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PERMIAN PRODUCTIDINA OF BRITAIN AND MALAYSIA

by

Mohd Shafeea Bin Leman

**A Thesis submitted in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy**

Department of Geological Sciences

**The University of Durham
1990**

1 5 NOV 1991

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Permian Productidina of Britain and Malaysia

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Abstract

The British Permian Productidina have not been revised in detail since 1858. In the present study some 2000 specimens from 29 localities in north east of England have been collected and prepared in the laboratory and used together with museum collections. The fauna consists of four species of *Strophalosia*, one new species of *Eostrophalosia*, six species of *Heteralosia* (four new), three species of *Craspedalosia* (one new), two species of *Howseia*, four species of *Horridonia* (one new) and two species of *Spinohorridonia* new genus. The Strophalosiacea and Horridoniinae are divided according to a new classification produced in this research. British Permian productidinid species are often strongly variable. Some variants suggest possible sexual dimorphism while others are probably of ecological forms. The fauna as a whole is unique and exclusive to the Upper Permian Zechstein Sea. The British Permian fauna shows major radiation periods during the early EZ1a Ca and early EZ1b Ca. In conjunction with these radiations, the Productidina become divided into two distinct assemblages, marking two biozones introduced in this thesis, the *Horridonia horrida* and *Strophalosia excavata* biozones.

Little is known of the Malaysian Permian Productidina. They comprise one species each of *Strophalosia, Craspedalosia, Institella, Antiquatonia, Reticulatia, Echinoconchus, Linoproductus, Stepanoviella, Striatifera, Liosotella* (with new species), *Marginifera?, Paucispinifera, Retimarginifera* (with new species) and *Costispinifera*, two species of *Dictyoclostus, Waagenoconcha* and *Echinauris* and three species of *Cancrinella*. Lower Permian productidinids are associated with Artinskian fusulines and show links with the South Tethyan cold water fauna. Upper Permian productidinids contain a mixture of North Cathaysian elements and the warm South Tethyan lyttoniid fauna. Variation occurs within some of the Malaysian species, but owing to lack of material, no final deductions can be made. Similarly, although significant differences are observed in Malaysian productidinid distributions, tabulation of biostratigraphic zonation is left until more data is available.

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Declaration

The contents of this thesis are the original work of the author and no other work is included without acknowledgement. This thesis has not been previously submitted for a higher degree at this, or any other University.

Mohd Shafeea bin Leman

December 1990

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CHAPTER 1

INTRODUCTION

The Scope of Study

The object of this study is to revise, redescribe and reclassify, when ever necessary, the Permian brachiopod Suborder PRODUCTIDINA from Britain and Malaysia. In achieving this goal, the study is concentrated on close examination of various morphological features within different productidinid taxa. This, in turn, contributes to the understanding of morphological variation, functional morphology and their significance in ontogeny, phylogeny and taxonomy of the group. One of the main purposes of this research is to tackle the long standing problems in taxonomic classification of the brachiopod Suborder Productidina, by establishing a more systematic scheme of classification and less ambiguous definitions of different taxa studied based on widely developed and reliable morphological criteria.

The brachiopod Suborder PRODUCTIDINA

Phylum BRACHIOPODA Dumeril, 1806
Class ARTICULATA Huxley, 1869
Order STROPHOMENIDA Opik, 1934
Suborder PRODUCTIDINA Waagen, 1883

Diagnosis. Strophomenida with open tubular spines.

Discussion. The Productidina range from the Lower Devonian to Upper Permian and has a world wide distribution particularly during Carboniferous and Permian time. The suborder Productidina was introduced in the Lower Devonian of North America (Quebec) for two strophalosiacean genera *Devonalosia* and *Spinulicosta*. The

Productidina diversified steadily during Devonian time, and during the Carboniferous they became very rich and diverse, dominating in most of the Carboniferous paralic environments. Among the celebrated Carboniferous productidinids is the largest brachiopod genus *Gigantoproductus.* The Productidina declines slightly at the end of Carboniferous period with the closure of some Carboniferous Seas, but it regains its diversifying momentum in the Permian, introducing many new taxa including the aberrant Family Richthofeniidae. At its peak of diversification at the end of the Permian period, sadly the Productidina dwindled and became extinct together with many other Palaeozoic invertebrates.

The Productidina has a very wide range of modes of life from sessile (attached by various technology, but not by the pedicle) to free living (adapted to various attitudes suiting various types of substratum), and possibly vagrant forms too. In conjuntion with these variable modes of life, the Productidina adopts a very wide range of morphological variation, the study of which has produced a series of never ending hyphotheses. The earlier group (the Strophalosiacea), however, are more primitive and somewhat close to some of the advanced Chonetidina. Although Muir-wood (1965) related the origin of Productidina to the strophomenidinid genus *Leptaenisca* (via the construction of brachial ridges), the possible link between Productidina and Chonetidina cannot be ruled out. Current observation shows that some of the primitive Strophalosiacea have much closer affinities towards some of the advance chonetids such as *Neochonetes* than towards the Strophomenidina.

Owing to its very diverse morphological variation, the taxonomic classification of the Productidina becomes very complicated and the scheme of classification is very difficult to erect systematically. At present, most of the productidinid taxa seem to be very dynamic, and many new methods of nomenclature have been introduced from time to time. It is noticeable, that many authors prefer to split the older nomenclature and introduce their own new names without attention to the possible extinction of a former name. There are so many cases in which we can see once popular and diverse genera being reduced to a mono-specific genera or to worst producing empty genera (see discussion on genus *Strophalosia*).

The Permian Productidina

The study of Permian Brachiopoda or the study of Permo-Triassic extinction seems to be incomplete without mentioning a word about the remarkable variation of somewhat bizarre Permian Productidina. It is especially during the late Permian time that the Productidina became very diverse and produced some of the most bizarre forms of all brachiopods. Such a great ability to evolve did not guarantee the Productidina a safe passage through the Permo-Triassic event which eliminated most of the marine invertebrates from the earth's surface. The Productidina finally disappeared from the sea at the end of the Palaeozoic era.

It is certainly very interesting as well as challenging to study this vast group, the morphology of which is very difficult to interpret because of its strong variation and because of the occurrence of so many cases of convergence, parallelism, etc. which require extra close attention.

The British Permian Productidina

The British Permian Productidina are not as diverse as they are in some other parts of the world (e.g. the Texas or the Salt Range Faunas). The fauna is restricted to the lowermost horizons of the Upper Permian, and they belong to the Zechstein fauna, where similar forms are found in East Germany, Poland and the USSR (Lithuania).

Major systematic classifications of the British Permian Productidina have been set up and revised several times since the work of Sowerby (1823). Several catalogues and monographs on the British Permian brachiopods have been published by Howse (1848, 1857, 1858), King (1846, 1848, 1850) and Davidson (1853, 1858, 1880). Some very useful descriptions and remarks have also been been produced by various authors including Trechmann (1921, 1945, 1954), Logan (1962), Smith & Francis (1967), Hollingworth (1987) and Hollingworth & Pettigrew (1988). In addition to all these, British Permian faunal lists have been compiled in a countless number of papers and memoirs.

The British Permian Productidina is dominated by the Strophalosiacea and the productacean Subfamily Horridoninae, with a few member of the aulostegacean Genus *Howseia*. Although various species names are encountered in the past literature, only some of them were generally accepted prior to this thesis. They include *Horridonia horrida, Howseia latirostrata, Strophalosia morrisiana, Orthothrix excavata, Orthothrix lewisiana, Dasyalosia goldfussi* and *Craspedalosia lamellosa.* However, as a result of current revision, several new taxa are introduced, while some generic names are changed. In Chapter 3, 22 species of 7 genera of the British Permian Productidina are described and revised.

Besides pure taxonomic treatment, the British Permian Productidina has also in the last few years, been the subject of palaeoecological study by Hollingworth (1987) and Hollingworth & Pettigrew (1988). Unfortunately, these authors give very little consideration to variation within and between species of Productidina.

The Malaysian Permian Productidina

In contrast to the British forms, the Malaysian Permian Productidina have received very little attention in the past. Although the Permian Productinida of Malaysia are much more widely distributed spatially as well as stratigraphically than they are in Britain, detailed information about them is not well known. Lack of local palaeontologists is the primary reason for the poor understanding of the Malaysian macrofauna in general. From the list given in table 4.2, it can be seen that more than half of the Permian productidinids listed are undetermined species while some of the determined species also prove to be a hasty identifications.

The Malaysian Permian Productidina range from the lowermost to the uppermost Permian, but their affinities are not very clear. This has partly resulted from the poorly understood Permian geology of the region. The Malaysian Permian Productidina are dominated by various productacean species, with rare species of Strophalosiacea and Aulostegacea. Described in Chapter 5 are 23 species of 19 genera of the Malaysian Permian Productidina, tentatively identified from all the available material during this study.

Methods of Study

Productidina is a brachiopod suborder in which most of the individuals are normally macroscopic in size and can be easily observed with the naked eye. As in many other studies in macrofossils, the working techniques employed are rather conventional and do not require much modern and expensive equipment. Microscopic study of the brachiopod shell is not stressed because the published information on the shell microstructure is sufficient for use in this research. Those species which perhaps deserved microscopic treatment, were unfortunately not well preserved because of their thin shells (e.g. the British Genus *Heteralosia*).

In this research, a great deal of attention was given to mastering every single morphological detail of the studied faunas in order to make detailed comparisons between individuals, between species, genera and between higher taxonomic ranks. Functional morphology is a very useful tool for this comparison. Here, models and deductions introduced by earlier workers were examined and compared with the available material, and whenever necessary new models were introduced. The knowledge gathered on the variation of morphological features and the published data on its functional morphology were then carefully and systematically scrutinized to establish new schemes of classification wherever possible.

In general, the preservation of the British and Malaysian Permian Productidina is not particularly good. Therefore, in this study, the results very much depend on good observation and good sample treatment. Samples are cleaned and prepared at various stages, both in the field and in the laboratory.

Field Sampling

Since this study is taxonomically orientated, the sampling work was carried out at random at places where the productidinids could be collected. The Productidina were collected entire as far as possible without leaving fragments of shells on the site. No measure was taken on the population density. Notes, however were taken on the faunal assemblages, lithological types as well as the types of preservation.

In the field, the productidinids can easily be recognized by naked eye or with the aid of a hand lens Loose samples were cleaned thoroughly with a brush or with water whichever is suitable. As far as possible, the fossils were prepared (loosened) in the field by using hammers and chisels of various weight and size, without harming the specimens. Delicate fossils were usually taken straight away to the laboratory for finer treatment. Labelling specimens in the field is the normal practice.

Laboratory treatment.

In the laboratory, , the productidinids were extracted or cleaned by various techniques. Each technique was carefully chosen depending on the mode of preservation, the nature and composition of the shell and the enclosing rock to avoid further damage to the fossil.

Loose, friable and highly weathered rocks were removed from the specimens by repetitive washing and brushing. Some very fragile and soft fossils were cleaned by blower (sandblast). When the shell is tough, friable matrix was sometime freed from the shell by using the ultrasonic bath.

The drilling method is the most commonly used to extract specimens. This is primarily because most of the specimens are preserved in forms of mould and cast. Some other specimens needed this technique because the shells and the matrix have the same solubility to acid reaction, or the same hardness (either too soft or too hard). Treatment with hydrochloric acid (5-10%) was tried on some of the shells preserved in limestone, but in many cases it failed to produce good results; parts of the shells being disolved together with the matrix. Some specimens were also treated with high heat and cold water, but again the result was far from satisfactory; the rocks tend to crack at random and the fossils were damaged.

In the drilling method, needles of various sizes, fine blades, small chisels and dentist's drills were used to remove the rock matrix from fossils. Chisels and blades are useful for those fossils preserved in shaly or cleaved rocks. Hard dolomite can be roughly removed from the fossils by using dentist's drills, followed by finer drilling with needles.

Thin and polish cross-sections of the shell were made to study the shell microstructure. This study is not stressed partly because of the homogeneity of the inner structure in Productidina, and partly because of the lack of shelly material available. The sections are sometime used for the reconstruction of the shell profile. Partial serial sections of some shelly fossils were made to monitor the development of the shell, but the results do not seem to be any better than observations made on naturally preserved shell interiors.

In contrast, negatives produced by rubber latex impressions or acetate peels are very helpful in reproducing very fine morphological details of the shells. Since many specimens are preserved in the form of moulds (external or internal moulds), the rubber latex casts made give better details than the actual moulds. This is a very good technique especially in reproducing projecting morphology such as the cardinal process and the spines from hollow moulds.

Several parameters of the brachiopod shells were measured (see text-figure 1.1), mainly to give data about dimensions of the fossils to support the descriptive work.

Illustration

Because variation occurs within the brachiopod species, reconstruction is necessary to illustrate the average morphology of each species. Average dimensions and collective morphological details were combined together to form the reconstruction of the species. To add to the precision of the reconstruction, details from photographs and camera lucida drawings were also used in preparing the reconstruction. Camera lucida drawings and photographs were also used to reveal some detailed features or the whole shell of selective specimens, when reconstructions were difficult to make. These techniques are also very useful to illustrate variation in ontogenic development and variation within species.

Photography is essential in all palaeontological work. For this purpose, the specimens were usually coated with ammonium chloride to produce a better picture and to hide unnecessary colour changes, label marks, etc. The coating was applied as lightly as possible, because thick coating gives poor definition to the photograph. The photographs were cut and arranged neatly on an A4 size hard backing, re-photographed and then printed as the final plate.

Taxonomic Classification Procedures

Problems in taxonomic classification

In the past, various criteria have been used to classify the productidinid brachiopods. However, no firm and systematic scheme of classification has ever been produced for the recognition, sub-division and understanding of the group. The schemes used in the past are always complicated and very difficult to apply. In general, experts agree that the classification above the generic level should be based on the presence or absence of a single or several morphological features. Most commonly, however, more than one feature is used and often more than one standard is employed at the same taxonomic level.

To accommodate all the features used in these classifications, the past diagnosis and definition of genera, subfamilies, families and superfamilies are usually very long and rather ambiguous. Recently, however, there are attempts to simplify and produce a schematic sub-division of Productidina, whilst works such as those of Muir-wood and Cooper (1960), Muir-wood (1965) are not always directly applicable. This is partly because these authors give little explanation of the scheme of classification, and mainly because the major part of their work still uses the older non-schematic methods of classification. As a result, the schematic classification introduced by them has been much debated by many later authors.

Taxonomic classification employed in this study

In this study, the author has outlined a scheme for classification of the superfamilies in Productidina, the families in Strophalosiacea and all the subfamilies in Strophalosiidae. The limited time available, does not permit the author to tackle the problems in family ranking of the productaceans and aulostegaceans. It is hoped that the successful division of the Superfamily Strophalosiacea will be used in the future, as the basis in producing similar scheme for Productacea and Aulostegacea.

Most of the criteria used in these schemes of classification have already been employed by previous workers, but here the author emphasizes the use of as few criteria as possible and applies this as rigidly as possible. Each morphological criterion is chosen carefully to avoid any overlapping in its usage. The lower ranking (genus, species and variety) are not greatly linked by a scheme of classification, and as much preference as possible is given to the original description. In addition to this, a study on the ontogeny is introduced to solve some of the problems on variation.

Some taxonomically important morphological features

Interarea. The presence of the interarea in some productidinids has long been considered as an important feature that linked this suborder with its possible strophomenidinid or chonetidinid ancestor. One important feature shown by productidinid evolution is that this group progressively looses its interarea. The presence or absence of the interarea has been widely used in determining the superfamilies in the large group of the Productidina (see Muir-wood & Cooper, 1960, Muir-Wood, 1965). Cooper & Grant (1975a,b) recognised that a large number of interarea bearing productidinids have interarea on their ventral valve only, and thus suggested that superfamilies of Productidina should be based not only on the presence or absence of interarea, but also whether both the ventral and dorsal interareas or only the ventral interarea are present.

These sub-divisions of Suborder Productidina based on the presence or absence of interarea on each valve reflects relationship between superfamilies as well as showing the evolutionary path in which each superfamily lies. With four possible groupings of interarea occurrence, only three groups are known. They are Productidina with 1) interarea on both ventral and dorsal valves (Superfamily Strophalosiacea); 2) interarea on ventral valve only (Superfamily Aulostegacea); and 3) no interarea (Superfamily Productacea); no productidinid is known to have the interarea only on the dorsal valve.

There is another small, but very important group owing to its abberant nature, the Richthofeniacea, which since it was elevated to a superfamily by Muir-Wood (1955) has not been questioned as to its validity. The Superfamily Richthofeniacea was not erected on the basis of the interarea, but detailed study on the group shows that it generally has a ventral interarea, but no dorsal interarea. Therefore, to maintain the consistency in classification of Productidina, it is suggested that the Family Richthofeniidae be included to the Superfamily Aulostegacea. This is very important, in order to prevent the creation of separate superfamily on a basis other than by the presence of interarea.

Also in accordance with this rigid scheme, some of the interarea-bearing families, subfamilies and genera which were included by Muir-Wood & Cooper (1960) into the Superfamily Productacea, should be redistributed into the other two superfamilies (see p. 137 in chapter 3). The Superfamily Strophalosiacea which has both ventral and dorsal interareas is sub-divided into families based on interarea-related morphology, the teeth and sockets. Other criteria should be chosen for subdivision of the Superfamilies Aulostegacea and Productacea because of the absence of teeth and sockets in these groups.

Teeth and sockets. In this research, in which a large collection of strophalosiaceans are studied in great detailed, the author found that the interarea and related features at the cardinal region show some degree of evolution within the group. With Family Productellidae (interarea present on both ventral and dorsal valves) considered as a strophalosiacean (see also page 36 & 137), this superfamily comprises two large groups with different strengths of development of the interarea, teeth and sockets. The Productellidae, with its degenerate interarea, teeth and sockets provides a possible intermediary form between Strophalosiacea and Productacea.

Another strophalosiacean family introduced in this study is a small, but interesting mono-generic group Ctenalosiidae which was classified by Muir-Wood & Cooper (1960) as a strophalosiid Subfamily Ctenalosiinae, based on the presence of a series of hinge teeth while other subfamilies was classified on the basis of spine distributions. The unique hinge teeth in *Ctenalosia* should not be lowly regarded, because it provides an excellent example of possible link between Productidina and the rest of Strophomenida (see further discussion on page 36).

Spine distributions. Classification based on spine distribution has been introduced by Muir-Wood & Cooper (1960) at the subfamily level of Strophalosiidae, and since then has gained various opinions, both pro- and contra- (a long discussion on this matter is written in Chapter 3, page 36 and so on). The importance of spines in productidinids has been stressed by many authors although their significance in the evolution of the group is scarcely known. However, the important function of hollow spines described by Rudwick (1970) and the consistent pattern of distribution should clear any doubt about the significance of spine distribution in sub-dividing subfamilies of Strophalosiacea.

The new scheme introduced in this thesis, suggests that only the presence or absence of body spines in each of the valves should be used in the classification of strophalosiacean subfamilies. Similar to the case of the interarea, there should be a maximum of four groups in each strophalosiacean family, but for the family Strophalosiidae, studied in this thesis, only two groups are commonly known. They are Strophalosiidae with 1) body spines on both ventral and dorsal valves (Subfamily Strophalosiinae); and 2) body spines on ventral valve only (Subfamily Heteralosiinae); *Lialosia* which has no body spines at all is suggested in this thesis to represent a new Subfamily Lialosiinae; no strophalosiids are known to have body spines on dorsal valve only. This scheme seems to work well in the other big strophalosiacean Family Productellidae, but the author has delayed this sub-classification until more material is available for comparison.

The distribution of body spines and marginal spines are also tentatively used for classifying the genera in subfamily Horridoniinae (see p. 144), while species within these genera are subdivided on the basis of the density of the body spines as well as on the dimensions of the shell.

Other morphological features. Other features are limited to use at generic and lower categories. There is no valid scheme of sub-division at these lower taxonomic ranks, but generally features closely associated with the interarea, cardinal extremities and surface ornamentation, such as the presence of squamose lamellae, are highly considered at generic level. The dimensions and shape of the shell, the growth pattern, including the growth of the cicatrix as well as the detail of types of spines, their arrangement and distribution are usually used in describing the species.

Morphological features like **cardinal process and brachial ridges** are often used in the past to described productidinid taxa at various level. At the same time, many workers described the variable nature of these two internal morphological features. The variation in the configuration of the cardinal process and brachial ridges is described in many places in this thesis. The development of the alveolus and antron, anterior to the cardinal process might have some taxonomic significance, but the lobation of the cardinal process is variable even within the same species. The size of the brachial loop probably has a little taxonomic value, but the configuration of the brachial loop seems to depend on the shape of the shell. *Howseia umbonillata*, described in this thesis gives a good example of how the shape of the brachial impression differs between the male and female dimorphs. Therefore, in this study the cardinal process and brachial ridges are not highly regarded in outlining the scheme of classification. These morphological features, are only used as supporting features to describe some of the highly variable species.

Research Problems

Apart from the problems of the taxonomic classification procedures, the author faced great problems with variation within the studied species. Some of the variants of one species sometimes seem to be very close to varieties of other species. This is particularly problematic in the rich and abundant species such as *Strophalosia excavata* and *S. lewisiana*, which Logan (1962) suggested had hybrid forms in between them. In order to avoid error in assigning a hybrid form or extreme variant, the author has tried to use several alternative features in describing the two species.

The problem of variation is made worse by the problem of preservation. Often, even the various alternative distinguishing features are not helpful owing to poor preservation. The reef fauna from Durham is very commonly preserved in the form of moulds and casts in which many morphological features are destroyed during their formation. The dolomitization of the reef is responsible for the formation of these moulds and casts, while the development of coarse-grained dolomite destroyed the shell even further. Some fossils on the bedding plane in the Raisby Formation and most of those from Malaysia are very difficult to study owing to burial deformation as well as tectonic deformation in the case of Malaysian fauna. Some of the fragmentary material from allochtonous assemblages in Malaysia are sometimes hardly recognisable.

Glossary of Productidinid Terminology

Adductor muscle platform - platform to which the muscle for closing the valves are attached.

Adductor muscle scars - impression of adductor muscle attachment areas.

Alveolus - pit formed anterior to cardinal process when the cardinal process shaft is not supported by a median ridge.

Antron - triangular gap due to incomplete fusion of cardinal process buttress plates and breviseptum as in *Buxtonia.*

Auricle - Flat or arched posterolateral extension of the shell, separated by a break of slope from the convex visceral disc (termed as wing or ala in some past literature).

Beak - pointed or incurved extremity of the umbo.

Brachial ridges - ridges of brachial apparatus originating from adductor muscle platforms, extending laterally and forming open loop (*brachial loop*) anteriorly; often only their impressions (*brachial impressions*) are preserved.

Breviseptum - median ridge not supporting the cardinal process.

Cardinal process - a more or less elevated boss for attachment of the diductor muscle; also assisting in articulation. It consists of a shaft and lobate myophore.

Chilidium - flat or concave plate closing the nothyrium.

Cicatrix of attachment - flattened scar in the ventral umbonal region for cementation against foreign objects.

Costae - coarse (less than 15 in 10mm) radial ridges on the exterior shell surface. It is called *costellae* when the radius is smaller (more than 15 in 10mm).

Delthyrium - triangular opening of the ventral interarea.

Diaphragm - thin crescentic plate developed around visceral disc of brachial valve, bridging the gap between the trail of ventral and dorsal valves.

Diductor muscle - Muscle for opening the valves, attached to the cardinal process myophores on the dorsal valve and to the large low flabellate scars on the ventral valve.

Dorsal valve - formerly brachial or small valve which bears cardinal process and lophopore, commonly concave or flat in nature.

Elytridium - Convex puckered cover of the delthyrium in Aulostegacea.

Endospines - Fine spines or protruding taleolae in interior of both ventral and dorsal valves. The coarser outer rims of endospines probably serve as strainers.

Fold - major radial ridges such as median fold.

Geniculate - sharp bend of the shell at the begining of the trail.

Ginglymus - secondary interarea? in ventral valve of some large Productacea; the function is not fully understood.

Hinge - posterior line of the valve junction.

Hinge teeth - a pair of articulating process at posterolateral margin of delthyrium.

Interarea - formerly cardinal area.

Lamellae - thin dead shell layer overlapping the newly developed outer layer.

Lateral ridges - thick ridges extending laterally from the cardinal process, probably for strengthening the shell and assisting in articulation.

Lophidium - triangular plate projecting posterior to the hinge line of the dorsal valve to form a posteriorly extended muscle attachment base and to close the opening in the delthyrium of the Aulostegacea.

Marginal ridges - concentric interior ridge bounding the visceral disc of Marginiferidae, often bearing coarse strainer endospines.

Median septum - median ridge of varying extent in both ventral and dorsal valves.

Myophore - distal expanded part of cardinal process to which diductor muscles were attached.

Notothyrium - triangular opening in interarea of dorsal valve.

Pseudodeltidium - single flat or convex plate covering part of the delthyrium.

Reticulation - nodelike enlargement formed by intersection of concentric rugae and radial costae or costellae.

Rugae - concentric wrinkles or thick overlapping growth lamellae.

Sockets - excavation for placing teeth at the lateral base of cardinal process of Strophalosiacea, bounded by *socket ridges* which often buttress the cardinal process.

Spine - hollow tubular projection out of the shell, classified according to their angle against the shell surface at point of origin: *erect spines (75-90°); recumbent spines (0-45°); suberect (45-75°).* by their nature: *clasping spines* (concentrically arranged marginal and body spines that clasped foreign objects, exceptionally well developed in almost all productidinid juveniles); *Halteroid spines* (long large spines, four or six in number, symmetrically placed and acting as a strut-like support); *prostrate spines* (straight spines that lie prone on shell surface); *rhizoid spines* (root-like spines for attachment by entanglement or cementation against foreign objects) or by their position: *auricular spines* (erect to suberect spines born on the auricle except for the row at posterior margin); *body spines* (all spines apart from auricular and marginal spines); *marginal spines* (a row of spines on the posterior margin, acting as cementing, clasping, balancing or supporting spines).

Squamose - ragged concentric structure of overlapping lamellae or rugae.

Sulcus - major depression in either valve, normally median in position.

Taleolae - non-fibrous calcite rods, commonly with median perforation and embedded in fibrous shell layer or protruded as endospines on the interior of the shell.

Trail - extension of shell of either valve beyond the visceral disc.

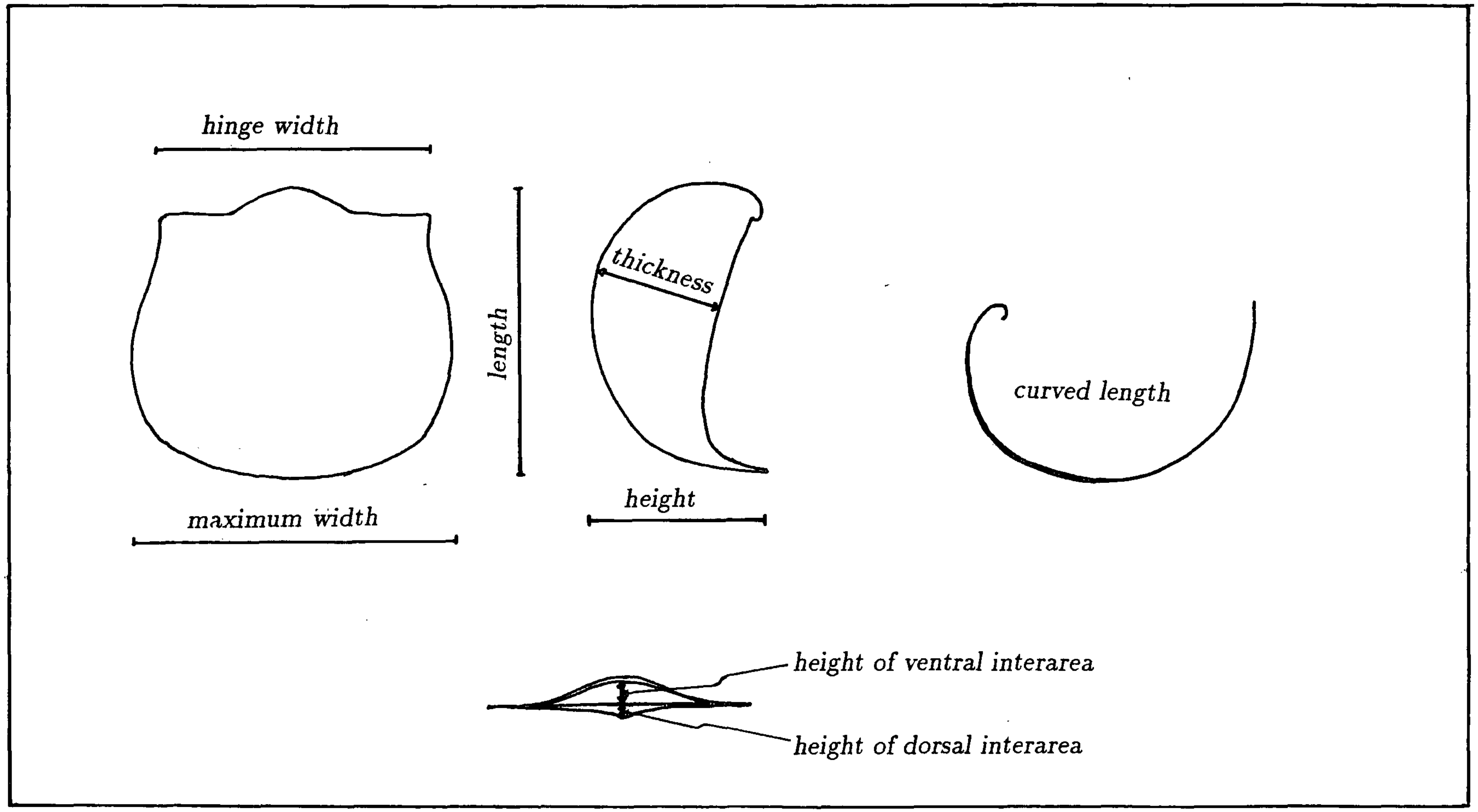
Umbo - posterior region just anterior to the beak.

ventral valve - formerly pedicle or larger valve, commonly convex in nature.

Visceral cavity - includes body cavity and mantle or brachial cavity.

Visceral disc - exterior equivalent of visceral disc.

[Most of the terminology listed above was taken from Muir-Wood (1965) and William & Rowell (1965)]



Text-figure 1.1. Measured dimensions

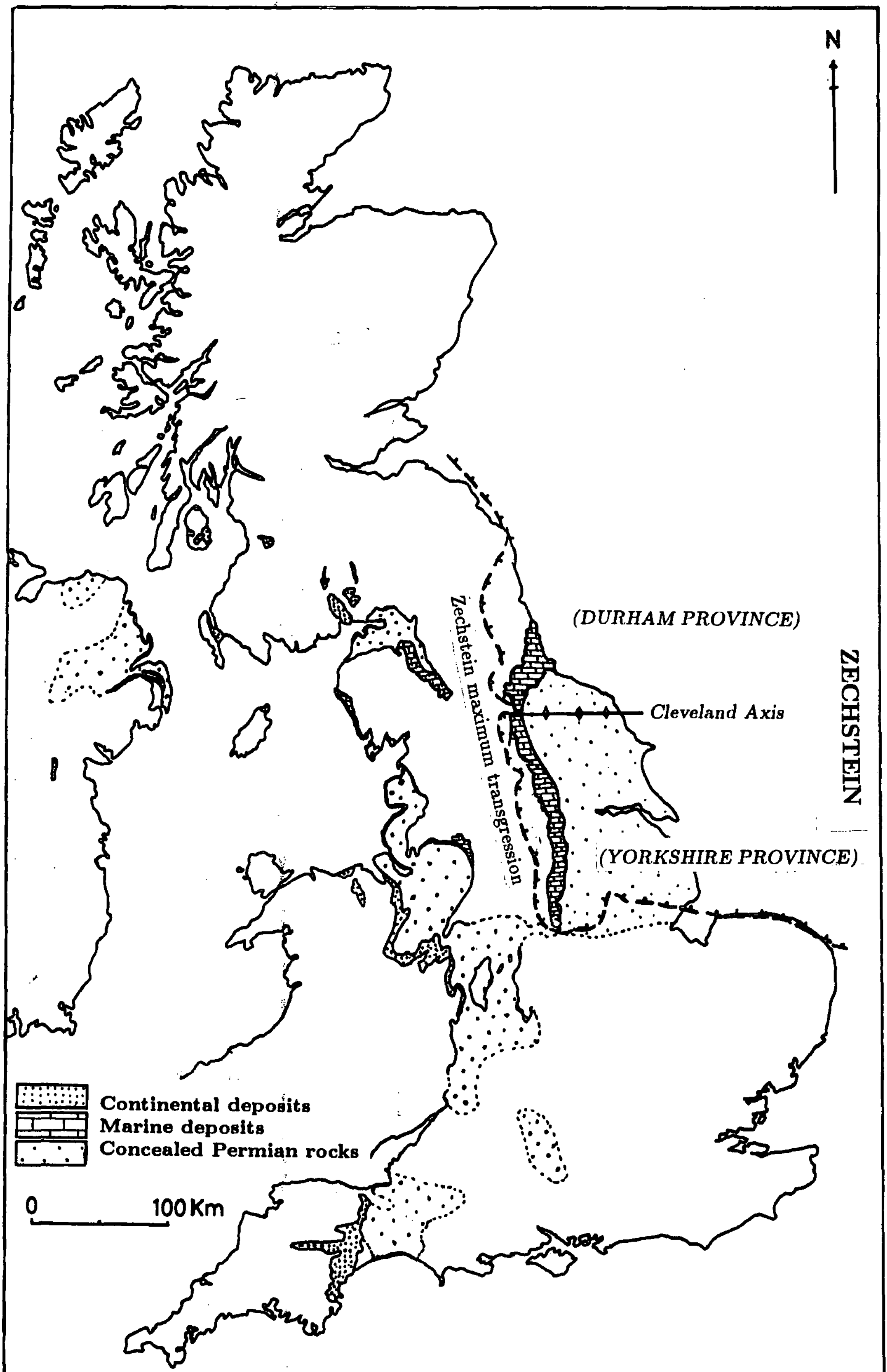
CHAPTER 2

THE BRITISH PERMIAN AND ITS PRODUCTIDINA

Introduction

The British Permian began with the development of a desertland, after the closure of the sea way across Europe during the Upper Carboniferous time (Johnson, 1981, 1982). This was later followed by the development of confined marine basins, in which lived all the Permian productidinids described in this study. The Permian rocks are well developed in the northeast, northwest, Midlands and southwest of England as well as in southwest of Scotland, North Wales and Northern Ireland (see text-figure 2.1). They consist largely of continental breccias or sandstones and marine dolomitic (magnesian) limestones, evaporites and mudstones. The desert sandstone deposition takes place during Lower Permian time, while the emergence of the confined hypersaline Bakevelia and Zechstein basins marked the begining of the Upper Permian in Britain. The Lower and Upper Permian in Britain have been well described in a countless number of individual papers and memoirs of British Geological Survey, and has been summarized several times by various authors including the works of Smith (1980b, 1981, 1989 etc.), Smith *et al.* (1974) and Smith *et al.* (1986) which are the main sources of reference for this chapter.

British Permian brachiopods are well known in past literature, and they have been studied in great detail over the last two centuries. Despite their very limited lateral and vertical distribution, the brachiopod fauna is very rich and diverse in composition. Up to the present time, the British Permian brachiopods are restricted to the English Zecshtein Cycle 1 (EZ1), and their occurence in the Bakevelia Sea in Northern Ireland, has been reported to be questionable (Pattison, 1970). For this reason, the author will discuss only the English Zechstein Cycle 1 in this chapter, while other Permian rocks will only be mentioned in relation to it.



Text-figure 2.1. Distribution of Permian strata in Britain [After Smith *et al.* (1974) and Smith (1989)]

The English Zechstein

During Lower Permian time, an arid climate produced widespread piedmont and eolian as well as fluvial deposits in Britain. Marine trangression which takes place during the Upper Permian time, submerged the northern part of England and Northern Ireland. This newly formed basin was divided into the Zechstein Sea to the east and the Bakevelia Sea in the west. The English Zechstein represents the western shelf of the larger Zechstein Basin wich extends to the east as far as Poland and Lithuania. In Britain, the Zechstein Sea is known to cover most of the old County Durham, Yorkshire and Nottinghamshire. The Bakevelia Sea is widespread in northwest England, the Irish Sea and part of southern Scotland and Northern Ireland. It is in these two basins that the celebrated British Magnesian Limestone and the associated evaporites were deposited.

The English Zechstein was deposited in two provinces, the Durham and Yorkshire Provinces which were separated by a palaeo-high called the Cleveland High or Cleveland Axis (Smith *et al.*, 1986). Five cycles of carbonate - evaporite deposition are recognised in both provinces, with substantial differences in lithology between the two provinces. Several names have been used to described these carbonates and evaporites in the past, but for the purpose of this study the nomenclature proposed by Smith, *et al.* (1986) is employed.

English Zechstein Cycle 1

The Marl Slate

The begining of the Zechstein trangression is marked by the deposition of water laid Yellow or Basal Permian Sands (Smith, *et al.* 1974), followed by the deposition of thinly bedded or laminated sapropelic dolomite (Turner & Magaritz, 1986) of the Marl Slate. The Marl Slate occasionally gains thickness of more than 5m, although it is normally about 1m in thickness. This formation is generally thicker in County Durham and thinning towards the west and south, and towards the basin in the east.

The Marl Slate in County Durham was in places anoxic and yields fish faunas, land floras and shallow marine invertebrate faunas. Among brachiopods commonly known from the Marl Slate are the inarticulates *Lingula credneri* and *Discina konicki*, but Mills & Hull (1976) also reported some *Horridonia horrida* as well as *Dielasma elongatum* and *Streptorhynchus pelargonatus* from the Marl Slate at Eldon Hill in County Durham. Bells *et al.* (1979) also recorded the occurrence of *H. horrida* from the Marl Slate at Middridge. The Marl Slate is succeded by the deposition of the Cycle 1 carbonate (Raisby and Ford Formations in Durham Province, and Cadeby Formation in Yorkshire Province), followed by Cycle 1 anhydrite, Cycle 2 carbonate and so on (see text-figure 2.3).

The Cadeby Formation

Although the current study does not involve any collecting or field work in the Cadeby Formation, several important specimens studied and figured in this thesis were obtained from several BGS boreholes from Yorkshire and Nottinghamshire. These faunas came either from the lower part of the Lower Magnesian Limestone or from the Lower Permian Marl (probably equivalent to the Wetherby Member of the Cadeby Formation of Smith *et al.*, 1986). Limited time available, did not permit the author to gather detailed information on the lithology and fauna of these boreholes.

Productidinids encountered in these boreholes include *Horridonia horrida*, *H. hoppeiana*, *Strophalosia goldfussi*, *Craspedalosia lamellosa*, *?C. langtonensis*, *?Heteralosia morrisiana*, and *?H. aycliffensis*. The occurrence of these productidinids has been recorded in various memoirs of the Geological Survey of Great Britain, but some of the species names used in these memoirs differ from the above list (see Edwards (1951, p. 98-101, & 1967, p. 149), Eden, Stevenson & Edwards (1957, p. 141) and Smith, Rhys & Goosens (1973, pl. 10,11); see also table 2.1). Fossils from the higher section (Sprotborough Member (EZ1b Ca)) are not very well known.

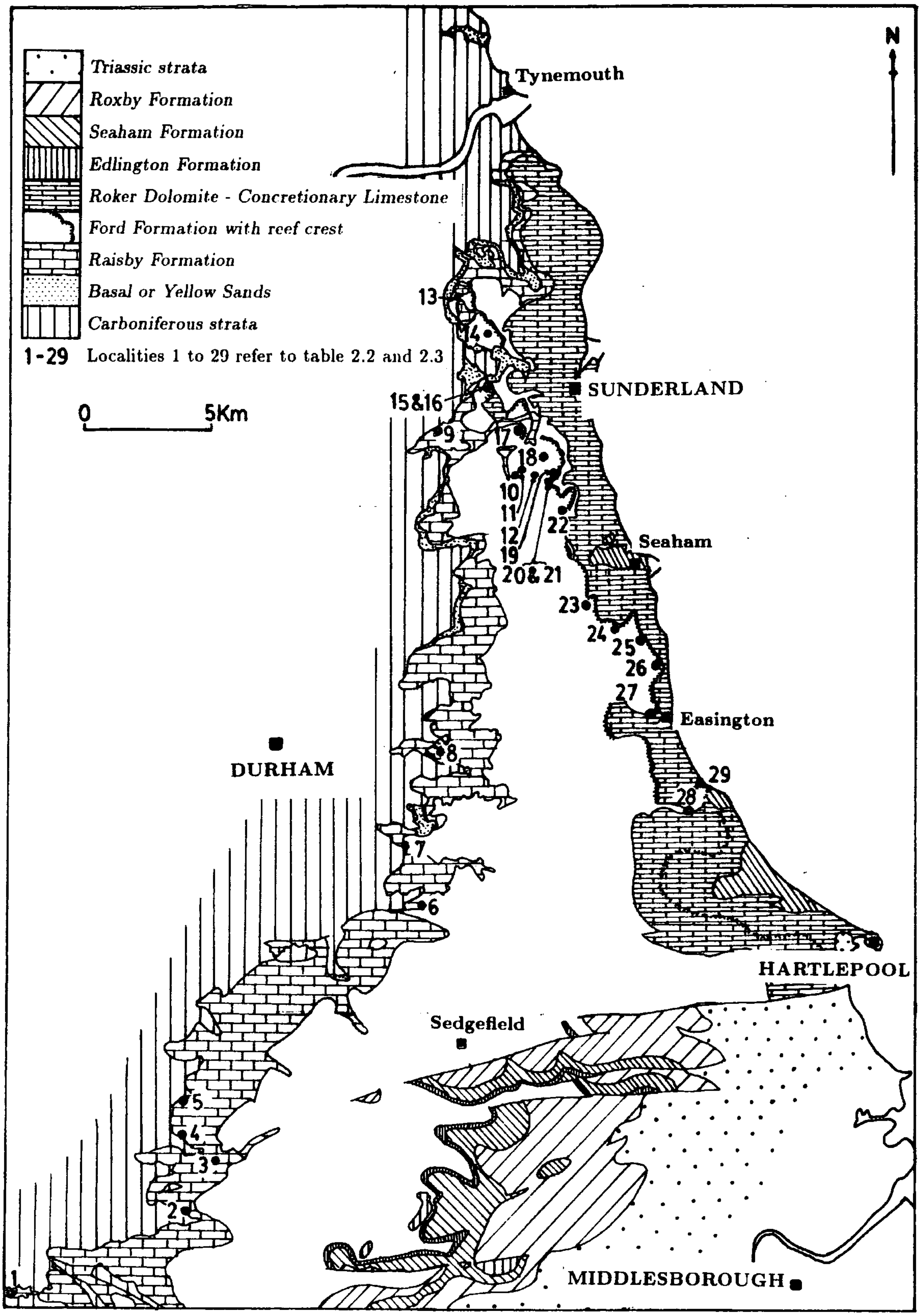
The Raisby Formation (EZ1a Ca)

The Raisby Formation which is more popularly known in the past as the Lower Magnesian Limestone, is well developed in County Durham (Smith & Francis, 1967; Smith, *in* Johnson, 1970, 1972; Mills & Hull, 1976; etc.), and it extends to the north to Tyne and Wear (Land, 1974; Smith (in publication), Smith *in* Robson, 1980; etc.) and to the south to North Yorkshire (Smith *et al.*, 1986) (see text-figure 2.2).

This formation was defined by Smith *et al.* (1986) as strata of cream, brown and grey fine-grained dolomite with thick grey fine-grained limestone in the lower part. The base of the formation is a sharp boundary above the finely laminated Marl Slate, and in its lower half the Raisby Formation is thinly bedded, locally sparingly to richly fossiliferous. Toward the top the Raisby Formation becomes medium to thickly bedded and less fossiliferous, and the top of this formation is overlain by the oolitic dolomite of the Ford Formation. The dolomite of the Raisby Formation commonly shows abundant replacive gypsum and anhydrite, and thin argillaceous dolomite beds and small scale cross-lamination in lower part. Evidence of eastward slope movements are also found at various levels especially at the bottom and the top of this formation.

Fossil occurrences have been recorded from numerous localities by various authors. During the tenure of this research, most of these localities have been visited. The author managed to collect specimens of productidinids from eight localities mentioned by earlier authors, while two new productidinid localities were also found for the first time during this study. These localities are Sherburn Hill Quarry (GR. NZ 345417) and White Quarry (GR. NZ 257245). The later locality had been studied by Mills & Hull (1976), but these authors did not find any brachiopods here.

All the fossils collected by the author during this research come from the lower part of the Raisby Formation. The faunas are usually found in limestones, either in biocoenosis assemblages (e.g. East Thickley Quarry, White Quarry and Raisby Hill Quarry faunas) or a thanatocoenosis assemblages like that of the Penshaw Hill, Sherburn Hill and Old Quarrington Quarry faunas. The fauna at Langton Quarry has been interpreted as a lagoonal or near-shore fauna. The list of productidinid brachiopod species collected and studied from the Raisby Formation can be seen in



Text-figure 2.2. Zechstein rock formations in Durham Province [After Smith (1980) and Smith *et al.* (1986)]

table 2.2 at the end of this chapter.

The Sherburn Hill Quarry (NZ 345417)

Sherburn Hill Quarry displays a good section of the top of the Yellow Sands, the Marl Slate and the base of the Raisby Formation. At the northeast corner of the Quarry (around NZ 345417), the quarry face cuts through about 1m of Marl Slate which is directly overlain by thin to medium-bedded buff to brown dolomite. The strata dip at about 5^o to the east. There are no macrofossils found in the finely laminated Marl Slate, but numerous shelly fossils are found at the top of the first bed of the Raisby Formation. Fortunately, the excavation has left a substantial surface of this first bed on the abandoned quarry floor. This bed ranges from 8 to 12cm thick and the top 3 or 4cm yields various fossils randomly distributed. The fauna is disorientated and includes some fragmentary bryozoans and many disarticulated brachiopods and bivalves suggesting that they have been transported, probably by downslope movement from the west. The fauna includes *Fenestella retiformis, Heteralosia? quarringtonensis, Pterospirifer alatus, Crurythyris clanyana, Stenoscisma schlotheimi, Horridonia horrida, ?Lingula credneri, Streblochondria pussila and Peripetoceras freieslebeni.*

The White Quarry (NZ 257245)

At southeast corner of White Quarry (or Old Town Quarry in Mills & Hull (1976)), the top of the Marl Slate is exposed at the quarry floor, yielding a rich fauna of inarticulate brachiopods *Lingula credneri* and *Discina konicki.* The Marl Slate is succeeded by thin to medium bedded bluish grey, fine-grained limestone of the Raisby Formation. The limestone sequence is about 10m thick and 30m wide in the quarry and passes gradually laterally and upwards into a thin to medium bedded pale cream to brown dolomite. Scattered fossils are found in the limestone over an interval of 1.5m, begining at about 2m above the base of the Raisby formation. Most of the fauna is found on bedding planes except for the large *Horridonia horrida* and some other large productidinids and bivalves. The fauna is dominated by *Horridonia horrida* which is commonly orientated with its trail on top. Other fossils include *Horridonia hoppeiana, Horridonia* sp. A, *Heteralosia aycliffen-*

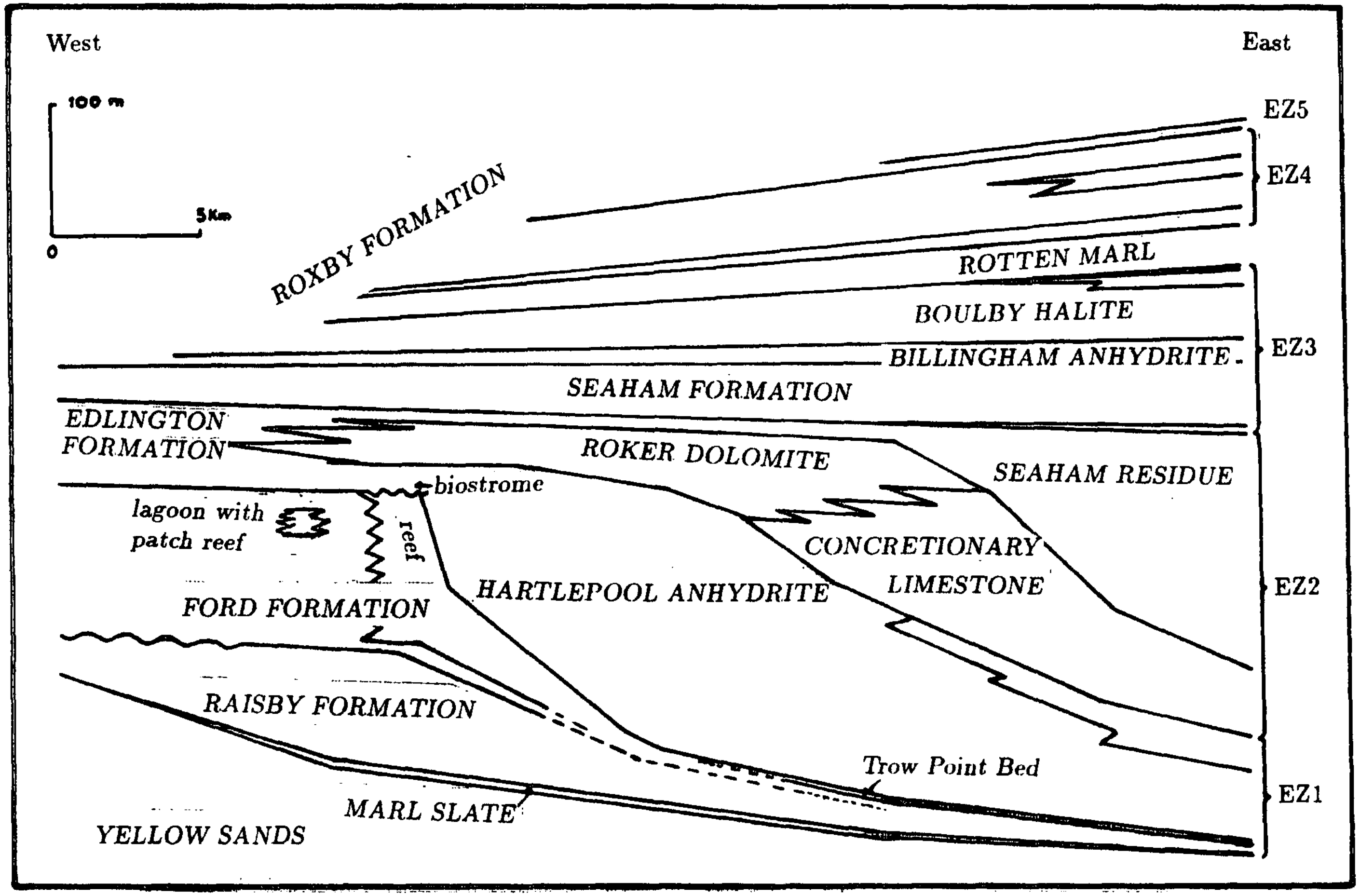
sis, Strophalosia goldfussi, Craspedalosia lamellosa, Pterospirifer alatus, Stenoscisma schlotheimi, Dielasma elongatum, Cleiothyris pectinifera, Crurithyris clanyana, Permophorus costatus, Peripetoceras freieslebeni, Fenestella retiformis, Synocladia virgulacea, Discritella columnaris, Acanthocladia sp. and *Kingopora?* sp. Burrowing traces are also commonly observed on the shell of larger *Horridonia horrida*

The Ford Formation (EZ1b Ca)

Formerly known as the Middle Magnesian Limestone of County Durham, Tyne & Wear, Cleveland and northern-most Yorkshire, the Ford Formation is defined by Smith *et al.* (1986) as the Upper Permian carbonate strata lying between the Raisby Formation and the Edlington Formation in the west and the Hartlepool Anhydrite in the east. The Ford Formation is divided into two interdigitate main facies, the reef and back-reef facies, and a minor basinal facies. Each of these three facies contains its own distinct fauna and the reef facies has produced most of the Permian fossils found in Britain. Productidinid brachiopods are well known from this formation and the vast majority of described specimens came from the reef facies of this formation. From the current research twenty productidinid localities (all of which have been recorded earlier by various authors) have been studied and the productidinid faunas encountered are listed in table 2.3 at the end of this chapter. The distribution of the Ford Formation can be seen on text-figure 2.2, while the lithostrathigraphic correlation between various facies in the Ford Formation and between Zechstein rock formations in Durham Province is illustrated on text-figure 2.3.

Reef facies - Tunstall Member

The Durham Permian reef is developed on a more or less north-south trend, extending from West Boldon in the north as several elongate discontinuous outcrops for more than 30 km to Hartlepool in the south. Erosion of the younger cover exposes the reef in the north in several low hills, whereas beyond Castle Eden Dene in the south the reef was covered by the younger Zechstein sediments. Owing to the difficulty in determining the actual boundaries between the reef and its surrounding rock formations, the lateral extension of the Zechstein reef cannot be precisely mapped. The



Text-figure 2.3. Lithostratographic correlation in the Zechstein of Durham Province [Modified from Smith (1989)]

best known limit is the outline of the reef front which was illustrated by Smith (1978), and this outline has been used successfully by Hollingworth (1987), Hollingworth & Pettigrew (1988) and Hollingworth & Tucker (1987) to reconstruct the paleoecology of the reef. The western limit of the reef is known to interdigitate with the back-reef or lagoonal rocks, but such feature is only known at the type locality of the formation, i.e. at Ford Quarry (NZ 36355130) and Claxheugh Rock (NZ 363514).

The Durham Permian reef is made of buff to brown altered dolomite with conspicious bryozoan frameworks and dominant algal encrustation, laminae and stromatolite at the top. Several reef sub-facies are recognisable in the field, where each subfacies displays different faunal assemblage from the other (see Hollingworth (1987), Hollingworth & Pettigrew (1988)). Productidinid brachiopods are dominant in places in the lower part of the reef, especially at the reef base and the lower reef core, while towards the reef flat and the fore-reef the brachiopods decline significantly in number and diversity. The last brachiopod to survive on the reef in upward succession is the terebratulid *Dielasma elongatum* which disappears not long after the last Permian productidinid *Strophalosia excavata.* Extinction was caused by changing environmental conditions particularly the increase in salinity of the Zechstein Sea towards the top of EZ1.

Basal Coquina. An excellent exposure of undolomitized limestone at Tunstall Hill Rock Cottage (NZ 392545) provides a good example of lithology and fauna of the reef base. This locality is formed of bedded shelly or coquina layers of various faunal elements. Although the coquina bed is not a part of the actual reef (Smith, in publication), its role in the development of the eventual reef is undeniable. The basal coquina at Tunstall Hill Rock Cottage yields a very rich brachiopod fauna, and a striking feature of this fauna is the nesting habit of *Dielasma elongatum.* The productidinids are not a very prolific group at this locality (see list in text-figure 2.3) with the sessile *Howseia latirostrata* and *Heteralosia morrisiana* dominated the suborder.

Hollingworth & Pettigrew (1988) mention that the Rock Cottage fauna was previously unknown, but the author believes that most of the specimens in Howse and Kirkby collections (marked from Tunstall Hill) formed in the nineteenth century might have come from an extension of this locality. The preservation of brachiopods in this huge collection by Kirkby and Howse (studied by the author in Hancock Museum), shows remarkable resemblaces with those collected by the author from the coquina bed at Tunstall Hill Rock Cottage. Pattison (1977) also suggested a locality around the present Rock Cottage coquina bed for the origin of the King collection labelled from Tunstall Hill. Although the King collection is not as big as the Kirkby collection, the fauna and its mode of preservation is unique as far as is known and suggests that it belongs to no other locality, but the Tunstall Hill Rock Cottage.

Reef-core sub-facies. Massive buff to brown autochthonous dolomite (biolithite, boundstone) forms much of the Durham Permian shelf-edge reef (Smith, in publication). The reef-core exposures, sometimes display turbid dolomite surrounding the framework of bryozoa, and pockets of detritus or sometimes pockets of *Horridonia dunelmensis* and / or *Strophalosia excavata - S. lewisiana. H. dunelmensis*, however does not appear in the upper reef-core (Hollingworth, 1987). Also very common in the reef core, is lamellar encrustations of dolomite of different sizes, which are often confused with the primary frame organisms.

Among the well known reef core exposures are Hylton Castle road cut (NZ 360589) and Humbleton Hill (NZ 381553) in which a rich and diverse productidinid fauna are encountered. The well preserved spines in most of the productidinid brachiopods strongly suggested that the fauna belongs to a biocoenosis. Comparison in faunal elements (especially the productidinids) between the two localities above and Tunstall Hill old trench (NZ 397541) suggests that the later locality is positioned much closer to the reef-core. Tunstall Hill old trench (NZ 397541) has been tentatively positioned at the reef crest by Hollingworth (1987) and Hollingworth & Pettigrew (1988), although they mentioned elements of uncertainty in their proposal. For a detail list and the relative abundance of productidinid brachiopods from these three localities see text-figure 2.3.

Reef-flat sub-facies. Uneven, more or less horizontal, thick-bedded, complex assemblages of encrusted bryozoan biolithite and algal stromatolite of the reef-flat are exposed in many localities in the vicinity of Ryhope, Seaham, Hawthorn and Easington. The sequence of this sub-facies sometimes reaches more than 10m thick (e.g. at

Hawthorn Quarry (NZ 438463), but the actual thickness is not known due to surface erosion of the reef. In places, the reef-flat contains pockets of derived debris, and quite often these pockets are full of molluscs and brachiopods. While Smith (in publication) suggests that the fauna is part of the debris, the presence of nests, very rich in fauna including *Strophalosia excavata - Strophalosia lewisiana* such as that exposed at Ryhope Mental Hospital (NZ 40055215) (or Quarry Heads in Smith, 1958 and Smith, in publication), suggests that some of the fauna might belong to biocoenosis assemblages, living in a pocket sheltered by algal bushes.

Current research encountered several productidinid localities in the reef-flat sub-facies, but only *S. excavata* and *S. lewisiana* are known from them. Among these localities include the Ryhope Mental Hospital, Stony Bank cut (NZ 41854740), Hawthorn Quarry (NZ 438463), Townfield Quarry (NZ 431438) and ?Garden of Eden Bridge (NZ 43803975). In general, the fossil occurrences are rare and scattered, while in some of the localities only stunted *S. excavata* recorded. This suggests that the rich fauna at Ryhope Mental Hospital might be positioned at the lower part of the reef-flat.

Reef-front sub-facies. Smith (in publication) divided the reef-front sub-facies into the reef-crest, the mid reef-slope and the lower reef-slope.

The reef-crest and uppermost slope are seen in the eastern part of the exposure of Claxheugh old railway cut (NZ 363574) and Ford Quarry (NZ 36355730). The lithology and the productidinid fauna of the reef-crest are quite similar to that of the reef-flat, except that the bedding of the dip-crest is highly lenticular with the dip changes from nearly horizontal in the reef-flat to 45^o or more in the reef-crest. *S. excavata* from the reef-crest is very small in average size and often shows a twisted umbo.

The mid reef-slope sub-facies exposes in several localities at Tunstall Hill, while the best exposure for the productidinids is exposed at the railway cut at Beacon Hill east NZ 442454 The rocks comprise thick to massive sheets of encrusted bryozoan biolithite with thinner sheets of laminated dolomite. The beds is often irregular, but generally dip very steeply (45-90^o) indicating the contemporary slope of the original reef front. A rich and diverse productidinid fauna is seen at Beacon Hill railway cut, with several faunal assemblages found within a close proximity. An assemblage of rich *S. excavata* - *S. lewisiana* - *Eostrophalosia permiana* exposed at the southern exposure (NZ 44214528), while an assemblage of *Heteralosia seahamensis* - *Howseia latirostrata* with less abundant *Strophalosia* is found less than 50m to the north of the first assemblage. *Horridonia dunelmensis* and *Howseia umbonillata* are also found in very small number.

The lower reef-slope or reef-talus subfacies is well exposed at the old railway cut at Ryhope (NZ 39605385). The rocks comprise multi-range of reef rock types, fallen from the higher part of the reef, ranging from blocks of several metres across to sand and silt-size fragments. The rocks usually contain authochtonous biota derived from the reef-slope and reef-crest as well as some indigenous fauna living in pockets of rubble between larger biolithite blocks. Although not rich, the productidinid fauna of the reef-talus at Ryhope old railway cut (NZ 39605385) is quite diverse and this suggests that it is positioned quite low in the Durham reef.

Back-reef or lagoonal facies

The back-reef and lagoonal facies forms most of the Ford Formation. However, owing to lack of interesting elements in this sub-facies it is probably the least known part of the formation. In many exposures of the lagoonal facies, the rocks are made of thin to medium-bedded,pale cream and buff granular and oolitic dolomite with abundant cavities from the dissolution of former sulphates. Fossils are very rare except for a few bivalves. Smith (in publication) suggests that the thick-bedded soft shelly granular dolomite below the reef dolomite at Gilleylaw Plantation Quarry (NZ 376536) and Humbleton Hill (NZ 381553) to belong to this facies. From the thick-bedded dolomite at Humbleton Hill the author found rare occurences of *S. excavata* as well as numerous bivalves and gastropods. Should this proposal of Smith (in publication) be true, the reef core of Humbleton Hill must be substantially younger than the underlying lagoonal deposits, and the reef must have been retrograding towards the shore.

Patch Reef sub-facies. The lagoonal facies of Ford Formation also includes several patch reefs and the best examples of patch reefs are shown at the Gilleylaw Plantation Quarry (NZ 376536) and at High Newport old railway cut (NZ 387538). The patch reefs developed in the east, at least 30m above the base of the lagoonal facies. The patch reef at Gilleylaw Plantation Quarry is made of about 5m of thick-bedded stromatolite and bryozoan biolithite with a wedge of highly fossiliferous rubbly talus at the northern margin, from where a rich fauna of *S. excavata* and *S. lewisiana* is found. The patch reef is overlain by coarsely oncolitic dolomite.

The High Newport patch reef comprises a rigid arched core of bryozoan and algal biolithite in which numerous remarkably preserved *S. lewisiana* and *S. excavata* with hairy spines are found. The flank of the reef is made of bedded dolomite of uncertain origin. The dolomite is locally fossiliferous and from a grey bedded dolomite the author found several specimens of small *Horridonia hoppeiana* with very strongly curved ventral valve together with some *Strophalosia lewisiana.*

From a temporary builder's trench (or Newport Hill of Smith (in publication) - NZ 379539), the author examined a large collection of fossils in Dr. G. A. L. Johnson's possession. This collection included the productidinids *H. latirostrata, H. umbonillata* and a few *S. excavata.* It should be noted that Hollingworth (1987) recorded that *Horridonia* is absent from these patch reefs.

Off-reef facies - Hesleden Dene Member

The off-reef facies of the Ford Formation is not well known and its relation to the other formations is also not well established. At Dene Holme (NZ 455405), algal-laminated dolomite is exposed, forming a large stromatolite dome (Smith & Francis, 1967), overlying basal conglomerate (up to 2m thick). The conglomerate comprises encrusted rolled cobbles and boulders of dolomite of the underlying reef with very little matrix. Some of the cobbles and boulders contain reef fauna includes some *S. excavata* and *S. lewisiana.* The basal conglomerate is deposited on the eroded surface shelf-edge reef.

Thick-bedded dolomite exposed at foot of the cliff at Chourdon Point (NZ 442468) was suggested by Smith & Francis (1967) as an off-reef basinal equivalent of the reef. However, the presence of inarticulate brachiopods such as *Lingula credneri* and *Discina konicki* indicates a shallow water origin of these beds. Also included in the biota is *Neochonetes* sp. cf. *N. davidsoni* which are commonly found in the lagoonal facies in Sunderland area. The rest of the fauna consists of *?Streptorhynchus pelargonatus, ?Heteralosia quarringtonensis, Bakevelia ?antiqua, Strophalosia ?excavata, Permophorus costatus, Crurythyris clanyana* (majority) and *Fenestella retiformis.*

Trow Point Bed. A thin layer of oncoids, peloids and columnar stromatolite named as Trow Point Bed by Smith (1986), extensively covers the Zechstein Cycle 1 and Smith (in publication) includes this thin layer as part of Ford Formation. Although it is better known off the reef, Smith (in publication) indicated that there is no evidence to suggest that this layer is a basinal equivalent of the reef, and according to him the whole layer might be younger than reef and other facies of the Ford Formation.

Post EZ1 Ca sediments

The Trow Point Bed is in turn overlain by the Cycle 1 evaporite (The Hartlepool Anhydrite of Durham Province and Hayton Anhydrite of the Yorkshire Province). The evaporite is thicker towards the basins and is succeeded by the Cycle 2 carbonates (the Concretionary Limestone and the Roker Dolomite of Durham Province and Edlington Formation of Yorkshire Province). However, none of these formations yields any brachiopods and thus the author will not described them in this thesis. These carbonates are in turn succeeded by the cycle 2 evaporite, cycle 3 carbonates and so on.

British Permian Productidina

The hypersaline nature and the very short life of the Pemian marine basin did not allow the British Permian productidinids to expand. The fauna is unique and has very little equivalent outside the Zeschstein. All British Permian productidinids occur in the English Zechstein carbonate Cycle 1, with the base of the reef developing the most rich and diverse fauna. The list of British Permian productidinids studied in this thesis, is separated in two tables, 2.2 for the Raisby Formation and 2.3 for the Ford Formation.

Table 2.1. Permian productidinids listed in Geological Survey Memoirs.

Sheet number Species list	15	21	27	32	100	101	113
Craspedalosia lamellosa			?F(r)			C	
*Dasyalosia goldfussi *1*						C	
*Horridonia horrida *2*	R	R,F(r)	R,F(l,r,b)	M,R	C	C	C
*Howseia latirostrata *3*			?R	R			
*Orthothrix excavata *1*	?R	F(l,r)	F(r,b)				
*Orthothrix lewisiana *1*			F(r,b)				
*Strophalosia morrisiana *4*	R	R,F(l)	R, F(l,r,b)	R		C	C

Memoir sheet 15, Land (1974)
Memoir sheet 21, Smith (D. B.) (in publication)
Memoir sheet 27, Smith (D. B.) & Francis (1967)
Memoir sheet 32, Mills & Hull (1976)
Memoir sheet 100, Eden, Stevenson & Edwards (1957)
Memoir sheet 101, Smith (E. G.), Rhys & Goosens (1973)
Memoir sheet 113, Edwards (1967)

M - Marl Slate
R - Raisby Formation
C - Cadeby Formation
F(l,r,b) - Ford Formation (lagoonal, reef, basinal facies)

*1 === *Dasyalosia goldfussi, Orthothrix excavata* and *O. lewisiana* are described under the genus *Strophalosia* in this thesis.

*2 === The genus *Horridonia* is represented by four species in the studied British Permian (see lists in table 2.2 and 2.3).

*3 === In this thesis two species of *Howseia* are accepted (see table 2.3).

*4 === *Strophalosia morrisiana* is now referred to the genus *Heteralosia* in which the author has introduced 4 new species from the Permian of Britain, as well as upgrading King's (1850) variety *humbletonensis* into a species (see table 2.2 and 2.3).

Table 2.2. Productidina from the Raisby Formation (author's collection)

Localities List of species	1	2	3	4	5	6	7	8	9
Craspedalosia lamellosa			r	r					
Craspedalosia langtonensis	c								
Heteralosia aycliffensis		?	c	r		r			
Heteralosia? quarringtonensis				r			c	c	?
Horridonia hoppeiana	r		r	?			?		
Horridonia horrida	c	r	c	c	c	r	c	r	c
Horridonia sp. A	r		r						
Strophalosia goldfussi			r	r			r		

c = common r = rare

Localities in Raisby Formation;

1 — Langton (or Hobgate) Quarry, Langton Village (NZ 165189)
2 — High Bank Quarry, Heighington (NZ 24002265)
3 — White (or Old Town) Quarry, School Aycliffe (NZ 257245)
4 — East Thickley Quarry, Shildon (NZ 24082564)
5 — Eldon Hill Quarry, Eldon (NZ 24202715)
6 — Raisby Hill Quarry, Coxhoe (NZ 346353)
7 — Old Quarrington Quarry, Coxhoe (NZ 326381)
8 — Sherburn Hill Quarry, Sherburn Hill (NZ 345417)
9 — Dawson Plantation Quarry, Penshaw (NZ 335544)

Table 2.3. Productidina from the Ford Formation

List of species Localities	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Craspedalosia sp. A					r															
Eostrophalosia permiana									?	r	r	r	?	c			c			
Heteralosia humbletonensis					r			c												
Heteralosia hyltonensis					c															
Heteralosia morrisiana									c											
Heteralosia seahamensis										r		r		c			c			
Horridonia dunelmensis					r			c	r	c	r	?					r			
Horridonia hoppeiana			r		r			?	?	r	r									
Horridonia sp. A										r										
Howseia latirostrata		c			r				c					r			r			
Howseia umbonillata		c			r				r					r			?			
Spinohorridonia geinitziana					r			r		r										
Spinohorridonia sp. cf. *S. laspeana*								r		r										
Strophalosia excavata	c	r	c	c	c	c	c	c	r	c	r	r	c	c	r	r	c	c	c	r
Strophalosia goldfussi								r		r										
Strophalosia lewisiana	c	?	c	r	c	?	?	c	r	c	r	?	c	c			c	c	c	r
Strophalosia? parva								r												

r = rare c = common

Ford Formation facies and related localities;

Back-reef or lagoonal facies (patch reef subfacies) — 10)-Gilleylaw Plantation Quarry, Silkworth; 11)-Gilleylaw builder's trench (temporary exposure), Silkworth; 12)-High Newport old railway cut

Reef facies — 13)-Downhill Quarry, West Boldon; 14)-Hylton Castle; 15)-Claxheugh old railway cut; 16)-Ford Quarry (east); 17)-Humbleton Hill; 18)-Tunstall Hill (rock cottage); 19)-Tunstall Hill (old trench); 20)-Ryhope old railway cut; 21)-Tunstall Hill sewage tunnel (temporary exposure); 22)-Ryhope Mental Hospital; 23)-Dalton-le-Dale; 24)-Stony bank cut, Seaham; 25)-Hawthorn Quarry, Hawthorn; 26)-Beacon Hill railway cut, Easington; 27)-Town Field Quarry, Easington; 28)-Garden of Eden Bridge, Castle Eden Dene.

Basinal or transitional facies — 29)-Dene Holme, Blackhall.

CHAPTER 3

SYSTEMATICS

Suborder PRODUCTIDINA Waagen

Superfamily STROPHALOSIACEA Schuchert

Diagnosis. Productidina with an interarea on both dorsal and ventral valves. Hinge operated by teeth and sockets.

