THE TAXONOMY, PHYLOGENY AND PALAEOBIOGEOGRAPHY OF THE TRILOBITE FAMILIES PLIOMERIDAE AND ENCRINURIDAE:

Reconstructing the Ordovician world using evolving lineages.

Volume 1 and Volume 2 together

Submitted for the degree of Ph.D.
by
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September 1997

DECLARATION

This thesis is the result of research carried out between October 1993 and September 1997 in the Department of Geology and Applied Geology, University of Glasgow, under the supervision of Dr. Alan W. Owen

This thesis is the result of my own independent research and any published or unpublished material used by me has been given full acknowledgement in the text.

Simon Peers
September 1997

ABSTRACT

The phylogeny of the Family Pliomeridae and the Ordovician representatives of the Encrinuridae was investigated using cladistics. This resulted in the diagnosis of seven subfamilies; five of pliomerids (including one erected herein) and two subfamilies of encrinurid: the Cybelinae and Encrinurinae. Some 75 genera and 12 subgenera are also diagnosed on the basis of cladistic analysis of over 180 relatively complete species. This facilitated the placement of numerous incomplete or anomalous species such that the overall analysis allowed the systematic placement of over 300 species including 159 species of pliomerid and 149 species of encrinurid. The phylogenies produced by this analysis are robust, being resistant to disruption by the addition of incomplete taxa and in showing a close match between branching order and stratigraphy. A recurring evolutionary pattern is demonstrated. Very short initial periods of rapid diversification of clades, accompanied by reduced levels of character burden, were followed by steady ramification of the newly developed subclades. This pattern of development is observed to be independent of scale, occurring at all levels of systematic hierarchy. As a result many taxa are expressly paraphyletic which may be the norm in cladistic analyses.

The taxa studied provide an excellent geographical and temporal spread for the investigation of Ordovician palaeobiogeography; the Pliomeridae being particularly useful for the early Ordovician, the Encrinuridae for the middle and late Ordovician. The palaeobiogeography was investigated by first elucidating the phylogeny of the clades and subclades through time and then assessing the palaeogeographical distribution of the taxa in the light of their evolutionary relationships. This palaeobiogeographical assessment was made both qualitatively and by means of geographical character optimisation and calculated gain/loss ratios. The two approaches supported each other. In addition to the detailed terrane-by-terrane results for each subclade, the following recurring patterns were observed: During the early Ordovician, Laurentia was juxtaposed to the eastern margin of Gondwana and close to areas of South America. Towards the end of the early Ordovician, Laurentia and Gondwana diverged, and did not subsequently re-approach each other during the Period although the Argentine Precordillera was situated in a position between Laurentia and Gondwana in the Llanvirn. This supports a modified verision of the model of Dalziel for the early Ordovician in which Laurentia and Gondwana are close, but not in contact, but that of Scotese & McKerrow and others for the mid- and late Ordovician. Throughout the Ordovician oceanic islands provided stepping stones for faunal migration between the main continental plates.

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CHAPTER 1

INTRODUCTION

1. Introduction:

The aim of this thesis is to explore the palaeobiogeography, and hence the palaeogeography of the Ordovician using selected groups of trilobites. Various possible approaches to reconstructing palaeobiogeography are discussed by Fortey & Mellish (1992). The approach which is utilised here is the 'key taxon' approach which involves reconstructing the detailed phylogenetic history of individual groups and linking this to their changing temporal and stratigraphical locations in order to make inferences about their palaeobiogeography, and hence the changing pattern of palaeogeography through time.

Used carefully, trilobites have been demonstrated to be excellent indicators of biogeography during the Ordovician (Fortey & Mellish 1992, Fortey & Cocks, 1992). The families Pliomeridae and Encrinuridae were selected for investigation in the present study for the following reasons:

1. They are species-rich clades.
2. They are known from many localities across a very wide geographical spread, both at the present and during the Ordovician.
3. Together they ranged throughout the Ordovician, from the early Tremadoc to the late Ashgill.
4. The taxa display a large number of discrete characters which are amenable to coding for cladistic analysis.
5. Some recent attempts have been made to elucidate the major relationships of the subfamilies Cybelinae and Encrinurinae within the Encrinuridae, e.g. Evitt & Tripp (1977), Temple & Tripp (1979), Strusz (1980), Fortey (1980b), Edgecombe *et al* (1988), Edgecombe & Chatterton (1990), Temple & Hong-Ji (1990), Edgecombe & Chatterton (1992), Lespérance & Desbiens (1996) but it is clear that many of the taxa, from species upwards, require more rigorous definition if their phylogeny (and hence biogeography) are to be understood.

The approach taken to resolving the detailed phylogeny and biogeography of the groups considered here was as follows:

1. Cladistic analyses were carried out for each of the Pliomeridae, Cybelinae, Dindymeninae, *Atractopyge*, *Cybeloides* and the Ordovician Encrinurinae, based on illustrations in the literature and specimens borrowed from museum collections, the datasets of which are included in the appendices. Any features particularly critical to the coding are illustrated by scanned images, line drawings or photographs.
2. The confidence which can be placed on the results of the cladistic analyses was assessed by means of the various consistency indices generated by the cladistic package used (PAUP) and by comparison of the branching order of the phylogeny with the stratigraphical ages of the taxa.
3. Informal inferences about the paleobiogeography and hence palaeogeography were made by comparison of the branching order with the stratigraphical ages of the taxa and their locations.
4. These informal inferences were followed by formal gain/loss ratio analyses of the ancestral areas of various nodes within the phylogenies following the method outlined by Smith (1994).
5. The results of the formal, and informal, analyses of palaeobiogeography are then discussed in terms of the likely palaeogeographical relationships and plate movements implied for each group.

CHAPTER 2

METHODS

2. Methods;

2.1 Cladistic Methodology;

The initial analyses in this thesis were carried out using PAUP version 3.1.1 on an Apple Macintosh Performa computer. The characters employed in the analysis were unweighted (except by the process of character selection and coding itself). The great majority of the characters were of unordered type. Where characters were ordered, the reasons for doing so and the logic behind their ordering is explicitly discussed within the character listing. All of the datasets were too large to allow exhaustive or branch and bound searches to be used in their analysis so heuristic searches were utilised instead.

It has been stated by a variety of authors that the order of entry of taxa into a dataset affects the results of a heuristic search. (e.g. Lespérance & Desbiens, 1995). As a basic check of the data, the taxa were re-ordered and the analyses run again. The order of display of the taxa was indeed altered, with the species being displayed in the order in which they were entered, but the relative branching order of the taxa on the cladogram was unchanged Hence the phylogenetic structure of the results was unaffected.

2.1.1 Selection of taxa for analysis:

When investigating the large scale relationships of taxa it is not possible to include all of the species in the analysis (see Edgecombe *et al.* 1988, Edgecombe & Chatterton 1990, Edgecombe & Chatterton 1992, Lespérance & Desbiens 1996, Smith 1994). As the taxa included affect the patterns of character change which develop on the cladogram, and hence the topology of the cladogram derived by the analysis, it is important to select which taxa to include carefully. In the large scale analysis of the Pliomeridae and Cybelinae there were too many taxa for it to be practicable to code them all. My approach to this problem was to include the following species:

1. The oldest known representative(s) of any clearly recognised, unambiguously monophyletic genus which displays a character coding fully shared by the majority of the taxa in the genus, including the type species, and which is as close to being complete as is practical.

2. Any members of the genus whose features differ from those of the oldest known member of the genus in the characters analysed.
3. Any taxa which are not part of a clearly recognised monophyletic sub-clade.

This selection of taxa for inclusion means that, for example, where a genus is clearly recognised as being unambiguously monophyletic only the basal species and any species which differ in their character codings from the basal species will be included. In contrast, a poorly understood group, or group made up of species of highly variable morphology may have all of its members coded and included in the analysis.

In the detailed relationship analyses, all of the species which are complete enough for coding were included in the analysis. These analyses include the following; *Atractopyge*, Dindymeninae, *Cybeloides* and Ordovician Encrinurinae.

Largely different suites of characters were employed in the detailed relationship analyses as, if the species and characters were coded correctly, the majority of the taxa in the analysis should have uniform character codings in those characters which were employed in the large scale analysis. Exceptions to this uniformity of character coding are those pleisiomorphic taxa which are basal to the monophyletic subclade and any taxa which subsequently developed new forms of one or more of the characters included in the large scale analysis. The characters in which these taxa differ from the other members of the subclade should be the only characters which are common to both scales of analysis. This method of choosing characters for analysis is strongly controlled by the burden of the characters employed in the analysis (See Section 2.1.9)

A number of taxa of uncertain affinity are too incompletely known for a sufficiently large number of characters to be coded to allow their inclusion in the main analyses. These taxa were added to the data sets separately after the main analysis had been run in order to discern their most likely taxonomic placement

2.1.2 Selection of characters for analysis:

Phylogenetic analysis using PAUP have been described as 'objective' (Lespérance & Desbiens, 1995). Unfortunately this is not the case. While it is correct to say that the actual program used in the analysis proceeds objectively, the choice of characters employed, the division of those characters into character states and decisions about the type of characters employed (i.e. ordered/unordered/stepmatrix etc.) is subjective. Only unordered and simple, reversible, ordered characters are utilised herein. The majority of the characters employed are of 'unordered type'. The method of character selection and coding employed in these analyses is largely that outlined in Smith (1994). The majority of the characters employed are discrete and either presence/absence or based on clearly defined different states of a single homologous feature. In a small number of characters, the character states which are defined are discrete, but divided arbitrarily. An example of this is the character 'Number of pygidial pleurae' in the Encrinurinae analysis, in which the number of pleurae is divided up into equally sized, arbitrary divisions.

Also included in the analyses are a small number of continuous characters which describe the shape of features. Their use has been avoided wherever possible because of difficulties in defining the boundaries between character states. Examples of these characters include 'Outline of the glabella = Concave/Parallel/Convex outwards' in the Encrinurinae analysis. Continuously variable characters have only been included where they are either inferred to be heterochronically controlled - i.e. a sequence of progression through the character states is observed in the ontogeny of one or more of the taxa involved - or where the character appears to be of high burden within monophyletic subclades of the taxa studied at the level of the analysis. For example if the analysis is largely performed at species level (detailed analysis) the character states must be stable within the species studied, similarly in the larger scale analysis, such as that of the Pliomeridae, continuous characters are required to be stable at genus level. Once again, the definition of the terms of the conditions controlling the analysis are to an extent controlled by the resolution at which the study is being conducted.

2.1.3 The ordering of characters;

There are three lines of evidence which can enable a character to be ordered (see below). In the present study characters were only set to be ordered where at least two (and usually three) out of the three possible lines of evidence were both available and in agreement.

1. Inferred logical sequence of development of a character. In this method a logical, parsimonious pathway for the development of one of the characters from

another is determined, e.g. if four recognisable states of a character are noted, and a logical sequence of development from one to the other may be inferred, and this inferred sequence does not conflict with the observed stratigraphical order of appearance of the taxa (see **2**), and the sister groups to the group in question display the form of the character which is inferred to be the most 'primitive', it is reasonable to regard these characters as representing an ordered sequence. A rare example of such ordering from these analyses of such ordering is the form of the anterior border of the cranidium in *Atractopyge* (see Chapter 5).

2. Stratigraphical evidence. The stratigraphical order of appearance of the character states in the fossil record may provide information on the proper ordering of the character.

3. Ordering of characters on the basis of ontogenetic information. The sequence of development of the various states of the character in the ontogenetic history of one of the taxa involved provides strong evidence for the correct ordering of the character states in the sequence. When a heterochronic sequence is observed it also provides evidence of the mechanism for its derivation.

On completion of the analysis, the effect and validity of ordering the character was assessed by comparing both the branching order of the phylogeny and the order of development of the various character states to the stratigraphical order of the taxa and any anomalies are investigated.

2.1.4 Problems encountered in the coding of characters for analysis and the resolutions employed;

An area which does not receive the coverage that it deserves in published cladistic studies is that of how problems encountered in the coding of characters for analysis were addressed. Discussion of these problems is crucial as the techniques employed in coding the characters may strongly affect the outcome of the analysis.

2.1.4.1 Coding characters which are applicable to only some sections of the group studied:

The problem of how to code characters which only apply to subsections of the group under study is frequently encountered and it is unfortunate that PAUP has no mechanism for coping with it. Such characters are those that refer to states of a feature which is not present in all of the taxa. An example of this used by Smith (1994) is that of the structure of crinoid pinnules, which cannot be coded for species which do not display pinnulate arms. These characters are then additional characters which depend on the previous acquisition of another character. The possible ways to handle this problem are as follows:

A. To add an extra state representing 'N/A' for those taxa in which the character is not applicable. This has the unfortunate effect of lumping together all those species for which the character concerned is not applicable. This is because PAUP treats the 'Not Applicable' character state as a statement of positive linkage. This may or may not be desirable depending on the character and its distribution amongst the taxa involved.

In addition, if a set of several related characters is not applicable to certain species because of a single factor, then repeatedly adding an 'N/A' character state to all of the characters affected will have the effect of heavily weighting the single (absent) feature. For example, in the case of the Encrinurinae the group of characters which relate to the ordering of the tubercles on the frontal lobe is not applicable to a large number of species in the lower portion of the cladogram in which these tubercles are not ordered. Adding a 'N/A' character state to all 4 or 5 of the characters affected by this would have the effect of introducing the character 'Frontal lobe tubercles Ordered/ Unordered' and weighting by a factor of five.

Finally, and most importantly, the amalgamation of all of the dependent characters into a single multistate character, together with the 'Present/Absent' character, entirely obscures the primary linkage of the taxa involved - which is the presence or absence of the character upon which the non-ubiquitously applicable characters depend. This is undesirable as it is obviously a highly important character in an evolutionary sense as it has spawned other, dependent characters. To further utilise the example used by Smith (1994): if the non-ubiquitously applicable character 'Form of the Pinnules' is coded as 'pinnules absent/pinnules present and terminating in a hook/pinnules present and terminating bluntly' the primary character 'pinnules present/absent' is masked by the splitting up of the 'pinnules present' state of the character, obscuring the lower resolution apomorphy (Pinnules present/absent) for the sake of the dependent character which is, by definition, evolutionarily 'less important'.

B. To only employ ubiquitously applicable characters in the analysis, only include the basal taxa of such groups in the analysis (if they are known to be monophyletic), and run separate sub-analyses to discern the relationships within such groups. This method fails in that there are insufficient characters which are derived unambiguously once and not then secondarily lost again to make up a useful data set.

C. To include a binary presence/absence character for the feature upon which the non-ubiquitously applicable character depends and a second character to describe the states of the dependent character. This second, descriptive, character is then coded as '?' (missing/unknown) in those species for which it is not applicable.

This is the approach adopted herein although it is recognised that PAUP attempts to apply all possible states of the descriptive, non-ubiquitous, character to taxa in which it is coded as '?'. This is sub-optimal for two reasons:

1. The character is not applicable to the taxon and so applying a value to it is misleading.
2. The large number of apparently missing data in the data set ('?') may result in the production of a greater number of trees by PAUP, which attempts to fit all possible character states to characters coded as ? (missing) to allow for the apparent uncertainty in the data set.

2.1.4.2 The coding of paedomorphic sequences:

In a number of cases it is possible to determine similarities between the adults of one taxon and the juveniles of a closely related taxon, i.e. the characters observed are heterochronically controlled. This obviously provides useful information on the relationships of the taxa concerned which should, if possible be included in the analysis. The problem of how to code this type of character is similar to that of coding non-globally applicable characters discussed above - except in this case, rather than simply being present or absent, the various character states may be present or absent in the organism as a whole, in all stages of its life, or present at various developmental stages in one taxon and other stages in a different taxon.

The method employed by Edgecombe *et al* (1988) in their broad-brush analysis of the Cybeline and Encrinurinae was to code the appearance of characters at a particular stage as a isolated event. This method avoids the directional forcing and bias introduced when characters are ordered simply or set to user defined character transformation paths. This method does however lose the sense of changes in developmental timing and of a developing sequence of events, treating each character state as a unique feature rather than being part of a dynamic system.

Because of the reliance of these characters on knowledge of the character states prevalent at different stages of development, they are particularly susceptible to missing data. The low preservation potential of juvenile stages relative to that of the adults and the difficulty of assigning the various juvenile morphologies to the correct adult taxon means that for any group of taxa, the ontogenies of the component taxa are unlikely to be known in full for more than a small number of those studied. This high proportion of missing data reduces the breadth of applicability and hence the usefulness of characters which are based on ontogenetic information.

2.1.4.3 Autapomorphic characters:

Autapomorphic characters (as opposed to autapomorphic character states of broadly applicable characters) are excluded from the analyses wherever possible as they provide no information on the relationships of the taxa. The only occasions in which they are included is when they are the only feature differentiating a taxonomic group from its sister group (e.g. see the Cybelinae and *Cybeloides* analyses concerning the pulvinus of *Cybeloides*).

2.1.4.4 Outgroup selection and character polarisation:

The only polarisation of characters which has been employed in the present study is in those rare cases where a character is explicitly defined as being of ordered type. Outgroups have not been used to polarise the characters in any way. Because of this, the same phylogeny results in each of the analyses irrespective of whether any of the species in that analysis are defined as an outgroup or not.

Obviously, it is useful during interpretation to view the phylogeny from the same 'angle' each time to allow comparison of the features on the cladograms and to allow comparison of the position of the taxa in the phylogeny to their stratigraphical age. To facilitate this, the cladograms and phylograms have been oriented by positioning the oldest taxon in the analysis at the base of the diagram. It should be stressed that this in no way affects the results of the PAUP analysis or the relative positions of the taxa within the phylogenetic tree and is purely a matter of representational convenience.

Similarly, when the characters employed in the analyses are defined, there is no ordering of the character states presumed - beyond any explicit ordering of characters which is stated in the character definition. For example, this means that if a character has two states which are defined as being '0' and '1' there is no presumption that state '0' is more 'primitive' than state '1'.

There has also been no polarisation of characters by means of the definition of ancestral taxa as this also introduces another level of subjectivity into the analysis beyond the levels already present in taxon selection, character selection and any explicit character ordering.

2.1.5 Assessment of the cladograms produced by the analyses:

The level of confidence which could be placed in the cladograms produced by the analyses was assessed in a number of ways:

1. The Consistency Index (C.I.) and the rescaled Consistency Index (R.C.I.) of each cladogram were compared to the C.I. expected from analyses of the same number of taxa and characters made using random data. (Klassen *et al.*, 1991).
2. The number of trees produced by the analysis was evaluated. If a large number of trees was produced for an analysis, little confidence could be held in any one of the resulting trees. If more than one tree was produced, the cause of the generation of multiple trees was identified and evaluated. The inferred cause of the production of multiple trees was stated and its impact on the reliability of the phylogeny was informally estimated.
3. The branching order of the phylogeny was compared to the stratigraphical ages and ranges of the component taxa (see Wagner, 1995). This provided an independent check on the phylogeny, the closer the match of the branching order of the phylogeny to the stratigraphical order of the taxa, the more confidence could be held in the topology of the tree. This technique also highlighted areas of anomaly in the cladogram which were not identifiable in any other way. Where this occurred, the source of the anomaly was investigated and stated, whether due to the topology of the tree or the age assigned to the taxa.

2.1.6 Systematic conventions employed:

All attempts have been made to restrict the taxa recognised in this thesis to monophyletic taxa. While no polyphyletic taxa are retained, it has proved impossible to avoid the recognition of a number of paraphyletic taxa as successful groups give rise to descendants and so are, by definition, paraphyletic as they do not include all ancestors of the taxa included.

2.1.7 Basal 'stem' taxa:

In many cladistic analyses there are 'stem taxa' i.e. pleisiomorphic intermediates which display some, but not all, of the characters of the subclade of which they are at the base. These taxa may or may not have any autapomorphies of their own. Their placement is problematical when attempting to define higher taxonomic units such as genera or subfamilies as these taxa may lack all but one of the apomorphies by which members of the derived clade are recognised and so more closely resemble taxa in more pleisiomorphic groups. The system followed here has been to assign these taxa as *sensu lato* members of the higher level group at the base of whose subclade they are situated. I do not favour the erection of monospecific higher groups, such as genera and subfamilies, as this results in redundancy of information with, for example, the species and genus diagnoses overlapping. As a result the generic diagnosis provides no further information about the relationships between various taxa than does the specific diagnosis, making the generic assignment redundant. In spite of this, there is a potential benefit in recognising monospecific genera in the case of stem taxa which have accumulated a number of significant autapomorphies as this allows recognition of the large difference between the pleisiomorphic taxon and the crown group of the subclade.

On completion of the analysis, it is clear that a number of the monospecific genera which have been erected in the past are stem taxa which are basal to monophyletic groups. These taxa lack most of the diagnostic apomorphies of the groups which they base and so, without cladistic analysis, have proved difficult to convincingly assign correctly to inclusive monophyletic systematic units.

2.1.8 Hierarchies:

Different hierarchical levels are recognised in the evolutionary history of taxa and are reflected in the hierarchical nature of systematics - individuals, populations, subspecies, species, genera, subfamilies etc. The hierarchical levels employed in an analysis determine the resolution with which the relationships of taxa are examined. For example, a study of the family level relationships of a group does not clarify the relationships of taxa within a particular family. Moreover, there may be a degree of independence of the characters utilised at different taxonomic levels and the taxonomic burden of a character may vary from level to level.

2.1.9 Polychotomies:

In cladistics it is often assumed that cladogenesis occurs as a result of dichotomous branching events. This assumption is not made for these analyses.

Smith (1994, p. 134) recognised that a trichotomy (and, by inference, a polychotomy) could be formed in a cladogram for two basic reasons: character conflict and lack of information. He stated that trichotomies resulting from character conflict (i.e. consensus trees) could not be used in the creation of phylogenetic trees. This view is followed herein. Smith (1994 p. 134, fig. 6.3) outlined three main evolutionary cases in which a lack of information in the relationships of three taxa (A, B and C) could lead to a trichotomy in a cladistic analysis: A being ancestral to both B and C, giving rise to them at a classic bifurcating node with A not persisting beyond the time of bifurcation. A being ancestral to both B and C in sequence and persisting beyond the time of development of both of them. A being a sister group to both B and C.

Wagner & Erwin (1995) provided examples of stasis resulting in the presence of polychotomous nodes within species-level cladograms and Hoeizer & Meinick (1994) discussed various methods by which polychotomous nodes could result in cladistic analysis as a result of normal evolutionary processes. These latter examples included both stasis and the situation where one ancestral species simultaneously gives rise to multiple descendent species, resulting in a polychotomous branching pattern. Polychotomous nodes are present in some of the minimum length trees which result from the present analyses and are discussed in the relevant chapters.

2.2 Biogeographical methods:

2.2.1 Informal analysis of the data:

This involves comparison of branching order of the taxa on the cladogram with the stratigraphical ages of the taxa and their geographical, or palaeogeographical, locations. In this method, the biogeographical history of the taxa is effectively read straight off the cladogram. This approach has the drawback that when a large number of palaeobiogeographical areas are represented on the cladogram it may be difficult to discern a pattern and to interpret the overall pattern of changing palaeobiogeographical affinity on the cladogram. Additionally, there is a high risk of the researcher 'seeing' what is expected in the data.

2.2.2 Formal Gain/Loss ratio analysis:

These were conducted according to the technique outlined by Smith (1994 p. 194 and references therein). After construction of the cladogram using morphological data, the geographical, or palaeogeographical areas in which the taxa were found were coded as being present or absent and optimised on the cladogram. Each area was then treated as if it was not part of the ancestral area and had subsequently been inhabited. The number of these gains was then recorded. Next, each area was treated as if it was part of the ancestral area and the number of times that the area must have been 'lost' to give the pattern observed on the cladogram was recorded. Lastly, the gain/loss ratio for each area was calculated. This gives some, relatively impartial, measure of the probability of each location having been part of the ancestral area of the node under study. This process is then repeated for all nodes of interest in the cladogram. As the branching order up the cladogram should roughly correspond to the age of the taxa, the gain/loss ratios for the nodes throughout the cladogram can be used to determine the pattern of biogeographical change through time. The age of the nodes for which the ancestral areas have been determined are identified allowing successively changing ancestral areas to be charted against a time axis to reconstruct the changing biogeographical pattern.

There are several problems affecting palaeobiogeographical studies which utilise Gain/Loss ratios, reducing the level of 'impartiality' of the technique, the principal ones being:

1. The technique depends upon the accurate assignment of fossil localities to either geographical or palaeobiogeographical units. These units are potentially open to some subjectivity - should localities be grouped together which are a few metres apart?, a few kilometres?, on the same terrane?, on the same continent? on the same palaeocontinent? While the level at which geographical areas are grouped together for the gain/loss analysis was originally thought likely to affect the outcome of the study this has, in fact, proved not to be the case (See Chapter 6).
2. Selection of nodes for examination in the gain/loss study. Unless the gain/loss ratios of all of the nodes are studied, the subjective selection criteria employed by the researcher will influence the result obtained.
3. All of the perennial problems of the quality of palaeontological data, such as differential preservation, sampling bias, taphonomic and taxonomic bias are present in Gain/Loss analyses.
4. Polychotomous nodes on the cladogram make it difficult to optimise areal data.

While not entirely free from bias, the gain/loss ratios have an explicit methodology and are a useful method of verifying and formalising biogeographical conclusions.

CHAPTER 3

THE PLIOMERIDAE RAYMOND, 1913

3.1 Introduction:

The Pliomeridae is a geographically widespread family which was at its most diverse during the Tremadoc and Arenig. Many of the genera which make up the Pliomeridae are poorly known because of the limited material available of each species. This means that the variability, or otherwise, of many of the characters employed in their taxonomy is uncertain.

The Pliomeridae have not previously been subject to a cladistic analysis and the present analysis is intended to be a 'first attempt' at a phylogeny for the family. The main aim of is to cast light on relationships between genera and to determine which, if any, of the pliomerids might be regarded as potential outgroups to the Subfamily Cybelinae.

The pliomerids have proved to be a problematic group to analyse cladistically. Genera within the Pliomeridae have traditionally been diagnosed on the basis of a small number of characters many of which are subjective, commonly being based on the interpretation of relative shapes or proportions. In addition, on analysis of the data matrix it is clear that a large number of the character states are independently derived within several of the subclades. A number of the remaining characters employed are only poorly known as they are situated on areas of the exoskeleton, such as the hypostome, which are only rarely preserved in association with other body parts.

The definition of the Pliomeridae itself, and that of other groups such as the Cybelinae is also problematical. There are no unique apomorphies supporting the Pliomeridae and Cybelinae as currently defined.

None of the pliomerid genera display all of the characters which might be expected in an outgroup to the Cybelinae as determined from the Cybelinae analysis (see chapter 4) such as; a glabella which is subparallel sided or which widens forwards; four lateral glabellar furrows or a bifurcate S3; an anteromedian complex - particularly a longitudinal anteromedian furrow; straight eye ridges cutting the adaxial side of the genal field; genal spines; a smooth hypostome with two raised areas, one either side of the middle body; broad anterior hypostomal wings; anterior pleural fields on the pygidium; an elongate terminal piece on the axis of the pygidium with transverse furrows and out turned tips to the pygidial pleurae. All of these characters are found scattered within various members of the Pliomeridae. This makes the selection of the pliomerid genus best suited as an outgroup to the Cybelinae difficult.

Further work also needs to be done to resolve both the relationship of offshoot groups, such as the Cheiruridae, to the main body of the Pliomeridae and the species level relationships within pliomerid genera. Time constraints prevent these analysis being done as part of the present project.

3.2 Methodology employed in the analysis:

The methodology followed in this analysis is that outlined in Chapter 2. While it has been suggested that the Pilekiinae were ancestral to the Pliomeridae the boundary between the two groups is poorly defined and so representatives of the Pilekiinae were included in this analysis. As in all of the analyses in this study, none of the characters are polarised and no ancestral state has been forced for any of the characters. Because of this, the same phylogeny results from this analysis whether any of the species are defined as an outgroup or not. Obviously, it is useful during interpretation to view the phylogeny from the same 'angle' each time and so, for display purposes only, the phylogeny was oriented so that the oldest known pilekiid, *Parapilekia olesnaensis* (Růžička, 1935), was placed at its base It should be stressed that this in no way affects the results of the PAUP analysis or the relative positions of the taxa within the tree and is purely a matter of representational convenience.

3.3 Current systematic position of the taxa studied in this analysis:

3.3.1 The current systematic situation of the taxa studied here;

The oldest taxa in this analysis are members of the Pilekiinae, a group which was originally placed as a subfamily within the Pliomeridae (Harrington *in* Moore 1959). Lane 1971 subsequently classed the Pilekiinae with the Cheiruridae although without description or discussion of the characters linking the to two groups. Demeter (1973), Terrell (1973), Young 1973 and Fortey (1980) followed Harrington (1957) in regarding the Pilekiinae as a subfamily within the Family Pliomeridae. Přibyl *et al.* (1985) concurred with Lane (1971) in the assignment of the Pilekiinae to the Cheiruridae but highlighted the indistinct nature of the boundary between the Subfamily Pilekiinae and the Family Pliomeridae (and in particular, the Subfamily

Protopliomeropinae). They recognised the numerous similarities between the Pilekiinae and Pliomeridae but were uncertain as to whether these similarities were the result of a close evolutionary relationship or of convergence. They thus regarded the Pilekiinae/Pliomeridae boundary as being, to an extent, one of convention. This raised questions as to the systematic relationship of the Pliomeridae to the Cheiruridae which they declined to explore until further work on the systematics of the Pliomeridae had been done. They did however (1985 p. 116), highlight a few inconsistencies between the systematic placement of some taxa by Demeter (1973) and the evolutionary relationships inferred by him.

3.3.2 Systematic groupings employed in the Treatise (Moore, 1959):

The systematic groupings utilised in the Treatise are listed in order to allow comparison with the phylogeny derived from this analysis.

Family	**Subfamily**	***Genus***
Pliomeridae	Pliomerinae	*Pliomera* *Cybelopsis* *Pliomerina* *Pliomerops* *Pseudomera*
	Pilekiinae	*Pilekia* *Anacheirurus* *Metapilekia* *Metapliomerops* *Parapilekia* *?Emsurina* *?Seisonia* *?Tesselacauda*
	Protopliomeropinae	*Protopliomerops* *Hintzeia* *Kanoshia* *Leiostrotropis* *Pliomeroides* *Protopliomerella* *Pseudocybele* *Rossaspis* *Strotactinus*
	Pliomerellinae	*Pliomerella*
	Placoparinae	*Placoparia*
	Diaphanometopinae	*Diaphanometopus*

3.4. Listing/discussion of the Pliomeridae considered in this analysis:

3.4.1 Species included in the analysed data set:

The criteria upon which selection of which taxa were to be included in the analysis were based were discussed in section 2.1.

Alwynulus perigrinus	Tripp, 1967 Stinchar Limestone (uppermost Llanvirn - lowest Caradoc), Girvan, S.W. Scotland
Anacheirurus plutonis	Bulman & Rushton, 1973 Deanshanger Borehole, England *A. tenellus* graptolite Zone (Tremadoc).
Anapliomera shirlandensis	DeMott, 1987 Platteville Group, Grand Detour Formation, *foliaceus* graptolite Zone (M. Caradoc) Winnebago County, Illinois, USA
Canningella hardmani	Legg, 1976 Emanuel Formation (Arenig) Australian graptolite Zone Be1/Be2, =L./Mid. *deflexus* graptolite Zone (American shelly Zone G1 or G2) Prices Creek Area, Canning Basin, Australia
Colobinion julius	(Billings, 1865) (see Whittington, 1961) in a boulder in a conglomerate from the Cow Head Group, Whiterock Stage, Lower Head, Newfoundland of *D. hirundo*-L./Mid. *artus*(='*bifidus*'), graptolite Zone age, so *Colobinion julius* must either be contemporaneous or older than this.

Cybelopsis speciosa	Poulsen, 1927 (see Hintze, 1953) Pogonip Group (Shelly Zone J) =Mid. *nitidus* graptolite Zone Western Utah and Eastern Nevada
Ectenonotus progenitor	Fortey & Droser, 1996 *Psephosthenaspis zone* above 'K' coquina bed =Upper *nitidus* graptolite Zone Utah, Eastern Nevada
Encrinurella reedi	Legg, 1976 Emanuel Formation (Arenig), Australian graptolite Zone Be 3/4, = Upper *deflexus* -Lower *nitidus* graptolite zones, (USA shelly Zone G2-H) Price's Creek, Canning Basin, Australia
Evropeites hyperboreus	Fortey, 1980 Valhallfonna Formation, Profilbekken Member, V_{4a-b} =Shelly Zone K-M, Upper *nitidus*-Mid. *artus* graptolite zones. Northern Ny Friesland, Spitsbergen
Gogoella wadei	Legg, 1976 Emanuel Formation (Arenig), Australian graptolite Zone Be1/Be2, Lower *deflexus* graptolite Zone, (USA shelly Zone G1 or G2) Prices Creek area, Canning Basin, Australia
Hintzeia celsaora	(Ross, 1951) [= *H. aemula* (Hintze, 1953)] Garden City Formation

	Shelly Zone G1- G2, Migneintian -Top *deflexus* graptolite Zone (U. Tremadoc-L. Arenig), Utah
Hintzeia firmimarginis	Hintze, 1953 Pogonip Group (Shelly Zone G1) U. Tremadoc, Mid. *superbus*-Mid. *phyllograptoides* and *approximatus* Baltoscandian graptolite zones, W. Utah & E. Nevada
Hintzeia taoyuanensis	Liu, 1977 Lower part of the Madaoyu Formation, M.-U. Tremadoc, Hunan, S. China.
Ibexaspis brevis	(Young, 1973) Fillmore Limestone Shelly Zone H =Mid *nitidus* graptolite Zone. Ibex in Utah
Kanoshia kanoshensis	Hintze, 1953 Pogonip Group American Shelly Zone M, =M.-U. *artus* British graptolite Zone. Western Utah and Eastern Nevada
Landyia elizabethae	Jell, 1985 Digger Island Formation, Australian Lancefieldian Zone 1, *K. meridionalis* Argentinian Zone, =M. Cressagian Stage of the Tremadoc, =Upper *flabelliformis socialis* - *flabelliformis flabelliformis* Baltoscandian graptolite zones. Waratah Bay, Victoria, Australia.
Metapilekia bilirata	Harrington, 1938 *Notopeltis orthometopa* Zone, Upper Tremadoc

Quebrada de Coquena, West of
Purmamarca, Argentina (see Fig. 3.1)

Parahawleia insculpta Zhou, 1978
Ashgill, Eastern China,

Parapilekia anxia Sdzuy, 1955
Leimitz shale =*tenellus* graptolite Zone,
Germany

Parapilekia speciosa * (Dalman, 1827)
L. Ord, Upper Tremadoc, Sweden

Perissopliomera maclachlani Ross, 1970
Antelope Valley Limestone,
American shelly Zone N,
D. murchisoni graptolite Zone.
Hot Creek Canyon, Nevada, USA

Pilekia apollo (Billings, 1860)
Tremadoc, Canada

Recognised as a junior synonym herein:
(?*Pilekia sp.* Jell, 1985)

Digger Island Formation,
Australian Lancefieldian Zone 1,
K. meridionalis Argentinian Zone,
=M. Cressagian Stage of the Tremadoc,
=Upper *flabelliformis socialis* -
flabelliformis flabelliformis
Baltoscandian graptolite zones.
Waratah Bay, Victoria, Australia.

This is the oldest recorded species of *Pilekia* and appears to be identical to *Pilekia apollo* (Billings, 1860), although differences may become evident with the discovery of further material.

Pilekia olesnaensis (Růžička, 1935)
Třenice and Mílana Formations
(L -U. Tremadoc), Bohemia

Recognised as a junior synonym herein:
Pilekia ferrigena Mergl, 1994

	Třenice Formation (L Tremadoc), Bohemia
Placoparia (Placoparia) cambriensis	Hawle & Corda, 1857 Llanvirn, Armorican Massif
Pliomera fischeri	(Eichwald, 1825) Serpentine Conglomerate, Arenig/Llanvirn boundary Otta, Norway.
Pliomerella girvanensis	Reed, 1930 Basal Superstes Mudstones Aldons Quarry, *Nemagraptus gracilis* graptolite Zone Girvan, S.W. Scotland
Pliomerina austrina	Webby, 1971 Caradoc (post *N. gracilis*) Utilised for coding as complete while *martelli* is very incomplete.
Pliomeridius? lacunatus	Dean, 1989 Outram Formation American Shelly Zone J =Mid *nitidus* graptolite Zone. Wilcox Pass, Alberta
Pliomeridius sulcatus	Leanza & Baldis, 1975 Llanvirn, Argentina See Fig. 3.1
Pliomeroides deferrariisi	(Harrington, 1938) L. Ord, Argentina see Fig. 3.1
Pliomerops senilis	(Barrande, 1852) (see Shaw, 1968) Šárka Formation, Llanvirn ? Vosek, Czech Republic
With hypostome coded from	*Pliomerops canadensis* (Billings, 1859) (see Shaw, 1968 and Whittington, 1961)

	Chazy Formation upper Llanvirn-Lower Caradoc Little Hammer Island, Champlain Valley, Isle La Motte, New York, Crown Point Valcour Island, St Lawrence Lowlands, USA & Canada
Protoencrinurella maitlandi	Legg, 1976 Emanuel Creek, Canning Basin, Australia, Nambeet Formation, Australian Bendigonian Zone, Australian graptolite Zone Be2, Mid *deflexus* graptolite Zone, Lower Arenig, (USA shelly Zone G2)
Protopliomerella contracta	Ross, 1951 Garden City Formation Shelly Zone G2, Mid *phyllograptoides*- Upper *deflexus* graptolite zones, Utah
Protopliomerops hamaxitus	Jell & Stait, 1985 Florentine Valley Formation, Late Tremadoc-Early Arenig, Approx. Lancefieldian Zone 1.5- Lancefieldian Zone 2 or pos. Lancefieldian 3 Australian zones = *sedgwickii* /*salopiensis* shelly Zone- '*phyllograptoides*' graptolite Zone Tim Shea area, Tasmania,
Protopliomerops lindneri	Jell, 1985 Digger Island Formation, Australian Lancefieldian Zone 1, *K. meridionalis* Argentinian Zone, =M. Cressagian Stage of the Tremadoc, =Upper *flabelliformis socialis* -

	flabelliformis flabelliformis Baltoscandian graptolite zones. Waratah Bay, Victoria, Australia.
Protopliomerops quattuor	Hintze, 1953 Pogonip Group Shelly Zone G2 and H =Mid *phyllograptoides*- Mid *nitidus* graptolite zones. Western Utah and Eastern Nevada
Protopliomerops seisonensis	Kobayashi, 1934 Lower/Mid Tremadoc South Chosen, China
Pseudocybele lemurei	Hintze, 1953 Pogonip Group (Shelly Zone H,I) =Lower-Mid *nitidus* graptolite Zone. Western Utah and Eastern Nevada
Pseudomera cf P. insolita	Poulsen (in Hintze, 1953) Pogonip Group American Shelly Zone J, =Mid *nitidus* graptolite Zone. Western Utah and Eastern Nevada
Pseudomera barrandei	(Billings 1865) see Hintze, 1953 Upper Pognip Group Utah and Nevada American Shelly zones M, N = Mid *artus*- Mid *murchisoni* graptolite zones. also see Whittington (1961) American Shelly zones J,K,L =*nitidus-gibberulus* graptolite zones. also see Tremblay & Westrop (1991) American Shelly Zone M Mid - Upper *artus* graptolite Zone.
Quinquecosta williamsi	Tripp, 1965 Doularg Formation

	Nemagraptus gracilis graptolite Zone (L. Caradoc), Girvan, S.W. Scotland
Rossaspis ? pliomeris	Demeter, 1973 Fillmore Limestone, Ibex, Western Utah, USA. American shelly Zone D - E? =*tenellus* graptolite Zone.
Rossaspis superciliosa	(Ross, 1951) Garden City Formation, Utah Shelly Zone F Upper Tremadoc, Lower Migneintian, *supremus* Baltoscandian graptolite Zone.
Strotactinus insularis	(Billings 1865) (see Fortey, 1979) Catoche Formation (L. Arenig) Shelly Zone (?G),H,I =Lower-Mid *nitidus* graptolite Zone, Port au Choix, W. Newfoundland
Strotactinus salteri	(Billings, 1861) Cassinian, shelly Zone G2-J Eastern Canada. see also Ingham *et al.*1986) Dounans Limestone, Cassinian, Highland Border Complex, Scotland
Tesselacauda depressa	Ross, 1951 Garden City Formation, American Shelly Zone E (=Mid *hunnebergensis* - Mid *supremus* Baltoscandian graptolite zones. Utah, USA,
Tesselacauda sp.	Jell, 1985
Synonymised with *Tesselacauda depressa* Ross, 1951 in this analysis	
	Digger Island Formation, Australian Lancefieldian Zone 1,

K. meridionalis Argentinian Zone,
=M. Cressagian Stage of the Tremadoc,
=Upper *flabelliformis socialis - flabelliformis flabelliformis*
Baltoscandian graptolite zones.
Waratah Bay, Victoria, Australia.

Victorispina holmesorum Jell, 1985
Digger Island Formation,
Australian Lancefieldian Zone 1,
K. meridionalis Argentinian Zone,
=M. Cressagian Stage of the Tremadoc,
=Upper *flabelliformis socialis - flabelliformis flabelliformis*
Baltoscandian graptolite zones.
Waratah Bay, Victoria, Australia.

*** = Coded only from the Treatise diagram**

3.4.2 Taxa known from relatively complete material but synonymised/included separately in the analysis:

Pseudopliomera Lu & Chien, 1978
Guizhou Province, China
Type species: *Pseudopliomera bifurcata* Lu & Chien, 1978

There are no characters differentiating this genus from *Parapilekia* and as a result *Pseudopliomera* is here regarded as a junior synonym of *Parapilekia* and is not included separately in the analysis.

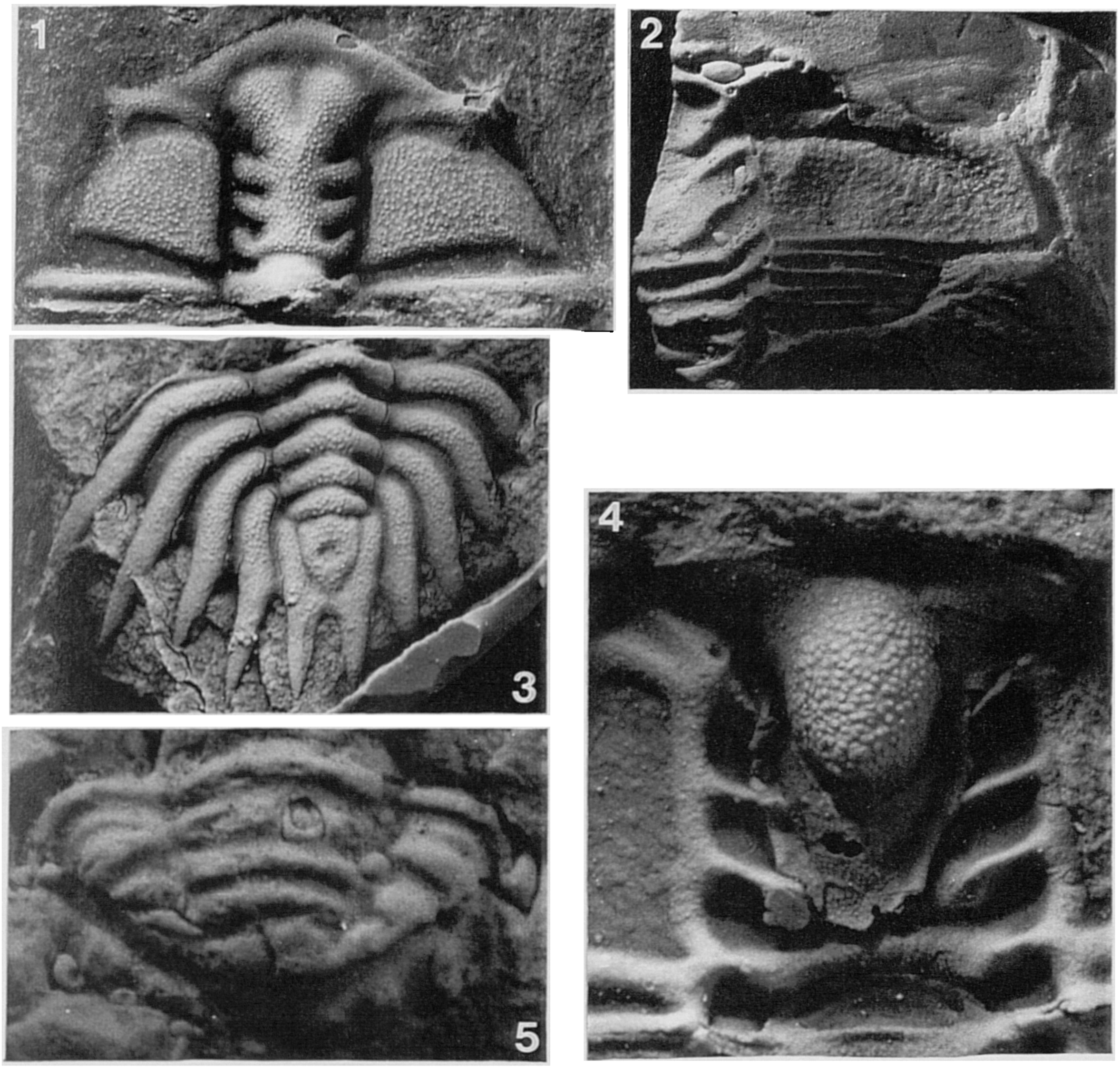


Fig. 3.1. Species of members of the Pliomeridae.
1, 3. *Pliomeridius sulcatus* Leanza & Baldis, 1975, Llanvirn, Argentina, Natural History Museum collection - un-numbered. 1. latex cast of mature cranidium, x6. 3. latex cast of pygidium, x6. 2. *Metapilekia bilirata* Harrington, 1938, Zone of *Nutopeltis orthometopa* (U. Tremadoc), Quebrada de Coquena, W of Purmamarca, Argentina, plaster impression of holotype partial cranidium and anterior thorax, Natural History Museum collection, It 11622 (original of Harrington & Leanza 1957, fig. 119:26), x4. 4. *Pliomeridius sulcatus* Leanza & Baldis, 1975, Llanvirn, Argentina, Natural History Museum collection - un-numbered. Ventral view of latex cast of cephalon and hypostome, x3. 5. *Pliomeroides deferrariisi* plaster cast of external mould of pygidium, Argentina, Natural Hstory Museum collection, It 11621, x24

Guizhoupliomerops Lu *et al.*, 1978
China, Guizhou Province,
Type species: *Guizhoupliomerops guizhouenis* Lu & Chien, 1978

Guizhoupliomerops comprises two species which are known from a few specimens and differ from *Pliomerops* only in the possession of three rather than five pygidial pleurae (see discussion of this character in section 3.5). As the number of pygidial pleurae by itself is a poor basis on which to differentiate a genus, *Guizhoupliomerops* is regarded as a subgenus of *Pliomerops* and excluded from the main analysis.

Guizhoupliomerops guizhouenis	Lu & Chien, 1978
Guizhoupliomerops shiqianensis	Lu & Chien, 1978

Chashania Lu & Sun, 1977
in Sheng, 1977
Nantsinkwan Formation (Tremadoc)
R. flabelliformis graptolite Zone.
Central Southern China
Type species: *Chashania chashanensis* Lu & Sun, 1977

The glabella of *Chashania* is identical to that of *Anacheirurus*. The only feature which differentiates *Chashania* from *Anacheirurus* is the apparent elongation of the terminal pygidial pleurae seen in a single, fragmentary pygidium figured by Lu & Sun (1977, plate 76, figure 12). Short lived variation in the degree of elongation of pygidial pleurae has been recorded in *Protopliomerops* by Demeter (1973) who regarded this elongation as being a subspecies level variation. This makes elongation of the pygidial pleurae a weak character upon which to diagnose a separate genus. Thus *Chashania* Lu & Sun, 1977 is here regarded as a subgenus of *Anacheirurus* and is therefore excluded from further consideration in this analysis.

Species are	*Chashania chashanensis*	Lu & Sun, 1977
	Chashania fusus	Sheng, 1977

Kanoshia reticulata Fortey & Droser, 1996
'K' shelly Zone, *glabrior* Subzone of the *Psephosthenaspis* Zone.
Nevada/Utah, W. USA

This species displays an unusual combination of characters. It was independently added to the analysis to determine whether it was, in fact, best assigned to *Kanoshia*.

Sinoparapilekia Peng, 1990
Lower part of the Madaoyu Formation,
M.-U. Tremadoc, Hunan, S. China.

The type species of this genus is unclear due to an apparent typographical error which is likely to render the genus, and hence the Subfamily Sinoparapilekiinae erected in the same paper, systematically invalid (see Section 3.6.2). In spite of this, the species that was probably intended to be the type species, *Sinocybele panjiazuiensis* Peng, 1990, was added to the analysis to determine its best placement within the phylogeny. The results of this analysis are discussed in Section 3.6.2.

Species are	*Sinoparapilekia panjiazuiensis*	Peng, 1990
	Sinoparapilekia expansa	Peng, 1990

3.4.3 Taxa known from incomplete material which is synonymised/considered in this analysis:

Emsurella Rosova, 1960
Type species: *Emsurella humilla* Rosova, 1960

This taxon was not included in the analysis as it is represented by only a single cranidium which is poorly preserved and illustrated. I can observe nothing on the cranidium to preclude the inclusion of this taxon within the Pliomeridae suggested by Přibyl *et al.* (1984), although I can determine no evidence for their suggestion that

Emsurella may prove to be situated as an intermediate between the Pilekiinae and the Pliomeridae as an ancestor to the Pliomeridae.

Emsurella? laevigata Rosova, 1960

This taxon is known from only a single, fragmentary cranidium which differs markedly from the type species *E. humilla* Rosova, 1960. *Emsurella? laevigata* appears to be most closely related to *Anacheirurus* Reed, 1896 and is provisionally placed within that genus (see Section 3.8.1.1).

Emsurina Sivov, 1955
Type species: *Emsurina sibirica* Sivov, 1955

Listed as U. Cambrian, probably L. Tremadoc (Moore, 1959), Siberia

Eocheirurus Rosova, 1960
Type species: *Eocheirurus salairicus* Rosova, 1960

This genus may prove to be close to the ancestral form of the Cheiruridae Salter, 1864 and is further discussed in Section 3.6.3.3.

Other assigned species;
Eocheirurus probus Rosova, 1960
Eocheirurus subtilis Rosova, 1960
These latter two taxa may be syonymous with *Eocheirurus salairicus* Rosova, 1960 (see Přibyl *et al.* 1985 p119)

Koraipsis Kobayashi, 1934
Type species: *Koraipsis spinus* Kobayashi, 1934
Tremadoc, South Chosen, China

This genus was erected on the basis of a single, incomplete, glabella and anterior margin. There is so little of this specimen preserved that it is not even possible to ascertain whether the glabella narrows anteriorly or is parallel sided. It is thus not possible to assign *Koraipsis* even to a rough position in the phylogeny of the Pliomeridae.

Other assigned species;	
Koraipsis taiziheensis	Kuo & Duan, 1982
Koraipsis shaniensis	Chang, 1966

I have been unable to obtain copies of the references depicting these two species and so am unable to do more than list them as having been assigned to this genus.

Strototropis	Raymond, 1937
Type species: *Strototropis laeviuscula*	Raymond, 1937 Upper part of the Highgate Formation, Upper Tremadoc/Lower Arenig, Grange Farm, Vermont, USA
Other assigned species;	
Strototropis elevata	Raymond, 1937 Location and age as for *laeviuscula*

As intimated by Moore (1959) *Strototropis* is identical to *Protopliomerops* and is here regarded as its junior synonym.

Leiostrototropis	Raymond, 1937
Type species: *Leiostrototropis phlegeri*	Raymond, 1937 Vermont, USA Location and age as for *Strototropis*
Other assigned species;	
Leiostrototropis laevis	Raymond, 1937 Vermont, USA Location and age as for *Strototropis*

Macrogrammus	Whittard, 1966
Type species: *Macrogrammus scylfense*	Whittard, 1966 Mytton Formation, Shelve Group, Arenig, *D. extensus* Graptolite Zone.

This genus is known from relatively poor material and so is excluded from the pliomerid analysis. It is appears to be closely related to *Parapilekia anxia*, and may prove to be a junior synonym of *Parapilekia*.

Metapliomerops	Kobayashi, 1934
Type species: *Metapliomerops extenuata*	(Raymond, 1924) Highgate Formation, U. Tremadoc Grange Farm, Vermont, USA
Other assigned species;	
Metapliomerops latidorsatus	Raymond, 1937 Location etc as of *extenuata*

3.4.4 Genera assigned to the Pliomeridae but not considered in this analysis as their references were either unavailable to me or contained no illustrations, descriptions or plates.

Diaphanometopus	Schmidt, 1881
Type species: *Diaphanometopus volborthi*	Schmidt, 1881

This genus was reassigned to the monospecific Subfamily Diaphanometopinae by Jaanusson in Moore (1959) and subsequently to a new Family Diaphanometopidae (Jaanusson, 1975). The genus has only been illustrated by a line drawing and is based on a single, enrolled, specimen. Despite earlier statements to the contrary, Schmidt's original species has been recorded as being extant in a recent catalogue of the Schmidt collection. (Bruton *et al.*, 1997) thus holding the prospect of some resolution of its taxonomic position.

Placoparina	
Placoparina taxinensis	Zhou, 1982
	Middle Ordovician,
	Shaanxi Province, Northwest China

Pliomerullus	
Pliomerullus amplissimus	Petrunina *et al.*, 1984

Genus and species erected with no description, illustrations or plates. I am therefore unable to code, or assess their validity.

Parapliomera	Petrunina *et al.*, 1984
Parapliomera anossiana	Petrunina *et al.*, 1984
Parapliomera sibirica	Petrunina *et al.*, 1984
Parapliomera tumulosa	Petrunina *et al.*, 1984

Genus and species erected with no description, illustrations or plates. I am therefore unable to code, or assess their validity.

Tienshifuia	
Tienshifuia sindabaoensis	Lu *et al.*, 1976
Tienshifuia penchiensis	Lu *et al.*, 1976
	Both from the Tremadoc of China

Genus and species erected with no description, illustrations or plates. I am therefore unable to code, or assess their validity.

3.4.5 Outgroup selection;

In these analyses there has been no polarisation of characters by the definition of ancestral forms. The analyses produce the same results regardless of whether an outgroup is defined or not and, if an outgroup is defined, which taxon is designated as the outgroup. In order to allow easy comparison of the branching order of the taxa with their stratigraphical ages and to provide a standard display format across all of the phylogeny diagrams, the oldest taxon included in the analysis is designated as the outgroup. This designation of outgroup for display in no way affects the outcome of the analyses. It merely serves to orient the phylogeny for display.

Although the Pilekiinae have been suggested as potential ancestors of both the Pliomeridae and Cheiruridae (Přibyl *et al.*, 1985 and references therein), there have been no clear suggestions as to which taxa are likely to prove to be ancestral to the Pilekiinae. This is a question which there has not been time to explore in this study and, as a result, there are no clear candidates to utilise as outgroup taxa when displaying the cladograms produced by this analysis. In the light of this the only practical option is to utilise the oldest member of the ingroup (Pliomeridae+Pilekiinae) as the outgroup taxon for display purposes.

Eocheirurus Rosova, 1960 has been assigned to the Pilekiinae (Přibyl *et al.*, 1984 and references therein) and is of late Cambrian age. It has also been suggested to be close to the ancestor of the Cheiruridae. However, *Eocheirurus* is only known from a poorly illustrated cranidium which displays features reminiscent of both the Pilekiinae and the Cheiruridae and its correct systematic placement is unknown until further material, including a pygidium, is recovered.

Parapilekia anxia Sdzuy (1955) has been described as the oldest known member of the Pilekiinae and Pliomeridae by Romano *et al.* (1993). However, comparing the age of *Parapilekia anxia* with the stratigraphical table given by Vaněk (1965, p. 292) it is apparent that it is younger than both *Pilekia olesnaensis* (Růžička, 1935) and *Pilekia bohemica* (Růžička, 1926). *Pilekia bohemica* is very poorly known and illustrated, *Pilekia olesnaensis* is both well preserved and relatively completely known and so was utilised as the outgroup for display purposes and to arrange the phylogeny for display in a consistent fashion in the various figures.

3.5 Discussion/list of characters utilised in this analysis;

3.5.1 List and discussion of characters included in the analysis;

For a discussion of the criteria employed in the choice and coding of the characters utilised in this analysis see Section 2.1.2

1. Form of the anterior border; '0'= angular/'1'=rounded.

2. Mid-part of the anterior border of the glabella is of nasute form;
'0'= no/'1'= yes.

3. Anterior margin of the glabella denticulate; '0'= no/'1'= yes.

The depressions between the denticulations on the anterior border of the glabella act as sockets to receive the tips of the pygidial pleurae during enrollment. This prevents lateral shearing forces being applied to unroll the trilobite Henry (1985)

4. Position of the posterior termination of the facial suture.
'0'= proparian/'1'= gonatoparian/'2'= facial suture is marginal.

5. Depth of the anterior border furrow;
'0'= uniformly deep.
'1'=shallows strongly mesially.
'2'= shallowed to obsolescence mesially

6. Mesial deepening in the anterior border furrow; '0'= no/'1'= yes.

7. Presence and form of the anteromedian complex on the frontal lobe of the glabella;
'0'= none present on external surface.
'1'= longitudinal anteromedian furrow or anteromesial indentation in the frontal lobe of the glabella.
'2'= Median pit in the frontal lobe of the glabella.

8. Outline of the glabella;

'0'= glabella narrows forwards.
'1'= glabella parallel/sub-parallel sided.
'2'= glabella widens forwards.

In some species, there is an element of subjectivity inherent in the coding of this character but in spite of this, it has been retained because of its usefulness in the diagnosis of the majority of the genera studied.

9. Width of glabella across L1 > one half of the total cranidial width;

'0'= no/'1'= yes.

10. Width of the frontal lobe of the glabella greater than that across the L3 lateral glabella lobes;

'0'= no/'1'= yes.

11. Sagittal length of the frontal lobe of the glabella (measured from the corner of the intersection of the S3 lateral glabellar furrow and the longitudinal axial furrow) is greater than the sagittal length of the L3 lateral glabellar lobes (measured at an equal distance from the axis);

'0'= no/'1'= yes.

12. Number of lateral glabellar furrows present; code the number of furrows (e.g. 2/3/4).

13. Position of the S3 lateral glabellar furrow relative to the anterior corners of the glabella;

'0'= anterior to the angle.
'1'= cutting the angle.
'2'= posterior to the angle.

The boundaries between the states are somewhat subjective in taxa which do not display an abrupt break in slope between the lateral and anterior portions of the glabellar margin. This problem is not common and so the character has been included.

14. Form of the S3 lateral glabellar furrow;
    '0'= un-branched and straight.
    '1'= sinuous.
    '2'= branches adaxially.
    '3'= poorly developed, represented by an apodeme or indentation in the lateral margin of the glabella.

15. Isolation of the S3 lateral glabellar furrows;
    (S3 furrows do not reach the axial furrows)
    '0'= no/'1'= yes.

16. Orientation of the S2 lateral glabellar furrows;
    '0'= adaxial ends directed transversely or to the posterior.
    '1'= adaxial ends directed towards the anterior.

17. Form of S1 lateral glabellar furrows;
    '0'= simple/'1'= forked/'2'= reduced to notches

18. Size of eyes (as indicated by the size of the palpebral lobes);
    '0'= absent/'1'= small/'2'= large
    (Large = longer sagittally than any one of the lateral glabellar lobes).

19. Eyes raised above the librigenal field on short stalks; '0'= no/'1'= yes.

20. Eye ridge and palpebral lobe confluent with the posterior portion of the border of the cranidium, with the furrow which backs the eye ridge being confluent with the cranidial border furrow;
    '0'= no/'1'= yes.

21. Eye ridges present; '0'= no/'1'= yes.

22. Presence of a furrow separating the anterior, adaxial portion of the eye ridge from the anterior border of the cranidium;
    '0'= not present/'1'= present.

23. Length of the eye ridge;
    '0'= eye ridge longer than the length of the palpebral lobe.
    '1'= eye ridge shorter than the length of the palpebral lobe.

24. Form of the eye ridge (if present); '0'= curved/'1'= straight.

25. Position at which the anterior, adaxial portion of the eye ridge (or trace of eye ridge indicated by an area which lacks pitting or a faint furrow) or anterior termination of the palpebral lobe if the eye is marginal and lacks an eye ridge) terminates;
    '0'= in the anterior, adaxial corner of the fixed cheek.
    '1'= posterior to the anterior, adaxial corner of the fixed cheek, cutting the lateral margin of the fixigenal field.
    '2'= cutting the anterior margin of the fixigenal field.

    When the eye ridge is depressed anteriorly (Character 28) the course originally taken by the, now flattened, section is indicated by an absence of reticulation or pitting. This allows the position of anterior termination of the eye ridge to be assessed.

26. Eye ridge dies out adaxially; the course of the adaxial portion of the eye ridge being indicated by a narrow, smooth, area of fixigenal field;
    '0'= no/'1'= yes.

27. Fixigenal spines present; '0'= no/'1'= yes.

28. Size of the genal spines; '0'= large/'1'= small.

29. Orientation of the genal spines (if present);
    '1'= spines directed to the posterior/'2'= spines directed laterally.

30. Sagittal length to width proportions of the rostral plate;
'0'= wider than long/'1'= longer than wide.

This character is poorly known in the Pilekiinae and their descendants, as well as in many of the other taxa, because of a lack of material which is sufficiently complete for these measurements to be made.

31. Outline of the hypostome; '0'= rounded, oval/'1'= angular, shield shaped.

32. Position of the middle body of the hypostome relative to the anterior border;
'0'= middle body situated far back on the hypostome relative to the anterior border, resulting in the anterior border being complete.
'1'= middle body of the hypostome situated far forward relative to the anterior border, dividing that border into two.

33. Expansion of the anterior border of the hypostome and of the associated hypostomal wings; '0'= no/'1'= yes.

34. Hypostomal wings depressed posteriorly relative to the anterior margin of the hypostome; '0'= no/'1'= yes.

35. Spines present on the lateral margins of the hypostome;
'0'= none present/'1'= marginal spines present on lateral border.

The angular corners of those hypostomes which do not display spines are situated in the same position as the spines of those which do possess them. Although not specifically linked in the character definition, it is likely that the lateral angles are equivalent to the lateral spines. Their number may prove to be a useful diagnostic character on recovery of more material.

36. Mesial spine or angle present on the posterior margin of the hypostome;
'0'= no mesial spine present, mesial edge of hypostome rounded.
'1'= mesial spine or mesial angle present.

37. Size of the mesial spine, if present, on the posterior margin of the hypostome.
'0'= short or represented only by an angle/'1'= long (See Figure 3.2).

Figure 3.2; Hypostome of *Pseudocybele nasuta* Ross (1951 pl. 33 fig.14) approx. x 11.5 showing the elongate mesial spine characteristic of this genus. In this specimen the distal section of the spine has been broken off.

38. Longitudinal width of the posterior border of the hypostome; **Ordered**
'0'= posterior border represented by a narrow rim.
'1'= posterior border broadened to a flat field.
'2'= posterior border sagittal length greater than width of hypostome middle body (see Fig. 3.7).

The breadth of the posterior border of the hypostome appears to be strongly controlled by heterochrony. The best example of this is in specimens of *Pseudomera barrandei* in Tremblay & Westrop (1991, figs 16-6,16-8 and 16-10), all of which are from the same locality, where the small hypostomes of immature individuals display narrow posterior borders while larger, and thus presumably more mature, specimens have increasingly broad posterior hypostomal borders. This heterochronic pattern of development from narrow posterior hypostomal borders in small (immature) specimens to broad borders in larger, more mature, hypostomes is also seen in specimens of *Hintzeia* Harrington, 1957.

The increase in breadth of this posterior hypostomal border in *Pseudomera barrandei* may be seen in Figs 3.3 and 3.4. With the exception of *Pseudomera barrandei* and one or two other species the width of the posterior hypostomal border is a character of very high burden, not varying within species, or within subclades. As such it is a useful character to utilise as an apomorphy to diagnose large scale relationships in this analysis.

Figure 3.3; Schematic representation (not to scale, but in proportion) of the development of the form of the hypostome of *Pseudomera barrandei* (Billings) after Tremblay & Westrop 1991 figs 16-6,16-8 and 16-10. Note the increasing breadth of the posterior border of the hypostome.

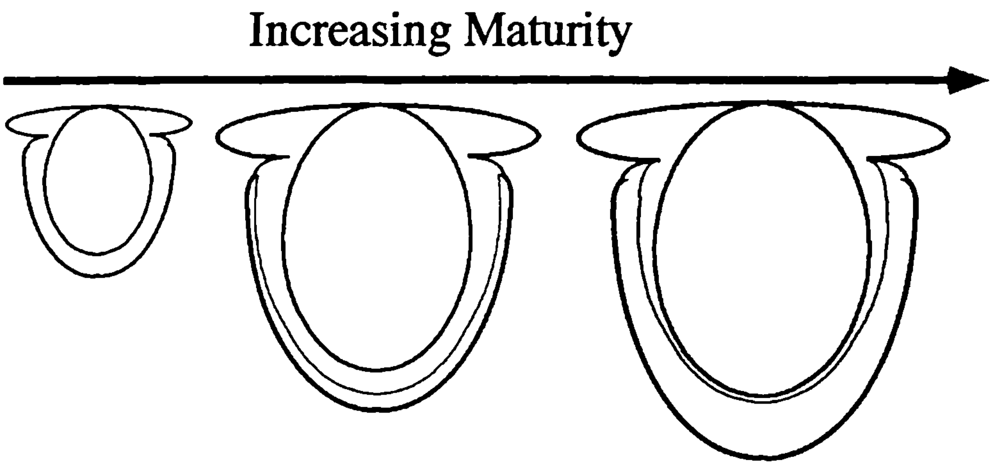


Figure 3.4; Schematic cross sectional view (not to scale, vertical dimension exaggerated) of the posterior border of the three hypostomes of *Pseudomera barrandei* (Billings) illustrated in Fig.3.3 showing increasing breadth of the posterior border.

The development of the posterior border of the hypostome is at its most extreme in specimens of *Hintzeia insolita* Poulsen (see Hintze, 1953 pl. 23, figs 5 and 7, Figure 3.7a herein) and *Kanoshia kanoshensis* Hintze, 1953 pl. 23 fig. 1 where the extreme development of the posterior border of the hypostome is one of the primary diagnostic characters.

Figure 3.5; Hypostome of *Rossaspis superciliosa* (Ross, 1951 pl. 31, fig.18) with a narrow posterior border and lateral, but not mesial, spines. (Approx x 14.5)

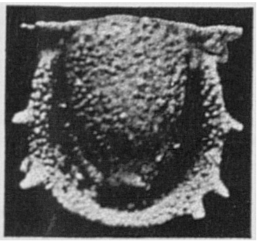


Figure 3.6; Slightly abraded hypostome of *Hintzeia celsaroa* Ross, 1951 (*Hintzeia aemula* of Hintze, 1953 pl. 22 fig. 13, (Approx. x 7.5)) illustrating a posterior border of medium breadth with lateral and mesial spines.

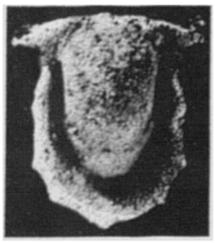
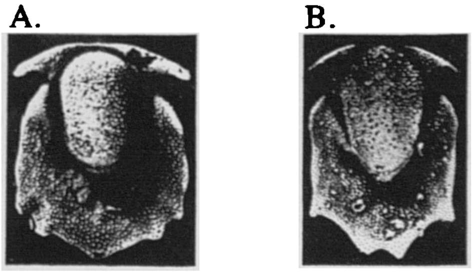


Figure 3.7; Illustration of the very broad posterior border of the hypostomes of;

A. *Pseudomera insolita* Poulsen (now *Hintzeia insolita*) (From Hintze, 1953 pl. 23, fig.7 (Approx. x4)).

B. *Kanoshia kanoshensis* Hintze, 1953 pl. 23, fig.1 (Approx. x5)



Clearly, given this strong evidence for the heterochronic control of the form of this feature and the clear developmental sequence it is reasonable to order this character in the PAUP analysis of this dataset.

39. Posterior border of the hypostome displays a mesial indentation;
'0'= no.'1'= yes.

40. Number of complete pleural ribs on the pygidium; Code the observed number. e.g.4/5/6/7/8 etc - there appear to be no pygidia with 7 pleurae

This has been employed as a diagnostic character at a range of systematic levels in different taxa. It was used at subspecies level in the systematics of *Placoparia* by Romano (1976) and differences in the number of pygidial pleurae are also apparent in short lived variants of *Protopliomerops* described by Demeter (1973 pl. 3, figs 1,2 and 3). The number of pygidial pleurae has also been employed as a species level diagnostic character in members of the genus *Ectenonotus* Raymond, 1920, and as a genus level character diagnosing *Demeterops* Přibyl *et al.*, 1985.

In spite of this range of variation in these few groups, this character is also relatively stable at higher systematic levels with genera found in the lower section of the cladogram predominantly displaying four pygidial pleurae, with the exception of *Anacheirurus*, *Metapilekia* , *Demeterops* (recognised herein as a junior synonym of *Pilekia*) and *Pilekia* which have three pleurae and *Rossaspis*, which possesses five. In contrast, those genera placed in the upper section of the cladogram predominantly posses five pygidial pleurae, with the exception of *Pseudomera* which has six and *Placoparia*, which has four.

In the light of the usefulness of the character in genus level diagnosis it is retained in the analysis but should not be employed as the sole character differentiating two genera. This particularly applies in situations where the population of the new genus is only poorly sampled.

41. Number of pygidial ribs equals the number of rings on the pygidial axis;
'0'= no, number of pygidial ribs less than the number of pygidial axial rings.
'1'= yes.

There are two possible mechanisms by which the number of axial rings could exceed the number of pleural ribs.

The first of these is the development of additional axial rings on the terminal area of the pygidial axis. This involves the elongation of the terminal piece of the axis and is the mechanism envisaged for all of the taxa displaying more rings than ribs, except *Demeterops*.

The second possible mechanism, which may have operated in *Demeterops*, is the loss of the terminal pair of pygidial pleurae accompanied by the retention of the axial ring originally associated with those pleurae.

There is no way to differentiate between these mechanisms in cases such as that of *Demeterops* where older taxa display a greater number of pygidial rings and ribs than the descendent taxa which have more axial rings than pygidial ribs it is reasonable to infer that the second of the two processes took place. In cases where the ancestors display the same number of pygidial pleurae as their descendants, it is reasonable to infer that the derived condition was achieved by the addition of additional rings to the axis of the pygidium without the addition of any associated pygidial pleurae.

Note: The multiple pits seen in the elongate terminal axial section of pygidia of the *Cybelopsis* are treated as multiple axial rings in this character.

42. Pygidial pleural areas divided by furrows into ribs and anterior fields;
'0'= no/'1'= yes.

The furrows on the pygidial pleural areas exhibit a variety of forms, varying in the position at which they originate and terminate, in the number of pleural areas which display them and in the course which they follow. Although this area of morphology may provide a fruitful source of further characters, stable character states did not emerge in the present study.

43. Shape of the pygidial pleurae;
'0'= strongly bent rearwards/'1'= not bent rearwards.

44. Form of the pygidial pleurae;
'0'= gradually narrowing distally.
'1'= broadening distally to the mid point at which the pleurae bend, then narrowing distally to the tips.

While this character is set to '0' in *Tesselacauda* there is a degree of similarity between the pygidial form of that genus and those genera (members of the Pilekiinae) for which this character state is set to '1'. This reflects the close proximity of the genera in the tree resulting from this analysis. The pygidium of *Tesselacauda* is not coded as '1' as the distal, narrowing, portions of the pleurae are reduced from long free spines to being mere mesial angles on otherwise broad pleurae. Altering this coding has little effect on the result of the analysis, merely reinforcing the phylogenetic position of *Tesselacauda* derived herein. The inferred homology of the pygidial pleurae of *Tesselacauda* and other members of the Pilekiinae provides independent support for the phylogeny derived.

45. Dorso-ventral curvature of the pygidial pleurae;
'0'= curved downwards.
'1'= flat lying.
'2'= horizontal adaxially, bending down vertically halfway along their length.

In some species of *Pliomerops* and *Pseudomera*, the form of the pygidial pleurae, normally state '0', closely approaches that of state '2'. This is to be expected as, in the analysis, *Pliomerops* and *Pseudomera* plot as the two closest sister groups to the *Placoparia* subclade. The form of the pleurae in these cases is differentiated from that found in the *Placoparia* subclade because the curvature of the pygidial pleurae is less extreme and more gradual. This is a useful, but subjective, character and is included in the analysis.

46. Tips of the pygidial pleurae turn out; '0'= no/'1'= yes.

State '1' of this character includes two closely similar forms:
That seen in *Quinquecosta*, amongst others, where the pygidial pleurae begin to turn outwards only a short distance from their terminations and the form seen in *Pliomeridius* where the pleurae begin to turn out slightly, approximately a quarter of the way in from the pleural terminations (Fig. 3.1).

47. Form of the tips of the pygidial pleurae;
    '0'= tips blunt, not tapering gradually to a point.
    '1'= tips sharp, tapering gradually to a point.

48. Size of the terminal piece of the pygidial axis relative to the total sagittal length of the pygidium;
    '0'= short (less than, or equal to, one third of the total length).
    '1'= elongate (more than one third of the total sagittal pygidial length).

Note that this character relates to terminal sections of the pygidium which are composed of areas which are determined to be structurally part of the axis of the pygidium. The character state 'elongated terminal piece' does not include situations where the posterior two pygidial pleurae have fused together distally. (See character 51).

49. Transversely oriented pair of pits present at the posterior of the pygidial axis;
    '0'= no/'1'= yes.

50. Additional transversely oriented pairs of pits on the axis of the pygidium, in addition to the terminal pair of pits;
    '0'= no /'1'= yes.

This is an autapomorphy of *Cybelopsis*. The pits are similar in form to the apodemes found on other part of the trilobite's exoskeleton and may represent muscle insertion structures. The spacing of these pits is similar to that of axial ring furrows and these structures are likely to be homologous.

51. Terminal pair of pygidial pleurae which are poorly differentiated from the terminal piece of the axis and which are fused together distally (Fig. 3.8);
    '0'= no/'1'= yes.

The presence of fused terminal pleurae on the pygidium may be differentiated from the presence of an elongate terminal axial piece in several ways:

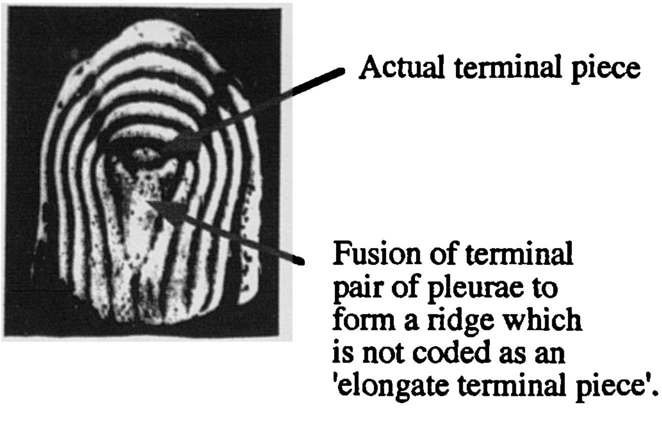
A. The 'axial furrow' separating the fused pleurae from the rest of the axis is concave forwards, as is the normal posterior margin of the axis, rather than being oriented concave rearwards as are the true axial rings. For example in *Pseudomera barrandei* (see Whittington 1961 pl. 100 fig. 6).

B. The segment anterior to the fused terminal pleurae continues the convexity of the pygidial axis while the fused terminal pleurae display an independent convexity. This posterior pair of pleurae may be depressed as in *Pseudocybele nasuta* Ross (1952 pl. 34 fig. 27).

C. A longitudinal line of may rarely be discerned bisecting the fused pygidial pleurae (e.g. Hintze 1953 pl. 24 figs 10, 11). This is here interpreted as a relict of the line of contact of the adaxial margins of the posterior pair of pygidial pleurae.

D. The anterior, adaxial, terminations of the 'fused terminal pleurae' are level with, and abaxial to an axial ring positioned anterior to the inferred true terminal piece of the pygidial axis. In this way they resemble pygidial pleurae rather than an elongate terminal section of the axis itself. An example of this may be seen in *Pseudocybele lemeuri* Hintze, 1953 (pl. 24 figs 7a, 7b), and in some specimens of *Pseudomera*. It is interesting to note that the axial ring with which the 'fused terminal pleurae' are confluent appears to be greatly reduced or lost in many, more derived, pygidia. An example of this reduction/loss of the axial ring may be seen in a pygidium of *Pseudocybele nasuta* Ross, 1951 (in Hintze 1953 pl. 24 figs 11a-d). On the external surface

Figure 3.8: Detail of terminal section of pygidium of *Pseudocybele nasuta* Ross from Hintze (1953 pl. 24, fig. 11d (Approx. x6)).



(pl.24, figs 11b, c, d) there is no trace of a posterior axial ring level with the termination of the fused terminal pair of pleurae. On an internal surface, however, (pl. 24 fig. 11a), immediately anterior to the small terminal piece, an axial ring may be seen, narrowing to obsolescence mesially.

3.5.1.1 Commonly discussed character not included in the analysis: Form of the thoracic pleurae.

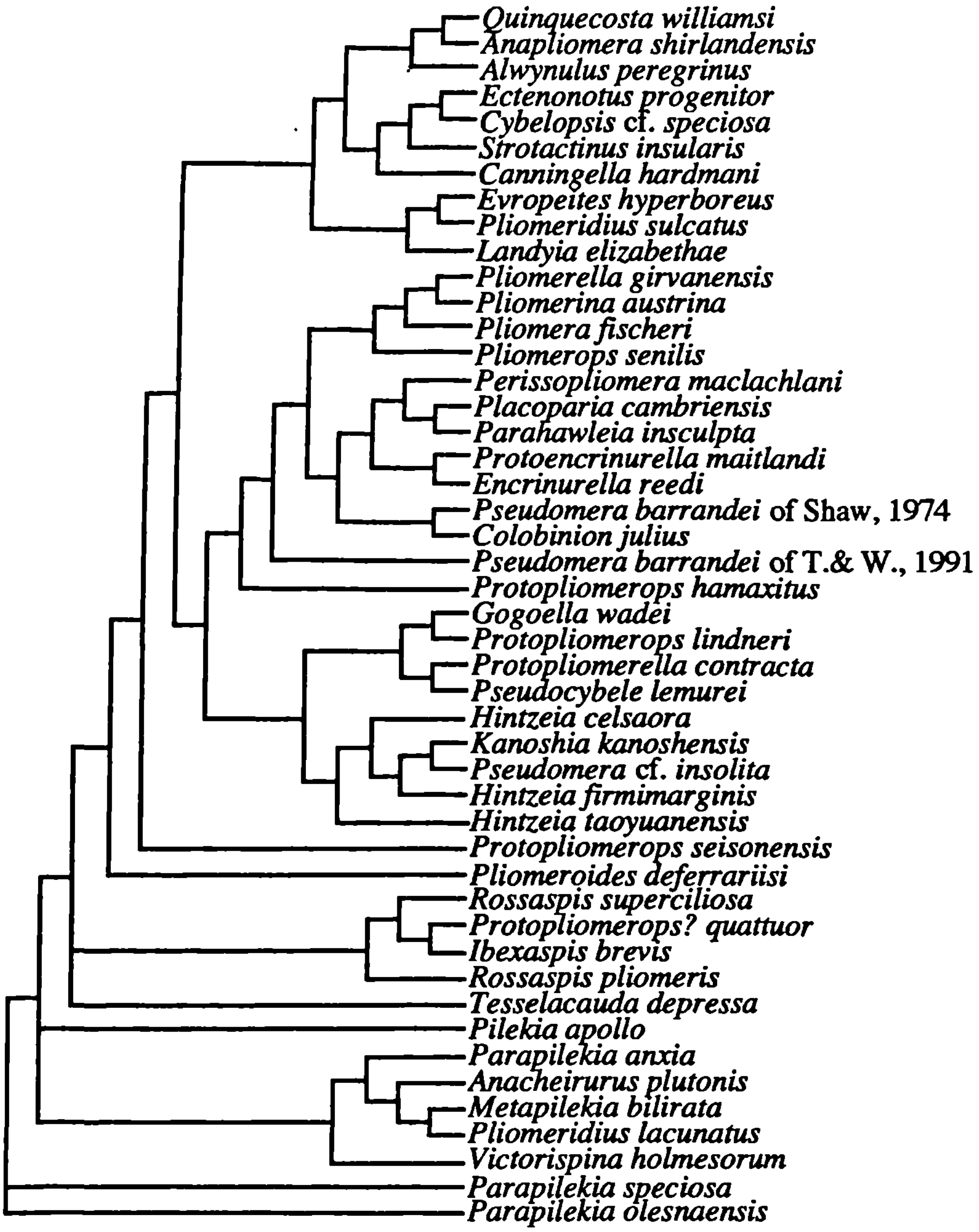
The absence of raised anterior bands on the thoracic pleurae were cited by Ross (1951) as a feature diagnostic of the Pliomeridae. However a significant number of pliomerids do display raised anterior fields on the thoracic pleurae. In addition, the recognition of this character is highly subjective, depending on the degree of overlap of successive thoracic pleurae in articulated specimens, the degree of inflation of the anterior field, the preservation of the specimen and the definition of 'anterior thoracic field' employed. It is clear that structures which are, in some specimens, called an anterior field are not defined as such in other specimens where they are of differing size or shape. Preservation plays a strong role in the recognition of different forms of thoracic pleurae, even within specimens of the same species.

3.6 Discussion of the results of the analysis:

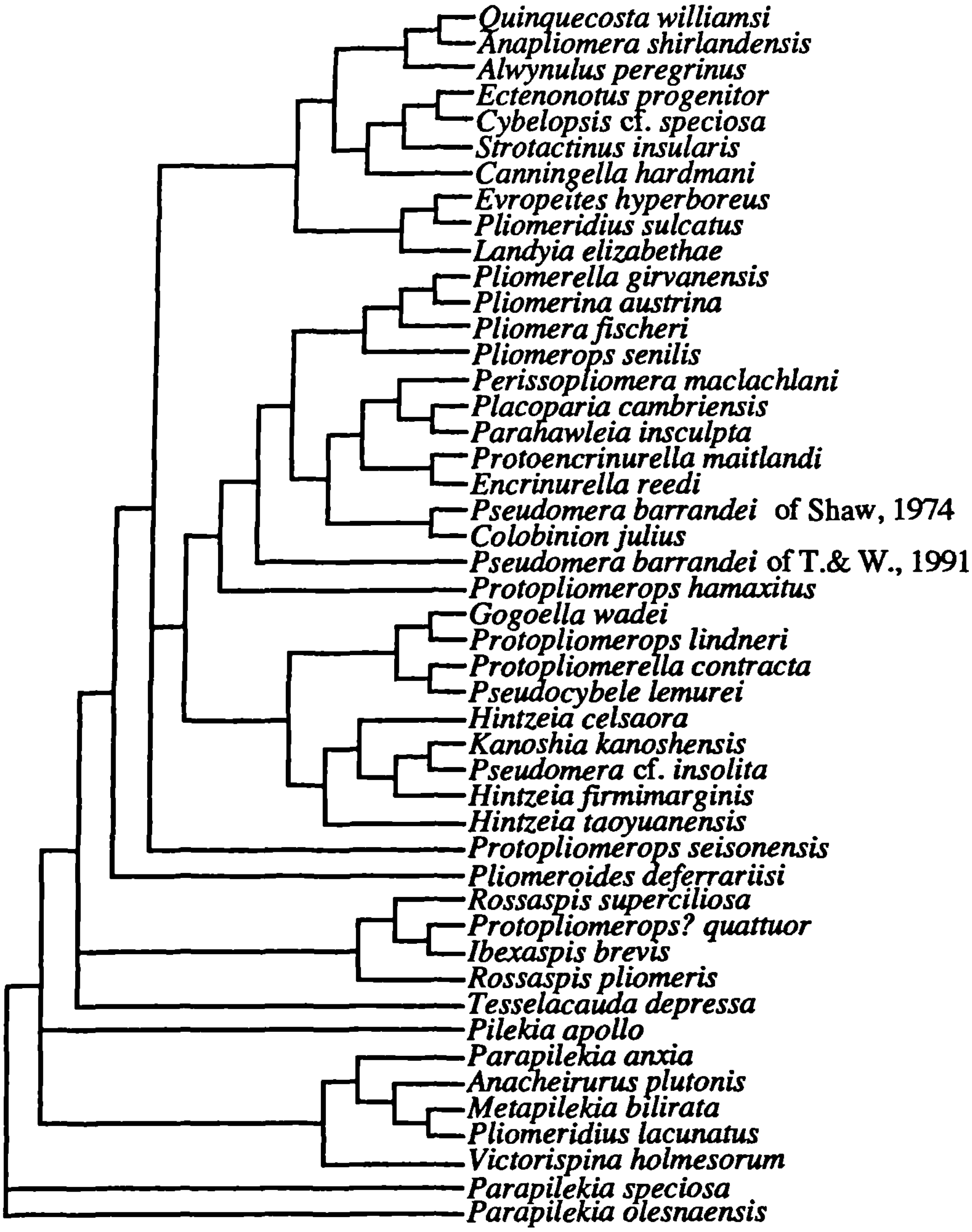
PAUP analysis of the characters and taxa outlined in the previous sections results in the production of two minimum length trees of Consistency Index of 0.491, a Consistency Index excluding uninformative characters of 0.433, a Rescaled Consistency Index of 0.360 and a Tree Length of 163. The two trees produced by this analysis are shown in Figure 3.9 and differ only in the resolution of the position of *Protopliomerops seisonensis*. In tree 2, *seisonensis* is represented as being situated at a trichotomy, while in tree 1, *seisonensis* is separated out at an additional node. On examining the character state changes across this part of the cladogram it is clear that there is no character support for the more highly resolved topology seen in tree 1 (see Fig. 3.11) and as a result, the topology of tree 2 will be employed in the diagrams in the remainder of this report.

Figure 3.9: The two minimum length trees for the Pliomeridae produced by PAUP analysis of the pliomerid dataset.

1.



2.


Quinquecosta williamsi
Anapliomera shirlandensis
Alwynulus peregrinus
Ectenonotus progenitor
Cybelopsis cf. speciosa
Strotactinus insularis
Canningella hardmani
Evropeites hyperboreus
Pliomeridius sulcatus
Landyia elizabethae
Pliomerella girvanensis
Pliomerina austrina
Pliomera fischeri
Pliomerops senilis
Perissopliomera maclachlani
Placoparia cambriensis
Parahawleia insculpta
Protoencrinurella maitlandi
Encrinurella reedi
Pseudomera barrandei of Shaw, 1974
Colobinion julius
Pseudomera barrandei of T.& W., 1991
Protopliomerops hamaxitus
Gogoella wadei
Protopliomerops lindneri
Protopliomerella contracta
Pseudocybele lemurei
Hintzeia celsaora
Kanoshia kanoshensis
Pseudomera cf. insolita
Hintzeia firmimarginis
Hintzeia taoyuanensis
Protopliomerops seisonensis
Pliomeroides deferrariisi
Rossaspis superciliosa
Protopliomerops? quattuor
Ibexaspis brevis
Rossaspis pliomeris
Tesselacauda depressa
Pilekia apollo
Parapilekia anxia
Anacheirurus plutonis
Metapilekia bilirata
Pliomeridius lacunatus
Victorispina holmesorum
Parapilekia speciosa
Parapilekia olesnaensis

3.6.1 Assessment and discussion of the trees produced by this analysis;

A comparison of the order of branching of the taxa in the phylogeny produced by this analysis with the stratigraphical positions of those taxa allows a rough idea of how 'good' the phylogeny produced is. The comparison of branching order to stratigraphical position highlights areas of anomaly in the cladogram which require explanation, either in terms of incompleteness of the data set ('ghost ranges') or in terms of inaccuracies in the derived phylogeny.

The cladogram produced by this analysis can be seen in Figure 3.10 where it is represented as a phylogram (In which the lengths of the branches are proportional to the number of apomorphies supporting each branch). In Figure 3.11 this phylogram is annotated with the broad stratigraphical positions of the taxa.

As can be seen, the general branching order of the phylogram closely matches the stratigraphical order of the taxa. There are few areas of anomaly, or conflict, between the branching order of the phylogeny and the stratigraphical position of the taxa. Those conflicts which are identified are of the order of, at most, a few American shelly zones. The absolute time span of these American shelly zones has not been ascertained but is certainly short. This close match of branching order to stratigraphical position provides strong support to the derived phylogeny.

One slightly anomalous branching position on the cladogram is that of *Pliomeridius sulcatus*. This species is of Llanvirn age while its sister taxon, *Evropeites hyperboreus*., is of Mid Arenig-Llanvirn age and is inferred to be 'more derived'. This anomaly either implies that the age assignment of *Pliomeridius sulcatus* is slightly inaccurate or requires the postulation of a 'ghost range' or a 'ghost taxon'. If the latter is the case, then the most likely explanation is the presence of a 'ghost taxon' which is ancestral to both *Pliomeridius sulcatus* and *Evropeites hyperboreus and* which would be expected to be of Early/Mid Arenig age.

Another taxon whose position in the branching order and stratigraphical position is anomalous is that assigned to *Pseudomera barrandei* by Tremblay & Westrop (1991). It is most likely that this stratigraphical anomaly is caused by lack of material, with more primitive 'ghost taxa', intermediate in form between *Protopliomerops* and the daughter subclade, not yet having been recovered.

Figure 3.10: Pliomeridae phylogeny in phylogram form.

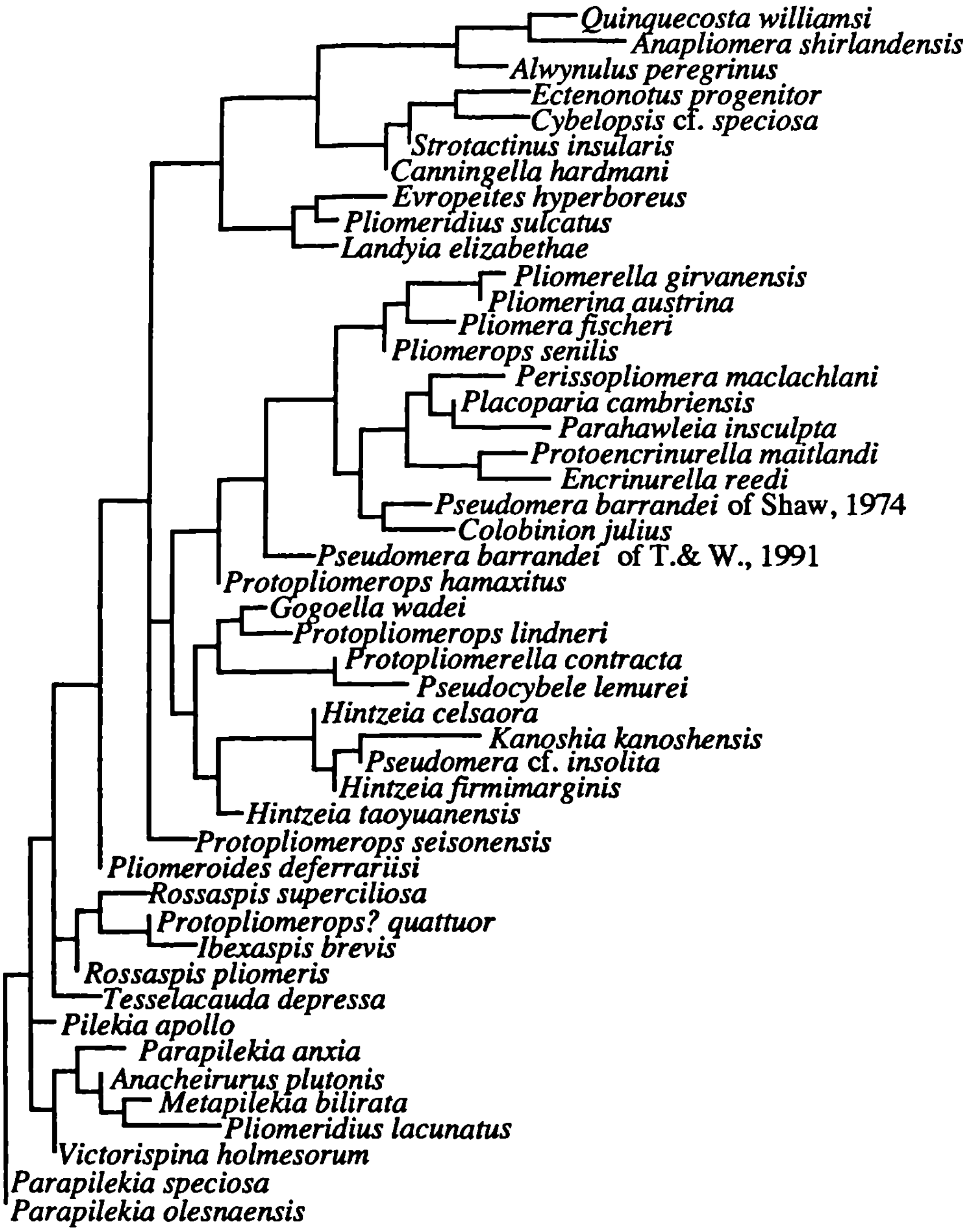
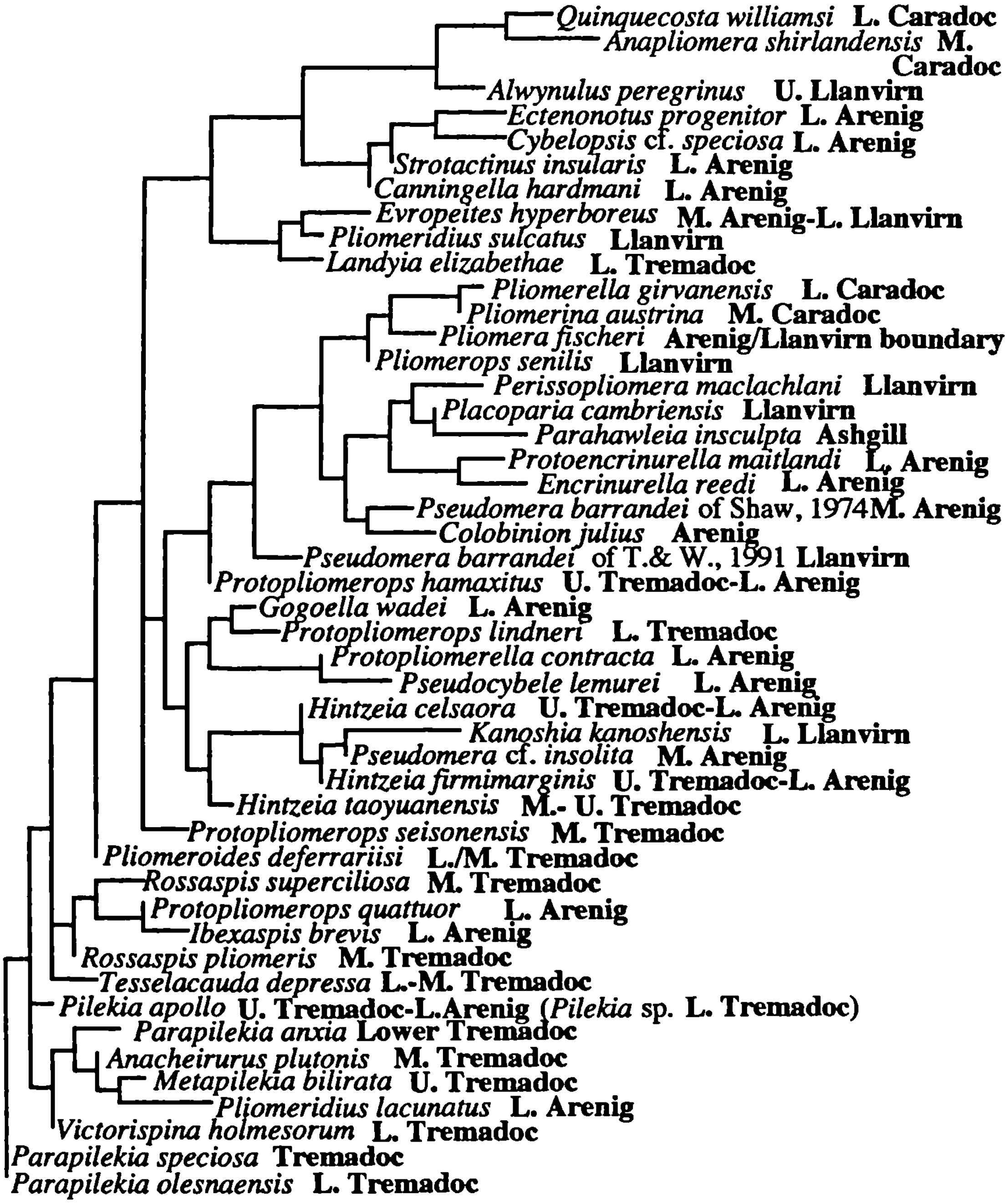


Figure 3.11: Pliomeridae phylogeny in phylogram form annotated with the stratigraphical ages of the included species..



The large number of characters employed in the analysis makes the concise annotation of a cladogram difficult and so the full list of character state changes are listed and annotated in Figure 3.12.

Figure 3.12: Tree 2 of the 'Pliomeridae' main analysis in phylogram form, annotated with all of the character state changes.

(Tree length = 163, Consistency index (CI) = 0.491, Homoplasy index (HI) = 0.595, CI excluding uninformative characters = 0.433, Rescaled CI = 0.360)

```
                                                 /---- Quinquecosta stincharensis
                                          /-----89-------- Anapliomera
                                          |                 shirlandensis
                             /-----------88---- Alwynulus peregrinus
                             |            /------- Ectenonotus progenitor
                    /-------87       /---84------- Cybelopsis cf. speciosa
                    |        |     /85 Strotactinus insularis
                    |        \----86 Canningella hardmani
             /-----83        /------ Evropeites hyperboreus
             |      |     /-81-- Pliomeridius sulcatus
             |      \----82----- Landyia elizabethae
             |                              /-- Pliomerella girvanensis
             |                       /-----48 Pliomerina austrina
             |                     /49----- Pliomera fischeri
             |                 /--50 Pliomerops senilis
             |                 |        /------ Perissopliomera maclachlani
             |                 |     /-52 / Placoparia cambriensis
             |          /-----57     |  \51--------- Parahawleia insculpta
             |          |      | /--54      /----- Protoencrinurella maitlandi
             |          |      | |   \-----53------- Encrinurella reedi
             |      /--58      \56 /----- Pseudomera barrandei of Shaw1974
        /---80      |   |        \55------- Colobinion julius
        |    | /---59   \----- Pseudomera barrandei of T & W 1991
        |    | |    \ Protopliomerops hamaxitus
        |    | |      /-- Gogoella wadei
        |    | |    /60---- Protopliomerops lindneri
        |    +68 /-62          / Protopliomerella contracta
        |    | | |  \----------61----- Pseudocybele lemurei
    /--79    | | |           / Hintzeia celsaora
    |   |    | \67           |   /----------- Kanoshia kanoshensis
    |   |    |   |  /-------65 /63 Pseudomera cf. insolita
    |   |    |   \-66        \64 Hintzeia firmimarginis
    |   |    |      \-- Hintzeia taoyuanensis
    |   |    \---- Protopliomerops seisonensis
  /78   \ Pliomeroides deferrariisi
  | |   /----- Rossaspis superciliosa
  | | /76    / Protopliomerops quattuor
  | +77 \---75---- Ibexaspis brevis
  | | \ Rossaspis pliomeris
/74 \---- Tesselacauda depressa
| +-- Pilekia apollo
| |   /----- Parapilekia anxia
| | /72 / Anacheirurus plutonis
69| | \71  /-- Metapilekia bilirata
| \73   \-70--------- Pliomeridius? lacunatus
|   \ Victorispina holmesorum
+ Parapilekia speciosa
\ Parapilekia olesnaensis
```

```
Apomorphy lists:

     Branch                         Character     Steps   CI  Change
    node_69 --> node_74             41.RibsequalR    1  0.250 0 ==> 1
    node_74 --> node_78             44.PleurBr+Na    1  0.500 1 ==> 0
    node_78 --> node_79             13.S3 Posit      1  0.250 1 ==> 2
                                    45.PleuraeCur    1  0.500 1 ==> 0
    node_79 --> node_80             40.NoPygRibs     1  0.333 4 ==> 5
                                    42.RibFurretc    1  0.400 1 ==> 0
    node_80 --> node_83             14.S3 Form       1  0.700 0 --> 2
                                    48.TermElong     1  0.250 0 ==> 1
                                    49.Post2Pits     1  1.000 0 ==> 1
    node_83 --> node_87             27.Fixi spine    1  0.167 1 --> 0
                                    41.RibsequalR    1  0.250 1 ==> 0
                                    46.RibTipOut     1  0.750 0 ==> 1
                                    47.FreeTipsSh    1  0.500 1 ==> 0
    node_87 --> node_88             8.Glab Outli     1  0.455 0 ==> 2
                                    10.FLWiderL3     1  0.500 0 ==> 1
                                    11.FLLongerL3    1  0.500 0 ==> 1
                                    16.S2DirAnt      1  1.000 0 ==> 1
                                    23.EyeRShort     1  0.250 0 --> 1
                                    34.HypWingsDe    1  0.500 0 --> 1
    node_88 --> node_89             7.Anteromed      1  0.286 0 ==> 2
                                    19.EyeRaised     1  1.000 0 ==> 1
                                    25.EyeR Term     1  0.500 0 ==> 1
    node_89 --> Quinquecosta        23.EyeRShort     1  0.250 1 --> 0
                stincharensis       40.NoPygRibs     1  0.333 5 ==> 4
    node_89 --> Anapliomera         12.NumGlaFurr    1  0.500 3 ==> 4
                shirlandensis       17.S1 Form       1  1.000 0 ==> 2
                                    32.MidBodAnt     1  0.250 0 ==> 1
                                    39.HypBordInd    1  0.500 0 ==> 1
    node_88 --> Alwynulus           27.Fixi spine    1  0.167 0 --> 1
                peregrinus          40.NoPygRibs     1  0.333 5 ==> 8
    node_87 --> node_86             14.S3 Form       1  0.700 2 --> 0
                                    35.MargSpines    1  0.333 1 ==> 0
                                    38.PostBordExp   1  0.500 0 ==> 1
    node_86 --> node_85             13.S3 Posit      1  0.250 2 ==> 0
    node_85 --> node_84             26.ERdies        1  1.000 0 ==> 1
                                    32.MidBodAnt     1  0.250 0 --> 1
    node_84 --> Ectenonotus         1.AB Shape       1  0.500 1 ==> 0
                progenitor          40.NoPygRibs     1  0.333 5 ==> 8
                                    41.RibsequalR    1  0.250 0 ==> 1
    node_84 --> Cybelopsis cf.      7.Anteromed      1  0.286 0 ==> 1
                speciosa            8.Glab Outli     1  0.455 0 ==> 2
                                    50.Add2Pits      1  1.000 0 ==> 1
    node_83 --> node_82             6.MesDeepeni     1  0.500 0 ==> 1
                                    7.Anteromed      1  0.286 0 ==> 1
                                    33.AntBordExp    1  1.000 0 ==> 1
    node_82 --> node_81             8.Glab Outli     1  0.455 0 ==> 1
    node_81 --> Evropeites          15.S3isolated    1  0.333 0 ==> 1
                hyperboreus         24.ERStraight    1  0.500 0 ==> 1
                                    28.Spine size    1  0.250 0 ==> 1
    node_81 --> Pliomeridius        11.FLLongerL3    1  0.500 0 ==> 1
                 sulcatus
    node_82 --> Landyia             40.NoPygRibs     1  0.333 5 ==> 4
                elizabethae         42.RibFurretc    1  0.400 0 ==> 1
    node_80 --> node_68             13.S3 Posit      1  0.250 2 ==> 0
    node_68 --> node_59             8.Glab Outli     1  0.455 0 ==> 2
                                    34.HypWingsDe    1  0.500 0 ==> 1
    node_59 --> node_58             27.Fixi spine    1  0.167 1 ==> 0
                                    32.MidBodAnt     1  0.250 0 ==> 1
```

Branch	**Character**	**Steps**	**CI**	**Change**
node_58 --> node_57	31.Hyp Outlin	1	1.000	0 ==> 1
	35.MargSpines	1	0.333	1 ==> 0
	38.BotBordExp	1	0.500	0 ==> 1
node_57 --> node_50	25.EyeR Term	1	0.500	0 ==> 2
	30.RostPlate	1	1.000	0 ==> 1
node_50 --> node_49	4.FacSut	1	0.667	0 ==> 1
	21 ER present	1	1.000	1 ==. 0
node_49 --> node_48	18.EyeSize	1	0.667	1 ==> 2
	47.FreeTipsSh	1	0.500	1 ==> 0
	48.TermElong	1	0.250	0 ==> 1
node_48 --> *Pliomerella girvanensis*	9.Glab/CephP	1	0.333	0 ==> 1
node_49 --> *Pliomera fischeri*	3.ABDenticul	1	0.500	0 ==> 1
	7.Anteromed	1	0.286	0 ==> 1
node_57 --> node_56	5.Abfdepth	1	1.000	0 ==> 1
node_56 --> node_54	4.FacSut	1	0.667	0 ==> 1
	45.PleuraeCur	1	0.500	0 --> 2
node_54 --> node_52	43.PygPleurSt	1	0.750	0 ==> 1
node_52 --> *Perissopliomera maclachlani*	3.ABDenticul	1	0.500	0 ==> 1
	12.NumGlaFurr	1	0.500	3 ==> 4
	48.TermElong	1	0.250	0 ==> 1
node_52 --> node_51	40.NoPygRibs	1	0.333	5 ==> 4
node_51 --> *Parahawleia insculpta*	4.FacSut	1	0.667	1 ==> 2
	5.Abfdepth	1	1.000	1 ==> 2
	9.Glab/CephP	1	0.333	0 ==> 1
	18.EyeSize	1	0.667	1 ==> 0
node_54 --> node_53	13.S3 Posit	1	0.250	0 ==> 2
	14.S3 Form	1	0.700	0 --> 1
	25.EyeR Term	1	0.500	0 ==> 1
node_53 --> *Protoencrinurella maitlandi*	42.RibFurretc	1	0.400	0 ==> 1
	44.PleurBr+Na	1	0.500	0 ==> 1
node_53 --> *Encrinurella reedi*	10.FLWiderL3	1	0.500	0 ==> 1
	14.S3 Form	1	0.700	1 --> 3
	45.PleuraeCur	1	0.500	2 --> 0
node_56 --> node_55	6.MesDeepeni	1	0.500	0 ==> 1
node_55 --> *Pseudomera barrandei* Shaw, 1974	15.S3isolated	1	0.333	0 ==> 1
	51.Term fused	1	0.333	0 ==> 1
node_55 --> *Colobinion julius*	13.S3 Posit	1	0.250	0 ==> 2
	41.RibsequalR	1	0.250	1 ==> 0
	48.TermElong	1	0.250	0 ==> 1
node_58 --> Pseudomera *barrandei* T & W, 1991	15.S3isolated	1	0.333	0 ==> 1
	51.Term fused	1	0.333	0 ==> 1
node_68 --> node_67	36.MesSpine	1	1.000	0 ==> 1
node_67 --> node_62	23.EyeRShort	1	0.250	0 ==> 1
node_62 --> node_60	18.EyeSize	1	0.667	1 ==> 2
node_60 --> *Gogoella wadei*	7.Anteromed	1	0.286	0 ==> 1
node_60 --> *Protopliomerops lindneri*	28.Spine size	1	0.250	0 ==> 1
	40.NoPygRibs	1	0.333	5 ==> 4
node_62 --> node_61	12.NumGlaFurr	1	0.500	3 ==> 4
	13.S3 Posit	1	0.250	0 --> 1
	27.Fixi spine	1	0.167	1 ==> 0
	47.FreeTipsSh	1	0.500	1 --> 0
	51.Term fused	1	0.333	0 ==> 1
node_61 --> *Pseudocybele lemurei*	2.AB Nasute	1	1.000	0 ==> 1
	37.MesSpineSi	1	1.000	0 ==> 1
	46.RibTipOut	1	0.750	0 ==> 1
node_67 --> node_66	38.PostBordExp	1	0.500	0 ==> 1

```
 Branch                           Character  Steps    CI Change
node_66 --> node_65               27.Fixi spine     1  0.167 1 ==> 0
                                  28.Spine size     1  0.250 0 --> 1
                                  29.GenSp/angO     1  0.500 1 --> 2
                                  32.MidBodAnt      1  0.250 0 ==> 1
node_65 --> node_64               38.BotBordExp     1  0.500 1 ==> 2
node_64 --> node_63               43.PygPleurSt     1  0.750 0 ==> 1
node_63 --> Kanoshia              7.Anteromed       1  0.286 0 ==> 1
            kanoshensis           8.Glab Outli      1  0.455 0 ==> 1
                                  13.S3 Posit       1  0.250 0 ==> 1
                                  23.EyeRShort      1  0.250 0 ==> 1
                                  27.Fixi spine     1  0.167 0 ==> 1
node_66 --> Hintzeia              40.NoPygRibs      1  0.333 5 ==> 4
             taoyuanensis
node_80 --> Protopliomerops       8.Glab Outli      1  0.455 0 ==> 1
            seisonensis           40.NoPygRibs      1  0.333 5 ==> 6
node_78 --> node_77               20.PalLatBor      1  1.000 0 ==> 1
node_77 --> node_76               28.Spine size     1  0.250 0 ==> 1
node_76 --> Rossaspis             29.GenSp/angO     1  0.500 1 ==> 2
            superciliosa          40.NoPygRibs      1  0.333 4 ==> 5
node_76 --> node_75               35.MargSpines     1  0.333 1 --> 0
                                  42.RibFurretc     1  0.400 1 ==> 0
node_75 --> Ibexaspis             8.Glab Outli      1  0.455 0 ==> 1
            brevis                45.PleuraeCur     1  0.500 1 ==> 0
node_78 --> Tesselacauda          22.ER ABFurr      1  1.000 1 ==> 0
            depressa              39.HypBordInd     1  0.500 0 ==> 1
node_74 --> Pilekia apollo        9.Glab/CephP      1  0.333 0 ==> 1
node_74 --> node_73               14.S3 Form        1  0.700 0 ==> 2
node_73 --> node_72               13.S3 Posit       1  0.250 1 ==> 2
node_72 --> Parapilekia           8.Glab Outli      1  0.455 0 ==> 1
            anxia                 17.S1 Form        1  1.000 0 ==> 1
node_72 --> node_71               40.NoPygRibs      1  0.333 4 ==> 3
node_71 --> node_70               25.EyeR Term      1  0.500 0 ==> 1
node_70 --> Metapilekia           24.ERStraight     1  0.500 0 ==> 1
             bilirata
node_70 --> Pliomeridius?         1.AB Shape        1  0.500 1 ==> 0
            lacunatus             7.Anteromed       1  0.286 0 ==> 1
                                  14.S3 Form        1  0.700 2 ==> 1
                                  40.NoPygRibs      1  0.333 3 ==> 5
 Branch                           Character  Steps    CI Change
```

3.6.2 Discussion of *Sinoparapilekia* Peng, 1990

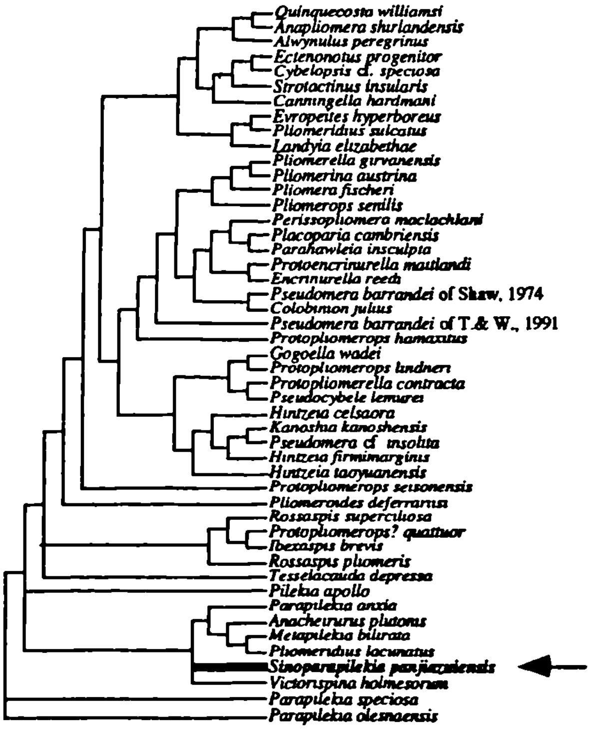
The work by Peng (1990) on 'Trilobites from the Panjiazui Formation and the Madaoyu Formation in Jiangnan Slope Belt' includes the establishment of a new Subfamily Sinoparapilekiinae (discussed in section 3.7), a new genus *Sinoparapilekia* and two species *S. panjiazuiensis* and *S. expansa.* This paper was not seen until the present work was largely finished, thus the diagrams in this chapter were not all re drawn and the biogeographical gain/loss analysis was not remade to incorporate *Sinoparapilekia* as this would have resulted in considerable delay in the production of this thesis. However, as will be demonstrated, inclusion of this taxon does not affect the phylogeny produced by this analysis. Moreover the systematic validity of both *Sinoparapilekia*, and the Subfamily Sinoparapilekiinae are questionable.

