THE GRYPHAEA PLEXUS IN THE LOWER LIAS OF THE VALE OF BELVOIR, NOTTINGHAMSHIRE

by

Henry Hurd Swinnerton

Summary

The material for this investigation was collected from temporary exposures made in 1940 in fields south of Granby, in the Vale of Belvoir. The strata involved belong to the Lower Lias, from the Angulata Zone up to the Semicostatum Zone. They therefore correspond very closely with the beds from which the fossils were obtained that were used by A. E. Trueman for his important pioneer paper, in which he first described the evolutionary development of the "*Gryphaea* Lineage". The present paper is concerned with the "*Gryphaea* Plexus"; a much more comprehensive conception than the "Lineage", the importance of which has become increasingly recognised in recent years. The plexus is shown to exhibit during its history in the Lower Lias two phases; a shorter earlier one, in which the main mutational changes took place; and a longer later one in which these changes extended to an increasing number of individuals. The principal changes are described and their importance assessed.

Introduction

The fossil *Gryphaea* is a bivalve shell closely related to the Oyster (*Ostrea*) from which it differs in that its left valve is sharply curved and pointed, thus resembling the beak of a mythical creature known as the Gryphon, often portrayed in ancient decorative carvings. The value of *Gryphaea* for the study of evolutionary problems was first established by Trueman (1922).

The material for this study of the *Gryphaea* plexus was collected from a small area, less than a mile long, lying in the Vale of Belvoir south of *Granby and* north of Plungar, near to the boundary between Nottinghamshire and Leicestershire (Swinnerton 1964, p. 409). The major part of it came from a criss-cross of trenches excavated in 1940 on the outcrops of those Lower Liassic strata described by Kent as "The Granby Limestone Series" (Swinnerton & Kent 1949, p. 40). These have an estimated thickness of about 70 feet and are situated within the Schlotheima Angulata and the lower part of the Arietites Bucklandi Zones. A smaller quantity of material was obtained from a higher horizon, from beds exposed in a number of bomb craters lying north of Plungar and separated from the trenches by less than half a mile occupied by barren clays. These craters were situated on the outcrop of the Ferruginous Limestone Series in the Arnioceras Semicostatum Zone. Table 1 summarizes the stratigraphy of the localities.

TABLE 1

STRATIGRAPHICAL COLUMN OF THE TWO LOWEST STAGES OF THE LIAS

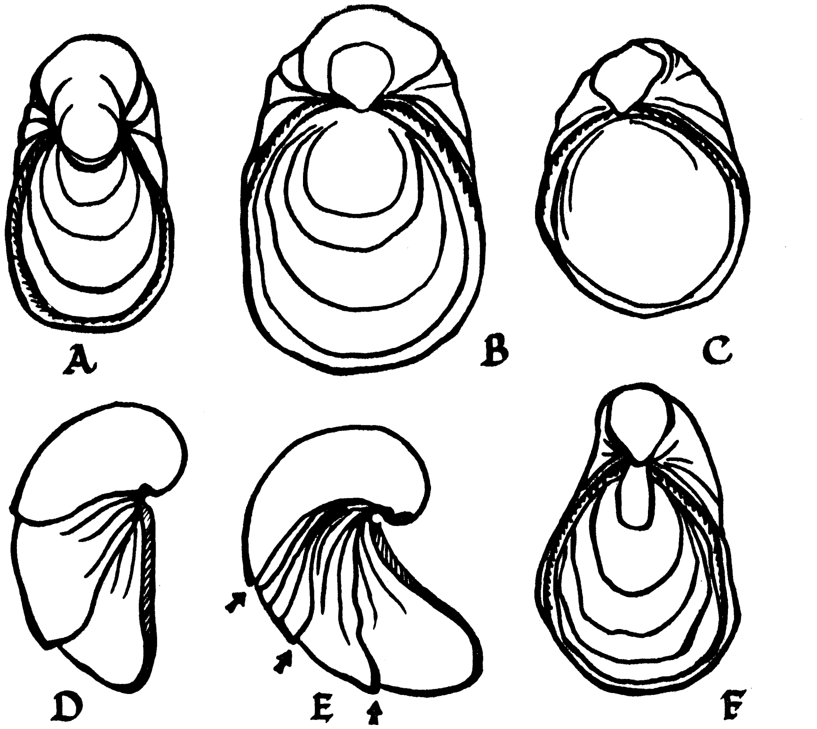
Lower Lias (Lower part)	Sinemurian	*Echioceras raricostatum*	Shales
		Oxynoticeras oxynotum	
		Asteroceras obtusum	
		Caenisites turneri	
		Arnioceras semicostatum	Ferruginous Limestone Series
		Arietites bucklandi	Shales
	Hettangian	*Schlotheima angulata*	Granby Limestone Series
		Alsatites liasicus	Shales
		Psiloceras planorbis	Hydraulic Limestones
			Preplanorbis beds

To guard against unconscious selection every recognisable fragment was collected. After careful cleaning those specimens were rejected that were too imperfect for useful measurement. Many of the others were practically perfect. The remainder were sufficiently complete for safe estimates to be made.

