A thesis entitled

THE SUPERFAMILY BEYRICHIAEAE (OSTRACODA)
FROM THE SILURIAN AND DEVONIAN SYSTEMS
OF BRITAIN

Submitted for the degree of

DOCTOR OF PHILOSOPHY

IN THE

FACULTY OF SCIENCE

UNIVERSITY OF LEICESTER

BY

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Volume 1

1974
To my wife, Pauline,

and my Parents,

for all they have given.
ABSTRACT

A study of the British members of the superfamily Beyrichiacea Matthew, 1886 (Ostracoda) has been undertaken. Nearly all of the taxa are Silurian in age; others are, very rarely, found in the Devonian. Wherever possible, extant type material has been located and a primary revision made. Such work has been augmented by studies on new collections, chiefly made from Central England and the Welsh Borderland.

The thesis is arranged on a taxonomic basis; the subfamily is taken as the basis for each major section of the work. Other chapters deal with finds of British valves which exhibit intermediary stages in the metamorphosis of the crumina, and with a new beyrichiacean genus which is unique in its apparent lack of dimorphism. One section discusses the faunal distribution of the British Beyrichiacea and compares it with established successions elsewhere.

Most of the techniques used, involve standard micropalaeontological practices. Casting methods, and the use of the scanning electron microscope for illustration of the casts, have proved invaluable for working with mould material, and provide an optimistic sign for the future study of ostracode mould faunas.

Representatives of the Craspedobolbininae, Amphitoxotidinae, Treposellinae, Beyrichiinae and Kloedeniinae are present. Over 75 named species and some 15 other forms are described; many of the species and genera are new.
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ACKNOWLEDGEMENTS

To my mentor, Professor P.C. Sylvester-Bradley, I owe a special debt of gratitude for his encouragement and advice; the privilege of his supervision throughout all stages of this work is deeply appreciated. I would also like to thank Professor Sylvester-Bradley and, lately, Dr. C.H. James for the use of the facilities of the Department of Geology at Leicester.

Special thanks are due to Professor A. Martinsson, Department of Palaeobiology, Uppsala, Sweden, for the considerable material placed at my disposal, for his expert introduction to the field of Palaeocene ostracodes and, not least, for his generous hospitality.

I am grateful to Dr. J.H. McD. Whitaker for suggesting a study of British Silurian ostracodes, and for his guidance in the field.

To the following I wish to record my appreciation for allowing access to material under their care: Dr. R.H. Bate, British Museum (Natural History) London; Dr. A.W.A. Rushton and Dr. D.E. White, Institute of Geological Sciences, Geological Survey and Museum, London; Dr. R.B. Rickards and Dr. C.L. Forbes, Sedgwick Museum, Cambridge; Dr. M.G. Bassett and Dr. R.M. Owens, National Museum of Wales, Cardiff; Dr. J.K. Ingham and Dr. W.D.I. Rolfe, Hunterian Museum, Glasgow University; Dr. C. O’Riordan, National Museum of Ireland, Dublin; Dr. M.L.K. Curtis, Bristol City Museum; Dr. R.B. Wilson, Institute of Geological Sciences, Edinburgh; Professor A. Martinsson (formerly of the Palaeontological Institute), University of Uppsala, Uppsala, Sweden.

Others have generously donated specimens or loaned material for study from their private collections: Dr. Derek J. Siveter, Trinity College, University of Dublin; Dr. J.E. Robinson, University College, London; Dr. R.F. Lundin, University of Arizona, Tempe, U.S.A.;
Mr. B. Abbott, The Open University; Mr. & Mrs. R. Marsh, Norwood Technical College, London; Mr. J. Tipper, University of Edinburgh; Dr. R.M. Owens; Dr. J.H.McD. Whitaker.

Drs. D.C. Palmer and G.D. Sevastopulo (Trinity College, Dublin) kindly supplied assistance during a visit to Eire, as did Dr. M.C. Keen (University of Glasgow) during field-work in Scotland. I am grateful to the many friends and geologists, particularly members of the Ludlow Research Group, whose company I have enjoyed in the field.

I wish to thank Mr. W.M. Teasdale and his staff for the technical services they have rendered, Mrs. A. Boustead for translating foreign texts, Mr. R. Branson and Mrs. J. Westerman for drafting services, and Mrs. E.M. Barratt for her general assistance. I am indebted to Mr. G.L.C. McTurk for all his work and expertise on the scanning electron microscope at Leicester. To Miss Sally Ward, my trusty typist, I owe - amongst other things - my sincere thanks for her skill and patience.

Most of this work was undertaken under the tenure of a Research Studentship from the Natural Environmental Research Council. I gratefully acknowledge this award.

Above all others, I am deeply grateful to my wife, Pauline, for her tireless help and encouragement, and to my parents for the constant support they have given.
INTRODUCTION

The Beyrichiacea are a group of fossil, straight-hinged Ostracoda (Crustacea, Arthropoda). In essence, the major unifying characteristic of the superfamily is the development (in all but one case - see chapter F, herein) of a specialised form of sexual dimorphy. The presumed female acquires a so-called "brood pouch" (= crumina) in the anteroventral (- ventral) region of each valve during the last moult, whereas the male merely suffers an increase in size during this ecdysis.

Within the group, which now numbers over 75 genera, there are myriad varieties of carapace morphology (well discussed and illustrated by Kesling 1969).

Beyrichiacean ostracodes are almost exclusively Silurian and Devonian in age; recently, they have been shown to range into the Carboniferous. Records occur from especially N America and Europe, with finds coming also from Asia, Africa, S America and Australia.

Beyrichiacean species constitute important elements in many ostracode faunas and have for long since attracted the curiosity of Palaeozoic micropalaeontologists. The long history of diverse research devoted to these palaeocopes, beginning in 1769 when C.F. Wilckens figured kloedeniine valves - together with trilobites - under the name Agnostus pisiformis, has been summarized in detail elsewhere (Martinsson 1962, pp. 13-38).
The first mention of ostracodes from the Siluro-Devonian of Britain appears to be a reference by Sowerby (in Murchison 1839, p. 604) to "Agnostus tuberculatus" together with a figure (op. cit., pl. 3, figs. 17, 17a) of "Agnostus pisiformis". The specimens - from the Downtonian near Downton, the Welsh Borderland - probably represent a kloedeniine beyrichiacean ostracode.

Many early students of Palaeozoic ostracodes treated material from the Silurian of Britain. Amongst these were Salter (1846), Haswell (1865), and McCoy (1846, 1851). The latter erected the first beyrichiacean genus, Beyrichia, and his B. kloedeni from Ireland subsequently became accepted as the type species of the type Palaeocope superfamily. Undoubtedly, T.R. Jones stands high on the list of pioneer workers in this field. In a legion of papers spanning the second half of the last century, he more than any other added to our knowledge of British Silurian and Devonian ostracode faunas. The reports most relevant to British beyrichiacea are those of Jones 1855a, 1869, 1879, 1881, 1881c, 1887a, 1887b, 1888a, 1890, and Jones & Holl 1886, 1886a. The material described included specimens from all parts of Britain with a concentration on the Silurian outcrops of the Welsh Borderland. This emphasis was, in part, due to Jones's treatment of material donated by other avid collectors (see also Vine 1882, 1887, 1888, and Smith 1881, 1892). The full scope of Jones's publications may be gathered in detail from the bibliographic lists of Bassler & Kellett (1934). His work embraced all forms of Palaeozoic ostracods, though a substantial proportion of the taxa he described were Beyrichiacea.
Between the long series of "Palaeozoic Bivalved Entomostraca" papers of Jones, and the second half of the present century, there was an almost complete hiatus in the study of Siluro-Devonian ostracodes from Britain. Amongst the exceptions were the researches of Straw (1928, 1933) who restudied *Beyrichia kloedeni* McCoy and described a late Silurian borehole fauna from Buckinghamshire, and Harper (1940) who reported on Llandovery ostracodes (including a number of beyrichiacean species) from the Welsh Borderland. Sylvester-Bradley & Levinson (1960) reviewed the official status of the genus *Beyrichia* McCoy and its type species.

After the work of Martinsson (1962) had revealed the wealth of Silurian Beyrichiacea in the Gotland succession, much interest was rekindled in the group. Much of our understanding of beyrichiacean taxonomy is due to Martinsson's significant contributions in this field (q.v. reference list). A number of papers (1960b, 1962, 1963, 1965a, 1967, 1968) by this author deal specifically, or in part, with British species of the superfamily. Following Martinsson, Shaw described Beyrichiacea from both the Downtonian of the Welsh Borderland (1969) and from the Ludlovian and Downtonian of the Lake District (1971a). In a paper on the new genus *Coplandella* - the only known Carboniferous member of the group - Bless & Jordan (1971) hinted that material from Ireland, originally described by Jones & Kirkby, may also belong within the beyrichiacean system. More recently, Siveter (1973, 1973a, 1973b) has re-illustrated and revised other Llandovery and Wenlock beyrichiacean species; to the authors knowledge the latter papers represent the first occasion that palaeocopes have been figured using scanning electron micrographs.

This thesis attempts the first revision and monographic treatment of Beyrichiacean taxa from Britain.
OUTLINE OF RESEARCH

It soon became apparent that the most important task confronting the researcher was a primary systematic rationalization of the British beyrichiacean fauna. To this end a search has been undertaken in all the major national and provincial museums of Britain to locate any relevant type collections. Wherever possible, species have been reappraised and type specimens designated. In part to aid such revisional studies, large amounts of new material was collected from the Silurian and processed for ostracodes.

Field collections were made from: Scotland (the Pentland Hills, the Lesmahagow inlier and the Girvan area); Central England (the Walsall, Dudley and Sedgley districts); the Welsh Borderland (including the Ludlow-Much Wenlock region, the Mayhill and Woolhope inliers, the Malverns and Abberley Hills); SW England (Tortworth and E Mendips); Pembrokeshire. An attempt has been made - for the first time since 1846 - to collect *Beyrichia kloedeni* McCoy from the type locality in Galway, Eire. For a number of reasons field-work activities have been concentrated on the N Welsh Borderlands, around the Ludlow anticline, Wenlock Edge, and Benthall Edge. This area is the home of much of the hitherto described beyrichiacean material, the local succession holds special historical significance in terms of Silurian stratigraphy as a whole, and the area has a traditional reputation for the richness of its fauna.

The Silurian samples taken from the N Welsh Borderland embraced Llandovery, Wenlock, Ludlow and Downton deposits. Collections elsewhere were governed mostly by the need for additional material to help species revision. Time did not permit the sampling of all parts of the succession; in the Ludlovian of the Welsh Borderland emphasis was, therefore, placed on the collection of material from across the Wenlock/
Ludlow boundary, from the middle part of the Ludlow Series (the Upper Leintwardine Beds), and from across the Ludlow/Downton boundary (i.e. at the level of the Ludlow Bone Bed). *Kyamodes* Jones, 1888 - representing the only probable beyrichiacean genus from the British Devonian - is revised.

The location of the main areas samples, and a general outline of the British Silurian succession are given text-figs. 3, 14.

It is hoped to eventually publish all of the major sections of this thesis.
Text-fig. 1  TERMINOLOGY OF THE NON-KLOEDENIINE BEYRICHIACEAN VALVE
(from Martinsson, 1962)

Text-fig. 2  TERMINOLOGY OF THE KLOEDENIINE BEYRICHIACEAN VALVE
(from Martinsson, 1963)
The specialised terminology introduced by Martinsson (1962, 1963) for description of the beyrichiacean carapace is adopted throughout this thesis. See text-figs. 1, 2.

One new term is introduced: the adductorial tubercle. This term denotes the single, isolated tubercle found near, or at the hinge line, above the main (adductorial) sulcus in some Craspedobolbininae, Amphitoxotidinae and Beyrichiinae; for example, as in Sleia Martinsson, 1962.
METHODS AND TECHNIQUES OF STUDY

I FIELD COLLECTING AND LABORATORY PROCESSES:

These activities varied with each of the three types of material encountered.

1. "Washed" material:

a) Collecting: This category comprises most of the samples treated. It includes all that material which can be broken down — with or without the aid of chemicals — washed, sieved and picked for ostracodes (e.g. the Wenlock Shale, and samples from bentonitic and clayey horizons). Sampling the localised marl pockets, the weathered rubble, and the shaley bands was the most profitable — and often the only — method to obtain abundant and well preserved material from many limestone horizons (e.g. the Wenlock Limestone at the Wren's Nest).

   Samples were collected usually with the aid of a trowel. This implement was especially useful when sampling marly or weathered material. Most of the samples were taken from about 0.5 - 2 metres of each exposure. The average weight for each sample was about 3 - 4 pounds. The number of samples processed from each locality varied from two, to over twenty from the Wren's Nest. It proved necessary to resample some localities numerous times in order to obtain particular dimorphs.

b) Processing: In the laboratory the samples were disintegrated using merely hot water in the case of marls, soft shales, clays and weathered material, or with the aid of hydrogen peroxide for the more calcareous shales. The residue was fractioned through sieves (meshes sizes of 2000, 1000, 500, and 125 microns). The fractions were transferred to evaporating dishes, allowed to dry slowly overnight in a heating cupboard, and then 'picked' for microfossils. Much time was saved during the later stage by the use of an automatic feeder and conveyor belt system attached to the binocular microscope. The flow
of the feed and the speed of the belt could be easily regulated
to suit the individual requirements of different particle sizes.
The ostracodes were picked using the alcohol method (see Martinsson
1956, p. 4; 1962, pp. 39, 40). Extracting was concentrated on the 1000
micron mesh as this, throughout the study, proved to be the most
profitable screen size in terms of adult beyrichiacean valves.
Demands on time prevented the finer fractions being worked, though
they were checked to see that they contained no surprises with regard
to the fauna. A number of samples lacked ostracodes completely
and receive no further mention here; from others a day's extracting
would be rewarded with just one or two, or sometimes many hundreds,
of valves. All ostracodes were picked though only the Beyrichiacea
are described herein.
c) Preparation of individual valves: Almost without exception,
valves from washed samples are covered to various degrees with
foreign matrix. The internal regions of the valves are always
packed with sediment, as are most of the concave, external parts of
the valves, the sulci, and some areas of the lobes. High importance
is therefore placed on the technique of cleaning, as a prelude to
successful photography. The method devised by Martinsson (1962,
pp. 40-42) has largely been followed, with good results.

As used by the present author the details are as follows.
The well of a small "embryo-dish" (obtainable from any standard
biological suppliers) is completely smeared with "Durofix" cellulose
adhesive (manufacturers: The Rawlplug Co. Ltd., Kingston, Surrey),
and allowed to harden for about 5 minutes, though the longer the
better. Black embryo-dishes are undoubtedly preferable to the
uncoloured, glassy types for reasons concerning light reflection and
specimen definition. A small blob of Durofix (some 2-3 times larger
than the valve to be cleaned) is then placed in the centre of the
embryo-dish well, and the ostracode - orientated appropriately for
cleaning - is attached to this point. The greater the amount of cleaning needed, the greater the length of time the now mounted specimen should be allowed to stand while the glue is hardening; in any case, 20 minutes should be the minimum period. It is at this stage that the weaker specimens may fragment irreparably, due to the tension factors within the hardening glue; often, incipient cracks (obscured by matrix) in the specimen, or excessive immersion of the specimen in the glue, will exacerbate this fragmentation.

The valve is then totally covered in distilled water and cleaned manually in the manner described by Martinsson (op. cit.) with a series of prepared brushes and fine needles. The water is changed frequently.

After cleaning, the glue around the specimen is circumscribed with a sharp point and the outer 'skin' of Durofix removed from the well with the aid of a film of water. The specimen - remaining in the centre of the well - is then immersed two or three times in acetone in order to dissolve the central blob of Durofix and complete the cleaning process.

These stages are repeated many times to clean a carapace completely, the fossil being reorientated and remounted after each successive cleaning. The whole procedure may take a few minutes, or, in the case of particularly delicate or valuable specimens (e.g. valves displaying cruminal metamorphosis), many hours.

2. Mould Material:
a) Collecting: Most of the Ludlovian material falls within this category. The rock type can vary from fine siltstones crowded with "rottenstone" fossil bands, to the weathered surfaces of limestones. Having ascertained the presence of ostracodes in the field, bulk sampling was adopted. In the localities with prolific faunas, e.g. the Upper Leintwardine Beds at Bengry Track, near Aymestrey (loc. 63), many tens of pounds of rock was collected.
b) **Processing:** In the laboratory, material would be broken up mechanically and examined for ostracodes under a binocular microscope.

c) **Preparation of valves:** For too long, important Palaeocene mould faunas such as those in the Welsh Borderland have received but scant attention, in part because of their mode of preservation. Techniques for the study of moulds of microfossils have been proposed by Martinsson (1964a), who described a method of obtaining photographic "casts" of ostracodes. The procedure of studying moulds employed by the present author consists of some casting practices standard to macro-palaeontologists, combined with unexplored techniques of illustration.

High priority is of course given to the collection of external moulds which, prior to casting, are normally dusted slightly with fine, dry sable brushes to expel any foreign particles. The actual casting procedure may be found in any standard technique manual. One additional point should be noted; the silicone gel was coloured dark grey/black by the addition of carbon black before application to the mould. The casting medium is obviously an important consideration; "Silcoset" 105 silicone rubber (manufactured by ICI; obtainable from Sasco Ltd., P.O. Box 20, Gatwick Road, Crawley, Sussex) has proved excellent for this task. Silcoset is not particularly cheap, but the high standard of the results are equal to the expense; ornamental details less than five microns in size are reproduced with faithful accuracy, provided, of course, that the original mould is of good quality. Many hundreds of valves from, for instance, the Wenlock and Llandovery of Scotland and the Ludlovian and Downtonian of the Welsh Borderland have been thus treated, either individually or - on slabs - many tens of valves at a time.

Each selected cast would then be cut from its Silcoset surround and mounted ready for stereoscan photography in the same way as any normal ostracode valve (see below for details). The quality of illustration obtained from this technique is far superior to previous
methods, and provides an optimistic sign for the future study of all mould faunas. Some of the results of this approach to the examination of microfossil moulds have already been published (Siveter 1973c). Similar methods were developed independently and published simultaneously by Chaloner & Gay (1973); these authors were concerned particularly with fossil plant impressions.

3. Limestone Material:

a) Collecting and Processing: This category consists of that limestone material which is impossible to sample from weathered or marly outcrops (e.g. the limestone band at the base of the Brinkmarsh Beds in the Tortworth inlier). As with the mould faunas a large number of slabs are collected, broken up mechanically in the workshop, and then scanned for ostracodes under a binocular microscope.

b) Preparation of individual valves: In most cases limestone matrix covers large areas of the valves and is too hard to allow cleaning by hand preparation alone. The use of finely ground needles in a 'Burgess' Vibro-tool has been used to overcome such problems, though considerable time and skill is needed to prepare microfossils in this way. The vibrations themselves in some cases tend to shatter valves or 'dislodge' lobes at the slightest lack of concentration.

A square is then cut around the prepared valve and the limestone chip prized from the slab. The microsaw "Microtome II" (manufactured by Metals Research Ltd., Melbourne, Royston, Herts.) is ideally suited for the cutting process; almost paper thin rock slices are obtainable and the slab to be cut may be tilted or rotated to more or less any desired position. In practice, limestone chips of about 0.7 cm sq. were cut - free movement within the specimen chamber of the Scanning Electron Microscope being impossible for larger specimens.
II PHOTOGRAPHY:
1. Stereoscan Photography:

The Scanning Electron Microscope at Leicester, the "Stereoscan Mark II" manufactured by Cambridge Scientific Instruments, has been extensively employed throughout this study. Illustration by Stereophotography has been used almost exclusively.

a) Mounting: After some experimenting, small domed rivets were found to be the most practical type of (aluminium) stub; they are a cheap, unlimited source of supply and have the distinct advantage (over flat stubs) that dorsal, ventral and end views may be taken in the correct plane without dorsal interference.

Three types of mounting medium were used:

i) A thin film of "Kodaflat 500" (manufactured by Kodak Ltd.).
   Advantages: remains sticky - never hardens completely - and therefore always allows reorientation of the specimen.
   Disadvantages: often too insecure for large specimens, especially carapaces; tendency for the glue to "creep" and obscure, at the very least, the edges of the valve. Method used initially.

ii) A tiny blob of Durofix glue. Advantages: specimen always secure; far fewer problems about masking the specimen with glue.
   Disadvantages: the glue has to be applied in amounts less than the size of the ostracode; such amounts are fast drying, rapid mounting and orientation needed. This method is recommended for Palaeocope ostracodes; used extensively in preference to Kodaflat solution.

iii) "DFL Exact" (brown grade). Used for all those valves resting on limestone or other rock chips. The stub is slightly heated over a flame, a small piece of Exact mounting compound (made by Dental Fillings Ltd., Grayling Road, London, and supplied through Metals Research) is dropped onto the stub, followed by
the placing and orientation of the rock chip in the now soft gel with the aid of hand tweezers. Durofix, in the amount needed to hold fast a sizable rock fragment, hardens much too slowly, during which time the specimen at hand swims to numerous undesired angles. Exact functioned perfectly for its job, giving about a minute for specimen orientation before hardening very quickly; rock chips of any irregular shape can be mounted at the appropriate orientation using this method. Disadvantage: Exact extremely difficult to remove from rock surfaces.

b) Coating: The N.G.N. 12" Coating Unit was used for all specimens. Almost without exception, specimens were coated with aluminium. Gold, although applied to a few valves, was not preferred due to the cleaning problems inherent in this method.

c) Photography: The vast majority of films were taken at 20 kv. The considerable "charging" effects encountered with some valves were combated either by recoating, lowering the voltage (down to 10 kv. or less), or by the use of an antistatic spray.

A noticable drawback to the "drop in voltage" option is that this method produces negatives which lack contrast, in many instances, excessively so.

d) Procedure for removing and cleaning the specimen: For those valves mounted in Kodaflat or Durofix and coated in aluminium:

i) Apply acetone to the stub to loosen the specimen.

ii) Remove glue from specimen by cleaning 1-2 times in embryo-dish of acetone.

iii) Remove aluminium coat by immersing in an embryo-dish of the cleaning concentrate "Decon 75" (manufactured by Medical Pharmaceutical Developments Ltd., Portslade, Brighton). The Decon is applied dilute (approximately 1:3) with distilled water.

iv) Cleanse specimen of decon by thorough washing 2-3 times in distilled water.
The specimens mounted in Exact may easily be taken from the stubs after briefly reheating the compound until it returns to a soft gel condition. Metals Research recommend the use of methylated spirits to finally dissolve the Exact; this has been tried, but without success.

2. 'Normal' Light Photography:

This method is needed to illustrate some specimens as it is in most cases inadvisable - and often impossible without damage to the specimens - to remove type material from their parent slabs for the purpose of SEM work. Technical details:

a) Leitz Aristophot equipment.

b) Leica 35 mm camera used with Kodak Panatomic-X film.

c) Milar 6.5 cm lens.

d) A single fluorescent ring light used in conjunction with a single arc light.

e) All specimens were painted with a thin film of "Opaque" (manufacturer Phillips & Jacobs, inc., Philadelphia, PA.) and later, just before photography, gently coated with ammonium chloride.

f) A base stage, capable of tilting through about 5-10 degrees to facilitate stereophotography.

3. Developing and Printing:

All films were developed with Patersons Acutol; for the printing process Patersons Acuprint, Amfix fixer, and Kodak photo-flo solution were used. Prints were made using a Leitz Focomat Ic enlarger and a Kodak 15TC rotary glazer. All enlargements were calculated from measurements taken from the specimen itself. Kodak bromide paper grade 2 (normal) was most often used, along with grades 1, 3 and 4. For negatives of very high or very low contrast, Ilford paper grades 0 and 5 respectively were especially valued.
III MEASUREMENTS:

The measurements given are of three types:

1. Valve length, along the hinge line.

2. Valve height, measured over the adductorial sulcus and including the width of the velum.

3. Valve height, as for 2, but excluding the velar width.

Type 1 is a standard measurement. Type 3 is normally given for those species with a broad velum - in which the distal edge is nearly always broken away.
The material used in this thesis was obtained from three main sources:

1. Museum Collections:

Very few of the major British museums have collections of British Silurian ostracodes. The most significant collection is housed at the British Museum (Nat. Hist.), London; here, much of the classic material of workers such as Jones, Holl, Smith, and Vine has been found. In most cases repository numbers for such material are recorded (herein) for the first time. All reference and catalogue information relevant to such museum specimens is given in the appropriate parts of the systematic section of this thesis.

Abbreviations of Repositories:

- Bristol City Museum, Bristol (CMB)
- British Museum (Natural History), London (BM)
- David J. Siveter, personal collections (DAS)
- Geological Survey, Canada (GSC)
- Institute of Geological Sciences, Edinburgh (GSE)
- Hunterian Museum, Glasgow (HM)
- Institute of Palaeontology, University of Lund, Sweden (MPL)
- Institute of Palaeontology, University of Uppsala, Sweden (IPU)
- National Museum of Ireland, Dublin (NMI)
- National Museum of Wales, Cardiff (NMW)
- Sedgwick Museum, Cambridge (SM)
Where, in the case of GSM material, a number of specimens have been prepared by the writer from a single slab, the endings /1, /2 etc. have been added to the slab number and assigned to the valves in question. These are not official Inst. Geol. Sci. suffixes; the relevant specimens may receive individual numbers at a later date.

2. **Samples donated by Professor A. Martinsson:**

A large number of samples collected (1957, 1962) by Prof. A. Martinsson from the Wenlock Series of the Welsh Borderland were generously placed at the authors disposal. The locality data for these samples has been obtained from information on the sample bags and 2\(^{\text{1/2}}\)" Ordnance Survey maps provided by Prof. Martinsson.

3. **Authors collections:**

Formed most of the material; full locality and faunal details are given in Volume 2, Appendix 1.

It is intended to donate the figured and referred material in the authors collections (DAS) to national museums upon publication of this thesis.

In order to eliminate lengthy repetition of information in the main text, the localities will mostly be referred to only by their field designation and locality number.
Subclass OSTRACODA Latreille, 1802 (nom. correct. Latreille, 1806)


Type Superfamily: Beyrichiacea Matthew, 1886 (designated by Henningsmoen, 1954).

Superfamily BEYRICHIACEA Matthew, 1886 (nom. transl. Ulrich & Bassler, 1923)

DIAIQIOSIS: Palaeocopa with cruminal dimorphism (and including possible non-dimorphic offshoots).

REMARKS: Ametrobeyrichia schizopyge gen. et sp. nov. (Chapter F) is firmly allied to the beyrichiacean group by many lobal and velar homologies and yet the evidence indicates that it lacks dimorphism. This species provides the first strong case (excluding possible examples of parthenogenesis) that the Beyrichiacea may have to accommodate non-dimorphic members.

FAMILIES: Craspedobolbinidae Martinsson, 1962

Beyrichiidae Matthew, 1886

Family CRASPEDOBOLBINIDAE Martinsson, 1962

DIAIQOSIS: Beyrichiacea primarily with tubular structures in the velum which may occasionally be reduced. Crumina originating by invasion of the velar fold along tubules in the anteroventral region; an earlier phylogenetic stage with a dolonoid pouch, tending to be closed by a flap, may be traced in all subfamilies by a dolonoid scar or a deflection of the velar edge on the crumina. (After Martinsson, 1963, p. 54).
BRITISH CRASPEDOBOLBINAE

REMARKS: Only one craspedobolinine species, "Bollia" (= Craspedobolbina) interrupta Jones, 1887, has previously been recognised and described (Martinsson 1965a) from Britain, although Harper's paper (1940) did hint that other forms similar to the Gotland "Beyrichia" (= Craspedobolbina) clavata Kolmodin, 1869 exist in the Silurian of Shropshire.

The genus Craspedobolbina is now known to have representatives in Scotland and Wales, with additional species coming from the Welsh Borderlands and associated inliers. In general the British Craspedobolbina species manifest several trends observed in closely related 'Baltic' taxa, though the development of some features (for instance, the form of the subcircular ridge in Craspedobolbina (Artiocraspedon) subgen. nov., or the lobes in Craspedobolbina turpis sp. nov.) is clearly uncharacteristic of the large majority of other members of the genus.

Significant similarities between craspedobolinines and the primitive amphitoxotidine Sleia Martinsson, 1962 are illustrated in Parasleia gen. nov.

The most important and diagnostic feature of Stroterobolbina gen. nov. is the distinctive morphology of its velum. In Stroterobolbina floribunda sp. nov. at least, the tubulous frill consists essentially of a series of hollow spine-like extensions, radially arranged around the shell and linked in web-like fashion.

Dictyobolbina gen. nov. is one of the few reticulate craspedobolbinine genera; its dolonoid closing mechanism is almost obsolete.
SYSTEMATIC PALAEONTOLOGY

Subfamily CRASPEDOBOLBININAE Martinsson, 1962

TYPE GENUS: Craspedobolina Kummerow, 1924, p. 427; from the Silurian of NW Europe.

BRITISH GENERA: Craspedobolina Kummerow, 1924
Parasleia gen. nov.
Dictyobolina gen. nov.
Stroterobolina gen. nov.

DIAGNOSIS: Craspedobolbinidae with cruminal metamorphosis passing a complete dolonoid stage, implying a completed closing off of the dolonoid space by a flap (after Martinsson 1962, p. 133).

DISCUSSION: The concept of this subfamily has been thoroughly presented in a series of papers by Martinsson (1962; 1963, p. 54; 1965, p. 17; 1965a) and Martinsson and Berdan (1965, p. 347) to which the reader is referred. Contrary to most other opinions, Abushik (1971) regards the group as a family containing only the type subfamily.

The variation in velar, lobal and ornamental structures in the Craspedobolbininae is seemingly unlimited (see Kesling 1969, pp. 284-287 for a summary), though all of its members are characterised and allied by the possession of a dolonoid scar. This feature indicates that the ostracode has experienced a dolonoid stage in the formation of the crumina - a development held by current workers (including the writer) to be of a "primitive" nature and to testify to the phylogenetic relationship between these less advanced members of the superfamily and members of the Ordovician Eurychilinaccea Ulrich & Bassler, 1923.

OCCURRENCE: Known from England, Wales and Scotland; Llandovery and Wenlock Series.

The Craspedobolbininae are dominantly found in the Silurian of N Europe and, less frequently, the eastern parts of N America.
Mesomphalus Ulrich & Bassler, 1913 occurs in the Devonian of the United States.

Genus **CRASPEDOBOLBINA** Kummerow, 1924

**TYPE SPECIES:** By monotypy; Craspedobolbina dietrichi Kummerow, 1924, p. 427, pl. 20 (numbered 21 in error), figs. 27, 28; lectotype designated by Martinsson 1962, p. 33, fig. 13A; drift boulder, S Baltic, of supposed late Llandovery - early Wenlockian age.

**BRITISH SUBGENERA:**
- **Craspedobolbina** (Artiocraspedon) subgen. nov.
- **Craspedobolbina** (Craspedobolbina) Kummerow, 1924
- **Craspedobolbina** (Mitrobyrichia) Henningsmoen, 1954

**DIAGNOSIS:** Craspedobolbininae with the preadductorial knob connected with the syllobium by a zygal arch; a syllobial groove occurs frequently. Anterior lobe always separated from the knob by a prenodal sulcus. Dolonoid scar admarginal; there is a ridge on the crumina, usually parallel to and below the scar. Velar constrictions (at the sides of the crumina) are normally present. (Modified after Martinsson 1962, p. 146).

**DISCUSSION:** This important and varied genus has British representatives of its two largest subgenera, **C.** (Mitrobyrichia) and **C.** (Craspedobolbina). **C.** (Clavobolbina) Martinsson, 1962 and **C.** (Odoniobolbina) Martinsson, 1962 - both monotypic (Gotland) taxa - are at present unknown from Britain. The generic diagnosis given by Martinsson (1962) has been modified slightly (with respect to subcruminal morphology) in order to accommodate forms such as **C.** (Artiocraspedon) and **C.** (Mitrobyrichia) interrupta (Jones, 1887).

**OCCURRENCE:** In Britain **Craspedobolbina** is restricted to strata of Llandovery and Wenlock age.
European members of the genus are known mostly from the Silurian of Gotland, the East Baltic states and Baltic drift material, with rare occurrences in the Silurian of Norway and Podolia. One species, C. kirki (Ulrich & Bassler, 1923), is recorded from America (see Martinsson 1968).

Subgenus Craspedobolbina (Artiocraspedon) subgen. nov.

**DERIVATION OF THE NAME:** From the Greek artios, complete, and craspedon, edge; with reference to the continuous ridge over the crumina.

**TYPE SPECIES:** Beyrichia glabra Harper, 1940, p. 392, pl. IX, fig. 8; from the late Llandovery of the Welsh Borderlands.

**SPECIES:** Only the type species.

**DIAGNOSIS:** Craspedobolbina species in which velar constrictions adjacent to the crumina are absent; the persistent ridge over the crumina appears continuous, both posteriorly and anteriorly, with the velum. Admarginally there is a long dolonoid scar. Anterior lobal cusp and syllobial dorsal plica gently rounded. Lobes granulose with scattered verrucae.

**DISCUSSION:** The new subgenus is established in order to express conspicuous differences in the ventral morphology of the crumina between C. glabra (Harper) and the great majority of Craspedobolbina species.

**OCCURRENCE:** The upper part of the Llandovery Series, the Welsh Borderlands.
Craspedobolina (Artiocraspedon) glabra (Harper, 1940)
Pl. A4, figs. 1-12.

1940 Beyrichia glabra, sp. n.; Harper, p. 392,
pl. IX, fig. 8.

HOLOTYPE: Harper selected a left valve tecnomorph (GSM 70328),
his only figured specimen (1940, pl. IX, fig. 8), as holotype.

TYPE LOCALITY AND TYPE STRATUM: "The Purple Shales .... in the
Church Preen Brook 55 yd W of its confluence with Hughley Brook"
(Harper, op. cit., p. 393); see loc. 30 of this paper.

DIAGNOSIS: As for the subgenus.

DESCRIPTION: Anterior lobe and syllobium are broad, rather flat, with
the conspicuously developed preadductorial node interposed as the most
elevated lobal element. The short, fairly weak zygal arch, runs from
the base of the preadductorial node around the ventral part of the
adductorial sulcus and fades out as it meets the syllobium. The best
defined boundary of the zygal arch is around its ventral periphery
but this line is not projected posterodorsally into any form of syllobial
groove. In late stage tecnomorphs and females a weakly rounded cusp
terminates the anterior lobe above the hinge line. The rounded cuspidal
plica on the syllobium of small instars lies along the hinge line, and
in more mature specimens, becomes somewhat flatter above the hinge line,
concealing the latter for some distance. The syllobium is broader
in its dorsal half, tapering ventrally; the reverse is true of the
anterior lobe. Syllobium and anterior lobe join in a wide area below
the zygal arch.

A narrow and shallow, but well defined adductorial sulcus reaches
almost two-thirds of the way to the velum from the dorsal margin; the
sulcus is anteriorly inclined and is of constant depth. The shallow
prenodal sulcus, its course obvious only at its junction with the
curved anterior face of the preadductor node, merges into the
adductorial sulcus just below the hinge line. Adductorial sulcus
twice as wide as prenodal sulcus. The lobate area has an evenly
curved outline; valves lack any trace of an anteroventral depression.

In tecnomorphs from posterodorsal to anterodorsal corners of
the shell a medium-wide velum is present, with short, quite wide
tubules distinctly visible throughout most (especially the ventral
part) of its length. Near its fusion with the lobate area the velum is
superimposed with scattered granules; distally a series of extremely
fine, discontinuous striae are arranged subparallel to the velar edge.
Concentric striae and radiating tubules give a frill-like / wrinkled
appearance to the velum. In large valves an outer ornamental ridge,
sited very close to the velar edge, is sometimes developed. The
crumina only just annexes the zygal arch, but (in the three females
found) does not constrict the velum to any degree; the ridge over the
crumina is in topographical continuation with precruminal and post-
cruminal velar edges and lies below the long dolonoid scar.

Irregularly scattered verrucae, in a ground pattern of dense
granulation, are found on all lobes. The prenodal sulcus is more
finely granulose, the adductorial sulcus remains smooth. In some
specimens the dorsal part of the anterior lobe has finer granules than
elsewhere, or can even be devoid of granulation. Cruminal ornament-
ation, like the distal parts of the velum, consists of rows of fine,
discontinuous striae arranged subparallel to each other along the
crumina.

Morphological changes between instars are gradual and relative
to size increase. In the smallest tecnomorph found the valve lacks a
zygal arch, the preadductor node is fused almost directly to the
anterior lobe, lobal cusps above the hinge line are absent, the
velum is relatively narrower without visible tubules, but the granulation
All specimens from Hughley Shales, N Welsh Borderlands.

- Church Preen Brook (loc. 30), 25 valves.
- Church Preen Brook (on GSM 70328), 3 valves.
- Devil's Dingle (loc. 29), 1 valve.

Text-fig. 4 SIZE DISPERSION OF CRASPEDOBOLBINA GLABRA TECNOMORPHS
is distinguishable. Generally however, in all immature tecnomorphs collected (other than in this very early instar) one can soon recognise a faint prenodal sulcus, a weakly suggested zygal arch, and a tubulous, wrinkled velum; the cusp on the anterior lobe and dorsal plica on the syllobium appear to delay their strongest development until late in ontogeny.

MATERIAL: This species occurs as moulds in shales (Devil's Dingle, Church Preen Brook) and as beautifully preserved valves in limestone (Church Preen Brook). The description given is based on all extant material, with most of the information on the fine detail of valve morphology coming from the specimens in the limestone.

MEASUREMENTS: No complete female valve has yet been obtained. Hinge length - sulcal height (excluding velar width) in microns of measurable tecnomorphs from the Hughley Shales.

Church Preen Brook (on GSM 70328): 1370-940 (holotype); 1300-875, 1200-775 (only approximate measurements).
Devil's Dingle (loc. 29): 1070-690.

DISCUSSION: Even though the holotype, resting on shale, is mostly an internal mould with very little shell remaining, and in spite of the fact that the writers personal collections from Harper's type locality came from a limestone band (not shale), there can be little doubt surrounding the correct identification of Beyrichia glabra. On the same slab as the holotype there are other moulds of tecnomorphs belonging to C. glabra and C. hipposiderus sp. nov.

The subcruminal morphology of C. glabra is quite unique, though numerous homologies (the presence of a ridge and dolonoid scar on the
crumina, a zygal arch and other lobal, sulcal and velar similarities) indicate its inclusion within Craspedobolbina. Hyrsinobolbina, Parasleia, and Craspedobolbina are all craspedobolinina genera with a ridge on the crumina below a dolonoid scar. However, apart from C. glabra, the species C. (Mitrobeyrichia) kirki, C. (Mitrobeyrichia) interrupta and C. (Mitrobeyrichia) hipposiderus are the only taxa in which the velar edge is continuous with that ridge - and then not in its precruminal section. Although, as stated by Martinsson (1965a, p. 323 and 1968, p.307-8), forms such as C. kirki and C. interrupta can be related to the more common type of Craspedobolbina subcruminal morphology through intermediate forms like the early C. unculifera Martinsson, 1962, the distinguishing feature of C. glabra cannot be readily allied to C. (Mitrobeyrichia) species and this is thought best illustrated by a break at the subgeneric level.

In lateral view the general carapace morphology of C. glabra is very much like C. (Odoniobolbina) lativelata Martinsson, 1962; both species possess a prominent preadductorial node, an inconspicuous zygal arch of like shape, a shallow adductor sulcus of narrow width, comparable anterior lobes and syllobial morphologies, similar velar morphologies and granulose-verrucose patterns of ornamentation. Although Martinsson does not figure the subcruminal morphology of C. lativelata, it is interesting that he notes (1962, p. 178) "... the egg-shaped crumina does not cause a very pronounced constriction of the velum." The species differ in subcruminal morphology and in other smaller details. C. lativelata has a slightly more inflated preadductorional node, an adductor sulcus which becomes deeper ventrally, a syllobial cuspidual plica which is cristate, and a wider velum (especially anteroventrally) giving the valves a more preplete outline.
OCCURRENCE: All the material obtained comes from the Llandovery Series (upper part).

Hughley Shales: Devil's Dingle (loc. 29), mid-Telychian; three tecnomorphs, one female.
Church Preen Brook (loc. 30), Telychian; about thirty complete and other broken tecnomorphs, two incomplete females.

Harper also recorded *Beyrichia glabra* from, "The Pentamerus Beds of Morrell's Wood Brook immediately N of Morrell's Wood Farm, and the Purple Shales at the junction of the Merrishaw and Harley Brooks", and, "in the stream ¼ mile W of the junction of Brook House and Hughley Brooks"; none of these occurrences have been investigated by the author.

Subgenus *Craspedobolbina* (*Craspedobolbina*) Kummerow, 1924

TYPE SPECIES: As for the genus.

BRITISH SPECIES: *Craspedobolbina* (*Craspedobolbina*) sp. nov. A.

DIAGNOSIS: *Craspedobolbina* species with a zygal crista reaching onto the preadductoril knob (after Martinsson 1962, p. 146).

OCCURRENCE: The Llandoveryan of Pembrokeshire.

The subgenus occurs mostly in the Llandovery and Wenlock deposits of Gotland and is also recorded from the Jaani (Wenlock) stage of Estonia.

*Craspedobolbina* (*Craspedobolbina*) sp. nov. A

Pl. A3, fig. 10.

REMARKS: The extant material consists of only three tecnomorphs and the ventral part (including crumina) of what is presumed to be the corresponding female (found on the same piece of rock) as one of the
Although these valves represent a new taxon it is left unnamed until more specimens, especially females, are obtained.

DESCRIPTION: A long, relatively wide adductorial sulcus, slightly inclined forwards, separates a somewhat slender preadductorial node from a syllobium which has a gently rounded posterior outline and a much sharper anterior cuspidal plica. Prenodal sulcus well defined but noticeably narrower than the main sulcus. Cusp of anterior lobe just projecting above the hinge line. A cristate zygals arch joins the syllobium to the preadductorial node. There is only a short distance between the zygals arch and the nearest point on the velum. No trace is seen of a syllobial groove, and the anteroventral depression is hardly discernible.

The zygals crista trends across the preadductorial node, round the ventral part of the adductorial sulcus and continues dorsally along the posterior margin of that sulcus for over half the height of the syllobium. The zygals crista is more diffuse on the preadductorial node than at any other point along its length. The syllobial cusp is pointed rather than cristate. In the small amount of material available there seems to be an ill-defined crista on the dorsal part of the anterior lobe, which fades ventrally, only to reappear in a weak form anteroventrally.

A moderately wide velum, at least in the extant tecnomorphs, lacks externally visible tubules. In the single female specimen a toric ridge runs parallel to the postcruminal part of the velar edge for a considerable length. The dolonoid scar lies close to the marginal structure and is complemented by a gently arched ridge. This ridge rests in line with, but appears to be separate from, the postcruminal section of the velum.

All lobes appear to have an even granulosity. The ventral part of the anterior lobe (if any) has tiny verrucae. Cruminal ornament not detected.
MATERIAL: All material, preserved as internal and external moulds, comes from the Turnbull collection, Sedgwick Museum, Cambridge. Casts were taken of all specimens.

SM A32744a and counterpart A32744b; tecnomorph, right valve.
SM A32745a and counterpart A32745b; tecnomorph, right valve.
SM A32746a and counterpart A32746b; tecnomorph, left valve.
SM A32746b also contains the (unnumbered) external mould of the ventral part of a female left valve.

Unsuccessful attempts have been made to collect more material.

MEASUREMENTS: Hinge length - sulcal height in microns of cast of SM A32745b: 1210-880.

DISCUSSION: Its lobation is comparable with Gotland species such as *C. perornata* Martinsson, 1962. However, not considering minor lobal and sulcal differences, the nature of the cristal system in itself is sufficient to distinguish the British species from other closely related taxa. The form of the zygal crista in the British species - extending considerably up the posterior margin of the adductorial sulcus - is unique; in *C. perornata* it continues far across the syllobium, in *C. mucronulata* Martinsson, 1962 and *C. juguligera* Martinsson, 1962 it becomes obsolete just on the syllobium, while in *C. ornulata* Martinsson, 1962 and *C. dietrichi* (Kummerow, 1924) it fades out before reaching the syllobium.

No other *Craspedobolbina* (*Craspedobolbina*) species is known from Britain.

OCCURRENCE: Turnbull loc. K, below the path SW of Uzmaston Farm, the Frolic, Haverfordwest, Pembrokeshire; upper part of the Llandovery Series (probably the Uzmaston Beds).
Subgenus Craspedobolbina (Mitrobeyrichia) Henningsmoen, 1954

TYPE SPECIES: Original designation of Henningsmoen 1954, p. 46;
Beyrichia Jonesii Boll, 1856, p. 322, figs. 1, 2; lectotype (Boll, op. cit., fig. 1) designated by Martinsson 1962, p. 18, fig. 3B;
N German drift boulders, Silurian (early Ludlovian?).

BRITISH SPECIES: Craspedobolbina (Mitrobeyrichia) interrupta (Jones, 1887)
Craspedobolbina (Mitrobeyrichia) hipposiderus sp. nov.
Craspedobolbina (Mitrobeyrichia) impendens (Haswell, 1865)
Craspedobolbina (Mitrobeyrichia) vallecula sp. nov.
Craspedobolbina (Mitrobeyrichia) turpis sp. nov.
Craspedobolbina? sp. nov. A

DIAGNOSIS: Craspedobolbina species without cristae but with a clearly distinguished anterior lobe, protruding over the hinge line with a cusp. Velum medium-wide, with edge thickened by the torus and a usually distinctly developed ornamental ridge, simply constricted on at least one side of the crumina (modified after Martinsson 1962, p. 154).

OCCURRENCE: The Midland Valley Scotland, Pembrokeshire and Carmarthenshire S Wales, the Welsh Borderlands, and the E Mendips inlier; Llandovery and Wenlock Series.

Craspedobolbina (Mitrobeyrichia) interrupta (Jones, 1887)


1887b Bollia interrupta, sp. nov.; Jones, p. 408, pl. XII, fig. 14.
1888 Bollia interrupta Jones; Vine, pp. 399, 403.
1892 Bollia interrupta, Jones; Smith, table opposite p. 158.
1908 Beyrichia interrupta (Jones); Ulrich & Bassler, p. 285, pl. XXXVIII, fig. 6; text-fig. 47.
1908 Beyrichia interrupta (Jones & Holl); Ulrich & Bassler, p. 299.
1934 *Beyrichia* (Zygobolba) *interrupta* (Jones); Bassler & Kellett, pp. 195, 217.

1936 *B. (?) interrupta* (Jones); Swartz, p. 546, pl. 78, fig. 8h.

1954 *Bollia interrupta* Jones 1887; Henningsmoen, p. 27, tentatively assigned to *Craspedobolbina* (*Mitrobeyrichia*) subgen. nov.

1965a *Craspedobolbina* (*Mitrobeyrichia*) *interrupta* (Jones 1887);

Martinsson, p. 321, fig. 6.

LECTOTYPE: A female carapace, BN IN 27474 (Vine coll.); designated by Martinsson 1965a, p. 322, fig. 6A; illustrated herein Pl. 1A, fig. 12.

TYPE LOCALITY AND TYPE STRATUM: (designated herein). On the N bank of the River Severn meander, 400 m SE of Buildwas Church, Shropshire (loc. 35); Buildwas Beds (Wenlock Shale).

According to Martinsson (1965a, p. 322) precise locality information for the type material is absent. However this material, washed by G.R. Vine from samples collected by G. Maw, was described by Jones as coming from the Buildwas Beds, box no. 37. Vine (1887, p. 229-34) gives a comprehensive list of Maw's locality details and corresponding bed and box numbers. Washing no. 37 and consequently the type locality for *C. interrupta* is clearly stated (op. cit. p. 233) by Vine (quoting Maw) as, "From Buildwas Beds near the base of Wenlock Shale, N end of exposure, side of River Severn, above Buildwas Bridge, Shropshire."

Moreover (topotype) material collected by the author permits an exact type locality designation as stated above.

DIAGNOSIS: *Craspedobolbina* (*Mitrobeyrichia*) species in which the ridge running below and subparallel to the dolonoid scar appears as a continuation of the postcruminal part of the velum; this ridge is never found to be touching, or encroaching into the scar. From a point immediately beneath the zygal arch a well marked groove projects across the sylobium.
DESCRIPTION: The reader is referred to a recent revision and description of this species by Martinsson (1965a).

MEASUREMENTS: Hinge length - sulcal height of females (in microns) from the Buildwas Beds.

- Buildwas (loc. 35): 2265-1520, 2255-1460, 2235-1350.

DISCUSSION: The form of the subcruminal morphology (see diagnosis) is almost sufficient to distinguish this species from all other members of the genus. Only *C. kirki* (Ulrich & Bassler, 1923) - see Martinsson 1968 - from the late Llandoverian Rose Hill Formation of the Appalachians, *C. hipposiderus* and *C. glabra* are comparable species in this respect. All four taxa have a ridge (on the crumina) which is seemingly continuous with the postcruminal part of the velar edge. However, in the American species this ridge appears to trend into and not run subparallel with, the dolonoid scar. In *C. glabra* the ridge apparently passes over the crumina uninterrupted and is in continuity even with the precruminal part of the velar edge.

In lateral view the general morphology of *C. interrupta* is typical of many well known *Craspedobolbina* spp. from Gotland such as *C. percurrens* and *C. lembodes*, but it can be distinguished from these taxa on details of lobation and ornamentation.

Features separating *C. interrupta* from *C. hipposiderus* are given under the latter species.

Some mould material of supposed low Wenlock age from near Llandeilo, kindly sent to the author for examination by Dr. D.E. White (Inst. Geol. Sci., London), has proved to belong to *Craspedobolbina* and (of the British species) recalls the morphology of *C. interrupta*. Unfortunately these specimens (on GSM DEX 7851-3, 7855, 7856) are too ill-preserved to allow further specific identification.
OCCURRENCE: All known material comes from the Buildwas Beds (lower Wenlockian) of Shropshire.

Buildwas Beds: Buildwas (loc.35).

Harley Brook (loc. 36).

Over 150 valves have been obtained from these localities.

Other material: BM IN 27474-27479, 27480-27483 and 27488, Vine coll.; material mentioned by Martinsson (1965a, p. 322). BM I 2214 from the, "Wenlock Shales, Vine box no. 22; purchased R.J. Damon 1891"; Vine (1888, p. 403) records C. interrupta from Buildwas box no. 22 which (Vine 1887, p.233) is a "Washing from the base of the fossiliferous zone of Buildwas beds, Harley, Near Wenlock."

HM A 12379/1-3. A small collection of Silurian ostracodes was found at the Hunterian Mus., Glasgow which included three females of C. interrupta. The collection is probably that sent by Maw and Vine to J. Young and referred to by Jones and Holl (1886, p. 345) and Vine (1887, p. 229).


Craspedobolbina (Mitrobeyrichia) hipposiderus sp. nov.

Pl. A2, figs. 1-12.

1940 Beyrichia clavata, Kolmodin; Harper, p. 391, pl. IX, figs. 5-7.

DERIVATION OF THE NAME: From the Greek hipposideros, horseshoe; referring to the shape of the zygal arch.

HOLOTYPE: A left female valve, BM IO 4758; Pl. A2 , figs. 1,2,4,9. The holotype and the tecnomorph, BM IO 4757, were prepared from the same piece of limestone.

The upper part of the Llandovery Series outcrops in the well known Shineton Brook section; Kenley Grit, Pentamerus Beds, and Hughley Shales are present. Most probably the small limestone chip from which the holotype was obtained came from the Hughley Shales of this locality, although there is no direct evidence to prove this. The specimen from Shineton was selected as holotype in preference to better localised material because of its excellent preservation.

DIAGNOSIS: Craspedobolbina (Mitrobeyrichia) species in which the post-cruminal part of the velar edge is weakly connected to the long ridge on the crumina. A U-shaped zygal arch travels some distance up the anterior margin of the syllobium (along its junction with the adductorial sulcus). Syllobium with a conspicuous cusp anteriorly but lacking a syllobial groove.

DESCRIPTION: Valves have a gently curved preplete outline. Anterior lobe shows tendencies (in the ornamentational pattern and by a slight drop in lobal elevation below the cuspidal area) towards differentiation into ventral and cuspidal regions. Anteriorly, the moderately pointed cuspidal plica on the syllobium bends away from the hinge line, and reaches the same height above the hinge line as the anterior lobal cusp. The knob-like preadductorional node is almost vertical, and is usually stoutly connected with the zygal arch below. Syllobium broad dorsally, narrowing quickly ventrally; anterior lobe tapers dorsally. Syllobial groove not discernible, even within the granulose ornamentation. Adductorial sulcus quite deep, vertical, and approximately twice the width of the prenodal sulcus. In males the long adductorial sulcus terminates a short distance from the velum; in females this sulcus is attenuated somewhat by cruminal development. In tecnomorphs the zygal arch (very strongly developed in some specimens) is symmetrically U-shaped, rounded in transverse section,
and runs dorsally along the junction of adductorial sulcus and syllobium for some distance before merging with the syllobium. The development of the zygal arch appears to be minimal in female valves, even where the crumina has not interfered with lobation.

Tubules, developed along the length of the velum, are best seen (especially when valves are viewed obliquely) anteroventrally in tecnomorphs and, to a lesser degree, in the postcruminal velar section of females. The velar edge has an inner toric ridge (seen in both dimorphs) and an outer ornamental ridge. The long dolonoid scar, very near the marginal structures, has a corresponding flap whose sides are squeezed into the former opening (cf. conditions found in *C. unculifera* - see Martinsson 1962, p. 156, fig. 42:4). The anterior part of the ridge on the crumina is curved abmarginally and terminates close to, but not in contact with, the precruminal velar section. The posterior part of this ridge is long and appears to just connect with the postcruminal velar section, although the ridge at this junction is probably weaker than at any other point along its length. Medioventrally the marginal structures are represented by a row of closely spaced, minute tubercle-like features along each valve.

A coarse, dense granulation evenly covers the syllobium; the pre-adductorial node, prenodal sulcus and velar areas immediately adjacent to the lobate area have finer, scattered granules. In adults small verrucae cover the ventral lobule of the anterior lobe; the posterior part of the cuspidal region is finely granulose. The anterodorsal part of the anterior lobe and deeper regions of the adductorial sulcus are smooth. Distal parts of the velum even outside the ornamental ridge, are covered with fine, impersistant, sub-parallel striae. Cruminal surface smooth where it meets the lobes, but otherwise contoured by fine striae.
MATERIAL: The species is found as well preserved valves in limestone (Church Preen Brook, Shineton), as moulds in shales (Devil's Dingle) and as washed material from shales (Domas, River Onney and Boathouse Coppice).

MEASUREMENTS: Hinge length - sulcal height in microns of representative specimens from the Hughley Shales.

Shineton (type locality): 1610-1015 (holotype), 1620-1000 (tecnomorph)


DISCUSSION: Tecnomorphs of this species do show variation from the description given above. When compared with BM IO 4757 (from the type locality), some specimens from Devil's Dingle have a greater extension of the velum anteroventrally, finer ornamentation on the ventral part of the anterior lobe, and a less conspicuously developed zygal arch. However these minor variants do not alter significantly the overall morphological picture of C. hipposiderus and have no special basis for separation.

Indeed, Craspedobolbina - abundantly present on Gotland - is a genus which exhibits, "...considerable variation in many species, geographically as well as stratigraphically, affecting size as well as ornamental and minor lobal features" (Martinsson, 1962, p. 154).

C. variolata like C. hipposiderus has a zygal arch whose width varies (see Martinsson 1962, p. 164 and figs. 61C, 62B), but is distinguished in having a sharper syllobial cusp, a faint syllobial groove, and a different subcruminal morphology and ornamentation.

C. insulicola Martinsson, 1962 differs from C. hipposiderus in having a greater lobular differentiation of the anterior lobe, a syllobial groove and a granulose crumina.
The subcruminal morphology of *C. interrupta* shows obvious similarity to that of *C. hipposiderus*, but the species are separated quite readily in lateral view. In *C. interrupta*, for example, a marked syllobial groove is present, and a strongly inclined preadductorial node is sited quite low on the valve. Furthermore, adults of *C. hipposiderus* are much smaller than those of *C. interrupta*.

**OCCURRENCE:** Known from the upper part of the Llandovery Series in the northern Welsh Borderlands.

Hughley Shales: Church Preen Brook (loc. 30), Telychian.
- Devil's Dingle (loc. 29), mid-Telychian.
- Domas (loc. 32), upper Telychian.
- R. Onny (loc. 33), *turriculatus* Zone, upper Fronian.
- Boathouse Coppice (loc. 31), mid-Telychian.
- "Shinerton", the type locality (probably from the Hughley Shales).

Over one hundred valves, mostly tecnomorphs, of *C. hipposiderus* have been collected; Devil's Dingle and Boathouse Coppice provided most of the material.

Harper's figured specimens of "*B. clavata*" came from a "limestone near the base of Purple Shales in the brook to the E of Claybrook Farm, Ticklerton," (GSM 70324; pl. IX, fig. 5) and from, "Purple Shales of the Onney River section," (GSM 70325-6; pl. IX, figs. 6, 7). Harper also recorded "*B. clavata*" from the, "Pentamerus beds in Morrell's Wood Brook immediately N of Morrell's Wood Farm"; attempts by the writer at collecting ostracodes from this locality proved unsuccessful.
Craspedobolbina (Mitrobeyrichia) impendens (Haswell, 1865)

Pl. A3, figs. 1-7, 9.

1865 Entomis impendens n. sp.; Haswell, p. 38, pl. III, fig. 11.

? 1869 Beyrichia impendens, sp. nov.; Jones, p. 11; p. 13, fig. 4.

1873 Entomis impendens, Haswell; Jones, p. 415.

1874 Entomis impendens, Haswell; Jones, p. 512.

1884 Entomis impendens, Haswell; Jones, p. 399, pl. XV, fig. 19.

? 1884 Beyrichia impendens; Jones, p. 400.

1934 Entomis impendens Haswell; Bassler & Kellett 1934, p. 302.

non 1968 Entomis impendens Haswell; Greig et al., p. 354.

LECTOTYPE: (designated herein) An external mould of a tecnomorphic left valve, BM I 6300b, Haswell 1865, pl. III, fig. 11; cast figured Pl. A3, fig. 5.

Haswell's type material was found in the Brit. Mus. (Nat. Hist.). Slab I 6300a contains many moulds of tecnomorphs including (according to label information) the specimen figured by Haswell. I 6299 consists of two identical sealing wax casts of this type slab; each cast has a number of valves, all of which are conspecific, one of which is ringed. This ringed specimen - a poorly preserved left valve - is taken to be the original of Haswell's figured cast and its external mould (now numbered I 6300b) is selected as lectotype.

TYPE STRATUM AND TYPE LOCALITY: Area adjacent to the North Esk Reservoir, the Pentland Hills, Scotland. If as seems likely Haswell's material came from Deerhope Burn or Wetherlaw Linn; the type stratum would have a probable late Llandovery age.

As Haswell did not give exact locality details a more precise restriction of the type locality cannot be made. The species is, however, commonly found in the mudstones of Deerhope Burn and Wetherlaw Linn and,
indeed, Jones (1884, p. 400) refers to its occurrence, "... in the Upper Silurian mudstone of Deerhope (?) ."

**DIAGNOSIS:** Small species of *Craspedobolbina (Mitroheyrichia)* whose lobes are covered with fine, crudely prismatic processes. Syllabial cuspidal plica rounded, anterior lobal cusp weak. Adductorial sulcus very narrow. No syllabial groove or lobular differentiation. Velum of constant width.

**DESCRIPTION:** Almost amplete outline with a large postadductorial area. Anterior lobe broad and flat with a weak, rounded cusp. The broad syllabium has a gently rounded dorsal plica. Both anterior lobe and syllabial plica reach to, or just above the hinge line. The relatively small preadductorial node is inclined towards, and nestles, against the anterior lobe. A zygal arch, narrow but discernible, joins the base of the preadductorial node to the anterior margin of the syllabium around the ventral periphery of the adductorial sulcus. The adductorial sulcus is narrow, deep and long, reaching two-thirds of the way to the velum from the dorsal border. This sulcus curves forward and becomes wider both above and below the preadductorial node, whose presence constricts the width of the sulcus. A very shallow, almost obsolete prenodal sulcus separates the anterior lobe from the preadductorial node. Even within the ornamentational pattern, no syllabial groove can be detected. Anteroventrally in tecnomorphs a faint change in the outline of the lobate area can be traced and is suggestive of the anteroventral depression sometimes found in *Craspedobolbina* species.

The narrow velum has a fairly constant width throughout its length. An ornamental ridge (seen in better preserved casts) occurs on the dorsal surface of the anterior and anteroventral parts of the velum, subparallel and close to the velar edge. Near the lobate area the dorsal surface of the velum has scattered granules; a close pattern of small transversal ridges contour its periphery. In well preserved
material short tubules are visible on the anterior and ventral regions of the velum. A narrow toric structure is present near to the ventral margin of the velum. Marginal structures consist of a row of small isolated tubercles near the ventral contact margin of each valve. Cruminal morphology is of the well known Craspedobolbina type; a dolonoid scar (close to the marginal structure) and corresponding ridge. Velum simply constricted both sides of the elongate crumina.

One specimen (on the slab BM I 2855) of C. impendens exhibiting cruminal metamorphosis has been found.

The ground pattern ornamentation appears to be granulation. Closer inspection of good casts reveals that the "granules" are merely the bases of minute prismatic processes which evenly cover nearly all the lobate area. Only the cuspidal part of the anterior lobe, with its small scattered granules, and the unornamented adductorial sulcus lack these delicate structures. The prismatic processes measure approximately 8 µm across and lie about 5 µm apart; they are spine-like but do not appear to taper distally. Many of them are broken; some reveal hollow centres. Crumina covered with discontinuous striae. Immature tecnomorphs are similar in essential respects to adult specimens.

DISCUSSION OF SYNONYMY: Beyrichia impendens Jones, 1869 was erected on, "casts of this little three lobed valve,... from the Upper Silurian Rocks of the Pentland Hills collected by Messrs. Haswell, Brown and Henderson of Edinburgh ..." Jones figured (op. cit., p. 13, figs. 4a, b) a left tecnomorphic and a left female valve and states that the material "closely resembles that of Entomis impendens Haswell." Jones (1884, p.400) confirms his opinions by saying E. impendens occurs, "as minute casts and impressions .... closely resembling those of B. impendens in the same strata."
Although the repository for the type material of *B. impendens* is unfortunately not known it seems highly probable that this species is synonymous with *C. impendens* (Haswell). For the present, *B. impendens* is questionably placed in the synonymy list.

Specimens recorded and figured by Jones (1874, p. 322; 1874a, p. 511, figs. 2a, b) as *B. impendens* and *B. impendens* var. *tuberosa* from Peeblesshire have not been located and, consequently are not commented on here.

*B. ? impendens* was also cited and figured by Jones from the Silurian of the Girvan area (in Nicholson & Etheridge 1879, p. 219, pl. XV, figs. 10a, b; not fig. 10c - see Jones 1893a, p. 300). The specimens were, "found by Mr. A. Macconochie at the hillside, opposite Blair Farm, about 8½ miles NE of Girvan". One slab (GSE 10803 = M1920) in the Inst. of Geol. Sci. (Edinburgh) is labelled *B. impendens* and *Entomis globulosa*. The locality data accompanying this slab read, "On hillside opposite Blair Farm 3½ miles E by S of New Dailly". This data is considered erroneous as GSE 10803 contains the two syntypes of *E. globulosa* Jones, 1879 whose type locality is the same as that stated for the Girvan specimens of *B. impendens*. The *B. ? impendens* specimens on slab GSE 10803 are thus considered to be part of Jones's referred material (1879, p. 219); however, they do not resemble his figured (1879) specimens. These four specimens (all tecnomorphic moulds) are badly preserved and more material is desirable; however their general morphology is suggestive of *Craspedobolbina*. If the Blair Farm locality is the same as that of Lapworth (1882, pp. 656-6) this material would be from the Blair flags and shales which according to present views (Cox *et al.*, 1971, fig. 2) should be near the base of the Wenlockian.
MATERIAL: The material of *C. impendens* consists of many hundreds of valves all of which are external and internal moulds. Many tens of valves have been cast.

MEASUREMENTS: In spite of the abundant extant material accurate measurements are difficult to obtain because nearly all valves and casts are squashed or distorted. Representative measurable female specimens (in microns).

Deerhope Burn: 1075-690, 1070-710, 1070-700, 1060-670.
Wetherlaw Linn: 1125-775, 1060-705, 1050-680.
Lyne Water: 1160-750, 1080-780.
Baddingsgill Reservoir: 1240-820.

DISCUSSION: The ornament of *C. impendens* is distinctive and this feature alone separates it from congeneric species. It also differs from most *Craspedobolbina* species by the lack of a syllobial groove or well developed anterior cusp and by its almost obsolete prenodal sulcus. In these respects *C. impendens* represents a rather isolated species within the genus. However, other homologies in the lobation and particularly the subcruminal morphology assign this species to the subgenus *Craspedobolbina* (Mitrobeyrichia).

*C. impendens* is similar to *Craspedobolbina* (Mitrobeyrichia)*jonesi* (Boll, 1856) in having a rounded cuspidal plica on the syllobium, a small anterior lobal cusp, and the lack of a well developed prenodal sulcus. The species are distinguished by the anteroventrally wider velum, broader adductorial sulcus and a tendency towards lobular differentiation of the anterior lobe in *C. jonesi*; furthermore, in *C. impendens* the ornamentation is different and there is a greater obsoletion of the prenodal sulcus.

The general carapace morphology of *C. unculifera* Martinsson, 1962 with its rounded cuspidal plica on the syllobium is not unlike *C. impendens*, but the presence in the former species of a faint syllobial groove, a
wider adductorial sulcus and a more pronounced anterior lobal cusp and prenodal sulcus clearly separates the two taxa.

**OCCURRENCE:** All material is found as moulds in mudstones from the Pentland Hills, Scotland. Mykura & Smith (in Mitchell et al., 1962, p. 21) consider these deposits to be late Llandovery in age.

Mudstones, Llandovery age: Wetherlaw Linn (loc. 9).

Deerhope Burn (loc. 8).

Other material: Each of the following numbers refer to a slab containing, in most cases, many specimens; locality data from respective catalogues.

GSE 10808 - 10811. Right bank of River Esk above junction of Wetherlaw Linn.

GSE EM 1186 and 1187. Deerhope Burn, left bank; 625 yd W 22° N of North Esk Cottage.

GSE EM 1369 - 1373, EM 1392 and 1393. Deerhope Burn, left bank; 1180 yd W 10° N of North Esk Cottage. About 60 ft from the bottom of the sequence.

GSE EM 1802, EM 1811 and 1812; EM 1820 and 1821. NE corner of Baddingsgill Reservoir. Deep cliffs in mudstones in stream which runs into reservoir; about 315 yd E 3° N of Hareslow Cottage (ruins).

GSE EM 1689. Lynslie Burn; near head, and 450 yd NW of Grain Head summit.

BM I 2855. Lynewater, Pentland Hills. This slab contains a specimen which exhibits an intermediary stage in cruminal metamorphosis.


SM A 35350, A 88250-1. Wetherlaw Linn. This slab contains many tecnomorphs and one female valve, all excellently preserved, showing fine details of ornamentation.

Extensive collections made by Mr. J.C. Tipper in connection with thesis work in the Pentlands were also kindly made available for study.
Craspedobolbina (Mitrobeyrichia) vallecula sp. nov.
Pl. A3, figs. 8, 11-15.

DERIVATION OF THE NAME: From the Latin vallecula, a little valley; alluding to the form of the depression on the syllobium.

HOLOTYPE: An external mould of a female right valve, DAS M 144; cast figured Pl. A3 , fig. 11.

TYPE LOCALITY AND TYPE STRATUM: Old railway cutting SE of Moon's Hill Quarry, Stoke St. Michael, Mendips (loc. 10); shale of supposed Wenlock age (Ziegler et al., 1968. p. 765).

DIAGNOSIS: Craspedobolbina (Mitrobeyrichia) species whose syllobium is markedly dissected by a broad sulcular-like depression which lies above a line projected from the zygal arch. Anterior lobe differentiated into two; cuspidal and anteroventral lobules. Anteriorly inclined preadductorial node occupies a low position on the valve. Evenly granulose lobes with verrucae anteroventrally and posteroventrally.

DESCRIPTION: Adult specimens noticably preplete. Strong anterior lobe projects above hinge line with a weakly pointed cusp. A broad, shallow sulcule together with differentiation in fields of ornamentation (see below) help divide the anterior lobe into an almost vertical dorsal part and an anteroventral lobule. The relatively small, anteriorly inclined preadductorial node is positioned low on the valve surface. A rounded zygal arch connects syllobium to preadductorial node. Cuspidal plica of the syllobium gently undulating, ending in a stout cusp near the adductorial sulcus.

A deep diagonal sulcule separates the broad, dorsal section of the syllobium from a smaller, lower posteroventral area. From a point just above posterior mid-height the sulcule trends anteroventrally, meeting the posterior margin of the adductorial sulcus approximately three-quarters
of the way down its length. This conspicuous sulcule occupies a more dorsal position than the syllobial groove of other *Craspedobolbina* species.

The long, quite deep adductorial sulcus is inclined forwards and is separated from the velum by a narrow area containing the zygal arch. The shallow, crescent-shaped prenodal sulcus occurs where the preadductorional node nestles against the anterior lobe; the dorsal part of this sulcus emerges into the adductorial sulcus, some distance from the hinge line. Anteroventral depression hardly discernible even in adults.

The medium-wide velum (greatest width anteroventrally) has a distally positioned toric ridge inside its thickened edge. Short, wide velar tubules are seen (especially anteroventrally) when mature tecnomorphs are viewed obliquely. Medioventrally two rows of marginal structures are present, which widen anteriorly and posteriorly into well developed, finely tubulous frills. The oval-shaped crumina has a long, faintly curved, dolonoid scar near the marginal structure and a corresponding ridge of typical *Craspedobolbina* form. On the only female obtained which exhibits its subcruminal morphology, the long arched ridge over the crumina appears to terminate only just short of the postcruminal velar section; in view of the mould nature of the material more specimens are needed to verify this interpretation of an important morphological feature. Velar constrictions inconsiderable. Cruminal presence eliminates zygal arch.

A dense granulation covering all lobes tends to be finer or effaced in the sulcules and cuspidal part of anterior lobe, and lacking on most of the adductorial sulcus and velum. Verrucae help differentiate an anteroventral lobule and are also found (less commonly) below the syllobial sulcule. Crumina striate between scar and ridge.

The sulcule on the syllobium, the verrucosity, and the differentiation of anterior lobe into lobules are all less pronounced in immature tecnomorphs. The zygal arch is more set off from the valve in young instars.
MATERIAL: *C. vallecula* occurs in shale as moulds. Most of the valves were obtained from shale material collected and donated to the writer by Dr. R.M. Owens. Casts were made of all external moulds. Of the females obtained only the holotype shows the complete lateral surface of the valve and one other specimen exhibits the subcruminal morphology of the species.

MEASUREMENTS: Hinge length - sulcal height of two undamaged adults from the type locality (in microns).

Female: 1780-1080 (Holotype).

Tecnomorph: 1770-1240.

DISCUSSION: *C. vallecula* has many general features of lobation and ornamentation known from Gotland *Craspedobolinina* (*Mitrobeyrichia*) spp. Its dorsal syllobial plica and relatively small anterior cusp are similar to *C. lembodes*, its inconspicuous zygal arch is not unlike *C. insulicola* while its velar morphology is comparable to *C. lembodes* and some forms of *C. percurrons*.

A near relative is *C. interrupta*, known only from the Welsh Borderlands. Both have a similar shape, velar and cuspidal morphologies. The form and position of sulci, preadductorional node and zygial arch and the lobular differentiation of the anterior lobe in these two species all invite close comparison. Their ornamentation - dense, evenly covered granules with superimposed verrucae - and its distributional pattern, again are very much alike. They differ in the following respects. The cuspidal part of the anterior lobe in *C. interrupta* (in lateral view) is posteriorly inclined, in *C. vallecula* it is more vertical. The velum, seemingly interrupted across the crumina in *C. vallecula*, is continuous (postcruminally) in *C. interrupta* (though confirmation of the former case is needed). The main differential character between these two British species is the nature and position of the depression running
diagonally across the syllobium. In *C. interrupta* the syllobial groove lies below a projected line marking the continuation of the zygal arch onto the syllobium; the prominent sulcule in *C. vallecula* lies above such a line and in adults almost bisects the syllobium to its junction with the adductorial sulcus. This sulcular depression distinguishes *C. vallecula* from all other *Craspedobolbina* species except *C. turpis* (in which the corresponding feature is even more extremely developed).

The stratigraphical occurrence of *C. interrupta*, *C. vallecula* and *C. turpis* is noticably similar; each is known only from argillaceous deposits (shales and mudstones) of Wenlock age.

**OCCURRENCE:** Known only from one locality, in the E Mendips inlier, Somerset.

*Shale, Wenlockian age:* Stoke St. Michael (loc. 10); over fifty complete and broken valves.

*Craspedobolbina (Mitrobeyrichia) turpis* sp. nov.

Pl. A4, figs. 13-16, 18-20.

1855a *Beyrichia Kloedeni*, M'Coy var. *torosa*, Jones, p. 167, pl. VI, fig. 12, (non figs. 10, 11).

1916 *Beyrichia cf. kloedeni* McCoy; Cantrill, Dixon, Thomas & Jones, p. 76.

**DERIVATION OF THE NAME:** From the Latin *turpis*, ugly; alluding to the morphology of the syllobium.

**HOLOTYPE:** An external mould of a female right valve, SM A 39574; cast figured Pl. A4, fig. 20.
TYPE LOCALITY AND TYPE STRATUM: Catalogue information read, "Coralliferous 'Series', 350 ft above the top of the basal conglomerate, Wooltack Park, Pembrokeshire; coll. D. Gibby".

This locality would lie on the S side of Deadman's Bay; siltstones of presumed Wenlock age.

DIAGNOSIS: Large Craspedobolbina (Mitrobeyrichia) species with a syllobium completely divided by a wide, deep sulcule into a ventral lobule and a dorsal region which has an elevated, knob-like feature anteriorly. Ventral lobule connected directly to the distinct, open, zygal arch. Syllobium and anterior lobe are capped by very small cusps. Adductorial sulcus and velum are wide; preadductorional node slender.

DESCRIPTION: Adult valves are large and noticeably preplete. The adduction sulcus is deep, wide and inclined forwards. The prenodal sulcus, occurring as a narrow, shallow tract adjacent to the anterior and dorsal margins of the preadductorional node, emerges into the adductorional sulcus a considerable distance from the dorsal margin of the valve. A stout, vertical, anterior lobe tends to be differentiated into a smaller ventral section (below the preadductorional node), and a wider cuspidal region which does not taper appreciably until about the level of the hinge line. The anterior lobal cusp is small.

Across the syllobium runs a wide, deep sulcule cutting the lobe in two and meeting the main sulcus about two-thirds of the way down the length of this sulcus. Above the sulcule the dorsal part of the syllobium is dominated by a large knob-like element which is mostly situated anteriorly - adjacent to the adductorional sulcus - and which forms the most elevated area of the valve; this conspicuous lobal element terminates in a cusp above the hinge line. Posterodorsally above the sulcule the syllobium is of much lower elevation and has a gently curved outline which just reaches the hinge line. Below the sulcule the smaller ventral lobule is connected directly to the "thick"
zygal arch (in lateral view this lobule appears merely as a higher and wider extension of the zygal arch). In females the crumina eliminates the zygal arch, and the ventral lobule of the syllobium takes the form of an isolated, elongate node between sulcule and velum. Positioned low on the valve surface and markedly anteriorly inclined is the small, slender preadductorional node. A slight anteroventral depression is discernible below a point where the ventral margin of the zygal arch meets the anterior lobe.

The velum is quite wide, especially anteriorly and anteroventrally, and tubules are visible ventrally and anteroventrally. A toric ridge occurs near the thick velar edge. The comparatively small crumina has a conspicuous dolonoid scar and a corresponding ridge which is long but which fails to connect with the velum. Simple constrictions of the velum are present on both sides of the crumina. A row of minute, isolated tubercles represents the marginal structures along each valve. Valve ornamentation cannot be determined. The small tecnomorphs cannot be distinguished from male valves except by size.

MATERIAL: All extant material consists of internal and external moulds on cleaved siltstones. Many specimens are squashed and distorted. Numerous attempts to collect more material from Deadman's Bay have not been successful.

MEASUREMENTS: Hinge length – sulcal height in microns of two females (valves slightly distorted).

2410-1390 (holotype), 2450-1410 (on GSM HT 1360).

DISCUSSION: The female left valve (GSM 26904) figured by Jones (1855a, pl. VI, fig. 12) as Beyrichia Kloedeni, var. torosa is not conspecific with "torosa" (based on the specimen selected herein as lectotype of that species). In the British Museum (Nat. Hist.) the box I 6356 contains two wax casts of the female mould on GSM 26904. These casts
(according to label information) formed the basis of the original illustration of Jones, 1855, pl. VI, fig. 12.

The far-reaching dissection of the syllobium in *C. turpis* is not common within *Craspedobolbina* and comparable conditions are found only in *C. vallecula*. *C. turpis* differs from *C. vallecula* in the morphology of its adductorial sulcus (wider), syllobium (in particular the sulcule is more pronounced) and zygal arch.

**OCCURRENCE:** Siltstones of probable Wenlock age (Ziegler et al., 1969; Cocks et al., 1971) from the Coralliferous 'Series' of Pembrokeshire. All known material is housed at the Sedgwick Museum, Cambridge and Inst. Geol. Sci. (London).

SM A 39561-74. From the type locality at Deadman's Bay; over twenty specimens on slabs. Coll. D. Gibby.

GSM 26904. Figured by Jones 1855a, pl. VI, fig. 12. A poorly preserved female left valve (external mould) from the "Wenlock Shale, Wooltack Bay, Pembroke".

GSM HT 1339, 1348, 1350, 1354, 1356, 1359, 1360, 1364, 1366, 1370. All from top of cliff, S side of Deadman's Bay (loc. 7 of Cantrill et al., 1916, p. 76); these numbered slabs contain approximately fifteen valves and other fragments.

*Crasedobolbina ? sp. nov. A*

Pl. A4, fig. 17.

**REMARKS:** The only known specimen (a tecnomorph) has a distinct morphology and represents a new taxon, but because of the lack of material - particularly a female - its taxonomic position cannot be decided with certainty. Its features are comparable to *Craspedobolbina* (see below). For the present **nomenclatura aperta** is used for the species.
DESCRIPTION: Anterior lobe well formed with a stout cusp above the hinge line. Small club-shaped preadductorional node, anteriorly inclined and relatively low on the valve. Below the long adductorional sulcus, a zygal arch joins the preadductorional node to the narrow base of the syllobium.

The morphology of the syllobium is distinctive; below the well developed anterior cusp, and lying mostly above the level of the preadductorional node, there is a conspicuous conical shaped node of approximately the same size as the preadductorional node. The posterdorsal outline of the syllobium is evenly rounded. Syllobial groove not discernible. Easily the most elevated part of the valve surface is the node on the syllobium, the majority of the syllobial area and the preadductorional node are of equal elevation, while the anterior lobe and dorsal region of the syllobium are the least elevated parts of the lobal elements.

Velum medium-wide with tubules visible externally along ventral and anteroventral sections. All lobes are coarsely granulose; the sulci and velum appear to be smooth.

MATERIAL: Just one tecnomorph, a left valve mould (part and counterpart). CMB unnumbered specimen; coll. M.L.K. Curtis.

MEASUREMENTS: Hinge length - sulcal height (excluding velar width) in microns.

1980-1210

DISCUSSION: The form of the anterior lobe, preadductorional node, zygal arch, sulci, velum and ornamentation all place this species closer to Craspedobolbina than to other genus. The taxon differs from most Craspedobolbina species particularly in syllobial morphology where the lack of a syllobial groove is unusual and the presence of a distinct node is unique. (The knob-like element found on the syllobium of
C. turpis is a larger yet less distinct feature than this node). The species differ in other respects; the Tortworth species lacks a syllobial sulcule, has larger lobal cusps and a narrower adductorial sulcus.

**OCCURRENCE:** From the upper part of the Llandovery Series, the Tortworth inlier, Gloucestershire; Palaeocyclus band, base of the Tortworth Beds (upper Telychian). Loose blocks in bank of stream about 150 yd E 30° N of the SW corner of Daniel's Wood, near Tortworth.

*Craspedobolbina* ? sp. indet. 1

Pl. A4, fig. 21.

1869 *Beyrichia Kloedeni*, M'Coy; Jones pp. 11-12; p. 14, fig. 6b.

**REMARKS:** The large female right valve figured by Jones in 1869 (plate reversed) as *Beyrichia Kloedeni* is an internal mould. Its general morphology argues strongly in favour of its inclusion within *Craspedobolbina*, but because of the nature of preservation this assignment is made with doubt.

**DESCRIPTION:** The syllobium is broad with a dorsal outline which is curved posteriorly and which terminates anteriorly in a well developed cusp. The presence of a syllobial groove is not indicated on the mould. A conspicuous cusp, the same height above the hinge line as the syllobial cusp, occurs on the anterior lobe. Syllobial cusp slightly smaller than anterior lobal cusp. Both the long adductorial sulcus and the preadductorional node are weakly inclined forwards. The preadductorional node appears to nestle against the wide ventral part of the anterior lobe but is separated from it by a shallow prenodal sulcus. The crumina is relatively small and has an elongate-ovoid shape. Other morphological details are not discernible.
MATERIAL: One female right valve, internal mould (BM I 6292).

MEASUREMENTS: Hinge length - sulcal height in microns.

3075-2060 (approximate measurement).

DISCUSSION: Although this specimen probably belongs to Craspedobolbina it is difficult to compare it with other species until the external form of the valve is known. However, this female is extremely large and lies appreciably outside the known size ranges of the adults of large Craspedobolbina spp. such as C. lembodes, C. cf. lunata of Martinsson (1962, p. 158) and C. turpis. The specimen may represent a new taxon.

OCURRENCE: "Llandovery at Darnery Bridge, Tortworth", Gloucestershire. The specimen occurs in a hard sandstone and probably comes from the Damery Beds (Telychian).

Craspedobolbina ? sp. indet. 2

Not figured.

1881c Beyrichia Kloedeni, M'Coy; Jones, p. 345, pl. X, fig. 12

(non fig. 13).

1928 Beyrichia kloedeni McCoy; Straw, p. 198 (partim).

REMARKS: This internal mould of a tecnomorphic valve figured by Jones (op. cit., fig. 12) has the general shape and lobal characteristics of the genus Craspedobolbina; in particular the presence of a zygal arch (connected to a knob-like preadductorial node) is strongly suggested (see Jones"s illustration). Unfortunately the mould is very poorly preserved and further identification is not possible.

MATERIAL: One internal mould of a tecnomorphic right valve, BM I 143; coll., H.A. Wyatt-Edgell.
MEASUREMENTS: Approximate hinge length.

1035 microns.

DISCUSSION: This indeterminate beyrichiacean is described for completeness. If its assignment to *Craspedobolbina* is correct it represents the only known specimen of the genus from the Malverns.

OCCURRENCE: Howler's Heath, about 1 km W of Chase End Hill, the S Malvern area; brown sandstone of Llandovery age (Cowleigh Park or Wych Beds).

Genus **PARASLEIA** gen. nov.

DERIVATION OF THE NAME: From the Greek *para*, near, and the genus *Sleia*; referring to the resemblance of (particularly) the (type) species to the amphitoxotidine *Sleia*. Gender, feminine.

TYPE SPECIES: *Parasleia artemum* sp. nov., Pl. A5 ,fig. 2.

from the Wenlockian of Staffordshire.

SPECIES:

- *Parasleia artemum* sp. nov.
- *Parasleia degener* sp. nov.
- *Parasleia angiportus* sp. nov.
- *Parasleia ? grandicalcar* sp. nov.
- *Parasleia* sp. A

DIAGNOSIS: Verrucose Craspedobolbininae with a short dolonoid scar admarginal to a long gently curved ridge. All lobes (anterior lobe, preadductor node, syllobium) and sulci (prenodal sulcus, pre-adductor sulcus) fully developed. Lobal connections weak; valves lacking a zygal arch. A calcarine protuberance and an adductorial tubercle frequently occur.
Text-fig. 5  SIZE DISPERSION OF FEMALE SPECIMENS OF *PARASLEIA* SPECIES

- **P. artemum.** Hay Head Farm (loc. 25), Barr Limestone.
- **P. angiportus.** Brinkmarsh Qy., limestone band (loc. 11), Brinkmarsh Beds.
- **P. degener.** Brinkmarsh Qy., *Pycnactis* band (loc. 12), Brinkmarsh Beds.
- **P. ? grandicalcar.** Brinkmarsh Qy., limestone band (loc. 11), Brinkmarsh Beds.
DISCUSSION: The presence of a dolonoid scar in Parasleia clearly places the genus within the Craspedobolbininae.

Parasleia like Craspedobolbina is one of the few members of the subfamily in which all the main lobes and sulci are well represented; in addition both genera have well developed velar structures. The occurrence of calcarine spurs and adductorial tubercles, and the lack of a zygal arch, distinguish Parasleia from the type genus. Calcarine spines or homologous structures are not unknown in the Craspedobolbininae; they occur in Aitilia and Hamulinavis though in these genera the spines occur medioventrally on the male velum, and in the female on the posterior part of the crumina. The occurrence of a single tubercle at the top of the adductorial sulcus has not previously been noted in the subfamily.

If the subcruminal morphology of Parasleia is ignored, the valve morphology, especially that of the type species, is very reminiscent of the primitive amphitoxotidine genus Sleia. Both genera have conspicuous developments of calcarine spines, and adductorial tubercles; Sleia (like all amphitoxotidines) and the new genus lack a zygal arch. Even the difference in the subcruminal morphology of these genera is not too marked. Lobation (especially the syllobium) and sulcation again invite comparisons between the two taxa.

OCCURRENCE: From the Silurian inliers near Walsall (Staffordshire) and Tortworth (Gloucestershire). All known species occur in lower Wenlockian deposits.

Parasleia artemum sp. nov.

Pl. A5, figs. 1-7, 9, 11, 12.

DERIVATION OF THE NAME: From the Greek artemon, a foresail; alluding to the rather wide anterior part of the velum.

HOLOTYPE: A left female valve, DAS 47231; Pl. A5 , fig. 2.
TYPE LOCALITY AND TYPE STRATUM: The old workings, about 400 m NW of Hay Head Farm, near Walsall, Staffordshire (loc. 25); Barr Limestone.

DIAGNOSIS: Large Parasleia species with a conspicuous tubercle at the top of the adductorial sulcus, a calcarine spur in tecnomorphs and an anterior lobe projecting above the hinge line. The tubulous velum is wide, especially anteroventrally in tecnomorphs and precruminally in females. Verrucae on all lobes.

