

THE INTERRELATIONSHIPS OF 'COMPLEX' CONODONTS (VERTEBRATA)

Philip C. J. Donoghue

Department of Earth Sciences, University of Bristol, Wills Memorial Building, Queen's Road,
Bristol BS8 1RJ, UK

Mark A. Purnell

Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK

Richard J. Aldridge

Department of Geology, University of Leicester, University Road, Leicester LE1 7RH, UK

Shunxin Zhang

Canada – Nunavut Geoscience Office, 626 Tunit Plaza, Suite 202, PO Box 2319, Iqaluit, Nunavut,
Canada XoA oHo

SYNOPSIS Little attention has been paid to the suprageneric classification for conodonts and existing schemes have been formulated without attention to homology, diagnosis and definition. We propose that cladistics provides an appropriate methodology to test existing schemes of classification and in which to explore the evolutionary relationships of conodonts. The development of a multi-element taxonomy and a concept of homology based upon the position, not morphology, of elements within the apparatus provide the ideal foundation for the application of cladistics to conodonts. In an attempt to unravel the evolutionary relationships between 'complex' conodonts (prioniodontids and derivative lineages) we have compiled a data matrix based upon 95 characters and 61 representative taxa. The dataset was analysed using parsimony and the resulting hypotheses were assessed using a number of measures of support. These included bootstrap, Bremer Support and double-decay; we also compared levels of homoplasy to those expected given the size of the dataset and to those expected in a random dataset. The dataset was analysed in three hierarchical tranches, representing three levels of certainty concerning multi-element reconstructions and positional homologies. There is much agreement between the results derived from the three partitions, but some inconsistency, particularly in the precise composition of the three main evolutionary grades traditionally recognised (Prioniodontida, Prioniodinina, Ozarkodinina). This is considered to result from (a) the progressive inclusion of data that is increasingly uncertain and (b) the inclusion of increasingly distantly related taxa, introducing spurious hypotheses of homology. We tested for these by partitioning the dataset into the three main evolutionary grades and in each instance resolution was seen to increase substantially, especially among prioniodinins. Our concluding scheme of relationships is a tree derived from a compilation of the three component subtrees, which is directly compatible with the most-parsimonious trees derived from the initial second tranche analysis with the exception of the position of *Hibbardella*. This is compared in detail to the main extant schemes of suprageneric classification. A formal scheme of suprageneric classification is presented and the distribution of characters with respect to component clades is considered as a basis for identifying diagnostic characters.

Key words conodont, cladistics, classification, vertebrate, evolution

Contents

Introduction	120
Historical perspective	121
A prescriptive approach: cladistics	121
Homology and conodonts	121
Phylogenetic analysis	123
Introduction	123
Previous phylogenies	123
Taxon sampling	124

Characters	124
Methods	124
Rooting	128
<i>A posteriori</i> reweighting	128
Bootstrap	128
Bremer support and Double Decay Analysis	128
Homoplasy: CI expected	129
Homoplasy: CI random	129
Results	129
Analysis of taxa for which there is direct evidence of topological homologies (Tranche 1)	129
Analysis including taxa for which topological homologies may be inferred with confidence (Tranche 2)	130
Analysis including taxa for which topological and orientational homologies are uncertain (Tranche 3)	130
Discussion of the primary results	132
Analysis of subgroups	135
Prioniodontida	135
Prioniodinida	136
Ozarkodinida	136
Summary of hypothesis of relationships	136
Comparison with previous phylogenies and classification schemes	139
Comparison with Sweet's phylogeny and classification	139
Sweet's Prioniodinida	140
Sweet's Prioniodontida	140
Sweet's Ozarkodinida	140
Quantitative testing of Sweet's phylogeny	140
Comparison with Dzik's phylogeny and classification	141
Dzik's Prioniodontida	141
Dzik's Ozarkodinida	141
Comparison with other classifications and hypotheses of relationship	141
Character distributions, higher taxa and homology	142
Ozarkodinida	142
Prioniodinina	142
Ozarkodinina	143
Final reflections on homology	143
Acknowledgements	143
References	143
Appendix 1: Conversion of Sweet and Dzik phylogenies to trees	147
Appendix 2: Positional homology assignments	148
Appendix 3: Character descriptions	151
Supplementary data	153

INTRODUCTION

In the century and a half following the first discovery of conodont remains, palaeobiological study has concentrated, quite naturally, on the question of the affinity of the group. Although debate continues, vertebrate affinity is now widely recognised (Aldridge *et al.* 1993) and phylogenetic analysis indicates that conodonts are basal stem-gnathostomes (Donoghue *et al.* 2000). Thus conodonts are now recognised as a major group of early vertebrates and their significance to our understanding of early vertebrate evolution

has begun to unfold. Phylogenetic analysis has revealed that the mineralised tooth-like elements that comprise the conodont feeding apparatus represent the earliest expression of a mineralised skeleton among vertebrates. As such, they not only hold the key to our understanding of how the skeletal system first evolved, but also provide a critical record against which patterns of vertebrate skeletal evolution may be calibrated. Furthermore, conodonts record the only firm evidence of the evolution of feeding strategies among extinct early vertebrates. However, our understanding of these events is hampered by the lack of knowledge of conodont

interrelationships. Rudimentary schemes of suprageneric classification have begun to emerge only relatively recently.

HISTORICAL PERSPECTIVE

The earliest attempt at a comprehensive scheme of suprageneric classification was made by Ulrich & Bassler (1926) as an aid to the development of conodonts as a tool in detailed biostratigraphy. In their acknowledgement that the new scheme would be artificial, at least in part, Ulrich & Bassler believed it unlikely that elements occupying the mouth of a conodont would be more dissimilar than left–right pairing would require. Their belief was proved wrong when, in 1934, Scott and Schmidt independently discovered and described articulated skeletal remains of conodonts, demonstrating that individual conodonts possessed a number of elements and that all elements exhibited various degrees of dissimilarity from each other. This possibility had been mooted by Branson & Mehl (1933: 5–6), although they argued that an artificial scheme of classification should, nevertheless, be maintained because 'The likelihood of finding the teeth in their original associations is remote, and in order to make the conodonts of greatest use both to systematists and stratigraphers it seems best to describe the readily distinguishable kinds as species'. Although the discovery of complete apparatuses provided a template for reconstructing other taxa, artificial schemes of classification persisted until the early 1970s, perpetuated by the first edition of the *Treatise on Invertebrate Paleontology* to tackle conodonts (Hass *et al.* 1962).

The greatest shake-up in the systematic classification of conodonts emerged as a result of the move towards a multi-element taxonomy, pioneered by Huckriede (1958) and followed by Walliser (1964), Bergström & Sweet (1966), Webers (1966), Jeppsson (1969) and Klapper & Philip (1971), among others. The first attempt to revise conodont systematics in line with burgeoning data on the multi-element composition of conodont taxa was undertaken by Lindström (1970), later succeeded by the second (and presumably final!) edition of the *Treatise on Invertebrate Paleontology* dealing with conodonts (Clark *et al.* 1981). The 1981 *Treatise* classification was roundly criticised for its violations of the International Code of Zoological Nomenclature (ICZN) (Stoll *et al.* 1964), and for the lack of a clear philosophical basis for its construction. Fåhræus (1984) highlighted the lack of a methodological approach in the hierarchical ranking of taxa and considered that proposed taxa were either too broadly or too narrowly defined. A prescriptive approach toward the adoption of paraphyletic, let alone monophyletic, groupings, is absent and, above all, the *Treatise* classification has been criticised for its failure to measure up as a scientific theory (Fåhræus 1984). The *Treatise* classification has been superseded by a scheme proposed by Sweet (1988), which represents the basis for the modern concept of conodont suprageneric relationships, although it has been revised in parts by Dzik (1991, 1994), Aldridge & Smith (1993) and Stouge & Bagnoli (1999).

Many of the criticisms levelled at the *Treatise* by Fåhræus (1984) are equally applicable to current schemes, although perhaps the most vexing of all remains the lack of a prescriptive methodological approach for the identification and diagnosis of groupings. In most cases, morphological

data have played a role in recognising groupings of putatively related taxa, but, whether implicitly (e.g. Sweet 1988) or explicitly (e.g. Dzik 1991), the process of reconstructing relationships and building a phylogenetic tree has leaned heavily on stratigraphic succession. The greatest limitation to this approach is its reliance upon (or assumption of) the completeness of the conodont fossil record (Wickström & Donoghue 2005). While it may be defensible to support the view that the conodont fossil record is relatively complete compared to, say, that of birds (e.g. Foote & Sepkoski 1999), this is not the same as absolute completeness (Purnell & Donoghue 2005 and references therein). This is not to say that stratigraphy has no place in phylogenetic reconstruction. Stratigraphy provides an important test of hypotheses of relationship based upon morphological datasets; at the same time, the hypotheses themselves can provide one of the few independent tests of stratigraphic data. The failure of one dataset to corroborate the other would suggest that the hypothesis of relationships is incorrect, that the fossil record is incomplete, or that both datasets are flawed. Only by maintaining a distinction between stratigraphic and morphological data can such tests be employed.

A PRESCRIPTIVE APPROACH: CLADISTICS

Phylogenetic systematics provides the prescriptive methodological approach that Fåhræus stipulated as a requirement for the systematic classification of conodonts, as it explicitly seeks to reflect evolutionary relationships through the recognition of groupings that meet the criterion of strict monophyly. These groupings, and the statements of the attributes (characters) on which they are based, are open to test, through scrutiny by peers and through congruence with other characters under global parsimony.

This approach promises many benefits to conodont palaeontology and biostratigraphy. Cladistic analysis at a multi-element level highlights the fact that, while the P₁ element may evolve more rapidly than any other element in the apparatus, consideration of changes in the entire apparatus can deliver an even more refined biostratigraphy (Klapper & Philip 1971; Donoghue 2001). Numerical cladistics also provides a test of multi-element reconstructions through congruence. Congruence is a measure of the fit of codings from one multi-element reconstruction to another. A failed test of congruence can arise if a reconstruction is incorrect because element morphotypes have been assigned incorrect positional homologies or because the reconstruction contains elements belonging to the apparatuses of other species.

HOMOLOGY AND CONODONTS

Cladistics relies upon the recognition of homologies. There has been considerable debate in the recent literature regarding the concept of homology, although the most prevalent view is that a homology is a shared attribute that reflects common ancestry. However, to then use homology to recognise relationships is circular and highlights the epistemological error in this definition of the concept. The original concept of

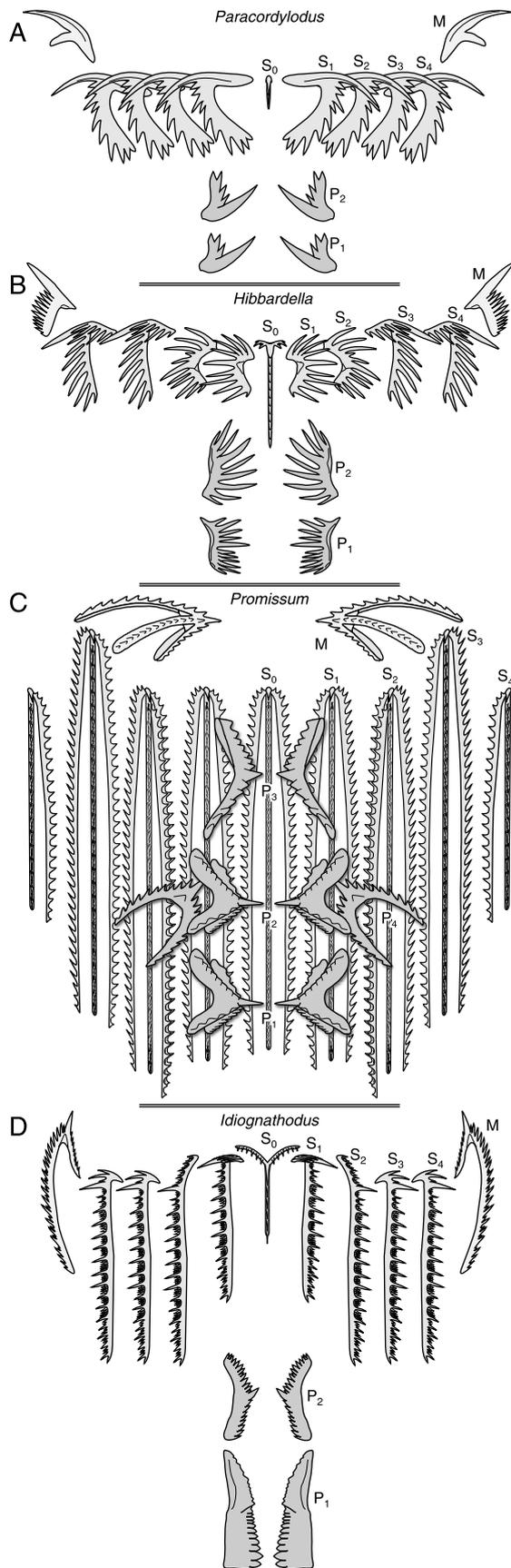


Figure 1 Representative templates for each of the main grades of ‘complex’ conodonts. Each is based on natural assemblage data with direct evidence of topological homologies, following the scheme

homology, as coined by Owen (1843), does not include common ancestry in its definition, which is not surprising given its pre-Darwinian origin, but emphasises instead structure and location, i.e. topology. Indeed, the consistent recognition of a common relationship of parts from one organism to another provided Darwin (1859) with one of the most compelling arguments in support of his theory of descent with modification. Many authors (e.g. Rieppel 1988, 1994; Panchen 1992) have argued that we should return to Owen’s concept of homology as it maintains a distinction between the explanation (evolution) and that which is to be explained (the common relationship of parts – homology). This is not a semantic issue relating merely to whether one is working within the paradigm of evolution, or actively testing it. Although many may argue that conodont phylogeny is at least known in part, the lack, to date, of a formalised approach to the recovery of relationships produces an absence of recognised homologies, of an Owenian type or any other.

Until very recently, there was no formalised scheme for the recognition of homologous elements from one taxon to another. Various notational schemes have been erected since the late 1960s (Jeppsson 1971; Klapper & Philip 1971; Sweet & Schönlaub 1975; Barnes *et al.* 1979) although they were only intended to reflect homology on a notional level that was more phenetic than phylogenetic (see e.g. Sweet 1981). With the discovery and description of the complete skeletal remains of more and more disparate taxa (e.g. Aldridge *et al.* 1995; Purnell & von Bitter 1996; Purnell & Donoghue 1998; Repetski *et al.* 1998; Orchard & Rieber 1999; Tolmacheva & Purnell 2002; Stewart & Nicoll 2003; Dhanda 2004), it has been possible to formalise a scheme for the recognition of homology based on topology (Purnell *et al.* 2000; Fig. 1). Thus, we are able to recognise the correspondence of individual element positions from the apparatus of one taxon to the next (Fig. 1). Furthermore, the discovery of fossils preserving complete apparatuses together with remains of the unmineralised soft tissues of the head and body of conodonts has provided the basis for biological orientation of the apparatus and of the elements within the apparatus, as well as for the description of element morphology using terms that reflect *in vivo* anatomy (Purnell *et al.* 2000). Nevertheless, problems remain. For instance, in the absence of phylogenetic information, it is not possible to resolve homology between the P elements of *Promissum pulchrum* and other complex conodonts for which there is definitive evidence of positional homology. *Promissum pulchrum* possesses four pairs of P elements, whereas just two pairs of P elements occur in the apparatuses of all other complex conodonts known from natural assemblages (Fig. 1). Which elements correspond to which? Are the two extra element pairs in *P. pulchrum* serial homologues (duplicates) of the other two pairs (which correspond to the P₁ and P₂ of other conodonts), or are they fundamentally different element positions? There is no homology in an Owenian sense because there is no direct topological similarity, although there may be homology

devised by Purnell *et al.* (2000). **A**, *Paracordylodus*, based on Tolmacheva & Purnell (2002), is used as the outgroup. **B**, *Hibbardella*, based on Nicoll (1977), is a representative prioniodinid. **C**, *Promissum*, based on Aldridge *et al.* (1995), is a prioniodontid. **D**, *Idiognathodus*, based on Purnell & Donoghue (1998), is a representative ozarkodinid.

in an evolutionary sense (transformational homology *sensu* Patterson 1982). Comparison of the component processes of homologous elements is even more vexing in the absence of a known phylogeny. Traditionally, the presence of processes has been described with respect to their disposition relative to the cusp; it is assumed that the landmark (the orientation of the cusp) does not move. However, within groups of taxa that possess similar apparatuses, it is possible to identify homologous processes that lie in different orientations in different taxa (relative to the landmark), but it is not possible to identify which process (if any) is homologous in more dissimilar taxa (Purnell *et al.* 2000; Wickström & Donoghue 2005). This problem is exacerbated by the occupation of homologous orientations by non-homologous processes in closely related taxa, so reliance upon orientation will probably include some false homology (homoplasy). However, it is likely that such instances of homoplasy will be identified in a test of congruence during parsimony analysis. Failure to recognise homologous processes deprives us of a tier of characters relating to their presence/absence (Wickström & Donoghue 2005). However, it is anticipated that this initial analysis will provide a basis for their recognition so that subsequent analyses may incorporate them.

In the absence of a hypothesis of relationships on which to base homology assessments for this paper, we have had to adopt an operational concept of homology that is identical to that proposed by Lankester (1870), i.e. based upon generality, similarity and the common relationship of parts. Our analyses lead to phylogenetic hypotheses that provide a context within which the homologies of conodont elements and their component parts can be further explored.

PHYLOGENETIC ANALYSIS

Introduction

Cladistic methods of phylogenetic analysis have only very recently been applied to the study of conodont interrelationships (Donoghue 2001; Zhang & Barnes 2004; Wickström & Donoghue 2005). Donoghue (2001) dealt with the relationships of palmatolepids, a taxonomically diverse, although conservative, group of ozarkodinid conodonts whose phylogenetic relationships have been considered in greater detail than for any other group. That study highlighted the effect of low taxonomic sampling density upon the resolution of relationships through cladistic analysis. The results corroborated many aspects of earlier hypotheses of relationships that were arrived at by stratophenetic methods, but it identified implied gaps in a fossil record that had hitherto been considered complete. That analysis also highlighted the need for multi-element treatment of conodont taxa in phylogenetic analysis given that much of the phylogenetic signal recovered stemmed from characteristics of elements other than the diagnostic P₁ element. Furthermore, it identified the need for a modular approach to the study and description of conodont elements given the possibility of identifying homology of individual processes that was potentially independent of their position relative to the cusp. This was taken further by Wickström & Donoghue (2005) who discriminated between processes occupying common positions in their assessments of homology, such as between the 'lateral' processes of pri-

oniodinid and ozarkodinid P₁ elements. However, these considerations were limited to problems of rooting in what was otherwise a focussed analysis of the inter- and intrarelationships of the Silurian Family Kockelellidae.

This paper addresses the relationships of conodonts on a much broader scale, with the aim of testing hypotheses of relationship between taxa that are currently ranked as families and between orders (e.g. Sweet 1988; Dzik 1991). The best approach to this would have been to undertake an analysis of relationships across as broad a range of taxa as possible, but this is constrained by the fact that different schemes for identifying homologies are currently in place for different types of conodont apparatus. The 'PMS' scheme established by Sweet & Schönlaub (1975) and formalised by Purnell *et al.* (2000) can be applied most readily to those groups of conodonts in which elements of the apparatus possess a number of processes that, in most taxa, bear denticles. A separate scheme of homological notation was established by Barnes *et al.* (1979) for taxa bearing only coniform elements and this was modified by Sansom *et al.* (1994) using the genus *Panderodus*. According to this scheme coniform elements are differentiated only by cross-sectional shape, curvature and the distribution of costae and sulci, which provide few discrete characters. It is not known precisely how these homology schemes compare (Purnell & Donoghue 1998; Sansom *et al.* 1994). We have decided, therefore, to focus upon taxa to which the PMS scheme can most readily be applied, i.e. those that have traditionally been accommodated within the orders Prionodontida Dzik, 1976, Prioniodinida Sweet, 1988 and Ozarkodinida Dzik, 1976. We have not been able to identify an out-group taxon or taxa in which unequivocal positional homologies for the element morphotypes can be determined. We have also excluded putatively plesiomorphic members of the group (e.g. *Rossodus*, *Tripodus*) for which positional homologies are extremely uncertain.

Previous phylogenies

Our intention with this work is to test, using cladistic methods, existing hypotheses of relationships between groups of morphologically complex conodonts. In order to compare our results, previous phylogenies (which incorporate assumptions regarding ancestry and descent) need to be converted to trees (which do not). Of the current schemes of classification of conodonts, only that of Sweet (1988) was presented in sufficient detail for it to be possible to derive a well resolved tree summarising the underlying hypothesis of relationships. Dzik (1991) also presented a broad overview of relationships and higher level classification of conodonts, but his scheme is more generalised in that he routinely outlined relationships at the level of the family, rather than the genus. In a few cases, however, he proposed more specific hypotheses of ancestry.

As noted by Donoghue (2001), the conversion of a phylogeny to a tree is not a simple matter. The process requires that all hypotheses of ancestry and descent are excluded from the hypothesis of relationships, with ancestral taxa translated into sister-taxa and hard polytomies converted to soft polytomies. In many instances, Sweet (1988) identified the genera to which putative ancestors and descendants belong, through single or multiple evolutionary events, and one approach in such cases is to reconstruct the clade as an unresolved polytomy. Strict application of this, however, results in loss of much of the information on relative branching

order that both Sweet and Dzik incorporated into their hypotheses of relationship. In order to retain this information, which is, after all, what we wish to investigate, we have reconstructed relationships so that hypothetical ancestors are included within the cladogram in a way that satisfies both Sweet's and Dzik's hypotheses regarding common ancestry. To do this, we have mapped the range of unidentified ancestral species that fall within the 'ancestral genus' onto a series of nodes in our tree in concordance with the original phylogenetic hypotheses. Genera treated this way are clearly paraphyletic and, while this may be undesirable from a cladistic perspective, it is true to both Sweet's and Dzik's original hypotheses. The summary trees derived from Sweet's (Fig. 2) and Dzik's (Fig. 3) hypotheses of phylogeny include only those taxa that are part of our most inclusive analyses (see below). A few of our taxa are excluded, such as the multiple species of *Ozarkodina*, because it is not clear where within their *Ozarkodina* lineage either Sweet or Dzik would place them. An additional assumption of our process for deriving a tree is that members of a genus share a single common ancestor. Because Dzik (1991) outlined fewer specific hypotheses of relationship, the tree derived from his hypotheses inevitably contains more polytomies, most of which indicate our ignorance of his view of relationships between taxa within families. In Appendix 1 we detail the decisions on which we converted both Sweet and Dzik's hypotheses of phylogeny to trees.

Taxon sampling

It would have been our preference to include as many taxa as possible into the analysis, thereby ensuring that sampling density did not impact upon our results. However, with increasing taxon number, the number of potential solutions increases exponentially (Felsenstein 1978), making even computer-based cladistic analyses computationally unfeasible. Thus, we instead emphasised taxonomic breadth, attempting to test existing families and higher taxa for monophyly by including at least three of their best-known constituent species. For this reason, our results convey only hypotheses of relative relationships, among which other taxa will be inserted in light of analyses that employ greater taxon sampling of local relationships. Subsequently, in the text, we often refer to taxa by their generic affiliation alone as a shorthand; the conclusions drawn should not be interpreted to be general to the genus as a whole.

Taxa selected for analysis fall into three categories, each based on the degree of confidence that we have in hypotheses of element homology. Firstly, there are taxa that are known from natural assemblages. Only for these do we have direct evidence of the *in vivo* orientation and topological position of individual elements: direct evidence of homology. Secondly, there are taxa of known multi-element composition that are sufficiently similar to taxa known from natural assemblages for homologies to be inferred without equivocation. Thirdly, there are taxa representing groups that are otherwise unrepresented in the analysis, but for which hypotheses of homology are less reliable. Our analysis proceeded by successively incorporating each of these three categories into the datasets analysed.

Appendix 2 includes all taxa analysed, together with notes on the multi-element reconstruction that we have followed and our interpretation of element topological homolo-

gies following the notational scheme of Purnell *et al.* (2000; Fig. 1).

Characters

The strategy by which characters are coded can emplace *a priori* assumptions of transformation, or apply potentially undue weight on certain character states (Pimental & Riggins 1987; Forey & Kitching 2000). We have chosen to avoid multi-state characters as they imply *a priori* knowledge of transformational homology between character states. Strict binary characters (Pleijel 1995) are also problematical because of the possibility that taxa are united on the absence of a character, rather than its presence. We have therefore decided to adopt contingent coding as a strategy (Hawkins *et al.* 1997) as it avoids the pitfalls of strict presence/absence coding by first querying the presence of a character and subsequently querying the nature of the character. Contingent coding is the only strategy that is both theoretically and operationally valid (Hawkins *et al.* 1997; Lee & Bryant 1999; Strong & Lipscomb 1999; Hawkins 2000).

Although the standard morphological categories used to describe conodont elements, such as pastinate and digyrate, serve well in distinguishing between taxa, in phylogenetic systematics the aim is to resolve similarities rather than differences. For this reason it is inappropriate to use standard terms as they serve to mask similarities. For instance, if we were to use the standard terms carminate, pastinate and stellate to characterise P_1 elements, this would mask the fact that stellate elements are pastinate elements with an additional lateral process and that many pastinate elements are also carminate. We have, therefore, chosen to reduce conodont elements to their component parts: 'anterior', 'posterior', 'inner' and 'outer' processes. Although this reflects well the hierarchical nature of biological characters, it also introduces a host of inapplicable character codings, e.g. if a process is not present, a second character, which pertains to whether or not that process is denticulate, is inapplicable. The introduction of question marks into the data matrix represents the greatest drawback to the contingent coding strategy. Computer algorithms treat question marks as unknown data rather than inapplicable characters and this can result in taxa being united on 'optimised' codings of the inapplicable characters (Platnick *et al.* 1991a, b). In an attempt to identify potential artefacts the results of the phylogenetic analysis have been assessed for corroboration by analysing the dataset using NONA (No Name) (Goloboff 1999).

Character descriptions are provided in Appendix 3.

