THE MORPHOLOGY OF THE BRACHIOPOD SUPERFAMILY TRIPLESIACEA

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ABSTRACT. The calcareous structures of the triplesiaceid shell are discussed and interpreted in terms of the soft parts of the living animal. Special attention is paid to the pseudodeltidium, the pedicle tube, the muscle scars and pallial sinuses, which have received little consideration in the past. Relationships of the superfamily to other brachiopod stocks are considered. A new species of *Cliftonia*, *C. oxoplecioides*, from the Ashgillian, the earliest known for that genus, is described.

IN a study of the Ashgillian Brachiopoda of the Chair of Kildare Limestone, County Kildare and of the Portrane Limestone, County Dublin, Eire, material of the brachiopod superfamily Triplesiacea Cooper 1944 has been found which has yielded information hitherto unknown for the group. At the same time, this information has been supplemented by work of a somewhat broader nature, carried out by the author in preparation of the superfamily for the forthcoming brachiopod part of the Treatise on Invertebrate Palaeontology, including a study of the triplesiaceids of the Norwegian Lower Palaeozoic. Concerning the latter, a species of the genus *Streptis* has already been reassessed (Wright 1960), and a redescription of other Norwegian forms is at present in preparation.

Although species of three genera of the superfamily were known and described before the turn of the century, the only attempt at a comprehensive survey has been that of Ulrich and Cooper (1936), who dealt with the Silurian genera. While not wishing to be unduly critical of their valuable contribution, the author feels that a more interpretative approach to the group would be of value. In the present paper, this type of approach has been used, where practicable, in an attempt to reconstruct the anatomy of the animals by studying the mode of secretion of the various hard parts and the part performed by them in the living creature.

THE SUPERFAMILY TRIPLESIACEA

The brachiopod genera centred around the genus *Triplesia*, although only nine in number, were considered by Cooper (1944, p. 307) sufficiently different from all others to deserve superfamilial status.

The various species of the genera now placed in this superfamily were originally distributed amongst genera of widely separated brachiopod families, from *Orthis* to *Atrypa*, from *Strophomena* to *Spirifer*. This resulted from the close external resemblance between the triplesiaceids and species of these other genera. With the discovery of the internal structures of the group, it was realized that the animals all belonged to a closely

knit unit quite different in character from any of the families with which they had been previously associated, these associations being simply the result of homeomorphy. Accordingly, Schuchert (1913, p. 387) placed the genera in the Tripleciinae, as a subfamily of the Strophomenidae, but the marked differences between this subfamily and the other strophomenids prompted Öpik (1932, p. 69) to raise the group to familial level.

Following Cooper, who as stated above erected the superfamily, the status of the group was further raised to an order by Moore (1952, p. 221). This was subsequently reduced to subordinal level by Muir-Wood (1955, p. 89). The writer here follows Williams (1956, p. 285), in believing that with the present knowledge of the phylum the superfamily forms the most convenient larger unit. Williams (1956, p. 284) cites the triplesiaceids as one of the superfamilies which does not fall easily into place in his method of grouping the superfamilies around one of six well-known genera, and suggests that the Triplesiacea may belong to either the '*Orthis*' or the '*Pentamerus*' group.

Superfamily TRIPLESIACEA Cooper 1944

Family TRIPLESIIDAE Schuchert 1913 [*nom. correct.* Quenstedt 1931 (*ex.* TRIPLECIINAE Schuchert 1913 *nom. imperf.*)]

Diagnosis. Biconvex to markedly dorsibiconvex, impunctate shells, normally with a prominent undulation in the anterior commissure. Ventral interarea with a delthyrium closed by a flat pseudodeltidium possessing a narrow median fold running anteriorly from the small apical foramen. Dorsal interarea obsolete. Cardinal process long, forked, and directed posteriorly, with a saddle or hood often developed on the posterior side of its base, and with short divergent processes on either side forming the inner boundaries to the sockets.

Range. Ordovician (Llanvirn) to Silurian (Wenlock).

Remarks. The above diagnosis emends that given by Ulrich and Cooper (1936, p. 332). Perhaps the most outstanding single feature of the family is the unusual forked nature of the long cardinal process, which is unique amongst the Brachiopoda. This feature is well developed in the earliest member of the family (Cooper 1956, p. 529) as well as in the youngest stages known in the growth of an individual (Wright 1960, p. 275). Thus no indication has been given so far of how this feature developed, or from what ancestral stock it could have arisen.

Whilst the cardinalia are very conservative features of the family, the external appearance is extremely varied, and it is this that provides the basis for generic distinction. The nine genera into which the triplesiids are at present divided are given below, together with a brief description of the generic characters.

Generic diagnoses.

BICUSPINA Havlíček 1950: transverse, uniplicate, multicostellate shells of spiriferoid appearance.

BRACHYMIMULUS Cockerell 1929: smooth, like *Triplesia* but sulcate.

CLIFTONIA Foerste 1909: subcircular outline, with strong concentric lamellae imposed on radial costellae.

ONYCHOPLECIA Cooper 1956: small, of tear-shaped outline and lenticular profile, smooth, uniplicate.

ONYCHOTRETA Ulrich and Cooper 1936: claw-like outline with greatly elongated ventral valve and long interarea; dorsal valve short; ornament of coarse costellae.

OXOPLECIA Wilson 1913: roundly elliptical to transverse outline, uniplicate, ornament of costellae and fine elevated concentric growth-lines.

PLECTOTRETA Ulrich and Cooper 1936: subcircular outline, ornament of strong concentric lamellae, and strong radiating plications.

STREPTIS Davidson 1881: small, subcircular to transverse, strong concentric lamellae and superimposed radial ribs. Uniplicate, usually with marked asymmetry.

TRIPLESIA Hall 1859: smooth, uniplicate, strongly convex shells with marked trilobation.

THE MORPHOLOGY OF THE VENTRAL VALVE

The interarea and delthyrium. All members of the superfamily are characterized by the presence of a well-developed interarea on the ventral valve which varies in attitude from orthocline to apsacline. The external surface of the interarea is flat to concave, and is usually clearly marked by growth-lines parallel to the hinge, together with striae at right angles to them. Within the triangular delthyrium, situated medianly and delimited on either side by growth-tracks of the teeth, the small pedicle foramen is restricted to the apex; it may, however, resorb part of the ventral umbo thus becoming situated anterior to the beak (Ulrich and Cooper 1936, p. 333). The remainder of the delthyrium is covered by a triangular calcareous plate which lies flush with the interarea and which possesses a narrow median fold running anteriorly from the apex to the middle of the hinge-line (Pl. 109, fig. 1). This plate has been alluded to both as a 'deltidium' and a symphytium, but it is here shown to be a pseudodeltidium which was an integral part of the interarea, and which was quite independent of the development of the pedicle.

The pedicle tube. Havlíček (1950, p. 87) in erecting his genus *Bicuspina*, states that the essential difference between it and *Oxoplecia* is the presence of the pedicle tube in the former; this is totally lacking in the type species of *Oxoplecia*. The specimens of *Bicuspina* in which this 'pedicle tube' has been observed are all in the form of internal moulds (e.g. Pl. 109, figs. 5, 9) where a thin rod of matrix extends from the posterior end of the adductor scars to the pedicle foramen. This type of rod is open to two interpretations; in life it may have been surrounded by a cylinder of calcite, or, alternatively, it may have been simply a cylindrical hole in a solid wedge of calcite. In both cases, the pedicle would have occupied what is now a thin rod of matrix.

Both of these interpretations of the pedicle tube are to be found within the superfamily, and diagrammatic reconstructions of these, as well as the more common type of pedicle opening, are shown (text-fig. 1). The different arrangements depend essentially on the attitude of the pediculate–outer epithelial junction. The pediculate epithelium is responsible for the secretion of cuticular chitin and the external surface of the pedicle, while the outer epithelium secretes the calcareous shell (Williams 1956, p. 255).

The more usual relationship for the triplesiaceids (as in *Triplesia* itself) is seen in text-fig. 1B. With growth of the shell, the ventral junction of the pediculate epithelium with

the outer epithelium moves anteriorly; whilst on the dorsal side, where the delthyrial cover is being secreted, the junction remains stationary at its apex. Thus, with increasing size, proliferation of pediculate or outer epithelial cells takes place without affecting the position of the junction. Thus, in the median zone a calcareous plate is secreted to fill the delthyrium, the pedicle itself being enclosed within a chitinous tube, so that when the soft parts are destroyed only the apical foramen remains.
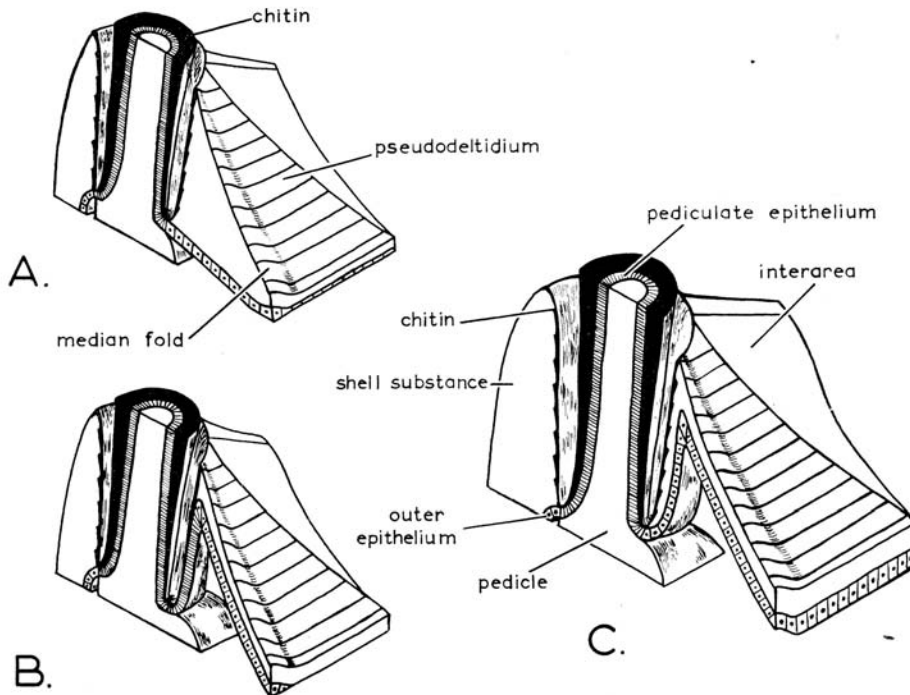

TEXT-FIG. 1. The nature of the triplesiaceid pedicle opening. Generalized block diagram reconstructions with oblique median views showing (A) development of a pedicle passage, (B) the 'normal' arrangement, (C) development of a pedicle tube.

