CONODONTS MEET CLADISTICS: RECOVERING RELATIONSHIPS AND ASSESSING THE COMPLETENESS OF THE CONODONT FOSSIL RECORD

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ABSTRACT. A numerical cladistic analysis of the conodont family Palmatolepidae has been undertaken to determine the applicability of the technique to group-wide systematic revision. Results suggest a new hypothesis of relationships that is considerably more parsimonious than trees compatible with existing hypotheses of relationships, or trees that are even loosely constrained stratigraphically. This may occur either because the fossil record is incomplete, because taxon sampling for the cladistic analysis is low, or because the most parsimonious trees approximate the true tree less well than do stratigraphically-constrained trees (or because of a combination of these factors). Although more taxa and more characters would be preferable in choosing between these possibilities, the tree derived solely from morphological data is adopted. Thus, stratigraphic data can be used to test hypotheses of relationships and construct phylogenies; hypotheses of relationships can be used to test the completeness of the conodont fossil record. Existing schemes of classification within the Palmatolepidae are rejected because most groups within them are either polyphyletic or paraphyletic. A new scheme is presented. Character changes suggest correlated, progressive and mosaic evolution within the Palmatolepidae. Parsimony analysis of partitioned datasets indicates that more phylogenetic information can be recovered from S rather than P or M element positions, although data from all three positional groups are preferable to data from just one. Thus, multielement taxonomy is essential to the resolution of conodont interrelationships.

KEY WORDS: conodont, cladistics, systematics, *Palmatolepis*, completeness, fossil record, extinction.

ALTHOUGH it is usually only the mineralised feeding elements that are preserved, conodonts have a fossil record that rivals any other group for completeness (Foote and Sepkoski 1999). This is due largely to the properties of the tissues from which the elements are composed. Like mammals, which have a fossil record similarly dominated by dentition, the 'teeth' of conodonts are largely composed from enamel, a brittle but highly wear-resistant tissue. Experimental analysis of conodont enamel (Broadhead and Driese 1994) demonstrated that mechanical abrasion has little effect. With this wealth of data it might be expected that the interrelationships of conodonts would be well understood. However, even though the conodont fossil record is relatively rich, until quite recently taxonomy has been limited to single-element morphospecies. Attempts to replace this with a biologically valid multielement taxonomy have been under way since the mid 1960s (Walliser 1964; Bergström and Sweet 1966), but we remain far from the utopian state where the apparatus composition of all conodont taxa is known in full. Because of this, most phylogenetic schemes still concentrate on the P_1 element (*sensu* Purnell *et al.* 2000), the element on which most conodont taxa are erected. However, because P_1 elements are usually the most informative for species discrimination, they are not necessarily the most useful in reconstructing conodont phylogeny (Merrill *et al.* 1990).

Because the conodont fossil record is perceived to be so good, the primary approach adopted to resolve the interrelationships of conodonts has been to assume that faunas from a single rock succession, or suite of coeval rock successions, represent a sequence of ancestor-descendant relationships. Amongst other examples, Dzik has presented compelling evidence for the gradual evolution of a number of multielement conodont lineages within the Middle–Late Ordovician Mojcza Limestone of the Holy Cross Montains (Dzik 1991*a*, 1994, 1999). These demonstrate well the gradualistic pattern of anagenetic change within

species as well as from one species to another (at least within the limitations of sampling). However, the lack of intermediates in these successions requires a leap of faith to understand the relationship between taxa of higher rank. Despite this problem, schemes of suprageneric classification have been in place for many years (Lindström 1970; Clark *et al.* 1981; Fåhraeus 1984; Sweet 1988; Dzik 1991*b*); explanations for discrepancies have ignored the possibility that the conodont fossil record is incomplete, and frequently overlooked constraints of palaeoecology and palaeobiogeography (cf. Gould and Eldredge 1977), placing ultimate faith upon the order of stratigraphic appearance when morphological data are mute. Notwithstanding problems with the methodology by which they have been erected, existing hypotheses of conodont relationship and schemes of classification serve no purpose other than to summarise loose concepts of genealogy; they express nothing pertinent to resolving evolutionary patterns and processes. Nor do they provide any of the data upon which existing phylogenies and schemes of classification were based.

There is a real need to reappraise our current understanding of conodont relationships with the view to erecting a cohesive and consistent scheme of classification. Such a reappraisal should meet three main criteria: (1) it should consider the evolution of conodonts in light of the universal shift towards multielement taxonomy; (2) it should formally constrain the influence of morphology and stratigraphy upon the resolution of relationships; and (3) a resulting classification scheme should consider the universal shift towards phylogenetic systematics in the rest of systematic biology and palaeontology. This last criterion is particularly pertinent as the true conodonts (=euconodonts) do not constitute a monophyletic taxon in either evolutionary or phylogenetic systematics (e.g. Miller 1980, 1984).

Conodont researchers (Dzik 1991*a*, 1999), like other micropalaeontologists (Steineck and Fleisher 1978; Lazarus and Prothero 1984), have often argued that iterative patterns of phenotypic evolution are so rampant within the fossil record of their subjects that morphological analysis alone (i.e. exclusion of stratigraphic data) is insufficient to resolve interrelationships. Furthermore, micropalaeontologists frequently argue that the temporal and spatial nature of the fossil record of the groups they are studying is sufficiently complete that stratigraphic data must be incorporated into the analysis of relationships and elucidation of phylogeny. For instance, the celebrated Late Devonian Standard Conodont Zonation (Ziegler and Sandberg 1990) rests upon the assumption that complete gradation between ancestors and their descendents can be discerned; individual zones are defined as ranging from the 'global phyletic first occurrence of the zonal name-giving species to the global phyletic first occurrence of the next younger, descendant species' (Ziegler and Sandberg 1994, p. 105). That such gradations between taxa are discernible and commonplace suggests a stratophenetic basis for their recognition, though like many schemes that might claim to be stratophenetic, this is a misnomer (cf. Pearson 1998). Indeed, Ziegler and Sandberg (1994) have attempted to discredit a competing zonation that utilises phenetically-defined taxonomic divisions as the basis for a graphically-correlated global composite standard (Klapper and Foster 1986, 1993; Klapper 1988; Klapper *et al.* 1995, 1996; Klapper and Becker 1999). If homeomorphy is so prevalent in the conodont fossil record, we might rightly question the biostratigraphic potential of the group, and yet conodonts are used as index fossils throughout a significant fraction of the Phanerozoic (cf. foraminifera; MacLeod 1993).