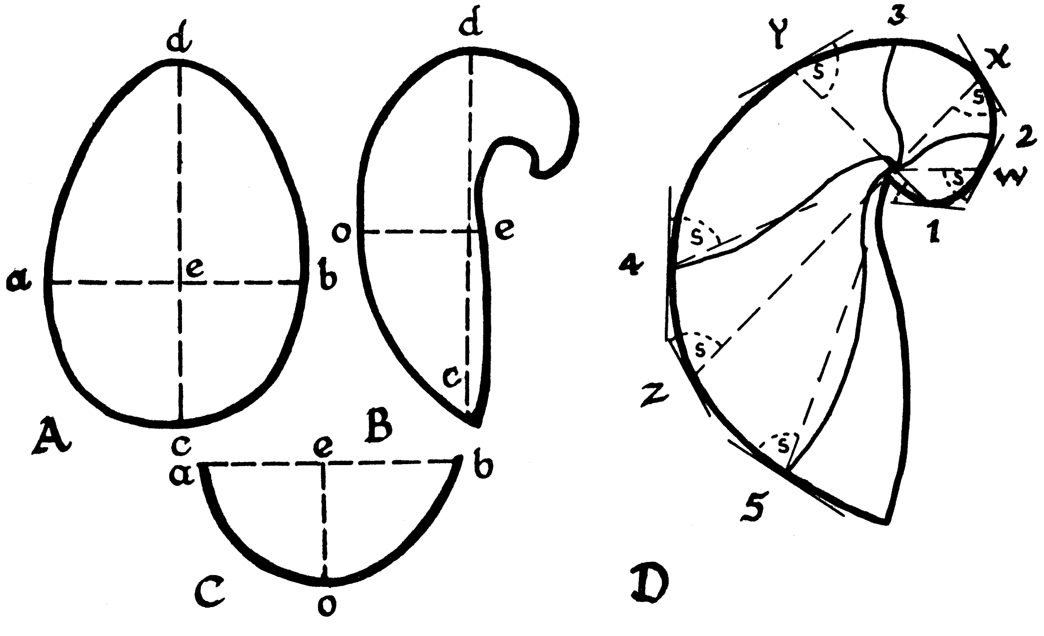
The fossils were unevenly distributed. A few came from the Lower Angulata Clays below the Granby Limestone Series. These had the same general characteristics as *Liostrea (Ostraea) irregularis* (Munst). but were larger than typical examples from Lavernock collected for *me by Dr. Trueman.* A *few* more came from a level 50 feet higher up in the base of the Granby Limestone Series. These were slightly smaller than those just mentioned, but nevertheless larger than the typical examples. Unfortunately even they did not suffice to throw any light on Trueman's view that '*O. irregularis*' was the ancestral stock of *Gryphaea.* Apart from this, the material discussed below came *from a sequence* of rocks stratigraphically *comparable* with those from which the *Gryphaea* specimens studied by Trueman (1922) were obtained.

It will be evident from the following descriptions and discussions that this material is representative of a compact closely related whole; that is to say of a plexus within which the various species of *Gryphaea* known as *G. obliquata* (Sow.), *G. incurva* (Sow.), and *G. maccullochi* (Sow.) have been *recognised.* These forms are *illustrated in text-fig. 1.* (The name *G. incurva* is used throughout, although *G. arcusta* has priority, to facilitate comparison with Trueman's work).

It is important to note that, though such a series of morphological changes can be recognised, no corresponding sequence of genetically related individuals can be isolated from the actual interbreeding



Text-fig. 1 The main variants in the *Gryphaea* plexus of the Lower Lias. A-C, right-hand views of *G. incurva*, *G. obliquata* and *G. maccullochi*, showing the variations in breadth. D-E, Posterior sketches of C and A showing disjunctions in the sequence of growth lines. F - a variant which tends to broaden near the ventral margin.



Text-fig. 2 Dimensions and measurements used in the text. A. Dorsal aspect, B & D. lateral aspect and C, cross-section. c-d, length; a-b, breadth; o-e, height; s, spiral angle - W.X.Y.Z. at 45, 90, 180 and 270° respectively, and 1, 2, 3, 4, 5 at growth stages, only disjunctions shown. The vector line is drawn from the point of origin of the shell to the first growth lamella, then rotated through 45, 90, 180 and 270° to give the spiral angles at these points.

communities preserved in the fossil state. Trueman showed that he realised this when he emphasised that a "lineage is a bundle of lines" and even suggested that a new name should be adopted (1924, p. 258). While discussing this question with him in 1940, I pointed out to him that the term "plexus" was the one required for the purpose but he definitely refused to use it. This was unfortunate for, in the absence of any precise statement of the differences in meanings, the continued use of these terms has resulted in a confusion of thought in the minds of various workers. The purpose of this article is to attempt a precise description of the plexus which fundamentally forms the background of the Gryphaea incurva lineage as he portrayed it.

Attention can be drawn at this stage to similar cases which have been described by Sylvester-Bradley (1958, 1959) from specimens obtained elsewhere from rocks higher in the sequence, throughout the Jurassic, suggesting that the 'Ostraea' - Gryphaea plexus is not confined to the Lower Lias.

