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Figs. 1-7, September, 1963

FACTORS AFFECTING THE DISTRIBUTION OF OPPOSING MOLLUSK VALVES[1]

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ABSTRACT

Statistical treatment of collections of valves of the clam *Dinocardium robustum* deposited on the beach of Mustang Island, Texas, indicates the differences in the number of left and right valves are significant at the 0.05 level of probability. A relationship is shown to exist between average valve length and the percentage of excess valves, with the number of excess valves being significant only in collections having an average valve length greater than 69.5 mm. This relationship is attributed to a similarity in surf requirements for separating opposing valves and transporting large valves, namely a high energy surf. Differences in weight, ornamentation, and fragility between opposing valves do not affect their distribution. Boring snails attack left and right valves in equal numbers, but seem to prefer small sizes. The size-frequency distribution of collections are varied, but highly skewed curves predominate.

INTRODUCTION

The occurrence of excess left or right valves in accumulations of clam shells has been noted in ancient sediments (Richter, 1922, 1924) and on recent beaches (Van Del Meulen, 1947; Martin-Kaye, 1951; Lever, 1958). Excess valves were also noted in an assemblage of fossil brachiopods by Boucot and others (1958), who suggested the possibility of locating the source area of the valves by contouring the ratio of disarticulated opposite valves, on the assumption that the ratio should increase with distance from the source.

The pelecypod valve is usually asymmetric so that it will tend to travel oblique to the direction of a current competent to transport the valve and, as opposing valves are mirror images, continued transport will tend to separate them. Boucot and others (1958) compared the diverging movement of the valves to the port and starboard tack of a sailboat. Lever (1958) suggests other causes of shell accumulations containing excess left or right valves such as differences in weight between opposite valves, and differences between valves caused by projections from one of the valves.

The objective of the investigation reported upon in this paper was to determine whether or not the left-right phenomenon (a term used by Lever, 1958) occurred on Mustang Island beach, Texas, and, if it did, to estimate the relative importance of properties of the shell and the environment in causing this phenomenon.

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COLLECTING SITE

The beach of Mustang Island near Port Aransas has a 1 to 2 percent slope with one or more sand bars about a thousand feet offshore (Hedgpeth, 1953, p. 183, fig. 38, p. 184). The beach profile varies considerably seasonally. The jetty north of the collecting area probably affects adjacent topography and current structure. The beach sand is well sorted with a median diameter in the very fine sand or fine sand size and consists predominantly of quartz particles (Shepard, 1960). The collecting area is shown in figure 1.

Detailed current movement in the collecting site is not known. According to Curray (1960, p. 231), during January, February, and March a strong westward and southward flow from across the shallow Louisiana shelf converges with northward flowing cur-

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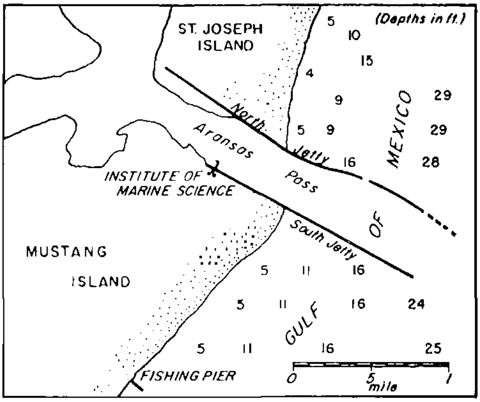

FIG. 1.—Map showing beach of Mustang Island where valves of *Dinocardium robustum* were collected.

rents in the vicinity of the collecting area. In May the convergence moves northward because of southeast winds so that currents in the collecting area would be mostly flowing north. In September, when winds shift to the east, the convergence again occurs near the collecting site. This generalized picture of circulation given by Curray (1960) indicates the complexity of current movements in the study area.

A tide station is maintained on South Pier at the southern end of the collecting site. Tidal wind, temperature, salinity, and tide staff data from December 1958 to May 1960 were analyzed, but as no relationship could be found between these parameters and the distribution of opposing *Dinocardium robustum* valves in the beach collections, the data from the tide station are not discussed in this paper.

