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[99]

A STUDY OF VARIATION AND RELATIVE GROWTH IN THE BLASTOID *ORBITREMITES*

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[Plate 2]

CONTENTS

Previous workers have described five species of the blastoid genus *Orbitremites* from the Lower Carboniferous of Britain. The original aim of the present work was to study the variation and relative growth in each of these species, and the supposed evolutionary differences between the species from successive geological horizons.

The recorded distribution of these five species has been reviewed, and where possible the older records have been confirmed by collecting new samples. The type species *Orbitremites derbiensis* has been collected from four localities, all in the D_2 Subzone (Upper Visean). Another species, *O. ellipticus*, has been collected at three localities, all in the C_2 Subzone (Lower Visean). But the other three species, *O. orbicularis*, *O. campanulatus* and *O. mccoyi*, have been found only in association with *O. ellipticus*.

Two samples of *Orbitremites* were collected, comprising 581 specimens of *O. derbiensis* from the Middle Limestone of Grassington, Yorkshire, and 112 specimens from the Upper Clitheroe Limestone of Clitheroe, Lancashire, which included representatives of the other four species.

Examination of the Clitheroe sample revealed that the forms previously described as distinct species are connected by intermediate forms. *O. ellipticus* and *O. orbicularis* are merely shape variants of the adult form of a single species, the difference in shape being described by their respective names. In many young individuals the base of the calyx is broad relative to that in larger specimens, and it is concluded that *O. mccoyi* is a young form of *O. ellipticus* and similarly

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O. campanulatus is a young form of *O. orbicularis*. As *O. orbicularis*, *O. mccoyi* and *O. campanulatus* are junior synonyms of *O. ellipticus*, only two British species of *Orbitremites* were available for the later part of the study.

Measurements of height, diameter, the sizes of the component plates and counts of the number of the ambulacral plates were made on all specimens sufficiently well preserved (Grassington 188 specimens, Clitheroe 40 specimens). Slight differences in the sizes of the component plates in each of the interambulacra of an individual were found to contribute to the errors of measurement.

There is considerable variation in size because each of the samples consists of an assemblage of individuals which died at various ages, and so constitutes a growth series. The sample mean and the sample variance could not be used as a basis of comparison between the samples because the frequency distribution of size bears an unknown relationship to that in the original living community, due to bias resulting from differential mortality and further bias arising during preservation and collection.

There is a strong positive correlation of all the variates with the size of the individual, so masking the true relationship between them. This difficulty has been overcome by the use of partial correlation. In *O. derbiensis* it was found that some variates are correlated, but in all cases the relationship appears to be based on the mechanical necessity that the component plates of the blastoid should fit together.

None of the scatter diagrams for pairs of variates show any curvature in their general trend, and so in each case the relative growth relationship has been expressed as an equation for a straight line. The slope and intercept of the reduced major axis, and the standard error of each of these parameters, has been calculated for all pairs of variates in both samples. Growth is isometric for some pairs of variates, but in other cases the intercept of the relative growth line is significantly different from the origin, indicating important changes in shape during the young stages.

The slope and intercept of the relative growth curves have been used as a basis of comparison between the samples. There is no significant difference in shape, as expressed by height and diameter, between *O. derbiensis* and *O. ellipticus*. In *O. derbiensis* the number of ambulacral plates relative to size is slightly greater than in *O. ellipticus*, due to an increase in the relative number on the deltoid region. There is no significant difference in the relative number of ambulacral plates on the radial region. As would be expected from the general appearance of the two species, there are large significant differences in the relative sizes of the component radial and deltoid plates.

As only two British species, instead of five, were available for the later part of the work, the comparison inevitably fell short of one of its original aims as an evolutionary study. However, fifteen species of *Orbitremites* have been recorded from North America, all of which are geologically older than the two British species, and in common with *O. ellipticus* the deltoid is never larger than the radial plate. In contrast, in *O. derbiensis*, and also in *O. malaianus* from the Permian of Timor, the deltoid is larger than the radial plate. Whether this sequence indicates a general evolutionary trend within the genus can only be determined by a similar study based on the American species of *Orbitremites*.

1. INTRODUCTION

Blastoids are not normally regarded as being common fossils, but during recent years large numbers of them have been collected at several localities in northern England. These blastoids are of Lower Carboniferous age, and the geological factors which influence their distribution have been described in detail elsewhere (Joysey 1955). The blastoids are often associated with knoll-forming limestones, being most abundant in the crinoid bank deposits which cap the knolls, although they also occur in laterally equivalent rocks of different lithology.

Seven blastoid genera are known to occur in northern England, but the majority are rare, and only *Codaster* and *Orbitremites* have been collected in large numbers. *Codaster* formed the basis of a previous study (Joysey 1953), in which it was found that two described

species were different stages in a single growth series. Observations on the shape of the specimens were supplemented by a biometrical study of the relative growth of height, diameter and the number of hydrospires. Biometrical methods have also been used in the present study of *Orbitremites*, which was undertaken with a threefold aim.

(i) To study the variation within a blastoid community.

(ii) To investigate the changes in shape during growth, and to study the relative growth of the characters.

(iii) To study the differences between species of the same genus, from different geological horizons.

The results of these related investigations, together with discussion of other problems which inevitably became apparent during the course of the work, are presented in this paper.

2. Source of the material

(a) *The distribution of* Orbitremites *in Britain*

The generic name *Orbitremites* was first published by Austin & Austin (1842), who selected *Pentremites derbiensis* Sowerby, from the Lower Carboniferous of Britain, as the type species of their new genus. Etheridge & Carpenter (1882, 1886) gave a generic diagnosis and comprehensive descriptions of the species included in this genus, under the name *Granatocrinus*. This generic description has required only insignificant revision by subsequent authors, though the name *Orbitremites* clearly has precedence.

At present 23 species are referred to the genus *Orbitremites*, which has now been recorded from Britain, North America, Australia and Timor (Bassler & Moodey 1943). Five of these species have been described from Britain, all in rocks of Visean age.

In order to collect samples of each of the British species, a list of localities was compiled from the previous literature. It soon became apparent that most of the type localities were poorly defined, and that there were conflicting records of the source of some figured specimens. This was aggravated by the misidentification of species and uncritical perpetuation of errors by successive authors. Records of the distribution of each of the five species are briefly reviewed below.

(i) Orbitremites derbiensis (*Sowerby*)

The type locality of *O. derbiensis* is indicated by the trivial name. The type specimens were collected by White Watson from the twenty-sixth bed of limestone in the Carboniferous succession of Derbyshire (Sowerby 1825); but the exact locality was not recorded. Many museum collections contain specimens of *O. derbiensis* from Derbyshire, but it has been possible to trace only one sample with additional locality data. This is a collection of nine specimens in H.M. Geological Survey Museum (95670 to 95678) from Sheldon Moor, near Bakewell. The area has been visited in the course of the present work, and several specimens were collected from a wall, but all nearby exposures were overgrown and so no specimens were found *in situ*.

Phillips (1836) figured a specimen from the Gilbertson Collection, but he did not state any locality for the specimen. However, he gave 'Grassington; Derbyshire' as localities for the species. This is the earliest reference to Grassington, and Bather (1899) has suggested

that this may be the source of Gilbertson's specimen. Grassington is situated in the West Riding of Yorkshire, about 10 miles north of Skipton.

In subsequent literature, there has been some confusion as to whether Grassington or Derbyshire is the type locality. Several authors (Roemer 1851; Dujardin & Hupé 1862) quoted Grassington as a locality for the species but omitted any reference to Derbyshire. The confusion was made worse when a succession of authors (Baily 1875; Etheridge & Carpenter 1886; Bassler & Moodey 1943) gave 'Grassington, Derbyshire' as the type locality, as though Grassington were situated in Derbyshire, rather than Yorkshire.

In 1948, Mr P. Manning and the author rediscovered large numbers of *O. derbiensis* in the Grassington area, Yorkshire, so confirming Phillips's (1836) original record. Elsewhere in Yorkshire, Bather's (1913) record of *O. derbiensis* at Limley in Nidderdale has been confirmed by further collecting, and a new locality for the species has been found near Malham (Joysey 1955).

There has been some confusion regarding the source of other specimens of *O. derbiensis* in the Gilbertson Collection. In 1828 Sowerby quoted Gilbertson as saying: 'The *Pentatremites* are *all* from the Calamine Mines, belonging to the Duke of Buccleugh, near Whitwell in Bolland, on the Lancashire side of the Odder'. Bather (1899) states that neither Gilbertson's own manuscript list, nor the Register of the Zoology Department, British Museum, gave the locality of his specimens of *O. derbiensis*, but when transferred to the Geology Department, the specimens were registered as from 'Bolland'. It has been indicated above that Gilbertson's specimens of *O. derbiensis* probably came from Grassington, but as Phillips did not give this locality until 1836, it is quite likely that the specimens were found subsequently to the quoted conversation between Gilbertson and Sowerby.

Etheridge & Carpenter (1886) recorded *O. derbiensis* from several localities in Lancashire, but Bather (1899) has subsequently amended several of these records. For example, some specimens in the Tennant Collection are recorded as from 'Lancashire' by Etheridge & Carpenter, but are from Derbyshire according to the British Museum Register. Similarly, Etheridge & Carpenter (1886) gave 'Clitheroe, Lancashire' as the locality for some specimens in the Rofe Collection, but Bather (1899) clearly had doubts and merely gave 'England' as the locality. In the course of the present work no specimens of *O. derbiensis* have been found among the collections of blastoids made at either Bolland or Clitheroe, in Lancashire.

O. derbiensis has been recorded from several localities in Ireland (Griffith 1862; Baily 1875), but none has been confirmed by recent work, although the superficially similar species *Monoschizoblastus rofei* (Etheridge & Carpenter) has been recorded at the same localities (Etheridge & Carpenter 1886; Oswald 1955).

(ii) Orbitremites ellipticus (*Sowerby*)

In 1825, Sowerby stated that the type specimens were: 'communicated to me by Mr Joseph Kenyon of Preston, Lancashire, near which place they are found'. Preston is situated in an area of terrestrial Triassic rocks, but specimens have subsequently been recorded and confirmed from two localities, Whitwell in the Bolland district and Clitheroe, both of which are about 15 miles from Preston (Phillips 1836; Etheridge & Carpenter 1886; Parkinson 1926, 1936; Joysey 1955). Although Phillips's (1836) locality at Bolland is the earliest record, the type locality will always remain uncertain.

