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MORPHOLOGY, PALAEOECOLOGY AND EVOLUTION OF THE GENUS *GRYPHAEA* IN THE BRITISH LIAS

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[Plates 10 to 12]

CONTENTS

A comprehensive study has been undertaken of Liassic *Gryphaea* specimens collected from various localities in Great Britain at stratigraphical horizons ranging from Upper Hettangian to Upper Pliensbachian.

Study of the area of attachment, which is generally small, but increases in mean size up the succession, shows no discernible natural selection effect. Measurements of the length, breadth and height of the left valve of over a thousand specimens from thirteen different samples were subjected to statistical analysis with the aid of a computer. The regression of breadth and height on length is shown to be expressible more accurately in terms of logarithmic than normal values. Statistical comparison of samples reveals that geographical variations, though sometimes important within the limits of one or two adjacent ammonite zones, are insignificant compared with a major trend up the succession towards broader shells with a looser coiling. The spiral angle tends to decrease in stratigraphically younger forms and increase during individual ontogeny, which indicates that the coiling of the left valve cannot be accurately represented by a logarithmic spiral.

The gryphaeas of the British Lias are divided into three species, in ascending stratigraphical order *G. arcuata*, *G. mccullochii* and *G. gigantea*, the first two each being divided into chronological subspecies.

Field evidence indicates that gryphaeas tend to be commoner in stratigraphically thicker sequences and in 'ferruginous' rather than 'calcareous' facies. The fairly symmetrical size frequency distributions are best interpreted in terms of low juvenile mortality following the successful settling of spat. Most shells are disarticulated, small ones more so than large. Taken in conjunction with orientation data, this suggests that post-mortem disturbance has frequently been

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important. It is deduced on various grounds that the life orientation of all species was with the left valve convex downwards.

Flow channel experiments on shell stability gave support to the common sense presumption that there is a trend of increasing stability from *G. arcuata* to *G. gigantea*, that *G. arcuata* became progressively less stable with growth and that the posterior sulcus and lobe of *G. arcuata incurva* could have had a stabilizing influence. Regional variations in shape of contemporaneous populations of *G. arcuata* may possibly relate to variations of turbidity and sedimentation rate, and it is argued that food supply was the major factor controlling distribution.

Several evolutionary trends up the stratigraphical succession are suggested in the lineage *G. arcuata—G. mccullochii—G. gigantea*. These are increase of size, reduction in degree of incurvature of the left valve, broadening of the shell and thinning of both valves, together with less notable changes in area of attachment and the development of a posterior sulcus. The evolutionary change from the Hettangian *Liostrea* is thought to have been relatively sudden and genetically simple. It was clearly adaptive in raising the mantle margins above the sediment bottom, but led to a reduction of stability. The subsequent evolutionary history of *Gryphaea* largely can be interpreted as an attempt to rectify this and achieve, by the steady operation of selection pressure, a paradigmatic condition.

I. Introduction

It is doubtful if any species of fossil invertebrate has attracted more attention than the Liassic oyster *Gryphaea arcuata*. Although it had long been familiar to palaeontologists and amateur naturalists on account of its curious and highly distinctive shape, its major scientific interest dates from 1922, the year of publication of a paper by A. E. Trueman, which became accepted as a classic of evolutionary palaeontology and provoked a large literature (Joysey 1959). Trueman's hypothesis, that gryphaeas of the *arcuata* type evolved progressively from normal oysters by a gradual increase in incurvature of the left valve, together with a reduction of the area of attachment, remained unchallenged until 1959, since which time it has been the subject of lively controversy (Hallam 1959, 1960, 1962; Joysey 1959, 1960; Swinnerton 1959, 1965; Philip 1962, 1967; Burnaby 1965).

In my 1959 paper I rejected Trueman's hypothesis on the following grounds: (1) there were no systematic changes up the Hettangian succession in *Liostrea* of the type Trueman claimed; (2) there was no evidence of a gradual transition from *Liostrea* to the highly incurved *arcuata*-type gryphaeas that first appear just below the top of the Hettangian; (3) a statistical analysis of *Gryphaea* samples suggested that the apparent increase in tightness of coiling (i.e. incurvature) up the stratigraphic succession was attributable to a combination of allometric growth and size increase. It is the third contention which has provoked nearly all the argument. While Joysey had independently arrived at the conclusion that Trueman had erred in failing to take the possibility of allometric growth into account, he nevertheless questioned my statistics, in particular objecting, with Swinnerton, to the practice of pooling samples from different localities in Great Britain, thereby disregarding possible geographic variations. This criticism seemed to me somewhat disingenuous bearing in mind the clear implication, embodied in the title of Trueman's paper, that he thought that geographical changes were sufficiently insignificant to be disregarded. Nevertheless, the criticism, once made, demanded further statistical study (Hallam 1960). Subsequently Philip attempted to resurrect the Trueman interpretation by criticizing aspects of the work of Joysey and myself, and claimed on the basis of a new analysis of my data that they indeed showed a significant evolutionary increase in coiling up the succession. Philip's

TABLE 1. GRYPHAEA COLLECTION LOCALITIES AND HORIZONS

S signifies sample for statistics. X signifies small amount of material collected for general study.

stages	zones	Dorset	Glamorgan	Somerset	Gloucestershire	Warwickshire	Lincolnshire	Yorkshire	Skye and Raasay
Pliensbachian	*Spinatum*	.	.	X	X	.	.	X	S
	Margaritatus	X	.	.	X	.	.	.	.
	Davoei	.	.	.	.	.	.	S	.
	Ibex	.	.	.	.	S	.	.	.
	Jamesoni	.	.	.	.	.	.	S	S
Sinemurian	*Raricostatum*	.	.	.	.	.	.	X	X
	Oxynotum	.	.	.	.	.	.	X	.
	Obtusum	X	.	.	.	.	S	X	.
	Turneri	.	.	.	.	.	.	.	.
	Semicostatum	.	S	.	.	.	.	.	S
	Bucklandi	X	.	.	S	.	.	S	X
Hettangian	*Angulata*	S	S	S	.	.	X	S	.
	Liasicus	.	.	.	.	.	.	.	.
	Planorbis	.	.	.	.	.	.	.	.

statistics were in turn criticized by Burnaby, who accepted the earlier contention that Trueman had been misled by allometric growth, and that if there was a coiling trend at all, it was likely to be in the reverse direction to that originally proposed. Philip (1967) has in turn contested Burnaby's criticisms. In his last paper, Swinnerton (1965) reported the results of a study of a large number of Nottinghamshire gryphaeas, which caused him to accept belatedly that Trueman had been misled by allometric growth.

This brief summary of the recent controversy, though inadequate to do justice to the arguments of the various protagonists, is sufficient to indicate the currently reigning state of confusion, and the need for more work on the subject. What has not, however, been widely appreciated is that discussion has concerned only the earliest gryphaeas in the Lias, leaving unconsidered the many forms, varying widely in size and shape, that occur higher in the Sinemurian and Pliensbachian stages. No hypothesis of Liassic *Gryphaea* evolution is satisfactory that fails to take these latter into account.

This paper presents the results of a comprehensive study of the genus *Gryphaea* in the Lias of Great Britain. It has entailed the collecting and measurement of over a thousand specimens, taken from a number of different horizons and localities (tables 1 and 2) together with examination of museum material. Ammonite zones were considered sufficiently precise stratigraphical units for the study undertaken, but subzonal horizons are given for completeness in table 2.

TABLE 2. COLLECTION DETAILS

S.M. = Sedgwick Museum, A.H. = author's collection.

sample	zone	subzone	locality	grid reference	collection
Ay	*Angulata*	*Complanata*	Foreshore at Redcar, Yorkshire	NZ 616252	S.M., A.H.
Ag	*Angulata*	*Complanata*	Foreshore at Stout Bay, Glamorgan	SS 975670	S.M.
As	*Angulata*	*Complanata*	Quarry at Corston, Somerset	ST 683650	S.M.
Ad	*Angulata*	*Complanata*	Seven Rock Point, Dorset	SY 327908	S.M.
By	*Bucklandi*	*Bucklandi*	Foreshore at Redcar	NZ 614254	S.M., A.H.
Bgl	*Bucklandi*	*Bucklandi*	Hock Cliff, Fretherne, Gloucestershire	ST 725093	A.H.
Sg	*Semocostatum*	*Reynesi*	Cliffs at Southerndown and Gwter Fawr, Glamorgan	SS 886728	S.M.
Ss	*Semicostatum*	*Reynesi*	Foreshore east of Broadford, Skye	NG 680246	S.M., A.H
Ol	*Obtusum*	*Stellare*, *Denotatus*	Ironstone quarries near Scunthorpe, Lincolnshire	SE 907133	A.H.
Jy	*Jamesoni*	*Jamesoni*	Foreshore at N.E. of Robin Hoods Bay, Yorkshire	NZ 956056	A.H.
Jr	*Jamesoni*	*Taylori*	Foreshore below Hallaig, Raasay	NG 592390	A.H.
Iw	*Ibex*	*Luridum*	Quarry near Blockley Station, Warwickshire	SP 182371	A.H.
Dy	*Davoei*	*Figulinum*	Cliff at Castle Chamber, Yorkshire	NZ 960066	A.H.
Sr	*Spinatum*	*Apyrenum*	Cliff S. of Rudha na'Leac, Raasay	NG 600381	A.H.

Though abundant at certain horizons, gryphaeas are generally sparser in the higher zones and hence are less well represented in the collections than those from the lower zones. The earliest gryphaeas are considered to be the arcuatiform types that enter the succession in the upper *Angulata* Zone. The so-called *Gryphaea dumortieri* Joly that occurs spasmodically lower in the Hettangian is thought to be merely a gryphaeiform variant of *Liostrea* with a small attachment area. In its relatively weak incurvature and thinness of the left valve it is readily distinguishable from the *G. arcuata* group.

Table 3. Statistical data

		$L-B$			$\log L-\log B$			$L-H$			$\log L-\log H$		
sample	number	slope	intercept	coeff. of least squares fit	slope	intercept	coeff. of least squares fit	slope	intercept	coeff. of least squares fit	slope	intercept	coeff. of least squares fit
Sr	20	1·022	5·035	0·9437	0·8513	0·6135	0·9612	1·741	14·53	0·9311	0·8062	1·514	0·9527
Dy	31	0·9857	6·301	0·9708	0·8471	0·7047	0·9705	—	—	—	—	—	—
Iw	38	1·092	6·208	0·9683	0·9060	0·5668	0·9735	1·658	17·03	0·9430	0·7931	1·641	0·9508
Jy	54	1·125	2·256	0·9357	0·9784	0·2487	0·9539	1·721	11·78	0·8731	0·8076	1·429	0·9087
Jr	60	1·129	6·654	0·9017	0·9774	0·3548	0·9459	1·567	10·73	0·9473	0·7466	1·515	0·9553
Ol	90	1·414	−1·358	0·9780	1·078	0·0346	0·9867	1·522	6·401	0·9885	0·7737	1·334	0·9863
Ss	158	1·514	−3·182	0·8975	1·086	0·0386	0·9219	1·367	8·934	0·9634	0·7994	1·198	0·9689
Sg	85	1·715	−4·073	0·9717	1·109	−0·0742	0·9626	1·510	5·208	0·9834	0·8225	1·117	0·9871
Bgl	61	1·748	−6·230	0·9658	1·212	−0·3173	0·9834	1·340	8·594	0·9735	0·7274	1·441	0·9902
By	98	1·761	−5·617	0·9269	1·179	−0·1649	0·9481	1·366	7·849	0·9771	0·7696	1·271	0·9807
Ay	190	1·548	−2·063	0·9613	1·091	−0·0825	0·9650	1·562	3·416	0·9796	0·8171	1·086	0·9782
As-d	61	1·784	−6·124	0·9469	1·193	−0·2050	0·9615	1·525	4·888	0·9744	0·8576	1·006	0·9726
Ag	37	1·398	1·033	0·9196	1·037	0·2391	0·9456	1·676	3·463	0·9641	0·9065	0·8964	0·9744

II. Shell morphology

(1) *General features*

The most notable generic character is that the left valve is more or less strongly convex, with the umbo incurved and sometimes orthogyrous, though frequently it is opisthogyrous (figure 1). An area of attachment or cementation truncates the umbo, usually to a limited extent, signifying that the animal was free-lying during most of its benthonic life. Occasionally, however, the attachment area is large relative to the size of the left valve, rendering it ostraeiform in appearance. A radial sulcus on the posterior side of the valve, defining a posterior lobe, is variably developed (figure 1). The dorsal or umbonal part of the left valve may show pronounced thickening. The right valve is opercular in character and is flat or, more usually, concave. The surface is ornamented by growth rugae.

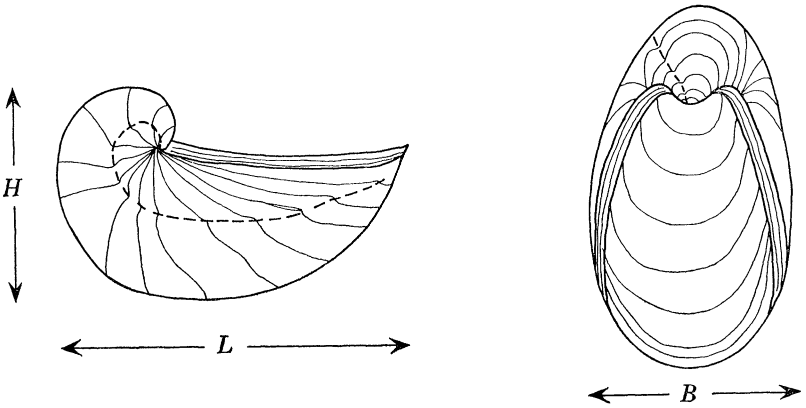

Figure 1. Diagram to illustrate general morphology of *Gryphaea* and the measurements used in the statistical analysis. L = length, H = height, B = breadth. Broken line indicates position of sulcus.

Underlying the umbo is a triangular ligament pit on a shelf with growth striae (there is a corresponding zone in the right valve). This signifies movement of the contained animal during growth away from the original hinge-line, as is clearly seen in modern oysters (Yonge 1960, p. 27). The shell is composed of calcite exhibiting crossed lamellar structure (Bøggild 1930). The ovoid shape viewed normal to the plane of commissure, and the subcentral, ovoid adductor muscle scar signify a closer relationship with *Ostrea* than with *Crassostrea*, among living oysters.

(2) *Area of attachment*

The size of the area of attachment of the left valve has been a subject of great interest since Trueman suggested a systematic change up the succession. It also has an important bearing on the measurement of shape because a high incidence of shells with large attachment areas would seriously interfere with the measurement of curvature in a given sample. Furthermore, Joysey (1959) has suggested that a study of this feature in young and adult shells might show whether or not there existed significant differences between 'unsuccessful' individuals and those that survived to maturity; such a difference might signify the operation of natural selection.

The length of the attachment area was measured parallel to the length of the valve in ten of the thirteen samples, and length-frequency distributions are plotted in figures 2 and 3. Figure 2 includes samples from the older horizons, from the *Angulata* to the *Semicostatum* Zone, and figure 3 younger ones, from the *Obtusum* to the *Ibex* Zone.

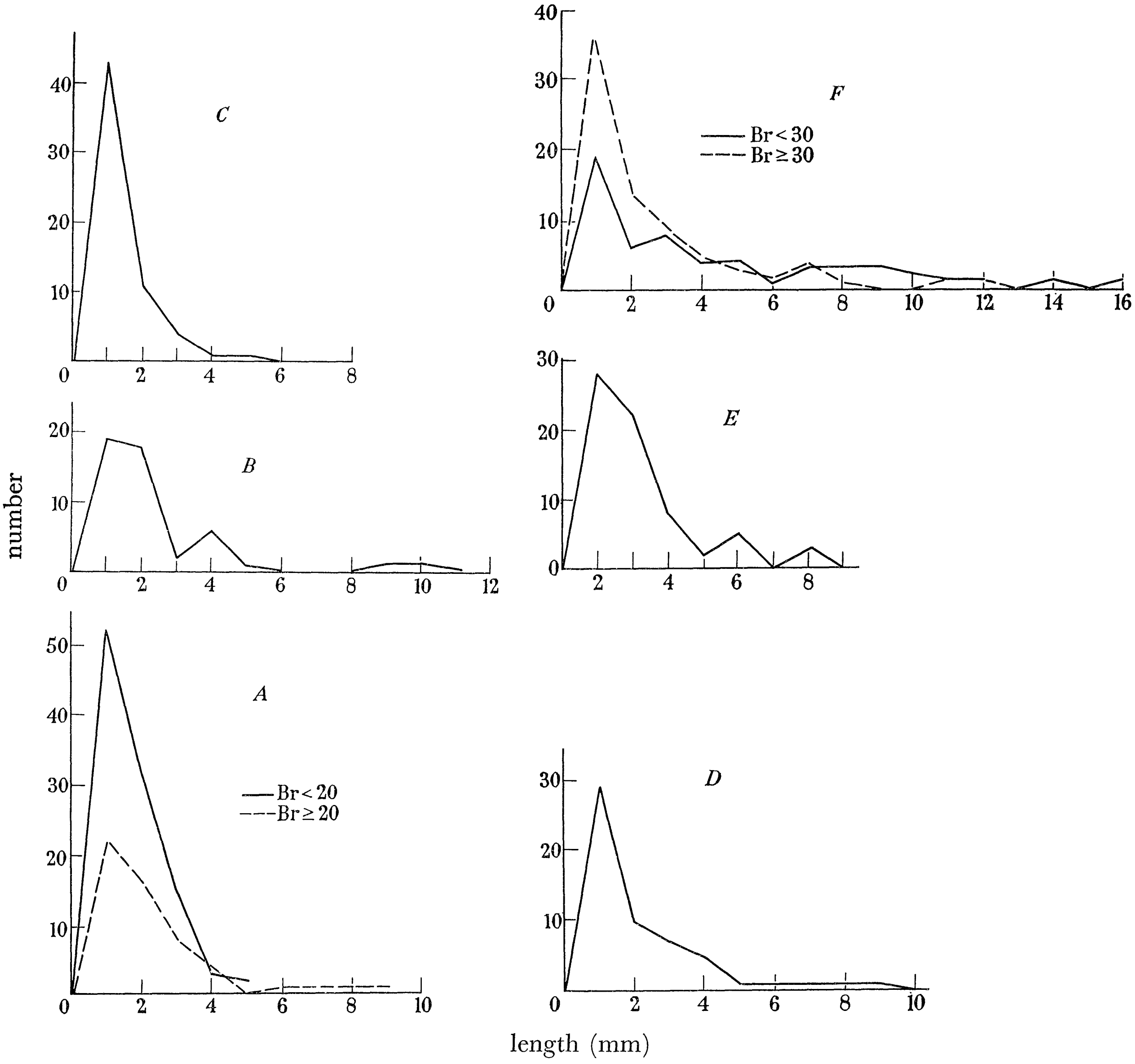

FIGURE 2. Length-frequency distributions of attachment area of left valve for earlier zonal samples of *Gryphaea*. *A* = *Angulata*, Yorks., *B* = *Angulata*, Somerset–Dorset, *C* = *Buckandi*, Yorks., *D* = *Bucklandi*, Gloucs., *E* = *Semicostatum*, Glamorgan, *F* = *Semicostatum*, Skye.

It is readily apparent from figure 2 that, for the older gryphaeas, there is a strong mode at 1 to 2 mm, above which a sharp fall-off signifies that only a minute fraction has an attachment area sufficiently large to obscure the incurved form of the shell. Similar modal values were obtained by Swinnerton (1939, fig. 5) and McLennan & Trueman (1942, fig. 5) for gryphaeas from the *Bucklandi* Zone of Fretherne and the *Semicostatum* Zone of Loch Aline respectively. There is no difference between the *Angulata*, *Bucklandi* and

Semicostatum horizons, as might have been predicted if Trueman's hypothesis were correct. The younger gryphaeas (figure 3) have a notably wider spread in size of attachment area, with a high proportion showing values up to 8 mm.

