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LIFE AND DEATH ASSEMBLAGES AMONG FOSSILS*

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ABSTRACT. Discrimination of fossil bivalve life assemblages and death assemblages comparable to Recent biocoenoses and thanatocoenoses is difficult. Size-frequency distributions have been analyzed in terms of the biocoenosis of the following: wave action, solution and abrasion, lower survivorship curve, in addition to the biological and physical factors tending to modify the initial distribution. The ratio of articulated shells to disarticulated shells is considered to be a function of time and to be related to the ease with which the shell may be disarticulated by biological and physical agencies. The departure from unity of the ratio of matching opposite valves is thought to be caused by the disruptive effects on the biocoenosis of the following: wave action, solution and abrasion, lower limit of observation, selective action of predators, scavengers and boring or triturating organisms. Comparison of the population densities observed among living forms may aid in differentiating between life and death assemblages among fossils. Application of some of these criteria to assemblages obtained from the Lower Devonian of northern Maine suggests the presence of five death assemblages plus one life assemblage.

INTRODUCTION

A paleoecologic study should attempt, as far as possible, to reconstruct the total environment for the particular time and place in question, including the physical and biological factors that affect the life and relationships of organisms.

Research in ecology has shown that detailed studies are necessary for understanding the relationships between organisms and their environment. In such studies the term "biocoenosis" has been used. A biocoenosis, meaning community of life, comprises the living organisms situated within a particular area. Much of the work of ecologists interested in marine benthonic organisms has centered upon the composition and functioning of the biocoenosis.

The paleontologist is handicapped in ecologic studies by the necessity for distinguishing ancient biotic assemblages comparable to the biocoenosis from what Wasmund (1926) has termed the "thanatocoenosis." Strictly speaking, the term "thanatocoenosis" implies a community of death; as used by Wasmund, however, it has come to mean the aggregated remains

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of organisms that in many cases never constituted a biocoenosis, but were brought together by physical agencies, such as wave and current action, which operated after they died. An excellent example of a thanatocoenosis is the miscellaneous assortment of organic debris gathered on most marine beaches. The fact, however, that fossils are commonly not preserved in their proper habitat need not deter the paleontologist from seeking to differentiate between assemblages comparable to the biocoenosis and the thanatocoenosis of the neontologist.

It is here suggested that the terms "life assemblage" and "death assemblage," respectively, be employed as the paleontological equivalents of biocoenosis and thanatocoenosis.

Clearly, the first task facing the student of paleoecology is to distinguish between associations comprising a life assemblage and those making up a death assemblage; this requires detailed observation and comparison of results with those obtained in studies of Recent ecology.

One of the best ways to determine the nature of a community is to subject certain of its properties to statistical analysis. Statistical analysis is an extended means of observation, the results of which enable the worker more easily to comprehend the type of community with which he is dealing. This paper is an attempt to deal statistically with assemblages of marine bivalves, referring especially to fossil brachiopods.

The writer wishes to express his gratitude for the aid and counsel of P. E. Cloud, Jr., Russell Olsen, Henry C. Stetson, George E. Clarke, and Bruce Nelson. In addition, particular thanks are extended to L. M. J. U. van Straaten, of the Rijks-Universiteit, Groningen, for the loan of unpublished data collected during the course of his studies on the Dutch coast.

CRITERIA FOR DISCRIMINATING BETWEEN A LIFE ASSEMBLAGE AND A DEATH ASSEMBLAGE

To interpret the results of this statistical analysis, one must first consider what conditions will be of importance in producing any given assemblage of hard parts of marine bivalves such as brachiopods.

Size-frequency distributions.—The simplest example of a size-frequency distribution is that of the assemblage of hard parts left behind by a single set[1] at a given locality. The two primary circumstances governing the size-frequency distribution of any set are the rate of reproduction and the death rate. In addition, the vagaries of the transporting current that brought the planktonic larvae to the locality where they finally became members of the benthos must be considered. The following discussion does not take into consideration the possibility of sexual dimorphism among dioecious species, such a phenomenon probably being too rare to be significant in most cases.