O. ellipticus has been recorded from Derbyshire (McCoy 1851), Staffordshire (Ludford 1951) and Ireland (Griffith 1862; Bassler & Moodey 1943) but none of these records has been confirmed in the course of the present work.

(iii) Orbitremites orbicularis (*Sowerby*)

In 1834, Sowerby did not name the type locality in his original description of *O. orbicularis*. Two years later Phillips (1836) figured both *O. ellipticus* and *O. orbicularis* from the Gilbertson collection and gave Bolland as the source of both species.

Roemer (1851) recorded *O. orbicularis* from 'Bolland in Yorkshire', and subsequently several authors have given 'Yorkshire' as a locality for the species. At Whitwell, in the Bolland area, the River Hodder marks the boundary between Lancashire and Yorkshire. Hence, apparently distinct records from Lancashire and Yorkshire may refer to one and the same locality. Etheridge & Carpenter (1886) recorded *O. orbicularis* from Clitheroe, Lancashire, where it has been confirmed in the course of the present study.

(iv) Orbitremites campanulatus (*McCoy*)

In 1849, McCoy gave Derbyshire as the type locality for this species, which was stated to be rare. The exact locality is unknown, and no further specimens have been recorded from Derbyshire.

Etheridge & Carpenter (1886) recorded this species from both Bolland and Clitheroe, and it has been confirmed at the latter locality in the course of the present study.

Five specimens, one of which is abnormal in having tetramerous symmetry, have been recorded from Haw Crag, Bell Busk, near Skipton, Yorkshire. (H.M. Geological Survey Museum, Rhodes Collection 1405 to 1407 and 1463.)

(v) Orbitremites mccoyi (*Etheridge & Carpenter*)

This species was originally described from two specimens in the Rofe Collection, and the type locality was stated to be Clitheroe, Lancashire (Etheridge & Carpenter 1882). Bather (1889) has indicated that the source of some of Rofe's material is questionable and so this type locality is open to doubt. However, this form has been collected at Clitheroe in the course of the present work.

Reviewing the distribution of *Orbitremites* in Britain, it is of stratigraphical significance that all of the localities at which *O. derbiensis* has been collected in the course of the present work (Sheldon Moor, Grassington, Limley and Malham), are in rocks of Upper Visean (D_2 Subzone) age. In contrast, *O. ellipticus*, *O. orbicularis*, *O. campanulatus* and *O. mccoyi* have been collected (Whitwell, Clitheroe and Slaidburn) only in rocks of Lower Visean (C_2 Subzone) age. The occurrence of these four species at the same horizon at Clitheroe gave the first disappointing indication that it would be possible to study the genus at only two geological horizons, instead of at five.

(b) Collection of the samples

As a result of the foregoing review of *Orbitremites* localities, and of visits to the various sites, it was clear that *O. derbiensis* was abundant at Grassington, and that specimens of *Orbitremites*, including all of the other four species, were fairly common at Clitheroe. These

two localities were chosen as the source of the samples for biometrical study. An account of the geology and distribution of *Orbitremites* in these two areas has been given elsewhere (Joysey 1955), and so it is only necessary to describe the actual collection of the samples.

(i) *Grassington, Yorkshire*

The sample of *O. derbiensis* was collected from the Middle Limestone (D_2 Subzone) near Yarnbury, north of Grassington, Yorkshire. The specimens were obtained from two outcrops, a few yards apart, at a locality a quarter of a mile bearing 150° from Bare House. The blastoid *Codaster acutus* McCoy is also common at this locality. The blastoids occur in a matrix of highly crinoidal limestone, and are very difficult to extract, being infilled with calcite which cleaves when the rock is hammered. However, the debris derived from the weathering of the outcrops contains many more or less complete specimens. Several hundred blastoids were collected from the soil below one crag, and there is no doubt that all this material was derived from the weathering of a thickness of only 2 ft. of limestone, along an exposure 4 ft. in length. A few yards away the same bed outcrops in a small stone digging, where the original bedding is recognizable in the thin subsoil which consists of weathered limestone blocks. This matrix easily crumbles, because the binding calcite cement has been leached out, and again several hundred blastoids were collected by stripping off the turf to expose this weathered material. These specimens were all obtained from a thickness of about 4 in. of limestone and from an area of not more than 3 sq. ft.

In order to obtain the smallest specimens, which are not found at all by such collecting, a few pounds of the friable matrix from the subsoil was broken down mechanically. The debris was passed through graded sieves and each portion examined on a sorting tray and picked in the manner employed by micro-palaeontologists. By this method three specimens smaller than 3 mm in height were found and added to the collection.

(ii) *Clitheroe, Lancashire*

The specimens of *Orbitremites* were collected from the Upper Clitheroe Limestone (C_2 Subzone) at the disused eastern end of Bellman Park Quarry in the Salt Hill knoll. They are most abundant on the almost inaccessible upper part of the face, but all loose fragments dropping from this position fall on to a small area of scree, from which the blastoids were collected. This area was then excavated but the material was so muddy that further collection was impossible. Accordingly, the locality was visited on several occasions during the period 1949 to 1951. On each visit the scree was examined and then dug over in preparation for the next visit, by which time the rain had washed the excavated material, and made further collecting possible.

3. Treatment of the material

(a) *Preparation*

At the time of collection most of the blastoids were enveloped in grass roots, coated with mud, or overgrown with lichen. In order to clean the specimens, they were boiled for some hours in a saturated solution of potassium hydroxide to destroy organic material. Constant washing in water for several days was necessary to remove the alkali, and then each specimen was thoroughly brushed with a medium-grade nylon tooth-brush, to remove the softened dirt.

After drying, the specimens were numbered with indian ink. It may be noted that the specimens were not numbered at random. The most weathered specimens were ready first, for these had been used for trial experiments in cleaning methods; and, in addition, specimens of about the same size tended to be prepared together, as it was found more convenient to group them for brushing.

(b) *Examination*

(i) *The Grassington sample*

In order to assess the value of the material for biometrical study, each specimen was examined under a binocular microscope. A catalogue was constructed which contained observations as to whether particular characters were preserved, and whether or not they could be measured.

Of the 581 specimens of *O. derbiensis* from Grassington it was found that 225 showed some distortion of shape due to crushing, and these specimens were, therefore, rejected.

The remaining 356 specimens, which showed no distortion, were by no means perfect. Of these, 186 were fractured or badly weathered. In many cases the fracture involved loss of a character, and so the specimen had to be rejected, while in other cases the specimen could be used. As most of the specimens were weathered there was a heavy loss of the ambulacral plates, but this did not seriously affect the plate counts as they often leave clear impressions on the underlying lancet plate. Of the original 581 specimens, it was possible to make all measurements and counts on 188—or about a third of the collected sample.

In the course of the individual examination of this large number of blastoids, several abnormal specimens of *O. derbiensis* were found, some of which are worthy of special note, as the syndrome is present in more than one individual. For example, four specimens have a small additional plate lying in a depression at the junction of the radial-deltoid and inter-radial sutures. This abnormality may be present in one or two inter-rays on the same individual, and is sometimes associated with a median groove on the deltoid, leading into the abnormal depression (nos. 39, 191, 428 and 499).

Another three individuals have the deltoid plate in one of the inter-rays divided by a curved transverse suture, which is pointed above. The lower part of the deltoid between the abnormal suture and the radial-deltoid suture is invariably swollen (nos. 156, 226 and 500).

In contrast to these individuals with additional plates, three specimens have been found lacking one or more plates. In one of these an entire ambulacrum is absent, so bringing the adjacent deltoid plates into lateral contact, although the associated radial plate is present. Another specimen similarly lacks an entire ambulacrum, but the associated radial plate is also absent and one of the adjacent deltoids is reduced to a narrow splint. The most abnormal specimen of all lacks one plate in each of the basal, radial and deltoid circlets, but retains all five ambulacra, two of them lying side by side and arising in the same radial sinus (nos. 576, 577 and 578).

Among the normal specimens of *O. derbiensis* some portion of the hydrospire system was exposed in 162 individuals and the single hydrospire fold on each side of the ambulacrum was found to be a constant character.

The structure of the summit and the details of the basal plates were visible in 89 individuals and it was, therefore, possible to check the orientation of the small basal plate in the left anterior inter-radius (in basal view). This character was found to be constant in

87 individuals. In the remaining two specimens (nos. 172 and 570) the orientation is doubtful, due to their poor state of preservation.

The top columnal ossicle was preserved in 40 specimens, and of these a few retained a very short length of stalk.

(ii) *The Clitheroe sample*

Of the original 112 specimens of *Orbitremites* collected from Bellman Park Quarry, Clitheroe, it was possible to make all linear measurements on 55 specimens, and, of these, 40 were sufficiently well preserved for the ambulacral plates to be counted.

The Clitheroe sample contains specimens which could be referred to the four species:

Orbitremites ellipticus (Sowerby 1825)
Orbitremites orbicularis (Sowerby 1834)
Orbitremites campanulatus (McCoy 1849)
Orbitremites mccoyi (Etheridge & Carpenter 1882)

There is no sign of heterogeneity of the sample, and there is no reason to suppose that all the individuals were not part of the same community. Strong support for merging these

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EXPLANATION OF PLATE 2

Magnification of all figures, × 2.

FIGURES 10 TO 24. Specimens of *Orbitremites ellipticus* from the Upper Clitheroe Limestone of Bellman Park Quarry, Clitheroe, Lancashire, arranged to illustrate the intergradation between forms previously described as distinct species. The numbers of the specimens in the author's collection are indicated in parentheses.

10. A narrow specimen of *ellipticus* (44).
11. A broad specimen of *ellipticus* (37).
12. An intermediate form between *ellipticus* and *orbicularis* (47).
13. A narrow specimen of *orbicularis* (42).
14. A broad specimen of *orbicularis* (32).
15 to 19. A graded series of specimens intermediate in size and shape between the series in figures 10 to 14 and that in figures 20 to 24 (26, 12, 8, 19, 9).
20 and 21. Specimens of *mccoyi* (27, 45).
22. An intermediate form between *mccoyi* and *campanulatus* (14).
23 and 24. Specimens of *campanulatus* (51, 13).

FIGURES 25 TO 32. Figures reproduced from Etheridge & Carpenter (1886), converted to the standard scale, for comparison with figures 10 to 24.

