A BIOMETRICAL STUDY OF *MICRASTER CORANGUINUM* AND *M.* (*ISOMICRASTER*) *SENONENSIS**

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CONTENTS

The echinoid *Micraster* shows one of the best examples of an evolutionary series among the invertebrates. The broad lines which this evolution took were demonstrated by Rowe in 1899. In the present paper the work of Rowe is extended and developed, using statistical methods where

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* One copy of the original data upon which this work is based will be deposited in the Library of the British Museum (Natural History), and another is available in the author's Ph.D. thesis, deposited in the Library of the University of London.

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these are appropriate. In addition to the species considered by Rowe, the paper deals with the closely related species *M.* (*Isomicraster*) *senonensis*, and with the zones of the English Chalk above that of *M. coranguinum.*

A sample of 516 specimens of *M. coranguinum* and *M.* (*Isomicraster*) *senonensis* was used for the biometrical studies. These specimens were collected by Rowe from Northfleet, Kent, and are now in the British Museum. Ten measurements, or as many of these as the state of preservation allowed, were made upon each specimen. Tests were made upon each of these ten sets of measurements to determine their accuracy and reproducibility. After a consideration of the results of these tests, three of the ten measurements were rejected. A discussion is given of the effects of errors of measurement on the interpretation of results.

The validity of applying the conclusions reached from the study of a sample of fossil material to the original living community is dealt with in two stages: (*a*) a study of the degree to which the sample of fossils is representative of the fossil population, and (*b*) a discussion of the degree to which the fossil population is representative of the living population from which it was derived.

Rowe's sample shows a bias due to unrepresentative collection. The larger specimens are over-represented, while *M. senonensis*, and the transitional forms between that species and *M. coranguinum*, are similarly over-represented with respect to *M. coranguinum* itself. Such bias is probably common to most palaeontological samples.

The bias due to an 'unrepresentative fossilization' of the living population is shown to be much reduced if samples are compared on the basis of estimates of 'shape' parameters defined in terms of allometric growth, rather than, as is usual, on the basis of 'size' parameters such as means.

Seven shape characters were considered, each defined by a pair of variates. These characters were: relative breadth, defined by the variates length and breadth; relative height, defined by the variates length and total height; relative height of the apical system, defined by the variates length and height of the apical system; degree of projection of the labrum, measured by the variates length and length to the tip of labrum; relative depth of anterior groove, measured by length and length to bottom of groove; degree of development of sub-anal fasciole, defined by length and area of fasciole; and degree of the posterior rise of the test, defined by the height and the apical height. In six of these seven characters the ranges of variation of the two species (*M. coranguinum* and *M. senonensis*) overlap. The exception is when the character 'degree of development of the sub-anal fasciole' is considered. On this basis the two species can be sharply separated—*M. coranguinum* having a well-developed fasciole, while in *M. senonensis* this is vestigial or absent. The intergrading between the two species in respect of the other six characters is possibly due to hybridization. A biometric study has also been made to investigate the differences between the anterior, unpaired, ambulacra in the two species. Here again there is complete intergrading. The study throws some light on the formation of a petal. It is suggested that the differences between the species are due to their occupying different ecological niches. These differences are not considered great enough to warrant placing the two species in separate subgenera.

The sample was divided between the two species on the basis of the area of the sub-anal fasciole; and the equation of allometric growth ($y=\beta x^{\alpha}$) was fitted by the method of Kermack & Haldane (1950) to the pairs of variates defining each of the seven characters under consideration.

In none of these seven cases did the estimates of α differ significantly for the two species. If, then, the values of α are assumed to be identical in both cases, the estimates of β so obtained differ significantly in the two species for five of the six pairs of variates considered. These differences between the two species would normally be obscured by the effects of allometric growth, *M. senonensis* being, on the average, larger than *M. coranguinum.*

The changes in shape which occur during growth are important in elucidating the systematics of the genus. They show, for instance, that *M. praecursor* Rowe is a synonym for *M. cortestudinarium* Gold., the former author having been misled by the effects of allometric growth. His division of *M. coranguinum* into a narrow and a broad variety is indefensible for the same reason.

The shape changes due to allometric growth are different from those seen in evolution. These echinoids do not show recapitulation.

By the technique of partial correlation, it has been demonstrated that the seven characters under consideration are so related, in *M. coranguinum*, that specimens which are more advanced than the general level of evolution of their time in some of them will be behind it in others. The result is that the sum total of the characters in any individual 'average up' to a level of evolution characteristic of the time at which the individual lived.

A discussion is given of the evolution and systematics of the English members of the genus *Micraster*. In southern England the main line of evolution of this genus passes through the lineage *M. leskei—M. cortestudinarium—M. coranguinum. M. corbovis* forms a branch phylum in the Turonian, and *M. senonensis* in the Senonian. In the north of England (the Northern Faunal Province of Wright 1952), the evolution of the genus follows a parallel, but not identical, line to that followed in the south. The northern forms culminate in *M. glyphus* and *M.* (*Isomicraster*) *stollyei* of the *mucronata* chalk. The study of the whole genus gives no grounds for assuming that these echinoids followed undeviating evolutionary trends, as some authors have supposed.

I. Introduction

As Watson (1949) has pointed out, the Cretaceous echinoid *Micraster* gives one of the best examples of an evolutionary series among the invertebrates. *Micraster* is a spatangoid, and lived on, or burrowed in, the bed of the Chalk sea. This sea persisted for a very long time, with some changes in depth, and the conditions within it appear to have been relatively uniform for long periods. As a result there is found in the White Chalk of southern England a continuous series of fossils, extending through several hundred feet of the chalk. This series contains, as usually defined, four species of *Micraster*: *M. corbovis* Wright, *M. leskei* Desm., *M. cortestudinarium* Gold. and *M. coranguinum* Leske. The closely related *M.* (*Isomicraster*) *senonensis* Lambert, always incorrectly called *Epiaster gibbus* by Rowe, is to be found in the higher zones of these deposits. The vertical range of this complex of species is from the zone of *Cyclothyris cuvieri* to that of *Marsupites testudinarius*, comprising the Turonian and a large part of the Senonian (see figure 1). These forms inhabited the area, which is now southern England, continuously for this long period of

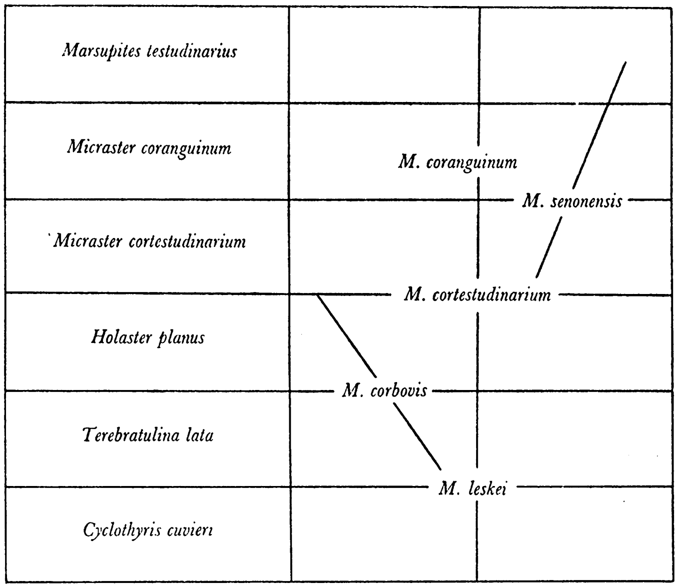

Figure 1. Diagram indicating the phylogenic lines in the evolution of the genus *Micraster* through the zones of the chalk in southern England. It should be noted that *M. coranguinum* persists, although it is very rare, above the zone of *Marsupites*.

time, and as there are no signs of immigrations into the area from the outside, the differences which are to be observed between the forms from the upper and lower zones must have been produced by evolutionary changes taking place within the area.

To the student of evolution this particular complex of species has yet other attractions. The test of an echinoid has a complex structure and shows a number of definable characters, although, unfortunately, far fewer than are to be found in a vertebrate skull. A large number of such characters are necessary to enable reliable lineages to be drawn up. This fact explains why our knowledge of the phylogeny of the vertebrates is so much better than that of any invertebrate phylum. In the outcome, as will be seen, *Micraster* had just enough definable characters to enable useful conclusions to be drawn. In addition the fossils of *Micraster* in some parts of the English chalk are reasonably abundant and usually uncrushed, while often the matrix is soft and the specimens may be prepared easily and without damage.

In 1899, Rowe published his classic account of evolution in *Micraster*. This was the first attempt to deal with the process of the evolution of species in *Micraster* on the basis of the study of populations rather than individuals; and to the present day it remains the only one. With the exception of the work of Hayward (1941 *a*, *b*, 1943, 1951) and Kongiel (1949) on *Echinocorys*, this statement appears to be true for all echinoids. The genus *Micraster* is a large one—Lambert & Thiéry (1924) give fifty-two species, which they consider to be good ones, and, in addition, seven associated subgenera with altogether thirty-eight species more—and Rowe limited his account to the study, in the English chalk, of the five species of *Micraster* mentioned above. Before discussing his work a brief description of *Micraster* is necessary.*

Micraster, like all spatangoids, shows a bilateral symmetry superimposed upon the primitive pentamerous symmetry of the echinoderms. Viewed from above, in plan (figure 12, plate 24), the outline of the test is seen to be heart-shaped, with an anterior groove, or notch. The floor of this groove is formed by the unpaired ambulacrum (ambulacrum III of Lovén (1874)). This ambulacrum does not show the formation of a fully developed petal; and it is, at the most, only sub-petaloid in its development. The other four ambulacra are paired, and show the formation of the typical spatangoid petal. The five ambulacra commence at the apical system, where the formation of new plates takes place. This system consists of the five ocular plates, one at the termination of each ambulacrum, and the four genital plates, each bearing a gonopore. The genital plate of the posterior interambulacrum (5) has been suppressed. The genital plate of the right anterior interambulacrum (2) bears the madreporite. Viewed from below (figure 16, plate 26) the position of the mouth is seen to be well anterior, and it is covered by a projecting labrum, formed from the posterior interambulacrum (5). Posteriorly can be seen a narrow ring of fine tubercles, which in life supported the small, club-shaped and densely ciliated spines of the sub-anal fasciole. Ambulacra I and V, on the ventral surface of the animal, spread out and form the so-called periplastronal area, the second pair of plates of interambulacrum 5 forming the plastron. Viewed from the side (figure 16, plate 26) the

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* The systematics of the genus *Micraster* are in a very unsatisfactory state, largely owing to the practice of making species of slightly unusual individual specimens. Purely for motives of convenience the classification of Lambert & Thiéry (1924) will be followed in the present work.

test is seen to be domed, with the posterior interambulacrum (5) forming a ridge or keel, from the posterior end of which the test falls sharply. The periproct is in this vertical face, just below the posterior termination of the keel.

Rowe demonstrated that certain changes took place in the micrasters as he passed from the lower to the upper strata, and that these changes took place in a regular manner, all the species perfectly intergrading. He studied the changes in a large number of characters, of which the following are important here:

(1) The forms became relatively broader, and the position of the broadest part of the test moved progressively backwards.

(2) They became relatively taller, and the keel became more pronounced. The highest part of the test, originally the apical system, moved posteriorly.

(3) The anterior groove deepened.

(4) The mouth moved anteriorly and the first plate of the posterior interambulacrum grew forward to cover it and form the labrum, which then continued to extend forward and became progressively more pronounced.

(5) The sub-anal fasciole became broader.

(6) The test increased in thickness.

(7) The periplastronal areas, originally smooth, became ornamented with small tubercules. This ornamentation became progressively more pronounced.

(8) The petals became shallower and increased in length.

(9) The petals became more ornamented, passing through the stages called by Rowe smooth, sutured, inflated, subdivided and divided.

It is clear from his paper that Rowe considered his *Epiaster gibbus* to be very closely related to *Micraster*, and, in fact, to be derived from it. He intended, in a subsequent paper, to deal with this species, along with the high zonal micrasters, but this paper was unfortunately never written.

The present paper will deal with four main topics:

(1) The relationship between *M. senonensis* and *M. coranguinum.*

(2) The relative growth rates of a number of characters in *Micraster*. A consideration of these was found to be of value in elucidating the systematics of the genus.

(3) The relationships between a number of characters, considered in a population from a single locality and a single zone. The results, when compared with the relationships between the same characters determined by Rowe for an evolutionary series, throw much light upon the interrelations between evolving characters in a stock.

(4) In addition, the investigation was of general value methodologically, and methods have been dealt with very fully.

The conclusions, to be valid, needed to be based on a large sample. This involved the use of statistical methods, and thus the study was confined to those characters which could be expressed in metrical terms, since the methods available for the treatment of non-metrical data were found to be neither powerful enough, nor precise enough. The required large sample of *Micraster* was not easy to obtain. The ideal would be one from a single large interbreeding population, but this was impossible and some zonal spread had to be accepted. This zonal spread will tend to obscure the relationship between the characters at any one time by superimposing upon them the relationships due to evolution, but if not too great the spread can be tolerated.

A suitable large sample had been collected by Rowe from Northfleet, Kent, and is now in the British Museum. It was kindly made available for study by the Trustees.

II. Material and methods

(a) Material

The Northfleet sample consisted of 516 specimens, stored in the British Museum in Rowe's original cabinet. His label gave the locality of the specimens as the *Micraster coranguinum* zone of Northfleet, Kent. The cabinet had four drawers, each separately labelled. Two were labelled simply '*Micraster coranguinum* (Leske)', and contained 274 specimens (E32865 to 33078, E33103 to 33133, E33191 to 33217, E33880 and E33881). The third, labelled '*Micraster coranguinum* (Leske) var. *latior*', contained 106 specimens (E32759 to 32864). The last drawer was divided by transverse slats of wood into a number of compartments, and contained 136 specimens in all. Of these Rowe had noted 27 specimens as being '*Epiaster gibbus*' (E32513 to 32539), and the remaining 109 specimens as 'Passage forms connecting *M. coranguinum* with *Epiaster gibbus*'. This last group was further subdivided by Rowe, and labelled as follows: (1) '*M. coranguinum* nearing *Epiaster* shape, but in no other way resembling it', 40 specimens (E32410 to 32449); (2) '*M. coranguinum* still nearer to *Epiaster* shape, but in no other way resembling it', 13 specimens (E32450 to 32462); (3) '*M. coranguinum* nearing or actually reaching *Epiaster* shape, and having a feebly developed fasciole', 23 specimens (E32463 to 32485); (4) '*M. coranguinum* with anterior ambulacrum in process of modification, and the shape of *Epiaster*, but with a slight but definite fasciole', 9 specimens (E32486 to 32494); (5) '*Epiaster gibbus* save for anterior ambulacrum', 18 specimens (E32495 to 32512); and finally (6) '*M. coranguinum* in all respects, save that there is no fasciole. Not even true *Epiaster* shape', 6 specimens (E32540 to 32545). The specimens had not been individually registered at the British Museum, and this had to be done before work on the collection could be commenced. The specimen reference numbers quoted above, and elsewhere in this paper, are those given by the Museum on registration.

On being received at University College, the specimens were cleaned of any adhering matrix. Owing to the uniformly soft nature of the chalk in which the specimens were embedded, this cleaning could be carried out by the use of a rotating dental brush. This treatment removes the soft Northfleet chalk without damage to the surface ornament of the specimen. As the rotating brush is only effective in soft chalk, while any more drastic treatment removes the surface ornament along with the matrix, one great merit of the Northfleet sample becomes apparent. After cleaning, the specimens were given a preliminary examination under a binocular microscope. One specimen (E32512) was seen to be a specimen of *M. cortestudinarium*, which must have been put into the cabinet by accident, probably after Rowe's death. It has been made no use of here. E33078 is the dorsal part of a hollowed out test, showing the structure of the petaloid portions of the ambulacra and of the apical system with unusual clarity; and E33123 and E33125 are flint casts. These three specimens were useless for the biometric work. In addition, a very badly damaged *M. senonensis* (the *Epiaster gibbus* of Rowe) was included among the forms labelled *Micraster coranguinum.* This specimen (E33108) had been preserved because it shows very clearly the details of the petals; it was quite impossible to make any measurements on it. It has been used here only in the compilation of table 3, where it has been left, perhaps rather perversely, under Rowe's classification as *M. coranguinum.* The specimens arrived from the British Museum in batches of about one hundred. There was almost a year between the arrival of the first group and that of the last. As each batch arrived it was divided, following the serial numbers, into sections each containing twenty specimens. These sections were then selected for measurement in an order obtained by the use of Fisher & Yates's (1948) table of random numbers. The random sampling of individual specimens would have been very inconvenient, and was not attempted; randomization of the major groups was impossible owing to the long time between the arrival of the first group and that of the last. The groups arrived in the following order: '*Epiaster gibbus*' and its passage forms (E32410 to 32538 and E32540 to 32545), then two batches of *M. coranguinum* proper (E32989 to 33109 and E32865 to 32988), then the batch of *M. coranguinum* var. *latior* (E32799 to 32864), and finally two more batches of *M. coranguinum* itself (E33110 to 33133 and E33191 to 33217). E32539, E33880 and E33881, which were on exhibition at the Museum, were measured separately at a later date.

(*b*) *Measurements*

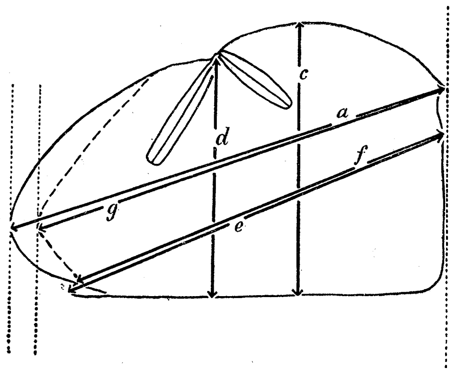
After each batch of specimens had been cleaned and examined, as many as possible of the following thirteen measurements were made on each. All are in millimetres except (*m*), which is in square millimetres, and (*n*) and (*o*), which are numbers of plates.

(*a*) The total length of the animal. This was measured from the most anterior point of the specimen to the tip of the rostrum (see figure 2).

(*b*) The breadth of the specimen (see figure 3).

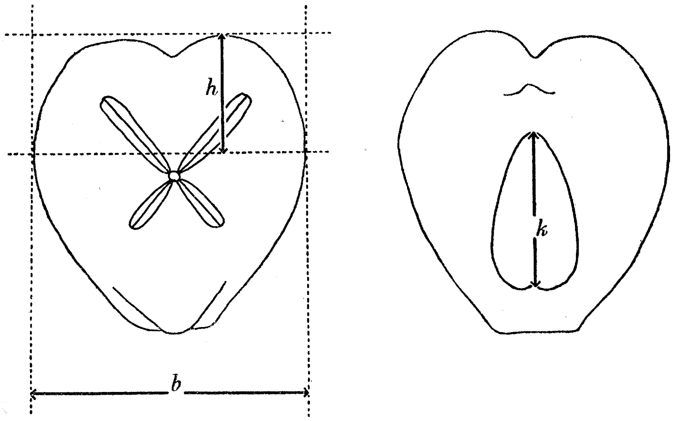
(*c*) The total height of the specimen (see figure 2).

(*d*) The height of the apical system (see figure 2). This measurement was always taken independently of (*c*), even if the apex appeared to be the highest point. This was done to



lateral

FIGURE 2. Lateral view of the specimen showing the positions of the measurements *a*, *c*, *d*, *e*, *f* and *g*.



dorsal

ventral

FIGURE 3. Dorsal and ventral views of specimen showing the positions of measurements *b*, *h* and *k*.

avoid the bias which would otherwise occur when using the difference of measurements (*c*) and (*d*).

(*e*) The distance from the tip of the labrum to the lowest point of the periproct (see figure 2).

All the above measurements were taken to two places of decimals. They were made with vernier callipers, which were graduated to 0·02 mm.

(*f*) The distance from the anterior point of the peristome to the lowest point of the periproct (see figure 2).

(*g*) The distance from the bottom of the anterior groove or sulcus to the tip of the rostrum (see figure 2).

These two measurements were taken with outside callipers and read under a binocular microscope, on a steel rule graduated in half millimetres. The measurements are given to one place of decimals.

(*h*) The distance of the greatest breadth of the test from its most anterior point (see figure 3). This was estimated with the millimetre rule, and the results are given to the nearest millimetre.

(*k*) The length of the plastron. This measurement was taken from the most anterior point of the plastron to the small eminence at its posterior end (see figure 3). Except in specimens E32410 to 32545 the measurement was made with a pair of blunt dividers, and then transferred to a rule exactly as with (*f*) and (*g*). In specimens E32410 to 32545 the measurements were taken with the points of the knife-edges of a pair of vernier callipers. The alteration in technique was due to an unavoidable change, at this point, in the pattern of vernier callipers used. The measurements taken with the dividers were recorded to one place of decimals; those taken with the vernier callipers were recorded to two places.

In all the above measurements the last decimal place has been estimated by interpolation between the scale divisions.

(*m*) The area of that part of the sub-anal fasciole which lies on interambulacrum 5. The fasciole forms a ring below the periproct, crossing interambulacrum 5 twice, once orally and once aborally. It is most clearly marked where it crosses interambulacrum 5 orally, and this was the part chosen for measurement (see figure 4). Owing to the irregular outline of the fasciole it was not feasible to measure its breadth; and the metrical attribute chosen was the area of that part lying on interambulacrum 5 at the oral crossing. This was done by projecting a virtual image of the relevant part of the fasciole on to the bench by means of a camera lucida, and then measuring the area of the image. The magnification being known the area of the fasciole is easily obtained. The area of the image was measured by a radial planimeter, set so that it gave the actual area of the fasciole directly in square millimetres, to one place of decimals. As a check on the accuracy of the work, the planimeter was run around each area twice, once clockwise and once anticlockwise. The mean of these two measurements was recorded as the area of the fasciole. The specimens were measured in the order of their serial numbers. Specimens E32410 to 32545 were then randomized and the measurements repeated; in the case of these specimens the mean of the two separate determinations was taken as the area for the tables and computations.

The last sets of characters to be measured concern the anterior ambulacrum in specimens E32410 to 32545, inclusive.

(*n*) The number of plates in the petaloid portion of this ambulacrum. The counts were made under a binocular microscope, and, in fact, pore-pairs were counted and not plates, as it is often impossible to distinguish the boundaries of individual plates. The end of the petal was taken as the point at which the pore-pairs showed no sign of petaloid modifications.

(*o*) The length of the petal. This was measured with dividers as in (*h*). The measurement was taken from the commencement of the ambulacrum at the apex, to the end of the petal as determined in the course of the pore counts.

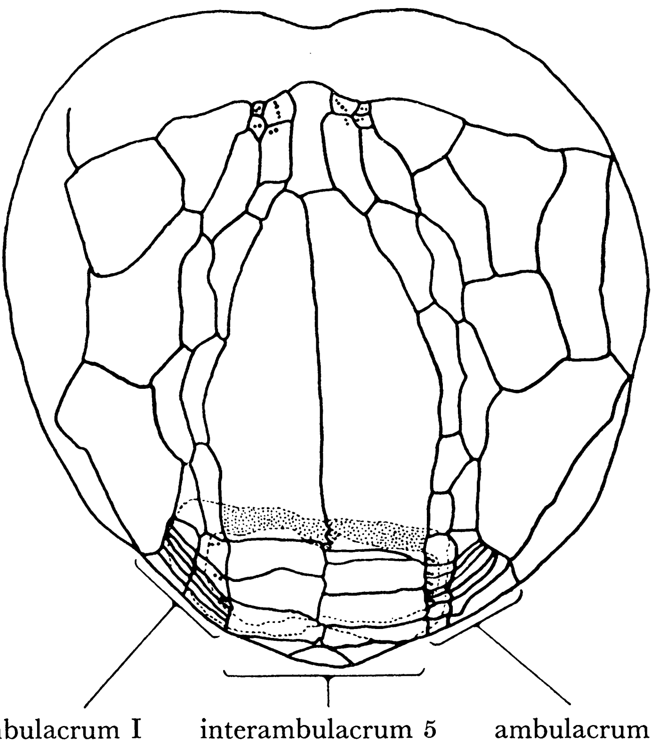


FIGURE 4. Ventral of specimen to show part of sub-anal fasciole measured. The limits of the fasciole are indicated by dotted lines, and the area actually measured is stippled.

Certain measurements, considered important by Rowe, could not be made with callipers. Rowe attached great importance to the backward movement, during evolution, of the apical disk, and of the highest and broadest points of the test. Making these measurements with an ordinary rule, e.g. measurement (*k*), was found to be unsatisfactory (see below under *Errors*). Rowe himself (1899) used a similar technique. An attempt was made, in the course of the present work, to devise a method of taking the measurements as projections upon a suitable plane. If successful, this would have made it possible to use a travelling microscope with great gain of accuracy. The method depends, however, on being able to define a plane with sufficient precision to give reproducible measurements. This it was found impossible to do, and the method therefore had to be abandoned.*

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* This does not mean that Rowe's results are valueless; it simply means that his technique would not give sufficiently accurate results for the analyses carried out in the present paper.

III. THE VALIDITY OF THE EVIDENCE

The special value of the study of the Northfleet specimens lies in the information they provide about the living community which inhabited the Cretaceous seas more than fifty million years ago. How valid may this information be? The answer to this turns upon the answers to three subsidiary questions which will be dealt with successively in the paragraphs which follow, viz.:

(*a*) *Errors of measurement.* To what degree do the measurements made upon our museum specimens adequately and accurately define their metrical properties?

(*b*) *Bias in the sample.* Is the sample of museum specimens truly representative of the population of fossils embedded in the chalk?

