# Studies on structural variation in the common European earwig (forficula auricularia Linn)

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# Studies on Structural Variation in
# the Common European Earwig
# (*Forficula auricularia* Linn.)

by

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# Abstract

From Scarborough in the south to the most northerly site, Berwick-on-Tweed, a series of samples of earwigs were collected in the years 1966, 1967 and 1968. Several parts of the anatomy of the earwigs collected were measured to gain overall information about the variability of this species spatially and from year to year. The results of this investigation may be summarised as follows: there was no evidence from the measurements taken, that the male Earwig is polymorphic in any respect except in the size distribution of the cerci. This polymorphism is restricted to the lengths of the cerci: no evidence was found to show that the lateral axes of the male cerci were polymodally distributed in any sample. Other findings indicated that the occurrence of the high male at the same place, was variable in different years. There was evidence that the earwigs collected in the south were larger than those in the north, and the populations contained proportionately more high males. The female earwigs were shown to be significantly larger than the males in almost all respects except in the cerci which are also dimorphic in shape.

Comparisons were made between the Farne Islands' populations of earwigs and those sampled on the mainland. The Farne Islands' earwigs are remarkably different from the mainland populations being much larger on average and containing far more high males.

Other work included the development of techniques to permit the objective separation of the populations of males into the separate morphs. Studies of the variation in shape of the cerci indicated the presence of three morphs of the male and two morphs of the female.

## Contents

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## General Introduction

Even before the concept of the species was first derived explicitly and applied to groups of different animals, it was a commonplace of experience, that in the living world there were many examples of groups of individual animals which were more similar to each other than any of them were to other animals. This practice of classifying different events into types is of great importance, and was first considered in detail by the Greeks. Aristotle, in particular, made a close study of the problem of the Universal, an ideal manifestation of a class of events, and considered the reality of the Universal in metaphysical terms. Indeed, the term species is derived directly from Aristotelian philosophy and in many cases the use of the species concept reflects precisely the use of the term Universal in the writings of the mediaeval scholastic philosophers.

The hierarchy of Universals, a concept which illustrates some of the paradoxes inherent in the notion of the Universal itself, corresponds in many ways to the hierarchy of taxa used in the classification of animals and plants, making use of their varying degrees of similarity. The species concept is in some ways a nominalist solution to the problem the Universal ( Russell 1946 ).

As all individual events differ from each other to a greater or lesser extent, so do all animals, and the problem of dividing animals or events into groups can admit of no really satisfactory solution. The concept of the species, from the viewpoint of expediency, neglecting for the meantime the philosophical validity of the notion, is a useful tool which allows the systematic organization of discovered data about individual animals. It becomes necessary therefore, if some classification of animals into a smaller number of groups than there are individuals, is to be derived, to classify differences between animals. Since the term animal itself implies underlying similarities between individuals belonging to the particular class of events, and since all animals are more or less different it is necessary to divide such differences into two classes: those that are relevant to the purpose of classification, and those that are not. In other words, the differences which necessitate the division of animals into more than one group, but into fewer groups than there are individuals become relevant, while those which would necessitate the division of the individuals into as many groups as there are individuals must be considered to be irrelevant.

This separation in a pragmatic fashion is fairly simple in terms of the species taxon, a group which may be limited in ways other than simple anatomical and physiological similarities among individuals, but the division of the higher taxa, or rather the assignment of individual groups to the higher taxa, is carried out despite the asseverations of taxonomists to the contrary, in an arbitrary fashion; there is simply no other way to do it.

From an implicit acceptance of the concept of relevant and irrelevant differences the whole edifice of taxonomy has developed. Unfortunately, students of the different types of animals have not necessarily agreed on which differences are relevant and for this reason not only is the animal kingdom classified in an arbitrary fashion but it is also classified inconsistently.

The refinement of this concept of classification leads to a subtle change in attitude; where originally there was a sample of animals all different but displaying many similarities, there is a species of animals which contains individuals. The species concept is therefore a two-edged sword; it allows on one hand the systematic classification of animals into groups, but on the other hand it fosters the conception of animals not as varying individuals, but, and it is a misleading metathesis, as members of groups. In this way the individual animal has come to be seen as the species writ small, and that the population of animals is nothing more than a series of ciphers, indistinguishable from each other, and simply supplying the biomass which makes up the real entity, the species.

This view of the individual as the species is particularly prevalent in much of the taxonomic work carried out even today and certainly many earlier workers have made this unwarranted assumption. Similarly many morphological studies ostensibly of particular species have been carried out on only a few individuals.

This error persists even now despite the fact that the unifying key to the whole of theoretical biology, the theory of evolution by natural selection, demands that the individuals which together make up a species must vary, and that such variability is of literally vital importance to the survival of the species in the long term.

Recently however, some work has been carried out on the importance of individual variability in populations of animals. Coulson ( 1968 ), working on the breeding biology of the colonial cliff nesting gull, the kittiwake (*Rissa tridactyla*) has shown that individuals which nest in the centre of a colony, in the most optimal sites, are of better "quality" than those nesting in less favourable areas at the edges of the colony. The birds which nest at the centre tend to be significantly larger, and tend to be significantly more successful in reproductive terms, than those that nest at the edges. Similarly Jenkins ( 1963 ) has shown that the size of the territory held by the Red Grouse (*Lagopus* l. scoticus) is closely related to the endocrine status of the individual male, and that by varying the titre of testosterone in the blood the size of the territory held could be varied. The males which were most aggressive held the largest territories and by increasing the titre of testosterone in the blood stream of individual males their agression was increased and they expanded their territories at the expense of less aggressive neighbours. Since the survival of the individual grouse depends on the ability to hold a territory, individual variation is of considerable importance to the continued existence of the population. Cain and Sheppard ( 1952 ), working on populations of the mollusc Cepaea nemoralis have determined the significance of the polymorphism observed in this species in ecological terms. Thus in ecology there is a growing awareness of the fact that the animals, which together comprise a species, vary and that this variation plays an important part in the life of the species itself. In many of the fields of biology the fact that individual animals vary is still neglected, and very many statement are made about species of animals, when observations have been derived from extremely small samples of individuals.

The problem of identifying and describing in detail the variability of certain external features within a population of insects is considered in this thesis. The characters described are morphological, and the animals which have been used in this study were collected from various populations of the common European Earwig (Forficula auricularia Linn). This species more than most has attracted considerable interest owing to the pronounced variability in form of the terminal cerci.

The terminal cerci protrude from the distal end of the abdomen and in the adult earwig are sexually polymorphic. The cerci of the female Earwig are short and straightish organs: the inner edge which is slightly curved lies approximately parallel to the long axis of the abdomen. At the proximal end of the cercus the base is fairly broad and the outer edge, which is again slightly curved, converges towards the inner edge meeting it at the tip. The inner edge of the cercus is finely serrated. The cerci in the male earwigs exist in at least two distinct forms, the so-called low form and the high form. This nomenclature follows Bateson and Brindley ( 1892 ). The low form of the cercus is somewhat sickle-shaped, the base of the cercus corresponding to the handle of the sickle, the bow corresponding to the blade. In situ, on the abdomen, the low cerci together enclose a subcircular area. From the proximal end of the organ, corresponding to the end of the handle of the sickle, to the proximal end of the bow, the shaft of the cercus is heavily dentated, but there are no serrations on the inner edge corresponding to those found on the cerci of the females.

The second form of the male cercus, the high form, which is almost always rarer in the population than the low form, is much longer than the longest cerci of either of the two types described previously, and indeed members of this type of cerci may be twice the length of low types. The cercus is similar in form to the low male cercus with the exception that it is considerably and disproportionately elongated. As a result of this extension the space enclosed by the cerci in situ on the abdomen is subelliptical instead of subcircular; in all other particulars the high form is similar, superficially at least, to the low form. These descriptions are necessarily vague; the curves and shapes of these organs are studied in detail in a later section.

Throughout this study the terms polymorphism and dimorphism are used to describe morphological phenomena only; this use of these terms represents a return to the generalized meanings of these words, and in no way implies a necessary corresponding genetic difference between individuals of the different types. The purpose of the studies described in this thesis has been to attempt to elucidate the manifestation of structural variability within known populations over a given period. For until such an investigation has surveyed the varying nature of the individual animals, no study of any depth can be begun to discover the interrelationships between individuals within the species.

## Variability in Size of the Earwig

### Introduction

While Bateson and Brindley ( 1892 ) were the first workers to state the facts about polymorphism in the Earwig in a modern fashion, the polymorphic forms of the earwig had been previously recognized, and had been classified variously as varieties of the species *Forficula auricularia* or as separate species of the same genus.

During the nineteenth century there was considerable interest in systematic entomology and indeed the history of the taxonomic relations of the species within the genus *Forficula* during this period is a testimony to the enthusiasm rather than the discretion of the early entomologists.

Linnaeus erected the species *Forficula auricularia* in 1758, and by 1802 Marsham had erected the species *Forficula neglecta*. This species was erected on the mistaken premise that the shape of the cerci of the female, which are sexually dimorphic characters in the species *Forficula auricularia*, indicated that the females belonged to a different species from the males. At the same time Marsham erected the species *Forficula media*, individuals of which were similar in all respects save one to the males of the species *Forficula auricularia*: this one difference was in the form of the terminal cerci. The cerci of individuals he assigned to the species Forficula media were larger and better developed than those of members of the species Forficula auricularia.

In 1835 Stephens erected the species Forficula borealis and Forficula forcipata: members of these species were also indistinguishable from males of the common earwig except by the differing development of their cerci: the individuals assigned to the species Forficula borealis had larger cerci than those placed by Marsham into Forficula media, and Forficula forcipata contained individuals with the largest cerci of all.

The major disadvantage of all this activity is the fact that there are no such readily recognizable corresponding differences in the form of the female cerci, and it was not until the time of Bateson, the late 19th Century, that the implications of this fact were realised. And even as lately as 1961 Ramamurthi comments that analogous errors were being made in the classification of the Indian Dermaptera.

Brindley ( 1892 ) was one of the first pioneers in the field of statistical biometrics, and towards the end of the nineteenth century there was the beginning of what was later to become considerable interest in biometrical studies. Following Brindley's work Giard ( 1894 ), was the first worker to try to explain the causes that lead to the development of the polymorphic forms of the earwig. He suggested in effect, that the high form was the normal expression of the genotype, and that the low form was produced by exhaustion of some individuals by parasitic gregarine protozoa.

Smith ( 1905 ) indicated that the polymorphism of some crustacea can be explained as variation in proportions due to varying functional states of the gonads, and suggested that the dimorphism of the males was produced in an analogous fashion.

Semenov Tian-Shansky ( 1910 ) suggested that the origin of the polymorphic forms of the Earwig is no more than the result of fortuitous accidents happening to individuals in the population and which cause the modifications of the cercus form for example, by physical injury and by shortage or superabundance of food. As a result, he considered the dimorphic individuals to be randomly deviant in form.

Wheeler ( 1910 ) combining elements from both Giard's work and Smith's proposed that the modification in the development of the cerci which leads to the dimorphism of the male cercus was due to parasitic castration in the high males.

During the period between the publication of Bateson's paper on the subject ( 1892 ) and the middle of the 1920's there had been much speculation concerning the causes and significance of the dimorphism observed in the cerci of the male Earwig. Many of these speculations were supported only by the most meagre experimental work. It was not until Diakonov ( 1925 ) investigated the problem that critical work on the causes of polymorphism was carried out, and the distribution of the polymorphic forms investigated.

Diakonov ( 1925 ) investigated the causes of polymorphism in the Earwig and although his career was cut short by his untimely death he showed that some of the speculations of earlier workers were untrue.

He showed that Giard's suggestion that the low polymorph was produced by exhaustion due to infection of the males by parasitic gregarines was at least an oversimplification of the facts, and probably erroneous altogether. He states, "The presence of Gregarines (Clepsidrina ovata) in the intestine has no influence on the size of the forcipes or on the state of the testes." It is, of course, possible that the infection, to cause sufficient damage, might have to occur at a particular period in the life of the nymph, and if this is the case, then Diakonov's statement is hardly more conclusive than Giard's. Diakonov did however show that those individuals infected with the larvae of the parasitic tachinid fly Digonochaeta setipennis Fall. always developed cerci of the low form.

Diakonov suggested the explanation that had previously been implicitly accepted by many investigators of the problem of the origin of the dimorphism of the Earwig. He supported this suggestion with evidence from observations made in the field of the occurrence of the high male in relation to the availability and quality of the food supply exploited by the Earwigs.

He showed that under unfavourable conditions a smaller proportion of the male population was made up of high males than was found in the same population in a more optimal feeding situation. Diakonov was unable to make clear though, whether this fact was due to a differential mortality of the nymphs which were destined to become high males, or whether an unfavourable environment prevented the manifestation within many of the nymphs of the potentially high form of the cercus. Diakonov did not restrict his study entirely to the dimensions and development of the cercus, and he discovered one of the most puzzling aspects of structural variation in the Earwig; the dimensions of all external characters measured in populations of male Earwigs, with the single exception of the cerci, were normally distributed.

After Diakonov's death, Huxley ( 1927 ), in one of a series of papers on the subject of heterogonic growth, made use of Diakonov's data and ttried to show that the dimorphism of the male cerci was a special case of the law of heterogonic growth, and suggested again that the cause of this dimorphism must be some kind of physiological switch mechanism, such that on one side of the threshold the low form is developed, while if the threshold is exceeded the high form is developed.

Przibram ( 1927 ) supported Huxley's main conclusions but introduced the suggestion that the origin of the polymorphic forms bears some relation to the possibility that certain individuals in the population reached maturity after a varying number of larval ecdyses, and that such individuals if present would tend to vary in fixed proportion according to the number of moults required to achieve sexual maturity. This ingenious explanation of the causes of polymorphism has unfortunately never been experimentally corroborated; there appears to be no evidence of varying numbers of larval instars, although there has in the past been some disagreement as to the actual number of larval instars in this species.

Kuhl ( 1928 ) investigated the occurrence of polymorphism in detail and came to several surprising conclusions. He made the point, and it is very relevant, that any biometrical investigation on a population should be carried out on samples collected in a rigorously random fashion, to exclude the unconscious selection of individuals, and to avoid the concommitant biassing of samples. His work was based on samples containing prodigious numbers of individuals, and he suggested that, on the evidence he had obtained, in all cases of dimorphism described in the Earwig, the dimorphism first demonstrated by Bateson and Brindley, as well as almost all subsequent workers was an artifact, produced by careless sampling techniques. He stated that the frequency distributions of the lengths of the cerci from the samples of males he collected, were not bimodal but were, on the contrary, skewed normal distributions; the skew being accounted for by a continuous sequence of intermediate forms which made impossible any valid separation of the cerci into the polymorphic types. Kuhl suggested that instead of the two classes into which male Earwigs had been separated, a classification of four separate and independent types reflected the real situation more precisely. In this classification the width of the bases of the cerci were taken into account, as well as the correlated presence or absence of a gap between the distal tips of the paired cerci when they were fully closed. The statistical reasoning behind this classification is not at all clear.

Kuhl studied the development of the cercus and presented evidence that the final form the cercus took was controlled by pressure of haemolymph, during the period immediately following the last larval ecdysis. The cerci are inflated by the pressure of the haemolymph which is developed by the rapid inspiration of air immediately after the ecdysis and before the cuticle begins to tan. The tanning process is sufficiently advanced after only ten minutes to prevent further inflation of the cerci. Kuhl suggested that if the conditions were not optimal during the critical ten minutes, and as a result the individual was not capable of inflating the cerci to their fullest extent in this short period, the cerci would remain small.

Why the effects of the pressure distend only the cerci, in this way, without producing corresponding changes in the external parts is not explained, and as a result this explanation is necessarily incomplete.

Lhoste ( 1943 ) studied polymorphism in the Earwig, and attempted to raise broods of eggs in the laboratory, in the hope of discovering and isolating the environmental factors which control the occurrence of the high male form. Other investigators including Beall ( 1932 ), and Singh ( 1967 ) have also made this approach to the problem. In all cases they failed to produce any of the high form of the male and indeed I know of no report of success in this experiment in the literature.

Since 1943 there has been little research to investigate the occurrence and causes of polymorphism in the Earwig, despite the fact that a survey of the literature makes it clear that there are many questions still only imperfectly answered.

The problem of the nature of the frequency distribution of the lengths of the male cerci has not been investigated since Kuhl's study in 1928, and since then there has been considerable interest in the analysis of polymodal and other distributions. Buchanan-Wollaston and Hodgson ( 1929 ) published the first work in this field and since then several methods for the analysis of frequency distributions have been developed.

Harding ( 1949 ) realized the potential of making use of arithmetic probability paper for dividing polymodal distributions of biological data, and since then various methods have been derived to simplify the analysis of such distributions. Cassie ( 1954 ) combining the techniques of Buchanan-Wollaston with the graphical method of Harding, has produced a simple and elegant method for separating polymodal distributions into their component normal distributions, as well as providing a method for determining the theoretical form of truncated and skewed normal distributions.

Mathematical methods for this type of analysis have been devised by Preston ( 1953 ) and Tanaka ( 1962 ).

The frequency distributions of the dimensions of a mumber of external characters of the Earwig have been investigated making use of some of the techniques described above.

## Study Area

The samples of earwigs examined in this study were collected from a series of sites on the North-East coast of England. The coast was chosen because it proved fairly easy to collect large samples of animals in this region, despite the highly aggregated spatial distribution of the earwig. A number of towns on the coast between Scarborough in the south and Berwick in the north were chosen as bases and samples were collected from sites chosen at each site in 1966, 1967 and 1968. The sampling areas were chosen by applying three criteria; each site visited was between approximately ten and fifteen miles to the north of the adjacent southerly collecting area, earwigs were fairly abundant, and each site was accessible to public transport.

Table 1 lists the sampling sites, their national grid references, and their approximate latitudes and longitudes, and Plate 1 shows a map of the collection areas. In 1967 all areas were visited and sampled, but in 1966 it was possible to visit only four of them while in 1968, owing to circumstances beyond my control, it proved impossible to sample the populations at Whitby and Beal.

The collections themselves were carried out in rough meadows and little difficulty was found in collecting considerable numbers of animals. The scrub which grows in the shelter of sand-dunes is made up of a number of species of hollow stemmed umbellifers including Hemlock but these did not prove to yield very large numbers of Earwigs. The best source of animals was in the stems of Cow-parsley Heracleum sphondylium found growing on the sides of railway cuttings and embankments. Collections were made as far as possible in sight of the sea in areas which were as similar as was possible to find. In this way some differences due to such factors as differences in altitude were controlled.

A further reason for collecting the samples from the coast was due to the proximity of the Farne Islands, a group of basaltic islands in the North Sea, between 1½ to 5 miles off the coast of Northumberland at Seahouses. Populations of Earwigs on the Farne Islands are unique in Northern England owing to the presence of an unusually large proportion of the high male polymorph, and it was of interest to compare the populations on the Farne Islands with those collected on the mainland.

The main problem encountered in collecting the samples of Earwigs on which this study is based was due to the spatial aggregation of this species. It was possible to search for long periods without finding sufficient animals for even a small sample, while in other circumstances it was possible to collect a thousand or more in an hour. This difficulty of finding the animals accounts for the variations in the sample sizes from the different areas.

Despite the proximity of adjacent sampling sites, the evidence derived from the study of size variation suggests that even within the small range over which the samples were collected, the variation in population from one area to another is considerable.

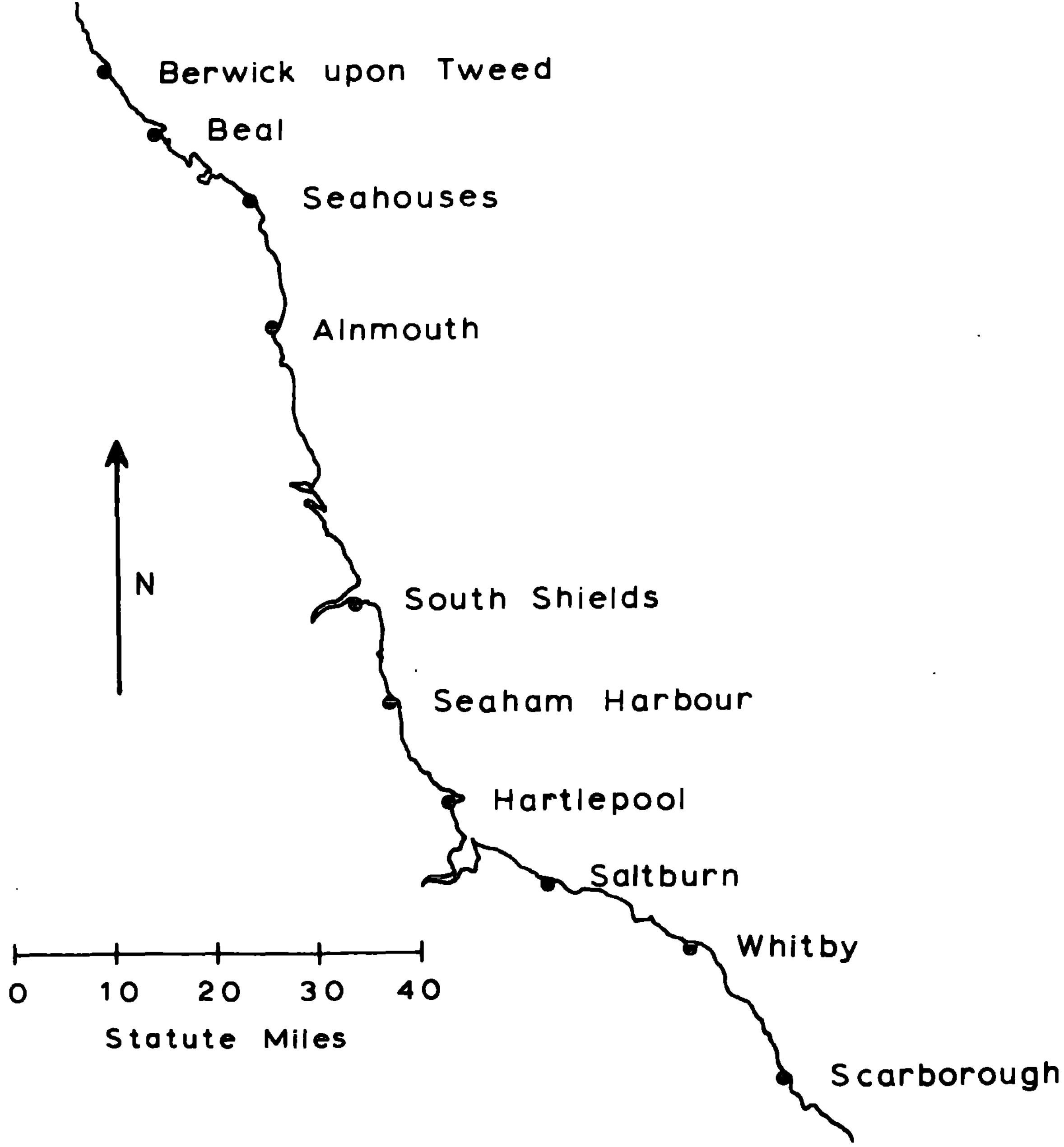
## Sampling Sites for Earwigs in N. E. England

Table 1

| | Grid Ref. | Lat. | Long. |
|---|---|---|---|
| Scarborough | TA 051893 | 54 -17.5 N | 0 -22.5 W |
| Whitby | NZ 908113 | 54 -29.3 N | 0 -35.6 W |
| Saltburn | NZ 658215 | 54 -35.7 N | 0 -59.0 W |
| Hartlepool | NZ 497358 | 54 -42.8 N | 1 -13.2 W |
| Seaham | NZ 431498 | 54 -50.5 N | 1 -19.7 W |
| South Shields | NZ 375675 | 54 -55.0 N | 1 -25.6 W |
| Alnmouth | NU 252108 | 55 -23.3 N | 1 -36.4 W |
| Seahouses | NU 223322 | 55 -35.0 N | 1 -38.2 W |
| Beal | NU 081425 | 55 -40.5N | 1 -52.8 W |
| Berwick | NT 982532 | 55 -46.4 N | 2 -1.8 W |

Plate 1. Map of the Coast of North-Eastern England Showing the Collection Sites on the Mainland.

## Map of North-East Coast of England Showing Relative Positions of Sampling Sites.

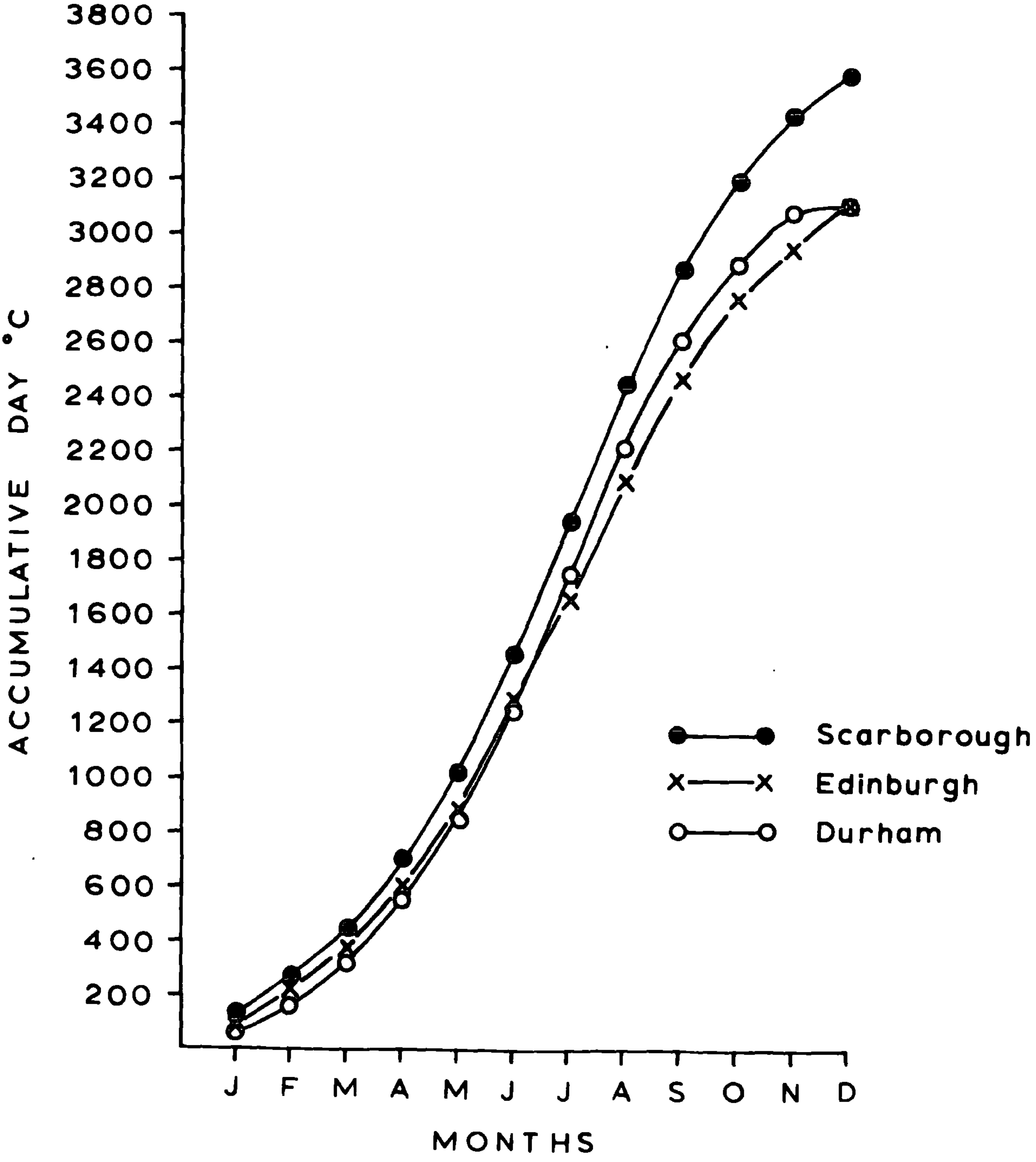


## - The Climate of the Study Area. -

Detailed information about the climate of the study area is difficult to obtain, owing to the paucity of recording stations in the area. The curves indicating the temperature are constructed from the averages of the mean daily temperature of the nearest stations, month by month, and are based on the published averages of the meteorological office, for the period 1931 to 1960. In order to indicate the heat gained by the environment throughout the year, the monthly mean temperatures have been converted to day degrees: in other words the effect of the temperature has been converted into temporal terms in order to facilitate the direct comparison of the temperature of the limits of the sampling area. The day degrees are plotted accumulatively to further facilitate comparison. Since the earwig life cycle takes almost a full year to be completed, in terms of temperature, the important measure of the temperature of the environment must be the total number of day degrees the environment has received. There are considerable differences between the total temperature received in these terms, between the most southerly collecting area, and the most northerly. Even allowing for the fact that Edinburgh is a fair distance to the north of Berwick the evidence suggests that the more southerly sampling areas are considerably warmer than those in the north. Plate 2 shows the curves of accumulated day degrees, plotted against months in which the temperatures were recorded.

Plate 2. Mean Annual Temperatures of Scarborough, Durham, and Edinburgh Plotted as Accumulated Day Degrees.

DAY DEGREES PLOTTED AS ACCUMULATIVE FREQUENCY CURVES AGAINST DATE



## Collection Methods

It is well known that the Earwig exhibits thigmotactic behaviour (Weyrauch 1929 and Lhoste 1944), placing itself in any container so that a large part of the body is closely apposed to the substratum. Lhoste indeed described in some detail "l'éffet de groupe" which arises as a consequence of this type of behaviour; the individuals often pack tightly into restricted hollows and can form groups of several hundred animals. The reasons for this behaviour are not clearly understood but grouping in this way may be expected to produce marked changes in the microclimate in which the group is formed. Lhoste comments that the activity of the individuals in the centre of the group is reduced, the metabolic rates are reduced even to the point of individuals in the centre of the group dying. Lhoste does not however, make clear whether death is caused by the mechanical consequences of crowding, for example by the restriction of available oxygen to members in the centre of the group, or whether there is some endogenous factor in the physiology of the individual earwig that reacts unfavourably to crowding at densities beyond a given threshold.

This crowding behaviour allows the collection of large numbers of Earwigs over short periods of time. One of the environments where this type of activity is often manifested, as was previously mentioned, is in the stems of certain umbelliferous plants. The Earwigs appear to play quite a prominent part in the ecology of the animal community which exploits this environment. It is from such stems that the majority of the samples of Earwigs were collected.

When the growth of a given year has finished, and the woody stems have stood for the following year, until the autumn, the Earwigs are readily collected by opening the stems and shaking the contents into some container and by transferring the Earwigs into 90% alcohol to fix them. Because all Earwigs which were found were collected ahd fixed there was no danger of selecting individuals and no risk of biassing the sample.

## Methods

The variability in size of the various parts considered was measured using samples of 100 Earwigs, or as many individuals as were available if there were fewer than 100. The samples were collected from the sampling sites and using the methods described above. The sample size of 100 individuals was a compromise between the minimum number acceptable for the analysis, and the amount of time available for the measurement of the animals.

The parameters that were measured on each individual animal were as follows:-

(i) The total body length from the anterior edge of the pronotum to the posterior end of the abdomen.

(ii) The gross length of the line joining the distal tip of the cercus to the inflection in the outer edge at the base of the cercus, parallel to the long axis of the body.

(iii) The length of the chord which joins the distal tip of the cercus to the proximal end of the bow at the inner edge of the organ.

(iv) The maximum length of the line produced at right-angles to the chord joining the proximal and distal ends of the bow along its inner edge, and extending to cut the outer edge of the cercus.

(v) The width of the cercus base from the point of inflection of the outer edge of the cercus, the point at which the cercus protrudes from the abdomen, at right-angles to the long axis of the body, to the line parallel to the long axis of the body that intersects the innermost extension of the base of the cercus.

(vi) The length of the pronotum from the anterior edge to the posterior edge measured along the midline of the body.

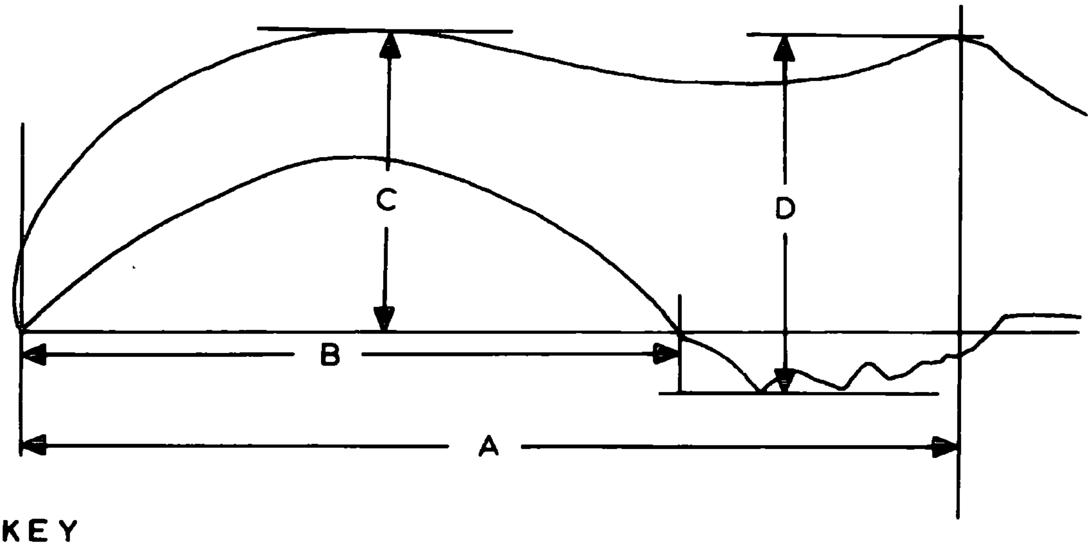
(vii) The width of the cercus at its widest point.

(viii) The minimum distance between the eyes on the head of the insect, from the inner edge of the faceted region of one eye to the inner edge of the faceted region of the other.

See Plates 3 and 4.

This sequence of measurements was taken for several reasons: owing to the primary importance of the variation in the cerci particular care was taken to record the maximum relevant information about this organ. This information was recorded in terms of widths, measured at right-angles to the long axis of the body, and lengths, parallel to the midline; this method supplied information about the growth of the cerci in these two directions only. No attempt was made to record the radii of curvature of the organ in this part of the study for two reasons; the curves of the inner and outer edges of the cerci are not simple, and any method making use of a micrometer eyepiece marked with concentric circles would lead to considerable inaccuracies of recording, and secondly because

Plate 3. Figure Showing the Measurements Derived from the Cercus of the Male Earwig.



**KEY**

A – Cercus length
B – Length of Cercus Bow
C – Width of Cercus Bow – Curvature Measure
D – Width of Cercus Base – Width

Plate 4. Figure Showing the Measurements Recorded from the Body of the Earwig.

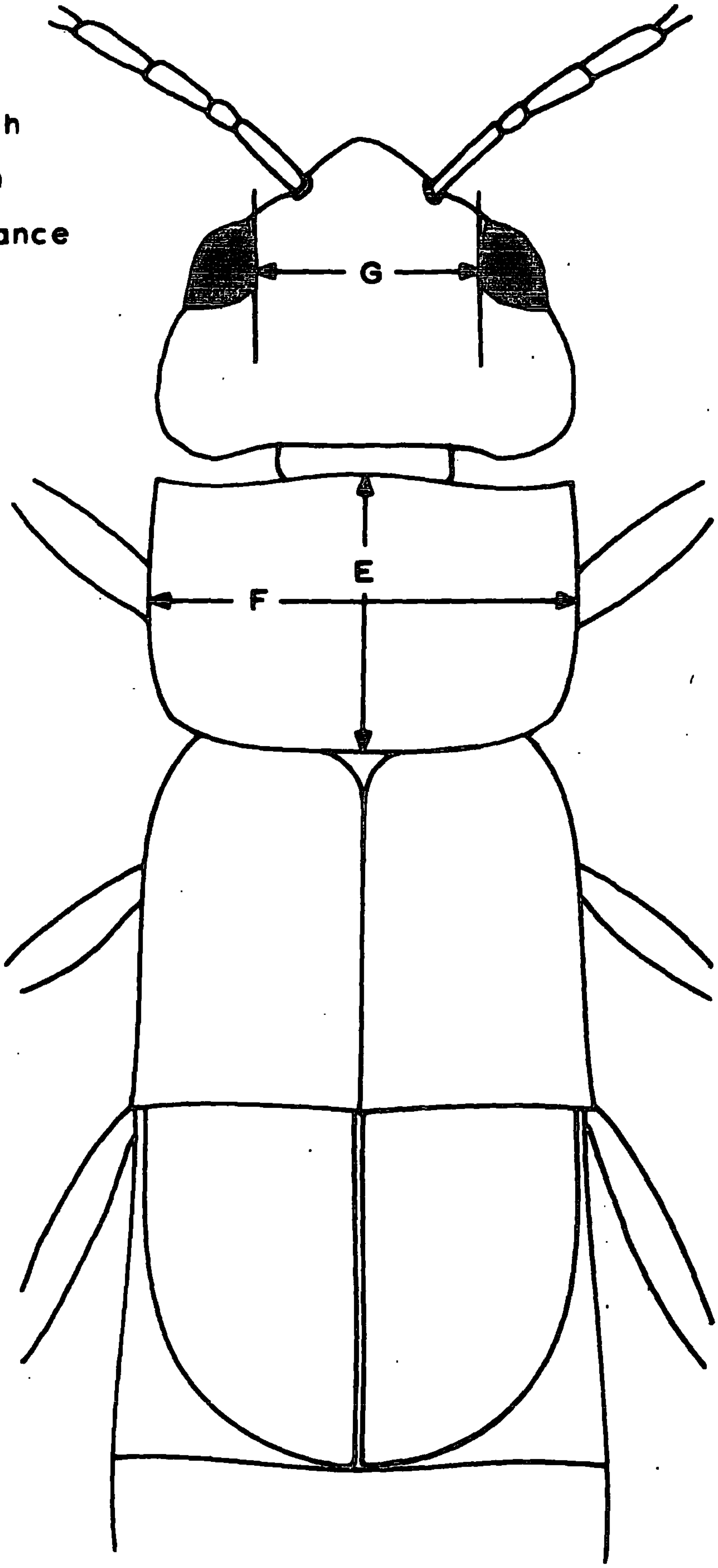
**KEY**

E - Pronotum length

F - Pronotum width

G - Interoptical distance

- head capsule



such data would necessarily be a combination of the effects of growth along both of the axes used as bases for measurement. In any case, the variation in the curves of the cerci is considered in detail in a later section which deals specifically with variation in shape.

The measurements of the other structures were made in order to obtain a clear picture of the variability of other normally distributed features of the earwig body, and to make comparisons between the variation of these parts and variations of the cerci.