Methods

The data matrix reproduced in Table 1 was analysed using PAUP 4.0b10a (Swofford 2002). The matrix was analysed in total and in partitions and the search algorithm employed depended upon how many taxa were included in the analysis and, thus, how long the search took to complete. In all instances, approximate search options were employed due to the size of the matrix and the branch-and-bound search option was employed in only the smallest partition of the dataset. In all other instances, an heuristic search option was implemented using random stepwise addition (100 replicates). All characters were unweighted in primary analyses of the data set and subjected to successive rounds of

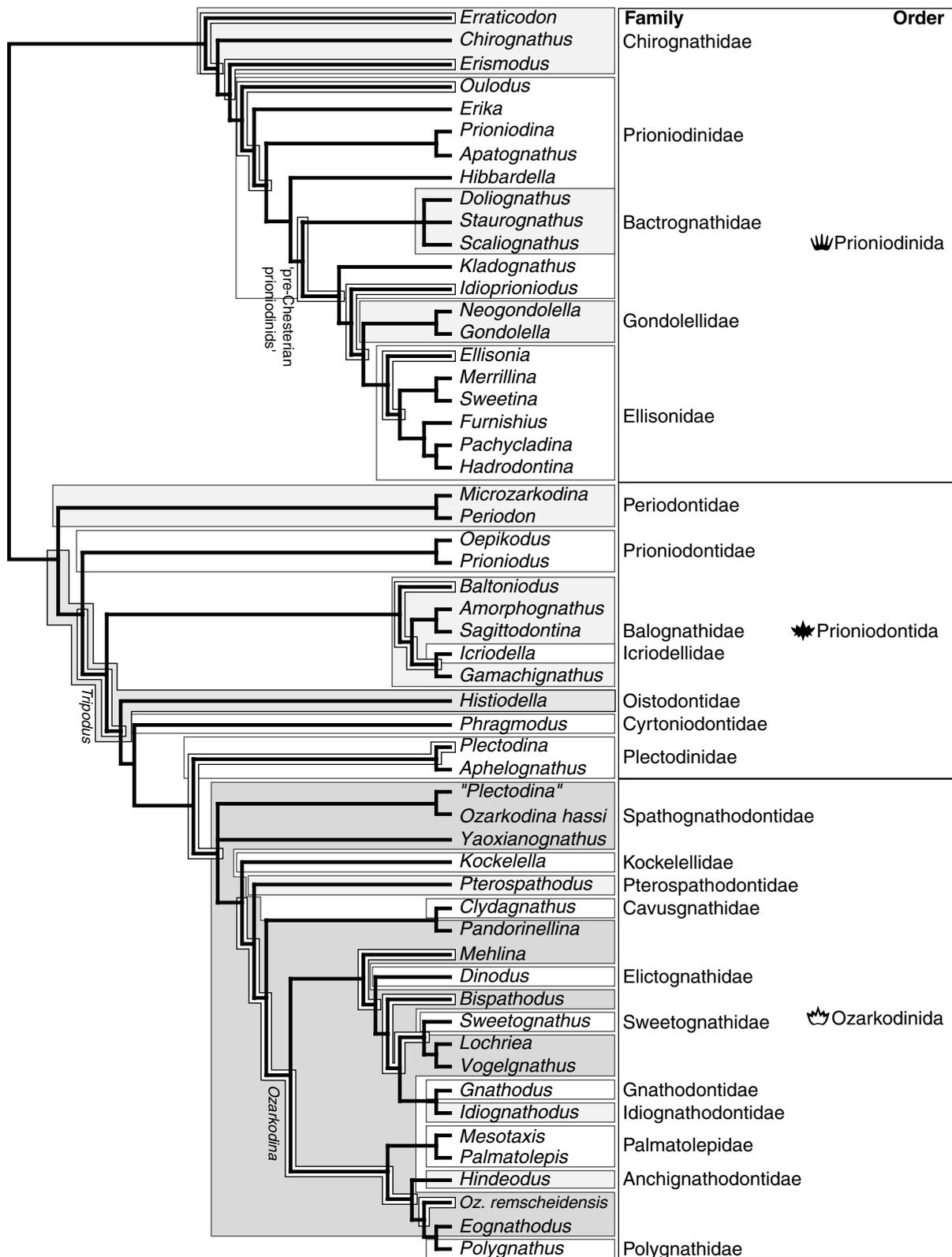


Figure 2 Summary tree reflecting hypotheses of relationship proposed by Sweet (1988) but showing only those taxa included in our analyses. Sweet's classification is also shown; shading and boxes indicate the boundaries of his higher taxa. 'Ancestral genera' from which Sweet derived multiple descendant taxa are shown as paraphyletic, spanning several nodes on the tree. Icons in this and in Figs 3–13 indicate the taxa assigned by Sweet to Prioniodontida (*), Prioniodinida (crown), and Ozarkodinida (crown with flame), respectively (see Appendix 1 for details).

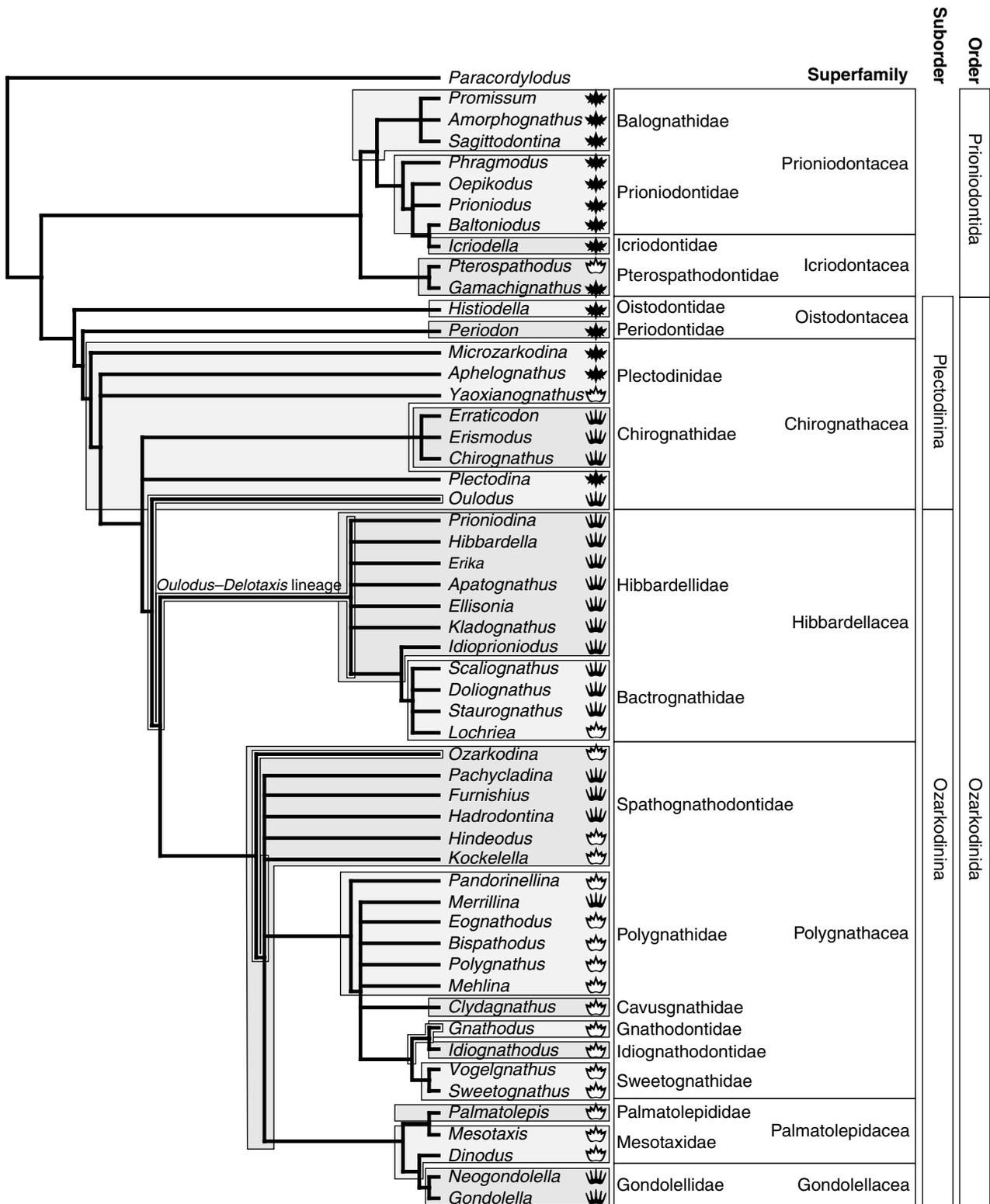


Figure 3 Summary tree reflecting hypotheses of relationships proposed by Dzik (1991) but showing only those taxa included in our analyses. Dzik's classification is also shown; shading and boxes indicate the boundaries of his higher taxa. 'Ancestral genera' from which Dzik derived multiple descendant taxa are shown as paraphyletic, spanning several nodes on the tree (see Appendix 1 for details).

a posteriori reweighting according to rescaled consistency indices derived from character fit arising from the preceding analysis. For small dataset partitions, bootstrap analyses were based upon 1000 replicates of a simple addition se-

quence heuristic search option with 10 trees held at each step. For the largest partitions, and for the complete dataset, bootstrap analyses were performed in 100,000 replicates of the 'fast' heuristic search option of PAUP 4.0b10.

Table 1 Data matrix

	1	2	3	4	5	6	7	8	9	
	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	1234567890	
<i>Amorphognathus</i>	1111101010	10?0000010	01101110??	010?011011	01000?1111	0110101100	1010110010	0000011010	????1?0?00	000??
<i>Apatognathus</i>	0??11010??	11111?0?11	100110?100	0110001000	1101??????	?001100110	01101000??	0?0?00?01	10????0?01	0110?
<i>Aphelognathus</i>	11100100?1	10?0100010	010100?000	01??011000	1101??????	?110011000	001110001?	0?00000?01	0??0?0?00	000??
<i>Baltoniodus</i>	11101100?1	10?0111000	011010?0??	010?011001	00?00?1111	0010001000	00?0001110	0?00000000	????1?0?00	000??
<i>Bispathodus</i>	1110010101	1110000100	011000?000	0011011000	1111101000	0110011000	0001101010	1101010101	1110010111	1001?
<i>Chirognathus</i>	0??11010??	1100111?11	000110?100	0110001100	11110?0101	1110011000	0011100001	0?0?00?01	0??0?0?00	01100
<i>Clydagnathus</i>	1100010101	10?0000100	011000?000	0111011000	11110?0101	1110011000	0001001010	1101110?01	10?010010	?0011
<i>Dinodus</i>	1110110101	1100000?11	0110011000	01110110??	????101000	0110011000	0011100010	0100110?01	11010????0?	100?0
<i>Doliognathus</i>	1110110100	1100100011	0110011000	0110011100	1101100100	0110011000	0011101000	0000010001	11010?0?00	00000
<i>Ellisonia</i>	0??11010??	1111111?11	100110?100	1110011000	11110?0101	111001100?	?????????11	0?0?00?0?	????0?0?0?	01100
<i>Eognathodus</i>	1110010101	10?0000110	011000?000	0111001000	11110?0101	1110011000	00011010??	1101110001	11010?0?11	00011
<i>Erika</i>	0??11010??	1101111?11	100110?100	1110001000	11110?0101	1001100110	01101010??	0?0?00?01	11010?0?0?	01100
<i>Erismodus</i>	0??11010??	10?0111?10	000110?100	1110001000	11010?0101	1110011000	0?10100001	0?0?00?01	00?0?0?00	00100
<i>Erraticodon</i>	0??11010??	10?0111?10	010110?100	0110011000	1100??????	?011001100	00111010??	0?0?00?01	0??0?0?00	0?1??
<i>Furnishius</i>	0??110111?	11111???11	100110?100	1110001000	11010?0101	111001100?	??????????	0?0?00?0?	????0?0?0?	01101
<i>Gamachignathus</i>	11101100?1	10?0111010	011010?0??	01??011001	11000?1101	0010001000	00110000??	0?00000?01	00?0?0?00	000??
<i>Gnathodus</i>	1110010101	10?0000100	011000?000	0011011000	1111101000	0110011000	0001101010	1101110101	1101011110	1001?
<i>Gondolella</i>	0??0010110	1100111010	011000?000	0110011000	11010?0101	1110011000	0011101010	0?0??10?01	11010?0?00	10000
<i>Hadrodontina</i>	0??110111?	1111111?11	100110?100	1110001000	11110?0101	111001100?	??????????	0?0?00?0?	????0?0?0?	01110
<i>Hibbardella</i>	0??11010??	10?1111?10	110100?000	1110011000	11010?0101	1011001100	00110010?1	0?0?10?01	0??0?010?00	01?00
<i>Hindeodus</i>	11100100?1	10?0000100	011000?000	0011001000	11110?0101	1110011000	0001101010	1?01010?01	11010?0?00	00000
<i>Histiodela</i>	01100000?1	00?0111?00	000000?0??	00?000?00	00?0000000	0000000000	00?0000110	0?00010?00	????0?0?00	000??
<i>Icriodela</i>	1110010100	10?0111010	011000?0??	01??011001	1100??????	?0111????0	10111100??	0000111?00	?????0?00	000??
<i>Idiognathodus</i>	1100010101	10?0000000	011000?000	0011011000	1111101000	0110011000	00?1101010	1101110101	1101011111	1001?
<i>Idioproniodus</i>	0??11010??	1111111?11	110100?000	1110011000	11010?0101	1110011000	0111001001	0?0?00?01	10??010100	?1100
<i>Kladognathus</i>	1??10000??	1111111?11	101100?000	1110011001	10?00?1100	0110011000	0001000001	0?00000?01	0??000000	011??
<i>Kockelella</i>	11100100?1	00?0010000	011000?000	1010001000	11010?0101	1110011000	0111101010	0?00010?01	0??0?0?00	00000
<i>Lochria</i>	1100010101	10?0000000	011000?000	0011011000	1111000101	1110011000	0011000010	1101110101	10??010?10	?0011
<i>Mehlina</i>	11100100?1	1110000011	011000?000	0111011000	11110?0101	1110011000	0011101010	1?00010101	11010?0?11	10011
<i>Merrillina</i>	10000100?1	10?0111010	011000?000	0110011011	00?0111000	0110011000	001010101?	0?00110001	10??0?0?10	10000
<i>Mesotaxis</i>	1110010111	1100000???	0110011000	0111011000	11010?0101	1110011000	0001100010	11??110001	11100?0?00	10001
<i>Microzarkodina</i>	11100100?1	10?01110??	????????00	010?001000	11010?0101	1001000100	00?0001110	0?00000?00	????0?0?00	00?00
<i>Neogondolella</i>	0??0010110	111011101?	011000?000	0110011000	11010?0101	1110011000	0011100010	0?0??10001	1101010?00	10000
<i>Nicollidina brevis</i>	11100100?1	00?0111000	011000?000	0011001000	1111111000	0110011000	0001101010	0?10010101	11100?0?11	?001?
<i>Oepikodus</i>	11101100?1	00?0111000	01101000??	010?010?01	00?00?1000	0010001000	00?0001110	0?00100?00	????0?0?00	000??
<i>Oulodus</i>	0??11010??	10?0111?10	000110?100	1110001000	1101??????	?110011000	0011001010	0?0?00?01	0??0?0?00	0110?
<i>Ozarkodina confluens</i>	11100100?1	00?0111010	011000?000	0010001000	11010?0101	1110011000	0001101010	0?10010?01	11010?0?00	00000
<i>Oz. excavata</i>	11100100?1	10?0111010	011000?000	0110001100	11110?0101	1110011000	0011101010	0?00010?01	0??0?0?00	00011
<i>Oz. hassi</i>	11100100?1	00?0111010	011000?000	0010001000	1101?????0?	?110011000	0011101010	0?00010?01	11010?0?00	0000?
<i>Oz. remscheidensis</i>	11100100?1	00?01?0100	011000?000	0011001000	11110?0101	1110011000	0001101010	0?10010?01	11010?0?11	00011
<i>Paracordylodus</i>	11100000?0	10?0111?10	001000?000	0110010?01	00?0001000	0010001000	00?0000110	0?00000?00	????100000	?00??
<i>Pachycladina</i>	0??11010??	1111111?11	100110?100	1110001100	11110?0101	111001100?	?????????0?	0?0?00?0?	????0?0?0?	00100
<i>Parapachycladina</i>	0??11010??	1111111?11	100110?100	1110001100	11010?0101	1?????????	?????????10	0?0?00?0?	????0?0?0?	01100
<i>Palmatolepis</i>	1110110110	1100100?11	0110011000	0010101110	11110?0101	1110011000	0011100010	10?0110001	1110010000	10010
<i>Pandorinellina</i>	11100100?1	1110000111	011000?000	0111011000	1111101000	0110011000	0011101010	1?01010101	11010?0?11	10011
<i>Periodon</i>	0??01100?1	00?0111000	010010?000	01??011000	11010?0101	1010001000	0010101110	0?0?00000	????0?0?00	000??
<i>Phragmodus</i>	11101000?0	10?0111?10	001010?000	0111010?01	00?00?1000	0010001000	0010101010	0?00000?00	????000000	?00??
<i>Plectodina</i>	11101000?1	10?0111010	001010?000	0110001000	11010?0101	1110011000	01111010??	0?00?00?01	0??0?0?00	00000
<i>'Plectodina'</i>	11100100?1	10?0111010	011000?000	0110001000	11010?0101	1010001000	0011001010	0?00?00?01	0??0?0?00	00000
<i>Polygnathus</i>	1110010101	0110000111	011000?000	0111011000	11110?0101	1110011000	0011101010	1101110101	1101010111	10011
<i>Prioniodina</i>	11100100?1	10?0111011	110100?000	11100110??	????0?0101	1110011000	00110?10??	0?00010?0?	????0?0?0?	001?1
<i>Prioniodus</i>	11101100?1	10?0111010	011010?0??	01????1001	0100101111	0010001000	00101011??	0000001001	0??1?0?00	000??
<i>Promissum</i>	1111110110	10?01?1010	0110111011	010?011001	11000?1111	0011101100	10111100??	0000001?00	????100000	000??
<i>Pterospathodus</i>	1110110110	10?0000010	011001101?	0?0?0110??	???????????	???????????	0011001010	0000010?11	0????0?0?0	000??
<i>Sagittodontina</i>	1111110110	10?0111010	01101110??	01??011001	11000?1111	0011101100	10111100??	0000010?10	????1?0?00	000??
<i>Scaliognathus</i>	0??11101010	10?0111010	011000?000	0011???????	???????????	?110011000	0011001010	0?0?00?01	10????0?0?	?00??
<i>Staurogathus</i>	1001110100	1100000010	0110011000	0110011000	1101100100	0110011000	0011101000	0100010001	11010?0?00	00000
<i>Sweetina</i>	1??01100?1	10?0111011	011000?000	0110011011	00?0???????	?110011000	01101010??	0?00000001	11010?0?10	100??
<i>Sweetognathus</i>	1110010101	10?0000110	011000?000	0011011000	1111???????	?110011000	0001001010	1101110101	10??0?0?10	1001?
<i>Vogelgnathus</i>	11100100?1	10?0000010	011000?000	0011011100	11110?0101	1110011000	0011101010	1?01010001	1101010?11	10000
<i>Yaoxianognathus</i>	11100100?1	00?0111000	011000?000	0011001000	11010?0101	1110011000	0011100010	0?00000001	0??0?0?00	00011

Rooting

By far the most widely used method of 'indirect' rooting is by outgroup. An ideal outgroup is composed of more than one taxon and all should be among the most closely related sister-taxa identifiable. Thus, in the selection of outgroup taxa we must have some *a priori* knowledge of relationships. This is where existing hypotheses of relationships are particularly useful and the validity of assumptions regarding the 'primitiveness' of proposed outgroup taxa can be tested through unrooted analysis. However, although hypotheses of conodont intrarelationships have been long established, their unifying weakness lies in failure to recognise how each of the major groups recognised root into each other. This is particularly problematical with respect to the 'complex' conodonts. For instance, Sweet (1988) was unable to identify the ancestry of his new order Prioniodinida.

The cladistically least-derived, and oldest taxon for which we have direct evidence of positional homologies, is *Paracordylodus*, which was not treated systematically by Sweet (1988), but is generally thought to be allied with taxa that would make it a very primitive prioniodontid (see Tolmacheva & Purnell 2002). Dzik (1991) placed *Paracordylodus* (with question) within Cordylodontidae Lindström. If Dzik (1991) was correct, *Paracordylodus* would not represent a member of the ingroup under either of the hypotheses of relationships proposed by Sweet (1988) or Dzik (1991). However, it may also be too distantly related to the ingroup to serve as an effective outgroup member. Nevertheless, due to the level of uncertainty surrounding possible outgroup status of taxa, as well as the paucity of data regarding element number and positional homologies among other possible outgroup candidates (*Rossodus*, *Tripodus*), we decided to use *Paracordylodus* as the sole outgroup taxon. However, it is noted that among the ensuing cladograms, the topology of relationships of basally-branching taxa is extremely stable. It remains possible that these taxa comprise a grade rather than a clade, but their relative branching order is unlikely to change with inclusion of additional outgroup taxa.

A posteriori reweighting

This is a technique for testing character consistency and support for a solution based upon a primary, unweighted analysis. Weights are assigned to characters based on their performance in an initial, unweighted parsimony analysis. Characters that exhibit close accordance with overall character distribution are deemed to record a more reliable phylogenetic signal than those that do not and are assigned high weighting relative to those characters that exhibit poor accordance. Poorly performing characters are assigned relatively low weight, or even no weight, reducing their influence upon subsequent parsimony analysis, or excluding them altogether. Weights were assigned according to the rescaled consistency index.

Historically, *a posteriori* reweighting has been used as a method for resolving between multiple equally most-parsimonious trees (e.g. Carpenter 1988). Platnick *et al.* (1991b) demonstrated that this is clearly not appropriate when they discovered that the most-parsimonious tree found after *a posteriori* reweighting need not necessarily coincide with one of the competing optimal trees found after parsimony analysis of the unweighted dataset. Furthermore, if a dataset includes many characters that exhibit a poor degree

of fit to the most-parsimonious tree(s), *a posteriori* reweighting will assign low weighting to those characters and subsequent analysis is likely to yield more, rather than fewer trees (Kitching *et al.* 1998). For this reason, Platnick *et al.* (1991a) and Goloboff (1993) have argued that *a posteriori* reweighting is essential in order to achieve results that are internally consistent, even when the primary analysis yields a single most-parsimonious tree. Indeed, Platnick *et al.* (1996) have gone even further in suggesting that analysis using equal weights can only be considered a preliminary and crude estimate of the relative value of the data. For this reason, we routinely used *a posteriori* reweighting in our analysis of relationships and although we present and discuss the results of both unweighted and reweighted analysis, we direct the reader in preference to the reweighted results.

Bootstrap

Bootstrap analyses operate by randomly sampling the dataset for subsets of characters that are subsequently subjected to parsimony analysis. This is undertaken 1000 times and groups recovered in 70% or more of the replicate analyses are considered to be well-supported. It should be remembered, however, that bootstrap analyses measure the degree of repeatability of putative phylogenetic signal within a dataset and are not a measure of the historical reality of the groups recognised.

Bootstrap analyses were performed in PAUP using branch-and-bound or heuristic search options, depending upon how many taxa were included within the analyses. In the case of heuristic searches, the simple addition sequence option was used, with 10 trees held at each step. In both branch-and-bound and heuristic search options, 1000 replicate analyses were undertaken and all groups compatible with the 50% majority-rule consensus were recognised.

Bremer support and Double Decay Analysis

Also known as decay index, length difference, or clade decay, Bremer support values assess the measure of character support for nodes within a cladogram when strict parsimony is relaxed.

Bremer support values were obtained using TreeRot (Sorenson 1999). The file includes a constraint statement for each node based upon a given strict consensus or most-parsimonious tree, as well as a command to search for trees that are incompatible with each of the constraint statements. The Bremer support index for a given node is obtained by calculating the difference between the length of the given tree (most-parsimonious tree(s)) and the length of the shortest tree(s) found to be inconsistent with that node. Unresolved portions of consensus trees have a Bremer support index of 0. The higher the Bremer support index for a specific node, the better supported it is deemed to be.

As with the bootstrap values, Bremer support values are not a measure of the historical reality of a group, but instead provide a measure of the degree of support for a clade when strict parsimony is relaxed. While this is an accurate measure of support, in instances where membership of an individual is suspect, otherwise strongly supported clades will be assigned low Bremer support values. In such instances it may be desirable to ascertain the underlying, more strongly supported, component topology. To this end, Wilkinson *et al.*

(2000) developed Double Decay Analysis (DDA), which reduces a tree to its many possible component subtrees and analyses these for Bremer support. The results can then be sifted for components that exhibit high support; these may exceed the total level of support exhibited by the original source tree. Wilkinson *et al.* (2000) suggested various criteria on which to measure the support for various components, of which Cladistic Information Content (CIC; Thorley *et al.* 1998) and Total Decay (TD) are the most compelling. CIC provides a measure of the information content in a tree as a function of the number of trees that it permits and the number of possible trees, calculated as the negative logarithm of this ratio and expressed in bits or nats depending on the base of the logarithm. While trees with the greatest number of taxa will often exhibit the highest CIC, this will not be the case in instances where there are many equally most parsimonious trees and the summary strict consensus tree is poorly resolved. Otherwise, CIC is best used in combination with other measures of overall support for trees, such as TD, where it can be used to select between trees with equal levels of support. TD is simply the sum total of Bremer support indices exhibited by all the nodes in any one component tree; because it is independent of numbers of taxa it is a suitable measure for identifying reduced component consensus trees that may exhibit higher overall support than the strict component consensus tree from which they are derived.

Homoplasy: CI expected

The Consistency Index (CI) provides a measure of the overall consistency of the data as explained by a phylogenetic hypothesis (Kitching *et al.* 1998). Thus, its reciprocal provides a measure of homoplasy within the dataset for a given tree and is sometimes referred to as the Homoplasy Index (HI) (Kitching *et al.* 1998). The CI is artificially inflated by uninformative characters (e.g. continuous or invariable characters) and so in all instances we quote the Consistency Index excluding uninformative characters (CIE). Although the CI provides a useful measure of the amount of homoplasy within a dataset, it also varies in proportion to the number of taxa included in an analysis. Sanderson & Donoghue (1989) plotted the CI for 60 cladograms derived from the literature and were able to derive a linear regression and, ultimately, a predictive formula for the expected CI:

$$\text{CI}(\text{exp}) = 0.9 - 0.022 (\text{number of taxa}) + 0.000213 (\text{number of taxa})^2$$

For each of the analyses described below, CI(exp) has been calculated on the basis of this formula for comparison with the tree statistics presented.

Homoplasy: CI random

Although the regression provided a formula by which it is possible to compare expected with actual CI values, it does not provide a lower estimate of what constitutes a significant value. Klassen *et al.* (1991) have provided a formula for determining the expected CI of an analysis derived from a matrix containing random data. Thus, if a CI is found to exceed this value, it can be inferred that the matrix contains phylogenetic information. The CI random (CI(ran)) value may be determined using the following formula:

$$\text{CI}(\text{ran}) = 2.937(\text{number of taxa})^{-0.9339}$$

For each of the analyses described below, CI(ran) has been calculated on the basis of this formula for comparison with the tree statistics presented.

