

# ROLE OF SHELL STRUCTURE IN THE CLASSIFICATION OF THE ORTHOTETIDINE BRACHIOPODS

by ALWYN WILLIAMS and C. H. C. BRUNTON

ABSTRACT. The secondary shell of the spire-bearing *Davidsonia* is fibrous, whereas in all true orthotetidine brachiopods it is laminar. For this reason, *Davidsonia* and related genera, which constitute the Davidsoniidae, are transferred to the spire-bearing brachiopods, the Atrypidina. The oldest known orthotetidines are impunctate, but the Ashgillian *Fardenia scotica* rarely bears incipient pseudopunctae, which apparently arise through spiral perpetuation of screw dislocations. This origin seems appropriate for orthotetoid pseudopunctae as a whole, which have not yet been found to contain undoubted taleolae. Among schuchertellids, inwardly projecting pseudopunctae were replaced by outwardly pointing extropunctae which could have evolved by changes in the rate of shell secretion relative to a different kind of organic holdfast. Koskinoid perforations also penetrate most orthotetidine shells, but they do so without deflecting lamination and were probably drilled mechanically by boring organisms.

Assuming shell structure and the loss of a functional pedicle foramen each to have the same taxonomic weight as all the morphological features developed for articulation and muscle support, phylogenetic analysis confirms that the orthotetidines belong to two superfamilies: an older paraphyletic Chilidiopsoidea, and a younger monophyletic Orthotetoidea. Both groups were affected by homeomorphic trends resulting from cementation and conical deepening of the ventral valves of many independent stocks. They can, however, be distinguished by phylogenetic analysis which provides cladograms consistent with their stratigraphic distribution.

THE orthotetidine brachiopods have always been the subject of taxonomic confusion. The distinctiveness shared by core genera, like *Orthotetes* Fischer de Waldheim, 1850, *Hipparionyx* Vanuxem, 1842, and *Streptorhynchus* King, 1850, has never been in doubt, but their precise affinities with other brachiopod groups have repeatedly given free rein to taxonomic practices bordering on the eccentric. These have been well documented by Manankov (1979a) and will not be reiterated except where they touch upon amendments of recent classifications which have led to the one being offered here.

The first authoritative grouping of the orthotetoids within the Brachiopoda as a whole was that presented by Schuchert (*in* Schuchert and Le Vene 1929, p. 16), who accepted the Orthotetinae of Waagen (1884) as a strophomenoid subfamilial repository, not only for all orthotetoid genera then known but also for an orthoid (*Orthidium*) with a vaguely 'orthotetoid' cardinal process, and for all resupinate strophomenides!

In the 1950s, when the Superfamily Orthotetacea was first proposed (Williams 1953, p. 9), a number of families were erected by various students of the group so that, by the end of the decade, seven such taxa were recognized (Williams 1953; Stehli 1954; G. A. Thomas 1958; Boucot 1959). These new taxa largely clarified the definitive orthotetoid character states, although further complications arose with the assignment to the Superfamily of the Davidsoniidae, Gemmellaroiidae, Scacchinellidae and the Thecospiridae by Williams (1953), for no better reason than that they were cemented, strophic stocks allegedly without spines but with a pseudopunctate shell.

By 1965, when the brachiopod volumes of the *Treatise on invertebrate paleontology* were published, the Superfamily had acquired the name of Davidsoniacea in place of Orthotetacea, in accordance with nomenclatorial rules of priority. The Gemmellaroiidae and Scacchinellidae had

both been found to be spinose and had been removed to the Productidina (Muir-Wood and Cooper 1960, p. 66); and, although the Triassic spire-bearing Thecospiridae had been retained in the Superfamily, the orthotetoids could be generally typified as: strophic, biconvex to resupinate, articulate brachiopods; initially with a supra-apical foramen which was lost in all younger, cementing species; and invariably with a secondary laminar shell, initially impunctate but later becoming pseudopunctate.

Since the *Treatise* study of the davidsoniaceans in 1965 (Williams, pp. H405–412), the number of genera assigned to the group has more than doubled to one hundred and four. However, only Cooper and Grant (1974) and Manankov (1979a) have offered a comprehensive revision of the classification to cope with this generic proliferation. The most important steps taken by Cooper and Grant were: (1) to transfer to the Strophomenidina all impunctate genera which were assembled, within an amended Davidsoniacea, into two Families, the Davidsoniidae and Fardeniidae (a junior synonym of the Chilidiopsidae); and (2) to erect a new Suborder, Orthotetidina, for all pseudopunctate genera which were grouped into two Superfamilies, the Orthotetacea and Derbyiacea, containing seven families and seven subfamilies. On the other hand, Manankov (1979a) retained both impunctate and pseudopunctate taxa within an amended Davidsoniacea which embraced four families and ten subfamilies, after the removal of the Thecospiridae and its promotion to the rank of superfamily with the Strophomenida.

The differences between these two classifications are much more fundamental than differences in the number of suprageneric taxa recognized by their authors. Manankov's classification is essentially phylogenetic in theme and prompted him to identify several recurrent trends, especially in changes in shell shape and in the elaboration of dental plates and cardinalia. In contrast, Cooper and Grant (1974) paid much less attention to taxonomic complications that could have arisen from the recurrence of parallel trends, particularly in the development of the cardinalia. Indeed, their approach is basically monothetic, as is exemplified by their exclusion of all impunctate species from their Orthotetidina (1974, p. 256). (Their reassignment of such stocks to the Strophomenidina disregards that that Suborder is pseudopunctate *par excellence*.)

At present then, three very different, flawed classifications are being used in systematic studies of orthotetidines and/or 'davidsoniaceans', as the case may be. Their deficiencies have now been brought into sharp focus by our attempts to update the taxonomy of the orthotetoids for the revised edition of the *Treatise* on the Brachiopoda. Thus the oldest classification currently in use, which was drawn up by one of us (A.W.) for the first edition of the *Treatise*, is not only incapable of accommodating all valid genera erected since 1965, but is also flawed in its use of shell structure for taxonomic purposes. In particular, the classification did not take into account the important discovery by Thomas (1958, p. 36) that in *Streptorhynchus* and allied genera microscopic conical flexuring of the laminar shell points outwardly, not inwardly as in the true pseudopunctate condition. To compound a more general indictment, our own studies of shell structure and morphology and our use of phylogenetic analysis to assess the merits of the two other commonly used classifications, those of Cooper and Grant (1974) and Manankov (1979a), reveal that they are also deficient in one way or another. In fact, we now know enough about this seemingly monophyletic group to conclude that orthotetidine phylogeny is much more complicated than can presently be deduced from the variability and range of known species; and, as the course of orthotetidine evolution becomes unravelled by future studies of new and extant collections, it will continue to prompt changes in taxonomy. Nonetheless, classifications, ephemeral though they may be, have to be put to the test. We have, therefore, decided to publish our current findings, before committing ourselves to a final version for the *Treatise*, in the hope that the model will be improved by the critical appraisal of a wider audience.

#### MATERIALS AND METHODS

Apart from recourse to literature, supplemented by the vast collections of specimens readily available to one of us, this study entailed the preparation of material for the computer as well as

for the electron microscope. It, therefore, seems appropriate to outline the processing of data for both lines of investigation in this section.

#### *Shell structure*

The study of shell structure was undertaken in two ways. Gross identifications, like the presence of pseudopunctae or koskinoid perforations, could adequately be made under the binocular microscope. Consequently, the shell structure of all genera of strategic taxonomic importance was routinely checked by this means except, of course, that of species which are presently known only as moulds or silicified replacements. The data obtained from such surveys have been used in this paper without reference to their precise source, unless they have been incorporated into text-figures.

More detailed studies to determine the basic biomineral units and any other microscopic features of the shell successions were carried out under the scanning electron microscope (SEM). Some whole or fractured specimens were examined in an environmental chamber (WETSEM), using an ISI ABT 55 machine, and required no special preparation. The shell structure of many genera, however, including all those illustrated in this paper, were studied under a Cambridge Stereoscan 360. For this purpose, some specimens were embedded in London resin and, after polymerization of the resin, were cut along preferred planes, which were then polished with alumina (Gamma 100) and etched in 2 per cent EDTA for about 30 minutes. Other specimens were broken to provide fracture sections through the shell or fragments of external and internal surfaces. These pieces were sonicated for 10 to 15 minutes, first in a weak detergent and then, after washing, in acetone, to remove adherent particles before mounting on stubs. All such surfaces and etched sections were coated with gold before examination under the microscope.

In addition to obtaining information on the shell structure of representative orthotetidines, it was necessary to ensure that the features being studied were not the result of changes during the fossilization and subsequent diagenesis of entombing sediments. Control specimens chosen to monitor this possibility were either contemporaneous but unrelated species from the same lithofacies and preferably the same locality, or species with well studied shell structures which could serve as standards for comparison. Details of the specimens used in the SEM studies for this paper are as follows:

#### Cranioidea

*Neocrania anomala* (Müller), Recent, near Oban, Scotland. L14924.

*Petrocrania scabiosa* (Hall), Upper Ordovician, Maysville Formation, Cincinnati, Ohio, USA. L14920a.

#### Strophomenida

*Leptagonia caledonica* Brand, Lower Carboniferous, Great Limestone Shale, Cocklaw Quarry, Scotland. L10106/1.

*Rafinesquina alternata* (Hall), Upper Ordovician, Maysville Formation, Cincinnati, Ohio, USA. L14920b.

*Strophomena planumbona* (Hall), Upper Ordovician, Trenton Group, Cincinnati, Ohio, USA. BMNH 73834.

#### Orthotetidina

*Apsocalymma shiellsi* McIntosh, Lower Carboniferous, Lower Limestone Group, Trearne Quarry, Beith, Scotland. L14922.

*Brochocarina trearnensis* McIntosh, Lower Carboniferous, Lower Limestone Group, Trearne Quarry, Beith, Scotland. B42729.

*Fardenia scotica* Lamont, Upper Ordovician, Lower Drummuck Subgroup, Craighead Inlier, Scotland. L4835/40.

*Orthopleura* sp., Upper Devonian, Cedar Valley Limestone, Washington Highway 11, 12 miles north of Cedar Rapids, Iowa, USA. L14921.

*Schuchertella lens* (White), Mississippian, Louisiana Limestone, Louisiana, Missouri, USA. L14923.

*Streptorhynchus pelargonatus* (Schlotheim), Upper Permian, Gera, Germany. B9329.

*Streptorhynchus pelicanensis* Fletcher, Upper Permian, Kazanian limestone, Pelican Greek, Queensland, Australia. B1749.

*Xystostrophia umbraculum* (Schlotheim), Middle Devonian (Eifelian), Gerolstein, Eifel, Germany. B39585.

#### Atrypidina

*Davidsonia verneuli* Bouchard, Middle Devonian (Eifelian), Gerolstein and Romersheim, Eifel, Germany. B5484, B39660.

#### Spiriferidina

*Spinocyrtia astiolata* (Schlotheim), Middle Devonian (Eifelian), Germany. B2677.

Repository numbers prefaced by L and B or BMNH refer to specimens housed in the Hunterian Museum, Glasgow and The Natural History Museum, London, respectively.

#### Phylogenetic analysis

There are many reasons for attempting a comprehensive reclassification of the Orthotetidina at the present time. Certain basic assumptions, which play a crucial role in shaping the three extant classifications, are no longer tenable. The shell structure of genera assigned to the Orthotetidina (and/or Davidsoniacea) has proved not to be exclusively impunctate or pseudopunctate as current taxonomic practices dictate. Furthermore, convergent dental plates, which characterize many of the later Palaeozoic stocks, did not always function as 'spondylia', although all such morphological features are generally given the same taxonomic weight within a classification, whereas relatively minor changes in the cardinalia may be assigned widely differing values. In short, although recurrent transformations of shell shape and, concomitantly, of articulatory and muscle-bearing devices were widespread, each of the prevailing classifications had been proposed in the expressed belief that homeomorphy affected only those characters which were not important to the erection of the favoured hierarchy!

In the face of such conflicting taxonomic treatment of homeomorphy, it was decided to reclassify the orthotetidines by phylogenetic analysis, deriving the cladogram(s) by parsimonious means and rooting it (them) to outgroups chosen on inferred symplesiomorphies. The program used (PAUP, Version 3.0n) was created and updated by David L. Swofford (January 1991). Each search for the optimal tree (or equally parsimonious trees) was carried out heuristically with ten branch-swapping entrances into the data set; and information was also sought on consistency and homoplasy indices, apomorphic homologues and consensus cladograms of rooted trees.

*Taxonomic and diagnostic data.* Notwithstanding the flexibility of the PAUP program, the orthotetidine data at our disposal were not instantly amenable to phylogenetic resolution at the generic level. By 1992, according to the databases being maintained at the Smithsonian Institution, Washington D.C. and the University of Glasgow, one hundred and four genera had been assigned to the orthotetidine (*s.l.*) group of brachiopods. Of these, eighty-seven (including twenty-five classified as junior synonyms) are, in our opinion, true orthotetidines; eight, including *Davidsonia*, are best assigned to the Atrypidina; two to the Strophomenidina (*s.l.*); and seven to the Articulata.

The sixty-two 'valid' genera constituting the orthotetidines (*s.s.*) can be uniquely described by thirty-seven characters in two to five transformational states. These states were our version of the variability in diagnoses distinguishing genera from one another. In effect, they varied among two or more genera constituting the orthotetidine set although, as the same assemblage of characters was used in analyses of superfamilial subsets, a changing minority became 'uninformative'. They defined transformations in: (1) shell size, shape and ornamentation; (2) shell structure; (3) the cardinal areas, particularly delthyrial and notothyrial features; and (4) all internal features which,

in this suborder, were exclusively those of articulation and musculature. The characters were not programmed as being in ordered states, but a minority were weighted as twice the standard default unit. These included: seven defining the articulatory and muscle supports in the program analysing the Orthotetoidea (transformations in these characters are linked to the conical elongation of ventral valves which was common in this superfamily); and four defining changes in the pedicle foramen, shell structure and dental plates in the primitive Chilidiopsoidea.

Notwithstanding these adjustments, analysing a  $62 \times 37$  matrix (exclusive of outgroups) would have been a prohibitively formidable exercise for the Apple Macintosh IIcx at our disposal, especially as we wished to vary the weighting of characters and the ordering of their states to test the effects of certain assumptions. In any event, a matrix where the number of taxa is almost double that of the characters identifying them is not amenable to meaningful analysis. We, therefore, decided to explore the prospects for assembling suprageneric units into a taxonomic framework, within which genera could be segregated into several, small groups for analysis.

The operational units chosen were the sum total of mutually exclusive families and subfamilies recognized by Cooper and Grant (1974) and Manankov (1979a) in their classifications of the Orthotetidina and/or Davidsoniacea. The Alectorhynchidae, which had been later erected by Henry and Gordon (1985, p. 36), was also included, but not the monotypic Dorsoscyphinae (Roberts 1971, p. 49), which, possibly through oversight, had been omitted from both classifications. (The subfamily is cited as a synonym of the Derbyiinae in the classification proposed in this paper.) The Thecospiridae (retained by Cooper and Grant in their classification, but see Brunton and MacKinnon 1972) were also excluded, as were all spire-bearing genera assigned to the Davidsoniidae, except *Davidsonia* itself which was retained as an outgroup. The Triplesiidae were also chosen as an outgroup. This family, which is typically a biconvex, laminar-shelled stock with a supra-apical foramen restricted by a monticular pseudodeltidium and a bilobed cardinal process, is assumed by us to be the sister group of the Orthotetidina, descended from a billingselloid ancestor.

In all, four families and ten subfamilies constituted our terminal taxa. They could all be diagnosed uniquely by an assemblage of fifteen characters in two to four transformations (Table 1). Of course, the precision with which taxa can be so defined depends upon the way they are represented. Ideally, a family (or subfamily) should be categorized by the sum total holomorphologies of its constituent species. But it is not feasible to retrieve data (much of it imperfect) on this scale. We have, therefore, assumed that each family (or subfamily) involved in our analysis is monophyletic and can be adequately represented by its type genus and/or well described, closely related species. Admittedly, this assumption rules out any immediate phylogenetic appraisal of the variability inherent in monophyletic clusters of genera. However, this deficiency has been partly mitigated by our subsequent use of all well-founded genera to refine, and determine the contents of, those suprageneric taxa which survived the first round of analysis.

The choice of characters for the first stage segregation of orthotetidine taxa was determined partly by the extent to which they have been used in previous suprageneric classification; and partly by the new information provided herein, especially on shell structure. Leaving aside classifications which are strictly monothetic, like those of Likharev (1932) and He and Zhu (1986), a general consensus has emerged on which characters are reliable for taxonomic discrimination at the suprageneric level. The presence then loss of a supra-apical foramen, signalling pedicle atrophy, the distinction between fibrous and laminar secondary shell, and the development of pseudopunctae (or extropunctae as defined in this paper) in an impunctate stock, have usually been perceived as synapomorphies, at subfamily level at least. However, there is a wide divergence of opinion on the relative taxonomic weight of most of these characters. The presence of pseudopunctae, for example, is accorded subordinal and subfamilial recognition by Cooper and Grant (1974) and Manankov (1979a), respectively, in their placing of the Chilidiopsidae within the orthotetidine (*s.l.*) hierarchy.