DINOCARDIUM ROBUSTUM

The clam chosen for the study was *Dinocardium robustum* Solander, whose shells are usually fairly abundant on the beaches along the Texas coast. According to Parker (1960, p. 321) this species is common in 2–12 fathoms of water from the east Mississippi Delta to Mexico. Specimens grow to about 4 inches, are oval, inflated, and have many ribs. The species is figured by Abbott (1954, pl. 32, fig. 2). Measurements of left and right valves of two specimens of *D. robustum* are compared in table 1. The shape of valves remains about the same during growth, but the sphericity may decrease slightly (fig. 2).

METHODS

Valves of *Dinocardium robustum* were collected from the water's edge on the beach of Mustang Island each month from December 1958, to August 1960. Collections were made while afoot and the attempt was made to pick up all valves, regardless of size, in a traverse along the water's edge. Collecting was discontinued after roughly 100 valves had been obtained. If, because of scarcity of valves, fewer than 100 valves could be picked up during a collecting trip, additional collections were made on following days. Collections made in the same month were lumped together for statistical treatment of the data.

In addition to counting the number of left and right valves in each collection, the length of each valve was measured parallel to the central rib in collections made up to March 1960, and it was noted whether or not the valve contained a hole made by a boring organism. From March 1959, to March 1960, a record was kept of the position of the valves on the beach, i.e., whether

TABLE 1.—*Comparison of dimensions of left and right valves of* Dinocardium robustum[a]

Measurement	Specimen No. 3		Specimen No. 6	
	Left Valve	Right Valve	Left Valve	Right Valve
Valve length cm[b]	6.20	6.29	9.15	9.36
Valve width cm[c]	5.78	5.80	8.27	8.36
Valve height cm[d]	2.52	2.62	3.46	3.57
Nominal diameter cm[e]	4.5	4.6	6.4	6.5
Sphericity[f]	0.73	0.73	0.71	0.70
Average wall thickness cm[g]	0.19	0.19	0.25	0.25
Weight gm	12.8	12.9	49.9	54.2
Cup volume cc[h]	31.0	29.0	90.0	105.0

[a] Data from Kornicker and Armstrong (1959).
[b] Valve length was measured in the plane of commissure parallel to the longest rib in the central portion of the valve.
[c] Valve width is the greatest distance between anterior and posterior margins measured in the plane of commissure and normal to the length.
[d] Valve height is the maximum dimension of the individual valve measured perpendicular to the plane of commissure; height as used here is one-half height of closed articulated shell.
[e] Nominal diameter is the cube root of the product of the length, width, and height of each valve.
[f] Sphericity is intercept sphericity as defined by Krumbein (1941).
[g] Wall thickness is roughly the average distance between the inner and outer surface of each valve obtained from three measurements with a micrometer.
[h] Cup volume is the internal volume of the disarticulated valve measured by filling the valve with water while the plane of commissure is held horizontal.

they were concave upward or concave downward.

SEASONAL DISTRIBUTION OF OPPOSING VALVES

If clam shells are deposited on a beach in a random manner most accumulation would contain about the same number of left and right valves, but in a few one valve would be greatly in excess. Therefore, it was necessary in the present investigation to determine whether variations in the proportion of opposing valves in individual samples were significant. This was done by using a Chi square test designed for more than 30 degrees of freedom (Edwards, 1958, p. 113). This test indicated a significant difference at the 0.05 level of probability in the numerical distribution of left and right valves in the monthly collections considered *in toto*, and specifically in collections obtained in December 1958, March 1959, June 1959, February and June 1960. Right valves were in excess in the December and March collections, whereas left valves were in excess in the June and February collections (table 2).

Although it seems quite likely that seasonal variations in current movement would be reflected in the distribution of opposing valves on the Mustang Island beach, there is no clear-cut evidence of a seasonal effect from the data. More closely spaced samples might have brought out seasonal trends, but it is possible that currents in the collecting area are sufficiently variable each month to mask seasonal effects. The data suggest that significant differences in the number of opposing valves occur on the Mustang Island beach during any season, and that either the left and right valve can be predominant at any time of the year.