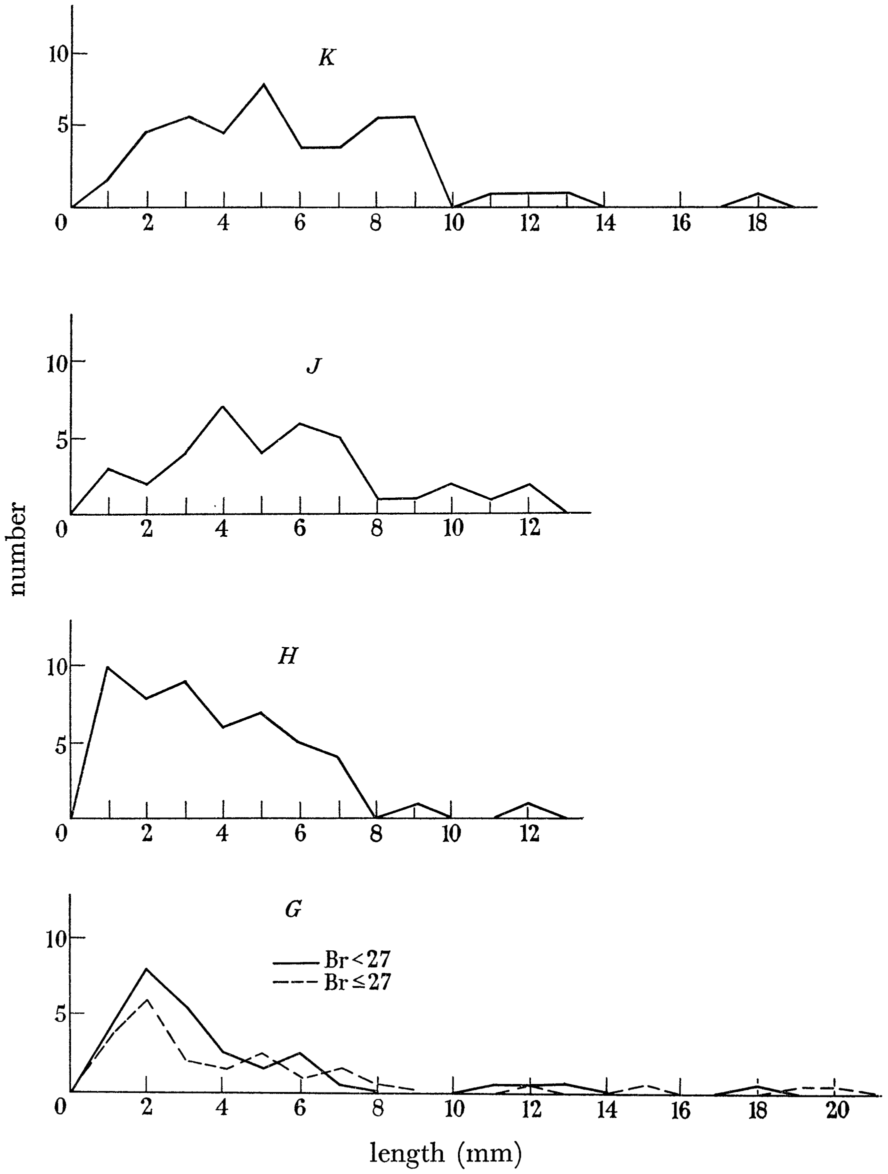

FIGURE 3. Length-frequency distribution of attachment area of left valve for later zonal samples of *Gryphaea*. *G* = *Obtusum*, Lincs., *H* = *Jamesoni*, Raasay, *J* = *Ibex*, Warwicks., *K* = *Jamesoni*, Yorks.

In three samples it proved possible to test adequately for a selection effect by dividing specimens into two sizeable groups, on either side of a mean value for the sample as a whole. For this purpose, breadth was taken as a more reliable measure of shell size than length, because of the distortion produced by large attachment areas. In all three cases, from the *Angulata* Zone, Yorkshire, the *Semicostatum* Zone, Skye and the *Obtusum* Zone, Lincolnshire, the modes for the larger and smaller subsamples are identical, signifying that natural selection with regard to this character is imperceptible.

(3) *Statistical analysis of shape of left valve*

It appears upon qualitative inspection that gryphaeas from the higher Liassic zones differ markedly from those from the lower zones in two important respects—the left valves are relatively broader and less incurved. Those from certain intermediate zones are, moreover, more or less intermediate in character.

These changes are readily amenable to statistical analysis, the three necessary measurements of length, breadth and height (figure 1) being quickly undertaken using vernier calipers. Plotting length against breadth gives, of course, a measure of relative breadth. The height:length relationship is, perhaps less obviously, a measure of degree of incurvature. It was first shown by D'Arcy Thompson (1917) that the spiral angle $\propto$ can be determined accurately from these two measures (see § II (4)).

As both L and H can be more accurately and quickly determined than the periphery P and radius R, the former are better parameters to measure than those I employed previously. The only qualification is that specimens with large areas of attachment give misleading data. However, as has been shown, these form only a very small proportion of the samples and have been neglected in the analysis to be described. A small minority of specimens, on which only two of the three parameters mentioned are measurable, are represented in the graphical plots (figures 6 to 19) but not included in the statistics. Care was taken to avoid measuring specimens whose shape had been distorted through crushing (cf. Burnaby 1965).

Before progressing further it is desirable to deal with an objection Burnaby (1965) makes against the conventional type of regression analysis employed in the study of fossil populations. He states that it is essential where possible to obtain data relating to the early growth stages of individual specimens, because no sample of single sets of 'adult' measurements can convey any direct information concerning the law of individual growth. Without such information he claims that one cannot define a truly growth-invariant measure of shell coiling.

The growth of individuals can readily be studied by cutting median longitudinal sections and marking out the growth lines. The specimen illustrated in figure 4 was selected as a representative adult of the sample from the *Bucklandi* Zone, Gloucestershire. Other sectioned specimens confirm that the pattern of growth lines so revealed is normal (note also the resemblance to the sectioned specimen illustrated by McLennan & Trueman (1942, fig. 4). Measurements of L, H, P and R were made on the illustrated specimen, and the results are plotted in figure 5. A comparison with figure 10 shows that the L:H scatter diagram gives a reliable indication of the growth of individual specimens. The same is true of the P:R relationship (cf. Hallam 1963, figs. 1 and 2).

Furthermore, the earliest and latest gryphaeas in this study are strikingly distinct (compare, for instance, figures 6, 18 and 19 and plates 10 and 12) and statistics are primarily required for greater precision and for distinguishing relatively subtle changes, as between adjacent zones or different geographical regions at the same zonal horizon. This is in marked contrast to my P:R studies of the early gryphaeas, which look much alike, except for size, on qualitative inspection. Accordingly statistics played a dominant role in the controversy.

Previously, the regression of R on P was studied by the reduced major axis method. A similar method of regression analysis has been undertaken with the L, H, and B measurements, using a KDF 9 computer. Both linear and logarithmic relationships were analysed, the best fit being determined by the coefficient of least squares method. Using mean

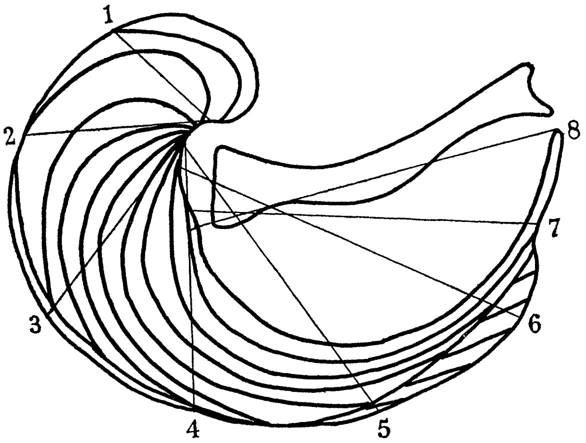

FIGURE 4. Diagram to illustrate the changing pattern of growth lines of *Gryphaea arcuata*. Traced from actual specimen which had been sectioned longitudinally. Compare figure 5.

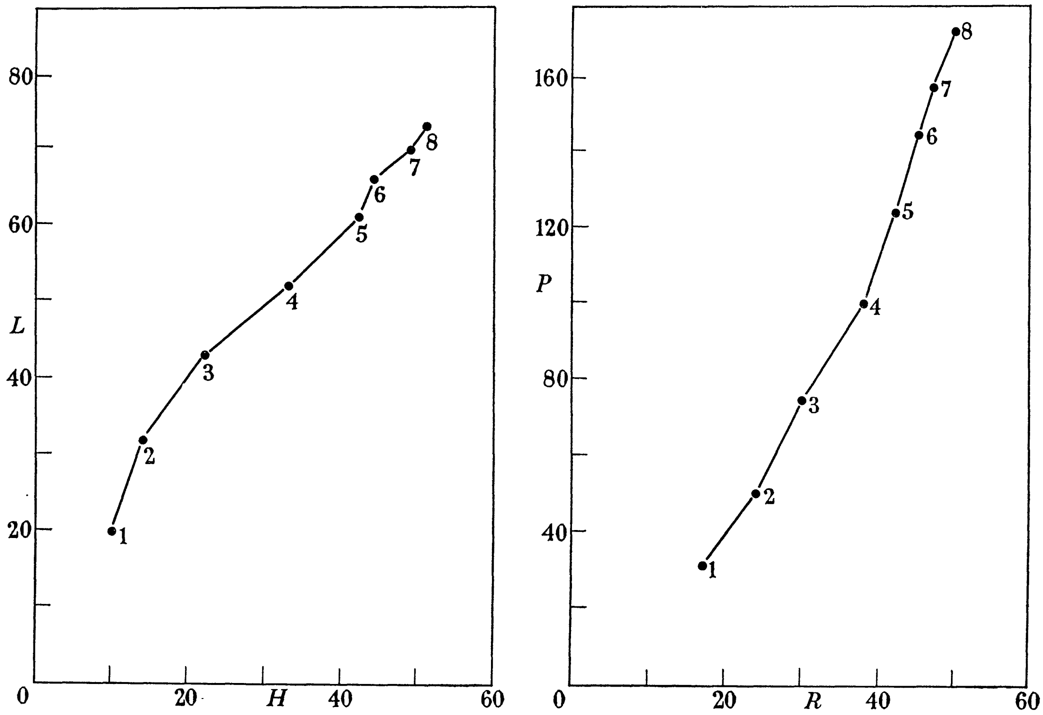

FIGURE 5. Length–height and periphery–radius relationships of sectioned *Gryphaea* of figure 4.

and variance data, significant differences for slope and intercept between different samples at the 5 % probability level were determined. The *Angulata* Zone specimens of Somerset and Dorset are pooled for the same reasons as formerly (Hallam 1960); in the case of the sample from the *Davoei* Zone, Yorkshire, it was not possible to determine height accurately

TABLE 4. STATISTICAL COMPARISON OF SAMPLES

Slope	log $L-\mathrm{H}$	log $L-B$
Intercept	log $L-H$	log $L-B$

N = Difference not significant
S = Difference significant

Samples	Sr	Dy	Iw	Jy	Jr	Ol	Ss	Sg	Bgl	By	Ay	As-d	Ag
Sr													
Dy	— N — N												
Iw	N N N N	— N — N											
Jy	N S N S	— S — S	N S N S										
Jr	N S N S	— S — S	N S N S	N N N N									
Ol	N D S S	— S — S	N S N S	N S N S	N S N S								
Ss	N S S S	— S — S	N S S S	N N S S	N N S S	N N N N							
Sg	N S S S	— S — S	N N S S	N S S S	S N S S	N N S N	N N N N						
Bgl	S S N S	— S — S	S S N S	S S N S	N S N S	N S N S	S S N S	S N S S					
By	N S S S	— S — S	N S S S	N S S S	N S S S	N N N S	N N N S	N N N N	N N S N				
Ay	N S S S	— S — S	N S S S	N N S S	S N S S	N N S N	N N N N	N N N N	S N S S	S N S N			
As-d	N S S S	— S — S	S S S S	N S S S	S S S S	S S S S	N S S S	N N N N	S N S N	S N S N	N N N N		
Ag	S S S S	— S — S	S S S S	S N S N	S N S N	S N S S	S N S S	S N N S	S S S S	S S S S	S N N S	N S N S	

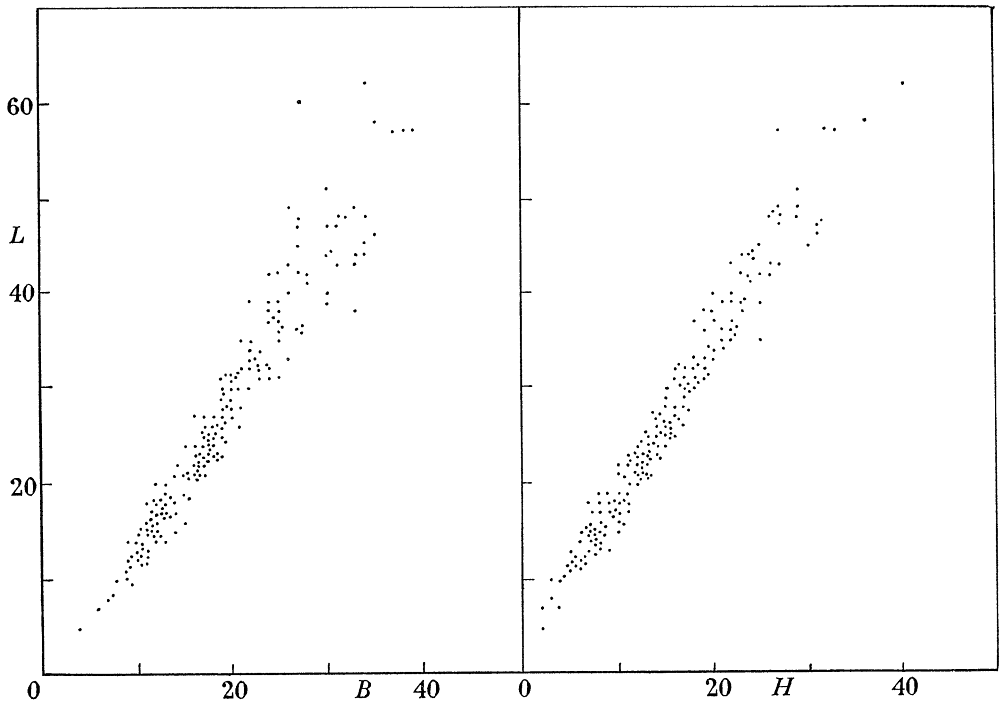

Figure 6. Scatter diagram showing relationship of length (*L*) to breadth (*B*) and height (*H*) in sample from *Angulata* Zone, Yorks.

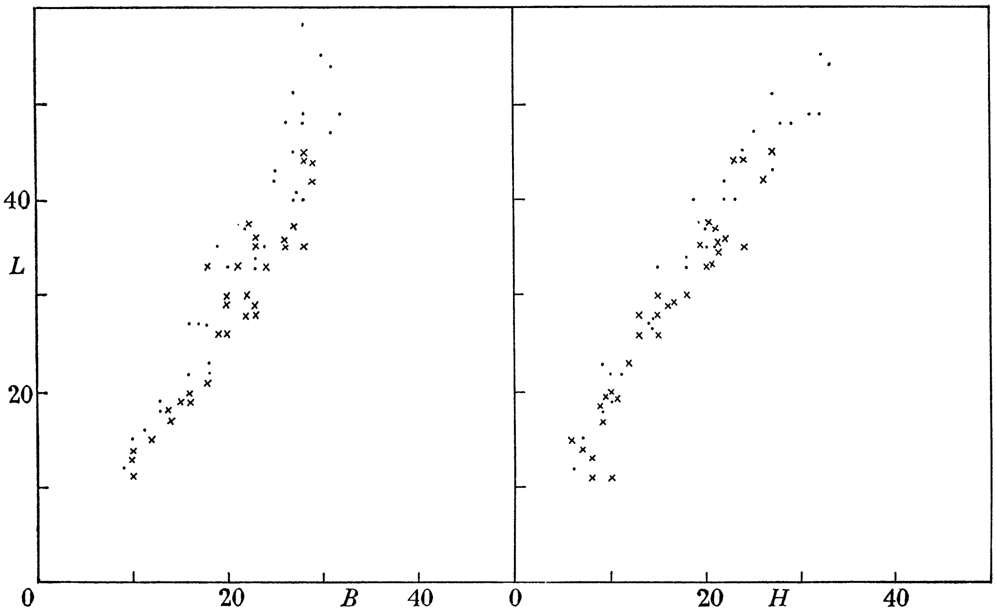

Figure 7. Scatter diagram cf. figure 6 for sample from *Angulata* Zone, Somerset–Dorset. Dorset specimens signified by crosses.

because of crushing and partial loss of shell. The basic results are presented in tables 3 and 4.

For many of the samples whose scatter diagrams are shown in figures 6 to 19, a simple linear fit is suggested upon inspection. Indeed, the coefficient of least squares fits are consistently high, and for most practical purposes no serious misinterpretation would result

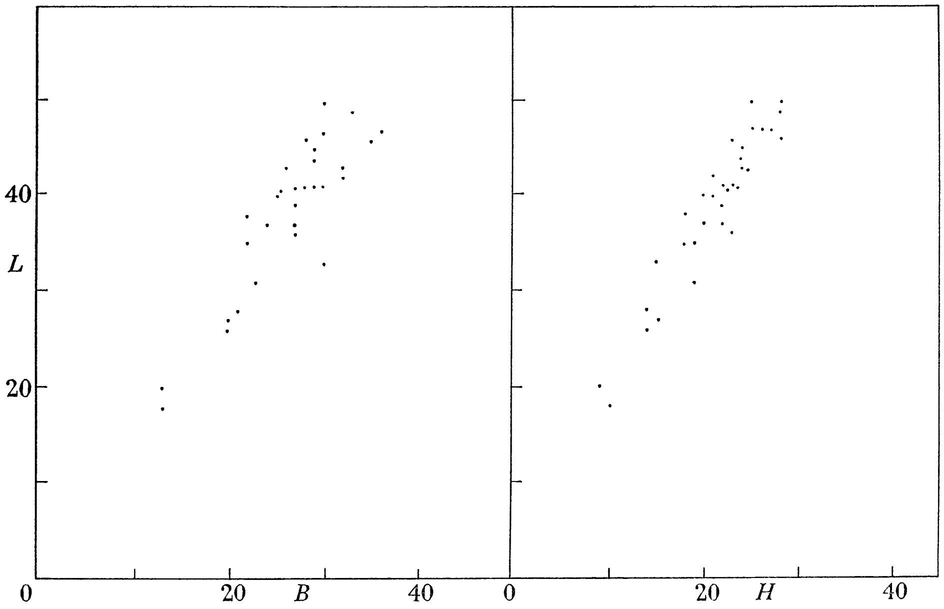

FIGURE 8. Scatter diagram cf. figure 6 for sample from *Angulata* Zone, Glamorgan.

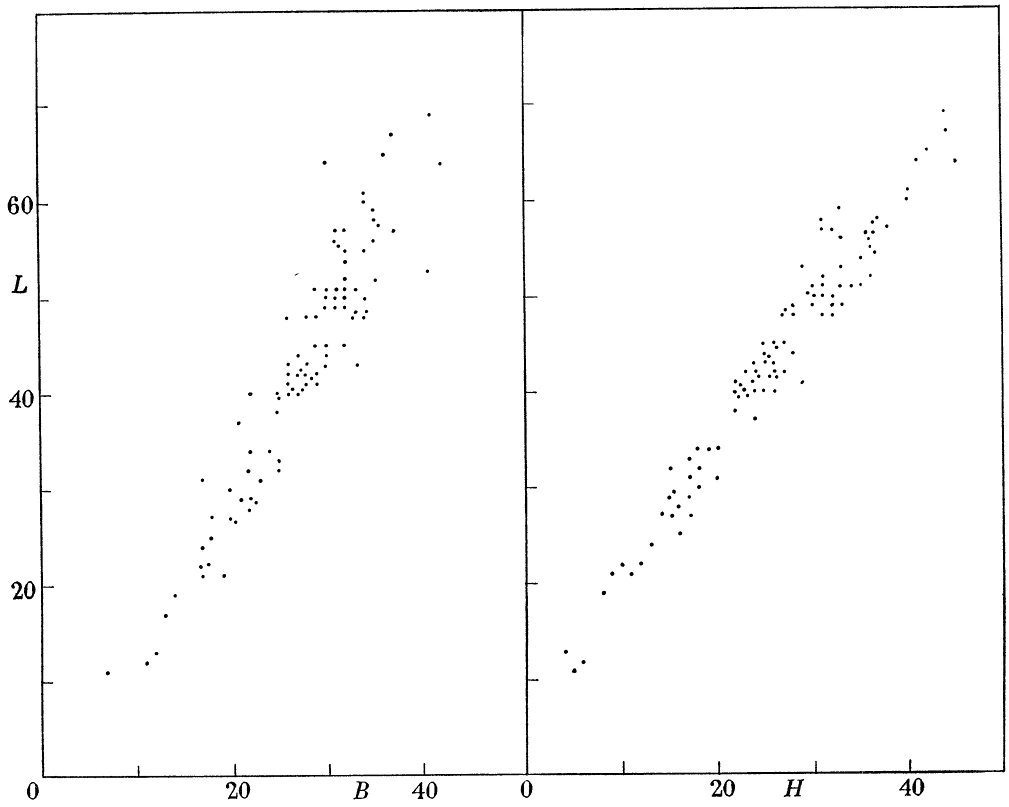

FIGURE 9. Scatter diagram cf. figure 6 for sample from *Bucklandi* Zone, Yorkshire.

if linear relationships were assumed. However, table 3 shows that the coefficient of least squares fits for the relationships of logarithmic values are usually even higher, and in the minority of instances where they are not the differences are very slight. Apparent linearity may result from the lack of a wide size range, with juveniles under-represented. Therefore, the

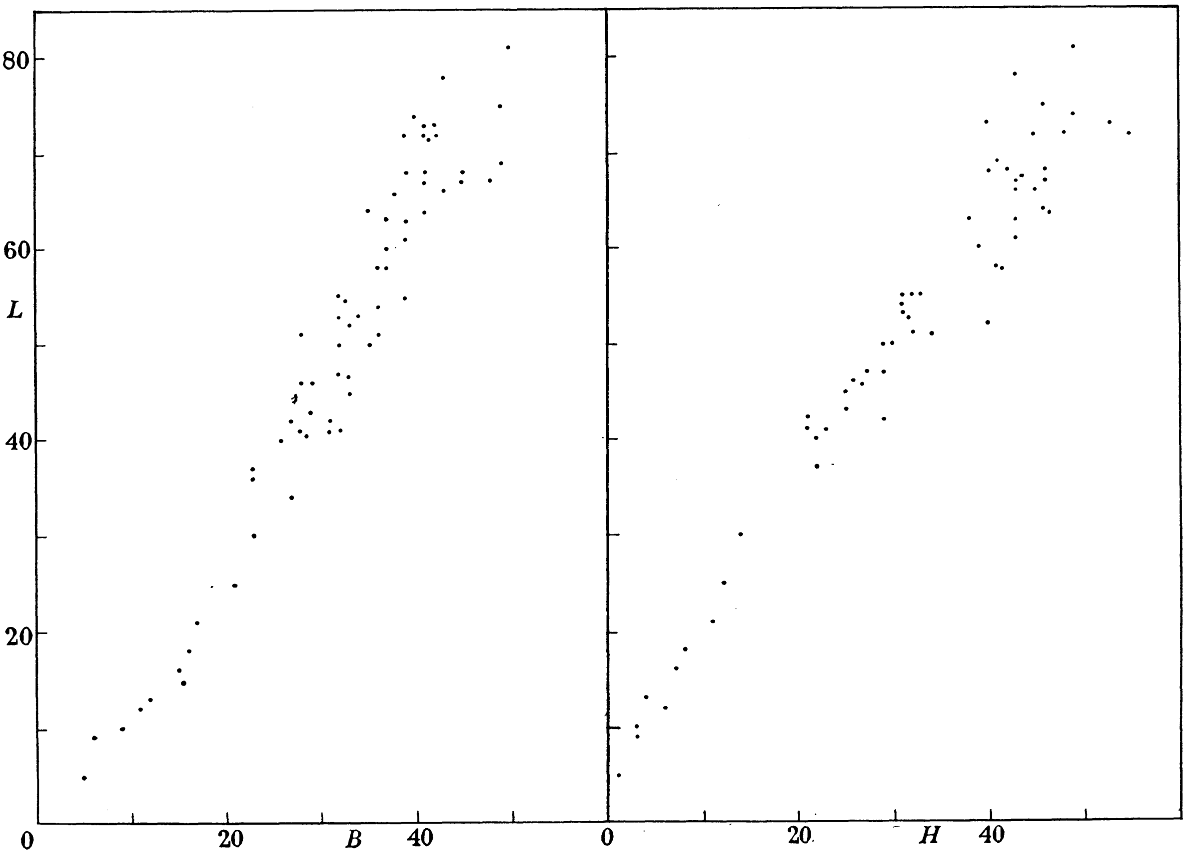

FIGURE 10. Scatter diagram cf. figure 6 for sample from *Bucklandi* Zone, Gloucs.