DESCRIPTION: Evenly curved outline to the preplete valves. Anterior lobe, preadductorial node and syllobium all strongly developed and separated by well marked sulci. The syllobium has a larger, pointed anterior cusp and a lower, rounded posterior cuspidal outline; the posterior syllobial cusp shows, in some specimens, a tendency to be higher and more pointed. In adult specimens all cusps (and the prominent, isolated adductorial tubercle) protrude above the hinge line. Below mid-height the broad syllobium narrows rapidly in an anteroventral direction; there is a small calcarine tubercle in the female and the remnants of a corresponding spur is found in the male. The shallow syllobial groove above the calcarine element is bounded dorsally by a large raised area forming the widest part of the syllobium; no callus is seen.

A low col connecting the knob-like preadductorial node with the syllobium, separates the adductorial sulcus from the inconsiderably developed anteroventral depression. A tendency towards isolation from the preadductorial node is shown by the crescent shaped anterior lobe; the prenodal sulcus is not much narrower than the adductorial sulcus. The preadductorial node in the tecnomorphs is almost vertical and is slightly more anteriorly inclined in the females. The broad velum, widest anteroventrally in tecnomorphs, is prominently developed in the precruminal region. Short tubules are seen along the ventral section of the velum in tecnomorphs and in its pre- and post-
cruminal parts in heteromorphs. A faintly developed ridge occurs on the outside of the velar edge. The toric structure runs parallel and very close to the edge of the velum for some considerable distance in tecnomorphs, and is also present in the post-cruminal velar section of heteromorphs. In anterior and posterior views the velum "flares" away from the postero- and anterodorsal corners of the tecnomorphic valve with an almost straight outline.

Simple constrictions of the velum are present on both anterior and posterior sides of the relatively small, rounded crumina. Effects of the crumina on lobation are inconsiderable. Below the small dolonoid scar, there is a long ridge, very gently arched about its mid-length. The vertical marginal structures are represented by a row of small, isolated tubercles on each valve.

Ornamentation consists of sparse granulation with superimposed verrucosity. The syllobium is covered with scattered verrucae; the syllobial groove remains unornamented. Verrucae also occur on the pre-adductorial node and on most of the anterior lobe (on the more anterodorsal regions of the lobe ornament tends to be effaced). Both sulci and velum are smooth; crumina faintly striate, particularly admarginally.

Young tecnomorphs have a well developed calcarine spine which becomes relatively smaller and less sharp with maturity. The lobal cusps in immature specimens reach to, but do not project above, the hinge line. In general the lobal, velar and ornamental features of small tecnomorphs are like those of adults.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of females from the Barr Limestone (two samples approximately 0.5 m vertically apart).

DISCUSSION: Variation within the extant material is negligible; the form of the posterior syllobial cusp represents the most variable character.

In common with *P. degener* and *P. angiportus* a zygal arch is absent and all lobes and sulci are well developed. *P. artemum* is also similar to *P. degener* in having a shallow syllobial groove above a calcarine spur in the tecnomorphs, an adductorial tubercle and a similar subcruinal morphology. *P. artemum* is distinguished from *P. degener* by its wider velum, its higher anterior lobe (projecting above the hinge line) and its more conspicuous ornamentation. Furthermore, while too much importance cannot be attached to absolute size as a specific character, adults of *P. artemum* lie far outside the known size range of *P. degener*.

OCCURRENCE: Known at present only from the lower Wenlockian of the type locality, Staffordshire.

Barr Limestone: Hay Head Farm (loc. 25); over seventy female and tecnomorphic specimens.

*Parasleia degener* sp. nov.

Pl. A5, figs. 8, 10, 13-20.

DERIVATION OF THE NAME: From the Latin *degener*, departing from its kind; with reference to the less prominently developed calcarine element in mature valves.

HOLOTYPE: A right female valve, DAS 47200; Pl. A5, fig. 10.

TYPE LOCALITY AND TYPE STRATUM: The SW side of the disused Brinkmarsh Quarry, near Whitfield, the Tortworth inlier, Gloucestershire (loc.12a); *Pycnactis* band near the base of the Brinkmarsh Beds.

DIAGNOSIS: *Parasleia* species with an anterior lobe just reaching the hinge line, a calcarine spur in tecnomorphs, and a moderately wide velum which is very weakly developed in its precruminal section. A small
adductorial tubercle is present. Acroidal processes occur in tecnomorphs.

DESCRIPTION: Not all of the morphological features described herein are found in every specimen; the material is generally poorly preserved and in most cases valves are crushed and broken.

All lobes and sulci easily distinguishable. Gently curving anterior lobe just reaching the hinge line. The syllobium has a simple morphology; its moderately pointed anterior cusp is the only lobal element which markedly projects above the hinge line. The postero-dorsal portion of the syllobium is most often rounded, but it can have a sharper contour. Syllobium and to a lesser extent anterior lobe, joined to the preadductorional node by low connections. The prenodal sulcus, separating distinctly the anterior lobe from the preadductorional node, is inconsiderably narrower than the adductorial sulcus. A shallow depression occurs anteroventrally in tecnomorphs. The preadductorional node and the most swollen part of the syllobium are approximately the same elevation; the lowest lobal element on the carapace is the anterior lobe.

Posterior acroidal processes are commonly found in young tecnomorphs. A small adductorial tubercle is present throughout ontogeny; in some specimens it is hardly - if at all - developed. The prominent calcarine spine found in immature specimens persists into adult males in a shorter, less developed, spur-like form; its place in the female is occupied by a smaller, ill-defined conical shaped element, rather like a blunted calcarine tubercle. A shallow syllobial groove occurs above the calcarine spine in the tecnomorphs, and a broad, shallow tract trends diagonally between the calcarine element and the larger part of the syllobium in the females.

From antero- and posterodorsal corners of the carapace the velum runs almost parallel to the contact margin for approximately half the height of the valve, before flaring out lateroventrally. The velar edge
is thick with a toric ridge along its ventral side. If tecnomorphic valves are viewed obliquely, short wide tubules are visible along the ventral parts of the velum. In young tecnomorphs the velum is relatively wider, giving a deeper appearance to the valves. Constrictions of the velum exist each side of the crumina, the posterior one being quite marked in lateral view. In females the velum is very narrow in front of the crumina. There is a small dolonoid scar admarginal to a long evenly curved ridge. Small isolated tubercles form the vertical marginal structures in each valve.

The ornamentation, often effaced from valve surfaces because of poor preservation, consists of a very sparsely granulate ground pattern superimposed with verrucosity. Scattered verrucae are seen on all lobes, especially the syllobium. The cruminal ornamentation consists of mostly effaced striae. Sulci and velum are smooth.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of female specimens from the *Pycnactis* band, Brinkmarsh Quarry. Each set of figures represents a different sample, approximately 2m apart along the strike.

1270-740 (holotype), 1125-710, 1065-670 (loc. 12a).
1230-770, 1170-685, 1065-660 (loc. 12b).
1220-745, 1040-680, 1035-640 (loc. 12c).
1140-690, 1050-670 (loc. 12d).

DISCUSSION: A comparison of this taxon with *P. artemum* and *P. angiportus* is made under those species. *P. degener*, with its adductorial tubercle and calcarine spur is most like the type species, but differs from it especially in the nature of the velum; furthermore, acroidal processes have been observed only in tecnomorphs of *P. degener*. Both species occur at approximately the same horizon, though at present they are separated geographically.
OCCURRENCE: Known only from near the base of the Wenlockian, the Tortworth district.

Brinkmarsh Beds: Brinkmarsh Qy., Pycnactus band (locs. 12a-d); over two hundred valves.

Parasleia angiportus sp. nov.
Pl. A6, figs. 1-7, 9-11.

DERIVATIŒ OF THE NAME: From the Latin angiportus, a narrow street; alluding to the appearance of the syllobial groove.

HOLOTYPE: A left female valve, DAS 47279; Pl. A6 , figs. 3, 7.

TYPE LOCALITY AND TYPE STRATUM: The NW side of Brinkmarsh Quarry near Whitfield, the Tortworth inlier, Gloucestershire (loc. 11); the sandy limestone band at the base of the Brinkmarsh Beds.

DIAGNOSIS: Parasleia species with a syllobial groove typically consisting of two fine furrows; these furrows are short and faint in females, longer and more conspicuous in tecnomorphs. Protuberances in the calcarine region are lacking. Lobal cusps rounded. Verrucae found mostly on the syllobium.

DESCRIPTION: The anterior lobe, broad in its ventral region, tapers evenly to a fine cusp reaching to, or just above, the hinge line. The generally rounded, anterior syllobial cusp projects above the hinge line. The gently contoured posterodorsal part of the syllobium skirts the hinge line. There is a prominent preadductorital node separating the two main sulci. Adductorial sulcus inconsiderably wider and deeper than prenodal sulcus; both are well developed. The lobal connections below the preadductorital node are practically obsolete, though the anteroventral depression (conspicuous in lateral view, but quite shallow) is never linked directly to the more elevated sulci above.
The syllobial groove in tecnomorphs is distinct and long; it curves diagonally from a point on the syllobium above the ventral end of the adductorial sulcus, to a point above the posterior mid-height of that lobe. In one small instar the groove almost reaches the posterior cardinal corner. Most tecnomorphs have this main (ventral) groove bordered dorsally by a second, finer, shorter groove; the intervening area is like (though is not considered to be) a callus. In some tecnomorphs the more dorsal, less distinct groove is seemingly absent. The syllobial groove in the extant females is represented only by two short, parallel, hairline furrows. The syllobium immediately below the grooves in tecnomorphs is quite elevated - almost as high as that part of the syllobium just dorsal of the grooves - though there is never any tendency to form calcarine spines, spurs or tubercles. The most elevated part of the syllobium occurs at its widest point (between its groove and cuspidal region). In a single enigmatic female specimen (referred with doubt to P. angiportus) a small blunt tubercle exists in the upper part of the adductorial sulcus near the hinge line; the valve is otherwise similar to the other female specimens.

The moderately-wide velum has a thickly rolled appearance to its rim, and is simply constricted both anterior and posterior of the oval-shaped crumina. Velar tubules are hardly discernible externally. A toric ridge is present close to the velar edge in both sexes. The short dolonoid scar lies admarginally to a longer, narrow, slightly curved ridge. All of the four female valves prepared appear to have a short groove on the crumina immediately below the preadductorial node. Vertical marginal structures present in both valves.

Most of the valve surface is smooth, especially sulcal and velar areas. Verrucosity is variably developed. A typical valve has scattered verrucae only on the posterior and posteroventral parts of the syllobium, below the groove. Other variants have verrucae extended to the more posterodorsal regions of the syllobium or, more rarely, appear to lack
verrucae. Crumina mostly smooth, some striae venterolaterally.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of undamaged specimens from the limestone band, Brinkmarsh Quarry (loc. 11).

Females: 1305-830 (holotype), 1260-800, 1255-820, 1210-770.

Tecnomorphs: 1260-845, 1020-760, 1015-720, 940-675, 850-605, 780-610.

DISCUSSION: This species, known only from the type locality, exhibits noticeable variation in minor details of morphology and ornamentation. Variation in ornamentation combined with that shown by the syllobial groove produces many phena with minor morphological differences. However, the variational groups have not proved to be discontinuous enough within the extant material for them to be considered as separate taxa; they are described and figured here as one species. Preparation of these Brinkmarsh specimens is extremely difficult, though preservation is generally good and is not considered to have "hidden" anything within the variants discussed.

*P. angiportus* has a more rounded syllobial cusp than *P. degener*. Moreover in lacking an adductorial tubercle or traces of a calcarine process, this species is unlike *P. artemum* or *P. degener*, and its assignment to *Parasleia* may be questioned. The writer prefers at present to refer this species to *Parasleia* mainly because of similarities in ornament, lobation (e.g. the lack of a zygal arch), and subcruminal morphology. If excluded from *Parasleia*, a new genus would be needed to receive this species.

A comparison of *P. angiportus* with *Parasleia* sp. A is given under the latter species.

OCCURRENCE: So far only from the type locality (basal Wenlockian) in the Tortworth inlier.

Brinkmarsh Beds: Brinkmarsh Qy., Limestone band (loc. 11); seven females (four complete), over forty tecnomorphs.
Parasleia ? grandicalcar sp. nov.

Pl. A7, figs. 1-4, 6, 9.

DERIVATION OF THE NAME: From the Latin grandis, large, and calcar, a spur; referring to the well developed calcarine spine in both females and tecnomorphs.

HOLOTYPE: A female right valve, DAS 47292; Pl. A7, figs. 4, 9.

TYPE LOCALITY AND TYPE STRATUM: The NW side of the old workings at Brinkmarsh Quarry, near Whitfield, Gloucestershire (loc. 11); the lowermost limestone band at the base of the Brinkmarsh Beds.

DIAGNOSIS: Parasleia ? species with a prominent calcarine spine in the female and in the tecnomorphs. The syllobium has two small, rounded cusps which are equal in size and project slightly beyond the hinge line. There is a bold adductor tubercle.

DESCRIPTION: The relatively large preadductorial lobe is evenly rounded and slopes forward slightly. Lobal connections are barely developed. The preadductorial node and anterior lobe are virtually isolated from each other, though the former is vaguely confluent with the syllobium via a low, ill-defined connection beneath the adductorial sulcus. The presence of an anteroventral depression is crudely outlined above the widest, anteroventral part of the velum. Although lobes are distinctly set apart, the sulci do not, because of their higher elevation, link directly with the region of this depression. The sickle-shaped anterior lobe tapers gradually to an indistinct, posteriorly projecting point, on or just above the hinge line.

Both adductorial sulcus and prenodal sulcus are narrow but well delimited; the adductorial sulcus is marginally wider and deeper and broadens a little towards the pap-like adductorial tubercle on the hinge line. The prenodal sulcus characteristically has a constant width and is
gently bent around the preadductorional node. The two cusps (see "Diagnosis") and the calcarine spine constitute the most salient features of the syllobium. A spine, or its remains, has been found in all extant specimens; it is sited on the ventral-most part of the syllobium and projects stoutly posterolaterally. Immediately above the spine, at least in tecnomorphs, a syllobial groove is discernible. The hair-like groove is markedly inclined to the dorsal margin of the shell and fades out before reaching the posterior boundary of the syllobium.

In tecnomorphs the fine, moderately-wide velum is best developed below the preadductorional node; anteriorly and posteriorly it becomes narrower and ridge-like. Along the ventral velar section, tubules are faintly visible externally. The female velum is narrow and ridge-like (particularly precruminally) and is - in lateral view - quite conspicuously constricted just behind the egg-shaped crumina. Ventrally on the crumina, some distance from the valve margin, there is a fairly long ridge which is curved abmarginally in a manner reminiscent of Craspedobolbina species. The existence of a complimentary scar has not, in the material at hand, been verified (see "Discussion" below). The gap between calcarine spine and crumina is extremely narrow.

The mostly smooth surface of the lobes if broken by variable developed verrucae. Typically these blunt cones are unevenly distributed over the syllobium (particularly posteroventrally), and the ventral parts of the anterior lobe. The sulci and velum lack ornamental features.

Apart from smaller - in some valves virtually obsolete - syllobial cusps, the early instars are identical to more mature specimens.

MEASUREMENTS: Hinge length - sulcal height (including velar width) of female valves from the type locality.

1120-780, 1025-765 (in microns).
DISCUSSION:  *P.? grandicalcar* is not common and the preparation of its few valves has provided many obstacles; access to crucial taxonomic areas on the crumina is almost impossible, unless - as in one specimen - this is permitted by a fortunate fracture of the limestone. Of the female valves obtained, two were complete, one had its crumina missing and the fourth had only the anterior part of the crumina remaining. The latter specimen was unprepared and showed a distinct curved ridge on the distal part of the crumina and, close to the margin, what could possibly be interpreted as part of a small dolonoid scar (the crumina is unfortunately broken across this point). In spite of the careful exposure of the crumina of the well preserved holotype, only the ridge was observed. The existence of the dolonoid scar has therefore not been positively determined. For the present this species is tentatively assigned to *Parasleia*.

The calcarine spine, found in all of the females and tecnomorphs collected, is the most obvious diagnostic feature of this species. The cuspidal morphology of the syllobium is another important distinguishing character.

OCCURRENCE: Confined, as yet, to the base of the Wenlock Series at the type locality in the Tortworth inlier.

  Brinkmarsh Beds: Brinkmarsh Oy., limestone band (loc. 11); four females and fourteen tecnomorphs.

  Parasleia sp. A.
  Pl. A6, figs. 8, 12, 13.

REMARKS: Probably one more *Parasleia* species exists from the limestone band at Brinkmarsh, but because of the small amount of extant material and considering the variation shown by *P. angiportus* from the same locality, it is thought best at present not to propose another new species.
MATERIAL: Five valves, two females and three tecnomorphs (one poorly preserved).

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of all extant material.

Females: 1110-775, 1080-695.

Tecnomorphs: 1150-825, 1145-830, 1120-770.

DISCUSSION: In shape, and general lobal features these specimens are much like P. angiporta and P. degener, but they differ from both species in the following details.

Verrucae (found on all parts of the syllobium and lower regions of the anterior lobe) cover much more of the valve surface than in P. angiportus. A syllobial groove, apparently lacking in the two females, occurs in the three tecnomorphs in a more ventral position than in P. angiportus; moreover (in contrast to conditions in P. angiportus) the elevation of that part of the syllobium below the groove is noticeably less than that part immediately above it. A conspicuous adductorial tubercle is present in all five specimens of Parasleia sp. A, whereas only one problematic specimen from the much larger amount of material assigned to P. angiporta shows this feature.

Parasleia sp. A differs from P. degener mainly by the lack of a calcarine spine or spur in the tecnomorphs and in the form of the syllobial groove.

OCCURRENCE: The basal Wenlockian of the Tortworth inlier.

Brinkmarsh Beds: Brinkmarsh Qy., limestone band (loc. 11); two females, three tecnomorphs.
Genus DICTYOBOLBINA gen. nov.

DERIVATION OF THE NAME: From the Greek dictyon, a net, and the generic name bolbina; referring to the reticulate ornament. Gender, feminine.

TYPE SPECIES: Dictyobolbina incuspidata sp. nov., Pl. A7, figs. 10, 11; from the Wenlock Shale of Shropshire.

SPECIES: Only the type species.

DIAGNOSIS: Reticulate Craspedobolbininae with a tiny, distally sited scar on the crumina. The continuation of the velum over the crumina can be traced in the pattern of ornamentation. All lobes inconspicuous; cusps absent. Adductorial sulcus narrow but distinct. Velum long and prominently tubulous.

DISCUSSION: A discussion of the cruminal morphology of this genus and a comparison with other Craspedobolbininae is given under D. incuspidata below.

OCURRENCE: The Welsh Borderlands; from the Coalbrookdale Beds and Buildwas Beds of N Shropshire.

Dictyobolbina incuspidata sp. nov.

Pl. A7, figs. 5, 7, 8, 10-14.

DERIVATION OF THE NAME: From the Latin in, without, and cuspidatus, pointed; referring to the absence of cusps along the hinge line.

HOLOTYPE: A female left valve, DAS 47238; Pl. A7, figs. 10, 11.

TYPE LOCALITY AND TYPE STRATUM: The N bank of the River Severn, about 15 m upstream from Buildwas Bridge (loc. 34), Buildwas, Shropshire; Coalbrookdale Beds.
DIAGNOSIS: As for the genus.

DESCRIPTION: Valves quite large with relatively flattened lateral surfaces. Lobation consisting of a wide syllobium of low elevation, a small preadductorial node and a flat anterior part of the shell constituting the anterior lobe. All lobes merge in the flat anteroventral area. The preadductorial node is quite sharply delimited on its posterior margin and is joined to syllobium by a wide, weakly defined connection. Valves lack a zygal arch or syllobial groove.

The narrow, short adductorial sulcus - at mid-length on the valves - is deepest and most conspicuous as it bends around the ventral part of the preadductorial node; it shallows rapidly dorsally and becomes obsolete before reaching the hinge line. Prenodal sulcus only vaguely suggested by a narrow shallower tract between preadductorial node and anterior lobe. The greatest elevation of the syllobium occurs in its ventral half, gradually becoming lower towards the hinge line where, like the the anterior lobe, it terminates without a dorsal projection. Anteroventral depression weakly indicated by a slight curve in the otherwise evenly rounded outline of the lobate area.

The well developed velum - extending in tecnomorphs from anterodorsal corner to posterior mid-height - has long, narrow tubules throughout its length. No torus is seen, though the velar edge is broken in all of the few tecnomorphs obtained. In heteromorphs the velar morphology matches that of the tecnomorphs except for the interruption by the large, rounded crumina which is well set off from the domicilial wall.

Distally on the crumina there is a very short, fine, arcuate scar whose length is approximately one-seventh of the cruminal length; in some specimens the scar is almost obsolete. The scar hugs against a fine admarginally deflected line which can be vaguely traced between the pre- and postcruminal velar sections. Typically this feature is not so much a ridge, more a demarcation line between patterns of
ornamentation (admarginally the crumina is smooth, abmarginally it has a dense, evenly covered granulation; characteristically this difference is less distinct near the scar).

The deepest ventral portion of the adductorial sulcus is the only part of the valve surface completely devoid of reticulation, though the meshes are effaced or less developed on the anterior lobe. Prenodal sulcus also reticulate. The crumina is mostly granulose, but ventrally and near its junction with the lobes it is smooth. Marginal structures consist of a row of small, isolated tubercles along each valve.

MEASUREMENTS: Hinge length - sulcal height of two tecnomorphs (in microns).

Coalbrookdale Beds: Buildwas Bridge (loc. 34): 1190-755.


DISCUSSION: Dictyobolbina is placed in the Craspedobolbininae because of the presence of what is interpreted to be a dolonoid scar. The subcruinal morphology of D. incuspidata indicates a developmental stage similar to that found in cruminae of the craspedobolinine Leptobolbina Martinsson, 1962, especially L. quadricuspidata; the dolonoid scar sited distally on the crumina is very small - almost obsolete - and flap insertion reduced to a minimum. In L. quadricuspidata the velar edge enters the dolonoid scar; some cruminae of Dictyobolbina appear to have a similar type of arrangement (involving the 'line' dividing the cruminal pattern of ornamentation - see description above).

Reticulation is not unknown in craspedobolinines; it occurs in Bolbineosia Kesling, Heany, Kauffman, & Oden, 1958, Dolichoscapha Kesling & Ehlers, 1958 and in females of a Gotland Clintiella species. Like Bolbineosia, Barymetopon Martinsson, 1962 and Hyrsinobolbina Martinsson, 1962 (Craspedobolbininae), Dictyobolbina has a well developed velum with long narrow tubules. Its narrow adductorial sulcus, bent around an inconspicuous preadductorial node is comparable to that found in Hyrsinobolbina and three other craspedobolinine genera, Aitilia Martinsson, 1962,

Dictyobolbina differs from Dolichoscapha and Bolbineossia by having full lobation; moreover, the velar morphology of Dolichoscapha (comparatively narrow and flange-like) is quite different. Barymetopon, Hyrsinobolbina, Aitilia, Hamulinavis and most Clintiella spp. are either smooth or punctate and lack the noticeable reticulation of Dictyobolbina.

OCCURRENCE: Known from the lower Wenlockian of the N part of the Welsh Borderlands. Specimens are fragmentary, complete ones are rare. The extant material, extracted from a large amount of washed samples, consists of five almost complete valves, numerous cruminae and other fragments.

Genus STROTEROBOLBINA gen. nov.

DERIVATION OF THE NAME: From the Greek stroter, crossbeam, and the generic name bolbina; alluding to the system of spines across the velum. Gender, feminine.

TYPE SPECIES: Stroterobolbina floribunda sp. nov., Pl. A8, figs. 1, 2, 5; from the Landovery of the Welsh Borderlands.

SPECIES: Only the type species.

DIAGNOSIS: Craspedobolbininae with a wide, entire velum which is crossed by a system of strut-like spines along its length. Most of the long, sausage-shaped crumina lies in front of the adductorial sulcus. The preadductorial sulcus is defined anteriorly by an indistinct prenodal sulcus.
DISCUSSION: The genus with which Stroterobolbina shows most affinities (at least in the females) is the monotypic Barymetopon Martinsson, 1962. Tecnomorphs of B. infantile Martinsson, 1962 are unknown, but it is still possible to distinguish Stroterobolbina from Barymetopon (as defined by Martinsson 1962, p. 194). In Stroterobolbina both pre-adductorial node and prenodal sulcus are more distinct, its adductorial sulcus is completely developed to the dorsal margin of the valve, its crumina is longer, and it lacks acroidal processes. At least the tecnomorphs (and possibly the females) of Stroterobolbina have ornament, whereas the known specimens of Barymetopon are smooth.

The system of spines on the velum (see diagnosis and description) is a unique characteristic of Stroterobolbina. I am unaware of a comparable feature in any other genus. The possible relationship of the spines - radiating from the edge of the lobate area - to velar tubulosity in general, is especially interesting and requires further study. Its cruminal morphology places Stroterobolbina within the Craspedobolbininae.

OCCURRENCE: Late Llandovery deposits in the N Welsh Borderlands.

Stroterobolbina floribunda sp. nov.

Pl. A8, figs. 1-7.

DERIVATION OF THE NAME: From the Latin floribundus, abounding in flowers; fancied resemblance of lobal ornament.

HOLOTYPE: A male right valve, DAS M 259; cast figured. Pl. A8 , figs. 1, 2, 5.

TYPE LOCALITY AND TYPE STRATUM: A large temporary section at Devil's Dingle, approximately 1200 m N of the river (Severn) bend at Buildwas, N Shropshire (loc. 29); Hughley Shales (upper part of the Llandovery Series).

DIAGNOSIS: As for the genus.
DESCRIPTION: The valve surface is fairly flat, and all lobes are of low elevation. The preadductorional node is narrow, elongate and markedly anteriorly inclined. This node is separated from the wide, flat anterior lobe by an almost obsolete prenodal sulcus, and from the syllobium by a wider and deeper adductorial sulcus. There is a characteristic swelling of the preadductorional node on the lower part of its posterior margin, which, in lateral view, slightly constricts the adductorial sulcus. The prenodal sulcus is discernible only as an extremely narrow, shallow tract around the anterior margin of the preadductorional node. The adductorial sulcus is narrow, inclined forward, deepest ventrally, and widens towards the hinge line. The width of the syllobium is approximately equal to its height. All of the lobes terminate without projections along the hinge line. In the broad region (reaching almost to mid-height) below the adductorial sulcus the large syllobium is connected to the anterior part of the valve.

At each hinge corner, particularly posteriorly, the velum is extended (at a slight angle) above the hinge line. Throughout almost its entire length the velum is wide (though it does taper towards the anterior hinge corner) and is crossed from base to edge at regular intervals by slender spines. In well preserved tecnomorphs the spines are seen to occur on the upper (laterally facing) surface of the velum in a manner suggestive of beam-like supports. Most of these spines are broken off, each revealing its former path across the velum in the form of two, fine, subparallel lines which in turn are traversed by fine striae. The striae cover the entire velum parallel to its edge; the velum, as in many craspedobolbinines, has a wrinkled appearance. The radial lines give an impression of tubulosity to the velum.

The long sausage-shaped crumina tapers slightly posteriorly, and impinges on the valve surface to an increasing degree in an anterior direction; approximately two-thirds of its length lies in front of the adductorial sulcus. The anterior face of the crumina is noticably blunt.
So far as can be determined the velum is simply attached to each end of the crumina and then continues towards the hinge corners in the same way as in the tecnomorphs. On a cast of the ventral part of a crumina (specimen assumed to be *S. floribunda* on the basis of the concomitant ostracode fauna) a long fine furrow — interpreted as the dolonoid scar — occurs close and parallel to the margin; the scar becomes obsolete near the end of the crumina.

Well-preserved tecnomorphs show that the anterior lobe, the syllobium and the area of lobal connection have fine granulose ornament. Near the central regions of the valves in particular, the granules form crude (?) five-sided polygons; elsewhere they are randomly distributed. Across the face of the preadductorional node the granules are arranged into sinuous, forwardly inclined rows. None of the females show surface ornament, though this is probably a reflection of poor preservation.

The velar spines, if anything, tend to be more pronounced in smaller instars, and the velum itself wider.

**MATERIAL:** Occurs only in mould form. Some 35 valves have been collected (and cast) from the type locality. The state of preservation varies considerably, even between individuals on the same slab. Fine ornamental details are visible on only a few specimens, though lobal, sulcal and velar outlines are clearly recognisable on all valves.

**MEASUREMENTS:** Approximate hinge length — sulcal height of topotype material (in microns).

Female: 975-640 (to mid-height of crumina).

Males: 1000-540 (670), 960-560 (650), 940-510 (630).

For the males, the sulcal height is given both exclusive and inclusive (in parentheses) of the velar width.
DISCUSSION: The velar morphology is singularly important as a diagnostic character. It is unfortunate that the extant material (all moulds) prevents access to a cross-section of the velum; it would be interesting to see how the trace of the spines relates to any tubulosity present.

All of the females obtained are fragmentary and less well preserved than most of the males. The possible existence of lobal ornament in females is a feature which needs further attention in connection with ? S. floribunda described below.

OCCURRENCE: Restricted, as yet, to localities in the late Llandovery of N Shropshire.

Hughley Shales: Devil’s Dingle (loc. 29); mid-Telychian.

? Domas (loc. 32); upper Telychian.

Material from Devil’s Dingle consists of approximately twenty tecnomorphs and fifteen females (complete and fragmentary valves). Poor internal moulds were found at Domas and are included with doubt. Church Preen Brook (loc. 30) may yet be added to this list (see ? S. floribunda below).

? Stroterobolbina floribunda
Pl. A8, figs. 8-11.

REMARKS: In those parts of the valve which remain (the edges of the velar sections above the crumina are largely missing) this single specimen is identical to the females of S. floribunda. However, this valve – found in limestone and exceptionally well preserved – has fine surface ornament, a feature not confirmed in the females of S. floribunda. Until adequately preserved moulds prove the presence (or absence) and nature of ornamentation in females of S. floribunda, or tecnomorphs have been found at Church Preen Brook, a more positive evaluation of this female cannot be made.
DESCRIPTION: Only ornamental features need be given. Most of the anterior lobe and syllobium have a delicate network of meshes (vaguely polygonal), superimposed by unevenly scattered verrucae. The latter also occur near the hinge line above the sulci. The preadductorial node is traversed by very fine striae (individual granules can hardly be detected) in exactly the same way as described for tecnomorphs of S. floribunda. Almost all of the crumina is finely striate, the striae running parallel to the cruminal length.

MATERIAL: Just one female left valve.

MEASUREMENTS: Hinge length - sulcal height (to the mid-height of the crumina).

965-660 (in microns).

DISCUSSION: The ornament of this female differs from tecnomorphs of S. floribunda by the occurrence of verrucae. However, dimorphism affecting ornament cannot be ruled out in this respect.

In spite of careful preparation of nearly all the ventral region of the crumina a dolonoid scar was not exposed; it apparently lies immediately adjacent to the margin.

OCCURRENCE: Upper part of the Llandovery Series, N Welsh Borderlands.

Hughley Shales: Church Preen Brook (loc. 30).
REMARKS: All of the genera discussed below, with the exception of *Strepula*, are recorded from Britain for the first time. Their study has revealed a more widespread existence of cristal systems and tubulous vela within the Treposellinae. Cristae have been observed in the early instars of *Bolbiprimitia* and *Garniella* species and in both the young and adults of *Pemphibaris* gen. nov.; yet another cristate Wenlockian form may provide the monotypic *Strepula* with its second species (*Strepula? sp. nov.*, herein). In the primitive *Strepula* and *Pemphibaris* the cristae are combined with full lobation; moreover in both these genera the velum is obviously tubulous in structure - signifying the early position they occupy within the beyrichiacean system. Radial tubulosity to the extent it is developed in *Pemphibaris* is paralleled only in *Treposella stellata* Kesling, 1955 from the Centerfield Limestone (Devonian) of W New York.

The morphology of the crumina in *Pemphibaris* and *Cavisella* gen. nov. is especially interesting; in both cases it is comparable with that found in craspedobolbinine genera such as *Clintiella*. On the other hand, the form taken by the adductorial sulcus in *Pemphibaris* is almost unique (cf. conditions in the amphitoxotidine *Berolinella* Martinsson, 1962). In *Cavisella*, as in the Devonian treposelline *Phlyctiscapha*, lobal features are lacking.

SYSTEMATIC PALAEONTOLOGY

Subfamily TREPOSELLINAE Henningsmoen, 1954

TYPE GENUS: *Treposella* Ulrich & Bassler, 1908, p. 134; from the Devonian of Ohio, U.S.A.
BRITISH GENERA: Cavisella gen. nov.
Pemphibaris gen. nov.
Strepula Jones & Holl, 1886
Garniella Martinsson, 1962
Retisacculus Martinsson, 1962
Bolbiprimitia Kay, 1940

DIAGNOSIS: Craspedobolbinidae tending to incorporate, or incorporating, a large part of the syllobium with an originally anteroventral crumina, the dolonoid closing mechanism of which has largely become obsolete (after Martinsson 1962, p. 196).

DISCUSSION: Henningsmoen (1954, p. 33) established the Treposellinae to include those beyrichiaceans with a, "... mainly ventrally situated pouch", which is, "... rather confluent with the rest of the valve". The subfamily is a relatively well knit unit - although exhibiting considerable diversity in lobal and ornamental features (see Kesling 1969, pp. 296-8) - and its original concept has remained quite stable and acceptable to most subsequent authors (Martinsson 1962, Henningsmoen 1965, Gailite 1967, Sarv 1968, Kesling 1969; herein). Abushik (1971) alone prefers to give the group family rank.

It is generally agreed (Henningsmoen 1954, Martinsson 1962, Kesling 1969, Abushik 1971; herein) that the Treposellinae descended from, or had ancestors closely similar to, certain craspedobolbinine genera.

OCCURRENCE: In Britain the subfamily is recorded mostly from the Wenlock Series, and rarely from the base of the Ludlovian.

Treposelline genera are documented mainly from Siluro-Devonian deposits of N Europe. Important members of the Treposellinae also occur in the Silurian and Devonian of N America.
Genus **CAVISELLA** gen. nov.

**DERIVATION OF THE NAME:** From the Latin *cavus*, hole, and *sella*, a little seat; referring to the adductorial pit - the only definable sulcal (or lobal) element. Gender, feminine.

**TYPE SPECIES:** *Cavisella clithridium* sp. nov., Pl. B1, fig. 1; from the Wenlockian of the Welsh Borderlands.

**SPECIES:** Only the type species.

**DIAGNOSIS:** Reticulate Treposellinae with sulcation diminished to a small central pit; lobation defunct. Velum attached simply to the ends of the long, smooth, ventrally situated crumina; a ridge, forming part of the marginal structure, runs along the base of the crumina.

**DISCUSSION:** This genus displays particularly interesting taxonomic features. In lateral view it could readily be considered a member of the *Aitilia* (Craspedobolbininae) group of genera. However, the ventral morphology of its crumina shows no trace of a dolonoid scar or any structure which could be interpreted as such. In the context of its overall morphology *C. clithridium* has to be considered a member of the Treposellinae in which - somewhat unusually for the subfamily (but also seen in its type genus *Treposella*) - the crumina encroaches onto the syllobial area but does not become markedly confluent with it; as Martinsson has stated (1962, pp. 190, 208), the species "Bolbiprimitia" limbata Swartz & Whitmore, 1956 and "Bolbiprimitia" teresaccula Swartz & Whitmore, 1956 are "perfectly intermediate" between the Craspedobolbininae and Treposellinae in this respect, though unfortunately their subcruminal morphology has not been described.

In lateral view the monotypic genus *Dolichoscapha* Kesling & Ehlers, 1958 - inferred by Martinsson (1962, p. 75) and stated by Kesling (1969, pp. 286, 310) to belong to the Craspedobolbininae - is remarkably similar
to Cavisella. D. escharota, known from a single female valve from the middle Silurian of America, differs from C. clithridium in having its valve surface weakly arched above the hinge line, a central smooth spot representing the adductorial sulcus, and a "velate ridge" which is either "complete or separated into two parts" (Kesling & Ehlers 1958, p. 153) along the base of a reticulate crumina. The only published illustration of the ventral view of the holotype (Kesling & Ehlers 1958, pl. 24, fig. 19) does show a ridge on the anterior part of the crumina (above a fairly continuous marginal ridge), but its precise course and structure cannot be discerned.

Non-lobate forms are known from the Treposellinae eg. Phlyctiscapha Kesling, 1953, but one has to look to the Craspedobolbininae (Bolbineossia Kesling, Heany, Kauffman & Oden, 1958) for an adductorial pit comparable to that found in Cavisella.

OCCURRENCE: The Wenlock Series of the Welsh Borderlands and English W Midlands.

Cavisella clithridium sp. nov.
Pl. Bl, figs. 1-12.

DERIVATION OF THE NAME: From the Greek clithridium, keyhole; alluding to the size of the adductorial sulcus.

HOLOTYPE: A female left valve, DAS 47327; Pl. Bl, fig. 1.

TYPE LOCALITY AND TYPE STRATUM: A small disused quarry on the N side of the A. 458 road, top of Harley Hill, approximately 1.2 km NW of Much Wenlock, Shropshire (loc. 51); a thin shale-parting in the Wenlock Limestone.

DIAGNOSIS: As for the genus.
DESCRIPTION: Small instars are quite deep; in more mature valves
the length of the hinge increases relative to the valve height. Valves
have a characteristic forward swing. All lobes are completely obsolete.
The lateral surface of the valves terminates dorsally along the straight
hinge line. At mid-length there is a very small, forwardly arched pit;
this represents the adductorial sulcus and is the only trace of
sulcation. In females the pit is separated from the crumina by one or
two meshes in the reticulate ornament. Acroidal processes are commonly
seen, particularly in small instars, above both anterior and posterior
hinge corners. In tecnomorphs a velar structure can be traced all around
the non-dorsal part of the shell. Near the hinge corners and for most
of its length anteriorly and posteriorly, the velum is ridge-like;
ventrally it is extended slightly into a narrow frill. There is no sign
of velar tubules. The velum is attached to each end of the crumina in
simple fashion. The ridge along the base of the crumina bends below
the points of velar attachment and dies out, anteriorly and posteriorly,
along the region of the free margin; scars or furrows are absent.

The sausage-shaped crumina extends for three-quarters of the valve
length and has a fairly constant width. In ventral view the crumina has
an evenly rounded profile; dorsally, it is well set off from the rest
of the valve and shows no marked tendency towards absorption within
the postadductorial region.

A network of medium-sized meshes evenly covers most parts of the
carapace. In some specimens the reticulation is somewhat effaced near
the anterior hinge corner. The velum and adductorial pit lack ornament;
the crumina is smooth.

MEASUREMENTS: Approximate hinge length - sulcal height (to the base of
the crumina) in microns of female valves from the Wenlock Limestone.
DISCUSSION: Very rarely, some tecnomorphs do show finer reticulation than is normal for the species. These are treated at the moment as intra-specific variants.

OCCURRENCE: The Wenlock Series of the Welsh Borderlands and English W Midlands.

Wenlock Limestone:
- Wren's Nest (loc. 27c).
- Gleedon Hill (loc. 50).
- Harley Hill Qy. (loc. 51).
- Hobbs Ridge (locs. 15a, b).
- Whitman's Hill (loc. 19b).
- Croft Farm (loc. 18).

Tickwood Beds:
- Harley Hill Road (locs. 48b, c).
- Tickwood (locs. 44c, d).
- Benthall Edge, East (loc. 43a).
- Acklands Coppice (loc. 42a).

Genus PEMPHIBARIS gen. nov.

DERIVATION OF THE NAME: From the Greek pemphix, an air-bladder and baris, a flat-bottomed boat; fancied resemblance of female crumina and lobes to a small rubber boat. Gender, feminine.

TYPE SPECIES: Pemphibaris malata sp. nov., Pl. B2, figs. 1, 4, 7; from the Wenlockian of the Welsh Borderlands.

SPECIES: Only the type species.
DIAGNOSIS: Treposellinae with an adductorial sulcus extending from the hinge line to the base of the velum. The crumina is long, smooth and ventrally situated. Velum wide and tubulous. Syllobium, pre-adductorial node and anterior lobe each with a crista; all lobes reticulate.

DISCUSSION: This very interesting treposelline finds its closest relative, at least in lobal morphology, in the genus Strepula. Both genera have a full complement of lobes adorned by cristae, but other features in their morphology are so significantly different that a break at generic level has to be made. In contrast to Strepula, Pemphibaris has no real lobal connection between the pre- and postadductorial areas, it has a more reduced cristal system (e.g. there is no lateral crista or cruminal cristae), and its crumina is long and not completely assimilated within the syllobium. Interestingly the velar morphology in the new genus is more comparable to conditions found in certain genera of the Amphitoxotidinae than to most other treposellines, and its form is undoubted proof that some members of the subfamily Treposellinae had far from dispensed with the practice of developing tubules. In Strepula the tubulosity is considerably fainter, though still not entirely obsolete. The width of the velum is another characteristic feature of Pemphibaris which distinguishes it from all other treposellines.

A special feature to note is the shape of the crumina. It is markedly similar to that found in the craspedobolbinine Clintiella, and corroborates Martinsson's suggestion (1962, p. 197) that, "The Treposellinae had probably close ancestors in common with the craspedo-bolbinines with a long crumina and a tendency to punction and reticulation".

OCCURRENCE: The Wenlockian of the Welsh Borderlands.
**Pemphibaris malata** sp. nov.


**DERIVATION OF THE NAME:** From the Latin *malus*, provided with masts; alluding to the appearance of the crista.

**HOLOTYPE:** A female left valve, DAS 47347; Pl. B2, figs. 1, 4, 7.

**TYPE LOCALITY AND TYPE STRATUM:** The large quarry at Whitman's Hill, approximately 300 m S of the Church (on the A 4103 road) at Storridge, Herefordshire (loc. 19b); Wenlock Limestone.

**DIAGNOSIS:** As for the genus.

**DESCRIPTION:** Both the syllobium and the slightly lower preadductorial node are steeply elevated features and have a maximum elevation well above the level of the anterior lobe. The intervening adductorial sulcus appears quite deep and in tecnomorphs, extends vertically from the hinge line to the proximal part of the velum. This sulcus shallows gradually and inconsiderably down its length but there is essentially no definable lobal connection linking anterior and posterior parts of the valve. A much narrower and very shallow prenodal sulcus separates the anterior lobal region from the elongate preadductorial node. Only the syllobium manages to reach beyond the hinge line, the preadductorial node terminates just short of the hinge line, and the anterior lobe has no cusp. The anterior lobe slopes very gently away from its posteriorly positioned crista. Like the syllobium, the anterior lobe and the preadductorial node merge gradually with the velar region.

The velum is very wide (especially in small instars), tubulous, and symmetrically arranged around the domicilium; its widest point occurs below the adductorial sulcus and it is here, too, that its long narrow tubules are best discernible. In the female the velum is unaffected in front of, or behind, the crumina. Typical "treposelline bridges"
(cf. Martinsson 1962) fuse the velar edge to each end of the crumina. There is a ridge connecting these points ventrally, along the crumina. For most of its considerable length (it occupies a distance almost equal to the hinge length), the sausage-shaped crumina is distinctly set off from the adjacent lobes; posteriorly it seems to merge a little more successfully—though far from completely—with the syllobium. The preadductorial node is unaffected by cruminal development.

Reticulation covers all of the preadductorial node, most of the syllobium, and a narrow strip (about two meshes wide) both sides of the anterior lobal crista; the size of each mesh is similar to that found in Garniella and Strepula. The lower regions of the syllobium, both sulci, and nearly all of the anterior lobe are smooth. Each lobe is capped by a crista; those on the syllobium and preadductorial node are prominent and vertical, that on the anterior lobe is faint and weakly curved along its length. As with the lobes, all of these ridges are isolated from each other (in contrast to Strepula where there is an interconnecting cristal system). The crista on the anterior lobe is situated very close to the prenodal sulcus. Ornament lacking on the crumina.

MEASUREMENTS: Hinge length—sulcal height (to the ventral margin of the crumina) of the female holotype.

970–845 microns.

DISCUSSION: See generic discussion.

OCCURRENCE: Known from one locality in the May Hill inlier and from the type locality in the Malverns area.

Wenlock Limestone: Whitman's Hill (loc. 19b).

Hobbs Ridge (loc. 15b).

The material is well preserved but difficult to prepare.
Genus STREPULA Jones & Holl, 1886

TYPE SPECIES: Subsequently designated by Miller 1892, p. 711;

Strepula concentrica Jones & Holl, 1886, p. 404, pl. XIII, fig. 6, non fig. 1; from the Wenlock Series, near Woolhope, Herefordshire.

SPECIES: Strepula concentrica Jones & Holl, 1886.

Strepula ? sp. nov. A

DIAGNOSIS: Treposellinae whose adults have cristae on the syllobium, preadductorial node, anterior lobe and crumina. All lobes are reticulate. The tecnomorphic velum shows very faint tubules and is otherwise smooth. Crumina well assimilated with the syllobium.

DISCUSSION: Martinsson (1962) was the first author to recognise that Strepula exhibits cruminal dimorphism and to correctly place the genus with conviction within the beyrichiacean system. Weyant (1965, pp. 71, 81) erected Strepula platyloba and Strepula roualti from the Middle Siegenian of Contentin, France. From the figures it seems to me that these two species are not congeneric with S. concentrica. There appear to be significant differences in cruminal morphology, lobation and ornamentation; furthermore, stratigraphically, the French species are far removed from the British generotype. The type species would then remain the only formally described species of Strepula.

OCCURRENCE: Strepula occurs in the Middle Silurian of the Welsh Borderlands and W Midlands of England.

Strepula concentrica Jones & Holl, 1886

Pl. B3, figs. 1-13; Pl. B7, fig. 10.

1886a Strepula concentrica, sp. nov.; Jones & Holl, p. 404, pl. XIII, fig. 6, non fig. 1.

1886a Strepula irregularis, sp. nov.; Jones & Holl, p. 404, pl. XIII, figs. 7, 8.
1886a Strepula beyrichioides, sp. nov.; Jones & Holl, p. 405, pl. XIII, fig. 2, (non fig. 3).

1892 S. concentrica; Miller, p. 711.

1908 Strepula concentrica Jones & Holl; Ulrich & Bassler, p. 296, fig. 35.

1908 Strepula irregularis Jones & Holl; Ulrich & Bassler, p. 296, fig. 36.

1962 Strepula concentrica Jones & Holl 1886; Martinsson, p. 198, figs. 2E-F, 89A, 90, 92A-B.

1973 Strepula concentrica Jones & Holl, 1886; Siveter, p. 45; pl. 1:8:46, figs. 1-4; pl. 1:8:48, figs. 1, 2; pl. 1:8:50, figs. 1-3; pl. 1:8:52, figs. 1, 2.

LECTOTYPE: A tecnomorphic carapace, BM IN 52531 (Smith coll. no. 553); figured by Jones & Holl 1886a, pl. XIII, fig. 6. Lectotype selected by Martinsson 1962, p. 25 and figured p. 16, fig. 2F; figured herein Pl. B3, fig. 12.

For the designation of a lectotype of S. beyrichioides Jones & Holl, 1886 see "Discussion" below.

DISCUSSION OF SYNONYMY: Jones & Holl (1886a) erected three species in their new genus, S. concentrica, S. irregularis and S. beyrichioides. Without realising the significance of their figured material, they had in fact illustrated a male, a female and a small tecnomorph of one species (S. concentrica of this paper) under three separate names.

Martinsson (1962, p. 25) designated lectotypes for S. concentrica and S. irregularis (a female right valve, BM IN 52509, Smith coll. no. 115, from Lincoln Hill, Shropshire) and demonstrated that they are conspecific.

An examination by the present author of the two figured specimens (again, both from the Wenlock Limestone of Lincoln Hill) of S. beyrichioides...
revealed that they belong to two different genera. Specimen BM IN 52507 (Jones & Holl 1886a, pl. XIII, fig. 2) is a small left valve tecnomorph and is herein selected as the lectotype; specimen BM IN 52506 is a squashed tecnomorphic carapace of *Sleia pauperata* (Jones, 1869) (figured from the left side by Jones & Holl 1886a, pl. XIII, fig. 3). Based on the selected lectotype, *S. beyrichioides* is herein considered to be synonymous with *S. concentrica*. No advantage would be gained by selecting BM IN 52506 as the type-specimen.

**TYPE LOCALITY AND TYPE STRATUM:** Near Woolhope, Herefordshire; Wenlock Series.

The lectotype from the Smith collection is stated (Jones & Holl 1886a, p. 404) as coming from Woolhope and the label information accompanying the specimen agrees with this. Martinsson (1962, p.25) expressed doubt that this is correct as, "... the specimen was half buried in matrix of the Ironbridge type ...". Smith (1892, p. 148) in his paper summarising the localities and species of "English Upper Silurian Ostracoda" lists a number of localities in the Woolhope area but *Strepula concentrica* is recorded only from his locality 18. This locality is given as "Woolhope, Herefordshire (about a mile east from the inn on the Ledbury Road).... a very small opening in the Woolhope limestone, situated in a wood at a little distance from the road ...". Although the type provenance information has to be accepted, the horizon given is very probably wrong (the Woolhope Limestone outcrops to the north, south and west of Woolhope in the inlier) and the lectotype almost certainly comes from a higher horizon within the Wenlockian Series.

**DIAGNOSIS:** As for the genus.

**DESCRIPTION:** This species is one of the few British beyrichiacean ostracodes to have received a modern description and only a little additional information to that provided by Martinsson (1962, p. 198) is given here.
Text-fig. 6  SIZE VARIATION OF FEMALE SPECIMENS OF STREPULA CONCENTRICA

30 valves (left & right) from one sample (coll. Prof. A. Martinsson).
Harley Hill, N. Shropshire.
Externally the flange-like velum in tecnomorphs, can be seen to have radial tubulosity (cf. Martinsson 1962, p. 199). Moreover one specimen has been found which has its longest crista (from anterior cusp to posterodorsal part of the syllobium) broken; like the velum it is composed of radial tubules (in cross-section the elongate-ovoid shaped lumen are packed adjacent to each other along the length of the crista). Small tecnomorphs, half the size of adults, are observed to have an almost completely developed cristal system (only the very fine crista on the anterior margin of the syllobium is absent), but the reticulation is not so conspicuously present.

MEASUREMENTS: Hinge length - sulcal height (to base of crumina) in microns of female specimens.


DISCUSSION: One of the most important features shown by the Treposellinae is the tendency to incorporate parts of the syllobium within an antero-ventrally derived crumina. In "S." platyloba Weyant, 1965 and "S." roualti Weyant, 1965 not only is this trend lacking but their cruminae project quite markedly anterodorsally, assimilating parts of the anterior lobal complex as they do so. This difference alone (emphasized by Weyant 1965, p. 80) is a significant factor in the decision not to assign the French species to Strepula. Other reasons for the separation include noticeable differences in the number and position of the cristae (the French species lack some of the cristate lobes of S. concentrata and have many more ridges on the crumina), the general form of the cristal system, and differences in the patterns of reticulation. From the figures however, "S." platyloba seems to be congeneric with "S." roualti.

Elton Beds: Stretton Westwood (loc. 60).
Shadwell Rock Qy. (loc. 61).

Wenlock Limestone: Wren's Nest (locs. 27c, d, e, f).
Hurst Hill (loc. 28).
Hobbs Ridge (loc. 15b).
Little Hill (loc. 17d).
Gleedon Hill (loc. 50).
Harley Hill Qy. (loc. 51).
Coates Qy. (locs. 53a, b).
Lincoln Hill (locs. 49a, b, c).
Benthall Edge, West (loc. 47).
Presthope (loc. 58).
Audience Wood (loc. 57).
The Bank Qy. (loc. 56).
Much Wenlock, Windmill (loc. 54).
Much Wenlock (loc. 55).

Tickwood Beds: Harley Hill Road (locs. 48b, c).
Tickwood (locs. 44a, c, d).
Benthall Edge, East (loc. 43a).
Acklands Coppice (loc. 42a, b).

Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39).

Strepula? sp. nov. A
Pl. B7, figs. 1, 6, 7, 9.

REMARKS: This material possesses some of the basic features found in Strepula concentrica and may be congeneric with that species. As no female has yet been found, and in view of the fact that other cristate
treposelline genera occur in the British Wenlockian, its assignment to *Strepula* is treated with caution and its formal description is meanwhile deferred.

**DESCRIPTION:** Valves are preplete, and, in the smaller specimens, rather deep. In contrast to the elongate knob-like anterior lobe and the inflated dorsal region of the syllobium, the anterior lobe is flat and indistinctly developed. The syllobium attains maximum elevation and height just behind the posterodorsal margin of the adductorial sulcus, and - unlike the two other lobes - extends above the hinge line (mostly with the aid of its strongly developed crista).

The adductorial sulcus is narrow in smaller specimens and relatively wider in the larger valves; dorsally the sulcus widens somewhat above the preadductorial node, ventrally it is weakly curved around the base of this lobe. A not very wide connection below the adductorial sulcus links the syllobium to the anterior part of the shell. In the smaller valves the prenodal sulcus is discernible as a narrow, shallow depression hugging the anterior face of the preadductorial node; in the larger specimens examined this sulcus is effectively lost in a more complete fusion of the anterior lobe and preadductorial node.

The velum is quite wide. Short, faint tubules are observable along most of the ventral section of the velum. These tubules are seen when valves are viewed obliquely. Cristae occur on all the tecnomorphs examined. The most prominent crista begins above the hinge line on the crest of the syllobium; it then runs down the anterior part of the syllobium towards the base of the adductorial sulcus, where - particularly in the smaller valves - it appears to link up with the crista which travels across the top of the preadductorial node. Down the anterior lobe, at least in the small tecnomorphs, there is a weaker crista; in the larger tecnomorphs this ridge is much reduced or obsolete. All of the cristae reach the hinge line.
The lobal connection and each of the lobes are - in typical treposelline fashion - reticulate. The adductorial sulcus and velum are smooth.

**MEASUREMENTS:** Hinge length - sulcal height (including velar width) of the two figured tecnomorphs.

1120-750 (DAS 47352), 890-625 (DAS 47198) (microns).

**DISCUSSION:** A number of features ally this species more closer to *S. concentrica* than to any other taxon; they include the width of the velum and its faint tubulosity, the association of cristae and reticulation in late and early instars, and the general arrangement of the lobes and lobal connection. It differs from *S. concentrica* mainly in its reduced cristal system (especially the lack of a lateroventral crista) and in its shape. Until a female is known, the material is tentatively referred to *Strepula*.

**OCCURRENCE:** The Wenlock Series of the N Welsh Borderlands.

- **Wenlock Limestone:** Harley Hill Qy. (loc. 51).
  - Audience Wood (loc. 57).
- **Tickwood Beds:** Tickwood (loc. 44d).
  - Benthall Edge, East (43a).

The total material consists of nine specimens.

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**Genus **Garniella** Martinsson, 1962**

**TYPE SPECIES:** Original designation of Martinsson 1962, p. 199; *Garniella lineolata* Martinsson, 1962, p. 201, figs. 92C, D; from the Ludlovian (Hemse Beds) at Hammarudden, Gotland.
BRITISH SPECIES: Garniella concinna (Jones & Holl, 1886)
Garniella arthrodes sp. nov.
Garniella? sp. nov. A

DIAGNOSIS: Treposellinae with reticulate lobes and - in adult
specimens - cristae only on the crumina (modified after Martinsson,
1962, p. 219).

DISCUSSION: Garniella consists of a fairly compact group of treposellines
with only small differences between each species. It was erected in 1962
to contain the type species and the new taxa G. jugata, G. uniseriata,
G. biseriata, and G. strepuloides. G. concentrica from the Cobleskill
Limestone of Central New York was added later (Berdan, 1972).

Garniella like Strepula has cristae on the crumina. In all essential
respects the material herein referred to G. concinna has the characteristics
of the genus Garniella, yet this species has a system of cristal ridges on
its lobes (younger instars only) - a feature previously confined to
Strepula and used to distinguish it from Garniella. These genera are
obviously closely related to each other (cf. also the subcruminal
morphology of G. concentrica with the British Garniella species) but
it is still possible to retain them as discrete units using the arrange­
ment, complexity and ontogenetic development (or disappearance) of the
cristae.

There is perhaps another Garniella species in the British Wenlockian.
At the moment it is known from only two valves and is not dealt with in
detail here. The tecnomorph bears close resemblance to G. uniseriata.

OCCURRENCE: Not previously cited from Britain; exists in the Wenlockian
of the Welsh Borderlands and English West Midlands.

It has now been demonstrated that the genus is found in the Wenlockian
(Musksha Horizon) and Ludlovian (Malinovtsy Horizon) of Podolia (Abushik
1968, p. 309; 1971, p. 64). Prior to these records, all European occurr­
ences of Garniella were confined to a few localities in Wenlockian and
Ludlovian horizons on Gotland. *G. concentrica* represented the first non-European (American) occurrence of the genus.

**Garniella concinna** (Jones & Holl, 1886)

Pl. B4, figs. 1-14; Pl. B7, fig. 13.

1886 *Beyrichia concinna*, sp. nov.; Jones & Holl, p. 356, pl. XII, figs. 22a, b.

1892 *Beyrichia concinna* Jones & Holl; Smith, p. 149, table opposite p. 158.

1908 *Kloedenia concinna*; Ulrich & Bassler, p. 301.

1934 *Kloedenia concinna* (Jones & Holl); Bassler & Kellett, p. 361 (partim).

**REMARKS:** *Beyrichia concinna* was founded on the basis of a single tecnomorphic carapace from the Wenlock Series of Dormington, in the Woolhope inlier. This poorly preserved specimen (hinge length, 580 microns) represents a very small instar of a *Garniella* species which has cristae on its lobes.

A cristate (younger instars only) *Garniella* species has been collected in some quantity from the Wenlock Limestone of the Welsh Borderlands and English W Midlands. Of this material, the smallest specimens obtained (620 microns from the Wren's Nest; 610 microns from Benthall Edge) are essentially indistinguishable from the type specimen of *G. concinna*. All of this material is treated herein as one species; ideally, additional material is needed from Woolhope.

There are prominent morphological changes during the ontogeny of this species. The description below is based almost entirely on the material from the N Borderlands and W Midlands. The section describing the smallest instars is based on the holotype and the single valve (referred to above) from Wren's Nest.
HOLOTYPE: A small tecnomorphic carapace, BM I 2379 (Smith coll.); illustrated by Jones & Holl 1886, pl. XII, figs. 22 a, b; herein Pl. B4, fig. 6.

TYPE LOCALITY AND TYPE STRATUM: "Dormington Wood" according to Brit. Mus. (Nat. Hist.) records; about 3 km NNW of Woolhope, Herefordshire (Nat. Grid Ref. approx. SO 390600); Wenlock Limestone.

DIAGNOSIS: Garniella species with a cristal system of three ridges in the younger instars. Dorsal parts of the lobes are arched above the hinge line. Preadductorial node discernible but not prominent. There are two distinct and other diffuse cristae below an unornamented groove on the crumina.

DESCRIPTION: The more mature valves will be described first (see remarks above). The syllobium is evenly curved above the hinge line, reaching its maximum height just in front of syllobial mid-width; the dorsal part of the anterior lobe is profiled in a similar manner, though only just above the hinge line. The widest section of both lobes occurs on, or a little way above, valve mid-height; from this point (in tecnomorphs) the posterior margin of the syllobium swings gently forward into the cuspidal section or, ventrally, towards the fairly wide "neck" which connects anterior and posterior regions of the valve below the adductorial sulcus. The anterior lobe and preadductorial node are fused as one unit, though the node is always recognised by its higher elevation, its shape, and by the outline it gives to the anterior boundary of the adductorial sulcus. There is (in larger instars) no definable sulcus in front of the preadductorial node. This anterior lobal complex is quite wide, but never equal to the widest part of the syllobium.

The area of the lobal connection linking the syllobium with the anterior part of the shell normally contains three (more rarely four) rows of meshes. Along the most dorsal of these rows (immediately below
the adductorial sulcus) and projecting posteriorly for a small distance onto the syllobium, a shallow depression is variably developed (it is mostly present, never prominent, and sometimes obsolete). The presence of this groove is accentuated somewhat by the ridge which, in mature tecnomorphs, skirts the ventral end of the adductorial sulcus and becomes obsolete on reaching the preadductorial node. This zygal-like ridge forms part of a more extensive cristal system in younger tecnomorphs (see below). A tendency for a faint crista to develop, along the boundary between the rows of meshes below the groove, has been observed in some specimens. The adductorial sulcus in tecnomorphs extends about two-thirds of the way down the valve; in females it is a little shorter and narrower because of cruminal interference, and in both dimorphs it bends forward around the site of the preadductorial node.

Across part of the female syllobium, from a point opposite the ventral termination of the adductorial sulcus, there is a shallow, indistinct depression which can be traced in the reticulation. The syllobial reticulation continues with no recognisable pattern to the unornamented groove on the crumina; just below the adductorial sulcus this groove becomes poorly defined. Between the well developed crista marking the ventral margin of the groove, and the prominent ventral cruminal crista (which is affixed at both ends to the "treposelline bridges" and together with the velar ridge encloses a long, slender "panel" along the base of the crumina) there is a network of about four inconspicuous cristae. Each of these weak cristae stems from the crista at the base of the unornamented groove, curves forward, and coalesces with the ventral cruminal crista and / or the next crista in line, thus producing intercristal areas which are crudely "diamond-shaped".

Throughout its length the velum is thickened near its edge, and quite deeply concave. Very near its ventral edge in tecnomorphs, a faint toric structure can be traced. Both the posterior and - to a lesser degree - the anterior cardinal angles are obtuse. The velum is
interrupted and fused to the ends of the base of the crumina with typical "treposelline bridges". The adductorial sulcus, like the velum, is smooth. In all but the smallest instars coarse reticulation covers all parts of the lobes. The crumina below the unornamented groove lacks reticulation.

The earlier instars have three cristal ridges on their lobes, and both preadductorial node and the depression in front of it are more pronounced than in adult valves. The most prominent crista runs from the dorsal region of the syllobial cusp down the lobe and around the base of the adductorial sulcus, where it becomes confluent with a second crista which then continues dorsally, across the face of the preadducorial node. A third, generally weaker ridge trends down from the cuspidal part of the anterior lobe to join the other combined cristal unit below the adductorial sulcus. The extant material does not permit an objective assessment of exactly when these cristae are lost during ontogeny, but certainly remnants of the cristal system have been observed in quite large tecnomorphs.

In the smallest instars observed (see "Remarks" above) the crista on the preadductorial node extends to the hinge line, very close to the ridge on the anterior lobe. Moreover, there is only a single (vertical) row of meshes on the anterior lobe, in front of an unornamented prenodal sulcus. Reticulation is also reduced from other parts of the lobes, particularly the posterior part of the syllobium. The preadductorial node is reticulate and well developed.

MEASUREMENTS: Hinge length - sulcal height (including cruminal width) in microns of females from the Wenlock Limestone.

1015-750 (Harley Hill), 1145-880 (Wren's Nest).

DISCUSSION: Neither the text or figures of the five ("rare" / "very rare") Garniella species erected by Martinsson give any indication of the presence of a cristal system in tecnomorphs. The occurrence of such
cristae in the earlier growth stages of *G. concinna* is its most distinguishing character and is almost unique for the genus (*G. concentrica* has a vague crista below the adductorial sulcus). There are other minor differences which aid separation of the more mature valves from the closely similar Gotland species, *G. uniseriata* and *G. strepuloides*. It differs from the former by the nature of the cristae on the crumina, in having a narrower velum, and in lacking a distinct single row of meshes on the crumina; *G. strepuloides* is discriminated on its cruminal ornament which consists of posteroventral reticulation and "only a comparatively slight differentiation of cristae" (Martinsson 1962, p. 204). Compared to the other British *Garniella* taxon (*G. arthrodes*) established herein, *G. concinna* has a different overall shape and lobal proportions, higher cuspidal regions, and a narrower, more concave velum.

The lobal cristae of this species illustrates the close relationship between *Garniella* and *Strepula* (see generic discussion).

**OCCURRENCE:** The Welsh Borderlands and inliers of the English W Midlands; Wenlock Series.

**Wenlock Limestone:** Dormington Wood (type locality).

Wren's Nest (locs. 27c, d, f).

Lincoln Hill (loc. 49b).

Benthall Edge, West (loc. 47).

Hurst Hill (loc. 28).

Whitman's Hill (loc. 19a).

Croft Farm (loc. 18).

**Tickwood Beds:** Harley Hill Road (loc. 48c).
Garniella arthrodes sp. nov.
Pl. B5, figs. 1-12, 14.

1886a Primitia seminulum, Jones; Jones & Holl, p. 413, pl. XIV, figs. 14a-c.

DERIVATION OF THE NAME: From the Greek, *arthrodes*, well-knit; referring to the fusion of the anterior lobe and the preadductorial node.

HOLOTYPE: A female right valve, DAS 47150; Pl. B5, fig. 1.

TYPE LOCALITY AND TYPE STRATUM: From the crest of the exposed ridge on the W side of the Wren's Nest, Dudley, Worcestershire (loc. 27c); Nodular Beds (of Butler 1939), Wenlock Limestone.

DIAGNOSIS: Garniella species with a broad, entirely fused, anterior lobar structure, and two distinct and other minor cristae on the crumina. Reticulation covers all the broad syllobium and terminates abruptly along a line across the dorsal part of the crumina. Dorsal parts of lobes broad and flat along the hinge line. Adductorial sulcus comparatively short; in the tecnomorphs the area below this sulcus is wide.

DESCRIPTION: The dorsal parts of the lobes are wide, almost straight, and terminate along the hinge line. The preadductorial node is virtually obsolete; its position is indicated merely by the outline of the anterior margin of the adductorial sulcus and, perhaps, by a faint rise in elevation. There is no trace of a depression separating this central, posterior part of the anterior lobar structure from the anterior section of the complex. The syllobium gradually narrows and swings forward from its widest section about the hinge line, to its ventral confluence with the crumina in females or with the area of lobar connection in tecnomorphs. This latter area, joining - without interruption - the syllobium to the fused anterior complex, is relatively wide and normally contains three (or four) rows of quite coarse meshes. The widest part of the anterior
complex occurs at mid-height. The anterior lobal complex lies at a slightly lower elevation than the syllobium.

In both dimorphs the adductorial sulcus bends forward in its ventral and dorsal regions. The ventral closure of this sulcus is gently rounded in tecnomorphs; it is noticeably more constricted and appears to be slightly higher in females. The sulcus is not too deep and is of constant depth throughout its length (to just below mid-height in tecnomorphs).

In tecnomorphs the rather wide velum is of constant width; in females the velum narrows slightly as it approaches the crumina. Characteristically, the anterior cardinal corner is obtuse and is complemented by an acute posterior cardinal angle. Radial streaks, indicating tubulosity, can be detected in some tecnomorphs (particularly small instars) when valves are viewed obliquely. In both dimorphs the velum is gently concave, becoming thickened near its edge.

The ventral extent of the crumina is marked by two "treposelline bridges", where the otherwise continuous velar ridge is tenuously attached to the crumina. In lateral view these points of fusion occur below the mid-length of the anterior lobal complex and below the mid-length (or just behind the mid-length) of the syllobium. Syllobial ornament ends along a line across the dorsal part of the crumina. Below this line, again across the face of the crumina, there is a narrow, unornamented groove (less well defined anteroventrally) which is bounded ventrally by a long fairly continuous crista. Between this crista and the substantially developed ventral crista (which together with the velar ridge below it, forms a long slit-like panel in ventral view) the crumina lacks reticulation but is ornamented with 2-3 short, indistinct cristae. The latter tend to branch off and run vaguely parallel with the dorsal crista, often coalescing towards the anteroventral point of origin of the crumina.
The adductorial sulcus and velum are smooth. All of the anterior lobal complex and the syllobium have quite coarse reticulation. On the syllobium, in a line roughly opposite the ventral extremity of the adductorial sulcus, there is a tendency in a few females for a very faint depression to develop and for the reticulation to be less conspicuous (though it is never absent). Minute tubercle-like processes form the marginal structures along each valve.

MEASUREMENTS: Hinge length - sulcal height (including cruminal width) in microns of female specimens from the Wenlock Limestone.

Wren's Nest (loc. 27c): 1660-1020 (holotype).

Audience Wood (loc. 57): 1310-820, 1300-770.

DISCUSSION: The length of the crumina between the "treposelline bridges" tends to vary. In the holotype this distance is quite short, compared with the same feature in specimens from Audience Wood. Many of the features of G. arthrodes can be found in the various Gamiella taxa from Gotland. The species closely resembles G. strepuloides from the Hemse Beds, most noticeably in the occurrence of a broad, completely integrated anterior lobal complex, a wide area of lobal connection below the adductorial sulcus in tecnomorphs, and in its general syllobial morphology. G. arthrodes is separated from G. strepuloides by the more postively differentiated cristal ridges and lack of reticulation (posteroventrally) on its crumina, and by its slightly shorter, narrower adductorial sulcus in females.

Jones & Holl (1886a) figured two tecnomorphic carapaces (Smith coll. no. 54 from Woolhope) of this species under the name Primitia seminulum; they are, BM I 2404 (op. cit., pl. XIV, figs. 14a, b) and BM IN 52527 (op. cit., pl. XIV, fig. 14c).
OCCURRENCE: Welsh Borderlands and the English W Midlands; Wenlockian.

Wenlock Limestone:
- Wren's Nest (locs. 27c, d, f).
- Hurst Hill (loc. 28).
- Lincoln Hill (locs. 49b, c).
- Harley Hill Qy. (loc. 51).
- Gleedon Hill (loc. 50).
- Benthall Edge, West (loc. 47).
- Little Hill (loc. 17d).
- Audience Wood (loc. 57).
- ? Presthope (loc. 58); only one broken tecnomorph.

Tickwood Beds: Tickwood (loc. 44d).

Garniella? sp. nov. A
Pl. B7, figs. 2-5, 8.

REMARKS: The extant material consists of a broken, fragmentary female valve and 1-2 immature tecnomorphs, all from the same locality. These specimens most probably represent another (undescribed) Garniella species. It seems best to defer its formal treatment until additional material has been collected. The female and the best tecnomorph are figured.

DESCRIPTION: The anterior lobal complex is flat and slightly narrower than the syllobium. The preadductorial node cannot be recognised; it is totally fused to the anterior lobe. The area below the adductorial sulcus in tecnomorphs, joining anterior and posterior parts of the valve, is quite wide (containing about three rows of meshes). A narrow depression (quite deep in the female; hardly developed in the smaller, figured tecnomorph) extends onto the syllobium from beneath the adductorial sulcus. As far as can be determined, the lobal areas do not extend above the hinge line. The adductorial sulcus is almost straight, consistently narrow and shallows slightly at its dorsal end.
In the female below the groove on the syllobium, there is a narrow zone of reticulation, which is bordered ventrally by a smooth groove; the latter extends across the length of the crumina. Unfortunately the remainder of the crumina is missing. The tecnomorphic velum is medium-wide, and gently concave.

The lobes are evenly covered with relatively fine reticulation. The velum, and adductorial sulcus are smooth. Along the shallow syllobial depression, ornamentation is mostly effaced.

MEASUREMENTS: Hinge length - sulcal height in microns of the two figured specimens.

Female (DAS 47038): 1300-1000 (hinge length estimated).

Tecnomorph (DAS 47153): 1010-720 (includes velar width).

DISCUSSION: The form (especially width) of the adductorial sulcus and the size of the meshes in the reticulation, effectively separate this material from all other described Gamiella species. The occurrence of cristae on the female crumina has yet to be confirmed.

OCCURRENCE: Only from the Wren's Nest inlier, Worcestershire.

Wenlock Limestone: Wren's Nest (locs. 27c, f).

Genus RETISACCLUS Martinsson, 1962

TYPE SPECIES: Original designation of Martinsson 1962, p. 204; Retisacculus commatatus Martinsson, 1962, p. 206, fig. 95A; from the Eke Beds (Ludlovian) at Lau Backar, Gotland.

BRITISH SPECIES: Retisacculus sp. nov. A

DIAGNOSIS: Treposellinae with reticulation over the whole carapace, including the crumina; crista absent. Smooth, narrow velar flange. Prenodal sulcus completely obsolete, adductorial sulcus may be constricted. (Modified after Martinsson 1962, p. 205).
DISCUSSION: There are three established species in the genus - the type species and *R. semicolonatus* Martinsson, 1962, both erected on Gotland material, and *R. sulcatus* Gailite, 1967 from the E Baltic. These species are differentiated on ornamental details and the morphology of the adductorial sulcus. *Retisacculus* is distinguished from *Garniella* by its lack of cristae and by the complete coverage of reticulation on the crumina. The entirely reticulate crumina is also the main feature which separates *Retisacculus* from *Bolbiprimitia*.

OCCURRENCE: In Britain from the Wenlock Series (Wenlock Limestone). All records outside Britain are confined to Gotland (upper parts of the Ludlovian), Latvia (upper part of the Ludlovian) and Estonia (high Whitcliffian - Downtonian).

*Retisacculus* sp. nov. A
Pl. B5, figs. 13, 15-17.

REMARKS: This species is known from only one female specimen from the Wren's Nest Dudley. Tecnomorphs of this species can be expected to closely resemble small instars of *Garniella arthrodes*, but with a more obtuse posterior cardinal angle and, perhaps with some form of constriction to the adductorial sulcus. As yet, no *Retisacculus* tecnomorph has been identified within the many small treposelline valves collected from Wren's Nest. The species is not raised until additional material becomes available.

DESCRIPTION: Preadductorial node almost entirely assimilated within the anterior lobal complex; it rises very slightly above the level of the anterior lobe. The prenodal sulcus is obsolete. The anterior lobal structure is not much narrower than the syllobium. Both pre- and postadductorial lobal areas terminate (without projections) along the hinge line. The syllobium is widest along the hinge line and narrows
considerably only below valve mid-height, where it is completely confluent with the crumina. The widest part of the anterior lobal complex occurs at mid-height. The adductorial sulcus is rather narrow, shallow and apparently lacks constrictions (the specimen is unfortunately broken along the line of the sulcus); ventrally, the sulcus is evenly curved, dorsally, it breaks through to the hinge line.

The velum is weakly concave, about twice as wide as the adductorial sulcus, and fused to the crumina by small "treposelline bridges" antero-ventrally and posteroventrally. A ridge along the base of the crumina links the anterior and posterior sections of the velum. The crumina is set off from the valve surface only along its margin with the lower part of the adductorial sulcus.

All lobal elements and the entire crumina above the basal ridge are coarsely reticulate; the meshes are consistently large. The velum is smooth.

MATERIAL: One female right valve (DAS 47037).

MEASUREMENT: Hinge length - sulcal height (to the ventral border of the crumina; lateral view).

950-630 (in microns).

DISCUSSION: Differs from *R. commatatus* by its larger adductorial sulcus and by having the meshes in its reticulation pattern of uniform size. It lacks the mid-length constriction of the adductorial sulcus found in *R. semicolonatus*. The British specimen is very much like *R. sulcatus*, a species established from the upper part of the Pagegiai Beds (= top of the Ludlovian) of Latvia, and subsequently found in Estonia (Sarv 1968; Kaljo 1970) and Ohesaare (Sarv 1971) at similar and somewhat higher horizons. The adductorial sulcus in the British female is, however, not so positively demarcated or incised as in the Baltic species.

The single known British valve is considerably older than the records of the genus from Gotland and the E Baltic area.
OCCURRENCE: From the inlier at Wren's Nest, near Dudley, Worcestershire.

Wenlock Limestone: Wren's Nest (loc. 27c).

Genus BOLBIPRIMITIA Kay, 1940

TYPE SPECIES: Original designation of Kay 1940, p. 234; Halliella fissurella Ulrich & Bassler, 1923, p. 514, pl. XXXVII, figs. 22, 23; from the Tonoloway Limestone (Upper part), Keyser, West Virginia, U.S.A.

BRITISH SPECIES: Bolbiprimitia juvenicristata sp. nov.

DIAGNOSIS: Treposellinae with a flattened, reticulate anterior lobal complex, a flattened, reticulate syllobium, and with a connection between these elements below the adductorial sulcus. The preadductorial node forms a small bulge in the anterior margin of the sulcus. Crumina mostly smooth, without cristae. Reticulation typically effaced near the anterior cardinal corner. (Modified from Martinsson 1962, p.207).

DISCUSSION: The history of the genus was outlined in some detail by Martinsson (1956, pp. 23, 24) when he described the Gotland species Primitia inaequalis Jones, 1888 and assigned it to Bolbiprimitia. In a later paper Martinsson (1962, p. 207) included both P. inaequalis and his new species Bolbiprimitia falculata provisionally within the genus because although - as he correctly states - lateral views of these species invite very close comparison with the generotype (Bolbiprimitia fissurella) the subcruminal morphology of the type species has yet to be investigated and confirmed as being the same as that found in the Gotland species. Undoubtedly the British species is congeneric with the two Gotland taxa and following Martinsson they are all provisionally assigned to Bolbiprimitia (pending a revision of the type species).
From published material (Sarv 1962, pl. VIII, figs. 3-7; Sarv 1968, pl. V, figs. 1, 2) it is not certain that Bolbiprimitia tamsaluensis Sarv belongs to that genus; no complete female valve, or a view of its ventral morphology, has been figured. As commented on by Martinsson (1962, p.190) the American taxa Bolbiprimitia limbata Swartz & Whitmore, 1956 and Bolbiprimitia teresaccula Swartz & Whitmore, 1956, although close to Bolbiprimitia, more correctly should be considered the basis of a new genus; they differ from the British and Baltic species of Bolbiprimitia especially in the morphology of the adductoral sulcus.

OCCURRENCE: The British member of the genus exists in the northern Welsh Borderlands in deposits of Wenlockian age.

The genus is also known from the Wenlock of Gotland and Estonia. B. tamsaluensis is found in the lowest Llandovery rocks of Estonia.

The type stratum for B. fissurella - the Tonoloway Limestone of West Virginia - is probably of Pridoli age (Berry & Boucot 1971, p. 230).

Bolbiprimitia juvenicristata sp. nov.

Pl. B6, figs. 1-11.

DERIVATION OF THE NAME: From the Latin juvenis, young and cristata, crested; referring to the crista found in the young tecnomorphs.

HOLOTYPE: A female right valve, DAS 47168; Pl. B6, figs. 4, 5, 7.

TYPE LOCALITY AND TYPE STRATUM: The cutting (just S of the old railway bridge) on the E side of the road (W side of Tick Wood) from Wyke to Lawleys Cross, about 3 km N of Much Wenlock, Shropshire (loc. 44d); Wenlock Shale (Tickwood Beds).

DIAGNOSIS: A species of Bolbiprimitia with a comparatively wide velum which is faintly tubulous in tecnomorphs. Between the long adductorial sulcus and the velum below, there are about two meshes in the reticulation.
All lobes terminate abruptly at the hinge line. A crista can be traced in small tecnomorphs.

DESCRIPTION: Valves, even in females, are only slightly preplete in outline. Lobation is reduced, but all the main elements can be recognised. The fairly wide anterior lobal complex consists of a pear-shaped pre-adductorial node which is fused almost completely with the flat anterior lobe. A prenodal sulcus as such, is absent - the greater height and distinctive shape of the preadductorial node serves to differentiate this feature from the anterior lobe. Below mid-height the syllobium narrows fairly quickly but in its dorsal regions it is quite broad, its greatest width occurring just above mid-height. In tecnomorphs the syllobium is joined to the anterior part of the valve in the moderately wide area below the adductorial sulcus. Like the anterior lobal complex, the syllobium has a dorsal margin which is straight and which does not appear above the hinge line. The conspicuous adductorial sulcus, just in front of mid-length, extends for about two-thirds of valve height. This sulcus is fairly wide and deep and, especially in females, is curved forward in its ventral regions. The outline of the anterior margin of the adductorial sulcus betray the presence of the preadductorional node. The anterior lobal complex lies below the level of the syllobium. Gradually increasing in elevation away from its dorsal margin, the syllobium reaches maximum inflation around mid-height in tecnomorphs and in the more ventral, cruminal part of the valve in females.

The comparatively wide velum is of constant width. In lateral view the female velum appears confined to the anterior and posterior margins of the valve, but ventrally it is seen to be continuous along almost all the length of the crumina. Only the very fine "treposelline bridges" (sited at each end of the crumina) prevent the existence of a continuous velar edge from posterior to anterior corners of the valve. From a point immediately below the anterior lobe, the crumina extends
posteriorly, attenuating the lowermost parts of the adductorial sulcus and absorbing a large, ventral section of the syllobium. In lateral view the crumina does not interfere with the ventral outline of the valve. Many of the better preserved tecnomorphic specimens show externally visible tubules (especially ventrally) along the velum. Marginal structures on each valve seem to consist of a single row of closely spaced, tiny tubercles.

The reticulation, which is not particularly fine, covers all of the lobate area (except anterodorsally on the anterior lobe) quite evenly; both the velum and the adductor sulcus are smooth. The crumina is smooth and the reticulation of the female syllobium begins opposite the ventral margin of the adductorial sulcus. Across the syllobium, from adductor sulcus to the velum, there are about seven meshes in the reticulate network. Across the anterior lobal complex there are about five meshes, and in the area connecting posterior and anterior parts of the tecnomorphic valve there are two rows of meshes.

Small instars are observed to have an indistinct crista which begins near the dorsal margin of the syllobium close to the adductorial sulcus, trends down the syllobium, around the ventral margin of the main sulcus, and then across the preadductorial node. The crista travels along the side of each mesh it encounters. Adults do not show any remains of a cristal system.

**MEASUREMENTS:** Hinge length - sulcal height (to base of crumina) in microns of female specimens from the type locality.

1100-785, 940-680, 870-660.

**DISCUSSION:** Prof. A. Martinsson has indicated (personal communication) that *B. inaequalis* and *B. falculata*, both from the Wenlock of Gotland, may be conspecific. Additional material has proved to be intermediate in size and morphology between the two species. Indeed when Martinsson
erected *B. falciculata* he stated in remarks (1962, p. 210) that some of the features (such as the number of meshes in the reticulation pattern) which distinguish this species from *B. inaequalis*, "could be functions of... size". Considering this, and the fact that the generic assignment of *Bolbiprimitia tamsaluensis* has not yet - in my opinion - been adequately proven, the known species of the genus are few in number.

*B. juvenicristata* resembles the Gotland forms mentioned above but differs in the following respects. It has a wider more tubulous velum, a narrower area (with fewer reticulate meshes) joining the syllobium to the anterior lobal complex beneath the adductorial sulcus, and dorsal margins to its lobes which are not ridge-like and which do not protrude above the hinge line. From the figures of *B. inaequalis* (Martinsson 1956, pl. III, figs. 16-19) it is apparent that its early instars do not have any cristae. The size and distribution of the reticulation takes the same form in the British and Baltic species, moreover all these *Bolbiprimitia* taxa have exactly the same small area (anterodorsally on the anterior lobe) where the reticulation is completely effaced (see Martinsson 1962, figs. 96A-B (*B. inaequalis*), fig. 96G (*B. falciculata*) and herein Pl. B6 , figs. 1, 3).

The type species (from considerably younger deposits in the United States) requires modern revision and illustration, though it can be distinguished from the European species in having a greater part of the lateral surface of its crumina covered by reticulation, a narrower adductorial sulcus and a less prominent preadductorial node (see Ulrich & Bassler, 1923, pl. XXXVII, figs. 22, 23).

**OCCURRENCE:** Wenlock Series of the N Welsh Borderlands.

*Wenlock Limestone:* Harley Hill Qy. (loc. 51).
Gleedon Hill (loc. 50).
Lincoln Hill (loc. 49b).
Audience Wood (loc. 57).
Much Wenlock, Windmill (loc. 54); two poorly preserved tecnomorphs.

Tickwood Beds:

- Harley Hill Road (loc. 48c).
- Tickwood (locs. 44b, d).
- Benthall Edge, East (loc. 43a).

**TREPOSELLINAE INCERTI GENERIS**

*"Bollia" uniflexa* Jones & Holl, 1886

Pl. B7, figs. 12, 14.

1886 *Bollia uniflexa*, sp. nov.; Jones & Holl, p. 361, pl. XII, figs. 17a, b.

1892 *B. uniflexa*; Miller, p. 706.

1923 *Bollia uniflexa* Jones & Holl; Ulrich & Bassler, p. 301.

1934 *Bollia uniflexa* Jones & Holl; Bassler & Kellett, pp. 17, 220.

1948 *B. uniflexa* Jones & Holl; Warthin, p. 646.

1953 *B. uniflexa* Jones & Holl, 1886; Henningsmoen, p. 233.

1968 *B. uniflexa*; Guber, p. 360.

**HOLOTYPE:** A tecnomorphic carapace, BM I 1945 (= Vine coll. no. XXXVIII), figured by Jones & Holl 1886, pl. XII, figs. 17a, b; herein Pl. B7, figs. 12, 14.

**TYPE LOCALITY AND TYPE STRATUM:** From a locality in the vicinity of Tickwood (3 km N of Much Wenlock), Shropshire; Wenlock Shale (Tickwood Beds).

The type and only specimen was picked by G.R. Vine from the washings of G. Maw's box no. 25. Notes on the localities of this and other boxes were sent to Vine by Maw and were subsequently published (Vine 1887). The material in box no. 42 was said to be from, "... the roadside at
Tickwood, between Buildwas and Wenlock" and that of box no. 25 from, "... strata similarly described" (Vine 1887, p.230). There is no firm evidence that the locality of J. Young's washing no. 25* - material supplied to him by Maw and quoted (Maw's description) by Vine (1887, footnote, p. 230) to be from "Tickwood Beds, Wenlock series; Shale from east end of Benthal Edge, opposite Ironbridge, Shropshire" - is the same as the type locality. Vine states that, "... I have no doubt that ..." Young's, "... no. 25* may have been obtained from a similar locality or horizon" to Maw's box no. 25.

DIAGNOSIS: A treposelline with a deep narrow carapace. The slender syllobium is linked by a U-shaped connection (below a prominent adductorial sulcus) to a narrow anterior lobal complex. Fine reticulation extends to most other regions of the valve surface from the lobes.

DESCRIPTION: The hinge line is straight and relatively short; the carapace is deep, narrow and preplete. All lobes are slender and the lobal area fails to occupy large parts of the valve surface.

The adductorial sulcus is always quite wide and deep but narrows ventrally to its base just below valve mid-height. A stout, U-shaped lobal connection (which is unlike a zygal arch) joins the slender syllobium directly to the anterior lobal complex. At its widest point this lobal complex is as broad and as high as the syllobium; both lobal features project above the hinge line with well developed, somewhat sharply rounded cusps. The anterior margin of the syllobium is straight; its posterior margin is a gently curved continuation of the dorsal cusp. The presence of the preadductorial node is indicated only by a slight bend in the outline of the anterior margin of the adductorial sulcus; the node is otherwise fused completely with the anterior lobe without a trace of a prenodal sulcus.
The velum is not particularly wide, although adjacent, non-lobal, parts of the valve falsely (in lateral view) increase its width. Very close to, and almost inseparable from the ventral edge of the velum there is a toric structure. The velar edge extends all around the free margin. Velar tubules are not visible and traces of an anteroventral depression are hardly, if at all, suggested.