Diametrically opposed to stratopheneticists are pure cladists such as Siddall (1998), who argue that the vagaries of the fossil record are such that temporal data, including the stratigraphic order in which fossils are found, have no place in resolving relationships. Other cladists, such as Smith (1994) and Forey *et al.* (1992) have argued that stratigraphy can be invoked to fine tune a cladistic analysis based upon morphology alone, and/or in choosing between multiple equally most-parsimonious trees. However, these are a world apart from those systematists who are prepared to use stratigraphy to choose any tree less parsimonious than the shortest tree(s) (e.g. Wagner 1995, 1998). The school of stratocladistics (Fisher 1992, 1994) incorporates stratigraphic data into the analysis by scoring presence or absence as for morphological data. However, as has been pointed out elsewhere (Forey 1998), this implies that co-occurrence in a temporal plane reflects potential monophyly.

Irrespective of the relative merits of stratophenetics (*sensu lato* or *sensu stricto*) over cladistics or *vice versa*, the only practical way in which to simultaneously analyse a large volume of data, such as those provided by conodont multielement taxonomy, is using numerical cladistics. Conveniently, a homology-based

approach of multielement taxonomy, which reconstructs conodont taxa by identifying elements that fill specific apparatus positions, is an ideal framework in which to conduct cladistic analyses. However, conodonts have remained unscathed by the cladistic revolution thus far largely because taxonomists persist in using a scheme of element orientation that has long been acknowledged as entirely arbitrary (e.g. Müller 1956a). This need no longer be the case. The apparatus architecture of many taxa is now known in great detail (Aldridge et al. 1987, 1995; Purnell 1993; Purnell and Donoghue 1997, 1998; Sansom et al. 1994) and the position of this apparatus relative to principal body axes is similarly well constrained (Aldridge et al. 1993; Purnell and Donoghue 1997; Purnell et al. 2000; see also Dzik 1994). We are therefore well positioned to introduce cladistic methodology into the classification of conodonts.

THE CONODONT FAMILY PALMATOLEPIDAE SWEET, 1988

The Late Devonian conodont family Palmatolepidae was chosen as the subject for a case study because its interrelationships are widely considered the best known of all conodont groups. Yet this knowledge is based entirely upon stratophenetic analysis limited to the element occupying the P_1 position. A cladistic analysis of relationships based upon multielement taxonomy will, therefore, provide not only an interesting comparison of methodologies, but also a test of the effectiveness of total versus partial evidence. The family Palmatolepidae is also an interesting group to study because many of its species comprise the backbone of the Late Devonian Standard Conodont Zonation (Ziegler and Sandberg 1990) and the Frasnian Global Composite Standard (Klapper et al. 1995, 1996; Klapper and Becker 1999). The stratigraphic ranges of palmatolepid species are, therefore, sufficiently well known to provide a corroborative test of any hypothesis of relationships. Furthermore, although the multielement composition of relatively few palmatolepid species is currently known and so only a small proportion of species are available for cladistic analysis, the results will provide an assessement of the reliability of cladistic methodology in resolving relationships when sampling density is artificially low and an approximately complete fossil record is known. It is hoped that this study will provide the impetus for those who work on palmatolepids to test the results of this paper by repeating the analysis incorporating multielement reconstructions for taxa currently known only from P_1 elements. Such an on-going project could provide a model study of the effect of improving sampling density upon the resolution of relationships ($sensu$ Fortey and Jefferies 1982) using cladistic methodology.

The family Palmatolepidae is conventionally perceived to be composed of four genera: $Schmidtognathus$ (c. 6 species), $Klapperina$ (c. 5 species), $Mesotaxis$ (c. 6 species) and $Palmatolepis$ (c. 110 species). Almost all species are assigned to $Palmatolepis$, which, in terms of sheer numbers, represents one of the most taxonomically diverse conodont genera. As such, $Palmatolepis$ has been the focal point of interest in conodont suprageneric taxonomy, particularly as a model in which to explore the levels at which subgenera, genera, subfamilies and families are defined (e.g. Merrill et al. 1990). A brief history of this debate follows.

By studying the morphological transformation of the $Palmatolepis$ P_1 element in successive stratigraphic samples through the Late Devonian, Müller (1956b), Helms (1959, 1963) and Ziegler (1962) were able to recognise several well-defined lineages, graphically expounded in the two editions of the Treatise (Helms 1962; Helms and Ziegler 1981). Müller (1956b) chose to assign each lineage to a new subgenus, erecting $Deflectolepis$, $Manticolepis$ and $Palmatolepis$ as new taxa defined on morphological characteristics of the P_1 element. Helms' (1963) reconstruction of the phylogeny of $Palmatolepis$ P_1 elements established $Panderolepis$ as a new group of palmatolepids. As opposed to the stratophenetic approach adopted by earlier workers, van den Boogaard and Kuhry (1979) were able to find support for subgeneric groupings of palmatolepids through cluster analysis of recurrent element associations. Each of the subgenera erected by Müller (1956b) and Helms (1963) was further refined by establishing the morphology of the P_2 element which was often found to be more distinctive than the P_1 element on which the groupings had been defined. The subgenus $Conditolepis$ was also established, and $Tripodellus$ was recognised to be a senior synonym of $Deflectolepis$, based on P_2 element morphology. However, multielement reconstructions of taxa hitherto assigned to $Deflectolepis$ indicate that not all species possessed a P_2 element with three processes (e.g. Metzger 1994: $Palmatolepis$ $loba$ Helms, 1963 and

Palmatolepis subgracilis Bischoff, 1956). Whether this is a primitive or derived characteristic can only be resolved by calibration against a hypothesis of relationships. For the purposes of this study, the subgenus *Deflectolepis* is retained for taxa which possess a P_1 element of the form subgenus '*Deflectolepis*' but which lack a three-processed P_2 element.