It is, nonetheless, universally conceded that all such characters are of greater taxonomic importance than, say, incremental changes in the articulatory devices or in the muscle supports of the shell, which have hitherto largely determined the structure of the orthotetidine taxonomic hierarchy. Clearly, a differential weighting would have to be introduced to strike a balance between,

TABLE 1. Characters used in the suprageneric classification of the orthotetidine brachiopods showing: types (I = irreversible; O = ordered; U = unordered); weights (13 or 1); and states (0–4).

Type	Weight	State
I	13	(1) supra-apical foramen present (0), usually present in young stages (1), absent (2)
U	13	(2) shell structure impunctate (0), pseudopunctate (1), extropunctate (2)
U	1	(3) dental ridges discrete (0), sporadically convergent (1), homeospondylium (2)
O	1	(4) dental plates absent (0), short, apical (1), parallel (2), parallel, long (3), convergent (4)
O	1	(5) spondylium absent (0), sessile (1), with median septum (2), free (3)
U	1	(6) ventral median septum absent (0), low to variable (1), high (2), ankylosed to pseudodeltidium (3)
I	1	(7) cardinal process bases discrete (0), becoming fused in later stocks (1), with single shaft (2)
I	1	(8) cardinal process lobes separate, associated with chilidium and hingeline (0), fused, myophore slots postero-ventral of chilidium and hingeline (1)
O	1	(9) socket plates absent or vestigial (0), short, variably disposed (1), recurved (2), recurved to divergent (3), divergent (4)
O	1	(10) fusion of socket plates distinguishable from cardinal process lobes (0), fused with lobes (1)
U	1	(11) chilidium large, discrete plates or single convex arch (0), large, grooved arch (1), narrow convex arch (2), narrow, grooved arch (3), vestigial or residual boss (4)
O	1	(12) brachiophores absent to vestigial (0), developing in later stocks (1), present (2), with promontorium (3)
O	1	(13) ventral umbo symmetrical, low interarea (0), variable (1), asymmetrical, high interarea (2)
O	1	(14) dorsal median septum absent or vestigial (0), low (1), high with raised muscle margin (2)
U	1	(15) radial ornamentation coarsely costate or costellate (0), costellate (1), finely costellate (2), secondarily plicate to costate (3), smooth to costellate (4)

for example, the five characters delineating the detailed morphology of the dorsal cardinalia and the single character defining the microtexture of the shell. In the circumstances, we decided that personal judgement could be at least as telling as reweighting characters commensurate with their rescaled consistency indices. We, therefore, decided to give each of the two basic characters in our analysis – the loss of pedicle and the development of pseudopunctae and extropunctae – a weighting equal to the total scored by the other thirteen characters of the assemblage (Table 1).

The states of the majority of characters used for suprageneric analysis could also be placed in an ordered transformation; in our estimation, some even irreversibly so. Irreversible transformations were the loss of the pedicle and the proximal development of a shaft for an elevated pair of fused cardinal process lobes. The recurrence of many of these trends during orthotetidine evolution was, of course, responsible for the extraordinary amount of homeomorphy affecting the Suborder, which is well shown by identifying ordered characters used in the analysis (Table 1).

TABLE 2. A matrix of sixteen suprageneric units (including the Triplesiidae and Davidsoniidae as outgroups)  $\times$  fifteen characters. It is based on taxa recognized by Cooper and Grant (1974), Manankov (1979) and Henry and Gordon (1985), but diagnosed according to the interpretation of shell structure and morphology given in this paper.

	111111
	123456789012345
Adectorhynchinae	20000021413?212
Pulsiinae	2102000020000?1
Hypopsinae	210420002002211
Derbyiidae	211003214132212
Orthotetidae	212002002000012
Areostrophinae	200001102040102
Chilidiopsinae	100100001000011
Derbyoidinae	210001002002112
Diplaninae	210000212131200
Schuchertellidae	220000002042111
Omboniinae	210400214132212
Meekellinae	210300214143213
Triplesiidae	000100210040104
Orthotetellinae	210430004122112
Streptorhynchidae	220000214132221
Davidsoniidae	000002000140224

Before analysing the assembled matrix of sixteen suprageneric units  $\times$  fifteen characters (Table 2), the classifications of Cooper and Grant (1974) and Manankov (1979a) were each subjected to a PAUP run involving only those families or subfamilies which were orthotetidine in our sense and distinguished by thirteen sets of character states which had been used by all three authors to define their suprageneric units. The triplesiid outgroup was used for both exercises. The operational taxonomic units of the Cooper and Grant classification consisted of twelve families and subfamilies which formed five equally parsimonious trees with a consistency index of 0.596 and a homoplasy index of 0.404. Of the three superfamilies recognized by them, the Orthotetacea was polyphyletic and the Derbyiacea and 'Fardeniaceae' (in lieu of Davidsoniaceae) were paraphyletic in the sense of Farris (1974). Ten orthotetidine families and subfamilies recognized by Manankov were used to test his classification which was based on one superfamily. Two equally parsimonious trees were derived with a consistency index of 0.788 and a homoplasy index of 0.212. Yet all three orthotetidine families featured in the classification, the Orthotetidae, the Schuchertellidae and the Meekellidae, were paraphyletic (Farris 1974).

The phylogenetic analysis of the suprageneric matrix shown in Table 2, identified nine equally parsimonious trees of 132 steps. A strict consensus of the nine trees was then obtained. It revealed that differences among the trees arose from transpositions in the two outgroups relative to the Chilidiopsidae and from some variation in the phylogenetic distance between the Derbyoidinae and the Hypopsinae and Orthotetellidae branch. One of the trees, which was comparable with the consensus cladogram except for the placing of the outgroups relative to the Chilidiopsidae, was chosen to provide further information on reconstructed states for internal nodes and the apomorphic relationships between them and the terminal taxa.

The taxa composing the chosen tree (Text-fig. 6), which had consistency and homoplasy indices of 0.652 and 0.348 respectively, segregated into three groups on the microtexture of the shell. They were: (1) the impunctate Chilidiopsidae and Adectorhynchidae (including the Areostrophinae); (2) the pseudopunctate Orthotetidae (including the Pulsiinae), Orthotetellidae (including the Hypopsinae and Derbyoidinae), Meekellidae (including the Omboniinae) and Derbyiidae (including the Diplaninae); and (3) the extropunctate Schuchertellidae and Streptorhynchidae.

The taxonomic validity of this microtextural segregation was then tested by phylogenetic analyses of the genera that could be unhesitatingly assigned to one or other of the groups, which will be conveniently referred to as the chilidiopsoid, orthotetoid and schuchertelloid groups. Not all genera accepted as orthotetidines were involved in the exercise. Some of the more obvious junior synonyms were withheld, such as the many genera erected by Likharev (1934) as variants of *Derbyia* Waagen, 1884. Others, however, were explicitly included to test the validity of synonymy as in the case of *Chilidiopsis* Boucot, 1959, which is currently suppressed in favour of *Coolinia* Bancroft, 1949. Poorly known genera which had been founded on inadequate diagnoses and/or material were also excluded from the initial analyses. Thus, only twenty-four of the thirty-seven characters used to define orthotetidine genera could be ascertained from the description and illustrations of *Magicothropia* Zhu (1985, p. 51). This lack of data increased the number of cladograms retained at the end of a program involving *Magicothropia*, without giving any indication which generic combinations were attributable to the deficiency. However, when the genus was fed into the chilidiopsoid program after the preferred cladogram had been derived, it was found to be synonymous with *Iridiostrophia* Havlíček, 1965, although the nature of features presently unknown, like the pseudodeltidium and chilidium, may eventually determine otherwise.

The same set of thirty-seven orthotetidine characters were used to build up a matrix for each group. The numbers of orthotetidine genera involved were nineteen, twenty and ten for the chilidiopsoid, orthotetoid and schuchertelloid matrices, respectively; while the Triplesiidae and the pseudopunctate laminar-shelled Stropheodontidae (in place of the unrelated Davidsoniidae) served as outgroups. Much of our information on genera was obtained from diagnoses and illustrations; their variable quality is reflected in the low consistency indices of 0.474, 0.534 and 0.678 for three chilidiopsoid, eight orthotetoid and four schuchertelloid equally parsimonious trees, respectively. The generic tree chosen to typify each group was that nearest to the consensus cladogram. Finally, the clustering of genera within each chosen tree was compared with the contents of currently recognized subfamilies and families and attempts were made to reconcile or rationalize the many differences between the cladograms and published taxonomic hierarchies of the orthotetidines as a whole, although some genera required transfer from one group to another or even removal from the Suborder.

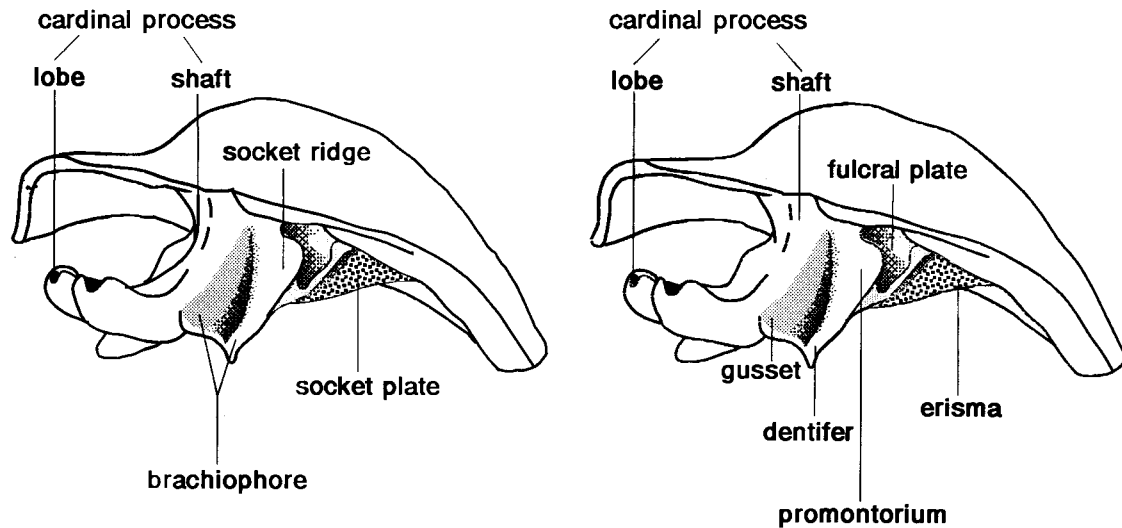
### Terminology

*Morphology.* The terminology used to describe orthotetidine morphology is essentially that compiled for the brachiopod volumes of the *Treatise on invertebrate paleontology* (Williams and Rowell 1965, pp. H139–H155). The glossary has been widely accepted and applied with little emendation. However, Cooper and Grant (1974, pp. 255–256) claimed that a number of terms were inconsistently defined; they coined new ones in their place or to describe features, especially of the cardinalia, which in their opinion were important enough to warrant formal recognition. The application of these new terms has caused difficulty. They have been ambiguously defined, especially in relating the newly named structures to one another and to the cardinal process (Cooper and Grant 1974, p. 352); also the labelling of 'gusset' in figure 40 (Cooper and Grant p. 351) is at variance with the text and with relevant plate figures (compare Cooper and Grant, pl. 110, figs 18–22 with pl. 104, figs 13–17). Our understanding of the terms as used by Cooper and Grant is based on their more succinct definitions (Cooper and Grant, pp. 257–260), insofar as they are consistent with the plate figures.

We see no advantage in accepting the radical terminological changes proposed by Cooper and Grant. Indeed, we share Manankov's concern (1979, pp. 28–29) over their introduction. Their terms, as well as those others used to define features that previously had not been formally named, have been applied without regard for the dynamic relationship between shell and secreting epithelium. Thus, the so-called 'erismata', introduced to distinguish divergent plates associated with the cardinal process from those labelled 'socket plates' by Thomas (1958, p. 19, fig. 6), must have been secreted in exactly the same way as the socket plates, irrespective of their early ontogenetic



appearance. There are, of course, differences in the size of these plates and in the disposition of their constituent facets, but these variations do not warrant a new terminology. We have, therefore, continued to describe orthotetidine cardinalia in terms defined in the *Treatise*, which incidentally have the same meaning as those of Thomas (1958, p. 9). Our correlation of such terms with those employed by Cooper and Grant (1974, p. 351, Fig. 40) is given in Text-figure 1.



TEXT-FIG. 1. Stylized representations of the cardinalia of *Meekella attenuata* Cooper and Grant (1974, pl. 104, fig. 16), identifying the terms used by these authors for the various parts of the structure in the right-hand diagram and those used in this paper in the left-hand diagram.

We also share Manankov's (1979) reservations about the interpretations offered by Cooper and Grant (1974) on other orthotetidine morphological features, especially those involving 'dental plates', 'ridges', 'septa' and 'spondylia'. The definitions of these terms have been amended to take into account whether the features, to which they refer, are of 'primary' or 'secondary' origin. This distinction appears to be based solely on the size of silicified specimens, in which they were first observed, as no shell sections have been described or figured. We do not, therefore, know the nature of the secondary shell accretion or resorption which various features are alleged to have undergone. In these circumstances, we have stuck to the more traditional definitions of the terms in question.

*Taxonomy.* In classifying the Brachiopoda, it has been the practice to use the suffix '-acea' for superfamilies. However, the International Code of Zoological Nomenclature has recently recommended the general adoption of '-oidea'. This recommendation has been accepted by all contributors to the revision of the brachiopod volumes of the *Treatise on invertebrate paleontology*. It is implemented in this paper except when referring to superfamilies in the way they had been taxonomically defined in published works.

#### ORTHOTETIDINE SHELL STRUCTURE

Ultrastructural studies of the shell provide information on its microtexture and its micromorphology. The microtexture is the basic pattern resulting from the periodic secretion of biomineral constituents by the outer epithelium of the mantle. This pattern can be modified by regularly occurring micromorphological features which usually result from microscopic extensions or

invaginations of the mantle into the shell. Both types of microstructure play a crucial role in brachiopod classification, and current investigations of them have also prompted a reappraisal of orthotetidine phylogeny.

#### *Microtexture of the orthotetidine shell*

Our preliminary survey showed that the microtexture of *Davidsonia verneuilli* Bouchard was not laminar in the manner of strophomenides in general and other orthotetidines in particular (Williams 1968, 1970, 1973). The taxonomic position of *Davidsonia* has been controversial since the discovery of calcareous spiralia in *Davidsonia* (Garcia-Alcalde 1973). The two most authoritative consequential reviews of *Davidsonia* itself have been contradictory, with Copper (1979) advocating its transfer to the atrypidines and Johnson (1982) its retention within the orthotetidines. It was, therefore, decided to compare the skeletal ultrastructure of *Davidsonia* with those of the spiriferide *Spinocyrtia astiolata* (Schlotheim) and the orthotetide *Xystostrophia umbraculum* (Schlotheim) from, the same Middle Devonian (Eifelian) successions of Gerolstein and Romersheim, to check the effects of any diagenetic changes on shell microtextures.

The microtexture of the three specimens of *Davidsonia* available for study under the SEM was fibrous. The specimens had been recrystallized so that the calcitic internal matrix formed a sharp micritic boundary with the floors of the dorsal and ventral valves, which were 0.5 mm and 2 mm thick respectively in the best preserved shell. Recrystallization, however, had not obscured details of individual fibres, which were orthodoxly stacked and more or less radially disposed with some flexuring (Pl. 1, fig. 1). The fibres were up to 20  $\mu\text{m}$  wide and 7  $\mu\text{m}$  thick and the externally facing saddles were gently concave and about 6  $\mu\text{m}$  wide.

This fibrous aggregation was characteristic of all fracture surfaces examined. Here and there, however, fibres were interleaved with lenses of more vertically disposed components (Pl. 1, fig. 2), which were up to 35  $\mu\text{m}$  thick and first appeared about 200  $\mu\text{m}$  internally of the outer surface of the dorsal valve. These have been interpreted as impersistent lenses of prismatic calcite. Further study of *Davidsonia* is likely to confirm a first impression that the margin of the ventral valve is thickened by interleaves of prismatic calcite.