(*c*) *The age distribution of the sample.* To what extent is the population of fossils representative of the successive living populations of which they represent the only tangible remains?

(*a*) *Errors of measurement*

In the exact sciences, such as physics and chemistry, the only inaccuracies in a series of measurements will be due either to random errors of measurement or to errors in the construction of the measuring instrument itself. For example, the length of a metal rod can be defined exactly as the distance between two clearly identifiable points, and the accuracy with which this distance can be measured is limited only by the accuracy of the measuring instrument. The actual results recorded for each individual measurement may vary, because of errors of measurement; but, if the rod is kept at a constant temperature, the mean of one set of measurements will not differ significantly from that of another set made at a different time.

As well as these random errors of measurement (usually called the *accidental* error of a set of measurements), there may be another error due to inaccuracies in the scale of the measuring instrument itself. This is called the *systematic* error and will be a constant for all similar measurements taken on the same instrument.

There is, however, a third type of error, which is usually ignored by physicists and chemists, although astronomers have long recognized its importance. This is due to the idiosyncrasies, psychological and physical, of the observer. These errors are often taken as constant and included in the *systematic* error. However, the work of Karl Pearson (1902) and others has shown that these personal errors are not, in fact, constant, but show a secular trend with a rather slow, irregular rhythm. As 'Student' (1917) says: 'After considerable experience, I have not encountered any determination which is not influenced by the date on which it is made; from this it follows that a number of determinations of the same thing made on the same day are likely to lie more closely together than if the repetitions had been made on different days.'

In biological work, these slowly fluctuating errors, called by 'Student' the *secular* error of the observations, are of great importance. This is because in biometrical studies it is usually impossible to define exactly what is actually being measured. The more accurately a character can be defined the more objective the measurements of it are likely to be. In this sense the measurements of, say, the length of the test of an echinoid are less objective than the measurements of the length of the metal rod, since in the first case it is more difficult the define the exact limits between which the measurements are being made.

If the secular error forms too large a part of the total observational error, there is always a danger that the means of comparable measurements on two samples may differ significantly, although this difference, in fact, is due mainly to the slowly fluctuating idiosyncrasies of the observer. If, however, the effect of the latter is swamped by the random accidental errors, spurious differences of this sort, due simply to the slowly fluctuating secular error, will not be liable to occur. The measurements can then be said to be reproducible.

Accuracy is equally important, however, which means that the total error, from all sources, must be small. In reproducible measurements much the greater part of the total error is contributed by the accidental errors. These accidental errors, which are usually to all intents and purposes normally distributed, produce no systematic bias in the means of sets of observations. What does happen is that these random errors increase, on the average, the scatter of the observations about their mean. Due to this increased scatter the estimates of the variance of such sets of observations will be systematically too large. Thus if a pair of variates is being considered, there will be no systematic bias in the estimates of their means, while the estimates of their variances will be systematically too large. However, if the errors in the two variates are independent, as is usually the case, so that making a large positive error in the measurement of, say, x does not increase the chances of making a similar error in measuring the corresponding value of y, then, on the average, no bias will be produced in the estimate of the covariance of x and y. These facts mean that the magnitude of the coefficient of correlation between x and y will be systematically underestimated. This is important, and the point is worth developing more formally.

As we have seen, observational errors produce no systematic bias in the means; but they add to the expectations of x^2 and y^2 additional terms ϵ_x and ϵ_y respectively. The errors of x and y being independent, there is no addition to the expectation of xy. Then if σ_x^2, σ_y^2 and $\sigma_x \sigma_y \rho$ are these expectations in the ideal case where there are no errors of measurement; and $\sigma_x'^2$, $\sigma_y'^2$ and $\sigma_x' \sigma_y' \rho'$ are the corresponding expectations in the practical case, which includes errors of measurement:

$$\sigma_x'^2 = \sigma_x^2 + \epsilon_x^2,$$

$$\sigma_y'^2 = \sigma_y^2 + \epsilon_y^2,$$

$$\sigma_x' \sigma_y' \rho' = \sigma_x \sigma_y \rho;$$

and so

$$\rho'^2 = \rho^2 \left(1 - \frac{\epsilon_x^2}{\sigma_x'^2}\right)\left(1 - \frac{\epsilon_y^2}{\sigma_y'^2}\right).$$

Thus, on the average, the estimated magnitude of the coefficient of correlation will be too small, unless allowance be made for the effect of errors of observation (Jeffreys 1948). In a large sample, where the value of the correlation coefficient is close to unity, the uncertainty of the exact value of the latter introduced by errors of measurement might easily be much greater than the uncertainty due to the fluctuations of random sampling. This would render inadmissible the use of the usual tests of significance, which are based on the assumption that the uncertainty of knowledge of the exact value of a parameter is entirely due to these sampling fluctuations. The coefficient of correlation is the worst sufferer from errors of measurement; but similar troubles may occur in the estimation of other parameters, for example, the regression coefficients, from the sample data. In addition, this bias in the estimation of the coefficient of correlation will cause the significance of estimates whose sampling variance contains the term $(1-\rho^2)$ to be systematically underestimated. Thus it is clear that the use of data in which the observational errors are at all large must be avoided. To make sure of this involves the estimation of ϵ^2 in each case.

The intrusion of an undesirably large secular error, and also the total contribution of all the errors of measurement to the estimate of the population variance, was estimated for measurements (*a*) to (*k*) inclusive, in the following way. Fifty specimens were selected by the use of Fisher & Yates's (1948) table of random numbers. The specimens were then measured for a second time; there were then available some fifty pairs of observations for each of the nine measurements. As some of the specimens chosen were damaged in one way or another, it was impossible to obtain the full fifty pairs of observations, the number actually obtained varying from forty to forty-six. Then, for each of the nine measurements in turn, the value of the mean difference between the first and second series of observations, as well as the standard error of this difference, was computed. If this mean difference does not differ significantly from zero, the observations are reproducible and the secular error is negligible. The significance of the difference in each case was tested by means of 'Student's' *t*-test. The results are given in table 1. They show that the probability corresponding to the value of '*t*' falls between the 5 % and 2 % points for measurement (*g*) and approaches the 0·1 % point for measurement (*f*); in no other case does the probability fall below the 5 % point. Thus only for measurements (*f*) and (*g*) is the secular error not negligible. The best estimate of the total contribution of the errors (ϵ^2) to the estimate of the population variance, in each case, is half the mean of the squares of the differences between the first and second series of observations. The table shows that only in measurements (*h*) and (*k*) does the value of ϵ^2 exceed 1 % of the estimate of the population variance; this value of 1 % has been chosen as the point at which the errors of observation become undesirably large. On these grounds measurements (*f*), (*h*) and (*k*) were rejected, and no further use was made of them. The secular error in measurement (*g*) does not certainly differ from zero, although it probably does so. This measurement was, therefore, retained.

After an inspection of these results, measurement (*a*) was chosen as the standard measure of length. It was preferred to measurement (*g*), which is similar to Rowe's measure of length, because its secular error is clearly not significant, while that of measurement (*g*) may be so $(0{\cdot}05>P>0{\cdot}02)$, and because the value of ϵ^2 for (*a*) is about three-quarters of the value for (*g*).

For measurement (*m*), the area of the sub-anal fasciole, the comparison was made between the first and second series of observations on specimens E32410 to 32545, inclusive. Each measurement in the two series is itself the mean of a clockwise and an anticlockwise reading of the planimeter. Thus three sets of comparisons are possible: between the clockwise and the anticlockwise readings of the first series; the same for the second series; and, between the means of the pairs of clockwise and anticlockwise readings

TABLE 1

measurement	number of pairs of measurements in the two series	mean difference between first and second series (mm)	standard error of mean difference (mm)	't' = $\frac{\text{mean diff.}}{\text{standard error}}$	total contribution of errors to estimate of population variance (ϵ^2) (mm²)	estimate of population variance (mm²)
(*a*) total length	45	+0·002222	±0·03825	0·0581	0·03218	107·23
(*b*) breadth	46	+0·02304	±0·05758	0·4002	0·07487	110·55
(*c*) total height	42	−0·01476	±0·04349	0·3394	0·03889	24·76
(*d*) apical height	42	+0·07714	±0·06172	1·2500	0·07401	22·41
(*e*) labrum-periproct distance	40	+0·09325	±0·04795	1·9447	0·049185	72·81
(*f*) peristome-periproct distance	46	+0·2087	±0·06034	3·4588	0·1037	77·22
(*g*) sulcus-rostrum distance	45	+0·09111	±0·04105	2·2199	0·04122	85·99
(*h*) length of plastron	42	+0·08000	±0·1577	0·5073	0·5131	30·41
(*k*) distance of greatest breadth of test from its most anterior point	46	−0·2826	±0·2594	1·0894	1·5544	20·175

TABLE 2. MEASUREMENT (*m*)

	mean difference between clockwise and anticlockwise measurements (mm²)	standard error of mean difference (mm²)	't' = $\frac{\text{mean diff.}}{\text{standard error}}$	sampling variance of single mean (mm⁴)
first series (A) (83 pairs)	+0·12048	±0·12740	0·9457	0·33639
second series (B) (83 pairs)	−0·22530	±0·10080	2·2351	0·22099
	mean difference between means of (A) and means of (B)			
individual means of both series (83 pairs)	−0·59458	±0·68942	0·8624	19·66387

Total contribution of errors (ϵ^2) to estimate of population variance (128·0873 mm⁴) = sampling variance of single mean due to differences between clockwise and anticlockwise measurements + sampling variance due to differences between series (A) and series (B) $= \frac{0{\cdot}33639+0{\cdot}22099}{2}+19{\cdot}66387=19{\cdot}94256$ mm⁴.

for both series together. In each case the significance of the difference between the two sets of observations was estimated by means of a 't' test, and an estimate was made of ϵ^2. The results are given in table 2. They show that the difference between the clockwise and the anticlockwise readings in the first series is not significant, while in the second series the significance of the difference lies only just beyond the 5 % point. The difference between the means of the clockwise and the anticlockwise measurements in the two series is not significant. The estimate of ϵ^2 obtained by considering the pairs of readings in the first series is 0·3364 mm^4, and that obtained from the pairs in the second series 0·2210 mm^4. If, however, the means of the pairs in both series are considered, the estimate of ϵ^2 is then 19·6639 mm^4. This is a good example of 'Student's' point that 'a number of determinations of the same thing made on the same day are likely to lie more closely together than if the repetitions had been made on different days'; and the danger of leaving out a large part of the error in assessing the accuracy of the results is clearly shown.

In measurement (m) the secular error is negligible, as the table shows, but the total observational error is undesirably large. Despite this the measurement has been retained. It is the measure of the degree of development of the sub-anal fasciole, a character of great importance, which it has, unfortunately, been found impossible to define in any more objective way.

(*b*) *Bias in the sample*

In collecting *Micraster*, most of the specimens that are found are damaged in one way or another. If the collector considers the damage to be too severe, he throws the specimen away. The level of damage which he is prepared to tolerate will depend upon a number of different factors. Three of the most important of these factors are: the rarity of the specimen, the collector's interest in the species it represents, and his unconscious bias towards favouring particularly large or particularly small specimens. The ideal sample is unbiased, but in practice the best that can be hoped for is to get some idea of the nature and extent of the bias which the sample will inevitably contain. An attempt has been made to do this for the present sample.

Two species are represented here, the one very common (*M. coranguinum*) and the other rare (*M. senonensis* i.e. Rowe's '*Epiaster gibbus*'). *Micraster coranguinum* was further divided by Rowe into the narrower forms, which he called *M. coranguinum* auctorum, and the broader forms called *M. coranguinum* var. *latior*. In addition, the sample contains Rowe's 'Passage forms connecting *M. coranguinum* with *Epiaster gibbus*'. These transitional forms between *M. coranguinum* and *M. senonensis* would have been of particular interest to Rowe, with his then new concept of intermediate forms between well-established species. It might therefore be expected that *senonensis*, and its passage form, would comprise a higher proportion of the sample than of the collectable specimens of both species in the Northfleet pit. To test this hypothesis the sample was first divided between Rowe's four groups (*Micraster coranguinum* auctorum, *M. coranguinum* var. *latior*, *Epiaster gibbus* and the passage forms between *Epiaster* and *Micraster*); and then each group was itself subdivided into those specimens upon which it had been possible to make all standard measurements (a) to (f) and (m), and those upon which, owing to damage of the specimen, one or more of these measurements had had to be omitted. The first subdivision may therefore be considered to consist of effectively undamaged specimens, and the second to consist of those which are damaged in some way or another.

Table 3 gives the number of specimens in each of the eight subgroups, together with the numbers that would have been expected if Rowe's standards of selection had been independent of the position of a specimen in his classification. The table shows that there are more damaged specimens of *Micraster senonensis* and the passage form and fewer damaged specimens of *Micraster coranguinum* auctorum and *M. coranguinum* var. *latior* than would be expected if this were so. The value of χ^2 for the table is 10·46, and the probability of exceeding this value on the basis of random sampling is between 0·01 and 0·02. Thus Rowe's standards of acceptability were, in fact, lower for his *Epiaster gibbus* and the passage form than for *Micraster coranguinum*, and, on the basis of the collectable specimens in the pit at Northfleet, the first two groups are over-represented in the sample.

Another factor may have been important, and, if so, it would have reduced this bias in the sample. *Micraster senonensis*, and the passage forms, tend to have thinner tests than the typical *Micraster coranguinum*. This would make them more liable to damage in collection, and so, with uniform standards of selection, under-represented in the sample.

If there had been, for any reason, preferential collection of either large or small specimens, bias of another sort would exist in the sample. The analysis which follows shows that this is indeed the case; the more damaged specimens tend to be larger than the less damaged. Rowe, or his collectors, had lower standards of selection for large specimens than for small.

Table 4 shows all the specimens upon which measurement (*a*) could be made, arranged as a two-fold table. In the rows the specimens are divided among Rowe's four main classificatory groups; and in the columns according to the number of measurements (*b*) to (*f*) and (*m*), which were made upon each. For each of the twenty-eight classes into which the sample is thus divided the following statistics are given: the number of specimens in each class; the class means and variances, with the standard error of the mean; the row and column unweighted means, with their standard errors; the row weighted means with their standard errors; and the weighted mean variances.

A number of points are obvious on examination of this table. The class means, with four exceptions, become greater as the rows are passed over from left to right, the more damaged specimens tending to be longer than the less damaged. The variances, as may be checked by the application of Fisher's z test, do not differ significantly within each row. The mean of *Micraster senonensis* is always the largest in each column. The means of the passage forms are larger than the corresponding means of *Micraster coranguinum* auctorum in three cases out of five; and the means of *M. coranguinum* var. *latior* are always larger than the corresponding means of *M. coranguinum* auctorum. The class variances in each column differ greatly, and the z test shows that these differences are significant. This is the reason that weighted means and weighted mean variances have been given only for the rows. The class variances are seen to be, on the whole, smallest for *Epiaster gibbus* and largest for *Micraster coranguinum* auctorum.

The trends in the class means are shown more clearly by the unweighted means of the rows and columns. The methods of the analysis of variance are not fully admissible, owing to the heterogeneity of the row variances, and these unweighted means are the

TABLE 3

		Epiaster gibbus (*Micraster senonensis*) E 32513–32539	transitional forms between *Epiaster* and *Micraster coranguinum* E 32410–32511 E 32540–32545	*Micraster coranguinum* auctorum E 32865–33078, E 33103–33107, E 33109–33122, E 33124, E 33126–33133, E 33191–33217, E 33880–33881	*Micraster coranguinum* var. *latior* E 32759–32864	total of rows
forms on which all measurements (*a*) to (*f*) and (*m*) were made	actual number of specimens	6	40	128	54	228
	expected number of specimens	12·0234	48·0938	120·6797	47·2031	
forms on which it was impossible to make all measurements	actual number of specimens	21	68	143	52	284
	expected number of specimens	14·9766	59·9063	150·3203	58·7969	
total of columns		27	108	271	106	512

$\chi^2 = 10{\cdot}46$; $0{\cdot}02 > P > 0{\cdot}01$.

TABLE 4

		specimens upon which all six measurements could be made	specimens upon which five measurements could be made	specimens upon which four measurements could be made	specimens upon which three measurements could be made	specimens upon which two measurements could be made	specimens upon which one measurement could be made	specimens upon which no measurements could be made	weighted means of rows, standard errors based on weighted variances	weighted variances of rows	number in each row	unweighted means of rows with standard errors based upon individual sampling variances
'*Epiaster gibbus*' (*Micraster senonensis*) (E 32513–32539)	mean (mm)	56·005	59·352	56·025	59·657	61·710	63·353	—	59·408			59·350
	standard error	±2·013	±2·497	—	±3·092	±2·942	±3·996	—	±1·199			±1·474
	variance (mm²)	24·324	31·187	—	28·867	43·291	47·903	—		33·710 (D.F. = 17)		
	number in group	6	5	1	3	5	3	0			23	
transitional forms between *Epiaster* and *Micraster coranguinum* (E 32410–32511, 32540–32545)	mean (mm)	50·625	51·741	52·773	53·000	52·611	56·941	—	51·691			52·949
	standard error	±1·158	±1·340	±2·216	±2·699	±1·513	±0·569	—	±0·712			±0·706
	variance (mm²)	53·651	52·118	54·018	58·286	20·611	0·647	—		50·166 (D.F. = 93)		
	number in group	40	29	11	8	9	2	0			99	
'*Micraster coranguinum* auctorum' (E 32865–33078, 33103–33133, 33191–33217, 33880 and 33881)	mean (mm)	48·588	49·886	52·909	47·485	59·137	—	—	49·641			51·601
	standard error	±0·929	±1·182	±1·705	±3·557	±4·625	—	—	±0·663			±1·253
	variance (mm²)	111·382	121·473	84·323	50·620	64·194	—	—		110·708 (D.F. = 247)		
	number in group	129	87	29	4	3	0	0			252	
'*Micraster coranguinum* var. *latior*' (E 32759–32864)	mean (mm)	51·773	50·219	53·217	57·86	—	—	—	51·646			53·267
	standard error	±0·880	±1·424	±1·355	—	—	—	—	±0·665			±1·764
	variance (mm²)	41·789	58·778	33·036	—	—	—	—		45·125 (D.F. = 98)		
	number in group	54	29	18	1	0	0	0			102	
unweighted means of columns, with standard errors based on unweighted means of individual sampling variances		51·748 ±0·663	52·800 ±0·846	53·731 ±1·646	54·501 ±2·161	57·819 ±1·896	60·147 ±2·018		50·960			
	numbers in columns	229	150	59	16	17	5	0			476	

best estimates of column effects. Row effects may be estimated by taking either the weighted or the unweighted means of the rows, since the variances within each row do not differ significantly. To each unweighted mean is attached its standard error. These standard errors were calculated by taking the unweighted mean of the sampling variances of the individual class means in each row and column, and then dividing this by the number of classes in the row or column to give the sampling variance of the unweighted mean. Where the class contained but a single specimen, the best estimate of its sampling variance is the unweighted mean variance of the row in which it falls. An alternative treatment, which has much to recommend it, is to take the weighted row variance as the best estimate of each of the individual class variances in the row, and to use those values in the computation of the sampling variance of the individual class means. Such a treatment will, in this case however, make no difference to the conclusions arrived at by a consideration of the table.

The unweighted means of the columns show in a striking manner the trend described above, increasing as they do in value as the columns are passed over from left to right. This confirms the conclusion arrived at above by the consideration of individual class means, namely, that the more damaged specimens tend to be larger than the less damaged. It should be added that, in unconsciously relaxing his standards for the larger specimens, Rowe was influenced by taxonomic considerations that turn upon relative growth rates.

To anticipate a little here, it may be said that Rowe defined both *Epiaster gibbus* and *Micraster coranguinum* var. *latior* in terms of characters which show allometric growth. Thus in selecting for *Epiaster gibbus*, for the passage forms between this species and *Micraster coranguinum*, and for *M. coranguinum* var. *latior* he was led to favour large specimens, because, other things being equal, the larger the specimen the better developed the diagnostic characters would be. This is numerically demonstrated in table 4 by the fact that, in these three cases the row means are larger, and the row variances smaller, than for *M. coranguinum* auctorum. In addition, on this hypothesis *Epiaster gibbus* should have a larger mean and a smaller variance than its passage form, the selection of large forms having been more marked in the former than in the latter. And so it has, as is demonstrated by the table.

(*c*) *The age distribution of the sample*

The Northfleet population of fossils itself is already unrepresentative of the original living community from which it was derived. A specimen which is now preserved in the chalk must have survived many hazards since it was part of a living echinoid. To start with, the animal must have died in some way which did not involve the destruction of its test; a specimen eaten by a fish would leave little to be fossilized. After death, the test must have fallen upon an area of the sea bed where deposition and not erosion was taking place; and, finally, the specimen must have escaped being crushed and destroyed during the consolidation of the chalk. Thus the probability of an individual specimen being preserved as a fossil is very small, and there is no reason to assume that this probability will be the same for specimens of all ages. If it is not, then the fossil population in the chalk at the present day will not show the same age distribution as the population of dead specimens on the floor of the Chalk Sea.

It is equally unlikely—and this is a separate problem—that the age distribution of individuals of the dead population on the floor of the Chalk Sea was the same as that of the living population. The distribution of ages in a dead population will only be the same as in the living population from which it arose if the likelihood of dying within any age interval, i.e. the force of mortality, were a constant independent of the age of the individuals.* Were this the case, the same proportion of individuals would die in all age groups, so that the age distribution of the dead population should be the same as that of the living. This is known to be true of some adult birds (Deevey 1947), but enough data have been collected to show that it is not at all common in the animal kingdom. As no life tables have been drawn up for any echinoderm, no more can be said than that it seems most unlikely that the force of mortality in *Micraster* would have remained constant during post-larval life. Nor is it likely that the force of mortality varied with age in the same manner in the two species in Rowe's sample, or that the chances of fossilization were the same for both, since one was probably a burrower, while the other crawled about on the surface of the sea-bed (see p. 406).

In general, the length, breadth or height of an animal, or the size of any part of it, will be highly correlated with its age, older animals being, on the whole, larger. Thus to compare one sample with another, or one species with another, by comparing the means or medians of variates which are highly correlated with the size of the animal, will involve making quite unjustified assumptions, and may give very misleading results.

In fact, in quantitative palaeontology the assumption is often made, although not explicitly, either that the age distribution of the sample is the same as that of the living population, or that all the samples have been biased in exactly the same way. Means or medians are then employed for purposes of comparison. The defence of this practice would appear to be that, from the very nature of palaeontological material, it is impossible to do any better. In fact, however, it is possible to avoid making any such assumptions about the age distribution of the sample if 'size' parameters, such as means and medians, are abandoned for the purpose of comparison, and 'shape' parameters are used instead. The age distribution of the sample will have little effect, if any, upon the values of the estimates of 'pure' shape parameters. This makes the use of the latter of particular value in quantitative palaeontology, where the age distribution of the sample is dependent upon that of the original living population in a very complex and indirect way. Ratios of two variates are often used as shape parameters in this way, but they suffer from the disadvantage that if the relationship between the two variates be allometric, and this is usually the case in practice, the value of the ratio depends on the age of the animal. Shape parameters may be obtained by a consideration of the equation of allometric growth ($y=\beta x^{\alpha}$) which are free from this disadvantage. In this paper the practice has been

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* Let L_x be the probability of living at least to age x, and let D_x be the probability of dying between the ages x and $x+\mathrm{d}x$. Then,

$$D_x = -\frac{\mathrm{d}L_x}{\mathrm{d}x},$$

and

$$\text{force of mortality } (\mu x) = \frac{D_x}{L_x} = -\frac{1}{L_x}\frac{\mathrm{d}L_x}{\mathrm{d}x}.$$

adopted of expressing all metrical variates as allometric functions of each other, and comparing the values of the estimates of the parameters so obtained.

IV. THE RELATIONSHIP OF *MICRASTER CORANGUINUM* AND *M.* (*ISOMICRASTER*) *SENONENSIS* ('*EPIASTER GIBBUS*')

As stated above, Rowe had divided his Northfleet specimens between three main groups: the first contained those specimens which he considered to be true *Epiaster gibbus* (*Micraster senonensis*) (E32513 to 32539); the second forms which he believed to be typical examples of *Micraster coranguinum* (E32759 to 33078, E33103 to 33133, E33191 to 33217, E33880 and E33881); and the last consisted of the transitional forms between these two species (E32410 to 32511, E32540 to 32545). The distinction between the *M. coranguinum* auctorum of Rowe and his *M. coranguinum* var. *latior* may be disregarded. As Rowe himself says (1899), the latter is only the broad form of the former. This difference does not warrant a separate varietal name. It is important, however, to decide whether Rowe was justified in considering his sample to consist of two closely related species which overlap in some morphological characters, or whether, in fact, it consists of a single, very variable, species. *M. senonensis* is stated to differ from *M. coranguinum* in the general shape and proportions of its test, in its possession of a petaloid anterior ambulacrum, and in its lack of a sub-anal fasciole (Lambert 1895, 1901). These three sets of characters will now be dealt with separately.

(*a*) *The shape of the test in the two species*

The sample was divided into Rowe's three groups, and the following correlation tables were drawn up for each group separately. The first set of these consisted of measurements (*b*) to (*e*) and (*g*) plotted against measurement (*a*). The second set consisted of measurements (*c*) to (*e*) and (*g*) plotted against measurement (*b*). The last set consisted of only a single correlation table for each group, measurement (*c*) being plotted against (*d*). This gave a total of ten tables for each of the three groups. The use of correlation tables for making comparisons between the groups enables both size and shape to be compared. As has already been shown (§ III*c* above) more reliable comparisons are possible on a basis of shape than on a basis of size.