In one of the two most recent revisions of conodont suprageneric taxonomy, Sweet (1988) maintained the single genus approach to classifying the species, but regarded *Palmatolepis* and its close relatives *Klapperina*, *Mesotaxis* and *Schmidtognathus*, as sufficiently distinct from other conodonts to merit erection of a family Palmatolepidae. Dzik (1991*b*) believed that the lineages derived from *Manticolepis* differ in apparatus composition sufficiently profoundly that there can be no doubt that they deserve separation at generic level. A similarly empirical approach was adopted by Merrill *et al.* (1990) who argued that apparatus variation in *Palmatolepis* is greater than in most conodont families, and that the Palmatolepidae is 'a genetically related group of conodonts that....underwent intense morphological convergence among their Pa [P_1] elements' (Merrill *et al.* 1990, p. 399; as opposed to the established phylogeny which portrays the evolution of P_1 element morphology as divergent, e.g. Helms 1962, 1963). Merrill *et al.* (1990) based their approach on the hypothesis that different elements in a conodont apparatus hold different value. They contended that the P_1 element is of value only for species level taxonomy, while the P_2 and M elements are more useful at the generic level, and S elements at the family level.

The cladistic analysis presented here includes a range of reconstructed taxa that encompass all the proposed genera and subgenera. As such, it holds the potential to discover any monophyletic subclades within the Palmatolepidae, and if so, whether these coincide with any of the existing subgeneric or multigeneric schemes. Furthermore, because the characters used in the analysis incorporate all elements of the apparatus, the study provides an independent test of phylogenies based solely on P_1 element morphology, and also of the proposal that different components of a conodont apparatus hold different taxonomic value (Merrill *et al.* 1990).

MULTIELEMENT CONCEPTS AND RECONSTRUCTIONS OF *PALMATOLEPIS*

The origin of conodont multielement taxonomy rests firmly with the discovery of natural assemblages of elements that represent the articulated remains of individual conodonts (Schmidt 1934; Scott 1934). Later workers were able to reconstruct multielement apparatuses by using the ratio of element types present in the natural assemblages as a template for comparison with recurrent associations of element types in discrete collections of elements (e.g. Huckriede 1958). Further discoveries of natural assemblages of differing age and taxonomic assignment [see appendix in Purnell and Donoghue (1998) for a reasonably comprehensive list of natural assemblages assigned to the order Ozarkodinida] have provided greater confidence in reconstructions of widely divergent taxa.

The 'official' multielement concept of *Palmatolepis* which appears in the Catalogue of Conodonts (Ziegler 1973) is that the apparatus is unimembrate, 'consisting of one or more pairs of left and right palmatolepiform elements' (Ziegler 1973, p. 255). Ziegler (1972, 1973) rejected Klapper and Philip's (1972) multielement reconstruction of the *Palmatolepis* apparatus by discounting Lange's (1968) cluster, on which the reconstruction is based, as coprolitic; the association of the articulated pair of *Palmatolepis bogartensis* P_1 elements with elements of other morphologies was considered fortuitous. Other authors who have followed a unimembrate concept of the *Palmatolepis* apparatus include Clark and Ethington (1967), Sandberg and Ziegler (1979), and Fåhraeus (1982).

