

# TAXONOMIC SIGNIFICANCE OF THE PSEUDODELTIDIUM IN TRIPLESIIACEAN BRACHIOPODS

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**ABSTRACT.** The recent proposal by Amsden (1968) to subdivide the Triplesiidae on the basis of the presence or absence of the pseudodeltidial fold is critically reviewed. Consideration is given to the variation in the development of the fold, and its absence or sporadic development is noted in several species; while in some forms the fold is even lost during ontogeny.

The belief that the pseudodeltidium and chilidium are very intimately related is supported by reference to several brachiopod stocks, and the form of the chilidium of the davidsoniacean *Meekella* is reinterpreted. The term 'perichilidial area' is proposed for a structure observed on the dorsal interarea of this genus which mirrors the perideltidial area of the pedicle valve. Comparison with *Meekella* leads to a reinterpretation of the chilidium of the triplesiaceans, and the structure is regarded as quite distinct from the cardinal process hood.

The pseudodeltidial fold is principally regarded as a reflection of the form of the cardinal process in stocks with a generally obsolete dorsal interarea, although other associated factors affect its development or lack of it; accordingly its variable loss in a few triplesiaceans is not regarded as providing a sound basis on which to subdivide the family.

THE articulate brachiopod *Triplesia* and its allies have long been known to possess a pseudodeltidium in the form of a flat plate with a narrow median fold extending anteriorly from the apex to the middle of the hinge-line. The recent observation by Amsden (1968, p. 39) that the species *Triplesia praecipecta* Ulrich and Cooper, from the Wenlock St. Clair Limestone of Arkansas, does not possess this characteristic median fold led him to erect a new genus, *Placotriplesia*, and also a new subfamily, the Placotriplesiinae, to contain this genus.

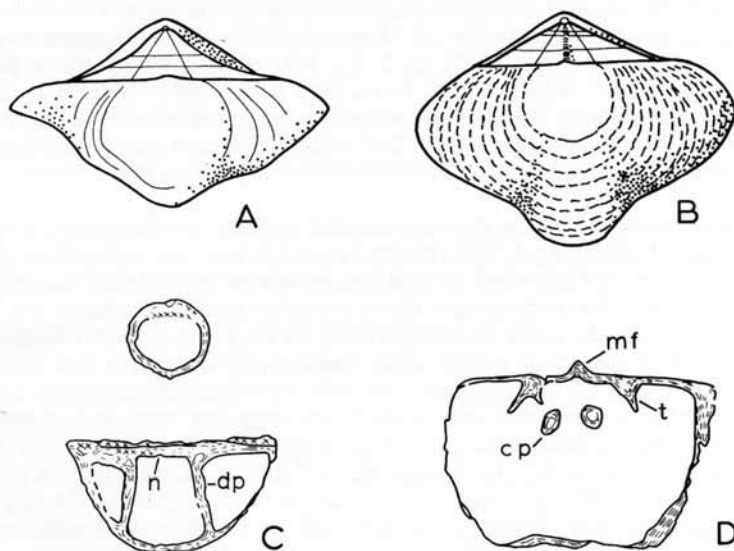
According to Amsden (1968, p. 40), 'As the new genus and new subfamily have essentially the same internal characters as the subfamily Triplesiinae and *Triplesia*, this emendation is concerned only with the structure of the pseudodeltidium: the family Triplesiidae should be emended to include triplesiids having the pseudodeltidium flat, either with or without a median fold, and the subfamily Triplesiinae to include only Triplesiidae in which the pseudodeltidium bears a median septum. The only genus presently referred to the new subfamily is *Placotriplesia*.'

In addition to *T. praecipecta*, the only other species which Amsden places with certainty in his new genus is *T. juvenis* Ulrich and Cooper. Only a single specimen of this form is known, and as this was obtained from a St. Clair Limestone locality which has also yielded fairly abundant *T. praecipecta*, its separation as an independent species is somewhat dubious; indeed, Amsden comments that it may simply be a morphological variant of *T. praecipecta*.

Ulrich and Cooper (1936, p. 333) state that the median fold is possessed by 'well preserved specimens', the implication being that any absence of the structure is a reflection of preservation. But Amsden (1968, p. 41) maintains that its absence in the case of *T. praecipecta* is not the result of preservation, a view which my own studies of this and other triplesiid species would support.

[Palaeontology, Vol. 14, Part 2, 1971, pp. 342-56, pls. 62-63.]

With some reservations, Amsden's observation of the flat nature of the pseudodeltidium in this species then is essentially acceptable. What should be questioned, however, is whether there is any justification for erecting a separate subfamily solely on the absence of the pseudodeltidial fold, or whether a diagnosis of the family (e.g. Wright 1963, p. 741; 1965, p. H358) should be emended to read 'delthyrium closed by a flat pseudodeltidium *commonly* possessing a narrow median fold'. ('Commonly', as although a handful of the hundred-odd described triplesiid species are insufficiently known from this viewpoint, the overwhelming majority do undeniably possess this median fold.)



TEXT-FIG. 1. Comparisons of the smooth pseudodeltidium of *Triplesia praecipecta* Ulrich and Cooper (A, C) with the medianly folded one of *Streptis altosinuata* Høltedahl (B, D). A, B, illustrations of postero-dorsal views of the conjoined valves.  $\times 7.5$ . C, D, transverse serial sections taken at 0.3 mm and 0.7 mm from the ventral umbones through specimens of *T. praecipecta* (QUB 25491), St. Clair Limestone, Cason Mine, Arkansas, and *S. altosinuata* (QUB 25492), Stage 6a-b, Kunglungen, Asker, Oslo, respectively.  $\times 20$ . cp—cardinal process; dp—dental plate; mf—median fold of pseudodeltidium; n—indentation on inner surface of pseudodeltidium; t—tooth.

If one accepts that an interpretative approach to shell morphology is desirable, the reason for the presence or absence of a morphological structure is at least as important as the taxonomic usage of such variation. In the case of *T. praecipecta* it is desirable to ascertain why this species apparently lacks the pseudodeltidial fold of the other triplesiids (text-fig. 1). Such an inquiry can only be conducted by discovering if the variation in the development of the pseudodeltidial fold is significant; if any variation correlates with other morphological changes; and if similar features are developed in other, related brachiopod stocks. Only when one has attempted to answer these questions will one be in a position to consider any taxonomic implications which may derive from the absence of the pseudodeltidial fold.