The body length was measured as an index of the general size of the individual, but this measurement was of only marginal usefulness owing to the considerable variability caused by distortions in fixation: the muscles of the abdomen often become very distorted, and as a consequence the abdomina of individuals were themselves often twisted. In such cases it was difficult to make even an approximate estimate of the overall length of the body of these individuals. To avoid this problem the pronotum, a very heavily sclerotised platelike structure, was used as an index of the variability of the body, as it did not distort sensibly as a result of even prolonged immersion in alcohol.

The interoptic distance was measured to record the variability of the head-capsule, which owing to its speroidal shape presents difficulties in measurement. This measurement was recorded particularly to investigate the possibility that some individuals of the population reached maturity after varying numbers of larval instars according by making use of the variation accounted for by Dyar ( 1890 ).

The measurements were carried out on subsamples of approximately 100 individuals selected from the samples obtained at all sites visited in a given year. When the sample was too small to yield 100 individuals the complete sample of all the animals of the appropriate sex was measured.

One of the difficulties encountered in the subsampling routine was due to the fact that not all the animals collected were alive at the time of fixation. Within the stems from which the animals were collected there were always a few individuals recently dead from natural causes. After a few hours the abdomina of the dead earwigs shrink considerably in length, unless they are kept in preservative, and consequently these animals introduce a bias into the sample. This bias is noticeable only in the frequency distributions of the total body length, the amount of shrinkage undergone by the hard parts being negligible. Nevertheless it was decided that such individuals should be excluded from the sample. With a little experience it becomes possible to recognize such individuals, both by their disproportionately short abdomina and by the fact that in comparison with individuals alive at the time of fixation, the cuticles of which were glossy, the cuticles of the recently dead individuals were very dull.

In almost all cases the newly dead individuals have been excluded and the absence of this bias can be demonstrated statistically.

The measurements were made using a micrometer eyepiece and a Watson "Zoom" Stereomicroscope. As far as possible the animal was kept intact in order to return if necessary to a particular samples if this was deemed necessary, and was laid in a dish, half filled with ballotine damped with 90% alcohol. The specimens were laid in a trough moulded in the wet ballotine, and care was taken to align them so that the measurements were taken in the horizontal plane. The damp ballotine could be moulded so as to align the specimens with great accuracy.

The sections which deal with the variation in shape and size of the various parameters of the Earwig body make no mention of the variation in the larval forms of the Earwig. The life history of the earwig is divided up into six phases; the pre-hatching phase when it is still in the egg, four larval instars, and the imago.

The larvae, in common with the rest of the Orthoptera resemble the adult form quite closely. The similarity increases with age, the last larval instar being far more similar to the adult than any of the earlier stadia. The similarities which can be observed between the adult forms and the larval forms are limited. In particular, the immature forms show no superficial sexual dimorphism, as well as lacking wings, and the cerci are short, delicate organs which are only lightly sclerotised, and in both sexes these organs are slightly curved. The larvae are not studied in detail in the following sections for the following reasons; above all, the larvae are difficult to collect, they distort violently in fixation, and finally, owing to a desire to culture the animals, I was unwilling to sacrifice many of those collected for straightforward biometrical studies.

The difficulties encountered in collecting adequate samples of the larvae were due to the circumstances in which earwigs overwinter. The female overwinters in a cavity in the soil, usually about five centimeters in diameter and between five to fifteen centimeters deep and it is here that she tends her eggs. As the earwigs are solitary animals at this phase in their lives, it is exceedingly difficult to discover adequate numbers of larvae by hand sorting. Since it is essential for the survival of the eggs and probably for the first instar larvae as well, that they are attended by a female, it was not possible to extract the larvae by any mechanical means. Nevertheless, with help, it proved possible to procure small samples of larval earwigs. Each year most were kept in the laboratory under controlled conditions but owing to difficulties encountered in the culturing techniques, it did not prove possible to keep a significant number alive to reach maturity. This culturing was attempted to clarify the role of environmental conditions in the development of the adult and in particular, to investigate the possibility of a genetic basis for the considerable variations in the mean sizes attained by samples of adult animals from different geographical areas.

Nevertheless, a few individuals were fixed, from the first three larval instars in an attempt to produce some biometrical information concerning the variability in size of these forms. The second and overwhelming difficulty encountered was in the fixation of the larvae. As mentioned previously, the larval cuticle is much less heavily sclerotised than the adult cuticle, and this difference is nowhere so clearly manifested as in the cuticle of the larval cerci: these organs distorted violently in the fixatives used. These included 70% ethyl alcohol, Bouin's solution, Petrunkevitch's solution, Duboscq Brazil solution and 90% alcohol. The delicate tissues of the larvae were distorted so violently, that even superficial scrutiny of the larvae indicated that the biometrical investigation would yield results of only dubious value.

Under other circumstances a study of the variation of the body size and the shapes of larval cerci would have been attempted. The techniques developed to study the variability in shape of the adult cerci are, as described in the section on shape variability, limited in their precision; indeed the study of the variation of the female cercus indicates the order of the limitations beyond which the methods so far developed cannot resolve. Even with the most sanguine hopes it appears doubtful whether the application of such techniques, without refinement to the variability in shape of the larval cerci would yield much positive evidence.

The delicacy of the cerci in the larval forms of the earwig precludes any of the functions described for the adults, and it may be that the cerci in the larvae are vestiges which attain their function, like the wings and the sexual organs in the adult.

Table 2 Body Measurements of Adult Male Earwigs collected from the coast of North-Eastern England in 1966

Body Measurements of Male 1966

All measurements in mms.

Based on sample sizes of 100 individuals

| | Body Length | | | Cercus Length | | |
|---|---|---|---|---|---|---|
| Sample Site | Mean | St.Dev. | St.Err | Mean | St.Dev. | St.Err. |
| Hartlepool | 9.829 | 0.881 | 0.088 | 3.396 | 0.410 | 0.041 |
| S. Shields | 10.729 | 0.861 | 0.100 | 3.241 | 0.254 | 0.030 |
| Alnmouth | 9.977 | 0.681 | 0.068 | 3.095 | 0.218 | 0.022 |
| Seahouses | 10.435 | 0.919 | 0.092 | 3.071 | 0.222 | 0.022 |

| | Length of Cercus Bow | | | Curvature | | |
|---|---|---|---|---|---|---|
| Sample Site | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Hartlepool | 2.212 | 0.309 | 0.031 | 1.170 | 0.121 | 0.012 |
| S. Shields | 2.139 | 0.168 | 0.020 | 1.212 | 0.099 | 0.012 |
| Alnmouth | 2.040 | 0.189 | 0.019 | 1.138 | 0.911 | 0.009 |
| Seahouses | 1.975 | 0.165 | 0.016 | 1.188 | 0.096 | 0.010 |

| | Cercus Width | | | Pronotum Length | | |
|---|---|---|---|---|---|---|
| Sample Site | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Hartlepool | 1.082 | 0.108 | 0.011 | 1.447 | 0.104 | 0.011 |
| S. Shields | 1.138 | 0.124 | 0.015 | 1.497 | 0.087 | 0.010 |
| Alnmouth | 1.044 | 0.097 | 0.009 | 1.378 | 0.114 | 0.012 |
| Seahouses | 1.106 | 0.121 | 0.012 | 1.417 | 0.112 | 0.011 |

| | Pronotum Width | | | Head Capsule | | |
|---|---|---|---|---|---|---|
| Sample Site | Mean | St. Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Hartlepool | 1.785 | 0.098 | 0.010 | 1.295 | 0.053 | 0.006 |
| S. Shields | 1.788 | 0.103 | 0.012 | 1.296 | 0.054 | 0.006 |
| Alnmouth | 1.717 | 0.092 | 0.009 | 1.281 | 0.061 | 0.006 |
| Seahouses | 1.783 | 0.092 | 0.009 | 1.310 | 0.067 | 0.007 |

Table 3 Body Measurements of Adult Male Earwigs collected from the coast of North-Eastern England in 1967

Body Measurements of Males 1967

All measurements in mms.

Based on sample sizes of 100 individuals

| Sample Site | Body Length | | | Cerci Length | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 10.964 | 0.895 | 0.091 | 3.188 | 0.200 | 0.020 |
| Whitby | 11.848 | 1.069 | 0.106 | 3.215 | 0.208 | 0.021 |
| Saltburn | 10.851 | 0.822 | 0.088 | 3.258 | 0.197 | 0.021 |
| Hartlepool | 10.944 | 0.9101 | 0.096 | 3.231 | 0.171 | 0.018 |
| Seaham | 10.692 | 0.925 | 0.095 | 3.242 | 0.207 | 0.021 |
| S. Shields | 10.953 | 1.026 | 0.105 | 3.336 | 0.266 | 0.027 |
| Alnmouth | 10.982 | 1.161 | 0.143 | 3.249 | 0.219 | 0.027 |
| Seahouses | 10.265 | 0.779 | 0.111 | 2.992 | 0.129 | 0.018 |
| Beal | 10.828 | 0.786 | 0.080 | 3.010 | 0.183 | 0.019 |
| Berwick | 10.867 | 1.020 | 0.132 | 3.040 | 0.187 | 0.024 |

| Sample Site | Length of Cercus Bow | | | Curvature | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 2.075 | 0.128 | 0.013 | 1.227 | 0.102 | 0.010 |
| Whitby | 2.107 | 0.148 | 0.015 | 1.247 | 0.104 | 0.010 |
| Saltburn | 2.151 | 0.169 | 0.018 | 1.222 | 0.107 | 0.012 |
| Hartlepool | 2.127 | 0.123 | 0.013 | 1.208 | 0.094 | 0.010 |
| Seaham | 2.115 | 0.164 | 0.017 | 1.214 | 0.105 | 0.011 |
| S. Shields | 2.173 | 0.190 | 0.019 | 1.218 | 0.101 | 0.010 |
| Alnmouth | 2.127 | 0.145 | 0.018 | 1.233 | 0.101 | 0.013 |
| Seahouses | 2.033 | 0.121 | 0.017 | 1.114 | 0.071 | 0.010 |
| Beal | 2.030 | 0.132 | 0.013 | 1.148 | 0.094 | 0.010 |
| Berwick | 2.003 | 0.128 | 0.017 | 1.147 | 0.097 | 0.013 |

Body Measurements of Males 1967 cont'd

All measurements in mms.

| Sample Site | Cercus Width | | | Pronotum Length | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err | Mean | St.Dev. | St.Err. |
| Scarborough | 1.097 | 0.099 | 0.010 | 1.571 | 0.079 | 0.008 |
| Whitby | 1.168 | 0.118 | 0.012 | 1.561 | 0.089 | 0.009 |
| Saltburn | 1.080 | 0.097 | 0.011 | 1.545 | 0.082 | 0.009 |
| Hartlepool | 1.099 | 0.096 | 0.010 | 1.569 | 0.089 | 0.010 |
| Seaham | 1.100 | 0.102 | 0.011 | 1.499 | 0.087 | 0.009 |
| S. Shields | 1.127 | 0.114 | 0.012 | 1.513 | 0.094 | 0.010 |
| Alnmouth | 1.147 | 0.138 | 0.017 | 1.514 | 0.110 | 0.014 |
| Seahouses | 1.035 | 0.096 | 0.014 | 1.482 | 0.067 | 0.010 |
| Beal | 1.068 | 0.096 | 0.010 | 1.484 | 0.075 | 0.008 |
| Berwick | 1.026 | 0.097 | 0.017 | 1.483 | 0.073 | 0.010 |

| Sample Site | Pronotum Width | | | Head Capsule | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 1.864 | 0.078 | 0.008 | 1.336 | 0.046 | 0.005 |
| Whitby | 1.852 | 0.099 | 0.010 | 1.330 | 0.059 | 0.006 |
| Saltburn | 1.785 | 0.080 | 0.009 | 1.305 | 0.051 | 0.006 |
| Hartlepool | 1.849 | 0.105 | 0.011 | 1.336 | 0.049 | 0.005 |
| Seaham | 1.778 | 0.087 | 0.009 | 1.303 | 0.058 | 0.006 |
| S. Shields | 1.811 | 0.110 | 0.011 | 1.323 | 0.064 | 0.007 |
| Alnmouth | 1.798 | 0.100 | 0.013 | 1.320 | 0.063 | 0.008 |
| Seahouses | 1.767 | 0.091 | 0.013 | 1.283 | 0.045 | 0.007 |
| Beal | 1.755 | 0.084 | 0.009 | 1.295 | 0.050 | 0.005 |
| Berwick | 1.757 | 0.086 | 0.011 | 1.285 | 0.045 | 0.006 |

Table 4 Body Measurements of Adult Male Earwigs collected from the Coast of North-Eastern England in 1968

Body Measurements of Males 1968

All measurements in mms.

Based on sample sizes of 100 individuals

| Sample Site | Body Length | | | Cercus Length | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err |
| Scarborough | 10.813 | 0.817 | 0.083 | 3.302 | 0.209 | 0.021 |
| Whitby | - | - | - | - | - | - |
| Saltburn | 10.146 | 0.686 | 0.071 | 3.240 | 0.182 | 0.019 |
| Hartlepool | 10.948 | 0.776 | 0.079 | 3.303 | 0.200 | 0.020 |
| Seaham | 11.015 | 0.927 | 0.097 | 3.309 | 0.155 | 0.016 |
| S. Shields | 11.351 | 0.994 | 0.099 | 3.381 | 0.240 | 0.024 |
| Alnmouth | 10.135 | 0.677 | 0.068 | 3.266 | 0.193 | 0.019 |
| Seahouses | 9.734 | 0.765 | 0.091 | 3.193 | 0.202 | 0.024 |
| Beal | - | - | - | - | - | - |
| Berwick | 9.492 | 0.790 | 0.079 | 3.137 | 0.189 | 0.019 |

| Sample Site | Length of Cercus Bow | | | Curvature | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 2.128 | 0.157 | 0.016 | 1.205 | 0.100 | 0.010 |
| Whitby | - | - | - | - | - | - |
| Saltburn | 2.139 | 0.142 | 0.015 | 1.180 | 0.094 | 0.010 |
| Hartlepool | 2.144 | 0.178 | 0.018 | 1.185 | 0.113 | 0.012 |
| Seaham | 2.155 | 0.117 | 0.012 | 1.175 | 0.100 | 0.010 |
| S. Shields | 2.206 | 0.171 | 0.017 | 1.205 | 0.123 | 0.012 |
| Alnmouth | 2.131 | 0.148 | 0.015 | 1.173 | 0.103 | 0.010 |
| Seahouses | 2.084 | 0.150 | 0.018 | 1.156 | 0.091 | 0.011 |
| Beal | - | - | - | - | - | - |
| Berwick | 2.054 | 0.147 | 0.015 | 1.128 | 0.101 | 0.010 |

Body Measurements of Males 1968 cont'd

All Measurements in mms.

| Sample Site | Cercus Width | | | Pronotum Length | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | Et.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 1.147 | 0.112 | 0.011 | 1.521 | 0.077 | 0.008 |
| Whitby | - | - | - | - | - | - |
| Saltburn | 1.109 | 0.099 | 0.010 | 1.492 | 0.074 | 0.007 |
| Hartlepool | 1.137 | 0.116 | 0.012 | 1.527 | 0.085 | 0.009 |
| Seaham | 1.079 | 0.111 | 0.011 | 1.489 | 0.079 | 0.008 |
| S. Shields | 1.118 | 0.123 | 0.012 | 1.516 | 0.093 | 0.009 |
| Alnmouth | 1.088 | 0.099 | 0.010 | 1.470 | 0.076 | 0.008 |
| Seahouses | 1.085 | 0.113 | 0.014 | 1.472 | 0.087 | 0.011 |
| Beal | - | - | - | - | - | - |
| Berwick | 1.072 | 0.109 | 0.011 | 1.448 | 0.095 | 0.010 |

| Sample Site | Pronotum Width | | | Head Capsule | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 1.853 | 0.090 | 0.009 | 1.320 | 0.053 | 0.005 |
| Whitby | - | - | - | - | - | - |
| Saltburn | 1.755 | 0.089 | 0.009 | 1.301 | 0.047 | 0.005 |
| Hartlepool | 1.819 | 0.094 | 0.009 | 1.312 | 0.049 | 0.005 |
| Seaham | 1.776 | 0.089 | 0.010 | 1.289 | 0.048 | 0.005 |
| S. Shields | 1.813 | 0.097 | 0.010 | 1.317 | 0.056 | 0.006 |
| Alnmouth | 1.757 | 0.093 | 0.009 | 1.295 | 0.053 | 0.005 |
| Seahouses | 1.788 | 0.094 | 0.012 | 1.305 | 0.053 | 0.007 |
| Beal | - | - | - | - | - | - |
| Berwick | 1.751 | 0.095 | 0.010 | 1.283 | 0.056 | 0.006 |

Table 5 Body Measurements of Adult Female Earwigs collected from the Coast of North-Eastern England in 1968

Body Measurements of Females 1968

All measurements in mms.

Based on sample sizes of 30 individuals

| Sample Site | Body Length | | | Cercus Length | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 11.240 | 0.694 | 0.127 | 3.097 | 0.159 | 0.029 |
| Saltburn | 11.090 | 0.722 | 0.132 | 3.140 | 0.155 | 0.028 |
| Hartlepool | 11.180 | 0.617 | 0.113 | 3.063 | 0.192 | 0.035 |
| Seaham | 11.700 | 0.863 | 0.158 | 3.170 | 0.210 | 0.038 |
| S. Shields | 11.467 | 0.949 | 0.173 | 3.127 | 0.195 | 0.036 |
| Alnmouth | 10.623 | 0.759 | 0.139 | 3.027 | 0.248 | 0.045 |
| Seahouses | 10.417 | 0.683 | 0.125 | 2.920 | 0.161 | 0.029 |
| Berwick | 10.097 | 0.781 | 0.143 | 2.943 | 0.174 | 0.032 |

| Sample Site | Cercus Width | | | Pronotum Length | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 0.876 | 0.050 | 0.009 | 1.612 | 0.0068 | 0.013 |
| Saltburn | 0.865 | 0.055 | 0.010 | 1.600 | 0.067 | 0.012 |
| Hartlepool | 0.897 | 0.056 | 0.010 | 1.612 | 0.074 | 0.014 |
| Seaham | 0.852 | 0.067 | 0.012 | 1.577 | 0.073 | 0.014 |
| S. Shields | 0.842 | 0.060 | 0.011 | 1.569 | 0.060 | 0.011 |
| Alnmouth | 0.855 | 0.055 | 0.010 | 1.549 | 0.067 | 0.012 |
| Seahouses | 0.844 | 0.099 | 0.009 | 1.547 | 0.070 | 0.013 |
| Berwick | 0.825 | 0.097 | 0.018 | 1.532 | 0.067 | 0.012 |

Body Measurements of Females 1968 cont'd

All measurements in mms.

| Sample Site | Pronotum Width | | | Head Capsule | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Scarborough | 1.900 | 0.072 | 0.013 | 1.367 | 0.044 | 0.008 |
| Saltburn | 1.860 | 0.093 | 0.017 | 1.354 | 0.042 | 0.008 |
| Hartlepool | 1.904 | 0.080 | 0.015 | 1.365 | 0.044 | 0.008 |
| Seaham | 1.889 | 0.107 | 0.020 | 1.357 | 0.054 | 0.010 |
| S. Shields | 1.859 | 0.070 | 0.013 | 1.350 | 0.037 | 0.007 |
| Alnmouth | 1.844 | 0.074 | 0.014 | 1.354 | 0.032 | 0.006 |
| Seahouses | 1.987 | 0.047 | 0.009 | 1.334 | 0.071 | 0.013 |
| Berwick | 1.824 | 0.077 | 0.013 | 1.325 | 0.047 | 0.009 |

Tables 2, 3, 4 and 5 summarise the results obtained from the measurements of the various body parts of the earwigs collected from the sampling sites in 1966, 1967 and 1968.

As these results form the basis of a large number of subsequent sections, the derivation of the statistics deserves some detailed description. The results are composites of two separate calculations. Concurring with Diakonov ( 1925 ) and other workers, it was found that with the exception of the bimodal distribution of those parameters of the cercus concerned with the length of this organ, each set of body measurements was closely approximate to a normal distribution. This fact was utilised in the calculation of the mean sizes of the body dimensions of all features except the lengths of the cerci, and of the cercal bows. With the exception of the last two measurements, therefore, where a mean and standard deviation is quoted, it is the mean of the particular body measurements for the entire sample of the given sex. The length of the cerci were measured and making use of the computer programme "APPROX" described in Appendix (ii), the high males were excluded from the sample, the mean cercus lengths of the remaining low males and the standard deviation of these measurements were calculated.

This approach was chosen for the following reason; by the inclusion of the normally distributed measurements of the high males, avoidable skew was not introduced into the distributions of the body measurements of the total male sample, and owing to the paucity of the high males in the mainland population, they were for statistical purposes treated as abberant members of the low male population only in terms of their cercal parameters and as indicated in the tests of normality applied in all particulars other than these they were normal low males.

The significance of the discovery that the head-capsule size as well as all the other body sizes were normally distributed within all samples of a given sex, is in the indication of the extreme improbability of the high form of the male being developed by the mechanism postulated by Przibram in 1927. He suggested that a varying number of larval instars in different individuals was the prime cause for the development of the two morphs of the male Earwig. It is extremely improbable that individuals undergoing differing numbers of ecdyses should all catch up with each other in such a way as to render the adults inseparable on statistical grounds other than the bimodal distribution of the cerci of the males. It might be argued that the paucity of the high males in the mainland samples precludes discovery of such morphological discontinuity: there is however, evidence derived from the populations of earwigs collected on the Farne Islands that there is no such discontinuity present in the distributions of the body dimensions of the male Earwig. These populations contain large numbers of high males, yet the distribution of, for example, the head capsule size, as indicated by the inter-optical distance, is closely approximate to the normal curve. This confirmatory evidence indicates the improbability that Przibram's hypothesis is valid.

## Variability in Size Related to Geographical Location

Before considering the differences in the means of the body dimensions of the samples of Earwigs collected from different areas, it was necessary to discover whether or not there were any significant differences in the sizes of the animals from a given sample when compared with the sizes of animals in other samples. The technique used to determine the significance of the observed differences between samples was the method known as the analysis of variance. Analysis in this way allows the partitioning of the variance of a population into two distinct components; the variance due to differences between individuals within all the members of a group of samples, and the variance due to differences between the individual samples. In the case of all samples being derived from a single population the variances partitioned in this way are approximately equal, and indeed in the ideal theoretical case the variances partitioned in this way, must by definition be equal.

The null hypothesis to be tested making use of this technique is, therefore, that all samples belong to the same population. Making use of the electronic computer, each set of measurements recorded of a given body dimension from all individuals in all samples collected in a given year was regarded as being a single population, while the measurements for the given body dimension taken from a single sample of Earwigs collected in the given year were considered to be a sample of the whole.

Treating the data in this way the variances within and between the samples were partitioned and by making use of Snedecor's "F" test the significance of the differences between the two component variances for each type of body measurement was calculated.

Table 6 Analysis of Variance Males 1966

Degrees of Freedom within the samples = 297

Degrees of Freedom between the samples = 3

| Measurement | Intrasample variance | Intersample variance | F | p |
|---|---|---|---|---|
| Body Length | 0.7019 | 9.9817 | 14.222 | 0.001 |
| Cercus Length | 0.0893 | 3.2986 | 36.956 | 0.001 |
| Length Cercus Bow | 0.0532 | 1.5826 | 29.721 | 0.001 |
| Cercus Curv. | 0.4367 | 0.2520 | 5.771 | 0.01 |
| Cercus Width | 0.0479 | 0.3967 | 8.278 | 0.001 |
| Pron. Length | 0.0485 | 0.4788 | 9.870 | 0.001 |
| Pron. Width | 0.0355 | 0.6913 | 19.448 | 0.001 |
| Head Capsule | 0.0148 | 0.0870 | 5.864 | 0.01 |

Males 1967

Degrees of Freedom within the samples = 827

Degrees of Freedom between the samples = 9

| Measurement | Intrasample variance | Intersample variance | F | p |
|---|---|---|---|---|
| Body Length | 0.8952 | 12.7077 | 14.196 | 0.001 |
| Cercus Length | 0.0411 | 1.0609 | 25.831 | 0.001 |
| Length Cercus Bow | 0.0220 | 0.2419 | 10.996 | 0.001 |
| Cercus Curv. | 0.0099 | 0.1382 | 14.270 | 0.001 |
| Cercus Width | 0.0446 | 0.6059 | 13.593 | 0.001 |
| Pron. Length | 0.0289 | 0.4367 | 15.111 | 0.001 |
| Pron. Width | 0.0342 | 0.5726 | 16.748 | 0.001 |
| Head Capsule | 0.0116 | 0.1222 | 10.538 | 0.001 |

Table 6 cont'd Males 1968

Degrees of Freedom within the Samples = 734

Degrees of Freedom between the samples = 7

| Measurement | Intrasample variance | Intersample variance | F | p |
|---|---|---|---|---|
| Body Length | 0.6503 | 40.4773 | 62.244 | 0.001 |
| Cercus Length | 0.0346 | 0.5022 | 14.509 | 0.001 |
| Length Cercus Bow | 0.0215 | 0.1803 | 8.372 | 0.001 |
| Cercus Curv. | 0.0102 | 0.0619 | 6.068 | 0.001 |
| Cercus Width | 0.0482 | 0.2948 | 6.116 | 0.001 |
| Pron. Length | 0.0272 | 0.3036 | 11.162 | 0.001 |
| Pron. Width | 0.0337 | 0.5168 | 15.335 | 0.001 |
| Head Capsule | 0.0107 | 0.0634 | 5.925 | 0.001 |

FeMales 1968

Degrees of Freedom within the Samples = 232

Degrees of Freedom between the Samples = 7

| Measurement | Intrasample variance | Intersample variance | F | p |
|---|---|---|---|---|
| Body Length | 0.5852 | 8.9985 | 15.378 | 0.001 |
| Cercus Length | 0.3566 | 0.2512 | 7.056 | 0.001 |
| Cercus Width | 0.0156 | 0.0542 | 3.474 | 0.01 |
| Pron. Length | 0.0185 | 0.1157 | 6.254 | 0.001 |
| Pron Width | 0.1350 | 0.1551 | 1.149 | 0.05 |
| Head Capsule | 0.0097 | 0.0252 | 2.598 | 0.05 |

## Results

The results of the analysis of variance displayed in Table 6 indicate that the probability that a particular set of measurements taken from a given sample of Earwigs, belonged to the same population as all the other samples of the same type of measurement was very small; usually the probability was less than 0.001, and in no cases was it greater than 0.1. The two exceptions where the variance ratios were not indicative of a significant difference between the samples were to be found in the population of females. There were far fewer females measured the sample size being 30 individuals, than there were males, sample sizes of around 100, and this fact may account partially for this discrepancy in the results. Nonetheless, the remaining four variance ratios, which do differ to a significant extent indicate that the samples of animals as a whole belong to different populations. These large variance ratios indicate the improbability that the samples are derived from the same population, and conversely imply that each sample was derived from a separate and different statistical population. In other words, the morphological characters of each of the samples differ so profoundly amongst each other that they appear to belong to different populations of animals. The causes for these differences reflect the combination of the genetic potentialities of the population from which each sample was derived, and the manifestation of such potentialities, which is to a large extent controlled by the environment. There is no way of separating these two factors by field observation, so the statement that the samples of earwigs, on the evidence of the disparate mean dimensions of the body, appear to belong to separate statistical populations in turn implies that they belong to separate morphological populations, i.e. earwigs from one area are a different size from the earwigs which occur in another.

This conclusion, that the Earwigs collected from the various sampling sites belong to different populations is not surprising when it is remembered that Earwigs are secretive animals which seldom, if ever fly. What is surprising is that the populations, all ten of them over such a short distance, approximately 110 miles, should be so distinct. This fact in itself indicates some of the dangers of generalizing widely from morphological information derived from samples of Earwigs collected in a given area.

Such generalized aspects of the growth of an individual as the size it attains at maturity, are profoundly affected by the environment, and since earwigs are poikilotherms the temperature in which they grow will be of importance in determining the rates of the chemical reactions involved in the maintenance of life. Since the rates of such reactions are greatly modified by even small changes in temperature it may be expected that the temperature in gross terms, of the environment, would be correlated in some way with the body sizes of the Earwigs collected from the particular environment, provided that the genetically determined potential size does not also vary significantly from place to place.

The temperature regime, for example, under which the Earwigs develop and live is composed of two components; the component due to the absolute differences in the environmental macroclimate and the alteration produced in this component by modifications of the microclimate due to the presence of the Earwigs themselves. Some changes of the microclimate due to the presence of Earwigs are greatly exaggerated by the crowding behaviour of the insects as described in the introduction to this chapter. Lhoste ( 1943 ) has suggested that the metabolic rates and the behaviour of Earwigs are modified when the animals crowd together: whatever the significance of this fact is, one effect will be to modify the microclimate in which the animals live. To some extent therefore, the modification of the microclimate must be related to the density of the population of Earwigs.

The spatial distribution of the Earwigs is densely aggregated and the varying densities of the populations found in different areas appear primarily, to be a difference in the density of the aggregations of the animals, rather than due to a varying density of animals in aggregations which themselves occur with the same density. Owing to the fact that it was not possible to enclose areas, it was impossible to test this hypothesis thoroughly, nevertheless, for the purposes of argument, and on the basis of subjective personal experience gained collecting Earwigs, it seems justifiable, as a first hypothesis to assume that the gross modification of the macroclimate is much the same throughout the collecting area. In other words, although the microclimate within which the Earwigs live is a modification of the macroclimate, the degree to which the animals modify the macroclimate is approximately the same throughout the collecting area, and as a consequence, the net effects of the environment on the growth of the animals may be correlated with the gross environmental conditions.

There are few temperature records available for the sampling sites, or indeed records of changes in any aspect of the environment at a given place. The correlation of body size with geographical position was calculated in this way, the geographical location serving as a modulus of the environment at a given place was related to the mean body sizes of the samples of earwigs collected there. This effect of the environment, particularly when manifested as areas with successively lower mean annual temperatures at the sites progressing northwards gives an indication of the effect of the environment on the growth of the Earwigs.

The correlation of body size with geographical location was calculated using Spearman's rank correlation coefficient. The collecting areas were ranked by their southerliness, such that the most southerly, Scarborough, had the lowest rank and the most northerly site, Berwick, had the highest. The means of each set of measurements were similarly assigned ranks such that for each sampling site, the highest mean body size of the set of measurements considered was assigned the lowest rank and the smallest mean was assigned the largest rank. Thus each sampling site was ranked and each of the sets of means was ranked. The hypothesis being tested was that the animals from the southerly sites lived in the most favourable environments and as a consequence were expected to be larger in all particulars than individuals living in more northerly and therefore less favourable conditions.

Table 7

Males 1967

| | Rank Corr. Coeff | T | p |
|---|---|---|---|
| Body Length | 0.5879 | 2.055 | 0.1 |
| Cercus Length | 0.3697 | 1.125 | 0.1 |
| Lgth Cercus Bow | 0.4303 | 1.348 | 0.1 |
| Cercus Curv. | 0.7091 | 2.844 | 0.05 |
| Cercus Width | 0.5515 | 1.870 | 0.1 |
| Pron. Length | 0.8788 | 5.209 | 0.01 |
| Pron. Width | 0.8545 | 4.654 | 0.01 |
| Head Capsule | 0.7697 | 3.410 | 0.05 |

Males 1968

| | Rank Corr. Coeff. | T | p |
|---|---|---|---|
| Body Length | 0.5476 | 1.603 | 0.1 |
| Cercus Length | 0.4524 | 1.242 | 0.1 |
| Lgth Cercus Bow | 0.4048 | 1.084 | 0.1 |
| Cercus Curv. | 0.8333 | 3.693 | 0.01 |
| Cercus Width | 0.7619 | 2.881 | 0.05 |
| Pron. Length | 0.8095 | 3.378 | 0.02 |
| Pron. Width | 0.5238 | 1.506 | 0.1 |
| Head Capsule | 0.5714 | 1.706 | 0.1 |

Females 1968

| | Rank Corr. Coeff. | T | p |
|---|---|---|---|
| Body Length | 0.6190 | 1.9311 | 0.1 |
| Cercus Length | 0.6667 | 2.191 | 0.1 |
| Cercus Width | 0.8095 | 3.3781 | 0.02 |
| Pron. Length | 0.9762 | 1.024 | 0.001 |
| Pron. Width | 0.6190 | 1.931 | 0.1 |
| Head Capsule | 0.9048 | 5.203 | 0.01 |

The significance of the rank correlation coefficient was tested making use of a transformation which produces Student's "t". Due account was taken of the fact that the number of samples was small in the calculation of "t".

## Conclusions

The results of calculating the rank correlation coefficient and the related "t" are summarised in Table 7.

With the exceptions of the lengths of the pronota of all samples and the measure termed the "curvature" of the male cercus there is no consistent evidence of the correlation between the sizes of the various parameters measured and the geographical position from which the samples were derived. These two consistent correlations are particularly interesting in the light of the information derived from the analysis of variation in size of the male earwigs collected on the Farne Islands as there are parallels to be found concerning the variation of the same parameters.

This variation, even in the absence of any clear pattern of correlation between the other measurements taken, and the geographical position from which the samples were derived, may be taken to indicate the possibility of the consistent variability of a species over a geographical range that is termed a cline. The cline is not clearly demonstrated by the great majority of the results and so caution must be used in applying it to the populations of earwigs under consideration in this section. If the variation manifested is truly of the type described by the word cline, there must be some factor which distorts the manifestation of the overall consistent variability which would otherwise be observed.

The correlation between the mean body lengths of the samples was not expected to be significant owing to the distortions produced in the abdomina of the individuals by fixation and the concommitant difficulties of measuring the lengths of the bodies precisely. It was however, unexpected that there should be no significant degree of correlation between the lengths of the cerci themselves and the position of the sites from which they were collected. The theory that the environment was the main cause for the development of the high form, and that the more favourable, and southerly sampling sites should produce larger individuals, as well as larger numbers of high males, led to the expectation, not confirmed, that there would be a significant correlation in this case. Similarly the mean length of the bows of the cerci were not significantly correlated with the positions of the sampling sites. The curvature of the cerci, being significantly correlated in this way further complicates the analysis, furthermore, the widths of the cerci of samples of both sexes collected in 1968 are also significantly correlated with the geographical positions of the sites from which the samples were derived. These facts present difficulties of interpretation owing to the lack of consistency in the results, and the evidence may be assessed in two ways, and this evidence also sheds some light on the problem concerning the distribution of the polymorphic forms of the Earwig.

The fact that the lengths of the cerci are not significantly correlated with geographical position, combined with the evidence that the curves are so correlated indicates that throughout the sampling range there is at least some consistent change in the shapes and sizes of the cerci. This is evidence which supports the suggestion that there is a cline in this species.

The various parameters of the cerci measured, need not necessarily vary in proportion to each other; it may be that the absolute length of the cercus is less critical to the function of the organ than the absolute radius of curvature, in which case the spontaneous variation of parameters such as curvature will be more restricted than those such as length, in which case over the geographical range considered, there may be a consistent variation masked so to speak, by the spontaneous variability of less critical parameters. This concept is developed further in the section dealing with the variation in shape of the cerci.

If this thesis is correct, the variation occurring randomly in the forms of the cerci of the earwigs collected over the restricted geographical range may well be sufficient to overlay the correlated relationship between the lengths of the cerci, and indeed all other measurements of the body, with the site from which the animals were derived.

An alternative suggestion with respect to the measurements of the cerci and possible correlations with sampling areas may be stated thus: if small departures from a standard shape interfere radically with the function of the cerci, variability related to geographical separation will be improbable. This suggestion, receives little support from the evidence since the curvature of the cerci of both the samples of males collected in 1968 are also significantly correlated with geographical position from which the samples were derived.

It is difficult to understand the functional significance of the remaining consistent correlation, between the length of the pronotum and the source area: it is difficult to envisage the situation in which this parameter might be of critical importance to the survival of the individual earwig.

In the face of this evidence, despite the lack of overall consistency, it is inevitably concluded that the species exists as a cline, although it is not possible to isolate the factors which cause the consistent variability in body parts.

It was expected that the hard parts of the animal, those which should have been changed least by the distorting action of the fixative, would show the highest correlation with geographical position, and indeed the mean lengths of the pronota were correlated in both sexes with the geographical position of the sampling area, although the correlation was not sustained; the mean widths of the pronota were not significantly correlated in this way, despite the expectation, predicted by the simple form of the hypothesis.

The cline, if there is adequate reason to term this variability as such, is not manifested in all the body parameters, but despite the lack of overall evidence, there is a distinct suggestion that the variability of the earwig body is of this type.

This study was designed as a first attempt to produce a rationale with which to describe the principles involved in causing variation in the earwig. As it made use of animals collected from the natural environment, the study escaped the problems of mimicing the environmental conditions in the laboratory. Evidence mentioned elsewhere indicates the ignorance of the critical factors in the earwig environment c.f. Lhoste's failure to raise high males in the laboratory, and for this reason it was deemed necessary as far as possible to avoid laboratory culturing in environments which are almost certainly travesties of the natural conditions the Earwigs live in.

The consistent variability of the body dimensions of the mainland populations of earwigs is very different from the variation seen in the populations collected on the Farne Islands. These anomalous populations indicate that the application of the term cline to the mainland populations must be used with circumspection, as these populations are so variant from the mainland populations as to be impossible to relate the information from this source, with the forms of the mainland populations.

While this study has failed to produce an entirely consistent pattern of the variability of the earwig, it has shown that although consistency is lacking, there is evidence that in some of the measured parameters of the earwig body, there are correlations between the mean body sizes of the samples and the geographical positions of the sampling sites, along a north-south axis.

## Comparison of the Body Dimensions of Males and Females

Despite the fact that considerable interest has been shown in the structural variation of the male Earwig, little research has been carried out on the corresponding variability of the female.

In the course of preparing data for the study of variability in shape of the female cerci a sample of 30 female Earwigs from each of the sampling areas visited in 1968 was measured. The means of the corresponding parts of the two sexes were compared using Student's "t" test. Of the eight separate measurements taken of body dimensions in the male, only six could be used for comparison owing to the difference in the overall form of the cerci in the two sexes; the female cercus lacks a bow and therefore the parameter termed "length of cercus bow" is meaningless, the width of the cercus bow, for the same reason, is also meaningless when dealing with female specimens. The remaining six measurements described in the list above were used in the following comparison.

Table 4 indicates the results of the measurements of males collected in 1968, Table 5 the corresponding results obtained from measuring the females. Table 8 shows the values of "t" obtained in the comparison of corresponding measurements taken from samples of males and females collected from the same area for each sampling site visited.