Many marine invertebrates, especially among the pelecypods, have reproductive and initial death rates that are high compared with those of mammals (Deevey, 1947). It is probable that many brachiopods and pelecypods have a concave or steeply negative sloping survivorship curve, such as that inferred for oysters by Deevey (1947, p. 312). Of importance to the paleontologist is the point on the survivorship curve at which the organism first develops hard parts capable of being preserved as fossils. Percival (1944) presented graphs of size-frequency distributions for the living brachiopod *Terebratella inconspicua* that indicate a survivorship curve that is concave. Under normal conditions, therefore, one may expect a size-frequency distribution curve for individuals past the larval stage that is concave, representing a large number of immature individuals, a moderate number of adults, and a relatively minor number of gerontic individuals, or a steeply sloping negative curve that approaches the asymptotic only for the gerontic individuals as is indicated by the right-hand portion of figure 1. If the larvae are included in the study one will have to consider the left-hand portion of figure 1 that is asymptotic to the vertical coordinate. The size-frequency distribution of a life assemblage that has experienced optimum conditions of preservation and no physical disturbance should approximate its mortality curve.

Most deposits contain more than one set, so one must consider the additive effects of sets with different population densities upon the expected size-frequency distributions of the final assemblage. Three types of increment are to be expected: static,

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[1] The term "set" as used by the marine biologist refers to the larvae, of one species, that settle down on a particular portion of the bottom after they have passed through a planktonic stage. The larvae spawned at any one time and place may be the source of the set at a number of localities, their distribution being dependent upon the transporting currents. Set is not synonymous with rate of reproduction.

cyclic, and irregular. For all three types it is assumed that the mortality rate will be of the same order of magnitude, especially among the immature individuals, excluding the larvae from consideration. Assuming the mortality curve to remain about constant, the size-frequency distribution for all three types will be similar to that for the single set, except that the size of the modal class will be exaggerated by the cumulative effect of the additional sets (fig. 2).

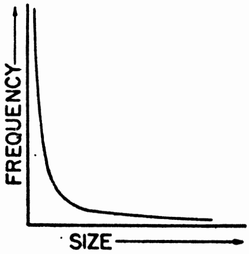

Fig. 1.
Normal survivorship curve.

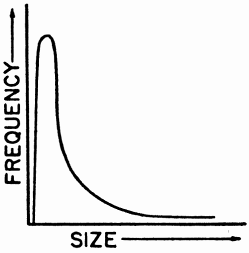

Fig. 2.
Mortality curves for two sets with differing initial population densities and unvarying mortality rate.

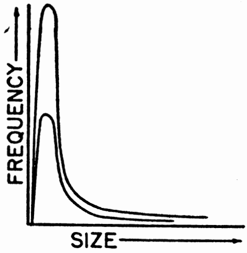

Fig. 3.
Mortality curves for sets with differing mortality rates.

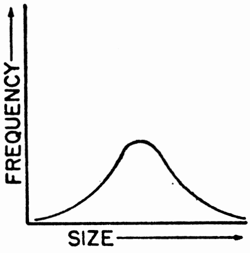

Fig. 4.
Bell-shaped normal distribution curve.

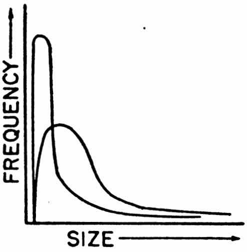

Fig. 5.
Predicted size-frequency distribution for a life assemblage.

The cumulative effect of additional sets with differing mortality rates introduces a slight modification of the size-frequency distribution. This modification will result in right-skewed, concave curves having peaks with variable curvature (fig. 3) as opposed to those showing an unvarying mortality rate. It is conceivable that under certain rare conditions the mortality curve may approach the bell-shaped condition rather than being strongly skewed to the right, with a corresponding effect upon the size-frequency distribution. Such a bell-shaped curve would imply that most of the members of a set had reached at least moderate size and age, an occurrence that seems to be almost unknown among marine bivalves under natural conditions, in which the mean life span is short.