25 and 26. *O. ellipticus* (plate VIII, figures 16 and 19).
27 and 28. *O. orbicularis* (plate IX, figures 12 and 11).
29 and 30. *O. mccoyi* (plate X, figures 7 and 5).
31 and 32. *O. campanulatus* (plate IX, figure 10 and plate VIII, figure 14).

FIGURES 33 TO 36. Specimens of *O. derbiensis* from the Middle Limestone of Yarnbury, near Grassington, Yorkshire, illustrating forms similar to those which occur within *O. ellipticus*. The numbers of the specimens in the author's collection are indicated in parentheses.

33. A specimen similar in shape to *O. ellipticus* (450).
34. A young specimen similar in shape to *O. mccoyi* (462).
35. A young specimen similar in shape to *O. campanulatus* (291).
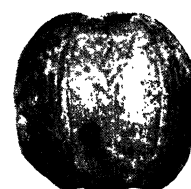36. A specimen similar in shape to *O. orbicularis* (541).
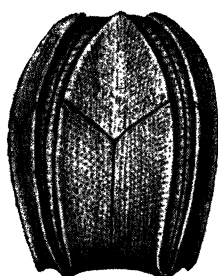
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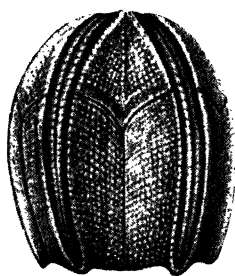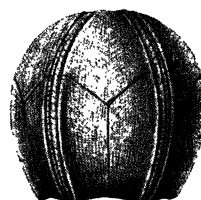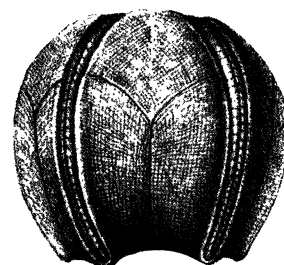
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four species is provided by the following descriptions by Etheridge & Carpenter (1886), which serve to illustrate the intergradation between these forms:

p. 253. 'This little species [*Granatocrinus McCoyi*] is intermediate in its characters between *G. ellipticus* and *G. campanulatus*. It possesses the elongated calyx of the former, and the truncated and flattened base of the latter type'.

p. 254. 'Furthermore the concave and narrow base [in *G. ellipticus*] is altogether different from the broad flat base of *G. campanulatus* and of *G. McCoyi*. The nearest ally of *G. ellipticus*, in the characters of the summit as well as those of the base, is unquestionably *G. orbicularis*. But it is readily distinguished by its more globular calyx and larger size.'

Examination of specimens in the Clitheroe sample (see figures 10 to 24, plate 2), shows that the forms previously described as *O. ellipticus* and *O. orbicularis* are merely shape variants of the adult form of a single species, the difference in shape being aptly described by their respective names. Figures 10 to 14 illustrate a graded series between specimens of *O. ellipticus* (figures 10 and 11) and *O. orbicularis* (figures 13 and 14), in which figure 12 is an individual completely intermediate between these two forms. In many of the young individuals (figures 20 to 24), the base of the calyx is broad relative to that in larger specimens. It is evident that *O. mccoyi* (figures 20 and 21) is a young form of *O. ellipticus*, and similarly *O. campanulatus* (figures 23 and 24) is a young form of *O. orbicularis*, while figure 22 is an individual which is intermediate in form between *O. mccoyi* and *O. campanulatus*.

The series of specimens illustrated in figures 15 to 19 represent an intermediate growth stage and serve to connect the adult series (figures 10 to 14) with the juvenile series (figures 20 to 24).

For the purposes of comparison with the Clitheroe sample, Etheridge & Carpenter's (1886) figures of these four species have been converted to the same scale (figures 25 to 32, plate 2).

Etheridge & Carpenter also described some differences between the species in the shape and surface structure of the ambulacral plates, and the position of the ambulacral pores. In fact, the structure of an ambulacrum is not constant along its length, there being a gradation between the two ends. The ambulacral plates are all formed at the radial tip of the ambulacrum within the radial sinus, and during subsequent growth they occupy a position first below the radial-deltoid suture, and then above it. The individual plates undergo considerable modification in shape and structure as they change their relative position on the ambulacrum. Furthermore, the ambulacral pores do not bear a constant relationship to the side plates, and, in any case, the number of pores is not exactly equivalent to the number of plates, the two structures being independent of one another in their formation.

The relative shape and size of the side-plate and outer side-plate also change according to the depth of abrasion, or weathering, as may be seen by examination of different ambulacra on the same individual. In the Clitheroe sample, it has been possible to match Etheridge & Carpenter's figures to various regions of the ambulacra, in different degrees of weathering, although it has not been possible to interpret all the features shown. The Clitheroe specimens are not sufficiently well preserved to allow a revision of the detailed morphological structure of the ambulacra, but a few specimens of *O. ellipticus*, collected

from the Phynis Shale of the Slaidburn anticline, are unique in the preservation of every detail of original structure and ornamentation.

It is concluded that the trivial names *orbicularis*, *mccoyi* and *campanulatus* describe shape variants and juvenile forms of the species *O. ellipticus* (Sowerby). No useful purpose is served by distinguishing these forms as they are recorded from the same localities, and so do not appear to have any stratigraphical or geographical significance. Accordingly, all the individuals in the Clitheroe sample are referred to the species *O. ellipticus* (Sowerby) and the use of the other specific names has been abandoned.

(c) Measurement of the samples

The following variates were studied: (1) height (H); (2) diameter (D); (3) height of the deltoid plate (Del); (4) height of the radial plate (Rad); (5) total number of ambulacral plates (A); (6) number of ambulacral plates on the deltoid region ($A.Del$); (7) number of ambulacral plates on the radial region ($A.Rad$).

Measurements (1), (2), (3) and (4) were made by the use of a traversing microscope fitted with cross-wire and a vernier scale. The scale readings were recorded to an accuracy of 0·1 mm.

In order to measure the total height and the heights of component plates the specimen was laid on a bed of Plasticine, with the best-preserved surface uppermost. The axis of the specimen was placed parallel to the direction of traverse and adjusted by eye to a horizontal position. The microscope was then traversed along the specimen and scale readings were taken at four points: (i) summit, (ii) top of the radial plate, (iii) base of the deltoid plate, and (iv) the base of the specimen. The microscope was always traversed back to the first position and the summit reading registered for a second time as a precaution, to check that neither the specimen nor the microscope stand had been accidentally displaced during the operations. The required measurements were then obtained by taking differences between the scale readings. It will be realized that the measurements of the deltoid and radial plates obtained by the above method are projections upon a plane parallel to the axis of the specimen and are not the lengths of the actual curved surfaces.

Next, the specimen was reorientated on the Plasticine bed and the axis put in a vertical position with the summit uppermost. The correct position was easily judged by eye when viewed through the microscope as the mouth is the centre of radial symmetry. The microscope was then traversed across the specimen, from the tip of one of the ambulacra to the middle of the opposite interambulacrum. As previously, the microscope was traversed back and the first reading taken again as a precaution against displacement.

All counts of ambulacral plates were made under a binocular microscope, using a needle point as a guide, to ensure that the eye did not jump a plate. The only difficulty encountered was in those specimens which had lost some or all of the plates, but it was often possible to count the depressions in which these had been situated. It should be noted that the pores along the margins of the ambulacra, which lead to the hydrospires, do not bear a constant numerical relationship to the ambulacral plates and cannot be used to estimate the number of the latter.

The original data are available (Joysey 1952), in a thesis for the degree of Ph.D., in the Library of the University of London.

(d) *Errors of measurement*

The errors of measurement encountered in work of this kind have been discussed by Kermack (1954) and classed in three groups:

(1) Systematic errors, which are related to the instrument of measurement. They are constant and similarly affect all measurements.

(2) Random observational errors or accidental errors.

(3) Secular errors, which are due to a personal factor in the observer and vary in magnitude from time to time.

'Student' (1917) found that a number of determinations of a measurement made on the same day are likely to lie more closely together than if they were made on different days.

The secular error may be important if it is different in magnitude when two sets of observations are made. This may lead to a conclusion that there are significant differences, where actually none exist, except in the secular error. However, the secular error need not be considered if its effects are swamped by random observational errors. This may be tested by repeating the same series of measurements at a different time to discover whether significant differences appear between the two sets of measurements. In fact, one wishes to test whether or not the series of measurements can be repeated. For this reason, the whole of the Clitheroe sample and a subsample of 50 specimens from Grassington were remeasured. The subsample was chosen as those specimens which were lying in the collection tray with their registration numbers uppermost. This choice is not quite random as the same individual could not be picked more than once, but it is certainly independent of either size or degree of weathering.

For the Grassington subsample differences were taken between the homologous measurements of the first and second series of observations, and the mean difference and its standard error were calculated. Student's 't' test was applied to test whether the mean difference was significantly removed from zero, as this would indicate whether or not the measurements could be repeated.

In two cases (*D.* and *Del.*) the mean difference is probably significantly different from zero ($P = 0.05$ to 0.02), and therefore the measurements were not repeatable. At first this was assumed to be due to the effects of the secular error. However, it was then found, in some cases, that the differences between the two series were correlated between the variates.

There was no significant correlation between the errors of height and diameter ($r = 0.08$), but there was a correlation between the errors of height, and those of the deltoid ($r = 0.29$) and radial ($r = 0.19$) plates. These correlations are to be expected, as an observational error on the scale readings would affect both variates. However, the strong negative correlation ($r = -0.47$) which exists between the errors of the radial and deltoid plates can only be interpreted on the assumption that there is an internal correlation within the individual. It seems that the deltoid plate varies slightly in length in the different inter-rays of the same individual. Where the deltoid is longer, the radial is correspondingly shorter, for the purely mechanical reason that the plates of the animal must fit together. Such variation within the individual would also contribute to the differences between the two series of measurements of the diameter and the counts of the number of ambulacral plates.

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As no precautions had been made to ensure that the second series of measurements were taken on the same side of the specimen as the first series, the actual differences which exist on the same individual swamped the errors of measurement.

The best estimate of the total contribution of both internal variance and error variance to the estimate of the population variance is half of the mean of the square of the difference between the first and second series of observations (Kermack 1954). These estimates for each variate are given in table 1, and expressed as a percentage of the estimated population variance.