Table 8

Comparison of Mean Body Dimensions of Male and Female Earwigs Collected in 1968

| | | | "t" | | |
|---|---|---|---|---|---|
| Sampling Site | B.L.* | C.L.* | P.L.* | P.W.* | H.C.* |
| Scarborough | 2.815 | 5.753 | 0.728 | 3.004 | 4.841 |
| Saltburn | 6.298 | 2.926 | 7.632 | 5.459 | 5.880 |
| Hartlepool | 1.683 | 5.954 | 5.297 | 4.875 | 5.671 |
| Seaham | 3.695 | 3.371 | 5.608 | 5.187 | 6.082 |
| South Shields | 0.582 | 5.985 | 11.628 | 2.898 | 3.707 |
| Alnmouth | 3.154 | 6.028 | 5.583 | 5.270 | 7.187 |
| Seahouses* | 4.417 | 7.252 | 4.564 | 1.702 | 1.961 |
| Berwick | 3.703 | 5.213 | 5.160 | 4.844 | 4.198 |

Degrees of Freedom within the sample = 128

* Seahouses samples

Degrees of Freedom within the sample = 98

if t is greater than 2.576 p is less than 0.001

Key

B.L. = Body Length
C.L. = Cercus Length
P.L. = Pronotum Length
P.W. = Pronotum Width
H.C. = Head Capsule

## Results

With the exception of the body lengths of the males and females collected at Hartlepool and South Shields, and the pronotum lengths of males and females collected at Seahouses, all samples show that in every measured parameter the males are significantly different in size from the females. In all body measurements except those of the cerci the females are larger than the males; the male cerci, by contrast are significantly larger than those of the females. While the biological significance of these facts is not clear, certain conclusions may be drawn from this variability. The larger mean size of the female body may be accounted for partially at least by the reproductive role of the female sex.

The female, of course, supplies all the food requirements of the ova it produces, and despite the fact that few eggs are laid, usually between approximately 30 and 50, they are comparatively large; the abdomen which contains 50 eggs must be fairly capacious. Furthermore Guppy ( 1947 ) amongst many others remarks that Earwig eggs fail to develop unless they are attended throughout the incubation period by a female, and since the eggs overwinter before hatching, it is essential that the female survives at least until hatching. There is thus a strong selective pressure in favour of robust, long-lived females, and this fact may account at least in part, for the larger body size of the females. Similarly a difference in the role of the cerci of the female earwig, during copulation in particular, may account for the significant difference in the mean sizes of the male cerci and those of the females from a given area, although this difference is far more radical, being composed of pronounced differences in shape as well as size.

## Earwigs and the Farne Islands

The Farne Islands are a group of small islands situated off the coast of Northumberland. Their primary claims to zoological interest are derived from the fact that they provide the environment for large colonies of breeding seabirds in the spring and summer and are used in the autumn and early winter by a large population of grey seals (Halichoerus grypus Fabr. ) also for breeding. They are outcroppings of basalt derived from the great Whin sill, a prominent geological feature of the north eastern area of England. As well as supporting the seabird colonies and the seals the islands support a very unusual population of earwigs. Indeed a population from one of the islands was sampled by Bateson and Brindley and was described by them in 1892; this first focussed attention on the polymorphism manifested in the common earwig. Of particular interest is the fact that the high males occur in the populations found on these islands vastly more frequently than in any of the mainland populations. The proportions described by Bateson and Brindley ( 1892 ) indicate that approximately 40% of all the males collected were of the high form. This is very different from the populations collected at any point on the mainland coast, including the collections made at Seahouses in Northumberland which is separated from the Farne Islands by only a few miles of open sea.

The volatile behaviour of the North Sea makes the Farnes a fairly inaccessible group of islands, despite which when conditions permitted, collections were made from some of the islands and these populations were studies in a similar fashion to the populations collected on the mainland.

The main source of samples of Earwigs was the Brownsman, one of the members of the outer group of the Farnes.

This island is separated from its nearest neighbour Staple by a gut of approximately 200 yards and which is possible to cross on foot at low water. Collections of earwigs were made at every opportunity, and the material was taken back to the laboratory for study. Owing to the lack of suitable vegetation, and the uncertainty of being able to return to the island within specified periods, it was not possible to trap the earwigs in the manner described for the mainland populations. In fact, the course of action followed was to take small jars, and search for dense populations of earwigs under stones and driftwood and to scoop as many individuals as possible into the jar. This method yielded a fair number of individuals but had the extremely undesirable effect of disturbing very large numbers of earwigs just before the beginning of mating, and in weather conditions of considerable harshness. To supplement the samples and in full awareness of the dangers, a quantity of earwigs was collected by hand in the pious hope that the bias produced in the sample would be minimal.

Because the sampling methods were unconventional and owing to the fact that the populations sampled were exceedingly different from the mainland earwigs, the results of this part of the study are given separately. The collections then, were made in conditions which were not ideal, and indeed it was not possible to make a collection in 1967. In that year the weather was so bad that only one foray was made to the islands; this was late in the season and the small numbers of adults obtained were used in the abortive attempts to culture the Farnes' earwigs in the laboratory. The information obtained from all sampling except that carried out on the Brownsman is so sketchy as to be of only anecdotal interest. The Brownsman samples, being incomplete are not of great service in clarifying the nature of this island population. It was unfortunate that the two samples obtained were separated temporally by the intervening year, nevertheless there are major differences between the populations of earwigs on the Farne Islands and all those found on the mainland. The observations made on the Farnes of populations other than those found on the Brownsman were too scanty to permit statistical analysis so it is proposed that a subjective description, based on the observations made in the field is the best way to summarise the small amount discovered about these populations.

## Results

Observations were made of the earwigs on the following islands of the Farne group; Inner Farne, Staple, South Warmses as well as on the Brownsman. On all islands visited there was present a large proportion of the high males in the populations observed in 1966 and 1968. This conclusion is supported by direct observation of the earwigs in the live state and by observations of the remains of earwigs to be found in the soil: the cerci are heavily sclerotised and lie in the soil for a considerable time after the death of the individual.

Subjective considerations suggest that if there is any significant variation there appears to be a smaller proportion of high males in the population on the Inner Farne, than on any of the other islands. The population on Staple seemed similar to the population on the Brownsman, a conclusion, it must be admitted which is coloured by the proximity of the Brownsman to Staple. There was a high proportion of high males on the South Warmses. In all these populations the proportions of high males appeared to be in the range of 20 - 40% of the male population.

The populations collected on the Brownsman were analysed statistically in the manner already described for the samples of earwigs collected from the mainland. These results are summarised in the following Tables, 9, 10 and 11.

Table 9

Body Measurements of Earwigs Collected on the Brownsman in 1966, from sites under Kittiwake nests.

All measurements in millimeters.

The sample of earwigs collected on the Brownsman was composed of 31 females and 38 males of which 24 were of the high form

| | High Males | | | Low Males | | |
|---|---|---|---|---|---|---|
| | Mean | St. Dev. | St. Err. | Mean | St.Dev. | St.Err. |
| Body Lgth | 10.729 | 0.799 | 0.130 | | | |
| Cercus Lgth | 6.896 | 0.457 | 0.093 | 3.636 | 0.311 | 0.083 |
| Lgth cercus bow | 4.558 | 0.319 | 0.065 | 2.350 | 0.172 | 0.046 |
| Curvature | 1.488 | 0.136 | 0.028 | 1.321 | 0.101 | 0.027 |
| Cercus Width | 1.419 | 0.084 | 0.017 | 1.296 | 0.106 | 0.028 |
| Pronotum lgth | 1.735 | 0.090 | 0.014 | | | |
| Pronotum width | 2.126 | 0.158 | 0.025 | | | |
| Head Capsule | 1.530 | 0.072 | 0.016 | | | |

| | Females | | |
|---|---|---|---|
| | Mean | St. Dev. | St. Err. |
| Body Lgth | 11.142 | 0.972 | 0.175 |
| Cercus Lgth | 3.422 | 0.186 | 0.033 |
| Lgth Cercus bow | - | - | - |
| Curvature | - | - | - |
| Cercus Width | 1.089 | 0.104 | 0.018 |
| Pronotum Lgth | 1.716 | 0.096 | 0.017 |
| Pronotum Width | 2.151 | 0.084 | 0.015 |
| Head Capsule | 1.513 | 0.050 | 0.009 |

Table 10

Body Measurements of Earwigs Collected on the Brownsman in 1966 from sites under stones, amongst campion.

All measurements in millimeters

The sample contained 61 males of which 22 were of the high form

| | High Males | | | Low Males | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St. Err. | Mean | St.Dev. | St.Err. |
| Body Lgth | 10.118 | 1.078 | 0.138 | | | |
| Cercus Lgth | 6.555 | 0.779 | 0.166 | 3.541 | 0.362 | 0.057 |
| Lgth cercus bow | 4.373 | 0.545 | 0.116 | 2.285 | 0.259 | 0.041 |
| Curvature | 1.495 | 0.136 | 0.029 | 1.233 | 0.128 | 0.021 |
| Cercus width | 1.427 | 0.067 | 0.014 | 1.238 | 0.127 | 0.020 |
| Pronotum Lgth | 1.665 | 0.140 | 0.018 | | | |
| Pronotum width | 2.030 | 0.185 | 0.023 | | | |
| Head capsule | 1.485 | 0.082 | 0.010 | | | |

Table 11

Body Measurements of Earwigs Collected on the Brownsman in 1968

All measurements in millimeters

The sample contained 50 females and 80 males of which 25 were of the high form

| | High Males | | | Low Males | | |
|---|---|---|---|---|---|---|
| | Mean | St.Dev. | St.Err. | Mean | St.Dev. | St.Err. |
| Body Lgth | 11.066 | 0.958 | 0.107 | | | |
| Cercus Lgth | 6.420 | 0.878 | 0.176 | 3.609 | 0.274 | 0.037 |
| Lgth cercus bow | 4.268 | 0.569 | 0.114 | 2.318 | 0.195 | 0.026 |
| Curvature | 1.499 | 0.100 | 0.020 | 1.287 | 0.106 | 0.014 |
| Cercus Width | 1.409 | 0.089 | 0.018 | 1.259 | 0.133 | 0.018 |
| Pronotum Lgth | 1.757 | 0.098 | 0.011 | | | |
| Pronotum Width | 2.063 | 0.137 | 0.015 | | | |
| Head Capsule | 1.538 | 0.073 | 0.008 | | | |

| | Females | | |
|---|---|---|---|
| | Mean | St.Dev. | St.Err. |
| Body Lgth | 11.742 | 0.851 | 0.120 |
| Cercus Lgth | 3.338 | 0.196 | 0.028 |
| Lgth cercus bow | - | - | - |
| Curvature | - | - | - |
| Cercus Width | 1.007 | 0.058 | 0.008 |
| Pronotum Lgth | 1.882 | 0.097 | 0.014 |
| Pronotum Width | 2.133 | 0.103 | 0.014 |
| Head Capsule | 1.554 | 0.058 | 0.008 |

The results of the analysis of the body sizes of the earwigs found on the Brownsman indicate the profound difference between this population and any of the populations found on the mainland. There are some similarities between the populations which deserve some note. All the body dimensions of the males and females collected on this island, with the exception of those of the cerci of the males, appeared to be normally distributed. The means are quoted for the males under the heading "high males" but the measurements apart from the cercal parameters are derived from both forms of the male. When the two forms of the male separable by direct measurement are considered separately it is discovered that the mean sizes of the body dimensions of all parameters of the high male are consistently larger than those of the low males collected in the same place. This fact leads to a paradox; the high and low male appear to belong to the same population as far as the body measurements excluding the cerci are concerned, yet the means of these body dimensions are different when each population is considered separately: a situation which seems to contradict the statement that the body dimensions are normally distributed.

The problem of separating the earwigs sheds some light on this question. If the populations are separated by making use of the bimodality evident when the length of the cercus is considered, and by this external evidence the normal distributions of other characters such as overall body length are separated, not on the evidence derived from the distribution of the body length of the sample, it will be clear that with reference to the distribution of body length alone, the population of animals which was measured to produce this distribution is being, as far as the given normal distribution of body length is concerned, divided into two components in an arbitrary fashion. When a normal distribution is divided into two components in this way there is bound to be a separation of the means of the components. The lower end of the distribution having a lower mean than the whole distribution considered as a single entity, while the high component, having a higher mean than the parent population. It is, furthermore, possible to calculate standard deviations, standard errors of the mean, etc. for two such arbitrarily separated components. Such parameters are meaningless except when applied to normal distributions; the application of these concepts therefore, to populations which have been separated into components on the basis of evidence external to the distribution under consideration is bound to lead to the production of fallacious results. For these reasons the means of the body dimensions of both types of earwig, except where justification in the form of internal evidence, as in the case of the bimodality in form of the cerci, have been quoted for the entire male sample.

Notwithstanding the unwillingness expressed in the previous paragraph to analyse, in statistical terms the components contributed by the two separable morphs to the normally distributed body dimensions, it is illuminating to make some general observations concerning the overall body form of the two morphs. To this end the histograms of the distributions of body lengths, pronotum lengths and widths, and interoptical distances have been prepared for the two samples collected from the Brownsman in 1966 and 1968. The histograms are drawn such that the distribution of the chosen body measurements are shown for the entire sample of male animals collected in a given year; this is the histogram shown in outline. The shaded histogram indicates the frequency of occurrence of the high form of the male within a given size class.

For the reasons discussed above I am unwilling to separate the two histograms and to consider them as separate and skewed distributions, and also it is true that the distributions could be transformed and the means and standard deviations could be calculated, but in the absence of internal evidence within the distributions in question the application of such techniques would not necessarily yield meaningful results.

Even without the artifice of statistics the general point emerges from consideration of the histograms shown in Plates 5, 6, 7 and 8, that the high form of the male is more commonly found amongst the larger individuals in the population than amongst the small. This finding concurs to some extent with the hypothesis of the physiological switch mechanism for the production of the high male, and this in turn relates to the correlation between the numbers of high males found in a given population on the mainland, and the mean size of the low male cerci in those samples.

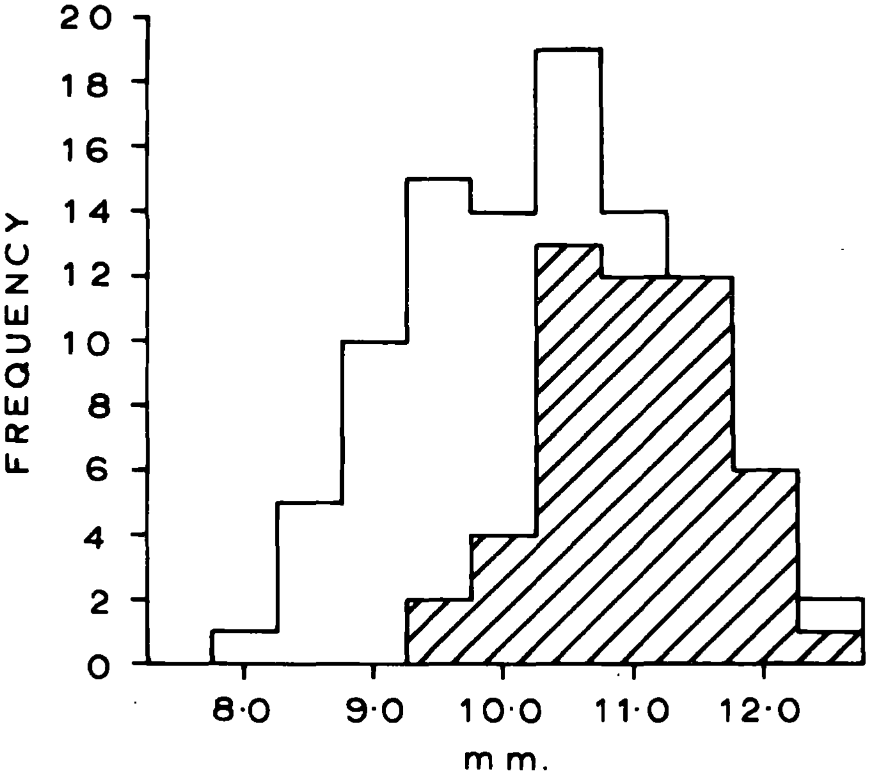
It would be tempting to try to determine the probability of the occurrence of the high form in relation to the absolute sizes of the size-classes in which the high males occur: the marked differences between the mean sizes of all the body measurements from the two samples collected in the different years unfortunately precludes any such numerical analysis. In itself, this does not invalidate the general hypothesis that large individuals are more likely to be high males than are small individuals.

The third low polymorph described in detail in the section dealing with variability in shape introduced a further complicating factor to the hypothesis of the physiological switch and

Plate 5. Histograms Showing the Frequency Distributions of the Body and Pronotum Lengths of Male Earwigs Collected from the Brownsman in 1966. The contribution Made to the Total Distributions by the High Males are Shown by the Hatched Areas.

## BROWNSMAN MALE EARWIGS 1966

BODY LENGTH



PRONOTUM LENGTH

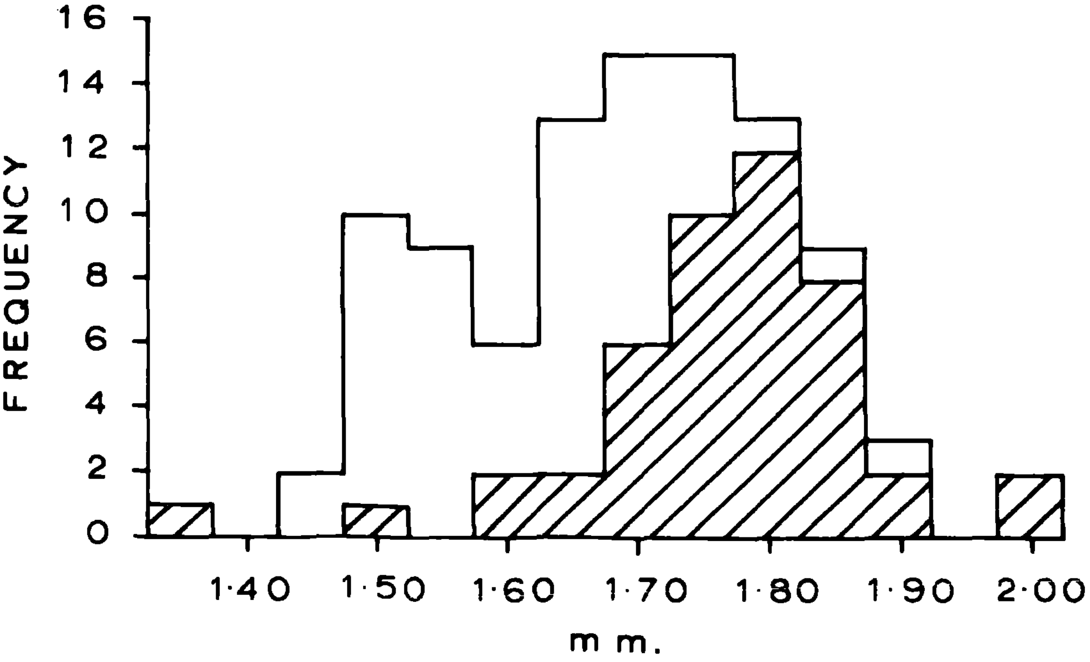
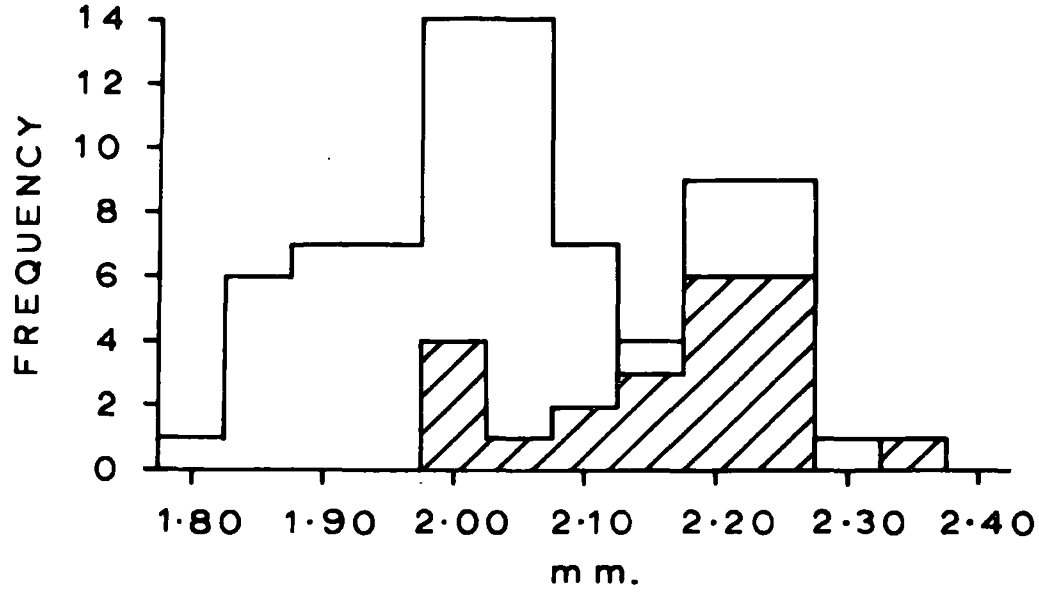


Plate 6. Histograms Showing the Frequency Distributions of the Pronotum Widths and Head Capsule Sizes of Male Earwigs Collected from the Brownsman in 1966. The Contributions Made to the Total Distributions by the High Males are Shown by the Hatched Areas.

# BROWNSMAN MALE EARWIGS 1966

## PRONOTUM WIDTH



## HEAD CAPSULE

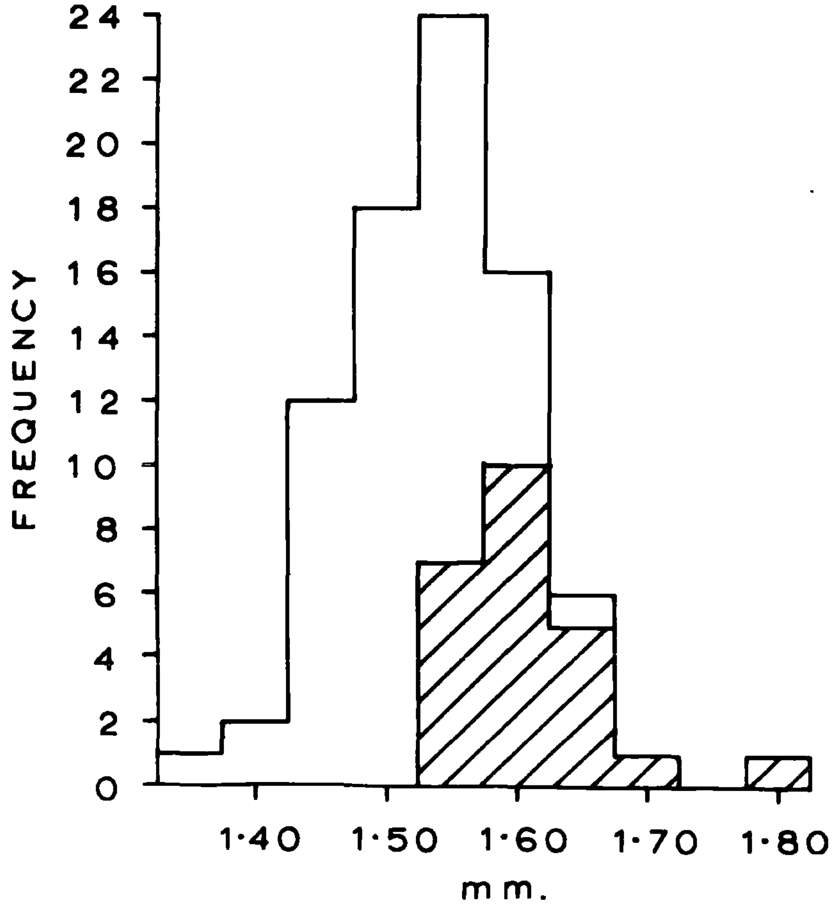


Plate 7. Histograms Showing the Frequency Distributions of the Body and Pronotum Lengths of Male Earwigs Collected from the Brownsman in 1968. The Contributions Made to the Total Distribution by the High Males are Shown by the Hatched Areas.

BROWNSMAN MALE EARWIGS 1968

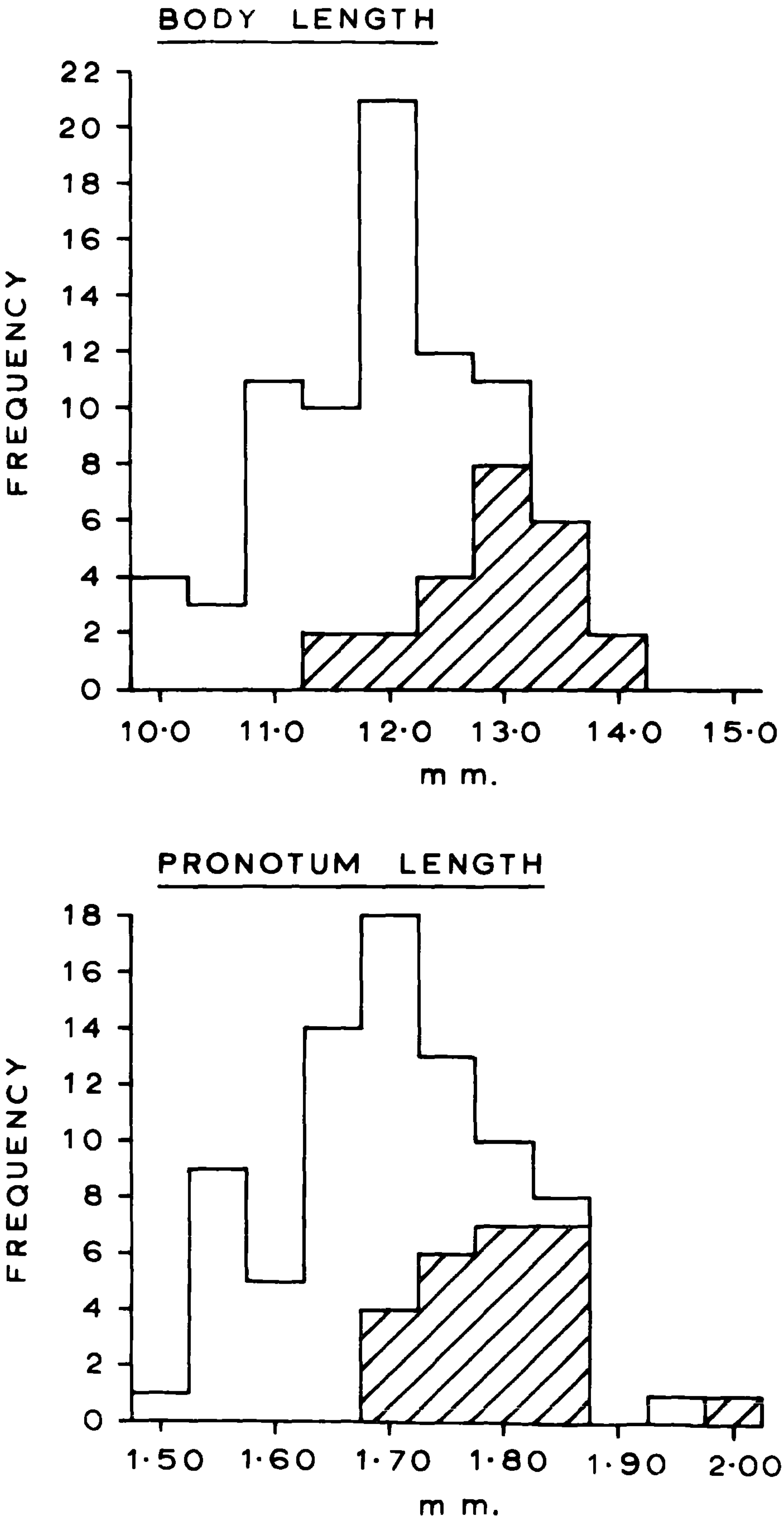
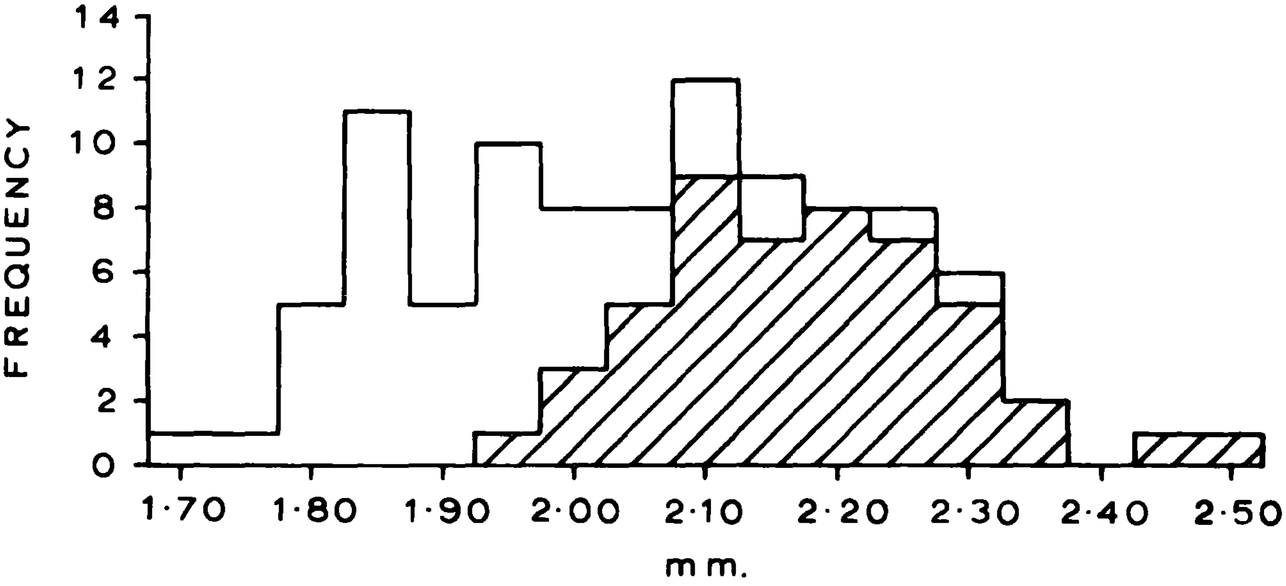


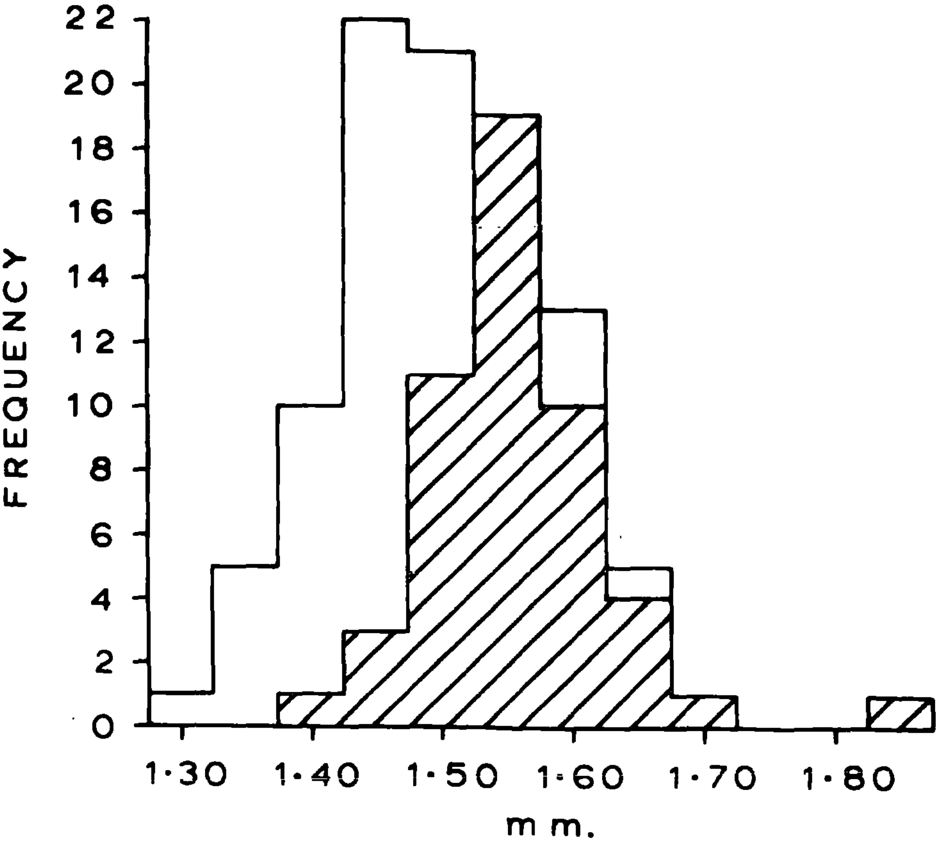
Plate 8. Histograms Showing the Frequency Distributions of the Pronotum Widths and Head Capsule Sizes of Male Earwigs Collected from the Brownsman in 1968. The Contributions Made to the Total Distribution by the High Males are Shown as Hatched Areas.

# BROWNSMAN MALE EARWIGS 1968

## PRONOTUM WIDTH



## HEAD CAPSULE



and until the interrelationship amongst the male morphs is more fully understood it is pointless to speculate further about the significance of the two male morphs, which are far more similar to each other than to the high form, in the development of the high male, low male dichotomy.

To summarise then; in general terms it appears that the high males are usually larger than low males in body dimensions other than cercal parameters, but that the disparity between the morphs in these features can only be determined by making use of evidence derived from the cercal variability. The finding may be best expressed by stating that the body measurements of males are normally distributed, but the occurrence of high males is more frequent in animals which lie towards the larger end of the distribution.

Owing to the subjective collection methods no great weight can be placed on the quoted results. In particular, while there is a great discrepancy between the proportion of the high males in the populations in 1966, and 1968, this may be accounted for by a combination of bias in the collections; as well as a real difference between the samples collected in these years; realizing that bias was bound to be introduced care was taken to avoid preferential collection of high males. Nevertheless, the very abundance of high males indicates that there must be a far greater proportion of high males in the population on the Brownsman than in any of the mainland populations. To have collected 25 high males from the mainland, even from a population where they were comparatively abundant would have necessitated collecting in the order of three to four hundred males.

Subjective methods of collection, even when statistical evidence indicates only a small bias, must,be suspected. Indeed Bateson and Brindley who derived the samples of male earwigs used in their first study of polymorphism from the Brownsman, which they described in the paper of 1892, were castigated by Kuhl for this very reason. They collected earwigs in a manner similar to that described above, in this section. They did find a large proportion of high males in the population and despite the shortcoming of the techniques there is some parity between the percentages of high males found at this population in 1892 and 1968. The main interest in the Brownsman population is the very evident difference between this population and the mainland populations. The earwigs are far larger than any found on the mainland and the cerci of the high males are prodigious in size, compared even with the largest of the high males found on the mainland. The population is very different from the mainland populations of earwigs, but although considerable anatomical observation has been undertaken there appear to be no morphological characters other than simply the abundance of the high male, and the overall size of the individuals to indicate that they belong to a different taxon from the mainland group.

Certainly, the conditions on the islands are very different from those on the mainland, and furthermore the populations of earwigs on the Farnes are separated geographically from the mainland, and therefore genetically as well, and these two factors may well be sufficient to account for the considerable differences observed between the mainland earwigs and those of the islands. It is chastening that the overall picture of variation related to geographical location is so violently distorted by these remarkable populations of earwigs. Until the causes of the polymorphism are more clearly understood these animals present a very considerable enigma to the investigator.

The problem of the Farne Islands' earwigs is a sidetrack which would repay considerable investigation, and this is particularly desirable in the light of the mainland investigations described elsewhere in this thesis. The inaccessibility of these populations is the main problem to be overcome.

## Comparisons between Some of the Samples of Male Earwigs Collected on the Brownsman in 1966 and 1968

Despite the smallness of the collections made in 1966, and despite the fact that they were not random samples, the measurements derived from the collection of earwigs from under old Kittiwake nests on the cliffs of the Brownsman have been compared with samples collected in the same year, in the centre of the island from under stones in the Sea-campion, (Silene maritima) which forms one of the main constituents of the vegetation on this island.

The samples were compared making use of Student's "t" test and the results of the application of this test are quoted in Table 12. The samples from the different sites on the island differ significantly in certain particulars. The body lengths of the samples of males from the two areas are exceedingly different, and this difference is shown by the "t" test to be very significant; it is very unlikely indeed that this difference is due to the distortion of the abdomina of the earwigs in question, produced by the fixation of the material. The parameters measured on the cerci of the earwigs in the two samples indicate that there is no significant difference between the sizes of the cerci in the high males of the two samples. The samples of the low male cerci, which are not significantly different in both samples, with the exception of the curvature of the cerci of the two groups of low males, indicate the similarity of the low cerci in the same samples. The pronotum lengths of the animals collected from under the nests are also markedly different from the pronotum lengths of the males collected from the centre of the island.

This fact again indicates the way in which a particular feature of a structure can vary with out necessarily being closely related to other features of the same structure. The widths of the pronota of the two samples of earwigs are shown not to be significantly different. The head capsules of the two samples are also significantly different.

The significance of the pronounced variability of some of the characters measured, when compared with the relative constancy of others is an intriguing puzzle: it should be remembered, that in connection with the variability of the mainland populations, in every case the pronotum length was correlated with the geographical location. This feature, may be, fortuitously, one of the more variable anatomical features of the male earwig. And that this particular character is modified by the environmental conditions is possible. The curvature of the cerci of the low males from the two sampling areas is another of the characters that differs significantly in the two samples. It will be seen in a later section that the shape units, which are calculated to describe the variability in shape of the cerci, are derived in the same axis as the curvature of the cerci. This measurement, it will be remembered, is derived from the maximum length of the line at right-angles to a pair of parallel lines, one joining the distal and proximal ends of the bow of the cercus and the second grazing the outer edge of the cercus in a tangential fashion. Rectification of the sizes in the shape study means that the absolute sizes of the organs are distorted, but the evidence derived from the samples on the Brownsman indicates that this particular measurement is very variable in populations separated by only a matter of 200 meters, approximately.

The variability of the head capsule size is of importance: the head capsules are also shown to be significantly different in size. This character reinforces the suggestion that the two samples manifest very different morphological characters. The classical explanation of this phenomenon would be to suggest that Dyar's law ( 1890 ) applied, and that the members of the two samples underwent different numbers of larval instars to reach maturity. This speculation is not lacking in piquancy but there is unfortunately no evidence available to support or deny this speculation; for the

Table 12

Comparisons between the Farne Islands Populations of Earwigs

Comparisons between the two samples of males collected in 1966 *

| | t. | probability |
|---|---|---|
| Body Lgth | 5.429 | less than 0.001 |
| Cercus Lgth (High Males) | 0.558 | greater than 0.6 |
| Cercus Lgth (Low Males) | 1.001 | greater than 0.4 |
| Lgth cercus bow (High Males) | 0.646 | greater than 0.5 |
| Lgth cercus bow (Low Males) | 0.680 | greater than 0.6 |
| Curvature (High Males) | 0.114 | greater than 0.9 |
| Curvature (Low Males) | 2.140 | less than 0.05 |
| Cercus Width (High Males) | 0.789 | greater than 0.5 |
| Cercus Width (Low Males) | 0.780 | greater than 0.5 |
| Pronotum Lgth | 4.361 | less than 0.001 |
| Pronotum Width | 1.202 | greater than 0.2 |
| Head Capsule | 4.139 | less than 0.001 |

* Samples collected from two habitats, under kittiwake nests on the cliffs, and under stones amongst the sea-campion

Table 12 cont'd.