EFFECT OF DIFFERENCES IN WEIGHT, FRAGILITY, AND PROJECTIONS BETWEEN LEFT AND RIGHT VALVES

Lever (1958) brings out that excess valves can result from differences in weight or fragility between left and right valves, and from differences in mobility caused by projections. As shown in table 1 opposing valves of *D. robustum* are quite similar in weight and shell thickness. Ornamentation and projections such as teeth also seem sufficiently the same not to cause significant differences in the mobility of opposing valves.

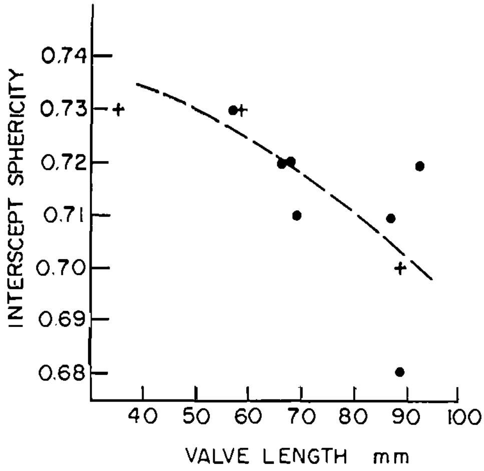

Fig. 2.—Value intercept sphericity as a function of valve length (from data in Kornicker and Armstrong, 1959). Crosses represent right valves, circles left valves.

It is possible to show that differences in weight and projections had little effect on the distribution of opposing valves by plotting the average length of right valves in each sample against the average length of left valves (fig. 3). The graph approximates a 45 degree slope with a slight indication of right valves being in excess in samples having large average valve lengths. The similarity in average length of opposing valves indicates that they have not been separated according to differences in projections or weight.

The wall thickness of left valves is similar to that of right valves (table 1) indicating that neither valve is materially more resistant to destruction than the other. The fact that the total number of left and right valves collected on Mustang Island was about the same (1,152 left valves *vs.* 1,161 right valves) is considered as evidence that the distribution of opposing valves of *D. robustum* is not affected by differences in fragility.

THE RELATIONSHIP BETWEEN VALVE SIZE AND DISTRIBUTION OF OPPOSING VALVES

It was noted that the average valve length in collections having a significant difference

TABLE 2.—*Distribution of left and right valves of* Dinocardium robustum *on Mustang Island beach by month*

Month-Year	No. of Left Valves	No. of Right Valves	Total No. of Valves Collected	Excess Valves[a] percent	Average Valve Length[b] mm	No. of Collecting Trips
1958						
Dec.	39	11	50	56 L[c]	82	1
1959						
Jan.	85	64	149	14 L	66	1
Feb.	55	49	104	6 L	63	2
March	106	48	154	38 L[c]	80	1
April	33	38	51	7 R	35	7
May	45	47	92	2 R	67	1
June	31	62	93	33 R[c]	75	2
July	76	50	126	21 L	32	1
Aug.	58	57	115	1 L	31	3
Sept.	65	56	121	7 L	22	3
Oct.	76	54	130	17 L	48	1
Nov.	58	72	130	11 R	34	1
Dec.	68	53	121	9 L	37	4
1960						
Jan.	92	83	175	5 L	42	2
Feb.	18	140	158	77 R[c]	82	1
March	54	54	108	0	54	1
April	—	collection made but shells not counted				—
May	78	51	129	21 L	—	1
June	28	68	96	42 R[c]	—	1
July	33	45	78	15 R	—	1
Aug.	54	59	113	4 R	—	1
Total	1152	1161	2313			36

[a] Percentage of excessive valves equals | number of left valves − number of right valves | divided by total number of left and right valves, multiplied by 100. The letter "L" or "R" after the percentage indicates which valve is in excess.

[b] Valve length was measured parallel to the longest rib in the central portion of the shell in the plane of commissure.

[c] Difference in the number of excess valves is significant at the 0.05 level of probability.

in the number of excess valves was greater than the average valve length in remaining collections (fig. 4, table 3). At first it was thought that this relationship might be due to small valves being more spherical (less asymmetrical) than large valves (fig. 2), but the difference in sphericity between large and small valves is so small that this seems unlikely. Furthermore, when the number of large and small opposing valves in the same sample are compared, their distribution is not significantly different (table 4). Therefore, it is concluded that environmental conditions conducive to depositing large valves upon the beach are also conducive to separating opposing valves. If this conclusion is correct, consideration of factors that lead to the deposition of large valves upon a beach might elucidate the mechanism that separates left and right valves.