Certain triplesiaceids show a quite remarkable thickening of the shell in the umbonal regions; the thickness of the shell in the umbo of a dorsal valve of *Triplesia ortoni* (Meek) observed by the author being about 7 mm. Young specimens are also thick, so that the thickening would seem to be a specific rather than a gerontic character, at least in this species. In the case of *Oxoplecia multicostellata* Cooper (Pl. 109, figs. 12, 15) thickening may also be observed in the umbonal regions. Here the delthyrial cover becomes very thick towards its apex, so that in these silicified specimens a neat cylindrical hole passes through the plate to connect the foramen with the interior of the valve. Text-fig. 1A shows the arrangement envisaged for this. The pediculate–outer epithelial junction advances anteriorly all round the pedicle as the animal grows, and thus the cylindrical

hole is formed with the delthyrial cover thickened on the ventral side. This cylindrical hole is here termed the *pedicle passage*.

The third variation observed is the development of the pedicle tube as used by Havlíček; whilst characterizing his genus, it is by no means restricted to it. Williams
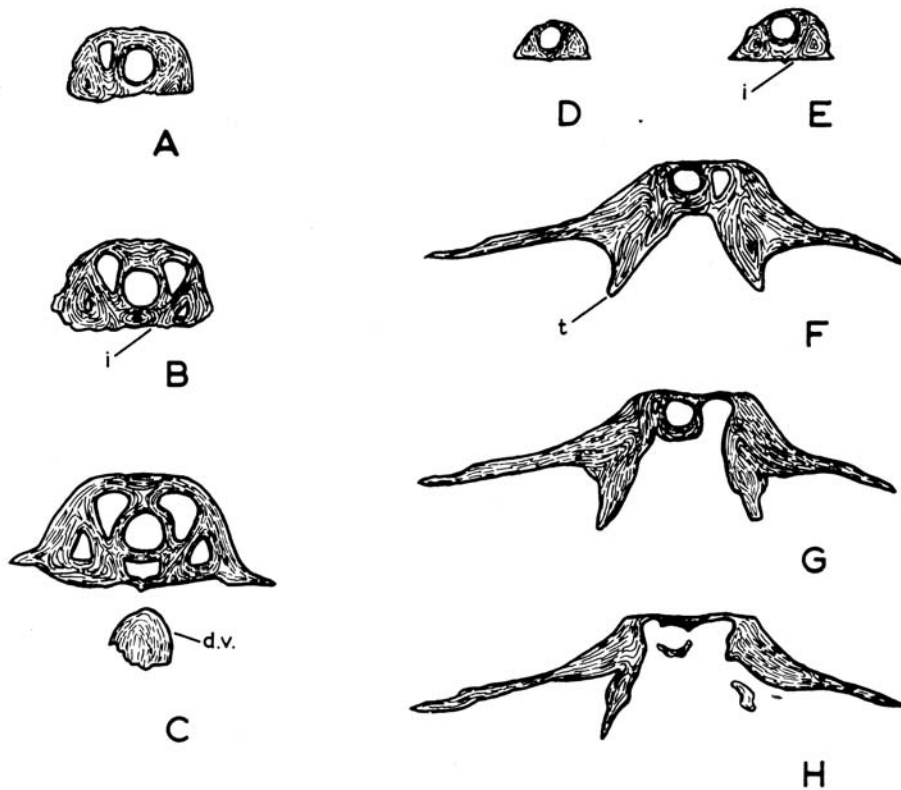

TEXT-FIG. 2. Transverse serial sections of *Cliftonia oxoplecioides* sp. nov. to show the pedicle tube. A–C: sections of a complete shell where the tube is lifted well clear of the valve floor by an isthmus of shell substance. A at 0·3, B at 0·45, and C at 0·6 mm. from the umbo. ×8. D–H: sections of a ventral valve cut slightly obliquely; the tube lies much closer to the valve floor. D at 0·6, E at 0·75, F at 1·5, G at 1·65, and H at 1·8 mm. from the umbo, ×7·7. d.v.—dorsal valve; i—interarea; t—tooth.

(1951, p. 105) describes a short tube in his species *Cliftonia lamellosa*, as does Wright (1960, p. 274) in *Streptis altosinuata* Holtedahl, and in *Cliftonia oxoplecioides* sp. nov. described below. This last species occurs in the form of complete shells in a limestone matrix, so that it is possible to produce serial sections. This technique gives a very satisfactory picture of the tube, substantiating the evidence obtained from the internal moulds. The ventral side of the tube (text-fig. 2) is formed by a thickening of the valve floor. The edges of this thickening are continued dorsally to form a discrete ring or

cylinder around the pedicle. The tube is usually situated close to the internal surface of the ventral valve, dependent on the somewhat variable thickening on the valve floor, which may take the form of a fairly high narrow isthmus between the valve and the pedicle. Posteriorly, the dorso-lateral sides of the tube especially tend to be in contact with the inner edges of the teeth, and the growth-lines (text-fig. 2B, C) show the two structures to be united; but anteriorly the tube becomes quite free, except for its contact with the valve floor on the ventral side (text-fig. 2H).

It will be noticed (text-fig. 2) that the pedicle tube is circular in section in *Cliftonia oxoplecioides*. Havlíček (1950, p. 88), in describing that of *Bicuspina*, says that the tube is slightly flattened in a dorso-ventral direction. Examination of a large number of specimens of *B. spiriferoides* (M'Coy) reveals that flattening may occur in the direction
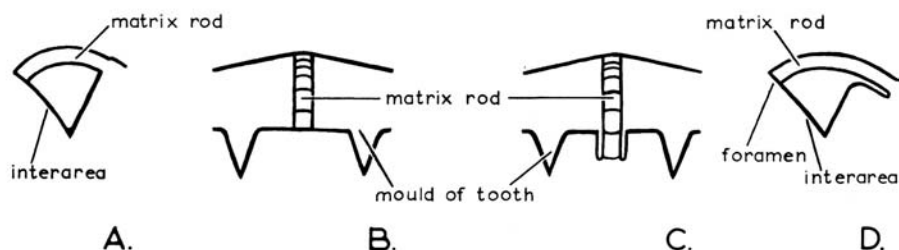
TEXT-FIG. 3. Diagram showing the relationship of the rod to the surrounding matrix of internal moulds for a pedicle passage (A, B) and a pedicle tube (C, D). A, D are median longitudinal sections through the rod; B, C show the rods in ventral aspect.

indicated by Havlíček, perpendicular to it, or else there may be no indication of flattening whatever. It would seem then, that this feature is due to squashing of the matrix filling the tube; or that the flattened tubes are variants of a cylindrical tube. In any event, dorso-ventral flattening is not a diagnostic property of the tube.

The diameter of the undeformed tube appears to be fairly constant over its length in most specimens of *B. spiriferoides*, and in *C. oxoplecioides*; that of *C. lamellosa* becomes relatively rapidly larger in an anterior direction.

Text-fig. 1C is a representation of the disposition of the soft parts where a pedicle tube is developed. Whilst the delthyrial cover is of a fairly even thickness, the pediculate–outer epithelial junction moves anteriorly with growth, so that the thin calcareous tube sheaths the pedicle dorsally and laterally, passing into the shell substance of the valve floor ventrally.

Although both a pedicle passage and a pedicle tube would produce a matrix rod when the material is in the form of internal moulds, the relationship of the rod to the surrounding matrix at its anterior end enables the two forms to be differentiated (text-fig. 3). In the pedicle passage (text-fig. 3A, B), the matrix rod abuts against a flat surface of matrix which marks the internal surface of the delthyrial plate. Where a pedicle tube is developed this surface will be seen to be hollowed out around the pedicle on its dorsal and lateral sides (text-fig. 3C, D), this space being occupied in life by the calcite of the pedicle tube. Posteriorly the two matrix rods will look similar; but where there is evidence of a pedicle tube in the anterior part it is reasonable to assume that this would continue to the umbo as in *C. oxoplecioides*.

The delthyrial cover. The study of the pedicle tube, which has enabled the reconstructions of the soft parts to be produced, has, as a corollary, shed light on the nature of the delthyrial plate. The pediculate–outer epithelial junction (text-fig. 1) occupies a position in the ventral valve ventral to the delthyrial plate throughout development, with the foramen occupying an apical or supra-apical position. Thus the plate within the delthyrium is secreted by a primary isthmus of outer epithelium quite independent of the pedicle and so is a *pseudodeltidium*. That this pseudodeltidium is an integral part of the interarea is supported by the fact that growth-lines may be traced right across the pseudodeltidium on to the interareas on either side of the delthyrium.

The narrow median ridge (Pl. 109, fig. 1) on the pseudodeltidium appears to be simply a median fold of that plate; certainly the growth-lines of the pseudodeltidium pass over the fold without any break. Ulrich and Cooper (1936, p. 333) believe the narrow fold to be associated with the 'chilidium', but it is here considered more closely related to the highly convex and incurved dorsal umbo.

With the establishment of pseudodeltidia in the triplesiaceids, this structure is now known to be a feature of four independent stocks, the others being the strophomenoids, the thecidaceids, and the nisusiids (Williams 1956, p. 258). Differences in the various pseudodeltidia do exist; those of the thecidaceids, the nisusiids, and the earlier strophomenoids are convex, while those of the triplesiaceids are flat with a median fold, although at the same time it must be remembered that the pseudodeltidia of the later strophomenoids are also flat. Again, the foramina of the first three groups are supra-apical whereas many of the triplesiaceids possess an apical foramen, though, as already noted, the ventral umbo may be resorbed so that the foramen moves out of the apex of the delthyrium.

These differences, however, do not alter the basic features of a pseudodeltidium; in fact they serve to emphasize further the different ways in which this feature may arise and the polyphyletic nature of the structure.

The muscle scars. The pattern of the ventral muscle scars in the triplesiaceids is unknown for the majority of species. This lack of information is so real that while Ulrich and Cooper (1936, p. 331), in discussing the relative values of characters in the group, rightly stress the familial level value of characters of the region around the ventral beak and of the pallial markings of both valves, neither the muscle scars nor the pallial markings receive more than an occasional mention in the rest of their paper.

The muscle scars are completely unknown for several genera; in others, only poorly preserved scars have been described for an occasional species, so that the information is scanty and of necessity the words 'obscure' and 'indistinct' are frequently used.

The occasional species, however, does indicate the muscle distribution within the valves. Pl. 109, fig. 5 shows a clearly defined ventral muscle area in a specimen of *Bicuspina spiriferoides*. This consists of a pair of flabellate diductor scars enclosing elongatedly cordate adductor scars laterally, and almost uniting in front of the latter. The diductor scars do not coalesce, but remain separate, as may be seen more clearly in Pl. 110, fig. 7. Through the narrow space separating the two diductors passes a pair of *vascula media* which arise immediately anterior to the adductor scars. Pl. 109, fig. 5 also shows two pronounced scars within the diductor scar postero-lateral to the adductors, which mark the position of the ventral adjustor muscles.