## VARIATION IN FOLD DEVELOPMENT

Although Amsden (1968, p. 40) was not aware of any triplesiid which lacks a median pseudodeltidial fold other than those which he places in *Placotriplesia*, there are scattered occurrences, and recordings in the literature, of other forms with smooth pseudodeltidia. The single specimen (British Museum B5634) from the Wenlock Shale of Wenlock described by Davidson as *Triplesia? wenlockiensis* (1883, p. 144) is apparently without a fold on the pseudodeltidium, although this is certainly not obvious from Davidson's figures (pl. 8, fig. 23), and additional specimens revealing the internal structures would be needed to confirm the generic placing. More importantly, the smooth pseudodeltidium is shown on Wiman's figure (1907, pl. 2, fig. 14b) of his *Triplesia plicata* from the 'Leptaena Limestone' of Öland. This form, with strong radial ribbing, is currently regarded as an *Oxoplecia*. This species has also been described from the Ashgill Portrane Limestone of Ireland (Wright 1964, p. 247) with the relevant part of the description stating 'delthyrium closed by flat pseudodeltidium, with median fold only occasionally developed'.

A further examination of the Portrane material confirms this description, a specimen being shown in Plate 62, fig. 3. This specimen does not show any median fold, although it does show a series of fine raised vertical lines orientated perpendicular to the growth-lines of the hinge. The specimen also shows a median notch at the hinge-line. It may be that this notch is the result of etching during the extraction of these silicified shells, but even so its presence does suggest some weakness, or thinness, in that position on the original shell. Of the ten specimens available, one whose pseudodeltidium is about 2.5 mm long has a fold developed by the 1 mm stage but which is apparently lost anteriorly; a smaller specimen shows a fold developed at the front, in this case at about 1 mm from the apex; a third may have an abraded fold, but the other seven specimens show no sign of a fold. At the same time it may be noted that two show an irregular fracture medianly, while three show a slight median notching effect anteriorly. The specimen previously illustrated (Wright 1964, pl. 11, fig. 17) has a faint trace of a fold umbonally but there is no sign of a fold in front of this, although there are again several vertical lines developed across the surface of the pseudodeltidium. It may be argued that the Portrane silicified material is poorly preserved, and that the general absence of the fold is a preservational effect, but this does not seem acceptable. Apart from tracing occasional growth-lines straight across the pseudodeltidium of *Oxoplecia plicata*, the flat pseudodeltidium of an associated *Triplesia*, etched by the same methods from the same limestone blocks, invariably possesses a median fold (Wright 1964, p. 245).

Further evidence is available to show that, in some species, different individuals may or may not possess this median fold. An *Oxoplecia*, probably closely related to the Portrane species, occurs in the younger Chair of Kildare reef limestone, where it is fairly abundant at the 'quarry', about 115 m to the east of the Chair itself. This material is not silicified, and the specimens are usually exfoliated because they have to be 'cracked out' of the fairly hard reef limestone. Thus although the overwhelming majority of the sixty or more *Oxoplecia* show no indication of a median fold on the pseudodeltidium, one is unsure as to whether or not this is the result of exfoliation. Plate 62, fig. 1 is of a specimen with a fold, and Plate 62, fig. 2 of a specimen apparently without a fold.

In order to verify the two conditions existing in this *Oxoplectra* several specimens were serially sectioned. The sections of the specimen illustrated in text-fig. 2 clearly show the fold developed on the exterior of the pseudodeltidium but, more importantly for the present argument, also show the fold to be traceable in the 'growth-lines' of the laminar secondary shell and on the interior surface of the pseudodeltidium. A section through the pseudodeltidium of a specimen which did not appear to possess a median fold is illustrated in text-fig. 3. The laminae here extend almost straight across the pseudodeltidium, which shows neither fold on the exterior nor groove on the interior. Thus, although exfoliation could account for the absence of an external fold, the lack of folding in the shell laminae and of a median groove on the interior can only be attributable to growth.

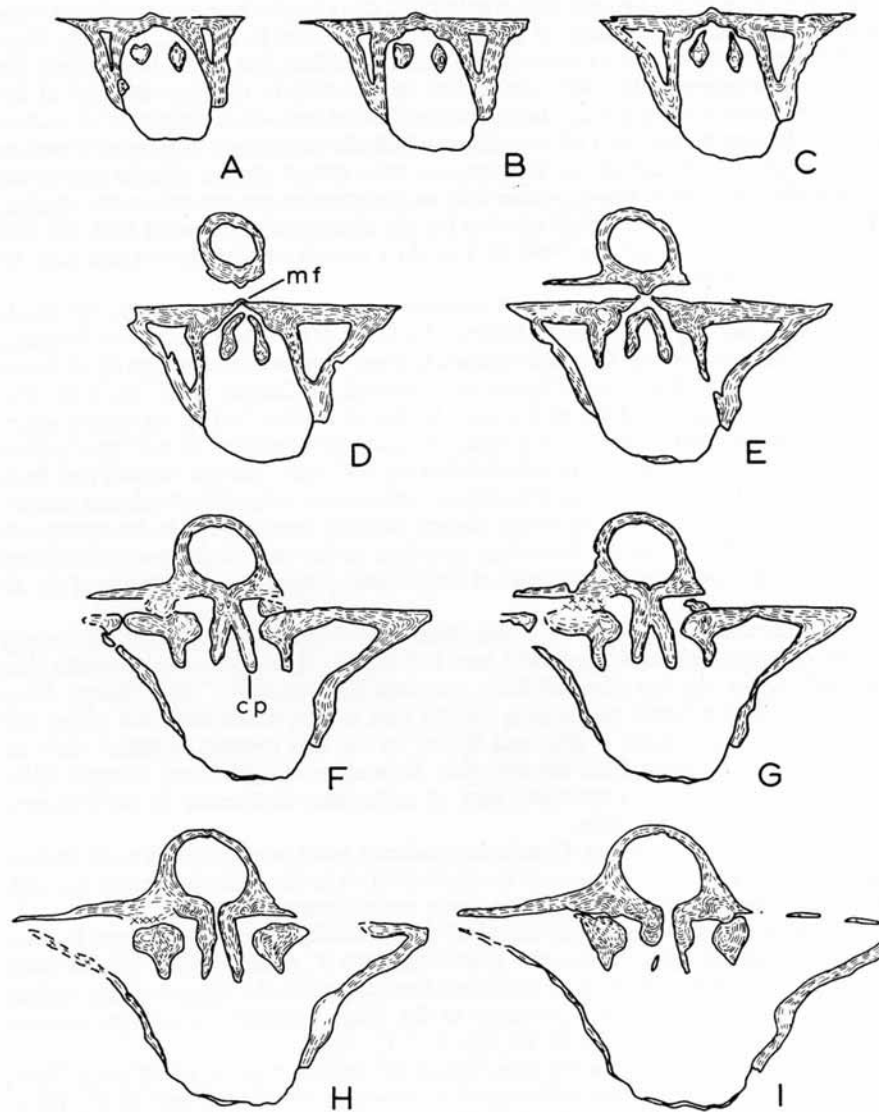
With respect to variation in pseudodeltidial morphology, several of the *Oxoplectra* species of Caradoc age described by Cooper (1956) are of considerable interest. A sketch of the pseudodeltidium of *O. multicostellata* Cooper is shown here as text-fig. 4, based on one (fig. 20) of the several illustrations provided by Cooper (1956, pl. 105). This species has a pseudodeltidium with a well-developed median fold in the young stages (at the umbonal end) which is lost in later growth stages. Judging from Cooper's illustrations, the median part of the pseudodeltidium may then become smooth and flush with the lateral parts of the pseudodeltidium, or possess a variably developed median groove anterior to the fold. Although Cooper did not mention this in his systematic description of the species, he does draw attention to the part of the pseudodeltidium laid down anterior to the anterior end of the elevated ridge in his description of fig. 20 (p. 1112).