Despite the discovery of many other natural assemblages (Puchkov *et al.* 1982; Delfour and Gigot 1985; Zvereva 1986; Orchard 1996), the Lange cluster (assigned to *Palmatolepis bogartensis* by Klapper and Foster 1993) remains the primary reference for homology in *Palmatolepis*. Some post-mortem movements have disrupted the relative arrangement of the component elements, but this cluster retains more three-dimensional architectural information than any single natural assemblage of any other conodont taxon. This is important because many of the component elements are morphologically unusual in comparison with the vast majority of ozarkodinids. The positional information that is provided allows the identification of homologies with the standard template for ozarkodinid apparatuses (Purnell and Donoghue 1997; Purnell *et al.* 2000).
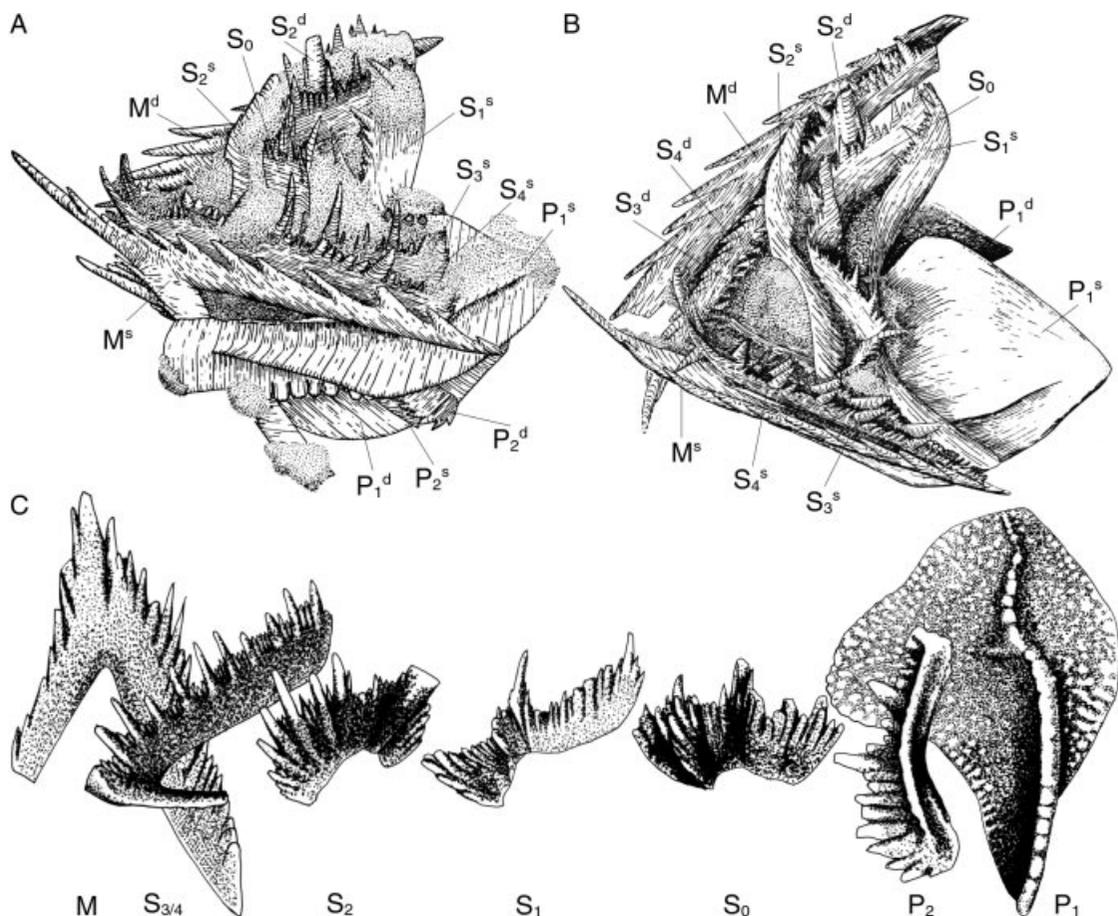
TEXT-FIG. 1. A–B, lateral and oblique-lateral view of cluster of *Palmatolepis bogartensis* (from Lange 1968, reproduced with permission). C, morphology of elements filling the principal apparatus positions of *P. bogartensis*; all elements in abaxial (dextral) view except the S_0 and P_2 which are shown in caudad and rostrad views (respectively); from right to left: P_1, P_2, S_0, S_1, S_2, S_{3-4}, M (after Klapper and Foster 1993).

It has not proven possible to restudy the Lange (1968) cluster of *Palmatolepis bogartensis* and so the interpretation of positional homology of distinct element morphologies has been limited to study of the original line drawings which are refigured here (Text-fig. 1A–B). Both pairs of P elements remain articulated suggesting little post-mortem disruption. The rostro-caudal axis of the P elements is oriented obliquely to the dorso-ventral axis of the S and M element array [note that the axes referred to are biological, not the traditional arbitrary scheme; see Donoghue and Purnell (1999) and Purnell *et al.* (2000) for discussion and explanation]. The lobed margin of the P_1 elements lies uppermost (as drawn) suggesting that this represents the rostral margin of the elements and it follows that the denticulation of the P_2 elements is directed adaxially and ventrally as in other ozarkodinids (e.g. Purnell and Donoghue 1997, 1998). The M elements flank two pairs of closely associated bipennate S_{3-4} elements and the caudal processes of all three element pairs appear to have been arranged in parallel *in vivo*. The morphology of the elements filling positions S_{1-2} is least clear due to some disruption in their arrangement relative to the axial S_0 element. Although both falcodontan elements are present, the dextral asymmetrical scutulan element is missing or obscured; the sinistral scutulan and falcodontan elements are displaced across the

axis, lying either side of the S_0. However, the asymmetrical scutulan element bears a strong resemblance to the *Polygnathus* S_1 element (e.g. Text-fig. 2B) but with an additional adaxial process; the asymmetrical scutulan element is, therefore, homologised with the occupants of the S_1 position and the falcodontan element with the occupants of S_2 positions. The orientation of the S_2 is not obvious but as the denticulation in ozarkodinid S elements consistently inclines towards the cauda (e.g. Purnell and Donoghue 1998), it appears most likely that the cusp is caudal relative to the process (Text-fig. 1A–B). The morphology of the elements and their homological notation is outlined in Text-figure 1C.

PHYLOGENETIC ANALYSIS

Reconstructions included in the analysis

Outgroup. Aside from *Palmatolepis*, with its many species, Sweet (1988) also placed a number of less diverse genera within the family Palmatolepidae. These include (from putatively less to more derived) *Schmidtognathus*, *Klapperina* and *Mesotaxis*. Only the last of these is known in multielement form (*Mesotaxis asymmetrica asymmetrica*, following the reconstruction by Klapper and Philip 1971), so the others are not represented in this cladistic analysis. Convention has it that the Palmatolepidae evolved from *Polygnathus latifossatus* Wirth, a species Sweet (1988) also included in the family, but which has conventionally (e.g. Ziegler and Lane 1987) been allied to *Polygnathus varcus* stock (Weddige 1977; Weddige and Ziegler 1979). No reconstruction for *P. latifossatus* exists, but following convention for the evolution of *Palmatolepis* from *Polygnathus*, it is preferable to include a polygnathid in the outgroup. *Polygnathus xylus xylus* is the best known of all polygnathids because it is represented in numerous natural fused clusters of elements (Nicoll 1985); it is also a member of *P. varcus* stock (Weddige 1977) and so an ideal outgroup candidate. However, *P. latifossatus* was originally thought to have evolved directly from *Ozarkodina* (=?*Mehlina*) *semialternans* (Wirth, 1967), a hypothesis also supported by Ziegler *et al.* (1976) and Sweet (1988). To assess the viability of such a hypothesis, a coding for *Mehlina gradata* Youngquist (following the reconstruction by Uyeno, *in* Norris *et al.* 1982) has been included as the only reconstructed species of the genus *Mehlina*.