Unfortunately, little is known about the effect of environmental conditions on the size of valves deposited on a beach. However, it would seem safe to assume that a relationship exists between available energy in the surf and valve size, with larger valves deposited when the available energy is greater. Therefore, it is likely that when the sea's conditions are such that sufficient energy is available to carry large shells to the beach, forces are at work separating left and right valves. It is too early to speculate concerning whether the separation is due directly to waves or to currents created by

TABLE 3.—*Relationship between valve length and percentage of excess valves*

Collection Period	Range of monthly mean valve lengths mm	Statistical comparison of numbers of left and right valves	Range of percentage of excess valves[a]
Jan., Feb., April, May, July, Aug., Sept., Oct., Nov., Dec. 1959; Jan., Mar. 1960.	22–67	0–3.2 (not significant)	0–21
Dec. 1958; Mar., June, 1959; Feb. 1960	75–82	4.8–46.2 (significant)	33–77

[a] Percentage of excess valves equals | number of left valves—number of right valves | divided by total number of left and right valves multiplied by 100.

waves, or what is more likely, a combination of both.

Kornicker and Armstrong (1959, fig. 3) determined experimentally the force required to move valves of *D. robustum*. The required force increased linearly with valve weight. Therefore, it seems reasonable to infer that more force is required to transport large valves to a beach than is required to transport small valves. And if the assumption is made that both large and small valves have the same source area, which seems a reasonable assumption for valves of *D. robustum*, large valves will require more

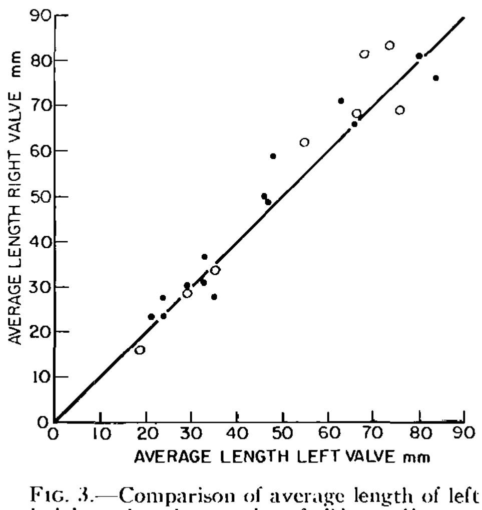

FIG. 3.—Comparison of average length of left and right valves in samples of *Dinocardium robustum* valves in collections from Mustang Island. Open circles indicate that right valves were in excess in the sample; filled-in circles indicate that left valves were in excess.

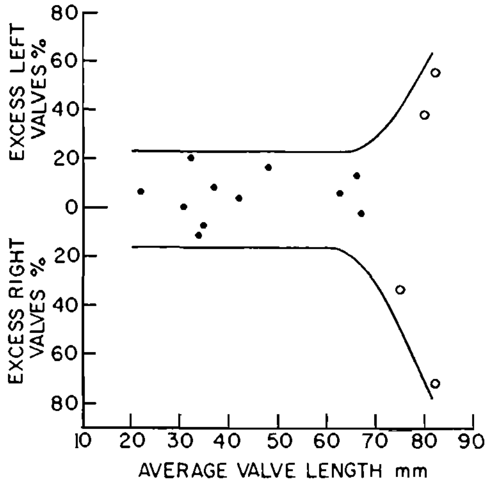

FIG. 4.—Relationship between average valve length and percentage of opposing valves. Samples containing differences in the number of opposing valves significant at 0.05 probability level are indicated by open circles.

energy to be transported to the beach than will small valves.

By using the experimentally derived forces necessary to move shells determined by Kornicker and Armstrong (1959), it was possible to estimate the force required to move 100 valves having the size-frequency distribution observed in samples collected from Mustang Island. The percentage of excess valves in each collection is shown as a function of the force that would be required to move 100 shells in figure 5. At the top of figure 5 an arbitrary scale indicates surf energies that might correspond to the force levels required to move the shells.

