# BRACHIOPOD LIFE ASSEMBLAGES FROM THE MARLSTONE ROCK-BED OF LEICESTERSHIRE

*by* A. HALLAM

ABSTRACT. Clusters of brachiopods in the Marlstone Rock-bed of Leicestershire are interpreted as life assemblages. It is tentatively suggested that at least three successive annual broods may be present. The colonies came to a sudden end, probably through burial by sediment.

THE Marlstone Rock-bed of the Middle Lias is well known for the richness and variety of its fauna, most notably brachiopods (Ager 1956). A striking feature of the Marlstone in the Midlands is the common occurrence of brachiopods in discrete and often tightly packed clusters of beautifully preserved shells. The present study of some of these clusters in Leicestershire follows on an earlier tentative inference (Hallam 1955) that they represent true colonial associations.

The Marlstone in the Midlands consists predominantly of oolitic ironstone, more specifically a calcitic, sideritic chamosite oolite (Whitehead *et al.* 1952) but in parts of Leicestershire and south Lincolnshire the lower few feet are made up of calcareous sandstone. It is generally accepted that the oolite was deposited in conditions of strong current action in a warm, shallow sea enriched in iron.

Fossils are distributed in the ironstone as follows:

(1) *Brachiopod clusters*. These consist of small clusters of closely packed brachiopods exhibiting wide size variation and random orientation. Disarticulation is slight and almost all the shells have their interiors filled with coarsely crystalline calcite. Signs of disturbance by currents are slight. Details of the location of some of these clusters or 'nests' in Leicestershire are given in Hallam (1955). In the rail cutting near Tilton is a 1-foot band composed of brachiopods (band A) about 2½ feet above the base of the Marlstone. This has been formed by the lateral coalescence of clusters of *Tetrarhynchia tetrahedra* and *Lobothyris punctata* (J. Sowerby). These clusters form the subject of the next two sections.

(2) *Disturbed shell bands*. These consist mainly of pelecypods, brachiopods, and belemnites. The first two groups are mostly disarticulated, especially the pelecypods. The interiors of articulated brachiopod shells are often filled with sediment; broken and crushed shells are common. Separated valves are usually oriented parallel to the bedding, e.g. band B near Tilton (Hallam 1955). The bands are usually less than an inch thick and are rarely traceable for more than a few hundred feet. Brachiopod clusters may grade into bands.

(3) *Scattered fossils*. Crinoids, an important component of the rock, are always disarticulated into small ossicles. These ossicles commonly occur as lenses and may mark out current bedding. A wide variety of other fossils occur as scattered shells.

## DESCRIPTION OF THE BRACHIOPOD CLUSTERS

Samples of several brachiopod clusters, containing the species *Tetrarhynchia tetrahedra* and *Lobothyris punctata* (J. Sowerby), were collected from two quarries in the neigh-

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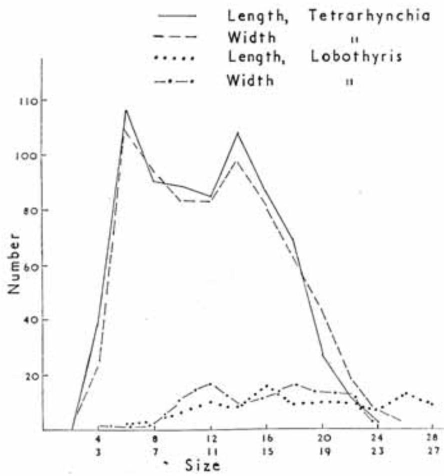
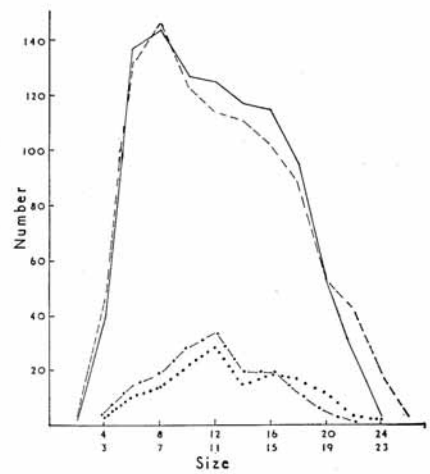
bourhood of Branston in north-east Leicestershire (N.G. 814295 and 806288), a particularly favourable locality. Clusters are commonest near the base of the ironstone but they are not confined to any one level. They tend to be subspherical or ellipsoidal in shape, with the long axis parallel to the bedding. They range in size up to 50 cm. in width and 15 cm. in height. The shells are almost all infilled with crystalline calcite and separate valves are rare. Distortion in shape is fairly common but fracture rare. No variation in shell size is readily discernible in different parts of the clusters. The clusters




Text-fig. 1. Sample 1 from Branston.