Comparisons between the samples collected from under stones in 1966 and 1968 from the Brownsman.

| | t. | probability |
|---|---|---|
| Body Lgth | 3.227 | less than 0.01 |
| Cercus Lgth (High Males) | 1.792 | less than 0.1 |
| Cercus Lgth (Low Males) | 0.943 | greater than 0.8 |
| Lgth cercus bow (High Males) | 1.391 | greater than 0.2 |
| Lgth cercus bow (Low Males) | 1.055 | greater than 0.3 |
| Curvature (High Males) | 0.174 | greater than 0.9 |
| Curvature (Low Males) | 2.573 | less than 0.02 |
| Cercus Width (High Males) | 0.363 | greater than 0.8 |
| Cercus Width (Low Males) | 1.686 | greater than 0.1 |
| Pronotum Width | 2.826 | less than 0.01 |
| Head Capsule | 2.385 | less than 0.02 |

present it seems that the safest conclusion to be drawn is that the pronounced differences between the head capsule sizes of the two samples of males indicates simply the magnitude of the morphological differences which separate them.

The short distance separating the two collecting areas lends support to the theory that the environment plays a very large part indeed in determining the final body dimensions of the adult earwig. It seems very unlikely that a distance of a few hundred meters at the most should be sufficient to isolate two genetically distinct populations of even such sedentary animals as the earwigs.

Similar comparisons were made between the sample of earwigs collected on the centre of the island in 1966 and the sample collected in the same place, two years later in 1968. A similar overall pattern was observed to that described for the two populations collected in 1966. It was modified by the fact that the two populations differed significantly in the matter of pronotum width as well as all the other characters described above. This fact is of particular interest when it is remembered that the two samples were collected in the same place, but in different years and lends emphasis to the suggestion that the overall conditions produce profound variation in the sizes of the adult earwigs.

## The Occurrence of High Males in Mainland Populations

In 1966, at the beginning of this study, it was not possible to make a thorough collection of earwigs from all the sampling sites, and so it was determined that a small number of samples should be collected from the sites near Durham. These sites sampled in 1966 were: Hartlepool, South Shields, Alnmouth and Seahouses. The samples collected contained between 200 and 300 individuals. In all of the four samples there was not one high male present: the records for the occurrence of high males of the Earwig are scanty, and have usually been published as asides in papers dealing with different aspects of the biology of this species, and although the discovery that there were no high males present in any of the samples collected on the mainland was disappointing it was not completely unexpected.

Subsequently, in 1967, when collections were made on a large scale it was superficially obvious that most, if not all the 10 samples collected contained a small proportion of high males. Attempts were made to determine precisely the proportion of each polymorphic form which made up the population of males in each sample.

Searches in the literature indicated that in general high males had been separated from the low males by eye in most cases, and this method, depending on the subjective behaviour of the investigator seemed rather untrustworthy. Arbitrary division of normal distributions is a dangerous practice and can lead to the production of very spurious results, the effects of inaccurate division of the complex distribution of the lengths of the male cerci from a sample of earwigs would be bound to be equally spurious.

In order to develop a consistent method of isolating the high males by making use of the variant form of their cerci, the computer programme "APPROX" was devised. The mode of operation and a flow diagram of this programme are contained in Appendix II.

Making use of this programme, the populations of male earwigs in each of the samples collected in 1967 were separated into the high and low polymorphs. The proportions of high males in each sample of the males collected in 1967, and 1968 are summarised in Table 13.

Table 13 Numbers of high males in samples* collected in 1967 and 1968 from Mainland Populations

1967

| Sample Site | Sample Size | No. High Males | % |
|---|---|---|---|
| Scarborough | 100 | 4 | 4.0 |
| Whitby | 112 | 10 | 8.9 |
| Saltburn | 100 | 13 | 13.0 |
| Hartlepool | 100 | 10 | 10.0 |
| Seaham | 100 | 6 | 6.0 |
| S. Shields | 100 | 4 | 4.0 |
| Alnmouth | 70 | 4 | 5.8 |
| Seahouses | 50 | 0 | 0 |
| Beal | 100 | 3 | 3.0 |
| Berwick | 63 | 2 | 3.5 |

1968

| Sample Site | Sample Size | No. High Males | % |
|---|---|---|---|
| Scarborough | 100 | 3 | 3.0 |
| Whitby | - | - | - |
| Saltburn | 100 | 7 | 7.0 |
| Hartlepool | 100 | 4 | 4.0 |
| Seaham | 100 | 7 | 7.0 |
| S. Shields | 100 | 6 | 6.0 |
| Alnmouth | 100 | 0 | 0 |
| Seahouses | 70 | 1 | 1.4 |

* Samples of males

Table 13 (cont.)

1968

| Sample Site | Sample Size | No. High Males | % |
|---|---|---|---|
| Beal | - | - | - |
| Berwick | 100 | 1 | 1.0 |

## Results

The results summarised suggest that the numbers of high males, small as they are in every case, decrease in number from the south with increasing northerliness. This distribution of high males with a lower proportion of them in the most northerly samples, compared with the southerly locations fits neatly into the general predictions concerning the causes for the origin of the high form of the male. If the environment plays a part in the production of the high male, as has been so widely suggested, then the more favourable southerly environments should allow the development of proportionately more high males than the less favourable northerly environments. Crumb, Bonn and Eide ( 1941 ) refer to a suspicious sample of common earwigs collected at Bergamo in Italy, this sample which contained 9,600 individuals contained exclusively high males. The significance of this sample is difficult to decide, it is mentioned in passing and must be viewed with scepticism, although if the causes of polymorphism of the type characterised by the occurrence of high males, are closely involved with environmental conditions, then it is possible, that under such ideal conditions a population entirely composed of high males might develop.

In order to test the hypothesis that the high males were more common in the southerly populations than in those at the north of the sampling area Spearman's rank correlation coefficient was calculated in a manner similar to the analysis of the relationship of mean size and geographical position. Each sampling site was assigned a rank such that the most southerly site had the lowest, and each site proceeding in a northerly direction was assigned a higher rank, the most northerly site of all receiving the highest rank of all. The populations of earwigs were given ranks such that the population which contained the highest proportion of high males received the lowest rank, and the population of males which contained the fewest high males was given the highest rank.

1967 males

Spearman's rank correlation coefficient = 0.6818

$p$ less than 0.05

1968 males

Spearman's rank correlation coefficient = 0.6369

$p$ greater than 0.05

The results of the application of this test to the results are ambiguous. The correlation of the proportions of high males in the samples collected in 1967 is probably significant. The fact that there are two fewer samples in the 1968 collection may account in part for the lack of significant correlation. The evidence suggests overall that there is some correlation of the type discussed above and the presence of a correlation between high proportions of high males and southerliness of position adds to the evidence in support of an environmental cause at least in part to the production of the high male.

The factor which tends to obscure the picture is the rarity of the high male. To produce a satisfactory picture of the occurrence of the high male much larger samples are necessary, indeed the minimum for this kind of work is of the size of one order of magnitude greater than the samples used in this preliminary investigation. The sizes of the samples have been limited in this study in order that an attempt, however superficial, could be made to try to understand the general effects of the environment on a whole series of populations from similar areas, and in order to derive a general notion of the variability of the Earwig body in geographical terms rather than the precise understanding of variation within one particular population, when the population of earwigs only ten miles away may vary in a completely different way.

## Occurrence of high males at the sampling sites in Different Years

The discovery in 1967, that a few high males occurred in most of the samples, was surprising in the light of the absence of this polymorph in the 1966 samples. As a result of this discovery it was decided that the constancy of occurrence at each of the sampling sites of high males collected in 1967 and 1968 should be determined. The environment, if it varied from year to year, was expected to influence the overall frequency of occurrence of the high males, while variations in local conditions were expected to be related to the overall climate of the particular year. In other words the year, if it was "good" was expected to produce more high males, than a "bad" year, but that in either good or bad years the proportions of high males would remain constant in rank terms: the sites which produced the most high males in good years producing the most, though fewer in proportion, high males in bad years. This hypothesis was tested by comparing the proportions of high males, ranked in relation to geographical position in the samples collected in 1967 and 1968. The ranked proportions were then considered to be independent ranks of the same data. Only the sampling sites used in 1968 were utilised, and the 1967 samples from Whitby and Beal were neglected in this calculation.

The rank correlation coefficient is very low in this case, and this value, 0.6074, is depressed by a single result, the proportions of high males in ranked terms are very similar for both years with the exception of the samples collected from Alnmouth in Northumberland. In 1967 there were 5.8% high males in the population, in 1968, with a larger sample size not one high male was discovered. It may be that the absence of high males in this sample indicates the random variability of the subsampling method and application of the binomial theorem indicates that it is unlikely that even if only 2% of the male population were of the high form they would be absent entirely from the sample (probability of 0.1318 that a sample of 100 males containing 2% high males should not contain any high polymorphs).

The besetting problem is still the paucity of high males, and the dependence on direct measurement of the length of the cerci to allow accurate separation of the high males. For this reason what analysis I have permitted myself has been non-parametric, and the correlation while being independent of the form of the distributions of high males, does not utilise the evidence to the full. With more time to devote to accurate measurement the tentative conclusions that have been arrived at in the study of the general factors relating to variability in the occurrence of high males would be more easily tested. If larger sample sizes were used, the data would also be amenable to more subtle parametric analysis.

## Correlation between the Cerci lengths of the Samples of Low Males Collected in 1968 and 1969 and the occurrence of high males.

The effects of environment on the development of the high form of the male Earwig have been investigated in some detail and although the conclusions are tenuous it appears that there is some relationship between geographical position of a given sampling site and the occurrence of the high male. The interrelationship of the two forms of the male Earwig are further illustrated by relating the overall mean cercus length of the low males in a sample with the occurrence of high males. If there is a relationship between the occurrence of the high male and favourability of the environment, then it might be expected that in favourable environments, the low males would be larger, and that this larger size of the low males would be correlated with the relatively large numbers of high males found in these areas. This hypothesis was tested making use of Spearman's rank correlation coefficient.

The data were analysed in the following way. For the samples collected in 1967 and 1968, the mean lengths of the cerci of the low males were ranked against the occurrence of high males such that the sample which contained the highest number of high males was assigned the lowest rank, and the ranks increased in magnitude such that the sample in which there was the lowest proportion of high males, was thus given the lowest rank. The samples were also ranked in order of mean cerci lengths of the low males, the highest mean receiving the lowest rank, the ranks increasing in magnitude, the sample with the lowest mean cerci length, being given the highest rank.

## Results

Males 1967 Correlation between the Occurrence of High Males and the mean lengths of the Cerci = +0.6757

p less than 0.05

Males 1968 Correlation between the Occurrence of High Males and the mean lengths of the Cerci = +0.5535

p greater than 0.1

These results indicate somewhat ambivalently that there is some possible correlation between the size of the low males and the occurrence in the population of the high male. This is very clearly indicated in the population from 1967, which shows a probably significant degree of correlation but this is not shown by the population collected in 1968. Reasons for this lack of convincing statistical evidence include the fact that the 1968 population contained only eight sample while the 1967 population contained ten. Furthermore, the relationship between the mean length of the cerci need not be linear, and this fact also may help to explain the discrepancy between the results of 1967 and 1968. The conditions which produce high males must be distributed about some kind of mode, which signifies the optimum conditions: in 1967, the conditions which went to produce the high males may have been more optimal than they were in 1968, and this in graphical terms, might be interpreted as lying on the distribution of conditions described above, on a part of the slope of the curve closer to the mode, than the conditions in 1968. Furthermore if the slope of this curve describing the optimum conditions varied, in a manner analogous to the normal curve for example, this could have the effect on the correlation of the high males of depressing it, simply because the number of samples is too few to fit the shallower part of the curve.

This explanation, that the occurrence of the high male is unlikely to be linearly related to the conditions supplies part of the reason for the inconsistency of the results of all the studies of the occurrence of the high male.

## Variation in the Shapes of the Cerci of Earwigs

Owing to the overall curved profile of the organs it was, possible to record only a few measurements from each individual cercus, and there were insufficient of these to allow a detailed analysis of the relative proportions of the structures. This difficulty is due to the fact that there are few recognizable anatomical features on the cercus which may be used as baselines for measurement. Observation of the cerci suggested that the evidence derived from the study of absolute variation in size accounted only partially for the total variation of these structures; that the variation in form of the cerci was of a complex nature.

The techniques described in this section were developed expressly to elucidate more clearly than the direct methods, the overall variability of the cerci. It is comparatively easy to measure the sizes of the cerci of a sample of earwigs, and it is on the consideration of size alone that most of the work has been done in the investigation of the occurrence of the polymorphic forms of the Earwig. By far the most detailed study of the occurrence of the polymorphic forms of the Earwig was carried out by Kuhl ( 1928 ). Kuhl, using samples of earwigs collected in Germany attempted to justify the separation of the male earwigs into four separate types. He suggested that the high form of the male, described by Bateson ( 1892 ), Diakonov ( 1925 ), Huxley ( 1927 ), and others was in fact separable using criteria derived from the width of the cerci into two separate populations. He further suggested that the low form of the male was also separable in this way. For this separation of the males into four distinct types to be valid the characters which allow such a separation must be very subtle indeed; there was no evidence of a bimodal distribution in the widths of the cerci of any of the samples of males collected over the three years of my study (each set of measurements having been tested for normality as a matter of course before standard deviations were calculated). Furthermore, a second argument Kuhl erected on the evidence of his investigation, that the distribution of the lengths of the cerci of a given sample of Earwigs was not bimodal but approximated to a skewed normal distribution presents logical difficulties. He introduced a further factor into the separation of the polymorphic types of the Earwig, by considering the presence or absence of a gap between the closed cerci to be diagnostic of a real polymorphic difference between the individual Earwigs. Kuhl's analysis of the problem thus presents two major difficulties: the fact that he considered the lengths of the cerci of his samples of males as a skewed normal distribution makes it impossible to divide the populations into polymorphic types using this measurement, and a character such as the gap between the tips of the cerci makes it essential to separate the animals of a given sample into two separate groups since a gap is either present or absent. It is perhaps unfortunate that the first biological work on the analysis of frequency distributions was published a year later by Buchanan-Wollaston in 1929. A current view of Kuhl's work is supplied by Wynne-Edwards ( 1962 ) who wrote "Notwithstanding the unassailable evidence to the contrary, Kuhl persuaded himself that the bimodality previously established was nothing but an illusion, and that in fact there was a continuous range in forceps length, which Bateson, Diakonov, and the rest had never been mathematically justified in dividing into two sections".

The evidence considered in the previous section of this work supports the older view and vindicates the validity of approaching the variability of the cercus in this way. Indeed, it is impossible to understand the theory by which Kuhl separates the four types, a theory which requires not one bimodal distribution, but a distribution with four separate modes.

It was to solve this enigma that this aspect of the study was carried out. The shapes of structures such as the cerci are inextricably linked with the variation in absolute sizes of the organs and if the shape is to be studied some method is necessary by which the sizes of different cerci may be reduced to some standard. This standard reduction may be carried out in two ways; either the influence of the absolute size may be cancelled out altogether by considering the different dimensions of the cerci in terms of proportional relations, or the sizes of different cerci may be reduced to some arbitrary standard, and the relative sizes of different parts of the cerci may then be considered in absolute terms.

## Methods

Several methods were tried in an attempt to derive some index of the shape of the individual cercus: they fall into two groups; arithmetic methods and projection methods. The arithmetic methods which made use of the four direct measurements of the cerci proved unsatisfactory because, despite the fact that by considering proportions, the problems of varying size were solved, difficulties of a statistical nature arose. Further it was impossible to describe the shapes of the cerci even approximately from the limited number of measurements available.

The methods which were based on projection of images of the cerci were more satisfactory than the arithmetic methods. Permanent preparations were made of the fixed cerci, by dehydrating them in absolute alcohol, clearing the specimens in xylol and mounting them permanently as whole-mounts with Canada balsam. Subsequently it was found that the permanent preparations were not altogether satisfactory; the mounts were of necessity thick and as a result took an inordinate time to harden, also it was not possible to align the the cerci accurately in the mountant. The cercus is not only curved in the lateral plane but is also curved to a lesser extent dorsoventrally and if a true image is to be projected, it is essential that the specimens be controlled at the time of projection. The most satisfactory and simplest method was to store the cerci in alcohol until they were needed and at the last possible moment to dry the specimen on tissue paper, align it on the slide, and draw its image. The cerci do not distort sensibly in the short period required to trace them, owing to the presence of the heavily sclerotised cuticle.

By using a camera lucida in conjunction with a Zeiss "zoom" binocular microscope, it was possible to align the images of the preserved cerci very accurately within a standard grid. The alignment was carried out by making use of the salient features of the cerci, which also served as baselines for the direct measurement. See Plate 3. Making use of the "zoom" facility of the microscope it was possible to control the magnification of the image and in this way each image was rectified to a standard grid; this grid was 10 cms. long and the cerci were set up in the following manner. The main landmarks by which the cerci were aligned are the distal tip of the cercus, the proximal end of the bow of the cercus, and the inflection of the outer edge of the proximal end of the cercus adjacent to the point along the cercus body where it emerges from the abdomen of the animal in life.

The distal tip of the cercus and the proximal end of the cercus bow were aligned on a straight line, the baseline, and the magnification was modified such that the line parallel to the baseline, intersected by a line produced through the tip of the cercus image, and at right-angles to the baseline and similarly intersected by a second line which intersected the proximal inflection of the outer cercus edge, was ten centimetres long;(i.e. the line marked A in Plate 3). By tracing a series of the images of different cerci within the same grid it was possible to obtain some subjective impression of the overall variation in shape, and as the cerci proved to be very variable, a technique was devised to quantify the data.

Making use of the rectified images of the cerci, each image being traced separately within a separate grid, the silhouette obtained was considered as a graph, the distal tip of the cercus being located at the intersection of the axes. At points, termed locations, separated from each other by a distance of 5 mms. along the abscissa of the graph, the ordinates of the curves produced by the inner and outer edges of the cercus were recorded using a "D Mac" pen-follower, and in this way 42 pairs of coordinates, 21 from the inner edge and 21 from the outer, were recorded.

The coordinates were output on to five hole paper-tape with the precision of 0.1 mms., and were processed as follows: the sets of coordinates were themselves rectified to a standard grid, rounded to the nearest 10 units and output in sets, each set of coordinates indicating the total variation of the edges of all the cerci considered, at a particular location along the long axis of all the cerci in the sample. Rounding of the coordinates was necessary owing to the fact that the co-ordinates were first projected through an optical system, then traced twice, once on to the standard grid, and once with the pen-follower. A certain amount of experimental error was unavoidably introduced into the co-ordinates for this reason, and rounding was used to minimise it.

Each set of rectified co-ordinates from a chosen location indicated the distribution of a series of points on the edges of all cerci, in the line produced from the location on the baseline, and at right-angles to the baseline. These co-ordinates were calculated for two series of samples of cerci, one series for each sex. The samples were constituted as follows: approximately 30 individuals of each sex were randomly selected from each of the samples collected over the entire study area in 1968, making a sample size of approximately 240 individuals of each sex. The samples were selected to indicate the overall variability of the cerci, particularly in the light of the ambivalent results derived from the study relating the variability of mean sizes of the populations of Earwigs with their geographical distribution throughout the collecting range.

The distributions of the populations of co-ordinates derived from all of the individuals were investigated using Harding's ( 1949 ) method of analysing polymodal frequency distributions as modified by Cassie ( 1954 ). This method makes use of the properties of arithmetic probability paper.

Each set of coordinates was plotted as an accumulative frequency percentage curve on arithmetic probability paper. The distributions could be isolated into their component normal sub-distributions. The method is described in detail in Appendix (i).

## Results

The results of this study are best summarised in two separate sections; one section dealing with the results of the analysis of shape for each of the sexes.

### Males

Plates 9 to 17 indicate the distributions of the points recorded from 36 of the locations selected around the edges of 256 rectified cercus images, plotted as accumulative percentage frequency curves on arithmetic probability paper. The component normal distributions for each location have been calculated and in each case these distributions have been plotted in addition to the compound distributions and within the same axes. It will be observed, on referring to the graphs that the frequency distributions fall into three groups. The distributions of points recorded from locations 16 to 20 Plate 11, are approximately normal, the distributions of the points recorded from locations 2 to 13, Plates 9, 10, and from 22 to 33, Plates 11, 12, 13, 14 and 15, are bimodal, and the distributions of points recorded from locations 34 to 41, Plates 15, 16 and 17, are trimodal. The positions of the inflections and the proportions of the populations which the component distributions account for are summarised in Table 14.

Owing to the fact there is considerable variability in the ease and accuracy with which the coordinates at the proximal end of the cercus can be recorded, particularly at locations 21 and 42, these locations have been excluded from the analysis. The proximal end of the cercus often, despite strenuous efforts to remove them, had strands of muscle attached to it, and this made precise determination of the edge impossible. Locations 14 and 15 also presented problems of analysis, owing to the fact that these locations lie close to one of the key features of the cercus used to align it within the grid. As described above, the proximal end of the inner curve of the bow is one of the features used to fix the image of the cercus; for this reason very small differences of shape effect considerable and disproportionate variations in the co-ordinates. This fact is explained when it is remembered that the cercus is so shaped that the edge at this point runs very nearly at right-angles to the long axis of the organ, and in this case, since the co-ordinates are recorded as a population of points in a line at right-angles to a given fixed point on the long axis, it becomes evident that small errors of tracing and recording will produce large variations in the co-ordinates recorded for such locations. For these reasons, despite the desirability of including these locations, the results from locations 14 and 15 have been excluded from the analysis.

Table 15 summarises the division of the distribution of the points recorded at each location and indicates the means and approximate standard deviations of the component normal distributions when they occur. Except for the unimodal distributions at the proximal end of the inner edges of the cerci, corresponding to locations 16 to 20, Plate, 11, and the distribution at location 2, all the distributions are at least bimodal; the populations are all divisible into at least two normal components. These components are consistently divisible at one inflection which accounts for approximately 10% of the total population in each case. In other words the populations, in toto, are made up of at least two populations of cerci, in the proportions of 10 percent and 90 percent.

If the means of the smaller component population are plotted graphically in order on the standard grid the mean shape, of one of the polymorphic forms of the cerci is produced. As mentioned above however, some of the populations of points are only unimodally distributed, and in this case the mean shape of all the different polymorphic cerci at such locations must be the same, therefore this mean is used in the reconstruction of all the polymorphic cercus types.

The form of the cercus produced by plotting the means of the populations with the lowest means is the high form of the cercus, because retification of the lengths of cerci of this type reduced the width of the cerci to a greater extent than rectification of the images of the low form. This will be obvious when it is remembered that the length of the high form of the cercus is always greater than that of the low form. At certain locations it is clear that the compound divisions must be divided in a fairly arbitrary fashion; in some it is not clear where the inflection falls on the curve. Such arbitrary division is particularly noticeable in the analysis of the distributions at locations 2, Plate 9, and 33, Plate 15. At location 2 there is no evidence that there are in fact two component normal distributions, as there is no hint of a definite inflection of the curve, it is impossible to infer the presence of two component distributions. It is possible to suggest on the strength of the evidence from most of the locations that the inflection separating the high form from the low lies somewhere near the 10 percent point on the curve, but owing to the lack of internal evidence from the population at location 2, this suggestion must be ignored.

At locations 33 and 34, Plate 15, the composition of the total distributions changes from being bimodal to being trimodal. The presence of the third mode is indicated by a second inflection. The division of the distributions at 33 and 34 is again partially arbitrary as there is some indication that the population of points at location 33 is also trimodal, but in this case the means of the two upper populations are too closely similar to admit of separation by graphical means. Nonetheless, at location 34 and beyond to location 41 there is evidence that the populations of points are separable into three separate distributions indicating the presence of three distinct populations of cerci: these populations may also be reconstructed and the mean shape may be plotted for both of them in the fashion described for the reconstruction of the high form of the cerci. Plate 27 shows the reconstructed cerci of the high form and the two low forms of the cerci.

The statistical significance of these differences is difficult to evaluate. In particular the distributions of the two forms of the low cerci are exactly similar over large areas of the structures and they are markedly different only at the proximal ends of their outer edges. Furthermore, even the characters which necessitate separation of the low males at all overlap considerably. These distributions do however display distinct differences, the means of each of the distributions are consistently different for the locations 34 to 41. It is therefore necessary to postulate that the polymorphic group of male earwigs known as the low males is composed, not of a unimodally distributed single population but is in fact composed of two morphologically distinct and separate populations of animals.

Table 14 Shape Distributions Males * Cerci

1968

* Showing the occurrence of component distributions and their proportions in the total populations indicated by the prescence and absence of inflections in the arithmetic probability paper plots.

| Location | % | Inflection | % | Inflection | % |
|---|---|---|---|---|---|
| 1 | - | - | - | - | - |
| 2 | 0-100 | 0 | 0 | 0 | 0 |
| 3 | 0-10 | 10 | 90 | 0 | 0 |
| 4 | 0-10 | 10 | 90 | 0 | 0 |
| 5 | 0-10 | 10 | 90 | 0 | 0 |
| 6 | 0-12 | 12 | 88 | 0 | 0 |
| 7 | 0-12 | 12 | 88 | 0 | 0 |
| 8 | 0-12 | 12 | 88 | 0 | 0 |
| 9 | 0-15 | 15 | 85 | 0 | 0 |
| 10 | 0-10 | 10 | 90 | 0 | 0 |
| 11 | 0-10 | 10 | 90 | 0 | 0 |
| 12 | 0-9 | 9 | 91 | 0 | 0 |
| 13 | 0-10 | 10 | 90 | 0 | 0 |
| 14 | - | - | - | - | - |
| 15 | - | - | - | - | - |
| 16 | 0-100 | 0 | 0 | 0 | 0 |
| 17 | 0-100 | 0 | 0 | 0 | 0 |
| 18 | 0-100 | 0 | 0 | 0 | 0 |

Table 14 cont'd.

| Location | % | Inflection | % | Inflection | % |
|---|---|---|---|---|---|
| 19 | 0-100 | 0 | 0 | 0 | 0 |
| 20 | 0-100 | 0 | 0 | 0 | 0 |
| 21 | - | - | - | - | - |
| 22 | 0-12 | 12 | 88 | 0 | 0 |
| 23 | 0-12 | 12 | 88 | 0 | 0 |
| 24 | 0-12 | 12 | 88 | 0 | 0 |
| 25 | 0-12 | 12 | 88 | 0 | 0 |
| 26 | 0-13 | 13 | 87 | 0 | 0 |
| 27 | 0-12 | 12 | 87 | 0 | 0 |
| 28 | 0-12 | 12 | 88 | 0 | 0 |
| 29 | 0-12 | 12 | 88 | 0 | 0 |
| 30 | 0-12 | 12 | 88 | 0 | 0 |
| 31 | 0-10 | 10 | 90 | 0 | 0 |
| 32 | 0-10 | 10 | 90 | 0 | 0 |
| 33 | 0-10 | 10 | 90 | 0 | 0 |
| 34 | 0-9 | 9 | 56 | 65 | 35 |
| 35 | 0-8 | 8 | 62 | 70 | 30 |
| 36 | 0-10 | 10 | 50 | 60 | 40 |
| 37 | 0-9 | 9 | 56 | 65 | 35 |
| 38 | 0-9 | 9 | 63 | 72 | 28 |
| 39 | 0-9 | 9 | 66 | 75 | 25 |
| 40 | 0-10 | 10 | 62 | 72 | 28 |
| 41 | 0-9 | 9 | 66 | 75 | 25 |
| 42 | - | - | - | - | - |

Table 15 Means and Standard deviations of the component Sub-distributions derived from the analysis of the Shape distributions of Male Cerci for each Location.

| | 1st distribution | | 2nd distribution | | 3rd distribution | |
|---|---|---|---|---|---|---|
| Location | Mean | St.Dev. | Mean | St.Dev. | Mean | St.Dev. |
| 1 | - | - | - | - | - | - |
| 2 | 61.0 ± | 10.0 | 0 | 0 | 0 | 0 |
| 3 | 72.0 ± | 5.0 | 111.0 ± | 10.0 | 0 | 0 |
| 4 | 102.0 ± | 5.0 | 150.0 ± | 14.0 | 0 | 0 |
| 5 | 122.0 ± | 10.0 | 175.0 ± | 15.0 | 0 | 0 |
| 6 | 137.0 ± | 20.0 | 205.0 ± | 15.0 | 0 | 0 |
| 7 | 150.0 ± | 20.0 | 220.0 ± | 15.0 | 0 | 0 |
| 8 | 145.0 ± | 20.0 | 235.0 ± | 20.0 | 0 | 0 |
| 9 | 130.0 ± | 20.0 | 245.0 ± | 20.0 | 0 | 0 |
| 10 | 130.0 ± | 20.0 | 235.0 ± | 20.0 | 0 | 0 |
| 11 | 110.0 ± | 35.0 | 220.0 ± | 20.0 | 0 | 0 |
| 12 | 100.0 ± | 20.0 | 185.0 ± | 20.0 | 0 | 0 |
| 13 | 85.0 ± | 20.0 | 155.0 ± | 15.0 | 0 | 0 |
| 14 | - | - | - | - | - | - |
| 15 | - | - | - | - | - | - |
| 16 | -5.0 ± | 15.0 | 0 | 0 | 0 | 0 |
| 17 | -20.0 ± | 25.0 | 0 | 0 | 0 | 0 |
| 18 | -45.0 ± | 15.0 | 0 | 0 | 0 | 0 |
| 19 | -45.0 ± | 15.0 | 0 | 0 | 0 | 0 |
| 20 | -30.0 ± | 20.0 | 0 | 0 | 0 | 0 |

Table 15 cont'd.

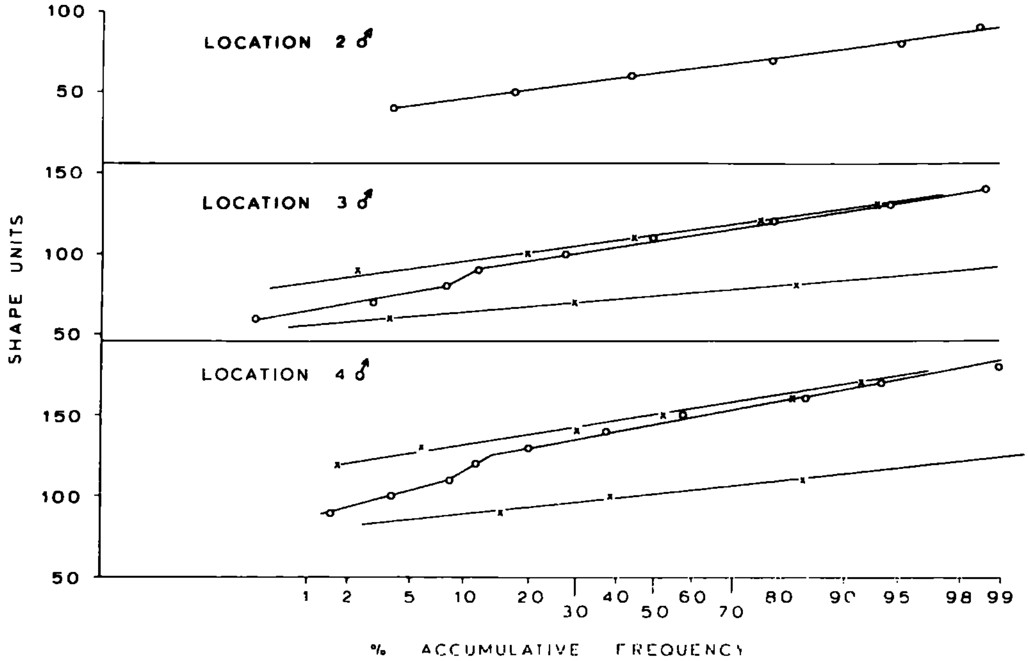
| Location | Mean | St.Dev. | Mean | St.Dev. | Mean | St.Dev. |
|---|---|---|---|---|---|---|
| 21 | - | - | - | - | - | - |
| 22 | 60.0 ± | 15.0 | 140.0 ± | 25.0 | 0 | 0 |
| 23 | 125.0 ± | 15.0 | 205.0 ± | 25.0 | 0 | 0 |
| 24 | 155.0 ± | 20.0 | 250.0 ± | 20.0 | 0 | 0 |
| 25 | 185.0 ± | 20.0 | 285.0 ± | 25.0 | 0 | 0 |
| 26 | 205.0 ± | 25.0 | 315.0 ± | 25.0 | 0 | 0 |
| 27 | 220.0 ± | 35.0 | 335.0 ± | 25.0 | 0 | 0 |
| 28 | 230.0 ± | 30.0 | 350.0 ± | 25.0 | 0 | 0 |
| 29 | 230.0 ± | 30.0 | 365.0 ± | 30.0 | 0 | 0 |
| 30 | 240.0 ± | 35.0 | 370.0 ± | 30.0 | 0 | 0 |
| 31 | 225.0 ± | 25.0 | 370.0 ± | 30.0 | 0 | 0 |
| 32 | 215.0 ± | 40.0 | 370.0 ± | 30.0 | 0 | 0 |
| 33 | 210.0 ± | 20.0 | 360.0 ± | 35.0 | 0 | 0 |
| 34 | 195.0 ± | 30.0 | 330.0 ± | 25.0 | 375.0 ± | 20.0 |
| 35 | 180.0 ± | 15.0 | 320.0 ± | 30.0 | 365.0 ± | 30.0 |
| 36 | 170.0 ± | 25.0 | 300.0 ± | 20.0 | 355.0 ± | 25.0 |
| 37 | 160.0 ± | 20.0 | 285.0 ± | 30.0 | 345.0 ± | 20.0 |
| 38 | 145.0 ± | 15.0 | 275.0 ± | 30.0 | 340.0 ± | 25.0 |
| 39 | 145.0 ± | 20.0 | 270.0 ± | 35.0 | 340.0 ± | 25.0 |
| 40 | 145.0 ± | 25.0 | 270.0 ± | 30.0 | 345.0 ± | 25.0 |
| 41 | 145.0 ± | 20.0 | 280.0 ± | 35.0 | 360.0 ± | 20.0 |

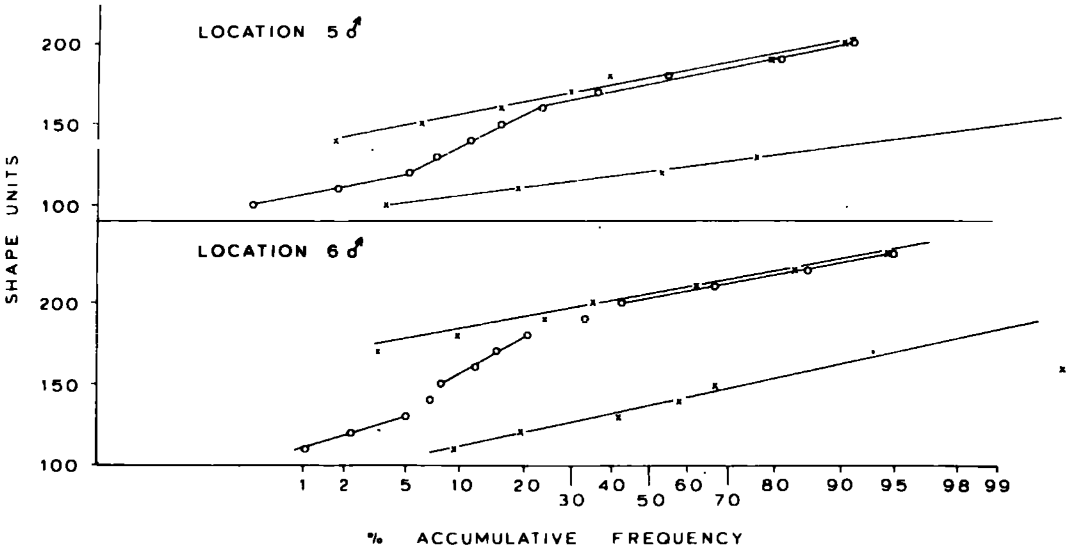
Plate 9. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 2, 3, 4, 5, 6 and 7, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.