The scars in *B. spiriferoides* appear to be better impressed than in other species of the genus (Havlíček, p. 88), but a similar muscle distribution is found in those species of the genus *Triplesia* for which muscle scars have been observed; the diductor scars are flabellate and divergent to a greater or lesser extent, while the adductors are smaller and are situated between the diductors.

Cooper (1956, p. 557), in a description of *Oxoplecia simulatrix* (Bassler), states that the diductor scars of this species are flabellate also; for the other twenty-one species of the genus described in this work, no reference is made to the muscle scars which are presumably not impressed on the valves. Whittington and Williams (1955, p. 412) in describing their species, *Oxoplecia mutabilis*, find that whilst in most specimens the muscle scars are not impressed, one specimen does show a narrow, rather long muscle scar with a median lanceolate adductor scar enclosed by narrow diductor scars. Rather narrow diductor and adductor scars have also been recorded for a species of *Streptis* (Wright 1960, p. 273).
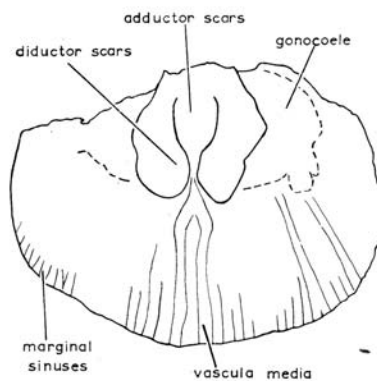
The pallial sinuses. The specimens of *Triplesia* from Kildare, which show, in the dorsal valve, by far the most complete pallial markings of any triplesiaceid known to the author, are completely devoid of these impressions in the ventral valve. Indeed, of the large number of specimens of the superfamily examined, evidence of the ventral pallial sinus patterns was only seen in four specimens of *Bicuspina spiriferoides*. The best of these is shown in text-fig. 4, and Pl. 110, fig. 7.

The branching canals take the form of grooves on the internal mould, thus the sinuses were situated on raised calcareous ridges on the inner shell surface. This indicates that the outer epithelial cells of the mantle, over which the sinuses passed, must have secreted calcite at a faster rate than in the intersinal areas.

Öpik (1934), in his outstanding work on pallial sinus patterns, is concerned principally with the clitambonitaceids and their relationships to the orthaceids, and does not mention the triplesiaceids in this connexion. Earlier, in a summary

TEXT-FIG. 4. The ventral muscle scars and pallial markings of *Bicuspina spiriferoides* (M'Coy), taken from the specimen figured in Pl. 110, fig. 7, ×2·4.

the characters of the triplesiids, he states that both the muscle scars and pallial markings to be little known for the group and ventures no further information (1930, p. 61).

The pallial markings on the specimen of *B. spiriferoides* here figured, while being clearly shown, are unfortunately incomplete. The *vascula media* arise anterior to the adductor scars, between the fronts of the diductors, and soon bifurcate. The pair diverge for a short distance, when they change direction and continue towards the anterior margin of the shell in a subparallel fashion, occupying only a relatively narrow sector of the shell.

The remainder of the pallial markings observed consist of marginal sinuses, while on the right-hand side two longer sinuses are preserved. These appear to arise at about midvalve where a shallow groove, marked in text-fig. 4 by a dashed line, is believed to

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mark the anterior limits of the area occupied by the gonocoeles. There is no evidence of an arcuate branch of the *vascula media* being directed in the same way as the *vascula myaria* of the dorsal valve, so it would appear that these two long sinuses form part of a series arising directly from the gonocoele as *vascula genitalia*. This is the lemniscate condition of Williams (1956, p. 275). The possibility of the two sinuses being given off from an arcuate sinus cannot entirely be ruled out due to the incomplete preservation of the pattern; but there is no trace of such a branch arising from the *vascula media*. The shallow groove, which has been taken as the anterior and lateral margin of the gonocoele, might possibly be an arcuate sinus, but its apparent termination against the lateral edge of the diductor scar, and not on the *vascula media*, would seem to make this interpretation unlikely.

THE MORPHOLOGY OF THE DORSAL VALVE

The hinge region and cardinalia. This region of the triplesiaceid shell includes the hinge-line, the 'brachiophores', the 'chilidium', and the cardinal process. Apart from these structures it is necessary here to consider the valve-opening mechanism and the role performed by the calcite processes, together with their effects on the intimately connected ventral structures (e.g. pseudodeltidium) during opening and closing of the valves.

As already stated, one of the outstanding features of the superfamily is the development of an exceedingly long, forked cardinal process (Pl. 109, fig. 14). This structure curves round backwards, from its variably thickened base at the posterior of the dorsal valve, to extend into the ventral umbo. The myophores are located on each prong at its distal end, usually as deep grooves on the dorsal surface. The actual mechanism of the muscles is discussed later.

Ulrich and Cooper (1936, p. 333) state that the cardinal process has been greatly elongated owing to the unusually great convexity of the dorsal valve.

This explanation for the development of the cardinal process is inadequate when other brachiopod stocks are considered, especially in the light of the function of the cardinal process and the leverage systems by which the valves are opened.

In such a brachiopod as *Dalmanella* Hall and Clarke, to cite a widely known stock with relatively simple organization, the cardinal process is situated posterior to the hinge-line with the myophore filling, and often protruding from, the notothyrium. This arrangement gave rise to a lever system of the first order, with the fulcrum (hinge) between the mass to be moved and the force to be applied. The required force was produced by a contraction of the diductor muscles, which pass from the cardinal process through the anterior part of the delthyrium to their ventral seat of attachment on the floor of the ventral valve in the beak region. This is a similar lever system to that found in most modern terebratulaceids and rhynchonellaceids (Thomson 1927, p. 29), the principal difference being that the muscle bases in the ventral valve are situated much further forward than in *Dalmanella*.

A first-order lever system exists also in the triplesiaceids; the *interarea is obsolete* in the dorsal valve, and the cardinal process projects posteriorly from the hinge into the ventral valve. This posterior growth of a cardinal process to project into the ventral umbo is by no means restricted to the Triplesiacea. Many stocks of productids develop in a similar fashion, although of course their cardinal process is bilobed and not forked. Here again it should be noted that in the majority of productids the dorsal interarea is

obsolete, as in the triplesiaceids; but when valve convexity is considered, the dorsal valve with cardinal process is flat or concave, which would instantly contradict Ulrich and Cooper's hypothesis.

The Triassic genus *Thecospira* also possesses a posteriorly directed cardinal process, combined with a concave dorsal valve and vestigial dorsal interarea. Again in some orthotetaceids, e.g. *Meekella* White and St. John, the cardinal process is directly similar. Here the convex nature of the dorsal valve would lend some support to Ulrich and Cooper's idea, although it is not developed to the extent seen in the triplesiaceids. But what would seem to be more fundamental is that, as in the productids and triplesiaceids, the development of a posteriorly directed cardinal process is found in association with the loss of interarea in the dorsal valve.

It would be unwise to say that the posterior elongation of the cardinal process was a *result* of the loss of interarea in those stocks where it is developed, as its development depends on various factors, including, for example, the growth of a sufficiently high ventral beak to accommodate this type of cardinal process. It would certainly seem, however, that there is a closer correlation between an elongated cardinal process and a reduced interarea, than between the length of the cardinal process and the convexity of the valve.

The great convexity of the dorsal valve at the umbo was, however, responsible for the median fold of the pseudodeltidium. The external edge of the pseudodeltidium (text-figs. 5A and 6A) extends straight to the hinge, where the tooth fits into the socket of the dorsal valve, bounded on the inside by the 'brachiophore'. Here the convexity of the dorsal valve is by no means marked, but it increases medianly so that the entire valve is strongly incurved in the median plane (text-figs. 5F, G, and 6B). The pseudodeltidium is now situated more dorsally (the section being through the median fold of that plate), and the dorsal umbo is in fact tucked inside the ventral valve. Thus, it becomes apparent that, if no median fold had been developed, the anterior part of the pseudodeltidium would have been jammed between the dorsal umbo and the hood of the cardinal process ('chilidium'). If the latter had not been developed, as it is envisaged below to be a complementary structure to the pseudodeltidial fold, the dorsal umbo would have been pressed against the flat pseudodeltidium and, due to its strongly convex nature and position, would certainly have impeded, if not prohibited, the opening of the valves.

To allow the dorsal umbo to be tucked into the ventral valve and also to enable the valves to open freely, it is necessary both to lift the median portion of the pseudodeltidium above the level of its lateral parts and to shorten it, producing the arrangement seen in text-fig. 5G and H.

As may be observed from the longitudinal sections (text-fig. 5F, G, H) and transverse sections (text-fig. 7F, G, H) of *Triplesia extans* (Emmons), there is developed, on the posterior side of the shaft near its base, a calcareous structure which takes the form of a saddle or hood, arching over the shaft with its dorsal edge parallel with the edge of the dorsal umbo (text-fig. 7F). The actual hood may be seen in the various silicified specimens of *Triplesia sp.* from Portrane, County Dublin, figured in Pl. 109, figs. 13, 16–19.