Discussion. In 1844, when W. King described the first Strophalosiacean genus *Strophalosia*, he gave broad diagnostic features which allow it to include almost all the described strophalosiaceans (for further detail see discussion on *Strophalosia*, later in this chapter). *Strophalosia* was well known in the nineteenth century and the increasing numbers of new interarea bearing productidinid genera needed to be grouped together into one subfamily. Schuchert (1913) introduced subfamily **Strophalosiinae** to describe the **Productidae** (family) which is anchored to foreign objects by their spines or by cementation of the pedicle valve. Genera included in this subfamily were *Chonopectus, Strophalosia, Aulosteges* and *Etheridgina.* This subfamily was upgraded to family **Strophalosiidae** by Stehli (1954), but no further subdivision of this new family was given.

Superfamily **Strophalosiacea** was introduced by Muir-Wood & Cooper (1960) to include Strophalosiidae and seven other families, most of which were new. One of the new families introduced, the **Aulostegidae** was later upgraded to a separate superfamily **Aulostegacea** by Cooper & Grant (1975a) in which they include five other families previously belonging to Strophalosiacea.

Detailed diagnostic features of the superfamily Strophalosiacea given by Muir-Wood and Cooper (1960), also covers those forms now known as aulostegaceans. Unfortunately, Cooper & Grant (1975a) did not give a new or amended diagnosis of the superfamily Strophalosiacea when they extracted some of the former strophalosiaceans to form their new superfamily Aulostegacea. The above diagnosis is therefore important for future reference.

Note: Family **Productellidae** Schuchert & le Vene was considered in the past to be a primitive productacean by having low dorsal and ventral interareas, vestigial teeth and sockets and reduced cardinal process shaft. Having all these features, the Productellidae seem to have much more in common with the Strophalosiacea than with the Productacea. The degenerate interarea, teeth and sockets and cardinal process shaft seem to mark the transition between Strophalosiacea and Productacea. Some other productidinids which have interareas on both ventral and dorsal valves, like *Kansuella* which was classified as a gigantoproductid by Muir-Wood & Cooper (1960) should also be included into the family Productellidae.

Family STROPHALOSIIDAE Schuchert 1913

Amended diagnosis. Strophalosiacea with one pair of strong hinge teeth and sockets and a stalked cardinal process.

Discussion. For a long time, the Strophalosiidae has been accepted as a sole family of Strophalosiacea and several criteria have been used for dividing strophalosiids into their subfamilies. The presence or absence of body spines on dorsal valves, which was suggested by Muir-Wood & Cooper (1960), seems to play an important role in the subfamily division of the strophalosiids. However, at the same time they also introduced the Ctenalosiinae Muir-Wood & Cooper as another subfamily on the basis of its hinge criteria. *Ctenalosia* Cooper and Stehli, the sole genus of ctenalosiinids has a spineless dorsal valve and in fact looks very similar to some of the Heteralosiinae Muir-Wood & Cooper, but this genus has a series of teeth and sockets along the hinge line, a character which has never been seen in any other strophalosiaceans. All other strophalosiaceans have only one pair of teeth on either side of the delthyrium and a pair of sockets at the base of the cardinal process. The unique nature of hinge teeth seem to have a greater meaning in terms of the evolution of the strophalosiaceans than the body spines. The presence of the hinge teeth link the strophalosiaceans with their possible chonetoid ancestor although the ctenalosiinids appear in the Permian, much younger than the first strophalosiaceans. At present state of knowledge ctenalosiinids are only recorded from the North American Permian while strophalosiids *Devonalosia* and *Leptalosia* have flourished from the Middle Devonian times. For these reasons, subfamily Ctenalosiinae should be upgraded to a separate family Ctenalosiidae (see note I at the end of this discussion), and the diagnosis for the remaining Strophalosiidae amended as the above.

With the exclusion of Ctenalosiinae, the Strophalosiidae can now be divided into its subfamilies solely based on the presence or absence of body spines on dorsal and ventral valves. Here, it would be best to exclude the hinge or marginal spines from discussion at this level of classification for it is almost essential for all strophalosiaceans to posess these spines. Two subfamilies, the Strophalosiinae Schuchert (1913) and Heteralosiinae Muir-Wood & Cooper (1960) have been introduced for strophalosiids with body spines on both valves and on the ventral valve only, respectively. To complete the sub-division of family Strophalosiidae, another subfamily should be introduced for those forms that have no body spines on either of the valves. *Lialosia* Muir-Wood & Cooper from the Australian Permian lacks spines except the hinge or marginal spines. The subfamily Lialosiinae is hereby suggested to fill this gap in strophalosiid classification for forms with no body spines on either dorsal or ventral valves (see note II at the end of this discusion).

When Dr. C. H. C. Brunton discovered that Muir-Wood & Cooper's (1960) type-species of *Strophalosia* W. King i.e. *S. gerardi* W. King has a spineless dorsal valve he amended the diagnosis of the genus *Strophalosia* and the subfamily Strophalosiinae (Brunton, 1966). He believed that the subfamily Heteralosiinae should be included into his newly defined subfamily Strophalosiinae and for this reason he suppressed the name Heteralosiinae for being a junior synonym of Strophalosiinae. Brunton (1966) included all those strophalosiids without spines on the dorsal valve in subfamily Strophalosiinae, while in place of what was formerly known as Strophalosiinae he introduced a new name Dasyalosiinae for strophalosiids with spines on both valves.

In my opinion, when the type-species of any genus appears to be misidentified, the case should be referred to the International Commission on Zoological Nomenclature (see the rule set by ICZN (1961) - Article 70 (b)) to designate another species as a new type-species, rather than changing the diagnosis of the genus. It should be noted that Brunton was not the first to notice that *S. gerardi* bears no spines on its dorsal valve. Further details regarding this problem will be discused under the heading of genus *Strophalosia*.

In contrast to Muir-Wood & Cooper's (1960) subfamily classification, Waterhouse (1967, 1969 and 1982a) and Waterhouse & Shah (1966) have stressed that spine distribution patterns are unreliable beyond generic classification. Waterhouse & Shah (1966) have shown that *Costalosia argentea* Waterhouse & Shah possesses spines on its dorsal valve whereas the type and all other *Costalosia* Waterhouse & Shah are spineless on their dorsal valves. On this evidence they considered that the spinosity of the dorsal valve as only a variable feature of the genus. Waterhouse (1969) further shows that the spinosity of the dorsal valve is of no generic value when he described a *Craspedalosia pulchella* (Dunbar) with spines on dorsal valve whereas Dunbar's early description of this species clearly shows that this species has a spineless dorsal valve. Waterhouse (1969) also mentioned the resemblence between *Craspedalosia* Muir-Wood & Cooper and *Dasyalosia* Muir-Wood & Cooper apart from the difference in the spinosity of their dorsal valves. However, he did not consider the possibility that his *C. pulchella* with spinose dorsal valve might belong to a different genus in another subfamily.

Having seen a large number of Zechstein species assigned to *Craspedalosia* and *Dasyalosia* by Muir-Wood & Cooper, I have to agree with Waterhouse's opinion, that apart from the difference in dorsal valve spinosity, both have a very similar internal and external morphologies. However, I cannot refute the genetic importance of body spines in the subfamily division given by Muir-Wood & Cooper (1960) and Brunton (1966). In particular, it is important to note that strophalosiacean spines are hollow throughout most of their life and a prolongation of the mantle is thought to continue to the tip of the spine and performs a sensory function (Rudwick, 1970). As they involve both external morphology and internal organs, the presence and distribution of spines is clearly genetically important and should be highly regarded in taxonomic classification of strophalosiaceans. Similarities in external and internal morphology between Muir-Wood & Cooper's *Craspedalosia* and *Dasyalosia* should thus be regarded as morphological convergence between two separate subfamilies as is commonly shown in many other productinid brachiopods.

Note I. Family : CTENALOSIIDAE new family

Diagnosis. Strophalosiacea with articulation provided by more than one pair of teeth and sockets along the hinge.

Discussion. To simplify later descriptive work it is more convenient to leave the distribution of spines to be discussed at subfamily level, similar to the systematic classification of other strophalosiaceans.

Note II: Subfamily : LIALOSIINAE new subfamily

Diagnosis. Strophalosiidae with marginal spines only on ventral valve. Body spines absent on both dorsal and ventral valves.

Discusion. At present state of knowledge lialosiinids are restricted to the Permian of Australia.

Subfamily STROPHALOSIINAE Schuchert 1913

Synonymy;
1938 Productellinae Schuchert & le Vene; Sutton, p. 548
1954 Strophalosiinae Schuchert: Maxwell, p 538
1960 Strophalosiinae Schuchert: Muir-Wood & Cooper, p 72
1966 Dasyalosiinae Brunton, p 190

Diagnosis. Strophalosiidae with body spines on both dorsal and ventral valves.

Type-genus. *Strophalosia* W. King, 1844, p. 313.

Other genera. *Echinalosia* Waterhouse, *Eostrophalosia* Stainbrook and *Crossalosia* Muir-Wood & Cooper.

Genus *STROPHALOSIA* W. King 1844

Synonymy;
1844 *Strophalosia* W. King, p. 313
1846 *Strophalosia* W. King; W. King, p. 92-94
1847 *Orthothrix* Geinitz, p. 84-86
1848 *Orthothrix* Geinitz; Geinitz, p. 14-15
1850 *Strophalosia* W. King; W. King, p. 93-96
1853 *Strophalosia* W. King; Davidson, p. 115-6
1858 *Strophalosia* W. King; Geinitz, p. 208
1861 *Strophalosia* W. King; Geinitz, p. 93
1913 *Strophalosia* W. King; Schuchert *in* Zittel, p. 391
1932 *Strophalosia* W. King; Dunbar & Condra, p. 190
1938 *Strophalosia* W. King; Sutton, p. 549
1943 *Strophalosia* W. King; Prendergast, p. 37-41
1943 *Strophalosia* W. King; Stainbrook, p. 57-58
1947 *Strophalosia* W. King; Stainbrook, p. 38
1954 *Strophalosia* W. King; Maxwell, p. 538-42
1955 *Strophalosia* W. King; Dunbar, p. 80-81
1960 *?Strophalosia* W. King; Muir-Wood & Cooper, p. 72-75
1960 *Orthothrix* Geinitz; Muir-Wood & Cooper, p. 79-80
1960 *Dasyalosia* Muir-Wood & Cooper, p. 76-77
1965 *?Strophalosia* W. King; Muir-Wood, p. 450
1965 *Orthothrix* Geinitz; Muir-Wood, p. 450-1
1965 *Dasyalosia* Muir-Wood & Cooper; Muir-Wood, p. 450
1966 *Dasyalosia* Muir-Wood & Cooper; Brunton, p. 192-3
1967 *Orthothrix* Geinitz; Smith & Francis, p. 181

Amended diagnosis. Strophalosiinid with heavy spines on both dorsal and ventral valves arranged in two series on ventral valve in younger stages, specialized in adults. Dorsal valve variously shaped, moderately convex with umbo either flattened and pointed or incurved. Cicatrix of attachment commonly absent, the shell is attached by means of its clasping and cementing spines. Dorsal valve moderate to weakly concave and smaller than the ventral valve. Dorsal interarea is lower than ventral interarea and they face each other at various attitudes depending on the shape of the umbo. Pseudodeltidium and chilidium are well developed. Teeth stout. Cardinal process with trilobed or bilobed myophore set on small shaft. Adductor muscle platforms smooth or striated and weakly elevated. Brachial loops large. Shell surface covered with growth striae or lamellae.

Type-species. *Productus lewisianus* de Koninck 1847a

Other species. *Spondylus goldfussi* Munster, *Orthis excavata* Geinitz, *Dasyalosia panicula* Brunton, *D. lamnula* Brunton, *Strophalosia butlerensis* Stainbrook, *S. multispinifera* Prendegast and *S. inexpectans* Cooper & Grant.

Branson (1948) listed about 60 specific and subspecific names once associated with the genus *Strophalosia*. Some of these names have been assigned to other genera while the identity of others is not certain. It should be noted that many of these uncertain species were described on an inadequate basis due to lack of multiple specimens.

Discusion and revision. Various names given in the synonymy show that this genus has been the subject of long misunderstanding by various authors, and revision is needed to clarify controversial elements regarding status and diagnosis of the genus as well as its much debated type-species. In this context, it is important to quote some of the points made by various authors to strengthen their particular argument.

The genus *Strophalosia* was first proposed by W. King in 1844 for **a *Productus*-like shell with an area and possessing a condyloid hinge as in terebratulas and not a simple one as in true productuses.** Unfortunately, that is all we know about *Strophalosia* until 1846 when W. King added further diagnostic features for the genus and for the first time listed several species under the name *Strophalosia*.

In 1846, W. King described *Strophalosia* as **both valves possess an area, that of the ventral being merely a hinge-plate thickened; the area of the dorsal valve is furnished with circatrized deltidium, at the base of which are situated two condyles which fit into sockets excavated in the hinge plate of the opposite valve, one on each side of the cardinal muscular fulcrum; the umbone of the large valve is generally flattened or irregularly indented and the entire face of ventral valve is often furnished with spines.**

If we follow W. King's statements closely, it is clear that he was actually addressing his **ventral valve** which bears thickened hinge plate as an area, cardinal muscular fulcrum (or cardinal process) and sockets to the brachial valve or what is currently accepted as the **dorsal valve**. Similarly, the **dorsal valve** of W. King which carries deltidium and condyles (or teeth) corresponds to the **pedicle or ventral valve.** This point should be stressed because W. King mentioned that **entire face of ventral (which should be called dorsal) valve is often furnished with spines.** The spinosity of this valve distinguishes it from the closely allied genus *Heteralosia* R. H. King which has no spines on dorsal valve. The word **often** should be cancelled in W. King's 1846 diagnosis after 1938 when R. H. King introduced the genus *Heteralosia* and the word **entire face** should carry meaning that spines are numerous on this particular valve.

It is most regrettable that in his 1846 publication W. King only described one of his strophalosiid species i.e. *S. gerardi* W. King, a species in which he said that **the spines on ventral (now dorsal) valve are not known.** R. H. King (1938) later discovered that this species has a spineless dorsal valve and included it into his newly described genus *Heteralosia.*

Other species listed by W. King (1846) as *Strophalosia* include; *S. spinifera* n. sp., *S. morrisiana* n. sp., *S. subaculeata* (Murchison), *S. productoides* (Murchison) and *S. ?spinulosa.* W. King did not choose any type-species for genus *Strophalosia* in his 1846 publication. So it is up to later authors to choose any of W. King's validly listed species as the type-species of this genus. However, all species listed by W. King (1846) under the name *Strophalosia* are invalid to be chosen as type-species for the following reasons.

1) *S. spinifera* and *S. morrisiana* were not described in the 1846 paper and had not been previously described, thus these species cannot be considered as valid nominal species;

2) *S. subaculeata* and *S. productoides* were later proved to be species of *Productella* Hall by Hall & Clarke (1893) and *Hamlingella* Reed by Reed (1943);

3) *S. gerardi* was proved to be a *Heteralosia* by R. H. King (1938);

4) The identity of *S. spinulosa* is not known, but it is beleived that W. King might have referred it to the present *Krotovia spinulosa* (Sowerby).

Meanwhile, in 1847 de Koninck described *Productus lewisianus* from English and German Zechstein for forms similar to Geinitz's *Orthis excavatus*, but with a curved umbo (see de Koninck, 1847a, 1847b). In 1847, Geinitz described a new genus *Orthothrix* which is characteristically very similar to W. King's genus *Strophalosia* and in 1848 he described and figured several species which fall into his genus *Orthothrix*. Among these species are *O. excavatus* (Geinitz) (including both forms with flattened umbo and the curved one), *O. lamellosus* n. sp., *O. goldfussi* (Munster) and *O. horrescens* (de Verneuil). However, in his following papers, Geinitz (1857, 1861) accepted the priority of W. King's genus *Strophalosia* above his own genus *Orthothrix* and re-described all his species as *Strophalosia*.

In his 1848 catalogue, Howse described for the first time two of W. King's invalidly assigned species of *Strophalosia* into *P. spiniferus* (W. King) and *P. morrisianus* (W. King). These two species appeared to be very similar descriptively with W. King's description of his *S. morrisiana (= P. spiniferus* Howse) and *S. spinifera (= P. morrisianus* Howse) which was published two days after Howse's work, except that the species name was applied in opposite to each other. Although Howse was probably unaware that W. King's name was still invalid at the time of his own publication, his names should still have priority above W. King's names. It is regrettable that Muir-Wood & Cooper asked for permission from the ICZN to suppress Howse's name *P. spiniferus* in favour of W. King's *S. morrisiana* and their request was granted by ICZN 1962, opinion 625.

Since de Koninck (1847a,b), Geinitz (1848) and Howse (1848) did not acknowledge *Strophalosia* in their publications, the discussion will be focussed more on W. King's work. In his 1848 catalogue, W. King only described two species of *Strophalosia* (*S. spinifera* and *S. morrisiana*) and mentioned the occurrence of *S. goldfussi* (Munster) in England. Out of this list of *Strophalosia*, *S. morrisiana (= P. spiniferus* Howse) should now be included into R. H. King's genus *Heteralosia* for it does not bear any spines on the dorsal valve. W. King (1850) and Davidson (1858) mentioned that there are a few examples of this species (or variety as it is described by Davidson) which bear spines on dorsal valve. From my current study, it appears that these specimens which bear spines on their dorsal valves, come from a separate population than that of *H. morrisiana*, and a new species *Eostrophalosia permiana* is established here for them (see further discussions under the heading of this species later in this chapter). The other described species, *S. spinifera (= P. morrisianus* Howse) seems to be a junior synonym of *P. lewisianus* de Koninck. Regarding *S. goldfussi* (Munster), it was not until 1850 that it was realised that W. King actually mis-used this name for the species which actually belongs to *S. excavata* (Geinitz). It is important to note that no one in England recognised the true *S. goldfussi* before Trechmann (1921).

Even though his description of *S. spinifera* does not contradict the description of the genus, W. King did not make any attempt to choose any type-species for his genus *Strophalosia* until 1850 when he subsequently chose this species as the type-species of *Strophalosia.*

In W. King (1850), *S. excavata* (Geinitz) was chosen as the type-species of *Strophalosia* with full list of synonymy including his own *S. spinifera* and de Koninck's *P. lewisianus.* W. King was obviously confused with the names given by Munster (1839), Geinitz (1842, 1848) and de Koninck (1847a,b) when he described *S. excavata* (Geinitz) for forms which actually belong to *S. lewisiana* (de Koninck), while *S. goldfussi* (Munster) was described for the true *S. excavata* (Geinitz). W. King's mistake was probably triggered by Geinitz's(1848) paper in which he included de Koninck's *P. lewisianus* together with his own form of *O. excavatus* into a single species without acknowledging de Koninck's work. Apart from W. King (1848, 1850), Howse (1848) and de Koninck (1847a,b) the form *S. lewisiana* has not been accepted as a separate species by various authors (Geinitz (1848, 1861), Davidson (1853), Maxwell (1954)). However, based on Dr. A. Logan's unpublished thesis (Logan, 1962), this species was re-introduced by Smith & Francis (1967) under *Orthothrix lewisiana* (de Koninck) and has since then commonly been used locally by various authors. Current study on these forms strongly supports the validity of this species as is discussed in the following pages.

Later authors were divided in their usage of the type-species of *Strophalosia.* Some tried to avoid this confusion by not mentioning the type-species at all. Davidson (1853), Hall & Clarke (1892), Scuchert & Le Vene (1929), Dunbar & Condra

(1932), R. H. King (1938), Sutton (1938), Prendergast (1943) and Dunbar (1955) chose *S. excavata* as the type-species of *Strophalosia.* Davidson's *S. excavata*, however is ascribed to that of W. King and not to the original Geinitz's species. It is not known to which forms that other authors referred their *S. excavata.* Other authors like Quendstedt (1871, 1885), Gaudry (1883), Koken (1896), Zittel (1913) and Maxwell (1954) chose *S. goldfussi* (Munster) while Muir-Wood & Cooper (1960, 1965) and Brunton (1966) used *S. gerardi* W. King as the type-species of *Strophalosia.*

In 1960, Muir-Wood & Cooper split the previously known genus *Strophalosia* into several genera, some of them are new and many of them consist of one or two species only. They also discussed the uncertainty of species previously assigned to *Strophalosia* and concluded that only *S. gerardi* should definitely belong to this genus, hence it was elected as the type-species. All other species previously assigned to this genus were transfered to either new or re-established genera, while the status of *S. morrisiana* was undecided.

If we follow Muir-Wood & Cooper's classification, we end up with a very well-known genus (i.e. *Strophalosia*) without any species in it. *S. gerardi* (W. King) was proved by R. H. King (1938) to belong to genus *Heteralosia* while with similar reasoning W. King's *S. morrisiana* should also be included in this genus.

The emendation of Brunton (1966) of the generic diagnosis mentioned earlier, does not seem to be the best solution to the problem created by Muir-Wood & Cooper. Brunton (1966), however, clearly stated that the younger stage of *S. gerardi* (W. King) is not very different from the juveniles of *Heteralosia.* This fact shows how close they are ontogenically, and as often shown in many other genera, the shape of the adult differs from one species to another and quite commonly it is influenced by the mode of life and other ecological factors.

From current study, I have also collected evidence that the development of spines in younger stages of *S. lewisiana* and *S. goldfussi* (previously known as *Orthothrix lewisiana* and *Dasyalosia goldfussi*) are very similar to each other. The hairy and vermiform spines in the adults of *S. lewisiana* and *S. goldfussi* are therefore acquired separately during ontogeny. There is little doubt that the mode of life and ecological factors play an important role in the specific development of spines in these two species of *Strophalosia.* For comparison, see plate 2, figure 8 which shows two sets of spines at the umbonal region in *S. goldfussi* and compare it with similar spine arrangement in *S. lewisiana* in plate 1, figure 10 to 12.

New type-species. Since *Strophalosia gerardi* W. King is no longer a valid species of the genus *Strophalosia* W. King (for reasons discussed earlier), it is also become invalid as the type-species of the genus. Therefore, it is important to find a more genuine and suitable species to replace this invalid type-species. The most sensible way to do this is go back through the history of the genus.

The first name that was elected as the type-species of *Strophalosia* is *S. excavata* (Geinitz; W. King, 1850). However, it is very clear that W. King misidentified this name (i.e. *S. excavata*) for the form which actually belongs to *S. lewisiana* (de Koninck). Since they are both genuine species of *Strophalosia*, we have to choose the correct name for the species described by W. King (1850) rather than the wrong name given by him for type-species of the genus. Thus *S. lewisiana* (de Koninck) should be chosen as the type-species.

Another reason for this assignment is that W. King (1848)'s *S. spinifera (=P. lewisianus* de Koninck) is the first species that was correctly described by any author as belonging to *Strophalosia* W. King. All names assigned to *Strophalosia* prior to this have been proven invalid for various reasons given before. The identity of *S. goldfussi* (Munster) mentioned in W. King (1848) is uncertain. As W. King (1850) misidentified his *S. goldfussi* with Geinitz's original *O. excavatus* (Geinitz, 1842), it is therefore inappropriate to choose this name to be the type-species of the genus as did many authors. Although *Spondylus goldfussi* Munster is the first described species of *Strophalosia*, it is not until 1857 that it is correctly assigned to this genus. Based on the work of W. King (1850), choosing *S. goldfussi* as the type-species of *Strophalosia* would create a very similar problem as to choose W. King's *S. excavata* for they both were mistakenly identified by him. Again, in my opinion the best way to solve this problem is to accept W. King's proposal of type-species by its description only. I suggest that the name which fits W. King's description, *Productus lewisianus* de Koninck should be elected as the type-species of the genus *Strophalosia* W. King.

Since Muir-Wood & Cooper (1960) and Brunton (1966) have changed the generic diagnosis of *Strophalosia* for the wrong reasons, the amended diagnosis for the genus given above is necessary to clarify the true morphology.

To summarize this lengthy discussion I would like to propose the following;

1. The diagnosis of genus *Strophalosia* W. King should be referred as far as possible to the original proposed by W. King in 1844 and supplemented by him in 1846;

2. In King's 1846 diagnosis, the sentence **entire face of ventral valve is often furnished with spines** should be interpreted as **dorsal valve surface is heavily spinose**;

3. All strophalosiid species without spines on dorsal valve should be regarded as heteralosiinid;

4. From the original description, the type-species of *Strophalosia* suggested by W. King in 1850 should be accepted as *S.lewisiana* (de Koninck), not *S. excavata* (Geinitz);

5. *Productus lewisianus* de Koninck should be elected as the new type-species of the genus *Strophalosia* W. King.

6. The names *Orthothrix* Geinitz and *Dasyalosia* Muir-wood & Cooper should be regarded as junior synonyms of *Strophalosia* W. King and therefore should be suppressed.

7. Subfamily Strophalosiinae and Heteralosiinae should stand as they were redefined and introduced by Muir-Wood & Cooper (1960) but their diagnoses should be revised as stated in this thesis.

STROPHALOSIA LEWISIANA (de Koninck)

(Text-figures 3.1 and 3.3A, Plate 1, figures 1-12, Plate 2, figure 1)

Synonymy:
1847a *Productus lewisianus* de Koninck, p. 262-4, pl. 15, fig. 5a-e
1847b *Productus lewisianus* de Koninck; de Koninck, p. 150-2, pl. 15, fig. 5a-e
1848 *Orthothrix excavatus* (Geinitz); Geinitz, pl. 5, fig. 35, 37-38
1848 *Productus morrisianus* Howse, p. 257
1848 *Strophalosia spinifera* W. King, p. 9
1850 *Strophalosia excavata* (not-Geinitz); W. King, p. 98-99, pl. 12, fig. 13-22
1853 *Strophalosia excavata* (not-Geinitz); Davidson, pl. 8, fig. 203-5
1858 *Strophalosia goldfussi* (not-Munster) var. *lewisiana* (de Koninck); Davidson, p. 43-4, pl. 3, fig. 19-22
1857 *Strophalosia excavata* (Geinitz); Geinitz, p. 209
1857 *Strophalosia goldfussi* (not-Munster); Howse, p. 47-8
1858 *Strophalosia goldfussi* (not-Munster); Howse, p. 251-3
1861 *Strophalosia excavata* (Geinitz); Geinitz, p. 93-4, pl. 17, fig. 5, 7-12, 14-15
1937 *Strophalosia excavata* (Geinitz); Malzahn, p. 53-4, pl. 2, fig. 19-20
1967 *Orthothrix lewisiana* (de Koninck); Smith & Francis, p. 181
1988 *Strophalosia* sp. Hollingworth & Pettigrew, p. 19, fig. 5

Diagnosis. Small to medium size *Strophalosia* with almost circular outline. Ventral valve moderate to strongly convex with poorly developed sulcus and incurved umbo covering most of the ventral interarea. Ventral interarea high with elongate triangular pseudodeltidium. Teeth stout. Ventral adductor muscle platform narrow and low. Ventral surface covered with growth striae or lamellae and closely packed hair-like spines arranged in two series posteriorly and one series anteriorly. Dorsal valve moderately concave with poorly developed fold and very low interarea. Cardinal process with short and posteriorly inclined shaft and trilobed or bilobed myophores. Dorsal adductor muscle platform lobed or spoon-shaped with smooth or striated scar. Brachial loop wide and median septum low, extending to the middle of the dorsal valve.

Type specimen. Specimen described and figured by de Koninck in 1847a should be elected as the holotype of the species.

Type locality. The material described by de Koninck (1847a) came from M. A. Lewis collection from Humbleton Hill, and this locality should be named as the type locality for the species. The actual point of origin of this species is not known, but it is very likely to be the same as that of W. King and Kirkby. As suggested by Pattison (1977) for W. King's collection, Humbleton Hill (GR. around NZ 381553) is tentatively suggested here as the type locality of *S. lewisiana* (de Koninck).

Other localities. This species has been reported from various localities in the Ford Formation of County Durham and around Sunderland including Tunstall Hill (?Rock Cottage) and Dalton-le-Dale (Howse, 1848; W. King, 1848) ?Garmondsway (Howse, 1848) ?Hylton North Farm, ?Tynemouth and Whitley (W. King, 1848) Ford Quarry (Pattison Smith & Warrington,1970) and Dene Holme and ?Garden of Eden Bridge (Smith & Francis, 1970)

Among localities in which this species is first recorded include Downhill Quarry (GR. NZ 348642), Hylton Castle road cut (GR. NZ 360589), Claxheugh abandoned railway cut (GR. NZ 363574), Tunstall Hill's old trench (GR. NZ 397542), Ryhope abandoned railway cut (GR. NZ 397538), Gilleylaw Plantation Quarry (GR. NZ 376536), High Newport abandoned railway cut (GR. NZ 387538), Ryhope Mental Hospital (GR. NZ 40055215) and Beacon Hill railway cut (GR. NZ 442454).

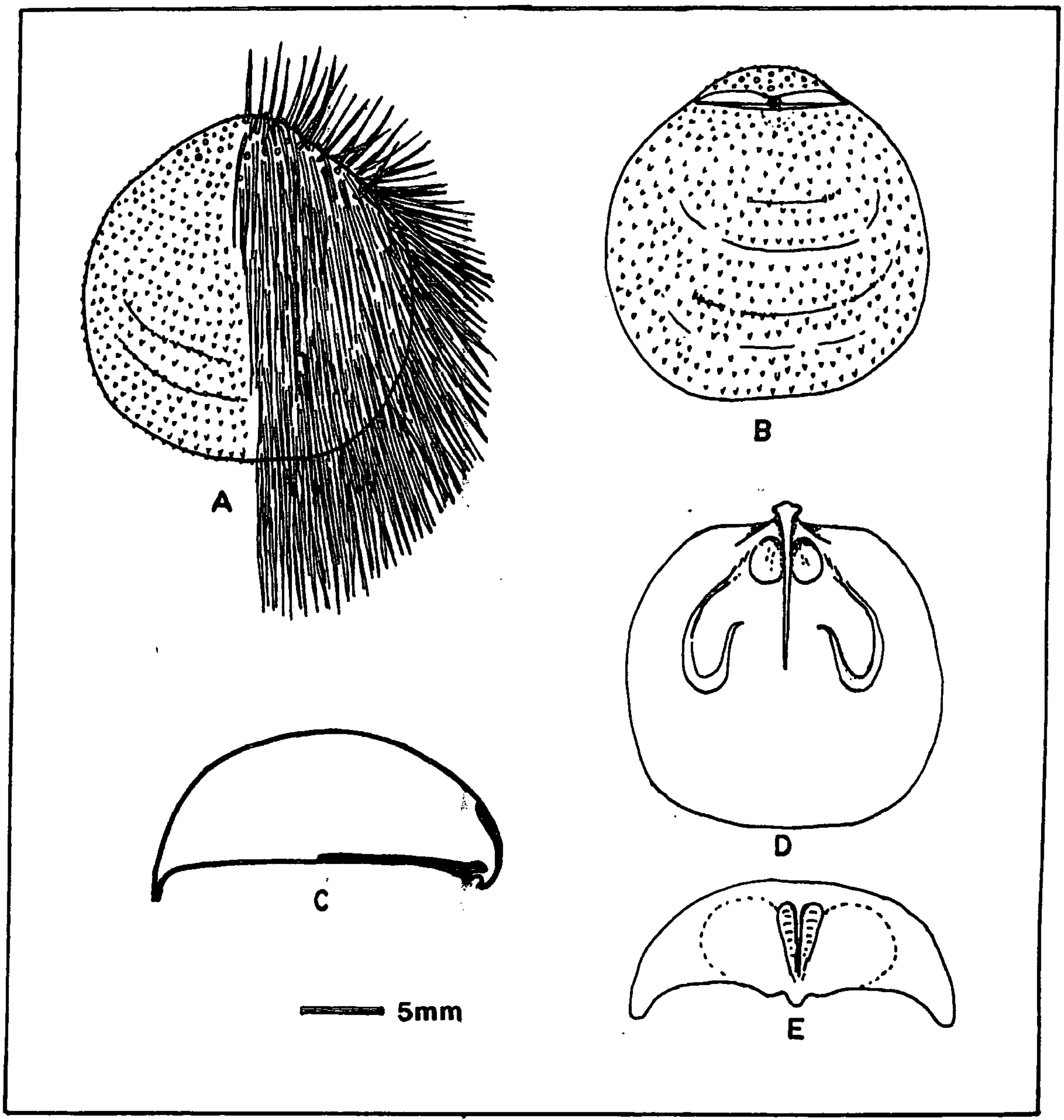
This species is also known from the Zechstein Dolomite of Posneck, Konitz, Liebenstein and Hirschberg in Germany.

Material. Most of the specimens studied are preserved in the form of moulds and casts. The original shell material has been found in some of the specimens from Rock Cottage, Tunstall Hill.

Horizon. Ford Formation (England).

Age. Upper Permian (EZ1).

Description. The shell is small to medium in size with the largest individual attaining a length of about 20 mm. The average size differs from one locality to another. The shell is generally sub-circular in outline, but it may vary from sub-elliptical to sub-triangular. Occasionally, the shape becomes slightly asymmetrical due to uneven



Text-figure 3.1. Reconstruction of ***Strophalosia lewisiana*** **(de Koninck)**
A - Exterior of ventral valve. B - Exterior of dorsal valve. C - Lateral profile. D - Interior of dorsal valve. E - Interior of dorsal valve (posterior view).

Table 3.1. *Strophalosia lewisiana* **(de Koninck) - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	thickness	height VIA
MSLHH1	e22.0	e32.0	e20.8	e12.5	10.0	6.5	e1.5
MSLHH2	9.6	14.2	11.0	e7.5	5.1	na	na
MSLHH3	e13.5	e17.0	e11.4	e7.8	e6.2	4.5	0.9
MSLHC1	21.7	29.4	21.5	e11.9	9.8	e6.5	e1.4
MSLHN1	6.4	7.4	6.8	e4.8	2.6	na	na
MSLHN2	14.9	21.1	15.5	na	7.3	na	na
MSLot1	8.6	na	e9.9	e 6.4	na	na	0.8
MSLot2a	11.3	16.9	13.4	e7.2	5.9	na	na
MSLot2b	12.1	16.6	13.2	e8.3	e5.4	e3.0	na
MSLot3	21.9	na	24.7	11.7	na	na	e1.7

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na = not available

growth of the umbo and the anterior margin. The shell width is maximum at the mid-length or immediately anterior to it.

The ventral valve is moderate to strongly convex. The wing is not developed although the lateral posterior margin is slightly concave in profile. The rest of the valve is smoothly and positively curved in all directions. From longitudinal section, the ventral valve attained maximum convexity posteriorly and its convexity weakens as the shell grows anteriorward. In most cases, the sulcus is very poorly developed and hardly perceptible to naked eye. When preserved, the sulcus is very shallow and originated at about the mid-length anteriorward. The beak is less gibbous and wide in sub-circular forms and more gibbous and narrower in elongated forms. There is no cicatrix scar on the beak. The umbo is half-incurved dorsally and covers the posterior half of the interarea. The ventral interarea is high but being hidden by the umbo, the actual height is impossible to measure. The delthyrium is covered by a narrow and low triangular pseudodeltidium.

Internally, the ventral valve is provided with a pair of stout teeth, divergent at an angle of about 50°. The adductor muscle platform is narrow and low and divided into two halves by a shallow median furrow. The attachment scar is smooth. The adductor muscle platform is surrounded by a pair of very low fan-shaped diductor muscle platforms, the surface of which is covered by distant radial striae.

The surface of the ventral valve is covered by thin concentric striae which sometimes turn to coarser growth lamellae and occasional rugae. The anterior margin of the larger adult is sometimes folded into several (less than 10) broad ridges and grooves. The ventral valve is covered with sub-erect and erect, posteriorly directed spines. The sub-erect spines are distributed throughout the whole valve while the the erect and posteriorly directed spines are arranged concentrically at the posterior region only. The spines are very fine and hairy in nature, extending to about 10 to 15mm in length. In most cases only the spine tubercles are preserved. These spine tubercles have a diameter of about 0.5mm. They are very closely spaced with more than 100 tubercles being counted in one square cm in the middle of the valve in some cases. In a smooth growing shell the tubercles are normally roughly arranged in staggered rows, while in most cases the tubercles are controlled by the development of growth lamellae or rugae. The number of spines in the rugate forms is normally less than those which have smoother striate shell-growth.

The dorsal valve has a sub-circular outline, truncated at the hinge line which has a length of about two thirds of the maximum width or slightly shorter. The shell is moderately concave with maximum depression immediately posterior to its mid-length. Anteriorly the valve follows the curvature of the ventral valve without any geniculation. The median fold is only weakly developed, best seen at the anterior margin and extended to about one third of the valve length posteriorward. The umbo is small, raised and pointed. The interarea is very low.

The interior of the dorsal valve is furnished with a shafted cardinal process with trilobed or bilobed myophores and very narrow muscle attachment base. The cardinal process shaft is small and usually stands at a low angle to the imaginary shell plane posteriorly. The diductor muscle scar runs along this shaft and converges toward its base. At the base of the shaft there are a pair of fairly deep sockets. These sockets are confined by a slightly raised posterior margin and a pair of strong socket ridges which seem to buttress the cardinal process shaft. The posterior margin develops a weakly raised ridge laterally. The socket ridges are short, narrow, straight or hook-shaped and separated by furrows from the raised oval-shaped concentrically striated or smooth adductor muscle platform. Medianly, the cardinal process shaft is buttressed by a strong median ridge which extends anteriorly as a low median septum to the mid-length of the valve or shorter. The brachial loop is wide with its outer ridge parallel to the lateral shell margin and its anterior ridge extending beyond the mid-length of the valve. It is not known excactly where the brachial ridges meet medially, but the posterior extensions of these ridges seem to fade into the furrows in between the muscle boundary ridges and the muscle platforms.

The dorsal surface is ornamented the same way as that of the ventral, except that it does not possess erect and posteriorly directed spines.

Ontogeny and variation. The ontogenic history of *S. lewisiana* cannot be described with certainty owing to the lack of a good collection of juvenile growth stages. From the available material, it can be seen that only limited variation occurs during growth to the adult. Apart from the development of ribs at the anterior margin of larger adults, the only noteworthy variation occurs in the development of the beaks of the adult. However, there is no particular trend in this variation. It is more likely, therefore, that this variation represents self-adjustment to the slightly different niches in which the individuals lived. The degree of incurving of the umbo changes from one individual to another and depends on the convexity and the general shape of the beak.

Regarding the development of spines, it is assummed that *S. lewisiana* clasped other objects only during the juvenile stages. The erect and posteriorly directed clasping spines are only developed posteriorly and as the shell grows larger the production of further clasping and cementing spines ceases. This suggests that the species adopted a free living mode during adulthood. The multiple occurrences of this species together with *S. excavata* at some localities suggests that both these species lived together in the form of a nest one on top of another. The nest is usually associated with reef building algae and occasionally with bryozoan colonies with which they might live together symbiotically. The dense body spines that were developed on both valves of this species might also have functioned as anchors that interlocked themselves into algal and bryozoan mats or into the spines of neighbouring individuals of the same species or of *S. excavata.* At the same time, these dense spines would protect the species from the attack of predators.

An interesting phenomenon is observed in the development of *S. lewisiana* through time. General decrease in size of individuals of this species is observed from the bottom to the top of the Durham Permian reef. In the upper reef flat fauna, the size of the largest individuals is commonly less than half of those found at the base of the reef. The dwarfing of the species toward the reef top is usually associated with faunal intolerence of the steadily increasing salinity of the Permian sea.

Discussion. When de Koninck first described this species in 1847, he only based his description on a single ventral valve. However, this description is sufficient to recognise the species from other strophalosias and productuses. De Koninck mentioned that without its dorsal valve it is difficult to distinguish the species from *P. granulosus* Phillips, *P. murchisonianus (= P. productoides* Murchison) and *P. geinitzianus* de Koninck. Since only *P. geinitzianus* has the same age range as *S. lewisiana*, it is unlikely that it belongs to either of the other two species. As for *P. geinitzianus* de Koninck, although there is a possibility that de Koninck's ventral valve of *P. lewisianus* might belong to a small specimen of his *P. geinitzianus*, all the rest of the collection from the type locality with similar ventral valves have the interarea on both valves and thus are true strophalosiaceans. De Koninck's *P. geinitzianus* on the other hand is a true productacean (see de Koninck (1847a, b), Geinitz (1861), W. King (1856) and also this thesis under the name *Spinohorridonia geinitziana* (de Koninck)). A few remains of *Sp. geinitziana* recently found at Humbleton Hill are much larger in size when compared to *S. lewisiana*, and also have a distinguishable productacean shape.

S. excavata (Geinitz) is the closest species to *S. lewisiana* and it is not suprising that many previous authors have described them both as a single species. The differences between the two species is only limited to the general shape of the shell and umbo while the shell ornament and most of the internal features are almost identical between the two species.

The first description of *S. lewisiana* by de Koninck (1847a) clearly stated that the shape of the shell is rounded sub-semiglobulose and the umbo is regularly curved upon itself, not prominent and pointed to its end. These features sufficiently distinguish *S. lewisiana* from *S. excavata* which has a sub-triangular shape and rather flattened and pointed umbo. With the dorsal valve and internal details now available for comparison, the differences between *S. lewisiana* and *S. excavata* can be further established. *S. lewisiana* has most of its ventral interarea hidden by the umbo and its cardinal process shaft strongly inclined posteriorward, while the ventral interarea of *S. excavata* is high and open and its cardinal process shaft is raised and more vertical than that of *S. lewisiana* (see text-figure 3.3A and 3.3B).

The Visean *S. panicula* (Brunton) and *S. lamnula* (Brunton) resemble *S. lewisiana* in having sub-rounded shape and very similar dorsal valve ornamentation, but the ventral valve of these Visean species retain their juvenile spines throughout their whole life. Thus, *S. panicula* and *S. lamnula* have two series of spines on the ventral valves in the adult stages. *S. panicula* and *S. lamnula* also differ from *S. lewisiana* in having an open interarea and a bilobed cardinal process myophore.

The Texas Permian *S. inexpectans* Cooper & Grant differs from *S. lewisiana* in having a transversely sub-oval shape, a geniculated dorsal valve, an open interarea, a bilobed myophore and a much longer median septum.

S. goldfussi (Munster) differs from *S. lewisiana* in having an open ventral interarea, a higher dorsal interarea and most important of all, specialization of the adult spines. The vermiform clasping and cementing spines on the ventral valve and concentric spines on the dorsal valve has led Muir-Wood & Cooper (1960) to isolate this species further from other *Strophalosia.* Muir-Wood & Cooper created a genus *Dasyalosia* to accommodate this species. However, detailed studies on the arrangement of spines at the umbonal region and the distribution of spines on both valves shows that *S. goldfussi* is ontogenically very close to all other species of *Strophalosia*. The specialization of the spines in *S. goldfussi* is an adaptational feature linked to its special way of life. It should be noted that *Craspedalosia lamellosa* (Geinitz) which is usually found together with *S. goldfussi*, also has very similar spines on the ventral valve. Although it is uncommon to find *S. goldfussi* preserved without spines, when all its spines are stripped off the shell ornament is identical with other species of *Strophalosia*.

STROPHALOSIA EXCAVATA (GEINITZ)

(Text-figures 3.2 and 3.3A, Plate 1, figures 13-19, Plate 2, figures 2-6)

Synonymy;
1842 *Orthis excavatus* Geinitz, p. 578-9, pl. 10, fig. 12 - 13
1848 *Orthothrix excavatus* (Geinitz); Geinitz, p. 14-15, pl. 5, fig. 36, 39-40 not 35, 37-38, pl. 6, fig. 23 not 20-21
1848 *?Productus asperimus* Howse, p. 257-8
1850 *Strophalosia goldfussi* (not-Munster); W. King, p. 96-98, pl. 12, fig 1-12
1853 *Strophalosia goldfussi* (not-Munster); Davidson, pl. 8, fig. 206, 209
1856 *?Strophalosia excavata* (Geinitz) var. *whitleyensis* W. King, p. 268
1857 *Strophalosia goldfussi* (not-Munster); Howse, p. 47-48
1858 *Strophalosia goldfussi* (not-Munster); Howse, p. 251-253
1858 *Strophalosia goldfussi* (not-Munster); Davidson, p. 39-43, pl. 3, fig. 1-18
1858 *Strophalosia goldfussi* (not-Munster) var *whitleyensis* W. King: Davidson, pl. 3, fig. 23
1861 *Strophalosia excavata* (Geinitz); Geinitz, p. 93, pl. 1-4, 13, 16-19 not 5-12 and 14-15
1937 *Strophalosia excavata* (Geinitz); Malzahn, p. 53-54, pl. 2, fig. 18
1960 *Orthothrix excavata* (Geinitz); Muir-Wood & Cooper, p. 79-80, pl. 7, fig. 7-16
1965 *Orthothrix excavata* (Geinitz); Muir-Wood p. 450-1, fig. 304,2a-d

Diagnosis. Small to medium size *Strophalosia* with variable sub-triangular shape. Ventral valve moderately convex with broad shallow sulcus and pointed umbo. Ventral interarea high with narrow triangular pseudodeltidium. Ventral surface with fine concentric striae or coarser growth lamellae and closely spaced hairy spines with two series posteriorly and one series anteriorly. Dorsal valve moderately concave with broad fold posteriorly. Dorsal interarea low. Dorsal surface concentrically striated or lamellose with one series of fine closely spaced sub-erect spines. Cardinal process with nearly vertical shaft and trilobed myophores. Teeth stout.

Type specimen. The specimen described by Geinitz in 1842 as *Orthis excavatus* should be elected as the type of the species.

Type locality. The Zechstein-Dolomite at Altenburg near Posneck in Germany has been mentioned as the locality of the material first described and figured by Geinitz (1842) as *Orthis excavata.* Therefore this locality should be selected as the type locality of the species.

British localities. In Britain, this species commonly occurs together with *S. lewisiana* although the relative abundance is different from one locality to another. In general, when they occur together *S. excavata* is found to be more abundant than *S. lewisiana.* However, difficulty in distinguishing some of the moulds of the species might lead to error in determining the rate of occurrence. There are also a few localities in which only *S. excavata* is found and these include Stony Bank Cut (GR. NZ 41854740), Hawthorn Quarry (GR. NZ 438463), Townfield Quarry (GR. NZ 431438) and Gilleylaw Builders Trench (GR. NZ 379539). Smith & Francis (1970) also recorded *S. excavata* without *S. lewisiana* from New Hesledon, Fox Cover Quarry, Easington Colliery, Craggy Bank, Chourdon Point and various boreholes from County Durham and West Hartlepool. Most of these localities are stratigraphically positioned rather higher in the Permian reef than those localities in which both *S. lewisiana* and *S. excavata* occur together.

Horizon. Ford Formation.

Age. Upper Permian (EZ1).

Description. The shell is small to medium in size with the largest individual reaching a length of about 23 mm. The shell outline varies considerably from one individual to another but generally maintains its more or less triangular shape. The length to

Table 3.2. *Strophalosia excavata* **(Geinitz) - dimensions in mm.**

Specimen number	length	curved length	maximum width	hinge width	height	thickness	height VIA
MSLBH2	15.5	18.4	15.0	6.5	6.6	3.8	2.2
MSLBH3	20.6	26.3	16.4	7.3	e7.4	4.2	3.0
MSLBH4	14.4	e21.5	13.6	6.0	e5.6	e4.2	1.8
MSLBH6	13.4	14.2	12.6	6.6	e4.9	3.2	2.3
MSLBH7	e17.7	e22.9	e16.7	7.2	e6.8	4.6	e2.3
MSLBH8	e15.7	e18.0	e13.8	7.1	e4.9	3.2	e2.6
MSLBH9	16.8	na	e12.0	5.6	e5.0	e3.4	e2.8
MSLot4	10.7	na	10.0	4.5	na	na	e2.1
MSLot6	e18.3	e22.1	16.0	8.5	6.1	3.6	e2.5

dimensions = refer to appendix
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na = not available

width ratio of the shells shows a great variation from the strongly elongated form to those which have a nearly trigonal shape. The maximum width of the shell is usually positioned at the anterior quarter of the shell.

The ventral valve is moderate to weakly convex with its maximum convexity at about its mid-length. The longitudinal curvature of the valve weakens both posteriorly and anteriorly. The sulcus is broad and shallow, extended almost to the whole shell-length, but sometimes too weak to be distinguished. The beak is commonly narrow and swollen, but in the shorter form it is broad and flattened. The umbo is normally posteriorly pointed, but it may vary from slightly curved and postero-dorsally pointed to raised and postero-ventrally pointed. Sometimes the umbonal growth is stunted and laterally twisted. The ventral interarea is high, orthocline to anacline with narrow weakly raised triangular pseudodeltidium covering its delthyrium. The internal morphology and surface sculpture of the ventral valve are similar to that of *S. lewisiana*.

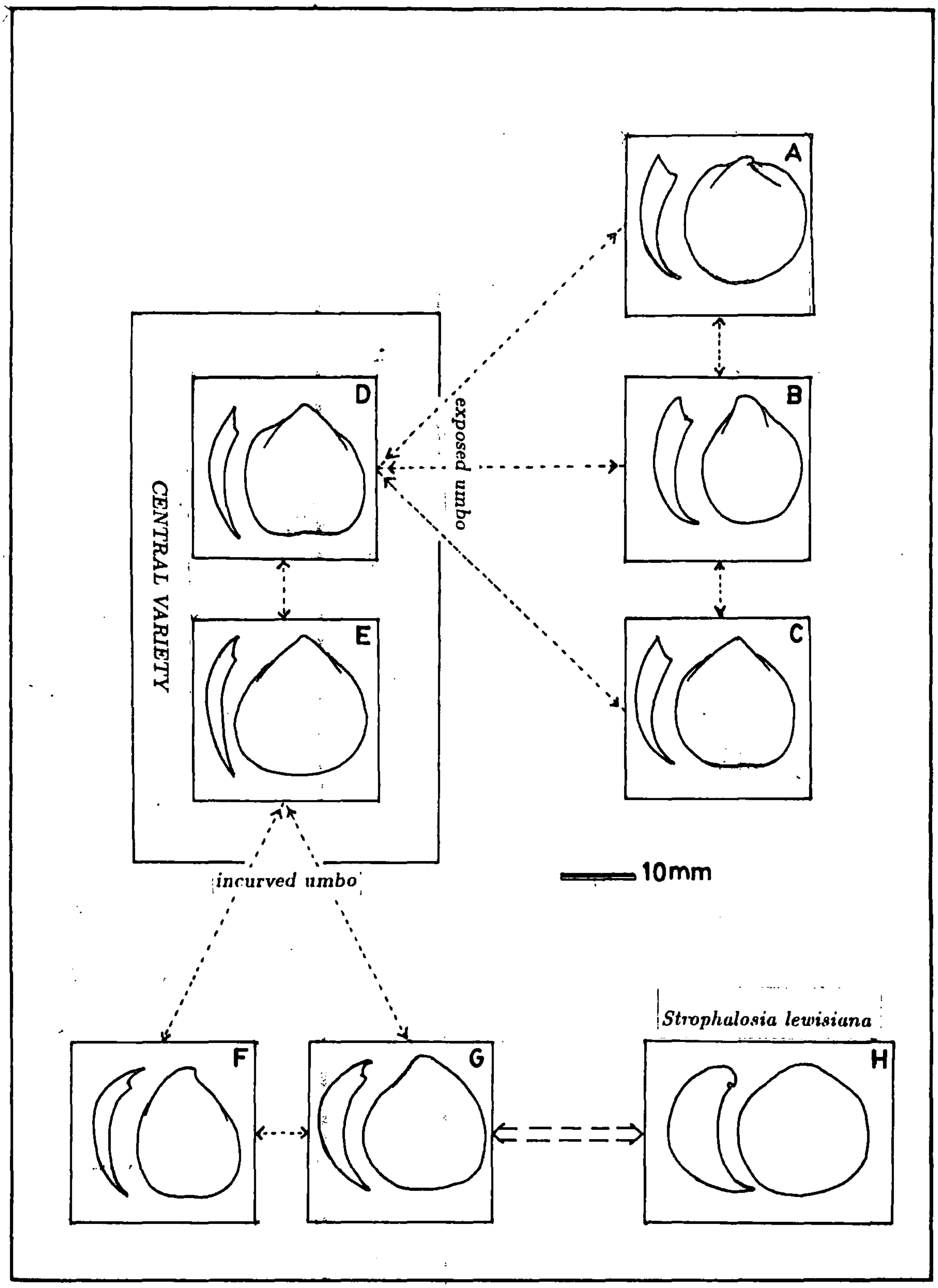
The dorsal valve is sub-trapezoidal in shape, moderate to weakly concave with its maximum depression just a little posterior to its mid-length. The median fold is low and broad, appears on the anterior half of the valve only. The umbo is small and weakly raised. The dorsal interarea is very low and only perceptible medially, facing the interarea of the ventral valve at various angles. Internally, the cardinal process shaft points to the posterior at an angle between 60^o to vertical to the shell plane. The rest of the internal features fall within variations of those found in *S. lewisiana.* The dorsal surface is similar to that of *S. lewisiana.*

Ontogeny and variation. For similar reason to those discussed on *S. lewisiana* the ontogenic history of this species cannot be precisely illustrated. Apart from the development of the umbo, the changes during the ontogeny of *S.excavata* are very similar to that of *S. lewisiana.*

The degree of variation on the umbonal development of *S. excavata* seems to be much greater than on *S. lewisiana* (see text-figure 3.2). Self-adjustment to very crowded niches might play an important role in the development of the highly diversified shape and attitude of the umbo of this species. This variation is less apparent in places where the species is a minority in the fauna.

Stunting of the species is also observed toward the top of the Permian reef where it became the last representative of the suborder Productidinae in this region.

Discussion. When Geinitz first described *S. excavata* in 1842, he clearly stated that **Die Rucken-Schale ist gleichmasig gewolbt nach dem kleinen erhabenen Wirbel zu.......or The ventral valve is symetrically arched toward that small raised umbo.......** This feature is well presented in his figure 12, but his figure 13 does shows a slightly curved umbo. He also mentioned that the shell has a pocket shape like *Orthis testudinaria.* Unfortunately, when Geinitz (1848) elaborated his earlier description, he mentioned that **Rucken-Schale halbkugelig quer-oval, mit einem kleinen niedergebogenen spitzen Wirbel.......or Ventral valve hemispherically transverse oval, with a small weakly curved pointed umbo........** In his figures he included some of the forms which have a rather sub-circular shape with strongly curved umbo, the form which has already been described by de Koninck (1847a,b) as *P. lewisianus* (see Geinitz (1848, pl. 5, fig. 35, 37-48 and pl. 6, fig. 20). Since then, the name *S. excavata* has been



Text-figure 3.2. Variation in *Strophalosia excavata* (Geinitz) from Beacon Hill railway cut

- - - - - - possible intervariety relationship. ====== possible relationship with *Strophalosia lewisiana* (de Koninck).

confused by various authors with forms that should be called *S. lewisiana*, while these same authors usually describe this species as *S. goldfussi* (see W. King (1850, 1856), Davidson (1853, 1858), Howse (1857, 1858) etc.). Some other authors chose to follow Geinitz (1848) in grouping these two species together as *S. excavata* (see Geinitz (1861), Malzahn (1937)).

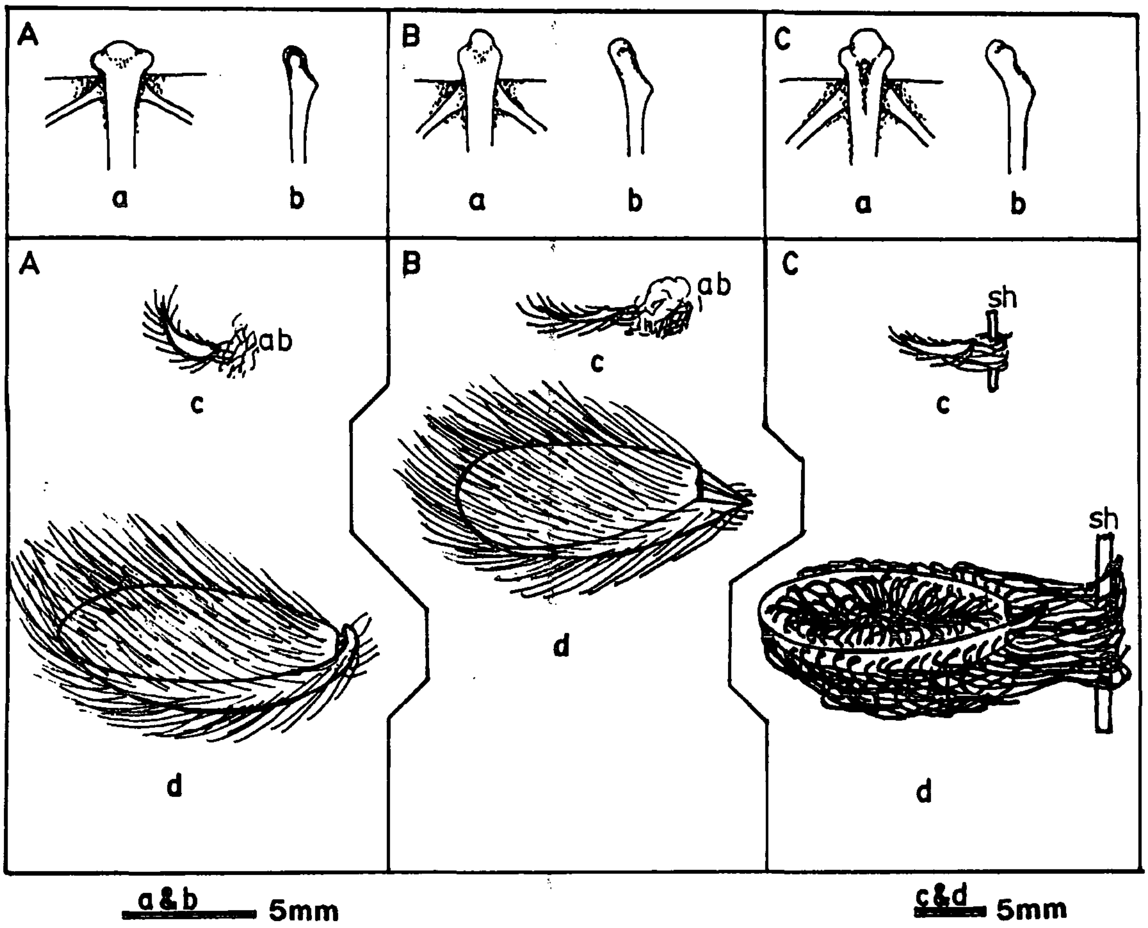
The most closely related species is *S. lewisiana* and a comparison between the two species has already been given. *S. panicula* and *S. lamnula* differ from *S. excavata* in having two series of spines on the ventral valve of the adult, a lower ventral interarea and a bilobed myophores. *S. goldfussi* differs from *S. excavata* in having vermiform and tangled spines in the adult. *S. inexpectans* differs from *S. excavata* in having a transversely sub-oval shape, a geniculated dorsal valve, a bilobed myophore and a very long median septum.

S. excavata reported from the Salt Range by Waagen (1884) and Reed (1944) seems to have fewer, but more stout and recumbent spines than the *S. excavata* described in this thesis. These very rare specimens described as *S. excavata* from the Central Asian Permian, might belong to a distant variation of other species in the area.

STROPHALOSIA GOLDFUSSI (Munster)

(Text-figure 3.3C, Plate 2, figures 7-13)

Synonymy;
1839 *Spondylus goldfussi* (Munster), p. 43, pl. 4, fig. 3a-b
1847a *Productus goldfussi* (Munster); de Koninck p. 257-9, pl. 11, fig. 4a-e and pl. 15, fig. 4a-b
1847b *Productus goldfussi* (Munster); de Koninck p. 148-151, pl. 11, fig. 4a-e and pl. 15, fig. 4a-b
1848 *Strophalosia goldfussi* (Munster); Geinitz, p. 14, pl. 5, fig 27-28
1861 *Strophalosia goldfussi* (Munster); Geinitz, p. 96-97, pl. 17, fig. 21-29
1871 *Productus goldfussi* (Munster); Quenstedt, p. 639, pl. 20, fig. 16-20,22
1921 *Strophalosia goldfussi* (Munster); Trechmann, p. 542, pl. 12
1901 *Strophalosia goldfussi* (Munster); Zittel, p. 391, fig. 581a-c



Text-figure 3.3. Comparison of cardinal process and mode of life between species of British Permian ***Strophalosia***

A - *Strophalosia lewisiana* (de Koninck). B - *Strophalosia excavata* (Geinitz). C - *Strophalosia goldfussi* (Munster). a,b - plan and side view of cardinal process. c,d - juvenile and adult mode of life. ab - algal mat or bryozoan colonies. sh - spine of *Horridonia*. *[Ad and Bd are not attached by spines]*

1937 *Strophalosia goldfussi* (Munster); Malzahn, p. 50-52, pl. 2, fig. 12-15
1960 *Dasyalosia goldfussi* (Munster); Muir-Wood & Cooper, p. 76-7, pl. 6, fig. 12-15
1965 *Dasyalosia goldfussi* (Munster); Muir-Wood, p. 450, fig. 304,4a-c
1985 *Dasyalosia goldfussi* (Munster); Cocks, p. 64, pl. 5.2.36A,B,C
1988 *Dasyalosia goldfussi* (Munster); Turek, Marek & Benes, p. 146-7, fig. 1-2

Diagnosis. Small to medium size *Strophalosia* with sub-triangular to sub-circular shell outline. Ventral valve moderately to strongly convex with poorly developed sulcus and small pointed umbo. Ventral interarea high with weakly raised pseudodeltidium. Ventral surface covered with fine concentric striae to coarse growth lamellae with two series of spines in younger stages, but in adult stages nearly all the spines are vermiform and posteriorly directed. Dorsal valve moderate to strongly concave. Dorsal surface with concentric striae or lamellae and vermiform spines centrally directed. Dorsal interarea low with small weakly raised chilidium and small triangular lophidium. Cardinal process large with trilobed myophores, shaft supported by strong lateral and median ridges. Adductor muscle platform highly elevated with radially grooved scars.

Type specimens. The original specimen described and figured by Munster in 1839 as *Spondylus goldfussi* should be elected as the type of the species.

Type Locality. Munster (1839) described and figured his *Spondylus goldfussi* from a specimen which came from Rospen near Gera. This locality should therefore be used as the type locality of the species.

Localities in Britain. *S. goldfussi* is a rare species in Great Britain and so far it has only been found at East Thickley Quarry (M. R. NZ 24082564), Old Town (=White) Quarry (M. R. NZ 257245), Old Quarrington Quarry (M. R. NZ 326381), Tunstall Hill old trench (M. R. NZ 397542) and Humbleton Hill (M. R. NZ 381553). The species was also obtained from the Mattersey Borehole in Nottinghamshire. Currently, there are about twenty specimens of this species known in Britain. The rarity of the species in this part of the world is the reason why it was poorly understood by British researchers in the last century. As mentioned earlier, the first true *S. goldfussi* in Britain was reported and figured in 1921 by Trechmann, long after most other British strophalosiids have been described.

Horizon. Raisby/Cadeby Formation and Ford Formation.

Age. Upper Permian (EZ1)

Material. The following description is not solely based on the local material. It is partly based on some well preserved specimens from Gera in Germany which were made available for detail study by the British Museum (Natural History), the Geological Survey Museum and the Hancock Museum. Local material in the author's collection include 3 specimens from East Thickley Quarry, 7 specimens from Old Town (=White) Quarry, 2 specimens from Old Quarrington Quarry and one specimen from Tunstall Hill old trench.

Table 3.3. ***Strophalosia goldfussi* (Munster) - dimensions in mm.**

Specimen number	length	curved length	maximum width	hinge width	height	thickness	height VIA
MSLot7	24.2	na	19.6	11.5	na	na	e5.5
MSLOQQ1	15.2	e18.9	e17.6	na	e7.2	na	na
MSLETQ1a	15.0	na	18.8	e8.8	na	na	e2.2
MSLETQ1b	16.9	na	18.0	8.9	na	na	e4.0
MSLETQ1c	18.0	na	19.6	na	na	na	na
MSLWQ1	14.8	na	15.3	7.8	na	na	2.1

dimensioms = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na =not available

Description. The shell is small to medium in size with the largest individuals sometimes reaching a length of 20 mm or more. The shell outline ranges from subtriangular to sub-circular. The maximum width is usually attained at the anterior half of the shell.

The ventral valve is moderately to strongly convex. The median sulcus is poorly developed and often imperceptible. The beak is weakly swollen with small flat cicatrix of attachment or without cicatrix. The umbo is small and usually pointed to the posterior, but sometimes the tip is slightly incurved or truncated. The ventral interarea is high and open with its surface transversely striated. The delthyrium is partly covered by a weakly swollen, narrow triangular pseudodeltidium. Internally, a strong pair of teeth are projected at a narrow angle to one another at the base of the pseudodeltidium.

The ventral surface is covered with fine concentric striae or with coarser lamellae. It is also covered with dense fine hollow vermiform spines. The straighter recumbent and adpressed spines can only be seen in the younger stages at the posterior region when the thick cover of the vermiform spines is stripped off. At this posterior region the spines are arranged in two series; the recumbent and anteriorly directed and the vermiform and posteriorly directed. In adult stages all spines are erect to sub-erect at their point of origin, but immediately turn posteriorward and become entangled with each other. These spines extend beyond the posterior shell margin before clasping or cementing themselves to other hard objects.

The dorsal valve has a sub-circular to sub-trapezoidal shape. It is moderate to strongly concave with obscure trace of a median fold anteriorly. The beak is small and moderately raised, so that the dorsal interarea is usually higher than that of any other *Strophalosia*. The dorsal interarea is about one-third to half the height of the ventral interarea. The width of the dorsal interarea is extended to the full length of the hinge line which is about two-thirds the maximum shell width or slightly shorter. The dorsal interarea has a transversely striated surface and furnished with a small weakly raised chilidium which is extended posteriorly as a small lophidium.

The dorsal surface is covered with fine concentric striae or coarser growth lamellae and a series of centrally directed vermiform spines, entangled with each others in the central depression of the shell.

The interior of the dorsal valve is provided with a large cardinal process which has a trilobed myophore. The cardinal process shaft inclines at a low angle towards the ventral, and is supported by a strong pair of posteriorly pointed lateral ridges which also act as the socket ridges. Medianly, the shaft is supported by a strong median ridge which narrows and continues anteriorly as a median septum. The adductor muscle platform is subtriangular in shape, highly elevated anteriorly with radially grooved scars.

Discussion. As discussed in Muir-Wood & Cooper (1960) the internal morphology of *S. goldfussi* seems to resemble very closely that of *S. lewisiana* and *S. excavata*, except that the exact form of the cardinal process is not well known in *S. goldfussi.* Brunton (1966) stressed that Muir-Wood & Cooper's description of the cardinal process was based on incomplete specimens. A single specimen from Tunstall Hill old trench collected during this research exhibits a well preserved internal morphology including the cardinal process which is very similar to that of *S. excavata* (see text-figures 3.3B and 3.3C).

Current study on some *S. goldfussi* from the German Zechstein in which the vermiform spines on the umbonal region are stripped off has shown that *S. goldfussi* has a very similar type and arrangement of spines to all other species of *Strophalosia* in the younger stages (see plate 2, figure 8). The vermiform nature of the spines seems to be a special character of the adult of this species. Furthermore, comparison with Brunton (1966) species from the Visean of County Fermanagh, shows that these Visean species actually show intermediate morphological features between *S. goldfussi* and *S. excavata* - *S. lewisiana.* For this reason I suggest that these three species be included in one genus and the best genus to fit them all is the genus *Strophalosia.* Other similarities and differences between the three species of *Strophalosia* from the British Permian have been described and discussed in earlier pages. In general *S. goldfussi* differs from all other species of *Strophalosia* in its unique vermiform spines which are slightly larger in diameter than in the other species.

Considering the small number of specimens of *S. goldfussi* available in the British Permian, one is inclined to speculate that these specimens might have been transported from a different part of the Permian sea. The specimens, however, show that they lived in the Durham Permian Sea at least during their adulthood. There are times in which a Zechstein storm might have transported larvae of this species westward from the east Zechstein. The British Zechstein Sea might not be the ideal environment for this species, but they certainly survived their adulthood here although they were probably not sufficiently numerous or fertile to further expand their generation. This is shown by the general dwarfing of the species in the British Permian as compared to average size of the adult of the species which lived in the East German Zechstein. Evidence shows that all the British *S. goldfussi* lived at more or less the same stratigraphic horizon in both East Thickley Quarry and Old Town (=White) Quarry. This indicates that they were probably carried westwards by the same storm current from the East Zechstein Sea.

Although the Old Quarrington Quarry *S. goldfussi* bearing bed is apparently lower than the other localities, evidence shows that this bed is not an *in situ* deposit. It is a slump deposit which was derived from a shallower sea to the west by downslope movement (Smith, 1970). Since the species is only known from a limited stratigraphic horizon in the British Zechstein, and the two localities with *S. goldfussi* bearing biocoenoces are situated to the west of the Old Quarrington Quarry, it is likely that this slump bed originated from the *S. goldfussi* bearing horizon in the west.

Rare occurrences of *S. goldfussi* in the Ford Formation is difficult to understand. More extensive study is needed in order to get a better understanding of this species, and to either prove or disprove various assumptions given above.

Genus *EOSTROPHALOSIA* Stainbrook 1943

Synonymy;
1943 *Eostrophalosia* Stainbrook, p. 58
1960 *Eostrophalosia* Stainbrook; Muir-Wood & Cooper, p. 77-79
1965 *Eostrophalosia* Stainbrook; Muir-Wood, p. 450

Amended diagnosis. Small to medium size productiform strophalosiinid with distant recumbent body spines on both valves and clasping marginal spines on ventral valve only. Ventral valve moderately to strongly convex with cicatrix of attachment small or absent. Interarea low with small pseudodeltidium and chilidium. Cardinal process with bilobed myophore on small shaft. Teeth moderately developed. Adductor muscle platform low. Brachial impression small. Shell surface smooth or lightly lamellose.

Discussion. Apart from the new species *E. permiana*, the genus *Eostrophalosia* has only been recorded from the Devonian of North America, and thus it holds the name "Eos" for being older than the true *Strophalosia*. It has been known as a rare genus and indeed all its species have also been considered as rare species by previous authors (Stainbrook, 1943; Muir-wood & Cooper, 1960). For this reason, the genus has not been fully described and currently only the external morphology is known with certainty. From the study of the external morphology of *E. permiana*, it seems that this species should best be described as *Eostrophalosia* rather than any other strophalosiinid. With a larger and better collection of specimens of this species, more details of the genus including the internal morphology can now be described.

