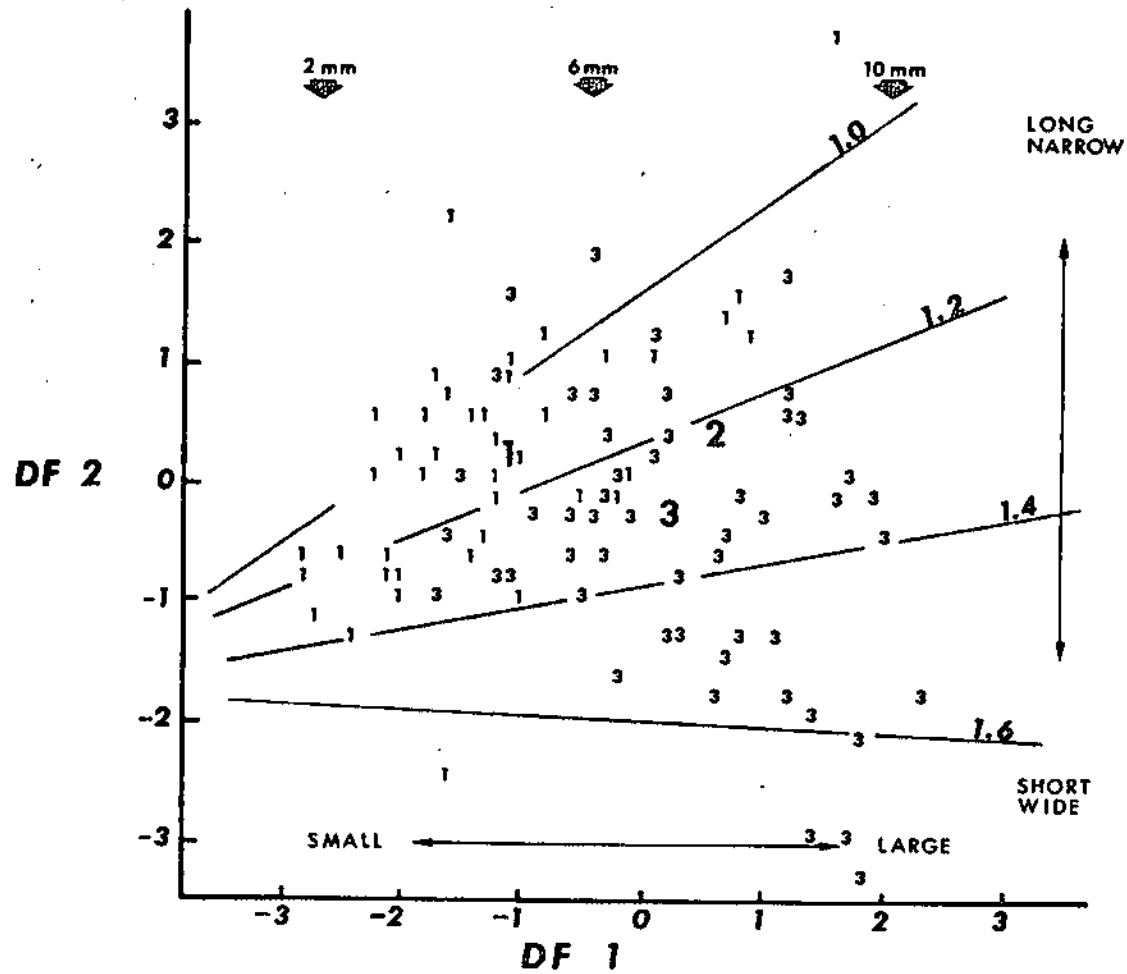
Samples (groups)	Keyser	loc. 57
loc. 57	48.887	-----
loc. 94	35.463	11.476

F values, comparing sample distributions, above 4.71 indicate that discrimination is significant at a level of better than 99%. Again, all three samples are statistically distinct groups.

The program plots the three groups (fig. 15) in terms of the discriminant functions used to distinguish them. An index of the relative importance of original variables in each of the discriminant functions may be calculated by multiplying raw coefficients of canonical variables (provided by the program) by the standard deviation of the appropriate original variable (table 2). These values indicate that both X and Y variables contribute equally to each discriminant function.

