THE PENTAMERACEA OF THE OSLO REGION

BEING

A DESCRIPTION OF THE KIÆR COLLECTION OF PENTAMERIDS

BY

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WITH 23 FIGURES IN THE TEXT AND 8 PLATES

Contents.

Preface.

The greater part of the material described in the present study was collected by the late Professor J. Kiær at the time of his detailed investigation of the Silurian rocks of South-eastern Norway. Kiær's stratigraphical results were published in his well-known monograph "Das Obersilur im Kristianiagebiete", and he had intended, apparently, to devote a separate work to a description of the fauna, especially the *Brachiopoda*. This projected work was unfortunately never completed, but Professor Kiær's entire collection, numbering several thousand specimens, is preserved at the Palaeontologisk Museum, Oslo. Of the *Brachiopoda*, the Pentamerids form the most widespread and important group, abundantly represented as they are in nearly all the different areas of the Norwegian Silurian. It appears that Professor Kiær had a few plates prepared, illustrating some of these Pentamerids, in view of a projected monograph on the *Brachiopoda* of Southern Norway: although many of the specimens had been identified, no notes exist, nor has it always been possible to determine the originals of Kiær's figures.

The Pentamerids are very abundant at many horizons in the Norwegian Silurian, but comparatively few genera and species are represented. All the material, however, is extremely well preserved, and instead of a state of preservation as casts, familiar in British specimens, not only do the interiors remain intact, embedded in matrix, but in many cases comparatively little exfoliation of the exterior shell has taken place. One further consideration enhances the special value of this collection. Nearly all the material has been very carefully labelled, so that the majority of specimens can be assigned to their original localities and horizons; with regard to the latter not only to a definite zone but often (by reference to the figures and tables in Kiær's monograph) to within a few feet in the succession.

With one or two exceptions the Pentamerids in question are not of great use for very detailed, stratigraphical zoning, and consequently a strictly palaeontological approach is adopted. By this means it is hoped the better to illustrate the facts that have been learnt concerning the evolution and origins of this group, and where necessary the work has been extended beyond the limits of this collection. Thus, with regard to the origin of the Pentamerids, specimens of

some of the early forms that occur in America and in Greenland have been examined, although without throwing much light on this problem. Again, the possibility that the essentials of the Pentamerid structures might be derived from such a form as the common Ordovician genus *Porambonites* led to an investigation of that genus. Representative specimens of each species and genus have, whenever possible, been compared with the type material, while an intensive search has been undertaken amongst the early literature on the subject with the aim of settling controversial points of nomenclature that have arisen.

The work, of which the results are here described, has been undertaken in the course of the last two years at the Sedgwick Museum, Cambridge. The writer wishes to express his thanks to Professor Holtedahl and Dr. A. Heintz for entrusting him with the description of this collection; and to the latter and to Dr. Leif Størmer for affording him facilities at the Palaeontologisk Museum, Oslo, and for guiding him over some of the classical Norwegian localities. He wishes, also, particularly to thank Professor O. T. Jones and Dr. O. M. B. Bulman for advice and kindly criticism, and Miss H. M. Muir-Wood and Mr. A. G. Brighton for access respectively to specimens in the British Museum (Natural History), London, and the Sedgwick Museum, Cambridge. Finally, he would express his thanks to the Department of Scientific and Industrial Research, London; to the Goldsmiths' Company, London, and to the Master and Fellows of Selwyn College, Cambridge, for the award of grants during the tenure of which this paper has been written.

Introduction.

The district of south-eastern Norway has long been recognized as a classic area for the study of the Silurian rocks, partly because of the continuous succession and the excellence of the exposures, and in part because of the abundance of the fauna, which is very largely of the shelly facies. This area early received the attention of geologists, but no detailed treatment appeared until comparatively recently. The original division of the Norwegian Lower Palaeozoic into nine groups was proposed by Kjerulf (1857 and 1865), and elaborated by later writers, but the first extensive treatment of the Silurian was due to Brøgger (1886 and subsequent papers) and Kiær,

who after two preliminary studies in 1897 and 1902, published his monograph "Das Obersilur im Kristianiagebiete" in 1908, and it is on this work that all subsequent advances must be based. His treatment was stratigraphical, and for the purposes of description he divided into seven districts the areas of occurrence of Silurian rocks, all of which lie within the down-faulted "Oslo region" extending from the mouth of the Oslo fjord northwards to Mjøsen. Since the faunas preserve a certain individuality as between district and district this division will be the subject of frequent reference in the present paper, and for convenience, the main characters of the successions in the different districts are summarized in Table I (p. 256). In the northern development the shelly fauna is scarcely represented, and it is mainly with the faunas of areas I, II, III and V that the present work is concerned.

The Pentamerids are characteristically fossils of the shelly facies, and to judge from a quantitative distribution — if this may serve as a general guide their most favourable habitat was in fairly clear water of quite moderate depth. Thus, it may be observed that it is in the relatively clear-water deposits of 6 c from Malmøy, Asker and Holmestrand that *Stricklandia lens* is represented most abundantly, while the distribution of the typical form of *Stricklandia lirata* shows a definite preference for clear-water formations. *Pentamerus borealis* is most abundant in this region (at Ringerike and Hadeland), as elsewhere, in shallow-water limestones, while *Pentamerus laevis* [=*P. oblongus*] is commonest in the most calcareous development of 7 b at Malmøy, Ringerike and Holmestrand. These considerations do not appear to apply with quite the same force to *Clorinda*.

In addition to the specimens in the Kiær Collection the writer has examined much duplicate material in the Palaeontologisk Museum, Oslo, and the Sedgwick Museum, Cambridge, as well as material in the Riksmuseum, Stockholm and the Palaeontological Institut at Kåbo, Uppsala. In all, several thousand specimens of *Pentamerus* and *Stricklandia* have been available for study. A comparison with British material has been made in order to correlate the Norwegian succession with the rocks in the type areas in Britain. Though this can only be done on a broad scale, the results of such a comparison appear to demonstrate the probable absence of true Lower Llandovery, at least in part, in Norway. Further anticipation would be premature, and these points are discussed more fully in a later section.

Of the genera that are present in the collection, *Pentamerus* is represented by three species, *Stricklandia* by two species, *Clorinda* by three species, *Conchidium* by one species and the interesting genus *Holorhynchus* by the only species that is yet known. After a detailed study it has been found necessary to propose only two new species, but within the limits imposed by the extent of the material it has been possible to arrange specimens in morphological series, which serve to illustrate in more than one case possible lines of evolution.

In the Kiær Collection the matrix in which the specimens are embedded, usually consists either of fine-grained calcareous sediment, or of a mosaic of calcite crystals formed subsequently to the fossilization of the specimen. In either case, the infilling is not very susceptible to removal by a dental drill, and such a method of preparation does not yield very satisfactory results. To meet the necessary requirements the obtaining of accurate and detailed information concerning the internal structure the technique of serial-sectioning has been adopted with the preservation of closely-spaced transfers, followed by the construction of enlarged scale-models. Brief references to this method have already been published (St. Joseph, 1935 a, p. 317), and it remains to be observed that the method is an exact one, in that a record of each cross-section can be retained as a transfer, the latter being even better than a photographic print as the growth-lines of the shell are preserved. The transfer method is suitable for any hard matrix, and the only circumstance under which it does not give satisfactory results is when recrystallization of matrix and skeleton together has taken place. For the specimens in this Collection which are of relatively large size, transfer series spaced at 0.1 or 0.15 mm intervals have mostly been used, though there is now no mechanical difficulty in obtaining serial sections of solid specimens at least down to 20 μ.[1]

Scale-models in beeswax of all the species, usually two of each species, have been constructed at magnifications between $\times$ 7 and $\times$ 15, in different cases. Many of these are illustrated in the plates, though figures can never demonstrate with the same conviction as

[1] For small specimens the grinding apparatus described and illustrated by Bulman ("British Dendroid Graptolites", *Palaeontogr. Soc. Lond.* [*Monogr.*], pt. 1, 1927, pp. 4—5), has been found very useful. This yields sections which may be drawn with a *camera lucida* attachment to a microscope.

the models themselves, the three-dimensional relations between the internal structures. Serial transfers have been taken from several individuals of each species, and in the case of the commoner specimens such as *Stricklandia* or *Pentamerus* these have been supplemented by thin-sections. In this way, the interiors of at least 12 examples of each of the more abundantly represented species have been examined, by one method or another; nor does this number include the specimens (which are quite numerous) that have fractured along the median plane, to expose part of the internal structures. It is to be understood with regard to this number of individuals that the expressions 'rare' or 'common' etc, are used in the sequel, when discussing internal variation.

The nomenclature adopted in this paper includes many technical terms that are already very familiar in the literature of the subject, and it is thought that reference to text-figures will leave no doubt as to their usage. Different systems of nomenclature, indeed, exist, and reference may be made to the list of terms given by Schuchert and Cooper (1932, pp. 6 11, 162 5), to quote a recent treatment. It seems unlikely that so detailed a terminology as that applied, for example, to Mesozoic Telotremata, may ever be necessary for the Pentamerids. It is, in fact, this very simplicity of structure that enhances their value, in that they provide a clear opportunity in which to study under simple conditions in a closely related group, the effect of processes of change over a considerable interval of time.

The specimens are illustrated by plates and drawings of serial transfers. Of the latter, considerations of space have necessitated that only each alternate, or every third transfer be figured. It is thought that these are sufficient to illustrate adequately the changes occurring through the series. The drawings are numbered to correspond with the serial numbers on the transfers. In these drawings the upper of the two valves is always the ventral; ['ventral' and 'dorsal' are used to describe the two valves in preference to 'pedicle' and 'brachial', with which terms they are synonymous]. 'Left' and 'right' in the text, and in the descriptions of figures, are to be understood as referring to the left and right of the animal, thus when the specimen is viewed from the dorsal side with the posterior end uppermost, the left of the specimen is on the observer's right, and *vice versa*. Usage is far from uniform in this matter with different authors.

All the models and serial transfers prepared in connection with this work have been deposited in the Sedgwick Museum, Cambridge (hereafter referred to as S. M. C.), while the collection of specimens remains in the Palaeontologisk Museum, Oslo (hereafter referred to as P. M. O.). Duplicates of two of the models, S. M. C., A. 13504, and A. 13518 have been deposited in the P. M. O.

Morphology.

The Delthyrium and Pseudodeltidium.

The nature of the pedicle-opening at present forms the basis of the commonly accepted division of the Phylum Brachiopoda into four Orders, and it is thus unfortunate that there has been considerable laxity in the use of terms describing this portion of the shell. In the present connection, it is the characters of the Protremata and Telotremata that are in question, and the nomenclature used applies particularly to these two Orders. It may be suggested that descriptive terms should be employed as far as possible in the sense in which they were used by their proposers, being modified only in so far as later work has tended to give a clearer conception of the structure or function of the feature in question. The morphology of the pedicle-opening (= foramen, in the Articulata) has been discussed recently by Thomson (1927, pp. 63 79), and the nomenclature there adopted is partly followed in the present account.

When the ventral cardinal-area is divided medianly by a triangular fissure, the latter is usually termed a 'delthyrium' (Hall and Clarke, 1892, pt. i, p. 189 footnote). The delthyrium extends from the hinge-line towards the umbo, and it appears to serve, primarily at least, for the passage of the pedicle. The shape and size of the pedicle-opening may be modified in different ways by the secretion of shell-material united to the ventral valve, and it is in connection with the terminology of these modifications that confusion has arisen. One of the first writers to discuss the morphology of this part of the shell was von Buch, who proposed the term 'deltidium'[1] (1834 [1835], p. 35) for the covering that constricted the pedicle-opening in certain Brachiopods, and he figures as examples some species of *Terebratula s. l.* He considered as distinct arrangements the cases in which the deltidium

[1] "Dieses schließende kleine Schaalstück nenne ich das 'Deltidium'.".

completely surrounded the foramen, bounded it only on its dorsal side, or was alternatively divided by the foramen into two entirely separate parts.

The term pseudodeltidium was first proposed by Bronn (1862, p. 242), who regarded it as distinct from von Buch's 'deltidium', defining it as follows:

> "Wo jenes [Schnabel-]Loch gar nicht vorhanden, da bleibt die dreieckige und bis in die Buckel-Spitze reichende Deltidial-Öffnung entweder ganz unverschlossen, oder sie schließt sich durch ein ungetheiltes mit dem rechten und linken Rande fest verwachsenes flaches und in der Regel queer-gewölbtes Pseudodeltidium, dessen Schloß-Rand gebogen ist und so, wie die ihm parallele Zuwachsstreifung des Deltidiums die Konvexität der Biegung nach hinten kehrt."
>
> (Bronn 1862, pp. 241 2).

Bronn was evidently describing an undivided plate attached to the sides of the delthyrium and partly covering the delthyrial opening. He refers for examples to figures of *Thecidium*, *Spirifer s. l.* and *Chonetes* (Bronn, *op. cit.,* pls. 23 and 24, figs. A, B, D and N). Quenstedt (1868, p. 10) interpreted this to mean that pseudodeltidium was partly synonymous with deltidium, while Davidson appears to have used deltidium in a general sense for any constriction of the pedicle-opening consisting of one or two pieces or 'plates' (cf. Davidson, 1853, p. 61; 1884, p. 289).

The two separate plates present in many Telotremata, that cover the delthyrial opening to a greater or lesser extent, have been termed generically by many different authors (*e. g.*, Schuchert, 1897, p. 74), deltidial plates (deltaria of Hall and Clarke, 1894), and when united they have been considered to form a 'deltarium' (of Hall and Clarke, 1894, p. 328), a 'pseudodeltidium' (of Schuchert, 1913, p. 359) or a 'symphytium' (of Buckman, 1918, p. 88). The term deltidium was taken by Beecher (1892, p. 142), Hall and Clarke (1892, p. 189; 1894, pp. 327 8), and Schuchert (1897, p. 74; 1913, p. 358) to include a superficially somewhat similar covering of the pedicle-opening in the Protremata, while pseudodeltidium was applied by Walcott (1912, p. 293) to a 'plate' which he considered to be the homologue in some Atremata and Neotremata, of the 'deltidium' of the Protremata.[1] In the same sense as this, Schuchert (1913, p. 358)

[1] This was Walcott's opinion, but it is very unlikely that the two structures are really homologous. Cf. *e. g.* Thomson, 1927, p. 66.

used the term homoeodeltidium. More recently, Thomson (1927, p. 68) and Schuchert and Cooper (1932, p. 7) restrict the term deltidium to a roughly triangular plate growing dorsally from the apex of the delthyrium in Protremata, and use the name deltidial plates for the structures which constrict the pedicle-opening in the Telotremata and which form a deltarium (of Hall and Clarke) or pseudodeltidium (of Schuchert) when united.

It will be seen from this that not only has there been little constancy in the usage of these terms, but that the meanings of 'deltidium' and 'pseudodeltidium' have come to be almost exactly interchanged. Deltidium first used by von Buch for a structure consisting of two plates covering the delthyrium of such forms as *Terebratula* and *Rhynchonella s. l.* now classed as Telotremata, has been used by recent authors for a single plate constricting the delthyrium in Protremata, while pseudodeltidium defined by Bronn as an undivided plate, has come to be used for the united condition of deltidial plates in Telotremata. Though it is likely, at least in certain genera, that the pseudodeltidium was secreted by a mantle-flap embracing the pedicle just as were deltidial plates, this is no reason for interchanging the meanings attached to these terms, while the only way to avoid further confusion is to use 'deltidium' and 'pseudodeltidium' in the sense in which they were employed by the proposers of these terms.[1] Pseudodeltidium, too, was used by Beecher as applying to the Protremata at the time that he proposed the four Brachiopod Orders at present in general use (1891, p. 355) and should be so employed for this reason as well.

The Pentameroidea are usually classed as Protremata, principally because of their close relationships with the Orthoidea: the presence

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[1] 'Deltidium' of von Buch (1834) in part, deltarium (of Hall and Clarke, 1894, and Schuchert and Cooper, 1932), pseudodeltidium (of Schuchert, 1913, *non* Bronn), and symphytium (of Buckman, 1918).

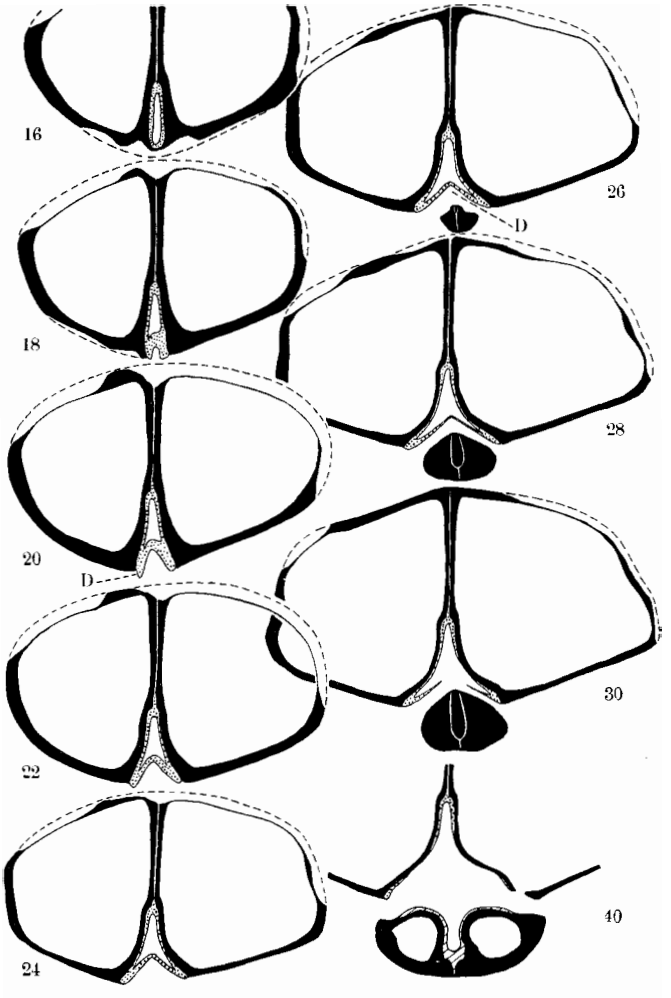
'Pseudodeltidium' of Bronn (1862) = in part, deltidium (of Hall and Clarke, 1894, Schuchert, 1897 and 1913, and Schuchert and Cooper, 1932; *non* von Buch).

The writer is very grateful to Mr. Henry Woods and Dr. O. M. B. Bulman for helpful discussion of a number of points in this section. Mr. Woods has always maintained that pseudodeltidium and deltidium should be used in their original sense [cf. Woods "Invertebrate Palaeontology" eds. I to VII (Cambridge 1893—1937), section Brachiopoda] while among American authors, pseudodeltidium has been correctly used *e. g.* by Girty 1908, "the Guadalupian Fauna", *Prof. Pap. U. S. geol. Surv.*, 58.

of any structures modifying the delthyrium has seldom been observed. Although Hall and Clarke (1894, pp. 247, 341 2) considered deltidial plates to be present in certain genera, such structures were not recorded by Schuchert and Cooper (1932, p. 163). The only instances in which these authors record a covering plate constricting the delthyrium are in a species of *Conchidium*, and in one species of *Harpidium*, in which they describe a rather large 'concave deltidium'. Kozlowski (1929, p. 130) has stated that deltidial plates (forming a 'deltarium discretum') are present in some species of *Gypidula*, *Clorinda*, *Pentamerella, Cymbidium* and *Harpidium*, and he considered that the single, concave plate in *Conchidium* and *Pentamerus* was formed by the fusion of two primitive plates composing a syndeltarium (= deltidium). He accordingly groups the Super-family Pentameracea with the Telotremata. Kozlowski's deltidial plates evidently correspond to the slight thickenings along the delthyrial margins termed by Schuchert and Cooper (1932, pp. 163, 176) 'incipient deltidial plates' and by Booker (1927, p. 134) 'pseudo-deltidial plates'.

In the Kiær Collection of Pentamerids the material is well preserved so that it has been possible to study in considerable detail the modifications of the delthyrium, and the origin of the structures concerned. A definite pseudodeltidium is present occasionally in *Pentamerus borealis*, as a general rule in *Pentamerus laevis* [= *P. oblongus*] and in *Pentamerus (Pentameroides)* cf. *gotlandicus*. In *Clorinda undata* and *Stricklandia lens* there are slight thicknings of the delthyrial margins. The occurrence of these structures is described under the separate species, only the more general considerations are noted here.

The presence of a pseudodeltidium in these species has been revealed by serial sectioning. It is in specimens in which the umbones are surrounded by matrix that the structure is best preserved; the pseudodeltidium is seldom visible when individuals have been cleaned of matrix since it is so fragile as easily to be removed. In closely-spaced serial-sections or transfers it is readily seen, however, as a thin covering at the apex of the delthyrium (text-figs. 1, 5 8), while in models its true form may be appreciated, that of a triangular plate which may be flat or concave outwards in different cases (Plate V, figs. 6 7). These sections reveal also the details of its structure. The pseudodeltidium is composed of a thin layer of shell-substance which lines the spondylial cavity, and which is described in the



Text-fig. 1. *Pentamerus (Pentameroides)* cf. *gotlandicus.* Lebedev.

Serial transfers (S. M. C., A. 13507) at 0.15 mm intervals from the posterior end of a specimen; zone 7 cβ, at Vesleøy, Ringerike. ×2⅓. Transfers 16—40. (For the complete series see text-fig. 8.) D pseudodeltidium.

succeeding part of this paper. This fine layer is best developed in the posterior portion of the spondylium, it is separated from the rest of the spondylial walls by a plane of discontinuity (text-figs. 1 and 2, where this thin shell-layer is stippled). Along the anterior part of the sides of the delthyrium the free edge may be thickened and as these thickened edges are traced towards the posterior they first constrict the delthyrial opening and finally form a complete cover over the apex of the delthyrium (text-fig. 1). This cover is a single structure crossed by continuous growth lamellae, and showing no trace of a median line of suture; it is thus not formed by the fusion of two pieces growing inwards from the margin but, apparently, rather by continuous growth anteriorly from the apex of the delthyrium; it is usually limited from the cardinal-area by small grooves. In *Pentamerus laevis* the covering is flat or gently concave (text-fig. 5, transfers 18 to 27), and lies very close to the incurved dorsal umbo. In *Pentamerus* cf. *gotlandicus* it is deeply concave (text-figs. 1 and 8) owing to the pronounced incurving of the umbo, which actually projects within the delthyrial cavity. In the typical thick-shelled *Pentamerus borealis* and in *Conchidium münsteri* the same thin layer is present lining the spondylial cavity (text-figs. 2, I II and 7, II), though in the specimens that have been sectioned it does not form a pseudodeltidium. In the species of *Clorinda* in the collection, this thin layer has not definitely been identified, and it is thus not altogether unexpected that a pseudodeltidium is never present.

The pseudodeltidium then, in these species of *Pentamerus* is composed of shell-substance continuous with that of the thin layer on the inside of the spondylium (text-fig. 1), which extends in some species even towards the anterior end of that structure. It would be in contact, in life, with the soft tissue, covering the surface of the spondylial cavity, and any increase in this layer subsequent to the formation of the spondylium could only take place by secretion by this mantle-tissue. The pseudodeltidium in these genera was thus probably formed by a small flap of the mantle which gradually extended anteriorly from the apex of the delthryium.[1] The covering evidently served to close the posterior part of the delthyrial opening above the dorsal umbo, and owing to the incurving of the umbo there

[1] Cf. the growth of the chilidium as inferred by Thomson (1927, p. 77).

would be no room for the passage of a functional pedicle[1] (cf. text-figs. 1, 5 and 7, I). In *P. borealis* the absence of a pseudodeltidium may possibly be explained by a closer approximation of the valves (cf. text-fig. 3, transfer 24), thereby perhaps obviating the need for such a structure. The difference, however, between this species together with *C. münsteri* and the later species of *Pentamerus* is more apparent than real, as may be seen by comparing text-figs. 1, 2 and 7. Thus, in all these forms, the thin layer lining the spondylial cavity is a constant feature and there is evidently a possibility that a pseudodeltidium might occasionally occur in *P. borealis* or in other species of *Conchidium*. It has, in fact, been observed in a *borealis-laevis* transitional form from zone 7 a at Asker (P. M. O. 53482; text-fig. 2, VI), while a deeply concave pseudodeltidium is present in the type species of *Conchidium*.

Detailed study of the typical genus of the Pentameracea gives no support to the view proposed by Kozlowski (1929, pp. 130 2) that *Pentamerus* and *Conchidium* possess a 'deltarium' [deltidium] composed of fused deltidial plates, and that the Super-family should be grouped with the Telotremata. The covering at the apex of the delthyrium in these two genera is an undivided plate or pseudodeltidium (in the sense of Bronn, 1862); while of the genera in which Kozlowski held that the narrow deltidial plates were present, in *Clorinda* and probably also *Gypidula* this appearance is produced by a slight thickening of the delthyrial margins which never approaches the structures in *e. g.* Palaeozoic Rhynchonellids or Mesozoic Terebratulacea.

If the study of these genera confirms the customary grouping of the Pentameracea with the Protremata it appears also to throw doubt on the value of the pseudodeltidium and of deltidial plates in so far as they are claimed to be of different origin, as distinguishing criteria between the Protremata and Telotremata. Beecher, when he proposed his four-fold division of the Brachiopoda, stated (1892, p. 142) "that the deltidium [= pseudodeltidium of Bronn] in all species possessing it (the Protremata) is an embryological, or nepionic feature", and he describes, with reference to Kovalevskii's work on the Development of the Brachiopoda, the origin of this structure. According

[1] The pseudodeltidium in these species is never perforated near its apex for the passage of a pedicle, as is the case, for example, in the Clitambonacea.

to Beecher (1892, pp. 142 5) the 'deltidium' is present in the cephalula just before its metamorphosis; it lies on the dorsal side of the pedicle close to the dorsal valve.

"The deltidium is not, therefore, primarily, on account of its manner of origin, an integrant part of the ventral valve, but is a shell growth from the dorsal side of the body, which afterwards becomes attached to the ventral valve, and is then considered as belonging to it.

"The further growth of the deltidium around the body and pedicle, and its consequent extension into the cavity of the ventral umbo, may explain the origin of the spondylium."

(Beecher, *op. cit.*, pp. 144 5.)

The deltidial plates of the Telotremata, however, according to the same author are neanic or ephebic features appearing at a much later period of growth.

"The ventral mantle gradually extends from each side as two prolongations partially covering the opening and enveloping the proximal portion of the pedicle. As this is an extension of the shell-secreting surface of the mantle, there naturally results the formation of two plates within the deltidial area. Their structure is commonly punctate whenever the valves are punctate.

"The true deltidial plates are formed on the side of the pedicle adjacent to the hinge by extensions of the ventral mantle lobe, and begin as two plates. They are likewise expressive of maturity, and are of secondary development, while the deltidium begins as a single plate in the median line, and is eminently a primitive character in the Protremata."

(Beecher, *op. cit.*, pp. 146 7.)

Beecher's account of the formation of a pseudodeltidium was based on Kovalevskii's observations of the development of the one living genus, *Thecidium (Lacazella)*, that is referred to the Protremata (Kovalevskii, 1874, pp. 1 40). This account has been frequently quoted by subsequent authors. It is difficult to understand from Beecher's description how a pseudodeltidium in such forms as the Pentamerids could be secreted on the dorsal side of the pedicle and 'become attached' to the ventral valve, so as to occupy the apex of the delthyrium and to be continuous with the inner layer lining the delthyrial cavity.[1] Recent authors (Thomson, 1927, p. 68; Schuchert

[1] The difficulties of Beecher's view have been fully discussed by Thomson, 1927, p. 78.

and Cooper, 1932, p. 7) define the 'deltidium' (= pseudodeltidium) as a plate growing from the apex of the delthyrium on the ventral side of the pedicle, and the latter suggest that it is formed by a flap of the ventral mantle. With regard to deltidial plates, there has been no such difference of opinion. Schuchert, 1913, Thomson, 1927, and Schuchert and Cooper, 1932, are all in accord with Beecher's view based on the study of living forms that these are secreted by extensions of the ventral mantle round the pedicle.

In *Pentamerus* and *Pentameroides* then, the pseudodeltidium was probably formed by a small fold of the mantle which grew anteriorly from the apex of the delthyrium. The structure in these genera, as in *Conchidium*, being a triangular plate attached to the sides of the delthyrium, covering the apex of the delthyrial opening, indeed, agrees closely with the original definition of a pseudodeltidium, but it occupies a different position from the (usually) rather convex covering over the anterior portion of the delthyrium (also commonly termed a pseudodeltidium), and the two may not necessarily have the same origin. However, to judge from published figures of, for example, the Clitambonitidae (Schuchert and Cooper, 1932, pls. 7 and 8) it would seem that the well developed pseudodeltidia occurring in that family could only have been secreted by a fold of the mantle surrounding the pedicle.

The condition in *Clorinda*, *Stricklandia* and *Gypidula* is different. Occasionally in these genera slight thickening may be present along the margins of the delthyrium (text-figs. 15 and 22). These are always small, never appreciably constricting the delthyrium, and do not merit the name 'deltidial plates'. In other Protremata, however, such as the Orthidae, larger, marginal plates are present constricting the delthyrium, structures which have been termed 'lateral plates' by Schuchert and Cooper (1932, p. 9). These authors cite *Glossorthis*, *Hesperorthis* and *Ptychopleurella* as genera in which they are well developed (1932, p. 23), and as far as may be seen from figures (*op. cit.*, pls. 4 and 6) these lateral plates are of the same form and occur in the same position as the deltidial plates of the Telotremata. They likewise appear to be formed by secretion by the mantle, and if they are truly homologous, Protremata evidently show occasionally a development of deltidial plates as well as a pseudodeltidium. While the presence of these structures may provide a useful guide in many cases, it would seem that distinctions between the two Orders based

on the development of pseudodeltidia or deltidial plates alone, are not of very fundamental value. Both structures are modifications of the delthyrium, both apparently secreted by the mantle. In the one case the constriction takes the form of a covering growing anteriorly from the apex of the delthyrium (*i. e.* a pseudodeltidium), in the other that of two plates which may remain separated (*i. e.* deltidial plates), approach each other, or coalesce along the median line (forming *e. g.* a deltidium [von Buch] = deltarium [Hall and Clarke], symphytium [Buckman], pseudodeltidium [Schuchert]).[1]

The Septum and Spondylium.

The characteristic structure in the ventral valve of the Pentamerids is the spondylium duplex. This is composed of a pair of plates, which are in contact ventrally, where they form a duplex septum attached to the valve-wall, while dorsally they separate to build the spoon-shaped structure known as the spondylium. Within the limits of the family, the length of the septum and the length and shape of the spondylium vary considerably in different genera. Both structures may be quite short, extending only for about one fifth or one sixth of the length of the valve as in *Clorinda*, *Barrandella* and *Stricklandia*: the spondylium may extend for about one third of the length of the valve (*Pentamerus borealis*), or be long, reaching from one-half to two thirds of the length, in late examples of *P. laevis*, in *P. gotlandicus* and *Conchidium münsteri*. The septum is usually shorter than the spondylium, supporting this structure for only part of its length (*Clorinda*, *Stricklandia*); in one genus it is entirely absent (*Holorhynchus*), while it may, on the contrary, approach (*P.* cf. *gotlandicus*) or exceed (*Conchidium*) the length of the spondylium. In cross-section, the spondylial cavity may be roughly equilateral in

[1] It is suggested that the first name 'deltidium' von Buch should be used preferably to the others, owing to the confusion that has arisen from the different meanings attached to these terms. Thus, Beecher was somewhat inconsistent in his use of 'pseudodeltidium' and 'deltidium' (1881, p. 355; 1892, p. 142). Walcott (1912, p. 293) used the first term to denote a plate in the Inarticulata; Schuchert (1913, p. 359), as a synonym of deltarium to describe the condition of united deltidial plates.

It seems hardly necessary to distinguish by different names the case in which the line of junction of the deltidial plates is still visible from that in which it is obliterated (cf. Thomson, 1927, p. 68).

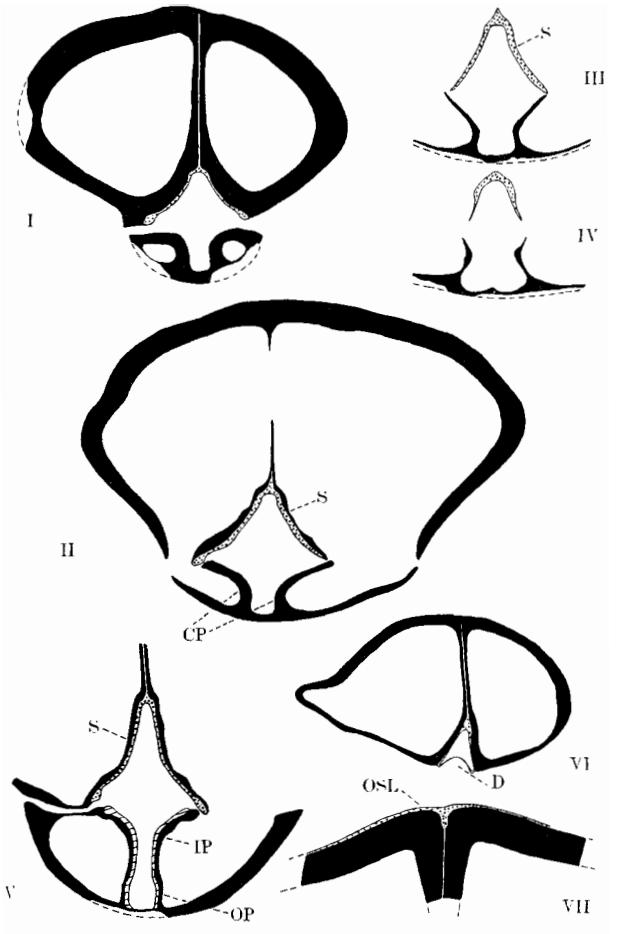
which case it presents a wide opening to the dorsal side, or narrow and with almost parallel walls, when the opening is much more restricted. Anteriorly, it terminates rather bluntly in a rounded end.

The septum is composed of calcareous material of prismatic structure; at the junction of the septum with the valve-wall, the growth-lines may sometimes be followed round into the material composing the wall. In all the species that have been sectioned, the septum may be traced as a separate structure, with its usual duplex character, as soon as the outermost layer of shell-substance has been removed at the posterior end (cf. *e. g.* text-fig. 10, transfers 12 20). The duplex character is marked by the presence of a plane of separation along the centre of the septum. This is particularly clear in *Pentamerus*, *Conchidium* and *Stricklandia lirata*; in the latter species it may be masked anteriorly, as also in *S. lens*; in this species and in *Clorinda*, the character though present, is not so well developed. The tendency for Pentamerids to split along the median plane is to some extent a measure of the degree of perfection of this duplex character. The plates composing the spondylium thicken slightly along the line at which they separate, so that the thickness of the spondylial walls is about the same as that of the septum. The walls may be further thickened at their free edges, particularly just below the corners of the delthyrium. The main part of the septum and of the spondylial walls is composed of material that appears to correspond to the inner shell-layer, but in the three species of *Pentamerus*, that have been investigated, in *Conchidium* and in some species, at least, of *Clorinda*, there is another layer of shell-material occurring as a thin sheath, lining the spondylial cavity (text-figs. 1, 2 and 7, where this layer is stippled).