Trueman regarded increase in size as one of the evolving characters of Gryphaea. His estimate of size was based mainly upon the length of the shell measured from the ventral margin of the left valve to a point directly opposite on the curving profile of the surface. This measurement is unfortunately influenced appreciably by the closeness or otherwise of the coiling. The length of profile of the left valve measured from the apex of the umbo along the middle line of the outer or curving surface to the ventral margin is not so affected and is correspondingly more reliable, even though it may include the area of attachment and possibly also a broken ventral margin. The extent of the latter may be closely estimated by extrapolation from the growth lines. Text-fig. 2 shows the various measurements which are used throughout this article.

Trueman's measurement were made upon 'adult' specimens, but his idea of adulthood seems to have been based upon size (Joysey 1959, p. 300). He thus tended to argue in a circle.

Growth of the Gryphaea shell

A close inspection of the growth lines of any well cleaned specimens reveals indications of stages of growth. Trueman's published figures show that he saw some of these and even drew them (Maclennan & Trueman, 1942, p. 216, text-fig. 3). As with other Mollusca, the shells of Gryphaea have their lamina secreted by the animal's mantle surface. As the lamina grew the edges of each one extended beyond that of its predecessor. This extension reached its maximum along the ventral margin. At intervals the rate of growth of the animal itself slowed down and the growth lines become correspondingly crowded. In Gryphaea this process seems to have culminated in a cessation of growth or possibly even a shrinkage in size of the animal. The evidence for this is seen along the anterior and posterior margins where the dorsal ends of these lines withdraw from the hinge area until only a small portion of the ventral margin remains visible,in the form of a narrow crescent near the middle of the profile surface. After a while growth was renewed and the margins of the laminae emerged once more at the surface as a succession of crescents increasing in size, with their horns progressing dorsalwards, until their points reached the hinge region. This sequence, as seen on the anterior and posterior aspects of the shell results in a disjunction, resembling an unconformity, in the midst of the growth lines (Text-fig. 1, E). This disjunction can also be traced across the outer surface of the shell. The two portions sometimes meet exactly across the outer surface of the shell; at other times they meet only approximately. Frequently the growth stage is emphasised by a freely projecting laminar margin showing occasional irregularities of growth. These features evidently reflect a halt or possibly even a set-back in the normal growth of the animal. It is tempting to associate them with an unfavourable season such as winter. Probably this was the case in some instances; but others may possibly reflect a slowing down of growth during the breeding season. The adoption of such a non-commital term as 'growth stage' therefore seems advisable.

On the surface near the umbo the growth lines may be obscured, for the earlier laminae were very thin and therefore the pattern of their growth was easily eroded or corroded. On the other hand, in old individuals the ventral margins often show distortions and irregularities which obscure the growth line pattern. The clear attainment of four or five growth stages is frequent but occasionally the number may be seven or eight.

The rate of growth

When measuring the length of the valve it is easy to mark the positions of growth stages with white ink and thus obtain a reliable basis for comparing rates of growth. In specimens from the lowest horizons, the middle and upper horizons of the Angulata Zone, such measurements showed that up to the first growth stage the normal length varied from 10 to 20 mms., but in some extreme individuals it varied from 4 to 35 mms.. For specimens from higher horizons (the lower part of the Bucklandi and the Semicostatum Zones), the corresponding figures were normally from 15 to 30 mms. and from 15 to 37 mms. respectively, but for the extreme cases, from 6 to 20 mms. and from 10 to 49 mms. respectively. Evidently the rate of growth in early life had already speeded up with the passage of generations, the first growth stages occurring progressively later in many specimens from the higher beds.

When growth rates and profile are plotted against one another (text-fig. 4), the resulting graphs are approximately straight lines, thus indicating that growth was normally regular. The growth lines for a collection of individuals from closely associated strata fall naturally into a cluster or stratigraphical group. Four such groups (Table 2, A, B, C, & D) were studied. When the corresponding clusters are superposed, it is found that they overlap one another in such a way as to indicate that a gradual increase in growth rate has taken place during the passage of generations.

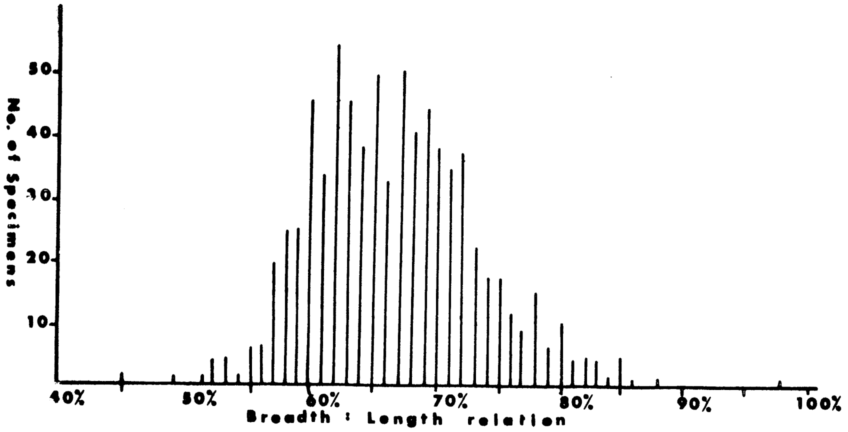
The number of individuals that lived long enough to attain the later stages of growth (numbers 6, 7, and 8) was very small; but those that reached adult stages (numbers 4 and 5) was much greater. These fell naturally into a stratigraphical sequence as shown in Table 2, in which the number of individuals found at successive levels is given.