While material of this species (from Sharon Springs in particular) is commonly heavily replaced by beekite, as is well seen in Cooper's figures, there is no doubt that the 'half ridges' on the pseudodeltidia are *bona fide* structures. This change from a pseudodeltidium which possesses a median fold to one which does not within the life-cycle of an individual is also well shown by the less coarsely replaced shells of *Oxoplectra filosa* Cooper from the Bromide Formation of Oklahoma (Cooper 1956, pl. 103, fig. 11), and is apparently also of infrequent occurrence in the Portrane *Oxoplectra* as mentioned above.

Another of Cooper's species, *Oxoplectra nevadensis*, has a pseudodeltidium which does not show a median fold. The species is commented on in the plate description (pl. 102, fig. 43) as having an 'interarea with (a) nearly smooth pseudodeltidium'.

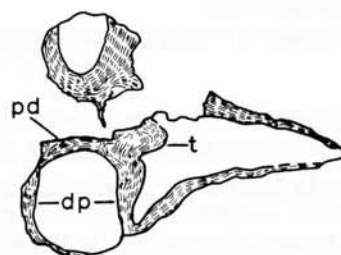
Text-fig. 5 shows another modification of the pseudodeltidium which occurs in some triplesiids such as *Triplesia insularis* (Eichwald) and *T. ortonii* (Meek). In this case, although the lateral parts of the pseudodeltidium extend to the hinge-line, the median fold terminates some distance posterior to the hinge producing a very pronounced notch or invagination (see also Pl. 63, figs. 5, 7, 15, 16).

Even specimens of *Triplesia praecipecta* figured by Amsden show some variation. Thus, although the pseudodeltidium of the specimen shown in Amsden's (1968) pl. 18, fig. 3*h* is essentially flat, an irregular median fracture such as has been noted in the Portrane shells above also occurs; while fig. 3*k* shows a faint raised line medianly. Doubts as to whether the pseudodeltidium of this species is invariably perfectly flat are supported by serial sections of a specimen from Cason Mine, Arkansas, prepared some time ago. These show the pseudodeltidium as a flat structure under low magnifications

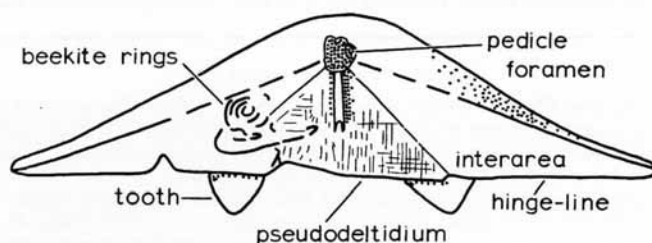


TEXT-FIG. 2. Transverse serial sections through a specimen of *Oxoplectra* sp., Chair of Kildare Limestone, Kildare (QUB 25493). Section A taken at 0.8 mm from the ventral umbo, others in sequence at 0.1 mm intervals,  $\times 8$ . cp—cardinal process; mf—median fold.

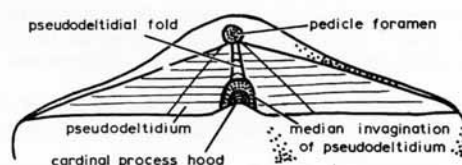
(text-fig. 1c). Under higher magnification however, a very small indentation may be observed on the inside of the pseudodeltidium which is only visible as a flexure in the shell laminae, the indentation itself being filled with micrite. Whether this small-scale



TEXT-FIG. 3. Transverse section taken at 0.9 mm from the ventral umbo of an *Oxoplectra* specimen from the same sample as that of text-fig. 2; left side broken away. QUB 25494,  $\times 8$ . dp—dental plate; pd—pseudodeltidium; t—tooth.



TEXT-FIG. 4. Stylized illustration to show the loss of the pseudodeltidial fold in *Oxoplectra multicostellata* Cooper, based on the specimen illustrated by Cooper (1956, pl. 20),  $\times 6$ .



TEXT-FIG. 5. Stylized illustration of the pedicle valve interarea of a *Triplesia* with a well-developed median invagination to the pseudodeltidium,  $\times 4$ .

fold can be traced through to the outer surface is uncertain, as poor detail in the shell laminae there together with a coating of micrite makes interpretation of the surface detail hazardous; nevertheless the indentation suggests that folding of the pseudodeltidium may be developed on a very small scale in this species, at least as a variant.

The relevant points arising from the above discussion with respect to the taxonomic value of the pseudodeltidial fold are that:

- (1) Individuals constituting the samples of certain species may or may not possess a variably developed median fold.
- (2) Certain species which possess a fold in the young stages, lose it in the adult.