A specimen of *E. permiana* has already been figured by Davidson (1858, pl. 3, fig. 38) as *S. lamellosa* (Geinitz) var. *humbletonensis* W. King, but since then the identity of this specimen has not been discussed by authors. In Logan's unpublished thesis (Univ. of Durham, 1962) the same specimen, as well as some other similar forms were figured and described as *S. morrisiana* W. King. Although the ornamentation on the ventral valve and the internal morphology of *E. permiana* and *S. morrisiana* (=*Heteralosia morrisiana* in this thesis) are very similar, the spinosity of the dorsal valve separates them into different genera and indeed a different subfamily. This is also supported by their distribution patterns in East Durham.

In terms of the external morphology *Eostrophalosia* can be best described as an intermediary between the slightly less productiform and larger strophalosiinid genus *Echinalosia* Waterhouse and the productellid genus *Orbinaria* Muir-Wood and Cooper. More detailed comparison is needed before any further conclusion on the true relationship between these three genera can be established.

Type-species : *Strophalosia rockfordensis* Hall & Clarke 1893

Other species : *Strophalosia callawayensis* Swallow, *S. littletonensis* Stainbrook, *S.*

independensis Stainbrook and *Eostrophalosia permiana* new species. All these species belong to the Devonian of North America except *E. permiana* which occurs in the British Permian.

EOSTROPHALOSIA PERMIANA new species

(Text-figure 3.4, Plate 3, figures 1-13)

The species is named after the Permian System, in which the genus was unexpectedly discovered.

Synonymy;
1858 *Strophalosia lamellosa* (not-Geinitz) var *humbletonensis* (not W. King); Davidson, pl. 3, fig. 38.

Diagnosis. Small to medium size *Eostrophalosia* with transversely sub-elliptical to sub-circular shell outline. Ventral valve moderate to strongly convex with inflated umbo and fully developed auricle. Sulcus absent. Cicatrix of attachment small or absent. Ventral interarea low with small pseudodeltidium. Ventral valve smooth or lightly lamellose with a row of clasping marginal spines, two to three discontinuous rows of auricular spines and scattered distant recumbent to adpressed body spines. Auricles lightly wrinkled. Dorsal valve moderately concave with small pointed umbo. Dorsal interarea low with small chilidium. Cardinal process with bilobed myophore set on small shaft. Dorsal adductor muscle platform low smooth or striated. Median septum short. Brachial impression small. Dorsal surface smooth or lightly lamellose with sparsely distributed adpressed body spines.

Type specimens. Specimens no.* MSLBH10, MSLBH11, MSLBH12, MSLBH13, MSLBH14 and MSLBH15 in the author's collection are chosen as a series of paratypes showing various important features of the species.

Type locality. Beacon Hill railway cut (GR. NZ 442454). This locality is chosen because from here most of the described specimens were collected, despite the fact that the first figured specimen (Davidson, 1858) came from Ryhope Field House.

Other localities. Material for this species has only been reported from Ryhope Field House (Davidson, 1858) and Fox Cover Quarry (Logan, 1962 unpublished thesis). Current study shows that there are a large number of specimens from Dalton-le-Dale in Kirkby's collection in Hancock Museum which were labelled as various species but belong to *E. permiana*. During the tenure of this research, the author also found this species from Tunstall Hill old trench (GR. NZ 397542) and Ryhope Mental Hospital (GR. NZ 40055215).

Material. The following description is mainly based on material collected personally by the present author which include 45 specimens from Beacon Hill, 3 specimens from Tunstall Hill old trench and 1 specimen each from Dalton-le-Dale and Ryhope Mental Hospital. Most of these specimens are preserved in form of moulds and casts, while a few show patches of original shell material.

Horizon. Ford Formation.

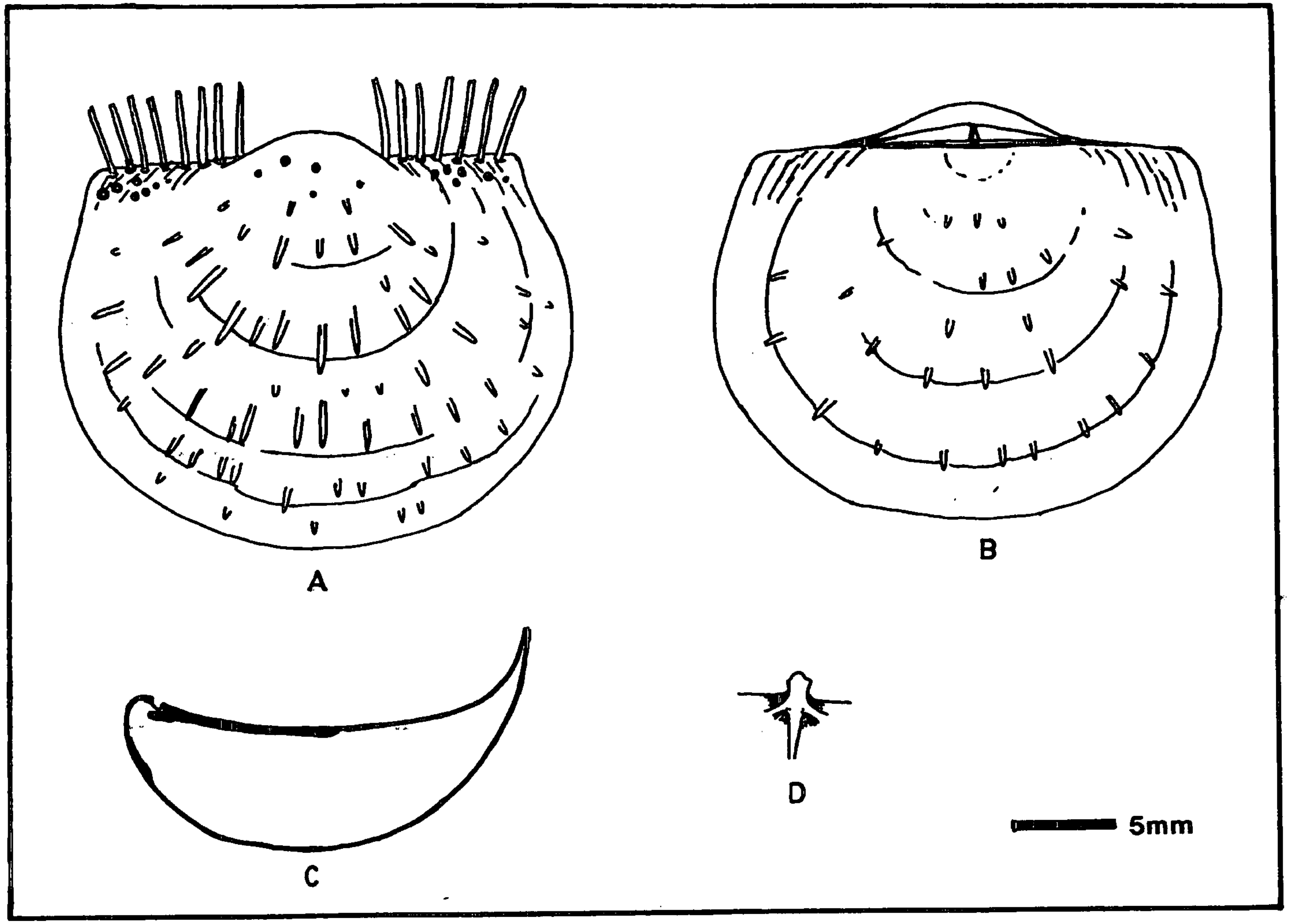
Age. Upper Permian (EZ1).

Table 3.4. *Eostrophalosia permiana* **new species - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	thickness	height VIA
MSLBH10	e24.5	e37.2	29.7	23.9	12.8	7.6	0.8
MSLBH11	19.6	e30.4	25.1	17.2	10.3	6.8	1.3
MSLBH12	16.5	24.0	22.8	e18.7	10.3	na	na
MSLBH13	10.2	11.9	11.5	e9.4	3.7	na	na
MSLBH14	23.8	34.6	27.4	na	12.8	na	na
MSLBH18	16.1	20.2	20.6	na	6.8	na	na
MSLot8	e20.0	na	e24.2	e17.6	na	na	e1.3

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na = not available

Description. The shell is small to medium in size with the largest individuals reaching



Text-figure 3.4. Reconstruction of *Eostrophalosia permiana* new species
A - ventral view (exterior). B - dorsal view (exterior). C - lateral profile. D - cardinal process.

a length of about 25 mm. The shell is usually transversely sub-elliptical to sub-circular in outline with the maximum width acquired at about the mid-length.

The ventral valve is moderate to strongly convex with maximum convexity shown posteriorly at the beak. The sulcus is usually absent, but sometimes a slight flattening in the median part of the shell is observed anteriorly. The auricles are not very prominent but they are fully developed. The beak is narrow and small, but it is strongly inflated. Vestiges of cicatrix of attachment can sometimes be traced on the umbo, but most commonly this scar is absent in this species. The umbo is slightly overhanging and incurved, but it does not cover the ventral interarea. The ventral interarea is low with smooth or transversely striated surface. The delthyrium is covered by a small weakly raised triangular pseudodeltidium.

The ventral valve interior is provided with a very narrow, short and low adductor muscle platform with smooth or lightly striated scar. This platform is divided in the middle by a shallow median furrow and laterally surrounded by a lower fan-shaped coarsely radially striated diductor muscle platform. Judged from the size of the socket on the dorsal valve, the teeth are quite small in size as compared to other strophalosiinids in this region.

The external of the ventral valve is smooth or lightly lamellose with occasional rugae. At the auricle the shell is lightly wrinkled. The shell is provided with the following spines; 1 - one row of clasping marginal spines which are erect, posteriorly and concentrically directed; 2 - two to three discontinuous radial rows of auricular spine bases in which the true nature of the spines is not fully known. The spine bases show that these spines are erect at their point of origin, but it is not known whether they provided additional clasping tools to the marginal spines or just posed as ornament; 3 - random and distantly distributed recumbent to adpressed body spines. In general, these body spines tend to be concentrated on the thicker growth lamellae or rugae. All spines are small with diameter around 0.7 mm and short and do not seem to be strong enough to support the large adult by their clasping mechanism.

The dorsal valve is moderately concave with maximum depression at about the centre of the valve. There are no traces of the median fold. The umbo is small, rounded and weakly elevated. The interarea is very low with a small chilidium.

The cardinal process shaft is small and posteriorly inclined, and the myophore is bilobed. The cardinal process is buttressed by a pair of low socket ridges and a low median ridge which continues anteriorly as a low and short median septum. The median septum extends to about one third of the valve length. The adductor muscle platform is roughly pear-shaped. It is weakly elevated with its scars either smooth or lightly concentrically striated. Brachial impressions are not completely preserved but are smaller compared to that of other strophalosiinids. The lateral and anterior margins only extended to about halfway to the lateral and anterior shell margins respectively. The rest of the internal features are not known.

The dorsal surface is smooth or lightly concentrically lamellose with very light wrinkles on the auricle. The shell is covered by very few (less than 30) distantly spaced adpressed spines. Sometimes, these spines are strongly adpressed and leave radial grooves on the shell surface to give the shell a rather costate appearence.

Discussion. The elongated form which is much more convex than the average form (see plate 3, figure 7), is normally found among the larger individuals, and therefore they might represent sexual dimorphs of the species. Apart from this, the complete ontogeny of this species is not well known because of the lack of younger individuals in current collection.

As compared to other *Eostrophalosia*, this species seems to resemble very closely to the type-species i.e. *E. rockfordensis* (Hall & Clarke) in its shape, surface sculpture and shape of the interarea. However, *E. rockfordensis* differs from *E. permiana* in its smaller size and more prominent cicatrix of attachment. Further comparison cannot be made because of the limited knowledge about the Devonian type-species. Other species of *Eostrophalosia* are also poorly described in past literature and thus no detailed comparison can be made. It is noteworthy that *E. permiana* is the largest and the youngest of all *Eostrophalosia* and it is also the most comprehensively collected species.

Subfamily HETERALOSIINAE Muir-Wood & Cooper 1960

Diagnosis. Strophalosiidae without spines on dorsal valve.

Type genus. *Heteralosia* R. H. King, 1838

Other genera. *?Devonalosia* Muir-Wood & Cooper, *Craspedalosia* Muir-Wood & Cooper, *Leptalosia* Dunbar & Condra, *Sphenalosia* Muir-Wood & Cooper, *Wyndhamia* Booker, *Costalosia* Waterhouse & Shah, *?Truncalosia* Imbrie and *?Oligorachis* Imbrie.

Discussion. The stability of the type genus i.e. *Heteralosia* R. H. King has contributed to the persistence of this subfamily since it was introduced in 1960 by Muir-Wood & Cooper. Only a few authors mentioned earlier in the discussion of the genus *Strophalosia* have argued about the validity of this subfamily. For reasons I have already given earlier, I have no doubt that this subfamily should stand as it is.

Note on the radial costae. One common phenomenon among the British Permian heteralosiinid is that the shell is almost always radially costate. The degree of the development of the costae is varied from one species to another, but generally the costae are developed stronger in the dorsal valve than in the ventral valve. The costae are regularly spaced with the width of each costa rarely exceeding 1mm. The costae are usually continuous from the umbo to the anterior margin, but bifurcation sometimes occurs anteriorly in the larger individuals. The ventral valve is usually weakly costate with the degree of costation sometimes usefull to divide some species from the others.

British Permian heteralosiinid. In previous papers, the subfamily Heteralosiinae is only represented by the genus *Craspedalosia* Muir-Wood & Cooper in the Zechstein Permian. More detailed study of W. King's *S. morrisiana* shows that it belongs to the genus *Heteralosia* R. H. King. Several other new species of *Heteralosia* have also been discovered during the present study on the British Permian productidinids.

Genus *HETERALOSIA* R. H. King 1938

Synonymy:
1938 *Heteralosia* R. H. King, p. 278.
1938 *Heteralosia* R. H. King; Prendergast, p. 41.
1952 *Heteralosia* R. H. King; Moore, Lalicker & Fischer, p. 252.
1960 *Heteralosia* R. H. King; Muir-wood & Cooper, p. 80-82.
1965 *Heteralosia* R. H. King; Muir-Wood, p. 451

Amended diagnosis. Small to medium size heteralosiinids with moderate to strongly convex ventral valve, recumbent to adpressed and erect body spines and umbonal cicatrix of attachment. Dorsal valve moderately concave to almost flat, sometimes geniculated. Interarea low on both valves with delthyrium partly covered by pseudodeltidium and lophidium and dorsal interarea with small chilidium. Cardinal process with bilobed or quadrilobed myophore. Teeth small. Adductor muscle platform moderately elevated. Brachial impressions medium to large in size.

Discussion. R. H. King (1938) described this genus as having interarea on both valves, spines on ventral valve only and umbonal cicatrix of attachment in order to distinguished it from *Strophalosia* W. King, *Aulosteges* Helmerson and *Leptalosia* Dunbar & Condra. With the above description he listed several species as *Heteralosia* including *H. sclocomi* n. sp. (as the type-species), *Strophalosia gerardi* W. King and *S. tenuispina* Waagen.

Later in 1960, Muir-Wood & Cooper revised the diagnostic features of this genus to distinguish it from many more new heteralosiinid genera introduced by them as well as various other authors (see the list of other genera above). Since not many of these genera are available in the present research collection, I cannot give any further comments on this subfamily division although some of the listed genera seem to lack a strongly convincing back ground.

The genus *Heteralosia* is known to have flourished from Mississippian time (Hinchey & Ray (1935)) and persisted through to the Upper Permian. Species of *Heteralosia* are usually zone restricted as well as spatially confined, except *H. tenuispina* (Waagen) which is known to have lived from Visean to Permian times. In general, it seems that the Carboniferous species have slightly more spines than those from the Permian. Variation in other features does not seems to be age related. In practice, the generic sub-division is based on the general size and shape of the shell, the size of cicatrix of attachment and the surface ornametation of the shell.

In Britain, the genus *Heteralosia* was only known previously from the Visean of County Fermanagh (Brunton, 1966). This is the first time that this genus is recognised in the Zechstein Permian, although one of its species, *H. morrisiana* (W. King) is famous in previous literature. This species is well described and illustrated by previous authors as a *Strophalosia*, probably because Davidson (1858) included in this species forms with spinose dorsal valves described here as *E. permiana* new species. The recognition of the genus *Heteralosia* has led the author to recognise four other species of the genus which might have been included by various authors in *S. morrisiana*. From the present study, *Heteralosia* is represented in Britain by *H. morrisiana* (W. King), *H. humbletonensis* (W. King), *H. hyltonensis* n. sp.. *H. seahamensis* n. sp. and *H. aycliffensis* n. sp. *Heteralosia? quarringtonensis* n. sp. is tentatively assigned to this genus although some of the features suggest that it might belong to one of the productellids.

Note. The above amended diagnosis is a simplified version of that given by Muir-Wood & Cooper (1960).

Type-species. *Heteralosia sclocomi* R. H. King, 1938, p. 278-9, pl. 39, fig. 15-18.

Other species. *Strophalosia gerardi* W. King, *S. morrisiana* W. King, *S. tenuispina* Waagen, *S. hystricula* Girty, *S. orbiculata* Hinchey & Ray, *S. subelliptica* Hinchey & Ray, *S. fortispinosa* Hinchey & Ray, *H. magnispina* Cooper & Grant, *H. paucispina* Cooper & Grant, *S. ?vidriensis* (=*H. subelliptica*) Cooper & Grant, *H. humbletonensis* (W. King), *H. hyltonensis* n. sp., *H. seahamensis* n. sp., *H. aycliffensis* n. sp. and *H?. quarringtonensis* n. sp.

HETERALOSIA MORRISIANA (W. King)

(Text-figure 3.5, Plate 3, figures 14-22).

Synonymy;

1846 *?Strophalosia morrisiana* W. King, p. 28.
1848 *Productus spiniferus* (W. King); Howse, p. 257.
1848 *Strophalosia morrisiana* W. King; W. King, p. 9.
1848 *Productus cancrini* (not-de Verneuil); Geinitz, p. 16, pl. 1, fig. 16-17.
1850 *Strophalosia morrisiana* W. King; W. King, p. 99-102, pl. 12, fig. 18-19.
1853 *Strophalosia morrisiana* W. King; Schauroth, p. 31, fig. 7.
1854 *Strophalosia morrisiana* W. King; Schauroth, p. 221.
1856 *Strophalosia morrisiana* W. King; W. King, p. 264-268.
1857 *Strophalosia cancrini* (not-de Verneuil); Howse, p. 49.
1858 *Strophalosia lamellosa* (not-Geinitz); Howse, p. 253-4.
1858 *Strophalosia lamellosa* (not-Geinitz) var. *morrisiana* (King); Davidson, p. 44-49, pl. 3, fig. 24-31, 33.
1861 *Strophalosia morrisiana* W. King; Geinitz, p. 98-100, pl. 18, fig. 8-22.
1871 *Productus morrisianus* (W. King); Quenstedt, p. 641, pl. 60, fig. 28.
1913 *Strophalosia morrisiana* W. King; Czarnocki & Samsonovich, p. 433, pl. 49, fig. 5.
1937 *Strophalosia morrisiana* W. King; Malzahn, p. 54, pl. 3, fig. 22.
1945 *Strophalosia morrisiana* W. King; Trechmann, p. 349, pl. 15, fig. 13.
1960 *Strophalosia morrisiana* W. King; Muir-wood & Cooper, p. 318.
1975 *?Heteralosia* sp. 4, Cooper & Grant, p. 802, pl. 193, fig. 9.

Diagnosis. Shell small to medium in size, sub-circular to transversely sub-elliptical in shape. Ventral valve moderately convex with small cicatrix of attachment on irregular and asymmetrical umbo. Ventral surface weakly lamellose and costate. Body spines rare, adpressed, or erect and posteriorly directed. Ventral interarea low with delthyrium partly covered by pseudodeltidium. Dorsal valve with radial costae and weak growth lamellae. Dorsal interarea low with small chilidium and lophidium. Teeth small. Cardinal process with bilobed myophore set on small shaft. Adductor muscle platform low. Brachial impressions wide. Median septum extended to half the length of the shell.

Type specimens. Pattison (1977) designated specimens no. D326A-C (three specimens) as syntypes of this species although he reports that the figured type of W. King is missing. All these specimens are kept in the Department of Geology, University of

Galway in Republic of Ireland. From my own examination of the specimens I have no doubt that none of them are illustrated in W. King's (1850) monograph. The specimen no. D326B is the most perfect syntype among the three and it shows very similar features to that of W. King's figure.

Type locality W. King (1850, 1856) stated that the type of his *Strophalosia morrisiana* should be chosen among the material from Tunstall Hill. According to Pattison (1977), W. King's Tunstall Hill locality is probably a fairly large area with quarries and natural exposures around NZ 392545. More new material was collected recently from this locality which is now known as the Rock Cottage (Hollingworth, 1986, 1987).

Other localities. *H. morrisiana* has also been reported from Humbleton Hill and Dalton-le-Dale (Howse (1848), Davidson (1858)), Ryhope Field House, Weston, Claxheugh and Midderidge (Davidson (1858). The species is also known from the German Zechstein (Geinitz (1848, 1861) Schauroth (1853, 1854), Quendstedt (1871) and Malzahn (1937)) and from ?Bone Spring Formation of West Texas (Cooper & Grant (1975)).

Material. This description is based on all the syntypes mentioned above and 48 specimens collected by the author from Tunstall Hill Rock Cottage. Most of these specimens are partly preserved with the original shell material and partly in form of moulds and casts. They are commonly preserved as complete shells and the internal details can be studied from original casts or artificial casts made from latex.

Horizon. Ford Formation.

Age : Upper Permian (EZ1).

Description. The shell is small to medium in size, sub-circular to transversely subelliptical in outline with posterior margin often irregularly developed. The lateral and anterior margins are usually smooth. The shell width is usually a little broader than its length, and widest at around mid-length. The shell profile is moderately concavo-convex with a narrow visceral cavity.

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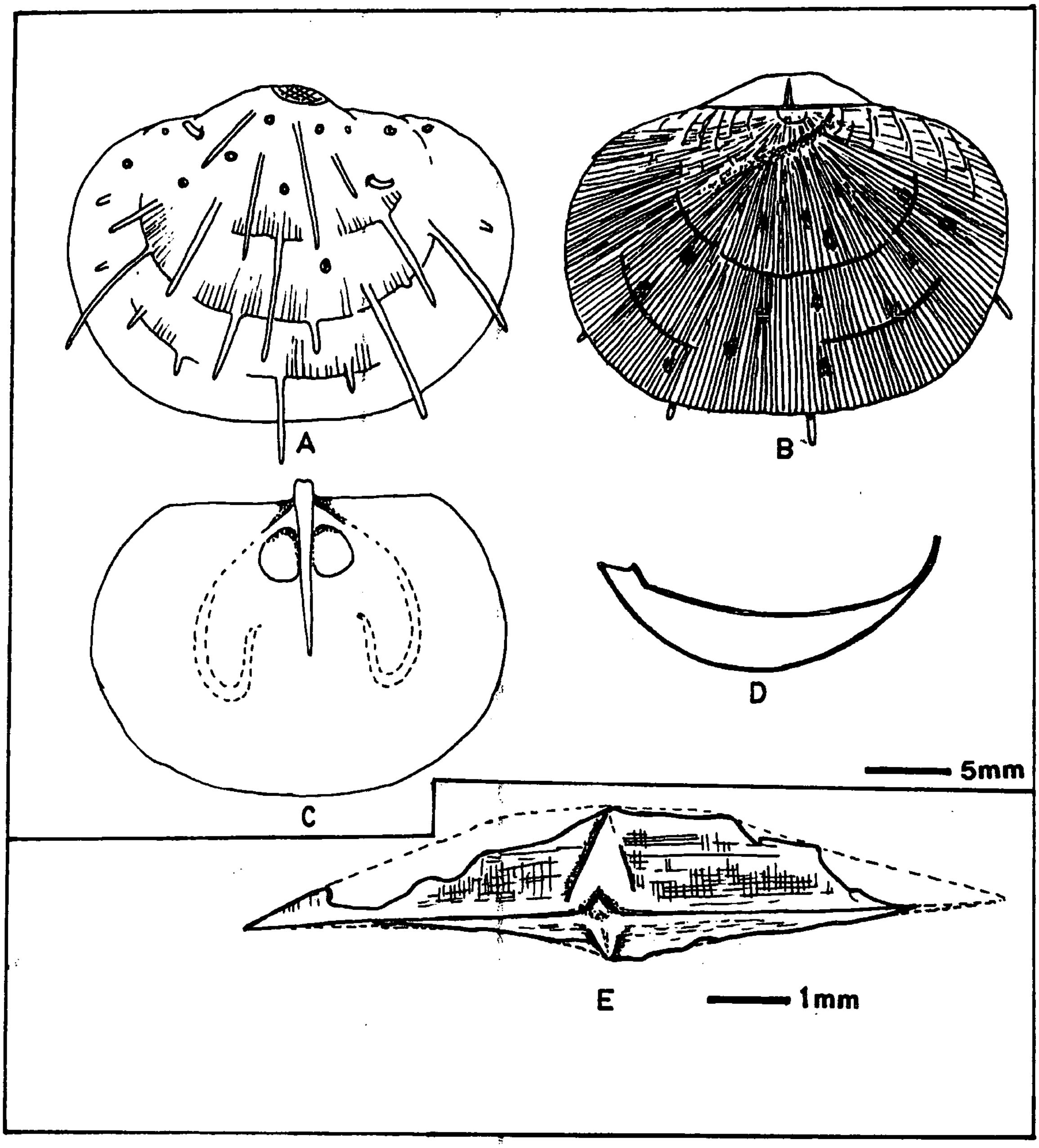


Text-figure 3.5. Reconstruction of *Heteralosia morrisiana* (King)
A - Exterior of ventral valve showing cicatrix of attachment (crossed). B - Exteriorof dorsal valve. C - Interior of dorsal valve showing endonodes. D - Lateral profile. E - Camera lucida reproduction of interarea of syntype no D326B (UCG collection).

Table 3.5. *Heteralosia morrisiana* **(W. King) - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	thickness	height VIA
MSLTH1	14.4	e23.0	18.6	13.2	6.8	2.5	1.8
MSLTH2	19.7	na	21.6	13.9	na	na	1.5
MSLTH3	e17.5	na	e20.5	13.2	na	na	na
MSLTH4	16.2	na	19.3	10.8	na	na	e1.0
MSLTH5	15.6	19.8	17.3	e12.3	8.1	na	na
MSLTH6	16.3	19.9	e21.0	e13.5	7.2	na	na
MSLTH7	6.9	9.0	8.6	5.3	2.7	na	na
MSLTH8	15.0	17.1	17.0	e10.4	10.4	na	na
MSLTH9	12.3	16.1	15.8	e10.6	7.7	na	na
MSLTH10	12.6	16.7	16.1	e10.3	7.1	na	na

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na = not available

The ventral valve is moderately convex and smoothly curved except for slight interruption at posterior region by the development of the cicatrix of attachment. The beak is broad and moderately inflated. It is irregular and asymmetrical in shape, sometimes truncated posteriorly or indented postero-ventrally by the cicatrix. The cicatrix is small, flat or weakly impressed, sub-circular to sub-elliptical in outline and often asymmetrically developed on the beak. Anteriorly and laterally, the valve is smoothly curved without forming a median sulcus or wing. However, sometimes the incisively developed body spines leave deep radial furrows which divide the valve into several broad ridges. Some of the fully grown individuals develop a long trail anteriorly and laterally to give the shell a quite gibbose appearance, but without increasing much of its visceral cavity thickness. The trail on the auricular region gives the shell an arch-like profile posteriorly.

The ventral surface of the shell is covered with fine concentric growth striae or lamellae but often this ornament is obscure and imperceptible. Sometimes the ventral valve shows a weak radial costae. The body spines are rare and irregularly distributed. They are small (less than 1 mm in diameter), but long hollow spines of two different types, the recumbent, adpressed and anteriorly directed spines and the erect and posteriorly directed spines. The second type is only developed posteriorly and probably functioned as clasping or cementing spines together with the marginal spines. The marginal spines are similar in sizes with the rest of the body spines and are of clasping or cementing types.

The ventral interarea is low and narrow with its full width about two thirds of the maximum shell width. It is apsacline to orthocline in profile with its surface longitudinally and transversely striated. The delthyrium is small and is partly covered by a slightly arched pseudodeltidium. The teeth are small. Other details of internal morphology of the ventral valve are not known.

The dorsal valve is slightly smaller than the ventral valve and moderately concave in profile. The valve curvature is smooth and continuous to both lateral and anterior margins. However, slight geniculation is sometimes shown in the larger individual. The concavity of the valve is usually interrupted posteriorly by a raised reflection of the cicatrix of attachment. The apex is always slightly raised above the plain of the valve. The dorsal surface of the valve is radially costate and weakly concentrically lamellose. The dorsal interarea is very low with small weakly raised chilidium, extended posteriorly to form a small triangular lophidium.

The cardinal process is small, with bilobed myophore elevated on a small postero-ventrally directed shaft which is butressed by a pair of slightly raised lateral ridges and a prominent median ridge. The median ridge extends anteriorly as a low median septum to about the mid-length of the shell. The adductor muscle platform is only slightly raised anteriorly. It has a pear-shaped outline and the muscle scars are lightly striated. The brachial impressions are wide with the lateral margin closely following the shell margin. The inner shell surface is smooth or covered with rare endonodes and traces of radial striae.

Discussion. Changes during **ontogeny** of *H. morrisiana* are not very obvious, except that the adult increases its gibbosity steadily by forming a trail anteriorly and laterally. Shell growth in the umbonal region seems to be very slow and limited probably due to its attachment strategies. The juveniles of *H. morrisiana* seem to be attached by cementation at the umbo to the hard objects, supported by clasping marginal spines. The restricted growth of the cicatrix of attachment in the species suggests that it freed itself from the host during early ontogeny. **Variation** occurs at the umbonal region where the shell is most unevenly developed. This might be due to shell adjustment to the very crowded niche in which the species lives, and it is not significant taxonomically. There are also small variations in the shell gibbosity, but it is difficult to determine whether this is a criterion for sexual dimorphism or merely another self adjustment feature. It is easy to mis-identify loose specimens of the visceral disk which are commonly much flattened, owing to the loss of the very thin and delicate trail.

Heteralosia sp. 4 (Cooper and Grant, 1975, p. 802, pl. 193, fig. 9) seems to be identical to *H. morrisiana* (W. King), though more detail is needed before a convincing deduction can be made regarding the relationship between these two separate populations. The material described by Cooper and Grant came from the Bone Spring Formation of West Texas (North American Permian).

H. morrisiana (W. King) differs from *H. humbletonensis* (W. King) in its smaller size, broader shell, narrower visceral cavity and less convex and less spinose ventral valve. The umbo of *H. morrisiana* is less inflated, irregular and asymmetrical with more pronounced cicatrix of attachment and a relatively higher interarea, compared to that of *H. humbletonensis.* As compared to *H. hyltonensis*, *H. morrisiana* differs in its larger size, lesser convex ventral valve and more symmetrical shape. *H. seahamensis* differs from *H. morrisiana* in its smaller size, more convex ventral valve and smaller cicatrix of attachment. *H. aycliffensis* differs from *H. morrisiana* in its larger size, larger cicatrix and denser, finer and longer spines. Both *H. morrisiana* and *H. aycliffensis* exhibit the best development of costae of all the British Permian *Heteralosia.*

HETERALOSIA HUMBLETONENSIS W. King

Text-figure 3.6. Plate 3, figure 23, Plate 4, figures 1-11.

The species name is taken from W. King (1850, 1856) Strophalosia morrisiana var. humbletonensis. W. King (1850) mentioned that if this variety is proven to be a separate species from the type of S. morrisiana, the given variety name should be promoted to the new species.

Synonymy;
1850 *Strophalosia morrisiana* var. *humbletonensis* W. King, p. 100-101, pl. 12, fig. 20-25, 29-30.
1856 *Strophalosia morrisiana* var. *humbletonensis* W. King; W. King p. 266-267.
1863 *Strophalosia lamellosa* (not-Geinitz) var. *humbletonensis* W. King; Davidson, p. 44-49, pl. 3, fig. 34-41 not 38.
1871 *Strophalosia morrisiana* W. King; Quendstedt, p. 641, pl. 60, fig. 23.

Diagnosis. Shell small to medium in size, outline variable elongate oval in plan. Ventral valve moderate to strongly convex with extensive trail. Umbo inflated, cicatrix of attachment very small or absent. Ventral body spines recumbent to strongly adpressed. Dorsal valve moderate to strongly concave. Interarea low and narrow. Cardinal process small with bilobed myophore. Median septum short. Dorsal adductor muscle platform slightly raised.

Type specimen. Pattison (1977) listed several specimens as syntypes of *S. morrisiana* var. *humbletonensis* W. King. They are specimen nos. D173A,C,D, D318A-F, D266A-F and D283A-C of W. King collection which are kept in the Department of Geology, University College of Galway, Republic of Ireland. All these specimens came from Humbleton Hill near Sunderland.

Type locality. All the type and figured specimens of this species came from Humbleton Hill, Sunderland. Pattison (1977) referred King's Humbleton locality as the quarry on the east side of Humbleton Hill around NZ 381553. A few specimens were recently collected from the above locality which has now become the private back gardens of several local houses.

Other Locality. Beside Humbleton Hill, this species was also found at Hylton Castle road cut (G R. NZ 360589).

Horizon Ford Formation

Age : Upper Permian (EZ1)

Material. The following description is based mainly on the syntypes of the species and several other specimens in Kirkby's collection in Hancock Museum, and the author's collection which include 3 specimens from Humbleton Hill and 7 specimens from Hylton Castle road cut.

Table 3.6. *Heteralosia humbletonensis* **(W. King) - dimensions in mm.**

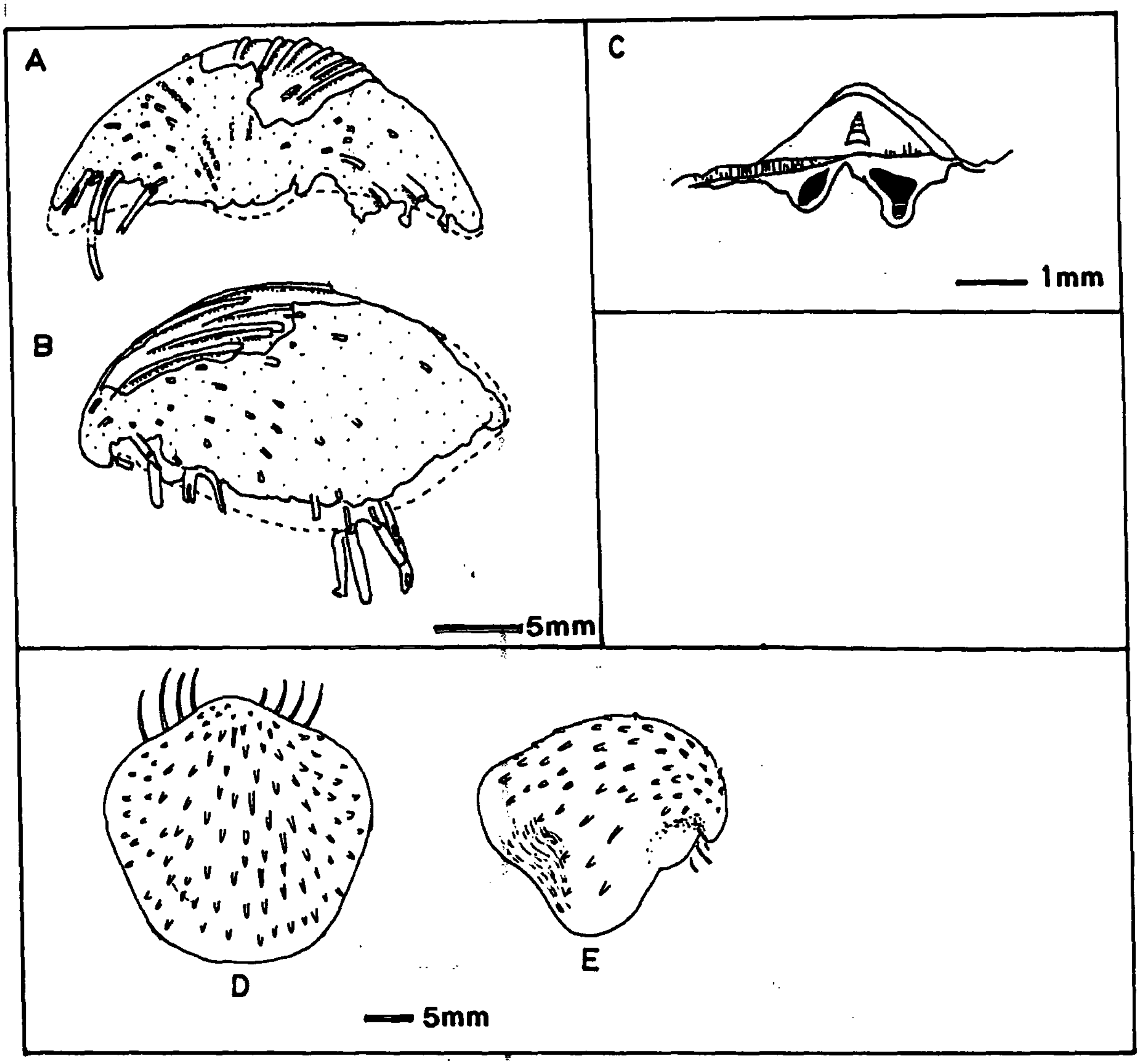
Specimen number	length	curved length	max. width	hinge width	height	thickness	height VIA
MSLHH4	e17.0	na	21.0	e8.0	11.5	4.1	e0.6
MSLHH5	7.8	10.4	7.7	e4.8	3.8	na	na
MSLHH6	e13.5	e16.8	e12.5	na	e8.0	na	na
MSLHH7	14.0	18.9	17.6	e11.4	5.6	na	na
MSLHC2	16.1	21.1	20.1	e10.9	8.0	na	na
G88.56a	28.8	42.0	27.7	e17.6	18.4	na	na
G88.56b	29.1	42.3	24.9	12.0	12.5	na	e1.5
G88.56c	27.9	39.8	27.9	e18.3	12.9	na	na
G88.56d	29.9	na	e24.4	e14.7	na	na	e1.7
G88.56e	na	na	e27.3	e17.3	na	7.9	e1.1

dimensions = refer to text-figure 1.1

specimen numbers = refer to appendix

VIA = ventral interarea e = estimated na = not available

(G88.56 = Hancock Museum collection)



Text-figure 3.6. Camera lucida reproduction of *Heteralosia humbletonensis* **(King).** A,B - Posterior and lateral views of syntype no D318B (UCG collection). C - Interior of ventral interarea of syntype no D318C (UCG collection) showing a pair of deep sockets (darken). D,E - ventral and lateral view of specimen no G88.56a (HM collection).

Description. The shell is small to medium in size, sometimes reaching a maximum length of more than 30 mm. The shell width is generally narrower than its length although in some flattened forms these dimensions are nearly the same. The maximum width of the shell is acquired at the posterior half of the shell. The shell outline varies considerably in shape from elongately subelliptical to vase shaped. The flatter forms are usually broad with a more or less subcircular plan outline.

The ventral valve is moderate to strongly convex with trail extensively developed especially anteriorly and on the auricular region. The anterior expansion sometimes forms a broad sinus due to the sudden increase in curvature of its lateral margin. The cross profile of the posterior region is strongly arched. The umbo is strongly inflated, overhanging and slightly curved, sometimes slightly dented or flattened by vestiges of cicatrix of attachment immediately posterior to the ventral interarea. The ventral interarea is apsacline, low and narrow with its full width often less than two thirds of the maximum shell width. The delthyrium is covered by a very small weakly raised pseudodeltidium.

The exterior of the shell is covered by distant recumbent and adpressed spines which sometimes leave deep grooves that disect the shell into several radial lobes. Posteriorly, beside the recumbent and adpressed spines, there are few erect and posteriorly directed clasping spines. The spines are hollow and very small in size (diameter less than 1 mm). Traces of radial costae and concentric growth lamellae are weak to obscurely developed, but occasional thickened growth lamellae or rugae are developed.

The dorsal valve is moderate to strongly concave, sub-rounded with even smooth curvature during the younger stages as shown by its growth lamellae. The curvature of the valve increases in the older stages, though geniculation is not very obvious. In general, the curvature of the dorsal valve follows that of the ventral valve quite closely. The exterior of the shell is radially costate and concentrically lamellose or occasionally rugate. The interarea on the dorsal valve is very low and almost imperceptible.

Interior of the dorsal valve is provided with a small shafted bilobed cardinal process with a small socket at its base. The adductor muscle platform is small and slightly raised. The brachial impression is small compared to the size of the shell. Its lateral margin is at a distance from the lateral shell margin while anteriorly it extends only slightly anterior to the mid-length. The median septum is low and short, extending to less than half the shell length. Exterior of the dorsal valve is similarly ornamented to the ventral valve except that it is spineless.

Discussion. The fact that the cicatrix of attachment is very small or absent suggests that *H. humbletonensis* adopted a free mode of living early in its ontogeny. During its ontogeny, steady increase in the shell gibbosity is observed. The dorsal valve becomes slightly geniculated and the shape of the shell becomes varied at a late stage in ontogeny, probably a characteristic of senility.

Comparison with *H. morrisiana* has been made earlier in this chapter. Although the flat and broad form of *H. humbletonensis* seems to resemble the shape of *H. morrisiana*, it differs from *H. morrisiana* in its more spinose ventral valve and smoother umbo without cicatrix of attachment. Other Zechstein species of *Heteralosia* are very small compared to *H. humbletonensis*, except *H. aycliffensis* n. sp. However, *H. aycliffensis* can be distinguished from *H. humbletonensis* by its denser, but less adpressed spines, larger cicatrix of attachment, smoother growth lines and stronger radial costae. The occasional development of the spine grooves, might lead one to confuse the juveniles or the younger individuals of *H. humbletonensis* with *H. hyltonensis* n. sp., but *H. hyltonensis* is characterised by its small size and asymmetrical shape.

HETERALOSIA HYLTONENSIS new species

(Text-figure 3.7, Plate 5, figures 1-13).

Named after Hylton Castle, the locality at which this species is found.

Diagnosis. Small, asymmetrical, transversely sub-elliptical to sub-circular shaped *Heteralosia* with small to minute cicatrix of attachment and strongly adpressed body spines. Some of the posterior body spines and the marginal spines are rhizoid in nature. Ventral valve strongly convex with broad unevenly plicated trail and lamellose exterior. Ventral interarea low and narrow, asymmetrical in shape. Dorsal valve weak to moderately concave with slightly geniculated margin, low interarea and lamellose and costate exterior. Cardinal process with stout shaft. Adductor muscle platform moderately elevated and pear shaped. Median septum short.

Type specimen. Specimens no.*MSLHC3, MSLHC4, MSLHC5, MSLHC6, MSLHC7 and MSLHC8 are chosen as a series of paratypes of *Heteralosia hyltonensis*, showing various morphological features of the species.

Type Locality. This species is only known from Hylton Castle road cut (G R. NZ 360589) and this locality should be named as the type locality of this species.

Material. The following description of the species is based on 59 specimens collected by the present author from the type locality mentioned above. Most of the specimens are preserved with the original shell material while a few are preserved in form of moulds.

Description. The shell is small in size with the largest individuals having a length of about 15mm, and characterised by strongly asymmetrical shell growth. The shell is variable in shape from asymmetrical transversely sub-elliptical to sub-circular. The shell width is usually greater than its length with the maximum width situated at anterior half of the shell. The hinge line is also asymmetrical in length and the beak is usually pointed toward the longer hinge line.

The ventral valve is strongly convex with maximum convexity at the umbonal region. The convexity of the valve is reduced toward the antero-lateral margin which shows evidence of strong growth. The posterior margin is provided with a poorly developed auricle. The anterior and lateral margins are usually broadly plicated. This plication is produced when the adpressed spines undercut the shell anteriorly to form several profound grooves at a distance away from one another. Generally, these grooves are bent following the twisted direction of the major shell growth. The umbo

Table 3.7. *Heteralosia hyltonensis* **new species - dimensions in mm.**

Specimen number	length	curved length (max.)	plane curved length	max. width	hinge width (HW1)	hinge width (HW2)	height
MSLHC3	11.5	18.2	14.6	15.1	3.9	6.5	6.8
MSLHC4	e11.9	e18.7	e15.1	e14.3	e3.9	na	7.5
MSLHC5a	11.4	16.0	13.6	12.8	na	5.2	6.2
MSLHC5b	9.6	e16.0	12.5	11.9	4.4	na	5.4
MSLHC6	7.8	14.7	12.4	e10.8	na	4.3	5.1
MSLHC10	6.8	e9.5	e7.5	8.5	e2.7	e3.2	3.4
MSLHC12a	3.9	e5.5	e4.2	4.8	na	na	1.8
MSLHC12b	4.9	6.5	e5.1	5.5	1.5	1.8	1.5

VIA = ventral interarea e = estimated na = not available
specimen numbers = refer to appendix

(see text-figure 3.7E,F for details on measured parameters)

is small, but usually broad and pointed toward the longer side of the hinge line which is also the major growth direction of the shell. The cicatrix of attachment small, flat or slightly concave and asymmetrically positioned on the umbo. Sometimes the cicatrix is so small as to be hardly observable.

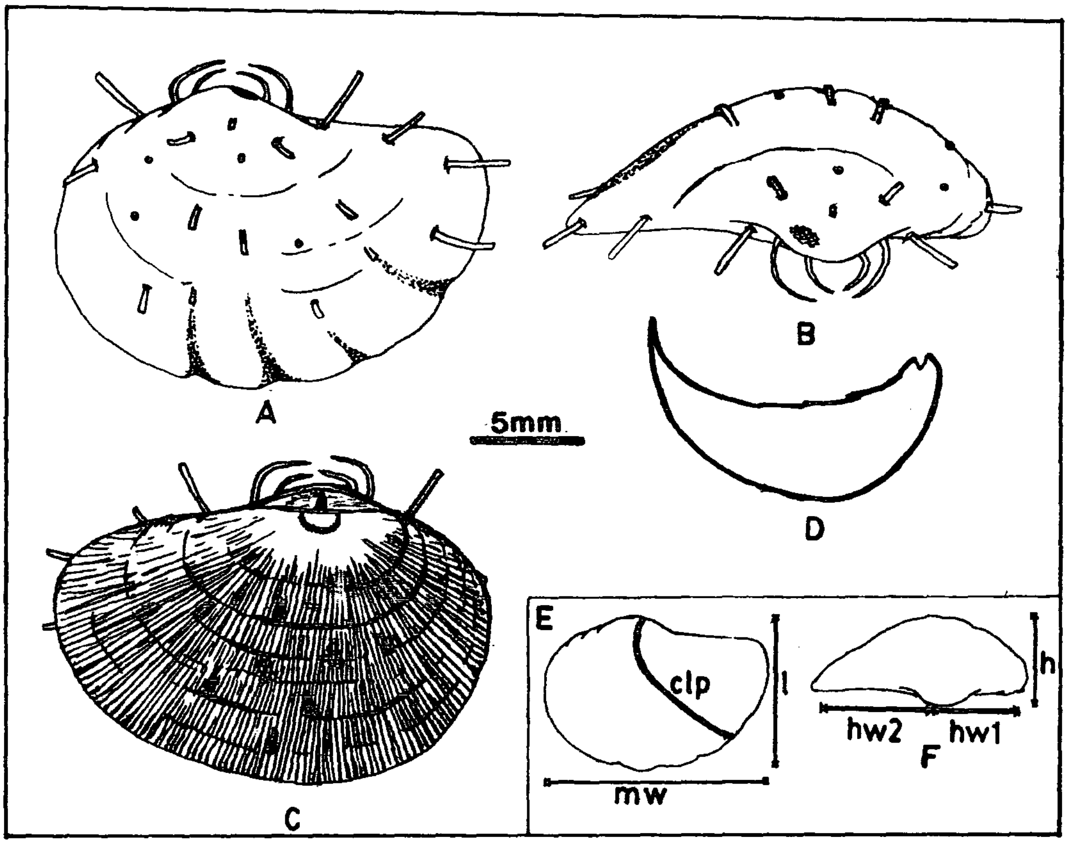
The ventral surface is lightly lamellose or smooth, wrinkled posteriorly. The valve is furnished with strongly adpressed to sub-erect body spines which are sparsely distributed over the convex part of the valve. These spines do not show radial growth, but are inclined toward the major growth direction of the shell. Posteriorly, some of the body spines are erect and posteriorly directed with their ends rhizoid in nature. The marginal spines are made of rhizoid spines.

The ventral interarea is low and narrow with slightly asymmetrical triangular shape. The surface is transversely striated and the delthyrium is covered by a small and pseudodeltidium. Adductor muscle platform is narrow and short. Full details of the internal morphology are not known.

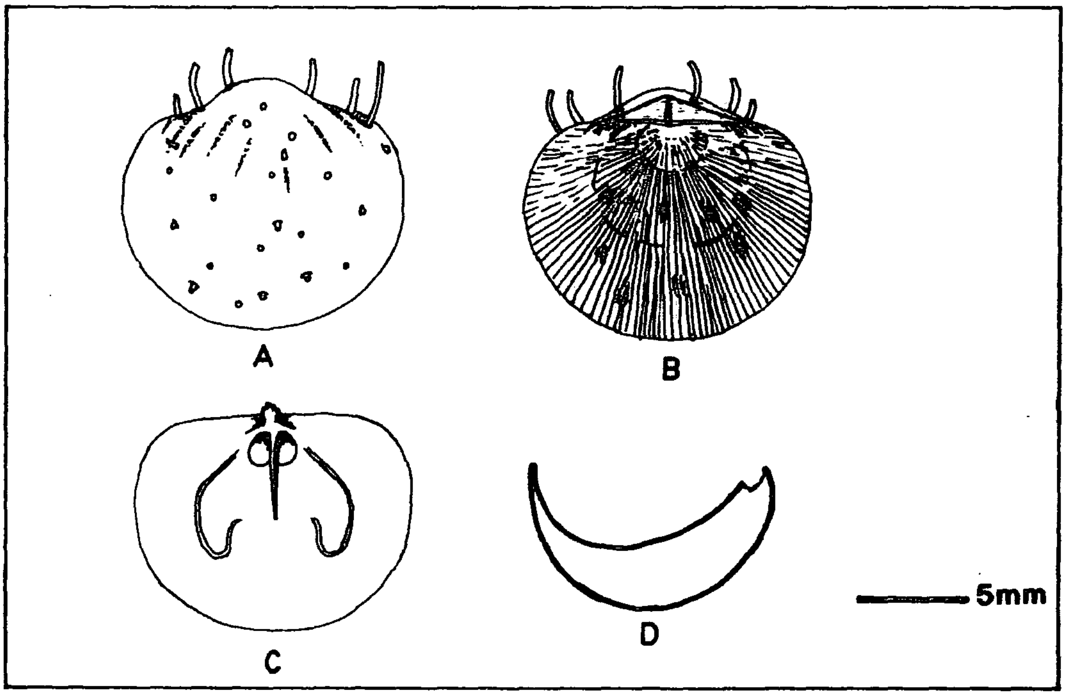
The dorsal valve is weak to moderately concave with slightly geniculated margin stronger at the lesser growing side. The umbo is small and weakly raised. The surface is prominently concentrically lamellose and finely costate. The dorsal interarea is very low with small chilidium. The interior of the dorsal valve is provided with a stout cardinal process shaft supported by a strong median ridge and a pair of lateral ridges which make an acute angle between them. The adductor muscle platform is pear shaped and is moderately elevated above the shell plane. The muscle scar is concentrically striated. The median septum is low and extends to the mid-length of the valve. Other internal features are not known.

Remarks. The asymmetrical shape of the shell and the position of the cicatrix of attachment clearly indicate that this species does not grow in a normal anterior direction, but laterally instead. The stronger growth of the shell at one lateral margin, creates a siphon-like structure at this margin. This adopted molluscan feature might have resulted from the very crowded niche in which this species lives. *H. hyltonensis* lived in a confined pockets within or under overgrown algal stromatolites or bryozoan colonies, where a type of siphonic apparatus would be beneficial for an immobile species to get fresh nutrient from the sea water. The reason for the development of a single lateral siphon in this brachiopod is not fully understood. It is possible that the attachment strategy employed by the species does not permit the re-positioning of the shell during ontogeny when the growth space was blocked. The attachment strategy of *H. hyltonensis* seems to be reinforced with the development of rhizoid spines at its posterior.

Comparison. The development of rhizoid spines and the strongly asymmetrical shell growth of *H. hyltonensis* is unique and have not been observed in any other *Heteralosia*. Apart from these, *H. hyltonensis* resembles some *H. humbletonensis* in its grooved trail and resembles *H. seahamensis* in its small globbose shell. However, *H. hyltonensis* can be distinguished from *H. humbletonensis* by its small size and asymmetrical shape, while it differs from *H. seahamensis* in its asymmetrical shape and its grooved trail.



Text-figure 3.7. Reconstruction of *Heteralosia hyltonensis* new species.
A - Exterior of ventral valve (plan view). B - Exterior of ventral valve (posterior view). C - Exterior of dorsal valve. D - Lateral profile. E,F - Measured parameters in table 3.7 [l = length clp = plane curved length mw = maximum width hw1 = shorter hinge width hw2 = longer hinge width h = height].



Text-figure 3.8. Reconstruction of *Heteralosia seahamensis* new species.
A - Exterior of ventral valve. B,C - Exterior and Interior of dorsal valve. D - Lateral profile.

HETERALOSIA SEAHAMENSIS new species

(Text-figure 3.8, Plate 5, figures 14-27).

Named after Seaham Harbour, peripheral to which the two major localities for this species are sited.

Synonymy;
1858 *Strophalosia lamellosa* (not-Geinitz) var. *morrisiana* (W. King); Davidson, pl. 3, fig. 32, ?33.

Diagnosis. Small globose *Heteralosia* with poorly defined cicatrix of attachment. Ventral valve strongly convex without sulcus or plicae. Ventral interarea high with small pseudodeltidium. Ventral surface lightly lamellose with sub-erect body spines. Dorsal valve moderately concave with slightly geniculated margin. Dorsal interarea low. Dorsal surface concentrically lamellose and finely radially costate. Cardinal process on small shaft. Teeth prominent. Adductor muscle platform moderately elevated with concentrically striated scar. Median septum short. Brachial impressions wide.

Type specimens. Specimens no MSLBH19, MSLBH20, MSLBH21, MSLBH22 and MSLBH23 are chosen as a series of paratypes representing various morphological features of *Heteralosia seahamensis.*

Type locality. The type specimens named above came from Beacon Hill railway cut (GR. NZ 442454), collected during the tenure of this research. This locality is chosen because of its availability for future collecting. Although a large collection of this species in Kirkby's collection in Hancock Museum came from Dalton-le-Dale, current research at Dalton-le-Dale failed to encounter any specimens of this species.

Other localities. Dalton-le-Dale (Kirkby's collection - probably the same as W. King's locality at around GR. NZ 40884744); Tunstall Hill old trench (GR. NZ 397541); temporary sewage tunnel at South Tunstall Hill.

Material. 49 specimens from Beacon Hill, 3 specimens from Tunstall Hill temporary tunnel and 1 specimen from Tunstall Hill old trench in my own collection. Most of the specimens are preserved in form of moulds and casts while a few are preserved with patches of original shell.

Table 3.8. *Heteralosia seahamensis* **new species - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	thickness	height VIA
MSLBH19	e12.3	e17.7	e12.5	6.9	5.9	3.1	1.1
MSLBH20a	12.2	18.1	13.1	9.9	6.6	na	na
MSLBH21	11.2	17.1	e12.3	7.0	5.2	na	na
MSLBH22	9.0	e10.9	9.1	6.7	4.0	na	na
MSLBH23	8.8	10.0	9.3	e5.4	3.3	na	na
MSLBH24	10.7	na	10.9	5.4	na	na	1.3
MSLBH25	9.6	na	10.0	9.3	na	na	0.9
MSLBH26	e11.2	na	e13.0	e8.5	na	na	na
MSLBH28a	12.1	17.4	13.1	e9.7	5.8	na	na
MSLBH28b	11.6	17.6	12.6	e8.7	7.1	na	na
MSLBH28c	e4.9	6.3	5.3	3.9	1.7	na	na
MSLBH28d	9.2	13.4	11.2	8.7	5.8	na	na

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na = not available

Description. The shell is small and rarely reaches 12 mm in dimensions. It is globose with almost circular outline but sometimes the shell outline is slightly asymmetrical in shape. The maximum shell width is situated at about the mid-length.

The ventral valve is strongly convex with maximum convexity normally situated posteriorly. There is no sulcus and no auricle. The beak varies from narrow to broad with overhanging and slightly curved umbo. Narrower beaks are commonly more inflated than the broader ones. The cicatrix of attachment is usually absent but when present it is small in size with sub-circular outline and flat profile. The umbo is not strongly incurved so that the ventral interarea is left open. The ventral interarea is quite high, but narrow with the hinge width about half to two thirds the maximum shell width. The pseudodeltidium is small and weakly raised.

The ventral surface is smooth or covered by fine concentric striae and sometimes lamellae or rugae. Traces of radial costae are occasionally seen. The ventral valve is furnished with sparse randomly distributed body spines and a row of posteriorly directed clasping marginal spines. Posteriorly, the body spines are divided into the recumbent to adpressed, and the erect posteriorly directed spines, while anteriorly, only suberect spines prevailed. The adpressed body spines sometimes leave radial grooves on the shell at the umbonal region. The spines are small and not extended very far beyond the shell margin. Interior of the ventral valve is provided with a pair of strong teeth and a short, but broad adductor muscle platform. The adductor muscle platform is moderately elevated and has a slightly flabellate shape, divided medianly by a well developed median ridge. The adductor muscle scar is smooth. Other internal features are not known.

The dorsal valve is moderately concave with slightly geniculated margin in the adult. The median fold is absent. Posteriorly, the umbo is slightly raised. The interarea is low and narrow with small chilidium. The dorsal surface is concentrically lamellose and finely costate. Interior of the dorsal valve is provided with a small, short shafted cardinal process with bilobed myophore. The cardinal process is supported by a pair of socket ridges and a low median ridge which is continued anteriorly by a low median septum to about the mid-length of the valve. The adductor muscle platform is pear shaped and moderately raised with the scar concentrically striated. The brachial impressons are wide. The interior surface is smooth, but sometimes it shows traces of radial striae and rare endonodes. The interior of the anterior margin is rimmed by numerous marginally pointed endospines.

Discussion. Not much ontogenic detail is known in *H. seahamensis* owing to the lack of completely preserved juveniles. However, it can be generalised that the globosity of the shell and the geniculation of the dorsal valve is achieved during the adulthood of the species. Regarding the attachment, it seems that the majority of *H. seahamensis* were only attached to other objects during their juvenile stages and by clasping spines only. A few individuals, however, are attached to the substratum for a much longer period of their lives. These attached forms usually show more irregular shell growth with small cicatrix on the umbo, and are often asymmtrical in its shape.

H. seahamensis closely resembles *H. hyltonensis* and the Mississippian *H. orbiculata* (Hinchey & Ray) from North America in its smaller size and globose shell. However, it differs from the *H. orbiculata* in its poorly developed cicatrix of attachment and the presence of radially costate ornament. The differences between *H. seahamensis* and *H. hyltonensis* has been outlined earlier in this thesis. *H. seahamensis* can be distinguished from other *Heteralosia* by its very small size, globose shell with almost circular outline and its less adpressed body spines.

H. seahamensis has probably been confused by Davidson (1858) with the juveniles or younger individuals of *H. morrisiana* because of its very small size. The geniculation of the dorsal valve and the globbosity of the ventral valve in very small individuals of this species indicate that they are adults and not juveniles of *H. morrisiana*, and that they belong to a separate species of *Heteralosia* which is characteristically very small in size. The juvenile or younger individuals of *H. morrisiana* are much flatter than *H. seahamensis* at the same size.

HETERALOSIA AYCLIFFENSIS new species

(Text-figure 3.9A,B,C, Plate 4, figures 12-22).

Named after Newton Aycliffe, the nearest town to the cited type locality of the species.

Diagnosis. Medium size *Heteralosia* with radial costae and weak growth lines on both valves. Ventral valve moderately convex with posterior margin truncated by cicatrix of attachment. Fine and long recumbent to adpressed body spines numerous. Ventral interarea low, trapezoidal in shape with small pseudodeltidium. Dorsal valve weakly concave with raised umbo and low interarea.

Type specimens. Specimens no MSLWQ4, MSLWQ5, MSLWQ6, MSLWQ7 and MSLWQ8 are chosen as a series of paratypes of *Heteralosia aycliffensis*, showing various morphological features of the species.

Type locality. Old Town (=White) Quarry (G.R. NZ 257245), where most of the specimens studied were collected is chosen as the type locality of this species.

Other localities include Raisby Hill Quarry (G.R. NZ 346353) and East Thickley Quarry (G.R. NZ 24082564).

Horizon. Raisby Formation.

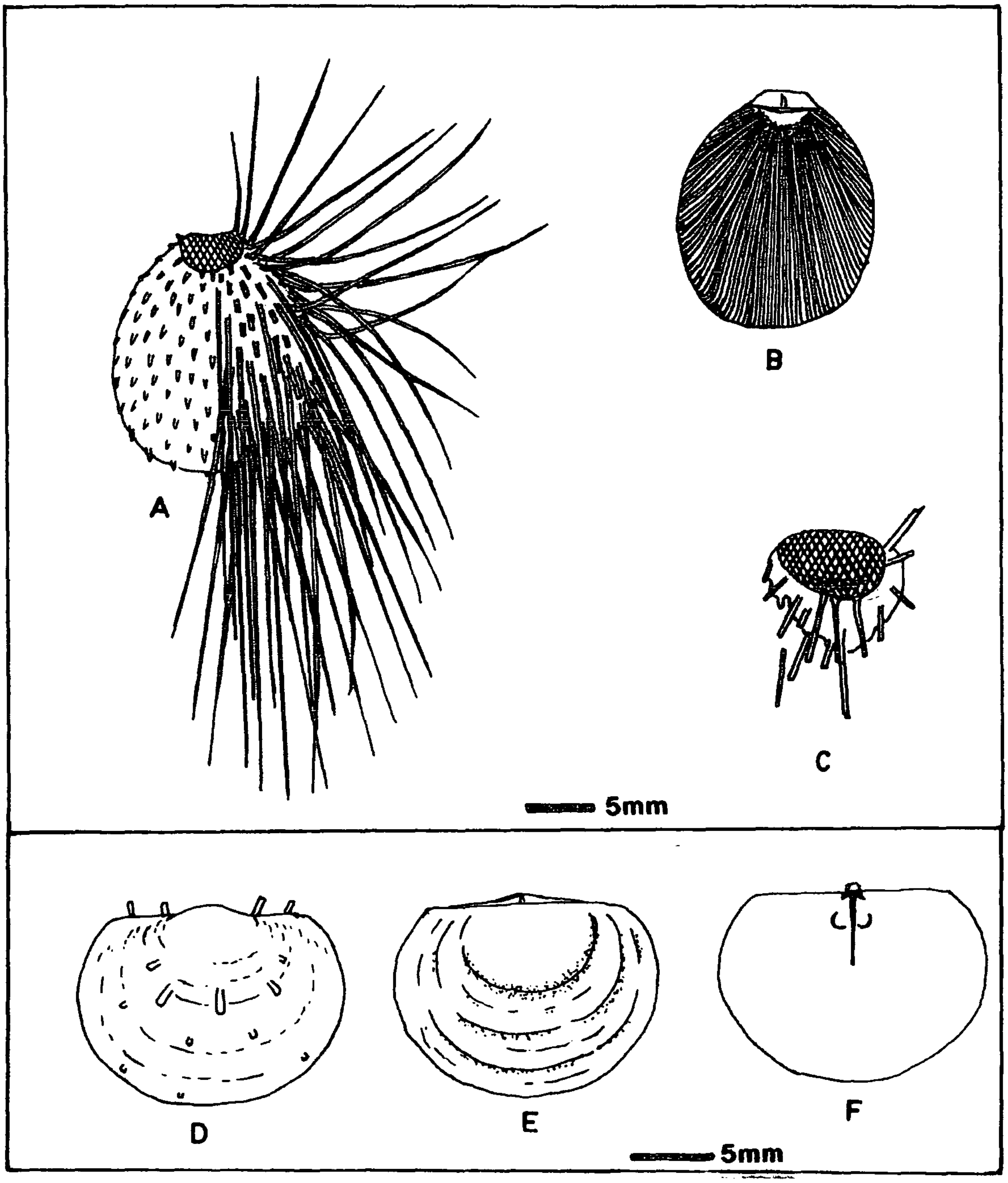
Age. Upper Permian (EZ1).

Material. 43 specimens from Old Town (=White) Quarry; 10 specimens from Raisby Hill Quarry; 5 specimens from East Thickley Quarry.

Description. The shell is of medium size with the length of the largest individual around 30 mm. It has a sub-elliptical to pear shaped outline with truncated posterior. The shell length is normally greater than the maximum shell width, although deformed specimens are sometimes *vice versa.*

The ventral valve is weakly to moderately convex longitudinally, but rather stronger in convexity transversely. The posterior margin of the ventral valve is truncated by a small sub-circular to transversely sub-elliptical cicatrix of attachment which is slightly concave or flat in profile. The sulcus and auricle are absent. The ventral interarea is low and narrow, trapezoidal in shape with small pseudodeltidium weakly raised above the plane of the interarea. Traces of a pair of small teeth are sometime seen at the base of the pseudodeltidium.

The growth lines of the ventral valve are obscure, but fine radial costae are usually



Text-figure 3.9. Reconstruction of *Heteralosia aycliffensis* new species (figure A to C) and *Heteralosia? quarringtonensis* new species (figure D to F).
A,B - Exterior of ventral and dorsal valves. C - Camera lucida reproduction of specimen no MSLWQ10 showing an overgrown cicatrix.
D - Exterior of ventral valve. E,F - Exterior and interior of dorsal valve.

Table 3.9. *Heteralosia aycliffensis* **new species - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	cicatrix length	height VIA
MSLWQ4	17.2	21.9	e16.4	na	7.3	na	na
MSLWQ6	15.7	18.8	e15.6	e9.1	6.0	2.0	na
MSLWQ7a*	20.0	na	17.0	7.0	na	na	0.8
MSLWQ8	4.8	5.2	5.6	3.1	1.3	1.5	na
MSLWQ9	e16.2	e19.0	e16.0	e10.5	5.2	5.0+	1.4
MSLWQ11a	5.8	na	7.0	4.0	na	e3.5	e0.5
MSLETQ2*	26.7	28.8	23.4	e7.8	e3.0	na	na

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na = not available

* badly deformed specimens + measured from dorsal valve.

well developed. The exterior shell surface is covered by fine recumbent and adpressed spines, but no spine groove is developed. The spines are long and sometime extend more than 20 mm beyond the shell margin. A few posteriorly directed clasping spines are also developed in some specimens.

The dorsal valve is weakly concave with semi-circular umbo raised on its posterior margin. The diameter of this raised umbo ranges from half to two thirds of the hinge width. There is no median fold. The interarea is low with small and weakly raised chilidium. The dorsal surface is radially costate with occasional traces of faint growth striae. The internal morphology of this species is unknown.

Discussion. This is the most ill-preserved species of *Heteralosia* in the Durham Permian. The currently available material, however, is sufficient to show that the external morphology is different from all known species of this genus. Therefore, it is without question that this material, as described above, should be placed in a new species of *Heteralosia*. Comparison with other species of *Heteralosia* has already been made earlier in this thesis.

H. aycliffensis might be confused with *C. langtonensis*, especially when the spines and the dorsal valve are missing. In this case *H. aycliffensis* can only be distinguished from *C. langtonensis* by its larger size, slightly smaller cicatrix of attachment and smaller number of spine bases.

Genus *CRASPEDALOSIA* Muir-wood & Cooper 1960

Synonymy;
1960 *Craspedalosia* Muir-Wood & Cooper, p. 82-83.
1965 *Craspedalosia* Muir-Wood & Cooper; Muir-Wood, p. 451.

Diagnosis. Small to medium size heteralosiinid with sub-pentagonal to sub-circular shell outline. Ventral valve strongly convex with no sulcus. Umbo usually truncated by cicatrix of attachment. Ventral interarea variable in height with small weakly raised pseudodeltidium. Ventral surface lightly lamellose with two series of spines posteriorly and specialized spines anteriorly. Dorsal valve with raised umbo, low interarea and squamose growth lamellae. Teeth prominent. Cardinal process with bilobed or trilobed myophore. Adductor muscle platform moderately elevated. Brachial impressions moderate to large in size. Median septum short. Dorsal valve with endospinose rim separated from geniculated margin by sulcus.

Discussion. The name *Craspedalosia* was suggested by Muir-Wood & Cooper (1960) to highlight the presence of the endospinose rim in the dorsal valve of this genus. It is well known that the internal features of the productidinids are unreliable, partly due to their ubiquity and partly due to their variable nature. It is very difficult to obtain the internal details of this genus, because individuals are usually preserved complete with the original shell and with both valves articulated. For this reason, it is not practicable to determine the genus *Craspedalosia* just by the meaning of its name. It is therefore, very important that other diagnostic features are considered in recognising the genus.

The genus *Craspedalosia* has been recognised in the past as heteralosiinid with strong squamose lamellae or rugae on its dorsal valve. This feature is not related to the name *Craspedalosia*. In past literatures, the sub-division of *Craspedalosia* has been based on the general shape and the nature of the adult spines. *C. pulchella* (Dunbar) is distinguished from the type-species *C. lamellosa* (Geinitz) by its triangular or wedge shaped and its two series of body spines in the adult.

The similarity of the dorsal valve of new species *C. langtonensis* with the other two species of *Craspedalosia* has led the author to assign the new species to this genus. With the new species the genus *Craspedalosia* is now represented in Britain by two species, *C. lamellosa* (Geinitz) and *C. langtonensis* n. sp. Another uncertain species of the genus is also recorded in this thesis.

Type species. *Orthothrix lamellosus* Geinitz, 1848, p. 18, pl. 5, fig. 16-26.

Other species. *Strophalosia pulchella* Dunbar and *Craspedalosia langtonensis* n. sp.

CRASPEDALOSIA LANGTONENSIS new species

(Text-figure 3.10B-E, Plate 6, Figures 1-10).

Named after Langton Village in which the type locality is sited.

Diagnosis. Small to medium sized, sub-circular to sub-triangular shaped *Craspedalosia*. Ventral valve moderately convex with large cicatrix of attachment and truncated umbo. Ventral interarea high and narrow with trapezoidal outline. Ventral surface with closely spaced spine bases. Dorsal valve with large and high umbo and very low interarea. Dorsal surface with radial costae and squamose concentric growth rugae anteriorly. Cardinal process small and shafted with prominent oblique lateral ridges. Adductor muscle platform weakly elevated. Median septum not extended beyond the first squamose rugae.