The presence of this additional layer is of considerable interest. In *Pentamerus borealis* (text-fig. 2, I IV), *P. laevis* [= *P. oblongus*] (text-fig.7, I), and *P.* cf. *gotlandicus* (text-fig. 1), it occurs in the posterior region of the spondylium as a thin surface-covering, usually it is thickest at the bottom of the spondylial cavity, where it may extend a short distance ventrally along the median plane of the septum. Anteriorly, it may compose the greater part, or the whole (at least in *P. borealis* and *P.* cf. *gotlandicus*), of the lower end of the spondylium. The condition is similar in *Conchidium münsteri*, except that the layer is rather thicker in the posterior region (text-fig. 7, II). In *Stricklandia lirata* (forma *typica*) the presence of this separate layer

has already been recorded (St. Joseph, 1935 b, p. 406 and text-figs. 2 and 3), and has been termed "secondary thickening". In this species, too, the layer may be prolonged for some distance as a thin selvage along the median plane of the septum. Similarly, material of the outer shell-layer may sometimes be seen extending for a short distance inwards along the plane of the median septum (text-fig. 2, VII). The presence of this thin selvage of material was apparently first recorded by Kozlowski (1929, fig. 37, V and VI and pp. 124 5) in *Clorinda pseudolinguifera* and *Sieberella* cf. *galeata* when he gave it the name "lame intraseptale".

In the Pentamerids, the spondylial walls meet the hinge-line at the antero-dorsal corners of the delthyrium, points which function in articulation, and a comparison with the structures in the ventral valve of related Protremata, *e. g. Porambonites* or of Telotremata, in which there are well developed dental-plates supporting the teeth, suggests that the two structures are homologous. Thus Kozlowski (*op. cit.*, p. 125) cites the example of *Porambonites*, in different species of which there is much variation in the width of the space between the dental-plates, and compares this with the typical, duplex spondylium of the Pentamerids. On this view, each dental-plate corresponds to one of the spondylial walls, together with one side of the duplex septum. This homology must be considered when attempting to determine the method of secretion of the spondylium by the mantle. The latter normally covers the whole of the interior surface of shell, and the part of the mantle that lines the spondylium of the Pentamerids, must thus correspond to the part which *e. g.* in *Porambonites* covers the inner surface of the valve-wall between the dental-plates, as well as those plates themselves. Similarly, the mantle lining the outer surface of the spondylium and septum in Pentamerids, should correspond to the part that in other families occupies the cavities between the dental-plates and the valve-wall. The dental-plates must have been formed within infolds of the mantle, usually they are not of very great size so that a slight increase of surface area of mantle would be sufficient to cover them. In the Pentamerids, the median septum is frequently of very large size compared with dental-plates, often entirely dividing the posterior region of the ventral valve, and presumably almost the whole of the body-cavity (as in late species of *Pentamerus* and in *Conchidium*). A septum of this character could only be formed within a very large mantle-infold,



Text-fig. 2. Septum and Spondylium. (All figures $\times 2^{1}/_{3}$.)

I—IV. — Transverse sections of *Pentamerus borealis*, zone 7 a, Ringerike. P. M. O., 58 550. V. — Transverse section of *P. laevis*, zone 7 a—b, Asker. P. M. O., 53 529. VI. Transverse section of *P. borealis* showing pseudodeltidium, zone 7 a, Asker. P. M. O., 53 482. VII. — Transverse section of *Stricklandia lirata* forma *typica*, showing outer shell-layer, from uppermost Llandovery, at Woolhope, England. S. M. C., A. 13 550.

CP = crural-plates; D = pseudodeltidium; IP = inner-plates; OP = outer-plates; OSL = outer shell-layer; S = spondylium.

and the structure of the septum may be considered to see whether it gives any indication of its mode of formation.

The internal structures in contact with the mantle would normally undergo some resorption and resecretion to be accommondated to the changing curvature, with growth of the valve-walls. In genera such as *Pentamerus* and *Conchidium* which possess a large, ventral septum (cf. text-figs. 8 and 10; Pl. V, figs. 10 11) this structure could never be covered by any small mantle-infold, but must have been secreted within an invagination of the mantle that could increase in size as along a free, growing edge. The first formed part of the septum must have been (in those forms in which it is present), the thin selvage of shell-substance occurring along the median plane (Kozlowski's "lame intraseptale"), and this appears to be continuous with the thin layer lining the spondylium (cf. text-fig. 1 and Kozlowski, 1929, fig. 7, VI). If the septum were formed within a mantle-infold with a free-growing edge, this layer should correspond to the first layer secreted by the mantle along the main shell-wall, *i. e.* the outer shell-layer, and it may be recalled that in *Stricklandia lirata* the outer layer sometimes extends for a short distance inwards along the median plane of the septum (text-fig. 2, VII). The shell-substance secreted subsequently and forming the main part of the median septum and of the spondylial walls (at least in the posterior region), will then correspond to the inner shell-layers of the valve-wall. Each of the two plates forming the septum is in contact with the mantle on its outer side only, and the plane of parting which causes the duplex character of the septum, separates the material secreted by the mantle on one side, from that on the other.

The origin and function of the spondylium may now be considered. Its duplex character distinguishes it structurally from the spondylium simplex of, for example, *Clitambonites* and *Skenidium*. In a recent discussion of spondylia, Kozlowski (1929, pp. 122 5, 126 7) derives the spondylium simplex from a pseudospondylium structure which is well exhibited in *e. g. Glossorthis*, by an enlargement of the genitalia owing to excessive testaceous deposit round the muscle impressions, with resulting resorption at the base of the pseudospondylium. The duplex spondylium of the Pentamerids, on the other hand, he considers to have been formed from a spondylium discretum (in *e. g. Huenella* and *Porambonites*), the dental-lamellae having been pushed together owing to an enlargement of the sexual glands:

"La cause de la transformation du *spondylium discretum* en *spondylium duplex* me semble résider dans l'hypertrophie des glandes sexuelles. Ces dernières, comme l'indiquent leurs impressions, souvent profondément imprimées, occupaient des espaces très grands de chaque côté. Leur développement de plus en plus grand et la pression qu'elles exerçaient sur les plaques dentales forçaient ces dernières à un déplacement progressif vers la ligne médiane, jusqu' à leur complète coalescence. A mesure que l'espace compris entre ces plaques se rétrécissait, les bases d'attache des muscles occupant cet espace étaient forcées de se déplacer sur les surfaces, internes des plaques dentales, et de s'y placer entièrement dès que ces plaques sont entrées en contact."[1]

This view as to the origin of a spondylium duplex is not without some difficulties. In living brachiopods there are four genital glands in each animal, two on the ventral and two on the dorsal side; they may be confined within the visceral cavity or may project for some distance into the pallial sinuses of the mantle. In certain genera the glands may be fixed to the shell by ligamentous ties which produce the familiar pitted appearance in the posterior region of the valves.[2] In Palaeozoic brachiopods, the inner surface in the posterior region of the valves just below the umbo is often pitted; this causes a rather roughened surface on internal casts especially in the ventral valve. Such pitted areas are prominent in the Clitambonitidae, while among the Pentamerids they are often readily seen on internal casts of *Stricklandia lens* and *S. lirata* and especially of *Holorhynchus*, and are probably due to the same cause. In the Pentamerids then, it may reasonably be assumed that the genitalia occupied the same position as in living brachiopods.

The Sub-order Pentameroidea is the first large group of brachiopods that possesses as a general character a strongly biconvex shell, enclosing a considerable space between the valves. The convexity affects proportionally the posterior region of the shell, so that when compared generally with the Orthoidea, the Pentameroidea have a much larger space available for the body and its associated structures. It is thus rather difficult to see how, if this group evolved from the Orthoidea, it was an enlargement of the genitalia that caused them to press on the dental-plates and unite them into a duplex septum. It might on the contrary be enquired whether it was not enlargement of the genitalia that was the cause of the change in shape from

[1] Kozlowski, 1929, p. 126.

[2] Cf. Thomson, 1927, p. 13.

the typical, gently biconvex, Orthid shell, perhaps through a markedly biconvex Orthoid such as *Porambonites* to the typical biconvex Pentamerid. Any argument based on the hypertrophy of the genitalia must take into account the disposition of the other soft parts in the body cavity, of some of which in the Palaeozoic Protremata the exact disposition must be very uncertain. One might have expected, too, evidence of proportionate enlargement of the genitalia in the dorsal valve owing to the more limited space in that valve, yet the Pentamerids show no general tendency for the cardinalia to take the form of a cruralium. Nor is the disposition of the secondary thickening around the muscle impressions and in the posterior region of the shell altogether in agreement with this theory. The secondary thickening in *e. g. Pentamerus borealis* and *Stricklandia lirata* occurs in the posterior region of valves, filling up the cavities on either side of the ventral median septum in just the position in which it is assumed there was occurring the enlargement of the genitalia. These facts raise the question as to whether there is not some other more likely explanation of the duplex spondylium.

The general function of a spondylium is not in question. Study of the relative positions of the two valves of a Pentamerid, when these are in apposition, shows that the divaricator muscles, which are attached to the dorsal valve below the umbo and posterior to the hinge-line, must have been bedded within the spondylial cavity (cf. text.-figs. 3, 5, 6, 8, and Plate V, figs. 1, 10). Similarly, the adductor muscles must have passed between the cardinalia also to the spondylial cavity.[1] The spondylium was, indeed, described by the proposers of the term as "an area of muscular implantation", and Hall and Clarke also stated that the impressions of the central adductor and lateral divaricator muscles were often clearly defined within the spondylium.[2] Muscle impressions in this position have seldom been observed in European material, but that the spondylium is an elevated area of muscle attachment the opinion of all recent writers on the subject there is no doubt.

A feature not frequently discussed in connection with the Pentamerids but characteristic of all the genera the writer has investigated *Clorinda*, *Barrandella*, *Gypidula*, *Sieberella*, *Pentamerus*, *Pen-*

[1] The musculature is discussed at greater length in a later section.

[2] Hall and Clarke, 1894, pp. 331–2, 335.

tameroides, *Holorhynchus*, *Conchidium* and *Stricklandia* — is the very degenerate nature of the dentition. This is described in a later section, but, in outline, articulation may be said to take place between the posterior edges of the spondylium where they commence at the antero-dorsal corners of the delthyrium, and the margins of the inner-plates in the dorsal valve, where these separate from the hinge-line. The articulation appears to be of a much more clumsy type than in the Orthoidea, and would have been of no use in maintaining the valves together, a function that must have devolved almost wholly on the muscles. The latter thus have to bear an extra strain apart from that consequent upon their function of opening and closing the valves. Further, in the Pentamerids, with their strongly biconvex profile, the muscles, and especially the divaricators would have to be of much greater length than those in the Orthids, but for some supporting structure. The development of an elevated muscle platform, formed by the union of the dental-plates might appear to be associated with the lack of normal articulation, and the resulting extra function of the muscles. The first stage in the process may be illustrated by reference to such a species of *Porambonites* as *P. ventricosus* in which the muscles are raised far above the floor of the ventral valve, by a solid deposit of shell-material between the dental-plates, to form the structure termed by Schuchert and Cooper (1932, p. 29) a spondyloid. *Porambonites* possesses the strongly biconvex profile typical of many Pentamerids, in contrast, however, to their inefficient dentition, it has well developed teeth and sockets. The necessity of keeping the valves together has thus not arisen in connection with the muscles; and when these are elevated above the valve-floor, it is on an adventitious deposit of shell-material rather than on any special structure.

The details of the different stages by which the typical, duplex spondylium of the Pentamerids has evolved cannot yet be studied for lack of suitable material. The variation in distance between the dental-plates in different species of *Porambonites*, to which Kozlowski has drawn attention (1929, p. 127), seems most apposite in the present connection. In some species of this genus the space between the dental-plates is sufficiently large for the muscles to rest on the floor of the valve, and there is every stage from this condition to that in which the intervening space has become so narrow that the muscles

rest almost entirely on the dental-plates themselves.[1] This stage is but a very little removed from the structure in a Pentamerid possessing a low and relatively short, ventral, median septum. Whether this may indicate the general lines on which the Pentamerid, duplex spondylium has developed must remain uncertain, but the writer would regard it as a more likely mode of origin than that suggested by Schuchert and Cooper (1932, p. 161), from the Syntrophiidae. If *Syntrophia* really possesses a spondylium simplex it is difficult to see how it can, by any means, have given rise to the Pentameracea.

Once the structure known as a spondylium duplex had arisen, it underwent many modifications. Two of these are represented in the specimens in the Kiær Collection. The gradual increase in length of the spondylium and septum in the *Pentamerus* series, reaches its greatest development in the latest *Pentamerus* species and in the related genus *Conchidium* (see text-figs. 5 8, 10 and Pl. V, figs. 7 11). This is a change which tends to raise the area of muscle attachment further above the valve-floor (especially in globose forms), the greater length of the septum at the same time affording an increased support. The second modification is a tendency to reduction or even complete loss of the supporting septum. This is seen in *Clorinda* and *Barrandella* (text-figs. 11, 13, 14, 19), and it is interesting that these are also the two forms with the least degenerate dentition of all the genera that have been investigated. The genus *Holorhynchus* (text-fig. 9), with a free spondylium, occupies an isolated position and its affinities are best discussed when considering the internal structures in the dorsal valve.

The Cardinalia.[2]

Of the assemblage of structures which characterize the Pentameracea, the cardinalia are perhaps the most important. In such typical genera as *Pentamerus* and *Conchidium* these consist of a pair of long, crural-plates arising almost at right-angles to the valve-floor

[1] Kozlowski, *op. cit.*, p. 127. For a description of the internal structures of *Porambonites* see Noetling, 1883, pp. 360 ff.

[2] This term, apparently introduced by Thomson (1927, p. 83), was used by Schuchert and Cooper (1932) in descriptions of Orthoidea and Pentameroidea. It may conveniently be applied in the Pentamerids to the assemblage of structures in the dorsal valve, which are often loosely called 'crural-plates' – a usage which does not conflict with the original definition.

and beyond which there may project the brachial-processes. The crural-plates frequently have a rather distinct, three-fold division into inner-plates, bases of the brachial-processes and outer-plates[1] (cf. text-figs. 8 and 15); the latter either join the floor of the valve or unite with each other, in which case the cardinalia form a cruralium (text-fig. 8). The inner-plates and outer-plates together form the greater part of the cardinalia, for the brachial-processes though long, are relatively narrow.

The inner-plates usually diverge from one another, being convex inwards to the centre of the valve; anteriorly the divergence may decrease so that the plates become almost parallel. Their free (inner) edges are often directed towards the margins of the spondylium and in different cases they lie a little inside (text-fig. 6) or outside (text-fig. 3) the latter. Just below the umbo they may have formed part of the area of attachment of the divaricator muscles, but anteriorly they become very thin. At the point at which they separate from the valve-wall their free edges may abut against the thickened margins of the spondylium, the arrangement serving for articulation. Their dorsal edges are fused with the bases of the brachial-processes. These are usually sub-parallel, and not always clearly separated from the outer-plates; they are less high[2] than the inner- or outer-plates, but extend beyond the latter often to about the end of the spondylium as free brachial-processes. The outer-plates lie in the same plane as the bases of the brachial-processes with which they are fused, and they extend to the valve-floor. They are generally rather thin, and parallel, but may be divergent (*Clorinda*: text-figs. 15, 18) or convergent (*Pentameroides*: text-fig. 8) and in the latter case they frequently form a cruralium. The development of a cruralium appears to be due to the gradual approximation and final union of the outer-plates, but in the one form (*Pentameroides* cf. *gotlandicus*) in which it has been studied in detail, it is interesting that even in their earliest stages of growth, embedded in the thickening of the shell-wall at the

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[1] These correspond respectively to the structures lettered Ip, BBP and Ops (or Op and Ms) in Figs. 26—28 of Schuchert and Cooper, 1932, p. 164: but in their discussion of the terms proposed by Leidhold (1928, pp. 51—3) these authors describe the cardinalia as composed of (1) inner-plates, united with (2) outer-plates which are separated by (3) a crural band or longitudinal thickening from (4) the septal or supporting-plates, united with the valve-floor.

[2] This refers to their dimension in a dorsal-ventral direction.

posterior end of the valve, the outer-plates are always united and retain no trace of the stage when they were separate (cf. text-fig. 1, transfers 26 30).

The genera *Clorinda*, *Holorhynchus* and *Stricklandia* depart from this standard type. In the first of these, the cardinalia are small and divergent, with very short inner- and outer-plates. Some species (*e. g. C. kjerulfi*) show no clearly defined junctions between the plates, and the outer-plates and the bases of the brachial-processes appear often to be fused together (text-fig. 13). *C. undata* possesses widely divergent outer-plates, brachial-processes that are concave to each other, and inner-plates that are often rather longer than the outer-plates. The edges of the bases of the brachial-processes often project slightly from the plane of the inner- and outer-plates to form small carinae (text-fig. 15). A closely similar arrangement has been described in species of '*Barrandina*' (*Clorinda*) from Australia (Booker, 1927, pp. 134 ff.).

In *Holorhynchus*, the structure is much less typically Pentamerid (text-fig. 9). Slender, rod-like, inwardly-inclined, brachial-processes occur, situated near to the valve-wall. These are attached posteriorly to a pair of diverging plates that approach the edges of the spondylium. These plates evidently correspond in position to inner-plates, but there are no traces of structures representing the outer-plates, since the bases of the brachial-processes arise very close to the valve-wall (text-fig. 9, transfers 100 to 124). The arrangement in *Stricklandia* is similar. In this genus (text-figs. 20 21, 23) the structures in the dorsal valve consist of slender, inwardly-inclined brachial-processes (crural-processes) which are fused to a second pair of plates (outer pair of plates, of St. Joseph, 1935 b, p. 413) directed towards the edges of the spondylium. A comparison of text-figure 21, transfers 23 to 33 with text-figure 9, transfers 104 to 116 illustrates the resemblance. In both these genera it would seem that the plates lying nearest to the spondylium correspond to the inner-plates of typical Pentamerids, while the outer-plates are either absent or represented in part by the bases of the brachial-processes. The internal structures of *Clorinda* represent a possible intermediate stage, for in some species of that genus there is a tendency for the outer-plates to be reduced, and not clearly separated from the bases of the brachial-processes, while the inner-plates may be somewhat lengthened (cf. text-fig. 14, transfers 20 to 24 and text-fig. 13, transfers 28 to 34

with text-fig. 21, transfers 23 to 29 and text-fig. 20, transfers 22 to 28).

The cardinalia in *Stricklandia* are thus not so anomalous as has hitherto been thought. They are very similar to the arrangement in *Holorhynchus* and though far removed from the typical Pentamerid development, the structure in some species of *Clorinda* may provide a possible, morphological intermediate. *Stricklandia* can hardly have given rise, however, directly to *Pentamerus* as Kiær considered (1908, p. 500) for the differences in internal structure are relatively great.

A thin layer of lamellar shell-material covers the inside of the cardinalia in some specimens of *Pentamerus laevis* and *P.* cf. *gotlandicus*, and appears to be of the same nature as the layer lining the spondylial cavity in those species. It is indicated by shading in text-figs. 1, (40) and 2, V. It may be present in other species of *Pentamerus*, and something evidently very similar was recorded by Hall and Clarke (1894, p. 238, fig. 171 in a specimen of *P.* '*oblongus*' [*laevis*]).

Musculature.

Muscle impressions are seldom well preserved in the Pentameracea. They are best studied in internal casts, and consequently this collection of material in which the shell-substance is largely present has yielded little, direct information. Evidence as to the position of the muscles, however, is also afforded by the relations between the various internal structures in the shell; relations which may easily be seen in the scale-models that have been constructed of the various species. Information derived from internal casts of species of *Stricklandia* and of *Clorinda undata* in which the muscle-scars are occasionally clear, shows that there is a median grouping of adductor-scars rather towards the posterior of the dorsal valve, while on the floor of the ventral valve, muscle-scars have never been observed. The muscles are usually considered to have been attached in this valve to the inside of the spondylium, in which position scars were recorded by Hall and Clarke (1894, pp. 331 5).

In the dorsal valve the position of attachment of the divaricator muscles must have occurred posterior to the hinge-line. A cardinal-process is always rudimentary or absent in this family and the area of attachment appears to have lain partly within the posterior end of the cavity defined by the cardinalia, and partly perhaps on the

inner-plates themselves, in species such as *P. borealis* and *P. gotlandicus* in which these structures diverge strongly from one another. From such a position the divaricator muscles can only have extended to the inside of the spondylial cavity, as is demonstrated by a study of serial drawings (text-figs. 3, 5, 6, and 8) showing the relative position of tho cardinalia and spondylium in life. Similarly, if the evidence of *Stricklandia* and the occasional presence of faint impressions on the floor of the valve, between the cardinalia in species of *Pentamerus* may be taken to demonstrate a normal grouping of adductor scars in this position, the arrangement of the internal structures shows that the course of the adductor muscles can only have run to the inside of the spondylium. The small, median ridge that occurs on the floor of the dorsal valve between the outer-plates possibly separated muscle impressions, just as did the rather similar ridge down the back of the spondylial cavity in *Stricklandia*. In *Pentameroides*, in which the cardinalia unite to form a cruralium, the area of muscle attachment was evidently elevated above the floor of the dorsal valve just as in the ventral.

Mantle Impressions:

Pallial and Genital Markings.

Traces of the soft parts other than muscle-scars can only seldom be studied in the Pentameridae and of these, the clearest impressions are usually the genital or ovarian markings. That the mantle, which lines the whole of the interior of the shell,[1] might retain its function of shell-secretion throughout the greater part of the life of the animal is illustrated by several species in this collection. Continual adsorption and re-secretion of shell-material must have occurred during the early stages of growth in order to accommodate the septum and spondylium to the changing curvature of the valves. In *Pentamerus borealis* and *Stricklandia lirata* which possess a greatly thickened shell in the posterior region, internal structures such as the septum in the ventral valve, or the cardinalia in the dorsal valve, can be traced embedded in the shell-wall almost to the exterior surface. At the time of their formation these structures must have been in

[1] The term 'mantle' is here used to include the dorsal and ventral surfaces of the body-wall.

contact with the mantle (cf. St. Joseph, 1935 b, p. 413), and the shell-material in which they are embedded must consequently be a later secretion.

One specimen of *P. gotlandicus* that was chosen for serial-sectioning is especially interesting in this connection. The median septum in this species is usually rather thin, especially towards the anterior, and in this individual both the septum and the left spondylial wall had fractured and been subsequently mended by additional secretion of shell-material, evidently by the mantle. The lines of fracture are now marked by thickenings due to this extra shell-substance (cf. text-fig. 8, showing an expansion on the left side of the septum).

Two individuals of *Stricklandia lens* show a peculiarity in the ventral valve. In these (cf. text-fig. 20, transfers 12 to 20 and text-fig. 22), there occurs for a short distance a second septum on the right side of the normal, median septum and there is also a trace of another septum on the other side (text-fig. 20, transfers 12 14). Evidently in these specimens there was a tendency to form more than one mantle-infold, and such conditions perhaps give some indication of the mode of formation of the structure in some Clitambonacea described by Öpik as a spondylium triplex.

Pallial Markings: Markings of the pallial sinuses have rarely been observed in this group of Brachiopods and of the specimens under immediate consideration have been described only in *Clorinda undata*. In large forms of that species, they frequently appear as irregular, longitudinal ridges. One specimen (S. M. C. A. 13551 from the Llandovery of Mathyrafal) exhibits a much more definite arrangement of main and auxilliary trunks, and although not included in the Kiær Collection, may for its general interest be described here. It is an internal cast of a ventral valve, showing (text-fig. 16) two antero-laterally directed trunks near the end of the median septum. Of the two branches formed at each first bifurcation, one is directed anteriorly where it dichotomizes further, the other towards the lateral margin. The arrangement is evidently closely similar to that in a specimen from the same locality figured by Davidson (1867, pl. xix, fig. 8 B).

Genital Markings: The impressions of the ligament-attachments, which bind the genital glands to the valve-wall usually produce a rather pitted appearance on the inner surface of the valves. Such

an effect is not uncommon in the Pentameracea; it is best studied in internal casts and may frequently be seen in species of *Stricklandia* over quite a large area at the posterior end of the shell, especially in the ventral valve. In *Holorhynchus* these impressions are very strongly developed, the whole of the inner surface of the ventral valve and also the sides of the spondylium being covered with small rugosities.

Stratigraphical Considerations.

The Pentamerids range in southern Norway between zones 5 b and 8 c, but it is from horizons 6 c, the maximum of *Stricklandia lens* to 7 b, the maximum of *Pentamerus laevis*, that they attain their greatest abundance. Their distribution is indicated in the following table:

Stratigraphical Distribution of Species.

Zone	8 a	c	*Clorinda malmøyensis*, new species.
»	7 c		*Pentamerus (Pentameroides)* cf. *gotlandicus* Leb. } especially in *Stricklandia lirata* (J. de C. Sow.) } 7 cβ. *Clorinda undata* (J. de C. Sow.), small, late variety.
»	7 b		*Pentamerus laevis* (J. Sow.), very common.
»	7 a	b	Early forms of *Pentamerus laevis* (J. Sow.), with *borealis-laevis* transients.
»	7 a		*Pentamerus borealis* (Eichw.), abundant.
»	6 c		*Stricklandia lens* (J. de C. Sow.), maximum development in 6 cα. Occasional, early examples of *Pentamerus borealis* (Eichw.). *Clorinda undata* (J. de C. Sow.), rarely.
»	6 b		Early forms of *Stricklandia lens* (J. de C. Sow.).
»	6 a		*Clorinda undata* (J. de C. Sow.) } maximum development in *Clorinda undata* (J. de C. Sow.) } 6 a b.
»	5 b		*Holorhynchus giganteus* Kiær. *Conchidium münsteri*, new species (Kiær MS). *Clorinda kjerulfi* (Kiær).

The three species from zone 5 b are as yet known from no other region. *Clorinda undata* which ranges through the whole of stage 6, and though less commonly through part of 7, is most abundant in the eastern development as at Malmøy and Asker. It attains its maximum about the top of 6 a, just before the first appearance of *Stricklandia lens*. The latter species is characteristic of zone 6 c being particularly common in the lower part of the zone, again in the eastern development. The earliest specimens of *Pentamerus* occur in 6 cβ at Asker, but the first general appearance of *Pentamerus borealis* is in 7 a in the western development at Ringerike, Hadeland

and Holmestrand (cf. Table I). The typical, thick-shelled *P. borealis*, indeed, does not occur at Asker and Malmøy. *Pentamerus laevis* in 7 b has the widest distribution of any of these species being known from all the different districts, even at Mjøsen in the north. Above this horizon the distribution of the Pentamerids becomes more restricted; *Pentamerus gotlandicus* and *Stricklandia lirata* which characterize 7 c β are most abundant in the western districts and unknown at Malmøy, while in the succeeding stage 8, *Clorinda malmøyensis* from 8 a and 8 c is almost the only species recorded.

It will be seen that the Pentamerids are typical of the eastern development in stage 6, being almost absent in the western districts and that they occur abundantly in the west (Ringerike and Skien and Porsgrund) for the first time at the base of stage 7, the "*Pentamerus*-kalk" of 7 b being a rather constant horizon. Above this their distribution becomes more restricted, but this time to the western development. This distribution is directly related to the conditions prevailing in the several areas when the rocks were formed. In stage 5 a considerable shallowing of the sea took place in the Oslo region; a fact that is indicated by the occurrence at horizon 5 b of such shallow-water deposits as sandy and oolitic limestones, pebble-beds with a matrix of oolitic limestone and even a breccia facies (Kiær, 1901, pp. 96 8). At the top of 5 b a depression of the sea-floor commenced and continued through stage 6. The effect is least marked in the Ringerike and Hadeland districts in the west, where calcareous sandstone and shale and arenaceous limestone are the commonest rock-types (Table I); ripple-marked surfaces occur, and the rocks seem to have been formed at no great distance from a shore line. In the east, much deeper-water conditions prevailed, mudstones with some calcareous beds and shales being accumulated, and it is these rocks that yield *C. undata* and *S. lens* most abundantly. The limestones and mudstones of stage 7 with *Pentamerus*, in the eastern district, would seem to be of slightly shallower-water formation, but deeper-water conditions commence again in 7 c and continue in the graptolite shales of 8 a and b. In the west, especially at Ringerike and Skien and Porsgrund relatively shallow-water conditions persisted, and the rocks are mostly calcareous. The shell banks of 7 a composed of *Pentamerus borealis* valves would appear to have been formed under the action of relatively strong currents, and this together with the presence of ripple-marked surfaces may

Table I.

Zone	Southern	
	Western development I Ringerike	Eastern II. Malmøy[1]
9 a—g	Limestones and some shale with Ostracods, *c.* 250 m	(At Holmestrand, limestones with Ostracods, 106—116 m)
8 d	Dark limestone, 2—12 m	"Malmøykalk", 10- 15 m
8 c	"Wenlockkalk", coral-reef limestone & shale, 4—25 m	*Rhynchotreta cuneata* limestone, 6—8 m
8 b	Arenaceous limestone, 45 m	Beds with *Monograptus*, *c.* 80 m
8 a	Greenish shale and arenaceous limestone, 70 m	
7 cγ	Upper red *Crotalocrinus* shale, *c.* 35 m	Limestone and shale with *Crotalocrinus*, *c.* 50 m
7 cβ	*Stricklandia lirata* beds, or upper coral limestone, 25 m	
7 cα	Lower red *Crotalocrinus* shale, 20 m	
7 bβ	Lower Coral limestone, 17 m	Beds with *Pentamerus laevis*, 35 m
7 bα	Limestones with *P. laevis* (= *oblongus*), 25 m	
7 a	Limestones & shale (*P. borealis* beds), 10 m	Grey *Pentamerus* limestones, 30 m
6 c	Arenaceous limestone and shale, 45 m	Shale & limestone with *S. lens*, 30—40 m
6 b	Calcareous sandstone, 50 m	Shales, *c.* 50 m
6 a	Calcareous sandstone and shale, 20 m	Shales & mudstones with *C. undata*, 50—60 m
5 b	Calcareous sandstones, *c.* 45 m	Calcareous sandstones with conglomeratic 'pebble bed' facies

[1] The succession at Holmestrand (III) is generally similar to that at Malmøy in stage 6, and to that at Asker and Bærum in stages 7—8.

Norway		British shelly facies
development V. Asker and Bærum[2]	Northern development VII. Mjøsen	
Limestones and calcareous shales, *c.* 200 m	Red and yellow sandstones	Ludlovian
"Malmøykalk", 8—10 m *Chonetes* beds, 30 m Shales with *Monograptus*, *c.* 90 m	Thick succession of red and yellow sandstones Calcareous sandstones with shale bands	Wenlockian
Stricklandia lirata beds, or upper coral limestone, *c.* 50 m Red *Crotalocrinus* shales, 12 m Lower Coral limestone, 30 m *Pentamerus* limestone, *c.* 60 m	Shales with graptolites, 80 – 100 m Lower Coral limestone, 9—10 m *Pentamerus* limestone, 9 15 m	Upper Llandoverian
Calcareous shale & limestones, 60—70 m Calcareous sandstones and shales, *c.* 42 m Mudstones & calcareous beds, *c.* 65 m	Sandstones, calcareous sandstones & shales, *c.* 9—30 m	? Middle Llandoverian
Calcareous & sandy beds with oolitic limestone & breccia facies	Calcareous mudstones & shales; arenaceous towards the top	? Lower Llandoverian

[2] In stages 7—9, the succession at Asker and Bærum is partly eastern, partly western in character.

be taken to indicate quite shallow-water conditions. The limestones of 7 cβ with large, isolated valves of *Stricklandia lirata* and *Pentamerus gotlandicus* belong to the same facies. Finally, the tendency to deeper-water conditions in the lower half of stage 8, which is so marked at Malmøy, is found also at Ringerike, but not to the same degree. The fauna of these rocks is thus closely related to the varying lithology, which appears to be a direct expression of the changing conditions under which the rocks were accumulated.

The details of the stratigraphy are given in Table I, which is based on Kiær's monograph (Kiær, 1908, pp. 472 3, 494 5, 576 7). The inclusion of zone 5 b in the Silurian, a course later adopted by Kiær and now commonly accepted, is justified by its faunal content, especially the three Pentamerid species. The suggested correlation with the British shelly-facies differs from that proposed by Kiær in that stage 6 is equated with the Middle rather than the Lower Llandovery. This seems to be indicated by the distribution of the shelly fossils. Thus, *Clorinda undata* and *Stricklandia lens* characteristic respectively of zones 6 aβ and 6 cα in southern Norway, attain their maximum in Britain at the top of the Lower Llandovery and in the Middle Llandovery. *Meristina crassa* the zone fossil of 5 b is commonest in Britain at the top of the Lower Llandovery, while the recorded occurrence of *Atrypa reticularis*, *Leptaena rhomboidalis* and *Strophomena euglypha* from 6 a onwards support this view. The beds with *Meristina crassa* in Britain occur nearly 2000 feet above the Ordovician, and it would seem as if there were a break of some importance between 5 a and 5 b, for the former which has yielded *Trinucleus* and Asaphids must certainly be Ordovician.

At higher horizons the maximum of *Pentamerus oblongus* in 7 b and of *Stricklandia lirata* forma *typica* in 7 cβ are useful guides in correlation, and appear to correspond respectively to the *Pentamerus* limestone of Shropshire and the topmost beds of the Llandovery.

Description of Genera and Species.

The History of the Genera *Conchidium* and *Pentamerus*.

These two names are so familiar and so well established in the literature of the Silurian Brachiopoda that it is the more regrettable that neither has ever received proper definition in accordance with

the International Rules of Zoological Nomenclature. The early descriptions of the Pentamerids are greatly confused, but the histories of these two forms have so much in common that they may conveniently be considered together. The treatment is purposely detailed, in the hope that if the nomenclature be stabilised in the light of a full discussion, later writers may conform to the system of names here adopted, and that further confusion may be avoided.

The most recent treatment of these genera (Schuchert and Cooper, 1932, pp. 177, 181) ascribes *Pentamerus* to J. Sowerby (1812, p. 73, pl. 28) with genolectotype (Hall and Clarke, 1894, p. 236) *P. laevis* J. Sow. and *Conchidium* to Linnaeus (1760 [*sic*, *err. pro* 1768], p. 163) with genotype *C. biloculare* Linn. 1753 (pl. 5, fig. 8) ascriptions which both require qualification. The earliest reference to *Conchidium* appears to be in Linnaeus' *Museum Tessinianum* 1753 [p. 90, Tab.V, figs. 8 A and B], where, under the entry *Conchidium biloculare* there is a concise and appropriate description in Latin, a reference for localities to "Oelandia, Gotlandia *frequens*", and two recognizable figures of a ventral valve, the one showing a spondylium supported on a long septum. In considering the origin of both genus and species this reference cannot be taken into account, for the publication antedates 1758, the accepted starting-point for zoological nomenclature under Article 26 of the International Rules.[1]

The next reference to this form is in Linnaeus' *Systema Natura* Ed. XII, Tomus III, 1768, p. 163, when he again gives a short description, as follows:

"41 Helmintholithus

Conchidium 3. Helminthol. Patellae? bilocularis Conchidium. Mus. Tess. 90, t. 5. f. 8. *Habitat in Mari* Balthico; *certe petrificatum in* Oelandia, Gothlandia *frequens; deperditus.*

Testa *antiquata fere Cardii edulis, solitaria, repleta calce solida; facillime findatur longitudinaliter in partes duas aequales; at vero, ubi non farcta calce a parte inferiore s. interiore, sepimento longitudinali divitur in duo loculamenta.*"

[1] The references to this code are to the reprint of the International Rules of Zoological Nomenclature, in *Proc. biol. Soc. Wash.*, Vol. 39, pp. 75—104 (1926), hereafter referred to as the "International Rules", and the Articles are cited as numbered there.

