THE INTERPRETATION OF GROWTH AND FORM IN SERIAL SECTIONS THROUGH BRACHIOPODS, EXEMPLIFIED BY THE TRIGONIRHYNCHIID SEPTALIUM

by PETER WESTBROEK

ABSTRACT. Some possible misinterpretations of serial sections through brachiopod shells are discussed; the trigonirhynchiid septalium is taken as an example. Growth-lines in transverse sections suggest that a septalium may have arisen either by fusion of the inner hinge plates or by division of the septum. However, it can be shown that, when the whole structural complex is considered and not only sections through it, the question whether the septalium has grown in either of the two manners becomes meaningless. The suggestion given by the growth-lines in the sections depends on a number of factors, such as the direction and the location of the section, the ontogenetical age of the specimen, and the three-dimensional shape of the septum and septalium. The shape of the septalium in the transverse sections is determined by the same factors as the manner of growth, and the same applies to the size. It is therefore dangerous to distinguish between septalia which are wide and narrow in transverse sections and to use this distinction as a character in systematics. A good description can be given when a three-dimensional reconstruction is taken as a starting-point. Measurements of the septalium and the septum which may be used for statistical treatment, can be performed on a projection of the septalium and the septum on the plane of symmetry and on specially selected sections.

THE serial sectioning technique is commonly applied to the study and interpretation of the internal structure of fossil brachiopod shells. Generally, transverse sections are taken through the shell, and acetate peels taken of the sectioned surfaces. These peels may show the form and structure of the internal elements very clearly, but interpretation of the sections is liable to error, and it is, therefore, opportune to point out and to correct possible misinterpretations more methodically.

The problem can best be elucidated by considering transverse serial sections through the septalium of, for instance, trigonirhynchiid rhynchonellides. Williams and Rowell (1965) define this term as: 'troughlike structure of brachial valve between hingeplates (or homologues) consisting of septalial plates (or homologues) and buttressed by median septum; does not carry adductor muscles' (text-fig. 1).

It is of interest to examine how earlier authors have considered the septalium. The following selection of quotations may demonstrate that there is disagreement as to how a septalium grows. Leidhold (1920, p. 354) introduced the term in the following manner:

> Als Septalium bezeichne ich die löffelförmige bis dreieckige Aushöhlung zwischen den geteilten Schlossplättchen der Dorsalen, entstanden durch eine Gabelung des Dorsalseptums an seinem hinteren Ende und Verschmelzung der Gabelstücke mit den Schlossplättchen. Das Septalium ist nicht zu. verwechseln mit dem Cruralium der Pentameraceen, das durch Verwachsung der Cruralplatten entsteht.

In 1928 (p. 11) he gave the following definition:

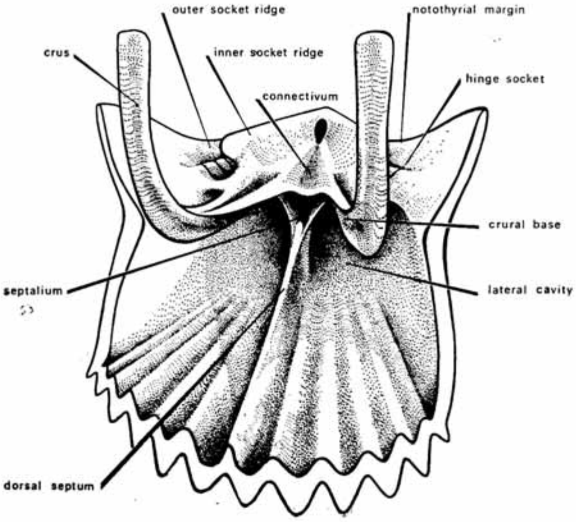
> Eine durch Spaltung der Dorsalseptums an seinem hinteren Ende hervorgegangene dreieckige bis löffel-förmige Aushöhlung zwischen den beiden Schlossplättchen.

[Palaeontology, Vol. 12, Part 2, 1969, pp. 321–32, pl. 61.]

This definition is charged with a statement about the genesis of the structure: it is formed by division of the median septum. This led to a small yet significant confusion in brachiopod literature.

1. Wiśniewska (1932, p. 6) stated:

Par le nom de septalium Leidhold a désigné une fossette formée par des lamelles allant de la plaque cardinale au septum, avec lequel elles s'unissent en forme d'un Y. En apparence le septalium est formé par la bifurcation du septum, mais en réalité, comme on le constate dans les sections transparentes, le septum ne se divise pas, ce sont les rebords internes infléchis de la plaque cardinale qui viennent se souder à son extrémité postérieure.