KEY

—o———o— Observed polymodal frequency distribution

—x———x— Component normal distributions derived by Cassie's Method





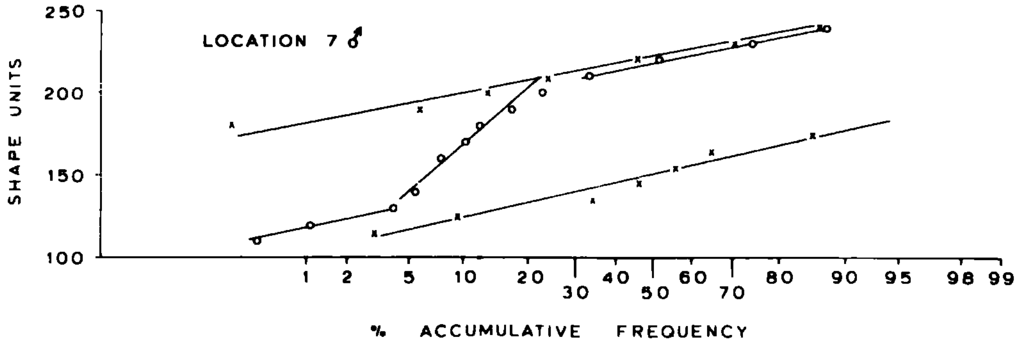
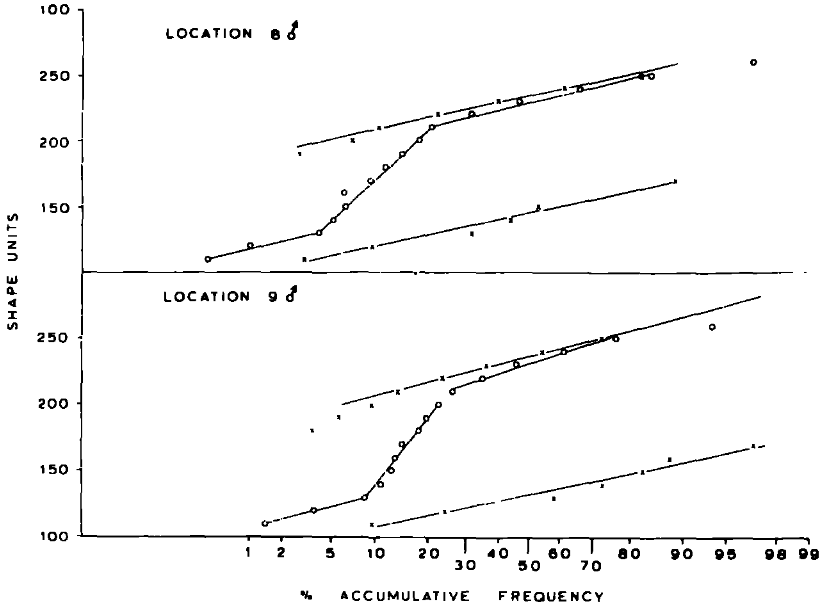


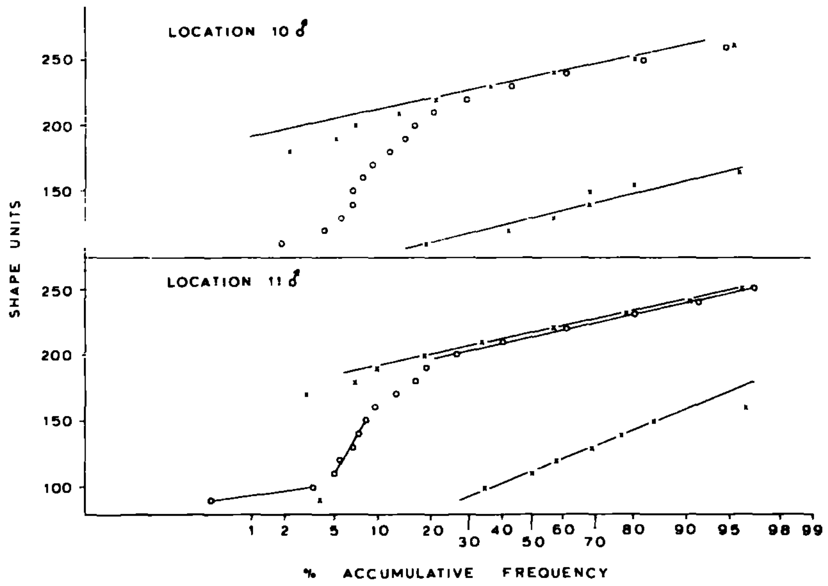
Plate 10. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 8, 9, 10, 11, 12 and 13, of the Sample of Male Cerci Plotted on Arithmetic Probability Paper.

KEY

—o——o— Observed polymodal frequency distribution

—x——x— Component normal distributions derived by Cassie's Method.





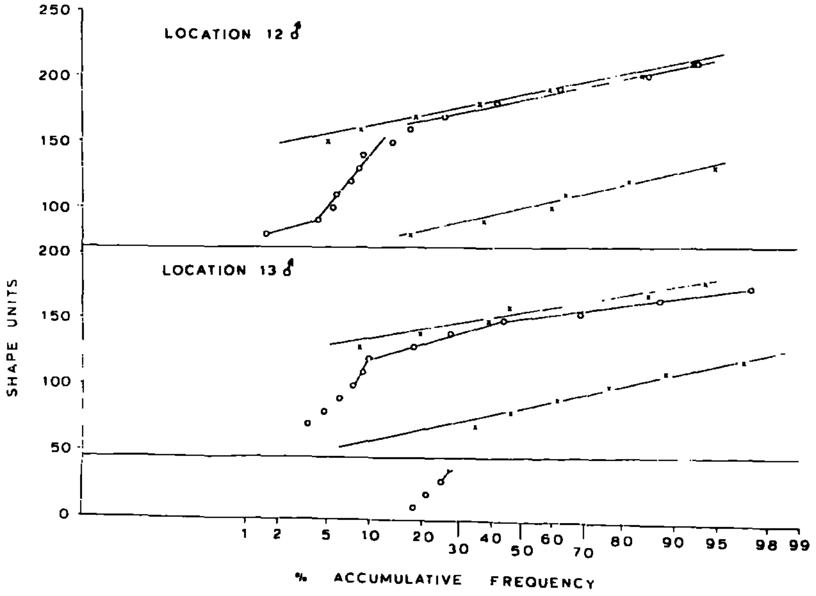
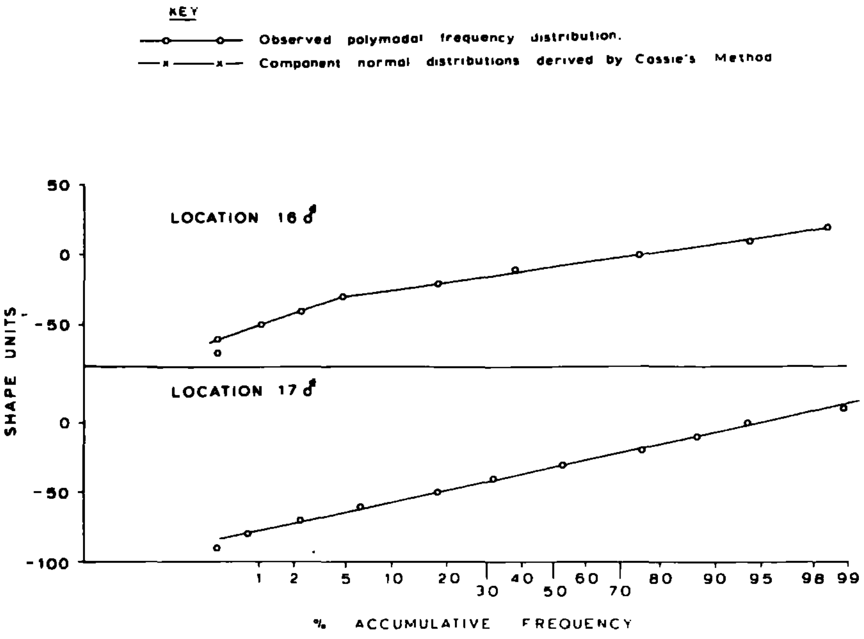
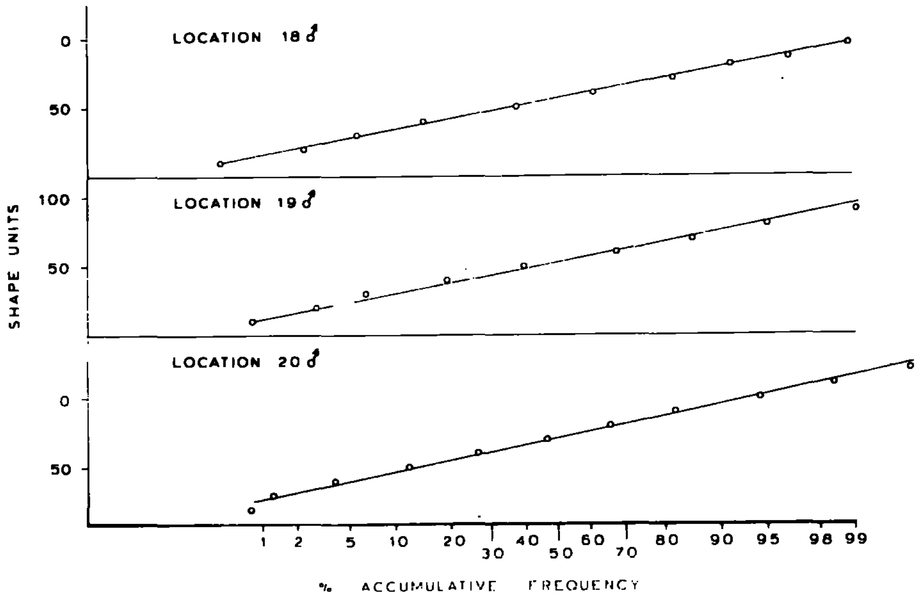


Plate 11. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 16, 17, 18, 19, 20, 22 and 23, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.


KEY
—o—o— Observed polymodal frequency distribution.
—x—x— Component normal distributions derived by Cassie's Method
LOCATION 16 ♂
LOCATION 17 ♂
SHAPE UNITS
50
0
-50
0
-50
-100
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY


LOCATION 18 ♂
LOCATION 19 ♂
LOCATION 20 ♂
SHAPE UNITS
0
50
100
50
0
50
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY

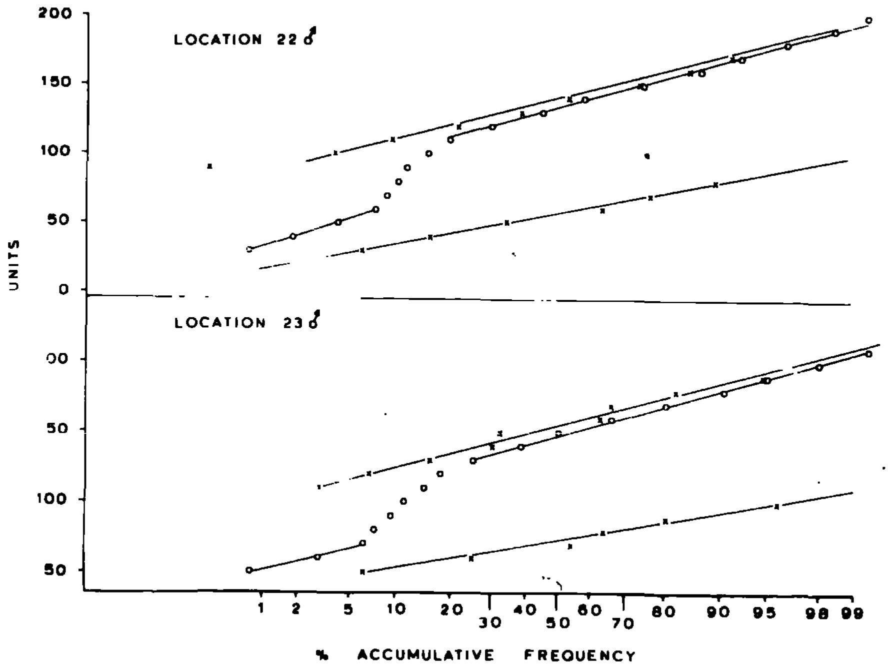
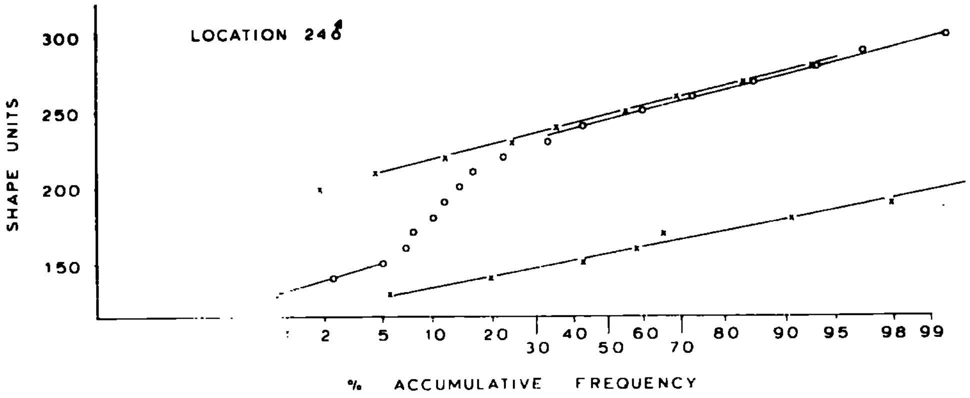

LOCATION 22 ♂
LOCATION 23 ♂
UNITS
200
150
100
50
0
00
50
100
50
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY

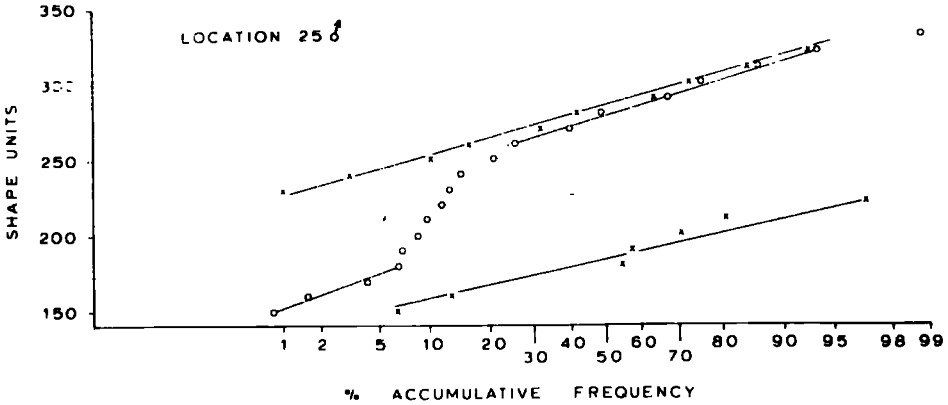
Plate 12. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 24, 25 and 26, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.

KEY

—o———o— Observed polymodal frequency distribution.

—x———x— Component normal distributions derived by Cassie's Method.





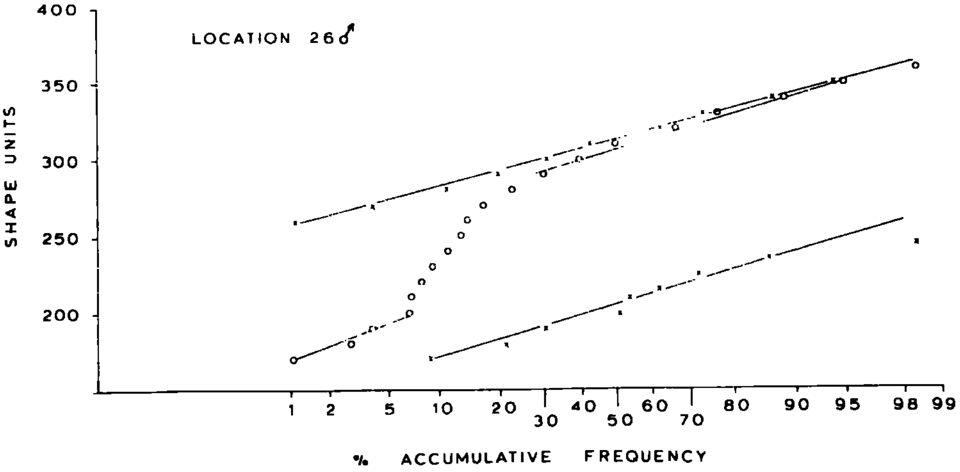
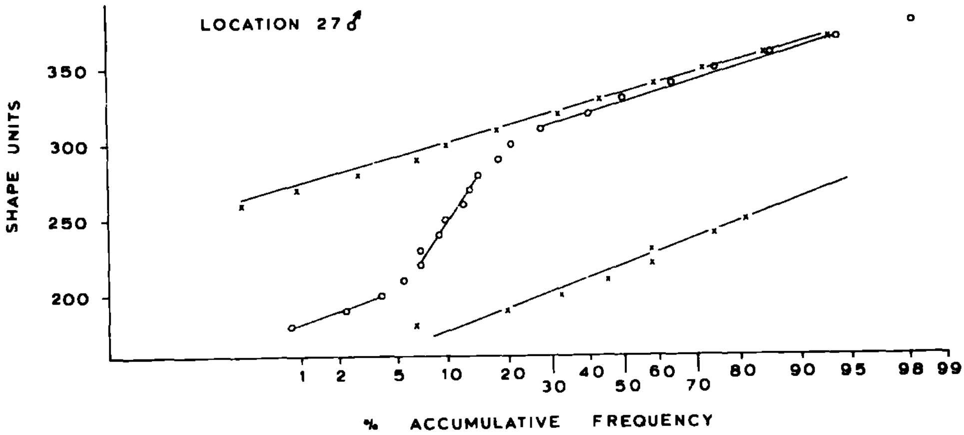


Plate 13. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 27, 28 and 29, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.

KEY

—o———o— Observed polymodal frequency distribution.

—x———x— Component normal distributions derived by Cassie's Method.



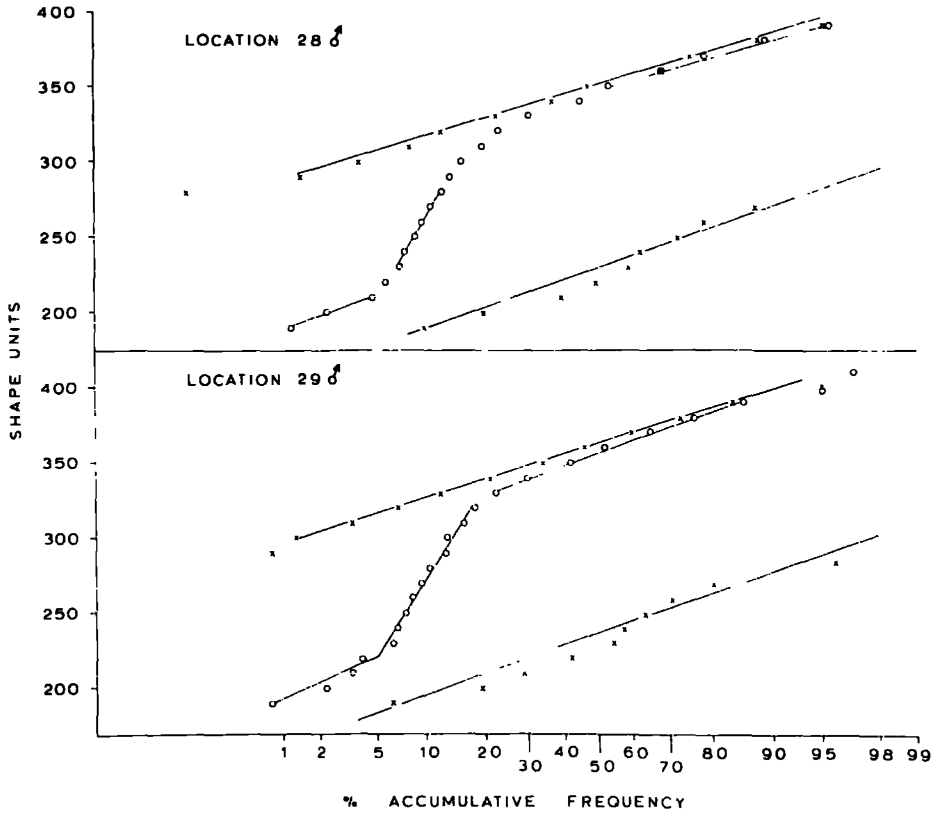
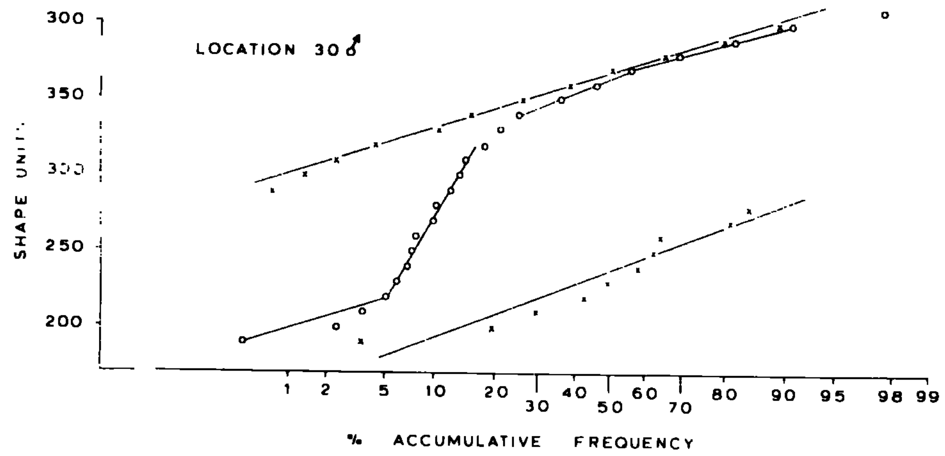


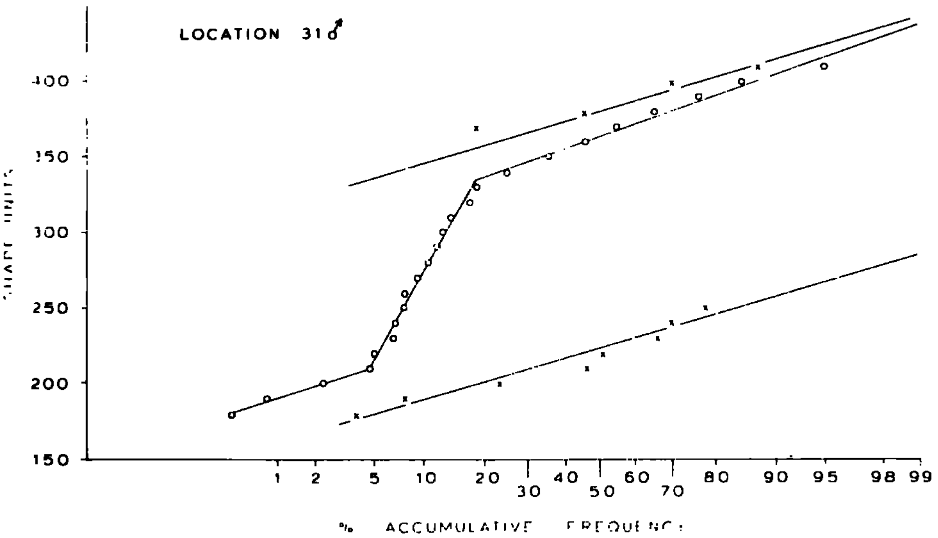
Plate 14. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 30, 31 and 32, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.

KEY

—o——o— Observed polymodal frequency distribution

—x——x— Component normal distributions derived by Cassie's Method





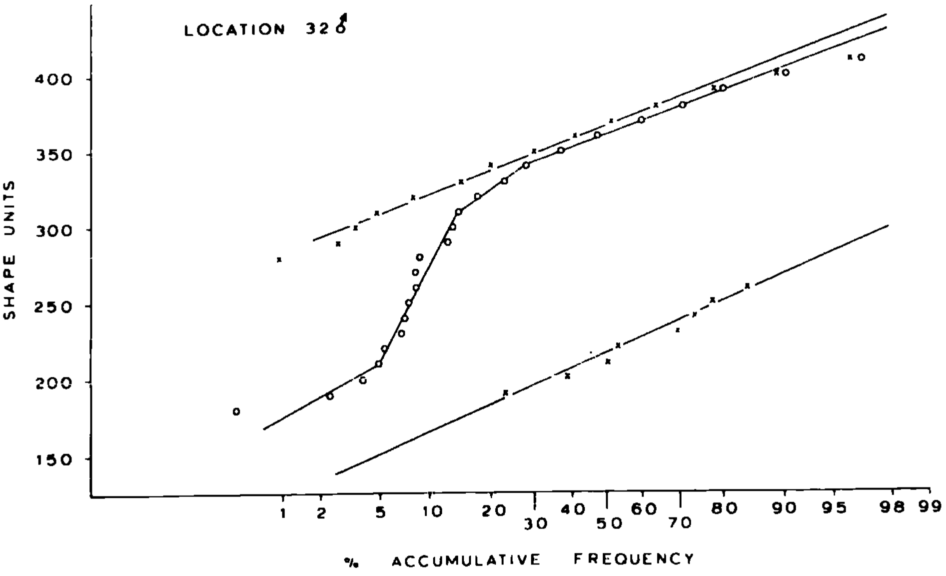
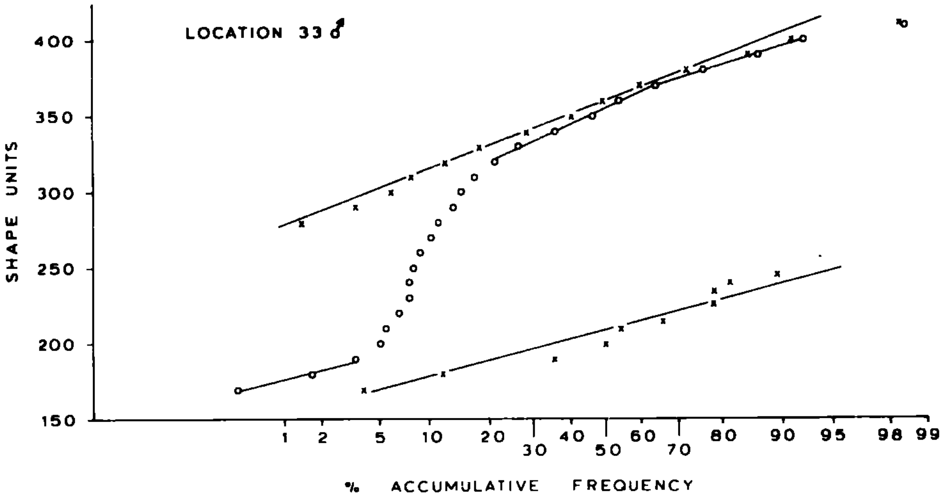


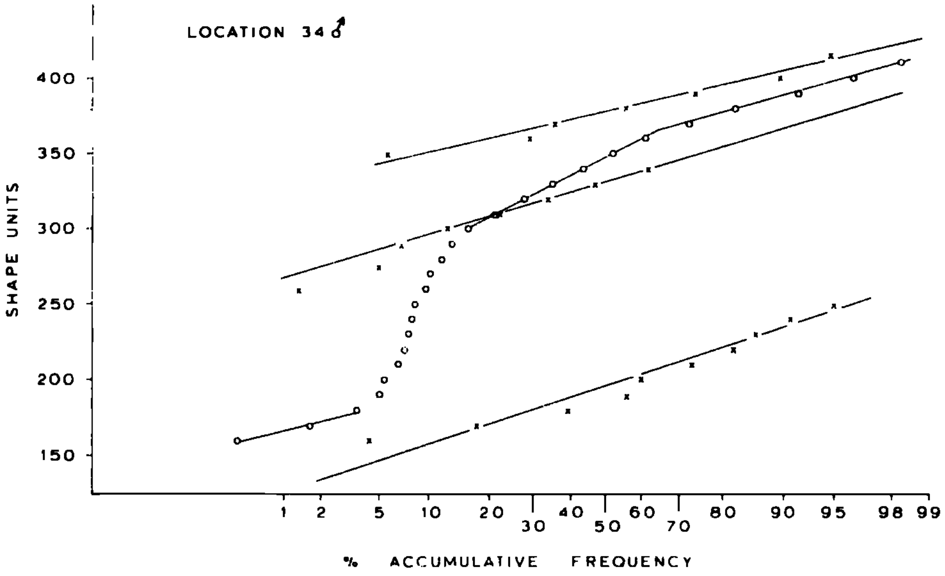
Plate 15. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 33, 34 and 35, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.

KEY

—o——o— Observed polymodal frequency distribution

—x——x— Component normal distributions derived by Cassie's Method.





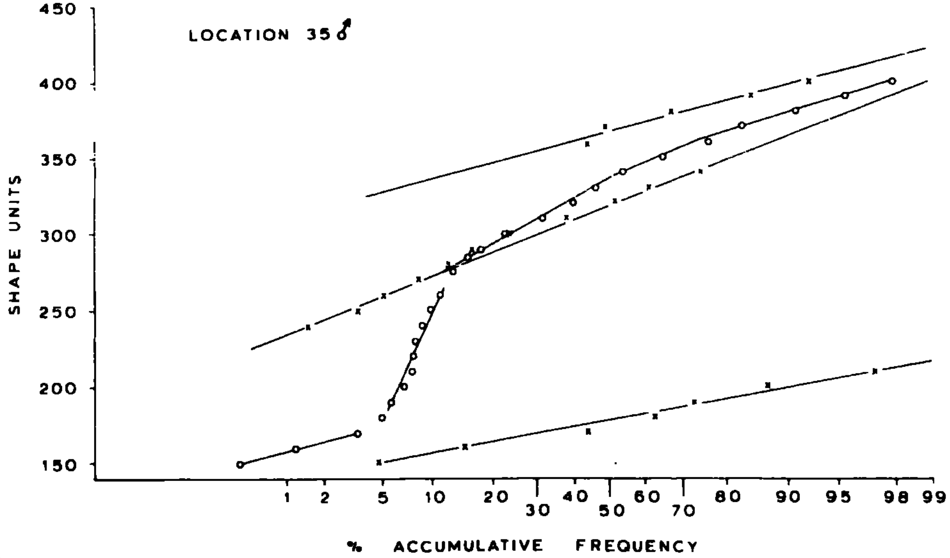
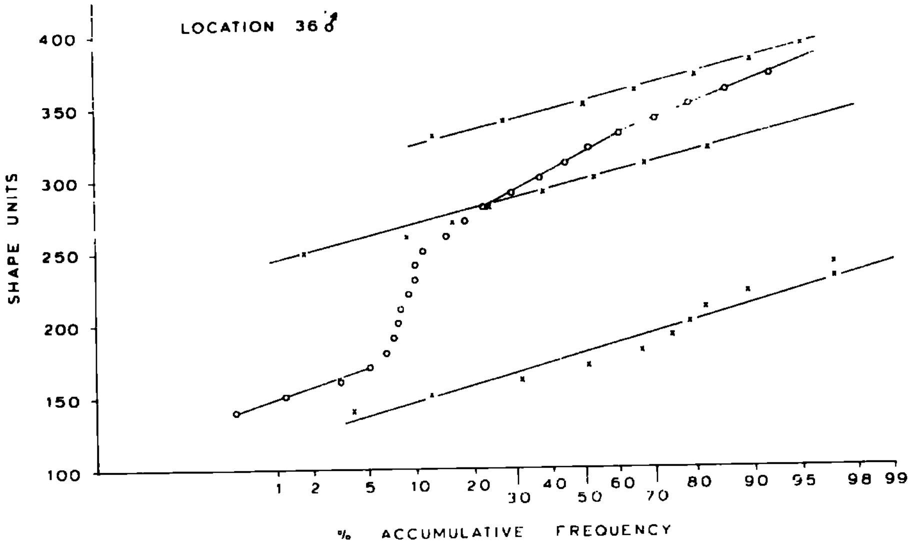


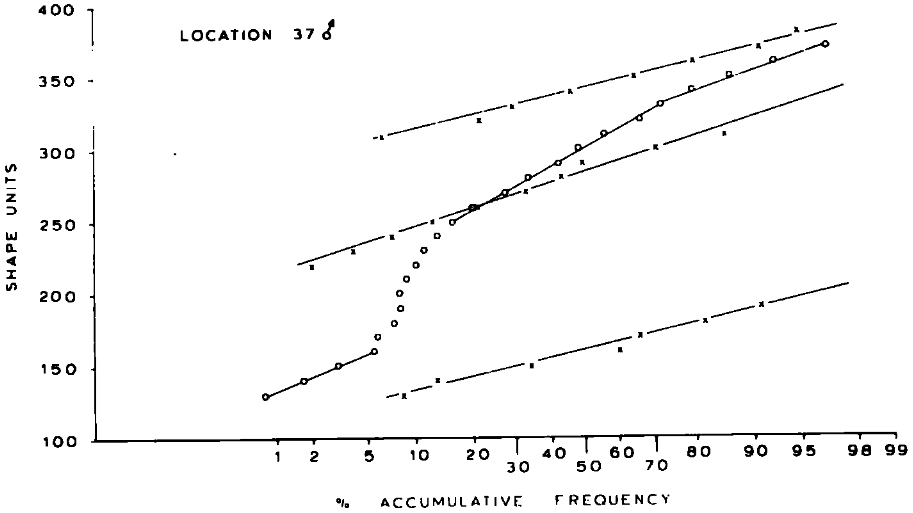
Plate 16. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 36, 37 and 38, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.

KEY

—o——o— Observed polymodal frequency distribution

—x——x— Component normal distributions derived by Cassie's Method





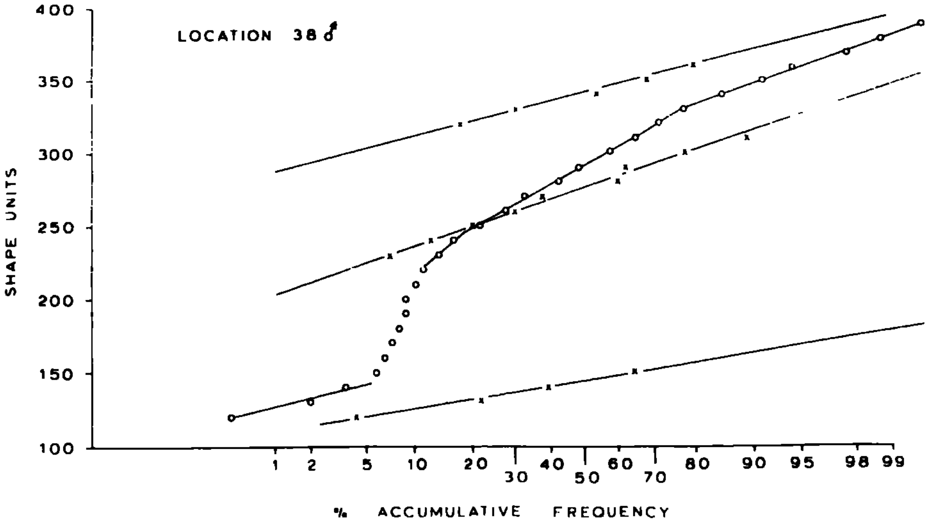
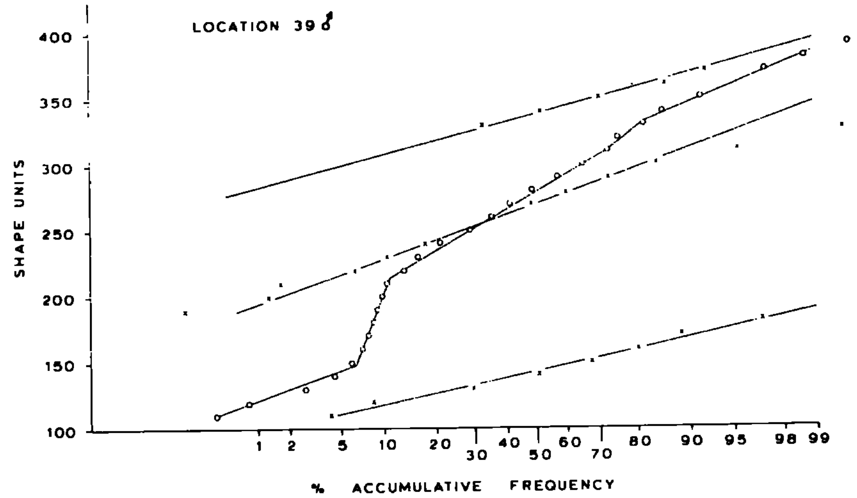


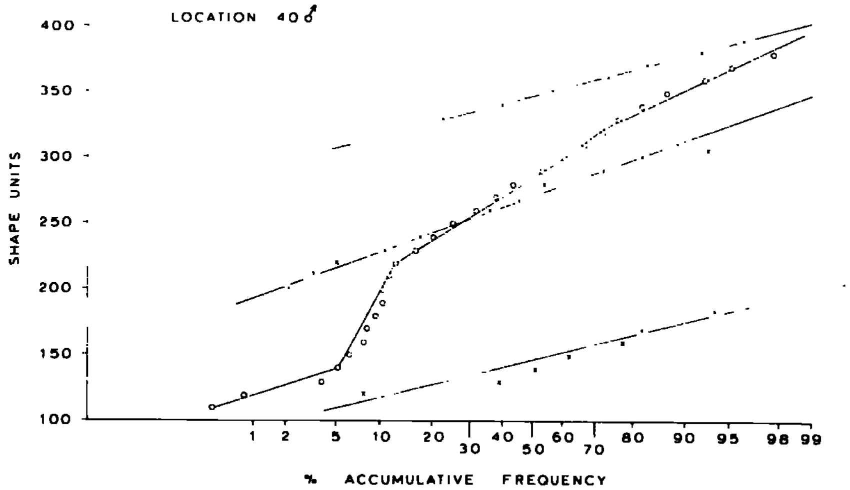
Plate 17. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 39, 40 and 41, of the Sample of Male Cerci. Plotted on Arithmetic Probability Paper.

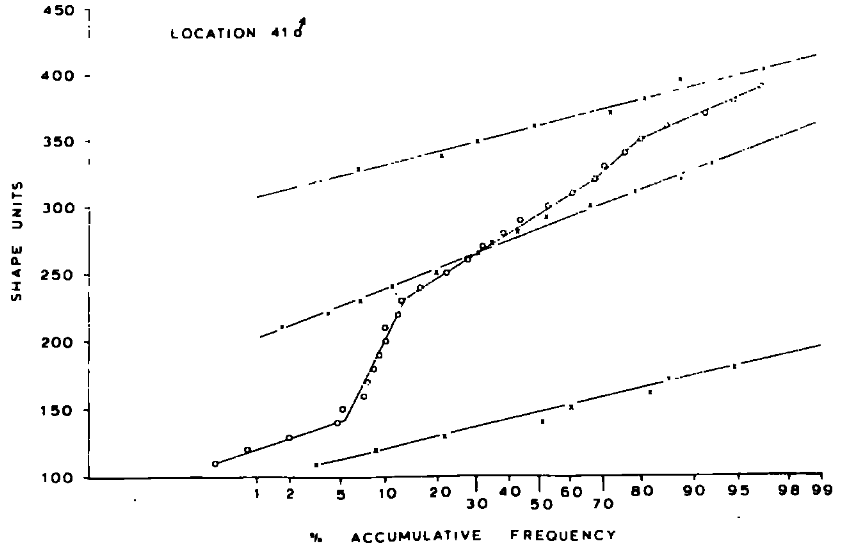
**KEY**

—○——○— Observed polymodal frequency distribution

—×——×— Component normal distributions derived by Cassie's Method







Concerning the units used in Tables 15 and 17, they are termed "shape units" because of their derivation. The units represent the mean lengths of the ordinates constructed at each location in the grid. The grid is ten centimetres along the abscissa, and this measurement corresponds to 1000 shape units. Each unit represents 0.1 of a millimetre. This bears no relation to the absolute sizes of the organs used in this study since the absolute sizes of these specimens are modified in the preparation of the rectified image.

## Females

The investigation of the variability in shape of the female cercus was carried out making use of the same techniques as those used in the analysis of the variability of the male cercus, with one modification. The coordinates output by the computer were rounded to the nearest 3 units, corresponding to 0.3 mms. on the rectified image. This rounding is much less drastic than the corresponding rounding applied to the coordinates derived in the study of variation in shape of the male cercus, but represents nonetheless the same compromise between smoothing the effects of random experimental error while retaining the maximum information derived from the computer.

The cerci of the sample of females used in this investigation were far less variable than the cerci of the males, and as there was even less evidence derived from direct measurement, to suggest the presence of polymorphism the absolute minimum of smoothing, concommittant with a consistent pattern was essential.

The coordinates were plotted on arithmetic probability paper in a manner exactly similar to the coordinates of the male cerci.