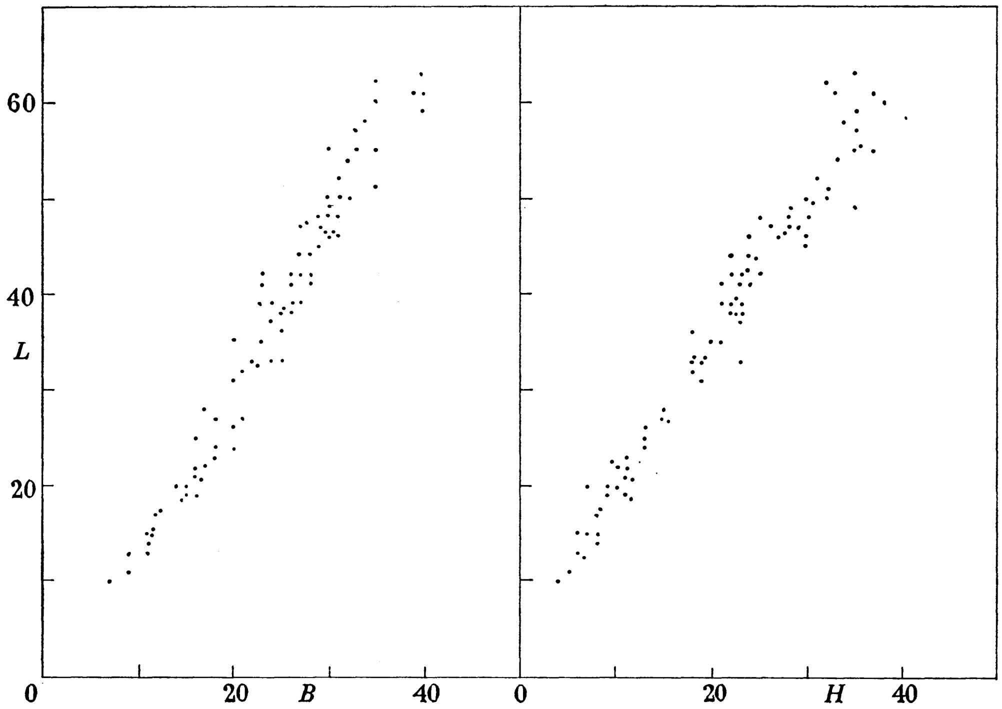

FIGURE 11. Scatter diagram cf. figure for sample from *Semicostatum* Zone, Glamorgan.

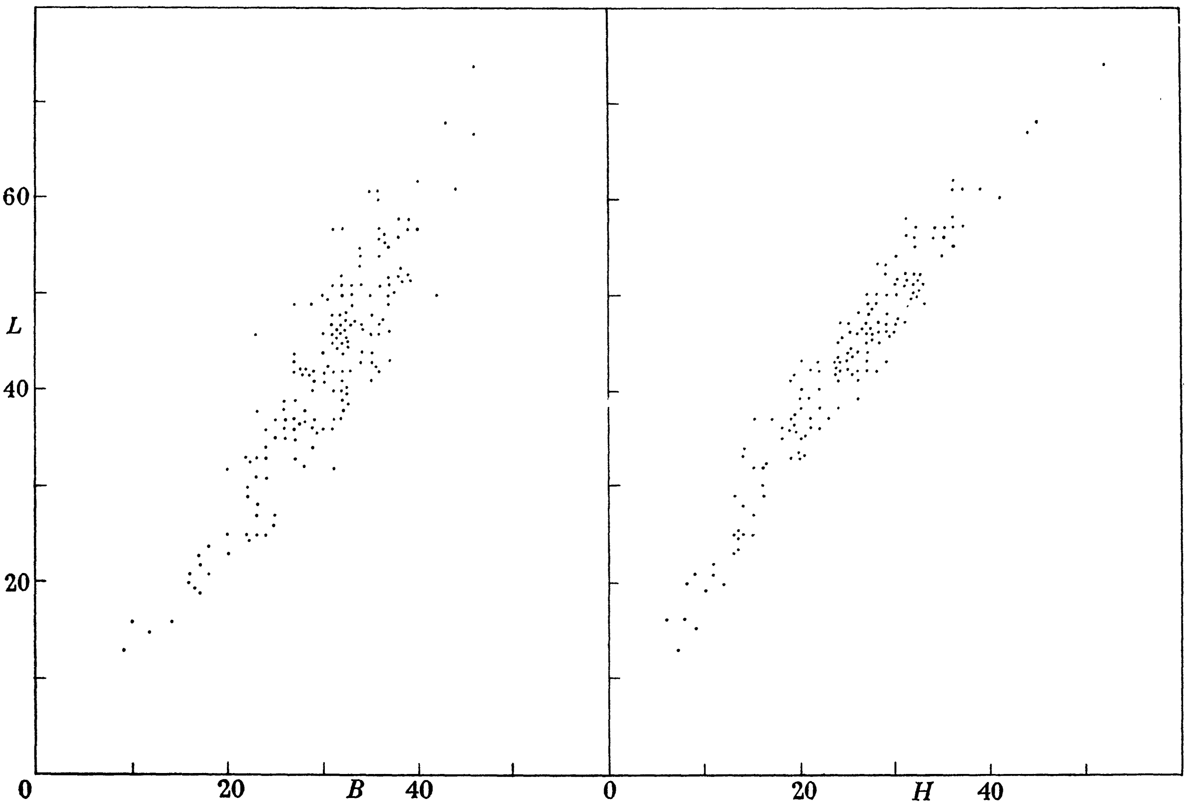

FIGURE 12. Scatter diagram cf. figure 6 for sample from *Semicostatum* Zone, Skye.

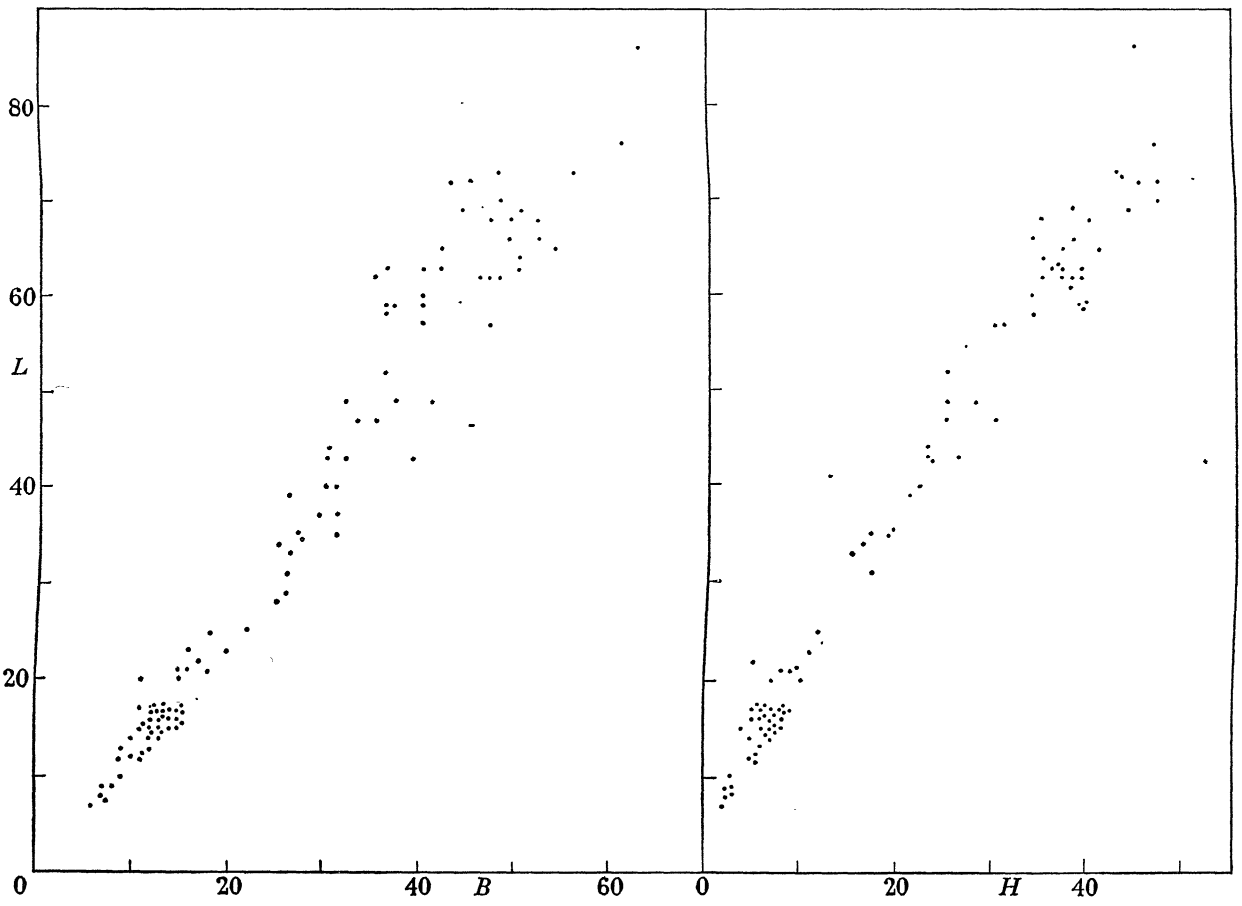

FIGURE 13. Scatter diagram cf. figure 6 for sample from *Obtusum* Zone, Lincs.

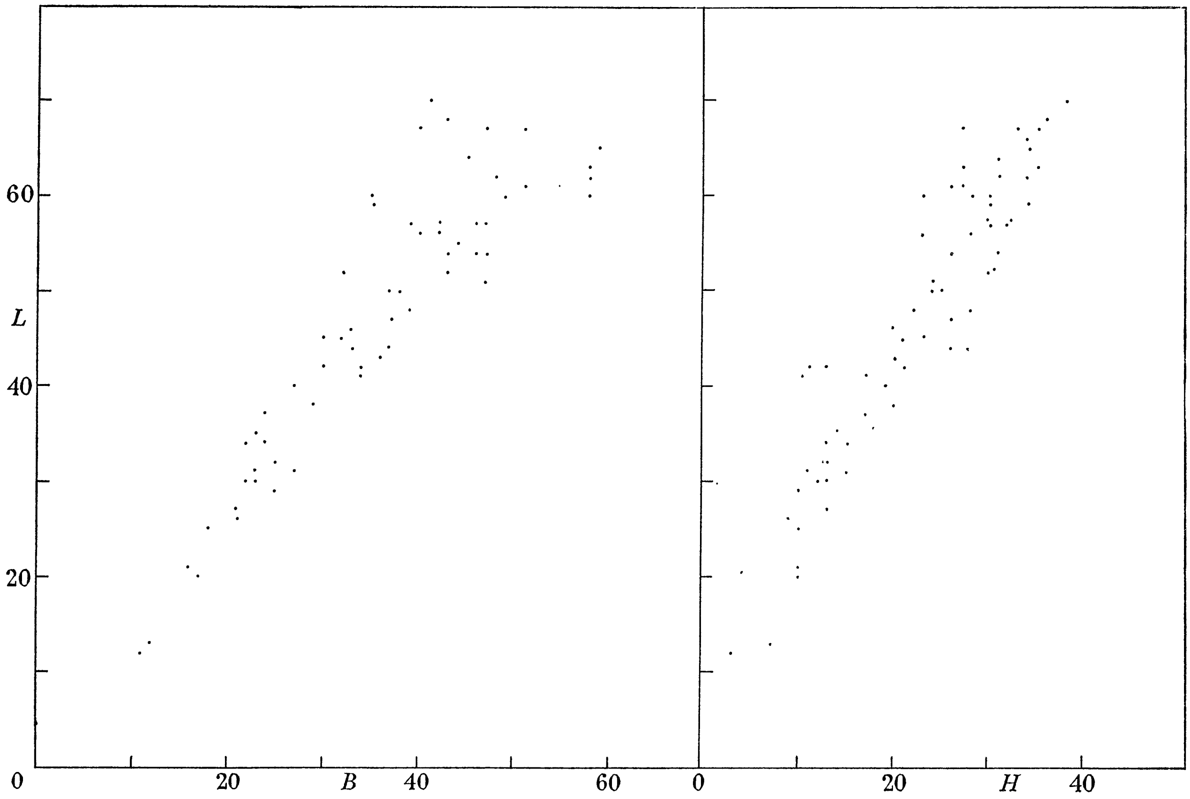

FIGURE 14. Scatter diagram cf. figure 6 for sample from *Jamesoni* Zone, Raasay.

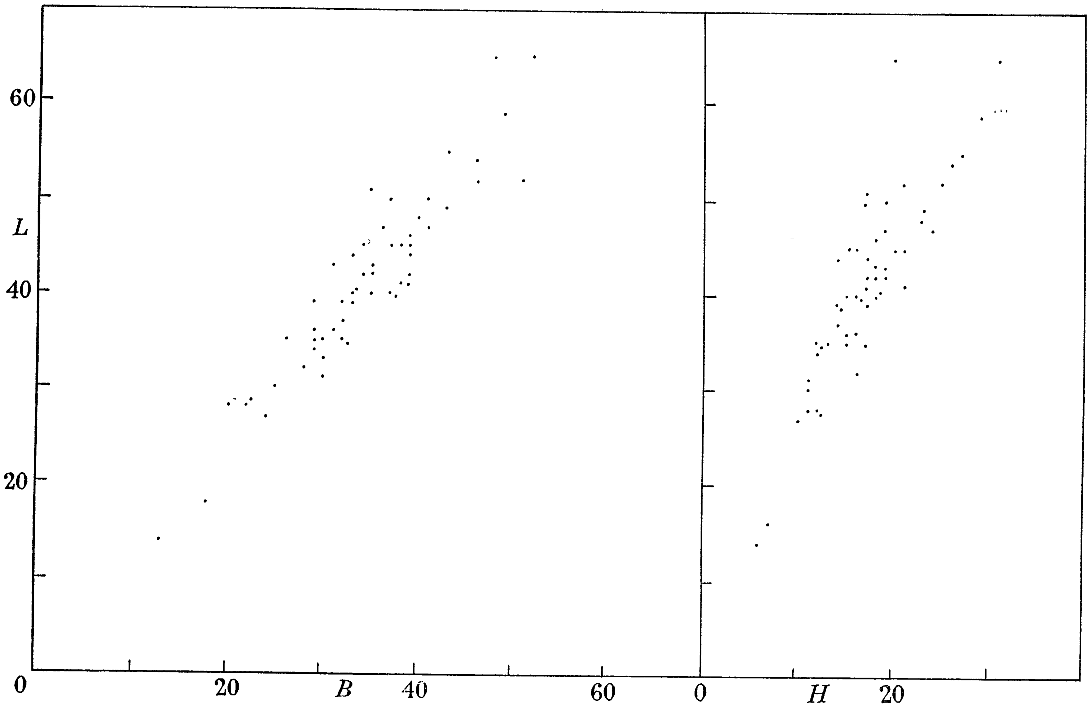

FIGURE 15. Scatter diagram cf. figure 6 for sample from *Jamesoni* Zone, Yorks.

relationships of $L{:}H$ and $L{:}B$ are more accurately described as exponential, and can be represented by the equation,

$$L = 10^{i} \log (H \text{ or } B)^{s},$$

where s = slope and i = intercept.

Accordingly, in table 4 the determination of significant differences is based upon logarithmic data, but substantially similar results are obtainable from the normal data.

We can now use the information provided in tables 3 and 4 to compare the samples both geographically and stratigraphically.

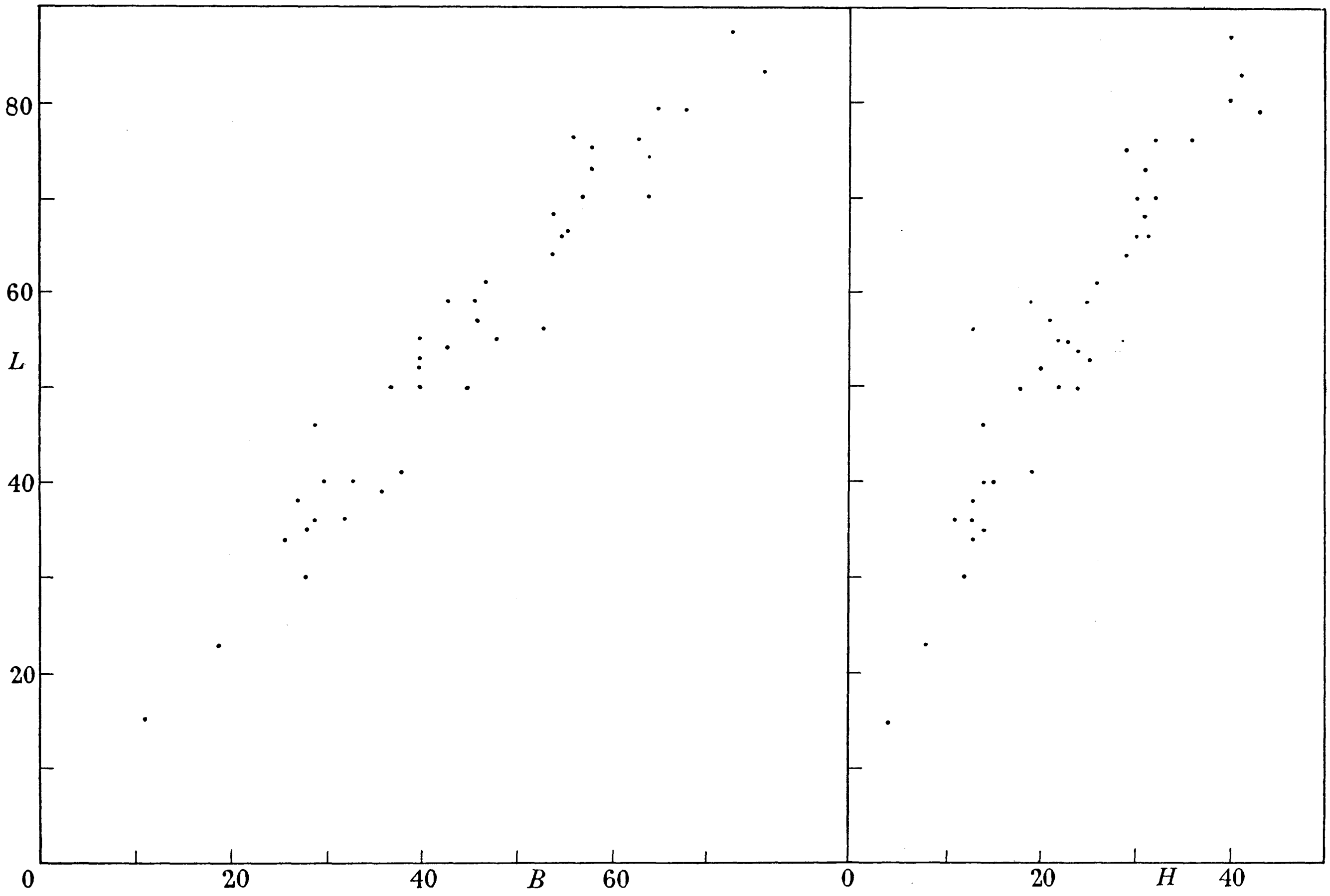

Figure 16. Scatter diagram cf. figure 6 for sample from *Ibex* Zone, Warwicks.