The distribution of ornament is notably unusual and distinctive. The adductorial sulcus is smooth but the fine lobar reticulation (most easily seen when the valve is immersed in water) extends to all other non-lobal and velar regions of the valve.

MEASUREMENTS: Hinge length - sulcal height (velum included) of the single extant specimen.

1115-880 (in microns).

DISCUSSION: In earlier literature "Bollia" uniflexa Jones & Holl, 1886 was not widely acknowledged as the type species of the genus Bollia Jones & Holl, 1886. Although "B." uniflexa was chosen as type species in 1892 (Miller, p. 706) the concept of the genus has developed around the other "new" species, Bollia bicollina Jones & Holl, 1886 (Bassler & Kellett 1923, pp. 17, 215, first cited "B." uniflexa then B. bicollina as type species). Guber (1968) recognised these facts and after examining the type material of "B." uniflexa he concluded that it was a beyrichiacean ostracode. In a recommendation to the International Commission on Zoological Nomenclature (I.C.Z.N.) he argued that the concept of the family Bolliidae Boucek, 1936 (Drepanellacea Ulrich & Bassler, 1923) and the taxonomy of the Beyrichiacea would suffer large (and unnecessary) upheaval if "B." uniflexa remained the type species of a genus which would then have to be transferred to the latter superfamily. His recommendation, "to set aside all designations of type species for ... Bollia Jones & Holl, 1886 and ... designate B. bicollina Jones & Holl, 1886 to be the type species" was subsequently adopted in Opinion 934.
In spite of attempts by the writer and other authors (see Guber 1968, p. 362) to collect more material of "B. uniflexa" the extant material consists merely of the type specimen. I agree with Guber that this species is a beyrichiacean ostracode but, without a female valve, it is hardly possible to decide conclusively its localised taxonomic position. As Guber points out (1968, p.361) it displays features which are found in both the Amphitoxotidinae and the Treposellinae. In its valve shape (rather deep), the presence of a toric structure, the form of the syllobium and the strongly developed adductorial sulcus it is not close to many treposellines, but more similar to several amphitoxotidines. Like members of both subfamilies it is reticulate (in treposellines, however, the meshes are often quite coarse). Although treposelline lobes are often rather broad and tend to fill out the surface of the valve, the slender lobal arrangements (especially the form of the anterior lobal complex) in "B. uniflexa" do invite close comparisons with tecnomorphs of the treposelline, Garniella lineolata. This particular form of fused preadductorial node - anterior lobe (with a direct - often slender - link to the syllobium) occurs frequently in the Treposellinae, but, to my knowledge, is unknown amongst amphitoxotidines. A conspicuous anteroventral depression is absent, and the velum is not particularly wide and lacks externally visible tubules; these are other aspects which, arguable, ally "B. uniflexa" closer to the Treposellinae than to the Amphitoxotidinae. Pending the collection of a female specimen I provisionally refer this species to the subfamily Treposellinae. For the same reason its assignment to a genus is deferred, although its unusual morphology and unique ornamentation pattern may prove best expressed as a new genus.

The two specimens from the Buildwas Beds ("no. 22") of Harley, Vine coll. no. LXII2 (BM I 1969), referred to in a list of Errata (Jones...
1887b, pp. 414, 415) as extra material of "B." uniflexa are not beyrichiaceans and do, in fact, belong to Bollia s.s.

OCCURRENCE: The Wenlockian (Tickwood Beds) of the type locality.

"Beyrichia" seminulum Jones, 1855

Pl. B7, fig. 11.

1855a Beyrichia seminulum nov. sp.; Jones, p. 173, pl. VI, fig. 24.

1865 Primitia Seminulum, Jones; Jones & Holl, p. 418.

1869 Primitia seminulum, Jones; Jones, p. 13, fig. V.

non 1886a Primitia seminulum, Jones; Jones & Holl, p. 413, pl. XIV, figs. 14a-c.

non 1887 Primitia seminulum, Jones, var.; Jones, p. 5, nomen nudum.

non 1888 Primitia seminulum, Jones; Jones, p. 406, pl. XXII, figs. 17a, b.

1934 Halliella seminulum (Jones); Bassler & Kellett, pp. 206, 323 (partim).

LECTOTYPE: A mould of a left valve tectomorph, BM I 6367; Pl. B7, fig. 11. Figured by Jones 1855a, pl. VI, fig. 24. On the slide the internal and external moulds of the type specimen, both bearing the same catalogue number, are labelled "Co-types". This figured specimen was chosen as lectotype by Henningsmoen (1954, p. 57).

TYPE LOCALITY AND TYPE STRATUM: Given by Jones (1855a, p. 173) as Wenlock schists of the Town Hill, Montgomery.

DESCRIPTION: This description is based on a cast of the external mould of the type specimen in which the posterior and anterior extremities are missing.
Valve outline almost symmetrical. Sylobium slightly broader than the anterior lobal complex. The relatively wide, but shallow, adductorial sulcus dissects the valve for about two-thirds of its height. No differentiation of a preadductorial node can be detected within the anterior lobal complex, (though this may be due, in part, to aspects of preservation). Behind and in front of the adductorial sulcus, the valve surfaces are fairly flat and are of equal elevation. All lobes appear to reach the hinge line. The velum is smooth and approximately the same width as the adductorial sulcus. The sylobium and the anterior lobal complex are reticulate, with the connection between the two having about 3-4 meshes from the velum to the ventral part of the adductorial sulcus.

DISCUSSION: Ulrich & Bassler (1923, p. 524) and Bassler & Kellett (1934, pp. 206, 323) allied "Beyrichia" seminulum to Halliella. Henningsmoen (1954, p. 57, pl. 6, fig. 12; pl. 8, fig. 24) described a Norwegian treposelline as Halliella? seminulum (Jones, 1855). Martinsson (1956, p. 25) inferred that the British material could be a Bolbiprimitia species, and from its lobation and ornamentation there is little doubt that it is a treposelline species. However, such is the nature of the existing material that in my opinion it is not possible to describe the taxon adequately nor indeed assign it with certainty to a particular genus. The type specimen has a morphology which is most easily referred to tecnomorphs of Bolbiprimitia or Garsiella, but unless further work reveals more topotype material it may be necessary to declare "Beyrichia" seminulum a nomen dubium.

OCCURRENCE: Known only from the type locality. The poorly preserved lectotype is the only extant specimen.
BRITISH AMPHITOXOTIDINAE

REMARKS: The Amphitoxotidinae from Britain are considerably diverse in all aspects of morphology, and hold importance in constituting a large proportion of its beyrichiacean fauna. A significant amphitoxotidine element is now established in the British Wenlock and Ludlow Series - this, in contrast to the mostly post-Wenlockian occurrence of the subfamily on Gotland and elsewhere in Europe.

Comparatively primitive amphitoxotidine features, involving disturbances and deflections of the velar edge, can be traced in the subcruminal morphology of many of the early British forms such as Tinotoxotis gen. nov., Undipila gen. nov., and Nudista gen. nov. The genera Equicastanea gen. nov., Aetholicotoxotis gen. nov., Sarmatotoxotis gen. nov., and Tinotoxotis are now to be listed with Sleia Martinsson, 1962 as amphitoxotidines possessing tuberculation - in most cases combined with reticulation. Both Sleia and Tribotoxotis gen. nov. have - rarely for the subfamily, but as with most Beyrichiinae - a syllobial groove.

Tropidotoxotis gen. nov. and Charitoxotis gen. nov. belong with the group of genera embracing Dibolbina Ulrich & Bassler, 1923 and Berolinella Martinsson, 1962. A denticulate border crest is known in Zorotoxotis gen. nov., Lophoctenella Martinsson, 1962, Osmotoxotis gen. nov., and Sarmatotoxotis gen. nov. In the latter three genera a prominent precruminal velar constriction is also developed. Of particular interest is the incipient lobulation of the anterior lobe in some British Sleia species.

The many and varied forms of velar morphology and lobation shown by British amphitoxotidines are equalled by an associated galaxy of subcruminal morphologies. Rather atypical is the
development in *Gongylostonyx* gen. nov. of a flange-like velum.
and - as in *Sleia* - a calcarine spine.

SYSTEMATIC PALAEONTOLOGY

Subfamily AMPHITOXOTIDINAE Martinsson, 1962

**TYPE GENUS:** *Amphitoxotis* Martinsson, 1962, p. 229; from the Ludlovian of Gotland.

**BRITISH GENERA:** *Sleia* Martinsson, 1962

- *Equicastanea* gen. nov.
- *Tinotoxotis* gen. nov.
- *Nudista* gen. nov.
- *Undipila* gen. nov.
- *Aetholicotoxotis* gen. nov.
- *Osmotoxotis* gen. nov.
- *Sarmatotoxotis* gen. nov.
- *Hensiella* Martinsson, 1962
- *Zorotoxotis* gen. nov.
- *Huttoniella* Shaw, 1971
- *Tribotoxotis* gen. nov.
- *Tropidotoxotis* gen. nov.
- *Charitoxotis* gen. nov.
- *Atterdagia* Martinsson, 1962
- *Gongylostonyx* gen. nov.
DIAGNOSIS: Craspedobolbinidae in which the closing procedure in the dolonoid stage of the cruminal metamorphosis was much reduced or absent. Traces of the ancestral dolonoid flap, if present at all, are deflections or constrictions of the velar edge on the distal part of the crumina, and the closing of a dolonoid pouch never occurred; the tubulous velum was invaded and inflated more or less directly into the crumina. (After Martinsson 1962, p. 214).

DISCUSSION: Many of the genera proposed herein are based on single species. The question of monotypy in the Amphitoxotidinae is a problem not confined to Britain. In his taxonomic treatment of the Gotland fauna, Martinsson maintained (1962, pp. 214-6) that the combination of a stable lobal and subcruminal pattern - found in groups regarded as genera in other beyrichiacean subfamilies - was not apparent in the Amphitoxotidinae where, "Most of the species ... are so different in both lobation and cruminal morphology that it is impossible to associate one of this species more closely with any particular species than with others." The material from Britain again demonstrates this pattern and re-affirms Martinsson's decision to "split", rathern than "lump", amphitoxotidines at the generic level.

The considerable variation of lobal, cruminal and velar morphology within the subfamily has been comprehensively outlined by Kesling (1969, pp. 287-291).

OCURRENCE: In Britain ranging from the Wenlock Series into the Downtonian. Known mostly from the Welsh Borderland; so far, not recorded from Scotland or Ireland.

Found in the Silurian of Australia (Öpik 1953), N and S America, and Europe.
Genus *Sleia* Martinsson, 1962

**TYPE SPECIES**: Original designation of Martinsson 1962, p. 216;

*Sleia equestris* Martinsson, 1962, p. 218, fig. 102B; from the Ludlovian (Hamra Beds) at Sles, Gotland.

**BRITISH SPECIES**: *Sleia pauperata* (Jones, 1869)

*Sleia grumula* sp. nov.

*Sleia cf. S. equestris* Martinsson, 1962

*Sleia procincta* sp. nov.

*Sleia ancon* sp. nov.

*Sleia troglodytophila* Martinsson, 1962

**DIAGNOSIS**: Amphitoxotidinae having an adductorial tubercle, vertical marginal structures composed of small, isolated tubercles and a subcruminal morphology which has, or is derived from, a velar edge gently curved in an arc-like shape, either side a point at its mid-length. Below the site of the syllobial groove, calcarine spines or tubercles frequently occur. Ornament typically consists of tuberculation, often combined with reticulation.

**DISCUSSION**: Martinsson (1962) included *Beyrichia kochii* Boll, 1862, and the two new species *S. equestris* and *S. troglodytophila* within *Sleia*. Later (Martinsson 1964, p. 130), *S. inermis* from the Leba I borehole of Pomerania was added to the genus.

The Wenlockian and Ludlovian of Britain have produced a moderate number of hitherto unrecognised species which fall readily into *Sleia*. Previous to this paper only *S. troglodytophila* has received modern recognition and description although the presence of other congeneric species had been suspected (see Martinsson 1962, p. 221, and Martinsson 1964, p. 133). No other area which has recently been collected and studied for beyrichiacean ostracodes has revealed so many species of the genus. While nearly all of the British *Sleia* species morphologically...
All specimens from the same sample,
Wenlock Limestone, Wren's Nest (loc. 27c).

Text-fig. 7 SIZE DISPERSION OF FEMALE SPECIMENS OF SLEIA SPECIES
lie well within the current concepts of the genus, *S. procincta* and *S. ancon* do show an unusual trend in the lobular differentiation of the anterior lobe. However, many valve features relate these two taxa to other congeneric species and any possible separation from *Sleia* based on this lobular differentiation alone is not justified. Some of the British species are tuberculate but the associated reticulation is less apparent than that found in *Sleia* taxa from the Baltic area, e.g. *S. kochi* or *S. inermis*; this may, however, be due in part to aspects of preservation.

**OCCURRENCE:** In Britain the genus occurs in the upper part of the Wenlockian and in parts of the Ludlovian; it is found in the northern part of the Welsh Borderland (Ludlow - Much Wenlock area) and in the inliers of central England and the southern Welsh Borderland.

In the Baltic area (Gotland, Estonia, Latvia, Lithuania, and Poland) the genus is exclusively post-Wenlock in age. *Sleia* is also recorded (Abushik, 1971) from Podolian deposits of Ludlow-Downton age. Martinsson (1971, *in* Berry & Boucot, p. 42) notes the presence of *Sleia* species in eastern coastal areas of North America in beds which are of late Ludlow - early Downton age. Copeland (1960, p. 98, pl. 23, fig. 23; 1964, pp. 4, 8) described a *Sleia* species as *S. kochi*? (Boll, 1862) from the Stonehouse Formation of Nova Scotia, Canada.

*Sleia pauperata* (Jones, 1869)


1869 *Beyrichia Kloedeni*, var. *pauperata*, nov.; Jones, p. 12; p. 14, fig. 8.

1869 *Beyrichia Kloedeni*, var. *torosa*, Jones; Jones, p. 14, fig. 11b.

?1886 *Beyrichia Kloedeni*, var. *intermedia*, Jones; Jones & Holl, p. 352, pl. XII, fig. 4 (*non* fig. 3).

1886a *Strepula beyrichioides* sp. nov.; Jones & Holl, p. 405, pl. XIII, fig. 3 (*non* fig. 2).
LECTOTYPE: Here designated. A damaged right valve tecnomorph, BM IN 51761, Jones 1869, p. 14, fig. 8 (plate reversed); herein Pl. Cl, fig. 12. The lectotype rests on a small piece of limestone and required a moderate amount of preparation before photography.

The label and catalogue information state that this is the figured specimen of Jones (1869, fig. 8); however, the corresponding locality details - Wenlock Limestone, Malverns - contradict those given by Jones (1869, p. 12), which were Upper Ludlow Shales near Kingston and Aymestrey. The label and catalogue information is taken as correct for the following reasons. Firstly, Jones illustrated only one specimen of his new var. pauperata; secondly, another specimen (BM IN 51760, an unfigured right valve tecnomorph, Holl coll.) was labelled Beyrichia Kloedeni var. pauperata, Wenlock Limestone, Malverns, and this valve is undoubtedly conspecific with the type specimen; lastly, this same species occurs quite commonly in the writers collections from the Wenlockian of the Malverns and elsewhere in the Welsh Borderlands.

TYPE LOCALITY AND TYPE STRATUM: The Malvern District, England; Wenlock Limestone (as interpreted above). Information for a restriction of the type locality is missing.

DIAGNOSIS: Slea species whose narrow syllobium is ridge-like from anterior cusp to the very shallow syllobial groove; the two syllobial cusps are of subequal size. Females have a rounded calcarine tubercle, adult tecnomorphs lack any conspicuous corresponding feature. Velar edge on the crumina long, uninterrupted, with a small abmarginal curve at mid-length. Sparse tuberculation scattered on all lobes.

DESCRIPTION: The conspicuously narrow syllobium protrudes over the hinge line with an anterior cusp and a noticeably smaller posterior cusp. Anterior lobal cusp attains the same height as the anterior syllobial cusp. The main (anterior) part of the syllobium is ridge-like and sharply
defined posteriorly. Extending from the anterior cusp, this ridge is interrupted at the site of the almost obsolete syllobial groove, below which in the females there is a rounded calcarine tubercle, and in the males a more pointed though not very prominent remnant of a posteriorly directed calcarine spine. A callus is not developed. Behind the main part of the syllobium is a smaller posterior lobule, conspicuous only in its cuspidal region. Lobal cusps are not pointed. The long anterior lobe is slender and appears isolated from the preadductorial node. All lobes stand high above the level of the sulci. Prenodal sulcus almost as wide as the adductorial sulcus. Sulci are of equal depth. Only a very low and broad connection between syllobium and preadductorial node prevents the adductorial sulcus linking directly with the marked antero-ventral depression. All valves have an adductorial tubercle near the hinge line.

The moderately wide velum is widest below the anteroventral depression; a well developed toric ridge is present along the ventral edge in tectomorphs and postcruminally in females. Velar tubules are visible externally when tectomorphic valves are viewed obliquely. The angle between the velar edge and the valve contact margin is noticeably greater at the posterior cardinal corner than at anterior cardinal corner. The narrow area of the velum between its edge and the lobes is as deeply concave as the adductorial sulcus. The velum is constricted on both sides of the rather well rounded crumina. The pattern of the velar edge on the crumina is very similar to that of the type species; in well preserved material a small, isolated tubercle is seen admarginal to the mid-length curve of the velar edge. A row of isolated but densely spaced tubercles form the marginal structures in each valve.

Ornamentation of the lobes consists of coarse, scattered tubercles and faint reticulation. Tubercles are distributed on the syllobium (especially posteriorly) and, to a lesser extent, on the preadductorial node (mainly anteriorly) and lower parts of the anterior lobe. The
All specimens from Wenlock Limestone, Welsh Borderlands & Central England.

Text-fig. 8  SIZE VARIATION OF FEMALE SPECIMENS OF *SLEIA PAUPERATA*
faint reticulation (when present) occurs on the calcarine and cuspidal regions of the syllobium and on the crest of the preadductoridal node. Areas of tuberculation and reticulation appear to be mutually exclusive. Fine, discontinuous, subparallel striae ornament the crumina.

The small calcarine spine present in young tecnomorphs is gradually reduced during ontogeny; its occurrence is weakly suggested in adult tecnomorphs. One valve has been collected which shows an intermediary stage in the metamorphosis of the crumina.

**Measurements:** Significant variations in the size of adult (female) specimens from different localities have been recorded. The Croft Farm (loc. 18) specimens from the Malverns are appreciably larger than those collected from Lincoln Hill (loc. 49), N. Shropshire, while intermediate in size between these two are valves from the Wren's Nest (loc. 27), Dudley. All three localities lie within the Wenlock Limestone. Between each of the three sets of valves measured the size ranges do not show overlapping to any noticeable degree.

Hinge length - sulcal height (including velar width) in microns, of representative female valves; all from the Wenlock Limestone.

- **Croft Farm (loc. 18):** 1330-825, 1310-780, 1280-780, 1275-810, 1255-745, 1245-765, 1225-770, 1200-765, 1160-735 (all from same sample).

- **Lincoln Hill (loc. 61c):** 1130-680, 1125-710, 1090-635, 1060-670, 1035-640, 1020-625, 1010-650, 985-615, 970-595 (all from same sample).

- **Wren's Nest (loc. 27c):** 1175-660, 1150-695, 1125-685, 1100-625 (two samples).

**Discussion:** Jones, apparently not realising their true relationship, figured both dimorphs of this species in the same paper (1869) under separate names (*B. Kloedeni*, var. *pauperata* and var. *torosa*). The specimen figured (p. 14, fig. 11b, plate reversed) as *Beyrichia Kloedeni*, var. *torosa* Jones is a female right valve, BM IN 51763, which label
information states as coming from the Wenlock Limestone of the Malverns; the original of figure 11a of the same paper has not been found. The tecnomorph BM I 52506, illustrated by Jones & Holl (1886a, pl. XIII, fig. 3) as *Strepula beyrichioides*, is conspecific with these specimens (see under *Strepula concentrica* for lectotype designation of *S. beyrichioides*).

The small tecnomorphic carapace (BM IN 52532) illustrated as a right valve by Jones & Holl (1886, pi. XII, fig. 3) and assigned by them to *Beyrichia Kloedeni* var. *intermedia* is a *Sleia* species. Its preservation is poor and it can only be referred to *S. pauperata* with doubt.

The form of the subcruminal morphology, marginal structures, adductorial tubercle and ornamentation in *S. pauperata* is typical of the genus *Sleia*. *S. pauperata* is immediately distinguished from other members of the genus by its syllobial morphology, which differs considerably from species such as *S. inermis*. Moreover, it differs from *S. equestris* in the lack of a calcarine spine in females, from *S. kochi* in lacking a calcarine process on the crumina and in having lobal cusps above the hinge line, and from *S. troglodytophila* in its subcruminal morphology.

**OCCURRENCE:** W Midlands of England and the Welsh Borderlands; Wenlockian and lowermost Ludlovian.

**Elton Beds:** Shadwell Rock Qy. (loc. 61).

**Wenlock Limestone:** Wren's West (locs. 27a-f).
Lincoln Hill (locs. 49a-c).
Benthall Edge, West (loc. 47).
Hurst Hill (loc. 28).
Croft Farm (locs. 18b, d).
Hobbs Ridge (locs. 15a, b).
Whitman's Hill (locs. 19a, b).

**Tickwood Beds:** Harley Hill Rd. (loc. 48c).
Benthall Edge, East (loc. 43a).
Tickwood (locs. 44a-d).
Acklands Coppice (locs. 42a, b).

**Coalbrookdale Beds:** Benthall Edge, Severnside (loc. 39).
Sleia grumula sp. nov.

Pl. C2, figs. 1-10, l3.

1886 Beyrichia tuberculata, (Kloden) var. gibbosa, Reuter; Jones & Holl, p. 349, pl. XII, fig. 1a (non lb).

DERIVATION OF THE NAME: From the Latin grumulus, a small hillock; alluding to the form of the calcarine element in the female.

HOLOTYPE: A female left valve, DAS 47062; Pl. 02 , figs. 1, 2, 5, 6, 10.

TYPE LOCALITY AND TYPE STRATUM: The W side of the Wren's Nest (loc. 27c), Dudley, Worcestershire; Nodular beds (of Butler, 1939) within the Wenlock Limestone.

DIAGNOSIS: Sleia species in which the female has a large calcarine tubercle and the male has only remnants of a calcarine spine. Syllobium lacking a noticeable groove or sharply defined lobules. Velar edge on the crumina well developed and abmarginally curved at mid-length. Anterior lobal cusp and the single, prominent anterior syllobial cusp are of equal height. Lobes only slightly tuberculate.

DESCRIPTION: Anterior lobe and preadductor node strongly developed; both show a tendency to become slender along their crests. The connection between preadductor node and syllobium is broad and faint; that between anterior lobe and preadductor node is obsolete. Width and depth of prenodal sulcus is almost that of the adductor sulcus. The anterior lobal cusp reaches the same height above the hinge line as the anterior syllobial cusp. Cusps are rounded rather than pointed. Preadductor node just touches the hinge line. A small, yet distinct, tubercle is found on the hinge line at the dorsal end of the adductor sulcus. The width of the syllobium varies somewhat, though it is usually quite broad, tapering gradually towards the calcarine region. There is a single, stoutly formed, syllobial cusp adjacent to the
adductorial sulcus. The uncular region is rounded and its dorsal projection into a second (posterior) syllobial cusp is only weakly suggested. Between the main syllobial cusp and the central part of the syllobium there is a shallow depression which appears to be wider in females than in tecnomorphs. The prominent calcarine tubercle of the female is large and mostly rounded, though sometimes its distal part is more acuminate; in the male there is vestige of a posteriorly projected calcarine spine. In the female a diagonal depression separates the calcarine tubercle from the elongate node-like feature which forms the ill-defined central syllobial lobule. The syllobial groove in males is nearly obsolete; only a shallow depression above the calcarine element denotes its presence. The central syllobial region of the male is slightly larger but less tumid than that of the female. In young tecnomorphs there is a conspicuous calcarine spine; its length gradually diminishes throughout ontogeny.

Faintly developed tubules are visible below the anteroventral depression, on the widest part of the velum. The preplete outline of the valves is most noticable in the smaller tecnomorphs. A toric structure is found along the tecnomorphic velum and postcruminally (for a short distance) in females. On the rounded crumina the velar edge is faintly arched (towards the margin) either side its small, mid-length, abmarginal curve (cf. conditions in S. equestris). Adjacent to the crumina there are velar constrictions. A row of small, isolated tubercles form the marginal structures along both valves.

Ornamentation consists of sparsely scattered tubercles on the syllobium and, to a lesser degree, on the anterior lobe and preadductorional node. Within the extant material, reticulation is hardly - if at all - discernible on the lobes. The ventral part of the crumina does, in a few specimens, appear to be very faintly reticulate; the crumina is otherwise smooth.
MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of female valves from the Wenlock Limestone.

Wren's Nest (loc. 27c): 1560-910, 1540-870, 1530-890, 1525-885, 1525-880, 1510-900.

DISCUSSION: The specimen (BM I 2359) from Dudley Castle considered by Jones & Holl (1886, pl. XII, fig. 1a) as Deyreichia tuberculata, (Kloeden) var. gibbosa, Reuter is a broken female right valve of S. grumula.

This species is readily distinguished from S. trogodytophila in subcruminal and syllobial morphology, and, among other differences, it lacks the differentiation of the anterior lobe found in S. procincta and S. ancon. Compared with Sleia kochi (Boll, 1862) the species has a wider velum, a calcarine spine (or tubercle), more prominent lobal cusps but lacks a well defined syllobial groove. A distinct lobular differentiation of the syllobium and a lack of conspicuous calcarine elements characterise Sleia inermis and distinguish this species from S. grumula. The syllobial morphology in itself is sufficient to separate S. grumula from S. pauperata. S. grumula most closely resembles S. equestris but differs from that species by its much reduced tuberculation, its lack of reticulation, the absence of a strongly developed callus above the syllobial groove, and in the form of the female calcarine element. Furthermore, S. grumula is somewhat removed stratigraphically from the younger S. equestris.

OCCURRENCE: From the Wenlockian of the English W Midlands and Welsh Borderlands.

Wenlock Limestone: Wren's Nest (locs. 27a-d, f, g).

Benthall Edge, West (loc. 47).

Crofts Farm (loc. 18).

Ledbury (loc. 23).
Sleia cf. S. equestris (Martinsson, 1962)
Pl. C2, figs. 11, 12.

REMARKS: The occurrence of a Sleia species in the Upper Leintwardine Beds of Great Britain has previously been indicated (Martinsson 1967, p. 371). Collections made by the writer from the Upper Leintwardine of the Ludlow area confirm that a species very close to, if not conspecific with, S. equestris is present.

MATERIAL: All the material collected consists of external and internal moulds. Casts were taken of specimens from all localities.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of casts of female specimens from the Upper Leintwardine Beds.


DISCUSSION: The specimens referred to herein as S. cf. S. equestris are very similar to the type species from Gotland. Tecnomorphs belonging to the British form cannot be distinguished from those of S. equestris. Females too, are very much alike in lobation and in the ventral morphology of the crumina. However, as yet, the presence of a spur-like calcarine tubercle - a diagnostic character of S. equestris - has not been confirmed in any of the extant heteromorphs from Britain, whose calcarine tubercle, although large and prominent, tends to be rounded. To what extent its absence is due to preservation (all the British material occurs as moulds) is somewhat uncertain, though even the better preserved British specimens (from near Tripletton Farm (loc. 68), Leintwardine) seem to lack a truely spur-like tubercle. Until the presence (or absence) of this feature is confirmed in additional material, the British specimens will be referred to S. equestris with a confer.
OCCURRENCE: *S. cf. S. equestris* has been collected from localities in the northern Welsh Borderlands around Ludlow.

Upper Leintwardine Beds: Tripleton Farm (loc. 68).

Bengry Track (loc. 63).

Forestry Track, Ludlow (loc. 62).

The Goggin (loc. 64).

Also identified in J.H. McD. Whitaker's colls. (loc. 811) from the Upper Leintwardine along Marlow Lane (SO 4080 7676), near Leintwardine, Herefordshire.

*S. equestris* has been recorded and figured from a number of Baltic and adjacent areas subsequent to Martinssons original description from the Ludlovian (Hemse, Eke, Hamra, and Sundre Beds) of Gotland. Occurrences are reported from Latvia (Gailite 1967, p. 119, pl. VII, figs. 8a-c), the region of the southern Baltic encompassing Lithuania and Kaliningrad (Pranskevichuis 1972a, p. 41), Podolia (Abushik 1971, p. 67, pl. XIV, figs. 9-11), Estonia (Sarv 1968, p. 21, pl. V, figs. 10, 11) and Saaremaa (Osel) Island, (Sarv 1971, p. 353, table 1). All these findings occur in deposits ranging from fairly high in the Ludlovian to low Downtonian.

*Sleia procincta* sp. nov.

Pl. C3, figs. 1-9, 11.

DERIVATION OF THE NAME: From the Latin *procinctus*, girded for battle; alluding to armour-like spine in the male.

HOLOTYPE: A female left valve, DAS 47218; Pl. C3, figs. 3, 4, 7, 8.

TYPE LOCALITY AND TYPE STRATUM: Old quarry on Hobbs Ridge, about 0.7 km NE of Longhope, Gloucestershire (loc. 15a); Wenlock Limestone.

DIAGNOSIS: *Sleia* species with a strongly developed calcarine spine in the male and a rounded calcarine tubercle in the female. Distinct
lobular differentiation of the anterior lobe. Syllobium with a shallow groove and a single, prominent cusp isolated from the main part of the lobe by a depression. A central syllobial lobule is adequately defined in tecnomorphs but not in females.

DESCRIPTION: In males the anterior lobe is divided at mid-height by a broad, shallow sulcule into cuspidal and ventral parts. Cuspidal part slender, posteriorly directed, with a moderately pointed cusp above the hinge line; ventral part itself differentiated into a higher node-like, posterior area with coarse granules and a lower anterior region with sparsely scattered tubercles. Only the cuspidal part of the anterior lobe is present in females. Slightly anteriorly inclined, the slender preadductorional node just reaches the dorsal margin of the valve. Prenodal sulcus wide and comparatively shallow. Adductorial tubercle found at the hinge margin of the main sulcus. The connection linking the syllobium to the preadductorional node is very weak and that from anterior lobe to preadductorional node is obsolete. Anteroventral depression discernible but not prominent.

The syllobium is wide dorsally, narrowing rapidly towards the sharp spine on the calcarine lobule in tecnomorphs, or towards the corresponding large rounded tubercle in females. Above this spine in males there is a shallow syllobial groove which trends diagonally across the width of the lobe; a similar feature appears to be lacking above the large knob-like calcarine region of female valves. In tecnomorphs, between the syllobial groove and the sulcule which isolates the syllobial cusp, there is a large central lobule forming the largest and most tumid part of the lobe. In females this lobule is not distinctly present - the sulcular depression below the syllobial cusp being much broader than in tecnomorphs. The posterodorsal part of the syllobium is rounded about the level of the hinge line.
Toric ridge present postcrumenally in females and along the ventral edge of the velum in tecnomorphs. The velum in lateral view has a gently rounded outline below the anteroventral depression, and characteristically narrows appreciably towards mid-height. A single line of small tubercles is present along each valve margin. The velum is constricted each side of the round crumina. The precruminal section of the valve is very small and the velar ridge in this region particularly narrow. Velar edge on the crumina is long, curving abmarginally for a short distance at its mid-point before resuming its trend parallel to the valve margin. Velar tubules hardly discernible.

Sulci and velum are smooth, calcarine and central lobules of the syllobium with scattered tubercles on a ground pattern of fine granulation. Tuberculosity also present on anteroventral part of anterior lobe. The higher, posteroventral part of the anterior lobe and the preadductorial node appear (on the better preserved valves) to house coarse, densely packed granules. Crumina mostly striate.

**MEASUREMENTS:** Hinge length - sulcal height (in microns) of females from Hobbs Ridge (loc. 15).

1420-810, 1415-785, 1390-780 (holotype).

**DISCUSSION:** This taxon is notable for the lobular differentiation of its anterior lobe - an arrangement unknown in other *Sleia* species except *S. ancon*. Although this feature constitutes a significantly different and unusual trend, this species (like *S. ancon*) is erected within *Sleia* because of the many homologies (e.g. the occurrence of an adductorial tubercle and the form of the marginal structures, calcarine elements, ornamentation and subcruminal morphology) it has with species of that genus. Reticulation is seemingly lacking in *S. procincta*. The presence of such a well developed calcarine spine in males of *Sleia* taxa is rare; in *S. equestris* the females have the spine, while in *S. grumula* it is in the small tecnomorphs where such a spine is prominently displayed.
OCCURRENCE: Known so far only from one locality in the Mayhill inlier and one locality in the Malverns area.

Wenlock Limestone: Hobbs Ridge (locs. 15a-c).

Croft Farm (locs. 18a, b, d).

**Sleia ancon** sp. nov.

*Pl. C3, figs. 10, 12; Pl. C4, figs. 2-4.*

DERIVATION OF THE NAME: From the Latin *ancon*, elbow; alluding to the shape of the anterior lobe.

HOLOTYPE: A female left valve, DA^d 47254; *Pl. C3*, fig. 10.

TYPE LOCALITY AND TYPE STRATUM: Woodbury Quarry, the Abberley Hills, Worcestershire; from a 5" shale parting in the Aymestry Limestone. Material collected by Dr. J.E. Robinson.

DIAGNOSIS: *Sleia* species with a single, stoutly developed, syllobial cusp and an anterior lobe differentiated into ventral and cuspidal parts. Males have a small calcarine tubercle below a very weak groove, females have a large calcarine tubercle and a small, central syllobial lobule. Lobes are very sparsely tuberculate.

DESCRIPTION: In the tecnomorphs the anterior lobe is divided just above mid-height into cuspidal and ventral sections by a broad, shallow sulcule; females have only the posteriorly pointing cuspidal part. The preadductorial node nearly reaches the hinge line and is almost vertical. From dorsal margin to the anteroventral depression, the prenodal sulcus is quite narrow and shallow, but effectively separates the anterior lobe from the preadductorlial node. The wider adductorial sulcus has a tubercle on its dorsal margin. Syllobium very faintly joined to preadductorial node by a wide, low connection.

Posterodorsally the syllobium is curved and lacks a (posterior) cusp. Rather blunted and occupying a wide section of the dorsal part of
the syllobium, the anterior cusp - like the anterior lobal cusp - projects a little way above the hinge line. Below the syllobial cusp there is a broad shallow sulcule. A node-like calcarine element, below a shallow depression, forms the most elevated region of the comparatively slender female syllobium. The central lobule of the female syllobium is quite narrow and somewhat smaller than that of the male. The male has a very small calcarine tubercle - possibly the vestiges of a spine - below an inconspicuous groove.

The velum, present from anterodorsal to posterodorsal corners of the valve, is not appreciably wide; a toric ridge parallels the inside of the ventral edge. Small tubercles line the margin of each valve. The crumina tapers slightly posteriorly towards its junction with the syllobium and velum. Precruminally the velar ridge is particularly narrow. Constrictions of the velum occur at each side of the crumina. Subcruminal morphology is of the typical Sleia type (cf. conditions in S. equestris).

The surfaces of the extant specimens are generally poorly preserved, but even the best preserved valves do not show much ornamentation. A few dispersed tubercles are found mostly on the syllobium, and the crumina is covered with fine, discontinuous striae. Velar tubules are not visible externally in the extant tecnomorphs.

MEASUREMENTS: Hinge length - sulcal height of female valves (in microns) from the type locality.


DISCUSSION: S. ancon has much in common with the considerably older S. procincta; they have similar cruminal and cuspidal arrangements and are the only known Sleia species with a divided anterior lobe. The disparity between these taxa is expressed chiefly in the form taken by the syllobium and the velum. S. ancon lacks the long (tecnomorphic) calcarine
spine of *S. procincta* and, furthermore, has a more slender syllobium, a somewhat larger valve area in front of a slightly less well rounded crumina, and a narrower and thicker velum which at the cardinal corners is consistently more flaired away from the adjacent contact margins.

**OCCURRENCE:** Known only from the Aymestry Limestone of the type locality, the Abberley Hills, Worcestershire.

The material, consisting of 15 female valves and seven tecnomorphs, was collected and kindly forwarded to the writer for study by Dr. J.E. Robinson, University College, London.

*Sleia troglodytophila* Martinsson, 1962

Pl. C4, figs. 1, 5-13.

1886 *Beyrichia Kloedeni*, M'Coy var. *granulata*, Jones; Jones & Holl, p. 350, pl. XII, fig. 2.

? 1886 *Beyrichia tuberculata*, (Kloeden) var. *gibbosa*, Reuter; Jones & Holl, p. 349, pl. XII, fig. 1b, (non la).

non 1903 *Beyrichia kloedeni*, M'Coy, var *granulata*, Jones; Chapman, p. 110, pl. XVI, fig. 8.

1934 *Beyrichia granulata* (Jones & Holl); Bassler & Kellett, p. 193, (pars).

1962 *Sleia troglodytophila* n. sp.; Martinsson, p. 220, figs. 98B, 104A-C.


**HOLOTYPE:** A right female valve, IPU EW 11; figured by Martinsson 1962, p. 220, fig. 104A.

**TYPE LOCALITY AND TYPE STRATUM:** The Wren's Nest, Dudley, Worcestershire; marl within the Wenlock Limestone.
DIAGNOSIS: Sleia sp. with a very large calcarine tubercle in the female. The velar edge on the crumina is divided into one shorter, straight, anterior portion and one larger, posterior portion, the anterior half of which is bent out from the posterior portion. (After Martinsson 1962, p. 220).

DESCRIPTION: See Martinsson 1962, p. 221.

DISCUSSION OF SYNONYMY: In 1855 Jones illustrated (1855a, pl. VI, fig. 9) a specimen from Lincoln Hill, Shropshire under the name Beyrichia Kloedeni, M'Coy; its surface was said to be "granulated". This specimen (BM I 169) is herein referred to the species Beyrichia (Beyrichia) clausa Jones & Holl. Jones later (1881c, pp. 345, 6) synonymised the "Beyrichia Kloedeni (with granulated surface)" with Beyrichia Kloedeni, var. tuberculata (Sow. or Salter in Murchison 1839); his figured specimen of 1881c (pl. X, fig. 13) from Benthall Edge, Shropshire is now assigned to the species Beyrichia (Beyrichia) messis sp. nov. and is therefore not conspecific with the 1855a (fig. 9) specimen. The first formal citation of the variety granulata did not appear until Jones & Holl 1886 (p. 35, pl. XII, fig. 2), when it was termed Beyrichia Kloedeni var. granulata, Jones. The description of 1886 was based on a newly figured left valve female from Dudley Castle (BM IN 52504, Smith coll. no. 91; here considered conspecific with Sleia trogloodytophila Martinsson, 1962), the 1855 figured specimen, and numerous other referred specimens. All this material has to be regarded as the "type-series" of the species with Jones (in Jones & Holl) as the author of var. granulata. However there is little point in choosing a lectotype for B. granulata Jones, 1886 as this taxon, is a junior primary homonym of Beyrichia granulata Hall, 1859.
The female carapace from Dudley Castle (BM IN 52503; Smith coll. no. 93) illustrated as *Beyrichia tuberculata*, (Kloden) var. *gibbosa*, Reuter by Jones & Holl (1886, pi. XII, fig. 1b) is questionably referred to *S. troglodytophila* only because of its poor preservation. Its morphology is more similar to *S. troglodytophila* than to any other British *Sleia* species.

Martinsson (1962, fig. 98H) figured the subcruminal morphology of an undescribed British Wenlock species which he stated probably includes *Beyrichia Kloedeni*, var. *granulata*, Jones, as illustrated by Jones & Holl 1886. The amphitoxotidinum which Martinsson figures is not var. *granulata* of Jones & Holl and does not belong to *Sleia*.

**MEASUREMENTS:** Hinge length - sulcal height (including velar width) in microns of females from the Wren's Nest.


**DISCUSSION:** This taxon is separated without difficulty from other *Sleia* species by the morphology of the velar edge, distally, on the crumina; the anterior part of the velar edge is disconnected from its longer posterior portion.

**OCCURRENCE:** The Welsh Borderlands, and the W Midland inliers of England; Wenlock Limestone and lowermost Ludlovian.

Elton Beds: Shadwell Rock Qy. (loc. 61).

Wenlock Limestone: Wren's Nest (locs. 27b-f).

Hurst Hill (loc. 28).

Benthall Edge, West (loc. 47).

Gleedon Hill (loc. 50).

Much Wenlock (loc. 55).

Ledbury (loc. 23).
Genus **Equicastanea** gen. nov.

**DERIVATION OF THE NAME:** From the Latin *equus*, a horse, and *castanea*, a chestnut tree; alluding to the fancied resemblance of the ornament to the bur of a horse-chestnut tree. Gender, feminine.

**TYPE SPECIES:** *Equicastanea lappacea* sp. nov., Pl. C5, figs. 1, 2, 4, 5, 9; from the Wenlock Series of the Welsh Borderland.

**SPECIES:** Only the type species.

**DIAGNOSIS:** Amphitoxotidinae whose stoutly developed, moderately broad lobes are coarsely tuberculo-reticulate. The wide velum is strongly represented precruminally and is gradually restricted posteroventrally. The velar edge is vaguely traced across the crumina, where it has a faint, overall deflection towards the margin and on its mid-point a small, admarginal node. Toric structures are absent.

**DISCUSSION:** *Equicastanea* represents a primitive member of its subfamily. Its subcruminal morphology indicates that disturbances involving the distal part of the anteroventral section of the velum took place during cruminal metamorphosis.

Of particular interest is that this genus shows features which ally it to two beyrichiaceous subfamilies. The form of the velum, the subcruminal morphology, and the reticulation, clearly indicate that this genus belongs within the Amphitoxotidinae, whereas the widely distributed tuberculation is a feature more commonly associated with members of the Beyrichiinae. Only rarely does tuberculation or verrucosity occur in amphitoxotidines - it is found also, for example, in *Sleia* and *Tinotoxotis*, where again it is combined with reticulation. However, these genera are otherwise quite different to *Equicastanea* in lobal, velar and subcruminal characters and, furthermore, the form taken by the tuberculo-reticulation is different in each genus; in *Equicastanea* there
are coarse, ubiquitous tubercles on a network of medium sized meshes, in Sleia fine reticulation is variably developed on the tubercles, while the type species of Tinotoxotis has sparsely scattered tubercles over fine reticulation.

**OCCURRENCE:** So far only from the Wenlock Series of the N Welsh Borderland.

**Equicastanea lappacea sp. nov.**

Pl. C5, figs. 1-11.

**DERIVATION OF THE NAME:** From the Latin lappaceus, burlike; alluding to the similarity of the tuberculation to the short, stout spines covering the fleshy bur of a horse-chestnut tree.

**HOLOTYPE:** A female right valve, DAS 47214; Pl. C5, figs. 1, 2, 4, 5, 9.

**TYPE LOCALITY AND TYPE STRATUM:** N side of the Harley Hill road (A 458) cutting, approximately 1.2 km NW of Much Wenlock, Shropshire (loc. 48a); Tickwood Beds.

**DIAGNOSIS:** As for the genus.

**DESCRIPTION:** All of the moderately broad lobes are entire and stoutly developed. Both anterior lobe and syllobium have rounded cusps capped with tubercles which protrude just above the hinge line. The anterior lobe broadens ventrally and is joined - below the narrow prenodal sulcus - to the preadductorial node by a low, fairly wide connection. Below the preadductorial node a prominent curve in the outline of the lobes indicates the region of the anteroventral depression. From its narrow base near its junction with the preadductorial lobe the syllobium rapidly widens (dorsally) and at the same time, gradually loses elevation (its highest point occurs well below mid-height). The posterior margin of the syllobium is a gently curved continuation of the cuspidal region. The long, deep adductorial sulcus is about twice the width of the prenodal sulcus and distinctly separates the adjacent lobes.
In tecnomorphs the wide velum is conspicuously present from the anterior cardinal corner to the posteroventral part of the valve—where it is gradually restricted—and thereafter (to the posterior cardinal corner) is discernible as a velar ridge. Maximum velar width occurs below the anteroventral depression and the velum itself flairs quite prominently away from the valve margin. Precruminally the velum is well developed; behind the crumina its morphology is identical to that of tecnomorphs. Long, narrow velar tubules are visible externally, both anteriorly and ventrally. The crumina (in lateral view) narrows posteriorly and occupies the whole width of the velum, the lower part of the anterior lobe and the area of the lobal connections above the anteroventral depression. The velar edge can be traced across the crumina (albeit faintly), particularly using the ornamentational patterns. Marginal structures consist of a row of closely spaced, fine tubercles mounted on a fine ridge along each valve. Toric features are absent.

Each of the lobes and lobal connections are covered with a regular network of medium sized meshes; rather acute tubercles stem from the sides of the meshes, and are evenly and densely distributed over this ground pattern of reticulation. The velum and sulci are smooth. Most of the crumina is coarsely verrucose but there are two areas—one immediately adjacent to its junction with the lobes and another between the valve margin and the line marking the trace of the velar edge—which largely lack ornament. Above the preadductorional node, near the hinge line, a small tubercle often occurs.

MEASUREMENTS: Hinge length - sulcal height (excluding velar width) in microns.

Tickwood Beds: Harley Hill Road (loc. 48a): 1925-1100 (female holotype).
1960-1150, 1850-
1180 (tecnomorphs).

DISCUSSION: The only material found in the literature which can be assigned to this species is a single tecnomorphic carapace (Smith coll. no. 14; BM 12364, from the railway cutting, Coalbrookdale) referred by Jones & Holf (1886, p. 358) to "Beyrichia Maccoyiana, Jones".

In most respects this species shows a fairly stable morphology. The small elevation noted adjacent to the distal part of the velar edge on the crumina can, however, vary in size from an indistinct tubercle to a more conspicuous node-like feature. The reticulation, which in any case tends to be dominated by the (superimposed) tuberculation, is normally difficult to discern and is most easily seen when valves are immersed in a liquid (e.g. water or alcohol).

OCCURRENCE: Collected from Wenlockian localities just N and S of the River Severn, N Shropshire.

Tickwood Beds: Harley Hill Road (loc. 48a).
Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39).
Coalbrookdale (loc. 40).

Genus Tinotoxotis gen. nov.

DERIVATION OF THE NAME: From the Greek teino, spread and toxotis (as in the type genus Amphitoxotis); alluding to the width and extent of the velum. Gender, feminine.

TYPE SPECIES: Tinotoxotis velivola sp. nov., Pl. C7, figs. 2, 3, 7, 10; from the Wenlock Limestone of the N Welsh Borderland.

SPECIES: Tinotoxotis velivola sp. nov.

Tinotoxotis praegnans sp. nov.
Text-fig. 9  SIZE DISPERSION OF FEMALE SPECIMENS OF TINOTOXOTIS SPECIES
DIAGNOSIS: Amphitoxotidinae with an extensively developed velum; it is very wide (even precruminally), prominently tubulous, and virtually unrestricted. The velar edge traverses the crumina diagonally and, as it does so, is strongly curved towards the margin. The anterior lobe and syllobium are broad, fairly flat, and terminate without cusps along the hinge line. The fine lobal reticulation can be effaced or combined with tuberculation. Toric structure absent.

DISCUSSION: Amongst the array of figures showing the wide range of subcruminal morphologies encountered in the subfamily Amphitoxotidinae, Martinsson (1962, figs. 98D, 100E) illustrated and recognised the type species of this genus as an, "Undescribed Wenlockian genus from Britain". I concur with this view; two species, both new, are assigned to the genus.

The strongly developed velum in Tinotoxotis, running almost completely around the free edge (it narrows gradually posteriorly above mid-height, though it is well represented anteriorly), is also found in several reticulate American amphitoxotidines which Henningsmoen (1954, p. 24) gathered under his new subgenus Beyrichia (Velibeyrichia). Certainly the width of the velum in species such as "Beyrichia" waldronensis Ulrich & Bassler, 1908 (p. 286, pl. XXXVII, figs. 9, 10) appears (relatively) equal to conditions found in the present genus. Unfortunately, because important information on the type species - Velibeyrichia moodeyi (Ulrich & Bassler, 1908) from West Virginia - is lacking (an undisputedly conspecific female has never been described or figured), it is not possible to compare and contrast these genera in detail. Indeed, all of the taxa assigned to Velibeyrichia by Henningsmoen (see also Hoskins 1961) are in need of re-examination. Using those figures which have been published of V. moodeyi (Ulrich & Bassler 1908, pl. XXXVII, fig. 8 and 1923, pl. LXIII, fig. 27), the genera differ mostly in the shape and proportions of the lobes (in V. moodeyi the syllobium is rather vertical and comparatively narrow, whilst its preadductorial node is as wide as its...
anterior lobe), in ornament (*V. moodeyi* does not combine tuberculation
with its reticulation) and in velar width (*in V. moodeyi* Ulrich &
Dassler 1923, pl. LXIII, fig. 27 - "One of the original types" - the
velum is noticably narrower than in *Tinotoxotis* despite being practically
unrestricted).

OCCURRENCE: The Wenlock and Ludlow Series; the Welsh Borderland and
English West Midlands.

*Tinotoxotis velivola* sp. nov.


1962 Martinsson, figs. 98D, 100E (illustrated as an undescribed genus).

DERIVATION OF THE NAME: From the Latin velivolus, with flying sails;
alluding to the prominently developed velum.

HOLOTYPE: A female left valve, DAG 47317; Pl. C7 , figs. 2, 3, 7, 10.

TYPE LOCALITY AND TYPE STRATUM: The bottom of the well exposed, steeply
dipping, face at the old workings on the W side of Lincoln Hill,
approximately 250 m N of the River Severn and 500 m NW of the bridge
at Ironbridge, Shropshire (loc. 49c); Wenlock Limestone.

DIAGNOSIS: A *Tinotoxotis* species in which the continuity of the broad
admarginal deflection of the velar edge across the crumina is "broken"
at about mid-length by a small, almost indiscernible, abmarginal
deflection. The fine reticulation on the lobes is combined with sparse
tuberculation. The crumina is striate and elongate in a general antero­
posterior direction.

DESCRIPTION: The broadly crescent-shaped anterior lobe is widest ventrally
and narrows dorsally. From its widest region, dorsally, the syllobium
gradually narrows and increases slightly in elevation towards its incon­
spicuous junction with the preadductorional node. Both lobes are, overall,
quite broad and flat; the preadductorial node, by comparison, is inconsiderably higher, and slightly inclined forwards. The dorsal margins of both anterior lobe and syllobium lie straight along the hinge line. The shape of the syllobium is constant; characteristically it has a long, straight, posteroventral margin which at posterior mid-height is flexed upwards towards the hinge line.

The broad lobes help to give a narrow appearance to the sulci. The adductorial sulcus is always wider and marginally longer than the gently curved prenodal sulcus and, unlike the latter, widens dorsally; both sulci are reasonably shallow. Only a weak connection from the anterior lobe to the preadductorial node separates the prenodal sulcus from the moderately developed anteroventral depression.

But for a short distance posterodorsally, the tecnomorphic velum is very wide; typically, in posterior and anterior views, it flares away from the margin at quite a high angle. At its maximum extension (below the region of the anteroventral depression) the velar width is equal to about three-quarters the height of the remainder of the valve. In females the elongate, egg-shaped crumina occupies the velar width from a point below the posterior margin of the adductorial sulcus to a point below the anterior margin of the anterior lobe - a distance somewhat longer than the velar width. The velar edge passes over the crumina (in the manner stated in the diagnosis) to join the prominently developed precruminal velar frill. The crumina does not assimilate much of the valve surface (only the lower part of the anterior lobe and the region of the lobal connections and adjacent anteroventral depression) and is mostly accommodated within the velum. There is no toric structure in either dimorph.

Cruminal ornament consists of coarse, discontinuous striae admarginal of the deflected velar edge, and finer striae laterally. The fine concentric striae present on the outer and inner surfaces of the velum, combine with the tubulosity to produce a "wrinkled" pattern. In contrast to the smooth sulci, the lobes are typically covered with fine reticulation
though it is, at times, not easy to discern) and a variably developed tuberculation. Except for a tendency for the small tubercles to occur in a vague line just above, and parallel to, the straight posteroventral margin of the syllobium, there is no regular pattern for their distribution; they can be sparsely and randomly scattered over the syllobium and, sometimes, the lower regions of the anterior lobe.

MEASUREMENTS: Hinge length - sulcal height (excluding velum) in microns of female valves.


Wren's Nest (loc. 27c): 1600-870, 1570-870, 1550-875.


DISCUSSION: In addition to those localities given below, Tinotoxotis has also been collected from the Uenlock Limestone at Parkwood (loc. 22), Croft Farm (locs. 18a-d) and Whitman's Hill (loc. 19b) in the Malverns district, and Hobbs Ridge (locs. 15a, b) in the May Hill inlier; all this material - broken females and tecnomorphs, as yet is insufficient for description - probably represents a single species, and closely resembles T. velivola. The material in question differs from the latter species in size (larger) and ornamentation (its instars are tuberculo-reticulate and identical to those of T. velivola, but the extant females lack both the lobal reticulation and - except in rare cases, when even then it is hardly developed - cruminal striation so characteristic of that species); it is probable that a third Tinotoxotis species is represented in the British Wenlockian.
The differences between *T. velivola* and *T. praegnans* are discussed under the latter species.

**OCCURRENCE:** Jenlock and Ludlow Series; the Welsh Borderlands and the Midlands of England.

- **Elton Beds:** Millichope (loc. 59).
- Stretton Westwood (loc. 60).
- Shadwell Rock Qy. (loc. 61).

- **Wenlock Limestone:** Benthall Edge, West (loc. 47).
- Hurst Hill (loc. 28).
- Lincoln Hill (locs. 49a-c).
- Wren's Nest (locs. 27a-g).
- Coates Qy. (loc. 53b).
- Much Wenlock, Windmill (loc. 54).
- Croft Farm (loc. 18).

- ? Ledbury (loc. 23); cruminae only.

- **Tickwood Beds:** ? Harley Hill Road (loc. 48c); crumina only.
- Tickwood (loc. 44d).
- Benthall Edge, East (loc. 43a).

- **Coalbrookdale Beds:** Benthall Edge, Severnside (loc. 39); crumina only.

Also collected from the top of the (undifferentiated) Wenlock Shale at Storridge (loc. 20), the Malverns area.

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**Tinotoxotis praegnans** sp. nov.

Pl. C8, figs. 1-8.

**DERIVATION OF THE NAME:** From the Latin *praegnans*, pregnant; alluding to the extended (acuminate) crumina.

**HOLOTYPE:** A female carapace, DAS 47104; Pl. C8, figs. 3, 5, 7.

**TYPE LOCALITY AND TYPE STRATUM:** S side of the Harley Hill road (A 458) cutting, approximately 1.2 km NW of Much Wenlock, Shropshire (loc. 48b); Tickwood Beds.
DIAGNOSIS: A Tinotoxotis species in which the velum is exceptionally broad and the crumina bluntly acuminate across the velar width. The deflection of the velar edge is traced diagonally near the apical part of the crumina. Ornamentation is mostly lacking; the crumina, near the velar edge, is weakly striate.

DESCRIPTION: None of the lobes are extended above the hinge line. The anterior lobe is broad, flat, and elevated slightly above the shallow, fairly short, prenodal sulcus. The anteriorly inclined preadductorional node is both the smallest and (inconsiderably) the most elevated of the lobes. Below the preadductorional node are the moderately wide lobal connections - that to the anterior lobe being slightly wider and less distinct than that to the syllobium. The anteroventral depression is outlined as a curve along the margin of the lobal area beneath the anterior region of the preadductorional node. Above the bend in its posterior outline, the syllobium is broad, flat and - because its posterodorsal, dorsal and anterior margins are fairly straight - characteristically square - shaped. Below this bend the posteroventral syllobial margin is straight, and is projected in an anteroventral direction; ventrally, the syllobium narrows quite quickly. The rather shallow adductorional sulcus runs from the dorsal margin to a point on the valve opposite the anteroventral depression, and is longer, wider and deeper than the prenodal sulcus.

The velum is extremely wide (at its widest point equal to the height of the lobal area), long (only in the immediate posterodorsal region it is reduced), and tubulous. The tubules are quite narrow (about five of them stem from the region of the anteroventral depression) but distinctly visible throughout. In those specimens in which the edge of the velum remains (it is normally broken away) the widest part of the velum occurs posteroventrally. In anterior and posterior views, the velum flares from the free edge at a high angle.
Dorsally, the crumina extends from a point just below the posterior margin of the adductorial sulcus to a point approximately below the anterior cardinal corner. However, the length of the crumina gradually diminishes across the velum and, moreover, its width (across the velum) is typically equal to, and often greater than, its maximum length. As a result, the crumina appears extended anteroventrally across the velum, an arrangement which helps give its distal region a bluntly pointed outline (best seen in oblique dorsal view). The velar edge is followed, sometimes with difficulty, diagonally across the relatively short distal part of the crumina. The precruminial section of the velum although narrowing gradually towards the anterior cardinal corner is always quite wide.

But for the infrequent development of fine, sparse tubercles along the posteroventral part of the syllobium, the lobes appear smooth. The crumina lacks ornament except for the occasional presence of a small granulo-striate zone adjacent to the path marked by the velar edge.

MEASUREMENTS: Hinge length - sulcal height in microns of two female specimens from the type locality.

1770-1030 (holotype), 1670-1010. In both specimens the sulcal height excludes the considerable velar width.

DISCUSSION: The shape and proportions of the lobes of both species of Tinotoxotis are much alike. T. praegnans is distinguished from the type species by its size, the shape of its crumina (relatively wider), the form of its subcruminal morphology (cf. descriptions), and its less developed lobal and cruminal ornament.

OCCURRENCE: Wenlockian deposits in the N Welsh Borderlands. Material is not common and complete valves are rare. The distinctive crumina is often the only part of the valve remaining.

Tickwood Beds: Harley Hill Road (locs. 48a-c).
Acklands Coppice (loc. 42a).
Tickwood (locs. 44c, d).
Genus NUDISTA gen. nov.

DERIVATION OF THE NAME: From the Latin nudus, naked, and the suffix - ista, signifying an agent, one who; alluding to the appearance of the female valves - virtually stripped of ornament. Gender, feminine.

TYPE SPECIES: Nudista cariticuspis sp. nov., Pl. C6, figs. 1, 2; from the Wenlockian of Gloucestershire.

SPECIES: Only the type species.

DIAGNOSIS: Amphitoxotidinae with an entire, broad syllobium, dorsal margins of the lobes straight - along the hinge line, and a moderately wide velum restricted gradually posteroventrally and virtually absent precruminally. Females are smooth; tecnomorphs show a tendency to be reticulate. The velar edge across the crumina has an overall curve towards the margin, is disturbed at mid-length by a small deflection in the reverse direction, and becomes obsolete anteriorly. The torus remains behind the crumina.

DISCUSSION: The dimorphism in this genus affects not only the antero-ventral region of the carapace but also the ornamentation. This type of dimorphism has been illustrated in the craspedobolbinines Clintiella (especially C. hyrsiniana Martinsson, 1962 and C. cf. hyrsiniana of Martinsson 1962, figs. 86II-I, K, L) and Aitialia (see A. calcarata Martinsson, 1962, figs. 80A-C), and has been noted to a lesser extent in the amphitoxotidine, Vinculovaliger Martinsson, 1962. In C. hyrsiniana the females are reticulate, while the males are coarsely granulose.
Reticulostriation is found on the males of *Vinculoveliger*, but is much less conspicuous - if present at all - on the lobes of the corresponding females. The dimorphism in *Nudista* is quite marked, but from the evidence available there is little reason to doubt that the dimorphs have been "matched" correctly.

The lobes of *Nudista* bear close resemblance in shape to - but are more elevated than those of - *Tinotoxotis*. These genera are distinguished chiefly using the form of the velum (substantially wider and more extensive in *Tinotoxotis*) and, to a lesser extent, the subcruminal morphology (cf. respective diagnoses).

The ventral morphology of the crumina in *Nudista* is very similar to conditions prevailing in *Undipila*. *Nudista* differs from *Undipila* most importantly in the dimorphic nature of its ornament (involving a total lack of reticulation in its females), but also by the absence of lobal cusps, and the virtual obsoletion of the velum in front of the crumina.

*Nudista* is distinguished from *Aetholicotoxotis* by the obsoletion of its velar edge anteriorly on the crumina, the lack of a precruminal velar frill, and the absence of lobal cusps.

**OCCURRENCE:** The Wenlockian of the Tortworth inlier.

*Nudista cariticuspis* sp. nov.

*Pl. C6, figs. 1-11.*

**DERIVATION OF THE NAME:** From the Latin *caritus*, devoid of, and *cuspis*, a point; referring to the absence of lobal cusps.

**HOLOTYPE:** A female left valve, DAS 47276; *Pl. C6*, figs. 1, 2.

**TYPE LOCALITY AND TYPE STRATUM:** A small exposure on the NW side of Drinkmarsh Quarry, near Whitfield, the Tortworth inlier, Gloucestershire (loc. 11); the sandy limestone band at the base of the Drinkmarsh Beds.
DIAGNOSIS: As for the genus.

DESCRIPTION: All of the lobal and sulcal elements are easily distinguished. Dorsally the syllobium is broad; below mid-height it tapers fairly quickly, but gradually increases in elevation. The preadductorial node is elongate, knob-like and slightly inclined forwards. The anterior lobe and, more noticeably, the syllobium each have a low, narrow lobal connection to the preadductorial node. None of the lobes project above the hinge line; the syllobium terminates in a broad area along the hinge line and the dorsal region of the anterior lobe is never cusp-like though, characteristically, the anterior margin of this lobe is continued for a short distance along the hinge line above the prenodal sulcus. In tecnomorphs the ventral margin of the anterior lobe - bounded just below mid-height by the anteroventral depression - is noticeably wider than its dorsal region. Both syllobium and preadductorial node are more elevated than the anterior lobe.

The long adductorial sulcus is approximately twice as wide as, but not much deeper than, the prenodal sulcus. In some specimens the prenodal sulcus shallows slightly near the hinge line. The preadductorial node, almost touching the dorsal margin, never allows the two sulci to meet.

In well preserved tecnomorphs long narrow tubules are visible on the anteroventral and ventral parts of the velum; at least eight of them stem from the region of the well developed anteroventral depression. A very gradual posteroventral velar restriction is discernible in tecnomorphs; postcruminally in females (and posteriorly in tecnomorphs) the velum narrows gradually, becomes ridge-like and mostly lacks any signs of tubules. There is an ornamental ridge, parallel and close to the outer side of the velar edge, from the point of velar restriction to the anterior cardinal corner. Fine wrinkles occur concentrically near the velar edge. In front of the anterior lobe in females, a very narrow
ridge - presumably homologous with the velum - forms the anterior boundary of the shell in lateral view.

The conspicuous crumina is well set off from the valve surface, and normally extends from below the posterior limit of the adductorial sulcus to below the anterior margin of the anterior lobe. The crumina does vary slightly in shape, being rather more elongate in a number of specimens (including the holotype). A toric ridge is present postcruminally (near the velar edge) in females and on the ventral part of the velum in tecnomorphs. The subcruminal morphology is given in the generic diagnosis. It may be added that in most of the females examined, a small pit-like scar is found inside the velar edge at cruminal mid-length.

The great majority of females are completely smooth, though a few specimens show indistinct pimple-like processes sparsely scattered on the posteroventral margin of the syllobium or, rarely, a fine reticulo-striation on the crumina. Reticulation occurring mainly on the anterior lobe and on the ventral and posterior regions of the syllobium, is variably present in tecnomorphs; otherwise the valves are smooth.

**MEASUREMENTS:** Hinge length - sulcal height (including velar width) in microns of specimens from the type locality.


Tecnomorphs: 1230-875, 1225-880 (the only two specimens which could be considered as possible males).

**DISCUSSION:** Except for the random occurrence of small, blunt processes on some valves and slight differences in the shape of the crumina, the range of variation expressed by the females (over 60 complete and fragmentary specimens) is negligible.

The tecnomorphs, on the other hand, are more enigmatic. In spite of considerable efforts to find a reticulate female for these tecnomorphs
(or a smooth tecnomorph for the females in question), none was collected. Indeed, from the available evidence I have concluded that the few reticulate tecnomorphs are the dimorphs of the smooth females. There are no other concomitant specimens which could possibly be considered as alternative "partners" for either dimorph and, more importantly, apart from the obvious ornamentational differences, the reticulate tecnomorphs are in every respect morphologically harmonious with the smooth females. The relatively small number of tecnomorphs found is also somewhat perplexing. Over sixty females are known but, surprisingly, only about ten tecnomorphic valves (nearly all of which are damaged) were recovered from large amounts of limestone, and of these only two specimens could possibly be considered as adults (both were equal in size to some of the smaller females). The reticulation is much more prominent in some tecnomorphs than in others, though in lobal, sulcal and velar characteristics all of the tecnomorphs show homogeneity.

OCCURRENCE: Only from the Wenlockian deposits at the type locality, Gloucestershire.

Brinkmarsh Beds: Brinkmarsh Oy., limestone band (loc. 11);
about ten tecnomorphs and over sixty females.

Genus **UNDIPILA** gen. nov.

DERIVATION OF THE NAME: From the Latin *unda*, a wave, and *pila*, a ball; alluding to the shape of the deflected velar edge on the crumina. Gender, feminine.

TYPE SPECIES: *Undipila repanda* sp. nov., PI. C9, figs. 1-3, 8, 10, 12; from the Wenlock Series of Shropshire.
SPECIES: Undipila repanda sp. nov.

Undipila subspissa (Jones & H.Woll 1886)

Undipila cortinata sp. nov.

Undipila gibba (Salter, 1848)

DIAGNOSIS: Amphitoxotidinae having lobes entire and reticulate, and across the crumina a velar edge which is both broadly curved towards the margin and disturbed at mid-length, usually by a small, sharper deflection (associated with a round pit) pointing away from the margin. The velum is generally well developed; it is present precruminally and is restricted posteroventrally. The torus does not advance onto the crumina.

DISCUSSION: The type species of Undipila has been figured elsewhere (Martinsson 1962, figs. 98C, 100D); only the subcruminal morphology was illustrated and the unnamed species was said to belong to an undescribed genus. The new genus has known representatives in Britain, and specimens from the McKenzie Formation (of probable Wenlock - Ludlow age) of Pennsylvania which were treated by Swartz (1936, pl. 78, figs. 8i-1; pl. 84, figs. 3e, f) under the name Beyrichia moodeyi Ulrich & Bassler, 1908 - but which are not conspecific with the type species of Velibeyrichia (see Martinsson 1962, p. 232) - appear to be congeneric. Swartz's illustrations include a ventral view of a female valve showing the characteristic deflection (and disturbance?) to the velar edge on the crumina. It is also possible that some of the reticulate "Beyrichia" species (e.g. Beyrichia veronica) established by Ulrich & Bassler (1923) from the Silurian of Maryland may have close affinities to Undipila; However, these American taxa (see also Velibeyrichia in Hoskins 1961, and in Swartz & Whitmore 1956) would much benefit from a first hand revision where priority is given to the collection and description of female specimens, thus enabling generic assignments to be made with much more certainty than has been possible hitherto.
The velar and lobal arrangements and the ornamentation of this genus are closely similar to *Amphitoxotis* Martinsson 1962. The type genus is differentiated mainly on the absence of any disturbances to the distal regions of the velar edge on the crumina, together with minor differences in lobation (e.g. in *Amphitoxotis* the preadductorial node protrudes above the hinge line in both dimorphs) and cruminal ornament.

**OCCURRENCE:** In Wenlockian and Ludlovian deposits; the Welsh Borderland and English W Midlands. May also occur in the Silurian of America.

**Undipila repanda** sp. nov.

Pl. C9, figs. 1-16.

1886 *Beyrichia Maccoyiana,* Jones; Jones & Holl, p. 357, pl. XII, figs. 11a-c, 12, 13a, b.

1962 Martinsson, figs. 98C, 100D (illustrated as an undescribed genus).

**DERIVATION OF THE NAME:** From the Latin *repandus,* bent backwards; referring to the mid-point deflection of the velar edge on the crumina.

**HOLOTYPE:** A female left valve, DAS 47178; Pl. C9, figs. 1-3, 8, 10, 12.

**TYPE LOCALITY AND TYPE STRATUM:** The bottom of the well exposed face at the old workings on the W side of Lincoln Hill, approximately 250 m N of the River Severn and 500 m NW of the bridge at Ironbridge, Shropshire (loc. 49c); Wenlock Limestone.

**DIAGNOSIS:** *Undipila* species with a marked distal deflection to the curved velar edge on the crumina. All of the lobes are moderately wide; prenodal sulcus comparatively indistinct. Syllobial and anterior lobal cusps and posteroventral velar restriction are all variably developed. The lobal reticulation consists of a network of medium sized meshes. Crumina mostly granulose.
DESCRIPTION: The anterior lobe is rather flat, and wider than the preadductorial node. The adjacent prenodal sulcus is shallow and becomes distinct only in its dorsal regions. A low, indistinct lobal connection joins the preadductorial node to the syllobium, preventing the long, vertical adductorial sulcus from linking with the anteroventral region of the valve. This sulcus is much deeper than, and about twice as wide as, the prenodal sulcus. The elongate preadductorial node does not appear above - and in most specimens just fails to reach the level of - the hinge line. In tecnomorphs this node for much of its length is joined to the widest (central) part of the anterior lobe by a flat, vaguely defined area which includes the virtually obsolete, ventral section of prenodal sulcus; the occurrence of reticulation over this area makes it difficult to determine the exact limits of the sulcus and lobes. The preadductorial node is slightly more elevated than the anterior region of the valve. The anteroventral depression is only faintly developed; its dorsal boundary coincides with a curve in the outline of the lobate area.

The syllobium is broadest at mid-height and has an evenly curved posterior outline; its anterior margin is almost straight. Cusps on the anterior lobe and syllobium may be developed (e.g. most of the specimens from Lincoln Hill and Wren's Nest) or reduced (e.g. characterised by material from the Harley Hill road section) (see "Discussion" below). The cusps become less rounded the higher they project above the hinge line. The syllobial cusp is usually slightly larger than the similarly shaped anterior lobal cusp.

The velum is well developed and quite wide anteroventrally and ventrally; anteriorly and posteriorly it narrows and becomes ridge-like. Its restriction, posteroventrally, may be sharply angular (e.g. most Lincoln Hill material) or gradual (e.g. most Harley Hill material). In tecnomorphs long, narrow, tubules are seen along the widest regions of the velum; in females, tubules are visible in the short postcruminal
section (usually 4-5 in number) and in the ventral part of the precruminal section of the velum. The latter part of the velum is quite wide ventrally but becomes ridge-like towards the anterior cardinal corner. Both sides of the velum typically have fine, concentric striae on their surfaces. Well below the velar edge in tecnomorphs a weakly developed toric ridge occurs; in females a similar ridge is usually present for a short distance postcruminally.

The velar edge passes over the crumina slightly diagonally, linking pre- and postcruminal sections, in the manner given in the generic and specific diagnoses. Often seen is a minute, round cavity, tucked admarginal of the velar edge mid-point on the crumina. The crumina is striate immediately abmarginal of the velar edge, whilst laterally it is mostly evenly granulose; adjacent to the lobes, and between the velar edge and the margin, the crumina is smooth. The marginal structure in each valve consist of a single ridge (parts of which are commonly seen in lateral view) crowned with minute, closely spaced tubercles. Posteriorly, near the cardinal corner, these marginal ridges characteristically diverge away from the free margin for a short distance, and as a result the combined outline (in carapaces) of both ridges has (in posterior view) an elongate ovoid shape (comparable conditions also occur in U. subspissa and U. cortinata).

All of the lobes are reticulate (for further comments on the ornamentation see "Discussion"). The adductorial sulcus and dorsal part of the prenodal sulcus are smooth.

MEASUREMENTS: Variation in the size of adult specimens is characteristic of this species.

Hinge length - sulcal height (excluding velar width) in microns of representative female valves.

Harley Hill (loc. 48c): 1350-880, 1320-850, 1300-780, 1270-800, 1255-795, 1235-815, 1215-750, 1210-805, 1180-760, 1175-740.

Acklands Coppice (loc. 42a): 1295-845, 1275-840, 1260-775, 1250-815, 1210-810.

DISCUSSION: A considerable amount of variation has been noted in the hundreds of valves studied, though in practical terms it has proved unreasonable to define more than one species.

It is possible to recognise two main variational groups whose end members - in isolation - might be considered as separate species. The differences involved are typified by specimens from the Harley Hill road section and from the nearby Lincoln Hill locality. Compared with material from Harley Hill, most of the Lincoln Hill specimens are smaller, have a more angular restriction to the posteroventral part of the velum and have lobal cusps which appear higher and more pointed above the hinge line. In all other respects the material from both localities is identical. Moreover, intermediate forms exist - some specimens from Harley Hill tend to have more pointed lobes, while some valves from Lincoln Hill show rounded cusps and/or a gradual posteroventral velar restriction - and it has not been possible to isolate any one feature which consistently separates the two groups.

Variation in features such as the shape of the velum is not unusual in the Beyrichiacea. Fairly "stable variational groups" involving the shape of the syllobial cuspidal plica were discussed and illustrated for Craspedobolbina percurrrens by Martinsson (1962, p. 166, figs. 64-66); variation in the shape of the posteroventral part of the velar edge has been recorded (see Hemsiella loensis and H. hemsiensis in Martinsson 1962, figs. 106, 108) and substantial differences in the size of adult specimens within a species is also known (see measurements for Craspedobolbina unculifera and C. percurrrens in Martinsson 1962, pp.156, 166).
Another continuous variation concerns the amount of reticulation present on the dorsal region of the anterior lobe; the normal condition is that ornament is effaced from parts of this area, though the lobe in question - particularly in small instars - can be entirely reticulate. No correlation has been detected between the area of effacement and left or right valves, females or tecnomorphs.

In some tecnomorphs (from a number of localities including Lincoln Hill and Harley Hill) the velum shows a fine, incipient border crest involving, very delicate denticles. These tecnomorphs, most of which are small instars, are similar in all other features to - and have to be thought conspecific with - the large number of other tecnomorphs studied.

Jones & Holl in 1886 figured three specimens of _U. repanda_ under the name _Beyrichia Maccoyiana_, Jones: a tecnomorphic carapace, BM I 1950 (pl. XII, figs. 11 a-c); a right valve tecnomorph, BM I 2372 (pl. XII, fig. 12); a female right valve (anterodorsal part now broken off), BM I 2375 (pl. XII, fig. 13 a, b).

The differences between _U. repanda_ and _U. subspissa_ are discussed under the latter species.

**OCCURRENCE:** The Wenlock and Ludlow Series; the Welsh Borderland and English W Midlands.

- **Elton Beds:** ?Hillichope (loc. 59); fragmentary tecnomorphs.
  - Shadwell Rock Oy. (loc. 61).
- **Wenlock Limestone:** Much Wenlock, Windmill (loc. 54).
  - Lincoln Hill (locs. 49a-c).
  - Wren's Nest (locs. 27a, ?c).
- **Tickwood Beds:** Harley Hill Road (locs. 48b, c).
  - Longville (loc. 41).
  - Tickwood (locs. 44b-d).
  - Acklands Coppice (locs. 42a, b).
  - Benthall Edge, East (locs. 43a, b).
Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39).
Also present in topmost (undifferentiated) Wenlock Shale of Malverns area: Storridge (loc. 20).

**Undipila subspissa** (Jones & Holl, 1886)

Pl. C10, figs. 1-11.

1885 *Beyrichia Kloedeni*, M'Coy, var. *intermedia*, Jones, subvar. *subspissa*, nov.; Jones & Holl, pp. 337, 352, pl. XII, fig. 3.
1934 *Beyrichia intermedia subspissa* (Jones & Holl); Bassler & Kellett, p. 195.

LECTOTYPE: Designated hero. A tecnomorphic carapace, BM IN 52439 (= Vine coll. no. XLIV^), Jones & Holl 1886, pl. XII, fig. 3; herein Pl. C10^, fig. 5.

TYPE LOCALITY AND TYPE STRATUM: The literature relating to this matter is somewhat contradictory. The type (and only figured) specimen belongs to the Vine collection (obtained from Mr. Maw's washings) and was stated by Jones & Holl to be from, "Bed no. 46"; this "bed" represents, "washings from shale over the Wenlock Limestone .... obtained from the railway cutting between Wenlock and Buildwas" (Vine 1887, p. 233, referring to, "Mr. Maw's notes on the localities"). In contrast to this information, Vine himself (op. cit., table, p. 242) records "Beyrichia subspissa" from only two localities (nos. 43 and 25), both of which occur below the Wenlock Limestone (= Coalbrookdale Beds and Tickwood Beds respectively; see Vine, op. cit., for details). Material identified with the lectotype and described herein, supports Vine's data; consideration of the evidence available suggests that the locality details in Jones & Holl may have been given in error.
DIAGNOSIS: Undipila species with finely reticulate lobes and a comparatively narrow velum. Anterior lobe and prenodal sulcus well defined. The prominent preadductorial node reaches the hinge line. Both syllobium and anterior lobe always have cusps and are somewhat slender.

DESCRIPTION: All of the lobes are well developed and effectively separated by the sulci. There are two rounded cusps above the hinge line; one on the anterior lobe and a slightly larger one on the syllobium. The anterior lobe and syllobium each have low lobal connections to the preadductorial node; of the two, the connection to the anterior lobe is lower, narrower, and much less well defined, though the prenodal sulcus is always separated from the anteroventral depression. The preadductorial node is prominently developed - just reaching the hinge line - and in most cases is slightly inclined forwards. This node overlooks the anterior lobe and is almost as elevated as the higher, ventral part of the syllobium. The widest region of the syllobium occurs just above mid-height, away from which the lobe narrows gradually to its broadly U-shaped connection with the preadductorial lobe. The anteroventral depression is not deep but is recognised in the angle formed below the region of the lobal connections.

In almost all of the tecnomorphs collected, the velum is characteristically broken - its remnants appearing merely as a narrow, ridge-like structure - on the periphery of the lobes; even when reasonably well preserved, the velum is quite narrow. The velum has a very gradual posteroventral restriction and maximum width anteroventrally; velar tubules are sometimes visible. Both behind the posteroventral restriction and in front of the crumina the velum is ridge-like. A toric ridge is present in tecnomorphs; the line of fracture commonly present along the velum always occurs immediately next to the torus. In females a faint ridge occurs adjacent to the postcruminal part of the
velar edge. The path taken by the velar edge across the crumina is as given in the generic diagnosis.

All of the lobes and occasionally the ventral part of the adductor sulcus are evenly covered with fine reticulation (hardly preserved in the lectotype).

MEASUREMENTS: Hinge length - sulcal height (including velum) of female valves in microns.

Coalbrookdale Beds: Coalbrookdale (loc. 40): 1380-980, 1240-925.

DISCUSSION: Mention of "Beyrichia" subspissa in previous papers has been confined to lists (Smith 1892, table opposite p. 158; Ulrich & Bassler 1908; Bassler & Kellett 1934). Apart from the type specimen, four other valves now referable to subspissa have been noted in literature: three tecnomorphs in slide BM I 2370 (Smith coll. no. 20) from the railway cutting at Coalbrookdale, treated by Jones & Holl (1886, p. 358) under "Beyrichia Maccoyiana, Jones"; one of six specimens in slide BM I 2381 (Smith coll. no. 31) from the railway cutting, side of R. Severn, Ironbridge, referred by Jones & Holl (1886, p. 354) to "Beyrichia Kloedeni var. subtorosa, Jones".

A number of minor differences are used to separate this species from the type species. The velum in U. subspissa, although rarely preserved complete, is appreciably narrower than in the type species; generally U. subspissa also has a more elevated anterior lobe, a deeper, somewhat more distinct prenodal sulcus and a more conspicuous preaductor sulcus. U. subspissa further differs from U. repanda by the more slender appearance to its anterior lobe and syllobium, and perhaps most noticeably - by its finer reticulation. These differences are particularly apparent when the two species in question occur within the same sample (as at Benthall Edge, Severnside; loc. 39).
Undipila cortinata sp. nov.


DERIVATION OF THE NAME: From the Latin cortina, a curtain, and the suffix -atus, provided with; alluding to the appearance of the precruminal part of the velum.

HOLOTYPE: A female left valve, DAS 47203; Pl. C10, figs. 12, 14.

TYPE LOCALITY AND TYPE STRATUM: The SW side of the disused Brinkmarsh Quarry near Whitfield, the Tortworth inlier, Gloucestershire (loc. 12); Pycnactis band, near the base of the Brinkmarsh Beds.

DIAGNOSIS: Undipila species with a wide precruminal velar section, a wide adductorial sulcus, and a finely striate crumina. Quite coarse reticulation occurs on the lobal connections and all lobes except the preadductor nodal in females. Cusps weakly developed. Preadductor nodal slender.

DESCRIPTION: The shape of the syllobium is a characteristic feature. In adults the syllobial cuspidal region is rounded and situated anteriorly, overlooking the adductorial sulcus; the cusp lies on, or just above, the hinge line and continues posteriorly in a fairly straight line towards the posterocardinal corner. Below mid-height the syllobium narrows appreciably as it swings forward and connects with the preadductor lobe. The boundary between the anterior margin of the syllobium and the adductorial sulcus is normally well demarcated along a line (marking the rather abrupt termination of syllobial ornament) from the cuspidal region to the base of the adductorial sulcus.
From this boundary the adductorial sulcus characteristically slopes gently towards its deeper, central regions; this "shelf" is best developed in the curved, ventral half of the sulcus. The adductorial sulcus in lateral view often appears more open ventrally than dorsally.

The preadductorial node is slender, inclined forwards slightly, and almost reaches the dorsal margin of the shell. It is joined to both of the other lobes in the area above the indistinct anteroventral depression. The lobal connection to the syllobium is low and quite narrow, and the corresponding one to the anterior lobe is, in the larger tecnomorphs, obscured by reticulate ornamentation. The anterior lobe is inconspicuously developed; dorsally, its cuspidal region rests on or inconsiderably above the hinge line. The prenodal sulcus is narrow and much less prominent than the adductorial sulcus.

The morphology of the velum in tecnomorphs has to be reconstructed from numerous fragments. It is well developed and visibly tubulous from the anterior cardinal corner to the point of (fairly gradual) posteroventral restriction, after which it continues as a velar ridge to the posterocardinal corner. In females too, the position of the posteroventral restriction can be recognised - as a faint, change in the velar outline just behind the crumina. Precruminally the velum is wide and in lateral view its anterior outline is drooped down in a characteristic fashion. Tubules are present along nearly all the length of the female velum, but usually are visible only when valves are viewed obliquely. For some distance behind the crumina there is a toric ridge running close to the velar edge; a similar ridge occurs, ventrally, in tecnomorphs.

The crumina is inclined at an angle to the hinge line and incorporates very little of the valve surface (most of the anterior lobe and pre-adductorial node, and all of the adductorial sulcus are unaffected by its development). The velar edge across the crumina has a weak overall deflection towards the margin and just fails to connect with the precruminal
section of the velum. The disturbance to the distal region of the velar edge is - as far as can be discerned (most cruminae are ill-preserved) - minimal, though characteristically there is (just admarginally) a small pit associated with a slight swelling.

In the larger of the extant tecnomorphs the lobes and ventral part of the prenodal sulcus are coarsely reticulate. The few small tecnomorphs available lack ornament on the prenodal sulcus and lobal connections to the syllobium, and have a moderately well developed anteroventral depression.

All of the females have reticulation on the anterior lobe and syllobium; the meshes are large, and about eight in number across the widest part of the syllobium. Ornamentation is absent from the preadductorional node of extant females. Fine striae cover the crumina and parts of the velum.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of female specimens from the type locality.

1500-1080 (holotype), 1385-940, 1310-920 (all from the same sample).

There are only four reasonably complete female specimens available for measurement, but it is obvious even from the broken valves that the size range of adults is quite considerable.

DISCUSSION: There is no difficulty in separating this species from U. repanda or U. subspissa; its velar arrangement, sulcal width, and syllobial morphology are characteristic and the type of cruminal ornament is a further distinguishing feature. U. cortinata is much closer to U. gibba (see "Discussion" of the latter species).

The subcruminal morphology of U. cortinata is apparently nearer than other congeneric species to conditions found in Amphitoxotis.

OCCURRENCE: Known only from the basal Wenlockian at the type locality in the Tortworth district.
Brinkmarsh Beds: Brinkmarsh Qy., *Pycnactis* band (loc. 12a-d); over sixty specimens.

Complete valves are rare. Furthermore, the great majority of specimens collected are females; only about 15 tecnomorphs - most of them immature - were obtained from a considerable amount of washed material.

**Undipila gibba** (Salter, 1848)

Pl. C8, figs. 9-15.

1848 *Beyrichia gibba*, Salter; Salter in Phillips, p. 352, pl. VIII, figs. 17, 18.

1916 *Beyrichia Kloedeni* (McCoy); Cantrill et al., p. 176.

1934 *Beyrichia gibba* Salter; Bassler & Kellett, p. 192.

1938 *Beyrichia gibba* Salter; Stubblefield, p. 36.

**TYPE SPECIMENS:** This species was originally described using "two or three specimens" (Salter op. cit.), two of which - both internal casts of tecnomorphic left valves - were figured. Cantrill et al. (1916, p. 176) state that Salter's originals are (Inst. Geol. Sci.) nos. 26907 and 26908. In a later paper (Stubblefield 1938, p. 36) dealing specifically with, "The types and figured specimens in Phillips and Salter's palaeontological appendix", specimen no. 26907 is said to be the original of Salter, pl. VIII, figs. 17 upper, 17a and the only surviving syntype; specimen no. 26908 (of Salter pl. VIII, figs. 17 lower, 18a) could not be traced.

It is now known that both 26907 and 26908 are extant in the collections of the Inst. Geol. Sci., London; however, these specimens are at variance with the information documented in Cantrill (op. cit.) and Stubblefield (op. cit.). The rock piece GSM 26908 contains a "ringed" female left valve external mould (badly damaged by a previous attempt at preparation) and a very small, poorly preserved, tecnomorphic
left valve internal mould; the old label attached to the rock reads "Wenlock Shale, Slate Mill, Pembroke" and "pl. 8, fig. 17, Beyrichia gibba." A later hand has crossed through the plate data and written, "kloedeni with hypertrophied antero-ventral lobe" (= crumina) over the word gibba. The tiny rock piece GSM 26907 contains only the internal mould counterpart to the female on GSM 26908. None of this material is considered identifiable with Salters figures, though it is undoubtedly conspecific with the (solitary) beyrichiacean species present (in some abundance) at Slate Mill.

**TYPE LOCALITY AND TYPE STRATUM:** "Slate Mill", on the B 4327 road, about 3.5 km N of Dale, Pembrokeshire; Coraliferous 'Series', of probable Wenlock age.