There would seem to be several ways of interpreting the string of names that follows *Helmintholithus,* but following Sherborn (1902, p. 236), the usage is to be regarded as trinomial, "*Conchidium Helmintholithum*" constituting the species.[1] This diagnosis then, the reference commonly cited as the original description of *Conchidium*, must be rejected under Articles 2 and 25 (b) of the International Rules. Such a course means that the next earliest binomial usage after this date must be accepted as the original description. This seems to be in Hisinger's "*Minerographiske anmärkningar öfver Gottland*" (1799) p. 285:

"Anomia bilocularis, testa obovata convexa multisulcata, nate incurvata; valva longiore sepimento longitudinali in duo loculamenta divisa.

Finnes vid Klinteberg til myckenhet både med och utan hopsittande parskal, och är den samma hvars ena skal i Syst. Nat, T. III. 101. 33. β blifvit räknad til *Helminth. Patellaria. Conchidium.*"

That Hisinger was referring to the same form as Linnaeus is evident, the elements of his diagnosis can be recognized in Linnaeus' description. Further, "a multi-ribbed, fossil shell, with the larger valve divided by a long, median septum into two chambers" does not admit of many interpretations. There is also a reference at second-hand (through the *Systema Natura*) to a figure, while a locality is cited; all this must constitute "an indication, or a definition, or a description" within the meaning of Article 25 (a) of the International Rules [cf. also Opinion 1 (A) *Ibid.* p. 91].[2] This description then must be taken as the original diagnosis of the species and must, further, have priority over all subsequent accounts in determining to which genus the species should be attributed. Hisinger referred the species primarily to *Anomia* and stated that it had also been reckoned as *Helminth. [olithum]*, *Patellaria [err. pro Patella]* and *Conchidium.*

At that date a great number of both living and fossil bivalves were included under the names *Anomia* and *Anomites*: *bilocularis*

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[1] This is by no means the only case; Sherborn gives analogous interpretations for similar strings of names occurring elsewhere in the *Systema Natura.*

[2] This case does not come within the scope of Opinion 5 (*Ibid.* pp. 91–2) as Hisinger's definition is not a reprint from the *Museum Tessinianum*, but a new interpretation.

is not the type species and the name *Anomia* had even been used already by Linnaeus himself (1761, pp. 520 21) in a more restricted sense [for *A. craniolaris* and other living forms, there classed under Vermes (Testacea)]. It has since been restricted as a genus of Lamellibranchs (*Anomia* Müller ex Linn.). *Bilocularis* hence cannot now be referred to *Anomia*, but in determining to which genus it should be ascribed the three generic names cited by Hisinger have priority over all others, and it was open for any later author to choose between them in accordance with the International Rules. This choice has strictly never been made. Wahlenberg (1819, p. 67) quotes (apparently) the same species as *Anomites conchidium* and refers to Linnaeus (1753) and Hisinger (1799). Dalman (1828, p. 125) proposed a new genus *Gypidia* with *conchidium* as a specific name: his synonymy, description and figures show that it is the same form as that termed by Linnaeus (1753) *Conchidium biloculare* or by Hisinger (1799) *Anomia bilocularis*. The name *Gypidia conchidium* was subsequently adopted by Hisinger himself (1837, pp. 74 5). Later authors perpetuated the error by quoting the same species and referring them to different genera, chiefly *Pentamerus* J. Sowerby and *Conchidium* auctt. *Conchidium* was redefined by Oehlert (1887, p. 1311), and by him attributed to Linnaeus 1760 (*err. pro* 1768) the trinomial usage in the *Systema Natura* being waived.

Any choice made now between the three generic names to which Hisinger (1799) stated the species *bilocularis* had been referred, must be guided by the subsequent history of these terms as well as by general convenience. Of these three names, *Helminth. [olithum]* does not appear to be recognized as an existing genus. It was originally defined trinomially in the *Systema Natura* and had not been redescribed, at least up to 1850. *Patella* has already been restricted as a genus of gasteropods [*Patella* Linn. emend.]. The remaining name *Conchidium* is available and has, indeed, nearly always been used in this sense, although with incorrect ascription to Linnaeus on the basis of his trinomial description. Such a choice of name is thus most compatible with the subsequent history of the term and the genus is redefined on pp. 125 6 of the present paper and ascribed to Hisinger 1799, with genotype *Conchidium bilocularis* Hisinger 1799, the single original species mentioned by Hisinger.

This interpretation of the history of *Conchidium* is directly relevant to the history of the genus *Pentamerus*. The name *Pentamerus* was proposed by J. Sowerby (Aug. 1813, p. 73*) his generic definition being as follows:

Pentamerus.

"Gen. Char. An equal-sided inequivalved bivalve, one valve divided by a longitudinal internal septum into two parts, the other by two septa into three parts or valves. Beaks incurved, imperforate."

He referred to this genus three new species *Pentamerus knightii*, *P. aylesfordii* and *P. laevis* (*Ibid.*, pp. 73* 76*). No selection was made as to a genotype. Of these three species *P. knightii* is certainly referable to the then existing genus *Conchidium* Hisinger, while *P. aylesfordii* is now generally regarded as a synonym of *P. knightii*; in any case, it also is referable to *Conchidium*. Thus when Davidson (1853, p. 97) close *P. knightii* as the genolectotype of *Pentamerus* J. Sowerby, he selected a species that should have been referred to an already existing genus. The remaining species *P. laevis* was chosen as genolectotype by Hall and Clarke (1894, pp. 236 7). J. Sowerby's original description of this form is as follows (*Mineral Conchology* p. 76*, pl. 28, bottom, right-hand figure):

"Pentamerus laevis,

Spec. Char. Smooth, triangular, front rounding, beaks incurved. Much less gibbous than either of the last [i. e. than *P. knightii* and *P. aylesfordii*]; free from furrows, but having slight depressions over the septa; length generally less than an inch.

Not having found this in a perfect state, although I have had stones including hundreds of specimens, I have been doubtful whether I ought to admit it. The Rev. Dr. Abbot, of Bedford, in May, 1812, was so kind as to bring me pieces of rolled Limestone, with these small dividing shells, from near Hopton Court, where he thought they appeared to be left by the swell of the river Teme, and formed a bank three feet or more high.

Sometimes I think there are two species in the stone, a smooth and a furrowed one, but better chance than I have had must determine this; at the same time the formation is distinctly characterized.

The same stones contain the remains of Madrepores. The specimen figured is from Bildwas, Shropshire, collected by A. Aikin, Esq."

His figure shows a portion of a small ventral valve, rather triangular in outline, broken at the posterior to expose a long, median duplex septum.

It will be seen that while the majority of his specimens were from drift,[1] and thus assignable to no particular horizon, the figured example was from Buildwas, Salop. This latter place then, must be taken as the type locality, a conclusion of much interest, since the only beds exposed anywhere in the vicinity of Buildwas that contain Pentamerids are the 'Pentamerus Beds' and Purple Shales of the Upper Llandovery,[2] so that it was probably from this broad horizon that Sowerby's specimens came. Unfortunately, the original figured specimen appears now to be lost,[3] but although J. Sowerby's description is somewhat lacking in precision a study of his figure as well as of parallel material in the J. de C. Sowerby Collection leaves no doubt as to the characters of the species that he was describing. The figure shows the ventral valve of a smooth Pentamerid with (for its size) a long, median, duplex septum, while the specimens from the J. de C. Sowerby Collection labelled *Pentamerus laevis* in a contemporary hand[4] are forms which today would normally be referred to *Pentamerus oblongus* J. de C. Sow. 1839. Further, J. Sowerby's description of *P. laevis* is almost entirely applicable as a concise definition of *P. oblongus* J. de C. Sow. 1839,[5] the only

[1] The Hopton Court cited by Sowerby is most probably the Country House of that name situated six miles WSW of Worcester, England and about one mile south of the river Teme.

[2] Cf. Whittard, *Quart. J. geol. Soc. Lond.*, vol. LXXXIII (1927), p. 745, pl. lvii.

[3] It is not preserved with the rest of the J. Sowerby Collection in the British Museum (Natural History), London, nor in the Collection of the Geological Survey, London.

[4] The specimens in question are B. M. (N. H.) BB 126 (some three specimens in a block), which have on the label the date 1835 and in a contemporary hand "Pentamerus laevis. Long Mynd, Salop." BB 123, also dated 1835, has in the same handwriting "Pentamerus. Soudley, Salop". Further specimens in the J. de C. Sowerby Collection are BB 124 labelled "Boocaun. Cong." [Galway, Ireland]; BB 125 labelled "*P. knightii*, Madeley Coal Pits"; this specimen appears to be the original of pl. 19, fig. 9 (top figure) of "The Silurian System" 1839, there described as *Pentamerus laevis*; and BB 127 labelled "Marbury: R. I. M." All these specimens would today normally be referred to *Pentamerus oblongus*. The handwriting on BB 123 and 126 may well be J. de C. Sowerby's.

[5] *Pentamerus oblongus* J. de C. Sowerby 1839 is also invalidated as a homonym of *Pentamerus oblongus* Pander 1830, p. 94, though it may be seen from Pander's figures (*Ibid.* Tab. ix, fig. 5) that his species would certainly not now be referred to *Pentamerus s. s.* This produced the confusing result that there are identical specimens in the older collections, some labelled *Pentamerus conchidium* (after Pander) and others *Conchidium pentamerus* (after *e. g.* de Verneuil, 1845).

smooth *Pentamerus* (sensu *stricto*) now recognized as occurring in the British Silurian; the small average size of J. Sowerby's specimens was probably due to their being young individuals. When it is added that the identity of the two forms was expressed in an almost contemporary opinion[1] little possibility of doubt remains that *Pentamerus oblongus* J. de C. Sowerby 1839 is a synonym of *Pentamerus laevis* J. Sowerby 1813. The former name then must be rejected in favour of the latter under Article 25 of the International Rules (The Law of Priority). *Pentamerus laevis* J. Sowerby 1813 should also become the genotype of *Pentamerus*, on account of its being the one valid species referable to the genus at the time the latter was proposed.

The changes of nomenclature that are involved may conveniently be summarized here. The genus *Conchidium* which is to be retained, must be referred to Hisinger 1799 (ex Linnaeus 1768) rather than to Linnaeus direct. *Pentamerus laevis* J. Sowerby 1813, is a specific name that must replace the commonly used name *P. oblongus* J. de C. Sowerby 1839, the latter being rejected as a synonym. The genus *Pentamerus* J. Sowerby 1813 is apparently governed by Davidson's choice (1853) of *P. knightii* as type, though it is arguable whether in fact he conformed to the strict interpretation of Article 30 II (g) of the International Rules [cf. also Recommendation III (k)]. If his selection were allowed to stand, *Pentamerus* J. Sowerby 1813 would become a synonym of *Conchidium* W. Hisinger 1799, and a new generic name would be required for Pentamerids of the *P. laevis* group.[2]

[1] J. de C. Sowerby 1839, briefly described and figured *P. laevis* (p. 641, pl. 19, fig. 9) as well as proposing the name *P. oblongus* (p. 641, pl. 19, fig. 10) and evidently considered the forms as quite distinct. McCoy (1852, pp. 209, 211) also accorded the species separate descriptions, but the differences he mentions depend on the size of the individuals; but it was Davidson (1867) who was really responsible for perpetuating the error. He quoted in full (p. 153) J. Sowerby's description of *P. laevis* and stated "It is now admitted by most palaeontologists that *P. laevis* Sow. is the young of *P. oblongus*, and if it were necessary to strictly adhere to the rules of priority, James Sowerby's name published in August 1813, would perhaps require to be adopted in preference to that of *oblongus*, given to the adult shell by Mr J. de C. Sowerby in 1839". [Cf. also Davidson's footnote on p. 158, *Ibid.*]. Salter was of the same opinion (cf. Salter 1866, p. 276, and 1873, p. 80, "*P. laevis* is the young only" [of *P. oblongus*]).

[2] A recent author would interpret the genus *Pentamerus* in terms of Davidson's choice in 1853 of *P. knightii* J. Sow. as genolectotype, on the grounds that

With such a change of generic name there would have to be parallel changes in the designation of Family, Superfamily, and Suborder (under Article 5 of the International Rules), a course likely to "result in greater confusion than uniformity".[1]

The genus *Pentamerus* with type *P. laevis* J. Sowerby 1813 (after Hall and Clarke's choice, 1894) is accordingly retained in the present paper, and it is intended to submit a case for the retention of this name to the International Commission on Nomenclature.

Family *Pentameridae*.

Genus *Pentamerus* J. Sowerby 1813.

Sowerby, J., "Mineral Conchology", Vol. I, p. 73*, Aug. 1813.

Davidson, T., "British Fossil Brachiopoda", *Palaeontogr. Soc. Lond.* [*Monogr.*] I, 1853, p. 97; III, pt. vii, pp. 142—157 (1867); V, pt. ii, pp. 161 4 (1883).

Hall, J. and Clarke, J. M., *Palaeontology of New York*, VIII, pt. ii, 1894, pp. 236 240.

Schuchert, C. and Cooper, G. A., "Brachiopod Genera of the Suborders Orthoidea and Pentameroidea", *Mem. Peabody Museum nat. Hist. Yale*, IV, pt. i, 1932, pp. 177 9.

Synonym. *Pentastère* Blainville, H. D. de, in "Dictionnaire des Sciences Naturelles", Vol. 32 (Nov. 1824), p. 301.[2]

Nomina nuda. *Trimurus* Caldwell, F. E. S., in *Abstr. Diss. Univ. Camb.* 1933 4 (1934), p. 56.

Miopentamerus Alexander, F. E. S. (née Caldwell), *Abstr. geol. Soc. Lond.*, no. 1315 (July, 1936), p. 116.

Genotype: *Pentamerus laevis* J. Sowerby, "Mineral Conchology", Vol. I, p. 76*, pl. 28, bottom right-hand figure (1813). The original specimen came from Buildwas, Salop, England.

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up to that date the genus *Conchidium* had not received proper definition. [Cf. Alexander (née Caldwell) in *Abstr. geol. Soc. Lond.*, No. 1315, July 1936, pp. 116—7]. This overlooks the importance of Hisinger's paper of 1799. This author has proposed the name *Trimurus* for Pentamerids of the *P. oblongus* type (*Abstr. Diss. Univ. Camb.*, 1933—4 (1934), p. 56). *Trimurus* Caldwell 1934 has the same meaning as the name *Miopentamerus* Alexander (née Caldwell), *op. cit.*, 1936, over which it has priority, while both are nomina nuda under Article 25 c (1—2) of the Rules.

[1] Resolution of the Commission on Zoological Nomenclature, as reprinted in E. T. Schenk and J. H. McMasters 'Procedure in Taxonomy' 1936 p. 38.

[2] The status of this name is doubtful. De Blainville quotes it as 'Pentastère Sowerby', and it is possibly only a *lapsus calami*. Cf. the form 'Pentamère' in "Noveau Dictionnaire d'Histoire Naturelle", Tom. XXV, 1817, p. 161.

Generic description: (partly after Schuchert and Cooper, 1932). Large, smooth Pentamerids, shell depressed to ovate, outline quadragonal pentagonal, often trilobed anteriorly and frequently with a fold on either valve. Hinge-line gently or sharply curved; cardinal extremities rounded. Ventral valve always the higher, often considerably so. Ventral umbo prominent, curved over the dorsal. Shell-substance fibrous.

In the ventral valve, a long spondylium supported on a long and high duplex septum. A rather wide delthyrium, with (in some species at least) a small pseudodeltidium at its apex.

In the dorsal valve, long cardinalia commonly divided into inner-plates, brachial-processes and outer-plates. The cardinalia may be sub-parallel or slightly divergent, and usually arise at right-angles to the valve-wall. Between the outer-plates a very low, median septum may be present. Cardinal-process rudimentary. Dentition simple, the postero-dorsal edges of the spondylium abutting against the outer surfaces of the inner-plates near the posterior end of the dorsal valve.

European species:

Gypidia borealis C. E. Eichwald 1842.
Pentamerus esthonus C. E. Eichwald 1854.
Pentamerus laevis J. Sowerby 1813.
Pentamerus samojedicus A. Keyserling 1846.

[?] *Pentamerus integer* J. Barrande 1847.
Pentamerus schmidti N. Lebedev 1892 (? synonym of *P. borealis*).

Discussion: The genus *Pentamerus* is exceedingly variable in external shape and size, but that this variation is of little guide even for a discrimination between species, is illustrated by the range in shape of forms all to be included within the type species. The most diagnostic characters are the smooth exterior, the long, high, and often relatively narrow spondylium duplex and the arrangement of the cardinalia. The shape of the spondylium is very different from that in *Stricklandia* or *Clorinda.* In these two genera the spondylium is fairly wide relative to its length; in *Pentamerus* the spondylium is not only long compared with the whole shell, but very long also in proportion to its width (in early Pentamerids about three times as long as wide, in late species the proportion is much greater). The cardinalia serve to distinguish *Pentamerus sensu stricto* from *Pentameroides* Schuchert and Cooper 1931, here regarded as a sub-genus. The disposition of the secondary thickening and the

presence in some forms of a small pseudodeltidium is extremely interesting and is discussed in detail under the separate species.

The affinities of *P. integer* Barrande 1847, 464, Taf. xxii, fig. 7, are uncertain. This species may be referable to *Pentamerus s. s.*, to judge from Barrande's figures, but if so, it extends the range of the genus up to the Downtonian (Barrande's horizon F).

Pentamerus borealis (C. E. Eichwald) 1842.

Plates I and V, figs. 1 4; Text-figs. 2, i iv, vi, and 3.

1842. *Gypidia borealis* Eichwald, C. E., "Die Urwelt Russlands", II, pp. 74 5, Tab. I, fig. 14. [Advance copy, from *Beitr. Kenntn. Russ. Reiches,* VIII, 1843].
1860. *Pentamerus borealis* Eichwald, C. E., "Lethaea Rossica", vol. I, p. 787.
1892. [?] *Pentamerus schmidti* Lebedev, N., "Obersilurische Fauna des Timan," *Mémoires du Comité Géologique,* vol. XII, No. 2, pp. 22, 42, Taf. ii, figs. 9 a c, 10.
1908. *Pentamerus borealis* Eichwald, C. E., Kiær, J., "Das Obersilur im Kristianiagebiete", *Vidensk. Selsk. Skrifter, Math.-Naturv. Kl.* (1906), II, *passim.*

Material: P. M. O., specimens 21 605 09, 40 250 52, 40 410, 40 471 76, 44 821, 24, 27, 41, —99, 44 900, —02, 52 809 22, 53 482—85, 58 418 27, 58 445—72, 58 478—58 520, 58 550 54. (Kiær Collection), from southern Norway.
S. M. C., specimens A. 13 525 36, from Esthonia.

Types: The specimens figured by Eichwald, 1842, Tab. i, fig. 14 (according to Teichert 1928, p. 60, these are no longer existent).

Introduction: Eichwald's original description gives a brief account of the external characters of this species. He considered that it was closely related to '*Gypidia conchidium*' auctt. [*C. bilocularis*], and he refers to its mode of occurrence as isolated valves forming shell-banks at various localities on the Silurian outcrop in Esthonia. His figure shows specimens with a well developed septum in the ventral valve. The species was easily identified and was chosen by Schmidt (1858 and 1881), as the zone fossil for the horizon G 2 (*Borealis*-bank) in his classification of the Esthonian Silurian. It was soon recognized that its distribution extended to southern Norway.

Diagnosis: *Pentamerus* of rather small, average size. Ventral valve moderately convex; dorsal valve flat, or very slightly convex. Umbones low, a little incurved, approximate, the ventral somewhat the higher. Length always greater than the breadth, which is greater than the thickness. In the ventral valve a relatively short and wide

spondylium, supported on a short septum. In the dorsal valve the cardinalia which are about equal in length to the spondylium, are attached at right-angles to the valve-wall except at their extreme anterior end, where they may be free. The species often possesses an extremely thick shell, but this feature is not invariable.

Discussion: In normal adult individuals the breadth is about two-thirds of the length; the maximum breadth is frequently attained about half-way from the posterior to the anterior margin. This, together with the rather sharp, downward slope of the valve-margins from the umbones, tends to produce a sub-oval or rhombic outline (cf. Plate I, figs. 1, 4, 6 7). The hinge-line is short and strongly curved and there are no cardinal angles. The profile is plano-convex, or slightly biconvex; the curved shape of the ventral valve contrasting with the much flattened dorsal valve. The ventral valve is most curved posteriorly, where it is arched forwards to conceal the dorsal umbo. The greatest thickness may be attained in about the same plane as the maximum breadth or rather more posterior. The anterior margin is straight or slightly flexed to the ventral side.

The dorsal umbo is incurved and fits closely below the umbo of the ventral valve, covering a triangular, rather wide delthyrium, a feature that can only be seen when the valves are isolated (Plate V, figs. 3 4). The delthyrial angle is about 60°. On either side of the delthyrium the valve is strongly curved, but there is no real area, demarcated from the rest of the valve-surface.

The valves are always completely smooth, apart from occasional, inconspicuous, concentric growth lines; frequently there is hardly a trace of a median fold in either valve, but in some rather large specimens the ventral valve is elevated into a broad, gently arched fold, especially towards the anterior.

The articulation is simple, as is usual in the Pentamerids. There are slight projections at the antero-dorsal corners of the delthyrium, where the free edges of the spondylium separate. These projections, which have but slight dorsal extension from the commissure, fit against the margins of the inner-plates just below the umbo of the dorsal valve (text-fig. 3, transfers 42 8); and to allow for this there is a small inward curve of the dorsal valve-wall at those points.

Internal Characters: In the ventral valve there is a typical development of spondylium, supported on a high, duplex septum (Plate V, figs. 3 4). The spondylium is of the 'long' type, in which

the maximum width of the structure is less than half the length, and in this species the proportion of length to breadth varies between 2 ½ and 3, to 1. The spondylium is comparatively open, its shape is determined posteriorly by the rather wide delthyrium and by the height of the septum. Thus, the dental-plates, which join the valve-wall along the edges of the delthyrium, slope inwards to enclose the spondylial cavity which is roughly triangular in section. The inward slope of the spondylial walls continues to the anterior end of the structure, at the same time the spondylium gradually narrows and becomes less deep (text-fig. 3, transfers 48 to 99); so that the cross-sectional shape remains triangular throughout, with the dimension of width approximately equal to the depth. As seen in profile, the spondylium curves gently antero-dorsally towards the cavity of the dorsal valve (Plate V, fig. 1). It is supported on a septum for less than half its length. The spondylium of *P. borealis* is thus very different in shape and cross-section from the analogous structures in the later species of *Pentamerus* and it resembles much more closely the *Stricklandia* type, than do the later Pentamerid spondylia.

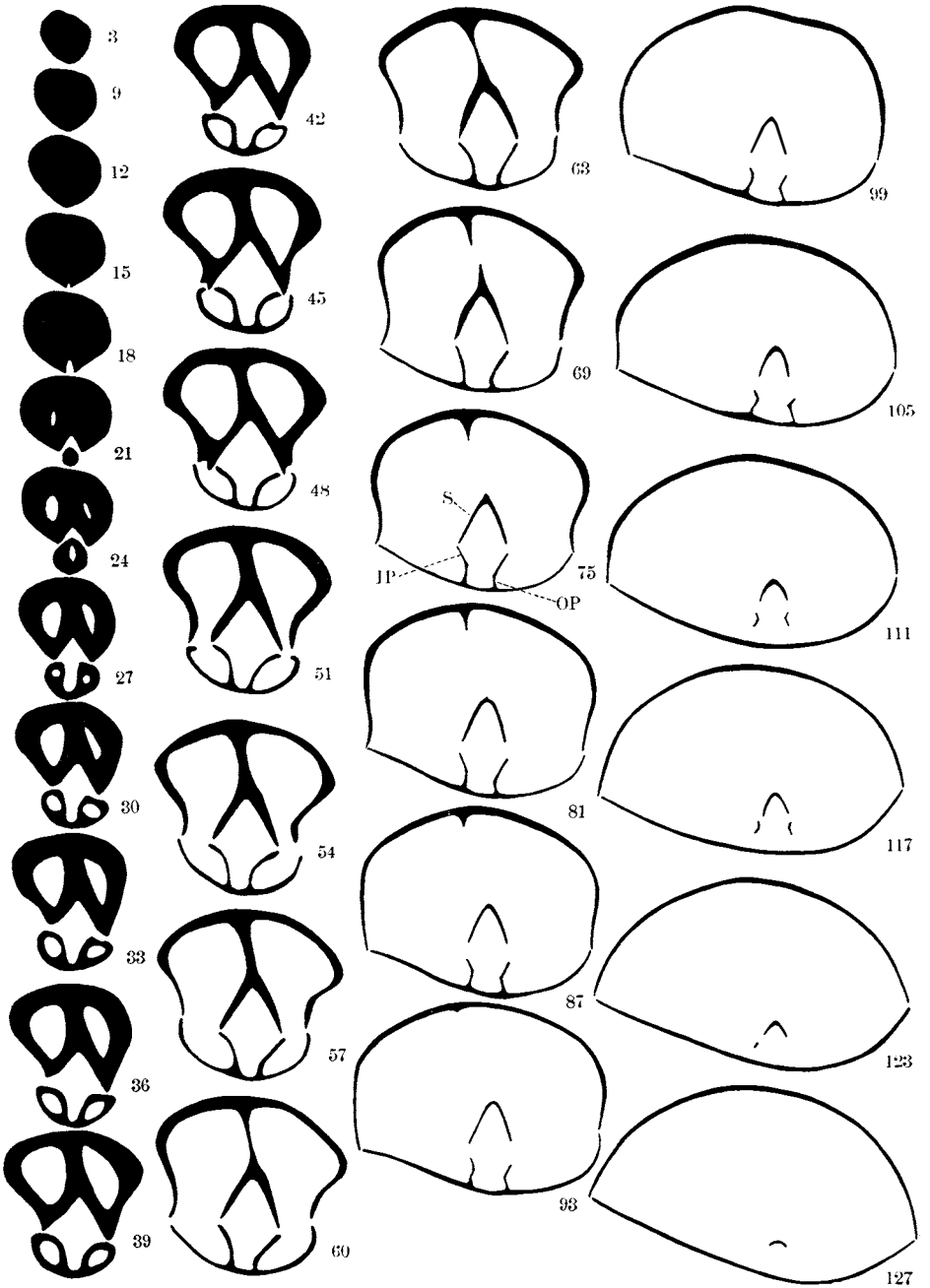
The detailed structure of spondylium and septum may be studied in thin sections and serial transfers (text-figs. 2 3). These show that most of the thickening of the valve-walls is due to an unusually great development of the main shell-layer. There may in addition be an inner layer of secondary shell-material, but this is comparatively thin. The thickness is thus due to continued secretion by the mantle after the early growth-stages. It affects the whole of the posterior region, especially of the ventral valve, including the septum and spondylium, the extent of the thickening gradually diminishing towards the anterior. The thickening is thus different from that present, for example, in *Stricklandia lirata* (forma *typica*). In that species (St. Joseph, 1935 b, p. 496) it was due to an increase in the amount of supplementary shell-material, while in *P. borealis* it is the primary shell-wall itself, which is thickened. The thickening is so extensive that it may, in advanced forms, fill completely the cavities on either side of the median septum almost to the level at which the spondylial walls separate from the valve-margin.

The development of the internal structures is clearly seen from serial transfers. These reveal the presence of two closely united plates forming a duplex septum, immediately within the outer shell-layer. This septum was thus initiated at a very early growth-stage,

as soon, in fact, as the mantle had secreted the outer shell-layer in the posterior region. The septum is present embedded in the thickened valve-walls, long before it separates as a visible structure supporting the spondylium. It is due to this extension of the septum through the thickened posterior region of the shell that the valve fractures so easily along the median plane.

As may be seen from the serial transfers (text-fig. 3) which form part of a series taken at 0.15 mm intervals, when the septum first appears (transfers 21 to 33) it is thick and short. It gradually thins, and becomes rather higher, elevating the spondylium above the valve-floor: it finally separates in transfer 69, to continue a short distance further as two ridges, one down the centre of the dorsal valve, the other down the back of the spondylium. In normal, adult specimens this separation of the septum occurs about 15 mm from the posterior end of the valve. The duplex character of the septum may be seen from sections and transfers to be very clearly marked throughout its length. The two walls of the spondylium do not fuse at the point at which they meet at the back of the spondylial cavity, but continue as two closely united plates to form the septum. The shell-material composing the greater part of the spondylial walls has a prismatic structure, and is continuous with the material forming the main valve-wall. Lining the whole of the spondylial cavity, however, and extending right to the apex of the delthyrium is another thin layer formed of calcareous lamellae laid down parallel to the spondylial walls (cf. text-fig. 2, I II, VI). This inner sheath is thickest at the bottom of the spondylial cavity, and may be prolonged a short distance ventrally along the median plane of the septum (text-fig. 2, II); it increases in thickness anteriorly, where it may build the greater part, or even the whole of the spondylial walls (text-fig. 2, III IV).

The homologies of this inner layer have been discussed in the systematic section, where it is shown that it is of this layer that the pseudodeltidium is formed, when such a structure is present. A pseudodeltidium has never yet been observed in a typical, thick-shelled *P. borealis*; the inward arching of the dorsal umbo covers the delthyrium almost completely, and perhaps obviated the need of this structure. However, in a thin section of a structurally rather more advanced specimen (P. M. O. 53 482), from zone 7a Sandvika, Asker, still referable to *P. borealis*, a very thin, deeply concave



Text-fig. 3. *Pentamerus borealis* (Eichwald)

Serial transfers (S. M. C. A. 13502) at 0.15 mm intervals from the posterior end of a specimen; zone 7a, Ringerike. ×1¼. Transfers 3—127. (Cf. text-fig. 2, I –IV and Pl. V, figs. 1—3.) IP = inner-plates; OP = outer-plates; S = spondylium.

pseudodeltidium may be observed, covering the apex of the delthyrium (text-fig. 2, VI). It is continuous with the inner layer lining the delthyrial cavity. In another specimen (P. M. O. 53 485) a small, concave pseudodeltidium may still be seen in place, in the apex of the delthyrium of a ventral valve.

In the dorsal valve the cardinalia commence at a similar early stage. Like the ventral septum, they remain embedded in shell-thickening for some distance below the umbo. They arise at right-angles to the valve-wall and at first remain roughly parallel or are slightly inclined inwards; as soon as they separate as visible structures they divide a median space from two lateral cavities, enclosed between them and the valve-wall (text-fig. 3, transfers 27 to 42). The plates gradually slope outwards (transfers 33 to 42), and finally separate (transfer 45), where they abut against the inner edges of the 'teeth' of the ventral valve. The cardinalia always remain low, and are directed approximately towards the free edges of the spondylium with which they almost come in contact (transfers 45 to 75). The outward inclination tends to decrease anteriorly, while at their anterior end the processes separate from the inner valve-surface and continue free for a short distance (transfers 105 to 127).

The material composing these processes is lamellar in fine structure and resembles that of the thin layer lining the spondylial cavity; it contrasts with the material of the inner shell-layer, which is in contact with the surface of these plates only at the posterior, before their free edges have separated from the valve-wall. Anteriorly (transfers 75 to 117) the plates are seen to have a two-fold division, rather than the tripartite arrangement characteristic of the later *Pentamerus* species.

Remarks: *Pentamerus borealis* is the earliest *Pentamerus* at present recognised and the first member of Kiær's *borealis*-'*oblongus*'-*gotlandicus* morphological series. The gradual lengthening of the septum and spondylium in the ventral valve and of the cardinalia in the dorsal valve, in passing from earlier to later members of this series, has been so often emphasized, that it is well to note that there are other characters in which this species differs from *P. laevis*, and which do indeed justify specific separation. Thus, of the characters that have served in the past to distinguish *P. borealis* from *P. laevis* one of the principal has been the length of the septum, which was considered to be 'short' compared with that in the latter species.

Dimensions of Typical Specimens
(in millimetres).

Length	Breadth	Thickness
53.7	37.9	25.6
50.0	39.4	24.2
45.8	33.4	25.0
74.0	41.4	-
42.0	32.5	-
47.7	38.2	-

Strictly, within each of these two species the length of the septum varies between certain limits, and the ranges would certainly overlap, so that on this feature alone the species merge into one another. Similar arguments apply to the structures in the dorsal valve. The characters which serve to separate *borealis* from *laevis* are rather the relative dimensions of the valves, the outline and profile, and also the shape of the spondylium.

Pentamerus borealis appears to be a relatively stable species, especially when it is compared with *P. laevis*, which shows a far greater range of variation. The characters that are least constant are the curvature of the valves, the development of the fold on the ventral valve, and the outline and profile. The variation is, however, limited; and for example, the form figured by de Verneuil (1845, pp. 119—20, pl. viii, figs. 1a c) as *P. borealis* is far from being typical of the species, as Teichert (1928) has pointed out. De Verneuil's figures, while agreeing well enough for the profile, show a far too 'pinched in' outline at the posterior, while his description is not wholly applicable.[1] He may have happened to have been dealing with specimens which constituted a variety of the typical *borealis*.

Pentamerus schmidti Lebedev 1892, would appear, as far as may be judged from Lebedev's description and figures,[2] either to be very closely related to *P. borealis*, or more probably to be the same form.

Eichwald's original material came from the Silurian of Esthonia (presumably horizon G) at various localities such as Hapsal and Dagö,

[1] Especially the first paragraph on p. 119 (*op. cit.*).

[2] These show a very thick-shelled form, of *P. borealis* shape and size, with short septum and spondylium [Lebedev, *op. cit.* Taf. ii, figs. 9a—c, 10]. The originals were in the Museum der Akademie, Leningrad.

and an examination of specimens (S. M. C. A. 13525 36) from this same general region leaves no doubt as to the identity of the material from southern Norway. In the Oslo region, *P. borealis* occurs at horizon 7a of which it is the zone fossil. The horizon is perhaps best studied in the western area at Ringerike and Holmestrand. At Hadeland and Ringerike the development is very characteristic, and it is from the latter district (Limåstangen) that most of Kiær's specimens have come. In a thickness of about 10 m of rock attributed to zone 7a, there are three or four bands varying from 15 to 120 cms in thickness, crowded with the thick shells of *P. borealis,* mostly in the form of isolated valves (cf. Kiær, 1908, pp. 53 6, pls. iii and xxiv). The shells were evidently swept along by currents to form shell-banks, a process in the course of which the valves were nearly always separated. As might be expected from such a method of formation, the area of this development is limited, and nothing quite like it is known in the neighbouring districts. The same conditions prevailed at times, however, in Esthonia, for there too, as was noted by Eichwald (1842, p. 75) *P. borealis* valves build entire shell-banks. At Holmestrand, *P. borealis* is present though it is not nearly so common as at Ringerike, occasional individuals are of the characteristic, thick-shelled form, but the greater number collected by the writer have a much thinner shell, and while still agreeing with the typical *borealis* in shape and type of spondylium, are a little closer to *P. laevis* (cf. Kiær, 1908, pp. 197 201). At Malmøy and Asker, the *P. borealis* development is rather less distinctly characterized (*op. cit.* pp. 152 3, 349 and 488).

The Baltic Provinces and southern Norway are the only areas from which *P. borealis* has been described. In Britain, though it has never been recorded, it is not impossible that a very similar form may be present in some Middle Llandovery horizon.

Pentamerus laevis J. Sowerby 1813.

Plates II, III, figs. 4 6, 10—11; V, figs. 5—6, 10; VI, figs. 16 17; Text-figs. 2, V, 4—7.

1813. *Pentamerus laevis* Sowerby, J., "Mineral Conchology" vol. I, p. 73*, pl. 28.
1839. *Pentamerus laevis* J. Sowerby. Sowerby, J. de C., in Murchison's "Silurian System", p. 641, pl. 19, fig. 9.
1839. *Pentamerus oblongus* Sowerby, J. de C., *ibid.* p. 641, pl. 19, fig. 10.