The *Angulata*, Yorkshire (Ay) and *Angulata* Somerset–Dorset (As-d) samples resemble each other, but the *Angulata*, Glamorgan (Ag) specimens are relatively less incurved than those of Ay and relatively broader than As-d. The $L{:}B$ intercept of Ag is also higher than Ay. It is interesting to note that Philip (1962), in his study of $P{:}R$ relationships, deduced that the *Angulata* Zone sample from Glamorgan was abnormal.

To all intents and purposes the *Bucklandi* and *Semicostatum* Zone samples may be considered to come from the same horizon, since they belong to stratigraphically adjacent subzones. The *Bucklandi*, Yorkshire (By), *Semicostatum*, Glamorgan (Sg) and *Semicostatum*, Skye (Ss) samples are almost identical, but the *Bucklandi*, Gloucestershire (Bgl) specimens differ notably from those of Sg and Ss in being narrower and more incurved, but differ only slightly from By specimens in the $L{:}H$ intercept value.

The relationships of the samples from the *Angulata* Zone on the one hand and the *Bucklandi–Semicostatum* Zone on the other are of particular importance in view of the controversy of recent years. The As-d specimens are less incurved than those of By and Bgl (i.e. $L:H$ slope is steeper) but not Sg or Ss, although the trend is in this direction. The Ag specimens are less incurved than any others and Ay less incurved than Bgl. There is little difference in relative breadth, except that Ag and to a lesser extent Ss specimens are broader. These results offer some support to Philip's (1962) contention that there is a discernible increase in tightness of coiling up the succession, but the general picture is complicated, with geographical differences seemingly as important as stratigraphical ones.

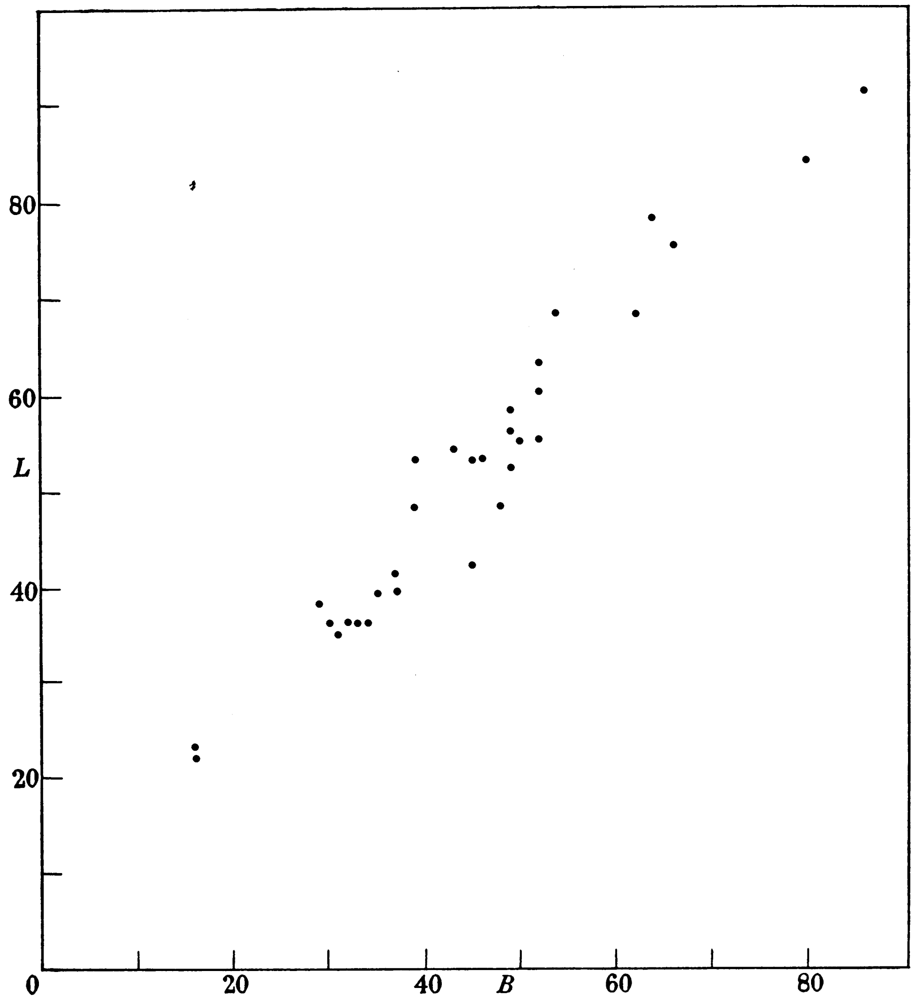

FIGURE 17. Scatter diagram showing length–breadth relationship for sample from *Davoei* Zone, Yorks.

The *Obtusum*, Lincolnshire (Ol) sample is indistinguishable statistically from that of Ss, and differs only slightly from Sg, By and Ay. Likewise, the difference from the *Jamesoni* Samples of Yorkshire (Jy) and Raasay (Jr) is not great, the specimens being somewhat less broad. Jr and Jy resemble each other, but the *Ibex*, Warwickshire (Iw) specimens are broader.

There is a trend towards lesser incurvature in the stratigraphically younger Iw sample, expressed in intercept value, which becomes significant in higher zones. The *Davoei*, Yorkshire (Dy) and *Spinatum*, Raasay (Sr) samples also show a significant trend towards

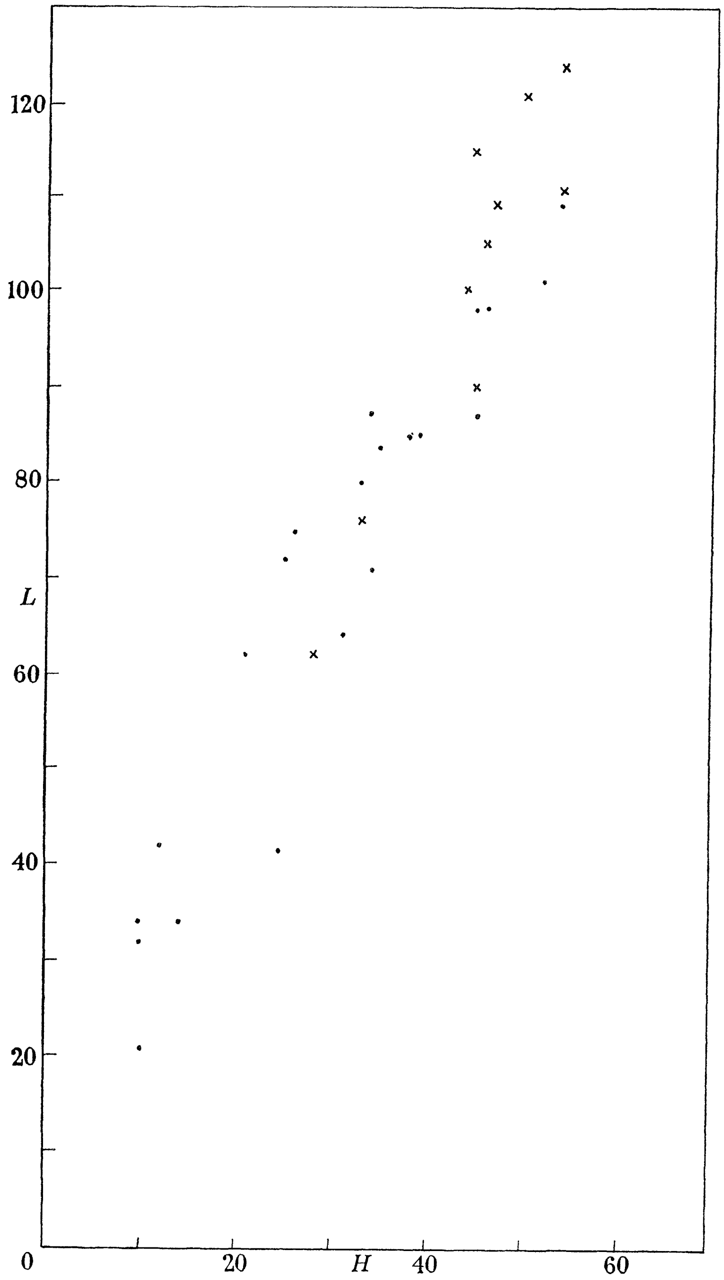

FIGURE 18. Scatter diagram showing length–height relationship for sample from *Spinatum* Zone, Raasay. Crosses signify British Museum specimens of U. Pliensbachian age from Gloucestershire and Somerset.

greater roundness than those in the *Jamesoni* Zone. The Iw sample looks intermediate in this respect but is not significantly different from Dy or Sr. The only accurate geographical comparison possible in these higher zonal samples is between Jy and Jr; they are statistically identical. In figures 18 and 19, however, plots of data from gryphaeas of *Margaritatus* or *Spinatum* Zone age from Gloucestershire and Somerset indicate that they could have come from the same population as the more or less contemporaneous Raasay specimens.

The general trend of change up the succession is brought out by figure 20. L:H and L:B regression lines have been plotted from the data given in table 3. This is more meaningful than plotting logarithmic values, since comparison can readily be made with the scatter diagrams and is accurate enough for the purpose of graphical illustration (the reader can confirm for himself that plotting the logarithmic data gives similar results). To avoid crowding, only data from six stratigraphically representative samples have been illustrated.

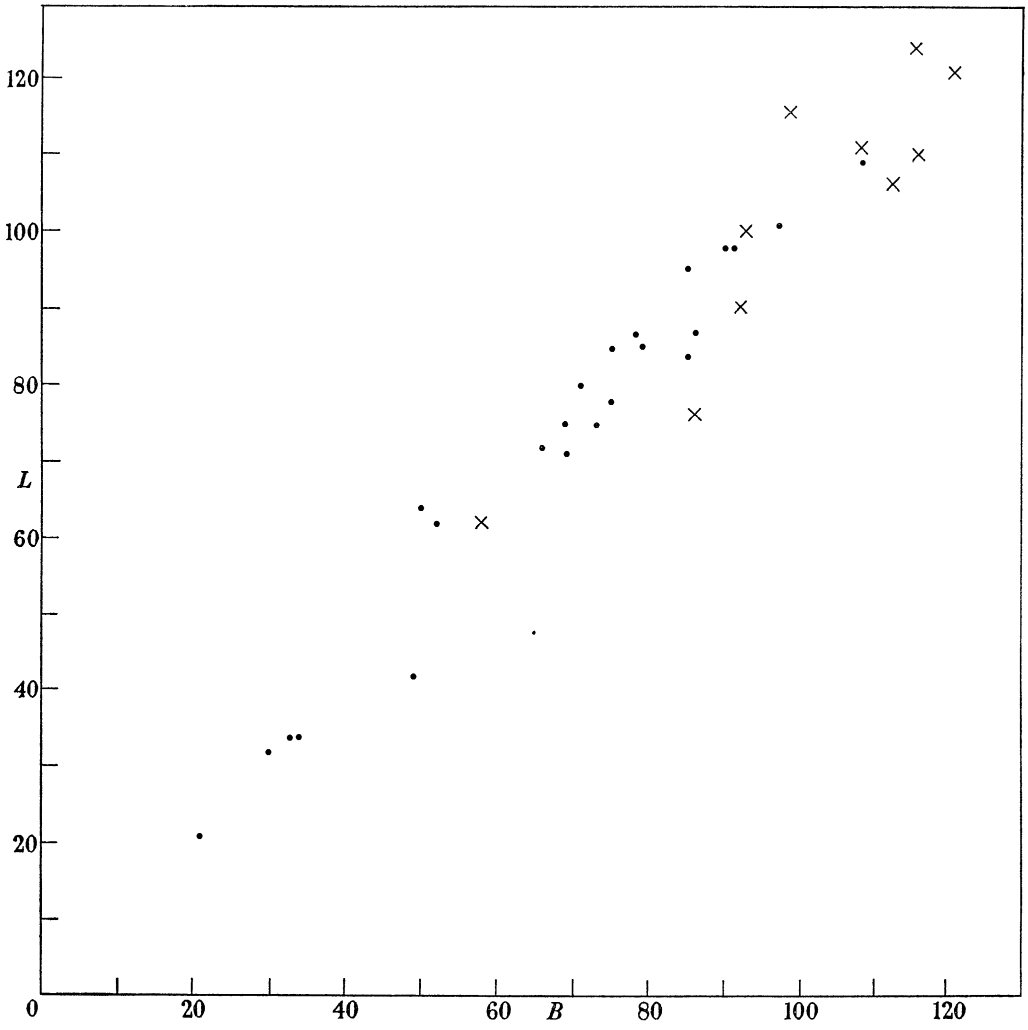

FIGURE 19. Scatter diagram showing length–breadth relationship for sample from *Spinatum* Zone, Raasay. Crosses signify British Museum specimens of U. Pliensbachian age from Gloucestershire and Somerset.

Figure 20 clearly indicates the two major trends up the succession. As the shells become relatively broader, there is a tendency towards a progressive ‘clockwise rotation’ of the regression lines approximately about a pivotal position in the region $L = 20$, $B = 15$ mm. The decrease in tightness of coiling or incurvature is expressed primarily by an increase in the $L:H$ intercept values, with only a slight increase in slope. The only notable anomaly in this simple pattern is that the *Bucklandi* sample is slightly more incurved than the *Angulata*. Compared with these striking trends, geographical variations are negligible, but we have seen that they may assume importance if only one or two adjacent ammonite zones are considered.

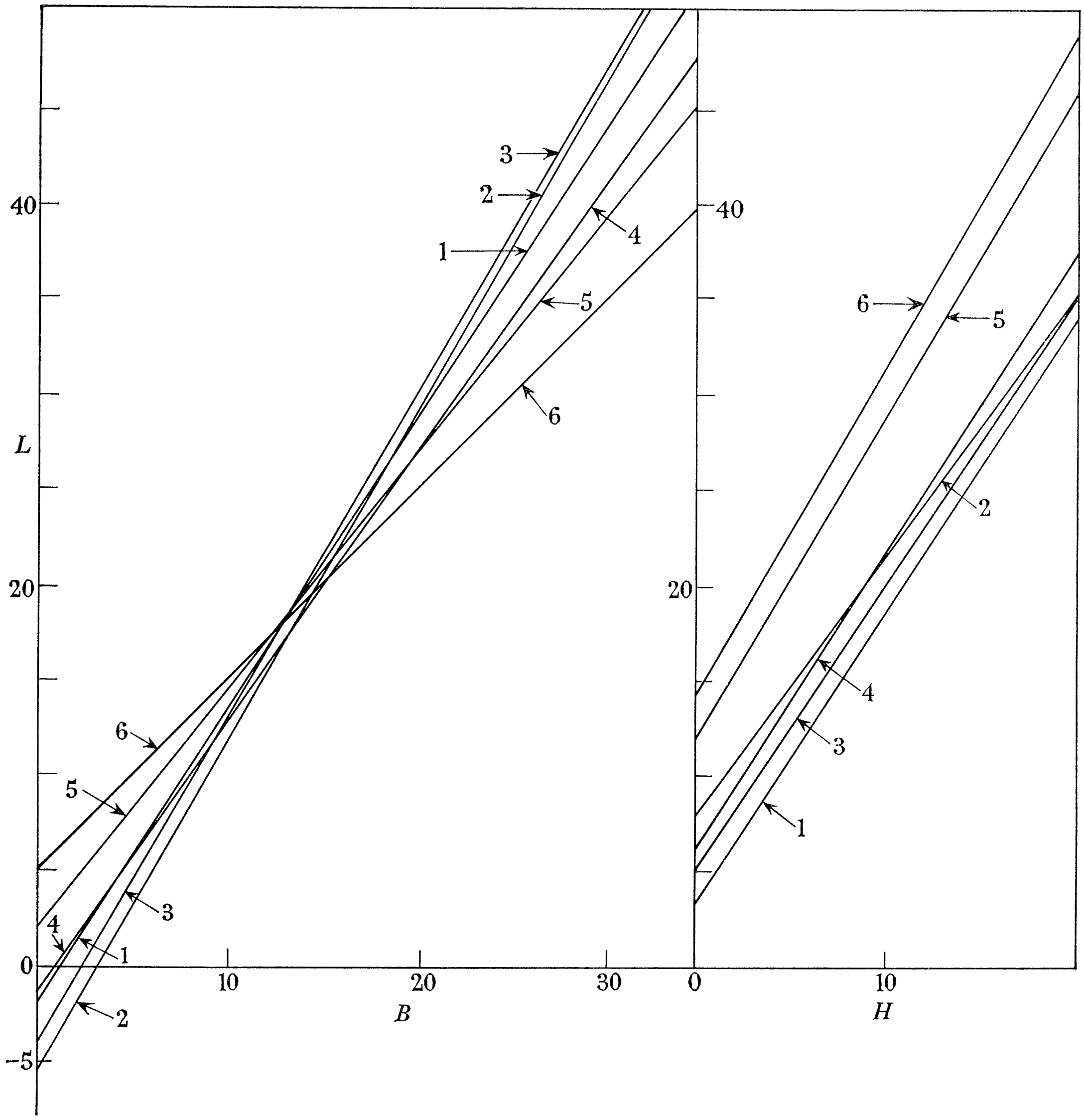

FIGURE 20. L–B and L–H regression lines for selected samples of *Gryphaea*. 1 = *Angulata* Zone, Yorks., 2 = *Bucklandi* Zone, Yorks., 3 = *Semicostatum* Zone, Glamorgan, 4 = *Obtusum* Zone, Lincs., 5 = *Jamesoni* Zone, Yorks., 6 = *Spinatum* Zone, Raasay.

(4) *Spiral angle*

Since D'Arcy Thompson (1917, p. 577) first made the suggestion that the left valve of *Gryphaea* corresponded to a logarithmic spiral, the spiral angle, i.e. the acute angle between the radius and a tangent to the shell, has been the subject of much discussion. If *Gryphaea* grows as a logarithmic spiral then the spiral angle should remain constant during ontogeny. If, however, the spiral angle increases during ontogeny, as the results of McLennan and

Trueman (1942) suggest, then this is an expression of increase in the tightness of coiling signifying allometric growth.

The spiral angle ∝ can be determined accurately from the equation.

$$\cot \propto = \frac{2 \log L/H}{\log e}.$$

(In the paper of McLennan & Trueman there is a misprint, with the positions of H and L reversed.)

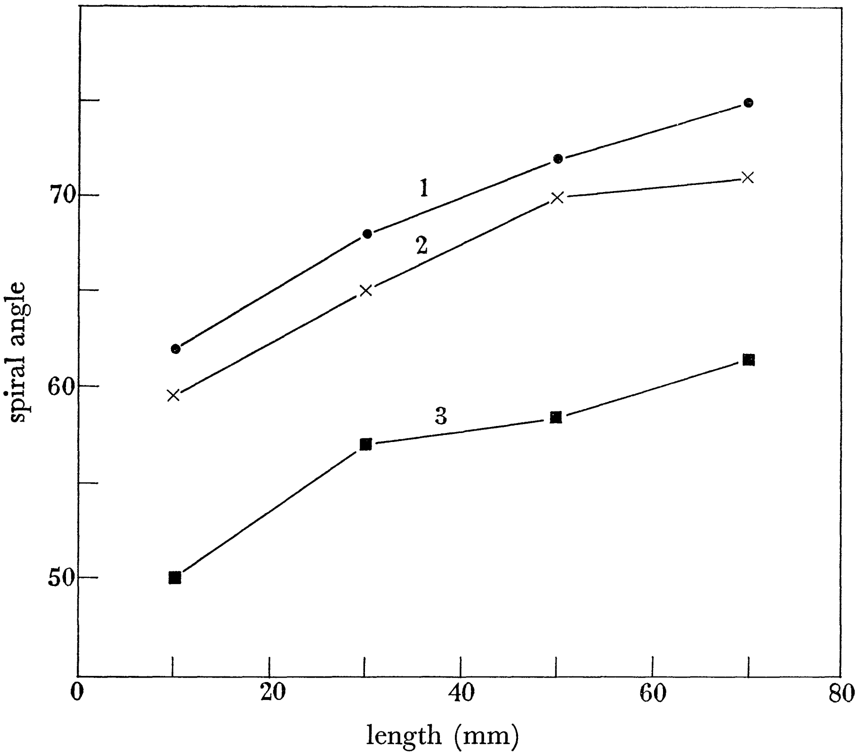

Figure 21. Diagram to illustrate change of spiral angle with growth, using sample mean values. 1 = *Bucklandi* Zone, Gloucs., 2 = *Obtusum* Zone, Lincs., 3 = *Ibex* Zone, Warwicks.

Three samples representing different horizons, Bgl, Ol and Iw, were chosen for detailed study. Mean values of H at lengths of 10, 30, 50 and 70 mm were taken and the spiral angle for each group computed. The results are plotted in figure 21. All three samples show a progressive increase in spiral angle with size, signifying that growth does not conform closely to a logarithmic spiral. Other points to note are that the rate of increase tends in a general way to slow down with age, and that the absolute values of spiral angle for a given size decrease up the succession. This is of course merely another expression of the degree of incurvature previously discussed.

McLennan & Trueman (1942), using a similar method of calculation for specimens from the *Semicostatum* Zone, obtained values of 71 to 81° for the spiral angle of adult specimens. This agrees fairly well with the results for the Bucklandi specimens illustrated in figure 20, allowing for the fact that they only measured specimens ranging in length from about

40 to 70 mm. That the progressive change in spiral angle with size related to individual ontogeny is readily confirmed by the study of sectioned adult specimens such as that illustrated in figure 4.