**DESCRIPTION:** The syllobium is broad dorsally, but tapers fairly quickly below mid-height. The rounded cuspidal region of the syllobium overlooks the adductorial sulcus, and is projected posteriorly along the hinge line. The shape of the syllobium, its boundary with, and morphology of, the adductorial sulcus is as described for *U. cortinata*. The prenodal sulcus is narrow, the lobal connections weak. The antero-ventral depression has an open, gently curved dorsal margin extending from the base of the wide, rather flat anterior lobe to the ventral end of the syllobium.

Numerous long, narrow tubules are discernible anteroventrally and ventrally on the wide tecnomorphic velum. Posteroventrally, the velum is gradually restricted. The velar edge on the crumina is weakly deflected towards the margin and at mid-length there is a small (ad marginal) pit. Knowledge is lacking of the form of the velum in front of the crumina.

Small instars are almost entirely reticulate; only the velum, the adductorial sulcus, and the dorsal part of the prenodal sulcus lack the large, polygonal meshes. With growth, reticulation recedes from
parts of the valve (viz. the narrow prenodal sulcus and the region of the lobal connections), and becomes much finer.

**MATERIAL:** All material is preserved as moulds. Moreover, every specimen is in some way incomplete or distorted. Casts were made of many tens of valves.

**MEASUREMENTS:** The nature of preservation precludes accurate measurement. Approximate hinge length (in microns) of some of the largest valves collected (Slate Mill; loc. 13).

- Female: 1660.
- Tecnomorphs: 1760, 1645, 1500, 1450.

**DISCUSSION:** *Beyrichia gibba* Salter, 1848 was one of the earliest described British beyrichiacean species, but it subsequently received little attention. McCoy (1851, p. 135) thought that, "The *B. gibba* figured by Mr. Salter ..." was "... a very trifling variety of ..." his own *B. kloedeni*. Jones too (1855b, p. 166; 1881c, p. 345), relegated the species to a junior synonym of *Beyrichia kloedeni* M'Coy, and its treatment by other authors (e.g. Bassler & Kellett 1934) has been merely superficial. In the original description the species was discussed under two names; in the text (Salter in Phillips 1848, P. 352) and plate explanation it was called *B. gibba*, elsewhere (op. cit. p. 234) the objective synonym *Beyrichia gibbosa* Salter was used.

A more detailed account of this taxon is prevented by the nature of its preservation and, by the same token, the positive identification of the species may not be possible outside the type area. The lobal arrangements (particularly of the syllobium) and sulcal morphology of *U. gibba* are seemingly very similar to conditions in *U. cortinata*. The latter species is distinguished by its coarser reticulation (adults), its slender preadductorial node and – in the extant females – its striate crumina. Furthermore, the lobal reticulation in *gibba* is more
extensive in the smaller - compared to the more mature - instars, whereas in *cortinata* this situation appears to be reversed (additional tecnomorphic material of the latter species is needed to confirm this observation).

**OCCURRENCE:** Only in the cleaved mudstones of the type locality (Minsle inlier), Pembrokeshire.

Coraliferous 'Series': Slate Mill (loc. 13); over 200 internal and external moulds.

Bassett (1971, p. 218) suggests that the locality is possibly high in the Coraliferous 'Series' (probably Wenlock age).

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**Genus AETHOLICOTOXOTIS** gen. nov.

**DERIVATION OF THE NAME:** From the Greek *aitholikos*, a pimple; and *toxotos* (as in the type genus *Amphitoxotis*); with reference to the (weak) tuberculation on the lobes. Gender, feminine.

**TYPE SPECIES:** *Aetholicotoxotis nidicola* sp. nov., Pl. C11, figs. 13,14,16, from the Wenlockian of the Wren's Nest, Worcestershire.

**SPECIES:** Only the type species.

**DIAGNOSIS:** Sparingly tuberculate Amphitoxotidinae with well developed lobes and sulci, a velum which is fairly wide - even precruminally, and a continuous velar edge over the crumina which has an overall curve towards the margin modified distally by a distinct deflection pointing away from the margin. Anterior lobe and syllobium with cusps. The torus does not traverse the crumina; there is no border crest.

**DISCUSSION:** In its subcruminal morphology this genus shows similarities to the British amphitoxotidines, *Tinotoxotis, Nudista, Osmotoxotis* and, particularly, *Undipila* (cf. the respective diagnoses). *Aetholicotoxotis*
is distinguished from each of these genera by either its lobal proportions, velar morphology, or ornamentation, or by a combination of these features. In particular it differs from Tinotoxotis in lobal and velar morphology, from Osmotoxotis by its ornamentation, the form of the velum (in front of the crumina) and the absence of a border crest, and from Nudista by the arrangement of the velum and the proportion and elevation of the lobes. In contrast to the entirely reticulate Undipila - with which it otherwise shows a likeness in both lobation and velar morphology, and also shares an almost identical form of subcruminal morphology - the genus Aetholicotoxotis is tuberculate.


Aetholicotoxotis nidicola sp. nov.

Pl. Cll, figs. 13-16.

DERIVATION OF THE NAME: From the Latin nidus, a nest, and the suffix -cola, an inhabitant; with reference to the type locality.

HOLOTYPE: A female right valve, DAS 47135; Pl. Cll, figs. 13,14,16.

TYPE LOCALITY AND TYPE STRATUM: The crest of the exposed ridge on the W side of the Wren’s Nest, Dudley, Worcestershire (loc. 27c); Wenlock Limestone.

DIAGNOSIS: As for the genus.

DESCRIPTION: Based on female valves only.

The anterior lobe is stoutly developed and extends above the hinge line to the same height as the anteriorly sited syllobial cusp. The preadductorional node is quite slender, has a narrow crest, and terminates just below the two adjacent lobes. Both cusps and the preadductorional node are weakly pointed. The sulci are fairly deep and prominent; none
of the lobes connect to each other. The syllobium gradually decreases in elevation and increases in width towards the hinge line; postero-dorsally this lobe has an evenly rounded margin around a field of low elevation.

In front of the crumina the velum is quite wide and faintly tubulous. Though the postcruminal velar section varies in width it is never very narrow, and often flares out some distance from the nearby syllobium. Immediately behind the crumina velar tubules are again discernible. The velar edge passes over the crumina to link together the pre- and postcruminal portions of the velum (see "Diagnosis"). A toric ridge is present, but only behind the crumina.

Very little ornamentation is present in the extant material. Small tubercles - hardly developed in the holotype - are scattered over the lower regions of the syllobium. No ornament has been detected on the other lobes or in the sulci. In well preserved specimens very fine striae are traced on the crumina, particularly ventrally. A minute hole is commonly seen just 'inside' the velar edge deflection on the distal part of the crumina.

MATERIAL: Tecnomorphs of this species have not been identified. Some ten female valves (mostly incomplete) and twelve cruminae have been collected.

MEASUREMENTS: Hinge length - sulcal height (including velar width) in microns of females from the Wren's Nest.

1510-980 (holotype), 1500-1010.

DISCUSSION: Sufficient material is known of this species to establish its morphology and taxonomic position; there is no point in leaving the species unnamed just because its tecnomorphs are unknown.

The extant material is fairly homogeneous; the width of the postcruminal part of the velum provides the most variable feature.
OCCURRENCE: So far, only from the Wenlock Series of the Wren's Nest inlier.

Wenlock Limestone: Wren's Nest (locs. 27c, d, f).

Genus OSMOTOXOTIS gen. nov.

DERIVATION OF THE NAME: From the Greek osmos, push, and toxotis (as in the type genus Amphitoxotis); alluding to the fancied resemblance of the precruminal section of the velum to the projecting blade of a bulldozer.

TYPE SPECIES: Osmotoxotis phalacra sp. nov., Pl. C11, figs. 1, 4; from the Wenlockian of the Wren's Nest, Worcestershire.

SPECIES: Only the type species.

DIAGNOSIS: Reticulate Amphitoxotidinae with a medium wide, evenly curved, denticulate velum, which in females is more or less confined to a short precruminal section widely separated from the crumina. All lobes entire and stoutly developed; both anterior lobe and syllobium have prominent cusps. Velar edge across the crumina gently deflected overall towards the margin and at mid-length very faintly curved in opposite direction; torus remains behind the crumina.

DISCUSSION: The subcruminal morphology of this genus is similar to conditions found in other British primitive amphitoxotidines such as Tinotoxotis, Undipila, and Nudista. Osmotoxotis is readily distinguished from all of these genera using a combination of lobal and velar characteristics; in particular the occurrence of a precruminal velar constriction or a border crest is unknown in the other genera mentioned. The two latter features do occur in the genus Sarmatotoxotis, which differs from Osmotoxotis in the form of its ornament (tuberculo-retication), subcruminal morphology (both velum and torus extend over
the crumina), and velum (much wider, with a posteroventral restriction).

OCCURRENCE: The Wenlock Series of the Welsh Borderland and English W Midlands.

Osmotoxotis phalacra sp. nov.

Pl. C11, figs. 1-12.

DERIVATION OF THE NAME: From the Greek phalakros, bald-headed; alluding to the somewhat effaced lobal ornament in the later instars.

HOLOTYPE: A female right valve, DAS 47058; Pl. C11, figs. 1, 4.

TYPE LOCALITY AND TYPE STRATUM: The mould-like exposures just N of the long ridge on the W side of the Wren's Nest, Dudley, Worcestershire (loc. 27d); Wenlock Limestone.

DIAGNOSIS: As for the genus.

DESCRIPTION: The anterior lobe, the preadductorial node and the syllobium (in its upper regions) are all vertical. The anterior lobe is about as wide as the preadductorial node and narrows only above the hinge line in its well developed cuspidal section. Just reaching the hinge line and hardly narrowing towards its base, the preadductorial node is linked with adjacent lobes by wide and low lobal connections. The lobal connection below the prenodal sulcus is poorly defined though it always separates this sulcus from the deep anteroventral depression. Ventrally, the prenodal sulcus shallows gradually. The adductorial sulcus is considerably wider and longer than the prenodal sulcus, and becomes somewhat deeper near its base. The syllobial cusp is approximately equal in size to the anterior lobal cusp, and is strongly represented throughout ontogeny; in the larger valves the syllobial cusp is sited anteriorly, is more or less acuminate, and shows a tendency (in some specimens) to be separated from the main section of the syllobium by a
faint depression. In late stage instars the dorsal part of the syllobium is considerably wider than its ventral region; posterodorsally this lobe is less elevated and is evenly rounded.

The velum has a characteristic profile in both anterior and posterior views, the form of which is best ascertained from the illustrations. In lateral view the tecnomorphic velum is widest anteroventrally and grades imperceptibly into a ridge-like feature posteroventrally; valves are gently preplete. In front of, and isolated from the crumina, there is a short section of the velum; postcruminally the velum continues as a ridge. The subcruminal morphology is as stated in the diagnosis; a tiny pit occurs 'inside' the faint curve of the velar edge on the distal part of the crumina. Behind the crumina, parallel to the velar edge, there is a toric ridge; in tecnomorphs the torus is well developed along the ventral part of the velum. The toric structure is normally seen to terminate on reaching the crumina, though perhaps the very faint bend occasionally observed (using special lighting conditions) below the velar edge, represents its continued trace. A denticulate border crest occurs precruminally in females and anteriorly (to approximately below the prenodal sulcus) in tecnomorphs. Velar tubules are seen when valves are viewed obliquely.

The anterior lobe is conspicuous throughout growth, but especially so in the small instars. Compared to the more mature valves, the earlier instars have a broader syllobial cusp which is more directly united with the main section of the syllobium. Modification of ornament is concurrent with the lobal changes. Lobes on the smaller valves are finely and evenly reticulate, sulci are smooth; with growth, this ornament gradually becomes less extensive and, if anything, acquires more of a fine reticulostriate arrangement, (not unlike the pattern found in Vinculoveliger Martinsson). In the largest valves collected the lobal surfaces are virtually unornamented. Abmarginal of the velar edge, the crumina is finely striate.
MEASUREMENTS: Hinge length - sulcal height (including velar width) in microns of specimens from the Wren's Nest.

Females: 1710-1260, 1680-1185.

Tecnornorphs: 1675-1160, 1560-1045, 1210-810, 920-630.

DISCUSSION: The form of the anterior lobe and the changes shown during ontogeny are distinctive feature of this species.

OCCURRENCE: The Wenlockian of the Welsh Borderland and English W Midlands.

Wenlock Limestone: Wren's Nest (locs. 27 b-d, f).

Ledbury (loc. 23).

Old Farm (loc. 16).

Croft Farm (loc. 18a).

Over 70 valves collected, mostly from the Wren's Nest (but including only 3 complete female valves from this locality).

Genus SARMATOTOXOTIS gen. nov.

DERIVATION OF THE NAME: From the Greek sarmatos, a chasm, and toxotis (as in the type genus Amphitoxotis); alluding to the gap between the crumina and the anterior part of the frill.

TYPE SPECIES: Sarmatotoxotis phracta sp. nov., Pl. C12 , figs.1-3,5,6; from the Wenlockian of the Welsh Borderland.

SPECIES: Only the type species.

DIAGNOSIS: Tuberculo-reticulate Amphitoxotidinae with a marked gap between the crumina and the precruminal velar frill. Both velar edge and torus traverse the crumina - the torus uninterrupted, the velar edge with a small mid-length deflection away from the margin. The velum is wide, has a denticulate border crest in both dimorphs, and is restricted posteroventrally in tecnornorphs.
DISCUSSION: The prominent precruminal velar constriction, the denticulate border crest, and the (almost) parallel passage of both velar edge and torus over the crumina, compares well with conditions found in Lophoctenella (cf. L. angustilaqueata), but in other characters, such as the form and ornamentation of the lobes (cf. the crystal system of Lophoctenella), the present material can in no way be regarded as congeneric with that genus. A comparison between Sarmatotoxotis and the other Wenlockian amphitoxotidines which manifests a considerable precruminal velar constriction is found under Osmotoxotis.

Sarmatotoxotis embraces a complex variational range of material, in which seemingly meaningful species boundaries are constantly eroded away. Only the type species, itself broadly based, is distinguished here, but other valves collected from the Malverns area indicates that there may be one, or possibly two more congeneric species.

OCCURRENCE: The Welsh Borderland and English W Midlands; Wenlock Series.

Sarmatotoxotis phracta sp. nov.

Pl. C12, figs. 1-12.

DERIVATION OF THE NAME: From the Greek phraktos, fenced in; alluding to the border crest around the velum.

HOLOTYPE: A female right valve, DAS 47163; Pl. C12 , figs.1-3,5,6.

TYPE LOCALITY AND TYPE STRATUM: The bottom of the well exposed face at the old workings on the W side of Lincoln Hill, approximately 250 m N of the River Severn and 500 m NW of the bridge at Ironbridge, Shropshire (loc. 49c); Wenlock Limestone.

DIAGNOSIS: As for the genus.
DESCRIPTION: The anterior lobal cusp and (anterior) syllobial cusp project above the hinge line. The preadductorional node almost reaches the dorsal margin, and is weakly inclined forwards. The node is linked to the syllobium by a low, slender connection; its attachment with the anterior lobe is much more tenuous. The anterior lobe is comparatively flat, and separated from the preadductorional node by a narrow sulcus. The anteroventral depression is well developed.

The syllobium is entire and has a characteristic shape. The extent and strength of the field of reticulation on this lobe is considerably variable, both between localities and between dimorphs. Typically (for example, at the type locality) in the more mature tecnomorphs it is limited to a narrow ridge-like strip down the anterior part (from cusp to below the adductorial sulcus) of the lobe. Sometimes this reticulate zone is 'broken' or effaced (particularly just below the cuspidal region) or occasionally (for example, in most of the Harley Hill material) it is obsolete or weakly and inconsistently developed. Characteristically the syllobial reticulation is less prominently developed in females; in most of the topotype female valves the reticulation is hardly - if at all - discernible, though in a few cases it approaches conditions found in the male. Elsewhere (for example, Croft Farm) the syllobial reticulation is much more consistently similar to that found in the male.

In tecnomorphs the velum is wide, especially anteroventrally; posteroventrally it is slightly restricted, behind which point it becomes ridge-like. Long, narrow tubules are seen along most of the velum. The precruminal velar section is long, tubulous and denticulate, and is separated from the crumina by a conspicuous gap. A border crest is continuous in tecnomorphs along the anterior and ventral parts of the velar edge. Behind the crumina the velum is ridge-like and its tubulosity is still discernible (under certain lighting conditions), though its width - as often occurs in amphitoxotidines - is variable.
(the typical arrangement is seen in the holotype). The tecnomorphic velum has a toric ridge; in females this ridge and the velar edge pass across the crumina (see "Diagnosis").

Tubercles are scattered over the syllobium (particularly postero-ventrally) and the lower parts the anterior lobe. Reticulation, in addition to that found on the syllobium, is commonly developed on the preadductorial node. The reticulation and the tuberculation are mutually exclusive. There is a small adductorial tubercle in each valve. The ventral part of the crumina is finely striate.

MEASUREMENTS: Hinge length - sulcal height (including velar width) of female valves from the type locality.

1280-950, 1250-880, 1235-920 (microns).

DISCUSSION: Much time has been spent trying to categorise the variations of the syllobial ornament, but it has not been possible to establish sufficiently stable specific groupings; a policy of "lumping" has therefore been adopted. The more important overall trends and some associated localities are given in the description.

OCCURRENCE: Wenlock Series of the Welsh Borderland and English W Midlands.

Wenlock Limestone: Lincoln Hill (locs. 49a-c).

Wren's Nest (locs. 27a, c).

Hurst Hill (loc. 28).

Croft Farm (locs. 18a, b, d).

Benthall Edge, West (loc. 47).

Harley Hill Qy. (loc. 51).

Gleedon Hill (loc. 50).

Much Wenlock, Windmill (loc. 54).

Ledbury (loc. 23).

Tickwood Beds: Harley Hill Road (loc. 48c).
Acklands Coppice (locs. 42a, b).
Tickwood (locs. 44c, d).
Benthall Edge, East (loc. 43a).

Genus **HEMSIELLA** Martinsson, 1962

**TYPE SPECIES:** Original designation of Martinsson 1962, p. 221;

**Hemsiella loensis** Martinsson 1962, p. 223, figs. 106A, 107; from the Ludlovian (Eke Beds) at Lau Backar, Gotland.

**BRITISH SPECIES:** 
- **Hemsiella maccoyiana** (Jones, 1855)
- **Hemsiella** sp. nov. A
- **Hemsiella** ? sp. nov. B

**DIAGNOSIS:** Reticulate Amphitoxotidinae with more or less coherent anterior lobe, preadductorial lobe, and syllobium; the syllobium is broad. The velar edge, but not the torus (if present), continues uninterrupted across the crumina without deflections. Velum in the male with a denticulate border crest. (After Martinsson 1962, p. 222).

**DISCUSSION:** The species groups recognised within **Hemsiella** and their relationships to each other have been extensively treated by Martinsson (1962, p. 223; 1964, p. 133, 1964a, p. 242). The definition of **H. maccoyiana** s. s. has still to be satisfactorily resolved.

**Hemsiella** material has been observed in the Whitcliffian of the Ludlow district but is too poorly preserved to be treated further here. The **Hemsiella cf. hemsiensis** distinguished by Martinsson (1967, p. 371) in mould material from the Upper Leintwardine Beds near Leintwardine has not been identified with certainty, though it may be the species **Hemsiella** ? sp. nov. B of this paper.

It is of general interest to note here that the (only) figured specimen of **Hemsiella dalmaniana** Jones, 1855 (pl. V, fig. 13) has been
located at the Brit. Mus. (Nat. Hist.); no. I 7018. The specimen, a complete female left valve, is well preserved and differs from the lectotype (BM I 7019) of the species (designated by Martinsson 1962, p. 17, fig. 2C) by the absence of reticulation on the crumina. The overall morphology of this specimen closely resembles the female figured as H. cf. maccoyiana from the Leba 1 borehole (Martinsson 1964, p. 134, fig. 4A).

**OCCURRENCE:** In Britain from the Lake District, the Long Mountain, and the Welsh Borderland.

*Hemsiella* is well represented on Gotland and in the nearby E and S Baltic States (Estonia, Latvia, Lithuania, Poland); its presence in the Podolian sequence has been established (Abushik 1971). The genus also occurs in Nova Scotia, Canada (Copeland 1960, 1964), and in Maine, U.S.A. (Berdan 1966; Martinsson in Berry & Boucot, 1971); with the erection of *Hemsiella andincola* Martinsson, 1964 its distribution was extended to South America.

Occurrences are confined to deposits of Ludlovian and Downtonian age; most records are from the Upper Ludlovian.

**Hemsiella maccoyiana** (Jones, 1855)

Pl. C13, fig. 17.

1855 *Beyrichia Maccoyiana*, nov. sp.; Jones, p. 88, pl. V, fig. 14.

1962 *Hemsiella maccoyiana* (Jones 1855); Martinsson, pp. 223, 16, 17, fig. 2B.

1971a *Hemsiella maccoyiana* (Jones 1855); Shaw, p. 597, pl. 109, figs. 1-4.

**LECTOTYPE:** Designated by Martinsson 1962, p. 17, fig. 2B; Jones 1855, pl. V, fig. 14; a poorly preserved tecnomorphic right valve, BM I 6953.
TYPE DATA: From the glacial erratic block no. 2 of Jones, found near Breslau; limestone (late Ludlovian?).


DISCUSSION: This species has not been collected by the writer and is included here on the basis of its treatment in the literature by Shaw (1969, 1971a). As noted by Martinsson (1962, 1964) *H. maccyiana* forms part of a long variational series - incorporating such taxa as *Hemisella dalmaniana* (Jones, 1855) and *Hemsiella elegans* (Boll, 1862) - in which the question of species variation and definition is particularly complex. Though its cruminal striation is perhaps somewhat coarser than is normally found in Baltic material, the female valve illustrated from the Lake District (Shaw 1971a, pl. 109, fig. 3) shows all the essential characteristics of the *H. maccyiana* group (as presently understood), and in accordance with Shaw the British material is given that name.

In his paper on the Leba 1 borehole, Martinsson (1964, pp. 134-5) outlined the differences between the Baltic *H. maccyiana* and the Gotland *H. hemsiensis* and *H. loensis*, and, moreover, indicated that a revisional survey of the first of these species had been undertaken (results as yet unpublished); any taxonomic refinement of the well preserved, but often poorly localised, *H. maccyiana* material from the Baltic will necessitate a reassessment of the British (and other) material. In this respect there has been no attempt to present an extensive list in the synonymy above.

The three amphitoxotidine tecnomorphs from the Wenlock Series of the Welsh Borderland figured as *Beyrichia maccyiana* Jones by Jones & Holl (1886, pl. XII, figs. 11-13) are now referable to *Undipila repanda* gen. et sp. nov.
OCCURRENCE: *H. maccoyiana* was recorded by Shaw (1971a) from the Upper Underbarrow Flags, the Kirkby Moor Flags and the Scout Hill Flags of Westmorland. Shaw (1969) also documents the species from the Whitcliffian and Downton Castle Sandstone of the Long Mountain district, and from the Whitcliff Beds of the Ludlow area.

*H. maccoyiana* and/or closely related (conspecific ?) forms have been described or recorded from N America and from numerous parts of N Europe; these include the Stonehouse Formation of Nova Scotia (Copeland 1960, 1964), throughout the Leba 1 borehole of Pomerania (Martinsson 1964), the Kaugatuma and Ohesaare Stages of Estonia and on Saaremaa Island (Sarv 1968, 1971; Kaljo 1970), and the Lebork and Wejherowo boreholes of N Poland (Uitwicka 1967). Martinsson (1967) has demonstrated that *H. maccoyiana* together with *Neobeyrichia regnans* Martinsson, 1962 forms a characteristic association - found in the submarine exposures just off the SW coast of Gotland - of late Whitcliffian age, and that the former species also occurs as a member of the younger, classic Beyrichienkalk fauna. All these finds are in deposits of late Ludlovian – late Downtonian age.

**Hemsiella** sp. nov. A

Pl. Cl3, figs. 1-5.

REMARKS: Because of the scarcity of material and the nature of its provenance the writer prefers to describe, but not name, the species.

DESCRIPTION: The main, ventral body of the syllobium is raised - though not appreciably so - above the cuspidal part of the lobe; posteriorly there is a narrow field of the syllobium which is conspicuously depressed. All lobes project slightly beyond the hinge line, the preadductorial lobe extending marginally above the anterior lobe and the syllobium. Lobal cusps are gently rounded. The adductorial sulcus, though
fully developed, is not very wide; the prenodal sulcus is much less prominent. Both the preadductorial node and the anterior lobe appear to have been considerably affected by the crumina; the anterior lobe, in particular, is very short.

The extremely large crumina dominates the valve in lateral view; beginning below the middle of the syllobial cusp, it extends (anteriorly) to just in front of the anterior cardinal corner, and (dorsally) far above valve mid-height. The crumina gradually widens anteriorly and acquires maximum width opposite the preadductorial node. The thick, ridge-like velar edge continues across the crumina, becoming obsolete anteriorly; the velum is absent in front of the crumina. Half-way over the crumina, the velar edge curves slightly away from the margin around - at least in one of the females - a minute pit. On the lateral surface of the crumina, along the velar edge, there is a wide, shallow depression.

All lobes and sulci are smooth. The lateral surface of the crumina is unornamented except for a few short, faint striae occurring above the lateral depression. The area between the velar edge and the ventral base of the crumina is indistinctly reticulate; the meshes are relatively fine.

MATERIAL: Just two complete female valves and two fragmentary female valves; all prepared from a single piece of hard, black limestone (GSM Bi 869).

MEASUREMENTS: Hinge length - sulcal height (to the ventral base of the crumina in lateral view) of the figured (female) specimens.

1240-1075, 1220-1020 (in microns).

DISCUSSION: The main features by which this species is distinguished are its total lack of lobal ornament, its very large crumina, and the form of its velar edge on the crumina. Of the previously figured Hemsiella material this species most closely resembles the female from
the Leba 1 core figured by Martinsson (1964, p. 134, fig. 4A) as _Hemsiella cf. maccoviana_ (Jones), but differs from that specimen in the size of the crumina and in details of ornamentation.

The female from Westmorland figured by Shaw (1971a, pl. 109, fig. 3) as _H. maccoviana_ has a crumina similar in shape and size to those described here, but is differentiated by the lavish ornament found on its lobes and crumina. The valves treated here seem sufficiently discontinuous from the _H. maccoviana_ complex to gain specific distinction. It is hoped to obtain more material, particularly a tecnomorph, before naming the species.

There is a difference in the shape of the postcruminal section of the velum between the two females figured here, but as this feature is also seen to vary in other _Hemsiella_ species (see _H. loensis_ Martinsson, 1962, figs. 106A, C-E and _H. hemsiensis_ Martinsson 1962, figs. 108A, _H_) it is considered of little taxonomic significance.

**OCCURRENCE:** Information accompanying the slab of limestone (GSM 869): Usk Valley Reservoir supply tunnel, 2160 ft from NE end, which is 200 ft SE of Dulch Urn, Carmarthenshire.

Concomitant with the _Hemsiella_ specimens are valves of an _Amygdalella_ (Primitiopsacea) species. The deposit in question is probably no older than late Ludlovian.

_Hemsiella ? sp. nov. B_

Pl. C13, figs. 6, 7, 14, 15.

**REMARKS:** This species is a characteristic member of the Upper Leintwardine beyrichiacean fauna. Its generic position is treated with caution and the species remains unnamed until a female valves becomes available.
DESCRIPTION: Both the crescent-shaped anterior lobe and the syllobium terminate along the hinge line; the large preadductorial node projects slightly higher. The lobal connections are low but distinct. The syllobium is entire - with no trace of a depression. The prenodal sulcus is well defined and is somewhat narrower, shorter and shallower than the adductorial sulcus. Below the preadductorial node there is a conspicuous anteroventral depression.

The velum - as seen in well preserved specimens - begins abruptly anteriorly (adjacent to the dorsal margin of the anteroventral depression) and then swings gently around the ventral part of the valve, narrowing (gradually) and becoming ridge-like posteriorly. When valves are viewed obliquely, broad tubules are discernible along the ventral part of the velum. The widest part of the velum occurs below the anteroventral depression. An extremely short border crest - consisting of about 10-12 fine denticles - occurs on the anterior part of the velum; the posterior section of the crest diverges away from the velar edge and then becomes obsolete.

Lobes are finely and distinctly reticulate. Very delicate striae traverse the velum parallel to its edge.

MATERIAL: All known valves are tecnomorphs and occur as moulds. Specimens, collected from three localities, are rare.

MEASUREMENTS: Approximate hinge length - sulcal height (including velar width) of a cast of the best preserved tecnomorph (DAS M 221).

1400-1000 (in microns).

DISCUSSION: The lobal and ornamental characteristics of this species could be accommodated within Henssiella. However, unlike all known Henssiella taxa this species has its denticulate border crest confined to but a small portion of the tecnomorphic velum (cf. conditions in Cryptolopholobus semilaqueatus Martinsson, 1962) and, furthermore, the velum itself is abruptly restricted anteriorly.
Genus **ZOROTOXOTIS** gen. nov.

**DERIVATION OF THE NAME:** From the Greek *zoros*, pure, and *toxotis* (as in the type species *Amphitoxotis*); alluding to the absence of torus or velum on the female crumina. Gender, feminine.

**TYPE SPECIES:** *Zorotoxotis sagena* sp. nov., Pl. C15, figs. 1, 2; from the Aymestry Limestone of the Abberley Hills, Worcestershire.

**SPECIES:**
- *Zorotoxotis mediculata* sp. nov.
- *Zorotoxotis sagena* sp. nov.
- *Zorotoxotis convallis* sp. nov.

**DIAGNOSIS:** Reticulate *Amphitoxotidinae* lacking a torus or velar edge on the crumina. The tecnomorphic velum is medium wide, shows no abrupt restrictions and has a denticulate border crest. Lobes entire, not particularly broad, and united by lobal connections; anteroventral depression conspicuous. Crumina striate or reticulo-striate.

**DISCUSSION:** In addition to those features noted in the diagnosis, the form of the velum in front of the crumina, the well developed pre-adductorial node, and the presence (in at least two of the species) of a short toric ridge behind the crumina also unite the species in question.

Other amphitoxotidine genera which lack both torus and velum across the crumina include *Atterdagia* Martinsson, 1962 (almost non-
lobate), Macrypsilon Martinsson, 1962 (with a velar flange, very broad lobes and a narrow sulci), Hammariella Martinsson, 1962 and Grogarnia Martinsson, 1962. It is evident that the emphasis for generic distinction is here placed on lobal and velar - rather than cruminal - characteristics. Zorotoxotis differs from Hammariella mainly by its narrower lobes, its narrower (denticulate) velum lacking an abrupt posteroventral restriction, and the presence in front of the crumina of a ridge representing the velum. The monotypic Grogarnia - which has an isolated anterior lobe, a sudden posteroventral restriction of the velum, combines a fine reticulation with verrucosity and lacks a denticulate border crest - obviously cannot accommodate the three present species. In most respects other than subcruminal morphology Zorotoxotis has affinities with Hemiella.


Zorotoxotis medioculta sp. nov.

Pl. C14, figs. 1-15.

DERIVATION OF THE NAME: From the Latin medius, middle, and cultus, cultivated; alluding to the ornamentation on the preadductorial node of the female.

HOLOTYPE: A female right valve, DAS 47132; Pl. C14 , figs. 3,4,7-9.

TYPE LOCALITY AND TYPE STRATUM: The ridge on the W side of the Wren's Nest, Dudley, Worcestershire (loc. 27c); the Wenlock Limestone.

DIAGNOSIS: Finely reticulate Zorotoxotis species with a velum which is narrow in tecnomorphs and only ridge-like in females. The crumina is large and entirely striate. The syllobium in females has a fairly constant width and is normally confluent ventrally with the edge of the velum. Syllobial cusp and preadductorial node both well developed and
subequal in height above the hinge line.

DESCRIPTION: Valves are preplete. Anterior lobe and syllobium are attached to the distinctly developed preadductorial node by lower lobal connections. The slightly wider, dorsal part of the syllobium is drawn above the hinge line into a single, stout, anterior cusp; ventrally, especially in females, the syllobium gains elevation but loses little in width. The preadductorial node is long and extends above the hinge line, often marginally higher than the syllobial cusp. The anterior lobe rarely projects above the hinge line, is the least elevated lobe, and is approximately of equal width to the widest part of the preadductorial node. There are no lobal grooves or depressions.

The anteroventral depression is well developed and is deeper than the sulci. The adductorial sulcus is slightly wider, deeper and longer than the prenodal sulcus, though both separate the lobes effectively. The syllobium is posteriorly inclined, the preadductorial node anteriorly inclined, and the anterior lobe appears to be vertical.

The tecnomorphic velum is narrow - it flares from the contact margin at right angles - and lacks the frill-like appearance characteristic of many amphitoxotidines; even so, tubules are discernible especially in the region of the anteroventral depression. There are no noticable changes to the velar outline in lateral view and throughout its length it closely hugs the adjacent lobal regions. Along the ventral part of the velum there is a border crest consisting of extremely fine denticles, and a well formed torus separated from the velar edge itself by a zone of striation. Immediately admarginal of this torus there seems to be, in the best tecnomorph from the Wren's Nest, another, shorter incipient toric structure; in the specimens from Ledbury (see "Discussion" below) a second toric ridge is clearly seen in adult valves. Behind the crumina the velum is manifest only as a narrow ridge or bend, continuing to the posterior cardinal corner;
this ridge - where it is joined to the posteroventral part of the syllobium - is often obsolete. Precruminally the velum is represented by a short, narrow ridge which seems to be more strongly developed in left, rather than right, valves. Apart from the striae which contour its entire surface, no other features traverse the crumina. Marginoventrally - at a point where in other amphitoxotidines there is often a small tubercle or deflection of the velar edge - there appears to be a minor disruption of the pattern of cruminal striation; this disturbance is seen to be (in well preserved specimens) associated with a minute slit-like depression. A short toric ridge occurs just behind the crumina.

Dimorphism is apparently present within the ornamentation arrangement. The well preserved, figured tecnomorph from the Wren's Nest is finely reticulate on the lateral parts of the syllobium, preadductorial node and the anterior lobe. In all the females studied only the (crest of) the preadductorial node has reticulation; ornament has not been detected on the other lobes. The marginal structure on each valve consists of a row of tiny tubercles.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of specimens from the Wenlock Limestone.

Wren's Nest (loc. 27c): 1360-870, 1320-840 (holotype), 1290-830, 1270-850, 1250-810 (females).
1355-860 (tecnomorph).

Ledbury (loc. 23): 1250-835 (female).
1240-820 (tecnomorph).

DISCUSSION: The material from Ledbury is worn and, compared to the Wren's Nest specimens, poorly preserved. The valves from both localities are, however, alike in all features except for the certain occurrence of a second toric ridge and a slightly deeper anteroventral
depression in the Ledbury tecnomorphs (the lack of ornament in the
Ledbury material is probably due to aspects of preservation). These
differences are not thought to be significantly important and all
the specimens are considered to be conspecific.

The features used to distinguish species of Zorotoxotis are
discussed under Z. sagena and Z. convallis.

OCCURRENCE: The Wenlockian of the Welsh Borderland and the W Midlands
of England.

Wenlock Limestone: Wren's Nest (locs. 27 c, f, g).
Ledbury (loc. 23).

Zorotoxotis sagena sp. nov.

DERIVATION OF THE NAME: From the Latin sagena, a fish-net; alluding
to the form of the cruminal ornament.

HOLOTYPE: A female left valve, DAS 47249; Pl. C15 , figs. 1, 2.

TYPE LOCALITY AND TYPE STRATUM: Woodbury Quarry, approximately 1500 m
NE of Shelsley Beauchamp, the Abberley Hills, Worcestershire (loc. 24);
a bentonite band in the Aymestry Limestone.

DIAGNOSIS: Zorotoxotis species with somewhat slender lobes.
Reticulation consists of medium (- fine) sized meshes. Ventrally and
dorsally the crumina is striate; lateroventrally it is reticulo-striate.
Preadductorial node and syllobial cusp project above the hinge line.

DESCRIPTION: Syllobium and anterior lobe are joined to the long
preadductorial node by fairly narrow connections. Both the adductorial
and prenodal sulcus are well developed; they curve gently around the
slightly anteriorly inclined preadductorial node with the adductorial
sulcus being the deeper and longer of the two. The distinct anteroventral depression fails to connect with the prenodal sulcus above. Only the anterior lobe lacks a portion above the hinge line; the fairly round, syllobial cusp is commonly not quite as high above the hinge line as the preadductorial node. The transition zone from the adductorial sulcus to the syllobium is gently rounded; by comparison the posterodorsal margin of the syllobium is (typically) sharply angled with the adjacent region of the velum. Across the syllobium, just below the cusp, there are sometimes traces of a shallow depression. The anterior lobe is the lowest and narrowest lobe; the ventral part of the syllobium has the same elevation as the preadductorial node, with its dorsal region somewhat lower. The crumina annexes a considerable section of the anterior lobe and almost a third of the preadductorial node; in tecnomorphs the anterior lobe and the preadductorial node are of approximately the same length.

The velum flares away from the valve margins at quite a high angle, but does not extend for any considerable distance away from the lotal area (in lateral view). In tecnomorphs a velar structure can be distinguished from anterior to posterior cardinal corner, although its frill-like development occurs only below mid-height. The postero-ventral restriction of the velum is very gradual; at anterior mid-height, however, the elevation of the velum diminishes abruptly. The major part of the velum in tecnomorphs is tubulous (seen distinctly when valves are viewed obliquely) and has a denticulate border crest; there are 2-3 small denticles per tubule. About three tubules are weakly visible postcruminally in females; in front of - and isolated from - the crumina there is a short, flange-like section of the velum next to the anterior lobe. A row of tiny, discrete, closely spaced tubercles form the marginal structures in each valve.

A narrow zone of the crumina immediately adjacent to the lobes is, like the sulci, smooth. Dorsally and ventrally the crumina is striate,
lateroventrally it is reticulo-striate. The subcruminal ornament is extended postcruminally in distinct fashion along the ventral side of the velum. Along the ventral part of the velar edge in tecnomorphs and behind the crumina for a short distance in females there is a toric ridge. Neither the torus or velar edge are found on the crumina itself. In the region of the stretched reticulate ornament on the most distal part of the crumina there appears to be, in a well preserved specimen (see figures) a small, weakly elevated area.

The syllobium and preadductorial node have medium sized reticulation. The anterior lobe has similar ornament on its lower regions; dorsally the reticulation becomes faint and is usually effaced.

MEASUREMENTS: Hinge length - sulcal height in microns of specimens from the type locality.


Tecnomorphs: 1120-820, 1120-810, 1110-805.

DISCUSSION: As a British Ludlovian ostracode species this material is exceptionally good in its state of preservation; it provides an optimistic sign for future collecting from similar Ludlovian lithologies.

Z. sagena is closely similar in several features to the much older (Wenlockian) Z. medioculta. Amongst other characteristics the narrower velum (e.g. in females behind the crumina), the slightly finer and less extensive reticulation, the cruminal ornament (striae), and the syllobial shape of the latter species all serve to distinguish the two forms.

OCCURRENCE: Recorded only from its type locality in the Ludlovian of the Abberley Hills.

Aymestry Limestone: Woodbury Qy. (loc. 24).

Some 100 valves have been collected from a conspicuous bentonite band in the type stratum.
Zorotoxotis convallis sp. nov.
Pl. Cl5, figs. 10-16.

DERIVATION OF THE NAME: Latin convallis, a coomb; alluding to the appearance of the anteroventral depression.

HOLOTYPE: A right tecnomorphic valve, DAS M 214; Pl. Cl5, figs. 12,14,16.

TYPE LOCALITY AND TYPE STRATUM: A small hillside exposure about 600 m SSE of Trippleton Farm and just 10 m W of the road from Burrington to Leintwardine, Herefordshire (loc. 68); Upper Leintwardine Beds.

DIAGNOSIS: Zorotoxotis species with well developed reticulation covering all lobes and lobal connections. Except for a narrow ventral opening, the marked anteroventral depression is totally enclosed by lobes. Dorsal margin of the syllobium gently rounded. Crumina entirely reticulate/reticulo-striate.

DESCRIPTION: The preadductorional node communicates with the other lobes via low but well defined connections; the connection between the preadductorional node and the anterior lobe is consistently wider than the corresponding feature joining the syllobium. The syllobium characteristically has a rather straight anterior margin, and an evenly curved posterior margin which continues in like fashion just above the hinge line. Ventrally, the anterior lobe is as wide as the preadductorional node, but its dorsal region is somewhat narrower and lacks a cusp. The well developed preadductorional node is inclined forwards and is produced over the hinge line just above the syllobial cusp. The ventral part of the syllobium directly below the adductorional sulcus is almost as wide as its main section (just above mid-height); it then tapers rapidly into the neck-like connection above the anteroventral depression.

Lobal depressions and grooves are absent. The adductorional sulcus is mostly vertical and is conspicuously longer and wider than the prenodal
sulcus; the latter bends evenly around the anterior face of the preadductorial node before becoming obsolete just above mid-height. Extending dorsally from the proximal margin of the velum, the narrow, finger-like anteroventral depression almost reaches opposite the base of the adductor sulcus. This deep depression appears nearly engulfed by the adjacent lobes.

The velum in tecnomorphs can be traced mostly as a narrow ridge, or (ventrally and anteroventrally) as a rather narrow, frill-like structure which carries a denticulate border crest. The transition, posteroventrally, from a ridge to a more extended velum is gradual. There are 2-3 denticles opposite each velar tubule. On the ventral part of the velum there is a toric ridge. No part of the postcruminal section of the velum is wider than a ridge; precruminally the velum is represented by a short, faint ridge. A torus behind the crumina has not been detected. Apart from the reticulate ornament, vaguely arranged in a linear manner, the crumina has no other structure across its surface.

The area of reticulation is well demarcated; it covers all the lobes and lobal connections except for the dorsal region of the anterior lobe which - like both sulci and the anteroventral depression - is smooth. Small instars are, in all essential details, similar to adult tecnomorphs.

MATERIAL: This species is known only from internal and external moulds. However, the excellent casts obtained permit a full and accurate description to be made.

MEASUREMENTS: Hinge length - sulcal height in microns of females from the Leintwardine Beds.

Trippleton Farm (loc. 66): 1140-750, 1130-710, 1110-720.

Martin's Shell (see occurrence): 1210-770.
DISCUSSION: Tecnomorphs of this species could easily be misplaced within *Hemsiella*; the form of the female subcristal morphology, however, prevents such an assignment.

*L. convallis* differs from congeneric species by the prominence and form of its anteroventral depression, and by differences in ornamentation and lobal and sulcal shapes.

OCCURRENCE: In the Leintwardine Beds of the Ludlow district.

Upper Leintwardine Beds: Tripleton Farm (loc. 68).
  The Goggin (loc. 64).
  Bengry Track (loc. 63).
  Forestry Track, Ludlow (loc. 62).
  Wigmore Rd. (loc. 66).

Also present in a small collection made from highest Lower Leintwardine Beds at Martin's Shell (SO 41097543; locality unnumbered), near Leintwardine.

The type locality provided both the best preserved and greatest number of specimens.

Genus *Lophoctenella* Martinsson, 1962

TYPE SPECIES: Original designation of Martinsson 1962, p. 239; *Lophoctenella angustilagueata* Martinsson, 1962, p. 240, fig. 121A; from the Ludlovian (Hamra Beds) at Hoburgen Ia (of Martinsson), Gotland.


DIAGNOSIS: Amphitoxotidinae with a strongly reduced anterior lobe, and long narrow cristal loops on the preadductorital lobe and the syllobium. Denticulate border crest along all the anterior and ventral parts of the male velum. The velar edge and the torus both continue parallel to
DISCUSSION: Undoubtedly, many taxonomic problems still exist with this genus. At present only two species of *Lophoctenella*, (*L. angustilaqueata* and *L. scanensis* (Kolmodin, 1869)) have been formerly erected. No difficulty exists with the identification of the type-species, but because of the nature of the type material of *L. scanensis* the presence of this species outside Scania is not certain. There may be a number of species "hiding" in the literature under the name of *L. cf. scanensis* (see "Discussion" below). Moreover, it has been suggested (Martinsson 1962, p. 240) that at least one more *Lophoctenella* species exists both in Scania and the N German erratics.

OCCURRENCE: This genus is known from the upper part of the Ludlovian and from the Downtonian. In Britain it ranges from the Upper Leintwardinian into the Downtonian. *Lophoctenella* occurs most noticeably in the Baltic area where it has been recorded from Gotland (Martinsson 1962) Latvia (Gailite 1967) and the Ohesaare borehole (Sarv 1971). Observations by Martinsson and Berdan on the Silurian ostracode faunas of the E coast of N America indicate that the genus is also found in the Ludlovian (Edmunds Formation) of Maine (see Martinsson 1971, in Berry & Boucot, p. 42).

*Lophoctenella cf. L. scanensis* (Kolmodin, 1869)
Pl. C13, figs. 8-13.

1971a *Lophoctenella cf. scanensis* (Kolmodin 1869); Shaw, p. 599, pl. 110, figs. 1-6.

REMARKS: The description given below is based on material collected by the writer from the Welsh Borderland.
DESCRIPTION: The dimorphism in this species influences the lobes, the velum and the anteroventral part of the valves; the dimorphs will therefore be treated individually.

The anterior lobe of the female is short, inconspicuous and lacks a crista. Both the anterior lobe and the preadductorional node are shorter in comparison to those of tecnomorphs; furthermore, the latter lobe is inclined as a result of cruminal development. The dorsal face of the preadductorial node has a weakly developed cristal loop (a shallow, narrow depression runs down the centre of the node; the higher surround to this lumen is particularly faint ventrally). The syllobium is stout, rounded dorsally and of fairly constant width; its lower half is raised into an elongate, crudely three-sided platform, well above the level of the cuspidal part of the lobe. The dorsal boundary of this platform is oblique to the hinge line. Between crumina and syllobium there is a prominent depression. All of the lobes project just above the hinge line. The adductorial depression is deep, vertical, and about as wide as the preadductorial node. Both in front and behind the crumina, the velum is represented as a non-tubulous, ridge-like feature, gently curved in lateral view. The large, coarsely striate crumina is rounded anteriorly, tapers posteriorly and normally reaches a height just below the dorsal limit of the raised section of the syllobium. The velar edge and toric ridge cross the crumina parallel to each other, to its most anterior point. The toric ridge extends some considerable distance posteriorly.

One extremely well preserved valve from Bengry Track (loc. 63) gives important additional information about the ornament of the female. Scattered on the upper regions of the syllobium in this specimen there are 6-7 faintly developed tubercles; the ventral, raised area is covered with medium sized striae haphazardly trending in many directions. In addition, the cuspidal region of the syllobium is seen to consist of
a larger anterior section above the hinge line, and a smaller (almost
obsolete) posterior part below this line.

In tecnomorphs a connecting ridge joins the preadductorional node to
the sylllobium, both lobes are crowned with a cristal loop. The width
of the area inside the sylllobial cristal loop is approximately
2-3 times as wide as the surrounding ridge. The velum is wide,
denticulate and distinctly tubulous for most of the distance from its
characteristic projection anterodorsally to the posteroventral part
of the valve; it continues posteriorly as a velar ridge. A very
narrow cristal loop - indiscernible in most specimens - has been
(rarely) observed on the isolated anterior lobe (see "Discussion"
below). All lobes are vertical and reach to, or just above the hinge
line. The anteroventral depression is strongly developed.

MATERIAL: Many tens of valves have been cast from the external moulds
collected in Shropshire. The number of females is large for the number
of tecnomorphs found.

MEASUREMENTS: Hinge length - sulcal height (including velar width)
of female valves collected from the Upper Leintwardine Beds.

Bengry Track (loc. 63): 1570-1050, 1510-1055, 1475-890, 1420-940,
1350-930, 1310-890.

Tripplenton Farm (loc. 68): 1240-780.

The Goggin (loc. 64): 1370-910.

DISCUSSION: In the material from Shropshire the females show a fairly
constant morphology and are easily identified, but it is difficult to
assess the significance of the occurrence of a cristal loop on the
anterior lobe of only a very few tecnomorphs (in most tecnomorphs
studied this lobe is vertical and finely ridge-like). It is possibly
a result of preservation (the loop is very fine and all of the material
occurs as moulds) or it maybe a reflection of the fact that most of the
tecnomorphs collected are small specimens (only one valve could possibly be considered as a male). Certainly the two specimens which best show the cristal loop are large and well preserved and the other, concomitant tecnomorphs are smaller and lack this feature. All of the tecnomorphs collected are alike in all other features and are thought to represent one species.

The moulds from Five Turnings (loc. 14) have a slightly narrower syllobium and the occurrence in the female of a cristal loop on the preadductorial node has not been confirmed. In general this material is less well preserved than that from the Upper Leintwardine Beds and it is included here with doubt.

The material described by Shaw (1971a) from the Lake District as _L. cf. scanensis_ is considered conspecific with the Welsh Borderland material. Study of Shaw's illustrations (pl. 110, figs. 1-6) and examination of two of his figured females (GSM Z19035, Z19036b) reveals no essential differences between the material from the two areas. It should be noted that the Lake District tecnomorphs too, appear to show some variation in the anterior lobe - in one of the figured tecnomorphs (GSM Z19036a, pl. 110, fig. 4) a cristal loop is clearly present, in the other (GSM Z19053, pl. 110, fig. 2) it is not discernible.

The female valve recorded from Gotland by Martinsson (1962, p. 242, figs. 122A-B) as _L. cf. scanensis_ may represent a separate species from that dealt with here; its preadductorial node shows no obvious sign of having a cristal loop, and the raised part of the syllobium is more markedly inclined forwards and appears to lack the randomly distributed striation characteristic of the British material.

_L. scanensis_ (Kolmodin, 1869) (see illustrations of two of Kolmodin's originals in Martinsson 1962, figs. 6A-C) differs from the British material presented here by the lack of coarse striae, laterally, on the crumina, the absence of a cristal loop on the tecnomorphic anterior lobe and by possibly having a slightly wider syllobial cristal
loop. There may appear to be sufficient grounds for distinguishing two separate taxa, but until the Scanian material has received adequate description from more completely preserved specimens (the only female in Kolmodin's collection is fragmentary) a confer is used with respect to the material described here.

OCCURRENCE: The authors' collections come from Ludlovian localities around Ludlow, The Welsh Borderlands.

Upper Leintwardine Beds: Trippleton Farm (loc. 68).
- Bengry Track (loc. 63).
- Forestry Track, Ludlow (loc. 62).
- The Goggin (loc. 64).

Whitcliffe Beds: ? Five Turnings (loc. 14), (included with some doubt).
? Ludford Lane I (loc. 69a), (only one small tecnomorph).

Also identified in J.H. McD. Whitaker's colls. (locs. 811 & 119a) from the Upper Leintwardine Beds of the Leintwardine area.

In the Lake District Shaw (1971a) recorded L. cf. scanensis from the Lower and Upper Underbarrow Flags, Kirkby Moor Flags, and the Scout Hill Flags; these deposits were regarded as equivalent to the Upper Leintwardine, the Whitcliffe and part of the Downton deposits of Shropshire. Lophoctenella sp. has also been documented from the Whitcliffian and Downton Castle Sandstone of the Long Mountain (Shaw 1969, pp. 67, 68, fig. 8).

Shirley and Shergold (1968, fig. 2) list "Lophoctenella spp." from the Upper Leintwardine Beds and the Upper Bringewood Beds of the Much Wenlock - Craven Arms district (material not seen).
Genus **Huttoniella** Shaw 1971

**Type Species:** Original designation of Shaw 1971a, p. 597;

**Huttoniella contracta** Shaw 1971, p. 598, pl. 109, fig. 5; from the Kirkby Moor Flags (late Ludlovian) of Westmorland.

**Species:** Only the type species.

**Diagnosis:** See Shaw 1971a, pp. 597, 598.

**Discussion:** When erecting this genus Shaw (1971a, p. 598) considered it probably allied to the Cryptolopholobus - Lophoctenella group of amphitoxotidines. A study of the figure of the female illustrated by Shaw supports such a comparison (cf. cruminal shape and lobal proportions). Unfortunately this female specimen (GSM Z1 9052) is now reported lost (Dr. D.E. White, pers. comm.). The other specimen figured by Shaw - the holotype - is an immature tecnomorph.

**Occurrence:** Late Ludlovian and Downtonian of Westmorland (Shaw, op. cit.).

**Huttoniella contracta** Shaw, 1971

Pl. C13, fig. 16.

1971 **Huttoniella contracta;** Shaw, p. 361, nomen nudum.

1971a **Huttoniella contracta** sp. nov; Shaw, p. 589, pl. 109, figs. 5, 6.

**Holotype:** A left valve tecnomorph, GSM Z1 9033, Shaw 1971, pl. 109, fig. 5.

**Type Locality and Type Stratum:** Approximately ½ mile S of Old Hutton, Kendal, Westmorland (N.G.R. 5642 8774); Kirkby Moor Flags.

**Diagnosis:** As for the genus.
DESCRIPTION: See Shaw 1971, p. 598.

OCCURRENCE: Not collected by the present writer. Shaw found this species in the Kirkby Moor Flags and Scout Hill Flags in the vicinity of Kendal; he considered these deposits to be Whitcliffian and Downtonian respectively.

Genus **TRIBOTOXOTIS** gen. nov.

DERIVATION OF THE NAME: From the Greek *tribos*, a track and *toxotis* (as in the type genus *Amphitoxotis*); alluding to the form of the velar edge and torus on the crumina. Gender, feminine.

TYPE SPECIES: **Tribotoxotis dorsistriata** sp. nov., Pl. C16, figs. 1, 2, 6; from the Wenlock Limestone of the Wren's Nest, Dudley, Worcestershire.

SPECIES: Only the type species.

DIAGNOSIS: Amphitoxotidinae with a velum which in tecnomorphs is fairly narrow, faintly tubulous and evenly curved, and in females is represented postcruminally merely by a velar bend. Both the velar edge and the nearby torus advance parallel to each other - without deflection - across the large crumina. The preadductorial node is very large; the lobal connections are slender. There is a syllobial cusp and a syllobial groove.

DISCUSSION: *Hogburgiella* Martinsson, 1962, *Lophoctenella* Martinsson, 1962, *Huntonella* Lundin, 1968, and *Sarmatotoxotis* are other amphitoxotidines which have torus and a velar edge across the female crumina, yet none of the wide variety of lobal and velar arrangements represented in these genera resemble those found in *T. dorsistriata*. 
Hogburgiella has a more extensive, distinctly tubulous velum, narrower lobes, different ornamentation, a considerably smaller crumina and a smaller preadductorional lobe. Huntonella differs from Tribotoxotis particularly in its velar morphology (being wider, abruptly restricted posterioventrally, and having a border crest) and in the form of the lobes (which are smaller and lack cusps). Amongst other differences, Tribotoxotis is distinguished from both Lophoctenella and Sarmatotoxotis in lobal proportions, lobal ornament, but its narrower velum, and in lacking a denticulate border crest.

Tribotoxotis, (like Sleia), is one of the few amphitoxotidine genera to have a syllobial groove. The very prominent preadductorional node - for which it is difficult to find a parallel amongst amphitoxotidines - and the large crumina (cf. Hammariella Martinsson, 1962) are other distinctive features of the genus.


**Tribotoxotis dorsistriata** sp. nov.

_PI. CL6, figs. 1-9, 12._

DERIVATION OF THE NAME: From the Latin *dorsistriatus*, referring to the lobal development of striae on the dorsal face of the preadductorial node.

HOLOTYPE: A female right valve (dorsal half of syllobium missing), DAS 47130; _PI. CL6_ , figs. 1, 2, 6.

TYPE LOCALITY AND TYPE STRATUM: From the ridge on the W side of the Wren's Nest, Dudley, Worcestershire (loc. 27c); the Wenlock Limestone.

DIAGNOSIS: As for the genus.
DESCRIPTION: The large preadductorial node, reaching a considerable
distance above the hinge line, is the dominant lobal feature. The
anterior lobe is vertical, narrow and only just attains the level of
the hinge line. In tecnomorphs the dorsal region of the syllobium is
wider than the preadductorial node, but ventrally this lobe narrows
appreciably and is not nearly so wide as the corresponding part of the
female valve. The ventral section of the female syllobium is directly
confluent with the edge of the valve, and a velar structure distinct
from this part of the lobe is not discernible; by comparison a narrow,
shallow depression is present between syllobium and velum in tecnomorphs.
All lobes are joined by slender connections in the region above the
anteroventral depression. The lateral surfaces of the syllobium and
preadductorial node are somewhat flattened. A shallow, rather open
syllobial groove runs (in tecnomorphs at least) from the gently
rounded, posterdorsal region of the lobe to immediately above the
base of the adductorial sulcus; the groove runs parallel to the long,
almost straight ventral boundary of the tecnomorphic syllobium.
The syllobium has a single, bluntly acuminate cusp overlooking the
adductorial sulcus; the cusp does not generally reach the same height
above the hinge line as the preadductorial node.

Both the adductorial sulcus and the prenodal sulcus are well
developed. The adductorial sulcus is considerably wider, longer, but
only slightly deeper than the prenodal sulcus. Appreciable parts of
the preadductorial node, anterior lobe and prenodal sulcus are annexed
by the crumina.

In posterior view (tecnomorphs) the velum typically travels
subparallel and close to the valve margin from cardinal corner to
approximately valve mid-height, where it abruptly flares away from the
margin leaving a conspicuous angle in the velar profile. In contrast,
the initial angle which the velum makes with the valve margin in
anterior view is steeper, and its overall profile lacks sharp flexures.
On the outside of the velar edge in tecnomorphs there is an indistinct, ornamental ridge - complemented on the inner, ventral side by a long, strongly developed torus nearly half-way between the velar edge and the marginal structure. In lateral view the tecnomorphic velum is evenly curved - lacking restrictions - throughout; valves are preplete. The velar structure is present postcruminally in the form of a velar bend and precruminally as a short, weak ridge divorced from the crumina. Velar tubules are best developed anteroventrally, and are most easily seen when valves are viewed obliquely; the tubules are short and quite wide (2-3 of them occupy the area of the anteroventral depression). The velar edge and adjacent toric ridge - which is extended for some distance postcruminally - continue undisturbed and without significant deflection across to the anterior-most part on the crumina.

Except for some fine striae consistently present around the dorsal face of the preadductorional node, ornamentation is absent from the lobal and cruminal surfaces of the extant specimens. The vertical marginal structure is not clearly seen, but appears to consist of a row of minute, densely spaced tubercles.

MEASUREMENTS: Hinge length (estimated) - sulcal height in microns of females valves from the type locality.

1400-910, 1375-880.

DISCUSSION: No female valve has yet been found in which the dorsal part of the syllabium (containing the syllabial groove) is preserved, though the morphology of the other lobes gives no reason to suppose that it would differ significantly from that in the tecnomorphs.

OCCURRENCE: Known only from the English W Midlands.

Wenlock Limestone: Wren's Nest (locs. 27c, f).

The extant material comprises of some 30 tecnomorphs and six incomplete female valves.
Genus TROPIDOTOXOTIS gen. nov.

DERIVATION OF THE NAME: From the Greek tropidos, a keel, and toxotis (as in the type species Amphitoxotis); with reference to the fancied resemblance of the velum on the crumina to the lowest longitudinal timber of a vessel. Gender, feminine.

TYPE SPECIES: Tropidotoxotis arga sp. nov., Pl. C16, figs. 10,13,19; from the Wenlockian of Shropshire.

SPECIES: Only the type species.

DIAGNOSIS: Entirely smooth Amphitoxotidinae in which a virtually unmodified velar edge crosses without interruption or deflection a crumina of disc-like form. The velum is very wide, sharply restricted posteroventrally, and present in front of the crumina. The broad syllobium - behind a narrow adductorial sulcus - is the only lobal element which is well defined. There is no toric structure or basal crest.

DISCUSSION: The completeness of the velar edge across the (discoid) crumina is an important characteristic of this genus - in which there is an obvious relationship with Berolinella Martinsson. Tropidotoxotis is separated from the much younger Berolinella by the absence of a basal crest or toric ridge, by its shorter, less conspicuous adductorial sulcus, and by the (almost) total disappearance of the prenodal sulcus. Tropidotoxotis differs from Dibolbina (to which it closely compares in lobation) in cruminal shape, velar morphology (it has a posteroventral restriction), and in lacking a torus or basal crest.

This genus was first suggested as a new taxon by Martinsson in the figure explanation to an illustration of a crumina of the type species (1962, fig. 100C).

OCCURRENCE: Wenlockian of the Welsh Borderland.
Tropidotoxotis arga sp. nov.

Pl. C16, figs. 10, 11, 13-19.

1962 Martinsson, p. 215, fig. 100C (unnamed species).

DERIVATION OF THE NAME: From the Greek argos, swift; alluding to the appearance of the valves.

HOLOTYPE: A female right valve, DAS 47337; Pl. C16, figs. 10, 13, 19.

TYPE LOCALITY AND TYPE STRATUM: A small exposure in the river bank on the S side of the R. Severn, opposite Coalbrookdale, approximately 700 m upstream from the Ironbridge at Ironbridge, N Shropshire (loc. 39); Coalbrookdale Beds.

DIAGNOSIS: As for the genus.

DESCRIPTION: Valves are rather flat and comparatively featureless. None of the lobes extend beyond the hinge line. At mid-length the adductorial sulcus, reduced to a narrow depression in the central region of the valve, bends forward around the site of the preadductorial node. Dorsally, this sulcus shallows slightly, ventrally it is prevented from reaching the base of the velum by a narrow lobal connection which joins the syllobium to the anterior part of the valve.

The syllobium is broad for most of its height, but then narrows rapidly below a line projected from the ventral end of the adductorial sulcus. The highest region of the valve occurs ventrally, on the syllobium; all lobal areas decrease in elevation towards the hinge line. The anterior lobe and preadductorial node appear as one complex, though there is between them an almost indiscernible depression marking the position of the prenodal sulcus. At the base of this flat, fused anterior lobal complex, just in front of the adductorial sulcus, a slight "hollow" in the valve surface represents the antero-ventral depression. The anterior lobal complex is equal in width to the syllobium.
The velum is very wide, abruptly terminated posteroventrally (though the exact velar shape at the point of restriction is not known), and flares from the valve at about 45° to the plane of the free margin. Anteriorly, the velum narrows gradually and ends just below the cardinal corner. Long narrow tubules radiate from the base of the velum throughout its length. There is no toric ridge. The crumina is ovoid in lateral view, discoid in overall form (its ventral surface is particularly flat) and is accommodated mostly within the velum. The velar edge traverses the crumina without interruption or significant deflection; it is hardly, if at all, influenced by cruminal occupation of the velum. In at least two specimens tubules have been observed even in the most distal part of the velar edge on the crumina. These tubules are seen where the velar edge is broken, normally the tubules on the crumina are not visible externally (cf. Berolinella where similar tubules are differentiated externally). The velum continues in front of the crumina as in the tecnomorphs.

All lobal and sulcal regions are smooth. No ornament has been detected on the crumina. Faint striae are concentrically arranged on the ventral surface of the velum. A line of very small, tubercle-like processes occurs along each valve margin.

**Measurements:** Few specimens were measurable. Hinge length - sulcal height (excluding velar width) in microns.

- Female holotype: 1350-900 (estimated).
- Tecnomorph: 1080-710 (BM I 2378).

**Discussion:** Some cruminae are more inflated than others, but all show the characteristic disc-like overall form. The width of the velar edge on the crumina also varies, though it is never insignificant and - distally - measures as much as 40-50 microns in some specimens.
The well preserved left valve tecnomorph (BM I 2378) from the old railway cutting, Ironbridge, figured herein, came from the Smith coll. (no. 28) and was referred by Jones & Holl (1886, p. 358) to Beyrichia maccoyiana Jones.

OCCURRENCE: Mostly from Wenlockian localities in the vicinity of the R. Severn, N. Shropshire. A few tecnomorphs and cruminae collected from the top of the (undifferentiated) Wenlock Shale at Storridge (loc. 20) in the Malverns area cannot be distinguished from the Shropshire material.

Tickwood Beds: Benthall Edge, East (locs. 43a, b).
? Tickwood (loc. 44c); 1 crumina.

Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39).
Coalbrookdale (loc. 40).

Specimens are not particularly common and, moreover, the distinctive crumina is often the only part of the valve remaining.

Genus CHARITOXOTIS gen. nov.

DERIVATION OF THE NAME: From the Greek charieis, graceful and toxotis (as in the type genus Amphitoxotis); with reference to the appearance of the type species. Gender, feminine.

TYPE SPECIES: Charitoxotis grvida sp. nov., Pl. C17, figs. 1,2,4,8,12; from the Wenlockian of the Wren’s Nest, Worcestershire.

SPECIES: Only the type species.

DIAGNOSIS: Amphitoxotidinae with a broad syllobium behind a small, narrow adductorial sulcus; the other lobal elements are indistinctly developed. The velum is wide – with a basal crest and basal toric ridge – in both dimorphs, abruptly restricted posteroventrally, and lacking pre-cruminally. The crumina is very large, reticulate, and untraversed by velum or torus.
DISCUSSION: This genus previously appeared in the literature when Martinsson (1962, p. 215, fig. 100A) figured a tecnomorph of the type species (from the type locality). In the figure explanation he commented that the species shows affinities to the Dibolbina - Berolinella group of the genera but noted that it should be assigned to a new genus; these views are accepted here.

Charitoxotis shows close relationships to Dibolbina in its lobal development and especially in the morphology of the small, curving adductorial sulcus (see Kesling 1956, pl. IV, figs. 11-13). Dibolbina is distinguished by having an entire, unrestricted velum which crosses the crumina without interruption, and by the presence of a ridge on the syllobium.

Berolinella differs from Charitoxotis in both lobal and subcruminal morphology; the former has exceptionally long sulci dividing the valve surface and retains part of the velar tubules, ventrally, on its "discoid-shaped" crumina.

Charitoxotis differs from Atterdagia chiefly in velar morphology (cf. females); in other respects these genera show affinities suggestive of a close phylogenetic relationship.

For further comments on the group of genera discussed here, see under A. versiculus sp. nov.


Charitoxotis gravida sp. nov.


1962 Martinsson, fig. 100A (illustrated as an unnamed genus).

DERIVATION OF THE NAME: From the Latin gravidus, heavily pregnant; alluding to the large and "full" crumina.

HOLOTYPE: A female left valve, DAS 47323; Pl. C17, figs. 1,2,4,8,12.
TYPE LOCALITY AND TYPE STRATUM: The crest of the exposed ridge on the W side of the Wren's Nest, Dudley, Worcestershire (loc. 27c); the Wenlock Limestone.

DIAGNOSIS: As for the genus.

DESCRIPTION: Specimens of *C. gravida* are rare. Those tecnomorphic valves which are reasonably complete do not show any traces of lobation in front of the adductorial sulcus, and in this respect are different to the females - though ideally more specimens are desirable for confirmation of this dimorphism.

In front of the adductorial sulcus in the female there are two small swellings near the hinge line marking the site of the pre-adductorial node and anterior lobe respectively; the prenodal sulcus is recognisable only as a very shallow depression. The anterior section of the valve in tecnomorphs is a very wide, flat area, (apparently) devoid of individual lobal elements. The adductorial sulcus is discernible as a narrow, shallow depression in the central part of the valve just behind mid-length. The syllobium is broad and in tecnomorphs is connected below the slightly curved adductorial sulcus to the anterior region of the shell. None of the lobes project above the hinge line.

The velum is wide and has a basal crest and a (basal) toric ridge in both dimorphs. In ventral view the posterior part of the toric ridge in tecnomorphs is characteristically arc-like in shape. The velum is joined directly to the posterior part of the crumina and absent in front of it. Posteroventrally the female velum has an abrupt restriction of the kind found in *Hammarieella* Martinsson (it has not been possible to figure it as this part of the velum is always broken); a similar restriction probably also occurs in the tecnomorphs. In the extant tecnomorphs the velum extends to at least anterior mid-height.
The crumina is large, and set off high above the domicilum. Neither toric ridge or velum pass over the crumina.

No ornament is observable on the lobes or sulci. Both sides of the velum have a pattern of fine, evenly distributed striae at right angles to the long, narrow tubules. The ventral part of the crumina has an impressive network of meshes arranged in rows roughly parallel to the free margin; this reticulation gradually becomes finer opposite the velar edge. On its dorsal regions, near to its junction with the lobes, the crumina is finely reticulostriate.

**MEASUREMENTS:** Hinge length - sulcal height (to the basal crest only) of two female valves from the type locality.

1380-750, 1360-710 (holotype).

**DISCUSSION:** This species seemingly displays dimorphism in its lobation. This is not an unusual condition; *Lophoctenella* Martinsson, 1962 and *Cryptolopholobus* Martinsson, 1952 are other amphitoxotidine genera whose species show differences between the lobation of heteromorphs and tecnomorphs. If dimorphism affects lobation in the amphitoxotidine *Atterdagia* (it appears to do so - see Martinsson 1962, p. 256, figs. 131 A, C - though it is not certain) then the form it takes is remarkably similar to that suggested in *Charitoxotis*.

**OCCURRENCE:** The Wenlockian of the W Midlands of England (and possibly the Welsh Borderland).

*Wenlock Limestone:* Wren's Nest (locs. 27c, d, f, g).

? Ledbury (loc. 23); cruminae (with vela) only.

? Old Farm (loc. 16); cruminae (with vela) only.

Extant material from the Wren's Nest consists of some 30 specimens (only five tecnomorphs), nearly all of which are incomplete.
Genus **Atterdagia** Martinsson, 1962

**TYPE SPECIES:** Original designation of Martinsson 1962, p. 254; **Atterdagia paucilobata** Martinsson, 1962, p. 255, fig. 131A; from the Ludlovian (Hemse Beds) at Tjängdarve, Gotland.

**BRITISH SPECIES:** **Atterdagia versiculus** sp. nov.

**DIAGNOSIS:** Amphitoxotidinae with the male velum very wide and abruptly restricted posteroventrally, and the female velum confined to a narrow, constricted, postcruminal wing. Both dimorphs have a basal crest and a basal toric ridge. Syllobium broad and fairly flat, anterior lobe and preadductorial node - if discernible - diminutive; dorsal margin straight, effectively without cusps. (Modified from Martinsson 1962, p. 255).

**DISCUSSION:** The British species shows such striking resemblance to **A. paucilobata** (hitherto the only known member of the genus) in valve, lobal, and cruminal shapes and proportions, and in ornament that - in this case - the differences in subcruminal morphology between the two species (see below) cannot be awarded generic importance. More particularly the velar morphology of the Welsh Borderland material is a facsimile of the distinctive form found elsewhere only in the **type species of Vinculoveliger.** If, as it seems (see Martinsson 1962, p. 256, fig. 131A), **A. paucilobata** has a short, ridge-like syllobial swelling similar to that found in **A. versiculus**, this would augment the generic characteristics given in the diagnosis above.

**Atterdagia** is related to a group of amphitoxotidines consisting of genera such as **Berolinella** Martinsson, 1962, **Dibolbina** Ulrich & Bassler, 1923 and **Charitoxotis** gen. nov. Features which characterise this group include: a well developed globular crumina, a rather flattened valve surface with (generally) indistinctly developed lobes
and sulci, and a wide, prominently tubulous velum (particularly in tecnomorphs) with a basal crest and a basal toric ridge. Some of the genera show affinities to each other in lobation but not in cruminal (or velar) morphology; others have subcruminal features in common but manifest different lobal and sulcal arrangements. Across the crumina in Berolinella (and probably Atterdagia versiculus) there are toric and velar structures, in Dibolbina there is - so far as we know (Berdan 1973, p. 23) - only a velum, whilst in Atterdagia paucilobata and Charitoxotis the crumina completely lacks such features. A postcruminal velar constriction is known only from Atterdagia; in the other genera mentioned here the velum is connected directly to the crumina. In Atterdagia, Berolinella, and Charitoxotis the velum is sharply terminated posteroventrally; in Dibolbina it is entire from anterior to posterior cardinal corners. Only in Dibolbina and Atterdagia is there a ridge-like structure on the syllobium.

OCCURRENCE: The Ludlovian of the Welsh Borderland and Gotland.

**Atterdagia versiculus** sp. nov.

Pl. C18, figs. 1-7.

DERIVATION OF THE NAME: Latin diminutive versiculus, a little furrow; referring to the appearance of the depression on the crumina.

HOLOTYPE: A female right valve, DAS M 284; Pl. C18, figs. 4, 7.

TYPE LOCALITY AND TYPE STRATUM: A small hillside exposure approximately 600 m SSE of Trippleton Farm and just 10 m W of the road from Burrington to Leintwardine, Herefordshire (loc. 68); Upper Leintwardine Beds.

DIAGNOSIS: A species of Atterdagia in which features (probably) corresponding to the torus and velar edge can be traced either side a narrow depression on the ventral part of the crumina. Adductorial sulcus long and shallow. Lobes discernible.
DESCRIPTION: The anterior and posterior margins of the valve are evenly curved. The fairly flat valve surface lies considerably below the lateral surface of the large, rounded crumina. Lobes are discernible but inconspicuously developed. The sulci are quite shallow (especially the prenodal sulcus).

The syllobium is broad, flat, and has no cusp. A short, ridge-like swelling is present - in females at least - on the posteroventral region of the syllobium. The preadductorional node in the female is represented by a small, very narrow, node-like feature near the hinge line; in the male the node is similar but somewhat longer. The anterior lobe is flat and wide, and is distinguished only as that region of the valve between the weakly developed prenodal sulcus and the anterior margin. The shallow, rather open adductorial sulcus is shortened in the females (to a length similar to the prenodal sulcus); in the tecnomorph it extends from the hinge line for a considerable distance - just failing to reach the basal crest of the velum. This sulcus is wider (dorsally) than the preadductorial node, and narrows gradually towards the velum. Valves lack an anteroventral depression.

Dimorphism is shown in the nature of the velum; in the tecnomorph it is long (from the lower part of the anterior margin to its abrupt restriction posteroventrally) and wide, but in the female it is represented simply as a short and narrow, postcruminal wing-like feature, separated from the crumina by a marked constriction. In both dimorphs the tubulous velum is adorned with a basal crest, a basal toric ridge and a concentric "wrinkle" pattern of fine striae. The latter, seen particularly in the tecnomorph, give the velum a frill-like appearance.

In lateral view the limits of the crumina lie (dorsally) just about valve mid-height, (anteriorly) directly below the anterior-most point of the valve margin, and (ventrally) below the valve margin. Crossing the ventral part of the crumina there is a narrow, shallow depression.
bounded along its length (abmarginally) by a rise to the lateral part of the crumina - which may mark the trace of the velar edge - and (admarginally) by an elevated zone which is taken to represent the toric structure. (For further comments on the subcruminal morphology see "Discussion" below).

As far as can be determined the lobal and sulcal surfaces are unornamented. Laterally and venterolaterally the crumina is reticulo-striate; in the shallow subcruminal depression ornament appears to be effaced.

MATERIAL: All specimens of A. versiculus are moulds. Particularly fine casts, were obtained from material from the type locality.

MEASUREMENTS: Hinge length - sulcal height (in microns) of valves from the type locality.

Females: 1480-890, 1450-880.

Tecnomorph: 1390-775.

DISCUSSION: A. versiculus differs from A. paucilobata in its more effectively developed sulcation (e.g. its longer adductorial sulcus), its reticulo-striate (as opposed to simply reticulate) cruminal ornament, and in the ventral morphology of its crumina (A. paucilobata has no subcruminal ridges or depressions). There may also be minor differences in lobation (it is not certain that the lobes of A. paucilobata tecnomorphs are differentiated dorsally).

The subcruminal morphology of A. versiculus has its nearest parallel in Vinculoveliger catenulatus Martinsson, 1962 (the type - and only species), where, "The crumina has ventrally a subequatorial ridge, corresponding to the velum, and a basal, broad, striate swelling which is probably of toric origin" (Martinsson 1962, p. 253, fig. 128B). The long adductorial sulcus of A. versiculus is reminiscent of conditions found in Berolinella.
OCCURRENCE: Obtained from a number of localities in the Leintwardinian around Ludlow.

Upper Leintwardine Beds: Tripleton Farm (loc. 68).
Bengry Track (loc. 63).
Forestry Track, Ludlow (loc. 62).
Fiddlers Elbow (loc. 67).
The Goggin (loc. 64).

Also identified in J.H. McD. Whitaker's collections (loc. 811) from the Upper Leintwardine of the Leintwardine area.

Genus MACRYSILON Martinsson, 1962

TYPE SPECIES: Original designation; Beyrichia Salteriana Jones, 1855, p. 89, (Martinsson's selected lectotype was not figured by Jones); from glacial erratics (limestone), near Breslau.

BRITISH SPECIES: Macrypsilon salterianum (Jones, 1855).

DIAGNOSIS: Amphitoxotidinae with very broad lobes. In the tecnomorphs the narrow sulci are united below the preadductor lobe into an equally narrow sulcus separating the syllobium and anterior lobe. Crumina very large. Velum forming a narrow flange from the anterior to the posterior hinge corner, but the tubulosity within it is discernible. All lobes finely reticulate. (After Martinsson 1962, p. 257).

OCCURRENCE: Deposits of late Ludlovian and Downtonian age.
Found in Britain, N America and the Baltic area.
Macrypsilon salterianum (Jones, 1855)

Pl. C18, figs. 14, 15.

1855 *Beyrichia Salteriana*, nov. sp.; Jones, p. 89, pl. V, figs. 15a, b, 16a, b.

1954 *B. salteriana* Jones 1855; Henningsmoen, p. 25 (assigned to *Beyrichia* (Neobeyrichia) subgen. nov.).

1957 *Neobeyrichia salteriana* (Jones) 1855; Kesling & Rogers, p. 1003, pl. 128, figs. 14-18.

1962 *Macrypsilon salterianum* (Jones, 1855); Martinsson, pp. 17, 257, fig. 2D.

1964 *Macrypsilon salterianum* (Jones, 1855); Martinsson, p. 133.

1964 *Macrypsilon salterianum* (Jones); Copeland, p. 5, pl. 1, figs. 4, 5.

1967 *Macrypsilon salterianum* (Jones) 1855; Witwicka, p. 48, pl. II, figs. 9a-c.

1967 *Macrypsilon salterianum* (Jones), 1855; Gailite, p. 128, pl. IX, figs. 5a, b.

1968 *Macrypsilon salterianum* (Jones); Sarv, p. 28, pl. IX, fig. 1.

1971a *Macrypsilon salterianum* (Jones 1855); Shaw, p. 599, pl. 109, figs. 7, 8.

1972a *Macrypsilon salterianum* (Jones); Pranskevichius, p. 441.

LECTOTYPE: Designated by Martinsson 1962, p. 17, fig. 2D;
unfigured by Jones; an almost complete tectonomorphic right valve,
BM I 7100.

TYPE DATA: From the glacial erratic block no. 5 of Jones, found near
Breslau; limestone, probably from the Beyrichienkalk.

DIAGNOSIS: As for the genus.
DESCRIPTION: See the generic diagnosis above, Kesling & Rogers 1957, and Shaw 1971a.

DISCUSSION: Both specimens figured by Jones in his original descriptions have been located at the Brit. Mus. (Nat. Hist.); they are BM I 7099 (Jones 1855, pl. V, figs. 15a, b) and BM I 7118 (Jones 1855, pl. V, figs. 16a, b).

In the last decade material from many countries has been illustrated in the literature under the name *M. salterianum*; as far as can be judged from the figures alone (cf. key references in synonymy list) the material is taken to represent one species. The two British valves (tecnomorph and female) figured by Shaw differ slightly from the Baltic material of Jones by the occurrence of a weak depression across the posterodorsal part of the syllobium. In all other respects the figured British tecnomorph (GSM ZL 9055) is indistinguishable from Jones's originals.

OCCURRENCE: Not collected by the writer but recorded by Shaw from two areas in Britain. In the Lake District (Shaw 1971a) *M. salterianum* ranges from the upper part of the Kirkby Moor Flags to the top of the Scout Hill Flags; in the Long Mountain region (Shaw 1969, fig. 8) it was observed in the Upper Whitcliffe Flags and Downton Castle Sandstone. In both regions its occurrence approximately spans the Upper Whitcliffian - Lower Downtonian sequence.

Elsewhere this species is known from the higher parts of the type section of the Stonehouse Formation, Nova Scotia (Copeland 1964), the Chlapowo borehole (Witwicka 1967) and Leba 1 borehole (Martinsson 1964) of Poland, the Kaugatuma and Ohesaare Stages of Estonia and Saaremaa (Sarv 1968, 1971), the Minija and Jura Beds of Latvia (Gailite 1967), and the Baltic Beyrichienkalk (Martinsson 1963, 1967).

Pranskevichius (1972a) records *M. salterianum* from the Minija strata of S Baltic (Lithuania and Kaliningrad) boreholes.
Genus *Gongylostonyx* gen. nov.

**DERIVATION OF THE NAME:** From the Greek *gongylos*, a ball, and *stonyx*, a spike; with reference to the prominently developed crumina and calcarine spine in the type species. Gender, masculine.

**TYPE SPECIES:** *Gongylostonyx exaggeratus* sp. nov., Pl. C19, figs. 3, 4, 8; from the Wenlockian of the Welsh Borderland.

**BRITISH SPECIES:** Only the type species.

**DIAGNOSIS:** Small Amphitoxotidinae with a prominent calcarine spine and a narrow, flange-like velum constricted behind a large crumina; the velum continues in front of the crumina. Anterior lobe, preadductory lobe and syllobium all entire and simply arranged; syllobial cusp variably developed.

**DISCUSSION:** The species cited by Martinsson (1962, p. 257, figs. 132A-C) as "*Incertae subfamiliae*, n.g., n.sp." from Sles and Lunde, Gotland, almost certainly belongs to this genus. The three females he figures display all the characteristics of *Gongylostonyx*, and on the basis of these illustrations (no description was given and the tecnomorph is unknown) it is hardly possible to distinguish the Gotland material from the type species; in subcruminal and velar morphology particularly, the material from each area appears identical. However, the Gotland material (six female valves) occurs at a much higher level (Hamra Beds = Whitcliffian) than *G. exaggeratus* (from the British Wenlockian) and it possibly represents another species.

As noted by Martinsson, the taxonomic position of this genus presents some problems - but it can hardly be placed in other than the Amphitoxotidinae or the Beyrichiinae. Prominent calcarine spines are present in parts of both subfamilies (cf. *Sleia* and *Beyrichia* (*Simplicibeyrichia*) spp.). *Gongylostonyx* is tentatively referred by the present
author to the Amphitoxotidinae (cf. velar morphology, the form of its cruminal ornament, and the nature of its marginal structure).

There is evidence, as yet inconclusive, to suggest that a second (congeneric) species occurs in the Wenlock Series of England. A few tecnomorphic specimens from one locality (Whitman's Hill; loc. 19b) differ from those included within *G. exaggeratus* by having a more isolated, ridge-like anterior lobe, a longer, distinctly posteriorly directed calcarine spine, and a syllobium showing no trace of cuspidal development. Additional material is needed before these differences can be confirmed and formally presented.

**OCCURRENCE:** The Wenlock Series of the Welsh Borderland and English W Midlands, and the high Ludlovian of Gotland.

*Gongylostonyx exaggeratus* sp. nov.

*Derivation of the Name:* Latin *exaggeratus*, exaggerate; alluding to the fact that the characters are emphasised.

**Holotype:** A female right valve, DAS 47354; Pl. C19, figs. 3, 4, 8.

**Type Locality and Type Stratum:** A small disused quarry on the N side of the A 458 road, top of Harley Hill, approximately 1.2 km NW of Much Wenlock, Shropshire (loc. 51); shale parting within the Wenlock Limestone.

**Diagnosis:** As for the genus.

**Description:** The preadductorial node is knob-like, slightly inclined forwards (particularly in females), and separated from the anterior lobe by a narrow, curving, prenodal sulcus. Both sulci are comparatively shallow, with the adductorial sulcus being somewhat longer (it extends for about two-thirds of valve height) and wider. The syllobium is
dominated by the single (hollow) spine found on its anteroventral region in tecnomorphs, and just behind the crumina in females. This calcarine spine is normally directed laterally, or slightly postero-laterally, and is always conspicuous. The only other feature on the syllobium is its variably developed cusp. Its position, just behind the main sulcus, is promptly recognised and normally the cusp is distinguished as a small, sub-angular process extending just above the hinge line; sometimes the cusp is not clearly differentiated and may appear as a tiny, blunt tubercle or - typically in immature valves - be lacking altogether. The anterior lobe is indistinctly developed; it does not project beyond the hinge line and is of lower elevation than either the syllobium or preadductorial node. All lobes vaguely coalesce (there are no well-defined lobal connections) in the region below the preadductorial node. The presence of an anteroventral depression is only very faintly suggested. Anterior and posterior acroidal processes are commonly seen in the smaller instars, but have not been observed in adults. These processes are confined in the extant material to the right valve.

The narrow velum is mostly flange-like and is widest ventrally, becoming somewhat narrower towards each hinge corner. In females the velum is fully constricted postcruminally, but reappears attached to the crumina precruminally, and can be traced as a narrow ridge to the anterior cardinal corner. Velar tubulosity is not visible. There are no signs of a toric structure in either dimorph. The crumina is large, well set off from the valve surface, and has expanded to the complete expense of the velum. Normally the vertical margin structures appear as fine ridges, capped with a row of minute processes. Some females show the vertical marginal structure well developed adjacent to the crumina, where it is about as wide as the velum, tubulous, and frill-like.

The lobes have a faint ground pattern of small granules and a sparse covering of rudimentary tubercles. Fine striae ornament the crumina and are best seen usually on its ventral surface.
MEASUREMENTS: Hinge length - sulcal height (to the edge of the velum) of female valves in microns.

Harley Hill Qy. (loc. 51): 1020-630.

Acklands Coppice (locs. 42a, b): 1060-670, 1050-655.

Benthall Edge, East (loc. 43a): 1035-620.

DISCUSSION: The most variable feature of this species is the strength of development of the syllobial cusp. It can be almost equal in size to the calcarine spine, or differentiated merely by an indistinct tubercle-like feature high on the anterodorsal surface of the syllobium. In immature tecnomorphs the cusp is invariably much reduced or obsolete.

A trend towards the isolation and elevation of the anterior lobe is shown within what is probably a second Gongylostonyx species (see generic discussion).


Wenlock Limestone: Harley Hill Qy. (loc. 51).

Gleedon Hill (loc. 50).

Benthall Edge, West (loc. 47).

Audience Wood (loc. 57).

Lincoln Hill (loc. 49b).

Wren's West (loc. 27a).

Hobbs Ridge (loc. 15b).

Whitman's Hill (loc. 19b).

Parkwood (loc. 22).

Tickwood Beds: Harley Hill Road (loc. 48c).

Tickwood (locs. 44a-d).

Acklands Coppice (locs. 42a, b).

Benthall Edge, East (loc. 43a).

Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39).
Amphitoxotidinae gen. et sp. nov. A
Pl. Cl9, figs. 9, 10, 12, 14, 15.

REMARKS: This large amphitoxotidine species is distinguishable from other members of the subfamily by its rather unique lobal arrangement. Unfortunately only three specimens (all females and only one complete) have been obtained from the large quantity of limestone prepared. Additional material - more especially a tecnomorph - is desirable before the species can be formally described.