Many secondary conditions, however, tend to alter the expected size-frequency distribution of hard parts. These conditions may be divided into two main groups: (1) non-selective conditions, such as the availability of food, temperature, and disease, all of which will ordinarily affect the size-frequency distribution of all the living forms in an area, and (2) selective conditions that will affect one size group more than another. These latter conditions may be further subdivided into the following categories: physical conditions, such as wave action, current action, solution, abrasion, biological conditions, such as the action of predators (Turner, *et al.*, 1948, pp. 43-45), scavengers, triturating organisms responsible for the destruction of hard parts, and hermit crabs; and experimental limitations such as the practical limits of observation. An attempt will now be made to discuss each of these selective conditions and to assess its effect upon size-frequency curves for the life assemblage and recognize its role in shaping the curves for death assemblages.

Wave action and current action, especially in the littoral zone, are potent agents in the destruction of the biocoenosis, both during the normal life cycles of the various organisms and after their death. Storm waves tend to disrupt the benthos either by burying it or by tearing its elements loose and scattering them. The effect of burial will be, presumably, to preserve a portion of the biocoenosis as a life assemblage. However, the scattering of the benthos will subject its elements to the same sorting processes that affect the accompanying sediments. Wave and current action will continually tend to remove the hard parts of dead individuals whose competent velocities are less than the competent velocity of the associated sediment (Menard and Boucot, 1951, pp. 146-148) and to redeposit them elsewhere at the dictate of local currents. This removal of hard parts will greatly alter the expected size-frequency distribution, because the greatest number of deaths will occur among the very young members of a set owing to their greater primary abundance. The result may then be a biocoenosis in which the size-frequency distribution curve may approximate a bell-shaped normal distribution[2] and a thanatocoenosis deposited elsewhere which will have the same type of distribution curve owing to sorting (fig. 4).

The effect of solution upon marine bivalves is not well understood. However, smaller hard parts having the same form as larger shells, will suffer disproportionately owing to their greater surface exposed per volume of shell material. This effect will tend to reduce the degree of right-skewness and slope of the curve expected in the size-frequency distribution of a life assemblage.

The effects of abrasion are hard to predict in the absence of adequate experimental data, but it is probable that they would tend to alter the expected size-frequency distribution.

An important factor that must be considered in paleontology is the lower limit of shell size that the methods of sampling and observation allow. In other words, just how small a specimen can be detected in the material? How finely can the sample be broken down in order not to miss any specimens, especially in a heavily indurated matrix? The answers to these queries probably vary for each worker and for each type of material, but some estimate of their effect needs to be taken into account.

The lower limit of shell size preserved may be controlled by

[2] Such an assemblage was observed by Mr. Henry Stetson, Mr. Sherwood Tuttle, and the author, during the spring oı 1951, in a salt-water pond at Cohasset, Mass. This pond, connected with the sea by a tidal sluiceway, contains large colonies of the mussel *Mytilus edulis*. Certain of the mussel beds are swept by currents competent to remove all the dead shells, and are underlain by relatively clean-washed sand and gravel. Others are apparently washed by weaker currents, capable only of removing the shells of small individuals. In these latter beds the dead shells of the larger mussels (approximately 3-5 cm in length) are buried below the thick mat of the living in a black, stinking mud. These deposits would give rise to a life assemblage characterized by a bell-shaped size-frequency distribution curve.

the grain-size of the enclosing sediment or the type of alteration (silicification, pyritization).

Two other conditions whose relative importance is not yet understood are the selective action of predators and scavengers in the abstraction of specimens of various sizes from the fauna, as well as the size preferences of boring and triturating organisms.

These modifying conditions indicate that a life assemblage may have a size-frequency distribution that is strongly right-skewed, negatively sloping, showing the predominance of small individuals (fig. 5). Their size-frequency distribution, therefore, may produce a strongly right-skewed or negatively sloping curve rather than the bell-shaped normal distribution curve common for particles of sediment and other materials that have undergone extensive sorting. However, death assemblages whose mode occurs among the small shells, i.e., transported assemblages comprised mainly of small shells, may strongly simulate or even be identical with the above-mentioned right-skewed size-frequency distributions.

The ratio of articulated shells to disarticulated shells.—Marine bivalves tend to become unhinged after death, some groups becoming unhinged more readily than others. Pelecypods equipped with a ligament or a resilium are prone to become unhinged after death, whereas many articulate brachiopods resist this tendency.

The biological and physical circumstances related to this tendency to become unhinged must be considered in interpreting the ecologic significance of the manner of preservation. Governing this event are such biological characteristics as the nature of the articulation between the valves and the rapidity with which the soft parts decompose. It is inferred that size and other biological characteristics are factors within a given species, although these points are not considered in the present paper.