Ingroup. Taxa included in the analysis, reconstructions followed, and subgeneric assignments are as follows: *Palmatolepis bogartensis* (Stauffer 1938) based on the reconstruction by Klapper and Foster (1993) and a fused cluster described by Lange (1968); assigned to the subgenus *Manticolepis* by Müller (1956b). *Palmatolepis deliculata deliculata* Branson and Mehl, 1934 based on a natural assemblages described by Puchkov *et al.* (1982; SUI 47281); many details of element morphology are not discernible in the natural assemblages and so related characters are scored as unknown; assigned to the subgenus *Manticolepis* by Helms (1962). *Palmatolepis falcata* (Helms 1959) based on a reconstruction by Metzger (1994); S_1 and M unknown and so related characters are scored as such [the M element assigned to this apparatus by Dzik (1991b) was considered by Metzger (1994) to belong to *Palmatolepis schindewolfi*]; assigned to the subgenus *Panderolepis* by van den Boogaard and Kuhry (1979). *Palmatolepis gracilis* Branson and Mehl, 1934 based on a reconstruction by van den Boogaard and Kuhry (1979) who assigned it to the subgenus *Tripodellus*. *Palmatolepis loba* Helms, 1963 based on the reconstruction by Metzger (1994); assigned to the subgenus *Deflectolepis* by Helms (1963). *Palmatolepis minuta minuta* Branson and Mehl, 1934 based on the reconstruction by Metzger (1994); assigned to the subgenus *Tripodellus* by van den Boogaard and Kuhry (1979). *Palmatolepis muelleri* Klapper and Foster, 1993 based on a reconstruction by Klapper and Foster (1993); assigned to the subgenus *Manticolepis* by Müller (1956b).

TEXT-FIG. 2. Morphology of elements filling the principal apparatus positions (right to left: P_1, P_2, S_0, S_1, S_2, S_{3-4}, M); all elements in adaxial (dextral) view unless otherwise stated. A, *Mehlina gradata* (after Uyeno, *in* Norris *et al.* 1982). B, *Polygnathus xylus xylus* (after Nicoll 1985); P_2 in caudad view. C, *Mesotaxis asymmetrica asymmetrica* (after Klapper and Philip 1971); S_1 rostral view. D, *Palmatolepis deliculata deliculata* (based on bedding plane assemblage described by Puchkov *et al.* 1982); S_0 and P_2 in rostrad view. E, *Palmatolepis falcata* (illustration from Dzik 1991 reproduced with permission); S_0 and P_2 in rostrad view. F, *Palmatolepis gracilis* (illustration from Dzik 1991 reproduced with permission) S_0 in rostrad and P_2 in caudad views.

M S3/4 S2 S1 S0 P2 P1

Palmatolepis perlobata perlobata Ulrich and Bassler, 1926 based on the reconstruction by Metzger (1994); no known S_2 element and so related characters are scored as unknown; assigned to the subgenus *Palmatolepis* by Helms (1962). *Palmatolepis perlobata maxima* Müller, 1956*b* based on the reconstruction by Metzger (1994); no known S_0 element and so related characters are scored as unknown; assigned to the subgenus *Palmatolepis* by Müller (1956*b*). *Palmatolepis quadrantinodosalobata* Sannemann, 1955 based on the reconstruction by Metzger (1994); no known S_1 element and so related characters are scored as unknown; assigned to the subgenus *Manticolepis* by van den Boogaard and Kuhry (1979). *Palmatolepis rugosa* Branson and Mehl, 1934 based on reconstruction by Dzik (1991*b*) and personal collections from the Fammenian of Ostrowska Quarry, Holy Cross Mountains, Poland (see Szulczewski and Skompski 1996); assigned to the subgenus *Palmatolepis* by Helms (1962). *Palmatolepis schindewolfi* Müller, 1956*b* based on the reconstruction by Metzger (1994); no known S_2 element and so related characters are scored as unknown; assigned to the subgenus *Palmatolepis* by Müller (1956*b*) and van den Boogaard and Kuhry (1979). *Palmatolepis subgracilis* Bischoff, 1956 based on the reconstruction by Metzger (1994); assigned to the subgenus *Deflectolepis* by Helms (1962). *Palmatolepis winchelli* (Stauffer 1938) based on the reconstruction by Klapper and Foster (1993); assigned to the subgenus *Manticolepis* by Müller (1956*b*). *Palmatolepis wolskae* Ovnatanova, 1969 based on the reconstruction by Metzger (1994); no known S_2 or M element and so related characters are scored as unknown; not assigned to a subgenus.

### Reconstructions excluded from the analysis

The reconstructions of *Mesotaxis* and *Palmatodella* by Philip and McDonald (1975) were not included in the analysis because these authors chose to use in their reconstructions a template modified from, but incompatible with, that of Klapper and Philip (1971, 1972). Philip and McDonald (1975) chose to replace the P_2 (their O element) with an element that had been placed in an M position (their N) by Klapper and Philip (1971, 1972), their M was replaced by an S_1 [one of their A elements (?A2)]. Whereas it is possible to resolve the correct positional homologies for these elements, most of the reconstructions lack both a P_2 and M, and by comparison with reconstructions of congeneric taxa, it is unlikely that some of the elements belong in some of the reconstructions (e.g. the S_1 in species of *Mesotaxis*). The bedding plane assemblage of a species of the *Polygnathus nodocostatus* group, figured by Habetín and Knobloch (1981) and Dzik (1991*b*), has also been excluded from this analysis because it is not possible to resolve the morphology of the P_2 and S_{1-2} elements. It was decided to exclude taxa known only from P_1 or P_{1+2} because of the problems associated with excessive missing data.

Character definitions

A total of 36 characters are used in the phylogenetic analysis of 16 species of *Palmatolepis*. Two putative ancestral taxa are included as outgroup taxa. Contingent coding strategy has been adopted as it is the only theoretically and practically valid method of character coding (Hawkins *et al*. 1996). Aspects of character morphology are described using both the biological and the traditional arbitrary schemes (see Purnell *et al*. 2000); arbitrary terms have been retained where precise biological terms cannot be applied until relationships are known.