Peng (1990 p.114) designated the type species of *Sinoparapilekia* (and hence of the Sinoparapilekiinae) as '*Sinoparapilekia taoyuanensis* n. g., n. sp.' but there is no description of a species with this name. *Protopliomerops taoyuanensis* (Liu 1977) was re- described (Peng 1990 p.116) and confirmed as belonging to *Protopliomerops* in the Subfamily Pliomerinae Raymond 1913 (See section 3.8.3.4 herein where the original assignment of *taoyuanensis* to *Hintzeia* is supported). The first of the *Sinoparapilekia* species to be defined by Peng was *Sinoparapilekia panjiazuiensis* n. g., n. sp. but it was not mentioned in the genus diagnosis. It thus seems likely that the type species of *Sinoparapilekia*, and hence of the Sinoparapilekiinae, was intended to be *Sinoparapilekia panjiazuiensis* Peng, 1990. The trivial name *taoyuanensis* may have been abandoned in favour of *panjiazuiensis* at a late stage of publication but its continued use in the type species designation overlooked. Irrespective of its taxonomic status, *Sinoparapilekia panjiazuiensis* was included in the Pliomeridae analysis to determine the position of '*Sinoparapilekia*' in the phylogeny.

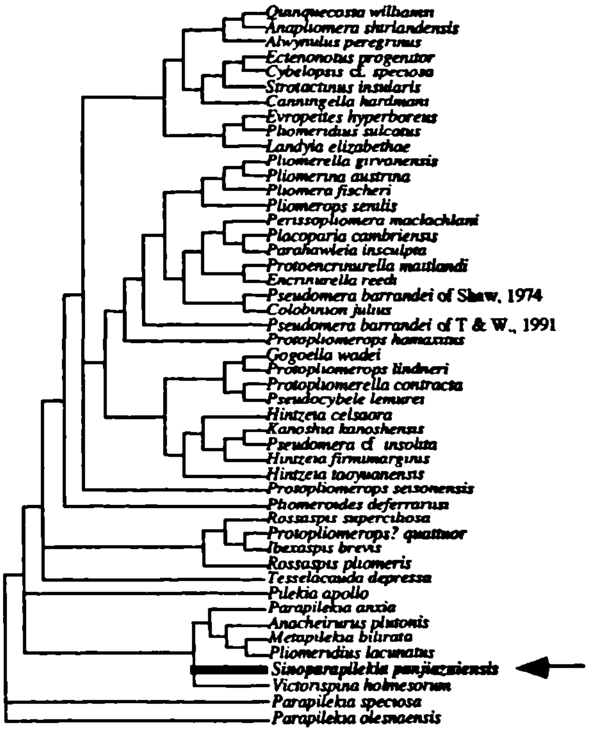
Adding *Sinoparapilekia panjiazuiensis* to the Pliomeridae analysis results in the production of two minimum length trees (Figure 3.13) which are both of length 164, C.I.= 0.482 and Rescaled C.I.=0.353. These trees are otherwise identical to those produced with *panjiazuiensis* excluded (see Figure 3.9). *Sinoparapilekia panjiazuiensis* is placed at a trichotomy, together with *Victorispina holmesorum* Jell, 1985 at the base of a subclade which contains the majority of the Pilekiinae. This placement of *Sinoparapilekia* matches well with the mid/upper Tremadoc age of the taxon and the juxtaposition of *Sinoparapilekia panjiazuiensis* from the Madaoyu Formation of north-western Hunan and *Victorispina holmesorum* Jell, 1985 from the Digger island formation of southern Victoria provides support for the close situation of Australia and Southern China at this time. Peng (1990) remarked on the close biogeographical affinities of Tremadoc faunas of the Panjiazui and Madaoyu formations from the Jiangnan Slope Belt of Hunan, S. China, with Tremadocian faunas of similar age in S. Korea, Australia, Tasmania, Argentina, the Anglo-Welsh area and Bavaria. He also remarked on the difficulty of correlating these formations with the shelly sequences of North America. This provides support for the biogeographical model outlined in Section 3.10.

Figure 3.13: The minimum length trees produced by analysis of the main pliomerid dataset with the addition of *Sinoparapilekia panjiazuiensis* Peng, 1990

1.



2.



Although invalidly erected, the 'Subfamily Sinoparapilekiinae' is discussed in Section 3.7. While it is likely that the taxa assigned by Peng to *Sinoparapilekia* do form a monophyletic group which lies outside currently defined genera, I will refrain from a formal diagnosis of *Sinoparapilekia* until its systematic status is clarified.

The remainder of the diagrams in this chapter do not include '*Sinoparapilekia*' for the reasons outlined earlier in this section.

3.6.3 The placement of highly incomplete taxa;

Various genera have been erected in the past on the basis of very limited and poorly preserved material. If these were to be included in the initial analysis, the sheer volume of missing data would result in the production of a large number of possible trees. To avoid this, such fragmentary taxa have been added to the analysis separately to determine their most likely position in the phylogeny. The discovery of further material may reveal unexpected features resulting in the placement of these taxa in positions other than those ascertained in this analysis.

3.6.3.1 *Emsurella* Rosova, 1960

Type species: *Emsurella humilla* Rosova, 1960

Emsurella humilla comprises one fragmentary cranidium, which is poorly illustrated. As a result there is too little information available to include it in this analysis. Přibyl *et al.* (1985) relocated *Emsurella* from the Pilekiinae to the Pliomeridae, without great discussion, and stated that it may ancestral to the Pliomeridae.

Included species:

Emsurella humilla	Rosova, 1960
Emsurella laevigata	Rosova, 1960

3.6.3.2 *Emsurina* Sivov, 1955

Type species: *Emsurina sibirica* Sivov, 1955

Emsurina is too incomplete to allow it to be coded. The most that can be said of it is that it is similar in form to both the early Pliomeridae and Pilekiinae. Přibyl *et al.* (1985 p. 116) reassigned *Emsurina* to the *Sphaerexochinae* as a possible ancestor of that group.

Included species:

Emsurina minuta	Rosova, 1960
Emsurina fulita	Rosova, 1960

3.6.3.3 *Eocheirurus* Rosova, 1960

Type species: *Eocheirurus salairicus* Rosova, 1960

Eocheirurus, from the Upper Cambrian of Siberia, was added to the analysis to get an indication of its likely placement in the phylogeny (see Figure 3.14). It is only known from a poorly illustrated cranidium which displays features reminiscent of both the Pilekiinae and the Cheiruridae and its correct systematic placement remains unknown until further material, including a pygidium, is recovered. Should *Eocheirurus* still plot at the same location on the cladogram this would indicate that the ancestor of the Cheiruridae lies within the Pilekiinae, close to *Parapilekia anxia*. A further impact of this placement would be that the outgroup to utilise for display purpose would best be *Eocheirurus* - or a closely related taxon.

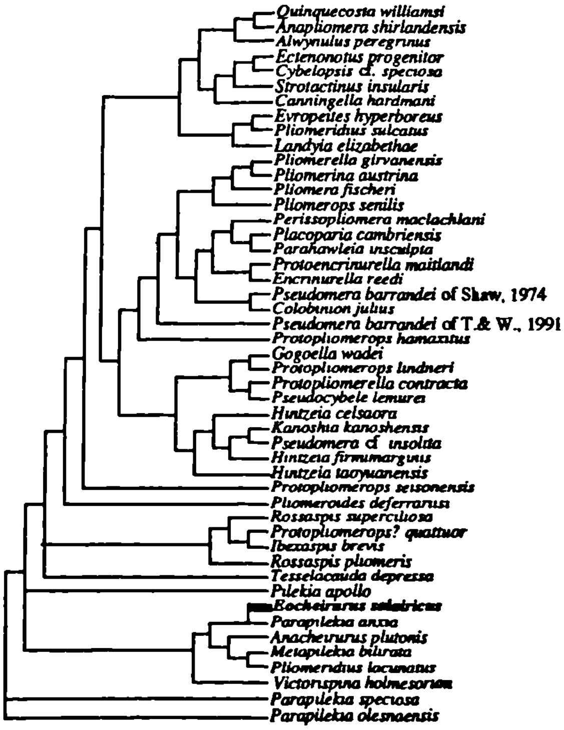
Included species:

Eocheirurus probus	Rosova, 1960
Eocheirurus subtilis	Rosova, 1960

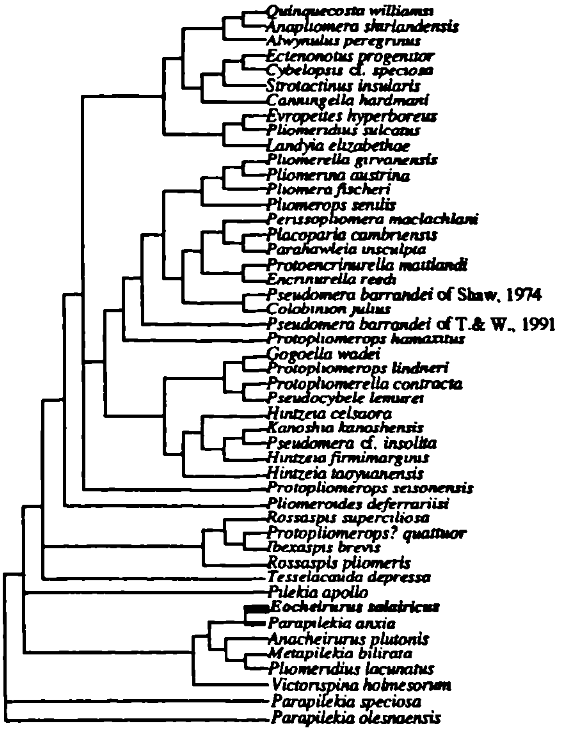
(These latter two taxa may be synonymous with *Eocheirurus salairicus* Rosova, 1960 (see Přibyl *et al.* 1985 p. 119))

Figure 3.14: Two minimum length trees resulting from the addition of *Eocheirurus salairicus* Rosova, 1960 to the pliomerid analysis. Length 167 CI=0.497 RCI=0.364 - Note: *Eocheirurus* material is very poor.

1



2



3.6.3.4 *Laticephalus* Pokrovskaya, 1960

Type species: *Laticephalus trapezoidalis* (Pokrovskaya in Rosova, 1960)

This genus is known from highly incomplete material and is here tentatively recognised as a synonym of *Macrogrammus* Whittard, 1966 from which it appears to be indistinguishable. Formal assignment of the specimens is deferred until more material is available for comparison.

Included species:

Laticephalus trapezoidalis	Pokrovskaya in Rosova, 1960
Laticephalus tuberosus	Pokrovskaya in Rosova, 1960

3.6.3.5 *Leiostrototropis* Raymond, 1937

Type species *Leiostrototropis phlegeri* Raymond, 1937

Leiostrototropis was thought by Raymond (1937) to be closely related to the genus *Strototropis* which he erected at the same time and which was regarded by Harrington (in Moore, 1959) as a junior synonym of *Protopliomerops* Kobayashi, 1934. Comparison of the character codings for *Strototropis* and *Protopliomerops* confirms that they are indeed identical. As *Leiostrototropis* is known only from two highly fragmentary cranidia there is not enough information available for a useful coding to be made. In spite of this, it seems to be differentiated from *Protopliomerops* Kobayashi, 1934 by its weakly developed and forward-directed S3 lateral glabellar furrows.

Other assigned species:

Leiostrototropis laevis	Raymond, 1937

3.6.3.6 *Seisonia* Kobayashi, 1934

Seisonia is a monospecific genus erected by Kobayashi (1934) at the same time as the type species *seisonensis*. The type material comprises only a fragmentary pygidium and cranidium. In addition, I was unable to obtain any illustrations of sufficiently high quality to allow this limited material to be coded. As a result *Seisonia* Kobayashi is here considered to be a valid taxon, as defined by Kobayashi but its affinities are not explored further here.

3.6.3.7 *Tumulina* Repina, 1960

Type species: *Tumulina tumidica* Repina (in Rosova, 1960)

This monospecific genus is known from highly incomplete material and is here tentatively recognised as a synonym of *Macrogrammus* Whittard, 1966 from which it appears to be indistinguishable. Formal assignment of the specimens is deferred until more material is available for comparison.

3.7 Revision of the systematics of the Family Pliomeridae Raymond, 1913 and Subfamily Pilekiinae Sdzuy, 1955:

3.7.1 General discussion.

The Pliomeridae have been divided up into eight subfamilies, including the Pilekiinae which has variably been assigned to the families Pliomeridae and Cheiruridae (see Lane 1971, Přibyl *et al.* 1985).

The subfamilies assigned to the Pliomeridae in the Treatise (Moore, 1959) and all subsequently defined groups which include taxa incorporated in this analysis are highlighted in Figure 3.16. They are largely poor cladistic groups, being variably monospecific, excluding basal members of subclades, polyphyletic or paraphyletic, or a combination of these. It is clear that the subfamily concepts within the Pliomeridae are in need of revision.

The options available for each subfamily are as follows;

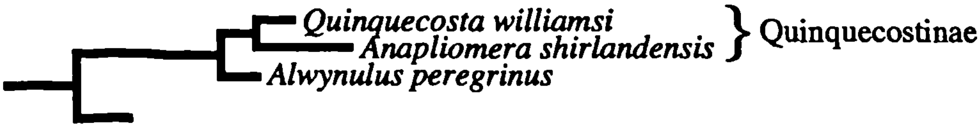
1. To abolish the subfamily.
2. To expand the concept of the subfamily to include all of the members of the subclade to which some members of the subfamily, as currently defined, belong.

3. To contract the concept of the subfamily to include all of the members of a portion of the main subclade to which some members of the subfamily belong.
4. To abolish all of the subfamilies and simply consider the Pliomeridae to be composed of related genera.

If the concept of subfamilies is to be successfully and usefully applied it must provide information about the relationships of the taxa to each other additional to that of the generic definition alone. It should also be possible to allocate unambiguously all, or virtually all, taxa within the Pliomeridae to a subfamily and it must be possible to define all of the subfamilies on the basis of at least one uniquely derived apomorphy. Further, these subfamilies should preferably be monophyletic although it would perhaps be naive to demand that none of the subfamilies be paraphyletic as any successful group, giving rise to large offshoot groups will be, by definition paraphyletic. In spite of this caveat I believe that it is desirable to approach, as closely as possible, monophyly in the definition of taxonomic groups, and that polyphyletic groups should not be allowed. The various problems inherent in the recognition of higher taxa within the Pliomeridae and Encrinuridae and the conventions employed herein are outlined in Section 2.1. An additional Subfamily, the Sinoparapilekiinae Peng, 1990, as discussed in section 3.6.2, is taxonomically invalid. The Sinoparapilekiinae was defined as including the invalid genus *Sinoparapilekia*, *Metapilekia*, *Pliomeroides*, *Eocheirurus*, *Macrogrammus* and *Chashania*. As can be seen from Figure 3.16, these taxa do not form a coherent phylogenetic unit and as such, had it been taxonomically valid, Sinoparapilekiinae would have been regarded as a junior synonym of the Subfamily Pilekiinae as it is within this subfamily that the probable type species of *Sinoparapilekia*, and hence the Sinoparapilekiinae, is placed (see Section 3.6.2).

Of the pliomerid subfamilies as previously defined, only the Quinquecostinae is monophyletic (see Fig 3.15).

Figure 3.15: Taxa currently assigned to the Quinquecostinae highlighted.



The definition of this subfamily is very tight, including only two genera, which are composed of only a small number of species. The Pilekiinae is the only other non polyphyletic subfamily, as currently defined, and is retained as an expressly paraphyletic subfamily herein.

As a result of this analysis I propose to recognise the following five subfamilies within the Pliomeridae (see Fig. 3.17)

Cybelopsinae	Fortey, 1979
Protopliomeropinae	Hupé, 1953
Pliomerinae	Raymond, 1913
New subfamily	Herein
Pilekiinae	Sdzuy, 1955

Of these five proposed subfamilies (see Fig. 3.17), only the Protopliomeropinae and the new subfamily are monophyletic; the remaining three being paraphyletic. Although in Figure 3.17 the Cybelopsinae do not appear to be paraphyletic, it is from within this subfamily that the Cybelinae are derived (See Chapter 4). The Protopliomeropinae and Pilekiinae, as proposed here, are both multiply paraphyletic, but not polyphyletic. The evolutionary significance of these subfamilies is discussed at greater length in section 3.7. In spite of their paraphyly, the subfamilies proposed here compose useful units of taxa with which to work, representing real evolutionary groupings.

3.7.2 Discussion and diagnosis of the five subfamilies here defined.

The presence of a pleisiomorphic plexus and the 'stepping in' of characters at the base of the subclades resulted in difficulties in defining the subfamilies. Those taxa situated in a position basal to the more derived subclades, intermediate between them and the pleisiomorphic plexus of taxa from which they were derived, were included in the definition of the subfamily which contained the more derived taxa. This results in a number of taxa which are superficially more similar to members of the pleisiomorphic plexus being assigned to the derived subfamilies whose subclade they are at the base of. The problem of the systematic placement of those taxa which are situated at the base of a derived subclade, possessing some, but not all, of that groups apomorphic character is not restricted to the Pliomeridae but which is widespread and is discussed in section 2.1.8.

Figure 3.16: Pliomeridae phylogram with the subfamilies of the Pliomeridae, as previously recognised highlighted.

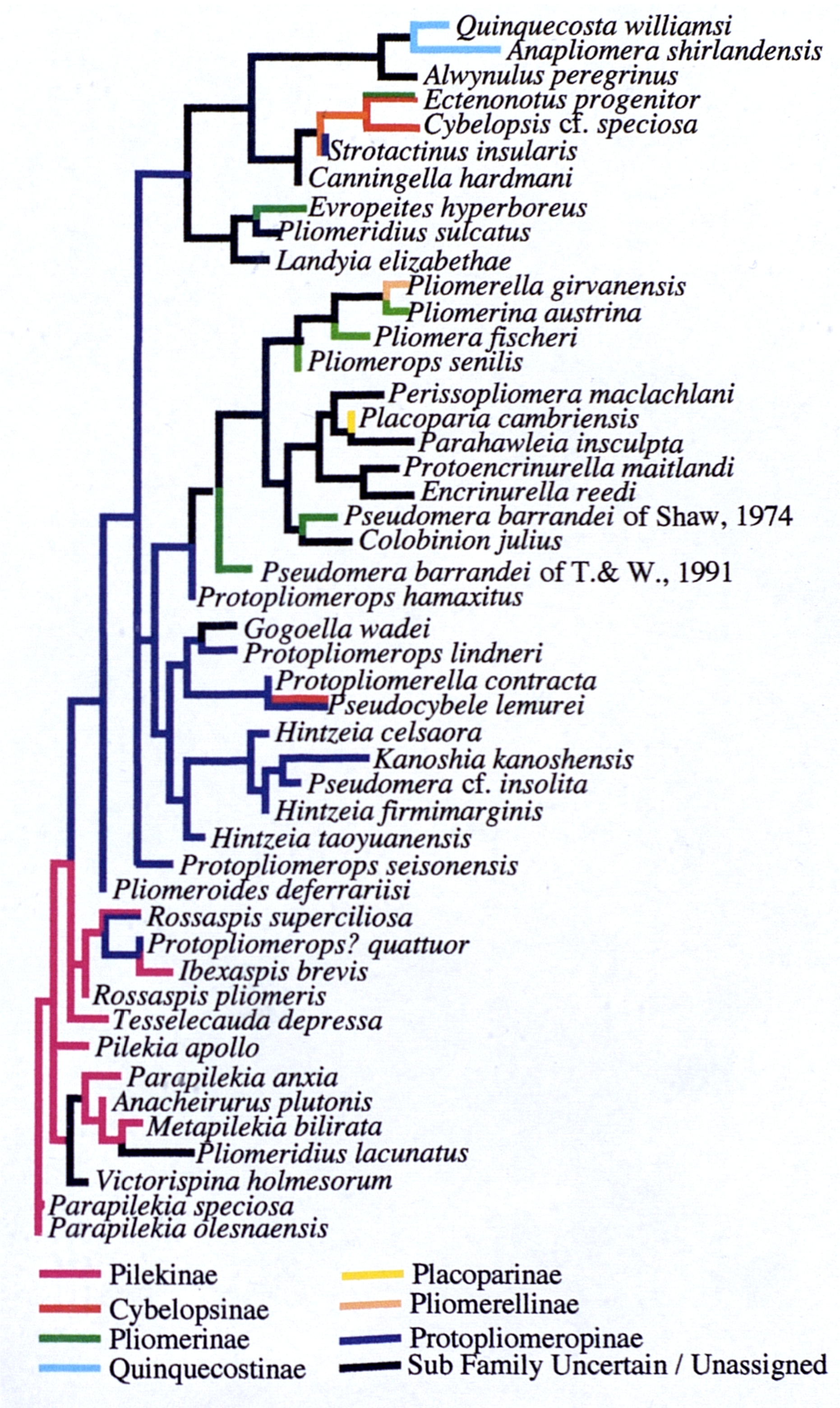
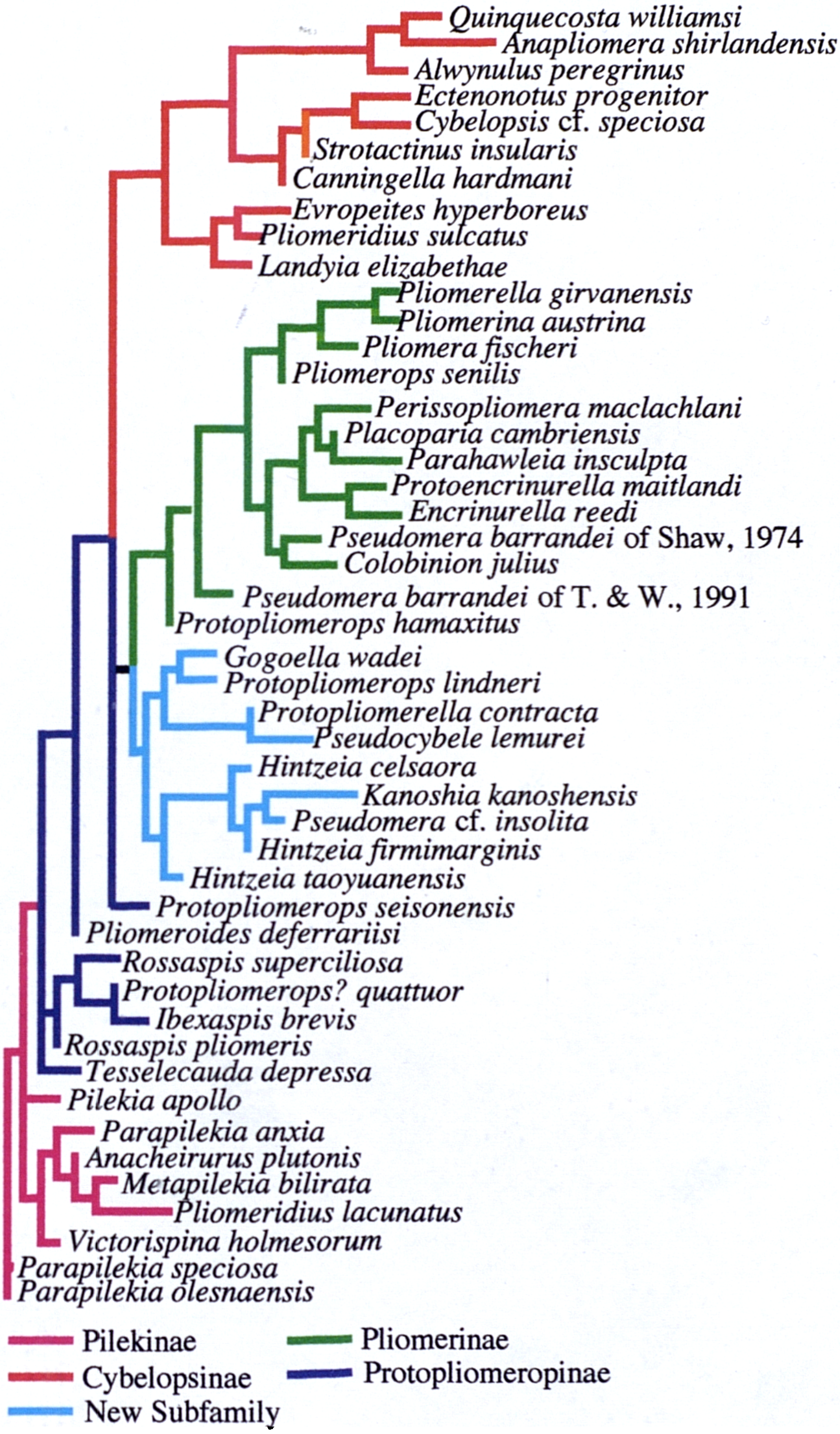


Figure 3.17: Phylogram with the re-defined pliomerid subfamilies highlighted.



3.7.2.1 **Pilekiinae** Sdzuy, 1955

It is debatable to which family the Pilekiinae should be assigned. They clearly gave rise to the undisputed subclades of the Pliomeridae and so could justifiably be placed within this family as suggested by Harrington in the Treatise (Moore, 1959).

However, the Pilekiinae also contains a good potential ancestor of the Cheiruridae in the incompletely known species *Rossaspis* sp. of Demeter (1973 pl. 2 fig. 5) on the basis of the course of the S1 lateral glabellar furrows which are oriented transversely in their abaxial portion, turn to the posterior at their midpoint, after which they are directed to the posterior, parallel to the axis. This results in the L1 lateral glabellar lobes exhibiting a distinctly square outline, similar to those of the Cheiruridae Hawle & Corda, 1852. If this species is close to the form ancestral to the Cheiruridae then the Pilekiinae gave rise to both the Cheiruridae and the Pliomeridae. It would also be reasonable to place the Pilekiinae within the Family Cheiruridae, as advocated by Lane (1971) and Přibyl *et al.* (1984). In spite of the complexity of the relationships of the Pilekiinae to their various daughter groups, I do not support the definition of the Pilekiinae as a separate family for two reasons:

1. The characters which unite the Pilekiinae are few and not of sufficient magnitude to support the separation of these taxa at familial level.
2. The complex nature of the relationship of the Pilekiinae to the other groups would not be further elucidated or resolved by definition of the Pilekiinae as a family rather than a subfamily. As the only justification for the erection of higher taxa is to provide simplicity, clarity and further information on the relationships of the component taxa, there is no reason for the elevation of the Pilekiinae above subfamily level.

The Pilekiinae are here regarded as a subfamily of the Pliomeridae.

The Pilekiinae *(sensu stricto)* is diagnosed primarily by distinctive pygidial pleurae which are swept back, broadening distally to the point at which they bend sharply to the posterior and taper until they form long free points. These pygidial pleurae are divided by pleural furrows which do not (normally) reach the margin of the pygidium.

Strictly utilising this character as the apomorphy diagnostic of the Pilekiinae results in the exclusion of *Tesselacauda* and *Rossaspis* from this subfamily. These genera display many of the features of the Pilekiinae but differ in the structure of the pygidial pleurae. While the pygidia of *Tesselacauda* display anterior fields on the pygidial pleurae which are defined by pleural furrows which terminate before reaching the margin of the pygidium (after the fashion of the Pilekiinae) they lack the characteristic long tapering free points. As a result, the pygidium of *Tesselacauda* has been coded as possessing anterior pleural bands on the pygidium but as not having 'Pilekiiform' pleurae. In most respects, however, the pygidia of *Tesselacauda* are very similar to those of the Pilekiinae, indicating a close relationship.

The pygidial pleurae of *Rossaspis (sensu stricto)* differ from those of both the Pilekiinae and of *Tesselacauda* and resemble those of such pliomerids as '*Rossaspis? pliomeris* ' of Demeter (1973). The mature pygidia of *Rossaspis* also bear a strong resemblance to immature pygidia belonging to *Tesselacauda*. This close similarity of pygidial form reinforces the close taxonomic juxtaposition of the two genera in the cladogram and supports the position of *Rossaspis* as being intermediate between *Tesselacauda*, the Pilekiinae and the Pliomeridae as intimated by Ross (1952). This taxonomic closeness is reflected in the geographical closeness of the oldest examples of the two taxa (see section 3.9).

In the light of the placement of these taxa on the cladogram as intermediate forms I propose the inclusion of *Rossaspis* and *Tesselacauda* in the Subfamily Protopliomeropinae rather than the Pilekiinae.

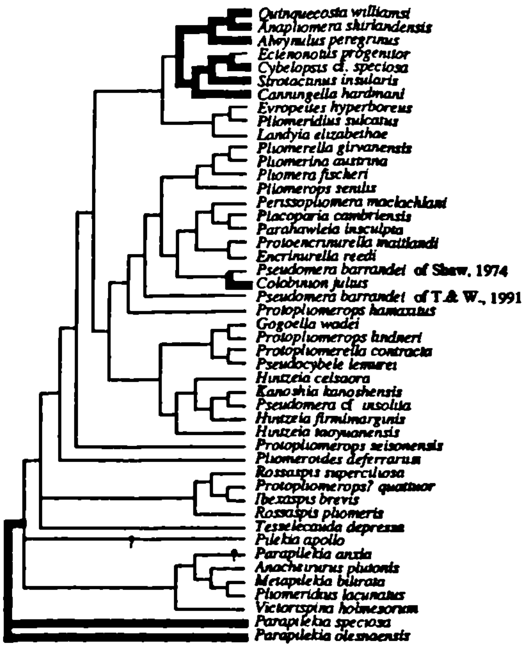
A feature which separates the genera *Pilekia* and *Parapilekia*, splitting the Pilekiinae into two sub-groups, is whether there are more rings on the axis of the pygidium than there are pygidial pleurae. In *Pilekia* and *Parapilekia* there is a degree of variation in this character at species level, and in some cases at subspecies level while in taxa further up the cladogram this character generally varies at genus level. Complicating the picture is the fact that in some species, such as *Pilekia apollo* Billings, 1859, in which the number of axial rings is equal to the number of pygidial pleurae, an area of the terminal piece of the pygidial axial termination displays a degree of independent convexity. As this area is not bounded by an axial furrow I do not regard it as an additional separate axial ring. In spite of this, some workers, notably Přibyl & Vaněk (1985), have regarded as this as being an additional axial ring.

It is clear that this character, although multiply derived, is of relatively high burden further up in the phylogeny but of relatively low burden within the Pilekiinae.

(see discussion of characters of variable burden in section 2.1.9.1). It is also clear that the genus *Parapilekia* as currently defined is polyphyletic and requires revision.

The apparently low burden of this character within some members of the Pilekiinae is important as it bears strongly on whether the genera *Pilekia* and *Parapilekia* should be synonymised (see Sdzuy (1955) and Lane (1971)) or retained as separate genera as favoured by Fortey (1980) and Mergl (1984).

Figure 3.18: Pliomerid cladogram with distribution of the character 'More axial rings than pleural ribs on pygidium' highlighted.



<u>The characters diagnostic of the Pilekiinae are:</u>

Glabella tapers anteriorly or is sub-oval/sub-square; S3 glabellar furrows branched or unbranched, cutting, or positioned posterior to, the anterior corners of the glabella; eye ridge not confluent with the lateral fixigenal border (except *Pilekia trio*); genal spines present, eyes sub-median to anterior; Hypostome with complete anterior border, narrow posterior border, lateral marginal spines but no mesial spine; 3-4 pygidial pleurae which flare strongly away from the pygidial axis to the point at which they curve rearwards and taper to free spines, flat pleurae bisected laterally by anterior pleural furrows which rarely reach the margins of the pygidium, Genera included in the Subfamily Pilekiinae:

Anacheirurus	Reed, 1896
Koraipsis	Kobayashi, 1934
Metapilekia	Harrington, 1938
Parapilekia	Kobayashi, 1934
Pilekia	Barton, 1916
Seisonia	Kobayashi, 1934
Victorispina	Jell, 1985
Eocheirurus	Rosova, 1960
Pliomeridius? lacunatus	Dean, 1989 (of uncertain genus) is included within the Pilekiinae.

Included provisionally in Pilekiinae, not included in this analysis:

Macrogrammus	Whittard, 1966
Metapliomerops	Kobayashi, 1934

Excluded from the Pilekiinae:

Ibexaspis	Přibyl & Vaněk, 1984
Tesselacauda	Ross, 1951
Rossaspis	Harrington, 1957

3.7.2.2 Protopliomeropinae Hupé, 1953.

As can be seen in Figure 3.16 the Protopliomeropinae as currently defined is both paraphyletic and polyphyletic. The paraphyletic aspect of the subfamily is less damaging than the fact that the group is polyphyletic and as such does not represent any meaningful evolutionary unit. I propose to limit the scope of this subfamily to those taxa highlighted in Figure 3.17 and any closely related taxa which were not included in that analysis.

The diagnosis of the Protopliomeropinae in the Treatise (Moore, 1959) is so broad as to provide no characters upon which to either recognise members of this subfamily as such, or to exclude many other pliomerids. The difficulty encountered in diagnosing this group, in essence reflects the evolutionary significance of the taxa assigned to it. Apart from subgroups such as that which includes *Rossaspis*, the Protopliomeropinae may be recognised by the pleisiomorphic morphology of its component taxa rather than by any uniquely derived apomorphies. Taxa belonging to this group form a long lived, evolving plexus which gave rise independently to the taxa forming the systematically more derived subfamilies.

The Protopliomeropinae is here restricted to a core of genera which excludes a number of taxa which are situated in a position which is basal to more derived subclades. The Protopliomeropinae is then a subfamily which represents a useful evolutionary group, the upper and lower bounds of which are defined by the loss and acquisition of apomorphies which define other subfamilies. As such, rather than being a monophyletic group defined by the acquisition of a unique apomorphy and truncated by extinction it is an arbitrary construct. In spite of this, the Protopliomeropinae is retained as being morphologically recognisable and evolutionarily meaningful.

The characters diagnostic of the Protopliomeropinae are:

Glabella longer than wide, tapering anteriorly or sub-parallel/sub-oval and non-tuberculate; Breadth of the glabella across L1 less than one third of the breadth of the cephalon across L1; S3 unbranched and directed either to the anterior glabella angle or posterior to it; Hypostome of rounded outline with a complete anterior border, small hypostomal wings, narrow posterior border, marginal spines present but no mesial spine; Pygidium of 4-6 pleurae; The number of pygidial pleurae equals that of pygidial ribs; Pygidial ribs are generally unfurrowed (*Rossaspis* and *Tesselacauda* furrowed); Tips of pygidial pleurae not turned out; Terminal piece of pygidial axis is small and unpitted.

Genera included in the Subfamily Protopliomeropinae:

Ibexaspis	Přibyl *et al.*, 1985
Rossaspis	Harrington, 1957
Pliomeroides	Harrington & Leanza, 1957
Protopliomerops	Kobayashi, 1934
Tesselacauda	Ross, 1951

3.7.2.3 Subfamily Nov. Herein.

In the Treatise (Moore, 1959) members of this subclade were assigned to the Subfamily Protopliomeropinae, as was *Pseudocybele* which was later re-assigned to the new Subfamily Cybelopsinae by Fortey, 1979 on the basis of the apparently elongate form of the terminal section of the pygidial axis. The results of the present analysis illustrate the close similarity in morphology of these taxa with those assigned to the Subfamily Protopliomeropinae (see section 3.7.2.2). In spite of this close relationship I propose the separation of members of this subclade from those of the Protopliomeropinae. Various apomorphies define successive subclades within this subfamily, but the primary defining character is the acquisition of a mesial spine on the posterior border of the hypostome. Although this feature is unique to this subfamily its usefulness is somewhat reduced by the infrequent preservation of hypostomes in association with matching cranidia.

Diagnosis of the Subfamily

Glabellar outline narrows forwards or is sub-parallel sided; glabella non-tuberculate; anteromedian complex may be present in frontal lobe of glabella; 3-4 lateral glabellar furrows; S3 either cuts or, in the case of *Kanoshia* Harrington, 1957, is situated to the posterior of the anterior angle of the glabella; Eye ridges present; Genal angles either spinose or rounded; Hypostome of oval outline; Anterior border of hypostome may be either continuous or cut by the middle body; posterior border of the hypostome either narrow or expanded; Marginal spines present on the hypostome; Mesial spine present on the posterior hypostomal margin; 4-5 pygidial ribs all of which end in free points and are not divided by pleural furrows into anterior and posterior fields; The number of rings on the pygidial axis is equal to the number of pygidial pleurae; The posterior pair of pygidial pleurae may be fused distally.

Genera included in the Subfamily Nov.:

Gogoella	Legg, 1976
Hintzeia	Harrington, 1957
Kanoshia	Harrington, 1957
Protopliomerella	Harrington, 1957
Pseudocybele	Ross, 1951

3.7.2.4 Pliomerinae Raymond, 1913

It can be seen from Figure 3.16 that the Pliomerinae, as defined in the Treatise (Moore, 1959) while largely supported by this analysis, is polyphyletic. The systematics of this subclade therefore require revision. *Cybelopsis* was removed from this subfamily by Fortey (1979) and placed in his new Subfamily Cybelopsinae, a reassignment supported by this analysis. The Pliomerinae as recognised herein comprises three subfamilies in the Treatise (Moore, 1959): The Pliomerinae Raymond, 1913, Pliomerellinae, Hupé 1953 and Placopariinae Hupé, 1953. This expanded Pliomerinae reflects the evolutionary history of a subclade whose members are descended from the same common ancestor, probably morphologically close to *Protopliomerops hamaxitus* Jell, 1985.

Protopliomerops hamaxitus is closely related to *Protopliomerops seisonensis* Kobayashi, 1934 and other members of the pleisiomorphic Subfamily Protopliomeropinae. The Protopliomeropinae also gave rise independently to the other derived subclades, while further evolving itself. The result of this is that all of the derived subclades, and hence the derived subfamilies, developed from very similar ancestral forms. As such it makes sense the define the base of all of the derived subfamilies (Pliomerinae, Subfam. Nov. and Cybelopsinae) as being at the point at which they acquired distinctive apomorphies setting them apart from the pleisiomorphic Protopliomeropinae.

Diagnosis of the Pliomerinae:

In common with the other diagnoses a number of characters 'step in' at the base of the subclade so some taxa at the base of the subclade may not display all of the characters included in this subfamilial diagnosis.

Glabella expands evenly forwards, approximately as long as wide; Anterior border furrow is shallow (*Pseudomera* subclade); 3 pairs of lateral glabellar furrows, S3 positioned anterior to the anterior angle of the glabella; genal angles rounded; eyes sub-median; Eye ridges terminate cutting the adaxial edge of the fixigenal field (*Pseudomera* subclade) or cutting the anterior, edge of the fixigenal fields (*Pliomera* subclade); Hypostome with anterior border intersected by the rounded middle body (except *P. hamaxitus*), posterior hypostomal border broad (except *Protopliomerops hamaxitus* and *Pseudomera barrandei*, no marginal spines (except *Protopliomerops* *hamaxitus* and *Pseudomera barrandei*; Hypostome of angular, shield-shaped outline (except *Protopliomerops hamaxitus* and *Pseudomera barrandei*) the angulations being situated in positions which correspond to those of the marginal spines found on the margins of the hypostome of members of other subfamilies; Pygidium with 4-6 unfurrowed pleurae and terminal axial piece.

Genera included in the redefined Pliomerinae:

Colobinion	Whittington, 1961
Encrinurella	Reed, 1915
Parahawleia	Zhou, 1978
Perissopliomera	Ross, 1970
Placoparia	Hawle & Corda, 1847
Pliomera	Angelin, 1852
Pliomerella	Reed, 1941
Pliomerina	Chugaeva, 1958
Pliomerops	Raymond, 1905
Protoencrinurella	Legg, 1976
'*Protopliomerops*' *hamaxitus*	Jell, 1985
Separate from *Protopliomerops* *(sensu stricto)*	
Pseudomera	Holliday, 1942

3.7.2.5 Cybelopsinae Fortey, 1979

The Subfamily Cybelopsinae was erected by Fortey (1979, p 106) to include the genera *Cybelopsis*, *Pseudocybele*, *Strotactinus*, *Canningella* and *Ectenonotus*. The validity of the Cybelopsinae is supported by this analysis, with some revision.

Fortey diagnosed the Cybelopsinae on the basis of the following characters: Pliomerids with elongate terminal piece on the pygidial axis or with more than five axial pygidial segments; a broadly rounded (rather than truncate) anterior glabellar outline; an anterior cranidial border which is nasute and highly convex or reflexed over the anterior of the glabella; a variably positioned palpebral lobe; a narrow pygidium of cybelid appearance and normally five pairs of pygidial ribs.

The distribution of the species originally included in the Cybelopsinae can be seen in Figure 3.16. The present analysis places the majority of these taxa in the same subclade, with the exception of *Pseudocybele* which is placed separately in an entirely different subclade, the new subfamily defined herein. The terminal section of the pygidial axis of *Pseudocybele* which is similar to be an elongate terminal section of the other taxa included in the Cybelopsinae by Fortey is not homologous, being formed by the fusion of the two posterior pygidial pleurae rather than by the elongation of the pygidial axis (Fig. 3.8). The terminal section of the pygidial axis itself is actually short (see Fig. 3.8).

Although the combination of characters originally employed in the diagnosis of the Cybelopsinae is unique, all of these characters are also found individually in other members of the Pliomeridae. In order that all of the members of the Cybelopsinae share at least one uniquely defined apomorphy the concept of the subfamily must be either expanded to include more genera, or restricted to include fewer.

I propose the expansion of the Subfamily Cybelopsinae to include *Cybelopsis, Ectenonotus, Strotactinus, Canningella, Quinquecosta, Anapliomera, Alwynulus, Evropeites, Pliomeridius* and *Landyia.* These taxa all posses a pygidium which displays a pair of pits on the relatively elongated axial terminal piece and pygidial pleurae which normally remain in contact until close to the tips. *Landyia, Evropeites* and *Pliomeridius sulcatus* display all of these characters, with the exception of the bluntly terminating pygidial pleurae remaining in contact for the majority of their length, in these taxa, the pleurae diverge shortly after their mid points. It is reasonable, then, to include these taxa within the Cybelopsinae.

The presence of a number of additional axial rings on the terminal piece of the pygidial axis of *Quinquecosta, Anapliomera* and *Alwynulus* makes determination of the presence or absence of paired pits on this posterior portion of the pygidial axis uncertain. As a result this character was coded as unknown for these taxa. It can be seen that the position of these taxa on the cladogram implies that either a small pair of pits is present on the terminal section of the pygidial axis and are simply difficult to ascertain due to their small size and the presence of numerous axial rings or that the terminal pair of pits has been secondary lost in these taxa.

Anapliomera was informally placed in a new subfamily, the Quinquecostinae, by Edgecombe & Chatterton, 1992. The erection of a new subfamily is considered to be redundant and not supported herein.

The inclusion of *Quinquecosta*, *Anapliomera* and *Alwynulus* in an expanded Cybelopsinae and the re-assignment of *Hunanencrinuroides* to the Encrinurinae (Tripp *et al.*, in press) results in the Subfamily Quinquecostinae being reduced to a junior synonym of the Cybelopsinae. It is probable that members of the Cybelopsinae gave rise to both the Encrinuridae Angelin, 1854 (from taxa close to *Evropeites*) and the Staurocephalinae Prantl & Přibyl, 1947 (from taxa close to *Alwynulus*).

Diagnosis of the Subfamily Cybelopsinae *sensu stricto*:

Glabellar outline variably narrows forward, is subparallel sided or expands forwards; Glabella longer than wide; Anterior border furrow is deep, with the *Landyia* subclade displaying a mesial deepening of the anterior border furrow; S3 lateral glabellar furrow is un-branched and obliquely oriented in the *Canningella* subgroup, dog-legged or forked in the other members; The early members of the subfamily, *Alwynulus*, *'Evropeites'*, *Pliomeridius* and *Landyia* display fixigenal spines which are directed towards the posterior while the more derived members display rounded genal angles; The hypostome has an oval outline; The anterior border of the hypostome is continuous, except in *Anapliomera* and *Cybelopsis* where it is bisected by the ovoid hypostomal middle body; Posterior border of the hypostome is expanded in the *Canningella* subclade, narrow in the other members of the subfamily; Similarly the *Canningella* subclade does not display marginal spines on the hypostome while the other members of the subfamily do; Mesial hypostomal spine absent; 4-5 pygidial pleurae present, except in *Alwynulus* and *Ectenonotus* where there are 8+ (see Fortey & Droser 1996); Number of ribs=number of axial rings on the pygidium in *Landyia* stem subclade, More axial rings than pleural ribs on pygidia of other Cybelopsinae; Pygidial pleurae not divided into anterior and posterior fields by longitudinal furrows (except *Landyia*); The tips of the pygidial pleurae are turned out (less strongly and consistently in the *Landyia* subclade than in the other members of the Cybelopsinae); Terminal piece of pygidial axis is elongate and bears a transversely oriented pair of pits;

Genera included in the Cybelopsinae:

Alwynulus	Tripp, 1967
Anapliomera	DeMott, 1987
Canningella	Legg, 1976

Cybelopsis	Poulsen, 1927
Ectenonotus	Raymond, 1920
Evropeites	Balashova, 1966
Landyia	Jell, 1985
Pliomeridius	Leanza & Baldis, 1975
Quinquecosta	Tripp, 1965
Strotactinus	Bradley, 1925
Genera Excluded from the Cybelopsinae:	
Pseudocybele	Ross, 1951

3.7.2.6 Assessment of the remaining pliomerid subfamilies presently defined.

The remaining subfamilies diagnosed in the Treatise (Moore, 1959) are as follows: Pliomerellinae Hupé, 1953; Placopariinae, Hupé, 1953 and the Diaphanometopinae Jaanusson, 1959. In addition, Peng, 1990 erected the Subfamily Sinoparapilekiinae.

3.7.2.6a Diaphanometopinae Jaanusson, 1959

See section 3.4.4

3.7.2.6b Placopariinae Hupé, 1953

As this subfamily is monogeneric, it provides no additional information on the relationships of the contained species above that of the basic generic assignment. Because of this, I propose that the Placopariinae should be regarded as a junior synonym of the Subfamily Pliomerinae.

3.7.2.6c Pliomerellinae Hupé, 1953

The diagnosis of this monogeneric subfamily employed in the Treatise contains no characters which are not found in taxa elsewhere in the cladogram. In common with the Subfamily Placopariinae, this subfamily is monogeneric and therefore all of the species assigned to the Subfamily Pliomerellinae are also automatically placed in the genus *Pliomerella*. This again makes the subfamily concept redundant as it provides no additional information on the relationships of the taxa to each other above that provided by the basic generic assignment. It is thus necessary to either incorporate the Pliomerellinae within an expanded concept of a larger subfamily or to expand the concept of the Pliomerellinae.

I propose that the Pliomerellinae be regarded as a junior synonym of the Subfamily Pliomerinae.

3.7.2.6d Sinoparapilekiinae Peng, 1990

As discussed in Section 3.6.2, this subfamily is taxonomically invalid as the name of the type species of the type genus was incorrectly designated. The components of the Sinoparapilekiinae were assessed in relation to the phylogeny derived by this analysis and do not form a coherent group (see section 3.6.2). [Peng defined the Sinoparapilekiinae as containing the following genera: *Sinoparapilekia*, Peng, 1990 (but see Section 3.6.2), *Metapilekia* Harrington 1938, *Pliomeroides* Harrington and Leanza 1957, *Eocheirurus* Rosova, 1960, *Macrogrammus* Whittard, 1966, *Chashania* Lu & Sun *in* Zhou *et al.* 1977.]

3.8 Discussion / diagnosis of the genera belonging to the various subfamilies assigned to the Pliomeridae Raymond, 1913:

3.8.1 Genera within the Subfamily Pilekiinae Sdzuy, 1953:

The relationship of *Parapilekia* to *Pilekia* has been the subject of debate in the literature with Sdzuy (1955) and Lane (1971) regarding *Parapilekia* as junior synonyms of *Pilekia* Barton. In contrast Destombes (1970), Hammann (1971), Fortey (1980) and Mergl (1984) supported the validity of *Parapilekia* as a genus distinct from *Pilekia* on the basis of the 'tumid and expanded glabella lobes, and anterior glabella taper' of the latter. In this analysis *Parapilekia speciosa*, and associated forms, are separated from *Pilekia* by a node on the cladogram. The character change which supports this node is that from there being more rings an the axis of the pygidium than there are pygidial pleurae, below the node, to there being an equal number of ribs and rings on the pygidia of the taxa above this node. While this character is of relatively high burden in the upper portion of the cladogram, it appears to be of low burden in this lower portion. This reduces the confidence with which the proportion of axial rings to pleural ribs on the pygidium may be used to make genus level distinctions in the lower portion of the cladogram without further supporting evidence.

As can be seen from Figure 3.16 various species assigned to *Parapilekia* plot at different locations within the Pilekiinae. This clearly indicates that the concept of *Parapilekia* requires revision. *Parapilekia* is composed of taxa of three distinct morphologies; *Parapilekia speciosa* and related forms, displaying a subsquare glabellar outline, *Parapilekia olesnaensis* and related forms (which are closely related to the *speciosa* form but which do not display the subsquare glabella form of those taxa in the *speciosa* group), and the *Parapilekia anxia* form which is closely related to *Anacheirurus*. It may ultimately prove useful to restrict membership of *Parapilekia* to those taxa of similar morphology to *speciosa*, with the *olesnaensis* form being regarded as a pleisiomorphic 'stem' group of *Parapilekia* and those taxa of similar morphology to that *olesnaensis* forming the basis of a new genus.

3.8.1.1 *Anacheirurus* Reed, 1896

Type species *Cheirurus (Eccoptochile) frederici* Salter, 1864

As noted in section 3.4.2 it is proposed that *Chashania* Sheng, 1977 be regarded as either a subgenus or junior subjective synonym of *Anacheirurus*.

Diagnosis of *Anacheirurus*:

Glabella narrows forwards, is longer than wide and has a breadth across L1 which is less than 1/3 of that of the cephalon across L1; S3 furrows bifurcate adaxially and positioned to the posterior of the anterior angle of the glabella; Palpebral lobe positioned abaxially; eye ridge present and curved; Genal spines large and directed to the posterior; Hypostome oval with an continuous anterior border, narrow posterior border and marginal spines; pygidium displays three pleurae of pilekiid form and confluent with three rings on the pygidial axis; small terminal section on axis.

Species included in *Anacheirurus*;

Cheirurus (Eccoptochile) frederici	Salter, 1864
Anacheirurus plutonis	Rushton, 1973
Hintzeia cf *H. insolita*	of Demeter, 1973, pl. 4 figs 9, 10
Cheirurus discretus	Barrande, 1868
P. bohemicus	Růžička, 1926
Emsurella(?) laevigata	Rosova, 1960

pos. new subgenus *Anacheirurus (Chashania)*

Anacheirurus (Chashania) chashanensis	(Sheng 1977)
Anacheirurus (Chashania) fusus	(Sheng 1977)

Taxa not examined herein, but assigned to *Anacheirurus* by other authors so tentatively assigned to *Anacheirurus* herein;

Anacheirurus discretus	Chang, 1966

3.8.1.2 *Macrogrammus* Whittard, 1966

Type species *Macrogrammus scylfense* Whittard, 1966

This taxon was too incomplete to include in the main analysis and its validity is not certain, however a broad discussion of its features is relevant here. As noted by Fortey (1980), there appears to be little to separate *Macrogrammus* from *Parapilekia* in terms of their cranidia. The main character supporting this differentiation, the position of the palpebral lobes and hence the length of the eye ridges, was highlighted as being a somewhat inadequate character for the differentiation of two genera by Fortey (1980 p. 81), particularly as it varies both between and within species. As intimated by Fortey, the exact subfamily/family assignment of *Macrogrammus* must await the discovery of a matching pygidium. It is worth noting, however, that both the form of the S1 lateral glabellar furrows which curve strongly rearwards, and the form of the glabella are reminiscent of those of the Cheiruridae. This may reflect the position of the ancestor of the Cheiruridae somewhere in the region of *Macrogrammus* and close to *Parapilekia*.

It is also worth simply noting the close resemblance between *Macrogrammus* and members of the genus *Laticephalus* Pokrovskaya in Rosova (1960) and *Tumulina* Repina in Rosova (1960) from the Lower Ordovician of the Gorny Altai region. These taxa are based on highly incomplete cranidia but one or other of them may prove to be a senior synonym of *Macrogrammus.*

Included species.

Macrogrammus scylfense	Whittard, 1966;
M. sp.	Lane (1971, p. 37 plate 7, fig. 21a,b);
M. sp.	Harrington & Leanza (1957, p.219, text fig. 121a,b)

Tentatively regarded as congeneric:

Tumulina tumidica	Repina in Rosova, 1960
Laticephalus trapezoidalis	Pokrovskaya in Rosova, 1960
Laticephalus tuberosus	Pokrovskaya in Rosova, 1960

3.8.1.3 *Metapilekia* Harrington, 1938

Type species *Metapilekia bilirata* Harrington, 1938

I was able to obtain a plaster cast of the partial cranidium type specimen of *Metapilekia bilirata* from Dr R.A. Fortey of the Natural History Museum and all of the codings for this taxon were made from this material and from the Treatise illustration of the pygidium (Moore, 1959). Codings made from this were verified against the illustrations of *M.(?) martelli* (Kobayashi, 1934) and *M.(?)* sp of Kobayashi (1959, p. 261, pl. 13, fig. 26). *Metapilekia* is closely related to *Anacheirurus* and has similar anterior fields on the thoracic pleurae.

Diagnosis of *Metapilekia:*

Glabella narrows forwards, is longer than wide and occupies less than 1/3 of the width of the cephalon across L1; S3 lateral glabellar furrows branched, anterior branch short and directed anteriorly, posterior branch long and directed transversely;

S3 furrows positioned posterior to the anterior corner of the glabella; Anterior border strongly 'W' shaped; eye ridges long, straight and adaxially terminating posterior to the adaxial corner of the fixigenal field; Arcuate fixigenal ridge extending from L3 to the posterior, abaxial corner of the fixigenal field; Long fixigenal spines present, directed to the posterior; Pygidium with three pleurae, of pilekiid form, confluent with three axial rings; small terminal axial piece.

Species included in *Metapilekia*;

M. bilirata	Harrington, 1938
M. (?) martelli	(Kobayashi, 1934)
M. (?) sp	Kobayashi, 1959 (p. 261, pl. 13, fig. 26)

3.8.1.4 *Parapilekia* Kobayashi, 1934

Type species: *Calymene ? speciosa* (Dalman, 1827)

On the basis of the currently employed characters *Parapilekia* is not supported as a good monophyletic group and is something of a 'dustbin' genus to which various, early, members of the Pilekiinae have been assigned. It encompasses morphologies ranging from that of the type species, *Parapilekia speciosa* (Dalman, 1827) to that of *Parapilekia anxia* Sdzuy, 1955 and this inclusion of a wide variety of morphologies renders the unambiguous diagnosis of the genus impossible and its revision is required.

Parapilekia is often diagnosed on the presence of a sub-square/oval glabella; a character employed by Fortey (1980 p.80) to differentiate *Parapilekia* from *Pilekia*, on the basis of the 'anterior glabellar taper' of the latter. Many of the taxa currently assigned to *Parapilekia* are not of this form, displaying instead either a glabellar outline with a distinct anterior taper, or with an elongate, sub-parallel outline.

Also often utilised in diagnoses of *Parapilekia* is the presence of non-bifurcate S3 lateral glabellar furrows. Unfortunately this feature is not unique to *Parapilekia* within the Pilekiinae, also being found in members of *Pilekia*, *Tesselacauda* and *Rossaspis*. Moreover, this character is not displayed by all of taxa currently assigned to *Parapilekia*. Those species with an elongate, sub-parallel glabella or with a strong anterior taper also display forked S3 lateral glabellar furrows. A character frequently employed in the diagnosis of *Parapilekia*, differentiating those *Parapilekia* species displaying an anterior glabella taper and forked S3 from *Anacheirurus*, is the presence of four, rather than three, pygidial pleurae. Indeed, on the current definition of *Parapilekia*, this is the only ubiquitously held character which differentiates *Parapilekia* from *Anacheirurus*. This character has been discussed at various points herein and its limitations as a sole diagnostic feature highlighted.

In order to address these points it is proposed to restrict the definition of *Parapilekia* to those species which closely resemble the type species *Parapilekia speciosa* (Dalman, 1827), with the remaining taxa being assigned to a new genus.

Taxa belonging to the proposed restricted *Parapilekia* exhibit a sub-square glabella which occupies approximately 1/3 of the total width of the cephalon across the L1 lateral glabellar furrows, an unbranched S3 lateral glabellar furrow which abaxially is directed obliquely to the anterior, cutting the anterior glabellar angle, an anterior border in which the portion which lies immediately to the anterior of the frontal lobe of the glabella is flat and straight and long, stout, genal spines which are directed parallel to each other to the posterior of the animal.

It is likely that *Anacheirurus* was derived from one of the taxa which it is proposed should be re-assigned outside *Parapilekia*. These taxa differ from *P. speciosa* in displaying an anterior border with no break in curvature, a glabella which is elongate, much less than 1/3 of the total width of the cephalon across the L1 lateral glabellar lobes and whose lateral glabellar margins are either sub-parallel or taper to the anterior. They have S3 lateral glabellar furrows which branch adaxially and cut the margin of the glabella posterior to the anterior glabellar angles and genal spines which are directed towards the posterior but which are less stout that those of *speciosa*..

Sheng (1977 pl. 77, figs 1 & 2) illustrated the species *Rossaspis latilus* and *Rossaspis longifrons* from the Nantsinkuen Formation of Central Southern China. These taxa are highly incomplete but appear to be related to *Parapilekia anxia*. Further material is required to make a definitive statement on their correct assignment, but it is likely that they will prove to belong to a single species which is best placed within this group of taxa closely related to *Anacheirurus*.

Parapilekia ferrigena Mergl, 1994 was diagnosed as differing from *Parapilekia olesnaensis* Růžička, 1935 which occurs together with *ferrigena* (see Vaněk, 1965 p. 292) and in the overlying horizons (see Vaněk, 1965 p. 292 and Mergl, 1994) in having the whole glabella rather than its margins tuberculate. This is a weak basis upon which to differentiate the two species, particularly given the poor state of preservation in both taxa. *Parapilekia ferrigena* is here regarded as a junior synonym of *Parapilekia olesnaensis*.

As *Parapilekia* is clearly not a monophyletic group, as presently configured, and as a detailed cladistic analysis of the Pilekiinae is not yet available, the genus *Parapilekia* is not formally re-diagnosed herein.

Taxa currently assigned to *Parapilekia*

?P. acetae	Hamman, 1971
P. afgahnensis	(Wolfart, 1970)
P. anxia	(Sdzuy, 1955)
P. discreta	(Barrande, 1868)
P(?). hunanensis	Peng, 1983
P. jacquelinae	Fortey, 1980
P. kazakhstanica	Ballashova, 1961
P. nana	Mergl, 1984
P. olesnaensis	(Růžička, 1935)
Junior synonym of *olesnaensis* herein *Parapilekia ferrigena*	Mergl, 1994
P. soguyi	Destombes, 1970
P. speciosa	(Dalman, 1827)

Taxa best placed with the taxa which are similar in form to *anxia*:

Rossaspis latilus	Sheng, 1977
Rossaspis longifrons	Sheng, 1977

3.8.1.5 *Pilekia* Barton, 1916

Type species: *Cheirurus apollo* Billings, 1860

The recovery of specimens of *Pilekia* from the Tim Shea area of Tasmania by Jell & Stait (1985), tentatively assigned to *Pilekia apollo* herein, means that *Pilekia* extended beyond the North American craton. In addition, as these specimens are the oldest known members of the genus, they provide important information on the development and area of origin of the genus. *Pilekia* may be diagnosed on the following characters in addition to those of the Subfamily Pilekiinae:

Diagnosis of *Pilekia*:

Glabella tapers strongly forwards (strawberry shaped) and is expanded to fill more than half of the breadth of the cephalon across the L1 lateral lobes; Genal spines present and directed obliquely laterally; Hypostome oval with complete anterior border, narrow posterior border and marginal spines; Three or four pygidial pleurae confluent with three or four continuous axial ring furrows; Number of rings on the axis of the pygidium equals the number of pygidial pleurae (except in *loella*); terminal piece small.

3.8.1.5a Discussion of Demeterops Přibyl & Vaněk, 1984

Type species *Pilekia loella* Demeter, 1973

This taxon was differentiated from *Pilekia* by Přibyl & Vaněk (1984) on the basis of its possession of three, rather than four pygidial pleurae. While the number of pygidial pleurae is stable in many pilekiid and pliomerid genera, it is a poor character to use as the sole basis for differentiation at genus level in taxa known only from limited, incomplete material (see Section 3.5). These reservations are highly relevant in this case as the number of pygidial pleurae appears to be variable within species of *Pilekia*. This may be seen in specimens illustrated by Terrell (1973) where the pygidium in his pl.6, fig. 15 ('*Pilekia loella?*') possess three pygidial pleurae while that in his pl.6, fig.16 ('*Protopliomerops sp*') has four. Apart from the number of pleurae present, there seems to be little to differentiate these two pygidia which I regard as belonging to *Pilekia loella*. This variation is also seen in *Pilekia*(?) sp of Demeter (1973 pl. 1 fig. 4) which possesses at least five or six pygidial pleurae. As both *Pilekia apollo* and *Demeterops loella* are only poorly known from limited material, it is not possible to assess their variability, or otherwise, in the number of pygidial pleurae.

In *Demeterops* the loss of the terminal pair of pygidial pleurae was not accompanied by loss of the associated axial ring. As a result of this axial ring retention, the pygidium must be coded as possessing more ribs than rings. In addition due to the short, broad nature of the pygidium, the retention of an additional pygidial axial ring results in the terminal piece of the axis exceeding one third of the total length of the pygidium which means that the pygidial axis must be coded as elongate. This collection of characters differentiating *Demeterops* from *Pilekia* stems from one morphological 'event', the incomplete effacement of the terminal pygidial pleurae. Additionally, '*Demeterops*' *loella* displays coarser tubercles on the glabella than other members of the Pilekiinae, which are generally smooth.

'*Demeterops*' *loella* is recognised from only a few specimens and the retention of the posterior axial ring after the loss of the posterior pygidial pleurae may prove to be a local variant of a main population in which this axial ring is also lost, as may the development of coarse tubercles on the glabella. There are no other species of *Pilekia* which share the features of *loella* and as a result any genera or subgenera erected to contain it will be monospecific and so will provide no further information on the relationships of the taxa. Thus *Demeterops* is here regarded as a junior synonym of *Pilekia*. Should any further taxa of similar form to *loella* be recovered, there would be a case for the resurrection of *Demeterops* as subgenus of *Pilekia*

Species included in *Pilekia*

Pilekia apollo	(Billings, 1860)
Pilekia loella	Demeter, 1973
Pilekia? trio	Hintze 1953
Pilekia transversalis	Zhou Tian-rong, 1981
cf *Pilekia*(?) *trio*	Demeter, 1973
Pilekia(?) sp.	Terrell, 1973
Pilekia(?) sp	Demeter, 1973
Pilekia sp.	Jell 1985
Pilekia sp.	Jell & Stait, 1985
Pilekidae gen et sp. nov.	Jell & Stait 1985

Species which were unavailable for analysis and which require examination

P. eryx	(Billings, 1860)

3.8.1.6 *Pliomeridius? lacunatus* Dean, 1989

Although this species resembles *Pliomeridius sulcatus* Leanza & Baldis, 1975, the type species of *Pliomeridius*, it is actually most closely related to the Pilekiinae, particularly the poorly known *Metapilekia bilirata* (Harrington, 1938). The similarity of *Pliomeridius? lacunatus* to *Pliomeridius sulcatus* is the result of the rapid development of the Pliomeridae from taxa closely related to the Pilekiinae during the early-mid Tremadoc which resulted in taxa at the base of derived clades resembling taxa basal to the whole Pliomeridae clade. Dean's species differs from *P. sulcatus* in a number of key features, the majority of which are associated with the pygidium which is flat; the terminal section of the pygidial axis lacks paired pits; the glabella narrows strongly forwards with the frontal lobe being narrower than all of the lateral glabellar lobes. *P.? lacunatus* also differs from *Metapilekia bilirata* Harrington, 1938 but I will refrain from erecting a monospecific genus to accommodate this species until more material of *Metapilekia* is available for comparison.

3.8.1.7 *Victorispina* Jell, 1985

Type species *Victorispina holmesorum* Jell, 1985

This genus and species from the Tremadoc of the Digger Island Formation, Waratah Bay, Victoria in Australia is remarkable for the extensive development of its genal and thoracic spines.

Diagnosis of *Victorispina*:

Glabella narrows forwards, is longer than wide and less than 1/3 of the total breadth of the cephalon across L1; Anterior border furrow of uniform depth; Three lateral glabellar furrows, S3 bifurcates adaxially and cuts the margin of the glabella abaxial at a point posterior to the anterior angle of the glabella; Eye ridge present, of curved form, terminating adaxially at the anterior, adaxial corner of the fixigenal field; Genal spines long and directed to the posterior, while at the same time being directed vertically at a large angle; Thoracic segments each carry a pair of long spines which are directed almost vertically upwards; Pygidium displays four pygidial pleurae of pilekiid form which correspond to four rings on the axis of the pygidium; Terminal section of the pygidial axis is small and, on some specimens displays a slight independent convexity which may be a relict of an additional axial ring. The surface of the exoskeleton is tuberculate.

Species included in *Victorispina*:

Victorispina holmesorum	Jell, 1985

3.8.2 Genera belonging to the Protopliomeropinae Hupé, 1953:

As discussed in the Pilekiinae section (3.8.1) the genera *Tesselacauda* and *Rossaspis* are situated in a position intermediate between the Pilekiinae and the Protopliomeropinae. *Tesselacauda* shares many of the features of the Pilekiinae, in particular its pygidium differs from those of the Pilekiinae only in its lack of long free pygidial spines. Similarly, immature pygidia of *Tesselacauda* are very similar to mature pygidia of *Rossaspis superciliosa*, indicating a probable close relationship between the two genera.

Taxa placed within the *Rossaspis* subclade have eye ridges which are confluent with the lateral cephalic border. From the pattern of character changes at the base of this subclade, it appears that the morphology of *Rossaspis? pliomeris* Demeter, 1973 is close to that of the ancestor of this subclade. The pygidium of this species is polymorphic, with some specimens displaying anterior fields on the pygidial pleurae while others lack them. It is likely that the species *Rossaspis superciliosa* (Ross, 1951) developed from an ancestor which was similar to the morph of *Rossaspis? pliomeris* which displays anterior pleural bands on the pygidium while the remainder of the subclade are derived from an ancestor which was similar to the morph of *Rossaspis? pliomeris* which lacks these bands.

This pattern of an ancestral form displaying a wide range of variation giving rise independently to descendants with reduced ranges of morphological variation is a common one which is discussed further in Section 2.1.9

3.8.2.1 *Pliomeroides* Harrington & Leanza, 1957

Type species: *Protopliomerops deferrariisi* Harrington, 1938

Pliomeroides is another monospecific genus defined around a 'stem' taxon. *Pliomeroides* bases the crown group and is envisaged as being part of the evolving pleisiomorphic plexus discussed in Section 3.7.1

Diagnosis of *Pliomeroides*;

Glabella longer than wide; Three lateral glabellar furrows; S3 single and situated behind the anterior glabella angle; Eye ridges long, curved and terminating anteriorly at the anterior, adaxial corners of the fixigenal fields; Pygidium with five unfurrowed pleurae which bend downwards and rearwards; Pygidial pleurae confluent with axial rings and terminate abaxially in long free points; Terminal section of the pygidial axis small.

Species included in *Pliomeroides*;

Protopliomerops deferrariisi	Harrington, 1938

I was unable to obtain the references containing the following taxa and so they are only provisionally assigned to *Pliomeroides*;

P. buceras	Anstygin *et al.*, 1973
P. modicus	Semenova, 1972
P. subdefensus	Anstygin *et al.*, 1973

3.8.2.2 *Protopliomerops* Kobayashi, 1934

Type species: *Protopliomerops seisonensis* Kobayashi, 1934

Because of the 'stem' position of this genus and the resultant lack of differentiating apomorphies on the cephalon, *Protopliomerops* has in the past been something of a 'dustbin' genus to which a variety of isolated cranidia of uncertain systematic position have been assigned. While the majority of these taxa belong to the

Subfamily Protopliomeropinae, most have been re-assigned to genera other than *Protopliomerops* herein. The remaining taxa form a relatively small and clearly defined genus.

Protopliomerops hamaxitus Jell & Stait, 1985 from the late Tremadoc-early Arenig of Tasmania is difficult to assign to a genus. If included in *Protopliomerops*, its position at the base of the *Pseudomera* subclade will render *Protopliomerops* paraphyletic. However to erect a monospecific genus to accommodate *hamaxitus* would not allow any further refinement of the diagnosis and will merely obscure the link between *Protopliomerops* and the *Pseudomera* subclade. I therefore propose to retain *hamaxitus* within *Protopliomerops* even though this renders the genus paraphyletic.

Diagnosis of *Protopliomerops* ;

Characters displayed by *Protopliomerops* in addition to the characters of the subfamily are:

Glabella sub-parallel sided; S3 lateral glabellar furrows positioned posterior to the anterior angles of the glabella; Eye ridges cut the anterior, adaxial, corners of the fixigenal fields; Small, posteriorly directed, fixigenal spines; Middle body of the hypostome does not bisect the anterior border of the hypostome; posterior border of the hypostome is narrow; Small paired marginal spines on the lateral sections of the hypostomal border and a mesial spine on the posterior border; Six unfurrowed pygidial pleurae curve downwards and rearwards.

Species included in *Protopliomerops* ;

Protopliomerops hamaxitus	Jell & Stait, 1985
?Protopliomerops? lata	Liu, 1977 in Sheng, 1977 - very poorly preserved and only a partial cranidium, so assignment uncertain but probably *Protopliomerops*.
Protopliomerops punctulifera	Kobayashi, 1935
Protopliomerops? radiatus	Kobayashi, 1955
Protopliomerops seisonensis	Kobayashi, 1934
Protopliomerops ? subquadratus	Kobayashi, 1955

3.8.2.3 *Rossaspis* Harrington, 1957

Type species: *Protopliomerops superciliosa* Ross, 1951

As currently defined *Rossaspis* is a monospecific genus. The fragmentary *Rossaspis? pliomeris* Demeter, 1973 is very closely related to *superciliosa*, but is of highly variable morphology in the characters upon which *Rossaspis* is recognised. An increased level of variation in characters which elsewhere in the cladogram are stable and of high burden at the same hierarchical level as that of the group being studied is common in taxa basal to a subclade and is further discussed in section 2.1.9.1.

Rather than define another monospecific genus with a diagnosis which would necessarily overlap that of *Rossaspis*, I favour the inclusion of *pliomeris* as a *sensu lato* member of *Rossaspis*, even though the characters diagnostic of *Rossaspis* are variably developed in *pliomeris*. This would result in *Rossaspis* being a paraphyletic genus, To avoid this I propose to further expand the concept of *Rossaspis* to include the monospecific genus *Ibexaspis* Přibyl *et al.*, 1984 and also *Protopliomerops? quattuor* Ross, 1951. The alternative to this is to either define a large number of monospecific genera, which will disguise he close relationship of the taxa to each other and result in the redundancy of the generic and specific diagnoses or to define paraphyletic genera. The expansion of the concept of *Rossaspis* also causes a number of problems as *Ibexaspis brevis* displays some distinctive autapomorphies, such as a hypostome border devoid of marginal or mesial spines and greatly reduced lateral glabellar furrows while the pygidia of *Ibexaspis brevis* and *Protopliomerops? quattuor* differ strongly from those of *Rossaspis superciliosa*. However, all of the taxa in this subclade are linked by a distinctive uniquely derived autapomorphy; the confluence of the lateral cephalic border and the palpebral lobes.

The cephala of mature specimens of the genus *Ibexaspis* are identical to those of immature specimens of *Protopliomerops? quattuor* Ross, 1951 and so it is logical to assume that *Ibexaspis* was derived from *quattuor* by paedomorphosis.

I propose to recognise three subgenera within *Rossaspis*; *Rossaspis (Rossaspis)*, *Rossaspis (Ibexaspis)* and *Rossaspis* (Subgen. nov.) as well as a *sensu lato* taxon.

Diagnosis of *Rossaspis* :

Glabella narrows forwards or is sub-oval, longer than wide and less than 1/3 of the total breadth of the cephalon across L1; Anterior border furrow of uniform depth; Three lateral glabellar furrows of which the S3 furrow is unbranched (dog leg form in *Rossaspis (sensu lato) pliomeris* and straight in *Rossaspis superciliosa,* and other derived members) and obliquely oriented, cutting the margin of the glabella at the anterior glabellar angle; Palpebral lobes confluent with the lateral border of the cranidium; Genal spines present, large and directed to the posterior in *pliomeris*, small, node-like and directed transversely in *superciliosa*; present but variably developed in the other taxa; Hypostome oval with an uninterrupted anterior border, narrow posterior border which displays marginal spines except (*Ibexaspis*), but no mesial spine; Pygidium of four or five pygidial pleurae which correspond with an equal number of axial rings and are divided into anterior and posterior fields by pleural furrows (not on all specimens of *pliomeris*); Pleurae are of simple (not pilekiiform) shape and of variable lengths, the free points of the pleurae may be exceptionally long Pygidial axial termination small and does not display any pits.

Species included in *Rossaspis* (*Rossaspis*):

Rossaspis superciliosa	Ross, 1951

In addition to the features of the genus, *Rossaspis* (Subgen. nov.) displays:

Lateral glabellar furrows straight, oriented obliquely; Posteriorly directed fixigenal spines present, often poorly developed; Pygidium subtriangular in outline; Little or no 'shoulder' on the pygidial pleurae which are elongate and diverging distally, commonly of different lengths.

Species included in *Rossaspis* (Subgen. nov)

Protopliomerops quattuor	Ross, 1951
Protopliomerops aff. *quattuor*	Demeter (1973)
Protopliomerops sp. I	Demeter (1973)
Protopliomerops sp, II	Demeter (1973)
Protopliomerops sp. III	Demeter (1973)
Protopliomerops punctilifera	(Kobayashi, 1935)

In addition to the features of the genus, *Rossaspis (Ibexaspis)* displays:

Glabella sub-parallel in outline; Glabella highly convex; Lateral glabellar furrows are very short; Posteriorly directed fixigenal spines present, often poorly developed; No spines on the margin of the hypostome; hypostome has a narrow, but complete, anterior border; Pygidium semicircular; Pygidial pleurae well spaced out and separated by depressed anterior bands;

Species included in *Rossaspis* (*Ibexaspis*):;

Protopliomerops quattuor brevis	Young, 1973

Species included in *Rossaspis* (*sensu lato*);

?Rossaspis pliomeris	Demeter, 1973

3.8.2.4 *Tesselacauda* Ross, 1951

Type species; *Tesselacauda depressa* Ross, 1951

Diagnosis of *Tesselacauda*;

Glabella narrows forwards/is sub-oval, longer than wide, less than 1/3 of the total breadth of the cephalon across L1; Three lateral glabellar furrows, S3 is unbranched and cuts the margin of the glabella at the anterior glabellar angle; No furrow separating the eye ridge from the anterior border; Genal angles rounded; Hypostome sub-oval with a complete anterior border and small hypostomal wings, narrow posterior border with a mesial indentation and marginal spines; Pygidium of four pygidial ribs which correspond to four axial rings; Pleurae broad and flat with the anterior two pairs being divided into anterior and posterior bands by furrows; Axial terminal piece is small.

Species included in *Tesselacauda*;

Tesselacauda depressa	Ross, 1951
Tesselacauda sp.	Jell, 1985

3.8.3 Genera placed within Subfamily Nov. herein:

3.8.3.1 *Gogoella* Legg, 1976

Type species: *Gogoella wadei* Legg, 1976

The morphology of this genus shows a degree of convergence on that of *Rossaspis* Harrington, 1957 in its glabellar shape and on *Pliomerella* Reed, 1941 in the shape and size of its eyes - possibly indicating similarities in aspects of its mode of life. Fortey & Shergold (1984) assigned the mid-Arenig species *brevis* to *Gogoella* and noted that its morphology was convergent upon that of *Pliomera*. The pygidium of *brevis* is indeed similar to that of *G. wadei*, but is also similar to that of *Pliomera*. The holotype cranidium of *brevis* is poorly preserved and, as noted by Fortey & Shergold (1984 p.356), differs markedly from that of *Gogoella wadei* but is very similar to that of *Pliomera*.

The diagnosis applied herein is that which applies to *wadei* and I have not followed Fortey & Shergold (1984) in expanding the diagnosis of *Gogoella* to accommodate *brevis* as there are no strong linking characters which would not also link *brevis* to the *Pliomera* subclade. Equally, due to the poor preservation of the holotype material, there is no conclusive evidence that *brevis* should be regarded as a related, but separate, genus to *Gogoella* or even whether or not it is a member of the subclade containing *Pliomera*.

In light of this uncertainty, am reluctant to extend the diagnosis of *Gogoella* to accommodate *brevis* until better preserved material is recovered and propose to propose to leave *brevis* tentatively assigned to *Gogoella*.

Diagnosis of *Gogoella*:

Characters displayed by *Gogoella* in addition to those of the subfamily:

Glabella wider than long and less than one third of the width of the cephalon across L1; Glabellar outline is sub oval/narrows forwards; Anterior border uniformly curved; Anterior border furrow of uniform depth; Longitudinal anteromedian furrow in the frontal lobe of the glabella; Eye ridges are very short, but present; Palpebral lobes very large; Fixigenal fields very narrow; Small, posteriorly directed fixigenal spines present; Librigenal borders broad; Oval hypostome with complete anterior border which is uninterrupted by the oval middle body; lateral and posterior hypostomal borders are narrow; Pygidium displays five unfurrowed pleural ribs which are associated with five axial rings and which curve down and rearwards to terminate in small free spines which do not turn out; Terminal section of the pygidial axis small and smooth.

Species included in *Gogoella*:

Gogoella brevis	Fortey & Shergold, 1984
Gogoella wadei	Legg, 1976

Species included as a *sensu lato* member of *Gogoella*:

Protopliomerops lindneri	Jell, 1985

3.8.3.2 *Hintzeia* Harrington, 1957

Type species:

Protopliomerops celsaora Ross 1951 [=*Protopliomerops aemula* Hintze, 1953]

Demeter (1973) demonstrated that *H. celsaora* (Ross, 1951) is the senior subjective synonym of the originally designated type species of *Hintzeia Protopliomerops aemula* Hintze, 1953. As the species *Pseudomera insolita* Poulsen (in Hintze, 1953) and *Protopliomerops firmimarginis* Ross, 1951 are placed by this analysis as pleisiomorphic to the *Kanoshia* subclade the genus *Hintzeia* is expressly paraphyletic. This is a common problem which I do not regard as preventing the recognition of *Hintzeia* as a valid genus, albeit one which is recognised largely by the absence of *Kanoshia* characters. It could be argued that *Hintzeia* and *Kanoshia* should be amalgamated into a single genus, but the wide morphological disparity between their members seems best represented by the retention of two separate genera.

The species *taoyuanensis* (Liu in Sheng, 1977) differs from *Hintzeia celsaora* in its possession of four, rather than five, pygidial pleurae (see discussion of this character in Section 3.5.1), in its possession of small fixigenal spines and a complete anterior hypostomal border which is not cut by the middle body. The retention of these primitive features by *taoyuanensis* is reflected by its position in the phylogeny as the basal member of the *Hintzeia* subclade. This combination of primitive and derived features supports the hypothesis that the *Hintzeia* and *Gogoella* subclades (amongst others) were independently derived from an ancestral form which would be placed by this analysis within the Protopliomeropinae.

Hintzeia was regarded by Fortey (1979) as a likely ancestor of the Cybelopsinae. It can be seen from Figure 3.16 that this is highly unlikely. The close linkage of these taxa recognised by Fortey results from two main causes; derivation from closely similar ancestral taxa (members of the Protopliomeropinae plexus) and a degree of convergence in the form of the posterior border of the hypostome.

Diagnosis of *Hintzeia* ;

Anterior border evenly curved; Anterior border furrow of uniform depth; Glabella of approximately subequal length and width, narrows forwards and less than one third as wide as the cephalon across L1; S3 lateral glabellar furrows situated anterior to the anterior glabellar angle, not branched adaxially and is oriented obliquely; Eyes sub-median; Eye ridges present and terminating at the adaxial, anterior corners of the fixigenal fields; Genal angles rounded (spinose in *taoyuanensis*); Hypostome of oval outline with a broad posterior border, lateral spines and a short mesial spine; Anterior border of hypostome is interrupted by the rounded hypostomal middle body (except in *taoyuanensis*); Four or five unfurrowed pygidial pleurae, all confluent with axial ring furrows; Pleurae curved rearwards and downwards; Tips of pygidial pleurae end in straight free points; Terminal section of axis small and smooth.

Species included in *Hintzeia* ;

Protopliomerops. celsaora	(Ross, 1951)
[=*Protopliomerops. aemula*	(Hintze, 1953)]
Protopliomerops firmimarginis	Hintze, 1953
Pseudomera cf. *insolita*	Poulsen, in Hintze, 1953
Protopliomerops taoyuanensis	Liu, in Sheng 1977

Tentatively included in *Hintzeia* ;

Cybele rotunda	Anstygin, 1978

The reproduction of the photographs of the type material of this species is rather poor but it appears that this species should be reassigned to *Hintzeia*.

3.8.3.3 *Kanoshia* Harrington, 1957

Type species: *Pseudomera kanoshensis* Hintze, 1953

Hintzeia grades into *Kanoshia* with stratigraphically later members of *Hintzeia* accruing some of the features which are diagnostic of *Kanoshia*. The result of this is that *Hintzeia* is a paraphyletic genus which may be best amalgamated with *Kanoshia*. *Kanoshia reticulata* Fortey & Droser, 1996 displays features characteristic of several different genera which are widely dispersed on the cladogram. This was recognised by Fortey & Droser who placed *reticulata* in the genus *Kanoshia* with which they argued it shared the largest number of apomorphies. Although the balance of apomorphies support this placement, *reticulata* has a large number of autapomorphies.

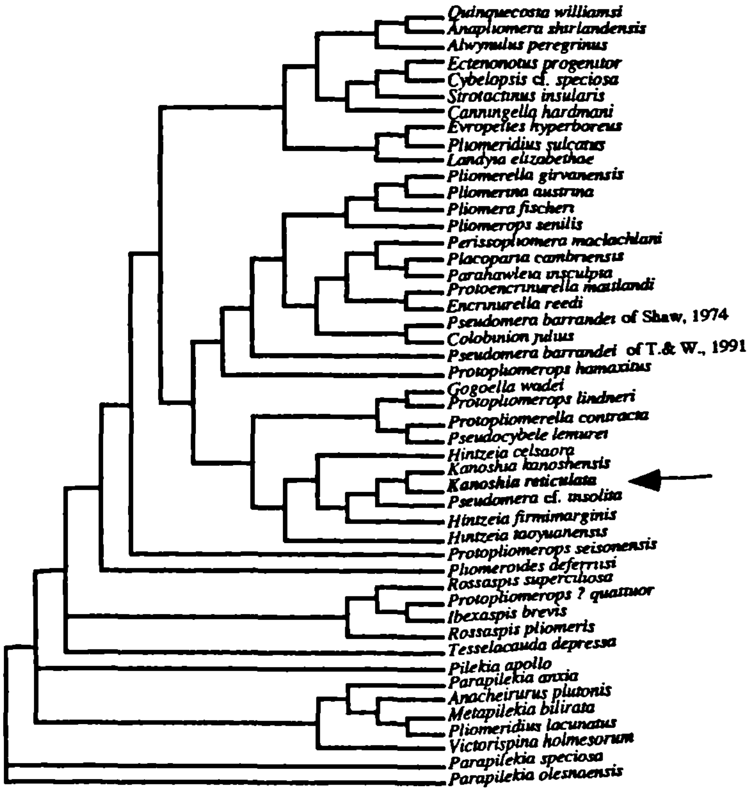
Inclusion of *reticulata* in the Pliomeridae data set and analysis in PAUP resulted in the production of two minimum length trees of length 178 and Consistency Index of 0.414 and a Rescaled Consistency Index of 0.331 (Figure 3.19). As can be seen, *reticulata* does indeed plot as a member of the genus *Kanoshia*. and, with the addition of *reticulata*, the resulting pair of trees are identical to those produced without *reticulata* included. It is interesting to note that immature members of *reticulata*, (Fortey & Droser 1996, fig. 17: 2, 3 and 9) strongly resemble members of the genus *Pliomerops* Raymond, 1905, differing substantively only in the presence of small fixigenal spines, and in the angle at which the pygidial pleurae are bent. This suggests that much of the similarity is the result of two features: a similar ancestral morphology (the Protopliomeropinae) to both subclades and the primary source of much of the variation within the Pliomeridae being ontogeneticaly sourced. This is further supported by the fact that all of the independently derived distinguishing apomorphies of *reticulata* are found in other members of the Pliomeridae, indicating that common developmental processes gave rise to these features in related taxa.

The development of much of the variation by alterations in ontogenetic timing resulted in variations in morphology accruing rapidly and the presence of a large amount of parallelism within the Pliomeridae, with the same features repeatedly developing in different, closely related, lineages. This extensive parallelism results in the difficulty in accurate systematic placement of species seen in the Pliomeridae.

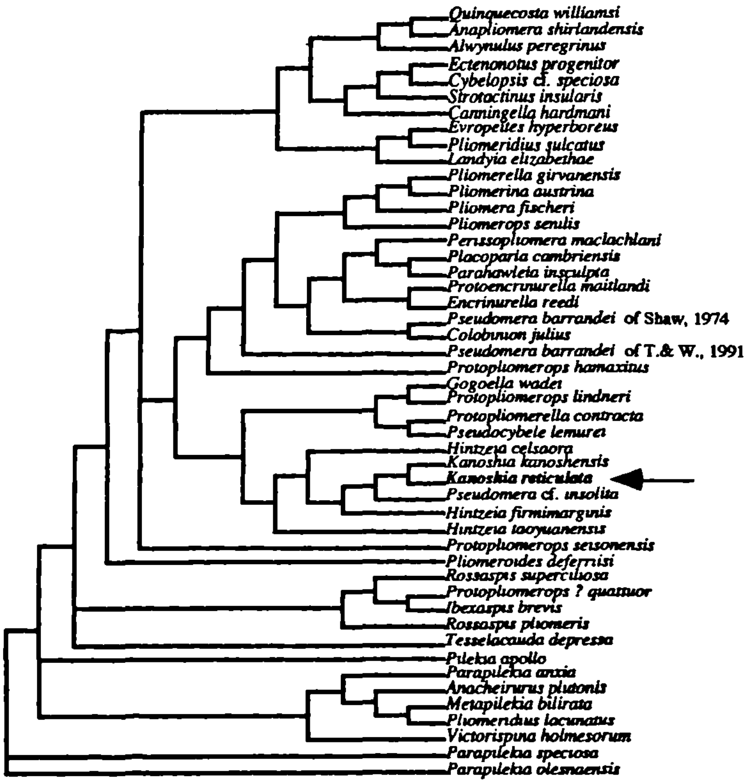
<u>Diagnosis of *Kanoshia*:</u>

Glabella parallel sided, longer than wide and less than one third of the total width of the cephalon across L1; Anterior border is smoothly curved; Anterior border furrow displays a median deepening; Furrow or pit present in the anteromesial area of the frontal lobe of the glabella; S3 lateral glabellar furrows situated at the anterior angles of the glabella, unbranched adaxially and oriented obliquely; Eyes positioned anteriorly (close to the glabella in *kanoshensis*); Eye ridges short, curving from the adaxial, anterior corners of the fixigenal field; Genal angles rounded; Hypostome outline is oval/sub-rectangular; Middle body of the hypostome cuts the anterior border; Posterior border of the hypostome is very broad and flat; Marginal spines present on the border of the hypostome; Mesial hypostomal spine bifurcate; Five unfurrowed pygidial pleurae present, terminating in sharp free spines; Pygidial pleurae do not bend to the posterior distally and are horizontal until their mid point after which they are strongly down curved; Terminal axial piece small and smooth.

Figure 3.19: Trees produced by inclusion of *Kanoshia reticulata* in the Pliomeridae analysis.



2.



Species included in Kanoshia;

K. kanoshensis	Hintze, 1953
K. reticulata	Fortey & Droser, 1996

3.8.3.4 *Protopliomerella* Ross, 1951

Type species: *Protopliomerella contracta* Ross, 1951

This genus is a pleisiomorphic sister group to *Pseudocybele*.

Diagnosis of *Protopliomerella*;

Characters displayed by *Protopliomerella* in addition to the characters of the subfamily are;

Elongate glabella narrows forwards, is longer than wide and less than one third of the total width of the cranidium across the L1 lateral glabellar lobe; anterior border gently rounded; Four lateral glabellar furrows normally present; S3 lateral glabella furrows cut the anterior angle of the glabella, do not branch adaxially and are directed obliquely; S4 lateral glabellar furrows are small and positioned anterior to the anterior glabellar angle; Anterior border furrow of uniform depth; Eyes oriented anteriorly and situated in the extreme anterior of the fixigenal fields, close to the glabella; Eye ridges curved and shorter than the length of the palpebral lobes; Fixigenal angles rounded or bluntly pointed, no genal spines; Hypostome very elongated; Anterior border of hypostome complete, not cut by the middle body but mesial portion of border may be reduced to a thread-like strip in some specimens; Posterior border of the hypostome narrow; Paired lateral spines and a single, short, mesial spine present on the margins of the hypostome; Pygidium with six, unfurrowed, pleurae, the tips of which are not turned out and may be blunt or pointed; The terminal pair of pygidial pleurae are fused together to form a pseudo-elongate terminal piece; Terminal section of the pygidial axis is small and does not display paired pits (some specimens display a pair of pits abaxial to the terminal piece).

Species included in *Protopliomerella* ;

P. contracta	Ross, 1951
P. pauca	Demeter, 1973

3.8.3.5 *Pseudocybele* Ross, 1951

Type species: *Pseudocybele nasuta* Ross, 1951

The form of the pygidium seen in *Pseudocybele* is highly convergent upon that of the Cybelopsinae, in spite of the elongate terminal piece being formed, like that of *Pseudomera*, by the fusion of the terminal pair of pygidial pleurae (see section 3.5). The extent of this convergence is illustrated by the pleurae of *Pseudocybele* which remain in contact for their full length, ending in blunt and turned-out tips which resemble the terminations of the pygidial pleurae in members of the Cybelopsinae. This degree of convergence must reflect a close similarity in function of the pygidium and therefore of life habit and / or environment.

Diagnosis of *Pseudocybele* ;

Characters displayed by *Pseudocybele* in addition to those characters of *Protopliomerella*: Anterior border nasute; Mesial spine on the posterior margin of the hypostome is elongate; The small terminal section of the pygidial axis becomes obsolete and is effaced in stratigraphically later species. This has the effect of making the differentiation of the terminal section of the pygidial axis into small terminal piece and fused posterior pair of pleurae difficult, the main indication being the change in slope from one to the other.

Species included in *Pseudocybele* ;

Pseudocybele altinasuta	Hintze, 1953
Pseudocybele lemeuri	Hintze, 1953
Pseudocybele nasuta	Ross, 1951

3.8.4 Genera placed within the Subfamily Pliomerinae Raymond, 1913:

3.8.4.1 *Colobinion* Whittington, 1961

Type species: *Amphion julius* Billings, 1865

Colobinion julius is very closely related to *Pseudomera* Holliday, 1942. In addition to the features noted in the diagnosis below are a number of less formally definable characteristics which are nevertheless useful in identifying *Colobinion*; The glabella is given a somewhat truncated appearance by the frontal lobe which is very short sagittally and which displays a very flat anterior margin, which is reflected in the very straight anterior cephalic border. In addition, in some specimens the anterior border immediately in front of the mesial deepening of the shallow anterior border furrow deflects to the anterior in a form reminiscent of the nasute anterior border form of *Pseudocybele* Ross, 1951.

Diagnosis of *Colobinion*;

Smoothly curved anterior border; Median deepening in a shallow anterior border furrow; Glabella expands forwards and is longer than wide; S3 lateral glabellar furrows terminate abaxially behind the anterior glabellar angle and may be isolated from the axial furrows; Curved eye ridges present, terminating adaxially at the anterior, adaxial fixigenal angle; Hypostome shield shaped and angular; Anterior border of the hypostome interrupted by the ovoid middle body; Hypostomal wings depressed; Lateral and posterior hypostomal border lacking marginal spines; Posterior hypostomal border broad; Pygidium displays five unfurrowed pygidial pleurae associated with a greater number of axial rings; The pygidial pleurae gently curve downwards but do not bend towards the posterior distally; Terminal section of the pygidial axis elongate and displays a number of axial rings.

Species included in *Colobinion*:

Colobinion julius	(Billings, 1865)

3.8.4.2 *Encrinurella* Reed, 1915

Type species: *Pliomera insangensis* Reed, 1906

Diagnosis of *Encrinurella*:

Anterior cranidial border smoothly curved; Anterior border furrow of uniform depth; Facial suture gonatoparian ; Glabella widens forwards, widest at the frontal lobe; S3 lateral glabellar furrows poorly developed, unbranched and positioned behind the anterior angle of the glabella; Eyes small, positioned sub-medially and close to the glabella; Eye ridges short, terminating adaxially behind the adaxial, anterior corner of the fixigenal field; No genal spines; Five pygidial pleurae without obvious anterior fields; Pygidial pleurae bent downwards and to the posterior; Small terminal axial piece.

Species included in *Encrinurella*:

E. exsculpta	Xiang & Ji, 1986
E. insangensis	Reed, 1906
E. liui	Sheng, 1974
E. pupiaoensis	Sheng, 1974
E. reedi	Legg, 1976
E. tetrasulcata	Ju, 1982 (in Lu & Zhou, 1982)

Tentatively included in *Encrinurella* - not seen in this study.

E. fenxiangensis	Xiang & Ji, 1987

3.8.4.3 *Parahawleia* Zhou, 1978

Type species: *Parahawleia insculpta* Zhou, 1978

Diagnosis of *Parahawleia* ;

Glabella very large relative to the total area of the cephalon; Three lateral glabellar furrows with the simple, unbranched, S3 situated in advance of the anterior glabellar angle; Eye ridges vestigial, terminating adaxially at the anterior, adaxial, angle of the fixigenal fields; Eyes absent; Anterior cranidial border is smoothly curved; Facial suture not obvious, presumably marginal; Anterior border furrow effaced, resulting in frontal lobe being confluent with anterior border; Four unfurrowed pygidial pleurae which do not bend towards the posterior distally and are curved down at right angles, ending in free points;

Species included in *Parahawleia* ;

P. insculpta	Zhou, 1978
P. shengi	Xiang & Ji, 1987

3.8.4.4 *Perissopliomera* Ross, 1970

Type species: *Perissopliomera maclachlani* Ross, 1970

It appears that *Perissopliomera* independently developed coapatative enrolment structures similar to those of *Placoparia*. Although the detail of some of the structures differ, this marked overall similarity makes it likely that this apparent convergence may be better described as parallelism, with the two closely related groups achieving very similar structures from similar developmental pathways.

Diagnosis of *Perissopliomera* ;

Four pairs of lateral glabellar furrows, S3 and S4 indent the anterior margin of the glabella longitudinally; Anterior margin of the frontal glabellar lobe straight and transverse; Anterior border furrow of uniform depth; Denticulations and associated longitudinal furrows present on the anterior cranidial border; Facial suture gonatoparian; Five unfurrowed pygidial pleurae which do not bend towards the posterior distally and are down curved at right angles; Posterior axial section elongated; Elongate section displays no transverse furrows or pits and bends sharply downwards halfway along its length, echoing the form of the pygidial pleurae.

Species included in *Perissopliomera* ;

Perissopliomera maclachlani	Ross, 1970

3.8.4.5 *Placoparia* Hawle & Corda, 1847

Type species: *Trilobites zippei* Boeck, 1828

The earliest species of *Placoparia* do not display denticulations on the anterior border of the glabella, such as those seen in *Pliomera* and *Perissopliomera*, but they are developed in stratigraphically later species (Henry, 1985, 1990). This is interesting as *Placoparia* plots separately on the cladogram from *Pliomera* and close to *Perissopliomera*. This indicates that similar enrolment locking structures (see Henry 1985) have developed independently in at least two related, but separate, lineages.

Placoparia has been subdivided into three subgenera; *Placoparia (Placoparia)*, Hawle & Corda, 1847, *Placoparia (Hawleia)* Prantl & Šnajdr 1957 and *Placoparia (Coplacoparia)*. The subgeneric relationships of *Placoparia* have not been investigated in this analysis and so subgeneric diagnosis are not given.

Diagnosis of *Placoparia*;

Anterior border smoothly curved; Anterior border furrow relatively shallow, but of even depth; Facial sutures gonatoparian; and positioned close to the margins of the fixigenal fields; Eyes very small; Genal angles rounded, no genal spines present;

Hypostome angular and shield shaped with no marginal spines; Anterior border of the hypostome is discontinuous, intersected by the oval middle body; Hypostomal wings depressed; Posterior border of the hypostome is expanded into a broad field; Four unfurrowed pygidial pleurae which do not bend towards the posterior distally and are roughly horizontal for approximately half of their length before curving down at right angles and terminating in sharp free spines;

Species included in *Placoparia:*

P. (Hawleia) grandis	Hawle & Corda, 1847
P. (Hawleia) irregularis	Moravec, 1990
P. (Hawleia) prantli	Kielan, 1960
P. (Placoparia) cambriensis	Hicks, 1875 (see Rabano, 1984)
P. (Placoparia) tecta	Hammann, 1971
P. (Placoparia) zippei	(Boeck, 1828)
P. (Coplacoparia) antiopa	Moravec, 1990
P. (Coplacoparia) borni	Hammann, 1971
P. (Coplacoparia) petri	Moravec, 1990
P. (Coplacoparia) tournemini	Rouault, 1847

3.8.4.6 *Pliomera* Angelin, 1852

Type species: *Pliomera fischeri* (Eichwald, 1825)

Bruton & Harper (1981) indicated the possibility of the currently known members of *Pliomera* forming two chronospecies but did not elect to formally erect them. Contrary to the description in the Treatise (Moore, 1959), the facial suture of *Pliomera* is proparian (see Bruton & Harper, 1981, pl. 5, figs 8, 9). The apparent gonatoparian course of the facial sutures in some dorsal views is due to the strong downwards curvature of the abaxial portions of the fixigenae. Species ascribed to *Pliomera* are known from the middle Urals (Anstygin, 1973) and from North East Russia (Rozman, 1970). If these taxa prove to belong in *Pliomera*, their locations are consistent with a latitudinally constrained palaeobiogeographical range encompassing Baltica, Siberia and a number of ocean islands.

Diagnosis of *Pliomera;*

Glabella subsquare, expanding forwards, and is wider than long and is less than one third of the width of the cephalon across L1; S3 lateral glabellar furrows do not branch adaxially and are situated in front of the anterior glabellar angle; Longitudinal anteromedian furrow in the frontal lobe of the glabella; The anterior margin of the glabella is not strongly bowed anteromesially; Anterior border furrow of uniform depth; Anterior border of cranidium denticulate; Facial suture gonatoparian; Eye ridges terminate anteriorly abaxial to the anterior fixigenal angle; Transverse furrow on the anterior of the librigenal border; Genal angles are rounded; Rostral plate wider than long; Hypostome angular and shield shaped with no marginal spines; Anterior border of the hypostome discontinuous, intersected by the oval middle body; Hypostomal wings depressed; Posterior border of the hypostome expanded into a broad field; Five unfurrowed pygidial pleurae present which curve gradually downwards and to the posterior, terminating in small free points; Number of rings on the axis of the pygidium equal to the number of pygidial ribs; Terminal section of the pygidial axis small and smooth.

Species included in *Pliomera;*

Pliomera fischeri	(Eichwald, 1825)

3.8.4.7 *Pliomerella* Reed 1941

Type species: *Pliomerella girvanensis* Reed, 1941

Diagnosis of *Pliomerella* ;

Glabella wider than long; Glabella widens anteriorly; Some specimens display median deepenings in the anterior border furrow; S1 and S2 lateral glabellar furrows long; S3 lateral glabellar furrows are either greatly reduced in length (some specimens of *girvanensis*) or effaced; Eyes very large; Eye ridges terminate anteriorly abaxial to the anterior fixigenal angle; Fixigenal fields very narrow; Rows of punctate granules on the librigenal borders; Genal angles are rounded; Rostral plate wider than long; Hypostome angular and shield shaped with no marginal spines; Anterior border of the hypostome is discontinuous, intersected by the oval middle body; Hypostomal wings depressed; Posterior border of the hypostome is expanded into a broad field; Five unfurrowed pygidial pleurae present which curve gradually downwards and to the posterior, terminating in small free points; Number of rings on the axis of the pygidium equal to the number of pygidial ribs; Elongate terminal piece lacking paired pits and rings.

Species included in *Pliomerella* ;

P. americana	Cooper, 1953
P. craigensis	(Reed, 1931)
P. girvanensis	Reed, 1941
P. serotina	Reed, 1941
Pliomerella	Qu, 1986 (not seen)

3.8.4.8 *Pliomerina* Chugaeva, 1956

Type species: *Pliomera martelli* (Reed, 1917)

The indentations in the frontal lobe of the glabella of *Pliomerina martelli* illustrated in the Treatise (Moore, 1959) are not seen in other specimens of *Pliomerina* and are likely to prove to be the result of the exoskeleton being crushed into the hypostome on compaction.