The program also provides the proportion of between group dispersion accounted for by each canonical variable. In this case, 85% of the dispersion is expressed by

Figure 15 - The computer plot of samples in terms of discriminant functions (DF 1 and DF 2) illustrates relationships between DF 1 and absolute size and DF 2 and beak/spondylium shape. For convenience only the first (Keyser) and third (loc. 94) groups are shown. The large numbers locate the centroids of each sample; diverging lines are lines of equal Y/X ratio; total X + Y is given in mm.

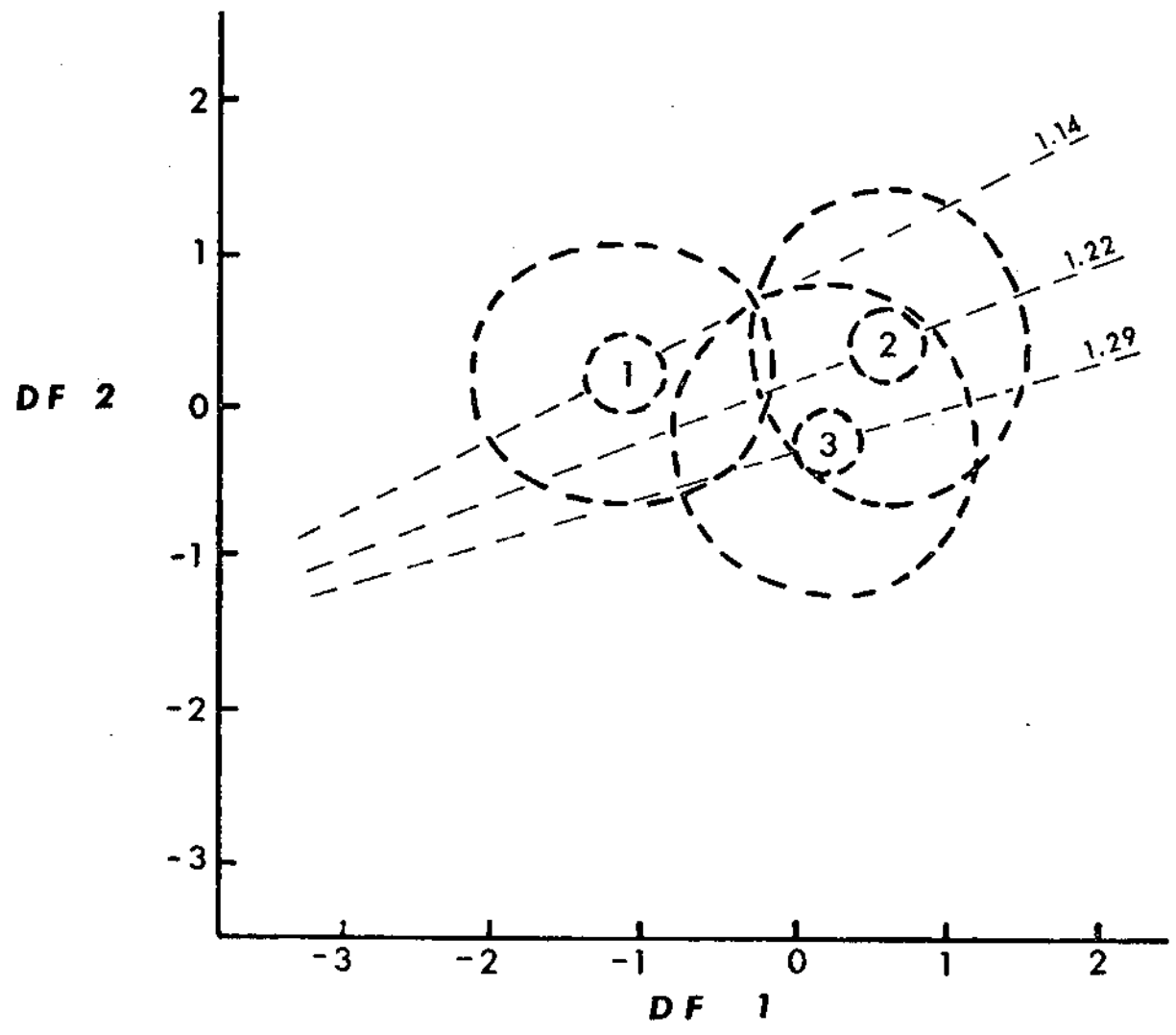


separation of groups along the first discriminant function (DF 1, fig. 15) and 15% is expressed along the second discriminant function (DF 2, fig. 15). Although canonical variates may be difficult to interpret biologically (Delany and Healy, 1964), it may be seen graphically (fig. 15) that the first discriminant function is largely, but not entirely, a function of absolute size as expressed by the total value of both X and Y variables. The second discriminant function is primarily a reflection of shape. This is indicated by the superimposed lines of equal Y/X values. Early samples are generally smaller with relatively narrow spondylia, while later samples are larger with relatively wider spondylia for a given length of beak.

When the groups are plotted in discriminant space the centroids are at their maximum separation (fig. 16). Sixty-eight percent of the members of each group will be enclosed by an ellipse which is one standard deviation away from the centroid. Ninety-five percent confidence intervals for the centroids do not overlap at all (fig. 16). In 95% of repeated random samples of the same populations, mean values (centroids) would fall within the small ellipses shown in figure 16.

A t-test may again be used to compare the significance of differences between centroids evaluated along each discriminant function. The null hypothesis in each test states that the means are equal. Values of t greater than 1.98 allow rejection of this hypothesis with 95% con-

Figure 16 - 95% confidence intervals (small ellipses) of sample centroids are plotted in terms of discriminant functions. The large ellipses are one standard deviation away from the centroids and enclose about 2/3 of each sample. Group 1 = Keyser, Group 2 = loc. 57, Group 3 = loc. 94