TABLE 2

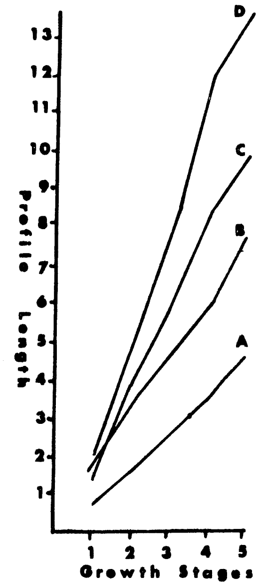
DISTRIBUTION OF ADULTS

Zone or Sub-zone	Group Thickness	A	B	C	D
Semicostatum		3	36	73	32
Lower Bucklandi	4 ft. 4 ins.	-	16	24	6
	18 ft. 6 ins.	5	51	121	39
	Base of Bucklandi Zone				
Angulata	13 ft. 9 ins.	3	29	8	7
	1 ft. 0 ins.	6	44	32	10
	6 ft. 0 ins.	209	257	25	-
	Gap of 50 feet				
	25 ft. 0 ins.	25	24	-	-

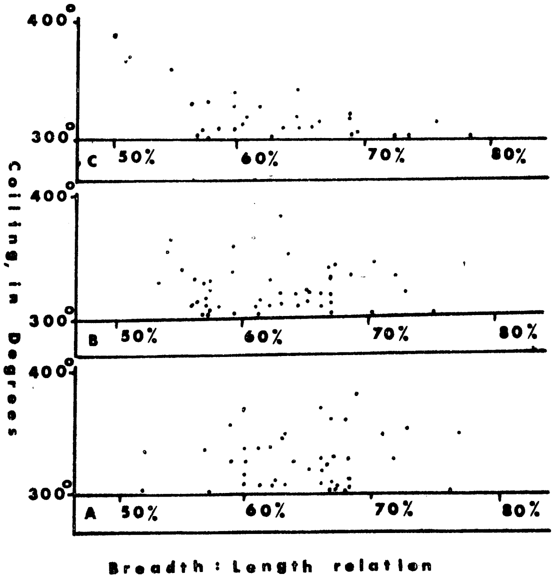
In interpreting this table, care must be taken to distinguish those levels at which individuals with new rates of growth first appear, from those later ones in which these rates have been merely extended to



Text-fig. 3 Histogram illustrating the relation of breadth to length in more than 760 specimens from all levels.



Text-fig. 4 Graphs illustrating the increase in rate of growth for the Angulata (A, B); Bucklandi (C); and Semicostatum (D) Zones respectively.



Text-fig. 5 Diagram illustrating the distribution of 300° or more of coiling for the corresponding groups of specimens in the successive zones of Angulata (A), Bucklandi (B), and Semicostatum (C).

number of individuals. Such a distinction marks off the actual process of evolution, as expressed by the entry of new mutations, from those subsequent increases in numbers of individuals in which the mutation merely finds continued expression. Table 2 shows that the rates represented in Groups A and B were already present in the lowest assemblage studied. The rates of growth represented in Groups C and D appear in the sequence in the two succeeding levels; thus indicating that evolution in size, due to the entry of new mutations in growth rate, was practically completed long before Angulata times.

The changes in numbers of individuals, though important, are merely a concomitant phenomenon associated with a decline in the number of those showing the lower rates of growth. Those exhibiting intermediate rates increase to a maximum of 56% in the lower horizons of the Bucklandi Zone and then decline to 50% in the Semicostatum Zone. The growth rate represented by Group C remained dominant while rate D rose to only 22% at the same level. The upshot of this was that the specimens with the higher growth rates attained maximum sizes and made up the dominant part of the *Gryphaea* population in the uppermost levels. This is the phenomenon that Trueman's graphs really record. The question naturally arises; should mere increase in relative numbers be strictly regarded as evolutionary or should the concept of evolution be confined to the process which brings about the first appearance of new stages in the development of fresh features? The latter view, as I understand it, is the one held by experimental biologists and is the one adopted here.

Transverse features

Trueman makes no specific reference to either breadth (width) or transverse profile in his list of progressive characters (1922, p. 258), but in his description of *G. obliquata* (Sow.), he mentions that the shell is broader in proportion than in *G. incurva* (1922, p. 266). In referring to other members of the grypheate series, he notes *G. macculloch*i (p. 264) and *G. cymbium* (p. 264), both of which are characterized by a similar or even greater breadth of shell. If we accept these as 'species', then breadth and transverse profile are among characters which contribute to the evolution of grypheate species not excluding *G. incurva* (see also Joysey 1959, p. 320).