The growth-lines, traced from photographs of cellulose peels, show that this hood is an integral part of the cardinal process. Text-fig. 5F shows the growth-lines on the hood to be abruptly truncated on the left, which is, as one would expect, at the side of the
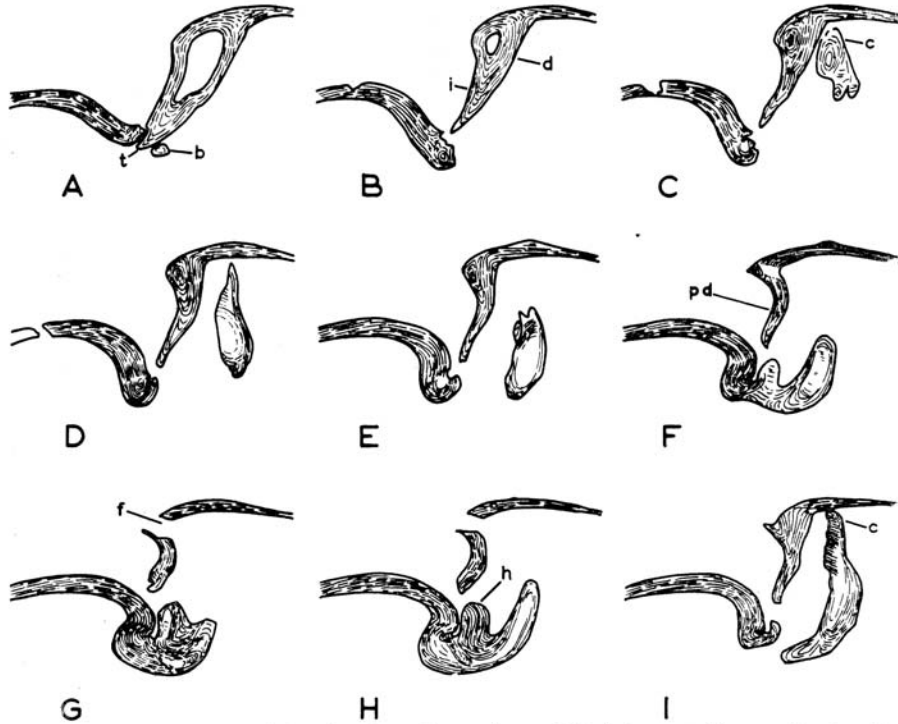
TEXT-FIG. 5. Longitudinal serial sections through a specimen of *Triplesia extans* (Emmons) to show the calcareous structures of the hinge region and their relationships. A is taken at the delthyrial edge, B at 0·5 mm. from it towards the median plane of the valve. The other peels follow B at 0·2-mm. intervals, ×8·1.

b—'brachiophore'; c—distal end of cardinal process; d—dental plate; f—pedicle foramen; h—cardinal process hood; i—interarea; pd—pseudodeltidium; t—tooth.
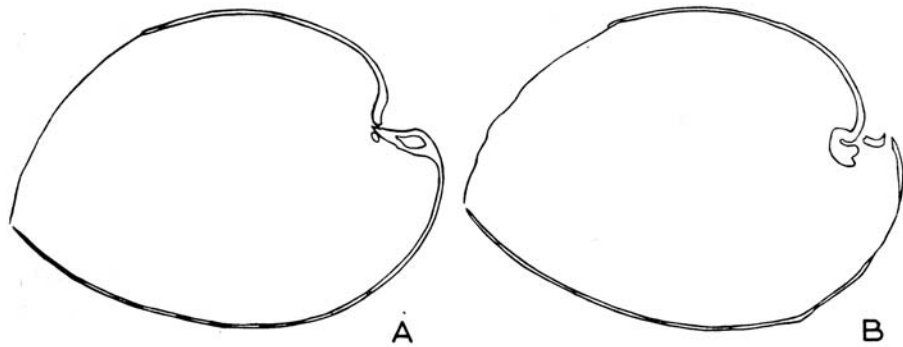
TEXT-FIG. 6. Longitudinal sections of *Triplesia extans* (Emmons) to show the hinge structures in relation to the rest of the valve. A and B correspond to text-fig. 5, A and G, respectively, ×3·3.
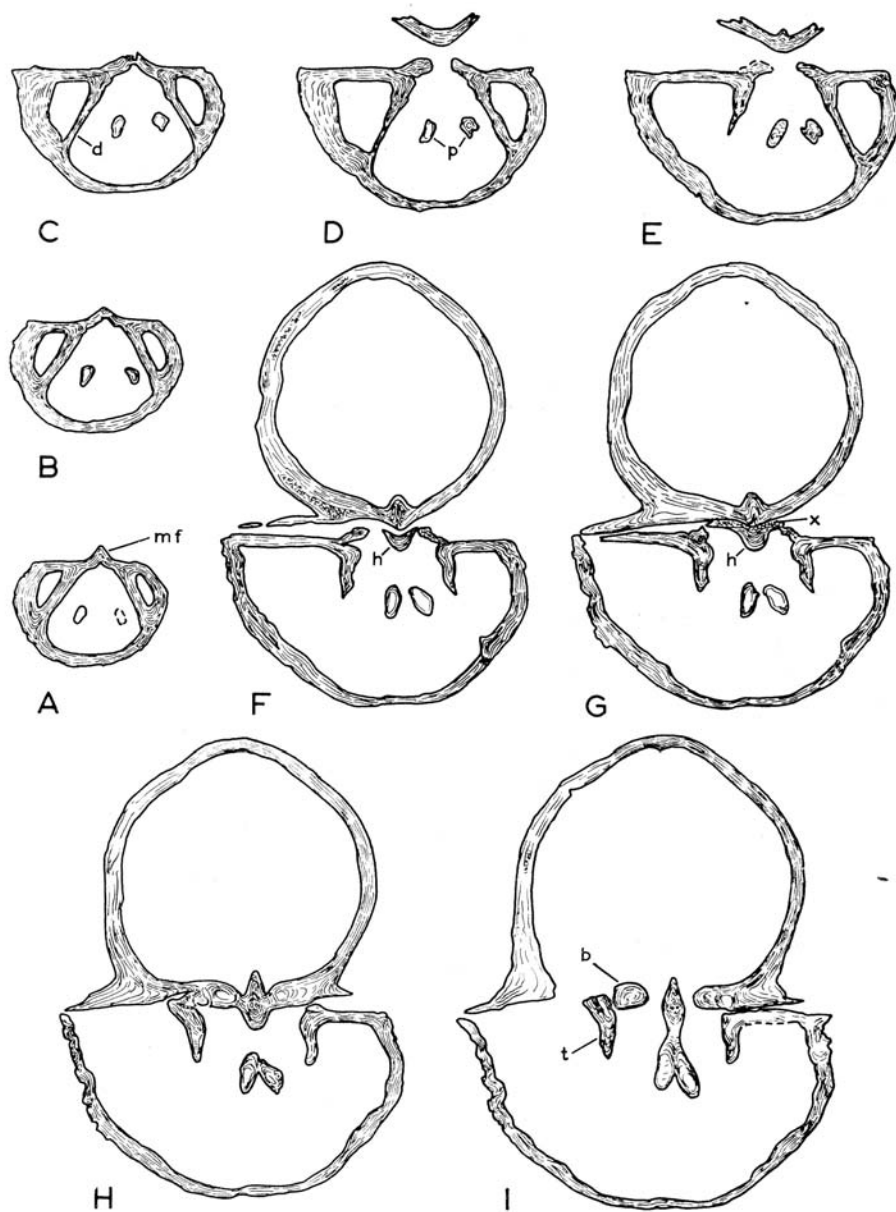
TEXT-FIG. 7. Transverse serial sections of *Triplesia extans* (Emmons) at 0·15-mm. intervals, A being taken at a distance of 1·05 mm. from the ventral umbo. A–E omit, or show only part of, the dorsal valve, ×8·1.

b—'brachiophore'; d—dental plate; h—cardinal process hood; mf—median fold on the pseudodeltidium; p—prongs of the forked cardinal process; t—tooth; x—crystalline calcite.

structure, while on the right the growth-lines flow smoothly into those of one of the process forks. The essential unity of the hood and the cardinal process is seen further in text-fig. 5, G and H. The sharp bend in the growth-lines at the base of the hood marks it off from the cardinal process proper, but there is no doubt that the growth-lines are continuous and that the hood is a process developing posteriorly from the cardinal process.

This hood has previously been identified as a much modified or vestigial chilidium (Ulrich and Cooper 1936, p. 333, and Muir-Wood and Cooper 1960, p. 134), but because the dorsal interarea is obsolete, and does not possess a notothyrium, it cannot possibly possess a chilidium. Moreover, the structure is an internal one, not visible on the exterior, and the growth-lines show that it is basically a development from the posterior surface of the cardinal process.

This is not to say that vestigial chilidia do not exist in some groups of brachiopods. Indeed, Williams (1953, p. 13) shows that the history of the stropheodontids exhibited a progressive reduction in the chilidium until it became obsolete. This is quite different from the triplesiaceids in which there is no such trend, for even the earliest known forms are without a dorsal interarea. Further, although the chilidium became obsolete in the stropheodontids, the dorsal interarea did not, although it may have decreased in size.

The variation in shape of the hood is discussed by Ulrich and Cooper (1936, p. 334). With respect to its function, it is here considered to be a complementary structure to the median fold of the pseudodeltidium. Lateral to the fold, where the convexity of the dorsal valve is not so pronounced, the pseudodeltidium reaches virtually to the hinge. Medially the pseudodeltidial fold is shorter and extends towards the posterior part of the dorsal valve, rather than the hinge. This gap is closed by the hood, which appears to act rather as the anterior portion of the pseudodeltidium, which is itself unable to develop as a consequence of the highly convex dorsal umbo.

The lophophore. No direct evidence of the feeding organ of members of the superfamily is available, as calcareous supports to it of any sort are totally lacking. In other super-families, the so-called brachiophores have been interpreted by some authors as being the most rudimentary type of lophophore support. Williams (1956, p. 264) has shown that, in the majority of orthaceids and dalmanellaceids, these brachiophores were far too short to have functioned as a support to the lophophore. In the case of the triplesiaceids, the brachiophores are not only directed laterally and ventrally but also become curved over in a posterior direction (Pl. 109, figs. 17, 19). Hence under these conditions, it is even more apparent that these structures acted merely as the inner walls to the sockets, and have no part in supporting the lophophore, which must have developed anteriorly from the body wall.

In the absence of any calcareous supports, and, of course, the soft parts themselves, the form of the lophophore may only be postulated by a consideration of the shape of the valves. In the case of closely apposed valves, such as the concavo-convex and resupinate strophomenoids, the lophophore must of necessity be flattened ventro-dorsally, and may have taken the form of a plane-spirolophe, a ptycholophe (as indicated, for example, by the ridges in the dorsal valves of *Leptaenisca* and *Plectodonta*, respectively), or a simpler schizolophe or trocholophe. Biconvex valves, where this ventro-dorsal restriction to growth is absent, show a much greater range of lophophore type

from trocholophous (*Gwynia*), schizolophous (*Argyrotheca*) to spirolophous (*Hemithyris*), plectolophous (*Terebratulina*), and deuterolophous (*Spirifer*).

Williams (1956, p. 272), in a consideration of Beurlen's (1952) classification of the articulate brachiopods (the major divisions of which are based on lophophore disposition, for which Beurlen relied principally on shell shape), demonstrates, with the Plectorthidae, the variation of shell shape within a family and the danger of homeomorphy when attempting to use this attribute as a means of classification. However, it is possible to determine some apparently valid relationships between the shape of biconvex shells and the lophophores of the animals, where the latter is known, and then apply them to extinct groups like the triplesiaceids, where the calcareous parts alone are known and do not themselves indicate the style of lophophore.

The following points are noted:

(1) In those spire-bearing brachiopods where the lophophore supports consist of spires which are directed laterally (*Athyracea, Spiriferacea*), the valves are more or less evenly convex.

(2) *Atrypa*, normally pronouncedly dorsi-biconvex, possesses spires which are directed dorso-medianly.