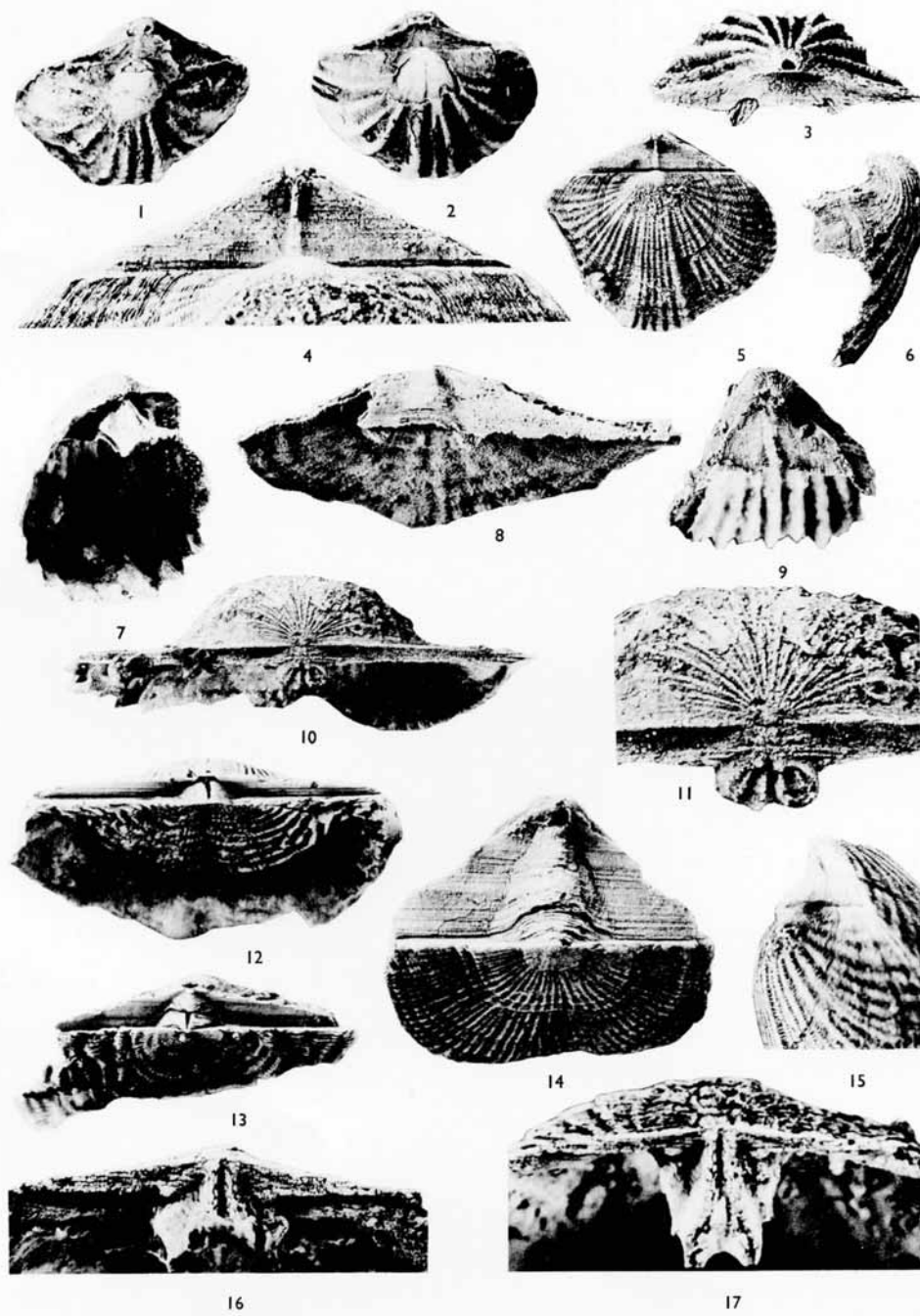
#### THE PSEUDODELTIDIUM AND ITS DORSAL COUNTERPART IN TRIPLESIAEANS AND OTHER STOCKS

Regardless of the variation in detail of the pseudodeltidium and its fold, a feature of the triplesiaeans is that, with the exception of the pedicle foramen which is essential for extrusion of the pedicle and attachment of the shell to the substrate, the postero-median part of the shell is closed to the exterior by shell substance. The interarea of the pedicle valve has the delthyrium closed by the pseudodeltidium which may extend more or less evenly to the hinge-line (Pl. 62, figs. 3, 5); or if it is indented medianly, this space is filled by the cardinal process hood (Wright 1963, p. 749) when the shell is closed (Pl. 63, figs. 7, 16). The interarea of the brachial valve is almost always obsolete and therefore

#### EXPLANATION OF PLATE 62

- Figs. 1, 2. *Oxoplectra* sp. Chair of Kildare Limestone (Ashgill), Ireland. Dorsal views of two shells with pseudodeltidial fold present and apparently absent, respectively,  $\times 3$ , QUB 25480 and 25481.
- Fig. 3. *Oxoplectra* cf. *plicata* (Wiman 1907). Portrane Limestone (Ashgill), Portrane, Ireland. Posterior view of pedicle valve showing pseudodeltidium,  $\times 3$ , QUB 25482.
- Figs. 4, 5, 15. *Oxoplectra gouldi* Ulrich and Cooper 1936. Bromide Formation (Upper Ordovician), Spring Creek, Oklahoma. 5, dorsal view of complete shell,  $\times 1.5$ , QUB 25483. 4, 15, enlarged dorsal and oblique lateral views to show detail of interarea and median pseudodeltidial fold.  $\times 4$ .
- Figs. 6, 7, 9. *Meekella* sp. Word Limestone (Permian), Glass Mountains, Texas,  $\times 2$ , BM B11899a, b. 6, 9, lateral and postero-dorsal views of pedicle valve showing form of interarea. 7, oblique lateral view of brachial valve, showing relation of cardinal process to hinge-line.
- Figs. 8, 10, 11. *Schellwienella radialis* (Phillips 1836). Lower Carboniferous, Bundoran, Ireland. 8, posterior view of pedicle valve,  $\times 1.5$ , QUB 25484. 10, 11, posterior view,  $\times 1$ , of brachial valve, and enlargement,  $\times 2$ , to show details of the chilidium-cardinal process relationships, QUB 25485.
- Fig. 12. *Leptaena depressa* (J. de C. Sowerby 1823). Dudley Limestone (Wenlock), Dudley. Posterior view of conjoined valves showing large, medianly grooved chilidium and small pseudodeltidium,  $\times 2$ , QUB 25486.
- Fig. 13. *Leptaena poulsoni* Kelly 1967. Dudley Limestone (Wenlock), Wren's Nest, Dudley. Posterior view of conjoined valves showing medianly grooved chilidium and relatively large pseudodeltidium,  $\times 2$ , QUB 25487.
- Fig. 14. *Vellamo diversa* (Shaler 1865). Ellis Bay Formation (Upper Ordovician), Junction Cliff, Anticosti. Postero-dorsal view of conjoined valves showing the relations of the pseudodeltidium and chilidium,  $\times 2$ , QUB 25488.
- Figs. 16, 17. *Meekella* sp., Leonard Formation (Permian), Old Word Ranch, Texas. Ventral and postero-ventral views of interarea and cardinalia of a brachial valve (cf. text-fig. 6),  $\times 4$ , QUB 25489.
- The photographs are not retouched, but all specimens were coated with ammonium chloride before photographing. Abbreviations of repositories: BM—British Museum of Natural History, London; PMO—Palaeontological Museum, Oslo; RMS—Riksmuseum, Stockholm; QUB—Queen's University Geology Department, Belfast.