Breadth in relation to length

The part played by the breadth of the shell in the general appearance of *Gryphea* may be appreciated by looking down upon the outer or curved surface of the left valve. In this aspect the umbo is partially hidden from view. The breadth of the shell is therefore seen, not in comparison with the true profile length, but with the length as Trueman measured it, i.e. from the centre of the ventral margin to a point on the opposite end, situated in the surface profile. As thus seen, the shape of the shell ranges from a relatively narrow oval, such as that seen in a typical specimen of *G. incurva*, to the wide, almost orbicular, outline of *G. macculloch*i (text-fig. 1, A & C). In very extreme individuals, the breadth, expressed as a percentage of length, may be as low as 30% or as high as 110%. For the majority it lies between 60% and 72% (text-fig. 3). Within this range the shape is further modified by slight variations in the position of maximum breadth, from lying nearer to the centre of the shell to a position nearer to the ventral margin (text-fig. 1, F).

These varieties are present at all levels, from near the base of the Granby Limestone Series up to the Semicostatum Zone. Apart from the absence of the extreme variants at the base and at the top of the sequence, there is apparently no progressive change in these breadth-length relations. All these variants lie within the genus *Gryphaea*, for they all exhibit the grypheate coil. From text-fig. 5, it will be seen that the high degree of coiling, 300° or more, is not confined to any one of these varieties but is so widely distributed amongst them as to indicate the breadth of shell and degree of coiling are not closely linked together.

The central mass of the plexus is made up of intermediate forms having the general features of *G. obliquata*, a species usually associated in literature with the Angulata Zone. These also are affected by the general increase in size referred to above, but there is no real necessity to distinguish between the *G. obliquata* of the lower and higher levels.

It should be re-emphasised that the main evolutionary change that takes place in this plexus is increase in size. Though all variants (? species) are found at all levels there is, as already noticed, a relative change in numbers. While *G. obliquata* is dominant in the Angulata Zone, *G. incurva* and *G. maccullochi* become more prominent in the Bucklandi and Semicostatum Zones by reason of a mere increase in number of specimens present. In the upper part of the Semicostatum Zone, *G. maccullochi* begins to merge into *G. cymbium.*

The *G.* aff. *obliquata* figured by Trueman (1922, text-fig. 1, C and text-fig. 2, A) really belongs to *G. maccullochi*; even so, as pointed out above (p.93) the sequence of changes he visualised certainly took place but was completed much lower down in the Angulata Zone, near to the base of the Granby Limestone Series. It did not, however, take place as a distinct line (so-called lineage) but as part of the general shuffling of characters within the communities which make up the plexus.

Apart from one or two very extreme and extraneous individuals (omitted from Table 3), the general range of variation of breadth remains relatively constant, as indicated by the figures given in Table 3.

TABLE 3

GENERAL RANGE OF VARIATION IN BREADTH OF SHELL
EXPRESSED AS A PERCENTAGE OF LENGTH OF THE SHELL

Stratigraphical horizon	No. of specimens	Range of variation
Semicostatum Zone		
Ferruginous Limestone Series	50	58.5% - 83.5%
Lower Bucklandi Zone		
Upper Granby Limestone Series	327	59.0% - 79.0%
Angulata Zone		
Middle Granby Limestone Series	135	62.0% - 77.0%
Lower Granby Limestone Series	514	60.0% - 82.0%

From all this it appears that though there is a considerable range of variation in breadth, there is no progressive change in this character within the period of time represented by these four levels. In this respect the species *G. incurva* lies on one side of the plexus and is not, as would be the case for the type specimen of a true species, a common or central variety. (See text-fig. 3).

Transverse profile

The dominant characteristics of the transverse profile may be expressed in terms of height as a percentage of breadth. By comparing the percentage for the umbonal or juvenile portions of the shell with that for the more fully grown portions, an estimate may be formed of the amount of change which took place during the individuals growth. Thus in a typical specimen from the middle part of the Angulata Zone, the variation in the proportion of height to breadth was from 40% to 73%. This fact indicates that even during the life time of one individual, the transverse profile became narrow and higher. The amount of this change was far from being the same for all individuals. Even without this assemblage from the Angulata Zone, the change in the relationship of height to breadth might range from as low as 7% during the lifetime of some individuals to as much as 34% in others.

The wider significance of these changes may be brought out by considering table 4. As the number of specimens of *Liostrea [Ostrea] irregularis* found near Granby was much too small for comparative purposes, I have included the measurements based upon a collection from Lavernock (Glamorgan) made for me under Dr. Trueman's supervision.

TABLE 4

GROWTH CHANGES IN TRANSVERSE PROFILE

Zone or sub-zone	Species	In Youth			In Later Life		
		No. of specimens	H/B Range	H/B Mean	No. of specimens	H/B Range	H/B Mean
Semicostatum	*G. incurva*	166	27-69	50%	166	52-88	70%
Bucklandi	*G. incurva*	171	24-70	45.8%	175	46-72	61.6%
U. Angulata	*G. obliquata*	556	25-70	41.9%	558	48-73	58.9%
M. Angulata	*G. obliquata*	67	16-68	45.4%	68	50-76	60.7%
L. Angulata	*L. irregularis*				87	24-68	45.4%

H/B - The relation of height to breadth of transverse sections .