TEXT-FIG. 1. *Trigonirhynchia pareti.* (De Verneuil, 1850), Emsian, NW. Spain. Three-dimensional reconstruction of brachial interior from serial sections. (After Westbroek, 1967.)

It is surprising, however, to observe that in at least one of the three drawings of these transparent sections through the brachial valve (Wiśniewska's fig. 1*b*) the course of the growth-lines clearly displays an incipient bifurcation of the septum, the two ends uniting halfway along the septalial plates with the dorsally growing ends of the hinge plates. This use of the term septalium by Wiśniewska is in contradiction with the original definition of Leidhold.

2. Cloud (1942, pp. 10–11) proposed a new term, crural trough, which more or less corresponds with the term cruralium as designated by Leidhold. Cloud's definition is:

A ventrally concave structure at the posterior of the dorsal valve of some terebratuloids, formed by the basal convergence of crural plates to form a duplex median septum, while their ventral ends remain in context with the edges of the outer hinge plates. The crural trough so formed is then the median portion of one kind of a cardinal plate . . . A crural trough is not the same as a septalium (Leidhold, 1920, p. 354), which is a structure of similar appearance in the Rhynchonellacea formed by the forking of the dorsal median septum at its posterior end.

It appears as though Cloud concluded that the crural trough is formed by basal convergence of crural plates because he found it associated with a duplex median septum. A duplex median septum consists of a median 'intraseptal lamella' and of laterally flanking shell deposits with a different structure and earlier thought to have arisen by an incomplete fusion of these flanks, which in this case would be dorsal prolongations of the crural plates. The underlying assumption that the flanks of the septum were first separately formed and then fused together is in plain contrast with the fact that septa are secreted in a single epithelial fold. Williams and Rowell (1965, pp. H113–H114) and Williams (1968, p. 35) have correctly observed that the difference in structure betweeen the intraseptal lamella and the flanks of the septum is due to a local difference in secretory activity of the surrounding epithelium. (See also Krans (1965, p. 104) and Westbroek (1967, pp. 30–4)).

3. Cooper (1959, pp. 9–10) makes, *inter alia*, the following statement concerning the septalium:

In a few genera of Recent and Tertiary, *Frieleia* for example, the median septum joins folds from the inside of the crural bases to form a small chamber at the posterior. . . . These [i.e. the hinge plates] do not seem to constitute a septalium in the true sense of the word as defined by Leidhold (1928, p. 11) who says that the median septum divides to produce the chamber. Wiśniewska (1932, p. 6), on the other hand, states that the septalium of the Mesozoic rhynchonelloids is formed by internal inflection of the hinge plate to meet the median septum. This seems to be the method of formation of this structure in *Frieleia* rather than division of the median septum.

4. Sartenaer (1961, p. 6), finally, wants the term to denote exclusively a certain form:

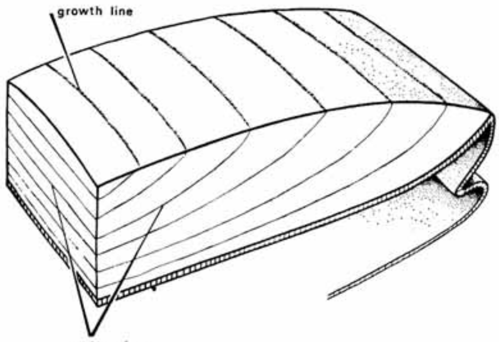
Ce terme n'est, à nos yeux, que descriptif, et nous estimons qu'il est prématuré d'en réduire la portée, vu que la signification morphologique et fonctionnelle est loin d'être comprise dans le groupe qui nous occupe.

Another interesting point is, that Sartenaer distinguishes in many of his descriptions between amphora-shaped and cupula-shaped septalia, the former enclosing a narrow and the latter a wide cavity in transverse sections. Actually, many authors make this distinction, but generally another terminology is used to designate both types of septalia.

Two conclusions can be drawn from this cursory survey of the relevant literature. Firstly, that uncertainty exists as to whether the septalium has originated by division of the septum or by fusion of the hinge plates, and secondly, that distinction is often made between septalia which are narrow and amphora-shaped or wide and cupula-shaped in transverse sections. In the following account these two matters are dealt with successively.