(3) In the Rhynchonellacea, whose lophophore is normally a dorsally-directed spirolophe, the shells are generally deeper in the dorsal than in the ventral valve.

(4) The inarticulate *Crania* possesses a flat ventral valve and a more or less conical dorsal valve into which the spirolophes are directed. *Discinisca*, with its ventrally directed spires and conical dorsal valve would seem to contradict the relationship of stronger valve convexity being in the direction of coiling. However, in the anterior third of the shell, where the coils are developed, the ventral valve becomes quite strongly convex, at least as much if not more so than the dorsal valve at this point.

(5) In the '*Terebratula*' group, with their characteristically plectolophous lophophore, the ventral valve may be deeper (e.g. *Dallina*) but more commonly the valves are about evenly convex. This situation is what one might expect from a shell possessing this type of lophophore.

It would seem, from the above examples, that the convexity of the valves does bear a relation to the kind of lophophore in many instances.

The plectolophous lophophore is a very advanced form, associated with a well-developed calcareous support in the form of a loop, a septum, or both, while the valve convexity is rather variable as already noted. The Triplesiacea, however, show no calcareous support, and are all dorsi-biconvex to a greater or lesser degree. Coupling these facts with the early occurrence of the superfamily—the terebratulids had barely commenced their existence when the triplesiaceids became extinct—it would seem highly improbable that the triplesiaceids possessed this type of lophophore.

Recent brachiopods which show no calcareous support for their feeding organ are to be found in the inarticulates, while the rhynchonellaceids only possess a simple support in the form of crura. The most complicated lophophore development in both these cases is a spirolophe, and this would seem to be the type of lophophore most likely to occur in the triplesiaceids. The genera *Gwynia* and *Argyrotheca*, with their simpler lophophores, are very small forms and, as a generalization, it may be said that the much larger size of most triplesiaceid genera is possibly another point in favour of the more advanced spirolophe, although it is appreciated that a small number of
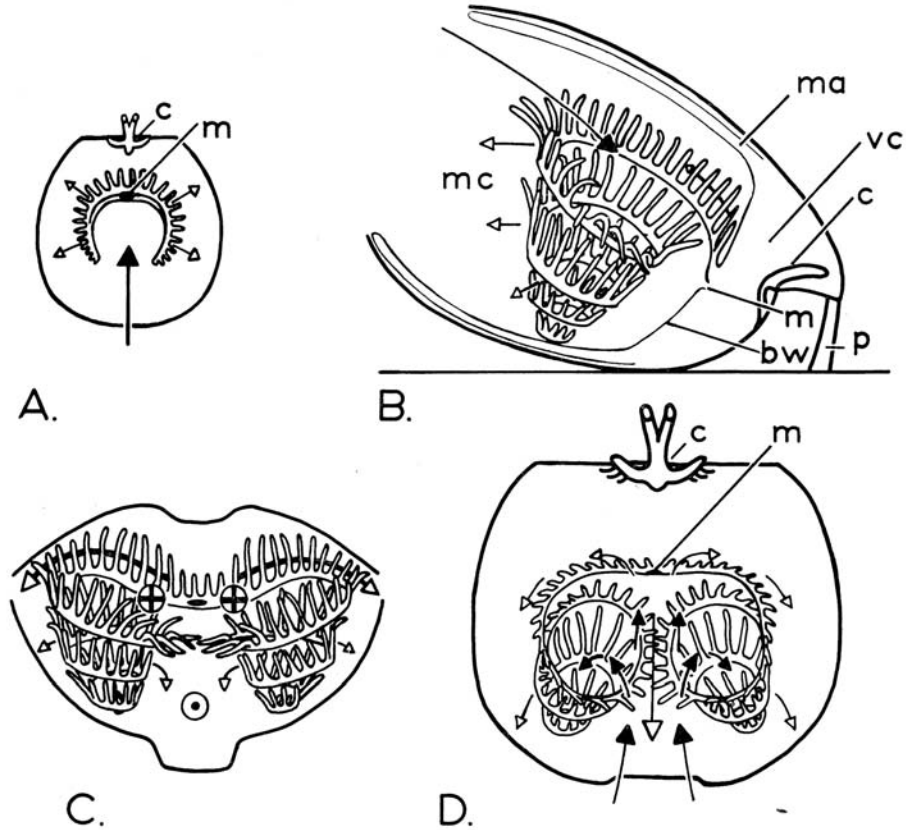
TEXT-FIG. 8. Diagrammatic reconstructions of the spirolophous lophophore and feeding currents envisaged for the Triplesiacea. (A) The trocholophous lophophore of a young individual with a median inhalant current (solid arrow), directed by the filaments to emerge as a lateral exhalant current (open arrow). The other figures represent an adult viewed, (B) laterally; (C) from the anterior commissure (posteriorly directed currents ⊕ anteriorly directed currents ☉); (D) ventrally.

bw—body wall; c—cardinalia; m—mouth; ma—mantle; mc—mantle cavity; p—pedicle; vc—visceral cavity.

larger brachiopods (e.g. *Rensselandia*) did possess a simple trocholophe in the adult stages.

The type of lophophore in Triplesiacea is considered to be that of a simple antero-dorsally directed spirolophe (text-fig. 8), rather similar to that of Recent rhynchonella-ceids. Now, during the early growth stages, i.e. where the trocholophous and early schizolophous condition exists, the inhalant current is a single median one, with the current then being directed through the filaments to emerge laterally (text-fig. 8A), as ascertained by Atkins (1956, 1958, 1959) for Recent brachiopods. With the development

of the spirolophe, the median inhalant current becomes divided and passes into the coils (text-fig. 8c, D). The possible advantage to certain brachiopods of a plication in the anterior commissure to assist the channelling of currents has been commented upon by Orton (1914, p. 295) and others; a plication is invariably present in the adults of the Triplesiacea. Possibly the stage of development of the lophophore associated with the division of the inhalant current is related to the appearance of the fold and sulcus. Should it be determined that the plication appeared at a definite stage in the development of the lophophore, it would prove useful in ascertaining the size attained before the development of an adult-type lophophore in the relevant extinct forms. For example, the fact that one species of *Streptis* develops its plication significantly later than another (Wright 1960, p. 269) would also mean that the former would be retarded in lophophore growth relative to the other, i.e. would possess its trocholophous stage for a longer period. As is well known, plicated commissures are far from being universal in the phylum, but it seems possible that in stocks where they are well developed, a co-ordination between the plication on the one hand and the feeding mechanism on the other may well have developed during the course of evolution.

Quite obviously this would have to be verified or disproved first of all with a sample of suitable Recent shells (rhynchonellaceids) which are unfortunately not available to the author at present.

The lophophore and current systems here envisaged for the Triplesiacea (text-fig. 8) is a mechanically efficient system (Rudwick 1960, p. 376), the filaments in the mouth region and on the first coil of the spires touching the ventral mantle to separate the inhalant and exhalant water there, whilst medianly the filaments of the first coils of the two spires interlock to separate the ventral inhalant current from the dorsal exhalant one.

The varying outline of the valves seen in the Triplesiacea, from the almost circular *Plectotreta* to the transverse *Bicuspina* with its spiriferoid outline, would not necessitate any fundamental reorientation of the brachial apparatus or the feeding currents; in the more transverse valves the angle subtended between the two cones would merely have to be increased.

The muscle scars and muscular system. The cruciform markings found on internal moulds of specimens of *Triplesia* and *Bicuspina*, especially from the British Llandeilian and Caradocian rocks, have been known to palaeontologists for many years. The cross has been taken, quite correctly, as dividing the anterior adductor pair from the posterior adductor pair, and the left scar from the right scar of each pair. The transverse bars of the cross, here shown to be *vascula myaria*, sweep round towards the posterior margin in the form of a pair of arcs. The whole of the area bounded by these arcs, which in many specimens attain considerable dimensions, was believed to be the posterior muscle scar.

The animal would thus have possessed a large pair of posterior adductor scars of sub-circular outline, together with a smaller subtriangular anterior pair, with the apices of the triangle directed postero-medianly towards the *nodus quadrivalis* (Öpik 1934, p. 38) as in text-fig. 10D.

While agreeing with the distribution of the latter, the present study shows that it is extremely unlikely that the posterior adductor scar did in fact cover the whole of the

area delimited by the *vascula myaria*. In the first instance, while the anterior pair of adductors are to be found in the form of raised areas on the internal moulds (Pl. 110, fig. 4), indicating a deep muscle insertion, the areas defined by the *vascula myaria* are lower on the moulds and thus are areas of greater secretion on the shell interior. This is contrary to what one would expect if they, too, were muscle scars. The lower level of the posterior areas is true, except for those parts of the area just inside the boundaries formed by the vascular arcs, where one finds a raised ridge in the mould. This becomes increasingly prominent when traced anteriorly from the umbo towards the *nodus*
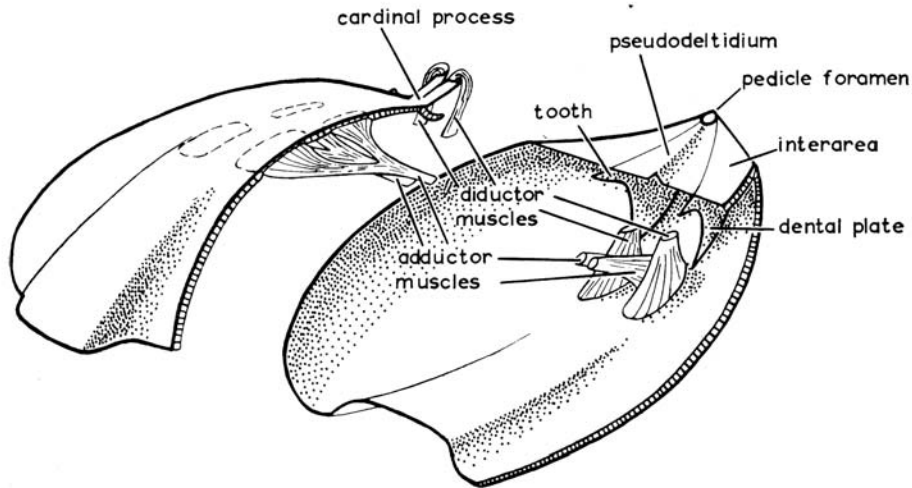
TEXT-FIG. 9. The muscle system of a generalized triplesiaceid. Antero-lateral view with the muscles cut and the dorsal valve lifted away from the ventral valve.

quadrivalis, where it is most marked, after which point it diminishes laterally to the valve margin. Thus on the shell interior the area is a raised one, clearly bounded anteriorly by a groove and by an area of deeper insertion postero-lateral to the 'cross' at the *nodus quadrivalis* (Pl. 109, fig. 2). These areas of deep insertion are here considered to be the location of the posterior adductor muscle attachments.