Results

Analysis of taxa for which there is direct evidence of topological homologies (Tranche 1)

This analysis included only taxa that are known from natural assemblages that preserve direct evidence of positional homologies (*Bispathodus*, *Clydagnathus*, *Gnathodus*, *Hibbardella*, *Idiognathodus*, *Idioproniodus*, *Kladognathus*, *Lochriea*, *Neogondolella*, *Nicollidina brevis*, *Palmatolepis*, *Paracordylodus*, *Phragmodus*, *Polygnathus*, *Promissum*). *Gondolella*, *Oepikodus*, *Sweetognathus* and *Vogelgnathus* are also known from natural assemblages but they do not preserve direct evidence of positional homologies (e.g. von Bitter & Merrill 1998 used natural assemblages of *Neogondolella* as a template for resolving positional homologies in natural assemblages of *Gondolella*); consequently, they were not used in this first phase of analysis. The initial analysis was treated as unrooted due to the lack of an unequivocal outgroup taxon or taxa.

The initial parsimony run under the branch-and-bound search option yielded two most parsimonious trees (Figs 4A, B) at 150 steps, a consistency index (CIE, i.e. Consistency Index excluding uninformative characters) of 0.53 (uninformative characters 2, 13, 27–30, 33, 35, 38, 39, 46, 49, 53, 55, 57, 59–62, 66, 68, 73, 77, 79), a retention index (RI) of 0.70 and a rescaled consistency index (RC) of 0.40. One round of *a posteriori* reweighting yielded a single most parsimonious tree compatible with one of these two trees (Fig. 4B). After two successive rounds, the tree statistics stabilised at a length of 64.02 steps, a CIE (a common suite of uninformative characters) of 0.75, a RI of 0.87 and a RC of 0.70. Figures 4A, B illustrate the results of bootstrap analyses based on 1000 replicates (branch-and-bound search) of the preliminary dataset and the reweighted dataset, respectively. In both there is good support for ingroup monophyly (92% and 100%), as well as for monophyly of the Ozarkodinida (90% and 98%). The Prioniodinida (*sensu* Sweet 1988) is resolved as paraphyletic, although if *Neogondolella* is excluded there is a well-supported (78% and 100%) monophyletic rump that could constitute a redefined Prioniodinida. The Prioniodontida is also resolved as a paraphyletic apical-lineage to the Ozarkodinida + *Neogondolella* and the rump of the Prioniodinida, corroborating the view that ozarkodinids and prioniodinids are derived prioniodontids (Donoghue *et al.* 2000; Sweet & Donoghue 2001). Internal support within the two main clades is variable, although there is good support for the internal topology of the prioniodinid rump (86% and 97%), for *Palmatolepis* plus all more derived ozarkodinids (90% and 98%) and for *Polygnathus* plus all more derived ozarkodinids (97% and 99%), as well as various internal nodes.

Bremer support indices were calculated for each of the nodes in the most-parsimonious tree and the results are presented in Fig. 4. One of the nodes has a Bremer support of 1 (internal node within the clade of ozarkodinids), while the ozarkodinid clade as a whole has a Bremer support of 4. The prioniodinids (bar *Neogondolella*) are also well supported with a value of 4, while the best supported clade is the

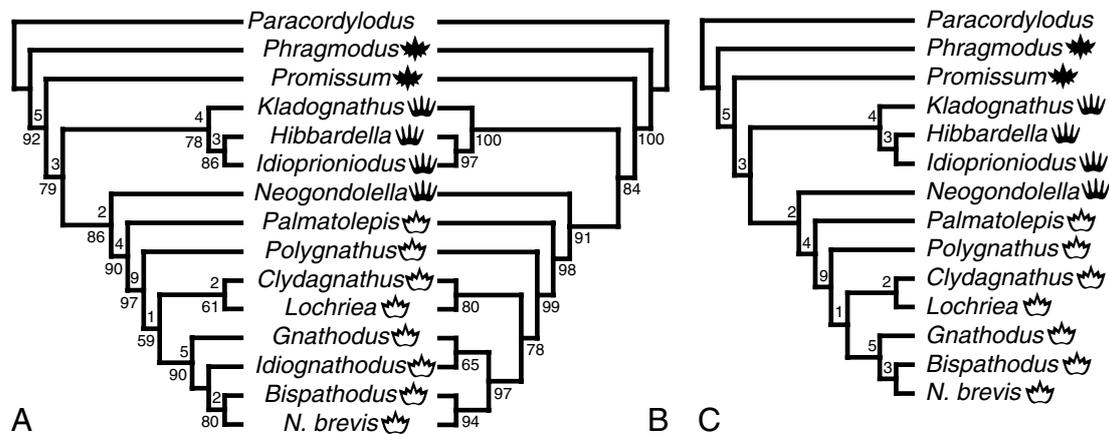


Figure 4 Cladograms derived from analysis of the taxa for which there is direct evidence of topological homologies (Tranche 1). Numbers adjacent to nodes represent their respective support values: the upper value is the Bremer support and the lower value is the Bootstrap Support. **A, B**, Two equally most parsimonious trees (MPTs) derived from analysis of the unweighted dataset; **B** also represents the MPT derived from analysis of the reweighted dataset; clade support values in **A** relate to the unweighted analysis and bootstrap values in **B** relate to the reweighted analysis. **C**, Tree derived from Double Decay Analysis that exhibits the highest Total Decay.

ozarkodinids (bar *Palmatolepis*), which has a Bremer support of 9.

DDA identified two reduced component consensus (RCC) trees that exhibit TD equal to the original strict component consensus (SCC) tree (TD = 40; lacking *Polygnathus* and *Neogondolella*, respectively). Although the SCC exhibits the highest CIC, by virtue of including the most taxa, DDA identified a single RCC tree with a higher TD (41; lacking *Idiognathodus*: Fig. 4C).

The CI(exp) for a dataset including 15 taxa is 0.52, while the CI(ran) is 0.23. Given that the actual CIe = 0.53, this indicates that there is no more homoplasy than would be expected of a dataset including this number of characters. The actual CIe also deviates significantly from the CI derived from an entirely random dataset.

Analysis including taxa for which topological homologies may be inferred with confidence (Tranche 2)

For this analysis we added the taxa for which there is very strong evidence that the multi-element reconstruction does not include any exotic components and for which the topological homologies are clear (*Aphelognathus*, *Baltoniodus*, *Dinodus*, *Gondolella*, *Hindeodus*, *Kockelella*, *Mehlina*, *Merrillina*, *Mesotaxis*, *Microzarkodina*, *Oepikodus*, *Oulodus*, *Ozarkodina confluens*, *Ozarkodina excavata*, *Ozarkodina hassi*, *Ozarkodina remschiedensis*, *Pandorinellina*, *Periodon*, *Plectodina*, 'Plectodina', *Prioniodus*, *Sweetognathus*, *Vogelgnathus*). For inclusion, we needed to be convinced that the topological homologies were consistent not merely between taxa with similar apparatuses (?closely related), but consistent with taxa in which we were certain of topological homologies (i.e. those taxa included in the first round of analyses). For this reason we excluded a range of taxa that are well known in multi-element terms (e.g. *Amorphognathus* – are the planate P elements homologous to the P₁, P₂, P₃ or P₄ elements of *Promissum pulchrum*; are they homologous to the P₁ or P₂ elements of others such as *Phragmodus* and *Idiognathodus*?). Most of the taxa currently assigned to the Prioniodinida (*sensu* Sweet 1988) were excluded because of such uncertainties regarding homology.

The increased size of the dataset precluded the use of the branch-and-bound search option and, thus, the heuristic search option was employed (tbr branch-swapping algorithm, steepest descent, random stepwise addition, 100 replicates, 10 trees held at each step). The initial parsimony run yielded six equally most-parsimonious trees at 268 steps, a CIe of 0.32 (excluding uninformative characters 2, 27–30, 35, 53, 55, 57, 59–61, 66, 79), a RI of 0.66 and a RC of 0.23 (strict consensus in Fig. 5A). These trees differ with respect to the phylogenetic positions of *Aphelognathus* and *Plectodina*. One round of reweighting yielded three most-parsimonious trees (strict consensus in Fig. 5B) and, after successive rounds, the tree statistics stabilised at a length of 61.79 steps, CIe of 0.49, a RI of 0.80 and a RC of 0.46. The trees differ with respect to the position of *Plectodina*, which is resolved as the sister-taxon to a clade of prionodinids, a clade of ozarkodinids and both, respectively. All three topologies are among the six most-parsimonious trees derived from the unweighted dataset. Figures 5A, B illustrate the results of the bootstrap analyses based on 100,000 replicates ('fast' heuristic search) of the preliminary dataset and the *a posteriori* reweighted dataset, respectively.

DDA identified 36 RCC trees with a higher TD than the source SCC (TD = 41), the highest of which (CIC = 55: Fig. 6) includes only 31 of the original 38 taxa; *Dinodus*, *Hindeodus*, *Merrillina*, *Mesotaxis*, *Nicollidina brevis* and *Palmatolepis* are excluded and it should be presumed their interrelationships, on the basis of this particular analysis, are poorly understood (*Paracordylodus* is excluded only because it is designated as the root in the analysis).

The CI(exp) for a dataset including 39 taxa is 0.37, while the CI(ran) is 0.10. This indicates that the dataset does not exhibit significantly more homoplasy than is expected of a dataset of this size (unweighted CIe = 0.32).

Analysis including taxa for which topological and orientational homologies are uncertain (Tranche 3)

Finally, we added the remaining taxa, for which multi-element composition is (to a greater or lesser extent) constrained, but topological homologies of the elements and, in particular, the orientational homologies, are less

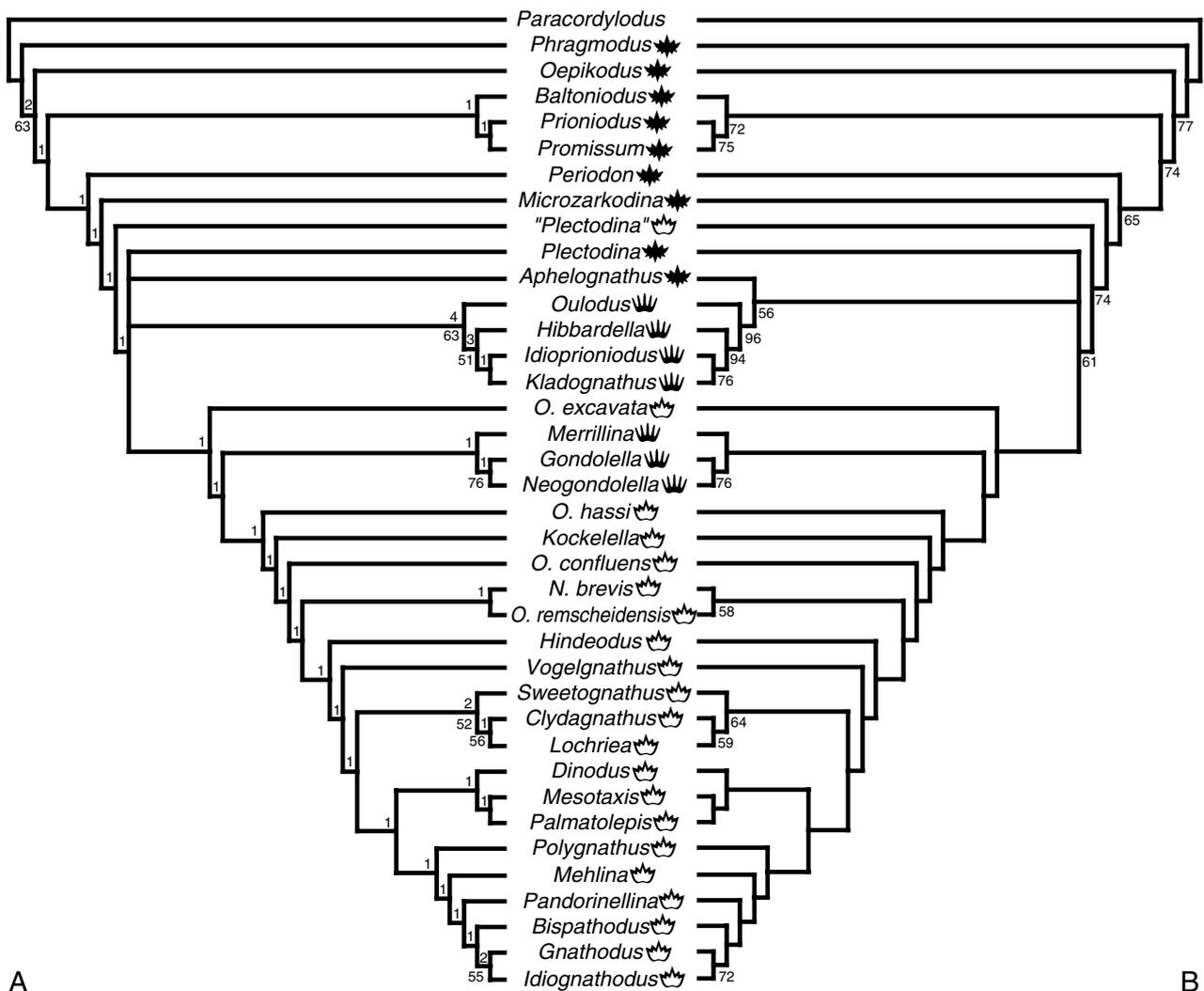


Figure 5 Cladograms derived from analysis of the Tranche 2 dataset (i.e. Tranche 1, plus taxa for which topological homologies may readily be inferred). **A**, Strict consensus of the six equally most parsimonious trees (MPTs) derived from analysis of the unweighted dataset. **B**, Strict consensus of the three equally MPTs derived from analysis of the reweighted dataset. Respective clad support values appear adjacent to nodes: Bremer support above and bootstrap values below.

well known (*Amorphognathus*, *Apatognathus*, *Chirognathus*, *Doliognathus*, *Ellisonia*, *Eognathodus*, *Erika*, *Erismodus*, *Erraticodon*, *Furnishiuis*, *Gamachignathus*, *Hadrodontina*, *Histiodellella*, *Icriodella*, *Pachycladina*, *Parapachycladina*, *Prioniodina*, *Pterospathodus*, *Sagittodontina*, *Scaliognathus*, *Staurogathus*, *Sweetina*, *Yaoxianognathus*). In particular, this list includes a large group of Ordovician and Permian/Triassic taxa that have previously been assigned to the Order Prioniodinida Sweet (1988).

The increased size of the dataset again precluded the use of the branch-and-bound search option and the heuristic search option was employed (tbr branch-swapping algorithm, steepest descent, random stepwise addition, 100 replicates, with 10 trees held at each step), but even under these circumstances the computation time required for the primary (unweighted) analysis was on the limits of acceptability (>120 h in some replicate analyses). The initial parsimony run yielded 195,727 equally most-parsimonious trees (the number of trees varied but the strict consensus was always the same: Fig. 7A) at 393 steps, a CIe of 0.23 (uninformative characters

27, 30, 35, 60), a RI of 0.69 and a RC of 0.16. Two rounds of reweighting yielded 1008 most-parsimonious trees and tree statistics that stabilised at a length of 63.54 steps, a CIe of 0.41 (common suite of uninformative characters), a RI of 0.82 and a RC of 0.36 (strict consensus presented in Fig. 7B). Most of the tree instability, under both weighted and unweighted datasets, arises from the interrelationships of relatively few taxa resolved in dramatically different positions in the competing trees; *Merrillina*+*Sweetina* are resolved in a relatively basal position within the ingroup, or else as basal members of the clade composed of bactrognathids (*Doliognathus*, *Scaliognathus*, *Staurogathus*), palmatolepids (*Mesotaxis*, *Palmatolepis*) and gondolellids (*Gondolella*, *Neogondolella*); in turn this entire clade is resolved either as the sister group to a large clade of ozarkodinids, or to the clade of prioniodinids. *Aphelognathus*, *Gamachignathus*, *Pterospathodus* and *Parapachycladina* also behave like rogue taxa, collapsing portions of the tree topology intermediate of the competing solutions to their affinity. All six taxa are among the most poorly known and/or understood of all taxa included in the

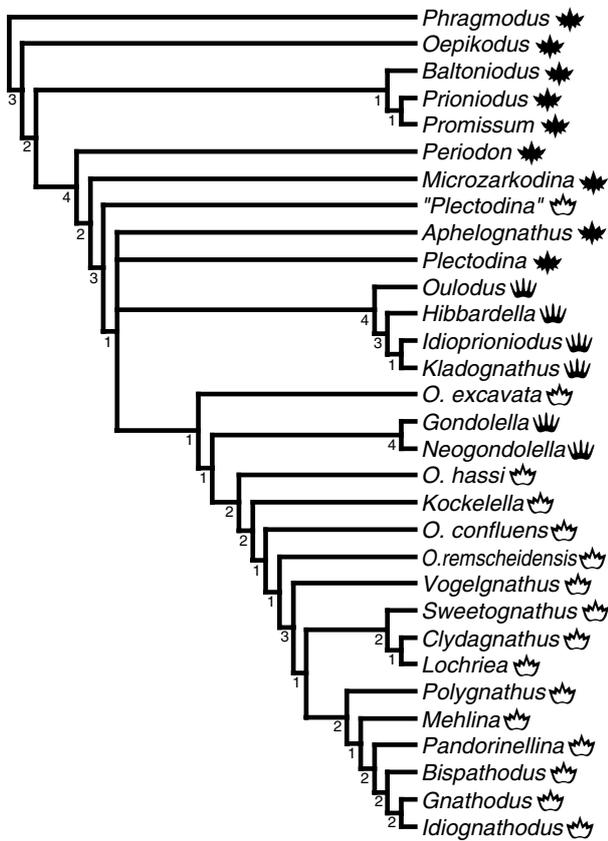


Figure 6 Reduced consensus tree with the highest Total Decay identified through Double Decay Analysis of the unweighted Tranche 2 dataset.

analysis, in terms of their multi-element composition or the homologies of the known elements.

It was not possible to apply DDA to the entire analysis because the number of included taxa is beyond the computational limitations of the available software and conflicting solutions to the affinity of the rogue taxa preclude DDA of even a partitioned dataset within an acceptable computation time. This results, undoubtedly, from the greater number of taxa in Tranche 3, but also from the uncertainty with which the additional taxa are known. Taxon deletion experiments in which the rogue taxa (*Aphelognathus*, *Gamachignathus*, *Merrillina*, *Parapachycladina*, *Pterospathodus* and *Sweetina*) were removed reduced the number of equally most-parsimonious trees of an unweighted dataset to 50 (353 steps; $CI_e = 0.25$; $RI = 0.70$; $RC = 0.19$; Fig. 8A), that reduced through 3 (67.94 steps; $CI_e = 0.41$; $RI = 0.82$; $RC = 0.38$; Fig. 8B) to 9 competing trees (66.86 steps; $CI_e = 0.43$; $RI = 0.83$; $RC = 0.40$; Fig. 9) after successive weighting. The strict consensus trees derived from the unweighted dataset and the first round of reweighting yielded compatible trees, but these differ significantly from the trees derived from successive rounds of reweighting, which ally the bactrognathid–palmatolepid–gondolellid clade with the ozarkodinids rather than the prioniodinids.

The CI_{exp} for a dataset including 61 taxa is 0.35, while the CI_{ran} is 0.06. With an unweighted CI of 0.23 the dataset therefore exhibits a greater level of homoplasy than

would be expected, but it clearly contains a relatively strong phylogenetic signal.

Discussion of the primary results

As additional taxa were included, they did not simply interleave among the branches of the preceding analysis but significantly changed the pre-existing hypotheses of relationships. For instance, between Tranche 1 and 2, *Nicollidina brevis* moves from a relatively derived position within a clade of ozarkodinids to a more plesiomorphic position. Similarly, the clade (*Lochriea* + *Clydagnathus*) shifts from a position more derived than *Polygnathus* and *Palmatolepis*, to a more plesiomorphic position; *Hibbardella* shifts from being the sister-taxon to *Idioproniodus*, to the sister to the clade (*Idioproniodus* + *Kladognathus*). These changes occur because the newly included taxa in the second tranche alter the pattern of character distribution. Thus, characters that united *N. brevis* with *Bispathodus*, *Gnathodus* and *Idiognathodus* in Tranche 1, such as the presence of bipennate rather than digyrate S_2 elements, are resolved as autapomorphies of *N. brevis*, although they are still synapomorphies of the remaining clade (*Bispathodus* + *Gnathodus* + *Idiognathodus*). Similarly, in the Tranche 1 analysis the absence of a ‘posterior’ process in the S_0 element is an autapomorphy of *N. brevis* and of *Palmatolepis*, but the additional taxa included in Tranche 2 reveal this to be a plesiomorphic condition for ozarkodinids (subsequently lost numerous times: see ‘Further reflections on homology,’ below). Indeed, the relatively large number of autapomorphies exhibited by both *N. brevis* and *Palmatolepis* in the Tranche 1 analysis (Fig. 4) may have been sufficient to raise doubts concerning their precise relationships, but these taxa exhibit just as many autapomorphies in the Tranche 2 results (Fig. 5B).

The addition of taxa in Tranche 3 leads to a reversion of the relationships of *Hibbardella*, *Idioproniodus* and *Kladognathus* to the topology derived from the Tranche 1 dataset (i.e. with *Kladognathus* as the more plesiomorphic taxon) and there are a number of other minor local changes (e.g. concerning *Baltoniodus*, *Prioniodus* and *Promissum*, and *Microzarkodina* and *Promissum*). The only other significant topological difference is in the referral of the palmatolepid clade (*Palmatolepis*, *Mesotaxis* and *Dinodus*) to a position plesiomorphic to most other ozarkodinids and united with the bactrognathids and gondolellids (Figs 7–9). This is supported, like much of the tree, largely on the basis of characters that change elsewhere in the cladogram. However, the significant characters that support the inclusion of *Palmatolepis* and *Mesotaxis* with gondolellids and bactrognathids include the possession of a recessive basal margin that is inverted rather than planar. Other common characters are also characteristic of *Polygnathus* and *Mehlina*. Indeed, to align the palmatolepids to *Polygnathus* costs as little as three steps in the parsimony argument that supports the results from the analysis of the Tranche 3 dataset.

Given the differences in the topology of relationships exhibited by the results of the three tranches of taxa, which are we to accept as the best available hypothesis? The first tranche dataset is based on taxa that are known from natural assemblages and so the positional homologies cannot be called into question. Indeed, the quality of this dataset is reflected in the strength of the underlying phylogenetic signal, as reflected in the Bremer support indices and the

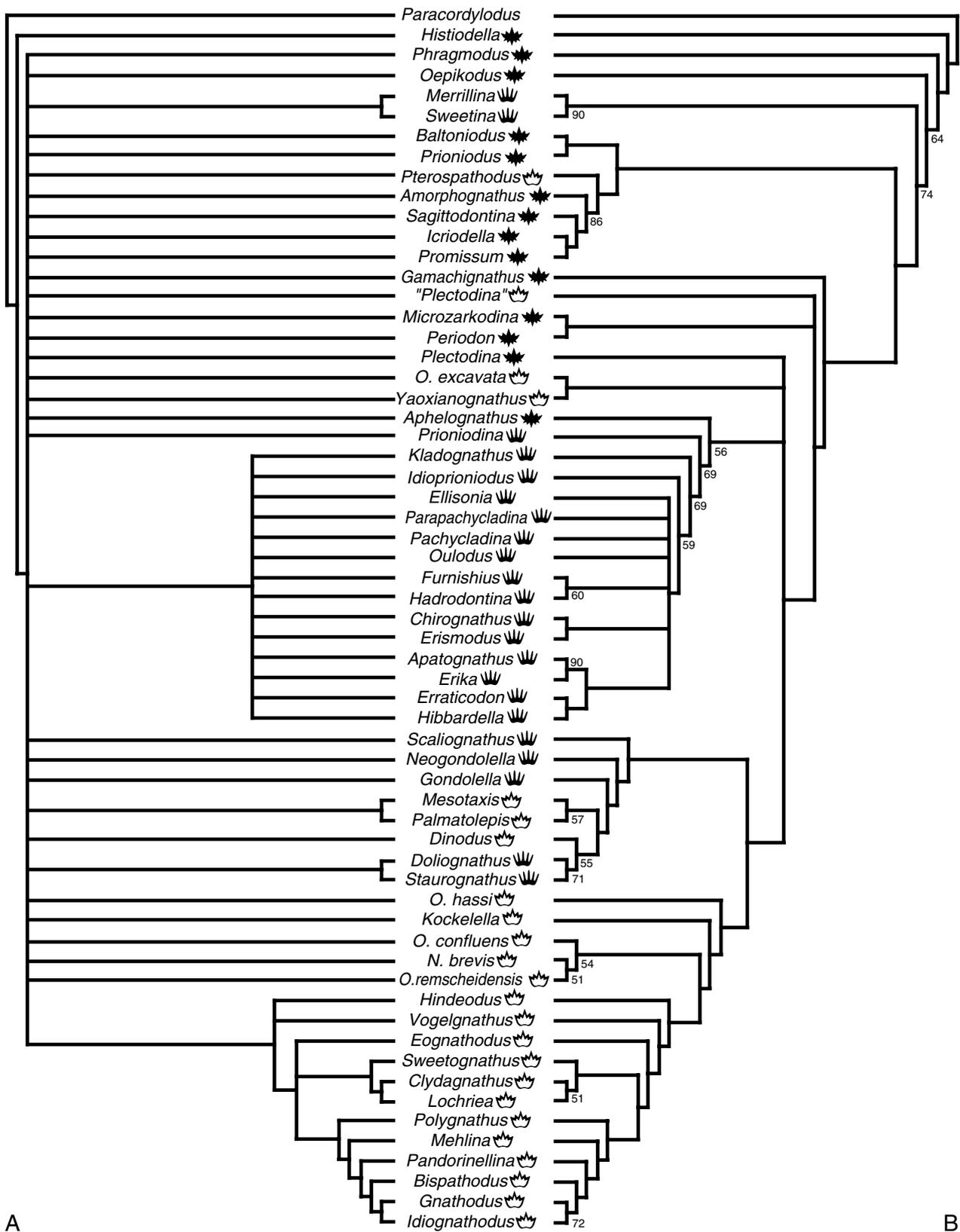


Figure 7 Cladograms derived from analysis of the Tranche 3 dataset (i.e. Tranches 1 and 2, plus those taxa for which topological and orientational homologies are uncertain). **A**, Strict consensus of the 195,727 equally most parsimonious trees (MPTs) derived from analysis of the unweighted dataset. **B**, Strict consensus of the 1008 equally MPTs derived from analysis of the reweighted dataset. The respective bootstrap support values appear adjacent to nodes.