DESCRIPTION: All of the lobes are elevated well above the level of the rest of the valve surface. The anterior lobe is stout, and almost constant in width from the base of the crumina to its rounded cusp some way above the hinge line. The small preadductorional node tapers to a vague point dorsally, and nestles against the lower regions of the anterior lobe in a manner reminiscent of many craspedobolbinines. The main, elevated section of the strongly developed syllobium is characteristically inclined forwards from its base to its broadly rounded cusp. Like the anterior lobe, the syllobium, in cross section, has a gently curved outline; the cusps of both lobes are similar in height and general shape. Posterodorsally the syllobium widens out into a lower, vaguely triangular area; ventrally it is not much wider than the anterior lobe. In posterior view the syllobium has a broadly arcuate ventero-dorsal profile.

Around the outside of the anterior lobe and syllobium, zones of appreciable width, but much lower elevation, occur; these areas are bounded by the velar bend. This sharply rounded ridge runs parallel to the free margin all around the valve except for its partial interruption by the crumina. In the best preserved female specimen the velum becomes obsolete for a short distance on the posterior part of the crumina, only to reappear again for most of the cruminal length as a fairly straight, weak ridge. There is no toric ridge.
The adductorial sulcus is deep, and widens dorsally above the preadductorional node. The prenodal sulcus is shallow, narrow and comparatively short (it opens dorsally into the adductorial sulcus, not the hinge line).

Apart from the fine reticulation - almost punctation - above mid-height on the main stem of the syllobium, the best preserved female valve lacks ornamentation (the crumina is also smooth).

**MATERIAL:** Just three female specimens; one complete but slightly damaged valve, and two other incomplete valves.

**MEASUREMENTS:** Hinge length - sulcal height (inclusive of cruminal width) of the only measurable female specimen.

2260-1650 (in microns).

**DISCUSSION:** On the basis of the general lobal arrangement and ventral morphology of the crumina, this species is considered to be an amphitoxotidine. Females of other genera such as *Grogarnia* Martinsson, 1962 show that the amphitoxotidine velum can be reduced to a low ridge or flange.

The details of its lobal pattern are unusual for the subfamily and it is not easy to find closely related genera. The form and position of the preadductorional node in particular is somewhat atypical, and we must look to the Craspedobolbininae and Treposellinae for comparable conditions. The morphology of the syllobium and anterior lobe, both rather stout and vertical, again, do not readily resemble any established amphitoxotidine genus (in genera such as *Vinculoveliger* the syllobium differs significantly in shape).

**OCCURRENCE:** Known from a single locality in the Tortworth inlier.

Brinkmarsh Beds: Brinkmarsh Qy., limestone band (loc. 11).
Amphitoxotidinae (gen. nov. ?) sp. nov. B

Pl. Cl8, figs. 8, 9, 12, 13.

REMARKS: Two female specimens collected from Lincoln Hill are referable to a new amphitoxotidine species. Its generic assignment is uncertain, but it probably represents a new genus. The species is not described in detail or named until more material becomes available. A female valve from Tickwood is congeneric with the specimens from Lincoln Hill, but may belong to another species (see "Discussion" below).

DESCRIPTION: The syllobium and anterior lobe are broad, and do not project above the hinge line. The preadductorial node is vaguely recognisable as a small, knob-like feature fused to the anterior lobe; there is no definable prenodal sulcus. The anterior lobal complex is slightly less elevated than the syllobium. The adductorial sulcus is almost as wide as the preadductorial node around which it curves; the sulcus appears to become obsolete before reaching the dorsal region of the valve (this is not certain as both specimens are damaged in this region).

In lateral view the small crumina is very nearly round. Long narrow tubules are radially arranged throughout the length of the velum. The frill-like velum extends from the anterior cardinal corner across the crumina - where just at mid-length it is weakly curved away from the margin - to its abrupt posteroventral restriction; posteriorly the velum can be traced as an indistinct ridge. The domicilium, excluding the adductorial sulcus, is covered by coarse reticulation. Cruminal ornament consists of fine striae.

MATERIAL: Two females - one crushed carapace and one slightly damaged right valve.

MEASUREMENTS: Estimated hinge length - sulcal height (including velar width) of the female right valve.

1050-820 (in microns).
DISCUSSION: *Hemsiella anterovelata* Martinsson, 1962 is perhaps the nearest known amphitoxotidine to this species; they are similar particularly in velar and subcruminal morphology, but differ in lobal and ornamental features. Assuming that the arrangement of the adductorial sulcus in the British species is correctly given above, the new genus would differ from *Hemsiella* in having a reduced adductorial sulcus, a fused anterior lobal complex and a network of reticulation whose meshes lie outside the size range of known *Hemsiella* species; knowledge of the tecnomorphs of the British species might provide other differences. One or two of these tecnomorphs may be "hiding" in the abundant material of *Undipila repanda* collected from Lincoln Hill.

The female from Tickwood (loc. 44d) - see "Remarks" above - is distinguished from the Lincoln Hill females by a more pronounced tendency towards obsoletion of the adductorial sulcus.

**OCCURRENCE:** Wenlock Series, N Shropshire.

Wenlock Limestone: Lincoln Hill (loc. 49c).

**Amphitoxotidinae (Incerti generis) sp. nov. C**

Pl. C18, figs. 10, 11.

**REMARKS:** This species is identified from a few tecnomorphs at a single locality. Of the known genera with a basal crest these Welsh Borderland valves most resemble the monotypic *Vinculoveliger* Martinsson from Gotland (cf. the proportions and isolation of the lobes, and the extent of the velum), but in the absence of information concerning the female dimorph it is not possible to assess with accuracy if they are congeneric. The British material can be distinguished from tecnomorphs of *V. catenulatus* Martinsson in ornament (more regularly reticulate, rather than reticulo-striate) and by slightly wider lobes.
DESCRIPTION: All lobes are broad and stout. The anterior lobe and to a lesser extent - lateral surfaces of syllobium and preadductorional node are flattened. All lobes are virtually isolated; in particular the long, well delimited prenodal sulcus - from hinge line to the moderately concave anteroventral depression - separates the anterior lobe from other lobal elements. The lobal connection from the syllobium to the preadductorional node is very weak. Adductorional sulcus shorter, but slightly wider and deeper than the prenodal sulcus. The anterior lobe has a rounded cusp inconsiderably above the hinge line; the syllobial cuspidal region is not seen.

No velum is preserved complete; characteristically it is broken immediately distal to the line of the basal crest. Like the velum, this crest is traced from anteroventral to posteroventral parts of the valve. The form taken by the posteroventral restriction, and the shape of the velum itself, is not known. Velar tubules are visible all along those parts of the velum preserved.

All lobes are finely reticulate and, so far as can be ascertained, the reticulation on the larger valves appears to be finer than the smaller tecnomorphs. The prenodal sulcus is conspicuously smooth.

MATERIAL: Five tecnomorphs, all moulds.

MEASUREMENTS: Approximate hinge length - sulcal height (excluding velum) of the largest tecnomorph.

1600-1000 microns.

OCCURRENCE: Leintwardinian near Aymestrey, Herefordshire.

Upper Leintwardine Beds: Bengry Track (loc. 63).
Family BEYRICHIIIDAE Matthew, 1886

DIAGNOSIS: Beyrichiacea lacking radial tubulosity in the flange- or ridge-like velum but sometimes with radial spines along the velar edge. Crumina originating by invasion of the region around the anteroventral portion of the velar fold. There are traces of the cruminal metamorphosis in the obsoletion of the marginal structure or in a plication breaking through this structure and the free margin of the valve, or these traces may be entirely absent. (After Martinsson 1963, p. 54).
BRITISH BEYRICHIINAE

REMARKS: The structure of the subfamily Beyrichiinae in Britain bears overall similarity to that from the Baltic region. Both areas are characterised by typical beyrichiines such as Beyrichia, Neobeyrichia, Nodibeyrichia and Calcaribeyrichia.

One British species (Beyrichiinae gen. et sp. nov. A, herein) is anomalous in that its affinities are best sought amongst the (mainly) American group of enigmatical beyrichiines which have a (variably developed) flange-like velum and an ornamental arrangement essentially different to that found in typical beyrichiines.

With the erection of the (early) Porcarichia gen. nov. (to accommodate two new species from one of the Scottish Silurian inliers) it is possible to retain the genera Neobeyrichia and Calcaribeyrichia as hitherto diagnosed.

The type genus, Beyrichia M'Coy, 1846 is quite well represented in Britain. The problem of its type species is discussed in some detail and collections of Beyrichia kloedeni M'Coy made from the type locality are described. Beyrichia (Jubatibeyrichia) subgen. nov. is established; a subcruminal ridge is now shown to occur within the genus.

The earliest known representative of Calcaribeyrichia (C. characta sp. nov.) is recorded from the Midland Valley of Scotland. Other Calcaribeyrichia species are documented from the Ludlow Series of England.

Most of the Neobeyrichia species from Britain are also well known members of Baltic faunas. The relatively young Nodibeyrichia occurs rarely, both in the Welsh Borderlands and in subsurface material from Buckinghamshire, but has (N. pustulosa Hall, 1860) proved to be important in intercontinental correlation.
SYSTEMATIC PALAEONTOLOGY

Subfamily BEYRICHIINAE Matthew, 1886

TYPE GENUS: Beyrichia M'Coy, 1846, p. 58; from the Silurian of Ireland.

BRITISH GENERA: Beyrichia M'Coy, 1846
Porcarichia gen. nov.
Neobeyrichia Henningsmoen, 1954
Nodibeyrichia Henningsmoen, 1954
Calcaribeyrichia Martinsson, 1962
Beyrichiinae gen. et sp. nov. A

DIAGNOSIS: Beyrichiidae forming the crumina by direct occupation of the anteroventral part of the shallow velar fold and adjoining parts of the carapace wall, without a dolonoid scar but often with a striate area on the ventral part of the crumina. Remains of the zygal ridge, if present at all, obviously influenced but sometimes only slightly displaced by the inflation of the crumina. (After Martinsson 1962).

DISCUSSION: As presented by Martinsson this subfamily consists of two morphological groups. The typical beyrichiines are granulose - spinose with a ridge-like velum and are mostly European (e.g. Beyrichia, Neobeyrichia, Calcaribeyrichia). The second group have a flange-like velum and are often reticulate; this group contains mostly American genera (e.g. Lophokloedenia Swartz & Whitmore, 1956, Zygobeyrichia Ulrich, 1916, and "Kloedenia" of American usage) but also includes the European Bingeria Martinsson, 1962. Martinsson and other workers (Kesling 1969, p. 291; Berdan 1972, p. 26) have suggested that with revision the latter group might form the basis of a subfamily distinct from the Beyrichiinae. In effect, this idea was largely implemented by Abushik (1971) who introduced the family Welleriellidae based on Welleriella gen. nov. from Podolia, and (amongst others) Zygobeyrichia, Welleria Ulrich & Bassler, 1923, Lophokloedenia and Welleriopsis Swartz &
Whitmore, 1956. As a thorough revision of this important group of
American genera is still needed, the present writer prefers to refrain
from using Abushik's taxon.

The morphological similarities between beyrichiines and amphitoxo-
tidines have been outlined elsewhere (Martinsson 1963, p. 56; Henningsmoen
Henningsmoen (1965) thought that the Amphitoxotidinae (with a tubulous
velum) may have descended from beyrichiines (without a tubulous velum)
and for this reason placed them in the same family.

OCCURRENCE: Known from throughout the Silurian in Britain. Distributed
widely in equivalent deposits of Europe, and also America. Recorded
from Asian regions of the U.S.S.R.

Genus BEYRICHIA M'Coy, 1846

TYPE SPECIES: Case to be submitted to the I.C.Z.N.; Beyrichia Klödeni
M'Coy, 1846, p. 58; from upper Llandovery sandstones, County Galway,
Ireland.

BRITISH SUBGENERA: Beyrichia (Beyrichia) M'Coy, 1846
Beyrichia (Scabribeyrichia) Martinsson, 1962
Beyrichia (Jubatibeyrichia) subgen. nov.

DIAGNOSIS: Beyrichiinae with an uninterrupted, more or less wide
connection between the anterior lobe and the syllobium, without any
significant lobular differentiation (slightly modified from Martinsson
1962, p. 268).

DISCUSSION - THE TYPE SPECIES: The complex nomenclatural history of
the genus Beyrichia M'Coy 1846 (non Beyrichia Boll, 1847) and the problem
of its correct type species has been discussed in much detail, notably
by Henningsmoen (1954), Kesling & Wagner (1956), Martinsson (1960b, p. 15;
1962, pp. 14, 269; 1965, pp. 111, 112), Spjeldnaes (1966) and by
Sylvester-Bradley & Levinson (1960).

Kesling & Wagner (op. cit.) maintained that Beyrichia kloedeni
M'Coy, 1846 has to be regarded as a junior synonym of Battus tuberculatus
Klöden, 1834; they pointed out that although M'Coy (1846) had given his
specimens (from Ireland, and some material from Wales which Sowerby in
Murchison 1839 had described as Agnostus (Battus) tuberculatus Klöd.)
a new generic and specific name, he had implied in both his text and synonymy
list that this material was conspecific with Klöden's form from the
Baltic area. Kesling & Wagner thus believed that B. tuberculatus was
the type species of Beyrichia and that B. kloedeni M'Coy, 1846 was an
invalid name. Moreover these authors recognised - as did M'Coy
(in a paper of 1851) and many later workers - that the material from
Ireland is referrable to a species separate from Beyrichia tuberculata
(Klöden).

Martinsson (1960b, pp. 15, 16; 1962, p. 14) and Sylvester-Bradley
& Levinson (1960) shared the opinion that Kesling & Wagner were incorrect,
that M'Coy's name was valid and - in agreement with nearly all previous
writers on the subject (such as Ulrich & Bassler 1923, Straw 1928,
Henningsmoen 1954) - that Beyrichia kloedeni M'Coy should be considered
the type species of the type genus Beyrichia.

The urgency to clarify this problem had received impetus by the
introduction (Henningsmoen 1954) of subgenera within Beyrichia.
B. (Nodibeyrichia) Henningsmoen,1954 which included B. tuberculata
(Klöden) was later (Kesling & Rogers 1957) elevated to generic rank.
If, as argued by Kesling & Wagner (op. cit.), B. tuberculata is the
type species this would mean changing the name Nodibeyrichia to Beyrichia,
changing the long and widely accepted concept of Beyrichia, and
renaming the genus now called Beyrichia.
Sylvester-Bradley & Levinson (op. cit.) in an application to the I.C.Z.N. held the view that *B. kloedeni* is a junior subjective synonym of *B. tuberculata*. Their application to place on the official lists of generic and specific names in zoology "Beyrichia M'Coy 1846" and "type species by monotypy, Beyrichia kloedeni M'Coy 1846" was never implemented; the authors did not invoke the use of the commission's plenary powers, but, in the opinion of Mr. R.V. Melville (secretary, I.C.Z.N.) should have done so. Mr. Melville (pers. comm., 21st. December, 1973) informs Sylvester-Bradley and the present writer that *B. tuberculata* must in his view be considered the type species of *Beyrichia* because the nominal species *B. kloedeni* is clearly a "replacement name" for *tuberculatus* and ipso facto is a junior objective synonym of *B. tuberculata* taking the same type specimen as that species.

As Klöden's originals are lost, Martinsson (1965, p. 123) designated a neotype for *Nodibeyrichia tuberculata* (Klöden, 1834). At present this specimen would, according to Mr. Melville, be the type specimen of the type species of *Beyrichia*. In order to preserve nomenclatural stability a new application (invoking the use of plenary powers) will be submitted to the commission by Sylvester-Bradley and the writer designed to avoid such action. It would invoke the general terms of Sylvester-Bradley and Levinson (op. cit.) but with the following amendments:

1. The specimen designated as lectotype of the nominal species *Beyrichia kloedeni* M'Coy, 1846 must now be designated as neotype.

2. Martinsson (1960b, pp. 15, 16) has discussed the authorship of the family name *Beyrichiidae* and has given reasons for ascribing this name to G.F. Matthew (1886) rather than to Ulrich, 1894. Sylvester-Bradley and the writer agree with the opinion of Martinsson and therefore in a new application it would be necessary to alter paragraph 15 (iii) "Beyrichiidae
Ulrich, 1894" and replace it with ".... Beyrichiidae Matthew 1886 ....".

Attention should also be drawn to the paper by Spjeldnaes (1966) in which he outlines the "publication" of the long forgotten "ostropod" species called Battus Kloedeni n. sp. by N.P. Angelin in 1838-9. This taxon is identified by Spjeldnaes with the species Craspedobolbinina (Mitrobeyrichia) clavata (Kolnodin, 1869). If Angelin's name had been used prior to 1960 in combination with Beyrichia, it could have been a senior secondary homonym of B. Kloedeni M'Coy. As it seems never to have been so used, and as it would now be regarded as a member of a different genus, it presumably can be ignored. This would especially seem so as there is considerable doubt about the validity of Angelin's publication, which was a printed list of fossils for sale, and the name does not seem to have been accompanied by "a description, definition, or indication" (article 12, International code of Zoological Nomenclature).

OCCURRENCE: The Llandovery, Wenlock and Ludlow Series of Britain. Many species of Beyrichia occur in the Silurian of Scandinavia and the Baltic area. Two species - Beyrichia arctigena Martinsson, 1960 and Beyrichia henningsmoeni McGill, 1963 - have been recorded from N America.

Subgenus Beyrichia (Beyrichia) M'Coy, 1846

TYPE SPECIES: Beyrichia Kloedeni M'Coy, 1846 (case to be submitted to the I.C.Z.N.).

BRITISH SPECIES: Beyrichia (Beyrichia) kloedeni M'Coy, 1846

Beyrichia (Beyrichia) messis sp. nov.

Beyrichia (Beyrichia) clausa Jones & Holl, 1886

Beyrichia (Beyrichia) obesa (Harper, 1940)

Beyrichia (Beyrichia) impacifica sp. nov.
DIAGNOSIS: Species of Beyrichia with a well delimited crumina and a broad syllobium. Verrucose, tuberculate, or spinose, without other differentiations in the ornamentation of the lobes than the distinction of a supravelar field or row of tubercles, between a calcarine and an uncular tubercle or spine. Velum never higher than a ridge; syllobial groove not exceptionally high. (After Martinsson 1962, p. 269).

OCCURRENCE: In Britain from the Llandovery, Wenlock and Ludlow Series; found in the Welsh Borderlands, English W Midlands, Midland Valley of Scotland, Ireland.

_Beyrichia (Beyrichia) kloedeni_ M'Coy, 1846
Pl. D3, figs. 13, 14.

1846 Beyrichia Klödeni. M'Coy; M'Coy, p. 58, three unnumbered text-figs.

1851 Beyrichia Klödeni (McCoy); M'Coy, p. 135 (partim).
non 1851 Beyrichia Klödeni (M'Coy); M'Coy, pl. 1E, fig. 2.
non 1855a Beyrichia Kloedeni, M'Coy; Jones; p. 165, pl. VI, figs. 7, 9.
non 1869 B. Kloedeni, M'Coy; Jones, p. 11, figs. 6a, b.
non 1881c Beyrichia Kloedeni M'Coy; Jones, p. 345, pl. X, figs. 12, 13.

1908 Beyrichia kloedeni McCoy; Ulrich & Bassler, p. 283, fig. 11.

1928 Beyrichia kloedeni McCoy; Straw, p. 198, pl. 1, figs. 1-4.

1936 B. kloedeni McCoy; Swartz, p. 548, pl. 78, figs. 8a, b.

1954 Beyrichia kloedeni McCoy 1846; Henningsmoen, p. 23.

NEOTYPE: To be designated by Sylvester-Bradley and the present writer in an application to the I.C.Z.N.; figured by Straw 1928, pl. 1, fig. 1; an internal mould of a tecnomorphic right valve, unnumbered, Griffith collection, Nat. Mus. Ireland, Dublin.
TYPE LOCALITY AND TYPE STRATUM: Boocaun, approximately 3 km WNW of Clonbur Village, near Cong, County Galway, Ireland; late Llandoverian sandstones. See loc. 1 of this paper.

DIAGNOSIS: A large Beyrichia (Beyrichia) species with a shallow depression immediately beneath the syllobial cuspidal region, and a deep syllobial groove; the intervening area appears as a conspicuously elevated part of the syllobium.

DESCRIPTION: Based on casts of external moulds. Both anterior and posterior cardinal angles are obtuse and posteriorly there is a characteristic bend in the valve outline. In the region below the preadductorial node, the anterior lobe is confluent with the broad syllobium. A narrow, curving prenodal sulcus separates the dorsal part of the anterior lobe from the preadductorial node. The anterior lobal cusp is equal in height above the hinge line to the anterior syllobial cusp. The adductorial sulcus extends for about two-thirds of valve height and is significantly wider and somewhat deeper than the prenodal sulcus. The cuspidal region of the syllobium is a direct continuation of the uncular ridge; behind the prominent anterior syllobial cusp there appears to be a smaller cusp which is represented merely as a faint undulation on the dorsal ridge.

From the base of the adductorial sulcus across just over half the syllobial width, there is a prominently developed groove which effectively separates the adjacent areas. Immediately below the cuspidal region there is a shallow depression. The mostly anterior part of the syllobium bounded by groove and depression appears as a conspicuously elevated feature. A callic ridge is not differentiated. The posterior part of the syllobium (below the uncular ridge) is of lower elevation and is united directly to the anterior lobe.
The velum is a thick, ridge-like structure easily separated ventrally from the lobal elements. There is little hint of an anteroventral depression. The crumina has a shape typical of Beyrichia (Beyrichia) spp. such as B. halliana. Medium-sized tubercles evenly and somewhat densely cover the lobes and crumina. Smaller tubercles are found along the velum. As far as can be discerned no individual spines or differentiation of rows of spines occurs. Subcruminal morphology not seen.

MATERIAL: All material of B. kloedeni sensu stricto occurs as moulds in the coarse sandstones of the type locality and nearby Capparcorcogoue, Co. Galway. A visit by the author to Boocaun produced additional topotype material consisting mostly of poorly preserved internal moulds and a few (mostly fragmentary) external moulds. The material is extremely difficult to cast successfully, though a reasonably complete female and large tecnomorph were obtained, together with a few other fragmentary casts. These specimens supply crucial information on the morphology of the species. Besides the material in the Nat. Mus. Ireland, specimens exist in other British Museums:

- SM A 3947. From Capparcorcogoue; presented by R. Griffith; figured Straw 1928, pl. 1, fig. 2.
- SM A 3948-51. As above; referred Straw 1928, p. 198.
- BM I 6286. From Capparcorcogoue.

MEASUREMENTS: Approximate hinge length - sulcal height (including velar width) in microns of casts of topotype valves. Author's coll.


DISCUSSION: Since its erection in 1846, confusion and debate concerning the nomenclatural status of this very important species has engaged much space in the literature. This matter remains unresolved (see generic discussion above) though B. kloedeni is generally accepted as
type species of the type genus of the Beyrichiacea. The morphology of the species - although discussed by many authors, notably Straw (1928), Henningsmoen (1954) and Martinsson (1960, 1962) - has not previously been treated in detail. The present study sustains most of the taxonomic interpretation of Beyrichia kloedeni made by Henningsmoen and by Martinsson, but some of the features of this species are considered atypical of the current literature concept of the subgenus Beyrichia (Beyrichia). An extensive synonymy list of Beyrichia kloedeni is not given above as the vast majority of citations would, in any case, be "non" references. The only true Beyrichia kloedeni in the literature are those specimens figured from County Galway, Ireland.

Straw's (1928) work was the first revision of Beyrichia kloedeni which involved the study of M'Coy's original material. In this paper he disassociated the Irish material from all other reported occurrences of the species except for the valve from the late Llandovery of the Malverns figured by Jones (1881c, pl. X, fig. 12) as Beyrichia kloedeni (this valve, BM I 143, is now referred to Craspedobolbina sp. indet.). In his revision of the Beyrichiacea, Henningsmoen (1954) also studied M'Coy's type material and noted that the moulds showed signs of a faint fissus (= syllobial groove), and a "granulose velate, ridge". The subgenus Beyrichia (Beyrichia) was diagnosed (in part) by Henningsmoen on the presence of a ventral connection between all three lobes, and those beyrichiids showing an isolation of the anterior lobe and a tendency for lobular differentiation and development of nodes were separated into the new subgenera Neobeyrichia and Nodibeyrichia. Henningsmoen's concept of Beyrichia (Beyrichia) included such species as Beyrichia verrucosa Kolmodin, 1869 and Beyrichia kloedeni var. bicuspis Kiesow, 1888 - an opinion which was strongly supported by Martinsson (1962). Martinsson thought that Beyrichia kloedeni must be very close to his new species Beyrichia halliana and that a species from the Welsh Borderlands which he termed Beyrichia cf. kloedeni (herein = Beyrichia messis sp. nov.) might even be conspecific with the Irish material.
Those casts in the writers collections show a marked swelling of that part of the syllobium which is bounded ventrally by a deep syllobial groove and dorsally by a shallow depression below the cuspidal region; ideally more topotype material should be collected. This syllobial morphology is unlike that found in the species (numbering over twenty) hitherto regarded as Beyrichia (Beyrichia) taxa, though it is perhaps not to be interpreted as lobular differentiation in the sense known from Neobeyrichia and Nodibeyrichia. Herein, stability of the currently accepted concept of Beyrichia and of the subgenus B. (Beyrichia) is maintained using slight emendations to Martinsson's (1962, p. 268) diagnosis of the genus.

OCCURRENCE: Late Llandoveryian deposits, Galway, Ireland.

Llandovery Sandstones: Boocaun (loc. 1).

Beyrichia (Beyrichia) messis sp. nov.

Pl. Dl, figs. 1-16.

1881c Beyrichia Kloedeni, M'Coy, var. tuberculata (Salter);
Jones, p. 345, pl. X, figs. 13a, b.

1886 Beyrichia Kloedeni, M'Coy, var. tuberculata, Salter; Jones & Holl, p. 354, pl. XII, figs. 8a, b.

1962 Beyrichia (Beyrichia) cf. kloedeni M'Coy; Martinsson, pp. 14, 269, figs. 1A-C.

DERIVATION OF THE NAME: From the Latin messis, a harvest; fancied resemblance of the ornament to a crop ready for harvest.

HOLOTYPE: A female carapace, DAS 47068; Pl. Dl , figs. 1, 2, 4, 7.

TYPE LOCALITY AND TYPE STRATUM: Top of the section on the N face of the large quarry at Gleedon Hill, approximately 150 m W of the B4378 road and 2 km NNE of Much Wenlock, Shropshire (loc. 50); Wenlock Limestone.
DIAGNOSIS: A large species of *Beyrichia* (*Beyrichia*) with comparatively fine tuberculation densely and evenly distributed on the lobes and crumina. Both the anterior cusp and syllobial cusps are rounded, equal in size, and project only slightly above the hinge line. There is an uncular tubercle or spine and (in immature valves) a calcarine spine. Syllobial groove weak. Velar edge with small tubercles.

DESCRIPTION: The anterior lobe is confluent below the preadductorial node with the syllobium. The width of the carapace diminishes quite noticeably from the syllobium to the anterior margin of the valve. Two syllobial cusps, virtually equal in size, project a little way above the hinge line. Apart from the occurrence of a very shallow syllobial groove - differentiated more clearly in the ornamentation pattern than by any other means - the broad syllobium is undissected. There is a tendency in some specimens for a short, weak callic ridge to develop on the upper margin of the groove. The anterior lobe is well defined only in its dorsal section, where its rounded, posteriorly projecting cusp attains the same height as the syllobial cusps. The short, narrow, prenodal sulcus curves gently around the anterior face of the preadductorial node and continues as a shallower depression towards the ventral end of the adductorial sulcus, thus tending to isolate the node. The adductorial sulcus is fairly straight and narrow, and is slenderly connected above the preadductorial node to the prenodal sulcus.

The ridge-like velum is generally indistinctly separated from the lobal areas and - particularly anteroventrally - has small tubercles scattered along its edge. An anteroventral depression is not present. The crumina, like most of the lobes, has a dense covering of relatively fine tubercles. The lobes have a ground pattern of tiny granules, and the subcruminal ornament is of the characteristic "finger-print" striation type. Tuberculation is less regularly present on the anterior
At each locality, all specimens from same sample.
All Wenlock Limestone, N Welsh Borderlands.

Text-fig. 11  SIZE DISPERSION OF FEMALE SPECIMENS OF BEYRICHA (BEYRICHA) SPECIES
margin of the anterior lobal cusp, and is slightly less pronounced on the preadductorional node. An uncular spine, or its remains, can be recognised (best seen in small instars) and there is a calcarine spine in the younger tecnomorphs. The right valve has a finely tubulous, marginal covering frill. A toric structure is hardly, if at all, discernible.

MEASUREMENTS: Hinge length - sulcal height (including velar width) in microns of female valves from the Wenlock Limestone.

Gleedon Hill (loc. 50): 2440-1710, 2370-1675 (holotype).
Harley Hill Qy. (loc. 51): 2460-1690, 2380-1660.

DISCUSSION: Throughout its known occurrence this species has a fairly stable morphology. It is best recognised by the form and pattern of its tuberculation and by its cuspidal morphology. It is interesting to note that whereas the uncular process is seldom difficult to distinguish at any growth stage, the calcarine spine is gradually lost as the ostracode approaches maturity and is not seen in adults or in the larger tecnomorphs.

This species is closely comparable to _B. halliana_ Martinsson, 1962 from which it differs by its denser tuberculation, by the occurrence of a calcarine spine and the persistence of its uncular process, and by the lack of spines along the anteroventral section of the velum in younger tecnomorphs. _Beyrichia messis_ is also similar to the Hemse Bed species _Beyrichia eteliana_ Martinsson, 1962; in particular an uncular spine can be recognised in both taxa. It differs from this Gotland species by the presence of a calcarine spine, by its cuspidal morphology, and again by the density of its tuberculation. The other common British _Beyrichia_ (Beyrichia) species which often occurs sympatrically with _B. messis_ in the Wenlockian of the N Welsh Borderlands is _B. clausa_ (Jones & Holl). These two
species are separated using such characters as cuspidal morphology
(syllobial cusps are higher and more pointed in B. clausa), and the
form of the tuberculation (sparser and coarser in B. clausa) and
its distribution (largely absent from the cuspidal region of the anterior
lobe in B. clausa).

Martinsson (1962) figured this species as B. cf. kloedeni;
in the light of the revision herein of B. kloedeni this assignment
is no longer tenable. The specimens from Benthall Edge and Woolhope
figured by Jones (1881c, pl. X, figs. 13a, b) and Jones & Holl (1886,
pl. XII, figs. 8a, b) as "B. kloedeni, M'Coy, var. tuberculata,
Salter" both belong to B. messis; these tecnomorphs are BM I 140 and
BM I 2368 respectively.

OCCURRENCE: Wenlock and Ludlovian Series of the Welsh Borderlands.

Elton Beds: Stretton Westwood (loc. 60).
Wenlock Limestone: Much Wenlock, Windmill (loc. 54).
Much Wenlock (loc. 55).
The Bank Qy. (loc. 56).
Gleedon Hill (loc. 50).
Harley Hill Qy. (loc. 51).
Coates Qy. (locs. 53a, b).
Little Hill (locs. 17a, d).
Benthall Edge, West (loc. 47).
Audience Wood (loc. 57).
Presthope (loc. 58).
? Wren's Nest (loc. 27c); one fragmentary
tecnomorph.

Tickwood Beds: Tickwood (locs. 44a, d).
Benthall Edge, East (locs. 43a, b).
Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39),
Beyrichia (Beyrichia) clausa Jones & Holl, 1886
Pl. D2, figs. 1-14.

1855a Beyrichia Kloedeni, M'Coy; Jones, p. 165, pl. VI, fig. 9, non fig. 7.
1886 Beyrichia Kloedeni, M'Coy, var. tuberculata, Salter, subvar. clausa nov.; Jones & Holl, p. 355, pl. XII, fig. 9b, (? fig. 9a).
1934 Kloedenia tuberculata clausa (Jones & Holl); Bassler & Kellett, p. 366.
1954 B. kloedeni var. tuberculata Salter subvar. clausa Jones & Holl 1886; Henningsmoen, p. 23 (referred to the subgenus Beyrichia (Beyrichia)).

LECTOTYPE: Here designated. A tecnomorphic carapace, BM IN 52441 (= Vine Coll. no. XLVII, Jones & Holl 1886, pl. XII, fig. 9b; herein Pl. D2, fig. 4.

TYPE LOCALITY AND TYPE STRATUM: Given by Jones & Holl as "Bed no. 46". According to Vine (1887, p.233) the washings from this bed are, "from shales over the Wenlock Limestone .... from the railway cutting between Wenlock and Buildwas".

The Lower Elton Beds it seems must be considered as the type stratum. B. clausa has been collected from this horizon at a locality between Buildwas and Much Wenlock, Shropshire (loc. 61 of this paper).

DIAGNOSIS: Beyrichia (Beyrichia) species with two stoutly developed syllobial cusps; the anterior syllobial cusp is larger than the posterior cusp. Lobal and cruminal tuberculation coarse and virtually undifferentiated; ornament mostly reduced on the cuspidal part of the anterior lobe. There is a marked uncular spine and (in the early tecnomorphs) a calcarine spine. Anteroventral depression absent. Syllobial groove shallow.

DESCRIPTION: All cusps are strongly developed; that on the anterior lobe and on the anterior part of the syllobium are approximately equal in
size and, typically, are slightly higher above the hinge line than the posterior syllobial cusp. Occasionally the latter cusp, representing the dorsal termination of the uncular ridge, approaches the same size as the anterior syllobial cusp. The syllobial cusps are bluntly pointed. Contact between the stout, dorsal region of the anterior lobe and the inflated, knob-like, preadductorial node is prevented by the presence of a short, curved prenodal sulcus. This sulcus can be traced as a shallower depression below the preadductorial node. The adductorial sulcus is vertical, noticeably wider than the prenodal sulcus, and extends from the hinge line for about two-thirds valve height. The syllobial groove, trending from the base of the adductorial sulcus towards the conspicuous uncular spine, is recognisable particularly by the gap it creates in the pattern of ornamentation. There are usually no traces of a callus. From the region of the characteristic bend posteriorly in the valve outline, to the anterior lobal cusp, the lobes and their connection lack any form of differentiation; an antero-ventral depression cannot be distinguished.

The velum is traced ventrally as a mostly unornamented ridge, and is usually well demarcated from the abutting lobes. At each end of the shell the velum merges more successfully with the lobal area. The region between velar edge and valve margin is faintly concave. Anteriorly and posteriorly, the velar edge in tecnomorphs is tuberculate or spinose; particularly characteristic are the small spines occurring posteroventrally just below the uncular region. In females velar tubercles are sparsely, but regularly distributed both in front of the crumina and posteriorly behind the ventral velar ridge.

Most of the lobes have fine granulation superimposed by coarse, isolated tubercles. There is no significant differentiation in the ornamental arrangement, though the field of tubercles below the syllobial groove can be vaguely aligned into some 3-4 rows, the most dorsal row of which is often more conspicuous than the rest. The uncular spine is
prominent throughout ontogeny, and a calcarine spine is distinguishable in the early instars. Ornament is usually absent from most of the cuspidal part of the anterior lobe, and is typically weaker on the preadductorial node. Near the valve margin the crumina is covered with "finger-print" striations, elsewhere it has the same ornamentation as the syllobium. The marginal covering frill is finely tubulous. In young instars there are generally more tubercles on the ventral part of the velum, though their arrangement on the lobes is largely consistent with that found in more mature valves.

MEASUREMENTS: Hinge length - sulcal height (including velar width) in microns of females from the Wenlock Limestone.


Coates Qy. (loc. 53b): 1810-1260.

DISCUSSION: Apart from its graphic treatment by Bassler & Kellett (1934) the subvar. clausa of Jones & Holl received no attention in the literature until it was ascribed by Henningsmoen (1954) to the subgenus Beyrichia (Beyrichia). Jones & Holl (1886) accompanied their description of this species with two figures; the original specimens, both small tecnomorphic carapaces, are in the collections of the Brit. Mus. (Nat. Hist.). BM IN 52441 (= Jones & Holl 1886, pl. XII, fig. 9b), although worn, can be identified with a ubiquitous Welsh Borderland Beyrichia (Beyrichia) species and is selected as lectotype. The original specimen of Jones & Holl 1886, pl. XII, fig. 9a (= BM I 1954) probably represents the same species but is too poorly preserved to include with certainty in the synonymy list. Jones had in fact previously illustrated B. clausa under the name B. kloedeni (1855a, pl. VI, fig. 9 = BM I 169, a large right valve tecnomorph from Lincoln Hill).
The material from Lincoln Hill is abundant, excellently preserved and has provided most of the information used in the description of this species. The specimens from Crofts Quarries are somewhat atypical in being wider and deeper, in having a less well demarcated velar ridge, and in showing a more consistent tendency to develop a fine callus; at present this material is treated within *B. clausa*.

In the valves from the higher part of the Lower Elton Beds at Millichope a calcarine spine can be recognised even in mature tecnomorphs. This material may form the basis of a taxon separate from *B. clausa* and, pending further study, it is referred to that species with doubt.

*B. clausa* most closely resembles *Beyrichia bicuspis* Kiesow, 1888, known on Gotland from Llandoverian and Wenlockian deposits. These taxa, characterised by coarse undifferentiated tuberculation and well developed subequal cusps, are discriminated using several minor morphological features. An anteroventral depression and a depression in the lobar connection above it, are absent in *B. clausa*; *B. bicuspis*, on the other hand, does not have a prominent uncular spine and seemingly lacks a calcarine spine in its early instars. A comparison between *B. clausa* and *B. messis* is given in discussion of the latter species.

**OCCURRENCE:** Wenlock and Ludlow Series; the Welsh Borderlands, English W Midlands.

**Elton Beds:**
- ? Millichope (loc. 59); see "Discussion".
- Stretton Westwood (loc. 60).
- Shadwell Rock Qy. (loc. 61).

**Wenlock Limestone:**
- Gleedon Hill (loc. 50).
- Harley Hill Qy. (loc. 51).
- Coates Qy. (locs. 53a, b).
- Benthall Edge, West (loc. 47).
- Hurst Hill (loc. 28).
- Lincoln Hill (locs. 49a-c).
- Wren's Nest (locs. 27c, f, g).
-250-

Audience Wood (loc. 57).
Presthope (loc. 58).
Much Wenlock, Windmill (loc. 54).
Ledbury (loc. 23).
Croft Farm (locs. 18a-d); see "Discussion".
? Little Hill (loc. 17d); fragmentary tecnomorph.
? Harley Hill Road (loc. 48d); fragmentary tecnomorph.

Tickwood Beds: Tickwood (locs. 44a-d).
   Benthall Edge, East (loc. 43a).

Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39).

**Beyrichia (Beyrichia) obesa** (Harper, 1940)
   Pl. D3, figs. 11, 12.

1940 Kloedenia obesa, sp. n.; Harper, p. 395, pl. IX, figs. 14, 15.
1954 Kloedenia obesa Harper 1940; Henningsmoen, p. 24 (included
   within subgenus Beyrichia (Beyrichia)).

LECTOTYPE: Here designated. A female left valve, GSM 70335, Harper
1940, pl. IX, fig. 14; herein Pl. D3 , fig. 11.

TYPE LOCALITY AND TYPE STRATUM: Given by Harper as Harley Brook SSW
of Domas, Shropshire; a limestone band in the Purple (Hughley) Shales.

DIAGNOSIS: **Beyrichia (Beyrichia)** species in which there is a relatively
wide gap between the crumina and the preadductorial node. Lobes, velum
and crumina with quite coarse, sparsely distributed tubercles. Lobal
cusps low.

DESCRIPTION: Both extant valves have quite deep outlines and lobes which
lack significant elevation. All lobal cusps are low and terminate on or
inconsiderably above the hinge line. The syllobium, at least in the
tecnomorph, has two tiny cusps of equal size; in the (larger) female valve
the dorsal part of the syllobium is not unquestionably bicuspidate - though this may be due to aspects of preservation. The anterior lobe is broad and flat; its cuspidal region is indistinctly developed. The preadductorial node is short and knob-like; its ventral margin is situated some distance from the dorsal base of the crumina. Both adductorial sulcus and prenodal sulcus are shallow, not too long (in the tecnomorph the main sulcus just succeeds in extending past valve mid-height) and lack for the most part well defined boundaries.

The crumina is comparatively small; subcruminal morphology not seen. Preservation of the surface ornament is not particularly good, though it is apparent that quite large individual tubercles were once sparsely scattered over at least the syllobium, the preadductorial node (weaker here), the crumina and the ventral section of the anterior lobe. Isolated, regularly placed tubercles are also visable (particularly in the tecnomorph) along the velar edge. In both extant specimens tubercles are absent from the dorsal region of the anterior lobe. The form of the syllobial groove is not discernible. There is no sign of an anteroventral depression. The narrow velum has a thick, ridge-like form and, ventrally, is not difficult to separate from the adjacent lobal region.

MEASUREMENTS: Hinge length - sulcal height (including velar width) in microns of the female lectotype: 2200-1590.

DISCUSSION: As far as the present writer is aware, the extant material of this species consists only of the female and the tecnomorph (GSM 70336) figured by Harper. Both valves are worn and do not permit a comparison in detail with other Beyrichia (Beyrichia) species, though they do provide enough information to establish that B. obesa is not conspecific with B. clausa or with B. messis. B. obesa may be separated from B. messis by its sparser, coarser tuberculation and, less completely, by its cuspidal morphology (its anterior lobal cusp remains on the
hinge line). Although closer to *B. clausa* in the form and disposition of its ornamentation, *B. obesa* lacks the stout cusps of that species. In addition *B. obesa* differs from both of these Welsh Borderland species in the extent to which the crumina assimilates parts of the carapace surface; there is a considerable gap present in *B. obesa* between crumina and preadductorial node. For these reasons *B. obesa* is retained as a distinct taxon; never-the-less this species would benefit from the collection of additional material (so far attempts have been unsuccessful).

**OCCURRENCE:** Restricted, as yet, to Harpers two localities along Harley Brook, Shropshire; the Hughley Shales, upper part of the Llandovery Series.

**Beyrichia (Beyrichia) impacifica** sp. nov.

Pl. D3, figs. 1-10.

**DERIVATION OF THE NAME:** From the Latin *impacificus*, war-like; alluding to the appearance given to the valves by the long spines.

**HOLOTYPE:** An external mould of a right tecnomorphic valve, DAS M 102; cast figured Pl. D3, figs. 1, 6.

**TYPE LOCALITY AND TYPE STRATUM:** An exposure on an unnamed stream, approximately 650 m E of Waterhead Farm, 3 km N of Muirkirk, Lanarkshire, Scotland (loc. 5); Blaeberry Formation (Priesthill Group).

**DIAGNOSIS:** A large, almost amplete *Beyrichia (Beyrichia)* species having three noticable, individual spines - a calcarine spine, an anteroventral spine on the velum, and a posteroveentral spine on the vela! edge below the base of the uncular region; in some specimens one, two or even all three of these spines can be reduced or absent. A small posterior cusp lies at the dorsal end of the uncular element; the anterior syllobial
The anterior syllobial cusp and anterior lobal cusp are of equal height. The usually small posterior syllobial cusp can vary in size but never attains the same height as the other two cusps; it lies at the end of a long, often ridge-like, uncular element. The presence of a syllobial groove is not even suggested in the ornamentational pattern of the broad syllobium.

The three spines mentioned in the diagnosis are mostly prominent - the calcarine spine in particular can be very long and unusually stout (in some specimens examined its base is almost as wide as the preadductorial node). There seems to be no regular pattern for the occasional reduction of these spines; the calcarine, anteroventral and posteroverentral spines may, independently or in any combination, be reduced or even absent. In female specimens the crumina eliminates the anteroventral spine, although the calcarine spine (just behind the crumina) and posteroverentral spine are normally present. Posteroverternally, the position of the spine marks a conspicuous bend in the valve outline. The small instars exhibit the same spinose arrangement as the adults.

The narrow adductorial sulcus is fairly straight, vertical and reaches just below mid-height. The narrower, shorter and shallow prenodal sulcus bends around the elongate preadductorial node to emerge from the lobes just below the hinge line. From its cusp the anterior lobe widens quite rapidly to attain maximum width at mid-height. All lobes are adequately connected in the broad region below the preadductorial node. There is no anteroventral depression and the depression below the preadductorial node is relatively shallow and not completely isolating. The calcarine region and dorsally adjacent parts of the syllobium, followed by the preadductorial node, are the most elevated areas of the carapace; by comparison the anterior lobe is flat.
In tecnomorphs along the edge of the velar ridge between the two marked spines there is a single row of densely spaced tubercles (also present for a short distance postcruminally in females). It is this part of the velum also, that characteristically flares out from the valve margin. The part of the velum lying dorsal to these two velar spines, has smaller and many fewer tubercles and lies subparallel to the valve margin. The crumina, whose long axis is noticeably inclined to the hinge line, is striate ventrally. Postcruminally in females and along the ventral part of the velum in tecnomorphs there is a fine toric ridge midway between the velar edge and the marginal structure. All the lobes (including most of the cuspidal regions) are covered with a fine, evenly scattered tuberculation; similar ornament is found on the crumina. The sulci are smooth.

MATERIAL: All the material collected of this species - some hundreds of valves - was in the form of external and internal moulds. Some of the moulds, especially those from Waterhead, were well preserved and afforded excellent casting material.

MEASUREMENTS: Hinge length - sulcal height in microns.

Blaeberry Formation: Waterhead (loc. 5); 2160-1410, 1965-1435 (females).

Blaeberry Burn (loc. 4b); 1955-1335, 1900-1360 (large tecnomorphs).

DISCUSSION: As noted in the diagnosis and description this taxon exhibits considerable variation in the development of its spines. The vast majority of specimens (tecnomorphs) have all three spines, but these are occasionally associated on the same slab with valves which - to varying degrees - have fewer spines. This type of variation is not unusual in the Beyrichiinae and has been previously documented in such species as Beyrichia (Beyrichia) dactyloscopica Martinsson, 1956 (here a supravelar spinose zone is involved - see Martinsson 1962, p. 283,
figs. 152, 153) and *Calcaribeyrichia caudata* Martinsson, 1962 (see Martinsson 1962, p. 332). Other features which are variably developed are the uncular region and the posterior syllobial cusp. Sometimes the uncular element is strong and ridge-like, in other specimens it is flat and relatively inconspicuous. The posterior syllobial cusp can appear very weakly represented and almost obsolete, but more normally it is a little less than half the size of the anterior syllobial cusp. If the uncular region is strongly developed then usually the posterior syllobial cusp is above average height.

Although this species is assigned to *Beyrichia (Beyrichia)* without any difficulty, the occurrence of so many well developed individual spines is unusual for the subgenus and is a feature more normally associated with *Calcaribeyrichia* species; however, all the lobes of *B (Beyrichia) impacifica* are entire and display no signs of lobular differentiation.

The morphology and position of the spines is in itself sufficient to distinguish this species from all other described *Beyrichia (Beyrichia)* taxa. The complete lack of a syllobial groove is also an important feature of valve morphology.

**OCCURRENCE:** Collected from three localities in the Priesthill Group of the Lesmahagow inlier, Scotland.

**Blaeberry Formation:** Waterhead (loc. 5).

Lamon Burn (loc. 6).

Blaeberry Burn (locs. 4a, b).

The total material from these localities consists of a few hundred valves of both dimorphs. The Priesthill Group is currently thought to be Llandoverian (or possibly Wenlockian) in age (Cox *et al.*, 1971, fig. 6).
Subgenus Beyrichia (Scabribeyrichia) Martinsson, 1962

TYPE SPECIES: Original designation of Martinsson 1962, p. 297;
Beyrichia tuberculata var. foliosa Jones, 1888, p. 403, pl. XXI, fig. 17;
from the Wenlockian (Slite Beds) at Slite, Gotland.

BRITISH SPECIES: Beyrichia (Scabribeyrichia) scotica Jones & Holl, 1886

DIAGNOSIS: Beyrichia species with a distinct zygal arch in the tecnomorphs, not considerably affected by the inflation of the crumina in the female, and with advanced differentiation of the supravelar syllobial tuberculation into a field or row of tubercles or spines below the syllobial groove (after Martinsson 1962, p. 297).

DISCUSSION: Eobeyrichia Henningsmoen, 1954 (which would benefit from redescription and re-illustration) from the early Silurian of Norway, is at present distinguished from Beyrichia (Scabribeyrichia) by its less complete cruminal inflation (the zygal arch is more clearly separated from the crumina) and by its more primitive, less differentiated form of supravelar ornamentation (for example, the individual uncular or calcarine spines of B. (Scabribeyrichia) spp. are lacking in Eobeyrichia spp.).

OCCURRENCE: Known from the Wenlockian of Gotland and from the upper parts of the Llandoveryian of Gotland and Scotland.

Beyrichia (Scabribeyrichia) scotica Jones & Holl, 1886

Pl. D4, figs. 9-11, 13, 15.

1886 Beyrichia Kloedeni, var. scotica, nov.; Jones & Holl, p. 356, pl. XII, fig. 10.
1893a Beyrichia Kloedeni, M'Coy, var. scotica, Jones & Holl; Jones, p. 302.
1893a *Ulrichia Gravae*, sp. nov.; Jones, p. 304, pl. XIV, fig. 9.

1908 *Kloedenia scotica*; Ulrich & Bassler, p. 302.

1934 *Kloedenia scotica* (Jones & Holl); Bassler & Kellett, p. 365.

1954 *Beyrichia kloedeni var. scotica* Jones & Holl, 1886;

Henningsmoen, p. 24 (assigned to the subgenus *Beyrichia* (*Beyrichia*)).

**TYPE MATERIAL:** Four specimens from the Gray collection, of which only one was figured (part of a right valve tecnomorph), formed the basis of the original description; none of this material has definitely been found. However, the Brit. Mus. (Nat. Hist.) catalogue records that the slab IN 20028 (Gray coll., from Bargany Pond Burn) contains not only the holotype of *Ulrichia grayae* Jones, 1893 but also a syntype of *Beyrichia kloedeni var. scotica*. This information contradicts that given by Jones (1893a, p. 304) when he says that the type-specimen of *U. grayae*, "Occurs with the cast of a small *Beyrichia Kloedeni* (?)." In actual fact the slab containing the figured type-specimen of *U. grayae* holds only one other specimen - a small fragment of a tecnomorphic right valve external mould, which is so poorly preserved that no objective identification could be made. If the catalogue information is accepted as correct then this fragment is the only specimen presently available as a syntype of *B. kloedeni var. scotica*. The present author does not consider the catalogue statement unquestionably acceptable and for this reason the selection of this specimen as a lectotype (which in any case, would serve no useful taxonomic purpose) is not made.

In spite of this difficulty regarding the type material, the description and illustration by Jones and Holl together with recent collections made by the present writer leave little doubt surrounding the identity of the species in question.

**TYPE LOCALITY AND TYPE STRATUM:** A small exposure on the banks of an unnamed tributary of Lauchlan Burn, approximately 900 m NW of Little Lane Cottage, near Old Dailly, Ayrshire (loc. 2); from the Wood Burn
Formation (sedgwickii Zone) of the Llandovery Series.

Jones & Holl stated (1886, p. 356) that the type material was collected by Mrs. Gray from Bargany Pond Burn near Girvan, in a 'limestone' of Llandovery age. After Dr. L.R.M. Cocks (Brit. Mus. (Nat. Hist.)) had informed the writer (pers. comm.; see also Cocks & Toghill 1973, p. 226) that the Gray locality "Bargany Pond Burn" still exists, a visit produced a few toptotype specimens. The exact collecting point for this material is given above as the restricted type locality.

DIAGNOSIS: A large Beyrichia (Scabribeyrichia) species with two (rarely three) rows of acute tubercles below a faintly represented syllobial groove, and 2-3 rows of tubercles and spines along the length of the velum. The syllobial cusps are small and subequal. The crumina has an even tuberculation. An uncular spine can be distinguished.

DESCRIPTION: The syllobium has two inconspicuous cusps. The anterior cusp is slightly smaller than the posterior syllobial cusp; both are weakly pointed and protrude just above the hinge line. The site of the syllobial groove, trending diagonally from the uncular spine to a point below the zygal arch, is clearly indicated by a line devoid of tuberculate ornamentation. The zygal arch is quite wide, present in both dimorphs, and joins the knob-like preadductory node to the syllobium above the syllobial groove. The preadductory node is slightly anteriorly inclined. The adductorial sulcus, whose length is a little more than half valve height, is wider and somewhat deeper than the prenodal sulcus. Curving around the prenodal sulcus is an anterior lobe which has a posteriorly directed cusp; this lobe becomes less well defined at valve mid-height. There is no anteroventral depression.

The velum is ridge-like and is prominently ornamented with about three irregularly aligned rows of tubercles and slender spines along its lateral and ventral sides. The more prominent spines form the lateral most row, with the finer tubercles occurring along the ventral
part of the velum. Particularly prominent are the velar spines near the uncular region and in the anteroventral region. In the only female so far obtained, the crumina has a fairly dense field of small, but high tubercles. These tubercles are seen to occur on the lateral and more ventral parts of the crumina; unfortunately that part of the crumina immediately adjacent to the valve margin is not exposed. The crumina does not eliminate the zygal arch which, even if a little less prominent than in the tecnomorphs, is undoubtedly present.

Above the syllobial groove the valve is sparsely, but evenly, tuberculate; below the site of the groove and continuing in a concentric manner below the zygal arch to the lower part of the anterior lobe there are small but high (a few are spinose) tubercles arranged in 2-3 rows. Above these rows of tubercles and continuing in the same concentric manner for a similar distance is a narrow zone (= a continuation of the syllobial groove) where ornamentation is lacking. An uncular spine is always recognisable though not always conspicuous.

MATERIAL: *B. scotica* is known from moulds and poorly preserved valves. Extant material is rare; besides the topotype material collected by the author, the following specimens belong to the species.

BM IN 20095-20101; IO 3339-44. This material, consists mostly of moulds together with a few specimens which have some shell remaining; all these valves are tecnomorphs. All specimens were obtained from Mrs. Grays brachiopod collection (presented 1920) by L.R.M. Cocks in 1966. The locality information of the label read, "Bargany Pond Burn, Girvan; Camregan Group (Upper Llandovery)."

MEASUREMENTS: Hinge length - sulcal height (in microns) of tecnomorphs.

2125-1320, 2115-1370, 1610-1120, 1560-1110 (measurements approximate).

Very few specimens are complete and available for accurate measuring.
DISCUSSION: This species, recorded from the upper part of the sedgwickii Zone, represents one of the earliest British beyrichiacean taxa. *Ulrichia grayae* Jones, 1893, established on the basis of one internal mould (BM IN 20028, a left valve tecnomorph) from the Gray locality of Bargany Pond Burn is herein considered to be conspecific with *B. scotica*.

The Gotland species *Beyrichia hirsuta* Martinsson, 1962 and *Beyrichia foliosa* Jones, 1888 are the only other known members of the subgenus. *B. scotica* is immediately distinguished from *B. foliosa* by its cuspidal morphology (for instance, the absence of a highly cylindrical syllobial cusp), its lack of a callus, the absence of tubercles above the adductorial sulcus, and by its different supravelar ornamentation (particularly in the calcarine region). The Scottish species is much closer to *B. hirsuta* from which it differs by its much larger size, its tuberculate crumina, its highly ornamented velum, and in lacking a singularly conspicuous row of supravelar spines in the female.

OCCURRENCE: Only from the type locality in the upper part of the Llandovery Series near Girvan, Scotland.

Wood Burn Formation: Little Lane (loc. 2), sedgwickii Zone (Fronian).

Subgenus *Beyrichia* (Jubatibeyrichia) subgen. nov.

DERIVATION OF THE NAME: From the Latin *jubatus*, crested, and the generic name *Beyrichia*; referring to the ridge on the ventral part of the crumina. Gender, feminine.

TYPE SPECIES: *Kloedenia salopiensis* Harper, 1940, p. 394, pl. IX, fig. 11 (lectotype designated herein); from the upper part of the Llandovery Series of the Welsh Borderlands.

SPECIES: Only the type species.
DIAGNOSIS: Elongate Beyrichia species in which the crumina both incorporates very little of the carapace wall and exhibits the remains of a velar fold. The wide syllobium and anterior lobe are crowned with spines. A weak syllobial groove is discernible in the pattern of ornamentation.

DISCUSSION: The lack of any lobular differentiation, the type of ornamentation, and the broad lobal connection between anterior and posterior parts of the valve ally this subgenus to the majority of Beyrichia taxa. However, it has characteristics which are comparatively unusual for the genus and which make is extremely difficult to place in any established subgenus (even with possible modifications to diagnoses). Perhaps its most interesting specialisation and one which immediately distinguishes it from other Beyrichia species is the remains of the velar fold or ridge found ventrally on the crumina (all other recorded Beyrichia species have a striate subcruminal ornamentation). But this feature in itself would not seem to justify the complete separation of this species from Beyrichia. It is already known that within a single Beyrichiinae genus it is possible to have some species with striate cruminae and others whose cruminae show remnants of the velum (cf. conditions found in Calcaribeyrichia spp.).

When compared with other subgenera of Beyrichia there are additional morphological differences which aid the separation of Beyrichia (Jubatibeyrichia) - briefly they are as follows. Beyrichia (Beyrichia) in particular has two well-defined cusps; Beyrichia (Altibeyrichia) has a relatively much higher carapace with noticeable differences in ornament and in the form of the syllobial groove; B. (Jubatibeyrichia) lacks a zygal arch or any differentiation of supravelar ornament which is found in Beyrichia (Scabribeyrichia); Beyrichia (Asperibeyrichia) has a zygal arch and a more completely assimilated crumina; Beyrichia (Simplicibeyrichia) is sufficiently different in ornament and cuspidal morphology;
a bicuspidate syllobium and an anteroventral depression are typical features of the elongate Beyrichia (Lunulibeyrichia) which do not appear in the new subgenus.

It seems to me that the individual morphology manifested by this species is best expressed at present by establishing a new subgenus of Beyrichia.

OCCURRENCE: The upper part of the Llandovery Series of the N Welsh Borderlands.

Beyrichia (Jubatibeyrichia) salopiensis (Harper, 1940)

Pl. D4, figs. 1-8, 12, 14.

1940 Kloedenia salopiensis, sp. n.; Harper, p. 394, pl. IX, figs. 11-12 (? fig. 13).

1954 Kloedenia salopiensis Harper 1940; Henningsmoen, p. 24, tentatively assigned to Beyrichia (Beyrichia).

LECTOTYPE: Designated herein; the right valve tecnomorph, GSM 70332; figured by Harper 1940, pl. IX, fig. 11.

TYPE LOCALITY AND TYPE STRATUM: Given by Harper as a limestone in the Purple (Hughley) Shales exposed in Hurley Brook SSW of Domas, Shropshire.

DIAGNOSIS: As for the subgenus.

DESCRIPTION: The long, low carapace has fairly shallow sulci, and lobes which are not well inflated. The anterior lobe in particular, is flat, broad and widens ventrally. A small preadductor node lies between a shallow, narrow prenodal sulcus and a slightly wider and deeper adductor sulcus. Both sulci curve very gently around a preadductor node which does not meet the hinge line. The syllobium is wide and has its greatest width and elevation just above mid-height. There is a
wide, flat area below the preadductorial node which connects anterior and posterior parts of the shell; no zygal structure is present.

There is no anteroventral depression. A low lying syllobial groove, whose anterior part ends below the ventral extremity of the adductorial sulcus (just below mid-height), is detected within the ornamentation pattern (tubercles are absent along its length). The anterior lobe and syllobium are represented above the hinge line (by a continuation of the lobal ornament) in the form of small but distinct spines; these number approximately two on the anterior lobe and four on the syllobium. On the hinge line above the preadductorial lobe an additional tubercle occurs.

The velum is easily delineated from the lobes and is slightly wider anteroventrally. Along the length of the velar edge there is a series of closely spaced tubercles and round, stump-like bases (presumably once extended into spines). These stout, spine bases are especially prominent posteroventrally in tecnomorphs and postcruminally in females. Ventrally, below the velar edge, there is a toric structure in tecnomorphs. On the crumina near the margin there is an arc-shaped ridge. Apart from the narrow region between this ridge and the valve margin, the crumina is covered with tubercles. The cruminal ridge is not connected to either the pre- or postcruminal sections of the velum. The crumina is relatively small and extends from below the adductorial sulcus to below the anterior part of the anterior lobe.

High tubercles, sometimes extending into fine spines, cover all the lobes; the sulci remain smooth. As far as can be seen within the extant material there is no differentiation or specialisation in the pattern of spines. The crumina incorporates very little of the carapace wall and its interference with lobation is minimal; the area between pre-adductorial node and crumina is relatively wide.
MEASUREMENTS: Hinge length - sulcal height (approximate measurements only) in microns of specimens on limestone pieces collected by Harper from the Hughley Shales.

Females: 1800-1110, 1750-1120, 1700-1100.

Tecnomorphs: 1780-1130, 1710-1130, 1640-1010, 1630-990.

DISCUSSION: When Harper erected Kloedenia salopiensis he figured three specimens, two of which came from a limestone and were designated syntypes (GSM 70332 and 70333). One of his syntypes is herein chosen as lectotype (see above). The third specimen (GSM 70334, a female left valve) lies in a shale and is herein included in the synonymy with doubt because of its preservation (it is an incomplete mould); those parts of the specimen which are visible suggest that it is probably B. (Jubatibeyrichia) salopiensis.

The simple lobal arrangement, the subcruminal ridge and the relatively small amount of carapace wall annexed by cruminal growth are significant morphological features of B. salopiensis. Certain other features of this species can be recognised elsewhere within the genus Beyrichia. The presence of spinose cuspidal areas is known from B. (Asperibeyrichia) spp. and Beyrichia (incerti subgeneris)erinacea Martinsson, 1962, and small tubercles scattered on the dorsal margin of the valve are seen in B. (Scabribeyrichia) spp. In its ornamentation, cuspidal morphology, and nature of the syllobial groove, B. erinacea manifests clear similarities to B. salopiensis; they differ most obviously in shape, and in the size, shape and ventral morphology of the crumina. Tecnomorphs which unquestionably belong to B. erinacea have not yet been found.

OCCURRENCE: This species is known only from those localities given by Harper (1940, pp. 399, 400) from the upper part of the Llandovery of N Shropshire.

GSM 70332, 70333; both from a limestone in the Purple Shales of Harley Brook SSW of Domas.
Genus PORCARICHTA gen. nov.

DERIVATION OF THE NAME: From the Latin porca, a ridge between two furrows, and the generic name Beyrichia; alluding to the ridge on the crumina. Gender, feminine.

TYPE SPECIES: Porcarichia fragum sp. nov., Pl. D5, figs. 2, 6; from the Dunside Formation of the Lesmahagow inlier, Scotland.

SPECIES: Porcarichia fragum sp. nov.

Porcarichia venefica sp. nov.

DIAGNOSIS: Beyrichiinae with lobes entire (lacking lobulation), and cruminae with a marginoventral ridge. Anterior lobe almost isolated; syllobium with one cusp and no groove. There are velar spines; individual lobar spines are absent. Small tubercles occur on the hinge line above the preadductorial lobe.

DISCUSSION: It has been found impracticable to assign the species described here to existing genera without amending current generic diagnoses to such an extent that these genera become too large and their boundaries obscure. The two species in question manifest characters known from both Neobeyrichia and Calcaribeyrichia, but lack important diagnostic features associated with these genera.
All specimens from the Priesthill Group, Lesmahagow inlier.

- **P. fragum.** Dunside (loc. 7), Dunside Formation.
- **P. venefica.** Dunside (loc. 7), Dunside Formation.
- **P. venefica.** Bleaberry Burn (on slab BM I 6379).

Text-fig. 12 SIZE DISPERSION OF FEMALE SPECIMENS OF PORCARICHTIA SPECIES
As in Calcaribeyrichia a ridge is found ventrally on the crumina, but Porcarichia differs from that genus in lacking both lobular differentiation and individual lobal spines.

In lateral view both species of Porcarichia could be considered as primitive members of Neobeyrichia. The lobal and sulcal features of P. venefica (e.g. the almost isolated anterior lobe, the anteroventral depression, the broad undivided syllobium with the small, anteriorly sited cusp, the ornamentation of the velum and the lack of lobal spines) distinctly resemble those found in Neobeyrichia ctenophora Martinsson, 1962. Porcarichia differs from Neobeyrichia primarily in its subcruminal morphology; Neobeyrichia is characterised (after Martinsson's 1965 revision) by species which have marginoventral "finger-print" striation but lack a subcruminal ridge. Furthermore, no lobular differentiation of the kind found in almost all Neobeyrichia species is present in the significantly older Porcarichia.

OCCURRENCE: The Priesthill Group of the Lesmahagow inlier, Scotland.

Porcarichia fragum sp. nov.

Pl. D5, figs. 1-8.

DERIVATION OF THE NAME: From the Latin fragum, a strawberry; fancied resemblance of the crumina to the fruit.

HOLOTYPE: An external mould of a female right valve, DAS M 151; cast figured Pl. D5, figs. 2, 6.

TYPE LOCALITY AND TYPE STRATUM: A small exposure by the side of Lochfennoch Burn, some 30 m S of the NE corner of the smaller E section of Dunside Reservoir and approximately 170 m NW of Dunside Farm, Logan Water, Lanarkshire, Scotland (loc. 7); Dunside Formation (Priesthill Group).
DIAGNOSIS: Porcarichia species with a marked ridge on the crumina. Anterior lobe never distinctly high. Velar spines short; a short row of conspicuous tubercles (or spines) occurs ventrally on the anterior lobe. Usually only one tubercle above the preadductorial node near the hinge line.

DESCRIPTION: The lobation is very simple. None of the lobes show differentiation into lobules, and there is no trace of a syllobial groove or callus. The dorsal part of the syllobium curves evenly towards its rather pointed cusp (adjacent to the adductorial sulcus). The main sulcus is vertical but not particularly wide. By comparison the prenodal sulcus is slightly shorter, narrower and bent around the preadductorial lobe. The dorsal part of the syllobium and the ventral part of the anterior lobe are approximately equal in width and elevation. In its more slender, ventral section the elevation of the syllobium increases to equal that of the preadductorial node. Dorsally, the flat anterior lobe is separated from the preadductorial node by the prenodal sulcus; ventrally, they are attached by a low, narrow connection which provides a dorsal border to the anteroventral depression. A completely isolated anterior lobe is never observed. In small tecnomorphs the prenodal sulcus is shallow, and the flat anterior lobe merges more or less directly with the higher preadductorial node. A small, weakly pointed cusp, subequal in height to the syllobial cusp, crowns the anterior lobe. In the larger tecnomorphs an anteroventral depression is recognised; it is delimited posteriorly by the low syllobial connection to the preadductorial node, and anteriorly by the end member of a single row of short lobal spines (or high tubercles) which occur on the ventral part of the anterior lobe, parallel to the velar edge.

The widest section of the velar ridge occurs behind the syllobium; in front of the anteroventral depression the velum becomes gradually
narrower, until its demarcation from the anterior lobe is hardly discernible. From the posteroventral part of the velum to the anterior corner of the valve the velar edge has a single row of short, isolated spines; the largest of these spines occurs ventrally and the smallest anteriorly. Anteriorly and posteriorly the velar edge is found close to the valve margins; in ventral view the base of the velum characteristically widens away from the margin, reaching maximum width below the preadductorional node. There is no toric structure.

The velar ornament in females is essentially the same as in the tecnomorphs. On the ventral part of the crumina there is a long, abmarginally curved ridge (discontinuous with the velar edge). In well preserved specimens (including the holotype) this "ridge" appears as a broad based, almost flap-like feature. High verrucae or weak tubercles are distributed over the lobes and most of the crumina; adjacent to its ridge the crumina lacks ornament. On the hinge line above the preadductorional node there is usually one (sometimes two) small tubercle(s). Certain features such as the prenodal sulcus, the anterior lobal cusp, the anteroventral depression, and the anteroventral row of spines are weakly developed or are hardly observable in very small instars, but become more distinct during ontogeny. The short velar spines are consistently present.

MATERIAL: All known material of this species occurs as moulds in the Lesmahagow inlier. Casts have been taken of well over fifty valves.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of casts of females from the type locality.

Dunside (loc. 7): 1770-1155, 1650-1000, 1585-990, 1540-1005, 1510-960 (holotype), 1500-970. 1460-945.

DISCUSSION: This species differs from P. venefica by its size (adults are appreciably smaller), ornament (e.g. the nature of the velar spines) and by the morphology of its anterior lobe and crumina (as indicated in
the respective diagnoses).

**OCCURRENCE:** Known from localities in the Priesthill Group of the Lesmahagow inlier, Scotland.

- **Dunside Formation:** Dunside (loc. 7).
- **Blaeberry Formation:** Waterhead (loc. 5).
- **Blaeberry Burn** (loc. 4c).
- **? Blaeberry Burn** (loc. 4b).

Nearly all the collected material, over 100 valves, came from the type locality at Dunside.

The species has also been identified on the slab BM I 6379 (old collection) which the label states to be from Blaeberry Burn.

The Priesthill Group is presently thought to be no younger than high in the Llandoverian or possibly low in the Wenlockian (Cox *et al.*, 1971, fig. 6).

**Porcarichia venefica** sp. nov.

*Pl. D5, figs. 9-14.*

**DERIVATION OF THE NAME:** From the Latin *venefica,* a witch; fancied resemblance of the anterior lobal cusp (of young instars) to a witch’s hat.

**HOLOTYPE:** An external mould of a female right valve, DAS M 148; cast figured *Pl. D5, figs. 9, 12.*

**TYPE LOCALITY AND TYPE STRATUM:** A small exposure by the side of Lockfennoch Burn, some 30 m S of the NE corner of the smaller E section of Dunside Reservoir and approximately 170 m NW of Dunside Farm, Logan Water, Lanarkshire, Scotland (loc. 7); Dunside Formation (Priesthill Group).
DIAGNOSIS: Large Porcarichia species with a stout, well developed anterior lobal cusp which is especially high in small tecnomorphs. Crumina with a ridge-like boundary between its lateral and margino-ventral surfaces. Stout velar spines, particularly long in small instars. Small tubercles, usually two, occur above the preadductorial node near the hinge line.

DESCRIPTION: Syllobium, preadductorial node and anterior lobe bear no traces of lobular differentiation. The anterior lobe is broad and flat; in adults its pointed cuspidal region reaches much higher above the hinge line than the small syllobial cusp. The pointed anterior lobal cusp is even higher in small tecnomorphs (its height above the hinge line can almost be equal to the length of the preadductorial node). An anteroventral depression is recognised throughout ontogeny, but is always separated from the (incised) prenodal sulcus above by a low, narrow lobal connection joining the anterior lobe to the preadductorial node. A similar, but wider connection unites the syllobium to the anteriorly inclined preadductorial node. Characteristically, on the hinge line above the preadductorial node, small tubercles (normally two though there may be one or three) are developed. The posterodorsal margin of the syllobium curves gently towards the pointed syllobial cusp overlooking the adductorial sulcus. The dorsal part of the syllobium is as wide as the ventral region of the anterior lobe. The elevation of the syllobium gradually decreases dorsally. There is no suggestion of a syllobial groove.

Along the edge of the velar ridge in tecnomorphs there are long, stout ventral spines and somewhat smaller anterior spines. In adults these spines are reduced in length but are still quite prominent. Immediately behind the crumina there is a row of (about four) stout spines. Posterovertrally there occurs a noticeable change in outline of the velum; between this point (usually the site of a spine) and the posterodorsal corner of the valve the velum is unornamented. An acroidal
spine (or its base) is often seen in young tecnomorphs and is sometimes discernible in adult valves. Ventrally, the velum is quite well delimited from the lobate area; anteriorly, the velum tends to merge with the anterior lobe.

The crumina is distinctly set off from the valve, and assimilates only the ventral part of the anterior lobe and the region of the antero-ventral depression. Lobes are sparsely covered by a low verrucosity. On the anteroventral part of the anterior lobe, trending subparallel to the velum, there is a tendency (in some of the larger valves) for a short row of more distinctive verrucae or tubercles to develop. The velum and sulci are smooth. Most of the crumina is ornamented with slightly more distinct verrucae, though its ventral part, near the margin, appears to be smooth. Two female specimens have been collected which show (in their casts) the ventral part of the crumina. In the holotype in ventral view the boundary between the lateral part of the crumina and its marginoventral section is admarginally curved and quite sharply angled, producing a fine ridge-like juncture (discontinuous with the velum). In the other female specimen this juncture is less sharp, lacking the ridge-like nature.

MATERIAL: All known material of _P. venefica_ occurs as moulds.

MEASUREMENTS: Hinge length - sulcal height (including velum) in microns of female specimens.

_Dunside Formation:_ Dunside (loc. 7): 2470-1380, 2340-1250 (holotype), 2325-1450, 2310-1325, 2250-1370.

Specimens on BM I 6379: 2550-1510, 2380-1380. 2340-1275.

DISCUSSION: During the ontogeny of this species noticable changes take place in the cuspidal regions; the anterior lobal cusp undergoes a considerable reduction in height, while the syllobial cusp becomes comparatively larger. The very high (pointed) cusp of the anterior lobe
is quite an unusual feature for which it is difficult to find comparisons within the Beyrichiacea. A similar form of cusp is found in Beyrichia (Scabribeyrichia) foliosa Jones, 1888, but here it belongs to the syllobium not the anterior lobe.

This species is close to P. fragum (from the same locality); characters used for separation are discussed under the latter species.

**OCCURRENCE:** Collected by the author only from the type locality in the Priesthill Group of the Lesmahagow inlier.

Dunside Formation: Dunside (loc. 7): this material consists of many tens of valves.

The species has also been identified on slab BM I 6379 which, according to the label information, comes from nearby Blaeberry Burn, Lesmahagow.

The Priesthill Group is presently regarded as high Llandoveryan or low Wenlockian (Cox et al., 1971).

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**Genus NEOBERRYCHIA** Henningsmoen, 1954

**TYPE SPECIES:** Original designation of Henningsmoen, 1954, p. 25; Beyrichia buchiana, Jones 1855, p. 86, pl. V, fig. 1; from erratic boulder no. 1 of Jones, collected near Berlin.

**BRITISH SPECIES:** Neobeyrichia lauensis (Kiesow, 1888) Neobeyrichia confluens Shaw, 1971 Neobeyrichia nutans (Kiesow, 1888) Neobeyrichia scissa Martinsson, 1962

**DIAGNOSIS:** Beyrichiinae with one cusp on the syllobium and an anterior lobe which is well set off from the other lobal elements. Uncular and calcarine spines missing. If lobulation in the anterior lobe occurs, the anteroventral lobule is separated from the rest of the lobe by an

DISCUSSION: Neobeyrichia was conceived (Henningsmoen 1954) as a subgenus of Beyrichia, but was soon used (Kesling & Rogers 1957, p. 998) at the generic level. Martinsson (1962) had tried to retain Neobeyrichia and Nodibeyrichia as subgenera (of Neobeyrichia), but subsequently (1965) abandoned this position in favour of the use of these taxa as distinct genera.

In contrast to Beyrichia, both Neobeyrichia and Nodibeyrichia have an anterior lobe largely (or completely) isolated from other lobal elements and an absence of individual (i.e. calcarine or uncular) lobal spines. The lack of such ornament, together with the absence of a marginoventral ridge on the crumina form major distinguishing features between these two genera and most Calcaribeyrichia species. The revision of, and the differences between, Neobeyrichia and Nodibeyrichia received considerable treatment in Martinsson's (1965) paper. These genera differ mainly in the type of subcruminal ornamentation present (striate in Neobeyrichia, tuberculate in Nodibeyrichia) and by the form taken by the anteroventral lobule (elongate - if present - in Neobeyrichia, rounded in Nodibeyrichia). It was also demonstrated (Martinsson, op. cit.) that these major distinguishing characters can be correlated with minor features of valve morphology (e.g. the rather narrow, spinose velar ridge in Neobeyrichia; the thickened, sparsely tuberculate velum - well set off from the lobes - in Nodibeyrichia; the postcruminal velar process in Neobeyrichia; the lack of granulose ground ornament in Nodibeyrichia and its occurrence in Neobeyrichia).

The close similarities between Neobeyrichia and Porcarichia are discussed under the latter genus.
OCCURRENCE: Known from the Lake District, Welsh Borderlands, and parts of Wales (Neobeyrichia tecnomorphs have been observed in Ludlovian material collected from the Usk district); almost exclusively Leintwardine - Whitcliffe deposits. N. confluens extends into the basal Scout Hill Flags (Downtonian) of the Kendal district.

Neobeyrichia, containing some thirteen named species, has wide geographical distribution. European occurrences are from Scania, the Baltic areas (Gotland, Poland, Lithuania, Latvia, Estonia and on Saaremaa), and Podolia; the genus has a Ludlovian - Downtonian range. Though not unknown in America (reported from the Leighton Shale Member of the Pembroke Formation of Maine; Martinsson in Berry & Boucot, 1971, p. 42), finds there of Neobeyrichia are, as yet, rare.

Neobeyrichia lauensis (Kiesow, 1888)

Pl. D6, figs. 1-7; Pl. D7, figs. 1-11; Pl. D8, figs. 1-11.

1881c Beyrichia Kloedeni, M'Coy, var. antiquata, Jones; Jones, p.345, pl. X, fig. 11.
1888 Beyrichia Lauensis nov. sp.; Kiesow, p. 8, pl. II, figs. 1, 2.
? 1928 Beyrichia cf. lauensis Kiesow; Straw, p. 200, pl. 1, fig. 5.
1954 Beyrichia lauensis Kiesow 1888; Henningsmoen, p. 25 (assigned to Neobeyrichia subgen. nov.).
1962 Neobeyrichia (Neobeyrichia) lauensis (Kiesow 1888); Martinsson p. 318, figs. 10, 177, 178).
1963 Neobeyrichia lauensis (Kiesow); Holland, Lawson & Walmsley, pl. 7, figs. 6, 10.
1965 Neobeyrichia lauensis (Kiesow 1888); Martinsson, p. 122.
1967 Neobeyrichia lauensis (Kiesow), 1888; Gailite, p. 135, pl. X, fig. 2.
1971a Neobeyrichia lauensis (Kiesow 1888); Shaw, p. 601, pl. 111, fig. 6.
NEOTYPE: A tecnomorphic left valve, IPU G 621; designated by
Martinsson 1962, p. 29, fig. 10.

TYPE LOCALITY AND TYPE STRATUM: Botvide in the parish of Lau,
Gotland; top of the Hemse Beds (Ludlovian).

DIAGNOSIS: Very large Neobeyrichia species with a narrow syllobium
which is dissected into unequal lengths by a considerable sulcule.
There is a stout anterior lobe which is completely isolated and a long
preadductorial node which fails to reach the hinge line. Anteroventrally,
the thick velum has large tubercles.

DESCRIPTION: See Martinsson 1962, p. 320.

MATERIAL: In the British sequence N. lauensis is seen only as moulds.
It is an abundantly represented and distinctive species and, if casts
are taken, the nature of preservation provides no handicap to its identifi-
cation.

MEASUREMENTS: Hinge length - sulcal height in microns of two of the
largest valves collected.

   Bengry Track (loc. 63): 3350-2240 (female).
       3960-2470 (an extremely large tecnomorph).

N. lauensis is easily one of the largest described members of its
superfamily.

DISCUSSION: Casts of external moulds of this species are unmistakable
and are recognised by their size and syllobial morphology. Internal
moulds provide additional problems as many of the valve features used
to separate N. lauensis from N. confluens are less apparent or are not
recorded in the morphology of the specimens. It has been found to be
unwise, especially in the case of small tecnomorphs, to identify either
one of these species based on internal moulds alone. The features
which separate N. lauensis from N. confluens have been outlined by Shaw
(1971a, p. 601).
Specimen BM I 141 from Leintwardine, Shropshire, described by Jones (1881c) as *Beyrichia Kloedeni* var. *antiquata* Jones, is in fact a mould of *N. lauensis*. In 1928 Straw figured (pl. 1, fig. 5) an internal mould of a tecnomorphic right valve as *Beyrichia cf. lauensis*. This specimen (SM A 3948) from Westmorland had originally been described by McCoy (1851, p. 135, Pl.1E, fig. 2) under the name of *Beyrichia kloedeni* McCoy. Its morphology cannot be differentiated from moulds of *N. lauensis* but in view of the similarity between internal moulds of the latter species and *N. confluens* it is included in the synonymy with doubt.

**OCCURRENCE:** This species is common in the Welsh Borderlands, where its presence has traditionally been regarded as an indicator of Upper Leintwardine age. It has been collected by the author from the following localities in the Ludlow, Leintwardine, and Aymestrey areas.

- **Upper Leintwardine Beds:** Tripleton Farm (loc. 68).
- Bengry Track (loc. 63).
- Forestry Track, Ludlow (loc. 62).
- Fiddlers Elbow (loc. 67).
- The Goggin (loc. 64).

Also found in J.H.McD. Whitaker's colls. (locs. 811 & 119a) of the Upper Leintwardine Beds from the Leintwardine area.

The distribution of *N. lauensis* and its relationship to the correlation of the Leintwardine Beds in the Welsh Borderlands engaged much comment in the papers by Shergold and Shirley (1968) and Lawson and Whitaker (1969). The latter authors disputed the proposition of Shergold and Shirley (op. cit.) that *N. lauensis* is confined to the high Upper Leintwardine Beds. As recorded (from published faunal lists) and correlated by Lawson and Whitaker the occurrence of this species is as follows: the upper part of the *Lingula lata* Beds (= Lower Leintwardine) and the succeeding "Chonetoidea" *grayi* Beds (= Upper Leintwardine) of Builth (Straw 1937); the *Leintwardinesia* Shales and the
Lower Dayia Beds (= Leintwardinian) of Kerry (Earp 1938); the Upper Leintwardine Beds at Leintwardine (Whitaker 1962) and Ludlow (Holland et al., 1963); the high Upper Leintwardine Beds of Wenlock Edge (Shergold & Shirley, op. cit.); the Woodbury Shale Member (= Upper Leintwardine) of the Malverns area (Phipps & Reeve 1967); the Lower Longhope Beds, (= Upper Leintwardine) of May Hill (Lawson 1955).

Other deposits which have yielded lauensis include the Dayia navicula Beds of the SW Clun district (Earp 1940), the Upper Leintwardine Beds along new forestry track exposures on the Ludlow anticline (Lawson 1973a), the Upper Leintwardine Beds at Aymestrey (Lawson 1973), the Upper Eppyant Beds (Leintwardinian) of the Cwm Dwfnant region, Breconshire (Marsh, 1973), and the "Chonetoidea" grayi Beds (= Upper Leintwardine) of Cwm Graig Ddu, Breconshire (Straw, 1953).

Two points should be noted with regard to this summary. Firstly, the record (Straw 1937, table, p. 452) from the Upper Lingula lata Beds at Builth is at variance with Straws text (op. cit., p. 413); speaking of the Orthonota Mudstones (the basal unit of which is the "Chonetoidea" grayi Beds) he comments, "Beyrichia lauensis" ..... is ....." restricted to it". Secondly, the occurrence of N. lauensis at May Hill (based on a single tecnomorph) is not conclusive; the specimen in question (kindly sent for study by Dr. J.D. Lawson) is a poorly preserved tecnomorphic internal mould. In this context it should be remembered that many of the records of N. lauensis given above are unrevised; this is particularly important as the closely similar N. confluens is now known to be both sympatric and synchronic with N. lauensis (see "Discussion" above and "Occurrence" of both species).

Shaw (1971a, p. 601) recorded N. lauensis from the Lower and Upper Underbarrow Flags of Westmorland - a range which he regarded as Upper Leintwardine to Lower Whitcliffe.
On Gotland *N. lauensis* is found in the Upper part of the Hemse Beds and in the overlying Eke Beds; in Scania it occurs at a correlative horizon in the Öved-Ramsåsa Beds (see Martinsson 1967, p. 371). The species is documented as a zone fossil for the lower part of the Pagegiai Beds of Latvia (Gailite 1967, Ulste 1968).

**Neobeyrichia confluens** Shaw, 1971

Pl. D6, figs. 8-13.

1869 Beyrichia Kloedeni, var. intermedia, nov.; Jones, p. 12; p. 14, text-fig. 9.

non 1886 Beyrichia Kloedeni var. intermedia, Jones; Jones & Holl, p. 352, pl. XII, figs. 3, 4.

1908 Beyrichia kloedeni intermedia Jones; Ulrich & Bassler, p. 285.

1934 Beyrichia intermedia (Jones); Bassler & Kellett, p. 195 (pars).

1971 Neobeyrichia confluens; Shaw, p. 362, nomen nudum.

1971a Neobeyrichia confluens sp. nov.; Shaw, p. 600, pl. 111, figs. 1-5.

**HOLOTYPE:** A tecnomorphic right valve, GSM Z19041, Shaw 1971a, pl. 111, figs. 2, 4.

**TYPE LOCALITY AND TYPE STRATUM:** About ½ mile S of Old Hutton, Kendal, Westmorland (Nat. Grid Ref. 5642 8774); Kirkby Moor Flags (Whitcliffian).

**DIAGNOSIS:** A Neobeyrichia species with a narrow syllobium which in adults is dissected by a shallow sulcule into unequal lengths; the ventral part of the lower lobule becomes confluent with the velum. There is a completely isolated anterior lobe, and a long preadductorial node which reaches the hinge line. Marked anteroventral velar tubercles are absent.

**DESCRIPTION:** See Shaw 1971a, p. 600.
MATERIAL: Around the Ludlow District the writer has collected only moulds of this species. In the Kendal area of Westmorland Shaw illustrated (1971a, pl. lll, figs. 1-5) valves in which the shell was still preserved. Many of the casts made from the Welsh Borderland moulds display a high amount of detail and, in my opinion, there is little doubt that this material is conspecific with that from the Lake District.

MEASUREMENTS: Hinge length - sulcal height in microns of female valves from the Ludlow area.

Upper Leintwardine Beds: Bengry Track (loc.63): 2410-1480.

The Goggin (loc.64): 2420-1515, 2440-1490.

The size of these adults is similar to the heteromorph from the Kirkby Moor Flags figured by Shaw (1971a, pl. lll, fig. 5).

DISCUSSION OF SYNONYMY: Some facts concerning the identification of the type specimen of Beyrichia Kloedeni var. intermedia Jones, 1869 should be explained. Slab BM I 6366, according to the catalogue information, contains Jones's (only) figured specimen of var. intermedia (1869, p. 14, fig. 9 - plate reversed); it is a left tecnomorphic valve from Upper Ludlow rocks near Kington (not Kingston cf. Jones 1869, p. 12 and Jones & Holl 1886, p. 353), Herefordshire. The box label to the slab read "Beyrichia kloedeni var. torosa, intermedia". This duplication of names is explained by the wax cast BM I 15552, labelled Beyrichia kloedeni var. torosa, (see Jones & Holl 1886, p. 353) which once filled the partly preserved female left valve (of a Neobeyrichia sp.) present on the slab in question. The other specimens on the slab - all of which are moulds - consist of part of a female left valve of a Lophoctenella sp., part of a tecnomorphic right valve of an ? Hemiella sp., and three tecnomorphs (two right valves, one left valve) of a Neobeyrichia sp.