III. Systematics

In this section the relatively brief written descriptions should be consulted in conjunction with both the photographic illustrations and the graphical plots of figures 6 to 19, which convey information on range of shape variation better than lengthy verbal accounts.

(1) Genus *Gryphaea* Lamarck, 1801

(*a*) *Gryphaea arcuata* Lamarck

Remarks. This is the type species of the genus (see opinion 338 of International Commission of Zoological Nomenclature).

In the absence of a specimen, L. R. Cox has accepted as lectotype figure 92, plate 15 of Bourguet's *Traité de Pétrifications* (1778). This illustration accords well with the interpretation of *G. arcuata* of Schäfle (1929), whose work should be consulted for a comprehensive survey, with extensive synonym lists, of European Liassic gryphaeas.

As regards the British specimens, the name may be used for those gryphaeas of late Hettangian and early Sinemurian age with strongly incurved left valves, greatly thickened in the dorsal region and with small areas of attachment, and relatively high length: breadth ratio. Two chronological subspecies can be distinguished.

Gryphaea arcuata obliquata J. Sowerby, figures 27 to 31, plate 10.
G. obliquata J. Sowerby (1815, pl. 112, fig. 3, p. 24).

Lectotype. Brit. Museum LL 26829.

Description. Relatively small in size, with an exogyroid twist and with sulcus feebly developed or absent. Max. length 62 mm. Length: height ratio approximately 1·5, length: breadth ratio approximately 1·3, area of attachment rarely more than 1 mm long. (See figures 2, 6, 7, 8 for fuller information.)

Remarks. This subspecies ranges from the *Angulata* Zone to the lower *Bucklandi* Zone (*Conybeari* Subzone). It is distinguishable from *G. arcuata incurva* by the absence or poor development of a sulcus and by the small size. At a given size, the difference of shape is too subtle to allow a ready distinction without measurement of many specimens. The lectotype came from St Donats Castle, Glamorgan, presumably from the shore section, where the *Angulata* and lower *Bucklandi* beds are well exposed. Sowerby's figured specimen is apparently lost. Sowerby's figures 3, 4 and 5, plate 1 give a better impression of the sub-species, however.

Gryphaea arcuata incurva J. Sowerby; figures 32 to 37, plate 10, figure 38, plate 11.
G. incurva J. Sowerby (1815, pl. 112, fig. 1, p. 23).

Lectotype. Brit. Museum LL 26828.

Description. Relatively large in size, with posterior lobe usually well defined by a pronounced sulcus. Max. length 81 mm. Length: height ratio approximately 1·5, length: breadth ratio approximately 1·3. Spiral angle in adult approximately 72°. (See figures 2, 9, 10, 11, 12 and 21 for fuller information.)

Remarks. This subspecies is found in the upper *Bucklandi* Zone (*Bucklandi* and ? *Rotiforme* Subzones) and the *Semicostatum* Zone. It may also range into the basal *Turneri* Zone. Because of allometric growth, a random collection of adults gives the impression that the left valves are much more tightly coiled or incurved than the smaller subspecies *G. arcuata obliquata*. The lectotype comes from Fretherne, presumably from the river cliff where sample Bgl was collected. It appears to correspond with Sowerby's figure 1. Its length: height ratio is abnormally low for the population at this locality and the specimen illustrated by figures 35, 36 and 37, plate 10 is more representative.

This is the familiar '*Gryphaea arcuata*' of numerous authors. Sowerby's species *G. incurva* is probably synonymous, but this cannot be established with any great confidence, since the exact horizon and location of the lectotype of *G. arcuata*, and the range of variation of the population from which it is drawn, are all unknown. Because of this it is rather unfortunate that this species was defined by Cox as the type species of the genus, particularly as the lectotype is based only on a drawn illustration. *G. arcuata* may also be regarded as the lectotype of the subspecies *G. arcuata arcuata*, which will have to remain as obscure as the species. Another subspecies name is required for the upper *Bucklandi* and *Semicostatum* zone forms described in this paper. Sowerby's name *incurva* is admirably suited for this purpose because it can be precisely defined.

(*b*) *Gryphaea mccullochii* J. de Sowerby

Gryphaea mccullochii mccullochii subsp.nov., figures 42 to 45, plate 11.
G. mccullochii J. de C. Sowerby (1829, pl. 547, fig. 3, p. 8a).

Neotype. Inst. Geol. Sciences, Scotland, 12281.

Description. Left valve moderately thin and incurved, sulcus poorly developed or absent. Max. length 83 mm. Length: height ratio approximately 2·2, length: breadth ratio approximately 1·3. Attachment area commonly up to 8 mm long (see figures 3, 14, and 15 for fuller information.)

Remarks. This subspecies appears to be confined to the *Jamesoni* Zone.

The specimen illustrated in Sowerby's figure 3 having been lost, a neotype is here designated from a specimen collected by the Geological Survey from the same locality, the Isle of Pabba (*Jamesoni* Zone). Figures 1 and 2 of Sowerby illustrate specimens collected from glacial drift in Northamptonshire and are obviously of no taxonomic value. The Jr sample, collected from the same zone in the neighbouring island of Raasay, gives a good idea of the range of variation of the species, and the Yorkshire specimens from a higher horizon in the *Jamesoni* Zone are closely similar.

Gryphaeas of this general shape, occurring in the higher part of the Lower Lias, have frequently been referred by palaeontologists to Lamarck's species *G. cymbium*. However, the specimen figured in the *Encyclopédie méthodique* (plate 189, figs. 1 and 2) is recorded as having come from Breuille, near St Jean d'Angely in Charente Inférieur. This is a region of Upper Jurassic rocks, so that either *G. cymbium* is not a Liassic fossil or its location is erroneous. Since both the stratigraphic and geographic location are uncertain the name cannot meaningfully be applied to any Liassic gryphaeas.

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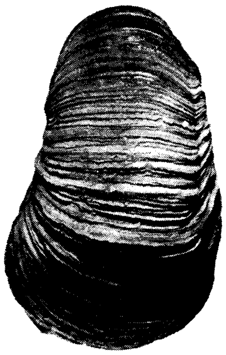

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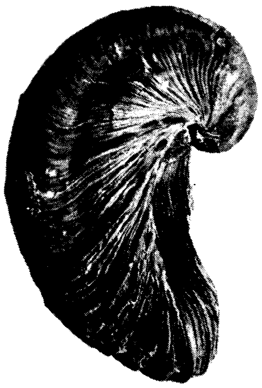

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FIGURES 27, 28. *Gryphaea arcuata obliquata* J. Sowerby. Lectotype, Brit. Museum (N.H.) LL 26829. Probably *Angulata* Zone, St Donats Castle, Glamorgan.

FIGURES 29, 30, 31. *G. arcuata obliquata* J. Sowerby. Sedgwick Museum J 48152 (34). *Angulata* Zone, Corston, Somerset.

FIGURES 32, 33, 34. *G. arcuata incurva.* J. Sowerby. Holotype, Brit. Museum (N.H.) LL 26828, *Bucklandi* Zone, Fretherne, Gloucestershire.

FIGURES 35, 36, 37. *G. arcuata incurva.* J. Sowerby. Author's collection. *Bucklandi* Zone, Fretherne. Gloucestershire.

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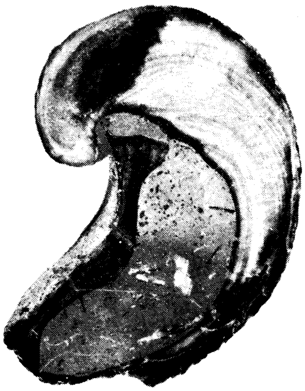
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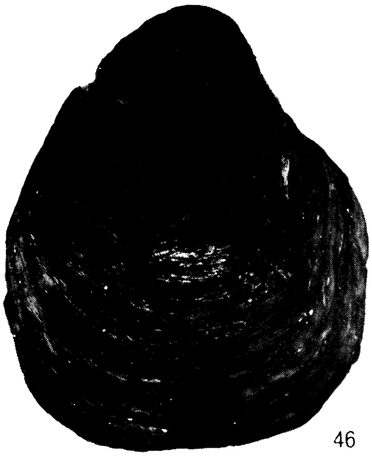
FIGURE 38. Median longitudinal section of *Gryphaea arcuata incurva*, *Bucklandi* Zone, Gloucs. Author's collection.

FIGURE 39. Median longitudinal section of *G. mccullochii arcuatiforme* subsp. nov., Author's collection. *Obtusum* Zone, Lincs. Shell margins marked by ink lines.

FIGURES 40, 41. *G. mccullochii arcuatiforme* subsp. nov. Holotype, Brit. Museum (N.H.) *Obtusum* Zone, Lincolnshire.

FIGURES 42, 43. *G. mccullochii mccullochii* J. de C. Sowerby. Lectotype, Geol. Survey Scotland 12281. *Jamesoni* Zone, Isle of Pabba, Inverness-shire.

FIGURE 44, 45. *G. mccullochii mccullochii*. External and internal views of right valve. Author's collection. *Jamesoni* Zone, Isle of Raasay, Inverness-shire.



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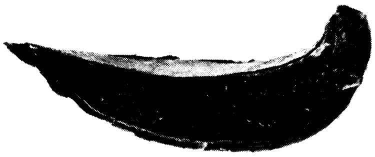

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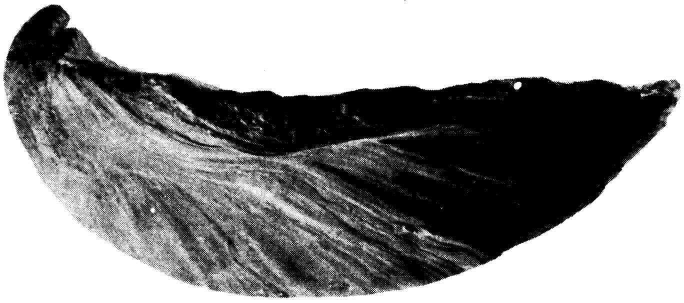

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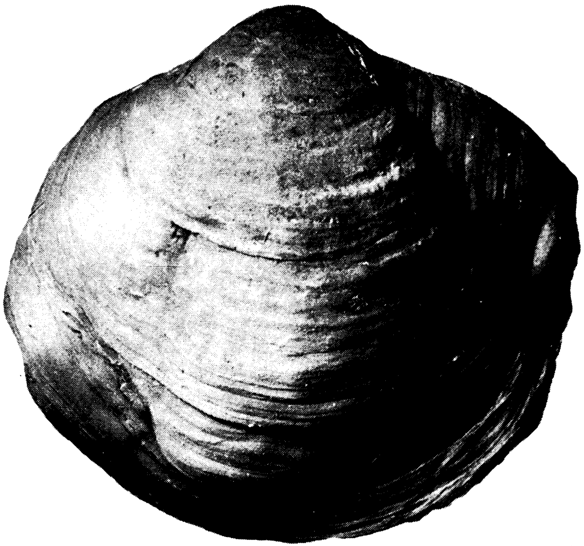

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FIGURES 46, 47, 48. *Gryphaea gigantea* J. de C. Sowerby. Author's collection. *Ibex* Zone, Blockley, Warwickshire.

FIGURE 49. Median longitudinal section of *G. gigantea*. Shell margins marked by ink lines. Author's collection. *Ibex* Zone, Blockley, Warwickshire.

FIGURES 50, 51. *G. gigantea* J. de C. Sowerby. Lectotype, Brit. Museum (N.H.) LL 26826. *Margaritatus* (or *Spinatum*) Zone, Churchdown Hill, Gloucestershire.

FIGURE 52. *G. gigantea* J. de C. Sowerby. Specimen showing posterior flange. Brit. Museum (N.H.) 67303. ?*Spinatum* Zone. Dursley, Gloucestershire.

Gryphaea mccullochii arcuatiforme subsp.nov., figures 39 to 41, plate 11.

HOLOTYPE. Brit. Museum LL 30989.

DESCRIPTION. Left valve moderately thick and incurved, sulcus poorly developed or absent. Max. length 86 mm. Length: height ratio approximately 1·7, length: breadth ratio approximately 1·4. Spiral angle approximately 70° in adult. Attachment area commonly up to 4 mm long. (See figures 3, 13 and 21 for fuller information.)

REMARKS. The range of this subspecies is from the *Turneri* to the *Raricostatum* Zone. Its recognition is based largely on a study of the Frodingham Ironstone (*Obtusum* Zone) sample, from which the holotype has been selected. I have found similar forms in small quantities in the *Obtusum* Zone of Yorkshire and Dorset, the *Raricostatum* Zone of Raasay and Yorkshire and the *Turneri* Zone of Lincolnshire, suggesting that the proposed stratigraphical subdivision of the species is valid.

It differs from *G. mcculochii mccullochii* in its higher length: breadth ratio, slightly greater degree of incurvature, thicker shell and smaller area of attachment. In these respects it is transitional to *G. arcuata incurva*, some relatively broad variants of which, e.g. from the *Semicostatum* Zone of Skye, it resembles quite closely. It is readily distinguishable, however, from the latter by the absence of a well developed sulcus and by the more loosely coiled umbo. There is considerable morphological overlap with *G. mccullochii mccullochii* which can only be satisfactorily resolved by the measurement of a large number of specimens. Therefore merely subspecific distinction is warranted.

(*c*) *Gryphaea gigantea* J. de C. Sowerby, figures 46 to 52, plate 12.

G. gigantea J. de C. Sowerby (1823, plate 391, figures 1, 2, p. 127; Corrigenda to *Min. Conch.*, p. 151).

LECTOTYPE. Brit. Museum LL 26826.

DESCRIPTION. Shell thin (figure 49, plate 12), large, ovoid to subcircular. Left valve only slightly incurved, with sulcus usually poorly developed or absent. Posterior part of shell may be splayed out to form a flange (figure 52, plate 12). Attachment area commonly ranged up to 8 mm. Max. length 137 mm (Brit. Mus. specimen 24390) in U. Pliensbachian, 90 mm. in L. Pliensbachian. Length: height ratio approximately 2·3, length: breadth ratio approximately 1·05 (1·2 in the *Ibex* Zone). Spiral angle in adults approximately 60°. (See figures 3, 16, 17, 18, 19 and 21 for fuller information.)

REMARKS. This species ranges from the *Ibex* to the *Spinatum* Zone. The unlocatable specimen figured by Sowerby and the chosen lectotype came from the ferruginous marlstone of Churchdown Hill Quarry, Gloucestershire. This rock unit is normally dated as *Spinatum* Zone, but C. P. Palmer (personal communication) has collected ammonites at this locality which suggest that it may here belong to the upper *Margaritatus* Zone. Large specimens of this species occurs commonly in the Upper Pliensbachian and specimens from south-west England are well represented in the British Museum collections.

Gryphaeas in the Lower Pliensbachian, from the late *Ibex* Zone upwards, are closely similar, but differ in their smaller maximum size and, in the case of the *Ibex* Zone of Warwickshire, in a slightly greater ratio of length to breadth. Further work in Britain and continental Europe might justify subdivision into chronological subspecies but at present geographical control is inadequate. Phillips's, species *G. depressa* (1829, plate 14, fig. 7), recorded as having come from the 'Marlstone Series' (= *Davoei* Zone) of the Yorkshire coast, is a synonym.

Gryphaea gigantea differs from *G. mccullochii* in its greater maximum size, lower length: breadth ratio, slightly lesser degree of incurvature and thinner shell. While *G. mccullochii arcuatiforme* is very different, there might be some difficulty in distinguishing *G. gigantea* from *G. mccullochii mccullochii* unless careful examination of whole assemblages is undertaken. Generally, however, the difference in length: breadth ratio is likely to be apparent even in small samples.

IV. PALAEOECOLOGY

(1) *Biostratonomic aspects*

(*a*) *Distribution of shells within sediment*

British Liassic gryphaeas occur in abundance in a variety of argillaceous facies, ranging from silty shales and siltstones in the Hebrides and Yorkshire to fine-textured shales, marls and marly limestones in the Midlands and south-west England. They are rare or absent, except sometimes as minute specimens, only in well-sorted sandstones and oolitic or shell-fragment limestones, where the sediments were presumably too unstable, and in laminated bituminous shales, which were laid down in anaerobic or at least very poorly aerated waters. The lack of intimate correlation between *Gryphaea* distribution and different types of argillaceous deposits is understandable in organisms which depended on water currents rather than the substrate for their sustenance.

Certain very general correlations are discernible, however. Gryphaeas tend to be more abundant in thicker successions and in ferruginous, as opposed to calcareous facies (where the associated carbonate is siderite rather than calcite). This is the more striking when it is borne in mind that condensed successions will give an exaggerated impression of faunal abundance.

Thus gryphaeas occur in enormous quantities in the relatively thick sequences of Skye, Raasay, Yorkshire and Glamorgan but are much less common, for instance, in the relatively thin sequence in Dorset. Whereas, moreover, prolific numbers of *Gryphaea* shells are found in the admittedly condensed Frodingham Ironstone, beds of an equivalent degree of condensation in the calcareous facies of south-west England are appreciably less fossiliferous in this respect. Within particular successions the shells tend to be concentrated into thin beds rather than dispersed uniformly throughout the rock. This most probably reflects periods of reduced sedimentation.

(*b*) *Size frequency distribution*

The method of collecting was not sufficiently intensive, nor confined to sufficiently thin horizons, to warrant the plotting of size frequency histograms, which would give a spuriously accurate picture. For example, most of the very small specimens from the Frodingham Ironstone came from a thin bed within the sequence. However, a general impression of size frequency can be obtained from a study of the scatter diagrams.

Only exceptionally, as in sample Ay, is there a strong predominance of juveniles and the most general pattern is a fairly symmetrical one which would plot as a more or less Gaussian distribution, as in most fossil samples. This is unlikely to be the result of a collecting bias since small specimens were consciously sought for. As it is unlikely that small, thick-shelled gryphaeas over a few millimetres in length could have been consistently swept away by water currents incapable of preventing the settling of mud, the most plausible interpretation is that juvenile mortality was in general relatively low after the organisms had broken free to commence their independent benthonic existence (cf. Craig & Hallam 1963). That spat mortality was probably very high has been shown for a sample of *Gryphaea arcuata* by Swinnerton (1964).

(*c*) *Articulation and orientation*

Table 5 gives the proportions of articulated and disarticulated shells (left valves) in the various samples. It will be seen that in most cases the disarticulated valves considerably exceed the articulated and only in one case, sample Bgl, are the latter in a majority. The proportions are influenced by size, large specimens having a much higher proportion of articulated shells than small ones, presumably as a consequence of the greater amount of energy required to separate the valves. Therefore the very low proportion of articulated shells in sample Ay is due in large part to the high proportion of juveniles.

TABLE 5. PROPORTIONS OF ARTICULATED AND DISARTICULATED VALVES

	articulated		disarticulated	
sample	number	percentage	number	percentage
Spinatum, Raasay	2	8·0	29	92·0
Ibex, Warwicks	12	28	31	72
Jamesoni, Yorks.	3	3·5	66	96·5
Jamesoni, Raasay	13	20	53	80
Obtusum, Lincs.	10	9·5	96	90·5
Semicostatum, Skye	8	5	147	95
Semicostatum, Glamorgan	7	7·5	85	92·5
Bucklandi, Gloucs.	35	54	30	46
Bucklandi, Yorks.	10	10	90	90
Angulata, Yorks.	3	1·5	191	98·5
Angulata, Glamorgan	2	6·5	37	93.5
Angulata, Somerset–Dorset	12	18·5	53	81·5
total	117		908	

Only in the Frodingham Ironstone have right valves been thoroughly searched for; the results quoted in Hallam (1963) signify a close approximation to a 1:1 ratio of left and right valves.

Zeuner (1933 *b*) was the first to make a systematic study of the orientation of left valves of *Gryphaea arcuata* in the sedimentary matrix. His principal finding was that the proportion of valves convex downwards (with the plane of commissure more or less horizontal) was greater in sandy than in clayey sediments, which he related to the more ready embedding of shells in the former as the result of stronger water movements.

A comparable study in two beds of the Frodingham Ironstone gave values of 43 % and 50 % convex downwards (Hallam 1963). Dr W. B. Heptonstall and Mr J. D. B. Cain obtained, in collaboration with myself, values of 50 % and 64 % respectively for several hundred gryphaeas in silty shales in the *Semicostatum* Zone on the Broadford shore in Skye. The tendency towards higher values in Skye can possibly be explained, following Zeuner, as the result of more rapid embedding, since the beds there signify a higher rate of sedimentation than in the case of the Frodingham Ironstone.

The strongest qualitative impression gained from collecting the other samples is one of randomness, with a higher proportion of valves lying on their side or convex upwards. The large saucer-shaped *Gryphaea gigantea* of the Raasay *Spinatum* Zone are dominantly convex downwards, however. It is also apparent that articulated specimens usually lie convex downwards.

It seems clear that post-mortem disturbance has played an important role, as suggested also by the disarticulation data. Granted a modest rate of sedimentation, the occasional large storm, perhaps as infrequent as once every decade, could have caused havoc amongst a shell assemblage while causing only a short-lived cessation of sedimentation. Such a factor was not taken into account by Zeuner.

With regard to the orientation assumed during life, the saucer-shaped gryphaeas of the higher Liassic zones are stable in only two positions, with the left valve convex downwards or upwards. As the animal could not have survived in the latter position it must have lived with its left valve on its underside and the plane of commissure more or less horizontal, as with modern oysters. This is confirmed by the stratonomic data for the *Spinatum* and *Ibex* Zones.