  1. P_1 morphology: carminate (0), pastinate (1). Although the P_1 elements of palmatolepids are conventionally interpreted as varieties of carminate morphology (e.g. Sweet 1988, p. 104), almost all species of *Palmatolepis* possess three processes, 'anterior', 'posterior' and 'lateral' (see Sweet 1988, p. 21, for the definition of these

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TEXT-FIG. 3. Morphology of elements filling the principal apparatus positions (right to left: P_1, P_2, S_0, S_1, S_2, S_{3-4}, M). A, *Palmatolepis loba* (based on Metzger 1994); $S_{1,\,0}$ and P_2 in caudad view. B, *Palmatolepis minuta minuta* (based on Metzger 1994); S_0 and P_2 in caudad view. C, *Palmatolepis muelleri* (based on Klapper and Foster 1993); $S_{1,\,0}$ and P_2 in caudad view. D, *Palmatolepis perlobata maxima* (based on Metzger 1994); P_2 in rostrad view. E, *Palmatolepis perlobata perlobata* (based on Metzger 1994); S_0 and P_2 in rostrad view.
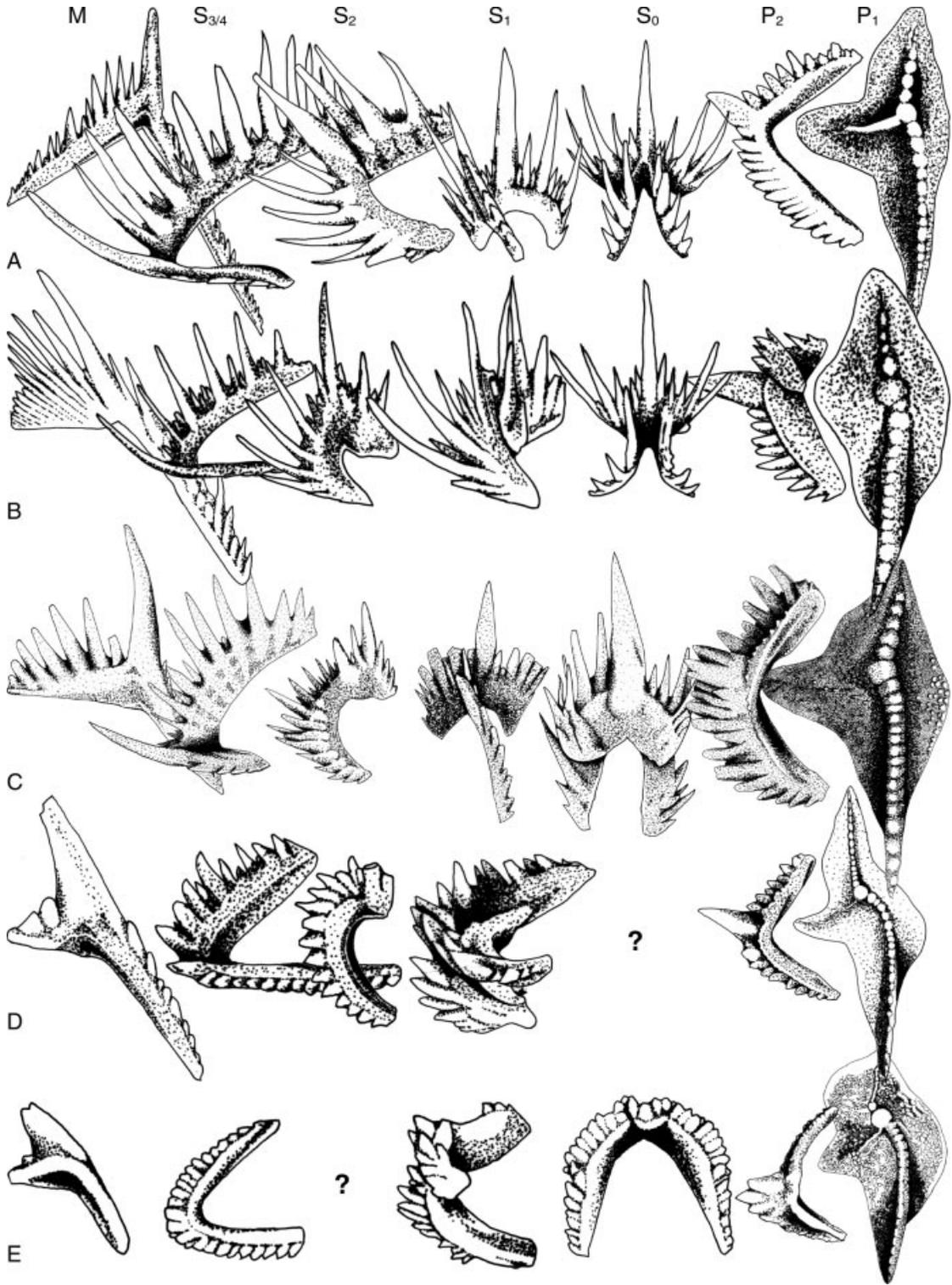
terms). Thus, these elements are of pastinate morphology. The 'lateral' process is represented either as a carina, a groove in the aboral surface, or both.

2. P_1 platform: absent (0), present (1). This character refers to the presence or absence of an expanded oral surface in the presence or absence of a blade or carina.

3. P_1 free blade ('inner'): absent (0), present (1). A free blade exists if the ventral ('anterior') process of an element does not exhibit platform development. This character refers only to the 'inner' surface which is the concave surface when the dorso-ventral ('anterior'–'posterior') axis of an element is bowed.

4. P_1 lobe: absent (0), present (1). A lobe is a 'lateral' process flanked by flanges or platforms.

5. P_1 offset in D-V axis: absent (0), present (1). This character refers to the sinusoidal trend of the dorsal and ventral processes of the P_1 of many taxa currently assigned to the genus *Palmatolepis*.