Type specimens. Specimens no MSLLQ1, MSLLQ2, MSLLQ3, MSLLQ4, MSLLQ5 and MSLLQ6 are chosen as a series of paratypes of *Craspedalosia langtonensis*, showing various morphological features of the species.

Type locality. The type specimens above are collected from Hobgate (= Langton) Quarry, south of Langton Village (GR. NZ 165189), near Barnard Castle.

Other Localities. Several specimens obtained from boreholes such as Fishburn BH, Welbeck Abbey BH, Sutton BH and Wressell BH which show close affinity to *C. langtonensis* are tentatively included in this species.

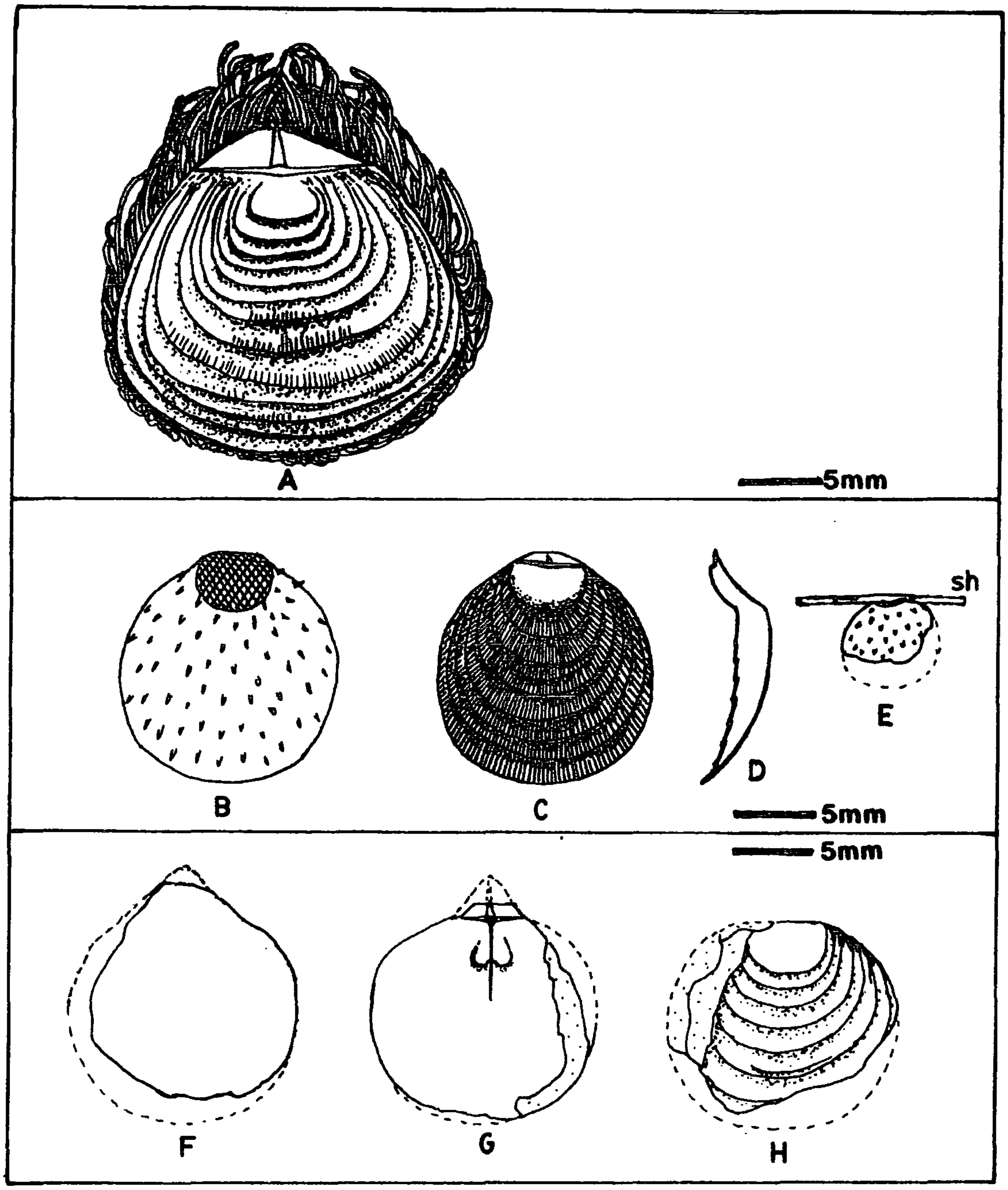
Horizon. Raisby Formation and Cadeby Formation.

Age. Upper Permian (EZ1).

Material. The following description is mainly based on 133 specimens in the author's collection from the type locality. Also observed are several specimens from Hobgate (=Langton) Quarry, Fishburn BH, Welbeck Abbey BH, Sutton BH and Wressell BH in the BGS Museum collection.

Description. The shell is small to medium in size with the largest individuals about 20 mm in length. It is sub-circular to sub-triangular in outline. The maximum width is reached at about its mid-length. The profile is often flattened with strong influence of the large cicatrix of attachment at the posterior. The visceral cavity is very narrow because of the development of a large cicatrix of attachment on the ventral valve and the strong undulation of the dorsal valve.

The ventral valve is weakly to moderately convex, surrounding the very large and



Text-figure 3.10. Reconstruction of British species of ***Craspedalosia.***
A - Dorsal view of *Craspedalosia lamellosa* (Geinitz)
B - E : *Craspedalosia langtonensis* new species; B - Exterior of ventral valve showing large cicatrix of attachment (crossed). B - Exterior of dorsal valve. D - Lateral profile. E - Camera lucida reproduction of juvenile specimen no MSLLQ5 attached to a spine of *Horridonia* (sh).
F - H : *Craspedalosia* sp. A (camera lucida reproduction of specimen no YEF 2367a,b - BGS collection): F,G - Internal mould of ventral and dorsal valves. H - External mould of dorsal valve.

Table 3.10. ***Craspedalosia langtonensis*** **new species - dimensions in mm.**

Specimen number	length	max. width	hinge width	height	cicatrix length	height
MSLLQ1	e14.3	e16.2	e8.8	na	na	1.6
MSLLQ2	e11.3	12.7	na	na	2.7+	na
MSLLQ4	e8.9	e9.9	6.8	na	2.8+	na
MSLLQ5	4.4	6.0	e4.8	e1.5	na	na
MSLLQ6	e5.3	6.7	4.5	2.1	na	na
MSLLQ7	e8.3	e8.3	e4.3	2.6	3.1	na
MSLLQ9	e12.8	12.9	e9.9	na	na	na
MSLLQ10	e12.3	e12.3	e9.0	na	3.6+	na

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA = ventral interarea e = estimated na = not available

+ measured from impression of cicatrix on the dorsal valve

smoothly concave cicatrix of attachment. The cicatrix of attachment usually covers a quarter to one thirds of the shell length, although in some individuals it is relatively smaller. It is sub-circular to semi-circular in outline with truncated posterior. The beak does not seem to be developed owing to the development of the large cicatrix. A few specimens, however, show a narrow and weakly inflated beak with flat or slightly concave attachment scar of varying shape, anterior to the umbo. The ventral interarea is high and narrow with trapezoidal shape and small weakly raised pseudodeltidium.

The exterior of the ventral valve is fine to moderately lamellose and weakly costate with some closely spaced spine bases whose points of origin suggest that they might range from erect to recumbent. A few spines were preserved in matrix a short distant from the lateral and anterior margins in some specimens and indicate the presence of recumbent spines in this species. These spines extend at a very low angle to the plane of the ventral valve. The marginal and clasping spines are not preserved.

The dorsal valve is sub-circular to sub-elliptical in outline with large sub-circular to semi-circular convex umbo, slightly smaller in size than the cicatrix of attachment. The umbo is rimmed anteriorly by several strong squamose growth rugae which are consistently developed toward the valve margin. These rugae give the valve a pronounced concentrically undulating surface. Beside these rugae the dorsal surface also shows traces of fine concentric lamellae and radial costae.

The dorsal interarea is very low and often compressed against the ventral interarea. The width of the hinge line is about two thirds the maximum width of the shell. The cardinal process has a small shaft, buttressed only by a pair of lateral ridges at an angle of 110^o to 130^o to each other. The adductor muscle platform is weakly elevated and has a radially striated surface and pear shape outline. The median septum is prominent but only extends to the first growth rugae, anteriorly.

Remarks. *C. langtonensis* shows an interesting ontogenic development (see text-figure 3.10D). It begins its early stage with a convexo-concave profile due to cementation of its umbo to smooth objects, probably rounded pebbles, plant fragments or on *Horridonia* or its spines (see Text-figure 3.10E). The normal productidinid profile is only produced half way through its life where at this stage the craspedalosian features begin to develop. At this stage, the dorsal valve begins to form undulations, owing to the development of consistent strong rugae which might correspond to a seasonal reduction of the shell growth. However, the growth reduction is not shown on the ventral valve. Unfortunately, owing to the absence of the original shell substance, it has not been possible to prove this assumption of growth behavior. The consistent truncation of the umbo in this species suggests that the shell is attached to the large host throughout its whole life. A few specimens, however, have a smaller attachment scar which is positioned a little anterior to the tip of the umbo, suggesting either that the host had a rather smaller surface area or perhaps these individuals might have adopted a free mode of life during the adult stage.

Comparison. Although the spines are not preserved in the available adults of this species, the spine bases show a roughly similar spine density with all other *Craspedalosia*. This species can easily be distinguished from other *Craspedalosia* by its large cicatrix of attachment, strongly truncated ventral umbo, trapezoidal shaped ventral interarea, large smoothly convex dorsal umbo and costate shell.

It is interesting that the incompletely preserved specimens and younger individuals of this species have been confused by previous authors with *H. morrisiana*. This has happened when only a few incompletely preserved specimens were obtained from various boreholes, from the Cadeby Formation in Nottinghamshire and from the Raisby Formation in County Durham. At a glance, these specimens in which the anterior half is missing or not developed look very similar to *H. morrisiana*, but they differ from *H. morrisiana* in the larger cicatrix of attachment and the much denser spines. In fact, it was not until I obtained a large collection of *C. langtonensis* from Langton (=Hobgate) Quarry, including several complete casts and moulds of dorsal and ventral valves of adult individuals, that I decided that this species should belong to the genus *Craspedalosia*.

CRASPEDALOSIA LAMELLOSA (GEINITZ)

(Text-figure 3.10A, Plate 6, figures 11-14).

Synonymy;
1848 *Orthothrix lamellosus* Geinitz, p. 14, pl. 5, fig 16-26, 33.
1861 *Strophalosia lamellosa* (Geinitz); Geinitz, p. 97, pl. 18, fig. 1-7.
1871 *Productus lamellosus* (Geinitz); Geinitz, p. 640, pl 60, fig 21.
1921 *Strophalosia lamellosa* (Geinitz); Trechmann, p. 541, fig. 2b.
1937 *Strophalosia lamellosa* (geinitz); Malzahn, p. 52, pl. 2, fig. 16-17.
1960 *Craspedalosia lamellosa* (Geinitz); Muir-Wood & Cooper, p. 82, pl. 6, fig. 1-9.

Material. Specimens studied include 1 incomplete specimen of my own collection from Old Town (=White) Quarry, and 5 specimens from Mattersey BH and 1 specimen from Barnby Moore BH in the BGS Museum collection. Trechmann's collections in British Museum (Natural History) have also been observed.

Table 3.11. ***Craspedalosia lamellosa*** **(Geinitz) - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	thickness	height VIA
YPF4168	e22.8	na	e22.9	e13.8	e8.4	7.8	2.8
BN8223d	20.2	23.2	18.2	na	7.7	4.7	na
BN8223i	20.0	24.9	22.4	e15.6	9.4	4.8	2.4

dimensions = refer to text-figure 1.1
(BGS collection)
VIA = ventral interarea e = estimated na = not available

Discussion. *C. lamellosa* was first correctly identified in the British Permian by Trechmann in 1921. It is a rare species in Britain and it is restricted to the lower part of the Raisby Formation and Cadeby Formation, commonly associated with the strophalosiinid *S. goldfussi*. Both of these species are known to be abundant in the East German Zechstein. As suggested for *S. goldfussi*, *C. lamellosa* was also probably carried to the British Zechstein Sea during its larval stage by westward storm currents from the Eastern Zechstein.

British *C. lamellosa* are generally smaller in size as compared to those from East Germany. They are commonly rather circular in shape with slightly overhanged umbo. The sub-elliptical and sub-triangular forms which are common in East Germany are less common in Britain. Other details of the surface ornamentaion of both valves are identical between the British and the German *C. lamellosa*. They both have ventral valves with a mass of tangled vermiform spines which are posteriorly directed and often still attached to the spines or shell of *Horridonia*. The dorsal valve is strongly squamose, except at the slightly raised umbo where it is only lightly lamellose.

Comparison with *C. langtonensis* has already been outlined in the previous section. Regarding *C. lamellosa* and *S. goldfussi*, it is fortunate that both species are almost always completely preserved, both in Germany and in Britain. Lack of external detail normally results from the process of weathering or preparation of the samples. Since the weathering process is not very severe in the present climate in which this species occurs and the preparational damage can be avoided, these two species can easily be distinguished by the spinosity of their dorsal valves. *S. goldfussi* is a strophalosiinid with its dorsal valve spinose, while *C. lamellosa*, as a heteralosiinid has no spines on its dorsal valve. It is noteworthy that there are no intermediate forms between these two species. This evidence strongly supports the sub-division of the family given earlier in this chapter.

CRASPEDALOSIA sp. A

Text-figure 3.10F-H, Plate 6, figures 15-19.

Material. 7 incomplete specimens from Hylton Castle temporary sewage trench in Dr. Denys Smith's collection, in BGS Museum collection (no. YEF 2367D).

Table 3.12. ***Craspedalosia* sp. A - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	height VIA
YEF2367Da	e15.0	na	14.2	e8.0	4.0	na
YEF2367Dc	13.1	15.0	13.4	e10.2	3.8	e1.6
YEF2367Dd	e13.8	e17.7	e16.0	e9.2	e3.5	e2.2
YEF2367De	e12.8	e16.7	e16.0	e8.6	e3.5	e2.0
YEF2367Df	e18.5	na	e17.5	na	e5.0	na

dimensions = refer to text-figure 1.1

VIA = ventral interarea e = estimated na = not available

Description. The shell is small in size with its outline almost conical or pear shaped. The ventral valve is weakly to moderately convex with flattened beak and sharply pointed umbo. Sometimes a poorly defined sulcus is also developed. The ventral surface is lamellose or occasionally rugate. The ventral interarea is high but narrow, the height of which ranges between one thirds to half the shell length. It is trigonal in shape with small weakly raised pseudodeltidium. Ventral adductor muscle platform is moderately raised, narrow and triangular in shape.

The dorsal valve is sub-circular to semi-circular in outline, rather flat or moderately concave with slightly geniculated margin. The umbo is slightly raised above the shell plane. The dorsal surface is covered with strong lamellae and squamose rugae. The dorsal interarea is low with small chilidium.

Discussion. The limited number of specimens available and lack of completely preserved specimens do not support the nomination of a specific name or the designation of a new species to the material described above. Although these specimens were labelled in the BGS Museum as *C. lamellosa*, I have a suspicion that they might belong to a separate new species.

Craspedalosia sp. A differs from *H. morrisiana* found at the same locality in its rugate and squamose dorsal valve and its high ventral interarea. In general, the shape of *Craspedalosia* sp. A might fall within the range of *C. lamellosa* or *C. pulchella*, except for its smaller size as compared to the other two species. Compared to *C. lamellosa*, *Craspedalosia* sp. A has a higher interarea, while compared to *C. pulchella*, *Craspedalosia* sp. A has no cicatrix of attachment and no radial ribs on the dorsal valve. The absence of a ventral valve preserved with spines in *Craspedalosia* sp. A makes further comparison impossible. More material and some completely preserved specimens are needed before the material described above can be named with certainty.

HETERALOSIA? QUARRINGTONENSIS new species

(Text-figure 3.9D-F, Plate 7, figures 1-11).

Named after Quarrington Village in which type locality of the species is sited.

Diagnosis. Medium size productiform heteralosiinid with weakly to moderately convex ventral valve, distinct auricles and small pointed umbo. Sulcus and cicatrix of attachment are absent. Ventral surface smooth or lightly lamellose with rare clasping marginal spines and sub-erect body spines which are rather recumbent in younger individuals. Interarea very low on both valves with parallel outline and minute pseudodeltidium and chilidium. Dorsal valve weak to moderately concave with light to strong growth lamellae. Teeth small. Cardinal process small and short shafted with poorly developed alveolus. Lateral ridges prominent but short. Median septum short. Adductor muscle platform pear-shaped with radially striated scar.

Type specimens. Specimens no MSLOQQ3, MSLOQQ4, MSLOQQ5, MSLOQQ6 and MSLOQQ7 are chosen as a series of paratypes of *Heteralosia? quarringtonensis*, showing various morphological features of the species.

Type locality. Old Quarrington Quarry (GR. NZ 326381) is selected as the type locality of this species because the outcrop is extensive and the specimens are better preserved here. Specimens from Sherburn Hill Quarry are commonly found in a deformed state. Specimens from the type locality have been previously recorded as *Strophalosia morrisiana* by Smith & Francis (1970) and Pattison *et al.* (1981).

Other localities. Sherburn Hill Quarry (GR. NZ345417), East Thickley Quarry (GR. NZ 24082564) and ?Chourdon Point (GR. NZ 44254650).

Horizon. Raisby Formation.

Age. Upper Permian (EZ1).

Material. 43 specimens from Old Quarrington Quarry; 42 specimens from Sherburn Hill Quarry; 3 specimens from East Thickley Quarry and 1 specimen from Chourdon Point.

Description. The shell is small to medium in size with transversely elongated subtrapezoidal to sub-elliptical in outline. The shell is less than 20 mm in length but the maximum width varies from slightly wider than the shell length to more than 1.5 times the length. The maximum shell width is at the anterior half of the shell, normally very close to the mid-length.

The ventral valve is weakly to moderately convex without sulcus or cicatrix of

Table 3.13. *Heteralosia? quarringtonensis* **new species - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height
MSLOQQ3a	7.8	9.0	10.2	e7.7	e2.5
MSLOQQ3b	11.5	14.8	e16.0	e12.5	4.7
MSLOQQ4	9.1	13.0	12.4	10.0	3.5
MSLOQQ6	9.0	10.3	12.3	9.7	3.0
MSLOQQ7	8.2	9.8	11.6	9.2	3.2
MSLSHQ1	7.4	8.1	10.2	8.0	e1.0
MSLSHQ2	14.3	17.4	20.0	e16.0	e5.0
MSLSHQ	11.0	13.4	15.0	e13.2	5.2
MSLSHQ	6.6	7.2	8.2	e6.2	e1.0

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
e = estimated

attachment. The umbo is small, flattened and pointed or slightly overhanging and incurved. The auricle is flat and narrow, triangular in shape and it is better developed in the less convex specimens. The ventral interarea in very low but wide, almost parallel in outline with minute weakly raised pseudodeltidium. The ventral surface is weakly lamellose and distantly spinose. The spines consist of not more than three pairs of posteriorly directed marginal spines and about ten or lesser sub-erect body spines. The body spines in younger individuals seem to be more recumbent and adpressed in nature than in the adults. A pair of small teeth are observed from the internal mould of the ventral valve.

The dorsal valve is weakly to moderately concave with lightly lamellose surface which sometimes becomes squamose anteriorly. The umbo is very small and hardly lifted above the concave dorsal valve plane. The dorsal interarea is very low and wide with parallel outline and poorly developed chilidium.

Casts from the internal mould of the dorsal valve show that the cardinal process is short shafted with poorly developed alveolus at its posterior. The myophore is not well preserved. It is knob-like in appearance but probably was originally trilobed with the lateral lobes broken in the specimens available. The cardinal process is only buttressed by a pair of strong, but short lateral ridges. The median septum is low, appears between the muscle platforms, and extends to about the mid-length of the valve. The adductor muscle platform is small, low and pear-shaped with the scars radially striated. Other internal features are unknown.

Discussion. The lack of completely preserved specimens prevents the present author from making a complete description of this species, but distinctive characters shown by the available material distinguish them from any other heteralosiinid species. The productiform shape with very rare spines and the reduced interarea, cardinal process shaft, teeth and sockets and a more strongly lamellose dorsal valve exclude this species from all other Zechstein heteralosinid species and probably from all known heteralosiinids elsewhere. Although the external features of the species shows a close resemblance to the productellids, the presence of a cardinal process shaft and functional teeth and socket in this species prove that it belongs to the family Strophalosiidae. The absence of spines on the dorsal valve place this species in the subfamily Heteralosiinae and distinguished it from the strophalosiinids genus *Eostrophalosia.*

STROPHALOSIA? PARVA W. KING

(Plate 7, figures 9-10).

Synonymy;
1850 *Strophalosia parva* W. King, p. 102, pl. 12, fig. 33

Note. The following description and discussion is based on the syntype of *S. parva* (specimen no. D 319 of W. King's collection in the Department of Geology, University College of Galway) and several specimens of Kirkby's collection in the Hancock Museum, all of which were collected from the Humbleton Hill, near Sunderland. The author only managed to find a single specimen during recent research on this type locality. The following description is given because it has been discovered that W. King (1850)'s description is incorrect.

Material. The syntype as well as other specimens available for study are only represented by internal moulds of the cicatrix of attachment of the ventral valve with moulds of several clasping spines. Most of the specimens are attached to the interior of the ventral valve of *H. horrida*, and in all cases the shell of the host is not preserved.

Description. The size of the cicatrix of attachment is large with the length in the syntype reaches 4mm. The mould of the cicatrix of attachment is usually larger than its actual size because of its convex nature. The outline of the cicatrix varied from hemispherical to truncated sub-elliptical shape with straight posterior. The profile of the cicatrix of attachment is weakly convex with a rather flattened posterior. However, when the shell is cemented to the convex exterior ventral valve of the host, the cicatrix is weakly concave or flat in profile. The internal mould is provided with a pair of large teeth and a moderately raised adductor muscle platform which is divided anteriorly into two halves by a median furrow. From the elongation of the muscle platform, it can be interpretted that the cicatrix of attachment is asymmetrically placed on the beak.

The mould of the rim of the cicatrix of attachment shows that the unattached or free ventral valve is more convex than the cicatrix.

The spines are numerous and consist of creeping rhizoid spines that emerge from the matrix lateral and anterior to the cicatrix of attachment. These spines appear from the matrix at various angles, but follow the curvature of the host immediately upon reaching it. They spread out randomly over the host, sometimes crossing one another. Individually, the spines are small in size (0.4 - 0.5mm in diameter), but long and hair-like with the longest spine reaching a length of about 20mm. The posterior of the cicatrix of attachment is devoid of spines, but some of the body spines are sometimes posteriorly oriented. Other details are unknown.

Discussion. W. King (1850) gave the following diagnosis of *S. parva*; **Form irregularly circular marginally. Large valve somewhat convex; umbone very small and much impressed; spines numerous, long and closely packed; area small. Rarely exceeding a quarter of an inch in diameter.** In this diagnosis W. King thought that his specimen (the syntype) represented the complete ventral valve. Detailed study of the syntype clearly shows that the actual ventral valve is partly hidden underneath the matrix, and the shell exposed is in fact a mould of the complete cicatrix of attachment. As shown by the point and angle of emergence of the spines, the ventral valve must extend beneath the matrix for at least another length of the cicatrix. Most of the cicatrix of attachment is convex because it is attached to a concave surface of the interior ventral valve of *H. horrida.* The convexity of the cicatrix of attachment might have confused W. King (1850) into thinking that it was the true free ventral valve.

Lack of completely preserved specimens prevent the full description of *S?. parva* and the status of the genus of this species remains uncertain. However, the existing information might be a basis for further investigation of the species. The large teeth and numerous hair-like spines put this species into the genus *Strophalosia.* However, there is no known *Strophalosia* s. l. or other strophalosiinid which has such a large cicatrix of attachment. The cicatrix is even larger than that of *Heteralosia* (possibly *H. humbletonensis*) sharing the same host with the syntype of the species; this later specimen shows smaller teeth and fewer spines than *S?. parva.* Although the above features suggest that this species might belong to the genus *Strophalosia* (if so the name *S. parva* should prevail), the possibility that it might belong to another genus in subfamily Heteralosiinae cannot be denied since the details of the dorsal valve are still unknown. It is important that full details of the shell are seen before the taxonomic status of this species is confirmed.

Superfamily AULOSTEGACEA Cooper & Grant

Diagnosis. Productidina with no teeth and sockets, interarea confined to ventral valve with delthyrium commonly closed by elytridium and lophidium.

Discussion. The superfamily Aulostegacea was elevated by Cooper & Grant (1975a) from the family Aulostegidae which was previously placed under the superfamily Strophalosiacea by Muir-Wood & Cooper (1960). According to Cooper & Grant (1975a) the aulostegaceans were derived from the strophalosiaceans by reduction and elimination of teeth and sockets, modification of pseudodeltidium and elimination of chilidium, but retaining the ventral interarea with its delthyrium open or closed by an elytridium and a lophidium. Unfortunately, Cooper & Grant did not give any formal diagnosis for the new superfamily.

In 1988, Brunton and Mundy elaborated the description of the Superfamily Aulostegacea and suggested that the relationship of the aulostegids should be reviewed. A case could be made, in their opinion for many of the genera being considered as productaceans specialized for living on hard surfaces rather than as strophalosiaceans which have lost their teeth and sockets. It appears that some of the features used by Brunton & Mundy are variable, and therefore the above diagnosis is introduced to avoid any use of variable features and to fit in with the diagnoses of other productidinid superfamilies.

Cooper & Grant (1975a) listed at least eight families in this superfamily based on several features. Some of the features however, seem to be adaptational and not significant at the family level. For instance, the size and shape of the family Ageleslidae might be acquired for adaptation to special living conditions, while some of the features of internal morphology which they used to describe this family can be highly variable, as is often shown by other productidinids (i.e. see Fagerstrom & Boellstorff 1964, etc.). With limited material available, no attempt can be made here to reclassify the aulostegacean families, but it is strongly suggested that a single or few criteria be chosen more systematically for this purpose.

Howseia, which seems to fit well to the above definition of Aulostegacea, should therefore be excluded from other productidinid superfamilies and the lengthy comparison with *Horridonia* by many previous authors now seems to be irrelevant. Similarities between the two genera are rather superficial as compared to the details of the development of the interarea. Here, *Howseia* clearly differs from *Horridonia* in having an interarea on the ventral valve, while as a productacean, *Horridonia* has no interarea. Therefore, *Howseia* should not be considered as a variety or a stunted form of *Horridonia horrida.*

Family AULOSTEGIDAE Muir-Wood and Cooper

Discussion. Muir-Wood & Cooper (1960) identified the Aulostegidae as a progressive Strophalosiacea having lost teeth, sockets and chilidium; interarea on pedicle valve only; delthyrium closed by elytridium (formerly pseudodeltidium) and lophidium; shell attached by umbo and anchored by spines. Brachial valve interior with trilobate to quadrilobate cardinal process; alveolus present, adductor scars dendritic, accessory diductor scars on cardinal process shaft, brachial ridges given off horizontally.

Most of the diagnostic features above have been used by Cooper & Grant (1975a) to describe the superfamily Aulostegacea. Therefore a new diagnosis is needed to describe and distinguish the family Aulostegidae from other aulostegaceans. Owing to lack of time and material available for the present study, the author cannot fulfil this requirement and for this work the diagnosis of the family Aulostegidae and its subfamilies is taken from Muir-Wood & Cooper (1960).

Subfamily ECHINOSTEGINAE Muir-wood & Cooper

Diagnosis. Aulostegidae with spines on ventral valve only.

Discussion. Muir-wood & Cooper (1960) gathered in this sub-family eight genera including *Xenosteges*, a genus which according to them is very different from other aulostegids in its specialized attachment strategies and the lack of ornamentation, as well as the simplicity of the internal morphology. The genus *Howseia*, revised in this thesis closely resembles the genus *Xenosteges.* They both differ from other echinostegids in having a shorter interarea, less advanced cardinal process, low adductor muscle platform and less spinose and ornamented shell.

Genus *HOWSEIA* Logan 1963

Synonym;
1963 *Howseia* Logan, p. 758.

Diagnosis. Echinosteginae with ventral valve moderately convex, weak median sulcus and poorly developed auricle. Dorsal valve weakly concave and slightly geniculate. Hinge-line short. Interarea on ventral valve low, delthyrium covered by lophidium with or without elytridium. Ventral adductor muscle scar dendritic or radially grooved. Brachial ridges given off at variable angle to horizontal. Ventral valve with two to three rows of posteriorly directed rhizoid spines and a few erect body spines.

Type species. *Productus latirostratus* Howse, 1848, p. 256 (chosen by virtue of being published two days earlier than King's *Productus umbonillatus*)

Other species. *P. umbonillatus* King.

Discussion. An examination of more than 200 specimens of *Howseia* s.l. recently collected from various localities in Durham and augmented by museum material clearly shows that they are ontogenically divided into two separate groups. This makes the need to erect two species out of them undeniable. When divided, it appears that each of these two species to some extent agrees with the earliest description of *P. latirostratus* (Howse) and *P. umbonillatus* (King), respectively. The major differences between the two species occurs mainly in the posterior region where overgrowing of the umbo affected the whole configuration of both external and internal morphology of the shell as reviewed later in this chapter. Since each species has its own series of ontogenic stages, any possibility of ecotypic variation should be ruled out.

Logan (1963) questionably assigned the Russian species *P. litkei* Licharev to the genus *Howseia*, but from the description and figures given by Licharev and Einor (1939), it seems that *P. litkei* is quite different from any species of *Howseia*. *P. litkei* has strongly concave dorsal valve with very thin visceral cavity, weakly elevated adductor muscle platform on the ventral valve and very long hinge line equal to the maximum width of the shell. *P. litkei* develops about twenty furrows on its ventral valve while the largest individuals of *H. latirostrata* only has about six furrows on its trail. More importantly, *P. litkei* does not have an interarea.

Further details of the spines and the internal morphology of *P. litkei* have not been described, and therefore, cannot be compared with *Howseia*. However, significant differences outlined above indicate that *P. litkei* lacks any relationship with *Howseia*, and perhaps it is not even related to the aulostegaceans. Licharev and Einor (1937) pointed out that this species is **somewhat reminiscent of *Chonetes* in shape**, but later compared it with *P. latirostratus*. More detailed study of the original material is needed to enable it to be assigned to its correct genus rather than to *Howseia*.

Background history of the genus *Howseia* and its species. The history of uncertainty involving *Howseia* s.l. has persisted since the middle of the nineteenth century when both Richard Howse and William King claimed priority for the species described by them at about the same time. A description of *Productus latirostratus* Howse was published on 17 August 1848, two days before an account of *P. umbonillatus* King was published. Although both species were described without illustration, *P. latirostratus* Howse can be readily recognised by its large and very much flattened umbo, while *P. umbonillatus* King has an umbo which is small, pointed and not incurved. The problem arises because all the past authors recognised only one species from this group, i.e *Howseia* s.l. Confusion started when King (1850) included in his Monograph, a figure which illustrates *P. latirostratus* under his species *P. umbonillatus* (see King, 1850, pl. 10, fig. 14), and when Howse figured his species *P. latirostatus* for the first time in 1857 and claimed that his species had never been described before his 1848 work.

Considering that King's (1850) monograph was based on imperfect material which was not properly illustrated, Davidson (1858) accepted the priority of Howse's

P.latirostratus. Davidson also gave a better description of *P. latirostratus* with some good illustrations to support his opinion. Regardless of this redescription, later authors remained uncertain about the specific name they should use to describe *Howseia* s.l. Among those who used King's name *P. umbonillatus* are Quenstedt (1871), Malzahn (1937), Trechmann (1945), Hill (1950) and Gobbett (1961) while Geinitz (1861), Licharev and Einor (1939) and Logan (1963) accepted Howse's name *P. latirostratus* in their work. Branson (1948) used both specific names, but unfortunately he did not give his reasons of doing so.

Despite uncertainty regarding the specific name, the search for the true taxonomic position of *Howseia* s.l. progressively acheived its goal. It was King who initiated the search for an alternative generic name for this group. In 1850, W. King mentioned that *P. umbonillatus* is distinct from both *Strophalosia* and *P. horridus* Sowerby and possibly belongs to Helmerson's genus *Aulosteges*, but it was not until 1856 that he firmly included his species into the genus *Aulosteges.*

Malzahn (1937) concluded that there were insufficient grounds for separating *P. horridus* from *P. umbonillatus*, and thus he assigned the latter as a variety of *P. horridus.* Based on similarities between *P. umbonillatus* from the Shell Limestone (=Ford Formation) and *P. horridus*, Trechmann (1945) placed the former into the genus *Horridonia* Chao, a genus name which was later adopted by him for his *P. horridus.* However, in the same paragraph he mentioned that *P. umbonillatus* from East Thickley has a well defined ventral area and that it might belong to a different genus.

In 1950, Dorothy Hill grouped *P. umbonillatus* together with *A. horrescens* (de Verneuil) *A. fragilis* (Netschajew) and *A. longa* (Netschajew) into a possible subgenus of *Aulosteges* which according to her, is characterized by a thin-visceraed shell with a low, wide area divided by oblique lines from the umbo. Gobbett (1961) gave the same opinion as Malzahn in that *P. latirostratus (= P. umbonillatus)* is only a variaton of *H. horrida* which differs from other forms of the species in its smaller size, low convexity of the ventral valve and flattened umbo. He added that **it appears to be a stunted form which perhaps lived in a less favourable environment.**

After a comprehensive study of this group, Logan (1963) finally erected a new genus called *Howseia* with *P. latirostratus* as the type species and the Russian *P. litkei* Licharev as the only other possible species of the genus. Logan (1963) refuted W. King's work and stated that figures in King (1850) monograph were rather inaccurate and were obviously drawn from very scanty material (see Logan, 1963, p. 754). Logan (1963) also gave a full account of the background history of the genus as well as detail comparison with genus *Horridonia*, with which many previous authors had confused it. Logan however, was not certain on the higher taxonomic position of the genus *Howseia*, and tentatively placed it in the subfamily Echinosteginae Muir-Wood & Cooper despite significant differences highlighted by him between *Howseia* and other genera in the subfamily (see Logan, 1963,. p. 756-8).

Conclusion from literature studies and results of the present sudies.

Uncertainty regarding the status of the genus *Howseia* in the past, was mainly caused by failure of previous authors to recognise the presence of a true interarea in the group. Only Trechmann (1945) recognised this feature within his *P. umbonillatus* King from Thickley, but unfortunately I have failed to locate his specimens in any possible depository museums in Britain. Specimen no. GSM 72557 (BGS Museum collection) from this locality which was donated by Trechmann in 1945 under the name of *P. umbonillatus* has interareas on both valves and thus could not be an aulostegacean. It is likely to be the strophalosiacean *Heteralosia? quarringtonensis* n. sp. with the dorsal valve lightly lamellose and non-spinose. Current attempts to collect more material from this well known locality failed to discover any further specimens of *Howseia*.

The works by King (1850), Howse (1857 and 1858), Davidson (1858), and Logan (1963) lack a full explanation of the interarea. While studying internal moulds of specimen no. GSM 59737 (BGS Museum collection), described and figured by Howse (1857, 1858), Davidson (1858) and Logan (1963), and more than a hundred other internal moulds from various collections, I have recognised that a substantial amount of the body cavity, lies posterior to the cardinal process, where the hinge line should generally be positioned in productidinids. Therefore, the umbo of the ventral valve must extend a little posterior to the hinge line. Since this umbo is never incurved, a flat extension of the shell is formed dorsally to enclosed this extended body cavity. This dorsally developed posterior margin of the ventral valve unquestionably represents the interarea.

The interarea of the ventral valve generally meets the hinge sheet of the dorsal valve at a very accute angle to leave only a very narrow space between them, possibly to accommodate a kind of resilium between the two valves. Logan also figured specimen no. BB 51034 (BM(NH) collection) (see Logan, 1963, pl. 108, fig. 4b) which undoubtedly has a true interarea with the posterior body cavity narrowed laterally on the wing and the hinge sheet being separated from the interarea by inclusions of foreign material. Logan (1963, p. 756) interpreted this as **a thickened hinge margin which tends to resemble an interarea** and related this structure with the **ginglymus** structure which is commonly found in true productaceans. The hollow body cavity which is clearly visible near the umbo of the specimen figured by Logan (1963, pl. 108, fig. 4b), indicates that this part of the umbo was not formed by only one thickened hinge margin and it must have been enclosed by a true interarea. The other specimen (no. BB 51041, Logan (1963), pl. 108, Fig. 13), which he used to described the same feature is pathologically deformed and should not be used for describing features of high taxonomic value.

During this study, the author identified some common generic features which should be highlighted in order to gain a better understanding of the genus including;
i) The development of a triangular lophidium which extends posterior to the hinge line of the dorsal valve and over which the posteriorly directed diductor muscle groove passes (see text-figure 3.11C).
ii) The prescence of a low interarea on the ventral valve (very low in *H. latirostrata* (Howse)) almost parallel to the shell of the dorsal valve. The interarea has a triangular aperture to match the lophidium on the dorsal valve. The delthyrium is either covered posteriorly by the elythridium (in some *H. umbonillata* (King)- see text-figure 3.14B) or closed entirely by the lophidium.
iii) The lophidium is extended beyond the hinge axis, therefore to open the valves the lophidium should be inserted into the triangular aperture on the interarea of the

ventral valve (see text-figure 3.12B,C). The posterior extension of the shell beyond the lateral ridges is very thin and possibly rather flexible in nature, so that it can be pressed against the ?resilium in the same process.

iv) The presence of rhizoid auricular (not marginal) spines functioning as both clasping (during the younger stages) and attaching or cementing spines for the older stages (see text-figure 3.11A and 3.12A).

v) In detail, most internal features vary considerably between individuals and therefore are not significant for the taxonomic classification. However, the cardinal process is generally vertical to the shell plane with bilobed myophores, while the ventral adductor muscle scars are generally dendritic.

Some of the listed features above do not seem to fit the earlier diagnosis of the genus given by Logan (1963). Logan (1963) identified *Howseia* as a **productoid, without cardinal and body spines on concave dorsal valve; cardinal process bilobate with each lobed grooved and extending at right angle to to the plane of the valve; hinge-line sometimes angulated and shell margin at hinge thickened, simulating an interaea; no delthyrium or elytridium; dendritic adductor scars in ventral valve only; ventral valve moderately convex with sinus weak; two to three cardinal spines, body spines are rare.** New observations highlighted above show that the genus *Howseia* needs a new diagnosis, and this is given on page 115.

HOWSEIA LATIROSTRATA (Howse)

(Text-figure 3.11, 3.12 and 3.13, Plate 7, figures 14-16, Plate 8, figures 1-11).

synonymy;
1848 *Productus latirostratus* Howse, p. 256.
1850 *Productus umbonillatus* King; King, pl. 11, fig. 14.
1856 *Aulosteges umbonillatus* (King); King, pl. 12, fig 6.
1857 *Productus latirostratus* Howse; Howse, p. 46, pl. 4, fig. 1-2.
1858 *Productus latirostratus* Howse; Howse, p. 18, pl. 11, fig. 1-2.
1858 *Productus latirostratus* Howse; Davidson, p. 36, pl. 4, fig. 1-12.
1861 *Productus latirostratus* Howse; Geinitz, p. 102, pl. 19, fig. 7-10.
1871 *Productus latirostratus* Howse; Quendstedt, p. 640, pl. 60, fig. ?8.
1963 *Howseia latirostrata* (Howse); Logan, p. 758, pl. 108, fig. 1-14 (not 2and 7).

Diagnosis. Shell small to medium in size, subquadrate, tapering posteriorly with short umbo. Ventral valve moderately convex with weakly developed sulcus, dendritic adductor muscle scars and low interarea. Dorsal valve weakly concave with poorly defined median fold, striated adductor muscle scars and a small triangular lophidium. Cardinal process with bilobed myophore facing posteriorly; shaft of cardinal process perpendicular to the plane of the shell and buttressed by lateral ridges. Shell smooth with concentric growth lines. Sparse body spines and two to three rows of rhizoid auricular spines developed on the ventral valve.

Type specimen. The lectotype of the species was chosen by Logan (1963) from the original material (GSM 59737 - BGS Museum collection) illustrated by Howse (1857, pl. 4, fig. 1-2). Out of seventeen topotype specimens (Logan, 1963) from Howse's collection, now kept in Hancock Museum, only seven of them belong to *H. latirostrata* (Howse), thus validating them to be assigned as topotypes. The rest of the specimens belong to *H. umbonillata* (King)

Type locality. All the type material of *H. latirostrata* (Howse) mentioned above came from Dalton-le-Dale (Howse, 1848), thus this locality should be designated the type locality. The map reference of the type locality was not given by Howse (1848), but Dr. Denys Smith (personal communication) recommends the locality around NZ 408477 as the possible origin of Howse's type species. A new attempt to uncover the position of the type locality has produced some specimens of *H. umbonillata* (King) from the old quarry face at South Farm, about 60 meters south of the waterwork buildings (NZ 40884744) and this gives better evidence for recognising Howse's type locality.

Comments. Although the type species and the type locality have been chosen as described above, only the type species has been figured by the past authors from this original type locality. Most other figured material for the species came from the second locality mentioned by Howse (1848), i.e. Tunstall Hill, Sunderland (see Davidson, 1858, pl. 4, fig. 1-4 and 6-12), probably from below the Rock Cottage (NZ 392545), the locality from which much of the current collection came.

Material. The following description covers a total of more than 200 specimens from various collections, including: The BGS Museum collection; specimens no. GSM 59737 from Dalton-le-Dale, GSM 10623-4 from Tunstall Hill and YGF 2460 from Hylton Castle: The BM(NH) collection; specimens no. B 13797 and 13830 from Tunstall Hill, B 13798 from Dalton-le-Dale and BB 51035-41 from Hylton Castle: The Hancock Museum collection; specimens no. G 86.57, G 86.64 and G 86.71 from Tunstall Hill and G 88.53 and some unnumbered specimens from Dalton-le-Dale: The University College of Galway (King's) collection; specimens no. D 184A,C,D from Tunstall Hill; The Tyne and Wear Museum and Art Gallery collection; specimens no. B 1902 from Tunstall Hill and B 1903 from Gilleylaw.

Also studied are 82 specimens from Gilleylaw builders trench (NZ 397539) in Dr. Johnson's collection; and from my own collection there are 5 specimens from Hylton Castle road cut (NZ 360589), 80 specimens from Rock Cottage, Tunstall Hill (NZ 392545) and 35 specimens recorded for the first time from Beacon Hill railway cut.

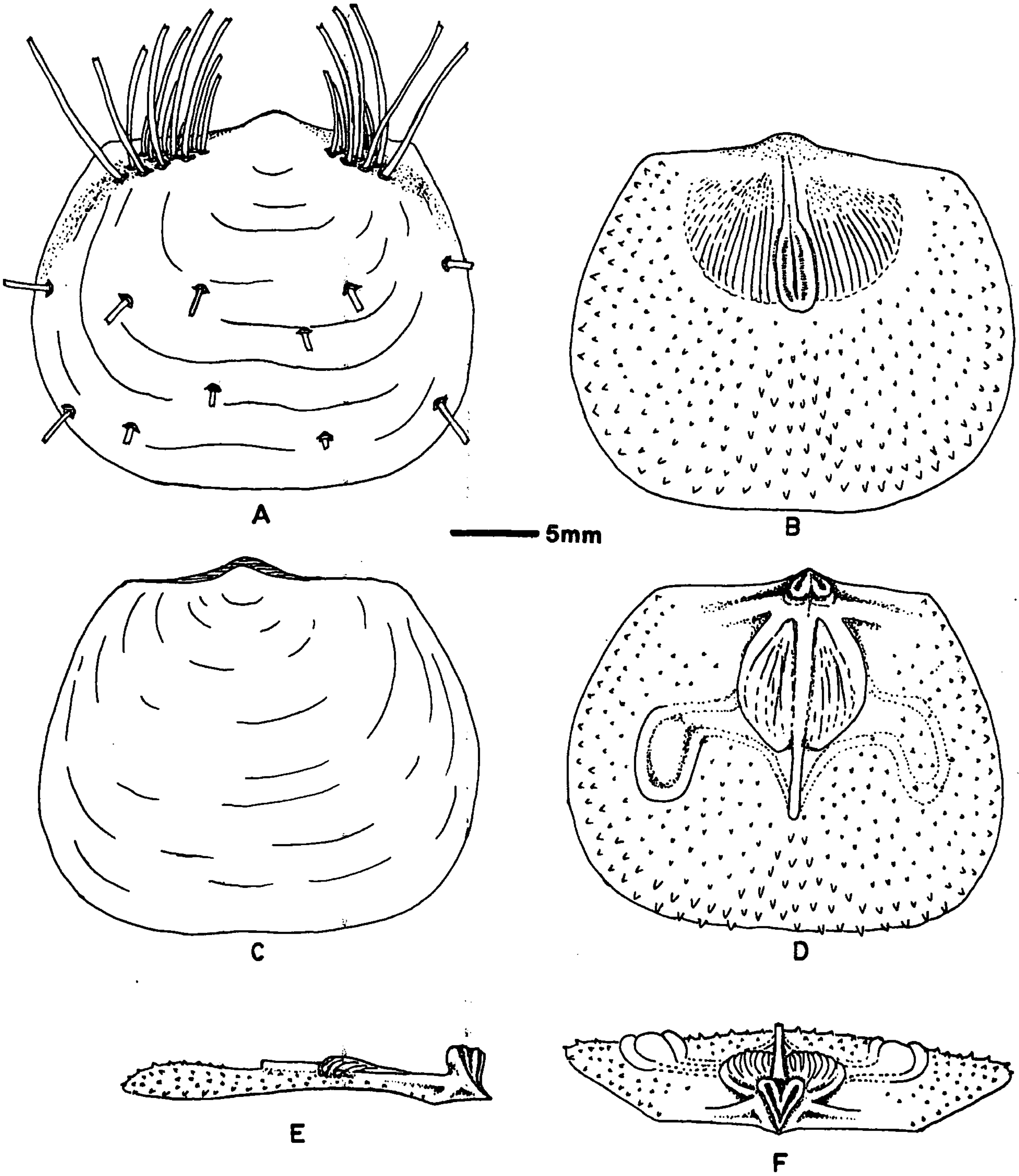
15 specimens from Poessneck, East Germany on loan from the BM(NH) (specimens no. 73160 and 73292) and Hancock Museum (specimens no. G 85.40, G 85.62 and G 85.69) are also included in this study.

Horizon. Ford Formation.

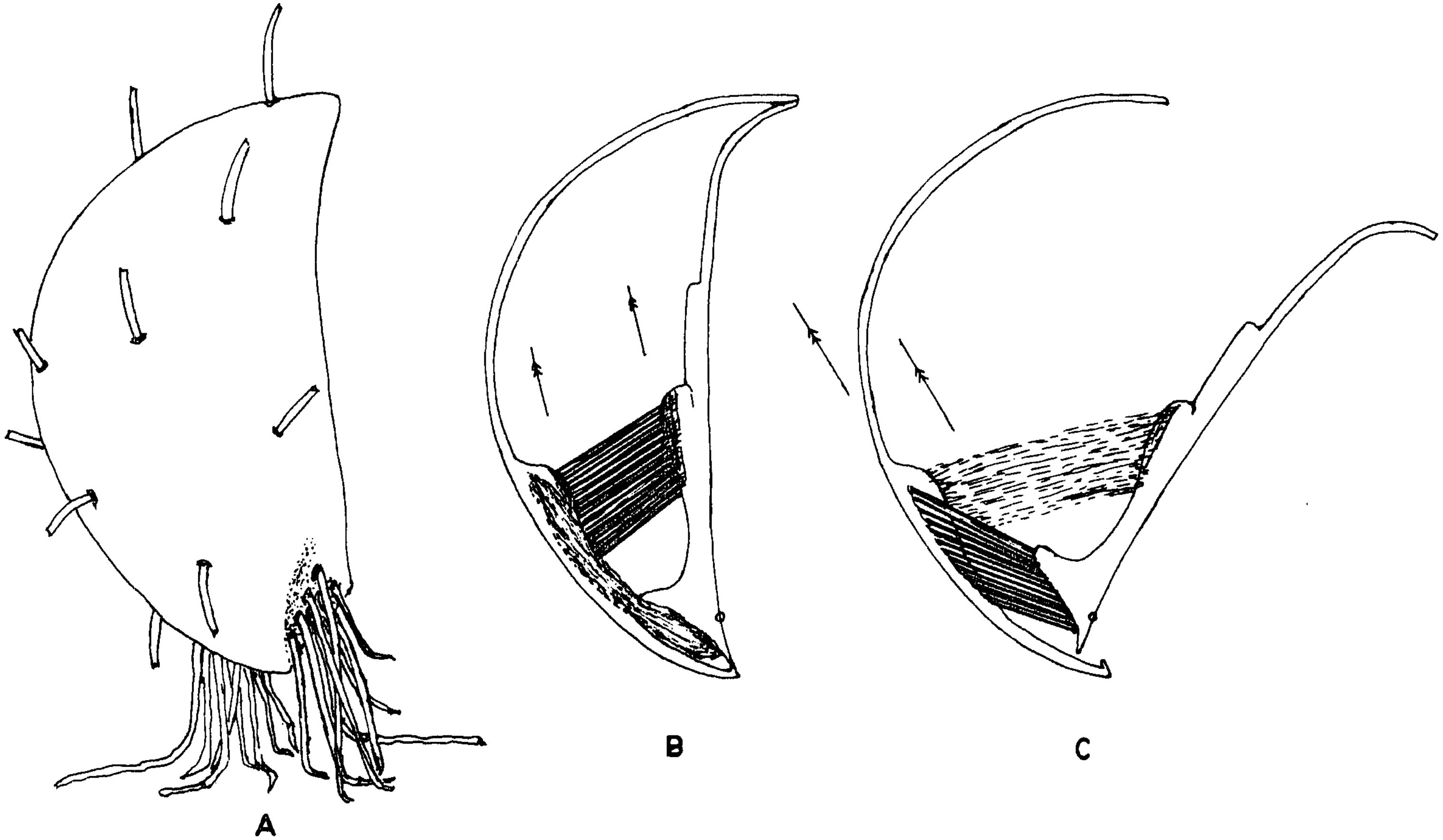
Age: Upper Permian (EZ1).

Description. The shell is small to medium in size, concavo-convex to plano-convex in profile with a narrow visceral cavity. The plan outline of the shell is slightly asymmetrically subquadrate with the lateral margin tapering slightly posteriorly. The shell length is slightly shorter than the maximum shell width which is acquired at the posterior quarter of the shell.

The ventral valve is moderately convex with the highest convexity at about the mid-length. The median sulcus only forms a shallow depression from about the mid-length anteriorward. The posterior margin only obtusely angulated. The beak is flattened or weakly inflated, extends slightly beyond the cardinal extremity, but does



Text-figure 3.11. Reconstruction of *Howseia latirostrata* (Howse).
A,B - Exterior and interior of ventral valve. C - Exterior of dorsal valve. D,E,F - Interior of dorsal valve; plan, lateral and posterior views.



Text-figure 3.12. *Howseia latirostrata*; A - Attachment by auricular spines; B - C - articulation mechanism.

Table 3.14. *Howseia latirostrata* **(Howse) - dimensions in mm.**

Specimen number	length	curved length	max. width	hinge width	height	thickness
MSLTH12	12.9	14.6	17.0	e13.4	3.7	na
MSLTH13	15.6	20.1	18.8	13.9	5.2	na
G88.57a	18.5	24.9	22.4	18.8	e8.7	6.0
G88.57b	19.0	31.2	e24.0	e19.1	11.6	na
MSLTH20	20.3	30.5	24.9	e20.5	9.8	5.3
MSLTH14	22.2	31.4	28.0	e21.8	10.3	na
MSLTH15	22.7	37.3	28.4	24.3	11.3	na
G88.57c	29.7	49.8	39.8	e32.0	19.6	na

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix (G88.57 = Hancock Museum coll.)
e = estimated na = not available

not overhang. The tip of the umbo normally points towards the shorter hinge line. The hinge line is slightly shorter than the maximum shell width, asymmetrical in length and interrupted medianly. Auricular expansions are formed by very thin shell laminae beyond the spinose edges of the shell. The interarea is very low with no elythridium, but with a small triangular aperture for recieving the tiny lophidium of the dorsal valve.

Interior of the ventral valve is covered with fine marginally pointed endospines, which become coarser towards the periphery of the shell. The adductor muscle platform is moderately to highly elevated with smooth or dendritic muscle field, divided into two elongated lobes by a median furrow. The muscle platform extends almost to the mid shell length anteriorly, while posteriorly it is preceeded by a low ridge of an aborted younger muscle platform. On each sides of the adductor muscle platform are the fan shaped, flat and radially striated diductor muscle impressions.

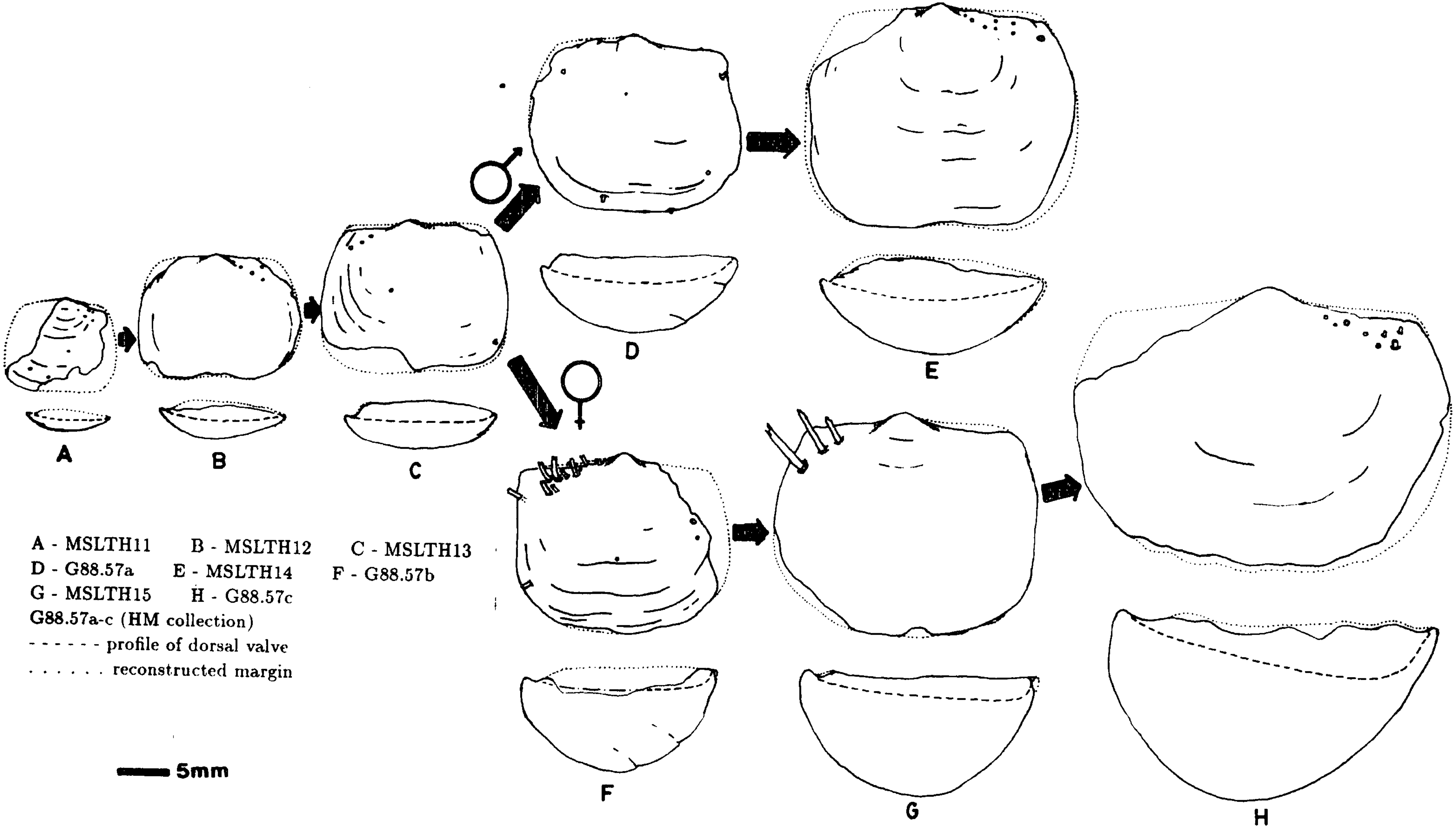
The exterior of the ventral valve is smooth apart from some concentric growth lamellae (very seldom rugate) and some sparsely distributed body spines and auricular spines. The body spines are erect and irregularly distributed. The auricular spines are made of two to three rows of not more than six rhizoid, posteriorly directed spines which are sometimes concentrically arranged or without particular arrangement. The spines are small (about 0.7mm in diameter), long (30mm or more) and hollow throughout.

The dorsal valve is slightly concave to flat in profile with poorly developed median fold and slightly geniculated margin. The posterior margin is straight or broadly angulated with small triangular lophidium developed medianly.

The interior of the dorsal valve is provided with a long shafted cardinal process which stands perpendicular to the plane of the shell. The myophore is bilobed with a deeply grooved diductor muscle attachment base on each lobe. Each lobe converges towards the plane of the shell to form a roughly triangular facet (button of Howse 1848, 1857 and 1858) with its sharp pointed tip bending almost at a right angles posteriorly. The cardinal process is buttressed by a pair of lateral ridges as well as the median ridge and a pair of accessory ridges which form the postero-lateral boundary for the muscle platform. The lateral ridges are highly elevated and narrow medially, flatter and broader laterally where they are flanged by thin hinge sheets which make the the posterior margin a straight line laterally. Medially, the posterior margin is interrupted by the development of a triangular lophidium.

The adductor muscle platform is pear-shaped with moderately elevated postero-lateral boundary and slightly lower muscle field which is furnished with striated muscle impressions. Medianly, the adductor muscle platform is divided into two halves by a low median furrow in which lies the median septum. The median septum extends anteriorly to about two-thirds of the shell length. The brachial ridges form a wide loop on each side of the visceral cavity, slightly closer to the lateral margin than to the median septum. The posterior point of origin of the brachial ridges varies from the edge of the muscle platform boundary ridges to the anterior end of the muscle platform, while the anterior pair run anterior to the muscle platform and unite medially near the extremity of the median septum.

The exterior of the dorsal valve is ornamented by several concentric growth lamellae which are weakly folded medially.



Text-figure 3.13. Ontogenic development of *Howseia latirostrata* from Tunstall Hill rock cottage.

A - H - Camera lucida reproduction of the listed specimens showing plan and lateral views (with profile of dorsal valve).

Ontogeny. The juveniles of *H. latirostrata* are generally flatter than the adults, with the convexity of the ventral valve and the size of the mantle cavity minimum at this stage. During its ontogeny, *H. latirostrata* develops sexual dimorphism. The male dimorph generally continues the growth trend of the juveniles, with slight increase in the convexity of the ventral valve and a little overgrowth of the umbo in the posterior region which sometimes exposes a very low interarea medianly. The female dimorph can only be recognised at the middle growth stages of the individual. It differs from the male form in its more convex ventral valve caused by enlargement of the visceral cavity, probably following the development of the ovary, brood pouch and related organs (Ferguson, 1969). As the convexity of the ventral valve increases the beak becomes more inflated and its posterior projection becomes less significant, thus the female form rarely exposes an interarea. To fit the non-pointed umbo, the cardinal process does not project strongly to the posterior, but instead grows vertically, restricting the development of the lophidium. Similarly, due to the increase in the convexity of the ventral valve, the dorsal valve becomes strongly geniculated to form a trail which gradually develops shallow furrows as the individual grows. Text-figure 3.13 illustrates well some of the changes during ontogeny of *H. latirostrata.*

Discussion. It is probably a female form of *H. latirostrata* which Trechmann (1945) considered very similar to *Horridonia horrida* Sowerby and led him to assume that there was convergence or mimicry between them.

Pathological effect. *H.latirostrata* commonly shows stunted development of the shell margin caused by predatory activity. This common injury among the species might have resulted from the absence of protecting spines on the dorsal valve, contrary to most other productidinids that live within the same ecological niche. Predatory attack often causes irregularities in the shape of the individual in this species. When this pathological effect occurs at the posterior region, the umbo usually becomes rather more strongly pointed. Posteriorly injured specimens of *H. latirostrata*, are therefore, difficult to be distinguished from *H. umbonillata* which is characterised by its strongly pointed umbo.

Besides the predatory marks, *H. latirostrata* also commonly shows occassional thickening of the growth lines. This phenomenon is caused by the occasional paucity of the shell growth which might be related with differential supply of calcium carbonate due to the high and low tide (Clark, 1974, Norton, 1988). This indicates that *H. latirostrata* must have been living in a relatively shallow water condition.

Related species. *H. umbonillata* (King) differs from *H. latirostrata* in having a narrower shell with shorter hinge line, narrower, but more pointed and overhanging umbo. The interarea of *H. umbonillata* is higher than that of *H. latirostrata* with the delthyrium sometimes partly covered by the elythridium posteriorly. The lophidium of *H. umbonillata* is larger than that of *H. latirostrata.* The two species are, however, similar in having a smooth dorsal valve and ventral valve with scattered body spines and two to three rows of rhizoid auricular spines. The general configuration of cardinal process, muscle scars and brachial ridges is very similar in these two species.

HOWSEIA UMBONILLATA (King)

(Text-figure 3.14, 3.15, Plate 8, figure 12-25).

synonymy;
1848 *Productus umbonillatus* King, p. 8.
1850 *Productus umbonillatus* King; King, pl. 11, fig. 14.
1854 *Productus umbonillatus* King; Schauroth, pl. 1, fig. 9-10.
1871 *Productus umbonillatus* King; Quenstedt, p. 640, pl. 60, fig. 8.
1937 *Productus horridus* var. *umbonillatus* (King); Malzahn, p. 34.
1963 *Howseia latirostrata* (Howse); Logan, pl. 108, fig. 2.

Diagnosis. Small, subquadrate to subtriangular *Howseia* with narrow, strongly pointed and overhanging umbo. Ventral valve moderately convex with faint median sulcus and high interarea. Delthyrium covered with elythridium posteriorly, open anteriorly. Ventral surface moderate to strongly lamellose, with few body spines and two to three rows of auricular spines. Dorsal valve weakly concave with large lophidium. Cardinal process low, but strongly extended posteriorly. Lateral ridges and brachial ridges usually oblique to growth axis.

Type specimens. Pattison (1977, p 38) selected all four of King's specimens in the University College of Galway collection (specimens no. D 184A-D) as syntypes of *P. umbonillatus* King (1848), which he renamed as *H. latirostrata* (Howse). Among these specimens, only specimen no D 184B (see King, 1850, pl. 11, fig. 15-18) and Logan (1963, pl. 108, fig. 2) belongs to *H. umbonillata* (King), while the remaining specimens belong to *H. latirostrata* (Howse). Therefore, specimen no. D 184B should be elected as the holotype of the species.

Type locality. The holotype of *H. umbonillatus* mentioned above, came from Tunstall Hill. Pattison (1977), suggested that King's collection from Tunstall Hill probably came from a large area with quarries and natural exposures, mostly from arround NZ 392545. Recent collecting work around Tunstall Hill produce a few specimens of *H. umbonillata* from an excavation site below the Rock Cottage (NZ 392544).

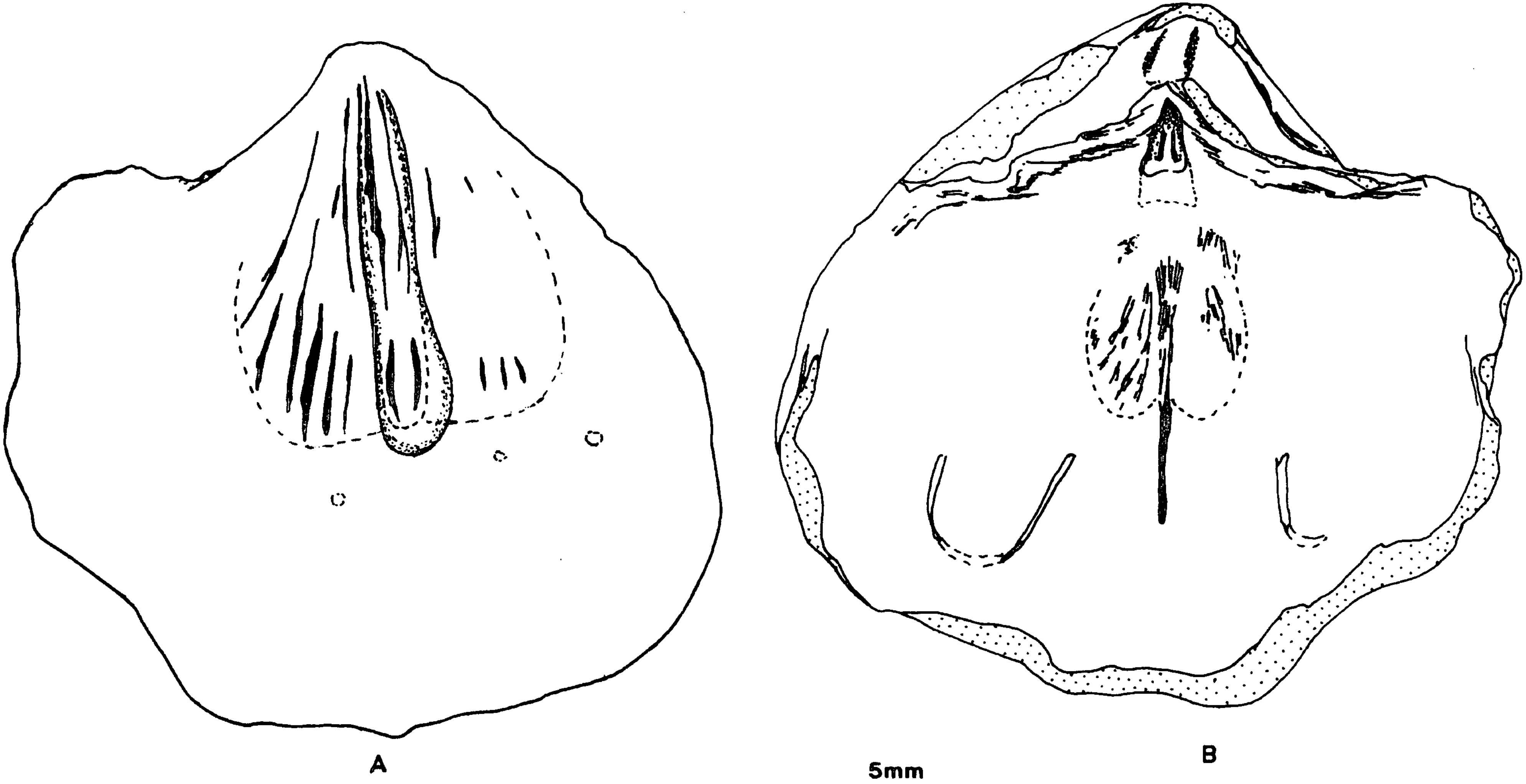
Material. The following description is based on about 80 studied specimens, including the holotype from Tunstall Hill (specimen no. D184B in University College of Galway collection), 36 specimens in Dr. Johnson's collection from Gilleylaw builders trench (NZ 379539), and in the author's collection are 12 specimens from the type locality, 7 specimens from Hylton Castle road cut (NZ 360589) and 5 specimens from Dalton-le-Dale (NZ 40884474). Also studied are several specimens in Hancock Museum collection from the type locality, Hylton Castle and Dalton-le-Dale (including specimen no G 88.53), and several specimens in BM(NH) collection from Hylton Castle and Dalton-le-Dale.

Horizon. ?Raisby Formation (Trechmann, 1945) to Ford Formation.

Age. Upper Permian (EZ1).

Description. The species is similar to that of *H. latirostrata* (Howse), except for the following details;

The plan outline of the shell ranges from subquadrate to subtriangular and it is almost always asymmetrical. The shell length is more or less equal to the maximum width which is normally acquired at the anteriormost part of the shell, but some



Text-figure 3.14 Camera lucida reproduction of the holotype of *Howseia umbonillata* (King); specimen no D184B (UCG collection).

A - ventral view. B - dorsal view *[rock matrix is dotted; - - - - - reconstructed outline of various internal morphology]*.

Table 3.15. *Howseia umbonillata* (King) - dimensions in mm.

Specimen number	length	curved length	max. width	hinge width	height	thickness	height VIA
MSLTH25	e9.0	na	e8.0	e7.3	e2.2	na	na
GALJ1	10.3	11.8	8.3	6.4	e3.2	2.4	e1.5
GALJ2	15.5	16.6	13.5	e9.9	4.2	na	na
GALJ3	e17.9	22.1	16.8	e13.5	e6.7	5.0	e2.4
MSLTH23	20.8	33.2	23.4	e20.2	e12.6	na	na
MSLTH24	21.3	25.5	23.0	e19.0	e5.7	na	na
GALJ5	e21.9	e33.2	e23.0	e19.5	e10.7	e8.9	e5.1
GALJ4	e22.5	e29.7	e22.8	e17.7	e9.1	e6.4	e4.6
GALJ6	e26.6	e45.0	e29.5	e23.8	e13.7	e9.8	e4.0

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
VIA =ventral interarea na = not available e = estimated

elongated forms show a greater length compared to the maximum width.