1867. *Pentamerus oblongus* J. de C. Sowerby. Davidson, T., "British Fossil Brachiopoda", *Palaeontogr. Soc. Lond.* [*Monogr.*], III, pt. vii, pp. 151 5, pls. xviii and xix, figs. 1 2 (with Bibliography). *Idem*, V, pt. ii (1883), pp. 161 2.

1894. *Pentamerus oblongus* J. de C. Sowerby. Hall, J. and Clarke, J. M., Palaeontology of New York, VIII, pt. ii, pp. 237 ff., pls. lxvii lxx (*pars.*).

1908. *Pentamerus oblongus* J. de C. Sowerby. Kiær, J., "Das Obersilur im Kristianiagebiete", *Vidensk. Selsk. Skrifter, Math.-Naturv. Kl.* (1906), II, *passim*.
Pentamerus oblongus of the generality of authors.
[?] Synonym. *Pentamerus beaumonti* Laporte, F. L. de, [=Castelnau, Comte de] Essai Syst. Silur. Amer. septent., 1843, p. 38, pl. 13, figs. 9, 9 a.

Material: P. M. O. specimens, 21 280 83, 88 90, 40 408 09, 40 509 16, 42 635 39, 50 53, 42 692 701, 42 788 93, 42 871 72, 42 913 16, 43 002, 43 038 41, 43 189, 43 319 22, 30 53, 43 456—59, 78 83, 43 549 56, 90 92, 43 619 28, 38 45, 53 454 55, 60 66, 53 496 503, 53 521 41, 50 52, 54 684 91, 54 726, 54 834, 58 65, 54 928 33, —44 46, 51 62, 58 555 59, 63. (Kiær Collection), from southern Norway.

Types: The original specimen figured by J. Sowerby (1813, p. 28, bottom, right-hand figure) is apparently lost. Plesiotypes. B. M. (N. H.), BB 125 (figured by J. de C. Sowerby 1839, pl. 19, fig. 9 as *Pentamerus laevis*), from the Silurian of Salop, England.

The history of this species has been fully recorded in the discussion of the synonymy of *Pentamerus* and *Conchidium* (pp. 60 63), and it is there shown that *Pentamerus laevis* J. Sow. 1813 must replace the commonly used name *P. oblongus* J. de C. Sow. 1839.

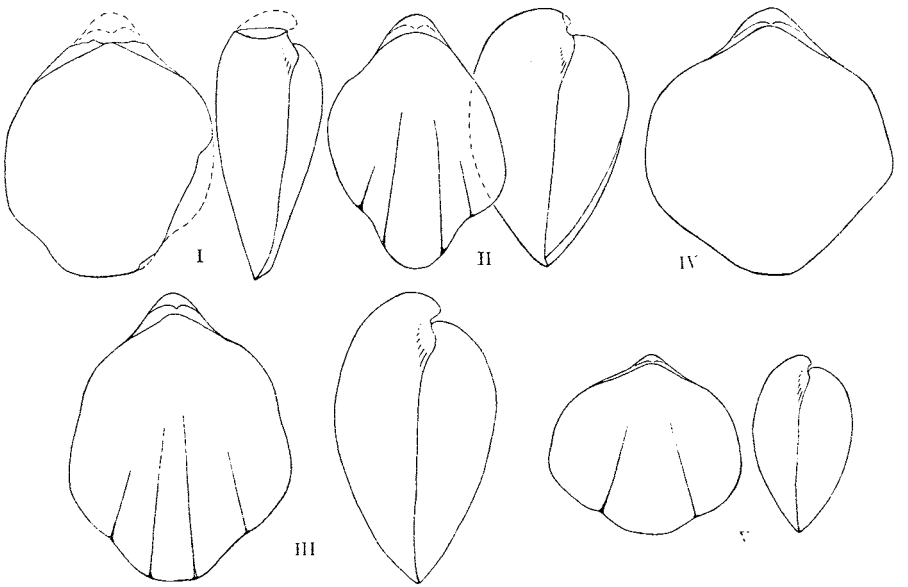
Diagnosis: Large-sized *Pentamerus*, oval, sub-pentagonal or even sub-rounded in outline. Breadth typically two-thirds of the length or rather more, and considerably greater than the thickness. The maximum breadth and thickness are often attained about halfway towards the anterior margin. Hinge-line short, curved. Profile always markedly biconvex, often about equi-convex. Ventral umbo rather high, curved forwards to conceal the dorsal umbo. A low, median fold usually present on both valves. Anterior margin rectimarginate; when the median folds are prominent, the margin may be drawn out into a small, anterior prolongation. Surface often marked by concentric lines of growth. In the ventral valve a triangular delthyrium partially covered by a small pseudodeltidium at

its apex (cf. pl. V, fig. 6). The sides of the delthyrium are supported by dental-plates which unite to form a long, narrow spondylium supported on a high, and relatively long, thin, duplex septum (Pl. V, figs. 6, 10). In the dorsal valve, long and often sub-parallel cardinalia (Pl. V, figs. 5, 10) composed of inner-plates, brachial-processes and outer-plates. Between the anterior portions of the cardinalia a low, median ridge may be present.

Discussion: The variability of *P. laevis* in such external characters as shape, size and profile has often been the subject of comment (cf. Davidson, 1867, pp. 152 3; Hall and Clarke, 1894, p. 237). The typical *P. laevis* is an elongate form, sub-oval in outline, with a biconvex profile, and a low, median fold on each valve. The maximum dimension of breadth thus falls about half-way between the maximum length and the thickness. The hinge-line is short and as in *P. borealis*, the valve-margins usually slope outwards and downwards from the ventral umbo, until the greatest breadth is attained. The characters which the early authors considered most important were the smoothness of the shell, the rounded and often trilobed anterior margin and the incurving of the umbones (cf. J. Sower by's description 1813, quoted *supra* p. 262, J. de C. Sowerby, 1839 p. 641, Davidson, 1867, p. 152). The great variation from the typical form is due to an accentuation of one more of the external characters. These may be described with reference to the drawings (text-fig. 4; cf. also Plates II and III), which represent the main variants in shape encountered in the Oslo region. The characters which are least constant are the outline and profile, the height of the ventral umbo, and the degree of trilobation of the anterior margin.

The specimens from southern Norway that most closely resemble the typical *P. laevis* (text-fig. 4, I and Pl. VI, figs. 16 17)[1] are perhaps those less trilobate forms from zone 7 b β at Malmøy. Thus P. M. O. 58 563 (cf. text-fig. 4, III) differs only in the slightly greater convexity of the shell and in a tendency towards trilobation. These two features are accentuated in the typical form from this locality and from Holmestrand at the same horizon, which is much more convex and strongly trilobate with a well-developed median fold in

[1] This is interpreted in terms of J. de C. Sowerby's figures in the "Silurian System" (1839, pl. 19, fig. 10), and those in Davidson's monograph (1867, pl. xviii and xix). The Norwegian material has been compared with actual, figured specimens.



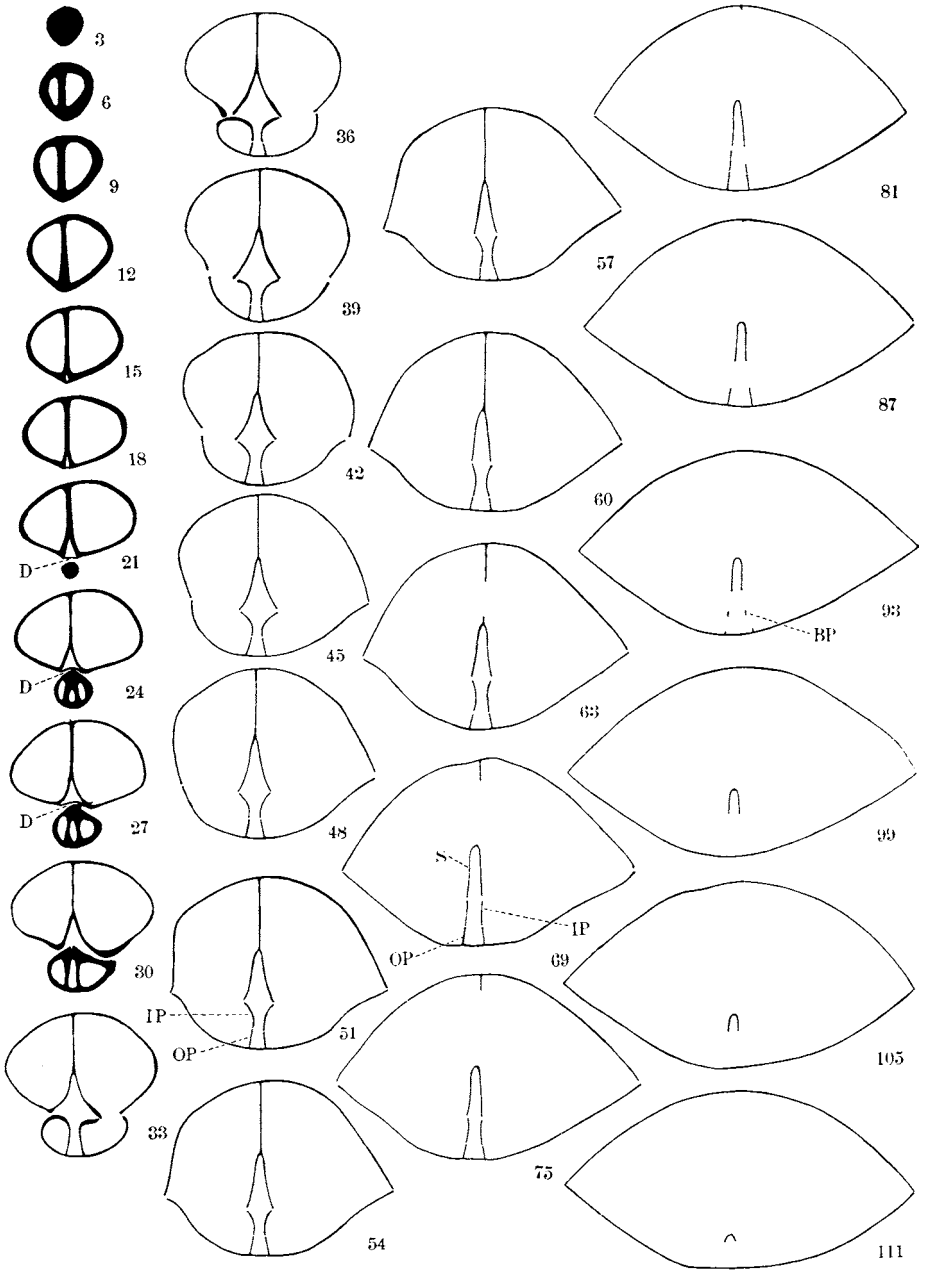
Text-fig. 4. *Pentamerus laevis* J. Sowerby. (All figures ×2/3.)
Outline drawings of the dorsal and right-lateral views of five specimens. I. Geol. Survey Coll., London, 6908 (Plesiotype); II. P. M. O. 58 558; III. P. M. O. 58 563; IV. P. M. O. 54 865; V. P. M. O. 40 520

each valve (P. M. O. specimens 58 555 9, 54 860, 42 789, 43 002 cf. text-fig. 4, II; and Pl. II, figs. 1 3). It is not represented in the collection from any of the other districts. Specimens from Ringerike (zone 7 b) and from Holmestrand in the lower part of this zone differ from the above in being relatively broader and less trilobate (text-fig. 4, IV; P. M. O. 44 910, 54 865). An even more extreme departure from the type is represented by material from 7 a and 7 b α at Malmøy, specimens 43 619 28, 21 280 81, 40 509 10, 40 520, which are less convex, with a rather lower ventral umbo, and broader, with the dimensions of breadth now tending to exceed the length (text-fig. 4, V; Pl. II, figs. 16 18). Individuals from zone 7 a at Sandvika, Asker, 53 521 41, 43 461 are not unlike the foregoing; the dimensions of length and breadth are about the same, the profile is gently biconvex, and there is a tendency to a general subcircular shape with a lengthening of the hinge-line. These specimens occur together with a few individuals (53 455) of about the same convexity but of much more triangular outline.

None of these variations, with the possible exception of the strongly trilobate form of 7 b β, is absolutely restricted to any one horizon. Nor do the extremes stand out distinctly from one another, they are connected by many intermediate types, which occur casually in the series. Text-figure 4 represents of necessity only a few of these shape variations but there are many specimens in the collection which serve to connect the forms that have been selected for drawing. The shape-variations thus merge into one another and have little or no stratigraphical significance; there is no division between the two extremes separating as it were, species from species. In internal characters they show great constancy, a statement that is based on an examination of specimens by serial transfers and thin-sections, specially selected to represent the widest range in external characters (S. M. C. A. 13 503 5, and sections of specimens P. M. O. 53 529 30, 42 914 etc.). These variants then are best regarded as all falling within the limits of the one species *P. laevis*, a conclusion which was evidently reached also by Professor Kiær, for they are so labelled in his collection, while in his monograph he describes them simply as varieties.

The articulation is of the generalized Pentamerid type. At the points where the free edges of the spondylium commence below the antero-dorsal corners of the delthyrium, the spondylial walls are slightly thickened and abut against the outer edges of the inner-plates where they separate at the hinge-line (text-fig. 5). The two points about which articulation takes place are rather closer together than in *P. borealis*.

Internal Characters: The spondylium in *P. laevis* is very constant in character and a feature by which the species may easily be recognized, a single cross-section usually sufficing for determination (text-figs. 5 and 6, Plate V, figs. 6, 10). The structure extends for about half the length of the valves or sometimes a little further. It is a much more advanced example of the 'long' type than that of *P. borealis*, the proportion of length to breadth is thus about 4 or 5, to 1. The spondylium attains its maximum width at the point at which its walls separate from the hinge-line (Pl. V, fig. 6). There, the spondylial cavity is approximately triangular in section (text-fig. 5, transfers 33 to 39), but anteriorly it narrows, the walls becoming nearly parallel and they continue so for the further half of its length (text-figs. 5 and 6, transfers 60 to 105 and 59 to 71 respectively).



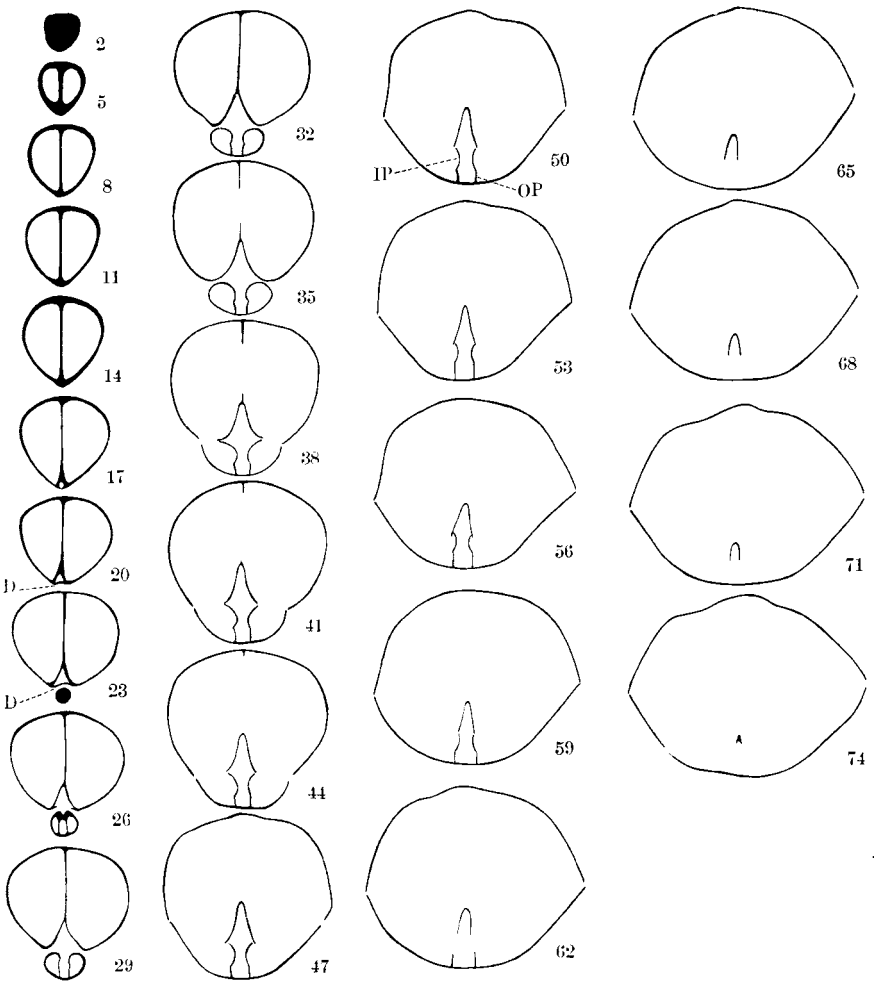
Text-fig. 5. *Pentamerus laevis* J. Sowerby.

Serial transfers (S. M. C. A. 13 503) at 0.15 mm intervals from the posterior end of a specimen; zone 7 b, Malmøy. $\times 1\frac{1}{3}$. Transfers 3—111. (Cf. Pl. V, fig. 10). BP = brachial-processes; D = pseudodeltidium; IP = inner plates; OP = outer-plates; S. = spondylium.

In its mid-portion the spondylium is thus frequently rather narrow and deep, the ratio of width at its free edges to depth being about 1 to 3. In profile, the front of the spondylium is almost straight, with the back curving gently forward to the cavity of the dorsal valve (Plate V, fig. 10). The structure is usually supported on a septum for about half its length.

The thickening of the valve-walls and internal structures in the posterior region which is commonly present in *P. borealis* hardly ever occurs in *P. laevis*. The shell in this species is usually very thin and the division into two shell-layers is seldom seen. Occasional individuals as, for example, from the lower part of zone 7 b at Ringerike show a thickening of the shell towards the posterior, but these may be types intermediate between the two species. The difference may be readily appreciated on comparing text-figs. 3 and 5. The late appearance of the septum as a visible structure in the series of transfers in the former figure, contrasts with its presence in the fourth transfer in the *P. laevis* series. In this species, as in *P. borealis*, the septum is encountered with its typical, duplex character, usually as soon as the outer shell-layer has been removed. It is always thin and relatively high, thus elevating the spondylium considerably above the valve-floor (text-figs. 5, 6), but its height depends to some extent on the convexity of the ventral valve. The duplex nature of the septum is maintained throughout its length, though this may be difficult to observe anteriorly owing to the thinness of the septum and the fine scale of its structure. When viewed in profile as in specimens fractured along the median plane, growth-lines may be seen parallel to its anterior margin.

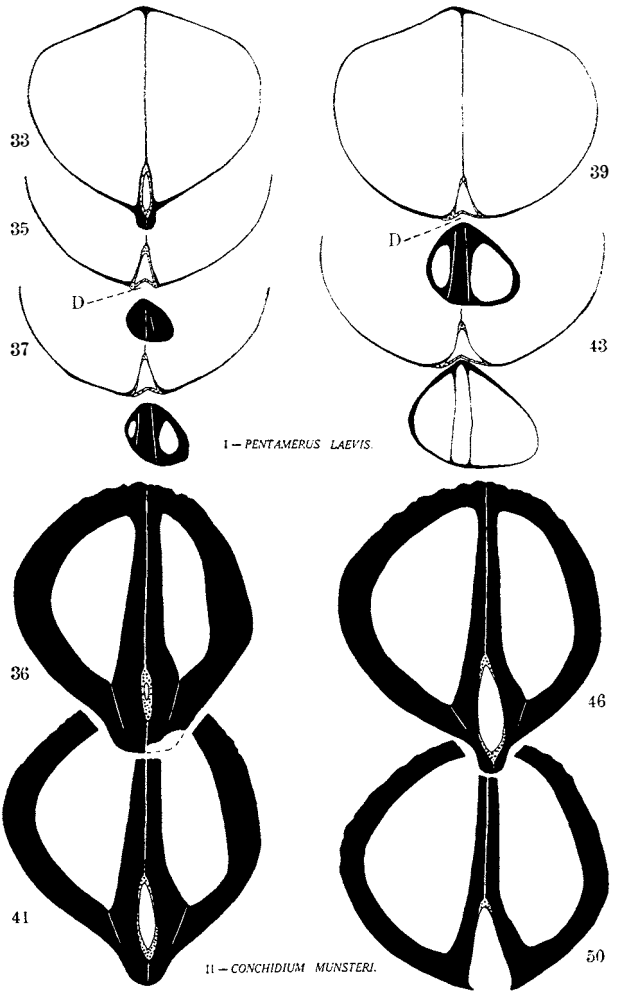
The whole of the interior of the posterior portion of the spondylium is covered by a very thin layer of lamellar material, which evidently corresponds to the similar feature seen in *P. borealis*. The layer is thickest near the umbo, where it may fill the whole of the delthyrial cavity, and along the base of the spondylium. A study of thin-sections and serial-transfers such as those shown in text-figs. 2, V and 7, I, leaves no doubt that the flat or slightly concave covering present at the apex of the delthyrium (cf. text-fig. 5, transfers 18 27) is formed of this same thin layer. This cover over the apex of the delthyrium is of the nature of a pseudodeltidium (Pl. V, fig. 6 and cf. the similar structure in *P.* cf. *gotlandicus*, fig. 7). In specimens with the two valves in apposition it may be seen to lie very close to the



Text-fig 6. *Pentamerus laevis* J. Sowerby.

Serial transfers (S. M. C. A. 13 504) at 0.15 mm intervals from the posterior end of a specimen; zone 7bβ, Malmøy × 2. Transfers 2—74. (Cf. Pl. V, figs. 5—6).
D pseudodeltidium; IP inner-plates; OP = outer-plates.

incurved umbo of the dorsal valve (cf. text-figs. 5 and 7, I). At the base of the spondylial cavity the thin, covering layer may be prolonged a short distance along the median plane of the duplex septum. Towards the anterior it appears to form the greater part of the spondylial walls, below the point at which the latter separate from the median septum.



Text-fig. 7. I. *Pentamerus laevis* J. Sow. II. *Conchidium münsteri* new species.
I. Serial transfers (S. M. C. A. 13 505) at 0.15 mm intervals from the posterior end of a specimen; zone 7 b β, Bjerkøy, Holmestrand. × 2⅓. Transfers 33—43. D = pseudodeltidium. II. Serial transfers (S. M. C. A. 13 509) at 0.125 mm intervals from the posterior end of a specimen; zone 5 b, Ringerike. ×3½. Transfers 36—50. (For the complete series see text-fig. 10.)

The cardinalia in the dorsal valve (Plate V, figs. 5 and 10) are clearly divisible into two pairs of plates, the inner-plates and outer-plates (text-figs. 2, V; 5 and 6). These commence at the dorsal umbo and form a tripartite division of the posterior region of the valve;

Dimensions of Typical Specimens
(in millimetres).

	Length	Breadth	Thickness	
Trilobate forms	50.0	40.6	21.5[1]	
	59.4	42.3	34.2	P. M. O. 58 563
	58.4	46.8	39.7	
	49.4	34.1	30.6	» 58 558
	38.6	34.3	24.2	» 54 859
	41.0	33.4	22.5	» 58 555
	48.2	36.0	33.4	
	51.0	49.4	34.6	» 54 865
Broad variety.....	32.5	35.4	18.5	» 40 509
	36.4	37.9	20.5	» 40 520
Variety from 7 a at Asker	34.2	33.4	19.9	
	30.7	27.3	15.7	» 53 524
	32.2	33.2	18.0	» 53 536

when they separate as distinct structures, at about the level of the hinge-line, the outer-plates are sub-parallel and arise roughly at right-angles to the valve-wall, while the inner-plates are markedly convex to one another and are directed towards the free edges of the spondylium (text-figs. 5 and 6, transfers 33 to 39, and 35 to 41 respectively; cf. also Pl. V, fig. 10), with which they almost come in contact. Further towards the anterior margin this convexity decreases, and the line of junction of the two pairs of plates becomes less distinct. The outer-plates are frequently continued for a short distance beyond the inner-plates, in contact with the valve-wall (text-fig. 5, transfers 81 to 93). The bases of the brachial-processes appear in these specimens to be fused with the outer-plates, but the presence of a double rather than a treble division (as is typical of the Pentamerids) may be due to the preservation of the material. The brachial-processes themselves may be seen in some specimens (P. M. O. 58 557, 42 653) continuing beyond the inner- and outer-plates (cf. text-fig. 5, transfer 93, and Pl. V, fig. 10).

Remarks: *Pentameris laevis* is by far the commonest and most widely distributed species of this genus in the Oslo region, as also in Britain. It occupies a middle position in Kiærs developmental series, and was considered by him to connect the short septate

[1] Present dimensions of the specimen (Geol. Survey Coll., London, 6908) figured by J. de C. Sowerby in the "Silurian System" 1839, pl. 19, fig. 10 (right-hand figure).

P. borealis with the long septate *P. gotlandicus*. The range of length of septum in *P. laevis* certainly falls between these two species and forms a convenient and useful guide for rough field-determinations. The biconvex profile, the frequent presence of a fold in both valves, the greater height of the ventral umbo, and usually the thinness of the valve-walls are characters which readily serve to distinguish the great majority of specimens of *P. laevis* from *P. borealis*. Detailed study reveals other important differences. A pseudodeltidium is normally present in *P. laevis* while it has never been observed in the typical, thick-shelled *P. borealis*. The spondylium in *P. laevis* is much narrower and deeper than the corresponding structure in *P. borealis*, in the former the spondylial walls are often parallel, in the latter they are always inclined to one another so that a cross-section of the spondylial cavity approximates to an equilateral triangle (cf. text-figs. 5 and 3). In the dorsal valve, the cardinalia have the same general form in the two species, but in *P. laevis* each process appears to consist of three plates which are fused along their edges, in *P. borealis* this multiple structure has not been observed.

The great range in shape and size exhibited by *P. laevis* has already been discussed (pp. 85 7), and it has been remarked that it is the constancy of the internal characters which indicates that all these variations should be included within the same species. A point of special interest is the relation between *P. laevis* and allied species of *Pentamerus* occurring at the same horizon. Thus, the existence of *P. samojedicus* Keyserling which closely resembles some shape-variations of *P. laevis* in external form while it differs internally, justifies the grouping of the *P. laevis* varieties under one species, quite as much as does the latter's constancy in internal characters. *P. samojedicus* differs according to Keyserling (1846, p. 236) from *P. laevis* in the greater thickness of the shell, in the possession of a relatively short septum and in the form of the spondylium. His figures (*Ibid.*, tab. 9, figs. 2 a b) show a form with a rather short, but high, septum and wide spondylium, in shape somewhat resembling that of *P. borealis*, and in the dorsal valve short cardinalia. This is, clearly, a short-septate form of *borealis* type, but in proportions and outline much closer to *P. laevis*[1]. Keyserling's

[1] Another point of resemblance to *P. laevis* is the prominence of the small median septum in the dorsal valve (cf. Keyserling *ibid.*, Tab. 9, fig. 2. f.).

specimens came from the Silurian limestones of northern Russia (Petschora) but are assignable to no precise horizon.

Pentamerus esthonus, to judge from Eichwald's description (1854, pp. 91 3; 1860, pp. 789 91) and from specimens in the British Museum (Natural History), London (B. 20, BB. 159 60), differs from *P. laevis* in its much larger average size, a feature which in itself might hardly justify specific separation, but this is combined, in the specimens that the writer has seen, with the presence of a curved cardinal-area in the ventral valve on either side of the wide delthyrium and apparently a much higher spondylium, but the internal structures have not been fully investigated. The form may be only a rather distinct variety of *P. laevis.*

In southern Norway, the beds with *P. laevis* comprise the zone 7 b, an horizon that is particularly well developed in the Ringerike, Holmestrand, Malmøy and Asker districts, and it is these areas that have yielded most of the specimens in the collection. At Ringerike a thickness of about 25 m was assigned by Kiær to 7 b, while at Malmøy this division is rather thicker (35 m). In the last locality two sub-zones are recognizable, 7 b α characterized by a broad and moderately short variety of *P. laevis* (Kiær, 1908, p. 489), and 7 b β with a large, strongly trilobate form, cf. text-fig. 4, II, and Plate II, figs. 1 3 (Kiær, *ibid.*), which apparently occurs also in the Holmestrand area (at Bjerkøy), high up in 7 b (Kiær, *ibid.* p. 203.) At Asker (Sandvika) in 7 a b there is an entirely different shape variation, a thinner and relatively broad form with a depressed ventral umbo (cf. text-fig. 4, V), but with internal structures identical with those of the typical *P. laevis* (cf. thin-sections of specimens P. M. O. 53529 30 (text.-fig. 2, V) and transfer series S. M. C. A. 13506). Most of these variations in external shape (Pls. II and III) appear to be entirely random in space as between district and district, and in time from one horizon to another; they thus have no real stratigraphical value. British material shows an analogous variation in external characters, again seemingly without stratigraphical significance, while to judge from published figures of specimens from the Baltic Provinces and from America, similar, great ranges of variation occur there also.

Sub-genus *Pentameroides* C. Schuchert and G. A. Cooper 1931.

Schuchert, C. and Cooper, G. A., *Amer. J. Sci.,* (5), vol. 22, 1931, p. 248.
Schuchert, C. and Cooper, G. A., "Brachiopod Genera of the Suborders Orthoidea and Pentameroidea", *Mem. Peabody Museum nat. Hist. Yale*, IV, pt. i, 1932, p. 179.
Genoholotype: *Pentamerus subrectus* Hall and Clarke, Palaeontology of New York, VIII, pt. ii, 1894, p. 238, pl. lxix, figs. 2 3, 8 10. The figured specimens came from the Niagara group of Iowa, U. S. A.

Schuchert and Cooper proposed in 1931 a new genus *Pentameroides* for specimens which externally are similar to *Pentamerus* but differ internally in the dorsal valve in that the cardinalia are united to form a sessile, or partly, or wholly, elevated cruralium. When studying internal casts such specimens can readily be distinguished from *Pentamerus s. s.* since they show a single median furrow in the dorsal valve, instead of the two in the latter genus.

The distance between the crural-plates in different species of *Pentamerus s. s.* is somewhat variable, and in the later forms in southern Norway (towards the top of zone 7 b), they may be close to one another, though never in contact. They unite, however, to form a sessile, or partly elevated cruralium in '*Pentamerus*' cf. *gotlandicus*, a species which Kiær considered to have descended from *P. laevis*. It would seem that *Pentamerus* gradually merges into *Pentameroides* through the approximation and final union of the cardinalia and until the limits of the latter form are more closely defined, the writer would prefer to regard it as a sub-genus.

Pentamerus (*Pentameroides*) cf. *gotlandicus* N. Lebedev 1892.

Plates V, figs. 7 8; VI, figs. 13, 15; text-figs. 1 and 8.

1892. *Pentamerus gotlandicus* Lebedev, N., "Obersilurische Fauna des Timan", *Mém. Com. géol. St.-Pétersb.*, vol. XII, No. 2, pp. 22, 42, Taf. II, figs. 11 a—b, 12.
1908. *Pentamerus gotlandicus* Leb. Kiær, J., "Das Obersilur im Kristianiagebiete", *Vidensk.-Selsk. Skrifter, Math.-Naturv. Kl.* (1906), II, pp. 66, 271 3, 356, 494, 500 etc.
1925. *Pentamerus gotlandicus* Leb. Munthe H., *et alii.* "Gotlands Geologi", *Sverig. geol. Unders. Afh.*, Ser. C, No. 331 (Årsbok 18: 1924), p. 19.

Material: P. M. O., specimens 21 675—79, 40 477 81, 45 380 81, 45 423 24, 66 67, 78, 80 81, 93 96, 58 560 62.
S. M. C., specimens A. 6755 58.

Types: The specimens figured by Lebedev 1892 (Taf. II, figs. 11 a b, 12). Of these, the originals of figs. 11 a—b were stated by him to be in the Museum der Akademie, of fig. 12 in the Museum des Berginstituts (Leningrad).

The original specimens came from Gotland; they are large forms, 8 10 cms long, with a high, ventral umbo and low, broad, median, ventral fold. The septum in the ventral valve apparently extended for more than half the length of the shell. The Norwegian examples were referred by Kiær to Lebedev's species and are here so described pending a re-examination of the Gotland material.

Diagnosis: Large-sized *Pentamerus*, generally subtriangular in outline. Breadth less than the length and considerably greater than the thickness. The maximum breadth is attained near the anterior margin. Profile gently biconvex. Ventral umbo moderately high; often a low, median fold in the ventral valve. A wide delthyrium, covered at its apex by a pseudodeltidium (see Pl. V, fig. 7). A long spondylium duplex, with a high, supporting septum, which in adult individuals extends at least for one-half of the length of the valve. Spondylial cavity posteriorly often Y-shaped in cross-section, anteriorly extremely narrow and with parallel walls. In the dorsal valve, high and very long cardinalia which meet to form a cruralium (Pl. V, fig. 8); this is sessile posteriorly, while anteriorly it is slightly elevated on a median septum, formed by the union of the outer-plates.

Discussion: There is insufficient material to permit of a full account of the variation in external characters, especially as most of the specimens occur as isolated valves. The species is more triangular in outline than *P. laevis*, the greatest width being attained close to the anterior margin (Pl. VI, fig. 15), but large specimens may be of an oval shape. In profile, the convexity is about the same in the two species (cf. Pl. VI, fig. 13 with fig. 16), strongly convex forms have not been seen. The median fold on the ventral valve is a late growth-feature, being most marked in the largest specimens; it may produce a slight extension at the anterior margin. There is a tendency in some individuals (P. M. O. 58 562) to form a small cardinal-area in the ventral valve, but this is not very sharply separated from the rest of the valve-surface. The dorsal valve fits

closely below the umbo of the ventral valve, almost touching the strongly concave pseudodeltidium. In the one specimen in which it has been measured, the delthyrial angle is about 70°. The antero-dorsal corners of the delthyrium are not thickened to serve as teeth, nor do there appear to be any other articulatory processes. The maximum possible movement about the hinge-line is very small, owing to the close approximation of the umbones.

Internal Characters: The internal characters readily identify this species among all other European Pentamerids. It is a thin-shelled form, while the changes in the spondylium and cardinalia that are apparent when a typical *P. borealis* is compared with *P. laevis*, reach a further expression in *P.* cf. *gotlandicus*. The spondylium is extremely long (Pl. V, fig. 7); in the few specimens of which the interior has been examined, it extends for about two-thirds of the length of the shell. The supporting septum which is thin and high (text-fig. 8), is typically duplex throughout its length. Its line of junction with the valve-wall may be traced on the exterior of specimens, from the ventral umbo usually for about two-thirds of the distance to the anterior margin. The septum itself divides above this level and continues as two ridges, one down the back of the spondylium, the other down the inner surface of the valve.

The shape of the spondylium may be seen from text-figure 8 and Plate V, fig. 7. It is at the anterior end of the delthyrium that the spondylial cavity attains its maximum breadth, a dimension that is abouth one-fifth of its length. There, the ventral part of the cavity is narrow, but dorsally the spondylial walls bend sharply outwards to conform to the edges of the delthyrium (cf. text-fig. 8, transfers 38 to 55). When the free edges of the spondylium separate at the hinge-line they gradually approach each other so that the spondylial cavity becomes narrow and parallel-sided, conditions which are maintained for the rest of its length (transfers 77 to 143). In lateral view, the dorsal edges of the spondylium appear almost straight, while the back of the spondylial cavity curves gradually forward towards the anterior part of the dorsal valve.