The microtexture of *Davidsonia* was identical with that of *Spinocyrtia*, except for the smaller size of the fibres of the latter, seldom more than 10  $\mu\text{m}$  wide. It was fundamentally different from the microtexture of *Xystostrophia*, which has been classified by Cooper and Grant (1974, p. 256) as a davidsoniacean within the Strophomenidina and by Manankov (1979a, p. 30) as a meekellid within the Davidsoniacea. The shell succession of *Xystostrophia* was laminar with individual laminae thinner than 100 nm although usually aggregated into sets, up to 30  $\mu\text{m}$  thick. Each lamina was composed of an amalgamated array of parallel-sided, platy laths 2–3  $\mu\text{m}$  wide (Pl. 1, fig. 3). The only

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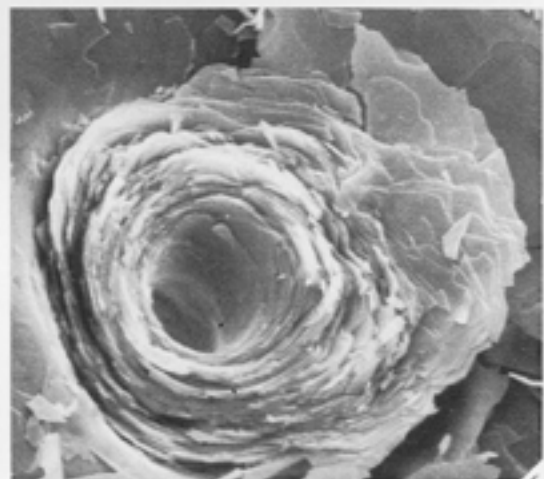
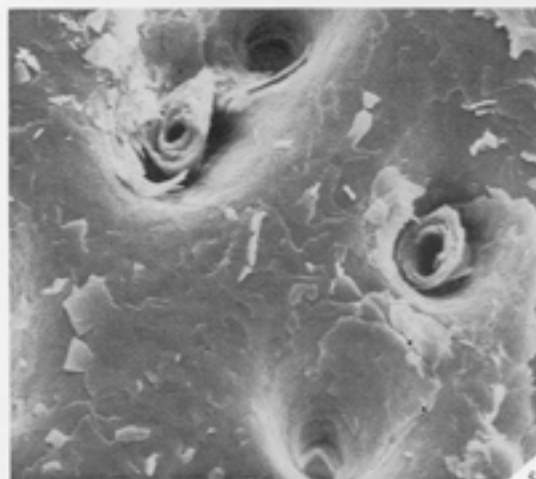
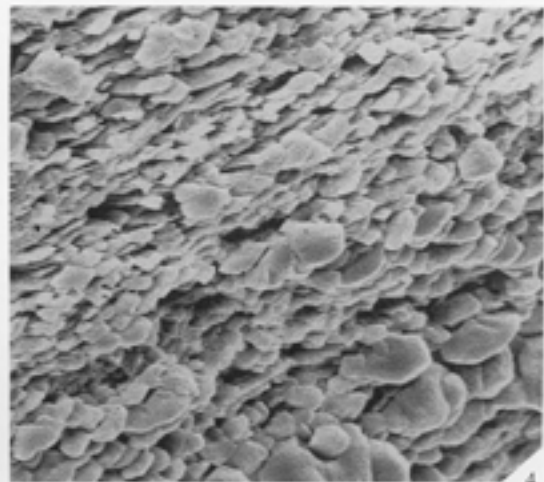
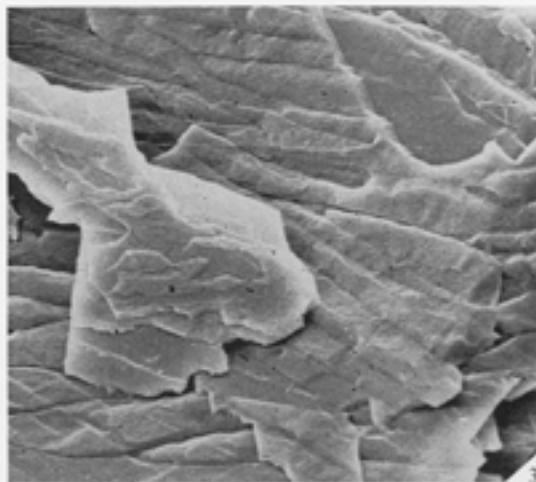
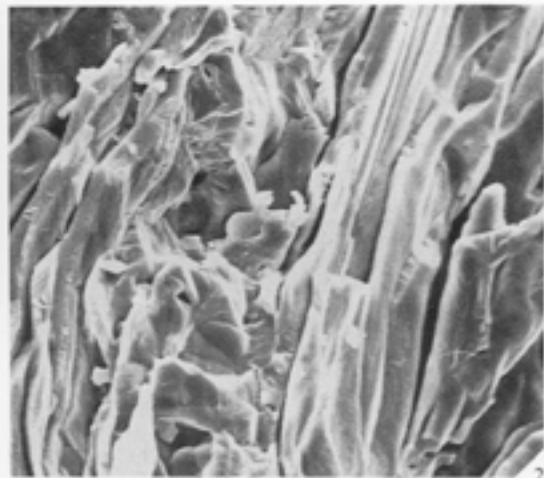
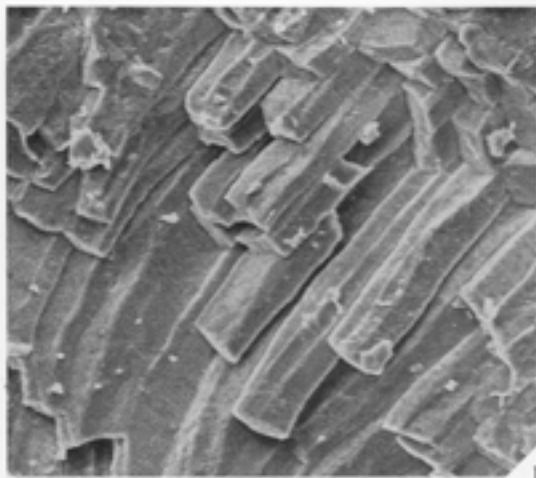
#### EXPLANATION OF PLATE 1

Figs 1–2. *Davidsonia verneuilli* Bouchard. Middle Devonian (Eifelian); Gerolstein, Eifel, Germany. 1, B39660; external fracture surface of dorsal valve, showing orthodoxly stacked fibres of secondary shell with well developed saddles directed externally,  $\times 380$ . 2, B5484; polished and etched subradial section of dorsal valve, with a lens of prismatic shell intercalated (submedially) within the fibrous succession of the secondary layer,  $\times 1470$ .

Figs 3–4. *Xystostrophia umbraculum* (Schlotheim). Middle Devonian (Eifelian); Gerolstein, Eifel, Germany; B39585; external fracture surface and polished and etched subradial section of dorsal valve, showing disposition and parallel-sided successions of impunctate cross-bladed laminae with some crested laths in the section (fig. 4) especially towards the bottom right-hand corner,  $\times 1200$ ,  $\times 1000$ .

Figs 5–6. *Neocrania anomala* (Müller). Recent; near Oban, Scotland; L14924; bleached interior of dorsal valve showing, in general view and detail, concentrically packed laminae forming the walls of punctae,  $\times 720$ ,  $\times 1350$ .

All scanning electron micrographs.



variations found were sporadic lenses of crested laths with gently convex outer surfaces and of highly inclined laths which are being studied further (Pl. 1, fig. 4). The laths within a set of laminae were aligned in the same direction, which usually changed at acute angles from one contiguous set to the next.

The microtexture of the *Xystostrophia* shell is identical with the standard cross-bladed laminar successions of all strophomenides and productides (except for the fibrous but pseudopunctate plectambonitoids and some early chonetidines). It is certainly typical of all orthotetid shells which have been studied ultrastructurally to date. For this paper, detailed microtextural surveys were restricted to a few representative genera, although these are sufficiently distant from one another phylogenetically to suggest that cross-bladed lamination is the hallmark of the Orthotetidina as amended herein. There was some variation in lath width with ranges of: 2.5–5  $\mu\text{m}$  for *Apsocalymma shiellsi* McIntosh; 3–4  $\mu\text{m}$  for *Fardenia scotica* Lamont; 4–6  $\mu\text{m}$  for *Streptorhynchus pelargonatus* (Schlotheim); and 4–7.5  $\mu\text{m}$  for *Schuchertella lens* (White); crested laths were also found in *Schuchertella*. In general, however, one micrograph of the shell structure of these species was indistinguishable from another so far as microtexture was concerned.

#### *Micromorphology of the orthotetidine shell*

**Terminology.** The main micromorphological features of the orthotetidines are conical deflections of the shell successions, which may point externally or internally; but before describing them, it seems appropriate to outline our interpretations of the terms currently used for such features.

In general, our usage conforms to that of the *Treatise* (Williams and Rowell 1965, H139–H155), except that the terms have been more precisely defined to take into account the new information obtained since 1965. Thus conical deflections of shell successions which point externally are usually referred to as punctae, on the assumption that they trace the paths of canals, accommodating extensions of the mantle. There are, however, several kinds of extensions. Papillose outgrowths (caeca) of the outer epithelium itself may either terminate at the periostracum, as in the Cranioida, or be separated from it by a canopy of shell perforated by microvillous canals, as in the Terebratulida and Thecideidina. This difference in the termination of the canals accommodating caeca warrants the restriction of the terms 'puncta' and 'endopuncta' to the cranioid and terebratulide types respectively. A system of canals permeating the brachiopod shell can also result from the secretion by outer epithelium of persistent proteinaceous strands. This system is especially characteristic of the organo-phosphatic brachiopods; and, although they have been described as 'punctae', it is more informative to refer to them simply as 'canals' (Williams *et al.* 1992, p. 87). Gaspard (1990, p. 54) has designated similar micro-morphological features, found in terebratulides,

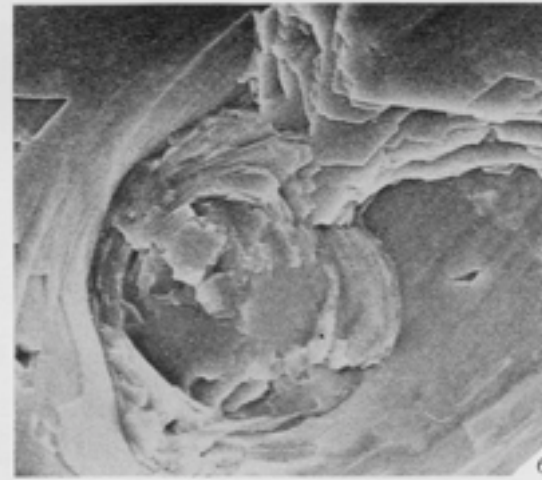
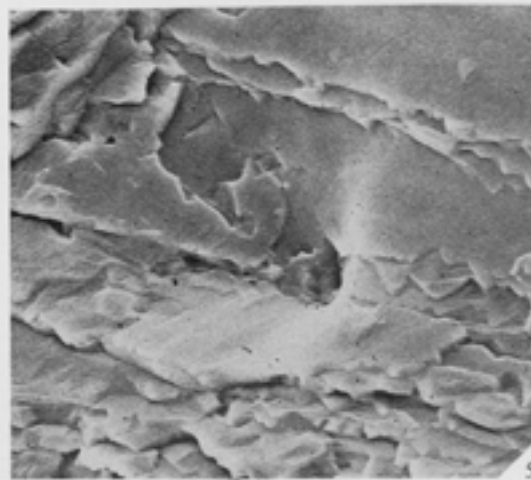
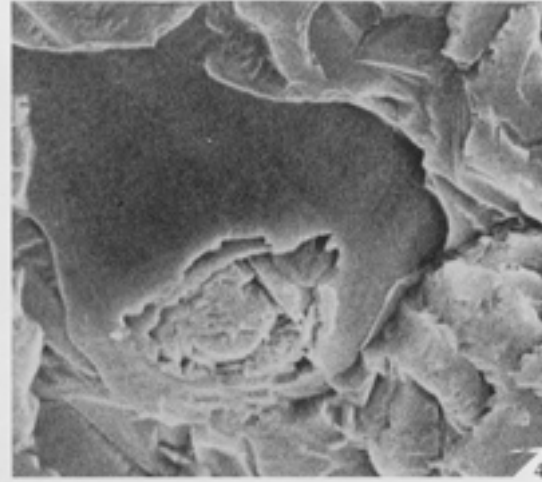
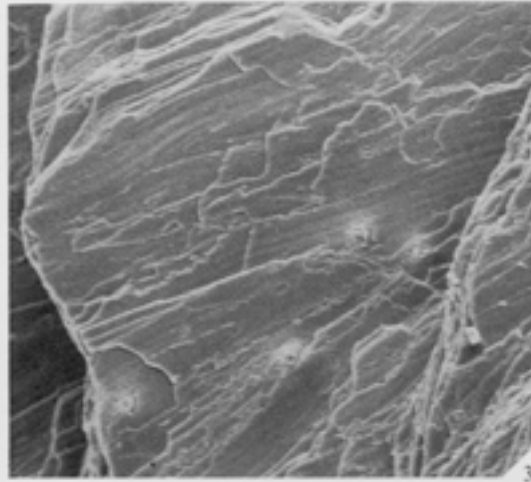
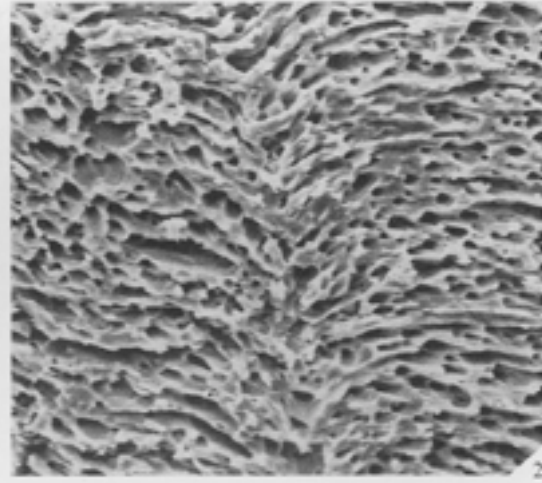
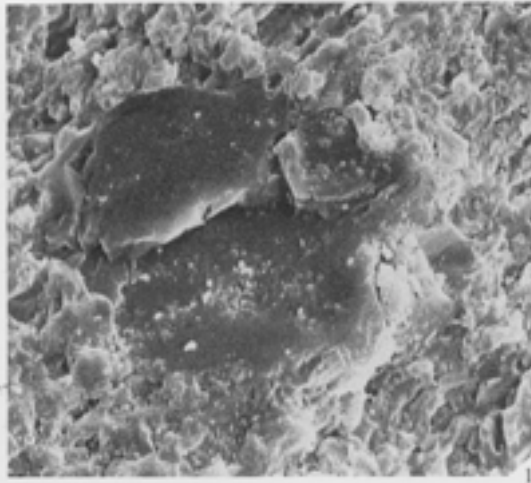
#### EXPLANATION OF PLATE 2

Fig. 1. *Petrocrania scabiosa* (Hall). Upper Ordovician (Maysville Formation); Cincinnati, USA; L14920a; external fracture surface of dorsal valve, showing calcitic infill of puncta within secondary laminar layer,  $\times 1750$ .

Figs 2–5. *Schuchertella lens* (White). Mississippian (Louisiana Limestone); Missouri, USA; L14923. 2, polished and etched lateral subradial section of dorsal valve, showing part of an extropuncta with conical deflections of secondary laminae directed towards the exterior beyond the lower edge of micrograph,  $\times 550$ . 3–4, external surface of fragment of laminar secondary shell, with general view and detail of radially arranged, externally directed tubercular structures of extropunctae,  $\times 275$ ,  $\times 2500$ . 5, internal surface of fragment of laminar secondary shell showing conical depression of extropuncta delineated by spirally disposed laminae,  $\times 1150$ .

Fig. 6. *Apsocalymma shiellsi* McIntosh. Lower Carboniferous (Lower Limestone Group); Beith, Scotland; L14922; external view of fragment of secondary shell of ventral valve, showing disposition of laminae around pseudopunctate depression filled with obliquely and spirally arranged laminae,  $\times 1500$ .

All scanning electron micrographs.



as 'micropuncta'. However, further study may show that, as in lingulides, they accommodate secretory products rather than membranous extensions of the outer epithelium.

Inwardly directed conical deflections of shell successions, which form tubercles on the valve floor, are pre-eminently characteristic of the strophomenides, productides and certain orthides. They are unknown in living species, the tubercles of thecideidines and terebratulides like *Megerlina* being unrelated, superficial outgrowths. Consequently, their inferred relationship with outer epithelium has always been a source of controversy, as has been well described by Manankov (1979b). Thus, the cores of pseudopunctae may be occupied by calcite rods (taleolae), which were probably a distinctive components of the shell *in vivo*. Pseudopunctae consisting exclusively of superimposed cones are also found, reputedly interspersed with those with taleolae in many species, and have been renamed 'propunctae' by Afaneseve (1980). However, we would not advocate the adoption of this term until a comprehensive study has established the true relationship between pseudopunctae with and without taleolae, as both kinds could have served as bases for fibrillar holdfasts of the mantle (Williams 1968, p. 41). In that respect, we do not subscribe to the idea that pseudopunctate tubercles acted as seats for 'setae' facilitating water flow within the mantle cavity (Grant 1968, p. 15). The inner epithelium of the strophomenide mantle would have been densely ciliated in the manner of living brachiopods and would have adequately performed all the functions envisaged for fimbriae.