This latter specimen is very similar (though not demonstrably identical) to the original line drawing of Jones and is the only tecnomorphic left
valve on the slab; it is therefore considered to be the figured specimen of var. *intermedia* Jones. Based on this specimen, *Beyrichia Kloedeni* var. *intermedia* Jones, 1869 is here regarded conspecific with, and a senior synonym of, *Neobeyrichia confluens* Shaw, 1971. However, B. Kloedeni var. *intermedia* - erected in a paper read to the Geologists Association on May 7th, 1869 - is also a junior primary homonym of *Beyrichia intermedia* Jones & Holl, 1869 (named in March of that year). There is no point in designating a lectotype for var. *intermedia* Jones. *N. confluens* remains the correct name for the species.

The merger of syllobium and velum differentiates *confluens* from other forms of *Neobeyrichia*.

**OCCURRENCE:** *N. confluens* has been collected by the writer from the following localities near Ludlow.

- Upper Leintwardine Beds: Bengry Track (loc. 63).
  - Forestry Track, Ludlow (loc. 62).
  - Fiddlers Elbow (loc. 67).
  - The Goggin (loc. 64).
  - Bow Bridge (loc. 65).
  - Uigmore Rd. (loc. 66).

See also comments in "Occurrence" of *N. lauensis*.

In the Kendal district of Westmorland, Shaw (1971; 1971a, p. 607) found this species almost exclusively in the Upper Underbarrow Flags and the Kirkby Moor Flags and he regarded its introduction into the sequence - along with *Hemsiella maccoyiana* - as indicative of the beginning of the Whitcliffian stage.
Neobeyrichia nutans (Kiesow, 1888)
Pl. D9, fig. 14.

1888 *Beyrichia Buchiana* var. *nutans* MIHI; Kiesow, p. 7, pl. 1, figs. 7-14.

1952 *Neobeyrichia (Neobeyrichia) nutans* (Kiesow, 1888); Martinsson, p. 321, figs. 40B, 179.

1965 *Neobeyrichia nutans* (Kiesow 1888); Martinsson, p. 122.

1971a *Neobeyrichia nutans* (Kiesow 1888); Shaw, p. 601, pl. 112, fig. 3.

**NEOTYPE:** A left tecnomorphic valve, IPU G 625; designated by Martinsson 1962, p. 321, fig. 179B.

**TYPE LOCALITY AND TYPE STRATUM:** Hammarudden (sensu Martinsson 1962), Gotland; Hemse Beds.

**DIAGNOSIS:** *Neobeyrichia* species with an almost completely isolated anterior lobe. There is a low elevation separating the main part of the prenodal sulcus from the anteroventral depression. *Syllobium* with two shallow sulcular depressions, one of them in the region of the syllobial groove the other subparallel to it and separating the cuspidal part of the syllobium. (After Martinsson 1962, p. 321).

**DESCRIPTION:** See Martinsson 1962, p. 321 and Shaw 1971a, p. 602.

**DISCUSSION:** As described by Shaw (1971a) the British material differs from that on Gotland by its tuberculate crumina and spinose velum. From the only figured British specimen (a cast of a left valve tecnomorph) it is not possible to discern whether or not the British material has the posteroventral velar bend so characteristically seen in the Hemse Bed valves illustrated by Martinsson (1962).
OCCURRENCE: Not collected by the writer. The inclusion here of this species is based on finds by Shaw from the Kendal area, Westmorland, where it was recorded from the Lower Underbarrow Flags.

*N. nutans* on Gotland is restricted to a few localities in the Hemse Beds. In Estonia and on Saaremaa it is reported (Sarv 1968, 1971) from the Paadla Stage.

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**Neobeyrichia scissa** Martinsson, 1962

Pl. D9, figs. 11, 12.

1962 *Neobeyrichia (Nodibeyrichia) scissa* n.sp.; Martinsson, p. 323, figs. 180A-D.

1965 *Neobeyrichia scissa* Martinsson 1962; Martinsson, p. 122.

1967 *Neobeyrichia scissa*; Gailite, pl. X, fig. 6.

1971a *Nodibeyrichia scissa* Martinsson 1962; Shaw, p. 603, pl. 112, figs. 1, 2.

**HOLOTYPE:** A left female valve, IPU G 621; figured by Martinsson 1962, fig. 180A.

**TYPE LOCALITY AND TYPE STRATUM:** From Hulte, Gotland; the Hemse Beds (Ludlovian).

**DIAGNOSIS:** A species of *Neobeyrichia* with an elongate anteroventral lobule below a diagonally trending sulcule. The sulcule just fails to completely cross the anterior lobe. The syllobial lobules are only faintly suggested. Syllobial cusp slightly larger than anterior lobal cusp.

**DESCRIPTION:** See Martinsson 1962, p. 323.

**MATERIAL:** In Britain *N. scissa* is known only from internal and external moulds, but the details of morphology and ornament on casts from the Ludlow area are adequate enough to allow a positive identification of this rather distinctive species.
MEASUREMENTS: Approximate hinge length - sulcal height of a cast of the only female specimen so far obtained from the Ludlow area.

Upper Leintwardine Beds: Forestry Track, Ludlow (loc. 62):

1460-970 microns.

DISCUSSION: Martinsson first suspected the presence of *N. scissa* in Britain when he recorded (1967, p. 371) *Neobeyrichia cf. scissa* from Upper Leintwardine Beds near Leintwardine, Shropshire. Later, Shaw (1971, 1971a) described material from the Lake District which he assigned without doubt to *Nodibeyrichia scissa* (sic). Martinsson could not positively identify *N. scissa* as he lacked an external mould of a tecnomorphic specimen - the morphology of which is vital in the identification of the species. The tecnomorphic moulds collected by the author from the Ludlow district are, in all essential respects, identical to the Gotland specimens and the confer applied by Martinsson to the Welsh Borderlands material may now be discarded. Only one female specimen (an incomplete right valve) has been obtained by the author from the Ludlow area; in every part of the valve that is visible, it resembles the *N. scissa* heteromorphs of Gotland.

Shaw (1971, 1971a) assigned the species in question to *Nodibeyrichia*, but the striate crumina and (especially) the anteroventral valve morphology would seem to place 'scissa' within the current concepts of *Neobeyrichia* (as outlined by Martinsson in his revision of *Nodibeyrichia*; 1965, pp. 112, 121,122). Following Martinsson the species is considered to belong to *Neobeyrichia*.

OCCURRENCE: Collected from two localities in the Middle Ludlovian near Ludlow. Only a small number of moulds were obtained.

Upper Leintwardine Beds: Bengry Track (loc.63).

Forestry Track, Ludlow (loc.62).

Shaw (1971; 1971a) recorded *N. scissa* from the Lower Underbarrow Flags, near Kendal, the Lake District.
In the Baltic area the species is known from the Hemse and Eke Beds of Gotland (Martinsson 1962) and from the lower part of the Pagegiai Beds of Latvia (Gailite 1967).

Genus **NODIBEYRICHA** Henningsmoen, 1954

**TYPE SPECIES:** *Beyrichia pustulosa* Hall, 1860, p. 157, text-fig. 19; cited herein as a senior subjective synonym of *Beyrichia Bronni* Reuter, 1885 (designated type species of *Beyrichia* (Nodibeyrichia) by Henningsmoen 1954, p. 26); from the Stonehouse Formation of Arisaig, Nova Scotia.

**BRITISH SPECIES:**
- **Nodibeyrichia verrucosa** Shaw, 1969
- **Nodibeyrichia pustulosa** (Hall, 1860)

**DIAGNOSIS:** Beyrichiinae in which the anterior lobe is generally well set off from other lobal elements and is divided into a cuspidal lobule and a prominent, rounded, anteroventral lobule. All kinds of lobular spines absent. Crumina with a tuberculate marginoventral field. Syllobium with usually one blunt cusp. (Modified slightly from Martinsson 1965, p. 122).

**DISCUSSION:** In 1954 Henningsmoen erected the subgenus *Beyrichia* (Nodibeyrichia) with *Beyrichia Bronni* Reuter as its type species; *Nodibeyrichia* was used as a subgenus by Martinsson (1962) and Copeland (1960). The taxon was elevated to generic level by Kesling & Rogers (1957). In a later paper Martinsson (1965, p. 122) cited *Beyrichia tuberculata* Boll var. *gedanensis* Kiesow, 1884 as a senior subjective synonym of *Beyrichia bronni* and type-species of the genus *Nodibeyrichia*. In this and subsequent papers (1967, p. 378; 1968, p. 308) Martinsson strongly suggested that the differences which separate *N. gedanensis* from *N. pustulosa* (Hall) are of infraspecific value. Indeed, in Copeland's opinion (1960, p. 98) the two forms are synonymous. *Beyrichia pustulosa* Hall,
1860 is considered herein as a senior subjective synonym of both *Beyrichia tuberculata var. gedanensis* and *Beyrichia bronni* and accordingly is regarded as the type-species.

Differences between *Nodibeyrichia* and the beyrichiines *Beyrichia*, *Neobeyrichia* and *Calcaribeyrichia* are outlined in the "Discussion" of *Neobeyrichia*. A comparison between *Nodibeyrichia* and *Porcarichia* gen. nov. is given under the latter genus.

**OCCURRENCE:** *Nodibeyrichia* is known in Britain from deposits which range from the top of the Whitcliffian to a level equivalent to the Beyrichienkalk (high in the Downtonian according to current correlation) of the Baltic region. The Beyrichienkalk is used throughout this paper as faunally defined and restricted in a number of papers by Martinsson (e.g. 1963, pp. 3-10).

Species of the genus have been described from the Baltic area (Poland, Estonia, Saaremaa, Latvia, Lithuania and the Hoburgs Bank off Gotland) in rocks of Whitcliffe - Downton age. Abushik (1971) established *N. torosa* from the Dzwinogorod and Rashkov Beds (Skala Horizon) of Podolia. *N. pustulosa* is found in Nova Scotia, Canada. Martinsson (in Berry & Boucot 1971, p. 43) has reported the occurrence of a *Nodibeyrichia* species in the Pembroke Formation of Maine, U.S.A.

*Nodibeyrichia pustulosa* (Hall, 1860)

Pl. D9, figs. 9, 10, 13.

1860 *Beyrichia pustulosa* n. sp.; Hall, p. 157, text-fig. 19.

1881b *Beyrichia tuberculata* (Klöden); Jones, p. 313.

1881c *Beyrichia tuberculata* (Klöden); Jones, p. 314, pl. X, figs. 8-10.

1884 *Beyrichia tuberculata* Boll var. Gedanensis; Kiesow, p. 277, pl. 3, fig. 5.

1885 *Beyrichia Bronni* n.sp.; Reuter, p. 638, pl. 25, figs. 6a, b.
1916 *Beyrichia cf. noetlingi* Reuter; Strahan, p. 45.

1933 *Beyrichia noetlingi* Reuter; Straw, p. 129, pl. X, figs. 10-12.

1954 *Beyrichia (Nodibeyrichia) bronni* (Reuter 1885); Henningsmoen, p. 26

1960 *Beyrichia (Nodibeyrichia) pustulosa* Hall; Copeland, p. 96, pl. 23, figs. 2-9.

1962 *Neobeyrichia (Nodibeyrichia) bronni* (Reuter 1885); Martinsson, p. 323.

1965 *Nodibeyrichia gedanensis* (Kiesow 1884); Martinsson, p. 127, figs. 2, 3, 5, 7, 8, 12-14, (q.v. for further synonymy).

1967 *Nodibeyrichia gedanensis* (Kiesow), 1884; Gailite, p. 140, pl. X, fig. 12.

**TYPE SPECIMENS:** The original of Hall 1860, text-fig. 19 is extant in the American Museum of Natural History, New York, no. 1657 (25.33). According to Martinsson (1967, p. 378) the specimen is an internal mould of a right valve female (not male as figured by Hall).

**TYPE LOCALITY AND TYPE STRATUM:** From near Arisaig, Nova Scotia; the Stonehouse Formation.

**DIAGNOSIS:** A *Nodibeyrichia* species whose lobuli have well developed nodes. A paracrumina may also be present.

**DESCRIPTION:** Very adequate descriptions are given by Copeland (1960) and Martinsson (1965). Martinsson, in particular, adds important information on ontogeny, the variation found between fossil populations, and the presence of a paracrumina in females. The following points should be noted with respect to the British material described herein.

In tecnomorphs the lower syllobial lobule has three rounded, nodal elements along its length, the middle lobule has two nodes, and both the syllobial cusp and the anterior lobal cusp have somewhat less distinct and less well-rounded elevations. Conspicuous tubercles are scattered over the lobes, though the nodes themselves and the syllobial sulcules appear largely devoid of ornamentation. The sulci and those parts of the
velum adjacent to the velar edge are smooth. Lobular and sulcral regions of the syllobium are easily distinguishable.

A paracrumina in the female is apparently absent. The disposition of lobal and nodal elements is similar in both dimorphs. In the small tecnomorph prepared, all nodes - except the posterior one on the lower syllobial lobule - are recognisable, an anteroventral lobule is developed (but not conspicuously so), but the ornamentation is much reduced compared with adult valves. In tecnomorphs the velar rim is thickened, particularly anteroventrally, and has indistinct tubercles along its edge. The "irregular pattern" noted by Martinsson (1965, p. 120, fig. 7) on the crumina of a female internal mould from the Baltic, is not present on the single British female specimen studied.

MATERIAL: Although material of this species is often well preserved (in a limestone matrix) most specimens available for study are broken, internal moulds. The shell of the valves easily breaks away from its mould when cracking open the limestone or during preparation of specimens.

MEASUREMENTS: Approximate measurement (in microns) of the only British female specimen seen by the author.


The specimen is from a depth of 1214 ft in the Little Missenden borehole.

DISCUSSION: As defined by Martinsson (1965) the only recognisable difference between the Baltic Beyrichienkalk species N. gedanensis, and N. pustulosa from Nova Scotia is the presence, posterroventrally, of a paracruminal inflation in the females of the former species. In the same paper Martinsson commented (1965, pp. 120, 131) that this difference was of questionable significance in separating these taxa at the specific level and that the correct name for the species should probably be N. pustulosa. In subsequent works (1967, p. 378; 1968, p. 308) Martinsson
confirmed his opinion that the two forms are almost certainly conspecific. Copeland (1960, pp. 96-98) in his study of the Arisaig fauna used *pustulosa* and *gedanensis* unquestionably as one species. Straw (1933, p. 130) considered the British material identical with both *Beyrichia neotlingi* Reuter (synonymous with *N. gedanensis*, see Martinsson 1965, p. 127) and with specimens 'coll. O.T. Jones) he had seen from the highest beds of the Stonehouse Formation of Arisaig.

The paracrumina, so characteristic of the Baltic specimens figured by Martinsson (1965, figs. 2D, C, 3A, 12A, 13A), is lacking in the only female specimen (a left valve internal mould) from Britain seen by the author. In this respect the British form is like the female specimens of Arisaig. The velar and lobal morphology (especially the nodal arrangement) of the larger tecnomorphs from Little Missenden agrees very closely with those specimens figured by Martinsson from the Baltic (1965, fig. 14). As moulds, the British material cannot be distinguished from the Arisaig tecnomorphs of Copeland (1960, figs. 2-6, 8, 9).

*Beyrichia pustulosa* Hall and *Beyrichia tuberculata* var. *gedanensis* Kiesow are thus generally held to be almost indistinguishable in terms of morphology. Furthermore, the strata in which they are found, particularly the Beyrichienkalk and the Stonehouse Formation, have similar concomitant faunas (e.g. the presence of *Kloedonia wilckensiana* (Jones, 1855); cf. Copeland 1960, p. 95, 1964, p. 8 with Martinsson 1963, p. 3, 1965, p. 136 and 1967, p. 377). Accordingly the present author prefers to treat the American and European specimens as one species.

*N. pustulosa* is readily differentiated from congeneric taxa by the occurrence and arrangement of the nodes on its lobes.
OCCURRENCE: In Britain from limestones of the Little Missenden borehole, Buckinghamshire; its occurrence would indicate an horizon equivalent to the Beyrichienkalk of the Baltic area i.e. above the lower part of the Downtonian but below the Gedinnian.

Straw (1933, p. 130) records his *B. noetlingi* as, "Abundant in the upper 29 ft of the borehole; rather rare below that level."

The borehole is believed to have passed through Palaeozoic rocks at a depth of between 1200 - 1264 ft (Strahan, 1916); Straw was presumably referring to this section of the core. The present author has seen many specimens of *H. pustulosa* (tecnomorphs) on the following material of the Little Missenden core (housed at the Inst. Geol. Sci., London):

GSM 51888. Slab containing the right valve tecnomorph of Straw, pl. X, fig. 12.

GSM 28269. Piece of limestone containing the right valve (internal mould) tecnomorph of Straw, pl. X, fig. 10).

GSM 28270. Small piece of limestone containing the left valve (internal mould) tecnomorph of Straw, pl. X, fig. 11.

All the figured specimens above came from a depth of between 1213' 6" and 1213' 9" in the core.

GSM Pl 4780. Limestone slab at 1214 ft.

GSM 51881. A large limestone slab at 1214 ft.

The species (as diagnosed herein) also occurs as a part of the Beyrichienkalk fauna (found commonly in erratics) of the Baltic. It is recorded from the lower part of the Jura Beds of Latvia by Gailite (1967, p. 140). Copeland (1964) gives a detailed account of its occurrence in the upper part of the Stonehouse Formation of Arisaig, Canada.
Nodibeyrichia verrucosa Shaw, 1969
Pl. D9, figs. 1-8.

1969 Nodibeyrichia verrucosa n. sp.; Shaw, p. 63, figs. 7A-C.

HOLOTYPE: An external mould of a tecnomorphic left valve, GSM 103262; rubber cast figured by Shaw 1969, figs. 7A, B.

TYPE LOCALITY AND TYPE STRATUM: Forge Bridge, near Downton, Shropshire; from just above the Ludlow Bone Bed, a Platyschisma bed, Downton Castle Sandstone.

DIAGNOSIS: A species of Nodibeyrichia with a callus and two subequal cusps on the undissected syllobium. Round, ventral lobule of the anterior lobe not severed by a distinct sulcule from the cuspidal region above. The edge of the narrow velum is finely corrugate.

DESCRIPTION: See Shaw 1969, pp. 64, 65.

MATERIAL: N. verrucosa is known only from internal and external moulds. The numerous features mentioned in the diagnosis are readily discernible in casts. No other known beyrichiine species in the British succession could be confused with N. verrucosa.

MEASUREMENTS: Approximate hinge length - sulcal height in microns of female valves from the very top of the Whitcliffe Beds.

Ludford Lane I (loc. 69a): 1950-1400, 1870-1330, 1850-1390, 1760-1310.

The holotype from Forge Bridge measures approximately 1600-1225.

DISCUSSION: As pointed out by Shaw (1969, p. 65), N. verrucosa shows features which can be regarded as incipient in the development towards species such as N. tuberculata (Klöden, 1834). It is separated without difficulty from other Nodibeyrichia species by the use of the diagnostic characters given above, particularly the form and number of the syllobial cusps.
Material very close to *N. verrucosa* exists high in the Silurian
of the E Baltic at an horizon (Ohessare) correlated with the British
Downtonian; Sarv (1968, p. 47, pl. XVII, figs. 5–9) illustrated this
material from Estonia under the name *Nodibeyrichia jurassica* (Gailite).
*Simplicibeyrichia jurassica* was treated by Gailite (1965, pp. 68, 70)
without illustration or description and is a *nomen nudum*; it is used
as a zone fossil in the Latvian Silurian. Using Sarv’s figures the
Estonian material appears to differ from *N. verrucosa* by the form of
the syllobial cusps (more unequal in size) and by the height of the
valve (*N. verrucosa* is "deeper").

**OCCURRENCE:** Collected by the author from the topmost Whitcliffian
immediately below the Ludlow Bone Bed at Ludlow.

Whitcliffe Beds: Ludford Lane I (locs. 69a, b); at 5cm and 10cm
respectively, below the Ludlow Bone Bed.

Over fifty valves, including some seven females, were obtained.

Most specimens were in some way incomplete or damaged.

Shaw (1969, pp. 65, 67, text-fig. 8) recorded *N. verrucosa*
from the Downton Castle Sandstone of two areas: the NW part of the
Ludlow anticline (at Forge Bridge, Downton), and the Long Mountain.

*Genus* **CALCARIBEYRICHIA** Martinsson, 1962

**TYPE SPECIES:** Original designation of Martinsson 1962, p. 326;
*Calcaribeyrichia bicalcarata* Martinsson, 1962, p. 328, figs. 183A,
184; from the Ludlovian (Hamra Beds) at Sles, Gotland.

**BRITISH SPECIES:** *Calcaribeyrichia characta* sp. nov.
*Calcaribeyrichia tegula* sp. nov.
*Calcaribeyrichia torosa* (Jones, 1855)
*Calcaribeyrichia ? antiquata* (Jones, 1855)
DIAGNOSIS: Beyrichiinae in which both velar and lobal spines, and lobular differentiation of the lobes are (variably) developed. Subcruminal morphology simply striate or, more typically, with a ridge, separated from the velar edge by a constriction.

DISCUSSION: In 1966a Martinsson added C. duplicicuspidata to the six species from Gotland he had originally included within the genus. Later C. katriensis Sarv, 1968, C. altonodosa Sarv, 1968, C. grebeni Abushik, 1970 and C. angusta Abushik, 1970 were erected.

Calcaribeyrichia is characterised by the development of lobules and lobal spines. Contrasts and similarities between Calcaribeyrichia and other beyrichiine genera occurring in Britain are made in foregoing generic discussions.

OCCURRENCE: I have collected the genus in Lower Silurian deposits of the Midland Valley, Scotland, and in the Ludlovian of the Welsh Borderlands. Also found in Westmorland & the Long Mountain (see C. torosa). Apart from C. duplicicuspidata (at the top of the Wenlock) all the Gotland species are of Ludlovian age. Other reported occurrences of Calcaribeyrichia come from the Ludlovian of Estonia, Saaremaa and Latvia, from the lower Ludlow and Skala horizons of Podolia, and from deposits of assumed post-Ludlow age on Vaygach Is. (off N. Russia). Calcaribeyrichia has also been recorded from subsurface material (Nøvling no. 1 borehole) in central Jutland, Denmark (Christensen 1971).

Calcaribeyrichia characta sp. nov.

Pl. Dll, figs. 1-6.

DERIVATION OF THE NAME: From the Latin charactus, provided with stakes; alluding to the rows of spines on the valve.

HOLOTYPE: An external mould of a female left valve, DAS M 114; cast figured Pl. Dll , fig. 1.
TYPE LOCALITY AND TYPE STRATUM: An exposure on the banks of an
unnamed stream approximately 650 m E of Waterhead Farm, 3 km N of
Muirkirk, Lanarkshire, Scotland (loc. 5); Blaeberry Formation
(Priesthill Group).

DIAGNOSIS: A small *Calcaribeyrichia* species in which faint lobular
differentiation of both anterior lobe and syllobium is traced in the
pattern of ornamentation. Anterior lobal cusp and the single syllobial
cusp are small and of equal height. Rows of lobal spines occur
anteroventrally, and also on the calcarine lobule; the calcarine
spine is prominent. Subcruminally there is a short, isolated ridge.

DESCRIPTION: Adult valves are comparatively small and slightly
preplete. The anterior lobal cusp and the anteriorly sited syllobial
cusp are small and of equal height; a posterior syllobial cusp is not
discernible. The anterior lobe is differentiated into a larger
dorsal section and a small anteroventral section by a shallow, narrow
sulcule (emphasized by the ornamentational pattern) which runs
obliquely from the region of the weakly suggested anteroventral
depression towards the velum at mid-height. Low connections join the
preadductorial node to the syllobium and anterior lobe respectively.
The adductorial sulcus is slightly wider, deeper and longer (it reaches
just below mid-height) than the prenodal sulcus. The preadductorial
node is weakly anteriorly inclined. Indistinct, lobular differentiation
of the syllobium occurs; it consists of a long calcarine lobule
below the site of the syllobial groove, and a larger, central lobule,
separated from a small cuspidal region by a faintly developed
depression.

Arranged at regular intervals along the velar edge there is a
sparse development of discrete, short spines; they are conspicuous
ventrally and continue (less prominently) anteriorly and posteriorly.
The largest velar spines in the females occur immediately behind the crumina. A line of spines (usually four, including the distinct calcarine spine) exists on the calcarine lobule, and a diagonal line of 3 - 4 spines is found anteroventrally on the anterior lobe. In both rows the largest spine occurs adjacent to the anteroventral depression; from here the spines get progressively smaller along each row, with each end member more or less of tubercle-form.

A small tubercle, sited directly below the preadductorial node and in line with the trend of the calcarine lobule, seems to be a constant feature of the carapace. The central lobule of the syllobium, the preadductorial node and the dorsal part of the anterior lobe have sparsely scattered, high tubercles. The sulcules are unornamented. Neither uncular or acroidal spines are developed.

The pattern of ornamentation in the female, apart from the coarsely tuberculate crumina, is like that of the tecnomorphs. Admarginal to the curved ridge found ventrally on the crumina, there is an area lacking ornamentation. This ridge is not connected to any part of the velar edge.

MATERIAL: All specimens collected are moulds. Many tens of valves were examined; casts were made of all the external moulds.

MEASUREMENTS: Approximate hinge length - sulcal height in microns of females from the Priesthill Group.


Lamon Burn (loc. 6): 1060-600.

DISCUSSION: In C. characta we have the beginnings in the trend towards the more complete lobulation and development of specialized spines seen in advanced Calcaribeyrichia species such as C. bicalcarata Martinsson, 1962. C. characta is recognised from congeneric species by its size (easily the smallest recorded member of the genus) and
by the form of its lobular differentiation and associated array of spines and tubercles. In having weakly defined lobules associated with a calcarine spine, this species is closely similar to the primitive C. simplicior from Gotland; the latter species is distinguished by the occasional presence of caudal and uncular spines and a posterior syllobial cusp, in the form and disposition of the lobules (particularly the anterior lobe), and in lacking a ridge on the crumina.

The occurrence anteroventrally of a marked spine is a feature which is known from only one other member of the genus - the early and distinctive Calcaribeyrichia duplicicuspidata Martinsson, 1966 from the Nalla Beds of Gotland. Like C. characta, C. duplicicuspidata has only one syllobial cusp. The absence in C. characta of a full complement of (calcarine, uncular and acroidal) spines is not a serious hindrance to its generic assignment (only half of the Calcaribeyrichia species are so well endowed).

The Priesthill Group is currently regarded as no younger than Llandoveryan or possibly lower Wenlockian (Jennings 1961, Walton 1965, Cocks et al., 1971). If this age is correct then C. characta is considerably older than other known Calcaribeyrichia species.

OCCURRENCE: Collected from two localities in the Priesthill Group of the Lesmahagow inlier, Scotland.

Blaeberry Formation: Waterhead (loc. 5); over 50 specimens of both dimorphs.

Lamon Burn (loc. 6); just 3 valves.

This species has also been identified on a slab (BM IN 24126) from an old collection in the Brit. Mus. (Nat. Hist.) labelled Loganwater (Lesmahagow) Lanarkshire, Scotland.
Calcaribeyrichia tegula sp. nov.
Pl. D10, figs. 1-8.

1962 Beyrichia Kloedeni (M'Coy) var. torosa (Jones); Holland, Lawson & Walmsley, pl. 7, figs. 8, 11, 12.

DERIVATION OF THE NAME: From the Latin tegula, a roofing tile; alluding to the imbricate nature of the granulose ornament on the cuspidal lobules and preadductorial node.

HOLOTYPE: An external mould of a female left valve, DAS M 288; cast figured Pl. D10, fig. 3.

TYPE LOCALITY AND TYPE STRATUM: A small hillside exposure, approximately 600 m SSE of Trippleton Farm and just 10 m W of the road from Burrington to Leintwardine, Herefordshire; Upper Leintwardine Beds (loc. 68) (Ludlovian).

DIAGNOSIS: A Calcaribeyrichia species with rounded lobular elements on the cuspidal sections of the syllobium and anterior lobe. Each cusp is capped with a spine. Syllobial cusp in front of an evenly curved posterodorsal syllobial region. A calcarine spine may occur. On the crumina there is a curved ridge.

DESCRIPTION: Anterior lobe divided into a larger, rather flat ventral part and a prominently elevated cuspidal area. The latter region - like the corresponding part of the syllobium - consists of a knob-shaped lobule extending from which (above the hinge line) there is a short spine. The lobular element of the anterior lobe extends to approximately opposite mid-height of the preadductorial node; the lobule on the cuspidal section of the syllobium is smaller and less elongate. The preadductorial node is elevated in similar fashion to the cuspidal lobular elements and is joined to the syllobium by a low lobal connection. There is no well defined connection between the
preadductorional node and anterior lobe.

The prenodal sulcus is short and obvious only when flanked by the (higher) preadductorional node and cuspidal lobule of the anterior lobe; the sulcus shallows ventrally and becomes obsolete on the ventral part of the anterior lobe. The adductorial sulcus bends gently around the preadductorial node, and is longer, deeper and slightly wider than the prenodal sulcus. The syllobial cusp is adjacent to the adductorial sulcus; posterodorsally the syllobium is evenly curved about the hinge line but fails to produce a second cusp. A narrow, oblique sulcule separates the cuspidal lobule of the syllobium from the remainder of the lobe; maximum syllobial width occurs just below this sulcule. Characteristically, there is a calcarine spine, and occasionally an acroidal spine can be recognised. Syllobial groove absent. The anteroventral depression is quite well developed.

A row of long, regularly spaced spines occurs around the velar edge. Marginoventrally the crumina has a curved ridge, which is separated from both pre- and postcruminal parts of the velum. A cast taken from a particularly well preserved mould gives much information about valve ornament. The ground ornament for the lobes is a dense granulation which takes on a contoured pattern and a scale-like form (with each granule overlapping the preceding one) on the crests of the lobules below the cusps and on the preadductorional node. The prenodal sulcus and the dorsal part of the adductorial sulcus have sparser, finer granulation; the deeper, ventral section of the main sulcus appears smooth. Even the dorsal spinose extensions of the syllobium and the anterior lobe are crowded with small granules. Superimposed on the granulation is a pattern of scattered tubercles; they are found on nearly all parts of the lobes and are especially noticeable on the syllobium and on the ventral part of the anterior lobe, but are absent on the lobules of the cuspidal regions.
MATERIAL: All extant material occurs as moulds.

MEASUREMENTS: Hinge length - sulcal height in microns of a female valve (cast) from the Upper Leintwardine Beds.

Bengry Track (loc. 63): 1780-1210

DISCUSSION: This species has been collected from a number of localities in the Leintwardine Beds. It is very similar to C. torosa and may have done much to (falsely?) extend (in published faunal lists) the range of "C. torosa" down into the Leintwardinian.

The extant material of C. torosa is larger than C. tegula. The syllobium in C. torosa is rather slender, ridge-like, and lacks a well developed posterodorsal region (its cuspidal section occupies almost all the syllobial width); by comparison C. tegula has a syllobium which is wider and flatter, with an anteriorly sited cusp adjacent to a posterodorsal lobal region. In C. torosa the crests of the cuspidal lobules and preadductorional node tend to be faceted and are rather more elongate than the equivalent knob-like lobules in C. tegula.

C. tegula is included within Calcaribeyrichia for reasons similar to those applied for C. torosa.

OCCURRENCE: Collected by the author from the Leintwardinian of the Welsh Borderlands.

Upper Leintwardine Beds: Bengry Track (loc. 63).
Forestry Track, Ludlow (loc. 62).
Fiddlers Elbow (loc. 67).
The Goggin (loc. 64).
Trippleton Farm (loc. 68).

Also identified in J.H.McD. Whitakers colls. (loc. 811) from Upper Leintwardine of the Leintwardine area.

Specimens figured by Holland et al. (1963) extend the range of this species into the highest Lower Leintwardine Beds (tecnomorph BM 10 885,
from Martin's Shell near Leintwardine, SO 41097543; also in small
collections made by the author from this locality) and the Lower
Whitcliffe Beds (female BM IO 886, from near Hollybush Cottage,
SO 41777328, the Leintwardine area).

Calcaribeyrichia torosa (Jones, 1855)

Pl. D10, figs. 9-16.

1855a Beyrichia Kloedeni, var. torosa; Jones, p. 167, pl. VI,
figs. 10, 11 (non fig. 12).

non 1869 B. Kloedeni, var. torosa, Jones; Jones, p. 14, fig. 11b.
1934 Beyrichia torosa (Jones); Bassler & Kellett, p. 208 (pars).
1954 Beyrichia tuberculata var. torosa Jones 1855; (sic)
Henningsmoen, p. 26 (assigned to Beyrichia (Nodibeyrichia)
subgen. nov.)

non 1962 Beyrichia kloedeni (M'Coy) var. torosa (Jones); Holland,
Lawson & Walmsley, pl. 7, figs. 8, 11, 12.
1971a Neobeyrichia torosa (Jones 1855); Shaw, p. 602, pl. 111,
figs. 7, 8.

TYPE SPECIMENS: The background to the rediscovery of these specimens
is somewhat complicated and needs explanation. In 1855a Jones
illustrated three specimens from two localities. The originals of
Jones pl. VI, figs. 10 (a tectomorphic left valve) and 11 (a female
right valve) came from the Upper Ludlovian of Frith Quarry, near
Presteign, in the Welsh Borderlands; the specimen in Jones pl. VI,
fig. 12 (a female left valve) was collected from cleaved siltstones
(currently regarded as Wenlockian deposits) at Wooltack, Pembroke-
shire.

The Pembrokeshire specimen was found in the Inst. Geol. Sci.
(London) on slab GSM 26904 along with brachiopods and a conspecific
tecnomorph; both ostracodes occur as moulds. Label information, a
cast made by the present author, and two wax casts (I 6356) found
in the Brit. Mus. (Nat. Hist.) which (label information) were
used for the original illustration of Jones 1855a, pl. VI, fig. 12,
leave no doubt that this is the figured heteromorph, although it
must be added that Jones apparently used some imagination to complete
the posterior extremity of this syntype.

Label information on another Inst. Geol. Sci. (London) slab
(GSM 36863) read, "Beyrichia kloedeni var. torosa Jones, Upper Ludlow,
Stapleton, Presteign - vide Ann. Mag. nat. Hist., 1855, pl. VI, fig. 10";
there was no additional information to indicate that this was type
material. All specimens on this slab were external moulds; a cast
revealed the following material: one female left valve of an Hemsiella
sp., part of a female right valve of a Lophoctenella sp., and two
female right valves and one tecnomorphic right valve of a beyrichiine.
The better preserved female specimen of the latter species is represented
by a wax cast in the Brit. Mus. (Nat. Hist.) (BM I 6355) - the original
of which is stated (catalogue information) to be that of Jones 1855a,
pl. VI, fig. 11 (sic); moreover, this specimen agrees in all essential
details with Jones's figure and consequently the external cast (on
GSM 36863) must be regarded as a syntype. To complicate matters,
another wax cast (of a tecnomorphic left valve) occurs in the same slide
and bears the same number (BM I 6355) and locality information as the
female. The original of this tecnomorph is stated to be that of Jones
1855a, pl. VI, fig. 10; it does in fact agree with Jones's figure.
However the external mould from which the cast of this tecnomorph was
taken has not been identified, even though - as given above - the
label information on GSM 36863 implies that it should contain the
original specimen of fig. 10.
In summary, the original moulds for figs. 11 and 12 have been identified at the Inst. Geol. Sci. (London) and their wax casts (which probably formed the basis of the figures) have been found at the Brit. Mus. (Nat. Hist.); a wax cast of the fig. 10 syntype is in the Brit. Mus. (Nat. Hist.) but the repository for its original mould remains unknown - all the evidence suggests that, like the other syntypes, it was deposited at the Inst. Geol. Sci. (London).

LECTOTYPE: Designated herein. *Beyrichia kloedeni* var. *torosa* is one of the few but often mentioned ostracodes in the literature on Ludlovian stratigraphy of the Welsh Borderlands. This traditional usage was an important consideration in the designation of a lectotype. The selection of the heteromorph from Wooltack Point as lectotype would result in 'torosa' becoming a Wenlockian *Craspedobolbina* species from Pembrokeshire (see *C. turpis* sp. nov.). Consequently the original of Jones 1855a, pl. VI, fig. 11, a female external mould (on GSM 36863) from the Upper Ludlow of the Welsh Borderlands is herein selected as Lectotype. Although attempts to recollect tootype specimens from Frith Quarry have not been successful, other material collected at a locality near Five Turnings (c. 5 miles N of Frith Quarry) in the Upper Chonetes Beds (Upper Ludlovian) of Stamp (1918), has produced moulds which are conspecific with 'torosa' based on the lectotype selected above and which permit an adequate definition and description of the species. It should also be added that within the limited amount of material available from Frith Quarry (only those specimens on slab GSM 36863), it is impossible to distinguish the *Lophoctenella* and *Hemiella* species present, from similar forms at the locality S of Five Turnings.

TYPE LOCALITY AND TYPE STRATUM: Frith Quarry, Stapleton about 0.5 km NNE of Presteigne, Radnorshire (Nat. Grid Ref.: 3190 6542); presumed upper part of the Ludlovian. The type locality lies in an unmapped
region to the SE of Holland's (1959) Knighton area; its fauna indicates an horizon high in the Ludlow.

DIAGNOSIS: A *Calcaribeyrichia* species in which both the elongate lobules of the cuspidal areas, and the preadductorional node, tend to be faceted. Each cusp is capped with a small spine. Syllobium slender and ridge-like, mostly lacking a distinct posterodorsal region. A calcarine spine may occur. On the crumina there is a curved ridge.

DESCRIPTION: All lobes except the fairly flat, anteroventral lobule, stand high above the sulcal and velar regions; cuspidal regions are prominently developed. The length of the lobular element of the syllobial cuspidal region is about two-thirds that of the lobule on the corresponding part of the anterior lobe. The lobule on the cuspidal part of the anterior lobe begins just above mid-height.

The lower part of the syllobium - below the oblique sulcule which isolates the cuspidal region - is long, slender and ridge-like. The shorter, cuspidal section forms almost the entire width of the narrow dorsal margin of the syllobium; the lobe lacks any significant posterodorsal area. The crests of the preadductorional node and of the lobular elements of the syllobial and anterior lobal cusps are elongate and characteristically are faceted. On the dorsal part of each cusp there is a single spine.

A low connection links the syllobium to the preadductorional node; the col between the anterior lobe and preadductorional node is weak. In its dorsal section - surrounded by the anterior lobal cusp and the preadductorional node - the prenodal sulcus is as deep as the adductorional sulcus; ventrally, the prenodal sulcus is discernible as a faint depression adjacent to the anteroventral lobule. A well developed anteroventral depression is squeezed between syllobium and anteroventral lobule. In heteromorphs the crumina assimilates the lower lobule of the anterior lobe but the almost vertical cuspidal
region remains unaltered.

The velum is well defined and, except for the cruminal region in heteromorphs, has a row of regularly spaced spines around its edge. The long axis of the crumina is inclined away from the horizontal. The arcuate ridge found on the crumina near to the margin is not attached to any part of the velum.

The crumina, the lower part of the syllobium, and the anteroventral lobule are covered with coarse tubercles. A calcarine spine is variably developed in both females and tecnomorphs; in most specimens it is inconspicuous, in other valves it is strongly represented. The tubercles appear smaller, or are absent, around the cuspidal areas and on the preadductorional node. Small tecnomorphs are essentially similar to adults.

**MATERIAL:** *C. torosa* is known only from mould material from the Lake District (Shaw 1971a) and the Welsh Borderlands. Specimens are not uncommon and often afford good casting material.

**MEASUREMENTS:** Hinge length - sulcal height in microns of casts from the Whitcliffian.

Five Turnings (loc. 14): 2280-1510, 2260-1490, 2240-1420 (females),
2245-1480 (male).

Approximate measurement of female lectotype: 2320-1500.

**DISCUSSION:** Shaw gave valuable assistance to the definition of the species when he described and figured material from Westmorland (1971a), but his synonymy list still included Jones's hetermorph from the Wenlockian of Pembrokeshire. No primary revision of the taxon has occurred since it was established in 1855.

Shaw attributed the species to *Neobeyrichia*. Although some of its features are relatively unusual and render generic assignment difficult, I prefer to refer the species to *Calcaribeyrichia* for the following reasons. A subcruminal ridge or a calcarine spine is
unknown from Neobeyrichia but both features are commonly found in Calcaribeyrichia. The occurrence of knob-like lobular elements in cuspidal regions has previously been recorded only from Calcaribeyrichia (cf. C. duplicicuspidata Martinsson and C. tegula sp. nov. - although in these species the lobules are not faceted). Trends towards the isolation of an anterior lobe or the development of an anteroventral lobule are seen in both genera, but the oblique sulcule which isolates and produces a long anteroventral lobule in Neobeyrichia does not occur in C. torosa; here the lobule is produced more by a difference in elevation between the cuspidal and ventral parts of the anterior lobe rather than by the positive intervention of a sulcule.

Unlike most Calcaribeyrichia species C. torosa has only one syllobial cusp (a situation common in Neobeyrichia) and its lobular differentiation has produced two, rather than the more normally observed three, syllobial lobules. Perhaps its most unexpected and diagnostic development is its faceted lobes - a feature found in no other Calcaribeyrichia species and more immediately associated with members of the Kloedeniinae.

C. torosa closely resembles C. tegula, from which it differs by details of cuspidal and syllobial morphology (see under C. tegula). The species lacks the anteroventral spine of C. duplicicuspidata and is further distinguished from that taxon by the form of the lobules and lobes, and by the presence of a ridge on the crumina.

Although in need of a critical first hand re-examination, it is obvious from the illustration alone that the female from the Öved-Ramsåsa Bed 4 of Scania figured as Deyrichia cuspidata Grönwall, 1897 by Moberg & Grönwall (1909, pl.IV, fig. 6) bears striking resemblance to C. torosa (Jones, 1855). Attention is drawn to the similar cruminal shape, velar morphology, ornament, and, in particular, to the depiction of faceting on the preadductorial node and on the cuspidal lobule of both anterior lobe and syllobium.
OCCURRENCE: Collected by the author from the following Ludlovian localities in the Ludlow, Downton and Bucknell districts.

Whitcliffe Beds: Five Turnings (loc. 14).

Stone Pitts Coppice (loc. 72).

Downton Castle Bridge (loc. 71).

Whitcliffe Oy. (loc. 70).

Although Beyrichia Kloedeni var. torosa Jones, 1855 is often recorded in Welsh Borderland faunal lists with a range from the Lower Leintwardine Beds to the top of the Whitcliffe Beds, the writer has seen C. torosa (as restricted herein) only from the rocks of Whitcliffe age.

The Neobeyrichia torosa (Jones, 1855) of Shaw (1971a) was documented from the Lower Underbarrow Flags, Kirkby Moor Flags and Scouthill Flags of the Lake District; according to Shaw (1971a) these beds represent Leintwardinian to Downtonian deposits. Shaw's figured material from the Scout Hill Flags (Downtonian) appears to be conspecific with the Welsh Borderland specimens described herein, but the possibility that the material recorded from the Lower Underbarrow Flags (Leintwardinian) could be assigned to C. tegula must be considered (material not studied in this connection). In the Long Mountain District Shaw (1969, pp. 67-8, text-fig. 8) noted the continuation of "N. torosa" into the lower part of the Downton Castle Sandstone from the underlying Upper Whitcliffe Flags.

Reported occurrences of C. torosa are exclusive to the British succession.

Calcaribeyrichia ? "antiquata" (Jones, 1855)

Pl. Dll, fig. 8.

non 1855 Beyrichia tuberculata, var. antiquata, Jones, p. 87, pl. V, fig. 12.

1855a Beyrichia Kloedeni, var. antiquata. Jones, p. 167, pl. VI, fig. 8.
1869 *B. Kloedeni*, var. *antiquata*, Jones; Jones, p. 14, fig. 7.
non 1881c *Beyrichia Kloedeni*, M'Coy, var. *antiquata*, Jones; Jones, p. 345, pl. X, fig. 11.
1886 *Beyrichia Kloedeni*, var. *antiquata*, Jones; Jones & Holl, p. 351 (pars).
1908 *Beyrichia kloedeni antiquata* Jones; Ulrich & Bassler, p. 285.
1934 *Beyrichia antiquata* (Jones); Bassler & Kellett, p. 186, (pars).

**HOLOTYPE:** A right valve tecnomorph, UM I 6353, figured Jones 1855a, pl. VI, fig. 8; herein pl. Dll , fig. 8.

Jones based his new variety on this single specimen.

**TYPE LOCALITY:** Given by Jones as, "Wenlock schists in the road cutting about half a mile from Montgomery towards Garth Mill."

This locality would probably be along the B4385 road on the E side of Ffridd Faldwyn (Nat. Grid Ref. 219973). Jones comments that the holotype was found in a, "calcareous nodule".

**DESCRIPTION:** Large, weakly preplete valve. **Syllobium** narrow ventrally - joined to the preadductorial node by an almost obsolete connection - but broadens rapidly towards mid-height. Anterior lobe isolated from preadductorial node by a shallow sulcus traced from the hinge line to the prominent anteroventral depression. The cuspidal section of the anterior lobe is faintly separated from the larger, ventral part of the lobe. The adductor(s) is slightly wider and deeper than the prenodal sulcus. The (anterior) cusp of the syllobium, like that of the anterior lobe, takes the form of a knob-like element, projecting just above the hinge line.

The velum is fairly narrow and has (the remains of) spines around its edge. All extant lobes - the preadductorial node and calcarine region of the syllobium are damaged - are tuberculate.

**MEASUREMENT:** Hinge length - sulcal height in microns. 2840-1660.
DISCUSSION: *Beyrichia Kloedeni var. antiquata* Jones, 1855a is a junior primary homonym of *Beyrichia tuberculata var. antiquata* Jones, 1855 from the Baltic Beyrichienkalk. It is preferred not to rename var. *antiquata* Jones, 1855a as this species - known only from one (worn and damaged) specimen - has not been identified elsewhere and has to be treated (for the moment at least) as a nomen dubium. This is done in the knowledge that attempts to recollect topotype material have met with no success.

As a temporary expedient the species is assigned to *Calcari-beyrichia* - mainly because of the resemblance of its lobar morphology (especially the cuspidal sections), anteroventral depression, and (spinose) velar ridge to conditions found in *C. tegula*. *C. tegula*, unlike *antiquata*, does not have a completely isolated anterior lobe. Unfortunately the calcarine region in the only extant specimen of *antiquata* is damaged and hence it is not possible to determine if, like *C. tegula*, it too had a calcarine spine.

OCCURRENCE: Only from the type locality.

*Beyrichiinae gen. et sp. nov. A*

Pl. 111, figs. 7, 10, 11, 14.

REMARKS: This species is represented by only one female specimen. Its morphology is unlike that of typical beyrichiines, and its occurrence in Britain is unusual. Its locality details are known in some detail; future collecting will almost certainly produce additional material which will permit a fuller description and the formal publication of the taxon.

DESCRIPTION: The valve has a regular rounded outline and (apart from the anteroventral crumina) appears almost symmetrical about its mid-length. Lobation is fully developed but the lobar elements do not
project above the hinge line. The anterior lobe is broad, flat and curves very gently for some distance along the hinge line. The preadductorial node (small by comparison with the two adjacent lobes) is more elevated than the anterior lobe but is lower than the syllobium. Although narrow and fairly short, the prenodal sulcus is by no means obsolete. Both the prenodal sulcus and the larger adductorial sulcus bend gently around the preadductorial node towards the crumina. The wide syllobium maintains a constant width until just below mid-height, when it begins to narrow gradually towards its junction with the crumina; even in this region the syllobium is still quite wide. The dorsal part of the syllobium lies flat along the hinge line, without a cusp; ventrally this lobe is quite tumid.

The flange-like velum is smooth, narrow and of nearly constant width; its presence from anterodorsal to posterodorsal corners of the valve is interrupted only in the cruminal region. There is no toric structure. The crumina is large, "full", and well set off from the valve. The posterior part of the crumina begins below the anterior margin of the syllobium and its dorsal region reaches just above valve mid-height. The surface of the valve is somewhat worn, but (as far as can be seen) there are no signs of subcruminal features such as ridges or striae. A marginal ridge runs parallel to the velum around the edge of the valve. The lobes and crumina appear to lack ornamentation. No form of groove is present on the syllobium.

MATERIAL: Just one female right valve, DAS 47160.

MEASUREMENTS: Hinge length - sulcal height in microns.  
1860-1080.

DISCUSSION: This species is characterised by a simple lobal arrangement, a simple flange-like velum, and an absence of ornamentation. Its morphology invites close comparison with problematical beyrichiines
such as the N American "Kloedenia" species and allied genera (see "Discussion, p. 233"). Berdan (1972) has recently published a much needed revision of some of the American taxa in which she erected the genus Kloenediopsis and recognised two other (unrevised) species groups largely on the basis of the form and position of the marginal and velar structures. In lateral view the British species could be placed in any one of Berdan's three groups, but its resemblance to "Kloedenia" normalis Ulrich & Bassler, 1923 - a species which characterises one of the groups - is especially apparent. From the published figures (Ulrich & Bassler, 1923, pl. LXXI, figs. 15, 16, 19; Berdan 1972, pl. 3, fig. 1) of this species it appears to differ from the British form mainly by the shape of the crumina and width of the syllobium. Moreover, according to Berdan's scheme the British female could not readily be referred to the "Kloedenia" normalis group or to Kloenediopsis, but would most probably be assigned to the third group (represented by forms such as "Kloedenia" montaguensis) where the, "velar ridge ... is separated from the marginal ridge so that a canaliculus is developed" (see Berdan 1972, p. 25, text-fig. 5).

Pending further revisional work on the large member of American taxa and the collection of more British material, the present species is referred to an unnamed genus and is provisionally (see Martinsson 1962, p.347, 1963, p. 19; Berdan 1972, p. 26) treated within the Beyrichiinae.

**OCCURRENCE:** From the Wenlockian near Ludlow, the Welsh Borderlands.

Wenlock Shale: Burrington (loc. 45); C. lundgreni Zone.
INCERTAE SUBFAMILIAE

Gen. et sp. nov. A
Pl. Dll, figs. 9, 12, 13.

REMARKS: The extant material of this species consists of a single tecnomorphic specimen; it is extremely well preserved and shows interesting lobal and velar features. Of the established beyrichiacean subfamilies its morphology is perhaps most comparable to some members of the Beyrichiinae but its taxonomic position cannot be decided until a female of the species is known.

DESCRIPTION: The large valve is gently preplete and fully lobate. The elongate preadductorial node is the smallest and most elevated lobe; it is bluntly pointed, inclined forwards, and rests against (and appears largely fused with) the anterior lobe. Separating these two lobes is a narrow (almost obsolete) prenodal sulcus. A rounded cusp caps the gently arched, anterior lobe; this lobe widens ventrally.

The anteriorly inclined adductorial sulcus is relatively narrow and quite deep; it reaches just below valve mid-height. Only near the hinge line - where it receives the dorsal part of the prenodal sulcus - does this sulcus widen slightly. The evenly curved cuspidal outline of the syllobium occupies (in lateral view) an appreciable part of the dorsal margin of the valve. In posterior view the syllobial profile is gently curved. Behind the ventral end of the adductorial sulcus there is a shallow, diagonally trending depression which houses at least one (possibly two) short, faint, hairline groove(s). The syllobium is joined first to the preadductorial lobe then the anterior lobe, along the fairly flat, ventral section of the valve. There are no indications of a zygal connection.
Outside the lobate area there is a narrow zone of nearly constant width on which the site of the velum is marked as an inconspicuous bend in the valve outline. The velum can be traced from anterior to posterior cardinal corners. There is a minor ridge-like marginal structure (which in lateral view forms the outline of the valve) along the free margin. Close examination of this ridge reveals it to have minute tubercles, closely spaced along its length.

The sulci and most of the valve surface are smooth. Areas of fine reticulation are confined to the dorsal part of the syllobium and along the main section of the anterior lobe.

MATERIAL: Only the figured specimen, a right valve tecnomorph (DAS 47295).

MEASUREMENTS: Hinge length - sulcal height (to the free margin) in microns.

1830-1380.

DISCUSSION: The form of the velum indicates that this species belongs to the Beyrichiidae rather than to the Craspedobolbinidae. Its fused anterior lobal complex, and the form of its adductorial sulcus and syllobium invite a superficial comparison with the zygo-bolbine genus *Slependia* Martinsson, 1962, but its sparse reticulation (not widely scattered reticulo-tuberculation), the structure of the velum and the presence of a syllobial groove are unlike anything found in that genus.

The closest relatives of this species may lie amongst the enigmatical reticulate beyrichiines such as the European *Bingeria* and "*Kloedenia*" (and associated genera) of American usage (cf. Martinsson 1962, p. 347 and 1963, p. 19). Many of these taxa tend to have a fused anterior lobal complex and a number of them - typified by "*Kloedenia normalis*" Ulrich & iassler, 1923 - appear to show a velar
bend similar to that found in the British species (see Berdan 1972, p. 25, fig. 5). In spite of these comparisons the British species cannot readily be assigned to any established genus and provisionally referred to an unnamed genus pending the collection of a female valve.

OCCURRENCE: From near the base of the Wenlockian, the Tortworth inlier, Gloucestershire.

Brinkmarsh Beds: Brinkmarsh Qy., limestone band (loc. 11).
BRITISH KLOEDENIINAE

REMARKS: Ploterichia gen. nov., in one sense dominates the finds of kloedeniines from Britain. This genus is assumed herein to represent a primitive member of the subfamily and its age (low Wenlockian) takes on special significance when considering the phylogeny of the superfamily in general and the Kloedeniinae in particular. Many of the characteristics of an idealised progenitor of the much younger kloedeniines hitherto described, are manifest in Ploterichia. The gap in morphology between this genus and, for example, Frostiella Martinsson, 1963 is not nearly so great as that provided by stratigraphy.

Baltic (and N American) elements are again in evidence in the form of Londinia Martinsson, 1963, Frostiella, and Kloedenia Jones & Holl, 1886.

The original specimens of Kyamodes Jones, 1888 have been located and revised, though the subfamilial position of the genus is still in doubt; accordingly it is dealt with under Incertae Subfamiliae.

The terminology applied to the Kloedeniinae is that used by Martinsson (1963, pp. 12-17, text-fig. 5; herein text-fig. 2).

SYSTEMATIC PALAEOENTHOLOGY

Subfamily KLOEDENIINAE Ulrich & Bassler, 1923

TYPE GENUS: Kloedenia Jones & Holl 1886, p. 362; from the Baltic Beyrichienkalk erratics.

BRITISH GENERA: Ploterichia gen. nov.
Londinia Martinsson, 1963
Frostiella Martinsson, 1963
Kloedenia Jones & Holl, 1886
DIAGNOSIS: Beyrichiidae with a longish, more or less distinctly anteroventral crumina, extending from anterior lobe to the mid-length of the syllobium, set off from the domiciliar part of the carapace - without any marked proximal constriction - as an ellipsoidal structure, or strongly assimilated with the domicilium. The formation of the crumina does not influence the free margin or marginal structures. The lobes tend to protrude considerably over the hinge line and to develop lateral facets or cristal loops. (After Martinsson 1963, p. 19).

DISCUSSION: The definition and restriction - excluding forms such as the "Kloedenia" of many American authors - of the Kloedeniinae put forward by Martinsson in his (1963) study of the group has found general acceptance in palaeoscope literature.

Abushik (1971) described many species in the new genera Cornikloedenina and Carinokloedenia, both erected within the new subfamily the Carinokloedeniinae. This subfamily was placed by Abushik within the Kloedeniidae Ulrich & Bassler, 1923 which - as with other beyrichiacean subfamilies - she had raised to family rank. Carinokloedeniinae was established on the basis of the occurrence of a spinose - wing-like extension along the ventral section of the tecnomorphic velar bend. Contrary to the opinion of Abushik it seems to me that Cornikloedenina and Carinokloedenia could be accommodated within the concept - as discussed at length by Martinsson (1963) - of the Kloedeniinae and the erection of a new subfamily for their reception seems, at present, unnecessary; similarly Ploterichia is assigned to the Kloedeniinae. These genera exhibit many features commonly associated with kloedeniine valves and the occurrence of a somewhat atypical velar morphology should not necessarily lead to their exclusion from the subfamily.

Apart from those conditions expressed in the diagnosis above, the following characteristics also serve to unify the group of genera in question. Characteristically it is the preadductorial node which is
protuberant; the adductorial sulcus is usually narrow and the syllobium usually broad - with a posterior lobule; the mostly smooth valve surface is often broken only by punctuation or, more rarely, lobal reticulation; subcraminal ornament generally consists of a variably developed striation; typically the velar structure is represented by a bend or ridge.

**OCCURRENCE:** Known from the Wenlock of the Tortworth inlier, the late Ludlow and Downton of the Welsh Borderlands and Wales, the Downton of the Lake District, and from borehole (Downton) material of Buckinghamshire.

Other records come from Podolia, Baltoscandia and the western coastal regions of Canada and the U.S.A. These finds mostly occur in Upper and late Silurian deposits.

**Genus PLOTERICHIA gen. nov.**

**DERIVATION OF THE NAME:** From the Greek Ploter, sailor and the suffix -richia (as in Beyrichia); with reference to the fancied resemblance of the (faceted) preadductorial node to a sailor's hat. Gender, feminine.

**TYPE SPECIES:** *Ploterichia pileata* sp. nov., Pl. El, figs. 3, 5, 6, 13, 14; from the Wenlockian of the Tortworth inlier, Gloucestershire.

**SPECIES:** Only the type species.

**DIAGNOSIS:** Kloedeniinae whose long crumina - quite well set off from the domicilium - has a wide field of fine striae ventrally and wide, coarse ridges laterally. A velar bend links the smaller posterior syllobial cusp to the anterior lobal cusp either side of the crumina in females, or via a short, narrow, lateroventral velar extension in tecnomorphs. The protuberant preadductorial node is faceted but lacks cristal loops. Sparse, blunt nodes and pimples often ornament the valves.
DISCUSSION: The occurrence of a genus with a morphology like Ploterichia in deposits of lowermost Wenlock age is somewhat unexpected. It is easily the earliest recorded member of the Kloedeniinae (commonly found in late Ludlovian and younger deposits) and the genus with which it shows closest affinities, Cornikloedenina Abushik, 1971 (see "Discussion" above), is unknown outside the Tchortkov Horizon (no older than Dittonian) of Podolia.

In general the valve outline, lobal distribution, and cruminal shape of Ploterichia is very comparable to Cornikloedenina. Ploterichia is distinguishable by the presence of a wide, subcruminal field of finger-print striation, the absence on its anterior syllobial cusp and (faceted) preadductorial node of cristae, the greater prominence of its other lobal cusps, and the occurrence of node-like structures on the valve surface. Furthermore, the wing-like tecnomorphic velum occurring in P. pileata is lacking in the type-species Cornikloedenina althi (Krândijevsky, 1963) and, although it is found in – and indicates its closer affinities to – species such as Cornikloedenina triangularis (Krândijevsky, 1963) the features outlined above effectively separate Ploterichia from Cornikloedenina.

See also "Discussion" under P. pileata below.

OCCURRENCE: The Wenlockian of the Tortworth inlier, Gloucestershire.

Ploterichia pileata sp. nov.

Pl. El, figs. 1-14.

DERIVATION OF THE NAME: From the Latin pileatus, "capped"; with reference to the fancied resemblance of the preadductorial node.

HOLOTYPE: A female right valve, DAS 47266; Pl. El, figs. 3, 5, 6, 13, 14.

TYPE LOCALITY AND TYPE STRATUM: A small exposure on the NW side of Brinkmarsh Quarry, near Whitfield, the Tortworth inlier, Gloucestershire (loc. 11); the sandy limestone band at the base of the Brinkmarsh Beds.
DIAGNOSIS: As for the genus.

DESCRIPTION: All of the lobate area is bounded by a conspicuous velar bend, outside which - in both dimorphs - there is a lower narrow zone extending to the free margin. Valve outlines are gently preplete.

The syllobium is broad, undissected and has two cusps - a smaller (in small tecnomorphs obsolete) posterior cusp appearing as the dorsal termination of the velar bend, and a more prominent anterior cusp which overlooks the adductorial sulcus and protrudes over the hinge line (although inconsiderably) more than any other cuspidal element. The adductorial sulcus is narrow, incised and continues from the dorsal margin to about mid-height on the valve. Stalk-like and easily the most elevated lobal feature, the preadductorial node tends to dominate the lateral surface of the valves. Its ovoid crest is generally faceted (though it can be slightly rounded), and lacks cristal loops. In lateral view, the dorsal margin of this crest fails to attain the level of the hinge line. Because of the narrowness of the adductorial sulcus, the preadductorial node - as in many kloedeniines - lies close to the syllobium.

By comparison with the main sulcus, the short prenodal sulcus is hardly discernible, appearing as a faint, gradually shallowing depression in the angle between the anterior lobe and the laterally projected preadductorial node. The anterior lobe is fairly flat, about two-thirds as wide as the syllobium, and is represented dorsally by a cuspidal termination to the anterior section of the velar bend. This anterior lobal cusp is small, subdued, and equal in size and form to the posterior syllobial cusp.

The velum is represented in both dimorphs by a bend or ridge-like structure which has an ovoid path (best described by the figures) parallel - except dorsally where its ends converge and terminate in lobal cusps - to the free margin. Ventrally the uniformly ovoid outline of the velar bend is interrupted by the occurrence of a short, wing-like velar
projection in tecnomorphs, and a long, posteriorly tapering crumina in females. This tecnomorphic velar projection extends laterally for a short distance as a thickened portion of the velar bend, from a point below the anterior margin of the preadductorial lobe to a point below the posterior syllobial cusp. The crumina extends from a point below the anterior cardinal corner, over a considerable length of the valve, to a point almost below the posterior syllobial cusp. Large areas of the domiciliar wall have been annexed by the crumina, especially in the region below the preadductorial node and in the anterior section of the shell. The long axis of the crumina is at a slight but consistently distinct angle to the hinge line. Ventrally, the crumina is completely separated from the free margin.

The ventral part of the crumina is evenly covered by a wide, regularly arranged field of fine striae. Laterally, the crumina has two large, rather rounded ridges along its length - an inconsiderably shorter dorsal one, and a prominent ventral ridge which, posteriorly, is typically projected as a weak spur-like feature off the crumina.

These two main ridges, in very well preserved specimens, are themselves, seen to be ornamented with fine striae. The remainder of the valve, except for the faceted crest of the preadductorial node, mostly lacks ornamentation. This crest has a weak but rather dense pattern of punctuation over its surface; this particular form of ornament has been detected only in the holotype. Blunt node-like structures varying much in size are scattered on the valves, particularly the females. Characteristically three or four are found over the dorsal regions of the crumina above (or even connected to) the dorsal ridge. One or two larger and somewhat irregularly shaped excrescenses are often found just below the anterior syllobial cusp. Sometimes (especially in many of the tecnomorphs) these structures may be lacking altogether. Small instars are similar in most essential respects to large tecnomorphs. Like adults, they have a velar bend and wing-like extension, though the
cusps on the anterior lobe and posterior part of the syllobium are hardly, if at all, recognisable.

MEASUREMENTS: Hinge length - height over the adductorial sulcus (females inclusive of crumina) in microns of specimens from the type locality.

   Females: 1820-1060 (holotype), 1500-895, 1450-900.

   Tecnomorph: 1810-1070.

Those female valves which were prepared did show an appreciable variation in size.

DISCUSSION: In his treatment of the Kloedeniinae Martinsson outlined (1963, p. 18) a series of morphological features which one might expect to find in an early member of the subfamily. The required structures, he suggested, occur in the genus Londinia Martinsson, 1962 (found in the high Ludlovian and Downtonian). In my opinion similar conditions are also apparent in the Wenlockian Ploterichia. It has a long crumina, quite well set off from - yet incorporating sizable parts of - the carapace, in much the same way as in Londinia. Moreover the ventral part of the crumina is striate, and does not interfere with the adjacent region of the free margin. The preadductorial node is protuberant (although radially rather than dorsally over the hinge line as in Frostiella and Kloedenia), faceted, and lies close to a wide syllobium, so that the adductorial sulcus is narrow and rather incised. The velum, too, - reduced to a bend - very much resembles homologous structures in Londinia and associated genera. From this evidence it is reasonable to assume that Ploterichia is both a very early and a primitive kloedeniine which lay at the root of a lineage from which other kloedeniines with a more complete velar and lobal reduction developed.

OCCURRENCE: Found, as yet, only from the base of the Wenlock Series at the type locality. Specimens are not uncommon, but are extremely difficult to prepare.

   Brinkmarsh Beds: Brinkmarsh Qy., limestone band (loc. 11).
Genus **LONDINIA** Martinsson, 1963

**TYPE SPECIES:** Original designation of Martinsson 1963, p. 20;

*Londinia reticulifera* Martinsson 1963, p. 24, figs. 7B, 12B, 13A;
from "Bed 1" (according to Moberg & Grönwall) near Klinta, parish of Bosjökloster, Scania.

**BRITISH SPECIES:**
- *Londinia fissurata* Shaw, 1969
- *Londinia lata* Shaw, 1969
- *Londinia arisaigensis* Copeland, 1964

**DIAGNOSIS:** Kloedeniinae with ellipsoidal crumina well set off from the domicilium. Preadductor lobe and anterior lobule of the syllobium subequal in size, more or less narrow, merging with the lateroventral part of the tecnomorphic valve on both sides of an adductorial sulcus. Anterior lobe and posterior lobule of the syllobium narrow, low, sub-equal in size and shape and merging with the lateroventral part of the tecnomorphic valve. A considerable field on the admarginal part of the crumina with undifferentiated finger-print striation. (After Martinsson 1963, p. 20).

**DISCUSSION:** *Londinia* was erected by Martinsson to include the type-species and "Kloedenia" kiesowi Krause, 1891. Subsequently *Londinia arisaigensis* Copeland, 1964, *Londinia lata* Shaw, 1969, and *Londinia fissurata* Shaw, 1969 were added to the genus. Martinsson has suggested (1963, p. 20) that "Kyammodes" tricornis Ulrich & Bassler, 1923 and "Kyammodes" swartzi Ulrich & Bassler, 1923 might also belong within *Londinia*, but Copeland (1964, p. 10) claimed generic distinction for these two American species when assigning them to the new genus *Pintopsis*, which he distinguished from *Londinia* by its less dissected syllobium and by the greater (ventral) constriction of its preadductor node. In other respects the two genera are closely allied and it may
be debatable whether a separation at the generic level is justified. *Londinia* differs from both *Frostiella* and *Kloedenia* by its wider, undifferentiated field of subcrominal striation, its less assimilated (within the domicilium) cromina of ellipsoidal shape, and its lack of cristae. The species described by Ijevant (1965) as *Londinia ? falcigera* n. sp. from the Siegenian of N France, should not be considered a member of the genus.

**DISTRIBUTION:** From Upper Silurian strata in Scania (Martinsson 1963, 1967), Pomerania (Martinsson 1964), Britain (Shaw 1969), and submarine exposures off Gotland (Martinsson 1964, 1967). In N America the genus has been recorded from the Edmunds and Pembroke Formations of Maine, U.S.A. (Berdan 1966; Martinsson, 1967 and Martinsson in Berry & Boucot, 1971) and from the lower part of the Stonehouse Formation of Nova Scotia (Copeland 1964).

*Londinia fissurata* Shaw, 1969

Pl. E2, fig. 11.

1969 *Londinia fissurata* n. sp.; Shaw, p. 58, figs. 4A-H.

HOLOTYPE: An internal mould of a tecnomorphic carapace, GSM 103242; illustrated by Shaw 1969, p. 60, fig. 4F, herein Pl. E2, fig. 11.

**TYPE LOCALITY AND TYPE STRATUM:** Norton Lane, Onibury, Shropshire; Temeside Bone Bed, Temeside Shales, Downtonian.

**DIAGNOSIS:** See Shaw, 1969, p. 58.

**DESCRIPTION:** See Shaw, 1969, p. 59.

**MATERIAL:** Occurs almost exclusively as moulds; rarely, some valves with traces of shell remaining.
MEASUREMENTS: Approximate hinge length - sulcal height in microns.

1600 - 1000 (female, internal mould, GSM 103237; Shaw 1969, p. 60, figs. A, D).

DISCUSSION: Separated from the closely allied *L. kiesowi* by its, "increased asymmetry ..... longer adductorial sulcus and shorter crumina" (Shaw 1969, p. 59). Distinguished from *L. arisaigensis* particularly by its gentler surface sculpture. Not collected by the writer (but see *L. cf. L. fissurata* below).

OCCURRENCE: Documented (Shaw, op. cit.) from the Downtonian at the type locality (Temeside Shales) and the Long Mountain area (Temeside Shales and Downton Castle Sandstone). Conspecific material may be present in Bed 4 at Ramsasa (Shaw, op. cit., p. 59), and in the topmost Whitcliffian at Ludlow (see *L. cf. L. fissurata*, herein).

*Londinia cf. L. fissurata* Shaw, 1969

Pl. E2, figs. 8, 9.

REMARKS: Concomitant with obvious (and common) *L. arisaigensis* valves in collections from the topmost Whitcliffian are a few *Londinia* specimens (of both dimorphs) which cannot be assigned with justification to that species.

The specimens in question show variation beyond the acceptable limits for *L. arisaigensis* - having gentler, more rounded lobal elements, a wider anterior syllobial lobule, and a total lack of lateral lobal facets. The overall morphology of these valves accords quite favourably with *L. fissurata* Shaw, though more material is needed for confirmation of this assignment.

OCCURRENCE: Topmost Whitcliffian, Ludlow.

Ludford Lane I (locs. 69a, b).
Londinia lata Shaw, 1969
Pl. E2, fig. 4.

1969 Londinia lata n. sp.; Shaw, p. 59, figs. 5A-K.

HOLOTYPE: An internal mould of a tecnomorphic right valve, GSM 103254; illustrated Shaw 1969, p. 62, fig. 5H, herein Pl. E2, fig. 4.

TYPE LOCALITY AND TYPE STRATUM: Norton Lane, Onibury, Shropshire; Temeside Bone Bed, Temeside Shales, Downtonian.


MATERIAL: Occurs mostly as moulds; occasionally some valves with shell remaining.

MEASUREMENTS: Approximate hinge length – sulcal height in microns.

2025 – 1350 (holotype).

1600 – 1050 (female cast, GSM 103255; Shaw 1969, p. 62, fig. 5J).

DISCUSSION: Not collected by the writer. The specimens figured by Shaw show noticable similarities to L. fissurata (from the same locality and horizon). Shaw distinguished L. lata by its wider syllobium and shorter adductorial sulcus.

L. lata must be considered very near to the concept (Copeland 1964) of Pintopsis, but apparently (Shaw 1969, p. 61) lacks the ventral constriction at the base of the adductorial sulcus found in that genus.

OCCURRENCE: Recorded (Shaw, op. cit.) from the Downtonian of the type locality (Temeside Shales) and the Long Mountain area (Downton Castle Sandstone and Temeside Shales).
Londinia arisaigensis Copeland, 1964
Pl. E2, figs. 1-3, 5-7, 10.

1964 Londinia arisaigensis n. sp.; Copeland, p. 11, pl. 1, figs. 16-26.

1967 Londinia cf. kiesowi; Martinsson 1967, p. 376.

1969 Londinia arisaigensis (Copeland 1964); Shaw, pp. 61, 63, figs. 6A-D.

HOLOTYPE: A female left valve, GSC 14562; figured Copeland 1964, pl. 1, fig. 18.

TYPE LOCALITY AND TYPE STRATUM: Shore of Northumberland Strait, near Arisaig, Nova Scotia, Canada; within the first 100 ft of the (type section of the ) Stonehouse Formation.

DIAGNOSIS: Londinia species with an (indistinctly) asymmetrical lobal arrangement. Anterior syllobial lobule long, slender and sloping forwards, preadductor node slightly broader and less elongate; both elements strongly elevated above other regions of the valve, with a tendency to develop lateral facets on their dorsal crests. Anterior lobe joined anteroventrally to the elevated area of lobal connection beneath the adductorial sulcus, and more prominent than the rather isolated posterior syllobial lobule; both elements lunate and ridge-like. Prenodal sulcus and syllobial sulcule fairly broad but not incisive.

DESCRIPTION: See Copeland (op. cit., p. 11), and also "Diagnosis" above and "Discussion" below. Some notes should be added with respect to the British material.

The adductorial sulcus is broad, long and deep; typically its edges are sharply defined (dorsally) due to the faceting of the preadductor node and anterior syllobial lobule. The lateral surface of the preadductor node is faceted obliquely, resulting in
an elevated, sharp posterior edge and a lower rounded anterior edge. Lobal faceting is generally less developed (sometimes practically absent) in material from below the Ludlow Bone Bed. The central lobal elements terminate on, or inconsiderably above, the hinge line.

Rarely (in 2-3 valves) very delicate reticulation - stretched dorso-ventrally in linear fashion (cf. conditions in *L. reticulifera*) - is detected on the preadductor node of females, while the corresponding syllobium appears to be finely and densely punctate; the absence of similar ornament in the extant tecnomorphs may be a dimorphic effect. The crumina is set off high above most of the valve, and is well demarcated proximally. Aspects of preservation prevent a determination of the subcruminal morphology.

MATERIAL: All known British material occurs in mould form.

MEASUREMENTS: Approximate hinge length (in microns) of casts of female valves.

Downton Castle Sandstone: Ludford Lane II (loc. 73b): 2100, 2075, 2000.

Whitcliffe Beds: Ludford Lane I (loc. 69b): 1900.

DISCUSSION: The British material varies from that described from Canada (Copeland 1964) by its longer adductorial sulcus and by the occurrence of (weak) lobal ornament; furthermore - and more significantly - though lobal facets would appear to be (faintly) present in the Arisaig valves (e.g. see Copeland, op. cit., pl. 1, fig. 21), this has not yet been confirmed with certainty. Notwithstanding these differences, there are marked similarities in lobal shape and arrangement between the material from each area, all of which is treated herein as conspecific; in particular the Welsh Borderland females are practically indistinguishable from the female holotype, as are the sympatric tecnomorphs in relation to the Arisaig right valve tecnomorph (G.S.C. 14564c) illustrated by Copeland 1964, pl. 1, fig. 21.
Copeland thought that *L. arisaigensis* displayed more affinities with *L. reticulifera* than *L. kiesowi*, whereas Martinsson (1967, p. 377) thought that the, "differences between *Londinia arisaigensis* Copeland 1964 and *Londinia kiesowi* are certainly at an infraspecific level".

From study of the published figures I am inclined to share the opinion of Copeland (op. cit.) and Shaw (1969, p. 70) that *L. arisaigensis* should be regarded as a species near to, yet distinct from, both *L. kiesowi* and *L. reticulifera*. In particular, it differs from the latter by its gentler (less incised) prenodal sulcus and syllobial sulcule, and by its considerably weaker lateral lobal facets, and is distinguished from the former mainly in details of the shape and the greater asymmetry of the lobal elements (in this respect and in the occurrence of - at least in the British material - faint reticulation, *L. arisaigensis* accords more closely with the type species than with *L. kiesowi*).

**OCCURRENCE:** Collected by the author from both above and immediately below the Ludlow Bone Bed at Ludlow.

- **Downton Castle Sandstone:** Ludford Lane III (loc.74).
- Ludford Lane II (locs. 73a, b).
- **Whitcliffe Beds:** Ludford Lane I (loc. 69a, b).

The best preserved material, showing prominent lateral lobal facets, was obtained at loc. 73b (about 1.5 m above the Ludlow Bone Bed).

Recorded by Shaw (1969, pp. 61, 67, 68, fig. 8) from the Downton Castle Sandstone at three localities: 5'6" above the Ludlow Bone Bed in Ludford Lane, Ludlow; Forge Bridge, near Downton; the Long Mountain region.

Records from outside Britain are limited, as yet, to the lower part of the Stonehouse Formation, Nova Scotia (Copeland 1964), though it must be remembered that its occurrence would extend to correlative horizons in the Baltic region if Martinsson’s synonymy (see "Discussion" above) were upheld.
Genus **FROSTIELLA** Martinsson, 1963

**TYPE SPECIES:** Original designation of Martinsson 1963, p. 29;

*Frostiella groenvalliana* Martinsson, 1963, p. 31, fig. 15B; from
"beds 3-4", sensu Grönwall, at Ramsåsa, Scania.

**BRITISH SPECIES:** *Frostiella groenvalliana* Martinsson, 1963

*Frostiella bicristata* Shaw, 1969

**DIAGNOSIS:** Kloedeniinae with crumina strongly assimilated with the
domicilium; crumina with a narrow, striate, and somewhat swollen
field between the distinct velar bend and the marginal structure.
Sylobium with protruding cusp. (After Martinsson 1963, p. 29).

**DISCUSSION:** The genus was erected to accommodate forms intermediate
between *Londinia* and *Kloedenia* and originally included the type species
and *F. plicata* (Jones, 1855). With the addition of *F. lebiensis*
Martinsson, 1965, to the genus, *F. plicata* was dubbed *nomen dubium.*
This list is augmented by *F. loodensis* Sarv, 1968 from Estonia,
*F. bicristata* Shaw, 1969 from Britain, and *F. modesta* Abushik, 1971
described from the mid-Skala horizon of Podolia.

**OCCURRENCE:** Most of the finds are in Downtonian and correlative
deposits of Britain and the Balto-Scandanavian area. Herein, the genus
is recorded for the first time from the (very top of the) British
Whitcliffian. The Leighton Shale (Pembroke Formation) of Maine,
U.S.A., and the Stonehouse Formation of Nova Scotia - both currently
regarded to be above the level of the Ludlow Bone Bed - also contain
*Frostiella* species (see Martinsson in Berry & Boucot 1971, p. 42).
Frostiella groenvalliana Martinsson, 1963
Pl. E2, figs. 12-14, 16-18.

1897 Kloedenia Wilckensiana Jones; Grönvall (passim).
1909 Kloedenia Wilckensiana Jones et var. plicata Jones; Moberg & Grönwall, p. 66, pl. VI, figs. 6a, b, 7.
1963 Frostiella groenvalliana n. sp.; Martinsson, p. 29, figs. 7C, 8, 14-17.
1963 Frostiella cf. groenvalliana; Martinsson, p. 34, figs. 18A-D.
1967 Frostiella groenvalliana; Martinsson, p. 376.
1968 Frostiella groenvalliana Martinsson; Sarv, p. 58, pl. XX, figs. 6-8.
1969 Frostiella groenvalliana Martinsson 1963; Shaw, p. 55, figs. 1A-F.
1971a Frostiella groenvalliana Martinsson 1963; Shaw, p. 603, pl. 113, figs. 1-5, 7.

HOLOTYPE: A female left valve, MPL LO 4084 T; illustrated Martinsson 1963, fig. 15B.

TYPE LOCALITY AND TYPE STRATUM: "Beds 3-4" (sensu Grönwall) at Ramsāsa, Scania.

DIAGNOSIS: A species of Frostiella with cristal loop tear-shaped, becoming pointed and posteriorly curved on the dorsal face of the pre-adductorial node. There is a cusp on the anterior part of the syllobium and a smaller one terminating the anterior lobe.

DESCRIPTION: See Martinsson 1963, p. 30 for a description of topotype specimens. The Welsh Borderland material was treated by Martinsson (1963, p. 34) under the name Frostiella cf. groenvalliana (the confer was subsequently dropped, Martinsson 1967) and later by Shaw (1969). F. groenvalliana has also been described from Westmorland (Shaw, 1971a). Only a few comments (see "Discussion" below) need be added to these descriptions.
MATERIAL: In Britain this species occurs only in mould form. Excellent casts have been obtained from material collected at Ludford Lane, Ludlow; even the fine ornament on the dorsal regions of the preadductorial node has been preserved.

MEASUREMENTS: Hinge length - sulcal height (in microns) of casts from the Downton Castle Sandstone.

Ludford Lane II (loc. 73b): 2200 (hinge only), 2010-1375 (females).
2130-1420, 2025-1490 (tecnomorphs).

DISCUSSION: The differences between the Welsh Borderland material and that from Scania have been outlined by Martinsson (1963) and Shaw (1969). I agree with Martinsson that the lateroventral lobal connection is slightly wider in the British specimens, and with Shaw when he comments that these specimens have a more rectangular outline, a rather elevated preadductorial node and an extended cristal loop.

The two most consistent differences between the authors material from Ludlow and those valves from Scania figured by Martinsson (1963) involve the lateroventral lobal connection and the cristal loop. In the Ludlow specimens - unlike the Scania material - the edge of the lateroventral lobal connection in tecnomorphs does not droop forward but runs roughly parallel (in lateral view) to the ventral margin of the valve and, furthermore, in most females the crumina does not swing below the valve margin; in addition, the cristal loop in the Ludlow material extends much higher across the dorsal face of the preadductorial node (in lateral view the terminal point of the loop is commonly unsighted). Martinsson places infraspecific value on these differences; having studied specimens from both areas he was of the opinion that the British material lies within the range of variation of that from Scania (see Shaw 1969, p. 55).

Shaw was apparently mistaken in concluding that the Welsh Borderland material lacked ornament "inside" its cristal loop; an arrangement
closely resembling the stretched striae pattern seen on the dorsal region of the preadductorional node of Scanian specimens (Martinsson 1963, figs. 7C, 8) has also been detected in casts from Ludlow. The width of the preadductorional node in the Ludlow specimens is variable, being quite wide in some specimens and comparatively slender in others.

OCCURRENCE: Found in collections made at Ludlow from the following localities.

- Downton Castle Sandstone: Ludford Lane III (loc. 74).
- Ludford Lane II (loc. 73a-c).
- Whitcliffe Beds: Ludford Lane I (loc. 69a, b).

*F. groenvalliana* has previously been cited from the Downton Castle Sandstone of the Ludlow area and the Long Mountain (Shaw 1969), and from the Scout Hill Flags of the Lake District (Shaw 1971a).

In N Europe it has been recorded from Scania, Estonia (Sarv 1968; Kaljo 1970), Ohesaare (Sarv 1971) and in glacial erratics from the floor of the Baltic. The Leighton Shale (Pembroke Formation) of Maine, U.S.A., also possibly holds the species (Martinsson 1967, p. 377). All of these records occur in deposits at present thought to be no older than Downtonian in age.

REMARKS: It should be noted here that a species of *Frostitella* - probably of the *groenvalliana- lebiensis* type - exists as poorly preserved moulds in the Llandeilo area of S Wales, in deposits traditionally considered to be of high Ludlow age. Preservation does not permit a more accurate identification. The material in question - kindly loaned for examination by Dr. D.E. White (I.G.S., London) - has a concomitant beyrichiacean fauna of *Lophoctenella* sp. and *Hemsiella* sp.

Locality data: Road cutting (A476), about three miles SW of Llandeilo, Carmarthenshire; National Grid Reference: SN 61031903.
Specimen numbers (all GSM): DEX 3474, DEX 3474A, DEX 3474B, DEX 3475, DEX 3478, DEX 3478 pars, DEX 3480, DEX 3480 pars, DEX 3485, DEX 3487, DEX 3487 pars.

Frostiella bicristata Shaw, 1969
Pl. E2, figs. 15, 19.

1969 Frostiella bicristata n. sp.; Shaw, p. 55, figs. 2A-G, 3A-D.

HOLOTYPE: A tecnomorphic carapace, GSM 103230, illustrated Shaw 1969, figs. 2E, F; figured herein Pl. E2, fig. 15.

TYPE LOCALITY AND TYPE STRATUM: Norton Lane, Onibury, Shropshire; Temeside Bone Bed, Temeside Shales, Downtonian.

DIAGNOSIS: Frostiella species whose early instars have a pronounced syllobial cusp, which is linked to the preadductorial node via an indistinct U-shaped lobal connection; both node and cusp have cristal loops. Adults have a smaller syllobial cusp lacking a cristal loop, and a well defined lateroventral lobal connection which is confluent from syllobium to anterior lobe. Posterior syllobial lobule weak. In adults the lateral facet of the preadductorial node is reticulate; shell punctate.


MATERIAL: Occurs mostly as moulds. In some specimens parts of the shell remain, giving important ornamental details which help to distinguish the species.

MEASUREMENTS: Approximate hinge length - sulcal height (in microns) of two tecnomorphs from the type locality.

1600-940 (GSM 103230; holotype).
800-470 (GSM 103228; Shaw 1969, fig. 2A).
DISCUSSION: The ontogenetic changes (outlined Shaw 1969, and in the diagnosis above) displayed by this species are unique for the genus. No other Frostiella species has two cristal loops or a syllobial cusp relative in size to that found in the small tecnomorphs of F. bicristata.

OCCURRENCE: Not collected by the writer. In addition to the type locality, Shaw (1969, pp. 67, 68, fig. 8) noted its presence in the Long Mountain succession.

All finds are restricted to the Temeside Shales, Downtonian.

Genus KLOEDENIA Jones & Holl, 1886

TYPE SPECIES: Subsequently designated by Miller, 1892. p. 708; Deyrichia Wilckensiana Jones, 1855, p. 89, pl. V, fig. 18; from a Beyrichienkalk erratic found near Breslau.

BRITISH SPECIES: Kloedenia wilckensiana (Jones, 1855)

DIAGNOSIS: Kloedeniinae with a syllobial cusp and with very reduced lobation. Preadductorail lobe very prominent, with an open cristal loop. Ventral ornamentation of the crumina consisting of three striate ridges the lateral of which may be reduced. (After Martinsson 1963, p. 41).

DISCUSSION: Following Martinsson, the genus is restricted herein to the sense of European usage and does not include the "Kloedenia" of most American literature. A thorough historical and taxonomical review of Kloedenia was given by Martinsson (1963); the type-species and Kloedenia leptosoma Martinsson, 1963 are its only known members. From the published illustrations it is not at all certain that Kloedenia? bacata Abushik, 1970 (from beds of approximately Downton age on Vaygach Is.) belongs to the genus. The specimens from the
British Silurian described by Harper (1940) as Kloedenia obesa sp. n. and K. salopiensis sp. n. are now referred to another subfamily, (see Beyrichia obesa and Beyrichia salopiensis of this paper). The original of Kloedenia intermedia var. marginata Jones & Holl, 1886 (pl. XII, fig. 21) from the Buildwas Beds at Buildwas has not been traced, though it is safe to assume it is not a kloedeniine; this species has to be considered, for the present at least, as a nomen dubium.

As presently understood, Kloedenia differs from Frostiella in having less developed lobation (e.g. the absence of a syllobial cusp), a greater differentiation of its subcruminal striation (into ridges), an ontogenetic development which suggests parthenogenesis (all adult valves have a comparatively swollen anteroventral region), and a different pattern of ornamentation on the preadductorial node.

**OCCURRENCE:** From in situ deposits (Ohesaare Stage) in Estonia and Latvia, the Beyrichienkalk drift material of the Baltic region, the Stonehouse Formation of Nova Scotia, the highest part of the Skala Horizon of Podolia, and subsurface material (Downtonian age) in Poland and Britain.