WRIGHT, Triplesiacean pseudodeltidium



without a notothyrium, although rarely, in such shells as the gerontic specimens of *T. orton* (Pl. 63), the essentially linear hinge-line is sufficiently lengthened to warrant the use of the term interarea.

Not all brachiopods have, nor appear to need, this effective closure of the delthyrium and the notothyrium by extension of the mineral skeleton. In the great majority of orthaceans, for example, these structures are open, and are only partially closed in the billingsellaceans, for the pseudodeltidium has a concave anterior margin which, despite the presence of a chilidium in the brachial valve, commonly leaves a gape in the middle of the hinge-line when the valves are closed. But in the plectambonitaceans and most of the strophomenaceans the pseudodeltidia and chilidia are sufficiently well developed as to close any such gap along the posterior margin, with an increase in the size of one being matched by a decrease in size of the other as was shown by Williams for the stropheodontids (1953, p. 14).

A change in the relative size of the two structures without resulting in a median gape is here illustrated by two specimens of *Leptaena* from the Wenlock Limestone of Dudley. The typical *Leptaena depressa* (Sowerby) shows a very small pseudodeltidium with the notothyrial and delthyrial openings largely filled by the medianly grooved chilidium (Pl. 62, fig. 12); while in the second form, which would be separated by Kelly as *L. poulsoni* (1967, p. 597), the size of the pseudodeltidium is much increased relative to the chilidium (Pl. 62, fig. 13). In this specimen at least, the increased size of the pseudodeltidium is largely a reflection of the doubling of the length of the pedicle valve interarea rather than any reduction of the chilidium. These specimens show firstly, that it is apparently important to the *Leptaena* not to allow a posterior gape and secondly, that the two plates are very intimately related.

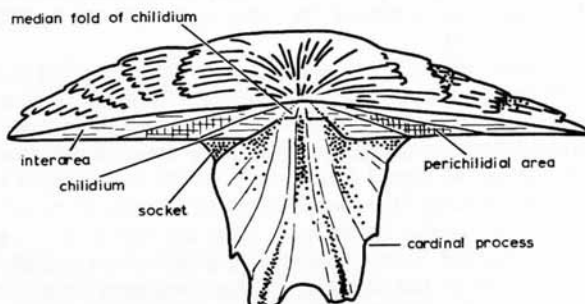
The illustration of the clitaenacean *Vellamo* (Pl. 62, fig. 14) also shows the very close relationship between the pseudodeltidium and chilidium. This specimen, from the Upper Ordovician of Anticosti Island, shows that the details of one are mirrored by the other; the chilidium is not evenly convex, but shows a distinct break in slope a little way in from the edge of the notothyrium on either side, a feature which is also displayed by the pseudodeltidium. This specimen is of interest with respect to the triplesiacean pseudodeltidium as it shows at least a stage in the differentiation of a pseudodeltidium.

The similarities to the triplesiaceans become clearer when the davidsoniaceans are considered. Although both stocks were regarded as subfamilies of the Strophomenidae by Schuchert (1913, p. 387) and Schuchert and Le Vene (1929, p. 16), various characters, but principally the impunctate nature of the shell, resulted in the Triplesiacea being regarded as aberrant orthides (Wright 1963). Recent study of the shell fabric strongly suggests that the triplesiaceans and davidsoniaceans are closely related, having diverged from the orthidine billingsellacean stock probably in late Cambrian times (Williams 1970); and although pseudopunctae are now known to occur rarely in the Triplesiacea (Wright 1970), the likely ancestry of the superfamily makes it difficult to regard them at present as being unequivocal strophomenides.

Two members of the davidsoniacean subfamily Meekellinae Stehli are illustrated to show the variation in the pseudodeltidium within the single subfamily, and the close relationship of the structure to the chilidium. *Schellwienella* shows a broad, evenly convex pseudodeltidium (Pl. 62, fig. 8), and a similarly broad and evenly convex chilidium occupies the centre of the short dorsal interarea (Pl. 62, figs. 10, 11). By

contrast, *Meekella* possesses a pseudodeltidium which is flat laterally and arched medianly (Pl. 62, figs. 6, 9) in the manner of the typical triplasiacean; this similarity to the triplasiaceans is again seen in the brachial valve where the interarea is obsolete (Stehli 1954, p. 303) or linear (Williams 1965, p. H405), while the chilidium, if developed, is regarded as vestigial.

One large brachial valve of *Meekella*, however, shows an interarea which is relatively long (Pl. 62, figs. 16, 17). Fragments of the chilidium in the hitherto accepted sense may be seen to cover the very proximal portions of the cardinal process ridges. But in addition a pair of clearly defined grooves extend across the interarea antero-laterally from the beak to reach the hinge-line at a position corresponding to that of the outside edge of

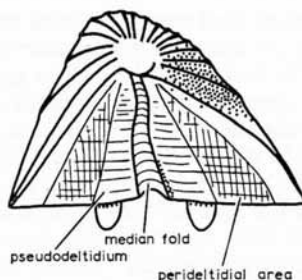


TEXT-FIG. 6. Stylized illustration of the posterior of a brachial valve of *Meekella* to show the features of the hinge region (cf. Pl. 62, figs. 16, 17).  $\times 6$ .

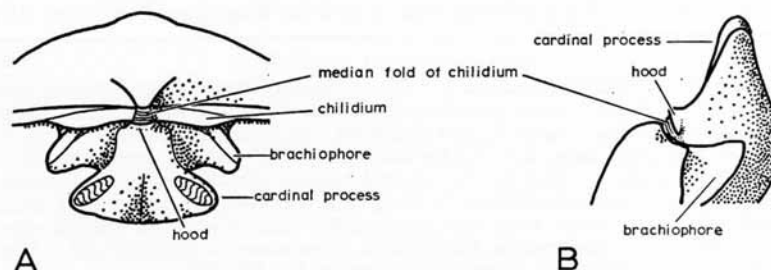
the ventral tooth when the valves are articulated. Reference to the *Meekella* pedicle valve shows that the flat part of the pseudodeltidium also extends to the outside edge of the tooth (Pl. 62, fig. 9). Thus the median area between the pair of well-defined grooves on the dorsal interarea, which is slightly raised relative to that part of the interarea lateral to it, must itself be the chilidium. According to this interpretation, the chilidium of *Meekella* is flat laterally with a median ridge (the 'vestigial chilidium' of authors) covering the posterior of the narrow cardinal process (text-fig. 6), and corresponds closely to the form of the pseudodeltidium in the manner already noted above for the pseudodeltidia and chilidia of *Vellamo*, *Leptaena*, and *Schellwienella*.