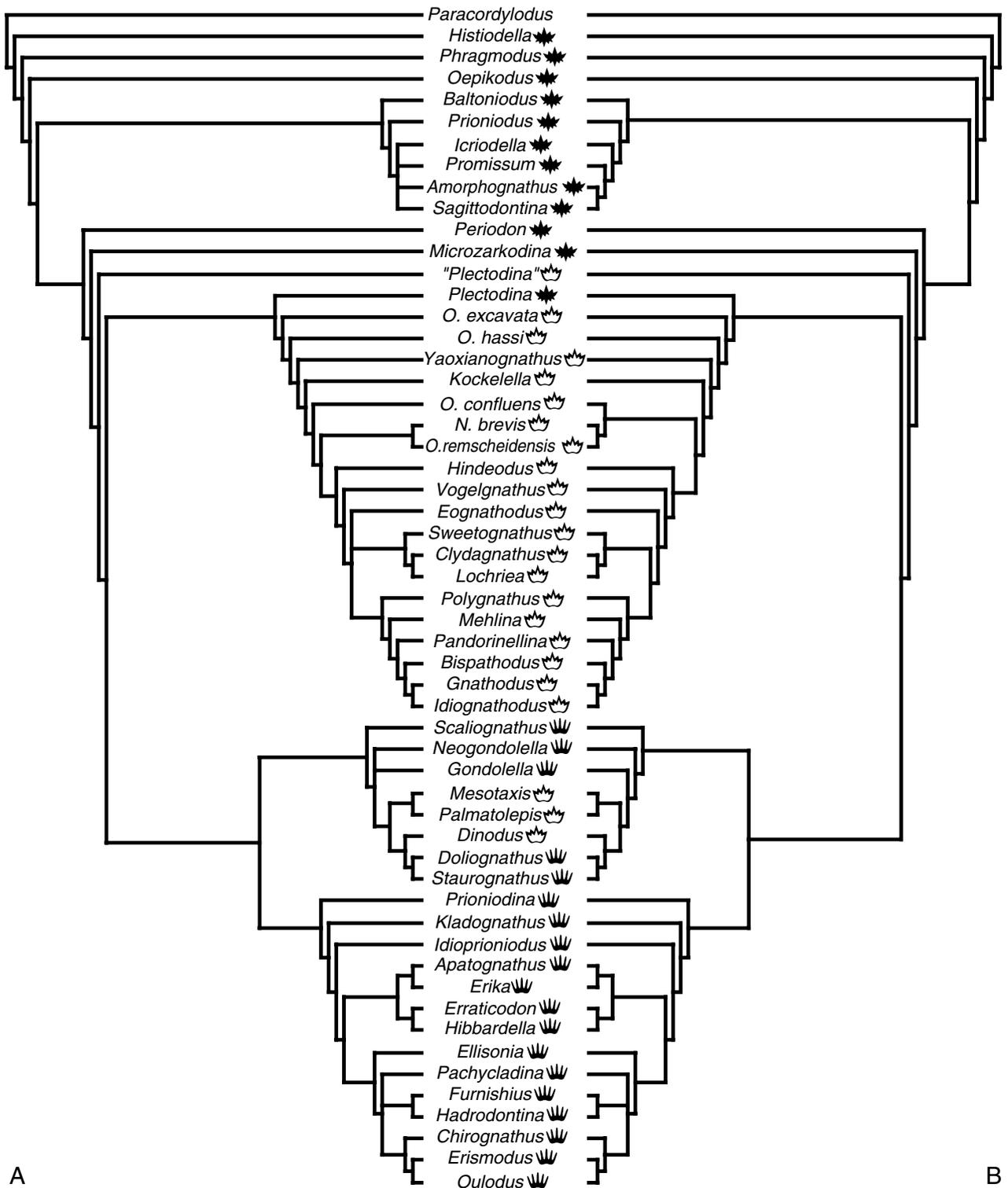


Figure 8 Cladograms from taxon deletion experiments on the Tranche 3 dataset. **A**, Strict consensus tree based on analysis of the unweighted Tranche 3 dataset after deletion of rogue taxa *Aphelognathus*, *Gamachignathus*, *Merrillina*, *Parapachycladina*, *Pterospathodus* and *Sweetina*. **B**, Strict consensus tree based on analysis of the reweighted Tranche 3 dataset after deletion of rogue taxa *Aphelognathus*, *Gamachignathus*, *Merrillina*, *Parapachycladina*, *Pterospathodus* and *Sweetina*.

bootstrap support values. This may be taken to imply that we should place greatest reliance on this hypothesis of relationships; the relationships of the taxa not known from natural assemblages could then be assessed by employing

the optimal tree derived from Tranche 1 as a backbone constraint underpinning subsequent analyses of more inclusive datasets. However, because the Tranche 1 dataset represents such a sparse sampling of distantly related taxa, it is possible

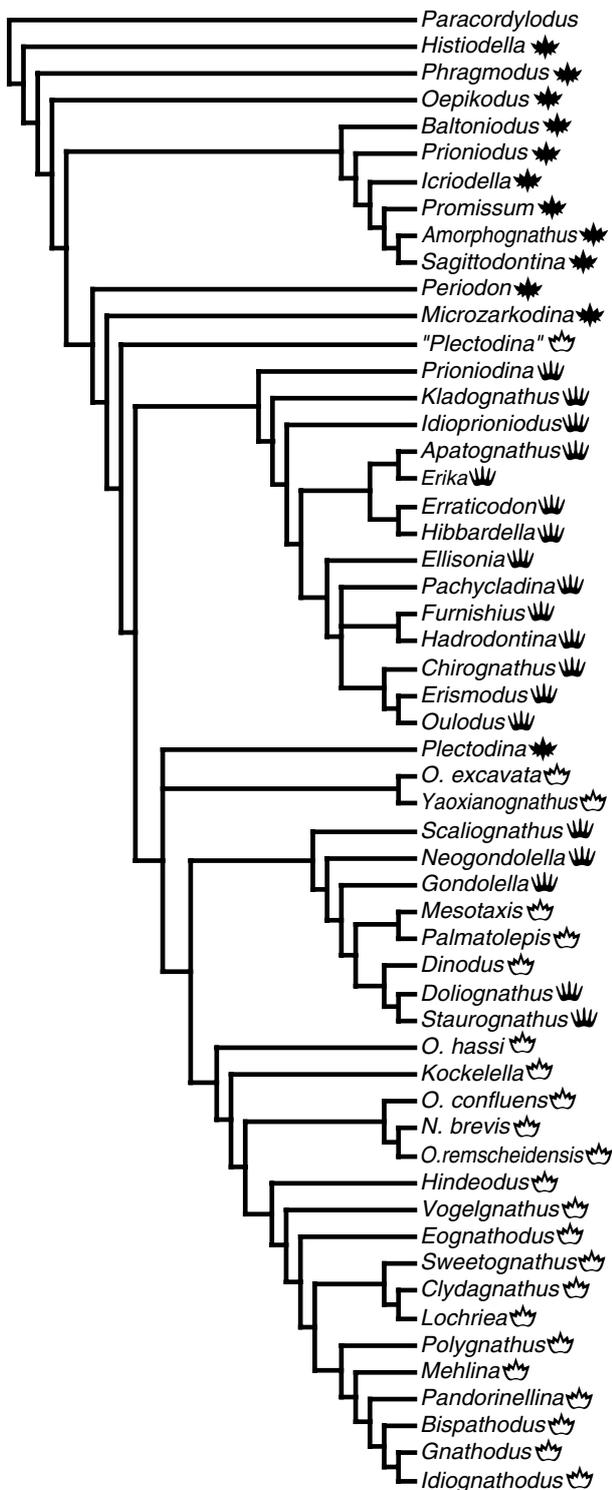


Figure 9 Cladogram from taxon deletion experiments on the Tranche 3 dataset, topologies stabilised after repeated rounds of successive weighting. Strict consensus tree based on analysis of the reweighted Tranche 3 dataset after deletion of rogue taxa *Aphelognathus*, *Gamachignathus*, *Merrillina*, *Parapachycladina*, *Pterospathodus* and *Sweetina*.

that some of the relationships resulting from this analysis are spurious. It might, therefore, be more appropriate to accept the best-supported hypothesis derived from the Tranche 3

dataset, which is the most inclusive and provides the most severe test of homology through character congruence. However, the trees derived from this analysis are the least well supported of any. Indeed, although there is good resolution in parts of the tree, at both fine and coarse scales, the results overall indicate that, as more and more taxa are included in the analysis, phylogenetic resolution decreases. This could occur for at least two reasons, which are not necessarily mutually exclusive. Firstly, resolution decreases with the inclusion of taxa for which element locations are less well-constrained and, thus, it is possible that spurious primary homology assessments are creating noise in the dataset. This undoubtedly occurs. Secondly, phylogenetic resolution decreases with the inclusion of taxa that are progressively more distantly related. We attempted to test both of these explanations by partitioning the dataset into three groups that equate approximately to the orders Prioniodontida, Prioniodinida and Ozarkodinida (*sensu* Sweet 1988), modified on the basis of the high-level relationships suggested by our results. We would expect homologies to be more consistently identified within each of these groups than between them; on independent analysis each group would be unaffected by the distribution of characters in outlying taxa.

Analysis of subgroups

Prioniodontida

The prioniodontid group analysis included all taxa from the total dataset excluding those resolved herein as members of an ozarkodinid or prioniodinid (except *Aphelognathus*) clade, or members of the clade including bactrognathids, gondolellids and palmatolepids; the analysis was rooted on *Paracordylodus*. The initial parsimony run yielded 48 most-parsimonious trees (147 steps; CIe = 0.42; RI = 0.63; RC = 0.29), the strict consensus of which (Fig. 10A) is poorly resolved. Deletion experiments (not shown) demonstrated

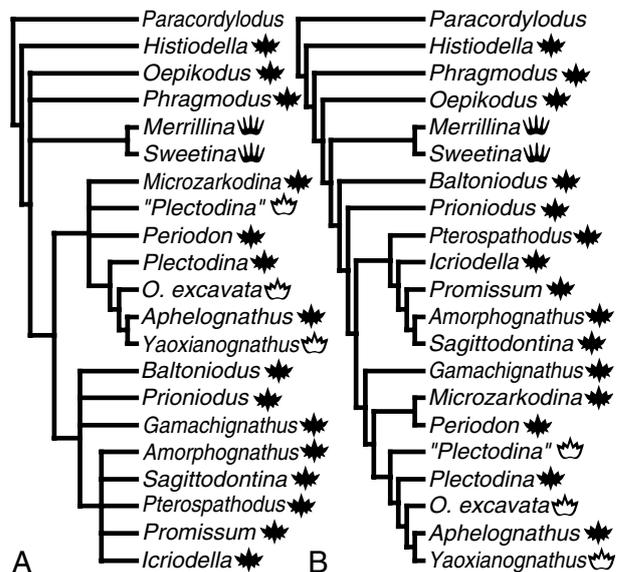


Figure 10 Intrarelationships of prioniodontids. **A**, Strict consensus of 48 trees derived from analysis of an unweighted dataset limited to a prioniodontid clade plus relevant outgroup taxa. **B**, Single most parsimonious tree arising from analysis of the reweighted dataset.

that this is not an artefact of the inclusion of *Merrillina* and *Sweetina*. A *posteriori* reweighting yielded a single most-parsimonious tree (Fig. 10B; 43.39 steps; CIe = 0.71; RI = 0.88; RC = 0.69) with a topology common to one of the competing optimal trees derived from analysis of the unweighted dataset. In comparison to the trees derived from analysis of the entire dataset, the most significant differences are the topology within the balognathid clade and the relationships of *Baltoniodus* and *Prioniodus* to this clade; in this respect the results are comparable to those of the Tranche 3 analysis with rogue taxa deleted (Fig. 9). This demonstrates that the exclusion of distant relatives has lessened the destabilising effect of poorly known taxa.

Prioniodinida

Using the results of the analysis of the entire dataset we identified a prioniodinid group, which included the taxa resolved as components of the rump prioniodinid clade, the clade including bactrognathids, gondolellids and palmatolepids, plus *Plectodina*, *O. excavata* and *Yaoxianognathus*; *Merrillina* and *Sweetina* were also included so that we could test whether their apparent plesiomorphic position resulted from primary signal or from homoplasy. *Microzarkodina*, *Periodon* and '*Plectodina*' were assigned to the outgroup. The initial parsimony run yielded six most-parsimonious trees at 213 steps, with a CIe of 0.35, a RI of 0.68 and a RC of 0.25; a strict consensus of these trees is presented in Fig. 11. The trees differ chiefly in that the relationships of *Plectodina* and the clade (*O. excavata* + *Yaoxianognathus*) are either unresolved or *Plectodina* is resolved as the more plesiomorphic. The only other difference between the trees concerns the position of *Pachycladina*, which is resolved as the sister to (*Ellisonia* (*Idioprioniodus* + *Kladognathus*)), or in an unresolved polytomy with this clade and (*Furnishius* + *Hadrodontina*). While *Merrillina* and *Sweetina* still form a clade, as they did in the Tranche 3 results, rather than being plesiomorphic they are now resolved as members of the in-group, positioned as the sister group to the bactrognathid – gondolellid – palmatolepid clade.

In this analysis, prioniodinid relationships are much better resolved than they are in the strict consensus tree derived from analysis of the entire dataset (Fig. 7) and some aspects of the topology differ between the two. In particular, analysis of the entire dataset resolved the oldest prioniodinid representatives in relatively derived positions. The partitioned analysis, however, resolved these taxa to relatively basal positions within the prioniodinid clade. Otherwise, the results from analysis of the entire dataset and the partitioned analysis share a common topology, especially in resolving a distinct bactrognathid – gondolellid – palmatolepid clade.

Ozarkodinida

The ozarkodinid group partitioned for separate analysis included all taxa comprising the core ozarkodinid clade, the bactrognathid – gondolellid – palmatolepid clade, *Aphelognathus*, *Plectodina*, *O. excavata* and *Yaoxianognathus*. As before, *Merrillina* and *Sweetina* were also included in the analysis to test their apparent plesiomorphic position. *Microzarkodina*, *Periodon* and '*Plectodina*' were assigned to the outgroup. The initial parsimony run yielded 44 most-parsimonious trees at 210 steps (CIe = 0.32; RI = 0.65; RC = 0.23). The trees differ in the resolution of the bactrognathid –

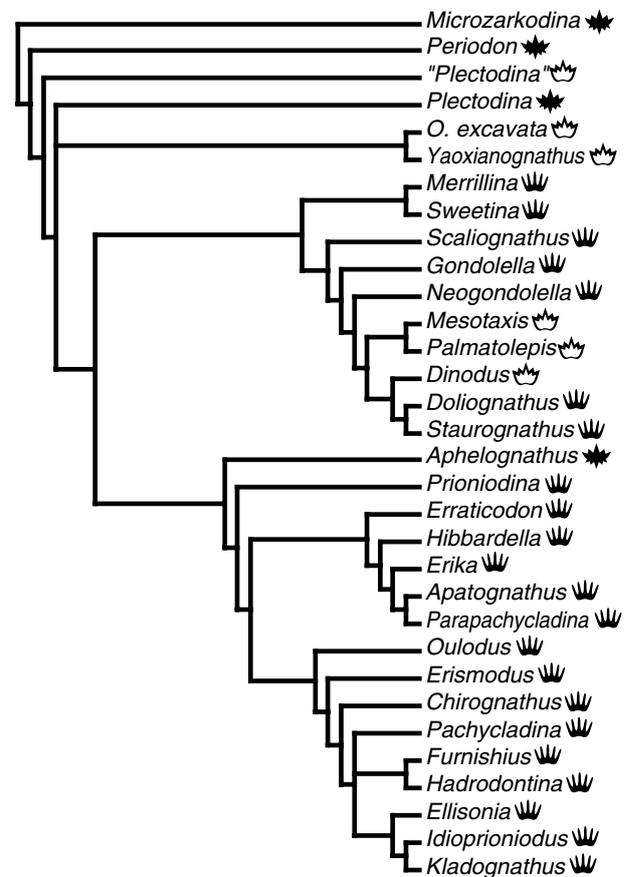


Figure 11 Intrarelationships of prioniodinids. Strict consensus of six trees derived from analysis of an unweighted dataset limited to a prioniodinid clade plus relevant outgroup taxa.

gondolellid – palmatolepid clade and in the interrelationships of *Plectodina*, *O. excavata*, *Aphelognathus* and *Yaoxianognathus*. *Eognathodus* is resolved either as the sister taxon to *Polygnathus* plus gnathodids, or in an unresolved polytomy with this and the clade (*Sweetognathus* (*Clydagnathus* + *Lochriea*)); a strict consensus is presented in Fig. 12A. Successive rounds of a *posteriori* reweighting yielded a single most-parsimonious tree (48.64 steps; CIe = 0.56; RI = 0.81; RC = 0.52; Fig. 12B) that is not the same as any of the most-parsimonious trees derived from the unweighted analysis, although it is the same as two trees that are three steps longer. The relative relationships of *Plectodina* and *O. excavata* plus *Yaoxianognathus* remain unresolved in this tree. *Merrillina* and *Sweetina* are again resolved as a sister clade to the bactrognathid – gondolellid – palmatolepid group, with *O. hassi* as the sister taxon to these two clades and *Kockelella* as sister taxon to this combined clade plus all more derived ozarkodinids. This differs from the result of the analysis of the complete data set (minus rogue taxa), which resolved the bactrognathid – gondolellid – palmatolepid clade as a distinct sister group to all remaining ozarkodinid taxa.

Summary of hypothesis of relationships

The results of the partitioned analyses demonstrate that, in all instances, the internal topologies of local clades have been affected by the inclusion or exclusion of distantly related taxa.

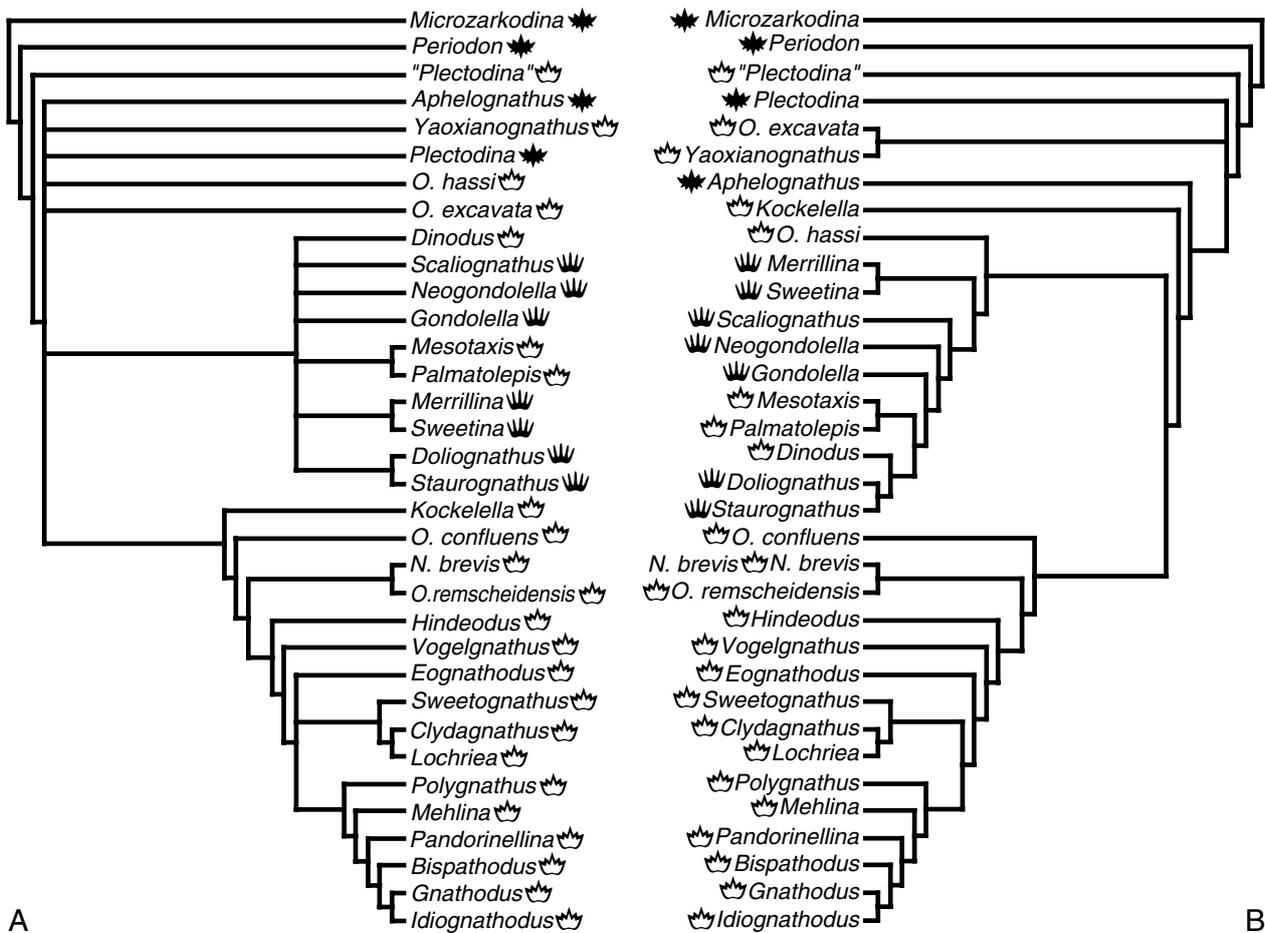


Figure 12 Intrarelations of ozarkodinids. **A**, Strict consensus of 44 trees derived from analysis of an unweighted dataset limited to an ozarkodinid clade plus relevant outgroup taxa. **B**, Single most parsimonious tree arising from analysis of the reweighted dataset.

While the complete dataset provides a more exacting test of character congruence than does analysis of local partitions, the likelihood that inferred homologies are spurious increases as more distantly related taxa are included. Consequently, where trees resulting from analysis of the partitioned dataset are not congruent with those from the Tranche 3 analysis, we generally have greater confidence in the topology of relationships derived from the partitioned datasets.

In order to provide a framework for discussion and comparison, we have produced a single tree that summarises all of the analyses (Fig. 13). This tree preserves the topology of the Tranche 2 analysis, probably our best substantiated hypothesis of relationships, except for *Hibbardella*, the position of which is shown as unresolved within core prioniodinids (because in the partitioned prioniodinid analysis and the Tranche 3 analyses it consistently formed a clade with taxa that were not included in the Tranche 2 analysis). The positions in the tree of taxa that were not included in the Tranche 2 analysis are based on the results of the Tranche 3 and/or the partitioned analyses; for many of these taxa the two analyses agree, as indicated by superscripts in the figure. For the clade identified as Prioniodinina we have taken the topology of the partitioned analyses as the most reliable guide to internal relationships within the group (for the reasons outlined above),

with the caveat that the relationships among prioniodinids are among the least well resolved of any in our analysis. Although they are consistently resolved as a clade, more work is needed to better constrain internal relationships. We also note that the position of palmatolepids shown in the tree is recovered only by the Tranche 3 analysis.

The classification derived from our results is indicated in Fig. 13 and detailed in Table 2. While traditional schemes of conodont classification have recognised both monophyly and paraphyly in formal nomenclature, we have chosen to recognise only monophyly. Although there are often problems associated with the application of strict monophyly in formal classification, in that traditional widely recognised taxonomic concepts are abandoned or fundamentally changed, the failure of most conodont specialists to utilise existing schemes of classification means that such problems do not obtain to the same degree. While it is possible to recognise each branching event in formal nomenclature, the resulting proliferation of names would not be helpful and, in almost all instances, is not required. Thus, we have chosen to recognise only major cladogenic events in formal nomenclature. Clades that would otherwise remain unnamed, but which equate in composition with pre-existing taxonomic concepts, are also recognised formally.

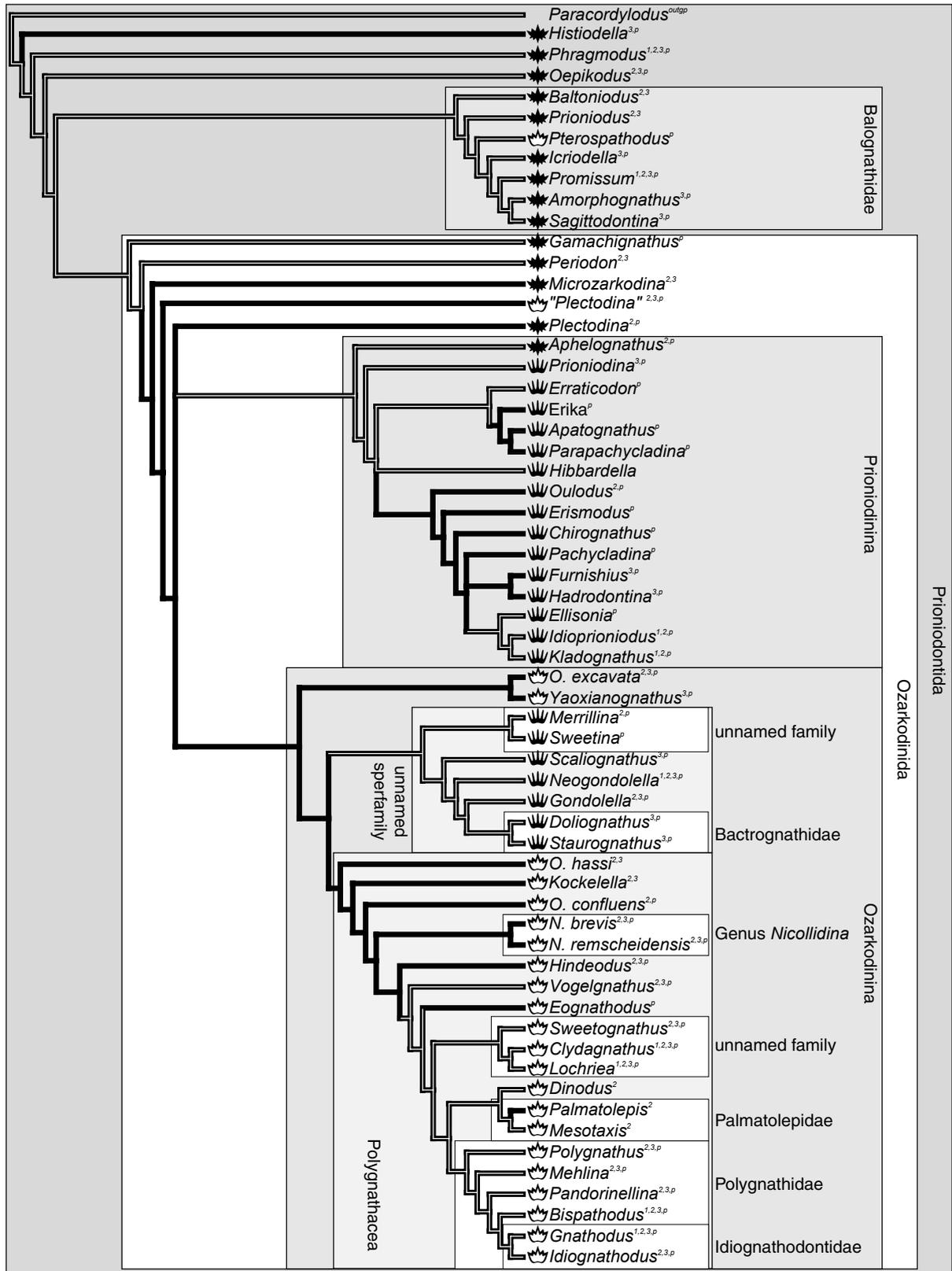


Figure 13 Tree summarising our hypotheses of relationships and our classification. Framework topology is based on Tranche 2 analysis; superscripts indicate which analyses recovered the relationships shown (1, 2, 3 and p indicate Tranche 1, Tranche 2, Tranche 3 and partitioned analyses, respectively), and thus provide a guide to how consistently clades are resolved under different conditions of analysis. Because *Nicollidina brevis* and *O. remschiedensis* are consistently resolved as a clade in our analyses we have provisionally reassigned the latter species to *Nicollidina*. Shading and boxes indicate inclusiveness of higher taxa. The figure also shows the inferred evolution of the 'posterior' process of the S_0 element (see the text for discussion); the presence of a 'posterior' process is indicated by fine white lines within the branches.