The detailed structure of the spondylium and septum is very well preserved in the specimens that have been sectioned, the divisions between the different shell-layers being usually more distinct than in the two previous species. The greater part of the septum and spondylium is composed of shell-material which appears to be similar

to that of the valve-wall, and it is continuous with the latter along the base of the septum. The additional, thin layer that is present in *P. borealis* and *P. laevis* is especially clear in this species (text-fig. 1, where the stippled portions indicate the layer in question). It is thickest at the back of the spondylial cavity in the posterior region, and may extend towards the valve-wall as a continuous selvage along the median plane of the duplex septum. This layer lines the whole of the delthyrial cavity, and is slightly thickened along the sides of the delthyrium. Below the apex the two sides join to form a deeply concave and rather large pseudodeltidium (text-figs. 1 and 8, transfers 18 to 30; Pl. V, fig. 7); this is demarcated by a slight furrow from the surface of the valve on either side. When the valves are in apposition, the dorsal umbo presses closely into the concavity of the pseudodeltidium (text-fig. 1, transfers 26 to 30), allowing no room for the passage of a pedicle. Towards the anterior end of the spondylium, the structure is less clear, but the inner layer appears to be present throughout and to form a thin lining to the spondylial cavity (text-fig. 1, transfer 40).

In the dorsal valve, the form of the cardinalia is very characteristic. These compose a thin-walled cruralium which is sessile posteriorly, and in some individuals for the greater part of its length, but slightly elevated anteriorly (text-fig. 8, transfers 39 143; Pl. V, fig. 8). The cruralium is closely similar in shape and size to the spondylium and its margins correspond roughly to the free edges of the latter (text-fig. 8). The structure of the cruralium is readily seen from thin-sections and transfers. It consists of three pairs of plates, inner-plates, brachial-processes and outer-plates (text-fig. 8, transfers 59 and 65), the latter unite and together with some adventitious shell-material, form the supporting septum. The structure is thus the same as that described by Schuchert and Cooper (1932, p. 164, fig. 27) as typical of *Pentameroides*. Posteriorly, the inner-plates, which are very thin throughout, are strongly convex to one another, while anteriorly they become almost parallel (Pl. V, fig. 8). Their lines of junction with the bases of the brachial-processes may be marked by a very slight flexure in the walls of the cruralium (text-fig. 8, transfer 59). The bases of the brachial-processes are similarly convex posteriorly and sub-parallel anteriorly. The sides of the cruralium change direction along the junctions of brachial-processes and outer-plates, the latter sloping sharply inwards to unite just above the

Dimensions of Typical Specimens
(in millimetres).

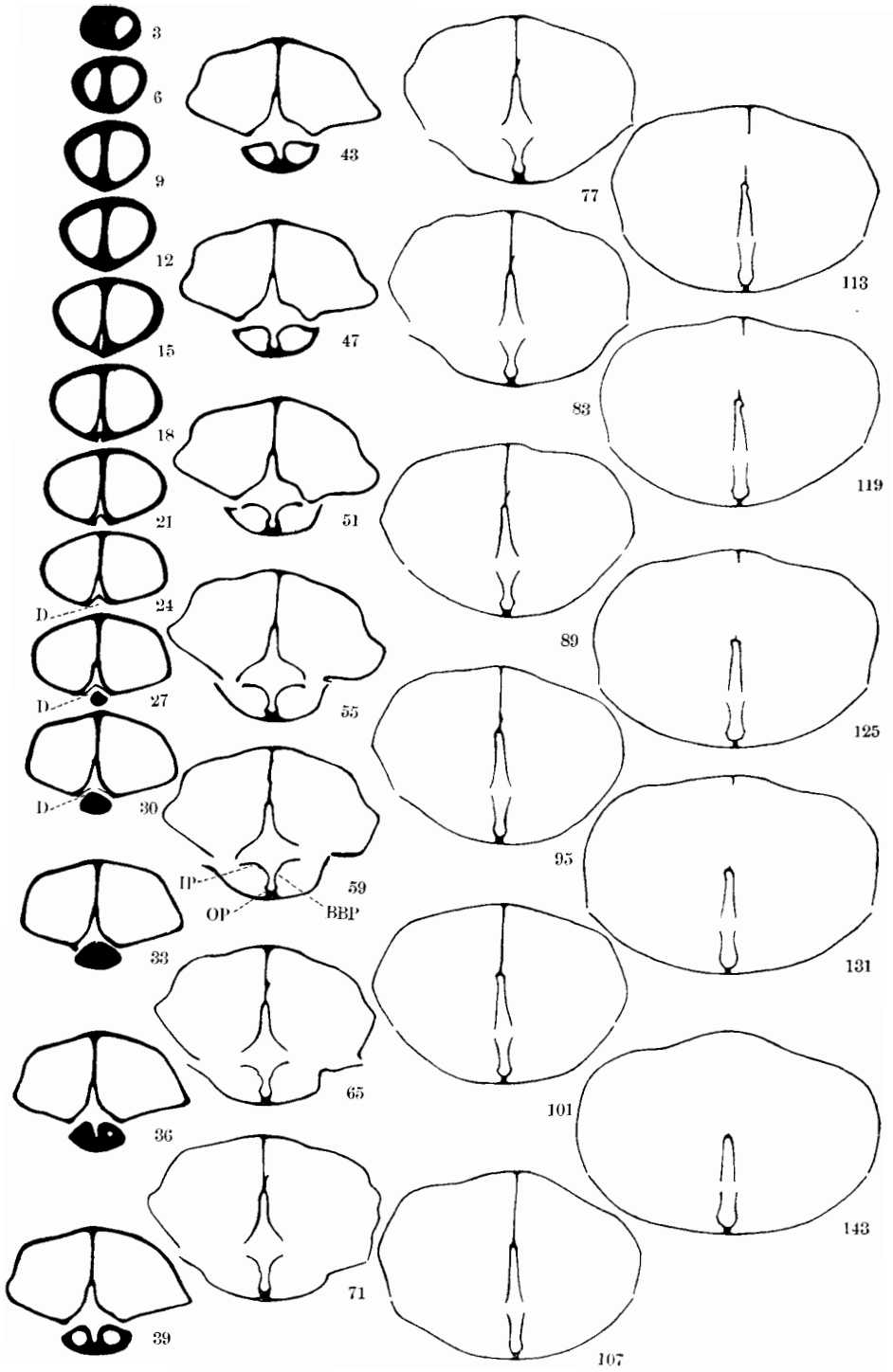
Length	Breadth	Thickness
45.5	37.4	19.1 (young specimen)
65.0	60.0	-
55.0	52.0	-
70.0	61.0	-

valve-floor (text-fig. 8). The development of the cardinalia may be traced in the earliest sections immediately below the dorsal umbo. The three-fold division is there maintained, while even as soon as they are visible embedded in the thickening of the valve-wall, the outer-plates unite just within the exterior surface of the valve (text-fig. 1, transfers 26 30).

Remarks: *Pentamerus* cf. *gotlandicus* is the latest species of *Pentamerus* to occur in southern Norway, and the end member of the morphological series traced out by Kiær in the smooth Pentamerids. It may easily be distinguished from *P. laevis*; the shape and usual large size of the valves, the long septum, spondylium and cardinalia are useful guides for rough determinations; in thin-sections, the deep and very narrow spondylial cavity and especially the presence of a cruralium are diagnostic characters (cf. text-fig. 8 with figs. 5 and 6). The pseudodeltidium appears generally to be larger than in *P. laevis*, but agrees closely in structure with that observed in a specimen of *P.* cf. *esthonus* in the British Museum, London (B. 50).

In southern Norway, *P. gotlandicus* was chosen by Kiær as a zone fossil for 7 c. It is common in the western development at Ringerike where it occurs with *S. lirata* in 7 c β, while Kiær records (1908, pp. 271 3) large individuals, that had been distorted by pressure, from horizons 7 c α γ at Skien and Porsgrund. The species is present also at Holmestrand in 7 c β, again associated with *S. lirata* (Kiær, *op. cit.*, p. 207). In the eastern development, as at Malmøy and

Text-fig. 8. *Pentamerus (Pentameroides)* cf. *gotlandicus* Lebedev.
Serial transfers (S. M. C. A. 13 507) at 0.15 mm intervals from the posterior end of a specimen; zone 7 c β, Ringerike. Natural size. Transfers 3—143.
(Cf. text-fig. 1 and Pl. V, figs. 7—8.)
BBP = bases of the brachial-processes; D = pseudodeltidium. IP = inner-plates; OP = outer-plates.


3
6
9
12
15
18
21
D
24
D
27
D
30
33
36
39
43
47
51
55
IP
OP
59
BBP
65
71
77
83
89
95
101
107
113
119
125
131
143

Text-fig. 8.

Asker it is hardly ever found, at the latter locality *P. laevis* appears to persist (in horizons 7 b β c γ) rather later than in the other districts.

In Gotland, the type area for *P. gotlandicus*, it has been recorded recently (Munthe, 1925, p. 19) from the Slite group it thus continues there rather later than *S. lirata*, its common associate. It does not appear to be known from Britain; in America species such as *P. subrectus* are generally similar in internal structure.

Genus *Holorhynchus* J. Kiær 1901.

Kiær, J., "Etage 5 i Asker ved Kristiania", *Norg. geol. Unders.* [Aarbog for 1902], No. 1, 1901, pp. 68 77, figs. 1 7 and pp. 103 9 (English trans.).

Schuchert, C. and Cooper, G. A., "Brachiopod Genera of the Suborders Orthoidea and Pentameroidea", *Mem. Peabody Museum. nat. Hist. Yale,* IV, pt. i, 1932, p. 180, pl. 27, fig. 20.

Genoholotype: *Holorhynchus giganteus* J. Kiær 1901, *op. cit. supra.*

This genus was proposed by Kiær, to include large specimens from the Lower Silurian of southern Norway, which are not unlike a transverse *Pentamerus*, but which differ internally in the possession of a free spondylium in the ventral valve. In the dorsal valve the cardinalia are of a generalized type, and free for almost their entire length.[1] Kiær's original description is quite detailed, and it is not proposed to give here a revised generic diagnosis, the new facts that have been learnt concerning the internal structures are presented under a discussion of the one species that is yet known.

Holorhynchus giganteus J. Kiær 1901.

Plate IV; Text-fig. 9.

1901. *Holorhynchus giganteus* Kiær, J., "Etage 5 i Asker ved Kristiania", *Norg. geol. Unders.* [Aarbog for 1902], No. 1, 1901, pp. 68 74, figs. 1 7.

1933. *Holorhynchus* cf. *giganteus* Kiær. Kulling, O., "Bergbyggnaden inom Björkvattnet -Virisen-området i Västerbottensfjällens centrala del", *Geol. Fören. Stockh. Förh.*, Bd. 55, pp. 242 3, Tavl. 10, figs. 1 5.

Material: P. M. O., specimens 12393 94, 12402—05, 08 09, 11, 12428 31, 34 37, 12452, 57, 12462, 66 67, 12488 91, 12505, 16656, 58, —82, 20823 24, 58604, 60021 (mostly fragmentary), from southern Norway.

[1] Not attached to the valve-floor, as Kiær thought (*op. cit.*, p. 72).

B. M. (N. H.). London, B 4214, B 4223 24, BB 143 46, (Kjerulf Collection), from southern Norway.

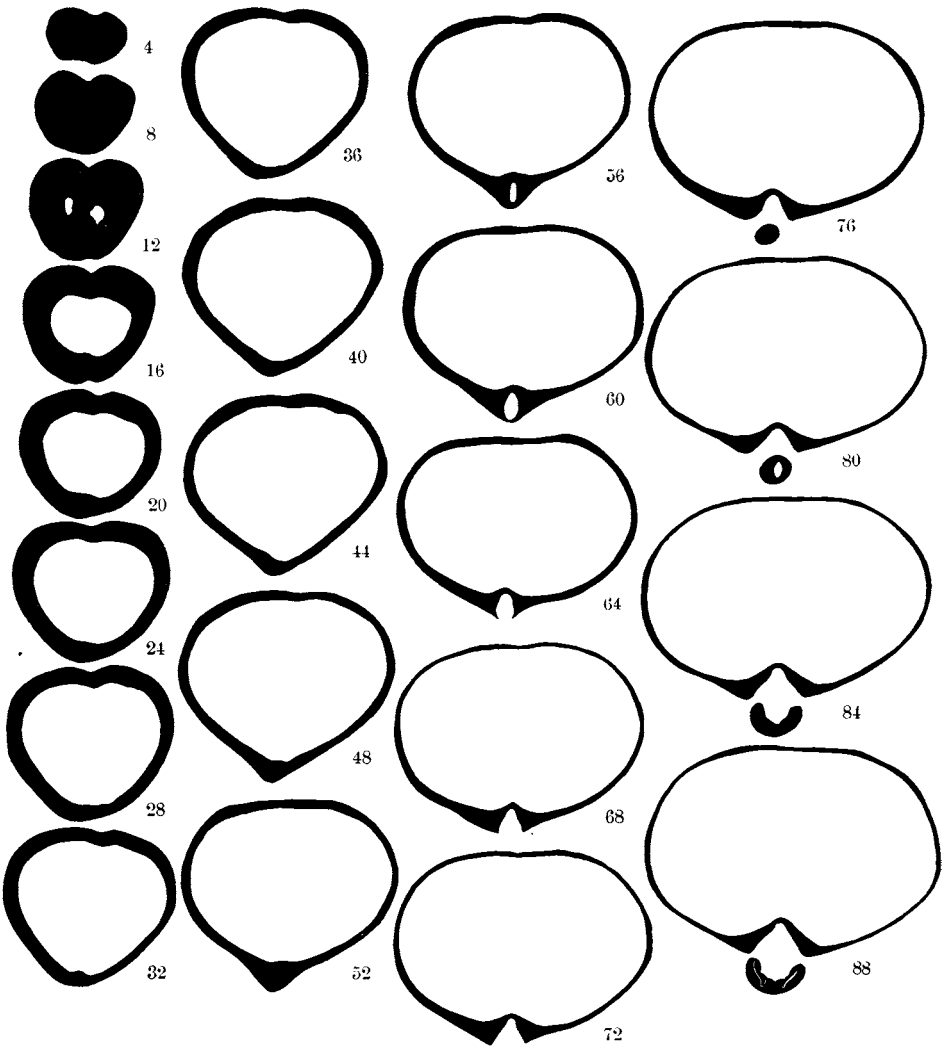
Lectotype (chosen by Dr. T. Strand in MS.): P. M. O., 12431, figured Kiær, *op. cit.*, pp. 70 71, figs. 1 3, Horizon 5 b, from Aspelund, Asker, Norway.

Kiær's original account was based on specimens mainly from the Kjerulf Collection that came from Asker and Ringerike, the only two districts in Southern Norway in which the species is known to occur. The material is preserved partly in the form of casts, partly with the shell still present, while not more than twelve specimens are reasonably complete.[1]

Diagnosis: Largely as for the genus. Outline subcircular: the breadth is rather greater than the length and about twice the maximum thickness. Profile biconvex. Ventral valve the higher, the umbo always well developed (Plate IV). Dorsal umbo low, carried forward beneath the ventral umbo, largely concealing the triangular delthyrium. Hinge-line short, nearly straight. In the ventral valve a rather large, free spondylium; the spondylial cavity is triangular in cross-section. In the dorsal valve long, slender brachial-processes which are free for the greater part of their length, also a second pair of plates inclined outwards from the processes towards the edges of the spondylium.

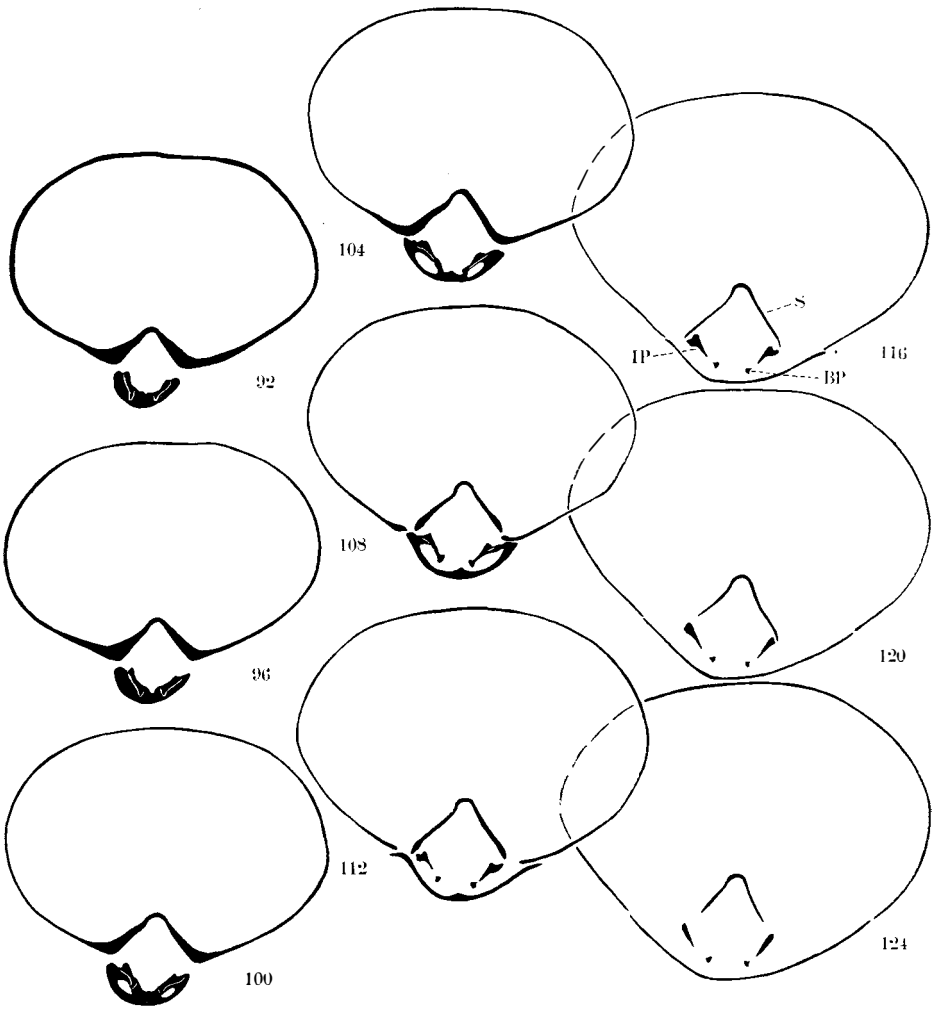
Discussion: This species was regarded by earlier authors as a large, transverse *Pentamerus* (Kjerulf, 1857, pp. 86 and 95; and 1865, p. 18), to which genus it shows a general, though superficial resemblance. Most of the specimens are of large size; the maximum breadth, which is attained about half-way from the posterior to the anterior border, usually exceeds the length. The edges of the valves curve round approximately as semicircles from the hinge-line to the anterior margin (Plate IV, figs. 1, 4). In profile, the ventral valve is generally more convex than the dorsal (Plate IV, figs. 2, 3, 5). Kiær described a narrow area occurring on each side of the delthyrium, and separated from the rest of the valve-surface by a small, raised line (1901, pp. 69, 72 and fig. 5), This feature is doubtfully present on the lectotype, but does not seem to occur of any of the other specimens.

[1] In view of the relative scarcity of the material one specimen only has been submitted to serial sectioning.



Text-fig. 9. *Holorhynchus*

Serial transfers (S. M. C. A. 13508) at 0.15 mm zone 5 b, Asker. Natural size. Transfers IP = inner-plates;



giganteus Kiær.

intervals from the posterior end of a specimen:
1 124. BP = brachial-processes;
S = spondylium.

The surface of the valves is smooth apart from occasional, slight, radiating furrows. In the ventral valve, a median furrow commencing just below the umbo is almost invariably present and frequently there is a furrow on either side. The development in the dorsal valve is generally similar. Concentric growth-lines may be prominent especially towards the anterior margin. Articulation is on the usual Pentamerid plan. The free edges of the spondylium just below the delthyrium approach the inner pair of plates in the dorsal valve, where these separate at the hinge-line (text-fig. 9, transfers 104 112).

Internal Characters: The spondylium in the ventral valve is free throughout its length (text-fig. 9, transfers 56 to 124), and there is no trace of a median septum in any of the specimens that have been examined.[1] The spondylium is thus only attached to the valve-wall along the sides of the delthyrium. A longitudinal furrow may be observed in some specimens (P. M. O. 16658) crossing the spondylial walls just below the delthyrium. This was observed by Kiær (1901, p. 72) who considered it to separate the growth-tracks of the antero-dorsal corners of the delthyrium, which functioned as 'teeth', from the rest of the spondylial walls. The latter are usually thin; they enclose a cavity which is approximately triangular in cross-section. Towards the anterior the spondylial cavity becomes less deep (transfers 150 to 170; not figured) and the walls tend to be more parallel, while the whole structure curves forward towards the dorsal valve. The thin layer lining the spondylial cavity that is present in *Pentamerus*, appears also to occur in *Holorhynchus*, though the structure is usually not so clear, and the layer is less sharply separated from the rest of the shell-material. A pseudodeltidium has never been observed, the sides of the delthyrium converging just below the umbo (text-fig. 9, transfers 60 to 64). The spondylium retains no trace of a duplex character, for the walls unite at the back of the spondylial cavity, without any indication of a median suture.

In the dorsal valve the cardinalia consist of two pairs of plates (text-fig. 9, transfers 104 124); a central pair in the form of long, slender rods, which constitute the brachial-processes ('crura'), and

[1] Text-fig. 9, transfer 12, does not represent a rudimentary median septum, but rather the slight infolding of the valve-wall, corresponding to the shallow, external furrow.

a second pair which posteriorly are in contact with the brachial-processes and which are directed towards the free edges of the spondylium. It is proposed to call this second pair of plates the inner-plates, without regard to their function. The development of the brachial-processes and inner-plates may be traced just below the dorsal umbo, where these structures are embedded in supplementary thickening (text-fig. 9, transfers 88 to 100). Two small cavities are present posteriorly between the inner-plates and the valve-wall (transfers 100 to 104); the brachial-processes and inner-plates then separate from the valve-wall (transfers 108 to 112) and continue anteriorly as free structures. They may at the same time separate from one another (transfer 112), or continue for a short distance in contact. The brachial-processes consist of flattened rods inclined inwards, and having a small projection towards the inner-plates. They continue as far anteriorly as the end of the spondylium,[1] a distance of some 15 mm from the dorsal umbo, while they diverge slightly from one another.[2] The inner plates maintain an approximately constant inclination to each other, of rather less than a right-angle. Anteriorly, they decrease in size and in the specimen that has been sectioned, they extend to only half the length of the brachial-processes.

The shell of *H. giganteus* is frequently very thick in the posterior region (text-fig. 9, transfers 1 to 32); near the ventral umbo it may attain as much as 6 mm in thickness, while it gradually thins away towards the anterior. The shell-material is seen from transfers to be coarsely prismatic in structure. The whole of the interior of the posterior portion of the shell, particularly of the ventral valve is covered with irregular pits or depressions. This feature may extend as far as half-way towards the anterior margin; it causes a very characteristic roughened surface on internal casts (specimens P. M. O. 12393, 12457; B. M. (N. H.) BB 124 5). Anteriorly, the rugosities often join together to form small, irregular ridges. The pits are of the same character as those formed by the ligamentous ties, which fix the genital glands to the valve-wall, in living brachiopods. In the

[1] In the series of transfers represented in text-fig. 9, the brachial-processes continue as far as transfer 170, the inner-plates as far as transfer 134.

[2] The "sloping, rising, longitudinal rib" mentioned by Kiær (1901, pp. 72, 106) as occurring on the "crural plates", is formed by the slight extension of the brachial processes from the plane of the inner-plates towards the centre of the valve.

Dimensions of Typical Specimens
(in millimetres).

Length	Breadth	Thickness
66.5	75.0	38.6 (Lectotype).
64.5	66.2	34.8
62.2	70.3	40.5
66.0	74.0	-
78.0	98.0	-
67.0	83.2	46.3
40.9	44.4	24.4

dorsal valve, faint, elongated, striated impressions as of muscles may sometimes be seen a short distance below the umbo.

Description of Lectotype: The lectotype, P. M. O. 12431 (Plate IV, figs. 1 3) is a well preserved specimen of average size, in which the shell-substance is present. The dorsal umbo is incurved beneath the ventral umbo; the hinge-line is short and nearly straight. The outline is sub-oval; in profile, the ventral valve is slightly the more convex. There is in each valve a shallow, median furrow with a lateral furrow on either side. Concentric growth-lines are prominent towards the anterior margin.

Remarks: *Holorhynchus giganteus* may be identified externally by its smooth, large shell, of sub-oval outline, with the occasional radiating furrows, while internally the absence of a median septum and the form of the cardinalia are characteristic. The possession of a free spondylium is a feature which it shares among Pentamerids only with *Cymbidium* Kirk. In that genus, too, there is no direct evidence that the spondylium had previously been sessile. In *Holorhynchus*, Kiær evidently considered that the septum had been secondarily lost (1901, pp. 77, 109), and he suggested that the development of the unusually thick shell in the posterior of the ventral valve, was a complementary effect which might, for example, afford a more rigid attachment for the spondylium at its junction with the valve-wall, along the margin of the delthyrium.

In the dorsal valve the cardinalia are of the greatest interest; these have but little, apparent relationship to the cardinalia of a *Pentamerus*, but are much more closely allied to the structures in the dorsal valve of species of *Stricklandia* (cf. text-fig. 9 with figs. 20 to 21). The common Norwegian *Stricklandias, S. lens* and *S. lirata*

have very short, ventral, median septa, while the prominence of the genital markings is another point of resemblance between the two genera, as Kiær noticed (1901, pp. 76, 108). Their relationships have been discussed at greater length in the morphological section.

Kiær recorded *Holorhynchus* from zone 5 b at Sandvika, Asker, the locality which has yielded most of the material in his collection, and also from Vestre Svartøy, Ringerike, at the same horizon. Outside Norway the genus has as yet been reported only from Northern Sweden (Kulling, 1933).

Genus *Conchidium* W. Hisinger 1799.

[ex C. Linnaeus 1768].

Linnaeus, C., Systema Natura, Ed. XII, Tom. III, 1768, p. 163. [Usage not binominal, cf. pp. 259 260 of present paper.]

Hisinger, W., "Minerographiske anmärkningar öfver Gottland", *K. svenska Vetensk. Akad. Handl.*, Tom. XIX for 1798 (1799), p. 285.

Wahlenberg, G., "Petrificata Telluris Svecanae examinata", *Nova Acta Soc. Sci. Upsal.*, VIII, 1821 (1819), p. 67 [*nomen nudum*].

Oehlert, D. P., in P. H. Fischer's "Manuel de Conchyliologie", 1887, p.1311

Hall, J. and Clarke, J. M., Palaeontology of New York, VIII, pt. ii, 1894, pp. 231 5.

Schuchert, C. and Cooper, G. A., "Brachiopod Genera of the Suborders Orthoidea and Pentameroidea", *Mem. Peabody Museum nat. Hist. Yale*, IV, pt. i, 1932, pp. 181 3.

Synonyms: *Gypidia* Dalman, J. W., *K. svenska Vetensk. Akad. Handl.* (for 1827), 1828, pp. 125, Taf. IV, figs. 1 a g.
[?] *Pentamerus* Pander, C. H., *partim.* [*non Pentamerus* J. Sow. 1813], Beitr. Geogn. Russ. Reiches, 1830, p. 94.
[?] *Antirhynchonella* Quenstedt, F. A. von, Petref. Deutsch, Vol. II, p. 231 (1869).
Pentamerus Caldwell, F. E. S. [*non Pentamerus* J. Sow. 1813; *non Pentamerus* C. H. Pander 1830], *Abstr. geol. Soc. Lond.,* No. 1315, 1936, p. 116.

Genoholotype: *Conchidium bilocularis* W. Hisinger 1799 [ex Linnaeus 1768], *K. svenska Vetensk. Akad. Handl.*, XIX for 1798, p. 285. The specimen figured by Linnaeus (Museum Tessinianum 1753, Tab. V, figs. 8 A and B), has the greatest value as a type.

Generic Description: (Partly after Schuchert and Cooper, 1932). Sub-oval to sub-triangular, multicostate Pentamerids, rather strongly biconvex. Hinge-line short. Ventral valve always the higher,

with a prominent umbo. Umbones often incurved, the ventral arched forward over the dorsal. A concave pseudodeltidium covering the apex of the delthyrium, is present in the type species (cf. Schuchert and Cooper, 1932, pp. 181 2). A long and rather narrow spondylium in the ventral valve, supported on an extremely long, duplex septum.

The cardinalia in the dorsal valve, seem to show the usual tripartite division into inner-plates, brachial-processes and outer-plates, but the division between the two last may be indistinct. Brachial-processes very long, extending beyond the inner-plates and outer-plates to about the same length as the spondylium. Dentition simple, similar to *Pentamerus*.

European Species:

Pentamerus bashkiricus E. de Verneuil 1845.
Anomia (Conchidium) biloculoris W. Hisinger 1799 [ex Linnaeus 1768].
Synonyms: *Anomites conchidium* G. Wahlenberg 1819.
Gypidia conchidium J. W. Dalman 1828.

Pentamerus hercynicus A. Halfar 1879. (Short septate form.)
Pentamerus (Gypidia) karpinskii T. N. Tschernyschew (= Chernuishev) 1893.
Pentamerus knightii J. Sowerby 1813.
Conchidium münsteri new species [J. Kiær MS.].
Pentamerus pseudoknighti T. N. Tschernyschew (= Chernuishev) 1893.
Pentamerus rossicus A. P. Karpinsky 1893 [?].
Pentamerus sculptus[1] N. P. Angelin and G. Lindström 1880.
Pentamerus tenuistriatus[1] N. P. Angelin and G. Lindström 1880.
Pentamerus vogulicus E. de Verneuil 1845.

[?] *Pentamerus aylesfordii* J. Sowerby 1813 (?Synonym of *P. knightii*).
[?] *Pentamerus firmus* J. Barrande 1879.

Of the European species referable to *Conchidium, C. münsteri* Kiær MS. is a *nomen nudum* and is described for the first time in the present paper. *Pentamerus pseudoknighti* Tschern., it would seem from Tschernyschew's figures may only be a small, incurved variety of *P. vogulicus* de Vern. *P. aylesfordii* J. Sow. is generally regarded as a synonym of *P. knightii* J. Sow. The fourteen species described by Pander (1830, pp. 92 5, pls. ix x) under the generic name

[1] These two species are mentioned by name only in Lindström 1861 pp. 365, 380.

Pentamerus, cannot belong to that genus. Being ribbed forms, it might be thought that they were species of *Conchidium*, but to judge from Pander's figures it is very doubtful whether they should be considered as Pentameracea at all, and some at least are probably more correctly referred to Lahusen's genus *Lycophoria.*

Conchidium münsteri new species [Kiær MS.].

Plates V, figs. 9 and 11; VI, figs. 10 11; Text-figs. 7 and 10.

1897. *Pentamerus münsteri* Kiær, J., "Faunistische Übersicht der Etage 5 des norwegischen Silursystems", *Vidensk. Selsk. Skrifter, Math.-Naturv. Kl.* (1897), No. 3, pp. 7, 30, 32, 76 [*nomen nudum*].

1901. *Conchidium münsteri* Kiær, J., "Etage 5 i Asker ved Kristiania", *Norg. geol. Unders.*, Aarbog for 1902, No. 1, 1901, pp. 80, 110 [*nomen nudum*].

Material: P. M. O., specimens 15132 42, 16644 52, 16665—74, 20821 (Kiær Collection), all from Vestre Svartøy, Ringerike, southern Norway.

Holotype: specimen P. M. O., 20821 a, cf. Pl. VI, fig. 11 from zone 5 b, Vestre Svartøy, Ringerike, southern Norway.

Paratypes: specimens P. M. O., 20821 b, c (originally from the same block as the holotype), cf. Pl. VI, fig. 10.

Topotypes: the remainder of the material as listed above.

The name *Conchidium münsteri* was twice mentioned by Kiær, when discussing the fauna of zone 5 b, but the species has never been described or figured. The specimens in the Kiær Collection occur as broken and isolated shells in a hard limestone matrix and are all ventral valves.

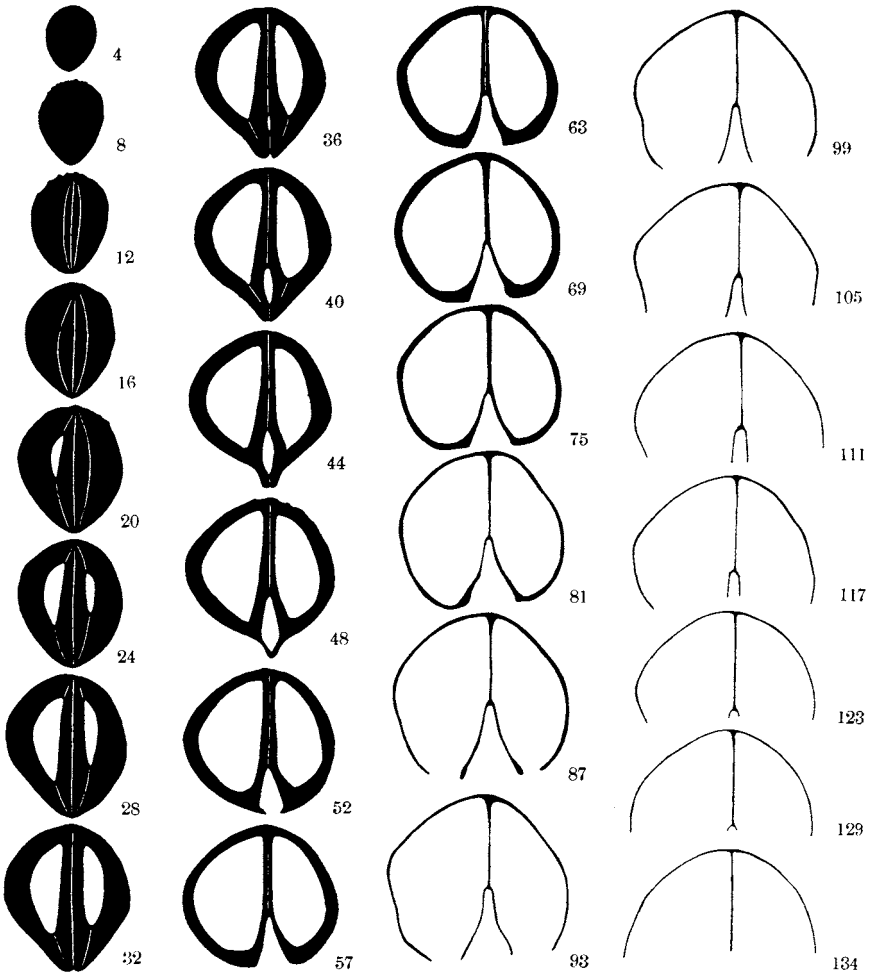
Diagnosis: Small *Conchidium* with a rather convex, ventral valve and moderately incurved umbo (Pl. VI, figs, 10 11). Outline sub-triangular, the greatest breadth is attained towards the anterior margin. Valve-surfaces with numerous small, radiating costae. In the ventral valve a large delthyrium of which the antero-dorsal corners are slightly expanded to serve as teeth. A long and deep spondylium, narrowing rapidly anteriorly to the delthyrium, supported on a thin, high, duplex, median septum, which extends beyond the spondylium almost to the anterior margin of the valve.

Discussion: The relative dimensions may only be estimated approximately since the dorsal valve is unknown. The species is rather elongate in outline, particularly so in young specimens. The

maximum length was probably considerably greater than both the breadth and the thickness. The ventral umbo is somewhat flattened and appears to have been only slightly higher than the dorsal. The surface of the ventral valve is folded into fine costae, most of which commence near the umbo (Pl. VI, fig. 10), but occasional new costae arise by bifurcation. 8 to 10 costae occur to the centimetre, and about 30 may be present round the anterior margin. The valve-surface is usually smooth below the umbo and also along the lateral margins. Concentric growth-ridges may be present. The shell-wall is thickened towards the posterior, but anteriorly is very thin.