In his survey of orthotetoid shell structure, Thomas (1958, p. 34) drew attention to the fact that the 'pseudopunctae' of *Streptorhynchus*, which are arranged radially along the axes of costellae, are deflected outwardly; he concluded that they were the sites of canals. In 1971 (p. 34), he recorded the same type of structures in *Schuchertella lens* (White) from the type locality; and in a personal communication (August 1992) he generously commented on his unpublished researches and listed the genera in which he had found these outwardly deflecting structures (now described by him as 'endopunctae'). They included *Arctitreta* and *Kiangsiella* as well as *Schuchertella* and *Streptorhynchus*. Manankov (1979b, p. 33) had already confirmed the existence of these microstructures in *Arctitreta*, *Kiangsiella* and *Streptorhynchus*, but was content to continue referring to them as pseudopunctae. Whether these outwardly deflecting features should be identified as 'endopunctae' or 'pseudopunctae' or should be given a new name, is dealt with later during discussion of our own findings.

*Micromorphology of representative orthotetidines.* Well preserved specimens of *Apsocalymma shiellsi* McIntosh and *Brochocarina trearnensis* McIntosh have been studied in detail to ascertain the micromorphology of the orthotetid (*s.s.*) shell. Pseudopunctae were openly distributed at 25–30 mm<sup>2</sup> and were uniformly asymmetrical in profile (Pl. 3, figs 2–3) in relation to the inferred stress couples set up between the mantle and the thickening shell (Williams 1968, p. 39). Where seen in transverse fracture sections on exfoliated surfaces, mature pseudopunctae formed rosettes, up to about 50 µm

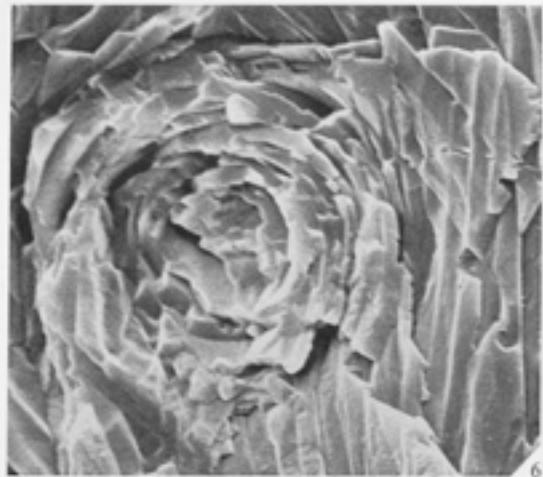
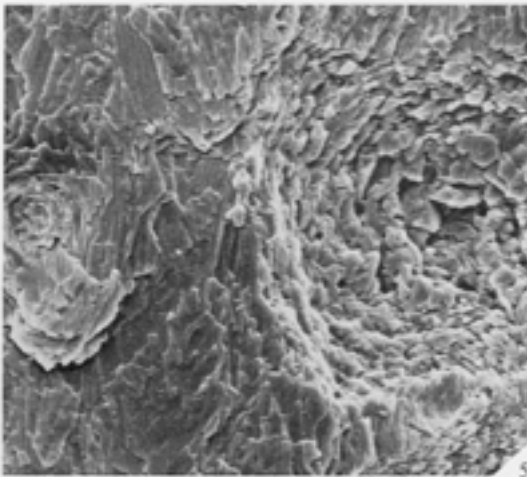
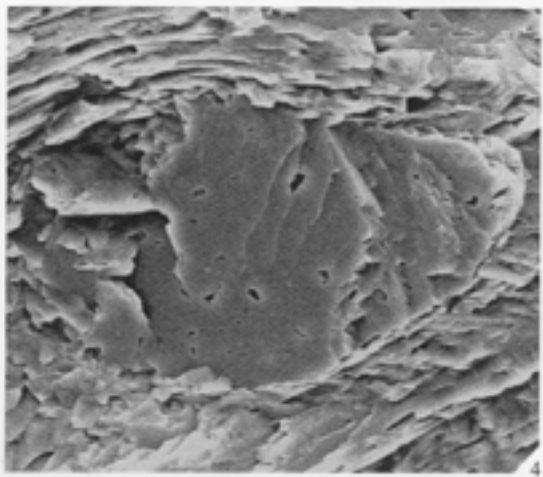
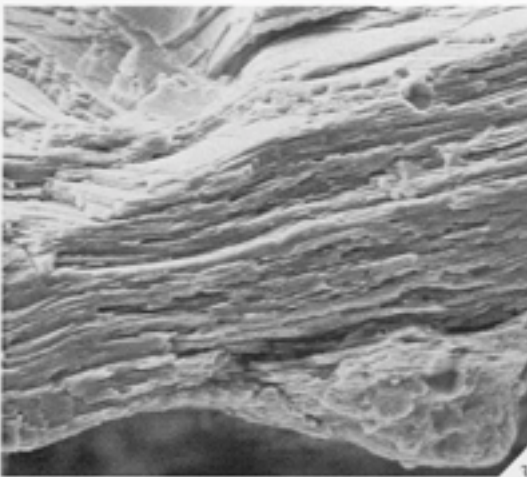
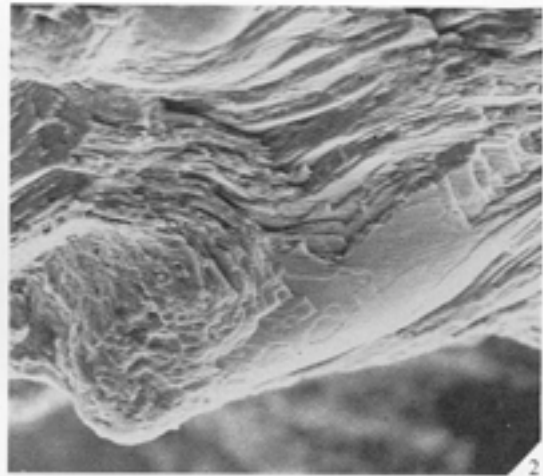
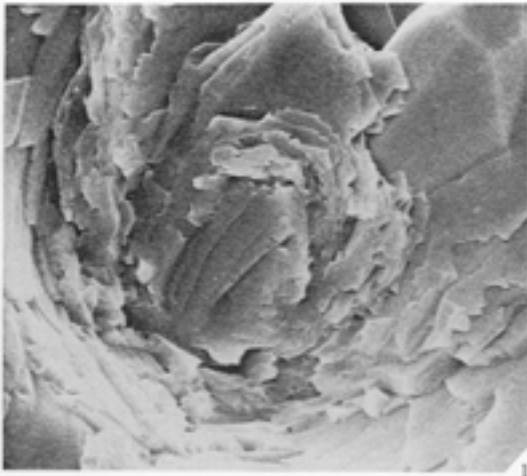
#### EXPLANATION OF PLATE 3

Figs 1–3. *Apsocalymma shiellsi* McIntosh. Lower Carboniferous (Lower Limestone Group); Beith, Scotland; L14922; 1, external view of fracture surface of secondary shell of ventral valve, showing disposition of laminae around pseudopunctate infill of inclined laminar fragments, × 1800. 2–3, views of subradial fracture section of ventral valve, showing laminar structure of inwardly projecting tubercles with externally facing pseudopunctate depression in top left-hand corner of figure 3, × 370, × 570.

Fig. 4. *Rafinesquina alternata* (Hall). Upper Ordovician (Maysville Formation); Cincinnati, USA; L14920b; external view of fracture surface, showing core of large pseudopuncta made up of recrystallized laminar fragments, parts of which are still identifiable along left-hand margin, × 900.

Figs 5–6. *Strophomena planumbona* (Hall). Upper Ordovician (Trenton Group); Cincinnati, USA; BMNH 73834; weathered and partly exfoliated exterior of ventral valve, with general view of pseudopunctate base on crest of costella flanked by granular interspatial depression (to left and right respectively of figure 5) and detail of pseudopunctate core composed of spirally inclined laminae (fig. 6), × 650, × 3000.

All scanning electron micrographs.



in diameter, of cortically disposed laminae which became increasingly inclined towards a core, 22–25  $\mu\text{m}$  across, consisting of a variety of calcitic structures. Up to twenty or so laminae and laminar sets made up the concentric layering around the core which formed a horizontal floor of solid calcite within a shallow hollow in some pseudopunctae seen from the exterior (Pl. 2, fig. 6). In others, the floor was tilted into discrete laminar sets, an arrangement which was well seen in some internal tubercles where tilted sets (Pl. 3, fig. 1) were enclosed within successive laminar cones with gently convex tops. Indeed, some tubercles were completely covered by dome-like laminae which, although affected by some diagenetic changes, seemed to have been unbroken in the original state (Pl. 3, fig. 2). We, therefore, conclude that orthotetid pseudopunctae typically consisted of a succession of superimposed laminar cones with gently convex peaks. Arrays of these cones have been traced for almost 0.5 mm, throughout a shell etched by EDTA, along a sinuous path about 40  $\mu\text{m}$  wide. There was no evidence of a core composed of anything other than the amalgamated peaks of successive laminar cones.

Schuchertellid micromorphology differs from the pattern of other orthotetoids in several respects. The immediately obvious difference is that although it also consists of arrays of asymmetrical conical deflections, they invariably point externally not internally. In recognition of this and other differences, which preclude any homology with punctation, we propose that these structures be called 'extropunctae'.

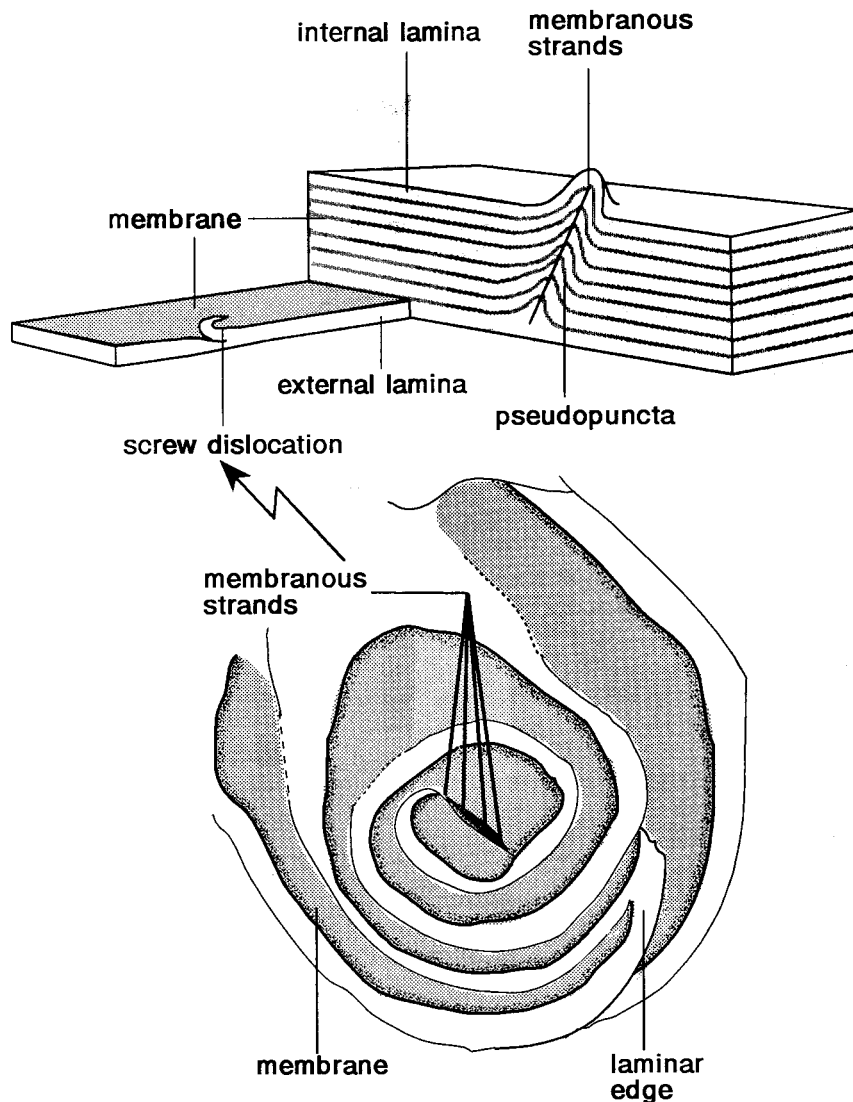
In specimens of *Schuchertella lens* (White) and *Streptorhynchus pelicanensis* Fletcher investigated by us, the extropunctae were densely arranged, more or less radially (Pl. 2, fig. 3), at about 150 per  $\text{mm}^2$ . On internal exfoliated surfaces, mature extropunctae formed shallow craters (Pl. 2, fig. 5), about 50  $\mu\text{m}$  in diameter, bounded by up to ten laminar sets arranged concentrically about elliptical cores, 4–5  $\mu\text{m}$  in maximum diameter, and usually with a medial slot. Exceptionally, a single lamina lined part of the crater sides and merged with the core as a spirally twisted band with a medial slot. On external exfoliated surfaces, extropunctae occurred as low domes, up to 30  $\mu\text{m}$  across (Pl. 2, fig. 4), which consisted of successions of curved laminae disposed around cores made up of oblique or twisted plates, some with medial slots. Extropunctate trails were also revealed by etching a transverse section of a shell with EDTA. These externally directed conical deflections, which were about 50  $\mu\text{m}$  wide, were seldom more than 200  $\mu\text{m}$  long (Pl. 2, fig. 2), although one could be traced for over 0.6 mm. The imperistence of extropunctae in such sections is probably due more to their sinuosity than to periodic lapses in their development.

The shell of *Xystostrophia umbraculum* has already been described as having a cross-bladed laminar microtexture. It is further characterized by an absence of micromorphological deflections of any kind; and this impunctate condition is typical of other genera assigned to the Chilidiopsidae (or its junior homonym Fardeniidae) by Cooper and Grant (1974) and Manankov (1979a). This impunctate condition had already been confirmed in *Floweria prava* (Hall) from the Upper Devonian of Iowa, and *Fardenia scalena* Williams from the Caradocian of Scotland. However, the present review also afforded an opportunity to ascertain the structure of the shell of one of the earliest orthotetidines, *Fardenia scotica* Lamont from the Ashgillian of Scotland, with intriguing results.

*Fardenia* is mostly represented in collections by moulds in a weathered siltstone, but a few specimens with adherent shell occur among topotypes in the Hunterian Museum, Glasgow. A fragment, about 2.4 mm long, adhering to the postero-median area of a dorsal valve, was prised away from a weathered shell, and four microscopic slivers were dislodged at the same time. All were mounted on the one stub for examination with the SEM. The large fragment and three of the four slivers were impunctate; the fourth was pseudopunctate!

There can be no doubt that the sliver in question (Pl. 4, fig. 5) came from the dorsal valve along with the other pieces. All five fragments have a cross-bladed laminar microtexture with laminae made up of monolayers of parallel-sided, amalgamated laths between 2 and 2.5  $\mu\text{m}$  wide and commonly aggregated into thick sets up to 3  $\mu\text{m}$  or so. However, two other features confirm that the pseudopunctate sliver was an integral part of the *Fardenia* shell. First, all fragments, and the adherent shell from which they were dislodged, were relatively coarsely recrystallized so that the





TEXT-FIG. 2. Diagrammatic reconstruction of the origin and essential structure of a pseudopuncta, based on those found on internal laminae of *Fardenia scotica* and illustrated in Plate 4, figure 6.

laminar surfaces were distinctly roughened by granules up to 300 nm in diameter (cf. Pl. 4, fig. 6). Secondly, the pseudopunctae are scattered along a gently arched feature about 250  $\mu\text{m}$  wide, which formed the long axis of the pseudopunctate sliver. This structure is an internally facing interspace, comparable in attitude and wavelength with those underlying the sharply crested costellae of the large fragment and of its counterpart mould on the dorsal valve.

The pseudopunctate sliver had an area of about 0.3 mm<sup>2</sup> and was less than 100  $\mu\text{m}$  thick. The surface studded with pseudopunctae (Pl. 4, fig. 5) was not part of the dorsal valve floor but an assemblage of freshly exfoliated facets of about ten laminar sets. The sliver was, therefore, a piece of the internal succession of the *Fardenia* shell. All the pseudopunctae were shallow and, at most, immature in development because the dome-like laminae accommodating them were seldom more

than 40  $\mu\text{m}$  across (Pl. 5, fig. 1) while their cores, with diameters of about 10  $\mu\text{m}$ , were usually encircled by fewer than seven laminar sets. Indeed, the most immature one was less than 13  $\mu\text{m}$  across and consists of only four or five laminae around a core with a diameter of 5  $\mu\text{m}$ . The most interesting feature of this incipient pseudopuncta is that the core was really made up of two spirally continuous laminae inclined towards a central slit which appeared to divide it into two halves (Pl. 4, fig. 6).