TABLE 1. ESTIMATE OF THE CONTRIBUTION OF INTERNAL VARIANCE AND
ERROR VARIANCE TO THE ESTIMATE OF THE POPULATION VARIANCE

	estimated contribution of internal and error variances $(mm)^2$	% estimate of population variances
H.	0·0109	0·22
D.	0·0201	0·52
Del.	0·0214	0·84
Rad.	0·0249	3·69
A.	0·85	1·55
A.Del.	0·50	1·73
A.Rad.	0·29	5·91

Some of the contributions of internal and error variance to the population variance are undesirably large, especially those for the radial plate and the number of ambulacral plates on the radial.

In those cases where the errors of two variates x and y are independent there is no addition to the expectation of the product xy, but there is an addition to the expectations of x^2 and y^2. In consequence, the estimate of the coefficient of correlation between the variates will be too small, and accordingly the significance of statistics based on $(1-r^2)$ will be underestimated.

(e) Computation

For the Grassington sample the data was transferred to punched cards and the initial stages of computation performed by a Hollerith tabulating machine. For the other sample, the required quantities were obtained using a Muldivo electrical computing machine. Throughout the work the maximum extent of the machine keyboard has been used, as it is preferable to carry too many insignificant figures, rather than too few significant ones.

All the machine computation has been carried out at least twice, and wherever possible a different method of scanning or working has been employed, in order to avoid the repetition of errors.

4. VARIATION

(a) The relationship between the sample and the living community

It is necessary to inquire to what extent the collected samples of blastoids are representative of the fossil population in the rock, and also to what extent these fossil populations are representative of the living communities of blastoids on the Carboniferous sea-floor.

Kermack (1954) and Haldane (1956) have pointed out that a dead population can only be fully representative of the living population if the force of mortality is constant through-

out life. Observation suggests that in the majority of animals the force of mortality varies with age, the individuals being more likely to die at one age than another. In all echinoderms we can be fairly certain that the larval mortality is very high, but we know nothing of changes in the force of mortality during the life history of a blastoid, subsequent to its metamorphosis. We do not know whether storms in the Carboniferous seas were more likely to break large or small blastoids from their anchorages, and we do not know whether disease took greater toll among the aged than among the young. The relationship between the dead accumulation of blastoids on the sea-floor and the living community from which it was derived, is analogous to that which exists between the buried occupants of a churchyard and the living members of the village from which it is derived.

Even after the initial accumulation of corpses, it is possible that the action of currents might sort and grade them according to their size, and so the fossil population may not even be representative of the original dead population lying on the Carboniferous sea-floor. Furthermore, large individuals would be more likely to suffer mechanical distortion by crushing before, during and after the consolidation of the sediment. There is no doubt that a fossil population is biased due to the action of many factors, and bears an obscure relationship to the dead but unfossilized population, and an unknown relationship to the original living community.

When this fossil population is sampled additional bias may arise during actual collection. A blastoid embedded in a fragment of rock is more likely to protrude from the matrix and be seen by the collector if it is a large specimen. This is an important consideration when collecting from the broken rock fragments on a scree, for the large specimens would be seen, whereas small specimens would be more likely to be completely enclosed within the rock fragments. Should these small specimens be free from matrix, then they would tend to fall in the crevices between the larger fragments and be lost. This may account for the complete absence of very young individuals in the sample from Bellman Park Quarry, Clitheroe, but their absence might equally be due to a low force of mortality among young individuals, or to the removal of small corpses by current action.

TABLE 2. MEAN VALUE OF EACH OF THE VARIATES IN *ORBITREMITES DERBIENSIS*
AND *O. ELLIPTICUS*

mean	*O. derbiensis*	*O. ellipticus*
H.	8·579	12·340
D.	8·127	11·175
Del.	6·439	5·688
Rad.	3·072	8·680
A.	29·527	39·725
A.Del.	20·309	16·100
A.Rad.	9·218	23·625

There is no doubt that the frequency distribution of size in the samples of blastoids is biased in relation to that in the original living community. The factors which produce the bias cannot be expected to be the same under different conditions or at different localities. Under these circumstances, the mean size (see table 2) and the variance (see tables 3 and 4) of the different characters can have little value for the comparison of the samples, and their application could easily produce misleading results.

This conclusion is of general application in the biometrical study of fossils where there are no criteria for age determination (Joysey 1956). Only a few structures which do not grow, such as the teeth of some mammals, form an exception to this general rule.

(b) *Correlation between the characters in* Orbitremites derbiensis

In a study of the Cretaceous echinoid *Micraster*, Kermack (1954) found that a pair of characters, which would both be regarded as advanced in the evolutionary sense, were often negatively correlated with one another in the individual. In other words, an individual which tended to be advanced in one character tended to lag behind in another.

Among living animals it is possible to investigate correlations between the various characters by studying individuals of the same age, but this is not possible in the blastoid samples as there is no criterion for age determination. Each blastoid sample contains individuals of different ages, and so constitutes a growth series. This is the explanation of the considerable variation shown by all the characters, the differences in size being largely due to differences in age. It follows that a strong positive correlation between the pairs of variates is to be expected (see tables 3 and 4), which will mask the actual relationship between the characters.

TABLE 3. VARIANCE (DIAGONAL), COVARIANCE (ABOVE DIAGONAL), AND CORRELATION COEFFICIENT (BELOW DIAGONAL) IN *ORBITREMITES DERBIENSIS*

	H.	D.	Del.	Rad.	A.	A.Del.	A.Rad.
H.	*4·967*	4·254	3·448	1·700	15·909	11·553	4·356
D.	0·967	*3·899*	2·925	1·482	14·013	10·135	3·878
Del.	0·971	0·929	*2·541*	1·082	11·073	8·133	2·940
Rad.	0·929	0·914	0·827	*0·675*	5·423	3·850	1·572
A.	0·965	0·959	0·939	0·892	*54·764*	39·382	15·382
A.Del.	0·964	0·955	0·949	0·872	0·990	*28·899*	10·483
A.Rad.	0·883	0·887	0·833	0·865	0·939	0·881	*4·899*

TABLE 4. VARIANCE (DIAGONAL), COVARIANCE (ABOVE DIAGONAL), AND CORRELATION COEFFICIENT (BELOW DIAGONAL) IN *ORBITREMITES ELLIPTICUS*

	H.	D.	Del.	Rad.	A.	A.Del.	A.Rad.
H.	*10·139*	8·319	4·022	7·529	27·624	11·004	16·621
D.	0·941	*7·711*	3·324	6·181	24·313	9·954	14·360
Del.	0·905	0·858	*1·946*	2·855	11·122	4·319	6·803
Rad.	0·991	0·933	0·857	*5·698*	20·435	8·143	12·292
A.	0·939	0·948	0·863	0·927	*85·333*	34·310	51·023
A.Del.	0·898	0·931	0·805	0·886	0·965	*14·810*	19·500
A.Rad.	0·930	0·921	0·869	0·917	0·984	0·902	*31·522*

This difficulty may be overcome by the use of partial correlation. Partition with respect to height eliminates the effect of the correlation of height with the other variates, and this is equivalent to studying individuals of the same height. The technique of partial correlation has been applied to the *O. derbiensis* sample from Grassington, in order to gain further information regarding the relationships between the variates. The values of the correlation coefficients, partitioned with respect to one or several factors, are given in tables 5 to 7, and the conclusions derived from the examination of these tables are summarized below.

In specimens of the same height (see table 5) those with a large diameter have a small deltoid plate and large radial plate. They also have a greater number of ambulacral plates, the increase being on both the radial and the deltoid regions. Individuals with a large deltoid have a small radial plate and hence more ambulacral plates on the deltoid and fewer on the radial. Similarly, those with a large radial plate have more ambulacral plates on the radial and fewer on the deltoid. The total number of ambulacral plates is, however, independent of the size of both the deltoid and the radial, and as would be expected, individuals with a large number of ambulacral plates have more both on the radial and deltoid.

TABLE 5. COEFFICIENT OF PARTIAL CORRELATION WITH RESPECT TO HEIGHT (ABOVE DIAGONAL) AND DIAMETER (BELOW DIAGONAL) IN *ORBITREMITES DERBIENSIS*

	H.	D.	Del.	Rad.	A.	A.Del.	A.Rad.
H.	0	—	—	—	—	—	—
D.	—	0	−0·142	0·172	0·393	0·335	0·280
Del.	0·763	—	0	−0·835	0·040	0·208	−0·210
Rad.	0·434	—	−0·152	0	−0·036	−0·237	0·258
A.	0·519	—	0·454	0·137	0	0·856	0·705
A.Del.	0·543	—	0·563	−0·005	0·882	0	0·237
A.Rad.	0·215	—	0·051	0·289	0·675	0·247	0

In specimens of the same diameter (see table 5) those which are taller are larger in all other characters as well. Those with a large deltoid plate have a larger number of ambulacral plates on it, and a larger total number of ambulacral plates, but they have a small radial plate. Those with a larger radial plate also have more ambulacral plates on the radial and a greater total number. As expected, it follows that those with a larger total number of ambulacral plates have more both on the radial and deltoid plates, and those with more on the radial also tend to have more on the deltoid. The number of ambulacral plates on the radial is independent of the size of the deltoid, and similarly the number on the deltoid independent of the size of the radial plate.

In specimens of the same height and diameter (see table 6), that is *specimens of the same size and shape*, those with a large deltoid have a small radial plate, with a small number of ambulacral plates on the radial and a large number on the deltoid. Similarly, those with a large radial plate have more ambulacral plates on the radial and fewer on the deltoid. Individuals with a large number of ambulacral plates have more both on the radial and deltoid, and those with more on the radial also have more on the deltoid. The total number of ambulacral plates is independent of the size of both the deltoid and the radial.

TABLE 6. COEFFICIENT OF PARTIAL CORRELATION WITH RESPECT TO THE TOTAL NUMBER OF AMBULACRAL PLATES (ABOVE DIAGONAL), AND BOTH HEIGHT AND DIAMETER (BELOW DIAGONAL) IN *ORBITREMITES DERBIENSIS*

	H.	D.	Del.	Rad.	A.	A.Del.	A.Rad.
H.	0	0·556	0·716	0·571	—	0·251	−0·251
D.	—	0	0·298	0·456	—	0·136	−0·136
Del.	—	—	0	−0·071	—	0·407	−0·407
Rad.	—	—	−0·831	0	—	−0·175	0·175
A.	—	—	0·105	−0·115	0	—	—
A.Del.	—	—	0·274	−0·318	0·836	0	−1·000
A.Rad.	—	—	−0·179	0·222	0·674	0·159	0

In specimens with the same total number of ambulacral plates (see table 6), individuals larger in either height or diameter are larger in all other characters except that they have a small number of ambulacral plates on the radial. Those with a large deltoid have more ambulacral plates on the deltoid and fewer on the radial, and similarly those with a large radial have fewer on the deltoid and more on the radial. As expected, there is a very strong negative correlation between the number of ambulacral plates on the radial and deltoid plates. The sizes of the radial and deltoid plates are independent.