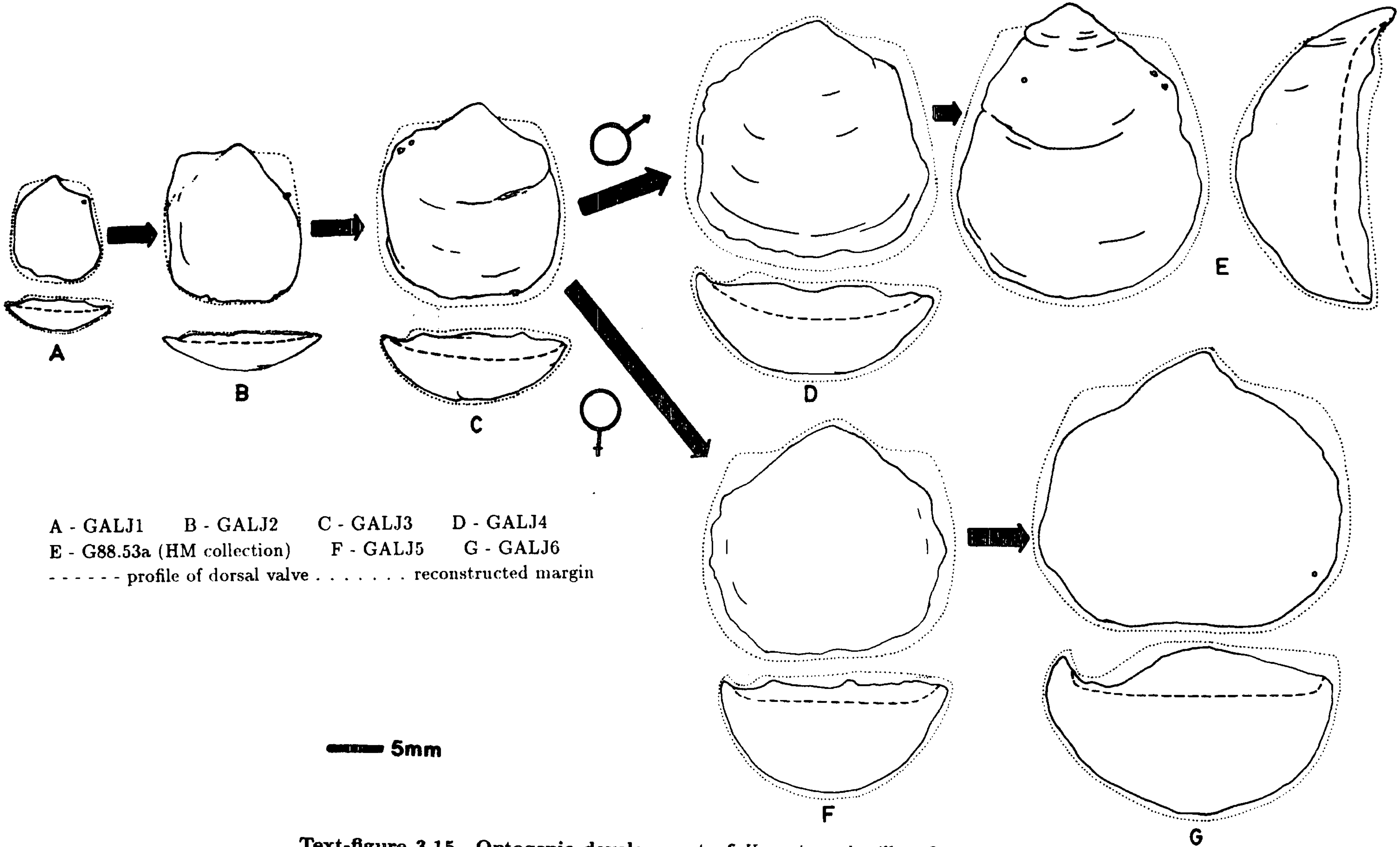
The ventral valve is moderately to strongly convex in profile with faint median sulcus developed anteriorly. In some of the juveniles and the male dimorphs, the sulcus is imperceptible. The posterior margin is asymmetrical with poorly developed auricle. The hinge line is about two thirds the length of the maximum width, with each side inequal in length. The beak is narrow, but long. It is strongly pointed and overhanging posterior to the hinge line. Usually the tip of the umbo twists and points toward the shorter half of the hinge line. The interarea is high, sometimes attaining a height of up to one fifth of the shell length. The delthyrium is provided with a large triangular aperture anteriorly and covered by a weakly raised triangular elytridium.

The interior of the ventral valve shows a moderate to highly elevated, smooth or dendritic adductor muscle platform surrounded by low radially striated diductor muscle field. The exterior of the ventral valve is moderately to strongly lamellose, often rugate. The true nature of the spines is unknown, but two to three rows of up to six spine bases are seen on the auricle, while the body spine bases are sparse and randomly distributed.

The dorsal valve is slightly concave in profile with poorly defined median fold and auricle. The posterior margin is provided by a large triangular lophidium. The interior morphology of the dorsal valve shows great variation between the male and female dimorphs, as shown in the remarks on the ontogeny below.

Remarks on the ontogeny (see text-figure 3.15). Similar to *H. latirostrata* the juveniles of *H. umbonillata* seems to be flatter than the adults. The juveniles of *H. umbonillata* differ from those of *H. latirostrata* in their more elongated shell and pointed umbo. These features are retained by the male adults with gradual curving of the umbo during growth. Changes during early maturity of *H. umbonillata* apparently produced very distinct dimorphs, and the male and female forms are characterised as follows;

The beak is gently curved in male forms and strongly curved in female forms. The cardinal process in male dimorphs is narrower, with lower shaft and longer posterior extension than it is in female forms. The lateral ridges are better developed in female forms than in male forms. They are developed at a right angle to the shell growth axis in female dimorphs, while in male dimorphs the lateral ridges are obliquely developed, sometimes making an angle of up to 60^o to the growth axis. The adductor muscle platform is normally wider in female forms, and slightly expanded longitudinally in the male forms. The brachial impressions of male forms also appear to be longitudinally expanded, where the brachial ridges are not given-off horizontally as they are in female forms.



A - GALJ1 B - GALJ2 C - GALJ3 D - GALJ4
E - G88.53a (HM collection) F - GALJ5 G - GALJ6
- - - - - - profile of dorsal valve . . . . reconstructed margin

Text-figure 3.15. Ontogenic development of *Howseia umbonillata* from Gilleylaw builders trench, except figure E which came from Dalton-le-Dale.
A - G - Camera lucida reproduction of plan and lateral view (with profile of ventral valve) of the listed specimens.

Superfamily PRODUCTACEA Gray

Amended diagnosis. Productidina with no interarea and no true teeth and sockets. Hinge operated by linear interlocking of the hinge margins.

Discussion. The above diagnosis is introduced for the superfamily Productacea in order to simplify the earlier diagnosis given by Muir-Wood & Cooper in 1960. Muir-Wood & Cooper (1960) stated that Productacea is **"Productoidea generally fixed by ringlike attachment spines in early growth stages and rarely cemented by beak, living free in adult stages supported by halteroid spines; interareas, teeth and sockets are normally absent but weakly developed in primitive forms; ginglymus in gerontic stages only; cardinal process of several types, bilobate or trilobate, rarely quadrilobate; diaphragm in brachial valve and crenulated marginal ridges in one or both valves in some genera".** This diagnosis appears to be ambiguous and not always applicable for distinguishing productaceans from other productidinids. For instance, the productacean mode of living varies from one species to another and the same modes of life are also observed in other productidinid superfamilies. It is important to consider ecological factors before conclusions are made on the mode of life of any productidinid. Similarly, as indicated in the original diagnosis, the cardinal process is very variable, and similar types of cardinal process occur in other productidinid superfamilies.

From the current investigation, the cardinal process seems to be relatively more sessile in Productacea than it is in Aulostegacea or Strophalosiacea, though there are exceptions. Likewise, Productacea generally tend to adopt a free mode of life, but exception is needed for those genera which fixed themselve to the substrate during most of their lives. Therefore, in my view, these generalised statements should not be used as diagnostic features of any superfamily of Productidina. Further, the diaphragm and marginal ridges are present in certain productacean families only, and therefore employing these criteria in the diagnosis of the superfamily is inappropriate.

Regarding the interarea, it has been stressed earlier about the importance of the presence of interarea, whether in ventral valve only or in both ventral and dorsal valves or absent in both valves. Therefore, suborder Productidina should be sub-divided on this basis, and the superfamily Productacea should be restricted to productidinid with no interarea and no true teeth and sockets. Muir-Wood & Cooper's (1960) interarea bearing productaceans should be placed in their appropriate superfamily based on the nature of the interarea. The family Productellidae and some members of the family Gigantoproductidae with interareas on both the ventral and dorsal valves should now be placed into the superfamily Strophalosiacea, while some members of the family Institidae, which develop the interarea only on the ventral valve should be regarded as aulostegaceans.

Table 3.16. Various criteria used by Muir-Wood & Cooper (1960) in subdividing the Superfamily Productacea.

Family	C.P.	B.R.	Add.	S.O.	Shape	Size	Diaph.	M.R.	I.A.
Productellidae	x		x						x
Institidae	x	x	x	x		x			x
Leioproductidae	x	x							
Overtonidae	x	x		x					
Marginiferidae	x			x				x	
Productidae	x		x			x	x		
Echinoconchidae	x				x				
Buxtoniidae	x			x					
Dictyoclostidae	x	x	x	x	x				
Linoproductidae	x		x	x	x				
Gigantoproductidae	x		x	x	x	x			x

C.P = cardinal process; B.R = brachial ridges; Add = Adductor; S.O = surface ornamentation; Diaph = diaphragm; M.R = marginal ridges; I.A = interarea.

Muir-Wood & Cooper (1960) listed and described eleven families in the superfamily Productacea, including strophalosiacean Productellidae and many new families based on various criteria. Unfortunately, none of their criteria were used consistently in their scheme of classification, except the cardinal process. The superfamily Productacea is divided by Muir-Wood & Cooper (1960) into Productellidae (now a strophalosiacean), Institidae (partly aulostegacean), Leioproductidae, Overtonidae, Marginiferidae, Productidae, Echinoconchidae, Buxtoniidae, Dictyoclostidae, Linoproductidae and Gigantoproductidae (partly strophalosiacean). The following table gives a full list of criteria used by Muir-Wood & Cooper (1960) for the diagnosis of their productacean families. It shows how inconsistent the used of these criteria were in acquiring the above sub-division.

Although the sub-division of the Productacea into families is unsatisfactory, limited time and material available during the current study has not allowed the author to proceed further on this matter. However, a major revision of the taxonomic classification of this large and problematic superfamily is required in the future, in order to gain a true understanding of its families and subfamilies.

From the British Permian, only one species of Productacea has been documented previously. This species is *Horridonia horrida* (Sowerby) from the subfamily Horridoniinae which is tentatively placed by Muir-Wood & Cooper into the family Dictyoclostidae. Current study, however, shows that *H. horrida* from the British Permian is made of several separate species of *Horridonia*, while a new genus *Spinohorridonia* is described from the area of study for the first time.

Family DICTYOCLOSTIDAE Stehli

Diagnosis. Usually strongly geniculated Productacea having reticulate visceral region, long trail, and brachial valve with sessile or short shafted strongly trilobed cardinal process, having large median lobe; adductor dendritic; brachial ridges given off horizontally.

Discussion. The above diagnosis is taken from Muir-Wood & Cooper (1960) without amendment. Limited time and material available prevented the author from elaborating or commenting in great detail about this diagnosis. Most of the criteria used are very variable and difficult and impractical to use to establish the family. However, until a better alternative is available, the family status of Dictyoclostidae and its sub-division, as introduced by Muir-Wood & Cooper (1960) will be maintained, but the diagnosis of the subfamily Horridoniinae must be amended as follows.

Subfamily HORRIDONIINAE Muir-Wood & Cooper

Amended diagnosis. Dictyoclostidae with no reticulate ornament on the visceral disc, often smooth or with weakly developed costae and rugae.

Type genus. *Horridonia* Chao (1927).

Other genera. *Sowerbina* Fredericks (1928), *Bailliena* Nelson & Johnson (1968) and *Spinohorridonia* new genus.

Discussion. Muir-Wood & Cooper (1960) introduced the subfamily Horridoniinae as **Dictyoclostidae mostly with smooth surface; pedicle valve with posterior spine rows and few scattered spines; brachial valve with large halteroid spines along posterior margin and ears; adductor dendritic.** With the large new collection of specimens from the Durham Permian and more information about horridoniinids currently available, some of these features have proved to be no longer reliable for the identification of the subfamily. The posterior spine rows, for instance, are not always present on both valves; in some species they are only found on the ventral valve while the same valve of other species are completely devoid of marginal spines. Similarly, the adductor has been found to be non-dendritic in some individuals of *Horridonia horrida*, a species which is known to develop a dendritic adductor. Therefore, the diagnosis of the subfamily Horridoniinae should be amended as above to avoid confusion.

The Horridoniinae was erected by Muir-Wood & Cooper (1960) as a mono-generic subfamily, with the sole genus recognised by these authors was *Horridonia* Chao. *Sowerbina* Fredericks and *Pleurohorridonia* Dunbar were considered by them as synonyms of *Horridonia.* Owing to poor description and illustration of *Horridonia horrida* (Sowerby) and related forms, the taxa at the generic level becomes uncertain. Therefore, to solve this problem, the background history of the development of *H. horrida* and related genera, must be studied.

It is important to note that only the external features will be employed to divide different genera of Horridoniinae. Needless to say, the internals of productaceans have often proved to be inconsistent from one individual to another. Such is the case with the *H. horrida* of the Durham Permian, where the cardinal process varies from bilobate to quadrilobate, and the adductor varies from dendritic to radially grooved. The extension of the median septum and the configuration of the brachial ridges are also individual rather than a specific or generic criteria. Regarding the external features, some are apparently more valuable taxonomically than the others. As discussed earlier in Strophalosiidae, the distribution of spines should be considered very important genetically and therefore, should be highly regarded in classifying the subfamily Horridoniinae.

Background history of *Horridonia horrida* and related forms. *Horridonia horrida* was first introduced as *Productus horridus* by Sowerby in 1823 although similar forms had been previously attributed to other names by various authors. As with most other early determinations, Sowerby's species has been subjected to prolonged discussion and changes. Similar to other early publications, it is either the wrong or insufficient description or the lack of sufficient supporting figures that contribute to the misunderstanding among the later authors. In Sowerby's (1823) paper, although he described *P. horridus* as having marginal and body spines on both the ventral and dorsal valves, his figures of the type specimen which came from the Cadeby Formation in Derbyshire clearly shows the lack of body spines on the dorsal valve. The absence of body spines is indeed very consistent among the British *Horridonia*, but unfortunately none of the later authors except Davidson (1858) give any note about it. Forms with a spinose visceral part of the dorsal valve are very rare in the British Permian, but they are quite often found in the East European Permian. Further discussion about these forms will be given later in this chapter.

Meanwhile, de Koninck (1846 and 1847) described *P. horridus* with body spines on the dorsal valve from the East European Zechstein. At the same time he also introduced *P. geinitzianus*, a species with a rather heavy spines on both valves but retaining some features of *P. horridus.* This species was accepted by King (1856) and Geinitz (1861), but was later considered by Eisel (1909), Malzahn (1937) and Gobbett (1961) to be one of the many varieties of *P. horridus* introduced by Eisel in 1909. In Geinitz's (1848 and 1861) papers on *P. horridus*, he also figured two different forms with body spines on the dorsal valve, which were later named by Eisel (1909) as *P.*

horridus var. *laspeanus* and *P. horridus* var. *geranus.*

In Britain, W. King and R. Howse both described *P. horridus* in a very similar way to Sowerby (1823), i.e. with marginal and body spines in both the ventral and dorsal valves, see King (1850) and Howse (1848, 1857 and 1858). However, none of King's (1850) figures show any sign of body spines on the dorsal valve. About the spines distribution, Davidson (1858, p. 34) mentioned that **on the dorsal valve they are confined to the vicinity of the cardinal edge where they assume much regularity in both valves, from being arranged in one or two rows in the proximity of the hinge line**, and illustrated well his *P. horridus* with body spines present on the ventral valve only.

In 1858, Haughton described *P. sulcatus* var. *borealis* based on two specimens, one of which belongs to the true *H. horrida* and the other one is a species of *Liosotella* (see Gobbett (1961)). Haughton's invalid name has unfortunately became a subject of confusion among later authors including Stepanov (1936, 1937) and Licharev & Einor (1939).

In 1875, Stuckenberg described *P. timanicus* from the Timan Tundra, the form of which differs from Sowerby's (1823) *P. horridus* only in detail of ornamentation and the shape of the shell. Later in the same year, Toula described *P. horridus* var. *granuliferus* from Spitzbergen, a form with no marginal or auricular spines on the ventral valve while the dorsal valve is devoid of body spines. Unfortunately, subsequent authors failed to realise the differences between the two species from Timan and Spitzbergen. Thus, assuming that Toula's *P. granuliferus* is similar to Stuckenberg's *P. timanicus*, authors like Wiman (1914), Frebold (1931a), Dunbar (1955) and Gobbett (1961 and 1963) described their species under Stuckenberg's name *P. timanicus.* Interestingly, as revealed later by Logan (1966) all those authors mentioned above were actually describing Toula's species as *P. timanicus*, while Stuckenberg's true species remained relatively unknown.

Eisel (1909) described and illustrated several varieties of *P. horridus* including var. *initialis*, var. *auritulus*, var. *laspeanus*, var. *bufoninus*, var. *hoppeianus* and var. *geranus.* He also considered that *P. geinitzianus* as a variety of *P. horridus.* Eisel's concept of varieties among *P. horridus* was well accepted by many later authors. Malzahn (1937), treated these varieties statistically, and found out that apart from *P. horridus* var. *hoppeianus*, all other varieties as well as it P. timanicus share a very similar growth patterns. He also proved that the varieties of *P. horridus* do not show any stratigraphical significance.

In 1927, Chao introduced the subgenus *Horridonia* to differentiate the only two accepted species, *P.(H.) horridus* and *P.(H.) timanicus* from other species of the overgrowing genus *Productus*. Probably ignorant of Chao's work, Fredericks (1928) introduced the genus *Sowerbina* which is similar to Chao's (1927) subgenus *Horridonia*, but with *P. timanicus* as the type species. In the same year, Chao elaborated his earlier definition of the genus *Horridonia*, while in 1929, Schuchert & le Vene chose *P. horridus* as the type species of this genus. To avoid confusion, Frebold (1931a,1931b and 1933), Malzahn (1937) and Trechmann (1944) used the original designation of the species prior to Chao's and Frederick's names. The name *Horridonia* was later used by Dunbar & Condra (1932) and Branson (1948), who listed 13 species of *Horridonia* in his Bibliograhic Index of the Permian Invertebrates.

In 1955, while working on horridoniinids from East Greenland, Dunbar found it important to separate those forms with marginal spines on both the ventral and dorsal valves from those with marginal spines on the dorsal valve only. He introduced the genus *Pleurohorridonia* for those forms with marginal spines on both the ventral and dorsal valves and with ribs on the trail of the ventral valve, while for those forms with marginal spines on the dorsal valve only he re-introduced Fredericks's name *Sowerbina* with amended diagnosis. Unfortunately, he gave little commentary about the actual genus *Horridonia* which had already been accepted by him in Dunbar & Condra (1932). In this paper, Dunbar introduced *P. scoresbyensis*, a form which was previously attributed by Frebold (1933) to both *P. horridus* var. *initialis* and *P. horridus* var. *hoppeianus*. Dunbar (1955) also introduced *S. maynci* which was identified by later authors as *H. granulifera*, and *S. rudis* which is a genuine new species. Although it is quite comprehensive, Dunbar's (1955) proposals have not been well received by other authors. Waterhouse (1982) employed the term *Sowerbina*, but unfortunately for just one uncertain species.

In 1960, Muir-Wood & Cooper re-established Chao's name *Horridonia* with new amended definition of the genus while at the same time they suppressed all other generic names once attributed to *H. horrida* and related forms. Muir-Wood & Cooper's (1960) amended diagnosis appeared to be very long and it covered all forms of Horridoniinae. Gobbett (1961) gave another amended diagnosis of *Horridonia* when he published a detailed account of the genus and its species. Unfortunately, Gobbett as many other authors before him, mistook Toula's *P. horridus* var. *granuliferus* with his *H. timanica* (not Stuckenberg's *P. timanicus*).

Following his unpublished PhD. thesis, Logan (1966) produced an account to clarify points of misunderstanding among earlier authors regarding the status of *H. timanica* and *H. granulifera*. Regrettably, he did not discuss the status of horridoniinids in the Durham Permian which he had studied in great detail.

Following Nelson's (1962) work on the horridoniinid stratigraphy of the Yukon Territory, Nelson & Johnson (1968) discovered a new horridoniinid genus *Bailliena*. Its new species *B. yukonensis* closely resembles *P. geinitzianus* de Koninck in many ways, but differs from the later in having no marginal spines on the dorsal valve. Nelson & Johnson (1968) apparently misunderstood the genus *Horridonia*, as they assigned two species, which they thought might fit Dunbar's (1955) description of the genus *Sowerbina*, into *H. bullocki* new species and *H. granulifera* (Toula). Both *H. granulifera* and *H. bullocki* have no marginal spines on the ventral valve and thus should be placed in the genus *Sowerbina*.

Conclusion: New scheme for generic classification of subfamily Horridoniinae.

The long and interesting history of interpretation of *Horridonia horrida* and related forms has given sufficient grounds to establish the following scheme of classification. It should be noted that one of the criteria used in the following taxonomic classification has already been used by Dunbar in 1955, but he failed to convince later authors of its value. Dunbar (1955) separated the genus *Sowerbina* from the rest of horridoniinids on the basis of the lack of marginal and auricular spines on the ventral valve. The genus *Sowerbina* is maintained in the following classification, so too is the genus *Bailliena* Nelson & Johnson (1968). With these two genera being extracted from the whole group of horridoniinids, it leaves us with a large genus *Horridonia* with marginal spines present on both the ventral and dorsal valves.

As stressed earlier, about the significance of the distribution of spines in taxonomic classification of the subfamily Horridoniinae, it is important to divide the subgenus not only on the distribution of the marginal spines, but also other spines including the body spines. With regard to the body spines, the remaining genus *Horridonia* can be divided into two groups; those with body spines on both the ventral and dorsal valves and those with body spines on the ventral valve only. The genus *Horridonia* should now include only the type species of *H. horrida* and related forms which have marginal spines on both the ventral and dorsal valves, and body spines on the ventral valve only. Forms with body spines on both the ventral and dorsal valves should be excluded from the genus *Horridonia.* A new genus *Spinohorridonia* is introduced here for those horridoniinids formerly assigned to *Horridonia,* but with both marginal and body spines present on both the ventral and dorsal valves. *P. geinitzianus* de Koninck is suggested in this thesis as the type species of the new genus *Spinohorridonia.*

This new scheme of classification reserves the size and shape of the shell and the detailed arrangement and type of the spines to descriminate at the specific level, as discussed later in this chapter. The generic scheme of classification can be generalized and tabulated as follows;

The British horridoniinid genera. Only *Horridonia* and *Spinohorridonia* are present in the British Permian.

Table 3.17. The classification scheme for subfamily Horridoniinae.

Genus (Type Species)	VVMS	VVBS	DVMS	DVBS
HORRIDONIA Chao (*P. horridus* Sowerby)	x	x	x	
SOWERBINA Fredericks (*P. horridus* var *granuliferus* Toula)		x	x	
BAILLIENA Nelson & Johnson (*B. yukonensis* Nelson & Johnson)		x	x	x
SPINOHORRIDONIA new genus (*P. geinitzianus* de Koninck)	x	x	x	x

VVMS: ventral valve marginal spines; VVBS: ventral valve body spines
DVMS: dorsal valve marginal spines; DVBS: dorsal valve body spines

Note on *Sowerbina*. The genus *Sowerbina* should be described as horridoniinids with marginal spines only present on the dorsal valve while body spines present on the ventral valve only. Since *Productus timanicus* Stuckenberg has been proved to have carried marginal spines on both the ventral and dorsal valves (Logan, 1966) and thus belongs to the genus *Horridonia*, it is no longer available as the type species of the genus *Sowerbina*. *Productus horridus* Sowerby var. *granuliferus* Toula, which genuinely belongs to the genus *Sowerbina* is proposed here to be the new type species of this genus. At present, apart from *S. granulifera* (Toula), the genus *Sowerbina* also includes *S. rudis* Dunbar, *H. bullocki* Nelson & Johnson and *H. texana* R.E. King.

Genus *HORRIDONIA* Chao 1927

Synonymy;
1927 *Productus subgenus Horridonia* Chao, p. 25.
1932 *Horridonia* Chao; Dunbar & Condra, p. 191.
1955 *Pleurohorridonia* Dunbar, p. 89.
1960 *Horridonia* Chao; Muir-Wood & Cooper, p. 292-294.
1960 *Pleurohorridonia* Dunbar; Muir-Wood & Cooper, p. 294.
1961 *Horridonia* Chao; Gobbett, p. 43.
1963 *Horridonia* Chao; Gobbett, p. 94.
1965 *Horridonia* Chao; Muir-Wood, p. 498.

Diagnosis. Horridoniinae with marginal spines on both the ventral and dorsal valves, and few smaller body spines on the ventral valve only.

Type species. *Productus horridus* Sowerby 1823 was assigned as the type species by Schuchert & le Vene (1929).

Other species. *Productus timanicus* Stuckenberg (1875), *Horridonia hoppeiana* (Eisel) and *H. dunelmensis* new species.

Discussion. Chao (1927) defined *Horridonia* as **Characterised by strong median fold, slightly convex (?) brachial valve and a few but very stout hollow spines**, but he did not single out the type species between *P. horridus* and *P. timanicus.*

In 1928, Chao corrected the above diagnosis and added that Horridonia **possess essentially the same characteristic outline of typical *Productus*, but is without either plicae or wrinkles. The median fold and sinus are rather pronounced and the surface is marked only by irregularly distributed, strong and erect spines. Some indefinite plicae are sometimes present, indicating occasional survival of the plicae making impulse**

Chao's diagnosis appeared to be very broad with many variable features, some of which are best used to described the differences between species while others seem to be more of individual characters. This unsatisfactory diagnosis has caused many later authors to write their own definition of the genus *Horridonia*, some short versions while others give a more detailed definition (see Dunbar & Condra (1932), Muir-Wood

& Cooper (1960), Gobbett (1961 and 1963) and Muir-Wood (1965)). However, none of these diagnoses suit the new scheme of taxonomic classification of the subfamily Horridoniinae. Therefore, the new diagnosis cited above is introduced to describe the genus *Horridonia* and comforming to the new scheme of classification introduced earlier in this chapter. In producing this diagnosis, care was taken to avoid the use of variable criteria which might cause confusion in the future. Features like the fold and sulcus, the shape of the shell, the detail surface sculpture and most of the internal features are left to be discussed at specific or variety level.

Specific division of the genus *Horridonia*.

Under the amended diagnosis above, the genus *Horridonia* is limited to the formerly known *Horridonia horrida* var. *initialis*, var. *auritulus*, var. *bufoninus* and var. *hoppeianus* and *H. timanica*. However, as mentioned earlier, Malzahn (1937) has clearly shown that *P. horridus* var. *initialis*, var. *auritulus*, var. *bufoninus* and *H. timanica* have a growth pattern which is very similar to one another; the only variety which seems to have its own growth pattern is the var. *hoppeianus*. Later in 1967, Kazmierczak pointed out that the whole Polish *H. horrida* belongs to the var. *hoppeianus*. The same variety has also been reported to dominate the Permian fauna of the East Greenland (Frebold (1933) and Dunbar (1955)).

Based on Malzahn's (1937) analysis, geographical distribution and new data which will be elaborated later under individual species, it is suggested that the specific status of the genus *Horridonia* can be described as follows;

1) At present, the genus *Horridonia* comprises four species, i.e. *Horridonia horrida* (Sowerby), *H. hoppeiana* (Eisel), *H. timanica* (Stuckenberg) and *H. dunelmensis* new species.

2) *Productus horridus* var. *hoppeianus* does not belong to *H. horrida* because it has a different growth pattern when compared to other varieties of *H. horrida* and because it has characteristic juvenile stages which was previously considered by Malzahn (1937) as mut. *hoppeianus*. The juvenile population has also been found from High Newport near Sunderland in Britain during this research. Furthermore,

the occurrence of var. *hoppeianus* alone in some region, strongly suggested that it belongs to a separate species, not only as a variety of *H. horrida*, see Kazmierczak (1967), Frebold (1933) and Dunbar (1955). Therefore, Eisel's (1909) var. *hoppeianus* should be elevated to form a separate species *Horridonia hoppeiana*, and a new full description is now required for this newly assigned species.

3) *Horridonia horrida* should be identified based on the type species and the remaining varieties *initialis*, *auritulus* and *bufoninus*) should not be used for the various reasons given below;

> a) the var. *initialis* appears to be easily recognised only among smaller individuals. Malzahn's (1937) term mut. *initialis* should therefore represent a juvenile population of *H. horrida*, whereas none of the other two varieties mentioned are recognisable among the juveniles of the species or as mutant varieties by some authors. Var. *initialis* should therefore, be regarded as juvenile and younger individuals of the species and, as might be expected, this supposed variety seems to be found more often than any of the other varieties.
>
> b) The var. *bufoninus* seems to be found among the very large *H. horrida* only, and it is not a common variety. From the White Quarry fauna, near Newton Aycliffe, the author found that none of the smaller individuals can be associated with var. *bufoninus*, but most of the very large individuals definitely belong to this supposed variety. Therefore, var. *bufoninus* can only be regarded as senile individuals of *H. horrida*.
>
> With regard to Malzahn's figure which shows the presence of body spines on the dorsal valve of var. *hoppeianus* (see Malzahn (1937, pl. 1, fig. 20)), this particular specimen might be regarded as the larger representative of his var. *laspeanus* or *Spinohorridonia laspeana* in this thesis.
>
> c) The difficulty in distinguishing var. *initialis* from var. *auritulus* in medium sized individuals is usually caused by the incomplete preservation of the delicate shell margins, especially around the auricle. Medium or large sized var. *initialis* always seem to have a broken auricle, while the impressively expanded

auricle in some var. *auritulus* could sometimes have resulted from the slight flattening of the shell close to the plane of the auricle, or due to damage of the anterolateral margin of the shell. Since var. *initialis* and var. *auritulus* are commonly based on differences of preservation, their varietal status are not significant and therefore should be suppressed.

4) The reasoning above suggests that the actual shape of adult individual of *H. horrida* should lie in between the supposed var. *initialis* - *auritulus*, perhaps closer to var. *auritulus* because of its more complete preservation, while the juvenile and senile stages have a less expanded auricle.

5) Similar growth patterns between *H. horrida* and *H. timanica* and the close resemblance of the external morphology (discussed later) show that these two species are much closer to each other than they are to *H. hoppeiana.* Gobbett (1961) considered that morphological similarities between var. *hoppeianus* and other varieties of *H. horrida* should put them closer to each other and further away from *H. timanica.* It should be noted, however, that Gobbett (1961) restricts this morphology to the distribution of the marginal spines and his description of *H. timanica* should be refered to *Sowerbina granulifera* (Toula), not *H. timanica* (Stuckenberg). More detail study is, however, required to clarify the true status of it H. timanica.

6) A new form of *Horridonia* recorded in this thesis from the British Permian, which differs from other known *Horridonia* in its more numerous body spines should be regarded as a separate species. *H. dunelmensis* is introduced for this new form.

British *Horridonia.* The genus *Horridonia* is only represented in Britain by *H. horrida, H. hoppeiana, H. dunelmensis* new species and another rare form (*Horridonia* sp. A) whose specific status is uncertain at the present time.

HORRIDONIA HORRIDA Sowerby

(Text-figures 3.16, 3.17, Plate 9, figures 1-14)

Synonymy;

1823 *Productus horridus* Sowerby, p. 17, pl.319, fig. 1.
1846 *Productus horridus* Sowerby; Geinitz, p. 52, pl. 21, fig. 17, pl. 22, fig.8.
1848 *Productus horridus* Sowerby; Geinitz, p. 15-16, pl. 6, fig. 1-14 not 8.
1848 *Productus horridus* Sowerby; Howse, p. 256.
1850 *Productus horridus* Sowerby; W. King, p. 87-92, pl. 11, fig. 2-7 and 10.
1853 *Productus horridus* Sowerby; Davidson, pl. 9, fig. 219-220.
1857 *Productus horridus* Sowerby; Howse, p. 44-46.
1858 *Productus horridus* Sowerby; Howse, p. 247-250.
1858 *Productus horridus* Sowerby; Davidson, p. 33-36, pl. 4, fig. 13-26.
1861 *Productus horridus* Sowerby; Geinitz, p. 103, pl. 19, fig. 11-12, 15-17.
1871 *Productus aculeatus* Quendstedt (not-Schlotheim), p. 635-6, pl. 60, fig. 1-4.
1909 *Productus horridus* Sowerby var. *initialis* Eisel, p. 33-34, fig. 1.
1909 *Productus horridus* Sowerby var. *auritulus* Eisel, p. 35, fig. 4.
1909 *Productus horridus* Sowerby var. *bufoninus* Eisel, p. 35, fig. 5, 8-10.
1933 *Productus horridus* Sowerby var. *initialis* Eisel; Frebold, p. 20-21, pl. 2, fig. 10-12.
1933 *Productus horridus* Sowerby var. *granuliferus* Frebold (not-Toula), p. 21-22, pl. 2, fig. 13.
1937 *Productus horridus* Sowerby var. *initialis* Eisel; Malzahn.
1937 *Productus horridus* Sowerby var. *auritulus* Eisel; Malzahn.
1937 *Productus horridus* Sowerby var. *bufoninus* Eisel; Malzahn.
1944 *Productus horridus* Sowerby; Trechmann, p. 349.
1955 *Pleurohorridonia scoresbyensis* Dunbar, p. 90-95, pl. 12, fig. 1-3.
1959 *Horridonia horrida* (Sowerby) var. *inicialis* Eisel; Stepanov, p. 192, pl. 1, fig 1 and 6.
1960 *Horridonia horrida* (Sowerby); Muir-Wood & Cooper, pl. 108, fig. ?8-11.
1961 *Horridonia horrida* (Sowerby); Gobbett, p. 43-46, pl. 3, fig. 1, ?2, 4, 6 and 8, pl. 5, fig. 5, 7-8.
1980 *Horridonia horrida* (Sowerby); Pettigrew, pl. 6g.
1988 *Horridonia horrida* (Sowerby); Hollingworth & Pettigrew, p. 18, fig. 3, text-fig. 5.
1988 *Horridonia horrida* (Sowerby); Turek, Marek & Benes , p. 147 , fig. c-f.

Diagnosis. *Horridonia* with trapezoidal shell outline in plan, moderate to well developed auricle and large and strongly incurved umbo. Ventral valve moderately convex in younger stages, strongly convex, but not geniculated in adult stages, with moderate to deep median sulcus. Ventral surface lightly to moderately lamellose with ribs developed on trails of senile individuals. Dorsal valve moderately concave with anterior slightly geniculated, median fold prominent and exterior lamellose. Cardinal process with trilobed, bilobed or quadrilobed myophore. Adductor muscle platform triangular in shape with dendritic or radially striated scars. Median septum short and low, and present between the muscle platforms. Brachial impressions small in size and variously originated. Marginal spines up to five pairs in each valve, auricular spines only one pair in the dorsal valve, up to three pairs in the ventral valve, ventral body spines less than ten in number.

Type specimens. Holotype: Specimen No. B60972 in BM(NH) was formally designated holotype by Gobbett (1961), this specimen was figured by Sowerby (1823, pl 319, fig 1a and 1b) and by many other authors.

Type locality. Limekiln Field, Bolsover, Derbyshire at GR. SK 474712 was designated type locality by Gobbett (1961).

Horizon. Cadeby/Raisby Formation and Ford Formation in England.

Age. Upper Permian (EZ1)

Other British localities. *H. horrida* has been reported from several localities within the Cadeby/Raisby Formation and the Ford Formation in Derbyshire, Nottinghamshire, County Durham and Tyne and Wear. Listed below are the localities from which the author has made his own collection of *H. horrida* with the number of specimens collected in brackets;
Langton (=Hobgate) Quarry, Langton - NZ 165189 (60)
High Bank Quarry, Heighington - NZ 24002265 (1)
White (=Old Town) Quarry, Newton Aycliffe - NZ 257245 (75)
East Thickley Quarry, Shildon - NZ 24082564 (9)
Eldon Hill Quarry, Eldon - NZ 24202715 (4)
Raisby Hill Quarry, Coxhoe - NZ 346353 (6)
Old Quarrington Quarry, Coxhoe - NZ 326381 (21)

Sherburn Hill Quarry, Sherburn Hill - NZ 345417 (1)
Dawson Plantation Quarry, Penshaw Hill - NZ 334544 (7)
? Tunstall Hill Rock Cottage, Tunstall - NZ 392545 (13)
? Ryhope old railway cut, Tunstall - NZ 39665385 (13)
? Hylton Castle roadcut, North Hylton - NZ 360589 (6)

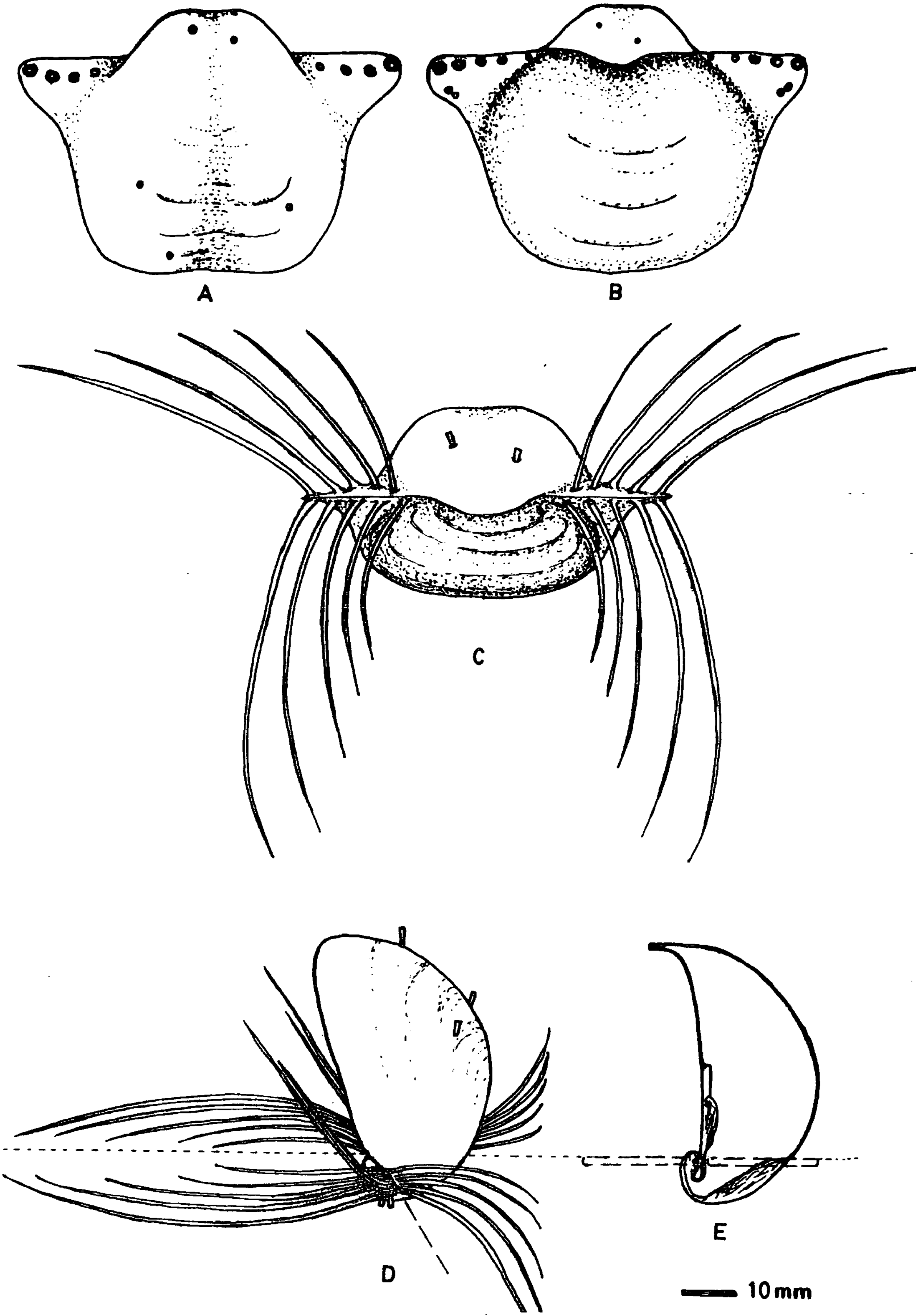
Table 3.18. *Horridonia horrida* **(Sowerby) - dimensions in mm.**

Specimen no	length	curved length	hinge width	height
MSLWQ14	6.0	e8.7	e7.2	e2.5
MSLWQ15	e11.1	na	e16.4	e5.3
MSLWQ16	22.5	e38.0	e30.6	e11.4
MSLWQ17	e33.5	e59.5	e38.5	e19.2
MSLWQ18	e40.0	e68.0	e50.0	e23.7
MSLWQ12	e45.0	e78.0	e59.0	e29.5
MSLWQ19	46.7	e88.0	e62.0	e31.2

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
na = not available e = estimated maximum width = hinge width

Description. The shell is medium to large in size with the maximum shell width reaching 65mm or more at the hinge line. The shell outline is anteriorly tapered sub-trapezoidal shape with the angle of anterior convergence varying from one individual to another. Posteriorly, the shell outline is marked by a sub-circular extension of the umbo beyond the hinge line. The maximum shell width is at the hinge line, and it is greater than the shell length.

The ventral valve is moderately convex in the smaller individuals and strongly convex in larger individuals. The convexity of the valve is strongest posteriorly, and weakens anteriorly. The ventral valve is divided into two visceral humps by a median sulcus which is deepest at about the mid-length, shallowing in both longitudinal directions, sometimes becoming very shallow and imperceptible at the umbo and on the trail. The umbo is large and tapers slightly towards the posterior across the hinge line. At the posterior extremity, the umbo is strongly incurved and convergent towards the dorsal and then towards the anterior. The tip of the beak usually covers



Text-figure 3.16. Reconstruction of *Horridonia horrida* (Sowerby).
A,B - Exterior of ventral and dorsal valves. C - Posterior view showing the special arrangement of marginal spines. D - Common life position of *Horridonia horrida* showing the role of marginal spines in supporting the shell *[- - - - - sediment interface; – – – – – hinge axis]*. E - Life profile *[= = = = = = spine horizon]*.

the slightly elevated posterior extension of the dorsal valve. The trail is generally smooth, but in larger individuals it is sometimes broadly ribbed. The auricle is well developed, but sometimes it appears to be fused with the visceral disc when the posterolateral margin of the valve slopes rather gently towards the auricle. When well developed, the auricle is triangular in shape and slightly arched in its longitudinal profile. Posteriorly, the hinge margin is straight laterally, but slightly bent towards the dorsal medianly, following the growth of the beak.

The exterior of the ventral valve is smooth or covered with light to moderate concentric growth lamellae or sometimes with unusual rugae. The assemblage of spines on the ventral valve consist of;

i) - a row of up to five pairs of coarse marginal spines, vertical to the shell plane longitudinally and inclined outwards at about 20^o to 50^o transversely. Three or four of the inner pairs however, occur slightly anterior to the margin and later join the other marginal spines to form a single plane of spines. The marginal spines are normally straight at the base and bend outwards at the end, but an exceptional case where these spines curve concentrically inward has also been observed. These spines are hollow throughout and increase in size from the inner pair to the outer pair. The largest outer spine pair observed has a diameter of about 2 mm, while the longest spines observed are more than 45 mm in length.

ii) - one to three pairs of large hollow auricular spines, very similar in many respects to those of the marginal spines, except that they are slightly inclined anteriorward.

iii) - Few (less than ten), irregularly distributed body spines on the beak, visceral humps and in the median sulcus. Owing to poor preservation, most of the specimens studied show hardly any traces of body spines except for very few small spine bases in the umbonal region. Judging from these spine bases, the body spines were erect to sub-erect in form.

The interior of the ventral valve is fully covered by short marginally pointed endospines, coarser at the anterior margin. In some larger individuals, the endospines at each side of the median sulcus are pointed medianly as well as anteriorly. Posteriorly, nearly one third of the valve is covered by large, low, radially striated diductor muscle platforms. In between this diductor muscle platforms lies the highly elevated adductor muscle platform which is divided into two halves by a low median furrow. Each half of the adductor muscle platform can be divided into the lower posterior section and the higher anterior section. The muscle scars are dendritic in pattern. At the posterior margin, an anteriorly inclined ridge appears at each sides of the umbo. This ridge is flattened and becomes broader laterally.

The dorsal valve is moderately concave, with the concavity stronger anteriorly; sometimes the trail is slightly geniculated. The median fold is well developed, appears shortly after the posterior margin and extends almost to the anterior margin. The posterior margin is straight laterally, but a little elevated medianly at the small triangular ?lophidium. The auricle is flat or concave in profile.

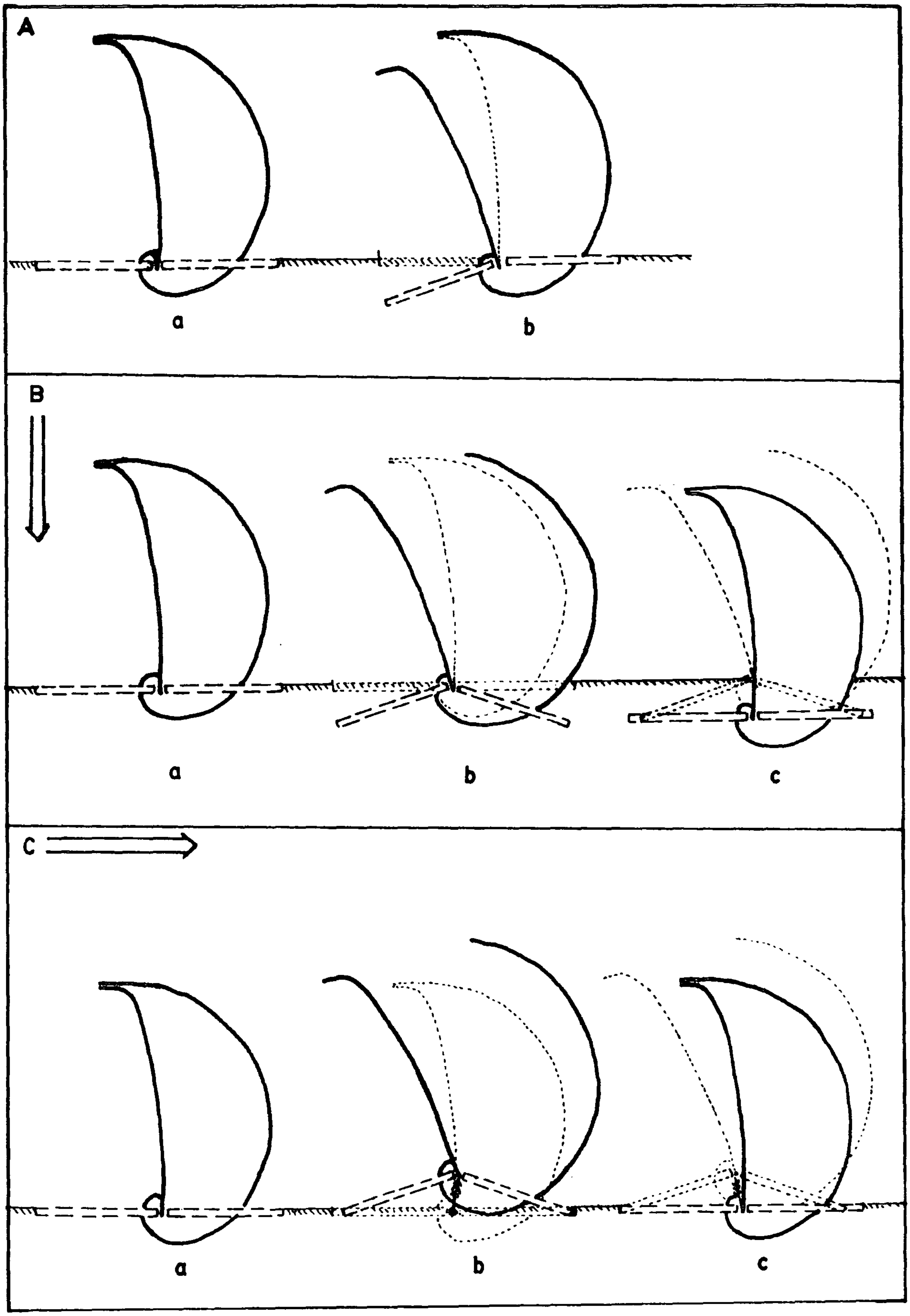
The exterior of the valve is smooth or lightly to moderately lamellose concentrically. The spines are restriced to a row of up to five pairs of large marginal spines and a pair of auricular spines. The nature of the marginal spines are similar to those of the ventral valve, so that when the valve is closed all marginal spines are set in a single linear plane. The dorsal marginal spines usually curve inward or concentrically arranged, but sometimes several outer pairs do curve outward. The auricular spines are larger than the marginal spines and develop at a low angle to both the shell plane and the plane of the marginal spines, and curve away from both planes.

Internally, the shell is covered by short, marginally pointed endospines, coarser at the margin of the viseral disc and on the trail. The cardinal process is large and short shafted or sessile with the myophore commonly trilobed, although some are bilobed or quadrilobed. The muscle attachment base is divided into two sections in the bilobed forms and four in the quadrilobed forms and some of the trilobed forms develop a very large median lobe. These divided muscle grooves converge toward the anterior into a small lophidium. The cardinal process shaft is posteriorly directed or inclined at a low angle (up to 20^o) either to the ventral or to the dorsal. The shaft is supported by a pair of strong lateral ridges and a weakly developed median ridge. The lateral ridges are thick and posteriorly inclined in the middle, but are flattened and broaden towards the lateral margins. The median ridge is sometimes very low and the median septum is separated from the cardinal process shaft by a low depression resembling an alveolus. The median septum appears in the middle of the adductor muscle platform and continues anteriorward to about two-thirds of the shell length. The median septum is thick and low posteriorly and sharp and moderately elevated anteriorly.

The adductor muscle platform is triangular in shape, and is divided into four sections. The anterior sections are more highly elevated than the posterior ones. The adductor muscle platform is divided centrally into two halves by a well developed furrow in which the median septum lies. The muscle scars are usually dendritic in pattern, but may be radially striated or grooved. In the non-dendritic forms, it is dificult to divide the adductor muscle platform into the posterior and anterior sections.

The brachial ridge is introduced posteriorly at various positions roughly at the anterior end of the adductor muscle platform. The ridge appears either horizontally or at a low angle towards the growth axis. The brachial impressions are small in size, and only occupy an area of about one quarter of the visceral disc.

Discussion. Ontogeny (see plate 9, figures 3 to 8). Juvenile and younger individuals of *H. horrida* compared to the larger adults, have a less convex ventral valve, smaller and poorly developed auricle, less concave dorsal valve and smoother external surface. As it grows larger, *H. horrida* increases the convexity of its ventral valve especially at the umbonal region, where the beak becomes strongly incurved. *H. horrida* also produces a better auricle and trail as it reaches adulthood. When it becomes very large or gerontic, *H. horrida* tends to develop a broadly ribbed trail, while the median sulcus fades away on the trail. The dorsal valve of the gerontic individuals are sometimes slightly geniculated. The trend of ontogenic development of the internal features of *H. horrida* are not well known because of the lack of material in which the internals are shown, especially among juvenile and senile individuals. Smaller adults, however tend to be more commonly found with bilobed cardinal process and non-dendritic muscle scars, but some of the larger adults of the species also inherited these features. The quadrilobed myophores are acquired only in very large individuals.



Text-figure 3.17. Postulation of various moving mechanisms in ***Horridonia horrida.***

A - simple opening of the valve.

B - Vertical movement *[a-b - all marginal spines sink into the sediment while the hinge axis is fixed; b-c - the shell sinks towards the new spine horizon: reversing the process will lift the shell upward].*

C - Lateral movement *[a-b - the shell is tangently lifted by pulling the dorsal marginal spines while holding the edge of the ventral marginal spines; b-c - by holding the edge of dorsal marginal spines the shell can be lowered tangently by pushing the ventral marginal spines;*

Note on the distribution and arrangment of spines and mode of life - material from East Thickley Quarry and White (=Old Town) Quarry. Based on material from East Thickley, Kazmierczak (1967) suggested that some *H. horrida* lived with its trail lifted above the surface and the marginal spines which are arranged in a single plane play the role of supporting platform. Similar interpretation has also been given by Muir-Wood & Cooper (1960) when they discussed the role of spines in *Horridonia* s.s. New material, which shows very similar preservation to that discussed by Kazmierczak, was collected from the White (=Old Town) Quarry (about 1.5km east of the East Thickley Quarry) during this research. With the shell and spines preserved in position exactly as figured by Kazmierczak (1967), these remarkable *H. horrida* must have been buried alive. It is also noted that *H. horrida* from these quarries only develop body spines at the umbonal region, whereas the rest of the ventral valve is smooth. Adopting the suggested living position of Kazmierczak, reduces the buried part of *H. horrida* to the umbonal region only, and this should reduce the significance of the body spines. The remaining body spines are very small in size as compared to the marginal spines and are usually preserved as spine bases in smaller individuals only. These spines were probably aborted during the ontogeny of *H. horrida* as they became less significant in supporting the larger individuals. The auricular spines were also probably aborted for a similar reason. Usually only a pair or two of auricular spines are left during the adult stage of this species. The nature of the auricular spines shows that they might have adopted a sensory function during part of the ontogeny, instead of supporting the shell.

The special arrangment of the marginal spines in *H. horrida* appears to have given it partial mobility including:-

i) By moving both valves equally and simultaneously, *H. horrida* could possibly lift itself up through muddy sediment to get clearer water conditions, and similarly it could bury itself further down in the mud to gain protection against predators or unfavourable environmental conditions (see text figure 3.17B).

ii) On a less muddy substratum, *H. horrida* could perhaps **plough** the mud surface by moving only one valve while holding the other still. In this way, it could move itself horizontally as well as vertically (see text-figure 3.17C). The ability to move horizontally would be of much advantage to secure a satisfactory substratum on which to settle down.

Comparison. *H. horrida* closely resembles the Carboniferous *H. timanica* in many respects, except that *H. timanica* has a slightly less convex ventral valve, slightly flatter dorsal valve, slightly broarder auricle and slightly better developed median sulcus and fold compared to *H. horrida*. *H. dunelmensis* differs from *H. horrida* only in its more numerous marginal and body spines, while the shape of the shell and the interior morphology of the two species are similar.

H. hoppeiana can be distinguished from *H. horrida* in its more convex ventral valve, more concave dorsal valve, less prominent auricle, median sulcus and fold and smaller marginal and auricular spines.

HORRIDONIA HOPPEIANA (Eisel)

[Text-figure 3.20, Plate 10, figures 1-11].

Synonymy;
1909 *Productus horridus* Sowerby var. *hoppeianus* Eisel, p. 34, pl. 2 and 3.
1933 *Productus horridus* Sowerby var. *hoppeianus* Eisel; Frebold, p. 18-19, pl. 3, fig 9 and pl. 5, fig. 1.
1933 *Productus* sp., Frebold, p. 19, pl. 1, fig. 7-8.
1937 *Productus horridus* Sowerby var. *hoppeianus* Eisel; Malzahn, pl. 1, fig. 18-23.
1955 *Pleurohorridonia scoresbyensis* Dunbar, p. 90-95, pl. 11 and pl. 12, fig. 4-13.
1959 *Horridonia horrida* (Sowerby) var. *hoppeiana* Eisel; Stepanov, p. 192, pl. 1, fig. 5.
1961 *Horridonia horrida* (Sowerby); Gobbett, pl. 3, fig. 3,5 and 7.
1967 *Horridonia horrida* (Sowerby); Kazmierczak, p. 239, pl. 1 and 2.

Diagnosis. *Horridonia* with sub-trapezoidal to rectangular shell outline, moderately developed auricles and large and strongly incurved umbo. Ventral valve very strongly convex , but not geniculated. Median sulcus poorly developed. Ventral surface lightly lamellose, sometimes ribbed on the trail. Body spines rare. Dorsal valve moderately to strongly concave, but not geniculated. Median fold poorly developed.

Type specimen. Specimens figured by Eisel (1909, pl. 2 and 3) as *Productus horridus* Sowerby var. *hoppeianus* should be elected as type specimens of this species.

British localities and current collection. Forms associated with *H. hoppeiana* have previously been recorded from Scar Lime Kiln Well, Ripon (Gobbett, 1961, pl. 3, fig. 7). During the tenure of this research, the present author managed to collect 44 specimens including 5 specimens from Langton (=Hobgate) Quarry (NZ 165189), 5 specimens from White (=Old Town) Quarry (NZ 257245), 17 specimens from High Newport old railway cut (NZ 387538), 1 specimen from Ryhope old railway cut (NZ 39665385), 14 specimens from Tunstall Hill old trench (NZ 397581) and 2 specimens from Hylton Castle road cut (NZ 360589).

There are several specimens labelled as material from Humbleton Hill in Kirkby's collection in the Hancock Museum which seem to belong to *H. hoppeiana.* However, the author believes that most of these specimens probably came from the Tunstall Hill (Rock Cottage), and not Humbleton Hill.

Horizon. *Horridonia hoppeiana* occurs in both the Cadeby/Raisby Formation and the Ford Formation in England.

Age. Upper Permian (EZ1).

Description. The shell is medium to large in size with the largest individuals reaching about 60mm in length. The shell has a sub-trapezoidal plan outline with the shell length is usually greater than the maximum shell width which is situated at the hinge line. Sometimes the hinge line is so short that the plan outline becomes an elongated rectangle.

The ventral valve is very strongly convex with the median sulcus generally weak, perceptible at the mid-shell length, but disappears on the trail and at the umbo. The auricle is small and triangular in shape. It is weakly inflated, often coalesced with the postero-lateral slope of the visceral disc. The umbo is large and strongly incurved

Table 3.19. *Horridonia hoppeiana* **(Eisel) - dimensions in mm.**

Specimen no	length	curved length	hinge width	height
MSLHN7	17.5	e27.8	17.8	9.7
MSLHN5	19.5	33.2	19.6	10.5
MSLHN4	e20.2	e29.0	17.0	10.0
MSLHN6	21.4	e37.4	20.7	10.8
MSLWQ24	31.4	e65.0	e30.4	21.2
MSLWQ25	e42.0	e90.0	e40.8	31.5
MSLLQ11	45.0	e84.0	e40.5	29.2
MSLLQ12	e49.5	e90.0	e48.8	e35.0

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
e = estimated

beyond the hinge line. The trail is long, weakly convex to almost flat in longitudinal profile.

The exterior of the ventral valve is covered with fine to moderate growth lamellae with occasional randomly distributed rugae developed. Rare spine bases are seen on the umbonal region and around the hinge area. Detail distribution and nature of the body spines as well as the marginal and auricular spines are not known in the British *H. hoppeiana*, except young specimens from High Newport old railway cut show that the marginal spines and auricular spines are laterally directed almost similar to those figured by Dunbar (1955). The interior of the ventral valve is only known in the younger population which will be discussed later.

The dorsal valve is moderately to strongly concave, but seldom geniculated. The median fold is absent or very poorly developed. The exterior of the valve is poorly known.

Discussion. Most of the material collected from the British Permian during this research is incompletely preserved. It can be differentiated from other *Horridonia* by the very strongly coiled shell with long trail and very shallow median sulcus.

Details of the distribution of spines and the internals are not fully known in British *H. hoppeiana*, except among the younger population of the species discussed below.

Note on *H. hoppeiana* from High Newport. A population of small *Horridonia*, majority of which have a strongly convex ventral valve have been found at an old railway cut at High Newport, near Sunderland. Considering this population of *Horridonia* alone, a case might be made that it belongs to a dwarf fauna or to a separate species. However, since a population of *S. lewisiana* from the same locality have average adult size for the species, these small *Horridonia* cannot be considered as part of a dwarf fauna. They should be considered as the juveniles of a species of *Horridonia* with very strongly convex ventral valve, i.e. *H. hoppeiana.* Other juveniles of *Horridonia* known from the British Permian are commonly much flatter than these particular juveniles. The largest individuals of the fauna has a length of about 21mm, and at this stage they have already developed a trail, some even show traces of radial costae on it. This evidence should clear any doubt in the authenticity of the species *H. hoppeiana*, and separates this species far from any other species of *Horridonia.*

Some of these young *H. hoppeiana* show a few large spine bases on the convex part of the ventral valve and two or more pairs each of marginal and auricular spines on the ventral valve, all of which are laterally directed. The nature of these spines are very similar to those figured by Dunbar (1955) for his *P. scoresbyensis* except that the auricular spines figured by him are very much larger than the marginal and body spines.

The ventral adductor muscle platform is divided into a highly raised anterior section and a low posterior section which are separated by a deep oblique furrow. The anterior section narrows posteriorly, continues in between the posterior section to the tip of the umbo. The anterior section or middle section (posteriorly) is divided into two halves by a shallow median furrow. The muscle scars are smooth, but may be dendritic in the larger adult stages. Surrounding the adductor muscle platforms are the radially striated scars of the diductor muscle platforms which are hardly raised from the shell plane. The dorsal adductor muscle platforms are pear shaped and moderately elevated, with the scars obliquely to radially striated or grooved.

The cardinal process is large with bilobed myophores. The shaft is supported by a pair of strong posteriorly inclined lateral ridges, but no median ridge is developed at the base of the shaft. The median ridges, however, appear shortly anterior to the cardinal process, in between the adductor muscle platforms, and continue as a moderately raised median septum to the mid shell length.

HORRIDONIA DUNELMENSIS new species

[Text-figure 3.18, Plate 11, figures 1-18].

[Named after the old County Durham where all the cited localities of this species lie].

Diagnosis. *Horridonia* with a very similar shape and profile to *H. horrida* but with up to 7 pairs of marginal spines on each valve, two rows of two to five pairs of auricular spines and thirty to fourty body spines on the ventral valve; dorsal valve with no auricular or body spines. Interior of the shell is similar to that of *H. horrida.*

Type specimen. Specimens no MSLHH8, MSLHH9, MSLHH10, MSLHH16, MSLHH17 and MSLHH18 are chosen as paratypes of *Horridonia dunelmensis*, to show variation in the morphology of the species.

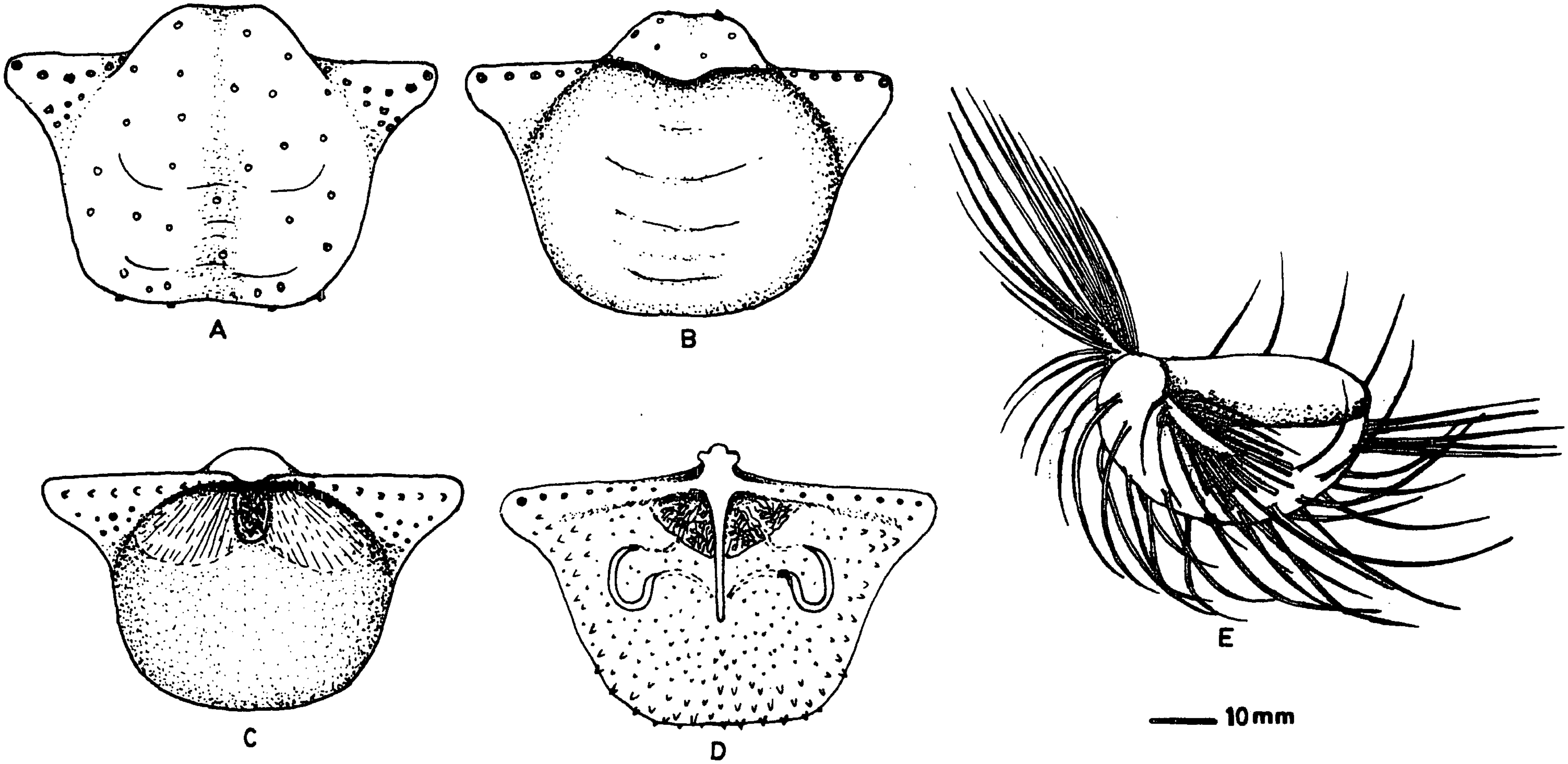
Type locality. The type specimens above came from Humbleton Hill (G.R. NZ 381553).

Other localities include Tunstall Hill old trench (G.R. NZ 397541), Ryhope old railway cut (G.R. NZ 39665385) and Beacon Hill railway cut (G.R. NZ 442454).

Horizon. Ford Formation.

Age. Upper Permian (EZ1).

Material. Humbleton Hill (?80 specimens), Tunstall Hill old trench (?90 specimens), Ryhope old railway cut (1 specimen) and Beacon Hill railway cut (4 specimens).



Text-figure 3.18. Reconstruction of *Horridonia dunelmensis* new species.
A,B - Exterior of ventral and dorsal valves. C,D - Interior of ventral and dorsal valces. E - Common life position of *Horridonia dunelmensis*.

Table 3.20. *Horridonia dunelmensis* **new species - dimensions in mm.**

Specimen no	length	curved length	hinge width	height
MSLHH12	8.7	14.6	e10.8	4.1
MSLR1	10.3	15.6	e12.2	3.8
MSLHH13	14.2	23.3	e17.0	e5.5
MSLHH14	e16.4	e25.5	e21.7	e7.0
MSLHH15	18.1	30.5	na	8.3
MSLHH16	24.3	40.2	e29.3	14.7
MSLHH9	26.3	44.7	e35.0	14.7
MSLot11	27.3	48.8	e37.5	16.8
MSLot12	29.3	52.0	e40.0	18.7
MSLot10	30.2	e52.0	e39.8	21.2
MSLHH17	33.8	e60.5	e48.0	22.3
MSLHH18	e41.0	e67.0	e53.0	27.5

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
na = not available e = not available

Description. Medium to large sized *Horridonia* with the largest individuals having a maximum shell width of 55mm or more at the hinge line. The range of shape and profile of the shell is similar to that of *H. horrida.* The ventral valve is similar in form to *H. horrida*, but differs in details of its external morphology. The exterior of the ventral valve is weakly lamellose, but often furnished with broad folding on the trail. The spines of the ventral valve consist of;

1) a row of up to seven pairs of large marginal spines usually pointed at a low angle towards the postero-lateral direction. The extremities of the marginal spines are usually laterally pointed, with no particular geometric orientation. However, occasionally more uniformly orientated postero-laterally pointing spines are seen. The outermost pair of spines have a diameter of up to 2mm and a length of 30mm or more, with the size and length of spines reducing gradually towards the inner pairs.

2) two rows of two to five pairs of auricular spines similar in many respects to the marginal spines.

3) thirty to fourty erect to sub-erect body spines, sparsely and often randomly distributed all over the valve. Sometimes, however, more systematic radial rows are developed over the convex part of the valve. Occasionally, a band of denser parallel erect spines is developed at a short distant from the anterior shell margin. These bands of spines apparently form on a parallel plane with the marginal and auricular spines.

The internal morphology of *H. dunelmensis* is similar to that of *H. horrida* except that the posterior shell substance is thicker in this species than it is in *H. horrida.*

The dorsal valve of *H. dunelmensis* is very similar to that of *H. horrida* except that the quadrilobed myophores have not been observed in this species. The cardinal process of *H. dunelmensis* has a trilobed or bilobed myophores. The marginal spines consist of up to seven pairs of spines which are dorso-laterally directed at their bases, but their extremities appeared to be pointing laterally to end up in a similar direction to the marginal spines of the other valve. The auricular spines are not developed.

Remarks. Up to the present time, this species is only known from the Ford Formation, and thus it is stratigraphically younger than *H. horrida.*

Although some individuals of *H. dunelmensis* retain the arrangement of spines of *H. horrida*, the majority of the species have all their marginal and auricular spines directed laterally instead of pointing longitudinally. This suggests that this species might be derived from *H. horrida*, but acquired more body spines and a new arrangement of marginal and auricular spines to adapt itself to the reef environment. The fact that *H. dunelmensis* has more numerous erect to sub-erect body spines and laterally directed marginal and auricular spines shows that it adopted a normal productidinid life position, with the ventral valve facing the sea floor and the dorsal valve exposed. The larger number of body spines was required to support the shell on the hard sea floor or to anchor into algal mats or loose sediment. The spine planes which develop at the postero-lateral margin and occasionally at the anterior margin provided a stronger anchoring system probably to suit a more muddy substratum or a denser algal mat.

Note on the articulation mechanism. The detailed articulation mechanism of the valves of *H. horrida* and related forms has never been described, probably owing to the lack of well preserved specimens especially those with their valves disarticulated. Several longitudinal sections and casts of some exceptionally well preserved moulds have been made during the present research and better reconstruction can now be made of the articulation mechanism of the valves of *H. horrida* and its related forms. The hinge elements of the ventral valve are formed of a pair of lateral ridges which bear a row of coarse endospines; these lateral ridges are sharp, anteriorly inclined medianly, and becomes gradually flattened and extended towards the lateral margins; in the middle, these ridges are divided by a narrow opening (see text-figure 3.18C and plate 11, figure 13).

On the dorsal valve, the cardinal process fits exactly into the median opening of the ventral valve. The lateral ridges that buttress the cardinal process are posteriorly inclined and form a well defined anteriorly dipping furrows in between the ridges and the posterior shell margin. These furrows receive the lateral ridges of the ventral valve when the shell is fully articulated. As the lateral ridges become flatter laterally these furrows also become obsolete. The flattened lateral furrows accommodate a row of apertures of marginal spines (see text-figure 3.18D and plate 11, figure 12). Although the number of these openings is less than the number of endospines on the ventral valve, they are placed in the right position so that when the valves are closed some of the endospines of the ventral valve fill or cover the spine openings of the dorsal valve and together they functioned as pseudo-teeth and -sockets.

HORRIDONIA sp. A

[Plate 9. figures 15-16].

Material. One specimen from Tunstall Hill old trench (GR. NZ 397541), two specimens each from White Quarry (GR. NZ 257245) and Langton Quarry (GR. NZ 165189).