Examination of these tables showed that in every case the observations relating to '*Epiaster gibbus*' do not fall altogether outside the area of the table occupied by *Micraster coranguinum*, that is, none of the characters under consideration enables us to distinguish between the two species with certainty. The sample of Rowe's *Epiaster* is too small for any bimodality to make itself apparent. In all these characters the 'transitional' forms appear to be intermediate between the other two groups.*

In addition to these characters there are some which have not been expressed in metrical form. It has been noticed that the specimens of '*Epiaster gibbus*' tend to have thinner tests than do the specimens of the other groups. Measurements of test thickness could only be made by cutting the specimens, so as to obtain a standard measurement in

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* Owing to lack of space six of these tables, 5 to 10, have been given as an example. The rest have been deposited in the archives of the British Museum (Nat. Hist.) or may be seen by consulting the author's Ph.D. thesis (Kermack 1950) at the University of London Library.

one position, and it was not possible or desirable to destroy the specimens in this way. As a consequence of the thinner test, the periplastronal area is less ornamented in '*Epiaster*' than in *Micraster*. The plastron is shorter in the former species than in the latter, and its posterior termination is more anterior. This difference is probably connected with the absence of the sub-anal fasciole in '*Epiaster*'. Finally, the paired ambulacra are rather deeper in '*Epiaster gibbus*' than in *Micraster coranguinum*. None of these characters, however, enables a clear-cut distinction to be made between Rowe's two species. Compare figures 12, 14 and 16 with figures 13, 15 and 17, plates 24 to 26.

TABLE 5. '*EPIASTER GIBBUS*' (E32513 TO 32539). TABLE OF LENGTH × BREADTH

breadth (mm)	48·995–49·995	49·995–50·995	50·995–51·995	51·995–52·995	52·995–53·995	53·995–54·995	54·995–55·995	55·995–56·995	56·995–57·995	57·995–58·995	58·995–59·995	59·995–60·995	60·995–61·995	61·995–62·995	62·995–63·995	63·995–64·995	64·995–65·995	65·995–66·995	66·995–67·995	total
66·995–67·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
65·995–66·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
64·995–65·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
63·995–64·995	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	2
62·995–63·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
61·995–62·995	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	2
60·995–61·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
59·995–60·995	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	2
58·995–59·995	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
57·995–58·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
56·995–57·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
55·995–56·995	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1
54·995–55·995	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1
53·995–54·995	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	3
52·995–53·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
51·995–52·995	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1
50·995–51·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
49·995–50·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
48·995–49·995	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
total	1	.	1	.	1	.	4	.	1	.	.	2	1	2	1	.	.	1	1	16

length (mm)

(*b*) *The anterior ambulacrum in the two species*

Both Lambert (1895, 1901) and Rowe considered the petaloid or subpetaloid nature of the anterior, unpaired ambulacrum in *Isomicraster senonensis* (*Epiaster gibbus*) to be one of the distinguishing characters between this form and the true micrasters. The analysis of the character will deal with only two of Rowe's three groups. These are the group which he considered as true *E. gibbus* (E32513 to 32539) and the group of transitional forms (E32410 to 32511 and E32540 to 32545). The restriction of the work to these two groups is due to the third group not being available at the appropriate time, as it was still awaiting registration at the Museum. It is the transitional forms which are of major interest for the present purpose, and the absence of this third group is not likely to affect the conclusions reached in this section of the paper. Two measurements were made on the anterior ambulacrum of each specimen: the total number of plates in its petaloid portion (n), and the length of this part of the ambulacrum (o). The method of making these measurements has already been described (§ II*b*).

TABLE 6. PASSAGE FORMS CONNECTING *MICRASTER CORANGUINUM* WITH *EPIASTER GIBBUS* (E32410 TO 32511, 32540 TO 32545)

TABLE OF LENGTH × BREADTH

breadth (mm)	35·995–36·995	36·995–37·995	37·995–38·995	38·995–39·995	39·995–40·995	40·995–41·995	41·995–42·995	42·995–43·995	43·995–44·995	44·995–45·995	45·995–46·995	46·995–47·995	47·995–48·995	48·995–49·995	49·995–50·995	50·995–51·995	51·995–52·995	52·995–53·995	53·995–54·995	54·995–55·995	55·995–56·995	56·995–57·995	57·995–58·995	58·995–59·995	59·995–60·995	60·995–61·995	61·995–62·995	62·995–63·995	63·995–64·995	64·995–65·995	total
62·995–63·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
61·995–62·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	1	4
60·995–61·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1
59·995–60·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	2
58·995–59·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1
57·995–58·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	3
56.995–57·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	1	.	.	.	.	.	7
55·995–56·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	1	.	.	.	.	.	.	.	.	4
54·995–55·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	1	.	.	.	.	.	.	4
53·995–54·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	3	.	.	.	.	.	.	.	.	.	4
52·995–53·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	.	.	1	.	.	.	.	.	.	.	.	5
51·995–52·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	2
50·995–51·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	1	.	.	.	.	.	.	.	.	.	.	.	4
49·995–50·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	.	.	.	.	.	.	.	.	.	.	.	.	3
48·995–49·995	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	4
47·995–48·995	.	.	.	.	.	.	.	.	.	.	.	.	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
46·995–47·995	.	.	.	.	.	.	.	.	.	.	1	.	2	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
45·995–46·995	.	.	.	.	.	.	.	.	.	.	.	2	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
44·995–45·995	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
43·995–44·995	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
42·995–43·995	.	.	.	.	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
41·995–42·995	.	.	.	.	.	.	.	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
40·995–41·995	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
39·995–40·995	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
38·995–39·995	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
37·995–38·995	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
36·995–37·995	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
35·995–36·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
34·995–35·995	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
total	2	.	1	4	2	1	2	3	5	2	2	3	6	6	1	4	2	6	6	1	5	5	6	5	1	.	1	3	1	1	87

length (mm)

TABLE 7. *MICRASTER CORANGUINUM* (E32759 TO 33078, 33103 TO 33133, 33191 TO 33217, 33880 TO 33881). TABLE OF LENGTH × BREADTH

breadth (mm)	23·995–24·995	24·995–25·995	25·995–26·995	26·995–27·995	27·995–28·995	28·995–29·995	29·995–30·995	30·995–31·995	31·995–32·995	32·995–33·995	33·995–34·995	34·995–35·995	35·995–36·995	36·995–37·995	37·995–38·995	38·995–39·995	39·995–40·995	40·995–41·995	41·995–42·995	42·995–43·995	43·995–44·995	44·995–45·995	45·995–46·995	46·995–47·995	47·995–48·995	48·995–49·995	49·995–50·995	50·995–51·995	51·995–52·995	52·995–53·995	53·995–54·995	54·995–55·995	55·995–56·995	56·995–57·995	57·995–58·995	58·995–59·995	59·995–60·995	60·995–61·995	61·995–62·995	62·995–63·995	63·995–64·995	64·995–65·995	65·995–66·995	66·995–67·995	67·995–68·996	68·995–69·995	69·995–70·995	70·995–71·995	total
66·995–67·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	2
65·995–66·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1
64·995–65·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	1	.	1	.	.	.	5
63·995–64·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	.	.	.	3
62·995–63·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	2	.	.	.	.	.	.	.	4
61·995–62·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	2
60·995–61·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	2	1	1	.	.	.	.	.	.	7
59·995–60·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	2	3	.	.	.	.	.	.	.	7
58·995–59·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	3	1	1	1	.	.	.	.	.	.	.	.	10
57·995–58·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	6	3	3	.	2	1	.	.	.	.	.	.	.	18
56·995–57·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	2	1	1	.	.	.	.	.	.	.	.	.	10
55·995–56·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	4	1	4	1	.	.	.	.	.	.	.	.	.	.	.	14
54·995–55·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	8
53·995–54·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	4	2	5	1	2	3	3	.	.	.	.	.	.	.	.	.	.	.	.	21
52·995–53·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	6	2	5	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	20
51·995–52·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	2	1	5	1	1	.	3	1	.	.	.	.	.	.	.	.	.	.	.	.	.	15
50·995–51·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	3	.	1	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	9
49·995–50·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	3	3	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14
48·995–49·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	4	4	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13
47·995–48·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	4	2	4	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14
46·995–47·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	2	1	3	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
45·995–46·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	3	1	4	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	14
44·995–45·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	5	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
43·995–44·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	2	1	3	1	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12
42·995–43·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	3	1	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
41·995–42·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	5	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10
40·995–41·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
39·995–40·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	3	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
38·995–39·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
37·995–38·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
36·995–37·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
35·995–36·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
34·995–35·995	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
33·995–34·995	.	.	.	.	.	.	.	.	.	.	.	1	5	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
32·995–33·995	.	.	.	.	.	.	.	.	.	.	1	2	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
31·995–32·995	.	.	.	.	.	.	.	.	.	.	.	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
30·995–31·995	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
29·995–30·995	.	.	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
28·995–29·995	.	.	.	.	.	.	1	4	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
27·995–28·995	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
26·995–27·995	.	.	.	.	.	3	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
25·995–26·995	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
24·995–25·995	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
23·995–24·995	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
22·995–23·995	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
total	1	1	2	.	2	4	6	6	1	3	1	6	8	3	12	3	6	2	10	9	14	10	9	5	14	13	15	19	10	18	13	13	11	14	15	19	12	6	4	9	7	6	3	.	1	.	1	1	348

length (mm)

The scatter diagram (figure 5) of the length of the petal (o) plotted against the length of the animal (a) shows both a reasonably high degree of correlation between the two variates ($r = 0{\cdot}8107$) and a slight, but noticeable, curvature in the trend of the plotted points. On a sample of this size (sixty-seven specimens), it is not possible to be certain whether the slight upward curve in the graph is significant. If it is, it means that the growth

TABLE 8. '*EPIASTER GIBBUS*' (E32513 TO 32539). TABLE OF LENGTH × MAXIMUM HEIGHT

height (mm)	48·995–49·995	49·995–50·995	50·995–51·995	51·995–52·995	52·995–53·995	53·995–54·995	54·995–55·995	55·995–56·995	56·995–57·995	57·995–58·995	58·995–59·995	59·995–60·995	60·995–61·995	61·995–62·995	62·995–63·995	63·995–64·995	64·995–65·995	65·995–66·995	66·995–67·995	total
42·995–43·995	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1
41·995–42·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1
40·995–41·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
39·995–40·995	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	1
38·995–39·995	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1
37·995–38·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
36·995–37·995	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1
35·995–36·995	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2
34·995–35·995	.	.	.	.	.	.	1	.	1	.	.	1	.	.	.	.	.	.	.	3
33·995–34·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
32·995–33·995	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
31·995–32·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
30·995–31·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
29·995–30·995	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
total	1	.	1	.	.	.	4	1	1	.	.	1	.	2	.	.	.	.	1	12

length (mm)

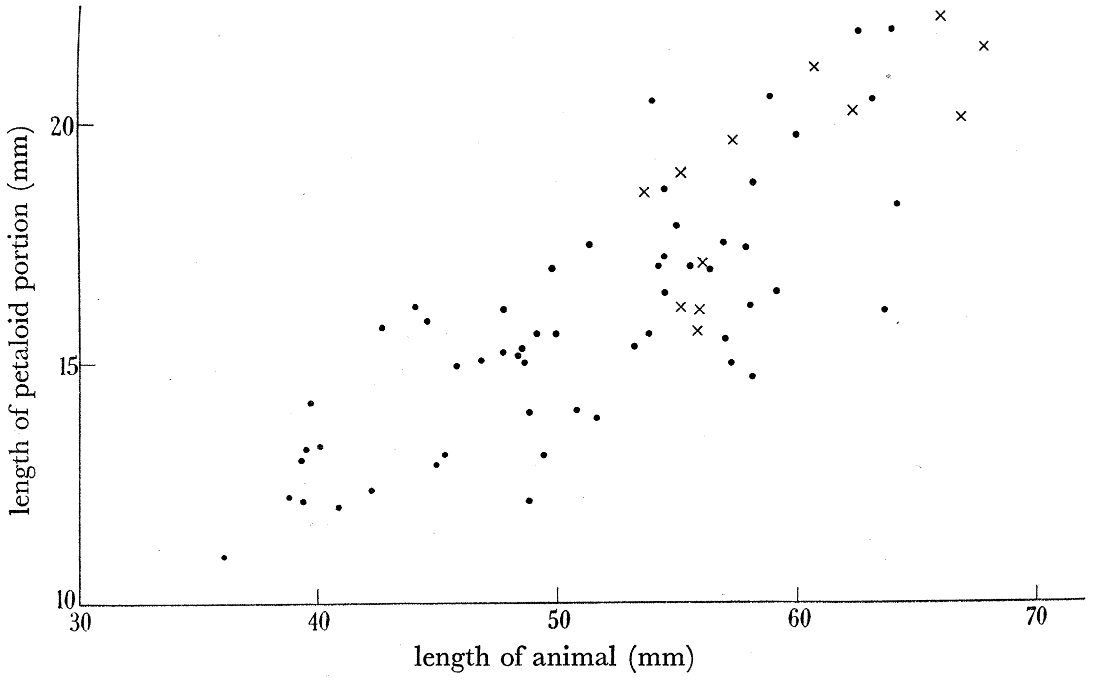

FIGURE 5. Scatter diagram showing the length of the petaloid portion of the anterior ambulacrum plotted against the length of the specimen (specimens E 32410 to 32545 inclusive). ×, specimens E 32513 to 32539 ('*Epiaster gibbus*' Rowe): •, other specimens.

TABLE 9. 'PASSAGE FORMS CONNECTING *M. CORANGUINUM* WITH *EPIASTER GIBBUS*' (E32410 TO 32511, 32540 TO 32545).

TABLE OF LENGTH × MAXIMUM HEIGHT

height (mm)	35·995–36·995	36·995–37·995	37·995–38·995	38·995–39·995	39·995–40·995	40·995–41·995	41·995–42·995	42·995–43·995	43·995–44·995	44·995–45·995	45·995–46·995	46·995–47·995	47·995–48·995	48·995–49·995	49·995–50·995	50·995–51·995	51·995–52·995	52·995–53·995	53·995–54·995	54·995–55·995	55·995–56·995	56·995–57·995	57·995–58·995	58·995–59·995	59·995–60·995	60·995–61·995	61·995–62·995	62·995–63·995	63·995–64·995	total
43·995–44·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1
42·995–43·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	1
41·995–42·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	3
40·995–41·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	2
39·995–40·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1
38·995–39·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	1	3	1	8
37·995–38·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
36·995–37·995	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	2	.	1	1	1	.	.	.	.	1	.	8
35·995–36·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	1	.	.	.	.	.	3
34·995–35·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	.	1	.	.	.	.	.	.	.	.	4
33·995–34·995	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	7
32·995–33·995	.	.	.	.	.	.	.	.	.	.	1	1	4	1	1	.	.	.	.	.	2	1	.	.	.	.	.	.	.	11
31·995–32·995	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	2	.	.	.	.	1	.	.	.	.	.	.	5
30·995–31·995	.	.	.	.	.	.	1	.	2	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	5
29·995–30·995	.	.	.	.	1	1	.	1	1	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	7
28·995–29·995	.	.	.	1	1	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
27·995–28·995	.	.	1	1	.	.	1	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
26·995–27·995	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
25·995–26·995	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
24·995–25·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
23·995–24·995	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
total	2	.	1	4	2	1	2	1	5	2	2	3	6	5	2	4	2	5	6	1	5	3	5	5	1	.	1	4	1	81

length (mm)

TABLE 10. '*MICRASTER CORANGUINUM*' (E32759 TO 33078, 33103 TO 33133, 33191 TO 33217, 33880 TO 33881).

TABLE OF LENGTH × MAXIMUM HEIGHT

height (mm)	23·995–24·995	24·995–25·995	25·995–26·995	26·995–27·995	27·995–28·995	28·995–29·995	29·995–30·995	30·995–31·995	31·995–32·995	32·995–33·995	33·995–34·995	34·995–35·995	35·995–36·995	36·995–37·995	37·995–38·995	38·995–39·995	39·995–40·995	40·995–41·995	41·995–42·995	42·995–43·995	43·995–44·995	44·995–45·995	45·995–46·995	46·995–47·995	47·995–48·995	48·995–49·995	49·995–50·995	50·995–51·995	51·995–52·995	52·995–53·995	53·995–54·995	54·995–55·995	55·995–56·995	56·995–57·995	57·995–58·995	58·995–59·995	59·995–60·995	60·995–61·995	61·995–62·995	62·995–63·995	63·995–64·995	64·995–65·995	65·995–66·995	66·995–67·995	67·995–68·995	68·995–69·995	69·995–70·995	70·995–71·995	total
41·995–42·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1
40·995–41·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	2
39·995–40·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	2
38·995–39·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	1	1	.	.	.	.	.	.	1	.	6
37·995–38·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	2	2	.	1	1	1	.	.	.	.	.	1	10
36·995–37·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	3	.	1	3	3	.	1	2	1	.	.	.	.	.	.	.	17
35·995–36·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	1	2	3	4	2	1	.	2	.	1	2	.	.	.	.	.	21
34·995–35·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	2	2	1	2	1	3	3	3	3	1	2	1	1	1	.	.	.	.	.	.	29
33·995–34·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	2	5	1	3	6	1	3	3	4	.	.	.	1	.	2	.	.	.	.	.	.	35
32·995–33·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	3	5	2	5	3	.	5	3	2	1	.	.	.	.	.	.	.	.	.	.	.	.	32
31·995–32·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	3	.	1	3	2	3	3	1	4	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	24
30·995–31·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	3	3	.	4	2	3	5	1	.	2	2	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	30
29·995–30·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	1	3	1	1	1	.	1	1	1	.	2	1	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	17
28·995–29·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	2	4	2	2	.	.	2	.	1	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
27·995–28·995	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	1	2	.	4	2	1	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	17
26·995–27·995	.	.	.	.	.	.	.	.	.	.	.	.	1	.	4	.	2	.	5	1	.	1	1	.	1	1	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	19
25·995–26·995	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	.	.	1	1	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
24·995–25·995	.	.	.	.	.	.	.	.	.	.	.	3	3	2	1	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11
23·995–24·995	.	.	.	.	.	.	.	.	.	2	.	1	2	1	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8
22·995–23·995	.	.	.	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
21·995–22·995	.	.	.	.	.	1	.	2	1	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6
20·995–21·995	.	.	.	.	.	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5
19·995–20·995	.	.	.	.	.	1	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
18·995–19·995	.	1	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4
17·995–18·995	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
16·995–17·995	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
15·995–16·995	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
total	1	1	2	.	2	4	4	6	1	3	1	6	7	3	10	3	6	2	10	9	13	11	9	5	13	11	14	19	11	17	12	12	12	13	14	20	11	6	4	9	6	6	2	.	.	.	1	1	333

length (mm)

in length of the whole animal fails quite to keep pace with the growth in length of the anterior petal. Figures 6 and 7 show the plate number (n) plotted against the length of the petal (o) and against the length of the whole animal (a), and these two graphs tell a very different

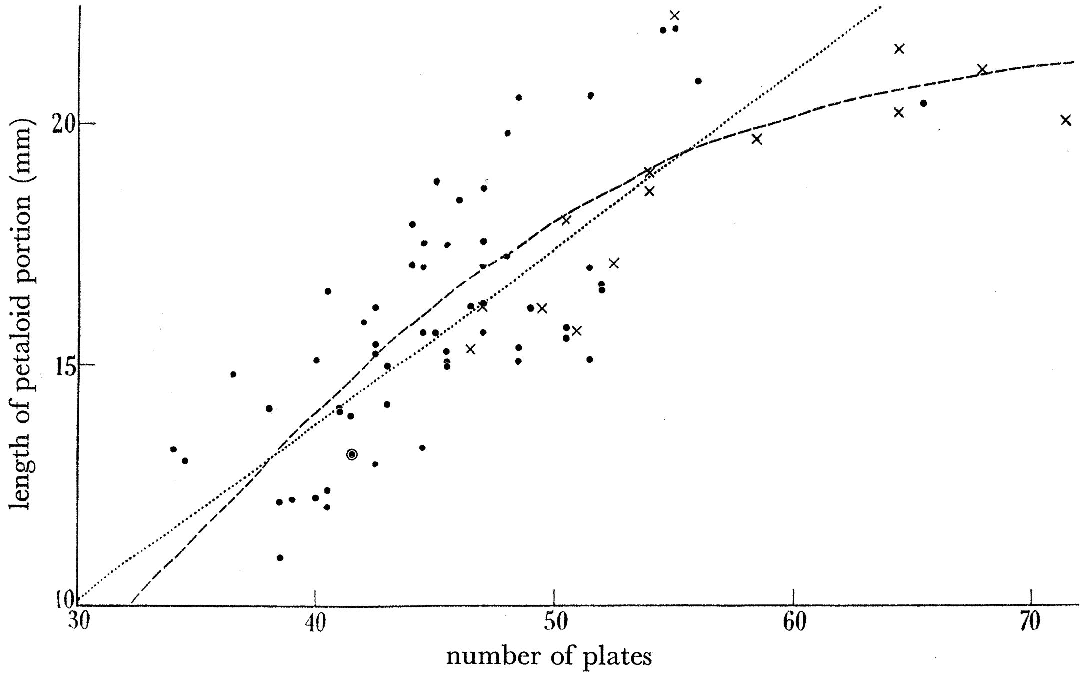

FIGURE 6. Scatter diagram showing the length of the petaloid portion of the anterior ambulacrum plotted against the number of plates in the petal (specimens E 32410 to 32545 inclusive). Symbols as in figure 5. – – – $l = \frac{1}{1+25{\cdot}003\,e^{0{\cdot}09447n}}$; ...... $l = 0{\cdot}2780n^{1{\cdot}05815}$.

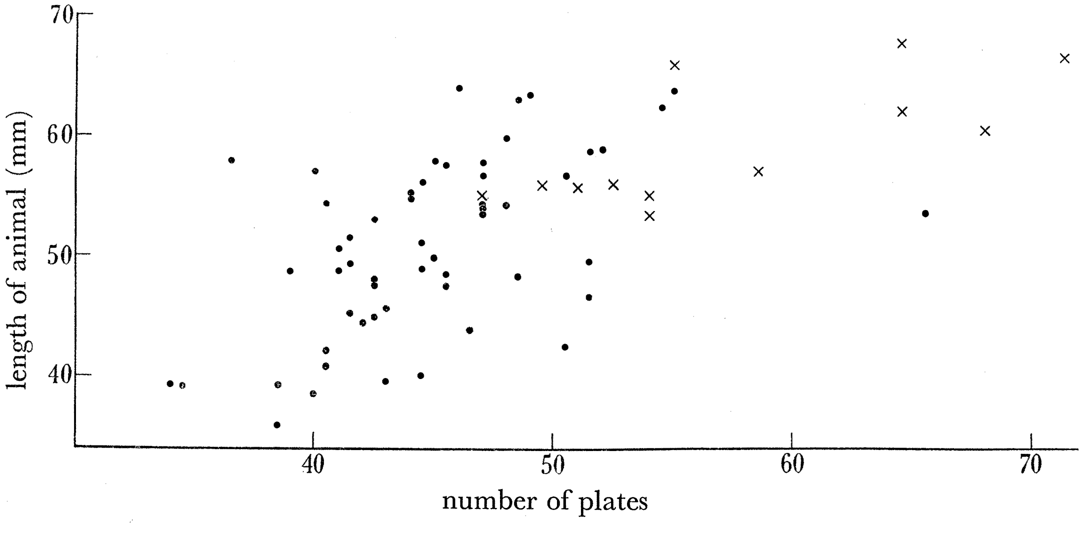

FIGURE 7. Scatter diagram showing the length of the specimen plotted against the number of plates in the petaloid portion of the anterior ambulacrum (specimens E 32410 to 32545 inclusive). Symbols as in figure 5.

story to figure 5. Until the petal contains a total of about fifty plates, the number of plates in it is roughly proportional both to the length of the petal and to the length of the specimen. When, however, the petal comes to contain something more than fifty plates, then the number of plates increases much more rapidly than the increase in length either of the petal or of the whole animal. In the graphs there is the well-marked bend in the line of points at this stage.

In these forms the plates of the anterior ambulacrum must have been produced at its apex, in the usual echinoid manner. Then they were pushed down the ambulacrum by the appearance of still further new plates behind them. As they moved down they grew in size and showed a considerable plasticity of shape. The ability of the ambulacral plates of echinoids to respond to pressure by changes in shape is well known, Hawkins (1919) giving an excellent account of it, although the mechanism by which it operates is unknown.