Internal Characters: The species shows a typical development of the long spondylium and very long septum that characterize the genus (Pl. V, figs. 9, 11). The septum may frequently be observed on the exterior of specimens, extending almost to the anterior margin. It has been traced by serial sections as in the case of *Pentamerus*, to the extreme posterior end of the valve, where it is embedded in the thickened valve-walls (text-fig. 10, transfers 8 to 24). Soon after it separates as a discrete structure, it divides to enclose the spondylial cavity below the umbo (transfers 36 to 57). The septum becomes higher and less thick towards the anterior, and for the greater part of its length is relatively thin (transfers 75 to beyond 150). Its duplex character is clearly maintained throughout its length. The spondylium decreases rapidly in size below the hinge-line (Pl. V, figs. 9, 11); posteriorly the spondylial cavity is rather acutely triangular in section (text-fig. 10, transfers 69 to 93), anteriorly, the walls may become parallel-sided. Where the edges of the spondylium first separate from the valve-wall (transfers 87), they are thickened to serve as teeth.

The thin layer within the spondylial cavity that has been observed in *P. laevis* and *P.* cf. *gotlandicus* is present also in this species of *Conchidium*. In specimen A. 13509 it can be seen in transfers 36 to 50 (cf. text-fig. 7, II) lining the apex of the delthyrial cavity; it may have a slight extension along the plane of the median septum. It decreases in thickness anteriorly and has not been definitely seen much below the hinge-line. In the few specimens that have been sectioned a pseudodeltidium is not present nor is the covering layer thickened along the delthyrial margins (as in *P. laevis* and *P. gotlandicus*), as would probably have been the case, had such a structure existed in life.



Text-fig. 10 *Conchidium münsteri* new species.

Serial transfers (S. M. C. A. 13509) at 0.125 mm intervals from the posterior end of a specimen; zone 5 b, Ringerike. × 1⅓. Transfers 4—134.
(Cf. text fig. 7 and Pl. V, figs. 9, 11).

Dimensions (in millimetres).

Length	Breadth	
24.8	22.9	(present dimensions of holotype)
25.0	22.0	Paratype 20 821 b
18.0	20.0	Paratype 20 821 c

Description of Holotype: The holotype, P. M. O. 20821a (Pl. VI, fig. 11) is the ventral valve of a specimen of average size, which is broken near the anterior margin almost at the end of the septum. The triangular delthyrium is clearly seen.

Remarks: This species, known only from zone 5 b in southern Norway, is the earlist *Conchidium* at present recognized; all the American forms as well as those from the Baltic States, belong to the Upper Silurian. Although it is separated in time from the other species of this genus by the whole of the Llandovery period, *C. münsteri* possesses the typical, long septum and spondylium of the later forms. It appears to be most closely allied to *C. bilocularis*, the type species from which it differs in its rather less triangular outline, in its lower and more incurved ventral umbo, and its finer costae.

Genus *Clorinda* J. Barrande 1879.

Barrande, J., "Systême Silurien du Centre de la Bohême", Vol. V, 1879, p. 109.

Hall, J. and Clarke, J. M., Palaeontology of New York, Vol. VIII, pt. ii, 1894, pp. 241, 245.

Kozlowski, R., "Les Brachiopodes Gothlandiens de la Podolie Polonaise", *Palaeont. polon.*, I, 1929, pp. 137 9.

Schuchert, C. and Cooper, G. A., "Brachiopod Genera of the Suborders Orthoidea and Pentameroidea", *Mem. Peabody Museum nat. Hist. Yale*, IV, pt. i, 1932, pp. 171 2.

Synonym: *Barrandina* Booker, F. W., *J. roy. Soc. N. S. W.*, vol. 60, 1926 (1927), p. 131.

Genoholotype: *Clorinda armata* J. Barrande, Syst. Sil. Bohême, vol. V. 1879, p. 109, pl. 119, figs. 1 4.

Generic Description: Barrande's original account is quoted in full:

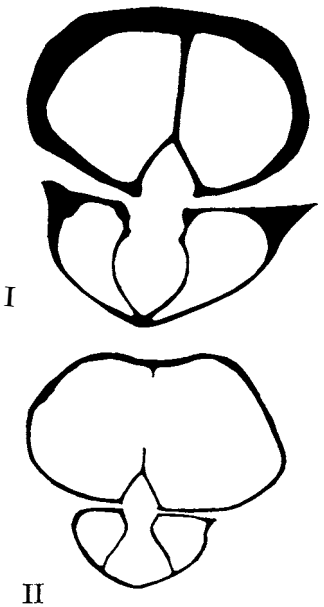
> "*Clorinda* Barr., Pl. 119 [of Syst. Sil. Bohême] reproduit par sa forme extérieure les apparences bien connues de *Pentam.*

linguifer Sow. Cette ressemblance est si trompeuse, que nous avons pendant longtemps rénui ces Brachiopodes sous les mêmes noms générique et spécifique. Mais, tandisque *Pentam. linguifer* figuré sur nos. Pl. 22 24. . . . . nous montre distinctement les cloisons et compartiments internes, charactéristiques de ce genre, *Clorinda* Pl. 119 est représentée par une série de spécimens, dont le moule interne offre une structure entièrement différente. Cette structure ne se retrouvant à notre connaissance, dans aucun autre Brachiopode figuré jusqu'à ce jour, nous avons cru devoir la considérer comme justifiant l'établissement du nouveau genre *Clorinda*.

Nous ferons remarquer, que les moules internes figurés sont composés de silice, qui s'est substituée au corps du mollusque. Par suite probable de la différence d'âge, ces spécimens, conservant les mêmes dispositions typiques, offrent cependant entre eux de notables différences individuelles. Dans tous, on reconnaît une partition médiane sous la forme d'un angle, compris entre des arêtes saillantes, dont le sommet est placé au crochet de la valve ventrale. La structure de la valve dorsale nous est inconnue.

Au type *Clorinda armata*, trouvé dans nos bandes f 2 g 1, nous adjoignons, avec quelque hésitation, une autre forme reproduisant aussi extérieurement celle de *Pentam. linguifer* et analogue au type *Clorinda* par les apparences moins prononcées de son moule interne. Nous la nommons *Clorinda ancillans* et elle est figurée sur la même pl. 119. Elle provient de notre bande e 2."

Barrande's figures (*op. cit.*, pl. 119, figs. 1 4) show four specimens from Hlubočep, horizon gl. There appears to be a short, median septum in the ventral valve, while in the only direct view (fig. 4 c) of a dorsal valve, the structure is not very clear. Externally, the specimens bear a close resemblance to *Barrandella linguifera* (J. de C. Sow.) 1839, the genotype of *Barrandella* Hall and Clarke, 1894 (p. 241). This latter genus has been considered a synonym of *Clorinda*, but more recently the name has been revived by Kozlowski (1929) and Schuchert and Cooper (1932). Kozlowski's detailed treatment (1929, pp. 127 9) of the Polish species *Clorinda pseudolinguifera* Koz. 1929, shows this to have a different arrangement of the brachial-processes in the dorsal valve from that in *Barrandella linguifera* (J. de C. Sow.) 1839, justifying their generic separation. After Schuchert and Cooper 1932, *Barrandella* and *Clorinda* are here regarded as distinct genera, rather than as genus and subgenus (as Kozlowski), because in each genus the structures in the



Text-fig. 11.

Transverse sections of (I) *Barrandella linguifera* (J. de C. Sow.) S.M.C.A.13521 × 5, and (II) *Clorinda undata* (J. de C. Sow.) S.M.C.A.13512, × 3.

dorsal valve have the same value in taxonomy there being nothing yet to show that either genus is descended from the other.

The two genera are generally similar in external form, and in the structures of the ventral valve, but the characteristic distinguishing feature is the dorsal interior. In *Clorinda* the dorsal septa are subparallel or divergent as they approach the valve-floor, while in *Barrandella* they are always markedly convergent, uniting to form an almost sessile cruralium (text-fig. 11). With regard to this difference the one *caveat* must be entered that the genoholotype of *Clorinda* is *C. armata* Barrande, a species in which Barrande stated (cf. the quotation above) that the structure of the dorsal valve was unknown. Should this species be found to have convergent cardinalia, *Barrandella* would become a synonym of *Clorinda* and a new generic name would be required for species with dorsal, internal structures of the type of *Clorinda pseudolinguifera* Koz. 1929.[1]

[1] Kozlowski (1929, p. 139, footnote 1) also states that the internal structures of *C. armata* Barr. and *C. ancillans* Barr. are unknown. His argument that they are probably as in *C. pseudolinguifera* Koz., because of their close external similarity to the specimens determined by Barrande as *Pentamerus linguifera* (and really *C. pseudolinguifera*) loses much of its force because of the marked similarity between *Pentamerus (Barrandella) linguifera* and *C. pseudolinguifera* themselves. Thus, the originals of Barrande's figs. 9 and 10 (*op. cit.* pl. 119), evidently possess two descrete septa in the dorsal valve (figs. 10 c and 10 e), and hence should be, apparently, *C. pseudolinguifera* rather than *B. linguifera* as he identified them. The species *Clorinda armata* is unrepresented in the collections of the British Museum (Natural History), London, and the Sedgwick Museum, Cambridge, and no specimens have been available to the present writer.

European Species:

Clorinda ancillans J. Barrande 1879.
Clorinda armata J. Barrande 1879.
Atrypa globosa J. de C. Sowerby 1839.
Clorinda groenlandica C. Poulsen 1934.
Barrandella kjerul J. Kiær 1901.
Clorinda malmøyensis new species.
Clorinda pseudolinguifera R. Kozlowski 1929.
Atrypa undata J. de C. Sowerby 1839.
[?] *Pentamerus bubo* J. Barrande 1847 (?synonym of *C. undata*).
[?] *Pentamerus krasnopolskii* T. N. Tschernyschew (= Chernuishev) 1893 (?synonym of *C. undata*).
[?] *Pentamerus sublinguifer* F. Maurer 1885 (*teste* Leidhold 1928).

Examination of the common Norwegian forms, "*Barrandella*" *kjerulfi* Kiær and "*Barrandella*" *undata* (J. de C. Sowerby), shows that they should more properly be referred to *Clorinda*. The last species and the closed allied "*Atrypa globosa*" J. de C. Sowerby, are also of widespread occurrence in Britain.

Clorinda kjerulfi (J. Kiær) 1901.

Plates VII, figs. 1 6. VIII, figs. 1 3; Text-figs. 12 and 13.

1901. *Barrandella kjerul* Kiær, J., "Etage 5 i Asker ved Kristiania", *Norg. geol. Unders.* [Aarbog for 1902], No. 1, 1901, pp. 63 8, figs. 1 7 on p. 64, and pp. 100 3, (English Summary).

Material: P. M. O., specimens 12545 51, 79, 83, 85 89, 12595 606, 12613 20, 26, 50, 53, 12673 90, 20508, 40466.

Lectotype (chosen by Dr. T. Strand in MS.): specimen P. M. O. 12598, figured Kiær, *op. cit.*, p. 64, figs. 1 4, from zone 5 b, south of Halden, Asker, southern Norway. Cf. Pl. VII, figs. 1, 4; text-fig. 12, I.

Paratypes: Specimens P. M. O. 12595 97, 12599 606, from the same horizon and locality, 40466 from zone 5 b, Jørgensløkken, Asker. Specimens 12595 and 40466 were figured by Kiær, *op. cit.*, p. 64, figs. 7 and 5 6 respectively. Cf. also Pl. VII, figs. 2, 3, 5, 6.

Diagnosis: Small, rather transverse *Clorinda* with the ventral umbo usually only slightly higher than the dorsal. Hinge-line, short, curved. Low, median, dorsal fold and ill-defined, ventral sinus. Valve-surfaces folded into a few, small, radiating costae which are mainly

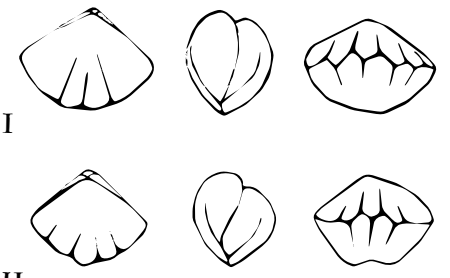
developed on the anterior half of the shell. In the ventral valve, a triangular delthyrium and small spondylium supported on a thin, very short, duplex septum. Spondylial cavity shallow. In the dorsal valve the cardinalia are slightly divergent, the carinae at the junction of the inner-plates with the brachial-processes are indistinct or absent. Brachial-processes lamellar.

Discussion: The dimension of breadth is commonly a little greater than the length and considerably greater than the thickness. The maximum breadth is attained about half-way towards the anterior margin, producing a sub-rhombic outline. Kiær (1901, pp. 65, 100) recognized two distinct forms a broad *e. g.* the lectotype; Pl. VII, figs. 1, 4), and a narrow form (*e. g.* paratype 40466, Pl. VII, figs. 3, 6). The differences may readily be appreciated by referring to the table of dimensions. The extreme types are connected by many intermediates, and have been proved by serial-sectioning to have precisely the same internal structure.

The ventral valve is generally more convex and a little higher than the dorsal valve. The ventral umbo is seldom prominent, it is usually slightly curved forwards, close to the dorsal umbo (Pl. VII, figs. 1 6). In a few individuals the umbones are of about the same height. There is no well-defined cardinal-area. The dorsal valve has a definite, but small median fold. This commences a little below the umbo and increases in width anteriorly; similarly in the ventral valve there is a shallow median sinus which projects as a slight tongue into the dorsal fold at the anterior margin (text-fig. 12). The anterior portion of the shell is folded into small, rounded, radiating costae, of which two to five may be present on either side of the fold and sinus. These are best developed in large specimens, but vary considerably in prominence and are sometimes indistinct or absent. The ventral sinus is usually divided by a small costa, while a very shallow furrow commonly bisects the dorsal fold.

Articulation takes place between the thickened margins of the spondylium just below the corners of the delthyrium and the inner-plates in the dorsal valve (text-fig. 13, transfers 26 to 30). There is usually a much closer fit between the two structures than in species of *Pentamerus*.

Internal Characters: The outline of the delthyrium is approximately that of an equilateral triangle (Pl. VIII, fig. 1). The dental-plates join the valve-wall along the margins of the delthyrium



Text-fig. 12.
Clorinda kjerulfi (Kiær).

Outline drawings of the dorsal, right-lateral and anterior views of (I) the lectotype P. M. O. 12598 and (II) paratype P. M. O. 12599 a. Natural size.

and continue anteriorly to form a short spondylium. At the level at which they separate from the hinge-line the spondylial walls meet almost at right-angles (text-fig. 13, transfers 22 to 30) and the spondylial cavity in thus relatively broad and shallow: towards the anterior it becomes very small as the edges of the spondylium approach each other (text-fig. 13, transfers 38 to 50; Pl. VIII, fig. 1). The spondylium may extend for a little more than a third of the distance from the umbo to the anterior margin. The supporting septum is very short, it usually ends before the spondylial walls separate from the hinge-line (text-fig. 13, transfers 16 to 18). In specimen P. M. O. 12673, it extended for rather less than 2 mm below the umbo, so that the spondylium is free for the greater part of its length.

The duplex character of the septum is never so distinctly marked as in the species of *Pentamerus*. It is clearest at the posterior margin where the septum is still embedded in the shell-material of the valve-wall, anteriorly it may be quite lost. A thin layer lining the spondylial cavity does not appear to occur in this species, or at least is not clearly separable from the rest of the shell-material. A pseudodeltidium has never been observed.

The cardinalia in the dorsal valve are divergent, as is usual in *Clorinda*. The junctions between the different plates are usually indistinct in thin sections; thus, in the specimens that have been serial-sectioned no division can be observed between the outer-plates and the bases of the brachial-processes. The inner-plates, however, may be seen sharply inclined outwards from the latter towards the margins of the spondylium (text-fig. 13, transfers 28 to 34). The brachial-processes (= 'crura') separate relatively early (transfers 30 to 32) from the valve-wall and continue for a long distance beyond the end of the inner-plates (transfers 36 to 54), often exceeding the length of the spondylium. The brachial-processes are in the form of flattened

Dimensions of Typical Specimens
(in millimetres).

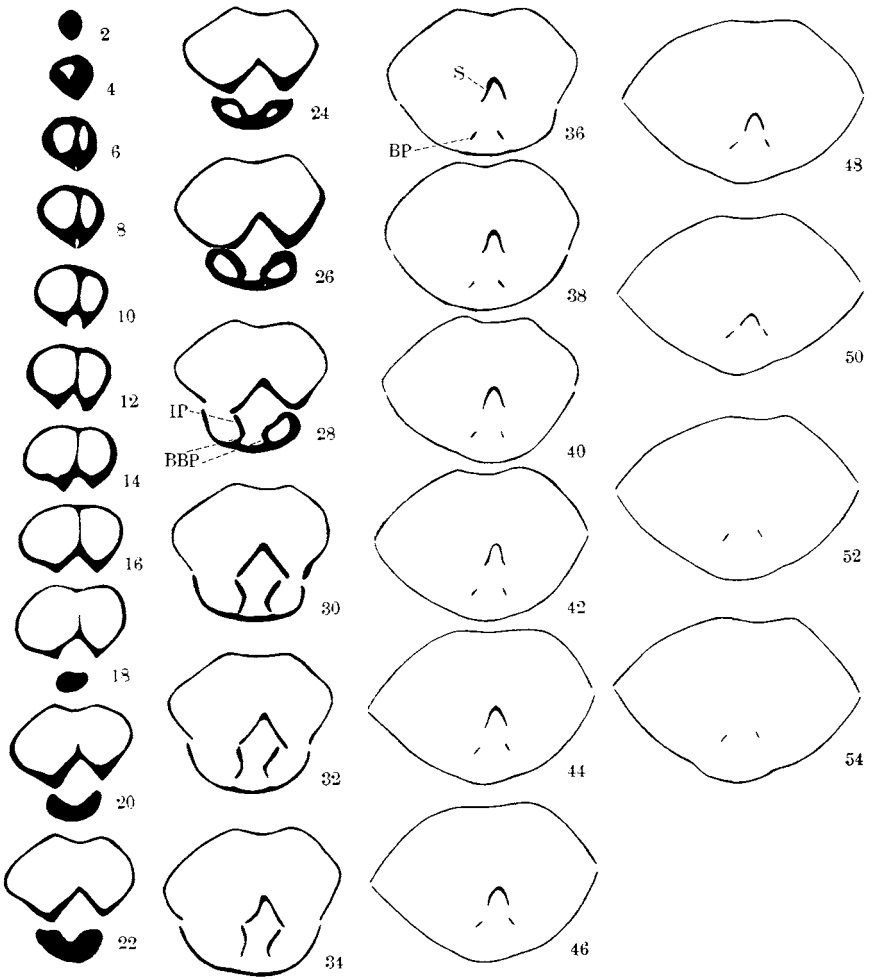
Length	Breadth	Thickness
12.8	16.8	11.3 (Lectotype)
8.3	9.1	6.0 (Paratype)
10.3	9.6	8.4 (Paratype)
9.7	12.3	6.7
14.1	18.0	11.0
16.6	16.3	11.1
11.6	13.9	11.0
10.4	9.6	8.8
12.0	11.0	7.4
20.0	21.5	-

rods, or narrow lamellae; they are sub-parallel, with their axes inclined inwards to one another.

Description of Types: The lectotype (Pl. VII, figs. 1, 4) is a rather large specimen of the broad variety. It is sub-rhombic in outline, the ventral valve is slightly the more convex, and the ventral umbo rather low. On each side of the median fold and sinus, which are clearly developed, two to three costae are present. The paratypes (Pl. VII, figs. 2, 3, 5, 6) include specimens of both broad and narrow shape variations.

Remarks: *Clorinda kjerulfi* differs from most other species of *Clorinda* in the presence of small costae on the anterior portion of the shell. These are always few in number and rather resemble the similar feature in certain species of *Gypidula* (*i. e. G. galeata*). The dorsal fold is often somewhat sharply delimited as in *C. pseudolinguifera,* though it never attains the proportions reached in that species. The small carina at the junction of the inner-plates with the bases of the brachial-processes, which has been described by Kozlowski in *C. pseudolinguifera*, and by Booker in certain Australian species perhaps to be referred to the same genus, is seldom well developed in *C. kjerulfi.* Kiær (1901, pp. 66, 102) considered that *C. kjerulfi* was most closely related to '*Barrandella*' *areyi* Hall and Clarke from the Clinton Group, U. S. A., a form of which the internal structure is unknown.

All the material in the Collection is from zone 5 b at various localities in the Asker district, the only area from which the species is recorded. The details of its distribution have been discussed by Kiær (1901, pp. 28—31).



Text-fig. 13. *Clorinda kjerulfi* (Kiær).

Serial transfers (S. M. C. A. 13510) at 0.125 mm intervals from the posterior end of a specimen; zone 5 b, Asker. Transfers 2–54. × 2. (Cf. Pl. VIII, figs. 1, 2 and 3).
BBP × bases for the brachial-processes; BP = brachial processes;
IP = inner-plates; S = spondylium.

Clorinda undata (J. de C. Sowerby) 1839.

Plates VI, figs. 1—9; VII, figs. 13 15; VIII, figs. 4 7;
Text-figs. 14 16.

1839. *Atrypa undata* Sowerby, J. de C., in Murchison's "Silurian System", p. 637, pl. 21, fig. 2.

1867. *Pentamerus undatus* (J. de C. Sow.). Davidson, T., "British Fossil Brachiopoda", *Palaeontogr. Soc. Lond.* [*Monogr.*], III, pt. vii, pp. 155 6, pl. xix, figs. 4 9 (with Bibliography). *Idem*, V, pt. ii (1883), pp. 162, pl. ix, figs. 10 20.

1908. *Barrandella undata* (J. de C. Sow.). Kiær, J., "Das Obersilur im Kristianiagebiete", *Vidensk. Selsk. Skrifter, Math.-Naturv. Kl.* (1906), II, *passim*.

[?] Synonyms. *Pentamerus bubo* Barrande, J., *Naturw. Abhandl.* (Haidinger), I, 1847, 472—4, pl. xxii, figs. 2a- d.

Pentamerus krasnopolskii Tschernyschew (= Chernuishev), T. N., "Die Fauna des unteren Devon am Ostabhange des Ural", *Mém. Com. géol. St.-Pétersb.*, vol. IV, No. 3, p. 79, Tab. XIII, figs. 1 4.

Material: P. M. O. specimens 20858 60, 63 65, 67, 69 71, 21242, 41253, 57 68, 41296 304, 41323 27, 52, 41650 65, 42490 91, 43400—02, —48 9, 43530, 52035 38, 42, 52101 08, 34, 36, 40, 52362, 52550 51, 52600, 03 04, 07, 52826, 52926, 29 31, 55, 53055 56, 53569 72, 53714 15, 54900 01, 06, 58564 65. From various localities in southern Norway.

Syntypes: The three specimens figured by J. de C. Sowerby *op. cit.*, 1839, pl. 21, fig. 2. The original of the bottom, left-hand figure is now preserved in the Collection of the Geological Survey, London (No. 7612, from the Lower Llandovery of Cefn-y-garreg, Carmarthenshire). Cf. Pl. VI, fig. 7; the other two specimens appear to be lost.

Clorinda undata is a very common fossil in the Llandovery of southern Norway as also in Great Britain; though it has in the past commonly been referred to *Barrandella*, an examination of its internal structures shows that it is really a species of *Clorinda*.

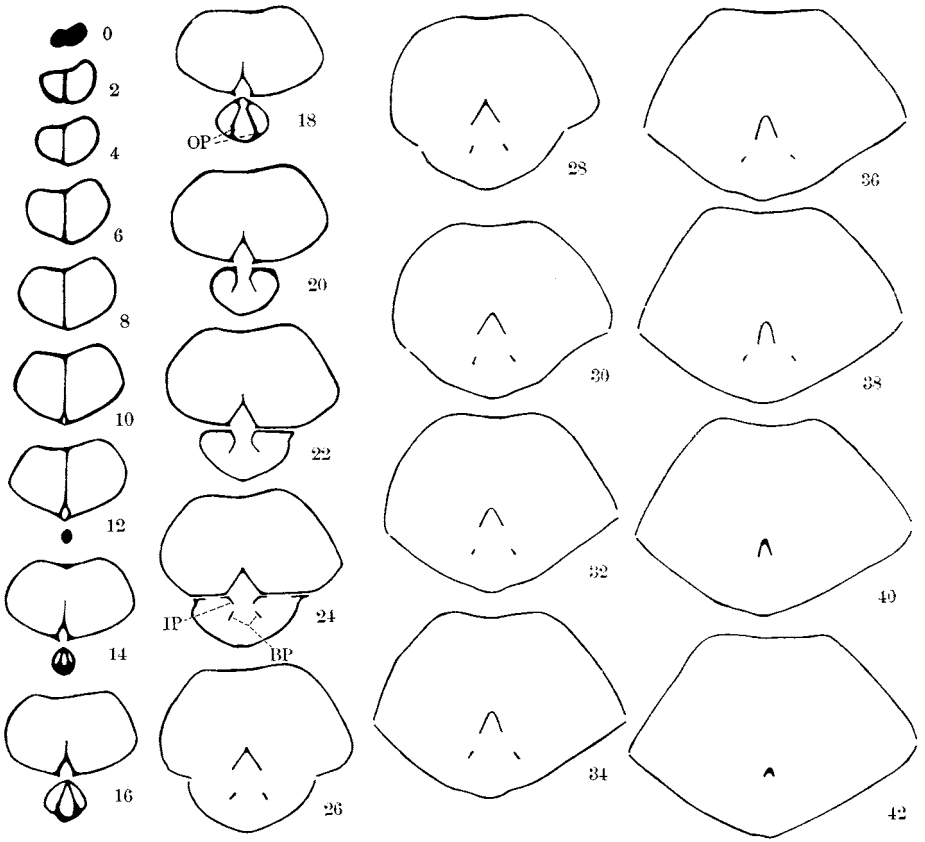
Diagnosis: Large, smooth, transverse *Clorinda* with the breadth usually much greater than the length, and the ventral valve considerably more convex than the dorsal (Pls. VI, figs. 1 9; VII, figs. 13 15). Umbones approximate, the ventral umbo rather low, incurved. Hinge-line long, straight. Large, prominent, flattened, median, dorsal fold, and shallow ventral sinus. Anterior margin strongly uniplicate. In the ventral valve a small delthyrium and short, narrow

spondylium, with short, supporting septum. In the dorsal valve the cardinalia consist of strongly divergent crural-plates, composed of inner-plates, brachial-processes and outer-plates (text-fig. 15). A small carina may be present at the junction of the inner-plates and the bases of the brachial-processes. Inner- and outer-plates very small: brachial-processes slender, diverging, rather long.

Discussion: The outline of this species is generally elongate-oval; the ventral valve is higher than the dorsal but seldom projects far above the hinge-line (Pls. VI, fig. 4; VII, fig. 13). The ventral umbo is much incurved and comes to lie in the adult considerably below the posterior end of that valve (Pl. VIII, figs. 4, 5). The hinge-line extends for about three-quarters of the maximum width of the shell. The lateral margins are nearly semi-circular; the anterior side of the valves when seen in the dorsal aspect, almost straight.

The fold in the dorsal valve is always well developed. It commences at the umbo and increases in width anteriorly, being generally rather triangular in outline, and with a flattened or gently convex surface. At the anterior margin the sides of the fold may be nearly parallel, arising almost at right-angles from the rest of the valve. The fold produces a strong, sub-rectangular plication of the margin (Pls. VI, figs. 3, 6, 8; VII, fig. 15). The sinus of the ventral valve is less prominent than the fold; it commences a little below the umbo and deepens anteriorly, where at the margin it extends as a tongue into the dorsal fold (Pl. VI, figs. 3, 6, 8). The sinus is frequently divided longitudinally by a low, median plication (*e. g.* P. M. O. 52 136). In some individuals (P. M. O. 41 262, 53 714) it is ill-defined or absent. In specimens in which the shell-substance is well preserved, concentric growth-lines are well marked especially towards the anterior.

Internal Characters: Owing to the incurving of the ventral valve the umbo does not lie far above the hinge-line and the delthyrium is consequently small. Occasionally, very slight ridges are present at the margins of the delthyrium (text-fig. 15), but these do not appreciably constrict the opening. When the valves are in apposition it is largely covered by the dorsal umbo. The spondylium is very short, and curves antero-dorsally towards the interior of the dorsal valve (Pl. VIII, fig. 5). The spondylial cavity is shallow, its cross-section approximates to an equilateral triangle (text-fig. 14, transfers 20 to 36). The supporting septum is thin and short (text-fig. 14, transfers 2 to 12), it seldom extends much below (*i. e.* anterior to) the level of the

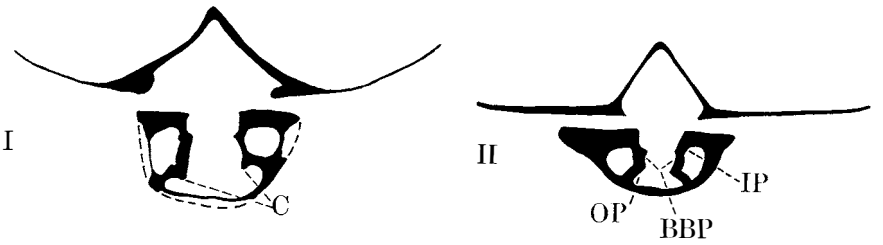


Text-fig. 14. *Clorinda undata* (J. de C. Sowerby).

Serial transfers (S. M. C. A. 13 512) at 0.125 mm intervals from the posterior end of a specimen; zone 6 a, Sjursøy, Oslo. × 2. Transfers 0 42. (Cf. VIII, figs. 4—7. BP = brachial processes; IP = inner-plates; OP = outer-plates.

apex of the delthyrium. It is seen to be duplex in character where it separates from the valve-wall, but anteriorly, the median plane of division along the septum is usually indistinct.

In the dorsal valve the crural-plates are very small, extending only for a short distance below the umbo. Posteriorly, they may often be seen to be rather distinctly divided into inner-plates, bases of the brachial-processes and outer-plates (text-figs. 14, transfer 18, and 15). At the junction of the inner-plates with the bases of the brachial-processes a small carina may be present and sometimes, also, at the junction of the latter with the outer-plates. The appearance



Text-fig. 15. *Clorinda undata* (J. de C. Sowerby).

Transfers from two specimens, × 5. From left to right S. M. C. A 13 513 (42) and A. 13 514 (36). BBP bases of the brachial-processes; C = carinae; IP = inner plates; OP = outer-plates.

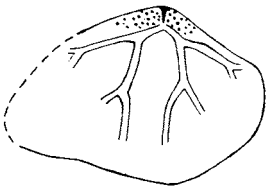
of these carinae is due to the bases of the brachial-processes being rather strongly concave to one another (text-fig. 15), and not entirely in the same plane as the inner- and outer-plates. The outer-plates always diverge strongly and are widely separated where they join the valve-wall. The brachial-processes consist of straight lamellae, which often continue as far as, or beyond the end of the spondylium (text-fig. 14, transfers 24 to 38).

Internal casts a common form of occurrence of the species in Britain show a short, median furrow in the ventral valve, which marks the position of the septum, while in the dorsal valve two extremely small slits may occasionally be seen, indicating the presence of the separate, crural-plates. Rather irregular, longitudinal ridges which appear to be pallial markings are often prominent in internal casts of the ventral valve. In one specimen (S. M. C. A. 13 551; text-fig. 16) they may be seen to conform to a definite arrangement. An area covered with small rugosities probably indicating ovarian markings commonly occurs on either side of the ventral, median, septum.

Description of Types: The syntype figured on Pl. 21, fig. 2 (bottom, left-hand figure) of "The Silurian System" 1839, is an almost complete internal cast of a rather transverse dorsal valve,[1] showing slight traces of median muscle-impressions (cf. Pl. VI, fig. 7).

Remarks: *Clorinda undata* is easily distinguished from other species of this genus by its smooth, transverse shell, its prominent

[1] [?] Not ventral as stated by Davidson. The specimen was republished by Davidson (1867, pl. xix, fig. 7), whose figure is a mirror image of the original.



Text-fig. 16.
Clorinda undata (J. de C. Sowerby).
Internal cast of a ventral valve showing pallial markings, S. M. C. A. 13551. × 1 1/4 approx.

dorsal fold and low ventral umbo. It is closely related to *Clorinda globosa* (J. de C. Sow.), which species, however, has a more strongly biconvex and less transverse shell and, apparently, a rather larger, ventral septum. Intermediate varieties do occur, and such specimens as P. M. O. 41323 and 53570 which are strongly inflated and less transverse than the typical *C. undata* serve to connect the two species. *C. pseudolinguifera* Koz. has a more rounded outline, a less convex dorsal valve and a higher ventral umbo.

Internally, *C. undata* possesses a septum of about the same length as that in *C. kjerulfi* (Kiær) and rather shorter than that of *C. malmøyensis*. The thickenings along the sides of the delthyrium appear to be similar to those in *C. pseudolinguifera* termed by Kozlowski 'deltidial plates'. In the dorsal valve there is a much more distinct tripartite division of the cardinalia than has yet been recorded in any other species of the genus. The crural-plates are more strongly divergent, than in the two other Norwegian species and most closely resemble the arrangement in the specimen of *C. pseudolinguifera* figured by Kozlowski (1929, p. 137, fig. 40).

Pentamerus bubo Barr. from the Silurian of Bohemia, seems from a study of Barrande's figures to be identical in external characters with the present species. The same is true of *Pentamerus krasnopolskii* Tschern. and both names appear to be synonyms of *C. undata* (J. de C. Sow.).

Clorinda undata is common in horizons 6 and 7 of the Norwegian Silurian. At Ringerike it occurs in 6a and was considered by Kiær to be especially characteristic of this zone (1908, p. 42). In the eastern development at Malmøy, he chose it as the zone fossil for 6aβ (*op. cit.*, pp. 135 7), and it continues in this district, though less commonly, through 6b to 6c. Its distribution in the Asker district is closely similar, it being particularly common in 6aα. The species occurs also in zone 7; there is a large, inflated form at Asker in 7a (P. M. O. 53569 70; cf. Kiær, *op. cit.*, p. 351) which approaches the related species *C. globosa*. The specimens in the upper part of this zone, referred by Kiær (*op. cit.*, pp. 155, 159) to *Barrandella linguifera* (J. de C. Sow.) are rather a variety of *C. undata*

Dimensions of Typical Specimens
(in millimetres).

Length	Breadth	Thickness
15.6[1]	23.3	-
18.3	24.8	15.6
22.5	28.3	18.7
19.0	21.6	15.2
14.7	18.4	10.5
18.2	22.9	14.4
19.3	25.3	15.0
26.1	27.4	21.1
11.5	16.2	8.3
17.3	22.4	14.3

as is shown by a study of their internal structure. Thus, individuals from horizon 7c at Malmøy are less transverse than the typical *C. undata*, with a slight, angular furrow at the anterior margin on either side of the dorsal, median fold (P. M. O. 43 401 20).

Clorinda malmøyensis[2] new species.

Plates VII, figs. 7 12; VIII, figs. 8—9; Text-figs. 17 19.

1908. *Barrandella ventricosa* (J. Hall). Kiær, J., "Das Obersilur im Kristianiagebiete", *Vidensk. Selsk. Skrifter. Math.-Naturv. Kl.* (1906), II, pp. 166, 171, 589.

Material: P. M. O. specimens 21 350 52, 21 388 89 (over 50 individuals) all from Malmøy.

Holotype: specimen P. M. O. 21 389a, cf. Pl. VII, figs. 7, 10; text-fig. 17. Horizon 8c, the lower part of the zone, from Malmøy (near Oslo).[3]

Paratypes: specimens P. M. O. 21 389b k, S. M. C. A. 13 515, from the same horizon and locality.