Table 3.21. ***Horridonia* sp. A - dimensions in mm.**

Specimen no	length	curved length	hinge width	height
MSLWQ26	38.2	65.0	e32.5	27.7
MSLot12	34.8	e52.0	e39.0	e22.0
MSLLQ14	46.0	73.0	e45.0	e 29.5

dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
e = estimated

Description. The shell is medium in size with the largest individual is 47 mm in length. The shell has a shield shape plan outline. The ventral valve is moderately to strongly convex. The median sulcus only developed posteriorly and is replaced by a fold anteriorly. Folding of the anterior margin has restricted the development of the trail to the lateral margins, thus giving the shell a proboscis shaped anterior. The auricle is small, arched in longitudinal profile, but fused with the slope of the visceral disc. The beak is large and strongly incurved. The exterior surface of the ventral valve is moderately lamellose, where the growth lamellae are concentric posteriorly, and wavy at the median fold anteriorly. About 16 (should be slightly more if all preserved) body spines are seen on the convex part of the ventral valve, and these spines are arranged in a more or less uniform radial rows. The dorsal valve is moderately concave and is not geniculated. Other details are unknown.

Remarks. *Horridonia* sp. A differs from other *Horridonia* in having a median fold on the ventral valve anteriorly. Other features of these specimens might fall within variations of other species of *Horridonia.* In my opinion, although this form is unique, more specimens are needed before it could be given as a new species status.

Genus *SPINOHORRIDONIA* new genus

Diagnosis. Horridoniinae with both ventral and dorsal valves densely covered with undifferentiated body and marginal spines.

Type species. *Productus geinitzianus* de Koninck 1846.

Other species. *Spinohorridonia gerana* new species and *S. laspeana* new species.

Discussion. Based on the type species *Productus geinitzianus* de Koninck, *Spinohorridonia* should be distinguished from other Zechstein and Arctic horridoniinids by its heavily spinose valves. *Spinohorridonia* seems to be an intermediary form between the dictyoclostinid genus *Tyloplecta* Muir-Wood & Cooper and the true *Horridonia.* For the same reasons given by earlier authors who included *P. geinitzianus* into the genus *Horridonia* and Nelson & Johnson (1968) who introduced the genus *Bailliena* in the Horridoniinae, I believe that *Spinohorridonia* should be included into the subfamily Horridoniinae instead of the Dictyoclostinae. Although the anterior region of *S. geinitziana* (de Koninck) is very similar to other *Tyloplecta*, the visceral and umbonal regions are characteristically horridoniinid in nature. The non-reticulate ornament on the visceral disc places this genus in subfamily Horridoniinae. The similar North American genus *Bailliena* differs from this genus in the absence of marginal spines on the dorsal valve.

As a horridoniinid, the above diagnosis is acquired using the taxonomic classification of the Horridoniinae previously stated (p. 144). *Spinohorridonia* is divided into its species on the basis of the density of the spines, the shape of the shell and the surface sculpture. On this basis, we can distinguish *S. geinitziana* (de Koninck) from *S. gerana* (Eisel) and *S. laspeana* (Eisel). The last two species were upgraded from Eisel's (1909) original *P. horridus* var. *geranus* and var. *laspeanus*, respectively.

Spinohorridonia and its species have not been reported from the British Permian in the past, but several species belonging to this genus have been described under different names in the East European Permian. In this thesis, *Spinohorridonia geinitziana* (de Koninck) and *S. laspeana* (Eisel) are described from the Permian of

Great Britain for the first time.

Note on *Spinohorridonia gerana* (Eisel). From Zone 4 of the East German Zechstein, Eisel (1909) described *P. horridus* Sowerby var. *geranus* for the forms which is very similar to de Koninck's (1847) *P. geinitzianus* in terms of the shape and profile of the shell and the distribution of spines, but differs from the later in having a more erect body spines and a non-costate anterior. Details of the internal morphology of *S. gerana* have not been discribed in the past, and therefore, cannot be compared with those of *S. geinitziana* which is discussed for the first time in this thesis. Up till now, *S. gerana* has not been found in the British Zechstein.

SPINOHORRIDONIA GEINITZIANA (de Koninck)

[Text-figure 3.19, Plate 11, figures 19-26].

Synonymy;
1846 *Productus geinitzianus* de Koninck, p. 264-266,, pl. 15, fig. 3.
1847 *Productus geinitzianus* de Koninck; de Koninck, p. 156-157, pl. 15, fig. 3.
1848 *Orthothrix excavatus* (part-Geinitz); Geinitz, p. 14-15, pl. 6, fig. 20-21.
1856 *Productus geinitzianus* de Koninck; King, p. 260-261, pl. 12, fig. 1-2.
1861 *Productus geinitzianus* de Koninck; Geinitz, p. 105, pl. 19, fig. 20-21.
1909 *Productus horridus* Sowerby var. *geinitzianus* de Koninck; Eisel, p. 36.

Diagnosis. *Spinohorridonia* with sub-trapezoidal to rectangular shell plan, moderately developed auricle and large and strongly incurved umbo. Ventral valve very strongly convex, but not geniculated. Median sulcus poorly developed. Ventral surface lightly lamellose with costate anterior. Marginal, auricular and body spines are numerous. Body spines in quincunx arrangement, erect to suberect on the convex part of the shell, recumbent on the trail. Dorsal valve moderately to strongly concave with flat auricle and poorly developed median fold. Dorsal surface lightly to moderately lamellose with undifferentiated spines all over the valve, and costate trail. Cardinal process with quadrilobed myophores, strong lateral and median ridges. Median septum highly elevated anteriorly. Adductor muscle platform triangular in shape with scars dendritic or radially grooved. Brachial impression small in size.

Type specimen. Material figured by de Koninck (1846, pl. 15, fig. 3) should be elected as type specimen of *Spinohorridonia geinitziana.*

Type locality. The type specimen of *S. geinitziana* mentioned above was acquired by de Koninck from Milbitz near Gera, where the type locality should be designated.

British Localities and Specimens Studied. Up till now, only 15 specimens of this species are known in Britain, all from around Sunderland; 7 of them were collected from Hylton Castle road cut (GR. NZ 360589), 6 came from Tunstall Hill old trench (GR. NZ 397541) and 2 came from Humbleton Hill (GR. NZ 381553).

Horizon. Ford Formation.

Age. Upper Permian EZ1.

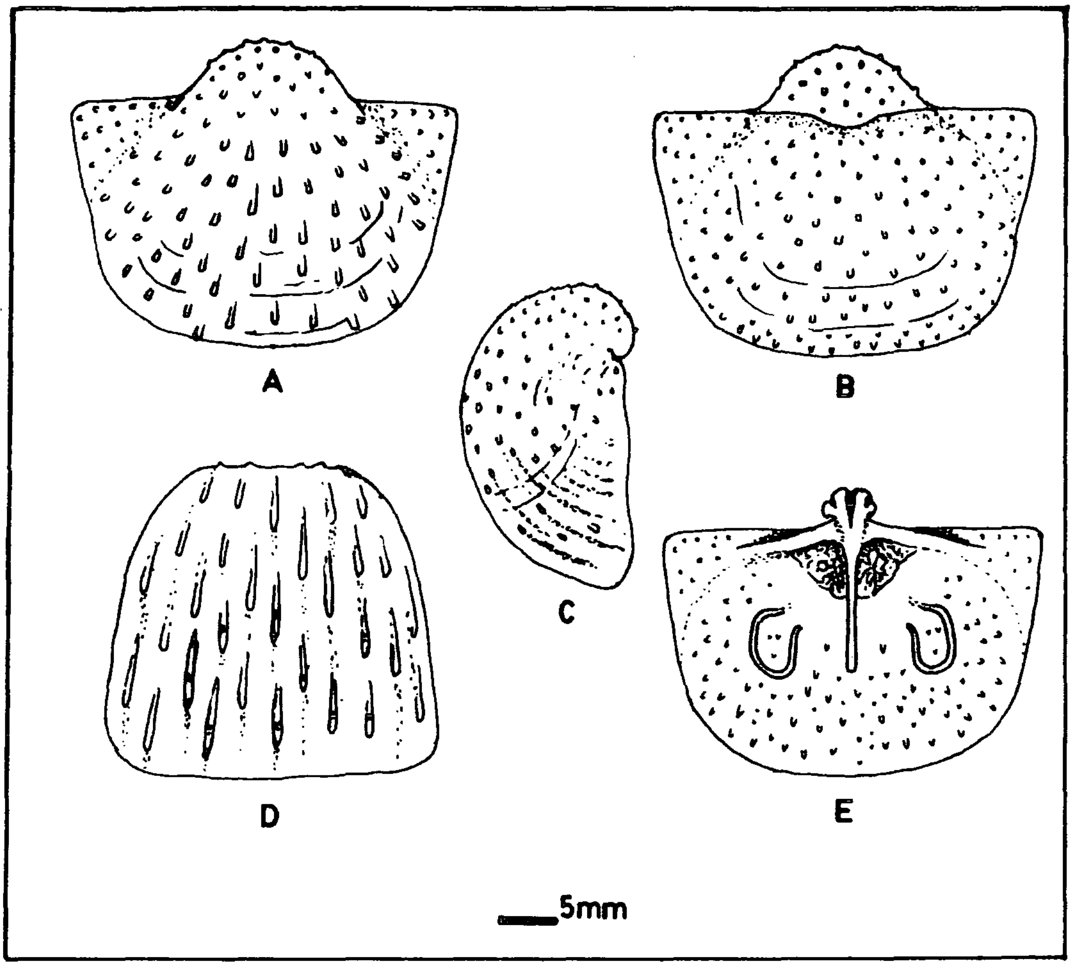
Table 3.22. *Spinohorridonia geinitziana* **(de Koninck) - dimensions in mm.**

Specimen no	length	curved length	hinge width	height
MSHot13	20.2	34.3	e24.5	9.7
MSLHC18	e22.5	e40.5	e26.5	13.7
MSLot14	23.0	e39.2	e29.0	13.5
MSLHC17	e25.0	na	e31.0	na
MSLHC14	30.0	57.2	e34.5	20.4

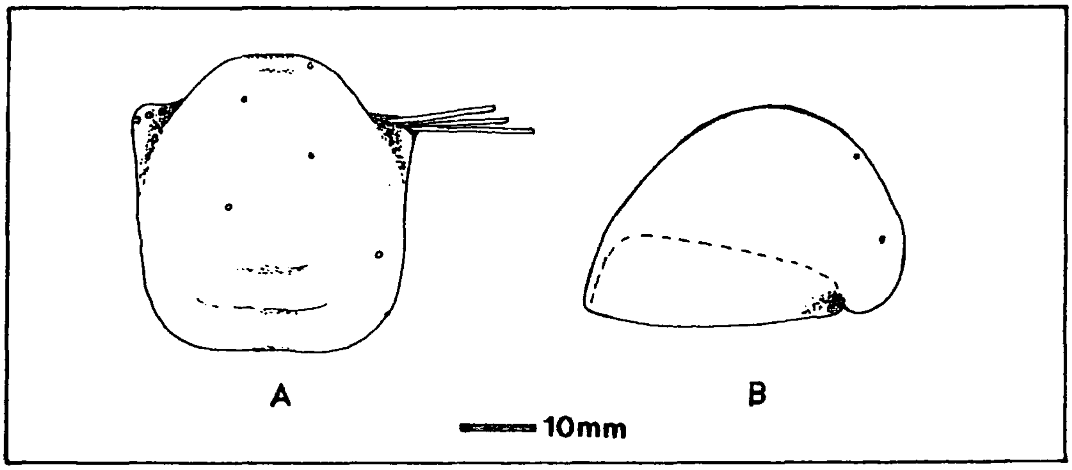
dimensions = refer to text-figure 1.1
specimen numbers = refer to appendix
na = not available e = estimated

Description. The shell is medium in size with the largest individual about 30mm in length and 36mm in maximum width which is at the hinge line. The shell has a sub-trapezoidal to rectangular plan outline with small auricle and large strongly incurved umbo.

The ventral valve is strongly convex with short trail and no geniculation. The



Text-figure 3.19. Reconstruction of ***Spinohorridonia geinitziana*** **(de Koninck).**
A,C,D - Exterior of ventral valve: ventral, lateral and anteroventral views. B,E - Exterior and interior of dorsal valve.



Text-figure 3.20. Reconstruction of ***Horridonia hoppeiana*** **(Eisel)**
A,B — Ventral exterior (ventral and lateral views).

median sulcus is shallow at the mid shell length, obscure posteriorly and anteriorly. The ventral surface is lightly to moderately lamellose and covered by numerous undifferentiated spines all over the valve. The spines are small, but long, sub-erect to erect in nature except on the trail, where they are more recumbent. On the convex part of the valve, the spines are a more or less quincunx in arrangement with a space of about 2 mm or less in between spines in the same concentric rows, and 2 to 3 mm in between spines in the same radial rows. There are about 40 rows of spines in the larger adult individuals. The trail of larger individuals has about the same number of sharp radial costae.

The interior of the ventral valve has a series of sharp radial furrows reflecting the costae on the exterior; the internal mould usually carries a series of radial blades. The adductor muscle platform is moderately elevated and is divided into two halves by a shallow median furrow. The muscle platform appears shortly after the tip of the umbo and it continues up to one third of the shell length anteriorward. The scars are concentrically striated or grooved. The diductor muscle platform is very low and radially scarred.

The dorsal valve is weakly to moderately concave with the median fold clear at the mid shell length, but fades away towards the posterior and anterior. The auricle is flat and triangular in shape. The exterior is regularly pitted in between sub-erect spines which are similar in arrangement and nature to those of the ventral valve. Shell surface is lightly to moderately lamellose. The trail is costate.

The interior of the dorsal valve is covered by fine, closely spaced , marginally pointed endospines which are coarser at the trail. The cardinal process bears a quadrilobed myophore, and its shaft is supported by strong pairs of posteriorly inclined lateral ridges and median ridge. The median ridge narrows anteriorly, and continues as the median septum which is highly elevated at its anterior extremities (at about the mid shell length). The adductor muscle platform is triangular in shape with dendritic or radially grooved scars. The brachial impression is small.

Comparison. *S. geinitziana* differs from *S. gerana* in having a recumbent body spines and costate anterior margin. This species differs from *S. laspeana* in its densely spinose shell with larger number of radial costae. The anterior ornamentation of *S. geinitziana* resembles the North American species *B. yukonensis*, but the latter is noted for its non-spinose posterior margin of the dorsal valve.

SPINOHORRIDONIA sp. cf. *S. LASPEANA* (Eisel)

[Plate 10, figures 12-16].

Material. 3 specimens from Humbleton Hill (GR. NZ 381553) and two specimens from Ryhope old railway cut (GR. NZ 39665385), all around Sunderland.

Table 3.23. *Spinohorridonia* sp. cf. *S. laspeana* **(Eisel) - estimated dimensions in mm.**

Specimen no	Length	max. (=hinge) width
MSLHH19	15.6	17.2
MSLHH20	14.1	16.0
MSLHH21	16.5	18.2
MSLR2	15.3	17.4
MSLR3	16.5	18.2

dimensions = see text-figure 1.1
specimen numbers = refer to appendix

Description. The British specimens are small in size with sub-trapezoidal to squarish in plan outline. The ventral valve is strongly convex with poorly developed median sulcus and auricle. The umbo is small, but is strongly incurved. The ventral surface is smooth or very weakly lamellose. Two pairs or more spine bases (probalby erect to sub-erect spines) are found in a marginal row, and up to twenty scattered spine bases of similar nature to the marginal spines are observed on the convex part of the valve.

The dorsal valve is moderately to strongly concave with no apparent median fold. The dorsal surface is smooth or lightly lamellose with scattered spine bases in a marginal row and on the concave part of the valve. The number and nature of these spines are similar to that of the ventral valve. Other details are not known.

Remarks. The small size of the specimens from Sunderland, might represent younger individuals of the species while some much larger specimens have been reported and figured from the East European Zechstein. The broad folding of the trail in the East European material is not seen in the British specimens, while the spines of the British specimens are more erect in nature as compared to those from East Europe. However, the distribution and density of the body spines on both valves is similar between the British and the East European *S. laspeana.*

CHAPTER 4

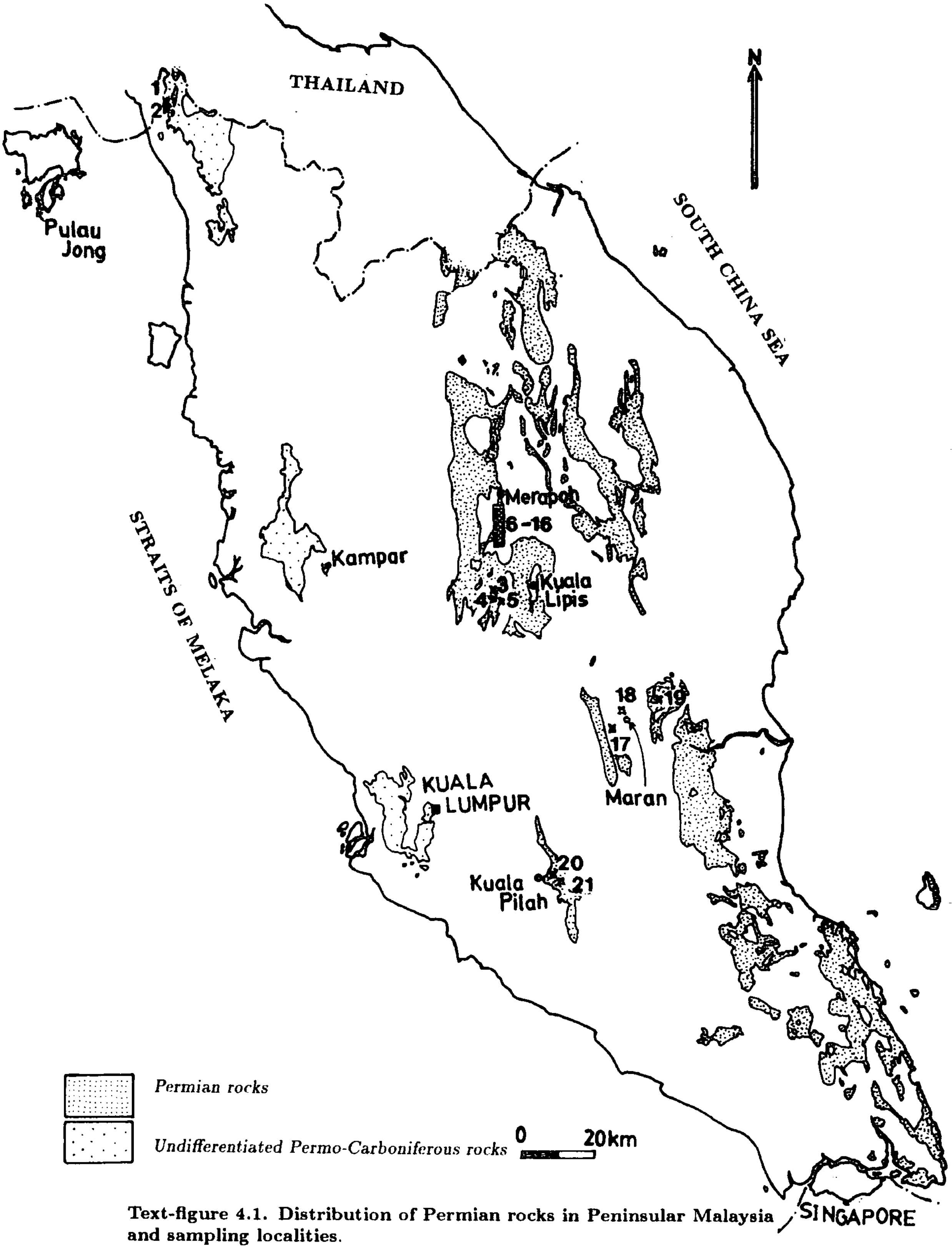
THE PERMIAN SYSTEM AND PERMIAN BRACHIOPODS OF MALAYSIA

The Permian System in Malaysia

The Permian System is well developed throughout West and East Malaysia. For the purpose of this study discussion will be limited to the Permian of West Malaysia from where a number of productidinid brachiopods have been described in the literature. The Permian of East Malaysia is restricted to the West Sarawak and no Permian brachiopods have been reported from there.

In West Malaysia or better known to geologists as Peninsular Malaysia (formerly Malaya or Malay Peninsula), Permian rocks crop out extensively to the west and east of the Main Range. However, due to lack of detailed studies, the lateral distribution and stratigraphic correlation are not fully understood and in many instances Permian occurrences are only inferred (see Table 4.1 for the correlation of Permian rock formations in Peninsular Malaysia). For the same reason, the Permian of Peninsular Malaysia is very seldom described as a separate system. It is usually discussed in a brief note under an Upper Palaeozoic or Permo-Triassic heading.

Gobbett (1973b) divided the Upper Palaeozoic of Peninsular Malaysia into four zones; the Northwest, Kinta Valley, Central and East Malaya (Peninsular Malaysia). Discussion will be focused on the first three zones, for the East Peninsular Malaysia Zone does not yield any productinid brachiopods. (The distribution of Permian rocks and the localities studied in Peninsular Malaysia are illustrated in text-figure 4.1, page 177).



Text-figure 4.1. Distribution of Permian rocks in Peninsular Malaysia and sampling localities.

The Northwest Peninsular Malaysia

In the Northwest Peninsular Malaysia, Permian rocks occupy part of Perlis and North Kedah and this outcrop extends across the border to the Thai Peninsula. The Permian sedimentary rocks of this zone are deposited on a more stable platform as compared to those of the Central zone. It is mainly made up of an unfossiliferous pure calcitic limestone of the Chuping Formation (Gobbett, 1973b). The basal part of this formation, however, is highly fossiliferous and the fauna gives an upper Lower Permian age to this horizon (Newton, 1926, Scrivenor, 1926, 1931, etc.). The exposed basal Chuping Formation comformably overlies the argillaceous Singa Formation in the Langkawi islands and the arenaceous Kubang Pasu Formation in Perlis. Although the detailed stratigraphy of these underlying formations is not fully understood, it is believed that the basal Permian lies somewhere within these beds. The top of the Chuping Formation is not well exposed, but in Kodiang area, North Kedah, it is in places comformably overlain by the impure Kodiang Limestone which is Lower Triassic in age (Metcalfe, 1981).

Several Permian fossil localities have been recorded from the transitional or passage beds from Singa and Kubang Pasu formations to the Chuping Formation in the Langkawi islands and in Perlis. Permian brachiopods have been reported from Pulau Jong, Pulau Singa Besar and Kisap in Langkawi islands and from Bukit Tungku Lembu and Bukit Temiang in Perlis (see table 4.2 for detail brachiopod lists).

The Kinta Limestone and Kenny Hill Formation

A series of limestone hills expose within the Kinta Valley in Perak, but the limestone has been subjected to a certain degree of metamorphism, such that fossils, especially the macrofauna, are scarce. However, from a series of a bioclastic limestones exposed in several tin mine pits in the 1960s, very rich and diverse macrofaunas have been recorded. These macrofaunas include many species of gastropods, bivalves, brachiopods, bryozoans, corals, algae, ostracods and fusulinid forams (see Toong, 1965, Suntharalingam, 1968, Batten, 1972, Runegar & Gobbett, 1975, and Ishii, 1966). The fusulines from H. S. Lee Beds belong to the *Parafusulina* Zone of late Artinskian

- early Kungurian Stages (Ishi, 1966) and the brachiopod limestones (= The Nam Loong Beds) below it are assigned to Sakmarian Stage by Gobbett (1973a, 1973b). The fossil record of the Kinta Limestone is not continuous and comprises of a range of fossils from Middle Devonian to Middle Permian time. Although detailed stratigraphy of the Kinta Limestone is not fully understood, Suntharalingam (1968) suggested that the basal Permian - Carboniferous boundary is best interpreted between Nam Loong Beds and the top of Kim Loong No.1 Beds. The youngest part of the Kinta Limestone (The H. S. Lee Beds) does not reach the Upper Permian (see stratigraphic column for Kampar in Table 4.1 of this chapter).

To the south, a sequence of unfossiliferous argillo-arenaceous rocks known as the Kenny Hill Formation represent the Upper Palaeozoic in Selangor. The discovery of *Agathiceras* sp. from this sequence proves that they extend to Permian in age (Geological Survey Department, 1986).

The Central Peninsular Malaysia

The Permian rock succession is well developed in Central Peninsular Malaysia or the Central Belt of the peninsula. Most of the Permian rock succession within this zone is associated with volcanic and pyroclastic rocks which indicates that they are deposited in a very unstable depositional basin. The common occurrence of plant remains to the east of this zone indicates that the shoreline is lying somewhere to the east.

In the west of this zone, the Permian rocks crop out extensively along the eastern foothills of the Main Range from Northwest Kelantan southward to Northwest Pahang. They are best known as the Gua Musang Formation and consist mainly of limestones, slates, indurated shales and mudstones, volcanic and pyroclastic rocks. The Gua Musang Formation often occurs as a roof pendant on top of granite bodies or as an underlying sediments beneath the younger Triassic rocks. They are generally folded and faulted and are very difficult to correlate either laterally or vertically (Richardson,1947, 1950; Gobbett, 1973b). From the several localities investigated, the Permian fauna of this area is mainly preserved in argillaceous rocks. The lime-

Table 4.1. Permian stratigraphic correlation of West and Central Peninsular Malaysia

SYSTEM		PERMIAN STAGES	WEST PENINSULAR MALAYSIA					CENTRAL PENINSULAR MALAYSIA					
		USSR platform	Langkawi Islands	Kedah/ Perlis		Kinta valley		Negeri Sembilan	Northwest Pahang		South Central Kelantan		Northeast Pahang
						Suntharalingam 1968					Aw *et al.* 1978		Fontaine *et al.* 1988
TRIASSIC				Kodiang Limestone	Semanggol Formation			Gemas Formation	Raub Group	Semantan Formation	Aring Formation		Upper Triassic Tembeling Gp
PERMIAN	UPPER	*Dorashamian*	Chuping Limestone Formation					Kepis Bed	Gua Musang Formation	*Leptodus* Bed		FSKN73	
		Dzulfian											Jengka Pass shale & sandstones
		Midian											
	MIDDLE	*Murgabian*											Jengka Pass limestones
		Kubergandian					H. S. Lee Bed						
		Bolorian											
	LOWER	*Artinskian*	Singa Formation (argillic)	Kubang Pasu Formation (arenic)		Kinta Limestone	Nam Loong Bed			metasediments		FSKN4	? ?
		Sakmarian											
		Asselian											
CARBONIFEROUS							Kim Loong Bed						Kuantan Group

stones, although they are locally fossiliferous, have not had detailed faunal studies. From this area, the Upper Permian *Leptodus* shales (in this thesis some of them are considered as weathered slates) are known in several places including Sungai Jemuru in Kuala Lipis, Sungai Yu in Merapoh and Sungai Galas in Gua Musang (Muir-wood (1948), Jones et. al. (1966)). Occurrence of similar *Leptodus* shales and slates are first recorded in this thesis from Kampung Gua, Kampung Garok and Terenggun near Kuala Lipis and from the Dada Kering - Gua Musang highway.

Southward, isolated Lower Permian rocks are exposed in Negeri Sembilan, nearly parallel to the strike of the Gua Musang Formation. The Permian rock succession here is called the Kepis Beds and it is mainly made of indurated mudstones and shales, interbedded with polymictic rudite, arenite and argillite and carbonaceous limestones. Lower Permian faunas have been recorded from Kampung Juaseh and Kampung Baharu Kepis in Kuala Pilah area (Khoo, 1985).

The east of the Central Peninsular Malaysia is mostly covered by Mesozoic rocks. Permian rocks commonly occur as patches in faulted blocks or as underlying sediments beneath the Triassic rocks. From south Central Kelantan, both Lower Permian and uppermost Permian faunas have been recorded by Aw *et al.* (1978), Toriyama *et. al.* (1975) and Yanagida & Aw (1979), while Maran Upper Permian faunas has been recorded by Fontaine *et al.*, 1988; Ichikawa *et al.*, 1966; Ishii, 1966; Nakazawa, 1973, etc. The south Central Kelantan faunas are found in tuffaceous limestones which are associated with slates and pyroclastic rocks while the Maran faunas are found in limestones, carbonaceous shales and in sandstones. In North Pahang, Middle to Upper Permian fauna have been recorded by Igo (1964) from Ulu Sungai Atok and Sungai Sepia. These fauna are found in silicified limestones and shales.

The southernmost fossil occurrences within this zone have been reported in the Geological Survey Annual Report 1987 from Permian tuffaceous sediments below the Triassic Gemas Formation in north and northwest Johor.

The Eastern Peninsular Malaysia

The eastern Peninsular Malaysian Permian rocks are well developed on top of the Boundary Ranges (at the border between Terengganu - Kelantan and Terengganu - Pahang), in Southeast Pahang and most of the East Johor. Besides its well known flora, Permian marine faunas (mostly corals and fusulinid forams) are found in several limestone hills in Terengganu and Johor (see Fontaine *et al*, 1988; Fontaine & Khoo, 1988; Kato & Ezaki, 1986).

Permian brachiopods

Brachiopods form an important element of the Permian faunas of Peninsular Malaysia. Extensive faunal lists cited by various authors have given a big catalogue of Permian brachiopods (see table 4.2). However, only a few of them have been described systematically.

The first and most comprehensive list of the Malaysian Permian brachiopod fauna was published by Jones *et al.* (1966) with most of the identifications made by Gobbett, one of the co-authors. In this first major summary of Malaysian fossils, more than half of the total recorded Permian brachiopods listed in table 4.2 are given. Prior to this publication, Permian brachiopods were not well known in Malaysia. The first work to mention the occurrence of Permian brachiopods in Malaysia was made by Wilbourn (1926) when he described the fauna of Bukit Temiang. Muir-wood (1948) noted another occurrence of Permian brachiopods from Sungai Jemuru, Pahang. The only descriptive work on the Malaysian Permian brachiopod fauna before Jones *et al.* (1966) was made by Igo (1964) on the late Middle Permian brachiopods from Sungai Sepia, Pahang in which he described three different *Dictyoclostus* sp. (renamed as *Antiquatonia* in this thesis) as well as several spiriferids.

Considering that very little is known about Permian brachiopods in Malaysia before Jones *et al.* (1966), the work is clearly a major breakthrough in this field. As in many other pioneer works their review is not very helpful for later workers. This is

Table 4.2 Lists of known Permian brachiopods in Malaysia.

Faunal list (productidinids)	Localities (refereuces)
Anidanthus **sp.***	12(h*)
Aulosteges **sp.***	4(d*)
Cancrinella cancrini **(de Verueuil)***	4(c.d*)
Cancrinella **sp. cf. *C. cancrini*** (de Verneuil)	5(a.b.c)
Cancrinella **sp.**	6(a.b.c)
Costiferina **sp.**	6(a).11(a)
Costispinifera **sp.**	6(f)
Dictyoclostus **sp.***	8(a.c,g).(15a.k*).(17l)
Echinauris **sp.***	12(h*)
?Echinoconchus fasciatus (Kutorga)	18(m)
Haydenella **sp. cf. *H. minuta*** Sarytcheva*	12(h*)
Horridonia **sp.**	14(a.b)
Krotovia **sp.**	13(c.l)
Linoproductus **sp. cf. *L. lineatus*** (Waagen)	6(a.f)
Linoproductus **sp.**	6(b.c.l).14(a,b.l).17(l)
Liosotella **sp.***	14(j*)
Marginifera **sp.**	4(a.c).8(a.c,g).9(a).17(l)
Monticulifera **sp.***	4(d*)
Proboliolina **sp.**	14(a.b)
'***Productus***' sp. cf. '*P*'. *gratiosus* Waagen*	12(h*)
Reticulatia **sp.** cf. ***R. uralica*** (Tschyernyschew)	13(c.l)
Reticulatia **sp.**	1(a.b.e).9(a)
Retimarginifera **sp.**	18(l.m)
Spinomarginifera kueichowensis Huang*	14(j*)
Spinomarginifera **sp. cf. *S. kueichowensis*** Huang	14(a.i)
Spinomarginifera **sp. cf. *S. spinocostata*** (Abich)*	12(h*)
Spinomarginifera **sp.**	14(a.i,j*,l)
Waagenoconcha **sp**	6(a.b.c)
Leptodus **sp. cf. *L. tenuis*** **Waagen**	8(a.c.g.l)
Leptodus **sp.**	9(a).10(a).14(a.b.l).18(l.m)
	continue

Faunal list (other brachiopods)	Localities(references)
Callispirina sp.	14(j)
Camerophoria sp.	6(a.f)
Camerotoechia sp.	6(a.f)
Chonetes sp.	6(a.f.l)
Composita sp.	2(a.e).6(a.f).16(a)
Crenispirifer sp.	14(j)
Derbyia sp.	4(d).6(a.b.c.f.l).7(a.f). 13(c.l).14(a.b).17(l)
Dielasma sp.	5(a.e).7(a)
Hamletella sp. cf. *H. alta* (Hamlet)	4(a.e).5(a.e)
Hustedia sp.	15(a.k)
Martinia sp.	6(a.f).12(h).14(j)
Micraphelia sp.	4(d)
Neophricodothyris sp.	14(j)
Neospirifer sp.	13(c.l).15(a.k)
Nothothyris sp.	14(a)
Orthothethina sp.	14(j)
Orthotichia sp. cf. *O. dorashamensis* Sokolskaya	14(c.j)
Orthotichia sp.	14(a.l)
Phricodothyris sp.	13(c.l)
Purdonella sp.	13(c.l)
Schellwienella sp. cf. *S. ruber* (Frech)	14(a.i.l)
Schizophoria sp.	13(c.l)
Spirifer sp.	6(a.b.c.f).8(a.c).17(l)
Spiriferellina cristata (Schlotheim)	15(a.k)
Spiriferellina sp.	8(a.c).12(h).18(m)
Spiriferina sp.	9(a).14(a.b)
Squamularia sp.	2(a.e)
Stenoscisma sp.	6(b.c)
Streptorhynchus sp.	2(a.e).9(a)
Uncinulus sp.	3(a.e).9(a)
Uncinunellina timorensis (Beyrich)	8(a.g)
Waagenites sp.	17(l)

List of localities	Age	Zone (locality)
1. Pulau Jong (Langkawi). Kedah	L. Permian	Northwest Zone
2. Pulau Singa Besar (Langkawi). Kedah	-do-	-do-
3. Kisap. Langkawi. Kedah	-do-	-do-
4. Bukit Tungku Lembu. Perlis	-do-	-do-
5. Bukit Temiang. Perlis	-do-	-do-
6. Kampar (Nam Loong Beds). Perak	-do-	Western Zone
7. Kampar (H. S. Lee Beds). Perak	-do-	-do-
8. Sungai Jemuru. Pahang	U. Permian	Central Zone
9. Sungai Yu. Pahang	-do-	-do-
10. Sungai Galas. Kelantan	M. Permian	-do-
11. Sungai Pergau. Kelantan	-do-	-do-
12. Sungai Relai. Kelantan	U. Permian	-do-
13. Sungai Ciku. Kelantan	L. Permian	-do-
14. Jengka Pass, Pahang	U. Permian	-do-
15. Sungai Remih. Pahang	M. Permian	-do-
16. Kampung Awah. Pahang	U. Permian	-do-
17. Kuala Pilah (area). Negeri Sembilan	L. Permian	-do-
18. Kubang. Johor	M. Permian	-do-

Note : * - described productidinids and descriptive work
(see list of referenceuces below):

List of references:
a. Jones. Gobbett & Kobayashi (1966)
b. Gobbett (1973a)
c. Toriyama et.al. (1975)
d. Ishi et.al. (1972) * *locality 4*
e. Jones (1976)
f. Suntharalingam (1968)
g. Muir-wood (1948)
h. Yanagida & Aw (1979) -- * *locality 12*
i. Ichikawa. Ishii & Hada (1966)
j. Nakazawa (1973) * *locality 14*
k. Igo (1964) -- * *locality 15*
l. Geological Survey of Malaysia (1987)
m. Ibrahim Amnan (1987)

because there are many differences of opinion on fossil identifications given by later workers for the same localities. Even Gobbett himself (Gobbett, 1973b) has identified different faunal elements and revised faunal lists for some of the localities which he listed in Jones *et al.* (1966).

Current research has failed to locate the collection of fossils identified and summarized in Jones *et al.* (1966) for the purpose of re-identification. For this reason the list of the Permian brachiopods in table 4.2 is not updated and a more reliable list of Permian brachiopod faunas that have been studied by the author is given in table 4.3.

Current research and material studied

The purpose of this research is to identify and determine the distribution of Malaysian Permian productidinid brachiopods and to study aspects of their ecology and evolution. During this research material from the collection of the Malaysian Geological Survey Department and the Geology Department of the University of Malaya were studied besides a large collection made by the author before and during the tenure of this research.

The Malaysian Geological Survey Collection (GSD collection).

Without their own palaeontologist to work on the local fossil collections, the Malaysian Geological Survey Department usually sends fossils overseas to be identified. Some of these fossils were described by foreign experts as a matter of personal interest. The identified and described collection is carefully labelled and well stored. With this excercise and with limited funds available, normally only part of the fossils collected are identified. Those which are not well preserved and those which are difficult to transport remain unidentified. Most of the unidentified material in the Malaysian Geological Survey collection comes from the states of Pahang, Kelantan and Negeri Sembilan.

During this research, with cooperation from the Malaysian Geological Survey officials, their geologists (En. Khoo Han Peng and En. Ibrahim Amnan) and their senior laboratory assistant En. Amran Nali, these collections were made available for a brief study. Owing to limited time available, attention was focused on material which came from remote localities which have not been visited during the current research. The good records kept by the Malaysian Geological Survey Department allow the excact location and origin of the large unidentified collection to be determined.

The University of Malaya collection (UMcollection)

A substantial collection of Permian fossils including some brachiopods was made over the last few decades by various collectors in the Department of Geology (University of Malaya), mostly undergraduates who studied a particular region for their final year thesis. Of all those collections, the Permian brachiopods from Kampar are the most interesting. This is partly because of the abundance and very diverse composition and partly because this particular collecting locality, which was once the floor of an open cast tin mine, is no longer available for further research due to the flooding of the site in 1966 (Runnegar & Gobbett, 1975). By consent of the keeper of this particular collection (Dr. Idris Mohamad) this material was brought to Durham for more detailed study. The record of the collector is not very clear, but I beleived that this material was gathered together by Suntharaligam, Toong and Gobbett before the pit was flooded.

Current Research collection (UKM-MSL collection)

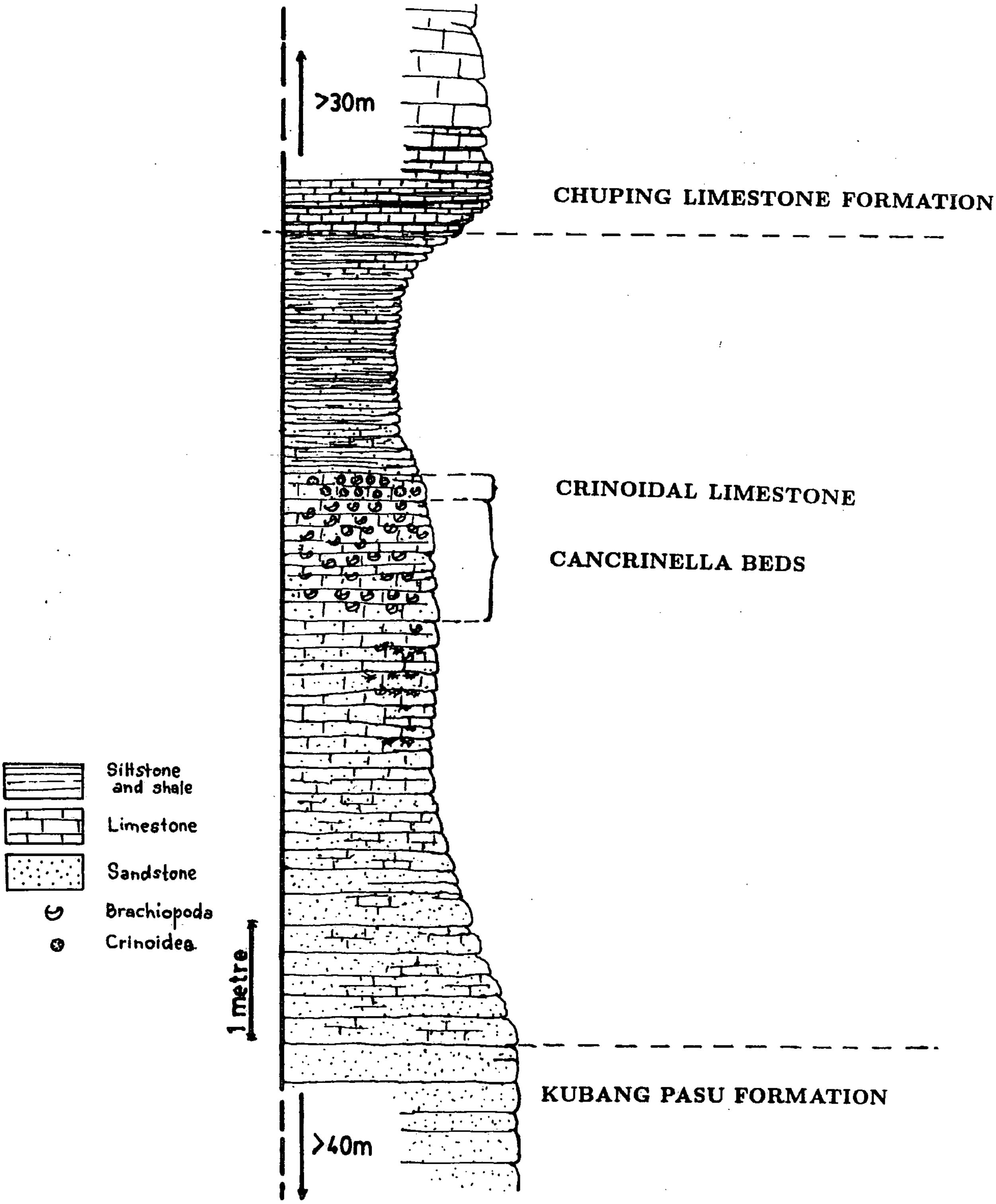
Owing to limited time and funds available collecting work for this research was restricted only to those easily accessible Permian brachiopod localities in Perlis, Pahang and Negeri Sembilan. Part of the collection has also come from field work made during the tenure of the University Kebangsaan Malaysia's Research Grants Nos 23/85 and 10/86 for the study of the general geology of the Kuala Lipis area and the Dada Kering - Gua Musang highway.

The current research collection comes from Bukit Tungku Lembu and Bukit Temiang in Perlis, from Kuala Lipis, Merapoh and Maran areas in Pahang and from Kampung Juaseh and Kampung Baru Kepis in the vicinity of Kuala Pilah, Negeri Sembilan. For further details on the distribution of these localities see text-figure 4.1, page 177. The geology of these collecting localities can be summarised as follows;

PERLIS AREA

Locality 1. Bukit Tungku Lembu, Perlis (GR. QN 247509)

About 40 meters above the base of the western foothill of Bukit Tungku Lembu the highly fossiliferous transitional or passage beds from the Kubang Pasu Formation to the Chuping Formation are exposed. At this point, the thickly bedded to massive quartzitic sandstones of Kubang Pasu Formation are seen to change gradually to recrystallized pure calcitic limestones of the Chuping Formation. The sandstone at the base of this exposure is about 20 to 30cm thick and it is overlain by about 3.5m of medium to thickly bedded brownish calcareous sandstone which in places contains small-scale, moderate to high angle cross-bedding of possible ripple origin. The top 1m of this bed is occasionally interbedded with shelly layers of *Cancrinella cancrini* (de Koninck). This calcareous sandstone is overlain by about 1.2m thin to moderate, irregularly bedded impure bioclastic limestones. The bottom 1m of this bed is dominated by *Cancrinella cancrini* with very few other accessory elements while the top of it is made of up to 20cm thick bed of very fragmented crinoid ossicles. This bioclastic limestone bed is followed by about 2m of eroded beds of softer rocks probably equivalent to the grey-green calcareous flaggy siltstone and shale beds of the Bukit Temiang succession (see Gobbett, 1973b). Above this eroded sequence are few meters of fine and irregularly bedded limestone interbedded with argillaceous and cherty laminae. Isolated fossils of unidentified gastropods, bivalves and brachiopods can be seen in these thin bedded limestones. These thinly bedded limestones gradually pass through to a more massive fine grain recrystallized limestone of the Chuping Formation. Here, gradual changes in colour from dark grey to light milky colour is seen from the bottom to the top of this limestone succesion. For further details, see



Text-figure 4.2. Stratigraphic column of the transitional beds at Bukit Tungku Lembu, Perlis.

text-figure 4.2.

Fossils and their preservation. The fauna of these transitional beds are mainly made up of brachiopods *C. cancrini* and fragmentary crinoid ossicles with very few accessory elements (see table 3 for the full faunal list). Most of the fossils are found in either the *C. cancrini* or the crinoid beds, some *C. cancrini* are also found in shelly layers on top of the calcareous sandstone beds and even on the flank of the crossbedded sandstones.

Most of the brachiopods and the bivalves are disarticulated and most of the productaceans have lost all their spines, while the crinoids and the bryozoans are very fragmentary in nature. This shows that the fauna has been subjected to a considerable degree of transportation before being laid down. In terms of preservation, some of the original shell material is still preserved showing good internal and external details, while some others are only preserved in the forms of moulds. Dissolution of the original shell material probably occurred partly during diagenesis and partly during weathering of the rocks after being exposed at the surface.

Locality 2. Bukit Temiang, Perlis (GR. QN 224508)

Very similar transitional beds has been reported by Gobbett (1973b) from Bukit Temiang, about 2.4 Km south of Bukit Tungku Lembu. From an isolated exposure of *C. cancrini* beds a few fossils mostly *C. cancrini* itself have been collected.

KUALA LIPIS AREA, PAHANG

The Gua Sai and Gua Bama limestones in the vicinity of Padang Tengku (in Kuala Lipis Map Sheet) has been considered to be of Carboniferous age since the work of Newton (1913), Procter (1975) (see also all the Geological Survey Annual Reports and Maps). Unfortunately, no further discovery of fossils has ever been reported to confirm Newton's findings. Procter (1975) divided his Raub Group into three formations in which he introduced the Padang Tengku Formation as the oldest formation, consisting the two limestone hills mentioned above and the surrounding non-calcareous rocks. He also generalized that his Raub Group is more or less younging westwards and assumed that his Triassic Lipis Group immediately east of Padang Tengku is unconformable over the Padang Tengku Formation. During my research on this supposed Lipis Group, I have failed to traced any unconformity between the non-calcareous rocks surrounding these two limestone hills and the overlying Triassic rocks. Furthermore, I also found that the limestone at Gua Sai pass laterally through to the non-calcareous rocks to the west in which a *Leptodus* shale is found; *Leptodus* bearing rocks in this area are known to be of Upper Permian in age (Muir-wood, 1948; Jones *et al.*, 1966; Gobbett, 1973b). Three *Leptodus* bearing fossil localities are reported for the first time in this thesis and they come from Kampung Gua, Kampung Garok and north Terenggun.

Note: Metcalfe (personal communication) suggests that the conodont assemblages of Gua Sai limestones are of Permian in age. The use of the term Raub Group at present is restricted to the Triassic formations and the term Lipis Group is no longer in use. The Permian rocks in Kuala Lipis area have much in common with the Gua Musang Formation found to the northwest of Kuala Lipis Map Sheet. Therefore, in this thesis the author employs the term Gua Musang Formation for the Permian rock succession in Kuala Lipis area (see also Mohd Shafeea Leman, 1987a).

Locality 3. Kampung Gua (GR. VE 65654355)

On the road (track) cut west of the Gua Sai limestone hill, thin to moderately bedded silty shales with a few fossils are exposed. About 30m south of it, on the track surface the shale becomes much finer and yields a much richer fauna with *Leptodus* present. The shale is reddish in colour and very highly weathered. The exact position of this shale is not known due to its highly weathered nature but it is estimated to be about 1 or 2m below the silty shales mentioned earlier. The fauna is preserved in the form of moulds probably as a result of weathering. The brachiopods, bivalves and solitary corals are normally preserved whole and scattered within the sediment body.

Locality 4. Kampung Garuk (GR. VE 642344)

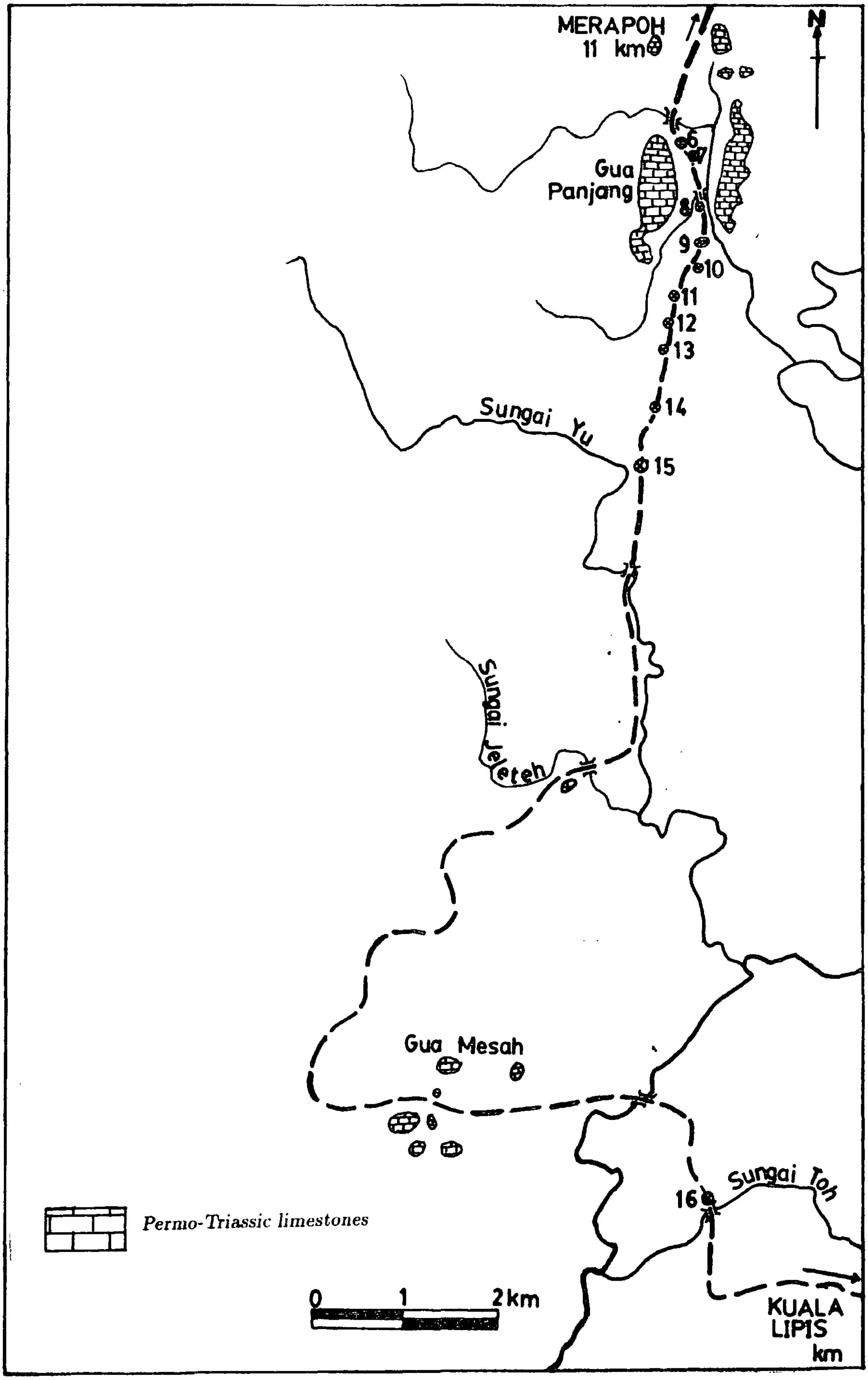
About 2.5 km south of Kampung Gua exposure, another track exposure revealed a slightly different fauna in a different kind of lithology. Here, fossils including *Leptodus* are found in a highly weathered tuffaceous siltstone and shale sequence which overlie a wedge of massive agglomerate and lappili tuff. The fauna in these highly weathered tuffaceous rocks are not well preserved. They are all preserved in form of moulds and [illegible] with traces of sulphide dissolution salt, indicating that the shell has probably been replaced by pyrite or other sulphide minerals prior to weathering process. The Kampung Garok fauna are also found as whole specimens and scattered within the sediment body.

Locality 5. North Terenggun (GR. VE 62454530)

About 0.9 km north-northeast of Terenggun Dam, lapilli tuff that is similar to those of the dam site is exposed. This lapilli tuff is overlain by tuffaceous silty shale which contains a few isolated brachiopods. The tuffaceous silty shale gradually becomes finer upward and at around GR. VE 62454530, which is about 5m above the lapilli tuff bed, it yields an interestingly rich fauna of dwarf brachiopods associated with some larger lyttoniids. This fauna is contained in a very fine tuff which is highly fractured and cleaved so that the large lyttoniids (mainly *Leptodus*) cannot be collected unbroken. Some of the fossils from this locality still have their original shell material preserved because the rock sequence was exposed only a short time before the collecting work was done. As in previous localities, most of the fossils are preserved in form of whole shells, scattered within the rock mass.

DADA KERING - GUA MUSANG HIGHWAY (MERAPOH MAP SHEET)

The Dada Kering - Gua Musang highway which connects Northwest Pahang and Southwest Kelantan passes through two major rock formations, the Permian - ?Lower Triassic Gua Musang Formation and the younger Bukit Tujuh granite which



Text-figure 4.3. Distribution of localities 6 to 16 along the Dada Kering - Gua Musang Highway, Northwest of Pahang.

baked part of the Gua Musang Formation during its intrusion (Mohd Shafeea Leman, 1987b). In between Bukit Tujuh and Merapoh, highway cuttings expose several Permian fossiliferous localities (see localities 6 to 16 below).

Locality 6 - 15. Gua Panjang - Sungai Yu halt

More than ten fossiliferous localities can be seen in several road cuts between Gua Panjang (Merapoh) and Sungai Yu halt (Km 12 to 16.2 Merapoh - Kuala Lumpur). An isolated fossiliferous locality is also found on the road cut immediately north of Sungai Toh (about Km 31.2 Merapoh - K. Lumpur). Details on lithology and fossil contents show that all these fossiliferous localities represent a singular fossil horizon within the Upper Permian of Gua Musang Formation. The most important faunal element in this horizon is *Leptodus* or related lyttoniids which can be found in almost all fossiliferous localities. Therefore this horizon can be tentatively related to the *Leptodus shale* of Muir-wood (1948).

Nearly all fossils from these localities are found in form of moulds which sometimes reveals accurate internal and external morphological details. The major problem faced in identifying these faunas is that they are usually strongly deformed by lateral compression in additon to the burial compression.

Locality 6 – GR. QZ 08174470. In between two mogotes of horizontal thinly bedded limestones (Gua Panjang hill in the west and unnamed hill in the east) lies a small exposure of highly weathered tuffaceous pebbly sandstones overlain by highly fossiliferous weathered slates. The fauna of these slates either accumulated in nearly horizontal layers or sometimes lie scattered within the sediments. In either case, they are generally highly deformed by lateral compression. This is shown by re-arrangement of fossil lineations into an almost vertical axis striking north-south, parallel to the secondary cleavage within this rocks. The fauna is made of brachiopods (mainly the spiriferids), bivalves, bryozoans and some remains of trilobite pygidia.

Locality 7 (GR. QZ 07854485) is an extension of the slates from locality 6, but the rocks here are much more weathered than that of the previous locality. However, a few remains of fossils including some brachiopods are still recognisable from these highly weathered rocks.

At **locality 8 (GR. QZ 07254485)** weathered indurated mudstones of less compressed nature than the slate from locality 6 are exposed in a drainage trench west of the highway. This slightly weathered indurated mudstones yields numerous brachiopods including some productidinids, gastropods and some bivalves. Accumulation of fossils into one particular layer is rather less common, but whenever this occurs, fragmented shells are conspicuous.

At **locality 9 (GR. QZ 069448)** the highway cuts about 35m of very hard yellowish grey slates which are rapidly softened and altered to reddish in colour by weathering. The highly weathered slates from this locality are very similar in appearance with that of locality 6 and 7. The fauna of this locality commonly accumulated on laterally compressed bedding planes, so that the fossils are highly distorted.

Locality 10 - GR. QZ 065447. The surface exposure afforded by an abandoned construction vehicles station at this locality reveals dark grey to reddish tuffaceous shales rich in brachiopods (especially large orthids), bivalves and gastropods. Also found here are bryozoans, trilobites and plant remains. Most of the fossils are well preserved with slight compression to the original shape following the shaly cleavage. Some of the fossils still have their original shell preserved.

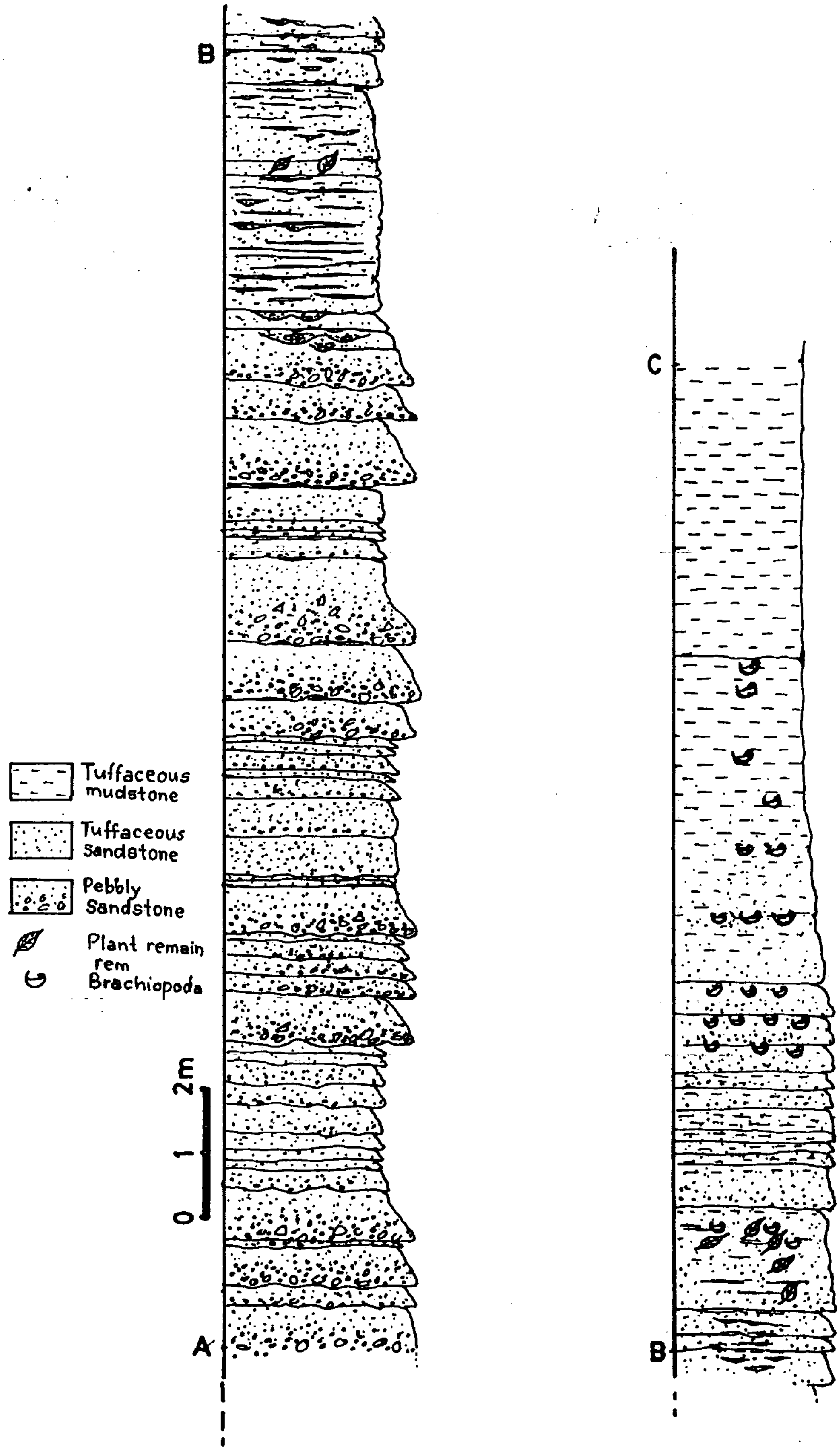
Locality 11 - 14 - GR. QZ 06084442, 05804435, 05604430 and 04804478. Weathered indurated mudstones similar to that of locality 8 are exposed at several places between locality 9 and Sungai Yu halt. Faunal elements of these localities vary from one another, but in general the fauna is dominated by brachiopods with *Leptodus* or related lyttoniids forming an essential element.

Locality 15 - Sungai Yu Halt - GR. QZ 04204405. A large road cut east of Sungai Yu halt exposes reddish weathered slates overlying less weathered dark grey calcareous slates with thin lenses of marl and oolitic limestone. Fossils are found in several layers within the weathered slates, calcareous slates and limestones. They are normally affected by a quite strong lateral compression, similar to that of locality 6 and 9.

Most of the brachiopods are found in the weathered slates and the less calcareous slates.

Locality 16. North Sungai Toh road cut (*GR. QZ 95204508)*

An isolated fossiliferous locality is also found in the road cut immediately north of Sungai Toh (about Km 31.2 Merapoh - K. Lumpur). At this locality, the highway cuts through about 230m of the western flank of folded tuffaceous pebbly sandstones, sandstones, siltstones, shales and indurated mudstones. The southern half of the exposure forms a normal open fold while toward the north end of the cutting it changes to an isoclinal fold. Fossils are found on both flanks of the open fold which are exposed on both sides of the highway. This open fold shows very interesting lithological and biotic changes from the bottom (south) to the top (north). The core of the fold is made of unfossiliferous tuffaceous pebbly sandstones and non-pebbly sandstones which are uniformly moderate to thickly bedded. This sandstone sequence is followed by an irregularly bedded tuffaceous sandstone, siltstones and mudstones commonly grading one into another, with occasional beds of coarser pebbly sandstones. At the top of this sequence, the coarser tuffaceous sandstones and pebbly sandstones occur as small scale channel lag deposits or in the form of small lenses within finer tuffaceous rocks. At these horizons the tuffaceous sandstone - siltstone - mudstone sequences are frequently interbedded with laminae of plant debris, some of which are replaced by recently developed iron pan. Above this sequence the flora becomes less fragmented and individual specimens are recognisable, while the sand grains become finer. The first fauna appears when the sediments becomes finer and regularly bedded about 6m above the first horizon of plant debris. At first, both fauna and flora are found together, but after about 0.5m the flora vanishes and is succeded by a succession about 7.4m thick containing an Upper Permian fauna. The sediments enclosing this fauna are made of tuffaceous siltstones or very fine sansdtones. They fine upwards continuously upwards until they finally become a very fine indurated white tuffaceous mudstone at the top of the whole succession. Within this faunal succession, several fragmentary shelly layers are traceable within the first 4.5m, while above it the fauna becomes scarce as the sediments become very fine. Most of the fauna are preserved



Text-figure 4.4. Stratigraphic column at locality 16, north of Sungai Toh, Merapoh, Pahang.

in the form of moulds. Details on the rock section from this locality is illustrated in text-figure 4.4.

MARAN AREA, PAHANG (EAST) (MAP SHEET 71, 89 & 90)

Several isolated Permian outcrops have been reported from this area including the well documented Jengka pass Permian. In this thesis, faunas from two other fossiliferous localities are introduced beside the Jengka Pass fauna. They are fauna from Bukit Jaya road cut and from Maran Oil Palm mill.

Locality 17. Jengka Pass (GR. WF 91651445) - Sheet 89

The Jengka Pass exposure and its celebrated unconformity in between the Upper Permian and the Upper Triassic has been illustrated in great detail by Gobbett (1973b), Kon'no & Asama (1970) and Nakazawa (1973), while its fauna and flora has been mentioned in so many publications and well described in Fontaine *et al.* (1988), Ichikawa *et al.* (1966), Ishii (1966), Kon'no & Asama (1970) and Nakazawa (1973). Permian brachiopods have recorded from both the limestones (Gobbett, 1973b), the carbonaceous shales and the tuffaceous sandstones (Ichikawa *et al.*, 1966 and Nakamura, 1973). The fauna in my collection comes from the carbonaceous shales formerly assigned to bed M40A by Kon'no & Asama (1970) and Yanagida (1973). They consist of productidinid and spiriferid brachiopods, bivalves, bryozoans and fusulinid forams and are preserved as moulds.

Locality 18. Bukit Jaya Road Cut (GR. WA 431967) - Sheet 71

Bukit Jaya road cut is mainly made of carbonaceous and pebbly slates, siltstones, mudstones and sandstones and cherts with a lot of down slope movement structures. At the eastern end of the road cut the sedimentary bedding becomes more uniform and at a locality around GR. WA 431967 thinly bedded pebbly chiastolitic slates interbedded with pebbly carbonaceous sandstones yield scattered fossils mostly fusulinid forams with a few bivalves and brachiopods. The brachiopods are generally poorly preserved and strongly flattened.

Locality 19. Timor oil palm mill (GR. WA 00753240) - Sheet 90

At the northeastern corner of the Timor Oil Palm mill, another exposure shows carbonaceous, cherty slates and siltstones interbedded with thickly bedded sandstones and faulted against a massive meta-arenite. The siltstones and slates are fossiliferous in places with the fauna dominated by fusulinid forams and a few brachiopods and bivalves.

KUALA PILAH AREA, NEGERI SEMBILAN

The Permian Kepis Bed is well exposed in Kuala Pilah area in between Kuala Pilah and Bahau. Several fossiliferous localities are found in Batu Kikir, Kampung Juaseh and Kampung Baru Kepis, but most of these fossiliferous exposures only yield Permian bivalves. Permian brachiopods are found at one locality in Kampung Juaseh and several localities in Kampung Baru Kepis.

Locality 20. Kampung Juaseh (GR. VK 35502295)

At the southern road cut of this locality, a wedge of polymictic conglomerate overlain by moderate to thickly bedded indurated mudstones are exposed. The mudstones yield a rich fauna of brachiopods and bivalves with very few other fossils. The fauna is preserved in the form of moulds and the specimens are commonly deformed and fractured by joint planes.

Locality 21. Kampung Baru Kepis (GR. VK 27853055)

A terrace cutting on a small hill east of Kampung Baru Kepis reveals a rather chaotic sedimentary sequence where angular blocks of various origins (sometimes reaching more than one metre in diameter) are randomly distributed in mudstones and siltstones matrices. Fossils are occasionally found in these blocks, but some brachiopods are also found in the matrix.

The Malaysian Permian brachiopods studied in this thesis

During this study, 23 species of productidinids are identified and described, the detailed of which comprise Chapter 5 of this thesis. All the studied species are listed in table 4.3 (below). Owing to shortage of time and material, less exact treatment is given to the Malaysian Permian Productidina as compared to those of Britain. This inevitably has left a number of uncertain species in the faunal list, partly due to lack of complete specimens and partly due to insufficient comparative material available. More detailed studies on some of the important faunas are suggested as a project to be pursued after the completion of this thesis, and this will be done by the author in Malaysia in the very near future, when access to more material will be possible (p. 241).

Table 4.3. List of the studied Malaysian Permian Productidina

Productidinid species	Localities*	Age ranges
Antiquatonia sp. A	10,20,21,26	L. - U. Permian
Cancrinella cancrini (de Koninck)	1,2	L. Permian
Cancrinella sp. cf. *C. cancriniformis* Tscher.	20	L. Permian
Cancrinella sp. A	23	L. Permian
Costispinifera sp. A	11,17,27	U. Permian
Craspedalosia sp. A	23	L. Permian
Dictyoclostus? gratiosus (Waagen)	5,8,10,11,14,16,25	U. Permian
Dictyoclostus sp. indet.	19,28	U. Permian
Echinauris sp. indet.	10,11,29	U. Permian
Echinauris? sp. A	23	L. Permian
Echinoconchus sp. A	23	L. Permian
Institella sp. A	22	L. Permian
Linoproductus sp. cf. *L?. sinosus* Huang	6,7,9,10,13	U. Permian
Liosotella nakamurai n. sp.	17,18	U. Permian
Marginifera? sp. A	20	U. Permian
Paucispinifera sp. A	29	U. Permian
Reticulatia sp.indet.	5,8,14,16,19	U. Permian
Retimarginifera lipisensis n. sp.	3,4,5,8,12,15,25	U. Permian
Striatifera sp. A	23	L. Permian
Stepanoviella sp. cf. *S. flexuosa* Waterhouse	24	L. Permian
Strophalosia sp. A	25	U. Permian
Waagenoconcha sp. cf. *W. abichi* (Waagen)	23	L. Permian
Waagenoconcha sp. indet.	16	U. Permian

Localities* — Localities 1 - 21 are described earlier in this thesis where the collection was made personally by the author. Localities 22 - 29 are localities in which the collection was made by other researchers, and the specimens are made available for this study by the Geological Survey Department and the Department of Geology, University of Malaya.

Locality 22 - Pulau Jong, Langkawi, Kedah.

Locality 23 - H. S. Lee mine pit no 8, Kampar. Perak.

Locality 24 - Kampung Baru, Kepis, Negeri Sembilan.

Locality 25 - Railway cut adjacent to Sungai Jeleteh, Merapoh, Pahang.

Locality 26 - Sungai Sepia, Kuala Lipis, Pahang.

Locality 27 - Ulu Lepar, Maran. Pahang.

Locality 28 - Sungai Galas, Gua Musang, Kelantan.

Locality 29 - Sungai Paloh, Kuala Krai, Kelantan.

CHAPTER 5

SYSTEMATICS OF THE MALAYSIAN PERMIAN PRODUCTIDINA

Suborder PRODUCTIDINA Waagen
Superfamily STROPHALOSIACEA Schuchert
Family STROPHALOSIIDAE Schuchert
Subfamily STROPHALOSIINAE Schuchert
Genus *STROPHALOSIA* King 1844
STROPHALOSIA sp. A
(Text-figure 5.1A, Plate 15, figure 1)

Material. A single poorly preserved specimen no. LF 176 (GSD collection) from railway cut adjacent to Sg. Jeleteh, Merapoh, Pahang shows the dorsal view of the internal mould of an undetermined species of *Strophalosia.*

Horizon and Age. Upper Permian *Leptodus* Bed.