In specimens of the same size and shape, and with the same total number of ambulacral plates (see table 7), those with a larger deltoid plate have a small radial plate. They have a large number of ambulacral plates on the deltoid and a smaller number on the radial. Similarly, those with a larger radial plate have a larger number of ambulacral plates on it and fewer on the deltoid. Those with a large number of ambulacral plates on the deltoid have a small number on the radial.

In specimens with the same size and shape and with the same size deltoid and radial plates (see table 7), those with a greater total number of ambulacral plates have more on both the radial and deltoid plates, presumably because in those forms the ambulacral plates themselves are smaller in size. It follows that those with more plates on the radial also have more plates on the deltoid.

TABLE 7. COEFFICIENT OF PARTIAL CORRELATION WITH RESPECT TO HEIGHT, DIAMETER AND THE TOTAL NUMBER OF AMBULACRAL PLATES (ABOVE DIAGONAL), AND HEIGHT, DIAMETER, HEIGHT OF DELTOID AND HEIGHT OF RADIAL (BELOW DIAGONAL) IN *ORBITREMITES DERBIENSIS*

	H.	D.	Del.	Rad.	A.	A.Del.	A.Rad.
H.	0	—	—	—	—	—	—
D.	—	0	—	—	—	—	—
Del.	—	—	0	−0·839	—	0·624	−0·464
Rad.	—	—	—	0	—	−0·748	0·555
A.	—	—	—	—	0	—	—
A.Del.	—	—	—	—	0·849	0	−0·247
A.Rad.	—	—	—	—	0·722	0·248	0

None of these results reveals any unexpected correlations between the characters. In all cases the relationship appears to be based on the mechanical necessity that the component plates of the blastoid should fit together.

5. RELATIVE GROWTH

(a) The nature of the fitted line

In a fossil sample we have a collection of individuals that died at various stages of growth. The trend line which may be fitted to a scatter diagram is representative only of the sample as a whole and provides no information about the development of an individual. The deviations of the individual points from the fitted line are not due to errors of measurement but mainly represent variation within the sample due to the real differences between individuals. We do not know whether the relative growth curve of an individual blastoid followed a course approximately parallel to the fitted line, or whether it followed an irregular course within the area of scatter.

A fitted line has no intrinsic properties of its own, but is merely a convenient way in which to express a relationship between two characters. Although such a line is used to

represent an average course of the individual relative growth curves, such an extension to its meaning is not necessarily justified, and may sometimes lead to difficulties in zoological interpretation.

The trend of the scatter diagrams of *Orbitremites* in no case showed any undoubted curvature, and so a straight line has been fitted in each case.

The growth formula for the sample can be expressed in terms of the equation for a straight line, $y = a + bx$ where a is the value of the intercept on the y axis and b is the slope of the line. These relative growth parameters a and b are independent of the size of the individuals and are, therefore, independent of the various biases which have been shown to affect the frequency distribution of size within a sample. The objections which were found to apply to the sample mean and the sample variance as a basis for comparison do not in any way affect the growth parameters, a and b.

In order to avoid possible confusion, it may be noted that Kermack & Haldane (1950) and Imbrie (1956) employ the equation in the form $y = b + ax$, and so the meanings of the parameters a and b are reversed. The alternative equation $y = a + bx$ is used here, in order to conform with Simpson & Roe (1939), and other papers by the present author (Joysey 1953, 1956).

When it is necessary to fit a straight line to a scatter distribution, it is common practice to employ one of the regression lines. However, Kermack & Haldane (1950) have shown that this method is often unsatisfactory in the study of organic correlation, since the terms 'dependent' and 'independent' variates have no real meaning in this case. As an alternative they have advocated the use of the reduced major axis. The application of this line to the study of organic correlation has been fully discussed by Kermack & Haldane (1950) and Kermack (1954).

The intercept (a) and the slope (b) of the reduced major axis, and the standard error of each of these parameters has been calculated for all pairs of variates in the *Orbitremites* samples (see tables 8 and 9). In general, it is difficult to attribute a zoological meaning to the values of the slope and intercept of a straight line which has been fitted to an arithmetical plot of a growth curve. Imbrie (1956, p. 234) has applied the terms 'growth ratio' and 'initial growth index' to the slope and intercept, respectively, but these terms correctly apply to the parameters a and b when used in the allometric growth equation $y = bx^a$ (Huxley 1932; Reeve & Huxley 1945). In order to facilitate the calculation of these allometric growth parameters, this equation is often expressed in the form

$$\log y = \log b + a \log x,$$

and hence a and b are the slope and intercept of the growth line when x and y are plotted on a double logarithmic scale. It cannot be too strongly emphasized that these allometric growth parameters are not identical with the slope and intercept of a rectilinear growth curve, when x and y are both plotted on an arithmetical scale, and so it is undesirable to apply the same terms to describe these two different pairs of parameters.

In the present equation, $y = a + bx$, it might appear at first sight that a represents the initial size difference between the variates, but in general this is not the case. The size difference between the variates may be expressed as follows:

$$y - x = a + x(b - 1).$$

TABLE 8. INTERCEPT (ABOVE DIAGONAL) AND SLOPE (BELOW DIAGONAL) OF RELATIVE GROWTH CURVE IN *ORBITREMITES DERBIENSIS*

	H.	D.	Del.	Rad.	A.	A.Del.	A.Rad.
H.	0	0·525* ±0·147	0·303* ±0·111	−0·090 ±0·089	1·040 ±0·566	−0·385 ±0·413	0·698* ±0·302
D.	0·886 ±0·017	0	−0·121 ±0·182	−0·309* ±0·103	−0·930 ±0·648	−1·815* ±0·494	0·109 ±0·316
Del.	0·715 ±0·013	0·807 ±0·022	0	−0·246 ±0·141	−0·367 ±0·775	−1·407* ±0·514	0·277 ±0·372
Rad.	0·369 ±0·010	0·416 ±0·012	0·515 ±0·021	0	1·851* ±0·946	0·204 ±0·745	0·941* ±0·314
A.	3·320 ±0·064	3·748 ±0·077	4·643 ±0·117	9·010 ±0·297	0	−1·140* ±0·228	0·387 ±0·228
A.Del.	2·412 ±0·047	2·722 ±0·059	3·373 ±0·077	6·545 ±0·234	0·726 ±0·007	0	0·857* ±0·299
A.Rad.	0·993 ±0·034	1·121 ±0·038	1·389 ±0·056	2·695 ±0·099	0·299 ±0·007	0·412 ±0·014	0

* Indicates values of the intercept which differ significantly from the origin, $P < 0·05$.

TABLE 9. INTERCEPT (ABOVE DIAGONAL) AND SLOPE (BELOW DIAGONAL) OF RELATIVE GROWTH CURVE IN *ORBITREMITES ELLIPTICUS*

	H.	D.	Del.	Rad.	A.	A.Del.	A.Rad.
H.	0	0·414 ±0·596	0·281 ±0·375	−0·570*† ±0·206	3·925 ±2·010	1·186 ±1·074	1·866 ±1·310
D.	0·872 ±0·047	0	0·073 ±0·471	−0·926 ±0·565	2·549 ±1·932	0·612† ±0·919	1·030 ±1·435
Del.	0·438† ±0·029	0·502† ±0·041	0	−1·051 ±0·817	2·065 ±3·103	0·411 ±1·522	0·736 ±1·851
Rad.	0·750† ±0·016	0·860† ±0·049	1·711† ±0·139	0	6·133* ±2·072	2·106 ±1·064	3·208* ±1·336
A.	2·901† ±0·158	3·327† ±0·168	6·622† ±0·529	3·870† ±0·230	0	−0·450 ±0·704	−0·519 ±0·703
A.Del.	1·209† ±0·084	1·386† ±0·080	2·759† ±0·259	1·612† ±0·118	0·417† ±0·017	0	0·137 ±1·647
A.Rad.	1·763† ±0·103	2·022† ±0·125	4·024† ±0·315	2·352 ±0·148	0·608† ±0·017	1·459† ±0·099	0

* Indicates values of the intercept which differ significantly from the origin, $P < 0·05$.
† Indicates values of intercept and slope which differ significantly from the corresponding value for *Orbitremites derbiensis*, $P < 0·05$.

It is clear that the initial size difference cannot be calculated unless the initial size of one of the variates is known, except in the special case where $b = 1$ and then a is the size difference which is maintained throughout growth.

Similarly, in the special case where $a = 0$ the relative growth curve passes through the origin, and it is clear that b is the ratio of the variates, which in this case remains constant throughout life.

In other cases, when a has a finite value, then

$$y/x = (a/x) + b.$$

When x is very large compared to a, the value of the term a/x is very small, and b closely approximates to the ratio between the variates. For small values of x, the term a/x is more

important and cannot be ignored. For example, it is not unreasonable to imagine a blastoid appearing at metamorphosis with a height of 0·5 mm and diameter 1·5 mm. Assuming b to have a value 1, as $1·5 = a + (1 \times 0·5)$, the intercept a would also equal 1, and so the ratio

$$y/x = (1/0·5) + 1 = 3.$$

After growth when $x = 1$ mm, the ratio

$$y/x = (1/1) + 1 = 2,$$

and after a longer period of growth when $x = 10$ mm, the ratio

$$y/x = (1/10) + 1 = 1·1.$$

It is clear that b is not a good approximation to the ratio unless a is small compared to x.

In the *Orbitremites* samples, of the 21 pairs of variates the value of the intercept of the relative growth curve differs significantly from the origin in 10 cases for the Grassington sample and in three cases for the Clitheroe sample (see tables 8 and 9). It is noticeable that considerably less of the Clitheroe values are significant, but this sample was very much smaller than that from Grassington.