Organisms that live deeply buried are more apt to be undisturbed after death than those that live on the sea floor. However, the presence of growth stages at different levels below the sea floor would tend to disturb the expected size-frequency distribution.

The chief physical conditions that affect unhinging are the velocity and the duration of current to which the shells are subjected after death (tending to unhinge the shells) and the rapidity of burial immediately after death (tending to prevent the valves from becoming unhinged).

It would be desirable to evaluate these biological and physical conditions among living bivalve faunas. In the absence of such information, an empirical means of evaluating the tendency of bivalves to become unhinged is found by counting the number of articulated shells and disarticulated shells or their impressions for each species in a particular assemblage.

Species that are easily disarticulated will be more delicate indicators of the amount of wave and current action that an assemblage has undergone than species that become disarticulated with difficulty. The occurrence of a single assemblage with a large percentage of articulated specimens of a species that is easily disarticulated would indicate a probable life assemblage. For example, in Devonian sandstones of west-central Maine the pelecypod *Nuculoidea* is usually found only as single valves. This is not remarkable because the resilium would tend to spread the valves apart after death. At one locality, however, a large number of valves are still hinged together, indicating the presence of a life assemblage that was buried before the resilium opened the valves.

A species which is disarticulated with difficulty will be a better indicator of the time during which disarticulating processes have been operative. The percentage of single valves is a function of the time elapsed.

It may be possible to determine the direction of shell movement at a given stratigraphic level by contouring values obtained for the ratio of whole shells and single shells.

The ratio of opposite valves.—An undisturbed deposit of shells containing unhinged shells should yield approximately equal numbers of opposing valves. The opposing valves should have dimensions that permit them to be fitted together. Sorting, on the other hand, will tend to segregate disarticulated valves according to their hydrodynamic behavior.

Field observations show that the opposing valves of different bivalve species may have widely variant hydrodynamic properties. Occasionally specimens of only one valve are found at a given locality; the other valve, because of differing hydrodynamic behavior, has been deposited elsewhere. A sorted deposit containing disarticulated bivalves will not, as a rule, yield equal numbers of matched opposing valves.

An empiric measure of these relationships can be obtained by counting the opposite valves in any particular shell deposit. Species whose opposite valves tend to be easily separated from each other will be more delicate indicators of the amount of sorting a deposit has undergone. A deposit containing nearly equal numbers of matching valves of a species whose valves ordinarily tend to become easily separated suggests a life assemblage.

By arranging in order of magnitude the opposite valve and articulated- to disarticulated-shell ratios of any one species taken from different fossil deposits, one may observe whether the same ratios for the accompanying species in each deposit show the same order or whether they vary erratically. If the ratios of the accompanying species in each deposit vary in the same manner as the ratios of the first species, the contents of each bed may have been derived from one source area. If the ratios of the accompanying species do not vary in the same direction as those of the first species at one or more of the deposits, diverse sources may be inferred.

Population densities.—The differentiation of a life assemblage from a death assemblage is aided by study of population densities on individual bedding planes. The population density of the fossils contained in a column of rock is a function of the rate of sedimentation, and consequently is of little value in discriminating between life and death assemblages. Normal population densities vary with the size of the growth stages of each species. For example, Percival (1944) in a biocoenosis of the brachiopod *Terebratella inconspicua* found about 400 individuals up to 3.5 mm long per 2.3 square decimeters and 30 to 40 individuals 10.5 to 13.5 mm per 2.3 square decimeters. Therefore a thanatocoenosis or death assemblage might be indicated by the occurrence of, for example, 160 individuals of this species with lengths of 10.5 to 13.5 mm per 2.3 square decimeters. This interpretation would be strengthened if the valves of this and other growth stages were disarticulated (assuming that this species is not easily disarticulated), if there were widely differing numbers of matching valves, and also if the size-frequency distribution were bell-shaped.

Another approach to this problem might be made by a study of the hydrodynamic behavior of the remains of benthonic organisms, in order to ascertain their competent velocities. Little work has been done in this direction (Menard and Boucot, 1951).