Extreme cases excluded.

The figures given for *L. irregularis* confirm the impression expressed by me some years ago (1939 p. xl), that this species shows a range of variation in transverse profile which lies near to that of the juvenile phases of *Gryphaea* species from higher stratigraphical horizons. (1939, p. lxv).

In *L. irregularis* this range is from low arched forms, in which the percentage for height against breadth is only 24%, to high arched forms, in which it may rise to 68%, or in extreme cases to as much as 79%, the average being 45%. The corresponding figures for the young in the earliest assemblages of *G. obliquata* that were examined is from 16 to 68% which is almost the same as for the adult stages of *L. irregularis.* It is noteworthy that for juveniles from higher stratigraphical levels, the figures lie sufficiently close to these to justify the view that this does indeed represent an ostreoid phase in the development of *G. obliquata* and *G. incurva.*

Though the variation in transverse profile in youth remains relatively close to that of its presumed ancestral stock throughout the period of time that stretches from the middle part of the Angulata to the lower part of the Semicostatum Zones, the range of variation of the height to breadth percentages tended to decrease and the average to increase slightly. On the other hand, marked changes took place during later growth. Thus the range of variation in height of profile may become reduced to about half that shown in earlier life. This change was brought about as the result of three factors. First there was the disappearance or non-development of those individuals which would exhibit the lower percentage height of profile. Secondly, and supplementary to the first, was the development only of those individuals having the higher percentages. The third was the apparent slowing down or even the non-appearance of new mutations for yet higher percentages. In the lower part of the Semicostatum Zone, where the adult range of variation in height of profile increased to as much as 107% and the height-breadth relation rose to over 70%, true *G. incurva* became most numerous. After that *G. incurva* declined and disappeared in the upper part of the of the Semicostatum Zone.

In the absence of such an analysis of variation, the general impression produced would have been that the height of profile was a progressive character in the evolution of *Gryphaea*. This, however, was not the case, for the various percentages exhibited in the latest assemblages were already present in the ancestral ostreoid stock. That fact implies the absence of new mutations in the later assemblages, and therefore the absence of progressive evolution in the strict sense. Here, as with the curvature of the left valve, the impression of evolution is produced by a relative increase in the numbers of the individuals exhibiting the higher percentages. This, however, is not what is usually understood by the term evolution. On the contrary *Gryphaea* shows the way in which nature shuffles the characters in a population during the individual development, and also the way new characters are produced.

The measurements of specimens from the middle beds of the Angulata Zone, as shown in Table 4, illustrate the variations in the direction of change in the height-breadth relations which may take place during growth. The fourth column brings out an important fact which may be obscured by average figures:- it is that, nothwithstanding the general tendency for the transverse profile to increase in height, the range of variation that lies behind this includes individuals in which the height actually diminishes as the breadth increases. Some examples of this contrary type of variation may even be regarded as leading to the formation of species such as *G.maccullochi* and *G. incurva* which represent some of the strands which make up the plexus. If this be so, then the plexus, with its relatively stable stock of genetic characters,is surely the true systematic unit and could be defined in terms embracing the various characters of the plexus. It would then follow that the so-called species are strictly variants or sub-species within the plexus. All this is equally true for the assemblages considered from other levels. Thus in the lower part of the Semicostatum Zone, where the range of variation of height to breadth may be from 52 - 88%, the central specific form is *G. incurva.*

Finally attention may be drawn to other peculiarities such as change in the height to breadth relationship. Individuals having the same length of profile, e.g. 7 cms., may show widely different shifts in height during growth, from as low as 33% to as much as 67%; that is to say there is a range of 34%. In others it was from 67 to 75%, a range of only 13%. Again in the collection as a whole, the specimens ranged in length from 38 cms. to 75 cms., but the change during growth varied from as low as 1% to as much as 36.5%. Thus within the plexus variation may proceed at such a rate as to produce negative or positive results in different specimens.

Concerning Coiling

Though Trueman listed several progressive features, his main emphasis was laid upon the arching of the left valve into a coil. This feature has accordingly received the lion's share of attention from subsequent workers. This was largely due to the fact, to which Trueman drew attention, that D'Arcy Thomson (1917) indicated the approximation of this coil to a logarithmic spiral. A superficial resemblance must be admitted, but unfortunately this has lain like a red herring across the path of various workers, including Trueman himself. In his first paper of the series he indicated the position of the point of origin around which the coil turns (1922, text-fig. 3). Later he amplifies this by writing "it is impossible to fit any portion of the later part of the shell to a curve unless the position of the origin *is changed from that of the first part*"(the emphasis is mine) (1942 p. 215). It seems to me that the necessity for such juggling definitely puts the logarithmic spiral out of account. Nevertheless later workers have continued to take this similarity seriously, even though it has no apparent biological or palaeontological significance.