From inspection of curves derived from the females, Plates 18-26, it is immediately evident that there is far less variability in the form of the female cerci, than is present in those of the male. It is however, possible to draw some general conclusions from a careful study of the curves. In almost all cases there is some indication of at least one inflection, sited at the lower end of the curve, approximately corresponding to the 5% - 10% points of the abscissa, and although it is almost completely absent in the distributions at locations 25 to 28, this inflection indicates the possibility that there may be some polymorphism in the female Earwig corresponding to the high form of the male, as well as a more numerous low form. In locations 23, 24, Plate 21 as well as 30, 31, 32, 33, 34 and 35, there is an indication of yet a second inflection, towards the upper end of the distribution in every case.

This second inflection is not easily seen and it is impossible to locate with any real accuracy for two reasons: the shape of the curve suggests that there are a large number of individuals present which are intermediates between the second (middle) distribution, and the third. For this reason there is no clear point of inflection, the second reason is that the inflection is so subtle that it is only marginally resolved even by the projection technique.

In view of the consistency with which the second inflection occurs, particularly as it does so in many adjacent locations the conclusion that the population of points at these locations is made up of three separate component normal distributions is unavoidable. As a consequence it must be concluded that the population of female cerci, considering the form of the complete cercus, must be made up of three separate polymorphic forms. Furthermore there is some similarity between the division of the males into three separate groups and the division of the females. The proportions of each population of Earwigs which are accounted for by a given sub-population of a single polymorphic type are similar. This similarity is most marked in the components in each distribution with the lowest means. As explained above, the populations of points derived from rectified images tend to invert the absolute sizes of the specimens, and that for this reason the component distributions with the largest mean size represent the smallest individual cercus population. Therefore the population of female cerci, corresponding to the high male cerci, are indicated by the lowest, and clearly marked sub-population of points derived from the separate locations. It is therefore concluded that in terms of the shape of cercus, there is a population of female Earwigs which correspond to the high form of the male, and that it appears approximately as frequently in the population as the high form of the male.

It would be piling Pelion on Ossa to suggest that the third population, which is at best only tenuously indicated, represented the third polymorphic form of the male in the female; the evidence hardly merits that degree of confidence, nonetheless, for the sake of uniformity between the sexes, a concept that has been ignored previously, in the study of Earwig polymorphism, it is a seductive speculation, which the evidence does not disprove.

The detailed analysis of the point distributions is far more problematical than the analysis of the males. Since it is impossible to locate all the inflections of the curves with precision, it would be sophistical to try to assign the inflections in an arbitary fashion, and to derive evidence from a circular statistical argument, in support of this analysis. It is for this reason that a complete statistical consideration of the curves produced for the shapes of the female cerci has not been attempted. The curves must stand by themselves, as evidence for the polymorphism of the females. Nevertheless, with respect to the variability of the female cercus, analogous to the high - low dichotomy of the male cercus types, it has proved possible to carry out some approximate analysis.

By neglecting the second inflection for statistical purposes and considering the population composition as being made up of two components, one corresponding to the high form of the male and the other corresponding to the two low types of the male combined, it is possible to divide the polymodal distributions of the ordinates from the different locations of the female cerci by methods of the type described in the section dealing with variability of the male cercus, and which are fully described in Appendix (i).

The results of such an analysis are given in summary in Tables 16 and 17. At most locations the ordinate distribution appears to be normal, but there are clear indications at locations 31 to 42, Plates 23 - 26, of bimodality. Furthermore the consistency with which this bimodality.is manifested indicates that there is some similarity between the situation observed in the high male - low male relationship, in terms of the proportion each of the component female distributions contributes to the total distribution at each of the bimodal locations.

Table 17 shows the means and standard deviations of the component distributions derived from each location along the edges of the female cerci. The two female cercus types which correspond to the generalized low male, and to the high male type are reconstructed in Plate 28. It is possible that the low cercus type of the female may be further separated into two components corresponding to the two low male types, unfortunately, there is insufficient evidence available for this task to be attempted at this time.

Table 16 Shape Distributions Females 1968

Cerci

| Location | % | Inflection | % |
|---|---|---|---|
| 31 | 0 - 10 | 10 | 90 |
| 32 | 0 - 11 | 11 | 89 |
| 33 | 0 - 12 | 12 | 88 |
| 34 | 0 - 12 | 12 | 88 |
| 35 | 0 - 12 | 12 | 88 |
| 36 | 0 - 7 | 7 | 93 |
| 37 | 0 - 10 | 10 | 90 |
| 38 | 0 - 12 | 12 | 88 |
| 39 | 0 - 11 | 11 | 89 |
| 40 | 0 - 8 | 8 | 91 |
| 41 | 0 - 7 | 7 | 93 |
| 42 | 0 - 5 | 5 | 95 |

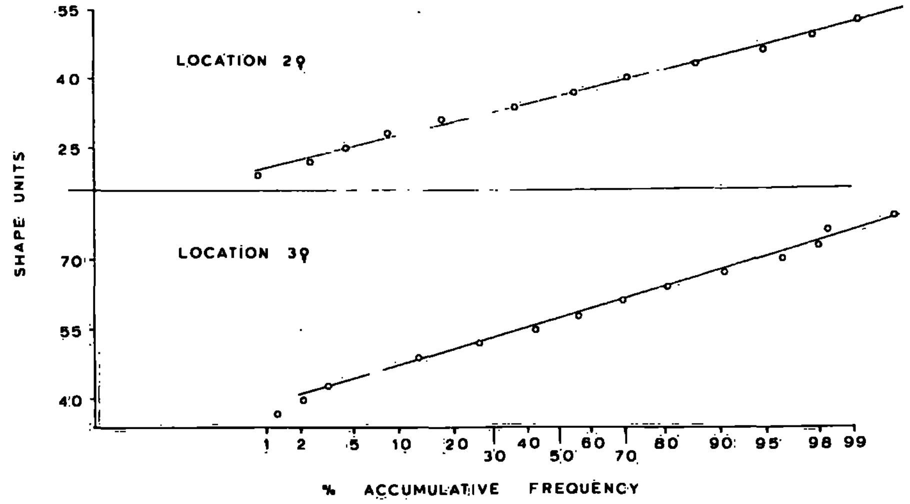
Table 17 Means and Standard Deviations of the Component Sub-distributions derived from the analysis of the Shape Distributions of Female cerci for each Location

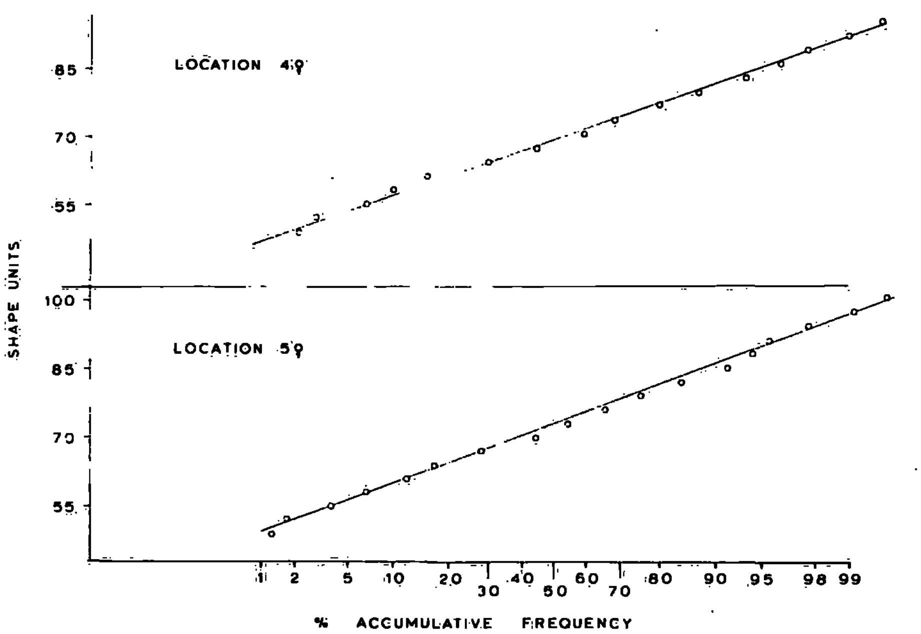
| Location | Mean | St.Dev. | Mean | St.Dev. |
|---|---|---|---|---|
| 1 | - | - | - | - |
| 2 | 37.0 ± | 6.0 | - | - |
| 3 | 58.0 ± | 9.0 | - | - |
| 4 | 67.0 ± | 6.0 | - | - |
| 5 | 73.0 ± | 9.0 | - | - |
| 6 | 73.0 ± | 12.0 | - | - |
| 7 | 67.0 ± | 18.0 | - | - |
| 8 | 61.0 ± | 12.0 | - | - |
| 9 | 52.0 ± | 9.0 | - | - |
| 10 | 46.0 ± | 9.0 | - | - |
| 11 | 40.0 ± | 12.0 | - | - |
| 12 | 34.0 ± | 12.0 | - | - |
| 13 | 28.0 ± | 9.0 | - | - |
| 14 | 22.0 ± | 9.0 | - | - |
| 15 | 13.0 ± | 6.0 | - | - |
| 16 | 7.0 ± | 3.0 | - | - |
| 17 | 1.0 ± | 6.0 | - | - |
| 18 | -5.0 ± | 3.0 | - | - |
| 19 | -2.0 ± | 6.0 | - | - |
| 20 | 28.0 ± | 9.0 | - | - |
| 21 | 28.0 ± | 9.0 | - | - |

Table 17 cont'd.

| Location | Mean | St.Dev. | Mean | St.Dev. |
|---|---|---|---|---|
| 22 | 55.0 ± | 12.0 | - | - |
| 23 | 112.0 ± | 9.0 | - | - |
| 24 | 139.0 ± | 9.0 | - | - |
| 25 | 154.0 ± | 9.0 | - | - |
| 26 | 166.0 ± | 12.0 | - | - |
| 27 | 172.0 ± | 12.0 | - | - |
| 28 | 175.0 ± | 12.0 | - | - |
| 29 | 175.0 ± | 12.0 | - | - |
| 30 | 157.0 ± | 6.0 | 178.0 ± | 9.0 |
| 31 | 154.0 ± | 3.0 | 178.0 ± | 9.0 |
| 32 | 157.0 ± | 3.0 | 181.0 ± | 12.0 |
| 33 | 160.0 ± | 6.0 | 181.0 ± | 9.0 |
| 34 | 160.0 ± | 6.0 | 184.0 ± | 9.0 |
| 35 | 166.0 ± | 9.0 | 187.0 ± | 9.0 |
| 36 | 166.0 ± | 6.0 | 193.0 ± | 12.0 |
| 37 | 178.0 ± | 12.0 | 202.0 ± | 9.0 |
| 38 | 187.0 ± | 12.0 | 214.0 ± | 15.0 |
| 39 | 202.0 ± | 15.0 | 232.0 ± | 18.0 |
| 40 | 217.0 ± | 9.0 | 253.0 ± | 18.0 |
| 41 | 232.0 | 12.0 | 274.0 ± | 18.0 |
| 42 | 235.0 ± | 15.0 | 289.0 ± | 18.0 |

Plate 18. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 2, 3, 4, 5, 6 and 7, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.


LOCATION 2♀
LOCATION 3♀
SHAPE UNITS
55
40
25
70
55
40
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY


LOCATION 4♀
LOCATION 5♀
SHAPE UNITS
85
70
55
100
85
70
55
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY

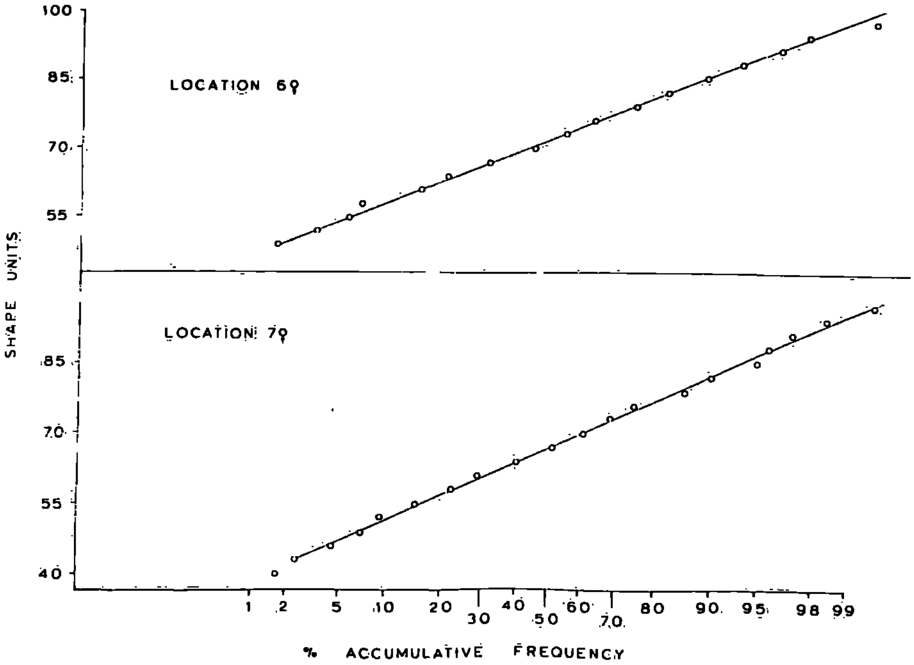
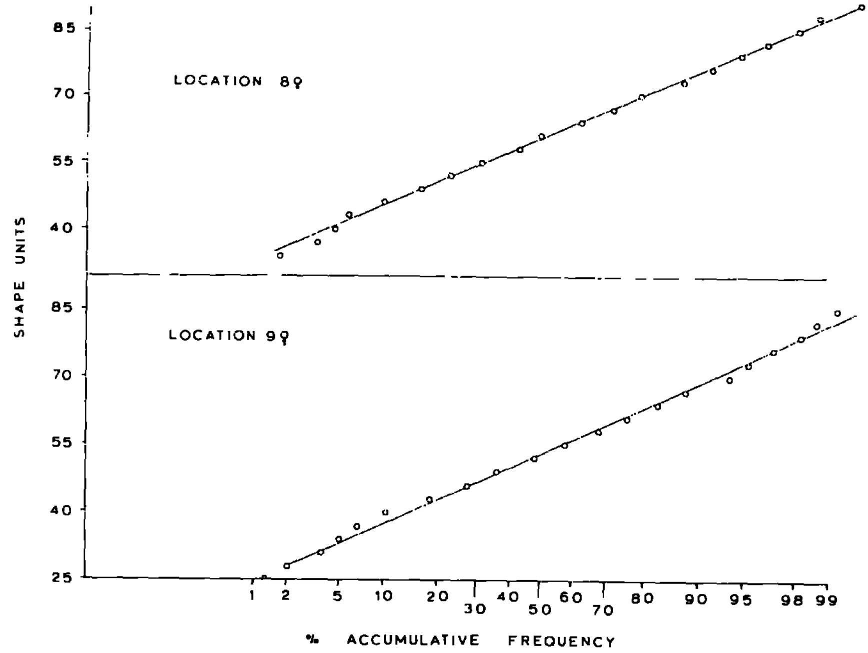
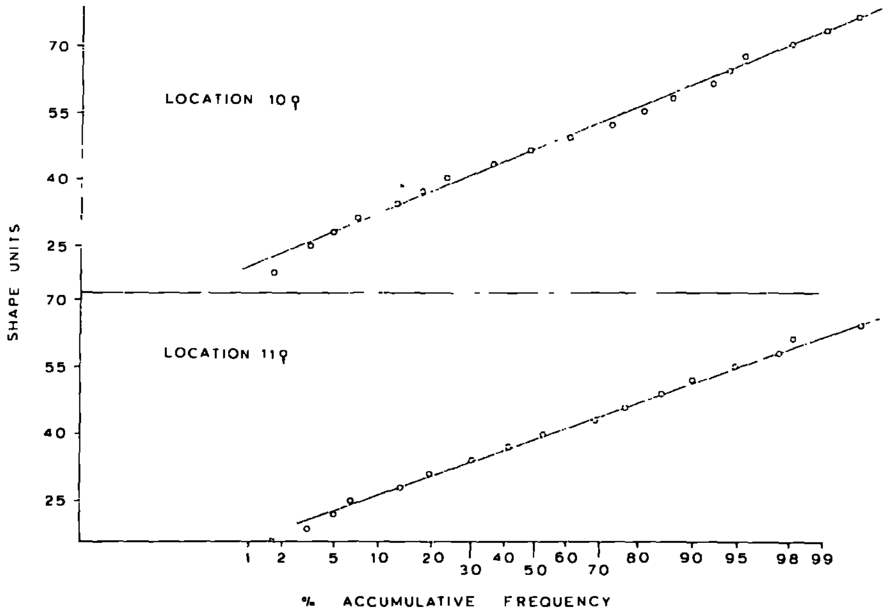

LOCATION 6♀
LOCATION 7♀
SHAPE UNITS
100
85
70
55
85
70
55
40
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY

Plate 19. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 8, 9, 10, 11, 12 and 13, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.


LOCATION 8♀
LOCATION 9♀
SHAPE UNITS
85
70
55
40
85
70
55
40
25
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY


LOCATION 10♀
LOCATION 11♀
SHAPE UNITS
70
55
40
25
70
55
40
25
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

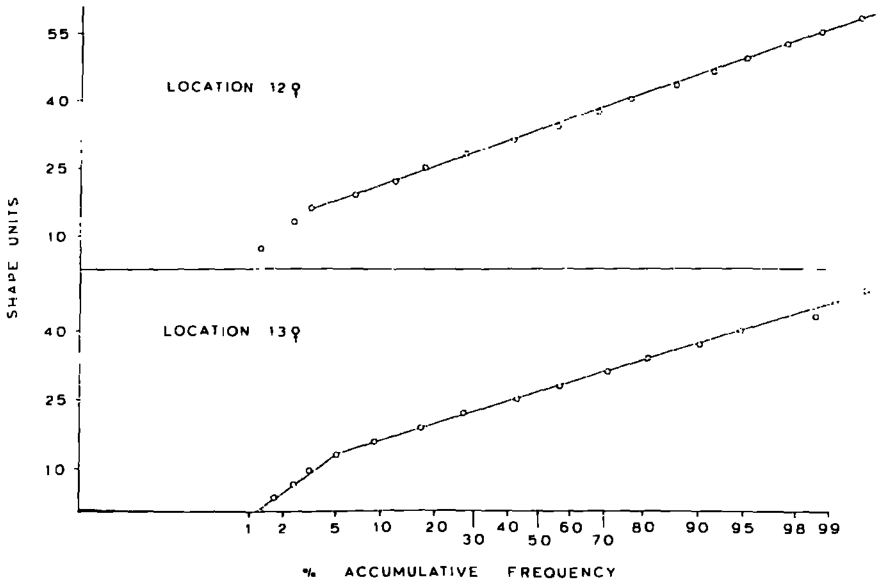
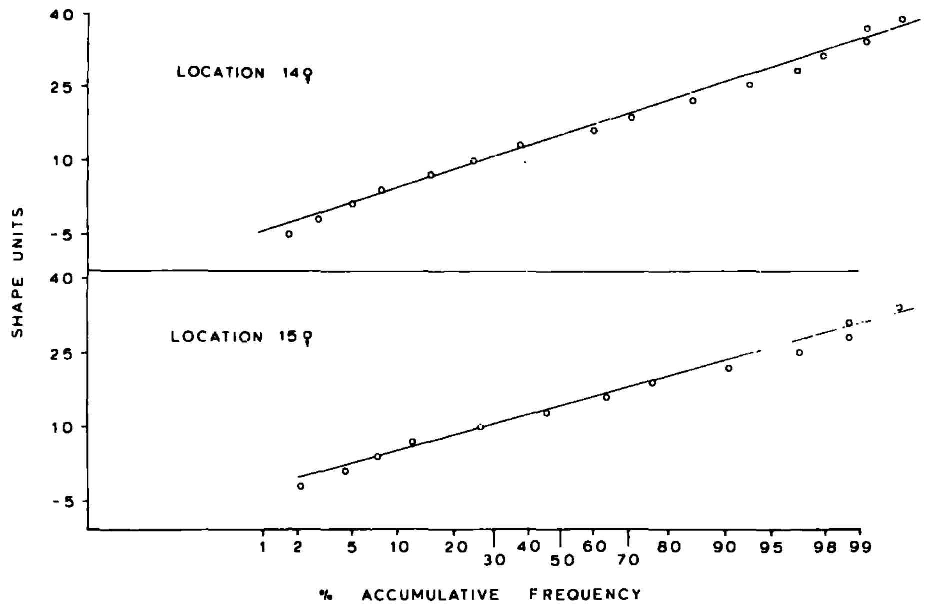
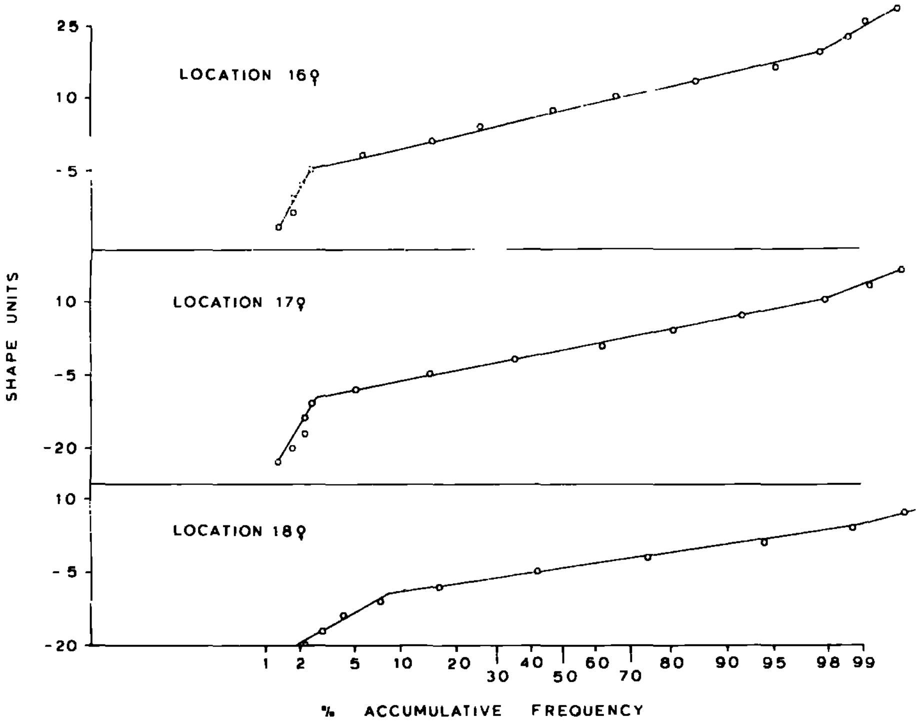

LOCATION 12♀
LOCATION 13♀
SHAPE UNITS
55
40
25
10
40
25
10
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

Plate 20. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 14, 15, 16, 17, 18, 19 and 20, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.


LOCATION 14♀
LOCATION 15♀
SHAPE UNITS
40
25
10
-5
40
25
10
-5
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY


LOCATION 16♀
LOCATION 17♀
LOCATION 18♀
SHAPE UNITS
25
10
-5
10
-5
-20
10
-5
-20
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY

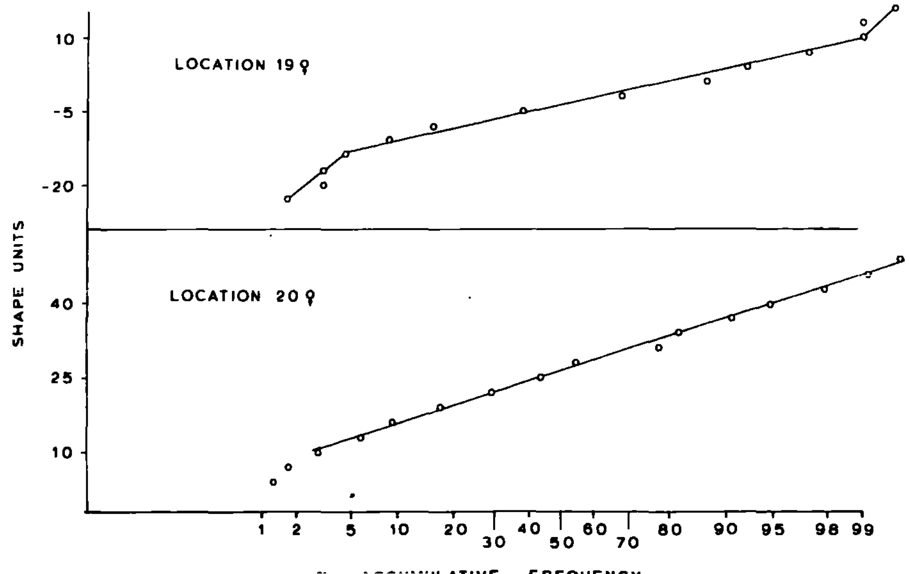
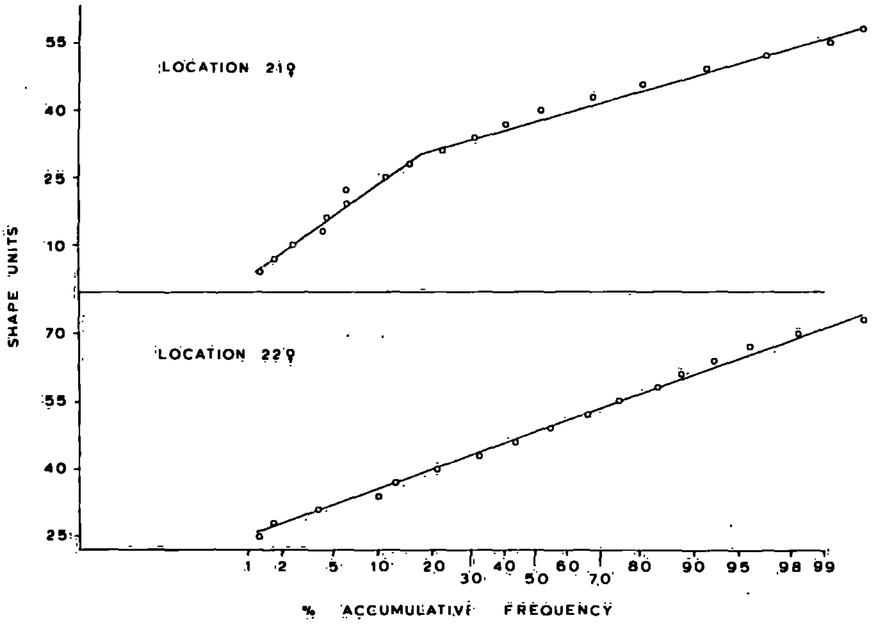
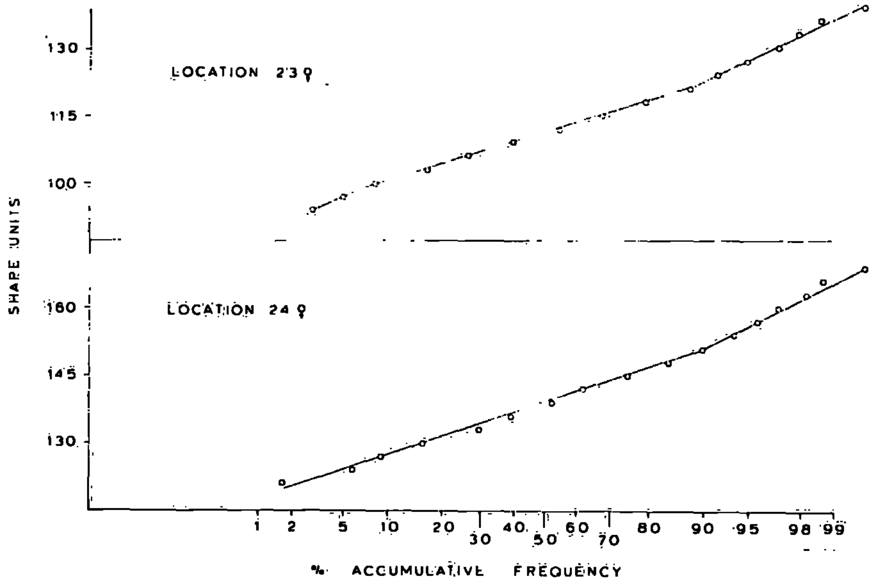

LOCATION 19♀
LOCATION 20♀
SHAPE UNITS
10
-5
-20
40
25
10
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99

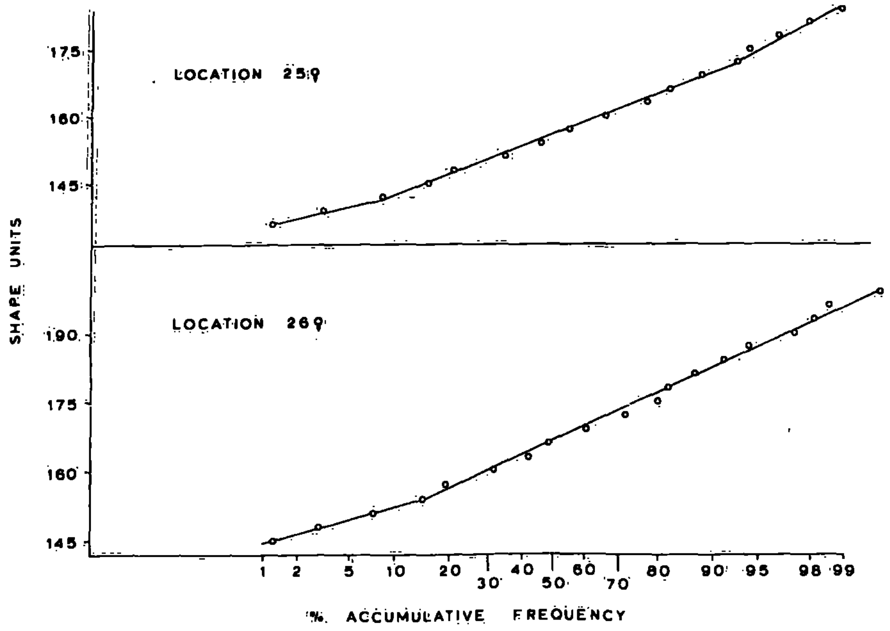
Plate 21. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 21, 22, 23, 24, 25 and 26, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.



LOCATION 21♀
LOCATION 22♀
SHAPE UNITS
55
40
25
10
70
55
40
25
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY

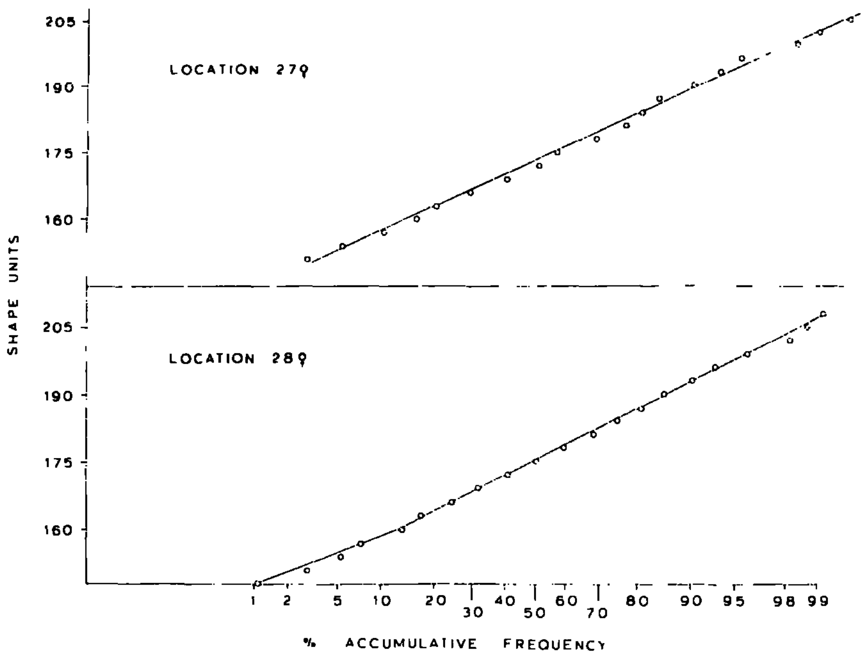


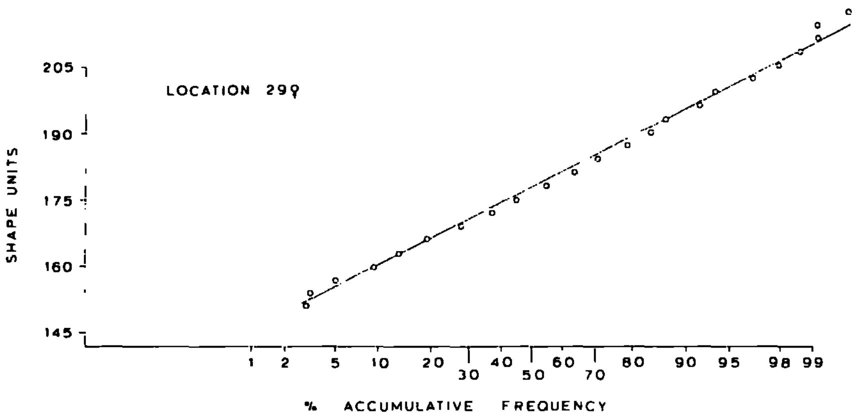
LOCATION 23♀
LOCATION 24♀
SHAPE UNITS
130
115
100
160
145
130
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY



LOCATION 25♀
LOCATION 26♀
SHAPE UNITS
175
160
145
190
175
160
145
1 2 5 10 20 30 40 50 60 70 80 90 95 98 99
% ACCUMULATIVE FREQUENCY

Plate 22. Accumulative Percentage Frequency Distribution of the Shape Indices of Locations 27, 28, 29 and 30, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.


LOCATION 27♀
LOCATION 28♀
SHAPE UNITS
205
190
175
160
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY


LOCATION 29♀
SHAPE UNITS
205
190
175
160
145
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

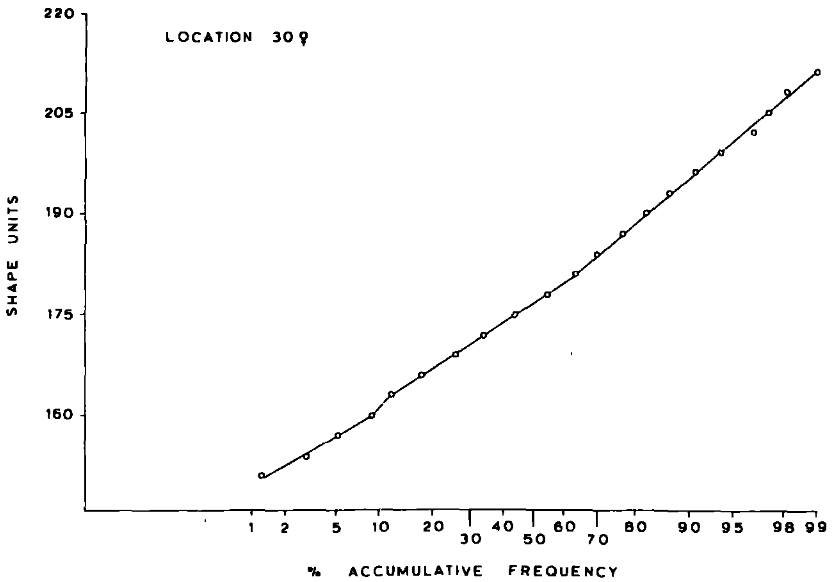
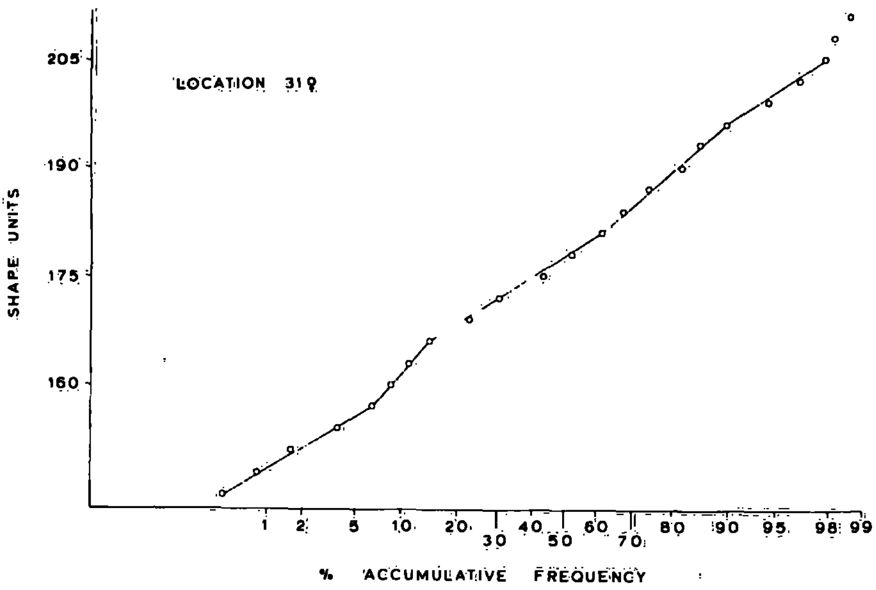
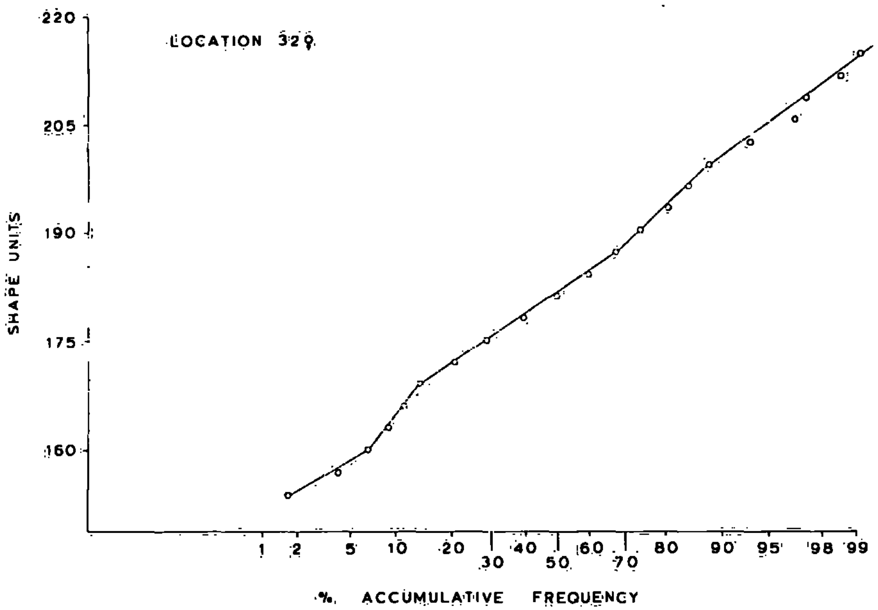

LOCATION 30♀
SHAPE UNITS
220
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

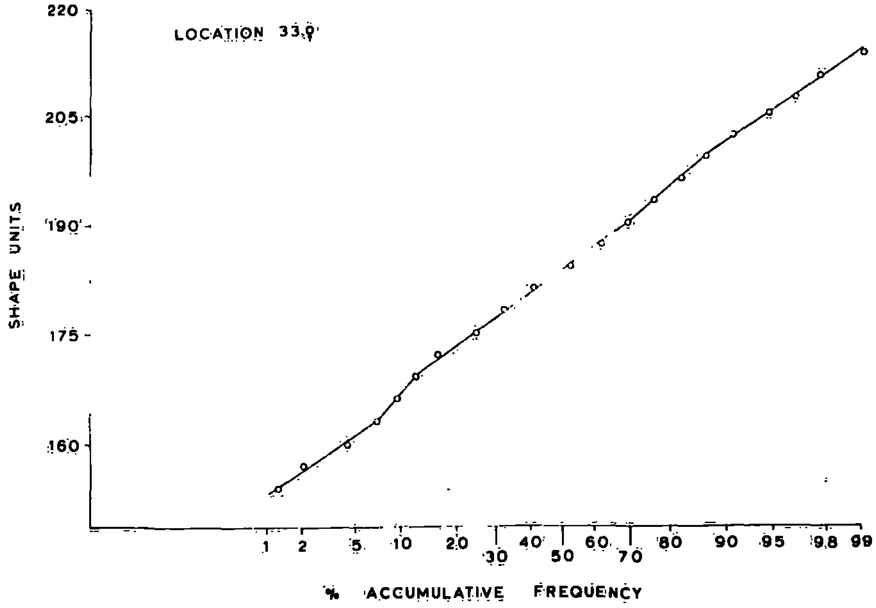
Plate 23. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 31, 32, and 33, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.