The ventral interarea of the Davidsoniacea is characterized by a perideltidial area, whose function is uncertain (Williams 1965, p. H364). The structure can be seen in the figured *Meekella* to extend from the edge of the pseudodeltidium at the outside of the tooth, to a position very close to the cardinal extremities of the shell (Pl. 62, fig. 9, text-fig. 7). The possibility of what is here regarded as the chilidium being a reflection of the perideltidial area in the brachial valve may be dismissed by virtue of the different positions occupied by these structures along the hinge-line. But what is interesting is that a close examination of the dorsal interarea reveals that this is also divisible into an area corresponding to the perideltidial area of the pedicle valve (Pl. 62, fig. 16, text-fig. 6), although the definition of its outside edge is much less obvious than its junction with the chilidium. The term *perichilidial area* is appropriate for this morphological feature.

Bearing in mind the normal very close relationship between the morphology of the chilidium and the pseudodeltidium, and the arrangement seen in *Meekella*, the dorsal hinge region of the triplesiaceans may now be examined. The hinge-line of the triplesiacean brachial valve is only rarely developed into an interarea; but as mentioned above the very thick shells of *Triplesia ortonii* (Meek) from the Brassfield Formation of Dayton, Ohio, do show some development of this region, and provide a picture of the basic arrangement.



TEXT-FIG. 7. Stylized illustration to show features of the pedicle valve interarea of *Meekella*.  $\times 4$ .



TEXT-FIG. 8. Stylized illustrations of posterior (A) and lateral (B) views of the brachial valve of *Triplesia ortonii* (Meek) to show features of the hinge region.  $\times 4$ .

From Plate 63, fig. 8 it can be seen that a pair of oblique furrows extend laterally across the very short interarea to reach the hinge-line at a position corresponding to the outside of the sockets. By comparison with the arrangement outlined for *Meekella*, these grooves may be regarded as marking the lateral edges of the notothyrium and also the chilidium. The first point then on this interpretation is that the chilidium is very much wider than has been previously supposed. The second point is that in the middle of this chilidium there is a fold developed (Pl. 63, fig. 6, text-fig. 8), which is in part the chilidium of earlier authors. The third point is that the cardinal process also develops a hood which, as stated before, is an internal structure (Wright 1963, p. 752) quite distinct from the median fold of the chilidium when both are developed. The latter is seen to occupy the space between the umbo and the hood in these shells (Pl. 63, fig. 6, and text-fig. 8) and is an external feature on those shells which have developed a short interarea.

Where the dorsal interarea is lacking, the only median structure which may develop at the posterior of the cardinal process is the hood. This hood is of very variable form even within a species (Pl. 63, figs. 2, 6, 8, 11), although it is commonly undercut on the umbonal side showing that it can develop *towards* the umbo in contrast to a chilidium which must develop towards the hinge-line.

#### FACTORS AFFECTING THE PSEUDODELTIDIAL FOLD DEVELOPMENT

The growth of any brachiopod shell must be related to an efficient opening of the valves to allow the circulation of water within the mantle cavity, and the various structures of the hinge-line must be looked at with this in mind. In the case of *Vellamo*, *Leptaena* and, to a somewhat lesser extent, *Schellwienella* the dorsal interareas are well developed, with the latter standing relatively high above the hinge-line so that when the valves open the chilidium will be displaced ventrally to slide under the anterior margin of the pseudodeltidium. But the very short interarea of *Meekella* means that the dorsal umbo is virtually on the hinge-line and will itself move in towards the pseudodeltidium when the valves open. At the same time the high, narrow cardinal process located immediately beneath the umbo and extending ventrally under an essentially catacline ventral interarea (Pl. 62, figs. 7, 6) suggests that the median fold of the pseudodeltidium in this case is a direct reflection of the need to accommodate this cardinal process. This is supported by the contrast with *Schellwienella*, where the broad chilidium covers a cardinal process which itself has a broad contact with the hinge-line (Pl. 62, figs. 10, 11).

#### EXPLANATION OF PLATE 63

Figs. 1-3, 6, 8-11, 15. *Triplesia ortonii* (Meek 1872), mainly from the Davidson Collection, localized as Clinton Group, North America, and Silurian, Dayton, Ohio. 1-3, lateral, dorsal, and ventral views of imperfect brachial valve,  $\times 3$ , showing features of the cardinalia, BM BB33840. 6, oblique lateral view of brachial valve,  $\times 3$ , showing chilidial fold and undercut cardinal process hood, BM B78618. 8, 9, postero-dorsal and oblique lateral views of a brachial valve,  $\times 3$ , showing interarea, chilidium, grooved cardinal process hood and other features of the cardinalia (cf. text-fig. 8), BM BB33841. 10, 11, oblique lateral and postero-dorsal views of imperfect brachial valve,  $\times 3$ , showing details of hinge and cardinalia, BM BB33842. 15, posterior view of pedicle valve,  $\times 3$ , showing pseudodeltidium and fold with deep median invagination, BM BB33843.

Fig. 4. *Oxoplectra multicostellata* Cooper 1956. Chatham Hill Formation (Upper Ordovician), Sharon Springs, Virginia. Lateral view of broken shell showing relation of forked cardinal process to umbo and interarea of pedicle valve,  $\times 4$ , QUB 25490.