Further, while in the majority of specimens in which the subcircular area is preserved it appears to be quite smooth, an occasional shell shows a series of alternating ridges and grooves, whose disposition is roughly radial from the direction of the umbo (text-fig. 10c, D, Pl. 110, figs. 1–3). These markings have a quite different appearance from the impressions left on the valve floor by muscle attachments. Moreover, their distribution seems to be closely related to that of the branches of the *vascula myaria* anterior to them.

It is thus concluded that the subcircular areas are principally the impressions of a pair of saccate gonocoeles, while the posterior adductor scars are restricted to the median portion as indicated in text-fig. 10A.

A reconstruction of the actual muscular system for a generalized triplesiaceid is shown in text-fig. 9. The striking feature of the system when compared with other con-

temporary stocks is that the seat of attachment of the diductor muscles in the dorsal valve is situated high inside the ventral umbo, at the distal ends of the cardinal process. This would maintain an efficient valve-opening mechanism for the group.
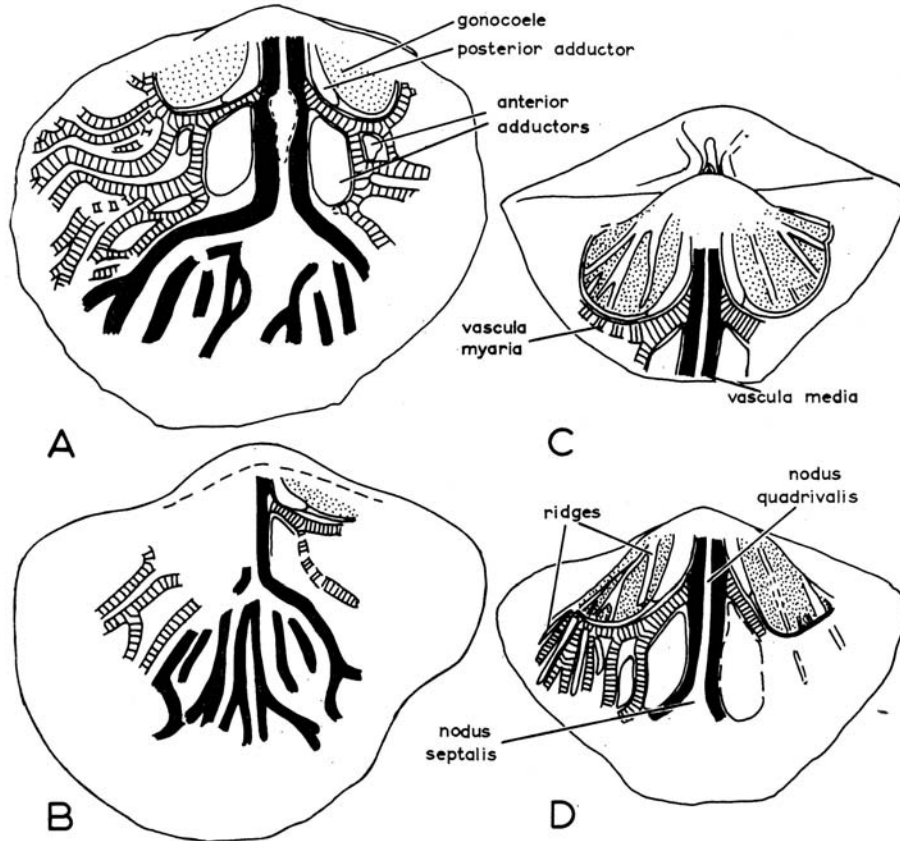
TEXT-FIG. 10. The dorsal pallial sinus patterns in the genus *Triplesia* taken from specimens figured in Pl. 110, figs. 2–4, 6. In (A) the *vascula myaria* (ornamented by closely spaced lines) and (B) the *vascula media* (solid black) are shown more completely. (C) and (D) are postero-dorsal and antero-dorsal views of an internal mould, showing clearly defined ridges traversing the floor of the gonocoele. ×4·9, ×4·7, ×1·9, ×1·9 respectively.

The pallial sinuses. The pallial sinus patterns in the dorsal valve have been established principally from internal moulds of a species of *Triplesia* from the Kildare Limestone (text-fig. 10, Pl. 110, figs. 4–6). The gonocoeles, described above, are delimited anteriorly by a ridge on the mould, exterior to which is a groove. This groove (corresponding to a ridge in the actual shell) is produced by an arm of the main vascular canals which

branches off from the latter at the *nodus quadrivalis* to pass laterally between the posterior and anterior adductor muscles, forming an arc which follows the anterior margin of the gonocoeles. This is the principal branch of the *vascula myaria*. This branches further, the first branch (text-fig. 10A, D) passing through the region occupied by the anterior adductor scar to divide it into a larger inner and a smaller outer portion as in *Clitambonites* (Öpik 1934, p. 39). The remaining branches are somewhat shorter, carrying out their circulatory function in that region of the shell between the first branch and the main arc. Some of these branches are seen to bifurcate at the periphery of the shell to produce marginal sinuses as in the ventral valve of the specimen of *Bicuspina* shown in text-fig. 4; but in the majority of specimens examined the marginal sinuses were not sufficiently strongly impressed for them to be visible. This was the case also with the marginal sinuses of the *vascula media*.

The *vascula media* again take the form of grooves in the cast. They are first observed a short distance anterior to the umbo, the left and right ones proceeding parallel to each other anteriorly along the middle of the valve, separated by a low, but clearly defined, ridge. This pattern continues until they reach the front of the anterior adductor scars (the *nodus septalis* of Öpik) when they diverge sharply to form a characteristic inverted 'Y' shape (Pl. 110, fig. 5). While this 'Y' is often clearly defined, the anterior markings within the fork of the 'Y' are usually only faintly impressed. Where impressions are found in this position, they take the form of a series of canals as seen in text-fig. 10B. Although it is not possible to be definite in stating how these canals arise from the main *vascula media*, due to their being indistinct at crucial points, it seems most probable that they do so at the *nodus septalis*. Here, at the point of divergence of the main trunks of the *vascula media*, two smaller canals appear to form a continuance of the same parallel course taken by those sinuses up to the *nodus septalis*. These smaller canals quickly produce three branches each, some of which show further branching as the shell margin is approached. The canal system thus developed within the limits of the main *vascula media* may be compared with that present in the orthaceid *Orthostrophia* Hall 1883. In this genus it takes the form of a pair of subsidiary median gonocoeles (Williams 1956, p. 278), whose finely fingered appearance corresponds closely with that of the postero-lateral gonocoeles.

In the case of *Triplesia*, although the canals occupy the correct position to be subsidiary gonocoeles (at least where *Orthostrophia* is concerned), it is not certain whether they did actually act as such. The appearance of these canals in *Triplesia* is coarser than that of the median gonocoeles of *Orthostrophia*, and in specimens where these canals have been observed, the postero-lateral gonocoeles are smooth. This prevents a close morphological comparison. It is interesting to note that wherever ridges are developed on the postero-lateral gonocoele in *Triplesia*, they are also coarser than the corresponding ones in *Orthostrophia*. Perhaps the coarser nature of the 'median gonocoele' is a reflection of this, and these median sinuses in *Triplesia* (and in the rest of the family, if the pallial markings prove to be similar to those of the type genus) did have a sexual as well as a circulatory function.

THE RELATIONSHIPS OF THE SUPERFAMILY

The assembly of familial features characterizing the genera of the Triplesiacea enable members of this superfamily to be differentiated easily from other groups. At the same

time this distinctive combination of characters poses difficulties when the relations of the superfamily to the rest of the class Articulata are considered. The nature of the cardinalia and the postero-median part of the ventral valve is extremely unusual, and so far no brachiopod has been described which shows transitional stages in the development of these features from an ancestral stock that could be placed with certainty in another definite group of brachiopods.

However, by a consideration of the stocks (*a*) which were potentially able to develop these more distinctive single features of the superfamily (*b*) which do themselves possess other features in common with the triplesiaceids and (*c*) which are known to be in existence in rocks older than, or that were deposited contemporaneously with, those in which the earliest specimens are found, the possible ancestral stock may be suggested. With the increasing knowledge of both the triplesiaceids and the stocks from which they may have evolved, certain groups are found to have more in common with them than others, and so the number of possibilities is reduced.

When demonstrating the close relation of stocks by a process of comparative morphology, it is imperative that the time factor, i.e. the stratigraphical distribution, is kept in mind. The earliest member of the triplesiaceids, *Onychoplecia*, makes its appearance in the Llanvirn Table Head Series of Newfoundland (Cooper 1956, p. 529). Thus, although its immediate ancestors are unknown, its closest relatives may be sought in the earlier Arenig or Tremadoc or in the contemporaneous Llanvirn stocks.

Thus, from a purely chronological standpoint, the stocks which arose later than the Llanvirn may be discounted in the search for potential ancestors. This eliminates the '*Rhynchonella*', '*Spirifer*', and '*Terebratula*' groups of Williams 1956. For the remaining three groups, the '*Pentamerus*' group is represented only by the Syntrophiacea, the '*Strophomena*' group by the Plectambonitacea and some early strophomenaceids, and the '*Orthis*' group by the three superfamilies Orthacea, Dalmanellacea, and Clitambonitacea.

In carrying out a morphological comparison between these stocks and the Triplesiacea, it is essential to consider which features of the latter are of high systematic value and must therefore be searched for in the potential ancestral stocks. In the Triplesiacea, perhaps, the most important features, which are to be found in other brachiopod groups, are the impunctate shell substance and the biconvex nature of the shell. A comparison of these features with the contemporaneous members of the '*Strophomena*' group renders a close relation with this group highly improbable. Although atrophy of the caeca in punctate stocks to produce impunctate shells is suspected to occur (Williams 1956, p. 253), it seems unlikely that the Dalmanellacea could have provided the ancestors to the Triplesiacea, for, whilst they are contemporaneous, they are not known in pre-Llanvirn times. Further, in North America, where *Onychoplecia* occurs, dalmanellaceids do not appear until the Llandeilo (Ashby stage, Cooper 1956, p. 137).

The Clitambonitacea are a very specialized superfamily. Some of the early forms, however (e.g. Tritoechiidae), do not possess all of the features associated with their superfamily, and seem to be transitional from an orthaceid ancestor (Ulrich and Cooper 1938, p. 161). While these forms and the triplesiaceids may possess a common ancestor, the former are clearly intermediate between the early Orthacea and the Clitambonitacea, and not the Triplesiacea.