LOCATION 31♀
SHAPE UNITS
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

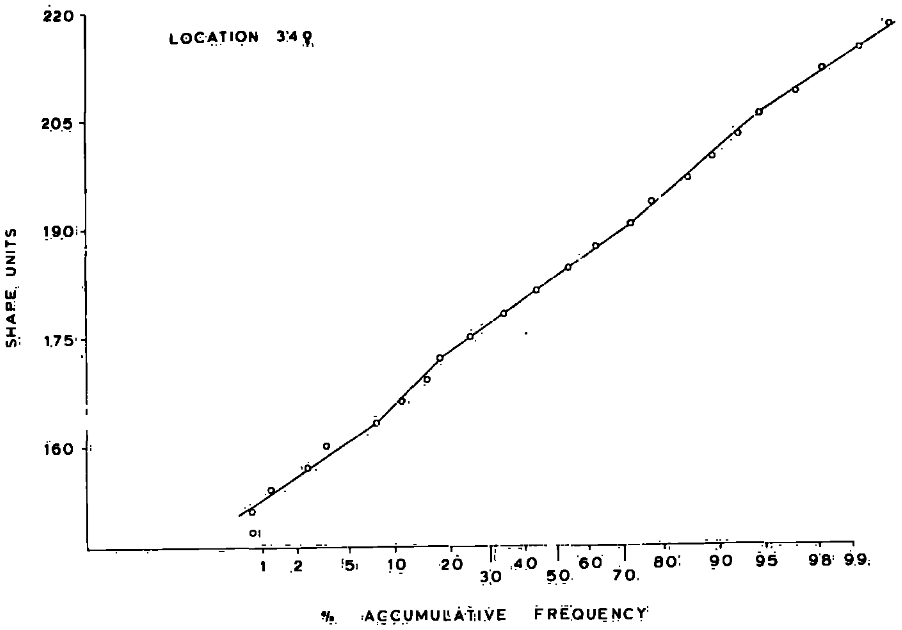


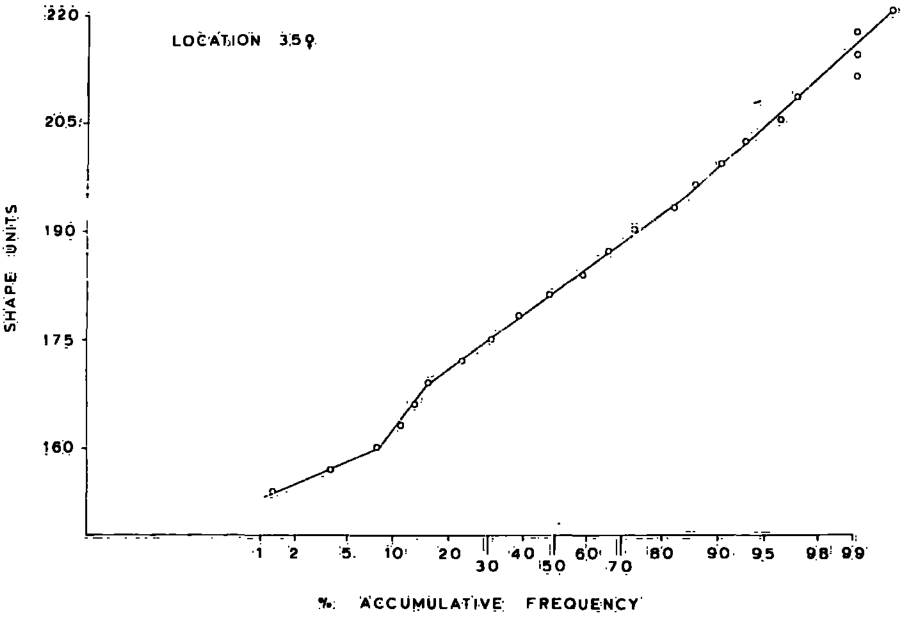
LOCATION 32♀
SHAPE UNITS
220
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY



LOCATION 33♀
SHAPE UNITS
220
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

Plate 24. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 34, 35 and 36, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.


LOCATION 34♀
SHAPE UNITS
220
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY


LOCATION 35♀
SHAPE UNITS
220
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

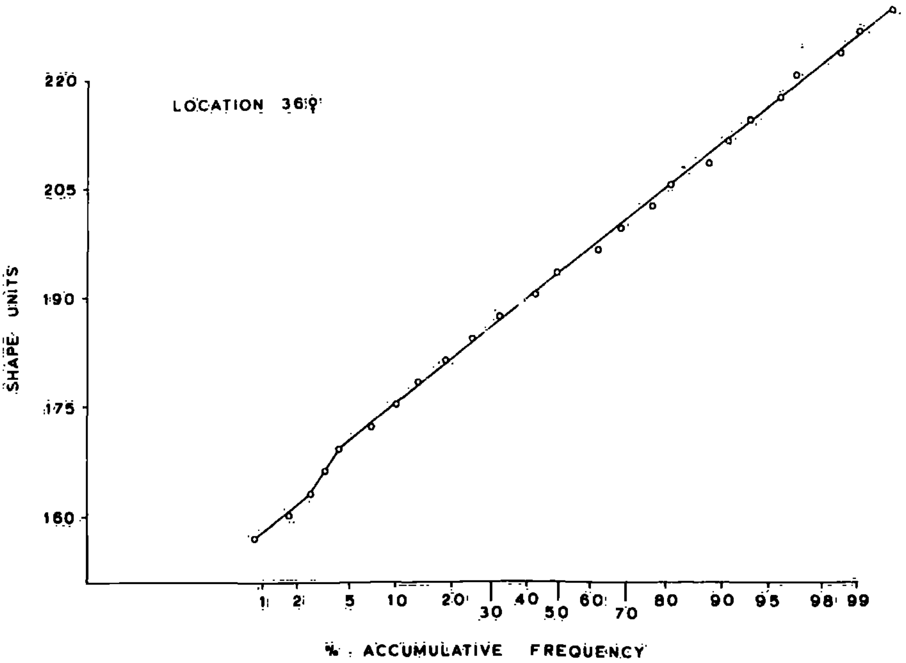
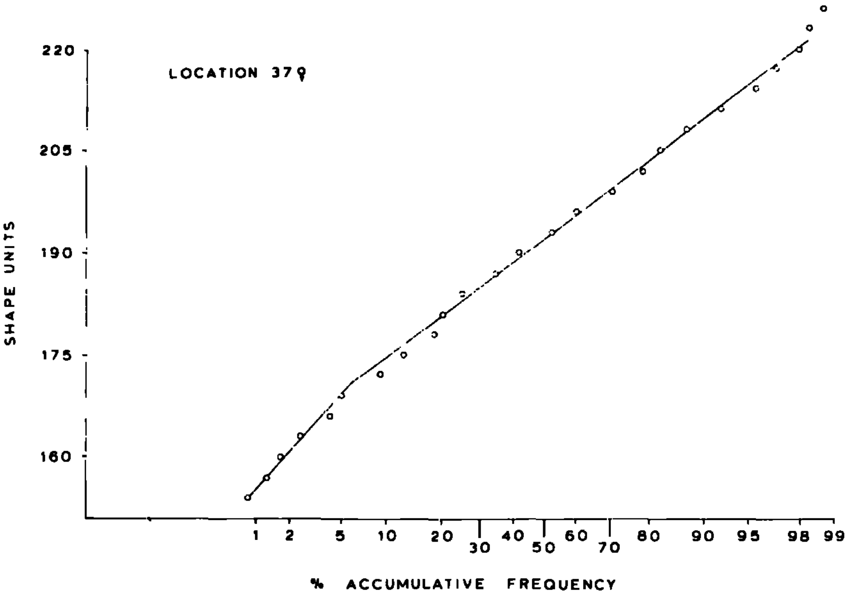
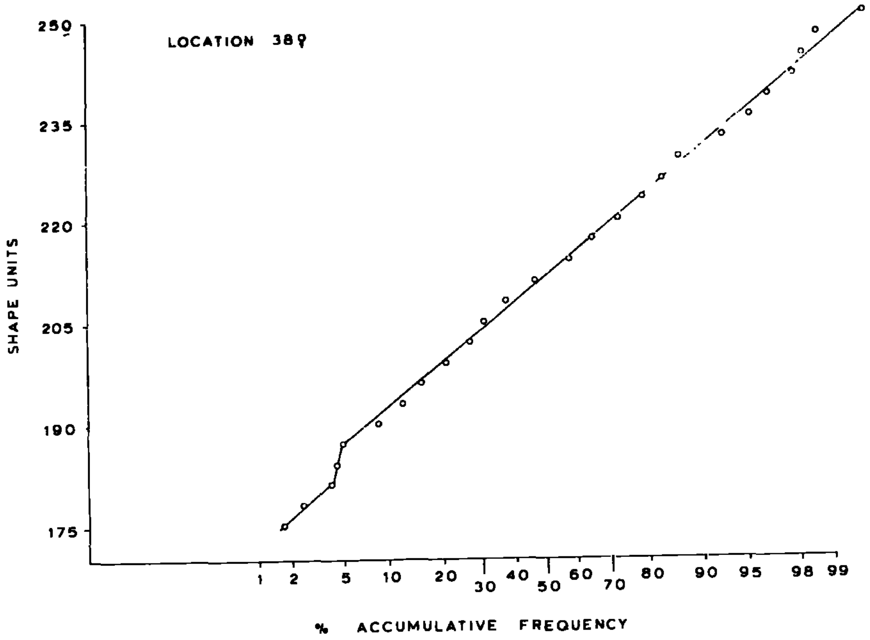

LOCATION 36♀
SHAPE UNITS
220
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

Plate 25. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 37, 38 and 39, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.


LOCATION 37♀
SHAPE UNITS
220
205
190
175
160
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY


LOCATION 38♀
SHAPE UNITS
250
235
220
205
190
175
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

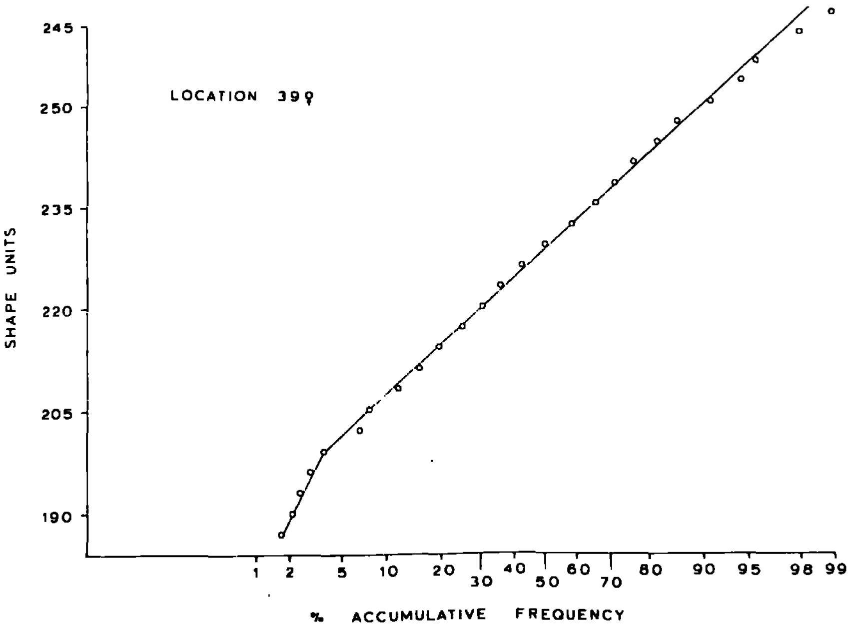
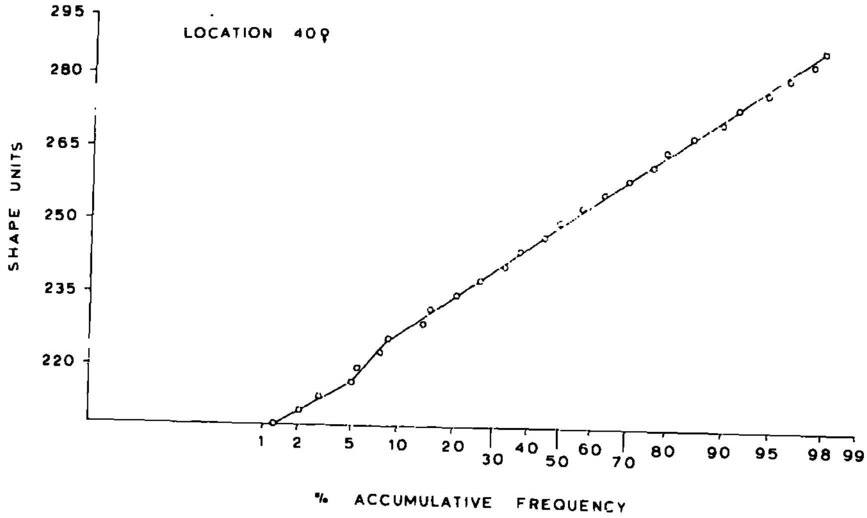
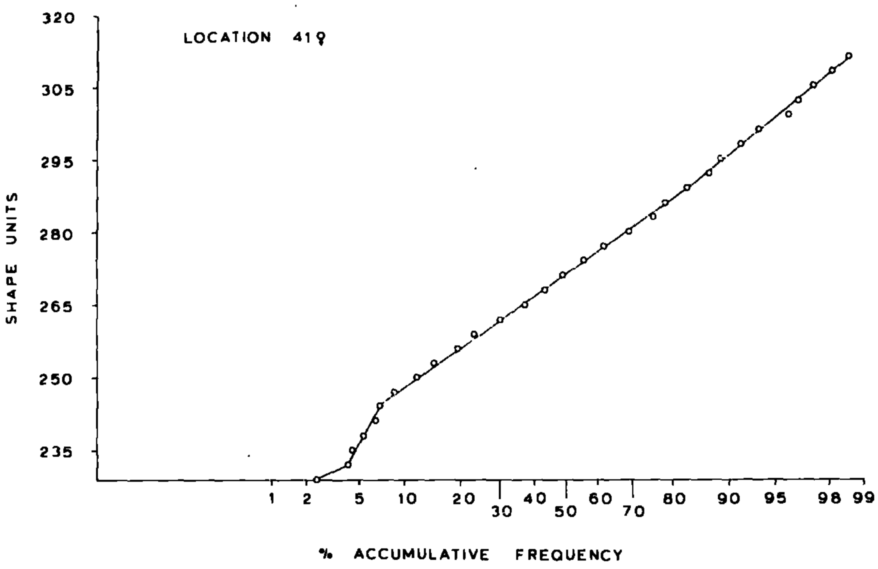

LOCATION 39♀
SHAPE UNITS
245
250
235
220
205
190
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

Plate 26. Accumulative Percentage Frequency Distributions of the Shape Indices of Locations 40, 41 and 42, of the Sample of Female Cerci. Plotted on Arithmetic Probability Paper.


LOCATION 40♀
SHAPE UNITS
295
280
265
250
235
220
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY


LOCATION 41♀
SHAPE UNITS
320
305
295
280
265
250
235
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

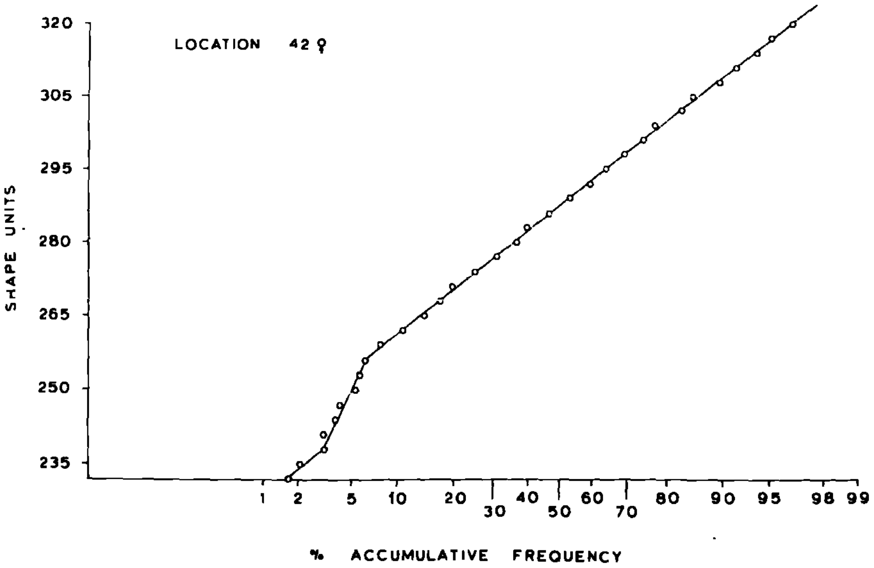
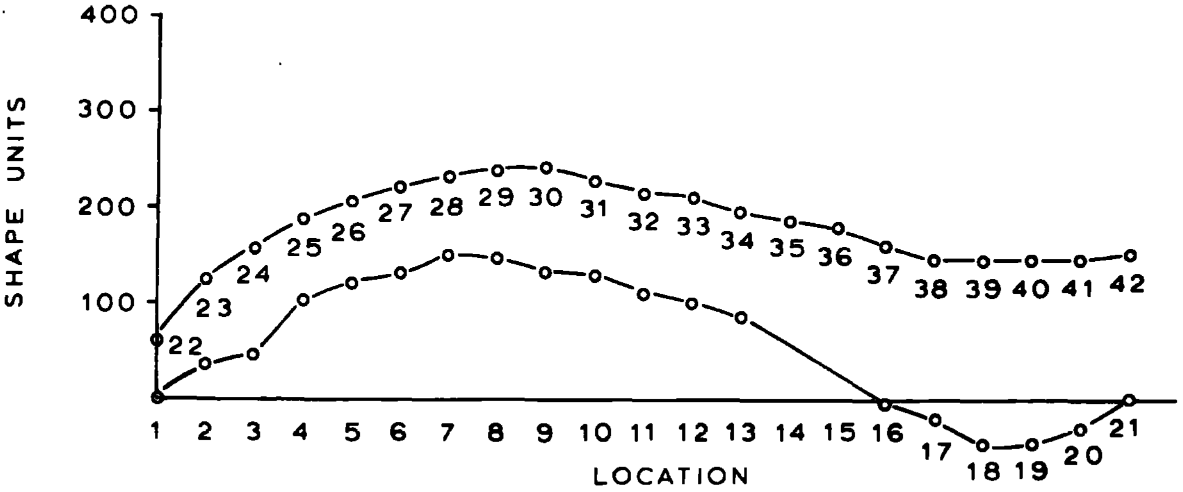
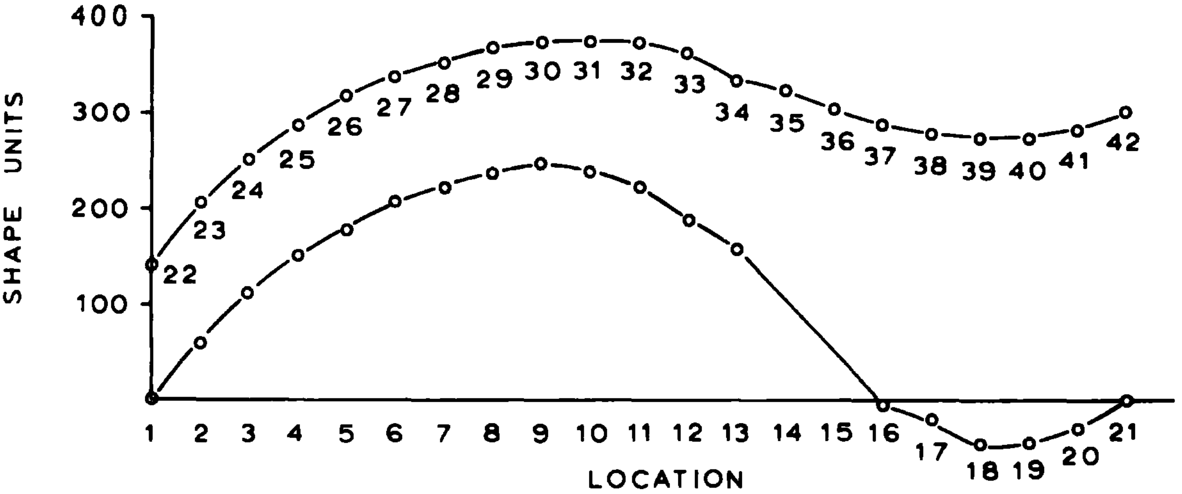

LOCATION 42♀
SHAPE UNITS
320
305
295
280
265
250
235
1
2
5
10
20
30
40
50
60
70
80
90
95
98
99
% ACCUMULATIVE FREQUENCY

Plate 27. Reconstructed Outlines of the Three Polymorphic Types of the Cerci of the Male Earwig.

The top reconstruction shows the mean shape of the cercus of the high male, the middle shows the mean shape of the more numerous low type, while the bottom shows the reconstructed form of the rarer low cercal type.

IMAGES OF HIGH MALE & LOW MALE CERCI RECONSTRUCTED TO SCALE.





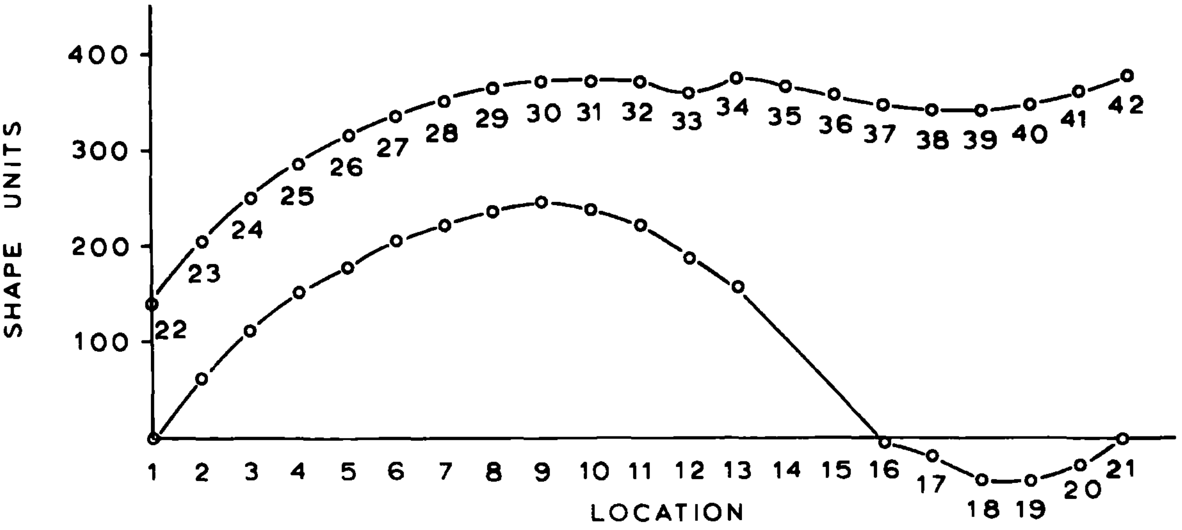
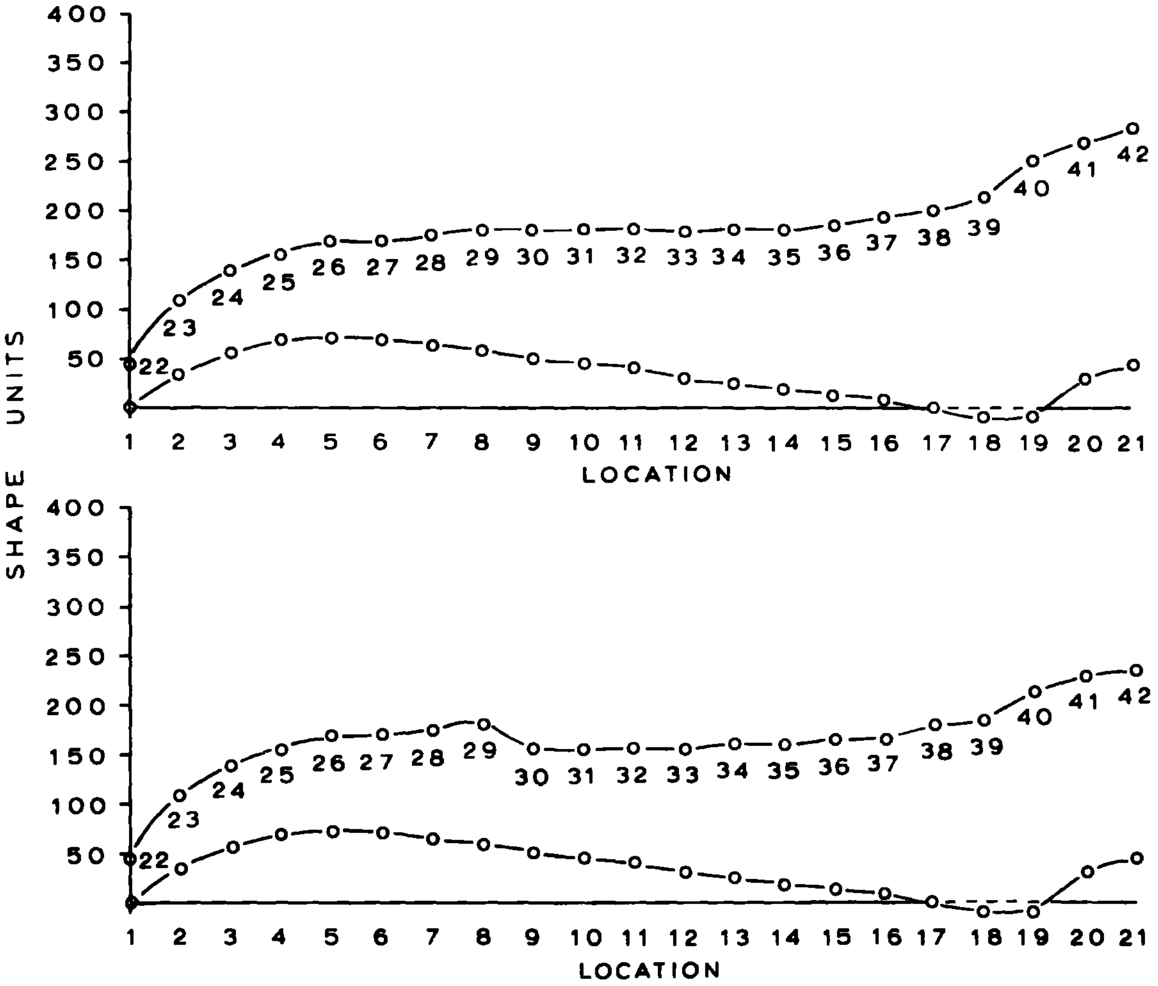


Plate 28. Reconstructed Outlines of Two of the Polymorphic types of the Cerci of the Female Earwig.

The upper reconstruction represents the commoner form which corresponds to the low male. The bottom reconstruction represents the form corresponding to the high male.

RECONSTRUCTED IMAGES OF TWO TYPES OF FEMALE CERCI



## Conclusions

The results of this study may be summarised as follows; the male Earwig appears to manifest three distinct polymorphic types of cerci, the female Earwig shows two polymorphs and there are indications of a third.

These polymorphic forms are all markedly different although the differences which separate the high form of the male cercus from either of the two low forms are more pronounced than the differences between the two separate low forms. The shape of the high form of the cercus is very distinctive owing to the considerable difference between the mean lengths of cerci of this type compared with the mean lengths of cerci of both the low types. This difference in shape is reinforced by the fact that the mean width of the bases, and the bows of cerci of the high type are disproportionate being similar to the corresponding absolute mean widths of the bows of low cerci.

The variability discovered within the low form of cercus was, by contrast, unexpected; as far as could be calculated all absolute size dimensions of that group of cerci, distinct from the population of high forms, were normally distributed. These measurements were investigated using Harding's method and the successive approximation method described elsewhere. The results of such investigation indicated that the distributions of all parameters measured on the cerci, with the exception of the length of the cerci were normal, or closely approximate to a normal distribution.

It is not altogether surprising that the bimodal distributions of the points at locations on the outer edges of the cerci of the low male sample remained unsuspected. The particular area where this variability is most clearly manifested does not lie close to any of the features used for direct measurement, and a further fact which also would tend to obscure this variability is the modifying effect of the variation in absolute size of the organs in the sample. Nevertheless, it is possible to measure the width of the base of the cercus with great accuracy, and any discontinuity in the distribution of this parameter would be expected on the evidence of the shape studies. In fact, the absolute sizes of the individual cercus bases appear to be normally distributed, although some slight evidence was found which might corroborate the results of the studies in shape variation.

It appears, then, that the absolute widths of the population of cerci studied were normally distributed, while paradoxically the shapes are not. This paradox is resolved only when it is realized that the methods are very different in their capabilities, and that they do to some extent show different things. The direct measurement method allows a restricted amount of rather inaccurate information to be derived from each cercus. The scales within which the measurements were taken were accurate to within 0.1 mms., and 0.05 mms. The scales used in the shape analysis, were variable but of the order of 0.003 mms. accuracy. This fact, combined with the effect of variation in size masking variation in shape, more than accounts for any apparent discrepancy.

The discovery of the three types of male polymorph concurs at least partially with Kuhl's suggestion that the polymorphic forms of the Earwig are divisible beyond a simple separation into high and low types, although the techniques used to separate the types are very different from the ones he used. There was in fact, no indication that the high males were also divisible into two separate types, although there were too few individuals available in this study to be certain that the high males themselves were not also further divisible.

It is of particular interest that the scatter of points recorded at each of the different locations on the cerci form different types of distributions, with one, two, or three modes, and the significance of this fact lies in information available about the sites of variability on the cercus itself. The most marked discontinuity is of course that which separates the high form of the male from the two low forms. In almost all cases, except for those locations at the proximal end of the inner edge of the cercus, from locations 16 to 20, this discontinuity is very marked. The distributions at locations 16 to 20 approximate closely to unimodal normal distributions viz. Plate 11. A similar effect may be observed in the comparison of the two low male types: considering the two types together, all the points at each location, with the exception of locations 35 to 41 along the outer edge of the cercus, again at the proximal end, are all normally distributed. At locations 35 to 41 the populations, from the low cerci alone, are bimodal, and it is this sequence of distributions which necessitates the separation of the low males into two morphologically separate populations.

The indications seen in many of the point distributions from the locations on the female cerci reflect a similar pattern to that discussed above, and the conclusions even without the strong statistical backing of those derived from the study of the males, are not without their confirmatory weight. Hitherto, the female Earwig has been considered to be a monomorphic sex, and this conclusion is not altogether surprising in the light of the difficulties which must be overcome to complete a thorough study of the variation in shape of the cercus.

It is incontestable that in many of the graphs derived from the cerci of the female, that there is at least one inflection, corresponding to the range 5% and 10% on the abscissa of each graph. The presence of the upper inflection, which by its presence would indicate the presence of a third distribution in some of the graphs, particularly those that plot the variability of the outer edge of the cercus, is much less certainly defined. Nonetheless, despite its tenuity, there is consistent evidence, from locations 23 to 33 on the sequence of graphs derived from the female cerci, Plates 21 and 22, that a second inflection is present, and that such inflections represent a real discontinuity. It is unlikely that an artifact produced for example, by careless sampling should produce so consistent a phenomenon. It is unfortunate that no further statistical evidence can be produced to reinforce this analysis. Nevertheless the presence of the first (lower) inflection is not called into doubt, by the tenuity of the second.

The evidence in toto, suggests that the cerci of a population of female Earwigs are not monomorphic, and indeed similarities are apparent between the polymorphism of the male, and that of the female. The fact that no previous worker, to my knowledge, has suggested that the female Earwig is polymorphic is evidence of the subtlety of the effect, and it is difficult to imagine the technique which would be essential to quantify completely the occurrence of the polymorphism of the female, and to reconstruct fully the mean shapes of all the types of polymorphic cerci, in the way that the male cerci have been reconstructed. Certainly the technique described above is too crude for such precise work, and indeed the sample studied is probably on the small side as well.

Despite the difficulties of quantifying the data farther than simply plotting the graphs it is useful to compare the positions in the curves of the shape distributions, of the inflections. On the very crudest level there are some similarities. The lowest inflections, occurring in the females within the range 5% to 10% and in the males 8% to 12%, indicate at least some similarity of proportions of such high individuals in the population: further, the occurrence of the second inflection when it is present, lies within the range 65% to 70% in the males, and within the much wider range 70% to 95% in the females. The positions of the upper inflections are all but indeterminable in the females; nevertheless there is some similarity in terms of the proportion of each of the three distributions in the populations of male and female Earwigs. Perhaps at this stage it is unwise to speculate further on the significance of these similarities.

The method of deriving these results is based upon an implicit assumption which is worth questioning. The assumption is this; that the cerci of Earwigs do not undergo allometric growth to any marked degree. The concept of allometric growth as applied to the growth of such structures as mollusc shells, or the skulls of vertebrates is a notion of considerable utility. Further, since D'arcy Thompson's eloquent explication of the significance of allometric growth in graphical terms ( 1942 ), no study of variability in the proportions of structures such as the cerci of earwigs, could be valid without taking into account the possibility that the polymorphic forms had arisen as a result of this types of growth. There are two facts to be considered; the cercus of the Earwig is inflated almost immediately after emergence from the last lar -

val ecdysis, and then is tanned, within the space of minutes, after which its form does not change barring accidental damage until death: in other words it does not grow in the sense that the form increases in size during the adult life. The second fact, based on theoretical grounds, is that the distributions recorded at the different locations on an organ which developed allometrically, could not on theoretical considerations alone produce polymodal curves, made up of normal components, but would produce curves which were skewed, according to the components of growth acting to produce the given point.

Huxley ( 1927 ) made an attempt to account for the variability of the male cercus in terms of his law of Heterogonic growth, but he was constrained to admit that polymorphism of the Earwig cercus was at best a special case.

The significance of these differences in proportions of the cerci is problematical, as there is no evidence to suggest that the functions of the cerci are different in the three groups and for this reason one may suggest that this considerable variability is a manifestation of the possible and non-critical variation of the organ. If the function of the cerci is the same in all the polymorphs of each sex, then presumably the critical areas of the organ are those that vary least. If this speculation is valid, owing to the fact that within the two low male populations the inner edges of the cerci must be the most critical, and therefore functional parts of the structure. Indeed, if this speculation is correct the inner edge of all types of cerci should be the most constant feature of the whole population of the cerci.

The inner edge of the high male cercus is markedly different in shape from the inner edges of both low male types, except for the proximal edge as described, at length, above, and this ntion of critical variability does not, per se, explain the variant form of the high cercus. It is however possible, that the shape of the cercus is not critical, and that it is the diameter of the bow of the cercus, measured at right-angles to its long axis that is the critical parameter. Certainly the width of the cercus bow is normally distributed within all types of males.

Behavioural considerations can be rallied to support this notion. During the behaviour that leads to copulation the male approaches the female and strokes her abdomen with his cerci closed round it. The movement of the cerci around the abdomen is similar to the movement of a curtain ring around a rod. The other major use of the cerci is during defence and while feeding with other individuals at a restricted food supply. The cerci are peculiarly ineffective weapons for grasping owing to the weakness of the muscles which close them, and because of the in-bowed shape. The cerci are used in the following fashion; when irritated by some tangible stimulus the earwigs of both sexes raise their abdomina and strike to left and right in a scorpion-like fashion at the source of the stimulus, and when a large number of earwigs are feeding at a restricted food supply they strike at each other in a similar fashion. It has been observed that earwigs with long cerci fare better at fending off competitors for food than those with shorter cerci. In this situation longer cerci are advantageous, and if, as suggested above, the diameter of the cercus bow is critical the development of the high form of cercus, with its disproportionate length, becomes comprehensible.

The significance of the difference between the two low forms of the male is much more enigmatic; there appears to be no obvious explanation that could elucidate in any way, the reasons or causes for the dimorphism of the cerci in the low group of males, although the significance of the two forms of low males may well be considerable.

One of the major unsolved problems in study of polymorphism in the Earwig, is the production of the high form of the male by culturing in the laboratory. No-one has yet succeeded in producing high males, Lhoste ( 1943 ), Singh ( 1967 ), although Crumb et al. ( 1941 ) did succeed in isolating mating pairs and observed that high males were produced. The pairs of earwigs were not kept in the laboratory, but in tins buried in the ground, under almost natural conditions. Evidence has been adduced to show that the key to this problem is at least partially environmental. Indeed Giard ( 1894 ), Diakonov ( 1925 ), Huxley ( 1927 ), D'arcy Thompson ( 1942 ) all in my opinion overstate the case, and allege, for no very clear reason that the polymorphism of the male Earwig is explicable entirely in terms of environmental effects. Crumb, Bonn, and Eide ( 1941 ) suggest that the polymorphism is entirely a genetic phenomenon. Callan ( 1941 ) noted the peculiarities of the chromosome number of the male Earwig but could find no correlation between the occurrences of the different chromosome numbers and the occurrences of the different polymorphic types.

All these investigations have probably been carried out using populations of earwigs which contained all three polymorphic types. Since the presence of the third polymorph has remained unsuspected until the present, it may well be that consideration of this hidden factor will both clarify the problem, and suggest new approaches to its solution.