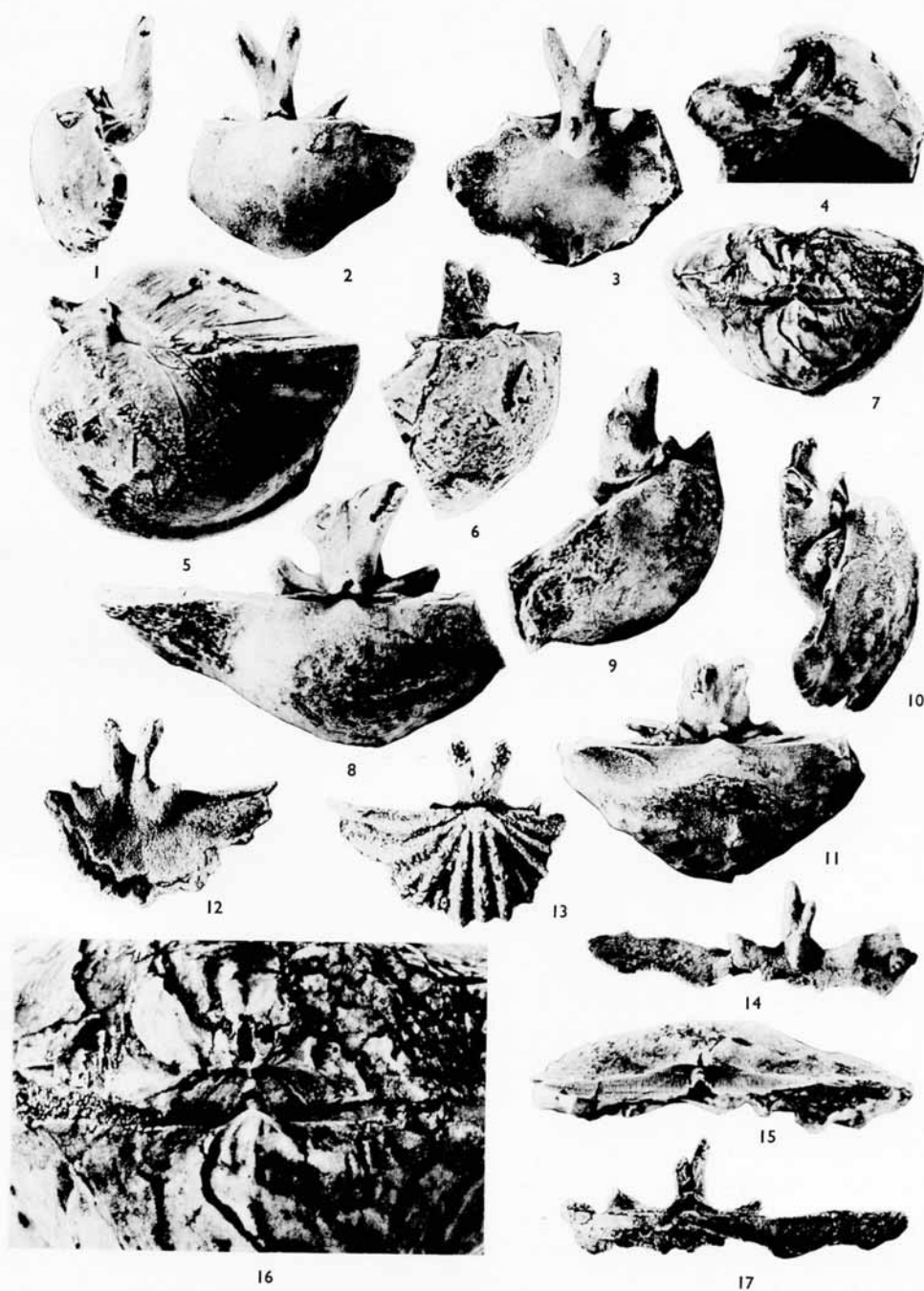
Fig. 5. *Triplesia insularis* (Eichwald 1842). ? F<sub>1</sub>C<sub>a</sub> (Upper Ordovician) Dagö, Estonia. Oblique lateral view showing the disposition of the brachial valve umbo relative to the pseudodeltidial fold,  $\times 2$ , RMS Br. 67848.

Figs. 7, 16. *Triplesia* sp. Stage ? 6 (Lower Llandovery), Brønnøy, Asker, Oslo. PMO 52179. 7, posterior view of partially exfoliated conjoined valves showing disposition of features of the posterior margin,  $\times 1.5$ . 16, enlargement,  $\times 4$ , to show detail of pseudodeltidial fold and cardinal process hood visible through median invagination of pseudodeltidium. PMO 52179.  $\times 4$ .

Figs. 12, 13. *Oxoplectra* cf. *plicata* (Wiman 1907). Portrane Limestone (Ashgill), Portrane, Ireland. Ventral and dorsal views of damaged brachial valve showing a 'grooved' cardinal process lacking hood development,  $\times 3$ , BM BB30340.

Figs. 14, 17. *Triplesia* cf. *insularis* (Eichwald 1842). Portrane Limestone (Ashgill), Portrane, Ireland. Ventral and dorsal views of hinge region showing 'keeled' cardinal process with well developed hood,  $\times 5$ , BM BB30335.

The photographs are not retouched, but all specimens were coated with ammonium chloride before photographing. Abbreviations of repositories as for Plate 62.



WRIGHT, Triplesiacean pseudodeltidium

The triplesiacean arrangement differs from that of *Meekella* in the basic attitudes of the ventral interarea and the cardinal process. The interarea is essentially apsacline with the cardinal process directed posteriorly into the ventral umbo (Pl. 63, figs. 1, 4). The position of the triplesiacean hood in the conjoined valves may be seen from the partially exfoliated specimen of *Triplesia* sp. through the anterior invagination of the pseudodeltidium (Pl. 63, figs. 7, 16).

This specimen shows that when the valves are closed, the hood serves to shut this median invagination and acts in place of the anterior part of the pseudodeltidium which is unable to develop in *Triplesia* as a consequence of the extremely convex and swollen dorsal umbo (Wright 1963, p. 752). When the valves open the hood moves antero-ventrally while the dorsal umbo moves into the space beneath the pseudodeltidial fold (Pl. 63, fig. 5). The very strong convexity of the dorsal umbo in these *Triplesia* species then accounts for a large measure of the antero-median shortening of the pseudodeltidium and its fold, rather than exerting any marked influence on the formation of that fold (cf. Wright 1963, p. 746). In forms lacking the very tumid dorsal umbo the indentation is very much reduced, as in *Oxoplectra gouldi* Ulrich and Cooper (Pl. 62, fig. 5).

In addition to the convexity of the dorsal umbo, the attitude of the ventral interarea is a further factor affecting relationships of the two valves along the hinge-line. At least some control on the pseudodeltidial fold by the interarea is suggested by the specimen *O. gouldi* cited above. The fold is pronounced posteriorly, but shows an abrupt reduction in stature during its development (Pl. 62, figs. 4, 15). The reduction corresponds to a well-marked growth-line on the interarea, and further marks the position of a break in slope on the interarea surface where the curved apsacline area flattens. Examination of a few specimens of *Oxoplectra multicostellata* coupled with Cooper's illustrations (1956, pl. 105) suggests the possibility that the loss of the pseudodeltidial fold on this form may be correlated with a change from curved apsacline to a much flatter almost catacline attitude of the ventral interarea. This is merely an impression whose significance could only be established from the detailed study of a large sample of this most interesting form.