The discovery of pseudopunctae on a sliver of shell of *Fardenia scotica* prompted us to check shell-bearing specimens of this and other *Fardenia* in Ordovician collections from Scotland and Anticosti Island in Canada. Yet only one other of the six shells systematically examined for micromorphological features under the SEM revealed any corroborative evidence: a solitary pseudopuncta in the postero-median area of a ventral valve of *F. scotica*. We have, therefore, concluded that *Fardenia* could be regarded as impunctate for classificatory purposes, but had a genetic propensity for pseudopunctation, albeit sporadically in impersistent patches in that part of the shell supporting the musculature.

The fragment has also presented a composite picture of the origin and development of at least one type of pseudopuncta. Starting with the spirally arranged laminae at the core of the incipient pseudopuncta, the most likely way for this arrangement to have originated would have been for a cell with a diameter of about 5  $\mu\text{m}$  to have started secreting, on an interlaminar membrane, not calcite but fibrillar proteins or filaments connected by hemidesmosomes, and to have continued to do so at a faster rate than the deposition of laminae by surrounding cells (Text-fig. 2). These rapidly lengthening proteinaceous strands (or filaments) would, in turn, have caused adjacent cells to secrete laminae in a steeply inclined coil around the organic strands to form the biomineralized core to the growing pseudopuncta. From time to time the process would have been stopped by the cessation of proteinaceous secretion which could have been selective or universal. This would account for those pseudopunctate tubercles, outcropping on the floors or on internal exfoliated surfaces of strophomenide valves, which are capped by entire as well as perforate laminae. This would not have precluded the growth of succeeding pseudopunctae on the same sites and at new loci, a concurrence which occurs during the maintenance of the micromorphological canal system pervading the shell of *Discina* (Williams *et al.* 1992, p. 98).

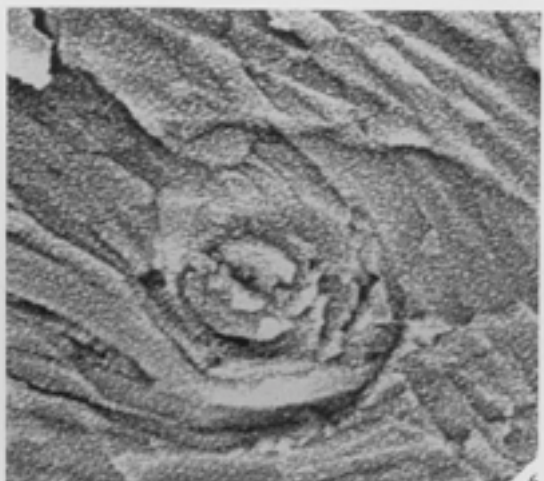
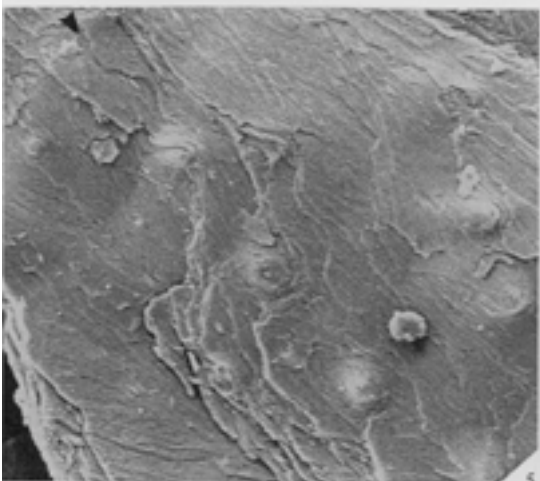
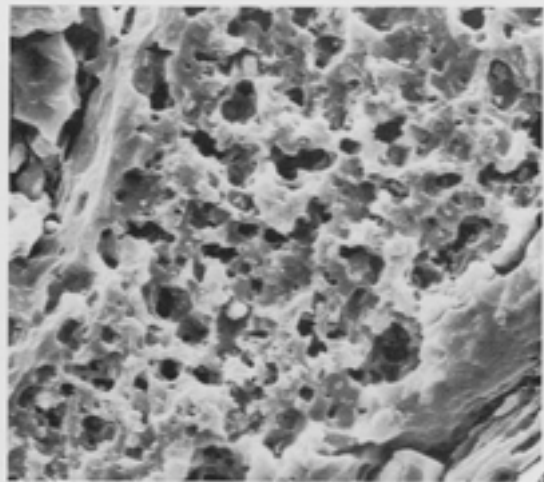
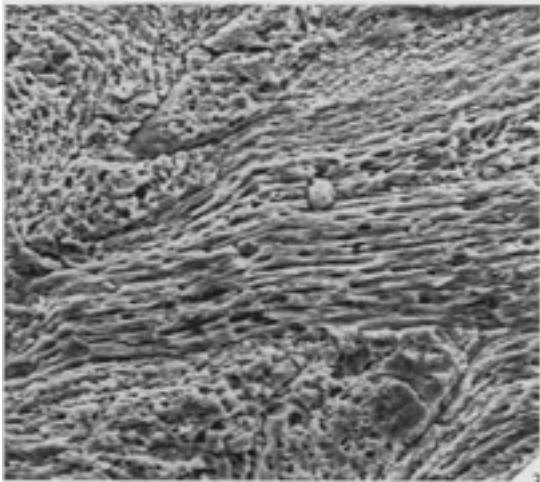
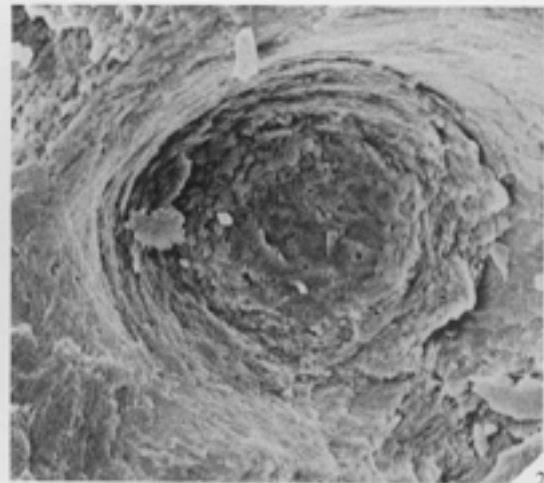
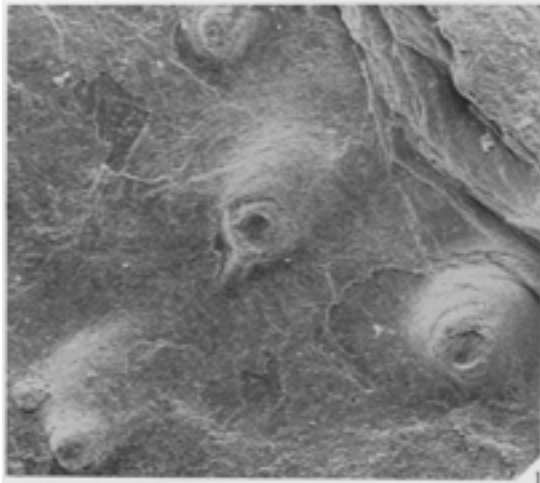
The postulated development of pseudopunctae in *Fardenia* is compatible with the micromorphology of the extropunctae of *Schuchertella* as well as the pseudopunctae of *Apsocalymma*. The conical deflections of both genera have cores consisting of tilted, discrete blocks of lamina; and spirally disposed laminae have been found lining extropunctate craters of *Schuchertella* (cf. Pl. 2, fig. 5). Both types may also be capped by entire laminae which could only have been secreted during interruptions of the processes responsible for the differentiation of the cores.

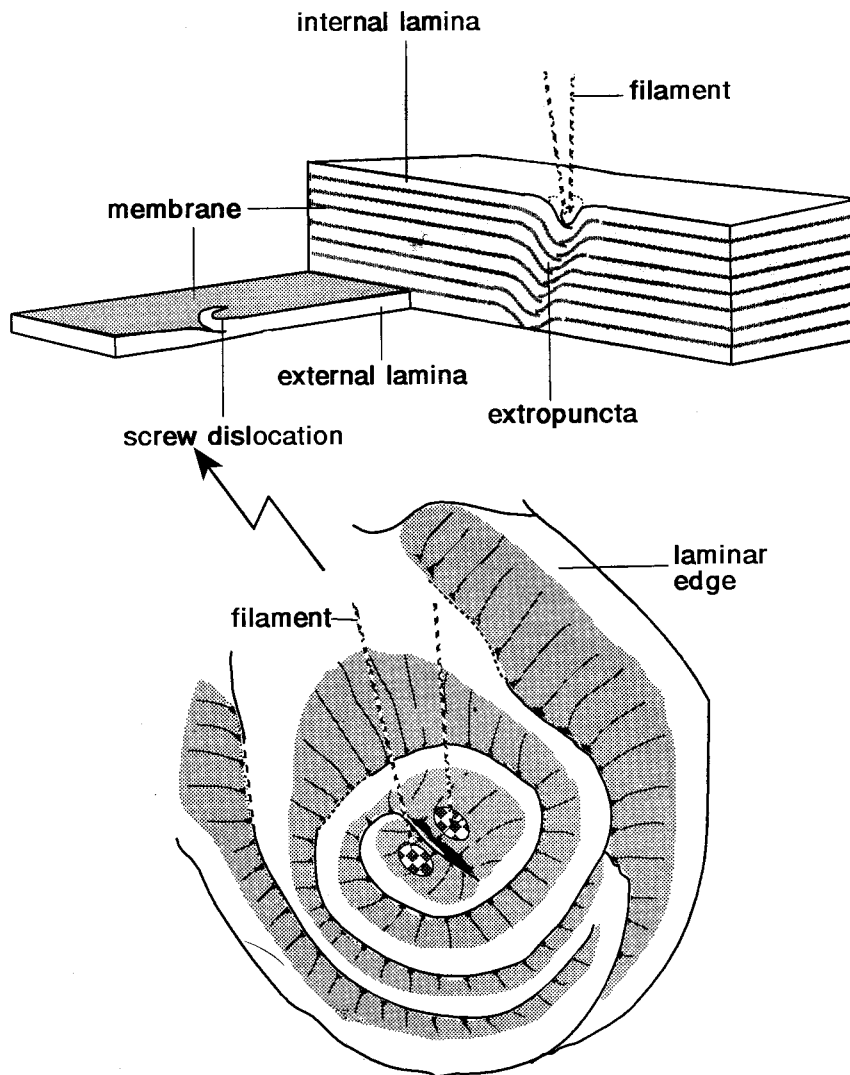
#### EXPLANATION OF PLATE 4

Figs 1–4. *Leptagonia caledonica* Brand. Lower Carboniferous (Great Limestone Shale); Cocklaw, Scotland; L10106/1. 1, general dorsal view of tubercles with taleolar cores on internal surface of ventral valve,  $\times 100$ . 2, external view of transverse fracture section of pseudopuncta with roughened, pock-marked surface to taleolar core,  $\times 470$ . 3–4, general view and detail of polished and etched subradial section of ventral valve showing disposition of laminae around taleolae (exterior towards the top); fully developed taleolar base secreted uncomfortably on horizontal laminae seen in bottom right-hand corner of figure 3,  $\times 410$ ; and taleola occupying much of figure 4, separated from laminae of top-left hand and bottom right-hand corners by patina and seamed with canals,  $\times 1700$ .

Figs 5–6. *Fardenia scotica* Lamont. Upper Ordovician (Lower Drummock Subgroup); Craighead, Scotland; L4835/40; general view and detail of granular internal surface of fragment of secondary shell of dorsal valve, showing incipient pseudopunctae breaking through cross-bladed laminae in spirally disposed arrangements perpetuating screw dislocations as in figure 6,  $\times 200$ ,  $\times 2750$ .

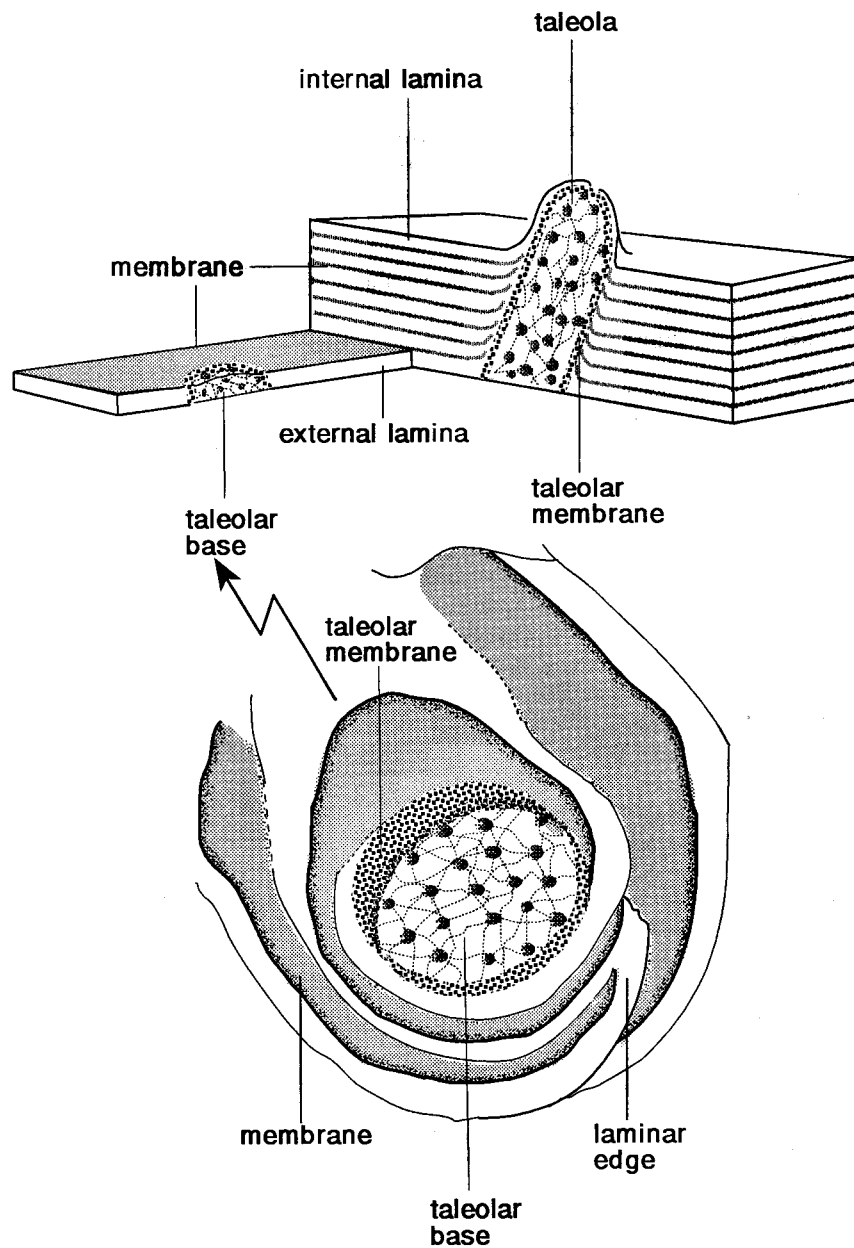
All scanning electron micrographs.





TEXT-FIG. 3. Diagrammatic reconstruction of the origin and essential structure of an extropuncta shown as a variant of the pseudopuncta illustrated in Text-figure 2 (note differences of the extropunctae of *Schuchertella lens* shown in Plate 2, figures 2-5).

There is, of course, a basic difference in the orientation of laminae around the cores. Thomas (pers. comm. 1992) has contended that *Schuchertella* was 'endopunctate' not pseudopunctate. In that respect, a comparative study of the punctate shell of *Neocrania*, which is laminar not fibrous, is instructive. At the internal surface of a bleached valve, punctae are delineated by concentric bands of laminae (Pl. 1, fig. 5). But aggregations of these form cylinders not cones (Pl. 1, fig. 6); and, although they can be dislodged by the chemical degradation of interlaminar membranes, they do not collapse into discrete blocks of laminae filling the canals which remain open to be filled by sediment or diagenetic precipitates during fossilization, as can be seen in *Petrocrania scabiosa* (Hall) (Pl. 2, fig. 1). If, therefore, the fine structure of the extropunctate core is the same as that of a pseudopuncta, the reversed orientation of deflection of the surrounding laminae must be due to different rates of secretion of the organic components of the cores. Thus, more slowly growing



TEXT-FIG. 4. Diagrammatic reconstruction of the origin and essential structure of a pseudopuncta containing a taleola, shown as a variant of the pseudopuncta illustrated in Text-figure 2 (note differences of the taleolae of *Leptagonia caledonica* shown in Plate 4, figures 1-4).

keratin filaments (with desmosomal attachments) may have been the dominant constituent in the extropuncta compared with rapidly secreted strands of membraneous proteins in the pseudopuncta (Text-fig. 3.).