Diagnosis of *Pliomerina* ;

Glabella longer than wide, expanding forwards; Three pairs of lateral glabellar furrows present; S3 furrows branched adaxially; S3 terminates abaxially in front of the anterior glabellar angle; Anterior border furrow of uniform depth; Anterior border of cranidium is gently rounded; Facial suture gonatoparian; Eye ridges curved, anteriorly cutting the anterior margin of the fixigenal fields, abaxial to the anterior fixigenal corner; Genal angles rounded; Rostral plate wider than long; Hypostome angular and shield shaped with no marginal spines; Anterior border of the hypostome intersected by the ovoid middle body; Hypostomal wings depressed; Posterior border expanded into a broad field; Five unfurrowed pygidial pleurae present which curve gradually downwards and to the posterior, terminating in small free points; Number of rings on the axis of the pygidium equal to the number of pygidial ribs; Terminal section of the pygidial axis is elongate and smooth.

Species included in *Pliomerina*

P. austrina	Webby, 1971
P. dulanensis	Chugaeva 1958
P. fupingensis	Zhou, 1982
P. longhuanensis	Chu *et al.*, 1979
P. martelli	(Reed, 1917)
P. prima	Webby, 1971
P. rigida	Kolobova, 1972
P. speciosa	Zhou, 1982
P. sulcifrons	Chugaeva 1958
P. tolenensis	Kolobova, 1972
P. unda	Chugaeva 1958
P. yaoxianensis	Chen, 1982
P. ?	Whittington 1966

3.8.4.9 *Pliomerops* Raymond 1905

Type species: *Amphion canadensis* Billings, 1859

Pliomerops, as currently coded in the analysis, is a pleisiomorphic genus which lacks apomorphies of its own. In this respect it is similar to the Cybeline genus *Deacybele*. As a result, *Pliomerops*, is differentiated from other similar taxa as much by the features which it lacks as by the positive features which it displays.

Pliomerops is very closely related to *Pseudomera* Holliday, 1942 with which it shares a common ancestor. Some species of *Pliomerops*, such as *P. canadensis* (Billings, 1859) display a pygidial morphology similar to that of *Pseudomera* with pygidial pleurae showing only a small degree of posterior curvature along their length and which curve strongly downwards. One species of *Pliomerops*, *P. praematura* Fortey, 1980, has an eye ridge which terminates adaxially at the anterior angle of the fixigenal field, after the fashion of most genera outside the *Pliomerops* subclade such as *Pseudomera.* The relatively late stratigraphical position of this species, together with its *Pliomerops*-like pygidium and lack of *Pseudomera* apomorphies indicates that *praematura* is indeed a member of *Pliomerops*, the eye ridge position possibly being a secondarily reversion.

Diagnosis of *Pliomerops:*

Glabella longer than wide, expanding forwards and is less than one third of the total width of the cephalon across L1; Three lateral glabellar furrows present; S3 glabellar furrows situated in front of the anterior glabellar angles and do not branch adaxially; anterior border furrow of uniform depth; anterior border smoothly curved; Facial suture proparian; Genal angles rounded and not spinose; Rostral plate wider transversely than it is long (sagittally); Hypostome angular and shield shaped with no marginal spines; Anterior hypostomal border intersected by the oval middle body; Hypostomal wings depressed; Posterior border of the hypostome is expanded into a broad field; Five unfurrowed pygidial pleurae present which curve gradually downwards and rearwards, terminating in small free points; Number of rings on the axis of the pygidium equal to the number of pygidial ribs; Terminal section of the pygidial axis small and smooth.

3.8.4.9a Discussion of *Guizhoupliomerops* Lu, 1975

Type species: *Guizhoupliomerops guizhouensis* Lu, 1978

Guizhoupliomerops differs from *Pliomerops* only by its possession of three rather than four pygidial pleurae. As discussed above (Section 3.8.4.9), the number of pygidial pleurae alone is not a strong basis for generic level diagnosis, in particular as the sample size of these taxa is very small. *Guizhoupliomerops* may best be regarded as a subgenus of *Pliomerops* until further information comes to light.

Species included in *Pliomerops (Pliomerops)*:

P.(Pliomerops) canadensis	(Billings, 1859) (see Shaw, 1968, pl.2, figs 1, 2)
P.(Pliomerops) dactylifera	Poulsen, 1927 (after Fortey, 1980)

P. (Pliomerops) escoti	(Bergeron)(re-described by Dean, 1966)
P. (Pliomerops) praematura	Fortey, 1980
P. (Pliomerops) senilis	(Barrande, 1872) (see Shaw, 1968)
P. (Pliomerops) shangortensis	Reed, 1945
P. (Pliomerops) sinensis	Chugaeva, 1964
P. (Pliomerops) toloubrensis	Pillet, 1988

Species included in *Pliomerops (Guizupliomerops)*:

P (Guizhoupliomerops) guizhouensis	Chu & Yin, 1978
P (Guizhoupliomerops) shiqianensis	Yin, 1978

Tentatively included in *Pliomerops (Pliomerops)* but not inspected:

P. (Pliomerops) indaurei	Barrande, 1846 (see Mergl, 1979)
P. (Pliomerops) parasiensis	Petrunina *et al.*, 1984
P. (Pliomerops) sichuanensis	Chu & Yin, 1978

3.8.4.10 *Protoencrinurella* Legg, 1976

Type species: *Protoencrinurella maitlandi* Legg, 1976

Although the sharply deflexed pygidial pleurae are very similar to those of the closely related genera *Perissopliomera* and *Placoparia* those of *Protoencrinurella* appear to have developed independently. There is no evidence of any denticulations on the anterior cephalic border such as those which facilitate firm enrolment of the other genera leaving unresolved the function of this unusual pygidial form.

Diagnosis of *Protoencrinurella*:

Glabella longer than wide, expanding forwards, widest across the L3 lateral glabellar lobes; S3 lateral glabellar furrows of sinuous form and positioned behind the anterior angles of the glabella; Frontal lobe large but exsagittal length does not exceed that of the L3 lateral glabellar lobes; Anterior border furrow of uniform depth; Anterior cranidial border is smoothly curved; Facial suture gonatoparian; Eyes small and positioned anteromedially; Eye ridges curved and terminating adaxially behind the anterior, adaxial, corner of the fixigenal field; No fixigenal spines; Pygidium with five pleurae, displaying anterior fields which are separated from the pleural ribs by strong furrows; Pleurae bend gradually rearwards and sharply downwards at right angles from their midpoint, terminating in straight, sharp free points; Small terminal axial piece.

Species included in *Protoencrinurella*:

P. maitlandi	Legg, 1976
P. subquadrata	(Kobayashi, 1940)

3.8.4.11 *Pseudomera* Holliday, 1942

Type species: *Amphion barrandei* Billings, 1865

Mature specimens of the taxa, from different localities, which are currently assigned to *Pseudomera* display a wide range of variation in hypostome morphology. The two extremes of these morphologies are:

1. Hypostomes of an oval outline, with a narrow posterior border and small spines on the lateral margins (e.g. *Pseudomera barrandei* of Tremblay & Westrop, 1991). These hypostomes are of similar form to those of the Protopliomeropinae from which this subclade was derived
2. Hypostomes of an angular 'shield shaped' outline without any marginal spines and with a broadly expanded posterior border (e.g. *Pseudomera barrandei* of Whittington, 1961). These hypostomes are of the same form as those of the Pliomerinae subclade as a whole.

A similar range of hypostomal morphologies can be seen in the ontogeny of *Pseudomera barrandei* with the smaller specimens displaying oval, spinose hypostomes with narrow posterior borders while the larger hypostomes are shield shaped, non spinose hypostomes with broad posterior borders (Tremblay & Westrop, 1991). This provides evidence that the form of the hypostome is, in this case at least, ontogeneticaly controlled.

From this it can be seen that the specimens assigned to *Pseudomera barrandei* are close in hypostomal morphology to that of the taxa which were ancestral to the whole subclade. The fact that this range of variation in hypostomal form is found in conjunction with an autapomorphy of*Pseudomera* - the fusion of the two posterior pygidial pleurae - indicates that, when examined at high resolution, the pattern of development of the 'shield shaped' hypostome is likely to have been somewhat more complicated than it appears at first sight. In the more derived members of this subclade this character has 'settled down' to be of high burden, not varying in mature specimens. This pattern of character variability - a character of previously high burden developing a new character state (often ontogeneticaly controlled) which is of low burden in early members of a clade, rapidly becoming established as a character of high burden in a subclade - is a common one which is discussed in Section 2.1.9.1.

Diagnosis of *Pseudomera:*

Characters displayed by *Pseudomera* in addition to the characters of the subfamily are:

Glabella expands forwards and is longer than wide; S3 lateral glabellar furrows terminate abaxially in front of the anterior glabellar angle without reaching the axial furrows; Median deepening in a shallow anterior border furrow (except *P. arachnopyge*); Smoothly curved anterior border; Curved eye ridges present terminating adaxially at the anterior, adaxial fixigenal angle; Hypostome shield shaped and angular (except some early specimens of *barrandei*); Anterior border of the hypostome interrupted by the ovoid middle body; Hypostomal wings depressed; The lateral and posterior hypostomal borders don't display any marginal spines; Broad posterior hypostomal border; The pygidium has six unfurrowed pygidial pleurae, five of which are distinct while the posterior pair are fused and enclose the small terminal section of the axis, giving the impression of a 'U' shaped furrow on the pygidial axis; The pygidial pleurae associated with an equal number of rings on the axis of the pygidium, gently curve downwards but do not bend to the posterior distally.

Species included in *Pseudomera:*

P. arachnopyge	Fortey & Droser, 1996
P. barrandei	(Billings, 1865)

3.8.5 Genera placed within the Subfamily Cybelopsinae:

3.8.5.1 *Alwynulus* Tripp, 1967

Type species: *Alwynulus peregrinus* Tripp, 1967

Tripp (1967) noted the resemblance of his new genus, *Alwynulus*, to the monospecific genus *Josephulus* Warburg, 1925 known from only a single cranidium of the species *J. warburgi*. Tripp argued that the pygidium of *Alwynulus* is distinctive and that it is unlikely that the stratigraphically younger *Josephulus* would possess a similar pygidium. While it is possible that the two genera will require to be synonymised in the future, *Alwynulus* is retained herein until pygidia belonging to *Josephulus* are recovered.

Alwynulus is morphologically very similar to *Oedicybele* Whittington, 1938 and may be a sister group of the Staurocephalinae Prantl & Přibyl, 1947, which may have developed from *Alwynulus* by inflation of the frontal lobe of the glabella.

Diagnosis of *Alwynulus*:

Glabella longer than wide; Sides of glabella sub-parallel posteriorly, expanding abruptly anteriorly; Frontal lobe wider laterally, and longer sagittally, than the L3 lateral glabellar lobes; S3 lateral glabellar furrows fork adaxially and abaxial terminate behind the anterior angle of the glabella; S2 and S3 lateral glabellar furrows directed forwards; Anterior border furrow of constant depth; Anterior border smoothly curved; Facial suture proparian; Eyes small, low and positioned close to the glabella and in the anterior portion of the fixed cheeks; Eye ridges present, shorter than the palpebral lobes; Eye ridges terminate adaxially at the anterior, adaxial corners of the fixigenal fields; Long, straight, fixigenal spines oriented to the posterior; Eight or more unfurrowed pleural ribs on the pygidium; More rings present on the pygidial axis than the number of pygidial pleurae present; Pleural ribs remain in contact until short, blunt, out-turned free spines; Terminal piece elongate, displaying furrows and possibly a pair of pits.

Species included in *Alwynulus*:

A. peregrinus	Tripp, 1967

3.8.5.2 *Anapliomera* DeMott, 1987

Type species: *Anapliomera shirlandensis* De Mott, 1987

Diagnosis of *Anapliomera:*

Glabella longer than wide; Sides of glabella sub-parallel posteriorly, expanding abruptly anteriorly; Frontal lobe wider laterally, and longer sagittally, than the L3 lateral glabellar lobes; S1 lateral glabellar furrows very short and positioned behind the posterior angle of the glabella; S2 lateral glabellar furrows directed to the anterior; S3 lateral glabellar furrows bifurcate adaxially; S4 lateral glabellar furrows present and situated on the anterior margin of the frontal lobe of the glabella, directed to the posterior; Median pit present in the anteromesial area of the frontal lobe; Anterior border furrow of constant depth; Anterior border smoothly curved; Facial suture proparian; Eyes small, low and positioned close to the glabella in the anterior portion of the fixed cheeks; Eye ridges present, terminating adaxially just to the posterior of the anterior fixigenal angle; Eyes small, close to the glabella and raised on short stalks; Long, straight parallel fixigenal spines directed to the posterior; Hypostome of rounded outline; Anterior border of hypostome bisected by the ovoid middle body; Hypostomal border has lateral, but not mesial, spines; Posterior section of the hypostome narrow, displaying a mesial indentation; Five unfurrowed pleural ribs present on the pygidium; More rings present on the pygidial axis than the number of pygidial pleurae; Pleural ribs remain in contact except for short, blunt, out-turned free spines; Terminal piece elongate, displaying furrows and possibly a pair of pits.

Species included in *Anapliomera:*

Anapliomera shirlandensis	De Mott, 1987

3.8.5.3 *Canningella* Legg, 1976

Type species *Canningella hardmani* Legg, 1976

This is a monotypic genus constituting a 'stem' taxon which occupies a basal position in the *Strotactinus* subclade.

Diagnosis of *Canningella*

Glabellar outline varies from narrowing forwards to sub parallel sided; Glabella longer than wide; Three lateral glabellar furrows present; L3 lateral glabellar furrows do not branch adaxially and terminate abaxially to the posterior of the anterior glabellar angle; Anterior border furrow of uniform depth; Anterior border smoothly curved; Facial suture proparian; Eye ridges curved, terminating adaxially at the anterior, adaxial corners of the fixigenal fields; Eyes present; Genal angles rounded; Hypostome oval; Anterior border of hypostome uninterrupted; No marginal or median spines present on the hypostomal border, the posterior section of which is broad and flat; Pygidium displaying five, unfurrowed, pygidial ribs associated with a larger number of rings on the pygidial axis; Pygidial pleurae in contact for their full length with blunt, out turned tips; Pygidial axis elongate.

Species included in *Canningella:*

Canningella hardmani	Legg, 1976

3.8.5.4 *Cybelopsis* Poulsen, 1927

Type species: *Cybelopsis speciosa* Poulsen, 1927

Diagnosis of *Cybelopsis:*

Glabella slightly longer than wide and expands forwards slightly; Frontal lobe area sagittally very short ; Longitudinal anteromedian furrow in the frontal lobe of the glabella; Three lateral glabellar furrows; S3 furrows terminate abaxially in advance of the anterior glabellar angle and do not branch adaxially; Anterior border furrow of uniform depth; Anterior border of cranidium smoothly rounded; Facial suture proparian; Eye ridges present, dying out anteriorly, represented by unpitted areas on the fixigenal fields; Genal angle rounded; Hypostome of oval, rounded outline; Anterior border of hypostome bisected by ovoid middle body; No marginal, or mesial, spines on the border of the hypostome; Posterior border of the hypostome produced into a broad, flat, field; Pygidium of five, unfurrowed, pygidial pleurae which are associated with an equal number of axial rings; Pleurae remain in contact until their bluntly out-turned free spines; Terminal section of the pygidial axis is elongated and bears multiple paired transverse pits.

Species included in *Cybelopsis*:

C. speciosa	Poulsen, 1927
*C.*cf. *C. speciosa*	of Hintze, 1953
C. sp.	Hintze, 1953
C. sp. nov.	Fortey, 1980
C. sp.	Shaw, 1978
C. sp	Fortey, 1992

Tentatively included in *Cybelopsis* but not examined in the present study:

C. sp aff. *speciosa*	McTavish & Legg, 1974
C.? shihuigouensis	Yanjiusuo *et al.*, 1979

3.8.5.5 *Ectenonotus* Raymond, 1920

Type species: *Amphion westoni* Billings, 1865

Diagnosis of *Ectenonotus*:

Glabella slightly longer than wide, tapering forwards; Three lateral glabellar furrows present, S3 situated in advance of the anterior angle of the glabella; Anterior border furrow of uniform depth; Anterior border of the cranidium 'prow shaped'; Facial suture proparian; Eye ridges present, dying out anteriorly where they are represented by unpitted areas on the fixigenal fields; Genal angles rounded; Hypostome not preserved in the species included in this analysis, but those of other species of *Ectenonotus* are of similar form to those of *Strotactinus*, with the exception of the anterior border which is bisected by the ovoid middle body in *Ectenonotus*; Eight or more unfurrowed pygidial ribs which terminate in blunt, out-turned, free spines; In all species of *Ectenonotus* except *progenitor* the number of rings on the axis of the pygidium exceeds the number of pygidial ribs; Terminal section of the pygidial axis is elongate and displaying a pair of pits, all species apart from *progenitor* also display rings on this elongate terminal section of the axis.

Species included in *Ectenonotus*:

E. connemaricus	(Reed, 1909)
[=*E. octocostatus*,	(Reed, 1910)]
(synonymised in Ingham *et al.*, 1985))	
E. progenitor	Fortey & Droser, 1996
E. marginatus	Holliday, 1942
E. whittingtoni	Ross, 1967
E. raymondi	Holliday, 1942
junior synonyms of *marginatus*	
(synonymised in Ingham *et al.*, 1985)	
E. westoni	(Billings, 1865)

3.8.5.6 *Evropeites* Balashova, 1966

Type species: *Cyrtometopus primigenus lamanskii* Schmidt 1907

Evropeites hyperboreus Fortey, 1980, as the oldest member of *Evropeites*, was used in the analysis as representative of the genus. Fortey & Droser (1996) informally re-assigned *hyperboreus* to *Pseudomera* Holliday, 1942 without detailed discussion, beyond stating that *hyperboreus* differed from the type species of *Evropeites*. I have been unable to obtain any photographs or specimens of the type material of *Evropeites* and so am unable to compare *hyperboreus* to it. Fortey's species is provisionally retained in *Evropeites*, its most recent formal systematic position.

In the present analysis, *hyperboreus* plots separately from *Pseudomera* and is placed within the revised Subfamily Cybelopsinae, as defined herein. Fortey (1980) suggested that *Evropeites hyperboreus* was a good contender for outgroup to the Cybelinae. It is indeed of similar morphology to that of the proposed ancestral form of the Cybelinae and has been used as an outgroup in the Cybelinae analysis (for display purposes only), although it seems likely that the actual ancestor of the Cybelinae was morphologically intermediate between *Evropeites hyperboreus* and *Pliomeridius sulcatus*.

Diagnosis of *Evropeites* -based on *E. hyperboreus*;

Glabella sub-parallel sided or narrowing forward; Mesial indentation in the anteromesial portion of the frontal lobe, extending rearwards from the mesial deepening in the anterior border furrow; Three pairs of lateral glabellar furrows; S3 furrows sinuous and positioned posterior to the anterior glabellar angle, containing one or two apodemes; The anterior, curved portion of the S3 furrows may become isolated from the rest of the S3 furrows in some specimens; The S3 furrows terminate abaxially before reaching the axial furrows; Anterior border furrow deepens mesially; Proparian facial suture; Anterior border is smoothly curved; Eye ridges long and straight, terminating adaxially at the anterior, adaxial corners of the fixigenal fields; No well defined furrow situated parallel to the posterior edge of the eye ridge; Eyes present; Very small fixigenal spines present, oriented to the posterior; Hypostome oval with small lateral spines on the border, but no mesial spine; Anterior border of hypostome continuous but narrows strongly mesially; Abaxial portions of the anterior border of the hypostome and lateral wings expanded into broad fields; Posterior border of the hypostome narrow; The posterior border furrow of the hypostome broad; Five pygidial pleurae which are all associated with an equal number of rings on the axis of the pygidium; In some specimens these pleurae display anterior fields; The terminal section of the pygidial axis is elongate and ornamented with a pair of pits.

Species included in *Evropeites*, as understood herein;

Evropeites hyperboreus,	Fortey 1980
Evropeites primigenus	(Angelin, 1854)
Pliomeroides sp.5	of Ross, 1958
Strotactinus sp.A	of Fortey, 1980

3.8.5.7 *Landyia* Jell, 1985

Type species *Landyia elizabethae* Jell, 1985

This monospecific genus from the Tremadoc of the Digger Island Formation, Waratah Bay, Victoria in Australia displays a unique form of furrow in the pygidial pleurae. These broad, deep furrows lie in the middle of the pygidial pleurae, parallel to the margins of the pleurae, bisecting the narrow ends of the pleurae adaxially. Abaxially the furrows die out just before the abaxial termination of the pleurae.

Diagnosis of *Landyia*;

Glabella narrows forwards/is sub-parallel sided, longer than wide and less than one third of the total breadth of the cephalon across L1; Indentation/furrow present in the anteromesial area of the frontal lobe of the glabella; Anterior border furrow is deep with a further deepening in its mesial section; S3 lateral glabellar furrow is variably adaxially bifurcate or of 'dog legged' form and cuts the margin of the glabella to the posterior of the anterior angle in mature (large) specimens. In small specimens S3 may cut the anterior glabellar angle; Curved eye ridges present, terminating adaxially at the anterior fixigenal angle; Palpebral lobes situated abaxial to the glabella; Fixigenal spines present and directed to the posterior; Hypostome oval with an uninterrupted, mesially narrowing, anterior border, narrow posterior border and marginal spines; Pygidium with four pleurae which correspond to an equal number of rings on the pygidial axis; Pygidial pleurae divided into two by furrows which lie parallel to the margins of the pleurae and which do not reach the margin of the pleurae at any point except through the adaxial end; Terminal piece of the pygidial axis elongate and displays a transversely oriented pair of pits.

Species included in *Landyia*;

Landyia elizabethae	Jell, 1985

3.8.5.8 *Pliomeridius* Leanza & Baldis, 1975

Type species *Pliomeridius sulcatus* Leanza & Baldis, 1975

Pliomeridius plots as sister group to *hyperboreus*. Dean (1989) assigned a new species, *lacunatus* to *Pliomeridius*, an assignment not supported by the analysis, which separates them widely on the cladogram, juxtaposing *lacunatus* and *Metapilekia bilirata* Harrington, 1938.

Diagnosis of *Pliomeridius:*

Glabella narrows gently forwards; The frontal lobe of the glabella is expanded laterally (although still narrower than the L3 lateral glabellar lobes) and longer, longitudinally, than the L3 lateral glabellar lobe; Strong longitudinal furrow in the anteromesial area of the frontal lobe, directed posteriorly from the mesial deepening in the anterior border furrow; S3 lateral glabellar furrows bifurcate adaxially; Anterior cephalic border furrow is deep with a mesial deepening; Anterior border of the cranidium curves smoothly; Proparian facial suture; Eye ridges curved and fairly short, terminating at the anterior, adaxial, corners of the fixigenal fields; Eyes small; Posteriorly directed fixigenal spines present; Hypostome outline oval; Anterior border of the hypostome complete with marginal, lateral, spines but with no mesial spine present; Posterior border of the hypostome narrow; Posterior border furrow is very broad; Five furrowed pygidial pleurae present, terminating in free spines and associated with an equal number of rings on the axis of the pygidium; Terminal section of the pygidial axis is elongate and has a pair of pits.

Species included in *Pliomeridius*

Pliomeridius sulcatus	Leanza & Baldis, 1975

3.8.5.9 *Quinquecosta* Tripp, 1965

Type species *Quinquecosta williamsi* Tripp, 1965

Quinquecosta williamsi Tripp, 1965 was utilised as the type of the Subfamily Quinquecostinae by Edgecombe & Chatterton (1992). This subfamily is subsumed into the Subfamily Cybelopsinae herein.

Diagnosis of *Quinquecosta:*

Median pit present on the anteromesial area of the frontal lobe; Glabella longer than wide; Sides of glabella sub-parallel posteriorly, expanding abruptly anteriorly; Frontal lobe wider laterally, and longer sagittally, than the L3 lateral glabellar lobes; S3 lateral glabellar furrows fork adaxially and abaxially terminate behind the anterior angle of the glabella; S2 lateral glabellar furrows directed forwards; Anterior border furrow of constant depth; Anterior border smoothly curved; Facial suture proparian; Eyes small, low and positioned close to the glabella in the anterior portion of the fixed cheeks; Eye ridges present, terminating adaxially posterior to the anterior fixigenal angle; Eyes small, close to the glabella and raised on short stalks; Long, straight fixigenal spines oriented to the posterior; Hypostome of rounded outline with an unbroken anterior border, lateral, but not mesial, spines and a narrow posterior border; Four unfurrowed pleural ribs present on the pygidium; More rings present on the pygidial axis than the number of pygidial pleurae present; Pleural ribs remain in contact until short, blunt, out-turned free spines; Terminal piece elongate, displaying furrows and possibly a pair of pits.

Species included in *Quinquecosta;*

Quinquecosta stincharensis	Tripp, 1967
Quinquecosta williamsi	Tripp, 1965

3.8.5.10 *Strotactinus* Bradley 1925

Type species: *Amphion salteri* Billings, 1861

As can be seen from Figure 3.20, the two named species ascribed to this genus are separated on the cladogram. As such *Strotactinus* is paraphyletic. Its transitional nature and the range of variation within its members in characters which are of higher burden in more derived members of the subclade was documented, but not formalised, by Ingham *et al.* (1985, fig. 14) and Fortey (1979). I will follow previous authors in regarding *Strotactinus* as a valid, but expressly paraphyletic, genus.

It is likely that *Strotactinus* sp. A of Fortey (1980) is more closely related to *Evropeites hyperboreus* Fortey, 1980 than *Strotactinus*, although without examining the associated hypostome, which was described but not illustrated by Fortey (1980), it is not possible to make a definitive statement. *Strotactinus* sp.A of Fortey (1980) is then tentatively retained within *Strotactinus* pending further study.

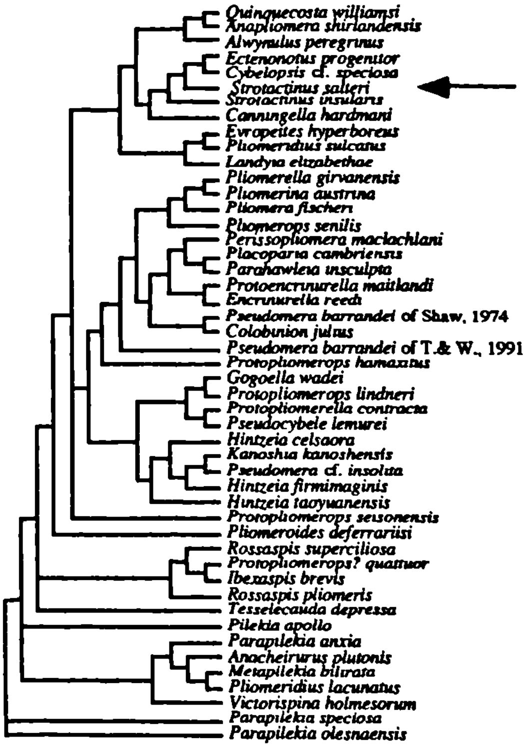
Diagnosis of *Strotactinus*:

Glabella slightly longer than wide, tapering forwards; Three lateral glabellar furrows present, S3 situated in advance of the anterior angle of the glabella; Anterior border furrow of uniform depth; Anterior border of the cranidium is smoothly rounded; Facial suture proparian; Eye ridges present, terminating adaxially at the anterior, adaxial, corner of the fixigenal field; Genal angles rounded; Hypostome rounded or sub-rectangular; Anterior border of the hypostome uninterrupted; No marginal, or mesial, spines on the hypostomal border; Posterior border of the hypostome produced into a broad, flat, field; Five unfurrowed pygidial pleurae terminating in out-turned, blunt points; Number of rings on the axis of the pygidium either equal to, or greater than, the number of pygidial pleurae; Terminal section of the pygidial axis elongate and bearing a pair of pits.

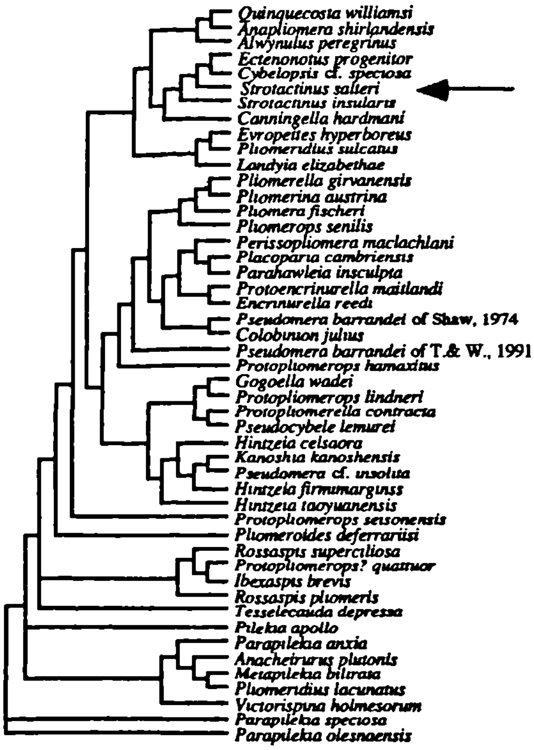
Species included in *Strotactinus*:

Strotactinus insularis	(Billings, 1865)
Strotactinus salteri	(Billings, 1861)

Figure 3.20: Results of addition of *Strotactinus salteri* to Pliomeridae dataset; 1.



2.



3.9 Broad evolutionary patterns seen in the Pliomeridae Raymond, 1913.

The Pilekiinae, which are here shown to have given rise to the other members of the Pliomeridae, originated in Gondwana in the early Tremadoc. It is clear from this analysis that there was a period of rapid diversification shortly after this, during the early and mid-Tremadoc. During this short period, all of the major pliomerid subclades were established from an evolving plexus of closely related taxa. During the remainder of the early and mid-Ordovician these established subclades continued to diversify, especially in the early Arenig. Only four subgroups, one of which is represented by a single species, survived beyond the Arenig/Llanvirn boundary. As far as I am aware, of the Pliomeridae, only *Placoparia (Hawleia) prantli* Kielan, 1960 survived into the Ashgill, although the Encrinuridae are both diverse and abundant at this time. In addition to the derived Pliomeridae, it is likely that a number of other major groups were derived from the Pilekiinae during the period of rapid diversification in the early Ordovician. *Rossaspis pliomeris* Demeter, 1973 from the

Lower Ordovician of Utah and *Macrogrammus* are both likely to be close to the ancestral form of the Cheirurinae. Similarly, the ancestral form of the Sphaerexochinae/Acanthoparyphinae/Cyrtometopinae is likely to be close to that of *Pilekia* sp. of Jell (1985). Pressure of time has precluded further detailed investigation of the development of these groups within the present study.

3.10. Palaeobiogeographical inferences:

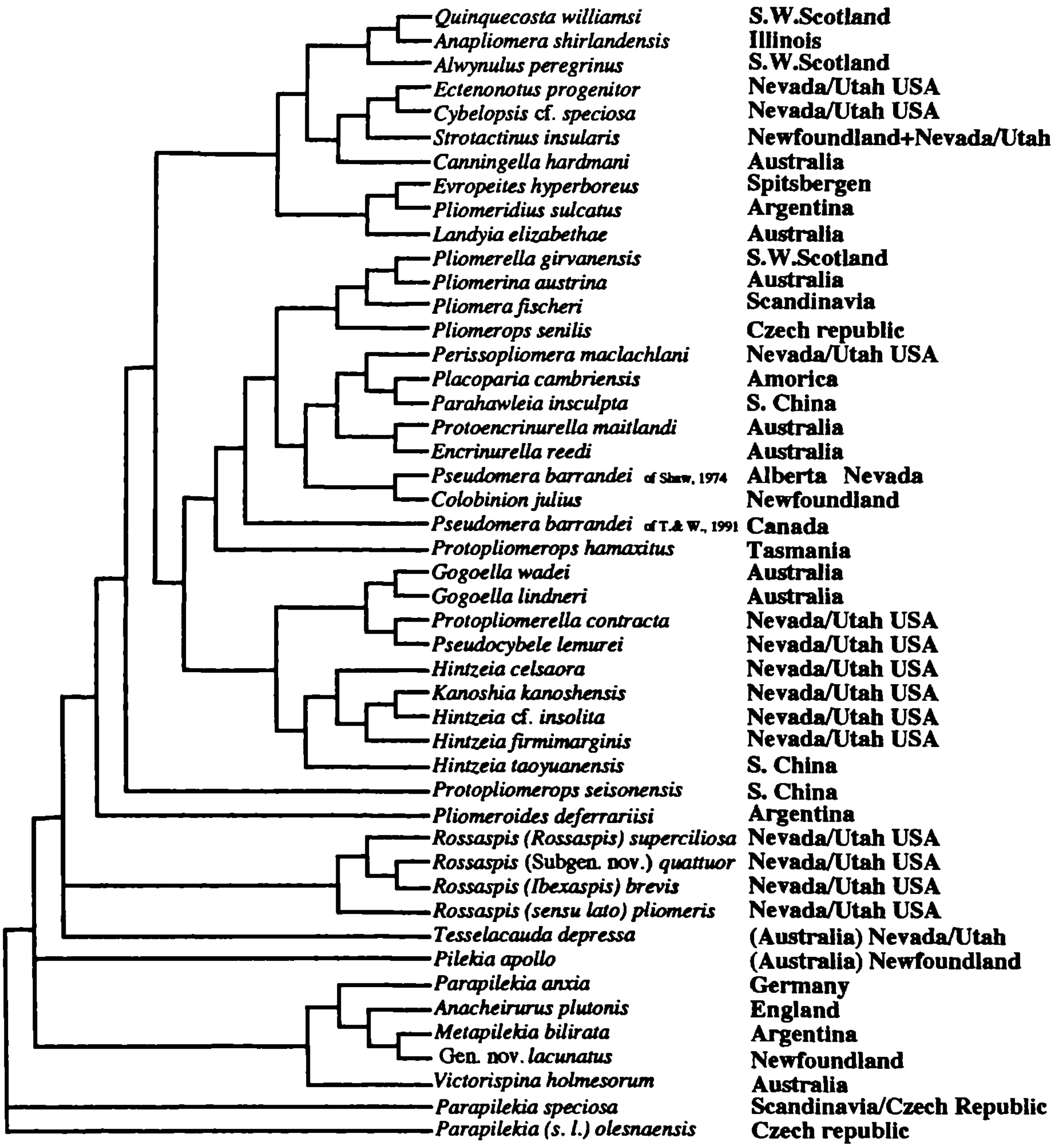
3.10.1 Informal palaeobiogeographical inferences:

Although often regarded as a predominantly Laurentian family, it is clear that the earliest members of the Pliomeridae are found in Gondwana during the early Tremadoc, later spreading into Laurentia - which must have been in biogeographical connection with Gondwana at this time. Shortly after this, the Laurentian members of the Pliomeridae become isolated from their Gondwanan relatives. In the mid-Ordovician this faunal isolation of Laurentia and Gondwana was replaced by communication, probably facilitated by the presence of intermediate terranes/continents which were used as stepping stones for dispersal.

The Pilekiinae developed in the Czech Republic area of Gondwana and Scandinavia (Baltic) in the earliest Tremadoc (Figs 3.21, 3.22), the apparent free communication between these areas indicates that the Czech Republic/Germany area of Gondwana and Baltica are likely to have been relatively close at this time. Shortly after this, in the early Tremadoc, the Pilekiinae gave rise to the other main groups of the Pliomeridae. At the same time the Pilekiinae became widespread in Gondwana where they expanded their range to include Australia and England. The recovery of Pilekiinae from England indicates that Avalonia was also close to, or part of, Gondwana at this time (Fortey & Mellish 1992; Torsvik *et al.*, 1996 Figs 10,11).

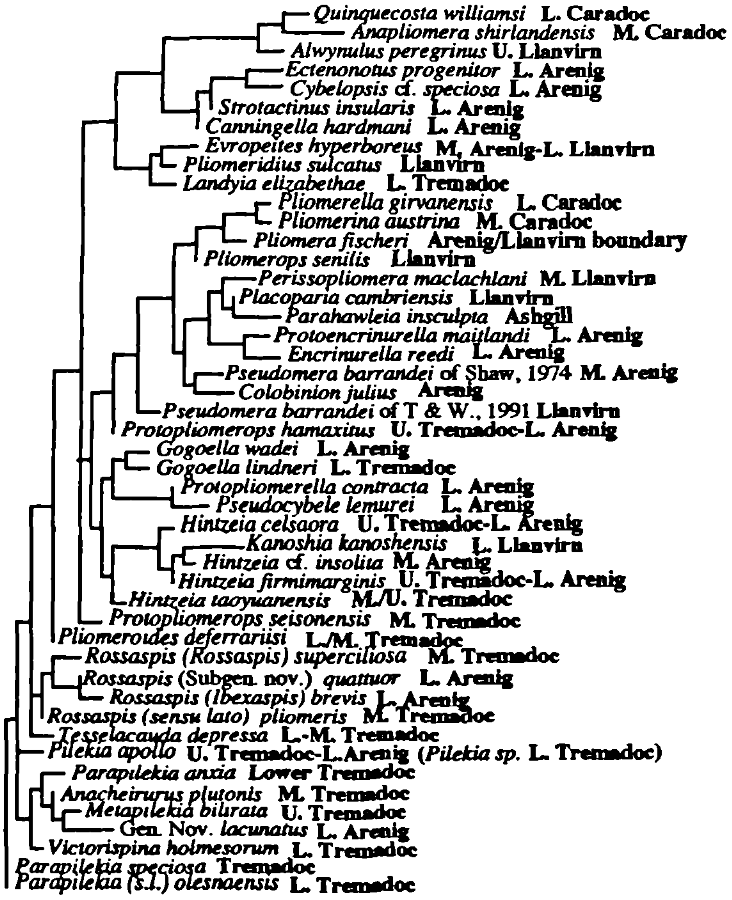
The early and mid-Tremadoc was a period of rapid diversification in which all of the major subclades of the Pliomeridae were established. This early diversification of the pliomerid groups which were derived from the Pilekiinae occurred in the Gondwanan southern Victoria/Tasmania area of Australia where the basal taxa of all of the major pliomerid subclades are now found and are of closely similar ages. There is a clear, repeated, palaeobiogeographical pattern evident in those Pliomeridae in a derived position above the Pilekiinae. At the base of every major subclade are taxa

Figure 3.21; Cladogram annotated with geographical locations of the taxa.



from Gondwana including areas such as the Czech Republic, Australia and China. The taxa which are situated higher in each subclade (and later in time) are predominantly Laurentian. It is generally the case with the Pliomeridae that when taxa are found in Laurentia they are exclusively found there, indicating isolation of Laurentia after its colonisation. It is similarly the case that when members of a

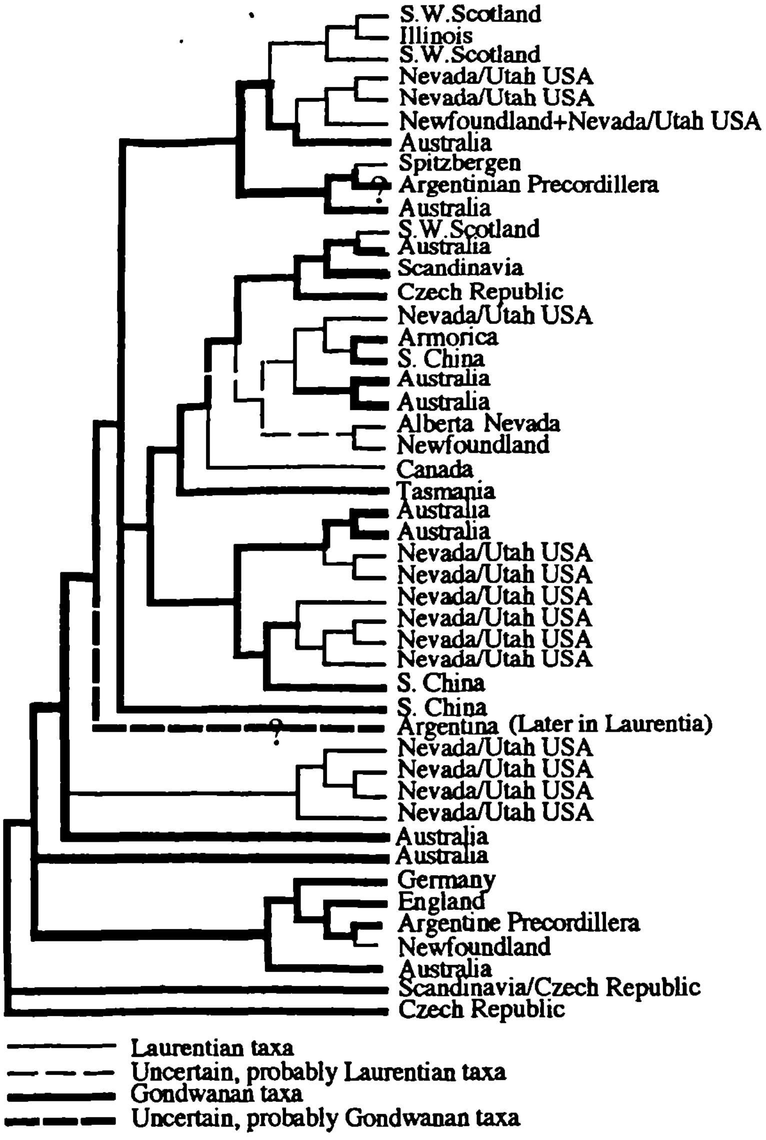
Figure 3.22: Pliomerid phylogeny derived from this analysis, annotated with the stratigraphical ages of the taxa for comparison to the biogeography.



subclade are found in Laurentia, they are the crown taxa while the taxa basal to the subclade are Gondwanan.

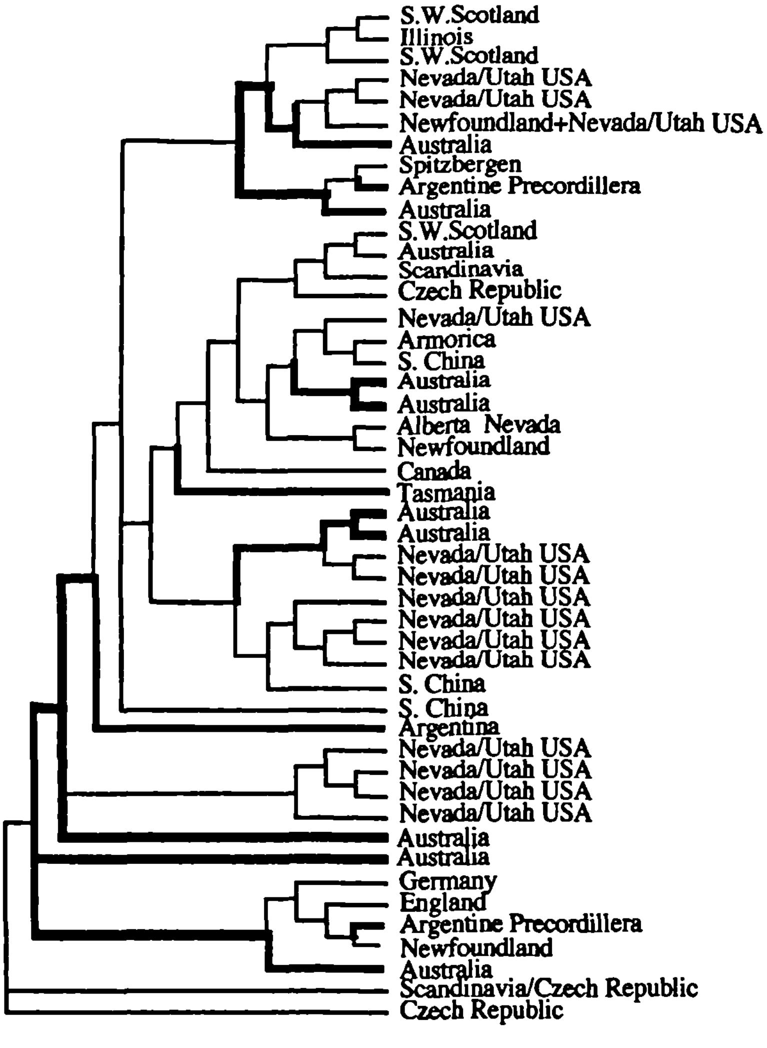
It is clear that during the Tremadoc Laurentia was closely juxtaposed to some areas of Gondwana; in particular the areas which now form Australia. This inference is further supported by the fact that a number of Tremadoc taxa, notably *Tesselacauda depressa* and *Pilekia apollo* are found in both Australia and N. America, with the oldest specimens of each being found in the southern Victoria/Tasmania area of Australia. After expansion from Australia into Laurentian N. America the Pliomeridae radiated strongly (Figure 3.23) but appear to have been isolated from Gondwana.

Figure 3.23: Cladogram annotated with the geographical localities of those taxa with Laurentian and non-Laurentian localities differentiated (see Fig. 3.21 for the taxa concerned).



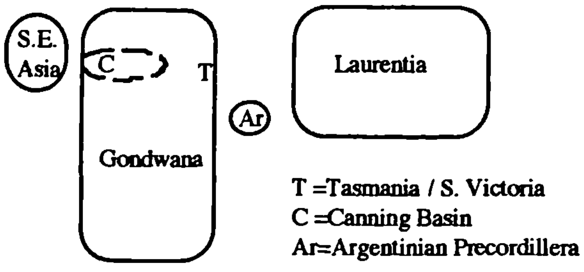
Taxa from the mid-Ordovician of the Argentine Precordillera are found phylogenetically 'sandwiched' between taxa from Australia and North America suggesting an intermediate geographical position by at least the Llanvirn (see Fig. 3.24 and 3.25)

Figure 3.24: Cladogram annotated with those taxa from Australia and S. America highlighted. (See Fig. 3.21 for the taxa concerned)



As indicated by Burrett & Stait (1985, p.188) and Burret *et al.* (1990 figs 3 & 4), the Canning Basin area of Australia did not lie close to Laurentia but was in close communication with the Sibumasu block (Malaysia and Thailand), Tibet and India. Proximity of the Canning Basin to the Eastern Asian terranes is supported by the development of *Protoencrinurella* and *Encrinurella* in the Canning Basin followed by the subsequent expansion of *Encrinurella* into these terranes. These taxa are not found in coeval Laurentian rocks, suggesting that the Canning Basin area was situated on the on the western side of Gondwana, while Laurentia lay on the eastern side.

Figure 3.25 Schematic diagram to indicate the relative positions of selected terranes discussed in the text. S.E. Asia includes China, India Sibumasu Block etc. in the Tremadoc.



The placement of the Canning basin as a marginal Gondwanan site was also indicated by Cocks & Fortey (1990) on the basis of the distribution of olenid trilobites at this time. A similar grouping of geographical areas during the Tremadoc was noted by Peng (1990 pp. 67-72) who emphasised a particularly strong correlation between the fauna of the Jiangnan Slope Belt of southern China and the formations of the Canning Basin of western Australia, the Digger Island Formation of southern Victoria, the Florentine Valley Formation of Tasmania, the Leimitz-Schiefer of Bavaria and the Tremadoc of South Korea. He also noted a weaker correlation between the faunas of the Jiangnan Slope Belt of southern China and those of the *Kainella meridionalis* Zone of Argentina and formations in Scandinavia and the Anglo-Welsh area, including the Shineton Shale fauna in England. Peng (1990) also noted that there was little faunal correlation between the Tremadoc fauna of the Jiangnan Slope Belt of southern China and the shelly sequences of N. America.

After the early/mid-Tremadoc, Baltica appears to have been isolated from both Laurentia and Gondwana. Laurentia and Eastern Gondwana were isolated from each other by the late Tremadoc-early Arenig when their pliomerid faunas become distinct from each other. Throughout this period both North and South China were close to Gondwana. Taxa from Siberia are not represented in this analysis, possibly indicating that it was distal to both Laurentia and Gondwana at this time. Similarly, the only pliomerids of which I am aware in Kazakhstan are a number of species of *Pliomerina* found there in the mid/upper Ordovician which, tenuously, may indicate that it lay at a moderate distance from the western margin of Gondwana during the early Ordovician.

The biogeographical pattern outlined here for the Tremadoc matches that of Dalziel (1997) fairly closely (see Fig. 3.30). Dalziel proposed that Laurentia (N. America) and Gondwana (Australia, Antarctica etc) were close in the early Tremadoc, with the Argentine Precordillera situated between the two. In Dalziel's reconstruction Gondwana stretched from low southerly latitudes to the equator, the northerly section of which was at a similar latitude to Laurentia. This orientation of Gondwana and latitudinal position of Laurentia also matches that outlined by Burret & Stait (1985), although they envisaged Laurentia as being longitudinally less close to Gondwana. In contrast, the continental reconstruction for the Tremadoc of McKerrow & Scotese (1991) with Laurentia situated at a distance from Gondwana, fails to explain the Australia-S. America - N. America linkage, the Canning basin-Sibumasu-India-China link and the isolation of their two sets of faunas from each other seen in this analysis.

More recent works such as those of Thomas & Astini (1996) (see Fig. 3.31 herein) and Astini *et al.* (1995) envisage the Argentine Precordillera as a terrane which rifted from Laurentia (which was widely separated from Gondwana) in the Cambrian and moved towards Gondwana in the Ordovician. They show the Argentine Precordillera approaching Gondwana closely enough for faunal exchange by the Llanvirn and with Laurentia never closely approaching Gondwana. This model fits well with the patterns observed in the Pliomeridae. The pattern seen in the subclades which contain taxa from the Argentinian Precordillera is as follows: the earliest known pliomerids are Gondwanan and were isolated from the Laurentian faunas. The first pliomerids in these subclades found in the Precordillera area are of Llanvirn age and later members of these subclades are Laurentian with no evidence of communication between Laurentia and Gondwana after this. This pattern supports the notion of a wide separation between Laurentia and Gondwana by the Llanvirn with the Argentinian Precordillera moving from Laurentia to Gondwana and acting as a stepping stone for faunal migration from Gondwana to Laurentia.

This synthesis suffers from the flaw that a different pattern is seen in the subclades which do not contain components from the Precordillera. In these subclades, there is evidence for direct migration between the southern Victoria/Tasmania area of Gondwana and Laurentia during the early/mid-Tremadoc followed by isolation of Laurentia and Gondwana from the mid/upper Tremadoc onwards. This evidence includes both the relative positions in the phylogeny of Gondwanan and Laurentian taxa and the presence of common species in both areas (eg

Pilekia apollo and *Tesselacauda depressa* (see Section 3.8.1). Clearly a migration route between Gondwana and Laurentia was available during the Tremadoc which did not involve the Argentinian Precordillera (as no pliomerids have yet been described there at this time) and which was not operable in the mid-late Ordovician, as none of the Laurentian Pliomeridae are found in Gondwana at this time. This pattern indicates that Laurentia and the Gondwanan southern Victoria/Tasmania area of Australia were close in the lower/mid-Tremadoc and that the separation between them increased to the point at which direct faunal exchange was impossible by the mid/upper Tremadoc.

It is possible, that a combination of the various models currently proposed is the correct answer. In this combined synthesis, Laurentia and the southern Victoria/Tasmania area of Gondwana were close in the early/mid-Tremadoc, as in the reconstructions of Dalziel (but with Gondwana not actually colliding with Laurentia). This is in marked contrast to the palaeogeographical reconstructions of McKerrow *et al.* (1991 text fig. 1) and Scotese & McKerrow (1991) in which Laurentia faces the area of Gondwana which includes England. In the mid. to late Tremadoc, the separation between Laurentia and Gondwana increased to the point at which faunal exchange could no longer occur between the two areas. Meanwhile, the Argentine Precordillera rifted off from Laurentia at some time prior to the Tremadoc and moved towards Gondwana, approaching it closely enough for faunal exchange to occur by the Llanvirn and thereby acting as a stepping stone between the two widely separated areas, as is shown in the biogeographical reconstruction of Thomas & Astini (1996) and Astini *et al.* (1995). The pivotal palaeobiogeographical role of Australia in the early Ordovician is more easily explained by its situation as a promontory jutting out from Gondwana as in Burrett *et al.* (1990 figs 3 & 4) than as part of a massive Gondwana such as depicted by Scotese & McKerrow (1990 fig.6)

The biogeographical patterns seen in this analysis for the Arenig and later do not support the continental position reconstructions of Dalziel (1996) for this period, in which Laurentia is shown as being situated close to Gondwana, with Spitsbergen and S.W. Scotland projecting out laterally. Dalziel's reconstruction is in conflict with the clear evidence of the complete isolation of the Laurentian and Gondwanan faunas seen in this analysis. The reconstructions of McKerrow & Scotese 1991, with later adaptations by other workers, in which Laurentia and Gondwana are well separated at this time closely matches the pattern seen in the Pliomeridae (see Fig. 3.29).

Figure 3.26 summarises the biogeographical history of the Pliomeridae, as inferred informally;

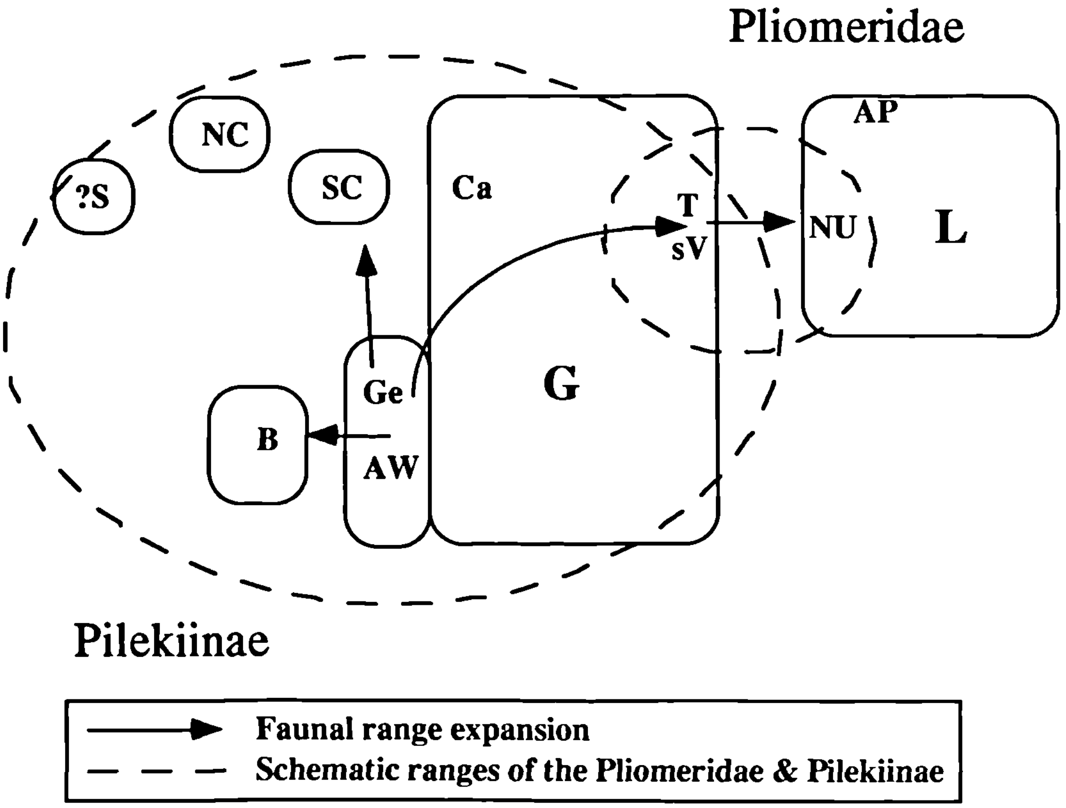
Figure 3.26: Inferred Position and movement of the main plates from this analysis.

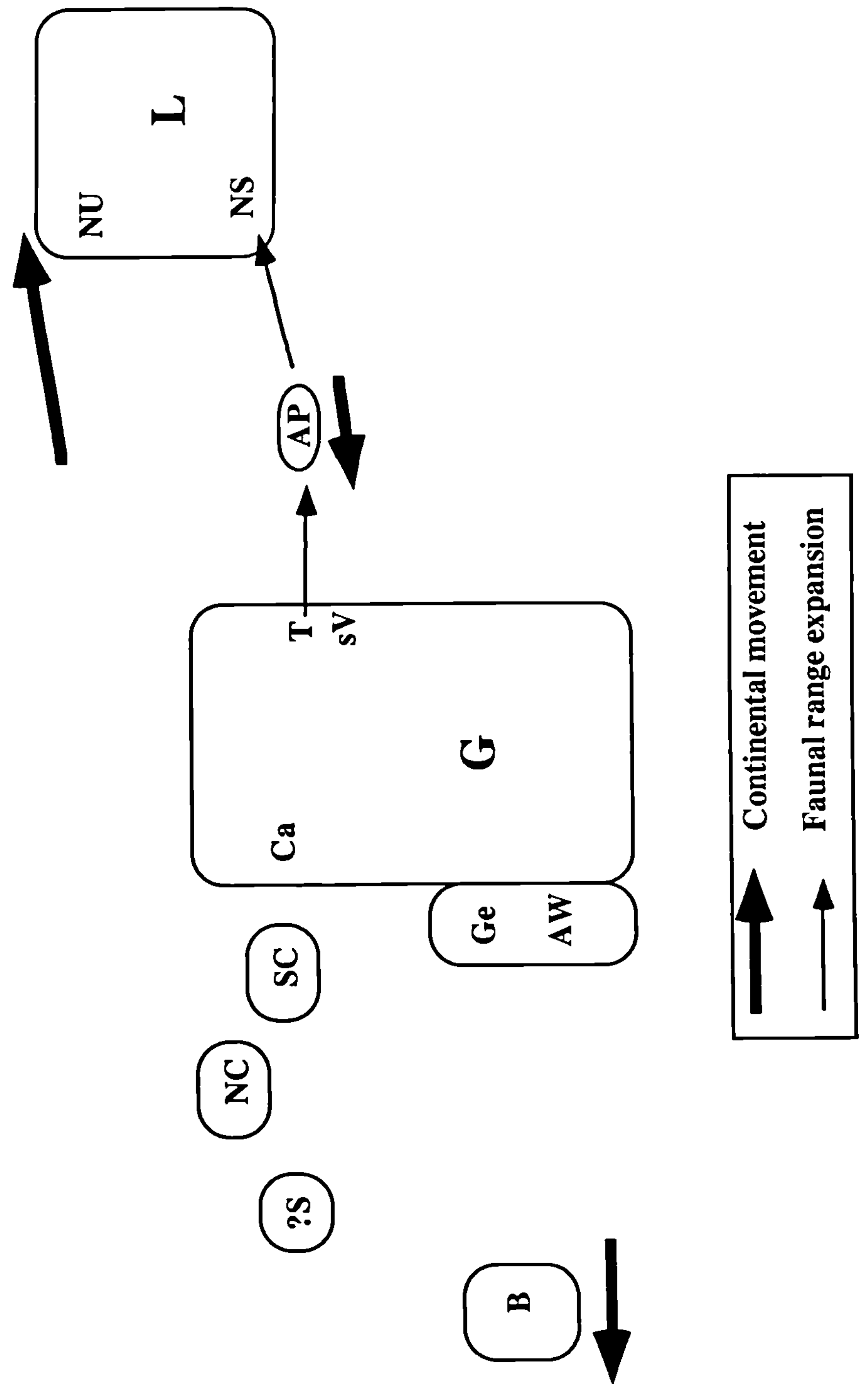
A. Early/mid Tremadoc.

B. Post/mid Tremadoc. (Baltica moving West <u>towards</u> Laurentia).

Note: L=Laurentia, G=Gondwana, AP=Argentine Precordillera, NU=Nevada & Utah, NS=Newfoundland & Spitsbergen, T=Tasmania, sV=southern Victoria, Ca=Canning Basin, SC=South China, NC=North China, S=Siberia, Ge=Germany (Bavaria), AW=Anglo/Welsh area, B=Baltica.

A.




L
NU
NS
AP
T
sV
G
Ca
Ge
AW
SC
NC
?S
B
Continental movement
Faunal range expansion

B.

3.10.2 Study of Gain/Loss Ratios:

3.10.2.1 Biogeographical Gain/Loss Study of the major pliomerid subclades:

The purpose of this section is to reduce the degree of subjectivity in the assessment of the palaeobiogeographical signal which may be discerned in the phylogenies produced by this analysis.

Figure 3.27: Cladogram annotated with the geographical localities of those taxa and with the nodes utilised in tables 3.3-3.6 of the gain/loss analysis.

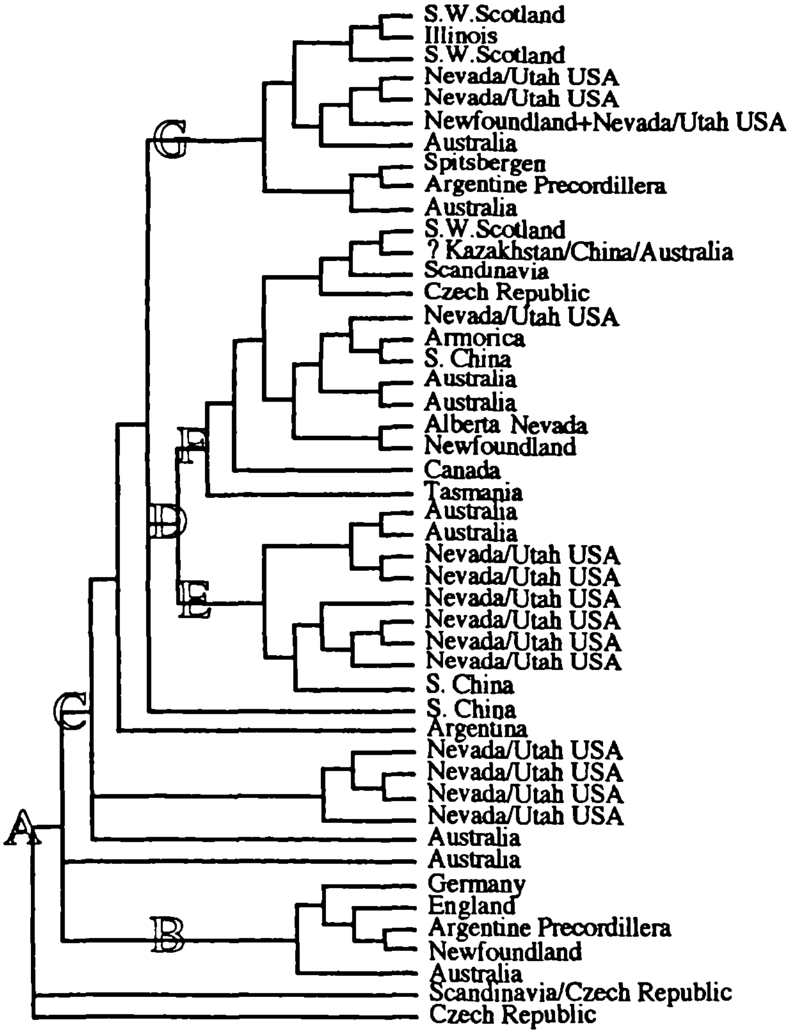


Table 3.1: Calculation of the geographical Gain/Loss ratios of nodes A and B. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	**Node A**			**Node B**		
	Losses	Gains	Gains / Losses	Losses	Gains	Gains / Losses
SW Scotland	18	3	0.17	0	0	0
Newfoundland	20	4	0.2	4	4	0.25
Alberta/McKenzie	12	1	0.08	0	0	0
Nevada/Utah	18	5	0.27	0	0	0
Illinois	13	1	0.08	0	0	0
Spitsbergen	12	1	0.08	0	0	0
Scandinavia	14	2	0.14	0	0	0
England	7	1	0.14	3	1	0.33
Australia	**17**	**9**	**0.53**	**1**	**1**	**1**
Czech Republic	12	3	0.25	0	0	0
Germany	6	1	0.17	**2**	**1**	**0.5**
Argentine Precordillera	14	3	0.21	4	1	0.25
S. China	20	4	0.2	0	0	0
Armorica	17	1	0.06	0	0	0
Oklahoma	15	1	0.07	0	0	0
Kazakhstan	16	1	0.06	0	0	0

The most probable ancestral area of node 'A' is Australia.

At node 'B' the area which is most likely to be part of the ancestral area is Australia with Germany having a lower likelihood of being part of, or close to, the ancestral area of the subclade.

Table 3.2: Calculation of the geographical Gain/Loss ratios of nodes C and D. Any areas scoring 0.5 or more highlighted in **Bold.**

Geographical area	**Node C**			**Node D**		
	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
SW Scotland	14	3	0.21	7	1	0.14
Newfoundland	14	2	0.14	6	1	0.17
Alberta/McKenzie	8	1	0.13	3	1	0.33
Nevada/Utah	14	5	0.36	8	3	0.38
Illinois	9	1	0.11	0	0	0
Spitsbergen	8	1	0.13	0	0	0
Scandinavia	11	1	0.09	6	1	0.17
England	0	0	0	0	0	0
Australia	**14**	**7**	**0.5**	**8**	**4**	**0.5**
Czech Republic	1	10	0.1	5	1	0.2
Germany	0	0	0	0	0	0
Argentine Precordillera	7	2	0.29	0	0	0
S. China	16	4	0.25	12	3	0.25
Armorica	13	1	0.8	8	1	0.13
Oklahoma	11	1	0.09	6	1	0.17
Kazakhstan	12	1	0.08	7	1	0.14

At nodes **C** and **D** it is, again, Australia which is the area most likely to have formed part of the ancestral range of the taxa which form this subclade.

Table 3.3: Calculation of the geographical Gain/Loss ratios of nodes E and F. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	Node E			Node F		
	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
SW Scotland	0	0	0	6	1	0.17
Newfoundland	0	0	0	5	1	0.2
Alberta/McKenzie	0	0	0	2	1	0.5
Nevada/Utah	**2**	**2**	**1**	6	1	0.17
Illinois	0	0	0	0	0	0
Spitsbergen	0	0	0	0	0	0
Scandinavia	11	1	0.09	5	1	0.2
England	0	0	0	0	0	0
Australia	**2**	**1**	**0.5**	**3**	**6**	**0.5**
Czech Republic	0	0	0	4	1	0.25
Germany	0	0	0	0	0	0
Argentine Precordillera	7	2	0.29	0	0	0
S. China	16	3	0.19	9	2	0.22
Armorica	0	0	0	7	1	0.14
Oklahoma	0	0	0	5	1	0.2
Kazakhstan	0	0	0	7	1	0.14

By node 'E' the area most likely to be part of the ancestral range is Nevada/Utah with Australia having a lower, but still considerable chance of having formed part of, or been situated close to, the ancestral range of the subclade.

At node **F** it is, again, the Australia area of Gondwana which is the area most likely to have formed part of the ancestral range of the subclade.

Table 3.4: Calculation of the geographical Gain/Loss ratios of node G. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	**Node G**		
	Losses	Gains	Gains Losses
SW Scotland	**3**	**2**	**0.67**
Newfoundland	4	1	0.25
Alberta/McKenzie	0	0	0
Nevada/Utah	3	1	0.33
Illinois	4	1	0.25
Spitsbergen	3	1	0.33
Scandinavia	0	0	0
England	0	0	0
Australia	**3**	**2**	**0.67**
Czech Republic	0	0	0
Germany	0	0	0
Argentine Precordillera	3	1	0.33
S. China	0	0	0
Armorica	0	0	0
Oklahoma	0	0	0
Kazakhstan	0	0	0

At node G Australia and S.W. Scotland are both equally likely to have formed part of the ancestral range of the taxa which comprise this subclade.

The results of this calculation of Gain/Loss ratios provides strong support for the informal inferences made earlier in this section and illustrated in Figures 3.25 and 3.26.

3.10.2.2 Investigation of biogeographical signal from the smaller subclades:

Figure 3.28: Cladogram annotated with the nodes examined in tables 3.7-3.11.

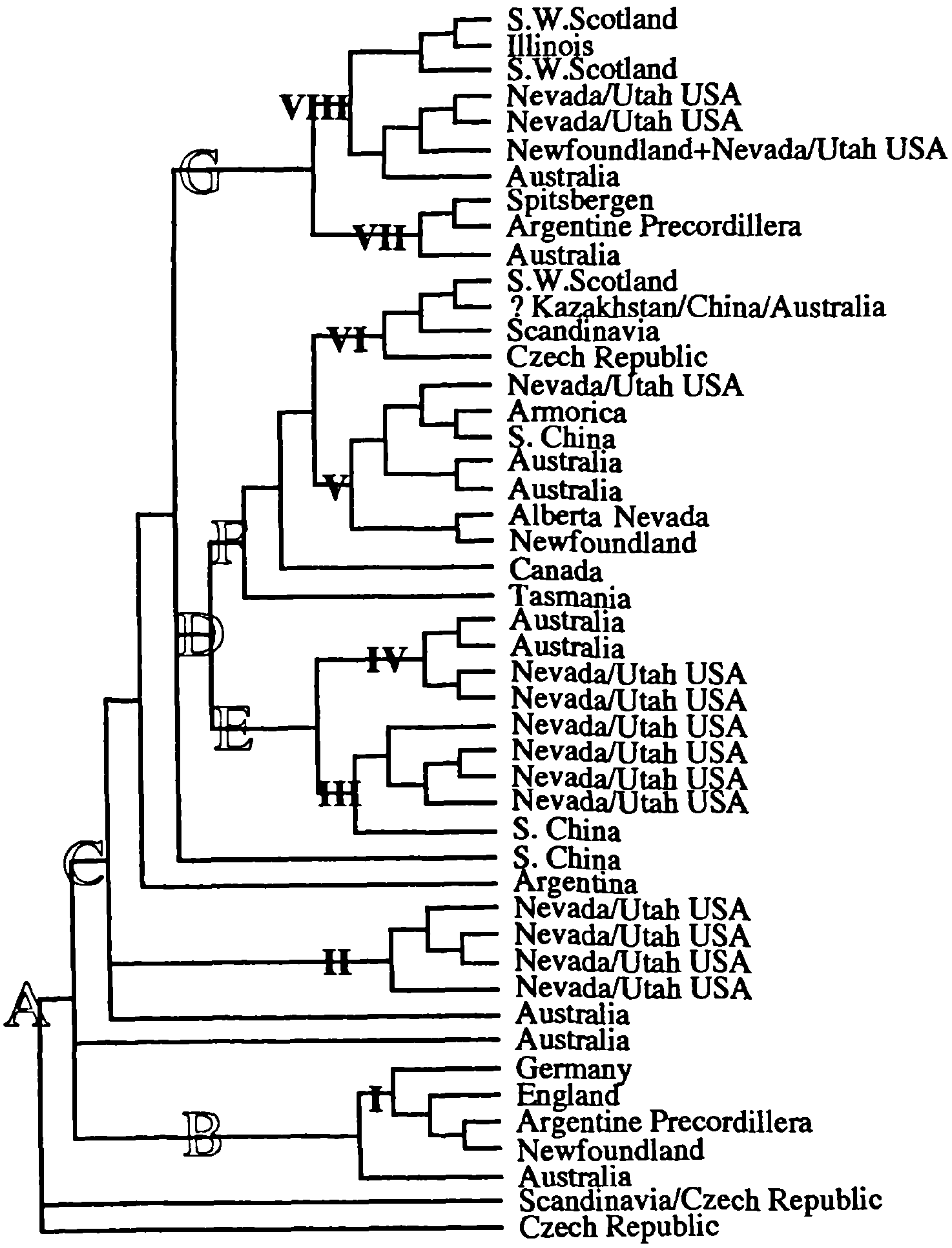


Table 3.5: Calculation of the geographical Gain/Loss ratios of node I. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	Node I		
	Losses	Gains	Gains Losses
Newfoundland	4	1	0.25
England	3	1	0.33
Germany	**2**	**1**	**0.5**
Argentine Precordillera	3	1	0.33

The area of Gondwana around Germany is the area most likely to have been part of the ancestral range of the taxa which make up subclade I. The taxa of subclade II were clearly restricted to the Nevada/Utah area of America, while those of subclade III are equally likely to have originated in China or the Nevada/Utah area of America. The ancestral area of the taxa of subclade IV is equally likely to have included Australia and the Nevada/Utah area of the USA.

Table 3.6: Calculation of the geographical Gain/Loss ratios of node VI. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	Node V		
	Losses	Gains	Gains Losses
Oklahoma	**2**	**1**	**0.5**
Newfoundland	**2**	**1**	**0.5**
Nevada/Utah	3	1	0.33
Australia	**2**	**1**	**0.5**
China	4	1	0.25
Armorica	4	1	0.25

It can be seen from table V that there is an equally high chance of Oklahoma, Newfoundland and Australia having formed part of the ancestral range of the subclade. This may indicate that members of this subclade were widespread at this time and that Laurentia (N. America) and Gondwana were in communication.

Table 3.7: Calculation of the geographical Gain/Loss ratios of node VI. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	**Node VI**		
	Losses	Gains	Gains Losses
S.W. Scotland	3	1	0.33
Scandinavia	**2**	**1**	**0.5**
Czech Republic	**1**	**1**	**1**
Kazakhstan/China/ Australia	3	1	0.33

At node VI both the Czech Republic and Scandinavia have high chance of having formed part of the ancestral area of the taxa belonging to this subclade.

Table 3.8: Calculation of the geographical Gain/Loss ratios of node VII. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	**Node VII**		
	Losses	Gains	Gains Losses
Spitsbergen	**2**	**1**	**0.5**
Argentine Precordillera	**2**	**1**	**0.5**
Australia	**1**	**1**	**1**

At node VII Australia has the highest chance of having formed part of the ancestral area of the taxa belonging to this subclade with the Argentine Precordillera and Spitsbergen both displaying the same, lower, probability.

Table 3.9: Calculation of the geographical Gain/Loss ratios of node VIII. Any areas scoring 0.5 or more highlighted in **Bold**.

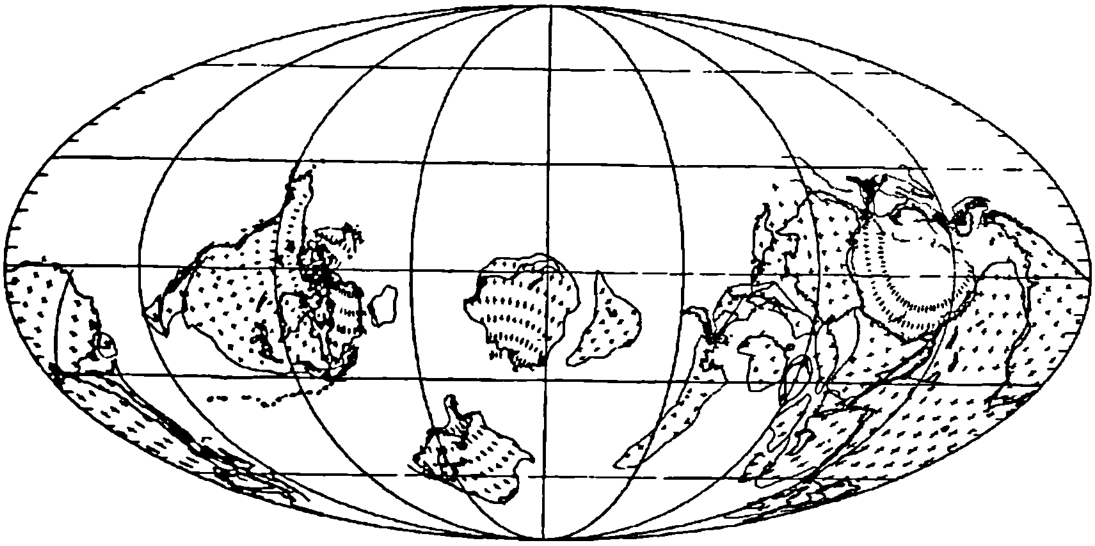
Geographical area	**Node VIII**		
	Losses	Gains	Gains Losses
S.W. Scotland	**3**	**2**	**0.66**
Illinois	4	1	0.25
Australia	**2**	**1**	**0.5**
Argentine Precordillera	3	1	0.33
Newfoundland	4	1	0.25
Nevada/Utah	3	1	0.33
Spitsbergen	3	1	0.33

At node VIII it is S.W. Scotland which has the highest probability of having formed part of the ancestral area of this subclade with Australia having a somewhat lower likelihood. This split may indicate that there are basal taxa to this subclade still to be found in early sediments from both S.W. Scotland and Australia.

The results of these gain/loss ration analysis strongly support the informal inferences made in section 3.10.1 and are summarised in Figure 3.26.

Figure 3.29: Palaeogeographical reconstructions of Scotese & McKerrow (1990). **Note:** Research subsequent to that upon which these reconstructions are based has resulted in much of these maps being revised and these maps are included only to facilitate comparison of the relative positions of Laurentia and Gondwana to each other through time with their position in the reconstructions of other workers.

A. Scotese & McKerrow, 1990 Fig. 6. Tremadoc



B. Scotese & McKerrow, 1990 Fig. 8. Early Caradoc

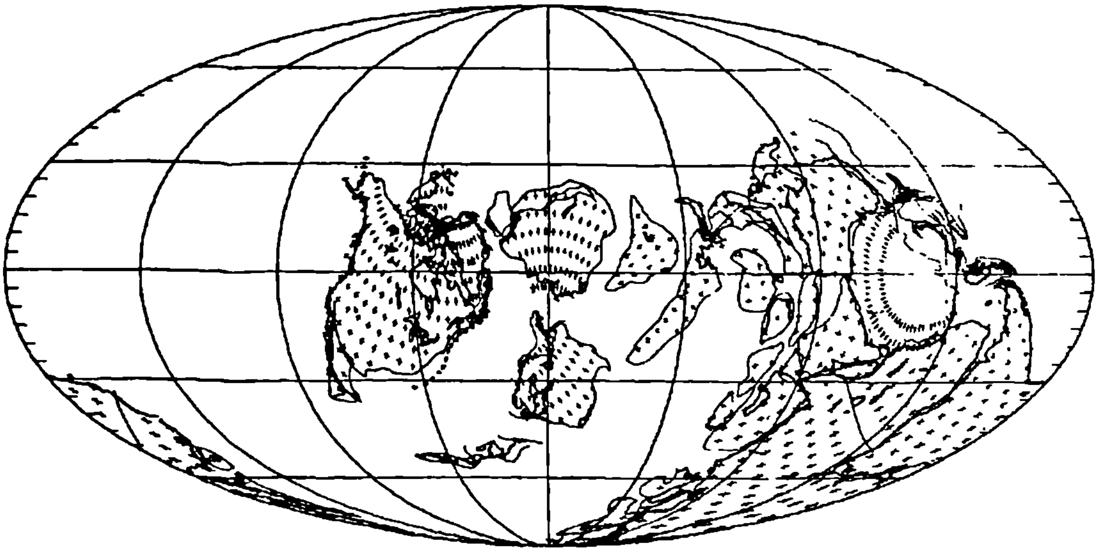
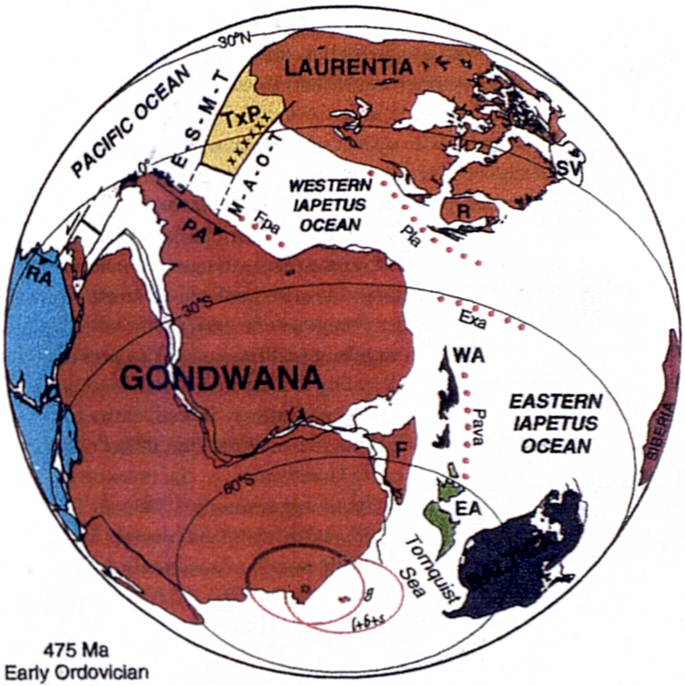
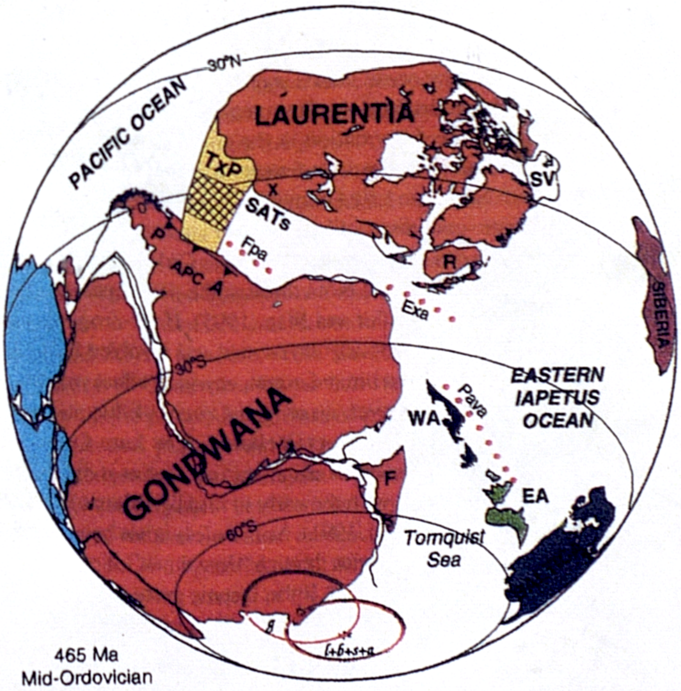


Figure 3.30: Palaeogeographical reconstructions of Dalziel (1997 figs 15a, 16).

Note: These maps are included purely to facilitate comparison of the relative positions of Laurentia and Gondwana to each other through time with their position in the reconstructions of other workers.



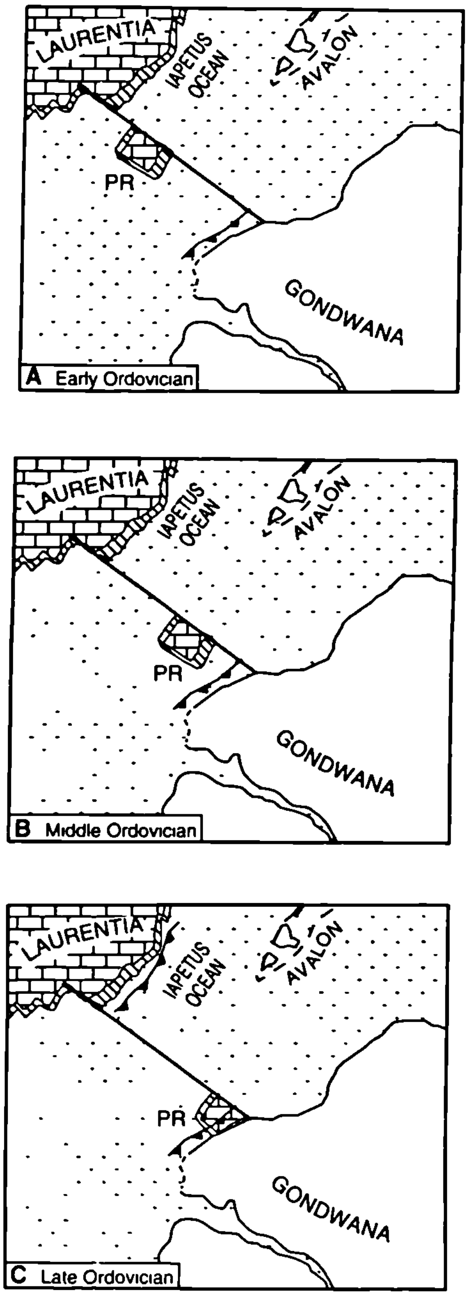
475 Ma
Early Ordovician
(Arenig)



465 Ma
Mid-Ordovician

Figure 3.31: Palaeogeographical reconstructions of Thomas & Astini (1996, fig.3)

Note: These maps are included purely to facilitate comparison of the relative positions of Laurentia and Gondwana to each other through time with their position in the reconstructions of other workers.



CHAPTER 4

THE CYBELINAE
HOLLIDAY, 1942

4.1 Introduction:

The objectives of this chapter are to;

1. Diagnose monophyletic genera to accommodate the approximately eighty species of Cybelinae.
2. Determine the intergeneric relationships.
3. Determine the interspecies relationships within those genera.
4. From these relationships, and the distribution of cybelines through time, draw conclusions about the palaeobiogeography of the Ordovician.

The Cybelinae was chosen as a suitable group for study as its taxa are geographically widespread and range throughout much of the Ordovician. This allows the palaeobiogeography of a large part of the globe to be examined over a critical period of ocean closure. Although inhabiting a range of environments, including shallow carbonate facies, they were concentrated in the deep shelf Nileid biofacies, making them likely to be good palaeogeographical indicators (Fortey and Mellish 1992). The Cybelinae consists of a large number of species which display wide variations in morphology which are amenable to coding as discrete characters.

The Cybelinae were chosen as the first group to be studied in the present project as an existing data matrix of characters and character states had been compiled for most members of the subfamily by R.P. Tripp and A.W. Owen. This was to have formed the basis of a multivariate statistical analysis similar to that undertaken by Temple and Tripp (1979) for the Encrinurinae. The data proved not to be amenable to multivariate analysis and so was made available to form the basis of a cladistic study. However the original data matrix was largely unsuitable for a cladistic analysis and most of the characters employed here are either new or are altered from those coded for the multivariate study.

4.2 Taxa considered in this analysis:

4.2.1 Taxa included in the Cybelinae analysis:

Atractopyge condylosa		Dean, 1971 Summerford Group, Upper Llanvirn, N.W. Newfoundland,
Atractopyge dentata		(Esmark, 1833) (See Whittington, 1965, Nikolaisen, 1961). Elnes Formation or Fossum Formation, Llanvirn-L. Caradoc, Oslo, Norway, Also M. Caradoc, Wales
Junior synonyms	*A. grewingki*	(Schmidt, 1881)
	A. reveliensis	(Schmidt, 1881)
Atractopyge gaoluoensis		Zhou *et al.*, 1977 Linxiang Formation, (Early Ashgill) Hupei, South China
Atractopyge sinensis		Lu, 1974 Shihtzupu Formation, Upper Llanvirn, *Calymenesun tingi* trilobite Zone, *G. teretiusculus* graptolite Zone, Guizhou Province, South China
Atractopyge scabra		Dean, 1962, Dufton Shales, Onnian Substage of the Streffordian Stage at Pus Gill in the *Onnia gracilis* and *Onnia superba* zones also in the Pusgillian. Top Caradoc-Lower Ashgill. N. England.
Bevanopsis ulrichi		Cooper, 1953. L. Champlain and Edinburg formations. Blackriveran (L. Caradoc), Virginia, U.S.A.

Cornovica didymograpti	Whittard, 1960 Uppermost Hope Shales, *Didymograptus artus* Zone (Llanvirn) Shelve inlier, West Shropshire,
Cybele aff. *bellatula*	Ancygin, 1973 U. Arenig, Middle Urals,
Cybele bellatula	(Dalman, 1827) Kunda Formation, (U. Arenig/L. Llanvirn) Sweden, Norway, Baltic.
Cybele pscemmica	Abdullaev *in*, Abdullaev & Khaletskaya, 1970, Chatkal'sky Range (Ashgill), Uzbekistan
Cybelella sp.	Tripp *et al.* 1981 Superstes mudstone, Lower *N. gracilis* graptolite Zone (Lower Caradoc). Girvan District, S.W. Scotland,

Material assigned to *Cybelurus expansus* by Tripp *et al.* (1981 pl.1 fig.14, 15) regarded herein as belonging to *Cybelella* sp. which is coded accordingly.

Cybelella sp.	Ingham, Undescribed material in prep. Bardahessiagh Formation, Middle Caradoc, Pomeroy, N. Ireland.
Cybeloides iowensis	Slocom, 1913. Maqouoketa Formation, Ashgill, E. USA.
Cybelurus batuensis	Levitskiy, 1962 Karakan Horizon (?=Llandeilan) Kazakhstan.
Cybelurus brutoni	Fortey, 1980 Valhallfonna Formation, V4a, Upper *hirundo* graptolite Zone N. Spitsbergen.

Cybelurus expansus	Reed, 1944 Basal Superstes Mudstones, L.-M. *gracilis* graptolite Zone (L. Caradoc) Girvan, S.W. Scotland
Cybelurus halo	Fortey, 1980 Valhallfonna Formation, V4b (*bifidus* graptolite Zone) N. Spitsbergen.
Cybelurus mirus	(Billings, 1865) *artus* graptolite Zone (L. Llanvirn) V4b in Spitsbergen (Fortey 1980)
Cybelurus planus	Levitskiy, 1962 (= *Cybele planifrons*; Weber, 1948; Semenova, 1960.) Bugryshikhinsk horizon (U. Llanvirn) Altai Mts. region of the former USSR.
Cybelurus shi	Zhou *et al.*, 1984 Shihtzupu Formation, Upper Llanvirn, Guizhou Province, South China
Cybelurus sokoliensis	Burskyi, 1970 *Megalaspides* trilobite Zone probably M. Arenig, Novaya Zemlya, Pai Khoya
Deacybele arenosa	(McCoy, 1846) Ballygarvan Bridge, New Ross, Co. Wexford, Longvillian (U. Burrellian)
and	Clashford House Formation, Caradoc. Near Herbertstown, Co. Meath, Eire.
Junior synonym (this analysis)	
Deacybele pauca	Whittington, 1965, Gelli-grîn Formation (Longvillian) Bala District.

Deacybele gracilis	(Nikolaisen, 1961) Solvang Formation (Upper Caradoc), Norway
Deacybele mchenryi	(Reed, 1899) Tramore Limestone (L. Caradoc)
And	Raheen Formation, (Upper Caradoc), Co. Waterford, SE Eire
Dindymene plasi	Kielan, 1960 Svarta Dobrotivá beds, Llanvirn-L. Caradoc, Bohemia
Encrinurus hornei	Dean, 1973 Summerford Group, Unit B Arenig/L. Llanvirn, Newfoundland, Canada
Evropeites hyperboreus	Fortey, 1980 Zone V4a-b of the Valhallfonna Fm, *hirundo* - *artus* graptolite zones U. Arenig - L. Llanvirn, Spitsbergen
Koksorenus kazakhstanensis	Koroleva , 1992 Mallisor lake deposits (Ashgill), N. Kazakhstan.
Libertella corona	Hu, 1971 Boutetort Formation, (=Edinburg Formation), Upper Llanvirn, Virginia, USA
Lyrapyge ebriosus	Fortey, 1980 Valhallfonna Formation, V2a = *bifidus* graptolite Zone N. Spitsbergen.
Plasiaspis bohemicus	(Barrande, 1872) $d\gamma_1$ beds (Arenig/Llanvirn) Šárka & Osek, Bohemia, Czech Republic

Sinocybele fluminis	Dean & Zhou, 1988 Ashgill, Sort Dere, Zap Valley, Turkey
Stiktocybele balclatchiensis	(Reed, 1914) Upper Balclatchie Group, *foliaceous* (=*multidens*) Zone, Lower Caradoc, Balclatchie, Girvan area, SW Scotland,
Stiktocybele bathytera	Ingham & Tripp, 1991 Jubilation Member, Doularg Formation, Albany Group, *gracilis* graptolite Zone. S.W. Scotland.

4.2.2 Taxa added separately as highly incomplete:

Sinocybele baoshensis	Sheng, 1974. L. Pupiao Formation, Upper Llanvirn/L. Caradoc Yunnan South China.

4.3 Characters considered in this analysis;

4.3.1 Character type and ordering:

The characters were all coded as unordered, apart from characters 1 and 3 which were ordered on the basis of inferred sequences of morphological development. These sequences were not based on ontogenetic evidence as the ontogeny of the majority of the Cybelinae is only poorly known. Instead, these morphological series were based on the observed states of homologous features in different groups descended from common ancestors. A sense of direction was provided to these successions of character states by comparing them to the states prevalent in potential outgroups, by looking for logical intermediaries between character states, by comparing the combinations of other characters accompanying those being ordered and by using stratigraphy.

These morphological series do not imply that species and genera displaying intermediate stages of character development are actual, direct *evolutionary* intermediaries but simply that many of the variations in form of associated structures in related groups may show a logical path of development. These series provide additional information about the relative relationships of genera to each other. For example, a genus whose members possess a structure developed from an earlier more 'primitive' structure is likely to be later than, and somehow descended from, members of that genus which possesses the more 'primitive' structure. This additional information may increase the level of confidence paced in a cladogram or indicate areas of anomaly within the cladograms generated by PAUP.

4.3.2 The position of the facial suture in the Cybelinae:

The position of the facial suture is a useful diagnostic feature in the systematics of the Cybelinae. The anterior border of the cranidium, the rostral plate and the lateral librigenal border are normally treated as separate structures but are here considered to be components of a single structure. This allows the full range of anterior cephalic morphologies found within the Cybelinae, and related groups, to be examined and derived within the same framework utilising only two developmental mechanisms; variations in the width of the marginal cephalic border and migration of the facial suture (Fig. 4.1).

In the Pliomeridae, and *Libertella* Hu, 1971, the anterior border is of constant breadth. In early members of the Cybelinae, such as *Cybelurus expansus* Tripp, 1976 (see Ingham & Tripp, 1991) the anterior border is a continuation of the lateral librigenal border. The anterior border is relatively broader than the librigenal border and there is a marked break in slope between the two. In early Cybelinae the facial suture passes abaxially to this break in slope. In more derived taxa the facial suture passes to the adaxial side of this break in slope resulting in the incorporation of a section of the broadened 'anterior border' into the librigenae as an anterior librigenal field. The break in slope is retained in the librigenae, marking the edge of these fields. In some members of the Encrinurinae this anterior field is further expanded and is strongly tuberculate. In a small number of taxa, including some members of *Cybeloides* and *Deacybele* this adaxial migration of the facial suture is taken to such an extreme that the anterior border of the cranidium is reduced to the width of a single tubercle (Fig. 4.13)

The rostral plate has no independent convexity of its own and its posterior edge follows the curvature of the posterior edge of the adjacent borders. It is therefore to be regarded as an area of the anterior border which is divided off from the rest by the facial suture. The result of this is that the size and shape of the rostral plate is dictated by the position of the facial sutures. This is highlighted by the morphology of the rostral plate of *Cybeloides (Cybeloides) virginiensis virginiensis* figured by Evitt & Tripp (1977 pl. 17 figs 1b,c, 12, 13, 14). In this case, the facial suture is positioned further adaxially and to the posterior than is the case in the early cybelines. This has the effect of incorporating most of the two median tubercles from the anterior border into the rostral plate, a clear example of the position of the facial sutures determining the form of the rostral plate.

From these points it can be seen that the librigenal border, the anterior border of the cranidium and the rostral plate are all essentially parts of the same structure, divided from each other by the facial suture, which defines their proportions.

In members of stratigraphically old genera such as *Cybelurus,* and in the Pliomeridae, the anterior portion of the facial suture is positioned abaxially, cutting the adaxial lateral margin of the fixigenal field (Figure 4.2) while in more derived taxa, there is a tendency towards adaxial migration of the anterior portion of the facial suture, resulting in a variety of different glabellar and librigenal morphologies including the highly attenuated anterior border of members of *Cybeloides* (see Figure 4.13), accompanied by the development of an anterior librigenal field and the frontal lobe morphology of *Libertella* Hu, 1971.

The utility of viewing the morphology of the rostral plate, librigenal border and anterior border as being part of a single structure may be seen when considering members of the genus *Libertella* Hu, 1971 (see Evitt & Tripp, 1977), where the hypostome is in direct contact with the anterior border, which lies along the base of the rostral plate and there are no librigenal anterior fields present. The rostral plate is situated within the convexity of the frontal lobe of the glabella .

In short, the position of the structures relative to each other is altered (see Figs 4.1a, 4.1b).

The unusual anterior morphology of *Libertella* is not unique. It has developed independently in members of both *Staurocephalus* Barrande, 1846 (see 1959 p.0449)) and *Dindymene pulchra* Olin, 1906.

Figure 4.1 a: Sequence of structures in the anterior of the majority of the Cybelinae

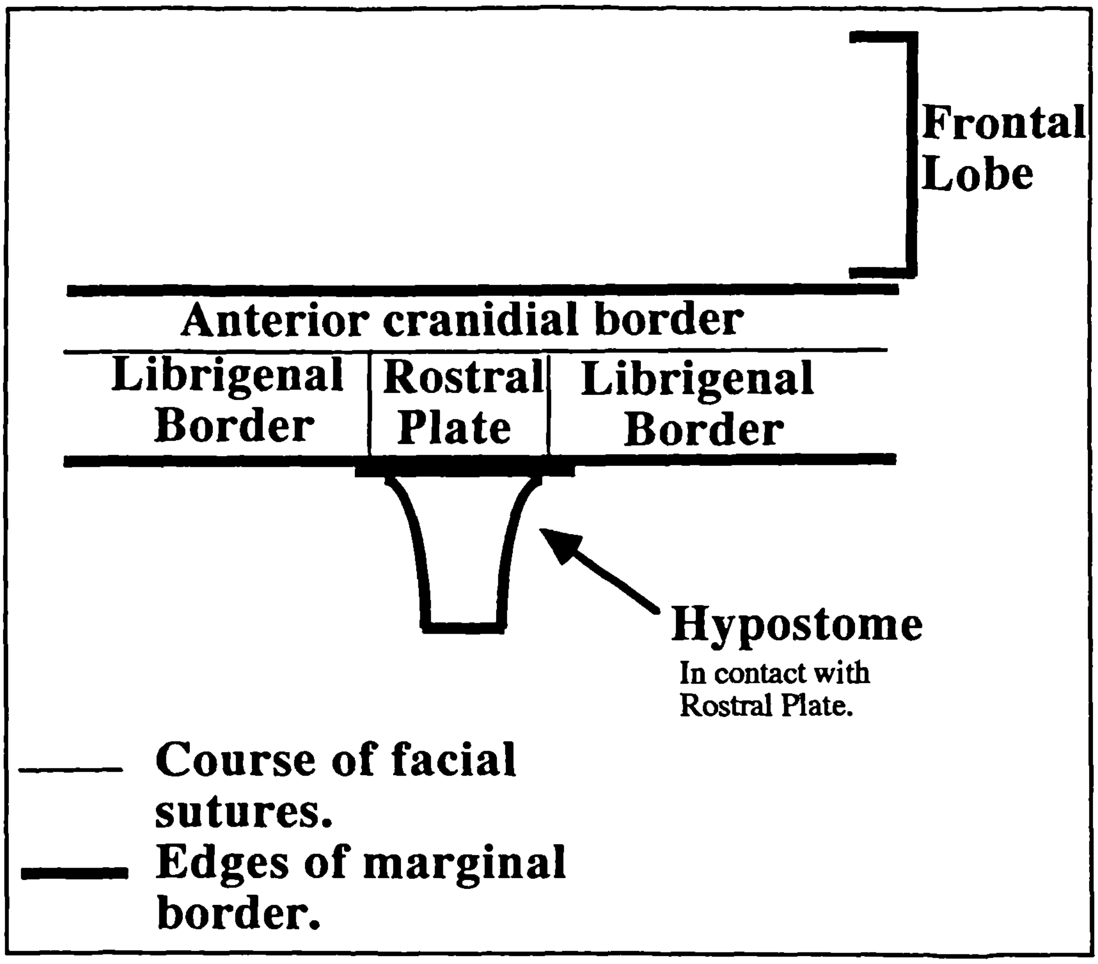
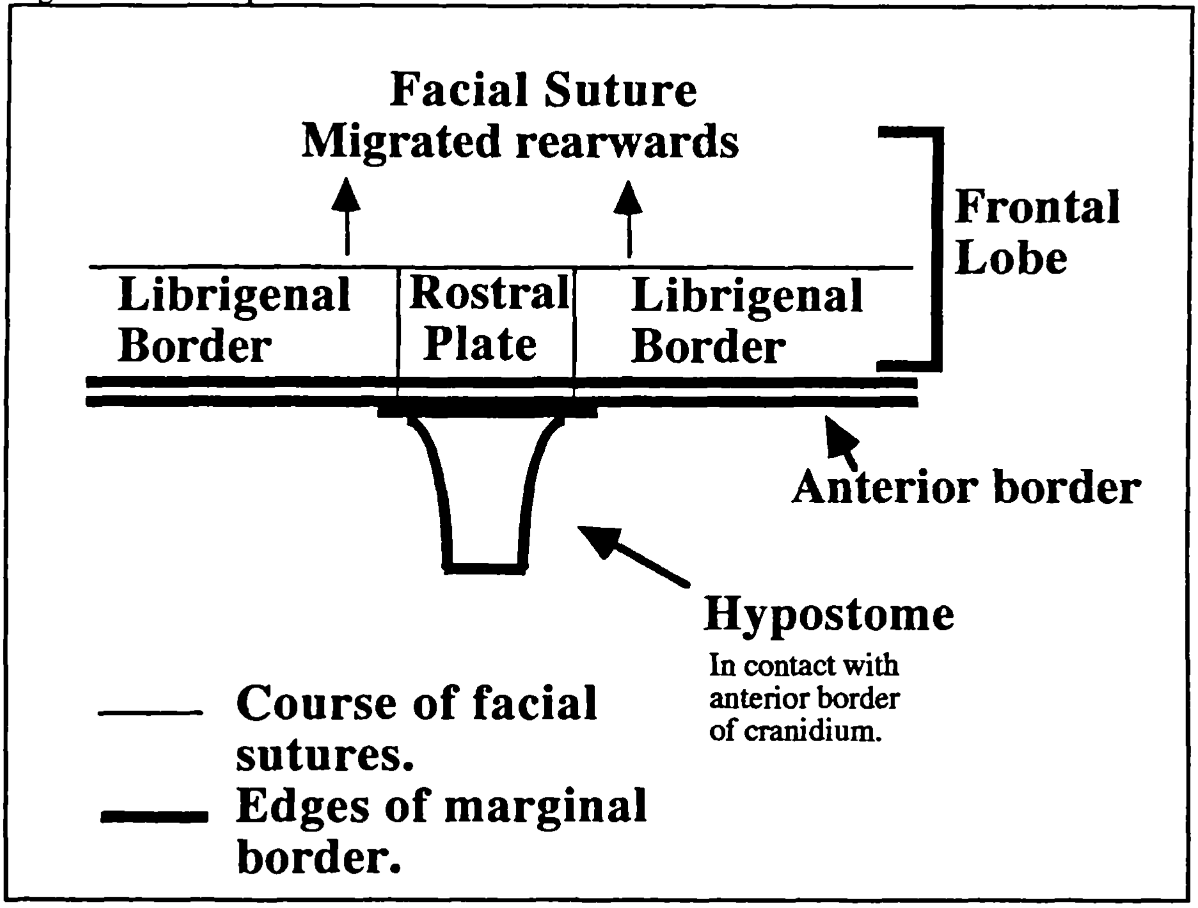


Figure 4.1 b: Sequence of structures in the anterior of *Libertella* .



4.3.3 List and discussion of the characters employed in this analysis:

As the choice and coding of characters is the main source of subjectivity in the analysis those characters chosen require to be justified where possible. A description and discussion of a number of the characters employed is given to highlight the reasoning behind their inclusion and their subdivision into character states.

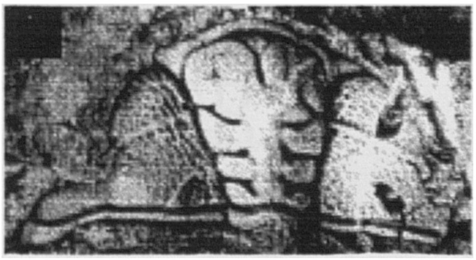
1. Adaxial migration of the facial suture resulting in the incorporation of a section of the anterior of the glabella as an anterior librigenal field; **Ordered**
   '0'=no.
   '1'=yes.
   '2'=yes, cuts frontal lobe of the glabella.

2. Median deepening present in the anterior border furrow;
   '0'=no.
   '1'=yes

The median deepening appears to be structurally separate from the furrow within which it sits. This inference is based upon the fact that the presence or absence of the median deepening in a specimen appears to be independent of the morphology of the anterior border furrow. For example; the median deepening is present in some species displaying a complete anterior border furrow, such as *Cybelurus mirus*, but is absent in others, such as members of the genus *Atractopyge*. It is also present in some species displaying a laterally shallowing anterior border furrow, such as *Cybele bellatula*, and in species in which the anterior border furrow has shallowed to obsolescence laterally, such as *Lyrapyge ebriosus*. As a result I have coded this as a separate character.

3. Form of the anterior border furrow; **Ordered** (See Figs 4.2-4.4)
   '0'= anterior border furrow of uniform depth.
   '1'= anterior border furrow shallows strongly laterally.
   '2'= anterior border furrow shallows to obsolescence laterally resulting in incorporation of the anterior border into the glabella.

Figure 4.2: *Cybelurus expansus* (Reed, 1944 from Ingham & Tripp, 1991 pl.12, fig. a) displaying complete anterior border furrow (Character state '0'). Note independent convexity of the frontal lobe of the glabella and the anterior border. Note also the break in slope of anterior border to right of glabella. X3.



In all potential outgroups to the Cybelinae, the anterior border furrow is complete and is of constant depth (state **0**). In taxa in which the anterior border is incorporated in the frontal lobe there is always a median deepening (see character 2) and faint traces of the relict anterior border furrow on both the abaxial and adaxial sides of the incorporated section. It is reasonable to code the state in which the abaxial sections of the anterior border furrow shallowed, but were still discernible (state **1**) as an intermediate between the extreme conditions.

Figure 4.3: *Deacybele gracilis* (Nikolaisen, 1961)
(from Owen & Bruton 1980 pl.8, fig.16)
displaying anterior border furrow partially effaced abaxially (Character state '1'). x4.5.

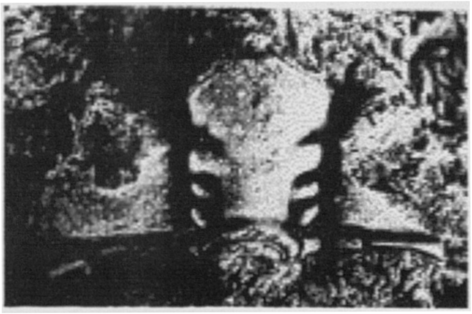
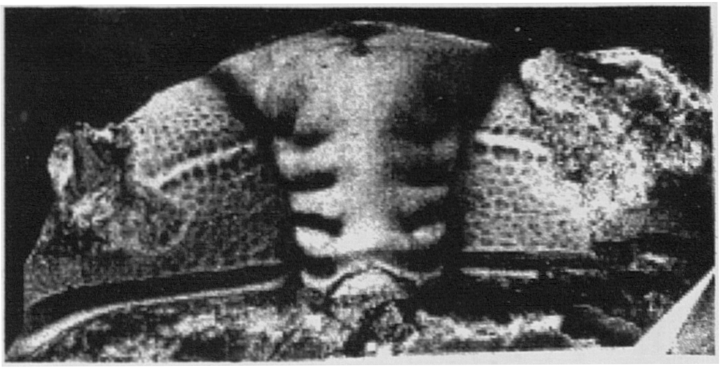


Figure 4.4: *Lyrapyge ebriosus* (Fortey 1980 pl.24, fig.1) displaying complete abaxial effacement of the anterior border furrow (Character state '2') x3.



4. Form of the S3 lateral glabellar furrow;
'1'=S3 furrow forks adaxially.
'2'=S3 furrow is unforked.
'3'=S3 furrow has a 'dog leg' form - i.e. is unforked but changes direction half way along its length.