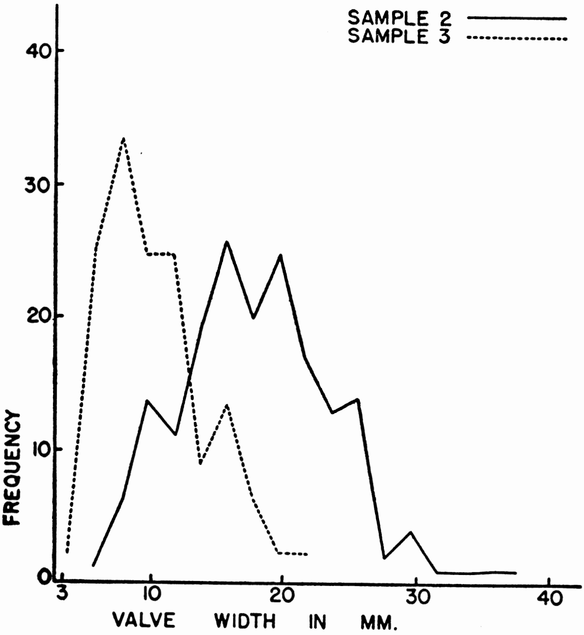

Fig. 6. Size-frequency distribution of *Mutationella sp.* (number of specimens per 10-cm cube).

Summary.—By considering certain statistical properties of an assemblage one should be in a better position to state the

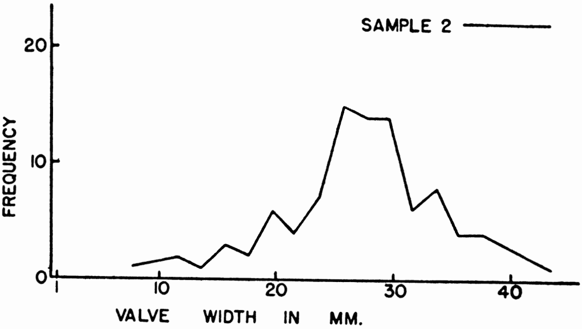

Fig. 7. Size frequency distribution of *"Spirifer" murchisoni* (number of specimens per 10-cm cube).

probability that the population from which the sample was drawn once formed part of a biocoenosis.

By considering also other pertinent information, such as that obtained from a study of the petrography and composition of the entombing sediments, one should be able to add further evidence. Of particular interest is the sulfur content. Sediments that run high in sulfur may have been deposited under reducing conditions, with consequent low oxygen content, and probable slight current activity, and therefore any benthonic animals found in them are apt to have belonged to the biocoenosis. These deposits will also be an excellent medium for the preservation of a thanatocoenosis composed of pelagic and planktonic organisms.

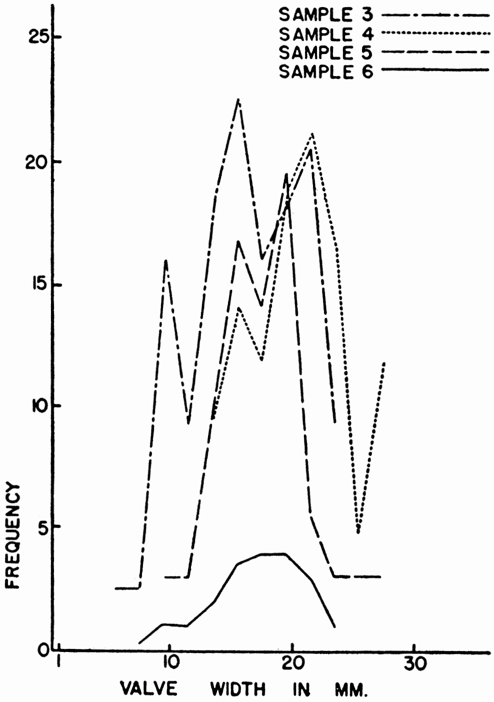

Fig. 8. Size-frequency distribution of *Antispirifer harroldi* (number of specimens per 10-cm cube).

DEATH ASSEMBLAGES AND A LIFE ASSEMBLAGE FROM THE LOWER DEVONIAN OF NORTHERN MAINE

Certain of the variables considered above were used in the study of fossil assemblages from Lower Devonian strata in Somerset County, Maine. Most of the material studied came from six different beds in Parlin Gorge, about 2 miles northeast of the village of Lake Parlin, Parlin Pond Township, Somerset County, Maine.