Table 2 Classification of the Prioniodontida Dzik, 1976.

Class Conodonta Eichenberg, 1930	
Division Prioniodontida Dzik, 1976	
<i>Paracordylodus gracilis</i> Lindström, 1955	
<i>Histiodella altifrons</i> Harris, 1962	
<i>Phragmodus inflexus</i> Stauffer, 1935a	
<i>Oepikodus communis</i> (Ethington & Clark, 1964)	
Family Balognathidae Hass, 1959	
<i>Baltoniodus clavatus</i> Stouge & Bagnoli, 1990	
<i>Prioniodus oepiki</i> (McTavish, 1973)	
<i>Pterospathodus amorphognathoides</i> Walliser, 1964	
<i>Icriodella superba</i> Rhodes, 1953	
<i>Promissum pulchrum</i> Kovács-Endrödy in Theron & Kovács-Endrödy, 1986	
<i>Amorphognathus ordovicicus</i> Branson & Mehl, 1933	
<i>Sagittodontina kielsensis</i> (Dzik, 1976)	
Order Ozarkodinida Dzik, 1976	
<i>Gamachignathus ensifer</i> McCracken <i>et al.</i> , 1980	
<i>Periodon aculeatus</i> (Hadding, 1913)	
<i>Microzarkodina parva</i> Lindström, 1971	
“ <i>Plectodina</i> ” <i>tenuis</i> (Branson & Mehl, 1933)	
<i>Plectodina aculeata</i> (Stauffer, 1930) <i>sedis mutabilis</i>	
Suborder Prioniodinina	
<i>Aphelognathus kimmswickensis</i> Sweet <i>et al.</i> , 1975	
<i>Prioniodina</i> cf. <i>P. recta</i> (Branson & Mehl, 1933)	
<i>Erraticodon patu</i> Cooper, 1981	
<i>Hibbardella angulata</i> (Hinde, 1879)	
<i>Erika divarica</i> Murphy & Matti, 1982	
<i>Apatognathus varians varians</i> Branson & Mehl, 1933	
<i>Parapachycladina obliqua</i> (Zhang in Zhang & Yang, 1991)	
<i>Oulodus rohneri</i> Ethington & Furnish, 1959	
<i>Erismodus arbucklensis</i> Bauer, 1987	
<i>Chirognathus duodactylus</i> Branson & Mehl, 1933	
<i>Pachycladina obliqua</i> Staesche, 1964	
<i>Furnishius triserratus</i> (Igo <i>et al.</i> , 1965)	
<i>Hadrodontina anceps</i> Staesche, 1964	
<i>Ellisonia triassica</i> Müller, 1956	
<i>Idioproniodus</i> sp.	
<i>Kladognathus</i> sp.	
Suborder Ozarkodinina Dzik, 1976	
<i>Ozarkodina excavata</i> (Branson & Mehl, 1933)	
<i>Yaoxaniognathus ani</i> Zhen <i>et al.</i> , 1999	
Unnamed Superfamily	
Unnamed Family	
<i>Merrillina divergens</i> (Bender & Stoppel, 1965)	
<i>Sweetina tricitum</i> Wardlaw & Collinson, 1986	
<i>Scaliognathus anchoralis</i> Branson & Mehl, 1941	
<i>Neogondolella momburgensis</i> (Tatge, 1956)	
<i>Gondolella pohli</i> von Bitter & Merrill, 1998	
Family Bactrognathidae Lindström, 1970	
<i>Doliognathus latus</i> Branson & Mehl, 1941	
<i>Staurognathus cruciformis</i> Branson & Mehl, 1941	
Superfamily Polygnathacea Bassler, 1925	
<i>Ozarkodina hassi</i> (Pollock <i>et al.</i> , 1970)	
<i>Kockelella ranuliformis</i> (Walliser, 1964)	
<i>Ozarkodina confluens</i> (Branson & Mehl, 1933)	
<i>Nicollidina brevis</i> (Bischoff & Ziegler, 1957)	
<i>Nicollidina remscheidensis</i> (Ziegler, 1960)	
<i>Hindeodus cristulus</i> (Youngquist & Miller, 1949)	
<i>Vogelgnathus campbelli</i> (Rexroad, 1957)	
<i>Eognathodus sulcatus</i> Philip, 1965	

Table 2 Continued

Unnamed Family	
<i>Sweetognathus expansus</i> (Perlmutter, 1975)	
<i>Clydagnathus windsorensis</i> (Globensky, 1967)	
<i>Lochriea</i> sp.	
Family Polygnathidae Bassler, 1925	
<i>Polygnathus xylus xylus</i> Stauffer, 1940	
<i>Mehlina gradata</i> Youngquist, 1945	
<i>Pandorinellina insita</i> (Stauffer, 1940)	
<i>Bispathodus aculeatus</i> (Branson & Mehl, 1933)	
Family Idiognathodontidae Harris & Hollingsworth, 1933	
<i>Gnathodus bilineatus</i> (Roundy, 1926)	
<i>Idiognathodus</i> sp.	
Family Palmatolepidae Sweet, 1988 <i>sedis mutabilis</i>	
<i>Mesotaxis asymmetrica asymmetrica</i> (Bischoff & Ziegler, 1957)	
<i>Palmatolepis bogartensis</i> (Stauffer, 1938)	
<i>Dinodus lobatus</i> (Branson & Mehl, 1933)	

Within this classification we have listed only those species that were used in the analyses presented in this paper; it provides a framework to which further taxa can be added as knowledge increases. The practice of using the suffix *sedis mutabilis* to indicate areas of ignorance in relation to relative branching follows Wiley (1979).

COMPARISON WITH PREVIOUS PHYLOGENIES AND CLASSIFICATION SCHEMES

Comparison with Sweet's phylogeny and classification

Comparison between our classification and that of Sweet (1988) is somewhat complicated by our recognition of more levels of nestedness of groups. For example, we recognise Idiognathodontidae within Polygnathidae within Polygnathacea within Ozarkodinina within Ozarkodinida within Prioniodontida. Sweet's classification is rather flat; he accommodated all the taxa under consideration here within his Class Conodonti, within which he recognised only orders, families, a few subfamilies and genera.

In spite of this, our analysis confirms, in broad terms, the framework of Sweet's classification, with two major clades (our Prioniodinina and Ozarkodinina are approximately equivalent to Sweet's Prioniodinida and Ozarkodinida, respectively) together with a paraphyletic array of more basal clades assigned by Sweet to Prioniodontida. We have chosen to recognise only monophyletic taxa in our classification, so we expand Prioniodontida to encompass all the taxa in our analysis (i.e. all conodonts with complex element morphologies) and recognise Ozarkodinida as a major clade within Prioniodontida, itself including both Ozarkodinina and Prioniodinina. One major difference concerns the relationships between prioniodinins and ozarkodinins. Sweet clearly derived his Ozarkodinida from among Prioniodontida, thereby implying that these two taxa are more closely related to one another than either is to Prioniodinida (although he did not explicitly say where Prioniodinida nested among complex conodonts). Our analysis, however, indicates that Ozarkodinina and Prioniodinina are sister groups.

Comparisons between the classifications at the family level are more difficult, partly because several of Sweet's families are massively paraphyletic, containing the ancestors of several other families. Sweet's Spathognathodontidae, for example, contains the ancestors of almost all the more derived families within his Ozarkodinida. Only by interpreting these multiple common ancestors as members of Spathognathodontidae is Sweet's taxon rescued from being polyphyletic. Our results are not compatible with the existence of a monophyletic (or paraphyletic) grouping that in any way resembles Spathognathodontidae.

In general, the relatively sparse taxon sampling of our analysis does not permit us to comment on the composition of families (but see Balognathidae, below). Nevertheless, we are able to test Sweet's hypotheses of ancestry and descent as resolved in our tree.

Sweet's Prioniodinida

Although relationships within the clade are problematical, our analysis agrees with Sweet's (1988) hypothesis that many of the taxa he assigned to Prioniodinida constitute a monophyletic group. Beyond that, our analysis is too poorly resolved to comment in detail except to say that we find no support for the view that Bactrognathidae are derived from a prioniodinid. Similarly, Gondolellidae and the clade *Merrillina* + *Sweetina* are resolved as members of Ozarkodinina, not Prioniodinina. None of our analyses support Sweet's hypothesis that *Idioproniodus* includes the common ancestor of Gondolellidae and *Ellisonia*. Our analysis suggests that *Aphelognathus kimmswickensis* is a basal member of the clade, contradicting Sweet's view that it is a close relative of *Plectodina* (see below).

Sweet's Prioniodontida

Of the taxa Sweet included within his Prioniodontida we are able to recognise only Balognathidae as a clade. Aside from that, and a relatively basal position for *Oepikodus*, Sweet's hypotheses of relationships and relative branching order of 'prioniodontids' (Fig. 2) are not supported by our analysis. *Histiodela* and *Phragmodus*, for example, are relatively derived 'prioniodontids' in Sweet's scheme, but are basal in our analysis. Regarding Balognathidae, although we recognise a clade to which we apply this name, the taxonomic composition of the family differs from that given by Sweet. Sweet's hypothesis of relative branching order of *Baltoniodus*, *Amorphognathus* and *Icriodella* is compatible with our tree, as is a close relationship between *Amorphognathus* and *Sagittodontina*.

Sweet's Ozarkodinida

In our analyses, Ozarkodinina (= Sweet's Ozarkodinida) was consistently resolved as a clade. In most cases, a clade including *Ozarkodina excavata* was resolved as the most basal branch, in some instances forming a polytomy with *Plectodina* and all other ozarkodinins. Our analysis does not support Sweet's hypothesis that '*Plectodina*' is the most basal member of the clade, but it is consistent with *Yaodianognathus* being among the most primitive. The position of *Kockelella* in our analysis accords well with Sweet's hypothesis in that it is a close relative of (although not actually derived from) species of *Ozarkodina* and it branches off early in ozarkodinina phylogeny. *Pterospathodus*, however, is resolved as a balognathid in our analysis.

Central to Sweet's concept of Ozarkodinida is the idea that members of Spathognathodontidae, especially *Ozarkodina*, are the 'rootstock' from which later ozarkodinids evolved. If this hypothesis is correct, we would expect species of *Ozarkodina* to be resolved as successive sister taxa to more derived members of the clade. *Ozarkodina confluens* and (*O. remscheidensis* + *Nicollidina brevis*) fit this pattern, but *O. excavata* and *O. hassi* do not. Our analysis confirms the view that *Ozarkodina*, as currently conceived, is polyphyletic (e.g. Murphy *et al.* 2004 *contra* Sweet 1988). We place little confidence in the reliability of our analyses in resolving the precise positions of palmatolepids, but none of our analyses accord with Sweet's hypothesis that they were derived from *Ozarkodina*. The alternative view, that they are closely related to *Polygnathus*, is consistent with some of our results.

Other 'ancestral' members of Spathognathodontidae, according to Sweet (1988; Fig. 2), include *Pandorinellina* (which arose from *Ozarkodina* and gave rise to *Clydagnathus*) and *Mehlina* (which arose from *Ozarkodina* or *Pandorinellina* and gave rise to *Dinodus* and *Bispathodus*, the latter giving rise in turn to *Gnathodus* and *Sweetognathus*). Our analysis supports a close relationship between some of these taxa within our Polygnathidae (*Mehlina*, *Pandorinellina*, *Bispathodus* and *Gnathodus*), but our trees are otherwise not compatible with Sweet (1988). As noted above, our analyses indicate that gondolellids, bactrognathids and the clade *Merrillina* + *Sweetina* lie among Ozarkodinina, not Prioniodinina.

Quantitative testing of Sweet's phylogeny

Quantitative comparisons of Sweet's hypotheses of relationship with ours have also been undertaken, using each of our three datasets. Sweet's pattern of relationships between the taxa in each tranche (Fig. 2, Supplementary Figs 1A, C) was enforced as a backbone constraint tree to determine how many extra steps were required to find the shortest compatible tree. In each instance, the data subsets were subjected to parsimony analysis constrained by the topology of the backbone constraint trees; the smallest data subset was analysed using the branch-and-bound search algorithm, while the larger datasets were analysed in 100 replicates of the random stepwise addition search algorithm.

Analysis of Tranche 1 under topological constraint of the first backbone constraint tree (Supplementary Fig. 1A) yielded a single MPT (185 steps; CI = 0.42; RI = 0.53; RC = 0.25; Supplementary Fig. 1B). This tree is clearly less parsimonious than the optimal trees found under unconstrained analysis (150 *versus* 185; 23% longer) and this is borne out by the significantly lower CI value. Nevertheless the CI value of the optimal trees found under constrained analysis is significantly higher than would be expected from a random dataset (0.23).

Analysis of Tranche 2 under topological constraint of the second backbone constraint tree (Supplementary Fig. 1C) also yielded a single MPT (341 steps; CI = 0.25; RI = 0.51; RC = 0.14; Supplementary Fig. 1D). Again, this tree is considerably less parsimonious than the optimal trees recovered under unconstrained analysis (268 *versus* 341; 27% longer). However, although the CI value of the constrained analysis is considerably lower than the CI value of optimal trees derived from unconstrained analysis, this value remains significantly higher than would be expected given a dataset containing no phylogenetic signal.

Analysis of Tranche 3 under topological constraint of the third backbone constraint tree (Fig. 2) yielded 28 equally most-parsimonious trees (545 steps; CI = 0.17; RI = 0.53; RC = 0.09), the strict consensus of which is reproduced in Supplementary Figure 2. Once more, these trees are significantly less parsimonious ($p = 0.05$) than the optimal trees recovered under unconstrained analysis (393 versus 545; 39% longer). Although the CI is again higher than that expected from a dataset containing no phylogenetic signal, it is very close to the value expected from an entirely random dataset.

Comparison with Dzik's phylogeny and classification

Dzik's Prioniodontida

Unlike Sweet's paraphyletic array, Dzik clearly considered many of the 'prioniodontid' genera included in our analysis to form a clade distinct from Ozarkodinida (see Fig. 3). This is partly supported by our results in that most of the taxa comprising our Balognathidae were assigned by Dzik to his Prioniodontacea (although his superfamily also included a range of taxa that we did not include in our analysis). Our clade differs in that we exclude *Phragmodus* and *Oepikodus* and include *Pterospathodus*. Our results also agree with Dzik's view that *Promissum*, *Amorphognathus* and *Sagittodontina* are more closely related to each other than to any other of the taxa under investigation. Otherwise, our hypotheses of relationships are incompatible with his. Our analysis does not support a close relationship between *Pterospathodus* and *Gamachignathus* and, although *Pterospathodus* and *Icriodella* do sit together in a clade, our hypothesis of relationships between the genera is not compatible with Dzik's view that Pterospathodontidae and Icriodontidae should be grouped together (although we note that Dzik's Superfamily Icriodontacea is polyphyletic even under his scheme of relationships).

Dzik's Ozarkodinida

Like Dzik, we recognise Ozarkodinida as a major clade of complex conodonts in a sister group relationship with a clade of 'prioniodontid' taxa. Within Ozarkodinida Dzik recognised two suborders, Plectodinina and Ozarkodinina and although we also recognise two major clades within Ozarkodinida, they do not correspond to Dzik's suborders. Our Prioniodinina includes many of the taxa Dzik assigned to his Superfamily Hibbardellacea and our Ozarkodinina includes many of the taxa assigned by Dzik to his other three ozarkodinid superfamilies (Polygnathacea, Palmatolepidacea and Gondolellacea). There are significant differences, however.

Of the taxa Dzik assigned to Plectodinina, representatives of most families are included in our analysis. They do not form a clade. *Periodon*, *Microzarkodina* and *Plectodina* are members of our Ozarkodinida but fall outside the clade Prioniodinina + Ozarkodinina. This is comparable to Dzik's placement of these taxa as a paraphyletic grouping of basal ozarkodinids.

As noted above, relationships within our clade Prioniodinina remain too uncertain for us to make detailed comparisons with previous classifications and hypotheses of relationship. But some comment is possible. For example, Dzik implied that the common ancestor of Hibbardellidae and *Ozarkodina* lay within the '*Oulodus*-*Delotaxis* lineage', thus deriving both major clades of ozarkodinids from this lin-

age. Expressed cladistically, this would place *Oulodus* as the sister group to the clade Prioniodinina + Ozarkodinina (respectively incorporating taxa assigned by Dzik to his Hibbardellacea and Polygnathacea; see Fig. 3). All our analyses that include *Oulodus* place it within the prioniodinin clade, which provides no support for Dzik's hypothesis. Our results also clearly contradict Dzik's hypothesis that Bactrognathidae form a clade with *Idioprioniodus* plus other taxa we assign to Prioniodinina (compare to comments regarding Sweet's classification above).

The taxonomic composition of our Ozarkodinina compares closely with a combination of Dzik's Polygnathacea, Palmatolepidacea and Gondolellacea. The most basal member of this group, according to Dzik's view, is *Ozarkodina*. The results of our analysis, with the *O. excavata* + *Yaoxianognathus* clade as most basal, are not entirely inconsistent with this, although polyphyly of *Ozarkodina* rather undermines the general hypothesis.

Comparison with other classifications and hypotheses of relationship

An exhaustive investigation of how our hypotheses of relationship compare with all those that have been proposed for various groups within Conodonta is beyond the scope of this paper but, in addition to the major overviews by Sweet (1988) and Dzik (1991) we also consider here two other works, namely those of Stouge & Bagnoli (1999) and Murphy *et al.* (2004).

Stouge & Bagnoli (1999) presented a hypothesis of relationships and a suprageneric classification of 'some Ordovician prioniodontid conodonts'. This was based on their identification of two distinctive and persistent apparatus styles. Although our taxon sampling was not designed to test their hypothesis, our analysis and theirs do have a number of taxa in common. These genera were assigned by Stouge & Bagnoli to two superfamilies, Prioniodontoidea and Balognathoidea, within their Order Prioniodontida. Stouge & Bagnoli were uncertain of the precise relationship between these two groups, but they clearly considered each to be monophyletic. There are some similarities between their phylogeny and our hypothesis: their Balognathidae (within Balognathoidea), for example, accommodates several of the taxa included within our clade Balognathidae, with *Sagittodontina*, *Amorphognathus* and *Promissum* as close relatives. However, the details of branching order differ and further differences arise from their placement of *Oepikodus*, *Phragmodus*, *Prioniodus* and *Baltoniodus* in their monophyletic Prioniodontoidea (Oepikodontidae + Phragmodontidae + Prioniodontidae). This grouping is not supported by our results; some taxa (*Baltoniodus*, *Prioniodus*) lie among our Balognathidae, others (*Oepikodus*, *Phragmodus*) are successively more basal sister taxa. Our analysis, therefore, does not support their hypothesis of relationships or their superfamilial divisions of prioniodontid conodonts. Stouge & Bagnoli (1999) also agreed with Dzik (1991) that oistodontids belonged among ozarkodinids, not prioniodontids, a hypothesis that is not supported by our results.

Murphy *et al.* (2004) proposed a series of new genera for taxa previously accommodated within *Ozarkodina* on the basis that they represent independent clades of conodonts. While the focus of their work is taxonomic, it is based on explicit hypotheses of relationship. Our analysis supports their assertion that *Ozarkodina* is polyphyletic, but this is where

agreement ends; several of their hypotheses of relationship are contradicted by our results and we have doubts about others. For example, of the taxa included in our analysis, they suggest that *Ozarkodina excavata*, *Pterospathodus* and *Kockelella* are close relatives, all branching off their *Wurmiella* lineage; they also assigned *Ozarkodina hassi* to *Wurmiella*. Our analysis does not support this. Even though we cannot fully resolve the position of *Kockelella*, in none of our analyses does it form a clade with *O. excavata* to the exclusion of other species of *Ozarkodina* and neither does *O. hassi*, while *Pterospathodus* is consistently resolved as a balognathid. Our analyses that include both *O. excavata* and *Yaoxianognathus* consistently resolve them as a clade and the latter genus may thus be the most appropriate taxonomic home for *O. excavata* and some of the other species assigned by Murphy *et al.* (2004) to *Wurmiella*. However, resolution of the relationships and nomenclature of this group of taxa awaits a detailed phylogenetic analysis at species level.

Murphy *et al.* (2004) designated *Ozarkodina remscheidensis* as the type species of their new genus *Zieglerodina*. In our analyses, however, this species consistently forms a clade with *Nicollidina brevis*, the type species of *Nicollidina* Dzik (2002). If this grouping is to be recognised at the generic level, then *Nicollidina* clearly has priority. (Interestingly, Dzik also proposed that *Hindeodus* may belong to the same lineage; our analysis is not completely congruent with this hypothesis, but *Hindeodus* is consistently resolved as being the next most derived ozarkodinid after the *Nicollidina* clade). Murphy *et al.* (2004) also suggested that *Pandorinellina*, *Eognathodus* and *Polygnathus* form a clade (together with their New Genus *Wurmiella* representatives of which, such as *O. eosteinhornensis*, were not included in our dataset). This hypothesis also finds no support in our analysis.

CHARACTER DISTRIBUTIONS, HIGHER TAXA AND HOMOLOGY

Much of the preceding discussion has focussed on taxa and relationships; here we consider the implications of our analysis for hypotheses of character evolution in complex conodonts and the distribution of characters with respect to major clades. Our approach to classification involves recognising higher taxa based on the relationship between their constituents, not their characters *per se*, but whether major clades are united by the possession of distinctive morphological characters is obviously important in the context of the more general applicability of our classification. Consideration of characters also allows us to evaluate previous hypotheses of homology between and within major taxonomic groupings and the reliability of characters thought to have diagnostic value.

Ozarkodinida

Synapomorphies of Ozarkodinida include the possession of 'inner lateral' and 'outer lateral' processes on the S_1 element (characters 41 and 42; acquired independently within the Balognathidae). Within Ozarkodinida, these processes are secondarily lost only in the *Merrillina* + *Sweetina* clade (*Kladognathus* loses only the outer lateral process). This pattern of character distribution raises an important issue with respect to

the homology of processes in conodont elements: although, strictly speaking, the S_1 element of *Merrillina* and *Sweetina* has lost its 'lateral' processes and gained 'anterior' and 'posterior' processes, it is far more likely that the 'anterior' and 'posterior' processes of *Merrillina* and *Sweetina* are homologues of the lateral processes of all other Ozarkodinida. This homology is masked by the convention of using the plane of cusp curvature as the landmark for determining process disposition. Our analysis highlights this as a widespread problem (see also Wickström & Donoghue 2005); the description of conodont element morphology needs to mature beyond the phenetic level and explicitly consider homology. Much more could be written on this topic, but given the preliminary nature of our analysis, detailed discussion is beyond the scope of this contribution.

Makellate M elements (character 80) were acquired at the base of the Ozarkodinida and almost all members possess them, but they are absent from *Periodon* and *Microzarkodina*, two of the most basal members. This pattern can be interpreted, with equal parsimony, either as gain at the basal node of Ozarkodinida, followed by loss in the common ancestor of *Periodon* and all more derived taxa, followed by regain in the common ancestor of 'Plectodina' and all more derived ozarkodinids, or as gain at the basal node of Ozarkodinida, followed by independent losses in *Periodon* and *Microzarkodina*. The reliability of makellate M elements as a synapomorphy of the clade is thus equivocal. (Makellate M elements were convergently acquired in some balognathids.)

Although the distribution of $S_{1/2}$ elements that are shorter than the accompanying $S_{3/4}$ elements (character 86) can only be coded unequivocally in taxa known from natural assemblages and the condition in the most basal members of the clade is thus unknown, this may prove to be a good synapomorphy of Ozarkodinida. Current information indicates that it is unknown outside the clade and exhibits only one reversal.

Prioniodinina

The possession of an 'inner lateral' process on P_2 elements (character 24) is a unique synapomorphy that unites all Prioniodinina. The absence of a posterior process (character 23) is almost as reliable as a prioniodinin synapomorphy, but is secondarily gained in *Kladognathus* and is homoplastically lost in *Histiodellella* and *Periodon*. All other synapomorphies of this clade, or slightly less inclusive subclades, are also P element characters. The clade encompassing all Prioniodinina except *Aphelognathus*, for example, is united by the possession of digyrate P_2 elements with an angle of less than *ca.* 135° between proximal parts of processes (character 93), a unique synapomorphy, and in possessing peglike denticles on P_2 elements (character 21; secondarily lost in *Erraticodon*, *Oulodus*, *Erismodus* and *Chirognathus*). Members of the clade comprising all prioniodinins more derived than *Prioniodina* share a number of synapomorphies (characters 1, 4, 5, 6, 7, 25, 28, 92) that pertain to possession of digyrate P_1 and P_2 elements (characters 7, 28, 92; unique to this clade; very few reversals) and their process disposition (characters 1, 4, 5, 6, 25).

These results lend some support to Sweet's (1988) view that members of his Prioniodinida (approximately equivalent to our Prioniodinina) were characterised by having digyrate elements in one or both P positions and by possession

of peglike denticles. Regarding the latter character, which also equates to the 'robust denticulation' considered by Dzik (1991) to be diagnostic of his Hibbardellacea, 14 out of 16 prionidinins have peglike denticles on the P₁ element, 11 out of 16 on the P₂ and 12 out of 16 on the S elements. Thus, despite some homoplasy and secondary loss, the possession of peglike denticles does appear to be a characteristic feature of prionidinins. Among the other characters considered by Sweet to be characteristic, we now know that possession of sexi- and septimembrate apparatus is no longer meaningful because the architectural stability of the apparatus within Ozarkodinina reduces these terms to nothing more than a subjective assessment of the morphological thresholds between element morphotypes. Natural assemblages have also revealed that the tendency for all elements to be the same size is an artifact of *post mortem* breakage. We have not investigated characters of 'robustness' or 'stoutness' because of the difficulty in scoring them consistently. It is also worth noting that the characters that our analysis revealed to be characteristic of prionidinins are absent from those taxa that were included by Sweet in Prioniodinida, but which our analysis placed elsewhere.