On completion of the analysis it appears that state 2, 'Unbranched S3 furrow,' has developed independently on at least two separate occasions - within the genus *Atractopyge* and in the *Plasiaspis-Cybele* subclade.

The bifurcate form of the S3 lateral glabellar furrow (Fig. 4.5) is found in all of the stratigraphically early taxa. I interpret this feature to have formed by the amalgamation of a non - bifurcate S3 lateral glabellar furrow with an anteriorly placed S4 furrow in the ancestor of the Cybelinae. This interpretation was suggested by Fortey (1980) and discussed by Edgecombe & Chatterton (1992) and is supported by two main features;

(i) Some members of early cybeline species, such as *Cybelurus halo* Fortey, 1980, display isolation of the anterior branch of the bifurcate S3 furrow from both the posterior branch of the fork and from the axial furrow. This isolation does not occur in any members of stratigraphically late species of *Cybelurus*.

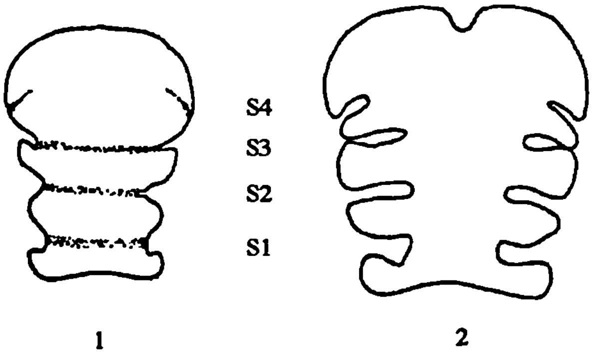
(ii) In addition, juvenile members of species in which the adults possess bifurcate S3 lateral glabellar furrows, start off with four separate, unbranched lateral glabellar furrows. During ontogeny the anterior two of these furrows (the S3 and S4) amalgamate to form the mature bifurcate S3 form (see Fig. 4.5). This pattern of ontogeny can be seen in *Cybelurus halo* Fortey, 1980.

The forked S3 furrows may take a range of forms, all of which are included in character state '1';

In *Cybelurus halo* Fortey 1980 there is a short stem, caused by the relatively poorly developed L3 lateral glabellar lobes followed to the anterior by a pair of lateral glabellar furrows (derived from the S3 and S4 furrows - see Figure 4.5) of approximately equal length, neither of which is obviously transverse.

Figure 4.5: *Cybelurus halo* Fortey, 1980 from the Lower Llanvirn of Spitsbergen (Scanned and adapted from Edgecombe & Chatterton, 1992).

1. Meraspid glabella, Fortey (1980 pl. 22, fig. 8). Approx. 0.5mm long. Note the presence of four distinct lateral glabellar furrows.
2. Small holaspid glabella, Fortey (1980, pl.22, fig. 5). Approx. 3mm long. Note that the anterior (S4) lateral glabellar furrow is now positioned close to the S3 lateral furrow. This, combined with the slight reduction in lateral length of the L3 lateral glabellar lobe relative to the other lateral lobes, results in the development of the characteristic 'bifurcate' S3 lateral glabellar furrow.



In *Koksorenus* Koroleva, 1992, the single abaxial stem of the fork is almost obliterated by the extreme reduction of the lateral glabellar lobes. This has the effect of making the morphology of the 'forked S3' approach that of two separate furrows, seen in juvenile specimens of *C. halo* Fortey 1980 or the discrete S3 and an S4 lateral glabellar furrows as seen in the outgroup Pliomeridae. The reduction in size of the lateral glabellar lobes, and associated inflation of the frontal lobe seen in *Koksorenus*, is here inferred to be paedomorphic.

Also seen in species such as *Atractopyge kutorgae* are S3 furrows reduced to rounded pits with a single apodeme, from which two shallow furrows diverge.

The forked S3 may also be asymmetrical with the posterior furrow directed transversely and the anterior branch directed obliquely towards the anterior. In taxa displaying this morphology the anterior furrow is normally considerably shorter than the transversely oriented one. This form of 'forked S3' is commonly seen in members of *Atractopyge*, such as *scabra*, and is extremely well developed in *Atractopyge sinensis* where the anterior branch is reduced to an indentation in the abaxial anterior part of a broadly transverse S3 furrow.

Character state **3**, 'dog-legged S3', is seen in members of the genus *Stiktocybele*, where this furrow contains two apodemes. This form is likely to have developed by the amalgamation of the two branches of the forked S3 seen in sister groups to *Stiktocybele*, and may have developed from an ancestor with asymmetrically forked S3 lateral glabellar furrows.

Character state **2**, 'Straight non-forked S3 furrow', contains three forms within it. These are not coded separately due to the difficulty of defining sharp boundaries between the individual states and the effects of distortion on the specimens. These non-branching forms are:

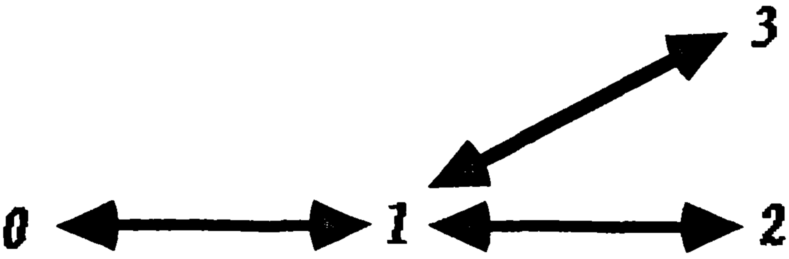
A. Single furrow directed obliquely to the posterior.

B. Single furrow directed obliquely to the anterior.

C. Single furrow represented by a pit and slight indentation of the lateral margin of the glabella.

In taxa with unbranched S3 lateral glabellar furrows the course of the S3 furrow pair varies within individual genera and species. This may be due to variation within a species where, for example, the orientation of the S3 furrows may vary from being directed obliquely to the anterior to being transversely oriented. Alternatively, the variation may be due to distortion of the specimen by fracturing and displacement during sediment compaction, or tectonic deformation. As the effects of such distortion are often hard to discern, both forms are incorporated into a single 'unbranched S3 lateral glabellar furrow' character state. The inferred, but not coded, relationship of these three main forms of S3 furrow is shown in Figure 4.6.

Figure 4.6: Inferred morphological development paths of the S3 glabellar furrow.



where;

0 = Four pairs of lateral glabellar furrows (outgroup).
In **1 to 3** there are only three pairs of lateral glabellar furrows.
1 = S3 furrow is forked adaxially.
2 = Unbranched (single) S3 pair.
3 = Unbranched S3 pair, of 'dog-leg' form; initially directed axially before turning obliquely to the posterior.

5. Number of apodemes in the S3 furrow; '0'=2 apodemes/'1'=1 apodeme.

6. L3 lateral glabellar lobe 20% larger than the other lateral lobes; '0'=yes/'1'=no.

7. Form of the anteromedian complex;
'0'= longitudinal anteromedian furrow.
'1'= median pit in the frontal lobe of the glabella.
'2'= no structures in the anteromesial part of the frontal lobe of the glabella.

It is important to again stress that this placement of morphologies into a sequence does not imply direct linear relationships of descent between successive species or genera displaying successive states of their anteromedian complex. The most 'primitive' form of this character in the Cybelinae is inferred to be longitudinal anteromedian furrow as seen in *Cybelurus* (Figure 4.2). The main reasons for this are as follows:

1. The longitudinal anteromedian furrow with associated median deepening of the anterior border furrow is the earliest form found.

2. Those stratigraphically old species which display a longitudinal anteromedian furrow (longitudinal furrow) also display what are inferred from other outgroup comparisons to be plesiomorphic forms of other characters.

Examples of this include:

A. A bifurcate S3 lateral glabellar furrow. Species displaying other forms of anteromedian complex possess one of the other forms of S3 furrow. In character 4 (Fig. 4.5) the bifurcate form of the S3 furrow was shown to be the most primitive state of that character with the other states being derived from it. This linkage of the longitudinal anteromedian furrow with the most primitive form of lateral glabellar furrow and the linkage of the other forms of anteromedian complex with the more derived forms of S3 furrow implies that the longitudinal anteromedian furrow is the most primitive form of the anteromedian complex.

Some stratigraphically younger taxa displaying a longitudinal anteromedian furrow, such as *Plasiaspis bohemicus* and *Encrinuroides hornei* - the oldest known encrinurine, also display non-bifurcate S3 lateral glabellar furrows. However, both also have a range of other characters, some of which are listed below, whose states are non-plesiomorphic (from outgroup comparison), indicating that it is the S3 furrows which are secondarily derived rather than the anteromedian furrow.

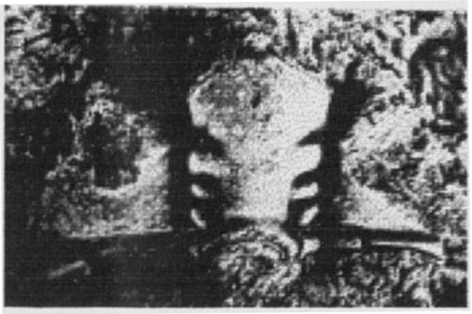
B. Non-tuberculation of the fixed cheek and librigenal border.

C. All of their pygidial pleurae are confluent with continuous axial ring furrows.

There are numerous others which can be read off from the annotated phylogram (Figure 4.16).

3. In some species which possess a longitudinal anteromedian furrow such as *Lyrapyge ebriosus* Fortey, 1980, the posterior part of the anteromedian furrow is gently expanded while the middle section of the furrow is attenuated almost to obsolescence (Figure 4.4). This results in the near isolation of the swollen posterior portion of the longitudinal anteromedian furrow. This posterior portion then greatly resembles a median pit, providing a possible mechanism by which the median pit found in the frontal glabellar lobes of cybeline genera such as *Stiktocybele,* some *Deacybele, Bevanopsis* and *Cybeloides* may be derived. Evidence of this can be seen in Figure 4.7 where the median pit in the frontal lobe of the glabella is clearly seen and the remains of an indentation in the anterior margin of the frontal lobe are visible. It is inferred that a longitudinal furrow once joined these two structures and has become effaced. This is direct evidence of the mode of derivation of the median pit from the anteromedian furrow, indicating that the longitudinal furrow is the more plesiomorphic of the possible states of this character.

Figure 4.7: *Deacybele gracilis* (Nikolaisen, 1961)
(From Owen & Bruton 1980 pl.8, fig.16), x4.5
Note the pit in the anteromesial area of the frontal lobe.

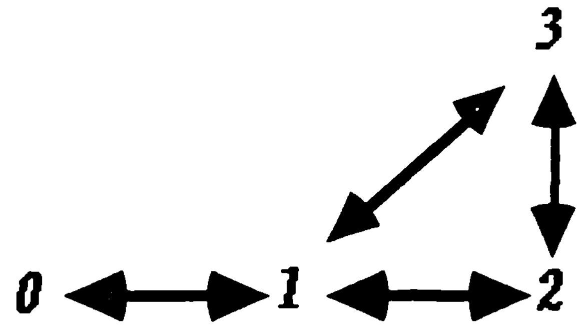


The most primitive ingroup form of this character is the longitudinal anteromedian furrow, from which the median pit in the frontal lobe of the glabella is derived. The final character state, the absence of anteromedian structures on the frontal lobe of the glabella, is seen in two groups, *Atractopyge (sensu stricto)* (see Section 4.5.1.6 and Chapter 6) and the *arenosa* form of *Deacybele* (see Section 4.5.1.12). It is inferred to be the most derived of the various states and to be derived from the median pit. In support of this theory the most primitive, and stratigraphically oldest, members of each of these group display median pit structures which are later lost - e.g. *Atractopyge sinensis* where some individuals display a small median pit (see Zhou *et al.*, 1984), while in other individuals it has been lost, resulting in the absence of anteromedian structures on the frontal lobe of the glabella (see Lu & Chang 1974).

In another possible mechanism of derivation of a frontal lobe which does not display any anteromedian features, the longitudinal anteromesial furrow may simply shallow gradually from the posterior end. Through time it becomes progressively shorter and is eventually lost, rather than the anterior end of the longitudinal anteromedian furrow shallowing to form a median pit before becoming effaced as outlined above. In this case, there will be no taxa displaying a median pit intermediate between the ancestral taxa (which display longitudinal furrows) and the descendent taxa which do not display any anteromedian structures. It is likely, that this latter is the process which acted in the development of the Encrinurinae and *Dindymene*.

The inferred sequence of development of this character can be seen in Figure 4.8

Figure 4.8: Possible pathways of development of the various forms of frontal lobe anteromedian complex characters (not ordered as such in analysis).



0 = Outgroup state.
1 = Longitudinal anteromedian furrow.
2 = Median pit.
3 = No anteromedian structures on the frontal lobe of the glabella.

Assuming that the longitudinal anteromedian furrow with associated anteromedian complex is the primitive form of this character, in the Cybelinae, any ancestral group, or outgroup, must possess some form of precursor anteromedian complex. Many of the taxa suggested as possible outgroups to the Cybelinae (e.g. *Evropeites hyperboreus* Fortey, 1980) display an indentation in the anteromedian area of the frontal lobe of the glabella with an associated median deepening of the anterior border furrow.

8. Triangular depression in the anteromedian area of the frontal lobe; '0'=no/'1'=yes.

The form of the anteromedian complex of *Cybele* comprises a median pit connected to the median deepening of the anterior border furrow by a broad, flat triangular depression. This triangular depression is differentiated from the relict indentation in the anteromesial area of the frontal lobe seen in a number of taxa (see Owen & Tripp, 1988) by its broad, flat base separated from the rest of the frontal lobe by a strong break in slope. In contrast, the indentation in the frontal lobe seen in other taxa is merely a cleft with no strong break in slope. The triangular depression seen in *Cybele* is inferred to have been derived from a form intermediate between the longitudinal anteromedian furrow and proto-median pit (similar to that found in *Lyrapyge*) by expansion of the broad, anterior portion of the furrow and reduction of the mesial part of the longitudinal furrow to give the depressed triangular area. A similar triangular depression is seen in some members of *Cybelurus* such as *Cybelurus expansus*.

9. Frontal lobe of the glabella inflated;
'0'=no/'1'=yes.

10. Furrow between the S1 furrow and the occipital furrow;
'0'=no/'1'=yes.

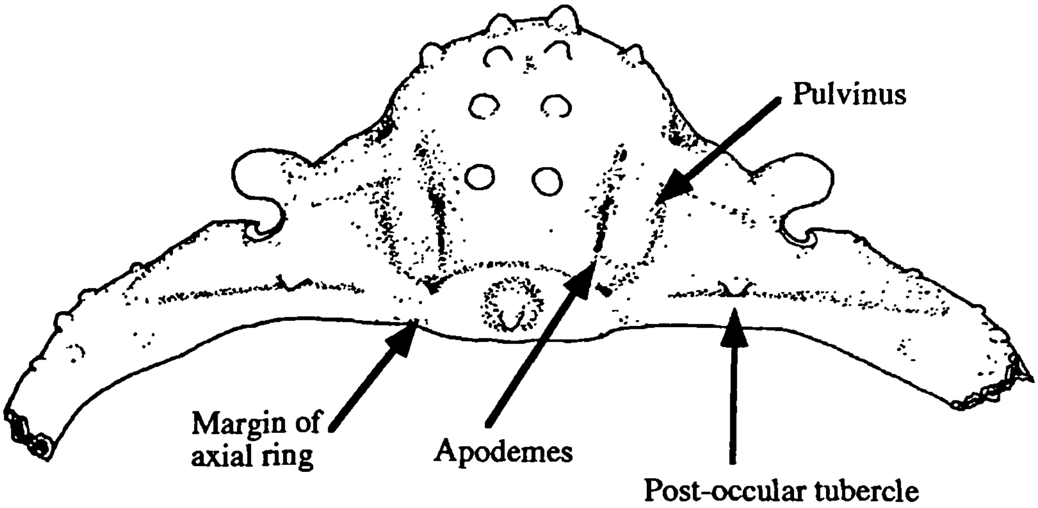
This furrow isolates the distal part of the S1 lateral glabellar lobes and may be linked to the development of the pair of longitudinal furrows seen partially, or completely separating the pulvinus from the rest of the glabella in the genus.

11. Eye ridges present;
'0'=yes, terminating adaxially at the axial furrows.
'1'=yes, adaxially confluent with the frontal lobe.
'2'=yes, adaxially confluent with the S3 lateral glabellar lobes.
'3'=no.

12. Pulvinus present; '0'=no/'1'=yes.

The pulvinus is a structure on the cephalon formed by the amalgamation and inflation of the abaxial portions of the lateral glabellar lobes, with or without the formation of longitudinal furrows separating the pulvinus from the axial region of the glabella (Figure 4.9).

Figure 4.9: *Cybeloides (Cybeloides) virginiensis virginiensis* Cooper, 1953 (from Evitt & Tripp, 1977)



The development of this feature is an autapomorphy of *Cybeloides* and is the only feature differentiating it from *Bevanopsis*. Although in groups such as *Atractopyge, Deacybele* some species display amalgamation of some, or all, of their lateral lobes none of these structures are termed pulvini as they display no inflation.

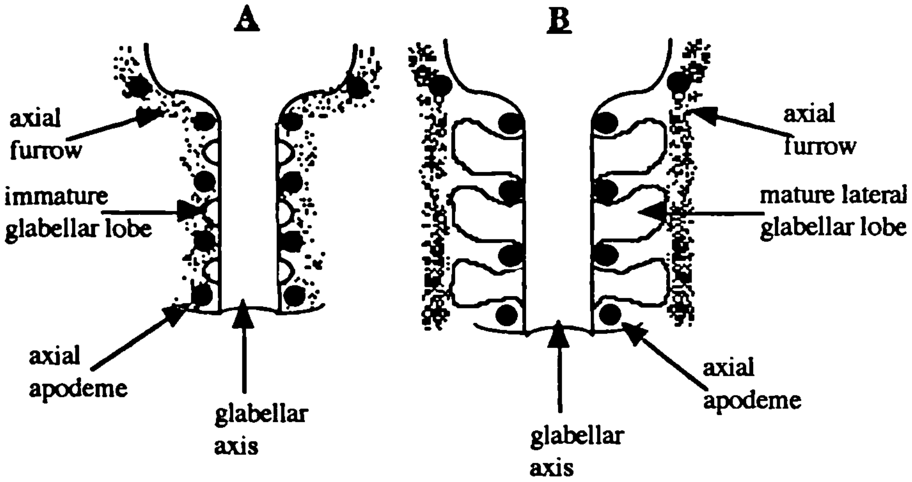
Evitt & Tripp (1977) studied the development of the pulvinus by examining silicified juveniles of *Bevanopsis* and *Cybeloides*. As the formation of a pulvinus is the only feature differentiating these genera any differences in their development should be related to the formation of this structure. By comparing the ontogeny of these two genera, Evitt & Tripp concluded that the development of the pulvinus was linked to the timing of the arrival and persistence of a structure termed the torulus - a swelling during ontogeny of the area around the torular tubercle on the fixigenae.

As members of *Bevanopsis* display no inflation of fused lateral lobes to form a pulvinus and no simple amalgamation of the abaxial portions of the lateral lobes, it would be useful to compare the ontogeny of *Cybeloides* with that of a species of *Atractopyge* or *Deacybele* which do display lobe amalgamation of this type, but no information on the ontogeny of these species is available. Evitt & Tripp (1977) also concluded that the pulvinus is not homologous with the lateral glabellar lobes found in other cybeline genera. They based this conclusion on the belief that the lateral lobes of other genera were purely formed of glabellar material while the pulvinus formed by the incorporation of areas of fixed cheek into the glabellar lobes which, they argued, occurs when the inflated 'torulus' is incorporated into the lateral glabellar lobes. This conclusion implies that the development of the pulvinus differs from the growth of glabellar lobes in other groups because it "occupies areas which were previously fixed cheek.".

This is challenged here on several grounds;

1. From illustrations in Evitt & Tripp (1977), it is clear that the incorporation of the torulus into the lateral glabellar lobes is in fact the amalgamation of the anterior two lateral glabellar lobes.
2. During the development of 'normal' lateral lobes, the lobes begin as small buds situated between the axial apodemes along the glabellar axis (see Fortey 1980 pl. 22 fig. 8 and Fig 4.10 herein) through which the axial furrows pass.

Fig. 4.10: Illustration of lateral axial furrow migration and lobe growth during ontogeny. (Not to scale.)



A = Immature state of glabella. Note the axial apodemes, through which the axial furrows pass, and the bud-like lateral glabellar lobes.

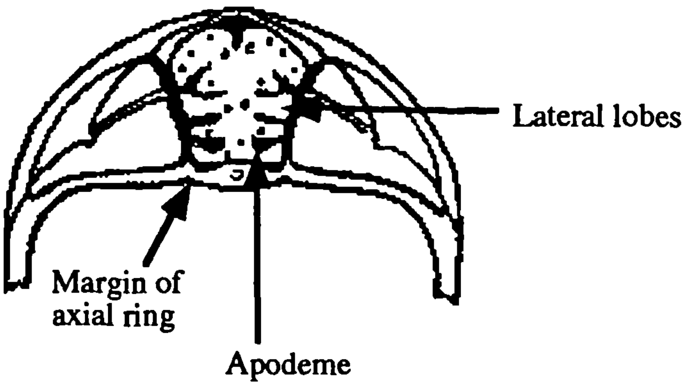
B = Mature state of glabella. The axial furrows no longer pass through the axial apodemes which are now isolated in the adaxial portions of the lateral glabellar furrows.

The area adaxial to this furrow is glabella while the area abaxial to this furrow is fixed cheek. During ontogeny the axial furrows migrate abaxially as the lateral lobes develop, leaving the axial apodemes behind in the adaxial ends of the developing lateral glabellar furrows. This process continues until the adult form is achieved. It can be seen that during ontogeny, areas which were previously termed fixed cheek become occupied by lateral glabellar lobes. This means that strictly, in all of the Cybelinae the lateral glabellar lobes incorporate an element of fixed cheek. These terms which are derived from studying adult specimens are not absolute concepts, but are flexible, during ontogeny.

3. Comparing the relative positions of the axial apodemes, the axial furrows, axial ring and the abaxial margins of the pulvinus in *Cybeloides* with those in groups displaying 'normal' glabellar lobes, such as *Cybelurus*, (Figure 4.11) it is clear that these structures occupy the same positions on the cephalon and are therefore homologous.

4. Many species of *Cybeloides* display both a pulvinus and a distinct tubercle in the same position as the torular tubercle described in Evitt & Tripp (1977) indicating that incorporation of the torular tubercles into the lateral glabellar lobes is not required for the development of a pulvinus.

Figure 4.11: *Cybelurus mirus* (Billings, 1865) (adapted from Whittington, 1965) showing relative position of axial furrows relative to the axial ring and apodemes.



From these points I conclude that:

1. The general terms 'glabella' and 'fixigenae' are not inflexibly applicable throughout ontogeny. This is common to all of the taxa in this study.
2. The pulvinae of *Cybeloides* are exactly equivalent to the lateral lobes of other Cybelinae.
3. The pulvinus is formed by the amalgamation of the lateral glabellar lobes followed by their secondary inflation and does not 'incorporate' any areas of 'fixed cheek'.

13. Fixigenal field tuberculate; '0'= no/'1'= yes.

14. Librigenal field tuberculate; '0'= no/'1'= yes.

15. Librigenal border tuberculate; '0'= no/'1'= yes.

16. Eyes present; '0'= no/1'= yes.

17. Post-ocular tubercles recognisable in mature specimens; '0'= no/'1'= yes.

(See Figure 4.9)This feature seems to be heterochronically controlled. The post-ocular tubercle is one of the suite of tubercles, including torular tubercles, which are prominent during the ontogeny of all Encrinuridae. These tubercles are the first to appear, normally subsiding to a less prominent size or being lost in the later stages of development. The post-ocular tubercle most regularly persists as an obvious, discrete, tubercle into mature specimens. Its retention may be associated with the retention of a generally 'juvenile' morphology into adulthood - most clearly seen in the case of *Libertella corona* Hu, 1971 (See Evitt & Tripp, 1977) indicating that its retention is due to simple paedomorphosis.

More commonly, species in which adults have post-ocular tubercles (such as members of *Cybeloides*) do not display a generally juvenile morphology. In these groups the pattern of heterochrony must be more complex. The complete ontogenetic stages of development of tuberculation on the fields of the fixed cheeks in may be as follows:

A. No tubercles on the fixed cheek.

B. Post-ocular and associated tubercles develop and swell.

C. Reduction in size of post-ocular and associated tubercles.

D. Development of numerous small, scattered, tubercles on the field of the fixed cheek. There is a degree of overlap between stage **C** and **D**.

Figure 4.12; Inferred full sequence of development of fixigenal tubercles.

A→B→C→D

18. Small, out-turned librigenal spine (see Ingham, 1968); '0'= no/'1'= yes.

19. Proportions of the pygidium (excluding free point spines);
'0'= Maximum pygidial width greater than the length of the pygidial axis.
'1'= Pygidial axis longer than the maximum width of the pygidium.

20. Number of pygidial pleurae confluent with in-sequence continuous axial ring furrows - coded as the actual number of confluent pygidial pleurae observed.

21. Pygidial axis tuberculate'; '0'= no/'1'= yes.

22. Pygidial pleural fields strongly pitted; '0'= no/'1'= yes.

This is another relatively subjective character as the pleural fields of the majority of the Cybelinae display some degree of pitting. Code '1' refers to the extreme development of those pits.

23. Width of the pygidial pleural fields;
'0'= pleural fields narrower than the ribs of the pygidial pleurae along their whole length.
'1'= pleural fields broader than the ribs of the pygidial pleurae along their whole length.

24. Paddle shaped pygidial pleurae - i.e. pygidial pleurae broaden into flat fields distally; '0'= no/'1'= yes.

25. Pygidium highly convex longitudinally;
'0'= no (Pygidium longer than maximum dorso-ventral height, excluding free spines).
'1'= yes (Pygidium shorter than maximum dorso-ventral height, excluding free spines).

26. Number of pygidial pleurae present;

This character is of relatively low burden. The 'normal' number of pygidial pleurae within the ingroup is four. It is, however, very common, for taxa to gain or loose a pleural rib; resulting in the multiple derivation of species with three or five pleural ribs on the pygidium. In spite of the 'noise' which this character introduces to the analysis of clade to clade relationships it has been retained as it is a useful diagnostic character, being stable and of high burden within the subclades.

27. Slim, upturned anterior projection on the anterior border of the glabella;
0'= no/'1'= yes.

In addition to this form of anterior projection, other forms are seen in the Cybelinae. *Sinocybele* Sheng, 1974 displays a large, straight, single anterior projection interpreted to be derived from the broadened anterior border of species of *Cybelurus* such as *C. halo* Fortey, 1980. Another form seen is the short, broad, flat, shovel shaped anterior projection of *Atractopyge sinensis* Lu, 1974. This structure is thought to have been derived from the form of anterior border seen in some members of *Cybelurus* such as *Cybelurus mirus* (Billings, 1865), and other taxa such as *Cybele bellatula* Dalman 1827, in which the anterior border bows out mesially.

28. Presence of pleural fields on the pygidium; '0'= no/'1'= yes.
(excluding the anterior pleural field seen on the most anteriorly positioned pair of pygidial pleurae)

29. Number of thoracic segments; '0'=10/'1'=11/'2'=12/'3'=13

30. Macropleural thoracic spine pair present; '0'= no/'1'= yes.

31. Tall mesial spine on the axis of the glabella; '0'= no/'1'= yes.

32. L1 lateral glabellar lobe; '0'= present/'1'= absent.

33. L2 lateral glabellar lobe; '0'= present/'1'= absent.

34. L3 lateral glabellar lobe; '0'= present/'1'= absent.

35. Facial suture positioned adaxially or marginally; '0'/'1'.

36. All pygidial pleurae confluent with in-sequence, continuous, axial ring furrows; '0'= no/'1'= yes.

37. Form of the V-shaped bar on the ventral surface of the pygidium;
'0'= bar begins abruptly.
'1'= bar begins as a continuation of the anterior pleural field.

38. Pair of ridges extending from the frontal lobe to the anterior border;
'0'= no/'1'= yes.

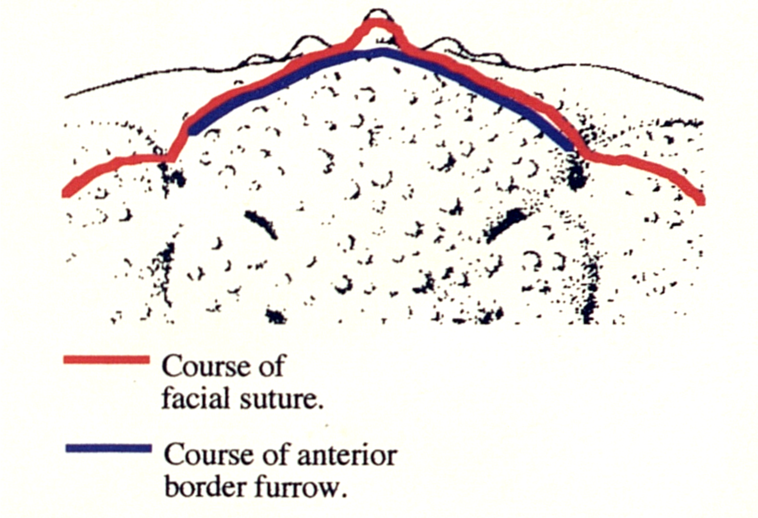
39. Mesial width of anterior border; '0'= constant.
'1'= narrows mesially.
'2'= widens mesially.

40. The facial suture lies along the anterior border furrow for part of its course;
'0'= no/'1'= yes.

In state '1' the posterior, adaxial, migration of the facial suture has progressed to the point where it lies along the anterior border furrow of the cephalon. This results in the formation of a large anterior librigenal field and may obscure the form of the anterior border furrow. In some species, such as

Cybeloides (Paracybeloides) girvanensis this is taken to extremes and has the effect of reducing the anterior border of the cranidium to a single tubercle.

Figure 4.13: Example of migration of the facial suture to a position within the anterior border furrow in *Cybeloides (Paracybeloides) girvanensis* (Adapted from Ingham, 1968)



41. Raised triangular area on the median part of the anterior of the frontal lobe of the glabella ; '0'= no/'1'= yes.

42. Tuberculation of the posterior border of the cephalon; '0'= no/'1'= yes.

43. Tuberculation of the anterior border of the glabella; '0'= no/'1'= yes.

44. Tuberculation of the glabella;
    '0'= no tubercles present on the glabella.
    '1'= tubercles present on the glabella.

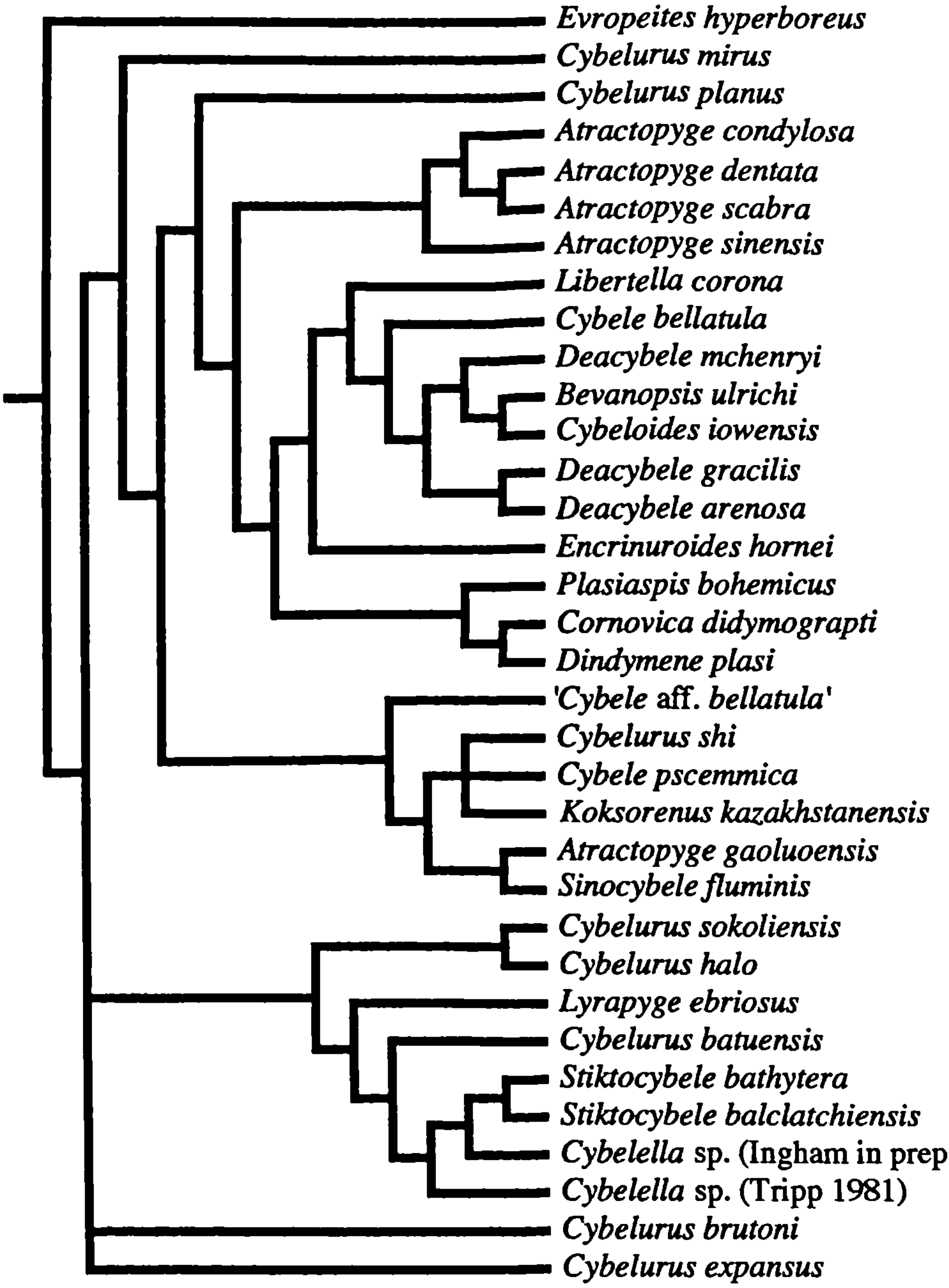
45. Constriction of the pygidial axis posterior to the axial rings which are confluent with the pygidial pleurae;
    '0'= no.
    '1'= yes.

4.4 Initial discussion of the results of the Cybelinae analysis;

4.4.1 Assessment and discussion of the tree resulting from this analysis;

Analysis of this data matrix in PAUP 3.1.1 resulted in the production of one minimum length tree of Length=110, CI=0.582 and RCI=0.482 (See Figure 4.14).

Figure 4.14 Minimum length tree produced by analysis of the Cybelinae data set.

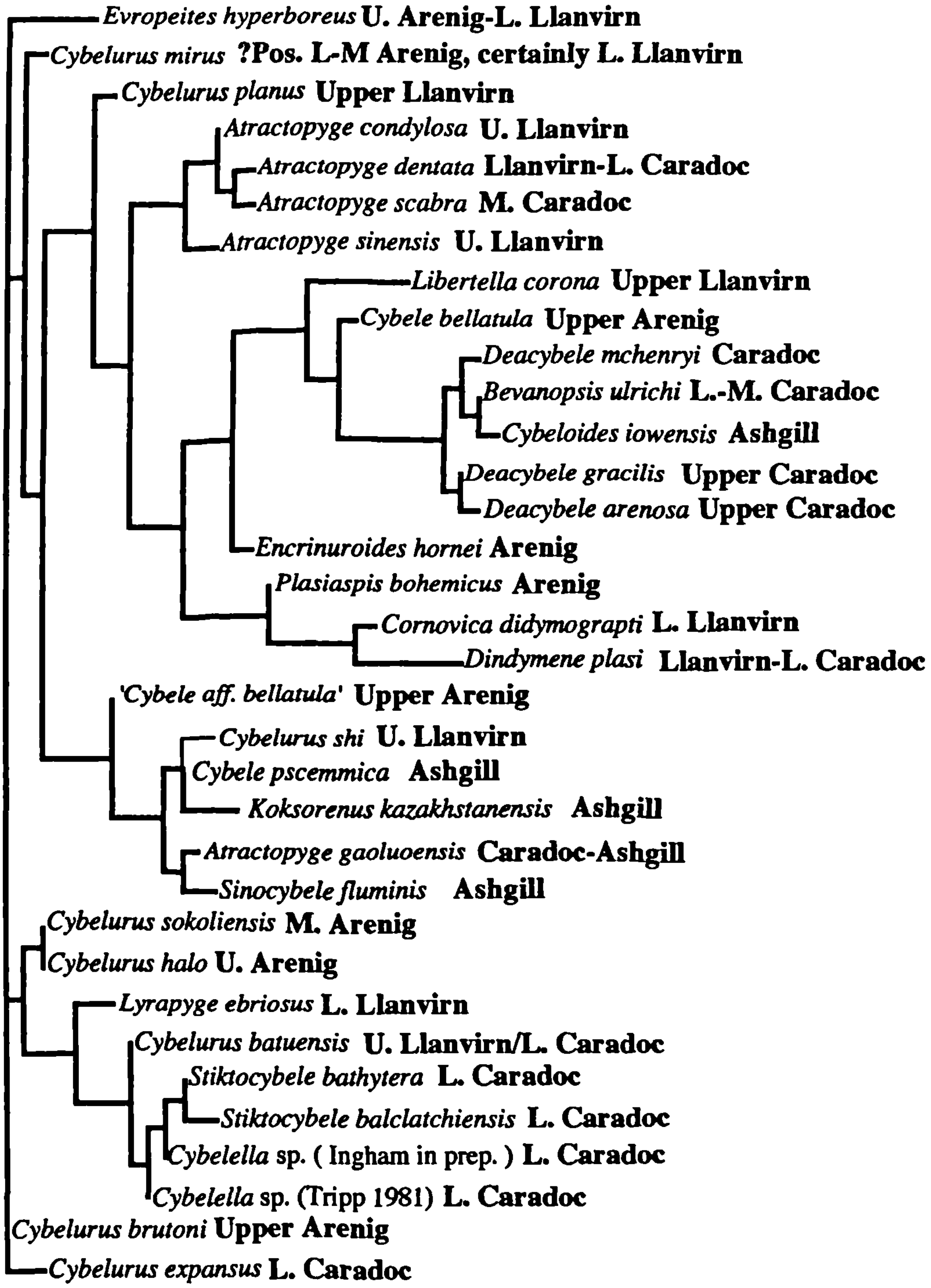


The consistency index is considerably higher than that to be expected from purely random data (Klassen *et al.*, 1991). In addition to the consistency index, an idea of the degree of confidence which can be placed in the phylogeny can be gained by comparing the branching order of the taxa in the cladogram with their stratigraphical ages. Any areas of anomaly, where the branching order conflicts with the stratigraphical order of the taxa must be explained either in terms of a problem with the derived phylogeny, missing taxa ('ghost ranges') or in terms of inaccurate ages assigned to the sediments which contain some of the taxa. The stratigraphy provides an independent data set against which to test the phylogenetic relationships derived by the analysis. As can be seen from Figure 4.15 there is a good match between the branching order of the phylogram and the stratigraphical ages of the taxa. There is a minor conflict between branching position and stratigraphical age at the base of the cladogram where members of *Cybelurus* morphologically similar to *C. planus* (see Section 4.5.1.1a) are marginally younger than taxa immediately above them in the branching sequence. This conflict is reduced to be within the resolution of the age dating of the Otta Conglomerate by consideration of a cephalon from the Elnes Formation ('*Ogygiocaris* Shale') (Llanvirn) of Norway figured by Nikolaisen (1961 pl.2, fig.4), described by him as '*Pliomerops* sp.', and a pygidium, from the Otta Conglomerate (Arenig/Llanvirn), figured by Bruton & Harper (1981 pl.5, fig.14). The probable ocean island, or marginal, environment of the Otta Conglomerate also supports the theory that other, older, taxa of this form existed in similar environments and are yet to be recovered.

The other anomaly between stratigraphical position and branching order is that of *Libertella* Hu, 1971 which is anomalously young for its position in the phylogeny. Its placement low on the cladogram is largely due to its possession of an anterior border furrow which does not shallow abaxially. The juveniles of taxa whose anterior border furrows shallow laterally display anterior border furrows of uniform depth. It is thus unclear whether the stratigraphical anomaly is due to 'ghost taxa' or to the strongly paedomorphic form of *Libertella*.

The branching, and stratigraphical, order of the taxa on the cladogram match closely providing additional confidence in the accuracy of the phylogeny.

Figure 4.15 Minimum length Cybelinae tree represented as a phylogram and annotated with the stratigraphical ages of the taxa.



One of the most striking features of the tree produced by this analysis is the polychotomy at its base. From stratigraphical evidence it is clear that this is partly the result of missing data. This polychotomy also occurs within the 'phylogenetic spread' of the expressly paraphyletic *Cybelurus*. For the majority of the genera included in the Cybelinae analysis, the oldest, relatively complete, species is analysed. Any species which differ from these species in the characters employed are also included. All members *Cybelurus* were included as they display variation in characters which are stable and of high burden higher up the phylogeny. The significance of such variations in character burden is discussed in section 2.1.9.1. The polychotomy within *Cybelurus* is likely to reflect its role in the development of the Encrinuridae. The character changes within this analysis are shown in Figure 4.16. This diagram may be used as a key for the identification of Cybelinae to generic, and in some cases species level.

Figure 4.16: Cladogram for the Cybelinae annotated with all character state changes. Numbers refer to those in the character list.

```
/----------------------------------------------------- E.hyperboreus
|    /------------------------------------------------ Cybelurus mirus
|    |       /---------------------------------------- Cybelurus planus
|    |       |                                 /------ Atractopyge condylosa
|    |       |                            /---36    /- Atractopyge dentata
|    |       |    /----------------------37    \---35- Atractopyge scabra
|    |    /-49    |                       \----------- Atractopyge sinensis
+---55    |  |    |              /-------------------- Libertella corona
|    |    |  |    |              |    /--------------- Cybele bellatula
|    |    |  |    |         /---43    |        /------ Deacybele mchenryi
|    |    |  \---48         |    \---42   /---39    /- Bevanopsis ulrichi
|    |    |       |         |         |   |    \---38- Cybeloides iowensis
|    |    |       |    /---44         \--41         /- Deacybele gracilis
|    \---54       |    |    |             \--------40- Deacybele arenosa
|         |       \---47    \------------------------- Encrinuroides hornei
|         |            |                       /------ Plasiaspis bohemicus
|         |            \----------------------46    /- Cornovica didymograpti
63        |                                    \---45- Dindymene plasi
|         |                               /----------- Cybele aff bellatula
|         |                               |         /- Cybelurus sp.
|         \------------------------------53    /---50- Cybele pscemmica
|                                         |    |    \- K. kazakhstanensis
|                                         \---52    /- A. gaoluoensis
|                                              \---51- Sinocybele fluminis
|                                                   /- C. sokoliensis
|                           /----------------------56- Cybelurus halo
|                           |    /-------------------- Lyrapyge ebriosus
+--------------------------62    |    /--------------- Cybelurus batuensis
|                           \---61    |             /- S.bathytera
|                                \---60        /---57- S.balclatchiensis
|                                     |   /---58------ C. sp(Ingham in prep.)
|                                     \--59----------- Cybelella sp(Tripp)
+----------------------------------------------------- Cybelurus brutoni
\----------------------------------------------------- Cybelurus expansus
```

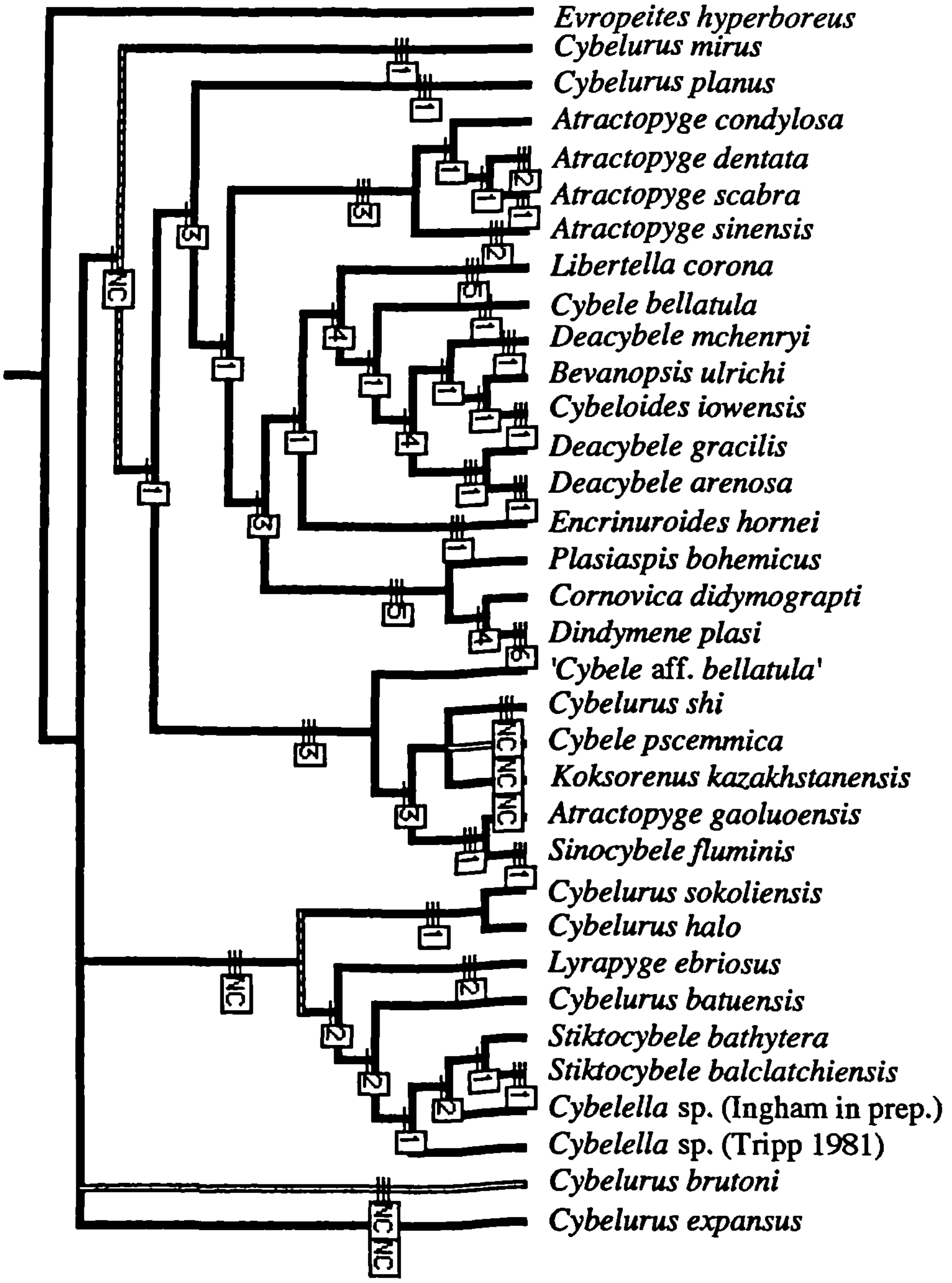
```
Character change lists:

 Character         CI      Steps                  Changes

 1.Facial suture 1.000      1           node_47 0 ==> 1 node_44
   migration                1           node_43 1 ==> 2 Libertella corona
 2.Median          0.500    1           node_48 1 ==> 0 node_37
   deepening in the         1           node_43 1 ==> 0 Libertella corona
   anterior border furrow
 3.Form of the     0.286    1           node_35 0 ==> 1 Atractopyge dentata
   anterior border          1           node_43 0 ==> 1 node_42
   furrow                   1           node_54 0 ==> 1 node_53
                            1           node_52 1 ==> 2 node_50
                            1           node_52 1 ==> 0 node_51
                            1           node_63 0 ==> 1 node_62
                            1           node_61 1 ==> 2 Lyrapyge ebriosus
 4.Form of the     1.000    1      E. hyperboreus 1 ==> 1/3 (within terminal)
   S3 lateral glabella      1           node_48 1 ==> 2 node_47
   furrow                   1           node_61 1 ==> 3 node_60
 5.S3 apodemes     0.500    1           node_35 0 ==> 1 Atractopyge scabra
                            1           node_48 0 ==> 1 node_47
 6.Size of the     0.500    1           node_49 0 ==> 1 node_48
   L3 lateral glabellar     1           node_53 0 ==> 1 node_52
   Lobes.
 7.Presence and    0.286    1           node_48 0 ==> 1 node_37
   form of structures       1           node_36 1 ==> 2 node_35
   in the anteromesial      1           node_44 0 ==> 1 node_43
   area of the frontal      1           node_40 1 ==> 2 Deacybele arenosa
   lobe                     1           node_46 0 ==> 2 node_45
                            1           node_54 0 ==> 1 node_53
                            1           node_60 0 ==> 1 node_59
 8.Triangular      0.333    1           node_49 0 ==> 1 Cybelurus planus
   depression in the        1           node_42 0 ==> 1 Cybele bellatula
   anterior of the          1           node_63 0 ==> 1 Cybelurus expansus
   frontal lobe
 9.Inflation of    0.333    1           node_43 0 ==> 1 Libertella corona
   the anterior of          1           node_46 0 ==> 1 node_45
   the glabella             1           node_50 0 ==> 1 K. kazakhstanensis
10.Presence        1.000    1           node_42 0 ==> 1 node_41
   of furrow from
   the S1 lateral glabellar
   furrows to the occipital
   furrow
11.Eye ridge       1.000    1           node_39 0 ==> 1 node_38
   present                  1           node_47 0 ==> 3 node_46
                            1           node_61 0 ==> 2 node_60
12.Pulvinus        1.000    1           node_38 0 ==> 1 Cybeloides iowensis
   present
13.Fixigenal       0.500    1           node_55 0 ==> 1 node_54
   field tuberculate        1           node_51 1 ==> 0 Sinocybele fluminis
14.Librigenal      0.500    1           node_54 0 ==> 1 node_49
   field tuberculate        1           node_43 1 ==> 0 Libertella corona
15.Librigenal      0.333    1           node_37 0 ==> 1 node_36
   border                   1           node_44 0 ==> 1 node_43
   tuberculate              1           node_46 0 ==> 1 node_45
16.Eyes present 1.000       1           node_47 0 ==> 1 node_46
17.Postoccular     0.500    1           node_48 0 ==> 1 node_47
   tubercles                1           node_41 1 ==> 0 node_40
   present                  1           node_50 0 ==> 1 Cybelurus sp.
                            1 S. balclatchiensis 0 ==> 0/1 (within terminal)
18.Librigenal      1.000    1           node_42 0 ==> 1 node_41
```

Character	**CI**	**Steps**	**Changes**
spines present			
19.Pygidial proportions	1.000	1	node_54 0 ==> 1 node_49
		1	*Cybelurus halo* 0 --> 0/1 (within terminal)
20.Number of pygidial pleurae confluent with axial rings	0.500	1	node_63 4 ==> 5 *E. hyperboreus*
		1	node_37 4 ==> 3 *A. sinensis*
		1	node_44 4 ==> 2 node_43
		1	node_42 2 ==> 1 node_41
		1	node_47 4 ==> 3 node_46
		1	node_45 3 ==> 2 *Dindymene plasi*
		1	node_53 4 ==> 3 node_52
		1	node_59 4 --> 1 node_58
21.Pygidial axis tuberculate	0.500	1	node_54 0 ==> 1 node_49
		1	node_45 1 ==> 0 *Dindymene plasi*
22.Pleural fields on the pygidium pitted	1.000	1	node_62 0 ==> 1 node_61
23.Broad anterior fields on the pygidial pleurae	1.000	1	node_62 0 ==> 1 node_61
24.Paddle shaped pygidial pleurae	1.000	1	node_52 0 ==> 1 node_51
		1	node_63 0 ==> 2 *Cybelurus expansus*
25.Convexity of the pygidium	1.000	1	node_61 0 ==> 1 *Lyrapyge ebriosus*
26.Number of pygidial pleurae	0.375	1	node_63 4 ==> 5 *E. hyperboreus*
		1	node_49 4 --> 3 node_48
		1	node_37 3 --> 4 node_36
		1	node_47 3 --> 5 node_44
		1	node_43 5 ==> 2 *Libertella corona*
		1	node_42 5 --> 4 node_41
		1	node_45 3 ==> 2 *Dindymene plasi*
		1	node_53 4 ==> 3 node_52
27.Upturned projection on the anterior of anterior cranidial border	1.000	1	node_58 0 ==> 1 node_57
28.Pleural fields present	0.333	1	node_63 1 ==> 0 *E. hyperboreus*
		1	node_44 1 ==> 0 *Encrinurus hornei*
		1	node_45 1 ==> 0 *Dindymene plasi*
29.Thoracic segments	0.750	1	node_42 2 --> 1 node_41
		1	node_46 2 --> 0 node_45
		1	node_45 0 --> 1 *C. didymograpti*
		1	node_62 2 --> 3 node_61
30.Macropleural spines present	0.500	1	node_63 1 ==> 0 *E. hyperboreus*
		1	node_47 1 ==> 0 node_46
31.Mesial spine on the glabella	1.000	1	node_46 0 ==> 1 node_45
32.L1 lateral glabellar lobes present.	1.000	1	node_50 1 ==> 0 *K. kazakhstanensis*
33.L2 lateral glabellar lobes present.	0.500	1	node_45 1 ==> 0 *Dindymene plasi*
		1	node_50 1 ==> 0 *K. kazakhstanensis*
34.L3 lateral glabellar lobes present.	0.500	1	node_45 1 ==> 0 *Dindymene plasi*
		1	node_50 1 ==> 0 *K. kazakhstanensis*

Character	CI	Steps	Changes
35.Facial suture marginal	1.000	1	node_47 0 ==> 1 node_46
36.All pygidial pleurae confluent with axial rings	0.333	1	node_47 1 --> 0 node_44
		1	node_43 0 --> 1 *Libertella corona*
		1	node_59 1 ==> 0 node_58
37.Raised rib around the underside of the pygidial margin	1.000	1	node_43 0 --> 1 node_42
38.Ridge between the frontal lobe and the anterior border of the glabella	1.000	1	node_35 0 ==> 1 *Atractopyge dentata*
39.Mesial width of the anterior glabelar border	1.000	1	node_55 0 ==> 1 *Cybelurus mirus*
		1	node_62 0 ==> 2 node_56
		1	*Cybelurus brutoni* 0 --> 02 (within terminal)
40.Facial suture runs along the course of the anterior border furrow for part of its course	1.000	1	node_42 0 ==> 1 node_41
41.Raised triangular section on the anteromesial section of the frontal lobe of the glabella	0.500	1	node_37 0 ==> 1 *A.sinensis*
		1	node_39 0 ==> 1 *Deacybele mchenryi*
42.Posterior border of the glabella tuberculate	1.000	1	node_41 0 ==> 1 node_39
43.Anterior border tuberculate	0.333	1	node_48 0 ==> 1 node_37
		1	node_44 0 ==> 1 node_43
		1	node_54 0 ==> 1 node_53
44.Glabella tuberculate	0.500	1	node_63 0 ==> 1 node_55
		1	node_57 0 ==> 1 *S. Balclatchiensis*
45.Narrow constriction in the pygidial axis immediately behind the posterior confluent pygidial pleurae/axial ring set	0.500	1	node_54 0 ==> 1 node_53
		1	node_50 1 ==> 0 *Cybelurus* sp

The number of unambiguous character changes along each branch may be read off Figure 4.17. As can be seen there is good character support for this phylogeny with most nodes displaying at least one, and usually more, character changes. The obvious exceptions to this are the polychotomous nodes which are supported by no unambiguous character state changes.

Figure 4.17: Cladogram for the Cybelinae annotated with the number of unambiguous character changes occurring along each branch, those with no unambiguous changes are labelled 'N/C'.



4.4.2 Discussion of the results of the Cybelinae analysis with reference to Edgecombe *et al.* (1988)

Edgecombe *et al.* (1988) concluded that, on the basis of ontogenetic evidence, the 'high clade' Cybelinae, including *Deacybele, Bevanopsis* and *Cybeloides* were more closely related to the Encrinurinae than to the 'low clade' Cybelinae, including such taxa as *Cybelurus* and *Lyrapyge*. This inference is supported by this analysis, which shows that the 'high clade' Cybelinae and Encrinurinae are sister clades. Edgecombe *et al.* also intimated that *Libertella,* should be included within the Encrinuridae and followed Fortey & Owen's (1987) inclusion of the Dindymeninae within the Encrinuridae. Both of these inferences are shown to be accurate by this analysis. Time has prevented my exploration of the relationship of the staurocephalines, suggested on the basis of ontogenetic characters to be closely related to the Cybelinae by Edgecombe *et al.* but it is likely that further study of these taxa may prove to be fruitful.

The majority of the characters utilised by Edgecombe *et al.* (1988) were not included in this analysis due to a lack of good specimens or illustrations of immature members of the majority of the taxa studied. It is thus extremely pleasing that the results of this analysis, which utilises only characters from mature adults, so closely mirror those derived by Edgecombe *et al.*, from an analysis made largely using developmental characters.

Edgecombe *et al.*'s (1988) suggestion that the Cybelinae is paraphyletic and requires revision is accurate but this revision is difficult to effect due to the paucity of sharply differentiated break points in the phylogeny of the Family Encrinuridae.

The Cybelinae may well prove to be a particularly useful group for comparisons of ontogenetic development and evolutionary history as most of the variation required for evolutionary change is supplied via heterochronic alterations in the timing of development of the Cybelinae.

4.5 Revision of the systematics of the Subfamily Cybelinae Holliday, 1942

4.5.1 Diagnosis of the genera included in this analysis

The majority of the genera originally assigned to the Cybelinae are retained on the basis of this analysis and are re-diagnosed here. There are also a number of genera whose taxonomic assignments have been somewhat uncertain which are here re-assigned to the Cybelinae.

4.5.1.1 *Cybelurus* Levitskiy, 1962

Type species - *Cybelurus planus* Levitskiy, 1962 = (*Cybele planifrons*; Weber, 1948; Semenova, 1960.). From the Burgryshikhinsk horizon (U. Llanvirn) of the Altai region of the former USSR.

It can be seen from the results of this analysis that the genus *Cybelurus* Levitskiy, 1962 is paraphyletic. As this paraphyletic group is not formed of morphologically homogeneous/similar taxa there is no advantage in uniting these taxa within a single genus, linked as they are purely by the retention of plesiomorphic characters. Instead I propose to split the expressly paraphyletic *Cybelurus* into two groups: *Cybelurus (sensu stricto)* and the *Sinocybele* plexus, although *Cybelurus (sensu stricto)* as here defined is expressly paraphyletic, which is less than ideal

5.1.1.a *Cybelurus (sensu stricto)* Levitskiy 1962

Cybelurus is retained as a genus and may be diagnosed on the following characters;

Diagnosis of *Cybelurus* :

Glabella expands forwards and may be either tuberculate or not; S3 lateral glabellar furrow pair bifurcate; Longitudinal anteromedian furrow in the frontal lobe of the glabella; Anterior border furrow of uniform depth, except for median deepening; Anterior cranidial border of variable width, non-tuberculate; Fixigenal field non-tuberculate (except *C. planus*); Eye ridge present, terminating adaxially at the axial furrows bordering the glabella; Librigenal fields non-tuberculate (except *C. planus*); Librigenal border non-tuberculate; Posterior cranidial border non-tuberculate; Thorax of twelve thoracic segments, the sixth macropleural; Pygidium wider than long, comprising four pygidial pleurae, all of which are confluent with continuous axial rings; Pygidial axis may be tuberculate or non tuberculate.

Species included in *Cybelurus (sensu stricto)*:

Cybelurus altaicus	Levitskiy, 1962
Cybelurus brutoni	Fortey, 1980
Cybelurus expansus	(Reed, 1944)
Cybelurus mira	(Billings, 1865)
= *Pliomerops sp.*	of Nikolaisen, 1961
= *Cybelurus* cf. *mirus*	of Wandås, 1983
Cybelurus planus	Levitskiy, 1962

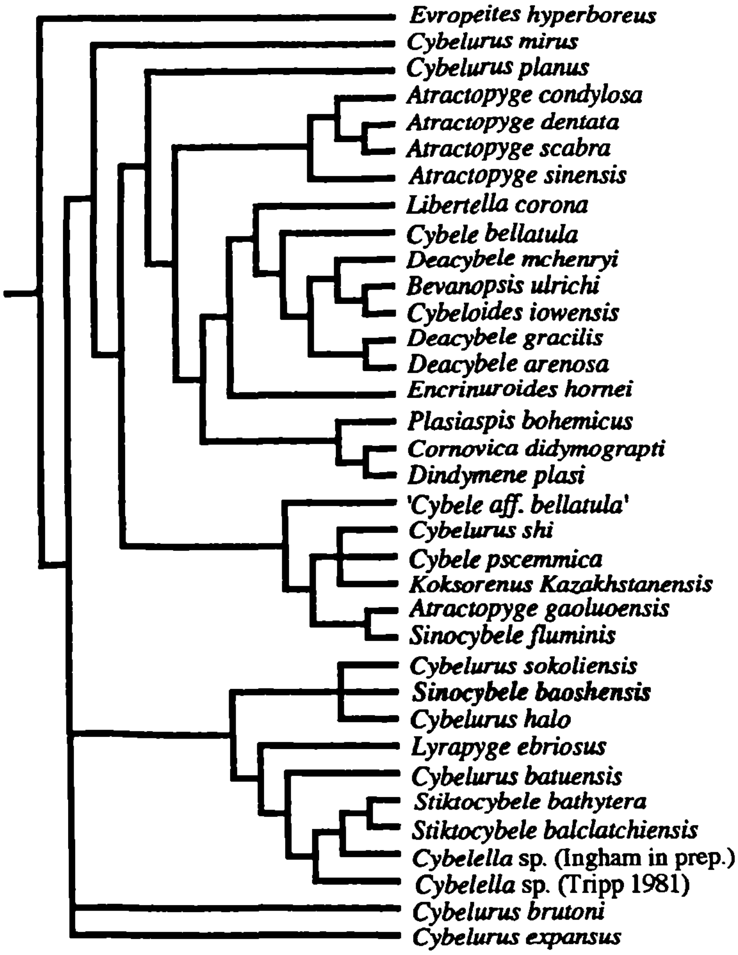
4.5.1.1b *Sinocybele* plexus

The second group of species which have been assigned to *Cybelurus* appears on the cladogram to be monophyletic, but is likely to be polyphyletic (see section 4.6). because of the close relationship of these species to each other and the close relationship and similar morphology of their respective ancestors it is likely that these taxa were derived from a morphologically conservative stock which was wide ranging, both geographically and temporally. They are retained within one group as there are no available characters with which to separate their origins, apart from the apparent stratigraphical anomaly of their ages.

In addition to those characters which diagnose *Cybelurus*, these taxa are united by their possession of a laterally shallowing anterior border furrow and of an anterior border which broadens mesially. This broadening of the anterior border extends to the full width of the mesial part of the anterior border which is positioned diametrically opposite the anterior edge of the frontal lobe of the glabella. As such it is differentiated from the anterior projection seen in some members of *Stiktocybele* which is upturned and has a much narrower base. The broadening of the mesial

The type material ascribed to *Sinocybele baoshensis* is very incomplete and I am reluctant to endorse a monospecific genus based on such fragmentary material. It does, however, seem reasonable to provisionally regard the group within which this taxon is placed as the '*Sinocybele* plexus' and to reserve judgement on the retention of the genus *Sinocybele* until better material is recovered.

Figure 4.18: Single minimum length tree resulting from analysis of the Cybelinae data set with the addition of *Sinocybele baoshensis* Sheng, 1974



The coding of the Llanvirn species *Cybelurus occidentalis* Dean, 1975 from unnamed Lower Llanvirn carbonates in the North-western Yukon region of Canada did not differ from that of *Cybelurus halo* Fortey, 1980 and comparison of the original material of the two species may show that the two species are conspecific.

Miracybele ? sp. of Ross (1967) and *Miracybele ?* sp. of Ross (1972) are both synonymised with *C. halo* herein as I am unable to differentiate any features in which they vary sufficiently from those of *C. halo* to exclude them from that species.

Species included in the *Sinocybele* plexus:

Sinocybele baoshensis	Sheng, 1974
Sinocybele grandispina	Xiang *et al.*, 1974 (Not examined)
Cybelurus halo	Fortey, 1980
Cybelurus occidentalis	Dean, 1975
Cybelurus sokoliensis	Burskyi, 1970

4.5.1.2 *Lyrapyge* Fortey, 1980

Type species : *Lyrapyge ebriosus* Fortey, 1980 of the Valhallfonna Formation (Middle Arenig), Spitsbergen.

Discussion of Lyrapyge.

Fortey (1980 p. 99) differentiated *Lyrapyge* from other cybelines primarily on the basis of its complete incorporation of the anterior border into the glabella and broad pygidium with wide fields and raised ribs ending in long upward turned free spines. Unfortunately, apart from the upward turned free spines, none of these characters are unique to *Lyrapyge*. Species in a range of other genera also possess some, or all, of these features; the genus *Koksorenus* Koroleva, 1992 and the, as yet unnamed, group of cybelines found in Kazakhstan and South China represented by *Lyrapyge? gaoluoensis* (Zhou *et al.*, 1977) also display an anterior border which is completely incorporated into the glabella, the whole of which is inflated. However, these groups do not have many of the other basic features of *Lyrapyge* such as the longitudinal anteromedian furrow, the forked S3 lateral glabellar furrows and the highly convex pygidium composed of uniformly broad pleural fields and narrow, raised pygidial ribs. These taxa instead have a median pit in the frontal lobe of the glabella and a vestigially forked S3 furrow pair. In addition, the pygidia of the group have only three pleurae (see diagnosis below). The general morphology of the pygidium of *Lyrapyge* is also not unique. Members of the genus *Stiktocybele* also have pygidia with narrow, raised pleural ribs, probably terminating in free spines, which separate broad flat pleural fields. The pygidia of *Stiktocybele* only differ markedly in the degree of their curvature, being almost flat while those of *Lyrapyge* are highly convex. It can be seen from the phylogeny derived here that the similarity in morphology of these taxa is due to their development from a common ancestor.

It is possible to see how the frontal lobe structure of *Lyrapyge* could have developed from an ancestor similar to that of *Stiktocybele* (and similar to *Cybelurus sokoliensis* although lacking the increased mesial width of the anterior border seen in *sokoliensis*) by further shallowing of the abaxial portions of the anterior border furrow resulting in the incorporation of the anterior border into the glabella. This incorporation was followed by a reduction in the sagittal length of the incorporated section of anterior border and by inflation of the frontal lobe.

The constriction of the central section of the longitudinal anteromedian furrow commonly leads to the near - isolation of the gently swollen posterior end of the anteromedian furrow, resulting in a morphology approaching that of the median pit seen in many Cybelinae; illustrating one of the potential mechanisms of formation of the median pit structures.

In short, although possessing a unique combination of characters, *Lyrapyge* has no unique apomorphies except the extreme convexity of its pygidium which is a somewhat subjective character on which to define it as a separate genus. In spite of this, the unique combination of characters found in *Lyrapyge* are here used to support its retention as a valid genus. It is worth mentioning that the closeness of the relationship of *Lyrapyge* to *Cybelurus* noted by Fortey (1980) is due to the retention by *Lyrapyge* of a number of plesiomorphic characters which signpost its development from *Cybelurus*. Fortey (1980, p100) noted that the pygidium assigned to *Dindymene(?) arenosa* by Lisogor (1965) and the incomplete cranidium assigned to *Cybele planifrons* by Weber (1948) occurred in similar areas and at similar horizons. He speculated that this pygidium and cranidium may have belonged to members of the same species. Although Weber's line drawing shows *Cybele planifrons* as having a complete anterior border furrow, the photograph in his plate 29, fig. 20, shows the anterior border furrow dying out abaxially. The general form of the cephalon of this species is very similar to that of *Cybelurus sokoliensis*, Burskyi, 1970 from Novaya Zemlya and is not inflated after the fashion of *Lyrapyge* although the abaxial effacement of the anterior border furrow appears to be almost complete as in *Lyrapyge.* The isolation of the S3 lateral glabellar furrows seen in *planifrons* is also seen in specimens of both *Lyrapyge* and taxa assigned to species similar in morphology to *sokoliensis* such as *Cybelurus halo.* It is unclear whether *Dindymene (?) arenosa* Lisogor, 1965 and *Cybele planifrons* Weber, 1948 belong to the same species. If they do, the morphology of this species would be close to that of the ancestor of both *Lyrapyge* and *Stiktocybele* Ingham & Tripp, 1991 and *planifrons* a sister taxon to *Cybelurus batuensis* Levitskiy, 1962.

Diagnosis of *Lyrapyge.*

The frontal lobe of the glabella is highly convex bearing an anteromedian complex composed of a longitudinal anteromedian furrow extending rearwards from a median deepening in the anterior border furrow, bisecting the frontal lobe of the glabella; The central section of the anteromedian furrow is constricted and the posterior end is gently swollen; S3 lateral glabellar furrow bifurcate adaxially and separate large, well formed lateral glabellar lobes; The relict adaxial anterior border is reduced to a narrow ledge; Anterior and posterior borders of the cranidium are devoid of tubercles, as are the glabella and free cheeks; Anterior border furrow shallowing to obsolescence abaxially resulting in incorporation of the anterior border into the glabella; Pygidium broad with wide pleural fields, strongly convex and crossed by stout, raised ribs which distally converge rearwards and project beyond the pygidial margin as upward turned spines; Four pygidial pleurae, all of which are confluent with continuous axial rings and none of which are tuberculate.

Species to be included in *Lyrapyge* :

Cybele planifrons	Weber (1948). Cranidium only. Not coded. Included by Fortey (1980)
Dindymene (?) arenosa	Lisogor, 1965 Pygidium only. Not coded. Included by Fortey (1980)
Lyrapyge ebriosus	Fortey, 1980

Possibly also ascribable to *Lyrapyge* :

'Atractopyge gaoluoensis ?'	of Lu, 1981

This pygidium does not belong to *gaoluoensis* and may belong to *Lyrapyge* .

4.5.1.3. *Stiktocybele.* Ingham & Tripp, 1991;

Type species: *Stiktocybele bathytera* Ingham & Tripp, 1991 from the Doularg Formation (Lower Caradoc, *gracilis* Zone) of Girvan, Scotland.

Stiktocybele is diagnosed on the following primary features:

The glabella, fixigenae and librigenae generally non-tuberculate; or tubercles developed are small and indistinct; Median pit in the frontal lobe of the glabella and associated median deepening in the anterior border furrow; S3 lateral glabellar furrow pairs are unbranched and directed obliquely with their adaxial ends to the posterior; These lateral glabellar furrows are of sigmoidal form in stratigraphically old members of this genus, straight and unbranched in younger, undescribed, taxa from Pomeroy collected by Dr Ingham. S3 furrow pairs contain supplementary apodemes except in some of the stratigraphically younger taxa; Lateral glabellar lobes large and well formed with the L1 lobes always the smallest; Anterior border furrow shallows abaxially; Two ridges extending from the frontal lobe to the facial suture, which cuts the cranidial border abaxially resulting in the absence of any anterior librigenal fields; In members of *Stiktocybele (sensu stricto)*, the median part of the anterior border is produced into a short, blunt, upturned spine with a rather globular end; The adaxial end of the eye ridge is positioned level with either the L3 glabellar lobe or the S3 lateral glabellar furrow, crosses the axial furrow and is confluent with the L3 glabellar lobe; The anterior and posterior cranidial borders are non-tuberculate; Thirteen thoracic segments, the seventh of which is macropleural; Pygidium of low convexity, broader than long with wide, depressed, pitted pleural fields which are crossed by narrow raised pygidial ribs extending beyond the edge of the pygidial shield as sharp free spines; Four pygidial pleurae, only one of which is confluent with a continuous axial ring furrow.

Discussion of *Stiktocybele*;

Stiktocybele balclatchiensis has been coded as variably displaying post-ocular tubercles, as these are seen on *Cybele (Cybelina) monoceras* Reed (1931 pl.5 fig.1) but not on other specimens assigned to this species The presence of post-ocular tubercles in the Reed's small specimen may be due to its being immature.

The morphology of basal members of *Stiktocybele* is close to that of the ancestors of this entire subclade, including *Lyrapyge*. The development of the distinctive broad, flat, anterior fields on the pygidial pleurae of *Stiktocybele* from pygidia such as those of *Cybelurus* may be seen in basal *Stiktocybele* species such as *Cybelella* sp of Tripp *et al.* (1981), the anterior pleural fields of which, while broad, flat and pitted, are intermediate in breadth between those of *Cybelurus* and those of more derived *Stiktocybele*. Thus a smooth path of development of this feature can be seen.

The gradual acquisition of characters which result in the development of *Stiktocybele (sensu stricto)* is well illustrated by this analysis (see Figure 4.16). As usual, the basal taxa of this subclade which display some, but not all, of the diagnostic characters are included as *sensu lato* members of the genus which they base. The continual development of new features in the stratigraphically younger taxa of the undescribed Pomeroy material illustrates that members this genus do not exhibit stasis but continued to develop.

Species included in *Stiktocybele* :

Stiktocybele balclatchiensis	(Reed, 1914)
Cybele (Cybelina) monoceras	Reed, 1931
Junior synonym of *S. balclatchiensis*	(Tripp 1980, Ingham & Tripp, 1991).
Stiktocybele bathytera	Ingham & Tripp, 1991

There is further material which forms part of unpublished material from the Bardahessiagh Formation of Pomeroy, County Tyrone collected by Dr K. Ingham which is to be included in *Stiktocybele* upon its description.

'Stem' taxa regarded as *Stiktocybele (sensu lato)*

Cybelurus batuensis	Levitskiy, 1962
Cybelella sp.	Tripp, 1981
Cybelella sp.	Tripp, 1976
Cybeline indet.	Romano & Owen (1993 pl. 4, fig. 7)

4.5.1.4 The *gaoluoensis* group

These taxa are all closely related to each other and form a monophyletic clade with *Koksorenus* Koroleva, 1992 from which they are readily distinguished.

Atractopyge? gaoluoensis	Zhou *et al.*, 1977
Cybele aff. *bellatula*'	Ancygin, 1973
Cybele pscemmica	Abdullaev, 1970
Cybelurus? shi	Zhou *et al.*, 1984
Sinocybele? fluminis	Dean, 1988

All of these taxa are linked by the morphology of their pygidia, which have three pleurae which are contiguous with continuous axial furrows and display a constriction in their pygidial axis immediately posterior to the hindmost of the axial rings which are confluent with the pygidial pleurae.

Sinocybele? fluminis and *Atractopyge? gaoluoensis* are linked by their 'paddle shaped' pygidial pleurae and may have developed independently, from a common ancestor, from the rest of the clade under discussion, as suggested by the anterior border furrow which does not shallow abaxially displayed by *fluminis*. This interpretation is not favoured by the cladistic analysis which shows the anterior border furrow form of *fluminis* as being a secondary reversion from the abaxially shallowing form of *gaoluoensis*. In spite of the strong similarities of the taxa, the material is too poor to allow the erection of a coherent genus concept accommodate them. In addition, any genus which is erected will be expressly paraphyletic as it is from this plexus that *Koksorenus* Koroleva, 1992 developed. It is not possible to expand the concept of *Koksorenus* to include these taxa as, although they are basal to the *Koksorenus* subclade, they do not display any of the primary apomorphies upon which *Koksorenus* is diagnosed. Furthermore, members of *Koksorenus* do not display the paddle shaped pygidial pleurae which distinguish this subclade.

I propose to erect a new genus 'Gen. Nov' to include *Atractopyge? gaoluoensis* (Zhou *et al.*, 1977) and *Sinocybele fluminis* of Dean, 1988 and to regard *Cybele* aff. *bellatula* 'of Ancygin (1973), *Cybelurus? shi* Zhou *et al.* (1984) and *Cybele pscemmica* Abdullaev (in Abdullaev & Khaletskaya, 1970) as members of a *Koksorenus* plexus until the recovery of further material allows their division into useful genera.

Gen. Nov. herein:

Type species : *Atractopyge? gaoluoensis* (Zhou *et al.*, 1977)

The best material upon which to diagnose the species '*gaoluoensis*' was figured by Tripp *et al.* (1989 fig. 16 a, b, c, d, e, f, g, j, m, n, fig. 17 a, i, j, o, u). who tentatively re-assigned it to *Lyrapyge* Fortey, 1980. This re-assignment is not supported by this analysis.

The frontal lobe morphology of *gaoluoensis* is unusual as it has a somewhat inflated frontal glabellar lobe which is separated from the anterior border by an anterior border furrow of uniform depth (not shallowing abaxially). This feature is well illustrated in Tripp *et al.* (1989 fig. 16 b, c, e, f, m, n and 17 a) and differs strongly from the condition in *Lyrapyge* Fortey, 1980 in which the anterior border furrow is effaced abaxially resulting in inclusion of the abaxial portions of the anterior border into the frontal lobe. In its retention of a separate anterior border and frontal lobe, *gaoluoensis* is most similar to *Dindymene* Hawle & Corda, 1847 although the two are not closely related. The juvenile illustrated in Tripp *et al.* (1989, fig. 16 b, c, f) very strongly resembles mature specimens of *Koksorenus* Koroleva, 1992 with anterior border furrows which shallow strongly abaxially.

Taxa assigned to this group are found in the Ashgill of Sort Dere, Zap Valley of Turkey while *gaoluoensis* is widespread in both North and South China, being known from the Lower Ashgill Linxiang Formation of Hupei, South China (Zhou *et al.*, 1977 and Xiang & Ji, 1986), the Caradoc Chedao Formation of Chedao, Gansu Province, N. China (Zhou & Dean 1986), the Ashgill Pagoda Formation of South China (Ji, 1986) and the Early Ashgill Tangtou Formation of South China

'Gen Nov ' is diagnosed on the following characters:

Frontal lobe of glabella tends towards inflation, is tuberculate and displays a median pit; Glabellar axis tubercles may be paired; Lateral glabellar furrows short, S3 forked and may be isolated; Anterior border furrow, continuous abaxially, median depression present; Anterior border continuous and tuberculate; Lateral glabellar lobes well formed; Librigenal fields non-tuberculate; Librigenal and posterior cranidial borders non-tuberculate; Pygidium wider than long; Pygidial axis non-tuberculate and constricted behind the third axial ring; Three 'paddle shaped' pygidial pleurae, all of which are contiguous with continuous axial rings and which have anterior fields.

Species included in 'Gen Nov':

Sinocybele fluminis	(Dean, 1988)
Atractopyge ? gaoluoensis	(Zhou *et al.*, 1977)

4.5.1.5 *Koksorenus* Koroleva, 1992;

Type species : *K. kazakhstanensis* Koroleva, 1992. From the Upper Ordovician deposits of Mailisor Lake in Kazakhstan.

Koksorenus is diagnosed on the following features:

Glabellar frontal lobe and axis inflated resulting in *Koksorenus* assuming a phacomorph morphology; Median pit in the frontal glabellar lobe; Lateral glabellar lobes reduced to rounded stubs and as a result the posterior and anterior branches of the S3 furrow both reach the axial furrow which has the effect of apparently splitting the forked S3 into an unbranched S3 furrow with an unbranched S4 furrow to the anterior; Mesial deepening of the anterior border furrow; Tuberculate anterior border of constant width incorporated into the glabella by effacement of the lateral parts of the anterior border furrow and displaying a small mesial projection; Glabella displays paired tubercles; Fixigenal fields tuberculate, postocular tubercles not enlarged. Posterior border of the cranidium, librigenal fields and librigenal borders non-tuberculate; Twelve thoracic segments, the sixth of which is macropleural; Pygidium wider than long, Axis of the pygidium is non-tuberculate and constricted immediately to the posterior of the third axial ring; Three pygidial pleurae, all of which are contiguous with continuous axial rings;.

Discussion of *Koksorenus* :

Cybele pscemmica Abdullaev, 1970 and the juvenile *gaoluoensis* illustrated in Tripp *et al.* (1989, fig. 16 b, c, f) very strongly resemble mature specimens of *Koksorenus*, displaying the same gross morphology with anterior border furrows which shallow abaxially. It thus seems likely that *Koksorenus* developed by paedomorphosis from some member of the '*gaoluoensis* group', probably a close relative of *Cybele pscemmica* as the pygidium of *Koksorenus* is similar to that of *pscemmica*, lacking the 'paddle-shaped' pleurae of *gaoluoensis*. This paedomorphosis resulted in the large frontal lobe area and in the minimised lateral glabellar lobes. The minimisation of the lateral lobes has resulted in the forked S3 furrow resembling the primitive form of an S3 furrow with an S4 furrow to the anterior. The development of this group by paedomorphosis accords well with the small size of the individuals.

Species included in this genus :

Koksorenus kassini	Koroleva, 1992
Koksorenus kazakhstanensis	Koroleva, 1992

4.5.1.6 *Atractopyge* Hawle & Corda, 1847

Type species: *Calymene verrucosa* Dalman, 1827, probably from the Crûg
Limestone (Ashgill) of S. Wales. (See Dean, 1974 p. 97-98,
Price 1984, p. 103)

The detailed relationships of the species assigned to *Atractopyge* are explored in a separate cladistic analysis (see chapter 5). As a result of this, discussion here is restricted to the relationship of *Atractopyge* as a whole to other taxa and to the development and differentiation of *Atractopyge* from its ancestors.

Atractopyge is diagnosed on the following features:

No anteromedian complex in the frontal lobe of the glabella or median deepening in the anterior border furrow; S3 lateral glabellar furrow pairs are forked; These forked S3 furrows display a strong, transversely directed furrow which has an anterior branch adaxially; The lateral lobes of some species may display some coalescence abaxially; Anterior border furrow of continuous depth, apart from the *A. dentata* subclade in which it shallows abaxially; The front of the anterior border of the glabella is multiply tuberculate or spinose; The glabella, fixigenal field and librigenal field are tuberculate, although the post-ocular tubercles are noticeably enlarged or distinguishable from other fixigenal tubercles; The librigenal border is tuberculate except for the species *A. sinensis* Lu, 1974 which may be independently derived (see discussion) and is certainly the most 'primitive' of the species of *Atractopyge;* Pygidium longer than wide; Four pygidial pleurae, all confluent with continuous axial ring furrows; The axis of the pygidium is tuberculate.

Species re - assigned.

Atractopyge tramorensis (Reed, 1895) has been re-assigned from *Cybele.* Its anterior projection displays five longitudinal ridges, and thus Reed (1895) considered it to be descended from *Atractopyge coronata* (Schmidt, 1881) which has five projecting spines on its anterior margin. *Atractopyge coronata* is likely to be closely related to *Atractopyge rex* (Nieszkowski, 1852) which possesses five tubercles on the anterior border of the cranidium (see Chapter 5).

Atractopyge gaoluoensis (Zhou *et al.*, 1977) has been re - assigned to a new, as yet un - named genus as a result of this analysis (see Section 5.1.4).

Atractopyge sinensis Lu, 1974 was re-assigned to *Cybelurus? sinensis* by Zhou *et al.* (1984) on the basis of material from the Shihtzupu Formation (Upper Llanvirn) in China. Its assignment to *Atractopyge* is supported by this analysis, although it is probable that it was derived independently to the other species of *Atractopyge* from a similar common ancestor (see Chapter 5), probably a geographically widespread form such as *Cybelurus.* This inference of the independent derivation of *sinensis* is supported by its considerable number of autapomorphies and by the apparently anomalous occurrence of this species in China while the rest of the early species of *Atractopyge* are found in Laurentia and Baltica.

Discussion of *Atractopyge sinensis*;

Atractopyge sinensis displays the following features which are unique (or very rare) within *Atractopyge*:

1. Anteromedian area gently swollen.
2. Median pit in the frontal lobe of the glabella.
3. Anterior border furrow shallow, broad and continuous with no median deepening
4. The abaxial anterior edge of each S3 furrows displays a nick.
5. Three pygidial pleurae, all confluent with continuous axial ring furrows.

The lectotype (see Lu, 1974) displays all of these features except the median pit in the frontal lobe of the glabella and the nick in the S3 furrows is much less pronounced. Zhou *et al.* (1984) argued that the variation from the type in the features of specimens in their material fell within an acceptable range for inclusion within the same species as *Atractopyge sinensis* but that *sinensis* should be tentatively re-assigned to *Cybelurus*.

I agree that these minor variations from the type fall within acceptable bounds for inclusion of the material of Zhou *et al.* (1984) within *Atractopyge sinensis*, particularly given the differing modes of preservation of the two sets of material. The proposed reassignment of *sinensis* to *Cybelurus* suggested by Zhou *et al.* is an interesting point. *A. sinensis* clearly differs from *Cybelurus* and to expand the concept of *Cybelurus* sufficiently to allow a diagnosis of *Cybelurus* to apply to it would result in the diagnosis being so broad as to be useless. Unfortunately there are also problems with incorporating *sinensis* within *Atractopyge*. The large number of autapomorphies displayed by *sinensis* as would seem to argue for a considerable developmental history which is separate from that of the other taxa assigned to *Atractopyge*. The anomalous palaeogeographical location of *sinensis* at the eastern extreme of the range of *Cybelurus* while the other members of *Atractopyge* at this time are found only in the western extreme of the range may also suggest that *sinensis* was derived independently from an ancestral member of *Cybelurus*. This interpretation would mean that to include *sinensis* within *Atractopyge* would result in that genus being polyphyletic.

Moreover, whilst it is clear that *sinensis* is morphologically intermediate between *Cybelurus* and its daughter genus *Atractopyge*, *A. sinensis* may have developed independently from a species of *Cybelurus* which was very similar to, and probably coexisting with, that ancestral to the other members of *Atractopyge*. But such a conclusion is tentative and because of its strong placement at the base of the *Atractopyge* subclade, I propose to retain *sinensis* within *Atractopyge*.

The species *Atractopyge grewingki* (Schmidt, 1881) and *Atractopyge revaliensis* (Schmidt, 1881) were placed in synonymy with *Atractopyge dentata* by Nikolaisen (1961). This synonymy is retained here although the remarkably long survival of this species compared to the rest of the Cybelinae must raise doubts as to whether they are actually conspecific.

Species included in *Atractopyge* :

Atractopyge adornata		(Törnquist, 1884)
Atractopyge affinis		(Schmidt, 1885)
Atractopyge aspera		(Linnarsson, 1869)
Atractopyge belgica		Lespérance & Sheehan, 1988
Atractopyge brevicauda		(Angelin, 1854)
Atractopyge celtica		Dean, 1965
Atractopyge condylosa		Dean, 1971
Atractopyge confusa		Owen, 1981
Atractopyge coronata		(Schmidt, 1881)
Atractopyge dalmani		Owen & Tripp, 1988
Atractopyge dentata		(Esmark 1833)
Junior synonyms	*A. grewingi*	(Schmidt, 1881)
	A. revaliensis	(Schmidt, 1881)
Atractopyge errans		(Öpik, 1937)
Atractopyge killochanensis		Tripp, 1954
Atractopyge kutorgae		(Schmidt, 1881)
Atractopyge michelli		(Reed, 1914)
Atractopyge pauli		Männil, 1958
Atractopyge petiolulata		Tripp, 1976
Atractopyge progemma		Owen, 1981
Atractopyge rex		(Nieszkowski, 1852)
Atractopyge scabra		Dean, 1962,
Atractopyge sedgwicki		MacGregor, 1962
Atractopyge sinensis		Lu, 1974

Atractopyge spicata	(Raymond, 1921)
Atractopyge tramorensis	(Reed, 1895)
Atractopyge vardiana	Männil, 1958
Atractopyge veneficus	Lespérance & Tripp, 1984
Atractopyge verrucosa	(Dalman, 1827)
Atractopyge williamsi	MacGregor, 1962
Atractopyge woehrmanni	(Vogdes, 1925)
Atractopyge woerthi	(Eichwald, 1840)
Atractopyge xipheres	(Öpik, 1937)

4.5.1.7 *Dindymene* Hawle & Corda, 1847;

Type species: *Dindymene fridericiaugusti* Barrande, 1852
M.-U. Ashgill, Bohemia

The detailed relationships of the species assigned to *Dindymene* are explored in detail in a separate cladistic analysis (see Chapter 6).

As traditionally defined, there are three genera which make up the *Dindymene* subclade. These are *Plasiaspis* Prantl & Přibyl, 1949, *Cornovica* Whittard, 1960 and *Dindymene* itself. Of these, *Plasiaspis* and *Cornovica* are both monospecific taxa, while *Dindymene* includes several species. There has been a lot of discussion as to the relationships of these taxa to each other, and even whether they are closely related at all (see Fortey & Owens, 1987). It is clear from this analysis that these taxa are closely related and that *Plasiaspis* and *Cornovica* are basal plesions to the *Dindymene* clade displaying some, but not all, of the characteristics of that genus. In general, I favour incorporating such taxa as *sensu lato* members of the monophyletic group which they base. *Plasiaspis*, however, lacks the majority of the defining characteristics of *Dindymene*, in particular the inflated frontal lobe of the glabella, and so looks very different to other members of the *Dindymene* subclade. As a result, it is proposed to retain the monospecific genus *Plasiaspis* Prantl & Přibyl, 1949. *Cornovica* is here regarded as a junior synonym of *Dindymene*. The species previously assigned to *Cornovica* differs from taxa classically assigned to *Dindymene* in only a few characters, all of which are consistent with its placement as a relatively plesiomorphic taxon at the base of the *Dindymene* subclade, these characters include:

1. The retention of three complete (non-fused) pygidial pleurae, rather than the two displayed by *Dindymene*. This is a primitive feature which is shared by *Plasiaspis bohemicus* which is basal to the whole *Dindymene* subclade.
2. The retention of L2 and L3 lateral glabellar lobes. The stratigraphically early species *Dindymene saron* Fortey & Owens (1987) also displays relict L2 and L3 lateral glabellar furrows defining lateral glabellar lobes and is clearly closely related to *Cornovica*.
3. Pleural fields retained.
4. Number of thoracic segments (12 in *Dindymene saron* Fortey & Owens, 1987, 11 in *Cornovica didymograpti* Whittard, 1960)

Dindymene pulchra Olin, 1906 is a highly derived member of *Dindymene* which is discussed and diagnosed in Chapter 6. It was not included in this large scale cybeline analysis and so is not separately discussed here.

Dindymene may be diagnosed on the following characters:

Frontal lobe and axis of the glabella inflated; Glabella tuberculate, with large mesial spine (Except the stem taxon *D. saron*); L2 and L3 lateral glabellar lobes absent (except the stem taxa *D. didymograpti* and *D. saron*); Frontal lobe lacking any anteromesial structures; Anterior border furrow of constant depth with the exception of a mesial deepening; Anterior border of constant breadth and non-tuberculate; Facial suture marginal, except in *D. pulchra* Olin, 1906 where the anteromesial portion of the facial suture cuts the frontal lobe of the glabella; Fixigenal field tuberculate with prominent post ocular tubercle; Eyes absent; Librigenal fields tuberculate; Librigenal border tuberculate; Posterior cranidial border non-tuberculate; Thorax of 10 segments (except the stem taxa *D. didymograpti* with 11 and *D. saron* with 12), none of which are macropleural; Pygidium longer than wide and displaying a characteristic 'bell shaped' outline; Two pygidial pleurae (except *D. didymograpti* which displays three) all of which are confluent with continuous axial rings; Pleural fields absent (except again for *D. didymograpti*).

Species included in *Dindymene*;

Dindymene cordai	Nicholson & Etheridge, 1878
Dindymene fridericiaugusti	Hawle & Corda, 1847
Dindymene heidingeri	Barrande, 1852
Dindymene hughesiae	Reynolds, 1894
Dindymene longicaudata	Kielan, 1960
Dindymene ornata	Linnarsson, 1869
Dindymene ovalis	Weir, 1959
Dindymene plasi	Kielan, 1960
Dindymene saron	Fortey & Owens, 1987
Cornovica didymograpti	Whittard, 1960
Dindymene saron	Fortey & Owens, 1987
Dindymene pulchra	(Olin, 1906)

4.5.1.8 *Plasiaspis* Prantl & Přibyl, 1949

Type species: *Plasiaspis bohemicus* (Barrande, 1872)
$d\gamma_1$ beds (Arenig/Llanvirn)
Sarka & Osek, Bohemia

Plasiaspis was assigned to a new sub-family, the Atractopyginae by Andreiva, 1985. Although I was unable to obtain a translation of this paper, it is clear that *Plasiaspis* lies within the *Dindymene* subclade and should be included within the Cybelinae (See Chapter 6 for a detailed discussion).

Diagnosis of *Plasiaspis*:

The glabella displays paired tubercles; Frontal lobe of the glabella bisected by a longitudinal anteromedian furrow directed posteriorly from the anterior border furrow; Three lateral glabellar lobes and furrows present; S3 bifurcates adaxially; S1 not cut by a longitudinal furrow; Tuberculate anterior border bounded by an anterior border furrow which does not shallow abaxially; Facial sutures cut the cephalic margin abaxially resulting in the absence of an anterior librigenal fields;

Fixigenal and librigenal fields also tuberculate, librigenal border granulate; Post-ocular tubercles enlarged relative to other fixigenal tubercles; Thorax of twelve segments, none macropleural; Pygidium longer than wide and displays three pleural ribs, all of which are confluent with continuous axial rings; Pygidial axis tuberculate.

Species included in *Plasiaspis* :

Plasiaspis bohemicus	(Barrande, 1872)

4.5.1.9 Encrinurinae Angelin, 1854

Genus: *Encrinuroides* Reed, 1931

The species coded here is the oldest known member of the Subfamily Encrinurinae,

Encrinuroides hornei	Dean, 1973 Summerford Group, Unit B (Arenig/Lower Llanvirn) Newfoundland, Canada.

This taxon is the basal member of the Ordovician-Silurian Subfamily Encrinurinae. The detailed relationships of the Ordovician representatives are explored in detail in Chapter 8 where the diagnosis of this species, and the genus *Encrinuroides* is given. The large scale relationship of the Encrinurinae to the Cybelinae is discussed in Chapter 8

4.5.1.10 *Libertella* Hu 1971

Type species: *Libertella corona* Hu, 1971 from the Botetort Formation of Virginia, USA, Upper Llanvirn (=New Genus B of Evitt, 1957, p. 1724).

Libertella is a highly unusual taxon whose morphology is discussed further in section 4.3.2

Libertella may be diagnosed on the following characters (based on Evitt & Tripp (1977) with additions):

Frontal lobe greatly inflated, sparsely tuberculate, displaying ordered pairs of tubercles with occasional inter-pair tubercles and a well developed median pit; Lateral glabellar lobes small; Facial suture cuts frontal lobe of the glabella, resulting in presence of large anterior librigenal field; Anterior border narrow and tuberculate; Anterior border furrow of uniform depth with no median deepening; Rostral plate large and its posterior margin is delineated by a raised, tuberculate border, made up of the median section of the anterior border; Hypostome broad with broad hypostomal wings and a narrow, tuberculate posterior border; The anterior border of the hypostome is interrupted by the oval median lobe; Fixed cheek granulate with post-ocular tubercles well developed; Eyes well developed and situated on long stalks; Librigenal fields very sparsely tuberculate; Librigenal borders tuberculate; Large backswept genal spines, the anterior portions of which are tuberculate; Posterior cranidial border non-tuberculate; Axial ring simple and non-tuberculate; Thorax of twelve segments, seventh macropleural; Pygidium longer than wide with two distinct pleurae and a large terminal axial piece within which may be seen relict portions of a third pair of pygidial pleurae fused with the terminal axis.

Species included in *Libertella*:

Libertella corona	Hu, 1971

Species not examined but tentatively included in *Libertella*:

Libertella syltensis	Krueger, 1979

4.5.1.11 *Cybele* Lovén, 1845

Type species: *Calymene bellatula* (Dalman, 1827) Kunda Formation (U. Arenig/L. Llanvirn) Sweden, Norway, Baltic. By subsequent designation of Vodges (1890). See Owen & Tripp (1988) for redescription.

Cybele may be diagnosed on the basis of the following characters:

Glabellar outline subparallel; Median pit in the frontal lobe of the glabella with associated triangular depression in the frontal lobe of the glabella stretching down from the median pit to the anterior border furrow. Glabella displays paired tubercles on its axis and scattered unpaired tubercles; The S3 furrow pair are unbranched and directed obliquely forwards; Anterior border furrow shallows strongly abaxially with a strong median deepening; Anterior border of the cranidium narrow, of uniform breadth and non-tuberculate; Anterior portion of the facial suture has migrated inwards resulting in the presence of a small anterior field on the Librigena; Eyes stalked; Fixigenae tuberculate with very prominent post-ocular and torular tubercles; Posterior cranidial border not tuberculate; Librigenal fields and borders tuberculate; Thorax of twelve segments, the sixth macropleural, all tuberculate; Pygidium longer than wide and composed of five pleurae, the first two of which are contiguous with continuous axial rings, axis and pleurae both tuberculate;

Species included in *Cybele*:

Cybele bellatula	(Dalman, 1827)
Cybele panderi	Schmidt, 1907

4.5.1.12 *Deacybele* Whittington, 1965

Type species - *Calymene arenosa* McCoy, 1846 from the Annestown Formation (Middle Caradoc) at Ballygarvan Bridge, New Ross, County Wexford.

As can be seen from the cladogram in Figure 4.14 the genus *Deacybele* is paraphyletic. In spite of this paraphyly, *Deacybele* is a useful, recognisable, taxonomic group and as such is retained as an expressly paraphyletic genus.

Deacybele may be diagnosed on the basis of the following features:

Glabellar outline sub-parallel sided; Large, well formed lateral glabellar lobes may display coalescence of the abaxial tips of any of the three lateral lobes on each side of the glabella; Glabella displays both paired and scattered unpaired tubercles; S3 furrow pair unbranched and directed obliquely with their adaxial ends to the posterior; A furrow or depression links the S1 lateral glabellar furrows to the occipital furrow; A median pit in the frontal lobe of the glabella may be present; Anterior border furrow shallows strongly abaxially and displays a median deepening; Anterior border tuberculate; Anterior portions of the facial suture adaxially placed, to a point where it runs along the anterior border furrow for much of its anterior section, resulting in the formation of anterior librigenal fields. This placement of the facial suture often results in the form of the abaxial portions of the anterior border furrow being obscured in isolated cranidia; Fixigenal fields tuberculate with the post-ocular tubercles being prominent; Posterior cranidial border tuberculate; Anterior librigenal fields present; Librigenal fields and borders tuberculate; Small, outwardly directed spines present on the librigenal borders; Thorax of twelve segments, the sixth macropleural; Pygidium longer than wide with four pygidial pleurae, of which one is confluent with a continuous axial ring; Pygidial axis tuberculate

Discussion of *Deacybele* ;

Deacybele was originally diagnosed (Whittington, 1965) to define a group of cybelines displaying large, well defined glabellar lobes. Such lobes are not restricted to *Deacybele* but they are one of the characteristics of the genus and so are included in this diagnosis.

There has been debate as to whether the lobes of *Deacybele* are homologous with those of other Cybelinae (see Harper *et al.*, 1985 p. 302) and whether the coalescence of the lateral glabellar lobes in some species, such as *D. conjuncta*, indicates derivation of *Deacybele* from *Cybeloides* (see Owen, 1981 p. 55).

From the results of this analysis it is clear that *Deacybele* is not descended from *Cybeloides* but is in fact ancestral to *Bevanopsis* which is in turn the sister taxon to *Cybeloides*. It can be seen that as the pulvinus is developed in taxa above *Bevanopsis* in the cladogram resulting from this analysis, the lateral lobes of *Deacybele* are homologous with those other cybelines. The coalescence of the abaxial parts of the lateral lobes seen in some species of *Deacybele* is the same as that seen in many species of *Atractopyge*, such as *Atractopyge dentata* (Esmark, 1833). This coalescence is similar to that seen to occur during the formation of the pulvinus in *Cybeloides* but the coalescence predates the pulvinus formation, rather than the other way around. One exception to this is *Deacybele conjuncta* Owen, 1981 which is herein reassigned to *Cybeloides* and is a species in which the lateral pulvinar structure is secondarily deflated.

Whittington (1965) separated his own species *Deacybele pauca* from the type species *Deacybele arenosa* on the basis of the possession or otherwise of a genal spine, the tuberculation, and the outline of the glabella. On study of the material upon which Whittington based these observations it is clear that the specimens do not actually differ in these features. As a result, *Deacybele pauca* is here regarded as a junior synonym of *Deacybele arenosa* from the Caradoc of Ballygarvan Bridge Co. Wexford, Eire and the Caradoc Clashford House Formation, of Co. Meath, Eire.

Bevanopsis phyllisae Tripp, 1993 displays a particularly interesting morphology although the type and associated material is poorly preserved, and so was not included in this analysis. It is here tentatively re-assigned to *Deacybele* because Tripp (1993) recorded it as lacking a median pit on the frontal lobe of the glabella. However, *phyllisae* is also recorded as displaying an eye ridge which is confluent with the frontal lobe of the glabella (Tripp, 1993). This feature is diagnostic of the genera *Bevanopsis* and *Cybeloides* and argues for the inclusion of *phyllisae* in the genus *Bevanopsis* as suggested by Tripp. This species is morphologically intermediate between *Deacybele* and *Bevanopsis* and is considered here to belong to the sub-group of *Deacybele* which gave rise to *Bevanopsis* in the Llanvirn. This morphological placement accords well with both the age and biogeographical situation of *phyllisae*.

Species included in *Deacybele* :

Deacybele arenosa	(McCoy, 1846)
Deacybele pauca	Whittington, 1965
Deacybele gracilis	(Nikolaisen, 1961)
Deacybele mchenryi	(Reed, 1899)
Bevanopsis phyllisae	Tripp, 1993

4.5.1.13 *Bevanopsis* Cooper, 1953

Type species: *Bevanopsis ulrichi* Cooper, 1953 from the Edinburg Formation (Lower Caradoc) of Virginia, USA.

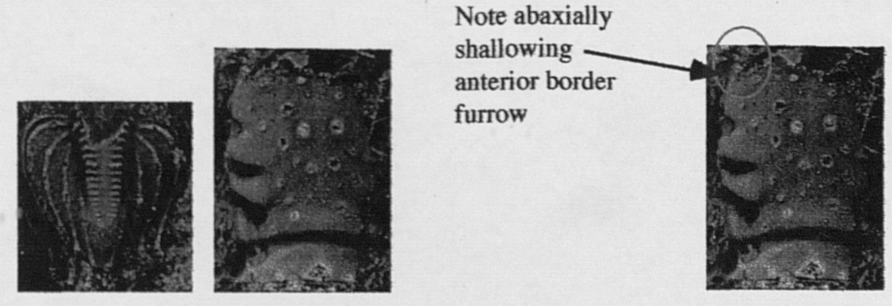
Bevanopsis is the genus most closely related to *Cybeloides (Cybeloides)*, from which it differs only in its lack of development of a pulvinus.

It is unclear as to whether the species *Bevanopsis phyllisae* Tripp, 1993, from the Platy Upper Stinchar Limestone (uppermost Llanvirn/basal Caradoc) of Girvan is best assigned to *Bevanopsis* or *Deacybele*. Until further material is recovered this species is tentatively re-assigned to *Deacybele* (see section 4.5.1.12).

Discussion of *Bevanopsis* sp. of Whittington (1965):

This material (Figure 4.19) from the Llanvirn Table Head Formation of Newfoundland displays an anterior border furrow which shallows strongly laterally which appears to have been cut by an adaxially positioned facial suture, there is a furrow linking the S1 and occipital furrows and the pygidium is of the form of those of the cybeline crown group, supporting its assignment to either *Deacybele* or *Bevanopsis*.

Figure 4.19: Pygidium and cranidium assigned to *Bevanopsis* sp. by Whittington (1965 pl.68, figs 6-11 (x9)).



The frontal lobe is fractured at the point where one would expect to find a median pit, if it was present, preventing the coding of this character. The cranidium is also fractured at the point where the eye ridge is closest to the glabella and the eye ridge is lost. However, it appears that the left S3 lateral glabellar furrow is isolated from the axial furrow and there is a fracture in the lateral portion of the frontal lobe at that point. This indicates that the eye ridge had indeed been confluent with the frontal lobe and, subject to any further material recovered displaying a median pit, this material should be assigned to *Bevanopsis*. This is roughly contemporaneous with *Deacybele phyllisae* and is the oldest *Bevanopsis* recorded.

Species included in *Bevanopsis* :

Bevanopsis ulrichi	Cooper, 1953
Bevanopsis thor	(Ludvigsen, 1979)
Bevanopsis sp.	of Whittington, 1965

4.5.1.14 *Cybeloides* Slocom, 1913;

Type species - *Cybeloides iowensis* Slocom, 1913

The detailed relationships of the species assigned to *Cybeloides* are explored in detail, and a more detailed diagnosis is given, in a separate cladistic analysis (Chapter 7).

Cybeloides may be diagnosed on possession of the following characters;

Glabella subparallel sided; Glabellar lobes coalesced and inflated to form pulvinae, associated with which are secondary axial furrows which divide off the pulvinae from the axis of the glabella. These are variably developed in different species, with the whole spectrum of strength from not developed to totally separating the pulvinae from the glabellar axis being seen; Glabella displays both paired and scattered unpaired tubercles; S3 furrows unbranched and diverging obliquely forwards; A furrow or depression links the S1 lateral glabellar furrows to the occipital furrow; Anterior border furrow shallows strongly abaxially and has a median deepening; Median pit present in the frontal lobe of the glabella; Anterior border tuberculate; Anterior portions of the facial suture adaxially placed, to a point where the suture lies along the anterior border furrow for much of its anterior section, resulting in the formation of anterior librigenal fields. This placement of the facial suture often results in the form of the abaxial portions of the anterior border furrow being obscured in isolated cranidia - in some species the rearward migration of the facial suture maybe taken to extremes e.g. *Cybeloides girvanensis* (Reed, 1906) where the anterior border is reduced to a single projecting tubercle (see Figure 4.13); Adaxial end of the eye ridge confluent with the frontal lobe of the glabella; Fixigenal fields tuberculate with the post-ocular tubercles being prominent; Posterior cranidial border tuberculate; Anterior librigenal fields present; Librigenal fields and borders tuberculate; Small, outwardly directed spines present on the librigenal borders; Thorax of twelve segments, the sixth macropleural; Pygidium longer than wide with four pygidial pleurae, of which one is confluent with a continuous axial ring; Pygidial axis tuberculate; V-shaped rib present running along the underside of the pygidial margin.

Species included in *Cybeloides* :

Cybeloides anna	Ludvigsen, 1979
Cybeloides attenuata	(Reed, 1897)
Species known only from pygidia and so not considered in this analysis.	
Cybeloides cimelia	Chatterton & Ludvigsen, 1976
Cybeloides conjuncta	(Owen, 1981) (See Chapter 7)
Cybeloides ella	(Narraway & Raymond, 1906)
Junior Synonym: *Cybeloides buttsi*	Cooper, 1953 (See chapter 7)
Cybeloides girvanensis	(Reed, 1903)
Cybeloides iowensis	Slocom, 1913
Cybeloides loveni	(Linnarsson, 1869)
Cybeloides parotti	Whittington, 1964
Cybeloides plana	Sinclair, 1944
Cybeloides prima	(Raymond, 1905)
Cybeloides rugosa	(Portlock, 1843)
Cybeloides seca	Evitt & Tripp, 1977
Cybeloides spinifera	Tripp, 1954
Cybeloides sulcata	(Troedsson, 1928)
Cybeloides terrigena	Tripp, 1962
Cybeloides virginiensis	Cooper, 1953

4.5.2 Species to be re-assigned as a result of this analysis;

1. *Atractopyge sinensis* Lu, 1974.