As stated earlier, Williams regards the superfamily as belonging to either the

'*Pentamerus*' or the '*Orthis*' group, and indeed many features present in the Triplesiacea are common to members of both the Syntrophiacea and the Orthacea—probably the latter, rather than the other two superfamilies, for reasons given above.

The external resemblance of some syntrophiaceids to triplesiaceids (e.g. *Syntrophia* Hall 1892, with *Triplesia*) is quite striking, and the two groups have often been confused. The biconvexity of the valves is also to be found in all three superfamilies, and the spirolophous lophophore, suggested for the Triplesiacea, gives no assistance in ascertaining relationships. Neither does the very distinctive pseudodeltidium or cardinalia, for both could develop equally well from the open delthyrium and simple cardinalia found in the other two stocks.

The presence of a spondylium in most Syntrophiacea, together with the general muscle distribution, would indicate that the affinities of the Triplesiacea lie rather with the Orthacea; but in the author's opinion it is the nature of the pallial sinuses, especially of the dorsal valve, which tips the balance in favour of inclusion in the '*Orthis*' group. The arcuate *vascula myaria*, curving posteriorly around saccate gonocoeles and giving off branches anteriorly, together with the branching nature of the *vascula media* possibly with subsidiary anterior gonocoeles, produces a pattern very close indeed to a lot of contemporaneous orthaceids, e.g. *Cyrtonotella*, and the later *Orthostrophia* (Williams

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EXPLANATION OF PLATE 109

The photographs are not retouched, but the specimens were coated with ammonium chloride before photographing. Abbreviations of repositories: B.B. = British Museum of Natural History, London; G.S.M. = Geological Survey and Museum, London; U.U.G. = Ústřední Ústav Geologický, Prague; I.G.S. = Irish Geological Survey, Dublin.

Fig. 1. *Triplesia extans* (Emmons 1842); postero-dorsal view of a complete specimen, showing the pedicle foramen and pseudodeltidium with median fold. Caradocian (Trenton), Watertown, New York State. B.B. 28215, ×1·5.

Fig. 2. *T. insularis* (Eichwald 1842); dorsal internal mould with muscle and vascular impressions. Caradocian, nr. Corwen, N. Wales. G.S.M. 10874, ×2·3.

Figs. 3, 4, 6–8, 10, 11. *Cliftonia oxoplecioides* sp. nov., Ashgillian, Chair of Kildare Limestone, Kildare, Ireland. 3, 4, 8, 10, Posterior, anterior, dorsal, and lateral views of the *holotype*. B.B. 28210, ×1·4. 6, Ventral valve (*paratype*). B.B. 28211, ×1·5. 7, Dorsal valve (*paratype*), partly exfoliated posteriorly to reveal the muscle scars. B.B. 28212, ×1·5. 11, Latex cast of an external mould, showing the strongly developed concentric ornament. B.B. 28213, ×3·0.

Fig. 5. *Bicuspina spiriferoides* (M'Coy 1851); internal mould of ventral valve. Caradocian, Allt Ddu Mudstone, Y Garnedd, Bala, N. Wales. B.B. 28200, ×1·3.

Fig. 9. *B. multicostellata* Havlíček 1950; internal mould of ventral valve. Llandeilian. Letná Beds, Chrustenice, Czechoslovakia. U.U.G. 1954. ×2·0.

Figs. 12, 14, 15. *Oxoplecia multicostellata* Cooper 1956; Caradocian, Chatham Hill Formation, Sharon Springs, Virginia, U.S.A. 12, 15, Two views of a ventral valve to show the posterior thickening of the shell and the pedicle passage. B.B. 28205, ×2·0. 14, View looking posteriorly into an articulated shell, showing the well-developed cardinal process directed into the ventral umbo. B.B. 28206, ×1·1.

Figs. 13, 16–19. *Triplesia sp.*, fragmentary silicified specimens from the low Ashgillian Limestone of Portrane, Co. Dublin, Ireland. 13, Posterior view of specimen B.B. 28209 showing cardinal process, 'brachiophores', hood, and dorsal umbo, ×4·8. 16, 18, Postero-ventral and posterior views of specimen B.B. 28208 showing a medianly cleft hood to the cardinal process, ×5·0. 17, 19, Oblique postero-ventral and posterior views of a specimen with a well-preserved hood (here concealing the dorsal umbo), broken cardinal process, 'brachiophore', and socket. B.B. 28207, ×4·7.

1956, p. 275, fig. 6 (3)). This is quite distinct from the digitate pattern of the Syntrophiacea.

While parallel development of this feature cannot be ruled out entirely, the present state of knowledge would suggest that the Triplesiacea developed from a stock of small biconvex orthaceids at the beginning of Ordovician times.

SYSTEMATIC PALAEONTOLOGY

Cliftonia oxoplecioides sp. nov.

Plate 109, figs. 3, 4, 6–8, 10, 11.

Diagnosis. Dorsi-biconvex *Cliftonia*, with outline varying from subcircular to transverse, the greatest width occurring just posterior to mid-valve. Well-developed dorsal fold and ventral sulcus, very variable in shape; the fold varies in form from a flat-topped one, standing well above moderately convex flanks, to a low one, passing almost imperceptibly into very convex flanks; anterior commissure varies accordingly. Varying degree of asymmetry present in about a third of the shells examined, occasional specimens being quite contorted. Ornament of fine, concentric growth-lines, and variably developed, coarser concentric lamellae which, when indistinct, due to fine development, abrasion, or exfoliation, give the shells the appearance of *Oxoplecia*. Radial ornament of costae and costellae branching laterally or dichotomously throughout shell growth, so that one large specimen (dorsal length 16·3 mm.) has over 55 ribs at the shell margin. At a distance of 5 mm. from the dorsal umbo, the modal number of ribs on the fold is 5 or 6, with 9 on flanks, although the former may vary between 4 and 8, and the latter between 6 and 12. At 10 mm. the mode is 8 (varying between 5 and 11) on the fold, and 14 on the flanks (varying from 10 to 19). The number of dorsal valves showing a frequency of 3, 4, or 5 ribs per 2 mm. medially at 5 mm. distance from the umbo is 26, 13, and 2; and 1, 2, 3, or 4 per 2 mm. at 10 mm. from the umbo 1, 11, 21, and 6 respectively.

Well-developed ventral interarea, pseudodeltidium with median fold and apical foramen; internally the foramen is continued in the form of a cylindrical pedicle tube (text-fig. 2).

Ventral interior with traces of muscle scars where exfoliated. Teeth supported by short dental plates.

Dorsal interior with cardinalia typical of the family; evidence of muscle scars and anterior edge of gonocoeles to be seen on some exfoliated specimens, but only sufficiently to state the pattern to be a normal one for the genus.

Type specimens (measurements in mm.):

	Max. length	Width
Holotype: Complete shell (B.B. 28210)	15·4	19·6
Paratypes: Ventral valve (B.B. 28211)	13·8	16·6
Dorsal valve (B.B. 28212)	12·4	15·7
External mould of dorsal valve (B.B. 28213)	..	..
Unfigured paratypes:		
Broken ventral valve (B.B. 28214)	12·8	..
Asymmetrical complete shell (B.B. 28216)	11·6	..
Dorsal valve (B.B. 28217)	12·1	13·7
Broken dorsal valve (B.B. 28218)	..	..

Horizon and locality. Ashgillian Chair of Kildare Limestone, Chair of Kildare, Co. Kildare, Ireland.

Discussion. The valve outline of the new species varies from subrounded (typical of *Cliftonia*) to transverse (like *Oxoplecia*) with the dorsal length: valve width ranging from 91 to 70 per cent. The radial ornament distinguishes the species from the very much finer ornament of *Bicuspina*, and although both possess a pedicle tube, the stronger concentric lamellae superimposed on the growth-lines indicate that the species belongs to the genus *Cliftonia*. A pedicle tube also exists in the type species of *Cliftonia*, *C. striata* Foerste (see Ulrich and Cooper 1936, pl. 48, fig. 25), as well as in *C. lamellosa* Williams, so it would appear to characterize the genus, although suitable material for investigation of other species is so far lacking. The genus *Bicuspina*, although possessing a pedicle tube, differs in outline and ornament from *Cliftonia*.

Cliftonia oxoplecioides, the earliest species of *Cliftonia* s.s. known at present, resembles the somewhat later basal Llandovery form *C. lamellosa*. This latter differs from the new species in being much more stable in outline, having a consistently stronger concentric ornamentation, and averaging fewer ribs at the margin for specimens of similar size. Internally, the pedicle tube becomes rapidly larger anteriorly in *C. lamellosa*.

The new species exhibits variation in many features, and although specimens may be picked up which appear at first sight to be possibly a different species, a statistical assessment of a sample of seventy or so specimens showed the variation to be continuous in all characters studied.

The variation in shape of the fold between being sharp-sided and from passing evenly into the flanks seems to suggest perhaps a specific difference; but as in *Streptis* (Wright 1960, p. 267) there is continuous variation, with some specimens showing a different type of relationship on either side of the fold. Specimen B.B. 28216 has one of these asymmetric folds. Where fold asymmetry occurs, it is often evident in the rib pattern on the fold. Specimen B.B. 28217 has five ribs on the fold at a distance of 5 mm. from the umbo. Of these, three are on the left and two on the right of the median line, the third on the right-hand side being on the flank at this stage, although passing on to the fold with increased growth of the shell. Additional ribs develop on the right-side only, by splitting off the existing ribs, chiefly away from the median plane (externally) so that at the commissure there are seven on the right and still three on the left side.

EXPLANATION OF PLATE 110

The photographs are not retouched, but the specimens were coated with ammonium chloride before photographing. Abbreviations of repositories as for Plate 109.

Figs. 1–3. *Triplesia anticostiensis* (Twenhofel 1914); dorso-lateral, dorsal, and postero-dorsal views of an internal mould showing the vascular markings of the dorsal valve. Upper Llandovery (C1 Beds), Sefin Footbridge, Llandovery, Wales. B.B. 28202, ×1·5, 1·5, and 1·6 respectively.

Figs. 4–6. *T.* cf. *insularis* (Eichwald 1842); dorsal valves from the Ashgillian Chair of Kildare Limestone, Kildare, Ireland, with the shell removed to reveal the pallial markings on the internal mould. B.B. 28203, ×4·6; I.G.S., ×3·2; and B.B. 28204, ×3·2, respectively.

Fig. 7. *Bicuspina spiriferoides* (M'Coy 1851); internal mould showing the muscle scars and vascular markings of the ventral valve. Caradocian Horderley Sandstone, Long Lane Quarry, Craven Arms, Shropshire, England. B.B. 28201, ×1·7.