Trueman's work indicates that the degree of coiling varied during individual development. In order to study this development, the point of origin for measurements must be fixed (see text-fig. 2). The best position for this is the apex of the umbo which is often precisely marked by the presence of the original larval shell situated at the umbo of the first shell lamella. In order to see this clearly it is essential that the *whole* of the earthy matrix about the apex be cleared away (Trueman 1922, p. 264). The line which may be taken to pass from this point to the ventral margin of that lamella may be adopted as the vector line. As this is rotated, the value of the spiral angle may be found for any point on the profile of the shell (text-fig. 2D). The varying size of the area of attachment makes no difference to the position of this line, though it does affect the total curvature of the shell. On the other hand, the ventral margin of the shell is often broken off, but as explained above (p.92) the original position of the edge may be estimated with reasonable accuracy. One useful outcome of the 'red herring' has been the realisation of the value of the spiral angle. Trueman states that in the development of the grypheate shell, this angle also tends to increase (1942 p. 214). The actual fact cannot be so simply stated, as will be seen from Table 5.

TABLE 5

THE SPIRAL ANGLE IN VARIOUS SPECIMENS

Ref. points Specimen nos.	45°	G.S.1	90°	G.S.2	180°	G.S.3	270°	G.S.4
G. bucklandi	42°		65°		76°	75° 83°	82°	74°
O. angulata	60°		65°	68° 68°	70°	75° 71° 80°	80°	89° 80° 90°
B.5 - 1	50°		60°	73° 76°	74°	78° 80°	87°	90°
AD 130 - 85	53°	61°	70°	61° 60°	70°	67°	67°	
AD 245 - 5	47°		55°		89°	78° 83°	73°	77° 75° 77°
AD 125 - 2	40°		55°	79°	82°	70° 75°	75°	
AD 125 - 8	50°	43°	60°	64° 70°	77°	74° 70°		

In this table, the points on the profile for which the angle was measured are those at regular intervals and those which mark the stages of growth (G.S.) giving eight points (text-fig. 2D) with certain additional reference points when possible.

From this it will be seen that the angle is at a minimum in early life and thus reflects a tendency towards the repetition of the conditions in an ostreoid ancestor (Trueman 1922, p. 261). Later on, this angle increases up to as much as 80° or 90° but may exhibit some marked irregularities.

Joysey (1959, p. 300) pointed out that Trueman must have included individuals of different ages in his sample and that therefore the continuity of variation in coiling indicated by him to some extent represented a growth series rather than a purely evolutionary one. I have tested this suggestion by making similar graphs for all the specimens collected from the two most fossiliferous horizons, viz. low down in the middle part of the Angulata Zone and in the lower part of the Bucklandi Zone respectively. The number of individuals that had attained to growth stages 6 to 8 proved to be too small for the purpose. Only by including those that had attained to stages 4 and 5 did the resulting graphs become comparable with those figured by Trueman. Indeed the resemblance to his graphs, drawn from specimens obtained from the Vermiceras and Rotiformis Sub-zones (lower part of the Bucklandi Zone) is so close as to leave no doubt, not only that the species were identical, but that Joysey's criticism was justified.

In the absence of a knowledge of growth stages it is evident that, for Trueman, the sizes attained at these stages were his unconscious criterion of adulthood. By reason of their much greater numbers, those in growth stages 4 and 5 exercised the dominating influence upon the positions of his modes. On the other hand, those that had attained to still later growth stages exercised a marked influence on the lower slopes of the right limb of his graphs. Because the majority of the specimens must have been in growth stages 4 and 5, the incidental inclusion of individuals of later ages did not affect the validity of his conclusions seriously. It may be pointed out that a failure to clear the apex of matrix completely may lead to a degree of error of 90° in an estimate of the total curvature of the shell (1922 p. 264, para. 1).

Joysey (1959, p. 301) states that Trueman's chart "does demonstrate progressive increase in the total range of coiling". My experience, however, tends to indicate that in this respect the chart is slightly misleading. In a collection of 509 specimens from the middle of the Angulata Zone, nearly 50 individuals already coiled between 300° and 380° (text-fig. 5). This upper limit was exceeded later by one specimen from the Semicostatum Zone, which appears to have reached 390°. These facts suggest that Trueman's charts do not represent quite correctly the ranges of variation in degrees of curvature that they are said to indicate.

The fact that, in the development of any individual, growth in size is accompanied by an increasing degree of coiling gives the impression that size and coiling are closely linked together. Phillips (1962) has shown mathematically that in the production of the total degree of coiling, increase in size plays an almost insignificant part as compared with tightness of coiling, as reflected by the increase of the tangential angle. The comparative figure he arrived at was 23% for increase in size and 143% for increase in the tangential angle. This is confirmed by the presence of high degrees of coiling in groups of smaller specimens found in lower stratigraphical levels. Thus one specimen, having a profile length of only 6.9 cms., attained to a coil of 380° in growth stage 6. This equals the maximum found higher up in the lower part of the Bucklandi Zone. Nevertheless, in a collection of 288 specimens from the Semicostatum Zone, one had a coil of 390°. Such facts indicate that the mutation in degree of coiling had almost reached its upper limit at the lower level. On the other hand, the number of individuals that attained to a curvature of 300° or more in the earlier communities formed only 15% of the population. In the later communities, this figure rose up to 31%.