DF 1 and DF 2 = discriminant functions.



fidence. Testing means along the first discriminant function (DF 1) gives the following results:

Centroids designated by C

- | | |
|----------------------|----------------------------|
| 1) Keyser : loc. 57 | $H_0 : C_K = C_{57}$ |
| t = 9.99 | $H_a : C_K \neq C_{57}$ |
| 2) Keyser : loc. 94 | $H_0 : C_K = C_{94}$ |
| t = 7.83 | $H_a : C_K \neq C_{94}$ |
| 3) loc. 94 : loc. 57 | $H_0 : C_{94} = C_{57}$ |
| t = 2.30 | $H_a : C_{94} \neq C_{57}$ |

In each case the null hypothesis is rejected with better than 95% confidence. The t values indicate that the first discriminant function maximizes differences between G. prognostica and G. coeymanensis. The second discriminant function would then be expected to maximize differences between samples of G. coeymanensis. This is demonstrated by the following tests of centroids evaluated along the second discriminant function:

- | | |
|---------------------|-------------------------|
| 1) Keyser : loc. 57 | $H_0 : C_K = C_{57}$ |
| t = 2.47 | $H_a : C_K \neq C_{57}$ |
| 2) Keyser : loc. 94 | $H_0 : C_K = C_{94}$ |
| t = 2.88 | $H_a : C_K \neq C_{94}$ |

3) loc. 57 : loc. 94

t = 4.10

 $H_0 : C_{57} = C_{94}$ $H_a : C_{57} \neq C_{94}$

The null hypothesis is again rejected with 95% confidence, the mean values are statistically distinguishable from one another, and discrimination is best between samples of G. coeymanensis.

Discriminant function analysis reveals that the three samples are statistically separable on the basis of measurements of spondylium width and beak length, and that discrimination may be better when larger individuals are compared.

Interpretation

The preceding tests all indicate statistically significant differences in both size and shape between G. prognostica and G. coeymanensis. Of the four tests used, discriminant function analysis provides the best resolution of morphologic differences between groups. G. prognostica differs from G. coeymanensis in size (as suggested by Swartz, 1929) and shape, while differences between samples of G. coeymanensis are mainly a function of shape. Shape changes are seen to be progressive in time.