Kloedenia wilckensiana (Jones, 1855)

Pl. E3, figs. 1-9, 14, 15.

1855 Beyrichia Wilckensiana, nov. sp.; Jones, p. 89, pl. V, figs. 17, 18.

non 1881c B. Wilckensiana, Jones; Jones, p. 343, pl. X, figs. 3, 6.

1886 Kloedenia Wilckensiana (Jones); Jones & Holl, pp. 347, 362.

1892 K. wilkensana; Miller, p. 708.

1933 Kloedenia wilckensiana (Jones); Straw, p. 130, pl. X, fig. 13.

1958 Kloedenia wilckensiana (Jones, 1855); Pribyl, p. 52 (pars).

1960 Kloedenia wilckensiana (Jones); Copeland, p. 99, pl. 23, fig. 17 (non 18).
non 1962 Kloedenia wilckensiana (Jones 1855); Martinsson, p. 352, fig. 201.

1963 Kloedenia wilckensiana (Jones 1855); Martinsson, p. 47, figs. 7F, 30-33.

1965 Kloedenia wilckensiana (Jones 1855); Martinsson, pp. 131, 136, fig. 17.

1967 Kloedenia wilckensiana (Jones)1855; Witwicka, p. 51, figs. 6a-d.

LECTOTYPE: A weathered left valve, BM I 7037; subsequently designated by Pribyl 1958, p. 52 (cf. Martinsson 1965, p. 136); figured by Jones 1855, pl. V, fig. 18 and by Martinsson 1965, p. 136, fig. 17.

TYPE PROVENANCE: The lectotype came from Jones's limestone erratic no. 4; found near Breslau.

DIAGNOSIS: Tumid Kloedenia species with two well developed ridges ventrally on the crumina; the lateral ridge is more or less reduced. Preadductorial lobe short, somewhat inclined backwards, and, owing to the tumid shape of the crumina, set off from the crumina by a distinct depression. Cristal loop present but indistinct. (After Martinsson 1963, p. 48).

DESCRIPTION: A description, based on many hundreds of valves from the Baltic drift erratics, is given in Martinsson 1963, p. 49; the ontogeny of the species and the evidence for the suspected presence of parthenogenesis is also dealt with in this paper.

There are some aspects of the British specimens which warrant description. Of the few specimens it has been possible to prepare completely, two fairly large valves (GSM 51881/4 and GSM 51888/1) show the following features on the ventral part of the lateroventral lobe: a fine, outer ridge (corresponding to the velar edge) which is comparatively short and sited about mid-length; a second, longer and
slightly thicker ridge close to - almost merging posteriorly with -
the edge of the lateroventral lobe. Between this latter edge and
the marginal flange there is a long, narrow depression. Another large,
but less well-preserved, valve (GSM 51881/3) has two broad ridges
on the ventral part of the lateroventral lobe; an inner one along
the edge of the lobe and an outer one of equal length and breadth.
In the large (adult ?) specimen (a left valve, internal mould)
figured by Straw (1933, pl. X, fig. 13) the slight posterior inclination
of the preadductorial lobe and the shallow depression at the base of
its lateral facet, are easily detected. In better preserved specimens
the ridge of the cristal loop is seen to run down the posterior
margin of the preadductorial node.

MATERIAL: Some 20 specimens are present in the three limestone
pieces studied from the Little Missenden borehole. Unfortunately,
the material is very difficult to clean; most valves are buried in
matrix and are commonly exfoliated - leaving internal moulds -
during preparation.

MEASUREMENTS: Hinge length - height over the adductorial sulcus
(from hinge line to ventral edge of the lateroventral lobe) of
some of the larger specimens prepared by the author. Measurements
in microns.

1680 (approximately) - 1220 (GSM 51888/1).
1710-1225 (GSM 51881/4).
1775-1260 (GSM 51881/3).
2050-1400 (approximate measurement; an internal mould).
2150-1620 (approximate measurement; GSM 51881B - the internal
mould figured by Straw, 1933, pl. X, fig. 13 - probably an adult
valve).
DISCUSSION: It should be noted that only 1 - 2 adults were available for study, and then occurring as internal moulds. Nevertheless, the morphology of the preadductor lobe and the ridge pattern on the lateroventral lobe (see above) indicate that the material should be assigned to *K. wilckensiana* rather than to the closely allied *K. leptosoma*.

A particularly interesting feature is the presence of *Nodibeyrichia pustulosa* (= *N. gedanensis*) as the (only) concomitant beyrichiacean to *K. wilckensiana* in the Little Missenden material seen by the author. Martinsson has previously noted (1965, p. 136; 1967, p. 377) that in the Baltic Beyrichienkalk (sensu stricto) only one *Kloedenia* species is found in each limestone erratic, and when such a species occurs with *N. gedanensis* it is always *K. wilckensiana*. The same faunal association is apparently present in Britain. Also present (as in the Baltic) is an *Amygdalella* (*Primitiopsacea*) species.

OCCURRENCE: In Britain only from the Little Missenden borehole, Buckinghamshire. According to Straw (1933, p. 130) *K. wilckensiana* is, "Fairly generally distributed throughout the boring, becoming abundant in the upper 29 ft", i.e. between 1200' and 1229' (the borehole went to a depth of 1264 ft, the last 64 ft of which were assumed to be Palaeozoic rocks). The writer has seen specimens of *K. wilckensiana* on the following slabs of limestone from the borehole.

GSM 51888. From a depth of between 1213' 6" and 12' 9" in the core.
GSM 51881. At 1214 ft (contains Straw's figured specimen).
GSM Pl. 4780. At 1214 ft.
GSM 51884. At 1234 ft.

It is also found in the Stonehouse Formation of Arisaig, Canada, in deposits of Downtonian age in the Chlapowa borehole of Poland, and as a part of the Beyrichienkalk fauna of the Baltic.
Genus KYAMODES Jones, 1888

TYPE SPECIES: Original designation of Jones 1888a, p. 296;

Kyamodes Whidbornei Jones 1888, p. 296, pl. XI, figs. 1-5; from the Devonian near Torquay, Devonshire.

BRITISH SPECIES: Kyamodes whidbornei Jones, 1888

Kyamodes elliptica Jones, 1888

DIAGNOSIS: Beyrichiacea with short sulci, a low, faint preadductorional node tucked against a posteriorly projecting anterior lobal cusp, and a syllobium with a weak posterior cusp behind a more distinct anterior cusp. Velum represented as a bend in the otherwise rather flat valve surface. Most lobal and sulcal elements are concentrated about the mid-dorsum.

DISCUSSION: Dimorphism is, as yet, unknown from the genus but its lobal and sulcal arrangements strongly favour its inclusion within the Beyrichiacea. The genus is important historically having received the attention of most authors reviewing the overall taxonomy of Siluro-Devonian ostracodes. In 1888a, Jones erected the type species and the varieties elliptica and obsolescens, all from the same locality. Ulrich & Bassler (1908) allied Kyamodes to Kloedenia and included within Kyamodes forms such as "Kloedenia" (= Londinia) kiesowi Krause. This view was later maintained by both Ulrich & Bassler (1923) - when they introduced the species "Kyamodes" tricornis and "Kyamodes" swartzi - and by Bassler & Kellett (1934). In his work on the Palaeocopete system, Henningsmoen (1953) included Kyamodes next to Welleria and Kloedenia in the subfamily Beyrichiinae (which encompassed the Kloedeniinae Ulrich & Bassler); later (1954), when dealing more specifically with the Beyrichiacea, he derived Kyamodes
from the Kloedenia wilckensiana group, assigning only the type species and possibly Welleria primitoides Kummerow, 1924 to the genus.

Copeland (1964) agreed with Henningsmoen, and referred "K". swartzi and "K". tricornis to a new genus Pintopsis, which he separated from Kyamodes on its more distinct velum and well developed preadductorional node. Martinsson (1963, p. 20) and Martinsson & Derdan (1965, p. 403) have, however, indicated the closeness of "K". swartzi and "K". tricornis to the kloedeniine Londinia.

I concur with these authors in their comparisons of Kyamodes with certain kloedeniine genera. In fact Kyamodes shows characteristics reminiscent of both beyrichiines and kloedeniines and it is perhaps unwise, without knowledge of the female morphology, to assign it to a particular subfamily. The genus differs from most established members of Kloedeniinae particularly in its diminutive preadductorional node. As suggested by Henningsmoen (1954, p. 32) and Copeland (1964, p. 10) Kyamodes is best restricted to Jones’s original (1888a) taxa, with the possible addition of W. primitoides (from glacial erratic material, N. Germany). The material described by Gross (1969, p. 19, figs. 9a, b) as Kyamodes? sp. has no sulci, and does not belong to the genus.

REMARKS ON THE TYPE MATERIAL: Jones’s specimens have been traced in the Sedg. Mus., Cambridge. Except for the (only) figured specimen of K. Whidbornei var. obsolescens and the smaller of the figured tecnomorphs of K. Whidbornei var. elliptica, all this illustrated material has been positively identified. Details are as follows (all Jones 1888a):

K. Whidbornei gen. et sp. nov., pl. XI, figs. 1-5 = SM H 9447.
K. Whidbornei gen. et sp. nov., pl. XI, fig. 6 = SM H 9448.
K. Whidbornei gen. et sp. nov., pl. XI, fig. 7 = SM H 9449.
K. Whidbornei var. elliptica nov., pl. XI, figs. 10a, b = SM H 9450.
K. Whidbornei var. elliptica nov., pl. XI, fig. 8 = possibly SM H 9451 (only the anterior part of the shell remains).

K. Whidbornei var. obsolescens nov., pl. XI, fig. 9 - now given the number SM H 9452, but specimens not identified.

SM H 9447 occurs as an isolated specimen. Valves SM H 9448-51 are all on one slab. The only additional material consists of a number of valves on the slab SM H 9453. Jones's illustrations proved to be very accurate records of the figured material. All material from Daddy Hole Oy., near Torquay.

OCCURRENCE: Middle Devonian limestone; Devonshire, England.

Kyamodes whidbornei Jones, 1888

Pl. E3, figs. 10-13, 16.

1888a Kyamodes Whidbornei, gen. et sp. nov.; Jones, p. 296, pl. XI, figs. 1-7.

1888a Kyamodes Whidbornei, var. obsolescens, nov.; Jones, p. 297, pl. XI, fig. 9.

1908 Kyamodes whidbornei Jones; Ulrich & Bassler, p. 304, figs. 59, 60.

1923 Kyamodes whidbornei Jones; Ulrich & Bassler, pp. 308, 643, 306, fig. 18 (10).

1934 Kyamodes whidbornei Jones; Bassler & Kellett, p. 371, fig. 9 (10).

1954 Kyamodes whidbornei Jones 1888; Henningsmoen, p. 32.

1964 Kyamodes whidbornei Jones; Copeland, p. 10.

LECTOTYPE: Here designated. A tecnomorphic carapace, SM H 9447, Jones 1888a, pl. XI, figs. 1-5; herein Pl. E3, figs. 10-13, 16.

TYPE LOCALITY AND TYPE STRATUM: Daddy Hole Oy., immediately SW of Meadfoot Beach, Torquay, Devonshire; Middle Devonian limestones.

For further details see Whidborne in Jones 1888a, p. 298; Ussher 1933, p.55; House & Selwood 1966, p. 57.
A visit to the type locality - still accessible at certain tide levels - by the writer failed to produce additional topotype material.

**DIAGNOSIS:** A species of *Kyamodes* with a very deep valve outline and a narrow adductorial sulcus.

**DESCRIPTION:** Based mostly on the selected lectotype. Valve outline very deep with most lobal and sulcal features arranged asymmetrically around the adductorial sulcus and near to the hinge line. Lobes are flat but are not faceted.

The dorsal part of the syllobium is divided into a low, indistinct, posterior "cusp" and a stronger, vertical, anterior cusp which reaches (slightly beyond the anterior lobal cusp) above the hinge line. The adductorial sulcus is narrow (especially ventrally), vertical, and extends to about valve mid-height. In its dorsal regions the adductorial sulcus receives a short, almost obsolete, prenodal sulcus. The preadductorial node is small (approximately half the length of the adductorial sulcus), weakly developed, and is tucked in against the (posteriorly curved) cuspidal region of the anterior lobe. Both anterior syllobial cusp and anterior lobal cusp tend to be somewhat angular.

Ventrally, all of the lobes quickly lose their identity as they merge into the broad, featureless region that links the pre- and postadductorial areas of the valve. The bend in the valve surface, parallel and near to the free margin, is taken to be the equivalent of the velar structure. Valves are seemingly unornamented.

**MATERIAL:** SM H 9447-9 and a few valves (nearly all fragmentary) on the same slab and on slab SM H 9453.
Text-fig. 13  SIZE DISPERSION OF SPECIMENS OF KYAMODES SPECIES

- Unnumbered (on same slab as H 9448-51).
- ? Heteromorph.
- KYAMODES WHIDBORNII
- H 9447
- Lectotype
- H 9448
- Unnumbered (on same slab as H 9448-51)
- KYAMODES ELLIPTICA
- H 9450
- Unnumbered (on slab H 9453).
- Lectotype

All specimens (Sedgwick Museum, Cambridge) on two toptype slabs.
MEASUREMENTS: Hinge length - sulcal height in microns.

1390-1090, left valve (SM H 9448).
1465-1145, right valve of lectotype (SM H 9447).
1755-1360, left valve (SM H 9449).
2080-1760, left valve unnumbered specimen on same slab as SM H 9448-51.

DISCUSSION: Measurements taken from the small amount of extant material clearly indicate the distinction in shape between K. whidbornei and K. elliptica (see text-fig. 13 ). Furthermore K. whidbornei appears to have a narrower adductorial sulcus. Apart from these differences, lobar and sulcal shapes and patterns are closely similar in both species.

After study of Jones's (1888a) illustrations and his toptype material, it is thought possible that K. whidbornei var. obsolescens (figured specimen not found) may represent a worn valve of K. whidbornei sensu stricto; it is included in the synonymy, but with doubt.

OCCURRENCE: Only from the type locality.

Kyamodes elliptica Jones, 1888
Pl. E3, figs. 17, 18.

1888a Kyamodes Whidbornei, var. elliptica, nov.; Jones, p. 297,
pl. XI, figs. 8, 10a, b.

1934 Kyamodes whidbornei elliptica Jones; Bassler & Kellett, p. 371.

LECTOTYPE: Here designated. A teconomorphic left valve, SM H 9450, Jones 1888a, pl. XI, figs. 10a, b; herein Pl. E3, fig. 17.

TYPE LOCALITY AND TYPE STRATUM: Daddy Hole Qy., immediately SW of Meadfoot Beach, "Torquay, Devonshire; Middle Devonian limestone. For further details see Whidborne in Jones 1888a, p. 298; Ussher, 1933, p. 55; House & Selwood 1966, p. 57.
DIAGNOSIS: A species of *Kyamodes* with a long hinge line and a shallow, elongate outline.

DESCRIPTION: General lobal and sulcal arrangement as for *K. whidbornei* (see generic diagnosis). The adductorial sulcus, if anything, is slightly less constricted than in *K. whidbornei*. The velum is represented in adults by a bend in the valve surface; in small instars this bend is more distinctly developed. Lobes are smooth.

MATERIAL: SM II 9450-1 and a few unnumbered specimens on the same slab, and also on slab SM II 9453.

MEASUREMENTS: Hinge length – sulcal height in microns.

- 2390-1320, right valve (on slab SM II 9453).
- 2260-1285, left valve (the lectotype).
- 1395-880, left valve (on same slab as lectotype).

DISCUSSION: Sufficient specimens (of various sizes) are available to establish that var. *elliptica* cannot belong to *K. whidbornei* sensu stricto. *K. elliptica* displays a trend in shape which is the reverse of that present in *K. whidbornei*.

OCCURRENCE: Only from the type locality.
ABSTRACT: The ostracode Anetrobeyrichia schizopyge gen. et sp. nov. is erected from the Silurian of Britain. Although seemingly non-dimorphic, its taxonomic position appears to be within the Beyrichiacea Matthew, 1886, a superfamily hitherto defined as possessing sexual dimorphism of the specialised cruminal type.

INTRODUCTION; THE PROBLEM:

It is more than 135 years (1838-39?; see Spjeldnaes 1966) since the first public indication was made - by the distinguished Swedish worker N.P. Angelin - that a species of a group now called the Beyrichiacea was in fact an "Ostrapod" and, moreover, that this animal (termed by Angelin Battus Kloedeni n. sp. = Craspedobolbina clavata Martinsson, 1962 from Gotland) displayed dimorphism. Many years - and numerous taxa - later, the concept that the Palaeocope superfamily Beyrichiacea is synonymous with ostracode dimorphism of the cruminal type is entrenched in the literature. Further, that the crumina (the domiciliar "brood pouch") housed larvae and that the dimorph (the heteromorph) with this specialised dimorphic structure - developed only during the ultimate mould - is the female has been proved in a number of independent studies (Hessland 1949; Spjeldnaes 1951; Martinsson 1956, 1962), and is now universally accepted.

It is against this background, that evidence from Britain of an apparently non-dimorphic beyrichiacean ostracode contradicts all previous records and statistics. Only non-cruminate specimens are represented (i.e. those valves - males and younger instars - which in dimorphic species lack the dimorphic structure and which are known as tecnomorphs).
The valve terminology adopted throughout follows that proposed by Martinsson (1962). If, as it seems, this ostracode is non-dimorphic, then strictly speaking the term tecnomorph (sensu Jaanusson & Martinsson 1956, pp. 401, 2; Jaanusson 1957, p. 190) should not be used in relation to the present material; if given in this context, the expression will be qualified thus: "tecnomorph" or "tecnomorphic form".

THE EVIDENCE:

The species in question is both ubiquitous and abundant; it is the most commonly encountered single palaeocope in the authors collections from Britain. To date, over 4100 specimens (valves and carapaces) have been picked from the larger size fractions of many samples representing more than 20 localities in the Wenlock and - much more seldom - Ludlow Series of the Welsh Borderland and English W Midlands. The species has been identified in washings from the Wren's Nest and Hurst Hill inliers, the Walsall district of Staffordshire, the Denthall Edge - Wenlock Edge area, the Malverns region, and the Woolhope and Mayhill inliers. Without exception all of the extant specimens are "tecnomorphs"; there is no trace in any of the concomitant ostracode faunas of a possible (cruminate) mate.

This situation is, as far as I am aware, unique amongst the Beyrichiacea. Triebel (1941) was of the opinion that when considering the sex ratio of beyrichiids the cruminate form was numerically inferior to the non-cruminate dimorph - which, incidentally, he (together with Schmidt 1941) believed to be the female (sic). Martinsson (1956, pp. 13-16) in an extensive investigation concerning the ontogeny of some of the magnificently preserved Silurian palaeocopes on Gotland, recorded that the sex ratios in the final instar for three of the species studied (one beyrichiacean and two primitiopsaceans) was approximately 50:50, and for a fourth species (a primitiopsacean) was 30:70 (male: female). Jaanusson & Martinsson (1956) reported a sex ratio of about 50:50
for the Gotland hollinid Triemilomatella prisca Jaanusson & Martinsson, 1956. In rejecting views similar to those proposed by Triebel, Martinsson concluded (1962, p. 84) that that author must have embraced subadult tecnomorphs in the count; he states, "A calculation based on metric analysis of Craspedobolbina clavata gave the ratios 50:50 and 51:49, and a rather similar distribution of the sexes seems to be normal in palaeocope ostracodes." By comparison, the sex ratio for recent ostracodes is summarised by van Morkhoven (1962, p. 94) thus: "The males of certain forms are extremely rare; occasionally, however, there are about equal numbers of the two sexes, or very rarely a preponderance of males, but in the large majority of cases the females are about three to ten times as abundant as the males."

Of course, there are beyrichiacean species elsewhere which are known from tecnomorphic valves only. In such cases, however, the total amount of material is itself very small (for example, fifteen complete and other fragmentary valves comprise the extant material of the American beyrichiine Tikiopsis denticulata Berdan, 1972) and in no way approaches the numerical and distributional situation observed in the British species.

It is also worthy of note that the reverse phenomenon - parthenogenesis - is documented or suggested for a few palaeocope taxa. They include: the beyrichiaceans Huntonella bransoni Lundin, 1968 (Craspedobolbinidae; see Lundin 1968, pp. 24, 25), Kloedenia leptosoma Martinsson, 1963 (Kloedeniinae; see Martinsson 1963, pp. 17-19, 41-47), and Kloedenia wilckensiana (Jones, 1855) (see Martinsson 1963, pp. 47-52) and the primitiopsacean Clavofabella reticristata (Jones, 1888) (see Martinsson 1956, pp. 16, 29). In each case the final instar consists of cruminate (or, as in C. reticristata, dolonate) specimens only.
POSSIBLE INTERPRETATIONS:

1. Sexes confused?: Could the non-cruminate adult beyrichiacean be the female?

   As discussed in the "Introduction" above, the weight of evidence now falls overwhelmingly against this hypothesis.

2. Collecting failure?: Many tens of pounds of material was processed. In most localities spot samples were collected from various points on the face/section exposed. Any possible error in human vigilance during the picking process is considered unlikely, considering over 4000 specimens of *A. schizopyge* alone were extracted from the samples in question.

3. Separation of dimorphs: Could the missing females have inhabited a geographical or ecological region distinct from that of their partners?

   An analogy may be found in the well known case of the Recent Myodocopid *Philomedes globosa*, the females of which live in the muddy benthos and ascend (over 100 fathoms) but once, to meet the always planktonic male for the copulatory act. Triebel (1941, p. 362) and Kesling (1952, p. 266) have previously indicated that some palaeocope dimorphs may be adapted for life in separate biotopes - a suggestion which has found some acceptance with Henningsmoen (1965, p. 356), but which was considered unlikely by Hessland (1949, p. 128). Almost all of the finds (see "Occurrence" below) of the British species occur in the shelf facies of the Wenlock Limestone, formed under shallow marine conditions (cf. Scoffin 1971, for details of depositional environment). Perhaps the females lived in the deeper, basinal environment which existed to the west of the shelf and slope during mid-Silurian times?

   This interpretation, although possible, is considered untenable for the case under review. It is thought extremely probable, in view of the numbers involved, that at least a few of the females would be preserved in the ecological niche of the male.
4. Taxonomic error: Is there an alternative group of palaeocopes which would accommodate the species?

The abundant material at hand permits an accurate description of the species to be made. The valves strikingly display all the classic characteristics (velum and marginal structures; syllobium, preadductorional node and anterior lobe; adductorial sulcus and prenodal sulcus) one could expect to find in a (lobate) beyrichiacean tecnomorph and, furthermore, contain no feature incompatible with the traditional concept of the group. This is to be contrasted with the obvious differences in both lobal and adventral structures between this species and supposed and confirmed cases of non-dimorphic palaeocopes; the species is not thought to show any close morphological affinities to groups such as the bassleratiides, quadrijugatorids, kirkbyaceans, drepanellaceans, and leperditellaceans.

It has been widely recognised (Swartz 1936; Henningsmoen 1953, pp. 194, 195; Jaanusson 1957, pp. 215, 216, 1966, pp. 67; Kesling 1969, p. 309) that the lobal patterns of many palaeocope taxa are subject to homeomorphy, and that it is the presence and type of dimorphism which expresses truer natural relationships; as Kesling (op. cit.) has stated in this context, lobation and ornamentation are "secondary to dimorphism". It is always possible therefore that convergent or parallel evolution has produced a remarkably successful example of homemorphy involving trends in both lobal and adventral structures; there are, however, no obvious candidates for the position of ancestor.

On morphological grounds there seems little margin for manoeuvre; the "tecnomorphs" cannot reasonably be included in any existing superfamily other than the Beyrichiacea.

5. An exception to the rule?: The exclusion from the Beyrichiacea of this species would seem to necessitate invoking a new higher taxon for its reception. While maintaining the established concept of the Beyrichiacea, this course of action is not quite in agreement with the
principles of evolutionary classification (cf. Mayr 1969, pp. 76, 77).

Alternatively, the balance of evidence suggests that here we have a unique beyrichiacean ostracode - one which has forsaken the formation of cruminae and the care of its brood therein. The reason for such an abandonment or rather non-development, let alone the physiological and phylogenetic paths for its accomplishment, remain speculative.

SYSTEMATIC PALAEOIgTOLOGY:

Superfamily BEYRICHIACEA Matthew, 1886
Family BEYRICHIIDAE Matthew, 1886

Genus AMETROBEYRICHIA gen. nov.

DERIVATION OF THE NAME: From the Greek *metra*, a womb, and the generic name *Beyrichia*; alluding to the absence of cruminae. Gender, feminine.

TYPE SPECIES: *Ametrobeyrichia schizopyge* sp. nov., Pl. Pl , fig. 8 ; from the Silurian of England.

SPECIES: Only the type species.

DIAGNOSIS: Beyrichiidae in which cruminae are absent.

DISCUSSION: The task of classifying further this species is not helped by the fact that heavy reliance is normally placed on the morphology of the crumina when deciding relationships within the beyrichiacea. Fortunately the type of subcruminal morphology expressed in each subfamily is to some extent correlated with lobal, velar and ornamental arrangements. In this respect *A. schizopyge* bears closest resemblance to the beyriiines, though in certain features a favourable comparison to the genus *Sleia* (Amphitoxotidinae) can similarly be made (cf. the form and isolation of the anterior lobe and preadductorial node, the relative prominence of the calcarine element, and the occurrence of a syllobial groove).
It is not too difficult to relate features of *A. schizopyge* to conditions in the beyrichiines *Plicibeyrichia*, *Gannibeyrichia*, and *Navibeyrichia* (established by Martinsson, 1962). The lateroventral lobe of the latter series is essentially an extension involving the slender calcarine lobule or plica below, again, a prominent syllobial groove. Other features in common with these genera include outline (cf. *Gannibeyrichia*), velar morphology (ridge-like with an "ornamental thickening", and traceable from the anterocardinal, to the posterocardinal corner; cf. *Plicibeyrichia* and *Gannibeyrichia*), ornamentation (a sparse verrucosity or tuberculation), and the appearance of the preadductorial node.

Much of the carapace morphology of *A. schizopyge* - for instance, the isolated anterior lobe, the syllobial lobules and sulcule - also recalls patterns in *Neobeyrichia* (cf. *N. lauensis* (Kiesow, 1888)).

**OCCURRENCE:** So far, only from Welsh Borderland & Central England; mid-Silurian.

*Ametrobeyrichia schizopyge* sp. nov.

Pl. F1, figs. 1-9; Pl. F2, figs. 1-8.

1886 *Beyrichia Kloedeni*, var. *subtorosa*, Jones; Jones & Holl,
p. 353, pl. XII, figs. 6, 7.

**DERIVATION OF THE NAME:** From the Greek *schizo*, split, and *pyge*, rump; alluding to the conspicuous division of the posterior lobe.

**HOLOTYPE:** A left valve, DAS 47358; Pl. F1, fig. 8.

**TYPE LOCALITY AND TYPE STRATUM:** The large, steeply dipping face at the old workings on the W side of Lincoln Hill, approximately 250 m N of the R. Severn and 500 m NW of the bridge at Ironbridge, N Shropshire, England.

**DIAGNOSIS:** As for the genus.
DESCRIPTION: Valves are preplete, and lack velar restrictions. The anterior lobe is long, slender, and has a cusp above the hinge line equal in height to the syllobial cusp. The ventral part of the anterior lobe swings backward and terminates abruptly, below the prenodal sulcus. The syllobium is divided into two parts by a conspicuous diagonal groove, which begins (anteriorly) opposite the base of the knob-like preadductorial node and ends (posteriorly) high up on the posterodorsal face of the lobe. Below the syllobial groove there is a long, fairly narrow, fold-like lobule whose trend - like that of the anterior lobe - is parallel to the adjacent section of the velum. The dorsal half of the syllobium is ridge-like, with the crest running from the posterodorsal edge of the groove to the tip of the cusp. In front of this crest there is a wide lateral facet forming the main element of the dorsal part of the lobe and sloping gradually towards the adductorial sulcus; posteriorly the ridge is sharply defined, dropping abruptly to a small posterodorsal syllobial lobule.

The sulci are long and are of equal width. The adductorial sulcus is connected with the prenodal sulcus below the preadductorial node, and both have access to the proximal region of the velum via the breach between anterior lobe and syllobium. There is no depression as such in the anteroventral region of the valve.

The velum is traced in a gentle curve from posterior to anterior cardinal corners; it is narrow, has a thickly rolled edge, and adjacent to the lobes is concave. A toric ridge hugs the ventral sections of the velar edge. Each valve has a row of tiny tubercle-like processes along the contact margin; in a few well preserved valves (e.g. at Whitman's Hill) these processes are seen to extend into wider, frill-like vertical marginal structures.
Small, sparse verrucae are characteristically developed on the syllobium, particularly posterodorsally, though their total absence is not too unusual. Ornament is not normally present on the other lobes. Occasionally (e.g. in some of the Hobbs Ridge and Whitman's Hill valves) one of the larger tubercles may assume the form and position of a diminutive posterior syllobial cusp.

The hinge structure is of a type similar to that generally found in beyrichiaceans (cf. Martinsson 1962, pp. 65-68, 75, figs. 16, 17, 20 & 1963, pp. 61, 62, figs. 35, 36; Adamczak 1968, p. 15). The hinge line is straight and consists in the right valve of a main groove of fairly constant width, bordered dorsally by a narrow ridge, which in turn is bounded by a very fine second groove. This upper groove is almost obsolete in its central region but becomes very slightly wider towards the cardinal corners. The hinge of the left valve, consists mostly of a single ridge; towards the cardinal corners, this ridge appears (in some specimens at least) to be weakly divided by a very faint groove. The covering frill of the left valve overlaps the right valve around the contact margin. The right valve has an extra-marginal shelf which compliments the contact groove of the left valve.

All valves collected, regardless of size, have essentially the same basic morphology as described above. Attempts at plotting the hinge length - sulcal height measurements for some of the more abundant, better preserved "populations" have not produced clearly defined growth stages (cf. Martinsson 1962, pp. 122, 123 for possible explanations of such dispersion patterns). The plots give no reason to suppose that a dimorphism involving merely size differences could be present.

MATERIAL: Single valves and carapaces totalling 4116 specimens; moderately well to excellently preserved. All but a few valves represent adult and late stage instars. Almost all samples produced over
ten specimens, with at least 100 valves collected from each of the localities Lincoln Hill, Harley Hill, Wren's Nest, Hobbs Ridge, Harley Hill Road, Crofts Farm, Tickwood and Benthall Edge East.

MEASUREMENTS: Hinge length - sulcal height (including velar width) in microns of some of the larger specimens (left and right valves) from representative localities. All Wenlock Limestone except Stretton Westwood (= basal Elton Beds).


DISCUSSION: Considering the large amount of material at hand, this species is noteworthy for its lack of variation in carapace morphology, other than that affecting ornamentation.

The species has previously been treated in a paper by Jones & Holl (1886 pp. 353, 354, pl. XII, figs. 6, 7) under the name "Beyrichia Kloedeni, var. subtorosa Jones". Beyrichia subtorosa Jones, 1869 was erected (Jones 1869, pp. 12, 14, figs. 10a, b, = male and female valves) on, "internal casts from Upper Ludlow Shales near Kingston and Aymestry", the Welsh Borderland. A search was made (particularly in the Jones collection at the British Museum) for the types, but with no success; they must be presumed lost. In the absence of any further
descriptive clue to its identity, this otherwise forgotten taxon must be declared a nomen dubium. There is, in any case, no likelihood of subtorosa Jones itself proving conspecific with the present material in view of its much later stratigraphic occurrence.

Repository details of figured and referred specimens (all B. kloedeni var. subtorosa Jones of Jones & Holl 1886, p. 354) now identified with A. schizopyge:

1. Vine coll. no. XLVI (Pl. XII, fig. 6), from Tickwood Beds, N Shropshire = BM I 1953 (left valve).

2. Smith coll. no. 34 (Pl. XII, fig. 7), from Silurian at Woolhope = BM I 2384 (left valve, only posterodorsal fragment now remaining). See also no. 5 below.

3. Smith coll. no. 17, from "Blue Holes, Rushal Canal, Walsall" (cf. loc. 26 herein, Daw End, Staffs; Wenlock Shale) = slide BM I 2376 (4 valves).

4. Smith coll. no. 32, from Silurian at "Stoke-Saye" (= Stokesay) Craven Arms, Shropshire = slide BM I 2382 (seven specimens).

5. Smith coll. no. 34 (part), from Silurian at Woolhope = slide BM IN 52517 (eight specimens).

6. Smith coll. no. 31, from Wenlock Shale at "Railway cutting, side of Severn, Ironbridge", N Shropshire = slide BM I 2381 (three of six valves).

OCCURRENCE: The Welsh Borderland and W Midlands of England; Wenlock and lowermost part of the Ludlow Series.

Elton Beds: Stretton Westwood (loc. 60).

Wenlock Limestone: Wren's Nest (locs. 27a-f).

   Lincoln Hill (locs. 49a-c).
   Gleedon Hill (loc. 50).
   Harley Hill Qy. (loc. 51).
   Coates Qy. (locs. 53a, b).
Parkwood (loc. 22).
Gold Hill Farm (loc. 21).
Whitman's Hill (locs. 19a, b).
Hobbs Ridge (locs. 15a-c).
Little Hill (locs. 17a-d).
Old Farm (loc. 16).
Hurst Hill (loc. 28).
Benthall Edge, West (loc. 47).
Croft Farm (locs. 18a-d).
Ledbury (loc. 23).
Much Wenlock, Windmill (loc. 54).
Much Wenlock (loc. 55).
Audience Wood (loc. 57).
Harley Hill Road (loc. 48d).

Tickwood Beds: Harley Hill Road (loc. 48c).

Tickwood (locs. 44a-d).
Benthall Edge, East (locs. 43a, b).
Acklands Coppice (locs. 42a, b).

Coalbrookdale Beds: Benthall Edge, Severnside (loc. 39).

_A. schizopyge_ has also been identified in the Jones & Holl/Smith Collections at the Brit. Mus. (Nat. Hist.) from the Wenlock Shale at Walsall, Staffs. (see "Discussion" above).
ABSTRACT:

Material representing intermediary stages in the development of the crumina (= "brood pouch") of the Palaeocope (Ostracoda) superfamily Beyrichiacea Mathew, 1886 is reported for the first time outside the Silurian of Gotland. These very rare valves are illustrated from the Craspedobolbininae, Amphitoxotidinae, and Beyrichiinae; a further specimen may, more doubtfully, represent a similar developmental state in the Treposellinae.

HISTORICAL REVIEW:

The studies of Martinsson (1956, 1960a, 1962) concerning the well preserved Gotland faunas have shown that the origin of the specialised domiciliar pouch (the crumina) in the heteromorphs (females) of beyrichiacean ostracodes is due (in most cases) to a metamorphosis occurring during the ultimate moult and - except in the rare "intermediate stages" such as those specimens described herein - before calcification is rife. Furthermore, trends in the development of the crumina were demonstrated to have fundamental bearing on the classification of the group. The reader is referred to those findings for a detailed background to the present paper and to the works of Jaanusson (1957), Henningsmoen (1965), Adamczk (1968), Kesling (1969) and Martinsson (op. cit.) for information relating to Palaeocope dimorphism and terminology.

Briefly, it was maintained by Martinsson that the order and mechanism of events during this metamorphosis strongly reaffirm the idea (Henningsmoen 1954, 1955; Jaanusson 1957; Kesling 1957a) that the cruminate palaeocopes (Beyrichiacea) - exclusively post-Ordovician - arose from Ordovician palaeocopes with an anteroventral, extradomiciliar pouch (the dolon). In both groups the dimorphic feature (crumina and
dolon respectively) is associated with the adventral structure, the velum; the most obvious candidates for the ancestral group are the (dolone) eurychilinacean ostracodes. The formation of the crumina in primitive beyrichiaceans (e.g. the Craspedobolbininae) was said to "recapitulate essential features in the phylogeny of the Palaeocope branch which comprises, at least, the Eurychilinacea and the Beyrichiacea" (Martinsson 1962, p. 116); here, the metamorphosis largely involves the inflation of anteroventral, intravelar tubules associated, at least in the initial stages, with the development of an atavistic dolonoid pouch. In more advanced members of the superfamily processes within the latter stage are progressively relinquished, and the crumina is now formed by a more direct inflation of the velar fold (as seen in the Amphitoxotidinae) and/or increasingly by an annexation of adjacent sections of the carapace wall (as in the Beyrichiinae and Kloedeniinae).

The sequence of cruminal metamorphosis was determined from very rare valves (estimated by Martinsson 1960, p. 3, at about 1 in 10,000 for adult specimens of *Craspedobolbina clavata*) in which the process has for some reason been interrupted and, moreover, preserved in its various states of development by the somewhat premature onset of calification.

This paper documents the first examples of "intermediary stages in cruminal metamorphosis" from the non-Gotland material. Initial estimates suggest that such valves are rather less scarce in Britain than on Gotland.

**THE BRITISH MATERIAL; DESCRIPTION AND INTERPRETATION:**

1. **SUBFAMILY CRASPEDOBOLBININAE:**

a) *Craspedobolbina (Mitrobeyrichia) impendens* (Haswell, 1865).

Pl. G1, figs. A-F.

One left valve internal mould (DAS M 270) on BM I 2855; dorsal part of valve missing. Lyne Water, the Pentland Hills, Scotland; presumed upper Llandovery age. Adult size; maximum length = c. 1300 microns.
Small dolonoid pouch developed, in lateral view incorporates only a tiny portion of carapace wall, and is some distance from zygal arch. Tubules not seen. Pouch moderately swollen, with well formed dolonoid cavity. Velar ridge traced at least onto the proximal region of both sides of pouch, without constrictions. Distal part of pouch broken off in the cast, but closing flap could not have been large, probably not yet affecting marginal structures. Torus absent.

This specimen is a remarkable compliment to the fossil record; it is the first example of cruminal metamorphosis from mould material. The description is taken from a silicone rubber cast.

Cruminal metamorphosis was interrupted at a fairly early stage. Most of the characteristics of a typical dolonoid pouch (see Martinsson 1962, pp. 92-98) are recognisable. The specimen has not yet reached the stage of flap insertion. Martinsson comments (1962, p. 96) that most of the incompletely developed cruminae recorded from Gotland were calcified at about this juncture. Comparable conditions are illustrated in: Craspedobolbina (Mitrobelichia) clavata (Kolmodin, 1869) (Martinsson 1962, figs. 26:1, 2 & 30A, 31A); C. (M.) variolata Martinsson, 1962 (Martinsson 1962, fig. 26:6); C. (M.) unculifera Martinsson, 1962 (Martinsson 1962, p. 112); C. (Clavobolbina) acuminulata Martinsson 1962 (Martinsson 1962, fig. 27:4). The ridge commonly developed at the base of the velar flap in the Gotland taxa is not discernible in the Scottish valve.

2. SUBFAMILY AMPHITOXOTIDINAE:


One left valve, DAS 47077. From Lincoln Hill (loc. 49c), N Shropshire; Wenlock Limestone. Adult size; hinge length - sulcal height (including velum) = 1045-600 microns.
Pouch is irregular in shape and irregularly inflated; in lateral view consisting of a small node-like inflation just below base of preadductorial node, joined ventrally to a much larger inflation occupying width of velum. Pouch well set off from adjacent areas, but inflated only as high as crest of syllobium. Anterior part of pouch (below prenodal sulcus) virtually undeveloped. No flap or dolonoid cavity. Anterior section of velar ridge joined directly to velar edge across pouch; this edge is weakly curved overall towards margin, with possible faint disturbance at mid-length. Posteriorly, the constriction of the velum is complete. Torus stops abruptly at anterior and posterior margins of pouch. In lateral view, pouch contained within velar outline.

Here a somewhat late intermediary stage is represented. The anterior section of the crumina has failed to inflate and the anterior velar constriction has, consequently, failed to develop. The form of the velar edge on the crumina is not too dissimilar to that found in normally developed females. Similar incompletely formed cruminae are known from *Sleia equestris* Martinsson 1962 (cf. dolonoid stages in Martinsson 1962, fig. 36). The failure of pouch inflation is accredited by Martinsson to the incomplete separation of the outer and inner layers of the velum. As in the Gotland material, the British *Sleia* species lacks a dolonoid cavity.

b) *Tinotoxotis velivola* gen. et sp. nov. Pl. G4 , figs. A-G.

One crumina only (left valve), DAS 47224. Lincoln Hill (loc. 49c), N Shropshire; Wenlock Limestone. Specimen width is approximately equal to that of a normal crumina.

Crumina large, but not fully inflated (cf. normal female crumina). Velar edge crosses the distal region of crumina and as it does so is strongly curved towards valve margin; the central parts of this edge obviously once extended into a small velar flap (now broken away). No cavity.
This crumina is in a fairly advanced developmental state. It shows, however, clear evidence that a vestigial dolonoid flap existed prior to the full expansion of the crumina. In the normal crumina such conditions are translated into a marked admarginal deflection of the velar edge.

c) Unipila repanda gen. et sp. nov. Pl. G5 , figs. A-I.

One incomplete left valve, DAS 47140. From Harley Hill (loc. 48c) near Much Wenlock, Shropshire; Tickwood Beds. Possible adult; height over adductorial sulcus (excluding velum) = 820 microns.

A small, well-formed dolonoid pouch in the region occupied in other tecnomorphs by the anteroventral depression and the adjacent section of the velum. Inflation barely influences the carapace wall, but affects about six velar tubules (cf. with the velum of normal adult tecnomorphs). Distal edge of pouch is curved gently in an admarginal direction and appears to be confluent anteriorly and posteriorly with edges of velum. Toric ridge continues into the region of the shallow dolonoid cavity. Junction between pouch and lobal areas is distinct.

But for the lack of a well developed dolonoid cavity, this intermediary stage displays a conspicuous similarity to the typical early dolonoid pouch of craspedobolbinines. The curved flap is again in evidence across the mature crumina in the form of a strongly deflected velar edge.

d) Sarmatotoxotis phracta gen. et sp. nov. Pl. G6 , figs. A-I.

One right valve, anterior regions of velum missing; DAS 47108. From Harley Hill (loc. 48c) near Much Wenlock, Shropshire; Tickwood Beds. Possible adult; hinge length - sulcal height (including velum) = 1170 - 840 microns.
Anteroventral pouch-like swelling from just below the preadductor node to edge of velum; approximately half the size of normal crumina. Inflation annexes most of the anteroventral tubules and a very narrow strip of the surrounding lobes. Distal margin of pouch continuous with posterior velar edge and is bent over slightly in a ventral direction. Toric ridge continuous into and completely across the very shallow "hollow" formed beneath ventral side of curved velum. Pouch inflated to just greater than crest of syllobium.

The cruminal metamorphosis of this valve has been preserved at a stage similar to c) above. It confirms that all aspects of the dolonoid mechanism are not yet abandoned in the Amphitoxotidinae. On the fully developed crumina this is reflected in the slight mid-length deflection (away from the margin) of the velar edge.

3. SUBFAMILY TREPOSELLINAE:

a) Bolbiprimitia juvenicristata sp. nov. Pl. G2, figs. A-H.

One carapace, DAS 47176. From Tickwood (loc. 44d), near Much Wenlock, N Shropshire; Tickwood Beds, Wenlock Series. Possible adult; hinge length - sulcal height (including velum) = 900-630 microns.

On right valve only of a carapace, a distinct posteroventral swelling affecting a short section of velum and narrow zone of adjacent syllobium. Distal boundary of the inflation is continuous with the velar edge, and is slightly extended venterolaterally in a vaguely flap-like manner. No cavity on ventral side of swelling.

The swelling occurs in an excellently preserved carapace at the position occupied in the normal female crumina by the posterior "treposelline bridge". Moreover, this tumid structure manifests in a striking fashion most of the characteristics normally associated with a typical dolonoid pouch (it lacks only the cavity), and an immediate reaction might be to regard this enigmatic specimen as the first record of an intermediary stage in cruminal metamorphosis from the Treposellinae. However, one or two facts do not agree with known
principles of beyrichiacean dimorphism and may be concluded that the morphology of this unique carapace was influenced by pathological or teratological factors.

Of primary importance is the fact that the swelling is sited posteroventrally; it is now fairly well established that the provenance of the beyrichiacean crumina lies in the anteroventral regions of the valve. Secondly, it might reasonably be expected that in the normal coarse of events the crumina develops simultaneously in both valves of the carapace - rather than diachronously, as would then be the case in this specimen. Teratological abnormalities are very often recognised by their asymmetrical mode of occurrence. The only other known complete carapace (C. clavata) showing interrupted cruminal metamorphosis also has an asymmetrical development of the dolonoid pouches (see Martinsson 1962, p. 112, no. 16); in contrast to the British valve, Martinsson found that, "Both pouches, as well as other parts of the valve ..." had, "... furrows and distortions of pathological origin."

4. SUBFAMILY BEYRICHIINAE:

a) Beyrichia (Beyrichia) clausa Jones & Holl, 1886. Pl. G7 , figs.A-g.

One fragment, the anteroventral part of a right valve, DAS 47225. From Lincoln Hill (loc. 49c), near Ironbridge, N Shropshire; Wenlock limestone. Specimen not measurable.

Extreme anteroventral part of valve wall and nearby region of velar fold are inflated slightly laterally and conspicuously so in a ventral direction. Boundary between incipient crumina and valve wall is considerably distant from base of preadductorional node (cf. conditions in normal females). Nearly all tubercles occuring anteroventrally in other large tecnomorphs can be recognised; lateral surface of the inflation is similarly tuberculate, whereas its distal and ventral regions are finely striate. Ventral side of the inflation, beginning at the margin, has a shallow hollow, (cf. dolonoid "pocket"). Anteroventral part of marginal ridge and contact margin bend sharply in towards the cavity; all nearby marginal features obsolete.
This specimen agrees in essential details with the only other confirmed beyrichiine valve (belonging to *Nodibeyrichia tuberculata* (Klod, 1834)) showing interrupted cruminal metamorphosis. In both cases the feature equivalent to the dolonoid cavity of primitive beyrichiaceans has moved perilously close to the margin. At the same time the adjacent marginal structures lose definition, or are drawn into the orifice and are lost altogether. The relationship between this migration of the "dolonoid pocket" - towards the margin in the Beyrichiidae and away from it in some Craspedobolbiinidae - and those carapace elements which eventually form the crumina is well discussed by Martinsson (1965, pp. 114-117; see also Martinsson & Berdan 1965). Here, the carapace wall obviously plays a much greater role in the metamorphosis than in the other specimens described.

**GENERAL CONCLUSION:**

The British material firmly supports the proposals advanced by Martinsson for the various ontogentic developments of the crumina, and the attendant implications these hold (see introduction) for the ancestry, phylogeny and general classification of the Beyrichiacea. A possible (notable) exception - the treposelline valve - more correctly probably represents a rare example of teratology in the Palaeocopa.
DISTRIBUTION AND AFFINITIES OF BRITISH BEYRICHIACEA

A. DISTRIBUTION:

This section summarizes the geographical and stratigraphical occurrence of beyrichiacean faunas of the British Isles. As with many like palaeontological studies, the known extent and abundance of the faunas is to some degree a reflection of bias in collecting. For example, particular emphasis has been placed— for reasons outlined previously— by the present author on obtaining material from the N Welsh Borderland. More intensive field work in such regions as the Midland Valley of Scotland and the southern Welsh Borderland inliers will doubtless augment the number of recorded beyrichiacean species from Britain. Moreover, having completed the taxonomic revision and established the nature and general succession of beyrichiacean faunas, future collecting can be expected to refine the results presented here concerning the N Welsh Borderland assemblages.

IRELAND: *Beyrichia kloedeni* from the Lower Owenduff Group, Annelid Grit (upper Llandovery, $C_4 - C_5$ age; see McKerrow & Campbell 1960) of Co. Galway is the only confirmed beyrichiacean taxon from Ireland. Bless & Jordan (1971) maintain that *B. hibernica* Jones & Kirkby from the Viséan of Cultra is synonymous with *Coplandella novascotica* and hence represents one of the rare Carboniferous members of the superfamily. Other as yet scarce and indeterminate beyrichiacean material is known in the form of moulds from the Lower Owenduff Group Finny School Beds (upper Llandovery) of Galway, the Silurian of the Anascaul inlier in the Dingle Peninsula and from the Kilbride Formation (upper Llandovery, $C_4 - C_5$ age) of the Kilbride Peninsula, Co. Mayo, Eire.

*Beyrichia kloedeni* is unknown outside its type locality.
SCOTLAND: The species occurring in Scotland are known from Midland Valley successions and, as yet, no taxon is mutual to the inliers in question.

The Pentland Hills has one known species, the upper Llandovery (Telychian) Craspedobolbina impendens. Similarly the Girvan area has but one named species, Beyrichia scotica from the Llandovery (Fronian) Woodburn Formation, though poorly preserved mould material from the Newlands Formation (gregarius Zone) represents the earliest occurrence of (probable) beyrichiacean ostracodes in Britain and the only known occurrence in rocks of middle Llandovery (Idwian) age. A second species of the genus Beyrichia has been identified from Girvan (Knockgardner district) but at present there is insufficient material for formal treatment.

The four species now recorded from the Lesmahagow inlier all occur in the upper part of the Priesthill Group (currently regarded as late Llandoverian, or possibly early Wenlockian; Jennings 1961, Cox et al., 1971). Beyrichia impacifica and Calcaribeyrichia characta occur only in the Blaeberry Formation; Porcarichia venefica has been collected only from the overlying Dunside Formation; Porcarichia fragum ranges from the Blaeberry into the Dunside Formation.

The Scottish fauna is "new"; none of the species from the Midland Valley are known elsewhere, though both Beyrichia and Craspedobolbina do occur in the upper Llandovery of the Welsh Borderland. If the proposed age of the Priesthill Group is correct, C. characta extends significantly the stratigraphic range of the genus (Calcaribeyrichia on Gotland is widely diversified and almost exclusively Ludlovian; in England two species of this genus occur high in the Ludlow).

LAKE DISTRICT: The ostracode succession of the late Leintwardinian to early Downtonian deposits (Underbarrow, Kirkby Moor and Scout Hill Flags) of the Kendal District, Westmorland has recently been described by Shaw (1971a).
EASTERN MENDIPS: **Craspedobolbina vallecula** from shale of Wenlock age is the only species known from the eastern Mendips. Its distribution is confined to this small inlier (but see "Pembrokeshire" below).

TORTWORTH: The composition of the basal Wenlock fauna obtained from Tortworth is particularly interesting and contrasts with the Beyrichiacea known from correlative horizons in Britain. Its ten known species, are unique to the inlier though congeneric material of **Parasleia** and **Undipila** is found at approximately similar Wenlockian horizons in the English Midlands and N Welsh Borderlands respectively, while another Tortworth Wenlockian species (**Undipila cortinata**) shows close affinities to a form found within the (Wenlockian) Coralliferous "Series" of Pembrokeshire. In the Telychian of Tortworth there are two known species, one of them new, and both probably referable to **Craspedobolbina**. The basal Wenlockian limestone band (Brinkmarsh Beds) contains the earliest British amphitoxotidines and the earliest recorded kloedeniine; the fauna consists of **Parasleia angiportus**, **Parasleia ? grandicalcar**, **Parasleia** sp. A, **Nudista cariticuspis**, **Amphitoxotidinae gen. et sp. nov. A**, **Gen. et sp. nov. A**, and **Ploterichia pileata**. The overlying (Wenlockian) **Pycnactis** band (Brinkmarsh Beds) is characterised by **Parasleia degener** and **Undipila cortinata**.

Should Beyrichiacea be obtained from higher horizons in the Tortworth district it will be interesting to observe whether or not the overall restricted nature of the faunal list is maintained.

PENBROKESHIRE: Two species, **Craspedobolbina turpis** and **Undipila gibba** are described from those parts of the Coralliferous "Series" presumed to be Wenlockian. Significant in this respect is the fact that **C. turpis** compares most closely with **Craspedobolbina vallecula**, a species known only from argillaceous sediments of assumed Wenlock age in the eastern Mendips inlier, while **U. gibba** appears to be very similar to the basal Wenlockian **U. cortinata** from the Tortworth inlier.
The unnamed *Craspedobolbina* (*Craspedobolbina*) species from the Llandovery Series (probably the Uzmaston Beds) of Haverfordwest is, like *C. turpis* and *U. gibba*, only documented at present from Pembrokeshire.

**CENTRAL ENGLAND:** Collections made from three of the four main inliers of the South Staffordshire/Worcestershire district (Dudley Castle inlier excluded) all produced Beyrichiacea.

*Parasleia artemum* and an undescribed amphitoxotidine are as yet confined to the Barr Limestone (Wenlockian) of Walsall. It is worth noting here that all species of the genus *Parasleia* (see "Tortworth" above) are recorded from deposits of Lower Wenlock age. The ubiquitous *Ametrobeyrichia schizopyge* is known from the Wenlock Shale of Walsall. Samples from the Wenlock Shale at Daw End provided only poorly preserved, indeterminate material, though the signs are that intensive collecting at this locality will substantially increase the number of beyrichiacean species from the Walsall district. The Wenlock Limestone exposed at Walsall (Daw End) did not lend itself to sampling procedures.

The Wenlock Limestone at Wren's Nest Hill, Worcestershire has long been renowned for the richness and preservation of its invertebrate fauna; the ostracodes have proved no exception. No less than twenty beyrichiacean taxa are described from the inlier; insufficient material prevents the treatment of a further three species. *Aetholicotoxotis nidicola*, *Tribotoxotis dorsistriata*, *Retisacculus* sp. nov. A and *Garniella ?* sp. nov. A are recorded exclusively from Wren's Nest. Four other species are known elsewhere (Welsh Borderlands) but are likewise confined to the Wenlock Limestone: *Sleia grumula*, *Osmotoxotis phalacra*, *Zorotoxotis medioculta* and *Charitoxotis gravida*. The taxa *Cavisella clithridium*, *Garniella arthrodes*, *Garniella concinna*, and *Sarmatotoxotis phracta* occur in the Wenlock Limestone at the Wren's Nest and are also faunal elements of the Wenlock Limestone and Tickwood Beds of the Welsh Borderland. Forms which are long ranging (Coalbrookdale Beds -
Lower Elton Beds) elsewhere and are present at Wren's Nest include Strepula concentrica, Beyrichia messis, Beyrichia clausa, Undipila repanda, Sleia pauperata, Tinotoxotis velivola and Ametrobeyrichia schizopyge. Sleia troglodytophila, the commonest beyrichiacean species at Wren's Nest extends in the Welsh Borderland from the Wenlock Limestone into the Lower Elton Beds.

All of the species (S. concentrica, G. concinna, G. arthrodes, B. clausa, S. pauperata, S. troglodytophila, T. velivola, S. phracta, A. schizopyge) present in the Wenlock Limestone of the Hurst Hill inlier are mutual to the closely adjacent Wren's Nest inlier to the south and to the N Welsh Borderland further to the west.

The general composition of both the Wren's Nest (excluding its distinctive members) and Hurst Hill faunas is seen to be in accordance with late upper Wenlockian associations known from the Wenlock Edge region.

N WELSH BORDERLANDS (SHROPSHIRE/HEREFORDSHIRE): This section deals essentially with the classic borderland region spanning from Ironbridge N of the R. Severn in the NW to the Ludlow-Leintwardine-Aymestrey area in the SW, and includes the famous scarps of Wenlock Edge and Benthall Edge. The collections were made from many isolated localities; sampling from the Llandovery and Wenlock Series was concentrated mostly on the Wenlock Edge-Benthall Edge-Ironbridge area, and that from the Ludlow Series from the region of the Ludlow anticline. Key references providing stratigraphical and lithological control for the localities samples are mostly given in Cocks et al. (1971) (see also appendix 1 herein). With the exception of the Downtonian elements (Shaw 1969) the distribution of the beyrichiacean faunas of this important type region are here outlined essentially for the first time. Future work will be aimed at both filling in gaps, by collecting from those parts of the succession not yet sampled (e.g. the Middle and Upper Elton Beds), and at refining the picture
presented here of particularly the Wenlockian faunas, which to date have furnished a much greater number of species than those faunas of the Llandovery or Ludlow Series of the region.

1. Llandovery Series:

The first known occurrence of a Welsh Borderland beyrichiacean species, Craspedobolbina hipposiderus, comes from near the base (topmost Fronian) of the Hughley Shales. This species together with Craspedobolbina glabra, Stroterobolbina floribunda, Beyrichia salopiensis and Beyrichia obesa is also a characteristic element of the top part (mid-late Telychian) of the Hughley Shales.

There is a striking faunal discontinuity with the overlying Wenlock Series, all five Hughley Shale species being confined to that formation.

No member of this late Llandovery fauna is known from outside the region in question.

2. Wenlock Series:

The original divisions of Davidson and Maw (1881) have been absorbed with minor modification (Pocock et al. 1938) into modern terminology. The (lower) Wenlock Shale Formation consists of three members, in ascending order, the Buildwas Beds, Coalbrookdale Beds and Tickwood Beds. Shergold and Bassett (1970) reappraised the facies and faunas of the overlying Wenlock Limestone Formation. The usage of the term Tickwood Beds herein follows that of the latter authors (cf. usage of Greig et al., 1968).

Opinions differ as to whether the Buildwas Beds in N Shropshire - historically regarded as the type area of the Wenlock Series - span the full complement of lower Wenlock standard graptolite zones as known elsewhere. Cocks and Rickards (1969) maintain that possibly all of the graptolite zones may be represented; Bassett (in Cocks & Rickards 1969) suggests that the age of the Buildwas Beds is probably slightly younger than the (lowest Wenlockian) centrifugus Zone (if correct this would, of course, place the described Tortworth fauna slightly older than those
Text-fig. 14. STRATIGRAPHICAL DISTRIBUTION OF BEYRICHIAECA IN THE WENLOCK EDGE - LUDLOW REGION
(Temeside Shale fauna from Shaw 1969; Zsagena and S. anchon records from Abberley Hills)
- 367-
taxa from the N Shropshire Buildwas Beds).

Samples from the Buildwas Beds generally are prolific in ostracodes but the faunas are dominated by both non-palaeocopes and non-beyrichiacean Palaeocopes - only two beyrichiacean species being present. *Craspedobolbina interrupta* is diagnostic of (the lower part of) the member; *Dictyobolbina incuspidata* is recorded from near the top of the Buildwas Beds. To reiterate, there are no Llandovery remnants found in the Wenlockian.

In common with other fossil groups the beyrichiaceae are seemingly not abundant for most of the Coalbrookdale Bed (mudstone) sequence. A single species, the transient *Dictyobolbina incuspidata*, is known from the basal part of the Coalbrookdale Beds though a significant fauna of undescribed non-palaeocopes is also evident from the latter horizon.

A distinctive group consisting of *Equicastanea lappacea*, *Undipila subspissa* and *Tropidotoxotis arga* - the first amphitoxotidines of the area - enter the succession in the upper part of the Coalbrookdale Beds. At the top of the Coalbrookdale Beds these three species encountered a significant number of other species - a faunal change heralding a large assemblage which essentially continues throughout the Tickwood Beds, the Wenlock Limestone Formation and, with modifications, into the lower Elton Beds (Ludlovian) above. A total of 23 species are known in that part of the sequence which spans from the top of the Coalbrookdale Beds to the top of the Wenlock Series (Wenlock Limestone). The Tickwood Beds contain 18 species; 61% of this fauna is in common with the top of the Coalbrookdale Beds, and 77% is mutual with the Wenlock Limestone. Of the 17 species found in the Wenlock Limestone, almost 50% range through to the Lower Elton Beds; furthermore, no new elements are introduced at this lowermost Ludlovian horizon. This picture of Wenlock/Ludlow faunal continuity corroborates the idea of the essentially 'Wenlockian' nature of the Lower Elton Beds along the Wenlock Edge region (Shergold & Bassett 1970) and contrasts sharply with the beyrichiacean ostracode changes (outlined above) at the Llandovery/Wenlock boundary of the region.
Undipila subspissa (as defined herein) is known only from the upper part of the Coalbrookdale Beds. Equicastanea lappacea, Tropidotoxotis arga and (probably) Tinotoxotis praegnans extend from the latter horizon only into the Tickwood Beds. Gongylostonyx exaggeratus occurs in the top of the Coalbrookdale Beds, the Tickwood Beds and the Wenlock Limestone, while a number of fairly long ranging elements (Strepula concentrica - the oldest British treposelline, Beyrichia messis, Sleia pauperata, Tinotoxotis velivola, Beyrichia clausa, Undipila repanda and the ubiquitous Ametrobeyrichia schizopyge) extend through the same horizons and into the Elton Beds. The species Cavisella clithridium, Bolbiprimitia juventicristata, Garniella concinna, Garniella arthrodes and Strepula ? sp. nov. A occur in samples from the Tickwood Beds and Wenlock Limestone only. Two comparatively scarce forms, Sleia grumula and Amphitoxotidinae (gen. nov. ?) sp. nov. B are unrecorded outside the Wenlock Limestone. Sleia trogodytophila is present in both Wenlock Limestone and Lower Elton Beds.

3. Ludlow Series:

Knowledge of all the Ludlovian faunas of the area are not yet complete. Within the time available, the policy has been to collect across the upper and lower boundaries of the Series and from the middle of the Series. In this way at least a more balanced overall assessment of the composition of Ludlovian faunas can be attempted.

The typical 'Wenlockian' aspect of the (basal) Lower Elton Beyrichiacea has been discussed (above). Substantiating this point one should note the occurrence (from one locality at Millichope) in the high Lower Elton Beds of a fauna consisting of Tinotoxotis velivola, Undipila repanda ? and Beyrichia clausa ? The Middle and Upper Elton Beds, and the Bringewood Beds of the area are uncollected. However, the Aymestry Limestone (Bringewoodian) of the Abberley Hills to the S, has yielded the amphitoxotidines Zorotoxotis sagena and Sleia ancon.
Extensive collections from the Upper Leintwardinian reveal a rich and distinctive fauna. The association of the very large beyrichiine Neobeyrichia lauensis with beds of Upper Leintwardine age has long since been recognised. Other diagnostic members of this fauna in the N Welsh Borderland include Neobeyrichia confluens, Neobeyrichia scissa, Sleia cf. S. equestris and Atterdagia versiculus. Associated with these species in the Upper Leintwardine Beds are the forms Lophoctenella cf. L. scanensis, the rarer Hemsiella ? sp. nov. B and Amphitoxotidinae sp. nov. C, together with Zorotoxotis convallis (common; known also from the highest Lower Leintwardine Beds) and Calcaribeyrichia tegula (common; present also in the Lower Whitcliffe Beds and highest Lower Leintwardine Beds). The reported occurrences (mostly unrevised) throughout the Welsh Borderland and parts of Wales of N. lauensis has been treated in full in the systematic section of this paper. The Lower Underbarrow Flags of Westmorland has the species N. lauensis, N. scissa, L. cf. L. scanensis and Hemsiella sp. in common with the Upper Leintwardine Beds of the Welsh Borderland and this deposit is concluded (Shaw 1971a) to be of Upper Leintwardine age. One significant anomaly concerns the distribution of N. confluens which in Westmorland.... "in the overwhelming number of cases ..... is indicative of Lake District strata (Upper Underbarrow and Kirkby Moor Flags) which correlate with the Whitcliffian stage" (Shaw 1971, p. 607); its occurrence in the Welsh Borderland is apparently earlier, otherwise some correlative adjustment of the Lake District strata has to be made (Hemsiella sp., L. cf. L. scanensis, and N. lauensis - but not N. scissa - do in fact also range into the Upper Underbarrow Flags; Shaw 1971).

What is known of the Whitcliffian elements indicates that the number of species this stage will yield in N Shropshire is not likely to be very large. The most commonly encountered species is Calcaribeyrichia torosa. A fauna characterised by C. torosa, Lophoctenella sp. and Hemsiella sp. is known from the high Ludlovian of the basinal area to
the W (Frith Quarry, Stappleton; Five Turnings, loc. 14 herein).

Shaw (1969) records *H. maccoyiana* from the Whitcliffian of the Ludlow District, but this has not been observed by the present author.

Particular attention has been given to the topmost Whitcliffian and the transition of its fauna across the boundary into the Downtonian. The important evidence provided by beyrichiacean ostracodes relates to the time gap represented by the Ludlow Bone Bed; it is now conclusively shown to be minimal. *Nodibeyrichia verrucosa* and the internationally important *Londinia arisaigensis* and *Froestiella groenvalliana* - previously recorded (Shaw 1969; see also Martinsson 1963, 1967) in Britain only from the Downtonian - are now known to appear first in the topmost Whitcliffian, immediately below (5-10 cm) the Ludlow Bone Bed at Ludlow itself (Ludford Lane). Concomitant with this fauna is *Londinia cf. L. fissurata* (*L. fissurata* occurs in the Temeside Shales of the Ludlow succession and in the Temeside Shales and Downton Castle Sandstone of the basinal Long Mountain District; Shaw 1969). At present there are no indications that this fauna is introduced into the Whitcliffe succession at any earlier point of time. This new data should not necessitate any major readjustment with regard to international correlation with the level of the Ludlow Bone Bed; rather it confirms the thoughts (Martinsson 1967) on the degree of faunal continuity across, and the brevity of the time interval within, the Ludlow Bone Bed as implied by the Baltic succession of palaeocene faunas.

4. "Downtonian":

As commented on above, a fauna consisting of *N. verrucosa*, *L. arisaigensis* and *F. groenvalliana* is known from the lowest levels in the Downton Castle Sandstone of the Ludlow area. Using the last named taxon an effective correlation has been achieved between the Scout Hill Flags of the Lake District and the Downton Castle Sandstone of the Welsh Borderlands (Shaw 1971a).

The succeeding Temeside Shales (Downtonian) of the Ludlow area contain the association of *Froestiella bicristata*, *Londinia lata* and *Londinia fissurata*. 
All of the Downton Castle Sandstone and Temeside Shale species of the Ludlow succession are recognised, with minor modifications in the order of their appearance, in the Long Mountain region to the West (Shaw 1969).

MAYHILL INLIER: The two Wenlock Limestone localities sampled produced a fauna (e.g. Cavisella clithridium, Sleia pauperata, Gongylostonyx exaggeratus, Ametrobeyrichia schizopyge) in accord with late Wenlockian associations of the Wenlock Edge region. The species Sleia procincta and Pemphibaris malata, known otherwise only from the Wenlock Limestone of the Malverns area, are exceptions to this comparison.

MALVERNS AREA: Samples from the Wenlock Limestone of the Malverns district (see Appendix 1, locs. 18, 19, 21-23) furnished no surprise elements for that formation. It is perhaps worthy of note that the occurrence in the area (Ledbury, loc. 23) of Zorotoxotis medioculta and ? Charitoxotis gravida provided the only (possible) record of these forms outside the type locality at Wren's Nest inlier.

A fauna (Tinotoxotis velivola, Undipila repanda, Tropidotoxotis arga) from the top of the Wenlock Shale at Storridge compares favourably with the faunal succession in N Shropshire.

WOOLHOPE INLIER: The species (Beyrichia messis, Ametrobeyrichia schizopyge, Strepula concentrica, Garniella arthrodes) here collected from the Wenlock Limestone are all characteristic of that formation in N Shropshire.

LITTLE MISSENDEN BOREHOLE: The two species originally described by Straw (1933) from subsurface material of Buckinghamshire are the last undoubted beyrichiaceans in Britain. As revised herein the British material (Kloedenia wilkensiana and Nodibeyrichia pustulosa (= gedanensis)) forms part of the classic Beyrichiankalk fauna of the Baltic and elsewhere. As currently understood (Martinsson 1967) this suggests a mid-late Downtonian age for this section of the borehole.
DEVON: The only known possible beyrichiacean taxon from the Devonian system of Britain is the genus Kyamodes from presumed middle Devonian Limestones of Devon.

B. AFFINITIES AND CORRELATION OF THE BRITISH FAUNA:


With the exception of the very rare Hexopthalmoidinae (known from only one Gotland species) and the Zygobolbinae (found dominantly in N America, with only scarce occurrence in Europe e.g. Noviportia and Slepandia) all of the recognised beyrichiacean subfamilies have representatives in the
British Isles. The most prominently found subfamily is the Amphitoxotidinae (approximately 36% of the British beynichiacean species), followed by the Beyrichiinae (c. 22%), Craspedobolbininae (c. 19%), Treposellinae (c. 12%) and Kloediniinae (c. 11%). The nature of the overall composition of the British Beyrichiacea, together with the prominence the group plays within British Silurian ostracode faunas as a whole, mirrors to a large degree the situation found in the Baltic area (Gotland, East Baltic states), and from a large scale geographical viewpoint these areas - to which may be added Podolia and certain western parts of N America - belong to one faunal province.

Llandovery times in Britain observes the occurrence of both craspedobolinines and beyrichiines, but by the beginning of the Wenlockian, the earliest representatives of the Amphitoxotidinae and - somewhat unexpectedly - Kloediiniinae make an appearance. The occurrence of the earliest known Kloediniine (Ploterichia pileata) in beds of basal Wenlock age presents somewhat of a biostratigraphical anomaly; specifically its nearest comparison is to be found with Podolian ostracodes of the Tchortkov horizon (no older than Dittonian) and, more generally, Kloediniine ostracodes of like morphology characterise European successions of post-Ludlovian age. Forms to bridge the time gap between this primitive "root stock" Kloediniine and the first flourish of Kloediniines (of late Ludlovian-Downtonian deposits) are as yet unknown. With the introduction at the top of the Wenlock Shale of the Treposellinae, all five subfamilies noted above are present within the British Wenlock Series. However, the presence of the Treposellinae is seemingly short-lived, the last British record coming, as yet, from the lowermost Ludlovian.

In Britain the amphitoxotidines are already much diversified in Wenlock times; in contrast, the Amphitoxotidinae on Gotland and in the Baltic region in general occur (except for rare, undescribed cases; Martinsson, pers. comm.) only in post-Wenlock deposits.
Most of the British Ludlovian species are amphitoxotidines and beyrichiines, with an in-rush of kloedeniines at about the level of the Ludlow Bone Bed. No craspedobolbinine has been encountered in British rocks of post-Wenlock age. British Downtonian faunas are monopolised almost exclusively by kloedeniines and some advanced beyrichiines.

Further analysis of the British beyrichiacean fauna reveals that about 43% of the genera are in common with the Baltic region, while at the specific level the amount (including "confer" material) is approximately 12%. The figure for the genus is influenced by the fact that many new members of the Amphitoxotidinae - a subfamily noted for its monotypic genera - occur in Britain. More significant is the fact that none of the Baltic species are found in the British sequence below the Leintwardinian. At the species level at least, there is apparently a provincialism which involves the British and Baltic regions during Llandovery, Wenlock, and lower Ludlow times; accordingly the British beyrichiacean faunas do not assist international correlation at these levels.

The first signs of the integration of faunal elements of the two regions may be correlated to within the Upper Leintwardinian (fauna containing Neobeyrichia lauensis and Neobeyrichia scissa; see Martinsson 1967, Shaw 1971a, and herein). N. scissa is now undoubtedly known to occur in the Upper Leintwardine Beds of the Welsh Borderland and the concomitant Sleia cf. S. equestris and Lophoctenella cf. L. scanensis also indicate the likelihood of the existence of other Gotland/Baltic species at this horizon. At the Upper Leintwardine level (Lower Underbarrow Flags) in the Lake District there is an additional Gotland species, Neobeyrichia nutans; its distribution in the British succession is seemingly slightly later than on Gotland, where it is characteristic of an association immediately preceding the lauensis-scissa association.
The occurrence in the Lake District of the Baltic species *Macrypsilon salterianum* and *Hemsiella maccoviana* has been treated by Shaw (1971a). Mostly by the control provided by the preceding and later faunas of the area, rather than by direct comparison with equivalent Baltic assemblages, the Lake District faunas (in the Kirkby Moor and Upper Underbarrow Flags) containing these two species were concluded to be of Whitcliffian age. The British species *Huttoniella contracta* and *Neobeyrichia confluens* were judged to be important diagnostic elements of this stage in the Lake District; the Welsh Borderland occurrence of *N. confluens* is, so far as is known, at variance with that situation (see under "Welsh Borderland" above).

Immediately preceding the level of the Ludlow Bone Bed (Ludlow/Downton boundary) British faunas take on a truly cosmopolitan aspect (cf. Martinsson 1963, 1963a, 1964). The diagnostic elements present in Britain include *Frostiella groenvalliana* and *Londinia arisaigensis*. As Martinsson (1967, p. 376) has stated these - or closely similar taxa - form part of an association which is present .... "in the Hoburg Bank area (limestone), Pomerania (shale), Scania (sandstones and siltstones with calcareous beds), and the Welsh Borderland (siltstones)..." and which ... "correlates beds at the floor of the Central Baltic with the intermediate Siluro-Devonian fauna in the Leba core, the uppermost Oved-Ramsasa Beds in Scania, and the Downton Castle Sandstone immediately above the Ludlow Bone Bed". The latter entry has now to be adjusted slightly with respect to the new data presented herein concerning the topmost Whitcliffian faunal elements. Faunas indicative of this association are also known from N America (lower part of the Stonehouse Formation of Nova Scotia, and the Leighton Shale Member of the Pembroke Formation of Maine ). Martinsson (1967, 1971) and Shaw (1969) have provided detailed analyses of palaeocene faunas about this horizon.
The occurrence of *Kloedenia wilckensiana* and *Nodibeyrichia pustulosa* (= *gedanensis*) in part of the Little Missenden Borehole, Bucks., the upper part of the type section of the Stonehouse Formation (Nova Scotia), and as elements in the Beyrichienkalk of the Baltic region, permits effective intercontinental correlation between these units (cf. Martinsson 1967, 1971), and implies a mid-late Downtonian age for the British deposits in question.


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After the text of this thesis had been completed and typed the following papers came to the notice of the present author.


An important, first hand reappraisal of the Wenlock series of the type area (Shropshire) has been undertaken by the authors. Briefly, the (lower) Sheinwoodian and (upper) Homerian Stages are introduced to cover the type Wenlock Series. The Homerian is itself divided into the (lower) Whitewell (= *Cyrtograptus lundgreni* Biozone) and (upper) Gleedon (= *Gothograptus nassa* and *Monograptus ludensis* Biozones) Chronozones. These divisions are established using boundary stratotypes. A new map of the area is given and its lithostratigraphical units receive modern terminology: "Buildwas Formation, Coalbrookdale Formation (including a new, upper, Farley Member) and Much Wenlock Limestone Formation." The *centrifugus*, *riccartonensis*, ? *flexilis*, *ellesae*, *lundgreni*, *nassa* and *ludensis* Biozones are demonstrated and, moreover, the graptolite biozone sequence for the Wenlock Series is said to be, "complete in the type area".

The new information and terms provided by Bassett *et al.* will, when published, obviously affect the terminology (e.g. of the lithostratigraphical divisions) used in certain sections of this thesis. However, such information should not modify the chronological order of events as presented herein.

This work describes a silicified fauna from the McCann Hill Chert of E Alaska and the Michelle and Prongs Creek Formations of Yukon Territory; the paper is important in that it provides knowledge about a fauna from the little studied Arctic province. The assemblages include a number of beyrichiacean ostracodes: *Beyrichia* (Beyrichia) *brabbi* sp. nov., *Beyrichia* (Scabribeyrichia) *churkini* sp. nov., *Yukonibeyrichia* *yukonensis* gen et. sp. nov., *Yukonibeyrichia* *solo* sp. nov. (Beyrichiinae); *Treposella* *borealis* sp. nov., *Treposella* sp. cf. *T. lyoni* (Ulrich, 1891) (Treposellinae); *Mesomphalus* sp. (Craspedobolbininae). The concomitant fauna (trilobites, conodonts, brachiopods, tentaculites) suggests an Emsian (late Early Devonian) age for the deposits, but the ostracodes, consisting of many new species, do not resemble published Emsian assemblages. It is concluded by the authors that the total ostracode fauna, "appears to represent a provincial fauna combining relict beyrichiaceans with ancestral hollinaceans and including elements that appeared later in widely separated areas".
A THESIS ENTITLED

THE SUPERFAMILY BEYRICHIACEA (OSTRACODA)

FROM THE SILURIAN AND DEVONIAN SYSTEMS

OF BRITAIN

Submitted for the degree of

DOCTOR OF PHILOSOPHY

IN THE

FACULTY OF SCIENCE

UNIVERSITY OF LEICESTER

BY

DAVID JOHN SIVETER B.Sc.

Volume 2

1974
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APPENDIX 1:

Field localities and fauna

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PLATE Al

Fig. | Page | Craspedobolbina (Mitrobeyrichia) interrupta (Jones, 1887)
--- | --- | ---
1. | 32 | Female carapace, DAS 47233. Buildwas Beds, Buildwas, Shropshire (loc. 35). Lateral (stereo-pair) view, right valve, X25.
5, 7, 8, | | Female carapace, from slide HM A 12379. Buildwas Beds, 10, 11. N Shropshire. From material donated by G. Maw to J. Young. Lateral detail of anteroventral ornament, X50; posterior, right lateral (stereo-pair), anterior and ventral (stereo-pair) views, X25.
6, 13. | | Tecnomorphic right valve, BM I 2214. Buildwas Beds, Maw box. no. 22 (= from Harley Brook; see Vine 1887, p. 233), N Shropshire. Lateral view, X25; lateral detail of pre-adductorial node and anteroventral ornament, X50.
12. | | Lectotype, female carapace, BM IN 27474. Buildwas Beds (Vine coll.), Buildwas, N Shropshire. Figured Martinsson 1965a, fig. 6A. Lateral view, left valve, X25.
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<th>Fig.</th>
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<td>1, 2</td>
<td>Holotype, female left valve, BM IO 4758 (ex. BM I 4514).</td>
</tr>
<tr>
<td>4, 9</td>
<td>Upper Llandovery (probably from Hughley Shales), Shineton, N Shropshire. Coll. Rev. C. Croft. Lateral (stereo-pair), anterior (stereo-pair), ventral (stereo-pair) and posterior views, X35.</td>
</tr>
<tr>
<td>3, 6, 7</td>
<td>Male left valve, BM IO 4757 (ex. BM I 4514). Prepared from same rock chip as holotype. Lateral (stereo-pair), ventral oblique, dorsal, posterior and anterior oblique (stereo-pair) views, X35.</td>
</tr>
<tr>
<td>8, 11</td>
<td></td>
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<tr>
<td>5, 12</td>
<td>Tecnomorphic left valve, DAS 47313. Hughley Shales, Church Preen Brook, Shropshire (loc. 30). Lateral detail of anteroventral lobal and velar ornament, X85; lateral view, X50.</td>
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PLATE A3 (continued)

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<tr>
<th>Fig.</th>
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<td>11.</td>
<td>Silcoset cast of external mould of holotype, female right valve, DAS M 144. Horizon and locality as fig. 8. Lateral view, stereo-pair, x27.</td>
</tr>
<tr>
<td>12, 13</td>
<td>Silcoset cast of external mould of male right valve, DAS M 134.</td>
</tr>
<tr>
<td>16.</td>
<td>Horizon and locality as fig. 8. Lateral (stereo-pair), posterior (stereo-pair) and ventral views, x27.</td>
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<tr>
<td>15.</td>
<td>Silcoset cast of external mould of female left valve, DAS M 139. Horizon and locality as fig. 8. 'Internal' ventral oblique view of crumina, x27.</td>
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Craspedobolbina (Mitrobeyrichia) vallecula sp. nov. 46

PLATE A3

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<th>Fig.</th>
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<td>Craspedobolbina (Mitrobeyrichia) impendens (Haswell, 1865)</td>
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</tbody>
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5. Silcoset cast of external mould of lectotype, a tecnomorphic left valve, now numbered BM I 6300b (on slab BM I 6300a). From area adjacent to N Esk Reservoir (probably Deerhope Burn or Wetherlaw Linn), Pentland Hills; Upper Llandovery. Figured Haswell 1865, pl. III, fig. 11 as Entomis impendens; designated lectotype herein. Lateral view, x45.

6. Silcoset cast of external mould of small tecnomorphic left valve, unnumbered (on same slab as SM A 88251 and A 88250). Horizon and locality as fig. 1. Lateral view, x55.

7. Silcoset cast of external mould of female right valve, GSE EM 1821. Presumed Upper Llandovery deposits, from streams, NE corner of Baddingsgill Reservoir, Pentland Hills. Lateral view, x45.

9. Silcoset cast of external mould of male left valve, unnumbered (on same slab as SM A 88251 and A 88250). Horizon and locality as fig. 1. Lateral view, x55.
PLATE A2

Craspedobolbina (Mitrobeyrichia) hipposiderus sp. nov. 35

1, 2. Holotype, female left valve, BM IO 4758 (ex. BM I 4514).


3, 6, 7. Male left valve, BM IO 4757 (ex. BM I 4514). Prepared from same rock chip as holotype. Lateral (stereo-pair), ventral oblique, dorsal, posterior and anterior oblique (stereo-pair) views, X35.

5, 12. Tecnomorphic left valve, DAS 47313. Hughley Shales, Church Preen Brook, Shropshire (loc. 30). Lateral detail of anteroventral lobal and velar ornament, X85; lateral view, X50.

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<td>Craspedobolbina <em>(Mitrobeyrichia) hipposiderus</em> sp. nov.</td>
<td>35</td>
</tr>
<tr>
<td>1, 2</td>
<td>Holotype, female left valve, BM IO 4758 (ex. BM I 4514).</td>
</tr>
<tr>
<td>4, 9</td>
<td>Upper Llandovery (probably from Hughley Shales), Shineton, N Shropshire. Coll. Rev. C. Croft. Lateral (stereo-pair), anterior (stereo-pair), ventral (stereo-pair) and posterior views, X35.</td>
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<td>3, 6, 7</td>
<td>Male left valve, BM IO 4757 (ex. BM I 4514). Prepared from same rock chip as holotype. Lateral (stereo-pair), ventral oblique, dorsal, posterior and anterior oblique (stereo-pair) views, X35.</td>
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<td>8, 11</td>
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11. Silcoset cast of external mould of holotype, female right valve, DAS M 144. Horizon and locality as fig. 8. Lateral view, stereo-pair, x27.

12, 13. Silcoset cast of external mould of male right valve, DAS M 134.

16. Horizon and locality as fig. 8. Lateral (stereo-pair), posterior (stereo-pair) and ventral views, x27.


15. Silcoset cast of external mould of female left valve, DAS M 139. Horizon and locality as fig. 8. 'Internal' ventral oblique view of crumina, x27.

PLATE A3

Fig.  Page

Craspedobolbina (Mitrobeyrichia) impendens (Haswell, 1865) 40


5. Silcoset cast of external mould of lectotype, a tecnomorphic left valve, now numbered BM I 6300b (on slab BM I 6300a). From area adjacent to N Esk Reservoir (probably Deerhope Burn or Wetherlaw Linn), Pentland Hills; Upper Llandovery. Figured Haswell 1865, pl. III, fig. 11 as Entomis impendens; designated lectotype herein. Lateral view, x45.

6. Silcoset cast of external mould of small tecnomorphic left valve, unnumbered (on same slab as SM A 88251 and A 88250). Horizon and locality as fig. 1. Lateral view, x55.

7. Silcoset cast of external mould of female right valve, GSE EM 1821. Presumed Upper Llandovery deposits, from streams, NE corner of Baddingsgill Reservoir, Pentland Hills. Lateral view, x45.

9. Silcoset cast of external mould of male left valve, unnumbered (on same slab as SM A 88251 and A 88250). Horizon and locality as fig. 1. Lateral view, x55.
Craspedobolbina ? sp. indet. 1

21. Internal mould of female right valve, BM I 6292. Damery Bridge, Tortworth inlier probably from the Damery Beds (Telychian). Figured Jones 1869, p. 14, fig. 6b, as Beyrichia Kloedeni, M' Coy. Lateral view, x8.
PLATE A4 (continued)

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<th>Fig.</th>
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<tr>
<td>Craspedobolbina (Mitrobeyrichia) turpis sp. nov.</td>
<td>49</td>
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</table>

13. Silcoset cast of external mould of female left valve, GSM 26904. From Wooltack, Pembrokeshire; presumed Wenlockian. Figured Jones 1855a, pl. VI, fig. 12 as Beyrichia Kloedeni, M'Coy var. torosa. Lateral view, x12.


Craspedobolbina ? sp. nov. A 52

Fig. 1, 10. Tecnomorphic right valve, DAS 47306. Hughley Shales, Church Preen Brook, N Shropshire (loc. 30). Lateral view, stereo-pair, x50; anterior oblique view of antero-ventral section of velum, showing concentric striae and velar tubules, x110.

2. Small tecnomorphic right valve, DAS 47302. Horizon and locality as fig. 1. Lateral view, x40.

3. Tecnomorphic left valve, DAS 47308. Horizon and locality as fig. 1. Lateral view, x35.

4. Small tecnomorphic left valve, DAS 47311. Horizon and locality as fig. 1. Lateral view, x40.

5. Small tecnomorphic left valve, DAS 47305. Horizon and locality as fig. 1. Lateral view, x40.

6. Crumina (only) of female right valve, DAS 47335. Horizon and locality as fig. 1. Ventral view, x30.

7. Tecnomorphic right valve, DAS 47304. Horizon and locality as fig. 1. Lateral view, x40.


9. Tecnomorphic left valve, DAS 47307. Horizon and locality as fig. 1. Lateral view, x40.

11. Holotype, tecnomorphic left valve, (shell almost completely absent), GSM 70328. Hughley Shales, Church Preen Brook, N Shropshire (cf. loc. 30 herein). Figured Harper 1940, pl. IX, fig. 8 as Beyrichia glabra. Lateral view, x25.
Parasleia artemum sp. nov.

1, 3. Male left valve, DAS 47229. Barr Limestone, Hay Head Farm, Staffordshire (loc. 25). Lateral (stereo-pair) and posterior views, x30.

2. Holotype, female left valve, DAS 47231. Horizon and locality as fig. 1. Lateral view, stereo-pair, x30.

5-7. Small tecnomorphic left valve, DAS 47234. Horizon and locality as fig. 1. Lateral, anterior and ventral views, x22.

4, 9. Female left valve, DAS 47230. Horizon and locality as fig. 1.

11, 12. Posterior, lateral, and ventral views, x30; detail of ridge and dolonoid scar on crumina, x70.

Parasleia degener sp. nov.


10. Holotype, female right valve, DAS 47200. Horizon and locality as fig. 8. Lateral view, x45.


15. Tecnomorphic right valve, DAS 47202. Horizon and locality as fig. 13. Lateral view, x35.

19, 20. Female right valve, DAS 47204. Horizon and locality as fig. 8. Lateral and posterior views, x50.
Parasleia angiportus sp. nov.

1, 5. Tecnomorphic left valve, DAS 47281. Limestone band, base of Brinkmarsh Beds, Brinkmarsh Quarry, Tortworth inlier (loc. 11). Lateral (stereo-pair) and dorsal oblique (note syllobial grooves) views, X45.

2, 10. Small tecnomorphic left valve, DAS 47284. Horizon and locality as fig. 1. Anterior oblique detail of syllobial ornament, X100; lateral view, X45.