Terminology. The term *septalial plates* is taken to mean the lateral walls of the septalium, irrespective of the way they have grown. The *inner hinge plates* are those parts of the septalial plates which have originated by dorso-medially directed growth starting from the sub-horizontal outer hinge plates or from the crural bases. This term approximately corresponds with the *crural plates* as conceived by Cloud (1942, p. 10). In the following account it is demonstrated that both terms—inner hinge plates and crural plates—when used in this sense are not helpful, and are best avoided altogether.

The problem of how the septalium grows can be investigated by the study of growth-lines in serial sections through the structures concerned. In living brachiopods the inner shell surface is lined with an outer epithelium which is responsible for the shell secretion. In both valves this epithelium extends towards the commissure and the growth of the outer shell surface is the result of a corresponding increase in size of the outer epithelium. Along the inner surface of the shell, and thus also along the surface of the internal shell structures such as the septum and the septalium, shell material is deposited at a rate which varies from one position to another. Old inner shell surfaces are thus buried in the subsequently deposited shell material. They intersect the outer shell surface as growth-lines and run more or less parallel to the actual inner shell surface which, of course, can be considered as the final one (text-fig. 2). Thus, they can only be studied in sections



TEXT-FIG. 2. The position of growth-lines and growth surfaces in the shell. (After Westbroek, 1967.)

through the shell and on the outer shell surface. Old inner shell surfaces which are recognizable as such are termed *growth surfaces* and in the sections they appear as *growth-lines*. These growth-lines enable the reconstruction of the growth process of the shell. It is, however, often far from easy to detect growth-lines in sections. Rhynchonellid shells mainly consist of calcite fibres which normally make very acute angles with the inner shell surface and intersect the growth surfaces. When the fibres are cut according to their long axes they are liable to be mistaken for growth-lines; when they are transversely cut, however, their arrangement may be such that the growth-lines can be more easily followed (Pl. 61, fig. 3). In the literature one often finds drawings of serial sections in which the fine structure has been indicated in some detail. Such drawings are certainly much more useful than the black spots which are normally given, but often the growth-lines and the fibres are not properly distinguished. In spite of the fact that they are

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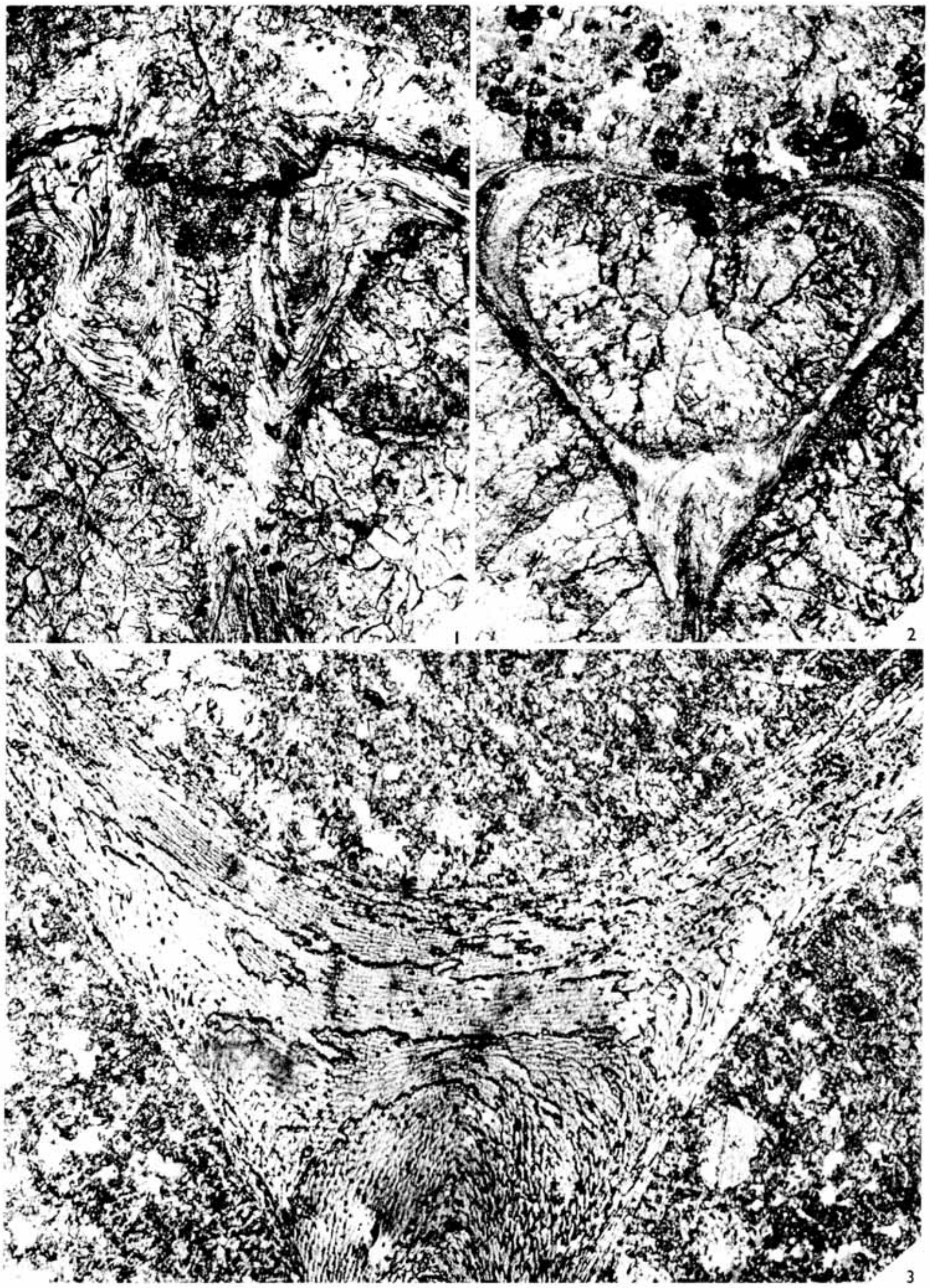
EXPLANATION OF PLATE 61