Five specimens, out of over 200 collected from a shell bank, show extremely pronounced concentric lamellae (Pl. 109, fig. 11) and might be thought at first to be different from the remainder. The pattern of development of the ribs is, however, identical to that of other specimens with the more usual less strongly pronounced lamellae.

Six dorsal valves with well-preserved umbonal regions showed the ribbing to originate on average at 2·15 mm. (variance 0·6) anterior of the umbo. Four primary ribs develop on the fold, the inner pair usually branching dichotomously, the outer pair externally, although branching may be delayed to a varying extent for any rib, producing a rib pattern which is almost invariably asymmetric to some degree.

Fine concentric growth-lines have been observed umbonally to number up to twenty-three per mm.; they would seem to be wider spaced in later growth (between seven and ten per mm. being observed at 10 mm. distance from the dorsal umbo), although a great deal depends on the preservation for the counting of such fine lines. The average wavelength (and variance) for the coarser concentric lamellae at 10 mm. distance from the dorsal umbo for seven specimens was 0·83 mm. (0·02).
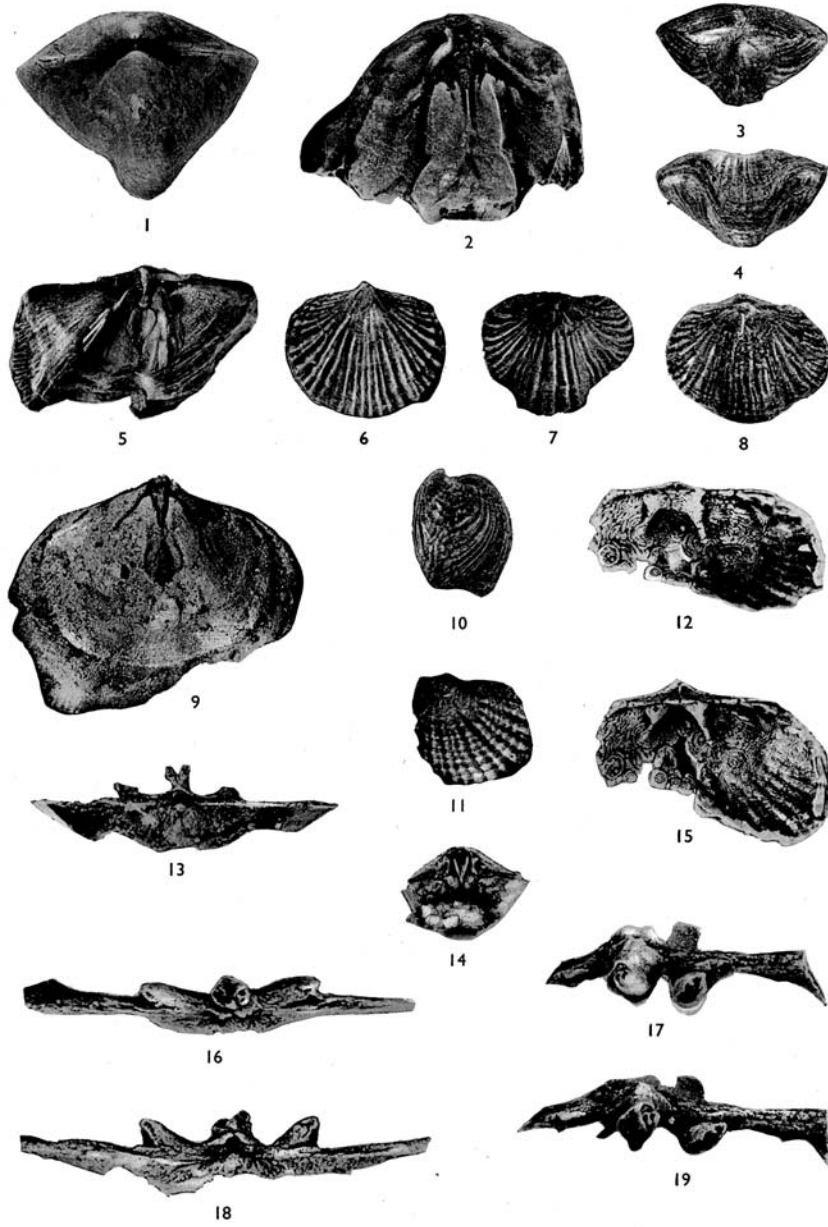
The following statistical data were obtained for a sample of about seventy specimens:

1. 23/70 specimens showed asymmetry.

2. Shell shape: bivariate analyses of (a) ventral length : width of valve. $n = 33$; $\bar{l}$ (var. l) = 11·58 (8·923) mm.; $\bar{w}$ (var. w) = 13·86 (13·43) mm.; $r = 0·9249$; a (var. a) = 1·227 (0·007); $b = -0·35$.

   (b) Dorsal length : width of valve.
   $n = 40$; $\bar{l}$ (var. l) = 11·29 (8·908) mm.; $\bar{w}$ (var. w) = 14·02 (15·63) mm.; $r = 0·9534$; a (var. a) = 1·324 (0·00577); $b = -0·93$.

   (c) Dorsal length : thickness of complete shell.
   $n = 14$; $\bar{l}$ (var. l) = 10·66 (8·55) mm.; $\bar{t}$ (var. t) = 6·89 (5·87) mm.; $r = 0·8762$; a (var. a) = 0·8285 (0·0133); $b = -1·943$.

   (d) Ventral length : distance anterior to ventral umbo of greatest valve width.
   $n = 23$; $\bar{l}$ (var. l) = 11·8 (7·223) mm.; $\bar{d}$ (var. d) = 5·48 (1·251) mm.; $r = 0·6763$; a (var. a) = 0·4161 (0·00447); $b = 0·57$.

3. The plication : bivariate analyses of (a) height of plication: width of plication.
   $n = 20$; $\bar{hp}$ (var. hp) = 3·115 (1·394) mm.; $\bar{wp}$ (var. wp) = 8·52 (3·62) mm.; $r = 0·7775$; α (var. α) = 0·602 (0·00796); $\beta = 1·458$.

   (b) Dorsal length : height of plication.
   $n = 15$; $\bar{l}$ (var. l) = 11·45 (5·72) mm.; $\bar{hp}$ (var. hp) = 2·96 (1·57) mm.; $r = 0·8046$; α (var. α) = 1·9666 (0·1048); $\beta = -3·708$.

   (c) Dorsal length : width of plication.
   $n = 16$; $\bar{l}$ (var. l) = 11·57 (5·53) mm.; $\bar{wp}$ (var. wp) = 7·98 (3·095) mm.; $r = 0·6813$; a (var. a) = 0·748 (0·0214); $b = -0·674$.

   (d) A univariate analysis of the position of origin of the plication showed that for forty dorsal valves the mean distance anterior of the dorsal umbo (with variance) was 4·63 (1·735) mm.

4. The ribbing: the variation in numbers of ribs with shell size made it necessary for counts to be taken at a definite position on the shell surface. The rib frequencies obtained at 5 and 10 mm. from the umbos of the dorsal valves have been given above; for the ventral valve at 5 mm. the modal number of ribs in the sulcus is 5–6 (range 3–8) and 8–9 (range 4–11) on the flanks. At 10 mm. the mode is 8 ribs in the sulcus (range 6–11) and 13 on the flanks (range 9–16). The density of ribs per 2 mm. taken medially at definite distances from the umbo has also been included in the diagnosis for the dorsal valve; for the ventral valve a frequency of 2, 3, 4, and 5 ribs was shown by 2, 19, 6, and 3 specimens at 5 mm. from the umbo; at 10 mm. 2, 3, and 4 ribs were present on 16, 10, and 3 specimens.
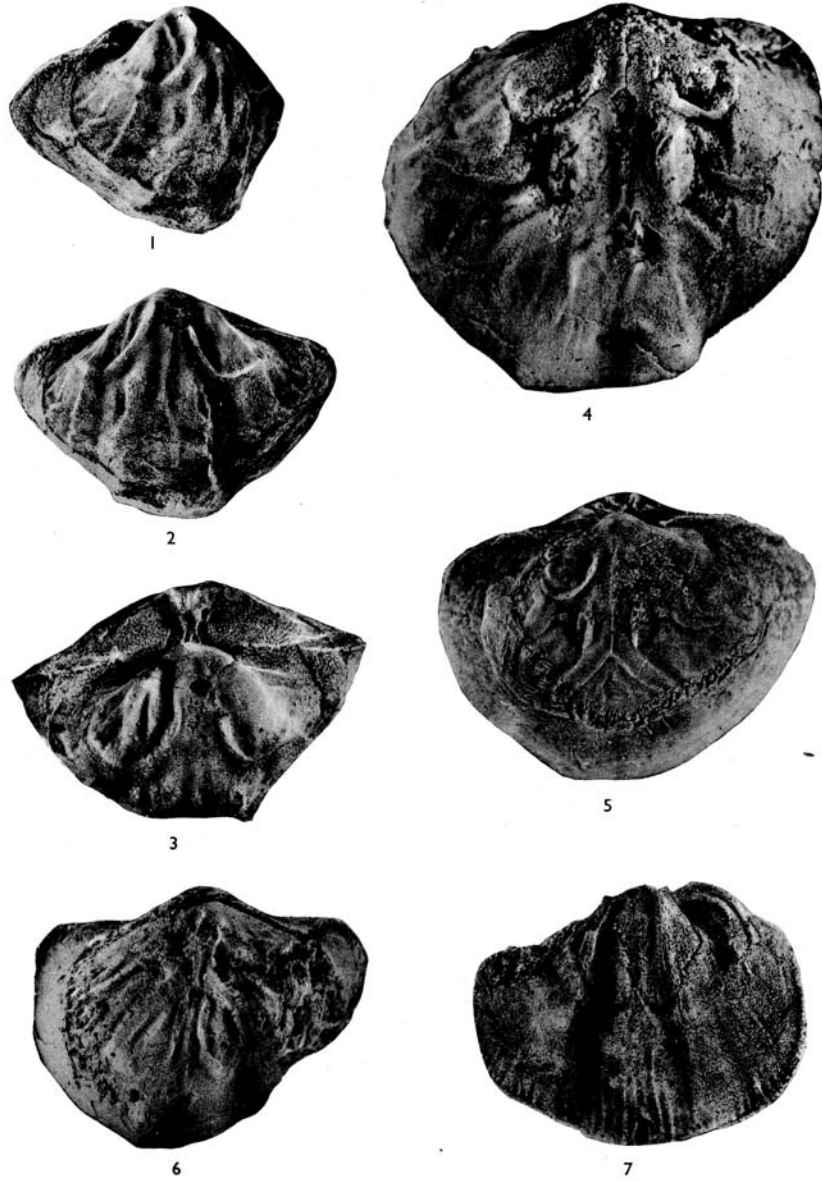
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