About 95 per cent of the rocks exposed in Parlin Gorge consist of medium-grained, dark blue-gray, argillaceous, brown-weathering, massive sandstone (subgraywacke). The remaining beds, scattered throughout the sequence, are slates. Fossils are ordinarily abundant in the slates, uncommon in the sandstone.

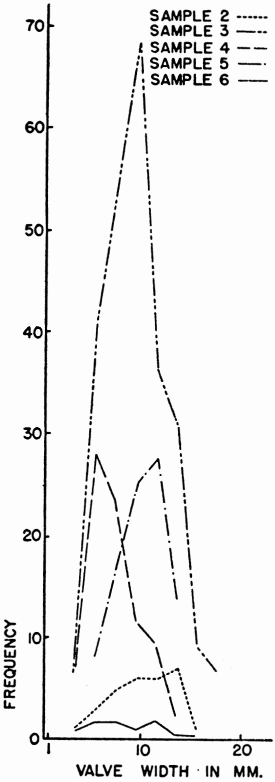

Fig. 9. Size-frequency distribution of *Leptocoelia flabellites* (number of specimens per 10-cm cube).

The ensuing paragraphs will attempt to analyze data from direct measurements of a number of specimens (table 1), taken from six samples of fossil-bearing slate and argillaceous sandstone, weighing 104 pounds. The fossiliferous samples were selected as being representative of the particular bed under investigation. All unfossiliferous rock adhering to the selected sample was removed in order to avoid a false picture of the population density, and the trimmed specimen was weighed. The weights of the samples ranged from 7¾ to 29 pounds. The weighed samples were then split parallel to the bedding, and records were kept of the number of valves belonging to each species and the maximum width of each valve.

TABLE 1

Number of Specimens Recovered from Six Fossil Beds in Parlin Gorge, Somerset County, Maine

Sample No.	1	2	3	4	5	6
Field No.	27	29	30	31	32	33
Antispirifer harroldi ..	...	...	59	50	24	92
"Spirifer" murchisoni..	...	96	...	...	...	...
Leptocoelia flabellites..	...	29	112	35	33	42
Mutationella sp.	...	176	64	1	2	2
Globithyris callida	231	...	...	...	...	...
f*	1.5	3.0	3.0	7.0	8.0	1.0
Sample weight in pounds	13.25	17.50	7.75	17.50	17.00	29.50

* "f" is the factor by which the observed values were multiplied to adjust for the estimated numbers of unobserved specimens in each sample.

It is not possible to count and measure some specimens in a given layer because they are packed so tightly that freeing one specimen breaks another, and some layers can be split only to a certain thinness. Therefore, an estimate "f" of the percentage of fossils not recorded was made.

Finally, these data were reduced to a common denominator, the number of specimens in a 10-cm cube, taking into account the estimated percentage of fossils not recorded and the varying weights of the initial samples. Specimens were measured to the nearest tenth of a millimeter, all measurements between each odd millimeter and the succeeding even one being combined before reducing to a common denominator.

For five of the six beds studied there was a distinct development of a bell-shaped size-frequency distribution, whereas the size-frequency distribution in the sixth (sample 1) was strongly skewed to the right and concave upward (figs. 6-11). The curves also demonstrate that the size-frequency distribution of each species has its own mode in the same bed, presumably because each species has its own hydrodynamic properties and behaves in characteristic fashion when subjected to the same forces.

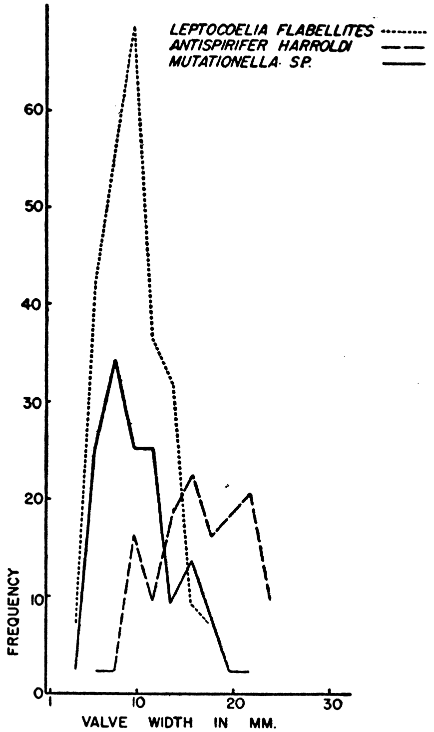

Fig. 10. Size-frequency distribution of fauna in sample 3 (number of specimens per 10-cm cube).