   This species was tentatively re-assigned to *Cybelurus* by Zhou *et al.* (1984) but is here confirmed as belonging to the genus *Atractopyge*.

2. *Bevanopsis phyllisae* Tripp, 1993

   Bevanopsis phyllisae is tentatively re-assigned to *Deacybele* (conditional on the recovery of further material) which makes *Deacybele phyllisae* both the oldest species of *Deacybele* currently known and the only one known from Laurentia. *Deacybele phyllisae* thus provides a link between the later species of *Deacybele* from Baltica and Avalonia, the sister groups of *Deacybele* and potential Laurentian ancestors of *Bevanopsis*.

3. *Cybele tramorensis* Reed, 1895.

   Cybele tramorensis is to be re-assigned to *Atractopyge*.

4. *Lyrapyge? gaoluoensis* Zhou *et al.*, 1977.

   Re-assigned to a new, as yet unnamed, genus

5. *Cybele pscemmica* Abdullaev, 1970.

   Re-assigned to a new, as yet unnamed, genus

6. *Cybelurus ?sp.* Zhou *et al.*, 1984.

   Re-assigned to a new, as yet unnamed, genus

7. *Cybele?* aff *bellatula* Ancygin, 1973.

   Re-assigned to a new, as yet unnamed, genus

8. *Sinocybele? fluminis* Dean & Zhou, 1988

   Re-assigned to a new, as yet unnamed, genus

9. *Cybelurus batuensis* Levitskiy, 1962.

   Reassigned as a *sensu lato* member of *Stiktocybele*.

10. *Cybelella* sp. Tripp *et al.*, 1981.

    Reassigned as a *sensu lato* member of *Stiktocybele*.

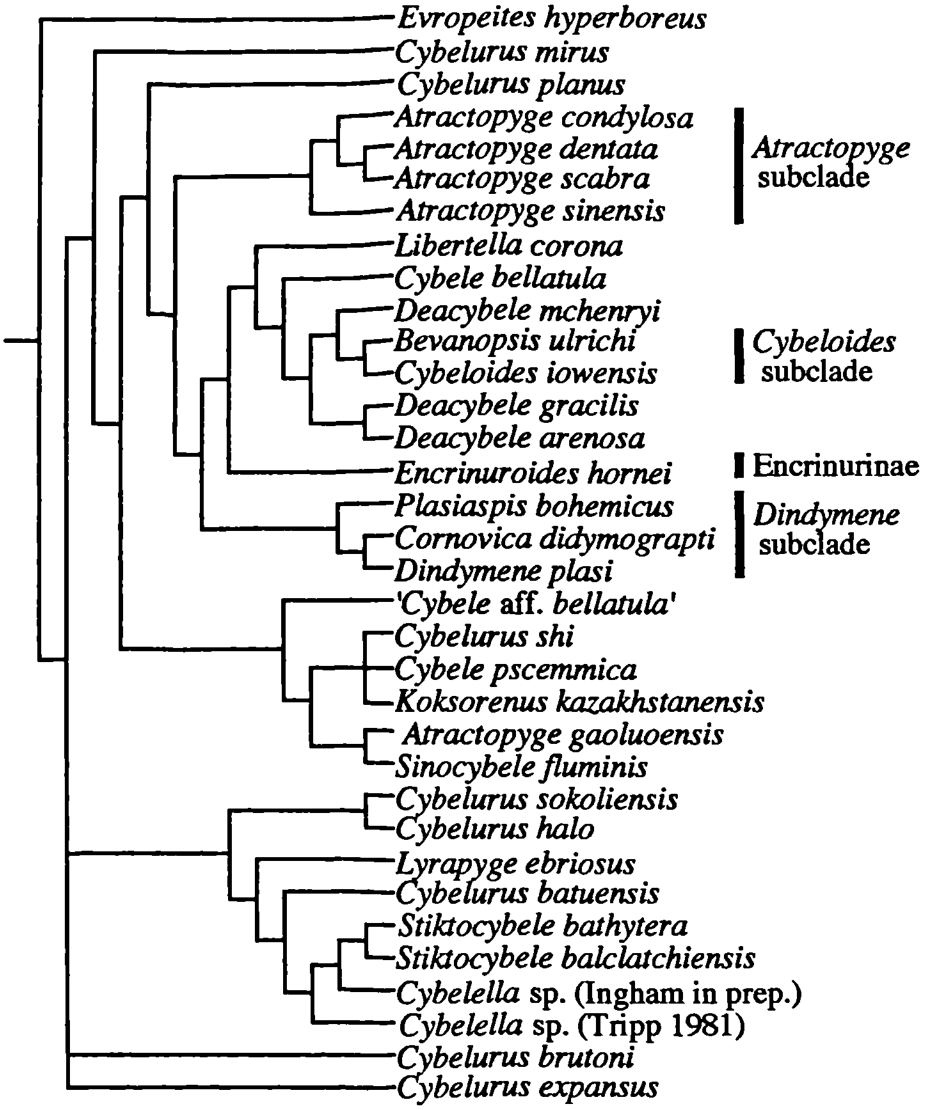
11. *Cornovica didymograpti* Whittard, 1960

    Reassigned to *Dindymene*

4.5.3 Broad evolutionary relationships of the Cybelinae:

The relationships of the taxa belonging to those subclades highlighted in Figure 4.20, *Atractopyge, Cybeloides, Dindymene* and the Ordovician representatives of the Subfamily Encrinurinae, are studied in further detail in separate cladistic analysis later on in the thesis in chapters 5, 6, 7 and 8 respectively.

Figure 4.20: Cladogram (minimum length tree) annotated with those subclades which are examined in more detail later in the thesis.



The history of the Cybelinae is one of convergence, of the repeated independent development of the same or similar features. In the past this has resulted in the relationships of the taxa being obscured. The simultaneous analysis of a large number of characters allows the identification and elucidation of such character convergence. Several of these convergent characters and the general relationships of the taxa are discussed here.

One of the most striking features of the phylogeny produced by this analysis is the polychotomous node at the base of the cladogram. There are several ways in which a polychotomy may result in an analysis. As only one tree results from analysis of this data set, this polychotomy is not the result of there being several possible equally parsimonious trees, which in turn means that the polychotomy is not the result of a character clash. The polychotomous node at the base of the cladogram reflects the actual evolutionary situation prevalent in the Cybelinae, where a morphologically diverse, widespread group of taxa has given rise to numerous offshoot taxa, rather than simply being an artefact of the method or characters employed.

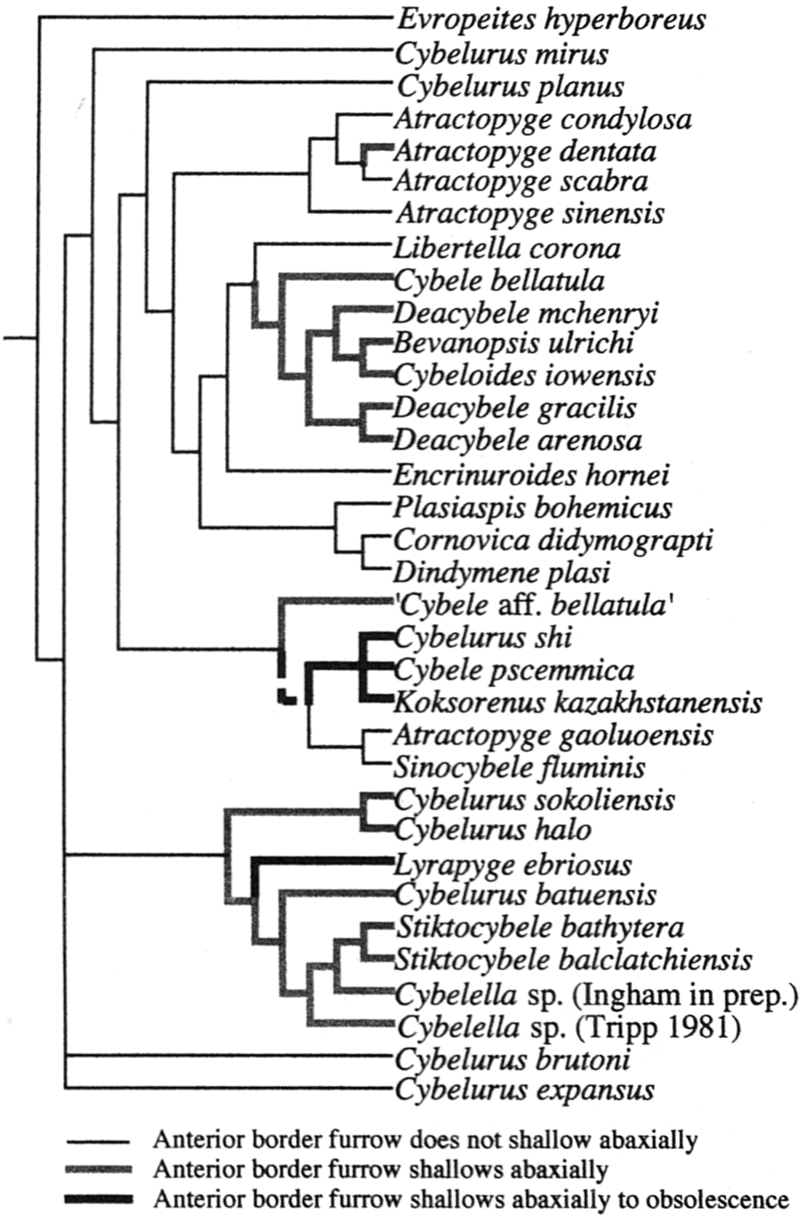
The basal, ancestral, taxon is thought to have been a species of *Cybelurus* that was similar in form to *planus* or *brutoni,* i.e. displaying a longitudinal anteromedian furrow in the frontal lobe of the glabella, a pair of forked S3 lateral glabellar furrows, an anterior border furrow which does not shallow strongly laterally (setting aside the median deepening in the anterior border furrow which is regarded as a separate character) and a pygidium which with an overall width greater than the length of its pygidial axis. This ancestral taxon is thought to have independently given rise to a forms possessing an abaxially shallowed anterior cranidial border furrow (Figure 4.21). Anterior borders of this form are found in the *Cybele* subclade, the *Cybelurus halo* subclade and the *Koksorenus* subclade.

Further complicating this picture is evidence that the laterally shallow anterior border furrow has developed independently more often than is apparent from the cladogram.

4.6. Discussion of convergent characters;

4.6.1 Lateral shallowing of the anterior border furrow;

Figure 4.21: Cladogram showing the pattern of character change of the form of the anterior border furrow.



The genus *Lyrapyge* displays an anterior border furrow that has shallowed to complete obsolescence laterally. It is inferred to have been derived from a state where the anterior border furrow shallows laterally but is still present. This appears to be reasonable, according to the pattern of character state changes on the cladogram, until the stratigraphical ages of the taxa involved are examined (Figure 4.15). It can then be seen that *Lyrapyge* is considerably older than the taxa which are placed below it in the phylogeny. The ages of these taxa are well constrained and are found in a conformable sequence of strata which crop out in the same geographical area. Fortey (1980) observed that the early Llanvirn transformation from complete anterior border furrow (*Cybelurus brutoni* Fortey, 1980) to abaxially shallow anterior border furrow (*Cybelurus halo* Fortey, 1980) was continuous, and assigned the two end members of the continuum to separate chronospecies. This morphological continuum results in the first occurrence of the species displaying a shallow anterior border furrow (*halo*) being tightly constrained stratigraphically, and not merely undiscovered in earlier strata. It must then be concluded that another, earlier, taxon, displaying an abaxially shallowed anterior border furrow, must have independently derived from the 'primitive' state and subsequently given rise to the genus *Lyrapyge*.

Cybelurus halo has been shown by Fortey (1980) to have been derived from *Cybelurus brutoni* (which has an anterior border furrow of uniform depth) in the early Llanvirn. If the Lower/Mid Arenig age assigned to *Cybelurus sokoliensis* is accurate, it is stratigraphically older than *Cybelurus halo* and yet the specimen has an anterior border furrow which shallows strongly laterally. This is therefore another example of the independent derivation of an abaxially shallow anterior border furrow.

It should be also be noted that in the unnamed new genus based on *gaoluoensis*, the anterior border furrow is depicted in PAUP as secondarily reverting to a uniform depth, while in MacClade it is represented as being of uncertain form in the node below this subclade (Figure 4.21). Given the multiple derivation of the abaxially shallow form of the anterior border furrow highlighted, the detailed history of this subclade may be slightly different to that illustrated here. It is likely that there are a number of undiscovered taxa in the Kazakhstan/Urals/Siberia areas with novel combinations of anterior border furrow and pygidial pleurae morphology which would resolve this uncertainty.

4.6.2 Migration of the facial suture to a point where it cuts the frontal lobe of the glabella;

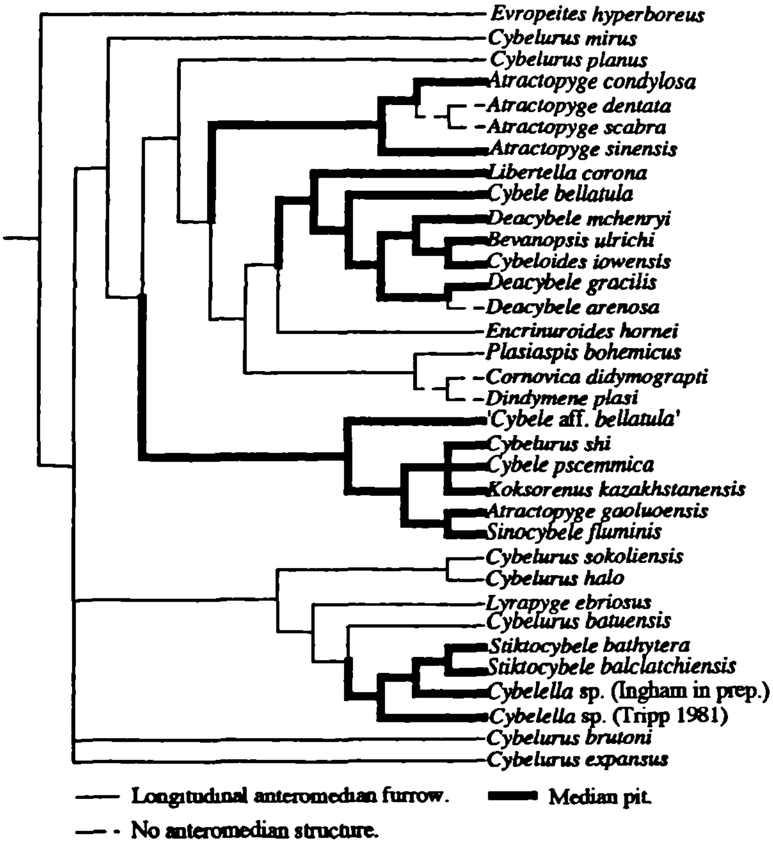
Rearwards migration of the facial suture to a point where it cuts the frontal lobe occurred independently within two separate lineages; *Dindymene* (*D. pulchra* Olin, 1906) and *Libertella* Hu, 1971. In *Libertella* this posterior migration occurred in a taxon which was descended from taxa in which the facial suture had already migrated posteriorly to a position which resulted in the development of an anterior librigenal field. In contrast, the taxa ancestral to *Dindymene pulchra* display marginal facial sutures.

Although I am unable to infer the functional use of a facial suture which cuts the frontal lobe of the glabella, the fact that two entirely different, independent, developmental routes have been taken to reach this facial suture morphology may indicate that its development addresses a common functional need in both taxa.

4.6.3 Median Pit;

Another feature which has proved to have been derived independently on a number of occasions (see Figures 4.22 and 4.3) is the median pit in the frontal lobe of the glabella. The distribution of median pits in the frontal lobe of the glabella is closely similar to the distribution of laterally shallowed anterior border furrows. The earliest members of *Atractopyge* display median pits but no abaxially shallow anterior border furrows (although *Atractopyge* (*Cybelella*) later develops an anterior border which gently shallows abaxially). In addition, the development of a median pit generally lags somewhat behind the development of abaxially shallow anterior border furrows. In spite of these differences it is likely that the independent development of these similar features relates to convergent adaptation of these subclades to similar modes of life.

Figure 4.22: Cladogram with the multiple derivations of a median pit in the frontal lobe of the glabella highlighted.

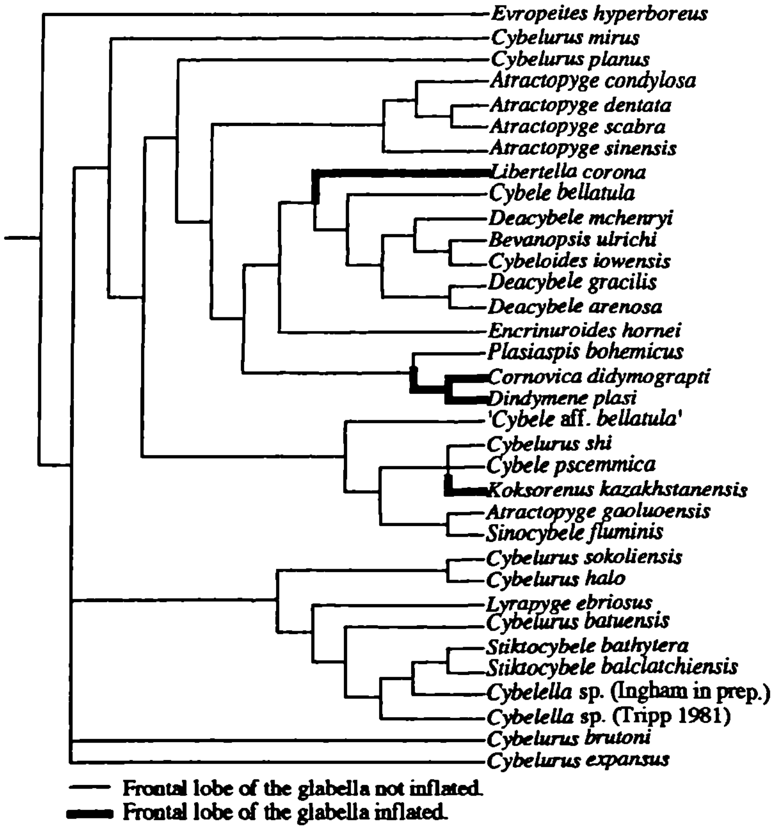


4.6.4 Inflation of the frontal lobe of the glabella:

Inflation of the frontal lobe of the glabella is seen to occur independently on at least four separate occasions within the Encrinuridae, of which three occur within the Cybelinae (including the Dindymene subclade (Figure 4.23)) and once within the Encrinurinae. Inflation of the frontal lobe of the glabella is also seen in taxa outside the Encrinurinae such as *Staurocephalus* and *Oedicybele*. The cybeline examples include the genera *Lyrapyge*, *Dindymene*, *Koksorenus* and *Libertella*. The encrinurine *Physemataspis* also displays strong inflation of the frontal glabellar lobe and other encrinurines display a degree of enlargement of the glabella.

Although the method of inflation of the frontal lobe is very similar in each case, the associated structures differ, supporting the interpretation that inflated frontal lobes were independently derived on several occasions. On each of these

Figure 4.23: Cladogram with taxa possessing an inflated frontal lobe highlighted.



occasions, inflation of the frontal lobe is accompanied by the retention of juvenile features into the adult stage including small body size. These juvenile characters include the retention of juvenile tubercle arrays into maturity, minimisation of the lateral glabellar lobes and reduction in the number of thoracic segments and pygidial pleurae present. The increased relative size of the frontal lobe of the glabella is itself also a juvenile feature. These points all indicate that relative inflation of the frontal lobe is paedomorphic. The evidence of early cessation in development indicates that the paedomorphosis is progenetic (see McKinney & McNamara, 1991, p.17). The developmentally controlled nature of this feature explains why such an apparently major morphological change could have developed independently on so many occasions within a closely related group of taxa and how it could develop with such apparent abruptness within some of the lineages. Both the *Dindymene* and the *Koksorenus* subclades display the full sequence of development of this feature.

In the *Dindymene* subclade the basal taxon *Plasiaspis* is very similar in form to other Cybelinae extant at the time, differing markedly only in its absence of eyes. Its daughter taxon *Dindymene didymograpti* (Whittard, 1960) and *Dindymene saron* Fortey & Owens, 1987 display a partially inflated frontal lobe which still clearly possesses lateral lobes. The crown group of this subclade displays a fully inflated frontal glabellar lobe and lacks, or has very weakly developed, lateral glabellar lobes.

Although the sequence of development of the inflated frontal lobe seen in the *Koksorenus* subclade is very similar to this, it differs in that the anterior border furrow shallows laterally to obsolescence while that of *Dindymene* does not. The frontal lobe of the basal taxon in this group, *Cybelurus shi* Zhou *et al.*, 1984 is not inflated, its upper surface being flat and level with the upper surface of the lateral glabellar lobes, the frontal lobes of its daughter taxa, *A. gaoluoensis* and *Cybele pscemmica*, are rather more convex with somewhat less prominent lateral glabellar lobes. The crown group, *Koksorenus*, whose members are very similar to juvenile specimens of *pscemmica* in both morphology and size, display highly inflated frontal glabellar lobes and minimised, but still present, lateral glabellar lobes.

The taxa displaying inflated frontal glabellar lobes are found in sediments deposited in a variety of different environments which may make it less likely that the inflated frontal lobe addresses a similar evolutionary problem in each group; *Libertella* is found in carbonate sediments deposited in a shallow water, well oxygenated environment; *Dindymene* in black shales deposited in poorly oxygenated deep water; *Koksorenus* appears to be preserved in sediments deposited in a siliciclastic environment.

4.6.5 Variation in the number of pygidial pleurae;

The number of pygidial pleurae varies from two to five between genera but is of high burden within genera, wherein the number of pygidial pleurae is constant (with the exception of the basal taxa of *Dindymene* Hawle & Corda, 1847). This is a relatively low burden character across the Cybelinae as a whole, the addition or loss of a pair of pygidial pleurae being easily achieved by slight alterations in developmental timing.

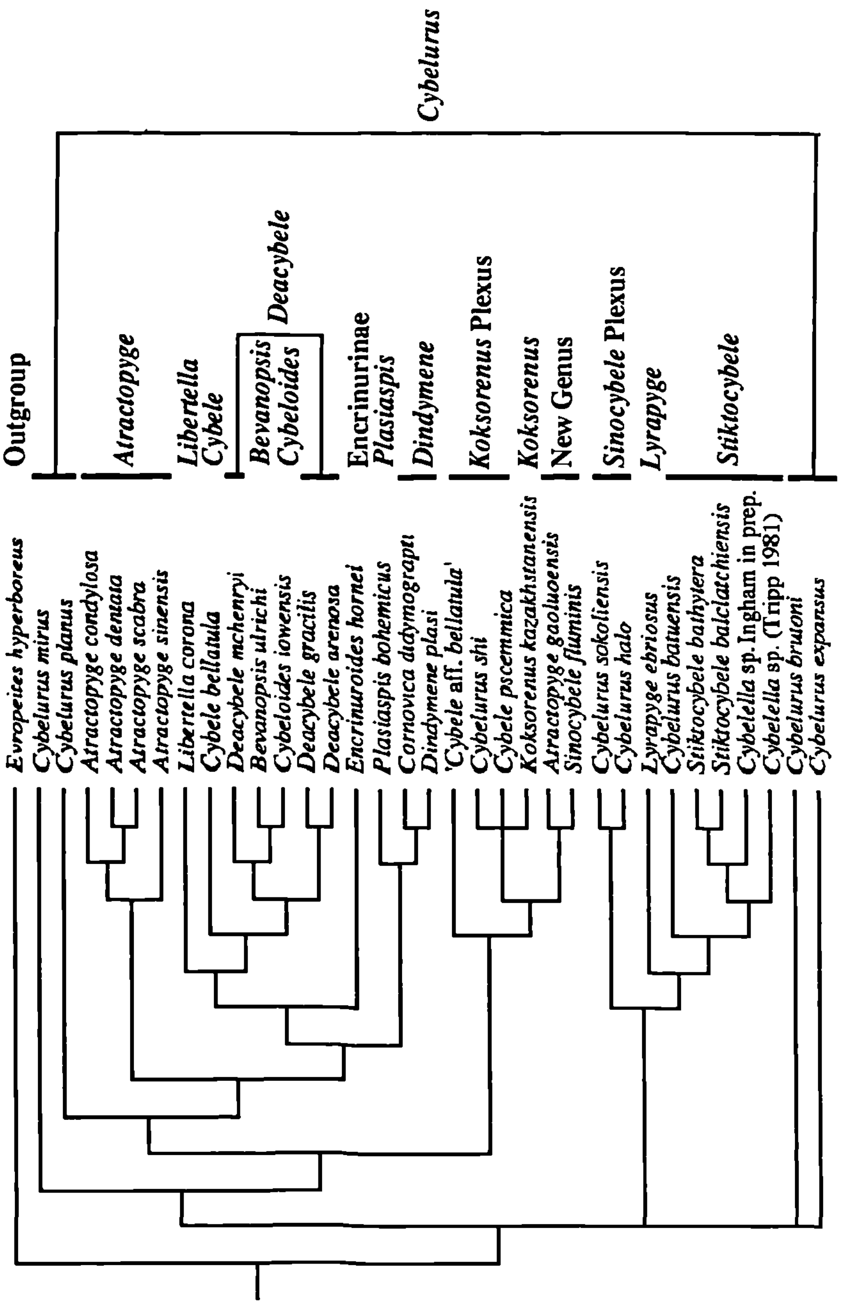
None the less, this character is useful in the differentiation of otherwise similar pygidia and so was utilised in the analysis. The outgroup taxa (the Pliomeridae) generally display five pygidial pleurae while those of the in-group (the Cybelinae) generally have four. Two members of the in-group independently reverted to possession of five pygidial pleurae, *Cybele* and *Encrinuroides hornei*, the oldest encrinurine. *Cybele* appears to have developed from an ancestor with four pygidial pleurae, of which only one was confluent with a continuous axial ring. The addition of a single pygidial axial ring/pleural rib at the end of the development of the pygidium leads to the unique combination of five pygidial pleurae of which the anterior two are confluent with continuous axial ring furrows. This implies the presence of an unrecorded ancestor with 4 pygidial pleurae (only one of which is confluent with a continuous axial ring furrow). Other characters suggest such an ancestor had a median pit in the frontal lobe of the glabella and probably displaying an anterior border furrow which does not shallow abaxially. This hypothetical ancestor would be present in the middle Arenig, probably of Baltica, Siberia and possibly Kazakhstan.

All of the Cybelinae recorded from China have three pairs of pygidial pleurae, all of which are confluent with continuous axial ring furrows. This morphology developed independently twice in taxa from China (*Atractopyge sinensis* and the *gaoluoensis-Koksorenus* subclade) and in the genus *Dindymene* from Bohemia and the Anglo-Welsh area. The inflated frontal lobes of the last two of these groups was earlier inferred to be paedomorphic (Section 4.6.4). As the number of pygidial pleurae present is developmentally controlled, it is interesting to note that, in *Dindymene* at least (see Chapter 6), the number of pygidial pleurae and degree of inflation of the frontal lobe of the glabella is strongly correlated.

4.7. General discussion of the large scale systematics of the Encrinuridae.

As can be seen from Figure 4.24, at least three of the genera recognised here are expressly paraphyletic as they give rise to descendent genera which are differentiated on the basis of one or more distinctive apomorphies.

Figure 4.24: Cybelinae cladogram (minimum length tree) annotated with the genera as defined in this report.

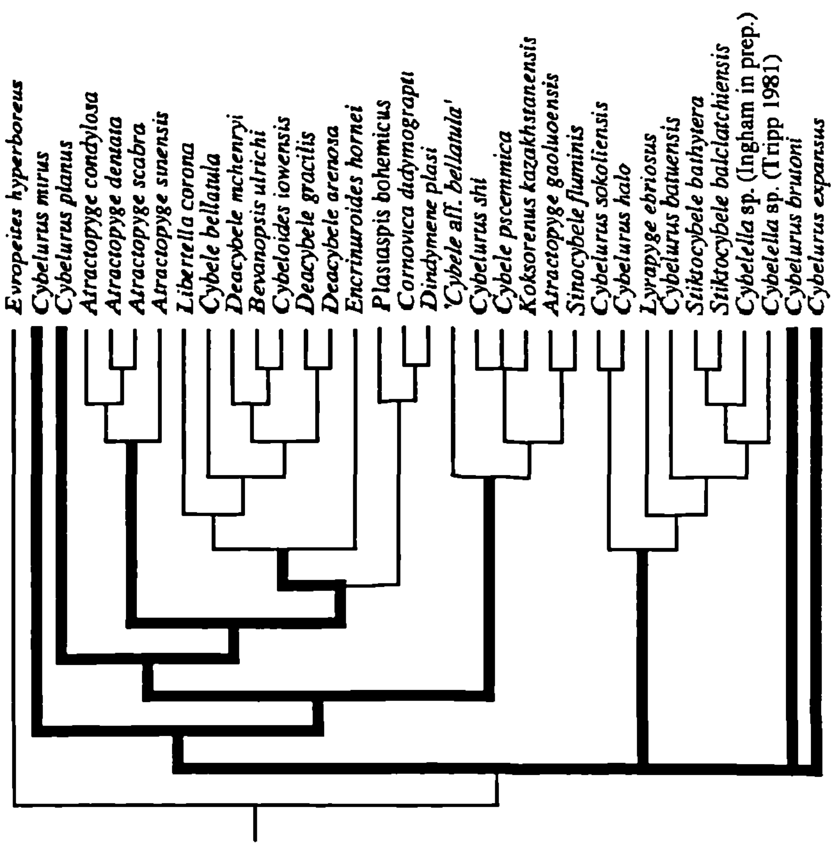


The recognition of expressly paraphyletic genera is necessary. It is inevitable that some of the taxa studied will give rise to descendants, rendering the parent taxon paraphyletic. To attempt to shoehorn all taxa into monophyletic genera can serve to obscure the evolutionary relationships, resulting in an artificial taxonomy which is more informative about the preferred systematic model of the researcher than the evolutionary history of the taxa. Paraphyletic taxa generally give rise to single offshoot taxon with which they coexist. *Cybelurus* is unusual as a number of coexisting daughter genera were derived from its member species.

4.8. The role of *Cybelurus* in the development of the Encrinuridae;

Cybelurus is geographically widespread, being found in platformal and marginal sediments from Laurentia to Siberia in a palaeoequatorial band and its component taxa are inferred to have independently given rise to all of the major subclades of the Encrinuridae.The express paraphyly of *Cybelurus* accurately reflects its evolutionary role in the development of the Encrinuridae (Figure 4.25).

Figure 4.25: Cladogram with the expressly paraphyletic genus *Cybelurus* and inferred "*Cybelurus*' ancestors to subclades highlighted.



As discussed earlier (section 4.6), many of the diagnostic features of the later taxa are independently derived from 'precursor' features seen in *Cybelurus*, for example the median pit which is nearly ubiquitous in the later Encrinuridae. This frequent independent adaptation of characters in *Cybelurus*, together with its widespread geographical range and occurrence in marginal and ocean island environments may indicate that *Cybelurus* was a generalist which independently gave rise to a number of more specialised descendants.

4.9. Definition and discussion of the subfamilies within the Family Encrinuridae;

As defined in the Treatise (Moore, 1959), the family Encrinuridae Angelin, 1854 contains the subfamilies Encrinurinae, Cybelinae, Dindymeninae and Staurocephalinae (see Figure 4.26).

As can be seen from Figure 4.27, the Family Encrinuridae, is supported by this analysis, with revisions. Fortey (1980) suggested that the species *Evropeites? hyperboreus* was close to the ancestor of the Cybelinae (and hence by implication the Encrinurinae as a whole). This is followed here and *Evropeites hyperboreus* Fortey, 1980 employed as an outgroup to that analysis. There are a number of other, closely related, taxa within the Pliomeridae, such as *Pliomeridius sulcatus* Harrington & Leanza, 1948, which are also possible outgroups to the Encrinurinae. Their substitution for *hyperboreus* has no effect on the phylogeny produced.

Evitt & Tripp (1977) suggested that the Staurocephalinae is closely related to the Cybelinae but that it should be regarded as a separate family, the Staurocephalidae. This suggestion is followed here. It appears likely that the Staurocephalidae derived from a (pliomerid) ancestor which, while closely related to that of the Cybelinae, was not common to both.

As is normal in these analyses, the transition from one group to another is not cleanly marked by the sudden acquisition of a number of characters. Rather, the characters diagnostic of the derived group are acquired gradually and are multiply derived independently in various other taxa. This makes diagnosing the Encrinuridae and subfamilies within it difficult without so many caveats as to make the diagnosis useless. In spite of this, the various groups are clearly differentiable 'by eye'; it is merely that the boundaries between them are indistinct.

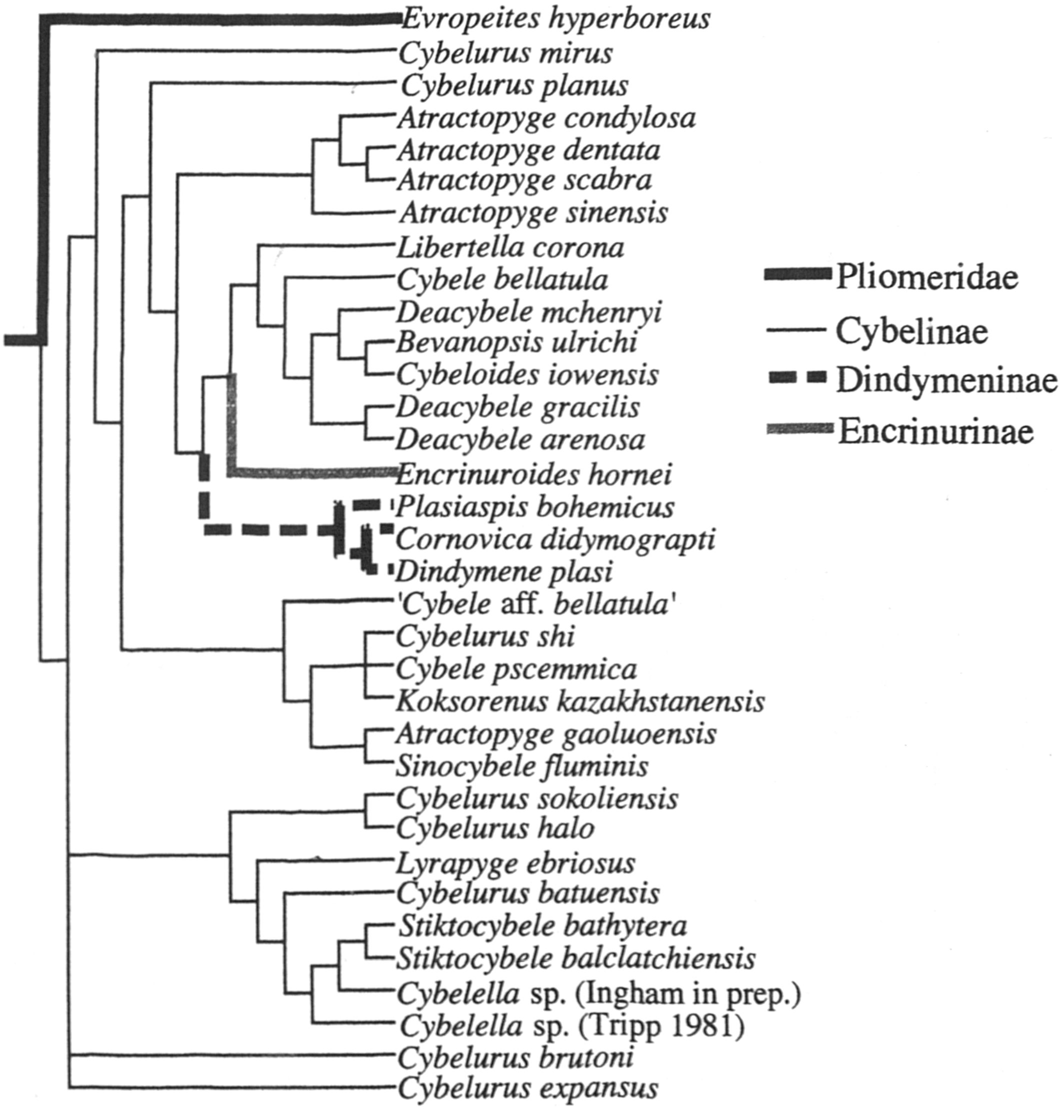
It can be seen from Figure 4.26 that the Subfamily Cybelinae as here defined is paraphyletic, giving rise to the subfamily Encrinurinae Angelin, 1854. As any higher group of taxa which is successful will inevitably give rise to offshoot groups, it seems reasonable to retain useful expressly paraphyletic higher taxa. I believe that the Cybelinae fall into this category and should be retained, with a degree of redefinition.

A number of characters, based upon ontogenetic information have been employed by Edgecombe *et al.* (1988) to investigate the relationships of the Encrinurinae. These characters are not discussed, or used, herein as there are very few species for which a sufficiently full ontogenetic history is known. However, should further material be recovered, this approach is the most likely to assist in the resolution of the large scale relationships.

The Encrinurinae is represented in this analysis by its oldest known species *Encrinuroides hornei* Dean, 1973. Although this species recognisably belongs in the Encrinurinae rather than the Cybelinae, this subjective differentiation is not supported by the acquisition of a large number of characters, or indeed a small number of major characters at a single node. The characters which have been thought to be diagnostic of the Encrinurinae as a whole were acquired sequentially both below and above the base of the 'Encrinurinae', defined here as being situated below *Encrinuroides hornei* .

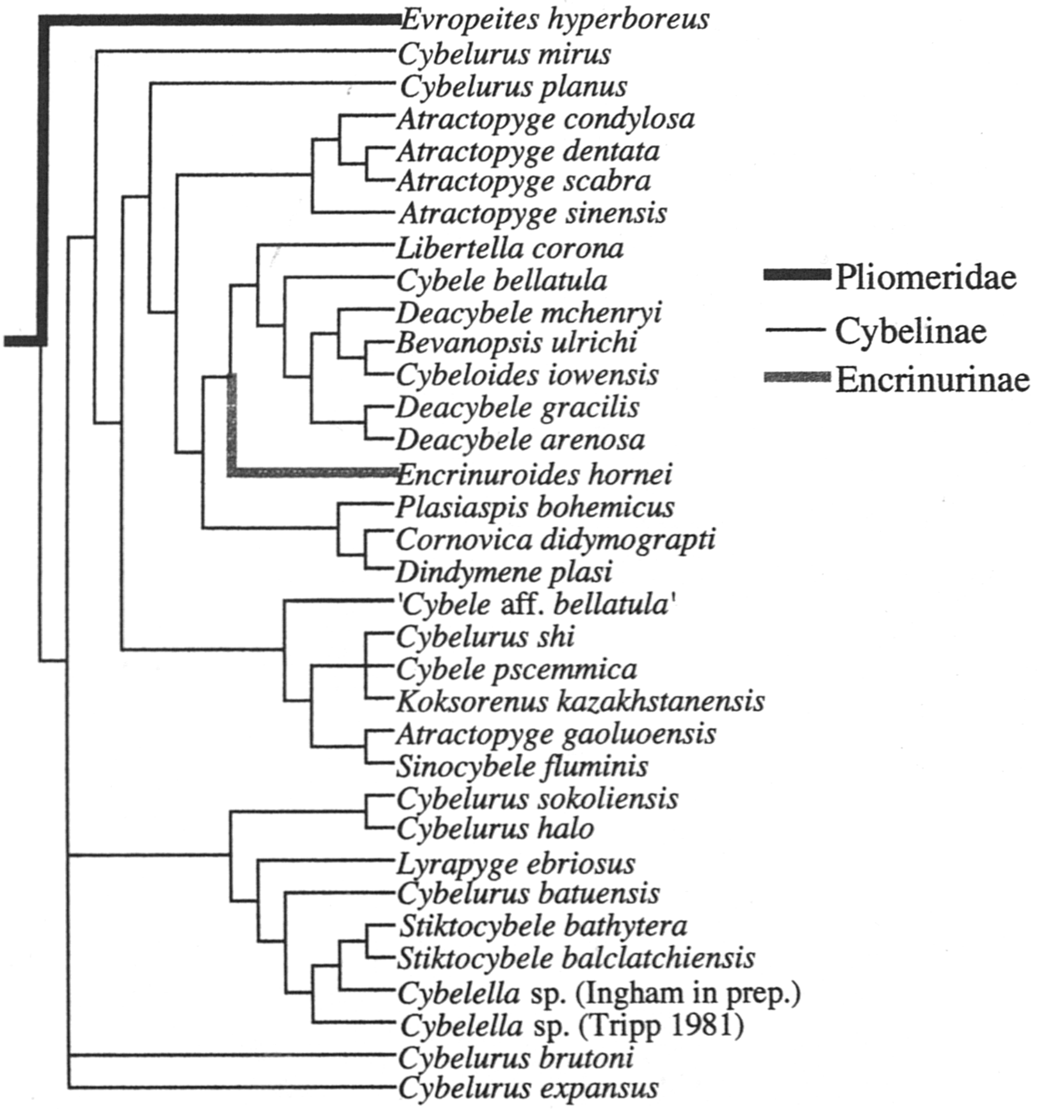
This poses the question of how, if at all, to separate the subfamilies Cybelinae and Encrinurinae. A number of characters have been employed but all of these have problems associated with them. The Encrinurinae is frequently described as differing from the Cybelinae by its lack of anterior fields on the pygidial pleurae, posterior to the anterior flange of the pygidium. As this character is independently derived in members of *Dindymene,* it cannot by itself, be used to diagnose members of the Encrinurinae. Another character employed is the absence of macropleural spines on the thoracic segments of the Encrinurinae. There are two problems with this character; it has again been independently derived in members of *Dindymene* and there are no thoracic segments known from the very earliest species of *Encrinuroides*, the most primitive of the Encrinurinae.

Figure 4.26: Minimum length tree with the various families and subfamilies as defined in the Treatise (Moore, 1959) highlighted.



The acquisition of a large number of pygidial pleurae and pygidial axial rings is diagnostic of the majority of the Encrinurinae but is not seen in *Encrinuroides hornei* and so does not coincide with the currently defined base of the Encrinurinae. The possession of a rhynchos on the hypostome has been described by Edgecombe *et al.* (1988) as linking the Encrinurinae with the derived forms of Cybelinae such as *Cybeloides*. However, the earliest members of the Encrinurinae do not have a hypostomal rhynchos, nor do *Libertella* or *Cybele*.

Figure 4.27: Minimum length tree with the various families and subfamilies as defined herein highlighted.



which are situated on the cladogram above the Encrinurinae, basal to the 'derived Cybelinae' subclade. This means that the hypostomal rhynchos must have been independently developed in both the cybeline crown group and the Encrinurinae. There are a number of characters which differentiate the more derived members of the Encrinurinae from the early members and the Cybelinae, but these characters are developed too high in the Encrinurinae subclade to be of use in differentiation from the Cybelinae.

It is clear that none of these characters provide a satisfactory basis for the diagnosis of a subfamily and so this is deferred.

Plasiaspis bohemicus and '*Cornovica*' *didymograpti* are placed as stem taxa intermediate between the Cybelinae and the Dindymeninae as currently defined. Although the monophyly of the latter group is supported by this analysis, even when expanded to include *Plasiaspis* and '*Cornovica*', there is little to support the retention of the Dindymeninae as a subfamily rather than incorporating it in the Cybelinae. The morphology of the cranidium is unusual in the Cybelinae, but inflation of the frontal lobe of the glabella and minimisation of the lateral lobes is also seen in *Libertella* and *Koksorenus*. The general form of the pygidium is distinctive but lacks any firm features upon which to found a subfamily diagnosis. The number of pygidial pleurae is variable with *Dindymene* and the most common number of pygidial pleurae (3) was independently derived in other groups on at least two occasions. The absence of eyes in *Dindymene* is unique within the Encrinuridae, but is considered insufficient justification for separating these taxa off as a separate subfamily, within which there is little morphological disparity. The Dindymeninae is here subsumed within the Cybelinae (see Chapter 6 for a detailed analysis).

A further systematic problem is the taxonomic separation of the Encrinuridae as a whole (and hence the Cybelinae, as the basal subfamily) from the Pliomeridae. This is difficult as all of the characters which have been proposed to differentiate the Pliomeridae and Encrinurinae are developed elsewhere within the Pliomeridae. For example, the feature most commonly quoted as being diagnostic of the Cybelinae is the tautologous 'cybeliform pygidium'. This is a pygidium which has more axial rings than pleural ribs, an elongate terminal axial section, anterior bands on the pygidial pleurae and out-turned free points. Unfortunately pygidia of this type are found in a number of pliomerid genera such as *Quinquecosta* Tripp, 1965, *Colobinion* Whittington, 1961 and *Pliomeridius* Leanza & Baldis, 1975.

One feature which does seem to differentiate the Pliomeridae from the majority of the Encrinuridae is the form of the anterior border which is of constant width and of the same width as the lateral librigenal border in the Pliomeridae . This contrasts with the Encrinuridae where the section of the anterior border immediately in front of the anterior of the frontal lobe of the glabella is considerably thickened vertically. Each side of this vertically thickened section is bounded by a strong break in slope (except *Dindymene* and *Libertella* in which the anterior border is of constant width). This character is still rather slim support for the definition of a family (and subfamily) and so the need for re-definition of the base of the Encrinuridae and of the Cybelinae is noted. Unfortunately, shortage of time precludes my pursuing this further here.

4.10 Summary of the general pattern of evolution of the Cybelinae:

The earliest Cybelinae developed from the Pliomeridae in the early or middle Arenig. *Cybelurus*, inferred to be the most primitive of the Cybelinae and containing some of the stratigraphically oldest species, was geographically widespread across a classic equatorial temperature zone; its members are found in a band including marginal Laurentia, through Spitsbergen (eg *Cybelurus brutoni* Fortey, 1980), Baltica (*Cybelurus mirus* in the Otta Conglomerate - see Wandås, 1983), Siberia (*Cybelurus planifrons* Rosova, 1960), the Altai region of the USSR (*Cybelurus planus* Levitskiy, 1962), Kazakhstan (*Cybelurus planifrons* Weber, 1948). There are indications that the geographical range of *Cybelurus* extended as far as South China where it gave rise independently to *Atractopyge sinensis* Lu, 1974 (see Chapter 5).

Cybelurus formed part of the relatively deep/offshore Nileiid association (Fortey, 1980), marginal continental shelf or ocean island palaeoenvironments. An example of this association is *Cybelurus occidentalis* Dean, 1973 which is found in sediments associated with a shallowing upwards classic ocean island sequence of ingneous and sedimentary rocks. The lavas in this sequence have a strong ocean island geochemical signature. This widespread basal group was morphologically conservative and independently gave rise to a number of daughter groups in different areas of its range during the Arenig. This diversification was extremely rapid with all of the major subclades being established by the late Arenig.

The earliest, members of *Cybelurus* were of the *C. planus* type with a complete anterior border furrow which does not shallow strongly abaxially, longitudinal anteromedian furrow and forked S3 lateral glabellar furrows. This 'primitive' form of *Cybelurus* survived from the late Arenig/Llanvirn until the early Caradoc. During this period *Cybelurus* gave rise to several offshoots, including *Atractopyge*, with which it co-existed for a time. *Atractopyge* and *Cybelurus* share a very similar morphology and existed in a similar range of conditions - predominantly moderately deep shelf environments - and it is possible that *Atractopyge* replaced *Cybelurus* in this niche.

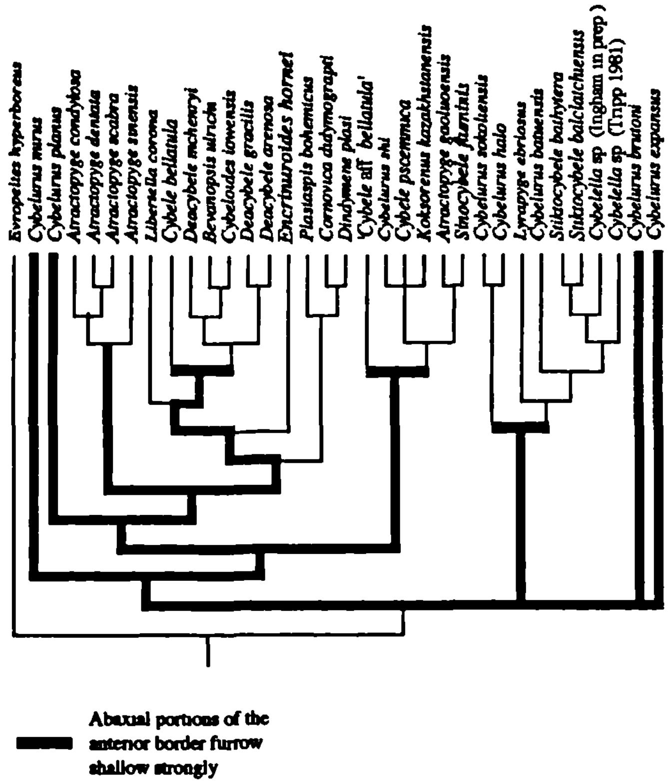
Another group which developed directly from *planus*-type members of *Cybelurus* was the paraphyletic and polyphyletic group of taxa termed in this report the *Sinocybele* plexus. These taxa are differentiated from the *planus* -type *Cybelurus* by the form of their anterior border furrows, which shallow strongly abaxially, almost to obsolescence. Many of these taxa, such as *Cybelurus halo* also display an inflated anterior border. The shallowed anterior border furrow developed independently on at least two occasions (See section 4.6.1 on the development of the anterior border furrow), and if the early age attributed to *Cybelurus sokoliensis* is correct, on more than two occasions. Members of this group appear to have been relatively restricted in their range, currently only being known from Laurentian and Siberian sediments. *Cybelurus* type taxa with abaxially shallowing anterior border furrows such as this gave rise to the majority of the Cybelinae.

Lyrapyge is one of those which developed from a form of *Cybelurus* which displayed abaxial shallowing of the anterior border furrow. The closest sister group to *Lyrapyge* is probably *Cybelurus batuensis* Levitskiy, 1962 which is basal to the *Stiktocybele* subclade. This inference of close relationship of *Lyrapyge* and *Cybelurus batuensis* is strengthened by the similar pygidial morphology of the sister taxa of these *batuensis*, which display depressed, pitted anterior bands on the pygidial pleurae similar to those of *Lyrapyge*.

Some of the main features of *Stiktocybele* are an S3 furrow displaying supplementary apodemes, which are a relic of the bifurcate ancestral form of the S3 lateral glabellar furrows, thirteen thoracic segments, the macropleural seventh of which is probably developed by delay in the cessation of the growth stage of ontogeny. This nileid biofacies group (see Ingham and Tripp, 1991) was limited in geographical range to an area (S.W Scotland and Northern Ireland) close to the margins of Laurentia.

Members of the *Koksorenus* plexus have an anterior border which is incorporated into the frontal lobe of the glabella as a result of the lateral obsolescence of the anterior border furrow. In spite of its similarity to that of *Lyrapyge* members of the *gaoluoensis* plexus were derived independently from an ancestral species of *Cybelurus*, as evidenced by the complete anterior border of their sister taxon, the new genus centred on *gaoluoensis,* and in particular in the form of the lateral glabellar lobes and pygidium. A stem group taxon with a form similar to

Figure 4.28: Cladogram with development of abaxially shallowing anterior border furrow highlighted. Each grey bar may represent more than one independent derivation of this feature.



that of the taxa ancestral to these taxa would be *Cybele* aff. *bellatula* of Ancygin, 1973

The genus *Koksorenus* from Kazakhstan developed by paedomorphosis from a member of the *Koksorenus* plexus. The adults of *Koksorenus* being morphologically identical to the juveniles of the *pscemmica* group, differing markedly only in size. *Koksorenus* shares many features with *Lyrapyge* and the *gaoluoensis* group but it is on the deep water genus *Dindymene* that *Koksorenus* is the most convergent. Both share a very similar general morphology of small size, minimised lateral glabellar lobes and highly inflated frontal glabellar lobe. Although clearly independently derived from different ancestors, *Koksorenus* and *Dindymene* are likely to have been adapted to very similar modes of life and habitats.

Cybele developed directly from an ancestor of broadly *Cybelurus* morphology with an anterior border furrow shallowing strongly abaxially. The main apomorphies of *Cybele* are a triangular, depressed, anteromedian area and five pygidial pleurae (which may be a reversion to a primitive state ancestral to the Cybelinae) two of which are contiguous with rings on the axis of the pygidium.

Deacybele developed from a similar, and possibly common, ancestor to that of *Cybele*. The main features developed in *Deacybele* are the loss of all anteromedian structures on the frontal lobe (an autapomorphy which is variably developed in the oldest members of this genus) and the migration of the facial suture adaxially, which is shared with later daughter genera.

Bevanopsis is sister group to *Deacybele* and is the first genus in which the eye ridge is confluent with the frontal lobe of the glabella.

Cybeloides developed from *Bevanopsis* from which it is differentiated by the formation of a pulvinus.

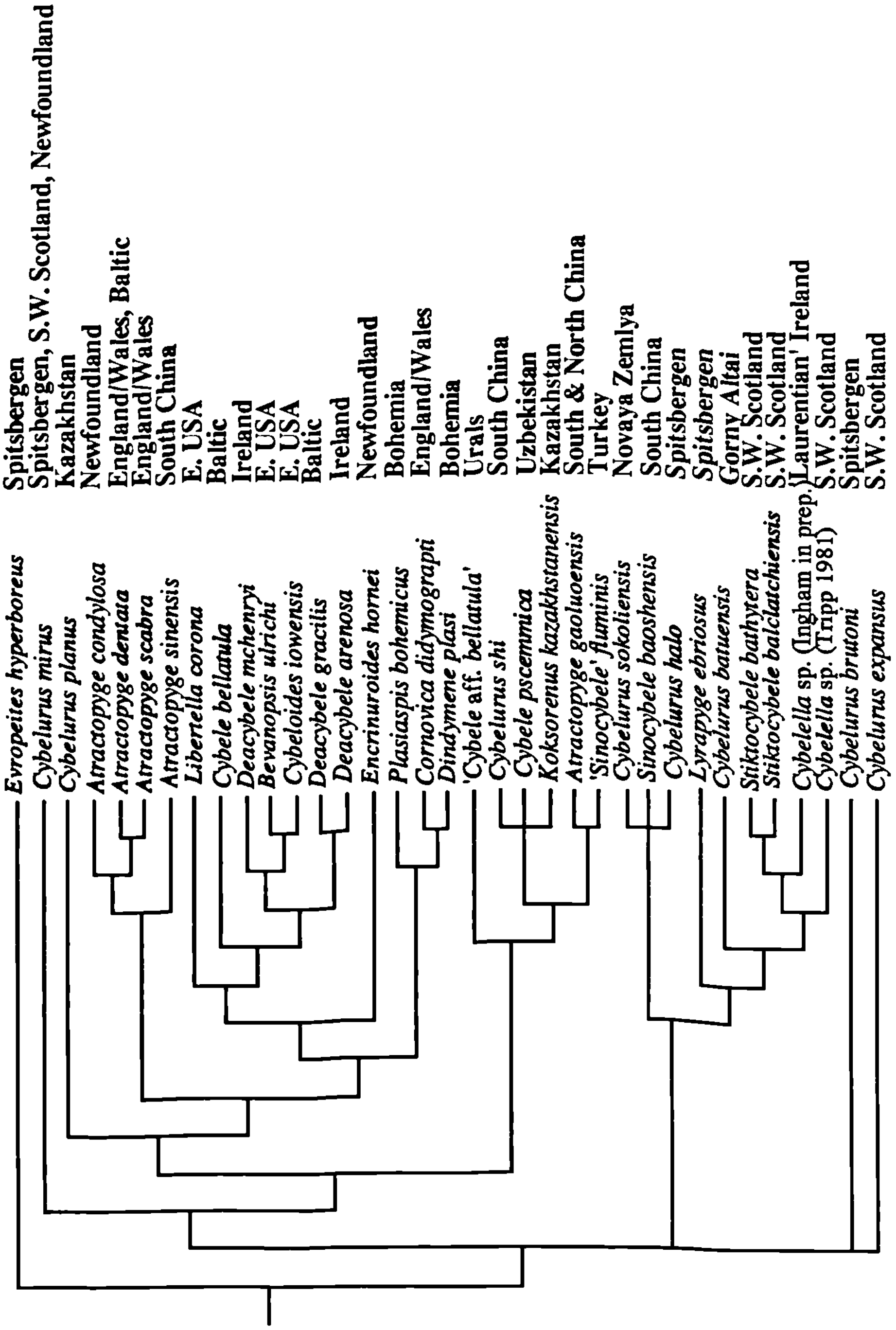
4.11 Biogeographical inferences.

4.11.1 Informal biogeographical inferences:

Informal biogeographical inferences may be drawn from the patterns of distribution of the taxa. These inferences will be tested against a formal gain/loss ratio analysis of the cladogram. The present day geographical locations of the taxa studied in this analysis are annotated on the cladogram produced by this analysis in Figure 4.28.

Cybelurus had a broad equatorial range which included Spitsbergen, Norway (Otta), Newfoundland, S.W. Scotland, Gorny Altai, Siberia, Novaya Zemlya, Kazakhstan and areas of the Urals. *Cybelurus* was restricted to these areas until the late Llanvirn and early Caradoc when it expanded into the Baltic region and Nevada. This pattern indicates that the former areas were in close communication with each other, and isolated from other areas from the Arenig until the late Llanvirn/early Caradoc when Baltica became close enough to allow taxa to 'hop over' from the group of equatorial areas.

Figure 4.29: Cladogram annotated with geographical locations of the Cybelinae.



The independent development of the various members of the *sokoliensis* group from different areas of the range of *Cybelurus* indicates that while these areas were in communication, they were not closely juxtaposed to each other. This supports the interpretation of the biogeography of these areas as being distributed in a long, narrow, equatorial band.

Cybele bellatula was an early shallow water migrant to the Baltic platform during the Arenig (see Figure 4.28). Although this short lived invasion is biogeographically anomalous it is not possible to determine what allowed this shallow water taxon to bridge the oceanic barrier which isolated Baltica from the equatorial band at this time. The appearance of *Cybele* in Sweden is interesting as it is difficult to see how it could have reached Baltica from the equatorial areas inhabited by its closest ancestor if the orientation of Baltica shown in Scotese & Mckerrow (1991) is correct. If Baltica is instead rotated through approximately 180 degrees, as suggested by Torsvik *et al.* (1990, 1991) the biogeographical signal makes more sense and provides further support for the rotation of Baltica at this time.

The Ashgill development of the *gaoluoensis* subclade in South China from late Arenig-L. Caradoc stock in the Urals and associated areas indicate that South China was close to the eastern extreme of the range of *Cybelurus* in the Caradoc/Ashgill. There is no evidence to indicate whether or not South China occupied this position before this time. The absence of *Cybelurus* from both South and North China coupled with the derived morphology of members of the *gaoluoensis*/*Koksorenus* subclade, may indicate that while South China in particular, was clearly proximal to the equatorial group of terranes which made up the range of *Cybelurus*, the two areas were either isolated from each other by a barrier or that an environment unsuitable for *Cybelurus* prevailed. The morphology of members of the *gaoluoensis* subclade is similar to that of members of the *Dindymene* subclade making it possible that this barrier was deep water. The presence of *gaoluoensis* in both South and North China when no other member of this subclade is found in North China may support the fact that this species at least was able to traverse deep water. The presence of members of the *gaoluoensis* subclade in South China without any early members of the group being found in North China indicates that North China is unlikely to have been situated in a vertical orientation between South China and the other equatorial terranes, as indicated by Scotese & McKerrow (1991).

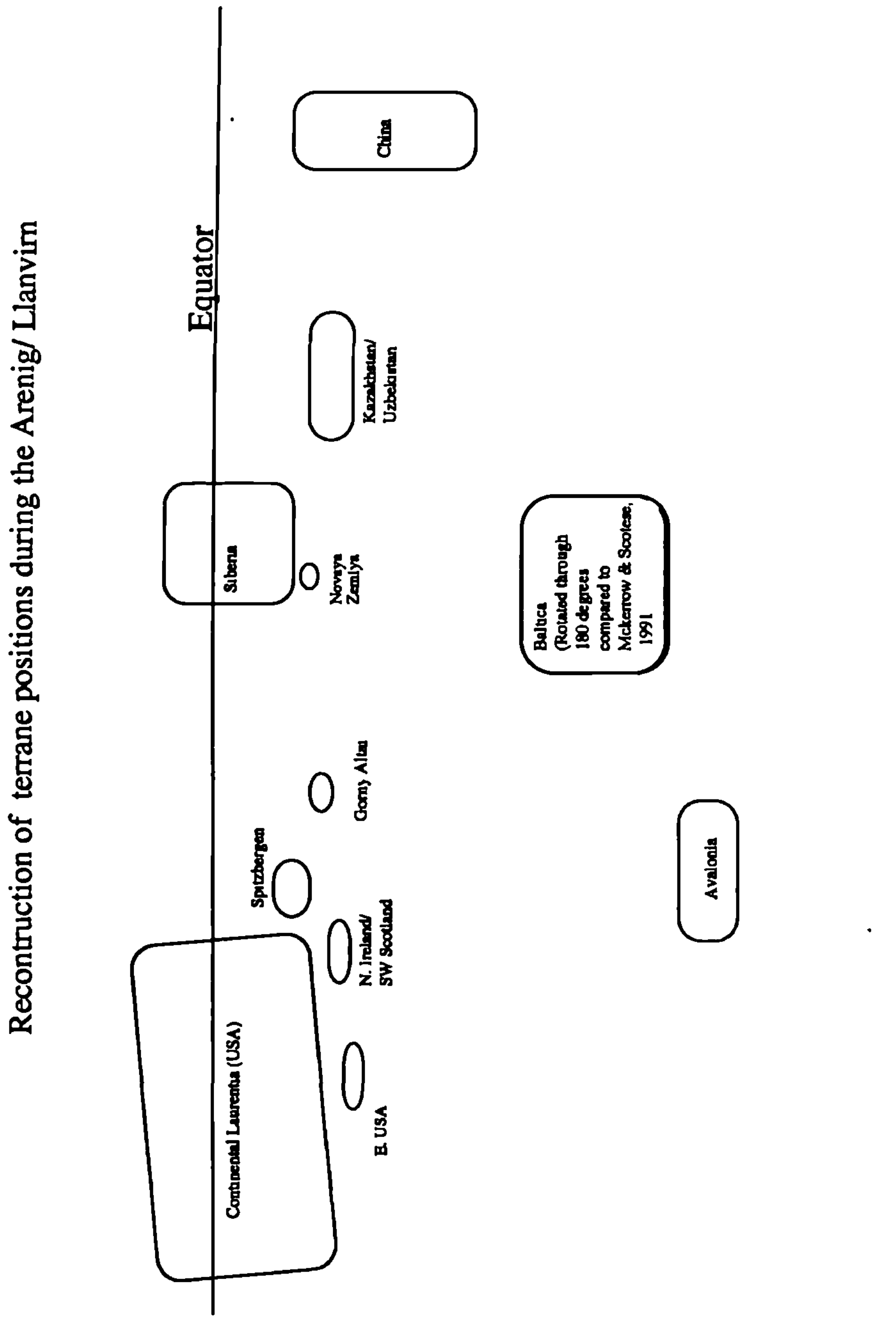
Members of the *Dindymene* subclade are found in deep water sediments and are the only Cybelinae found in Bohemia. It is likely that, during the early

Ordovician, Bohemia was isolated by deep water from the equatorial band of terranes and remained so throughout the middle and late Ordovician.

The development of *Atractopyge sinensis* in South China during the Llanvirn is interpreted (see section 5) as being independent of, and parallel to, the development of the other members of *Atractopyge*. This independent derivation of two similar daughter groups from two similar, or conspecific, ancestral taxa indicates that by the early Caradoc communication between the Western and Eastern extremes of the range of *Cybelurus* (Newfoundland and South China respectively) must have been strongly established. This also indicates that by the Llanvirn South China was part of the range of *Cybelurus* and close to areas such as Kazakhstan and Gorny Altai. The other *Atractopyge* species are found in Laurentia, Baltica and Avalonia, indicating that these areas were in relatively close proximity by the early Caradoc. In the subclade which includes *Deacybele, Bevanopsis* and *Cybeloides*. the biogeographical emphasis has switched from the broad equatorial band inhabited by *Cybelurus* to a narrower, but more cosmopolitan area concentrated in the western portion of that range. While the signature here is still primarily Laurentian, the centre has switched from Spitsbergen to E. USA. There is also evidence of expansion from Laurentia to both Avalonia and Baltica, although it is not possible to state from this analysis whether this expansion occurred to Avalonia via Baltica, to Baltica via Avalonia or to both simultaneously. It is, however, clear that by the Caradoc marginal Laurentia, Avalonia and Baltica were approaching each other.

While *Stiktocybele* is entirely Laurentian its sister taxon *Cybelurus batuensis* is found in the Gorny Altai, making it likely that these two areas were close during the early Ordovician. These inferences are summarised in Figure 4.30

Figure 4.30: Reconstruction of relative terrane positions during the early Ordovician.



4.11.2 Formal Gain/Loss ratio analysis of the Encrinuridae;

All of the inferences made in the preceding sub-section are entirely subjective. As such, it is useful to compare them to the results of a gain/loss analysis. This analysis does not minimise the biases inherent in the sampling of the data, but should minimise researcher bias (see section 2.2.2).

Figure 4.31: Cybelinae cladogram annotated with the nodes considered in the Gain/Loss analysis.

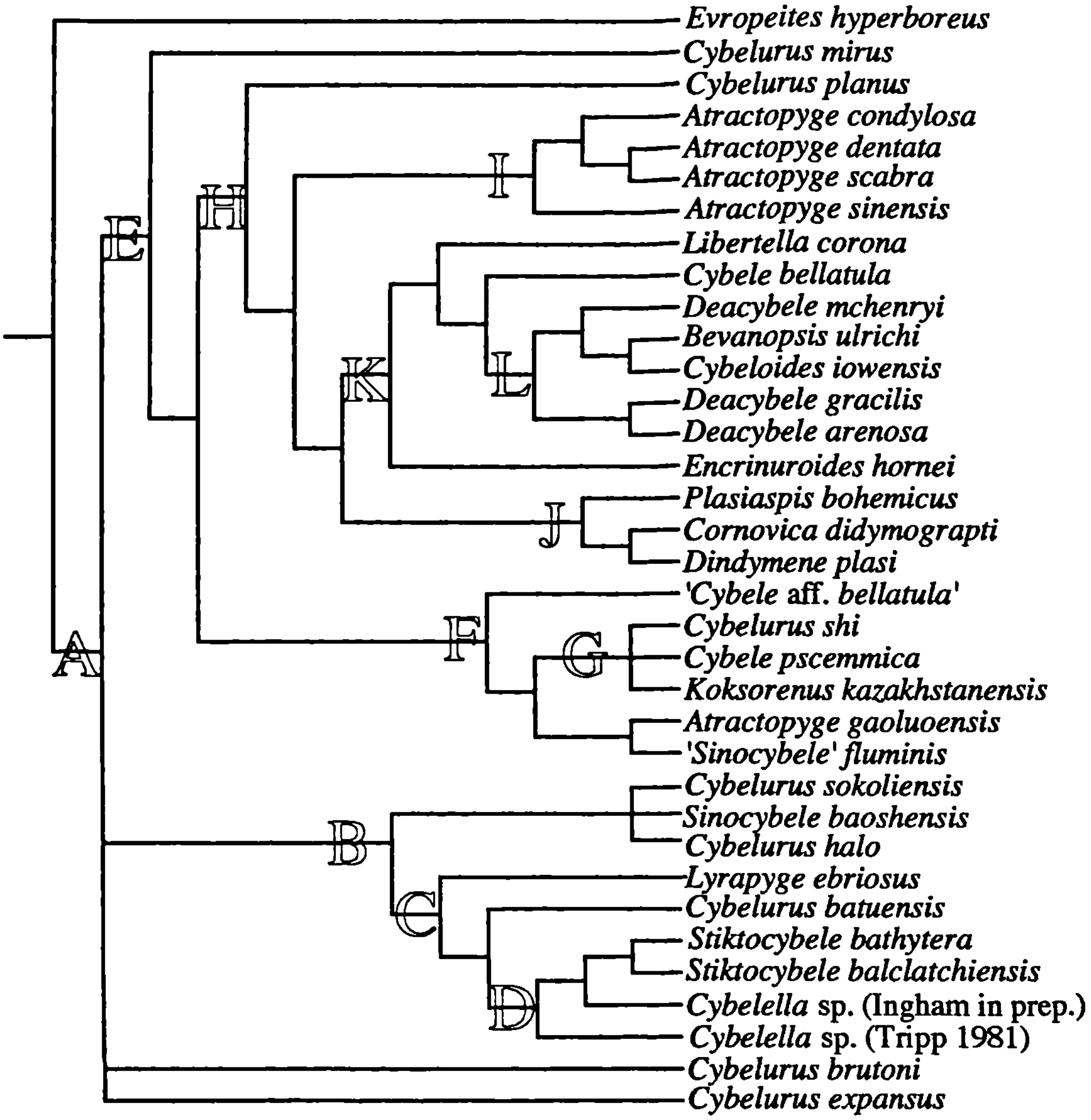


Table 4.1: Calculation of the geographical Gain/Loss ratios of nodes A and B. Any areas scoring 0.5 or more highlighted in **Bold.**

Geographical area	Node A			Node B		
	Losses	Gains	Gains/Losses	Losses	Gains	Gains/Losses
Spitsbergen	**5**	**5**	**1**	**3**	**2**	**0.66**
S.W. Scotland	**7**	**4**	**0.57**	**4**	**2**	**0.5**
E. USA	13	2	0.15	0	0	0
Newfoundland	3	10	0.33	0	0	0
Laurentian Ireland	9	1	0.13	5	1	0.2
Ireland	14	2	0.14	0	0	0
Baltic	14	4	0.29	0	0	0
England/Wales	12	2	0.17	0	0	0
South China	14	4	0.29	3	1	0.33
North China	9	1	0.11	0	0	0
Turkey	9	1	0.11	0	0	0
Kazakhstan	10	2	0.2	0	0	0
Novaya Zemlya	7	1	0.14	3	1	0.33
Uzbekistan	10	1	0.1	0	0	0
Altai	9	3	0.33	3	1	0.33
Bohemia	10	2	0.2	0	0	0

At node A Spitsbergen and S.W. Scotland are most likely to have formed part of the ancestral range of the taxa studied . This indicates that the most likely site of derivation of the Encrinuridae (and hence Cybelinae) was the south eastern margin of the Laurentian continent, probably in the shelf waters around island marginal to Laurentia (depending on which reconstruction of the history of S.W. Scotland in the Caledonides is favoured). This accords well with the biogeographical spread of those Pliomeridae inferred to have been ancestral to the Encrinuridae, which are morphologically closest to members of the Family Encrinuridae/ Subfamily

Cybelinae. These Pliomeridae include taxa such as that chosen as outgroup to the analysis *Evropeites hyperboreus* Fortey, 1980.

The areas most likely to have formed part of the ancestral range of taxa in the subclade based by node B are once again Spitsbergen and S.W. Scotland.

Table 4.2: Calculation of the geographical Gain/Loss ratios of nodes C and D. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	**Node C**			**Node D**		
	Losses	Gains	Gains / Losses	Losses	Gains	Gains / Losses
Spitsbergen	**1**	**1**	**1**	1	0	0
S.W. Scotland	**3**	**2**	**0.67**	**2**	**1**	**2(1)**
E. USA	1	0	0	1	0	0
Newfoundland	1	0	0	1	0	0
Laurentian Ireland	4	1	0.25	**2**	**1**	**0.5**
Ireland	1	0	0	1	0	0
Baltic	1	0	0	1	0	0
England/Wales	1	0	0	1	0	0
South China	1	0	0	1	0	0
North China	1	0	0	1	0	0
Turkey	1	0	0	1	0	0
Kazakhstan	1	0	0	1	0	0
Novaya Zemlya	1	0	0	1	0	0
Uzbekistan	1	0	0	1	0	0
Altai	**2**	**1**	**0.5**	1	0	0
Bohemia	1	0	0	1	0	0

Moving further up the subclade, at node C Spitsbergen and S.W. Scotland are still the areas most likely to have formed part of the ancestral range. although at this node, the ancestral range is also likely to have included the Altai region.

At node D, S.W. Scotland and the Laurentian Ireland region both formed part of the ancestral range of the taxa in the subclade above this node.

Table 4.3: Calculation of the geographical Gain/Loss ratios of nodes E and F. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	**Node E**			**Node F**		
	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Spitsbergen	**1**	**1**	**1**	1	0	0
S.W. Scotland	**1**	**1**	**1**	1	0	0
E. USA	9	2	0.22	1	0	0
Newfoundland	**6**	**3**	**0.5**	1	0	0
Laurentian Ireland	1	0	0	1	0	0
Ireland	10	2	0.2	1	0	0
Baltic	10	4	0.4	1	0	0
England/Wales	8	2	0.25	1	0	0
South China	8	3	0.38	**4**	**2**	**0.5**
North China	5	1	0.2	3	1	0.33
Turkey	5	1	0.2	3	1	0.33
Kazakhstan	6	2	0.33	4	1	0.25
Novaya Zemlya	1	0	0	1	0	0
Uzbekistan	6	1	0.17	4	1	0.25
Altai	**3**	**2**	**0.67**	**1**	**1**	**1**
Bohemia	6	2	0.33	1	0	0

Looking now at the subclade based by node E the ancestral range of the subclade is likely to have included Spitsbergen, S.W. Scotland, Newfoundland and the Altai region.

The ancestral range of the subclade based by node F is likely to have included South China and the Altai region. This subclade is inferred to have derived from taxa belonging to *Cybelurus* by various changes which step in through the subclade. This would indicate that the range of *Cybelurus* had expanded eastwards to include S. China, by the late Arenig (the age of the basal taxon of this subclade). This inference is supported by the inferred independent derivation of *Atractopyge sinensis* from *Cybelurus* in China during the early Llanvirn.

Table 4.4: Calculation of the geographical Gain/Loss ratios of nodes G and H. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	**Node G**			**Node H**		
	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Spitsbergen	1	0	0	1	0	0
S.W. Scotland	1	0	0	1	0	0
E. USA	1	0	0	7	2	0.29
Newfoundland	1	0	0	5	2	0.4
Laurentian Ireland	1	0	0	1	0	0
Ireland	1	0	0	8	2	0.25
Baltic	1	0	0	9	3	0.33
England/Wales	1	0	0	6	2	0.33
South China	3	1	0.33	3	1	0.33
North China	1	0	0	1	0	0
Turkey	1	0	0	1	0	0
Kazakhstan	3	1	0.33	**1**	**1**	**1**
Novaya Zemlya	1	0	0	1	0	0
Uzbekistan	3	1	0.33	1	0	0
Altai	1	0	0	**1**	**1**	**1**
Bohemia	1	0	0	**4**	**2**	**0.5**

Members of the subclade above node G were widespread throughout Uzbekistan, Kazakhstan and S. China with none of these areas being more likely than the others to have formed an ancestral range.

The ancestral range of embers of the subclade based by node H, is likely to have included Kazakhstan, Altai and Bohemia.

Table 4.5: Calculation of the geographical Gain/Loss ratios of nodes I and J. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	Node I			Node J		
	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Spitsbergen	1	0	0	1	0	0
S.W. Scotland	1	0	0	1	0	0
E. USA	1	0	0	1	0	0
Newfoundland	**2**	**1**	**0.5**	1	0	0
Laurentian Ireland	1	0	0	1	0	0
Ireland	1	0	0	1	0	0
Baltic	3	1	0.33	1	0	0
England/Wales	**2**	**1**	**0.5**	**2**	**1**	**0.5**
South China	**1**	**1**	**1**	1	0	0
North China	1	0	0	1	0	0
Turkey	1	0	0	1	0	0
Kazakhstan	1	1	1	1	1	1
Novaya Zemlya	1	0	0	1	0	0
Uzbekistan	1	0	0	1	0	0
Altai	1	0	0	1	0	0
Bohemia	1	0	0	**1**	**2**	**2(1)**

The ancestral range of the subclade based by node I is likely to have included Newfoundland, The Anglo/Welsh area and South China. The biogeography of this subclade is explored in detail in section 5.5.

The ancestral range of the subclade based by node J included the Anglo/Welsh area and Bohemia. This biogeographical spread differs markedly from that of the other cybeline subclades and is further explored in section 6.7.

Table 4.6: Calculation of the geographical Gain/Loss ratios of nodes K and L. Any areas scoring 0.5 or more highlighted in **Bold**.

Geographical area	Node K			Node L		
	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Spitsbergen	1	0	0	1	0	0
S.W. Scotland	1	0	0	1	0	0
E. USA	**4**	**2**	**0.5**	**2**	**1**	**0.5**
Newfoundland	**1**	**1**	**1**	1	0	0
Laurentian Ireland	1	0	0	1	0	0
Ireland	5	2	0.4	**2**	**2**	**1**
Baltic	**4**	**2**	**0.5**	**2**	**1**	**0.5**
England/Wales	1	0	0	1	0	0
South China	1	0	0	1	0	0
North China	1	0	0	1	0	0
Turkey	1	0	0	1	0	0
Kazakhstan	1	0	0	1	0	0
Novaya Zemlya	1	0	0	1	0	0
Uzbekistan	1	0	0	1	0	0
Altai	1	0	0	1	0	0
Bohemia	1	0	0	1	0	0

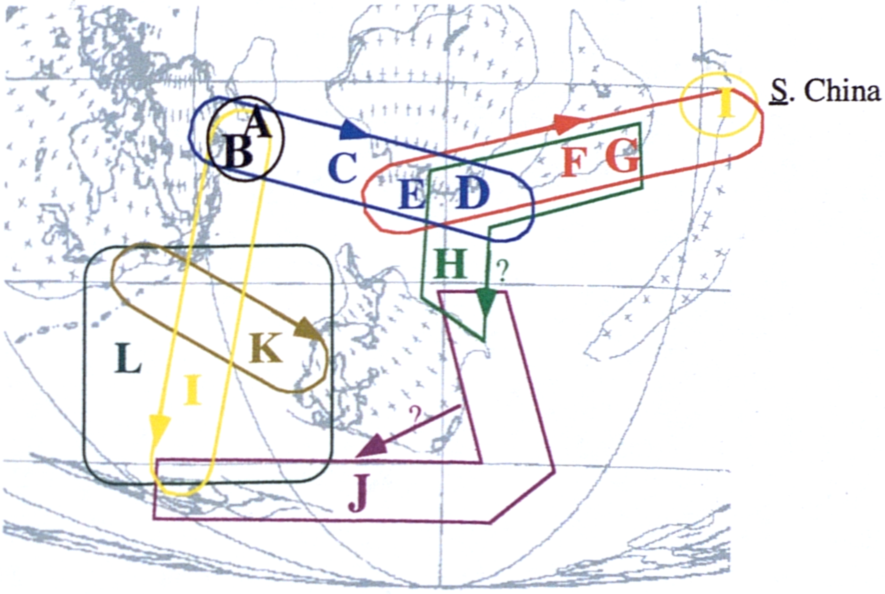
The ancestral range of the subclade based by node K included the Eastern USA, Newfoundland and Baltica.

The subclade based by node L had a similar ancestral range which included both Eastern USA and the Baltic region and Ireland.

The results of the gain/loss ratio analysis are illustrated graphically in figures 4.32 and 4.33. As can be seen, these results strongly support the subjective inferences made in section 4.1.3.

Figure 4.32: Geographical reconstruction of the Lower Ordovician (after Scotese & McKerrow, 1991) annotated with the ancestral ranges of the various nodes discussed previously.

Note: Colours and 'ovals' indicate ancestral ranges as at the nodes indicated by the associated letters. Alterations to some of the continent positions shown have been proposed by various authors which are supported by this analysis but which are not included in this diagram. Many of the taxa included are from the middle and upper Ordovician so superimposed ranges included a time element relative to the base reconstruction.



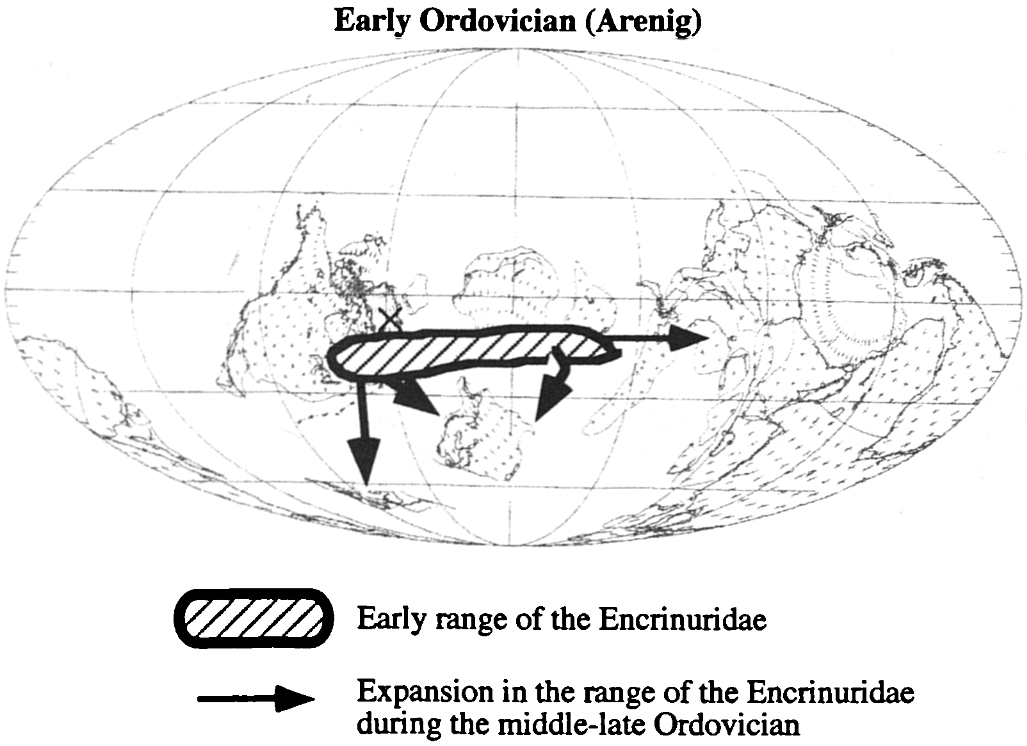
The age of the oldest taxon in each combined ancestral range is as follows:

Arenig	Arenig	Arenig
Arenig	Llanvirn	Caradoc
Arenig	Arenig	

Arrows indicate inferred directions of range expansion.

This diagram can be further simplified to show the broad pattern of distribution of the Encrinuridae through time as in figure 4.33.

Figure 4.33: Schematic representation of the changing extent of the range of the Encrinuridae in the Ordovician.



THE TAXONOMY, PHYLOGENY AND PALAEOBIOGEOGRAPHY OF THE TRILOBITE FAMILIES PLIOMERIDAE AND ENCRINURIDAE:

Reconstructing the Ordovician world using evolving lineages.

Volume 2

Submitted for the degree of Ph.D.

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CHAPTER 5

ATRACTOPYGE
HAWLE & CORDA 1847

5.1 Introduction:

In the initial analysis of the Cybelinae, groups known to be monophyletic were not resolved in detail. The three main groups treated in this manner were *Atractopyge*, *Cybeloides* and *Dindymene*. The relationships of the species within these groups were then resolved in separate analyses.

Atractopyge was derived from *Cybelurus* in the late Llanvirn. *Cybelurus* died out shortly after the development of *Atractopyge*, making it possible that the two groups occupied similar niches and that one effectively replaced the other.

5.2 Species considered in this analysis:

5.2.1 Species included in this analysis:

Genus *Atractopyge* Hawle & Corda, 1847
Type species - *Calymene verrucosa* Dalman, 1827, probably from the Crûg Limestone (Ashgill) of S. Wales. (see Dean, 1974 p. 97-98, Price 1984, p. 103)

Atractopyge belgica	Lespérance & Sheehan, 1988 Ashgill, Bande de Sambre-Meuse, Belgium.
Atractopyge brevicauda	(Angelin, 1854) Boda Limestone, U. Pusgillian-Rawtheyan (M. Ashgill), Sweden.
Atractopyge condylosa	Dean, 1971 Summerford Group Upper Llanvirn, N.W. Newfoundland.
Atractopyge confusa	Owen, 1981 Bønsnes Formation, Rawtheyan (Upper Ashgill), Norway.

Atractopyge coronata		(Schmidt, 1881) Baltic Zone C2, *N. gracilis* graptolite Zone, Lower Caradoc, Baltic.
Atractopyge dalmani		Owen & Tripp, 1988 Jonstorp Formation, M. Ashgill, Sweden.
Atractopyge dentata		(Esmark 1833), (See Whittington, 1965, Nikolaisen, 1961) Elnes Formation or Vollen Formation, M. Llanvirn-L. Caradoc, Oslo, Norway. Also Wales (M. Caradoc)
Junior synonyms	*A. grewingki*	(Schmidt, 1881)
	A. revaliensis	(Schmidt, 1881)
Atractopyge gracilis		Ancygin 1973 M. Caradoc, Middle Urals
Atractopyge kutorgae		(Schmidt, 1885) Baltic zones C3, D1, D2. Lower/M. Caradoc, *D. foliaceus* (=*multidens*) + Middle *D. clingani* graptolite zones.
Atractopyge michelli		(Reed, 1914) Balclatchie Group, Lower Caradoc, Girvan, S.W. Scotland.
Atractopyge petiolulata		Tripp, 1976 Superstes Mudstone, L. *N. gracilis* graptolite Zone. Lower Caradoc, Girvan, S.W. Scotland.

Atractopyge progemma	Owen, 1981 Lunner Formation, Pusgillian (Lower Ashgill), Norway.
Atractopyge rex	(Nieszkowski, 1852) Baltic Zone C2, *N. gracilis* graptolite Zone, Lower Caradoc, Baltic.
Atractopyge scabra	Dean, 1962, Dufton Shales, Onnian Substage (*Onnia gracilis* and *Onnia superba* trilobite zones) and Pusgillian Stage Top Caradoc-L. Ashgill, N. England.
Atractopyge sedgwicki	MacGregor, 1962 *N. gracilis* graptolite Zone, L. Caradoc, Berwyn Hills, Wales,
*Atractopyge sinensis**	Lu, 1975 Shihtzupu Formation, U. Llanvirn/L. Caradoc, China, Guizhou Province.
*Atractopyge tramorensis**	(Reed, 1895) Tramore Limestone, U. Llanvirn/Lower Caradoc, SE Eire
Atractopyge veneficus	Lespérance & Tripp, 1984 Whitehead Formation, Ashgill (Cautleyan), Eastern Canada.
Atractopyge verrucosa	(Dalman, 1827) Horizon etc as in type description.

Atractopyge williamsi	MacGregor, 1962 Lower Caradoc, Berwyn Hills, North Wales

5.2.2 Species for which the material was too fragmentary or poorly illustrated to be code able.

Atractopyge adornata	(Törnquist, 1884) Chasmops Limestone, M. Caradoc, Sweden.
Atractopyge affinis	(Schmidt, 1885) U. Llanvirn, Baltic.
Atractopyge aspera	(Linnarsson, 1869) Chasmops Limestone, M. Caradoc, Sweden.
Atractopyge celtica	Dean, 1965 Snowdon Volcanics M. Caradoc, Wales.
Atractopyge killochanensis	Tripp, 1954 Kiln Mudstones, Low *D. clingani* graptolite Zone. M. Caradoc, Girvan, S.W. Scotland
Atractopyge pauli	Männil, 1958 Baltic zones C1, C2 L. *D. murchisoni* - U. *N. gracilis* graptolite zones, M. Llanvirn to L. Caradoc, Baltic.

Atractopyge spicata	(Raymond, 1921) Collingwood/Lindsay Formation U. Caradoc, Ontario, Canada.
Atractopyge vardiana	Männil, 1958 Baltic zones F1, F2 Top Caradoc - Top Ashgill, Top *clingani* - Top *persculptus* graptolite zones, Baltic.
Atractopyge woehrmanni	(Vogdes, 1925) Baltic
Atractopyge woerthi	(Eichwald, 1840) Baltic zones C1a, b *D. murchisoni* graptolite Zone, Upper Llanvirn,

Reference obtained too late for inclusion in these analyses;

Atractopyge errans	(Öpik, 1937) Baltic zones E1, E2, F1 *D. clingani-D. anceps* graptolite zones, U. Caradoc - M. Ashgill, Baltic.
Atractopyge xipheres	(Öpik, 1937) Kukruse Formation (C2), *N. gracilis* graptolite Zone, Lower Caradoc, Baltic.

5.3 Characters employed in the *Atractopyge* analysis;

The following characters are employed in the *Atractopyge* analysis. Except for character 10, which is of simple ordered type, the characters used in this analysis are of simple, unordered, unweighted type. As far as possible the characters employed are discrete and discontinuous, however, as this is a species level analysis the use of some nominal characters such as character '1' was unavoidable but the use of truly continuous characters such as measurements and ratios was avoided.

1. Number of axial rings on the pygidium:

0-5= 0
6-10= 1
11-15= 2
16-20= 3
21-25= 4
26-30= 5
31-35= 6
Numerous
but faint = 7

2. Tubercles on the pygidial axis: 0/1 - n/y

3. Tubercles on the pygidial pleurae: 0/1 - n/y

4. Number of pygidial pleurae: 3/4

5. Development of 2nd anterior band on the pygidium: 0/1 - faint/distinct.

6. Course of the glabellar axial furrows: 0/1/2
diverging strongly forwards/parallel/biconcave.

7. Amalgamation of the adaxial portions of the lateral glabellar lobes: 0/1 - n/y

8. Form of the S3 lateral glabellar furrow: 0/1 - Forked/single.

The majority of the members of *Atractopyge* possess a forked S3, rather than the single furrow widely considered to be a defining characteristic of this genus. Unlike the forked S3 furrow found in many of the earlier Cybelinae, such as *Cybelurus,* the fork is not symmetrically bifurcate, instead the morphology is more commonly that of a single, straight S3 furrow, transversely directed, with a short anterior branch which does not normally contain an apodeme. This would seem to indicate that the anterior branch of the S3 lateral glabellar furrows may simply be a relict of the previously bifurcate form of the S3 furrows.

9. Presence of a furrow or depression joining the occipital furrow to the S1 lateral glabellar furrow: 0/1 - n/y

This feature is found in only one of the species in this genus, *Atractopyge dalmani,* although it is an autapomorphy of the crown group of the Cybelinae, which includes *Cybeloides* (see Section 7). It is noted that this furrow is only apparent in *A. dalmani* when the specimen is oriented in a certain direction. Rather than actually being a furrow as described in Owen & Tripp (1988), this is a strong break in slope, caused by the slight inflation of the abaxial part of the lateral lobe without any corresponding inflation of the adaxial part of the lobe. This raised, inflated abaxial portion of the L1 lobe casts a strong shadow on the adaxial section of the lobe when oriented towards the light source, giving the appearance of a furrow. From this it is clear that, this feature in *dalmani* is not analogous to the S1-occipital furrow of the Cybelinae crown group.

10. Unpaired tubercles present on the axis of the preoccipital glabella : 1/2 - n/y

This seems to be a primitive feature of the group, with the acquisition of additional, inter-pair tubercles being a derived feature. This may indicate that there are *Cybelurus* species (the ancestral sister groups of *Atractopyge*) which display adventitious, unpaired tubercles still to be found in the

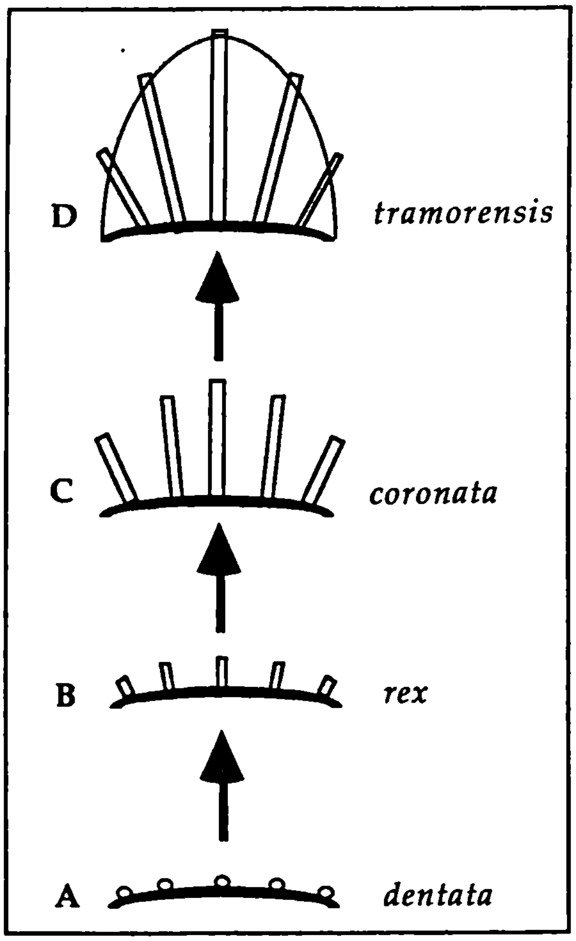
Llanvirn - L. Caradoc of Siberia, Kazakhstan, China and Laurentia. This character may be ontogenetically controlled as immature specimens of species in the crown group of the Cybelinae analysis, such as *Cybeloides*, display a small number of paired tubercles while more mature specimens display numerous scattered inter-pair tubercles in addition to the paired tubercles.

11. Tuberculation of L2: 0/1/2 - none/ monotuberculate/ multituberculate.

12. Anterior border: 0/1/2 - **ORDERED**
granulate/tuberculate/spinose anterior projections/spatulate, ribbed anterior projection

This sequence of character states may be seen in the *dentata* sub-clade. This continuity of charter state development was first noted by Reed (1895). The broad, flat, anterior projection displayed by *A. sinensis* is not included in this character which deals with the relative development of the anterior border tubercles. The broad, flat, anterior projection seen in *sinensis* is produced by the flat protrusion of the anterior border as a whole (see Figure 5.1). This border itself displays numerous small anterior border tubercles/ granules and it is these which are coded for this character in *A. sinensis*.

Figure 5.1: Schematic diagram of the inferred sequence of development of the long, ribbed, anterior projection seen on the anterior border of *A. tramorensis* from the anterior border tubercles of *A. dentata*.



13. Number of anterior border tubercles/projections:

0..8 = code as the number.
≥9 = code as 9.

14. Occipital ring is: 0/1/2 - simple/tuberculate/granulate:

15. Position of posterior edge of palpebral lobe:

level with occipital ring or furrow =0
L1, S1, L2 =1
anterior to and including S2 =2

16. Presence of a fixigenal spine: 0/1 - n/y.

17. All of the pygidial pleurae are continuous across the axial furrows: 0/1 - n/y

18. Posterior border of cranidium widens strongly into a field at the genal angle:
0/1 - n/y

19. Posterior border of cranidium (except the occipital ring) tuberculate: 0/1 - n/y

20. Median pit present: 0/1 - n/y

21. Enlarged, paired, tubercles on axis of glabella: 0/1 - n/y

22. Anterior border widens abaxially: 0/1 - n/y

23. Anterior border furrow shallows abaxially: 0/1 - n/y

5.4 Results of the analysis:

5.4.1 Assessment of the trees resulting from this analysis:

The analysis produced two equally parsimonious trees of length = 50, C.I. = 0.660, C.I. Rescaled C.I. = 0.521. The only difference between the trees being a slight uncertainty as to the position of *Atractopyge sedgwicki* MacGregor, 1962. These trees are shown in Figures 5.2 and 5.3, with a consensus tree given on Figure 5.4. It can be seen that Figures 5.2 and 5.4 are identical. This is because the presence or absence of the node immediately below *michelli* in Figure 5.3, which differentiates the cladogram in 5.2 from that in 5.3, has no effect on the length of the trees because of a degree of uncertainty in the character optimisations across this area of the cladograms resulting from a small absence of data and a degree of minor character conflict. As the node immediately below *michelli* in Figure 5.3 is not supported in both minimum length trees the strict consensus of the two trees does not include this node, and so is identical to the minimum length tree in Figure 5.2.

As can be seen from Figure 5.5, the fit of the phylogeny to the stratigraphy is very good with no conflicts in evidence, increasing confidence in the accuracy of the phylogeny.

The two species placed in the outgroup for display purposes are *'Atractopyge' sinensis* Lu, 1975 and *Atractopyge condylosa* Dean, 1971. These are placed as stem taxa to *Atractopyge* by the Cybelinae analysis and are distinguished from *Atractopyge (sensu stricto)* by their possession of a median pit in the frontal lobe of the glabella. *'Atractopyge' sinensis* is the earliest of the two stem taxa and is the only species of *Atractopyge* to be found in China, all of the other species being found in Laurentia/Baltica/Avalonia. The appearance of *sinensis* in China makes little biogeographical sense if *sinensis* is seen as *Atractopyge (sensu stricto)* but fits well if it is regarded as having been independently derived from a *Cybelurus* type common ancestor/ancestral form which was widespread at low latitudes in the Llanvirn. This seems likely as species of *Cybelurus*, known from the Llanvirn/L. Caradoc have just such a widespread equatorial distribution (*Cybelurus* mentioned, but not illustrated, as present in the Llanvirn of the North China Platform by Zhou *et al.*, 1989). The idea that *'Atractopyge' sinensis* has been derived independently from a form of *Cybelurus* close to, or the same as, that of the ancestor of the other species of *Atractopyge* is further supported by the large number of autapomorphies displayed by *sinensis* (represented in Figure 5.5 by the length of its branch). The derivation of *condylosa* and the other species of *Atractopyge* from a form close to that of, but not identical to, the ancestor of *sinensis* would result in the placement of *condylosa* as the closest ancestor to *Atractopyge (sensu stricto)* with *sinensis* as a sister group as shown in the cladogram.

Figure 5.2: *Atractopyge* minimum length tree 1.

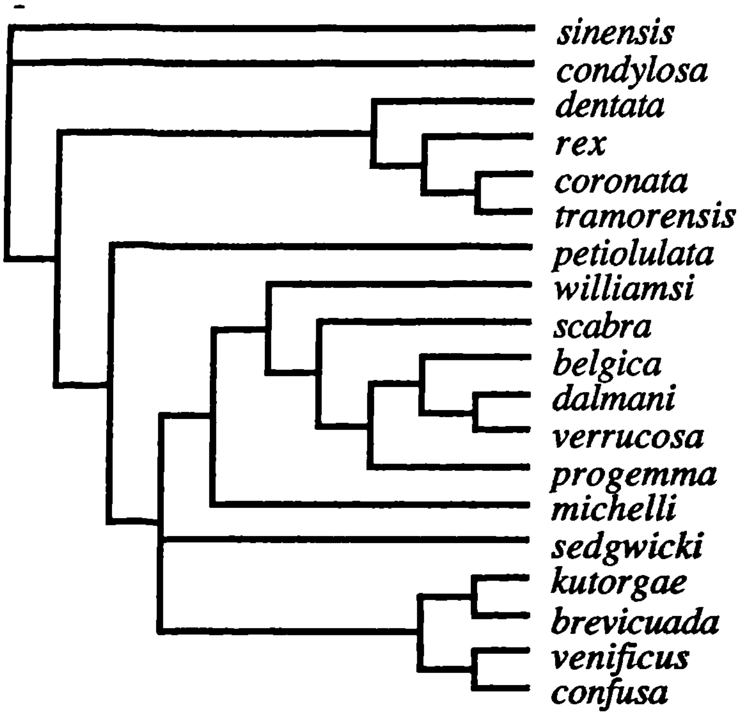


Figure 5.3: *Atractopyge* minimum length tree 2.

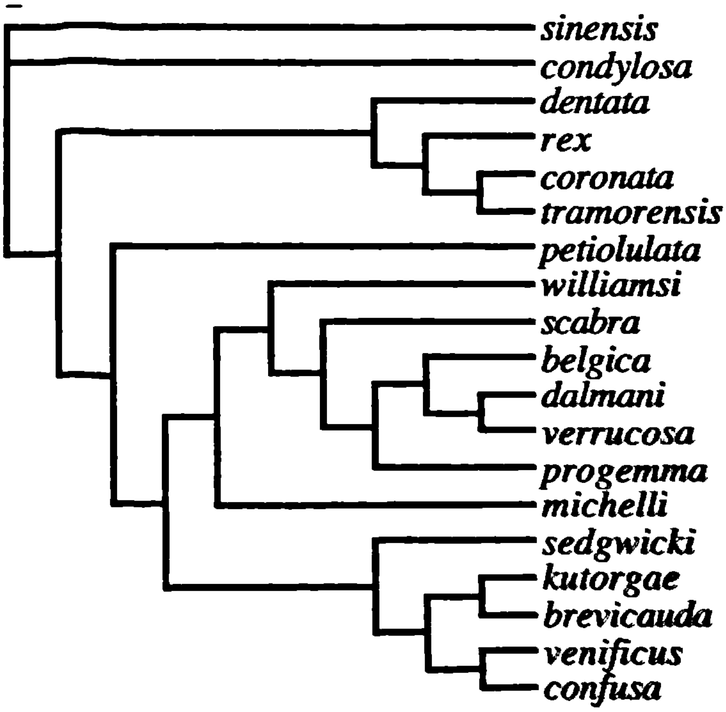
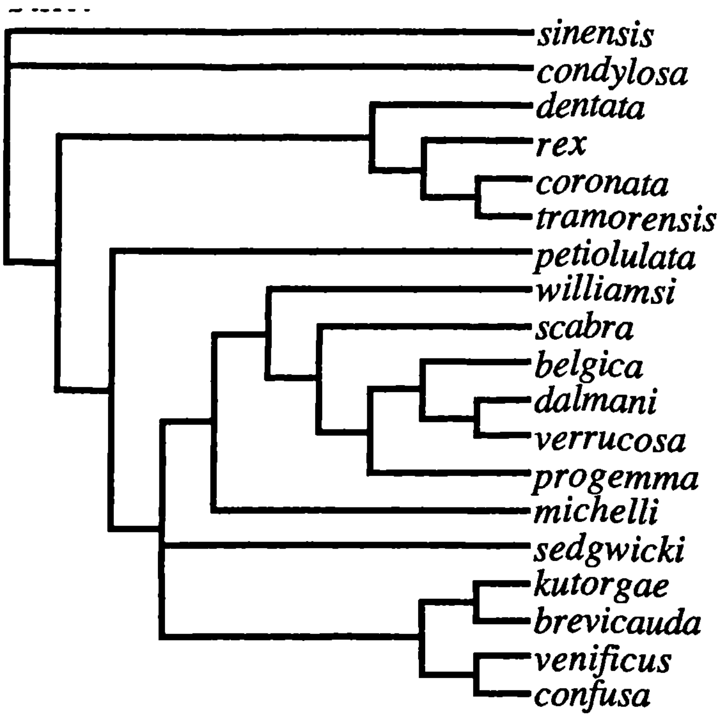


Figure 5.4: Strict consensus of the two minimum length trees; C.I. = 0.877



The following phylograms are based on tree two in which *sedgwicki* is raised by an additional node into the *kutorgae* subclade rather than tree one, where this extra node is not supported and *sedgwicki* is placed at a trichotomy with both the *kutorgae* and *verrucosa* subclades. I chose to employ tree two as the basis of these phylograms as, while the extra node basing *sedgwicki* is not supported in both trees, tree two illustrates the maximum possible information on character change in this group.

The character changes which form this phylogeny can be seen on the annotated phylograms in Figures 5.6 and 5.7 (numbers refer first to the character number, then the previous character state and then the value that it changed to).

Figure 5.5: Tree two represented as a phylogram. Tree 2 is employed here rather than tree one as tree 2 is more highly resolved, although the *sedgwicki* node is not supported in both trees.

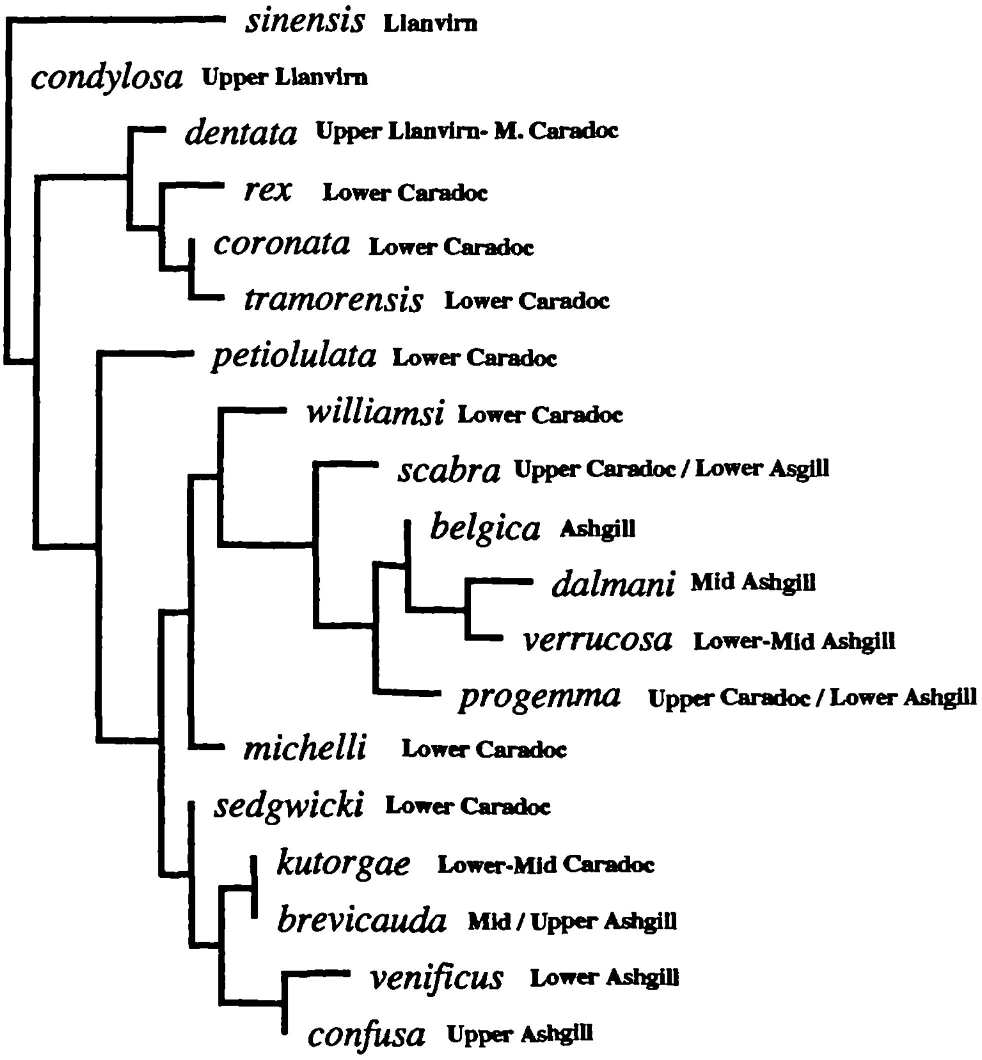


Figure 5.6: Phylogram based on tree two annotated with all character changes .