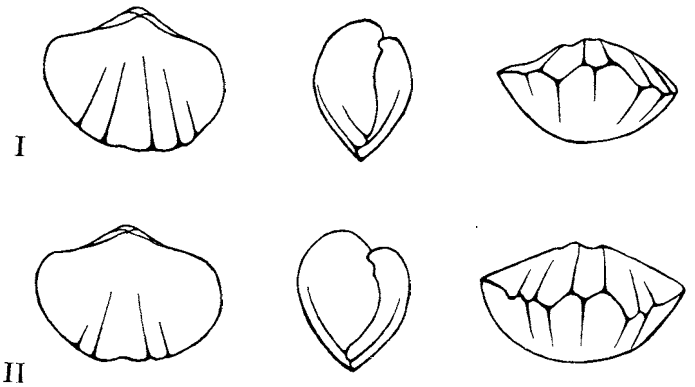
The species *Clorinda malmøyensis* is proposed to include specimens from Malmøy referred by Kiær to *Pentamerus ventricosa* J. Hall 1860, a form which agrees internally with *Barrandella*,[4] while the specimens in question have the internal structure of a *Clorinda*.

[1] Approximate, present dimensions of type.

[2] Named after Malmøy, the type locality.

[3] Just to the east of the summit of the island, according to Kiær's label. Cf. Kiær, *op. cit.*, Karte III.

[4] As may be seen from Hall and Clarke's figures. Cf. *e. g.*, 1894, pl. lxxi, fig. 5 showing in an internal cast, a single furrow in the dorsal valve, marking the junction of the united crural-plates with the valve-wall.



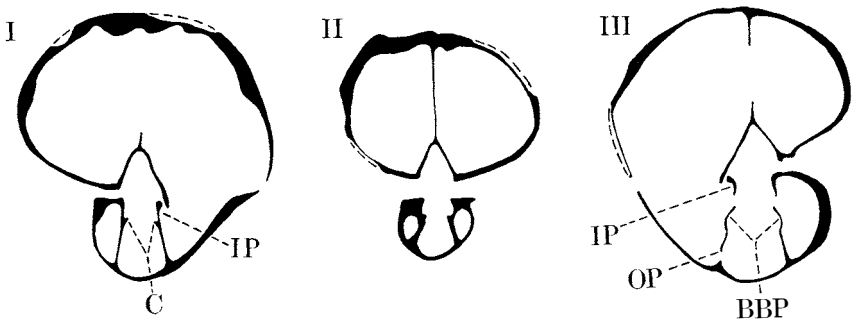
Text-fig. 17. *Clorinda malmøyensis* new species.

Outline drawings of the dorsal, right-lateral and anterior views of (I) the holotype P. M. O. 21389 a and (II) paratype P. M. O. 21389 c. ×2.

Diagnosis: Small, transverse *Clorinda*, with a straight hinge-line and rounded lateral margins. Anterior margin uniplicate, with a low, median, dorsal fold and ill-defined ventral sinus. The greater part of the valve-surface folded into radiating costae, which commence below the umbones. In the ventral valve, a narrow delthyrium and a small spondylium supported on a short, median, duplex septum. In the dorsal valve, the cardinalia consist of small, divergent crural-plates from which there project relatively long, lamellar brachial-processes (Pl. VIII, fig. 9).

Discussion: This species is generally rather elongate-oval in outline with the breadth always exceeding the length and equal to about one-and-a-half times the thickness (cf. table of dimensions). The ventral valve is the more strongly convex (Pl. VII, figs. 7 12). The hinge-line is relatively long and may approach the greatest breadth of the shell. The median dorsal fold, though small, is always present, and produces a slight plication of the anterior margin. The ventral sinus is rudimentary. The valve-surfaces are folded into rounded, radiating costae (text-fig. 17), of which two compose the dorsal fold, while six or eight may be present round the margin.

When the valves are in apposition the posterior part of the edges of the spondylium are seen to project slightly dorsally from the commissure (text-fig. 19, transfers 11 to 13) to fit outside the margins of the crural-plates in the dorsal valve, articulation taking place between the two structures.



Text-fig. 18. *Clorinda malmøyensis* new species.
Transverse sections of three specimens, × 5. From left to right P. M. O. 21 389 d—f, respectively.
BBP = bases of the brachial-processes; C carinae; IP = inner-plates; OP = outer-plates.

Internal Characters: The delthyrium is short and narrow and in life would be partially covered by the incurved dorsal umbo (Pl. VIII, fig. 8). No constriction of the delthyrial opening has been observed. The spondylium is very small, it may attain a length of 3 or 4 mm measured from the umbo of the ventral valve. The free edges of the spondylium are almost straight (Pl. VIII, fig. 8) and remain approximately in the plane of junction of the valves.

A thin, median septum is present supporting the spondylium for about half its length (text-fig. 19, transfers 3 to 15; cf. text-fig. 18). It breaks away rather suddenly about 2 mm below the umbo and does not appear to continue as a ridge down the interior of the valve-wall. The septum may be seen to be duplex where it separates from the wall of the valve; but anteriorly this duplex character is lost.

In the dorsal valve the cardinalia consist of a pair of divergent, crural-plates from the ends of which the brachial-processes continue anteriorly (Pl. VIII, fig. 9; text-figs. 18, 19, transfers 7 to 17). The crural-plates show no very distinct division into inner-plates, brachial-processes and outer-plates, but a study of transfers such as text-fig. 19, transfer 13, and of thin-sections (text-fig. 18), suggests that that part of each crural-plate lying ventrally to the base of the brachial-process corresponds to the inner-plate in the cardinalia in other Pentamerids and that the part between the base of the brachial-process and the valve-wall similarly corresponds to the outer-plate. This is supported by the occasional presence, in thin-sections, along the supposed line

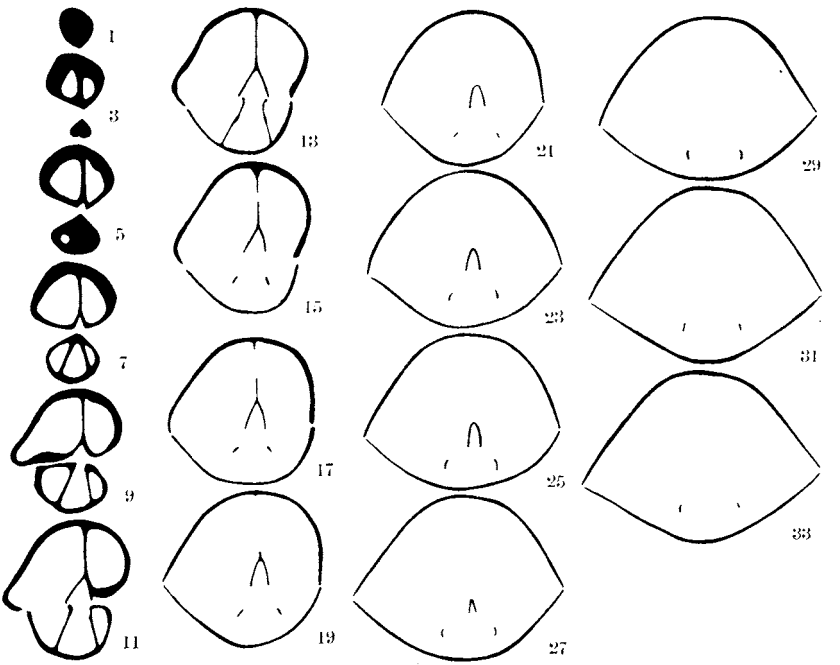
Dimensions of Typical Specimens
(in millimetres).

Length	Breadth	Thickness
9.1	11.5	6.4 (Holotype)
8.6	12.4	6.4 (Paratype)
10.7	12.9	8.1 »
10.0	13.7	9.3 »
9.5	12.7	6.9 »
9.3	11.6	7.6 »
8.2	11.8	7.2 »
9.6	12.8	8.5 »
9.3	12.1	7.6 »
8.8	10.5	6.5 »

of junction of the inner-plates and the bases of the brachial-processes of a small carina pointing ventrally (text-fig. 18); a feature similar to that recorded by Kozlowski (1929, p. 137, fig. 40) in *C. pseudolinguifera*. The lamellar brachial-processes diverge slowly (Pl. VIII, fig. 9) and frequently continue beyond the end of the spondylium (text-fig. 19, transfers 15 to 33).

Description of Holotype: The holotype (Pl. VII, figs. 7, 10; text-fig. 17, I), is a specimen of average size with a prominent, ventral umbo. The ventral valve is somewhat more convex than the dorsal. The hinge-line is only a little shorter than the maximum breadth. In the ventral valve the median sinus is scarcely developed, while six low plications occur round the anterior margin.

Remarks: *C. malmøyensis* most closely resembles *C. kjerulfi* (Kiær), described above, but it may be distinguished from this species externally by its more transverse shell, and almost straight hinge-line, and internally by its smaller delthyrium and narrower spondylium with a longer supporting septum (contrast text-figs. 13 and 19). In the dorsal valve of *C. malmøyensis* the cardinalia are more strongly divergent than in the second species, while the brachial-processes appear to be rather longer. The carina at the junction of the inner-plates and the bases of the brachial-processes has not been seen in *C. kjerulfi*. *C. malmøyensis* has in common with the earlier species *C. undata*, a transverse outline and long, straight hinge-line; it usually possesses a relatively longer septum than the latter, besides differing externally in its much smaller size and costate shell.



Text fig. 19. *Clorinda malmøyensis* new species.

Serial transfers (S. M. C. A. 13 515) at 0.10 mm intervals from the posterior end of a specimen; zone 8 c, Malmøy. × 3. Transfers 1—33. (Cf. Pl. VIII, figs. 8 9.)

The possession of a costate shell separates *C. malmøyensis* and *C. kjerulfi* from all other species of this genus. It is a feature which appears occasionally in some Pentamerid genera of which the majority of species are smooth. Thus, while most species of the closely allied genus *Barrandella* are smooth, *B. ventricosa* is costate and generally similar externally to the species under consideration. Costation is a somewhat variable character even within a species, and is often absent on young specimens, being attained only in the later stages of growth. Thus, a number of small specimens (P. M. O. 21 350 52) about 4 to 5 mm in length, collected by Kiær probably from horizon 8 a at Malmøy, and which have the internal structure of a *Clorinda* are considered provisionally to be young individuals of *C. malmøyensis* although they possess a much more rounded outline, while costation is hardly developed.

Family *Stricklandidae*.

Genus *Stricklandia* E. Billings 1859.

Billings, E., "On some new Genera and Species of Brachiopoda, from the Silurian and Devonian Rocks of Canada", *The Canadian Naturalist and Geologist,* vol. iv, 1859, pp. 132 5, figs. 8 9.

Davidson, T., "British Fossil Brachiopoda", *Palaeontogr. Soc. Lond.* [*Monogr.*] III, pt. vii, pp. 157 63 (1867); V, pt. ii, pp. 164—6, (1883).

Hall, J. and Clarke, J. M., Palaeontology of New York, VIII, pt. ii, 1894, pp. 249 51.

Schuchert, C. and Cooper, G. A., "Brachiopod Genera of the Suborders Orthoidea and Pentameroidea", *Mem. Peabody Museum nat. Hist. Yale*, IV, pt. i, 1932, pp. 186 8.

Synonym: *Stricklandinia* Billings, E., "On the genus Stricklandia; proposed alteration of the name"; *The Canadian Naturalist and Geologist*, vol. viii, 1863, p. 370.

Genolectotype: *Stricklandia gaspéensis* E. Billings, *The Canadian Naturalist and Geologist*, iv, 1859, p. 134. (Chosen by Hall and Clarke, *op. cit. supra*, p. 250.) Original from Gaspé peninsula, Quebec; horizon Upper Silurian.

Generic description: Transversely-oval to elongate-oval, large Pentameracea, with a straight hinge-line and rather flattened, biconvex profile; valves sub-equal, the dorsal valve frequently with the greater convexity. A small, median fold and sinus often developed. Delthyrium open. Cardinal-areas usually present; that in the ventral valve broad and curved; in the dorsal valve small or linear. Surface of the valves smooth or costate. Shell substance fibrous.

In the ventral valve a very small, dorsally curving spondylium supported on a short, duplex septum. Ovarian markings may be prominent on the posterior part of the inner valve-surface. In the dorsal valve the cardinalia consist of simple, slender brachial-processes and short strongly divergent, inner-plates. Dentition simple; articulation takes place between the thickened, antero-dorsal corners of the delthyrium and the margins of the inner-plates, where these join the valve-wall. Elongate muscle-scars, situated posteriorly, are often prominent.

European species:

Atrypa lens J. de C. Sowerby 1839.
Spirifer liratus J. de C. Sowerby 1839.
[?] *Pentamerus microcamerus* F. McCoy 1851 (? synonym of *S. lens*).

Discussion: *Stricklandia* is most readily recognized by its straight and often long, hinge-line, its low umbones and curved area. Internally, the form of the cardinalia is characteristic. This genus has, in the past, sometimes been regarded as a rather anomalous member of the Pentameracea, distinctly separated from the family Pentameridae (Schuchert and Cooper, 1932, p. 188). Study of the abundant material preserved in this collection suggests, however, that the relationship between *Stricklandia* and *Pentamerus* may be closer than has been imagined. The development of the cardinalia in the former genus, which has hitherto been considered quite distinct from anything represented in the same Super-family, seems on close examination to correspond to the general Pentamerid plan. The resemblance is closest, among known forms, to the cardinalia in *Holorhynchus*, and it would appear that the inner-plates in *Stricklandia* are homologous with the inner-plates of normal Pentamerids. Similarly, the relatively long hinge-line and the very short septum and spondylium are not characters which involve a distinct separation of the genus, for even in this collection both features are present in such species of *Clorinda* as *C. undata* and *C. malmøyensis*.

Stricklandia lens (J. de C. Sowerby) 1839.

Plates III, figs. 1 3, 7 9, 12 17; VI, figs. 12, 14; VIII, figs. 10 19; Text-figs. 20 22.

1839. *Atrypa lens* Sowerby, J. de C., in Murchison's "Silurian System", p. 637, pl. 21, fig. 3.

1867. *Stricklandinia lens* (J. de C. Sow.). Davidson, T., "British Fossil Brachiopoda", *Palaeontogr. Soc. Lond.* [*Monogr.*], III, pt. vii, pp. 161 3, pl. xix, figs. 13 23 (with Bibliography). *Idem*, V, pt. ii, 1883, p. 165, pl. ix, figs. 2 5.

1908. *Stricklandinia lens* (J. de C. Sow.). Kiær, J., "Das Obersilur im Kristianiagebiete", *Vidensk. Selsk. Skrifter, Math.-Naturv. Kl.* (1906), II, *passim*.

[?] Synonym: *Pentamerus microcamerus* McCoy, F., *Ann. Mag. nat. Hist.*, 2nd Series, vol. viii, 1851, pp. 390 1, reprinted in Sedgwick and McCoy "British Palaeozoic Rocks and Fossils", 1851 5, p. 210 (1852).

Material: P. M. O. specimens 21138 72, 74 99, 21201 02, 71, 40420 22, 93 95, 40555 62, 41375 76, 80 82, 41977 42031, 34 36, 69 77, 42087 101, 42103, 05, 52388 89, 91 99, 52401, 03, 08 11, 13 14, 16, 19 21, 23 28, 30 55, 52599, 52601 02, 05, 08,

19, 52730 45, 52828 39, 53199 202, 53265, 68 96, 53315 16, 53436 42, 54580 85, 94, 54605 09, 58354 69, 58525 49.

Syntypes: The two specimens figured by J. de C. Sowerby *op. cit.*, 1839, pl. 21, fig. 3. These are preserved in the Collection of the Geological Survey, London [No. 6905 (upper figure), from the Upper Llandovery of Mandinam, Carmarthenshire; No. 6678 (lower figure), from the Lower Llandovery of Cefn Rhyddan, S. E. of Llandovery, Carmarthenshire]. Cf. Pl. VI, figs. 14 and 12.

Diagnosis: Large, smooth *Stricklandia* usually sub-circular to elongate-oval in outline. Hinge-line straight, rather long. Valves about equi-convex, umbones low, approximate (Pl. III). A small cardinal-area in the ventral valve. Often a long, fan-shaped, median, dorsal fold which may cause a slight plication of the anterior margin. In the ventral valve an open delthyrium and small, dorsally-curving, spondylium partly supported on a short, duplex septum. In the dorsal valve slender, lamellar, brachial-processes, which are in contact for about half their length with a pair of divergent inner-plates.

Discussion: A number of different shape-variations are represented among the several hundred individuals of this species (mostly from zone 6 cα), that have been examined. The dimensions of length and breadth are commonly about equal giving an approximately sub-circular outline (Pl. III, figs. 1, 3, 12, 15), but some elongate forms occur with the dimension of length exceeding the breadth (Pl. III, fig. 17). Occasionally, as in specimens from 6 cα at Malmøy (P. M. O. 21174 8) it is the breadth that is increased, producing a transverse variety. In all these forms the maximum thickness is attained half-way or rather less from the hinge-line, to the anterior margin (Pl. III, figs. 2, 8 and 13). In profile, the valves are gently convex or somewhat flattened. The umbones are usually very small and low, often inconspicuous, rising only slightly above the hinge-line. The latter is always less than the greatest width of the shell, and the valve-margins curve slowly outwards until the maximum breadth is attained.

The surface of the dorsal valve is elevated into a low, median fold that commences a little below the umbo and increases considerably in width towards the anterior, where its sides are rather ill-defined (Pl. III, figs. 7, 12, 15, 17). In specimens in which the fold produces a plication of the margin a shallow sinus may be present in the ventral valve (Pl. III, figs. 3, 16). In a number of individuals

(*e. g.*, P. M. O. 21180, 53268) there are faint traces of secondary folds (costae) on either side of the median fold and sinus. Concentric growth-lines are often prominent towards the anterior margin.

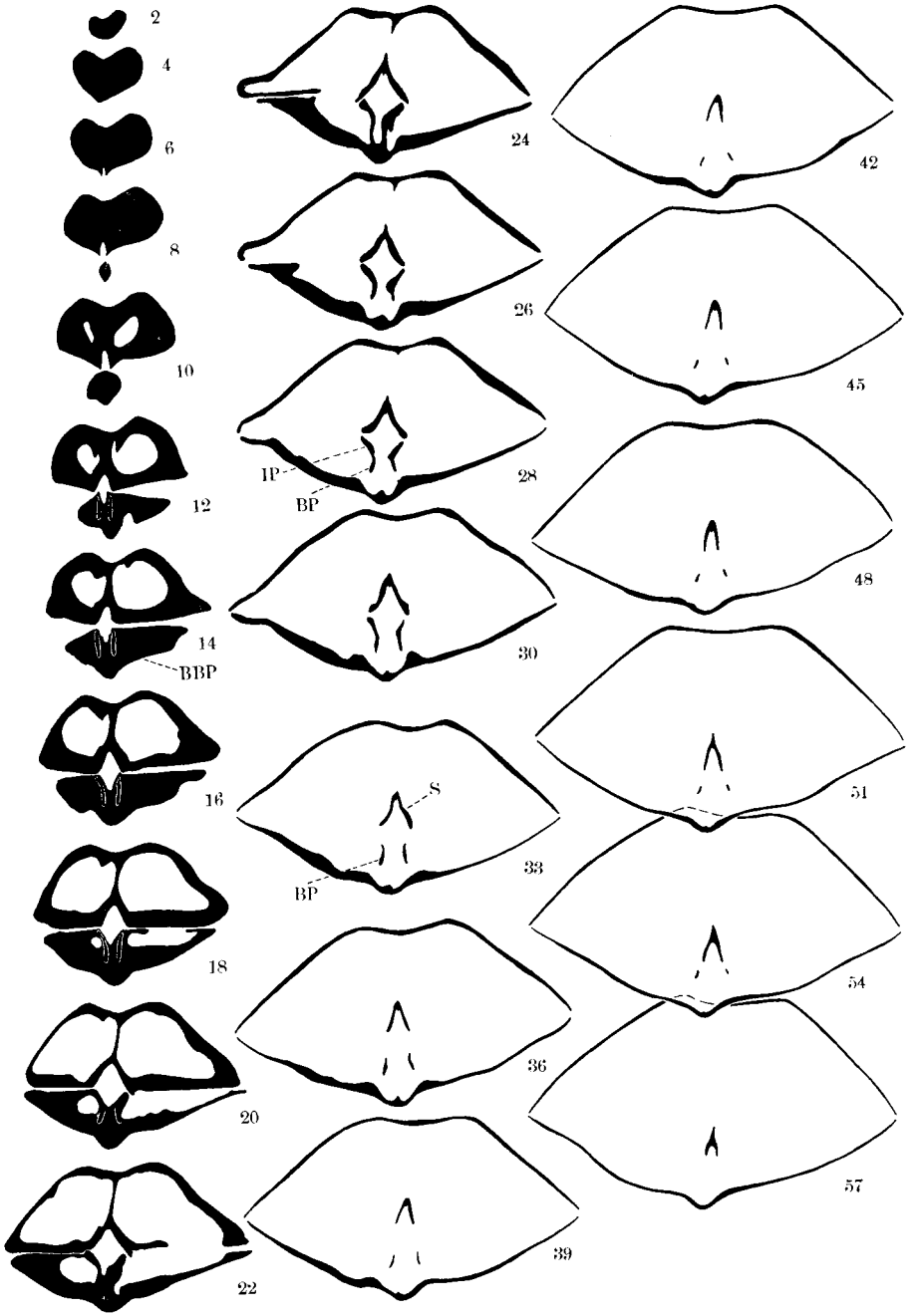
The extensive variation that occurs in this species is of a similar character to that observed in *P. laevis*. It is perhaps best illustrated by a description of a suite of specimens (P. M. O. 58529 49) all from the same horizon and locality (zone 6 c at Malmøy about 30 m thick) specially selected by Kiær to show the variation occurring between forms from different beds of rock. Thus, within this group, P. M. O. 58547 49 probably from the lowest level, are transverse forms, considerably wider than long, with inconspicuous umbones and a hinge-line approaching the greatest breadth of the shell. They possess a rather clearly developed, dorsal, median fold, while a shallow sinus is also present. P. M. O. 58543 46 from the next band, are of about the same average size, but with their dimensions of length and breadth approximately equal, producing a sub-circular outline. Specimens P. M. O. 58539 42 from the succeeding bed are elongated forms with the length considerably greater than the breadth, and with a short hinge-line. The cardinal-angles are rather prominent. The next group, P. M. O. 58534 38 are small and of rounded outline with a distinctly developed, median, dorsal fold. Finally, P. M. O. 58529 33 apparently from the top bed, are similar to the foregoing, but with the median fold forming a prolongation of the anterior margin, while the cardinal-angles again tend to be distinctly marked. All the specimens in this series have very small, inconspicuous umbones, but there is evidently a considerable variation from bed to bed, and similar series could probably be obtained from other districts.

Internal Characters: The delthyrium in this species is usually covered by the incurved dorsal umbo, which fits closely below the apex of the ventral valve when the two valves are in apposition (Pl. VIII, figs. 10, 19). The spondylium is or the short, open type which characterizes *Stricklandia* (Pl. VIII, figs. 12, 15). Its usually extends for between one-quarter and one-sixth of the length of the shell, always curving forward towards the cavity of the dorsal valve (text-fig. 20, transfers 24 to 57 and Pl. VIII, figs. 11, 16, 18). 'Teeth' are better developed in this species than in many other Pentamerids. The spondylial walls are often appreciably thickened at the point where they join the hinge-line, and may extend slightly dorsally from the commissure to make contact with the edges of the inner-

plates of the dorsal valve (text-fig. 20, transfers 20 to 24). The median, duplex septum is rather thin and short (text-figs. 20 and 21); in specimens of average size it may extend for 4 or 5 mm anterior to the umbo, supporting the spondylium for less than half the length of the latter (Pl. VIII, figs. 11, 17). The posterior portion of the inner surface of the spondylial cavity is covered by a thin layer of lamellar shell-material (text-fig. 22, where this layer is stippled), apparently of the same nature as that described in species of *Pentamerus*, though it is not so sharply separated from the shell-wall as in that genus. Along the margins of the delthyrium small ridges may occur, slightly constricting the delthyrial opening (text-fig. 22). They are evidently of the same nature as the "incipient deltidial plates" that have been described in certain species of *Clorinda* (Booker, 1927, p. 134). When the valves are in apposition the ridges lie close to the surface of the dorsal valve and fill the narrow gaps between the dorsal umbo and the delthyrial margins. A true pseudo-deltidium has not been observed.

In the dorsal valve the cardinalia consist only of brachial-processes and inner-plates. The bases of the brachial processes may be traced almost to the umbo, embedded in later deposited shell-substance (text-fig. 20, transfers 12 to 22). They separate from the valve-wall a little anterior to the hinge-line, and continue as flattened rods (Pl. VIII, figs. 13 14; text-figs. 20 and 21, transfers 24 to 54 and 25 to 57 respectively), which may embrace the anterior end of the spondylium when the valves are in the position of life (text-fig. 21, transfers 55 to 57; Pl. VIII, fig. 11). Attached to the ventral edges of the brachial-processes are a pair of divergent inner-plates (Pl. VIII, fig. 13; text-figs. 20 and 21, transfers 24 to 30 and 23 to 33 respectively). These are usually rather wider than the brachial-processes, but extend for only half their length. The junctions of the inner-plates with the hinge-line define two sockets into which there project the 'teeth' of the ventral valve.

Description of Types: Of the two syntypes figured by J. de C. Sowerby, No. 6905 in the Collection of the Geological Survey, London, is an incomplete, internal cast (with counter-part), of an average-sized specimen, with a very short septum in the ventral valve (cf. Pl. VI, fig. 14). A low, median, dorsal fold is present and there are traces of faint, secondary costae on either side. No. 6678 in the same Collection is an internal cast of a ventral valve, with a



Text-fig. 20. *Stricklandia lens* (J. de C. Sowerby).

Serial transfers (S. M. C. A. 13516) at 0.10 mm intervals from the posterior end of a specimen; zone 6 bβ, Asker. × 2. Transfers 2—57 (cf. Pl. VIII, fig. 17). BBP bases of the brachial processes; BP = brachial-processes; IP = inner-plates; S = spondylium.

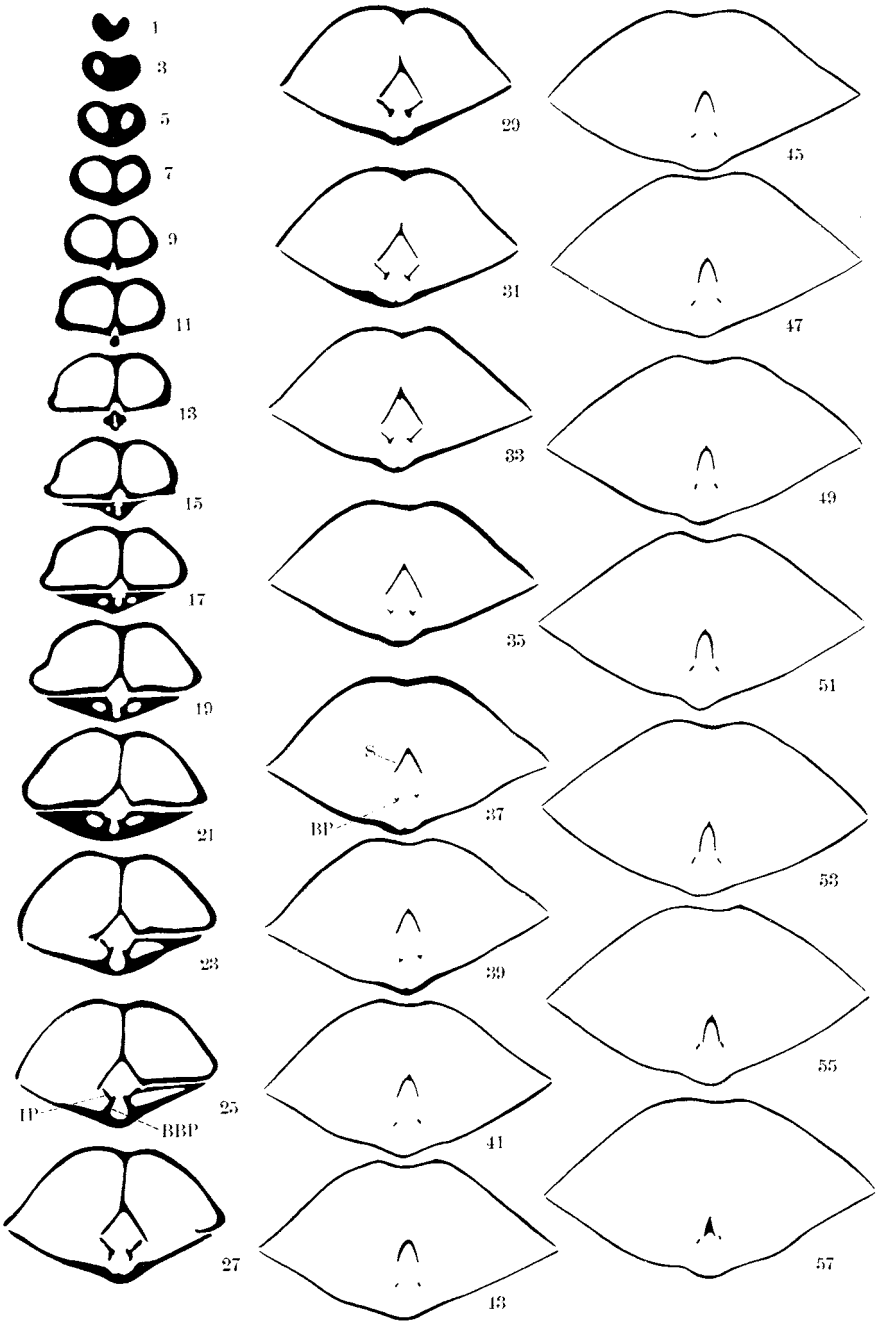
Dimensions of Typical Specimens
(in millimetres).

Length	Breadth	Thickness
c. 49.5	46.0	18.5 (present dimensions of types)
66.0	49.0	-
67.0	60.0	36.0
62.1	63.2	33.3
60.9	49.2	27.7
56.4	53.4	32.8
29.8	25.0	14.8
28.9	24.5	12.9
44.4	62.2	23.9
51.0	44.0	22.7

short septum (Pl. VI, fig. 12). Very slight, radiating folds and concentric growth-lines occur towards the anterior margin.

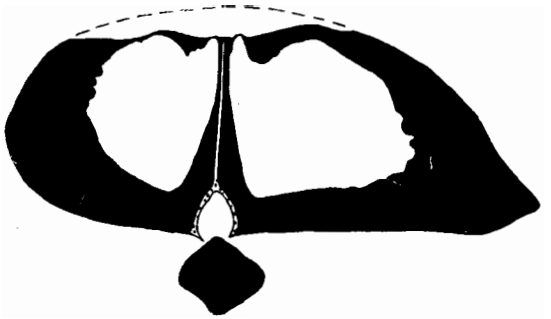
Remarks: In spite of its many shape-variations *S. lens* may be easily identified by its essentially lenticular profile, smooth shell, poorly developed fold and sinus and small incurved umbones. The slight plications that have been described as occurring round the anterior margins in some specimens never approach the size or prominence of the costae of a typical *S. lirata*.

S. lens is extremely common at horizon 6 c of the Norwegian Silurian being especially characteristic of the eastern development. There, at Malmøy and Asker, it may attain importance as a rock former (Kiær, 1908, pp. 142 3, 340 1). The earliest appearance of the species is at Asker, where in 6 bβ there occurs a small variety (Kiær, *op. cit.*, p. 326) often somewhat triangular in outline. It is the zone-fossil for horizon 6 cα in which it attains its maximum abundance, and most of the material in the Collection has come from the Malmøy and Asker districts at this horizon. The main variations at Malmøy have been described, and similar types occur in the Asker region. Kiær (*op. cit.*, p. 193) records that it is common also at Holmestrand in 6 cα. In the western development, as at Ringerike and Skien and Porsgrund, the species is almost entirely absent. In 6 cβ it is still present in the eastern areas, though much less common; it overlaps in this zone (at Asker) with the oldest member of the *Pentamerus* series (Kiær, *op. cit.*, pp. 342, 499). Rare examples are also found at horizon 7a at Malmøy, Asker and Holmestrand (Kiær, pp. 153, 351, 199- 200).



Text-fig. 21. *Stricklandia lens* (J. de C. Sowerby).

Serial transfers (S. M. C. A. 13518) at 0.125 mm intervals from the posterior end of a specimen; zone 6 c α, Malmøy. × 1⅓. Transfers 1 57 (cf. Pl. VIII, figs. 12—13). BBP bases of the brachial processes; BP = brachial processes; IP = inner-plates; S = spondylium.



Text-fig. 22. *Stricklandia lens* (J. de C. Sowerby).

Transfer from the posterior end of a specimen, S. M. C. A. 13519 (18). × 5.

S. lens does not appear to have been recorded from the Baltic Provinces, but in England it is very common, appearing first at the top of the Lower Llandovery, reaching its maximum in the Middle Llandovery, and extending also to the Upper Llandovery.

Stricklandia lirata (J. de C. Sowerby) 1839.

Text-figs. 2, vii and 23.

1839. *Spirifer liratus* Sowerby, J. de C., in Murchison's "Silurian System", p. 638, pl. 22, fig. 6.

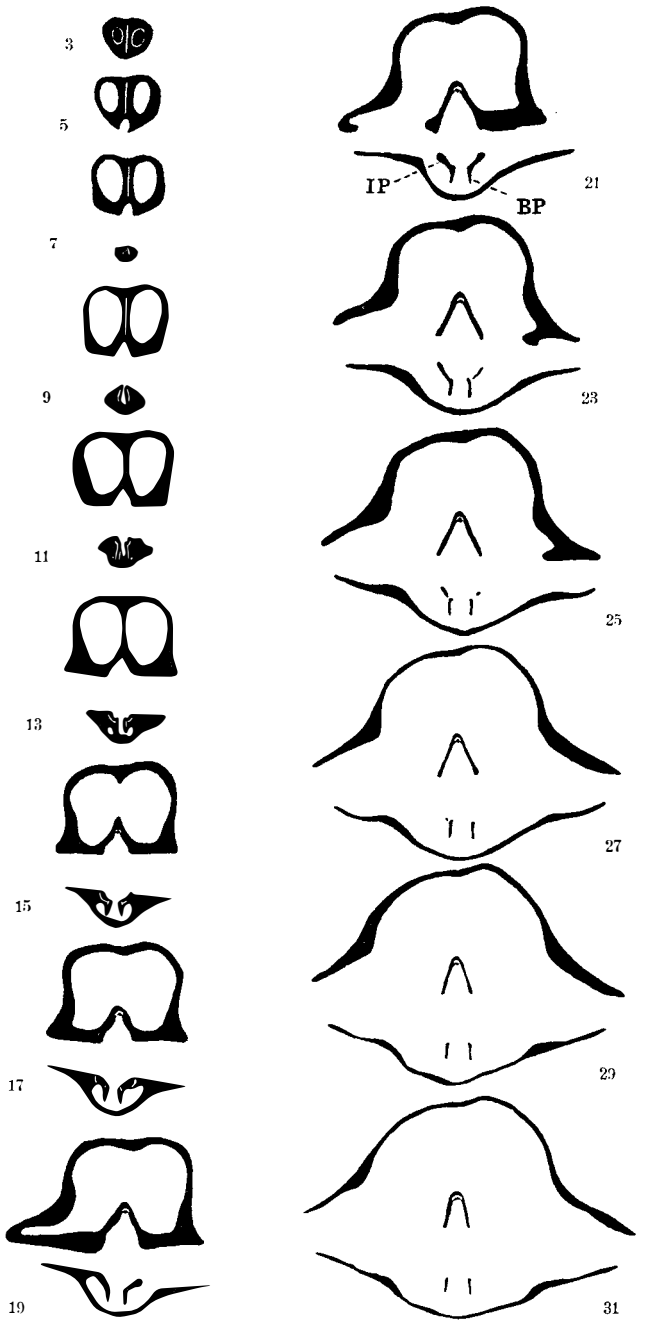
1867. *Stricklandinia lirata* (J. de C. Sow.). Davidson, T., "British Fossil Brachiopoda", *Palaeontogr. Soc. Lond.* [*Monogr.*], III, pt. vii, pp. 159 61, pl. xx, figs. 1 13. *Idem*, V, pt. ii (1883), p. 165, pl. ix, fig. 1.