Additional work will be required to document that large valves and a high percent of

TABLE 4.—*Comparison of number of left and right valves among small and large sizes in samples having significant differences in the numbers of opposing valves*

Month-Year	Valve length less than 79.5 mm		Valve length more than 79.5 mm	
	No. of left valves	No. of right valves	No. of left valves	No. of right valves
December 1958	13	6	26	5
March 1959	34	16	54	32
June 1959	14	28	17	34
February 1960	8	38	10	101

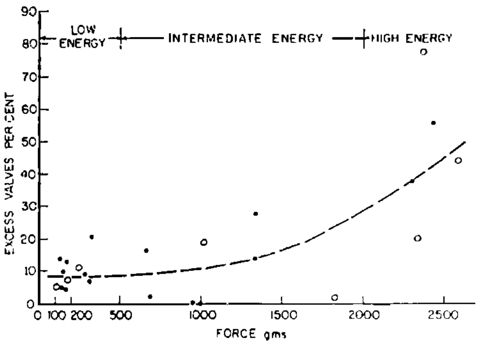

FIG. 5.—Percentage of excess valves as a function of calculated force required to move 100 valves having the size-frequency distribution of each collection of valves from Mustang Island. A scale indicating relative surf energy is at top of graph. Open circles indicate that right valves were in excess in the sample; filled-in circles indicate that left valves were in excess.

excess valves are related to high surf energy. If the relationship between energy levels, valve size, and excess valves is shown to exist, use might be made of the relationship in interpreting the energy levels at which fossil assemblages are deposited.

THE MECHANISM OF VALVE TRANSPORT

It seems to have been assumed that left and right valves are separated from each other by currents while the valves are in a concave downward position. However, Menard and Boucot (1951) observed that brachipod valves turned end over end when transported by water in a flume, and Kornicker and Armstrong (1959, p. 183) reported the overturning of *D. robustum* valves by waves in shallow water. Therefore, it would seem that the concept of valves being transported while they remain in a concave downward position is an oversimplification.

There appears to be a relationship between the rate of overturning and velocity of water current, with more overturning taking place at higher velocities (Menard and Boucot, 1951, table 1; Kornicker and Armstrong, 1959, p. 182). Therefore, it does not seem unlikely that when energy in the surf is sufficiently great to transport large valves to the beach it is also capable of overturning valves. A hypothesis that presents itself is that the overturning of valves may play an important part in the separation of opposing valves. Perhaps the opposite symmetry of left and right valves permits one valve to be more easily overturned than the other after they are oriented differently by prevailing currents, or perhaps separation takes place more easily when valves are in a concave upward position than when they are convex upward. The writers can only suggest these possibilities in absence of a complete understanding of the mechanisms that might be involved.

The fact that many valves collected on Mustang Island beach were found in a concave upward position (table 5) is considered to be an indication that overturning is probably occurring offshore, although some overturning may take place after the valve is deposited on the beach as described by Kornicker and Armstrong (1959, p. 183).

RELATIONSHIP BETWEEN DRILLED AND UNDRILLED VALVES

Kornicker and Armstrong (1959) and Lever and others (1961) observed that clam shells with holes behaved differently hydrodynamically than shells without holes. Apparently, in some situations valves with holes tend to lag behind shells without holes (Kornicker and Armstrong, 1959), whereas in other situations, the reverse occurs (Lever and others, 1961). Therefore a possible factor not previously considered in the separation of left and right valves would be a preference by drilling organisms of one valve over the other.