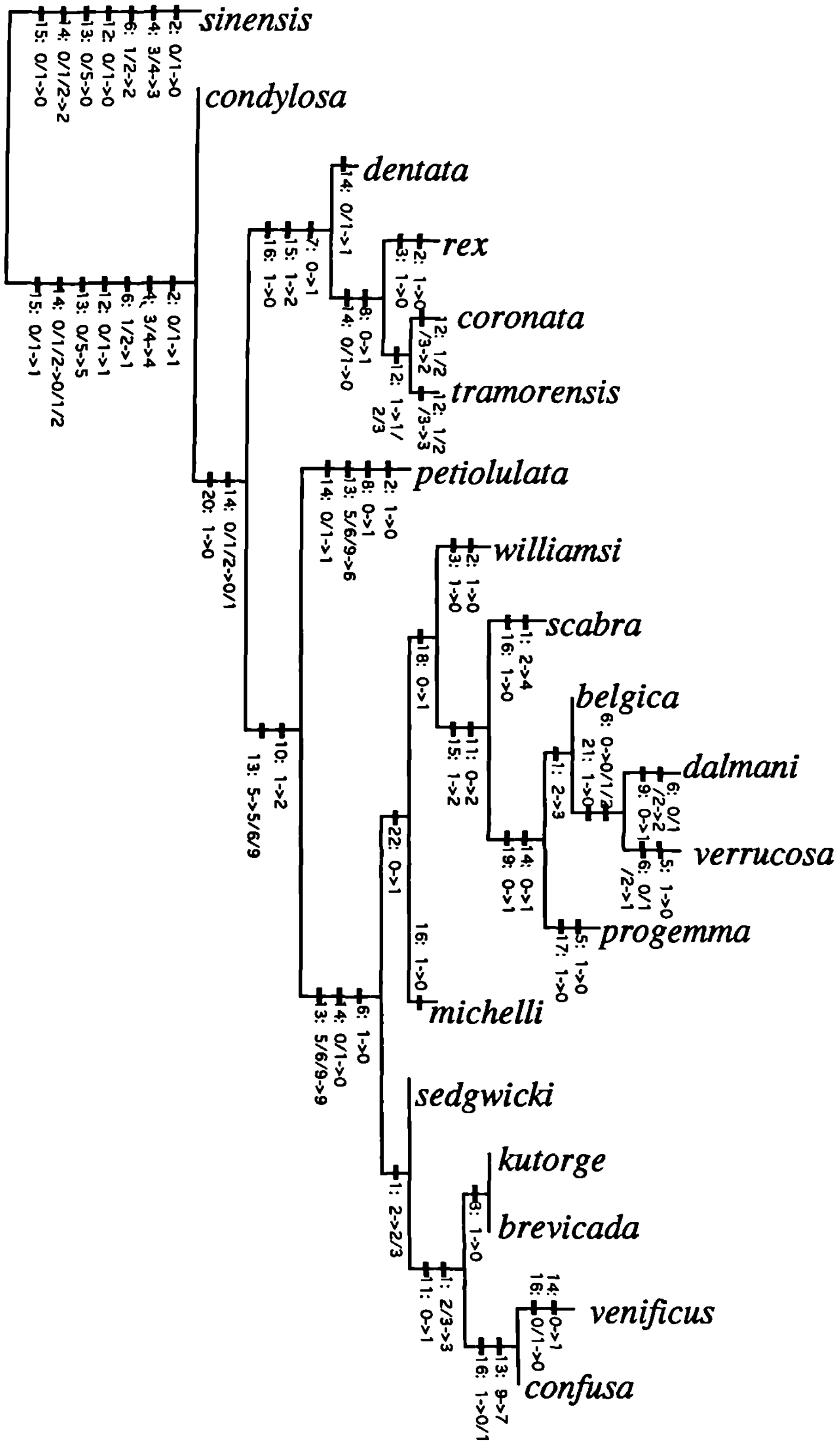
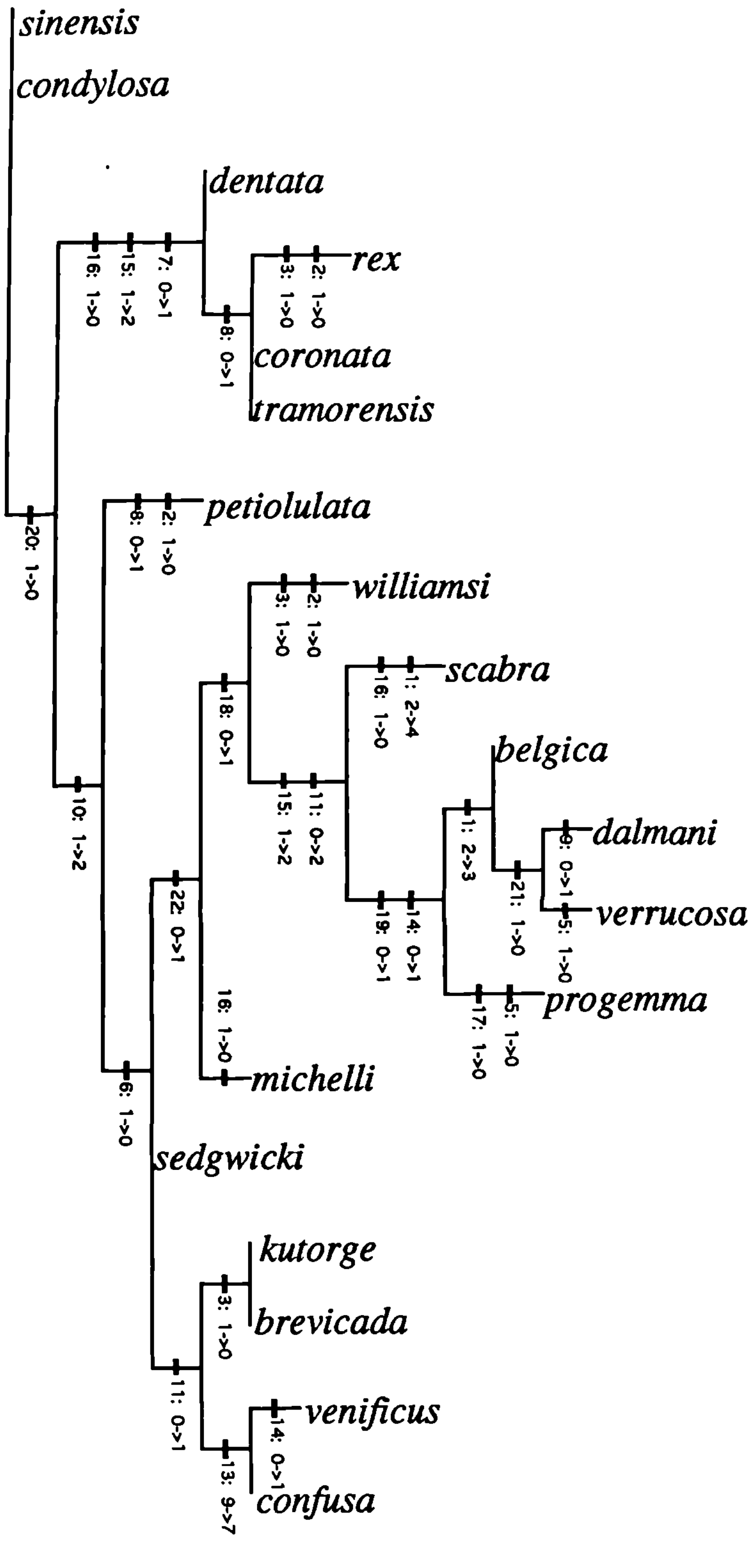


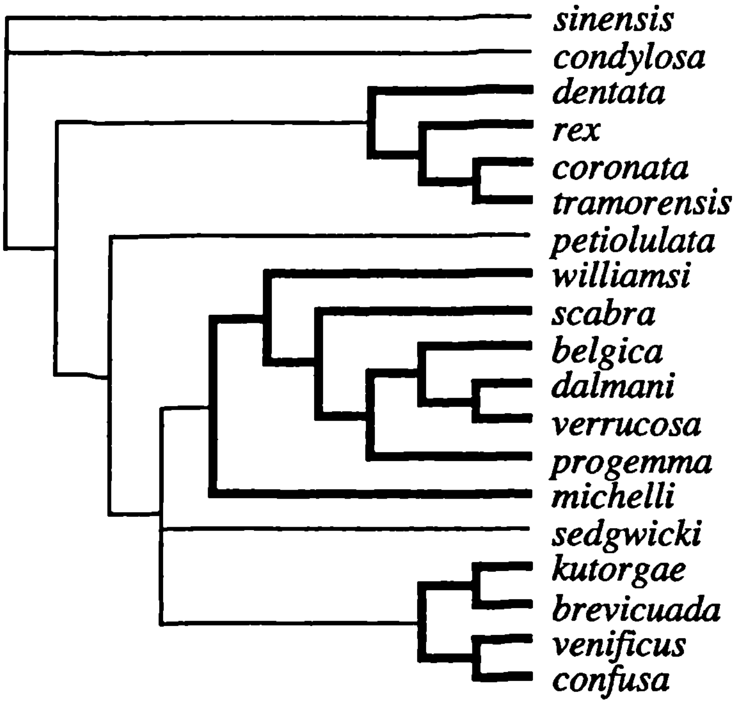
Figure 5.7: Tree two Phylogram annotated with all 'unambiguous' changes.



5.4.2 Systematic relationships of the taxa within *Atractopyge*:

As can be seen in Figure 5.8a three main subclades within *Atractopyge* may be recognised;

Figure 5.8a: The subclades within *Atractopyge*.



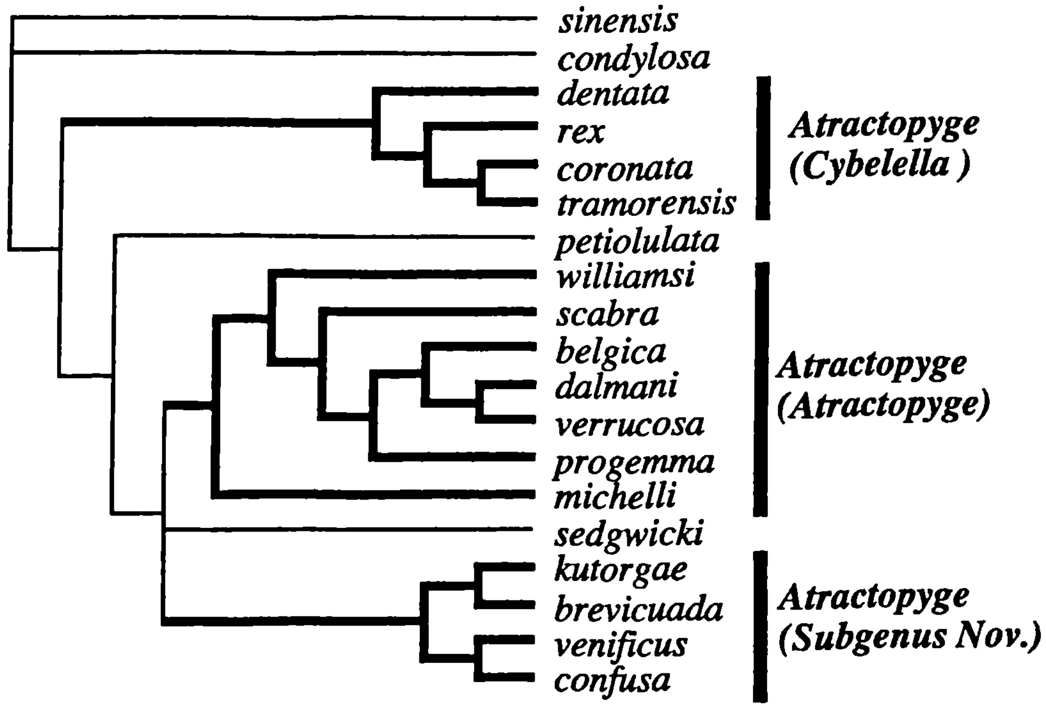
Each of these subgroups is easily recognisable on the basis of a few characters, making the initial placement of taxa simple. It is likely that these marked differences relate to the adaptation of *Atractopyge* to a number of different niches. I propose to recognise these three subclades herein as subgenera of *Atractopyge*:

Atractopyge (Atractopyge)
Atractopyge (Subgen. nov.)
Atractopyge (Cybelella)

In addition I propose to describe those basal taxa which are not situated within one of the subclades assigned to subgenera above as '*Atractopyge (sensu lato)*'.

The subgenera of *Atractopyge* proposed in this report are indicated in Figure 5.8b.

Figure 5.8b: The proposed subgenera of *Atractopyge*.



5.4.2.1 *Atractopyge (Atractopyge)*

Type species: *Calymene verrucosa* Dalman, 1827

Diagnostic features of *Atractopyge (Atractopyge)*

The S3 lateral glabellar furrows are oriented transversely, with an anteriorly directed branch situated abaxially; Polytuberculate lateral glabellar lobes. Adventitious, unpaired tubercles on the glabella; Anterior border widens abaxially and displays numerous, small, tubercles; The palpebral lobes are situated to the anterior of the fixigenal fields, in front of the S2 lateral glabellar furrows and project out into the librigenal fields; The posterior cephalic borders widen abaxially into broad, flat, genal areas which are tuberculate; More derived members of this group display a tuberculate occipital ring and a tuberculate posterior cranidial border;

Species included in *Atractopyge (Atractopyge)*:

Atractopyge belgica	Lespérance & Sheehan, 1988
Atractopyge dalmani	Owen & Tripp, 1988
Atractopyge michelli	(Reed, 1914)
Atractopyge progemma	Owen, 1981
Atractopyge verrucosa	(Dalman, 1827)

5.4.2.2 *Atractopyge (Cybelella)* **Reed, 1928**

Type species: *Zethus rex* Nieszkowski, 1852

This subclade includes the species *Atractopyge rex* (Nieszkowski, 1852) which was utilised as the type species for the genus *Cybelella* by Reed (1928). The taxa placed within this subclade are differentiated from those of the other subclades predominantly by the abaxial shallowing of the anterior border furrow and the development of anterior projections on the anterior border of the cranidium. Because the first of these features is independently derived by a number of taxa within the Cybelinae (see Section 4.6.1) and the anterior projections on the anterior border of the cranidiun are variably developed by the taxa placed in this subclade it is herein proposed to recognise *Cybelella* as a subgenus of *Atractopyge*. The original material of *rex* is still extant and available for examination (Bruton *et al.*, 1997), although time constraints have precluded this.

Diagnostic features of *Atractopyge (Cybelella)* are:

Sub-parallel glabellar outline; Glabellar axis sparsely tuberculate, with all of the tubercles being paired in a longitudinal row; The anterior border furrow shallows strongly abaxially; Anterior border with five tubercles or spines (basal members of this subclade may display 7, 9 or more); In the more derived section of this subgroup (excluding *dentata*) the S3 lateral glabellar furrows do not branch adaxially; In common with the *verrucosa* subclade, the palpebral lobes are positioned level with, or in front of, the S2 lateral glabellar furrow; There is a tendency towards amalgamation of the lateral glabellar lobes abaxially; There are no fixigenal spines.

Discussion;

Although the number of tubercles or spines on the anterior border is a useful character, it has the following limitations:

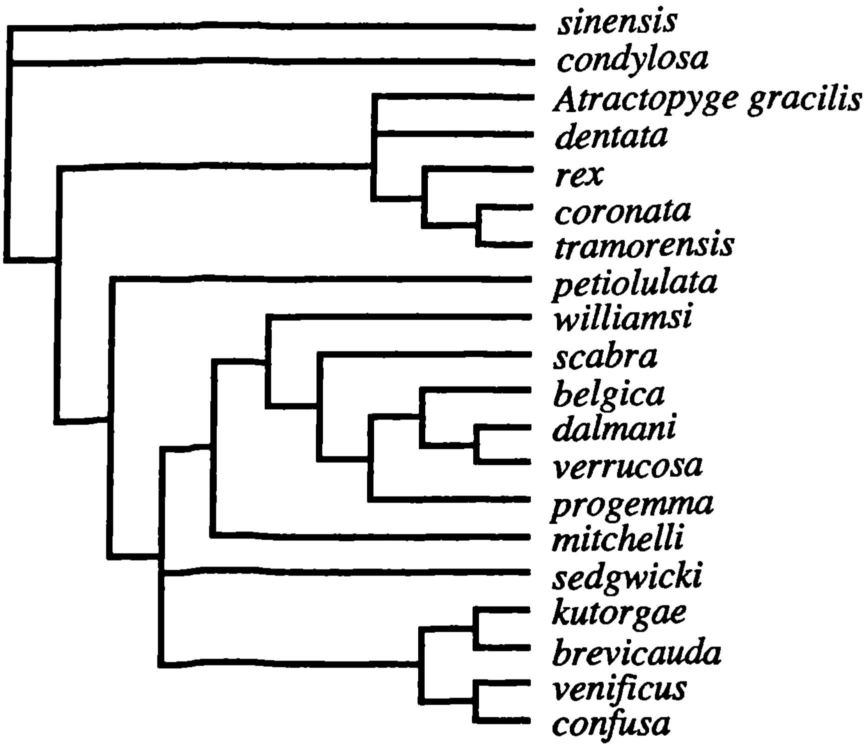
The species *A. condylosa*, which is outside *A. (Cybelella)* on the cladogram, also has five anterior border tubercles, highlighting the close relationship of *condylosa* to *A . (Cybelella)*. A number of unassigned, fragmentary cranidia, placed by this analysis in *A. (Cybelella)* (see 5.4.2.2a-c) display more anterior border projections than *dentata* but are otherwise very similar. These taxa with more than five anterior border tubercles or projections, are placed at an unresolved polychotomy at the base of the subclade possibly indicating that, with the recovery of further material, they may form an early subclade within *A. (Cybelella)*.

5.4.2.2a The taxon *Atractopyge gracilis* Ancygin 1973

Addition of the highly incomplete *Atractopyge gracilis* Ancygin, 1973 to the analysis resulted in the production of six minimum length trees of length 51 and C.I. of 6.47 (6.25, excluding uninformative characters, rescaled consistency index=0.512). It can be seen from the strict consensus of these six trees (Figure 5.9) that apart from a slight uncertainty as to the exact placement of *Atractopyge gracilis* within *A. (Cybelella)* the trees produced are identical to those which result when it is excluded. In spite of the uncertainty as to the exact placement of the taxon assigned to *Atractopyge gracilis* within *A. (Cybelella)*, this species should be regarded as belonging to that subgenus.

There are tubercles on the anterior border of *A. (C.) gracilis* which are organised in a similar fashion to the five of *dentata* and seven of *Atractopyge* aff. *dentata* of Whittington (1965) The poor preservation of this material precludes an exact count being made of the number of tubercles present but it is certainly more than the five exhibited by *dentata* and may be the same as that displayed by *Cybelella* sp. of Whittington (1965), to which it may be more closely related and is of a similar age.

Figure 5.9: Strict consensus of six trees produced by the addition of *Atractopyge gracilis* Ancygin, 1973 to the *Atractopyge* analysis.



5.4.2.2b *Atractopyge* sp. of Romano & Owen (1993);

Although too incomplete to add to this analysis, this specimen from the Lower Caradoc Clashford House Formation, near Herbertstown, Co. Meath, Ireland is clearly closely allied to the taxa discussed in Section 5.4.2.2.a. It displays a laterally shallowing anterior border furrow, bifurcate S3 and a number of peg-like anterior border tubercles. While there are certainly more than seven of these anterior border tubercles, their exact number is uncertain due to the fragmentary nature of the material.

5.4.2.2c *Cybelella* aff. *dentata* and *Cybelella* sp of Whittington (1965);

This material, from the Longvillian of the Bala area, is also too fragmentary to be included in the analysis but is clearly also closely related to *Atractopyge sp.* and Ancygin's *Atractopyge gracilis*. *Cybelella* sp of Whittington (1965), from the

M. Caradoc of Co. Wexford, is currently being assessed by Owen and Parkes (pers. comm. 1996) along with other material from the Leinster terrane and is also clearly closely related to these taxa.

Evidently, there is a large number of taxa which have a broadly similar morphology to that of *Atractopyge rex* (Nieszkowski, 1852), and therefore belong within the subgenus *Atractopyge (Cybelella)*, but which display more than the five anterior border projections which typify the other taxa included in this group. The material by which these taxa are known is highly fragmentary but it is likely that these taxa form a coherent subgroup within *Atractopyge (Cybelella)*.

Species included in *Atractopyge (Cybelella)*;

Atractopyge coronata	(Schmidt, 1881)
Atractopyge dentata	(Esmark 1833)
Atractopyge aff. *dentata*	Whittington, 1965
Atractopyge gracilis'	Ancygin 1973
Atractopyge rex	(Nieszkowski, 1852)
Atractopyge sp.	Romano & Owen 1993
Atractopyge tramorensis	(Reed, 1895)
Cybelella sp.	Whittington, 1965

5.4.2.3 *Atractopyge* (Subgen. nov.)

Type species: *Atractopyge kutorgae* (Schmidt, 1885)

The morphology of the glabella of members of *Atractopyge* (Subgen. nov.) is convergent upon that of the sub family Encrinurinae with both groups having numerous large, closely spaced tubercles on the glabella.

Diagnostic features of *Atractopyge* (Subgen. nov.) are:

The S3 lateral glabellar lobes branch adaxially, the branches and anterior portion being reduced so that the morphology of the S3 furrows approach that of a rounded pit connected to the axial furrow; Lateral glabellar lobes are poorly developed; Monotuberculate lateral glabellar lobes, except the basal taxon, *sedgwicki*; Glabellar tubercles are enlarged when compared to those of other species of *Atractopyge* and are situated close together; Adventitious, unpaired tubercles on the glabella; Anterior border displays seven, nine or more, closely spaced tubercles; Palpebral lobes are situated sub-mesially; 16 to 20 rings on the axis of the pygidium.

Species included in *Atractopyge* (Subgen. nov.):

Atractopyge brevicauda	(Angelin, 1854)
Atractopyge confusa	Owen, 1981
Atractopyge kutorgae	(Schmidt, 1885)
Atractopyge sedgwicki	MacGregor, 1962
Atractopyge venificus	Lespérance and Tripp, 1984

5.4.2.4 *Atractopyge (sensu lato)*:

As is usual with cladistic studies, a small number of the taxa do not neatly lie within one of the subclades. Rather than expand and water down any of the subgenus diagnoses I propose to assign these taxa to *Atractopyge (sensu lato)*. These taxa display the basic characters of the genus, without the derived apomorphies outlined in the subgenus diagnoses.

Species included in *Atractopyge (sensu lato)*;

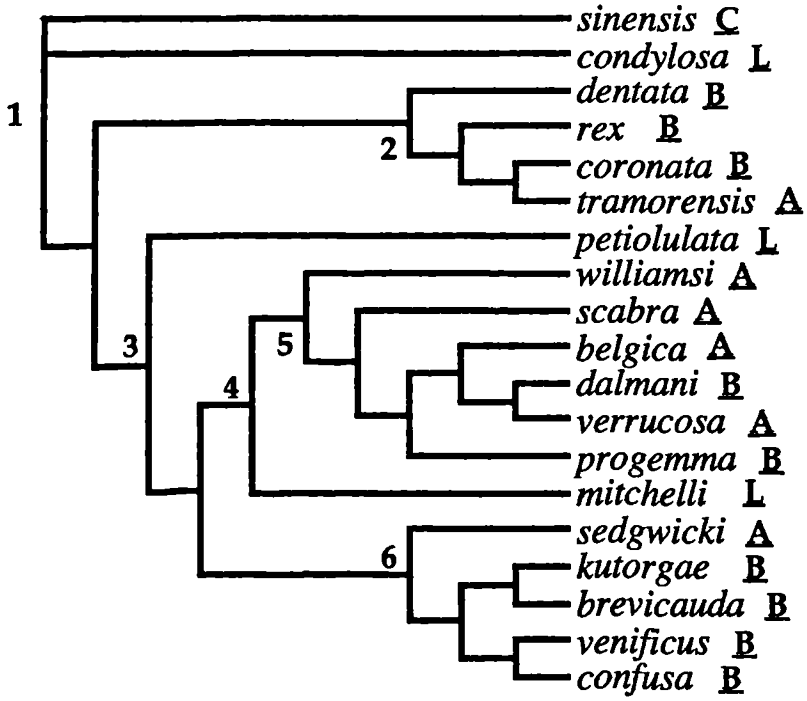
Atractopyge condylosa	Dean, 1971
Atractopyge petiolulata	Tripp, 1976
Atractopyge sinensis	Lu, 1975

5.5 The palaeobiogeographical history of *Atractopyge*

The three subgenera have different biogeographical histories (Figs 5.10-12) which may reflect the adaptation of the species within each of the three subclades to separate environments. In particular, *Atractopyge (Atractopyge)* and *Atractopyge* (Subgen. nov.) show similar, but not identical, biogeographical histories while that of *Atractopyge* (*Cybelella*) is distinct.

The more highly resolved second tree is employed in the biogeographical analysis as the calculation of gain/loss ratios over polychotomies is uncertain, introducing as much possible error as the assumption of validity of a node supported in one of two possible trees and not actively contradicted in the second.

Figure 5.10: Tree 2 annotated with palaeocontinent locations.
Numbers in **bold** are nodes discussed in text.
C = South China, **L** = Laurentia
B = Baltica, **A** = Avalonia



The study of the biogeographical history of *Atractopyge* may be somewhat formalised as outlined in Section 2.2.2. As the palaeobiogeographical affinities of the localities in which these taxa are found are well known the palaeobiogeographical, rather than the biogeographical, history of the group is analysed - ie the cladogram is annotated with the inferred palaeobiogeographical locations rather than with their modern day locations. The palaeobiogeographical locations of the taxa have been optimised on the cladogram. The results of this analysis may be seen in tables 4.1 to 4.4.

Tables 5.1-5.4. Gain/Loss ratio's for nodes 1-4.
(values rounded to nearest tenth, rounding up when a value is '_._5')

Node 1

Place	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	**4**	**3**	**0.8**
Baltica	**10**	**6**	**0.6**
Avalonia	**10**	**6**	**0.6**
China	**1**	**1**	**1**

Node 2

Place	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	0	0	0
Baltica	**1**	**3**	**3**
Avalonia	3	1	0.3
China	0	0	0

Node 3

Place	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	**2**	**2**	**1**
Baltica	7	3	0.4
Avalonia	**5**	**5**	**1**
China	0	0	0

Node 4

Place	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	**1**	**1**	**1**
Baltica	5	2	0.4
Avalonia	**3**	**4**	**1.33**
China	0	0	0

Node 5

Place	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	0	0	0
Baltica	**4**	**2**	**0.5**
Avalonia	**4**	**2**	**0.5**
China	0	0	0

Node 6

Place	Losses	Gains	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	0	0	0
Baltica	**1**	**1**	**1**
Avalonia	**1**	**1**	**1**
China	0	0	0

Taking each of the nodes in turn;

1. It can be seen that the both Laurentia, Baltica, Avalonia and South China are likely to have been found within the range of the ancestors of *Atractopyge*. Just such a range is observed in *Cybelurus*, inferred in the main analysis to be ancestral to *Atractopyge*. This supports the inference from the main Cybelinae analysis that *'Atractopyge' sinensis* may have developed independently in China while the main *Atractopyge* clade derived from a Laurentian ancestor, *condylosa*, by approximately the Llandeilan Stage of the Llanvirn.

2. After the origination of *Atractopyge* in Laurentia, *Atractopyge (Cybelella)* is obviously Baltic in derivation, later expanding into Avalonia. It appears that marginal Laurentia (the ocean island facies in which *condylosa* is found) was close enough to Baltica, for these taxa to expand into Baltica by the late Llanvirn, as evidenced by the presence of *dentata* in Norway.

Baltica and Avalonia were, in turn, relatively closely juxtaposed by the late Llanvirn or earliest Caradoc as *tramorensis* is found in the Tramore Limestone of County Waterford.

3. This large crown group, based by *petiolulata* is likely to have independently derived from Laurentian *Atractopyge* by the early Caradoc (*michelli* and *sedgwicki*). The high Gain/Loss ratio exhibited by Laurentia and Avalonia indicates that this expansion was initially from Laurentia to Avalonia .

4. This node highlights the order of appearance in Avalonia and Baltica of *Atractopyge (Atractopyge)*. The same biogeographical pattern, of origination in Laurentia being followed by rapid expansion into Avalonia, is seen as in node **3**.

5. By this node it can be seen that the inferred ancestral area of this restricted subclade included both Avalonia and Baltica, with no Laurentian component.

6. *Atractopyge* (Subgen. nov.) also shows no differentiation between Avalonia and Baltica as to which formed part of the ancestral range. It is likely either that expansion into these areas by members of *Atractopyge* (Subgen. nov.) was simultaneous (within the resolution of the stratigraphy) or that the picture is being distorted by missing data. The close fit of the branching order of the phylogeny to the stratigraphical order of the taxa mitigates against there being a large amount of missing taxa, lending support to the idea of a roughly simultaneous expansion of *Atractopyge* (Subgen. nov.) into these two areas. This biogeographical uncertainty is mirrored by the topological uncertainty about the exact placement of the species *sedgwicki*.

Discussion.

Atractopyge developed from a widespread group, probably *Cybelurus*, in the mid-to late Llanvirn. The genus developed in Laurentia with *'A'. sinensis* developing independently at the opposite side of the geographical range of *Cybelurus*..

There are at least two separate biogeographical histories within *Atractopyge*: the history of *Atractopyge (Cybelella)*, and that of the other taxa. These groups are morphologically distinct and are likely to have been adapted to significantly different environments. Time constraints preclude the detailed correlation of taxa to sedimentary environments within the present study, although some brief points may be noted:

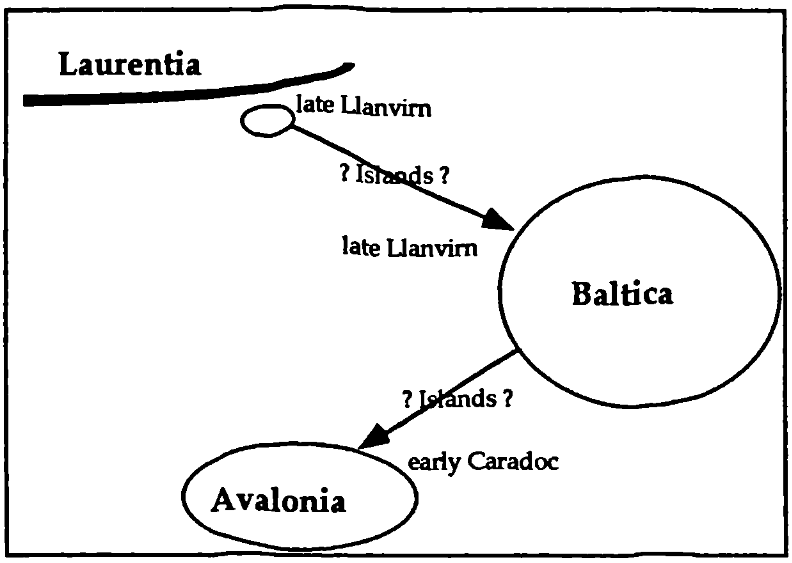
The earliest Laurentian *Atractopyge*, *A. condylosa*, inhabited a marginal cratonic or ocean island environment, similar to that envisaged for its ancestor *Cybelurus*. This interpretation of the environment in which *condylosa* lived is robust as the sediments in which it is found are part of a classic ocean island sequence of volcanic and sediments (Dean, 1971; Dean, 1973)

Members of *Atractopyge (Cybelella)* are similar in morphology to *A. condylosa* and are found in sediments which are inferred to have been from either ocean island environments or open shelf environments. This was the earliest subclade to develop after the Laurentian *condylosa* and was present in Baltica by the late Llanvirn, indicating either that at this point Baltica was either closer than Avalonia was to Laurentia or that Baltica was preferentially positioned with regard to ocean island chains or ocean currents. It is possible that members of *Atractopyge (Cybelella)* island hopped between the continents, inhabiting a slightly deeper facies than that of other *Atractopyge* and so being able to spread between the continents slightly before the other forms of *Atractopyge*.

This inference of members of *Atractopyge (Cybelella)* island hopping between Laurentia and Baltica is supported by the presence of taxa such as *Atractopyge* sp. (Romano & Owen 1993) in sediments from Co. Meath, Ireland and *Atractopyge gracilis* Ancygin 1973 from the mid-Caradoc of the middle Urals which are interpreted to have been marginal islands and all of which, when added to the analysis, plot as basal members of *Atractopyge (Cybelella).*

Member of this subgenus are found in Avalonia by the early Caradoc and as these taxa are inferred to have had a somewhat deeper water habit than other *Atractopyge* this may provide an indication of the earliest possible age of approach of Baltica and Avalonia, while the age of approach derived from the other taxa is likely to be the latest possible.

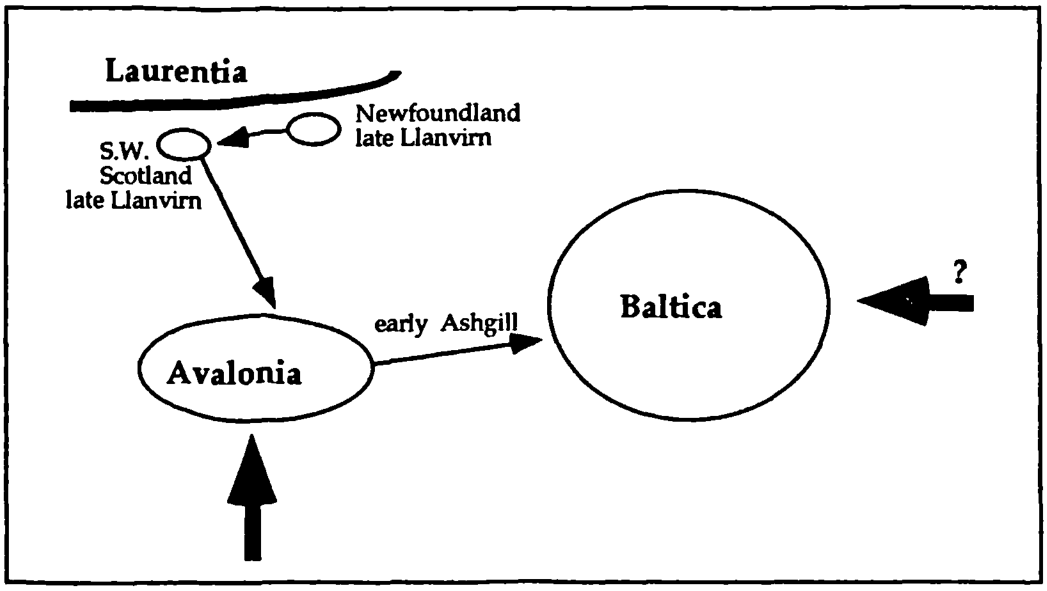
Figure 5.11: Expansion of *Atractopyge (Cybelella).* Thin arrows indicate 'range expansion.'



Members of the *Atractopyge* crown group (*A. (Atractopyge)* + A. (Subgen. nov.), which derived independently from the Laurentian ancestors, are found in sedimentary facies indicative of shallower water (possibly also reflected in their increased glabellar tuberculation). Their inferred inhabitation of slightly shallower water, more proximal, environments may explain why these taxa are not found outside Laurentia until the early Caradoc, by which time Baltica and Avalonia had moved to a position which was closer to Laurentia.

The first appearance of members of the crown group outside Laurentia was in Avalonia, identified as being the ancestral area of *Atractopyge (Atractopyge)*. This suggests that by the early Caradoc Avalonia was probably somewhat closer to Laurentia than was Baltica. It is not until the early Ashgill that members of *Atractopyge (Atractopyge)* are found in Baltica, which argues for either geographical separation of these continents or differing prevailing environmental situations until the early Ashgill.

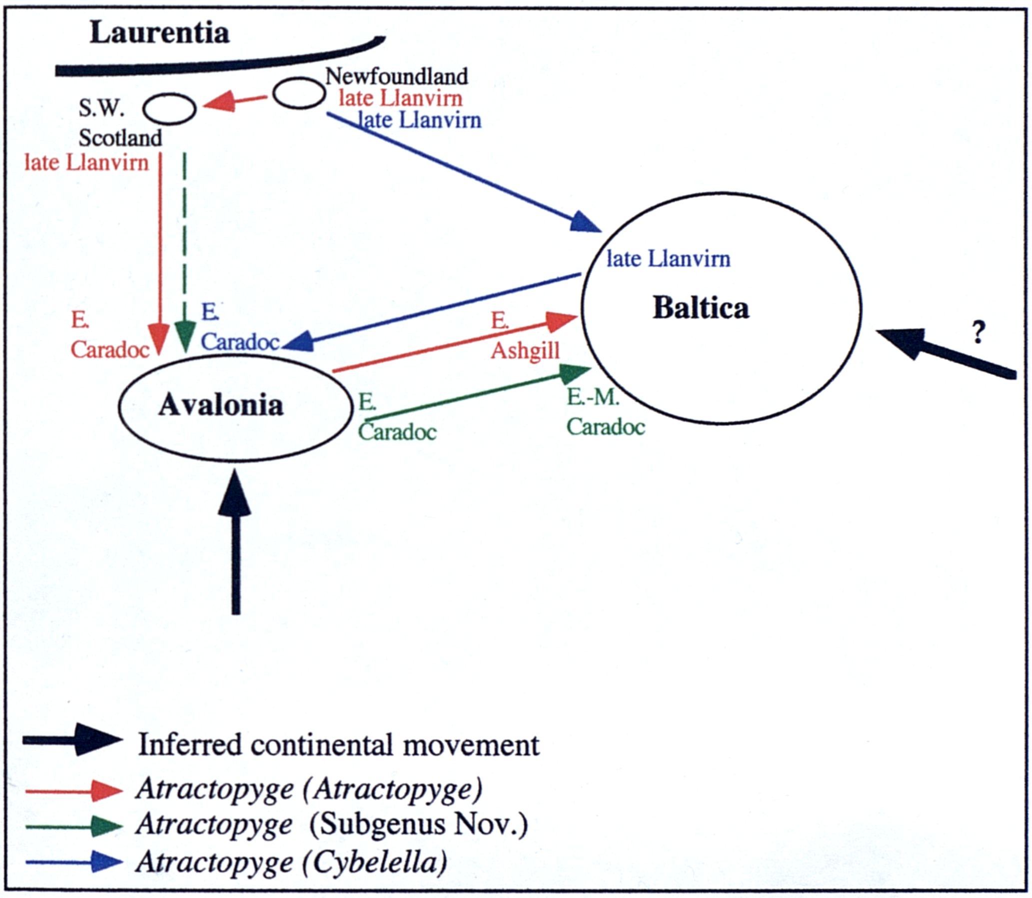
Figure 5.12 Sequence of expansion of *Atractopyge (Atractopyge)*.
Thin arrows show the sense of the 'range expansion.'
Thick arrows show the inferred sense of continental movement.



Apart from its common derivation from Laurentian stock, the biogeographical signal from *Atractopyge* (Subgen. nov.) is less clear with equal probability being given to a Baltic and Avalonian ancestry by the Gain/Loss ratio. It seems likely, but not certain, that the history of this subgenus mirrors that of *Atractopyge (Atractopyge)*, with common origination in Laurentia being followed by expansion into Avalonia then by diversification into Baltica - as this is the stratigraphical order in which the taxa are found.

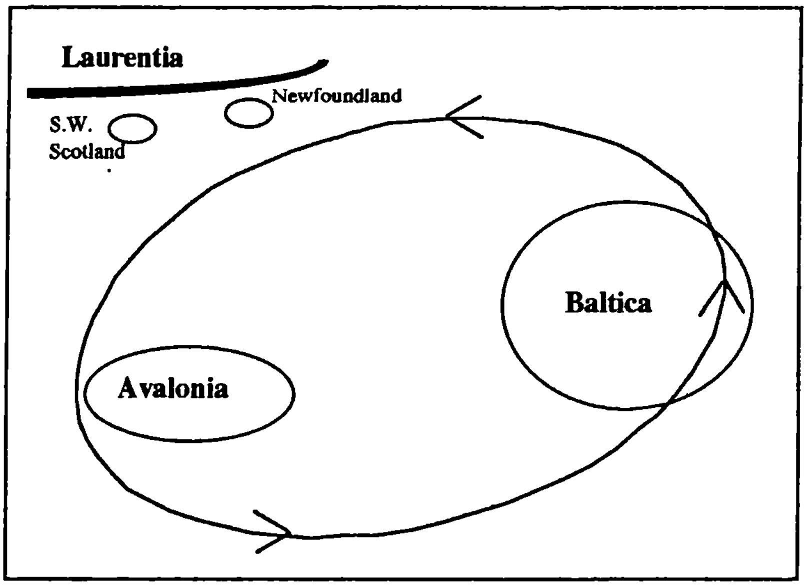
It can clearly be seen from Figure 5.13, that Avalonia closely approached marginal Laurentia by the early Caradoc at about the same time, or slightly later, Baltica moved close enough to Avalonia for the first exchange of faunas to occur. By the late Ashgill Baltica and Avalonia were sufficiently adjacent for mixing of the faunas to occur.

Figure 5.13: Diagram showing inferred 'range extensions' of the *Atractopyge* subgenera and schematic continental movements. Southern China is inferred to have been to the East of this area and not in direct communication with it.



The general pattern of range expansion seen is consistent with the presence of an anticlockwise southern hemisphere gyre although the early migration of *Atractopyge* (*Cybelella*) from Laurentia to Baltica and hence to Avalonia is anomalous in its sense, which is counter to the inferred southern hemisphere gyre.

Figure 5.14: Diagram of the inferred mid-Ordovician southern hemisphere gyre.



CHAPTER 6

ANALYSIS OF TAXA PREVIOUSLY ASSIGNED TO THE DINDYMENINAE

6.1 Introduction

In the discussion of the Cybelinae analysis (Section 4.5) the Dindymeninae was not recognised as a valid subfamily as its observed range of variation is comparable to that of genera within the Cybelinae. In addition, the only character which united all of the taxa in the Dindymene subclade was a negative one - the loss of eyes. As a result, the Subfamily Dindymeninae is here subsumed within the Cybelinae. The purpose of this chapter is to elucidate the relationships between those species which make up the '*Dindymene*' subclade. Members of this group are thought to have had a benthonic lifestyle in a deep water environment, indicated by the fine grained black shales in which the taxa are commonly found and in the absence of eyes in members of this clade.

6.2 Taxa considered in the analysis

6.2.1 Species included in this analysis

Taxa assigned to *Plasiaspis*, Prantl & Přibyl, 1949 herein

Type species: *Plasiaspis bohemicus* (Barrande, 1872)

Plasiaspis bohemicus	(Barrande, 1872) Šárka Fm. (Llanvirn) Šárka & Osek, Bohemia, Czech Republic

Taxa assigned to *Dindymene* Hawle & Corda, 1847 herein.

Type species: *Dindymene fridericiaugusti* Hawle & Corda, 1847

Dindymene cordai	Nicholson & Etheridge, 1878 Upper Drummock Group, Rawtheyan, M. Ashgill, Girvan, S.W. Scotland
Cornovica didymograpti	Whittard, 1960 Uppermost part of the Hope Shales,

	artus graptolite Zone Shelve inlier (Llanvirn), Wales
Dindymene fridericiaugusti	Hawle & Corda, 1847 Králův Dvur Formation, (M.-U. Ashgill), Bohemia
Dindymene heidingeri	Hawle & Corda, 1852 Králův Dvůr Formation, M.-U. Ashgill, Bohemia
Dindymene hughesiae	Reynolds, 1894 Zones 5,6,(&7?) of the Rawtheyan, M.-U. Ashgill, Cautley, Yorkshire, England
Dindymene longicauda	Kielan, 1960 *Staurocephalus clavifrons* trilobite Zone =*complanatus* graptolite Zone (Lower-M. Ashgill), Brzezinki (Poland), Bornholm, Scania and Västergötland (Sweden). Also Sholeshook Limestone, Cautleyan-Lower Rawtheyan (Ashgill) S. Wales (Price, 1980)
Dindymene ornata	Linnarsson, 1869 Lower - Middle Light Mudstones, *complanatus* graptolite Zone, (L. Ashgill), Holy Cross Mountains, Poland, (also Sweden),
Dindymene ovalis	Weir, 1959 Ashgill, County Clare, Ireland
Dindymene plasi	Kielan, 1960 Svarta Dobrotivá beds, Llanvirn-L. Caradoc, Bohemia
Dindymene saron	Fortey & Owens, 1987 Fennian Stage, Arenig, S. Wales

Eodindymene pulchra	(Olin, 1906) *Tretaspis* Shales, Tommarp(Sweden), Also Kielan, 1960 Lower Light Mudstones, *complanatus* graptolite Zone Lower Ashgill, Holy Cross Mountains, Poland

6.2.2 Discussion of included taxa

Dindymene ovalis is known only from relatively poorly preserved material and thus it was not possible to code many of the features used in the analysis. It was excluded from the initial analysis, but was added later to see where it was best placed.

Dindymene fridericiaugusti was largely coded from the excellent drawings of Barrande (1852) and was then checked against the lectotype figured by Šnajdr, 1983 (p. 156 and pl. 7, fig. 9 and pl. 15, fig. 2.). As a result, its coding is tentative and may be subject to revision at a later date. This, and *Dindymene heidingeri* were double checked against the drawings, photographs and descriptions in Kielan (1960). It is interesting to note that the cephalon assigned by Kielan to *D. fridericiaugusti* possesses a small genal spine which is directed to the anterior, while the specimen figured by Barrande has large genal spines which are directed to the posterior. From this it seems likely that the cranidium figured by Kielan does not, in fact, belong to *D. fridericiaugusti* but should be re-assigned elsewhere. While the material figured appears to be too fragmentary to form the basis of a new species it plots closest to the *D. longicaudata* subclade.

Dindymene saron Fortey & Owens, 1987 is somewhat difficult to code due to its small size. The diagrams and description in Fortey & Owens (1987) appear to diverge from each other in several key areas, such as the number of pygidial pleurae. As a result, the figured material was re-examined in order to clarify these points (see Figure 6.1) and used as the basis of the character coding for this analysis.

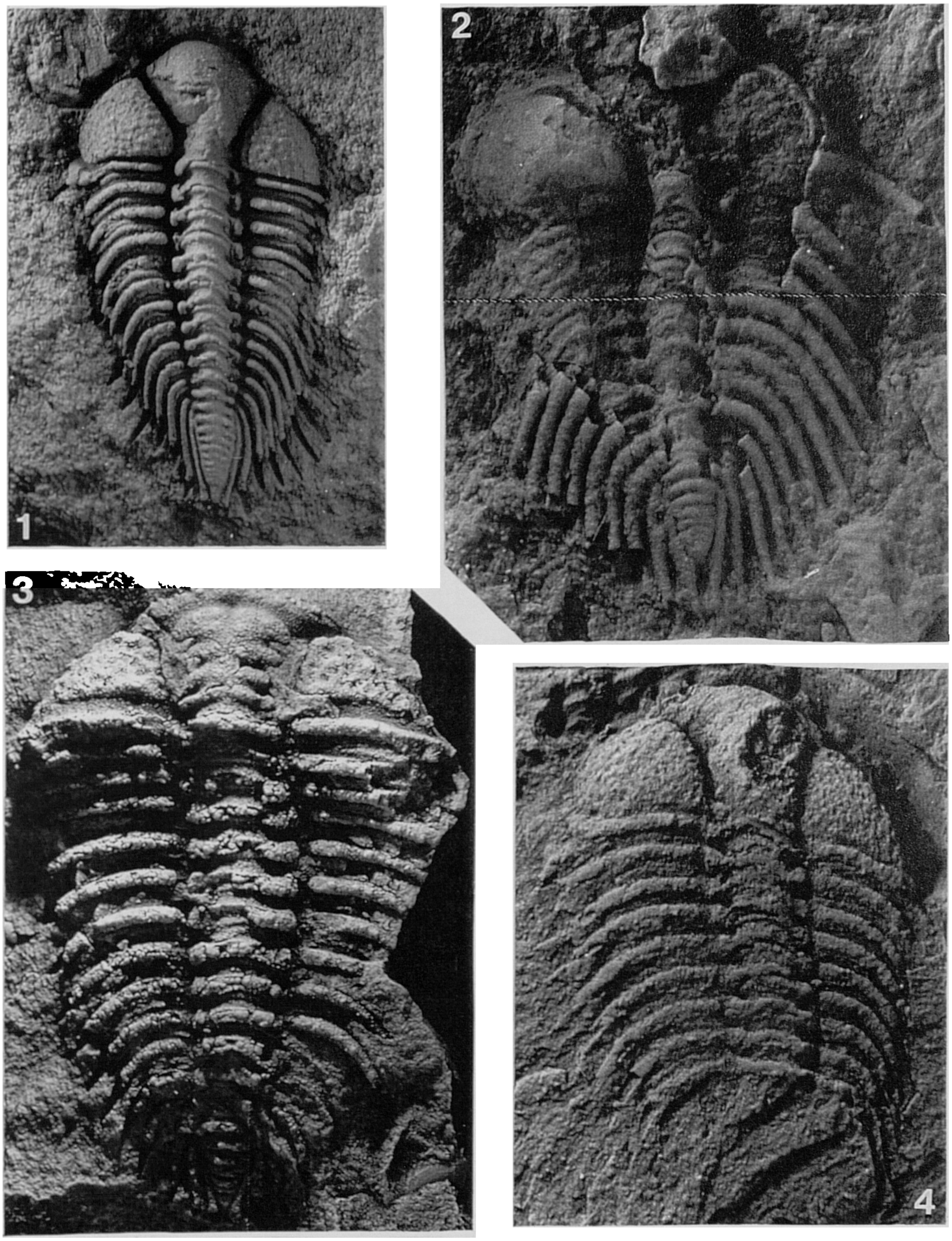


Fig. 6.1. Species of members of the *Dindymene* subclade.
1. *Dindymene ornata* Linnarsson, 1869, *Staurocephalus clavifrons* Zone (M. Ashgill), Brzezinki, Holy Cross Mountains, Poland, Natural History Museum collection, internal mould of complete individual In 56908, x9. 2. *Dindymene heidingeri* Hawle & Corda, 1852, Králův Dvûr Formation (Ashgill), St Benigna, Bohemia, Natural History Museum collection, partially exfoliated individual 3594, x9. 3. *Plasiaspis bohemicus* (Barrande, 1872), Šárka Formation (Lower to middle Llanvirn), Osek, Bohemia, Natural History Museum, External mould of complete specimen I 3432. 4. *Dindymene saron* Fortey & Owens, 1987, Fennian Stage, Pontyfenni Fm., Upper Arenig, Pontyfenni, Dyfed, South Wales internal mould of holotype cephalon and partial thorax, Natural History Museum collection, It 18984 (original of Fortey & Owens 1987, fig. 94a) x10

6.2.3 Taxa excluded from the analysis

Dindymene duftonensis	Dean, 1962 Dufton Shales, Cross Fell inlier, N. England, Marshbrookian Substage

Material too poor to allow sufficient characters to be coded for analysis.

Dindymene cf. *ornata*	Harper, 1956 Woolstonian Substage, Llanystwmdwy, N. Wales

Material too poor to allow sufficient characters to be coded for analysis.

6.3 Characters

6.3.1 Discussion and list of characters employed in the analysis

1. Lateral glabellar furrow pairs S2 and S3 present: '0' = yes/'1' = no.

2. Facial suture position:
   '0'= lying across free cheek and then cutting obliquely across the anterior border of the glabella.
   '1'= marginal
   '2' = situated inside the lateral border furrow before swinging inwards in its anterior portion, where it cuts across the frontal lobe of the glabella.

3. Presence of a rostral plate:
   Character disputed by Fortey & Owens (1987, p.235)
   '0' = rostral plate present.
   '1' = anterior, adaxial portions of the librigenae fused resulting in the absence of a separate rostral plate.

4. Inflation of the frontal lobe of the glabella: '0' = no/'1' = yes.

5. Frontal lobe of the glabella overhangs the anterior border furrow: '0'=no/'1'=yes.

The validity of this character has been disputed by Fortey & Owens (1987, p 234) who argued that the occurrence of this feature was dependent on the degree of post depositional compression of the glabella. While compression will affect the appearance of this character, it is thought to still be a useful character, with the caveat that care should be taken in determining its state and allowing for the varying effects of compression between specimens.

6. Presence of an anteromedian complex: '0' = no/'1' = yes.

7. Course of the axial furrows: '0' = concave outwards/'1'= convex outwards.

8. Glabellar tubercles large: '0' = no/'1' = yes.

9. Mesial spine present on the axis of the glabella: '0' = no/'1' = yes.

10. Size of the mesial glabellar spine: '1' = small/'3' = large.

11. Tuberculation of the fixed cheek: '0'= non tuberculate/'1'= tuberculate.

12. Density of tuberculation (This character is subjective but is still useful);
'0'= few tubercles/coarse granules.
'1'= many tubercles.

13. Size of the genal spines:
'0'= genal angles only.
'1'= small genal spines.
'2'= large genal spines.

14. Orientation of the genal spines (if present):
'0'= to the posterior.
'1'= to the anterior.

15. Tuberculation of the posterior cranidial border: '0'= no/'1'= yes.

16. Number of thoracic segments:
'0'= 10.
'1'= 11.
'2'= 12.

17. Row of tubercles on each of the thoracic axial sections: '0'= no/'1'= yes.

18. Axis of the fourth thoracic segment carries a large mesial spine:
'0'= no
'1'= yes.

19. Shape of the free points of the thoracic pleurae:
'0'= sharply curved to the posterior then directed directly to the posterior parallel to each other.
'1'= curved outwards (pleurae curve rearwards at a relatively low angle giving a splayed form).

20 Length of thoracic pleurae:
'0'= all short.
'1'= lengthening to the posterior. Pleurae terminate en echelon.
'2'= posterior pleurae highly elongate, Anterior pleurae less so. Pleurae terminate at a single transverse line.

21. Number of separate free pygidial pleurae confluent with axial rings: 1/2/3

22. Number of rings on the axis of the pygidium.

23. Axis of the pygidium is tuberculate: '0'= no/'1'= yes.

24. Pygidial ribs tuberculate: '0'= no/'1'= yes.

25. Additional pair of partially formed hindmost pleurae which are fused to the pygidial axis along their length: '0'= no/'1'= yes.

26. pygidial pleurae produced into elongate spines: '0'= no/'1'= yes.

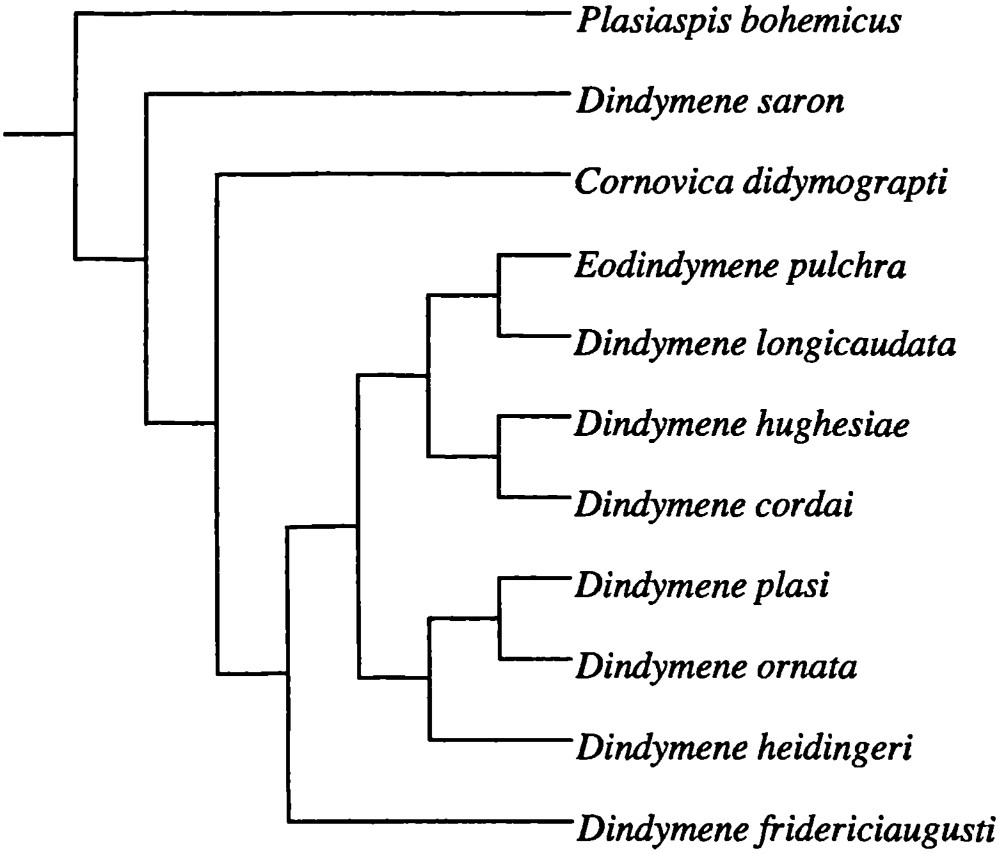
6.4. Results of analysis

6.4.1 Description of the cladograms resulting from the analysis

Analysis with the highly incomplete species *ovalis* excluded, producing one minimum length tree of length 38, CI = 0.842, Rescaled C.I. of 0.706 (Figure 6.2).

Note: that throughout this chapter, the names assigned to the taxa on the diagrams are those assigned to the taxa before this work.

Figure 6.2: Phylogeny of the *Dindymene* subclade.



The character changes comprising this minimum length tree strongly support all of the main subclades and are shown in figures 6.3 and 6.4.

Figure 6.3: *Dindymene* phylogram annotated with all occurring character changes. Character changes in bold ***italics*** are ambiguous (not unique or of uncertain value). Character changes in plain text are unambiguous.

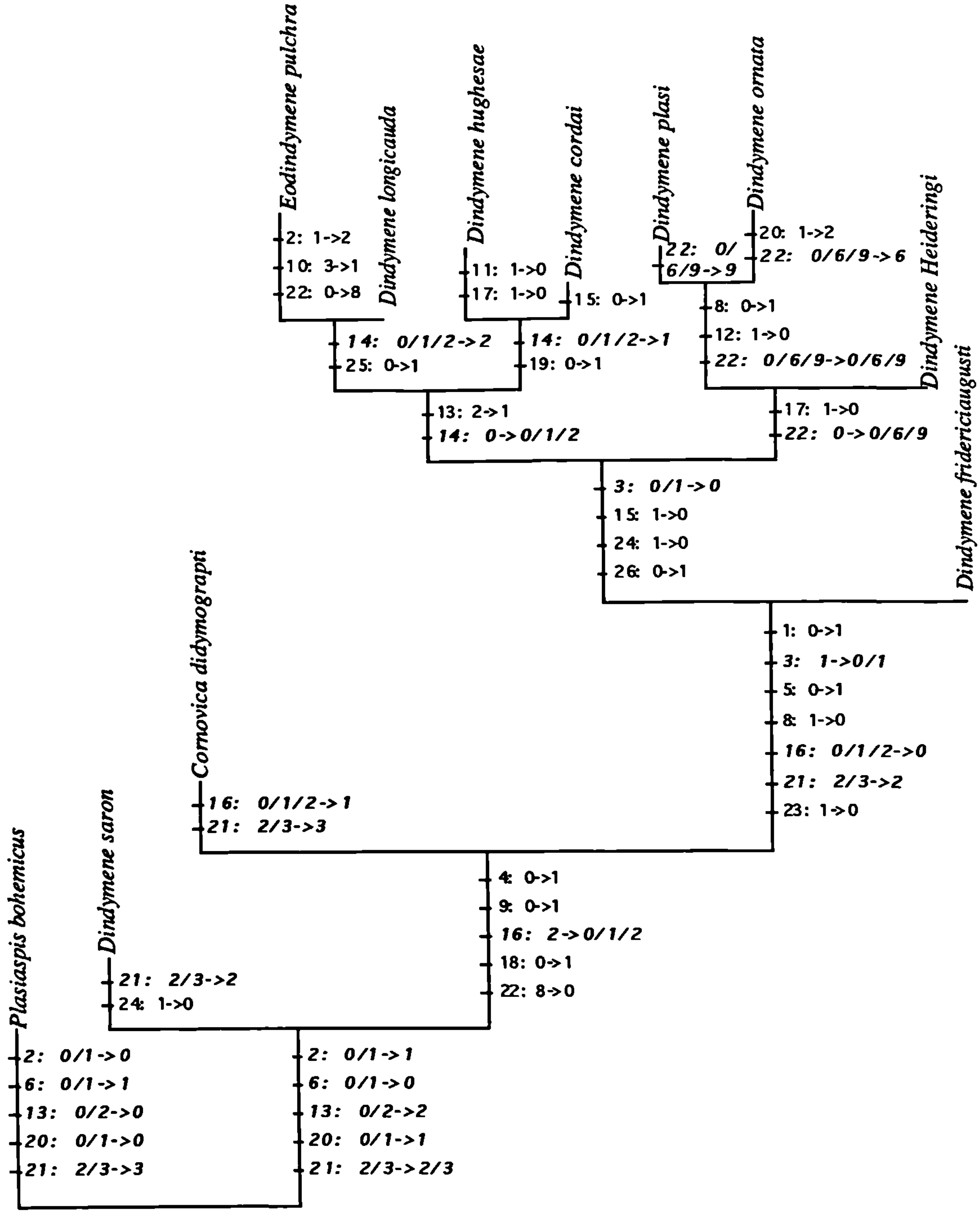
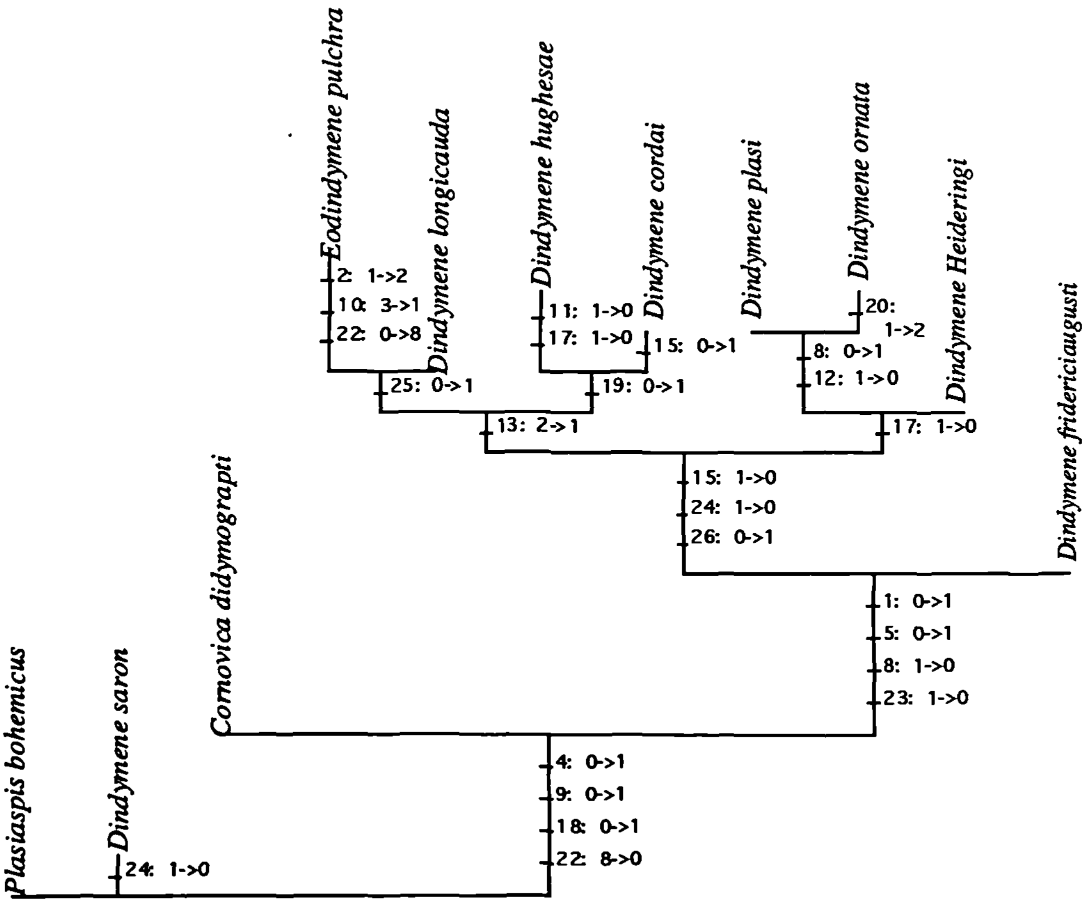


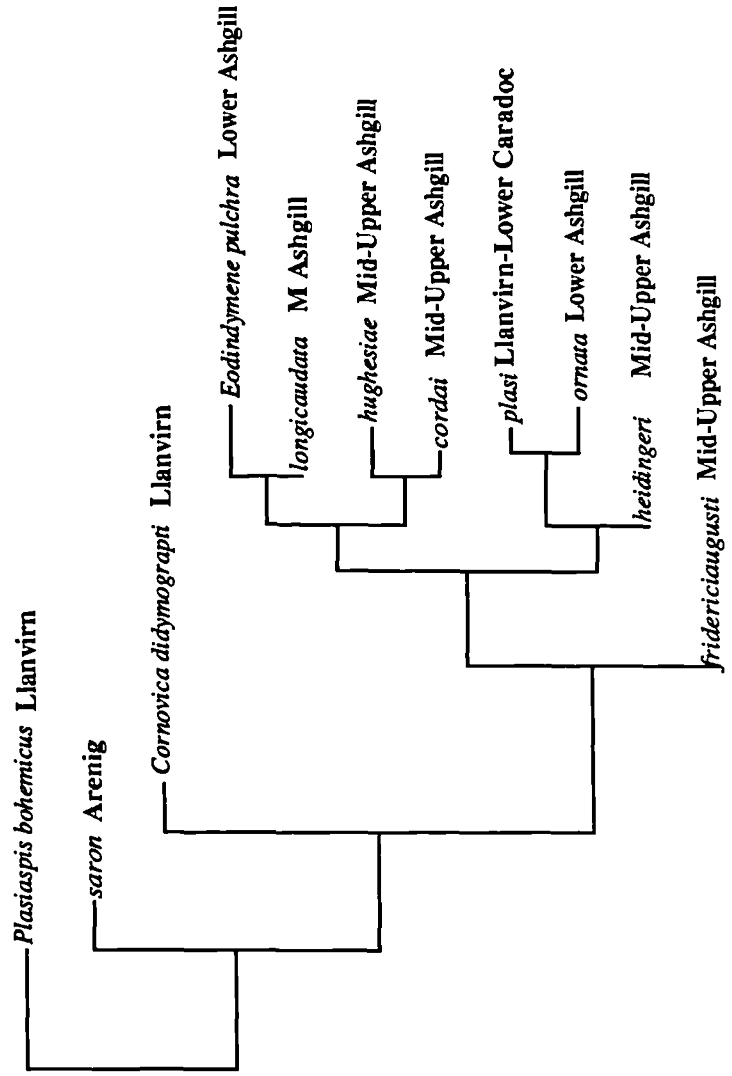
Figure 6.4: *Dindymene* phylogram annotated with all of the unambiguous character changes.



6.4.2 Comparison of the phylogeny derived from this analysis with the stratigraphical ages of the taxa:

As can be seen in Figure 6.5 the branching order of the phylogeny mirrors the stratigraphical ages of the species in the analysis. The only exception to this are the species *Dindymene plasi* and *Dindymene ornata* both of which are anomalously old for their position in the phylogeny.

Figure 6.5: Tree one from the analysis which excluded *D. ovalis*, represented as a phylogram and annotated with age of each of the component species.



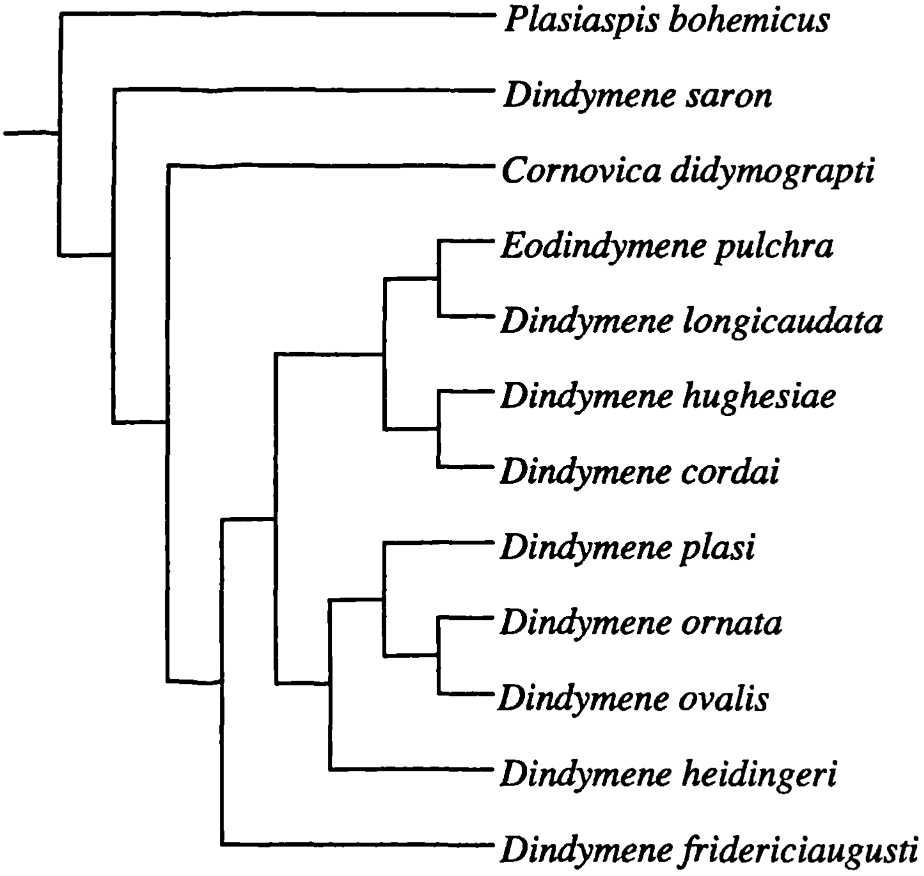
6.5 Assessment of *Dindymene ovalis* Weir, 1959

Dindymene ovalis is poorly known from a few, highly incomplete specimens and so was excluded from the main analysis. It was subsequently added to the matrix to determine its most likely position in the phylogeny, resulting in the production of the two trees shown in Figure 6.6. These trees are both of length 40, CI = 0.825 and Rescaled C.I. = 0.604.

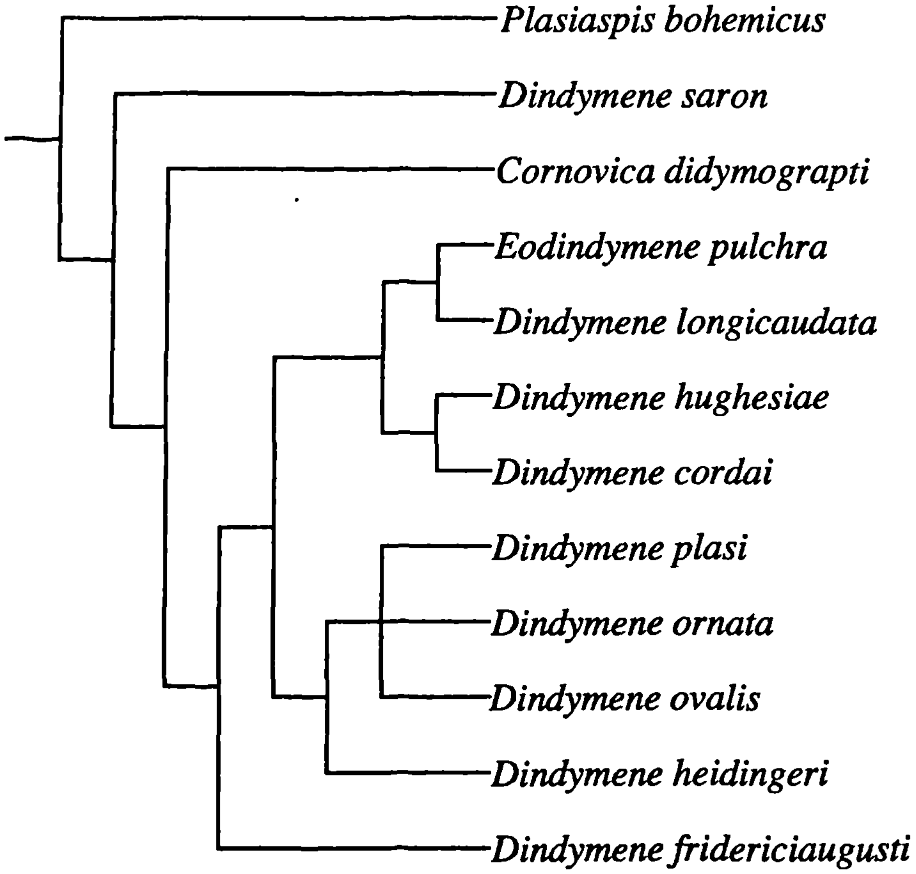
As can be seen *ovalis* plots in the *D. plasi* subclade and is likely to be a sister taxon to the species *ornata*.

Figure 6.6: Phylogeny of *Dindymene* with *ovalis included.*

1.



2.



6.6 Systematics of the taxa included in this analysis

6.6.1 Discussion of the systematic relationships of *Dindymene*

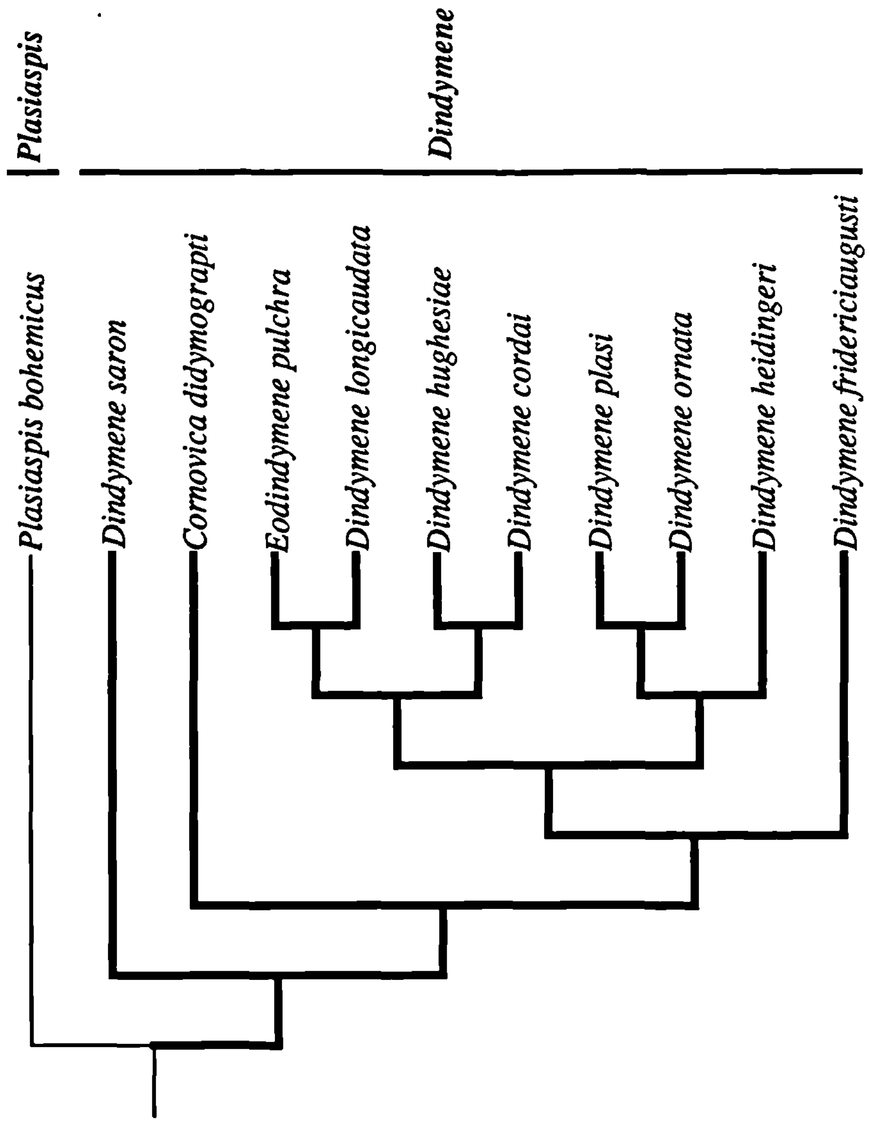
It is clear from the this analysis that Whittard (1960, p.123) was correct in recognising *Cornovica* as morphologically intermediate between *Plasiaspis* and *Dindymene (sensu stricto).* Fortey & Owens (1987) argued that *Cornovica* should be regarded as a junior synonym of *Dindymene* and that *Plasiaspis* is best placed within the 'Dindymeninae' group. As they assigned their new species *saron* to *Dindymene* and as *saron* and *Cornovica didymograpti* are very similar morphologically, it was logical to synonymise *Cornovica* with *Dindymene.* These proposals are followed here. Defining the base of *Dindymene* on the cladogram is difficult. *Plasiaspis* should certainly be classified as either a close sister group to *Dindymene* or a basal, pleisiomorphic member of that clade. The key to this question is which characters are regarded as being diagnostic of the genus *Dindymene* - where to draw the line. The loss of the S2 and S3 lateral glabellar furrows is not a suitable basal character as both *Dindymene didymograpti* and *Dindymene saron* display S2 and S3 lateral glabella furrows. The fusion of the anterior, adaxial portion of the librigenae, and the associated incorporation/loss of the rostral plate is potentially a useful character but it is the subject of some debate as to which, if any, species display this character (Kielan, 1960, Fortey & Owens, 1985). The development of a mesial glabellar spine is a feature which, in the Cybelinae, is restricted to *Dindymene*. Unfortunately, this spine is not present in *Dindymene saron* where, although the known material is rather poor, the spine appears to be truly absent rather than merely not preserved. This problem of the 'stepping in' of diagnostic characters is seen in all groups, and is discussed in section 2.1.8 The mesial glabellar spine is then also less than ideal as a basal apomorphy defining *Dindymene*.

Inflation of the glabella occurs in other members of the Cybelinae and Encrinurinae and so is a poor character upon which to define a genus. The absence of eyes in members of the *Dindymene* subclade, however, is unique within the Encrinuridae as is the abaxial migration of the facial suture, although the posterior migration of the facial suture in *Libertella* (Hu, 1971) results in a similar morphology of the anteromesial portion of the frontal lobe of the glabella. The small size of members of *Dindymene* is a useful secondary character but is not diagnostic.

Where complete specimens are known, the number of thoracic segments is a useful character, with *Plasiaspis bohemicus* and *Dindymene saron*, having 12, *Dindymene didymograpti* 11 and the other species 10 thoracic segments. The other Cybelinae all display 12 thoracic segments, including *Koksorenus* Koroleva, 1992 and *Libertella* Hu, 1971.

Other useful characters are the form of the pygidium, which displays small, or no anterior pleural fields, two or three pygidial pleurae and a slope-shouldered, bell shaped form. The pygidial form, while distinctive, has proved to be difficult to formally differentiate from that seen in other taxa while the number of pygidial pleurae and absence of anterior pleural fields on the pygidium are not unique to members of the *Dindymene* subclade. The result of this that the only unambiguous, abruptly appearing autapomorphy defining the base of *Dindymene* is the loss of eyes. It is sub-optimal to define a genus on the basis of the loss of a character. The most practical approach is to define *Dindymene* on the basis of a number of characters and allow for the inclusion of *sensu lato* species displaying some, but not all, of the diagnostic characters-as is common in other taxa in this suite of analyses.

Figure 6.7: *Dindymene* cladogram annotated with the proposed divisions.



The monotypic genus *Eodindymene* was erected by Kielan, 1960 to contain *Dindymene pulchra* Olin, 1906. *Eodindymene* was primarily differentiated from *Dindymene* by the position of the anterior portion of the facial suture, which cuts the anterior of the frontal lobe of the glabella. Fortey & Owens (1987) doubted if this character warranted generic distinction from *Dindymene*. Similar posterior migration of the facial suture is also seen in the cybeline genus *Libertella* Hu, 1971 and the mechanism of development of this feature in *Libertella* is discussed in sections 4.3.3 & 4.5.1.10. It is clear from this analysis that *Eodindymene pulchra* lies firmly within the *Dindymene* subclade and so the simplest way to deal with the development of this, probably developmentally controlled, novelty would be to regard *Eodindymene* as a subgenus of *Dindymene*. This would have the unfortunate result of making *Dindymene* paraphyletic, without any great increase in systematic clarity. It is proposed, therefore, to regard *Eodindymene* as a junior synonym of *Dindymene*.

Plasiaspis bohemicus (Barrande, 1872) is an extreme example of a taxon situated at the base of a subclade displaying few of the characters of that subclade. Such a taxon would normally be included as a member of the genus at whose base it is situated. *Plasiaspis*, however, looks very different to all of the other taxa assigned to *Dindymene* as it lacks the inflated glabella typical of *Dindymene*. As a result, I propose to retain *Plasiaspis* as a monotypic basal sister genus to *Dindymene*.

6.6.2 Diagnosis of the genera included in this analysis

6.6.2.1 *Plasiaspis* Prantl & Přibyl, 1949

Type species: *Plasiaspis bohemicus* (Barrande, 1872)
Šárka Fm. (Llanvirn),
Šárka & Osek, Bohemia, Czech Republic

Diagnosis (in addition to the basal diagnosis in section 5.1.7)

Anterior border furrow with median deepening; Facial suture lies along the marginal border furrow of the cephalon; Longitudinal anteromedian furrow present in the frontal lobe of the glabella; Glabella not inflated; Lateral glabellar lobes present and not reduced; Paired tubercles on the axis of the glabella; Genal spines absent; Posterior cranidial border tuberculate; 12 thoracic segments present, none macropleural; No mesial spine on the fourth thoracic segment: All of the thoracic pleurae are short and of equal length; Pygidial axis tuberculate with 8 axial rings.

Species included in *Plasiaspis*:

Plasiaspis bohemicus	(Barrande, 1872)

6.6.2.2 *Dindymene* Hawle & Corda, 1847

Type species: *Dindymene fridericiaugusti* Hawle & Corda, 1847
Králův Dvůr Formation,
Middle-Upper Ashgill, Bohemia

Diagnosis of *Dindymene* :

Glabella rounded, inflated and widens forwards; Lateral glabellar lobes L2 and L3 shallow, reduced to obsolescence in derived taxa; Large mesial spine on the axis of the glabella (except *saron*); Longitudinal anteromedian furrow in the frontal lobe of the glabella either very faint or absent; Anterior border furrow uniformly shallow; Anterior border of the glabella is of uniform width and may be tuberculate; Facial suture usually marginal (cuts the cheeks and frontal lobe in *pulchra*); Eyes absent; genal spines present, oriented either to the posterior or transversely; 10-12 thoracic segments (12 in all but basal taxa); No macropleural thoracic spines; Length of thoracic pleurae increases to the posterior, mesial spine on fourth thoracic segment; Pygidium of typical 'bell' shape with sloping, rounded anterior margin and terminating in a gentle curve, or transversely posteriorly; Two or three pygidial pleurae, anterior pleural fields on the pygidium small, number of pygidial axial rings variable, normally >10, pygidial axis non tuberculate.

Species included in *Dindymene*:

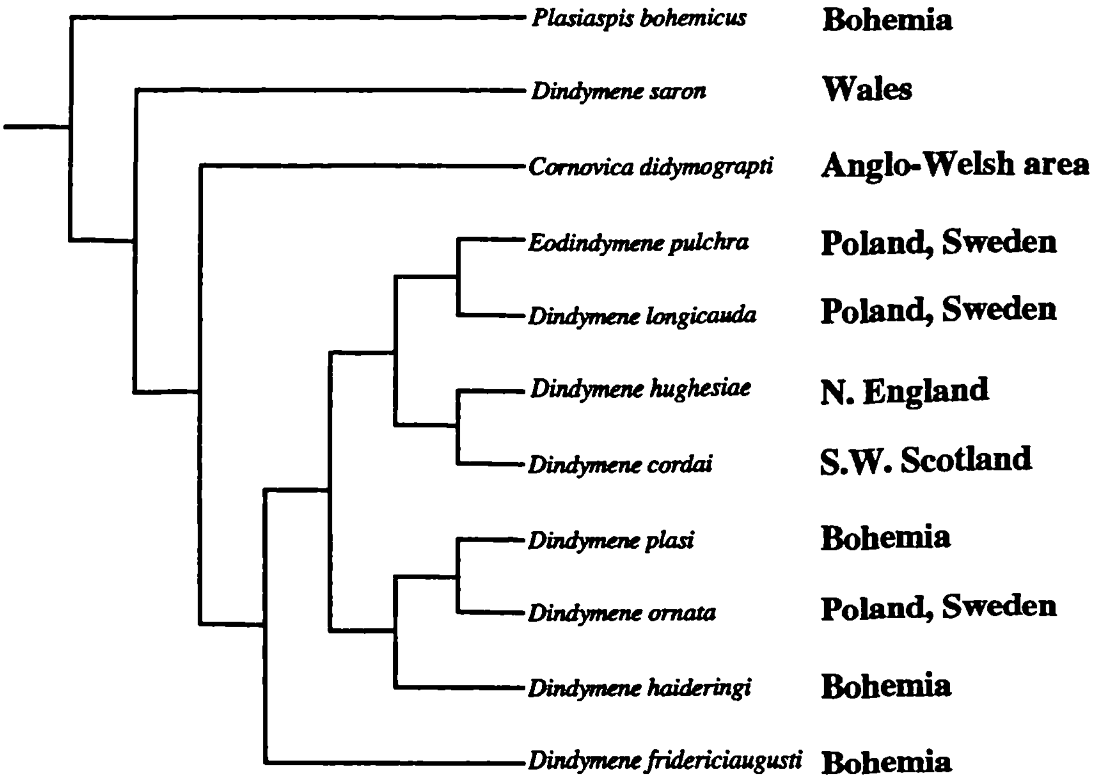
Dindymene cordai	Nicholson & Etheridge, 1878
Dindymene didymograpti	Whittard, 1960
Dindymene duftonensis	Dean, 1962
Dindymene fridericiaugusti	Hawle & Corda, 1847
Dindymene heidingeri	Hawle & Corda, 1852
Dindymene hughesiae	Reynolds, 1894
Dindymene longicauda	Kielan, 1960
Dindymene ornata	Linnarsson, 1869
Dindymene ovalis	Weir, 1959
Dindymene plasi	Kielan, 1960
Dindymene pulchra	Olin, 1906
Dindymene saron	Fortey & Owens, 1987

6.7. Biogeographical inferences:

6.7.1 Informal palaeobiogeographical inferences:

The close grouping of the ages of the *Dindymene* in the upper part of the cladogram, the incomplete nature of the range of taxa included in the analysis and their deep water habit make informal assessment of their biogeographical history difficult.

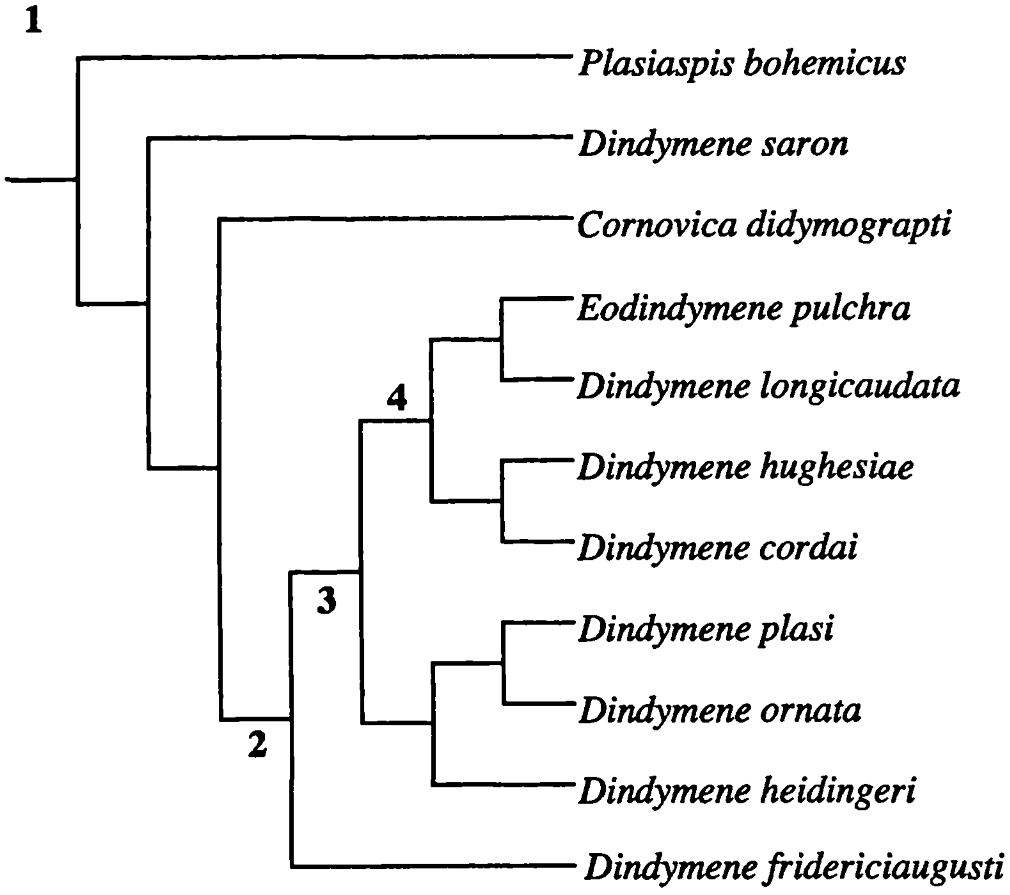
Figure 6.8: Cladogram annotated with the present day geographical distribution of members of the *Dindymene* subclade included in this analysis.



The species which forms the outgroup in this analysis (for display purposes only), *Plasiaspis bohemicus*, is found in Bohemia (Gondwana) while the basal in-group taxa, *didymograpti* and *saron*, are both found in Wales (Avalonia) (Figure 6.8), supporting the juxtaposition of Avalonia and Gondwana during the Arenig. Gondwanan taxa continue to figure strongly in the basal section of the cladogram with taxa of this age being found in Bohemia. By the mid. Caradoc *Dindymene* was found in Baltica, evidenced by an undescribed cranidium from Norway (A.W.Owen pers comm.) and reached the Laurentian margin by the late Caradoc/early Ashgill (undescribed material in the Whitehouse Group alluded to by Ingham (1974)). In the upper section of the cladogram there is evidence of roughly simultaneous appearance of *Dindymene* in Baltica (Poland and Sweden), Laurentia (S.W. Scotland) and Avalonia (N. England) from Gondwanan (Bohemian) ancestors, although this information is undermined by the undescribed material discussed earlier.

6.7.2 Gain/Loss ratio study of the taxa included in this analysis

Figure 6.9: *Dindymene* cladogram (without *ovalis*) annotated with the nodes for which gain/loss ratios are examined.



It can be seen from table 6.1 that Bohemia and Wales formed the ancestral area of *Dindymene*. At node 2, the ancestral area includes Bohemia, Poland and Sweden-Wales is unrepresented at this, or any higher, nodes.

By node 3, the ancestral area is most likely to include Poland and Sweden, with Bohemia assuming a secondary role. At node 4 Sweden and Poland form the ancestral area while Bohemia is unrepresented. From these two areas *Dindymene* appears to spread into N.E. England and S.W. Scotland. It is interesting to note that Poland and Sweden appear to be strongly linked, being combined in a single palaeocontinent, Baltica. At the base of the cladogram Bohemia and Wales appear to be combined in a single palaeocontinent, representing the juxtaposition of Avalonia (Wales) and Gondwana (Bohemia). The Gain/Loss ratio study repeats the same broad picture as that inferred informally, but provides no further information.

Table 6.1; Tables of gain/loss ratios for nodes 1 to 4.

Node 1			
Place	**Losses**	**Gains**	**Gains/Losses**
Bohemia	4	4	1
Wales	2	2	1
Poland	7	2	0.29
Sweden	7	2	0.29
N. England	7	1	0.14
SW Scotland	7	1	0.14

Node 2			
Place	**Losses**	**Gains**	**Gains/Losses**
Bohemia	2	2	1
Wales	0	0	0
Poland	4	2	0.5
Sweden	4	2	0.5
N. England	4	1	0.25
SW Scotland	4	1	0.25

Node 3			
Place	**Losses**	**Gains**	**Gains/Losses**
Bohemia	2	1	0.5
Wales	0	0	0
Poland	3	2	0.66
Sweden	3	2	0.66
N. England	3	1	0.33
SW Scotland	3	1	0.33

Node 4			
Place	**Losses**	**Gains**	**Gains/Losses**
Bohemia	0	0	0
Wales	0	0	0
Poland	1	1	1
Sweden	1	1	1
N. England	2	1	0.5
SW Scotland	2	1	0.5

CHAPTER 7

CYBELOIDES SLOCOM, 1913

7.1 Introduction:

The genus *Cybeloides* was recognised in the large scale cybeline analysis as a monophyletic group whose sister group was *Bevanopsis*, from which *Cybeloides* is distinguished by the formation of a pulvinus and development of a large post-axial spine on the pygidium While *Cybeloides* is poor in terms of large scale biogeographical information - being largely a Laurentian group - it is possible to infer a considerable amount of information on the relative geographical distributions of the Laurentian/marginal Laurentian terranes within the province.

It was also desirable to discover the species level relationships of this subclade to ensure a complete resolution of the relationships of the Cybelinae. The resolution of the species level relationships also clarified the division of *Cybeloides* into the two subgenera *Cybeloides (Cybeloides)* Slocom, 1913 and *Cybeloides (Paracybeloides)* Hupé, 1955

Both currently known species of the sister group *Bevanopsis* were included in the analysis.

7.2 Species considered in the analysis;

7.2.1 Species included in the analysis;

C. (Cybeloides) anna	Ludvigsen, 1979 Sunblood Formation, Upper Llanvirn, Southwestern District of Mackenzie, Western Canada
C. (Cybeloides) anna26	Ludvigsen, 1979 Sunblood Formation, Upper Llanvirn, Southwestern District of Mackenzie, Western Canada

This is a specimen figured and assigned by Ludvigsen (1979 figure 26) to *Cybeloides anna*. It differs from the holotype of *anna* in numerous features and has been coded separately for this analysis. The apomorphies by which it differs may be seen in the annotated phylogram, Figure 7.4

C. (Cybeloides) cimelia	Chatterton & Ludvigsen, 1976 Esbataottine Formation Chazyan/Blackriveran (U. Llanvirn/L. Caradoc) Southwestern District of Mackenzie, W. Canada
C. (Cybeloides) iowensis	Slocom, 1913 Maqouoketa Formation, Ashgill, E. USA
C. (Cybeloides) prima	(Raymond, 1905) Chazy Limestone, U. Llanvirn - L. Caradoc New York, USA
C. (Cybeloides) rugosa	(Portlock, 1843) Bardahessiagh Formation (M. Caradoc) *Climacograptus peltifer* -lower *Dicranograptus clingani* graptolite zones, Pomeroy, Northern Ireland.

This species was initially defined on the basis of a single pygidium from the Bardahessiagh Formation, re-illustrated by Ingham (1968, pl. 1 fig. 16). The rest of characters have been coded from an, as yet undescribed, almost complete specimen from the Bardahessiagh Formation which is currently undergoing preparation and description by Dr J.K. Ingham at the Hunterian Museum, University of Glasgow. Further specimens of *C. rugosa* have been described from mass flow deposits in the Kirkcolm Formation at Kilbucho and Wallace's Cast, Southern Uplands. L-M. Caradoc, *Climacograptus*

	peltifer -lower *Dicranograptus clingani* graptolite zones by Owen & Clarkson (1992)
C. (Cybeloides) spinifera	Tripp, 1954 Kiln Mudstone, M. Caradoc S.W. Scotland
C. (Cybeloides) virginiensis	Cooper, 1953 Edinburg Formation, Blackriveran (L. Caradoc) Virginia, USA
C. (Paracybeloides) conjuncta	(Owen, 1981) Lunner Formation L. Ashgill Hadeland, Norway
C. (Paracybeloides) ella	(Narroway & Raymond, 1906) Ottawa Formation, Blackriveran (Lower Caradoc), Ottawa-St. Laurence Lowland, Ontario, Canada
C. (Paracybeloides) buttsi	Cooper, 1953 Synonymised with *C. ella* in this analysis. Little Oak Limestone, Blackriveran (L. Caradoc), Virginia, USA
C. (Paracybeloides) girvanensis	(Reed, 1903) Upper Drummock Group, High Rawtheyan, (U. Ashgill) Girvan, S.W. Scotland, and Pusgillian to Rawtheyan (L.-U. Ashgill), Oslo, Norway (Owen, 1981), and Sholeshook Limestone Formation, Cautleyan-Rawtheyan (Ashgill), South Wales, (Price, 1980), and the Ashgill of the Cautley and Dent Districts of Westmorland and Yorkshire, England (Ingham, 1974)

Cybeloides parotti	Whittington, 1964 Synonymised with *girvanensis*, by Ingham (1968,) Ddolhir Beds, Rawtheyan (U. Ashgill), Wales
C. (Paracybeloides) loveni	(Linnarsson, 1869) Fjäcka Shale, Johnstorp & Ulunda Formations (L.-M. Ashgill) Sweden, Also reported from the Ashgill of Siberia by; Rosova (1960) Also reported from the Ashgill of Gorny Altai by Semenova *et al.* (1960)

7.2.2 Species excluded from the analysis due to poor illustration or degree of incompleteness;

Cybeloides attenuata	(Reed, 1897) Portrane Limestone (Cautleyan), Eire
Cybeloides plana	Sinclair, 1944 Sherman Falls Formation M. Caradoc, Canada
C. (Paracybeloides) rarissimus	Nan, 1985 Wulongtun Formation, Eastern Yilehuli Shan, Upper Ordovician (Ashgill) Heilo Ngjiang Province, China
C. (Cybeloides) seca	Evitt & Tripp, 1977 Lincolnshire Formation, Chazyan (U. Llanvirn), Virginia, USA
Cybeloides sulcata	(Troedsson, 1928) Cape Calhoun, N. Greenland Edenian/Maysvillian (L. Ashgill)
Cybeloides terrigena	Tripp, 1962 Confinis Flags (U. Llanvirn)

Girvan, S.W. Scotland

Specimens of this species are all highly abraded. It is likely that *terrigena* is a basal member of *Cybeloides (Paracybeloides)*, but it is not possible to confidently assign this species there until better specimens are recovered.

7.2.3 Outgroup species included in the analysis:

Bevanopsis thor	(Ludvigsen, 1979) Sunblood Formation, Upper Llanvirn, Southwestern District of Mackenzie, Canada
Bevanopsis ulrichi	Cooper, 1953 Edinburg Formation (L. Caradoc), Virginia, USA.

7.3. Characters employed in the analysis:

The characters employed are of simple, unordered type and are all of equal weight. They are as follows;

1. Anterior border tuberculation:
   '1' = median tubercle present.
   '2' = no median tubercle present.

2. Enlargement of the anterior border tubercles (n/y): '0'/'1'.

   This character is an autapomorphy of *iowensis*. Although it is unquantified, the separation in size of the anterior tubercles of *iowensis* from those of other species of *Cybeloides* is clear.

3. Tuberculation of the triangular area on the anterior of the frontal lobe (n/y): '0'/'1'.

The anterior of the frontal lobe of all species of *Cybeloides (Cybeloides)* displays a non-tuberculate, pitted, triangular area. This area is oriented with one side to the anterior and the apex of the triangle pointing towards the posterior, close to the site of the median pit. The shape and orientation of this area is similar to that of the depressed triangular area in *Cybele*, the raised triangular area in '*Atractopyge*' *sinensis* and the depressed triangular area in *Cybelurus mira*. The function of this area is unclear but may be a broad muscle attachment site.

4. Tuberculation of the axis of the glabella:
'0' = tubercles paired, with smaller adventitious tubercles.
'1' = tubercles predominantly unordered and of equal size, with the unordered 'adventitious' tubercles outnumbering any paired tubercles.

This is a somewhat unsatisfactory, imprecise, character which can be removed without damaging the relationship trees produced by the analysis. In spite of this it is retained in the analysis as it is an easily discernible diagnostic character of *Cybeloides (Paracybeloides)*.

5. Number of complete, ordered, columns of tubercles on the axis of the glabella:
'0' = tubercles either paired or with occasional paired tubercles in generally unordered glabellar axial tuberculation.
'1' = four columns, i.e. the tubercles are arranged in transverse lines of four tubercles.

6. Pulvinus present (n/y): '0'/'1'. (See Section 4.3.2)

The form of the pulvinus is variable in *Cybeloides*. This variability takes two forms;

A. Variation in the shape of the fused pulvinar lobes.

The variation in outline shape of the pulvinar lobes, i.e. whether their outer edges converge, are sub-parallel or diverge anteriorly, does not appear to be stable within species and is not included in this analysis.

Variation in the general shape of the pulvini - i.e. whether the component lateral glabellar lobes retain independent convexity and are discernible within the pulvinus - is stable within species and variable between some species and so was coded for in character 7.

B. Variation in the development of the longitudinal furrows which isolate the pulvini from the axis of the glabella.

The degree of development of the longitudinal furrows isolating the pulvinar lobes from the axis of the glabella was found to be variable within species. In addition, separation of a condition where the adaxial portion of the lateral glabellar lobe is depressed relative to the pulvinus and/or the axis of the glabella from one where there is development of a furrow across the adaxial portion of a lateral lobe seems overly subjective. As a result, a character describing variability in the development of these longitudinal furrows is not included in the analysis.

It is worth noting that this pair of variably developed longitudinal furrows that pass through the axial apodemes, separating the pulvini from the glabellar axis, exactly follow the course taken by the axial furrows during early stages of development. These axial furrows are initially parallel to and immediately beside the glabellar axis, passing through the axial apodemes (see Section 4.3.2). During ontogeny they migrate abaxially as the lateral glabellar lobes develop and are observed to be abaxial to both the pulvini and the axial apodemes in adult members of *Cybeloides*. These furrows are present in addition to the pulvinar furrows separating the pulvini from the glabellar axis. It is clear from the co-existence of these two structures that the pulvinar furrows and the axial furrows are two separate features. However, as the course of the pulvinar furrows exactly follows that of the axial furrows in juvenile individuals, and as pulvinar-type furrows are not seen isolating the lateral glabellar lobes of any other members of the Encrinuridae, it is likely that these pulvinar furrows developed by a 'reactivation' of the juvenile 'axial furrow' pair of early ontogeny.

If this proves to be the case, this reinforces the point that terms that are clearly defined in the adult may require to be flexibly applied, or to be inappropriate, when applied to different ontogenetic stages.

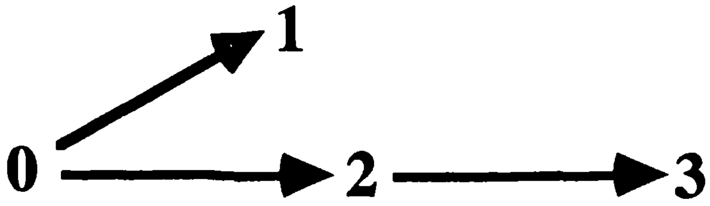
7. Form of the pulvinus:
'0' = Form of the component lateral lobes discernible as independent convexities within the pulvinus.
'1' = Pulvinus smooth and ovate with the convexity of the component lateral lobes not discernible.

8. Eyes positioned on tall, slender, stalks/ eyes unstalked: '0'/'1'.

9. Tuberculation of the pulvinus:
0 = Non-tuberculate, small granules present.
1 = Component lobes of the pulvinus monotuberculate (rare, isolated, large tubercles on the pulvinus).
2 = Pulvinus (and component lateral lobes) covered with numerous, scattered coarse granules.
3 = Pulvinus (and component lateral lobes) covered with numerous, scattered, small tubercles.

Initially, this character was coded as a user defined stepmatrix character (see Figure 7.1). On running the analysis it was found that in spite of the characters representing this feature being defined in this way, the inferred pattern of character change was not supported by the analysis or by any independent evidence. Rather than try to force the sequence of character state developments along the path originally envisaged, the character was reset to simple unordered type which produced the same topology of cladogram but with an increased C.I. In other words, the assignment of this character to an unordered state better represented the actual situation.

Figure 7.1: Inferred order of derivation of the inferred sequence of development of character 9 (coded as 'unordered' in the analysis).



10. Tuberculation of the fixigenal field:
'0' = Tuberculation restricted to torular, postocular and associated tubercles.
'1' = Field covered with numerous small tubercles in addition to the tubercles outlined above.

11. Tuberculation of the eye ridge:
'0' = Single large tubercle / '1' = numerous small tubercles.

12. Position of the eye:
'0' = posterior edge of the palpebral lobe behind S1 lateral glabellar furrow.
'1' = posterior edge of the palpebral lobe in advance of S1 lateral glabellar furrow.

13. Length of genal spine:
'0' = Short / '1' = Long.

14. Pleural fields on pygidium reticulate (n/y): '0'/'1'.

All species of *Cybeloides (Cybeloides)* display pleural fields which are pitted to some extent. However, this pitting is so extensive and deep in *C.(C.) rugosa* (Portlock, 1843) as to be described as reticulation. An intermediate between the normal pitted state and the reticulation seen in *rugosa* occurs in the species *Cybeloides (Cybeloides) spinifera* Tripp, 1954. In order to avoid forcing the topology of the tree, the intermediate character state seen in *spinifera* was not coded as such - merely being coded as 'non reticulate'. The fact that, in spite of this caution, *spinifera* is placed as a sister group to *rugosa* by the analysis supports the inferred path of derivation of this character.

15. Tuberculation of the librigenal lateral border:
'0' = Tuberculate / '1' = Non-tuberculate.

16. Post axial spine present on the pygidium (n/y): '0'/'1'.

17. Pleural rib tips on the pygidium extended into long, flaring, spines (n/y):

'0'/'1'.

18. Axis of the pygidium tuberculate (n/y): '0'/'1'.

19. Pygidial pleurae tuberculate: (n/y): '0'/'1'.

It may prove to be possible to add another character based upon the form of the hypostome, e.g. the presence of small denticles on the posterior margin or the form of the central body. Unfortunately, in the majority of species of *Cybeloides, Bevanopsis* and *Deacybele* the hypostome is either not known, or too poorly preserved to determine key features with confidence. As a result no characters based on the form of the hypostome were employed.

7.4. Results of cladistic analysis.

7.4.1 Assessment of the trees produced by the analysis:

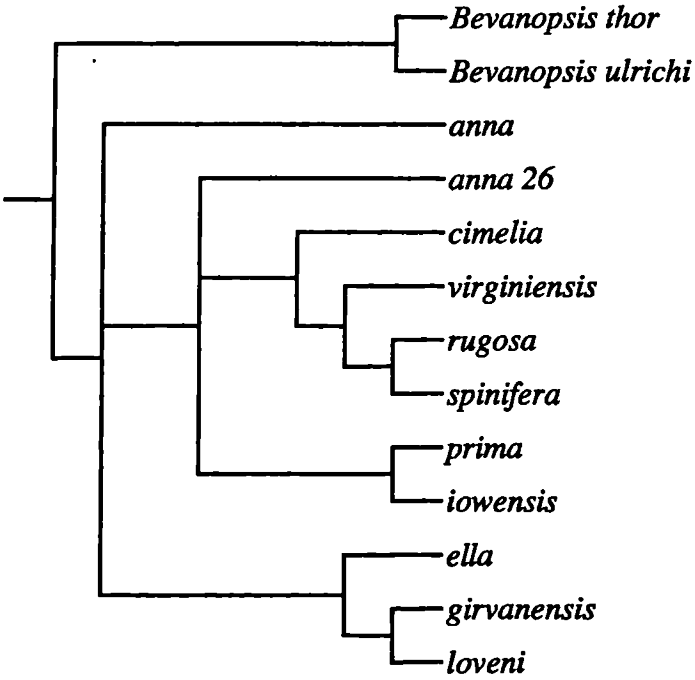
Analysis of the *Cybeloides* data matrix produced two equally parsimonious trees of length 25 and with a rescaled C.I. of 0.724 (Figure 7.2). These trees do not conflict in any way, tree 1 being merely a lower resolution version of tree 2, a resolution problem which results from this analysis being made at species level while one of the characters (presence of median tubercle on the anterior border of the glabella) varies at below species level in *Cybeloides (Cybeloides) anna*. variation in character burden such as this is further discussed in section 2.1.9.1.

