THE BIOMETRICAL ANALYSIS OF FOSSIL POPULATIONS

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ABSTRACT—The organisms which are fossilized are only a fair sample of the living population, under very special circumstances. The bias in other cases is considered. In fossils such as many molluscs where the earliest formed parts of the shell are preserved, it has been possible in living forms to measure the intensity of natural selection by comparing these parts in juvenile individuals and survivors. The same could be done with fossil populations.

A NON-PALAEONTOLOGIST who is asked to contribute to a palaeontological journal can say but little that is new. But one who had studied populations of living plants and animals can comment on certain aspects of palaeontology. A group of fossils is not usually a representative sample of the once living population. But a bone bed may sometimes contain a representative sample. Here we may hope to find the skeletons of a whole herd of mammals overwhelmed by a sandstorm or an eruption, or a large number of fish killed simultaneously by a change of salinity.

Generally the fossils found are those of animals at the age when they died from more normal causes, after allowance is made for the fact that usually, though not always, the skeletons or shells of smaller animals are less well preserved than those of larger ones of the same species. To make matters clear, what do we expect to find if we dig up a Christian or Muslim cemetery ? If we dug up an English urban cemetery of the 18th century, perhaps half the burials were of young children whose skeletons would, however, be poorly preserved. Many of the adults had died fairly young, for the age distribution of deaths was similar to that in many Indian cities today. Only a few had survived to old age. But if we studied a very modern English cemetery, the majority of skeletons would be of people over 60 years of age. Almost all would have lost some teeth. Many would show senile changes in the joints. Further, neither cemetery would contain the bones of those who were killed as soldiers fighting abroad, drowned at sea, judicially executed, and so on. Burial may, of course, be highly selective. Thus in India, Hindus are not buried except by a rare accident. However, I think that fossilization is, on the whole, even more selective. Molluscs killed by such predators as Hybodonts are at best represented by fragments. Those killed by predators such as starfish may be represented by complete shells, and so on.

A palaeontologist comparing these two sets of human skeletons from the 18th century and the modern age would perhaps conclude that the second sample represented a population in the last stages of "racial senility" when various degenerative changes were occurring. In fact palaeontologists have described such populations. The most notorious case is that of the oysters assigned to the genus *Gryphaea*. The gradual increase in the coiling of their shells culminated in forms which apparently could hardly open their shells at all. This may have been the cause of their extinction. But we can also conclude, if we find a population most of whose members reached this highly coiled condition, that they were so well adapted to their environment that most of them lived long enough to die from a "natural" death, that is to say a death from slowly operating physiological causes, rather than a "sudden" death due to predation, acute infection, cold, burial in mud, or other possible causes. In a number of mammalian groups, for example the Dinocerata, Brontotheria, and so on, a great development of horns preceded extinction. We can at least conclude that most of the animals whose skeletons are found, lived long enough to grow large horns.

Most palaeontologists probably believe that natural selection played at least some part in the process of evolution. But they would regard it as impossible to obtain any estimate of the intensity of natural selection in an extinct species. It is in fact possible. But first I must say a little about the operation of natural selection as we can observe it today. No doubt evolutionary changes in the sizes and shapes of hard parts of species living today are occurring, and a part at least of these changes is due to the operation of natural selection in the Darwinian sense of survival.

But evolution is such a slow process that it would be very hard to detect such a change even in a molluscan population. Let me describe the kind of selection which can be detected. Karn and Penrose (1951) recorded the weights of 13,730 London babies at birth and found which of them lived to four weeks old. They found that the mean weight of those which survived was about 1% above that of the total, but the variance of the survivors was no less than 13% smaller. The babies which were much lighter or heavier than the average had less chance of survival than those near it. The slight increase of average weight was due to the fact that a number of the light babies were premature. Rendel (1943) found just the same for ducks' eggs. Those whose weight was near the average had the best chance of hatching.

This kind of natural selection, which weeds out extremes, is very general. In such a case one can measure the intensity of selection for weight at birth very easily. Roughly speaking $1\frac{1}{2}$% of the babies near the optimal weight of 8 lbs. died, but $4\frac{1}{2}$% of all babies died. If they had all weighed between $7\frac{1}{2}$ and $8\frac{1}{2}$ lbs., only $1\frac{1}{2}$% would have died. The extra death rate of 3% represents the intensity of natural selection for weight over this short part of the life cycle.