Figs. 1, 2. *Ptychomaletoechia* cf. *gonthieri* (Gosselet, 1887), Crémenes Limestone (Frasnian-Famennian boundary), NW. Spain. 1, Transverse section through septum and septalium of gerontic specimen. Septalium consists entirely of hinge plates and is amphora-shaped, ×40. 2, Transverse section through septum and septalium of adult specimen. Bi-furcating septum; septalium is cupula-shaped and consists partly of outgrowths of septum and partly of inner hinge plates, ×40.

Fig. 3. *Trigonirhynchia pareti* (De Verneuil, 1850), Emsian, La Vid Formation, Cantabrian Mountains, Spain. Transverse section showing transition between septum and septalium. Fibres of secondary shell are transversely cut, and growth-lines can be traced. The course of these growth-line suggests a bifurcation of the septum. ×150.



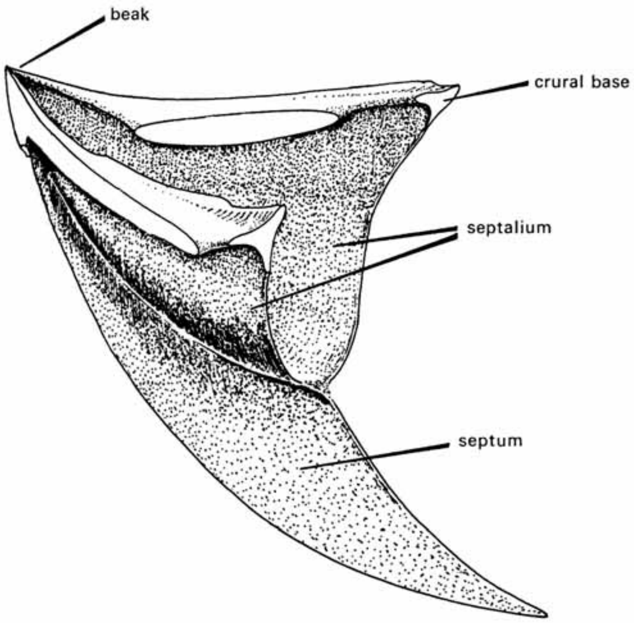
WESTBROEK, Transverse sections of septa and septalia generally not very clearly defined, the growth-lines in the sections can often be traced, though with some difficulty so that at least an impression can be obtained of how the different shell structures have grown.