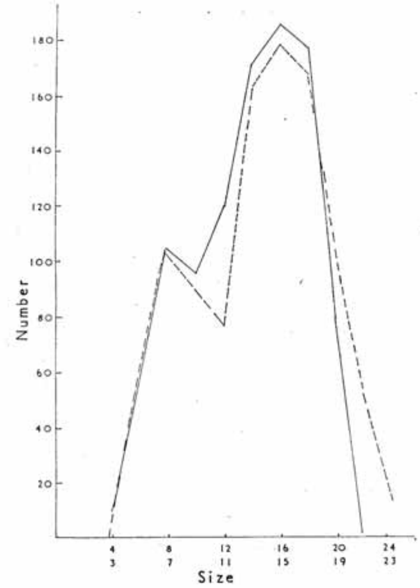

TEXT-FIG. 2. Sample 2 from Branston.

TEXT-FIGS. 1–6. Length and width frequency diagrams of samples of brachiopod clusters from Branston, Leicestershire. The key is given in text-fig. 1.

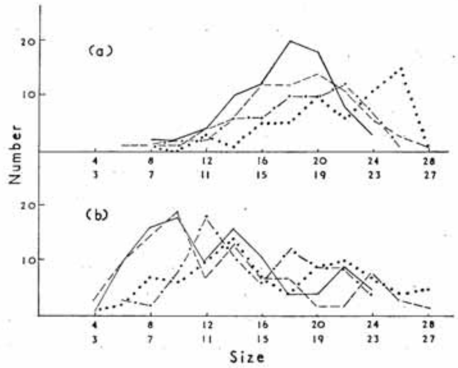
are isolated in much less fossiliferous rock containing scattered brachiopods and belemnites, sometimes concentrated into thin bands. The lithology throughout seems uniform. As the rock matrix is hard it was found impossible to collect complete clusters —indeed, a cluster is only visible if part has been removed by quarrying. The assumption is made that the samples collected are representative of complete clusters.

An attempt was made to extract all the brachiopods from the rock samples. This was effected by thorough mechanical breakdown, which is facilitated a little by immersing material in hot, concentrated evaporating solutions of $Na_2SO_4$ (no conventional chemical technique can be applied as the shells are composed of $CaCO_3$). Because of the hardness of the matrix some of the larger specimens were fractured during the process but with care the fragments could be fitted together, so that the number actually lost is very small. Particular care was taken to collect small specimens and the number missed below a length of 4 mm. is probably only small so that if anything there is a slight bias in collecting towards small size. In this way over 4,000 brachiopods were obtained.

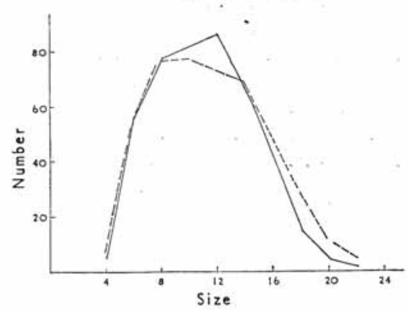
Size-frequency graphs of samples from seven different nests were plotted and are reproduced in text-figs. 1 to 6. Both length and width were measured and plotted to



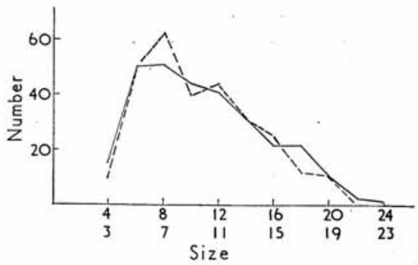

TEXT-FIG. 3. Sample 3 from Branston. For key see text-fig. 1.




TEXT-FIG. 4. (*a*) Sample 4 and (*b*) sample 5 from Branston.




TEXT-FIG. 5. Sample 6 from Branston. For key see text-fig. 1.




TEXT-FIG. 6. Sample 7 from Branston.

give a reliable index of size. It will be seen from the figures that the shape of the size-frequency curves is closely similar for both measurements.

Measurement was made in millimetres but in order to obtain a clearer picture of the broad features of the size frequency distributions and reduce the risk of incorporating accidental variations, the measurements were grouped together in pairs of millimetres in two ways, 3–4, 5–6, &c., and 4–5, 6–7, &c. Both sets give closely similar curves, so only one is illustrated.