Analysis of allometry is an important tool in documenting evolutionary (genetic) change in populations. Other statistical comparisons determine accurately the amount and significance of changes in measured characters, but fail to reflect the genetic basis, if any, for such changes. Characters or traits are not strictly inherited, but rather, a growth mechanism or a capability for development of a character is passed from generation to generation. Comparisons of relative growth of a character provide documentation of changes in growth mechanisms which reflect genetic change.

It is believed that spondylium width and beak length are measures of relative dorso-lateral and ^{ANTERIOR}~~POSTERIOR~~ shell growth in the hinge area. Allometric curves relate change of proportion to size for each population (figs.

13 and 14). The morphologic change documented by the various statistical tests is seen graphically as a change in proportions of larger individuals in successive populations. It is suggested that size and shape differences between populations are interrelated and adaptive. The adaptive advantage of the observed changes in shape may be due to two factors:

- 1) Greater width of the spondylium for a shell of given length increases the area of muscle attachments to accommodate either larger or more efficiently shaped muscles. This provides more efficient valve articulation.
- 2) In the gypidulid life position, wider shells with shorter beaks have a relatively lower center of gravity, providing increased stability on the substrate.

Many evolutionary changes in proportion are a result of increases in size, but the alternative; new proportions allowing size increase may also occur (Gould, 1966). Large individuals with shapes like those in the Keyser sample are suggested to be inadapative because of inefficient articulation and/or inability to maintain a stable position on the substrate. Selection would work against these individuals even though the same proportions in

smaller size ranges are adaptive.

It may be added that there can be adaptive value to size increases alone (Gould, 1966). Increased size may discourage predators or allow the animal to feed on larger sized particles. In the case of gypidulids, increased size in a relatively rough water environment may increase stability in the absence of a functional pedicle, provided that the shape of the animal is not inadapative.

Selection works throughout ontogeny, but allometric relationships indicate that selective pressure may vary at different growth stages (Gould, 1966). It is believed that selection for growth mechanisms allowing wider spondylia and shorter beaks in larger individuals permitted later populations of G. coeymanensis to reach larger sizes.

Conclusion

Progressive adaptive morphologic change in successive populations of gypidulid brachiopods parallels progressive decrease in restriction of the gypidulid environment. The Appalachian basin evolves from an area of tidal flat and evaporite deposition during pre-Keyser time to a more open epeiric sea during post-Coeymans time. This progressive opening of the basin would tend to improve circulation, limit salinity fluctuations and possibly increase food supply. All of these parameters appear to effect the distribution of gypidulids.

Although there may not be a cause and effect relationship between environmental change and progressive widening of the gypidulid spondylium, the evolution of the Appalachian basin would certainly provide the type of selection which must be the final cause of beak and spondylial shape changes.

Simpson (1953, p. 5) indicates that well-defined changes in morphology in successive populations extending over long periods of time reflect genetic change in those populations. Because spondylium/beak shape changes between G. prognostica and G. coeymanensis are statistically significant, persistent through a geologically significant period of time (Upper Silurian through Lower Devonian), and environmentally feasible, they are interpreted as evolutionary (genetic) and adaptive.

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APPENDIX I

Variables used in quantitative analysis

- X length of beak \bar{X}, \bar{Y} = sample means
 Y width of beak (distance between hinge teeth)
 s standard deviation
 N sample size
 a slope of reduced major axis
 b y intercept of reduced major axis
 r correlation coefficient
 k slope of allometric line
 B y intercept of allometric line

$$\Sigma Y^2 = \Sigma (y^2) - (\Sigma Y)^2 / N$$

$$s_Y = \sqrt{\Sigma Y^2 / N - 1}$$

$$b = \bar{Y} - \bar{X} a$$

$$s_a = a \sqrt{1 - r^2} / N$$

$$a = s_Y / s_X$$

$$r_{XY} = \Sigma XY / \sqrt{\Sigma X^2 \Sigma Y^2}$$

APPENDIX II

Original measurements of gypidulid samples

Keyser sample:

specimen #	Y	X	Y/X
1	4.3	4.7	.98
2	3.9	3.1	1.26
3	3.6	2.9	1.24
4	3.2	2.8	1.15
5	3.7	3.0	1.23
6	2.7	2.3	1.18
7	3.6	3.1	1.16
8	2.6	2.7	.96
9	2.9	2.4	1.21
10	3.3	2.7	1.22
11	2.6	2.4	1.09
12	2.6	2.2	1.18
13	3.6	3.1	1.16
14	1.8	1.8	1.00
15	2.5	2.3	1.09
16	2.1	1.8	1.17
17	2.1	2.0	1.05
18	2.8	2.6	1.08
19	2.7	2.4	1.13
20	2.4	2.5	.96
21	2.6	2.4	1.08
22	1.9	2.1	.91
23	3.0	2.2	1.36
24	2.6	2.3	1.13
25	2.4	2.3	1.04
26	1.6	2.4	.68
27	2.2	2.2	1.00
28	2.5	2.5	1.00

APPENDIX II (cont'd)

specimen #	Y	X	Y/X
29	2.1	1.8	1.17
30	1.6	1.6	1.00
31	2.4	2.2	1.09
32	1.8	1.6	1.13
33	2.0	1.8	1.11
34	1.9	1.6	1.19
35	2.9	2.4	1.21
36	2.6	2.1	1.24
37	2.4	2.2	1.09
38	1.8	1.3	1.39
39	1.5	1.3	1.15
40	2.9	1.6	1.81
41	1.8	1.6	1.13
42	1.9	2.0	.95
43	2.0	1.6	1.25
44	1.9	1.5	1.27
45	2.0	2.1	.95
46	2.0	1.9	1.05
47	1.5	1.7	.88
48	2.1	1.6	1.31
49	1.2	1.1	1.09
50	1.4	1.1	1.27
51	1.3	1.1	1.18
52	4.0	3.2	1.25
53	4.3	3.8	1.13
54	4.1	3.8	1.08
55	5.1	3.6	1.42
56	3.7	3.3	1.12
57	3.6	3.3	1.09
58	4.2	3.6	1.17
59	3.7	2.8	1.32
60	3.2	3.0	1.07
61	2.5	2.0	1.25
62	4.0	3.7	1.08

APPENDIX II (cont'd)

loc.57: specimen #	Y	X	Y/X
1	3.6	3.0	1.2
2	2.2	2.4	.92
3	2.4	2.1	1.15
4	3.3	3.2	1.03
5	2.4	2.1	1.44
6	3.1	2.9	1.07
7	3.3	2.9	1.14
8	2.5	2.2	1.14
9	2.3	3.0	.77
10	3.3	3.0	1.10
11	2.6	2.0	1.30
12	2.8	2.4	1.17
13	4.7	3.5	1.34
14	3.6	3.6	1.00
15	3.2	2.8	1.14
16	3.0	2.6	1.15
17	4.5	3.6	1.25
18	3.1	3.0	1.03
19	4.0	3.2	1.25
20	2.6	2.8	.93
21	3.7	3.3	1.12
22	3.6	3.2	1.12
23	4.0	3.3	1.21
24	4.6	3.8	1.21
25	4.2	3.6	1.16
26	3.9	3.6	1.08
27	3.2	3.2	1.00
28	3.9	3.2	1.22
29	4.0	3.5	1.14
30	4.1	3.3	1.24

APPENDIX II (cont'd)

specimen #	Y	X	Y/X
31	4.8	3.0	1.60
32	4.6	3.6	1.28
33	4.2	3.3	1.27
34	4.3	3.9	1.10
35	4.1	3.5	1.17
36	4.5	3.0	1.50
37	4.5	3.9	1.15
38	4.4	4.0	1.10
39	2.9	2.8	1.04
40	4.2	3.2	1.31
41	4.6	3.1	1.48
42	4.6	3.7	1.24
43	4.5	3.7	1.22
44	5.7	4.0	1.42
45	4.1	3.1	1.32
46	5.2	3.7	1.41
47	3.9	3.1	1.26
48	4.3	4.2	1.02
49	4.3	3.2	1.34
50	3.3	2.8	1.18
51	4.5	3.4	1.32
52	4.0	3.3	1.21
53	4.4	4.0	1.10
54	4.1	3.7	1.11
55	5.0	4.5	1.11
56	5.0	4.4	1.14
57	4.4	3.8	1.16
58	5.9	4.4	1.34
59	5.7	3.9	1.46
60	4.7	3.3	1.42