The initial size of *Orbitremites* is unknown. One of the smallest individuals in the Grassington sample has a height of 2·1 mm, but it already has seven ambulacral plates. Croneis & Geis (1940) have described microscopic stages of blastoids, the smallest forms being 0·1 mm diameter. There are three circlets of plates in the 'larval' stages—basals, radials and distals. The distals are either shed or resorbed at 'metamorphosis' and are therefore not homologous with the deltoids of the adult, which do not appear until after 'metamorphosis'. The component plates undergo considerable changes in shape and relative size before 'metamorphosis', which occurs at 0·4 mm diameter.

These dimensions are of the same order of size as the values of the intercept of the relative growth curves that have been calculated for the *Orbitremites* samples. It is, therefore, to be expected that there were considerable changes in shape and size of the component plates in the early period of growth, when the gross size was less than that of the smallest individual which has been collected. It seems that the smallest individual in the Grassington sample is perhaps 20 times the initial size of a blastoid, and 5 times the size at which the 'adult' plate arrangement was established.

It is quite likely that the relative growth curve changed in slope at the point which is referred to as 'metamorphosis', although some of the 'adult' plates were already present prior to this stage. Although it is speculative to produce the relative growth curve of *Orbitremites* into the region beyond the size of the smallest individual, it is possible to test the validity of such speculation. On the assumption that one of the variates was very near to zero at its initial appearance, then the following conclusions regarding the initial relative sizes of the variates in *Orbitremites* may be obtained from the graphs: (1) initial diameter was larger than initial height; (2) initial deltoid was larger than initial height; (3) initial radial was smaller than initial height; (4) initial radial was smaller than initial diameter. These conclusions would represent quite possible relationships, except that regarding the deltoid plate and initial height. It might be suggested that the deltoid plate was initially well developed, lying in a larval disk, but this is absurdly removed from the

original concept in which the height of the deltoid was measured as a component of the total height. The only possible conclusion is that the extrapolation was unjustified.

It is common practice in palaeontological studies to use the frequency distribution of the ratio between two variates as a basis for comparison of fossil samples. There is an inherent danger in this procedure, unless it can be demonstrated either that the individuals are all of the same age, or that there are no changes in shape during the course of development.

The sample available to the palaeontologist usually consists of individuals of many different ages. Since it is impossible to assess the age of an individual unless growth lines are present there is considerable difficulty in distinguishing between a small variant and a young individual. As most animals change their shape as they grow, the value of the ratio of a pair of variates changes during the life of the individual. The mean value of the ratio, for a given sample, will depend on the relative abundance of large and small individuals and is, therefore, subject to bias by the many factors which affect the frequency distribution of size during life, after death and during collection.

It is possible to assess whether there are any changes in shape during growth by determining whether the value of the intercept a differs significantly from the origin. It has already been shown that when a differs significantly from the origin there are important changes in shape during the young stages, especially while the intercept a is of similar magnitude to one of the variates.

In the present study, although several of the values of a differ significantly from the origin, it might have been possible to base some of the comparisons on the frequency distribution of the ratio between pairs of variates. This is because the difference between the two species is so great that in most cases it would have swamped the error due to changes in the value of the ratio during growth. However, this would not apply in all cases, and due to the inherent danger in the use of the frequency distribution of a ratio, it was preferred to base all the comparisons on the parameters a and b.

(b) Comparison between the samples

Comparisons have been made between analogous relative growth curves of the Grassington and Clitheroe samples. The slope of the relative growth curve is significantly different in 19 graphs, and not significant in the other two cases (see tables 8 and 9). Of the 19 significant differences 16 are highly significant, $P < 0.001$, and all of these involve as one of the variates, either the size of the radial or deltoid plate, or the number of ambulacral plates on the radial or deltoid region. These differences are all obvious from examination of the graphs, there being no overlap between the areas covered by the scatter of the points belonging to the two samples (see figures 1 to 4). The differences are due to the marked distinction between the two samples in the relative size of the component plates (see figure 5).

The remaining three cases that are significantly different ($P = 0.05$ to 0.01), involve either the relationship between gross size and the number of ambulacral plates (see figure 6), or the size of the deltoid plate and the number of ambulacral plates in its region (see figure 7). These differences cannot be detected by examination of the graphs, which show overlap in the area of scatter for the two samples. In *O. derbiensis* the number of ambulacral plates relative to size is slightly greater than in *O. ellipticus*, due to an increase in the relative number on the deltoid region.
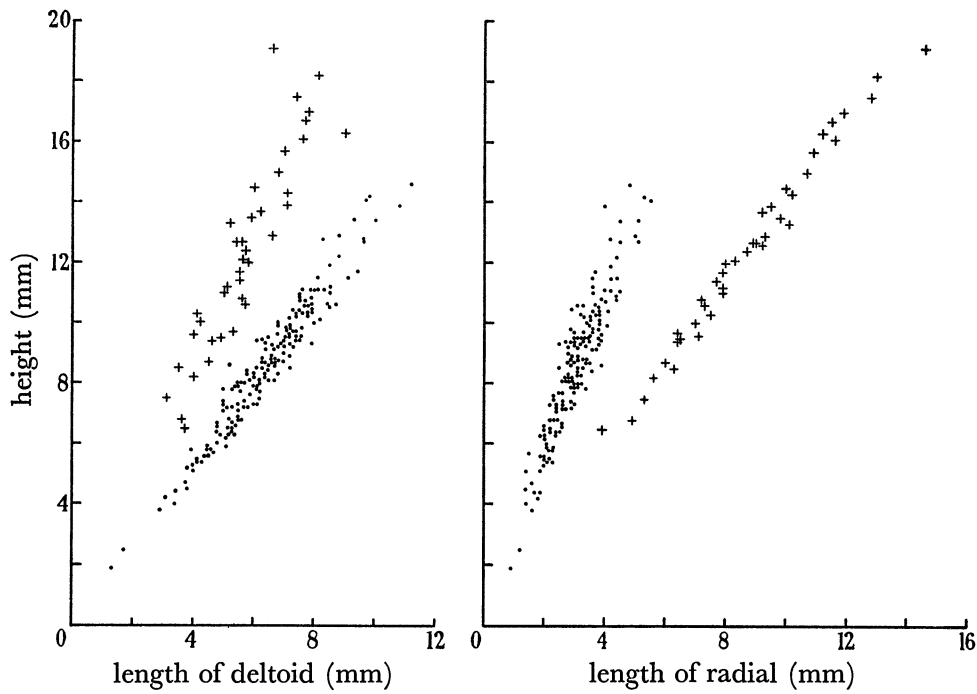
FIGURE 1

FIGURE 2

FIGURE 1. Scatter diagram showing the height of the specimen plotted against the length of the deltoid plate. ●, specimens of *Orbitremites derbiensis* from Grassington; +, specimens of *O. ellipticus* from Clitheroe.