It will be observed that in the Branston clusters *T. tetrahedra* is much commoner than *L. punctata*, which may be completely absent. There is no danger of confusing the two species even with the smallest specimens. The wide size range and the high percentage of small specimens in the samples is striking. Considering for the moment only *Tetrarhynchia*, the curves of samples 1, 2, 6, and 7 are slightly left-skewed and 3 and 4 roughly symmetrical. Those of samples 1 and 3 are clearly bimodal, with peaks at $\frac{5}{8}$, $\frac{13}{14}$, $\frac{7}{8}$, and $\frac{15}{16}$ respectively. The results for samples 4 and 5 are less reliable because of the much smaller number of specimens. They came from volumes of rock similar to the others but the percentage of small specimens is much lower.

An interesting feature is the rarity of specimens of length less than 5 mm.; $5\frac{1}{2}$ per cent. is the maximum in any sample for the $\frac{3}{4}$ mm. grade. No specimens of *Tetrarhynchia* of less than 3 mm. and *Lobothyris* of less than 5 mm. were discovered. This can be attributed to collection failure only to a limited degree, since the rock matrix was carefully scrutinized for such material.

## INTERPRETATION

There is strong evidence in favour of the clusters being genuine life assemblages (in the sense of Boucot 1953).

(1) There are few signs of physical disturbance of the shells.

(2) There is a wide size range in the shells, not suggestive of sorting by currents.

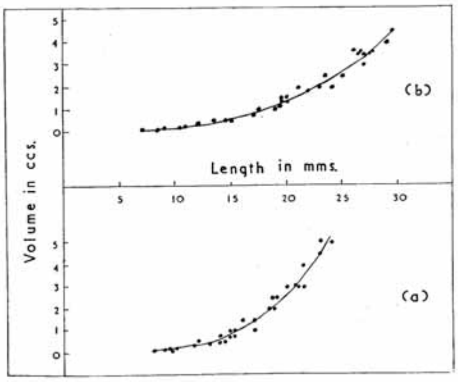
(3) The clusters are not random samples of the Marlstone fauna. It is highly exceptional for them to contain any fossils besides brachiopods.

(4) It is inherently improbable that clusters of brachiopods would be swept together by bottom currents. The evidence of the disturbed shell bands suggests rather the reverse.

(5) In three cases out of four, there is a pronounced lack of coincidence in the shape of the size-frequency curves for *Tetrarhynchia* and *Lobothyris* in the same cluster (text-figs. 1, 2, and 4). There is no reason to expect similarity if the fossils represent original living associations, whereas if the shells had been sorted to any extent after death they would tend to be grouped according to size regardless of biological differences. Variation in volume is the most important factor controlling the possible distribution of shells by currents (the more subtle factors of weight and shape, which are not readily measurable, may be disregarded in a rough analysis). Therefore, to test the supposition that the differences in the curves reflect genuine differences of volume, a volume/length curve was plotted for a number of specimens of *Tetrarhynchia* and *Lobothyris* from the samples (text-fig. 7). The most pronounced differences occur in sample 1. The two peaks in the *Tetrarhynchia* curve correspond to volumes of about 0·10 and 0·50 c.c., while the *Lobothyris* curve has a low mode at 0·65 c.c. While 57 per cent. of the *Tetrarhynchia* specimens have a volume less than 0·35 c.c. only 29 per cent. of the *Lobothyris* specimens fall in this range. The shapes of the two curves differ markedly also in sample 2, the mode for *Tetrarhynchia* being at about 0·10 c.c. and that for *Lobothyris* at about 0·25 c.c. Data for the much smaller samples 4 and 5 are naturally less reliable but at least in the case of sample 4 there appears to be an appreciable difference. Not only do the shapes of the curves differ but the mode for *Tetrarhynchia* (*c.* 1·7 c.c.) is less than that for *Lobothyris* (*c.* 2·8 c.c.). There is therefore justification for maintaining that differences in the shapes of the curves reflect genuine differences in the size distributions of *Tetrarhynchia* and *Lobothyris* from the same samples.

It follows from acceptance of the clusters as life assemblages that *Tetrarhynchia* and *Lobothyris* lived in intimate association.

The general shapes of the size-frequency curves may now be considered further. Boucot (1953) suggested that life and death assemblages may be distinguishable on the basis of size-frequency curves, the former tending to have strongly left-skewed distributions with the right-hand portion concave upwards, the latter having normal or gaussian distributions. The curves in text-figs. 1 to 6 do not correspond closely to either pattern. The reason is not far to seek. It is apparent from the work of Olson (1957) that fossil assemblages may approximate to theoretical predictions only if the factor of annual




TEXT-FIG. 7. Volume/length relationships in samples of (*a*) *Tetrarhynchia* and (*b*) *Lobothyris*.

broods and population fluctuations can be rendered negligible. But this is only possible if specimens are collected from beds deposited in a space of time considerably greater than a few years, in which case the chance of a genuine life assemblage being preserved and accurately sampled is slight. This is a serious defect of the technique Boucot proposed and one must endorse Olson's view that other criteria should be sought, as in the present work.