So it seems then, that as with the evolution of the rate of growth, so with the coiling, two stages may be distinguished in the plexus; an earlier and comparatively brief phase in which the major part of the mutation took place, and a later phase, in which the impression of further evolution is produced by a marked increase in the numbers of individuals which carry on the more advanced mutation.

Trueman put forward the view that coiling of the apex of the left valve developed to such an extent that the umbo, by pressing on the right valve, locked this in a closed position and thus led to the death of that individual. He even extrapolated this to the extinction of the "lineage" (1922 p. 265, para. 1). Though I have cleaned a great number of well grown specimens of Gryphaea, I must confess that to my disappointment, I have never had the good fortune to see any specimen in which such a locking had occured. On the other hand, I have been impressed by the fact that during growth of the cardinal area, this extends in such a way that the hinge line is carried out of range of such an eventuality. (Maclennan and Trueman 1942 p. 40, text-figs. 3 and 4).

Conclusions

The examination of specimens of Gryphaea from the Lower Lias of the Vale of Belvoir has resulted in the development of an improved method of measuring the length of the shell along the middle line of the outer or curving surface to the ventral margin. The measurement of the spiral angle has been facilitated by fixing the point of origin of the measurement at the apex of the umbo. Using 'disjunctions' in the growth of the shell it is possible to establish growth stages, which can be used to distinguish adult specimens. The spiral angle has been measured at the growth stages and at other fixed points and it is shown to be at a minimum in early shell life, increasing later; a feature also found in the ostreoid ancestor.

Breadth of the shell is considered to be an important character, unrelated to length. It has been used as a factor in the breadth - height relationship, expressed as a percentage. An analysis of the variation of transverse profile shows that the increase in height of profile, both in ontogeny and phylogeny, is a progressive character, but is present in the ancestral ostreoid stock. In later populations there is an increase in the numbers of individuals with higher percentages of the breadth to height ratio. This is accompanied by a decrease in the range of variation, the result being that most specimens are the high arched form.

Coiling can no longer be considered to be comparable to a logarithmic curve. Neither can excessive coiling be considered to cause the death of an individual or the extermination of the plexus. The curvature of the valve is best expressed by the spiral angle, rather than in terms of coils. Increase in coiling is manifest in specimens from lower horizons and becomes dominant in the higher horizons due to the increase in the numbers of individuals with this character. Some of the small specimens in the lower horizons have attained a coil of 300° or more, which suggests that no simple relationship exists between increase in size and coiling.

Evolution expressed by rates of growth, transverse profile and coiling occurred as mutations in the lower stratigraphical levels, which become dominant in the higher levels by increase in the numbers of individuals with these mutations.

It is emphasised that the arrangement and development of the characters occurs as a plexus rather than a lineage, the specific forms discussed being useful morphological species by which the plexus can be described, whilst the whole plexus is nearer the definition of a biological species.

H.H. Swinnerton, D.Sc., Ph.D., F.G.S.,
The Headmaster's House,
The Haberdashers Aske's School,
Elstree,
Hertfordshire

References

JOYSEY, K.A. 1959. The evolution of the Liassic Oysters - Ostrea - Gryphaea. Biol. Rev., Vol. 34, pp. 297 - 352, text-figs. 1-17 .

MACLENNAN, R.M. and TRUEMAN, A.E. 1942. Variation in Gryphea incurva (Sow.) from the Lower Lias of Loch Aline, Argyll. Proc. Roy. Soc. Edinburgh, Ser. B, Vol. 61, pt. 2, pp. 211 - 32, text-figs. 1 - 11.

PHILLIPS, G.M. 1962. The Evolution of Gryphaea. Geol. Mag., Vol. 101, text-figs. 1 - 3, tables, 1 - 3. No. 4, pp. 327 - 44.

SWINNERTON, H.H. 1964. The early development of *Gryphaea*. Geol. Mag., Vol. 101, No. 5, pp. 409 - 20, text-figs. 1 - 3, tables 1 - 3.

SWINNERTON, H.H. and KENT, P.E. 1949. The Geology of Lincolnshire. Trans. Lincolnshire Naturalists' Union, 126 pp. 19 text-figs.

SYLVESTER-BRADLEY, P.C. 1958. The descriptions of fossil populations. J. Palaeont., Vol. 32, pp.

1959. Iterative evolution in fossil oysters. Proc. XVth. Int. Congr. Zool., London, pp.

THOMPSON, D'ARCY W. 1917. On Growth and Form. Cambridge Univ. Press.

TRUEMAN, A.E. 1922. The use of *Gryphaea* in the correlation of the Lower Lias. Geol. Mag., Vol. 59, No. 6, pp. 256 - 68, text-figs. 1 - 7.

1924. The Species concept in Palaeontology. Geol. Mag., Vol. 61, No. 8, pp. 355 - 60.

(Manuscript received 18th March, 1965)