TABLE 5. *Comparison of number of* Dinocardium robustum *valves deposited on Mustang Island beach in concave up position with number deposited in concave down position*

Month	Year	No. valves in concave up position	No. valves in concave down position	Ratio of concave down to concave up valves: Left Valves	Right Valves	All Valves
March	1959	120	34	0.2	0.5	0.3
April	1959	47	14	0.4	0.2	0.3
May	1959	59	33	0.8	0.4	0.6
June	1959	33	60	0.6	3.4	1.8
July	1959	54	72	1.2	1.5	1.3
Aug.	1959	25	90	3.4	3.7	3.6
Sept.	1959	40	81	1.7	2.5	2.0
Oct.	1959	60	70	1.1	1.2	1.2
Nov.	1959	68	52	0.9	0.7	0.8
Dec.	1959	23	98	5.8	3.1	4.2
Jan.	1960	61	114	1.4	2.6	1.9
Feb.	1960	33	125	2.0	4.2	3.8
March	1960	34	74	2.2	2.2	2.2

In order to test this possibility in the present study the number of drilled left and right valves in a subsample of 1,871 valves were compared. Drilled holes were present in 125 left and 101 right valves, showing that the drilling organism (probably the snail *Natica polynices*) attacks through either valve. Therefore, it is concluded that the drilling of holes in valves of *D. robustum* has no major effect on the distribution of opposing valves.

Although no preference was apparent for left or right valves by drilling organisms, a preference is shown for small valves. Valves with lengths less than 49.5 mm contained a higher percentage of borings than larger valves (fig. 6). This relationship is reflected in the average length of drilled valves being smaller than the average length of undrilled shells in monthly collections (table 6). It is apparent from this that if valves should be sorted on a beach according to size, a higher percentage of drilled valves would be more likely to occur among the fraction containing small shells.

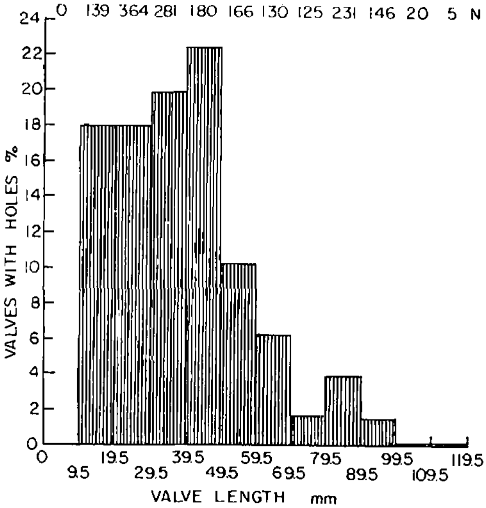

FIG. 6.—Histogram showing the percentage of *Dinocardium robustum* valves drilled by a boring organism as a function of valve length. Number of valves in each size class is given above each bar. Valves were collected from January 1959 through March 1960.

THE USE OF DISSOCIATED VALVES IN DETERMINING SOURCE

Boucot and others (1958, p. 332) state "Asymmetric mirror-image shells, as mentioned previously, will tend to diverge dextrally and sinistrally from the direction of the current. If the rate of disarticulation is high, so that the shells disarticulate almost instantaneously, then the angular divergence of the bulk of the original sample would be initiated at once. By contouring the frequency of right and left valves and drawing lines through the elongate directions of greatest frequency, one should obtain an intersection corresponding to the source bed. The bisectrix of the angle between the lines would be parallel to the direction of the current that moved the shells." Although the present authors are completely in agreement with the theoretical probability of the above statement, the data collected in the present study indicates that in nature, the mechanisms of shell transportation are too complex to permit application of the suggested method. The periodic collections of transported shells on Mustang Island beach sometimes contained almost equal numbers of opposing valves whereas at other times one valve was greatly in excess of the opposing valve. There is no indication that in water where sufficient currents exist to transport shells, a less complex situation prevails.

TABLE 6.—*Comparison of mean length of snail drilled and undrilled* Dinocardium robustum *shells in collections from Mustang Island, Texas*

Month-Year	*D. robustum* valves drilled by snails, %	Mean length mm.	
		Drilled	Undrilled
Jan. 1959	6	49.0	66.9
Feb. 1959	12	51.0	63.8
March 1959	7	55.9	81.5
April 1959	19	25.5	44.9
May 1959	17	37.1	73.4
June 1959	10	41.6	78.4
July 1959	13	27.3	32.8
Aug. 1959	8	24.0	24.0
Sept. 1959	8	21.0	21.8
Oct. 1959	11	39.0	48.7
Nov. 1959	19	33.9	34.4
Dec. 1959	24	28.6	40.2
Jan. 1960	22	42.7	70.4
Feb. 1960	4	76.8	91.2
March 1960	16	44.6	55.7