During growth the plates of the anterior ambulacrum were subjected to packing and crushing, which turned the initially square plates with closely placed circular pores into rectangular plates with widely spaced, elongated pores, the elongation being normal to the long axis of the ambulacrum. 'Plate pressure' would have eventually turned the unmodified ambulacrum into a typical 'petal'. The petal terminates quite suddenly, so that there must be a point in the ambulacrum beyond which the plasticity of plates becomes much reduced. In the young animal, plates which had once got beyond this point would thus have been protected from the effects of plate pressure and would not have 'packed down' and become petaloid. If it be assumed that this point is at a distance a from the apex of the ambulacrum, then the limiting length of petal is a. If l be the length of the petaloid portion of the ambulacrum already in existence, then the increase in its length for the addition of one new plate at the apex will be proportional both to l and to $a-l$. It will be proportional to l since the longer the petal the larger the animal (figure 5)—and hence the larger the plate; it must be proportional to $a-l$ since the more nearly l is equal to a the greater the plate pressure and the more plate 'packing' must have taken place. Then, for the addition of the $n+1$ plate,

$$l_{n+1}-l_n=kl_n(a-l_n),$$

and considering this as a differential equation (which is strictly inadmissible, but is convenient) we have

$$\mathrm{d}l=kl(a-l)\,\mathrm{d}n.$$

This equation integrates to give $$l=\frac{a}{1+b\mathrm{e}^{-\gamma n}},$$

which is the equation of the well-known logistic curve. This curve is of the shape required to fit figures 6 and 7, since, at first, it rises up with a fairly even slope, which then falls off sharply as the curve comes to its asymptote. Figure 6 shows a logistic fitted to the data. The logistic does not lend itself to fitting by the method of least squares, although Pearl (1930) gives a transformation which makes this possible, albeit by the employment of a certain amount of guesswork. Hartley (1948) gives an exact method, which is, unfortunately, only suitable if the observations are equally spaced, and so cannot be used here. In the present case the curve was drawn by guessing the upper asymptote (a), and then choosing three points through which the curve had to pass. This gives what appears to be not too bad a fit. The equation of allometric growth was also fitted to the data by the method of Kermack & Haldane (1950), and this curve is shown on the same graph. It can be seen that it does not follow the trend of the plotted points as well as does the logistic. An exponential equation has also been fitted and found to be unsatisfactory. Judging the goodness of fit by eye can be dangerous, as has been pretty thoroughly pointed out in the literature, but its use is not unreasonable in the present instance, since the labour of computation in any more exact method would be prohibitive.

The peculiar trend of the plotted points in figures 6 and 7 may be explained as follows. If at maturity there were a sudden decrease in the rate of growth in size of most parts of the echinoid, but the rate of production of new ambulacral plates was not affected by this general decrease, this would cause the sudden bend in the trend of the plotted points, as shown by the logistic in figure 6. It is only in those specimens which had reached a reasonable size that plate packing could have proceeded far enough to produce something resembling a typical petal in the anterior ambulacrum. In *Micraster*, the sole difference between the paired and unpaired ambulacra was that the former must have had a higher rate of production of new plates than the latter. This would have caused the paired ambulacra always to have had a petaloid portion as soon as the animal had exceeded a certain very small size.

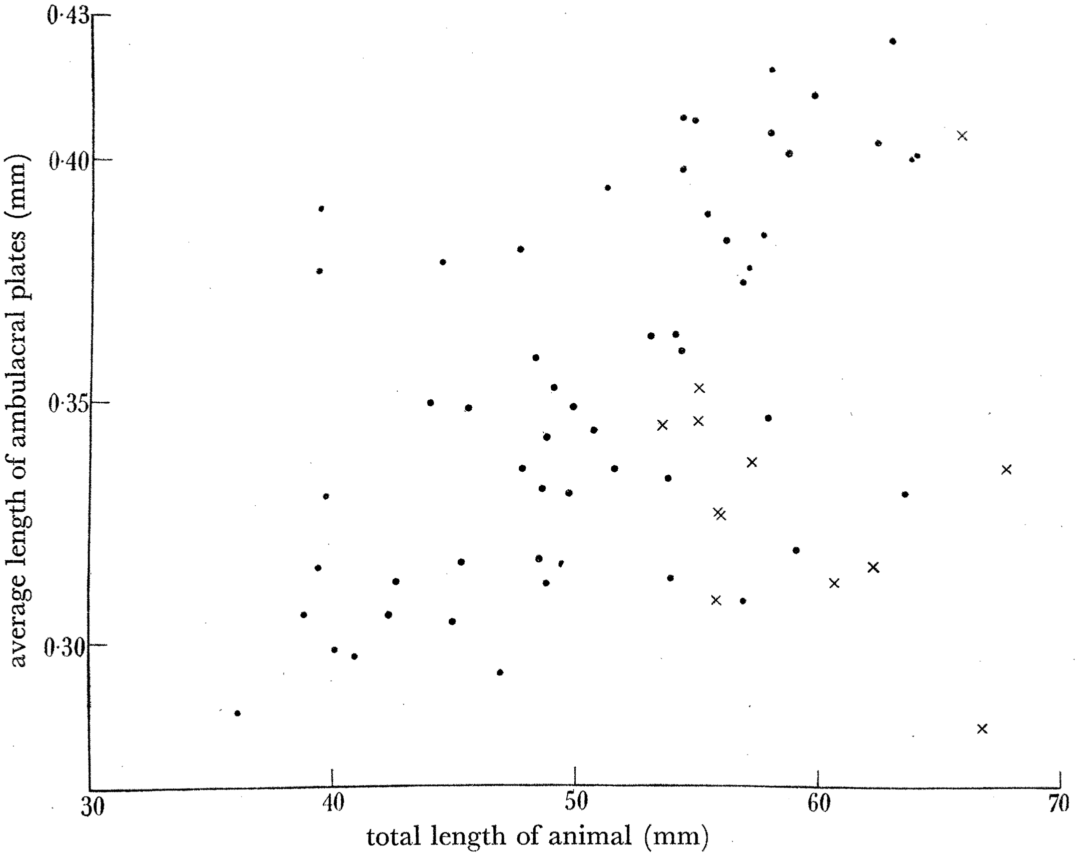

FIGURE 8. Scatter diagram showing the average length of the plates in the petaloid portion of the anterior ambulacrum plotted against the length of the specimen (specimens E32410 to 32545 inclusive).

In figures 5 to 10 those forms which Rowe regarded as true '*Epiaster gibbus*' (E32513 to 32539) have been represented by crosses, while his transitional forms (E32410 to 32511 and E32540 to 32545) have been marked by a dot. From figure 6 it can be seen that the examples of the former group all tend to have a large number of plates in proportion to the length of the petal. Thus considerable plate packing had taken place, and the anterior ambulacrum shows a well-developed petal. Figure 7 tells another version of the same story, in that Rowe's '*Epiaster gibbus*' have a large number of plates in the anterior ambulacrum, relative to the length of the specimen. Finally, figure 8 shows that these forms have rather narrower plates in the petaloid part of the anterior ambulacrum than do the transitional forms. These graphs show, however, that in respect of any of these characters of the unpaired ambulacrum, it is impossible to draw a dividing line between those forms classed by Rowe as *Epiaster gibbus* and those forms which he classed as *Micraster coranguinum*. The difference is only one of degree, and the two 'genera' intergrade perfectly with respect to this set of characters.

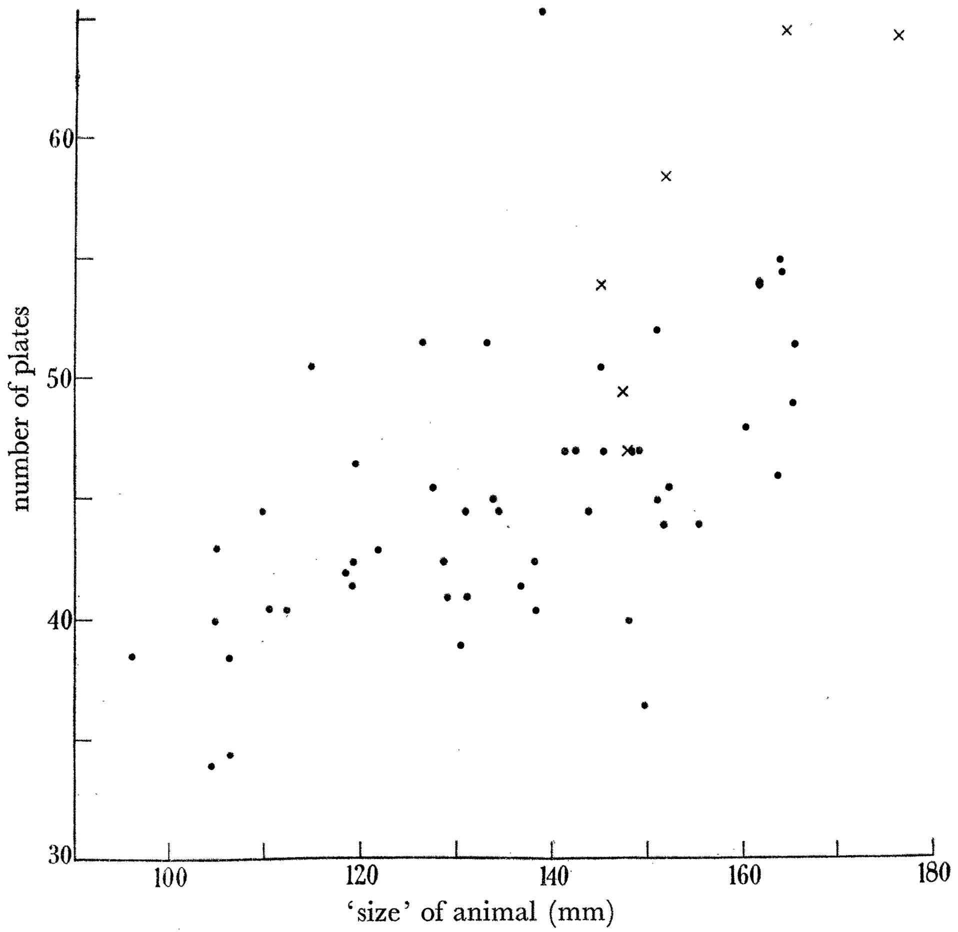

FIGURE 9. Scatter diagram showing the number of plates in the petaloid portion of the anterior ambulacrum plotted against the 'size' of the animal (specimens E32410 to 32545 inclusive). Symbols as in figures 5 to 7.

Rowe's epiasters are rather broad and tall for their length, as may be seen from tables 5 to 10. This raises the question whether Rowe's '*Epiaster gibbus*' tend to have more plates in their anterior ambulacra because they are larger than specimens of *Micraster coranguinum*, of the same overall length. To decide this it is necessary to have a measure of the overall size of the animal. The most obvious one to choose is the total volume of the test. In practice, the measurement of this character would have a number of disadvantages, one being to find a suitable liquid which would not penetrate the specimen. Another is that many of the specimens are incomplete, owing to damage, or have adhering to them Bryozoa, the tubes of serpulid worms, and small shells. These difficulties can be avoided by the use of some variate based on the length, breadth and height. One possibility would be to multiply all three together, and then to take the cube root of the product to give a variate of linear dimensions. Here a simpler alternative has been chosen—the three variates have simply been added together. This is equivalent to using the arithmetic mean instead of the geometric mean, and the sum is similar to the compound 'size' estimate of Penrose (1947). Figure 9 shows the number of plates in the anterior petal plotted against the size of the specimen, and it should be carefully compared with figure 7. In both cases '*Epiaster gibbus*' tends to have more plates in the petal of the unpaired ambulacrum than specimens of *Micraster coranguinum* of the same size. This tendency is less well marked, however, when the size is estimated from the compound size variate than when it is estimated from the total length of the specimen. The fact that the Epiasters tend to be rather larger for their length than the Micrasters will account for a part of the increased number of plates in the anterior ambulacrum of the former seen in figure 6. It will not account for all the difference, however, and at any rate a part of this is probably real and may have some unknown adaptive significance.

(*c*) *The area of the sub-anal fasciole*

In the analysis of the measurements of the area of the sub-anal fasciole, its area (measurement (*m*), § II*b*) was plotted against the length of the specimen (measurement (*a*)) as a scatter diagram (figure 10). Rowe's '*Epiaster gibbus*' and its passage forms (E32410 to 32545) were plotted as crosses, and the rest of the specimens as dots. These plotted points fall into two clearly separated groups. One contains all the dots and some of the crosses, and here the general trend of the points suggests that the area of the fasciole varies, to a first approximation, as the square of the length of the specimen. The second group is much smaller, and consists entirely of crosses. In these animals the area of the fasciole is either zero or else very small, and there is no sign of any trend in the points. Of Rowe's group of 'true *Epiaster gibbus*' (E32513 to 32539) the area of the fasciole could be measured in fourteen specimens. Of these three fall into the first group and eleven into the second.

The function of the sub-anal fasciole has been investigated by Gislén (1924); and the following account will be based upon his work, supplemented by observations made by myself at Plymouth and at Roscoff. The two regular echinoids observed, *Psammechinus miliaris* and *Echinus esculentus*, live on the sea bed. The whole surface of the animal, including the bases of the spines, is covered with fine cilia, which, except on the periproct, so beat as to drive a current of water towards the mouth. This current keeps the surface of the animal clean by removing detritus and the larvae of sessile and parasitic animals. This was demonstrated by placing particles of carmine, and tiny glass balls, on the surface of the animal. The ciliary current was the dominant factor in moving the carmine particles; gravity, and the shape of the animal, was more important in the case of the glass balls. The small spines and the pedicellariae assisted in moving troublesome particles.

Two spatangoids have been observed, *Spatangus purpureus* and *Echinocardium cordatum. Spatangus* resembles *Micraster* in having only a sub-anal fasciole, *Echinocardium* has both sub-anal and peripetalous fascioles. In both species the arrangement of the ciliary tracts over the surface is quite different from that in the regular echinoids. The arrangement in *Spatangus purpureus* is shown in figure 11. It can be seen that the ciliary currents sweep any small particles falling on the animal backwards to the sub-anal fasciole. The small, closely set spines which make up the fasciole are heavily ciliated, and cause an intense current of water directed backwards away from the animal. In *Echinocardium* the state of affairs is essentially similar, despite the presence of a peripetalous fasciole in this species.

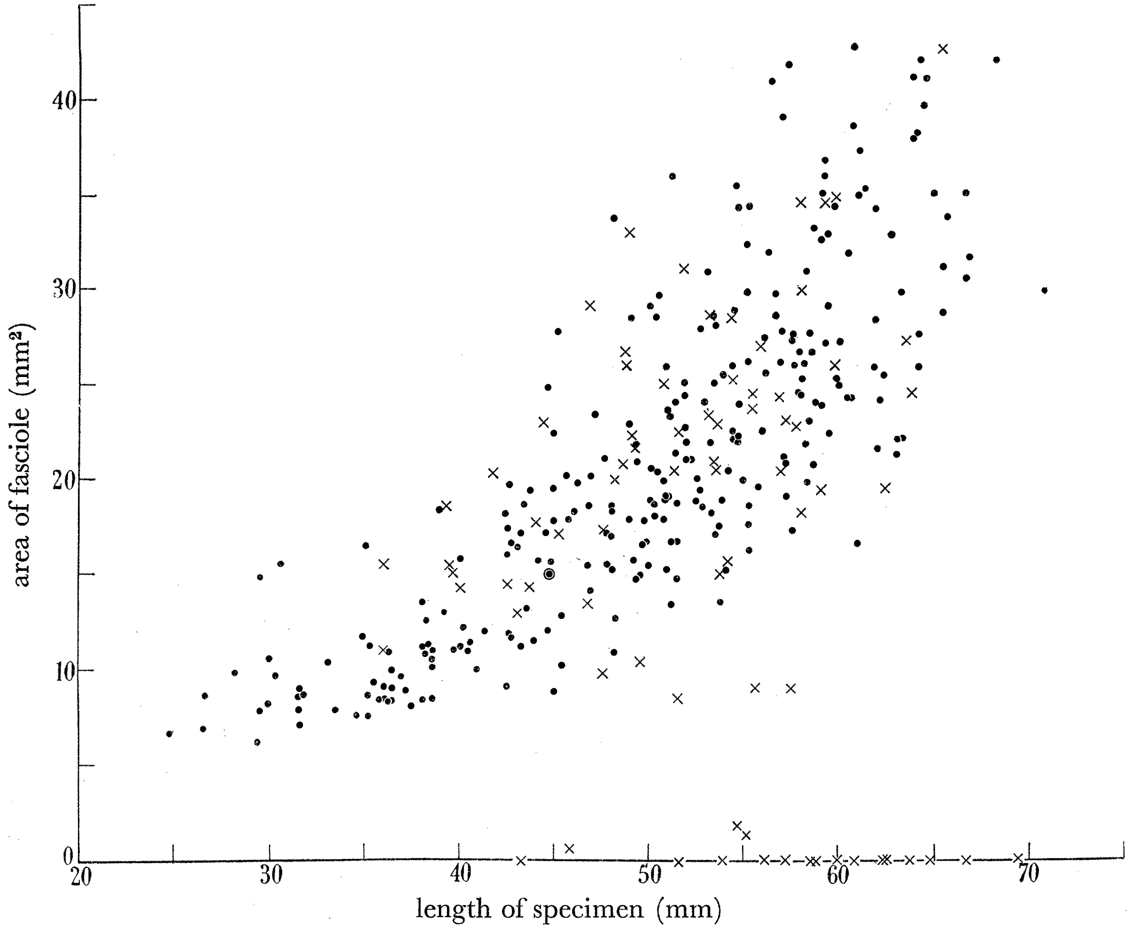

FIGURE 10. Scatter diagram of the area of the sub-anal fasciole plotted against the length of the specimen (specimens E 32410 to 32545, E 32759 to 33078, E 33103 to 33133, E 33191 to 33217, E 33880 to 33881). Symbols as in figures 5 to 7, 9.

The explanation of the difference between the spatangoids and the regular echinoids is obtained by a consideration of their modes of life. *Spatangus* and *Echinocardium* live in burrows. Under these conditions a continuous current of water is needed for respiration, for the removal of waste products, and to keep the surface of the animal clean. The ciliary tracts on the body, especially those of the sub-anal fasciole, produce a strong current of water backwards through the burrow and meet these needs. Any small particles which fall on the surface of the animal are swept backwards to the sub-anal fasciole and are there swept away. In this case gravity can be of no assistance in keeping the body clean. *Micraster coranguinum* much resembles *Spatangus* in shape, and it is reasonable to assume that the mode of life was similar in the two species. In this case the sub-anal fasciole would have had the same function in *Micraster* as in the present day spatangoids, namely, that of maintaining a powerful current of water backwards through the burrow.

The sub-anal fasciole in *Micraster senonensis* is absent or rudimentary, and the high conical shape of this species makes it unlikely that it was a burrowing form. It is worth noting here that the unrelated *Echinocorys*, also to be found in the chalk, has a markedly elevated shape and lacked fascioles. These elevated forms could not have been burrowers, and must have lived on, rather than in, the sea bottom. Under such a mode of life a sub-anal fasciole would be useless. The animals existed in a continuous rain of precipitating calcium carbonate, foraminiferal tests and other detritus. These particles were disposed of in the same way as in the modern regular echinoids, by orally directed ciliary currents, and by the general shape of the animal causing larger particles to roll down and off. The high, conical shape of *M. senonensis* seems well suited to this last function.

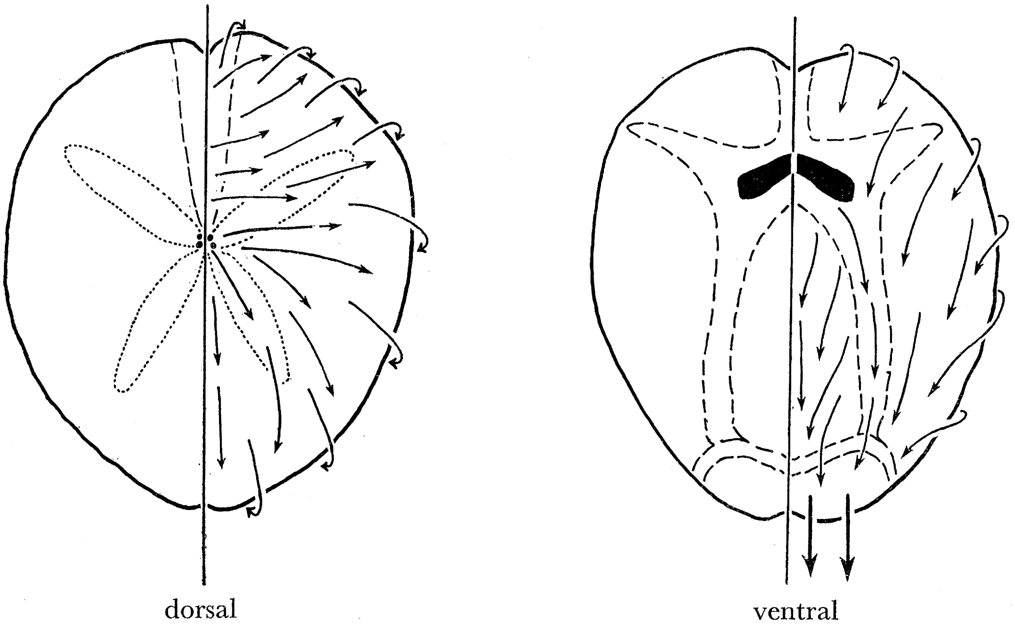

FIGURE 11. Ciliary tracts in *Spatangus purpureus*.

In all characters, except the area of the sub-anal fasciole, the two species completely intergrade. Such intergrading is due to hybridization and is not uncommon between species of recent echinoids: see, for example, Shearer, de Morgan & Fuchs (1913) and Mortensen (1927). *Micraster senonensis* and *M. coranguinum* may well have hybridized in the same way, thus producing the transitional forms. By analogy with the recent forms, however, there is no reason to deny to either the status of a good species, although they can only be certainly distinguished on the character of the sub-anal fasciole.

V. Allometric growth in *Micraster coranguinum* and *M. senonensis*

(*a*) *The estimation of the parameters of the equation of allometric growth*

Following upon the work of Huxley (1924), there has arisen a great interest in the part played by relative growth rates in evolution. Huxley's basic assumption is that the ratio of the relative growth rates of two organs of an individual is constant. If x be some metrical character of one organ, for example, its length, then its growth rate is the differential of x with respect to its age, and similarly for y, the corresponding character of another organ. The growth rates being $\frac{dx}{dt}$ and $\frac{dy}{dt}$, the relative growth rates are $\frac{1}{x}\frac{dx}{dt}$ and $\frac{1}{y}\frac{dy}{dt}$. Then Huxley's hypothesis gives the differential equation $\frac{1}{y}\frac{dy}{dt} = \alpha\frac{1}{x}\frac{dx}{dt}$, or $\frac{x}{y}\frac{dy}{dx} = \alpha$, where α is a parameter, called by Richards & Kavanagh (1945) the *growth ratio*. The solution of this equation is $y = \beta x^{\alpha}$, β being another parameter, the *initial growth index* of the above authors. Taking the logarithms of both sides the equation becomes

$$\log y = \alpha \log x + \log \beta.$$

This equation gives an excellent fit in many cases of relative growth, and for this reason it has been largely used in previous work on relative growth rates in evolution. Examples of this may be found in the work of Huxley himself (1924, 1932), and that of Hersh (1934), Robb (1935*a*, *b*, 1936, 1937), de Beer (1940), Lumer (1940), Phleger (1940), Phleger & Putnam (1942) and Reeve & Murray (1942). The following section of this paper deals with the application of the equation to the Northfleet samples of *coranguinum* and *senonensis*.

The parameters (α and β) of the equation of allometry are most conveniently estimated by fitting a straight line to the logarithmic data. In all previous work the line has either been fitted by eye, or is a regression line fitted by the method of least squares. The former practice has little to commend it, while the use of regression lines is open to a serious objection. A regression line is one about which the sum of squares of *one* of the two variates has been reduced to a minimum. This variate is called the *dependent* variate, the other the *independent* variate. The use of the regression line is only valid if all the error lies in the determination of the values of the dependent variate. Under these conditions it enables us to estimate the most probable value of the dependent variate for any given value of the independent variate. Usually in palaeontology we are dealing, not with the growth of a single specimen, but with a sample consisting of a number of specimens of different sizes. In this case by far the greater part of the residuals of the variates about the regression lines is due to the inherent biological variability of the material and not to errors of measurement. What is wanted is not a line for estimating the most probable value of one variate for a given value of the other, but a line that will represent satisfactorily the general trend of the observations. A suitable line for this purpose is the *reduced major axis* of Kermack & Haldane (1950).

The use of this reduced major axis fulfils the following conditions: (1) it does not postulate that one of the variates is dependent on the other, but is neutral as between them; (2) it is invariant to change of scale, although not to rotation of the axes of measurement; (3) both its slope, and its intercept with the y-axis, can be estimated about as efficiently as the comparable parameters of the regression lines. It has therefore been used in the present work in place of the latter.

In making use of the equation of allometric growth ($y = \beta x^{\alpha}$), the labour of first converting the observations into their logarithms, and then computing the required sums of squares and products, is considerable. If there be a number of variates, with many observations for each, this labour can easily become prohibitive. However, Kermack & Haldane (1950) give methods which enable the work involved to be much reduced. These methods have been employed in this present work.

In the equation of allometry $y = \beta x^{\alpha}$, the growth ratio (α) gives the slope of the straight line fitted to the logarithms of x and y. It has a clear biological meaning; it is the measure of the ratio of the specific growth rates of x and y. It is a pure number without dimensions, and its value may be compared in two different samples by a 't' test, based on the appropriate sampling variance. This will be the sum of the sampling variances of the pair of sample growth ratios.

The biological meaning of the initial growth index (β) is much less clear, as Huxley himself has pointed out. It is numerically equal to the value of y for which $x = 1$, or $\log \beta$ is the value of $\log y$ for which $\log x = 0$. This, incidentally, means that where all the observations are large multiples of the unit of measurement, as is usually the case in practice, it is impossible to estimate β from the data with any accuracy. β has dimensions, and these, as Lumer (1939) pointed out, depend upon the value of α. This follows since both sides of the equation $y = \beta x^{\alpha}$ must clearly have the same dimensions. It is thus difficult to assign a meaning to comparisons of the estimates of β from two samples, unless the value of α is taken as being the same in the two populations from which the samples were drawn. β, however, is a measure of an important property, measuring as it does the *inherent or initial shape* of the organism, irrespective of the changes in actual shape due to allometric growth. Better parameters than the initial growth index can be found, however, for comparing the inherent shape of two samples, when the growth ratios cannot be assumed to have the same value in both the populations from which the samples were drawn.