The analysis supports the monophyly of *Cybeloides* and its division into two subgenera; *Cybeloides (Cybeloides)* and *Cybeloides (Paracybeloides)* as discussed by Ingham (1974) is clearly also supported.

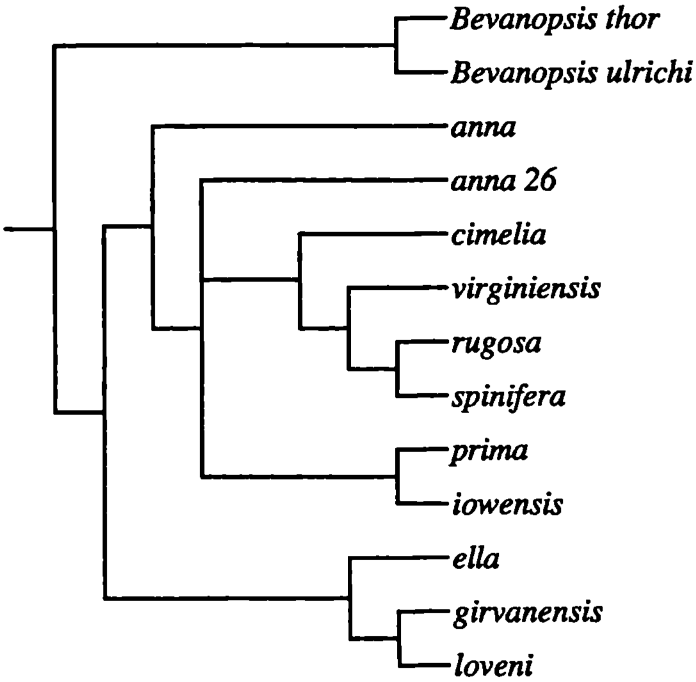
There has been debate about whether *Cybeloides (Paracybeloides) girvanensis* and *Cybeloides (Paracybeloides) loveni* are two separate species or merely sub-specific variants (see Ingham, 1968 and Kielan-Jaworowska *et al.*, 1991). The two taxa are clearly closely related, but the examination of a large amount of material is required to determine whether there is a continuous range of variation between them. The time constraints of this present study preclude this and so these taxa are added as separate species although the characters by which their codings differ are the subject of some debate.

Figure 7.2: Two minimum length trees produced by PAUP analysis of *Cybeloides*.

Tree number 1.



Tree number 2.

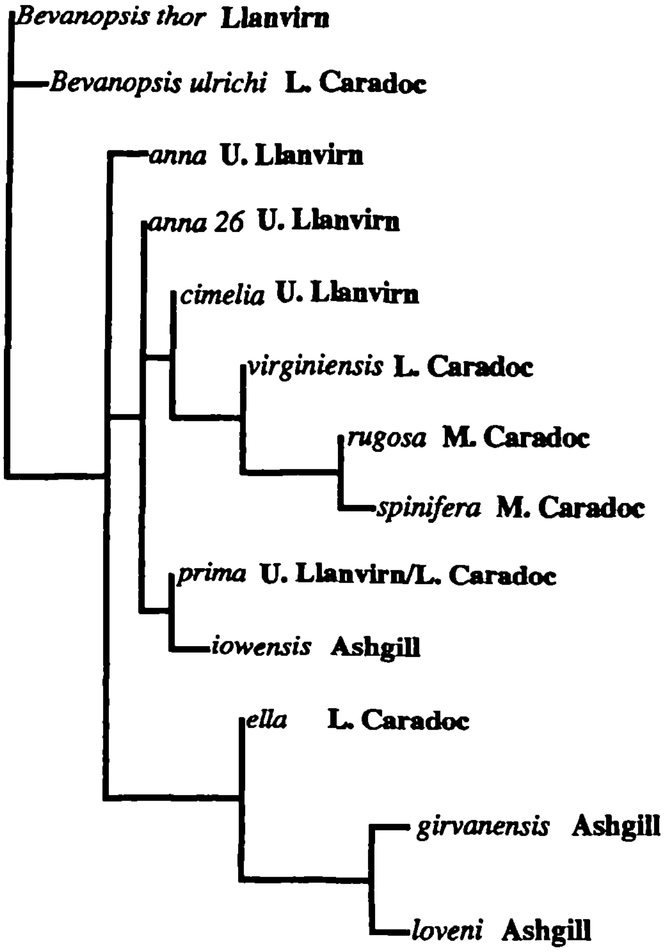


The lower resolution of these two trees (tree one) is adopted herein as it requires the fewest assumptions.

Match of biostratigraphy to phylogeny:

As can be seen from Figure 7.3, the sequence in which species develop in the phylogeny derived from this analysis very closely matches the stratigraphical sequence in which the species are found. This match provides strong additional support for the phylogeny.

Figure 7.3: Phylogram annotated with the ages of the *Cybeloides* species.



The match of stratigraphy to branching order is excellent. The fit of stratigraphy to branching order will be further enhanced if the highly incomplete, Upper Llanvirn taxon *C. terrigena* from the Confinis Flags of S.W. Scotland proves, as expected, to be a basal member of *Paracybeloides (Paracybeloides).*

The positions of the various apomorphies can be seen on the annotated phylogram below. The length of each branch is proportional to the number of apomorphies which support that branch.

Figure 7.4: Annotated phylogram representation of species relationships within *Cybeloides* .

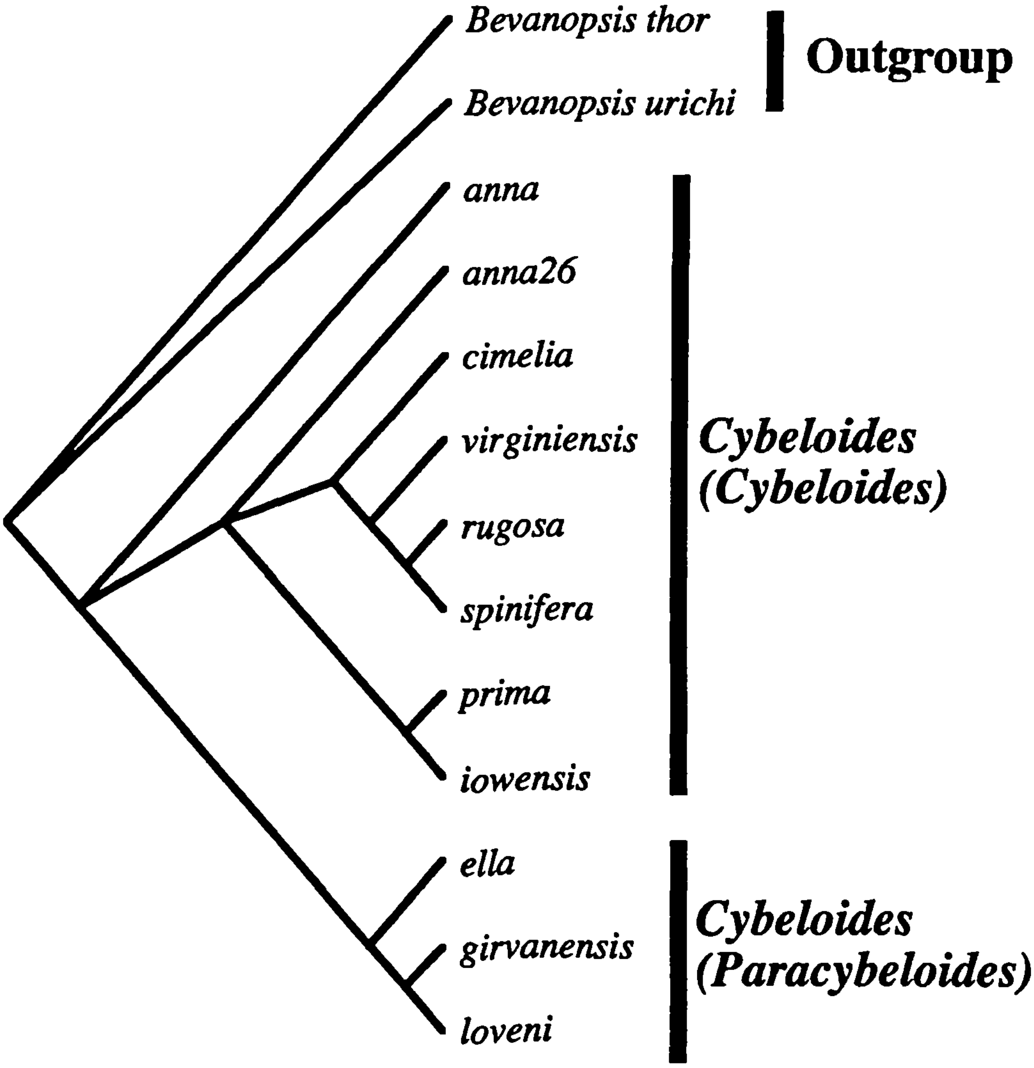
```
/ Bevanopsis thor
+---- Bevanopsis ulrichi
|             /----- anna
|             |    / anna26
22            |    |    / cimelia
|             |    +---16         / virginiensis
|             +---18   \-------15            /----- rugosa
\------------21    |              \------------14 spinifera
              |    |    / prima
              |    \---17----- iowensis
              |                   / ella
              \-----------------20                /----- girvanensis
                                  \-----------------19----- loveni
```

```
Apomorphy lists:

         Branch                    Character        Steps  CI   Change

         node_22 --> B. urichi     9.pulv tub          1  0.600 0 ==> 1
         node_22 --> node_21       3.triang tub        1  0.500 1 ==> 0
                                   6.pulvinus          1  1.000 0 ==> 1
                                   16.Pax ridge        1  1.000 0 ==> 1
         node_21 --> anna          13.spine legn       1  1.000 1 ==> 0
         node_21 --> node_18       1.ab tub            1  1.000 1 ==> 2
         node_18 --> node_16       7.ovate pulv        1  1.000 0 ==> 1
         node_16 --> node_15       5.+2 collumn        1  1.000 0 ==> 1
                                   9.pulv tub          1  0.600 0 --> 2
         node_15 --> node_14       8.tall stalk        1  1.000 0 ==> 1
                                   9.pulv tub          1  0.600 2 --> 3
                                   12.eye pos          1  0.500 0 ==> 1
         node_14 --> rugosa        14.retic fiel       1  1.000 0 ==> 1
         node_18 --> node_17       9.pulv tub          1  0.600 0 ==> 1
         node_17 --> iowensis      2.abtub enla        1  1.000 0 ==> 1
         node_21 --> node_20       12.eye pos          1  0.500 0 ==> 1
                                   15.libbor tub       1  1.000 1 ==> 2
                                   17.Paracyb pl       1  1.000 0 --> 1
                                   18.axis tub         1  1.000 1 --> 0
         node_20 --> node_19       3.triang tub        1  0.500 0 ==> 1
                                   4.glab tub          1  1.000 0 ==> 1
                                   9.pulv tub          1  0.600 0 ==> 3
                                   11.eyeridge t       1  1.000 0 ==> 1
         node_19 --> girvanensis   10.fixi tub         1  1.000 0 ==> 1
         node_19 --> loveni        19.pleurae tu       1  1.000 1 ==> 0
```

7.4.2 Diagnosis of the subgenera within *Cybeloides* Slocom, 1913;

The two subclades of *Cybeloides* are illustrated in figure 7.5 and are considered to be subgenera, supported by numerous synapomorphies.

Figure 7.5: Cladogram showing the subgenera of *Cybeloides*.



7.4.2.1 *Cybeloides (Cybeloides)* Slocom, 1913

Cybeloides (Cybeloides) is recognised on the basis of the following synapomorphies in addition to those features diagnostic of *Cybeloides* (see section 4.5.1.14):

Well developed longitudinal axial furrows adaxial to the pulvini; Anteromesial triangular area on the frontal lobe of the glabella lacks tubercles; Loss of the median tubercle on the anterior border of the glabella (Except *Cybeloides (Cybeloides) anna*.); Tubercles on the axis of the glabella arranged in pairs with rare adventitious tubercles; Tuberculate librigenal borders; Tuberculate pygidial axis; Free points of pygidial pleurae short;

Taxa included in *Cybeloides (Cybeloides)*.

C. (Cybeloides) anna	Ludvigsen, 1979
C. (Cybeloides) attenuata	(Reed, 1897)
C. (Cybeloides) cimelia	Chatterton & Ludvigsen, 1976
C. (Cybeloides) iowensis	Slocom, 1913
C. (Cybeloides) plana	Sinclair, 1944
C. (Cybeloides) prima	(Raymond, 1905)
C. (Cybeloides) rugosa	(Portlock, 1843)
C. (Cybeloides) seca	Evitt & Tripp, 1977
C. (Cybeloides) spinifera	Tripp, 1954
C. (Cybeloides) sulcata	(Troedsson,1928)
C. (Cybeloides) virginiensis	Cooper, 1953

The diagnostic features of each species may be read off from the annotated phylogram. Note that a number of the autapomorphic characters are not included in this list.

7.4.2.2 *Cybeloides* Slocom, 1913 (*Paracybeloides*) Hupé, 1955

Cybeloides (Paracybeloides) is diagnosed on the following apomorphies in addition to those features diagnostic of *Cybeloides* (see section 4.5.1.14):

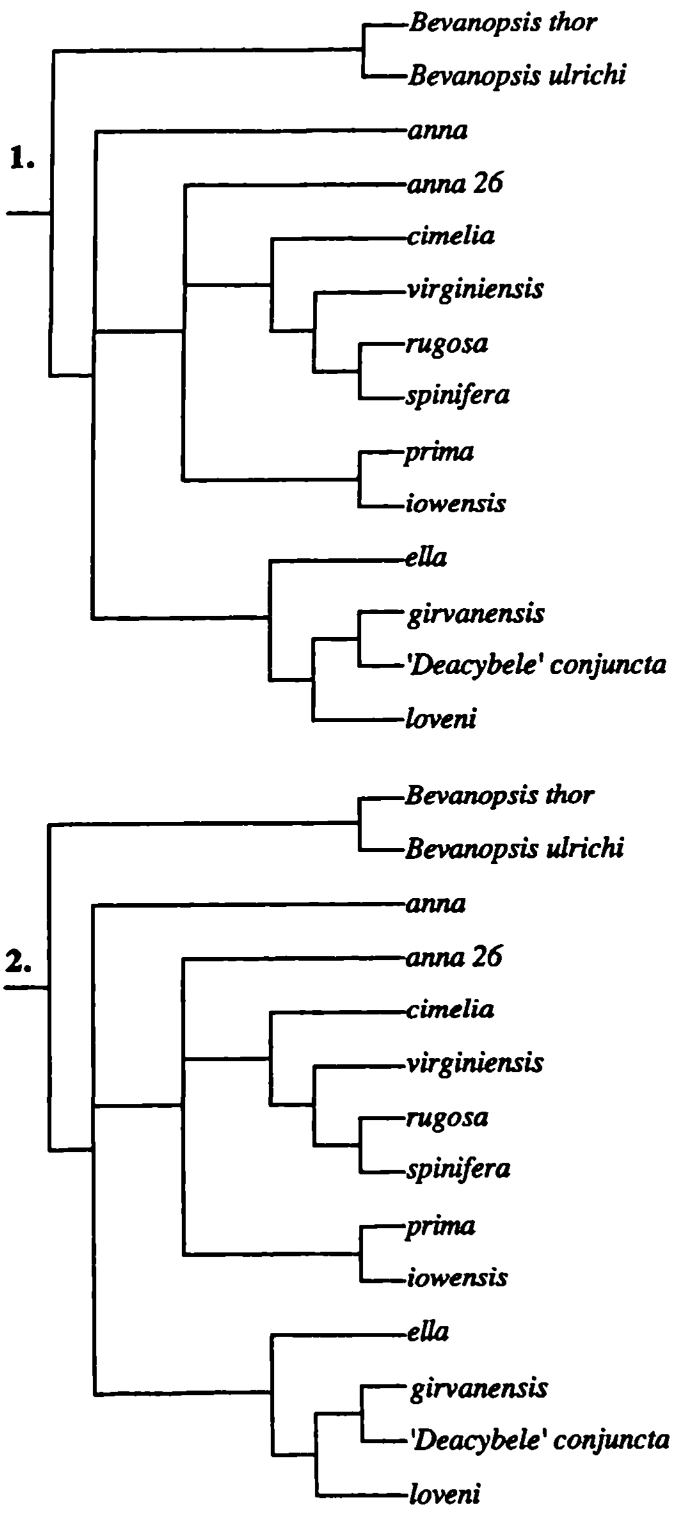
Tendency towards absence of the axial furrows adaxial to the pulvinus; Fine polytuberculation of the pulvinus; Tuberculation of the anteromesial triangular area; Tubercles on glabellar axis predominantly equisized and unordered; Forward placed palpebral lobes; Dense tuberculation of fixed cheek and eye ridge; Non-tuberculate librigenal border; Non-tuberculate pygidial axis; Development of elongate, flared pleural spines on the pygidium.

C. buttsi is here synonymised with *Cybeloides ella* which is most closely related to *Cybeloides (Paracybeloides)* and so is included in this subgenus despite displaying only some of the diagnostic characters. Although highly abraded, *Cybeloides terrigena* Tripp, 1962 displays enough apomorphies of *Cybeloides (Paracybeloides)* to also allow its assignment to this subgenus. *Cybeloides rarissimus* Nan, 1985 is too poorly illustrated to be reliably coded for analysis. In spite of this, the large pygidial spines, multiple, unordered tuberculation of the axis of the glabella and multiple tuberculation of the fixed cheeks and eye ridges, all indicate that *rarissimus* should be assigned to *Cybeloides (Paracybeloides)* and is probably an offshoot of either *girvanensis* or *loveni*.

7.4.3 Assessment of the species *Deacybele conjuncta* Owen, 1981.

Deacybele conjuncta was described by Owen (1981) from the Lunner Formation of Hadeland, Norway (L. Ashgill) and assigned to *Deacybele* rather than *Cybeloides* on the basis of the abaxial portions of the lateral lobes not being inflated into pulvini. Inclusion of *Deacybele conjuncta* in the *Cybeloides* analysis results in the two minimum length trees shown below. Both trees are of length 26, rescaled C.I. of 0.707 and are of identical topology to those produced without the inclusion of *conjuncta*.

Figure 7.6: Two trees produced by inclusion of *conjuncta* in this analysis.



It can be seen that *conjuncta* plots with *girvanensis*, with which it co-occurs. It is clear that *conjuncta* is the daughter taxon as all of the sister taxa to both *girvanensis* and *conjuncta* display lateral glabellar lobes which have coalesced and inflated to form pulvini. It is also clear from this placement that *conjuncta* has secondarily lost the inflation of the adaxial portion of the lateral lobe which makes up the pulvinus. This interpretation is consistent with the variable development, and varying degree of inflation, of the pulvinus seen in other species of *Cybeloides* such as *C. (C.) prima*, Raymond, 1905. As the deflation of the fused abaxial portions of the lateral lobes is a secondary feature, it is best to regard *'Deacybele' conjuncta* as a member of *Cybeloides (Paracybeloides)* rather than *Deacybele*. The fact that this species lacks the inflated pulvinus which is diagnostic of *Cybeloides* is unfortunate, but is the consequence of defining a genus on the basis of one primary character which is developed to a variable degree within the group.

Although poorly illustrated, it can be discerned that *C. rarissimus* Nan, 1985 from the Ashgill Wulongtun Formation of Eastern Yilehuli Shan Heilo Ngjiang Province, China, has multituberculate fixed and free cheeks and eye ridges and a single, mesially situated, anterior border tubercle and so is best placed within *Cybeloides (Paracybeloides)*. The inflated pulvinus seen in *C. rarissimus* makes it unlikely that it is a descendant of *'Deacybele' conjuncta* so it is most likely to be closely related to either *loveni* or *girvanensis*, if these latter two are in fact separate species.

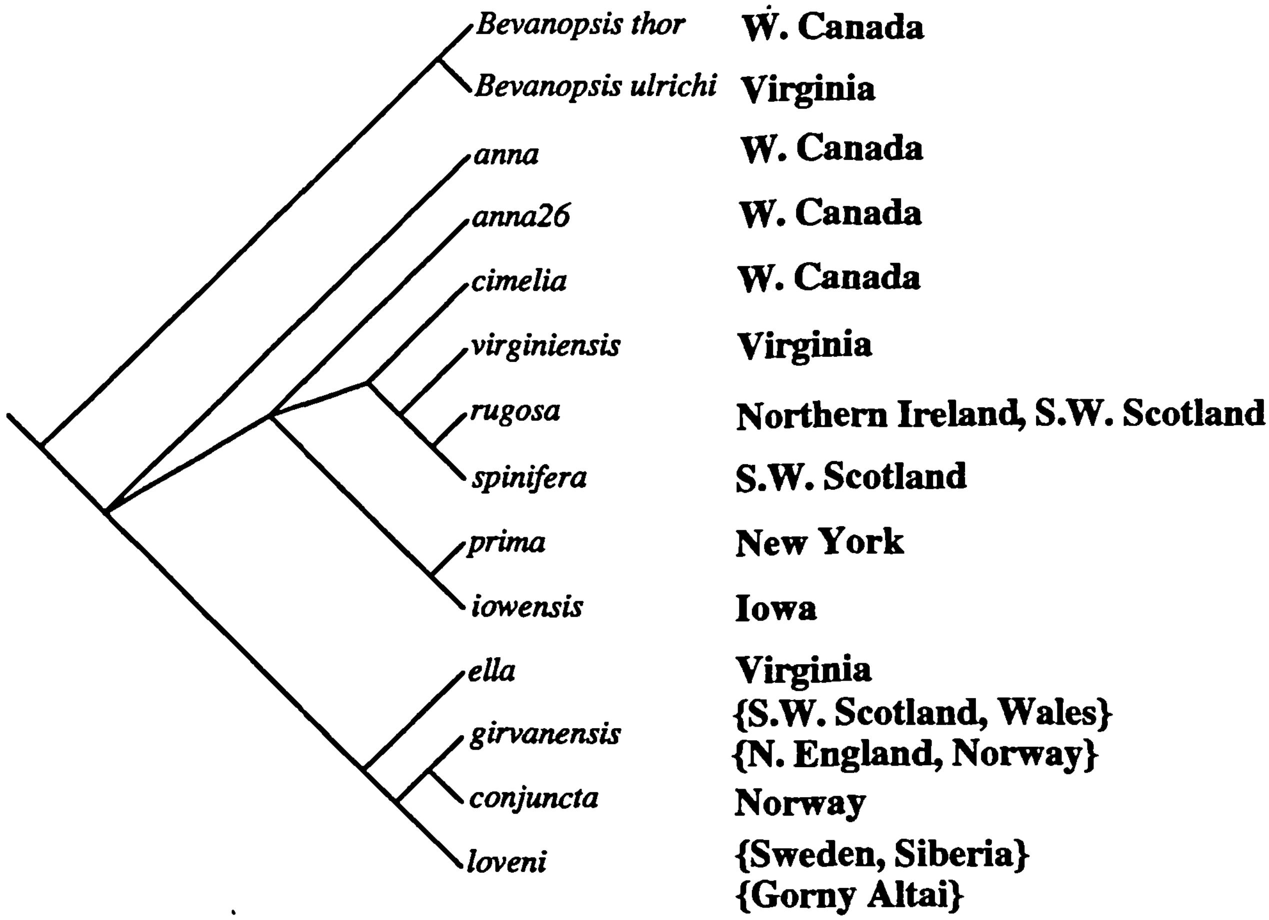
Taxa included in *Cybeloides (Paracybeloides)*.

C. (Paracybeloides) conjuncta	Owen, 1981
C. (Paracybeloides) ella	(Narroway & Raymond, 1906)
Cybeloides buttsi	Cooper, 1953
Synonymised with *(Paracybeloides) Cybeloides ella*. in this analysis.	
C. (Paracybeloides) girvanensis	(Reed, 1903)
Cybeloides parotti	Whittington, 1964
Synonymised with *(Paracybeloides) girvanensis* by Ingham 1968	
C. (Paracybeloides) loveni	(Linnarsson, 1869)
C. (Paracybeloides) rarissimus	Nan, 1985
C. (Paracybeloides) terrigena	Tripp, 1962

7.5. Palaeobiogeography of *Cybeloides*:

As the group as is largely Laurentian, there is little large scale biogeographical information to be extracted from *Cybeloides* but there is information on the detailed Laurentian biogeography.

Figure 7.7 *Cybeloides* cladogram annotated with the species localities.



7.5.1 Informal palaeobiogeographical inferences:

Inferences about biogeography can be made both by comparing the stratigraphical ages, geographical positions and branching order of the taxa and by a more formal method utilising Gain/Loss ratios. Taking the more subjective method first. *Cybeloides* originated in Western Canada (Laurentia) from where one branch of *Cybeloides (Cybeloides)* spread into Iowa and New York while the other branch spread first to Virginia and then to Pomeroy in Northern Ireland (marginal Laurentia, part of the Midland Valley terrane) and so to Girvan, South West Scotland (also part of the Midland Valley terrane). This indicates that Virginia and the Midland Valley terrane, while probably at some small distance from each other, were both situated close to Western Canada- although Virginia is likely to have been closer to Canada than was the Midland Valley terrane.

The slight faunal separation of Pomeroy and Girvan may indicate a degree of ecological differentiation of these two components of the Midland Valley terrane during the mid-Caradoc.

The *Cybeloides (Paracybeloides)* subclade also derives from ancestral taxa in Western Canada. The earliest members of *Cybeloides (Paracybeloides)* are found in Virginia, spreading to S.W. Scotland (*terrigena, girvanensis*) before reaching Avalonia (Wales etc, *girvanensis*). The species *loveni* is found almost simultaneously in Sweden (Baltica) and possibly slightly later in Siberia and Gorny Altai and is very closely related to, and possibly synonymous with, *girvanensis*. The close relationships of the *Cybeloides* species in Avalonia and Baltica, and the apparently widespread nature of *Cybeloides (Paracybeloides) girvanensis*, indicate that marginal Laurentia, Avalonia and Baltica were all in close proximity by the Ashgill. *Cybeloides (Paracybeloides) conjuncta* Owen, 1981 is found in Baltica but not in S.W. Scotland or Northern England. It seems most likely that the poorly known species *Cybeloides rarissimus* Nan, 1985 from the Upper Ashgill of China was derived from an ancestor situated at the eastern extremity of the geographical range of *Cybeloides (Paracybeloides)*. A likely contender for this is *Cybeloides (Paracybeloides) loveni* in Baltica Siberia and Gorny Altai. The presence of *Cybeloides* in China indicates a degree of communication between, and relative geographical proximity of S.W. Scotland, Sweden, Siberia, Gorny Altai and China by the late Ashgill. This communication is likely to have been the result of *Paracybeloides* expanding from S.W. Scotland (Marginal Laurentia) eastwards during the Ashgill until it occupied a large latitudinally constrained band.

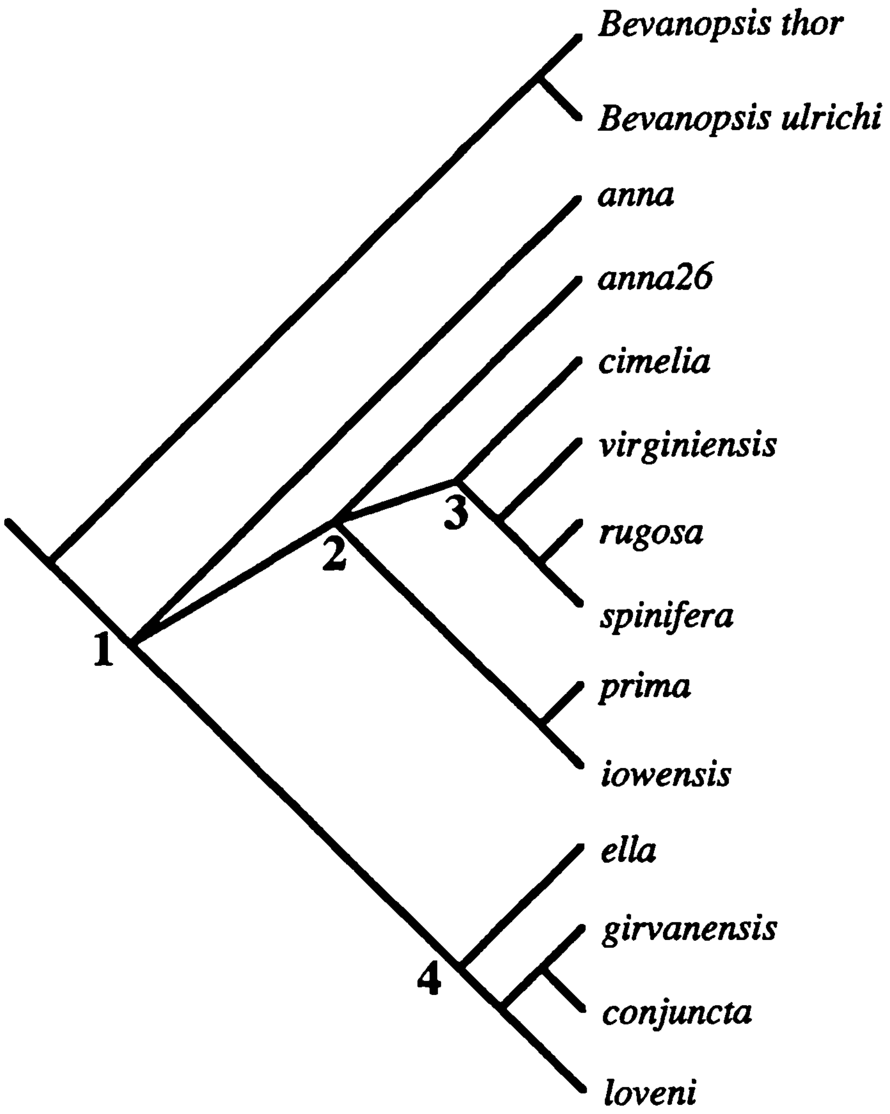
The biogeographical histories of the main *Cybeloides (Cybeloides)* subclade and the *Cybeloides (Paracybeloides)* subclade mirror each other, while the minor *Cybeloides (Cybeloides)* subclade has a similar, but distinct, history within the Laurentian province. The similarity of the independent biogeographical histories of

C. (Cybeloides) and *C. (Paracybeloides)* is likely to indicate that these two groups adapted to slightly different niches.

7.5.2 Gain/Loss ratio analysis of the palaeobiogeography of *Cybeloides*.

A gain/loss analysis was performed (see section 2.2.2). The nodes examined are illustrated in Figure 7.8 and their Gain/Loss ratios are listed in tables 1 - 4:

Figure 7.8: Minimum resolution cladogram, with *conjuncta* included and with the nodes examined highlighted.



Tables 7.1 - 7.2: Gain/Loss ratios for nodes 1-2. 'Scotland' refers to both the Girvan area of S.W. Scotland and the Southern Uplands.

Node 1			
Place	**Losses**	**Gains**	$\frac{\textbf{Gains}}{\textbf{Losses}}$
W. Canada	**3**	**3**	**1**
Virginia	6	2	0.3
Pomeroy	7	1	0.14
New York	7	1	0.14
Iowa	5	1	0.2
Scotland	9	2	0.22
Wales	5	1	0.2
Norway	5	1	0.2
Sweden	4	1	0.25
Siberia	4	1	0.25
Gorny Altai	4	1	0.25

Node 2			
Place	**Losses**	**Gains**	$\frac{\textbf{Gains}}{\textbf{Losses}}$
W. Canada	**2**	**2**	**1**
Virginia	4	1	0.25
Pomeroy	5	1	0.2
New York	3	1	0.33
Iowa	3	1	0.33
Scotland	5	1	0.2
Wales	0	0	0
Norway	0	0	0
Sweden	0	0	0
Siberia	0	0	0
Gorny Altai	0	0	0

The area most likely to form part of the ancestral range at **node 1** is Western Canada. Virginia appears to be close to the ancestral range but probably not actually in it.

Western Canada is again the most likely area to be part of the ancestral area at **node 2**. All the members of the subclade above this node are Laurentian.

Tables 7.3 - 7.4: Gain/Loss ratios for nodes 3-4. 'Scotland' refers to both the Girvan area of S.W. Scotland and the Southern Uplands.

Node 3

Place	Losses	Gains	Gains / Losses
W. Canada	**1**	**1**	**1**
Virginia	**2**	**1**	**0.5**
Pomeroy	3	1	0.33
New York	0	0	0
Iowa	0	0	0
Scotland	3	1	0.33
Wales	0	0	0
Norway	0	0	0
Sweden	0	0	0
Siberia	0	0	0
Gorny Altai	0	0	0

Node 4

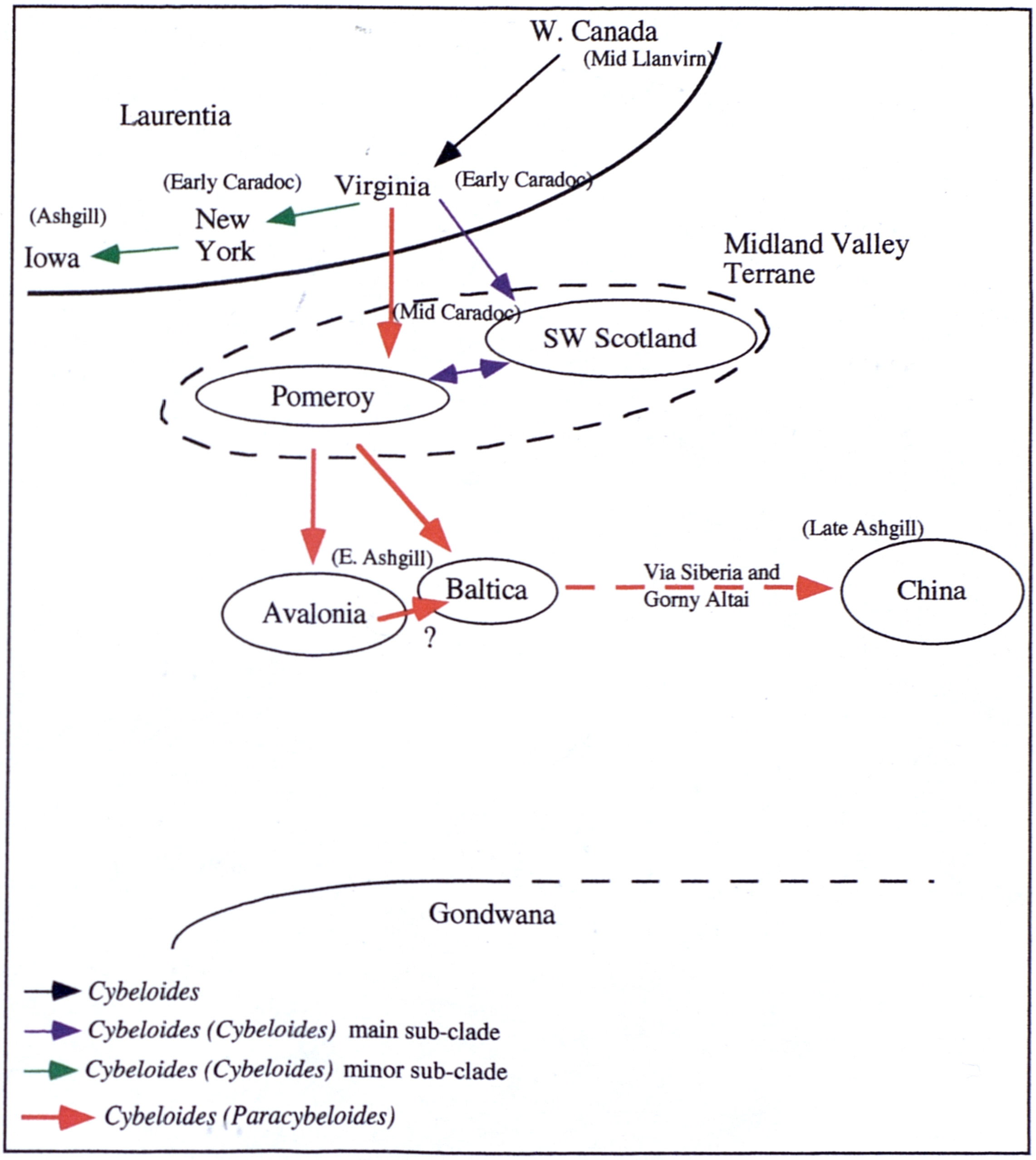
Place	Losses	Gains	Gains / Losses
W. Canada	0	0	0
Virginia	**1**	**1**	**1**
Pomeroy	0	0	0
New York	0	0	0
Iowa	0	0	0
Scotland	3	1	0.33
Wales	3	1	0.33
Norway	**2**	**1**	**0.5**
Sweden	**2**	**1**	**0.5**
Siberia	**2**	**1**	**0.5**
Gorny Altai	**2**	**1**	**0.5**

In **node 3** Western Canada is yet again the most likely area to be part of the ancestral area. The Gain/Loss ratios of the node immediately above this one gives Virginia as the area that is most likely to have given rise to the rest of the subclade with Girvan in S.W. Scotland and Pomeroy in Northern Ireland having the same value - as expected as both are part of the Midland Valley terrane.

At **node 4** Virginia certainly formed part of the ancestral range of this sub group while Norway, Sweden, Siberia and the Gorny Altai regions all have a lower probability of having formed part of the ancestral range indicating that these areas were in communication at this time.

The results of the Gain/Loss ratio analysis support the more subjective inferences made in the previous section and are summarised in Figure 7.9.

Figure 7.9: Summary of the inferred pattern of range expansion of the *Cybeloides* subclades. Not to scale.



7.5.1 Summary of the inferred sequence of events:

Cybeloides is inferred to have developed in Canada during the Llanvirn. An excellent contender for a sister group which is close to the ancestor of *Cybeloides* is *Bevanopsis* sp. figured by Whittington (1965b pl. 68, figs 6-11) which is the right age and comes from the right location. Their appearance in both Avalonia and Baltica in the early Ashgill indicates that these areas were not close to Laurentia until this time. The subsequent expansion of *Paracybeloides* during the Ashgill, from Baltica to Siberia and thence via Gorny Altai to China is interesting, as this sense of movement is counter to that of the postulated Southern Hemisphere gyres (see Fig. 7.10). This, together with the relatively shallow water habitat of *Cybeloides (Paracybeloides)*, would seem to indicate a chain of ocean islands linking the two areas to act as 'stepping stones' (see Fig. 7.11). The remains of these islands may be represented by the Gorny Altai sediments.

Figure 7.10: Schematic diagram of inferred anticlockwise gyre (not to scale).

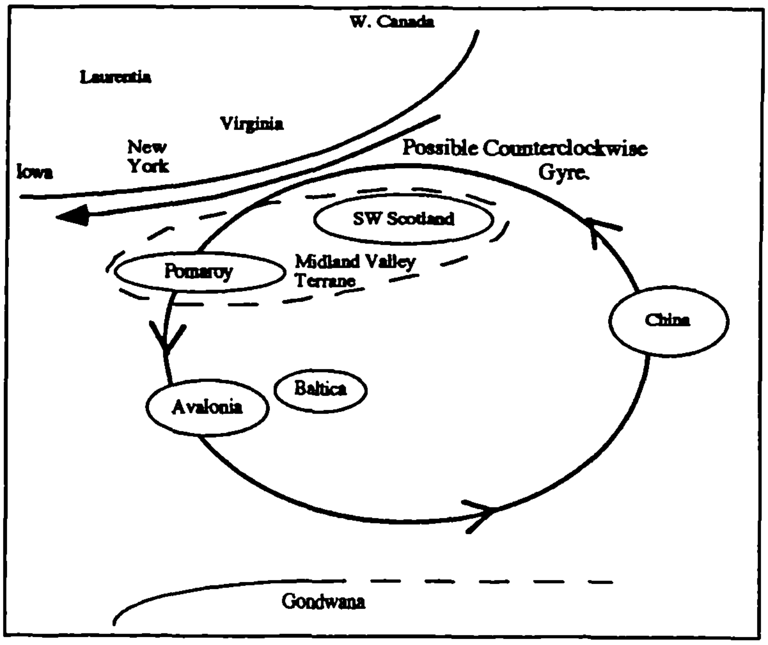
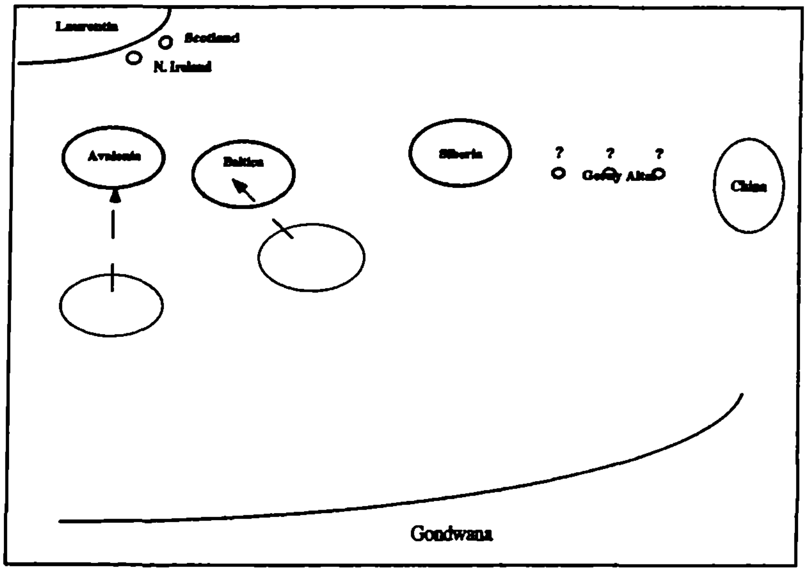


Figure 7.11: Schematic diagram of continental movements.



CHAPTER 8

ORDOVICIAN ENCRINURINAE

8.1 Introduction:

This section examines the relationships of the Ordovician members of the Subfamily Encrinurinae.

The analysis of the subfamily Cybelinae (Chapter 4) shows that the Encrinurinae were derived from cybeline ancestors during the late Arenig. This means that the Cybelinae must be regarded as an expressly paraphyletic group. In spite of this, the traditional placement of these groups as two subfamilies is provisionally retained as a useful working concept. This position is likely to be revised eventually, not only because of the paraphyletic nature of the cybelines but also because there are few apomorphies separating the groups. As a working hypothesis the main features which separate the Encrinurinae from the Cybelinae lie in the thorax and pygidium.

The Encrinurinae differ from the Cybelinae in lacking macropleural spines produced from the sixth or seventh thoracic segments. This is also seen in members of the *Dindymene* subclade, which are closely related to the Encrinurinae, although independently derived from the Cybelinae. The lack of macropleural spines is a reversion to the primitive state found in the pliomerids.

The Cybelinae have anterior pleural fields on the pygidium in addition to the single pleural field positioned at the anterior of the first axial ring segment on the pygidium. These additional pleural fields are not seen in the Encrinurinae in which the pygidia appear to have reverted to the ancestral pygidial form seen in pliomerids such as *Evropeites hyperboreus*. In addition, the fused bar which presumably stiffened and strengthened the margin of the pygidium is confluent with the anterior pleural field in the 'high clade' Cybelinae, while in the Encrinurinae this bar is not continuous with the anterior field. The Cybelinae and Encrinurinae also differ in the number of pleurae present on the pygidium. In the Cybelinae the maximum recorded number of pygidial pleurae is five, seen only in members of the genus *Cybele* Lovén 1845, In contrast, five is the smallest number of pygidial pleurae seen in members of the Encrinurinae and is only seen in *Encrinuroides hornei* Dean, 1973.

Although it is possible to assign cranidia to either the Cybelinae or Encrinurinae 'by eye', I have been unable to ascertain any discrete, unambiguous characters by which to separate the earliest encrinurine cranidia from those of the latest Cybelinae in a cladistic analysis. This is no doubt due to the changes in cranidial morphology occurring later than changes in the pygidium and thorax. Features such as the course of the axial furrows, the development of the lateral lobes and the development of glabellar tubercles have been cited in the past (Strusz, 1980; Evitt & Tripp, 1977), as being useful in differentiating the two groups. In practice, none of these characters are useful in defining a sharp cut off point based on cranidial characters between the two groups. This is because these characters are variably developed in both groups and there is a large degree of overlap and convergence- for example compare *Atractopyge brevicauda* (Angelin, 1854 - see Nikolaisen, 1961) with *Encrinuroides lapworthi* Tripp, 1980b .

These problems raise me concerns about the separation of these two groups into subfamilies and echo the thoughts of Edgecombe *et al.* (1988) that members of the Encrinurinae are more closely related to the more derived members of the Cybelinae than the latter are to the 'primitive' Cybelinae (see section 4). However, given the problems in defining any neat, monophyletic groups (see section 4.5) the divisions are retained as they currently stand.

8.2 Method employed in this analysis:

The method used in this analysis differs slightly to that employed in the analysis of the Cybelinae and Pliomeridae because of the smaller number of taxa being studied. In the case of the Cybelinae and Pliomeridae the stratigraphically oldest, reasonably complete, members of acceptably monophyletic sub-groups (genera) were coded as nominates for that subclade, and any taxa which are of uncertain assignment or which did not share all of the coded features of the nominate species were included. This was then (time permitting) followed up by individual analysis of the relationship of the members of these monophyletic groups to each other using an additional suite of morphological characters.

In contrast, the smaller number of Ordovician Encrinurinae allowed the inclusion of virtually all of the known taxa in a single analysis. Highly incomplete or poorly illustrated taxa of which the original material was not available were excluded from the initial analysis. If a sufficient number of characters could be determined to analyse these incomplete taxa, they were then added separately to the analysis to determine their best systematic placement.

8.3 Species considered in the analysis:

Those species which have been excluded from consideration in the analysis due to poor illustration or incomplete material, are listed separately at the end of this list.

8.3.1 List of species included

Celtencrinurus lamonti	(Tripp, 1957) Lower Drummuck Group, Cautleyan (M. Ashgill), Ayrshire
Celtencrinurus laurentinus	(Twenhoffel, 1928) (figured Tripp, 1957), Ellis Bay Formation, Gamachian (Top Ashgill), Anticosti Island, Quebec, Canada
Celtencrinurus multisegmentatus	(Portlock, 1843) (figured Tripp, 1957; Tunnicliff, 1978), Killey Bridge Beds (Lower Ashgill), Desertcreight, N. Ireland
Celtencrinurus perceensis	(Cooper, 1930 (in Schuchert & Cooper)) (figured Lespérance & Tripp, 1984), Ashgill, Percé, Quebec
Celtencrinurus praecursor	(Tripp, 1954) Kiln Mudstones, lower *clingani* graptolite Zone, Ayrshire. The various numbers of '*praecursor*' refer to figure numbers in Tripp (1954, plate 4) in which the morphological range of this species is illustrated.
Celtencrinurus trispinosus	(Reed, 1914) Starfish Beds, South Threave Formation

	Upper Drummuck Group, Rawtheyan (Ashgill), Ayrshire.
Cromus optimus	Webby *et al.*, 1970 Malongulli Formation, Late Eastonian (Late Caradoc), New South Wales, Australia
Encrinuroides sp.A	Tripp, 1974 (=Encrinurus Sp. Fig.s 10-11), Galena Formation, Upper Caradoc, Elkader, Iowa, USA
Encrinuroides sp.B	Lespérance & Tripp, 1984 White Head Formation, Matapédia Group, Lower Ashgill, Percé, Québec
Encrinuroides autochthon	Tripp, 1962 Confinis Flags, Llanvirn, Girvan, Ayrshire
Synonymised with *autochthon* herein.	
Encrinuroides polypleura	Tripp, 1967 Stinchar Limestone, U. Llanvirn-Lowest Caradoc, Ayrshire.
Encrinuroides capitonis	Fredrickson, 1964 (see Shaw, 1974) Bromide Formation, Llanvirn, Oklahoma, USA
Encrinuroides fallax	(Reed, 1899) see also Reed (1931) Tramore Limestone, Llanvirn - L. Caradoc, Co. Waterford, Ireland
Encrinuroides hornei	Dean, 1973 Summerford Group, Unit B, Arenig/early Llanvirn, Newfoundland, Canada
Encrinuroides lapworthi	Tripp, 1980b Sericoidea Mudstones,

	Basal *Dicranograptus clingani* graptolite Zone Craighead Quarry, Ayrshire
Encrinuroides neuter	Evitt & Tripp, 1977 Martinsburg Formation M.-Caradoc Virginia, USA
Encrinuroides obesus	Tripp, 1965 Doularg Formation, Early Caradoc (*N. gracilis* Zone), Ayrshire
Encrinuroides periops	Tripp, 1967 Upper Stinchar Limestone, latest Llanvirn/early Caradoc, Ayrshire
Encrinuroides rarus	Walcott, 1877 (?Blackriver Fm), Platteville Group, Lower-M. Caradoc, Wisconsin, USA,
&	Esbataottine Formation, (Chazy-Blackriveran), U. Llanvirn -L. Caradoc, Mackenzie District, Canada
Encrinuroides sexcostatus	Reed, 1931 (see Whittington, 1950) Sholeshook Limestone Formation, Cautleyan-L. Rawtheyan, M. Ashgill, South Wales
Encrinuroides spicatus	Tripp, 1974 Galena Formation, Edenian Stage of the Cincinnatian Series, Latest Caradoc, Duck Creek,Green Bay, Wisconsin,
And	Lespérance & Desbiens, 1995 Shipshaw Formation,

	Edenian/Maysvillian, (Latest Caradoc-Lower Ashgill) Lake St. John District, Quebec
Encrinuroides stincharensis	Reed, 1928 (see Tripp, 1979), Stinchar Limestone, latest Llanvirn-earliest Caradoc, Ayrshire, Scotland
Encrinuroides tholus	Evitt & Tripp, 1977 Boutetort Formation =Edinburg Formation (early Caradoc), Virginia, USA
Synonymised with *tholus* herein.	
Encrinurus gibber	Dean, 1979 Lourdes Limestone members II and III *D. multidens* graptolite Zone (Caradoc) Port au Port Peninsula, S.W. Newfoundland, Canada.
Walencrinuroides gelasi	Lésperance & Desbiens, 1995 Upper Caradoc, Lake St. John, Quebec
Encrinuroides torulatus	Evitt & Tripp, 1977 Boutetort Formation (=Edinburg Formation), early Caradoc, Virginia, USA
Encrinuroides uncatus	Evitt & Tripp, 1977 Oranda Formation, M. Caradoc, Virginia, USA
Erratencrinurus brutoni	Owen, 1981 Middle part of the Kjørrven Formation, Grina Shale Mbr, Lunner Formation, Rawtheyan, (Ashgill), Hadeland, Norway
Erratencrinurus capricornu	Krueger, 1971 Nabla Stage (=Baltic Stage E), Top *D. clingani* graptolite Zone,

	(U. Caradoc), N. German Drift
Erratencrinurus cornutus	(Ingham, 1974) (reassigned to *Celtencrinurus* by Evitt & Tripp, 1977), Cautley Mudstones, Cautleyan (M. Ashgill), N.W. England
Erratencrinurus imperfectus	Owen, 1981 Gagnum Shale Member, Lunner Formation, Pusgillian (early Ashgill), Hadeland, Norway The various numbers of '*imperfectus*' refer to figure numbers in plate 11 of Owen (1981) which illustrate the range of variation displayed by this species. Correlated with Baltic Zone F$_{\mathrm{Ia}}$ (L. Ashgill) by Krueger (1991)
Erratencrinurus inopinatus	Owen & Heath, 1990 Upper Kalvsjø Formation, U. Ashgill (prob. Late Rawtheyan), Hadeland, Oslo Region, Norway
Erratencrinurus jaegeri	Krueger, 1991 Nabla Stage (=Baltic Stage E), Top *D.clingani* graptolite Zone, (U. Caradoc), N. German Drift & Ostseekalk,
Erratencrinurus kaushi	Krueger, 1971 Baltic stages D2-D3 (Upper Caradoc), Top *foliaceus*-U. *clingani* graptolite zones. N. German Drift
Erratencrinurus kiaeri	Owen, 1981 Husbergøya Formation, Top Rawtheyan (Ashgill), Nyborg, Asker, Norway

Erratencrinurus kingi	(Dean, 1963) (see also McNamara, 1979) Stile End Formation, Cautleyan (middle Ashgill), Lake District, England
Erratencrinurus kummerowi	Krueger, 1971 Baltic Stage E (U. Caradoc), Upper *D. clingani* graptolite Zone. N. German Drift
Erratencrinurus moe	(Männil, 1958) (Figured Krueger, 1971 and Neben and Krueger, 1973), Vormsi Stage, (early Ashgill), Estonia and N. German Drift
Erratencrinurus nebeni	Krueger, 1971 Baltic stages D2-D3 (Upper Caradoc), Top *D. foliaceus*-U.*D clingani* graptolite zones. N. German Drift
Erratencrinurus postseebachi	Krueger, 1991 Baltic Stage F_{Ia}, Top Caradoc/Early Ashgill, Ostseekalk/N. German Drift
Erratencrinurus seebachi	(Schmidt, 1881) (see Krueger 1971, 1991) *seebachiI* coded from Krueger (1971), Rakvere Stage (Stage E), M. *D. clingani* graptolite Zone, (=U. Caradoc), Estonia, and the N. German Drift, Baltic Stage E, Top *clingani* graptolite Zone, *seebachiIII* coded from Krueger (1991), Estonia
Erratencrinurus vigilans	(Hall, 1847)

	Baltic Stage DIII (Caradoc) L.-M. *clingani* graptolite Zone. New York, USA, See also Rocklandian to Edenian (Caradoc) of S. Ontario, (Lespérance & Desbiens, 1995; Ludvigsen, 1978, 1979; Edgecombe & Chatterton, 1990),
Junior synonyms;	*Encrinurus cybeleformis* Raymond, 1921 *Encrinurus trentonensis* Walcott, 1877 (as indicated by Ludvigsen, 1979a p. 45, DeMott, 1987, p. 80, and Lespérance & Desbiens, 1995 p. 1)
Physemataspis coopi	Evitt & Tripp, 1977 Boutetort Formation, (=Edinburg Formation), L. Caradoc, Virginia, USA
Physemataspis insularis	Shaw, 1968 Lower Crown Point Formation, Upper Llanvirn, New York, USA
Physemataspis mirabilis	Tripp, 1980 Upper Balclatchie Group, Balclatchie Conglomerate, Lower Caradoc, (*D. foliaceous* graptolite Zone), Penwhapple Burn, Ayrshire

8.3.2 Species excluded from the analysis:

The following species were excluded from the analysis, either due to the incomplete nature of the material, or its poor illustration.

Encrinuroides permodosus	Slocom, 1913 Lower Maquoketa Formation,

	Late Caradoc or Ashgill, Iowa, USA
Encrinuroides sublanceolatus	Reed, 1935 (Figured Tripp, 1980b), Craighead Limestone, Lower *D. clingani* graptolite zone, Glenochrie Quarry, Ayrshire
Encrinuroides tuberculosis	Collie, 1903 Lower Trenton Group (Caradoc), Pennsylvania, USA
Encrinuroides waigatcshensis	Burskyi, 1966 Yugorsky Horizon, (Caradoc), Vaygach Island, Arctic USSR
Encrinuroides xillingensis	Xiang, 1987 Upper Ordovician, Yangtse Gorge area, China
Encrinuroides zhenxiongensis	Sheng, 1964 early Ashgill, Szechuan-Kweichow, China.
Encrinurus melzensis	Krueger, 1971 Baltic Stage F (U. Caradoc-Ashgill) N. German Drift
Erratencrinurus ceras	Krueger, 1971 Baltic Stage E (U. Caradoc), N. German Drift
Erratencrinurus paetzensis	Krueger, 1971 Baltic Stage E (U. Caradoc) N. German Drift
Encrinurus striatus	Angelin, 1854 (see Krueger, 1971) Kullsberg Limestone (Late Caradoc) Dalarne, Sweden

8.4 Characters employed:

8.4.1 Tubercle nomenclature:

The notation applied herein to the ordered glabellar tubercles, when present, of the Encrinurinae is largely that of Tripp (1957) and Evitt & Tripp (1977). These authors numbered the tubercles on the glabellar axis from the mid-line outwards, with those on the mid-line being '0' and in arcs from posterior to anterior, employing capital roman numerals for those tubercles which are situated opposite lateral glabellar lobes. Lower case numerals were allocated to those tubercles which lie between the major tubercle arcs. Tripp (1957) and Evitt & Tripp (1977) numbered these minor tubercles according to the numbers of the tubercle arc behind which they were situated. Tubercles which lie in distinct arcs on the frontal lobe of the glabella are allocated numbers by simply extending the tubercle row numbers forwards from those on the glabellar axis.

The only way in which the notation employed in this analysis deviates from that of Tripp (1957) and Evitt & Tripp (1977) is in the terminology of the inter-arc tubercles, to which the number of the lateral glabellar furrow pair between which they are situated is allocated. This has the effect of making the number assigned to the inter-arc tubercles in this analysis be one less than those assigned to the same tubercles by Tripp (1957) or Evitt & Tripp (1977). For example an inter-arc tubercle, situated sagittally and opposite the S1 lateral glabellar furrow pair is labelled 'i-0' herein rather than 'ii-0'. The first five of these tubercles make up the 'tubercle pentagon' of Owen & Heath (1990 p.227).

The pattern of tubercles on the glabella appears to be controlled by heterochrony. Juveniles of species such as *Encrinuroides fallax* (Reed, 1899) tend to have relatively few tubercles on the cranidium and these tubercles are generally large and well ordered. Mature specimens tend to develop more tubercles on the glabella and these are generally of a smaller size and display a lower level of symmetry. This ontogenetic control on glabellar tuberculation is the same as that discussed by Evitt & Tripp (1977) with regard to *Cybeloides* and this relationship is repeated wherever glabellar tuberculation is observed within the Pliomeridae, Encrinurinae and Cybelinae (including *Dindymene*).

Tubercles on the frontal lobe are commonly difficult to code. In taxa situated low on the cladogram, although the tubercles on the glabellar axis are ordered, the frontal lobe tubercles are commonly unordered. High in the *Celtencrinurus* subclade, the frontal lobe tubercles are large and well ordered. In the *Erratencrinurus* subclade, although the frontal lobe tubercles are relatively large and obviously well ordered, their coding into standard tubercle rows is problematic due to the development of numerous inter-row tubercles (indicated by lower case letters). Krueger (1971) assigned row names to these tubercles in some species on the basis of the enlargement of various tubercles. This method appears to be entirely subjective and unreliable, without ontogenetic information and so these characters have been coded as unknown ('?') in the species concerned.

8.4.2 List and discussion of the characters employed:

The characters in this analysis are unweighted and of either simple or ordered type.

1. Tuberculation of the anterior border of the cranidium;
   '0'=granulate.
   '2'-tubercles on the anterior border of the cranidium.

2. No. of tubercles on the anterior border of the cranidium;
   '1'=odd no/'2'=even no.

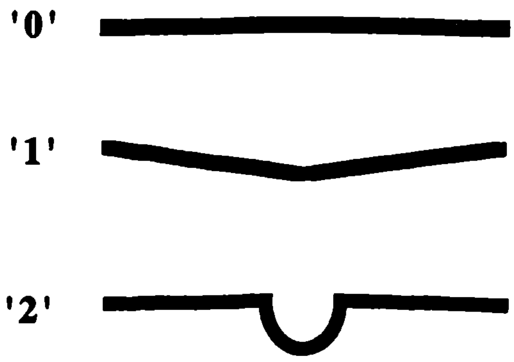
3. Number of tubercles on the anterior border of the cranidium; coded as the number of tubercles observed.
   (Only applies to species displaying a single row of anterior border tubercles)
   (Character state '1' = 10 tubercles on the anterior border of the cranidium)

4. Form of anterior border;
   '0'=constant width in the horizontal plane.
   '1'=narrows mesially in the horizontal plane.

5. Anterior border discontinuous (absent mesially); '0'=no/'1'=yes.

6. Median indentation in the anterior border;

Figure 8.1: Anterior view of the three possible states of the median part of the anterior border.



'0'=no.
'1'=broad, V-shaped indentation.
'2'=strong break in slope.

7. Longitudinal furrow on the anteromesial area of the frontal lobe; '0'=absent/'1'=present.

8. Depth of anterior border furrow; '0'=constant/'1'=shallows mesially.

9. Ventrally divergent rostral sutures; '0'=no/'1'=yes.

10. I-1 tubercle pair; '0'=absent/'1'=present.

11. i-0 tubercle (=ii-0 of Tripp (1957), Evitt & Tripp (1977)); '0'=absent/'1'=present.

12. II-1 tubercle pair; '0'=absent/'1'=present.

13. ii-0 tubercle (iii-0 of Tripp (1957), Evitt & Tripp (1977));
'0'=absent/'1'=present.

14. Size of the 'tubercle pentagon' tubercles listed previously relative to other tubercles on the glabella;
'0'=same size as the other glabellar tubercles (ignoring III-1)
'1'=smaller than the other glabellar tubercles.
'2'=bigger than all other glabellar tubercles ignoring III-1.
'3'=bigger than all other glabellar tubercles including III-1.
('3' only found in *ceras* and *paetzensis* which were not included in the main analysis as they were too incomplete.)

15. III-1 tubercle pair; '0'=absent/'1'=present.

16. III-1 tubercle pair extended into horns;
'0'=no/'1'=yes.

17. III-1 horns amalgamated; **ORDERED**
'0'=separate.
'1'=amalgamated at the base only (e.g. see *E. imperfectus* 2 Owen, 1981).
'2'=amalgamated (e.g. see *E. imperfectus* 2 and *E. brutoni* Owen, 1981)

18. III-1 tubercle pair enlarged relative to the other glabellar tubercles
'0'=no/'1'=yes.

19. Amalgamated III-1 horn bifurcates at the distal end; '0'=no/'1'=yes.

20. iii-0 tubercle present; (this is the iv tubercle of Tripp (1957))
'0'=no/'1'=yes.

21. I-0 tubercle present; '0'=no/'1'=yes.

22. II-0 tubercle present; '0'=no/'1'=yes.

23. III-0 tubercle present; '0'=no/'1'=yes.

24. IV tubercle pair (if present) enlarged relative to the other glabellar tubercles; '0'=no/'1'=yes.

25. v-o tubercle present; '0'=no/'1'=yes.

26. VI tubercle row present (VI 3 2 1); '0'=no/'1'=yes.

Erratencrinurus cornutus (Ingham, 1974) has been coded as 'no' rather than '?'. This character is illustrated as being present by Ingham, the row labelled in his diagram (1974, fig. 23) as row VI ends at the adaxial row V tubercle pair (see Ingham 1974, pl. 15) and therefore that row is row V. This being the case, *cornutus* has no row VI tubercles.

27. vi tubercle present; '0'=no/'1'=yes.

28. Row VII tubercles present; '0'=no/'1'=yes.

29. Abaxial lateral glabellar lobe tuberculation;
'0'=multiply tuberculate.
'1'=tuberculiform (i.e. lateral lobe represented only by a single large tubercle).
'2'=single tubercle sitting on a discernible lateral lobe.

The primitive form of this character appears to be state '0' - polytuberculate lateral glabellar lobes - with states '1' and '2' independently developing from this primitive state. The transformation from polytuberculate lateral lobes to monotuberculate lateral lobes can be seen in specimens of *Erratencrinurus seebachi* figured by Krueger (1991); with lobe tuberculation of the form of states '0' and '2' being referred to as *Seebachi III* and *seebachi I* respectively.

State '1' (tuberculiform) lateral lobes develop in the *Celtencrinurus* subclade from the polytuberculate lateral lobes displayed by *Encrinuroides lapworthi* Tripp, 1980. This character is not coded as being of ordered type.

30. L1 lateral lobes depressed below the level of the rest of the glabella;
'0'=no/'1'=yes.

31. Course of axial furrows;
'0'=concave outwards. - Frontal lobe = widest point of the glabella.
'2'=convex outwards. - L3 = widest point of the glabella.

This character seems to be heterochronically controlled. This may be illustrated by comparison of *Encrinuroides fallax* (Reed, 1899) (Fig. 8.8 herein), and *Encrinuroides obesus* (Tripp, 1965). The axial furrows in juvenile specimens of *Encrinuroides fallax* follow a convex - outwards course while in mature specimens the furrows follow a concave - outwards path.

The stratigraphically younger *Encrinuroides obesus* is very similar to *fallax* apart from in the course of the axial furrows, which are convex outwards, and in the more pronounced development of the post-ocular tubercles on the fixed cheek. There is a striking similarity between the juveniles of *fallax* and mature specimens of the stratigraphically younger *obesus*. It seems likely that *obesus* has been derived from *fallax* by means of paedomorphosis.

32. Tuberculation of the fixed cheeks; '0'=tuberculate/'1'=non-tuberculate.

33. Eye ridge distinct; '0'=no/'1'=yes.

34. Mid-point of the palpebral lobe positioned in advance of the mid-point of the L3 lateral glabellar lobes;
'0'=no/'1'=yes.

35. Ring of coarse granules/tubercles around the eye socle; '0'=no/'1'=yes.

This character is not equivalent to the 'circum-ocular tubercles' of Evitt & Tripp (1977) but refers instead to a ring of tubercles, or large granules around the eye stalk itself.

36. Eye reniform; '0'=no/'1'=yes.

37. Mid-section of eye stalk constricted; '0'=no/'1'=yes.

This character refers to the constriction of the mid-part of the eye stalk as seen in *periops* and *sexcostata*. Some members of *Erratencrinurus* appear superficially to display this characteristic but the apparent constriction at the base of the eye stalk in these species is an artefact of the presence of a ring of large tubercles rather than a constriction of the stalk itself.

38. Height of eye stalk; **ORDERED**
'0'=eye unstalked/'1'=eye stalk short/'2'=eye stalk tall.

39. Inflation of the palpebral lobe; '0'=no/'1'=yes.

40. Swollen transverse, ridge-like area to the rear of the fixigenae;
'0'=absent/'1'=present.

This feature is found developed, to a much lesser extent, in other species than these analysed here, both within the Encrinurinae and in the wider Encrinuridae such as the cybeline genus *Cybele*. It is likely that this ridge is a re-activated relict of the segments which are inferred to have fused together to form the cephalon.

41. Tuberculation of the posterior border of the cranidium
(with the exception of the tuberculation of the genal angles);
'0'=no/'1'=yes.

42. Length of fixigenal spine:
(Measured as a chord from the most posterior abaxial part of the posterior border furrow to the tip of the genal spine).
'0'=genal angle.
'1'=small (0=>49% of sagittal length of cranidium)
'2'=large (=>50% of sagittal length of cranidium)

43 Tuberculation of base of fixigenal spine;
'1'=granulate/'2'=tuberculate.

44. Tuberculation of the genal spines; '0'=no/'1'=yes.

45. Tuberculation of the librigenal field;
'0'=tuberculate/'1'=non-tuberculate (granulate).

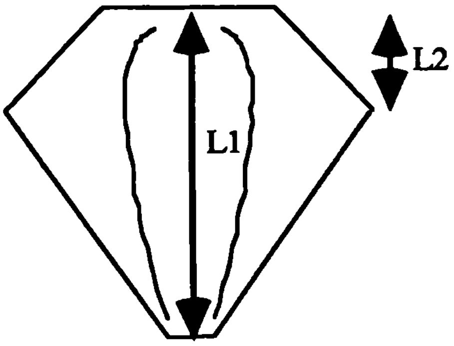
46. Tuberculation of the librigenal lateral border;
'0'=tuberculate/'1'=granulate.

47. Anterior, adaxial, extent of the tuberculate section of the librigenal border;
'0'=tuberculation does not extend to the full length of the librigenal border under the anteromesial section of the cranidium.
'1'=tuberculation extends to the full length of the librigenal border under the anteromesial section of the cranidium.

48. Number of rows of tubercles on the anterior field of the librigenae.
(Coded as the number of transverse rows of tubercles observed).

49. Shape of the pygidium;
'0'=subpentagonal $(L2>(0.5)L1)$.
'1'=subtriangular $((0.9)L1<L2<(0.5)L1)$.
'2'=triangular $(L2<(0.9)L1)$.

Figure 8.2: Definition of measurements employed in the definition of character 49.



Measured as:

L1= sagittal length of the pygidium
L2= length from the anterior of the pygidium to the end of the first pleurae, or break in slope - whichever is shortest.

50. Sagittal tubercles on the axial rings of the pygidium;
'0'=on successive rings.
'1'=on some rings, with regular numbers of 'blank' rings in between.
'2'=on no rings.

51. Number of pygidial axial tubercles per axial ring displaying tubercles;
'1'=single sagittal tubercles/'2'=sagittal tubercles paired/tripled etc.

52. Form of the tips of the pygidial pleurae;
'0'=straight-sided, blunt, not projecting beyond margin of pygidium.
'1'='spear-head shaped' or possessing free tips which turn out.

Species with only some pygidial pleurae ending in free points are coded as '1'.

53. Number of pygidial pleurae confluent with 'in sequence' continuous axial rings;

It would be possible to reduce the number of trees produced by this analysis to one by adding the state '>= 4' to link *Encrinuroides rarus* (Walcott, 1877) and *Cromus optimus* Webby *et al.*, 1970, resolving the ambiguous node. This has not been done as it would seem to be rather forcing the data.

54. Number of pygidial pleurae present;
'0'= 5
'1'= 6-8
'2'= 9+

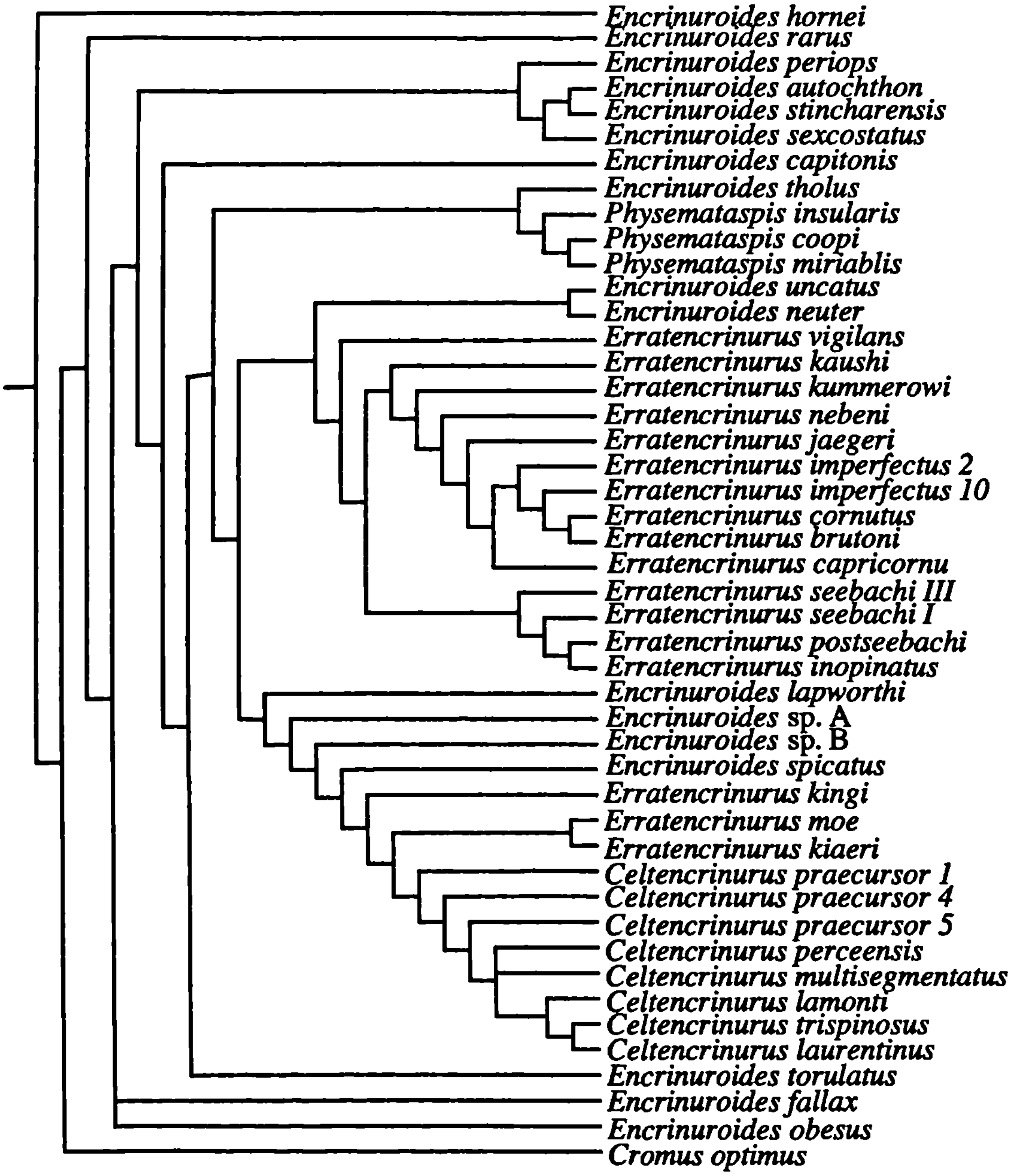
55. Single row of tubercles on the anterior border of the cranidium;
'0'= no/'1'= yes.

8.5 RESULTS:

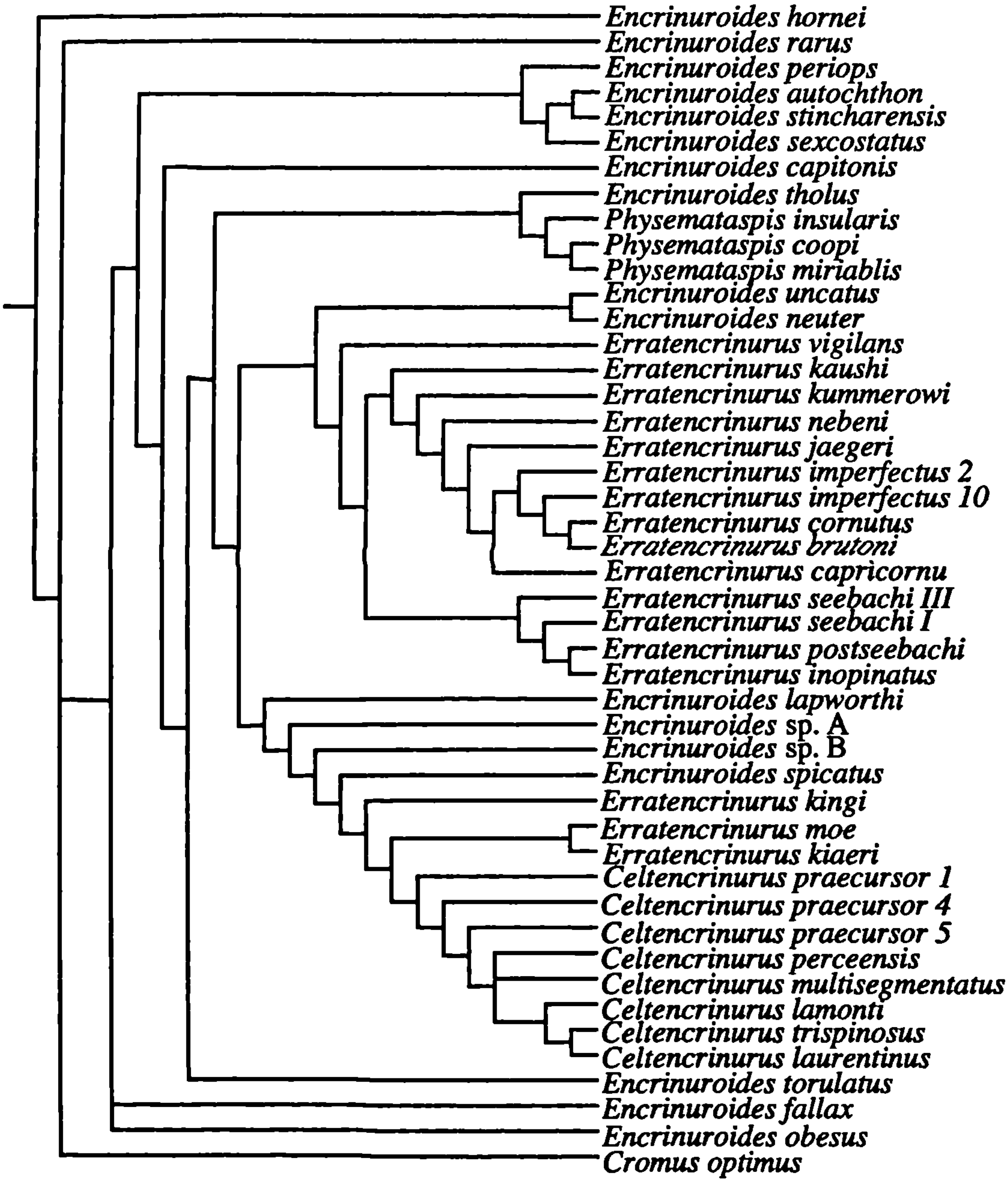
PAUP analysis of the Encrinurinae data set results in the production of the two minimum length trees seen in Figure 8.3

Figure 8.3: Two minimum length trees produced by the Encrinurinae analysis.

1.



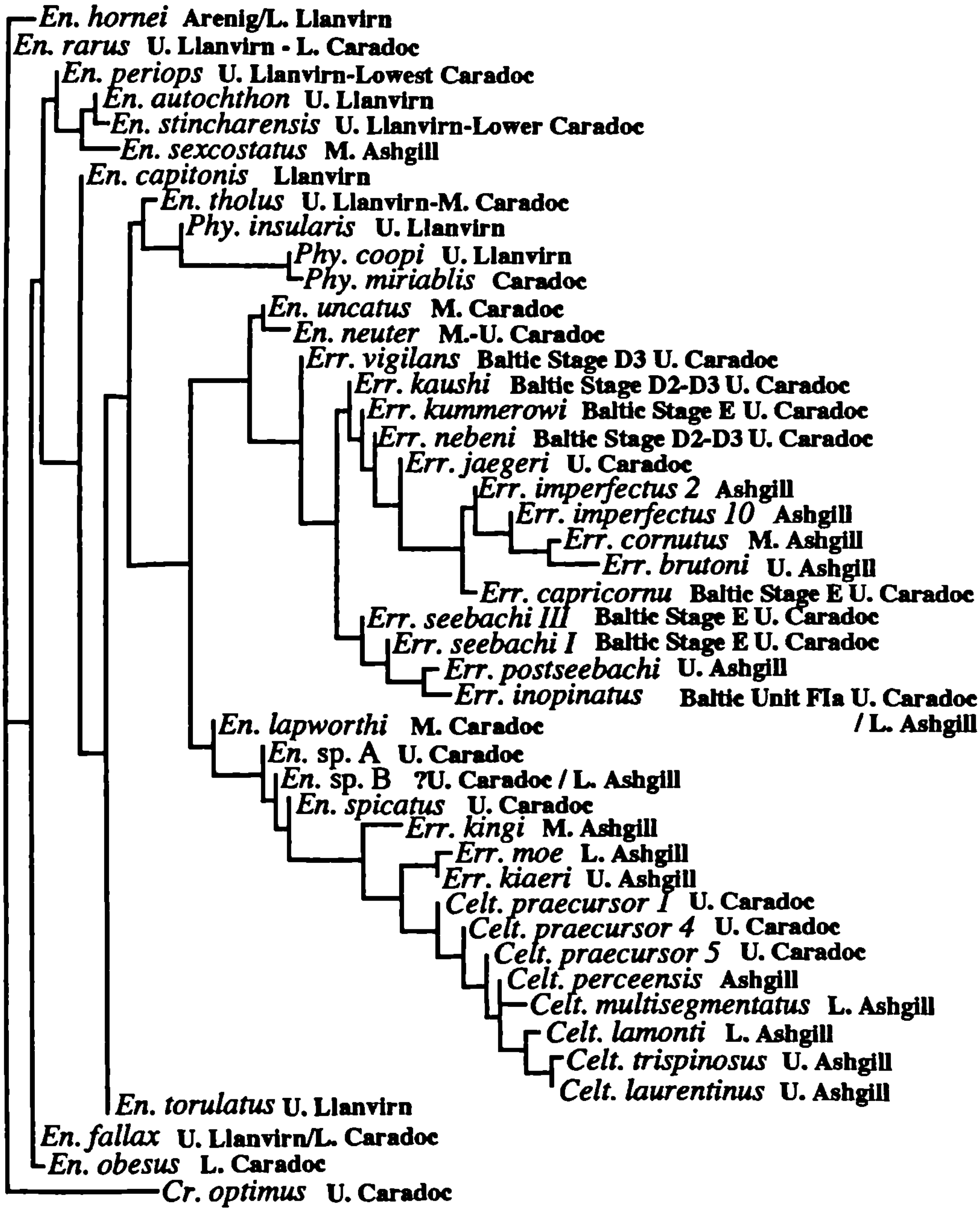
2.



The Trees are of length 139, C.I.=0.525 and Rescaled C.I.=0.452. The value of the CI is higher than that expected from purely random data (Approx 0.1 expected for this size of dataset (Klassen *et al.*, 1991), providing a measure of confidence in the phylogeny. Two trees, rather than one, are produced because of a degree of uncertainty in the position of *Encrinuroides rarus*.

A further assessment of the reliability of this phylogeny may be made by comparing the branching order of the taxa with their stratigraphical position. As can be seen from Figure 8.4, there is a very good fit between the branching order and stratigraphical position.

Figure 8.4: Phylogram annotated with the broad stratigraphical ages of the taxa.



There is an excellent match between the branching order and stratigraphy, with only a few areas of minor anomaly. The anomalies are of small scale, and include;

Cromus optimus is the taxon which displays the largest age anomaly in this analysis. It is assigned an age of late Caradoc while the taxa immediately above it are of late Llanvirn age.

'*Erratencrinurus kingi*' (Dean, 1963) is of mid-Ashgill age while the taxa immediately above it in the phylogeny are of early Ashgill (*Erratencrinurus moe* in Baltica) and late Caradoc (*Celtencrinurus praecursor* in S.W.Scotland) ages. This stratigraphical anomaly is likely to be due to lack of data resulting from the presence of a large unconformity immediately below the sediments containing *kingi*, requiring either downwards extension of the range of *kingi* or the inferred presence of ghost taxa The age anomalies of *E. vigilans* and *E. kummerowi* are less significant, particularly as both taxa are only known from specimens found in glacial drift deposits and as such their age assignments are somewhat uncertain. *E. vigilans* is assigned a stratigraphical position of Baltic Stage D3 (Upper Caradoc) while the taxon immediately above it in the phylogeny is assigned to Baltic stages D2-D3 (Upper Caradoc). Similarly *E. kummerowi* is assigned to Baltic Stage E (Upper Caradoc) while the taxon immediately after it in the phylogeny is assigned to Baltic Stage D2-D3 (Upper Caradoc), which immediately underlies Baltic Stage E. It can be seen that these stratigraphical anomalies are very minor and likely to result from either the age ranges of the taxa overlapping or, more likely, slightly inaccurate stratigraphical assignments of taxa from within the glacial drift deposits.

Of the two trees produced, that which is of the lowest resolution (tree 2) will be utilised as the basis of further discussion. This tree is selected as it involves the fewest assumptions.

Figure 8.5: Complete listing of all character state changes on the topology resulting from this analysis illustrated on tree number 2, represented as a phylogram. Names of taxa and character abbreviated.

```
Tree length = 141
Consistency index (CI) = 0.518
Homoplasy index (HI) = 0.482
CI excluding uninformative characters = 0.500
HI excluding uninformative characters = 0.500
Retention index (RI) = 0.859
Rescaled consistency index (RC) = 0.445
```

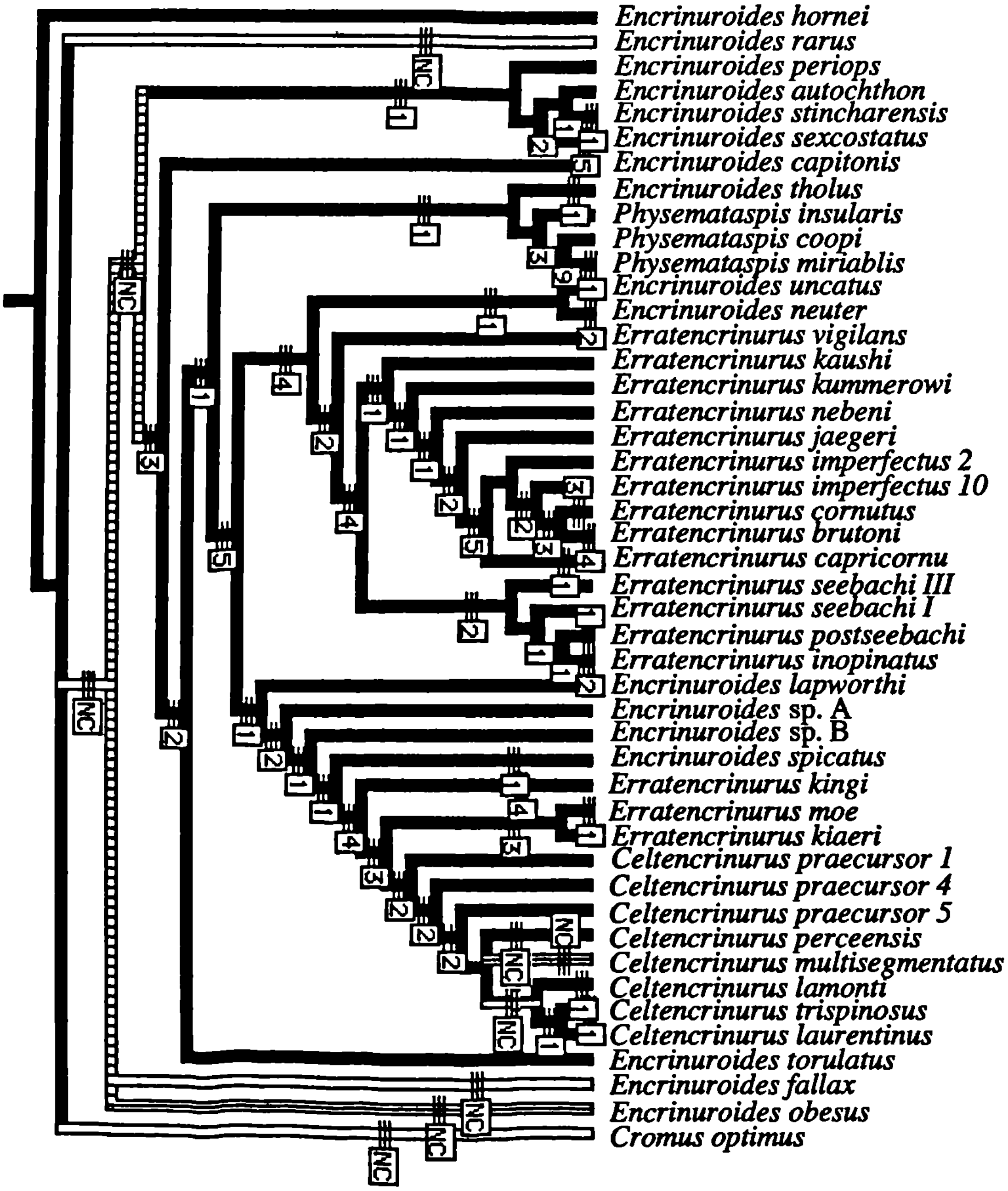
```
/-- En hornei
+ En rarus
|   / En periops
|   |   / En autochthon
|  49  47- En stincharensis
|  |\-48--- En sexcostatus
|  |   / En capitonis
|  |   |     /- Ph tholus
|  |   |    52  / Ph insularis
|  |   |    |\-51          / Ph coopi
|  |   |    |   \---------50-- Ph miriablis
| 85   |    |            / Er uncatus
| ||   |    |           53-- Er neuter
| ||   |    |           |    / Er vigilans
| ||   |    |           |    |   / Er kaushi
| ||   | /-82     /----67    |   | / Er kummerowi
| ||   | |  |     |     |    |  61 |/ Er nebeni
| ||   | |  |     |     \---66  |\60| / Er jaegeri
| |\--84 |  |     |          |  |  59 |      / Er imperfectus 2
| |    | |  |     |          |  |   \58     56   / Er imperfectus 10
| |    | |  |     |          \-65     |     |\--55   /- Er cornutus
| |    | |  |     |             |     \----57    \--54----- Er brutoni
| |    | |  \----81             |           \- Er capricornu
87|    | |        |             |  / Er seebachi III
| |    | |        |             \-64 / Er seebachi I
| |    | |        |                \63   /- Er postseebachi
| |    | |        |                  \--62-- Er inopinatus
| |    | |        | / Celt lapworthi
+86    | |        | |    / Celt sp.A
| |    \83        \80    |/ Celt sp.B
| |      |          \---79|/ Celt spicatus
| |      |               78|        /--- Celt Kingi
| |      |                77        |      /- Celt moe
| |      |                 \------76  /--68 Celt Kiaeri
| |      |                         |  |   / Celt praecursor 1
| |      |                         \-75   | / Celt praecursor 4
| |      |                            \--74 |  / Celt praecursor 5
| |      |                                \73  |/ Celt perceensis
| |      |                                  \-72+-- Celt multisegmentatus
| |      |                                     71 /- Celt lamonti
| |      |                                      \70  /- Celt trispinosus
| |      |                                        \-69 Celt laurentinus
| |      \ En torulatus
| + En fallax
| \- En obesus
\-------------- Cr optimus
```

```
Apomorphy lists:

             Branch                Character      Steps CI    Change

node_87 --> En hornei          53.PygPleur c       1  0.667 2 ==> 4
                               54.NoOf pleur       1  0.500 1 ==> 0
node_87 --> node_86            36.Eye renifo       1  1.000 1 ==> 0
                               38.Stalk high       1  0.333 0 ==> 1
node_86 --> node_85            38.Stalk high       1  0.333 1 ==> 2
node_85 --> node_49            37.Eyestalk f       1  1.000 0 ==> 1
node_49 --> node_48            48.LABFrow No       1  0.375 2 ==> 1
                               49.pygid form       1  0.286 0 ==> 1
node_48 --> node_47            38.Stalk high       1  0.333 2 ==> 1
node_47 --> En stincharensis   33.eye ridge        1  0.333 1 ==> 0
node_48 --> En sexcostatus     32.FixCheek t       1  0.250 0 ==> 1
                               52.pygpleur t       1  0.333 1 ==> 0
                               53.PygPleur c       1  0.667 2 ==> 1
node_85 --> node_84            1.abGranTube        1  1.000 0 ==> 2
                               13.ii0 presen       1  0.200 0 ==> 1
                               20.iii0 prese       1  0.333 0 ==> 1
node_84 --> node_83            35.eye ring         1  0.250 0 ==> 1
                               42.genal spin       1  0.500 1 ==> 2
node_83 --> node_82            3.No.AB tub         1  0.667 5 --> 8
                               6.ab indent         1  0.667 0 ==> 1
node_82 --> node_52            31.ax fur cou       1  0.500 0 ==> 2
node_52 --> Ph tholus          42.genal spin       1  0.500 2 ==> 0
node_52 --> node_51            30.L1 depress       1  1.000 0 ==> 1
                               39.palepr inf       1  1.000 0 ==> 1
                               48.LABFrow No       1  0.375 2 ==> 3
node_51 --> node_50            4.ant bord          1  1.000 0 ==> 1
                               7.long. fur         1  0.333 1 ==> 0
                               11.i0 present       1  0.250 1 ==> 0
                               13.ii0 presen       1  0.200 1 ==> 0
                               20.iii0 prese       1  0.333 1 ==> 0
                               40.Swoll Fixi       1  1.000 0 ==> 1
                               45.Libfield g       1  0.333 0 ==> 1
                               50.axTub            1  0.333 0 ==> 1
                               53.PygPleur c       1  0.667 2 ==> 3
node_50 --> Ph miriablis       5.AntMid mis        1  1.000 0 ==> 1
node_82 --> node_81            43.spineBase        1  1.000 1 ==> 2
                               46.lib bord t       1  1.000 1 ==> 0
                               50.axTub            1  0.333 0 ==> 1
                               51.axTubPairi       1  0.500 2 ==> 1
                               55.singleABro       1  1.000 0 ==> 1
node_81 --> node_67            3.No.AB tub         1  0.667 8 --> 9
                               9.ros plate         1  1.000 0 ==> 1
                               18.IIIl enlar       1  0.333 0 ==> 1
                               24.IV enlarg        1  0.500 0 ==> 1
                               38.Stalk high       1  0.333 2 ==> 1
node_67 --> node_53            26.VI tubercl       1  0.333 0 ==> 1
node_53 --> Er neuter          42.genal spin       1  0.500 2 ==> 1
                               52.pygpleur t       1  0.333 1 ==> 0
node_67 --> node_66            25.v0 tubercl       1  0.500 0 --> 1
                               33.eye ridge        1  0.333 1 ==> 0
                               51.axTubPairi       1  0.500 1 ==> 0
                               54.NoOf pleur       1  0.500 1 --> 2
node_66 --> node_65            7.long. fur         1  0.333 1 ==> 0
                               16.IIIl horns       1  0.500 0 --> 1
                               47.LibTubBand       1  0.500 0 ==> 1
node_65 --> node_61            38.Stalk high       1  0.333 1 ==> 2
node_61 --> node_60            50.axTub            1  0.333 1 ==> 2
```

Branch	Character	Steps	CI	Change
node_60 --> node_59	48.LABFrow No	1	0.375	2 ==> 3
node_59 --> node_58	14.Penttub si	1	1.000	0 ==> 1
	49.pygid form	1	0.286	0 ==> 1
node_58 --> node_57	2.OddEvABtub	1	0.333	1 ==> 2
	3.No.AB tub	1	0.667	9 ==> 8
	13.ii0 presen	1	0.200	1 ==> 0
	32.FixCheek t	1	0.250	0 ==> 1
	45.Libfield g	1	0.333	0 ==> 1
node_57 --> node_56	17.IIIlhorns	1	1.000	0 ==> 1
node_56 --> node_55	15.III1 prese	1	0.500	1 ==> 0
	17.IIIlhorns	1	1.000	1 ==> 2
	23.III0 prese	1	0.500	0 ==> 1
node_55 --> node_54	11.i0 present	1	0.250	1 ==> 0
	32.FixCheek t	1	0.250	1 ==> 0
	53.PygPleur c	1	0.667	2 ==> 3
node_54 --> *Er cornutus*	6.ab indent	1	0.667	1 ==> 2
node_54 --> *Er brutoni*	10.I1 present	1	0.500	1 ==> 0
	12.II1 presen	1	0.500	1 ==> 0
	19.IIIlhornBi	1	1.000	0 ==> 1
	48.LABFrow No	1	0.375	3 ==> 4
node_57 --> *Er capricornu*	53.PygPleur c	1	0.667	2 ==> 3
node_65 --> node_64	14.Penttub si	1	1.000	0 ==> 2
	35.eye ring	1	0.250	1 ==> 0
node_64 --> node_63	16.III1 horns	1	0.500	1 --> 0
	29.lobe tub	1	1.000	0 ==> 2
node_63 --> node_62	24.IV enlarg	1	0.500	1 ==> 0
	49.pygid form	1	0.286	0 --> 1
	50.axTub	1	0.333	1 --> 2
node_62 --> *Er postseebachi*	3.No.AB tub	1	0.667	9 ==> 7
node_62 --> *Er inopinatus*	18.III1 enlar	1	0.333	1 ==> 0
	35.eye ring	1	0.250	0 ==> 1
node_81 --> node_80	2.OddEvABtub	1	0.333	1 --> 2
	6.ab indent	1	0.667	1 ==> 2
node_80 --> node_79	11.i0 present	1	0.250	1 ==> 0
	29.lobe tub	1	1.000	0 ==> 1
	41.PostBor tu	1	0.500	0 --> 1
	48.LABFrow No	1	0.375	2 --> 1
node_79 --> node_78	13.ii0 presen	1	0.200	1 ==> 0
node_78 --> node_77	7.long. fur	1	0.333	1 ==> 0
node_77 --> node_76	33.eye ridge	1	0.333	1 ==> 0
	48.LABFrow No	1	0.375	1 --> 3
	49.pygid form	1	0.286	0 --> 1
	50.axTub	1	0.333	1 ==> 2
	51.axTubPairi	1	0.500	1 ==> 0
	54.NoOf pleur	1	0.500	1 ==> 2
node_76 --> *Celt Kingi*	18.III1 enlar	1	0.333	0 ==> 1
	26.VI tubercl	1	0.333	0 ==> 1
	32.FixCheek t	1	0.250	0 ==> 1
node_76 --> node_75	10.I1 present	1	0.500	1 ==> 0
	21.I0 present	1	1.000	0 ==> 1
	38.Stalk high	1	0.333	2 ==> 1
node_75 --> node_68	3.No.AB tub	1	0.667	8 ==> 1
	35.eye ring	1	0.250	1 --> 0
	44.TubGen spi	1	1.000	0 ==> 1
node_68 --> *Celt moe*	13.ii0 presen	1	0.200	0 ==> 1
node_75 --> node_74	20.iii0 prese	1	0.333	1 ==> 0
	41.PostBor tu	1	0.500	1 ==> 0
	49.pygid form	1	0.286	1 --> 0
node_74 --> node_73	12.II1 presen	1	0.500	1 ==> 0

```
            Branch                  Character          Steps  CI    Change

                                22.II0 presen      1  1.000 0 ==> 1
node_73 --> node_72             15.III1 prese      1  0.500 1 ==> 0
                                23.III0 prese      1  0.500 0 ==> 1
node_72 --> node_71             26.VI tubercl      1  0.333 0 ==> 1
node_71 --> Celt                2.OddEvABtub       1  0.333 2 ==> 1
            multisegmentatus    3.No.AB tub        1  0.667 8 ==> 9
node_71 --> node_70             27.vi tubercl      1  1.000 0 ==> 1
                                49.pygid form      1  0.286 0 ==> 1
node_70 --> Celt lamonti        47.LibTubBand      1  0.500 0 ==> 1
node_70 --> node_69             25.v0 tubercl      1  0.500 0 ==> 1
                                48.LABFrow No      1  0.375 3 --> 2
node_69 --> Celt trispinosus    28.RowVII tub      1  1.000 0 ==> 1
node_86 --> En obesus           31.ax fur cou      1  0.500 0 ==> 2
node_87 --> Cr optimus          8.abf depth        1  1.000 0 ==> 1
                                11.i0 present      1  0.250 1 ==> 0
                                34.eye pos         1  1.000 0 ==> 1
                                42.genal spin      1  0.500 1 ==> 0
                                45.Libfield g      1  0.333 0 ==> 1
                                48.LABFrow No      1  0.375 2 ==> 1
                                49.pygid form      1  0.286 0 ==> 2
                                50.axTub           1  0.333 0 ==> 2
                                51.axTubPairi      1  0.500 2 ==> 0
                                52.pygpleur t      1  0.333 1 ==> 0
                                53.PygPleur c      1  0.667 2 ==> 6
                                54.NoOf pleur      1  0.500 1 ==> 2
```

Figure 8.6: Cladogram 2 annotated with the numbers of unambiguous character changes on each branch. NC=No unambiguous changes on branch.

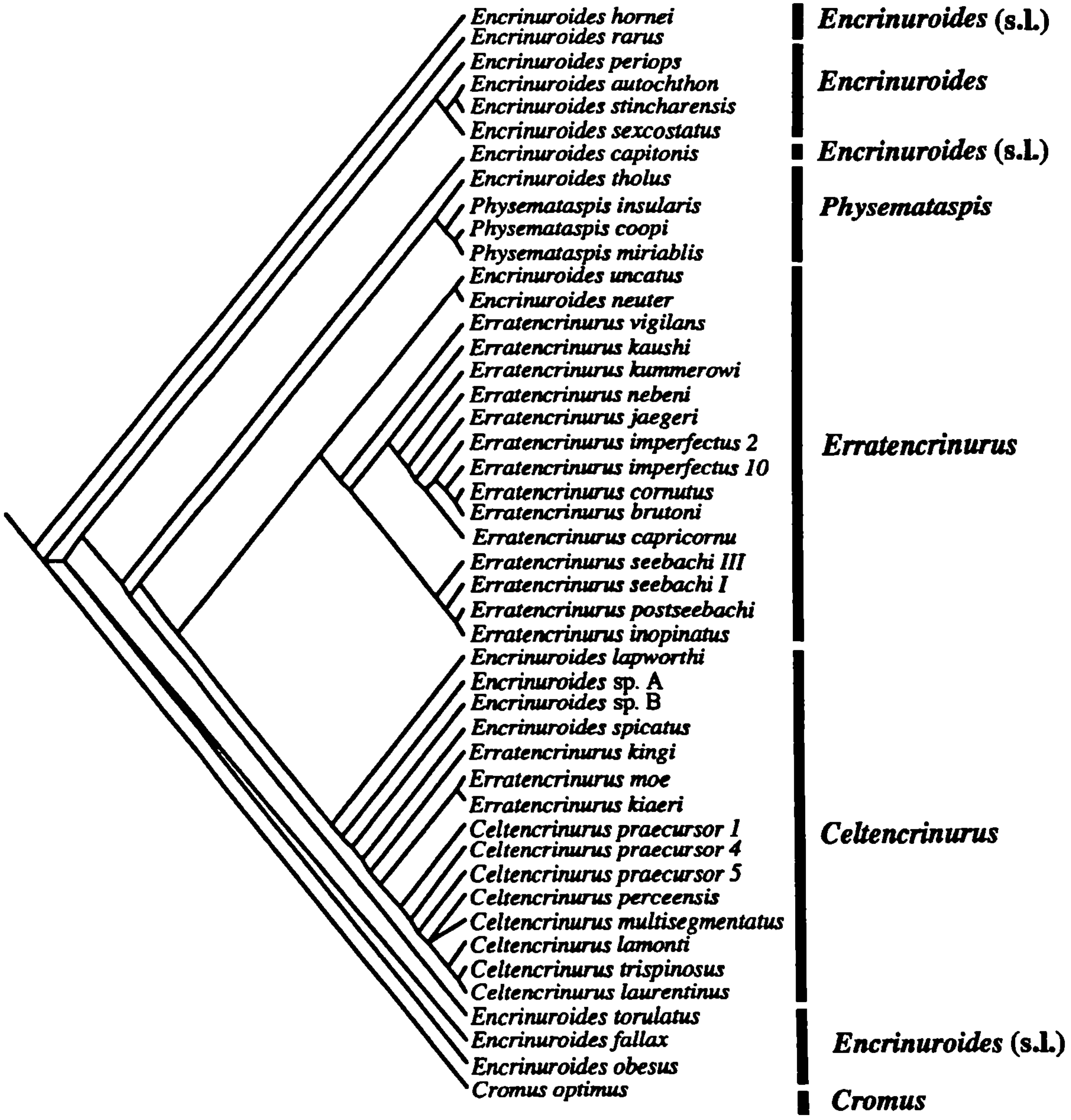


<u>8.6 Systematics</u>

<u>8.6.1 Discussion of the systematic implications of this analysis.</u>

One of the most obvious features of this phylogeny (Figure 8.3) is the paraphyly of *Encrinuroides*, supporting the contention of Edgecombe *et al.* (1990) that *Encrinuroides* requires revision. I propose to redefine the Ordovician Encrinurinae

Figure 8.7: Cladogram with the proposed systematic divisions highlighted.



as illustrated in Figure 8.7 with *Encrinuroides* being divided up into a tightly diagnosable '*sensu stricto*' subclade and those basal taxa which are not included in any one group placed in *Encrinuroides (sensu lato).* The definition of an *Encrinuroides (sensu lato)* group makes practical sense as all of these basal intermediate taxa are of similar gross morphology, merely acquiring one or more of the characters diagnostic of the subclades which they base (see section 2.1.8). It can be seen that the evolutionary role played by the genus *Encrinuroides* is similar to that fulfilled by the genus *Cybelurus* at the base of the Cybelinae and the Subfamily Protopliomeropinae at the base of the Pliomeridae. These taxa all form paraphyletic groups which rapidly give rise to all of the other major sub-groups in the respective analysis. As such the identification and understanding of these taxa and the patterns of character change which they display is crucial to the understanding of the relationships, and patterns of character change in the other taxa in the group. It can be seen that the same evolutionary mechanisms are occurring at different levels in the systematic hierarchy (see section 2.1.9).

8.6.2 The cladistic analysis of the Ordovician Encrinurinae by Lespérance & Desbiens (1995).

Lespérance & Desbiens (1995) carried out a cladistic analysis of 18 Ordovician encrinurine species, utilising 17 characters (some multistate). On the basis of this analysis they re-diagnosed *Encrinuroides* Reed, 1931 and *Physemataspis* Evitt & Tripp, 1977 and erected the following new genera and subgenera;

1. *Walencrinuroides*
   based on a new species *W. gelasi* Lespérance & Desbiens, 1995
2. *Frencrinuroides*
   based on *Encrinuroides capitonis* Fredrickson, 1964 (see Shaw, 1974)
3. *Physemataspis (Physemataspis)*
   based on *Physemataspis coopi* Evitt & Tripp, 1977
4. *Physemataspis (Prophysemataspis)*
   based on *Encrinuroides uncatus* Evitt & Tripp, 1977.

None of these new taxa are supported by the present analysis. Some fundamental problems of the analysis by Lespérance & Desbiens (1995) are as follows;

Methodological problems;

Because many of the characters employed are multistate, there are more character states than there are taxa, but there are very few characters employed relative to the number of taxa in the analysis.

Although the use of a number of non-discrete characters in an analysis is often unavoidable, they are not amenable to cladistic analysis as their definition is highly subjective and their use should be avoided wherever possible (see Smith, 1994 and references therein). Of the 17 characters employed by Lespérance & Desbiens (1995) 12 are non-discrete making any results of their analysis suspect.

Of the five remaining characters, character 11 ('adaxial tubercles on fixigenae') is poorly defined: it is not explained in what way adaxial fixigenal tubercles are non-analogous to abaxial fixigenal tubercles. Character 13 'Adaxial thoracic spines' groups together all thoracic spines in a single character - which is problematic as the spines on different segments may not all be analogous.

From the results of the Cybelinae analysis presented herein it is clear that, although the taxa employed by Lespérance & Desbiens (1995) to polarise their characters (*Lyrapyge* Fortey, 1980, *Cybelurus brutoni* Fortey, 1980 and *Cybelurus halo* Fortey, 1980) are situated below the Encrinurinae in the phylogeny of the Encrinuridae they are not sister taxa, nor are they closely related to the Encrinurinae.

Systematic problems;

Although the majority of the taxa included in this analysis by Lespérance & Desbiens are of very similar age, the phylogenetic position in the branching order of the only taxon whose age lies outside the 'Upper Llanvirn-M. Caradoc' spread of the other taxa (*Encrinuroides sexcostataus* Reed, 1931) is in conflict with its stratigraphical age. It is the youngest taxon but it is placed at the base of the phylogeny.

The diagnosis of the genera and subgenera are so loosely phrased as to overlap each other, they are supported by no uniquely derived apomorphies and they are dogged by reversal of many of the characters employed in the diagnoses.

The taxa included within *Frencrinuroides* are united by only the continuous character 'Glabella subequal', which is also derived independently within *Walencrinuroides.* The taxa included within *Walencrinuroides* are similarly only linked by their possession of subequal pygidia.