FIGURE 2. Scatter diagram showing the height of the specimen plotted against the length of the radial plate. Symbols as in figure 1.
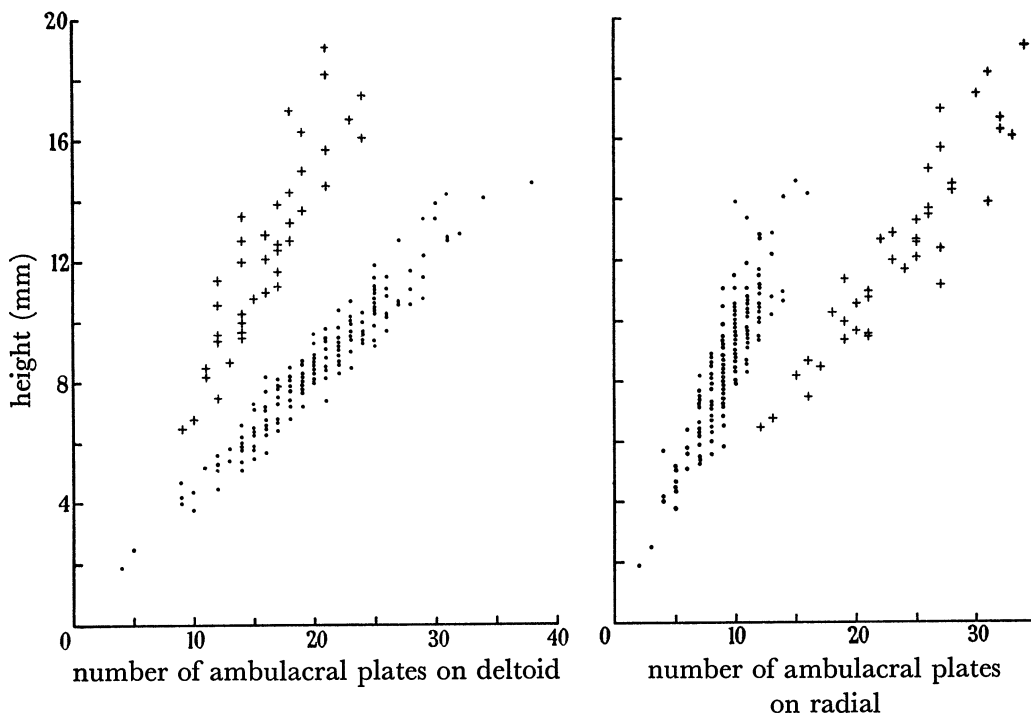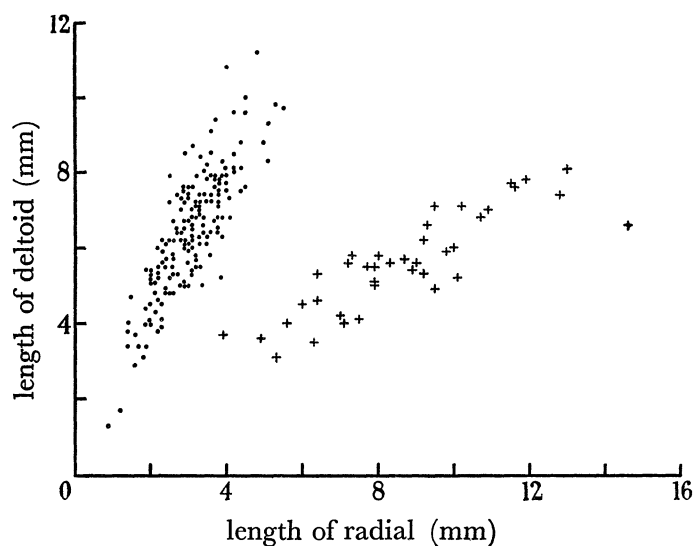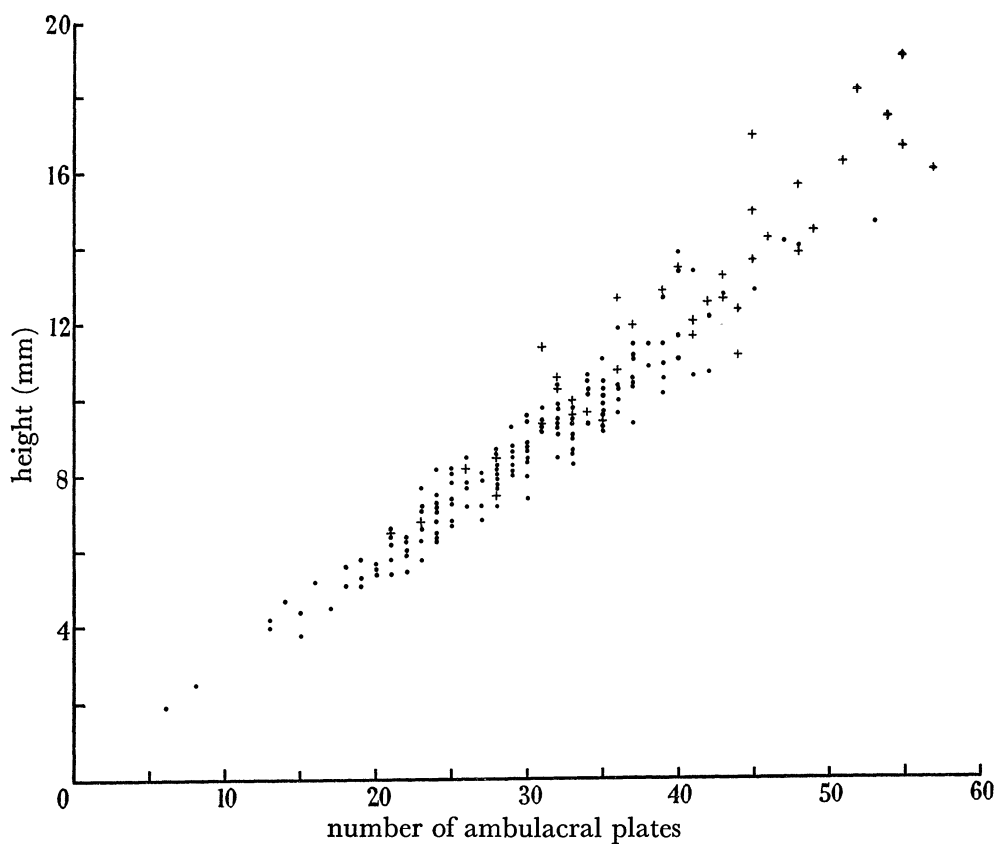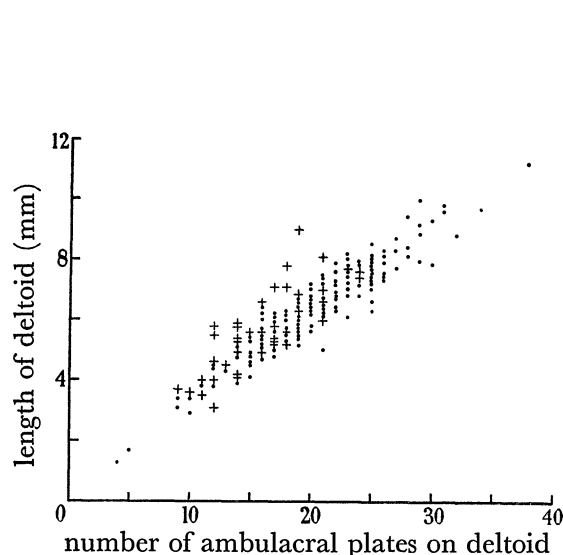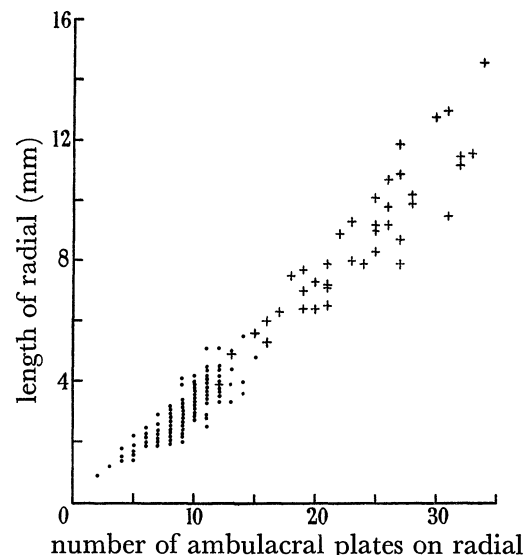

FIGURE 3

FIGURE 4

FIGURE 3. Scatter diagram showing the height of the specimen plotted against the number of ambulacral plates on the deltoid region. Symbols as in figure 1.

FIGURE 4. Scatter diagram showing the height of the specimen plotted against the number of ambulacral plates on the radial region. Symbols as in figure 1.

15-3

FIGURE 5. Scatter diagram showing the length of the deltoid plate plotted against the length of the radial plate. Symbols as in figure 1.

FIGURE 6. Scatter diagram showing the height of the specimen plotted against the total number of ambulacral plates. Symbols as in figure 1.

FIGURE 7

FIGURE 8

FIGURE 7. Scatter diagram showing the length of the deltoid plate plotted against the number of ambulacral plates on the deltoid region. Symbols as in figure 1.

FIGURE 8. Scatter diagram showing the length of the radial plate plotted against the number of ambulacral plates on the radial region. Symbols as in figure 1.
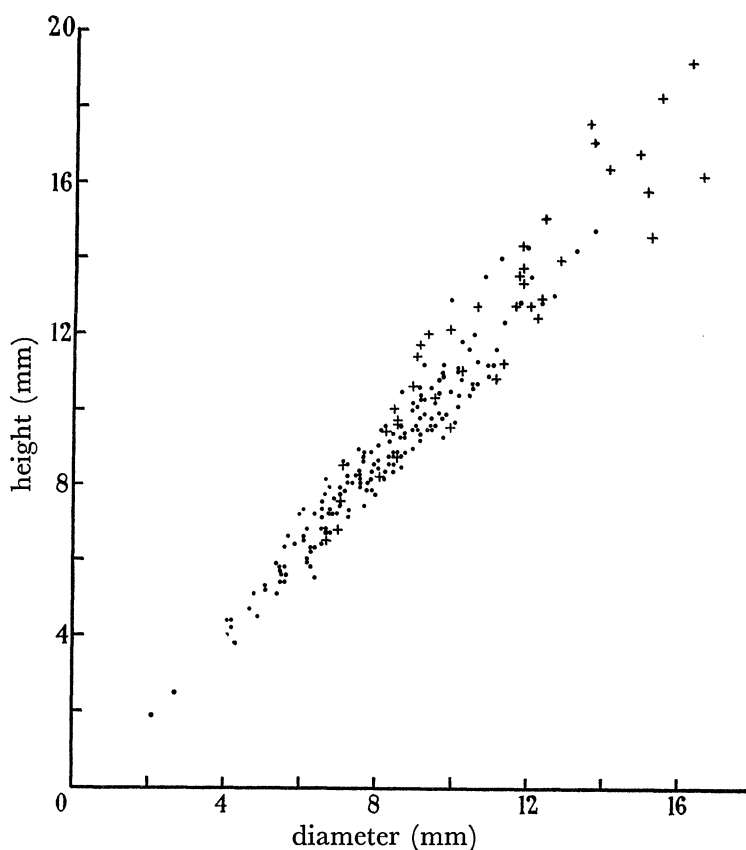
FIGURE 9. Scatter diagram showing the height of the specimen plotted against the diameter of the specimen. Symbols as in figure 1.

There is no significant difference ($P=0{\cdot}1$ to $0{\cdot}05$) in the relationship between the size of the radial plate and the number of ambulacral plates on it (see figure 8). The shape of the two species, as expressed by height and diameter (see figure 9), is not significantly different ($P=0{\cdot}8$ to $0{\cdot}7$).

The scatter-diagrams for the blastoid samples all 'fan out', because the range of variation of each character increases with size. This is to be expected, for when the mean size of a character is 1 mm an individual differing by 10% has a deviation of $0{\cdot}1$ mm, but a similar difference at a mean size of 10 mm would have a deviation of 1 mm. Although the range of variation increases with size, the coefficient of variation does not increase.

It is noteworthy that at equivalent sizes the two samples have the same range of variation (see figure 9). This lends support to the conclusion that the Clitheroe sample consists of only a single species, and is not an assemblage of four separate species. Furthermore, among the Grassington sample of *O. derbiensis* (figures 33 to 36, plate 2), some large individuals (figure 33) are comparable in shape with *O. ellipticus* and others (figure 36) with *O. orbicularis*, and all intermediate stages exist. Similarly, among the juvenile specimens of *O. derbiensis*, some individuals (figure 34) resemble the shape of *O. mccoyi*, and others (figure 35) can be matched with *O. campanulatus*. As in the Clitheroe sample, intermediate stages in the growth series are also present, connecting the juvenile and adult forms.

As only two British species, instead of five, were available for the later part of the work, the comparison inevitably fell short of one of its original aims as an evolutionary study. Although *O. ellipticus* and *O. derbiensis* are related species, there is no reason to believe that the former is directly ancestral to the latter. They both occur in the British area and inhabited a very similar environment, but they are separated by the time interval between the C_2 and D_2 Subzones, during which there are no records of *Orbitremites*. It is possible that the two species evolved independently outside the British area, and entered the region at different times and from different sources, as geographical and environmental conditions permitted.

The two species have much in common. Apart from their similarity in shape, they have a similar relationship between gross size and the number of ambulacral plates.

The highly significant differences between the species are all due to the difference in the relative size of the component plates. The radial plate is always larger than the deltoid plate in *O. ellipticus*, while the converse is true in *O. derbiensis*. This is the best criterion to distinguish between the two species. It is not easy to imagine what adaptive significance this might represent, but it is possible that the efficiency of the hydrospires may be modified as they bear a different relationship to the radial and the deltoid plates. In the deltoid region the hydrospires are further removed from the ambulacra and are connected to the ambulacral pores by canals which pierce the substance of the deltoid plates. But it would be unwise to speculate on these grounds as we have no real knowledge of the functional morphology of the hydrospires.