APPENDIX II (cont'd)

specimen #	Y	X	Y/X
61	5.6	3.8	1.47
62	3.9	3.7	1.05
63	4.8	3.8	1.26
64	5.2	3.7	1.41
65	3.6	3.2	1.12
66	4.2	3.9	1.08
67	5.2	3.6	1.45
68	5.3	3.9	1.36
69	5.9	4.4	1.34
70	5.1	3.2	1.60
71	4.6	4.0	1.15
72	5.0	4.0	1.25
73	5.4	4.8	1.13
74	4.6	3.5	1.31
75	6.0	5.4	1.11
76	5.9	4.2	1.40
77	5.5	4.4	1.25
78	6.2	4.7	1.32
79	5.8	3.6	1.61

loc.94:

1	2.0	1.8	1.11
2	2.5	2.2	1.14
3	2.5	2.2	1.14
4	1.8	1.6	1.12
5	2.7	2.3	1.17
6	3.3	2.5	1.32
7	2.1	2.1	1.00
8	2.3	2.6	.89
9	2.3	2.4	.96
10	3.5	2.6	1.35

APPENDIX II (cont'd)

specimen #	Y	X	Y/X
11	2.9	2.2	1.32
12	3.5	2.5	1.40
13	3.0	2.4	1.25
14	3.2	2.8	1.14
15	2.7	2.3	1.17
16	3.0	2.5	1.20
17	2.3	2.1	1.05
18	2.3	1.9	1.21
19	2.4	1.8	1.34
20	2.8	2.1	1.34
21	3.7	2.8	1.32
22	3.2	2.9	1.11
23	4.0	3.3	1.21
24	3.6	3.2	1.13
25	2.9	3.1	.95
26	3.6	3.1	1.16
27	4.7	3.5	1.34
28	4.5	3.5	1.29
29	3.5	2.6	1.35
30	3.0	2.8	1.07
31	3.9	3.1	1.26
32	3.4	2.9	1.17
33	3.5	3.3	1.06
34	3.6	3.6	1.00
35	3.9	3.1	1.26
36	3.0	2.5	1.20
37	4.0	2.6	1.54
38	3.3	2.6	1.27
39	3.4	2.7	1.26
40	4.4	3.0	1.47

APPENDIX II (cont'd)

specimen #	Y	X	Y/X
41	5.4	4.1	1.32
42	3.9	3.1	1.26
43	3.7	2.9	1.28
44	4.7	3.9	1.21
45	3.8	3.1	1.23
46	5.7	4.0	1.42
47	4.5	4.1	1.10
48	4.6	3.6	1.28
49	4.2	3.8	1.10
50	6.5	4.2	1.55
51	4.9	4.0	1.22
52	5.8	4.2	1.38
53	4.6	3.4	1.35
54	4.5	3.4	1.32
55	3.5	2.8	1.25
56	3.9	3.6	1.08
57	4.6	3.1	1.49
58	4.3	2.9	1.49
59	4.9	3.3	1.49
60	5.1	3.6	1.42
61	5.2	3.5	1.49
62	4.5	3.4	1.32
63	3.8	3.2	1.20
64	3.6	2.7	1.33
65	3.5	2.9	1.21
66	4.0	3.3	1.21
67	4.5	3.3	1.36
68	5.4	3.5	1.54
69	3.8	3.3	1.15
70	4.8	3.2	1.50

APPENDIX II (cont'd)

specimen #	Y	X	Y/X
71	4.2	3.8	1.10
72	5.3	4.0	1.32
73	4.8	3.6	1.33
74	4.8	3.1	1.55
75	4.8	3.8	1.26
76	5.4	3.7	1.46
77	4.2	3.5	1.20
78	5.3	3.6	1.47
79	4.6	3.5	1.31
80	5.4	3.7	1.46
81	5.9	3.4	1.73
82	5.6	4.2	1.34
83	6.4	3.6	1.77
84	4.5	3.6	1.25
85	4.8	3.9	1.23
86	4.3	3.1	1.39
87	5.7	3.6	1.58
88	5.3	3.6	1.47
89	6.2	3.6	1.72
90	6.1	3.8	1.60