Description. The shell is 13mm long and 10mm wide with the maximum width acquired at the anterior quarter of the shell. The shell plan outline is subtriangular in shape. The dorsal valve is weakly concave with the interior reflecting a few concentric growth rugae. The adductor muscle platform is roughly pear shaped and the median septum extends to about half the length of the valve. The interarea of the ventral valve is high and wide with triangular shape and sharply pointed tip. The delthyrium is poorly preserved, but posterior excavation of the interarea exposed a pair of large teeth at the base of the broken pseudodeltidium. Several randomly arranged posteriorly directed spines probably belong to the ventral valve are seen in the matrix posterior to the shell. Other details of the specimen are unknown.

Discussion. The large teeth and high ventral interarea shown by this specimen suggests that it belongs to the genus *Strophalosia.* However, until more details are known it is impossible to assign this specimen to any particular species or genus with absolute certainty.

Family STROPHALOSIIDAE Schuchert

Subfamily HETERALOSIINAE Muir-Wood & Cooper

Genus *CRASPEDALOSIA* Muir-Wood & Cooper 1960

CRASPEDALOSIA sp. A

(Plate 12, figures 1,2)

Material. One incomplete dorsal valve - specimen no 2727 (labelled as Echinosteginae?) collected by D. J. Gobbett and C. T. Tan from H. S. Lee Mine no 8, near Kampar, Perak (UM collection).

Horizon and Age. Nam Loong Bed, Lower Permian.

Dimensions. The dorsal valve of specimen 2727 is more than 22mm in length and 13mm in width.

Description. The profile of the dorsal valve is convex posteriorly and flat anteriorly. The dorsal valve shows an abraded rugate dorsal surface, which left the umbo smooth. The shaft of the cardinal process is long (2.7mm in length), and posteroventrally pointed. The cardinal process is buttressed by a strong median ridge which extends anteriorly as the median septum. The median septum is highly elevated at its anterior extremity. The adductor muscle platform is quite large in size and highly elevated anteriorly. Other details are unknown.

Discussion. Unlike that of other aulostegacean, the long shafted cardinal process without alveolus in *Craspedalosia* sp. A is genuinely a strophalosiacean feature. The non-spinose rugate and possibly squamose dorsal valve and long shafted cardinal process in the described specimen is characteristic of the genus *Craspedalosia.* As compared to other species of *Craspedalosia*, *Craspedalosia* sp. A has a dorsal valve with larger convex area, larger size adductor muscle platform and highly elevated median septum. Unfortunately, other details are not available for further discussion and possibly for designation of a new species.

Suborder PRODUCTIDINA Waagen
Superfamily AULOSTEGACEA Muir-Wood & Cooper
Family AULOSTEGIDAE? Muir-Wood & Cooper
Subfamily INSTITELLINAE Muir-Wood & Cooper
Genus *INSTITELLA* Cooper 1942
INSTITELLA sp. A

(Plate 12, figure 3)

Material. Specimen no 1353 (labelled as *Reticulatia* sp.) collected by D. J. Gobbett from Pulau Jong, Langkawi, Kedah (UM collection). This specimen might be the one refered as *Reticulatia* sp. by Gobbett (1973b), Jones (1976) and Jones *et al.* (1966).

Horizon and Age. Chuping Formation, late Lower Permian.

Description. The maximum shell width is about 60mm, positioned slightly anterior to the hinge line. The ventral valve is weakly convex with moderately developed median sulcus, small incurved umbo and large flattened auricle. The lateral trail is conjoined with the auricle, but it is slightly swollen. The umbo and the visceral disc are strongly reticulate, but the intensity of reticulation is fainter towards the anterior and lateral margins. The posterior margin is strongly wrinkled and weakly reticulate. Several large laterally directed spines are developed on the auricle. Marginal spines, when preserved are large, posteriorly directed and rhizoid in nature. The ventral interarea is very low, but wide, hidden under the incurved umbo medianly. The dorsal valve is weakly concave with depressed umbo and weakly developed median sulcus. The visceral cavity is limited in size. Apart from the absence of dorsal spines, the dorsal ornamentation is similar to that of the ventral valve. Other details are unknown.

Discussion. The very narrow visceral cavity and the development of flat trail dismiss the possibility of this specimen being associated with the genus *Reticulatia*. The presence of rhizoid spines and a very low ventral interarea indicate that it is an aulostegacean, while the nature of the trail suggests that it belongs to the genus *Institella*. *Institella* sp. A resembles the type species, *I. leonardensis* Cooper from the Permian of Texas, in its reticulate ornament, but *I. leonardensis* shows a more complete recurving of the trail and more numerous rhizoid cementing spines as compared to *Institella* sp. A. Until more specimens are available, the author will reserve opinion on the specific status of this material.

Suborder PRODUCTIDINA Waagen
Superfamily PRODUCTACEA Gray
Family DICTYOCLOSTIDAE Stehli
Subfamily DICTYOCLOSTINAE Stehli
Genus *DICTYOCLOSTUS* Muir-Wood 1930
DICTYOCLOSTUS? GRATIOSUS (Waagen) 1884

(Text-figure 5.1C-F, Plate 12, figures 4-9, Plate 15, figure 12)

Synonymy:
1884 *Productus gratiosus* Waagen, p. 691, pl. 72, fig. 3-7.
1916 *Productus gratiosus* Waagen; Broili, p. 12-13, pl. 66, fig. 4-5, 7-13.
1927 *Productus gratiosus* Waagen; Chao, p. 44, pl. 4, fig. 6-10.
1932 *Productus (Dictyoclostus)* aff. *gratiosus* Waagen; Huang, p. 32-33, pl. 2, fig. 3.
1933 *Productus (Dictyoclostus)* cf. *gratiosus* Waagen; Huang, p. 33-34, pl. 2, fig. 4-5.
1944 *Marginifera gratiosa* (Waagen); Reed, p. 98-99, pl. 19, fig. 6-7.
1979 *Productus* sp. cf. *"P". gratiosus* Waagen, Yanagida & Aw, p. 132-133, pl. 28, fig. 18.

Localities and Material. Locality 8 (2 specimens), locality 10 (6 specimens), locality 11 (4 specimens), locality 14 (1 specimen) and locality 16 (6 specimens), near Merapoh, and north Terenggun (6 specimens), near Kuala Lipis, Pahang (UKM-MSL collection).

Horizon and Age. Upper Permian *Leptodus* Bed.

Description. The shell is small in size, transversely subtrapezoidal to squarish in shape with the whole surface heavily costate and reticulate. The ornamentation is so strong that even the interior shows its reflection. The ventral valve weakly to strongly convex with short or long geniculated trail and well developed median sulcus

Table 5.1. *Dictyoclostus? gratiosus* **(Waagen) - dimensions in mm**

Specimen no	length	curved length	hinge width	height
MSL10.1a	10.4	na	e11.4	na
MSL10.1b	9.5	na	e13.5	e2.5
MSL10.1c	9.1	na	e16.2	e2.5
MSL16.1a	10.0	e13.7	e17.0	4.6
MSL16.1b	11.4	e14.4	e17.8	e3.5
MSL16.1c	9.9	e17.0	e15.6	7.5

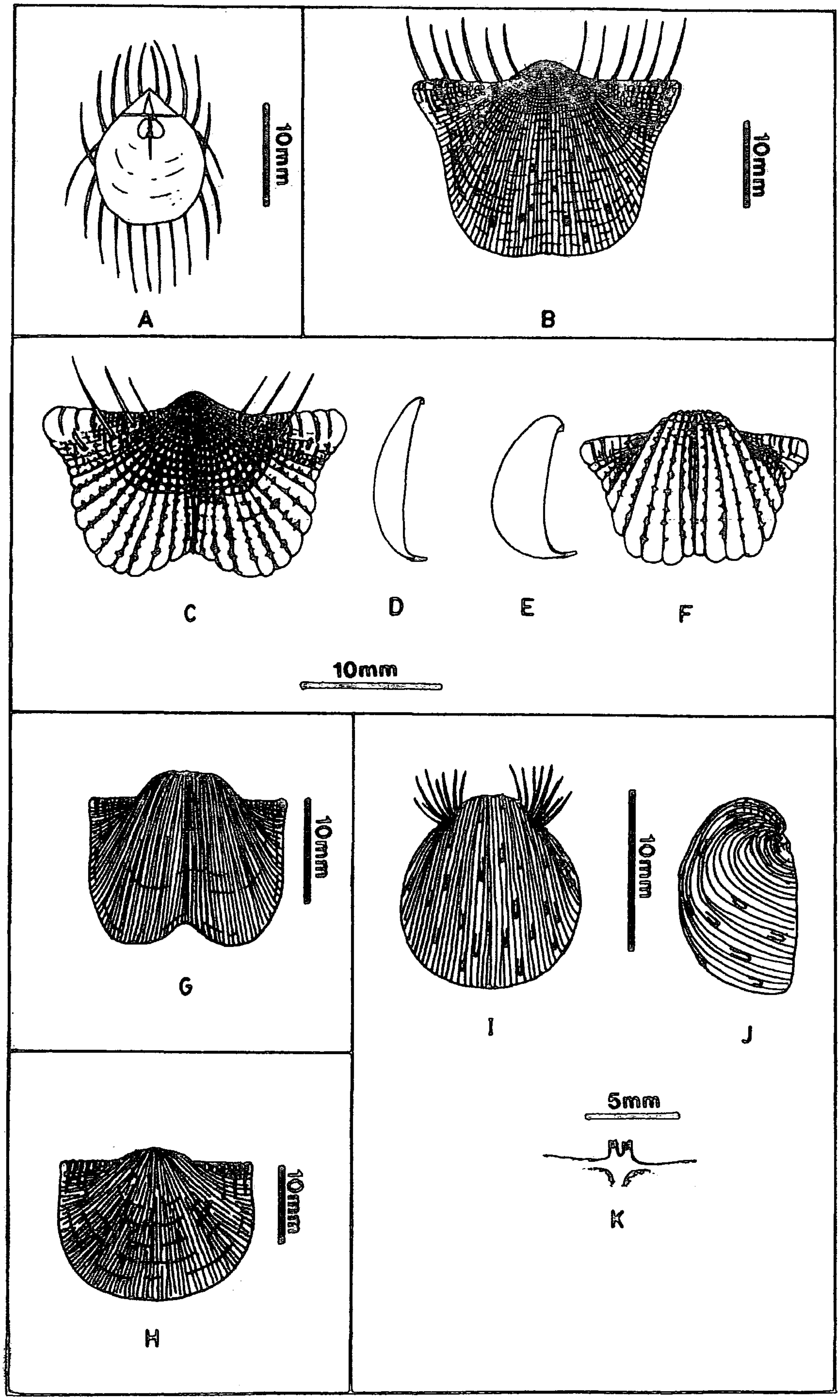
dimensions = refer to text-figure 1.1
na = not available e = estimated

dividing the visceral disc into two halves anteriorly. The median sulcus is shallower towards the posterior and becomes obsolete at the umbo. The very strong reticulation gives the ventral valve a rather grated appearence, especially at the umbonal region. The reticulation is weaker towards the anterior, but usually persists through to the anterior margin. The costae are coarse, bifurcate and radiate from two separate nuclei on each half of the visceral disc, thus the costae usually converge into the median sulcus medianly. The number of costae at the anterior margin of each half of the visceral disc ranges from 8 to 12.

The auricle is moderate to well developed, triangular in shape, and flat or slightly swollen in profile. It is provided with a fine reticulate radial costae and strong wrinkles at the posterior margin. The hinge line is wide and represents the maximum width of the shell. The auricular spines comprise a row of two or more spines (probably halteroid) at the base of the convex visceral disc. No other spines is known.

The dorsal valve is moderately concave and closely follows the curvature of the ventral valve, leaving a very limited visceral cavity between them. The spines are not known from the dorsal valve, but other surface ornamentation is very similar to that of the ventral valve. Other details are unknown.

Discussion. When Waagen (1884) described *P. gratiosus*, his figures seems to show two rather separate varieties, one with strongly convex ventral valve, long trail, small


A
10mm
B
10mm
C
D
E
F
10mm
G
10mm
H
10mm
I
J
10mm
5mm
K

Text-figure 5.1. Reconstructions of Malaysian Permian Productidina I

Figure A - *Strophalosia* sp. A - interior of dorsal valve and ventral interarea.

Figure B - *Antiquatonia* sp. A; ventral exterior.

Figure C - *Dictyoclostus? gratiosus* (Waagen); ventral exterior of variety II.

Figure D - lateral profile of C.

Figure E - lateral profile of variety I of the same species.

Figure F - ventral exterior of E.

Figure G - *Linoproductus* sp. cf. *L? sinosus* Huang; ventral exterior.

Figure H - *Stepanoviella* sp. cf. *S. flexuosa* Waterhouse; ventral exterior.

Figures I, J - ventral and lateral exterior of *Cancrinella cancrini* (de Koninck).

Figure K - cardinal process of the same species.

auricle and more spines on the ventral valve (see Waagen 1884, pl. 72, fig. 3-5), while the other has less convex ventral valve, short trail, large auricle and hardly any spines on the ventral valve (Waagen 1884, pl. 72, fig. 6-7). The generic status of this species was debated by later authors and some avoided discussion of this species in their general taxonomic classification. This is probably because the original description is incomplete and lacks features of high taxonomic value. *P. gratiosus* has been associated with the genus *Dictyoclostus* by Huang (1932, 1933) and Muir-Wood & Oakley (1941), and to the genus *Marginifera* by Licharev (1936) and Reed (1944), while other authors maintain its questionable relationship to the genus *Productus*.

The first variety of Waagen's (1884) species *P. gratiosus* seems to belongs to the family Dictyoclostidae, even though most dictyoclostids do not have a very strong median sulcus. It might belong to a separate new genus in this family, but until better and more complete specimens are available it is not possible for the author to place this species precisely in any particular genus. This variety is not very common in the Permian of Malaysia, and it is illustrated in text-figures 5.1E,F and plate 13, figure 9 under *Dictyoclostus? gratiosus* (Waagen) variety A.

The second variety of Waagen's (1884) *P. gratiosus* might represent an incomplete part of the first variety, but many more complete specimens similar to it figured by later authors seem to give it a rather separate identity from the first variety (see Broili (1916, pl. 66, fig. 5, 9-12), Huang (1932), Reed (1944) and Yanagida & Aw (1979)). The low visceral cavity in this variety is not a characteristic of the genus *Dictyoclostus*, but there are no other features which might associate this variety with other productacean families. Although Reed (1944) tried to illustrate the presence of a marginal ridge in this variety, his figures are not very convincing. If Reed's (1944) postulation is accepted, this variety should have its own specific identity, under a new genus very close to the paucispiniferinid genus *Reticulatia* Waterhouse. This variety is more common in the Permian of Malaysia, and it is illustrated in text-figures 5.1C,D and figured in plate 13, figures 4-8 and plate 16, figure 12.

Forms associated with Waagen's (1884) *P. gratiosus*, have been recorded from several Upper Permian localities in Asia, and it becomes an important element in the Upper Permian (Wuchiapingian) of South China. The Malaysian occurrences also seem to be restricted to those horizons associated with llytoniids, except that from South Central Kelantan which was dated as late Upper Permian by Aw *et al.* (1977) and Yanagida & Aw (1979). Because of its stratigraphic importance, *Dictyoclostus? gratiosus* must be studied in more detail in the future for clarification of its taxonomic status.

DICTYOCLOSTUS? sp. indet.

(Plate 15, figures 2,3)

Material. Several specimens in 3 rock slabs no FPhN 19 from Sungai Galas, South Kelantan (GSD collection) and 1 specimen from Bukit Jaya, near Maran, Pahang (UKM-MSL collection).

Horizon and Age. Upper Permian *Leptodus* Bed and unnamed formation of ?Upper Permian age.

Description. The ventral valve is very strongly deformed and not representing the true shape and curvature of the shell. Therefore, the dimensions of the shell are not easy to measure. Some of the large flattened specimens have a maximum shell width of about 20mm or more. The umbo and the visceral region is finely reticulate while the trail is broadly costate. The median sulcus is poorly defined. The auricle is small and often weakly wrinkled. No traces of body spines or auricular spines are known. The dorsal valve is unknown.

Discussion. Owing to a poor preservation, it is difficult to assign these specimens to their proper genus and species with absolute certainty. These specimens resemble *Antiquatonia* sp. A in their reticulate and costate ornamentation, but the absence of body spines differentiate this species from them. The fine body spines which characterise the genus *Dictyoclostus* might have been destroyed during fossilization.

Genus *ANTIQUATONIA* Miloradovich 1945

ANTIQUATONIA sp. A.

(Text-figure 5.1B, Plate 12, figures 10-13, Plate 15, figures 4-6)

Synonym:
1964 *Dictyoclostus* sp. A, Igo, p. 67, text-fig. 6.
1964 *Dictyoclostus* sp. B, Igo, p. 67-8.
1964 *Dictyoclostus* sp. C, Igo, p. 68.

Material. Specimens no L 1096 (26, 29a,b, 30, 31 and 32a,b) from Sg. Sepia, near Kuala Lipis, Pahang (GSD collection), 5 specimens from locality 10, near Merapoh, Pahang and 8 incomplete specimens from Kg. Juaseh, near Kuala Pilah, Negeri Sembilan (UKM-MSL collection)

Horizon and Age. The age ranges from late Lower Permian (Kepis Bed) to Upper Permian (*Leptodus* Bed).

Table 5.2. *Antiquatonia* **sp. A - dimensions in mm**

Specimen no	length	curved length	hinge width
MSL10.2a	e10.4	17.8	19.0
MSL10.2b	na	e18.7	26.7
L1096(26)	10.0	na	13.9

dimensions = refer to text-figure 1.1
e = estimated na = not available

Description. The shell is medium to large in size with maximum dimensions reaching 50mm. The plan outline is variable in shape due to deformation. The ventral valve is weakly convex with long and geniculated trail, moderately developed auricle and small umbo. The median sulcus is fairly deep at the convex part of the visceral disc, shallower towards the umbo and the anterior margin. The umbo and the posterior part of the visceral disc is furnished with reticulate ornament. The reticulation of the shell is fainter towards the anterior trail, where it is replaced by 40 to 60 well developed radial costae which sometimes bifurcate before reaching the shell margin. The auricle is strongly wrinkled, and the wrinkles are often crenulated. The body spines consist of less than ten large randomly arranged halteroid spines at the trail and a few smaller spines on the posterior part of the visceral disc. Five to six pairs of posteriorly directed marginal spines are developed on the posterior margin. Two rows of two to five auricular spine bases are seen at the base of the visceral disc, but the nature of the spines are not known. The ventral adductor muscle platform is moderately elevated and the muscle impressions are dendritic.

The dorsal valve is only depressed at the umbo, while the rest of the visceral disc is flat with strongly geniculated trail. The ornamentation of the dorsal valve is similar to that of the ventral valve, except that the dorsal valve has no spines. Interiorly, the cardinal process is large and sessile with the bilobed or quadrilobed myophore facing dorsally. Other details are unknown.

Discussion. The large body spines randomly set on the crest of the costae put this species into the genus *Antiquatonia*, instead of *Dictyoclostus* as it was previously assigned by Igo (1964). The genus *Antiquatonia* is widespread during the Carboniferous time, while only a few species of *Antiquatonia* are known from the Permian. *Antiquatonia* sp. A resembles the Upper Permian species *A. planumbona* Stehli from Word Formation of Texas, in its reticulate ornamentation, but the spines of *Antiquatonia* sp. A are slightly coarser and less in number as compared to *A. planumbona*.

Genus *RETICULATIA* Muir-Wood & Cooper 1960

RETICULATIA sp. indet.

(Plate 12, figures 16-18)

Material. Three incomplete external moulds (one of which contains broken internal mould of the cardinal process) from locality 16, near Merapoh, and one incomplete cast and/or mould of the exterior of ventral valve each from locality 8 and 14 near Merapoh, north Terenggun near Kuala Lipis and Bukit Jaya near Maran, all in Pahang (UKM-MSL collection).

Horizon and Age. *Leptodus* Bed (Upper Permian) and unnamed formation of Upper Permian age.

Remarks. The ventral valve is strongly reticulate, stronger at the umbonal region and slightly weaker towards the anterior and at the lateral posterior margin. The ventral valve is strongly convex with weak median sulcus, short smoothly curved trail, small incurved umbo and poorly defined auricle. The dorsal valve is weakly concave with poorly defined median fold. The cardinal process is short and sessile with ?bilobed or ?quadrilobed myophores, and dorsally facing muscle attachment base. *Reticulatia* sp. differs from the strongly reticulated *Dictyoclostus? gratiosus* in its poorly developed median sulcus and auricle. No attempt can be made to relate this uncertain species with any known species of *Reticulatia*, until a better collection of more complete specimens is available. [MSL16.2a - estimated dimensions; length = 17.2mm, width = 32.5mm].

Family ECHINOCONCHIDAE Stehli

Subfamily ECHINOCONCHINAE Stehli

Genus *ECHINOCONCHUS* Weller 1914

ECHINOCONCHUS sp. A

(Plate 12, figures 19-23)

Material. 18 unnumbered specimens from H. S. Lee Mine no 8, near Kampar, Perak (UM collection).

Horizon and Age. Nam Loong Bed, Lower Permian.

Description. The shell is small to medium in size, with posteriorly tapered subtrapezoidal to subtriangular shell plan. The ventral valve is strongly convex with poorly defined median sulcus and small and poorly defined auricle. The umbo is large and strongly incurved. The ventral surface is covered by a series of concentric bands on which are set several concentric rows of spines. In smaller individuals, only one concentric row of spines are usually preserved on each band, while in larger individuals each band usually carries one row of larger spines and two to three rows of much finer spines. The spines are very fine in size and are suberect in nature. The dorsal valve

Table 5.3. *Echinoconchus* **sp. A - dimensions in mm**

Specimen	length	curved length	max. width	hinge width	height
UM-1b	9.9	e18.9	11.5	na	3.8
UM-1d	14.7	23.9	e18.9	e13.2	8.4
UM-1f	5.9	9.5	e6.6	na	3.7
UM-1g	8.7	15.7	11.8	e8.9	4.5
UM-1h	11.9	e19.0	e17.5	na	5.5

dimensions = refer to text-figure 1.1
na = not available e = estimated

is moderately concave with prominent concentric bands which commonly represent the more or less uniform growth lamellae. Other ornamentation is similar to that of the ventral valve. The interior morphology is unknown.

Discussion. The available details on the external morphology of the described specimens above show that they belong to the genus *Echinoconchus.* However, lack of complete morphological details especially the internal morphology does not allow the author to give these specimens a more specific denomination.

Family ECHINOCONCHIDAE Stehli
Subfamily WAAGENOCONCHINAE Muir-Wood & Cooper
Genus *WAAGENOCONCHA* Chao 1927
WAAGENOCONCHA sp. cf *W. ABICHI* (Waagen) 1884

(Plate 12, figures 25-28)

cf:
1884 *Productus abichi* Waagen, p. 697, pl. 74, fig. 1-7
1927 *Waagenoconcha abichi* (Waagen); Chao, p. 87, pl. 7, fig. 7-8.
1960 *Waagenoconcha abichi* (Waagen); Muir-Wood & Cooper, pl. 89, fig. 1-5.
1966 *Waagenoconcha abichi* (Waagen); Grant, p. 660-662, fig. 1-2.

Material. 7 ventral valves of unnumbered specimens from H. S. Lee Mine no 8, near Kampar, Perak (UM collection).

Table 5.4. *Waagenoconcha* **sp. cf.** *W. abichi* **(Waagen) - dimensions in mm**

Specimen	length	curved length	max. width	hinge width	height
UM-2a	14.4	e22.0	e17.5	na	6.4
UM-2b	8.6	e11.5	10.8	e7.6	4.1
UM-2c	14.5	22.4	e17.0	e13.0	6.6
UM-2d	7.0	e9.0	e7.5	e6.5	2.5

dimensions = refer to text-figure 1.1
na = not available e = estimated

Horizon and Age. Nam Loong Bed, Lower Permian.

Description. The shell is small in size with subcircular to posteriorly tapered subtrapezoidal plan outline. The ventral valve is strongly convex with poorly defined median sulcus and auricle. The umbo is small, but strongly incurved. The ventral surface is marked by densely spaced fine spines which are set in quincunx arrangement. The spines are suberect in nature. Other ornament is inconspicuous. Details on the internal morphologhy and the dorsal valve is unknown.

Discussion. The density and arrangement of the spines in these specimens are typical of the genus *Waagenoconcha*, while the general shape and outline of the ventral valve resembles so much Waagen's *Productus abichi*. However, more details on the dorsal valve is needed before the described specimens can be reliably assigned to this species.

WAAGENOCONCHA sp. indet.

(Plate 12, figure 24)

Material. A single ventral valve from locality 15, near Sg. Toh, Merapoh, Pahang (UKM-MSL collection).

Horizon and Age. Upper Permian *Leptodus* Bed.

Description. Length = 28.5 mm, Max. width = 27mm. Medium size *Waagenoconcha* with poorly developed median sulcus and ventral surface covered by densely packed fine recumbent to suberect spines, set in quincunx arrangement.

Discussion. The specimen discussed is slightly compressed. If not compressed the length should be slightly shorter than the maximum width, and the specimens would appear to be more like those of the Lower Permian of Kampar. However, compared to the Kampar specimens the above specimen appears to be slightly larger in size.

Family LINOPRODUCTIDAE Stehli

Subfamily LINOPRODUCTINAE Stehli

Genus *LINOPRODUCTUS* Chao 1927

LINOPRODUCTUS sp. A, cf. *L? SINOSUS* Huang 1932

(Text-figure 5.1G, Plate 12, figures 29-31)

cf:
1932 *Linoproductus sinosus* Huang, p. 43-44, pl. 2, fig. 15-16.

Material. Ten specimens from localities 9, 2 specimens each from locality 10 and 13 and 1 specimen each from localities 6, 7 and 14, all from the road cut in between Gua Panjang and Sungai Yu halt, near Merapoh, Pahang, and 1 specimen from Bukit Jaya, near Maran, Pahang (UKM-MSL collection).

Horizon and Age. Upper Permian *Leptodus* Bed and unnamed formation of ?Upper Permian age.

Description. The shell is small to medium in size with strongly deformed shell plan outline and profile. The largest individual (MSL9.1a) has an estimated maximum shell width of about 30mm. The ventral valve is strongly convex with fine costae and costellae and occassional growth lamellae. The median sulcus is strongly developed anteriorly and weaker towards the umbo. The trail is long, linear and geniculate with the costae slightly coarser than that on the visceral disc. The umbo is large and strongly incurved. The hinge line is straight and possibly represents the maximum width of the shell. The auricle is moderately developed, flat and triangular in shape with prominent wrinkles and faint radial costae. Other details are unknown.

Discussion. Although the described specimens are all deformed in one direction or another, the essentially deep median sulcus, wide hinge line and strongly incurved umbo in *Linoproductus* sp. A closely resembles that of *Linoproductus sinosus* Huang. This species, however, has been assigned by Nakazawa (1973) to the genus *Anidanthus.* Unfortunately, the available specimens of *Linoproductus* sp. A do not show any convincing features which could associate them with the later genus. For this reason, the author will tentatively assign the studied specimens into the genus *Linoproductus* until further comparison with the Chinese type specimens of *L. sinosus* is made. The essential features outlined above distinguish *Linoproductus* sp. A from other Malaysian species of *Linoproductus.*

Genus *STEPANOVIELLA* Zavodowsky 1960

STEPANOVIELLA sp. A, cf. *S. FLEXUOSA* Waterhouse 1970

(Text-figure 5.1H, Plate 15, figures 7-9)

cf:
1970 *Stepanoviella flexuosa* Waterhouse, p. 45-48, pl. 14, fig. 1-8, 15-16.

Material. Seventeen moulds of disarticulated valves on 6 rock slabs no. KPF (1, 2, 3, 3a, 3b and 5) and some unnumbered specimens from Kuala Pilah area, Negeri Sembilan (GSD collection).

Horizon and Age. Kepis Bed, late Lower Permian.

Description. The shell is asymmetrically transversely elongated to subcircular in plan outline. The maximum shell width is at about the mid shell length. The ventral valve is weakly to moderately convex with short, broad and weakly incurved umbo, short and indistinct trail, small auricle and no median sulcus. The umbo is usually flattened by small rough surface of cicatrix in younger individuals, but the cicatrix is less pronounced in the larger individuals. The hinge line is inequal in length, and the umbo is usually pointing towards the shorter hinge line. The auricle is developed as a narrow flattened or slightly swollen strip along the hinge line. The exterior of the shell is furnished with broad flexuous costellae, irregularly intercepted by a series of discontinuous growth lamellae or occasional rugae. Concentric bands are also commonly developed. The posterior margin is usually strongly wrinkled.

The dorsal valve is weakly concave with very short trail, flattened auricle and no median fold. The curvature of the dorsal valve closely follows that of the ventral valve, thus the visceral cavity is narrow. The outline of the dorsal valve is usually transversely elongated. The surface ornamentation of the dorsal valve is very similar to that of the ventral valve. No spines are known in either ventral or dorsal valves. The interior details are unknown.

Discussion. The short trail and flexuous costellae distinguished *Stepanoviella* sp. A from the genus *Linoproductus*. *Stepanoviella* sp. A resembles *S. flexuosa* Waterhouse in its transverse shape, broad umbo, concave dorsal valve and coarse costellae. *Stepanoviella* sp. A differs from *S. flexuosa* in the development of a cicatrix in younger individuals. *S. flexuosa* is reported to be restricted to the Stage 3 of Waterhouse's (1970a) Permian brachiopod zonation, equivalent to the Sakmarian-Artinskian Stage of the Russian platform.

Genus *CANCRINELLA* Fredericks 1928

CANCRINELLA CANCRINI (de Koninck) 1842

(Text-figure 5.1I-K, Plate 13, figures 2-10)

Synonym:
1847 *Productus cancrini* de Koninck; de Koninck, p. 208-211, pl. 11, fig. 3a-f.
1973 *Cancrinella cancrini* (de Koninck); Ishii *et al.*, p. 69-70, pl. 2, fig. 2, 4-7.

Material. Hundreds of complete and partly complete disarticulated ventral and dorsal valves from Bukit Tungku Lembu and about 20 specimens of similar nature from Bukit Temiang, Perlis (UKM-MSL collection). These specimens are preserved in form of moulds, but occasionally the original shell at the cardinal area of the dorsal valve is preserved.

Horizon and Age. Chuping Formation, late Lower Permian.

Table 5.5. *Cancrinella cancrini* **(de Koninck) - dimensions in mm**

Specimen	length	curved length	max. width	hinge width	height
MSL1.1a(1)	14.0	24.8	e14.0	na	8.2
MSL1.1f	9.1	14.6	e9.5	na	4.1
MSL1.1g	8.7	14.7	9.0	na	6.5
MSL1.1a(2)*	11.5	na	14.5	12.8	na
MSL1.1b(1)*	e14.3	na	16.8	e15.0	na
MSL1.1b(2)*	e7.9	na	e9.3	na	na
MSL1.1c(1)*	e11.4	na	e14.7	e12.8	na
MSL1.1d(1)*	10.5	na	12.4	e10.6	na
MSL1.1d(2)*	7.9	na	9.0	e7.4	na

dimensions = refer to text-figure 1.1
na =not available e = estimated * = dorsal valve

Description. Small sized *Cancrinella* with maximum dimension reaching about 17 mm. The shell is roughly subcircular in its plan outline. The maximum width of the shell is at about the mid shell length. The ventral valve is moderately to strongly convex with no median sulcus, very short trail and small flat auricle. The umbo is large and strongly overhanging and incurved beyond the hinge line. The exterior of the ventral valve is covered by regular fine costae which sometimes bifurcate anteriorly, with little or no concentric bands or growth lamellae. Suberect spines are disposed at irregular intervals on the crest of the costae, without any systematic pattern of arrangement. The fully grown individual has about 20 to 30 body spines on the ventral valve. The erect and laterally directed auricular spines are concentrated in two or three rows at the base of the visceral disc. The auricle is wrinkled, with the strongest wrinkles developed at the posterior margin. The posterior margin is straight and provided with a row of posteriorly directed marginal spines.

The dorsal valve is weakly concave with depressed umbo, no median sulcus and short geniculate trail. The auricle is narrow, transversely elongated triangular in shape and flat in profile. The posterior margin is strongly wrinkled laterally. The dorsal surface is finely costate with occasional growth lamellae, and is sometimes wavy in nature. No traces of spines are observed. The cardinal process has a very short shaft, and is supported by a pair of strong lateral ridges. The myophore is bilobed with each lobe well separated and each tends to split into two smaller lobes. The muscle attachment bases face the dorsal. Other details are unknown.

Discussion. At Bukit Temiang and Bukit Tungku Lembu, *C. cancrini* forms cocquina beds with virtually no other faunal elements, within the passage beds between the arenaceous Kubang Pasu Formation and the Chuping Limestone Formation. As in many other brachiopod species which dominate their fauna (e.g. *S. excavata* and *S. lewisiana* from the British Permian), individuals of the species seem to show wide variation.

The Malaysian *C. cancrini* shows considerable variation in the shape and convexity of its ventral and dorsal valves. The ventral valve varies in its plan outline from subcircular to a slightly elongated pear shape, and in its strong to very strong convexity, but maintains its non-sulcate form with large incurved umbo. Furthermore, the ventral valve remains more or less smoothly curved with very little or no fluctuation, except for the auricular wrinkles. These general features, as well as the ornamentation of the shell which characterised the *C. cancrini* described from the Permian of Russia, distinguish the Malaysian forms from other species of *Cancrinella*. The thin shell at the auricle was probably damaged during the fossilization, thus the ventral valve seldom shows a well developed auricle.

The dorsal valve, on the other hand, shows a greater variation from longitudinally to transversely elongated shape and from moderately concave to nearly flat profile. The flatter forms are usually associated with longitudinally elongated shell with less geniculated trail. Since the ventral valve and the dorsal valve are always separated, it is very difficult to prove whether the strongly varied shape and profile of the dorsal valve belongs to an extreme variation of the species or merely a result of deformation.

It is also difficult to prove whether the fluctuate dorsal valve in some specimens belongs to another species of *Cancrinella* or is simply deformed shells. Although the degree of deformation is generally very low in the rock formations containing this fauna, it is still possible for individuals of these thin shelled brachiopods to be crushed upon one another. More detailed study on the taphonomy of this interesting fauna is needed before a better conclusion can be achieved on the variation of the morphology within the species.

CANCRINELLA sp. cf. *C. CANCRINIFORMIS* (Tschernyschew) 1902

(Plate 13, figure 11)

cf:
1916 *Productus cancriniformis* Tschernyschew; Broili, p. 13-14, pl. 66, fig. 6.

Material. Five incomplete moulds from Kg. Juaseh, near Kuala Pilah, Negeri Sembilan (UKM-MSL collection)

Horizon and Age. Kepis Bed, late Lower Permian.

Description. The shell is small to medium in size. The ventral valve is moderately convex with no median sulcus, small, narrow and weakly incurved umbo and poorly developed auricle. The surface of the ventral valve is covered with fine costae and several suberect body and auricular spines. The spines are small in diameter and distributed at irregular intervals at least 3 mm apart. The shell is concentrically banded with broad to sharp ridges and shallow to deep grooves. The ridges and grooves are often discontinuous. The grooves are sometimes overlapped by occasionally developed growth lamellae or rugae. The dorsal valve is flat or weakly concave with fine radial costae and irregular concentric bands. Other details are unknown. [MSL20.2a - estimated dimensions; length = 19.5mm, width = 22mm].

Discussion. The specimens described above are similar to some extend to *C. cancriniformis* from Timor, but incomplete preservation does not allow these specimens to be placed into the named species with confidence. The Juaseh specimens differs from the *C. cancrini* from Perlis in their larger size, smaller umbo and stronger fluctuation of their shell, although the shell fluctuation might be exaggerated by the deformation of the Kepis Bed which seems to be stronger compared to the Chuping Limestone Formation.

CANCRINELLA sp. A

(Plate 13, figures 12-13)

Material. 4 casts and 1 mould of unnumbered specimens from H. S. Lee Mine no 8, near Kampar, Perak (UM collection).

Horizon and Age. Nam Loong Bed, Lower Permian.

Description. The ventral valve is medium in size, moderately convex with small slightly pointed umbo, small flattened auricle and no median sulcus. Apart from the umbo, the whole ventral surface is covered with strong radial costae and concentric bands of ridges with sharp crest and profound grooves. Several large, distant suberect spines are arranged in radial as well as concentric rows on the crest of the costae. The auricular spines are not known. The auricle is strongly wrinkled and the posterior margin is provided with a row of posteriorly directed marginal spines. Other details are unknown. [UM-3a - dimensions; length = 22.5mm, width = 21.0mm].

Remarks. As compared to other Malaysian species of *Cancrinella*, *Cancrinella* sp. A is distinguished by its stronger radial costae and concentric bands, and larger and more systematically arranged body spines. The ornamentation in *Cancrinella* sp. A resembles the New Zealand species *C. halli* Waterhouse, but like *Cancrinella* sp. A, the New Zealand species was described from incomplete specimens, some features are thus unavailable for comparison (see Waterhouse, 1982). Therefore, the author will delay naming this species until a better collection of specimens is available.

Family LINOPRODUCTIDAE Stehli

Subfamily STRIATIFERINAE Muir-Wood & Coopper

Genus *STRIATIFERA* Chao 1927

STRIATIFERA sp. A

(Plate 13, figure 1)

Material. Two incomplete external moulds of dorsal valve from H. S. Lee Mine no 8, near Kampar, Perak (UM collection).

Horizon and Age. Nam Loong Bed, Lower Permian.

Remarks. The maximum shell width of large flattened specimen (UM-4a) is more than 60mm. The dorsal valve is large in size and partly impressed upon the contour of the rock. In general the dorsal valve is moderately concave with the maximum concavity situated at the umbo. The auricle is small and flat, while the hinge line is short and straight. The surface of the shell is covered by fine costae and costellae and occassional weak wrinkles. The costae and costellae bifurcate at various positions near the anterior margin. The wrinkles are stronger at the lateral posterior margin. Other details are unknown.

The incomplete preservation of the described specimens make comparison with any known species of *Striatifera* impossible.

Family MARGINIFERIDAE Stehli

Subfamily MARGINIFERINAE Stehli

Genus *LIOSOTELLA* Cooper 1953

LIOSOTELLA NAKAMURAI new species

Text-figure 5.2A-E, Plate 14, figures 6-15

Named after Nakamura who in 1973, described this species under Spinomarginifera kueichowensis Huang and Liosotella sp.

Synonym;

1973 *Spinomarginifera kueichowensis* Nakamura (not-Huang), p. 292-3, pl. 31, fig. 9.

1973 *Liosotella* sp. indet. Nakamura, p. 293, pl. 31, fig. 10-11.

1973 *?Spinomarginifera* sp. indet. Nakamura, p. 293, pl. 31, fig. 8.

Diagnosis. Medium sized *Liosotella* with 14 to 16 coarse costae, a row of 4 to 5 pairs of large halteroid auricular spines, rare smaller body spines including two concentric rows near the anterior margin where each row of spines is set on alternate costae. Ventral valve moderately to strongly convex with short trail, small smooth umbo, smooth auricle and weakly developed median sulcus. Dorsal valve weakly concave with no median fold, smooth umbo, costate anterior and very short trail. Marginal ridges of spinomarginiferid type. Cardinal process small with posteriorly pointed shaft. Adductor muscle platform subtriangular in shape. Brachial impression moderate in size.

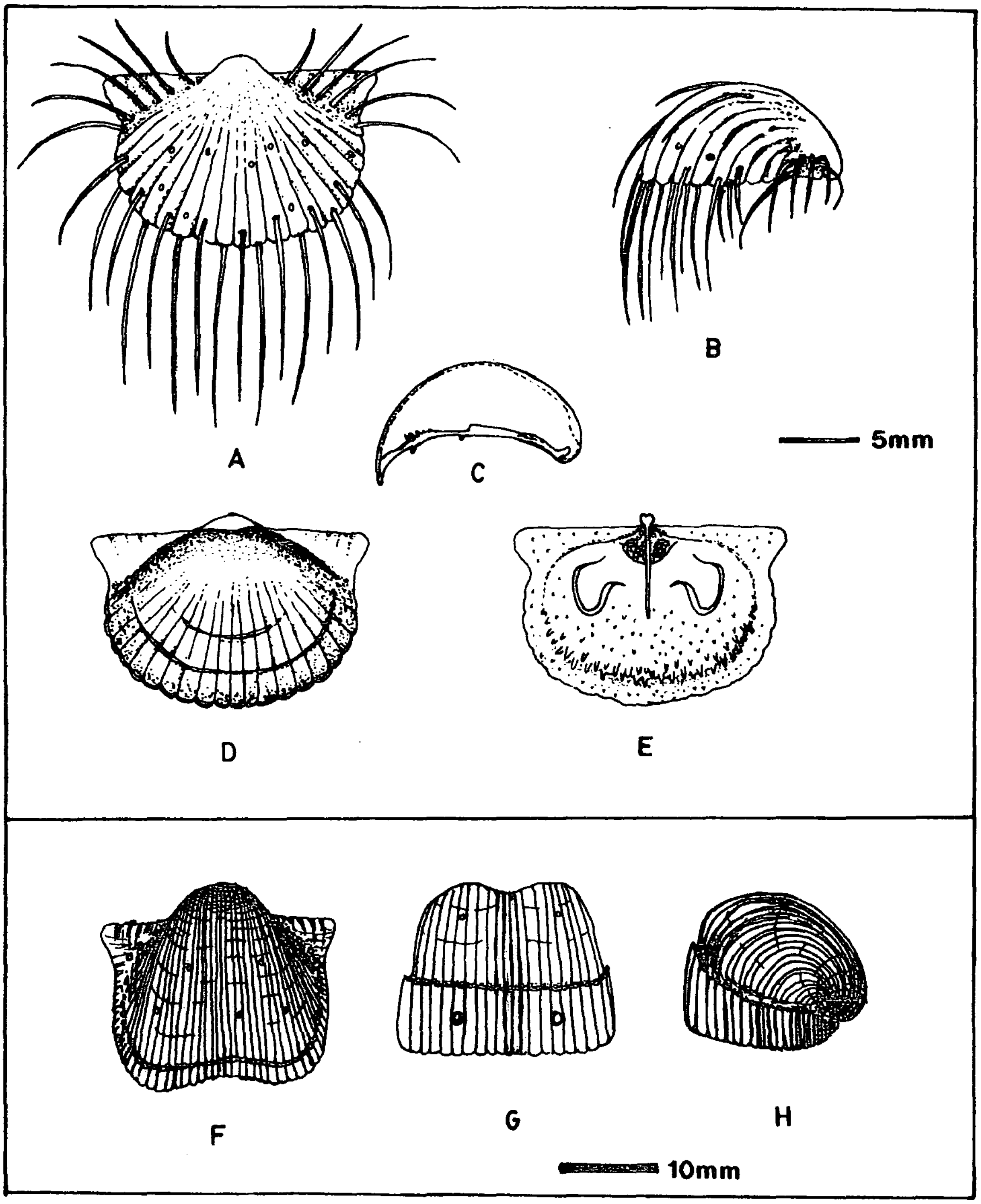
Material. Paratypes: Specimens no. MSL17.1a, MSL17.1b, MSL17.1c, MSL17.1d and MSL17.1e (UKM-MSL collection) from carbonaceous shale exposed at the Jengka Pass road cut, are chosen to represent a series of paratypes of *Liosotella nakamurai* n. sp., in the absence of a complete specimen. The following description also covers observations made on another 80 specimens from the type locality and 12 specimens from the Maran Oil Palm Mill exposure.

Type locality. The Jengka Pass road cut (GR. WF 91651445, Sheet 89) is chosen as the type locality of *Liosotella nakamurai* n. sp. because of the numerous occurrences of the species in this locality, though the newly cited locality, i.e. the Maran Oil Palm Mill produces a few well preserved specimens. The Jengka Pass road cut, in addition, is the locality in which Nakamura (1973) described this species under *S. kueichowensis* and *Liosotella* sp.

Horizon and Age. Unnamed formation of Upper Permian (Midian) age.

Description. The shell is transversely subtrapezoidal in shape, as inferred from the less distorted disarticulated dorsal valve. Owing to substantial deformation the plan outline of the ventral valve varies from transverse to elongate subelliptical to subtriangular shaped, and often twisted. The maximum shell width is at the hinge line, but the ventral valve often shows a hinge line shorter than the maximum width due to deformation.

The ventral valve is strongly convex, although it often shows a great variation in



Text-figure 5.2. Reconstructions of *Liosotella nakamurai* new species (figure A-E) and *Marginifera?* sp. A (figure F-H)

A,B — ventral exterior (ventral and lateral views); C — lateral profile; D,E — dorsal exterior and interior.

F,G,H — ventral exterior (ventral, anterior and lateral views).

Table 5.6. ***Liosotella nakamurai*** **new species - dimensions in mm**

Specimen	curved length	maximum width
MSL17.1a	27.3	e26.0
MSL17.1b	13.7	na
MSL17.1c	e31.7	na
MSL17.1f	25.7	27.9
	length	maximum (=hinge) width
MSL17.1d*	13.1	27.0
MSL17.1e*	e14.0	e27.0
MSL17.1g*	e15.0	e21.0
MSL17.1h*	13.6	e23.5
MSL17.1i*	e12.3	e20.7
MSL17.1j*	13.7	18.5

dimensions = refer to text-figure 1.1

* = dorsal valve e = estimated na = not available

curvature and convexity. The median sulcus is weakly developed at the convex part of the visceral disc, and becomes obsolete at the umbo and the trail. The umbo is small, but strongly incurved. The trail is short, with slight or no geniculation. The auricle is small, but well defined. The visceral disc is furnished with several large costae, some of which bifurcate at the trail. The total number of ribs at the trail ranges from 14 to 16. The costae narrow and become faint towards the posterior margin where the umbo is usually smooth. The auricle is smooth.

A row of 4 to 5 pairs of halteroid auricular spines are set on the break of slope between the convex visceral disc and the rather flat auricle. Body spines are rare and randomly distributed over the convex visceral disc. Anteriorly, there are two concentric rows of larger body spines with the spines usually set on alternate costae and each row is arranged on different set of costae (see text-figure 5.2A). The interior details of the ventral valve are unknown.

The dorsal valve is weakly concave with flat auricle and no median fold. The costae are weakly developed on the dorsal surface. The dorsal exterior is spineless. The external marginal ridge is sometimes developed as a narrow rim, a short distant from the anterior and anterolateral margins. The narrow trail beyond the external marginal ridge maintains the exterior curvature and morphology of the dorsal valve.

Interiorly, significant change can be seen in between the trail and the visceral cavity. At the visceral region, the dorsal interior is furnished with fine marginally pointed endospines. The interior marginal ridge is not very well developed. It is only slightly raised and marked by a rim of coarser strainer endospines. Anterior to the marginal ridge, the interior surface becomes smoother and the curve becomes weaker as such the anterior margin of the dorsal valve meets the ventral valve at a rather wide angle.

The cardinal process is small with posteriorly pointed shaft and bilobed myophore. The lateral ridges are weakly developed. The adductor muscle platform is subtriangular in shape with the lobate scars obscurely divided into the posterior and anterior sections. The brachial impressions are moderate in size with the inner ridges bent anteromedianly towards the edge of the median septum. The median septum is narrow and low, appears at the middle of the adductor muscle platform and extends to about the mid shell length.

Discussion. Although the actual shell is not preserved, the reconstruction based on the external and internal moulds of the dorsal valve shows that the marginal ridge of *Liosotella nakamurai* is similar to that figured by Huang (1931) for the genus *Spinomarginifera.* Under the present scheme of classification, however, the strongly costate ventral and dorsal valves with smooth umbo, and the absence of spines from the dorsal valve should placed this species in the genus *Liosotella*, not *Spinomarginifera* as was suggested by Nakamura (1973).

The marginal ridge of *L. nakamurai* is unique and has not been found in any other species of *Liosotella. L. nakamurai* resembles *L. grandicosta* (Chao) and *L. magnirugosa* Cooper in terms of the size of their costae. *L. nakamurai*, however, differs from the other two species in its smaller auricle, less profound median sulcus and the systematically arranged spines on its trail.

Genus *MARGINIFERA* Waagen 1884

MARGINIFERA? sp. A

(Text-figure 5.2F,G, Plate 14, figures 1-5)

Material. Two nearly complete and 3 incomplete ventral valves from Kg. Juaseh, near Kuala Pilah, Negeri Sembilan (UKM-MSL collection).

Horizon and Age. Late Lower Permian - Kepis Bed.

Dimensions. MSL20.3a; length = 21.0mm, width = 27.0mm; MSL20.3c; width = 36mm.

Description. The shell is medium in size with distorted shell plan outline. The ventral valve is strongly convex with moderately developed median sulcus and long geniculated trail separated from the visceral disc by the development of an internal marginal ridge. The umbo is small, but incurved. The auricle is moderately developed with strong wrinkles developed at the posterior margin. Exteriorly, the posterior part of the visceral disc is weakly reticulated, but the anterior part and the trail are uniformly costate, with costae seldom bifurcating. The impression of the marginal ridge is seen as a break of slope exteriorly, separating the convex visceral disc from a linear trail. The trail, however maintains the ornamentation of the posterior visceral disc, while the median sulcus divides the trail into two distinct ridges. A pair of large spine bases are seen on the inner slope of the trail ridges. No other body spines are observed. The lateral slope of the visceral disc develops two radial rows of auricular spines.

The ventral adductor muscle platform is quite wide and moderately elevated. The muscle impressions are coarsely dendritic in pattern.

The dorsal valve is not completely known, but a short concave diaphragm is partly exposed immediately after the break of slope of the ventral valve. The cardinal process has a small sessile bilobed myophores with the muscle attachment base facing the ventral. Other details are unknown.

Discussion. Although the very rare, large probably halteroid body spines in these specimens might characterise the subfamily Paucispiniferinae, the numerous auricular spines place them into the subfamily Marginiferinae. The rarity in body spines and the strong deflection of the trail in ventral valve allies these specimens with a marginiferinid genus *Alifera* Muir-Wood & Cooper, but the smaller auricle and very long trail in these specimens does not agree with the description of the genus *Alifera*. Despite the lack of body spines and the strongly deflected trail of the ventral valve, these specimens resembles other species of *Marginifera* in their general ornamentation, the auricular spines and the general shape. More better preserved and complete specimens are needed before these specimens can be placed into their proper genus and species with certainty.

Family MARGINIFERIDAE Stehli

Subfamily PAUCISPINIFERINAE Muir-Wood & Cooper

Genus *PAUCISPINIFERA* Muir-Wood & Cooper 1960

PAUCISPINIFERA sp. A

(Plate 15, figure 14)

Synonym:
1979 *Anidanthus* sp. Yanagida & Aw, p.131-132, pl.28, fig. ?5, 15-16.

Material. Specimens no. GS(F) 5, ?51, 52 and 53 from locality FSKN 73, Sg. Paloh, tributary of Sg. Relai in South Central Kelantan (GSD collection).

Horizon and Age. Late Upper Permian Aring Formation.

Dimensions. GS(F)5; length = 11mm, width = 24mm; GS(F)52; length = 16mm.

Description. The shell is small to medium in size with fusiform shape, with the maximum shell width slightly posterior to the hinge line and more than twice greater than the shell length. The ventral valve is strongly curved longitudinally, with poorly developed median sulcus, broad strongly incurved umbo and large flat or slightly swollen auricle. The trail is short and strongly curved at the anterior margin, but at the lateral margin it is flattened and coalesces with the auricle. The ventral surface is weakly costate, smoother at the trail. The auricle is smooth. A few (3 or 4 pairs) large spine bases are seen at the lateral and anterior slope of the visceral disc. No other spines are known. Specimen no 52 shows an interior mould with large radially striated diductor muscle scars and strong anterior marginal ridges which bend towards the posterior inside the median sulcus. Other details are unknown.

Discussion. The presence of marginal ridges and rare large body spines suggest that the described specimens belong to the marginiferid subfamily Paucispiniferinae, not to *Anidanthus* or other linoproductids. Although the marginal ridges of the described specimen resembles that of *Retimarginifera lipisensis* n. sp., the lack of reticulate ornament suggests that it belongs to the genus *Paucispinifera.* At present, the genus *Paucispinifera* is only known from the Upper Permian of North America. *Paucispinifera* sp. A resembles the type species, *P. auriculata* Muir-Wood & Cooper from Word Formation of Texas, in its general shape and convex auricle, but the spines of *Paucispinifera* sp. A are not systematically arranged as they are in *P. auriculata.*

Genus *RETIMARGINIFERA* Waterhouse 1973

RETIMARGINIFERA LIPISENSIS new species

(Text-figure 5.3A-F, Plate 14, figures 16-26, Plate 15, figure 13)

Named after Kuala Lipis District in which all the described specimens came from.

Diagnosis. *Retimarginifera* with finely reticulate umbonal region, moderately developed median sulcus and auricle. Ventral valve with three pairs of halteroid marginal spines and three pairs of halteroid body spines following the outline ot the interior marginal ridge. The marginal ridges are well developed in both ventral and dorsal valve, stronger on the ventral valves especially anteriorly.

Type specimens. Specimens no MSL15.1a, MSL15.1b and MSL15.1c from Sungai Yu halt road cut, near Merapoh, Pahang are chosen as a series of paratypes of *Reticulatia lipisensis*, representing various morphology of the species.

Type Locality. The Sungai Yu halt road cut (GR. QZ 04204405), near Merapoh, Pahang is chosen for type locality of the species, because some of the best preserved specimens of this species came from here.

Other material and localities. For the following description, reference are also made on several other specimens in UKM-MSL collection including 4 other specimens from the type locality, 5 specimens from locality 8 and 2 specimens from locality 12, near Merapoh; 5 specimens from Kg. Gua, 4 specimens from Kg. Garok and 1 specimen from north Terengun, near Kuala Lipis, all of which from the Kuala Lipis District in Northwest Pahang. Also studied are several specimens in GSD collection including 4 specimens from railway cut adjacent to Sungai Jeleteh, near Merapoh.

Wahid Abdul Rahman (1987) reported the occurrences of *Retimarginifera* sp. from Labis area in Northwest Johor, but the author failed to locate these specimens during the recent visit to the Geological Survey Department.

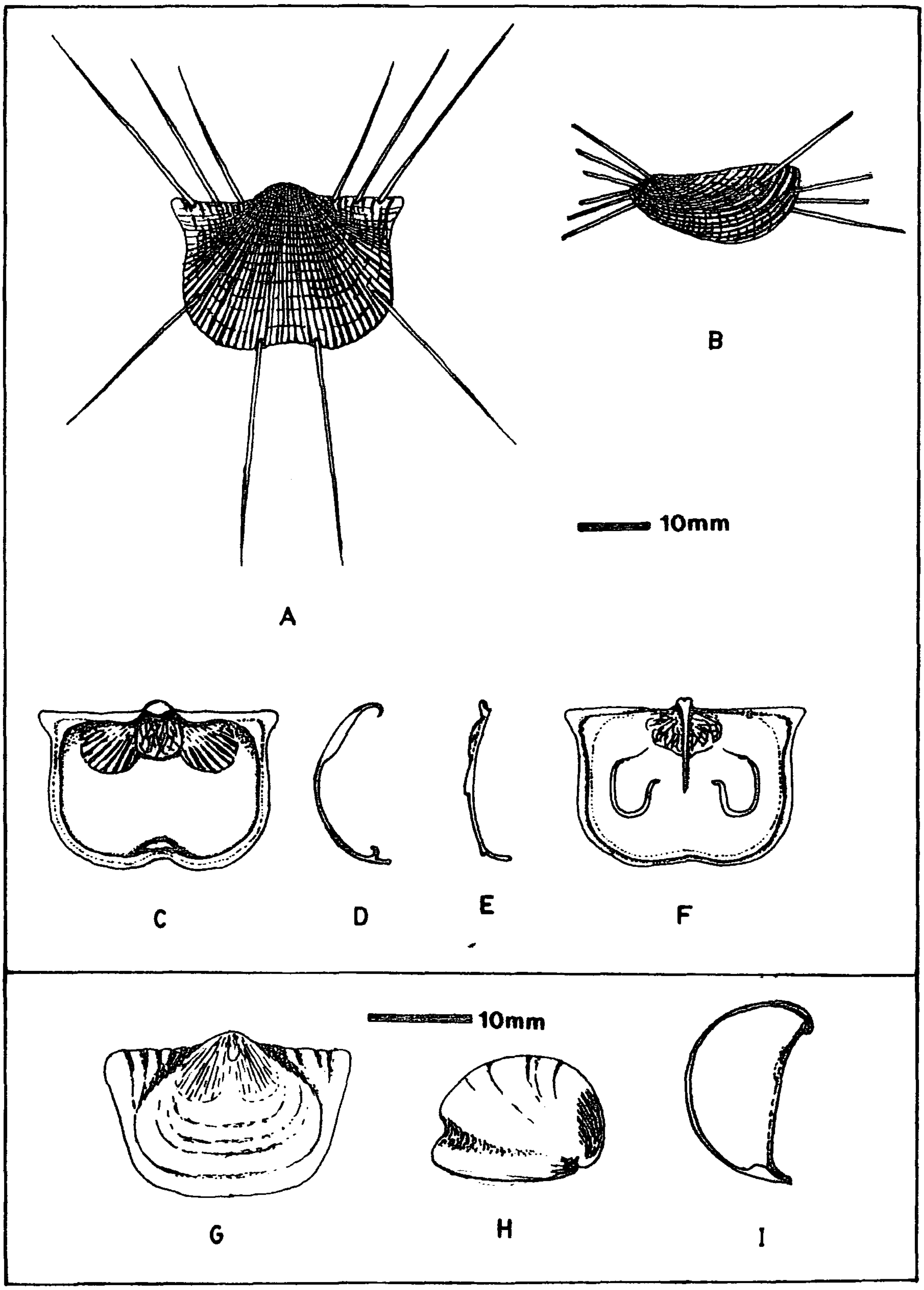
Horizon and Age. Upper Permian *Leptodus* Bed.

Table 5.7. *Retimarginifera lipisensis* **new species - dimensions in mm**

Specimen	length	curved length	maximum (=hinge) width
MSL15.1a	e23.8	e32.0	34.1
MSL15.1b	e25.0	na	24.0
MSL15.1c	na	na	e35.0
MSL8.3a	19.5	e37.5	28.5
MSL8.3b	e4.5	na	7.8
MSL3.1a	e17.4	na	e21.0

dimensions = refer to text-figure 1.1
e = estimated na = not available

Description. The shell is medium in size with the largest individual reaching 35mm in its maximum width at the hinge line. The shell plan outline is transversely subtrapezoidal in shape with the length of the shell about two thirds of its hinge width. The ventral valve is moderately convex with the anterior half is more convex than



Text-figure 5.3. Reconstructions of *Retimarginifera lipisensis* new species (figure A-F) and *Echinauris?* sp. A (figure G-I)

A,B—ventral exterior (ventral and lateral views); C—ventral interior; D,E—median section (ventral and dorsal valves); F—dorsal interior.
G,H—internal mould of ventral valve (ventral and lateral views); I—Lateral shell profile.

its posterior. From the mid shell length, the ventral valve curves gently towards the small umbo. The median sulcus is moderately developed, more profound anteriorly than posteriorly. The umbo is small, weakly inflated and incurved. The auricle is small and slightly swollen. The trail is short and poorly defined exteriorly.

The umbo and the central part of the visceral disc are furnished with fine reticulate ornament. The reticulate ornament fades away towards the margin where the visceral disc becomes regularly costate peripherally. The costae are about 0.5 to 1mm apart and never bifurcate, they fade towards the margin. The auricle is wrinkled. There are only twelve halteroid spines on the ventral valve. These spines are made of three pairs of marginal spines and three pairs of body spines. The marginal spines increases its diameter laterally, and they are posterolaterally pointed. Two pairs of large body spines are arranged in the same concentric row with the outermost pair of the marginal spines. These two pairs of body spines are anterolaterally pointed, forming one horizon of spines with the marginal spines. The anterior pair is the largest pair of spines with their diameter reaching 1mm. A pair of smaller spine bases are developed on the lateral slope of the visceral disc, and this pair seems to be formed on the same concentric row with the second pair of the the marginal ridges (see text-figure 5.3A).

The ventral adductor muscle platform is weakly to moderately elevated with coarsely dendritic muscle impressions. The adductor muscle platform is undivided, and is surrounded by a large pair of low radially striated diductor muscle platforms. The lateral ridges are moderatately developed, but the marginal ridge is well developed, especially anteriorly. The anterior and anterolateral marginal ridges are thick with their crest inclined towards the central visceral cavity. Medianly, the anterior marginal ridge curves towards the posterior and then towards the ventral (see text-figure 5.3D). The interior surface of the shell is endospinose.

The dorsal valve is weakly concave with weakly developed median sulcus and small auricle. Apart from the absence of spines, the surface ornamentation of the dorsal valve is similar to that of the ventral valve. The lateral ridges are well developed, broader laterally and become crenulated at the point it meets the lateral marginal ridge. The lateral marginal ridge is narrower and sharper towards the anterior marginal ridge. The cardinal process is small with the shaft pointing to the posterior. The adductor muscle platform is low to moderately elevated, subtriangular in shape with dendritic muscle impressions. The brachial impressions are medium in size.

Discussion. The genus *Retimarginifera* is not a very well known genus, and the number of species described in the past is small and their distribution is limited to the Permian of Asia and Russia. *R. lipisensis* differs from the type species *R. perforata* Waterhouse in its finer and more regular reticulate ornament and costae and less profound median sulcus. The interior details of the type species is not known and cannot be compared with this species. The spines arrangement is similar between *R. lipisensis* and *R. perforata*, although Waterhouse did not described the relationship between the body spines and the marginal spines.

Family MARGINIFERIDAE Stehli

Subfamily COSTISPINIFERINAE Muir-Wood & Cooper

Genus *COSTISPINIFERA* Muir-Wood & Cooper

COSTISPINIFERA sp. A

(Plate 13, figures 14-15, Plate 15, figures 10-11)

Material. Four incomplete specimens from locality 11, near Merapoh and 5 specimens from Jengka Pass road cut, near Maran, Pahang (UKM-MSL collection); and more than 20 fragmentary specimens from Ulu Lepar, near Maran, Pahang (GSD collection).

Horizon and Age. Upper Permian *Leptodus* Bed and unnamed formation of ?Upper Permian age.

Description. Small to medium size *Costispinifera* with strongly deformed and fragmented shell. The large specimens sometime have a maximum width of more than 20mm. The median sulcus is poorly developed. The umbo is strongly incurved, crenulated or sometimes costate. The ventral valve is furnished with wide crenulated costae and numerous spines. The auricle is small, smooth or wrinkled with three radial rows of auricular spines. The ornament of the dorsal valve is similar to that of the ventral valve, but very rare spines are preserved. No spines are observed on the dorsal auricle. Other details are unknown.

Discussion. The roughly crenulated costae and numerous spines placed these specimens into the genus *Costispinifera*. However, the shells are often distorted and incomplete, thus specific nomination of these specimens is difficult to attempt.

Genus *ECHINAURIS* Muir-Wood & Cooper 1960

ECHINAURIS sp. indet.

(Plate 13, figure 16)

Synonym;
1979 *Echinauris* sp. Yanagida & Aw, p. 129-130, pl. 28, fig. 7(not 6).

Material. Specimen no GS(F)54a,b from locality FSKN73, Sungai Paloh in South Central Kelantan and one specimen each from localities 10 and 11, near Merapoh, Pahang.

Horizon and Age. Upper Permian *Leptodus* Bed of Gua Musang Formation and Aring Formation.

Remarks. The shell is very small in size (usually less than 10mm in dimension) with subcircular plan outline. The ventral valve is strongly convex with small auricle, narrow, but incurved umbo, no median sulcus and short and indistinct trail. The ventral surface is smooth, with several large halteroid spines developed on the convex part of the visceral disc and on the auricle. Other details are unknown. The incomplete preservation of the described specimens prevent the author from describing and discussing more details about this species. It is quite possible that these specimens could be confused with the juveniles of other species with smooth shell surface, but such species have not been reported from the same horizon in which *Echinauris* sp. is found.

ECHINAURIS? sp. A

Text-figure 5.3G,H, Plate 13, figures 17-20, Plate 14, figures 27-28)

Material. Four external moulds of ventral valve and 5 internal moulds of dorsal valve of unnamed specimens from H. S. Lee Mine no 8, near Kampar, Perak (UM collection).

Horizon and Age. Nam Loong Bed, Lower Permian.

Table 5.8. *Echinauris?* **sp. A - dimensions in mm**

Specimen	length	curved length	maximum (=hinge) width	height
UM-4a	e15.3	e29.4	e20.6	9.6
UM-4b	e9.0	12.5	e13.7	4.1
UM-4e	13.6	27.0	e19.4	8.0
UM-4f	10.0	18.6	e15.5	e5.0

dimensions = refer to text-figure 1.1
e = estimated

Description. The shell is medium in size with transversely subtrapezoidal shaped plan outline. The maximum shell width is at the hinge line. The ventral valve is strongly convex with poorly defined median sulcus, small strongly incurved umbo and small flat auricle. Traces of wrinkles and rugae are often impressed on the internal moulds of the ventral valve, but no traces of costae are seen. The interior of the ventral valve is provided with short and narrow outline of the adductor muscle platform surrounded by a pair of larger radially striated diductor muscle fields. A few remains of spine pits show that the spines are quite closely spaced and suberect to erect in nature. The marginal ridge is thick and wide with its posterior slope nearly vertical to the growth axis. The lateral marginal ridges are lower and narrower than the anterior marginal ridge.

The dorsal valve is transversely elongated with its maximum width at the hinge line nearly twice greater than the shell length. The dorsal valve is weakly concave with no median sulcus and short geniculated trail. The dorsal surface is concentrically lamellose and provided with numerous erect spines which are set in a more or less concentric rows or randomly distributed.

Discussion. These specimens are tentatively assigned to the genus *Echinauris* because of their smooth, but quite heavily spinose shells, although the marginal ridge is quite distinct from any other species of this genus. The thick ventral marginal ridge is known in costispiniferinid genus *Rudinia*, but this genus has a weakly costate shell with rare spines. Lack of better preserved and more complete specimens, prevents the author from describing these specimens further.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Summary of the British Permian Productidina

The British Permian Productidina comprise 4 species of *Strophalosia*, 1 species of *Eostrophalosia*, 6 species of *Heteralosia*, 3 species of *Craspedalosia*, 2 species of *Howseia*, 4 species of *Horridonia* and 2 species of *Spinohorridonia* (see table 6.1). These productidinids are thought to be carried in with the marine incursion from the Boreal Ocean to the north, during a possible high eustatic sea-level at the end of the Lower Permian period (Ziegler, 1982; Taylor, 1984). A closely related fauna found in East Greenland and Spitzbergen might have been derived from similar source, but settled down there before reaching the Zechstein depression.

The earliest British Permian productidinid recorded is *Horridonia horrida* from the Marl Slate at Eldon Hill (Mills & Hull, 1976) and Middridge (Bells *et al.*, 1979). Fresh water influx (Turner & Magaritz, 1986) and the locally developed anoxic environment (Smith, 1988) during the early stages of the development of the Zechstein Sea, were not suitable for a breeding ground for exclusively marine articulate brachiopods like the Productidina.

As soon as the marine environment was fully established, the productidinids began to dominate the Zechstein fauna. The Raisby Formation (EZ1a Ca - Durham Province), in particular, is in places rich in *Horridonia* (including the peculiarly orientated *H. horrida*) and various species of Strophalosiidae. Interestingly, the early British strophalosiids are significantly different from those found in the east Zechstein (East Germany, Poland and Lithuania). *Strophalosia goldfussi* and *Craspedalosia lamellosa* which used their vermiform spines for attachment are abundant in the east Zechstein, but rare in the English (west) Zechstein. On the contrary, the large-cicatrix bearing strophalosiids *Heteralosia aycliffensis* and *C. langtonensis* are abundant in the English Zechstein, but are not known from the east Zechstein. This phenomenon is probably related to the relative abundance of dissolved carbonate in the sea water. Warm tropical currents circulated the carbonate better to the west than to the east of the confined Zechstein Sea.

In the Yorkshire Province, the productidinids are only known from boreholes. The fauna seems to be very similar to that of Durham Province. The early attempt of colonization of the Zechstein Sea was unsuccessful, and towards the top of the EZ1a Ca, the productidinids as well as other fauna decline significantly. This is probably the result of contemporary increase of salinity as the confined basin evolved.

However, immediately before the EZ1 Ca reef is developed, the productidinids as well as other faunal elements returned to the shallow margins of the Zechstein Sea. The productidinids as well as other brachiopods, molluscs and frame building bryozoans are responsible in forming the foundation of the reef by developing several shell or coquina banks on the edge of the Zechstein Sea shelf. This new fauna shows the first appearances of many productidinid genera including *Howseia, Eostrophalosia* and *Spinohorridonia* as well as many new species. Among the most notable, is the disapearance of *H. horrida* and the appearance of the new species *H. dunelmensis, S. excavata* and *S. lewisiana* which later dominate the benthic fauna of EZ1b Ca. The genus *Heteralosia* which was re-introduced by *Heteralosia morrisiana* in the basal coquina, later becomes very specialized, with many new species appearing in the different reef sub-facies.

These rich and diverse productidinid groups, however, did not persist through the life of the reef, except for *S. excavata* and its stunted variety that lived up to the reef-flat and reef-crest at many localities. No brachiopods are known to survive the hypersaline water conditions which eliminated the Durham Permian reef and its fauna before depositing the EZ1 anhydrite.

Biostratigraphic significance of British Permian Productidina

Interestingly, most of the British Permian Productidina have a very short vertical distribution, but no formal biostratigrahic subdivision has ever been erected for the Permian of Britain. In the east Zechstein, however, Karwowski & Klapcinski (1986) have introduce a biostratigraphy of the Polish Zechstein, in which the first two biozones were based on the brachiopods *Lingula credneri* and *Horridonia horrida.* It is not known how these Polish authors classified their *H. horrida*, but current study shows that the British *H. horrida* became extinct much earlier than is suggested in Poland.