Ozarkodinina

With very few exceptions, the taxa which comprise the Ozarkodinina are consistently resolved as a clade in all our analyses, yet unequivocal ozarkodinid synapomorphies are hard to find. P₁ elements with all processes in the same plane when viewed laterally (character 76), for example, are present in almost all ozarkodinins, but the condition in the common ancestor of the clade is unknown because the character is scored as absent in *Yaoxianognathus*, *Sweetina* and *Scaliognathus*. Furthermore it is homoplastically acquired four times outside the clade. Within Ozarkodinina, makellate M elements bearing two markedly downflexed processes (character 81) once acquired exhibit only a single reversal, but they are absent from the most basal members of the clade (*Ozarkodina excavata* + *Yaoxianognathus*) and are homoplastically acquired twice in prionidinins. Other characters, such as restriction of the basal cavity to the cusp in P₁ and S elements (characters 11 and 32) exhibit even more homoplasy and more reversal within the clade.

Dzik (1991) did not recognise a grouping of conodonts that equates to our ozarkodinins, but Sweet's (1988) Ozarkodinida is comparable. He considered that ozarkodinids were characterised by having carminate or angulate elements, or the equivalent platform morphologies, in P positions, which in our character set would correspond to the possession of an 'anterior' and 'posterior' process (characters 6 and 1) without 'lateral' processes. Our analysis broadly confirms this, in that most members of the clade have P₁ elements with this configuration of processes. However, several do not (e.g. *Scaliognathus*, *Neogondolella* and *Gondolella* lack the 'posterior' process; *Sweetina*, *Doliognathus*, *Staurognathus*, *Palmatolepis* and *Dinodus* have an additional 'outer lateral' process) and a number of taxa that lie outside Ozarkodinina also acquired this configuration of process through loss of the 'outer lateral' process (the common ancestor of Balognathidae and Ozarkodinida possessed P₁ elements with 'anterior', 'posterior' and 'outer lateral' processes). P₂ element process configuration follows a similar pattern. The common ancestor of *Oepikodus*, Balognathidae and Ozarkodinida possessed

'anterior', 'posterior' and 'outer lateral' processes and, although the subsequent history of process loss is not simple, the possession of only 'anterior' and 'posterior' processes is indeed a synapomorphy of Ozarkodinina.

Final reflections on homology

While our trees do not exhibit higher levels of homoplasy than would be anticipated given the sizes of the datasets from which they are derived, the existence of a number of homoplastic characters nevertheless indicates that many of the prior hypotheses of homology were unfounded, representing similarities that have arisen through convergence. A retrospective examination of these characters is a valuable tool for understanding why they might have evolved convergently and can inform their value for future cladistic analyses. This is particularly apt in consideration of conodont phylogeny because conodont skeletal anatomy and homology has rarely been considered beyond an aphylogenetic, phenetic level. We have briefly addressed the issue of process disposition and homology above and this problem is general to all conodont elements. As a final illustration of problems arising from aphylogenetic hypotheses of process homology we consider homology of the 'posterior' process of S₀ elements.

The presence or absence of the S₀ 'posterior' process has often been considered a character of high taxonomic value, distinguishing entire clades, such as the spathognathodontids, palmatolepids and polygnathaceans from their near relatives (Merrill *et al.* 1990; Dzik 1991; Zhang *et al.* 1997). Implicitly, this indicates that the S₀ 'posterior' process has evolved convergently, on a number of occasions, but our analysis suggests that some of these groups turn out to lack historical reality. Figure 13 presents the inferred evolution of the S₀ 'posterior' process, based on our preferred tree. This provides only a minimum estimate, because we have analysed only a small sample of species across conodont diversity, but it suggests that the S₀ 'posterior' process has evolved at least five times and may not be as useful a guide to relationships as has been thought.

ACKNOWLEDGEMENTS

For assistance in finding multi-element reconstructions, providing access to collections and/or discussion: Howard Armstrong (Durham), Gil Klapper (Iowa), Jeff Over (Geneseo), Charles Sandberg (Denver), Paul Smith (Birmingham), Walt Sweet (Ohio), Andrew Swift (Leicester). The Royal Society funded two visits by Shunxin Zhang to Leicester under the Sino-British Fellowship scheme (1993, 1995); this study was initiated during those visits. This research was supported by NERC (GT5/99/ES/2 to P.C.J.D., GT5/98/4/ES and NER/J/S/2002/00673 to M.A.P.). The comments of two referees and of the editor led to several improvements in the paper.

REFERENCES

- Albanesi, G. L., Hünicken, M. A. & Barnes, C. R. 1998. Bioestratigrafía, biofacies y taxonomía de conodontes de las secuencias Ordovícicas de Cerro Poterillo, Precordillera Central de San Juan, R. Argentina. *Academia Nacional de Ciencias* 12: 1–253.

- Aldridge, R. J. & Smith, M. P.** 1993. Conodonta. Pp. 563–572 in Benton, M. J. (eds) *The Fossil Record 2*. Chapman and Hall, London.
- , **Briggs, D. E. G., Clarkson, E. N. K. & Smith, M. P.** 1986. The affinities of conodonts – new evidence from the Carboniferous of Edinburgh, Scotland. *Lethaia* **19**: 279–291.
- , **Smith, M. P., Clarkson, E. N. K. & Clark, N. D. L.** 1993. The anatomy of conodonts. *Philosophical Transactions of the Royal Society of London, Series B* **340**: 405–421.
- , **Purnell, M. A., Gabbott, S. E. & Theron, J. N.** 1995. The apparatus architecture and function of *Promissum pulchrum* Kovács-Endrödy (Conodonta, Upper Ordovician), and the prioniodontid plan. *Philosophical Transactions of the Royal Society of London, Series B* **347**: 275–291.
- Armstrong, H. A.** 1997. Conodonts from the Ordovician Shinnel Formation, Southern Uplands, Scotland. *Palaeontology* **40**: 763–797.
- Barnes, C. R., Kennedy, D. J., McCracken, A. D., Nowlan, G. S. & Tarrant, G. A.** 1979. The structure and evolution of Ordovician conodont apparatuses. *Lethaia* **12**: 125–151.
- Barrick, J. E. & Klapper, G.** 1976. Multielement Silurian (late Llandoveryan – Wenlockian) conodonts of the Clarita Formation, Arbuckle Mountains, Oklahoma, and phylogeny of *Kockelella*. *Geologica et Palaeontologica* **10**: 59–100.
- Bassler, R. S.** 1925. Classification and stratigraphic use of conodonts. *Geological Society of America Bulletin* **36**: 218–220.
- Bauer, J. A.** 1987. Conodonts and conodont biostratigraphy of the McLish and Tulip Creek formations (Middle Ordovician) of south-central Oklahoma. *Oklahoma Geological Survey, Bulletin* **141**: 1–57.
- 1994. Conodonts from the Bromide Formation (Middle Ordovician), south-central Oklahoma. *Journal of Paleontology* **68**: 358–376.
- Bender, H. & Stoppel, D.** 1965. Perm-Conodonten. *Geologische Jahrbuch* **82**: 331–364.
- Bergström, S. M. & Sweet, W. C.** 1966. Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana. *Bulletins of American Paleontology* **50**: 271–441.
- Bischoff, G. C. O.** 1986. Early and Middle Silurian conodonts from mid-western New South Wales. *Courier Forschungsinstitut Senckenberg* **89**: 1–337.
- & **Argent, J. C.** 1990. Lower Devonian (late Lochkovian–Pragian) limestone stratigraphy and conodont distribution, Waratah Bay, Victoria. *Courier Forschungsinstitut Senckenberg* **118**: 441–471.
- & **Ziegler, W.** 1957. Die Conodontenchronologie des Mitteldevons und des tiefsten Oberdevons. *Abhandlungen hessisches Landesamt für Bodenforschung, Wiesbaden* **22**: 1–136.
- Branson, E. B. & Mehl, M. G.** 1933. Conodont studies. *University of Missouri Studies* **8**: 1–349.
- & — 1941. New and little known Carboniferous conodont genera. *Journal of Paleontology* **15**: 97–106.
- Briggs, D. E. G., Clarkson, E. N. K. & Aldridge, R. J.** 1983. The conodont animal. *Lethaia* **16**: 1–14.
- Carpenter, J. M.** 1988. Choosing between equally parsimonious cladograms. *Cladistics* **4**: 291–296.
- Chalimbadia, V. G. & Silantiev, V. V.** 1998. Conodonts from the Upper Permian type strata of European Russia. *Proceedings of the Royal Society of Victoria* **110**: 137–145.
- Chauff, K. M.** 1981. Multielement conodont species from the Osagean (Lower Carboniferous) in midcontinent North America and Texas. *Palaeontographica Abt. A* **175**: 140–169.
- Chauffe, K. M. & Nichols, P. A.** 1995. Multielement conodont species from the Louisiana Limestone (Upper Devonian) of west-central Illinois and northeastern Missouri, U. S. A. *Micropaleontology* **41**: 171–186.
- Clark, D. L., Sweet, W. C., Bergström, S. M., Klapper, G., Austin, R. L., Rhodes, F. H. T., Müller, K. J., Ziegler, W., Lindström, M., Miller, J. F. & Harris, A. G.** 1981. Pp. W1–W202 in Robison, R. A. (ed.) *Treatise on Invertebrate Paleontology. Part W Miscellaneous, Supplement 2, Conodonta*. Geological Society of America and University of Kansas Press, Lawrence.
- Cooper, B. J.** 1981. Early Ordovician conodonts from the Horn Valley Siltstone, Central Australia. *Palaeontology* **24**: 147–183.
- Darwin, C.** 1859. *On the origin of species*. John Murray, London.
- Dhanda, R.** 2004. The apparatus architecture of the prioniodinid conodont *Erimodus quadridactylus* and its implications. *Palaeontology Newsletter* **57**: 117–118.
- Donoghue, P. C. J.** 1998. Growth and patterning in the conodont skeleton. *Philosophical Transactions of the Royal Society of London, Series B* **353**: 633–666.
- 2001. Conodonts meet cladistics: recovering relationships and assessing the completeness of the conodont fossil record. *Palaeontology* **44**: 65–93.
- , **Forey, P. L. & Aldridge, R. J.** 2000. Conodont affinity and chordate phylogeny. *Biological Reviews* **75**: 191–251.
- Dzik, J.** 1976. Remarks on the evolution of Ordovician conodonts. *Acta Palaeontologica Polonica* **21**: 395–455.
- 1990. Conodont evolution in high latitudes of the Ordovician. *Courier Forschungsinstitut Senckenberg* **117**: 1–28.
- 1991. Evolution of oral apparatuses in the conodont chordates. *Acta Palaeontologica Polonica* **36**: 265–323.
- 1994. Conodonts of the Mójca Limestone. *Paleontologia Polonica* **53**: 43–128.
- 1997. Emergence and succession of Carboniferous conodont and ammonoid communities in the Polish part of the Variscan Sea. *Acta Palaeontologica Polonica* **42**: 57–170.
- 2000. The origin of the mineral skeleton in chordates. *Evolutionary Biology* **31**: 105–154.
- 2002. Emergence and collapse of the Frasnian conodont and ammonoid communities in the Holy Cross Mountains. *Acta Palaeontologica Polonica* **47**: 565–650.
- Eichenberg, W.** 1930. Conodonten aus dem Culm des Harzes. *Paläontologisches Zeitschrift* **12**: 177–182.
- Ethington, R. L. & Clark, D. L.** 1964. Conodonts from the El Paso Formation (Ordovician) of Texas and Arizona. *Journal of Paleontology* **38**: 685–705.
- & **Furnish, W. M.** 1959. Ordovician conodonts from northern Manitoba. *Journal of Paleontology* **33**: 540–546.
- Fähræus, L. E.** 1984. A critical look at the Treatise family-group classification of Conodonta: an exercise in eclecticism. *Lethaia* **17**: 293–305.
- Felsenstein, J.** 1978. The number of evolutionary trees. *Systematic Zoology* **27**: 27–33.
- Foot, M. & Sepkoski, J. J.** 1999. Absolute measures of the completeness of the fossil record. *Nature* **398**: 415–417.
- Forey, P. L. & Kitching, I. J.** 2000. Experiments in coding multistate characters. Pp. 54–80 in Scotland, R. W. & Pennington (eds) *Homology*. Taylor & Francis, London.
- Globensky, Y.** 1967. Middle and Upper Mississippian conodonts from the Windsor Group of the Atlantic Provinces of Canada. *Journal of Paleontology* **41**: 432–448.
- Goloboff, P. A.** 1993. Estimating character weights during tree search. *Cladistics* **9**: 83–91.
- 1999. *NONA (NO NAME)*, version 2. Programme and documentation. Published by the author, Tucumán, Argentina. Available at: <http://www.rladistics.com/abostNONA.htm>.
- Grayson, R. C. J., Merrill, G. K. & Lambert, L. L.** 1990. Carboniferous gnathodontid conodont apparatuses: evidence for the dual origin for Pennsylvanian taxa. *Courier Forschungsinstitut Senckenberg* **118**: 353–396.
- Hadding, A.** 1913. Undre Dicellograptusskiffern I Skane Jamte Nagre Darmet Ekvivalenta Bildninger. *Lunds Universitets Arsskrift, N. F.* **9**: 1–90.
- Harris, A. G., Repetski, J. E., Stamm, N. R. & Weary, D. J.** 1995. Conodont age and CAI data for New Jersey. *U.S. Geological Survey Open File Report* **95–557**: 1–31.
- Harris, R. W.** 1962. Subgenera of the conodont genus *Multioistodus* in Simpson-Burgen (Ordovician Arbuckle). *Oklahoma Geological Notes* **25**: 34–47.
- Harris, R. W. & Hollingsworth, R. V.** 1933. New Pennsylvanian conodonts from Oklahoma. *American Journal of Science* **25**: 193–204.
- Hass, W. H.** 1959. Conodonts from the Chappel Limestone of Texas. *U. S. Geological Survey Professional Paper* **294-J**: 365–399.

- , Häntzschel, W., Fisher, D. W., Howell, B. F., Rhodes, F. H. T., Müller, K. J. & Moore, R. C. 1962. Pp. W1–W259 in Moore, R. C. (ed.) *Treatise on Invertebrate Paleontology, Part W, Miscellanea*. Geological Society of America and the University of Kansas Press, Lawrence, 259 pp.
- Hawkins, J. A.** 2000. A survey of homology assessment: different botanists perceive and define characters in different ways. Pp. 22–53 in Scotland, R. & Pennington, R. T. (eds) *Homology and Systematics: Coding Characters for Phylogenetic Analysis*. Taylor and Francis, London.
- , **Hughes, C. E. & Scotland, R. W.** 1997. Primary homology assessment, characters and character states. *Cladistics* **13**: 275–283.
- Hinde, G. J.** 1879. On conodonts from the Chazy and Cincinnati Group of the Cambro–Silurian, and from the Hamilton and Genesee–Shale division of the Devonian, in Canada and the United States. *Quarterly Journal of the Geological Society, London* **35**: 351–369.
- Huckreide, R.** 1958. Die Conodonten der Mediterranean Trias und ihr stratigraphischer Wert. *Paläontologische Zeitschrift* **32**: 141–175.
- Igo, H., Koike, T. & Yin, E. H.** 1965. Triassic conodonts from the Kelantan, Malaya. *Mejiro Gakuen Women's Jr. College, Memoir* **2**: 5–20.
- Jeppsson, L.** 1969. Notes on some Upper Silurian multielement conodonts. *Geologiska Föreningens i Stockholm Förhandlingar* **91**: 12–24.
- 1971. Element arrangement in conodont apparatuses of *Hindeodella* type and in similar forms. *Lethaia* **4**: 101–123.
- 1974. Aspects of late Silurian conodonts. *Fossils and Strata* **6**: 1–54.
- Kitching, I. J., Forey, P. L., Humphries, C. J. & Williams, D. M.** 1998. *Cladistics: the Theory and Practice of Parsimony Analysis*. Oxford University Press, Oxford, 228 pp.
- Klapper, G. & Foster Jr., C. T.** 1993. Shape analysis of Frasnian species of the Late Devonian conodont genus *Palmatolepis*. *Paleontological Society Memoir* **32**: 1–35.
- & **Murphy, M. A.** 1974. Silurian–lower Devonian conodont sequence in the Roberts Mountains Formation of central Nevada. *University of California Publications in Geological Sciences* **111**: 1–62.
- & **Philip, G. M.** 1971. Devonian conodont apparatuses and their vicarious skeletal elements. *Lethaia* **4**: 429–452.
- & — 1972. Familial classification of reconstructed Devonian conodont apparatuses. *Geologica et Palaeontologica SB* **1**: 97–114.
- Klassen, G. J., Mooi, R. D. & Locke, A.** 1991. Consistency indices and random data. *Systematic Zoology* **40**: 446–457.
- Lange, F.-G.** 1968. Conodonten-Gruppenfunde aus Kalken des tieferen Oberdevon. *Geologica et Palaeontologica* **2**: 37–57.
- Lankester, E. R.** 1870. On the use of the term homology in modern zoology, and the distinction between homogenetic and homoplastic agreements. *Annals and Magazine of Natural History* **6**: 34–43.
- Lee, D. C. & Bryant, H. N.** 1999. A reconsideration of the coding of inapplicable characters: assumptions and problems. *Cladistics* **15**: 373–378.
- Leslie, S. A. & Bergström, S. M.** 1995. Element morphology and taxonomic relationships of the Ordovician conodonts *Phragmodus primus* Branson and Mehl, 1933, the type species of *Phragmodus* Branson and Mehl, 1933, and *Phragmodus undatus* Branson and Mehl, 1933. *Journal of Paleontology* **69**: 967–974.
- Lindström, M.** 1955. Conodonts from the lowermost Ordovician strata of south-central Sweden. *Geologiska Föreningens i Stockholm Förhandlingar* **76**: 517–604.
- 1970. A suprageneric taxonomy of the conodonts. *Lethaia* **3**: 427–445.
- 1971. Lower Ordovician conodonts of Europe. Pp. 21–61 in Sweet, W. C. & Bergström, S. M. (eds) *Symposium on Conodont Biostratigraphy*. Geological Society of America, Memoir 127. Geological Society of America, Boulder.
- Männik, P.** 1998. Evolution and taxonomy of the Silurian conodont *Pterospirifer*. *Paleontology* **41**: 1001–1050.
- McCracken, A. D. & Barnes, C. R.** 1981. Part 2: conodont biostratigraphy and paleoecology of the Ellis Bay Formation, Anticosti Island, Quebec, with special reference to late Ordovician–early Silurian chronostratigraphy and the systematic boundary. *Geological Survey of Canada, Bulletin* **329**: 50–134.
- , **Nowlan, G. S. & Barnes, C. R.** 1980. *Gamachignathus*, a new multielement conodont genus from the latest Ordovician, Anticosti Island, Québec. *Geological Survey of Canada Paper* **80–1C**: 103–112.
- McHargue, T. R.** 1982. Ontogeny, phylogeny, and apparatus reconstruction of the conodont genus *Histioidella*, Joins Fm., Arbuckle Mountains, Oklahoma. *Journal of Paleontology* **56**: 1410–1433.
- McTavish, R. A.** 1973. Prioniodontacean conodonts from the Emanuel Formation (Lower Ordovician) of Western Australia. *Geologica et Palaeontologica* **7**: 27–58.
- Merrill, G. K., von Bitter, P. H. & Grayson, R. C.** 1990. The generic concept in conodont palaeontology – growth, changes and developments in the last two decades. *Courier Forschungsinstitut Senckenberg* **118**: 397–408.
- Müller, K. J.** 1956. Triassic conodonts from Nevada. *Journal of Paleontology* **30**: 818–830.
- Murphy, M. A. & Matti, J. C.** 1982. Lower Devonian conodonts [*hesperius-kindlei* zones] central Nevada. *University of California Publications in Geological Sciences* **123**: 1–83.
- & **Valenzuela-Ríos, J. I.** 1999. *Lanea* new genus, lineage of Early Devonian conodonts. *Bollettino della Società Paleontologica Italiana* **37**: 321–334.
- , **Matti, J. C. & Walliser, O. H.** 1981. Biostratigraphy and evolution of the *Ozarkodina remscheidensis* – *Eognathodus sulcatus* lineage (Lower Devonian) in Germany and central Nevada. *Journal of Paleontology* **55**: 747–772.
- , **Valenzuela-Ríos, J. I. & Carls, P.** 2004. On classification of Pridoli (Silurian) – Lochkovian (Devonian) Spathognathodontidae (Conodonts). *University of California Riverside Campus Museum Contribution* **6**: 1–25.
- Nicoll, R. S.** 1977. Conodont apparatuses in an Upper Devonian palaeoniscoid fish from the Canning Basin, Western Australia. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics* **2**: 217–228.
- 1980. The multielement genus *Apatognathus* from the Late Devonian of the Canning Basin, Western Australia. *Alcheringa* **4**: 133–152.
- 1985. Multielement composition of the conodont species *Polygnathus xylus xylus* Stauffer, 1940 and *Ozarkodina brevis* (Bischoff and Ziegler, 1957) from the Upper Devonian of the Canning Basin, Western Australia. *Bureau of Mineral Resources Journal of Australian Geology and Geophysics* **9**: 133–147.
- 1990. The genus *Cordylodus* and a latest Cambrian–earliest Ordovician conodont biostratigraphy. *BMR Journal of Australian Geology and Geophysics* **11**: 529–558.
- 1995. Conodont element morphology, apparatus reconstructions and element function: a new interpretation of conodont biology with taxonomic implications. *Courier Forschungsinstitut Senckenberg* **182**: 247–262.
- Norby, R. D.** 1976. *Conodont apparatuses from Chesterian (Mississippian) strata of Montana and Illinois*. Unpublished PhD thesis: University of Illinois at Urbana-Champaign.
- & **Rexroad, C. B.** 1985. *Vogelgnathus*, a new Mississippian conodont genus. *Indiana Geological Survey, Occasional Paper* **50**: 1–14.
- Norris, A. W., Uyeno, T. T. & McCabe, H. R.** 1982. Devonian rocks of the Lake Winnipegosis–Lake Manitoba outcrop belt, Manitoba. *Geological Survey of Canada Memoir* **392**: 1–280.
- Nowlan, G. S. & Barnes, C. R.** 1981. Part 1: Late Ordovician conodonts from the Vaureal Formation, Anticosti Island, Quebec. *Geological Survey of Canada, Bulletin* **329**: 1–49.
- , **McCracken, A. D. & Chatterton, B. D. E.** 1988. Conodonts from Ordovician–Silurian boundary strata, Whittaker Formation, Mackenzie Mountains, Northwest Territories. *Geological Survey of Canada, Bulletin* **373**: 1–99.
- Orchard, M. J. & Rieber, H.** 1999. Multielement *Neogondolella* (Conodonts, upper Permian–middle Triassic). *Bollettino della Società Paleontologica Italiana* **37**: 475–488.
- Owen, R.** 1843. *Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals, Delivered at the Royal College of Surgeons, in 1843*. Longman, Brown, Green and Longmans, London.