Text-fig. 3*a* shows a section through the brachial valve of a specimen of *Ptychomaletoechia* cf. *gonthieri* (Crémenes Limestone, Frasnian–Famennian, N. Spain; see Westbroek, 1964). Growth-lines have been drawn wherever they could be identified. It appears that the septum grew from the bottom of the valve in ventral direction until point A was reached. There it divided into two elements which grew symmetrically in both

TEXT-FIG. 3. *Ptychomaletoechia* cf. *gonthieri* (Gosselet, 1887), Crémenes Limestone (Frasnian-Famennian boundary), NW. Spain. Transverse sections in umbonal part of brachial valves. Growth-lines have been indicated. *a*, Section through adult specimen, showing bifurcation of the septum, the cupula-shaped septalium consisting of the resulting outgrowths of the septum and of the inner hinge-plates. *b*, Section through gerontic specimen. Amphora-shaped septalium, consisting of inner hinge plates, which have united at their dorsal end and then have fused with the monocarinate septum.

ventro-lateral directions. Each outgrowth of the septum then met a corresponding inner hinge plate growing dorso-medially, so that a full-grown septalium arose (Pl. 61, fig. 2). This type of growth is intermediate between the manner of growth of Leidhold's septalium and Cloud's crural trough and might warrant a new term. However, inspection of text-fig. 3*b*, which represents a section through the brachial valve of another, more gerontic, specimen from the same locality and most probably also belonging to *P.* cf. *gonthieri* (Pl. 61, fig. 1) shows both septalial plates to consist entirely of the inner hinge plates which have grown in dorsal direction, then have united and finally connected with the median septum which has remained mono-carinate during its entire growth. This structure complies with the crural trough of Cloud and cannot be considered as a septalium as conceived by Leidhold.

The questions now arise as to how these differences may be interpreted and how important they are systematically. The relation between the structural types of the septalium becomes clear when the three-dimensional shape of this element and not only plane sections through it are taken into consideration. Text-fig. 4 gives a schematic three-dimensional representation of the septum and septalium. For convenience surrounding structures are omitted. The structural complex displayed radiates as a whole from the umbo, from which it has actually grown approximately anteriorly, whilst also thickening. Text-fig. 5*a* represents a projection of the septum and septalium on the median plane. Line *AB* represents the connection between the two elements. In this projection the structure has grown by a gradual anterior shifting and a concomitant enlargement of the anterior boundary. A series of growth stages is also represented in text-fig. 5*a*. They actually constitute the projections of the anterior boundaries of a series of successive growth surfaces which, as we have seen, envelop each other. By means of this figure two arbitrary points, *P* and *Q*, can be located so that *P* is the older and was first reached by the anteriorly growing structure. Assuming that the number of growth



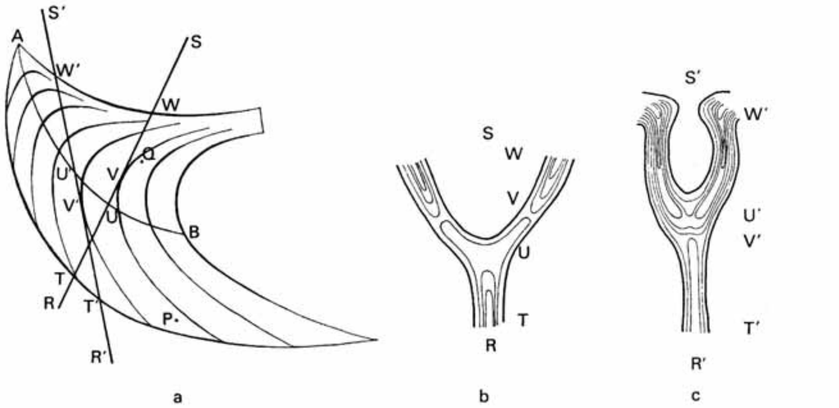
TEXT-FIG. 4. Schematic three-dimensional representation of septum and septalium.

surfaces at a particular point in the projection corresponds with the number of drawn anterior boundaries which are successively intersected by a line connecting that point with the final anterior boundary, then that number is 3 for *P* and 2 for *Q*. Consequently it is possible to reconstruct the course of the growth-lines in any section perpendicular to the plane of symmetry.

An attempt is made to reconstruct a section *RS* (text-fig. 5*a*). Point *T* obviously is the oldest point cut by the section; the number of growth-lines will be maximal here. From *T* in the direction of *S* progressively younger parts of the structure are cut, and the number of growth-lines decreases until *V* is reached, where the plane of the section is tangential to the anterior boundary of a growth surface. Consequently, *V* is the youngest point cut by the section and the number of growth-lines reaches its minimum here. From *V* to *W* the age of the structure and the number of growth-lines increases again. Point *U* represents the boundary between the septum and the septalium in the section. Since *V* is situated ventrally in relation to *U* the course of the growth-lines in the section must suggest a division of the septum (text-fig. 5*b*).