TABLE 7.—*Comparison of percent of four types of categories of size-frequency distribution found in 200 samples of fossil animals and shells of* Dinocardium robustum *from Mustang Island*

Category of Distribution	200 samples of fossil animals[a]—approx. percent	25 samples of *Dinocardium robustum* shells from Mustang Island—approx. percent
Roughly bell-shaped	75	25
Highly skewed	10	44
Bi- or polymodal	10	25
Highly irregular	5	6

[a] Data from Olson (1957, table 1).

SIZE-FREQUENCY DISTRIBUTION

A paleontologist working with fossil shells is often confronted with the problem of determining whether the shells under study are from animals that lived where the shells are found, or whether they have been transported after death of the animal. Several paleontologists (e.g., Percival, 1944; Boucot, 1953; Olson, 1957; Rigby, 1958; Johnson, 1960) have considered the meaning and use of size-frequency distribution of fossil shells.

Olson examined the size-frequency curves of 200 samples of fossil animals and approximated the percent that fell into four shape categories. The percentage noted by Olson for each category is compared with the percentage in the shell collections from Mustang Island in table 7. The shells collected on Mustang Island have in common the fact that they were transported from where they lived. The fossil collections examined by Dr. Olson were dominantly bell-shaped, whereas many collections from Mustang Island were strongly skewed. The presence of all categories in collections of beach shells, which are known to be transported, suggests that the size-frequency distribution of fossil shells may be of little use in interpreting the history of the original population (fig. 7). This supports conclusions of Olson (1957) and Boucot (1953, p. 31).

The many highly skewed size-frequency distributions in the beach collections were somewhat unexpected, as sorting is generally thought to result in a dominance of bell-shaped size-frequency distributions. It is also of interest that many beach samples had a size-frequency distribution similar to that observed for living populations, i.e. a predominance of small shells (see Percival, 1944).

SUMMARY AND CONCLUSIONS

Statistical treatment of collections of *Dinocardium robustum* valves from Mustang Island beach, Texas, obtained during December 1958 to August 1960, indicated that the difference in opposing valves considered *in toto* was significant at the 0.05 level of probability. No relationship was apparent between the occurrence of significant differences in the number of opposing valves and season. The absence of this relationship may be due to the occurrence of considerable variation in current direction each month in the collecting area, or may be the result of the samples not being sufficiently closely spaced.

The average length of left and right valves were similar in each collection indicating that observed numerical excesses of one valve over the opposing valve were not the result of differences in weight, ornamentation, or projections between opposing valves. About the same total number of left and right valves were collected from the Mustang Island beach indicating that one valve is not materially more resistant to destruction than the opposing one and, therefore, the observed distribution of opposing valves was not due to differences in fragility of opposing valves.

A relationship exists between average valve length in collections and the percentage of excess valves, with the number of excess valves being significant only in collections having an average valve length greater than 69.5 mm. This relationship is thought to indicate that environmental conditions conducive to the separation of opposing valves is also conducive to the deposition of large valves upon a beach. It is tentatively suggested that a high energy surf tends to separate opposing valves, whereas, a low energy surf does not. The overturning of valves in the surf during their transport inland may play an important part in the separation of opposing valves, but under-