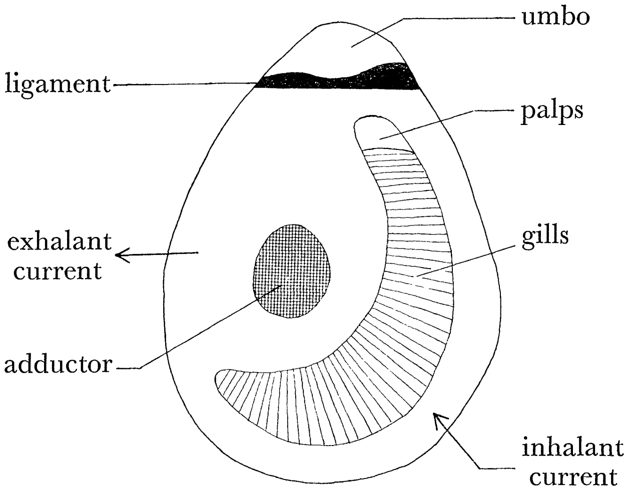

Figure 22. Simplified reconstruction of principal soft parts of *Gryphaea*, showing probable positions of inhalant and exhalant currents.

The case of *Gryphaea arcuata* is more difficult, because the shell is most stable lying on its side, with the plane of commissure approximately vertical. This has indeed been suggested as the life orientation by Pfannenstiel (1928) and Schäfle (1929). Zeuner (1933 *a*) criticized this view on the grounds that the convex left valve, subject to water movements, would tend to sink differentially in the sediment until its commissure was substantially horizontal. Zeuner's interpretation can be supported on different grounds. Since *Gryphaea* so closely resembles *Ostrea* in its hard parts one may reasonably deduce that the same was true of the soft parts. Figure 22 shows a simplified reconstruction of the latter based on Yonge (1960) and shows the probable positions of the inhalant and exhalant siphons. If incurved species of *Gryphaea* lay on their side one or other of these siphons would have been clogged by mud and the organisms would have quickly died since they had no means of righting themselves. Therefore the orientation must have been such as to allow both siphons free access to water currents. The stratonomic data also argue in favour of a subhorizontal commissure in that articulated specimens, i.e. those that have suffered the least post-mortal disturbance, are generally convex downwards.

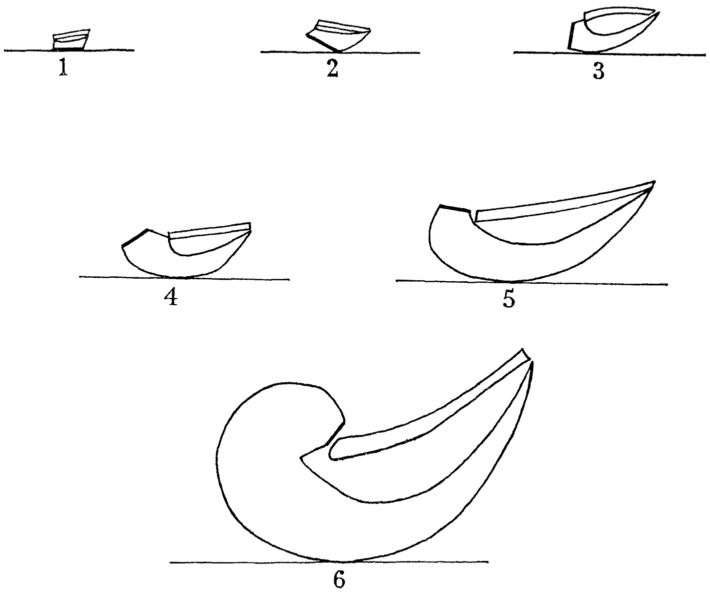

FIGURE 23. Postulated change in orientation of *Gryphaea arcuata* with growth. Area of attachment marked by thick line.

Figure 23 shows an attempt to reconstruct the most probable orientation of the living *G. arcuata* during ontogeny, from the time when it first broke free of its attachment surface. Bearing in mind the massively thickened dorsal part of the shell beneath the umbo it is most likely that the plane of commissure in the adult was tilted upward ventrally. This interpretation is subject to the amount of embedding having been minimal. Strong current disturbance would have led to partial burial of large specimens, as Zeuner's (1933 *a*) experiments demonstrated.

(*d*) *Stability*

On common sense grounds relatively round shells with a low degree of incurvature should be more stable on the sea bed than more incurved and narrower forms.

Likewise, the presence of a sulcus creates a posterior lobe which could have had a stabilizing function, as is easy to demonstrate on a hard surface. If an adult specimen of *Gryphaea arcuata incurva* is placed convex downwards and given a gentle push from the posterior side, it readily keels over to a stable position with its commissure approximately vertical. A push of comparable strength from the anterior side, however, only results in the shell settling in an oblique position because of the posterior lobe.

It was considered desirable to subject these ideas to experimental test and obtain some quantitative data on relative stabilities of different shells. A series of experiments were therefore conducted using a 12 ft. flow channel in the Grant Institute of Geology in Edinburgh. The following shells were used:

1. *Gryphaea arcuata obliquata*, $L = 53$, $H = 40$, $B = 32$ mm.
2. *G. arcuata incurva*, $L = 74$, $H = 47$, $B = 40$ mm.
3. *G. arcuata incurva*, $L = 51$, $H = 30$, $B = 34$ mm.
4. *G. mccullochii arcuatiforme*, $L = 72$, $H = 45$, $B = 46$ mm.
5. *G. gigantea*, $L = 83$, $H = 42$, $B = 71$ mm.

Care was taken to ensure that the shells were taxonomically representative.

All these specimens are articulated and contain sedimentary material in the interior. Therefore they do not correspond exactly to the living animal, but the bulk of the weight is still provided by the shell. The experiments, moreover, are not meant to simulate actual living conditions but are merely intended to inform on relative stability in controlled artificial situations. Therefore the shells are satisfactory for the purpose required. The floor of the flow channel was covered with about 8 cm of medium sand, which is a convenient material to work with.

If a shell of *Gryphaea arcuata* is placed on sand as in position 1 of figure 24 and subjected from one side to a moderately powerful current, a crescentic depression will develop on the upstream side as a result of scouring. As this deepens in the course of time, the shell is progressively undermined and tilts into it, coming to rest only when it reaches the position of stability shown in position 3. Following from the discussion in § IV 1 (*c*), this may be held to signify that death would rapidly ensue. In the series of experimental runs whose results are to be described, the time T taken for the shell to travel from position 1 to 3, or a comparable position with the commissure vertical, was measured for a variety of orientations and current velocities. At a velocity of 20 cm/s ripples began to form and at 25 cm/s a substantial proportion of sand went into suspension. The shells are thus quite likely to be buried before they are tilted over and the results obtained at this high velocity are only to be considered as very approximate. Such high velocities would have been intolerable to the great majority of, if not all, gryphaeas.

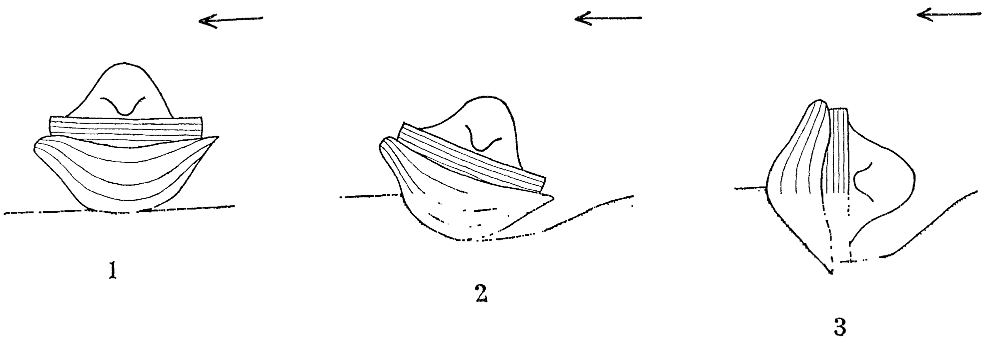

FIGURE 24. Diagram to illustrate the upstream tilting and partial burial of strongly incurved *Gryphaea* into stable position (3) with plane of commissure approximately vertical, consequent upon unidirectional current action.

In the first set of experiments the relative stability of the dorsal, ventral, anterior and posterior sides upstream of specimen 2, which has a posterior lobe, was studied by making eight runs for each orientation at 20 cm/s. The dorsal-ventral positions have comparable stability (mean $T = 2$ min 52 s), about twice that of the other two positions (mean $T = 1$ min 15 s). This is because lengthwise-oriented specimens of the relatively narrow *G. arcuata* provide less resistance. They tend, however, to rotate progressively towards the less stable position at right angles.

At 20 cm/s the posterior upstream orientation is slightly less stable ($T = 1$ min 6 s) compared with the anterior upstream (1 min 23 s). At 15 cm/s, however (20 runs), it is much the more stable (4 min 46 s compared with 2 min 28 s). At 10 cm/s the shell was still stable in both orientations after 30 min, having been subjected to only gentle tilting and slight burial.

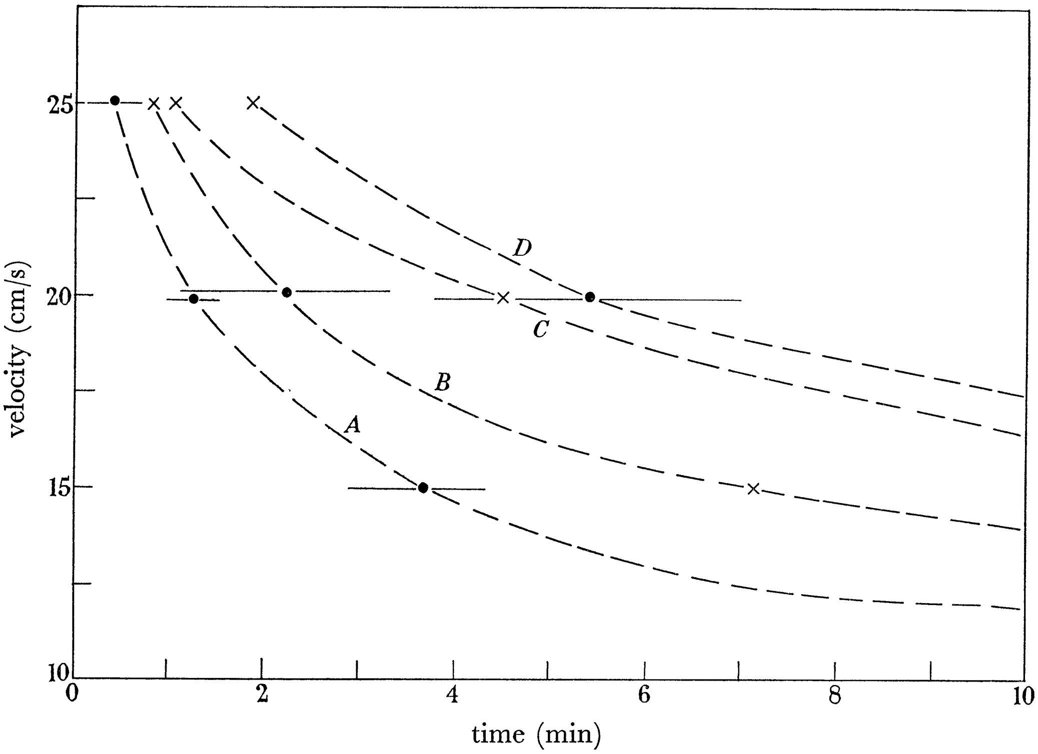

FIGURE 25. 'Instability curves' for various specimens of *Gryphaea*, for anterior or posterior side upstream, based on flow channel experiments. Curves mark the times, for given current velocity, at which specimens tilt into stable subvertical position. Horizontal lines signify 95 % confidence limits, crosses signify approximate values. A = large *G. arcuata incurva*, B = *G. arcuata obliquata*, C = *G. mccullochii arcuatiforme*, D = small *G. arcuata incurva*.

Specimen 1, which lacks a posterior lobe, was subjected to the same treatment. At 20 cm/s (10 runs) the posterior upstream orientation was found to be less than half as stable as the anterior upstream (1 min 17 s compared with 2 min 55 s) and at 15 cm/s (4 runs) there was effectively no difference between the two orientations (*ca.* 7 min).

Specimens 3 and 4 are more stable and fluctuations in successive runs for a given orientation greatly exceeded any possible difference between the two different orientations. Specimen 5 was found to remain stable in both orientations (in the sense defined earlier) after being subjected to a 20 cm/s current for 30 min, merely being tilted upstream to a moderate extent.

Figure 25 gives the results of a comparative study of the stability of specimens 1 to 4 in various current regimes, the data for both anterior- and posterior-upstream orientations being averaged. The 90° tilt from a horizontal plane of commissure was most decisive and rapid in the case of the large *G. arcuata incurva*. Hence a relatively large number of runs were undertaken and the results for this specimen are the most accurate.

It will be seen from the figure that the order of increasing stability is—large *G. arcuata incurva*, *G. arcuata obliquata*, *G. mccullochii arcuatiforme* and small *G. arcuata incurva* (the most stable of all, *G. gigantea*, cannot of course be portrayed in the diagram).

To summarize, the flow-channel experiments suggest the following conclusions:

1. The morphological trend from *G. arcuata* via *G. mccullochii* to *G. gigantea* is one of increasing stability.
2. *G. arcuata* became progressively more unstable with growth, as a result of the ontogenetic increase of incurvature.
3. The possession by *G. arcuata* of a posterior sulcus and lobe seems to increase stability on one side of the shell at low to moderately high current velocities, but this advantage is lost at high velocities and tends to be outweighed by growth of the shell to a large size.

It is of course arguable whether or not these results are relevant to natural conditions encountered in the Liassic seas. Indeed, experiments of this sort can never be more than suggestive, or do more than demonstrate feasibility. This is decidedly not an argument, however, for not bothering to attempt them.

(2) *Ecological interpretation*

Only in the case of *G. arcuata* does the sampling allow a consideration of regional variations in shape and size. The most striking difference is that the *Bucklandi*, Gloucestershire specimens tend to be narrower and attain larger sizes than their near contemporaries in Glamorgan and Skye. These differences correlate with disarticulation ratios and sedimentary thickness and hence mean rate of sedimentation. Both the Glamorgan and Skye sequences are appreciably thicker, zone for zone, than that at Fretherne and the proportion of articulated shells is very low, whereas the Gloucestershire sample has by far the highest proportion of these in any sample (table 5).

One can speculate that these differences may conceivably be related to the increased turbidity consequent upon higher sedimentation rate. Although the living *Ostrea* is well adapted to turbid conditions it cannot tolerate excessive turbidity, which beyond a certain point inhibits feeding and hence reduces the maximum size attained (Loosanoff & Tommers 1948). A high incidence of disarticulation suggests current disturbance, and, in the case of the silty shales of Skye, Dr W. B. Heptonstall (personal communication) has deduced moderately strong current activity from the preferred orientation of sand grains. The greater relative broadness of the Skye and Glamorgan shells might therefore possibly signify an adaptation towards achieving greater stability. In relatively disturbed conditions, moreover, organisms might die by being irrevocably tipped on their side upon the attainment of a certain size, since shell stability diminishes with growth.

A comparable explanation might be applicable to *G. arcuata obliquata* in the *Angulata* Zone of Glamorgan and Somerset–Dorset, because shells of the former are broader and have a slightly lesser maximum size, the proportion of disarticulated valves is appreciably higher and the stratigraphical thickness of the enclosing sediments much greater.

These geographical changes are, however, quite minor compared with those of the sequence of species up the succession and no secular environmental change of corresponding magnitude can be inferred from other fossils or from the rocks. Salinity is known to affect size, but any increase of this during the course of the Lias (Hallam 1967) must have been very slight, because marine conditions were established at the beginning of the Hettangian. It will be seen, moreover, that *Gryphaea* was very probably, like modern oysters, well adapted to conditions of slightly reduced salinity. Hence it may be deduced that the morphological changes in question are evolutionary in origin.

With regard to the factors controlling abundance, *Gryphaea* is much rarer in the Mediterranean region than in north-west Europe. It has been inferred on a variety of grounds that rocks of 'Mediterranean facies' were laid down in open-sea conditions distant from rivers. The varied facies of north-west Europe signify in contrast a region of shallow coastal and in-shore waters in which the influence of rivers was appreciable, with consequent slight reduction in salinity and faunal diversity (Hallam 1967). Such an environment, greatly enriched in suspended organic matter, favoured colonization by lamellibranchs in prolific numbers.

Gryphaea distribution, like that of modern oysters, must have been conditioned largely by the balancing of two intimately related factors, food supply and terrigenous sedimentation. This helps to explain why gryphaeas tend to be more abundant in deposits signifying a relatively high rate of sedimentation. The variable abundance within such successions might also be related to sedimentation. The more barren beds could signify episodes of sedimentation too rapid for successful colonization, either because of excessive turbidity or because the sea floor was too soft. That food supply was the dominant factor controlling distribution is also suggested by the fact that, for deposits of comparable rates of sedimentation, gryphaeas tend to be commoner in ferruginous than in calcareous facies, since the former was deposited closer to nutrient-bearing rivers (Hallam 1966).

V. Evolution

The following morphological changes up the Liassic succession are interpreted as evolutionary trends.

1. Size increase in *G. arcuata* and *G. gigantea*.
2. Lessening degree of incurvature of left valve, expressed by increase in length:height ratio and decrease of spiral angle.
3. Broadening of shell, expressible as decrease in length:breadth ratio. This trend continued after the length:height ratio became stabilized in the early Pliensbachian.
4. Thinning of both valves.
5. Increase in length of attachment area, stabilized in the early Pliensbachian.
6. Development of a well-marked posterior sulcus in the left valve of *G. arcuata incurva*, following by loss or reduction in stratigraphically higher forms.

Since the two subspecies of *G. mccullochii* are intermediate in these respects between the stratigraphical end members, we may consider the sequence as the lineage *G. arcuata obliquata—arcuata incurva—mccullochii arcuatiforme—mccullochii mccullochii—gigantea* (figure 26).

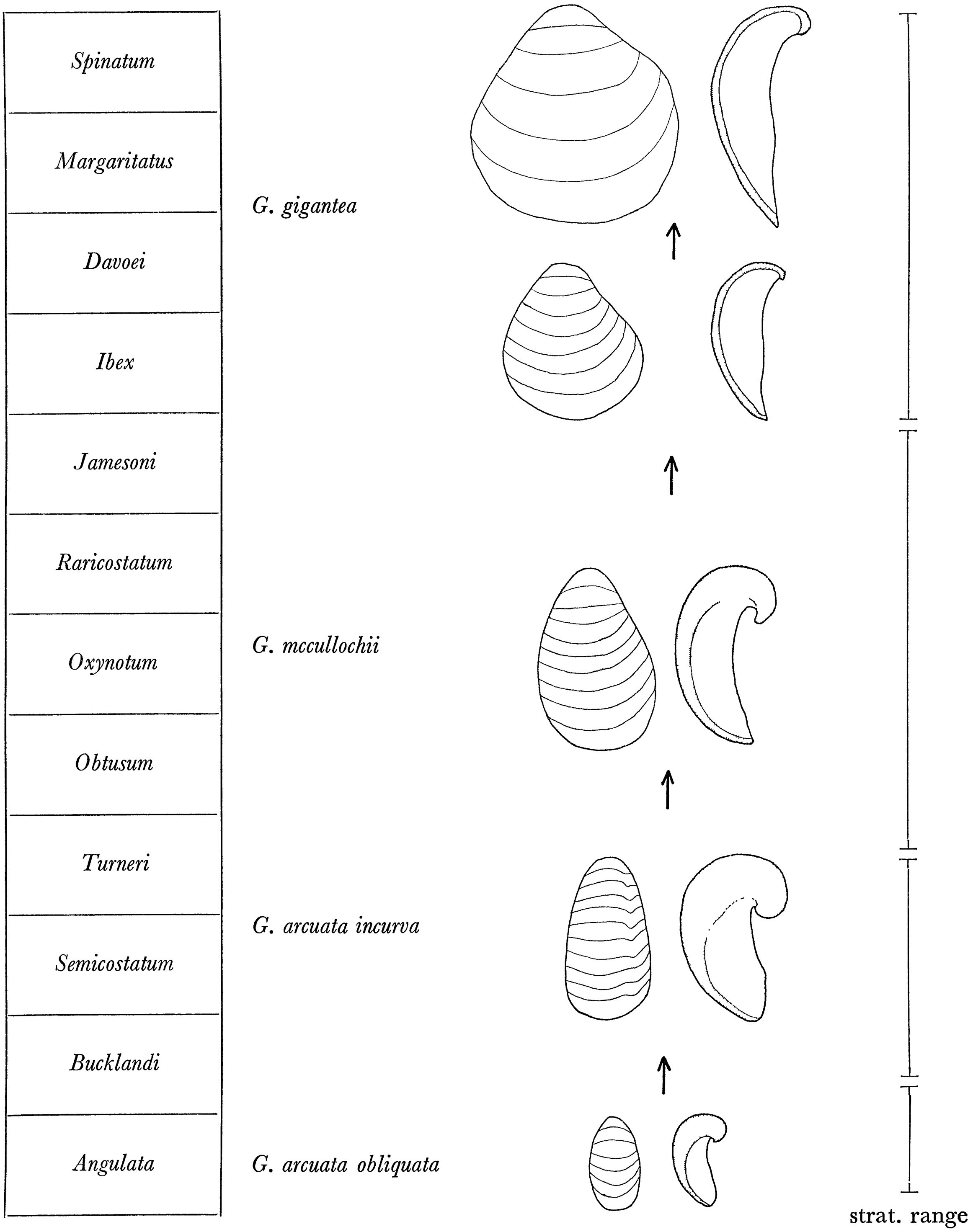

FIGURE 26. Diagram summarizing principal evolutionary trends in Liassic gryphaeas. Only left valve shown. Specimens in lateral orientation are seen in median section, with the area of shell stippled.