TU and *UW* are the projections of the section through the septum and the two septalial plates, respectively. Consequently the number of growth-lines is duplicated from *U* ventrally. This, of course, has not been taken into consideration in the above argument.

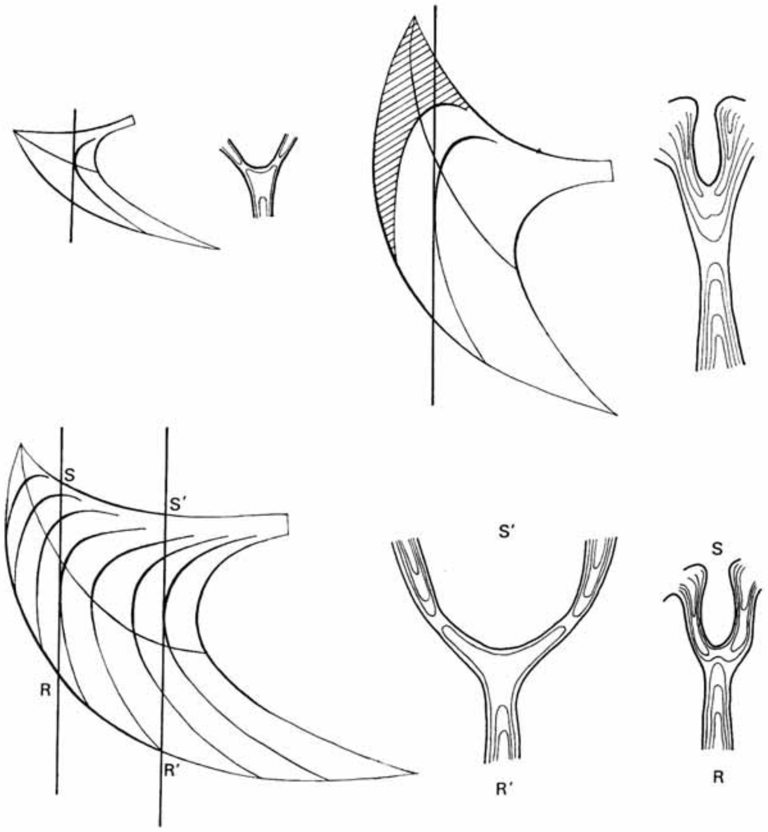
The course of the growth-lines can be reconstructed likewise in section *R′S′* (text-fig. 5*a*), and since in this section *V′* is situated dorsally in relation to *U′* the septalium will consist here entirely of the hinge plates; these plates even fuse to form the most ventral part of the septum (text-fig. 5*c*).



TEXT-FIG. 5. *a*, Projection of a septum and septalium on the plane of symmetry; a series of early growth stages is represented. *b*, Section *RS* through this septum and septalium. *c*, Section *R′S′* through same structure.

Thus, it is demonstrated that there is no fundamental difference between a septalium which is formed partly or entirely by bifurcation of the septum and one which has been brought about by fusion of the inner hinge plates. It all depends on the relative positions of *U* and *V* in the section: when *U* is situated dorsally in respect of *V* the septum bifurcates; when it is situated ventrally of *V* the hinge plates fuse together.