3, 7. Holotype, female left valve, DAS 47279. Horizon and locality as fig. 1. Lateral (stereo-pair) and ventral oblique views, X45.

4. Tecnomorphic right valve, DAS 47285. Horizon and locality as fig. 1. Lateral view, X45.

6, 9. Small tecnomorphic left valve, DAS 47282. Horizon and locality as fig. 1. Lateral (stereo-pair) and ventral oblique (note syllobial grooves) views, X45.

11. Female right valve, DAS 47280. Horizon and locality as fig. 1. Lateral view, X45.

8. Female right valve, DAS 47299. Horizon and locality as fig. 1. Lateral view, stereo-pair, X50.

12, 13. Tecnomorphic left valve, DAS 47297. Horizon and locality as fig. 1. Anterior oblique and lateral views, X50.
Fig. | Parasleia ? grandicalcar sp. nov. | Page
--- | --- | ---
1, 2. Tecnomorphic right valve, DAS 47291. Limestone band, base of Brinkmarsh Beds, Brinkmarsh Quarry, Tortworth inlier (loc. 11). Detail of calcarine spine and syllobial groove, dorsal oblique view, x95; lateral view, stereo-pair, x55.
3. Tecnomorphic left valve, DAS 47290. Horizon and locality as fig. 1. Lateral view, x55.
4, 9. Holotype, female right valve, DAS 47292. Horizon and locality as fig. 1. Ventral view of crumina, and lateral view, x45.
6. Female left valve, DAS 47289. Horizon and locality as fig. 1. Lateral view, stereo-pair, x55.

Dictyobolbina incuspidata gen. et sp. nov.

8. Small tecnomorphic carapace, DAS 47246. Horizon and locality as fig. 7. Lateral view, left valve, x35.
10, 11. Holotype, female left valve, DAS 47238. Horizon and locality as fig. 7. Lateral (stereo-pair) and anterior views, x35.
12, 13. Tecnomorphic right valve, DAS 47240. Horizon and locality as fig. 5. Posterior and lateral (stereo-pair) views, x35.
PLATE A8

<table>
<thead>
<tr>
<th>Fig.</th>
<th>Stroterobolbina floribunda gen. et sp. nov.</th>
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<tr>
<td>1, 2, 5.</td>
<td>Silcoset cast of external mould of holotype, male right valve, DAS M 259. Hughley Shales, Devil's Dingle, N Shropshire (loc. 29). Lateral view, stereo-pair, X55; detail of ornament on postero-central region of anterior lobe, stereo-pair, X220; detail of ornament on preadductorional node, X220.</td>
<td>74</td>
</tr>
<tr>
<td>7.</td>
<td>Silcoset cast of external mould of female right valve, DAS M 262. Horizon and locality as fig. 1. Lateral view, X55.</td>
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</tbody>
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? Stroterobolbina floribunda 77

8-11. Female left valve, DAS 47248. Hughley Shales, Church Preen Brook, Shropshire (loc. 30). Posterior (stereo-pair), lateral (stereo-pair), dorsal oblique and ventral views, X55.
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<th>Fig.</th>
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<tbody>
<tr>
<td><strong>1.</strong></td>
<td>Holotype, female left valve, DAS 47327. Wenlock Limestone, Harley Hill Quarry, N Shropshire (loc. 51). Lateral view, stereo-pair, x 55.</td>
</tr>
<tr>
<td><strong>2.</strong></td>
<td>Tecnomorphic carapace, DAS 47142. Tickwood Beds, Harley Hill Road, N Shropshire (loc. 48c). Lateral view, left valve, x 55.</td>
</tr>
<tr>
<td><strong>3, 5.</strong></td>
<td>Female carapace, DAS 47141. Horizon and locality as fig. 2. Left lateral and oblique ventral views, x 55.</td>
</tr>
<tr>
<td><strong>4.</strong></td>
<td>Small tecnomorphic carapace, DAS 47333. Tickwood Beds, Benthall Edge, East (N Shropshire) (loc. 43a). Lateral view, left valve, x 55.</td>
</tr>
<tr>
<td><strong>6.</strong></td>
<td>Male carapace, DAS 47328. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 55.</td>
</tr>
<tr>
<td><strong>7-9.</strong></td>
<td>Female left valve, DAS 47331. Wenlock Limestone, Wren's Nest, Worcestershire (loc. 27c). Anterior, lateral (stereo-pair), posterior and dorsal views, x 55.</td>
</tr>
<tr>
<td><strong>10.</strong></td>
<td>Tecnomorphic carapace, DAS 47334. Horizon and locality as fig. 4. Lateral view, left valve, x 55.</td>
</tr>
<tr>
<td><strong>11.</strong></td>
<td>Small tecnomorphic carapace, DAS 47330. Wenlock Limestone, Hobbs Ridge, May Hill inlier (loc. 15b). Lateral view, left valve, x 55.</td>
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</tbody>
</table>
1, 4, 7. Holotype, female left valve, DAS 47347. Wenlock Limestone, Whitman's Hill, near Storridge (Malverns area), Herefordshire (loc. 19b). Lateral (stereo-pair), dorsal and posterior oblique (stereo-pair) views, x55.

2, 5, 9. Tecnomorphic right valve, DAS 47348. Horizon and locality as fig. 1. Lateral (stereo-pair), dorsal and anterior oblique (stereo-pair) views, x70.

3. Female left valve, DAS 47350. Horizon and locality as fig. 1. Ventral view, x55.

6. Tecnomorphic right valve, DAS 47349. Horizon and locality as fig. 1. Lateral view, x55.

PLATE B3

1, 5, Male carapace, BM IO 4755 (ex. DAS 47100). Wenlock Limestone, Harley Hill Quarry, N Shropshire (loc. 51.). Figured Siveter 1973, pl. 1:8:46, figs. 1-4; pl. 1:8:48, figs. 1, 2. Left lateral (stereo-pair) and ventral oblique views, X55; detail of syllobial cristae and reticulation, X110; dorsal view, X55.

7, 8. Strepula concentrica Jones & Holl, 1886

2-4, 6. Female right valve, BM IO 4756 (ex. DAS 47103). Horizon and locality as fig. 1. Figured Siveter 1973, pl. 1:8:50, fig. 1-3, pl. 1:8:52, figs. 1, 2. Lateral (stereo-pair), posterior, anterior and dorsal views, X55.

9. Female right valve, BM IN 52509 (Smith coll. no. 115). Wenlock Limestone, Lincoln Hill, N Shropshire. Figured Jones & Holl, 1886a, pl. XIII, fig. 7 as Strepula irregularis and designated lectotype of that species by Martinsson 1962, fig. 2E. Lateral view, X45.

10. Small tecnomorphic carapace, BM IN 52507 (Smith coll. no. 115). Horizon and locality as fig. 9. Figured Jones & Holl 1886a, pl. XIII, fig. 2 as Strepula beyrichioides. Designated herein as lectotype of that species. Lateral view, left valve, X55.


12. Lectotype, tecnomorphic carapace, BM IN 52531 (Smith coll. no. 553). Wenlock Series, near Woolhope? Figured Jones & Holl 1886, pl. XIII, fig. 6 as Strepula concentrica and designated lectotype of that species by Martinsson 1962, fig. 2F. Lateral view, left valve, X45.

Garniella concinna (Jones & Holl, 1886)

1, 4. Tecnomorphic right valve, DAS 47147. Wenlock Limestone,

5, 8. Wren's Nest, Worcestershire (loc. 27f). Lateral (stereo-pair), posterior, dorsal and ventral views, x 50.

2, 3. Female right valve, DAS 47110. Tickwood Beds, Harley Hill Road, N Shropshire (loc. 48c). Anterior, lateral (stereo-pair) and ventral views, x 55.

6. Lectotype, small tecnomorphic carapace, BM I 2379 (Smith coll. no. 29). Dormington Wood, the Woolhope inlier. Figured Jones & Holl 1886, pl. XII, figs. 22a, b as Beyrichia concinna. Lateral view, right valve, x 55.

9, 11. Small tecnomorphic right valve, DAS 47149. Wenlock Limestone,

13. Wren's Nest, Worcestershire (loc. 27c). Posterior, lateral and posterior oblique views, x 55.

10. Small tecnomorphic carapace, DAS 47336. Horizon and locality as fig. 9. Right lateral view, stereo-pair, x 55.

12. Tecnomorphic carapace, DAS 47027. Horizon and locality as fig. 9. Lateral view, left valve, x 55.

14. Female right valve, DAS 47148. Horizon and locality as fig. 9. Lateral view, x 50.
### PLATE B5

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<td>Garniellia arthrodes sp. nov.</td>
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2-4, 7. Tecnomorphic left valve, DAS 47151. Horizon and locality as fig. 1. Lateral (stereo-pair), anterior oblique, anterior and ventral views, x40.


8. Small tecnomorphic carapace, BM IN 52527 (Smith coll. no. 54). From Woolhope inlier; Wenlock Limestone? Figured Jones & Holl 1886a, pl. XIV, fig. 14c as Primitia seminulum, Jones. Lateral view, left valve, x60.

11. Small tecnomorphic carapace, BM I 2404 (Smith coll. no. 54). From Woolhope inlier; Wenlock Limestone? Figured Jones & Holl 1886a, pl. XIV, figs. 14a, b as Primitia seminulum, Jones. Lateral view, x40.

12. Small tecnomorphic right valve, DAS 47152. Horizon and locality as fig. 1. Lateral view, x40.

Retisacculus sp. nov. A 106

13. Female right valve, DAS 47037. Wenlock Limestone, Wren's Nest, Worcestershire (loc. 27c). Ventral, anterior, lateral and posterior views, x60.
PLATE B6

Bolbiprimitia juvenicristata sp. nov. 109


2, 3. Female right valve, DAS 47169. Tickwood Beds, Tickwood, 6, 8. N Shropshire (loc. 44d). Anterior (stereo-pair), lateral (stereo-pair), ventral oblique and dorsal views, x 60.

4, 5. Holotype, female right valve, DAS 47168. Horizon and locality as fig. 2. Lateral, posterior (stereo-pair) and ventral views, x 60.

9, 11. Tecnomorphic carapace, DAS 47170. Tickwood Beds, Harley Hill, N Shropshire (loc. 48c). Ventral and right lateral views, x 60.

10. Small tecnomorphic carapace, DAS 47195. Horizon and locality as fig. 1. Left lateral view (showing cristal system), x 45.
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12, 14. Tecnomorphic carapace, BM I 1945 (Vine coll. no. XXXVIII). Tickwood Beds, vicinity of Tickwood, N Shropshire. Figured Jones & Holl 1886, pl. XII, figs. 17a, b as **Bollia uniflexa**. Right lateral (stereo-pair) and ventral views, x40.

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PLATE B7

Strepula ? sp. nov. A  

1. Tecnomorphic carapace, DAS 47352. Wenlock Limestone, 
   Harley Hill Quarry, N Shropshire (loc. 51). Lateral 
   (stereo-pair) view, right valve, x50.

6, 7, 9. Tecnomorphic carapace, DAS 47198. Tickwood Beds, Benthall 
   Edge, East (N Shropshire) (loc. 43a). Dorsal, anterior 
   oblique and right lateral (stereo-pair) views, x50.

Garniella ? sp. nov. A  

2-4, 8. Tecnomorphic right valve, DAS 47153. Wenlock Limestone, 
   Wren's Nest, Worcestershire (loc. 27f). Anterior, 
   posterior, lateral (stereo-pair) and ventral views, x55.

5. Incomplete female right valve, DAS 47038. Wenlock 
   Limestone, Wren’s Nest, Worcestershire (loc. 27c). 
   Lateral view, x40.

   Strepula concentrica (Jones & Holl, 1886)  

10. Female right valve, DAS 47070. Wenlock Limestone, 
    Gleedon Hill, N Shropshire (loc. 50). Lateral view, 
    x35.

"Beyrichia" seminulum Jones, 1855  

11. Silcoset cast of external mould of lectotype, tecno­ 
    morphic left valve, BM I 6367. Town Hill, Montgomery. 
    Figured by Jones 1855a, pl. VI, fig. 24 as Beyrichia 
    seminulum and designated lectotype of that species by 
    Henningsmoen 1954, p. 57. Lateral view, stereo-pair, 
    x30.
PLATE Cl

Sleia pauperata (Jones, 1869) 123

1, 2, 11. Male left valve, DAS 47082. Wenlock Limestone, Lincoln Hill, Shropshire (loc. 49c). Anterior oblique view (showing velar tubules), lateral (stereo-pair) and dorsal views, X45.

3. Female left valve, DAS 47080. Horizon and locality as fig. 1. Lateral view, stereo-pair, X45.

4. Female right valve, BM IN 51763. Wenlock Limestone, Malverns. Figured Jones 1869, p. 14, fig. 11b (plate reversed) as Beyrichia kloedeni var. torosa Jones. Detail of syllobium, preadductorional node, and part of crumina, X60.

5, 6. Female right valve, DAS 47122. Wenlock Limestone, Croft Quarries, Malverns (loc. 18). Lateral and posterior views, X45.

7. Male left valve, DAS 47120. Horizon and locality as fig. 5. Lateral view, X45.

8. Female carapace, DAS 47126. Horizon and locality as fig. 1. Ventral view, stereo-pair, X45.

9, 13. Tecnomorphic carapace, DAS 47124. Horizon and locality as fig. 1. Ventral and lateral views, X45.

10. Female left valve, DAS 47036. Wenlock Limestone, Wren's Nest, Dudley (loc. 27c). Lateral view, X45.

PLATE C2

Sleia grumula sp. nov. 128

1, 2, 5. Holotype, female left valve, DAS 47062. Wenlock Limestone, Wren's Nest, Dudley (loc. 27c). Lateral (stereo-pair), anterior, posterior, ventral and anterior oblique views, X35.

6, 10. Male left valve, DAS 47259. Horizon and locality as fig.1. Lateral view, stereo-pair, X35.

3. Female right valve, DAS 47022. Horizon and locality as fig. 1. Lateral view, X35.


8, 9. Small tecnomorphic right valve, DAS 47260. Horizon and locality as fig. 1. Lateral view, posterior view showing calcarine spine, X35.

13. Female right valve, slightly incomplete, BM I 2359. Wenlock Limestone, Dudley Castle. Figured Jones & Holl, 1886, pl. XII, fig. 1a as Beyrichia tuberculata (Klodan) var. gibbosa Reuter. Lateral view, X35.

Sleia cf. S. equestris Martinsson, 1962 131


Sleia procincta sp. nov.

1, 2, 5, 6. Male right valve, DAS 47219. Wenlock Limestone, Hobbs Ridge, Gloucestershire (loc. 15b). Lateral (stereo-pair), posterior, anterior, and ventral views, X45.

3, 4, 7, 8. Holotype, female left valve, DAS 47218. Wenlock Limestone, Hobbs Ridge (loc. 15a). Lateral (stereo-pair) and posterior views, X45; anterior oblique view, stereo-pair, X40; ventral oblique view, X45.

9. Tecnomorphic right valve, DAS 47226. Horizon and locality as fig. 1. Detail of anterior lobe, X75.

11. Female left valve, DAS 47220. Horizon and locality as fig. 3. Lateral view, X45.

Sleia ancon sp. nov.


12. Female left valve, DAS 47255. Horizon and locality as fig. 10. Ventral oblique view, X40.
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<td>Tecnomorphic right valve, DAS 47253. Horizon and locality as fig. 1. Lateral view, stereo-pair, X40.</td>
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<td>Figured Siveter 1973a, pl. 1:27:148, figs. 2-4. Posterior, lateral (stereo-pair) and ventral views, X45.</td>
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<td>Female right valve, BM IO 5806 (ex. DAS 47024). Horizon and locality as fig. 1. Figured Siveter 1973a, pl. 1:27:146, figs. 2, 3. Anterior oblique, dorsal, lateral (stereo-pair), ventral (crumina) and posterior views, X45.</td>
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<td>Female left valve, BM IN 52504. Wenlock Limestone, Dudley Castle, Dudley. Figured Jones &amp; Holl 1886, pl. XII, fig. 2, as Beyrichia Kloedeni var. granulata Jones. Lateral view, X35.</td>
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<td>Female right valve, BM IO 5805 (ex. DAS 47026). Horizon and locality as fig. 1. Figured Siveter 1973a, pl. 1:27:148, fig. 1. Internal lateral view, X45.</td>
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Equicastanea lappacea gen. et sp. nov. | 141

1, 2. Holotype, female right valve, DAS 47214. Tickwood Beds,

4, 5, 9. Harley Hill Road, N Shropshire (loc. 48a). Anterior
(stereo-pair), lateral (stereo-pair), posterior, ventral and dorsal views, x30.

3, 6, 8. Tecnomorphic carapace, DAS 47190. Coalbrookdale Beds,
Benthall Edge, Severnside (N Shropshire) (loc. 39). Right lateral (stereo-pair), ventral oblique and anterior oblique views, x30.

7. Female right valve, DAS 47213. Horizon and locality as fig. 1.
Detail of crumina, ventral view, x45.

10. Tecnomorphic carapace, DAS 47191. Horizon and locality as fig. 3. Lateral view, left valve, x30.

11. Male right valve, DAS 47320. Horizon and locality as fig. 1. Lateral view, x25.
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Fig.                  Page

Nudista cariticuspis gen. et sp. nov.    152

1, 2. Holotype, female left valve, DAS 47276. Limestone band, base of Brinkmarsh Beds, Brinkmarsh Quarry, Tortworth inlier (loc. 11). Posterior (stereo-pair) and lateral (stereo-pair) views, x45.

3, 8. Tecnomorphic left valve, DAS 47268. Horizon and locality as fig. 1. Lateral (stereo-pair) and anterior oblique (stereo-pair) views, x55.

4. Female right valve, DAS 47269. Horizon and locality as fig. 1. Lateral view, x45.

5, 6. Female right valve, DAS 47273. Horizon and locality as fig. 1. Lateral and posterior views, x45.

7. Female right valve, DAS 47325. Horizon and locality as fig. 1. Ventral view, stereo-pair, x45.

9. Tecnomorphic right valve, DAS 47270. Horizon and locality as fig. 1. Lateral view, x45.

10. Tecnomorphic left valve, DAS 47272. Horizon and locality as fig. 1. Lateral view, x45.

11. Tecnomorphic left valve, DAS 47271. Horizon and locality as fig. 1. Lateral view, x45.
PLATE C7

Fig.                     Page

Tinotoxotis velivola gen. et sp. nov. 145

1, 4. Male left valve, DAS 47316. Wenlock Limestone, Lincoln
      Hill, N Shropshire (loc. 49c). Lateral (stereo-pair)
      and anterior views, x 40.

2, 3, 7, 10. Holotype, female left valve, DAS 47317. Horizon and
    locality as fig. 1. Posterior, lateral (stereo-pair),
    dorsal and ventral oblique views, x 37.

5, 6. Female left valve, DAS 47315. Horizon and locality as
    fig. 1. Lateral and anterior views, x 40.

8. Male left valve, DAS 47314. Horizon and locality as
    fig. 1. Lateral view, x 40.

9. Female right valve (velum and crumina only), DAS 47044.
    Wenlock Limestone, Wren's Nest, Worcestershire (loc. 27c).
    Ventral view of crumina, stereo-pair, x 47.

11, 13. Tecnomorphic left valve, DAS 47158. Tickwood Beds,
    Tickwood, N Shropshire (loc. 44d). Ventral oblique
    and lateral views, x 40.

12. Female right valve, DAS 47362. Lower Elton Beds,
    Millichope, Shropshire (loc. 59). Lateral view, x 37.
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<td>Silcoset cast of external mould of a crumina, DAS M 145.</td>
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<td>Horizon and locality as fig. 9. Lateral view, stereo-pair, x25.</td>
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<td>Silcoset cast of external mould of large tecnomorphic right valve, DAS M 5.</td>
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<td>Horizon and locality as fig. 9. Lateral view, stereo-pair, x22.</td>
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Tinotoxotis praegnans sp. nov. 148


2, 4, 8. Female right valve, DAS 47244. Tickwood Beds, Harley Hill Road, N Shropshire (loc. 48b). Detail (stereo-pair) of crumina, ventral view, x42; anterior and lateral views, x30.

3, 5, 7. Holotype, crushed female carapace, DAS 47104. Horizon and locality as fig. 2. Left lateral (stereo-pair), dorsal oblique and ventral views, x30.

6. Female right valve, DAS 47319. Horizon and locality as fig. 2. Lateral view, x30.

Undipila gibba (Salter, 1848) 168


12. Silcoset cast of external mould of small tecnomorphic left valve, DAS M 27. Horizon and locality as fig. 9. Lateral view, stereo-pair, x25.
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<td>Holotype, female left valve, DAS 47178. Wenlock Limestone,</td>
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<td>Lincoln Hill, N Shropshire (loc. 49c). Posterior, anterior, lateral (stereo-pair), ventral and ventral oblique views, x 40; detail of crumina, ventral view, x 57.</td>
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<td>4-6</td>
<td>Male left valve, DAS 47185. Horizon and locality as fig. 1.</td>
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<td>9, 11</td>
<td>Posterior, anterior, lateral (stereo-pair), ventral oblique and ventral views, x 40.</td>
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<td>Female right valve, DAS 47182. Horizon and locality as fig. 1. Lateral view, x 40.</td>
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<td>13</td>
<td>Tecnomorphic right valve, BM I 2372 (Smith coll. no. 22\textsubscript{5}). Horizon and locality as fig. 1. Figured Jones &amp; Holl 1886, pl. XII, fig. 12 as Beyrichia maccoyiana, Jones. Lateral view, x 40.</td>
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<td>Male left valve, DAS 47186. Tickwood Beds, Harley Hill Road, N Shropshire (loc. 48c). Lateral view, stereo-pair, x 40.</td>
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<td>Female right valve, DAS 47181. Horizon and locality as fig. 14. Lateral view, stereo-pair, x 40.</td>
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<td>Small tecnomorphic carapace, DAS 47187. Horizon and locality as fig. 1.</td>
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Fig. 12, 14. Holotype, female left valve, DAS 47203. Pycnactis band, Brinkmarsh Beds, Brinkmarsh Quarry, Tortworth inlier (loc. 12). Lateral (stereo-pair) and ventral (stereo-pair) views, x 30.

13. Tecnomorphic carapace, DAS 47205. Horizon and general locality as fig. 12. Lateral view, stereo-pair, x 35.

15. Female right valve, DAS 47239. Horizon and locality as fig. 12. Lateral view, x 35.
Undipila subspissa (Jones & Holl, 1886) 162

1, 2. Female carapace, DAS 47192. Coalbrookdale Beds, Coalbrookdale, N Shropshire (loc. 40). Lateral (stereo-pair) and ventral views, x 35.

2-4. Tecnomorphic carapace, one of three conspecific specimens in slide BM I 2370 (Smith coll. no. 20). Coalbrookdale Beds, railway cutting at Coalbrookdale, N Shropshire. Referred by Jones & Holl, 1886, p. 358 to Beyrichia maccoyiana, Jones. Anterior, posterior, lateral (stereo-pair) and ventral views, x 35.

5. Lectotype, tecnomorphic carapace, BM IN 52439 (Vine coll. no. XLIV). Probably Wenlockian, N Shropshire. Figured Jones & Holl 1886, pl. XII, fig. 3 as Beyrichia Kloedeni, M'Coy, var. intermedia, Jones, subvar. subspissa nov.; designated lectotype herein. Lateral view (tilted slightly), x 35.

6. Male carapace, DAS 47326. Horizon and locality as fig. 1. Lateral view, x 35.

9. Tecnomorphic right valve, from slide BM I 2370 (Smith coll. no. 31). Wenlockian, from the railway cutting, S side of R. Severn near Ironbridge, N Shropshire. Referred by Jones & Holl 1886, p. 354 to Beyrichia Kloedeni var. subtorosa Jones. Lateral view, x 35.

**PLATE C11**

1, 4. **Osmotoxotis phalacra** gen. et sp. nov. 175

1, 4. Holotype, female right valve, DAS 47058. Wenlock Limestone, Wren's Nest, Worcestershire (loc. 27d). Lateral (stereopair) and anterior views, x35.


5. **Tecnomic right valve**, DAS 47159. Wenlock Limestone, Ledbury (Malverns area), Herefordshire (loc. 23). Lateral view, x35.

7, 8. Female right valve (anterior part only), DAS 47345. Horizon and locality as fig. 2. 'Internal' ventral oblique and ventral views, x30.

9. Female carapace, DAS 47066. Horizon and locality as fig. 1. Lateral view, left valve, x35.


11. Small tecnomic right valve, DAS 47343. Horizon and locality as fig. 2. Lateral view, x35.

12. Small tecnomic right valve, DAS 47344. Horizon and locality as fig. 10. Lateral view, x35.

**Aetholicotoxotis nidicola** gen. et sp. nov. 172


15. Female right valve, DAS 47057. Horizon and locality as fig. 13. Lateral view, x40.
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Sarmatotoxotis phracta gen. et sp. nov. 178

1-3. Holotype, female right valve, DAS 47163. Wenlock Limestone, Lincoln Hill, N Shropshire (loc. 49c). Anterior (stereo-pair), lateral (stereo-pair), posterior (stereo-pair), ventral (stereo-pair) and dorsal views, x 40.

4. Tecnomorphic right valve, DAS 47363. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 40.

7, 11. Female right valve, DAS 47235. Wenlock Limestone, Croft Farm, Malverns (loc. 18). Lateral (stereo-pair) and dorsal oblique views, x 40.

8. Female right valve, DAS 47165 (scratched along velum-syllobium junction during preparation). Horizon and locality as fig. 1. Lateral view, x 40.

9. Tecnomorphic left valve, DAS 47091. Horizon and locality as fig. 1. Lateral view, x 40.

10. Female right valve, DAS 47164. Horizon and locality as fig. 1. Lateral view, x 40.

12. Female right valve, DAS 47161. Tickwood Beds, Harley Hill Road, Shropshire (loc. 48c). Lateral view, x 40.
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<td>Female right valve, GSM Bi 869/b. From same slab as fig. 1. Lateral, posterior, ventral and anterior views, x 40.</td>
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<td>Silcoset cast of external mould of tecnomorphic left valve, 14, 15. DAS M 221. Upper Leintwardine Beds, Bengry Track, Aymestrey, Herefordshire (loc. 63). Lateral view, stereo-pair, x 35; detail of syllobial ornament, stereo-pair, x 465; detail of preadductorional node, x 80; oblique anterior view, x 35.</td>
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<td>Male left valve, DAS 47137. Wenlock Limestone, Wren's Nest, Worcestershire (loc. 27c). Lateral (stereo-pair), anterior (stereo-pair), dorsal, posterior, ventral and anterior oblique views, x45.</td>
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<td>Holotype, female right valve, DAS 47132. Horizon and locality as fig. 1. Anterior (stereo-pair), lateral (stereo-pair), posterior, ventral (stereo-pair), and dorsal views, x45.</td>
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<td>Female left valve, DAS 47134. Horizon and locality as fig. 1. Lateral view, x45.</td>
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<td>Female left valve, DAS 47042. Horizon and locality as fig. 1. Detail of crumina, ventral oblique view, x70; lateral view, x45.</td>
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<td>Female left valve, DAS 47172. Wenlock Limestone, Ledbury (Malverns area), Herefordshire (loc. 23). Lateral view, x45.</td>
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Zorotoxotis sagena gen. et sp. nov. 192

1, 2. Holotype, female left valve, DAS 47249. Aymestry Limestone, Woodbury Quarry, the Abberley Hills, Worcestershire (loc. 24). Lateral (stereo-pair) and anterior oblique views, x 50.

3-6, 9. Tecnomorphic left valve, DAS 47250. Horizon and locality as fig. 1. Lateral (stereo-pair), posterior, anterior, posterior oblique and ventral views, x 50.

7. Male left valve, DAS 47252. Horizon and locality as fig. 1. Lateral view, x 50.

8. Female carapace, DAS 47251. Horizon and locality as fig. 1. Ventral (stereo-pair) view of right valve crumina, x 55.

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10, 13. Silcoset cast of external mould of female left valve (cuspidal regions missing), DAS M 283. Upper Leintwardine Beds, near Trippleton Farm, Leintwardine, Herefordshire (loc. 68). Ventral view of crumina, and lateral view, x 40.


12, 14. Silcoset cast of holotype, an external mould of a tecnomorphic right valve, DAS M 214. Horizon and locality as fig. 10. Posterior (stereo-pair), ventral and lateral view, x 45.

15. Silcoset cast of external mould of female right valve, DAS M 215. Horizon and locality as fig. 10. Lateral view, x 40.
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Tribotoxotis dorsistriata gen. et sp. nov.  205

1, 2, 6. Holotype, female right valve, DAS 47130. Wenlock Limestone, Wren's Nest, Worcestershire (loc. 27c). Lateral (stereo-pair), anterior and ventral views, x45.

3-5. Tecnomorphic right valve, DAS 47129. Horizon and locality as fig. 1. Posterior, lateral (stereo-pair), anterior oblique, ventral and dorsal views, x45.

7. Tecnomorphic right valve, DAS 47313. Horizon and locality as fig. 1. Lateral view, x45.

12. Female left valve, DAS 47065. Horizon and locality as fig. 1. Lateral view, x40.

Tropidotoxotis arga gen. et sp. nov.  209


11, 14. Tecnomorphic left valve, BM I 2378 (Smith coll. no. 28). Wenlock Shale, old railway cutting, S side of R Severn, near Ironbridge, N Shropshire. Referred by Jones & Holl (1886, p. 358) to Beyrichia Maccoyiana, Jones. Ventral, lateral (stereo-pair), posterior and anterior views, x40.

15. Fragmentary female left valve, (anteroventral part only), DAS 47338. Horizon and locality as fig. 10. Lateral view, x29.

16. Tecnomorphic left valve, DAS 47339. Horizon and locality as fig. 10. Lateral view, x40.
PLATE C17

Charitoxotis gravida gen. et sp. nov. 212

1, 2, 4. Holotype, female left valve, DAS 47323. Wenlock Limestone, 8, 12. Wren's Nest, Worcestershire (loc. 27c). Lateral (stereo-pair), anterior (stereo-pair), ventral oblique and posterior views, x 40; detail of subcruminal ornament, x 70.

3, 5, 6. Tecnomorphic left valve, DAS 47054. Horizon and locality as fig. 1. Lateral (stereo-pair), anterior and ventral views, x 40.

7. Female left valve (crumina and velum only), DAS 47064. Horizon and locality as fig. 1. Ventral view, x 40.

9, 13. Female right valve, DAS 47324. Horizon and locality as fig. 1. Lateral (stereo-pair) and dorsal views, x 40.

10, 11. Tecnomorphic right valve, DAS 47322. Horizon and locality as fig. 1. Lateral and dorsal views, x 40.
Amphitoxotidinae (Incerti Generis) sp. nov. C

10, 11. Silcoset cast of external mould of tecnomorphic left valve, DAS M 227. Upper Leintwardine Beds, Bengry Track, near Aymestrey, Herefordshire (loc. 63). Detail of reticulation on preadductorional node, x 240; lateral view, stereo-pair, x 40.

**Macrypsilon salterianum** (Jones, 1855)


1, 2, 5. Silcoset cast of external mould of male right valve,
DAS M 187. Upper Leintwardine Beds, Trippleton Farm,
Shropshire (loc. 68). Lateral (stereo-pair), posterior
(stereo-pair), and ventral oblique (stereo-pair) views,
x 30.

3. Silcoset cast of external mould of female left valve,
DAS M 189. Horizon and locality as fig. 1. Lateral view,
stereo-pair, x 30.

4, 7. Silcoset cast of external mould of holotype, female right
valve, DAS M 284. Horizon and locality as fig. 1.
Lateral (stereo-pair) and ventral oblique (stereo-pair)
views, x 30.

6. Silcoset cast of external mould of female right valve
(ventral regions only), DAS M 186. Horizon and locality as
fig. 1. Ventral view, stereo-pair, x 30.

8, 13. Female right valve (slightly incomplete), DAS 47355.
Wenlock Limestone, Lincoln Hill, Shropshire (loc. 49c).
Lateral (stereo-pair) and posterior views, x 45.

9, 12. Female carapace (crushed), DAS 47356. Horizon and
locality as fig. 8. Detail of left valve crumina, ventral
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<td>11. Female carapace, DAS 47245. Horizon and locality as fig. 5. Left lateral view, x 55.</td>
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<td>13. Small tecnomorphic left valve, DAS 47139. Horizon and locality as fig. 5. Ventral view, x 55.</td>
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**Amphitoxotidinae gen. et sp. nov. A**

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<td>10. Incomplete female right valve (anterior part only), DAS 47301. Horizon and locality as fig. 14. Lateral view, x 20.</td>
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PLATE D1

Beyrichia (Beyrichia) messis sp. nov. 242

1, 2. Holotype, female carapace, DAS 47068. Wenlock Limestone, Gleedon Hill, N Shropshire (loc. 50). Lateral (stereo-pair) view, left valve, x 25; details of ornament on ventral regions of cruminae, x 55; detail of dorsal part of syllobium x 50; ventral oblique view, x 25.

3. Male carapace; DAS 47069. Horizon and locality as fig. 1. Lateral (stereo-pair) view, left valve, x 25.

5, 8. Small tecnomorphic left valve, DAS 47143. Horizon and locality as fig. 1. Lateral, posterior, anterior and ventral views, x 25.

6. Small tecnomorphic left valve, DAS 47067. Horizon and locality as fig. 1. Lateral view, x 25.

10. Male carapace, BM I 140. Wenlock Limestone, Benthall Edge, N Shropshire. Figured Jones 1881c, pl. X, figs. 13a, b as Beyrichia kloedeni, M'Coy, var. tuberculata (Salter). Lateral view, left valve, x 25.

11-14. Tecnomorphic left valve, BM I 2368 (Smith coll. 18, part). From the Woolhope inlier, probably Wenlock Limestone. Figured Jones & Holl 1886, pl. XII, figs. 8a, b as Beyrichia Kloedeni M'Coy, var. tuberculata, Salter. Lateral, posterior, anterior and ventral views, x 25.

16. Female carapace, DAS 47073. Horizon and locality as fig. 1. Lateral view, left valve, x 25.
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<td>Lectotype, small tecnomorphic carapace, BM IN 52441 (Vine coll. no. XLVII). &quot;Shales over Wenlock Limestone&quot; (= probably Lower Elton Beds), &quot;... between Wenlock and Buildwas&quot;, N Shropshire. Figured Jones &amp; Holl 1886, pl. XII, fig. 9b as Beyrichia kloedeni, M'Coy, var. tuberculata, Salter, subvar. clausa. Lateral view, right valve, X30.</td>
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<td>Female carapace, DAS 47118. Horizon and locality as fig. 1. Lateral view, right valve, X30.</td>
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<td>Tecnomorphic right valve, DAS 47083. Horizon and locality as fig. 1. Lateral view, X30.</td>
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<td>Tecnomorphic carapace, DAS 47116. Horizon and locality as fig. 1. Lateral view, left valve, X30.</td>
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PLATE D3 (continued)

Beyrichia (Beyrichia) obesa (Harper, 1940) 250


12. Tecnomorphic right valve, GSM 70336. Horizon and locality as fig. 11. Figured Harper 1940, pl. IX, fig. 15 as Kloedenia obesa. Lateral view, stereo-pair, x 30.

Beyrichia (Beyrichia) kloedeni M'Coy, 1846 238


1, 6. Silcoset cast of external mould of holotype, a tecnomorphic right valve, DAS M 102. Blaeberry Formation (Priesthill Group), Waterhead, near Muirkirk; Lesmahagow inlier, Lanarkshire (loc. 5). Lateral (stereo-pair) and ventral views, x 20.

2. Silcoset cast of external mould of female right valve, DAS M 123. Blaeberry Formation, Blaeberry Burn, Lanarkshire (loc. 4b). Lateral view, stereo-pair, x 17.

3-5. Silcoset cast of external mould of tecnomorphic right valve, DAS M 107. Horizon and locality as fig. 1. Lateral (stereo-pair), anterior (stereo-pair) and posterior (stereo-pair) views, x 20.

7. Silcoset cast of external mould of tecnomorphic right valve, DAS M 125. Horizon and locality as fig. 2. Lateral view, stereo-pair, x 20.

8. Silcoset cast of external mould of tecnomorphic right valve, DAS M 126. Horizon and locality as fig. 2. Lateral view, stereo-pair, x 20.

9. Silcoset cast of external mould of female right valve, DAS M 104. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 16.

10. Silcoset cast of external mould of tecnomorphic carapace, DAS M 98. Horizon and locality as fig. 1. Ventral view, x 20.
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<td>1, 2</td>
<td>Male left valve, GSM 70588/1. Hughley (= Purple) Shales, Harley Brook, SE of Domas, N Shropshire. Lateral (stereo-pair), posterior and ventral views, x30.</td>
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<td>Female left valve, GSM 70588/5. Horizon and locality as fig. 1. Posterior, lateral (stereo-pair) and ventral views, x30.</td>
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<td>Female right valve, GSM 70588/2. Horizon and locality as fig. 1. 'Internal' ventral oblique view of crumina, stereo-pair, x38.</td>
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<td>Small tecnomorphic left valve, GSM 70588/3. Horizon and locality as fig. 1. Lateral view, x30.</td>
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<td>Slightly incomplete female right valve, GSM 70588/4. Horizon and locality as fig. 1. Lateral view, x30.</td>
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<td>9, 10</td>
<td>Silcoset cast of external mould of incomplete female left valve, DAS M 30. Woodburn Formation (Fronian), NW of Little Lane cottage, near Old Dailly, Ayrshire (loc. 2), (i.e. Bargany Pond Burn). Ventral (stereo-pair) and lateral (stereo-pair) views, x20.</td>
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<td>Silcoset cast of external mould of male left valve, DAS M 33. Horizon and locality as fig. 9. Lateral (stereo-pair) view, x20.</td>
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10. Silcoset cast of external mould of female left valve, on slab BM I 6379. Catalogued as Beyrichia kloedeni var. antiquata from Blaeberry Burn, Lesmahagow inlier. Lateral view, stereo-pair, x 17.

11. Silcoset cast of external mould of female right valve, DAS M 72. Horizon and locality as fig. 9. Lateral view, x 17.

13. Silcoset cast of external mould of tecnomorphic left valve, on slab BM I 6379. Catalogue data as fig. 10. Lateral view, stereo-pair, x 17.


15. Silcoset cast of external mould of tecnomorphic right valve, DAS M 75. Horizon and locality as fig. 9. Lateral view, x 18.
PLATE D5

Porcarichia fragum gen. et sp. nov. 266


2, 6. Silcoset cast of external mould of holotype, female right valve, DAS M 151. Horizon and locality as fig. 1. Lateral (stereo-pair) and ventral (stereo-pair) views, x 25.


4. Silcoset cast of external mould of tecnomorphic right valve, DAS M 79. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 23.

5. Silcoset cast of external mould of tecnomorphic left valve, DAS M 159. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 25.

7. Silcoset cast of external mould of tecnomorphic left valve, DAS M 133. Blaeberry Formation (Priesthill Group), Blaeberry Burn, Lesmahagow inlier, Lanarkshire (loc. 4c). Lateral view, stereo-pair, x 25.

PLATE D6 (continued)

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Neobeyrichia lauensis (Kiesow, 1888) 274

1. Silcoset cast of external mould of tecnomorphic left valve, DAS M 164 [see also plate D8]. Upper Leintwardine Beds, Bengry Track, near Aymestry, Herefordshire (loc. 63). Lateral view, stereo-pair, x 20.

2. Silcoset cast of external mould of female right valve, DAS M 167. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 12.


4. Silcoset cast of external mould of tecnomorphic left valve, DAS M 166 [see also plate D7]. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 20.


7. Internal mould of tecnomorphic right valve BM I 141. From Leintwardine, Shropshire (presumed Upper Leintwardine Beds). Figured by Jones 1881c, pl. X, fig. 11, as Beyrichia Kloedeni var. antiquata, Jones. Lateral view, x 12.
Neobeyrichia lauensis (Kiesow, 1888) 274

1-11. Silicoset cast of external mould of tecnomorphic left valve, DAS M 166; showing fine details of "granulation" and tuberculation. Upper Leintwardine Beds, Bengry Track, near Aymestry, Herefordshire (loc. 63).

1. Lateral view, x 20.

2, 3. Lateral side of velum below adductorial sulcus; x 40 & x 280.

4. Anterior lobe and part of prenodal sulcus; stereo-pair, x 80.

5. Central part of valve [note presumed site of muscle scar in adductorial sulcus]; stereo-pair, x 40.

6, 7. Preadductorional node; stereo-pairs, x 80 & x 200.

8, 9. Central regions of prenodal sulcus; stereo-pairs, x 80 & x 200.

10, 11. Area of syllobial groove; stereo-pairs, x 80 & x 200.
Neobeyrichia lauensis (Kiesow, 1888) 274

1-11. Silcoset cast of external mould of tecnomorphic left valve, DAS M 164; showing fine details of "granulation" and tuberculation. Upper Leintwardine Beds, Bengry Track, near Aymestry, Herefordshire (loc. 63).

1. Lateral view, x 20.
2. Central region of anterior lobe, x 90.
3. Lateral side of velum below syllobium, x 100.
4 - 7. Ventral section of syllobium; stereo-pairs, x 60, x 120, x 300, x 600.
8, 9. Posteroventral face of syllobium and adjacent part of velum; stereo-pairs, x 120 & x 300.
10, 11. Crest of dorsal part of the preadductorial node; stereo-pairs, x 120 & x 600.
PLATE D9 (continued)

**Nodibeyrichia pustulosa** (Hall, 1860)  285

9. Small tecnomorphic left valve, GSM 51881/1. From slab GSM 51881, at 1214 ft in the Little Missenden borehole, Bucks. Lateral view, stereo-pair, x 25.


13. Female left valve, internal mould, GSM Pl. 4780/1. From slab GSM Pl. 4780, at 1214' in the Little Missenden Borehole. Lateral view, x 13.

**Neobeyrichia scissa** Martinsson, 1962  282


**Neobeyrichia nutans** (Kiesow, 1888)  281

PLATE D9

Fig.  Page

**Nodibeyrichia verrucosa** Shaw, 1969 290

1. Silcoset cast of external mould of female left valve, DAS M 292. Topmost Upper Whitcliffe Beds (5 cm below Ludlow Bone Bed), Ludford Lane I, Ludlow, Shropshire (loc. 69a). Lateral view, stereo-pair, x 19.

2. Silcoset cast of external mould of female left valve, DAS M 294. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 19.


4. Silcoset cast of external mould of tecnomorphic left valve, DAS M 297. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 19.

5. Silcoset cast of external mould of small tecnomorphic left valve, DAS M 298. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 19.


7. Silcoset cast of external mould of tecnomorphic right valve, DAS M 300. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 20.

8. Silcoset cast of external mould of small tecnomorphic left valve, DAS M 299. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 19.
PLATE D10 (continued)

Calcaribeyrichia torosa (Jones, 1855) 299

9. Silcoset cast of external mould of female right valve,
   DAS M 232. Upper Chonetes Beds, Five Turnings (near
   Knighton), Shropshire (loc. 14). Lateral view, stereo-
   pair, x 15.

10. Silcoset cast of external mould of female right valve,
    DAS M 237. Upper Whitcliffe Beds, Downton Castle Bridge,
    Herefordshire (loc. 71). Lateral view, stereo-pair, x 15.

11. Silcoset cast of external mould of female left valve,
    DAS M 229. Horizon and locality as fig. 9. Lateral view,
    stereo-pair, x 15.

12. Silcoset cast of external mould of lectotype, female right
    valve, on GSM 36863. Upper Ludlovian, Frith Quarry, Stapleton,
    near Presteigne, Radnorshire. Original cast (BM I 6355) figured
    Jones 1855a, pl. VI, fig. 11 as Beyrichia Kloedeni var. torosa.
    Lateral view, stereo-pair, x 15.

13. Silcoset cast of external mould of tecnomorphic right valve,
    DAS M 230. Horizon and locality as fig. 9. Lateral view,
    stereo-pair, x 15.

14. Silcoset cast of external mould of tecnomorphic left valve,
    DAS M 231. Horizon and locality as fig. 9. Lateral view,
    stereo-pair, x 15.

15. Silcoset cast of external mould of tecnomorphic left valve,
    DAS M 233. Horizon and locality as fig. 9. Lateral view,
    stereo-pair, x 15.

16. Silcoset cast of external mould of female right valve
    (ventral part only), DAS M 243. Horizon and locality as
    fig. 9. Ventral view of crumina, stereo-pair, x 34.
PLATE D10

Calcaribeyrichia tegula sp. nov.


4, 8. Silcoset cast of external mould of tecnomorphic left valve, (dorsal regions only), DAS M 246. Horizon and locality as fig. 1. Details of ornament on preadductorial node and anterior cuspidal region, and on dorsal regions of syllobium, stereo-pairs, x 52.

5. Silcoset cast of external mould of female left valve (ventral regions only), DAS M 249. Upper Leintwardine Beds, Fiddlers Elbow, near Leintwardine (loc. 67). Ventral detail of crumina, stereo-pair, x 40.


7. Silcoset cast of external mould of tecnomorphic left valve (dorsal regions only), DAS M 321. Horizon and locality as fig. 2. Detail of cuspidal part of syllobium. Lateral view, stereo-pair, x 75.
PLATE D11 (continued)

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8. Holotype, a tecnomorphic right valve, BM I 6353. From "Wenlock schists" near Montgomery, Wales. Figured Jones 1855a, pl. VI, fig. 8 as Beyrichia Kloedeni, var. antiquata, Jones. Lateral view, x 14.

Incertae Subfamiliae. Gen. et sp. nov. A 310

9. Tecnomorphic right valve, DAS 47295. Limestone band,

12. Brinkmarsh Beds, Brinkmarsh Quarry, Tortworth inlier (loc. 11).

13. Ventral, anterior (stereo-pair) and lateral views (stereo-pair), x 25.
PLATE D11

Calcaribeyrichia characta sp. nov. 292

1. Silcoset cast of external mould of holotype, female left valve, DAS M 114. Blaeberry Formation (Priesthill Group), Waterhead Farm, near Muirkirk, Lanarkshire (loc. 5). Lateral view, stereo-pair, x 35.

2. Silcoset cast of external mould of tecnomorphic right valve, DAS M 95. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 35.

3. Silcoset cast of external mould of female right valve, DAS M 110. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 35.

4. Silcoset cast of external mould of tecnomorphic carapace, DAS M 112. Horizon and locality as fig. 1. Ventral view, stereo-pair, x 35.

5. Silcoset cast of external mould of tecnomorphic left valve, DAS M 90. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 35.


7, 10, Female right valve, DAS 47160. Wenlock Shale, Burrington,

11, 14. Ludlow anticline (loc. 45). Ventral, lateral (stereo-pair), posterior and anterior views, x 35.
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<td>Small tecnomorphic right valve, DAS 47267. Horizon and</td>
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<td>Tecnomorphic right valve, DAS 47263. Horizon and locality</td>
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<td>Female right valve, DAS 47265. Horizon and locality</td>
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<td>18.</td>
<td>Silcoset cast of external mould of tecnomorphic left valve, DAS M 308. Topmost Upper Whitcliffe Beds (5 cm below Ludlow Bone Bed), Ludford Lane I, Ludlow, Shropshire (loc. 69a). Lateral view, stereo-pair, x 21.</td>
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**Frostiella bicristata** Shaw, 1969

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<td>Small, worn, tecnomorphic carapace, GSM 103228. Horizon and locality as fig. 15. Shaw 1969, fig. 2A. Right lateral view, stereo-pair, x 35.</td>
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PLATE E2 (continued)

Londinia lata Shaw, 1969


Londinia cf. L. fissurata Shaw, 1969


Londinia fissurata Shaw, 1969


Frostiella groenvalliana Martinsson, 1963

12. Silcoset cast of external mould of female right valve, DAS M 305. Downton Castle Sandstone (from about 1.5 m above Ludlow Bone Bed), Ludford Lane II, Ludlow, Shropshire (loc. 73b). Lateral view, stereo-pair, x 20.

PLATE E2

Londinia arisaigensis Copeland, 1964 324

1. Silcoset cast of external mould of tecnomorphic left valve, DAS M 311. Downton Castle Sandstone (from about 1.5 m above Ludlow Bone Bed), Ludford Lane II, Ludlow, Shropshire (loc. 73b). Lateral view, stereo-pair, x 19.

2. Silcoset cast of external mould of female left valve, DAS M 314. Horizon and locality as fig. 1. Lateral view, stereo-pair, x 20.


7. Silcoset cast of external mould of female left valve, DAS M 312. Horizon and locality as fig. 1. Lateral detail of preadductorional node, stereo-pair, x 40.

**PLATE E3**

**Kloedenia wilckensiana** (Jones, 1855)  
1, 2. Tecnomorphic left valve, GSM 51881/4. At 1214 feet in the Lower Missenden Borehole, Buckinghamshire; Downtonian. Lateral (stereo-pair), anterior (stereo-pair) and ventral oblique views, x35; detail of preadductorional node, dorsal oblique view, x35.

3. Large right valve, GSM 51881/3. Horizon and locality as fig. 1. Lateral view, x30. Note more tumid lateroventral lobe and higher preadductorional node.

4, 7. Tecnomorphic left valve, GSM 51888/1. From between 1213'6" and 12'9" in the Little Missenden core. Lateral, ventral (stereo-pair), posterior and dorsal views, x35.

8. Small tecnomorphic right valve, GSM Pl. 4780/2. Horizon and locality as fig. 1. Lateral view, x35.

9. Tecnomorphic left valve, GSM 51884/1. At 1234 feet in the Little Missenden core. Lateral view, x35.

**Kyamodes whidbornei** Jones, 1888  
10-13. Lectotype, a tecnomorphic carapace, SM H 9447. Middle Devonian limestones, Daddy Hole Quarry, near Torquay, Devonshire. Figured Jones 1888a, pl. XI, figs. 1-5; designated lectotype herein. Right lateral (stereo-pair), posterior, ventral, left lateral and dorsal oblique views, x25.
PLATE F1

Fig.  Page

Ametrobeyrichia schizopyge gen. et sp. nov. 343

3. Lateral view, stereo-pair, x 55. 4. Anterior view, stereo-pair, x 55. 5. Ventral view, x 55. 6. Dorsal view, x 55.

7. Left valve, DAS 47102. Tickwood Beds, Harley Hill Road, N Shropshire (loc. 48c). Lateral view, stereo-pair, x 55.


9. Left valve, BM I 1953. Tickwood Beds, Shropshire. Figured Jones and Holl 1886, pl. XII, fig. 6 as Beyrichia Kloedeni var. subtorosa, Jones. Lateral view, x 55.
Fig. 1. Carapace, DAS 47361. Wenlock Limestone, Hobbs Ridge, May Hill inlier, Gloucestershire (loc. 15b). Ventral view, stereo-pair, x 55.

2. Left valve, DAS 47359. Wenlock Limestone, Croft Farm, Malverns Area (loc. 18d). Lateral view, stereo-pair, x 55.


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<td>A.</td>
<td>Silcoset cast of external mould of male left valve, unnumbered (on same slab as SM A 88250). Upper Llandovery of Wetherlaw Linn, Pentland Hills, Scotland. Lateral view, stereo-pair, x55.</td>
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<td>B.</td>
<td>Silcoset cast of external mould of female right valve, SM A 88250. Horizon and locality as fig. A. Lateral view, stereo-pair, x55.</td>
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<td>C-F.</td>
<td>Silcoset cast of external mould of an incomplete left valve (dorsal part absent) exhibiting cruminal metamorphosis; on slab BM I 2855. Presumed upper Llandovery; Lyne Water, Pentland Hills. C. Lateral view, stereo-pair, x50.</td>
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<td>D. Anterior view showing profile of dolonoid pouch, stereo-pair, x50. E. Ventral oblique view, stereo-pair, x45.</td>
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<td>F. Ventral view, stereo-pair, x45.</td>
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**Craspedobolbina (Mitrobeyrichia) impendens** (Haswell, 1865) 40
PLATE G2

Bolbiprimitia juvenicristata sp. nov. 109

A. Male carapace, DAS 47175. Wenlock Limestone, Audience Wood, N Shropshire (loc. 57). A. Left lateral view, stereo-pair, x60.

B, D, H. Female right valve, DAS 47169. Tickwood Beds, Tickwood, N Shropshire (loc. 44d). B. Lateral view, x60. D. Posterior view, x60. H. Ventral view, x60.

C, E-G. Carapace with posteroventral pouch-like swelling (on right valve only), DAS 47176. Horizon and locality as fig. B. C. Right lateral view, stereo-pair, x60. E. Detail of swelling, ventral view, stereo-pair, x90. F. Posterior view, x60. G. Ventral oblique view, x60.
PLATE G3

**Fig.**  
**Sleia pauperata** (Jones, 1869) 123

A, B. Male left valve, DAS 47082. Wenlock Limestone, Lincoln Hill, N Shropshire (loc. 49c).  A. Lateral view, stereo-pair, x45.  B. Anterior view, x45.

C, D, G. Female left valve, DAS 47080. Horizon and locality as fig. A.  C. Lateral view, stereo-pair, x45.  D. Anterior view, x45.  G. Ventral view, x45.

E, F. Left valve exhibiting cruminal metamorphosis, DAS 47077.

H, I. Horizon and locality as fig. A.  E. Lateral view, stereo-pair, x45.  F. Anterior view, stereo-pair, x45.  H. Ventral view, stereo-pair, x45.  I. Oblique ventral view, x45.
Undipila repanda gen. et sp. nov.

A, E. Male left valve, DAS 47186. Tickwood Beds, Harley Hill Road, N Shropshire (loc. 48c). A. Lateral view, stereo-pair, x 40. E. Anterior view, x 40.

B, F. Female left valve, DAS 47179. Horizon and locality as I. fig. A. B. Lateral view, stereo-pair, x 40. F. Anterior view, x 40. I. Ventral view, x 40.

Sarmatotoxotis phracta gen. et sp. nov.

A, B. Male right valve, DAS 47097. Tickwood Beds, Harley Hill Road, N Shropshire (loc. 48c). A. Lateral view, stereo-pair, x 40. B. Posterior view, x 40.

C, D. Female right valve, DAS 47161. Horizon and locality as G. fig. A. C. Lateral view, stereo-pair, x 40. D. Posterior view, x 40. G. Ventral view, x 40.

E, F. Slightly incomplete right valve exhibiting cruminal metaporphosis, DAS 47108. Horizon and locality as fig. A. E. Lateral view, stereo-pair, x 40. F. Posterior view, stereo-pair, x 40. H. Ventral view, stereo-pair, x 40.

I. Oblique ventral view, x 40.
Beyrichia (Beyrichia) clausa Jones & Holl, 1886


B. Tecnomorphic carapace, DAS 47083. Horizon and locality as fig. A. B. Lateral view, stereo-pair, x30.

C-F. Anteroventral part of left valve exhibiting cruminal metamorphosis. Horizon and locality as fig. A.

C. Anterior view, x30. D. Lateral view, x30. E. 'Internal' ventral oblique view, x30. F. Ventral view, x30.
APPENDIX 1: FIELD LOCALITIES AND FAUNA.

As far as possible, the following information accompanies each of the cited localities.

a) A short "field designation" and locality number.
b) Geographical position, including National Grid Reference.
c) Stratigraphical position.
d) Type of material collected e.g. "washed samples".
e) Beyrichiacean fauna.

Stratigraphical control and information on most of the outcrops sampled is provided in a number of key papers (e.g. Ziegler, Cocks, & McKerrow 1968, document localities in the Llandovery of the Welsh Borderland); relevant references are appended.

A single asterisk (*) indicates where both Prof. Martinsson's and the author's samples are used. Two asterisks (**) denotes the use of Prof. Martinsson's samples alone. In this context it should be noted that any lack of knowledge regarding the exact sampling point for Prof. Martinsson's material, does not effect the general geographical or stratigraphical information given for the samples concerned.

Those localities sampled, but producing only non-beyrichiacean ostracodes or lacking ostracodes at all, receive no further treatment below.
Loc. 1. BOOCAUN: The vicinity of the (only remaining) cottage and nearby stream at Boocaun, about 3.5 km NNW of Clonbur village, near Cong, County Galway, Ireland. See McKerrow & Campbell, 1960. Loose blocks of coarse sandstone of upper Llandovery age. Mould material. 
Beyrichia kloedeni.

Loc. 2. LITTLE LANE: On an unnamed tributary of Lauchlan Burn, approximately 900 m NW of Little Lane cottage, 2.5 km SW of Old Dailly, Ayreshire, Scotland; NX 2500 9858. See Cocks & Toghill, 1973, p. 226.
Woodburn Formation, Monograptus sedgwickii Zone; Fronian, upper Llandovery. Mould material, occasionally parts of shell remaining. 
Beyrichia scotica.

Loc. 3. NEWLANDS: Cutting at Newlands Farm, near Girvan, Ayreshire; NS 2775 0434. See Cocks & Toghill, 1973, p. 215.
Newlands Formation, Monograptus gregarius Zone; Idwian, middle Llandovery. Poorly preserved moulds. Beyrichiacean sp. indet. Included because of its early stratigraphical position; not treated further.

Loc. 4. BLAEBERRY BURN: Exposures at W end of Blaeberry Burn, just E of Logan Reservoir, the Lesmahagow inlier, Lanarkshire, Scotland. See Jennings, 1961, pp. 11, 12.
Blaeberry Formation, Priesthill Group; of probable late Llandovery (or possibly early Wenlock) age. Moulds; in situ and scree material.
4a. NS 7342 3568. Beyrichia impacifica.
4c. NS 7381 3553. Porcarichia fragum.
Loc. 5. WATERHEAD: Exposure on bank of unnamed stream approximately 650 m E of Waterhead Farm, 3 km N of Muirkirk, the Lesmahagow inlier, Lanarkshire, Scotland; NS 7058 3085. See Jennings, 1961, pp. 11, 12.

Blaeberry Formation, Priesthill Group; of probable late Llandovery (or possibly early Wenlock) age. Mould material. Beyrichia impacifica, Calcaribeyrichia characta, Porcarichia fragum.

Loc. 6. LAMON BURN: Lamonburn Bridge, 600 m N of confluence of Lamon Burn and Greenock Water, 2.5 km N of Muirkirk, the Lesmahagow inlier, Lanarkshire, Scotland. Material from two exposures: NS 6900 2991, and NS 6903 2982. See Jennings 1961, pp. 11, 12.

Blaeberry Formation, Priesthill Group; of probable late Llandovery (or possibly early Wenlock) age. Mould material. Beyrichia impacifica, Calcaribeyrichia characta.

Loc. 7. DUNSIDE: Small exposure on bank of Lochfennock Burn, about 30 m S of NE corner of the smaller E section of Dunside Reservoir, and some 170 m NW of Dunside Farm, Logan Water, the Lesmahagow inlier, Lanarkshire, Scotland; NS 7492 3719. See Jennings 1961, pp. 12, 13.

Dunside Formation, Priesthill Group; of probable late Llandovery (or possibly early Wenlock) age. Mould material. Porcarichia venefica, Porcarichia fragum.

Loc. 8. DEERHOPE BURN: Near head of Deerhope Burn, approximately 1100 m W 10°N of N Esk Cottage, N Esk inlier, the Pentland Hills, Scotland; Nat. Grid Ref.: NT 143 580. See Mykura & Smith, 1962.

Mudstones of supposed upper Llandovery (Telychian) age. Mould material. Craspedobolbina impendens.
Loc. 9. WETHERLAW LINN: Side of Wetherlaw Linn Burn, 30 m from junction with the River N Esk, N Esk inlier, the Pentland Hills, Scotland; Nat. Grid Ref.: NT 148 586. See Mykura & Smith, 1962.
Plectodonta Mudstones of supposed upper Llandovery (Telychian) age. Mould material. Craspedobolbina impendens.


Four localities, a few metres apart along strike.
12a. ST 6737 9128. Parasleia degener, Undipila cortinata.
12b. ST 6739 9126. Parasleia degener, Undipila cortinata.
12c. ST 6741 9125. Parasleia degener, Undipila cortinata.
12d. ST 6744 9124. Parasleia degener, Undipila cortinata.

Loc. 14. FIVE TURNINGS: Exposures in field adjacent to A488 road, approximately 0.5 km S of Five Turnings (3 km N of Knighton), Shropshire; Nat. Grid Ref.: SO 288 479. Upper Chonetes Beds (upper Ludlovian) of Stamp (1918). Mould material. Calcaribeyrichia torosa, Lophoocenella sp., Hemsiella sp..

Loc. 15. HOBBS RIDGE: Line of old quarries immediately N of old road across crest of Hobbs Ridge, about 0.7 km NE of Longhope, May Hill inlier, Gloucestershire. See Lawson 1955. Wenlock Limestone (lower part). Washed samples. Three localities, about 10 m apart and approximately same horizon.


15c. SO 6946 1954. Sleia procincta, Ametrobeyrichia schizopyge.

Loc. 17. LITTLE HILL: Line of old quarries along ridge-crest of Little Hill, some 2.5 km N of Woolhope (Woolhope inlier), Herefordshire. See Squirrell & Tucker 1960.

Wenlock Limestone. Washed samples.

Four localities about 40 m apart along strike.

17a. SO 6096 3817. Beyrichia messis, Amentobeyrichia schizopyge.

17b. SO 6100 3815. Amentobeyrichia schizopyge.

17c. SO 6104 3813. Amentobeyrichia schizopyge.

17d. SO 6110 3810. Strepula concentrica, Garniella arthrodes, Beyrichia messis, Beyrichia clausa ?

Loc. 18. CROFT FARM*: Line of old quarries along ridge between Croft Farm and Cother Wood (0.5 km W of W Malvern), Herefordshire.

Wenlock Limestone. Washed samples.

Four localities, all pathside exposures.

18a. SO 7572 4650 (W side of middle path). Beyrichia clausa, Sleia pauperata, Sleia procincta, Osmotoxotis phalacra, Sarmatotoxotis phracta, Amentobeyrichia schizopyge.

18b. SO 7574 4646 (W side of middle path). Beyrichia clausa, Sleia procincta, Sarmatotoxotis phracta, Amentobeyrichia schizopyge.

18c. SO 7577 4627 (W side of upper path). Beyrichia clausa, Amentobeyrichia schizopyge.

18d. SO 7579 4623 (W side of upper path). Beyrichia clausa, Sleia pauperata, Sleia procincta, Sarmatotoxotis phracta, Amentobeyrichia schizopyge.

In addition to the above fauna, the species Cavisella clithridium, Garniella concinna, Sleia grumula and Tinotoxotis velivola are present in Martinssons samples from the Wenlock Limestone at Croft Farm.
Loc. 19. WHITMAN'S HILL: Large quarry at Whitman's Hill, approximately 300 m S of the church (on the A4103 road) at Storridge, Herefordshire. Wenlock Limestone. Washed samples.


Loc. 20. STORRIDGE: Road section approx. 300 m SW of church on the A4103 road at Storridge (N Malverns), Herefordshire; SO 4758 4853. Wenlock Shale (topmost part). Washed samples. 

*Tinotoxotis velivola, Undipila repanda, Tropidotoxotis arga.*

Loc. 21. GOLD HILL FARM: Roadside quarry 400 m W of Gold Hill Farm near Eastnor, the S Malverns, Herefordshire; SO 7322 3629. (cf. Bassett 1970, loc. 93).

Wenlock Limestone. Washed samples. 

*Ametrobeyrichia schizopyge.*

Loc. 22. PARK WOOD: Line of old quarries (largely overgrown), through Park Wood, c. 0.5 km N of Upper Wyche, the Malverns area, Herefordshire; SO 764 443. Wenlock Limestone. Washed samples.

*Gongylostonyx exaggeratus, Ametrobeyrichia schizopyge.*

Loc. 23. LEDBURY**: Disused quarry, opening onto the E side of the A449 road, 0.5 km NE of Ledbury, the Malverns area, Herefordshire; SO 7162 3775. (cf. Bassett 1970, loc. 90).

Wenlock Limestone. Washed samples.


Loc. 25. HAY HEAD FARM: Old workings c. 400 m NE of Hay Head Farm (and c. 120 m NE of northernmost water-filled quarries), near Walsall, Staffordshire; SP 0492 9890. See Cantrill, 1919. Barr Limestone (lower part of Wenlock). Washed samples. *Parasleia artemum.* Also fragments of an undescribed amphitoxotidine species.


Loc. 27. WREN'S NEST: Wren's Nest Hill, Dudley, Worcestershire. See Butler, 1939. Wenlock Limestone. Washed samples. Seven localities around the flanks of the pericline.

27a. Large, steeply dipping bedding plane, E side; Basement Beds (of Butler, 1939); SO 9382 9189. *Sleia pauperata, Sleia grumula, Tinotoxotis velivola, Undipila repanda, Sarmatotoxotis phracta, Gongylostonyx exaggeratus, Ametrobebyrichia schizopyge.*

27b. Large bedding plane, S end; Nodular Beds (of Butler 1939); SO 9370 9144. *Sleia pauperata, Sleia grumula, Sleia troglodytophila, Tinotoxotis velivola, Osmotoxotis phalacra, Ametrobebyrichia schizopyge.*


27e. Ridge crest, W side; Nodular Beds; SO 9357 9192. Strepula concentrica, Sleia pauperata, Sleia troglodytophila, Tinotoxotis velivola, Ametrobeyrichia schizopyge.


27g.** W flank of W side; Nodular Beds; SO 9394 9184. Beyrichia clausa, Sleia grumula, Tinotoxotis velivola, Zorotoxotis medioculta, Charitoxotis gravida.

Loc. 28. HURST HILL: Cutting on A463 road through Hurst Hill (inlier at Sedgley 4 km N of Dudley), Staffordshire; SO 9280 9405. See Butler 1939.

Wenlock Limestone (Nodular Beds). Washed samples.
Strepula concentrica, Garniella concinna, Garniella arthrodes, Beyrichia clausa, Sleia pauperata, Sleia troglodytophila, Tinotoxotis velivola, Sarmatotoxotis phracta, Ametrobeyrichia schizopyge.
*Craspedobolbina glabra, Craspedobolbina hipposiderus, Stroterobolbina floribunda.*

Loc. 30. CHURCH PREEN BROOK: Exposure in floor of Church Preen Brook, about 60 m W of its confluence with Hughley Brook, Shropshire; SO 5620 9764. Hughley Shales; Telychian, upper Llandovery. Well preserved valves on limestone slabs. 
*Craspedobolbina glabra, Craspedobolbina hipposiderus, Stroterobolbina floribunda.*

Loc. 31. BOATHOUSE COPPICE: Exposure along stream 1 km due E of Shineton, N Shropshire; SJ 6205 0398. Hughley Shales; C₅ (mid-Telychian), upper Llandovery. Ziegler et al., 1968, loc. 49. Mould material and washed samples. 
*Craspedobolbina hipposiderus.*

Loc. 32. DOMAS: W bank of Harley Brook, approximately 100 m SW of bridge at Domas, Shropshire; SJ 5934 0062. Ziegler et al., 1968, loc. 55. Hughley Shales; C₆ (upper Telychian), upper Llandovery. Washed samples. 
*Craspedobolbina hipposiderus, Stroterobolbina floribunda.*

Loc. 33. R. ONNY: E bank of River Onny, approximately 700 m SW of church at Wistanstow, Shropshire; SO 4260 8533. Ziegler et al., 1968, loc. 60. Hughley Shales; presumed *Monograptus turriculatus* Zone, upper Fronian, upper Llandovery. Washed samples. 
*Craspedobolbina hipposiderus.*

Loc. 34. BUILDWAS BRIDGE*: The N bed/bank of the River Severn, about 15 m upstream from the road bridge at Buildwas, N Shropshire; SJ 6451 0445. Coalbrookdale Beds (lower part); Wenlock Series. Washed samples. 
*Dictyobolbina incuspidata.*
Loc. 35. **BUILDWAS**: Exposure high above the river bed and just below road (B4380) level on the N side of the river (Severn) bend, some 400 m S of the church at Buildwas, N Shropshire; SJ 6400 0456. (cf. Pocock et al., 1938, p. 112. Buildwas Beds (lowermost part); Wenlock Series. Washed samples. **Craspedobolbina interrupta**.

Loc. 36. **HARLEY BROOK**: River bluff exposure on E bank of Harley Brook, approximately 200 m S of its junction with Merrishaw Brook, near Domas, Shropshire; approx. SJ 5925 0039. Buildwas Beds (lower part); Wenlock Series. Washed samples. **Craspedobolbina interrupta**.

Loc. 37. **BUILDWAS ABBEY**: Exposures on N bank of the R. Severn, c. 120 m upstream from road bridge and opposite Buildwas Abbey, Buildwas, N Shropshire; approx. SJ 6435 0450. (cf. Bassett 1970, loc. 4). Buildwas Beds (upper part); Wenlock Series. Washed samples. **Dictyobolbina incuspidata**.

Loc. 38. **BIRCHES COPPICE**: Slope above (N side of) B4380 road at the S end of Birches Coppice, and some 700 m E of Buildwas Bridge, N Shropshire; SJ 6523 0460. Coalbrookdale Beds (lower half); Wenlock Series. Washed samples. Two indeterminate beyrichiine species.

Loc. 40. COALBROOKDALE*: Very small exposure near cottage immediately
N of railway bridge, W side of Coalbrookdale valley, N
Shropshire; SJ 6555 0400.
Coalbrookdale Beds (upper part); Wenlock Series. Washed samples.
Equicastanea lappacea, Undipila subspissa, Tropidotoxotis arga.

Loc. 41. LONGVILLE: Exposure along the minor road between Longville
in the Dale and Stanway, Wenlock Edge, Shropshire; SO 5398 9272.
Tickwood Beds (topmost part), Wenlock Series. Washed samples.
Undipila repanda.

Loc. 42. ACKLANDS COPPICE: Well exposed section along the old railway
track, on the NW side of Acklands Coppice, between Buildwas
Tickwood Beds; Wenlock Series. Washed samples.
Two localities about 25 m apart, approximately same horizon.
42a. SJ 6379 0269. Strepula concentrica, Cavisella clithridium,
Sleia pauperata, Tinotoxotis praegnans, Undipila repanda,
Sarmatotoxotis phracta, Gongylostonyx exaggeratus, Ametro-
beyrichia schizopyge.
42b. SJ 6378 0267. Strepula concentrica, Sleia pauperata,
Undipila repanda, Sarmatotoxotis phracta, Gongylostonyx
exaggeratus, Ametrobeyrichia schizopyge.

Loc. 43. BENTHALL EDGE, EAST: Small exposures along path just above (S of)
the old railway track, S side of R. Severn below the E end of
Tickwood Beds; Wenlock Series. Washed samples.
43a.* Approximately 100 m W of Bower's Brook; SJ 6664 0352.
Strepula ? sp. nov. A, Strepula concentrica, Cavisella
clithridium, Bolbiprimitia juvenicristata, Beyrichia messis,
Beyrichia clausa, Sleia pauperata, Tinotoxotis velivola,
Tinotoxotis praegnans ?, Undipila repanda, Gongylostonyx
exaggeratus, Tripidotoxotis arga, Sarmatotoxotis phracta,
Ametrobeyrichia schizopyge.
Approximately 450 m W of Bower's Brook; SJ 6632 0356.

Beyrichia messis, Undipila repanda, Tropidotoxotis arga,
Ametrobeyrichia schizopyge.

Loc. 44. TICKWOOD: Cutting, E side of the minor road from Lawleyscross
to the Wyke, S of the old railway bridge on the W side of
Tick Wood, Shropshire.

Tickwood Beds; Wenlock Series. Washed samples.

Four localities, approximately the same horizon.

44a. SJ 6382 0278. Strepula concentrica, Beyrichia messis,
Beyrichia clausa, Sleia pauperata, Gongylostonyx exaggeratus,
Ametrobeyrichia schizopyge.

44b. SJ 6380 0285. Bolbiprimitia juvenicristata, Beyrichia
clausa, Sleia pauperata, Undipila repanda, Gongylostonyx
exaggeratus, Ametrobeyrichia schizopyge.

44c. SJ 6379 0290. Strepula concentrica, Cavisella clithridium,
Beyrichia clausa, Sleia pauperata, Tiniotoxotis praegnans,
Undipila repanda, Sarmatotoxotis phracta, Tropidotoxotis arga ?,
Ametrobeyrichia schizopyge.

44d. * SJ 6381 0281. Bolprimitia juvenicristata, Strepula concentrica,
Strepula ? sp. nov. A, Cavisella clithridium, Garniella
arthrodes, Beyrichia messis, Beyrichia clausa, Sleia pauperata,
Tiniotoxotis velivola, Tiniotoxotis praegnans, Undipila repanda,
Sarmatotoxotis phracta, Gongylostonyx exaggeratus, Ametro-
beyrichia schizopyge.

Loc. 45. BURRINGTON: Exposures along sunken trackway, 200 m S of church
at Burrington (Ludlow anticline), Herefordshire; SO 4424 7190.

Holland et al., 1963, loc. 90.

Wenlock Shale; Cyrtograptus lundgreni Zone, Wenlock Series.

Shale slabs.

Beyrichiinae gen. et sp. nov. A.

Beyrichia (Beyrichia) sp.

Loc. 47. BENTHALL EDGE, WEST*: Disused quarry along Benthall Edge, about 500 m NNW of Benthall Hall, N Shropshire; SJ 6587 0315. Wenlock Limestone; Wenlock Series. Washed samples. 

Strepula concentrica, Garniella arthrodes, Garniella concinna, Beyrichia messis, Beyrichia clausa, Sleia pauperata, Sleia grumula, Sleia troglodytophila, Tinotoxotis velivola, Sarmatotoxotis phracta, Gongylostonyx exaggeratus, Ametrobeyrichia schizopyge.


48a. N side of road; approx. SJ 6099 0037; Tickwood Beds (basal part). Equicastanea lappacea, Tinotoxotis praegnans.

48b. S side of cutting; approx. SJ 6101 0036; Tickwood Beds (middle part). Strepula concentrica, Cavisella clithridium, Tinotoxotis praegnans, Undipila repanda.

48c. N side of cutting; approx. SJ 6104 0036; Tickwood Beds (top part). Strepula concentrica, Cavisella clithridium, Garniella concinna, Bolbiprimitia juvencristata, Sleia pauperata, Undipila repanda, Tinotoxotis praegnans, Tinotoxotis velivola ?, Gongylostonyx exaggeratus, Sarmatotoxotis phracta, Ametrobeyrichia schizopyge.

48d. N side of cutting, just below small bioherm - see Bassett & Shergold 1970, fig. 7; approx. SJ 6107 0035; Wenlock Limestone. Beyrichia clausa ?, Ametrobeyrichia schizopyge.
Loc. 49. LINCOLN HILL*: The large, steeply dipping face at the old workings on the W side of Lincoln Hill (ridge), approximately 250 m N of the R. Severn at Ironbridge, N Shropshire. (cf. Bassett 1970, loc. 5).

Wenlock Limestone; Wenlock Series. Washed samples.

49a. Top of face (=ridge crest); SJ 6693 0381. Strepula concentrica, Beyrichia clausa, Sleia pauperata, Tinotoxotis velivola, Undipila repanda, Sarmatotoxotis phracta, Ametrobeyrichia schizopyge.

49b. Base of face, directly below 49a. Sleia concentrica, Garniella concinna, Garniella arthrodes, Bolbiprimitia juvenicristata, Beyrichia clausa, Sleia pauperata, Tinotoxotis velivola, Undipila repanda, Sarmatotoxotis phracta, Gongylostonyx exaggeratus, Ametrobeyrichia schizopyge.

49c. Base of face, 10 m SW of 49b. Strepula concentrica, Garniella arthrodes, Beyrichia clausa, Sleia pauperata, Tinotoxotis velivola, Undipila repanda, Sarmatotoxotis phracta, Amphitoxotidinae (gen. nov. ?) sp. nov. B, Ametrobeyrichia schizopyge.

Loc. 50. GLEEDON HILL*: Top of the section, NW side of Farley Quarry, on the E side of Gleedon Hill, 1.7 km NNW of Much Wenlock, Shropshire; SJ 6298 0169. (cf. Bassett 1970, loc. 8).

Wenlock Limestone; Wenlock Series. Washed samples.

Strepula concentrica, Cavisella clithridium, Garniella arthrodes, Bolbiprimitia juvenicristata, Beyrichia messis, Beyrichia clausa, Sleia troglodytophila, Sarmatotoxotis phracta, Gongylostonyx exaggeratus, Ametrobeyrichia schizopyge.

Loc. 51. HARLEY HILL QY: Small, disused quarry on the N side of the A458 road, crest of Harley Hill, Wenlock Edge, approximately 1.2 km NW of Much Wenlock Shropshire; SJ 6110 0034.

Wenlock Limestone; Wenlock Series. Washed samples.

Strepula concentrica, Strepula ? sp. nov. A, Cavisella clithridium,
Garniella arthrodes, Bolbiprimitia juvenicristata, Beyrichia messis, Beyrichia clausa, Sarmatotoxotis phracta, Gongylostomyx exaggeratus, Ametrobeyrichia schizopyge.

Loc. 52. HAYES QY*: Quarry on N side of B4371 road, approximately 2 km SW of Much Wenlock, Wenlock Edge, Shropshire; SO 6015 9915. (cf. Bassett 1970, loc. 2).
Wenlock Limestone; Wenlock Series. Washed samples.

Beyrichia (Beyrichia) sp.

Loc. 53. COATES QY: Large quarry on the N side of the B4371 road, about 1.7 km SW of Much Wenlock, Wenlock Edge, Shropshire; SO 6045 9935. (cf. Bassett 1970, loc. 1).
Wenlock Limestone; Wenlock Series. Washed samples.

53a. Prominent bentonite horizon; E end of main quarry face.

Material from this locality also kindly supplied by B.M. Abbot (Open University) & R. Marsh (Norwood Tech. Coll.).
Strepula concentrica, Beyrichia messis, Beyrichia clausa, Ametrobeyrichia schizopyge.

53b. W part of main quarry face. Strepula concentrica, Beyrichia messis, Beyrichia clausa, Tinotoxotis velivola, Ametrobeyrichia schizopyge.

Loc. 54. MUCH WENLOCK, WINDMILL*: N of the old windmill at Shadwell Rock quarry, on E side of B4378 road, about 1 km N of Much Wenlock, Wenlock Edge, Shropshire; SJ 6247 0090. (cf. Bassett, 1970, loc.6).
Wenlock Limestone; Wenlock Series. Washed samples.
Strepula concentrica, Bolbiprimitia juvenicristata, Beyrichia messis, Beyrichia clausa, Tinotoxotis velivola, Undipila repanda, Sarmatoxoxtotis phracta, Ametrobeyrichia schizopyge.

Loc. 55. MUCH WENLOCK**: Small, old quarry, c. 50 m SW of the old windmill at Shadwell Rock Quarry, on E side of B4378 road, approximately 1 km N of Much Wenlock, Wenlock Edge, Shropshire; SJ 6245 0078.
Wenlock Limestone; Wenlock Series. Washed samples.
Strepula concentrica, Beyrichia messis, Sleia troglodytophila, Ametrobeyrichia schizopyge.
Loc. 56. THE BANK QY.*: Old quarry on the N side of the path from the Bank to Blakeway Hollow, 1 km SW of Much Wenlock, Wenlock Edge, Shropshire; SO 6095 9973. Bassett 1970, loc. 17. Wenlock Limestone; Wenlock Series. Washed samples. 
  *Strepula concentrica, Beyrichia messis.*

Loc. 57. AUDIENCE WOOD**: Immediately N of the minor road from Lawleyscross to Wyke and c. 200 m due S of Tickwood Hall, 3.5 km NW of Much Wenlock, Shropshire; SJ 6436 0246. Wenlock Limestone; Wenlock Series. Washed samples. 
  Garniella arthrodes, Strepula concentrica, Strepula ? sp. nov. A, Bolbiprimitiajuvenicristata, Beyrichia messis, Beyrichia clausa, Gongylostonyxexaggeratus, Ametrobeyrichia schizopyge.

Loc. 58. PRESTHOPE**: Exposure near road junction at Presthope, about 4.5 km SW of Much Wenlock, Wenlock Edge; SO 5816 9741. Wenlock Limestone; Wenlock Series. Washed samples. 
  Strepula concentrica, Garniella arthrodes ?, Beyrichia messis, Beyrichia clausa.

Loc. 59. MILLICHOPE: Stream section about 600 m NW of Upper Millichope, Wenlock Edge, Shropshire; SO 5185 8987. (approximately loc. 295 of Shergold & Shirley, 1968, fig. 1.). Lower Elton Beds (higher part); Ludlow Series. Washed samples. 
  Beyrichia clausa ?, Tinotoxotis velivola, Undipila repanda ?

Loc. 60. STRETTON WESTWOOD: SE face of Stretton Westwood Quarry, S side of B4371 road, c. 2.5 km SW of Much Wenlock, Wenlock Edge, Shropshire; SO 5960 9838; (see Shergold & Bassett, 1970, p. 128, figs. 14, 15). Lower Elton Beds (lowermost part; Coralliferous strata); Ludlow Series. Washed samples. 
  Strepula concentrica, Beyrichia messis, Beyrichia clausa, Tinotoxotis velivola, Ametrobeyrichia schizopyge.
Loc. 61. SHADWELL ROCK QY.: Top of the N face of Shadwell Rock Quarry
(Wenlock Edge), just E of the B4378 road, approximately 1 km N
of Much Wenlock, Shropshire; SJ 6255 0090 (see Shergold & Bassett
Lower Elton Beds (lowermost part); Ludlow Series. Washed samples.
Strepula concentrica, Beyrichia clausa, Sleia pauperata, Sleia
troglodytophila, Tinotoxotis velivola, Undipila repanda.

Loc. 62. FORESTRY TRACK, LUDLOW: New forestry road section W of Batchott,
Ludlow anticline, Shropshire; SO 4883 7109. Lawson 1973a, loc. 62.
Upper Leintwardine Beds; Ludlow Series. Mould material.
Neobeyrichia confluens, Neobeyrichia lauensis, Neobeyrichia scissa,
Calcaribeyrichia tegula, Sleia cf. S. equestris, Zorotoxotis convallis,
Atterdagia versiculus, Hemiocella ? sp. nov. B, Lophoctenella cf.
L. scanensis.

Loc. 63. BENGRY TRACK: Exposures along the E end of Bengry track,
approximately 200 m W of the Crown Inn at Aymestrey, Herefordshire;
SO 4228 6544. See Lawson 1973, pp. 255, 262, fig. 3.
Upper Leintwardine Beds; Ludlow Series. Mould material.
Neobeyrichia confluens, Neobeyrichia lauensis, Neobeyrichia scissa,
Calcaribeyrichia tegula, Sleia cf. S. equestris, Zorotoxotis convallis,
Atterdagia versiculus, Hemiocella ? sp. nov. B, Lophoctenella cf. L.
scanensis, Amphitoxotidinae (Incertae generis) sp. nov. C.

Loc. 64. THE GOGGIN: Small exposure along track at "The Goggin" 2 km SE of
Elton (Ludlow anticline), Herefordshire; SO 4727 7004.
Upper Leintwardine Beds; Ludlow Series. Mould material.
Neobeyrichia confluens, Neobeyrichia lauensis, Calcaribeyrichia
tegula, Sleia cf. S. equestris, Zorotoxotis convallis, Atterdagia
Loc. 65. **BOW BRIDGE**: Small exposure 200 m from Bow Bridge along track towards Downton on the Rock (Ludlow anticline), Shropshire; SO 4290 7325.

Upper Leintwardine Beds; Ludlow Series. Mould material. **Neobeyrichia confluens**.

Loc. 66. **WIGMORE RD.**: Exposure along the Wigmore road (Ludlow anticline), Shropshire; SO 4930 7412 Holland *et al.*, 1963, loc. 27.

Upper Leintwardine Beds; Ludlow Series. Mould material. **Neobeyrichia confluens, Zorotoxotis convallis**.

Loc. 67. **FIDDLER'S ELBOW**: W side of A4113 road at Fiddler's Elbow, 3 km NE of Leintwardine, Herefordshire; SO 4266 7586. See Whittaker 1962.

Upper Leintwardine Beds; Ludlow Series. Mould material. **Neobeyrichia confluens, Neobeyrichia lauensis, Calcaribeyrichia tegula, Atterdagia versiculus**.

Loc. 68. **TRIPPLETON FARM**: A small hillside exposure approximately 600 m SSE of Trippleton Farm and just 10 m W of road from Burrington to Leintwardine, Herefordshire; SO 4145 7298.

Upper Leintwardine Beds; Ludlow Series. Mould material. **Neobeyrichia lauensis, Calcaribeyrichia tegula, Sleia cf. S. equestris, Zorotoxotis convallis, Atterdagia versiculus, Lophoctenella cf. L. scanensis**.

Loc. 69. **LUDFORD LANE I**: N side of "Ludford Lane", about 70 m W of junction with A49 road, Ludlow, Shropshire; SO 5119 7413.

Topmost Upper Whitcliffe Beds; Ludlow Series. Mould material.

69a. 5 cm below the Ludlow Bone Bed. **Nodibeyrichia verrucosa, Londonia cf. L. fissurata, Londinia arisaigensis, Frostriella groenvalliana, Lophoctenella sp.**

69b. 10 cm below the Ludlow Bone Bed. **Nodibeyrichia verrucosa, Londonia cf. L. fissurata, Londinia arisaigensis, Frostriella groenvalliana.**
Loc. 70. WHITCLIFFE QY.: Old quarry in Whitcliffe, 300 m WSW of Ludford Bridge, Ludlow, Shropshire; SO 5096 7414. Holland et al., 1963, loc. 6.
Upper Whitcliffe Beds; Ludlow Series. Mould material.
Calcaribeyrichia torosa.

Loc. 71. DOWNTON CASTLE BRIDGE: Trackside exposure just SW of Downton Castle Bridge, Herefordshire; SO 4445 7427. (cf. Holland et al., 1963, loc. 56).
Upper Whitcliffe Beds; Ludlow Series. Mould material.
Calcaribeyrichia torosa.

Loc. 72. STONEPITS COPPICE: Old quarry in Stonepits Coppice, 3 km NE of Leintwardine, Herefordshire; SO 4360 7730.
Upper Whitcliffe Beds; Ludlow Series. Mould material.
Calcaribeyrichia torosa.

Loc. 73. LUDFORD LANE II: N side of "Ludford Lane", about 70 m W of junction with A49 road, Ludlow, Shropshire, SO 5119 7413.
(Directly above locs. 69a, b).
Downton Castle Sandstone; Downtonian. Mould material.
73a. 0.5 m above Ludlow Bone Bed. Londinia arisaigensis, Frostiella groenvalliana.
73b. 1.5 m above Ludlow Bone Bed. Londinia arisaigensis, Frostiella groenvalliana.
73c. 2.0 m above Ludlow Bone Bed. Frostiella groenvalliana.

Loc. 74. LUDFORD LANE III: At junction of "Ludford Lane" and A49 (Leominster) road, Ludlow, Shropshire; SO 5123 7413. Holland et al., 1963, loc. 7.
Downton Castle Sandstone, about 2.75 m above Ludlow Bone Bed. Londinia arisaigensis, Frostiella groenvalliana.