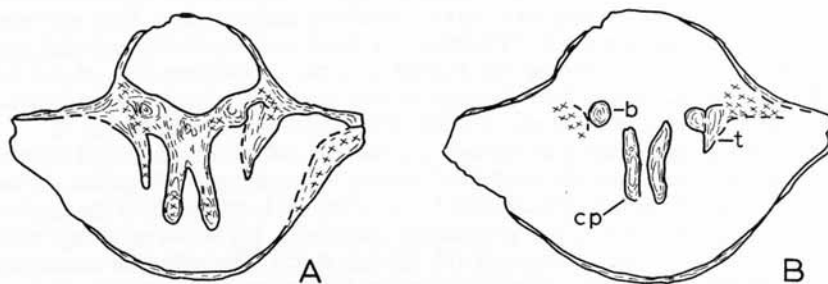
While the convexity of the dorsal umbo and the attitudes of the ventral interarea and cardinal process may all play a part in influencing the form of the pseudodeltidium, the principal factor appears to be the nature of the proximal part of the cardinal process on its dorsal side, and possibly also the cardinal process hood. Reference may be made again to the *Oxoplectra* and *Triplesia* from Portrane mentioned above (Pl. 63, figs. 12, 13, 14, 17). The *Oxoplectra*, which commonly lacks the pseudodeltidial fold, is characterized by a 'cardinal process (which is) broad proximally' and a 'hood (which is) not developed, commonly replaced by (a) small pit' (Wright 1964, p. 248). It may be noted that the broad process without a hood is also clear on Wiman's figure of *O. plicata* (1907, fig. 13); and that the *Schellwienella* discussed above also has a broad process. The Portrane *Triplesia* with its persistent pseudodeltidial fold has, on the other hand, a cardinal process which is narrow proximally relative to the width of the hinge-line, as in *Meekella*, and a hood which is 'invariably present' (Wright 1964, p. 246).

Although the chilidium and dorsal surface of the essentially posteriorly directed cardinal process are clearly the parts of the brachial valve most likely to be intimately related to the form of the pseudodeltidium, there is a further important difference between the cardinalia of these two Portrane triplesiids. The *Triplesia* has a forked



cardinal process which is fused proximally into a stout ridge, with the brachioophores or socket ridges well separated from the process laterally (Pl. 63, fig. 14). In contrast the *Oxoplecia* (Pl. 63, fig. 12) has no proximal ridge on its ventral surface, but is essentially cleaved into two lobes along its length with the lobes strongly ankylosed to their adjacent brachioophores rather than to each other.

The two cardinal processes, which for convenience may be referred to as 'keeled' in the *Triplesia* species and 'grooved' in the *Oxoplecia* are fundamentally different types within the broad concept of the triplesiacean cardinal process. The grooved form appears to be the much rarer development, although cardinal process details are unknown for the majority of species.



TEXT-FIG. 9. Transverse serial sections through a specimen of *Triplesia praecipecta* Ulrich and Cooper to show the grooved cardinal process. Peels for A, B, taken at 0.45 and 0.6 mm from the ventral umbo respectively. QUB 25491,  $\times 20$ . b—brachioophore; cp—cardinal process; t—tooth.

No mention is made of a hood or chilidium being present in *T. praecipecta* by Amsden (1968); neither is one apparent from his illustrated sections (text-figs. 23, 24), nor from my own serial sections. Not that this is conclusive, for although a well-formed hood is clearly distinguishable in sections of a large *Triplesia* like *T. extans* (Wright 1963, text-figs. 5, 7), a small hood in a small species such as *T. praecipecta* could be difficult to recognize in such sections. Although external appearances (Amsden, pl. 18, fig. 3k) suggest that the presence of a hood is unlikely, its absence would need to be confirmed from disarticulated brachial valves.

The cardinal process on this species is described by Amsden as being long and forked, and lying 'about at right angles to the valve commissure' (p. 41). This last point is interesting and may, along with the tendency for the ventral interarea to become almost catacline, have been a factor related to the non-development of the pseudodeltidial fold. But the interesting feature of the cardinal process revealed by Amsden's sections (text-figs. 23B, C; 24D, E) and shown here in text-fig. 9 is that it is of the grooved type. This immediately suggests that there may be a major subdivision of the triplesiids on Amsden's lines using as a basis the form of the cardinal process supplemented by the condition of the pseudodeltidium. Even if the variation in the pseudodeltidium could be ignored, the typical Portrane *Oxoplecia* shows a smooth pseudodeltidium and a grooved cardinal process; but specimens from the Kildare sample show beyond doubt a grooved process associated with a medianly folded pseudodeltidium (text-fig. 2).



Consideration of *Oxoplectra multicostellata*, whose pseudodeltidial fold is not developed in the later growth-stages, makes the situation more complex for the keel of the cardinal process is well developed before the pseudodeltidial fold is lost (Cooper 1956, pl. 105). The redistribution of calcite by resorption and secretion around the cardinalia to produce a grooved process would be exceptional; but clearly this species is one in which detailed study of population variation and growth of a large sample would help considerably towards the understanding of the group as a whole.

#### CONCLUSIONS

The study of variation of the triplesiacean pseudodeltidium shows that while in the overwhelming majority of species a pseudodeltidial fold is developed, in a few stocks it is more commonly absent but apparently not completely excluded. This variation of development within valves apparently from the same populations, together with the fact that some shells show a loss of the fold during ontogeny, indicates that the absence of the fold is not of major taxonomic importance in the group.

The structure which has most bearing on the development of the median fold is the cardinal process, in particular the position occupied by this structure in the region of the hinge itself. But other features such as the attitude of the cardinal process coupled with that of the ventral interarea, the cardinal process hood and the chilidium, and the convexity of the brachial umbo coupled with the drastic reduction in the dorsal interarea, also affected the fold development.

That the cardinal process and the loss of interarea in the brachial valve are closely related to the development of a pseudodeltidial fold may be seen by comparison with the related davidsoniacean, *Meekella*. It would seem that even within the Meekellinae the fold was formed as the need arose by the pressure of a similar suite of factors—all factors which are concerned with the fundamental operation of opening and closing the valves.

It seems, therefore, that the absence of a median fold on the triplesiacean pseudodeltidium is taxonomically only of value for specific differentiation at the most, i.e. one species consistently has a fold; another is characterized by its variable development; while another appears to lack a fold. Accordingly I cannot accept the establishment of either the subfamily Placotriplesiinae or the genus *Placotriplesia* on the basis of the absence of the pseudodeltidial fold.

Although it is again pointed out that there are two basic kinds of cardinal process in the triplesiaceans, they are certainly no more different than those of *Meekella* and *Schellwienella*; and until more data are accumulated on the development and distribution of the two types within the presently accepted genera, they cannot be regarded as a suitable means of subdividing the group.

*Acknowledgements.* It is a pleasure to record my thanks to Professor Alwyn Williams for making his extensive personal brachiopod collections available to me, and for his kindness in reading the manuscript; and to Dr. L. R. M. Cocks, Dr. G. A. Cooper, Professor Gunnar Henningsmoen, and Dr. Valdar Jaanusson for the loan of specimens from the collections within their care.

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Manuscript received 27 July 1970