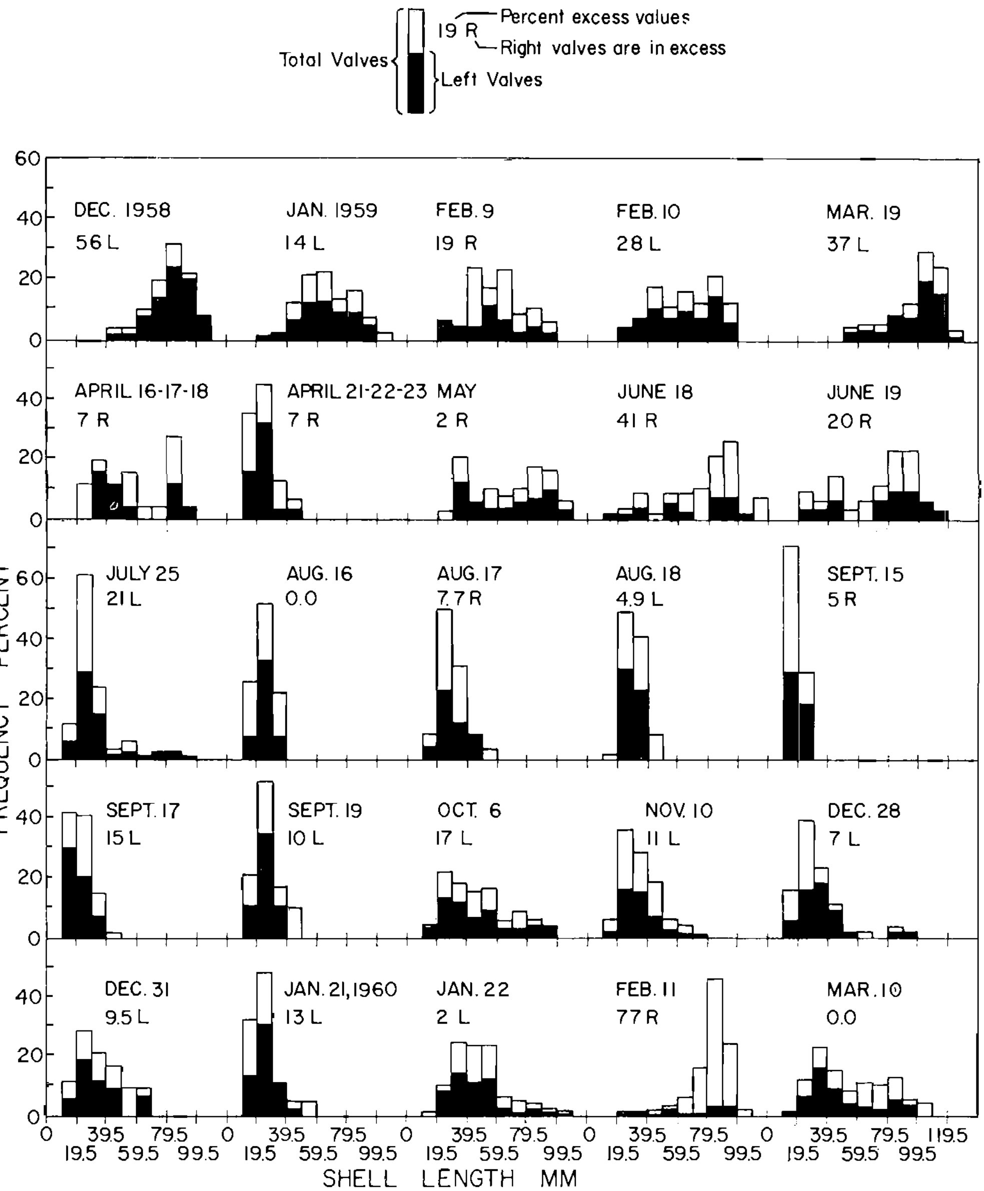

FIG. 7.—Histograms showing size-frequency distribution of valve length in collections of *Dinocardium robustum* from Mustang Island, Texas. The percentage of left valves in each size class is shown by a filling-in of the lower part of each bar.

standing of the mechanisms involved requires further study.

Boring organisms attacked both left and right valves in almost equal numbers so that the presence of a hole in some valves and not others had no major effect on the distribution of opposing valves. However, small valves contained a greater percentage of borings than large valves. Therefore, when shells are sorted according to size, more drilled valves may occur in the fraction containing the smaller shells.

The presence on Mustang Island of accumulations of shells containing almost equal numbers of opposing valves as well as accumulations containing significant inequalities in numbers of opposing valves suggests that the use of the relative number of left and right valves in assemblages of fossil shells to indicate shell source might not be feasible.

The size-frequency distributions of valves in the collections were quite variable. Many were strongly skewed and resembled the population structures of living populations. The considerable variation in the size-frequency distribution of valves known to have been transported indicates that size-frequency distribution is of limited use in interpreting the history of fossil assemblages.

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