- Panchen, A. L.** 1992. *Classification, Evolution and the Nature of Biology*. Cambridge University Press, Cambridge.
- Patterson, C.** 1982. Morphological characters and homology. Pp. 21–74 in Joysey, K. A. & Friday, A. E. (eds) *Problems of Phylogenetic Reconstruction*. Systematics Association Special Volume 21. Academic Press, London.
- Perlmutter, B.** 1975. Conodonts from the uppermost Wabausse Group (Pennsylvanian) and the Admire and Council Grove Groups (Permian) in Kansas. *Geologica et Palaeontologica* **9**: 95–115.
- Perri, M. C. & Andraghetti, M.** 1987. Permian–Triassic boundary and Early Triassic conodonts from the Southern Alps, Italy. *Rivista Italiana di Paleontologia e Stratigrafia* **93**: 291–328.
- Phillip, G. M.** 1965. Lower Devonian conodonts from the Tyers area, Gippsland, Victoria. *Proceedings of the Royal Society of Victoria* **79**: 95–117.
- Pimental, R. A. & Riggins, R.** 1987. The nature of cladistic data. *Cladistics* **3**: 275–289.
- Platnick, N. I., Griswold, C. E. & Coddington, J. A.** 1991a. On missing entries in cladistic analysis. *Cladistics* **7**: 337–343.
- , **Coddington, J. A., Forster, R. R. & Griswold, C. E.** 1991b. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). *American Museum Novitates* **3016**: 1–73.
- , **Humphries, C. J., Nelson, G. & Williams, D. M.** 1996. Is Farris Optimization perfect?: three-taxon statements and multiple branching. *Cladistics* **12**: 243–252.
- Pleijel, F.** 1995. On character coding for phylogeny reconstruction. *Cladistics* **11**: 309–315.
- Pollock, C. A., Rexroad, C. B. & Nicoll, R. S.** 1970. Lower Silurian conodonts from northern Michigan and Ontario. *Journal of Paleontology* **44**: 743–764.
- Purnell, M. A.** 1992. Conodonts of the Lower Border Group and equivalent strata (Lower Carboniferous) in northern Cumbria and the Scottish Borders. *Royal Ontario Museum, Life Sciences Contributions* **156**: 1–79.
- 1993. The *Kladognathus* apparatus (Conodonts, Carboniferous): homologies with ozarkodinids and the prioniodinid Bauplan. *Journal of Paleontology* **67**: 875–882.
- & **Donoghue, P. C. J.** 1998. Architecture and functional morphology of the skeletal apparatus of ozarkodinid conodonts. *Palaeontology* **41**: 57–102.
- & — 2005. Conodont biology and phylogeny – interpreting the fossil record. *Special Papers in Palaeontology* **73**: 1–218.
- & **von Bitter, P. H.** 1996. Bedding-plane assemblages of *Idioproniododus*, element locations, and the Bauplan of prioniodinid conodonts. Pp. 48 in Dzik, J. (ed.) *Sixth European Conodont Symposium (ECOS VI), abstracts*. Instytut Paleobiologii PAN, Warsaw.
- , **Donoghue, P. C. J. & Aldridge, R. J.** 2000. Orientation and anatomical notation in conodonts. *Journal of Paleontology* **74**: 113–122.
- Repetski, J. E., Purnell, M. A. & Barrett, S. F.** 1998. The apparatus architecture of *Phragmodus*. Pp. 91–92 in Bagnoli, G. (ed.) *Seventh International Conodont Symposium held in Europe (ECOS VII), Abstracts*. Tipografia Compositori, Bologna.
- Rexroad, C. B.** 1957. Conodonts from the Chester Series in the type area of southwestern Illinois. *Illinois State Geological Survey, Report of Investigations* **199**: 7–43.
- Rhodes, F. H. T.** 1953. Some British Lower Palaeozoic conodont faunas. *Philosophical Transactions of the Royal Society of London, Series B* **237**: 261–334.
- Rieppel, O.** 1988. *Fundamentals of comparative biology*. Birkhäuser, Basel.
- 1994. The role of paleontological data in testing homology by congruence. *Acta Palaeontologica Polonica* **38**: 295–302.
- Ritter, S. M. & Baesemann, J. F.** 1991. Early Permian conodont assemblages from the Wolfcamp Shale, Midland Basin, West Texas. *Journal of Paleontology* **65**: 670–677.
- Roundy, P. V.** 1926. Introduction, the microfauna in Mississippian formations of San Saba County, Texas by Roundy and others. *United States Geological Survey, Professional Paper* **146**: 1–63.
- Sanderson, M. J. & Donoghue, M. J.** 1989. Patterns of variation in levels of homoplasy. *Evolution* **43**: 1781–1795.
- Sansom, I. J., Armstrong, H. A. & Smith, M. P.** 1994. The apparatus architecture of *Panderodus* and its implications for coniform conodont classification. *Palaeontology* **37**: 781–799.
- Schmidt, H.** 1934. Conodonten-Funde in ursprünglichem Zusammenhang. *Paläontologische Zeitschrift* **16**: 76–85.
- Schülke, I.** 1997. Conodont clusters and multielement reconstructions from the Upper Kellwasser horizon at La Serre (Late Frasnian, Montagne Noire, Southern France). *Geologica et Palaeontologica* **31**: 37–66.
- 1999. Conodont multielement reconstructions from the early Fammenian (Late Devonian) of the Montagne Noire (Southern France). *Geologica et Palaeontologica* **SB 3**: 1–124.
- Scott, H. W.** 1934. The zoological relationships of the conodonts. *Journal of Paleontology* **8**: 448–455.
- Smith, M. P.** 1991. Early Ordovician conodonts of East North Greenland. *Meddelelser om Grønland, Geoscience* **26**: 1–81.
- Sorenson, M. D.** 1999. *TreeRot, version 2.0*. Programme and documentation. Boston University, Boston, MA.
- Sorentino, L.** 1989. Conodont assemblages spanning the Lochkovian–Pragian (Early Devonian) boundary at Eurimbla, central New South Wales. *Courier Forschungsinstitut Senckenberg* **117**: 81–115.
- Staesche, U.** 1964. Conodonten aus dem Skyth von Südtirol. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **119**: 247–306.
- Stauffer, C. R.** 1930. Conodonts from the Decorah Shale. *Journal of Paleontology* **4**: 121–128.
- 1935a. Conodonts of the Glenwood Beds. *Bulletin of the Geological Society of America* **46**: 125–168.
- 1935b. The conodont fauna of the Decorah Shale (Ordovician). *Journal of Paleontology* **9**: 596–620.
- 1938. Conodonts of the Olentangy Shale. *Journal of Paleontology* **12**: 411–443.
- 1940. Conodonts from the Devonian and associated clays of Minnesota. *Journal of Paleontology* **14**: 417–435.
- Stewart, I. & Nicoll, R. S.** 2003. Fifteen element septimembrate apparatus structure of the early Ordovician conodont *Oepikodus evae* Lindström from Australia and Sweden. *Courier Forschungsinstitut Senckenberg* **245**: 361–387.
- Stoll, N. R., Dollfus, R. P., Forest, J., Riley, N. D., Sabrosky, C. W., Wright, C. W. & Melville, R. V.** 1964. *International Code of Zoological Nomenclature*, 2nd edition. International Commission on Zoological Nomenclature, London.
- Stouge, S. & Bagnoli, G.** 1988. Early Ordovician conodonts from Cow Head Peninsula, western Newfoundland. *Palaeontographica Italica* **75**: 89–178.
- & — 1990. Lower Ordovician (Volkhovian–Kundan) conodonts from Hagudden, northern Öland, Sweden. *Palaeontographica Italica* **77**: 1–54.
- & — 1999. The suprageneric classification of some Ordovician prioniodontid conodonts. *Bollettino della Società Paleontologica Italiana* **37**: 145–158.
- Strong, E. E. & Lipscomb, D.** 1999. Character coding and inapplicable data. *Cladistics* **15**: 363–371.
- Sweet, W. C.** 1979a. Late Ordovician conodonts and biostratigraphy of the Western Midcontinent province. *Brigham Young University Geology Studies* **26**: 45–86.
- 1979b. Conodonts and conodont biostratigraphy of post-Tyrone Ordovician rocks of the Cincinnati region. *United States Geological Survey, Professional Paper* **1066-G**: 1–26.
- 1981. Macromorphology of elements and apparatuses. Pp. W5–W20 in Robison, R. A. (ed.) *Treatise on Invertebrate Paleontology, Part W, Miscellanea, Supplement 2, Conodonts*. Geological Society of America and the University of Kansas Press, Lawrence.
- 1982. Conodonts from the Winnipeg Formation (Middle Ordovician) of the northern Black Hills, South Dakota. *Journal of Paleontology* **56**: 1029–1049.
- 1988. *The Conodonts: Morphology, Taxonomy, Paleocology, and Evolutionary History of a Long-extinct Animal Phylum*. Clarendon Press, Oxford.
- & **Donoghue, P. C. J.** 2001. Conodonts: past, present and future. *Journal of Paleontology* **75**: 1174–1184.

- & Schönlaub, H. P. 1975. Conodonts of the genus *Oulodus* Branson & Mehl, 1933. *Geologica et Palaeontologica* 9: 41–59.
- , Thompson, T. L. & Satterfield, I. R. 1975. Conodont stratigraphy of the Cape Limestone (Maysvillian) of eastern Missouri. *Missouri Geological Survey, Report of Investigations* 57: 1–59.
- Swift, A. 1986. The conodont *Merrillina divergens* (Bender & Stoppel) from the Upper Permian of England. Pp. 55–62 in Harwood, G. M. & Smith, D. B. (eds) *The English Zechstein and Related Topics. Geological Society Special Publication No. 22*. The Geological Society of London, London.
- Swofford, D. L. 2002. *PAUP*: Phylogenetic Analysis Using Parsimony (and other methods)*, 4.0 beta 10, Programme and documentation. Sinauer, Sunderland, MA.
- Tatge, U. 1956. Conodonten aus dem germanischen Muschelkalk. *Paläontologische Zeitschrift* 30: 108–127.
- Theron, J. N. & Kovács-Endrödy, E. 1986. Preliminary note and description of the earliest known vascular plant, or an ancestor of vascular plants, in the flora of the Lower Silurian Cedarberg Formation, Table Mountain Group, South Africa. *South African Journal of Science* 82: 102–105.
- Thorley, J. L., Wilkinson, M. & Charleston, M. 1998. The information content of consensus trees. Pp. 91–98 in Rizzi, A., Vichi, M. & Bock, H.-H. (eds) *Advances in Data Science and Classification*. Springer, Berlin.
- Tolmacheva, T. Y. & Purnell, M. A. 2002. Apparatus composition, growth, and survivorship of the Lower Ordovician conodont *Paracordylodus gracilis* Lindström. *Palaeontology* 45: 209–228.
- Ulrich, E. O. & Bassler, R. S. 1926. A classification of the toothlike fossils, conodonts, with descriptions of American Devonian and Mississippian species. *Proceedings of the United States National Museum* 68: 1–63.
- Varker, W. J. 1994. Multielement conodont faunas from the proposed Mid-Carboniferous boundary stratotype locality at Stonehead Beck, Cowling, North Yorkshire, England. *Annales de la Société Géologique de Belgique* 116: 301–321.
- von Bitter, P. H. & Merrill, G. K. 1998. Apparatus composition and structure of the Pennsylvanian conodont genus *Gondolella* based on assemblages from the Desmoinesian of northwestern Illinois, U.S.A. *Journal of Paleontology* 72: 112–132.
- Walliser, O. H. 1964. Conodonten des Silurs. *Abhandlungen hessisches Landesamt für Bodenforschung, Wiesbaden* 41: 1–106.
- Wardlaw, B. R. & Collinson, J. W. 1986. Paleontology and deposition of the Phosphoria Formation. *Contributions to Geology, University of Wyoming* 24: 107–142.
- Webers, G. F. 1966. The Middle and Upper Ordovician conodont faunas of Minnesota. *Minnesota Geological Survey, Special Publication Series SP-4*: 1–123.
- Wickström, L. M. & Donoghue, P. C. J. 2005. Cladograms, phylogenies and the veracity of the conodont fossil record. *Special Papers in Palaeontology* 73: 185–218.
- Wiley, E. O. 1979. An annotated Linnean hierarchy, with comments on natural taxa and competing systems. *Systematic Zoology* 28: 308–337.
- Wilkinson, M., Thorley, J. L. & Upchurch, P. 2000. A chain is no stronger than its weakest link: double decay analysis of phylogenetic hypotheses. *Systematic Biology* 49: 754–776.
- Wilson, G. A. 1989. Documentation of conodont assemblages across the Lochkovian–Pragian (Early Devonian) boundary at Wellington, Central New South Wales, Australia. *Courier Forschungsinstitut Senckenberg* 117: 117–171.
- Youngquist, W. L. 1945. Upper Devonian conodonts from the Independence Shale (?) of Iowa. *Journal of Paleontology* 19: 355–367.
- & Miller, A. K. 1949. Conodonts from the late Mississippian Pella Beds of south-central Iowa. *Journal of Paleontology* 23: 617–622.
- Zhang, S. & Barnes, C. R. 2004. The post-mass extinction bioevents, cladistics and response to glacio-eustasy of conodonts across and after the Ordovician–Silurian boundary, Anticosti Basin, Québec. Pp. 73–104 in Beaudoin, A. (ed.) *The Micropalaeontology of Boundaries*. The Geological Society, London.
- & Yang, Z.-Y. 1991. On multielement taxonomy of Early Triassic conodonts. *Stratigraphy and Paleontology of China* 1: 17–47.
- , Aldridge, R. J. & Donoghue, P. C. J. 1997. An Early Triassic conodont with periodic growth? *Journal of Micropalaeontology* 16: 65–72.
- Zhen, Y.-Y., Webby, B. D. & Barnes, C. R. 1999. Upper Ordovician conodonts from New South Wales, Australia. *Geobios* 32: 73–104.
- Ziegler, W. 1960. Conodonten aus dem Rheinischen Unterdevon (Gedinnium) des Remscheider Sattels (Rheinisches Schiefergebirge). *Paläontologische Zeitschrift* 34: 169–201.
- 1981. *Catalogue of Conodonts*, volume IV. E. Schweizerbart, Stuttgart.

APPENDIX 1: CONVERSION OF SWEET AND DZIK PHYLOGENIES TO TREES

Conversion of Sweet's phylogeny

Although it may read a little like Matthew: 1 (*Oulodus* begat *Erika* etc) it is difficult to compare Sweet's hypothesis with ours and to follow Fig. 2 without more explicit explanation of how we derived a tree from Sweet's hypotheses of relationship. For the Prioniodinida, Sweet identified *Erraticodon* as the most basal member, with *Chirognathus* and *Erismodus* both being derived therefrom. The common ancestor of the latter taxa is, thereby, a species of *Erraticodon*, allowing us to resolve the relationship as shown in Fig. 2. *Oulodus* was derived from *Erismodus* and itself gave rise to *Erika*, followed by *Prioniodina* and *Hibbardella* (following our approach, the nodes subtending these 3 genera are thus considered to fall within the generic concept of *Oulodus*, allowing us to reconstruct the relative branching order, with all 3 genera arising from unspecified species of *Oulodus*). *Apatognathus* was derived from *Prioniodina* and these genera are reconstructed as sister taxa. Sweet provided no information concerning relationships between members of Bactrognathidae, so *Doliognathus*, *Staurogathus* and *Scaliognathus* are shown in an unresolved polytomy. Bactrognathidae and *Idioproniodus* shared a common ancestor among what Sweet identified as various pre-Chesterian species of the Prioniodinidae, with Bactrognathidae branching-off first. *Kladognathus* is also shown (Sweet 1988: fig. 5.28) as arising from within the same part of prioniodinid phylogeny. *Idioproniodus* includes the common ancestor of Gondolellidae (*Gondolella* and *Neogondolella*) and *Ellisonia*, the latter including the common ancestor of *Merrillina* + *Sweetina* and *Furnishius* + *Pachycladina* + *Hadrodontina*. Sweet's phylogeny (1988: fig. 5.28) suggests that the latter two taxa are more closely related to each other than either is to *Furnishius*.

Relationships among taxa Sweet assigned to Prioniodontida and Ozarkodinida are less straightforward. *Periodon* and *Microzarkodina* 'represent branches of the same stock' (Sweet 1988: 76) with roots among early oistodontids, making them the most basal of the prioniodontid taxa included in our analysis (Sweet did not consider *Paracordylodus*). *Prioniodus*, *Phragmodus* and *Plectodina* are 'heterochronous derivatives of *Tripodus*' (p. 75) from which Sweet also derived *Histiodella* (either directly (p. 62) or indirectly (fig. 5.11)) and *Baltoniodus*. *Baltoniodus* includes the ancestor(s) of *Amorphognathus*, *Gamachignathus* and (probably) *Icriodella*. *Amorphognathus* subsequently gave rise to *Sagittodontina*. Of the taxa that share *Tripodus* as a common ancestor, Sweet indicates that *Prioniodus* branched off first (and subsequently 'spawned' *Oepikodus*), followed by *Baltoniodus* and then the lineage leading to *Histiodella*. *Phragmodus* and *Plectodina* arose later. *Tripodus* is thus shown on Fig. 2 as ranging through the nodes representing the common

ancestors of these taxa. *Plectodina* gave rise to ‘*Plectodina*’, a basal member of Sweet’s Ozarkodinida; Sweet also considered that certain species of *Aphelognathus* (including *A. kimmswickensis*, the species used in our analyses) were more closely related to *Plectodina* than to *Aphelognathus sensu stricto* (which he placed among Ozarkodinida).

Being derived from *Plectodina* (within Prioniodontida), Sweet’s ‘*Plectodina*’ must be reconstructed as the most basal member of his Ozarkodinida. He also identified *Yaoxianognathus* as one of the earliest members of this clade, but did not provide any further details of its origins. We show it in a polytomy with ‘*Plectodina*’. *Ozarkodina hassi* is, according to Sweet, among the youngest species of ‘*Plectodina*’ and is thus resolved as sister to ‘*Plectodina*’ in Fig. 2. All more derived members of the clade have their ultimate origin in species that Sweet assigned to *Ozarkodina*. *Kockelella* branched off first, followed by *Pterospathodus*. *Pandorinellina* separated from contemporary populations of *Ozarkodina* in the earliest Devonian (Sweet 1988: 95) and subsequently gave rise to *Clydagnathus*. *Mehlina*, which may have arisen either from *Pandorinellina* or *Ozarkodina* (we follow the latter) gave rise to *Dinodus* (indirectly) and *Bispathodus*. *Bispathodus*, in turn, gave rise to *Gnathodus* and, indirectly, *Sweetognathus* (according to Sweet 1988: 96: ‘*Bispathodus*, the ancestor of Gnathodontidae and Sweetognathidae’). Sweet (1988: 111) acknowledged that there is some uncertainty surrounding the relationships of *Vogelgnathus* and *Lochriea* to other conodonts but ultimately considered that derivation from *Bispathodus* was a possibility for both, while at the same time implying that *Vogelgnathus* is more closely related to *Lochriea* than to anything else. Figure 2 is compatible with either of these hypotheses. For the palmatolepids (*Mesotaxis* + *Palmatolepis*), after discussing various scenarios, Sweet indicates a preference for origin from within Spathognathodontidae and connects them, with some uncertainty, to *Ozarkodina* (Sweet 1988: fig. 5.36). The same is true of the later *Hindeodus*. Indirectly, Sweet (1988: 95) implicates *Ozarkodina remscheidensis* as an ancestor to *Eognathodus* and *Polygnathus*, leading us to resolve their relationship as shown in Fig. 2.

Conversion of Dzik’s phylogeny

Dzik assigned *Paracordylodus* to Cordylodontidae, albeit with some reservation. This family sits outside the major clades of complex conodonts under investigation here and this assignment is thus consistent with our selection of *Paracordylodus* as the outgroup. *Phragmodus* is considered to have arisen from a balognathid (Dzik 1991: 290) and, by implication, this makes *Phragmodus* the most basal member of the Prioniodontidae (assuming a single origin for the family). It also means that Prioniodontidae and Balognathidae must be sister taxa with Prioniodontidae sitting in a relatively more derived position (*contra* Dzik 1991: fig. 18). Pterospathodontidae also appear to have arisen from within Balognathidae (Dzik 1991: fig. 18), even though Dzik considered *Pterospathodus* not to be directly related to *Amorphognathus* (p. 291). We have reconstructed Pterospathodontidae as sister taxon to Balognathidae (Fig. 3), with the latter taxon extended to include the common ancestor of all Dzik’s Prioniodontida. Dzik suggested that *Icriodella* (and Icriodontidae) may have evolved from *Baltoniodus* and this is how we show it.

Dzik (1991: 294) identified *Periodon* as the earliest undoubted ozarkodinid, with *Histiodella* as a potential ancestor.

Microzarkodina is ‘probably the ancestor of all remaining Ozarkodinida’. Along with *Microzarkodina*, *Aphelognathus* and *Yaoxianognathus* are accommodated within Plectodinidae, but other than indicating that they are more derived than *Microzarkodina* (the probable ancestor) Dzik did not discuss their relationships and they are shown in Fig. 3 in an unresolved polytomy with more derived conodonts. *Plectodina* and *Oulodus* are also members of Plectodinidae and, although *Oulodus* was interpreted as a ‘derivative of the *Plectodina* branch’ (Dzik 1991: 295), Dzik also noted in the same sentence that the apparatus of *Erraticodon* (a member of Chirognathidae, with *Erismodus* and *Chirognathus*,) ‘is not unlike that of *Plectodina*, being even more similar to *Oulodus*’. Relationships between *Plectodina*, *Oulodus* and Chirognathidae are thus shown here as unresolved except that *Oulodus* is taken to be the ancestor of Hibbardellidae. This last point is based on Dzik’s proposal (p. 296) that a change in M element morphology within the *Oulodus* lineage represents ‘a convenient point of demarcation of the lower boundary of the Hibbardellidae’. Relationships of taxa with this family were not discussed, nor were those of taxa within Bactrognathidae. The origins of Bactrognathidae are from within Hibbardellidae (Dzik 1991: fig. 18) and the evidence cited for this, possible reconstructions of bactrognathids which include *Idioproniodus*-like S elements, implies either that bactrognathids were descendants of *Idioproniodus*, or that they shared a recent common ancestor.

Ozarkodina developed from *Delotaxis*, part of the *Oulodus*–*Delotaxis* lineage (Dzik, 1991: 298) and is thus the most basal member of Dzik’s Polygnathacea. *Kockelella* and *Pandorinellina* both evolved from *Ozarkodina* (p. 300), but beyond this most of the relationships within Spathognathodontidae and Polygnathidae were not discussed and they are reconstructed here as unresolved polytomies. *Pandorinellina* is an exception in that, having evolved from *Ozarkodina*, it must be the most basal member of Polygnathidae. Cavusgnathidae and Idiognathodontidae were derived from somewhere within Polygnathidae (Dzik 1991: fig. 18); owing to the lack of details of the relationship they are reconstructed in a polytomous relationship with Polygnathidae. Dzik noted (p. 302) that only details of the S₀ element distinguish Gnathodontidae from Idiognathodontidae and, in the absence of further discussion, we take this to imply a close relationship. *Sweetognathus* and *Vogelgnathus* are together accommodated in Sweetognathidae and they are thus reconstructed as sister taxa; Dzik’s discussion (1991: 301–302) suggests that he considered *Sweetognathus* to be a derivative of *Gnathodus*. Finally, the ancestry of palmatolepids (Palmatolepididae and Mesotaxidae) lies somewhere among Spathognathodontidae, with *Mesotaxis* as the oldest member of the group (Dzik, 1991: 305). Gondolellidae (*Gondolella* and *Neogondolella* in our analysis) are related to this group in that *Pinacognathus* (questionably included among Mesotaxidae by Dzik; not included in our analysis) may be ‘close to the common ancestor of *Dinodus* and *Gondolella*’ (Dzik 1991: 304).

APPENDIX 2: POSITIONAL HOMOLOGY ASSIGNMENTS

Amorphognathus ordovicicus Branson & Mehl, 1933, following the reconstruction of Nowlan & Barnes (1981): P₁ = platform, P₂ = ambalodiform, S₀ = trichonodeliform, S₁ = cladognathiform, S₂ = tetraprioniodiform,

- $S_3 =$ cladognathiform, $S_4 =$ eoligonodiniform, $M =$ holodontiform) and Dzik (1994: $P_1 =$ sp, $P_2 =$ oz, $S_0 =$ tr, $S_1 =$ pl, $S_2 =$ ke, $S_3 =$ pl, $S_4 =$ hi, $M =$ ne).
- Apatognathus varians varians* Branson & Mehl, 1933, following the reconstruction of Nicoll (1980: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ M, $S_{3/4} =$ Sc, $M =$ Sb. We find the position of Nicoll's Sd is uncertain and interpret it as another Sb element morphotype).
- Aphelognathus kimmswickensis* Sweet *et al.*, 1975, following the reconstruction of Sweet (1988: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb, $S_{3/4} =$ Sc, $M =$ M).
- Baltoniodus clavatus* Stouge & Bagnoli, 1990, following their original reconstruction: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb, $S_2 =$ Sd, $S_{3/4} =$ Sc, $M =$ M.
- Bispathodus aculeatus* (Branson & Mehl, 1933), following a natural assemblage of elements figured by Purnell & Donoghue (1998: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb₁, $S_2 =$ Sb₂, $S_3 =$ Sc₁, $S_4 =$ Sc₂, $M =$ M).
- Chirognathus duodactylus* Branson & Mehl, 1933, following the reconstruction of Sweet (1982: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb, $S_2 =$ Sb, $S_{3/4} =$ Sc, $M =$ M).
- Clydagnathus windsorensis* (Globensky, 1967), following the assemblage of elements associated with soft tissue remains from the Lower Carboniferous Granton Shrimp Bed (Briggs *et al.* 1983; Aldridge *et al.* 1986, 1993); element morphologies taken from Purnell (1992: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_2 =$ Sb, $S_{3/4} =$ Sc, $M =$ M) and unpublished collections from the Granton Shrimp Bed.
- Dinodus lobatus* (Branson & Mehl, 1933), following the reconstruction of Dzik (1997: $P_1 =$ sp, $P_2 =$ oz, $S_0 =$ tr, $S_2 =$ pl, $S_{3/4} =$ hi, $M =$ ne (fig. 20D)).
- Doliognathus latus* Branson & Mehl, 1941, following the reconstruction of Chauff (1981: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb₁, $S_2 =$ Sb₂, $S_{3/4} =$ Sc, $M =$ M).
- Ellisonia triassica* Müller, 1956, following the reconstruction of Perri & Andraghetti (1987) with the following element positional reassignments: $P_1 =$ Pa, $P_2 =$ M, $S_1 =$ Sb, $S_{3/4} =$ Sc; following the reconstruction of Sweet (1988) with the following element reassignments: $P_1 =$ Pb, $P_2 =$ M, $S_0 =$ Sa, $S_1 =$ Sb, $S_2 =$ Pa, $S_{3-4} =$ Sc.
- Eognathodus sulcatus* Philip, 1965, following reconstructions by Klapper & Philip (1971: $P_1 =$ P, $P_2 =$ O₁, $S_0 =$ A₃, $S_1 =$ A₂ (Philip 1965: pl. 9, figs 11–12), $S_2 =$ A₂ (Philip 1965: pl. 9, figs 23–24), $S_{3/4} =$ A₁, $M =$ N), Murphy *et al.* (1981: $P_1 =$ P, $P_2 =$ O₁, $S_0 =$ A₃, $S_1 =$ A₂ (pl. 3, fig. 27), $S_2 =$?, $S_{3/4} =$ A₁, $M =$ N) and Bischoff & Argent (1990: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb (pl. 3, fig. 17), $S_2 =$ Sb (pl. 3, fig. 18), $S_{3/4} =$?, $M =$?).
- Erika divarica* Murphy & Matti, 1982, following the reconstruction of Murphy & Matti (1982) with the following (somewhat equivocal) element positional reassignments: $P_1 =$ Pa, $P_2 =$?Sb/Pb, $S_0 =$ Sa, $S_{1/2} =$ Sb, $S_{3/4} =$ Sc, $M =$?Pb/M.
- Erismodus arbucklensis* Bauer, 1987, following the reconstruction of Bauer (1987): $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sba, $S_2 =$ Sbb, $S_{3/4} =$ Sc, $M =$ M.
- Erraticodon patu* Cooper, 1981, following the reconstruction of Nicoll (1995): $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sd, $S_2 =$ Sb, $S_{3/4} =$ Sc, $M =$ M. Supplementary information provided by Sweet (1988).
- Furnishius triserratus* (Igo *et al.*, 1965), following the reconstruction of Sweet (*in* Clark *et al.* 1981); $P_1 =$ Pa (fig. 2f), $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb, $S_2 =$ Pa (fig. 2e), $S_{3/4} =$ Sc, $M =$?.
- Gamachignathus ensifer* McCracken *et al.*, 1980, following the original description: $P_1 =$ f, $P_2 =$ g, $P_3 =$?, $P_4 =$?, $S_0 =$ c, $S_1 =$ b, $S_2 =$ b, $S_3 =$ a₂, $S_4 =$ a₁, $M =$ e₁.
- Gnathodus bilineatus* (Roundy, 1926), following interpretations of natural assemblages published by Purnell & Donoghue (1998: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb₁, $S_2 =$ Sb₂, $S_3 =$ Sc₁, $S_4 =$ Sc₂, $M =$ M) with additional data on element morphologies from Grayson *et al.* (1990: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sd, $S_2 =$ Sb, $S_3/S_4 =$ Sc, $M =$ M).
- Gondolella pohli* von Bitter & Merrill, 1998, following the original reconstruction: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb₁, $S_2 =$ Sb₂, $S_3, S_4 =$ Sc, $M =$ M.
- Hadrodontina anceps* Staesche, 1964, following the reconstruction of Sweet (*in* Clark *et al.* 1981) and Perri & Andraghetti (1987): $P_1 =$ Pa+Sa, $P_2 =$ M, $S_0 =$?, $S_1 =$ Sb, $S_2 =$ Pb, $S_{3/4} =$ Sc, $M =$?.
- Hibbardella angulata* (Hinde, 1879), following the natural assemblage figured and described by Nicoll (1977: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb, $S_2 =$ M, $S_{3/4} =$ Sc, $M =$ N) and interpreted by Purnell (1993).
- Hindeodus cristulus* (Youngquist & Miller, 1949), following the reconstruction of Norby (1976: $P_1 =$ P, $P_2 =$ O, $S_0 =$ A₃ (pl. 16, fig. 5), $S_1 =$ A₃ (pl. 16, fig. 4), $S_2 =$ A₂, $S_{3/4} =$ A₁, $M =$ N).
- Histiodela altifrons* Harris, 1962, following the reconstruction of McHargue (1982: $P_1 =$ bryantodontiform, $P_2 =$ short bryantodontiform, $S_0 =$ trichonodelliform, $S_1 =$ zygognathiform, $S_2 =$ zygognathiform, $S_{3/4} =$ twisted bryantodontiform, $M =$ oistodontiform) supplemented by unpublished collections.
- Icriodella superba* Rhodes, 1953, following the reconstructions of Bergström & Sweet (1966: $P_1 =$ *Icriodella superba*, $P_2 =$ *Sagittodontus dentatus*, $S_0 =$ *Rhynchognathodus divaricatus*, $S_1 =$ *Rhynchognathodus typicus*, $S_2 =$?, $S_3 =$ *Rhynchognathodus typicus*, $S_4 =$?, $M =$ *Sagittodontus robustus*), Harris *et al.* (1995: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_{1/2/3/4} =$?, $M =$?) and Sweet *et al.* (1975: $P_1 =$ icriodelliform, $P_2 =$ sagittodontiform (pl. 3, fig. 4), $S_0 =$ trichonodelliform, $S_1 =$?, $S_2 =$?, $S_3 =$?, $S_4 =$?, $M =$ sagittodontiform (pl. 3, fig. 4)).
- Idiognathodus*, following natural assemblages published by Purnell & Donoghue (1998: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$ Sb₁, $S_2 =$ Sb₂, $S_3 =$ Sc₁, $S_4 =$ Sc₂, $M =$ M) with additional data on element morphologies from Grayson *et al.* (1990: $P_1 =$ Pa, $P_2 =$ Pb, $S_0 =$ Sa, $S_1 =$?, $S_2 =$ Sb, $S_{3/4} =$ Sc, $M =$ M).
- Idioprioniodus*, following the reconstruction of Purnell & von Bitter (1996); element morphologies based in part upon Chauffe & Nichols (1995: $P_1 =$ Pa (pl. 1, figs 1, 2, 4, 11, 13, 14), $P_2 =$ Sb₁, $S_0 =$ Sa, $S_1 =$ Sb₂, $S_2 =$ Pa (pl. 1, fig. 3), $S_{3/4} =$ Sc, $M =$ M), as well as collections on which