A number of specimens of their new species, *Walencrinuroides gelasi,* are described as being 'morphologically identical to *Encrinuroides tholus*', making the material that they describe a junior synonym of *Encrinuroides tholus* (Evitt & Tripp, 1977) (synonymy of these taxa is supported by the Encrinurinae analysis conducted herein). In spite of this, *gelasi* and *tholus* are placed in separate subclades at opposite sides of the phylogeny by Lespérance & Desbiens.

Finally, Lespérance and Desbiens assigned *Encrinuroides uncatus* Evitt & Tripp, 1977 and *Encrinuroides neuter* Evitt & Tripp, 1977 to *Physemataspis (Prophysemataspis)* on the basis of adaxial tubercles not being present on the fixigenae (the character defining their *Physemataspis* subclade), the presence of a straight-sided glabella (secondarily lost in *neuter*), possession of at least one tubercle on the pygidial axis (also independently developed in *Encrinuroides lapworthi*) and axial spines on at least one thoracic segment. *Encrinuroides uncatus* Evitt & Tripp, 1977 and *Encrinuroides neuter* Evitt & Tripp, 1977 are both assigned to *Erratencrinurus* in the Encrinurinae analysis outlined herein, as suggested by Evitt & Tripp (1977) and supported by Owen & Heath (1990).

In spite of these problems, there are some areas of agreement between the two analyses. The juxtaposition of *Encrinuroides uncatus* Evitt & Tripp, 1977 and *Encrinuroides neuter* Evitt & Tripp, 1977 by Lespérance and Desbiens is supported herein, as is the juxtaposition of *Encrinuroides autochthon* Tripp, 1962 and *Encrinuroides polypleura* Tripp, 1967, which are synonymised herein and the close association of *Encrinuroides gibber* Dean, 1979 and *Encrinuroides tholus* Evitt & Tripp, 1977 which are also synonymised herein.

8.6.3 Diagnosis of the genera:

8.6.3.1 *Encrinuroides* Reed, 1931

Type species; *Encrinuroides sexcostatus* Reed, 1931
Sholeshook Limestone, Cautleyan-Rawtheyan (M. Ashgill), South Wales

As suggested by Edgecombe & Chatterton (1990) it is clear that *Encrinuroides* as currently defined is paraphyletic and requires revision. A small number of the taxa currently assigned to *Encrinuroides* form a monophyletic clade which includes the type species *Encrinuroides sexcostatus* Reed, 1931. I propose to restrict *Encrinuroides (sensu stricto)* to the taxa *Encrinuroides autochthon* Tripp, 1962, *Encrinuroides periops* Tripp, 1967, *Encrinuroides sexcostatus* Reed, 1931 and *Encrinuroides stincharensis* Tripp, 1979. Of the taxa currently assigned *Encrinuroides* a number should be re-assigned to other genera:

1. *Encrinuroides tholus* Evitt & Tripp, 1977 is to be reassigned to *Physemataspis* Evitt & Tripp, 1977.
2. *Encrinuroides neuter* Evitt & Tripp, 1977 and *Encrinuroides uncatus* Evitt & Tripp, 1977 are to be reassigned to *Erratencrinurus* Krueger, 1971.
3. *Encrinuroides* sp. A of Tripp, 1974, *Encrinuroides* sp. B of Lespérance & Tripp, 1984, *Encrinuroides lapworthi* Tripp, 1980b, and *Encrinuroides spicatus* Tripp, 1974 are all to be reassigned to *Celtencrinurus* Evitt & Tripp, 1977.
4. The remaining taxa currently assigned to *Encrinuroides* are taxa which occupy positions in the phylogeny which cluster around *Encrinuroides* but which are intermediate between it and other genera. As is usual with pleisiomorphic stem (intermediate) forms, the systematic placement of these taxa is problematical. To avoid having to set up a large number of monospecific genera I propose to assign these taxa to *Encrinuroides (sensu lato)*, comprising the following taxa;

Encrinuroides (sensu lato) capitonis	Fredrickson, 1964
Encrinuroides (sensu lato) hornei	Dean, 1973
Encrinuroides (sensu lato) fallax	(Reed, 1899)
Encrinuroides (sensu lato) obesus	Tripp, 1965
Encrinuroides (sensu lato) rarus	(Walcott, 1877)
Encrinuroides (sensu lato) torulatus	Evitt & Tripp, 1977

As can be seen from Figure 8.7, *Encrinuroides (sensu lato) fallax* (Reed, 1899) (see Reed, 1931) and the stratigraphically younger *Encrinuroides (sensu lato) obesus* Tripp, 1965 are closely related. If adult specimens of *Encrinuroides (sensu lato) obesus* are compared to juvenile specimens of *Encrinuroides (sensu lato) fallax* (See figure 8.8.1) it is clear that they are almost identical, making it highly probable that *Encrinuroides (sensu lato) obesus* developed by paedomorphosis from *Encrinuroides fallax*.

Encrinuroides (sensu stricto) may be diagnosed on the following characters:

The outline of the glabella is concave outwards with the frontal lobe being the widest point; Longitudinal anteromedian furrow presentin the frontal lobe of the glabella; With the exception of *Encrinuroides periops*, the tubercles on the axis of the glabella are not obviously ordered. In *periops* the I-1, II-1 and III-1 tubercles are ordered but none of the tubercles is notably enlarged relative to the others; Lateral glabellar lobes multiply tuberculate; Anterior border furrow of constant depth; Anterior cranidial border continuous, of constant breadth and displaying scattered granules; Fixigenal fields tuberculate, except in *E. sexcostatus* in which they are granulate; Eye ridge present (except *stincharensis*); Mid-point of the palpebral lobes posterior to, or level with the mid-point of the L3 lateral glabellar lobes; Eyes stalked; The mid-section of the eye stalk is constricted; Fixigenal spine present, length less than 50% of the sagittal length of the cranidium; Base of the fixigenal spine granulate; Sub-parallel lateral margins to the rostral plate; Librigenal field tuberculate; Librigenal border granulate; One irregular row of tubercles on the anterior librigenal field (except *periops* in which the tubercle distribution is so irregular as to form two rows); Pygidium sub-triangular (except the stem taxon *periops* in which it is sub-pentagonal); Paired/tripled tubercles present on all successive rings on the axis of the pygidium; Two pleurae confluent with in sequence axial rings (except *sexcostatus* with one); 6-8 pygidial pleurae;

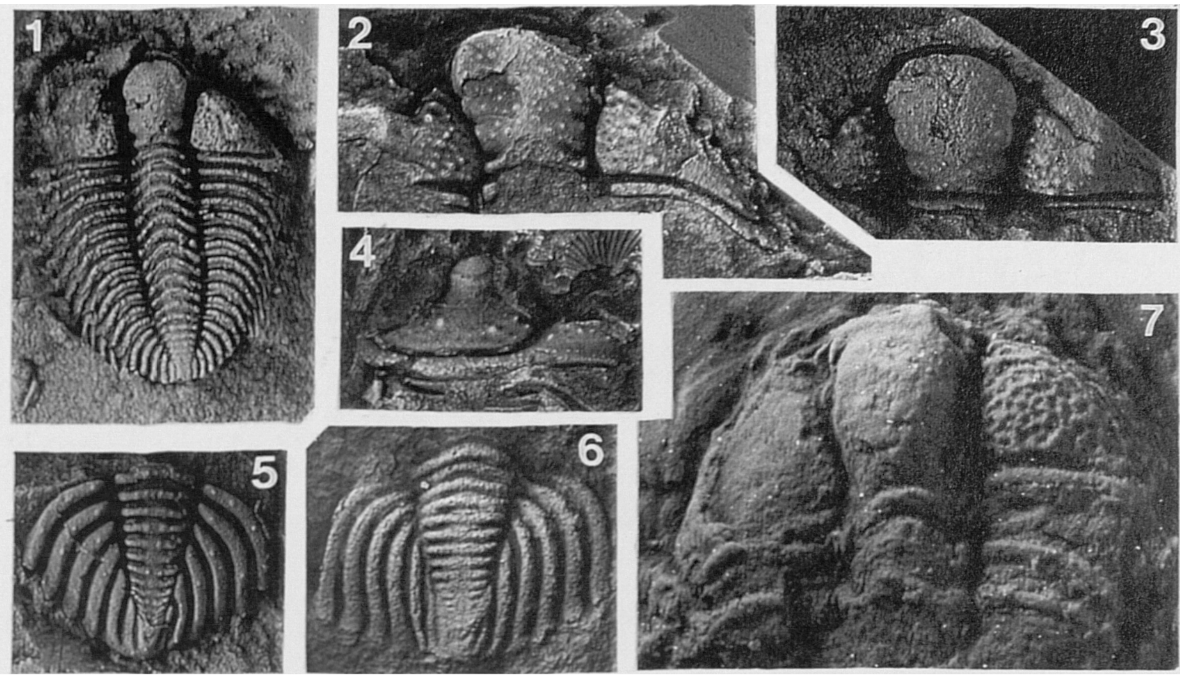


Fig. 8.8. *Encrinuroides fallax* and *Dindymene saron*.
1-6. *Encrinuroides fallax* (Reed, 1899), Tramore Limestone (upper Llanvirn - lowest Caradoc), Tramore, Co. Waterford, Ireland, National Museum of Ireland Collection (Photographs courtesy of Dr Alan W. Owen). 1. Internal mould of complete syntype specimen, NMI. G.15. 1983 (original of Reed 1899, pl. 49, fig. 12), x6. 2. Partially exfoliated cranidium, G. Murphy collection No. 269A, x6. 3. Internal mould of syntype cranidium, NMI. G.13. 1983 (original of Reed 1899, pl. 49, fig. 9), x4. 4. Internal mould of free cheek, G. Murphy collection No. 442, x4. 5. Internal mould of syntype pygidium, NMI. G.14. 1983 (original of Reed 1899, pl. 49, fig. 11), x4. 6. Latex peel of pygidium, G. Murphy collection No. 353A, x5.
7. *Dindymene saron* Fortey & Owens, 1987, Pontyfenni Fm. (Upper Arenig), Pontyfenni, Dyfed, Sweden. Partially exfoliated cranidium Note the similarity of the cephalon of this large specimen to that of small individuals of *E. fallax* (e.g. Fig.8.8.1).

8.6.3.2 *Physemataspis* Evitt & Tripp, 1977:

Type species: *Physemataspis coopi* Evitt & Tripp, 1977
Boutetort Formation (=Edinburg Formation),
early Caradoc,
Virginia, USA

Species of *Physemataspis*, together with the basal stem taxon *Encrinuroides tholus*, here reassigned to *Physemataspis (sensu lato)*, form a monophyletic subclade. Edgecombe & Chatterton (1990) suggested that the species *Encrinuroides gibber* Dean, 1979 may be related to an expanded *Physemataspis* and remarked on the similarity of cranidia assigned to *Ceraurus* sp. by Dean (1979). These inferences are supported herein. Evitt & Tripp (1977) and Edgecombe & Chatterton (1990) regarded *Encrinuroides insularis* as being closely related to *Physemataspis*, which is also borne out by this analysis. The subgenera *Physemataspis (Physemataspis)* and *Physemataspis (Prophysemataspis)* were erected by Lespérance & Desbiens (1995) but are not regarded as being valid herein (see section 8.6.2).

Crown group members of *Physemataspis* display inflated glabellae which may be functionally similar to those of the cybelines *Dindymene*, the *Koksorenus* group and *Libertella* within the Cybelinae. This feature is not sufficiently strong, in the Ordovician encrinurines, to allow a sharp division to be drawn between taxa with an inflated glabella and taxa without, and so was excluded from the analysis. The inflated transverse fixigenal ridge is morphologically very similar to the thoracic segments and may be a re-expression of a segment tagmatised to form part of the cranidium during ontogeny. Numerous other Encrinuridae display slight transverse ridges towards the posterior of the fixigenal fields but they are not inflated and raised after the fashion of those in *Physemataspis*. Edgecombe & Chatterton (1990) regarded the development of an inflated, round hypostomal middle body to be a useful synapomorphy of *Physemataspis*. This character was not included in this analysis because of problems in differentiating its definition from oval, non-inflated forms of hypostomal middle body.

8.6.3.2a Discussion of *Encrinuroides gibber* Dean, 1979

On setting up the new species *Encrinuroides gibber*, Dean (1979) included and described only pygidia. In the same formation and from the same locality as these pygidia are cephala which he considered to be of juvenile *Ceraurus* and which he assigned to *Ceraurus* sp. These cranidia are in fact of adult encrinurines, as noted by Edgecombe & Chatterton (1990). It seems logical to link these pygidia and cranidia as belonging to the same species and here include them both in the species *Encrinuroides gibber*. This species, as here defined, does not differ in any significant manner from *Encrinuroides tholus* Evitt & Tripp, 1977. As a result I propose that *Encrinuroides gibber* be considered a junior subjective synonym of *Encrinuroides tholus* Evitt & Tripp, 1977. This incorporation of *gibber* into *tholus* provides information on the form of the librigenae in *tholus*

8.6.3.2b Discussion of *Walencrinuroides gelasi* Lésperance & Desbiens, 1995

In their discussion of this new genus and species, Lésperance & Desbiens (1995, pp.9-11) noted that two of their specimens are identical to *tholus*. I can find no significant features separating these two species and so regard *Walencrinuroides gelasi* Lésperance & Desbiens, 1995 as a junior subjective synonym of *Encrinuroides tholus* Evitt & Tripp, 1977. In the analysis below, *Encrinuroides tholus* is reassigned to *Physemataspis* and thus the genus *Walencrinuroides* is a junior synonym of *Physemataspis*.

Physemataspis is diagnosed on the following characters:

(As a basal taxon, *tholus* lacks some of the diagnostic features)

Axial furrows convex outwards, widest at the L3 lateral glabellar lobes; Longitudinal anteromesial furrow in the anterior of the frontal lobe; Numerous tubercles on the axis of the glabella, some pairing evident, but no tubercles enlarged relative to the others, I-1, II-1, III-1 tubercles present without the associated interpair tubercles in the more derived members of the clade; Lateral glabellar lobes multiply tuberculate; L1 lateral glabellar lobes depressed relative to the other lobes; Anterior border furrow of constant depth; Anterior border with scattered tubercles and granules, not arranged in regular rows; Anterior border narrow mesially in the sagittal plane, in *miriabilis* it is discontinuous mesially; Rostral plate sub-parallel sided; Fixed cheeks tuberculate; Eye ridge distinct; Eyes situated posterior to the mid-point of the L3 lateral glabellar lobes, eye stalked, palpebral lobe inflated with a ring of coarse granules/tubercles; Derived members display an inflated fixigenal ridge; Posterior cranidial border non-tuberculate; Fixigenal spines long (>50% of the sagittal length of the cranidium), base of the fixigenal spine granulate, spine itself non-tuberculate; Librigenal field and border granulate; Three rows of tubercles on the anterior librigenal field; Pygidium sub-pentagonal; pygidial axial rings display paired tubercles, on stem taxa, tubercles on each of the axial rings of the pygidium, in other members of *Physemataspis* only alternate pygidial axial rings display tubercles; Two pygidial pleurae confluent with in sequence, continuous axial rings in stem taxa members of *Physemataspis*, three in crown group members; 6-8 pygidial pleurae.

Taxa included in *Physemataspis* :

Physemataspis coopi	Evitt & Tripp, 1977
Physemataspis insularis	(Shaw, 1968)
Physemataspis miriabilis	Tripp, 1980
Physemataspis tholus	(Evitt & Tripp, 1977)

8.6.3.3 Discussion of *Erratencrinurus* Krueger, 1971 and *Celtencrinurus* Evitt & Tripp, 1977

Erratencrinurus was established by Krueger, 1971 to accommodate a group of spinose species from erratics in the North German Pleistocene drift deposits. Evitt & Tripp, 1977 established the genus *Celtencrinurus*, based on the type species *Amphion multisegmentatus* Portlock, 1843, stating that they believed that *Erratencrinurus* and *Celtencrinurus* were developed from an evolutionary line which included *Encrinuroides uncatus* Evitt & Tripp, 1977. On the basis of the results of a multivariate analysis, Temple & Tripp, 1979 suggested that *Erratencrinurus* and *Celtencrinurus* be regarded as subgenera of *Erratencrinurus* but did not formally effect this change. Strusz (1980 p.9) agreed in principle but also did not formally define the subgenera and it was Owen (1981 p48) who diagnosed the subgenera *Erratencrinurus (Erratencrinurus)* and *Erratencrinurus (Celtencrinurus)*. Lespérance & Tripp (1984) agreed with the subgeneric assignment of *Celtencrinurus* and further restricted the diagnosis to only include five members. Owen & Heath (1990) did not follow this restriction of the diagnosis of *Erratencrinurus (Celtencrinurus)* and divided *Erratencrinurus (Celtencrinurus)* into two groups. They also recognised two informal groups within *Erratencrinurus (Erratencrinurus)* and an *Erratencrinurus (sensu lato)* group.

It is unsurprising that problems have been experienced by various authors as there is evidence of a large amount of convergence and parallelism in these two closely related groups which are not as apparent when non-cladistic methods of analysis are employed. Further hampering the definition of tight diagnoses is the fact that the majority of the characters which have previously been considered diagnostic 'step in' gradually at the base of the subclades, with the result that many of the basal members do not display all of the feature 'diagnostic' of the group. In spite of these difficulties *Erratencrinurus* and *Celtencrinurus* should be regarded as genera, rather than subgenera as the features which, in the past, have been regarded as uniting the two groups are independently derived in each:

1. The mesial deepening in the anterior border.

The basal taxa of both groups do not have a mesial deepening in the anterior border. In addition, the deepening in *Erratencrinurus* differs from that of *Celtencrinurus*. In the former, the anterior border slopes down adaxially to a narrow point in the middle to form a 'V' shape while in *Celtencrinurus* the anterior border is horizontal with a sharply delineated 'U' shaped depression.

2. Large ordered tubercles on the axis of the glabella.

Members of *Erratencrinurus* display axial glabellar tubercles arranged in a pentangle, enlarged relative to the other glabellar tubercles in the majority of the taxa while members of *Celtencrinurus* display regularly paired axial tubercles with interpair I-0 tubercles.

8.6.3.4 *Erratencrinurus* Krueger, 1971;

Type species: Subsequently designated (Krueger, 1972) *Erratencrinurus capricornu* Krueger, 1971
Baltic Stage E (Upper Caradoc)
Top *D. clingani* graptolite Zone. N. German Drift

Diagnosis of *Erratencrinurus*:

No anteromesial furrow in the frontal lobe, except the basal stem taxa *lapworthi*, sp.A and sp.B; I-1 (except in *brutoni*, where this area is non-tuberculate) , II-1 (except in *brutoni*, where this area is non-tuberculate) and III-1 (conservatively coded as absent in *imperfectus*, *brutoni* and *cornutus* although III-1 inferred to have fused together at their base to form a single, very large and broad based, horn topped by a pair of tubercles) tubercles present; III-1 tubercles enlarged or extended into horns in derived members; i-0 (ii-0 of Tripp), ii-0 (iii-0 of Evitt & Tripp 1977), iii-0 (iv-0 *of* Evitt & Tripp 1977) present in all but the most derived of the taxa; I-0, II-0 III-0 tubercles absent; III-0 conservatively coded as present in *imperfectus*, *brutoni* and *cornutus* as the fused III-1 tubercle pair occupies this position - although clearly differentiated from the single III-0 tubercle by both size and the presence of a tubercle pair in front of it; Pentagon of tubercles (Evitt & Tripp, 1977) enlarged relative to the other glabellar tubercles; IV tubercles enlarged; Lateral glabellar lobes polytuberculate, except in *inopionatus* subclade in which they are monotuberculate; Anterior border of constant breadth, gradually descending in a 'V' shape to its lowest point in the middle (in *capricornu* the lowest point of the anterior border is somewhat broader than in the other taxa, approaching the form seen in *Celtencrinurus* but still associated with a gently 'V' shaped anterior border); Anterior border generally displays an odd number of well developed tubercles (except *capricornu* crown group) which are organised symmetrically in a single row; Most have nine tubercles, except again for the *capricornu* crown group; Lateral margins of rostral plate diverge ventrally; Eye ridge poorly defined in derived members; Ring of tubercles present around the eye stalk; Eye stalk is short in low clade taxa, tall in more derived members; Long genal spine present, the base of which is tuberculate; Librigenal lateral border tuberculate; Tuberculation of the anterior portion of the librigenal border, underneath the anterior librigenal field, extends to the full adaxial extent of the librigenal border (except in the stem taxa *uncatus, neuter* and *vigilans*; Number of rows of tubercles on the anterior librigenal field increases from two to five in a regular fashion as taxa are increasingly derived; Low clade members of *Erratencrinurus* display tubercles on alternate axial rings while high clade members entirely lack axial tubercles; Pygidial pleurae 'spear shaped' and display tips which turn out laterally; Nine or more pygidial pleurae (6-8 in *uncatus* and *neuter*); Two pygidial pleurae confluent with in sequence, continuous axial pygidial rings;

Species included in *Erratencrinurus*:

Erratencrinurus brutoni	Owen, 1981
Erratencrinurus capricornu	Krueger, 1971
Erratencrinurus cornutus	(Ingham, 1974)
Erratencrinurus imperfectus	Owen, 1981
Erratencrinurus inopinatus	Owen & Heath, 1990
Erratencrinurus jaegeri	Krueger, 1991
Erratencrinurus kaushi	Krueger, 1971
Erratencrinurus kummerowi	Krueger, 1971
Erratencrinurus nebeni	Krueger, 1971
Erratencrinurus neuter	Evitt & Tripp, 1977
Erratencrinurus postseebachi	Krueger, 1991
Erratencrinurus seebachi	(Schmidt, 1881) (see Rosenstein, 1941)
Erratencrinurus uncatus	Evitt & Tripp, 1977
Erratencrinurus vigilans	(Hall, 1847)

8.6.3.5 *Celtencrinurus* Evitt & Tripp, 1977

Type species: *Amphion multisegmentatus* Portlock, 1843
Killey Bridge Beds, Cautleyan (M. Ashgill), Desertcreight, Co. Tyrone, N. Ireland (see Tripp, 1957, Tunnicliff, 1978),

As usual, many of the characters 'step in' resulting in the basal taxa not displaying all of the features listed in the diagnosis.

Diagnosis of *Celtencrinurus* :

No anteromesial furrow in the frontal lobe, except the basal stem taxa *lapworthi*, sp.A and sp. B; None of the glabellar tubercles are enlarged relative to other glabellar tubercles; I-1, II-1 and III-1 tubercles absent in more derived members of *Celtencrinurus*; III-1 tubercles (where present) not enlarged; i-0 (ii-0 of Evitt & Tripp, 1977) absent in all members except the most basal stem taxon *lapworthi*; ii-0 (iii-0 of Evitt & Tripp, 1977) absent in more derived members, as is iii-0 (iv-0 of Evitt & Tripp, 1977); I-0 tubercle present in more derived members, while II-0 and III-0 tubercles 'step in' in more derived taxa; lateral glabellar lobes tubercliform; Anterior border displays an even number of well developed tubercles organised symmetrically in a single row (except *multisegmentatus* which displays 9); The majority of *Celtencrinurus* have eight tubercles, while *moe* and *kiaeri* have ten; Horizontal anterior border of constant breadth, displaying an abrupt broad based 'U' shaped mesial deepening, approximately as broad as one of the anterior border tubercles; Eye ridge poorly defined in derived members; Ring of tubercles present around the eye stalk; Eye stalk is tall in low clade taxa, short in more derived members; Long genal spine present, the base of which is tuberculate; Lateral margins of rostral plate sub-parallel; Librigenal lateral border tuberculate; Tuberculation of the anterior of the librigenal border does not extend to the full length of the librigenal border under the anteromesial section of the cranidium; Between one and four rows of tubercles on the anterior librigenal field; Low clade members of *Celtencrinurus* display tubercles on alternate axial rings while high clade members entirely lack axial tubercles; Pygidial pleurae 'spear shaped' and display tips which turn out laterally; six or more pygidial pleurae (less than 8 in taxa belonging to the lower half of the subclade; Two pygidial pleurae confluent with in sequence, continuous axial pygidial rings.

Species included within *Celtencrinurus*:

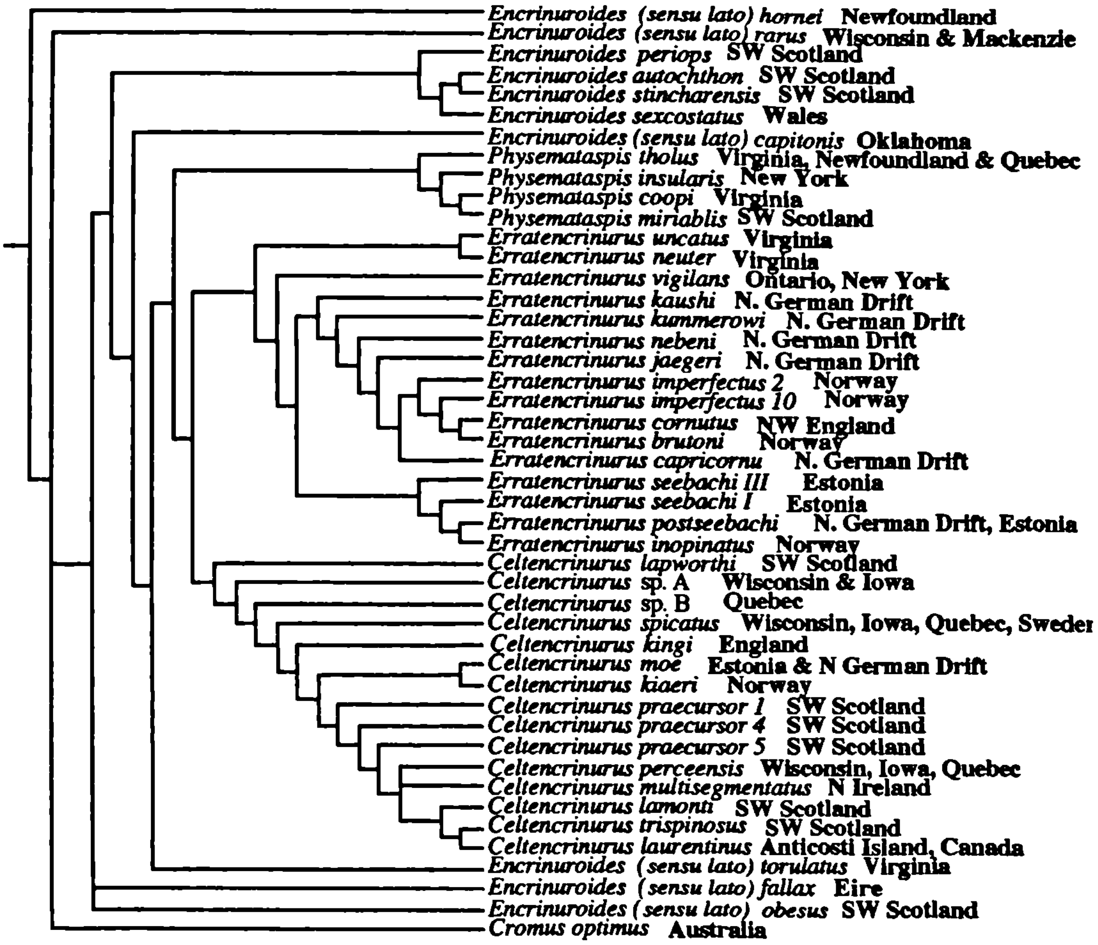
Celtencrinurus sp.A	of Tripp (1974)
Celtencrinurus sp.B	of Lespérance & Tripp (1984)
Celtencrinurus kiaeri	Owen, 1981
Celtencrinurus kingi	(Dean, 1963)
Celtencrinurus lamonti	(Tripp, 1957)
Celtencrinurus lapworthi	Tripp, 1980b
Celtencrinurus laurentinus	(Twenhofel, 1928)
Celtencrinurus moe	(Männil, 1958)
Celtencrinurus multisegmentatus	(Portlock, 1843)
Celtencrinurus praecursor	(Tripp, 1954)
Celtencrinurus perceensis	(Cooper, 1930)
Celtencrinurus spicatus	(Tripp, 1974)
Celtencrinurus trispinosus	(Reed, 1914)

8.8. Palaeogeographical inferences:

8.8.1 Informal palaeobiogeographical inferences:

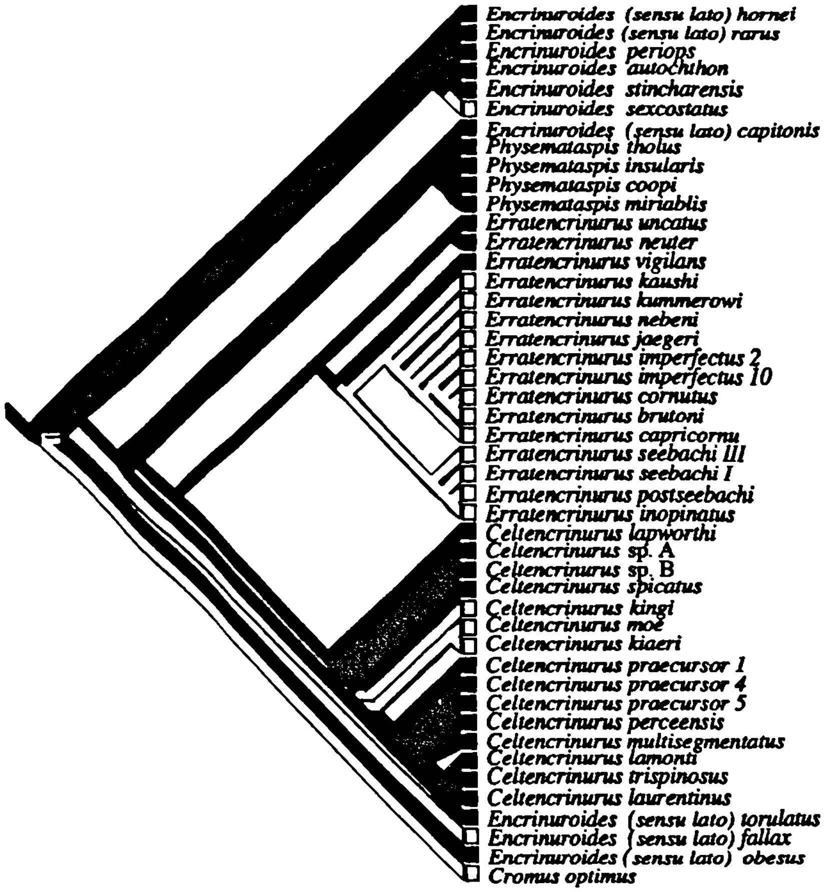
The Ordovician Encrinurinae are predominantly found in Laurentia and Baltica. Their shallow water habitat is reflected in the tendency for the subclades to be strongly localised with, for example, *Encrinuroides (sensu stricto)*, *Physemataspis* and *Celtencrinurus* being almost exclusively Laurentian subclades while members of *Erratencrinurus* is are largely to be found in Baltica (Figure 8.9). The oldest taxa in each subclade are invariably Laurentian. Any non-Laurentian taxa are successively from Baltica and then Avalonia.

Figure 8.9: Cladogram annotated with the geographical locations of the specimens.



This broadly repeated palaeobiogeographical pattern within the Encrinurinae (and Encrinuridae) of origination within Laurentia, followed by expansion into Baltica, followed in turn by expansion from Baltica into Avalonia during the Late Ordovician can clearly be seen in Figures 8.10, 8.11 and 8.12; the Encrinurinae cladogram 2 with the distributions of the palaeogeographical locations of these taxa optimised upon them. The close fit of branching position and stratigraphical age in this phylogeny provides a very rough sequence to the patterns of range alteration. *Cromus optimus* is the only Ordovician encrinurine found in Gondwana. It is a phylogenetically early species, although stratigraphically in the middle of the Ordovician range of the Encrinurinae The morphology of *Cromus optimus* is similar to that of other Ordovician Encrinurinae, inferred to have existed in shallow water (such as *Encrinuroides*) making it difficult to explain how *optimus* alone reached Gondwana.

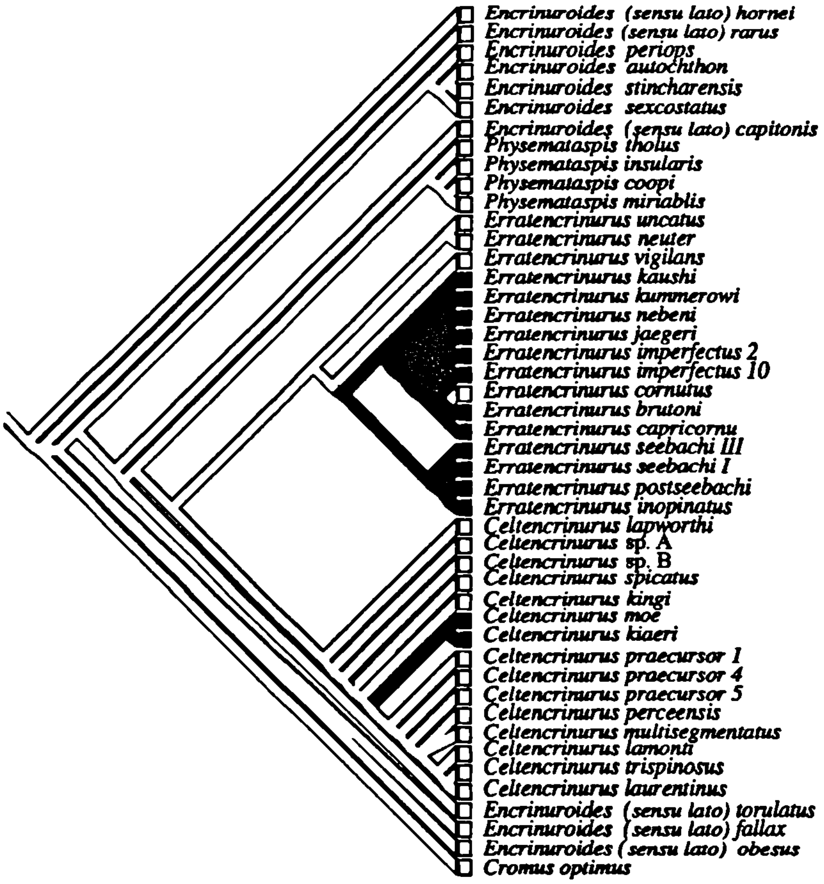
Figure 8.10: Cladogram 2 with the distribution of Laurentian Ordovician encrinurine taxa highlighted in black;



As can be seen from figure 8.10 the oldest Encrinurinae and the oldest members of each subclade are found in areas which are thought to have belonged to Laurentia. Taxa recorded from Baltica invariably developed from ancestors which were to be found in Laurentia (Figure 8.11).

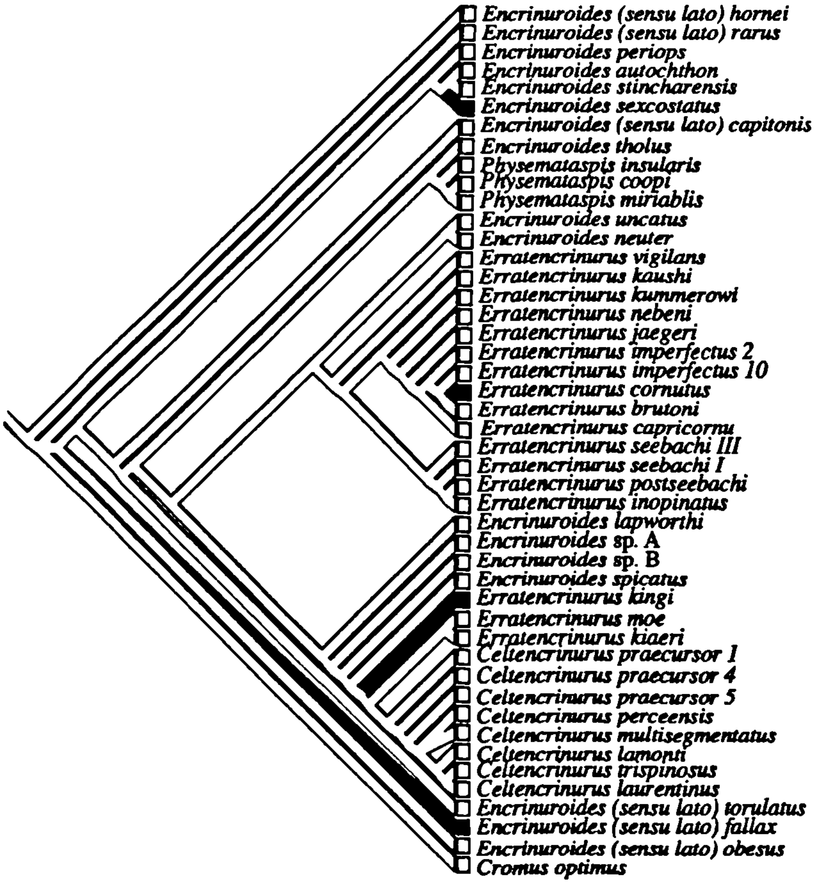
There is an obvious strong biogeographical division between members of *Erratencrinurus*, which are predominantly Baltic, and those of *Celtencrinurus*, which are largely to be found in marginal Laurentian areas, such as S.W. Scotland.

Figure 8.11: Cladogram 2 with the distribution of Baltic Ordovician encrinurine taxa highlighted in black;



This may well indicate that these two areas were sufficiently far apart that taxa which inhabited shallow water, such as *Erratencrinurus* and *Celtencrinurus* are inferred to have done, were not in full communication with each other.

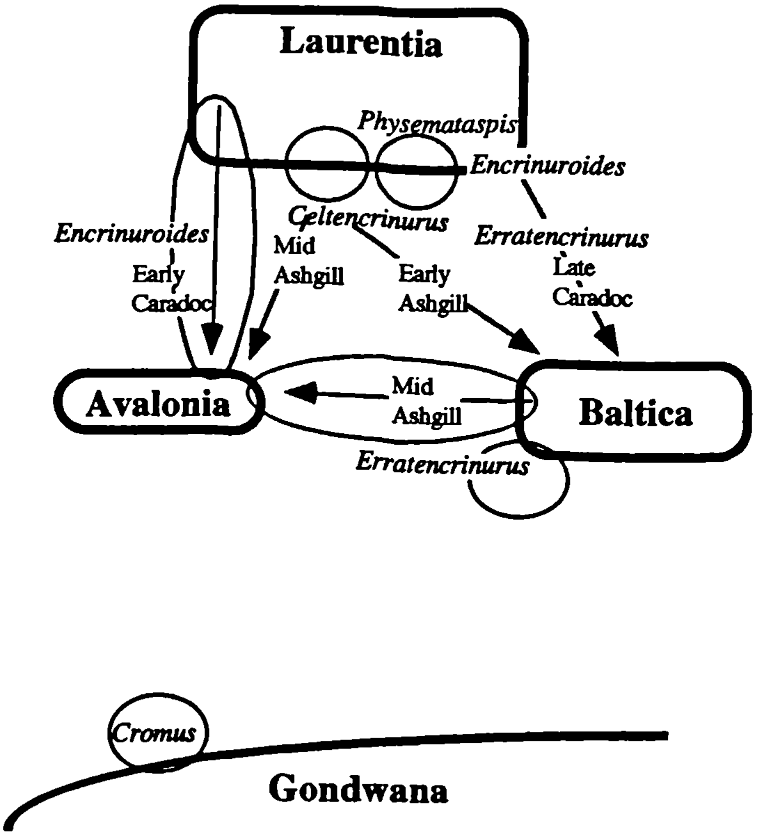
Figure 8.12: Cladogram 2 with the distribution of Avalonian encrinurine taxa highlighted;



The ranges of *Encrinuroides (sensu stricto)*, *Erratencrinurus* and *Celtencrinurus* do not include Avalonia until the late Ashgill when a small number of taxa, derived from both Laurentian and Baltic stock 'hop over' indicating that, for these taxa, Avalonia was not in communication with either Laurentia or Baltica until the Ashgill. This pattern may indicate the following scenario:

1. Origination of the Encrinurinae in Laurentia in the Arenig, at which time Laurentia was isolated from the other continents.
2. Close approach of Laurentia and Baltica in the late Caradoc/early Ashgill.
3. Isolation of *Celtencrinurus* in Laurentia and *Erratencrinurus* in Baltica during the, Caradoc/Ashgill - possibly due to environmental specialisation.
4. Close approach of Avalonia to both Laurentia and Baltica simultaneously during the late Ashgill.

Figure 8.13: Schematic diagram showing informally inferred distributions and timing of range expansion of the Ordovician encrinurine subclades.



The only feature of the Encrinurinae palaeobiogeographical history, as outlined here, which differs from that of the other taxa studied herein is the early communication between Laurentia and Avalonia in the Llanvirn/ early Caradoc where *Encrinuroides (sensu lato) fallax* (Reed, 1899) from the Tramore Limestone of Ireland (Avalonia) gave rise to *Encrinuroides (sensu lato) obesus* in the early Caradoc. This indicates that, for *Encrinuroides (sensu stricto)*, Laurentia and Avalonia were in communication by this time. A possible explanation of this anomaly is that Tramore was situated in a more marginal position than the rest of Avalonia or that Tramore was actually part of an island in Iapetus which allowed taxa to 'hop' between continents. This latter scenario finds some support in the other taxa in the Tramore Limestone; *Atractopyge tramorensis* has been shown to be derived from Laurentian ancestors (via Baltica) which made the journey far earlier than expected as it, and other members of its subgenus, were adapted to an ocean island setting. There are further taxa with strong Laurentian affinities in the Tramore Limestone and associated units in addition to characteristic Avalonian taxa (A.W. Owen pers. comm.)

8.8.2 Palaeobiogeographical Gain/Loss ratio analysis:

In order to somewhat formalise the palaeobiogeographical inferences a gain/loss study was carried out.

Figure 8.14: Ordovician Encrinurinae cladogram 2, annotated with the nodes utilised in the Gain/Loss ratio analysis.

The Gain/Loss ratios calculated for the various nodes on the cladogram are listed in tables 8.1 to 8.8.

Table 8.1: Showing Gain/Loss ratios for nodes A and B (see Fig. 8.14)

Geographical area	**Node A**			**Node B**		
	Gains	Losses	$\frac{\text{Gains}}{\text{Losses}}$	Gains	Losses	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	**15**	**6**	**2.5**	**13**	**5**	**2.6**
Baltica	**10**	**18**	**0.55**	**10**	**15**	**0.67**
Avalonia	4	25	0.16	4	22	0.18
Gondwana	1	3	0.33	0	0	0

At nodes A, B and C the ancestral range of the Encrinurinae included Laurentia and Baltica.

Table 8.2: Showing Gain/Loss ratios for nodes C and D (see Fig. 8.14)

Geographical area	**Node C**			**Node D**		
	Gains	Losses	$\frac{\text{Gains}}{\text{Losses}}$	Gains	Losses	$\frac{\text{Gains}}{\text{Losses}}$
Laurentia	**12**	**3**	**4**	**2**	**1**	**2**
Baltica	**10**	**13**	**0.77**	0	0	0
Avalonia	2	21	0.1	**1**	**2**	**0.5**
Gondwana	0	0	0	0	0	0

At node D the ancestral range included Laurentia and Avalonia.

Table 8.3: Showing Gain/Loss ratios for nodes E and F (see fig. 8.14)

Geographical area	**Node E**			**Node F**		
	Gains	Losses	Gains Losses	Gains	Losses	Gains Losses
Laurentia	**9**	**3**	**3**	**1**	**1**	**1**
Baltica	**10**	**11**	**0.91**	0	0	0
Avalonia	2	18	0.11	0	0	0
Gondwana	0	0	0	0	0	0

At node E the ancestral range of the Encrinurinae included Laurentia and Baltica while at node F the ancestral range was restricted to Laurentia.

Table 8.4: Showing Gain/Loss ratios for nodes G and H (see Fig. 8.14)

Geographical area	**Node G**			**Node H**		
	Gains	Losses	Gains Losses	Gains	Losses	Gains Losses
Laurentia	**7**	**3**	**2.3**	**2**	**1**	**2**
Baltica	**10**	**9**	**1.11**	**9**	**3**	**3**
Avalonia	2	17	0.117	1	11	0.09
Gondwana	0	0	0	0	0	0

At nodes G and H the ancestral ranges included Laurentia and Baltica.

Table 8.5: Showing Gain/Loss ratios for nodes I and J (see Fig. 8.14)

Geographical area	**Node I**			**Node J**		
	Gains	Losses	Gains Losses	Gains	Losses	Gains Losses
Laurentia	0	0	0	0	0	0
Baltica	**9**	**1**	**9**	**1**	**1**	**1**
Avalonia	1	10	0.1	0	0	0
Gondwana	0	0	0	0	0	0

At nodes I, J, K and L Baltica formed the ancestral range of the taxa.

Table 8.6: Showing Gain/Loss ratios for nodes K and L (see Fig. 8.14)

Geographical area	**Node K**			**Node L**		
	Gains	Losses	Gains/Losses	Gains	Losses	Gains/Losses
Laurentia	0	0	0	0	0	0
Baltica	**8**	**1**	**8**	**4**	**1**	**4**
Avalonia	1	8	0.13	1	4	0.25
Gondwana	0	0	0	0	0	0

Laurentia formed the ancestral range of the taxa above node M. While the ancestral range of the taxa above node N included Laurentia, Avalonia and Baltica.

Table 8.7: Showing Gain/Loss ratios for nodes M and N (see Fig. 8.14)

Geographical area	**Node M**			**Node N**		
	Gains	Losses	Gains/Losses	Gains	Losses	Gains/Losses
Laurentia	**5**	**2**	**5**	**2**	**1**	**0.5**
Baltica	1	6	0.17	1	**2**	**0.5**
Avalonia	1	5	0.2	**1**	**1**	**1**
Gondwana	0	0	0	0	0	0

Table 8.8: Showing Gain/Loss ratios for node O (see Fig. 8.14)

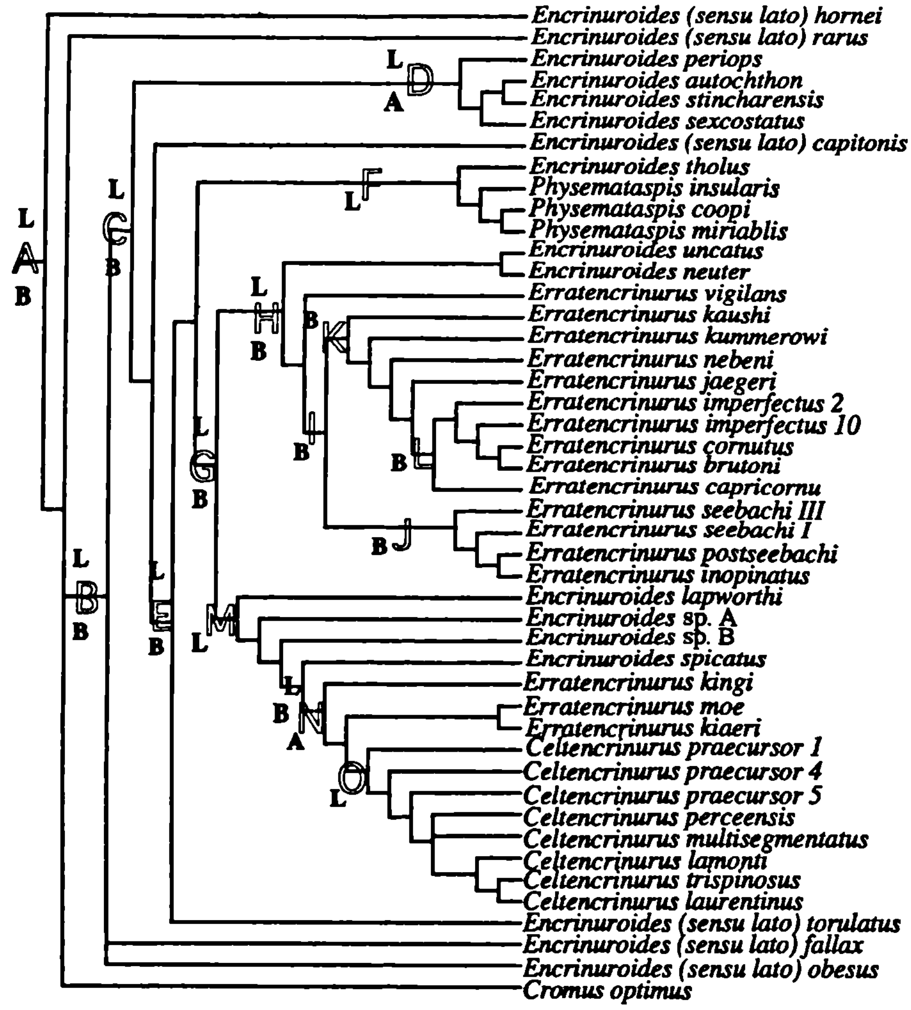
Geographical area	**Node O**		
	Gains	Losses	Gains/Losses
Laurentia	**1**	**1**	**1**
Baltica	0	0	0
Avalonia	0	0	0
Gondwana	0	0	0

The ancestral range of the taxa above node O includes Laurentia.

The mixed nature of the results indicates that both Laurentia and Baltica are likely to have formed parts of the ancestral range of the Encrinurinae right from the start of their development. There is a very clear palaeobiogeographical pattern of inclusion of both Baltica and Laurentia in the ancestral range of the early Encrinurinae, followed first by restriction, isolation and development of different subclades within these plates, finally followed by simultaneous range expansion to Avalonia from Laurentia and Baltica. The indication that both Laurentia and Baltica formed the ancestral range right from the inception of the Encrinurinae is surprising as the earliest Encrinurinae are of late Arenig age, at which time all of the other evidence, including the biogeographical signal of the Cybelinae, indicates that Baltica and Laurentia were well separated and the Encrinurinae are thought to have been relatively shallow water taxa. The immediate sister groups to the Encrinurinae within the Cybelinae are all Laurentian / equatorial, although *Cybele* Lovén, 1845 is also found in Baltica during the Arenig, indicating that some taxa were managing to hop from the Laurentia/equatorial belt range of the Cybelinae at this time.

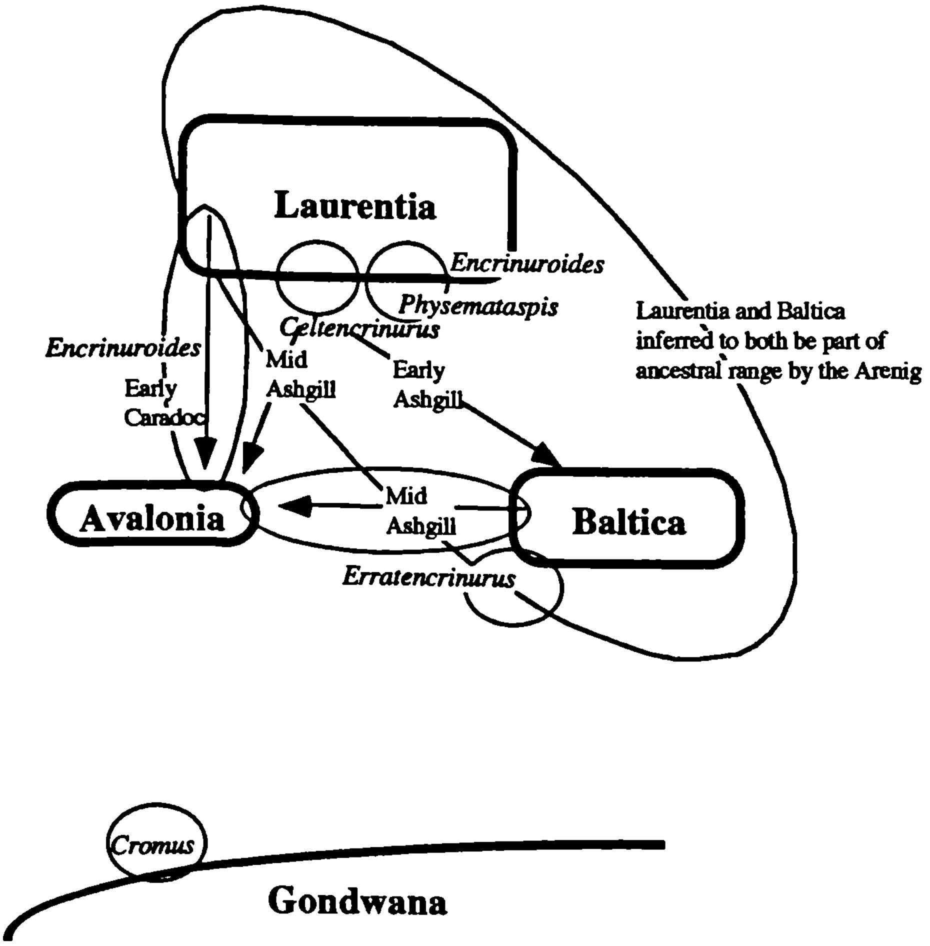
The fact that a large number of the gain/loss ratios are greater than '1' is a cause for concern, which may be a flaw in the gain/loss ratio method of assessment of palaeobiogeography which merits further investigation.

Figure 8.15: Cladogram annotated with the ancestral palaeobiogeographical ranges inferred for each node. **A**=Avalonia, **B**=Baltica, **L**=Laurentia



It can be seen that, with the exception of the common Laurentia/Baltica ancestral range of the early taxa, the pattern of change inferred is very similar to that inferred informally.

Figure 8.16: Schematic diagram showing distributions of the encrinurine subclades, inferred from the palaeobiogeographical gain/loss ratio analysis.



Laurentia and Baltica inferred to both be part of ancestral range by the Arenig

Because of the apparent anomaly in the early communication between Laurentia and Avalonia inferred by the Gain/Loss analysis, and in order to check that the results gained were not the result of my grouping of the areas into palaeoterranes, a second gain/loss ratio analysis was completed based on the current geographical locations of the taxa. This results in a completely different pattern of divisions of the data into locations and also provides a spatially more detailed study of the gain/loss ratios.

8.8.3 Gain/Loss ratio analysis utilising current geographical locations of the taxa:

Figure 8.17: Cladogram annotated with the nodes employed in the biogeographical gain/loss analysis.

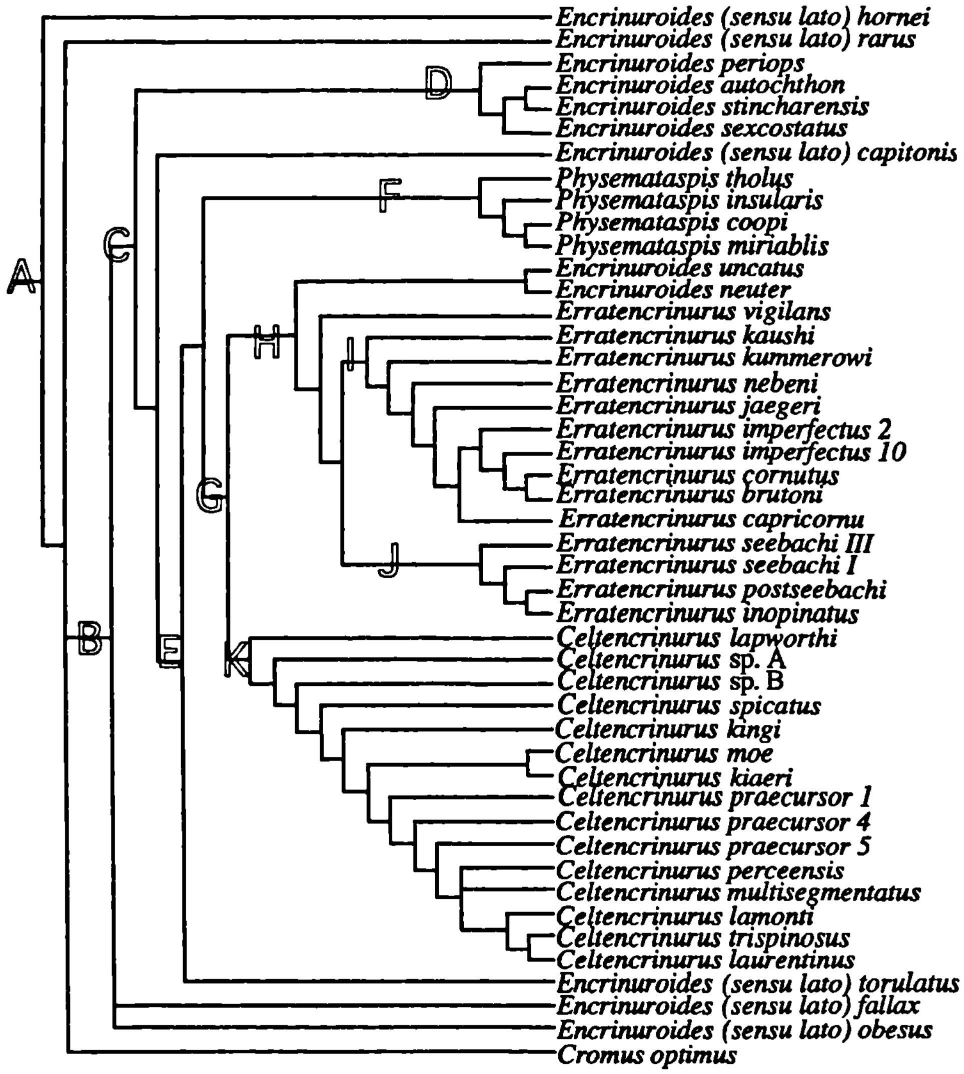


Table 8.9: Showing Gain/Loss ratios for nodes A and B (see Fig. 8.17)

Geographical area	**Node A**			**Node B**		
	Gains	Losses	$\frac{\text{Gains}}{\text{Losses}}$	Gains	Losses	$\frac{\text{Gains}}{\text{Losses}}$
New South Wales	1	3	0.33	0	0	0
S. Ireland	1	5	0.2	**1**	**2**	**0.5**
N.E. England	2	25	0.08	2	22	0.09
S. Wales	1	7	0.14	1	4	0.25
S.W. Scotland	**10**	**17**	**0.59**	**10**	**15**	**0.67**
Tyrone	1	21	0.05	1	18	0.06
Oklahoma	1	7	0.14	1	4	0.25
Virginia	4	11	0.36	4	8	0.5
New York	2	13	0.15	2	10	0.2
Iowa	1	12	0.08	1	9	0.11
Wisconsin	2	13	0.15	1	11	0.09
Quebec	5	20	0.2	5	16	0.29
Makenzie District	1	3	0.33	0	0	0
Ontario	1	12	0.08	1	9	0.11
Newfoundland	2	9	0.22	1	7	0.14
N. German Drift	9	20	0.45	**9**	**17**	**0.523**
Estonia	5	23	0.217	5	20	0.25
Norway	5	27	0.19	5	24	0.21

At node A the ancestral range of the taxa included South West Scotland while at node B the ancestral range of the taxa may have included S. Ireland (Avalonia) and the North German Drift (Baltica)

Table 8.10: Showing Gain/Loss ratios for nodes C and D (see Fig. 8.17)

Geographical area	**Node C**			**Node D**		
	Gains	Losses	Gains/Losses	Gains	Losses	Gains/Losses
New South Wales	0	0	0	0	0	0
S. Ireland	0	0	0	0	0	0
N.E. England	2	20	0.1	0	0	0
S. Wales	1	3	0.33	1	2	0.5
S.W. Scotland	**9**	**15**	**0.6**	2	1	2
Tyrone	1	16	0.06	0	0	0
Oklahoma	**1**	**2**	**0.5**	0	0	0
Virginia	**4**	**6**	**0.66**	0	0	0
New York	2	8	0.25	0	0	0
Iowa	1	7	0.14	0	0	0
Wisconsin	1	9	0.11	0	0	0
Quebec	5	15	0.33	0	0	0
Makenzie District	0	0	0	0	0	0
Ontario	1	7	0.14	0	0	0
Newfoundland	1	5	0.2	0	0	0
N. German Drift	**9**	**9**	**1**	0	0	0
Estonia	5	18	0.23	0	0	0
Norway	5	21	0.24	0	0	0

At node C the ancestral range of the taxa included the modern-day areas of South West Scotland, Virginia, Oklahoma (Laurentia) and the North German drift (Baltica). The ancestral range of the taxa above node D certainly included South West Scotland and may have included S. Wales.

Table 8.11: Showing Gain/Loss ratios for nodes E and F (see Fig. 8.17)

Geographical area	**Node E**			**Node F**		
	Gains	Losses	Gains/Losses	Gains	Losses	Gains/Losses
New South Wales	0	0	0	0	0	0
S. Ireland	0	0	0	0	0	0
N.E. England	2	18	0.11	0	0	0
S. Wales	0	0	0	0	0	0
S.W. Scotland	**7**	**13**	**0.54**	1	3	0.33
Tyrone	1	14	0.07	0	0	0
Oklahoma	0	0	0	0	0	0
Virginia	**4**	**4**	**1**	**2**	**2**	**1**
New York	2	6	0.33	**1**	**2**	**0.5**
Iowa	1	5	0.2	0	0	0
Wisconsin	1	7	0.14	0	0	0
Quebec	5	13	0.38	**1**	**1**	**1**
Makenzie District	0	0	0	0	0	0
Ontario	1	5	0.2	0	0	0
Newfoundland	1	3	0.33	**1**	**1**	**1**
N. German Drift	**9**	**12**	**0.75**	0	0	0
Estonia	5	16	0.31	0	0	0
Norway	5	20	0.25	0	0	0

At node E the ancestral range of the taxa included the modern-day areas of South West Scotland, Virginia, Quebec (Laurentia) and the North German drift (Baltica). While the ancestral range of the taxa above node F is profoundly Laurentian, including Virginia, New York, Quebec and Newfoundland.

Table 8.12: Showing Gain/Loss ratios for nodes G and H (see Fig. 8.17)

Geographical area	**Node G**			**Node H**		
	Gains	Losses	Gains/Losses	Gains	Losses	Gains/Losses
New South Wales	0	0	0	0	0	0
S. Ireland	0	0	0	0	0	0
N.E. England	2	16	0.125	1	11	0.09
S. Wales	0	0	0	0	0	0
S.W. Scotland	**6**	**9**	**0.66**	0	0	0
Tyrone	1	12	0.08	0	0	0
Oklahoma	0	0	0	0	0	0
Virginia	**1**	**2**	**0.5**	**1**	**1**	**1**
New York	1	3	0.33	**1**	**2**	**0.5**
Iowa	1	3	0.33	0	0	0
Wisconsin	1	5	0.2	0	0	0
Quebec	4	11	0.36	0	0	0
Makenzie District	0	0	0	0	0	0
Ontario	1	3	0.33	**1**	**2**	**0.5**
Newfoundland	0	0	0	0	0	0
N. German Drift	**9**	**11**	**0.82**	**8**	**4**	**2**
Estonia	5	14	0.36	**4**	**7**	**0.57**
Norway	5	17	0.29	4	10	0.4

At node G the ancestral range of the taxa included the modern-day areas of South West Scotland, Virginia, and the North German drift (Baltica). While the ancestral range of the taxa above node H included Virginia, Ontario, New York (First three are Laurentian), North German drift and Estonia (Baltica).

Table 8.13: Showing Gain/Loss ratios for nodes I and J (see Fig. 8.17)

Geographical area	**Node I**			**Node J**		
	Gains	Losses	Gains/Losses	Gains	Losses	Gains/Losses
New South Wales	0	0	0	0	0	0
S. Ireland	0	0	0	0	0	0
N.E. England	0	0	0	0	0	0
S. Wales	0	0	0	0	0	0
S.W. Scotland	0	0	0	0	0	0
Tyrone	0	0	0	0	0	0
Oklahoma	0	0	0	0	0	0
Virginia	0	0	0	0	0	0
New York	0	0	0	0	0	0
Iowa	0	0	0	0	0	0
Wisconsin	0	0	0	0	0	0
Quebec	0	0	0	0	0	0
Makenzie District	0	0	0	0	0	0
Ontario	0	0	0	0	0	0
Newfoundland	0	0	0	0	0	0
N. German Drift	**5**	**1**	**5**	**3**	**1**	**3**
Estonia	1	4	0.25	**3**	**1**	**3**
Norway	**3**	**6**	**0.5**	1	3	0.33

The ancestral ranges of the taxa above nodes I and J were Baltic and included the North German Drift deposits, Estonia and Norway.

Table 8.14: Showing Gain/Loss ratios for node K (see Fig. 8.17)

Geographical area	**Node K**		
	Gains	Losses	Gains / Losses
New South Wales	0	0	0
S. Ireland	0	0	0
N.E. England	1	5	0.2
S. Wales	0	0	0
S.W. Scotland	**6**	**8**	**0.75**
Tyrone	1	11	0.09
Oklahoma	0	0	0
Virginia	0	0	0
New York	0	0	0
Iowa	**1**	**2**	**0.5**
Wisconsin	1	4	0.25
Quebec	4	10	0.4
Makenzie District	0	0	0
Ontario	0	0	0
Newfoundland	0	0	0
N. German Drift	1	7	0.14
Estonia	1	7	0.14
Norway	1	7	0.14

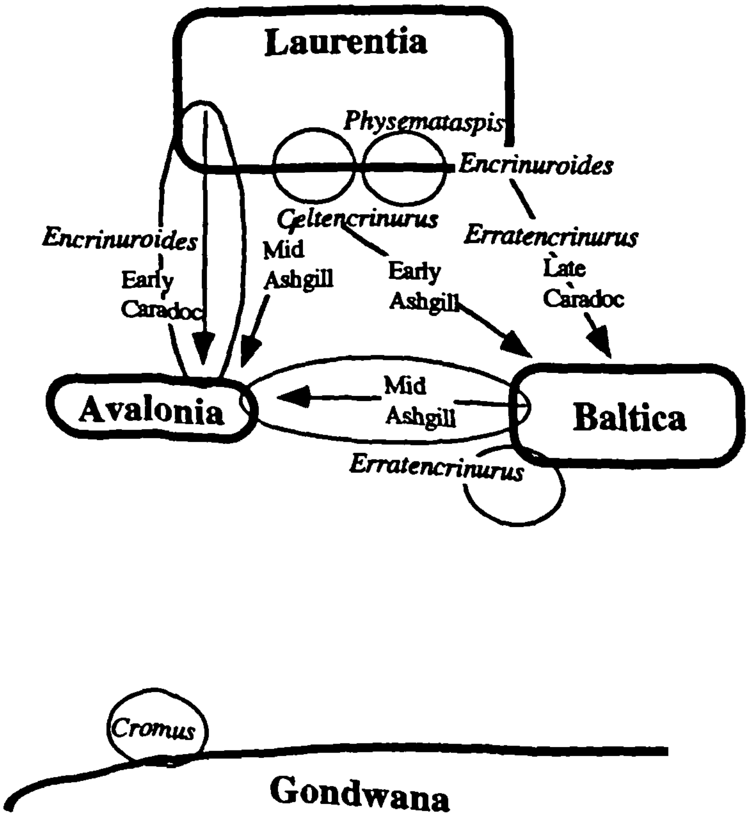
The ancestral ranges of the taxa above node K included S.W. Scotland and Iowa, both of which are Laurentian.

The results of this biogeographical gain/loss study reflect those of the palaeobiogeographical study with minor differences;

At the base of the cladogram (Node A) Baltica is not included in the ancestral range of the Encrinurinae, which accords with the relative positions of Baltica and Laurentia inferred from other sections of this study. The gain/loss ratio study still clearly indicates that Avalonia (Tramore Limestone) was part of the ancestral range (with Laurentian areas) by the early Caradoc. This early Caradoc age for communication between Laurentia and Avalonia, while still earlier than that indicated by many groups, is similar to that recorded for the *Atractopyge (Cybelella)* subclade (Section 5.5). The inference made for *Atractopyge (Cybelella)* was that the members of the subclade were adapted to slightly deeper water than the other *Atractopyge* groups and that it had 'island hopped' to S. Ireland (hence its occurrence in the Tramore Limestone).

In the upper part of the cladogram the broad pattern is the same as in the previous study but outlined in greater detail, with taxa not reaching Avalonia from Laurentia and Baltica until the Ashgill.

Figure 8.18: Schematic diagram showing inferred distributions and timing of range expansion of the Ordovician Encrinurinae subclades, inferred from the second encrinurine biogeographical Gain/loss ratio analysis.



I had been concerned as to the effect that variations in the definition of the areas employed would strongly affect this type of analysis (e.g. combining all of the American and associated areas into Laurentia versus listing S.W. Scotland, Iowa, Wisconsin, Quebec etc. individually) with the signal predominantly being determined by the groupings decided upon by the researcher. It can be seen, albeit informally, from comparisons of these two gain/loss studies that this is not the case and that the addition of further subdivisions merely adds to the detail gained from the study.

A final point is to note that there is an almost perfect match between the palaeobiogeographical history inferred using informal methods and that inferred using Gain/Loss ratio analysis.

CHAPTER 9

GENERAL CONCLUSIONS

9. Broad conclusions.

9.1 Large scale evolutionary relationships of the taxa considered in this analysis:

Detailed systematic inferences and conclusions are included in chapters 3 - 8, as are summaries of conclusions for each group; the broadest, overarching conclusions of which are as follows.

The earliest members of the Pliomeridae are herein included in the subfamily Pilekiinae from which all other major subclades of the Pliomeridae developed very rapidly during the earliest Tremadoc. At about the same time, a number of other groups are also likely to have developed from the Pilekiinae, including the Cheirurinae, Sphaerexochinae, Acanthoparyphinae and Cyrtometopinae (see Lane, 1971, p. 71; Pribyl *et al.* 1985).

The subclades within the Pliomeridae are diagnosed herein as the following subfamilies: Pliomerinae Raymond 1913, Protopliomeropinae Hupé, 1953, Pilekiinae Sdzuy, 1955, Cybelopsinae Fortey, 1979 and a new subfamily diagnosed herein.

After the initial period of very rapid, high level, diversification the pattern of evolution of the Pliomeridae is largely restricted to the further ramification of the established major subclades. A notable exception to this is the development of the Encrinuridae from the Cybelopsinae in the early part of the Arenig.

The Encrinuridae is herein divided into two subfamilies, the Encrinurinae and the Cybelinae, with the Dindymeninae being subsumed within the Cybelinae (see sections 4.5 and 6). The Encrinurinae as a whole are here regarded as being monophyletic, the Cybelinae as defined herein is expressly paraphyletic as it is from the Cybelinae that the Encrinurinae developed in the mid Arenig. It is likely that the Staurocephalinae Prantl & Pribyl, 1947 was also derived from the Cybelopsinae (as defined in Chapter 3) at approximately the same time as was the Cybelinae.

9.1a Repeated evolutionary patterns:

A regularly repeated evolutionary pattern may be clearly discerned within these analyses. This shows the very rapid diversification at the base of each of the major clades in which all of the major subclades of that clade are developed. This rapid diversification is then followed by ramification within those established clades. This

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A regularly repeated evolutionary pattern may be clearly discerned within these analyses. This shows the very rapid diversification at the base of each of the major clades in which all of the major subclades of that clade are developed. This rapid diversification is then followed by ramification within those established clades. This *pattern is most clearly illustrated* when the stratigraphical ranges of all of the taxa included in the main analyses are plotted, with the taxa arranged in the phylogeny derived herein. This is shown in Figure 9.1 (Foldout at back of thesis).

This repeated pattern is recognisable at a variety of systematic resolutions, from species level to subfamily level. The periods of rapid diversification are normally accompanied by change in the hierarchical level at which characters employed in the analysis vary where the burden of the characters employed in the analysis and diagnosis of the taxa is reduced.

9.2 Summary of large scale biogeographical conclusions:

Only the large scale relationships of the major areas during the Ordovician are summarised here. Detailed biogeographical reconstructions and terrane-by-terrane analyses are included in chapters 3-8, as are summaries of conclusions for each group.

9.2.1 Inferred relative positions of the major continental blocks throughout the Ordovician:

Tremadoc

- Gondwana (including the area later to become Avalonia), South China, Laurentia, and Baltica were situated close to each other.
- The Utah/Nevada area of Laurentia and the southern Victoria/Tasmania area of Gondwana were situated close to each other and were in faunal communication. The Newfoundland/Spitsbergen area of Laurentia was not in faunal communication with the southern Victoria/Tasmania area of Gondwana.
- The Argentine Precordillera was attached to, or situated close to, Laurentia but was not in faunal communication with the southern Victoria/Tasmania area of Gondwana.
- The Canning Basin area was close to South China and the Shan-Thai area but was probably not in faunal communication with Laurentia.
- Baltica was close to the area of Gondwana which was later to become Avalonia.
- Laurentia was not close to either Baltica or Avalonia.
- Southern China and Kazakhstan were close to Gondwana but not Laurentia.

- Southern China and Kazakhstan were not close to each other.

Late Arenig

- Laurentia was no longer close to Gondwana, the two areas were isolated from each other.
- Baltica was also no longer close to Gondwana.
- Laurentia and Baltica were not close to each other.
- Avalonia was still attached to Gondwana.
- Siberia, the Urals and Kazakhstan were close to each other and to Laurentia.
- North and South China were not close to Siberia/Kazakhstan or Laurentia.

Early Llanvirn

- Avalonia was not close to Gondwana, Laurentia or Baltica.
- China was isolated from Siberia and Laurentia but close to both the Urals and Kazakhstan.
- The Argentine Precordillera was situated between the Newfoundland/Spitsbergen area of Laurentia and the southern Victoria/Tasmania area of Gondwana, acting as a stepping stone between Laurentia and Gondwana.

Mid-Llanvirn-mid Caradoc

- Islands were present between Laurentia and Baltica.
- Baltica and Laurentia approached each other more closely - within range of 'island hopping' taxa.
- Avalonia was not close to Laurentia or Baltica.
- Islands were present between Avalonia and Laurentia and between Avalonia and Baltica.
- China was isolated from Siberia, the Urals, Kazakhstan and Laurentia.

Late Caradoc

- Avalonia was close to both Baltica and Laurentia.
- China was in communication with Siberia, the Urals, and Kazakhstan, and was probably closest to Kazakhstan.

Late Ashgill

- Avalonia, Baltica and Laurentia were close to each other.
- China was in communication with Laurentia, Siberia, the Urals, Uzbekistan and Kazakhstan.
- Turkey was close to China.

The biogeographical history of the taxa studied most closely fits the plate tectonic model of Dalziel (1995) for the period including the Tremadoc, and at least the early part of the Arenig, in recognising the close juxtaposition of Laurentia with Gondwana and portions of South America although his suggestion of a mid-Ordovician collision of Laurentia and Gondwana is not supported by the results of these analysis. During the Llanvirn the palaeogeographical reconstructions of Astini *et al.* (1995) and Thomas & Astini (1996) in which the Precordillera area was a microcontinent situated in an intermediate position between Laurentia and Gondwana are supported herein. In the post-Llanvirn Ordovician the results of these analyses favour the palaeogeographical model of Scotese & McKerrow (1990, 1991), with the subsequent alterations summarised in Fortey & Cocks (1992) and Harper *et al.* (1996) (and references therein), in showing the wide separation of Laurentia and Gondwana.

9.3 Further work arising from this study:

This analysis has resolved a large number of systematic problems including the definition and relationships of subfamilies, genera, and in many cases, species within the Pliomeridae and Ordovician Encrinuridae. Time constraints prevented various questions being explored in detail including: the detailed relationships of the Cheiruridae to the Pliomeridae, the identification of a likely sister group to the Pilekiinae, the rigorous revision/re-diagnosis and differentiation of the base of the Encrinuridae and Encrinurinae and the definition of the Cybelinae. Cladistic investigation of the relationships of species within *Pliomerops*, *Placoparia*, *Pliomerina* and *Encrinurella* will provide detailed information on the palaeobiogeography of Gondwana throughout the Ordovician.

There is great potential for further study of taxa from the Ordovician low latitude belt which includes Siberia, Kazakhstan and Uzbekistan as well as areas of Gondwana. Detailed palaeoecological study of the taxa considered herein will further enhance the palaeobiogeographical resolution attainable.

Finally, the tracing of lineages through time using cladistics provides an excellent tool for the study of evolutionary processes and patterns which is an aspect of this study which has not been explored in detail herein. The very rapid differentiation of taxa at the base of the major clades and the observed variations in character burden across the cladograms would repay further investigation and interpretation as would the numerous examples of convergence and parallelism observed in these taxa.

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APPENDICES

APPENDIX 1

Pliomeridae analysis PAUP dataset:

```
#NEXUS
[MacClade 3.04 registered to Taxonomy, Glasgow University]

BEGIN DATA;
DIMENSIONS  NTAX=47 NCHAR=51;
FORMAT MISSING=? GAP=-  SYMBOLS= " 0 1 2 3 4 5 6 7 8";
OPTIONS  MSTAXA=POLYMORPH ;

CHARLABELS
        [1]     AB_Shape        [2]     AB_Nasute       [3]     ABDenticulation  [4]
        FacSut  [5]     Abfdepth
        [6]     MesDeepening    [7]     Anteromed       [8]     Glab_Outli       [9]
        'Glab/CephProp'  [10]   FLWiderL3
        [11]    FLLongerL3      [12]    NumGlaFurr      [13]    S3_Posit         [14]
        S3_Form  [15]   S3isolated
        [16]    S2DirAnt        [17]    S1_Form  [18]   EyeSize  [19]    EyeRaised
        [20]    PalLatBor
        [21]    ER_Present      [22]    ER_ABFurr       [23]    EyeRShort        [24]
        ERStraight      [25]    EyeR_Term
        [26]    ERdies   [27]   Fixi_spines     [28]    Spine_size       [29]
        'GenSp/angOrient'       [30]    RostPlate_Prop
        [31]    Hyp_Outline     [32]    MidBodTop       [33]    TopBordExp       [34]
        HypWingsDepressed       [35]    MargSpines
        [36]    MesSpine        [37]    MesSpineSize    [38]    BotBordExp       [39]
        HypBordIndent   [40]    NoPygRibs
        [41]    RibsequalRings  [42]    RibFurretc      [43]    PygPleurStraight [44]
        PleurBr+Narr    [45]    PleuraeCurv
        [46]    RibTipOut       [47]    FreeTipsSharp   [48]    TermElong        [49]
        Post2Pits       [50]    Add2Pits
        [51]    Term_fused
        ;

MATRIX
Quinquecosta                100000220113220101101100100--?000110-00400000101?00
Anapliomera                 100000220114220121101110100--?010110-01500000101?00
Alwynus                     10000002011322010100111000101?0????????800000101?00
Pliomerellagirv             10010002100(23)0(03)0002000---2-0--1110100010510000001000
Pliomerina                  100100020003000002000---2-??-1110100010510000001000
Perissopliomera             1011?002000400000100110000??-??????????510102011000
Pliomera                    101100120003000001000---2-0--1110100010510000010000
Gogoella                    10000010000300000200111000101?0000???00510000010000
Pliomerops                  100000020003000001001100200--1110100010510000010000
Hintseia                    100000000003000001001100000--?010011010510000010000
Hintseia_taoyuanensis       10000000000300000100110000101?000011010410000010000
Pilekia_apollo              10000000100310000100110000101??????????411011010000
Parapilekia_speciosa        10000000000310000100110000101??????????401011010000
Parapilekia_olesnaensis     10000000000310000100110000101??0001??0?401011010000
Parapil_sensu_anxia         10000001000322001100110000101?0000???00411011010000
Anacheirurus_plutonis       10000000000322000100110000101?0000??-00311011010000
Victorispina                10000000000312000100110000101??????????411011010000
Metapilekia                 10000000000322000100110110101??????????311011010000
Rossaspis                   1000000(01)000310000101110000112?00001000051100101 0000
Teselacauda                 1000000(01)000310000100100000??-?00001000141100 10-0000
Protopliomerella            100000000004100001001110000--?00001100051000000(01)0001
Pseudocybele                110000000004?00001001110000--0000011100510000100001
Ectenotus_progen            000000000003000001001100010--00????????81000010?100
Cybelopsis_Cfspec           100000120003000001001100010--?010000010500000101110
Canningella                 1000000(01)000320000100110000???0000000105000000101100
Strotactinus_insul          100000000003000001001100000--?000000010500000101100
Kanoshia                    10000011000310000100111000112?010011020510100010000
P_cf_insolitaHintze         100000000003000001001100000--?0?0011020510100010000
PseudomeraShaw1974          100011020003001001001100000--0110100010510(01)00010001
Colobinion                  100011020003200001001100000--0110100010500000011?00
Pseudomera_Mk2              10000?020003001001001100000--0010110000510(01)00010001
Protopliomerops_hamaxitus   10000002000300000100110000101?000110-00510000010000
Evropeites                  1000011100032(12)100100110100111?0010100005100000(01)11100
pliomeridius_sulcatus       1000011100132(12)000100110000101?001010000510000011100
Landia                      1000011000032(12)000100110000101?0010100004110000(01)11100
Protoencrinurella           100110020003210001001100100--??????????511012010000
Encrinurella                100110020103230001001100100--??????????510000010000
Rossaspis?_pliomeris        10000000000310000101110000101?00001000041(01)001010000
Hfirmigensis                100000000003000001001100000--?010011020510000010000
Placoparia                  100110020003000001001100000--0110100010410102010000
Pliomeridius_lac            00000010000321000100110010??-??????????511011010000
Pliomeroides                10000000000320000100110000101??????????411000010000
Protopliom_quattor          10000000000310000101110000111??????????410001010000
'Protopliseison(type)'      10000001000320000100110000101?000010-00610?00010000
Ibexaspis                   10000001000310000101110000111?000000-00410000010000
Parahawleia                 1002200210030000000011-?000--??????????410102010000
Protoplio_lindneri          10000000000300000200111000111??????????410000010000
;
```

```
ENDBLOCK;
begin PAUP;
endblock;
BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;

        TYPESET  1  = unord: 1-51;
        TYPESET * UNTITLED  = unord: 1-37 39-51, ord: 38;

ENDBLOCK;

BEGIN TREES;

        TRANSLATE
                1       Quinquecosta,
                2       Anapliomera,
                3       Alwynus,
                4       Pliomerellagirv,
                5       Pliomerina,
                6       Perissopliomera,
                7       Pliomera,
                8       Gogoella,
                9       Pliomerops,
                10      Hintzeia,
                11      Hintzeia_taoyuanensis,
                12      Pilekia_apollo,
                13      Parapilekia_speciosa,
                14      Parapilekia_olesnaensis,
                15      Parapil_sensu_anxia,
                16      Anacheirurus_plutonis,
                17      Victorispina,
                18      Metapilekia,
                19      Rossaspis,
                20      Teselacauda,
                21      Protopliomerella,
                22      Pseudocybele,
                23      Ectenotus_progen,
                24      Cybelopsis_Cfspec,
                25      Canningella,
                26      Strotactinus_insul,
                27      Kanoshia,
                28      P_cf_insolitaHintze,
                29      PseudomeraShaw1974,
                30      Colobinion,
                31      Pseudomera_Mk2,
                32      Protopliomerops_hamaxitus,
                33      Evropeites,
                34      pliomeridius_sulcatus,
                35      Landia,
                36      Protoencrinurella,
                37      Encrinurella,
                38      Rossaspis?_pliomeris,
                39      Hfirmigensis,
                40      Placoparia,
                41      Pliomeridius_lac,
                42      Pliomeroides,
                43      Protopliom_quattor,
                44      'Protopliseison(type)',
                45      Ibexaspis,
                46      Parahawleia,
                47      Protoplio_lindneri
        ;
        TREE 1 =  [&R]
((((((((((((((((1,2),3),25),((23,24),26)),(33,34)),30),(((36,37),41),42)),((((4,8),7),9),((6,(40,46))
,29))),10,((27,28),39)),(21,22)),44),(38,(43,45))),(19,20)),13),12),(16,18)),15);
        TREE  * UNTITLED =  [&R]
(((((((((1,2),3),(((23,24),26),25)),((33,34),35)),((((((4,5),7),9),(((6,(40,46)),(36,37)),(29,30))),
31),32),(((8,47),(21,22)),((10,((27,28),39)),11))),44),42),((19,(43,45)),38),20),12,((15,(16,(18,41)))
,17)),13),14);

ENDBLOCK;


BEGIN MACCLADE;
v 3.0
-1305228012
1100&/0
0
0
ENDBLOCK;
```

APPENDIX 2

Cybelinae analysis PAUP dataset:

```
#NEXUS
[MacClade 3.04 registered to Taxonomy, Glasgow University]

BEGIN DATA;
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FORMAT MISSING=? GAP=-  SYMBOLS= " 0 1 2 3 4 5";
OPTIONS  MSTAXA=POLYMORPH ;

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        S3_form        [5]    S3_apodemes
        [6]     S3_biggest    [7]     Anteromed      [8]     Triang_depr    [9]
        Infl_front_lobe       [10]    S1_occ_fur
        [11]    Eye_ridge     [12]    Pulvinus       [13]    Fixi_field_tub
        [14]    Lib_field_tub [15]    Lib_borb_tub
        [16]    Eyes    [17]  Post_occ_tub  [18]   Lib_spine      [19]
        Pygid_prop     [20]   Pyg_pleur_confl
        [21]    Pyg_axis_tub  [22]    Pit_pleur_F    [23]    ant_band_wide [24]
        Paddle_pleur_rib      [25]    Pygid_conv
        [26]    No_pyg_pluer  [27]    up_ant_proj    [28]    Pleu_fields    [29]
        Thor_segments  [30]   Macropleurae
        [31]    Glab_spine    [32]    L1      [33]   L2      [34]    L3     [35]
        Marg.sut
        [36]    AllPleurConfl [37]    PygMargRib     [38]    FLABRidge      [39]
        AB_Width       [40]   FSABF
        [41]    RaisedTriangArea      [42]    PostBordTub    [43]    ABTub  [44]
        GlabTub        [45]   PygAxisConstricted
        ;

MATRIX
Evropeites_hyperboreus        010(13)000000000000000500000500?0011101?00000000
Cybelurus_mirus?              01010000000000000000400000401210111101?01000010
Cybelurus_planus              0101000100001100001410000401?1011101?00000010
Cybelurus_sokoliensis         0111000000000000000400000401??011101?02000000
Lyrapyge_ebriosus             0121000000000000000401101401??011101?00000000
Cybelurus_batuensis           0113000000200000000???????0??01110???0000000
Sticktocybele_bat             011300100020000000010110041131011100?00000000
Sticktocybele_balc            0113001000200000(01)0010110041??011100?00000010
Cybele_aff_bellatula          0111001000001??00?040000004012?011101?00000111
Cybelurus_shi                 0121011000001??01?0300000301??011101?00000110
Atractopyge_gaoluoensis       0101011000001000000300010301??011101?00000111
sinocybele_fluminis           010101?000000000000300010301??011101?00000111
Cybele_pscemmica              0121011000001000000300000301??011101?00000111
Koksorenus_kazahkstanen       012101101000?000000300000301210000001?00000111
Atractopyge_condylosa         0001011000001110001410000401??011101?00000110
Atractopyge_sinensis          0001011000001100001310000301??011101?00010110
Atractopyge_dentata           00110120000011100014100004012101101?10000110
Atractopyge_scabra            00011120000011100014100004012101101?00000110
Libertella_corona             2002111010001010101210000201210111010000000110
Encrinurus_hornei             1102110000001100101410000500??01110000000000010
Plasiaspis_bohemicus          01021100003011011013100003012001111?00000010
Cornvica_didymograpti         0102112010301111101310000301101111110000000010
Dindymene_plasi               01021-201030111110120000020000110011?00000010
Cybele_bellatula              111211110000111010121000050121011100?00000110
Deacybele_mchenryi            1112111001001110111110000401??011100?00111110
Deacybele_gracilis            1112111001001110011110000401??011100?00100110
```

```
Deacybele_arenosa           111211200100111001????????0???01110??0010011?
Bevanopsis_ulrichi          1112111001101110111110000401?1011100100101110
Cybeloides_iowensis         111211100111111011111000040111011100100101110
Cybelurus_brutoni           01010000000000000000400000401210111 01?0(02)000000
Cybelurus_halo              011100000000000000(01)40000040121011101?02000000
'Cybelella_sp(Tripp81)'     011300100020?000?0040110040131011101?00000??0
'Cybelella_sp(Oweneto)'     011300100020?000?0010110040131011100?00000??0
Cybelurus_expansus          01010001000000000000400020401210111 01?00000000
;
ENDBLOCK;

BEGIN ASSUMPTIONS;

        USERTYPE abf STEPMATRIX = 4
            0 1 2 3
         [0] . 1 2 1
         [1] 1 . 1 2               NOT UTILISED IN THIS ANALYSIS
         [2] 2 1 . 3
         [3] 1 2 3 .
        ;

        USERTYPE S3 STEPMATRIX = 4
            0 1 2 3
         [0] . 1 2 2
         [1] 1 . 1 1               NOT UTILISED IN THIS ANALYSIS
         [2] 2 1 . 2
         [3] 2 1 2 .
        ;

        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;

        TYPESET * UNTITLED  = unord: 2 4-45, ord: 1 3;

ENDBLOCK;
begin PAUP;

BEGIN TREES;

        TRANSLATE
                1       Evropeites_hyperboreus,
                2       Cybelurus_mirus?,
                3       Cybelurus_planus,
                4       Cybelurus_sokoliensis,
                5       Lyrapyge_ebriosus,
                6       Cybelurus_batuensis,
                7       Sticktocybele_bat,
                8       Sticktocybele_balc,
                9       Cybele_aff_bellatula,
                10      Cybelurus_shi,
                11      Atractopyge_gaoluoensis,
                12      sinocybele_fluminis,
                13      Cybele_psoemmica,
                14      Koksorenus_kazahkstanen,
                15      Atractopyge_condylosa,
                16      Atractopyge_sinensis,
                17      Atractopyge_dentata,
                18      Atractopyge_scabra,
                19      Libertella_corona,
                20      Encrinurus_hornei,
                21      Plasiaspis_bohemicus,
```

```
                22        Cornvica_didymograpti,
                23        Dindymene_plasi,
                24        Cybele_bellatula,
                25        Deacybele_mchenryi,
                26        Deacybele_gracilis,
                27        Deacybele_arenosa,
                28        Bevanopsis_ulrichi,
                29        Cybeloides_iowensis,
                30        Cybelurus_brutoni,
                31        Cybelurus_halo,
                32        'Cybelella_sp(Tripp81)',
                33        'Cybelella_sp(Owenetc)',
                34        Cybelurus_expansus
        ;
        TREE  * PAUP_1 =  [&R]
(1,((2,((3,(((15,(17,18)),16),(((19,(24,((25,(28,29)),(26,27)))),20),(21,(22,23))
))),(9,((10,(13,14)),(11,12))))),((4,31),(5,(6,(((7,8),33),32)))),30,34));

ENDBLOCK;


BEGIN MACCLADE;
v 3.0
1678318286
1000&/0
0
0
ENDBLOCK;
```

APPENDIX 3

Atractopyge analysis PAUP dataset:

```
#NEXUS
[MacClade 3.04 registered to Taxonomy, Glasgow University]

BEGIN DATA;
DIMENSIONS  NTAX=19 NCHAR=23;
FORMAT MISSING=? GAP=-  SYMBOLS= " 0 1 2 3 4 5 6 7 8 9";

CHARLABELS
        [1]    Ax_rings        [2]    Axial_tub.      [3]    Pleurae_tub     [4]
        No._of_plur    [5]     2nd_ant.
        [6]    Fur_course      [7]    Lobe_amalg.     [8]    S3_form         [9]
        S3_oc_fur     [10]     Non_pairT
        [11]   Lobe_tub        [12]   Ant_bord        [13]   No_ant_tub      [14]
        Occ_ring      [15]     Eye_pos
        [16]   Fixi_spine      [17]   Cont_pleur      [18]   Gen_field       [19]
        PostBor_tub   [20]     Med_pit
        [21]   PairAxTub       [22]   AB_Width        [23]   ABF_Shallows
        ;

MATRIX
[                     10        20  ]
[                      .         .  ]

sinensis        20131200010002011001100
condylosa       2114110001015?111001100
dentata         21141110010151201000101
rex             20041111010150201000101
coronata        21141111010250201000101
tramorensis     ????111101035020?000101
petiolulata     20141101020161111000100
williamsi       2004100002017011110017O
sedgwicki       ????0000201901???00100
michelli        21141000020190101000110
scabra          41141000022190201100110
kutorge         310410000211901110007OO
brevicada       31041000021190171?00?00
venificus       31141000021171101000100
confusa         3114100002117017100010O
belgica         31141000022191211110110
dalmani         31141200122191211110010
verrucosa       3114010002219121171OO1O
progemma        2114000002219127O110110
;
ENDBLOCK;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;

ENDBLOCK;
begin paup;
        set maxtrees=1000;
end;
BEGIN TREES;
```

```
        TRANSLATE
                1       sinensis,
                2       condylosa,
                3       dentata,
                4       rex,
                5       coronata,
                6       tramorensis,
                7       petiolulata,
                8       williamsi,
                9       sedgwicki,
                10      michelli,
                11      scabra,
                12      kutorge,
                13      brevicada,
                14      venificus,
                15      confusa,
                16      belgica,
                17      dalmani,
                18      verrucosa,
                19      progemma
        ;
        TREE  * PAUP_2 =  [&R]
(1,(2,((3,(4,(5,6))),(7,(((8,(11,((16,(17,18)),19))),10),(9,((12,13),(14,15))))))
));

ENDBLOCK;


BEGIN MACCLADE;
v 3.0
-1341593067
0000&/0
0
0
ENDBLOCK;
```

APPENDIX 4

Taxa previously assigned to the Dindymeninae.

```
#NEXUS
[MacClade 3.04 registered to Taxonomy, Glasgow University]

BEGIN DATA;
DIMENSIONS  NTAX=12 NCHAR=26;
FORMAT MISSING=? GAP=-  SYMBOLS= " 0 1 2 3 4 5 6 7 8 9";

CHARLABELS
        [1]     Lat_Glab_furr  [2]     Fac_Sut_Pos      [3]     RostralPlate   [4]
        FrontLobeInflated      [5]     FLOverhangs
        [6]     Anteromed      [7]     AxFurrPath       [8]     GlabTubLarge   [9]
        MesSpinePres  [10]     MesSpSize
        [11]    FixCheekTub    [12]    ManyTub          [13]    SizeGenSpine   [14]
        OrietGenSpine [15]     PostCranidBorTub
        [16]    ThorSegNo      [17]    ThorTubRow       [18]    4thSegSpine    [19]
        ThorPleurShape         [20]    pleuraelength
        [21]    NoSepFreePygPleur      [22]    NoPygAxRings   [23]    PygAxTub
        [24]    PygRibsTub     [25]    HindFusedPleur
        [26]    PygPleurLegnth
        ;

MATRIX
[                                    10         20      ]
[                                    .          .       ]

Plasiaspis_bohemicus        001001010-110-121000381100
D_saron                     01?0000?0-1120121001281000
Cornovica_didymograpti      01110001131120111101301100
Eodindymene_pulchra         12011000111112001101280011
D_plasi                     11011001131020000101290001
D_longicauda                11011000131112001101200011
D_hughesae                  11011000130111000111200001
D_fridericiaugusti          11?11000131120101101200100
D_cordai                    11011000131111101111200001
D_ornata                    11011001131020000102260001
D_ovalis                    11?110111?100-??????260001
D_haideringeri              11?1100013112000?012??001
;
ENDBLOCK;

BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;

ENDBLOCK;

BEGIN TREES;

        TRANSLATE
                1       Plasiaspis_bohemicus,
                2       D_saron,
                3       Cornovica_didymograpti,
                4       Eodindymene_pulchra,
                5       D_plasi,
                6       D_longicauda,
                7       D_hughesae,
```

```
            8       D_fridericiaugusti,
            9       D_cordai,
            10      D_ornata,
            11      D_ovalis,
            12      D_haideringeri
      ;
      TREE PAUP_1 =  [&R] (1,(3,(((4,6),(7,9)),(5,10))));
      TREE PAUP_1 =  [&R] (1,(3,(((4,6),(7,9)),(5,10))));
      TREE PAUP_1 =  [&R] (1,(3,((((4,6),(7,9)),((5,10),12)),8)));
      TREE  * UNTITLED =  [&R] (1,(2,(3,((((4,6),(7,9)),((5,10),12)),8))));

ENDBLOCK;


BEGIN MACCLADE;
v 3.0
-1365588432
0000&/0
0
0
ENDBLOCK;
```

APPENDIX 5

Cybeloides dataset.

```
#NEXUS
[MacClade 3.04 registered to Taxonomy, Glasgow University]

BEGIN DATA;
DIMENSIONS  NTAX=13 NCHAR=19;
FORMAT MISSING=? GAP=-  SYMBOLS= " 0 1 2 3";

CHARLABELS
        [1]    ab_tub [2]    abtub_enlar    [3]    triang_tub     [4]     glab_tub
        [5]    +2_collumns
        [6]    pulvinus      [7]    ovate_pulv     [8]    tall_stalk     [9]
        pulv_tub     [10]    fixi_tub
        [11]   eyeridge_tub  [12]   eye_pos        [13]   spine_legnth   [14]
        retic_field   [15]   libbor_tub
        [16]   Pax_ridge     [17]   Paracyb_pleurae      [18]    axis_tub
        [19]   pleurae_tub
        ;

MATRIX
[                               10        ]
[                               .         ]

Bevanop_thor            101000000000??10011
Bevanop_urichi          1010000010001?10011
Cybeloi_anna            1000010000000011011
Cybeloi_anna26          2000010000001011011
Cybeloi_ella            ?00001000001?021???
Cybeloi_cimelia         2000011000001011011
Cybeloi_prima           2000010010001011011
Cybeloi_virginensis     2000111020001011011
Cybeloi_iowensis        2100010010001011011
Cybeloi_rugosa          ?000111130011111011
Cybeloi_spinifera       2000111130011011011
Cybeloi_girvanensis     1011010031111021101
Cybeloi_loveni          ?011010030111021100
;
ENDBLOCK;

BEGIN ASSUMPTIONS;


        USERTYPE Pulv_tub STEPMATRIX = 4
            0 1 2 3
         [0] . 1 1 2                  not utilised in these analysis

         [1] 1 . 2 3
         [2] 1 2 . 1
         [3] 2 3 1 .
        ;

        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;

ENDBLOCK;
begin paup;
        set maxtrees=1000;
end;
```

```
BEGIN TREES;

        TRANSLATE
                1       Bevanop_thor,
                2       Bevanop_urichi,
                3       Cybeloi_anna,
                4       Cybeloi_anna26,
                5       Cybeloi_ella,
                6       Cybeloi_cimelia,
                7       Cybeloi_prima,
                8       Cybeloi_virginensis,
                9       Cybeloi_iowensis,
                10      Cybeloi_rugosa,
                11      Cybeloi_spinifera,
                12      Cybeloi_girvanensis,
                13      Cybeloi_loveni
        ;
        TREE  * UNTITLED =  [&R]
((1,2),((3,(4,(6,(8,(10,11))),(7,9))),(5,(12,13))));

ENDBLOCK;


BEGIN MACCLADE;
v 3.0
-1338749445
1100&/0
0
0
ENDBLOCK;
```

APPENDIX 6

Encrinurinae dataset.

```
#NEXUS
[MacClade 3.01 registered to GORDON B CURRY, UNIVERSITY OF GLASGOW]

BEGIN DATA;
DIMENSIONS NTAX=46 NCHAR=55;
FORMAT MISSING=? GAP=- SYMBOLS= " 0 1 2 3 4 5 6 7 8 9";

CHARLABELS
        [1]  abGranTubetc      [2]   OddEvABtub.      [3]   No.AB_tub         [4]
        ant_bord         [5]   AntMid_missing                abf_depth         [9]
        [6]  ab_indent         [7]   long._fur        [8]
        ros_plate        [10]  I1_present                    ii0_present       [14]
        [11] i0_present        [12]  II1_present      [13]
        Penttub_size     [15]  III1_present                  [18]  III1_enlarg
        [16] III1_horns        [17]  III1horns_amalg
        [19] III1hornBifurc          [20]  iii0_present      III0_present      [24]
        [21] I0_present        [22]  II0_present      [23]
        IV_enlarg        [25]  v0_tubercles                  RowVII_tubercles
        [26] VI_tubercles      [27]  vi_tubercle      [28]
        [29] lobe_tub          [30]  L1_depressed                eye_ridge         [34]
        [31] ax_fur_occur      [32]  FixCheek_tub     [33]
        eye_pos          [35]  eye_ring                      Stalk_hight       [39]
        [36] Eye_reniform      [37]  Eyestalk_form    [38]
        palepr_infl      [40]  Swoll_Fixi_ridge
        [41] PostBor_tubercle        [42]  genal_spine       [43]  spineBase_tub
        [44] TubGen_spine      [45]  Libfield_gran
        [46] lib_bord_tub      [47]  LibTubBand_ext              [48]  LABFrow_No.
        [49] pygid_form        [50]  axTub
        [51] axTubPairing      [52]  pygpleur_tips    [53]  PygPleur_confl
        [54] NoOf_pleurae      [55]  singleABrow
        ;

MATRIX
[                                  10        20        30        40        50  ]
[                                  .         .         .         .         .   ]

En_hornei               0--0001001110010-0-00000???0000100100000110??-?0021400
En_rarus                0--0001001110010-0-00000???00001001000001100 1-20021210
En_periops              0--00010?1110010-0-00000???00001000120001 1001-20021210
En_fallax               0--00010?1110010-0-?0000???00001000010001 1001-20021210
En_obesus               0--00010?1110010-0-?0000???00201000010001 1001-?0021210
En_autochthon           0--00010?----0-0-0-----0----0000100011000110 01-11021210
En_stincharensis        0--00010?----0-0-0-----0----0000000011000110 01-11021210
En_sexcostatus          0--000100----0-0-0-----0----0001100012000110 01-11020110
Cr_optimus              0--0001101010010-0-?0000???00001101000000 1011-122-0620
En_capitonis            2-?0001001111010-0-10000???00001000020001 1001-20021210
En_tholus               2--00110?1111010-0-100000000002010100200001001-20021210
Ph_insularis            2--0011001111010-0-10000???01201010021002 1001-30021210
Ph_coopi                2--1010001010010-0-000000000?12010100?11021011-30121310
Ph_miriablis            2--1110001010010-0-00000????12010100?11021011-30121310
En_torulatus            2-50001001111010-0-10000???00001010020002 1001-20021210
En_uncatus              2190011011111010-1-100010100000010100100022000020111211
En_neuter               2190011011111010-1-100010100000010100100012000020110211
En_lapworthi            22800210?1111010-0-100000000000010100200022000020111211
En_vigilans             2190011011111010-1-?0001???000000?001000?200002 0?01??1
Er_kaushi               219001001111101101-10001???000000100200022000?20101221
Er_kummerowi            219001001111101101-10001???0000001002000220001202-1221
```

```
Er_nebeni               219001001111101101-10001????0000001002000220001302-1221
Er_seebachiIII          219001001111121101-10001????0000000001000220001201012221
Er_seebachiI            219001001111121001-10001????2000000001000220001201012221
Er_postseebachi         217001001111121001-10000????20000000010002200012??????1
Er_inopionatus          219001001111121000-10000????2000001001000220001212-1221
Er_jaegeri              219001001111111101-10001????0000001002000220001?12-1221
Er_imperfectus1         228001001??1011111-10001????0001001002000220101?12-1221
Er_imperfectus10        228001001?1101012101001l????0001001002000220101?12-1221
Er_capricornu           2280010011?1011101-10001????0001001002000220101312-1321
Er_cornutus             228002001101010121 0?0011100000000001002000220101312-1321
Er_brutoni              228001001000010121110011100000000001002000220101412-1321
Er_Sp.A                 2280021071011010-0-1000000001000?0?00200??20???0111211
Er_Sp.B                 22800210?1010010-0-1000000001000?01002001?200????????1
Er_spicatus             2280020001010010-0-1000000001000101002001220000101 11211
Er_Kingi                ???0??0??101001001-1000001001001001 00200???00??12-122?
Er_moe                  22100200?0011010-0-1100000001000 00?001001221???12-1221
Er_Kiaeri               2210020000010010-0-1100000001000000001001221000312-1221
Er_praecursor1          22800200?0010010-0-0100000001000 00?001000220???02-1221
Er_praecursor4          22800200?0000010-0-0110000001000 00?001000220???02-1221
Er_praecursor5          22800200?0000000-0-0111000001000 00?001000220???02-1221
Er_parceentis           2280020000000000-0-01110010010000 0?001000220000?02-1221
Er_multisegmentatus     21900200?0000000-0-0111001001000 00?001000220???02-1221
Er_lamonti              2280020000000000-0-011100110100000 1001000220001312-1221
Er_trispinosus          2280020000000000-0-0111011111000001001000220000212-1221
Er_laurentius           22800200?0000000-0-01110111010000 01001000220?????????1
;
END;
begin PAUP;
endblock;
BEGIN ASSUMPTIONS;
        OPTIONS  DEFTYPE=unord PolyTcount=MINSTEPS ;

        TYPESET * UNTITLED  = unord: 1-37 39-55, ord: 38;

END;

BEGIN TREES;

        TRANSLATE
                1       En_hornei,
                2       En_rarus,
                3       En_periops,
                4       En_fallax,
                5       En_obesus,
                6       En_autochthon,
                7       En_stincharensis,
                8       En_sexcostatus,
                9       Cr_optimus,
                10      En_capitonis,
                11      En_tholus,
                12      Ph_insularis,
                13      Ph_coopi,
                14      Ph_miriablis,
                15      En_torulatus,
                16      En_uncatus,
                17      En_neuter,
                18      En_lapworthi,
                19      En_vigilans,
                20      Er_kaushi,
                21      Er_kummerowi,
                22      Er_nebeni,
```

```
                    23      Er_seebachiIII,
                    24      Er_seebachiI,
                    25      Er_postseebachi,
                    26      Er_inopionatus,
                    27      Er_jaegeri,
                    28      Er_imperfectus1,
                    29      Er_imperfectus10,
                    30      Er_capricornu,
                    31      Er_cornutus,
                    32      Er_brutoni,
                    33      Er_Sp.A,
                    34      Er_Sp.B,
                    35      Er_spicatus,
                    36      Er_Kingi,
                    37      Er_moe,
                    38      Er_Kiaeri,
                    39      Er_praecursor1,
                    40      Er_praecursor4,
                    41      Er_praecursor5,
                    42      Er_percentis,
                    43      Er_multisegmentatus,
                    44      Er_lamonti,
                    45      Er_trispinosus,
                    46      Er_laurentius
        ;
        TREE PAUP_1 =  [&R]
(1,((2,(((3,((6,7),8)),(10,(((11,(12,(13,14))),(((16,17),(19,((20,(21,(22,(27,((2
8,(29,(31,32))),30))))),(23,(24,(25,26)))))),(18,(33,(34,(35,((37,38),(39,(40,(41
,(42,43,(44,(45,46))))))))))))),15))),4,5)),9));
        TREE  * UNTITLED =  [&R]
(1,((2,(((3,((6,7),8)),(10,(((11,(12,(13,14))),(((16,17),(19,((20,(21,(22,(27,((2
8,(29,(31,32))),30))))),(23,(24,(25,26)))))),(18,(33,(34,(35,(36,((37,38),(39,(40
,(41,(42,43,(44,(45,46)))))))))))))),15))),4,5)),9));

END;


BEGIN MACCLADE;
v 3.0
-1338390442
0100&/0
0
0
END;
```

Fig. 9.1 Composite phylogeny including the results of all of the main analyses included within this report (excluding highly incomplete taxa etc) with the stratigraphical ranges of the taxa plotted against the stratigraphical table of Fortey et al. (1995, fig 1)

———— Inferred phylogeny

━━━━ Stratigraphical age

━━▶━━ The arrowhead section of the stratigraphical range shows the portion of the range supplied by a taxon highly likely, but not proven to be, conspecific with the taxon named at the head of the range.

············ Inferred extended range

•••••••••••• Age uncertain (or highly approximale)

The stratigraphy employed is that of Fortey *et al.* (1995). The chronostratigraphical table is adapted from Fortey *et al.* (1995) figure 1