(*b*) *The comparison of shape in the two samples*

It has already been shown (§ III above) that whereas the comparison of samples of fossil specimens by the use of size parameters is not valid, comparisons based upon differences in shape are unobjectionable. In comparing the shape of two samples, as measured by the variates x and y, it is the usual practice in quantitative palaeontology to compare the values of the ratio y/x in the two cases. In practice, however, the relationship between x and y is almost always allometric, that is $\alpha \neq 1$ in the equation $y = \beta\, x^{\alpha}$. Then $x/y = \beta x^{\alpha - 1}$, which is not a constant but depends on the value of x.

Then there are two possibilities. The first is to make the comparison between what may be called the *average shape* of the two samples, due to all causes. For each sample the best average shape statistic to choose is either the ratio of the geometric means of x and y, or, better still, the logarithm of this ratio. This statistic $(m'_Y - m'_X)$* has a sampling variance such that

$$\text{var. } (m'_Y - m'_X) = \frac{\sigma_Y^2 + \sigma_X^2 - 2\sigma_X\sigma_Y\rho}{n}.$$

The values of $(m'_Y - m'_X)$ for different samples may be then compared by a 't' test.

The other possibility is to compare the inherent shape of the two samples, eliminating as far as possible the changes in actual shape due to allometric growth. Here again there are two alternatives.

It has been shown by Teissier (1936) and by Chevais (1937), amongst others, that β is much more taxonomically sensitive than α. Thus if two samples were from related species, it would be reasonable to assume that the value of α was identical for both populations, supposing that the two sample estimates of it did not differ significantly.

Then, if the value of x at which the comparison is made be the same for both samples, $y_1/x = \beta_1 x^{\alpha-1}$ and $y_2/x = \beta_2 x^{\alpha-1}$. Thus

$$\frac{y_1}{x}\frac{x}{y_2} = \frac{y_1}{y_2} = \frac{\beta_1}{\beta_2}.$$

The ratio y_1/y_2 has the same value, irrespective of the value of x, and this value is always equal to β_1/β_2.

In practice the values of the estimates of α from the two samples are pooled, to give an overall estimate, and this pooled value is used to calculate a value of b for each sample. These two estimates of β have the same dimensions, and may be simply compared.

If a_1 is the estimate of α from the first sample, and a_2 that from the second, then, pooling the information from both samples, the best estimate of α $(\dot{a})$ is

$$\dot{a} = \frac{a_1 \text{ var } a_2 + a_2 \text{ var } a_1}{\text{var } a_1 + \text{var } a_2}.$$

The variance of $\dot{a}$ is

$$\text{var } \dot{a} = \frac{\text{var } a_1 \text{ var } a_2}{\text{var } a_1 + \text{var } a_2}.$$

Then the estimate of log β_1 $(\dot{B}_1)$ for the first sample is

$$\dot{B}_1 = m'_{Y,1} - \dot{a}m'_{X,1}.$$

And for the second the estimate of log β_2 $(\dot{B}_2)$ is

$$\dot{B}_2 = m'_{Y,2} - \dot{a}m'_{X,2}.$$

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* In the following account the population parameters will be denoted by Greek letters; and for their estimates, obtained from the samples, the equivalent Roman letter will be used. Thus σ_x^2 is the variance of x in the population, and s_x^2 is the estimate of this obtained from a sample. The population means are μ'_x, μ'_y, and the sample estimates of them are m'_x, m'_y. The covariance of x and y will be written $\sigma_x\sigma_y\rho$ for the population and $s_x s_y r$ for the sample. Where more than one population or sample is being considered, the parameters, and their estimates, will be distinguished by an additional suffix, e.g. $\sigma_{x,1}^2$ is the variance of x in the first population and $\sigma_{x,2}^2$ that of x in the second. The logarithms of x and y will be written X and Y, and the estimate of log β will be represented as B. The parameters of the logarithmic populations, and their sample estimates, will be denoted by the same symbols as are used for the populations and samples of x and y. They will be distinguished, however, by bearing the suffixes X and Y instead of x and y.

Then

$$\operatorname{var}(\dot{B}_1-\dot{B}_2)=\frac{\sigma^2_{Y,1}+\dot{\alpha}\sigma_{X,1}-2\dot{\alpha}\sigma_{X,1}\sigma_{Y,1}\rho_1}{n_1}+\frac{\sigma_{Y,2}+\dot{\alpha}\sigma_{X,2}-2\dot{\alpha}\sigma_{X,2}\sigma_{Y,2}\rho_2}{n_2}+(\mu'_{X,1}-\mu'_{X,2})\operatorname{var}\dot{a}.$$

$\dot{B}_1-\dot{B}_2$ is simply the distance, measured along the Y-axis, between two parallel straight lines, and the accuracy with which this distance can be estimated is not adversely affected by all the observations being large multiples of the unit of measurement. In this case $\dot{B}_1-\dot{B}_2$ is as efficient a measure of the difference in inherent shape between the two samples as any that can be found.

If the value of α is assumed to be different in the two species, then the difference in shape between the two is not constant for all values of x. This makes it necessary to choose the value of x at which the shapes are to be compared. In this work the value of x chosen is that of the geometric mean of the smaller sample (*Micraster senonensis*). This is equivalent to asking: if *Micraster coranguinum* grew to the same size as *M. senonensis*, would the two species then differ in shape for the character in question? This comparison is not only much more meaningful biologically than the comparison of shape when $x=1$ for both species, but it can be made much more accurately. If, for any value of X, $Y_1=a_1X+B_1$ and $Y_2=a_2X+B_2$, then

$$\operatorname{var}(Y_1-Y_2)=\frac{\sigma^2_{Y,1}}{n_1}(1-\rho_1^2)\frac{(X-m'_{X,1})^2}{\sigma^2_{X,1}}+\frac{\sigma^2_{Y,2}}{n_2}(1-\rho_2^2)\frac{(X-m'_{X,2})^2}{\sigma^2_{X,2}};$$

and this will be very much smaller if $X=m'_{X,1}$ than if $X=0$.

(*c*) *Preliminary discussion of results*

It has already been shown in this paper that the Northfleet sample is divisible into two separate groups on the basis of the area of the sub-anal fasciole. The first of these groups, in which this area exceeds 5 mm², can be equated with *Micraster coranguinum*; and the second, in which this area is less than 5 mm², with *M. senonensis*. In the following account the two species have been treated separately. Dividing up the sample in this way involves the rejection of those specimens in which the area of the fasciole, owing to damage of some sort, could not be measured. Out of a total of 511 specimens 147 have been so rejected. The maximum loss of information so caused has been about 28 %, which is not serious.

Table 11 gives the means, variances and coefficients of variation for the following seven variates: total length (*a*), breadth (*b*), total height (*c*), apical height (*d*), labrum-periproct distance (*e*), sulcus-periproct distance (*g*), and, for *M. coranguinum* only, the square root of the area of the fasciole.* These are defined, and the methods of measurement employed are discussed, in § II*b* above.

From the table it is seen that the means for *senonensis* are all significantly larger than those of the corresponding variates of *coranguinum*, whilst the variances and coefficients of variation for the first species are all smaller than the corresponding values for the second. The differences between the variances are not significant in any case; the differences

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* Throughout, the square root of the area of the fasciole is used instead of the area itself. This was done to give a variate with the dimensions of a length, and so facilitate comparison with the other variates, all of which are of linear dimensions.

between the coefficients of variation are significant, except in the case of variates (*c*) and (*d*) ($P<0{\cdot}01$ for variates (*a*), (*b*) and (*g*), $0{\cdot}05>P>0{\cdot}01$ for variate (*e*)).

The greater values of the means, and the smaller values of both the variances and the coefficients of variation in the sample of *M. senonensis*, is due largely to the absence of small individuals as is shown clearly by figure 10. This absence may well be an example of the effects discussed in § III above; and, in view of the generally unsatisfactory nature of size parameters in fossil populations, it should not be too lightly assumed that the differences between the two species described above as significant will hold for samples from other localities and horizons.

(*d*) *Relative growth rates in the two species*

Table 12 gives the result of fitting the reduced major axis to the logarithmic data by means of the transformations of Kermack & Haldane (1950). This gives estimates of the parameters α and $\log \beta$ of the equation of allometric growth ($y=\beta x^{\alpha}$). In the table, first the total length variate (*a*) has been considered as x and all the other variates in turn as y, and then the total height (*c*) has been considered as x and the apical height (*d*) as y. In each case the number of specimens used, the values of the estimates of α and $\log \beta$, their standard errors, and the estimates of the coefficients of correlation for the logarithmic distributions are given. These coefficients of correlation for the logarithmic populations were estimated directly from the original data by the methods of Kermack & Haldane (1950). As before, both species are treated separately in the table.

Considering first the sample of *Micraster coranguinum*, the values of the estimates of α differ significantly from unity ($P<0{\cdot}001$) in every case except two. These two exceptions are when the labrum-periproct distance (*e*) is considered as y and the total length (*a*) as x, and when the apical height (*d*) is considered as y and the total height (*c*) as x. Except for the two cases mentioned, the biological meaning of these results is that the characters in question would change as the animal increased in size. As an individual of *M. coranguinum* grew in length it became relatively broader and less elevated. At the same time the anterior groove became relatively deeper, and the area of the sub-anal fasciole relatively larger. The degree of projection of the labrum did not change with increase in total length; and the character measured when (*d*) is plotted against (*c*)—called by Rowe 'the posterior rise of the test'—did not do so either.

Turning now to consider the sample of *M. senonensis*, the table shows that none of the estimates of the growth ratios differ significantly in value from unity (P always greater than $0{\cdot}05$). The failure to demonstrate significant allometry here is almost certainly due simply to the very small size of the sample. It does not mean that allometric growth did not occur in *M. senonensis*; it does mean that a larger sample than the present would be required to demonstrate its existence. The differences between the corresponding values of the growth ratios for *coranguinum* and *senonensis* are also not significant (P always greater than $0{\cdot}05$). This again does not necessarily mean that the values are identical in the two species; it only means that they have not been proved different.

The existence of allometric growth in these two species may be checked by fitting the straight line to the original data instead of to the logarithms. If allometric growth be present the value of y/x for the character cannot be a constant but must depend upon the value of x. If this is to be true then the fitted straight line cannot pass through the

TABLE 11. ORIGINAL DATA

	variate ...	length	breadth	total height	apical height	sulcus-rostrum distance	labrum-periproct distance	√area of fasciole
forms with fasciole exceeding 5 mm² in area	number in group ...	328	338	315	321	314	251	346
	mean (mm)	50·27	48·68	32·06	31·41	47·43	42·52	4·499
		±0·51	±0·52	±0·27	±0·27	±0·47	±0·51	±0·051
	variance (mm²)	86·34	89·16	23·36	23·96	70·29	65·71	0·9052
	coefficient of variation (%)	18·48	19·40	15·07	15·58	17·68	19·06	21·15
forms with fasciole less than 5 mm² in area	number in group ...	18	17	12	12	15	12	—
	mean (mm)	58·07	57·13	37·17	36·90	54·22	46·45	—
		±1·60	±1·62	±1·17	±1·18	±1·53	±1·63	—
	variance (mm²)	46·28	44·59	16·43	16·67	34·96	31·75	—
	coefficient of variation (%)	11·71	11·69	10·90	11·06	10·90	12·13	—

TABLE 12. LOGARITHMIC DATA (NATURAL LOGS), $Y = aX + B$

variates ...		length	length	length	length	length	length	total height
	e^X	length	length	length	length	length	length	total height
	e^Y	breadth	total height	apical height	sulcus-rostrum distance	labrum-periproct distance	√area of fasciole	apical height
forms with fasciole exceeding 5 mm² in area	number in group ...	318	301	306	311	247	328	314
	a	1·0464 ± 0·0100	0·8312 ± 0·0219	0·8199 ± 0·0238	0·9624 ± 0·0047	1·0027 ± 0·0112	1·1368 ± 0·0263	0·9904 ± 0·0070
	B	−0·2189 ± 0·0390	+0·2122 ± 0·0857	+0·2365 ± 0·0927	+0·0892 ± 0·0184	−0·1673 ± 0·0435	−2·9547 ± 0·1025	0·0132 ± 0·0242
	r	0·9854	0·8889	0·8619	0·9962	0·9845	0·9083	0·9922
forms with fasciole less than 5 mm² in area	number in group ...	16	11	11	15	12	—	12
	a	1·0940 ± 0·0783	1·3009 ± 0·2710	1·3193 ± 0·2752	0·9666 ± 0·0172	1·0948 ± 0·0812	—	1·0107 ± 0·0139
	B	−0·3776 ± 0·3163	−1·6227 ± 1·0908	−1·7041 ± 1·1080	+0·0829 ± 0·0695	−0·5536 ± 0·1059	—	−0·0463 ± 0·0507
	r	0·9581	0·7230	0·7220	0·9976	0·9664	—	0·9989

TABLE 13. ORIGINAL DATA, $y = ax + b$

variates ...								
	x	length	length	length	length	length	length	total height
	y	breadth	total height	apical height	sulcus-rostrum distance	labrum-periproct distance	√area of fasciole	apical height
forms with fasciole exceeding 5 mm² in area	number in group ...	318	301	306	311	247	328	314
	a	1·0098	0·5279	0·5107	0·9071	0·8574	0·1017	0·09711
		±0·0097	±0·0140	±0·0149	±0·0045	±0·0096	±0·0024	±0·0069
	b	−2·290	+5·470	+5·702	+1·809	−0·1183	−0·6268	+0·3036
		±0·498	±0·717	±0·760	±0·230	±0·4871	±0·0384	±0·2233
	r	0·9851	0·8874	0·8600	0·9962	0·9843	0·9066	0·9921
forms with fasciole less than 5 mm² in area	number in group ...	16	11	11	15	12	—	12
	a	1·0977	0·8652	0·8711	0·9169	0·9217	—	1·0072
		±0·0789	±0·1085	±0·1821	±0·0163	±0·0686	—	±0·01349
	b	−5·404	−11·289	−11·894	+1·823	−4·435	—	−0·5424
		±4·519	±10·184	±10·272	±0·939	±3·813	—	±0·5042
	r	0·9578	0·7219	0·7208	0·9976	0·9662	—	0·9989

origin, since, as $y=ax+b$, $y/x=a+b/x$, which is only independent of the value of x if $b=0$.

Table 13 was obtained by fitting the reduced major axis to the original data, the same pairs of variates being used as in table 12. In every case is given: the number of specimens in the group, the values of a and b and their standard errors, and the value of the coefficient of correlation between x and y. In the sample of *coranguinum* the values of b differ significantly from zero ($P<0{\cdot}001$) in every case except when variate (*e*) is taken as y and variate (*a*) as x, and when variate (*d*) is taken as y and variate (*c*) as x. This confirms the results obtained above by a consideration of the growth ratios, that, except in these two instances, allometric growth is present in every case. In the sample of *senonensis* none of the values of b differ significantly either from zero or from the values obtained from *coranguinum*, and here again, the blame may be placed on the small size of the sample of the former.

(*e*) *The comparison of the shape of characters in the two species*

(1) *The comparison of mean shape*

The mean shape of a character (§V*b* above) is measured as the logarithm of the ratio of the geometric means of the two variates which define it. This mean shape is due to the interaction of a number of different factors: changes in the growth ratio, in the inherent shape as measured by the initial growth index and in the overall size of the species, will all produce changes in its mean shape. Table 14 gives, for both species, the mean shape of the characters defined by the seven pairs of variates considered in the previous section of this paper. In addition, the differences in mean shape between the two species are given for all the characters except the degree of development of the fasciole. By definition, *M. senonensis* lacks, or almost completely lacks, a fasciole. Thus no comparison needs to be made for that character. All estimates are given along their standard errors.

Comparing mean shape for the two species in this way, we see that when variate (*a*) is taken as x and variate (*b*) as y, and when variate (*c*) is taken as x and variate (*d*) as y, the differences between the two species are clearly significant ($P<0{\cdot}002$). None of the differences between the other pairs of variates are significant ($P>0{\cdot}05$).

Putting these results in biological terms we may say that *M. senonensis* differs from *M. coranguinum* in mean shape by being relatively broader and in having a less pronounced 'posterior rise to the test'. The two species do not differ in relative height, depth of the anterior groove or in the degree of development of the labrum (compare figures 12, 14 and 16 with figures 13, 15 and 17, plates 24 to 26).

(2) *The comparison of inherent shape*

As the comparable values of the estimates of α do not differ significantly (§V*d* above), the most obvious way of comparing the inherent shape of the two species is to assume that these values are identical in both. The values of α are estimated by pooling the information obtained from both samples, and the values of the initial growth indices are computed from these estimates. The comparison of inherent shape then consists of assessing the significance of the differences between these growth indices for each character. The methods involved are described in §V*b* above, and the results are given in table 14.

TABLE 14

variates ...	e^X	length	length	length	length	length	length	total height
	e^Y	breadth	total height	apical height	sulcus-rostrum distance	labrum-periproct distance	$\sqrt{\text{area of fasciole}}$	apical height
	number in group ...	318	301	306	311	247	328	314
(1) forms with fasciole exceeding 5 mm² in area (*M. coranguinum*)	$m'_{X,1}$	$3{\cdot}9006 \pm 0{\cdot}0104$	$3{\cdot}9007 \pm 0{\cdot}0104$	$3{\cdot}8967 \pm 0{\cdot}0105$	$3{\cdot}9000 \pm 0{\cdot}0104$	$3{\cdot}8864 \pm 0{\cdot}0121$	$3{\cdot}9007 \pm 0{\cdot}0101$	$3{\cdot}4569 \pm 0{\cdot}0085$
	$m'_{Y,1}$	$3{\cdot}8625 \pm 0{\cdot}0108$	$3{\cdot}4543 \pm 0{\cdot}0087$	$3{\cdot}4315 \pm 0{\cdot}0086$	$3{\cdot}8427 \pm 0{\cdot}0100$	$3{\cdot}7297 \pm 0{\cdot}0121$	$1{\cdot}4798 \pm 0{\cdot}0115$	$3{\cdot}4371 \pm 0{\cdot}0084$
	average shape $m'_{Y,1} - m'_{X,1}$	$-0{\cdot}0380 \pm 0{\cdot}0019$	$-0{\cdot}4464 \pm 0{\cdot}0048$	$-0{\cdot}4651 \pm 0{\cdot}0055$	$-0{\cdot}0057 \pm 0{\cdot}0010$	$-0{\cdot}1567 \pm 0{\cdot}0021$	$-2{\cdot}4209 \pm 0{\cdot}0048$	$-0{\cdot}0198 \pm 0{\cdot}0011$
	number in group ...	16	11	11	15	12	—	12
(2) forms with fasciole less than 5 mm² in area (*M. senonensis*)	$m'_{X,2}$	$4{\cdot}0360 \pm 0{\cdot}0275$	$4{\cdot}0247 \pm 0{\cdot}0261$	$4{\cdot}0247 \pm 0{\cdot}0261$	$4{\cdot}0393 \pm 0{\cdot}0291$	$4{\cdot}0049 \pm 0{\cdot}0319$	—	$3{\cdot}6101 \pm 0{\cdot}0311$
	$m'_{Y,2}$	$4{\cdot}0377 \pm 0{\cdot}0301$	$3{\cdot}6130 \pm 0{\cdot}0340$	$3{\cdot}6055 \pm 0{\cdot}0345$	$3{\cdot}9871 \pm 0{\cdot}0281$	$3{\cdot}8310 \pm 0{\cdot}0345$	—	$3{\cdot}6026 \pm 0{\cdot}0314$
	average shape $m'_{Y,2} - m'_{X,2}$	$+0{\cdot}0016 \pm 0{\cdot}0087$	$-0{\cdot}4118 \pm 0{\cdot}0235$	$-0{\cdot}4192 \pm 0{\cdot}0239$	$-0{\cdot}0052 \pm 0{\cdot}0022$	$-0{\cdot}1739 \pm 0{\cdot}0092$	—	$-0{\cdot}0075 \pm 0{\cdot}0015$
difference of average shape in two species $(m'_{Y,1} - m'_{X,1}) - (m'_{Y,2} - m'_{X,2})$		$-0{\cdot}0397 \pm 0{\cdot}0089$	$-0{\cdot}0346 \pm 0{\cdot}0240$	$-0{\cdot}0459 \pm 0{\cdot}0245$	$-0{\cdot}0005 \pm 0{\cdot}0024$	$+0{\cdot}0172 \pm 0{\cdot}0094$	—	$-0{\cdot}0123 \pm 0{\cdot}0019$
difference of inherent shape in two species	(i) on assumption that values of α are identical in both species $\dot{a}$	$1{\cdot}0471 \pm 0{\cdot}0099$	$0{\cdot}8342 \pm 0{\cdot}0219$	$0{\cdot}8326 \pm 0{\cdot}0237$	$0{\cdot}9627 \pm 0{\cdot}0046$	$1{\cdot}00445 \pm 0{\cdot}0117$	—	$0{\cdot}9945 \pm 0{\cdot}0062$
	$\dot{B}_1 - \dot{B}_2$	$-0{\cdot}0333 \pm 0{\cdot}0089$	$-0{\cdot}0552 \pm 0{\cdot}0243$	$-0{\cdot}0685 \pm 0{\cdot}0247$	$-0{\cdot}0104 \pm 0{\cdot}0022$	$+0{\cdot}0177 \pm 0{\cdot}0095$	—	$-0{\cdot}0131 \pm 0{\cdot}0019$
	(ii) assuming that values of α differ in two species, and making comparison when $x = m'_{X\,2}$	$-0{\cdot}0334 \pm 0{\cdot}0090$	$-0{\cdot}0556 \pm 0{\cdot}0258$	$-0{\cdot}0690 \pm 0{\cdot}0263$	$-0{\cdot}0104 \pm 0{\cdot}0022$	$+0{\cdot}0175 \pm 0{\cdot}0094$	—	$-0{\cdot}0137 \pm 0{\cdot}0021$

The values of the growth indices, as calculated in this way, are seen to be significantly greater for *senonensis* than for *coranguinum* when (*a*) is taken as x and the following as y: (*b*) ($P<0{\cdot}01$), (*c*) ($0{\cdot}05>P>0{\cdot}01$), (*d*) ($0{\cdot}05>P>0{\cdot}01$) and (*g*) ($P<0{\cdot}001$). This is also true when (*c*) is taken as x and (*d*) as y ($P<0{\cdot}001$). The difference between the two species when (*a*) is taken as x and (*e*) as y is not significant ($P>0{\cdot}05$).

Thus, in specimens of the same length, *senonensis* is broader and taller than *coranguinum*; and the former species has a shallower anterior groove and less of a posterior rise to the test than the latter. Finally, there is no difference in the degree of development of the labrum in the two species.

It is instructive to compare these differences in inherent shape with those obtained when comparable values of the growth ratios are assumed to be different in the two species. In this case, the values of α, for the two species, are estimated by their respective sample values. The comparison is best made by assuming the smaller species (*coranguinum*) to grow to the same size as the larger (*senonensis*). This is more sensitive than making the comparison the other way about, as may be seen from the equation for the standard error of $Y_1 - Y_2$, given in §V*b*.

The results are again given in table 14 and show that even were the average size of *Micraster coranguinum* the same as that of *M. senonensis* the two species would still differ in breadth ($P<0{\cdot}0005$), height ($0{\cdot}05>P>0{\cdot}01$), in the depth of the anterior groove ($P<0{\cdot}002$) and in the extent of the posterior rise of the test ($P<0{\cdot}002$). The two species would not differ in the degree of development of the labrum ($P>0{\cdot}05$).

Thus in the present instance the differences between the inherent shape of the two species are found to be the same by both methods. The fact that they differ both in relative height and in the degree of development of the anterior notch would have been obscured if the shape comparisons had been confined to taking means of ratios, as is the usual practice. This is due to the allometric growth of these two characters, along with the difference in size of the two species.

VI. INTERCORRELATIONS IN *MICRASTER CORANGUINUM*

The final analysis carried out on the data was to form all possible intercorrelations between the following seven variates: total length (*a*), breadth (*b*), total height (*c*), total height minus apical height [(*c*) − (*d*)], depth of the anterior groove [obtained by subtracting from the total length of the specimen (*a*) the length to the bottom of the groove (*g*)], the distance from the tip of the labrum to the periproct (*e*), and the square root of the area of the fasciole. For this work it was only possible to use those specimens upon which all the above measurements could be carried out. In addition, owing to the small size of the sample of *Micraster senonensis*, the analysis was confined to the sample of *M. coranguinum*. 220 specimens of the latter species fulfilled the required conditions and were used. After all the total correlation coefficients had been computed, certain partial correlations were formed from them.

The necessarily very laborious work of computation was much reduced by making use of the 'Hollerith' system of machine computation. This method has the further advantage that it avoids the necessity of grouping the data and applying Sheppard's corrections. The effect of grouping is to add, on the average, a term $\frac{1}{12}h^2$ to the estimates of the population variances, h being the grouping interval. But, since the average value of the estimates of the covariances is unaffected by grouping, this will cause the values of the correlation coefficients to be systematically under-estimated. Sheppard's corrections may be applied to correct this bias, but this only improves the values of the estimates *on the average*: in an actual individual case it may make them worse not better. A preliminary run was made on the present data, grouping the latter in the usual way with intervals of about a quarter of a standard deviation. In this case the values of some of the coefficients of partial correlation only differed significantly from zero if Sheppard's corrections were applied. As it is clearly unsatisfactory that the significance of an estimate should depend upon whether these corrections have been applied or not, a much finer grouping was essential. By the use of the Hollerith it was possible to ensure that the grouping interval never exceeded 0·1 mm. This could, at most, have produced an effect in the fourth decimal place of the estimates of ρ, which is perfectly satisfactory. As the effect of the grouping was too small to be of any importance, Sheppard's corrections were not employed in the Hollerith work.