In conclusion, it is of interest to review briefly the species of *Orbitremites* which have been found outside the British area. In North America *Orbitremites* is represented by a single species in the Kinderhook Stage and by fourteen species in the succeeding Osage Stage There are no records of *Orbitremites* occurring outside North America at this time, which is

equivalent to the Tournaisian of Europe (Moore 1948). In two of these American species the radial and deltoid plates are of equal size, but in all the other species, the radial plate is larger than the deltoid, as in *O. ellipticus*.

A single North American species, *O. spinuliferus* (Rowley), recorded from the Meramic Stage (which is equivalent to the Lower Visean in the European succession), is described as having 'eight small spiracles at the summit' (Rowley 1900), and so does not belong to this genus. Elsewhere during the Visean, records of *Orbitremites* are confined to the British species, which have already been discussed in detail.

There are no records of the genus throughout the Upper Carboniferous, with the possible exception of *Orbitremites? wachsmuthi* (Etheridge) from the Carbo-Permian of Australia. This imperfectly known form has been doubtfully referred to this genus, and the relative size of the radial and deltoid is not known.

A single species, *O. malaianus* Wanner, has been recorded from the Middle Permian of Timor (Wanner 1924). In this form, as in *O. derbiensis*, the deltoid plate is larger than the radial.

Thus, in the earlier species of *Orbitremites*, including all the American forms and the British *O. ellipticus*, the deltoid plate is never larger than the radial plate. In contrast, in the later *O. derbiensis* from Britain and in the Timor species, the deltoid plate is larger than the radial plate. Despite this change in the relative size of the component plates there is no change in the shape of the calyx as a whole, at least in the British forms.

Although there appears to be a general trend involving an increase in the relative size of the deltoid and a decrease in the relative size of the radial, it remains to be investigated whether this trend will be substantiated when the morphological and stratigraphical succession of the North American species has been studied in detail.

REFERENCES

Austin, T. & Austin, T. 1842 Proposed arrangement of the Echinodermata, particularly as regards the Crinoidea, and a subdivision of the class Adelostella (Echinidae). *Ann. Mag. Nat. Hist.* (1), **10**, 106.

Baily, W. H. 1875 *Figures of characteristic British fossils.* (Vol. 1, Palaeozoic.) London: Van Voorst.

Bassler, R. S. & Moodey, M. W. 1943 Bibliographic and faunal index of Palaeozoic pelmatozoan echinoderms. *Geol. Soc. Amer. Sp. Paper.* No. 45.

Bather, F. A. 1899 *List of genera and species of Blastoidea in the British Museum.* London: Trustees of the British Museum.

Bather, F. A. 1913 British fossil Crinoids IX. *Ann. Mag. Nat. Hist.* (8), **12**, 388.

Croneis, C. & Geis, H. L. 1940 Microscopic Pelmatozoa. I. Ontogeny of the Blastoidea. *J. Paleont.* **14**, 345.

Dujardin, F. & Hupé, H. 1862 *Histoire naturelle des Zoophytes Echinodermes.* Paris: Roret.

Etheridge, R. & Carpenter, P. H. 1882 On certain points in the morphology of the Blastoidea, with descriptions of some new genera and species. *Ann. Mag. Nat. Hist.* (5), **9**, 213.

Etheridge, R. & Carpenter, P. H. 1886 *Catalogue of the Blastoidea in the Geological Department of the British Museum.* London: Trustees of the British Museum.

Griffith, R. 1862 In Appendix to second edition of McCoy, 1844.

Haldane, J. B. S. 1956 The biometrical analysis of fossil populations. *J. Palaeont. Soc. India.* **1**, 54.

Huxley, J. S. 1932 *Problems of relative growth.* London: Methuen.

Imbrie, J. 1956 Biometrical methods in the study of invertebrate fossils. *Bull. Amer. Mus. Nat. Hist.* **108**, 217.

Joysey, K. A. 1952 *The geology, distribution and biometry of Carboniferous blastoid communities.* Thesis for degree of Ph.D. University of London.

Joysey, K. A. 1953 A study of the type-species of the blastoid *Codaster* McCoy. *Geol. Mag., Lond.,* **90**, 208.

Joysey, K. A. 1955 On the geological distribution of Carboniferous blastoids in the Craven area, based on a study of their occurrence in the Yoredale Series of Grassington, Yorkshire. *Quart. J. Geol. Soc. Lond.* **111**, 209.

Joysey, K. A. 1956 The nomenclature and comparison of fossil communities. In *The species concept in Palaeontology.* Edited by Sylvester-Bradley, P. C. London: Systematics Association.

Kermack, K. A. 1954 A biometrical study of *Micraster coranguinum* and *M. (Isomicraster) senonensis.* *Phil. Trans.* B, **237**, 375.

Kermack, K. A. & Haldane, J. B. S. 1950 Organic correlation and allometry. *Biometrika,* **37**, 30.

Ludford, A. 1951 The stratigraphy of the Carboniferous rocks of the Weaver Hills district, North Staffordshire. *Quart. J. Geol. Soc. Lond.* **106**, 211.

McCoy, F. 1844 *A synopsis of the characters of the Carboniferous limestone fossils of Ireland.* Dublin: University Press.

McCoy, F. 1849 On some new Palaeozoic Echinodermata. *Ann. Mag. Nat. Hist.* **3**, 244.

McCoy, F. 1851 *Systematic description of the British Palaeozoic fossils in the Geological Museum of the University of Cambridge.* Cambridge: University Press.

Moore, R. C. 1948 Palaeontological features of Mississippian rocks in North America and Europe. *J. Geol.* **56**, 373.

Oswald, D. H. 1955 The Carboniferous rocks between the Ox Mountains and Donegal Bay. *Quart. J. Geol. Soc. Lond.* **111**, 167.

Parkinson, D. 1926 The faunal succession in the Carboniferous Limestone and Bowland Shales at Clitheroe and Pendle Hill. *Quart. J. Geol. Soc. Lond.* **82**, 188.

Parkinson, D. 1936 The Carboniferous succession in the Slaidburn district, Yorkshire. *Quart. J. Geol. Soc. Lond.* **92**, 294.

Phillips, J. 1836 *Illustrations of the geology of Yorkshire.* Pt. 2. York: Murray.

Reeve, E. C. R. & Huxley, J. S. 1945 Some problems in the study of allometric growth. In *Essays on growth and form presented to D'Arcy Wentworth Thompson.* Edited by Le Gros Clark, W. E. and Medawar, P. B. Oxford: University Press.

Roemer, C. F. 1851 Monographie der fossilen Crinoidenfamilie der Blastoideen und der Gattung *Pentatremites* im besonderen. *Wiegmann. Archiv.* **17**, 323.

Rowley, R. R. 1900 New species of crinoids, blastoids and cystoids from Missouri. *Amer. Geol.* **25**, 65.

Simpson, G. G. & Roe, A. 1939 *Quantitative zoology.* New York and London: McGraw Hill.

Sowerby, G. B. 1825 Note on Crinoidea, together with a description of a new species of *Pentremites*. *Zool. J.* **2**, 316.

Sowerby, G. B. 1828 On some new species of *Pentatremites*. *Zool. J.* **4**, 89.

Sowerby, G. B. 1834 On *Pentatremites orbicularis*, *P. acuta* and *P. pentangularis*. *Zool. J.* **5**, 456.

'Student' 1917 Tables for estimating the probability that the mean of a unique sample of observations lies between $-\infty$ and any given distance of the mean of the population from which the sample is drawn. *Biometrika*, **2**, 414.

Wanner, J. 1924 Die Permischen blastoiden von Timor. *Jaarb. Mijnw. Ned.-Oost-Ind.* **51**, 161.

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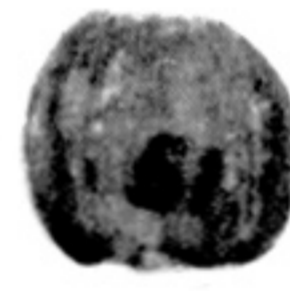15   16   17   18   19

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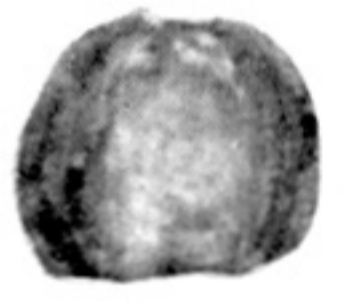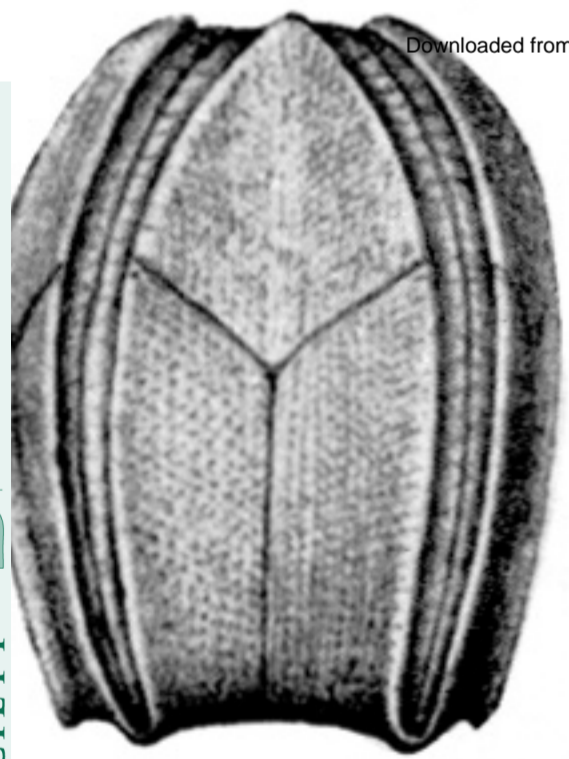
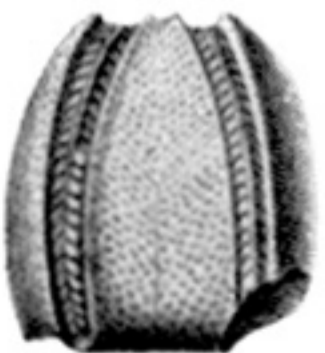25   26   27   28

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