6. P_2 platform: absent (0), present (1). As character 2.

7. P_2 free blade: absent (0), present (1). As for character 4, except that this character pertains to either the 'inner' and/or 'outer' surface of the ventral blade.

8. P_2 'lateral' process: absent (0), present (1).

9. S denticulation: fused at base (0), round and fused at tip (1), fine and fused at tip (2).

10. En echelon arrangement of denticles along $S_{0,1,2}$ elements: absent (0), present (1). This pertains to a pattern of denticulation in which the denticles occur in sets of three, arranged in parallel, but tangential to the long axis of the subtending process.

11. S incipient type iii growth: absent (0), present (1). This refers to the patterns of growth described by Donoghue (1998). Although the data have not been obtained through histology, existing work indicates that such patterns of growth are manifest in the pattern of denticulation in which intercalary denticles are vestigial.

12. S_0 caudal process: absent (0), present (1). This character refers to the presence or absence of the process traditionally termed 'posterior'.

13. S_0 horizontal caudal process: absent (0), present (1).

14. S_0 rostral processes: absent (0), present (1). This character refers to the presence or absence of primary or secondary processes that are rostrad in orientation or alignment relative to the cusp.

15. S_0 rostral processes: absent (0), primary (1), secondary (2). Pertaining to whether rostral processes, where present, branch directly from the cusp (primary) or from a distinct process which branches from the cusp (secondary).

16. S_0 bears distinct cusp: absent (0), present (1).

17. S_0 process displacement: absent (0), present (1). This character pertains to a rostral flexure of the abaxial ('lateral') processes immediately adjacent to the cusp followed by caudally-directed recurvature of the distal ends, such that the elements exhibit a broadly m-shaped outline when viewed from the dorsum.

18. S_1 'posterior' process: absent (0), present (1).

19. S_1 abaxial 'lateral' process: absent (0), present (1).

20. S_1 adaxial 'lateral' process: absent (0), present (1).

21. S_1 rostral processes 'posteriorly' recurved: absent (0), present (1). Pertaining to whether or not the 'anterior' process (where present) is curved to eventually face 'posteriorly'.

22. S_2 'posterior' process: absent (0), present (1).

23. S_2 'anterior' process: absent (0), present (1).

24. S_2 'lateral' process: absent (0), present (1).

25. S_2 vestigial 'lateral' process: absent (0), present (1).

26. $S_{3,4}$ prominent cusp: absent (0), present (1).

27. $S_{3,4}$ morphology: standard bipennate (0), reduced bipennate (1). Pertaining to whether the elements occupying S_{3-4} apparatus positions possess rostrad and caudad processes which are strongly unequal in length (standard bipennate) or approximately equal in length (reduced bipennate).

28. $S_{3,4}$ 'anterior' process: ventrally directed (0), ventro-caudal (1). Pertaining to whether the rostral processes of the S_{3-4} elements are orientated in a dominantly ventral or caudal orientation at their extremity.

TEXT-FIG. 4. Morphology of elements filling the principal apparatus positions (right to left: P_1, P_2, S_0, S_1, S_2, S_{3-4}, M). A, *Palmatolepis quadrantinodosalobata* (based on Metzger 1994); S_0 in caudad view, P_2 in rostrad view. B, *Palmatolepis rugosa* (illustration from Dzik 1991, reproduced with permission); S_0 and P_2 in rostrad view. C, *Palmatolepis schindewolfi* (based on Metzger 1994); S_0 and P_2 in rostrad view. D, *Palmatolepis subgracilis* (based on Metzger 1994); S_0 in caudad view, P_2 in rostrad view. E, *Palmatolepis winchelli* (based on van den Boogaard and Kuhry 1979; illustration from Dzik 1991, reproduced with permission); S_0 in rostrad view, P_2 in caudad view. F, *Palmatolepis wolskae* (based on Metzger 1994); S_0 and P_2 in rostrad view.

TABLE 1. Data matrix used in the phylogenetic analysis. See text for character descriptions.

	000000000 123456789	1111111111 0123456789	2222222222 0123456789	3333333 0123456
Mehlina gradata gradata	001000102	00100?1010	0111001000	1000000
Polygnathus xylus xylus	011000102	00110?1010	0001001000	1000000
Mesotaxis asymmetricus asymmetricus	011001102	00110?1001	0001101000	1010000
Palmatolepis bogartensis	111111102	000?121101	1001111010	1011101
Palmatolepis deliculata deliculata	111111?02	010???0?0?	??011?1010	0111111
Palmatolepis falcata	110011101	000?111???	??01101010	111????
Palmatolepis gracilis	011111111	000?121?01	1001111010	1011111
Palmatolepis loba	110111100	000?111?01	1001101011	0111111
Palmatolepis minuta minuta	111111112	000?121?01	1001101010	1111111
Palmatolepis muelleri	111111100	000?121101	1001111011	0111111
Palmatolepis perlobata maxima	110111001	11?????01	1111000110	01111?1
Palmatolepis perlobata perlobata	110111001	110?0?0101	11????0110	0111111
Palmatolepis quadrantinodosalobata	111111102	000?110???	??01111010	1011111
Palmatolepis rugosa	110111001	010?120101	1111001110	0111101
Palmatolepis schindewolfi	110111001	110?0?0101	11????1110	0111111
Palmatolepis subgracilis	101000102	000?111?01	1001101010	1111111
Palmatolepis winchelli	111111102	000?121101	1001111010	1111111
Palmatolepis wolskae	110111001	01????0???	??00101110	0??????