If, then, it may be accepted that the irregular character of the curves in text-figs. 1 to 6 is due to the influence of successive broods, there exists the possibility of recognizing annual groups in the populations. The only relevant published work on living brachiopods known to the author is that of Percival (1944). However, Dr. M. J. S. Rudwick has recently made a similar study of living brachiopod populations in New Zealand and obtained results much different from those of Percival. He has kindly offered the following remarks:

'The size distribution of my samples of *Terebratella inconspicua* is markedly two-peaked, in striking contrast to Percival's sample, which shows no trace of a peak of large shells. At all the localities I have seen, living populations are conspicuous for their high proportion of large and mature individuals. Percival's sample was, I believe, highly abnormal in this respect, probably because it was collected from such a small area of stones. Owing to the very patchy distribution of the shells, 2·3 square decimetres is far too small an area to ensure a representative sample of the population. I can only infer that the small stones from which his sample came happened to be occupied by a very dense patch of shells from the most recent spatfall, and did not include any of the patches of the large and mature individuals that comprise the bulk of the population. My samples were collected from areas of boulder-surface more than ten times Percival's area, yet even so there are individual differences between them that suggest that even they are not accurately representative, though much more so than Percival's.'

Dr. Rudwick believes that the troughs between the two peaks in his samples do not necessarily represent the interval between successive broods but could be due to the local failure of intervening broods.

In the case of *Tetrarhynchia*, the two peaks in samples 1 and 3 are probably reliable in view of the large number of specimens involved and the technique applied of grouping measurements in pairs of mms. It is interesting to note that the spacings of the peaks, $\frac{5}{6}$ and $\frac{13}{14}$ mm. in sample 1 and $\frac{7}{8}$ and $\frac{15}{16}$ mm. in sample 3, are identical, suggesting that they may reflect separate broods of slightly different ages. The uniformity and small amount of the spacing between the peaks suggests that we may indeed be dealing with successive broods. Bearing this in mind, the main features of the other large sample (2) could be accounted for by the presence of large first- and second-year broods with modes at $\frac{7}{8}$ and $\frac{15}{16}$, as in sample 3. The slight shallowing of the right-hand end of the curves in samples 1, 2, 3, 6, and 7 could be due to the presence of a few specimens of a third-year age group. Recognition of such a group is bound to be more difficult both because of the relatively small number of forms which would survive to the third year and because of a slowing down of growth.

If the assumption that annual groups are normally distributed is correct (Olson 1957) the possibility exists of separating different broods in a given sample. Unfortunately, one would have to work from the steep left-hand part of the curve and this may be the least reliable. In view of this and the number of uncontrollable variables involved, statistical analysis would be likely to give valid results only with a far greater number of samples. The evidence seems good enough, however, to allow the tentative suggestion that the clusters sampled are composed of at least three successive annual broods, but in view of Dr. Rudwick's remarks, confirmation will have to await the results of a much greater quantity of work on living brachiopod populations.

The absence of specimens of length less than 3 mm. and 5 mm. in *Tetrarhynchia* and *Lobothyris* respectively may be due to predation. It is questionable whether the rarity of small specimens in sample 4 is due to their selective removal by currents.

Recognition of the clusters as colonial associations poses an interesting problem. It is apparent from the work of Menard and Boucot (1951) that brachiopod shells filled with water are moved by currents much more readily than coarse sand. The critical velocity for effecting such movement is very low, no greater indeed than that of natural currents operating at a depth of more than 1,000 fathoms in the Pacific Ocean. But the sedimentary evidence for the Marlstone in general strongly suggests the operation of powerful bottom currents.

Presumably the colonies grew in periods of comparative quiescence. Yet as even weak currents could have sufficed to disperse shells after the pedicles had decayed, one is forced to the conclusion that the living colonies were killed by a sudden change of environment and preserved within the sediment as discrete clusters. Bearing in mind the nature of the Marlstone environment as deduced from the sedimentary evidence, it is quite probable that they were overwhelmed by the movement of sediment on the sea bottom. If growth were allowed to continue for long enough, the clusters would tend to spread over the sea floor and eventually coalesce. This appears to have happened in at least one case, that of band A near Tilton, which was mentioned earlier.

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A. HALLAM
Grant Institute of Geology,
King's Buildings,
Edinburgh, 9

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