The conclusions of this study in summary are these; that both the sexes of the Earwig are polymorphic. The males are divisible into three classes, two of which, the two low forms, are much more similar to each other, than either is to the high form. The females are polymorphic, although to a markedly lesser degree than the males. The female polymorphism allows the separation of the females into two separate groups which correspond to the high males and to the low males, and further, that there is some tenuous indication of a third polymorphic group in the female Earwig.

These conclusions may be condemned as being pragmatic, and certainly there is an element of pragmatism present in the analysis: the problem of the causes and significance of polymorphism in the Earwig is no nearer to solution than it was in Bateson's day, and the evidence adduced in these conclusions indicates some possible reasons why attempts to isolate the causes of the phenomenon have been failures in the past through lack of precise morphological knowledge.

The proposition that the findings of this study support is this; that the classical description of polymorphism in the Earwig is inadequate owing to the failure to recognize at least two and possibly three polymorphs, and that Bateson's and Brindley's ( 1892 ) description of secondary sexual characters in the Earwig was no more precise than the old division of the species into *Forficula media*, *Forficula borealis*, and *Forficula forcipata*.

## Discussion

Polymorphism, in its widest sense, is a very common phenomenon found in many species of animals. In sexually reproducing species individuals usually, although not always, belong to one of two sexes. The fact that in such cases the reproductive roles of the two sexes differ, necessitates the development of different organs to fulfill the different contributions the sexes make in the reproduction of the species. Furthermore, the functioning of the differing sex organs will partially depend on differing concentrations of sex hormones in the bodies of the two sexes, and these hormones may have associated side effects on the variation in shape and size of the individual animals.

Sexual dimorphism is so common as to obscure the fact that sexual differences are manifestations of a genetically controlled morphological and physiological dimorphism. Sexual dimorphism is a concept readily comprehensible from a human standpoint and there is no reason to separate dimorphism of this type from all other manifestations of polymorphism as there is no qualitative difference between the two types of variability.

Polymorphism in a given sex may take two separate forms: it may relate to the time at which an animal reaches maturity, or it may be independent of temporal conditions. Temporal polymorphism is observed in some species of the Heteroptera, and may be related to the time in the season when the individuals reach maturity; animals maturing early in the season may have a markedly different body form from those maturing later. This type of polymorphism is observed in some species of the genus Gerris. In this genus and indeed in many of the examples of polymorphism in the order Heteroptera the organs associated with flight seem to be particularly susceptible to polymorphic variation. Typically polymorphism in the gerrids is characterised by varying degrees of wing development, the early adults having smaller wings than those emerging later in the season. In some species of the Corixidae individuals appear to be polymorphic with respect to their wing muscles, some morphs being capable of flight, and others incapable. Another example of temporally displaced polymorphism, and one which shades into contemporary polymorphism is found in some species of aphids, a group of insects much studied on account of the agricultural importance of some pest species. Lees ( 1966, 1967 ) has studied the effects of the environment in the causation of polymorphism in this group and concludes that polymorphism is caused in the aphids by a complex of environmental factors. It is because there is considerable temporal overlap in the lifespans of these morphs that the situation shades into the second type of polymorphism.

The division of polymorphism into the two major types is an arbitrary one devised solely for the purpose of description; the class termed contemporary polymorphism contains such diverse examples as the genetically determined polymorphism of the African swallow tail butterfly, and the environmentally produced variety observed in many species of the social Hymenoptera. Contemporary polymorphism may be characterised by the presence of more than one morph of the given sex produced by the given generation.

The African swallow tail butterfly, Papilio dardanus is polymorphic in the female sex and the type of morph the individual becomes is genetically determined. The adult females of this species exist in about half a dozen different forms, and each morph is a Batesian mimic of a different and distasteful species of butterfly. Carpenter and Ford ( 1933 ) describe this example in detail. The significance of this polymorphism is enormous in ecological terms and its function in this case, the deception of predators, is fairly evident. This case is of particular interest, as it reveals not only the subtlety with which the different morphs fulfil a useful ecological function in terms of the species, but indicates the validity of this type of polymorphism as an interactive phenomenon.

The polymorphism of the social Hymenoptera is environmentally controlled, depending on the transfer of hormones from one individual to another during mutual feeding. Not only at the hormones distributed in this way, but the time in the life cycle of the individual when it receives the hormone is important in determining the effect of the dose. The temporal relationships between the administration of the form-determinant secretions and their effects is discussed by Weir ( 1959 ).

While the number of examples of polymorphism could be increased
astly, the examples cited above serve as a short survey of the ex-
ression of polymorphism in some species of insects. To summarise,
olymorphism may be controlled by either the environment or by gen-
tical factors, and may manifest itself in a progression of differ-
nt body forms being developed at different stages in the season,
r by the occurrence of all the different morphs together and simul-
aneously in the same generation.

Concerning the causes of polymorphism, in physiological terms,
here is little in the way of a theoretical framework within which
he different expressions of polymorphism in the insects may be re-
ated. Wigglesworth (1965) suggests that the differences between
he polymorphs of some species are due to varying degrees of per-
istence ofjuvenile hamone in the adult insect, and as a result
f precocious secretion of ecdysone in the larva, the former being
esponsible for the persistence of larval characters in the imago,
he latter producing adult characters in the larva. Such a theory
as a great deal to commend it in species that show a graded sequence
f polymorphic forms, but the discontinous polymorphism of the ear-
ig; described elsewhere in this thesis, does not lend itself to this
ype of interpretation at first sight. The presence or absence of a
haracter could, however, be accounted for in this way, by assuming
hat the response of some structures in the insect body depends upon
threshold concentration being exceeded, rather than upon the abso-

lute concentration of the hormone in the haemolymph. Such an explanation is of course, only applicable to environmentally controlled polymorphism, and represents the recasting of Huxley's ( 1928 ) hypothetical "physiological switch" mechanism in modern terms.

The three morphs of the male sample, and the evidence of shape variability of the cerci of the female Earwig may be interpreted in a further way. While the evidence for the causes of this shape variability is far from being completely assembled, the suggestion that the causes of polymorphism are genetically controlled has still to be conclusively disproved. Crumb et al. ( 1941 ) were the last workers to suggest an exclusively genetical control for this phenomenon, and as they adduced little evidence in support of their conclusions, little weight can be put on their analysis of the causes of polymorphism. Nevertheless inspection of the proportions of the three morphs isolated in the population of male cerci (approximately) 10%, 60%, and 30%) is somewhat similar to the proportions of offspring produced by a pair of heterozygous individuals, when both the homozygous as well as the heterozygous types have morphologically distinct phenotypes. The theoretical ratio in this case would be two groups representing both homozygous types, of 25% and one, representing the heterozygous individuals, of 50%. Mayr ( 1963 ), comments at length about the vigour of the heterozygote in many species of animal, suggesting that the superiority of this type of individual having the benefit of the products of two alleles of the same gene, is often more vigorous than either of the two corresponding homozygotes. If in the earwigs, the homozygote responsible for the production of the high male, is sub-lethal, in the populations found on the mainland, this may account for the distortion of the ratios of the three different morphs of the male earwig found on the mainland. If, in contrast, on the Brownsman, one of the Farne Islands, the conditions are such that the form homozygous for short cerci were similarly sub-lethal, then the high proportion of the high type male, homozygous for the long cerci could be accounted for.

These speculations depend upon the assumption that the commonest morph of the male, accounting for most of the low form, and intermediate in size between the smallest morph and the high morph, is in fact the vigorous heterozygote. This hypothesis is offered, not as an explanation, although it could well have a grain of truth in it, but simply as an illustration of the fact that despite all the work of the past, a purely genetic explanation of the causes of polymorphism is not disproved.

Concerning the evolutionary causes of polymorphism, very little is known in most cases. It might be suggested that the bivoltine gerrids are simply reacting to conditions of varying favourability, although in some cases of this type of polymorphism there appears to be some measure of genetic control. Polymorphism of the genetically controlled type appears often to be related to the capacity of the individual to mimic other individuals, or to blend into the environment, cryptically. The colonial polymorphism observed in the Hymenoptera is explicable in terms of the division of labour in the colony. These explanations, as well as being oversimplifications of the significance of this type of variation nevertheless represent the little that is understood of the function of polymorphism in the life of insects.

Within the framework of general studies of polymorphism in insects the results of the studies on the Earwig deserve a little further scrutiny. The conclusions drawn are simple; the major inference to be drawn is that instead of two polymorphic types of the Earwig there are three male morphs, as well as two and possibly three female polymorphs. This is the major conclusion to be drawn and at the risk of tediousness, it must be stated that the importance of precise morphological investigation is sine qua non in studies of this type. The identification of the three male morphs represents a new and different answer to the problem of the description of the polymorphic forms of the male Earwig. All workers before Kuhl ( 1928 ) were, without exception interested in the variability in the size of the various parts of the earwig body, and not in the shape. A problem is posed therefore, in the reconciliation of the two related answers to the two related questions. The paradox of the existence of three distinct polymorphs separable by shape, compared with only two morphs separable by size is discussed at length in the conclusion of the section dealing with variability of cercal shape.

The conclusion that the nature of the polymorphism of the earwig is not as simple as was thought previously, establishes a far more satisfactory basis for the significance of this type of structural variation in the Earwig. That the sexes are similar and possibly exhibit a complementary polymorphism restores at least partially some concept of uniformity. The notion that the males alone were polymorphic was disconcerting, in the light of the suspected enviromental causation of the polymorphism in this species. There are of course, examples of pronounced environmentally controlled polymorphism occurring in only one sex, for example, amongst many species of ants, only the females are polymorphic.

The significance of such polymorphism, and the division of labour in the colony amongst morphologically diverse individuals, is not to be found in the common Earwig. Although the behaviour of the female in tending her eggs, and the crowding behaviour of the adults before mating takes place, both indicate some analogies with a potentiality for a rudimentary colonial life; the essence of colonial living, division of labour has not been observed in this species.

For the reasons cited above it would appear to avoid the problem of hypothetical colonial behaviour if both the sexes were polymorphic, and the affects of polymorphism applied for both sexes at the individual level.

The other results to be discussed include the geographical and temporal variability of the mainland and island populations of earwigs.

These results represent the spadework, done in order to provide evidence of the natural variability of the Earwig, and to provide a yardstick by which the development of laboratory cultures may be compared with the development of the earwigs in the wild.

This work has progressed only slowly owing to the inconveniently long life cycle of the Earwig; it requires patience to build data about the variability of the Earwig in the field.

With regard to the tenuity of the correlations between the separate body dimensions with geographical location of the sample source, there are two statements to be made in extenuation for the slightness of the evidence; the first is that meteorological records are scanty, and that they are seldom available for a considerable period after the records for a particular year have been completed, the second is that the relationship between the climate at one geographical position and another is not entirely constant in differing years. The evidence is however, fairly convincing that there is a small degree of correlation between the mean body sizes of the samples with geographical location, although this correlation is not significantly manifested every year. On biometrical evidence alone, it seems fruitless to speculate about the nature of this correlation which may be caused by the variations in the environment of the population of animals, or by variation in the genetics with geographical position, or by a combination of both of these factors. Furthermore, there is only subjective prejudice to back the notion that the mainland variation of the Earwig of the same nature qualitatively, as the variation observed in the Farne Island population; certainly the two populations are quantitatively different to a very pronounced degree, but in the absence of data, the relation-ship between the mainland and the island population must remain obscure.

The failures in the attempts to culture the animals are particularly irksome in the context of this variation in body form as culturing the animals in the laboratory would have been very useful indeed in untangling the enigmas concerning the interation of the genetics and environment in the production of polymorphism in this species.

The correlation between the mean size of the cerci of a population of male earwigs and the occurrence within the population of high males is another aspect of the biology of the variation of the Earwig which is still not completely described; the correlation is significant in one year but not in the other, yet in sum the evidence suggests that there is such a relationship. Furthermore, the robust buil of the Farne Island earwigs, togther with the unique proportions of high males in these populations lends some support to this thesis. The traditional view which holds that the high males are produced by the effects of the environment, might lead one to expect that larger animals could well be more likely to develop into high males than smaller ones, and this receives some indirect support by this finding, although the third polymorph indicates the causes of the high male, low male dichotomy may well be more complex than was previously suspected.

While there is a beguiling temptation to speculate about the mechanism of the causes of the development in the species of the two important male morphs, circumspection is required, as any hypothesis is bound to be coloured by evidence from the very different populations found on the Farne Islands, and on the mainland.

In view of the positive correlation of the cerci sizes of the males with the occurrence in the various populations of the high males, a physiological switch mechanism of the type discussed above might be invoked to account for the two disparate forms of the male. For example, if there were a critical size below which the cercus development was automatically of the low form, and beyond which the males developed the high form of the cercus, part of the observed variability could be accounted for. Such a hypothesis, however, suffers from certain insuperable disadvantages, in the form stated above. If such a situation applied, then it may be expected that the distribution of the low form of the cercus would, in statistical terms, approximate to a truncated normal distribution. There is no evidence that the lower distribution is truncated in this way. The hypothesis in the simple form does not therefore hold.

While the conclusion of a thesis is not the place to start speculations concerning lines of future investigation, certain experiments do commend themselves very strongly. In particular, large scale culturing of earwigs under controlled conditions could give evidence for a clearer understanding of the genetics of the different populations.

With sufficient time devoted to this culturing there should be no insuperable problems, furthermore the Earwig in suitable environments, is capable of producing more than one brood a year, a fact which could be distinctly advantageous for certain experiments. The high male problem, and in particular the problem of culturing this form probably requires great care in controlling conditions, and until this form is cultured successfully there seems little hope of a solution to the problem of the causes of this polymorphism.

The male Earwig has a variable chromosome number Callan ( 1941 ). Callan found no correlation between the occurrence of the high male, and variable chromosome numbers: perhaps with a newer knowledge of the facts concerning the morphology of this polymorphism, there may be some correlation, taking into account the third polymorph, between the variation in the chromosome numbers and the overall variability of the Earwig body.

The ecological function of this variation deserves particular scrutiny, and this investigation could be backed up by a more intensive behavioural study. Wynne-Edwards ( 1962 ) suggests that polymorphism in the Earwig is a population-regulating device, and the significance of such a claim deserves investigation. This study is limited by the short season over which the adult earwigs are readily available.

Finally, as the nymphs have been excluded from this study an investigation of the varibility of the different larval instars should supply useful information concerning the development of the sexes, and with refinement to the techniques of shape study it may be possible to separate the sexes of the earwigs with confidence, in some of the later larval stages.

The difficulty of acquiring the nymphs in large enough numbers, presents problems in this type of study, although as dead material can be used for this type of investigation, some type of mechanical extraction of the larvae from the soil, for example by making use of a Berlese funnel or allied device, might be used to good effect.

It is a sombre thought that the research described in this thesis has done little to answer the main questions concerning the variability of the common earwig, but by approaching the basic problem of morphological description, it can serve as a stable base, upon which other workers can construct their studies, and add their own contributions to the study of the structural variability of the species Forfigula auricularia.

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## Appendix I Statistical Methods

The forms of the frequency distributions investigated in the body of this thesis have been analysed making use of Cassie's modification of Harding's method for the analysis of polymodal frequency distributions.

This method allows rapid and easy classification of any frequency distribution, demonstrating the normality of the distribution, the presence or absence of skew, and allows the determination and description of the component normal distributions within populations of statistics distributed polymodally. The technique is operated by sorting the data for a given distribution into size classes and converting them into an accumulative percentage distribution, such that a particular size class accounts not only for the percentage of the given size class in the distribution, but also for the total percentages of all size classes lower than the given one. When the distribution is normal, if the curve is plotted on arithmetic probability paper such that the percentage of a given size class is plotted as a modulus of the probability of occurrences of that size class the resulting curve is a straight line, if the distribution is normal in type. In the case of skewed distributions, the line plotted in the way described is slightly curved, positive skew being indicated if the slope increases to the right. Negative skew is indicated by a decrease in slope of the curve towards the right, and kurtosis is indicated by the presence of a sigmoidal curve.

Positive kurtosis is indicated by reversed "s" shaped curve, negative kurtosis by an "s".

If the distribution considered is polymodal, the curve plotted on probability paper is inflected. The inflections delimit areas of the curve which are more or less straight lines; these lines indicate the presence, and the magnitude of the component distributions which make up the polymodal curve in its entirety.

Inflections always have a greater slope than any of the component normal distributions, of the percentage probability of the occurrence of the size classes is plotted along the abscissa and the size classes themselves are plotted as the ordinates. This fact is due to the relative paucity of intermediate forms lying beyond the limits of the adjacent normal distributions.

The method used for separating the component distributions is a sequential process, started by determining the form of component distribution with the lowest mean, by making use of its exposed flank. The limits of this distribution are indicated by the position of the first inflection, which indicates the proportion of the total accounted for by the lowest component. For example, if one of the straight portions of the curve is separated from the other such portions by inflections at a% and b% on the abscissa ( a less than b ) the proportion of the total distribution accounted for by this component is equal to (a-b)%. This fact indicates the importance of accurate plotting in the determination of the exact point of inflection.

Making use of this information it is possible to calculate the values of the whole component distribution and to plot them as separate accumulative frequency curves. Since the percentage of individuals belonging to a given distribution may be limited, it is possible to calculate the standard deviation of the population and the mean size class of each component for example, since 50% of a normal population lies to one side of the mean, the size class at the ordinate which intersects the abscissa at the 50% point must be the mean size class.

The theory summarised above is derived from Harding's contribution. Cassies's modification to this method is best illustrated with an example. The example chosen to illustrate in detail the derivation of the component distributions from a polymodal curve, is the analysis of the distribution of the points recorded at location 39 from the sample of the males, see Plate 17.

Two inflections can be seen in this curve; one very clearly, at approximately 9% and the second at 76%.

Since the lowest distribution is terminated at the 9% point, this component accounts for 9% of the total distribution.

By multiplying the percentages of each of the size classes which account for less than 9%, such that the total percentage contributed by all of them is 100%, the component distribution may be plotted. All the percentages less than 9% are therefore multiplied by a factor of 100 / 9.

The second distribution, which is delimited by the first inflection and the second, at 76%, accounts for 67% of the total distribution (76% - 9%). It is treated in a similar way to the first, except that 9 is subtracted from the original percentages of all size classes lying within the range 9% to 76%, and the factor by which the percentages are subsequently multiplied, 100 /(76 - 9).

On inspection, it will be seen, that there is considerable overlap between the second component, when plotted, and the third and final component. Size class 320 occupies only 95% of the second distribution and therefore the contribution made to the third component distribution by this size class will be as follows:

since size class 320 accounts for only 95% of the second distribution, it accounts in the total distribution for (95 x 67)/100%. The total percentage accounted for by the first and second distributions up to this size class is equal to ((95 x 67)/ 100 + 9)% = k'. Therefore the remainder of the whole distribution, contributed by size class 320 is equal to the percentage that this, the 320, size class, contributes to the whole distribution, from which is subtracted the value k', multiplied, to raise the percentage of the third component distribution to 100%, by 24 / 100, i.e. (100 - 76) / 100. This method of solution is a considerable improvement on Harding's method which is based upon a similar basic premise, but which necessitates the fitting of the component distributions by eye, and reconstructing the compound distribution until the theoretically derived curve, is sufficiently similar to the observed.

While graphical methods provide the solution for most of the problems encountered in the analysis of frequency distributions, in one particular series of investigations they proved to be somewhat unsatisfactory. Many of the samples of male Earwigs collected along the coast contained only a few high males, usually approximately 10% of the males were of this form. When distributions of the lengths of the cerci were plotted for a given sample on probability paper, the inflections, thought they were often very distinct, fell around the 90% point of the scale. Owing to the paucity of high males it was not possible to calculate the mean and standard deviation of the high distribution, and it was inaccurate to calculate the means and standard deviations of the high male measurements using the graphical method described above; it was therefore decided that other methods of analysing polymodal distributions should be investigated.

With the exception of Kuhl ( 1928 ) most workers had been satisfied to assign individual male earwigs to the two types, high male and low male, in an arbitrary fashion, yet it is almost impossible to do either consistently or accurately by eye, particularly when large samples are to be sorted, and when sorting is carried out over a long period.

Ideally the system used to separate distributions should indicate the real difference in mathematical terms between the types of cerci, and in this case there is no difficulty in maintaining consistency. As a compromise however it was decided that an arbitrary method would be simpler to devise, and making use of electronic computation it was possible to design a technique which although possibly arbitrary in function, separated the component distributions consistently. The method finally devised separated the distributions both accurately and rapidly and was in the pragmatic sense at least, perfectly satisfactory. The methods by which this separation is achieved are summarised in appendix II.

In the course of this investigation the statistical techniques used included calculation of standard deviations, standard errors of the mean, correlation coefficients, and various tests of significance, including Student's "t", and Snedecor's "F" test. When the results of such calculations are quoted, in every case the distributions to which the results refer have been tested and shown to approximate closely to normality. In a few calculations dealing with distributions other than the normal curve non-parametric statistics have been used.

Appendix II Computer methods.

The computers used during this study were an "Elliott 803" and subsequently an I.B.M. series 360/67 with a satellite 1130. Electronic computation was used for two distinct purposes; for routine calculation of statistics and the analysis of the information produced in the study of shape variability, together with the analysis of bimodal distributions of cerci lengths.

As described previously the graphical methods proved to be unreliable for the precise separation of males into the high and low polymorphs, on the evidence of cercus length. The method developed to accomplish this was designed making use of the principle of successive approximation in the following manner.

Owing to the paucity of the high males, in the coastal populations, the effect on the total population, in numerical terms of these individuals is small. The mean and standard deviation of a sample of cerci therefore reflects closely the mean and standard deviation of the most common form, the population of low males. The computer was programmed to calculate the mean and standard deviation of the complete sample, including the high males, then to exclude from the population all lengths which lay beyond the range of the mean + 3 standard deviations. Owing to the far greater length of many of the high cerci in comparison with all the lengths of the low male cerci, many high males were excluded from the population. The process was repeated, each time excluding the individual lengths which lay beyond 3 standard deviations of the mean. This routine was repeated until on two successive cycles the same number of individuals were left, i.e. no more were excluded. This calculation produces two effects; with the exclusion of abberrant individuals, the mean and standard deviation are successively reduced in magnitude, and tend to approximate more and more closely to the mean and standard deviation of the more numerous low male population, and when the calculation is complete a measure of the probability of individuals belonging to one or other class may be calculated with precision. Since the probability that parameters which are normally distributed lie within the range of the mean ± 3 standard deviations is very high, in the order of $p = 0.9999$, the probability that the excluded values are members of the normal distribution is approximately 0.0001, hence individuals excluded from the total population are extremely unlikely to be members of the statistical population lying within these limits. This description applies precisely to the calculated division of the populations of earwigs. Where means and standard deviations are quoted, these apply, unless otherwise stated to the low males of the sample, separated in the manner described above.

The problem of defining the limits on the range of values assumed to contain all the members of the normal distributions, was never solved mathematically, and the limits were chosen to be sufficiently wide so as to leave very little doubt about the difference between the two types of polymorph separable by this means.

In fact the limits were so chosen that the low males were almost certainly all partitioned from the high males; the probability of a low male being assigned to the wrong class was less than 0.0001. The converse of this statement is undemonstrable owing to the paucity of high males in the mainland samples. There were too few animals to justify the calculation of means and standard deviations of the lengths of cerci of the different samples of high male polymorph and as a result it is not possible to calculate the probability of assigning high males to the wrong class. The problem of determining with confidence the accuracy of separation was approached indirectly. The The accumulative frequency distributions were plotted for the cerci as lengths of several samples of low male earwigs, the polymorphs being separated by means of the computer programme, and these were found to be sensibly approximate to straight lines. Had there been individuals assigned to the wrong class of polymorph, plotting the frequency distributions in this way would indicate errors, showing evidence of the truncation or extension of the distribution by producing curved lines, rather than the straight lines which were discovered.

This technique is limited in potential, representing rather than a general solution to the problem, a specific tool for a specific task, but provided that there is only a small proportion of variant individuals in a population, and that the values of these variant parameters are not orders of magnitude greater than the values of the variables in the numerous population, the results are consistent, and separation is obtained rapidly and easily. Other methods were contemplated, but without exception they proved too bulky or too time-consuming to develop.

Data used in the analysis of shape variation in the cerci were recorded using a "D Mac" pen follower. This device produced a pair of co-ordinates which corresponded to the position of a pen on a plotting area of 10,000 square centimetres (a square of 100 cms. side). The pen follower is accurate within the range ± 1mm. The co-ordinates produced were output on to paper tape and processed making use of the computer. Each rectified image of a cercus was aligned so that the axes of the grid were parallel to the axes of the plotting table. The co-ordinates of the intersection of the axes were recorded, and the relative co-ordinates of each location of each cercus were calculated, with reference to the intersection of the axes. In this way the co-ordinates were recorded independently of the absolute co-ordinates of the locations within the plotting field. In other words by this means it was necessary only to align the axes of each grid with the axes of the plotting field, without locating the grid at any precise spot within the field. In this way the cerci which had previously been rectified in size were located within the standard grid in a form suitable for calculation. It was thus possible to compare the points on all other cerci in the sample at the same location. The points recorded from all cerci for each location in turn were sorted, and the frequency of each size class was determined after a suitable smoothing factor had been introduced, this factor determining the separation between size classes. The computer then produced an accumulative percentage probability distribution, of the points recorded at each location, of every cercus in the sample. The distributions were plotted on arithmetic probability paper by hand.

## Appendix III The functions of the Cerci

The behaviour of earwigs, as the behaviour in all animals, may be divided for convenience into aspects; these aspects are not at all exclusive, and therefore when any one sub-division of behaviour is considered, e.g. feeding, the reactions of the individual cannot be wholly dissociated from reactions to other separate stimuli, e.g. threat. This fact emerges very clearly when a section of the behavioural repertoire, such as the uses to which the cerci are put, is considered.

An earwig is capable of moving its cerci in the vertical plane and in the horizontal, and because the cerci are borne on the end of a flexible abdomen, the combination of movements that the individual is capable of, with the cerci is large.

The use of the cerci in feeding serves to illustrate the way in which behaviour associated with different types of stimulus is combined during the feeding of the animal. The common Earwig does not make use of the cerci to capture prey, and I have found no reference in the literature to suggest that the Earwig ever grasps its food, in this way. Lhoste ( 1942 ) states that after 6 months study he never saw an earwig grasp prey. The Earwig when it feeds on animal material holds its victim with forelimbs and mandibles. The cerci are carried in the horizontal plane and are opened a little. If the prey is either quiescent, or moving only weakly, the individual feeds and finally abandons the remains of the prey. If the victim is moving more violently, the gape of the cerci is increased, and the cerci are lifted into the vertical plane. In cases when particular individuals had been starved for a few days, they would feed on struggling meal-worms, and in this case the cerci were used often to strike at the prey, scorpion fashion, the abdomen being bent double almost, over the thorax. This behaviour was observed on numerous occasions and in none of them did individuals of either sex grasp the prey with the cerci.

When one earwig was feeding at a restricted food supply, others collected and fed at the same source. The feeding individuals, if they reacted at all to the arrival of new comers to the source, reacted with differing degrees of violence. In some cases only the gape of the cerci was increased and the cerci were tilted, using the muscles intrinsic to the cerci, into the vertical plane. This reaction took place in varying degrees of violence, apparently dependent on the availability of the food. In the situation where food was in very short supply, particular individuals were jostled so as to be in danger of losing their positions at the food. In some cases such individuals raised their cerci as described above, into the vertical plane and bending their abdomina over forward scorpion fashion, struck to right and left with their cerci at the individuals around them. The development of the cerci has much influence on the effectiveness of this manoeuvre, those individuals with large cerci fending off the others most efficiently. Individuals with well developed cerci, particularly high males were occasionally observed to grasp other earwigs around the abdomen, with their cerci. The closing power as mentioned above, is weak, and no individual observed being gripped appeared to be suffering any damage due to the shearing or crushing forces exerted on it by the cerci of another. Nevertheless individuals attacked in this way usually fled precipitately.

Observations suggest that females and high males are more efficient than low males at defending food in this way, although too few observations were taken to quantify this suggestion.

The reaction to threat is complex, and it is comparable to the reactions invoked in certain phases of the feeding behaviour. When attacked with a mounted needle or other such instrument the individual earwig flees rapidly, and opens its cerci in the horizontal plane. If the stimulus is made more intense, the cerci, still gaping are raised into the vertical plane, the abdomen being held in its normal position parallel to the substratum, if trapped the earwig will raise its cerci over its thorax and strike downwards, and occasionally it will make grasping movements with its cerci. This sequence of events, naturally, is susceptible to much modification, and the order of the phases is not fixed. Some confirmation is given, however, by the fact that after the threatening stimulus is removed the phases are reversed in order as the time passes.

As well as mechanical reactions, the Earwig makes use of chemical secretions Eisner ( 1960 ). These secretions are emitted by glands on the body of the Earwig, and contain amongst other components 2 methyl, and 2 ethyl - p - benzo quinone.

Defence reactions are also manifested as part of the feeding behaviour, and in some aspects, with the exception of the grasping phase, these are similar to the behaviour of the Earwig struggling with its prey. In the case of feeding at a restricted food supply both males and females grasped the bodies of adjacent individuals, and in this case the feeding behaviour is analogous to the reactions to other threats.

This description of the defence behaviour is a composite derived from observations of 23 individuals, 10 males, 13 females.

The role played by the cerci in copulation is difficult to isolate. Certainly the results of extirpation experiments such as those of Lhoste ( 1942 ) in which he paired individuals of different degrees of mutilation in order to discover if copulation took place, are difficult to analyse; it is impossible to isolate the effects of extirpation on the whole animal, and simultaneously to study the effects of removing the cerci on one aspect of behaviour, for example mating. Some results do emerge however, and Lhoste has shown that earwigs with cerci missing can copulate. The most extremely mutilated pair that copulated successfully was comprised of a male with both cerci removed, and a female with both its cerci undamaged.

Observations made by Chapman ( 1917 ) showed that before copulation took place, the male touched the female with its cerci, and that occasionally the male was seen to grip with its cerci the abdomen of the female. The observations made in the course of this study of the cerci reveal that in every case of copulation watched, the cerci of the male had been utilised during the period immediately prior to mating. From the argument above, it will be understood that it is almost impossible to test the importance, or even the functions of these organs; there is however no justification that the cerci play little or no part in the mating syndrome as Singh ( 1967 ) suggested.

The description of the behaviour immediately before and during copulation is a composite of notes taken while observing 15 different pairs. Where an event was observed in only some of the pairs this fact is noted in the text below.

The male, when it is ready to mate searches for a female, by walking slowly and following a convoluted path, pausing every few seconds to wave its abdomen in the air. This movement takes place both in the vertical and horizontal planes; it is sinuous in appearance and often the male tends to reverse its path, and even on occasion to walk backwards. When a male comes into contact with another individual, it strokes the dorsal side of the other's abdomen. If the second individual is also a male, a fight, similar to combat over food usually develops, although such fights are usually much more apparently vehement over food than they seem to be in relation to pre-copulatory behaviour.

If the individual encountered is a female, it usually becomes quiescent after the stroking. The male at this stage begins to twist its abdomen about the long axis of the body so that the cerci open in the plane vertical to the midline of the abdomen. The male opens its cerci and closes them round the abdomen of the female, such that one cercus enclosed the dorsal, and the other the ventral side of the abdomen. Fulton ( 1924 ) states ambiguously that the cerci do not appear to be used as claspers, but he does not make clear what he considers the role of "claspers" to be. In the closed position the male grips the female, and moves the cerci along the long axis of the female's abdomen in a fashion reminiscent of a curtain-ring sliding along a rod. While carrying out this action, the male moves from its position at right-angles to the long axis of the body of the female, and comes to lie parallel with it, both animals at this stage are facing the same direction. The abdomen is released, and simple stroking of the female's abdomen, is continued. The male then worms it abdomen beneath the female body, such that their bodies cross each other, the male's beneath the female's, and twists, so that the ventral and dorsal surfaces of its abdomen are juxtaposed. In this way the ventral surface of the male's body is closely apposed to the ventral surface of the abdomen of the female. While the male had been carrying out the manoeuvre to align the ventral surfaces of the abdomina, it walked through 180 degrees and as a result faces in the opposite direction to the female, at the same time the abdomina being still pressed closely together.

At this point in the sequence one of two events takes place. Individuals of one group of males started to grip the body of the female from the ventral side with their cerci, and passed the cerci along the abdomen of the female, with the reciprocating motion described previously; this stage is often left out.

The females then twist their abdomina so that the ventral abdominal surfaces lie together in the vertical plane. At this stage, usually, pushing its abdomen against the abdomen of the female, the male slips its body along the long axis of the female's body. While the abdomina are still closely pressed together, the penis is extruded and penetration takes place.

Copulation takes place for a period between 20 minutes and two hours, and may be repeated several times before the eggs are laid. Unless the pair is disturbed, copulation takes place between the same pair of animals on each occasion.

Earwigs do not appear to mate under crowded conditions; the sequence of behaviour is complex and appears to be disrupted readily by interference at all stages. In the wild the insects mate in cavities in the ground separated from other pairs, and this fact accounts partially for the fact that when mating is repeated it tends to take place between the same pair.

The suggestion that the common Earwig (Forficula auricularia) uses the cerci to refold its wings after flight is fairly widely quoted, e.g. Imms ( 1925 ). Attributed by Chapman ( 1917 ) to Wood ( 1892 ) this fact has become slowly modified until the statement of the original is now usually completely misquoted. Wood ( 1892 ) states that he had observed an individual earwig, of the species Labia minor use its cerci to refold its wings after flight. Chapman ( 1917 ), stated that despite observing earwigs of this species opening and closing their wings, on several occasions, states that on every occasion he observed that the cerci were never used for either operation. He goes so far as to suggest that Wood was mistaken.

The problem of the possibility of the use of cerci to refold the wings is particularly difficult to solve as the adult common earwigs fly so seldom; indeed there is some controversy about flight in the common earwig. Chopard ( 1938 ) states that it is unlikely that individuals of the species Forficula auricularia can fly at all. Poulton ( 1931 ) and ( 1937 ) states that the evidence for flight is overwhelming but in the 1931 paper he quotes anatomical evidence supplied by Mallock (unpublished) that does not support the theory that the common earwig can fly. Mallock suggests that the musculature present in the thorax of the Earwig is inadequate to supply the necessary force to permit flight. Burr ( 1939 ) remarks that the evidence for flight is too plentiful for the idea that the Earwig flies on occasion, for this theory to be a chimaera. The problem of whether the cerci are used in the folding of wings or not, will remain insoluble until it is certain whether or not the Earwig ever unfolds its wings.

## Summary

Studies on the structural variation in populations of male and female earwigs, sampled in areas on the north-east coast of England, were carried out. There were ten sampling areas in all; in order, from the south to the north they were, Scarborough, Whitby, Saltburn, West Hartlepool, Seaham Harbour, South Shields, Alnmouth, Seahouses, Beal and Berwick-on-Tweed. Samples of earwigs were also collected from the Farne Islands, a group of basaltic islands, which lie off the coast of Northumberland, east of Seahouses. The samples were collected in the autumns of the years 1966, 1967 and 1968, from the hollow stems of species of umbelliferous plants, notably *Heracleum sphondylium*, where the individuals aggregate before returning to the soil to mate.

Subsamples of 100 males were taken from each of the samples collected in the three years, and a series of measurements of body dimensions was taken, making use of a microscope and an eyepiece micrometer. Eight measurements were taken from the body of each male earwig as follows:

(i) The overall length of the body from the anterior edge of the pronotum to the posterior edge of the abdomen.

(ii) The overall length of the cerci.

(iii) The length of the bowed section of the cercus from the tip.

(iv) The maximum width of the bowed section of the cercus.

(v) The maximum width of the shaft of the cercus.

(vi) The length of the pronotum, from its anterior to posterior edge.

(vii) The width of the pronotum.

(viii) The minimum interoptical distance.

This sequence of measurements was subjected to analysis of variance procedures and the results indicated that each sample of male earwigs belonged to a statistically distinct population. The statistical independence was investigated in an attempt to discover some underlying pattern. Accordingly, the correlation between the mean body dimensions of the sample of males with the geographical position of the sampling site, ranked by position north of Scarborough, was calculated and the samples collected in 1967 were shown to be significantly correlated (p less than 0.05) with geographical position, the samples from the south of the range containing larger individuals than those from more northerly locations. The results from the samples collected in 1966, added confirmatory evidence, while the evidence derived from the 1968 collection, despite the lack of statistical significance, did add some further confirmation to this hypothesis. It was concluded that the evidence suggested the presence of a cline in this species.

The mean body dimensions of the samples of males collected in 1968 were compared with the corresponding measurements from females sampled at the same place and it was shown that with the exception of the cercal parameters the females were generally significantly larger than the males.

The earwigs from some islands of the Farnes group were also measured in the same way as the mainland samples and were shown to be remarkably different from the mainland populations, both by virtue of having much higher mean sizes, and containing far higher proportions of the high male polymorph, than the mainland populations. On some of the island approximately 40% of the males belonged to the high type while on the mainland seldom even 10% of the males belonged to the high form. Comparisons were made between the body sizes of the male earwigs collected from two habitats on the Brownsman, one of the islands in the Farnes group. These comparisons showed that pronounced differences in the mean size of populations of male earwigs could be produced by environmental conditions.

The occurrence of the high males in the mainland populations was also examined in detail, and a computer method of separating the high males from the low males was devised, making use of the bimodal distribution of the cercal lengths of populations made up of mixtures of the morphs. The occurrence of the high form of the male was correlated both with the mean size of the low males in the same sample, and with the geographical position. It was shown that the populations with the larger individuals, the southerly populations, contained more high males than the northerly ones.

The variability of the occurrence of the high males from year to year was also investigated, and despite considerable variation in the occurrence of high males from year to year, the underlying pattern, (high males being more frequent in the south of the range), was sustained.

Evidence from the measurement of the body indicated that the male earwigs are polymorphic with respect to the cerci only and methods to quantify the polymorphism of the cerci in more detail than simple measurement were designed.

A sample of approximately 250 male earwigs made up of individuals from all the sites visited in 1968 provided a supply of cerci which were preserved in alcohol. The outline of each cercus was traced on a grid of standard size by making use of a camera lucida, and a "zoom" microscope. The cartesian coordinates of the outlines with respect to the standard grid were recorded using a pen-follower and by examining the distribution of the coordinates derived from corresponding locations on the cerci, the variability of the whole sample of cerci at the given point could be determined. This technique permitted the separation of the sample of male earwigs into three distinct morphs. These morphs accounted for approximately 10%, 65% and 25% of the sample of males. A sample of 240 female cerci were similarly processed and the females proved to be separable into two distinct morphs, accounting for 10% and 90% of the total female sample. Furthermore, there was some evidence, too slight to be quantified, of the possibility that the more numerous morph, may be further separable into two distinct morphs, each corresponding to one of the two more numerous male morphs.

This restatement of the morphology of polymorphism in the earwig may help to shed some light on the enigma of the causes of polymorphism in this species.