The *Fardenia* model of pseudopunctate development can also be used to explain the growth of the pseudopunctae of the Ordovician strophomenoids *Rafinesquina alternata* (Hall) and

*Strophomena planumbona* (Hall), which have been studied under the SEM for comparative purposes. In the former species, rosettes may be as much as 150  $\mu\text{m}$  across with a core about one-third of that diameter (Pl. 1, fig. 4). Yet there can be little doubt that the cores, even of these large structures, are mainly composed of tilted blocks of laminae. The pseudopunctae of *Strophomena* are smaller, with rosettes about 40  $\mu\text{m}$  in diameter and cores one-quarter or so of that length (Pl. 3, fig. 6). However, the specimen studied was well-enough preserved externally to provide information on the first-formed parts of *Strophomena* pseudopunctae. The cores and surrounds of those pseudopunctae originating in the interspaces tend to be coarsely granular, which we have taken to indicate recrystallized primary shell, at least in part (Pl. 3, fig. 5). In contrast, pseudopunctae exposed on exfoliated surfaces on the crests of costellae and beneath the ornamented superficial layer of the valve, have cores composed of obliquely stacked laminar blocks (Pl. 3, fig. 6) which, apart from size, are closely comparable with those of *Fardenia*.

The pseudopunctae of the leptaenid *Leptagonia caledonica* Brand are quite different (Pl. 4, fig. 1). Rosettes of inwardly inclined laminae, which can exceed 75  $\mu\text{m}$  in diameter, are grouped around taleolae, up to 30  $\mu\text{m}$  or so in diameter (Pl. 4, fig. 2), which can frequently be traced throughout the shell successions for 1.5 mm or more (cf. Pl. 4, fig. 3). Taleolae are demonstrably different from other pseudopunctate cores of laminar blocks or the matrix infill of punctae. A taleola is fully developed and differentiated from the microtexture of the host shell when first formed and its distinctiveness is further emphasized by the way its surface forms a calcified patina, which is sharply separated from the surrounding laminae even when traces of interlaminar boundaries are preserved upon it (Pl. 4, figs 3–4).

The most startling difference, however, was brought out by etching polished sections with EDTA. The bedded nature of the laminae was enhanced by etching, whereas a taleola became porous and remained free of any laminar traces. The etched pits within the taleola were commonly delineated by rhombohedral planes, but were clearly part of an interlacing series of canals, up to 300 nm in diameter, permeating the entire feature (Pl. 4, fig. 4). In the face of this evidence of heterogeneity in its original composition, we concluded that a taleola, *in vivo*, consisted of a calcitic mesh permeated by interconnected tunnels which were filled with organic materials; and was probably bounded by a membrane continuous with those between the calcitic components of the laminar succession (Text-fig. 4).

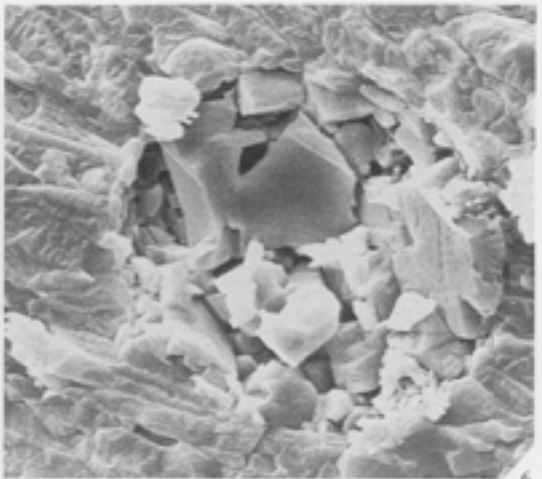
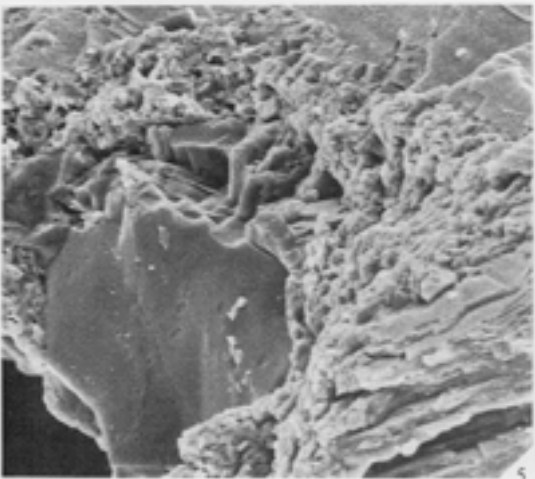
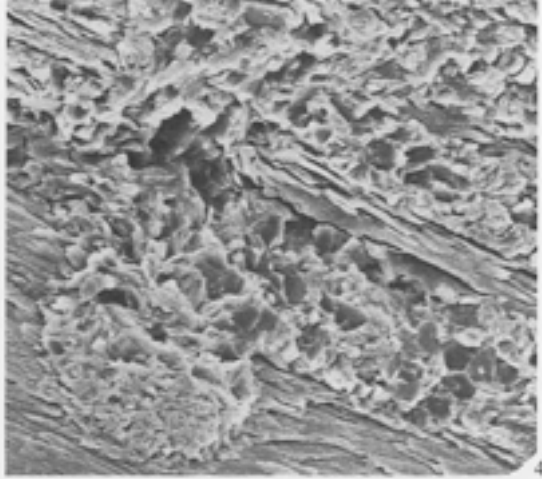
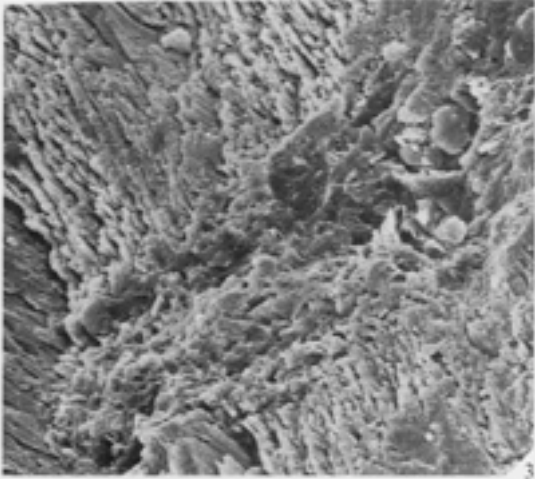
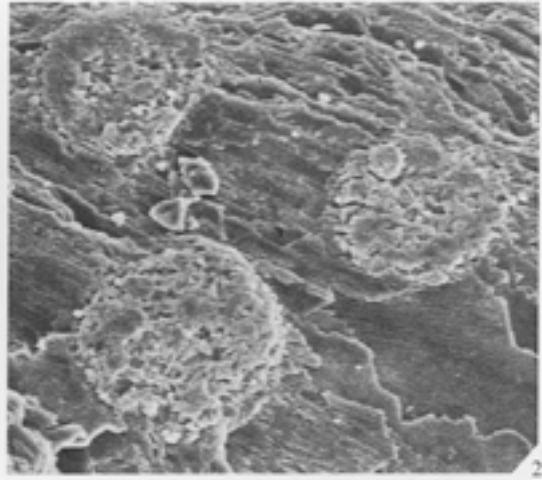
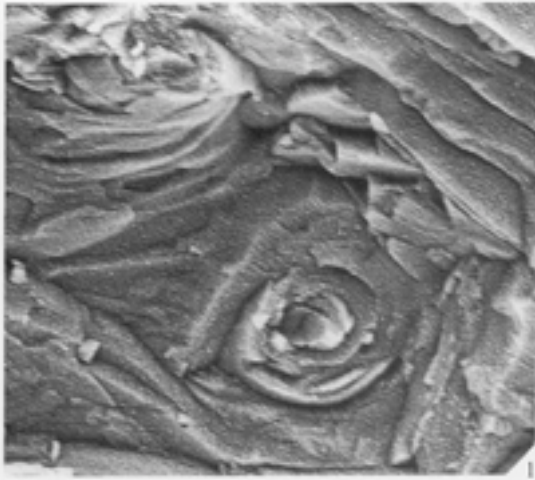
Tubercles with or without taleolae can also be partly or entirely capped by laminae, which, temporarily at least, terminated taleolar growth. This, and the fact that our interpretation of a

#### EXPLANATION OF PLATE 5

Fig. 1. *Fardenia scotica* Lamont. Upper Ordovician (Lower Drummock Subgroup); Craighead, Scotland; L4835/40; detail of internal surface of fragment of secondary shell (Pl. 4, fig. 5), showing two pseudopunctae, with spirally arranged laminae well seen in lower one,  $\times 1880$ .

Figs 2–6. Koskinoid perforations. 2–4, *Brochocarina trearnensis* McIntosh; Lower Carboniferous (Lower Limestone Group); Beith, Scotland; B42729; fracture surface and section near ventral umbo; 2, general view of three perforations in transverse section with bulbous surface to lower infill and circumferential rubbly surround to upper left,  $\times 340$ ; 3, canal with cleaved infill and boundary patina perforating undeflected laminar succession,  $\times 600$ ; 4, circular infill representing tunnel in bottom left-hand corner connecting with rubbly infill representing two lateral galleries separated by shelf of laminae which has been penetrated by the perforation in top left-hand corner,  $\times 475$ . 5, *Streptorhynchus pelicanensis* Fletcher; Upper Permian (Kazanian Limestone); Pelican Creek, Queensland, Australia; B1749; oblique view of part of perforation penetrating fracture section of secondary laminae, showing recrystallized core infill and the circumferential rubbly zone,  $\times 680$ . 6, *Orthopleura* sp.; Upper Devonian (Cedar Valley Limestone); Cedar Rapids, USA; L14921; internal fracture surface (external view), showing transverse section of koskinoid perforation with micritic interface between boundary laminae and recrystallized infill,  $\times 1600$ .

All scanning electron micrographs.



'living' taleola continues to involve the existence of a calcitic framework, affirms that the main function of tubercles was to provide holdfasts for mantle filaments.

#### *Koskinoid perforations*

Microscopic perforations penetrating the ventral valves of the atrypidine *Uncites* and many orthotetidine genera have been recognized for well over a century. The perforations tend to be concentrated in the umbonal region; and, since perforated species invariably lacked a functional pedicle opening, they have been variously interpreted as accommodating: (1) byssus-like threads (Jux and Strauch 1966); (2) finely divided distal branches of mature or juvenile internal pedicles (Schumann 1969; Martinez-Chacon and Garcia-Alcalde 1978); or (3) attachment fibrils secreted by papillae of outer epithelium, which first made the perforations by shell resorption (Grant 1980).

Within the context of this paper, the origin of these perforations has to be explored, as all three interpretations envisage features which could be critically important to orthotetidine classification. Indeed, Grant (1980, p. 314) has gone so far as to transfer the impunctate *Morinorhynchus* to the Orthotoidea solely on the grounds that it is the only chilidiopsoid, known to him, which has koskinoid perforations. In so doing, he has accorded these perforations greater taxonomic weight than the combined morphological and other structural features of *Morinorhynchus*.

During our own studies of specimens representing thirty or so orthotetidine genera, we were able to confirm a general but not a complete absence of koskinoid perforations from chilidiopsoids and their presence in orthotetoids. We further confirmed Grant's observations (1980, p. 315) that, although the perforations were concentrated in umbonal regions, they also occurred on cardinal areas and elsewhere on ventral valves (especially the flatter ones) but were absent from the dorsal valves. However, ultrastructural studies on the perforations in the orthotetid *Brochocarina trearnensis* McIntosh, the schuchertellid *Streptorhynchus pelicanensis* Fletcher and the chilidiopsid *Orthopleura* sp. suggest that they may not have been a growth feature of the brachiopods bearing them.

External and exfoliated surfaces, as well as fracture sections, show that the perforations are normally orthogonal to the shell and occur as close clusters of near perfectly circular transverse sections on laminar surfaces (Pl. 5, fig. 2). In *Brochocarina*, twelve perforations were counted in 0.25 mm<sup>2</sup>, with an average diameter of 69  $\mu$ m (for fourteen sections with a range of 52–78  $\mu$ m). They seldom overlapped and were normally dispersed at distances of 70–80  $\mu$ m from one another, although not in any discernible pattern. The most noteworthy aspect of the perforations is that they had been neatly drilled through the laminar successions of the shell without any deflection or general disturbance of the laminae themselves (Pl. 5, fig. 3), other than rare fracture cleavage in the vicinity of the perforations. In effect, the perforations are cylindrical tunnels seldom deviating from the vertical. Except for their chimney-like openings at the external shell surface, which were 30  $\mu$ m or so deep, they were filled with recrystallized, cleaved calcite disposed irregularly as foliated rhombs (Pl. 5, fig. 4) or as more regular arrays of cleaved plates more or less parallel to the long axes of the tunnels (Pl. 5, fig. 3); only occasionally were the medial regions of the infill occupied by irregular cavities, a few micrometres in size.

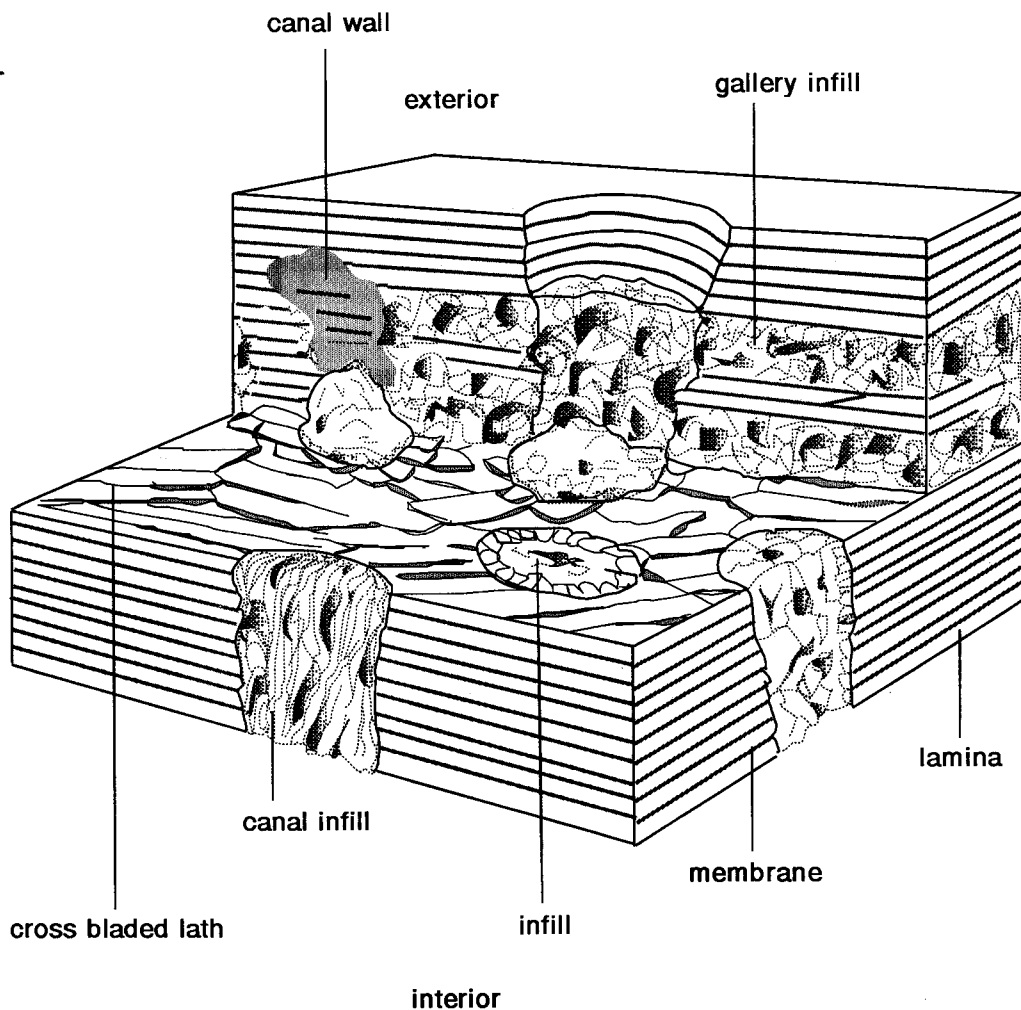
The sides of the tunnels, as revealed by oblique fractures, were relatively smooth and sharply distinguishable from the infill (cf. Pl. 5, fig. 6) which was bounded by either a micritic interface or a circumferential rubbly wall about 10  $\mu$ m thick consisting of smaller fragments of calcite. Some of these fragments were joined with the laminae defining the tunnel walls by thin isthmuses of calcite, but it was not possible to determine whether these junctions resulted from a post-depositional recrystallization of wall and matrix or were the residues of chemical solution occurring during tunnel formation.

In the samples at our disposal, the tunnels were almost always discrete. Even when overlap occurred, it is evident that one tunnel had been superimposed on another at a later time and there were few signs of branching. However, one vertical fracture section showed a horizontal gallery, up to 175  $\mu$ m high and extending for more than 760  $\mu$ m. The gallery, which contained a shelf of



laminae nearly  $20\ \mu\text{m}$  thick, was continuous with at least two tunnels about  $200\ \mu\text{m}$  apart so that all three structures were filled by an uninterrupted matrix of recrystallized calcite (Pl. 5, fig. 4).