1908. *Stricklandinia lirata* (J. de C. Sow.). Kiær, J., "Das Obersilur im Kristianiagebiete", *Vidensk. Selsk. Skrifter, Math.-Naturv. Kl.* (1906), II, *passim*.

1935. *Stricklandia lirata* (J. de C. Sow.). St. Joseph, J. K. S., "A Critical Examination of *Stricklandia lirata* (J. de C. Sowerby) 1839", *Geol. Mag. Lond.*, LXXII, pp. 401 24, pls. xvi xvii (with full Bibliography).

Synonyms: *Cardium multisulcatum* Hisinger, W., Lethaea Svecica, supplimenti secundi continuatio, 1841, p. 4, pl. xli, figs. 3 a b.
Spirifer ovatus McCoy, F., A. Synopsis of the Silurian Fossils of Ireland (1846), 1862, p. 37, pl. iii, fig. 24.

Material: P. M. O. specimens 21664 73, 45439 40, 68 71, 74 75, —77, 45515 16, 94 96.



Text-fig. 23. *Stricklandia lirata* (J. de C. Sowerby).

Serial transfers (S. M. C. A. 7039) at 0.15 mm intervals from the posterior end of a specimen; zone 7 c β, Ringerike. × 2 approx. (For the complete series, see St. Joseph 1935 b, pp. 407 9, text-fig. 2.). BP = brachial-processes; IP = inner-plates.

Holotype: Specimen 6618 in the Collection of the Geological Survey, London, from the top of the Llandovery at Marloes Bay, Pembrokeshire; figured by J. de C. Sowerby *op. cit.*, 1839, pl. 22, fig. 6.

The account of this species is condensed from St. Joseph, *op. cit. supra*, 1935. All the specimens of *S. lirata* in the Kiær Collection are of the forma *typica*.

Diagnosis[1]: Large, sub-circular to oval *Stricklandia*, the valves nearly equal, the ventral a little larger than the dorsal. Maximum breadth usually rather greater than the length. Hinge-line straight, somewhat less than the greatest breadth of the shell. Umbones approximate, the ventral slightly the higher. Ventral cardinal-area small, curved. Often a low, prominent, median fold in the dorsal valve, and corresponding sinus in the ventral. Valves multicostate. In the ventral valve a typical, small, open spondylium and duplex septum. In the dorsal valve the cardinalia consist of small inner-plates[2] and slender, parallel, brachial-processes (= crural-processes).

Discussion: The variation in external characters exhibited by this species has recently been discussed with particular reference to British material (St. Joseph, 1935 b, pp. 403 4, 418 21) and only special characteristics of the Norwegian specimens will be noted here. The Kiær Collection includes a few large individuals (P. M. O. 21664 6, 45594 6) identical with the forma *typica*, and also smaller specimens (P. M. O. 21667, 21671) with a somewhat more convex ventral valve and slightly less prominent ribbing a variation which is not very common in Britain. The umbones are sometimes a little incurved and there is a small, sloping cardinal-area on the ventral valve. The sinus is always developed, but the dorsal fold may be ill-defined, or present only at the anterior margin.

Internal Characters: The delthyrium appears to have been open as the dorsal umbo seldom curves far forward from the plane of junction of the valves, while in the few specimens in which the feature can be studied, no structures constricting the delthyrial opening have been seen. The spondylium is short compared with the length of the shell, it is free for the greater part of its length, the supporting

[1] This diagnosis applies particularly to *S. lirata* forma *typica*.

[2] These were termed previously 'outer plates' (St. Joseph, 1935 b, p. 413), referring to their lateral position relative to the brachial processes. The nomenclature is now altered to 'inner-plates', in order that the terminology may agree with that in use for other Pentamerids.

septum being very small (text-fig. 23). The low, median ridge at the back of the spondylial cavity is often distinct; it probably separated muscle impressions. The duplex character of the septum is generally well marked, and the median plane of separation may be traced right to the posterior end of the valve. The extensive, secondary thickening of the posterior portion of the shell that has been described in specimens of the forma *typica* from England has not been observed in the Norwegian material.

In the dorsal valve the cardinalia consist of rather slender, lamellar, brachial-processes and strongly divergent inner-plates (text-fig. 23, transfers 15 31). The former are approximately parallel and situated close to the valve-wall, they extend for about the same distance as the spondylium. The inner-plates are seen from sections to be quite distinct structurally from the brachial-processes of which they attain about half the length. The two may remain in contact, or separate slightly towards the anterior (text-fig. 23, transfers 19 to 27). The bases of the brachial-processes appear to be attached directly to the valve-wall, as if no structure were present, corresponding to the outer-plates of *Pentamerus*.

Remarks: The species may easily be distinguished from *Stricklandia lens*, the only other Norwegian form referred to this genus, by its strongly costate shell, and much more prominent umbones.

All the specimens of *S. lirata* in the Collection have come from Ringerike at horizon 7 cβ, of which it is characteristic, Kiær (1906, p. 64) choosing it as the zone fossil. It is common at that horizon, occuring together with *P.* cf. *gotlandicus*. The material consists for the greater part, of isolated valves, and adds little to the knowledge of the internal structure of the species. *S. lirata* is also recorded from Skien and Porsgrund (*op. cit.*, p. 273) and occasionally from Holmestrand (p. 207) and Asker (pp. 356 7), where the faunal development closely parallels that at Ringerike. It is absent in the eastern districts (Malmøy). Kiær reported rare examples of the species from the Wenlock horizon 8 b, in the western area (*op. cit.*, pp. 74 5, and 279), though none of these are contained in the Collection. It seems doubtful whether they are really typical specimens. *S. lirata* forma *typica* occurs also in Gotland, being common in the lower part of the Wisby group, and in England where it characterizes a narrow horizon at the junction of the Llandovery and Wenlock beds.

List of Works to Which Reference Is Made.

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Printed June 30th, 1938.

PLATES

PLATES I III ARE FROM FIGURES
PREPARED BY KIÆR

Plate I.

Pentamerus borealis (C. E. Eichwald).

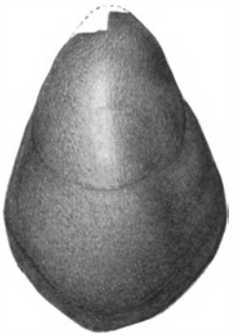
All figures natural size.

Figs. 1 2. Ventral and right-lateral views of specimen P. M. O. 54 726. Zone 7 a, Bjerkøy, Holmestrand.

» 3. Dorsal view of specimen P. M. O. 54 834. Zone 7 a, Bjerkøy, Holmestrand.

» 4—6. Dorsal, left-lateral and ventral views of specimen P. M. O. 58 553. Zone 7 a, Ringerike.

» 7 9. Dorsal, left-lateral and ventral views of a specimen. Zone 7 a, Bjerkøy. Original unidentified.



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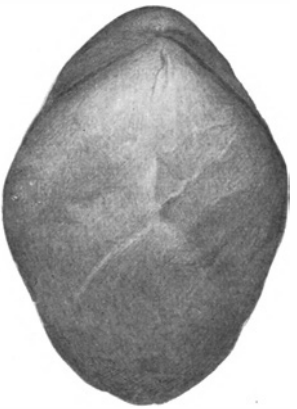

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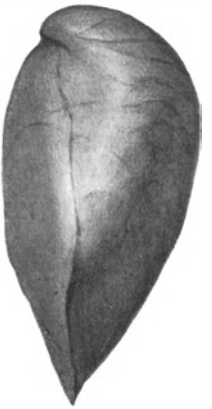

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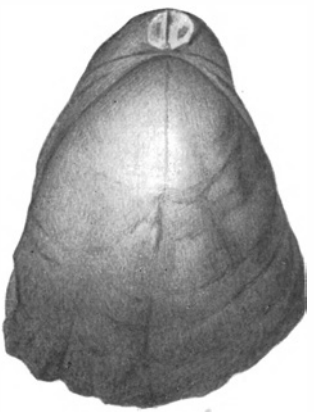

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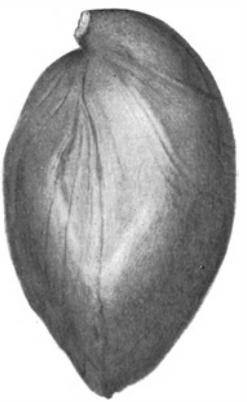

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Plate II

Pentamerus laevis J. Sowerby.

All figures natural size.

Figs. 1— 3. Dorsal, right-lateral aud ventral views of a rather trilobed specimen. Zone 7 b, Malmøykalv. Original unidentified.

» 4— 6. Dorsal, left-lateral and ventral views of a broad specimen, P. M. O. 42 639. Zone 7 a (?), Malmøy.

» 7— 9. Dorsal, right-lateral and ventral views of a young specimen. Zone 7 b, Malmøykalv. Original unidentified.

» 10—12. Dorsal, right-lateral and ventral views of a young specimen, P. M. O. 40 523. Zone 7 a Malmøy.

» 13—15. Dorsal, right-lateral and ventral views of a young specimen, P. M. O. 40 514 a. Zone 7 b 3, Malmøy.

» 16—18. Dorsal, right-lateral and ventral views of specimen P. M. O. 40 520. Zone 7 a (top), Malmøy.

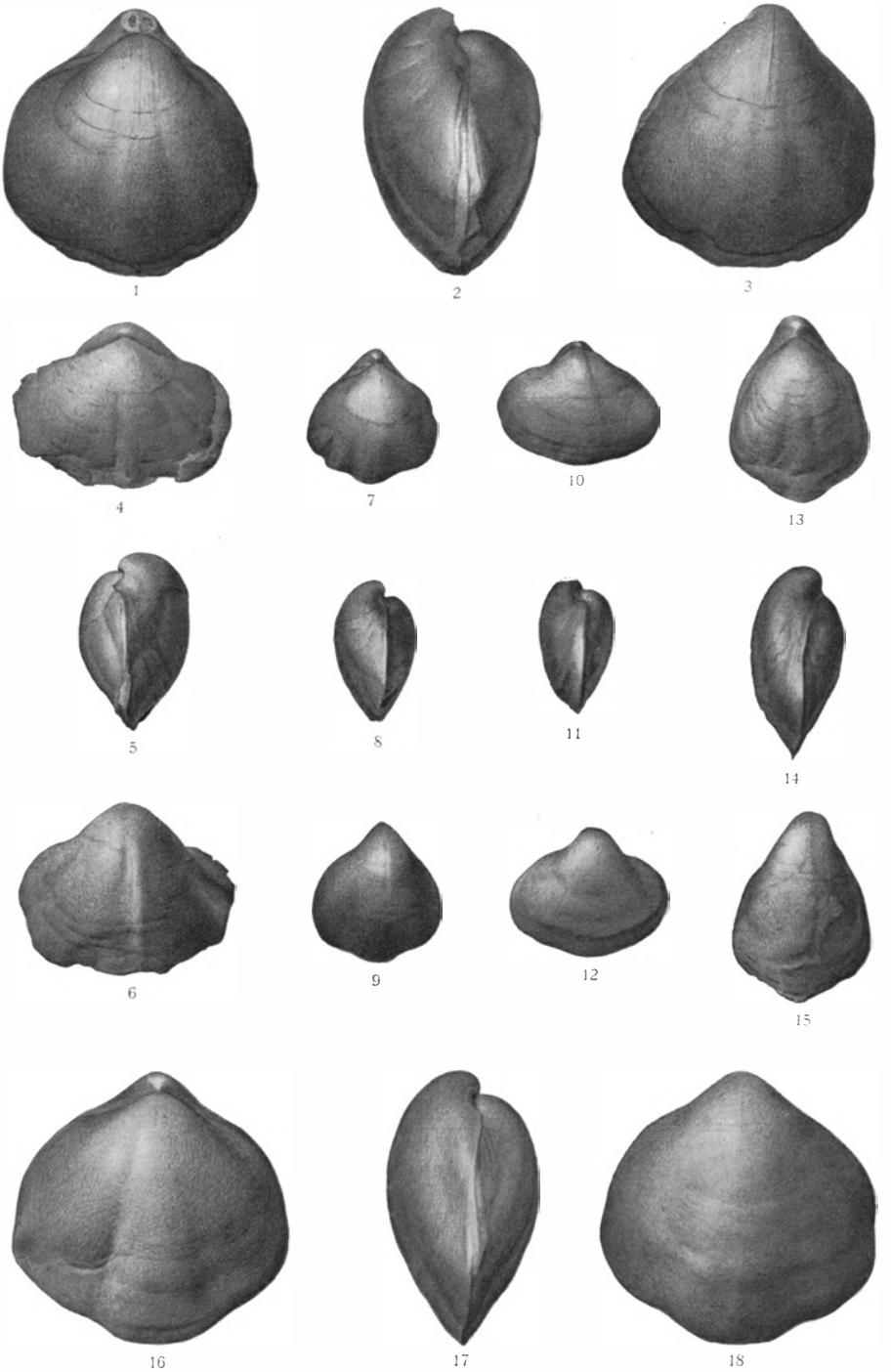
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Plate III

All figures natural size.

Stricklandia lens (J. de C. Sowerby).

Figs. 1— 3. Dorsal, left-lateral and ventral views of specimen P. M. O. 41 376. Zone 6 c, Malmøy.

» 7 9. Dorsal, left-lateral and ventral views of a specimen. Zone 6 (top), Asker. Original unidentified.

» 12—14. Dorsal, left-lateral and ventral views of a young specimen, P. M. O. 54 594 a. Zone 6 c, Bjerkøy.

» 15—16. Dorsal and ventral views of a specimen. Zone 6—7, Asker. Original unidentified.

» 17. Dorsal view of a specimen. Zone 6 c, Malmøy. Original unidentified.

Pentamerus laevis J. Sowerby.

» 4— 6. Dorsal, left-lateral and ventral views of a specimen. Zone 7 a (?), Malmøy. Original unidentified.

» 10—11. Dorsal and right-lateral views of a specimen. Zone 7 b (?). Original unidentified.

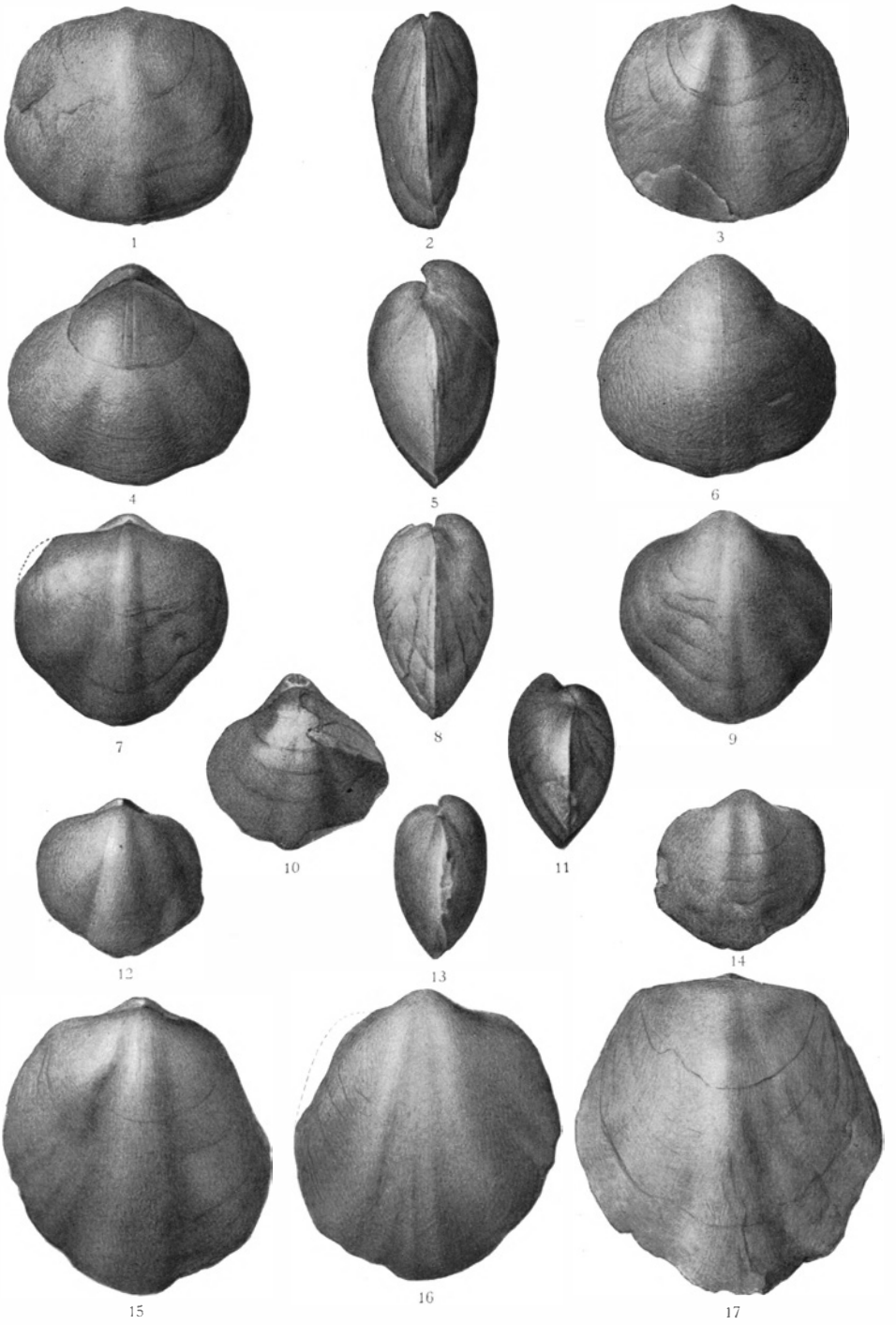
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Plate IV

Holorhynchus giganteus J. Kiær.

All figures natural size.

Figs. 1—3. Dorsal, left lateral and posterior views of the lectotype. P. M. O. 12431. Zone 5 b, Aspelund, Asker.

» 4—5. Dorsal and left-lateral views of specimen P. M. O. 12491. Zone 5 b, Asker. This specimen has been destroyed in obtaining the series of transfers shown in text-fig. 9.

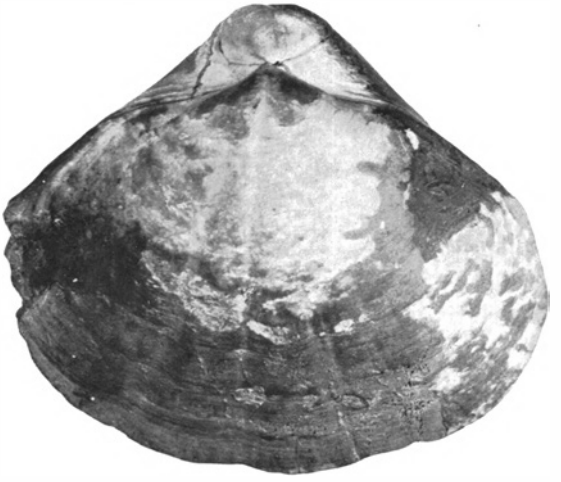

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Plate V

Wax models, constructed from serial transfers, of the posterior portions of the shells of various Norwegian Pentamerids.

Pentamerus borealis (C. E. Eichwald).

Fig. 1. Antero-lateral aspect, showing the spondylium, which is free for the lower half of its length, curving dorsally towards the cardinalia. × 1¼. S. M. C. A. 13 502; original from zone 7 a, Ringerike. Compare text-fig. 3.

» 2. Ventro-lateral aspect of the dorsal valve of the same specimen. × 1¼.

» 3. Dorso-lateral aspect of the ventral valve of the same specimen, showing the shape of the spondylium. × 1¼.

» 4. Dorsal aspect of a ventral valve of a young specimen. × 2. S. M. C. A. 13501; original from zone 7 a, Ringerike.

Pentamerus laevis J. Sowerby.

» 5. Ventral aspect of a dorsal valve of a rather young specimen. × 2½. S. M. C. A. 13 504; original from zone 7 b β, Malmøy. Compare text-fig. 6.

» 6. Dorsal aspect of the ventral valve of the same specimen. A small pseudodeltidium is present at the apex of the delthyrium. × 2½.

» 10. Antero-lateral aspect, showing the relative positions of the cardinalia and the spondylium. The latter is supported on a median septum for the greater part of its length. × 1½. S. M. C. A. 13 503; original from zone 7 b, Malmøy. Cf. text-fig. 5.

Pentamerus (Pentameroides) cf. *gotlandicus* N. Lebedev.

» 7. Dorsal aspect of a ventral valve, showing the narrow spondylium supported on a long, median septum. A concave pseudodeltidium covers the apex of the delthyrium. Natural size. S. M. C. A. 13 507; original from zone 7 c β, Ringerike. Compare text-fig. 8.

» 8. Ventral aspect of the dorsal valve of the same specimen, showing the long cruralium. Natural size.

Conchidium münsteri new species.

» 9 & 11. Dorsal and dorso-lateral aspects of a ventral valve, with a large delthyrium and spondylium and long median septum. × 2. S. M. C. A. 13 509; original from zone 5 b, Ringerike. Cf. text-fig. 10. Topotype.

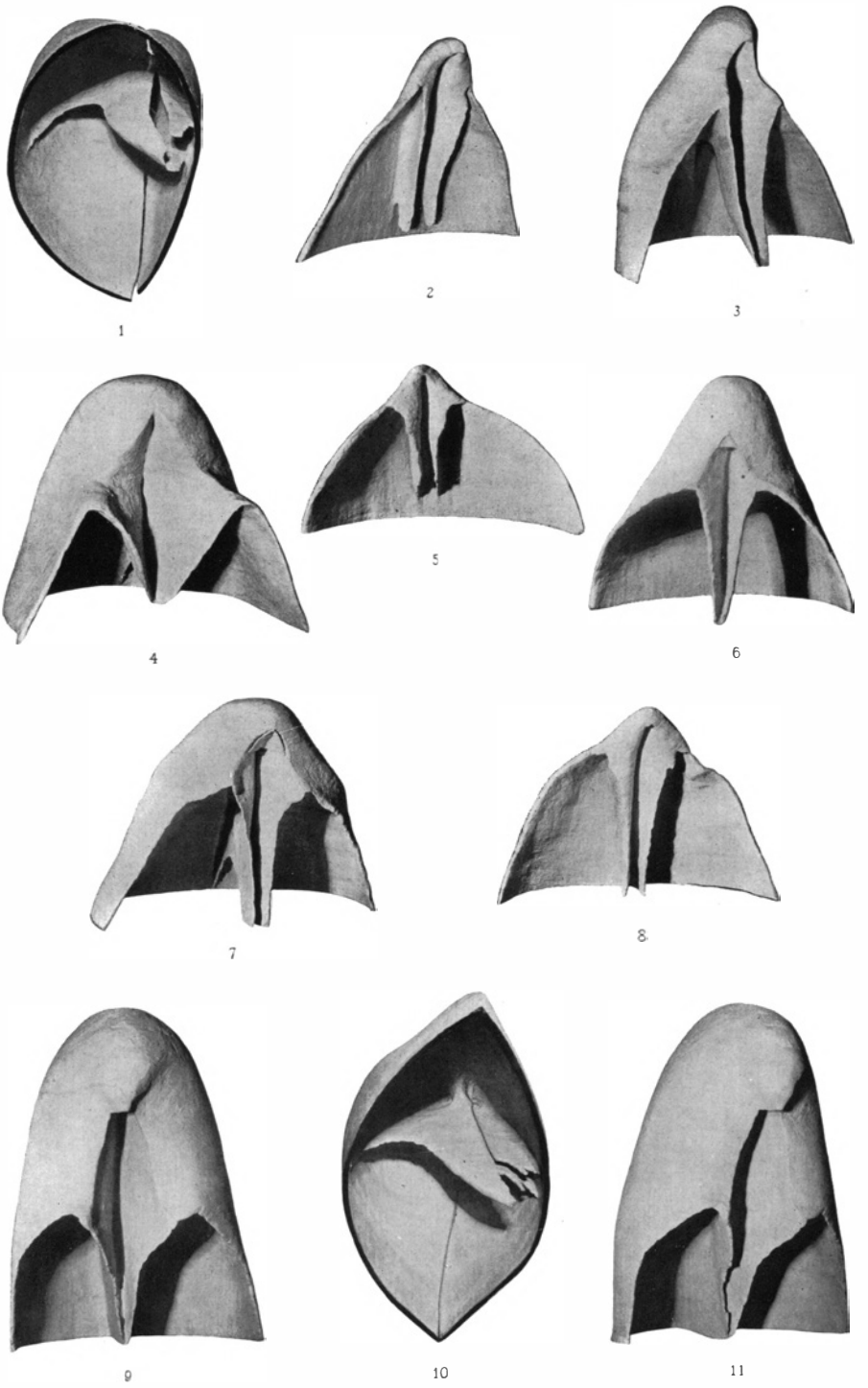
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Plate VI

Figures natural size, unless otherwise stated.

Clorinda undata (J. de C. Sowerby).

Figs. 1— 3. Dorsal, right-lateral and anterior views of specimen P. M. O. 52 136. Zone 6 a, Asker.

» 4 & 8. Dorsal and anterior views of specimen P. M. O. 41 262. Zone 6 b—c, Ulvøy.

» 5 6. Right lateral and anterior views of specimen P. M. O. 42 491. Zone 6 c β, Malmøy.

» 7. Syntype: an internal cast viewed from the dorsal side. Geological Survey, London 7612. Lower Llandovery, Cefn-y-garreg, Carmarthenshire.

» 9. Right-lateral view of specimen P M. O. 53 714. Zone 7 b, Barüm.

Conchidium münsteri new species [Kiær MS.].

» 10. The two paratypes: from left to right P. M. O. 20 821 b and c, respec tively. Zone 5 b, Vestre Svartøy, Ringerike.

» 11. Left-lateral view of the holotype. P. M. O. 20 821 a. Zone 5 b, Vestre Svartøy, Ringerike.

Stricklandia lens (J. de C. Sowerby).

» 12. Ventral view of syntype 2, × 3/4. Geological Survey, London 6678, from the Lower Llandovery (top part), Carmarthenshire. Cf. J. de C. Sowerby, 1839, pl. 21, fig. 3, bottom figure.

» 14. Dorsal view of syntype I. Geological Survey, London 6905, from the Upper Llandovery, Carmarthenshire. Cf. J. de C. Sowerby, 1839, pl. 21, fig. 3, top figure.

Pentamerus (Pentameroides) cf. *gotlandicus* N. Lebedev.

» 13 & 15. Right-lateral and dorsal views of a small specimen, P. M. O. 58 562. Zone 7 c β, Ringerike.

Pentamerus laevis J. Sowerby.

» 16 & 17. Right lateral and dorsal views of a plesiotype. Geological Survey, London 6908. Upper Llandovery, Salop (?), England. Figured by J. de C. Sowerby (1839, pl. 19, fig. 10) as a syntype of "*Pentamerus oblongus*"

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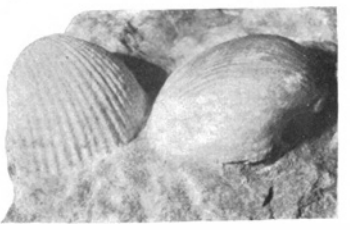

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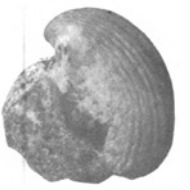

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Plate VII

All figures twice natural size.

Clorinda kjerulfi (J. Kiær).

Figs. 1 & 4. Dorsal and right-lateral views of the lectotype, P. M. O. 12598. Zone 5 b, Halden, Asker.

» 2 & 5. Dorsal and right-lateral views of paratype, P. M. O. 12595. Zone 5 b, Halden, Asker.

» 3 & 6. Dorsal and right lateral views of paratype, P. M. O. 40466. Zone 5 b, Jørgensløkken, Asker.

Clorinda malmøyensis new species.

» 7 & 10. Dorsal and right-lateral views of the holotype, P. M. O. 21389 a. Zone 8 c (lower part), Malmøy.

» 8 & 11. Dorsal right-lateral views of paratype, P. M. O. 21389 b. Same horizon and locality.

» 9 & 12. Dorsal and right-lateral views of paratype, P. M. O. 21389 c. Same horizon and locality.

Clorinda undata (J. de C. Sowerby).

» 13—15. Dorsal, right-lateral and anterior views of specimen P. M. O. 20863 a. Zone 6 b, Sjursøy, Oslo.

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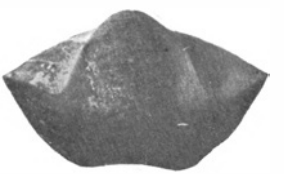

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Plate VIII

Wax models, constructed from serial transfers, of the posterior portions of the shells of various Norwegian Pentamerids.

Clorinda kjerulfi (J. Kiær).

Figs. 1—2. Dorsal and dorso-lateral aspects of a ventral valve, showing the short, wide spondylium. Fig. 1 × 2½; fig. 2 × 3. S. M. C. A. 13510; original from zone 5 b, Asker. Cf. text-fig. 13. Topotype.

» 3. Ventral aspect of the dorsal valve of the same specimen, showing the brachial-processes and inner-plates. × 2½.

Clorinda undata (J. de C. Sowerby).

» 4—5. Dorsal and dorso-lateral aspects of a ventral valve. The short spondylium curves dorsally from the commissure. Fig. 3 × 3; fig. 5 × 2. S. M. C. A. 13512; original from zone 6 a β, Sjursøy, Oslo. Compare text-fig. 14.

» 6. Ventral aspect of the dorsal valve of the same specimen, showing the slender brachial-processes. × 2.

» 7. Antero-lateral aspect of the same specimen. The brachial-processes separate the divergent outer-plates (near the wall of the dorsal valve) from the inner-plates (near the spondylium). × 2. Compare text.-fig. 14.

Clorinda malmøyensis new species.

» 8. Dorsal aspect of a ventral valve. × 4. S. M. C. A. 13515; original from zone 6 c (lower part), Malmøy. Compare text-fig. 19. Paratype.

» 9. Ventral aspect of the dorsal valve of the same specimen. × 4.

Stricklandia lens (J. de C. Sowerby).

» 10. Dorsal aspect of the exterior of specimen S. M. C. A. 13518; original from zone 6 c α, Malmøy. × 1⅕.

» 11. Anterior aspect of the same specimen. The spondylium curves dorsally towards the lamellar brachial-processes. × 1½. Cf. text-fig. 21.

» 12. Dorsal aspect of the ventral valve of the same specimen, showing the short, broad spondylium. × 1¼ approx. Cf. text-fig. 21.

» 13. Ventral aspect of the dorsal valve of the same specimen. The inner-plates are attached to the posterior portions of the brachial-processes. × 1¼ approx.

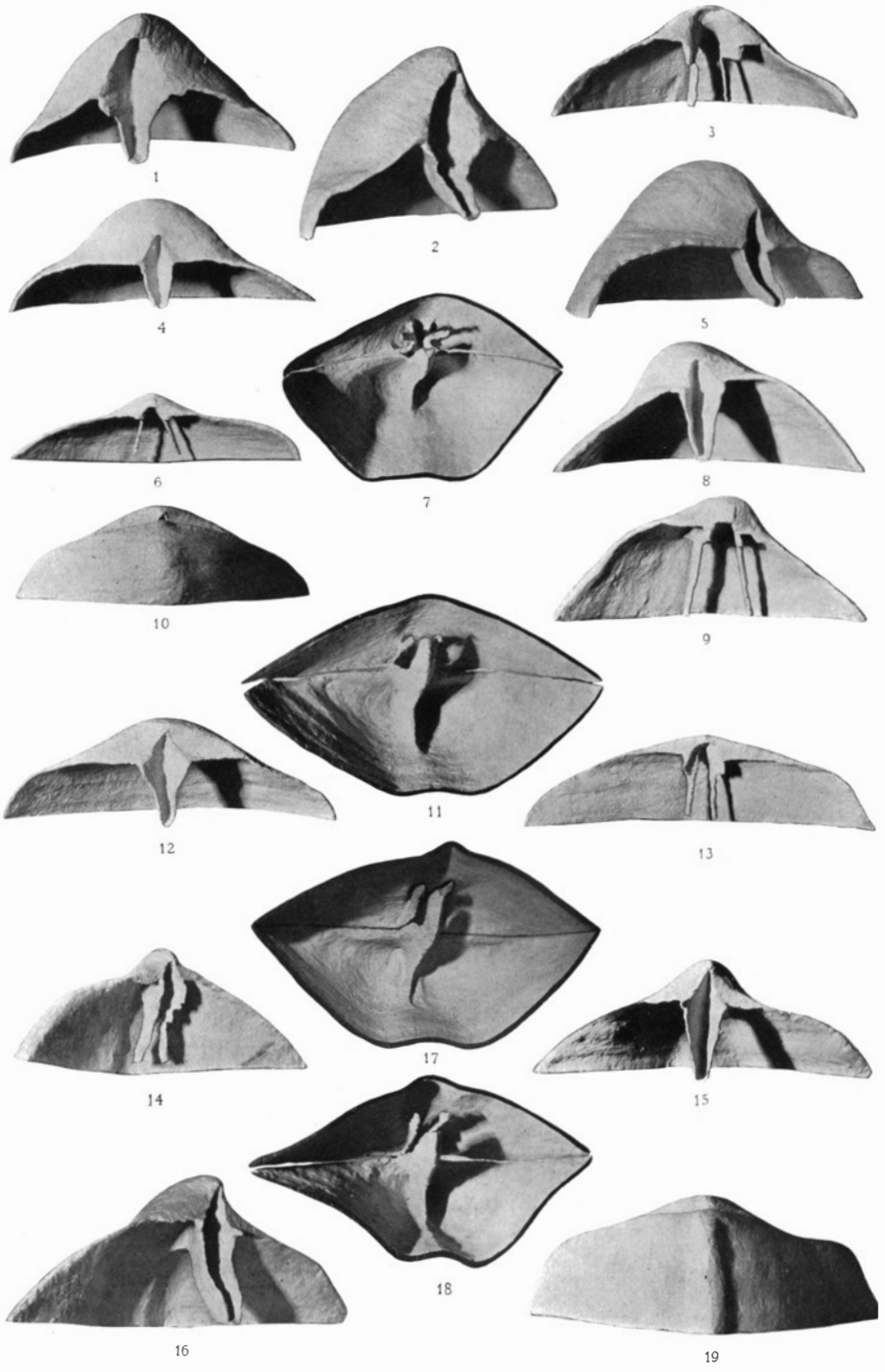
» 14. Ventro-lateral aspect of a dorsal valve. × 2. S. M. C. A. 13517: original from zone 6, Asker.

» 15 & 16. Dorsal and dorso-lateral aspects of the ventral valve of the same specimen, showing the spondylium and short, supporting septum. Fig. 15 × 2: fig. 16 × 2½.

» 17. Anterior aspect. The spondylium, supported on a short septum, curves dorsally towards the brachial-processes. × 2. S. M. C. A 13516: original from zone 6 b β, Asker. Compare text-fig. 20.

» 18. Anterior aspect of specimen S. M. C. A. 13517. × 2.

» 19. Dorsal aspect of the exterior of specimen S. M. C. A. 13516. × 2.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