Another possible minor trend is the slight increase in incurvature from *G. a. obliquata* to *G. a. incurva* but, as pointed out earlier, morphological variations between samples of the same age are of a comparable magnitude. More work, especially on the European Continent, is required to determine whether this apparent change in coiling is evolutionary or ecological. In a more general way, my own collecting in Swabia and Lorraine accords with the descriptions and illustrations of Schäfle (1929) and Charles & Maubeuge (1951) in suggesting the probability of similar trends at the same stratigraphic horizons in the Lias of both Germany and France.

Before the evolutionary trends are interpreted the possible origin of *Gryphaea arcuata* must be discussed. Either it evolved more or less *in situ* from the flourishing *Liostrea* populations of the Hettangian, as has been generally assumed since the early work of Trueman, or it migrated at the end of the Hettangian from another region after evolving from a pre-existing oyster stock.

Small gryphaeas, ranging up to about 40 mm in length, are known from Upper Triassic (pre-Rhaetian) deposits from various parts of the world (Böhm 1903; Scalia 1912; McLearn 1937; Kiparisova 1938). Some of these, such as *G. arcuataeformis* Kiparisova, have a fair resemblance to small *G. arcuata*. This is not especially significant since the young *G. arcuata* has a rather generalized gryphaeate form and no Rhaetian or early Hettangian Jurassic forms resembling *G. arcuata* having been recorded anywhere, i.e. there is an apparent absence of stratigraphical intermediates.

Lower Lias gryphaeas of *arcuata* type are indeed rare in most parts of the world including the Tethyan belt and Pacific margins, that is, the regions of open ocean. Around the Pacific, for instance, nothing resembling *G. arcuata* is known from Japan (Hayami 1961), New Zealand (Marwick 1953) or North America (Hallam 1965).

As the prevalent view among specialists is that Mesozoic gryphaeas have evolved from oyster stocks on a number of occasions (Sylvester-Bradley 1959) it seems more plausible to accept that *G. arcuata* has no close relationship to the Triassic gryphaeas but evolved from *Liostrea* in the only region where it is abundant, namely north-west Europe.

The following remarks must of course be treated as speculation but may provide a useful basis for discussion.

The primary ecological requirement of oysters of all types is to obtain maximum nutritional benefit from suspended organic matter in the sea. This is most easily achieved in the organics-rich waters in or close to estuaries, but at the expense of coping with problems of turbidity and a high sedimentation rate. It therefore appears self-evident that any change leading to the raising of the mantle margin above the sea bed would confer a selective advantage by reducing the chance of suffocation. The reduction of attachment area would also open up an extensive new niche, namely the muddy sea bed with only minute amounts of shell or other hard surface available for colonization.

In other words, the change from the flat *Liostrea irregularis* to the incurved *Gryphaea arcuata* was clearly adaptive. Its apparent suddenness (at least in geological terms) suggests the likelihood of a rather simple genetic change, conceivably even a single mutation. Essentially the only change required was a strong relative increase in the *transverse* component of growth (i.e. normal to the plane of commissure), to use the terminology of Owen (1953). This would lead to the early breaking-away of the left valve from the surface of cementation and the growth of a transversely coiled shell. The massively thickened shell in the dorsal region might be a mere metabolic by-product of this change.

However, the development of a tightly coiled spiral must have led to a reduction in stability. The subsequent evolutionary history of the lineage can be understood as an attempt to rectify this, coupled with increase in size, which is a common evolutionary trend in invertebrates, with several adaptive advantages (Gould 1966). (If the apparent increase in incurvature within *G. arcuata* is considered to be evolutionary, only slight modification is required to this statement.)

Initially a sulcus was developed, and the experimental results suggest that this could feasibly have increased stability to a small degree. This must have been more or less outweighed by the greater incurvature of the adults resulting from size increase and so was inadequate for the purpose. The subsequent increase in relative broadness was far more effective in conferring stability and hence the sulcus was reduced or lost. Decrease in incurvature, also aiding stability, was the result of a gradual decrease in the transverse growth component, with the result that the area of attachment increased in size because of delayed partition from the surface of cementation. The need for a massive shell having diminished, much less metabolic energy was expended in $CaCO_3$ secretion. The end-product was a thin-shelled saucer-shaped *Gryphaea* which expressed a good balance between stability and the need to keep the mantle margin above the muddy bottom.

These gradual changes up the succession must have been far more complex genetically than that which initiated *G. arcuata* and signify the slow operation of natural selection on a subtly changing gene pool. The evolution may be regarded as caenogenetic in so far as the adult *G. gigantea* has a similar spiral angle to the young *G. arcuata* (figure 21). It also signifies progressively closer approximation to a *paradigm* for *Gryphaea*, i.e. a structure that can fulfil a function with maximal efficiency under the limitations imposed by the nature of the materials (Rudwick 1961). It is probably significant in this respect that *G. gigantea* bears a much closer resemblance to most later Jurassic gryphaeas than does *G. arcuata*.

The lineage appears to have come to an end at or just after the close of the Pliensbachian, being subjected to extinction together with most other benthonic invertebrates by the widespread onset of stagnant bottom conditions in the early Toarcian (Hallam 1961). Possibly, however, this small chapter in evolution was not closed definitively, and certain survivors might have given rise to new flourishing stocks in later Jurassic times.

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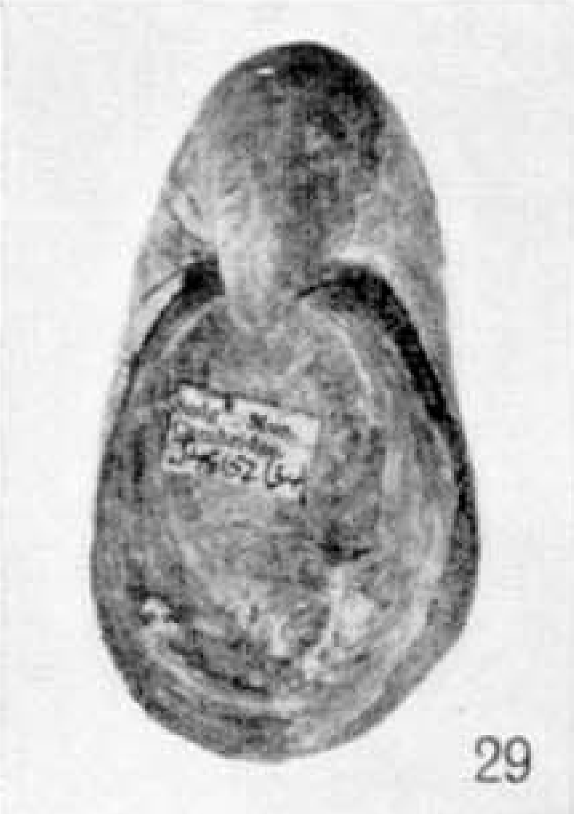
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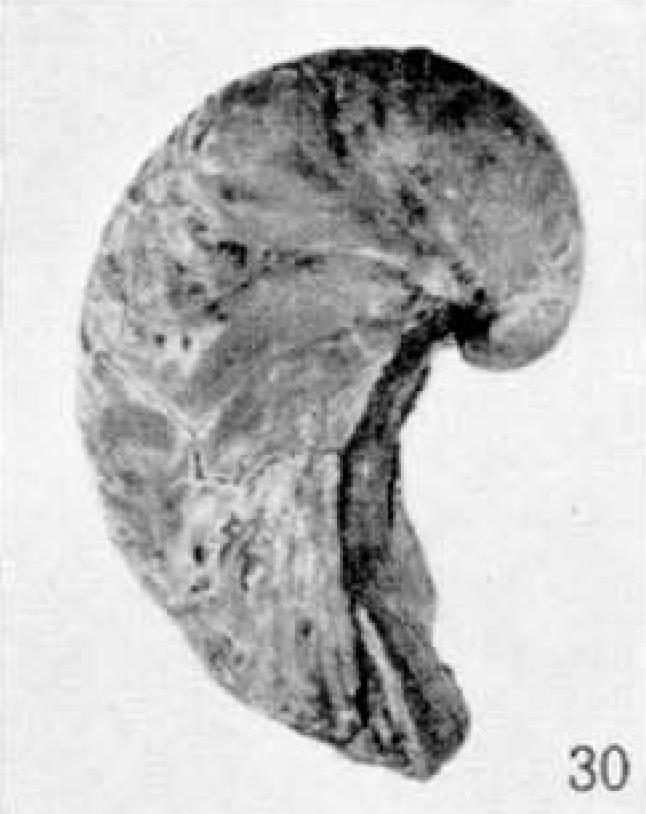
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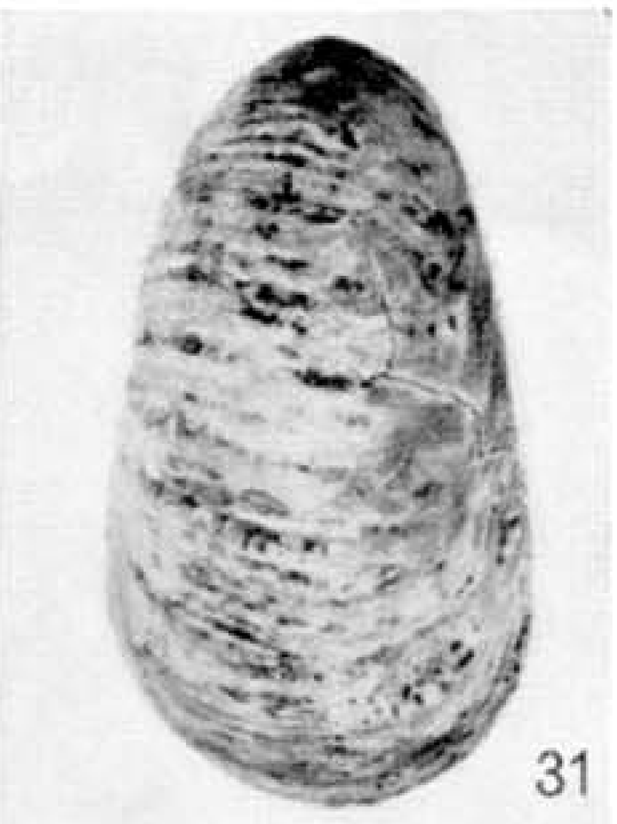
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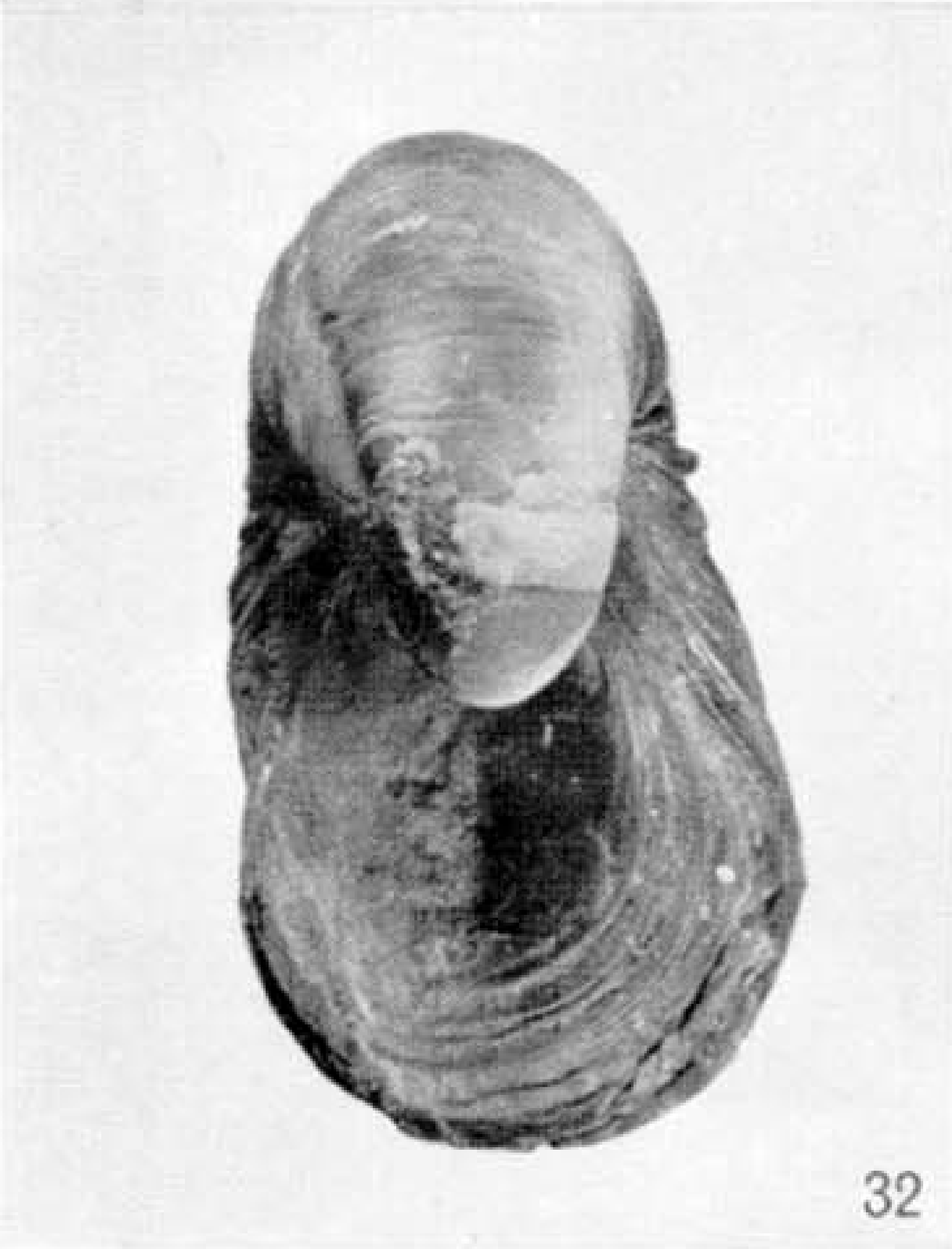
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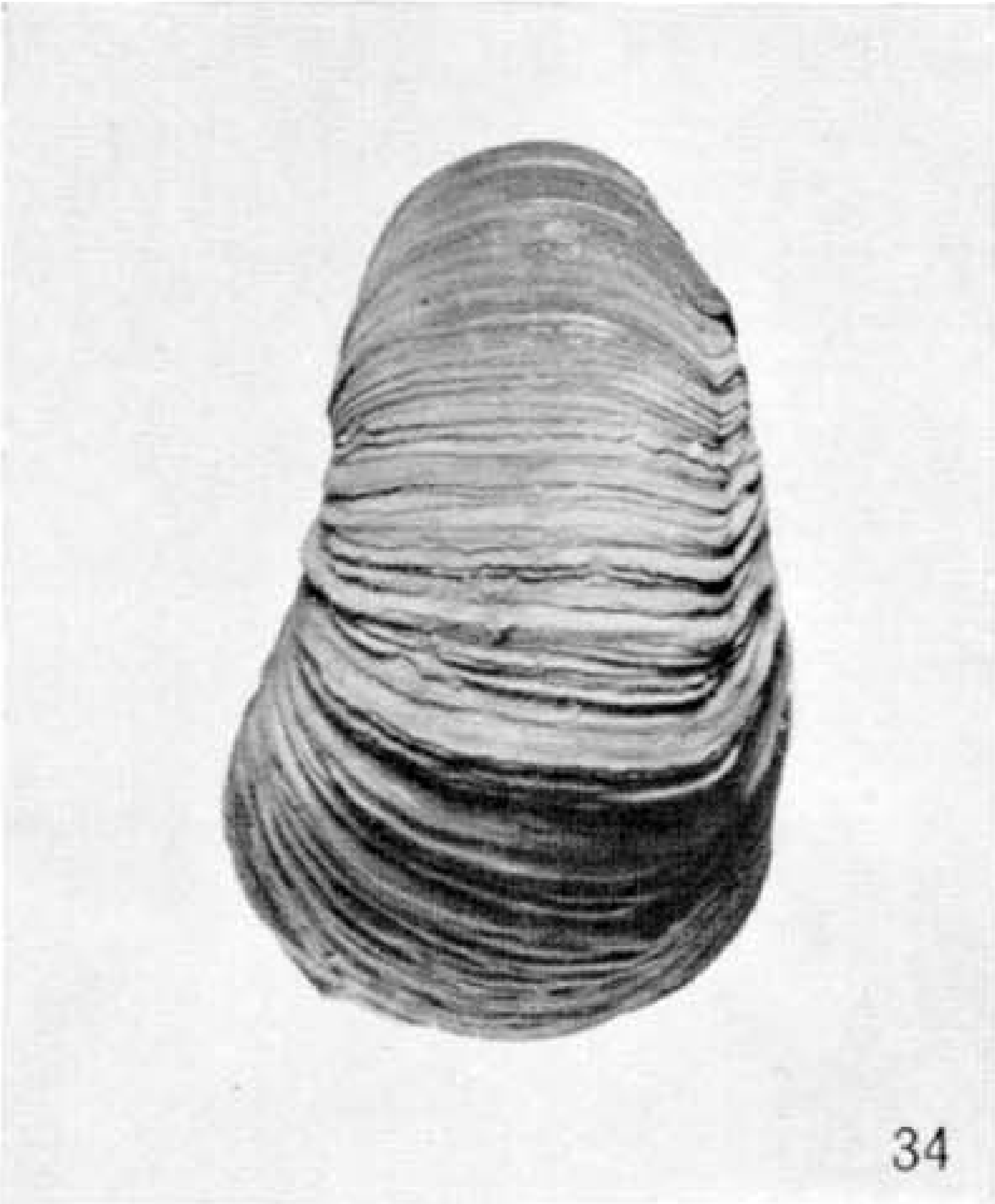
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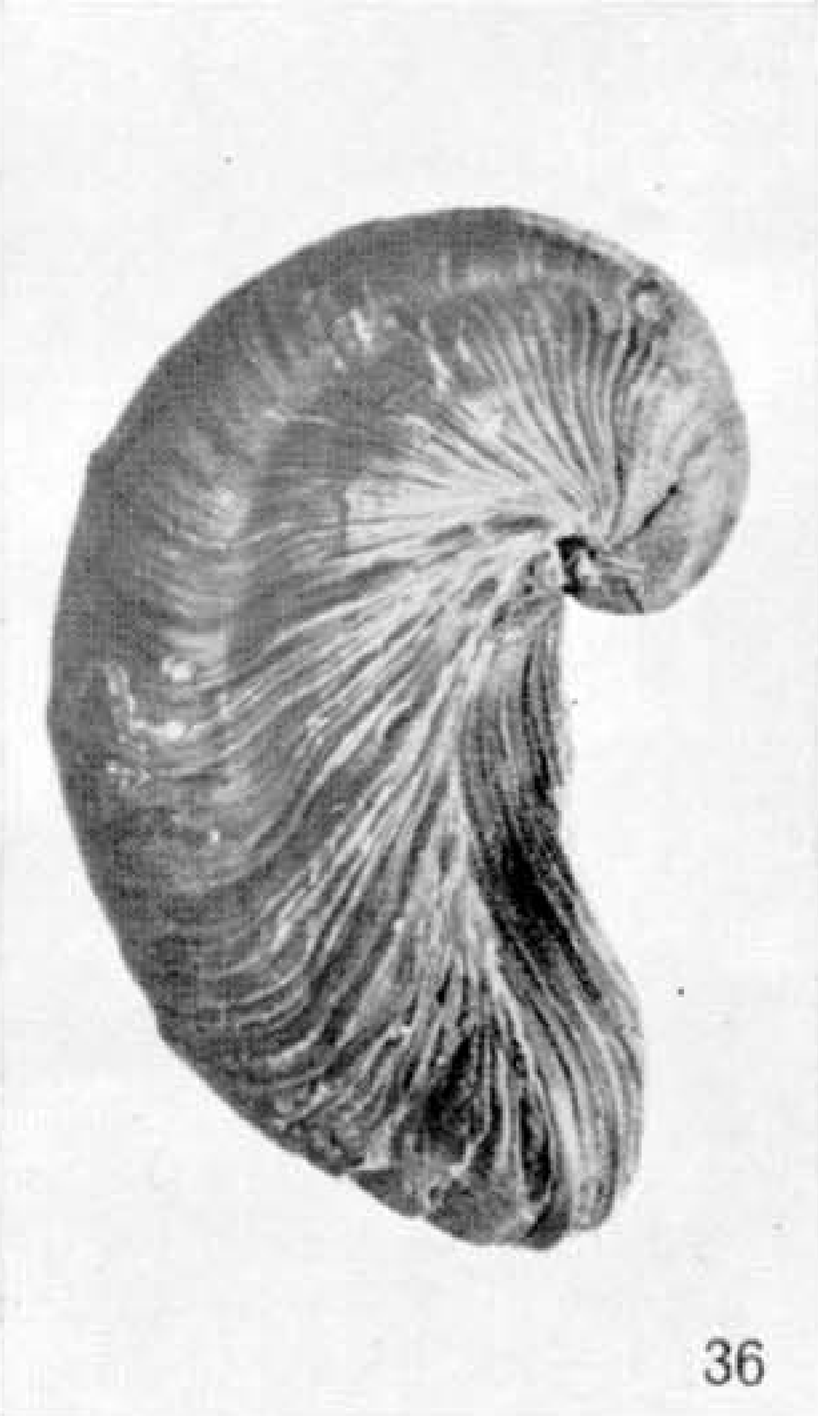
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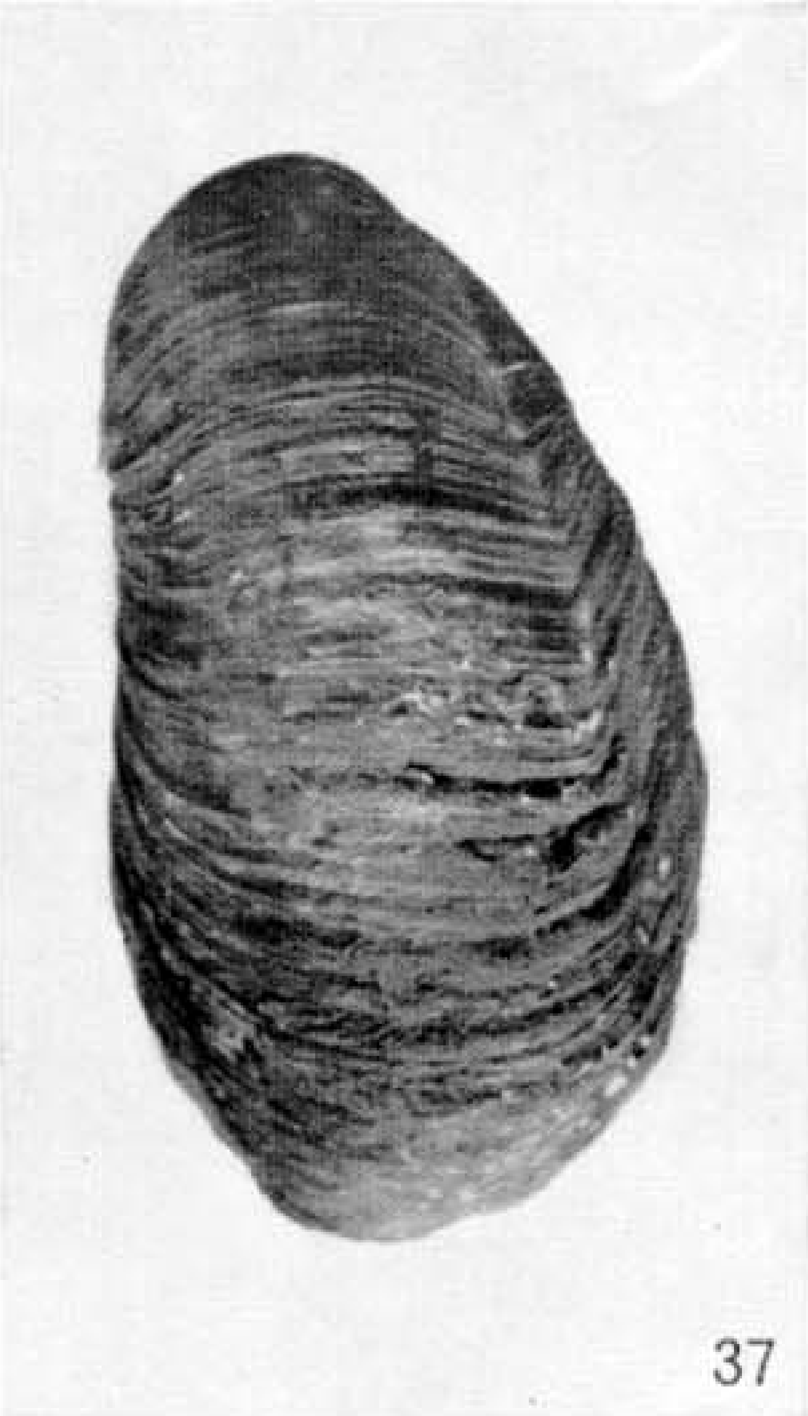
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FIGURES 27, 28. *Gryphaea arcuata obliquata* J. Sowerby. Lectotype, Brit. Museum (N.H.) LL 26829. Probably *Angulata* Zone, St Donats Castle, Glamorgan.