The koskinoid perforations found in *Orthopleura* and *Streptorhynchus* differ from those piercing *Brochocarina* shells only in the diameters of their almost perfectly circular outlines in transverse sections (Pl. 5, figs 5–6). Ten of the more densely distributed perforations in *Streptorhynchus* averaged  $11.8\ \mu\text{m}$  (range  $6.8\text{--}13.0\ \mu\text{m}$ ), compared with  $30.5\ \mu\text{m}$  (range  $26\text{--}34\ \mu\text{m}$ ) for seven such structures in the antero-medial region of *Orthopleura*. In both genera, the recrystallized blocky matrix filling the perforations do not deflect the laminae forming koskinoid walls. In effect, all koskinoid structures studied by us are consistent with the features represented in Text-figure 5.



TEXT-FIG. 5. Diagrammatic representation of koskinoid perforations, based on those found in *Brochocarina trearnensis* and illustrated in Plate 5, figures 2–4.

Assuming that the micromorphology of the koskinoid tunnels of *Brochocarina*, *Streptorhynchus* and *Orthopleura* is typical of other perforate orthotetoids (and *Uncites*), a number of constraints now have to be observed in forming any view on their origin.

First and foremost, the absence of any ordered deflection of the laminae forming the walls of koskinoid tunnels precludes the development of the perforations during the growth and thickening of the shell. Had the tunnels accommodated byssus-like threads or branching pedicles, they would have been lined with a membrane in continuity with the periostracum; and the differential secretion of the thickening shell around each byssus thread or pedicle branch would have resulted in outward conical deflections of the surrounding laminae and their interleaved membranes. In any event, the orthotetidines belonged to an order characterized by a general atrophy of the pedicle, which must have taken place before the emergence of cementing orthotetoids, so that, by the time koskinoid perforations began appearing, even the pedicle epithelium would have become modified to secrete an adhesive pad rather than any byssus-like structure (compare the development of *Neocrania* (Nielsen 1991, p. 12)).

The assumption by Grant (1980, p. 317) that papillae of outer epithelium could have resorbed koskinoid tunnels and then secreted fibrils in them is also untenable. Shell resorption in brachiopods cannot be so finely focused as to drill neat holes through an alternating succession of calcitic laminae and proteinaceous membranes as well as the external cover of tanned periostracum. In living brachiopods, resorption patches, associated with the advance of muscle bases or the growth of loops, are invariably surrounded by transitional zones of partially digested carbonate and proteinaceous membranes, which are many microns wide. No surface as cleanly cut as the typical interface between shell and koskinoid perforation has yet been attributable to resorption in living species. Moreover, had the same, randomly distributed patches of outer epithelium later secreted and sustained fibrils protruding through the koskinoid tunnels, the inner laminar successions bordering such perforations would have been deflected outwards.

The rejection of any role for the mantle and pedicle of the host brachiopod in the formation of its koskinoid perforations inevitably leads to the assumption that they were excavated by other types of organism, a conclusion shared with Thomas (1958, p. 37). The lack of any pattern to their distribution and of any regular interconnections suggests that the vertical tunnels were occupied by solitary organisms seldom more than 1 mm or so long and 130  $\mu\text{m}$  in diameter. Such an organism would have been capable of grinding through calcite as well as proteinaceous membranes, to account for the mechanically drilled nature of the perforations. Even so, the rarity of galleries joining the vertical tunnels suggests that the organism did not live by digesting the shell itself but was probably parasitic on the soft parts of its host.

This interpretation of koskinoid perforations does, of course, raise important questions which are not easily answered. In particular: why such structures should be restricted to ventral valves and concentrated in their umbonal regions; and why burrowing parasites, even if in symbiotic association, should be so selective of their hosts as to be known only in the later orthotetidines and *Uncites*.

We suggest that the ventral valve with its umbo cemented to, or buried within, substrates, would always have been susceptible to invasion by infaunal infestations. This would account for the relatively widespread distribution of perforations on flatter ventral valves and their absence from the upper dorsal valves. (It might also account for the absence of perforations from contemporaneous stropheodontoids which, although of comparable shape, were never cemented to the substrate and were probably capable of repeated movement of the entire shell (Williams 1953, p. 34).)

The apparent restriction of koskinoid perforations to later orthotetidines and *Uncites* is more difficult to explain. Both stocks differ from pedicle-bearing brachiopods in their attachment to substrates by cementation which, as already noted, would have facilitated infestation. On the other hand, contemporaneous productidines were also anchored and immobile and yet escaped koskinoid depredations. This could have been due to the relatively elevated habit of spinose productidine shells. Surface settlement might also have been repulsed by the nature of the productidine periostracum. In fact the periostraca of many extinct brachiopod groups might have been sufficiently robust and antibiotic to have deterred shell entry by boring organisms (a point overlooked by Owen and Williams (1969, p. 200) in their comparison of the distribution of

burrowing polychaetes and sponges in the shells of *Waltonia* and *Hemithiris*). Moreover, if burrowing parasites had been responsible for koskinoid perforations, they could also have infested many late Palaeozoic groups of pedicle-bearing brachiopods without leaving any trace on the shell by effecting entry at the junction between the pedicle and outer epithelium.

Tentative as our interpretation of koskinoid perforations may be, we feel that there is good reason for excluding this feature from the lists of characters used to classify the orthotetidines.

#### ORTHOTETIDINE CLASSIFICATION

The phylogenetic tree of suprageneric taxa, shown in Text-figure 6, was constructed in accordance with the criteria outlined in Materials and Methods and our interpretation of orthotetidine morphology and shell structure. The terminal taxa of the cladogram include all established orthotetidine subfamilies and families except for the Dorsoscyphinae Roberts, 1971, and the Tropidelasminae Waterhouse, 1983, which are judged to be synonyms of the Derbyiidae and the Streptorhynchidae respectively. The taxa were redefined in conformity with the character states listed in Table 1. Their relationships within the tree clarify some issues but raise others.

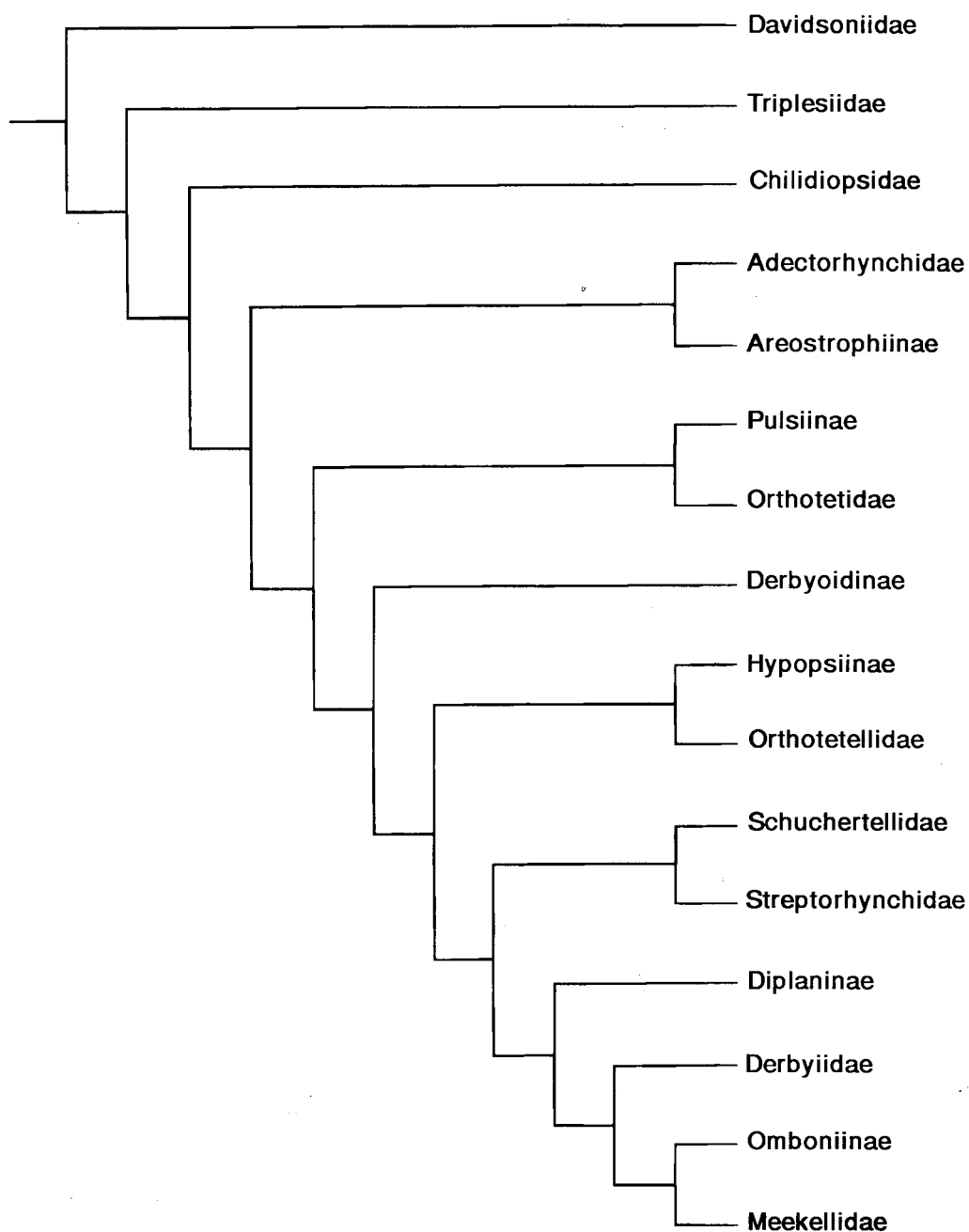
The fibrous-shelled Davidsoniidae are taxonomically distant from the Triplesiidae (the other outgroup) and the remaining orthotetidines, all of which are laminar shelled. The davidsoniids, therefore, can no longer be classified as orthotetidines.

The impunctate chilidiopsoid group, embracing the Chilidiopsidae and Areostrophiiidae (with the Adectorhynchinae), is paraphyletic. It includes the oldest known orthotetidines in which the pedicle remained functional in adult shells, although atrophy of the organ took place within the group and was signalled by the later emergence of free-lying chilidiopsids with no trace of a pedicle foramen and, in turn, by cementing areostrophiiids.

The pseudopunctate orthotetoid group consists of the Pulsiinae, Orthotetinae, Derbyoidinae, Orthotetellidae (with the Hypopsiinae), Derbyiidae (with the Diplaninae) and the Meekellidae (with the Omboniinae). The pseudopunctate condition, which immediately distinguishes the group from other orthotetidines, is invariably characteristic of at least the entire postlarval shell, albeit with varying density. Even so, the group is paraphyletic with the Derbyiidae and Meekellidae rooted with the extropunctate Schuchertellidae and Streptorhynchidae.

At first sight, this aggregation appears to support the recognition of four superfamilial groups: (1) impunctate chilidiopsoids normally with small cardinalia; (2) pseudopunctate orthotetoids with moderately developed cardinalia; (3) extropunctate schuchertellids with variably developed cardinalia; and (4) pseudopunctate derbyioids with elaborate cardinalia. Such a classification would have some common ground with that of Cooper and Grant (1974). In particular, they elevated the Derbyiidae to a Superfamily, the Derbyiacea, for orthotetidines with elaborately developed socket plates (their 'erismata', p. 259). These structures, however, must have evolved as repeatedly as convergent dental plates or elevated cardinal processes, which would explain why the 'Derbyiacea' (*sensu* Cooper and Grant) contains such dissimilar groups as the orthotetellids and the streptorhynchids.

Moreover, there is another basic reason for questioning the need to proliferate orthotetidine superfamilies. The pseudopunctate orthotetoids and the extropunctate schuchertellids together constitute a monophyletic group, immediately distinguishable from their ancestral, impunctate chilidiopsoids. Accordingly, we propose that superfamilial recognition be restricted to the Chilidiopsoidea and the Orthotetoidea with the latter embracing the extropunctate schuchertellids and streptorhynchids as well as all pseudopunctate orthotetidines. This would rationalize the taxonomic position of the schuchertellids (including the streptorhynchids) and, simultaneously, put micromorphological changes affecting the orthotetidine shell into perspective. Certainly, the previous classifications of this group could not have been more at odds. Williams (1965, p. H409) united both stocks as subfamilies of the Schuchertellidae which were characterized as lacking dental plates. Cooper and Grant (1974, p. 256) assigned the Schuchertellidae and Streptorhynchidae to the Orthotetacea and Derbyiacea respectively on differences in their cardinalia. Manankov (1979a, p. 31)



TEXT-FIG. 6. Cladogram of fourteen widely recognized orthotetidine subfamilies and families (with the Triplesiidae and Davidsoniidae as outgroups), diagnosed according to the fifteen character sets listed in Table 1 and derived from the matrix of Table 2.

having confirmed the researches on shell structure by Thomas (1958, p. 34), recognized the close affinity between the Schuchertellidae and the Streptorhynchidae. Yet he also included the impunctate Areostrophiinae within his version of the Schuchertellidae.

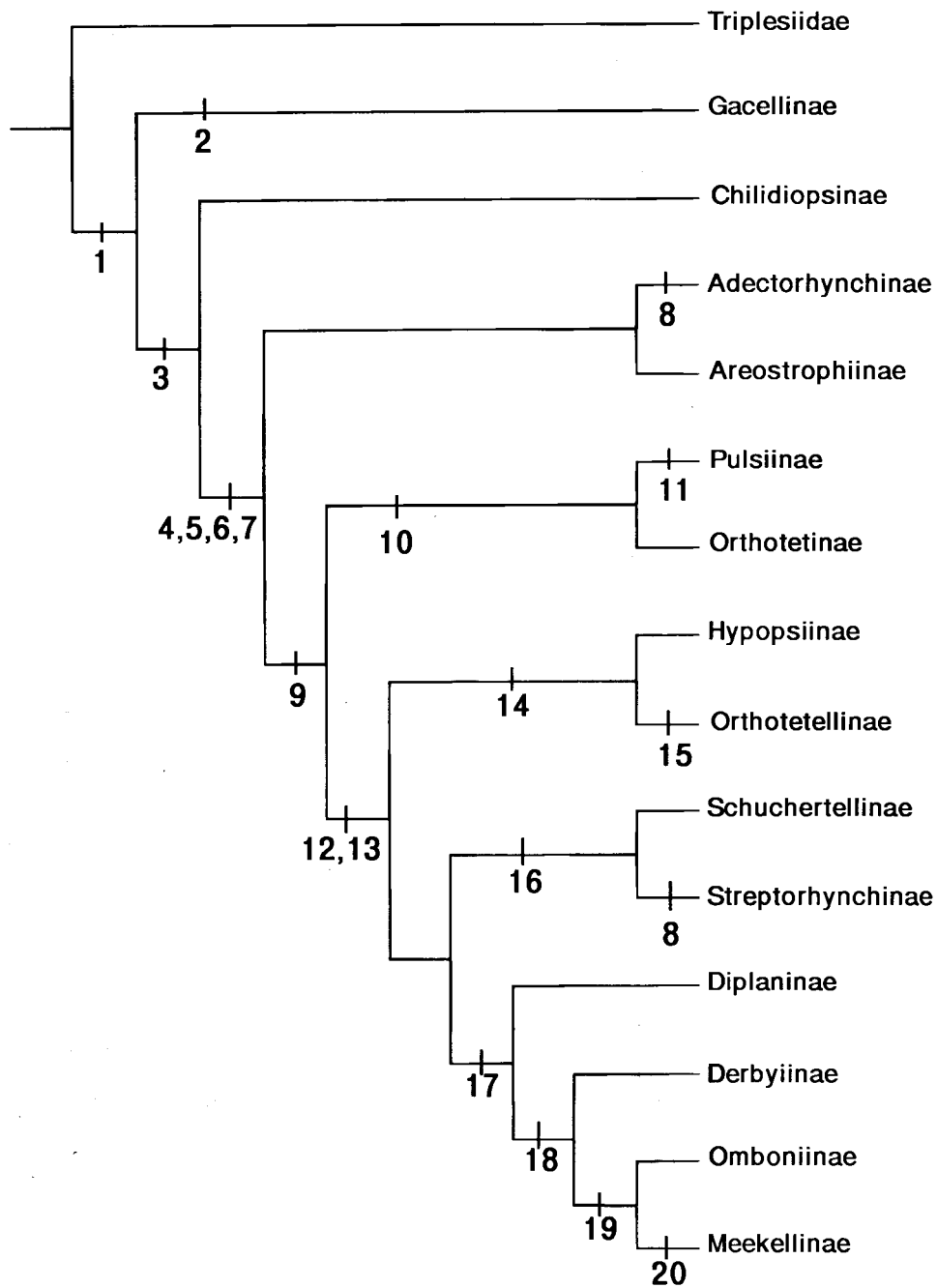
The use of generic programs to check the contents of the constituent subfamilies and families of the phylogenetic tree just described, resulted in a cladogram (Text-figure 7) based on the matrix of Table 3, which we now propose as the basis for orthotetidine classification. The character states determining the taxa are shown in Table 1. The cladogram is one of nine equally parsimonious trees of 128 steps and has consistency and homoplasy indices of 0.664 and 0.336 respectively. The changes are more profound than appears at first sight for, in its compilation, a number of genera were transferred from one family to another or indeed removed from the Orthotetida altogether (*Schuchertellopsis* Maillieux, for example, is probably an atrypidine). Generic reclassification, however, is not within the province of this paper. That part of our analysis will appear in the *Treatise* in due course, by which time it will certainly have undergone further changes to accommodate the new genera proposed in the intervening period.