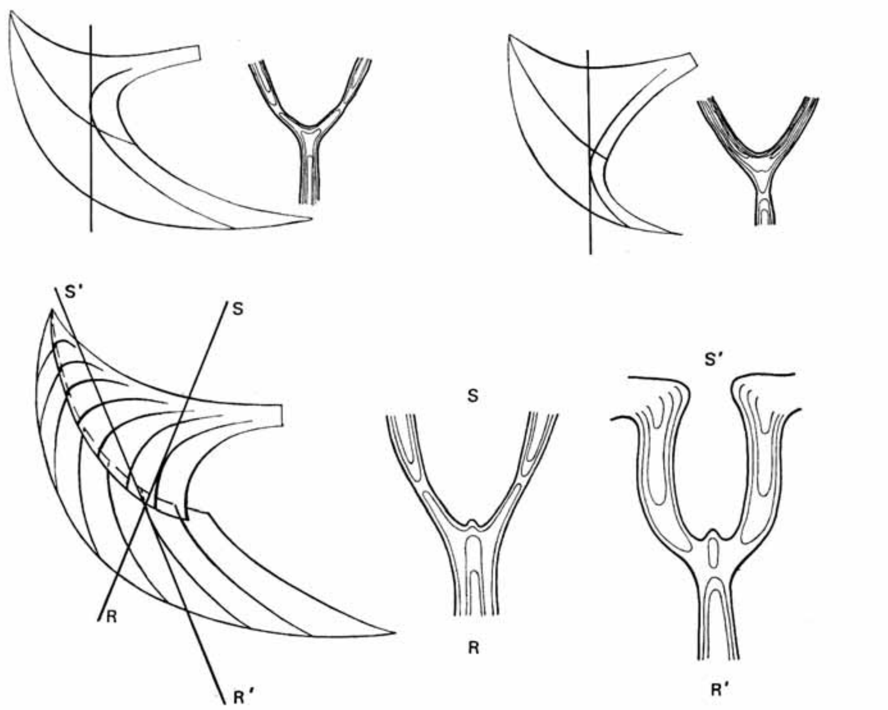
The relative position of *U* and *V* depends on a number of factors. As we have seen, the direction of the section is important (text-fig. 5). Since generally the sections are taken perpendicularly to the plane of the commissure and since the angle between the most posterior part of the outer surface of the brachial valve and the plane of the commissure increases according to the ontogenetical age of the specimen, *V* tends to be situated more dorsally relative to *U*, and thus the septalium tends to be more completely constituted by the hinge plates in older specimens (text-fig. 6 top). The effect of the location of the section is determined by the general curvature of the structure (text-fig. 6 bottom). Posterior sections generally show a septalium which consists more fully of the hinge plates than more anterior ones. Another important factor is, of course, the shape of the structural complex. Differences, for example in the course of the anterior boundaries of the growth surfaces, may have an effect on the sections, as represented in text-fig. 7 (top), and differences in the line of connection between the septum and the septalial plates naturally also affect the relative position of *U* and *V*. In many species the anterior boundaries of the septum and the septalium are not continuous: the septum protrudes a little beyond the septalial plates, anteriorly as well as ventrally, in lateral



TEXT-FIG. 6 (Top) The influence of the ontogenetical age of the specimen on the shape and structure of the septum and septalium in the section. (Bottom) The influence of the location of the section on the displayed shape and structure of the septum and septalium.

view, and it seems to have more individuality, to be a more 'primary' structure. Reconstructions of sections through a structural complex of this type are given in text-fig. 7 (bottom). It appears that a division of the septum may be suggested in certain sections, the septum then tending to divide ventrally into three parts. A growth pattern in which the septalial plates first unite and then fuse with the septum can hardly occur, the direct fusion of the septalial plates being prevented by the intermediate septum in the sections.

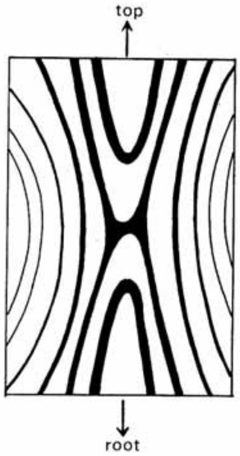
When in a piece of wood the annual rings run as indicated in text-fig. 8 there is no particular reason to conclude that the whole tree has originated by fusion of two originally independent structures, one growing upward from the root and the other downward from the top, although for the represented section itself this assumption certainly holds good. For the same reason the question whether the septalium has grown by bifurcation of the septum or by fusion of the hinge plates makes sense only as long as sections through the structure are considered and it becomes irrelevant as soon as the entire structure is taken into consideration. Campbell (1965, p. 13) appears to have



TEXT-FIG. 7 (Top) The influence of the shape of the anterior boundary of the septum and the septalium on the structure of these elements in tranverse sections. (Bottom) Two sections showing the effect of the protrusion of the septum beyond the septalial plates, anteriorly as well as ventrally.

understood this when he characterizes Cloud's distinction between a septalium and a crural trough as 'singularly unhelpful since it is concerned only with appearances and not with origins'. The cardinalia must be considered as a single though complicated structural complex which grows as a whole from the umbo anteriorly. During this process it increases in size but does not change essentially in shape. Division of a septum would mean that originally only one septum would occur in the shell, and that at a certain moment in the ontogenetical development two distinct septa would arise out of this single septum by accretional growth in front of it. This would mean that the cardinalia would change essentially in shape during growth. A similar reasoning can be applied to the process of fusion. In other words: terms like division and fusion are meaningless unless they refer to a process which takes place within a time-interval which is small relative to the entire period of growth: before this time-interval the structure concerned is not divided or fused, and afterwards it is.