I have shown (Haldane, 1953) how this kind of natural selection can be measured even where there is no information about death rates. In many molluscs the parts of the shell laid down in early life are preserved as the shell grows, and may be preserved with very little wear and tear. Weldon (1901) measured a shape parameter in 100 young members of a population of the gastropod *Clausilia laminata* and in the corresponding parts of 100 fully grown ones, that is to say in the apical portions of their shells, which they had formed in early life. He found that the young parts of the shell were less variable in the old snails. But the mean values did not differ. This means that death had weeded out those which diverged most from the average. If the selection had operated in one direction it could always be argued that the animals which died had been weakened by starvation or otherwise, and produced, for example, too thin shells. But if it is as dangerous to depart from the mean in one direction as the other, this argument cannot be used.

Weldon did not estimate the intensity of natural selection for the character in question. I have shown how to do so, but the formulae given, and still more the proof of them, involve statistical estimation, and would be out of place in this Journal until they have been applied to palaeontological material. Suffice it to say that Weldon's data show an intensity of natural selection of about 10%.

A palaeontologist could proceed as follows. Suppose, from the same horizon, we have a sample of 100 *complete* ammonites which have died after attaining a diameter of 5 cm. but before reaching one of 20 cm., and also a sample all of which have reached a diameter of 20 cm. or more, the following counts and measurements could be made on each of them :

1. Number of ribs in first complete turn inside diameter of 5 cm.
2. Number of sutures in first complete turn inside diameter of 5 cm.
3. Thickness at point where diameter reaches 5 cm.
4. Total angular distance between diameters of 1 and 5 cm.

These are only examples, and probably not the best possible. As for statistical methods India possesses one of the world's great schools of statistics, and it would be impertinent for me to make recommendations.

For gastropods similar measurements could be made in some species. Weldon's technique involved the destruction of the shells. In Lamellibranchs with well-marked growth lines one could measure such characters as maximal length along the line whose minimum distance from the umbo is 1 cm. The most favourable material might be a genus such as *Perna* with a very pronounced form where several shape parameters could be measured. Brachiopods could clearly be examined in the same way.

On the other hand echinoderms, for example, are unsuited for such work, since the plates, like vertebrate bones, undergo some remodelling during ontogeny. Foraminifera, which are available in very large numbers, and which can be ground down to examine sections, might be very favourable material.

When a few hundred fossil populations have been examined by such methods as these, it will be possible to answer certain questions, of which I give a few examples.

1. Is it often found that the mean of some measurable character in survivors differs from that of juveniles ? If so, does this change point in the direction in which this species or genus was evolving ? For example during a period when the complexity of suture lines was increasing in Ammonites, were the suture lines on an average more complex in the juvenile parts of individuals which grew large than in those which died young ? I should not expect that such an effect would often be observable, owing to the slowness of evolution.

2. Is stabilizing selection, that is to say selection against extremes, without much effect on the mean, generally found, or is it found for some characters and not for others ?

3. If stabilizing selection is (as I suspect) common, was it more intense in stable species or in rapidly evolving ones ? One can suggest arguments for either alternative.

I want to suggest that biometrical palaeontology has perhaps so far been rather narrow, concerned rather with problems of taxonomy than with those of evolution, and that any Indian palaeontologist who has a thousand or so specimens of a molluscan species from a given horizon can make an important contribution to the study of evolution.

It will, of course, be necessary to rule out certain possible causes of bias. One of these is the tendency, in large collections, to include an unduly high proportion of aberrant individuals, while keeping only the best preserved or least damaged specimens whose form and size are most typical. Such a bias would certainly operate on a series of specimens chosen for a museum. It should be completely absent in material collected by the worker who is subsequently making the measurements.

The validity of any conclusions based on the study of a sample depends in the most complicated and often unexpected manner on the precise details of the method by which the sample was obtained. Professor Mahalanobis and his colleagues have made this very clear in the case of economic data. The kind of bias to be expected will vary from one case to another. It is clear for example that thick-shelled molluscs will stand a better chance of preservation than thin-shelled members of the same species. A selection in favour of thick shells has occurred after death, and we can hardly hope to find evidence of such a selection during life.

However, such biasses will be more obvious to a palaeontologist than to a statistician, and I venture to hope that some of my Indian colleagues may lead the way in applying the methods which I have outlined here.

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