TABLE 15. FORMS IN WHICH THE AREA OF THE FASCIOLE EXCEEDS 5 MM^2.
VARIANCES AND CO-VARIANCES IN MM^2

	length	breadth	total height	total height minus apical height	depth of notch	labrum-periproct distance	$\sqrt{}$area of fasciole
length	85·67	85·87	39·06	2·710	7·919	72·81	7·126
breadth	—	88·55	39·10	2·502	7·761	72·43	7·257
total height	—	—	23·05	0·9611	3·879	33·79	3·311
total height minus apical height	—	—	—	0·3629	0·3327	2·441	0·2286
depth of notch	—	—	—	—	1·2307	7·026	0·6865
labrum-periproct distance	—	—	—	—	—	63·83	6·114
$\sqrt{}$area of fasciole	—	—	—	—	—	—	0·8999

TABLE 16. FORMS IN WHICH THE AREA OF THE FASCIOLE EXCEEDS 5 MM^2.
TOTAL CORRELATIONS

	length	breadth	total height	total height minus apical height	depth of notch	labrum-periproct distance	$\sqrt{}$area of fasciole
length	1·0000	+0·9860	+0·8790	+0·4860	+0·7713	+0·9846	+0·8116
breadth	—	1·0000	+0·8654	+0·4413	+0·7434	+0·9634	+0·8130
total height	—	—	1·0000	+0·3323	+0·7284	+0·8810	+0·7270
total height minus apical height	—	—	—	1·0000	+0·4978	+0·5072	+0·4000
depth of notch	—	—	—	—	1·0000	+0·7928	+0·6523
labrum-periproct distance	—	—	—	—	—	1·0000	+0·8067
$\sqrt{}$area of fasciole	—	—	—	—	—	—	1·0000

The only case where difficulties may arise in the application of normal correlation theory to the data is when one of the two variates is $(c)-(d)$ (total height minus apical height), since here the joint distribution is very skew. The work of E. S. Pearson (1931), however, suggests that even in such a case the theory appropriate to normal correlation may be applied without grave error.

Table 15 gives the matrix of variances and covariances for the seven variates; and table 16 gives all the total correlations between them. From this last table it can be seen that all the correlations are positive and significant, as would be expected.

TABLE 17. FORMS IN WHICH THE AREA OF THE FASCIOLE EXCEEDS 5 MM^2.
PARTIAL CORRELATION INDEPENDENT OF LENGTH

	breadth	total height	total height minus apical height	depth of notch	labrum-periproct distance	$\sqrt{}$area of fasciole
breadth	1·0000	−0·01627	−0·2591	−0·1599	−0·2525	+0·1313
total height	—	1·0000	−0·2277	+0·1661	+0·1857	+0·04869
total height minus apical height	—	—	1·0000	+0·2211	+0·1880	+0·01092
depth of notch	—	—	—	1·0000	+0·3002	+0·07092
labrum-periproct distance	—	—	—	—	1·0000	+0·07448
$\sqrt{}$area of fasciole	—	—	—	—	—	1·0000

Table 17 shows all the partial correlation coefficients, when the effect of the differences in the total length of the specimens has been eliminated. A number of points should be noted from this table: (1) there is no significant correlation between the breadth (*b*) and the height (*c*) of the specimens; (2) a significant negative correlation exists between the breadth and the three variates total height minus apical height ($P<0·01$), depth of groove ($0·05>P>0·01$), and labrum-periproct distance ($P<0·01$); (3) the positive correlation between the breadth and the square root of the area of the fasciole is barely significant ($P\simeq 0·05$); (4) the total height shows a significant negative correlation with the 'posterior rise of the test' (total height minus apical height) ($P<0·01$); (5) the total height is positively correlated both with the depth of the groove ($0·05>P>0·01$), and with the labrum-periproct distance ($P<0·01$); and (6) there is no significant correlation between the height of the animal and the square root of the area of its fasciole.

The biological meaning of these partial correlations is that, *in forms of the same total length*, the following relationships hold: (1) the breadth and the total height of the specimens are independent of each other; (2) the broader forms tend to have a less marked 'posterior rise to the test', a shallower anterior groove and a less pronounced labrum than the narrower ones; (3) the taller forms tend to have a less well-marked 'posterior rise to the test', a deeper groove and a more pronounced labrum than the less tall; (4) the broader forms may have a larger fasciole than the narrower; and (5) there is no relationship between the height of an individual and the degree of development of the sub-anal fasciole.

Table 18 shows the partial correlations when the effects of both total length (*a*) and total height (*c*) are eliminated; and table 19 shows the partial correlations when total height and breadth are both eliminated. Due to the negligible partial correlation between breadth and height, these two tables tell the same story, as far as the relationship of breadth and height to the other variates is concerned, as table 17.

Finally, table 20 shows the partial correlations when the effects of length, breadth and height are all eliminated. Here there are significant positive correlations between the three variates measuring 'the posterior rise of the test', the depth of the anterior groove and the degree of projection of the labrum (P in all cases less than 0·01). Thus, when considering animals of the same overall size, the degree of development of these three characters is associated. A specimen in which one of the three is well developed will tend to have the other two pronounced as well. None of these three variates is significantly correlated with the square root of the area of the fasciole.

Table 18. Forms in which the area of the fasciole exceeds 5 mm^2. Partial correlations independent of length and total height

	breadth	total height minus apical height	depth of notch	labrum-periproct distance	√area of fasciole
breadth	1·0000	−0·2699	−0·1595	−0·2539	+0·1322
total height minus apical height	—	1·0000	+0·2700	+0·2407	+0·02263
depth of notch	—	—	1·0000	+0·2779	+0·06380
labrum-periproct distance	—	—	—	1·0000	+0·06667
√area of fasciole	—	—	—	—	1·0000

Table 19. Forms in which the area of the fasciole exceeds 5 mm^2. Partial correlations independent of length and breadth

	total height	total height minus apical height	depth of notch	labrum-periproct distance	√area of fasciole
total height	1·0000	−0·2402	+0·1657	+0·1877	+0·05128
total height minus apical height	—	1·0000	+0·1884	+0·1311	+0·04692
depth of notch	—	—	+1·0000	+0·2720	+0·09393
labrum-periproct distance	—	—	—	1·0000	+0·1122
√area of fasciole	—	—	—	—	1·0000

Table 20. Forms in which the area of the fasciole exceeds 5 mm^2. Partial correlation independent of length, breadth and total height

	total height minus apical height	depth of notch	labrum-periproct distance	√area of fasciole
total height minus apical height	1·0000	+0·2384	+0·1848	+0·06110
depth of notch	—	1·0000	+0·2487	+0·08674
labrum-periproct distance	—	—	1·0000	+0·1046
√area of fasciole	—	—	—	1·0000

VII. General discussion

(a) *The systematic position of* Micraster senonensis

The nature of the sub-anal fasciole provides the only basis for sorting the individuals of a mixed sample of both *Micraster coranguinum* and *M. senonensis*. The fasciole is well developed in the former species, and absent, or vestigial, in the latter. Most of the other characters in the two species do differ, however; but the range of variation in them overlaps in all cases, so that they cannot be used to classify an individual specimen with certainty. For a metrical character such differences may arise in two ways. The characters may have different relative growth rates in the two species—that is, the values of the growth ratios are not the same in the two cases; or the species may differ in inherent shape for certain characters—using this term in the sense in which it is used in §V.

The work of Teissier (1936) and Chevais (1937) on local races suggests that closely related forms are more likely to differ in inherent shape than in the values of the growth ratios. This appears to hold between different breeds of dogs (Lumer 1940); and the work of Hersh (1934), Robb (1935*a*, 1936) and Reeve & Murray (1942) suggests that this is also true for the differences between related genera and species. Such populations may also differ in relative growth rates, but the differences in inherent shape are usually much more conspicuous.

The same thing is found by comparing the samples of *Micraster coranguinum* and *M. senonensis* from Northfleet. As has already been shown (§ IV*b*), they differ in inherent shape for a number of characters. The former species has a relatively narrower, less elevated test, with a deeper notch, and a more pronounced 'posterior rise' and labrum. However, the samples of the two species do not show any significant differences for any of the estimates of the growth ratios.

After considering the differences in the relative size of the body and large claws in two different races of the American lobster (*Homarus americanus*), Teissier (1936) suggested a mechanism by which such changes in proportion could be brought about. After the male lobster has become sexually mature it continues to grow, but the values of α for the claws undergo a sudden change at the final moult before maturity. This moult occurs in one of the races when the animal has, on the average, reached a larger size than in the other. Hence, although the values of α are the same for mature individuals of both races, the values of β, and so the relative size of the large claws, are different. The work of Chevais (1937) on species of *Corophium* gives similar results.

Something comparable may well have taken place in these echinoids. The different development, however, prevents an exact parallel. The work of Goldschmidt and the other developmental geneticists provides many examples of an alteration in the timing of a process resulting in differences of structure.

Other differences between the two species of echinoid are of a qualitative nature. *Micraster senonensis* has, compared with *Micraster coranguinum*, a rather thinner test, and, almost certainly associated with this, the periplastronal area is but lightly ornamented in the former species. These differences are not, however, clear cut. Some otherwise perfectly typical examples of *M. coranguinum* have a thin test and a relatively unornamented periplastronal area. In addition, there is a tendency for the specimens of *senonensis* to have deeper paired ambulacra. Finally, it seems that, even allowing for its greater size, *M. senonensis* shows a greater degree of packing of the plates of the anterior ambulacrum than does *Micraster coranguinum*.

In explaining these differences it will be assumed that natural selection is responsible for the changes that have taken place in these species; in other words, that the alterations in the *coranguinum-senonensis* complex are all adaptive.

The essential postulate on this hypothesis is that the two forms were occupying slightly different ecological niches. One species, *Micraster coranguinum*, was a burrower like the present-day *Spatangus*; the other, *M. senonensis*, lived on the surface of the sea bed, and burrowed little, if at all. In § IV above, evidence has been brought forward in support of this postulate. In any burrowing spatangoid a sub-anal fasciole is probably a necessity, while in forms which do not burrow the fasciole would have no selective advantage and would tend to disappear. The anterior groove, the labrum and the posterior rise of the test were probably, as Hawkins (1936) suggests, connected with the burrowing and feeding of the animal. The well-marked positive partial correlation between these three characters (table 20) suggests that their functions were interconnected, and hence supports Hawkins' hypothesis. Thus in *coranguinum* selection pressure would be acting on this complex of characters; while in the surface-living *senonensis* this pressure would have been much reduced, so that the whole complex of characters would be more 'old fashioned' in the latter forms than in the contemporaneous *coranguinum*. As has already been suggested above (§ III*c*), a tall conical shape was advantageous to an echinoid living on the bottom of the Chalk Sea, a more flattened shape was more advantageous to a burrowing form. This would explain the differences in inherent shape between the two species in relative height of the test. No explanation can be offered of the differences between the two in the breadth and thickness of the test, or in the ambulacra.

Except the area of the sub-anal fasciole, all the characters in the two species overlap in their ranges of variation. This is explained by assuming that they, like some recent echinoids, interbred to some extent in nature. Certain of the evolutionary implications of this fact will be discussed below.

Isomicraster was established by Lambert in 1901 as a subgenus of *Micraster*. In this description he did not nominate a subgenotype. In 1928 Lambert & Thiéry again define *Isomicraster* as a subgenus of *Micraster* giving *M.* (*Isomicraster*) *stollyei* as the subgenotype. The custom has arisen of referring to members of the subgenus *Isomicraster* as though the latter were the generic name. This custom has nothing whatever to commend it: it simply obscures the close relationship of these forms to the other members of the genus *Micraster*. *M.* (*Isomicraster*) *senonensis* itself was first described by Lambert in 1895 as *M. senonensis*. In 1901 he placed this species in his subgenus *Isomicraster*, the members of which were characterized by having the sub-anal fasciole absent or vestigial. *M.* (*I.*) *senonensis* is clearly so closely related to forms of the main *M. cortestudinarium*–*M. coranguinum* phylum, that it is undesirable to place it in a separate subgenus from them. It is much better to refer to it simply as *M. senonensis*, as has been done in the preceeding sections of this paper.

I have not studied the other members of Lambert's subgenus *Isomicraster* in sufficient detail to be able to say for certain that they too warrant not being placed in a separate subgenus from the typical micrasters, but I strongly suspect this to be the case. The above remarks may also be applied to the subgenus *Gibbaster* Gauthier. The genus *Micraster* is a large one, and could probably be usefully subdivided. Such subdivision should follow natural relationships: to make artificial divisions upon the basis of so variable a character as the sub-anal fasciole, or upon the basis of the general shape of the specimens, increases rather than lessens the confusion.

Mortensen (1950), on the grounds that the species comprising it completely lack fascioles, raises *Isomicraster* to generic rank. He then removes it from the family Micrasteridae and places it in the family Toxasteridae. This he is forced to do by his scheme of classification, since, by his definition, all members of his family Micrasteridae must have a sub-anal fasciole. He considers the absence of the fasciole in the toxasterids to be primitive, and for the members of this family to be among the most primitive spatangoids. In transferring the isomicrasters to the Toxasteridae, Mortensen is faced with the difficulty that Lambert & Thiéry (1924) note the presence of a vestigial sub-anal fasciole in some examples of *Micraster senonensis*. He endeavours to explain away this awkward observation by suggesting that Lambert was mistaken in attributing these specimens to *M. senonensis*. It is very unlikely that so acute an observer as Lambert would have made such a mistake; and, anyhow, perfectly good examples of *M. senonensis* may well have a slight fasciole—for example, specimen E32536.

Lambert (1895), in his original description of the species, comments on the fact that *M. senonensis* may have a rudimentary fasciole, although this appears to have escaped the attention of Mortensen. The fascioles in the Spatangoidea are of great adaptive significance, and, in the evolution of a stock, a sub-anal fasciole may easily disappear under the influence of natural selection. This has happened in the evolution of *M. senonensis*. The presence or absence of a fasciole is therefore a most unsuitable character upon which to build the major subdivisions of the amphisternatous spatangoids.

In the last volume of his *Monograph on the Echinoidea* (1952), Mortensen recants, to some extent. He was informed by Melville (1951) in a letter that a well-preserved specimen of *M.* (*Isomicraster*) *stollyei* showed a sub-anal fasciole. He therefore concludes that there must have been a typical sub-anal fasciole in the young *Isomicraster*. This, I think, is very doubtful—figure 10 in the present paper gives no indication that in *Micraster senonensis* a fasciole was present in the young form and later lost. The occasional presence of a fasciole in *M. stollyei* can be best explained by hybridization.

(*b*) *The evolution of the genus* Micraster *in England*

Micraster first appears in southern England in the zone of *Cyclothyris cuvieri*, where it is exceedingly rare. I have only seen three such specimens, best classed as *Micraster leskei*—two in the collection of Mr C. W. Wright, and one in the Sedgwick Museum at Cambridge. According to Rowe (1899), *Micraster* is only to be found in this zone at Beer, Devon, where all the specimens have the facies of *M. leskei*. In the next higher zone (*Terebratulina lata*), *M. leskei* is still excessively rare, Rowe (1899) reporting but one specimen from the Dover chalk; but another larger *Micraster*, *M. corbovis*, is to be found here in some numbers. In the zone above (*Holaster planus*), are found large numbers of another species, *M. cortestudinarium*, along with smaller numbers of *M. leskei* and *M. corbovis*. At this level *M. leskei* is more numerous than *M. corbovis*, and neither of these two species rises above the top of this zone. *M. cortestudinarium* is abundant in the next zone, of which it is the name fossil; and here too are to be found the first representatives of *M. senonensis*. In the next zone *M. cortestudinarium* passes into *M. coranguinum*, the name fossil of this zone; while *M. senonensis* passes on up through this zone, evolving parallel to the *cortestudinarium–coranguinum* phylum. In the succeeding zone (*Marsupites*) the two lines become rarer. In the two following zones (*Offaster pilula* and *Actinocamax quadratus*) *M. senonensis* is absent and *M. coranguinum* very rare (see figure 1). Then, in the succeeding zone of *Belemnitella mucronata*, two new species (*M. glyphus*, using this name in the broadest sense, and *M.* (*Isomicraster*) *stollyei*) are to be found in comparative abundance in Norfolk. Along with them go a few very aberrant examples of *M. coranguinum*. Elsewhere in southern England, *Micraster* is very rare in this zone, the only example which I have examined personally being a very large *glyphus* collected by Professor H. L. Hawkins from the Isle of Wight.

In the north of England *Micraster* is much less common than in the south. The stock appears to follow in the north a similar, although by no means identical, course of evolution to that followed in the south. I have not seen an example of *M. senonensis* from the north, but in view of the small number of specimens available that is not surprising—*M. senonensis* is a rare species in any event. The present paper deals mainly with the southern Micrasters, and the northern forms will only be discussed in as far as they throw light on the evolution of the southern forms.

The forms to which the name *M. leskei* is applied appear to be simply small examples of *M. cortestudinarium*. I have examined some two hundred specimens of *Micraster* from the zone of *Holaster planus* at Dover, and I was quite unable to divide these between the two species in any way except on size, which is not particularly satisfactory. In the south of England the main line of evolution of the genus *Micraster* is the phylum *leskei–cortestudinarium–coranguinum*, which passes up from the zone of *Cyclothyris cuvieri* to that of *Marsupites*. Coming off from this main stock are two branch phyla. One appears in the zone of *Terebratulina lata* and passes up into the succeeding zone of *Holaster planus*. At the top of this last zone it becomes extinct. This branch comprises the forms which are placed in the species *Micraster corbovis*. The typical members of this species are clearly distinct from the typical examples of *M. leskei* and *M. cortestudinarium*. Transitional forms exist, however, between the forms typical of the main and branch phyla, and these intermediates are more numerous than the typical *M. corbovis*. They may have been produced by hybridization. *M. corbovis* probably occupied a slightly different ecological niche from the species comprising the main phylum, although what this niche was remains a mystery. Like *M. senonensis*, *M. corbovis* had a thinner test than the contemporary forms of the main phylum; and, again like *M. senonensis*, it tended to lag behind the 'main-line' forms in the evolution of such details as the ambulacra, the labrum, the anterior groove, etc. *M. corbovis* differs from *M. leskei* and from *M. cortestudinarium* in shape, and, like *M. senonensis*, it is a rather large form.

At the end of the zone of *Holaster planus* there seems to have been a fairly sudden change in the conditions of life. The ecological niche occupied by *Micraster corbovis* vanished, and one opened suitable for the members of the other branch phylum. This phylum, which comes off from the main stock at the bottom of the zone of *M. cortestudinarium*, comprises the forms which are placed in the species *M. senonensis*. It goes on, evolving parallel to the main stock, until it disappears in the zone of *Marsupites*. If *Micraster senonensis* were more common, the fact that it is not found below the base of the zone of *M. cortestudinarium*, i.e. it is confined to the Senonian, might be of practical use to the field geologist.

As both *M. corbovis* and *M. senonensis* intergrade with their contemporaries of the main phylum, it is almost certain that interbreeding took place between the main and the branch phyla. This would be disadvantageous to both the stocks in which it took place by hindering them from becoming fully adapted to their environments. In addition, poorly adapted transitional forms would be produced. If a barrier arose to prevent this interbreeding, it would be advantageous to both stocks, since it would enable them to become more perfectly adapted. In this case a period of rapid evolution would take place; and the parent stocks, connected by transitional forms, would be replaced by two species which were completely separate from one another. The setting up of such a barrier, outside the English area, may have been the cause of the replacement, in the

Northern Province, of *M. coranguinum* and *M. senonensis*, which have transitional forms, by *M. glyphus* and *M. stollyei*, which have not.

According to Wright (1952), the Chalk Sea was divided into two faunal provinces by a barrier passing from east to west across the middle of England. The exact position of this barrier varied from time to time; and, during *mucronata* times, it had moved so far south as to include the area which is now Norfolk within the Northern Province. The barrier does not seem to have been of an absolute nature, and individuals could sometimes pass from one province to the other, despite its presence.* The Micrasters of the Northern Province are rather rare. Mr C. W. Wright has shown me the following specimens from his collection: some aberrant *M. corbovis*, with a peculiar pointed labrum, from the northern equivalent of the zone of *Holaster planus*; some forms of the age of the zone of *M. cortestudinarium*—these specimens having thicker and more elevated tests, with a more posterior apical system and shallower petals, than the southern, true, *M. cortestudinarium*; and a single specimen from the northern equivalent of the zone of *M. coranguinum*. These specimens appear to form an evolutionary series, and they are almost certainly specifically distinct from the forms of the same age in the Southern Province.

In the *mucronata* chalk of Norfolk, the northern forms become reasonably abundant. Here are to be found *Micraster glyphus*, *M.* (*Isomicraster*) *stollyei* and some aberrant forms, resembling in some ways *M. coranguinum*. The first two species are identical with those of the Hanover chalk described by Schlüter (1869). These three species may be taken as the end-products of the evolution of the northern stock. Up to, and including, the forms of the age of *M. coranguinum*, the northern forms follow a similar, although not identical, series of evolutionary trends to those described for the southern forms by Rowe (1899). These northern forms, however, seem to be more advanced than the forms of the Southern Province of the same age, among other respects in having rather thicker tests and shallower paired ambulacra. The *mucronata* forms, however, tend on the whole to have rather thin tests and deep open paired ambulacra. In addition, associated with the thin test, these forms tend to have a but lightly ornamented periplastronal area. For these two species, with their thin tests and open deep petals, to have evolved from their predecessors in the Northern Province would involve a complete reversal of the lower zonal evolutionary trends in these characters. There seems to be, however, no serious objection to such a reversal having taken place. For example, *Micraster senonensis* evolved from *M. cortestudinarium* at the top of the zone of *Holaster planus*. The parent stock shows a trend of progressive increase in the thickness of the test and increase in the area of the sub-anal fasciole during the whole period of its existence, from the zone of *Cyclothyris cuvieri* to the zone of *Marsupites*. The *senonensis* branch phylum, whose ancestors possessed these trends in the zone of *Holaster planus* and the lower zones, does not itself show them. The concept of undeviating evolutionary trends, such as is summed up in the term 'orthogenesis', finds no support from the study of these echinoderms, despite the opinion of Hawkins (1936).

The growth ratios, which have been determined for *Micraster coranguinum* may be assumed to apply, more or less, to the whole *Micraster* stock. On this assumption a number of anomalies are removed. In the first place it becomes clear that Rowe's 'species'

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* The solitary *Micraster glyphus* found by Hawkins in the Isle of Wight may perhaps best be accounted for by migration across the barrier from the Northern Province.

M. praecursor, and his variety, *M. coranguinum* var. *latior*, do not represent useful concepts. Any *M. praecursor* which grew to a large enough size would have turned into what Rowe would have regarded as a typical example of *M. cortestudinarium*; just as any specimen of Rowe's *M. coranguinum* would, given a life long and successful enough, have become a typical example of his *M. coranguinum* var. *latior*. Similarly, upon a consideration of the growth ratios, we can see why 'All broad forms, whether they be high-zonal or low-zonal, have a tendency to assume a large size' (Rowe 1899). Particularly striking examples of this are to be found in the zone of *M. cortestudinarium* at Dover, where very large, broad and flat Micrasters frequently are to be found.

The changes in the shape of the individual during growth bear little, if any, relationship to the changes in the shape of the species during evolution.

During growth an individual of *M. coranguinum* became relatively broader and flatter, with a deeper anterior notch and a more marked fasciole. There seems to have been little change in either the extent of the posterior rise of the test, or in the degree of projection of the labrum. During evolution, however, the animals became relatively broader and taller, with a deeper notch and a more pronounced labrum and posterior rise to the test. In addition, the sub-anal fasciole became larger in area. Kongiel (1949) noticed that in species of *Echinocorys* there was similarly no particular relationship between the relative growth rates in the individual and the evolutionary trends in the species. These echinoids, in fact, do not show recapitulation. Even attempts to explain evolutionary processes in terms of the speeding up or the slowing down of the process of allometric growth in the post-larval state are not supported by a study of *Micraster*.

(*c*) *The relationships between the characters in* Micraster coranguinum

We have already seen (§ VI above) that it is possible to discount the effect of the overall size of the animal in considering the interrelationships of certain of the characters. For example, there are significant positive correlations between the three characters 'depth of anterior groove', 'degree of development of the labrum' and 'extent of the posterior rise of the test', even in specimens of the same length, breadth and height. In this case the area of the sub-anal fasciole is uncorrelated with any of the above three variates.

We must now consider the correlations of height and breadth with the other variates, in forms of the same length. As Rowe (1899) has shown, during evolution the *leskei–cortestudinarium–coranguinum* phylum became relatively taller and broader; the depth of the anterior groove, the degree of projection of the labrum, and the 'extent of the posterior rise of the test' all increased, while the sub-anal fasciole became more prominent. Tables 17 and 19 show that the relatively taller forms are 'ultramodern' in the depth of the anterior groove and in the degree of development of the labrum, and 'old fashioned' in the 'extent of the posterior rise of the test'. In the degree of development of the fasciole they seem to be about the average for their time. The relatively broader forms, on the other hand (tables 17 and 18), seem to lag behind their relatively narrower contemporaries in all characters except height and the area of the fasciole. Rowe (1899) had noted this tendency of the broad forms to be 'old fashioned'; and, in addition to the characters considered here, he observed that they tended to lag behind their time in the state of evolution of the paired ambulacra.