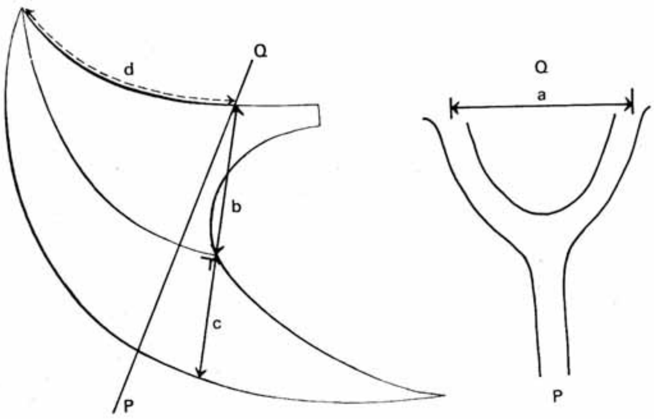
A few conclusions may be drawn concerning the terminology of the elements. Since the criteria by which the terms 'septalium' and 'crural trough' are distinguished are invalid, there is good reason to reject the term 'crural trough'. To denote the lateral walls of the septalium the terms 'inner hinge plates' and 'crural plates' are quite inappropriate for the reasons given above. Instead, the use of the term 'septalial plates' is recommended.



TEXT-FIG. 8. Annual rings in a piece of wood. The manner in which the tree has grown *in this section* differs from the manner of growth of the whole tree.

The *shape* of the septalium as it appears in the section is determined, as is the course of the growth-lines, by the direction and the location of the sections on the one hand and by the three-dimensional shape of the whole structure on the other, and the same applies to the size. The influence of the direction of the section on the shape can be visualized by reference to sections *RS* and *R'S'* in text-fig. 5, which show a wide, cupula-shaped, and a narrow, amphora-shaped, septalium, respectively. Text-fig. 6 (top) illustrates the influence of the age of the specimen: in young specimens the sections tend to show a wider septalium than in old ones. An extreme instance of this effect was demonstrated by Rouselle (1965), who showed the shape of the septalium to be affected beyond recognition in transverse sections through old specimens of mesozoic Rhynchonellida and Zeilleriacea. In view of the structure anteriorly from the umbo, sections through the posterior part of the septalium will be generally relatively narrower than more anteriorly located ones (text-fig. 6 bottom). Sartenaer's distinction between amphora-shaped and cupula-shaped septalia is therefore deceptive.

The shape of a septalium can only be illustrated accurately after a three-dimensional reconstruction. A method for the preparation of three-dimensional reconstructions after serial sections is described by Westbroek (1967, p. 12). Enlargements of the sections are drawn on thin glass plates which are then mounted in a way as to be appropriately situated relatively to each other. Stereophotographs are then prepared of this arrangement and the reconstruction is drawn by means of a stereoscope. The drawing of the reconstruction is, even under these circumstances, a difficult procedure, and probably the mere representation of the stereo-photographs will do as well, or sometimes even better. A shortcoming of the three-dimensional reconstructions is that they only provide a realistic impression of the shape of the structure, without giving measurable data which can be expressed numerically and are suited for computation. For such an elaboration, the projection of the septum and septalium on the plane of symmetry and the sections themselves together give a lot of reliable information. Such a projection can easily be constructed by drawing a lateral view of the specimen before sectioning, then by marking the location of the sections in this drawing as exactly as possible, and finally by indicating in the drawing the relevant data of each section, such as the point of fusion of the septum and the septalium, the youngest point cut by the section and the ventral boundary of the septalium. Connection of the corresponding points provides the projection requested. For statistical computation the following may serve as measureable variables: the depth of the septalium at its anterior boundary, the distance between the anterior boundary and the beak, the height of the septum at the anterior boundary of the septalium and the unrolled length of the base of the septum. The width of the septalium



TEXT-FIG. 9. Some variables, *a*, *b*, *c*, and *d*, which can be measured in the projection of the septalium and the septum on the plane of symmetry and on a specially selected section, and which can be used for statistical treatment.

at its anterior boundary is another important variable; it can be found in a selected section (text-fig. 9). A statistical treatment of these measurements would of course be a most laborious procedure, since serial sections must be made through a considerable number of specimens in order to obtain a significant sample. Consequently, this method can only be applied in very special cases, e.g. when the discrimination between two species is very difficult and when the collections are very large.

The considerations given above can be applied to many structures which increase in size by accretionary growth, especially to other brachiopod shell elements such as the pentamerid spondylium. Even in the interpretation of sedimentary structures—which often display a striking analogy to brachiopod shells—similar problems may arise.

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