- the multi-element reconstruction of *Bactrognathus* by Chauff (1981) was based.
- Kladognathus* sp., following the reconstruction of Purnell (1993: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sb$, $S_2 = Sb$, $S_3 = Sc$, $S_4 = Sc$, $M = M$).
- Kockelella ranuliformis* (Walliser, 1964), using the reconstructions of Barrick & Klapper (1976: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = ?$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$) and Bischoff (1986: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sb$ (pl. 14, figs 23, 25), $S_2 = Sb$ (pl. 14, fig. 24), $S_{3/4} = Sc$, $M = M$), supplemented by unpublished collections.
- Lochria commutata* (Branson & Mehl, 1941) following the natural assemblages figured in Purnell & Donoghue (1998: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sb_1$, $S_2 = Sb_2$, $S_3 = Sc_1$, $S_4 = Sc_2$, $M = M$) supplemented by data on element morphologies in Varker (1994: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = ?$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$).
- Mehlina gradata* Youngquist, 1945, following the reconstruction of Uyeno (*in* Norris *et al.* 1982: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = A_{1-2}$, $S_2 = A_2$, $S_{3/4} = Sc$, $M = N$).
- Merrillina divergens* (Bender & Stoppel, 1965), following the reconstruction of Swift (1986: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = ?$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$). S_1 based on unpublished collections.
- Mesotaxis asymmetrica asymmetrica* (Bischoff & Ziegler, 1957) following the reconstruction and element morphologies in Klapper & Philip (1971: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = ?$, $S_2 = A_2$, $S_{3/4} = A_1$, $M = N$; (1972: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = A_2$ (pl. 2, fig. 16), $S_2 = A_2$ (pl. 2, fig. 15), $S_{3/4} = A_1$, $M = N$).
- Microzarkodina parva* Lindström, 1971, following the reconstruction by Stouge & Bagnoli (1990: $P_1 = P$, $P_2 = ?$, $S_0 = Sa$, $S_1 = Sd$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$).
- Neogondolella mombergensis* (Tatge, 1956) following the reconstruction of Orchard & Rieber (1999: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sb_1$, $S_2 = Sb_2$, $S_3 = Sc_1$, $S_4 = Sc_2$, $M = M$).
- Nicollidina brevis* (Bischoff & Ziegler, 1957), following the natural assemblages of Nicoll (1985: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sd$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$) supplemented by the reconstruction of Uyeno (*in* Norris *et al.* 1982: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = A_2$, $S_2 = A_{1-2}$, $S_{3/4} = A_1$, $M = N$). Dzik (2002) erected *Nicollidina* to accommodate the taxon widely reported as *Ozarkodina brevis*.
- Oepikodus communis* (Ethington & Clark, 1964), following the natural assemblage of Smith (1991: $P_1 = P$ (fig. 24a), $P_2 = P$ (fig. 24b), $S_0 = Sa$, $S_1 = ?$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$) supplemented by Albanesi *et al.* (1998: $P_1 = ?$, $P_2 = Pb$, $S_0 = ?$, $S_1 = Sd$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$).
- Oulodus rohneri* Ethington & Furnish, 1959, following the reconstructions of Nowlan & Barnes (1981) and McCracken & Barnes (1981) ($P_1 = prioniodiniform$, $P_2 = oulodiform$, $S_0 = trichonodelliform$, $S_{1/2} = zygognathiform$, $S_{3/4} = eoligonodiniform$, $M = cyrtoniodontiform$; cordylodiform of McCracken & Barnes = $S_{3/4}$).
- Ozarkodina confluens* (Branson & Mehl, 1933), following the reconstructions of Klapper & Murphy (1974: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = A_2$ (pl. 4, figs 4–5), $S_2 = A_2$ (pl. 4, fig. 1), $S_{3/4} = A_1$, $M = N$) and Jeppsson (1974: $P_1 = sp$, $P_2 = oz$, $S_0 = tr$, $S_1 = pl$, $S_2 = ?$, $S_{3/4} = hi$, $M = ne$) and supplemented by unpublished collections. We retain the species name *confluens* for this taxon as it is the name that has been used by most workers; however, we note the case made by Murphy *et al.* (2004) for use of the name *typica* and recognise that this will have to be considered.
- Ozarkodina excavata* (Branson & Mehl, 1933), following the reconstruction of Klapper & Murphy (1974: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = A_2$ (pl. 6, figs 2, 4), $S_2 = A_2$ (pl. 6, fig. 1), $S_{3/4} = A_1$, $M = N$).
- Ozarkodina hassi* (Pollock *et al.*, 1970), following the reconstructions of McCracken & Barnes (1981: $P_1 = spathognathodontiform$, $P_2 = ozarkodiniform$, $S_0 = trichonodelliform$, $S_1 = zygognathiform$, $S_2 = ?$, $S_{3/4} = ligonodiniform$, $M = synprioniodiniform$) and Nowlan *et al.* (1988: $P_1 = g$, $P_2 = f$, $S_0 = c$, $S_1 = b$, $S_2 = ?$, $S_{3/4} = a$, $M = e$).
- Ozarkodina remscheidensis* (Ziegler, 1960), following reconstructions by Klapper & Murphy (1974: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = ?$, $S_2 = A_2$, $S_{3/4} = A_1$, $M = N$), Sorentino (1989: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = ?$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$), Wilson (1989: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = ?$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$) and Bischoff & Argent (1990: $P_1 = Pa$, $P_2 = Pb$, $S_0 = ?$, $S_1 = Sb$ (pl. 4, figs 3, 7), $S_2 = Sb$ (pl. 4, fig. 5), $S_{3/4} = ?$, $M = M$).
- Pachycladina obliqua* Staesche, 1964, following the reconstruction of Perri & Andraghetti (1987: $P_1 = Pa$, $P_2 = M$, $S_0 = Sa$, $S_1 = Sb$, $S_2 = Pb$, $S_{3/4} = Sc$, $M = ?$).
- Palmatolepis bogartensis* (Stauffer, 1938), following the natural assemblage figured by Lange (1968: $P_1 = Palmatolepis triangularis$, $P_2 = Ozarkodina regularis$, $S_0 = Scutula sinepennata$, $S_1 = Scutula venusta$, $S_2 = ?Falcodus variabilis$, $S_3 = Prioniodina smithi$, $S_4 = Prioniodina smithi$, $M = Prioniodina$ cf. *prona*) and the reconstructions of Klapper & Foster (1993: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sd$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$) and Schülke (1997, 1999: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sd$, $S_2 = Sb$, $S_{3/4} = Sc$, $M = M$).
- Pandorinellina insita* (Stauffer, 1940), following the reconstruction of Uyeno (*in* Norris *et al.* 1982: $P_1 = P$, $P_2 = O_1$, $S_0 = A_3$, $S_1 = A_{1-2}$, $S_2 = A_2$, $S_{3/4} = A_1$, $M = N$).
- Paracordylodus gracilis* Lindström 1955, following the fused natural assemblage described by Stouge & Bagnoli (1988) and the natural assemblage described by Tolmacheva & Purnell (2002).
- Parapachycladina peculiaris* (Zhang *in* Zhang & Yang, 1991), following the reconstruction of Zhang *et al.* (1997: $P_1 = Pa$, $P_2 = M$, $S_0 = Sa$, $S_1 = Pb$, $S_2 = Sb$, $S_{3/4} = ?$).
- Periodon aculeatus* (Hadding, 1913), following the reconstruction of Armstrong (1997: $P_1 = Pa$, $P_2 = Pb$, $S_0 = Sa$, $S_1 = Sb$ (inner?), $S_2 = Sb$ (outer?), $S_{3/4} = Sc$, $M = M$).

Phragmodus inflexus Stauffer 1935a, following the natural assemblages of Repetski *et al.* (1998) and discrete element reconstructions of Bauer (1994: P₁ = Pa, P₂ = Pb, S₀ = Sa, S₁ = ?, S₂ = ?, S_{3/4} = ?, M = M) and Leslie & Bergström (1995: P₁ = Pa, P₂ = Pb, S₀ = Sa, S_{1/2} = Sb, S_{3/4} = Sc, M = M).

Plectodina aculeata (Stauffer, 1930), following the reconstruction of Bergström & Sweet (1966: P₁ = ?, P₂ = ?, S₀ = trichonodella-like, S_{1/2} = zygognathus-like, S_{3/4} = cordylodus-like, M = ?), Ziegler (1981: P₁ = Pa, P₂ = Pb, S₀ = Sa, S₁ = Sb (*Plectodina* pl. 1, fig. 5), S₂ = Sb (*Plectodina* pl. 1, fig. 4), S_{3/4} = Sc, M = M) and Sweet (1982: P₁ = Pa, P₂ = Pb, S₀ = ?, S₁ = Sb, S₂ = Sb, S_{3/4} = Sc, M = M).

'*Plectodina*' *tenuis* (Branson & Mehl, 1933), following the reconstructions of Sweet (1979a: P₁ = PA, P₂ = PB, S₀ = Sa, S₁ = Sb, S₂ = ?, S_{3/4} = Sc, M = M) and Nowlan & Barnes (1981: P₁ = prioniodiniform, P₂ = ozarkodiniform, S₀ = trichonodelliform, S₁ = zygognathiform, S₂ = ?, S_{3/4} = cordylodiform, M = cyrtioniodiform) with supplementary material from unpublished collections. Sweet (1988) argued that species of *Plectodina* with angulate, rather than pastinate, P₁ elements represent the most plesiomorphic members of the Ozarkodina. Sweet suggested that the two be distinguished formally and, as a temporary measure, chose to reflect this distinction by referring the putatively ozarkodinid members of the genus *Plectodina* to '*Plectodina*'. We follow Sweet's distinction only as a means of highlighting his hypothesis of the ozarkodinid ancestry while undertaking our cladistic analyses. Note also that the apparatus of '*Plectodina*' *tenuis* reconstructed by Nowlan & Barnes (1981) includes a pastinate, rather than an angulate P₁ element – we have followed Sweet (1979a, 1988) in coding this element.

Polygnathus xylus xylus Stauffer, 1940, following the reconstruction of Nicoll (1985: P₁ = Pa, P₂ = Pb, S₀ = Sa, S₁ = Sd, S₂ = Sb, S₃ = Sc, S₄ = Sc, M = M).

Prioniodina cf. *P. recta* (Branson & Mehl, 1933), following the reconstruction of Schülke (1997: P₁ = Pa, P₂ = Sb, S₀ = Sa, S₂ = Pb, S_{3/4} = Sc; 1999: M = M).

Prioniodus oepiki (McTavish, 1973), following the reconstruction of Stouge & Bagnoli (1988: P₁ = Pa, P₂ = Pb, P₃ = ?, P₄ = ?, S₀ = Sa, S₁ = Sb, S₂ = Sd, S_{3/4} = Sc, M = M).

Promissum pulchrum Kovács-Endrödy in Theron & Kovács-Endrödy, 1986, following the natural assemblages and the interpretation by Aldridge *et al.* (1995: P₁ = Pa, P₂ = Pb, P₃ = Pc, P₄ = Pd, S₀ = Sa, S₁ = Sb, S₂ = Sd, S₃ = Sc₁, S₄ = Sc₂, M = M).

Pterospathodus amorphognathoides Walliser, 1964, following the reconstruction of Männik (1998: P₁ = Pa, P₂ = Pb₁, P₃ = Pb₂, P₄ = Pc, S₀ = Sa, S₁ = ?, S₂ = ?, S_{3/4} = ?, M = M).

Sagittodontina kielcensis (Dzik, 1976), following the reconstruction of Dzik (1994: P₁ = sp, P₂ = oz, P₃ = ?, P₄ = ?, S₀ = tr, S₁ = ke, S₂ = pl, S₃ = ke, S₄ = hi, M = ne).

Scaliognathus anchoralis Branson & Mehl, 1941, following the reconstruction of Dzik (1997: P₁ = sp, P₂ = oz, S₀ = ?, S₁ = ?, S₂ = ?, S_{3/4} = hi, M = ne).

Staurogathus cruciformis Branson & Mehl, 1941, following the reconstruction of Chauff (1981: P₁ = Pa, P₂ = Pb, S₀ = Sa, S₁ = Sb₁, S₂ = Sb₂, S_{3/4} = Sc, M = M).

Sweetina triticum Wardlaw & Collinson, 1986, following the reconstructions of Wardlaw & Collinson (1986) and Chalimbadia & Silantiev (1998): P₁ = Pa, P₂ = Pb, S₀ = Sa, S₁ = Sb, S₂ = Sb, S_{3/4} = Sc, M = M.

Sweetognathus expansus (Perlmutter, 1975), following the natural assemblages of Ritter & Baesemann (1991) and discrete element reconstruction of Perlmutter (1975: P₁ = P, P₂ = O₁, S₀ = A₃, S₁ = A₁ (pl. 3, fig. 23), S₂ = A₂, S_{3/4} = A₁ (pl. 3, figs 20–21), M = N).

Vogelgnathus campbelli (Rexroad, 1957), following the reconstruction of Norby & Rexroad (1985: P₁ = Pa, P₂ = Pb, S₀ = Sa, S_{1/2} = Sb, S_{3/4} = Sc, M = M).

Yaoxianognathus abruptus (Bergström & Sweet, 1966), following the reconstruction of Sweet (1979b: P₁ = *Bryantodina abrupta* (Bergström & Sweet, 1966, 'bryantodina-like'), P₂ = *Bryantodina abrupta* (Bergström & Sweet, 1966, 'prioniodina-like'), S₀ = *Plectodina? posterocostata* (Bergström & Sweet, 1966, 'hibbardella-like'), S₁ = *Plectodina? posterocostata* (Bergström & Sweet, 1966, 'zygognathus-like'), S₂ = *Plectodina? posterocostata* (Bergström & Sweet, 1966, 'trichonodella-like'), S_{3/4} = *Plectodina? posterocostata* (Bergström & Sweet, 1966, 'cordylodus-like'), M = ?; Sweet, 1988: P₁ = Pa, P₂ = Pb, S₀ = Sa, S₁ = ?, S₂ = ?, S_{3/4} = Sc, M = ?); see also Zhen *et al.* (1999: P₁ = Pa, P₂ = Pb, S₀ = Sa, S₁ = Sd, S₂ = Sb, S_{3/4} = Sc, M = M).

APPENDIX 3: CHARACTER DESCRIPTIONS

1. P₁: 'posterior' process: absent (0), present (1). Processes, as used here for P elements, must bear denticles; adenticulate costae and protuberances are not processes as we apply the term.
2. P₁: 'posterior' carina in early ontogeny: absent (0), present (1). As we apply the term here, where a platform is absent we take a 'posterior' process to be equivalent to a 'posterior' carina.
3. P₁: 'posterior' carina in late ontogeny: absent (0), present (1). Notes to character 2 also apply here.
4. P₁: 'inner-lateral' process(es): absent (0), present (1). 'Inner' is taken as the concave side of an element when viewed from 'above'.
5. P₁: 'outer-lateral' process(es): absent (0), present (1).
6. P₁: 'anterior' process: absent (0), present (1).
7. P₁: digyrate elements: absent (0), present (1). As we use it, 'digyrate' refers only to elements that have two processes, one of which is 'inner-lateral', one of which is 'outer-lateral' in position.
8. P₁: platform: absent (0), present (1).
9. P₁: platform: type A (0), type B (1). The types of platform development referred to are outlined in Donoghue

- (1998); type A is comparable to the icrion of Dzik (2000) and type B is comparable to his 'platform'. '?' signifies inapplicable.
10. P₁: 'anterior' free blade: absent (0), present (1). A free blade is considered present when a blade protrudes beyond the 'anterior' margin of the platform. Herein we consider the condition of free blade to be also present in elements lacking platform development.
 11. P₁: basal cavity: restricted to cusp (0), extends along processes (1). Almost by definition, incremental layers of crown tissue must open onto the aboral surface of element crowns and so in a strict sense, basal cavities almost always extend along the processes of elements. However, this character refers to an extensive area on the aboral surface of elements where successive layers of crown tissue have consistently failed to envelop the basal edge of the preceding lamella; in one condition the area of non-enveloped lamellae is limited to a region immediately below the cusp, in the other it extends along the aboral margin of all the processes.
 12. P₁: basal cavity recessive: absent (0), present (1). This character refers to an aboral area of non-enveloped lamellae that is approximately planar, as typified by *Palmatolepis*.
 13. P₁: recessive basal margin reversed: absent (0), present (1). This character refers to a convex aboral area of non-enveloped lamellae, as typified by *Pachycladina*.
 14. P₁: peg-like denticles: absent (0), present (1). In our usage, this character refers to the presence of denticles that are relatively long, thick, approaching round in cross-section and which have U-shaped (rather than V-shaped) spaces between them.
 15. P₁: centre of growth: indistinct (0), distinct (1). The centre of growth is defined by the tip of the basal cavity. When more than one basal cavity is present, the centre of growth is taken as the tip of the basal cavity in the oldest portion of the element. This character refers to the presence of a distinctive morphological structure on the 'upper' surface that immediately overlies the centre of growth.
 16. P₁: prominent cusp in early ontogeny: absent (0), present (1). Although the degree of cusp prominence is intrinsically a continuous variable, there are relatively few taxa in which the cusp dwarfs the surrounding denticulation as it does in some of the oldest species of *Ozarkodina*.
 17. P₁: prominent cusp in late ontogeny: absent (0), present (1).
 18. P₁: prominent 'anterior' crest: absent (0), present (1). This character refers to the presence of a denticle or series of denticles at the 'anterior' end of an element, larger than the cusp or any other denticles, otherwise referred to as a 'fan' by Murphy & Valenzuela-Ríos (1999). This character is inapplicable for taxa scoring absent for character 6 (P₁: 'anterior' process).
 19. P₂: basal cavity: restricted to cusp (0), extends along processes (1). See notes to character 11.
 20. P₂: basal cavity recessive: absent (0), present (1). See notes to character 12.
 21. P₂: peg-like denticles: absent (0), present (1). See notes to character 14.
 22. P₂: 'anterior' process: absent (0), present (1).
 23. P₂: 'posterior' process: absent (0), present (1).
 24. P₂: 'inner-lateral' process(es): absent (0), present (1).
 25. P₂: 'outer-lateral' process(es): absent (0), present (1).
 26. P₂: platform: absent (0), present (1).
 27. P₂: platform: type A (0), type B (1). '?' signifies inapplicable.
 28. P₂: digyrate elements: absent (0), present (1). See notes to character 7.
 29. P₃: absent (0), present (1).
 30. P₄: absent (0), present (1).
 31. S: peg-like denticles: absent (0), present (1). See notes to character 14.
 32. S: basal cavity: restricted to cusp (0), extends along processes (1). See notes to character 11.
 33. S: morphogenesis: type II (0), type III (1). See Donoghue (1998).
 34. S: type IV morphogenesis: absent (0), present (1). See Donoghue (1998).
 35. S₀: 'anterior' process: absent (0), present (1).
 36. S₀: 'posterior' process: absent (0), present (1).
 37. S₀: 'lateral' processes: absent (0), present (1).
 38. S₀: 'lateral' processes: vertical (0), horizontal (1). '?' signifies inapplicable.
 39. S₁: 'anterior' process: absent (0), present (1).
 40. S₁: 'posterior' process: absent (0), present (1).
 41. S₁: 'inner-lateral' process: absent (0), present (1).
 42. S₁: 'outer-lateral' process: absent (0), present (1).
 43. S₁: 'outer-lateral' process: vertical (0), horizontal (1). '?' signifies inapplicable.
 44. S₁: digyrate: absent (0), present (1). See notes to character 7.
 45. S₂: 'anterior' process: absent (0), present (1).
 46. S₂: 'anterior' process: vertical (0), horizontal (1). '?' signifies inapplicable.
 47. S₂: 'posterior' process: absent (0), present (1).
 48. S₂: 'inner-lateral' process: absent (0), present (1).
 49. S₂: 'inner postero-lateral' process: absent (0), present (1). This character refers to the additional process found on quadriramate elements.
 50. S₂: 'outer-lateral' process: absent (0), present (1).
 51. S₂: digyrate: absent (0), present (1). See notes to character 7.
 52. S₃: 'anterior' process: absent (0), present (1). '*Plectodina tenuis* is polymorphic for the presence of a denticulated 'anterior' process; we have taken this as indicative of the presence of a process.
 53. S₃: 'posterior' process: absent (0), present (1).
 54. S₃: 'inner-lateral' process: absent (0), present (1).
 55. S₃: 'outer-lateral' process: absent (0), present (1).
 56. S₄: 'anterior' process: absent (0), present (1).
 57. S₄: 'posterior' process: absent (0), present (1).
 58. S₄: 'inner-lateral' process: absent (0), present (1).
 59. S₄: 'outer-lateral' process: absent (0), present (1).
 60. M: 'anterior' process: absent (0), present (1).
 61. M: 'posterior' process: absent (0), present (1).
 62. M: peg-like denticles: absent (0), present (1). See notes to character 14.
 63. M: basal cavity: restricted to cusp (0), extends along processes (1). See notes to character 11.
 64. M: 'postero-lateral' process: absent (0), present (1).
 65. M: 'antero-lateral' process: absent (0), present (1).
 66. M: three or more processes: absent (0), present (1).
 67. M: adaxial bulge at base of cusp: absent (0), present (1).

68. M: oistodiform: absent (0), present (1).
69. True white matter (*sensu* Donoghue 1998): absent (0), present (1).
70. Fibrous enamel (pseudo white matter *sensu* Donoghue 1998): absent (0), present (1).
71. P₁: apex of basal cavity or pit of recessive basal margin lies in 'anterior' of cavity/basal margin OR aboral cavity or recessive basal margin more expanded 'posterior' of basal cavity apex than 'anterior': absent (0), present (1).
72. P₁: most of platform lies to 'posterior' of basal cavity apex: absent (0), present (1). This character is inapplicable for taxa scoring absent for character 1 (P₁: posterior process) and / or character 8 (P₁: platform).
73. P₁: pinched basal cavity: absent (0), present (1). 'Pinched' refers to a cavity that is 'laterally' expanded, with margins that project from the side of the element at close to 90°.
74. P₁: cupola or dome-shaped basal cavity beneath posterior process(es): absent (0), present (1).
75. P₁: different denticulation on 'anterior' and 'posterior' processes (where both present): absent (0), present (1).
76. P₁: all processes in the same plane when viewed laterally: absent (0), present (1).
77. S: 'sheath' or 'webbing' between processes extending distal to cusp: absent (0), present (1).
78. S₁: distal portion of anterior process (where present) recurved sharply 'inward': absent (0), present (1).
79. P₁: bifid outer-lateral process: absent (0), present (1).
80. M: makellate: absent (0), present (1). Makellate elements have a lateral process or two lateral processes, one on each side of the cusp. Unlike Nicoll (1990) we do not include elements that lack lateral processes.
81. M: asymmetrical makellate with down-flexed lateral process or processes: absent (0), present (1).
82. M: makellate with two down-flexed, lateral processes of markedly unequal length: absent (0), present (1).
83. M: makellate with two down-flexed, lateral processes of markedly unequal length that are straight: absent (0), present (1).
84. M: makellate with two down-flexed, lateral processes of markedly unequal length, the longer of which is curved and/or twisted: absent (0), present (1).
85. S₂: quadriramate: absent (0), present (1).
86. S₁₋₂: dominant process shorter than in S₃₋₄ elements: absent (0), present (1).
87. P₁: basal cavity lanceolate, tapering more posteriorly than anteriorly and with asymmetric lateral expansion (i.e. the outline of the cavity is reminiscent of the outline of Brazil): absent (0), present (1).
88. S₁: dominant process shorter than in S₂ element: absent (0), present (1).
89. S₁: 'bipenniform' – this includes elements that are strictly bipennate plus elements that are digyrate, but which strongly resemble bipennate elements in their overall morphology (i.e. the processes are oblique-lateral, but distally they are aligned with one another and 'horizontal': absent (0), present (1).
90. M: type IV morphogenesis: absent (0), present (1). See Donoghue (1998).
91. S₀: lateral processes: direct lateral (0), antero-lateral (1).
92. P₁: digyrate, with angle between proximal parts of processes less than *ca.* 135°: absent (0), present (1).
93. P₂: digyrate, with angle between proximal parts of processes less than *ca.* 135°: absent (0), present (1).
94. S₁: both processes 'horizontal' adjacent to cusp: absent (0), present (1). This character is only applicable to digyrate elements and refers to S₁ elements that are morphologically close to bipennate.
95. S₂: both processes 'horizontal' adjacent to cusp: absent (0), present (1). This character is only applicable to digyrate elements and refers to S₂ elements that are morphologically close to bipennate.

SUPPLEMENTARY DATA

Supplementary figures are available online on Cambridge Journals Online on: http://www.journals.cup.org/abstract_S1477201907002234