In Britain, *H. horrida* did not persist beyond EZ1a Ca and it was replaced by *H. dunelmensis* in the EZ1b Ca reef. Therefore, a tripartite zonation of the EZ1 seems to be appropriate and should be introduced as follows:

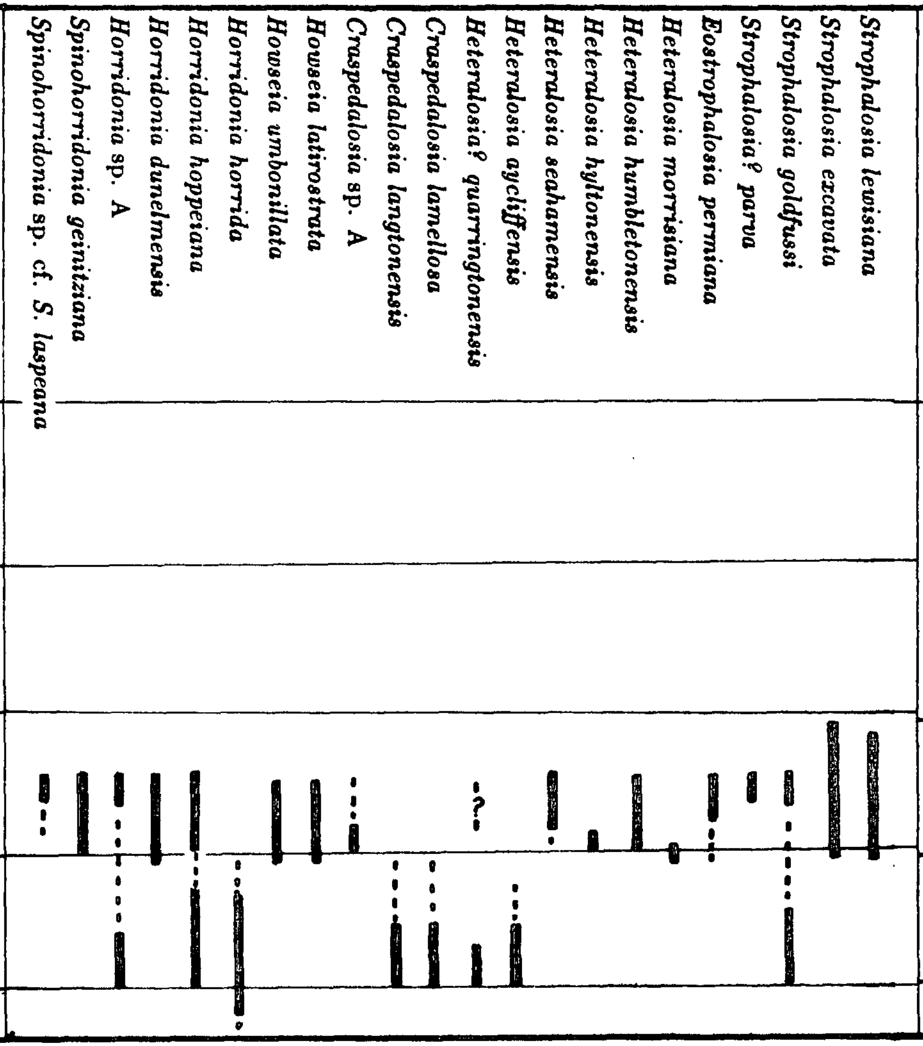
i) *The Lingula credneri Biozone* - commencing with the Marl Slate to the basal Raisby/Cadeby Formation. This biozone was proposed by Karwowski & Klapcinski (1986) for a zone equivalent to the White sandstone and Kuperschiefer of Poland.

ii) *The Horridonia horrida Biozone* - covering the main part of the Raisby Formation and Wetherby Member of Cadeby Formation (EZ1a Ca), except for the usually barren lowermost part and the coquina bed at the top of these formations. This biozone was originally assigned by the Polish authors to cover the Zechsteinkalk of Poland which is equivalent to the whole EZ1 Ca of England.

iii) *The Strophalosia excavata Biozone* - effective from the reef foundation (topmost EZ1a Ca) to the top of the reef (EZ1b Ca). This will include most of the Ford Formation and Sprotborough Member of Cadeby Formation. This biozone is introduced to cover the highly fossiliferous period of Zechstein beyond range of the English *H. horrida. S. excavata* is the most prolific species within this period and it is the last productidinid to become extinct in Britain.

Table 6.1. Stratigraphic distribution of British Permian Productidina

Zechstein Sedimentary Cycle	Durham Province	Yorkshire Province	English Biostratigraphic Zonation (this thesis)	Polish Biostratigraphic Zonation (after Karwowski and Klapcinski 1986
EZ2 Ca	Roker Dolomite Concretionary Limestone	Edlington Formation	*Lebeia squamosa*	*Lebeia squamosa*
EZ1 A	Hartlepool Anhydrite	Hayton Anhydrite		
EZ1b Ca	Ford Formation	Cadeby Formation (Sprotborough Member)	*Strophalosia excavata*	*Horridonia horrida*
EZ1a Ca	Raisby Formation	(Wetherby Member)	*Horridonia horrida*	
	Marl Slate	Marl Slate	*Lingula credneri*	*Lingula credneri*



The Lebeia squamosa biozone is used as it is defined by the Polish author, i.e. to cover the EZ2 Ca of both sides of the Zechstein.

The stratigraphic range of other British Permian Productidina is illustrated in table 5.1

Summary of Malaysian Permian Productidina

The Malaysian Permian Productidina is dominated by the Productacea with 20 species of 16 genera, while the Strophalosiacea and Aulostegacea are only represented by 3 isolated specimens. The productidinids occur in a wide stratigraphic range from the lowermost to uppermost Permian. They are usually asociated with the late Lower Permian (Artinskian) fusulines, and the Upper Permian fusulines as well as lyttoniids. Table 4.3 on p. 199 shows the distribution of the Malaysian Permian Productidina.

It is very difficult to trace the origin of the Permian Productidina in Malaysia owing to the mainly unfossiliferous Upper Carboniferous and Lower Permian strata of the region. The Lower Permian Productidinids are widespread in West Peninsular Malaysia, dominated by the linoproductid genus *Cancrinella.* In general, the fauna resembles the Lower Permian cold water fauna from southern Tethys in some respects (Metcalfe, 1988; Waterhouse, 1975, 1982b; Yanagida, 1967,1976), but elsewhere it resembles to some extent the Salt Range fauna. The Lower Permian genus *Stepanoviella* from Negeri Sembilan is exclusive to the Southern Gondwana (Waterhouse, 1970a).

The Middle Permian fauna is not well known, but the Upper Permian productidina are widespread in Central Peninsular Malaysia. The dictyoclostid genus *Liosotella* and its associated flora from Maran Area appear to belong to the northern Cathaysian elements, while the widespread lyttoniid fauna during the late Permian indicates the spreading of warm tropical condition in Malaysia where the fauna closely resembles those of the Salt Range and Southwestern China. Among the best described productidinid species are *Dictyoclostus? gratiosus* and *Retimarginifera lipisensis*. *D? gratiosus* and other productidinids from South Central Kelantan, the youngest known productidinids in Malaysia, nearly reached the Permo-Triassic boundary.

Some of the Malaysian Permian Productidina seem to have a short stratigraphic ranges, but owing to poorly known lithostratigraphic correlation no biostratigraphic zonation can be tabulated in this thesis.

Comparison between British and Malaysian Permian fauna

Being restricted to a confined basin, the British (or the Zechstein) fauna has no fully comparable equivalents outside its own basin. The fauna itself is unique and its development within the basin was not influenced from outside, similarly it did not affect others outside the basin. Nevertheless, the fauna was still dynamic, with several diversification periods attempted before increasing salinity of the sea caused the extinction of Zechstein brachiopods.

The Malaysian fauna, on the other hand, was part of a huge open realm, where many elements could be introduced or withdrawn from time to time. Furthermore, Malaysia was situated on the unstable and tectonically active periphery of the Gondwana super-continent. Volcanic activity features widely in the Malaysian Permian and thick sequences of ash are widespread. For these reasons, the Malaysian Permian Productidina belong to a special facies that cannot easily be correlated with neighbouring areas. From time to time, unexpected elements are found in the Malaysian fauna, but in general it is not greatly different from other Southern Tethyan faunas.

Further Research

Owing to the establishment of this field of study for over 150 years in Britain, little can be suggested for future research on British Permian Productidina. However, more detailed study on stratigraphical as well as paleogeographical distribution of the Productidina might produce new findings which would not necessarily support the conclusions of this thesis. Detailed paleoecological study of the British Permian Productidina, undoubtedly has much interest and would certainly produce a huge volume of results, especially if details of all variants of each species are taken into consideration.

The scale of study carried out on the Malaysian Permian Productidina clearly is only provisional and it cannot be compared with study of British forms. However, for a start to this field of study in Malaysia, the author has incorporated a short account in this thesis. The study of the Malaysian Permian Productidina will be caried out in more detail in the future and it is anticipated that these studies will solve some of the problems faced in this research concerning uncertain fossil identifications and stratigraphic horizons. Detailed geological mapping and more detailed stratigraphic correlation of the widespread Permian rocks of Malaysia should be tackled first in order to understand the distribution of its fauna. Other faunal elements besides the Productidina also need urgent attention. Only when all these various aspects of geology are better understood, will the Malaysian Permian Productidina be ready for detailed descriptive study.

EXPLANATION OF PLATE 1

Strophalosia lewisiana (de Koninck)

Reef Core of Ford Formation, Humbleton Hill

1 —— Internal morphology of the dorsal valve, MSLHH3

2-5 — Plan view of the ventral and dorsal valves, and posterior and lateral views of the ventral valve, MSLHH1.

6 —— Ventral exterior with posteriorly directed spines, MSLHH2

Reef base of Ford Formation, Hylton Castle

7 —— Internal mould of the dorsal valve, MSLHC1.

Patch reef of Ford Formation, High Newport

8 —- Closely spaced hair-like spines, MSLNH3 - preserved in life position.

9 —- Ventral exterior with recumbent to suberect spines, MSLHN2.

10 — A juvenile with some of the posterior spines erect and recurved to the posterior, MSLHN1.

Reef core of Ford Formation, Tunstall Hill old trench

11 — Part of the interior morphology of the dorsal valve and some spines from the ventral valve (dotted line represent the margin of the broken shell), MSLot1.

12 — Ventral valve, MSLot2a (showing plan view) and MSLot2b (showing anterior view).

Strophalosia excavata (Geinitz)

Reef core of Ford Formation, Beacon Hill railway cut

13-14 — Ventral and dorsal exterior, MSLBH8.

15-17 — Ventral, dorsal and lateral exterior, MSLBH3.

18-19 — Ventral and dorsal exterior, MSLBH9.

[All specimens are coated with ammonium chloride].

(specimen numbers = refer to appendix)

PLATE 1

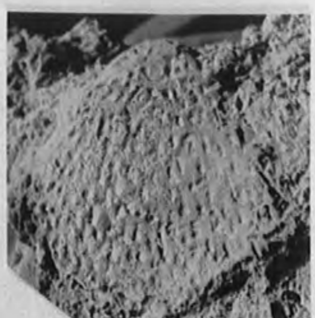

1


2


8


4


3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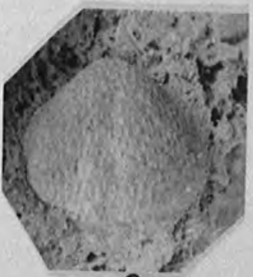
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7


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10


18


16


13


11


19


15


14


12

5mm

EXPLANATION OF PLATE 2

Strophalosia lewisiana (de Koninck)

Reef core of Ford Formation, Tunstall Hill old trench

1 — Internal morphology of the dorsal valve, MSLot3

Strophalosia excavata (Geinitz)

Reef core of Ford Formation, Tunstall Hill old trench

2 —— A hollow cardinal process, teeth and sockets, and other internal morphology of dorsal valve, MSLot4.

4 —— Dorsal valve interior, MSLot5.

5-6 — Ventral and dorsal interior, MSLot6.

Reef core of Ford Formation, Beacon Hill

3 — Sharply pointed umbo and irregular development of growth rugae, MSLBH1.

Strophalosia goldfussi (Munster)

Lower part of Raisby Formation, Old Quarrington Quarry

7 — Part of ventral valve exterior with posteriorly directed vermiform spines, MSLOQQ2.

Zechsteinkalk, Gera, E. Germany

8 — Two series of hair-like spines at posterior region and coarser erect and posteriorly directed vermiform spines at anterior region, G88.44a (Hancock Museum collection).

Lower part of Raisby Formation, East Thickley Quarry

9 —- Various mode of attachment shown by specimens MSLETQ1a,b,c.

10 — Enlargement of MSLETQ1a showing centrally directed dorsal body spines and posteriorly directed ventral body spines. *The ventral body spines are cemented to the ventral valve of Horridonia horrida (Sowerby) which is preserved in life position. This suggest that S. goldfussi in figures 9 and 10 might have been attached on a living H. horrida.*

Lower part of Raisby Formation, Old Town (=White) Quarry

11 — Open interareas, centrally directed dorsal body spines and posteriorly directed vermiform ventral body spines clasping a tubular object, probably a spine of *H. horrida*, MSLWQ1

Reef core of Ford Formation, Tunstall Hill old trench

12 — Internal mould of the dorsal valve, MSLot7.

13 — Enlargement of rubber latex cast of the same specimen showing a strongly shafted trilobed cardinal process and a pair of thick socket ridges.

[All specimens are coated with ammonium chloride]

(specimen numbers = refer to appendix)

PLATE 2

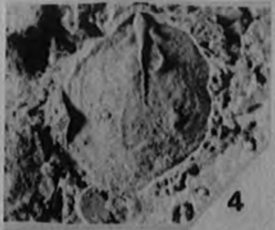
1

2

13

5mm

3



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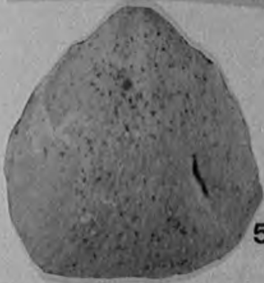

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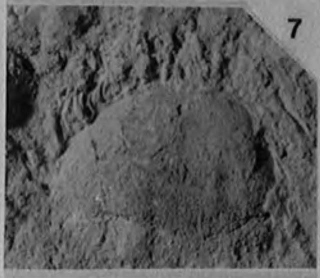

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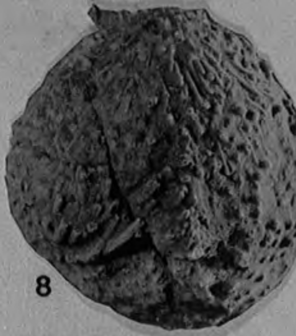

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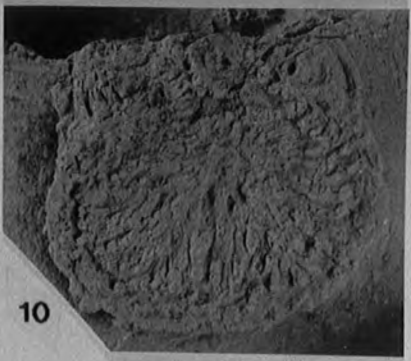

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EXPLANATION OF PLATE 3

Eostrophalosia permiana new species

Reef core of Ford Formation, Beacon Hill railway cut

1-2 — Ventral and dorsal exterior of paratype MSLBH10.
3 —— Dorsal external mould of the same paratype.
4 —— The smallest paratype, MSLBH13.
5-6 — Latex casts from the external and internal moulds of paratype MSLBH15 showing details of the exterior and interior of the dorsal valve.
7 —— Elongated spine bases and occasional growth rugae, paratype MSLBH14.
8 —— Dorsal exterior, MSLBH17.
9 —— Ventral exterior, MSLBH16.
10-11 - Ventral and dorsal exterior, paratype MSLBH11.
12 —— Ventral exterior, paratype MSLBH12.

Reef core of Ford Formation, Tunstall Hill old trench

13 —— Part of the interior and exterior of the dorsal valve, MSLot8.

Heteralosia morrisiana (King)

Reef base of Ford Formation, Tunstall Hill (rock cottage)

14 —— Ventral exterior showing strongly adpressed body spines which leave deep grooves on the shell, MSLTH1.
15 —— Dorsal exterior of the same specimen showing truncated ventral interarea and finely costate dorsal valve.
16 —— Ventral exterior, MSLTH7 - juvenile with large cicatrix.
17-18 - Ventral exterior (plan and lateral views), MSLTH5.
19 —— Internal morphology of the dorsal valve, MSLTH2.
20 —— Strongly adpressed body spines and occasional growth rugae, MSLTH6.
21 —— The thin shell of the dorsal valve and the finely costate external mould, MSLTH4.
22 —— Internal morphology of the dorsal valve, MSLTH3.

Heteralosia humbletonensis (King)

Reef base of Ford Formation, Hylton Castle

23 —— Ventral exterior very similar to *H. morrisiana*, but with more numerous body spines, MSLHC3.

[All specimens figured in this plate are coated with ammonium chloride].
(specimen numbers = refer to appendix)

PLATE 3


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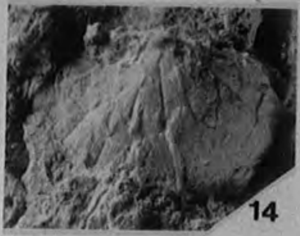
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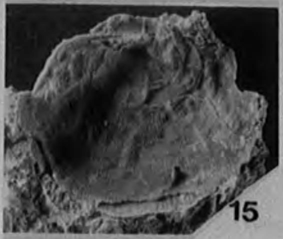
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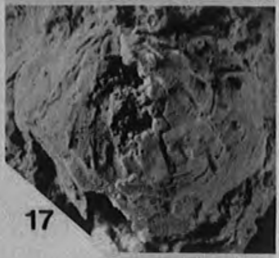
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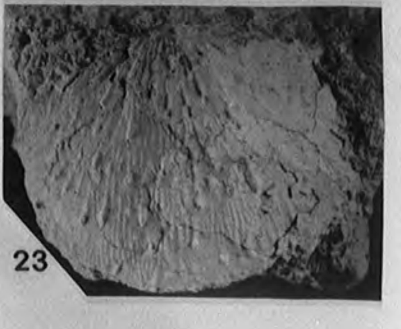
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EXPLANATION OF PLATE 4

Heteralosia humbletonensis (King)

Reef core of Ford Formation, Humbleton Hill

1-3 — Ventral exterior (ventral, posterior and lateral views), G88.56a.
4 —— Latex cast from the internal mould of the dorsal valve, G88.56d.
5 —— Concentric rows of spine bases developed on the growth rugae, G88.56c.
6 —— Ventral exterior, G88.56b.
7 —— Dorsal interior, G88.56e.
8 —— Ventral exterior from latex cast showing adpressed body spines and bases of erect body spines, MSLHH3.
9-10 - Ventral exterior and dorsal interior, MSLHH4.
11 —— Ventral exterior younger specimen, MSLHH5.

Heteralosia aycliffensis new species

Lower part of Raisby Formation, Old Town (=White) Quarry

12 — Several specimens on slab MSLWQ7 with dorsal exterior of paratype MSLWQ7a (marked as a).
13 — Deformed specimen with few very long fine hair-like spines, paratype MSLWQ5.
14 — Ventral exterior with elongate spine bases and fine costae, paratype MSLWQ6.
15 — Juvenile with large cicatrix of attachment, paratype MSLWQ8.
16 — Ventral exterior, paratype MSLWQ4.
17 — Overgrown cicatrix, MSLWQ10.
18 — Dorsal exterior with impression of large cicatrix, MSLWQ11a.
19 — Ventral exterior, MSLWQ9.

Lower part of Raisby Formation, East Thickley Quarry

20 — Ventral exterior, MSLETQ2.
21 — Ventral exterior, MSLETQ3.

Lower part of Raisby Formation, Raisby Hill Quarry

22 — Ventral interior with a pair of teeth, MSLRHQ1.

[Specimens in figures 1-3, 5, 9-10 and 22 are not coated; other specimens are coated with ammonium chloride]
(specimen numbers = refer to appendix)

PLATE 4


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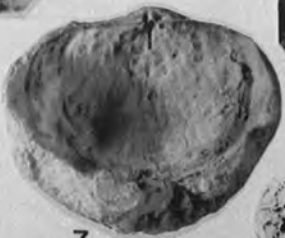
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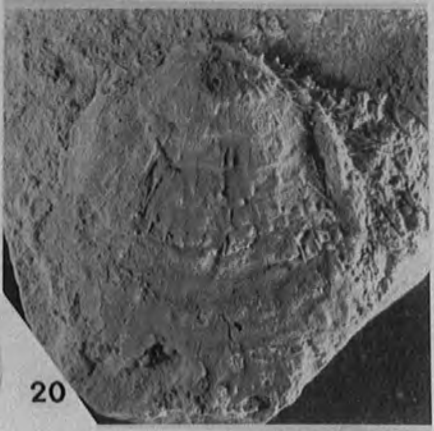
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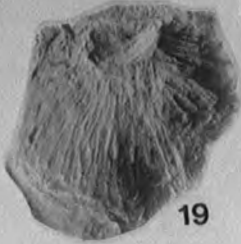
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EXPLANATION OF PLATE 5

Heteralosia hyltonensis new species

Reef base of Ford Formation, Hylton Castle

1-2 — Ventral exterior (plan and right lateral views), paratype MSLHC3.
3 —— Ventral exterior with deep grooves on the trail, paratype MSLHC5a.
4-5 — Ventral exterior (plan and posterior views), paratype MSLHC4.
6 —— Ventral exterior, paratype MSLHC8.
7 —— Latex cast from internal mould of the same specimen.
8 —— Ventral exterior, MSLHC10.
9 —— Ventral exterior (posterior view) with several rhizoid spines, paratype MSLHC6.
10-11 - Ventral and dorsal exterior, paratype MSLHC7.
12 —— Latex cast of the ventral exterior with strongly adpressed spines, MSLHC9.
13 —— Dorsal exterior with fine radial costae, MSLHC11.

Heteralosia seahamensis new species

Reef core of Ford Formation, Beacon Hill railway cut

14 —— Ventral exterior with concentrically directed marginal spines, paratype MSLBH22.
15 —— Dorsal interior, MSLBH25.
16-17 – Ventral and dorsal interior, paratype MSLBH19.
18 —— Latex cast from internal mould (figure 17) of the same paratype showing details of the internal morphology of the dorsal valve.
19-20 – Ventral interior (ventral and posterior views), MSLBH27.
21 —— Ventral exterior of younger individual, MSLBH20b.
22 —— Ventral interior, paratype MSLBH20a.
23-24 – Dorsal interior and lateral profile, MSLBH26.
25 —— External mould of ventral interarea and dorsal exterior, MSLBH24.
26 —— Ventral interior, paratype MSLBH21.
27 —— Ventral exterior, paratypes MSLBH23.

- - - - - - - reconstructed shell margin
[All specimens are coated with ammonium chloride]
(specimen numbers = refer to appendix)

PLATE 5


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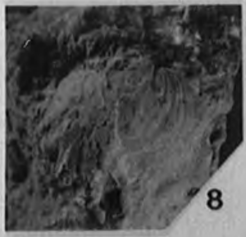
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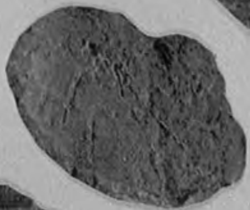
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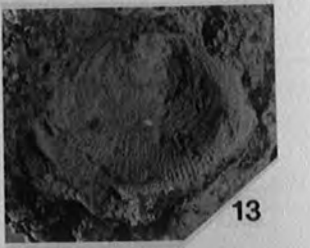
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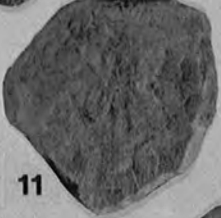
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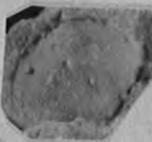
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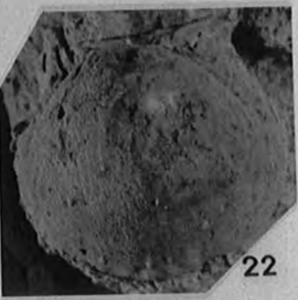
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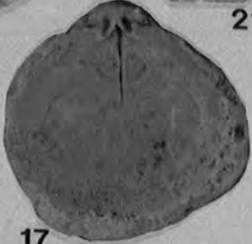
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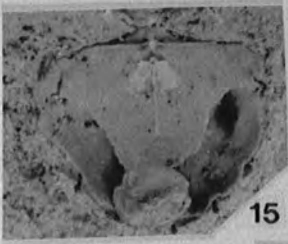
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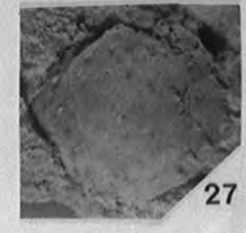
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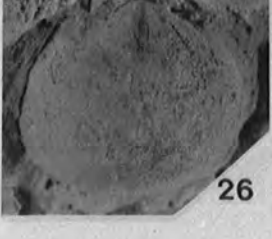
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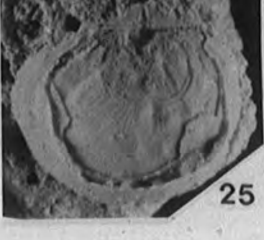
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EXPLANATION OF PLATE 6

Craspedalosia langtonensis new species

Lower part of Raisby Formation, Hobgate (=Langton) Quarry

1-2 — Ventral interarea and very thin visceral cavity, paratype MSLLQ1.
3 —— Strong impression of cicatrix upon the dorsal valve, paratype MSLLQ2.
4 —— Ventral exterior of small individual with large cicatrix covered by matrix, paratype MSLLQ6.
5 —— Dorsal exterior with strong growth rugae, paratype MSLLQ3.
6 —— Small individual attached to a spine of *Horridonia horrida* (Sowerby), paratype MSLLQ5.
7 —— Dorsal interior, paratype MSLLQ4.
8 —— Ventral exterior with large cicatrix, MSLLQ8.
9 —— Dorsal exterior showing squamose growth rugae and fine radial costae, MSLLQ9.
10 —— Ventral exterior, MSLLQ11.

Craspedalosia lamellosa (Geinitz)

Cadeby Formation, Nottinghamshire (BGS specimens)

11-12 — Ventral and dorsal exterior, YPF 4168, Barnby Moore borehole.
13-14 — Ventral and dorsal exterior, BN8223i, Mattersey borehole.

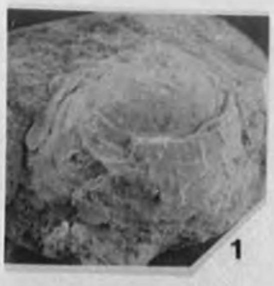
Craspedalosia sp. A

Ford Formation, Hylton Castle (BGS specimens)

15-16 – Internal moulds of ventral and dorsal valves, YEF 2367Da.
17 —— External mould of the same specimen showing squamose dorsal growth rugae.
18 —— Ventral exterior of two specimens, YEF 2367Dd,e.
19 —— Ventral interior with sharply pointed umbo, YEF2367Dd.
20 —— Ventral interior, YEF 2367Df.

[All specimens are coated with ammonium chloride]
(specimen numbers = refer to appendix)

PLATE 6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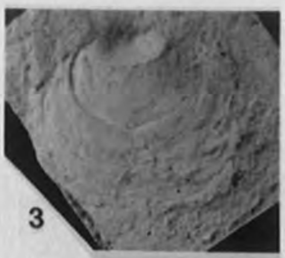
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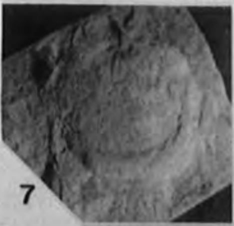
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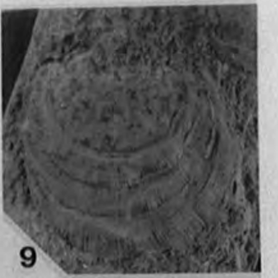
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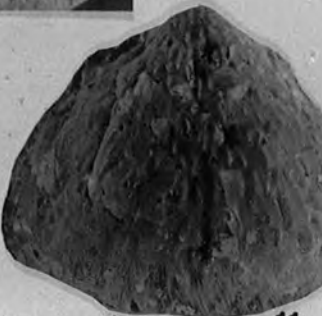
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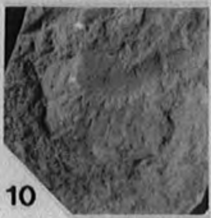
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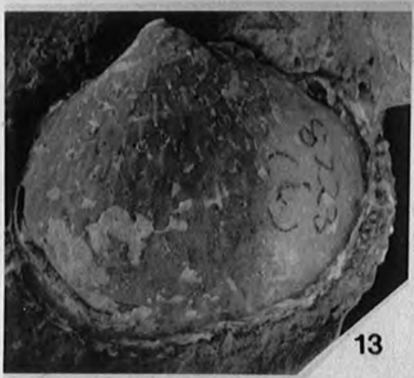
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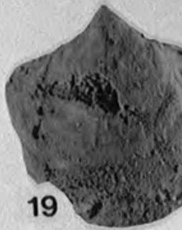
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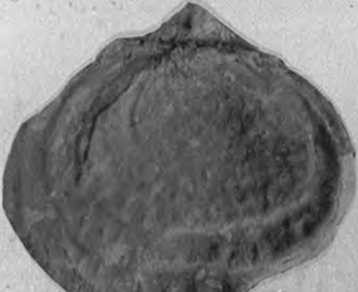
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EXPLANATION OF PLATE 7

Heteralosia? quarringtonensis new species

Lower part of Raisby Formation, Old Quarrington Quarry

1 — Ventral exterior, paratype MSLOQQ3a.
2 — Ventral exterior, paratype MSLOQQ4.
3 — Internal mould of dorsal valve, paratype MSLOQQ5a (marked as a) with two other specimens, MSLOQQ5b,c.
4 — Ventral exterior, paratype MSLOQQ6.
5 — Interior of dorsal valve, MSLOQQ8.
6 — External mould of dorsal valve and ventral interarea, MSLOQQ3b.
7 — Latex cast of ventral exterior, MSLOQQ3c.

Lower part of Raisby Formation, Sherburn Hill Quarry

8 — Latex cast of ventral exterior, MSLSHQ3a.
9 — Ventral exterior with elongate spine bases, MSLSHQ1.
10 — Ventral exterior, MSLSHQ3b.
11 — Latex cast of ventral exterior, MSLSHQ2.

Strophalosia? parva (King)

Reef core of Ford Formation, Humbleton Hill

12 — Ventral valve attached on the exterior umbo of *Horridonia dunelmemsis* new species, MSLHH8 - this latex reproduction shows the interior of ventral valve with large strongly elevated adductor muscle platform.
13 — Syntype of *S?. parva* (King collection in University College of Galway) showing large cicatrix cemented on the interior of *H.dunelmemsis.* this specimen shows numerous spines creeping on the host.

Howseia latirostrata (Howse)

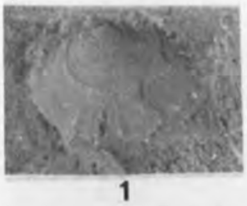
Patch reef of Ford Formation, Gilleylaw builder's trench (Dr. G. A. L. Johnson's specimens)

14 — Latex cast of dorsal exterior showing part of the ventral interarea and some rhizoid spines, GALJ7.
15 — Latex cast of dorsal interior, showing the internal morphology of the dorsal valve and some rhizoid spines from the ventral valve, GALJ8.
16 — Latex cast of specimens GALJ9a,b,c showing auricular spines of specimen marked **b** clasping on the shell of specimen marked **a**.

[All specimens are coated with ammonium chloride].

(specimen numbers = refer to appendix)

PLATE 7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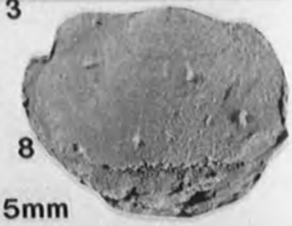
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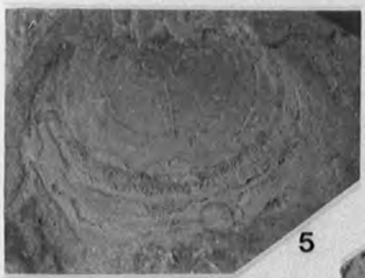
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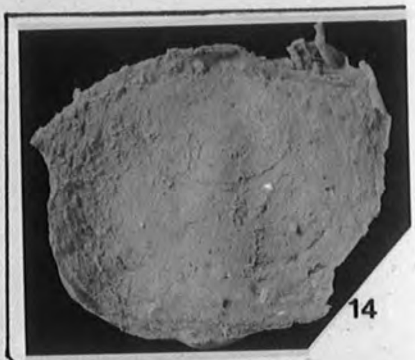
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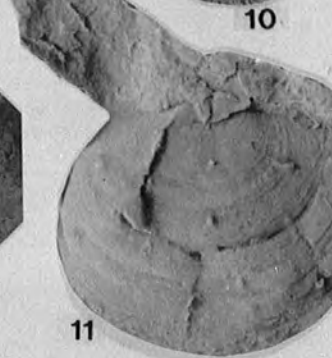
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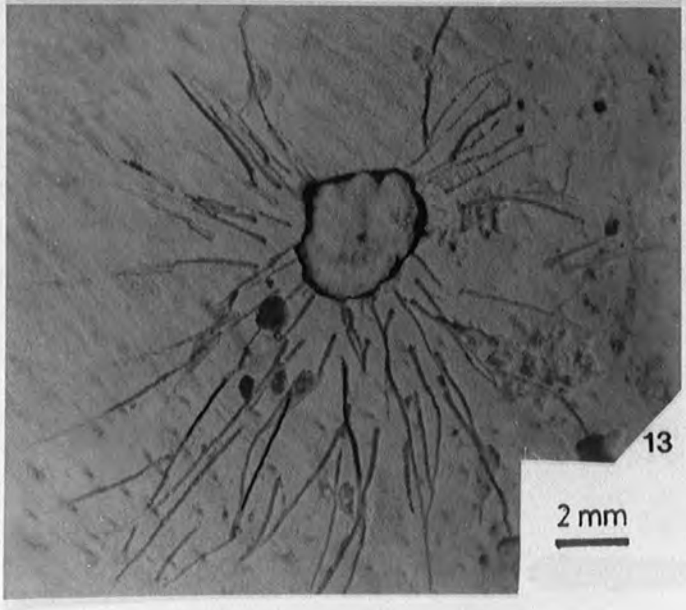
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EXPLANATION OF PLATE 8

Howseia latirostrata (Howse)

Reef base of Ford Formation, Tunstall Hill (rock cottage)

1 —— Ventral exterior, MSLTH12.
2 —— Ventral exterior, MSLTH13.
3-4 — Ventral and dorsal exterior of a male dimorph, G88.57a.
5 —— Ventral exterior of a male dimorph, MSLTH14.
6 —— Ventral exterior of a female dimorph, G88.57b.
7 —— Ventral exterior of a female dimorph, MSLTH15.
8 —— Ventral exterior of a senile female dimorph, G88.57c.
9 —— Ventral interior, MSLTH18.
10 —— Dorsal interior, MSLTH17.
11 —— Dorsal exterior and ventral interarea, MSLTH16.

Howseia umbonillata (King)

Reef base of Ford Formation, Tunstall Hill (rock cottage)

12 —— Dorsal exterior (male) with lophidium inserted into triangular opening of ventral interarea, MSLTH21.
13 —— Ventral interior (female), MSLTH22.
24 —— Ventral exterior of a juvenile, MSLTH25.
25 —— Ventral exterior (female), MSLTH23.

Ford Formation, Dalton-le-Dale (HM collection)

14 —— Dorsal interior (mould) and ventral interarea, G88.53b.
19 —— Ventral interior with shelly material (male dimorph), G88.53a.

Reef patch of Ford Formation, Gilleylaw builder's trench (Dr. G. A. L. Johnson's collection)

15 —— Ventral exterior of juvenile, GALJ1.
16 —— Ventral exterior of juvenile, GALJ2.
17 —— Ventral exterior of juvenile, GALJ3.
18 —— Ventral exterior of male dimorph, GALJ4.
20-21 – Dorsal interior and lateral view of ventral interior of female dimorph, GALJ6.
22-23 – Dorsal interior and lateral view of ventral interior of female dimorph, GALJ5.

[All specimens (except specimens in figures 14 and 19) are coated with ammonium chloride]

(specimen numbers = refer to appendix)

PLATE 8


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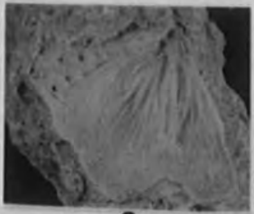
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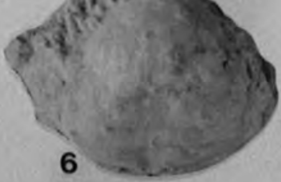
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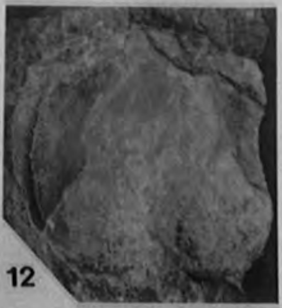
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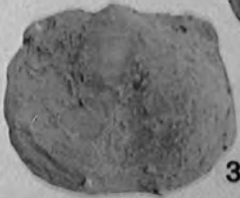
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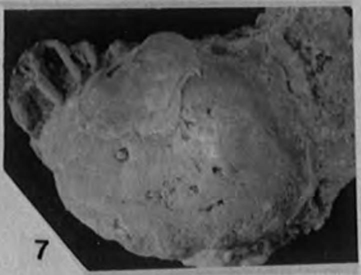
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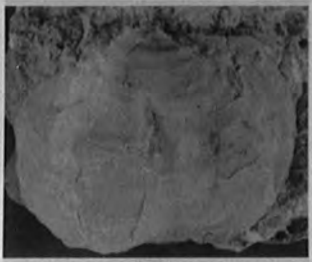
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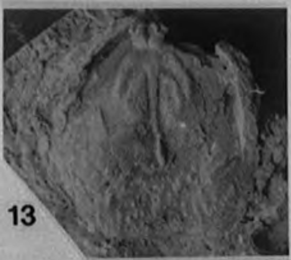
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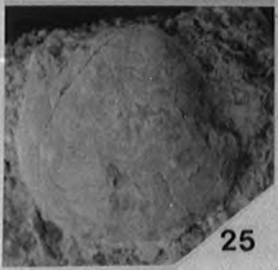
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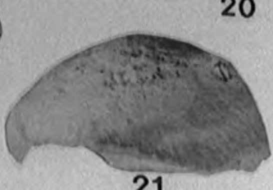
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10mm

EXPLANATION OF PLATE 9

Horridonia horrida (Sowerby)

Lower part of Raisby Formation, Old Town (=White) Quarry

1 —- Ventral exterior (posterior view) showing unique spines arrangement, MSLWQ12.
2 —- Ventral exterior (posterior view) showing unique spines arrangement, MSLWQ13.
3 —- Ventral exterior of juvenile, MSLWQ14.
4 —- Ventral exterior of juvenile, MSLWQ15.
5 —- Ventral exterior, MSLWQ16.
6 —- Ventral interior, MSLWQ17.
7 —- Ventral exterior, MSLWQ18.
8 —- Ventral exterior, MSLWQ19.
10 — Ventral exterior in life position, seen from the top, MSLWQ20 - exposed by natural erosion.
11 — Natural cross section, seen from the top, MSLWQ 23 -preserved in life position.
12 — Dorsal interior, MSLWQ21.
13 — Ventral exterior (posterior view) showing unique spines arrangement, MSLWQ22.
14 — Enlargement of figure 3.

Lower part of Raisby Formation, East Thickley Quarry

9 —- Dorsal exterior, MSLETQ4 (the two large spines have been repositioned during diagenesis).

Horridonia species A

Lower part of Raisby Formation, Old Town (=White) Quarry

15 — Ventral exterior, MSLWQ26.

Reef core of Ford Formation, Tunstall hill old trench

16 — Ventral exterior, MSLot12.

[All specimen are coated with ammonium chloride, except specimen in figure 2 which is immersed in water]
(specimen numbers = refer to appendix)

PLATE 9


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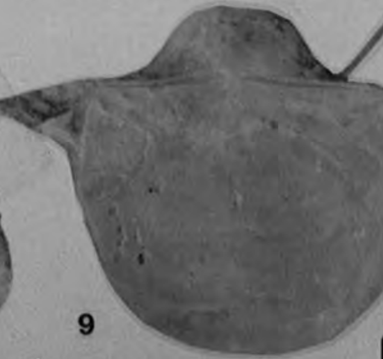
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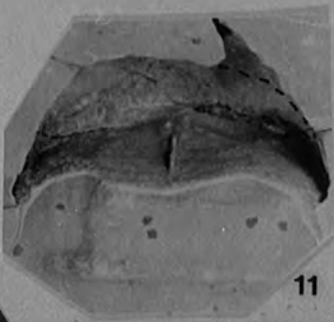
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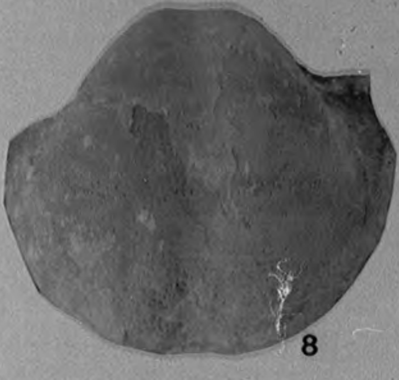
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5mm

10mm

EXPLANATION OF PLATE 10

Horridonia hoppeiana (Eisel)

Lower part of Raisby Formation, Hobgate (=Langton) Quarry

1-3 — Ventral exterior (posterior, lateral and plan views), MSLLQ11.

Lower part of Raisby Formation, Old Town (=White) Quarry

4-5 —– Lateral profile ventral exterior, MSLWQ24.
10-11 - Lateral and anteroventral views of ventral interior, MSLWQ25.

Patch reef of Ford Formation, High Newport old railway cut

6 —— Ventral exterior, MSLHN4.
7 —— Ventral exterior, MSLHN5.
8-9 — Ventral exterior (posterior and plan views), MSLHN6.

Spinohorridonia species cf. *S. laspeana* (Eisel)

Reef core of Ford Formation, Humbleton Hill

12 — Dorsal exterior (external mould), MSLHH21.
13 — Dorsal exterior (external mould), MSLHH19.
14 — Dorsal exterior (latex cast), MSLHH20.

?Reef core of Ford Formation, Ryhope old railway cut

15-16 — Latex cast of dorsal and ventral exterior, MSLR2.

[All specimens are coated with ammonium chloride]
(specimen numbers = refer to appendix)

PLATE 10


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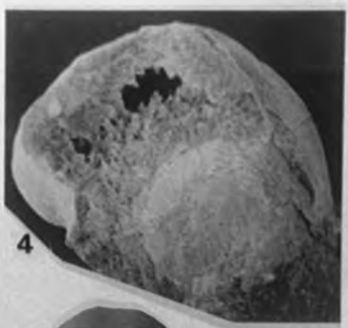
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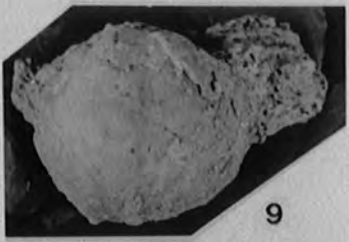
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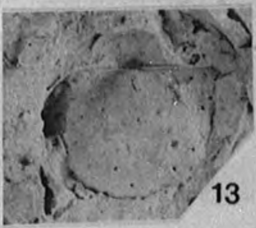
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EXPLANATION OF PLATE 11

Horridonia dunelmensis new species

Reef core of Ford Formation, Humbleton Hill

1-8 — Internal mould of ventral valves from a series of ontogenic development, MSLHH12-16,9,17-18. (MSLHH9 shows numerous spines set on a horizontal plane).
9 — Ventral internal mould, MSLHH18.
10-11 — Latex cast of dorsal and ventral exteriors, MSLHH8. (ventral exterior carries numerous body spines while dorsal exterior has no body spines).
12 — Dorsal interior showing a row of marginal spine apertures, latex cast from MSLHH10.
13 — Ventral interior showing a ridge with coarse endospines matching the apertures in figure 12, latex cast from MSLHH11.

Reef core of Ford Formation, Beacon Hill railway cut

14 — Ventral exterior (lateral view), MSLBH29b.
15 — Dorsal interior with quadrilobed myophore, MSLBH29a.
16 — Posterior view, latex cast of MSLBH30.

Reef talus of Ford Formation, Ryhope old railway cut

17 — Ventral internal mould with impression of spine bases, MSLR1.

Reef core of Ford Formation, Tunstall Hill old trench

18 — Ventral internal mould with patches of shell remain, MSLot11.

Spinohorridonia geinitziana (de Koninck)

Reef base of Ford Formation, Hylton Castle

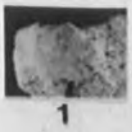
19-20, 22 — Ventral exterior (posterior, anterior and lateral views), MSLHC13.
21 — Dorsal exterior of the same specimen.
23 — Parts of dorsal interior, MSLHC16.

Reef core of Ford Formation, Tunstall Hill old trench

24 — Ventral internal mould, MSLot14.
25 — Parts of dorsal interior, MSLot15.
26 — Posterior region from ventral internal mould, MSLot13.

[All specimens figured in this plate are coated with ammonium chloride].
(specimen numbers = refer to appendix)

PLATE 11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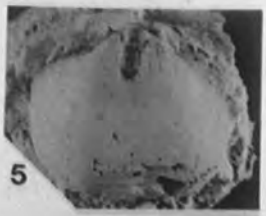
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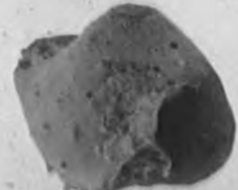
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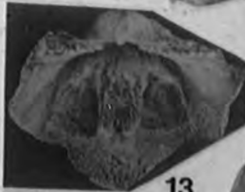
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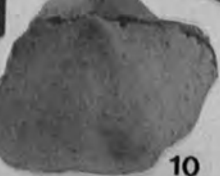
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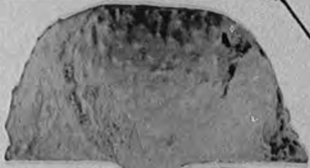
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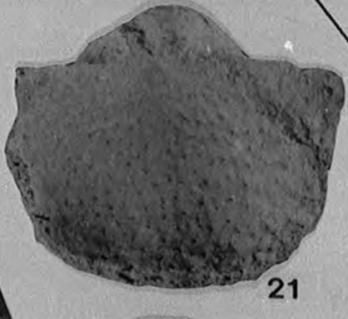
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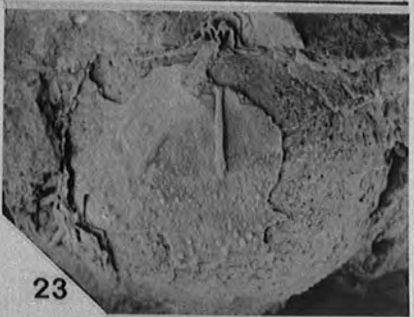
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EXPLANATION OF PLATE 12

Craspedalosia species A

Nam Loong Bed of Kinta Limestone, H. S. Lee mine no 8

1-2 — Exterior and interior of dorsal valve, D2727 (UM collection).

Institella species A

Base of Chuping Limestone Formation, Pulau Jong

3 —— Ventral exterior with large rhizoid marginal spine and smooth lateral margin, 1353 (UM collection).

Dictyoclostus? gratiosus (Waagen)

Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]

4 —— Ventral exterior, MSL10.1a (locality 10).
5 —— Dorsal interior, MSL10.1b (locality 10).
6 —— Ventral exterior, MSL8.1a (locality 8).
7 —— Ventral exterior, MSL16.1a (locality 16).
8 —— Dorsal interior, MSL16.1b (locality 16).
9 —— Strongly convex ventral valve with long trail, MSL16.1c (locality 16).

Antiquatonia species A

Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]

10 —— External mould of open ventral and dorsal valves, MSL10.2a (locality 10).
11 —— Internal mould ventral valve with a row of marginal spines, MSL10.2b (locality 10).

Kepis Bed, Kampung Juaseh

12 —— Ventral valve compressed against dorsal valve, MSL20.1a.
13 —— Dorsal interior, MSL20.1b.
14 —— Ventral external mould, MSL20.1c.
15 —— Ventral interior, MSL20.1a.

Reticulatia sp. indet.

Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]

16 —— Ventral exterior, MSL8.2a (locality 8).
17,18 — Ventral exterior, MSL16.2a,b (locality 16).

Echinoconchus species A

Nam Loong Bed of Kinta Limestone, H. S. Lee mine no 8

19,23 — Dorsal external moulds, UM-1a,e (UM collection).
20,21,23 — Ventral exteriors, UM-1b,c,d (UM collection).

Waagenoconcha sp. indet.

Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]

24 —— Ventral exterior, MSL16.3 (locality 16)

Waagenoconcha sp. cf. *W. abichi* (Waagen)

Nam Loong Bed of Kinta Limestone, H. S. Lee mine no 8

25,26,27,28 — Casts of ventral exteriors, Um-2a,b,c,d (UM collection).

Linoproductus sp. cf. *L?. sinosus* Huang

Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]

29 —— Cast of ventral exterior, MSL10.3 (locality 10).
30 —— Cast of ventral exterior (postero-lateral view), MSL9.1a (locality 9).
31 —— Several specimen from rock slab MSL9.1b (locality 9).

[All specimens figured in this plate are coated with ammonium chloride]

PLATE 12


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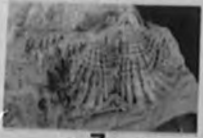
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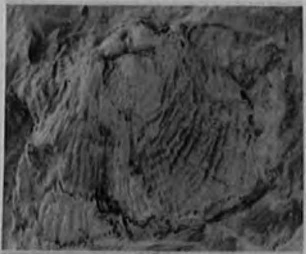
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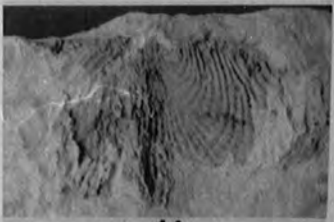
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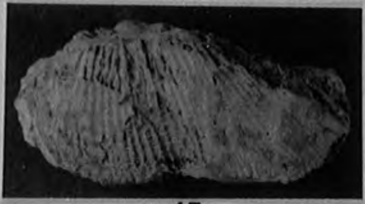
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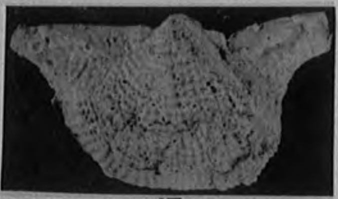
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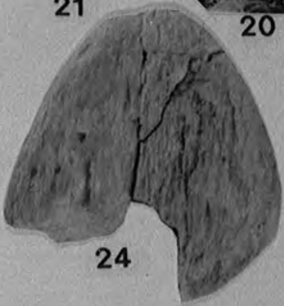
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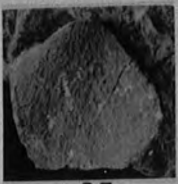
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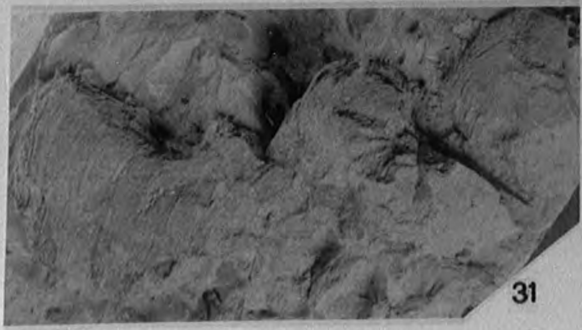
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EXPLANATION OF PLATE 13

Striatifera species A

Nam Loong Bed of Kinta Limestone, H. S. Lee mine no 8
1 — Ventral exterior, UM-4a (UM collection).

Cancrinella cancrini (de Koninck)

Basal Chuping Formation, Bukit Tungku Lembu, Perlis
UKM-MSL collection
2 — Cast of ventral exterior and dorsal external mould of different individuals, MSL1.1a.
3,4 — Cast of ventral exterior (lateral and posterior views), MSL1.1a.
5 — Cast of dorsal exterior, MSL1.1b.
6 — Dorsal external mould, MSL1.1c.
7 — MSL1.1d, coated with ammonium chloride.
8 — Part of MSL1.1d, covered with thin film of water.
9 — Ventral exterior (cast) with coarse costae and body spines, MSL1.1e.
10 — Several complete and fragmentary specimens, MSL1.1b.

Cancrinella sp. cf. *C. cancriniformis* (Tschernyschew)

Kepis Bed, Kampung Juaseh, Negeri Sembilan
11 — Cast of ventral exterior, MSL20.2a.

Cancrinellla species A

Nam Loong Bed of Kinta Limestone, H. S. Lee mine no 8
12,13 - Casts of ventral exterior, UM-3a,b.

Costispinifera species A

Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]
14 —- Part of ventral internal mould, MSL10.5, locality 10.

Unnamed formation, Jengka Pass, Maran, Pahang
15 — Cast of ventral exterior, MSL17.2.

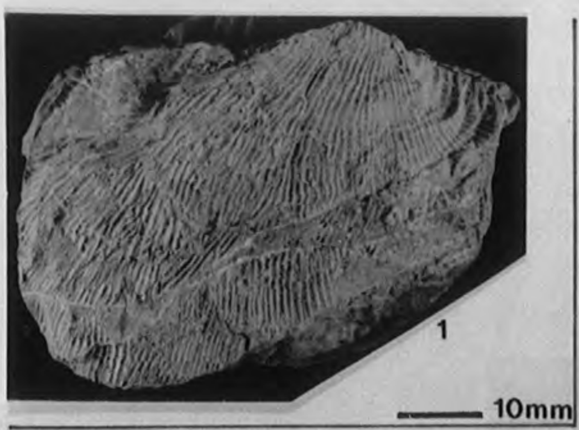
Echinauris sp. indet.
Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]
16 — Part of ventral valve, MSL11.2, locality 11.

Echinauris? species A

Nam Loong Bed of Kinta Limestone, H. S. Lee mine no 8
UM collection
17 — Ventral internal mould, lateral view showing deep groove of interior marginal ridge, UM-4a.
18 — Ventral internal mould showing striated diductors and wrinkled auricle, UM-4b.
19,20 — ~~Dorsal external mould showing numerous rugae and spine apertures, UM-~~4c,d.

[All specimens are coated with ammonium chloride except for specimen in figure 8 which is coated with thin film of water]

PLATE 13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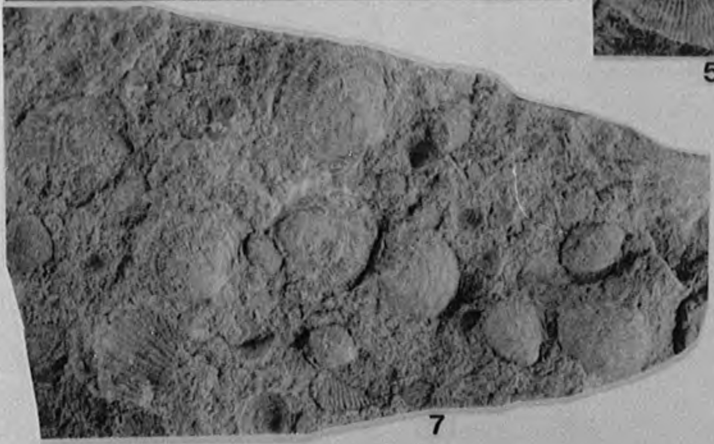
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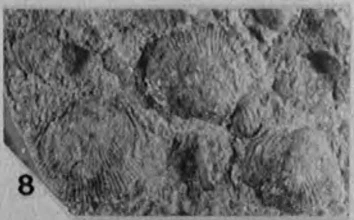
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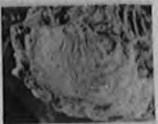
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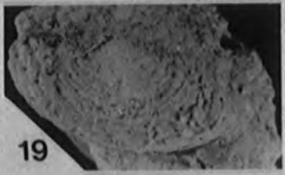
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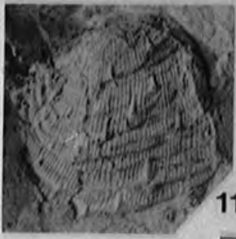
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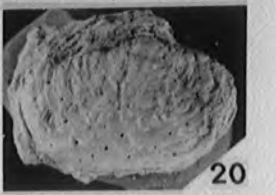
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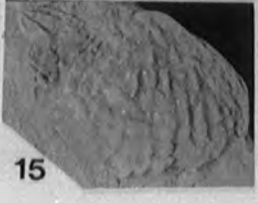
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EXPLANATION OF PLATE 14

Marginifera? species A

Kepis Bed, Kampung Juaseh - UKM-MSL collection

1,2,3,4 - Ventral internal mould with part of external cast - ventral, anterior, posterior and lateral views, MSL20.3a.
5 — Ventral internal mould of posterior region, MSL20.3b.

Liosotella nakamurai new species

Unnamed Upper Permian formation
Jengka Pass, Maran, Pahang, (UKM-MSL collection)

6 — Ventral exterior (cast), posterior view, MSL17.1a.
7 — Ventral exterior (cast), juvenile, MSL17.1b.
8 — Ventral exterior (latex cast) showing some spine bases, MSL17.1c.
9 — Dorsal interior (latex cast) showing some large endospines on the rim of internal marginal ridge, MSL17.1d.
10 — Dorsal interior with a break of slope at the trail, MSL17.1e.
11 — Ventral exterior (cast), MSL17.1c - compare with latex cast of similar specimen in figure 8.
12 — Ventral interior pitted with numerous fine endospines, MSL17.1f.

Unnamed Upper Permian formation
Timor Oil Palm Mill, Maran, Pahang (UKM-MSL collection)

13,14,15 — Ventral exterior (cast), dorsal internal mould and dorsal exterior cast, MSL18.1a (UKM-MSL collection).

Retimarginifera lipisensis new species

Leptodus Bed of Gua Musang Formation
Dada Kering - Gua Musang highway [UKM-MSL collection]

16 — Ventral internal mould with deep groove of marginal ridge and broad dendritic adductor, MSL15.1a, locality 15.
17 — Latex cast of the same specimen showing thick internal marginal ridge.
18 — Overlapping external and internal morphology of ventral valve, MSL15.1b, locality 15.
19 — Internal mould of both ventral and dorsal valve, MSL15.1c, locality 15.
20 — Latex cast of the internal morphology of the same specimen.
21 — External mould of the same specimen.
23 — Cast of external mould showing halteroid spines, MSL11.1, locality 11.
24 — Ventral valve of a juvenile showing a pair of marginal spines, MSL8.3a, locality 8.
25 — Ventral valve with three pairs of halteroid spines, MSL8.3b, locality 8.

Leptodus Bed of Gua Musang Formation
Kampung Gua, Kuala Lipis, Pahang (UKM-MSL collection)

22,26 — Ventral valves with deep groove of marginal ridge, MSL3.1a,b.

Echinauris? species A

Nam Loong Bed of Kinta Limestone, H. S. Lee mine no 8

27,28 — Ventral internal mould (ventral and lateral views), UM-4e (UM collection).

[All specimens figured in this plates are coated with ammonium chloride]

PLATE 14


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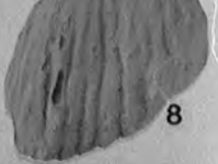
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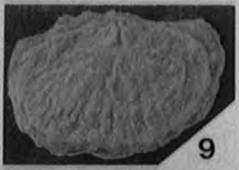
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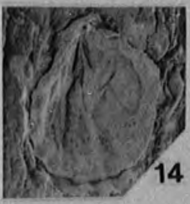
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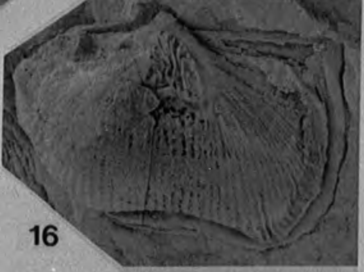
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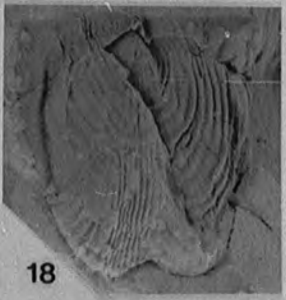
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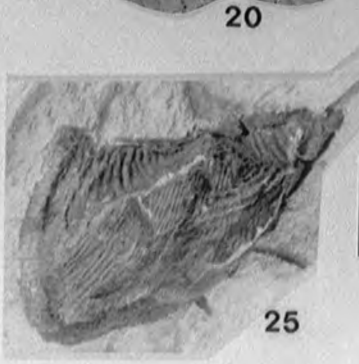

25


27


28


26

10mm

EXPLANATION OF PLATE 15

(Geological Survey Department (GSD) colection)

Strophalosia species A
Leptodus Bed of Gua Musang Formation
Railway cut adjacent to Sungai Jeleteh, Merapoh, Pahang

1 — Internal mould of dorsal valve with ventral interarea, LF 176.

Dictyoclostus sp. indet.
Leptodus Bed of Gua Musang Formation
Sungai Galas, Gua Musang, Kelantan

2,3 — Several undetermined specimens showing coarse costae and reticulate umbo, FPhN19a,b.

Antiquatonia species A
?Gua Musang Formation, Sungai Sepia, Kuala Lipis, Pahang

4,6 — Casts of ventral exterior, L1096(31,26).
5 —— Dorsal external mould, L1096(29b).

Stepanoviella sp. cf. *S. flexuosa* Waterhouse
Kepis Bed, Kampung Baru Kepis, Kuala Pilah, Negeri Sembilan

7 — Dorsal interior, KPF3b.
8 — Dorsal external mould, KPF3a.
9 — Ventral exterior (cast), unnumbered specimen.

Costispinifera species A
Unnamed Upper Permian formation, Ulu Lepar, Maran, Pahang

10,11 — Several fragmentary cast showing coarse corrugated costae with numerous spines especially on lateral slope of visceral disc, AN29a,b.

Dictyoclostus? gratiosus (Waagen)
Leptodus Bed of Gua Musang Formation
Railway cut adjacent to Sungai Jeleteh, Merapoh, Pahang

12 — Ventral exterior, 172/9c.

Retimarginifera lipisensis new species
Leptodus Bed of Gua Musang Formation
Railway cut adjacent to Sungai Jeleteh, Merapoh, Pahang

13 — Superimposed internal and external morphology of both ventral and dorsal valve, 172/7.

Paucispinifera species A
Upper Permian Aring Formation, South Central Kelantan

14 — Ventral internal moulds of three specimens GS(F)5,52,53.

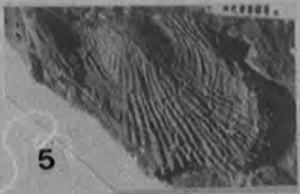
[All specimens are not coated]

PLATE 15


1


2


4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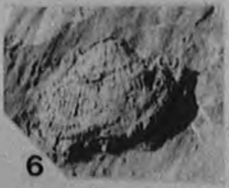
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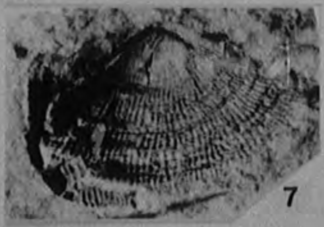
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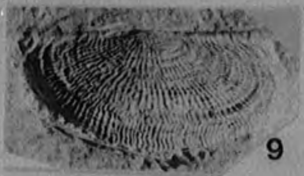
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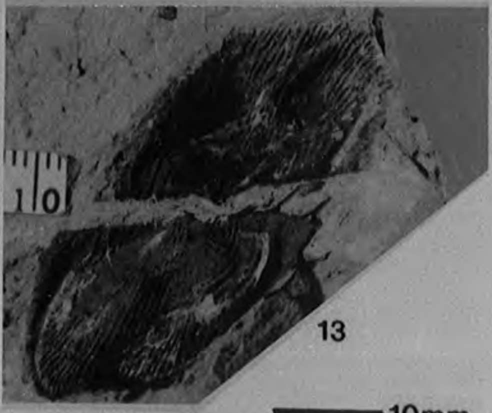
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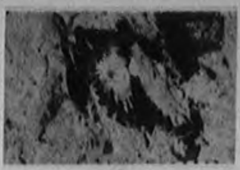
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APPENDIX

List of type, figured and measured specimens (author's collection) deposited in the British Museum (Natural History), London.

Author's numbers	BM(NH) numbers	
MSLHH1	BD 9141	Strophalosia lewisiana
MSLHH2	BD 9142	
MSLHH3	BD 9143	
MSLHC1	BD 9144	
MSLHN1	BD 9145	
MSLHN2	BD 9146	
MSLHN3	BD 9147	
MSLot1	BD 9148	
MSLot2	BD 9149	
MSLot3	BD 9150	
MSLBH1	BD 9151	Strophalosia excavata
MSLBH2	BD 9152	
MSLBH3	BD 9153	
MSLBH4	BD 9154	
MSLBH6	BD 9155	
MSLBH7	BD 9156	
MSLBH8	BD 9157	
MSLBH9	BD 9158	
MSLot4	BD 9159	
MSLot5	BD 9160	
MSLot6	BD 9161	
MSLot7	BD 9162	Strophalosia goldfussi
MSLWQ1	BD 9163	
MSLOQQ1	BD 9164	
MSLOQQ2	BD 9165	
MSLETQ1	BD 9166	
MSLHH8	BD 9292	S. parva
MSLBH10	BD 9167	Eostrophalosia permiana
MSLBH11	BD 9168	
MSLBH12	BD 9169	
MSLBH13	BD 9170	
MSLBH14	BD 9171	
MSLBH15	BD 9172	
MSLBH16	BD 9173	
MSLBH17	BD 9174	
MSLBH18	BD 9175	
MSLot8	BD 9176	
MSLTH1	BD 9177	Heteralosia morrisiana
MSLTH2	BD 9178	
MSLTH3	BD 9179	
MSLTH4	BD 9180	
MSLTH5	BD 9181	
MSLTH6	BD 9182	
MSLTH7	BD 9183	
MSLTH8	BD 9184	
MSLTH9	BD 9185	
MSLTH10	BD 9186	

Author's numbers	BM(NH) numbers	
MSLHH4	BD 9187	Heteralosia humbletonensis
MSLHH5	BD 9188	
MSLHH6	BD 9189	
MSLHH7	BD 9190	
MSLHC2	BD 9191	
MSLHC3	BD 9192	Heteralosia hyltonensis
MSLHC4	BD 9193	
MSLHC5	BD 9194	
MSLHC6	BD 9195	
MSLHC7	BD 9196	
MSLHC8	BD 9197	
MSLHC9	BD 9198	
MSLHC10	BD 9199	
MSLHC11	BD 9200	
MSLHC12	BD 9201	
MSLBH19	BD 9202	Heteralosia seahamensis
MSLBH20	BD 9203	
MSLBH21	BD 9204	
MSLBH22	BD 9205	
MSLBH23	BD 9206	
MSLBH24	BD 9207	
MSLBH25	BD 9208	
MSLBH26	BD 9209	
MSLBH27	BD 9210	
MSLBH28	BD 9211	
MSLBH29	BD 9212	
MSLBH30	BD 9213	
MSLBH31	BD 9214	
MSLWQ4	BD 9215	Heteralosia aycliffensis
MSLWQ5	BD 9216	
MSLWQ6	BD 9217	
MSLWQ7	BD 9218	
MSLWQ8	BD 9219	
MSLWQ9	BD 9220	
MSLWQ10	BD 9221	
MSLWQ11	BD 9222	
MSLETQ2	BD 9223	
MSLETQ3	BD 9224	
MSLRHQ1	BD 9225	
MSLOQQ3	BD 9226	Heteralosia quarringtonensis
MSLOQQ4	BD 9227	
MSLOQQ5	BD 9228	
MSLOQQ6	BD 9229	
MSLOQQ7	BD 9230	
MSLOQQ8	BD 9231	
MSLSHQ1	BD 9232	
MSLSHQ2	BD 9233	
MSLSHQ3	BD 9234	

continue

Author's numbers	BM(NH) numbers	
MSLLQ1	BD 9235	Craspedalosia langtonensis
MSLLQ2	BD 9236	
MSLLQ3	BD 9237	
MSLLQ4	BD 9238	
MSLLQ5	BD 9239	
MSLLQ6	BD 9240	
MSLLQ7	BD 9241	
MSLLQ8	BD 9242	
MSLLQ9	BD 9243	
MSLLQ10	BD 9244	
MSLLQ11	BD 9245	
MSLTH12	BD 9246	Howseia latirostrata
MSLTH13	BD 9247	
MSLTH14	BD 9248	
MSLTH15	BD 9249	
MSLTH16	BD 9250	
MSLTH17	BD 9251	
MSLTH18	BD 9252	
MSLTH19	BD 9253	
MSLTH20	BD 9254	
GALJ7	BD 9255	
GALJ8	BD 9256	
GALJ9	BD 9257	
GALJ1	BD 9258	Howseia umbonillata
GALJ2	BD 9259	
GALJ3	BD 9260	
GALJ4	BD 9261	
GALJ5	BD 9262	
GALJ6	BD 9263	
MSLTH21	BD 9264	
MSLTH22	BD 9265	
MSLTH23	BD 9266	
MSLTH24	BD 9267	
MSLTH25	BD 9268	
MSLWQ12	BD 9269	Horridonia horrida
MSLWQ13	BD 9270	
MSLWQ14	BD 9271	
MSLWQ15	BD 9272	
MSLWQ16	BD 9273	
MSLWQ17	BD 9274	
MSLWQ18	BD 9275	
MSLWQ19	BD 9276	
MSLWQ20	BD 9277	
MSLWQ21	BD 9278	
MSLWQ22	BD 9279	
MSLWQ23	BD 9280	
MSLETQ4	BD 9281	

Author's numbers	BM(NH) numbers	
MSLHN4	BD 9282	Horridonia hoppeiana
MSLHN5	BD 9283	
MSLHN6	BD 9284	
MSLHN7	BD 9285	
MSLWQ24	BD 9286	
MSLWQ25	BD 9287	
MSLLQ12	BD 9288	
MSLLQ13	BD 9289	
MSLot16	BD 9290	
MSLot17	BD 9291	
MSLHH8	BD 9292	Horridonia dunelmensis
MSLHH9	BD 9293	
MSLHH10	BD 9294	
MSLHH11	BD 9295	
MSLHH12	BD 9296	
MSLHH13	BD 9297	
MSLHH14	BD 9298	
MSLHH15	BD 9299	
MSLHH16	BD 9300	
MSLHH17	BD 9301	
MSLHH18	BD 9302	
MSLot10	BD 9303	
MSLot11	BD 9304	
MSLot12	BD 9305	
MSLBH32	BD 9306	
MSLBH33	BD 9307	
MSLR1	BD 9308	
MSLWQ26	BD 9309	Horridonia sp.A
MSLot13	BD 9310	
MSLLQ14	BD 9311	
MSLHC13	BD 9312	Spinohorridonia geinitziana
MSLHC14	BD 9313	
MSLHC15	BD 9314	
MSLHC16	BD 9315	
MSLHC17	BD 9316	
MSLHC18	BD 9317	
MSLot14	BD 9318	
MSLot15	BD 9319	
MSLot16	BD 9320	
MSLR2	BD 9321	Spinohorridonia sp. cf. S. laspeana
MSLR3	BD 9322	
MSLHH19	BD 9323	
MSLHH20	BD 9324	
MSLHH21	BD 9325	

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