In contrast, the suprageneric classification offered here may prove to be comprehensive enough to incorporate new taxa without disintegrating. Comparison of Text-figures 6 and 7 shows that the suprageneric groupings in the latter largely retain their initial phylogenetic relationship as determined by PAUP, although the suppression of the Derbyoidinae and the assignment of its constituent genera to the Orthotetinae has reduced the branching of the preferred tree. It has also been necessary to erect a new monotypic subfamily based on the earliest known orthotetidine, *Gacella*. These changes, however, have not affected our version of the chronology of the main events in orthotetidine history, which are outlined below.

The loss of a pedicle occurred early in the evolution of the most primitive orthotetidines, the Chilidiopsoidea. The presence of a supra-apical foramen in the adult ventral valve seems to have been restricted to early Upper Ordovician species of *Fardenia* and *Gacella* of Scotland and Virginia. Little is known about the occurrence of a functional foramen in young chilidiopsoids, except that supra-apical sheaths have been seen by one of us (A.W.) in immature shells of *Coolinia* from the Middle Silurian Waldron Shale of North America. However, other chilidiopsoids are almost invariably symmetrical in outline without any sign of distortion of the ventral umbo through cementation, and it seems safe to assume that they were free-lying on the substrate. This unattached habit was also probably the mode of life of many early orthotetids like *Pulsia*, *Schellwienella*, *Orthotetes* and related genera. Our inference is that a universal atrophy of the pedicle led to the widespread distribution of unattached stocks. Many of these became cemented to the substrate and independently developed distorted subconical ventral valves, a characteristic feature of the Areostrophidiidae, Orthotetellidae, Derbyiidae, Meekellidae and the Streptorhynchidae.

Micromorphological transformations of shell structure serve to particularize the emergence of a monophyletic family, the extropunctate schuchertellids, but the phylogenetic status of the pseudopunctate orthotetoid stocks relative to the impunctate chilidiopsoids is less certain. The rare occurrence of the impersistent pseudopunctae in a few specimens of *Fardenia*, which is otherwise impunctate, may be taxonomically unimportant, but it does support the assumption that the orthotetoids descended from the chilidiopsoids. Of course, pseudopunctae could also have developed in impunctate chilidiopsoids other than *Fardenia*; and we concede the possibility that the pseudopunctate condition was polyphyletic in origin, which would not be surprising in view of its development among other strophomenide stocks.

The development of extropunctae is of phylogenetic interest in several respects. On parsimonious grounds, one would expect the extropunctate condition to have been an apomorphy of the impunctate state. Indeed, Manankov (1979a, p. 31) showed that the extropunctate *Schuchertella* as having evolved from impunctate areostrophidiids, and the pseudopunctate *Schellwienella* (his stem stock for the orthotetoids) as having descended from the chilidiopsoids. The PAUP program, however, consistently showed extropunctae as homologues of pseudopunctae and obliged us to consider such a route for the micromorphological evolution of the orthotetidine shell. We subsequently found that the outwardly directed extropunctae could feasibly have been derived from inwardly directed pseudopunctae by assuming that an evolutionary change took place in the organic components of these structures. Our interpretation can be tested, because a number of Permian orthotetoid genera have been founded exclusively on silicified material, so that their shell



TEXT-FIG. 7. Cladogram of fourteen orthotetidine subfamilies (with the Triplesiidae as an outgroup) derived from the matrix shown in Table 3, based on characters as ordered, weighted and categorized in Table 1. The major character changes enumerated are: 1, development of short, variably disposed socket plates; 2, short socket plates parallel with hinge-line; 3, loss of pedicle foramen in adult shells; 4, loss of pedicle foramen; 5, loss of dental plates; 6, socket plates becoming recurved and longer; 7, ventral umbo distorted by cementation; 8, high cardinal process lobes directed postero-ventrally and supported by proximal shaft ankylosed to socket plates; 9, development of pseudopunctate shell; 10, ventral valves seldom distorted by cementation;

TABLE 3. The matrix of fifteen suprageneric units  $\times$  fifteen characters used in the orthotetidine classification proposed in this paper. The Triplesiidae served as an outgroup. The matrix was derived from that of Table 2 after the redistribution of some genera (see text), which did not affect any of the character states defining the taxa but did result in the suppression of the Derbyoidinae with consequential effects on the cladogram of Text-figure 7.

	111111
	123456789012345
Adectorhynchinae	20000021413?212
Pulsiinae	2102000020000?1
Hypopsinae	210420002002211
Derbyiidae	211003214132212
Orthotetidae	212002002000012
Areostrophinae	200001102040102
Chilidiopsinae	100100001000011
Diplaninae	210000212131200
Schuchertellidae	220000002042111
Omboniinae	210400213132212
Meekellinae	210300214143213
Triplesiidae	000100210040104
Orthotetellinae	210430004122112
Streptorhynchidae	220000214132221
Gacellinae	000200001000012

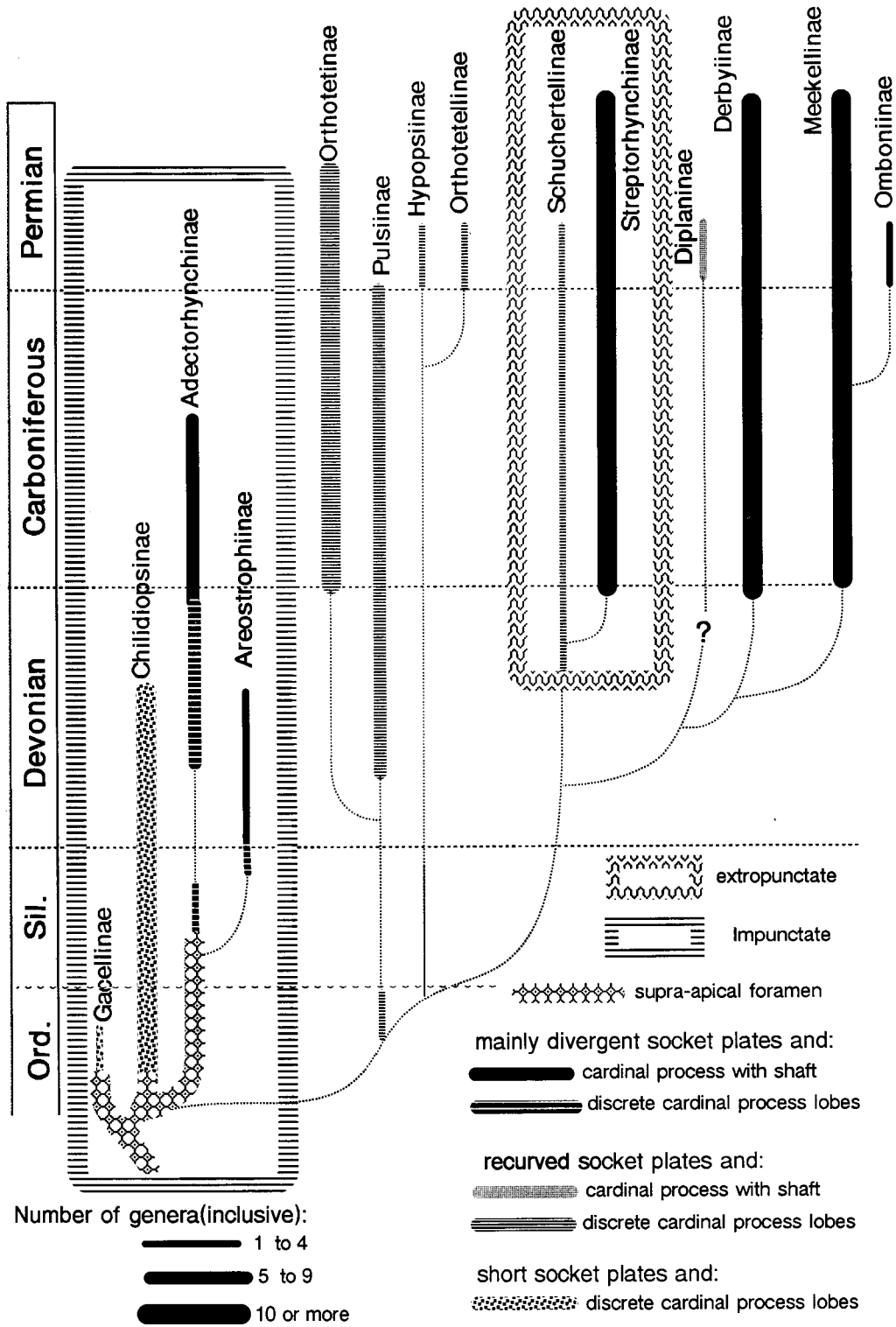
micromorphology is presently unknown. Future studies of unsilicified specimens of these genera will afford a check of both the shell structure and the merits of the classification now being proposed. In particular, we anticipate that *Diplanus*, which is provisionally assigned to the Derbyiidae, will prove to be extropunctate and more akin to the Schuchertellidae.

The other significant changes in orthotetidine morphology were essentially elaborations of the articulatory and muscle-supporting devices attendant upon increases in shell volume, especially through the conical deepening of the ventral valve. The features which most obviously underwent interrelated changes were the teeth ridges and dental plates, the bilobed cardinal process and the socket plates. Other structures also underwent compatible changes. Modifications of the pseudodeltidium and chilidium, for example, were in phase with the disposition of teeth ridges, and especially of the posterior face of the base of the cardinal process; but only the development of the socket ridges needs to be taken into account here.

The teeth ridges, which trace the growth of the hinge-teeth on either side of the delthyrial cavity, were supported by short dental plates in the comparatively shallow chilidiopsid ventral valves. The subsequent evolution of these dental structures seems to have been a widespread atrophy followed by independent recurrences of excessively developed plates. The plates were lost with the emergence of the areostrophiiids, the orthotetids, the schuchertellids and the derbyiids. Within these groups, exaggerated teeth ridges became convergent onto a ventral median septum to form the so-called homeospondylium of the orthotetids and a more sporadically developed apical chamber among adult *Derbyia*.

Post-chilidiopsid dental plates, on the other hand, arose secondarily on at least three different occasions in the orthotetidine history, and with subtly different manifestations. Among the pulsiids,

11, development of strong, parallel dental plates; 12, socket plates becoming ankylosed to cardinal process; 13, brachiophores well developed; 14, dental plates becoming convergent to form spondylium; 15, development of free spondylium and divergent socket plates; 16, development of extropunctate shell; 17, development of high cardinal process with fused lobes supported by proximal shaft; 18, socket plates becoming larger and divergent; 19, long dental plates becoming convergent; 20, cardinalia becoming flanked by promontoria.





the plates were of variable length and bounded the ventral muscle field. In our opinion, the orthotetellid dental structure evolved independently of that of the pulsiids, with a convergence of plates eventually to form a free spondylium accommodating the entire ventral muscle field. The convergent dental plates of the meekellids are superficially similar; but they must have developed independently of those giving rise to the orthotetellid spondylium, because the bases of the diductor muscles were inserted on the floor of the ventral valve, on either side of the convergent dental plates of *Meekella* or of the septum formed by the convergence of the plates in *Ombonia*.

The transformation of the chilidiopsid cardinal process, consisting of a pair of low, discrete lobes with broad, posteriorly facing myophores, to a high shafted, distally bilobed structure with slit-like myophores facing postero-ventrally, was clearly related to the conical deepening of the ventral valve. The elaboration of the cardinal process was, therefore, polyphyletic, with the high shafted version characteristic of the late chilidiopsid areostrophiids and the orthotetoid streptorhynchins, orthotetellids, derbyiids and meekellids. In these families, the elaboration of the cardinal process was accompanied by an extraordinary development of the socket plates (the erismata of Cooper and Grant 1974, p. 259) and other associated features, especially the oblique socket ridges with their brachiophore-like prolongation (the dentifers and ancillary plates of Cooper and Grant 1974). As a result, long, divergent socket plates were united with the shaft of the cardinal process into a single structure. Well developed socket ridges with ventral prolongations were ankylosed to the lateral faces of this device; and were also flared postero-laterally in the meekellids (the promontaria of Cooper and Grant 1974).

The cumulative effects of these trends are illustrated in Text-figure 8 in relation to the stratigraphic ranges of the main orthotetidine groups. The chronology of the Suborder is broadly consistent with the cladograms derived by phylogenetic analysis. The diagram also illustrates the extent of homeomorphy during orthotetidine evolution, with no fewer than four of the nine terminal families independently featuring cardinalia of closely comparable complexity.

### CONCLUSIONS

The orthotetidines constitute one of the few suborders of the Brachiopoda characterized by several basic differences in the ultrastructure of their shells. All true orthotetids have a secondary shell of cross-bladed laminae bearing closely distributed pseudopunctae, composed of microscopic conical deflections of the laminae which are directed inwardly. They evolved from the laminar-shelled chilidiopsoids, which are impunctate except for a few specimens of late Ordovician *Fardenia* which bear sporadically occurring, impersistent pseudopunctae. The pseudopunctate orthotetoids were in turn ancestral to the laminar-shelled schuchertellids, which are extropunctate with radially distributed microscopic conical deflections of the laminae pointing outwardly.

The typical orthotetoid shell is ultrastructurally indistinguishable from that of the strophomenids, although the pseudopunctae arose independently in both stocks. So far as is known, the extropunctate condition is unique to the orthotetidines; however, pseudopunctae with taleolae, so characteristic of the leptaenids, stropheodontids, chonetidines, productidines and related aberrant Permian forms, have yet to be positively identified in orthotetidines.

The orthotetidines were also closely related to the other strophomenidines in many basic morphological features. The presence, in the older species of both groups, of a pseudodeltidium with a supra-apical foramen is indicative of the existence of a ventral body wall in the living state (Williams 1956, p. 258), which was absent from other articulate brachiopods except for some primitive orthides. The sealing-off of the foramen in all later Palaeozoic strophomenides confirms that a universal atrophy of the pedicle had taken place throughout the Order by Carboniferous times. Subsequently, many strophomenides (including the orthotetidines) acquired a cementing

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TEXT-FIG. 8. Chronostratigraphy of orthotetidine phylogeny, based on the cladogram of Text-figure 7 and showing the main trends in the evolution of the pedicle foramen, shell structure and cardinalia; all taxa outside the designated boxes are pseudopunctate.

habit; and, since the davidsoniids were also cemented to the substrate and appeared to have a pseudodeltidium, they were widely accepted as orthotetidines and, indeed, gave their name to the Suborder under the priority rules of the International Code for Zoological Nomenclature. Yet, as Johnson (1982, pl. 1, figs 11, 14) illustrated, the so-called pseudodeltidium is a deltidium and, with the discovery that the shell is fibrous not laminar, *Davidsonia* and other related, cementing Middle Palaeozoic brachiopods with calcareous spiralia must now be transferred, without further demur, to the atrypines.

The widespread acquisition by many orthotetidines of a cementing habit led repeatedly to the elevation of their shells above the substrate by excessive conical deepening of the attached ventral valves. This conical deepening was accompanied by complementary extensions of skeletal articulatory devices. The morphological effects were quite dramatic, especially with regard to variations in the proportionate development of the ridges and plates supporting the teeth, the bilobed cardinal process accommodating the dorsal diductor bases, and other associated parts of the cardinalia defining the dental sockets.

Not surprisingly, these repeated trends gave rise to similar, spectacular structures in several independent stocks. The trends were broadly synchronous within a readily identifiable phylogeny that was evidently compatible with the stratigraphic ranges of constituent taxa (Text-fig. 8). As a result, previous classifications have been dominated by the preferential weighting of one kind of feature, for example dental plates or socket plates, at the expense of others. In effect, homeomorphy has played a more important role than homology in determining the structure of previous orthotetidine classifications.

These homeomorphic trends can be disentangled by paying due regard to morphology as a whole through phylogenetic analysis, and especially to the more stable changes attending the evolution of shell structure. The classification proposed herein is an attempt to meet these conditions. Even so, it is provisional on getting further information not only on the many poorly described genera currently in circulation but also on taxa like *Diplanus* and *Hypopsia*, whose exquisitely silicified morphology could well be at variance with their original shell structure which is as yet unknown.

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ALWYN WILLIAMS

Palaeobiology Unit  
Department of Geology and Applied Geology  
University of Glasgow  
8 Lilybank Gardens  
Glasgow G12 8QQ, UK

C. H. C. BRUNTON

Department of Palaeontology  
The Natural History Museum  
Cromwell Road  
London SW7 5BD, UK

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