Matthew (1926), discussing the evolution of the Equidae, pointed out that although in groups of contemporaneous species, e.g. of *Hipparion*, some will be found to be more specialized in some characters, and some in others, yet still the general level of evolution reached by each species is about the same. Much the same sort of thing is to be seen in *Micraster coranguinum*, although here we are considering individuals within a single species. Hawkins (1936) noted that in *Micraster* the sum total of the characters in an individual specimen added up, more or less, to the average level of evolution for its time, although specimens tended to be in advance of their time in some characters and to lag behind it in others. He did not observe, however, the systematic nature of the effect, in that given combinations of characters were always associated in the same way. For example, if an individual be broad, and so in advance of its time for this character, it characteristically lags behind in all the others except total height and area of fasciole; while forms which are advanced by having a well-marked 'posterior rise to the test' tend to be backward by being flatter and less broad than the average of their contemporaries, and so on.

In a population in approximate equilibrium under the action of natural selection genotypes of low fitness may be kept in being by mutation, but such mutants would rarely be found in a sample of a few hundred specimens. Apart from this, genetically determined variance may be due to genes which are almost neutral from the point of view of natural selection. Such genes, if they exist at all, must be very rare. There is a considerable body of evidence that extreme variants are, in most cases, less fit than more average ones. This suggests that genetic differences are usually kept in being because heterozygotes are more fit than homozygotes. If relatively broad forms of *M. coranguinum* were fitter than narrow, then, other things being equal, a gene reducing broadness could only have been kept in being if it had some other effect which increased fitness; and if these effects were so balanced that the heterozygote was fitter than either homozygote. For this to be possible, a gene which, in any individual, produces a positive selective advantage in one set of characters must, at the same time, produce a negative selective advantage in another set. Thus the gene differences which survive in a random mating population will tend to affect characters of selective value in opposite senses, so that characters which make for fitness will be negatively correlated at any given time. However, considered from the point of view of evolution, and therefore, necessarily, over a long period of time, selection pressure would be seen to be forcing an all-round adaptive 'improvement' in the stock. Thus, in an evolutionary series, such as the *Micraster* genus from the zone of *Cyclothyris cuvieri* to that of *Marsupites*, characters which convey a selective advantage would all appear to be positively correlated.

While any gene pair can give two characters a sizeable negative correlation, a considerable number of such characters cannot all show large negative correlations with each other. The general effect would probably be similar to that obtaining in the *Micraster* population, where some, but not all, of the characters which are positively correlated in evolution are negatively correlated at any one time.

Interpretation is more complicated if two species live in different habitats, in which selective influences differ, and interbreed to a limited extent. This was almost certainly true of *M. coranguinum* and *senonensis*. If, of two allelomorphs (*X* and *Y*), *X* makes for increased fitness in one habitat and Y for increased fitness in another, selection pressure will cause X to increase in number in the species inhabiting the first, and Y to increase in number in the species inhabiting the second. If, however, the two species hybridize in nature, there will be a leakage of genes between them. If this leakage be too large compared with the selective intensities, either X or Y will disappear in both species. Thus, under these conditions, genes making for increased fitness in one habitat or the other will be lost. On the other hand some genes may have such selective effects in relation to the migration frequencies that both allelomorphs will survive, in different ratios in the two species. In this case one species may be more advanced than the other in one respect, less so in another, just as we find in *M. coranguinum* and *M. senonensis*. But unless evolution is in the same direction in both habitats, this is not necessarily true.

In conclusion, I wish to thank all those who have assisted me in this work, and the following in particular: Professor D. M. S. Watson, F.R.S., who suggested this problem; the Trustees and Staff of the British Museum for allowing me to keep material on extended loans, and for much incidental assistance; Professor J. B. S. Haldane, F.R.S., for continued advice and encouragement; Professor P. B. Medawar, F.R.S. for reading through the manuscripts and giving me valuable criticism and advice; Dr K. A. Joysey for many useful discussions; Mr C. W. Wright for making available to me his superb personal collections and enlightening me on the palaeogeography of the Chalk Sea; and Dr H. O. Hartley for introducing me to the 'Hollerith' method of computation. The graphs and text-figures are due to my wife.

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EXPLANATION OF PLATES

PLATE 24

FIGURE 12. Dorsal view of a specimen of *Micraster coranguinum* (E 32980). Notice, that while the anterior ambulacrum is showing petaloid modifications, these have not become very marked.

FIGURE 13. Dorsal view of a specimen of *Micraster* (*Isomicraster*) *senonensis* (E 32533). Note that the test is relatively broader than that of the specimen shown in figure 10. Observe also that the modification to the anterior ambulacrum has here produced a definite petal.

PLATE 25

FIGURE 14. Lateral view of specimen E 32980. Note that the highest point of the test is not at the apical system, but lies a little behind it. In some specimens of *M. coranguinum* 'the posterior rise to the test' is much more accentuated than it is here.

FIGURE 15. Lateral view of specimen E 32533. Note that here the highest point of the test occurs at the apical system. Observe in addition the steep fall of the test from the apex to the periproct.

PLATE 26

FIGURE 16. Ventral view of specimen E 32980. Note: the prominent labrum, covering the mouth; the long plastron; the dense mammillated ornament of the periplastronal areas; and the ring of the sub-anal fasciole, with inside it the enlarged pore-pairs of ambulacra I and V.

FIGURE 17. Ventral view of specimen E 32533. Note: and compare with specimen E 32980—the rather shorter labrum and plastron; the lightly ornamented periplastronal areas; and the absence of the sub-anal fasciole, although the enlarged pore-pairs of ambulacra I and V remain.