FIGURES 29, 30, 31. *G. arcuata obliquata* J. Sowerby. Sedgwick Museum J 48152 (34). *Angulata* Zone, Corston, Somerset.

FIGURES 32, 33, 34. *G. arcuata incurva*. J. Sowerby. Holotype, Brit. Museum (N.H.) LL 26828, *Bucklandi* Zone, Fretherne, Gloucestershire.

FIGURES 35, 36, 37. *G. arcuata incurva*. J. Sowerby. Author's collection. *Bucklandi* Zone, Fretherne. Gloucestershire.


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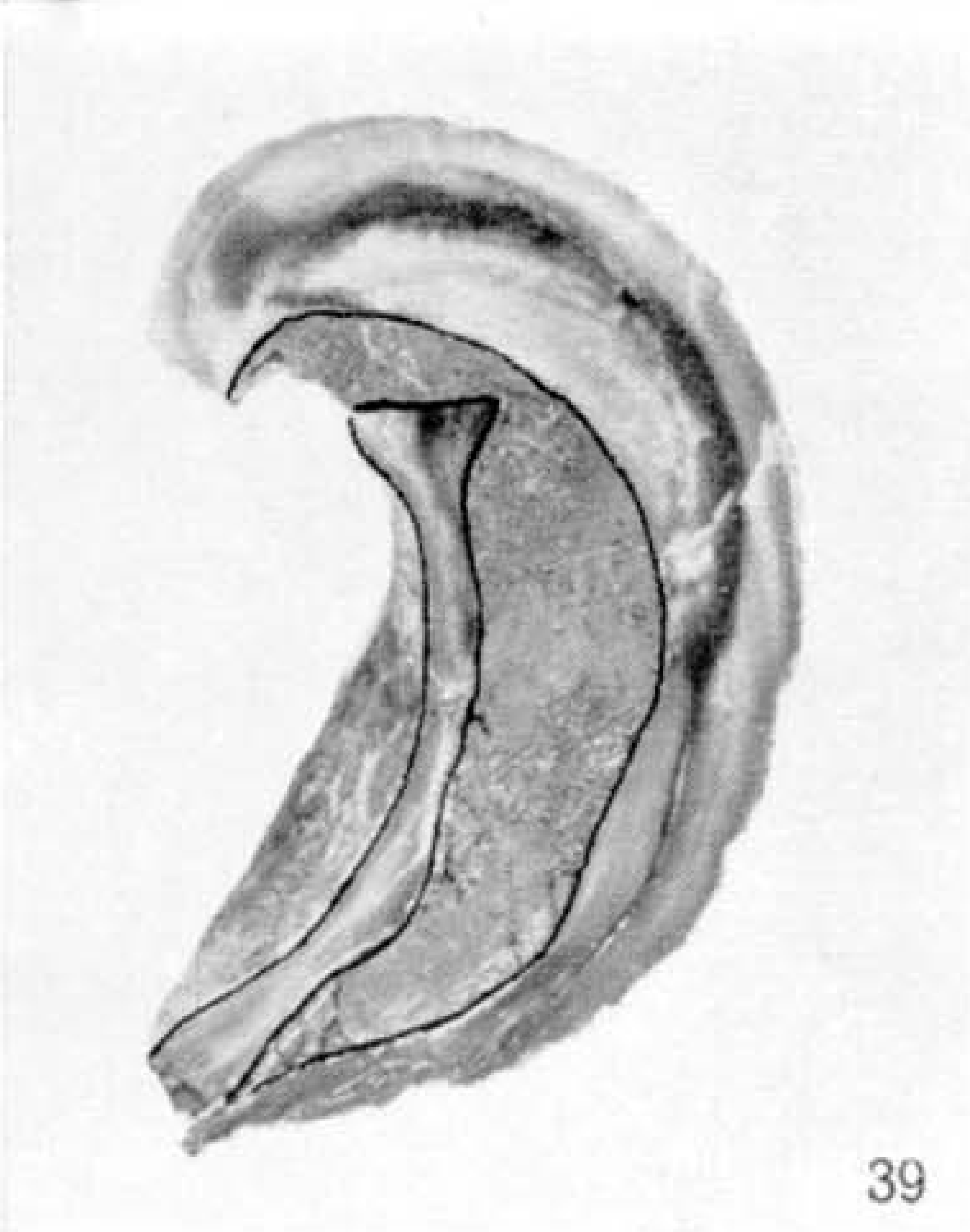
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FIGURE 38. Median longitudinal section of *Gryphaea arcuata incurva*, *Bucklandi* Zone, Gloucs. Author's collection.

FIGURE 39. Median longitudinal section of *G. mccullochii arcuatiforme* subsp. nov., Author's collection. *Obtusum* Zone, Lincs. Shell margins marked by ink lines.

FIGURES 40, 41. *G. mccullochii arcuatiforme* subsp. nov. Holotype, Brit. Museum (N.H.) *Obtusum* Zone, Lincolnshire.

FIGURES 42, 43. *G. mccullochii mccullochii* J. de C. Sowerby. Lectotype, Geol. Survey Scotland 12281. *Jamesoni* Zone, Isle of Pabba, Inverness-shire.

FIGURE 44, 45. *G. mccullochii mccullochii*. External and internal views of right valve. Author's collection. *Jamesoni* Zone, Isle of Raasay, Inverness-shire.


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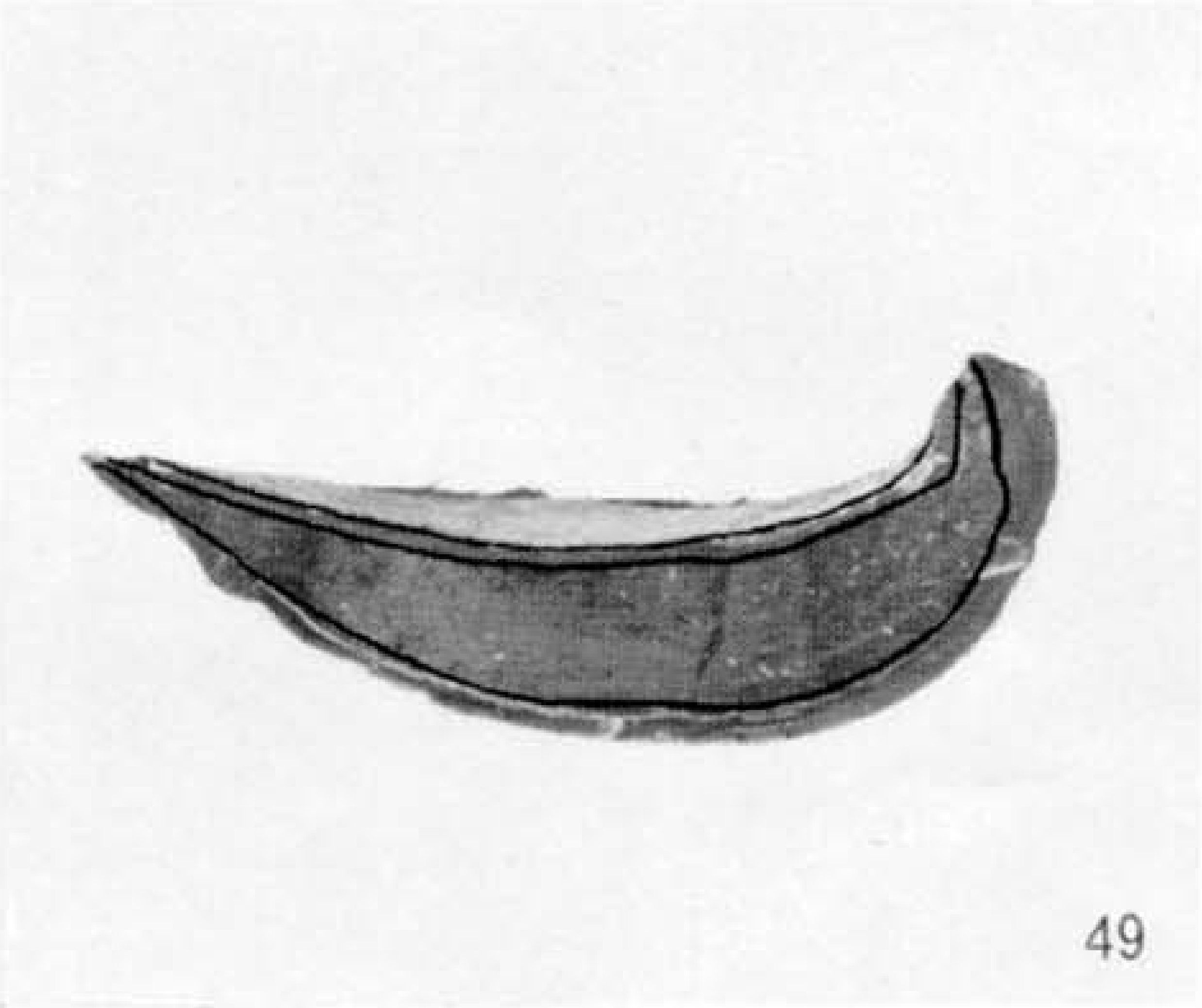
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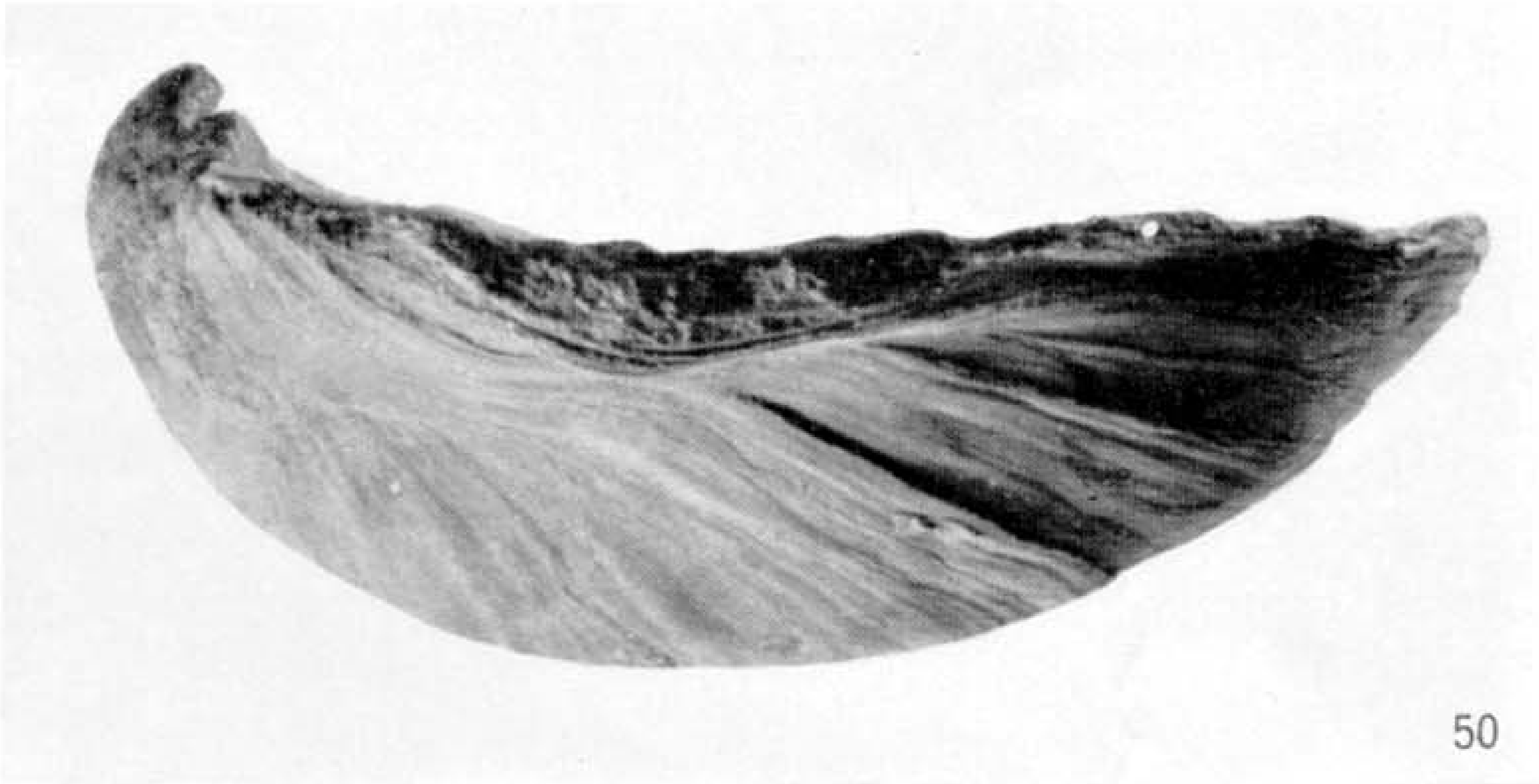
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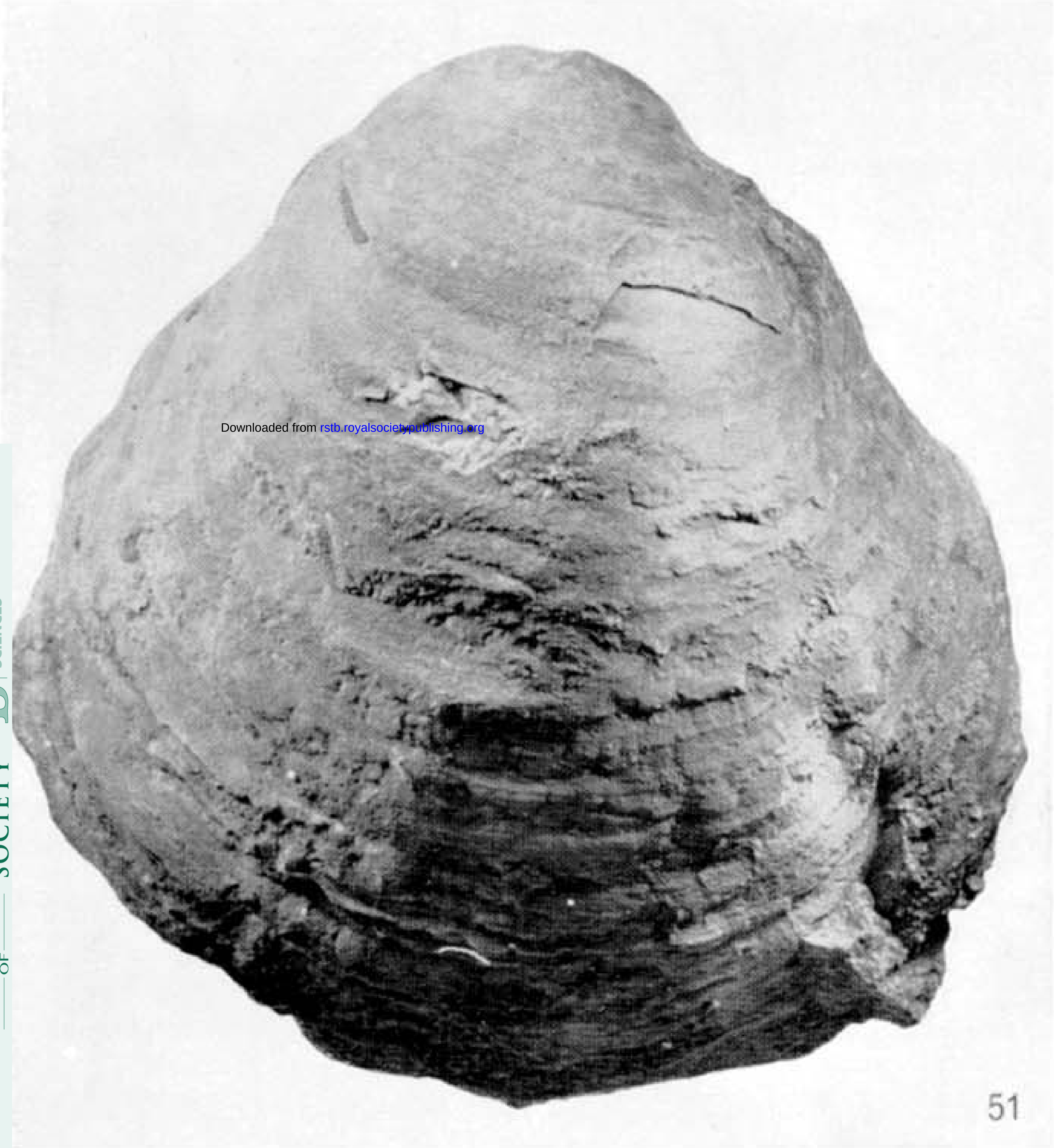
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FIGURES 46, 47, 48. *Gryphaea gigantea* J. de C. Sowerby. Author's collection. *Ibex* Zone, Blockley, Warwickshire.

FIGURE 49. Median longitudinal section of *G. gigantea*. Shell margins marked by ink lines. Author's collection. *Ibex* Zone, Blockley, Warwickshire.

FIGURES 50, 51. *G. gigantea* J. de C. Sowerby. Lectotype, Brit. Museum (N.H.) LL 26826. *Margaritatus* (or *Spinatum*) Zone, Churchdown Hill, Gloucestershire.

FIGURE 52. *G. gigantea* J. de C. Sowerby. Specimen showing posterior flange. Brit. Museum (N.H.) 67303. ?*Spinatum* Zone. Dursley, Gloucestershire.

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