In curves for certain beds the modes are farther to the right than in others, but the bell-shaped outlines of the size-frequency distribution curves are about the same. Herein may lie a partial explanation for certain "dwarf" faunas, as previously suggested by Cloud (1948). The same mechanism also accounts for some faunas composed mainly of large individuals, the Oriskany sandstone fauna of New York being an example.

All of the genera except *Leptocoelia* (fig. 6) are usually found as disarticulated shells. In none of the beds were many articulated shells found, with the exception of *Leptocoelia* and, in sample 1, of *Globithyris* (fig. 11). In other parts of Somerset County, *Globithyris* commonly occurs disarticulated. Sample 1 is composed of a rock rich in free carbon and iron sulfide.

The ratio of pedicle: brachial valves of the "*Spirifer*" (fig. 8) in sample 2 was approximately 3.5: 1.0.

Fig. 11. Size-frequency distribution of *Globithyris callida* (number of specimens per 10-cm cube).

The population density of *Globithyris* in sample 1 for shells more than 10 mm wide is much less than that found in the probable death assemblages of this genus elsewhere in Somerset County, Maine. In general, the population density of sample 1 is lower than that of samples from the other beds in Parlin Gorge, indicating that these other beds may contain the remains of more sets than sample 1.

It is concluded that the fossils in samples 2 to 6 (figs. 6-10) probably represent death assemblages because of their size-frequency distributions, the lack of articulated shells of those species which probably are easily disarticulated, and the ratio of opposite valves for "*Spirifer*" in sample 2, as well as the population densities. The beds represented by these samples are not very ferruginous or noticeably carbonaceous as compared with the bed that yielded sample 1. The fossils in sample 1 are thought to represent a probable life assemblage because there are numerous articulated shells of a species that is usually disarticulated with ease, the size-frequency distribution is strongly right-skewed, and the bed is rich in free carbon and iron sulfide.

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ERRATA

In the paper by Arthur J. Boucot entitled "Life and Death Assemblages among Fossils" (January 1953) the fourth line of the Abstract (p. 25), "biocoenosis . . ." should be deleted.

The author has asked us to point out the following errors:

Figures 1-5 (p. 28) should have been arranged as shown below:

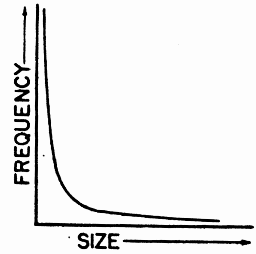

Fig. 1.
Normal survivorship curve.

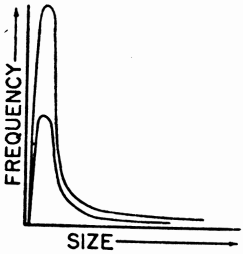

Fig. 2.
Mortality curves for two sets with differing initial population densities and unvarying mortality rate.

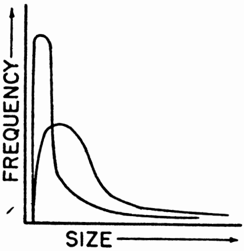

Fig. 3.
Mortality curves for sets with differing mortality rates.

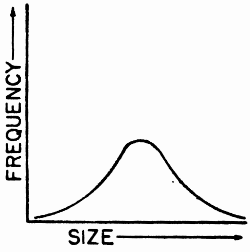

Fig. 4.
Bell-shaped normal distribution curve.

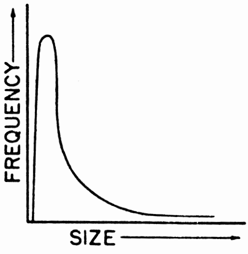

Fig. 5.
Predicted size-frequency distribution for a life assemblage.

On page 39, line 3, a "9" should be substituted for the "6"; line 9, a "7" should be substituted for the "8."