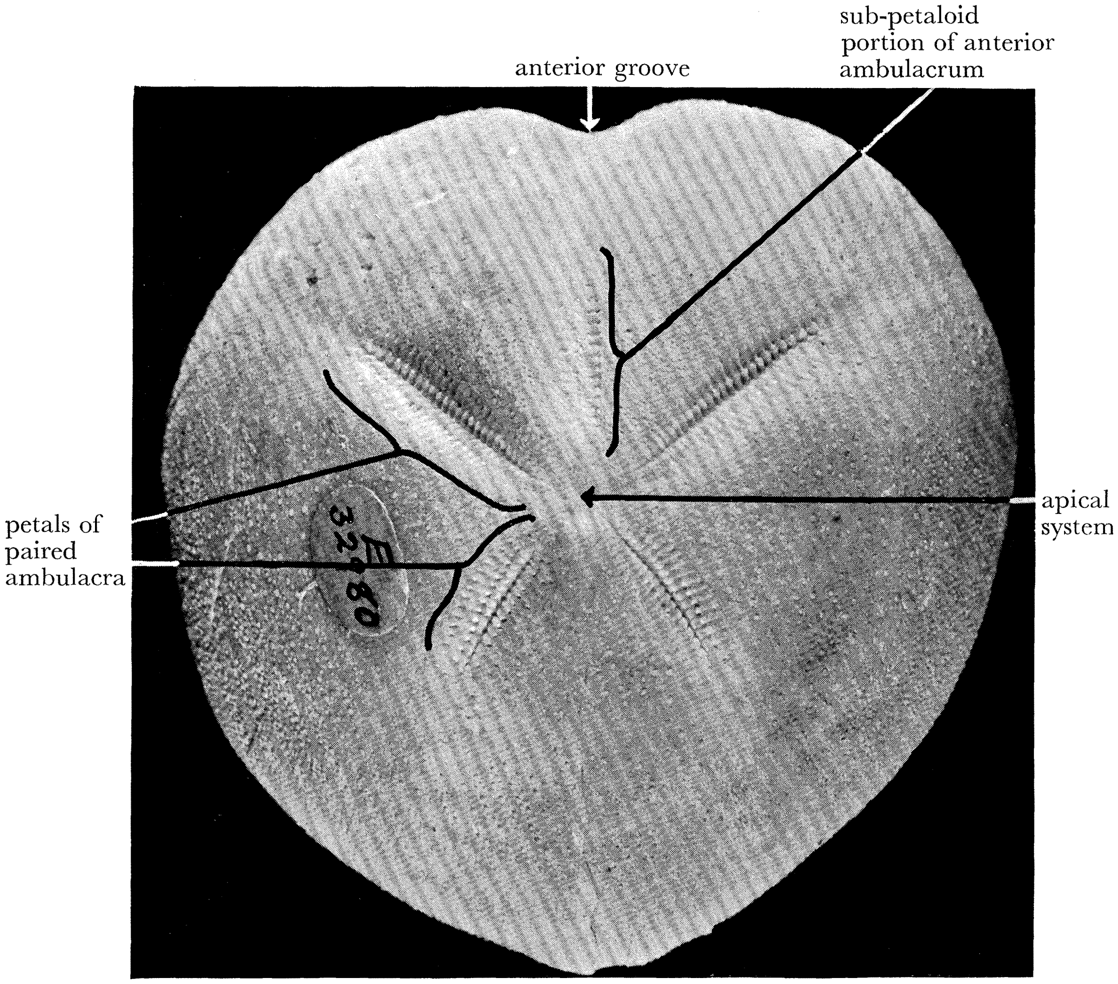

FIGURE 12

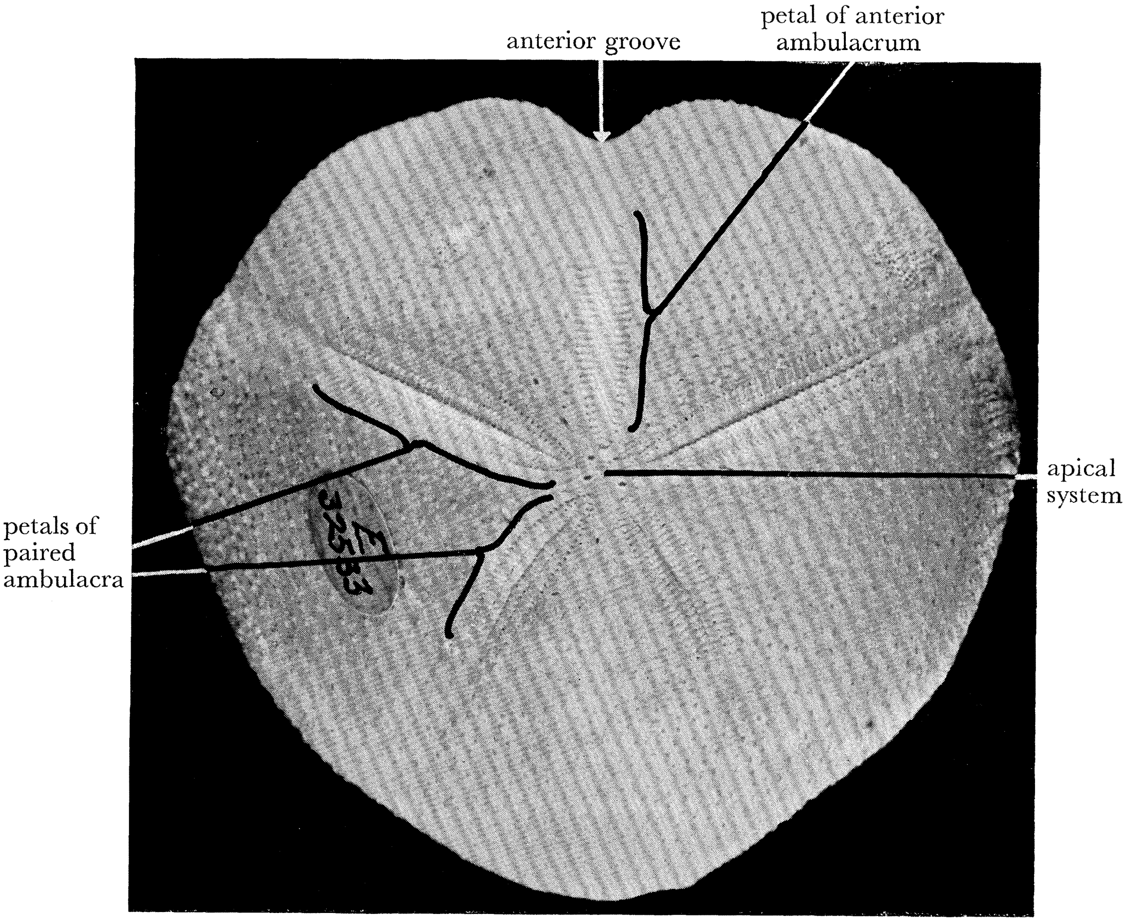

FIGURE 13

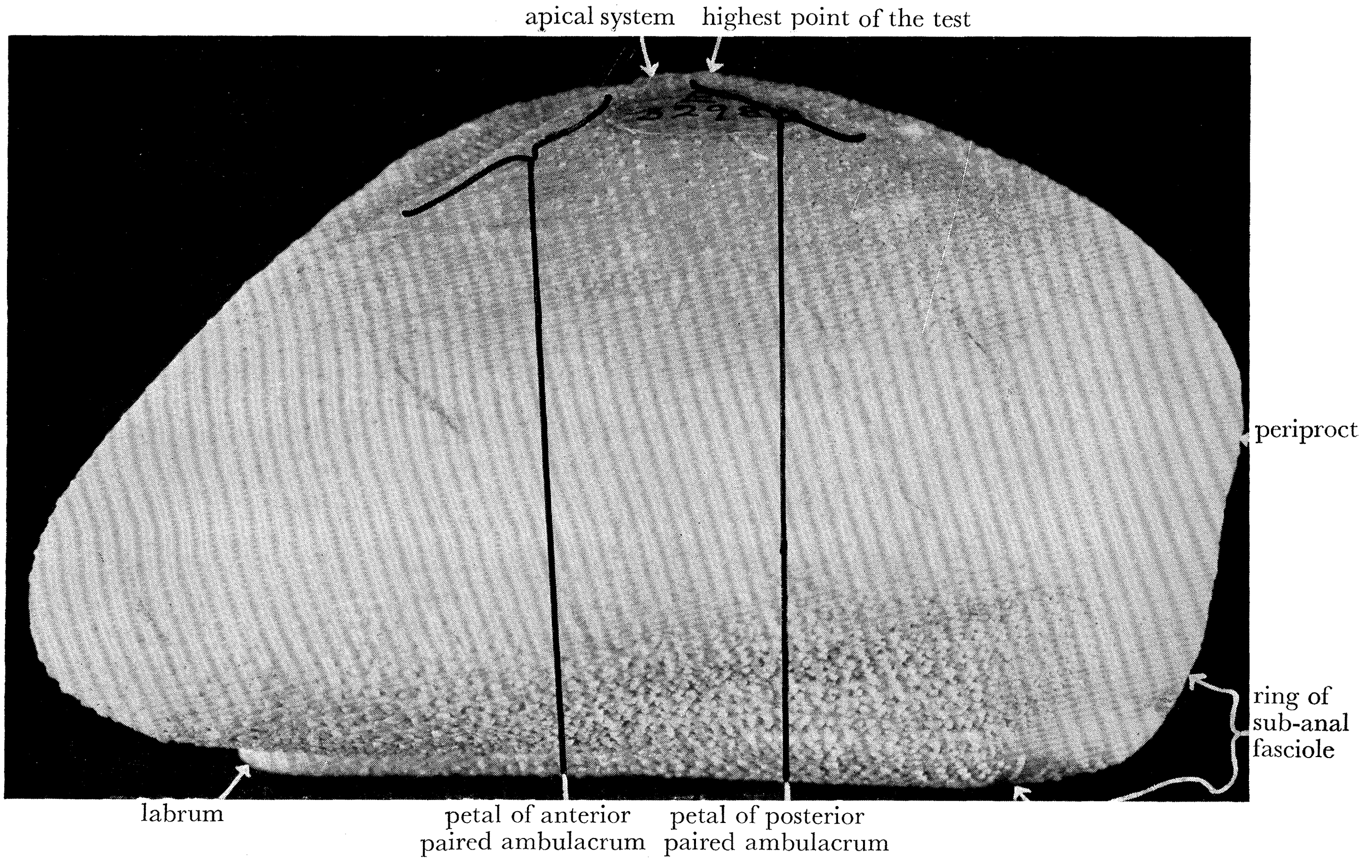

FIGURE 14

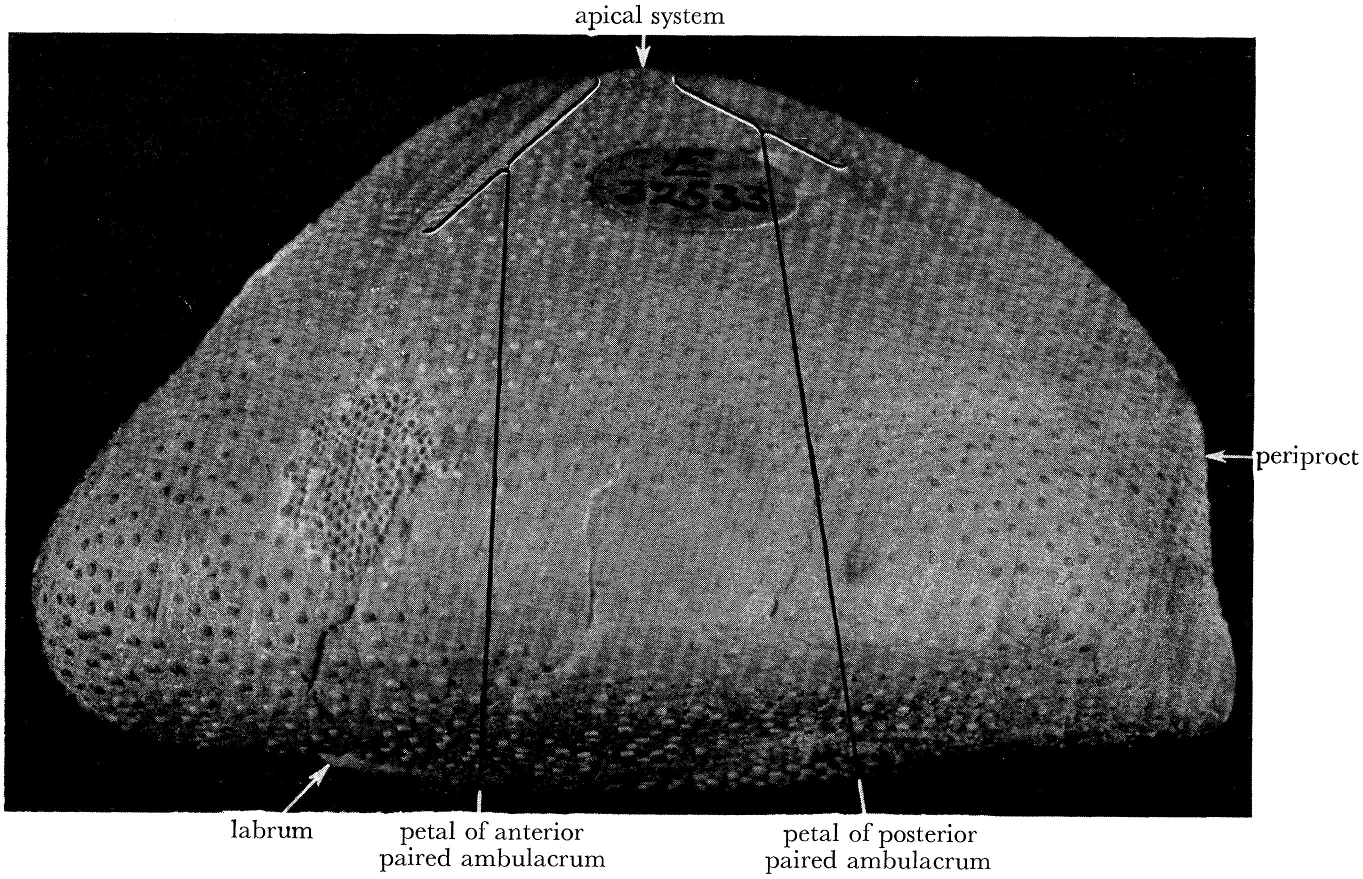

FIGURE 15

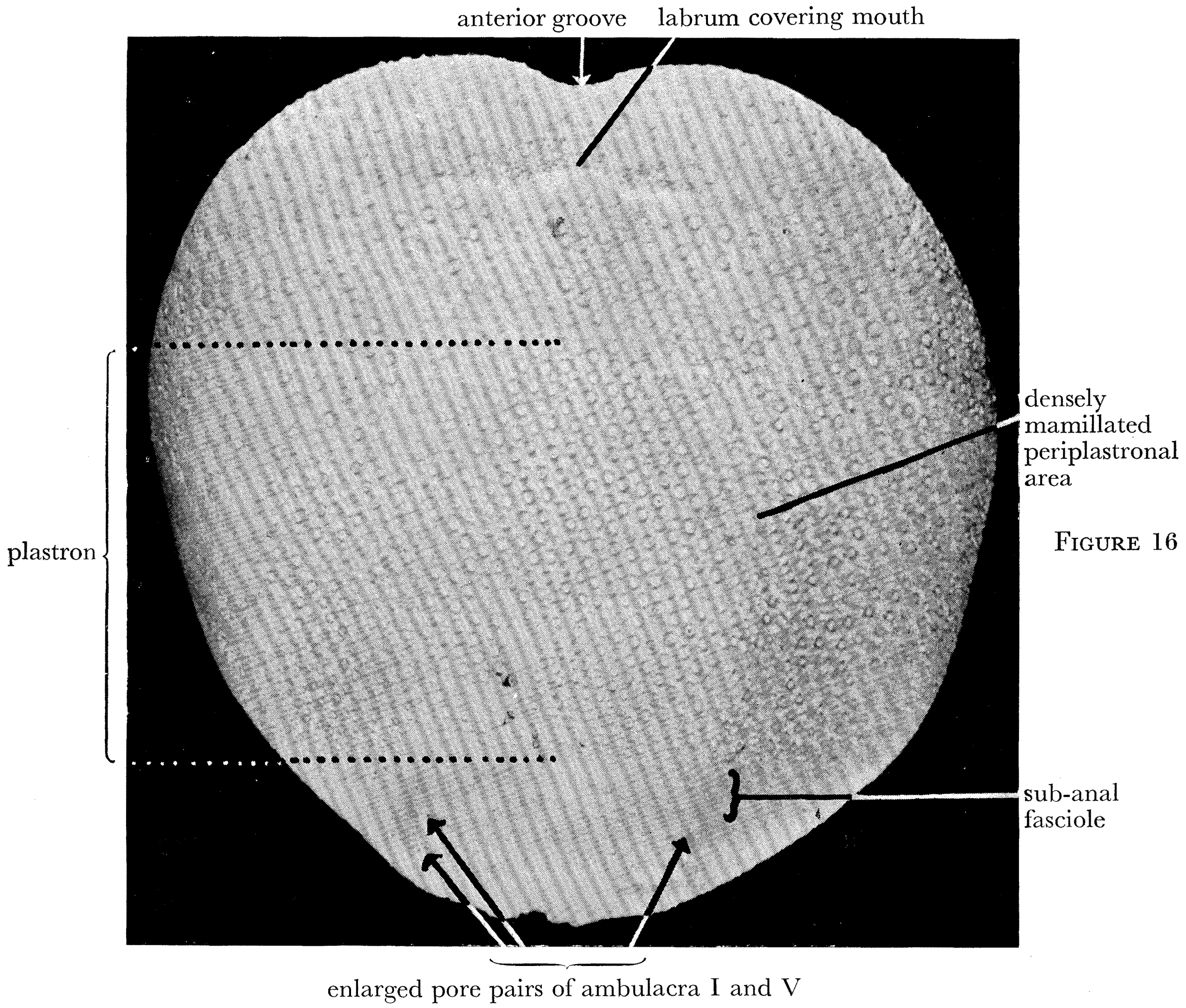

FIGURE 16

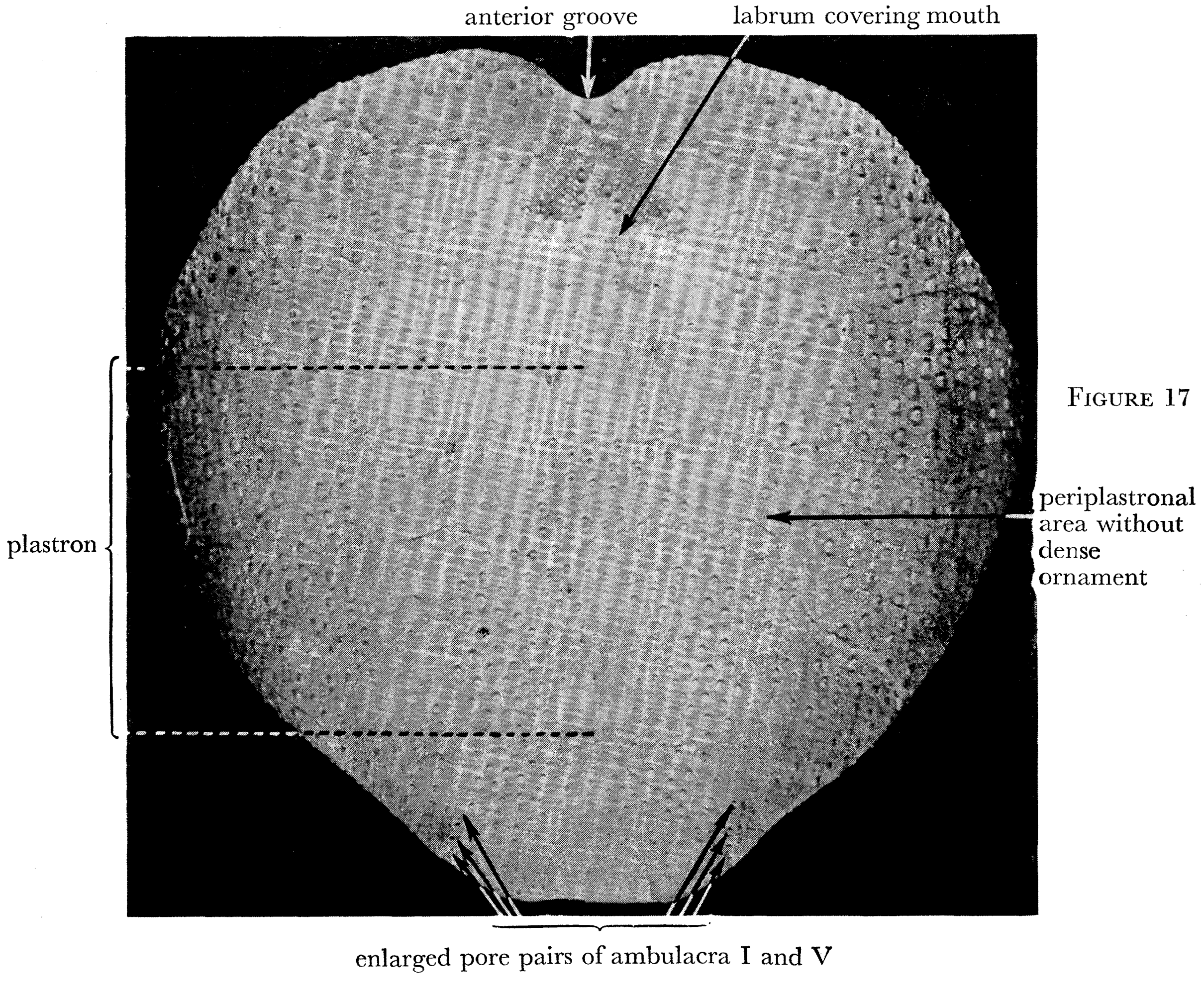

FIGURE 17

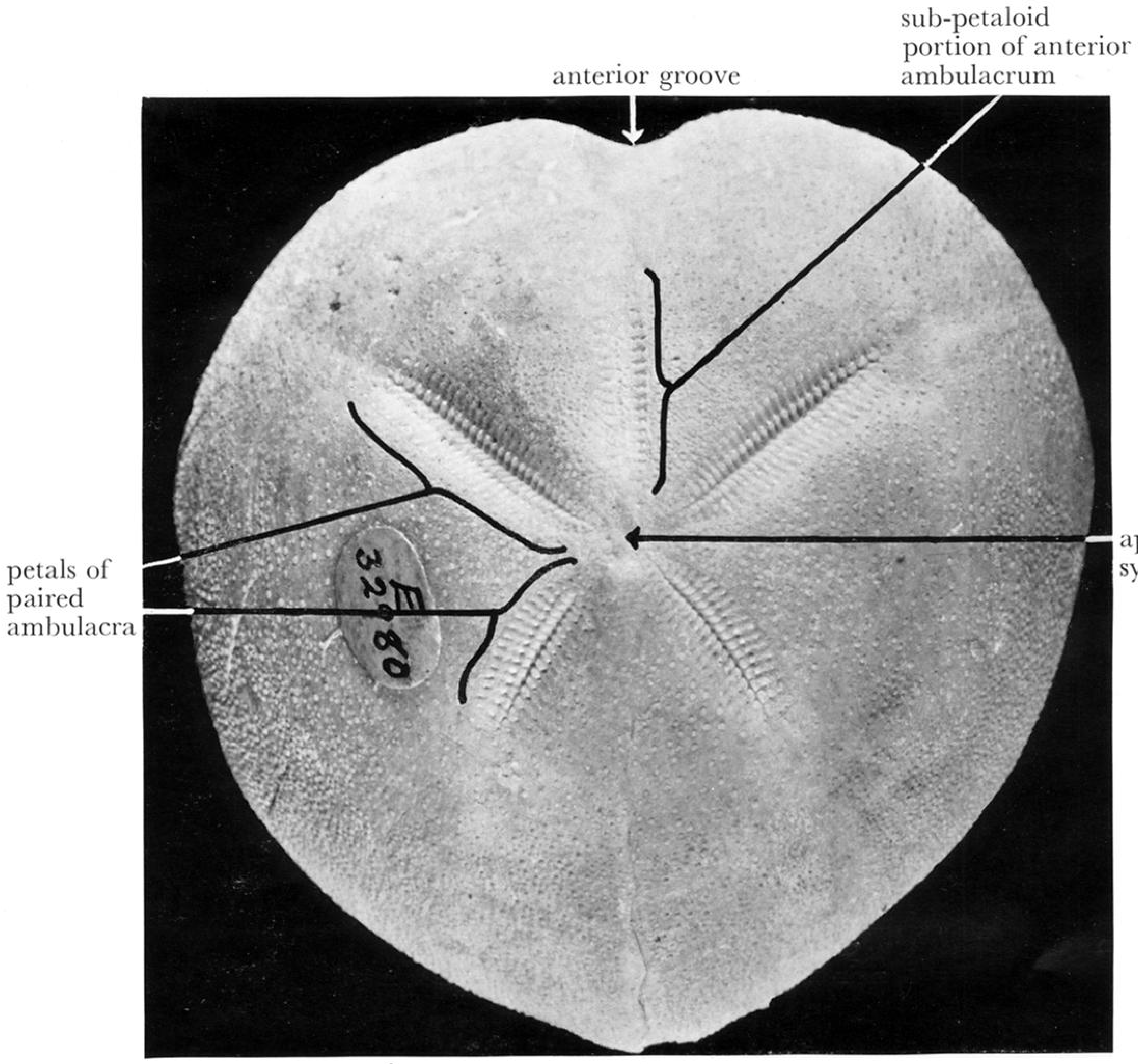

FIGURE 12

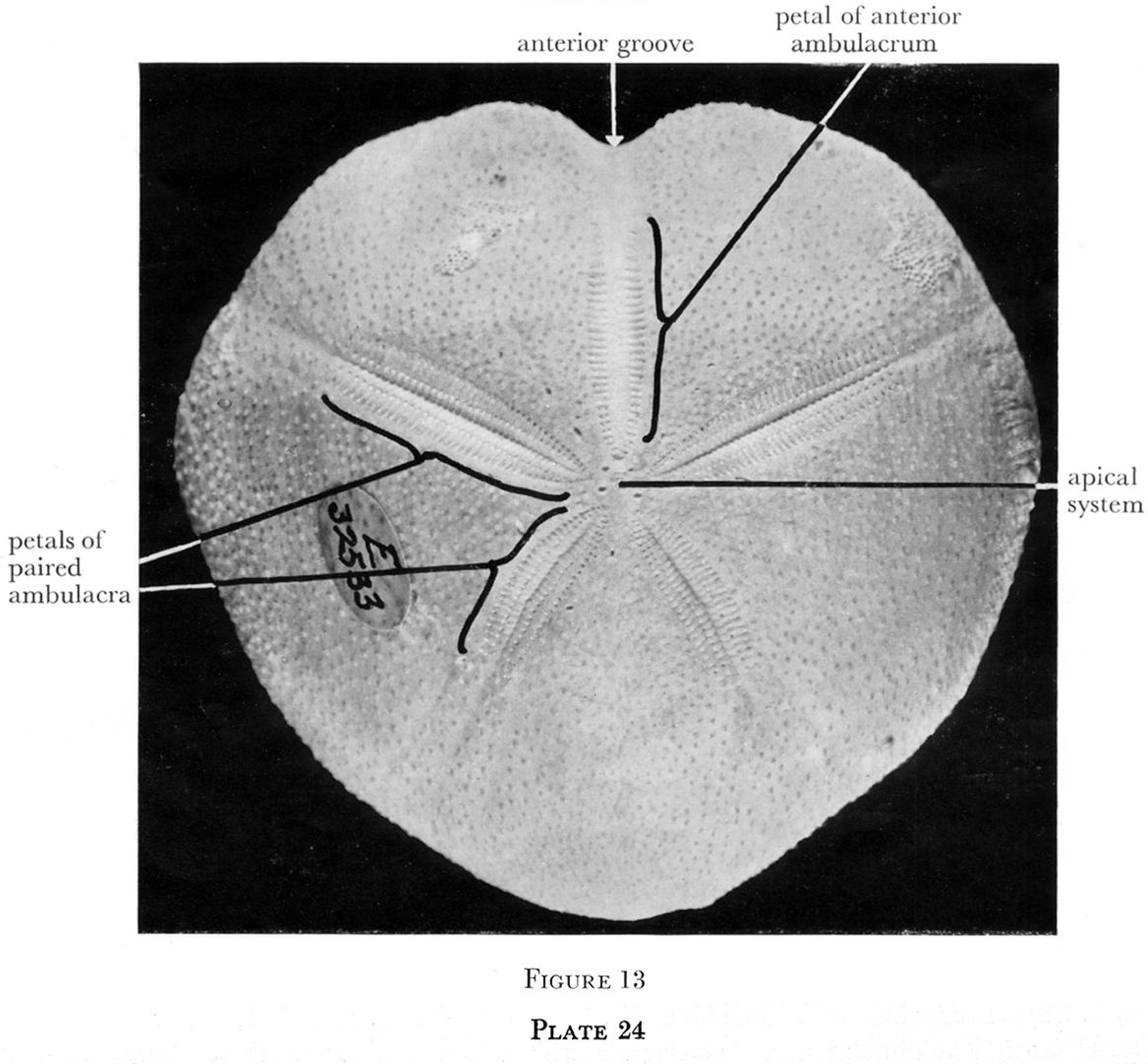

FIGURE 13

PLATE 24

FIGURE 12. Dorsal view of a specimen of *Micraster coranguinum* (E 32980). Notice, that while the anterior ambulacrum is showing petaloid modifications, these have not become very marked.

FIGURE 13. Dorsal view of a specimen of *Micraster* (*Isomicraster*) *senonensis* (E 32533). Note that the test is relatively broader than that of the specimen shown in figure 10. Observe also that the modification to the anterior ambulacrum has here produced a definite petal.

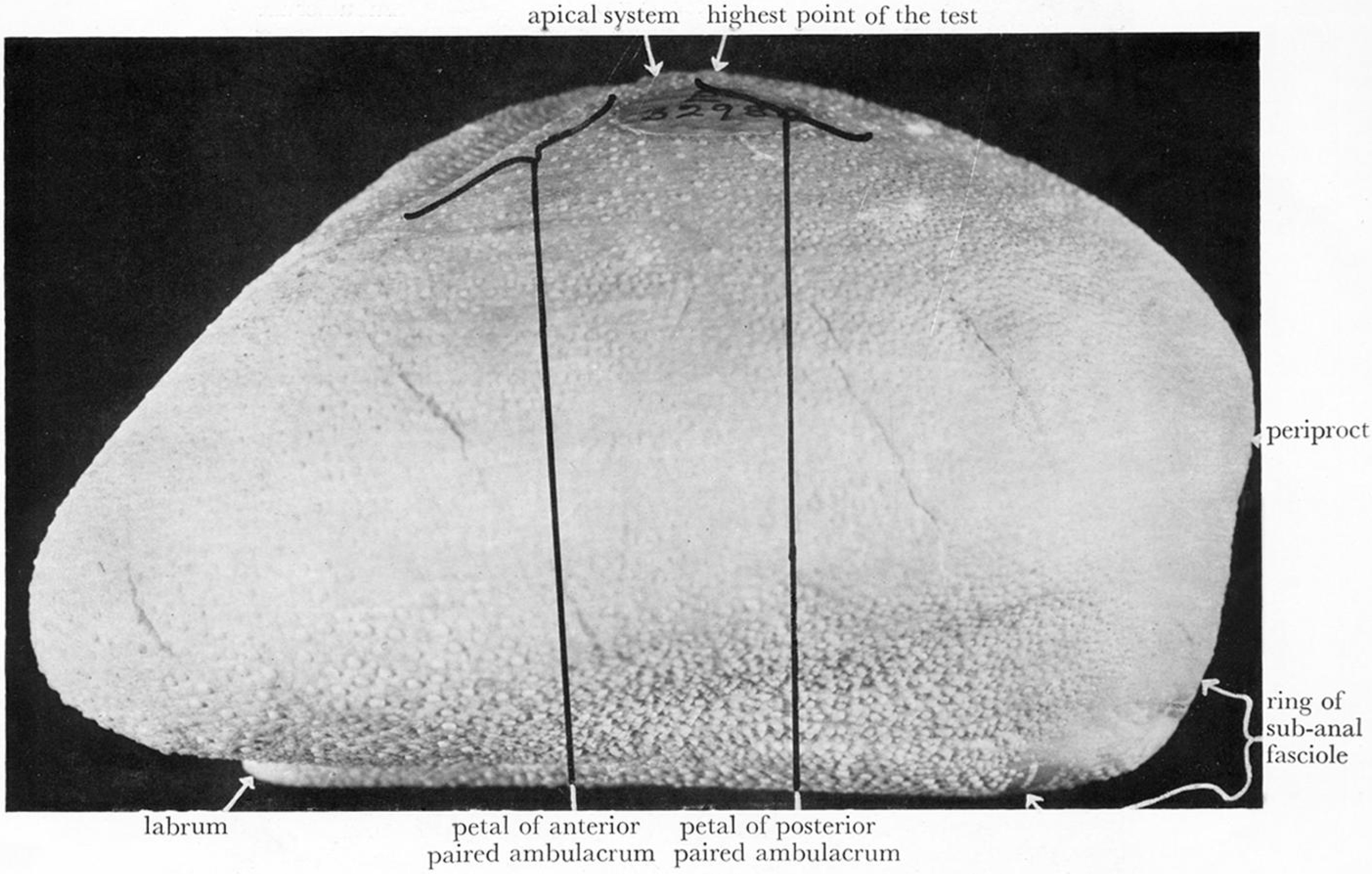

FIGURE 14

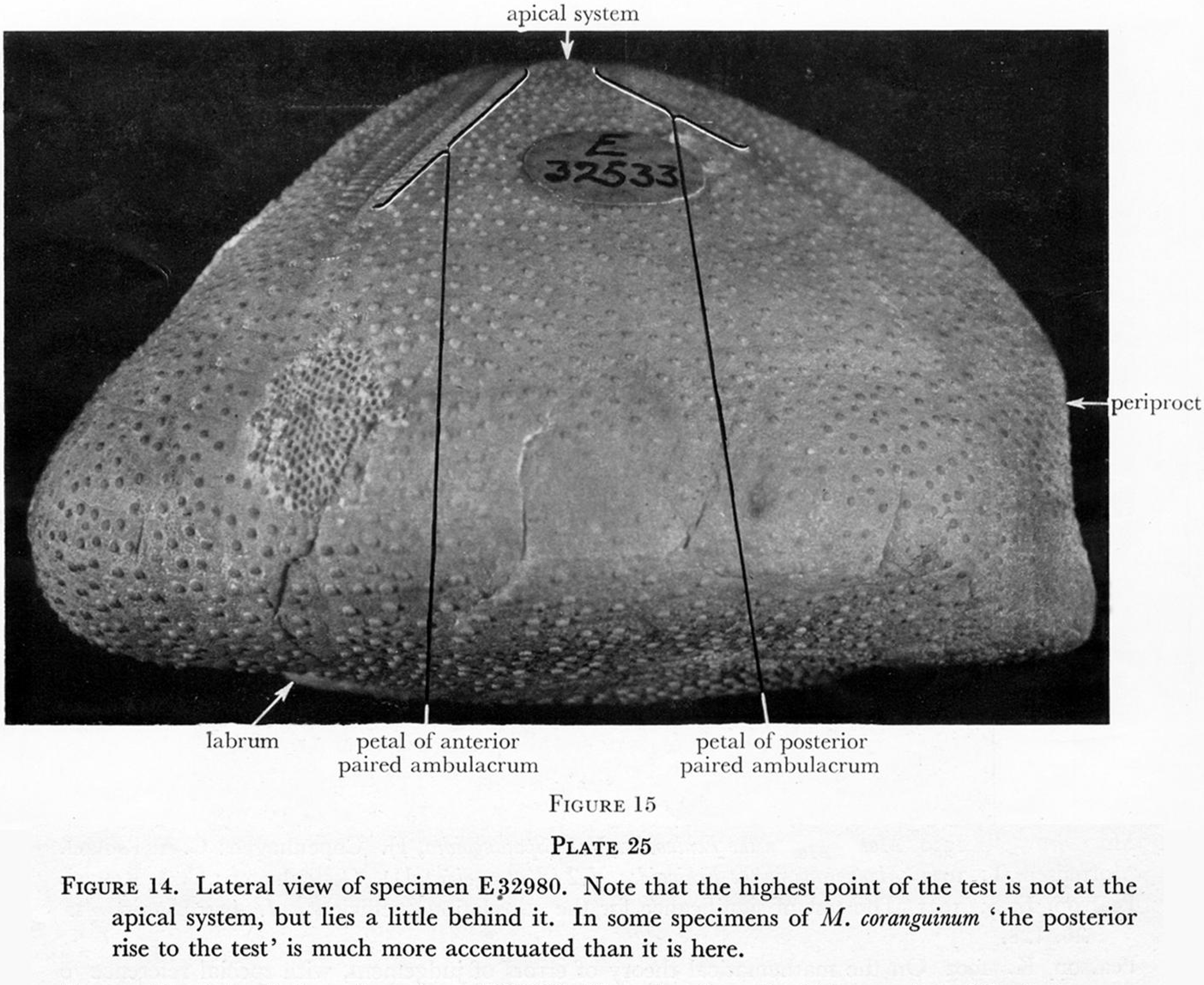

FIGURE 15

PLATE 25

FIGURE 14. Lateral view of specimen E 32980. Note that the highest point of the test is not at the apical system, but lies a little behind it. In some specimens of *M. coranguinum* 'the posterior rise to the test' is much more accentuated than it is here.

FIGURE 15. Lateral view of specimen E 32533. Note that here the highest point of the test occurs at the apical system. Observe in addition the steep fall of the test from the apex to the periproct.

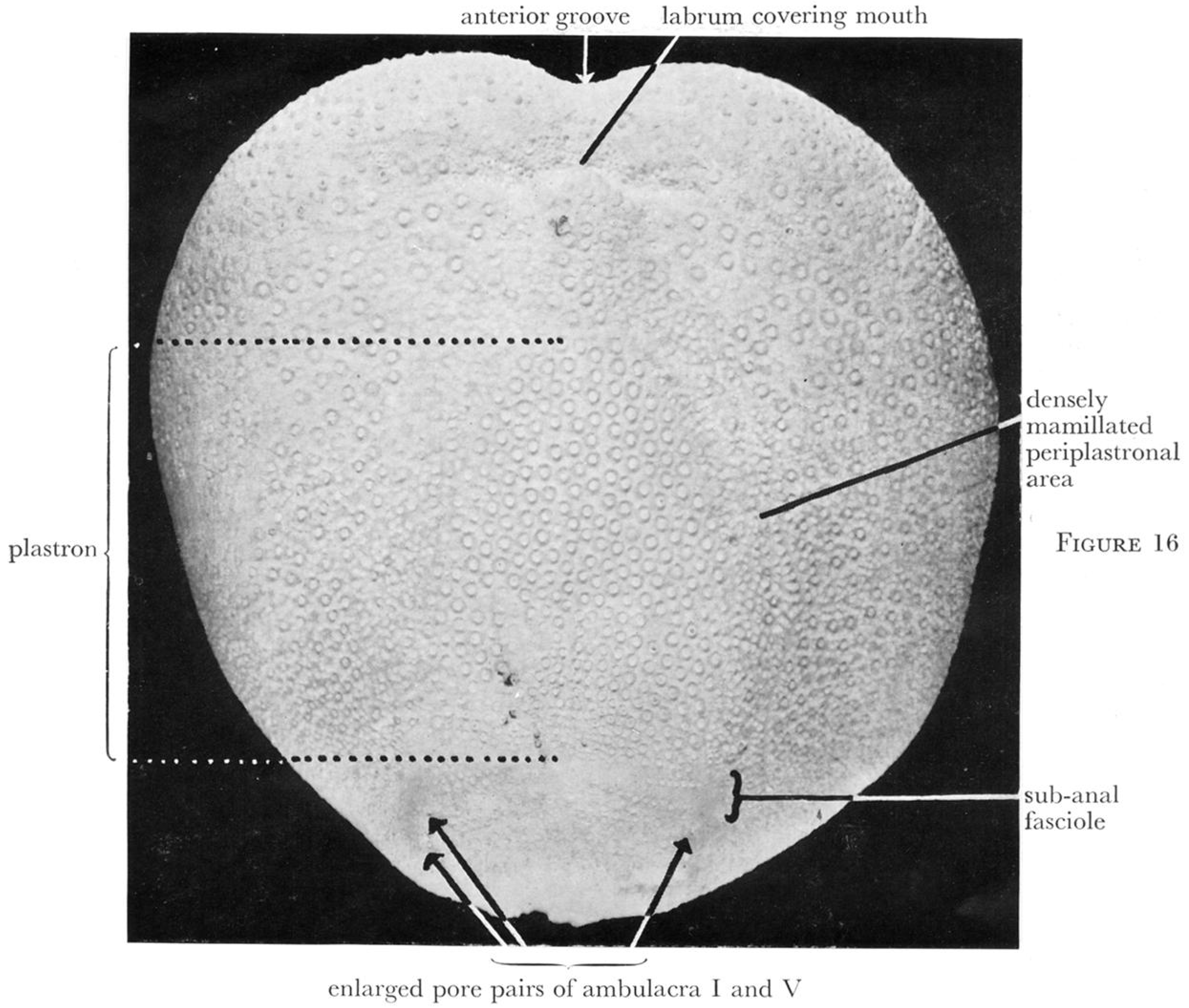

FIGURE 16

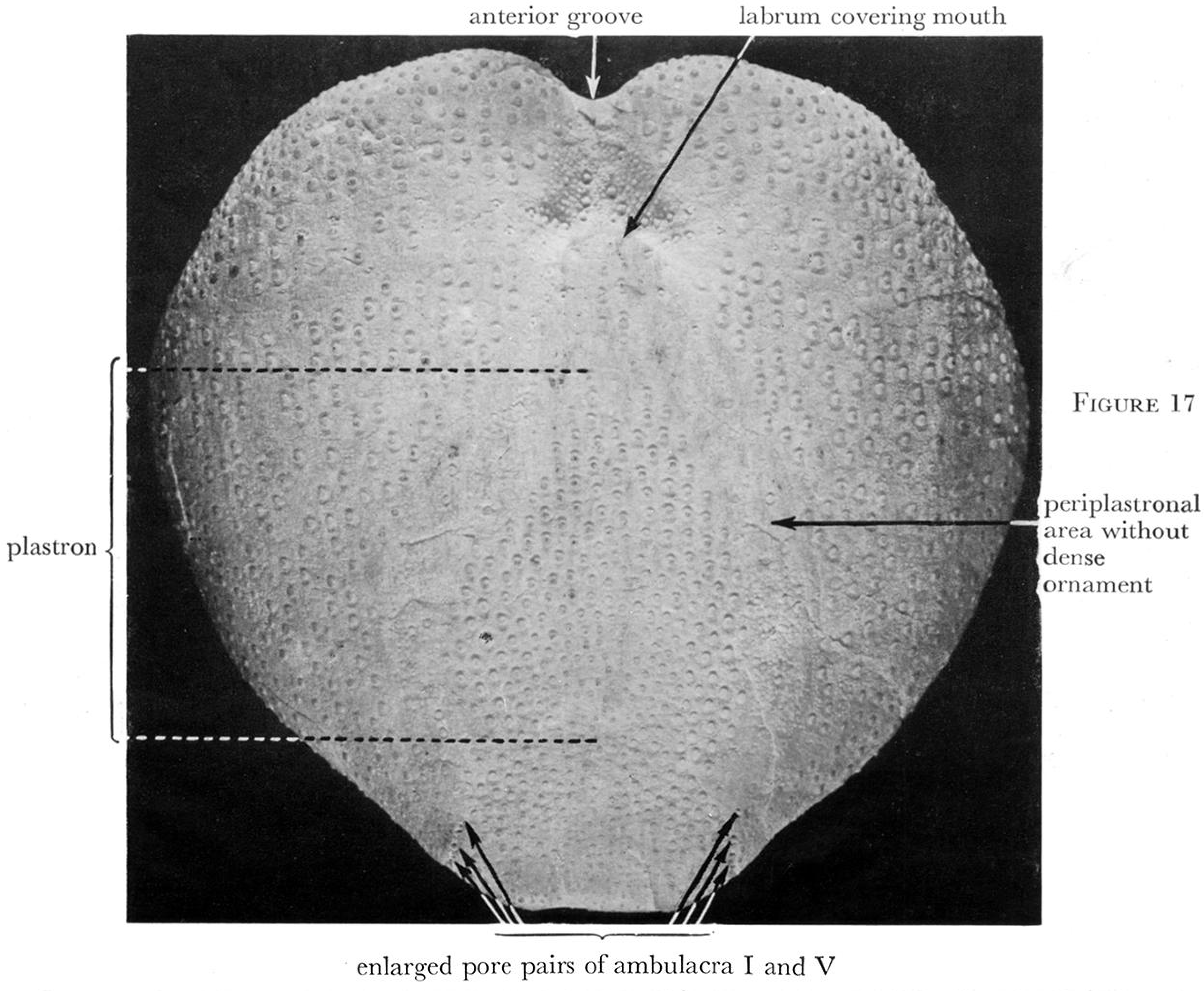

FIGURE 17

PLATE 26

FIGURE 16. Ventral view of specimen E 32980. Note: the prominent labrum, covering the mouth; the long plastron; the dense mammillated ornament of the periplastronal areas; and the ring of the sub-anal fasciole, with inside it the enlarged pore-pairs of ambulacra I and V.

FIGURE 17. Ventral view of specimen E 32533. Note: and compare with specimen E 32980—the rather shorter labrum and plastron; the lightly ornamented periplastronal areas; and the absence of the sub-anal fasciole, although the enlarged pore-pairs of ambulacra I and V remain.