29. S_{3-4} single intercalary denticles: absent (0), present (1).
30. S_{3-4} multiple intercalary denticles: absent (0), present (1).
31. M denticle orientation: erect (0), rostral (1). This character pertains to whether the denticulation is orientated perpendicularly (or approximately so) to the basal margin of the element (erect) or else, inclined subparallel to the basal margin of the element (rostral).
32. M lacks rostral: absent (0), present (1). This character refers to the presence or absence of a rostral process.
33. M 'anterior' process: twisted (0), straight (1).
34. M recessive basal margin: absent (0), present (1).
35. M rostral denticles > caudal denticles: absent (0), present (1).
36. M 'inner-lateral' process: absent (0), present (1).

Search techniques

Cladistic analyses were carried out using HENNIG86 (Farris 1988), PAUP 3.1.1 (Swofford 1993) and PAUP* 4b4a (Swofford 1999); results of the PAUP-based analysis are presented herein. Character evolution was resolved using MacClade 3.0 (Maddison and Maddison 1991). All characters were unweighted and unordered in preliminary analyses of the dataset. A paraphyletic outgroup composed of *Mehlina gradata* and *Polygnathus xylus xylus* (with *M. gradata* as the principle outgroup taxon in HENNIG86 analyses) was used to root the tree(s). It should be noted, however, that repetition of the experiments using consensus and monophyletic outgroups had no effect upon the topology of the ingroup. Bremer support values were calculated for each of the branch nodes using TreeRot (Sorenson 1996), and bootstrap values were calculated using PAUP*4b4a (1,000,000 'fast' heuristic search option); these values are present adjacent to the node to which they relate.

In all instances, results arrived at from an initial unweighted analysis of the dataset were subjected to *a posteriori* reweighting (equivalent to the successive weighting technique of Farris 1969). This technique assigns a weight to each character proportional to how the character performed in the primary analysis. Thus, characters that exhibit a relatively high degree of fit with the tree(s) produced in the primary analysis (and are therefore assumed to carry more phylogenetic information than those that do not) are assigned high weightings. Conversely, characters exhibiting poor fit to the original tree(s) are assigned relatively

low weights or no weight; where characters are assigned no weight they are essentially excluded from analysis. Although *a posteriori* reweighting is conventionally assumed to be a method for choosing between multiple most-parsimonious trees (e.g. Carpenter 1988), the prime objective of this technique is to test character consistency and character support for the original solution. If a dataset includes many characters that exhibit a poor degree of fit to the primary most-parsimonious tree(s), *a posteriori* reweighting will result in many characters with low weights; subsequent analysis of this dataset is likely to result in more, rather than fewer trees (Kitching *et al.* 1998). Thus Platnick *et al.* (1991) and Goloboff (1993) have argued that parsimony analysis requires *a posteriori* weighting to achieve self-consistent results, even if the primary analysis using equal weights produced a single most-parsimonious tree. Platnick *et al.* (1996) have argued further, that analysis using equal weights can only be considered a preliminary and crude estimate of the relative value of the data. In short, the effect of *a posteriori* reweighting is that characters are given the weights that they deserve.

Results and experimental analysis of the dataset

An initial analysis included only members of the ingroup in a search for an unrooted network. Excluding non-palmatolepid taxa from the analysis rendered 14 characters uninformative (2, 6, 12, 13, 17–20, 23, 28, 32–34, 36), and yielded two equally most-parsimonious networks, the consensus of which (Text-fig. 5A) supports a view that the genus *Palmatolepis* constitutes a monophyletic clade. *A posteriori* reweighting and subsequent analysis yielded the same two trees. Including all 18 terminal taxa in a search for an unrooted network rendered two characters uninformative (13, 23), and yielded two equally most-parsimonious unrooted networks, the consensus of which (Text-fig. 5B) supports a monophyletic Palmatolepidae and *Palmatolepis*, and the suitability of *Mehlina gradata* and *Polygnathus xylus xylus* as outgroup taxa.

Rooting the ingroup (Palmatolepidae) on *Mehlina gradata* and *Polygnathus xylus xylus* yielded two equally most-parsimonious trees (CIe = 0·6481; RI = 0·8137; tree length 56 steps) that differ in the relative arrangement of *Palmatolepis minuta minuta* to two terminal clades; the strict consensus of these trees is figured in Text-figure 6A. *A posteriori* reweighting had no effect upon tree topology.

Tree statistics (Text-fig. 6A–B) indicate that many of the nodes are poorly supported. Nevertheless, monophyly of the Palmatolepidae is supported by both high bootstrap and Bremer Support values, as is monophyly of taxa currently assigned to the genus *Palmatolepis*. The only other clades that have good statistical and character support are those composed from the terminal taxa previously assigned to the subgenus *Palmatolepis* (*Palmatolepis*) (see Text-fig. 9 for details of character changes).

Comparison with established phylogenies

Competing phylogenetic schemes stem from the work of Müller (1956*b*); the most comprehensive recent summary of the state of knowledge was published by Helms and Ziegler (1981), and so it was decided to employ this as the stratophenetic comparator. In order to compare the results of cladistic and stratophenetic analyses of the relationships of palmatolepids, an experiment was conducted that implemented a constraint tree summarising the relationships of taxa proposed by Helms and Ziegler (1981).

It is worth noting at this point that the results of cladistic and stratophenetic analysis are not directly comparable. Stratophenetic analysis results in the establishment of a phylogenetic hypothesis that incorporates assumptions of time and ancestry in its formulation; cladistics (phylogenetic systematics) makes no such assumptions. In constructing constraint trees it was necessary, therefore, to translate ancestral taxa into sister-taxa, and hard polytomies into soft polytomies. Where an individual taxon is interpreted as ancestral to a number of descendent taxa through separate evolutionary events and to have outlasted these more derived taxa, the clade is represented as an unresolved (soft) polytomy.

Implementation of a constraint tree for the hypothesis of relationships presented by Helms and Ziegler (1981; Text-fig. 6C) and analysis using PAUP's branch-and-bound search option (outgroup composition as before) yields 15 equally most-parsimonious trees (CIe = 0·5469; RI = 0·7157; 66 steps; Text-fig. 6D). *A posteriori* reweighting had no effect upon tree topology.
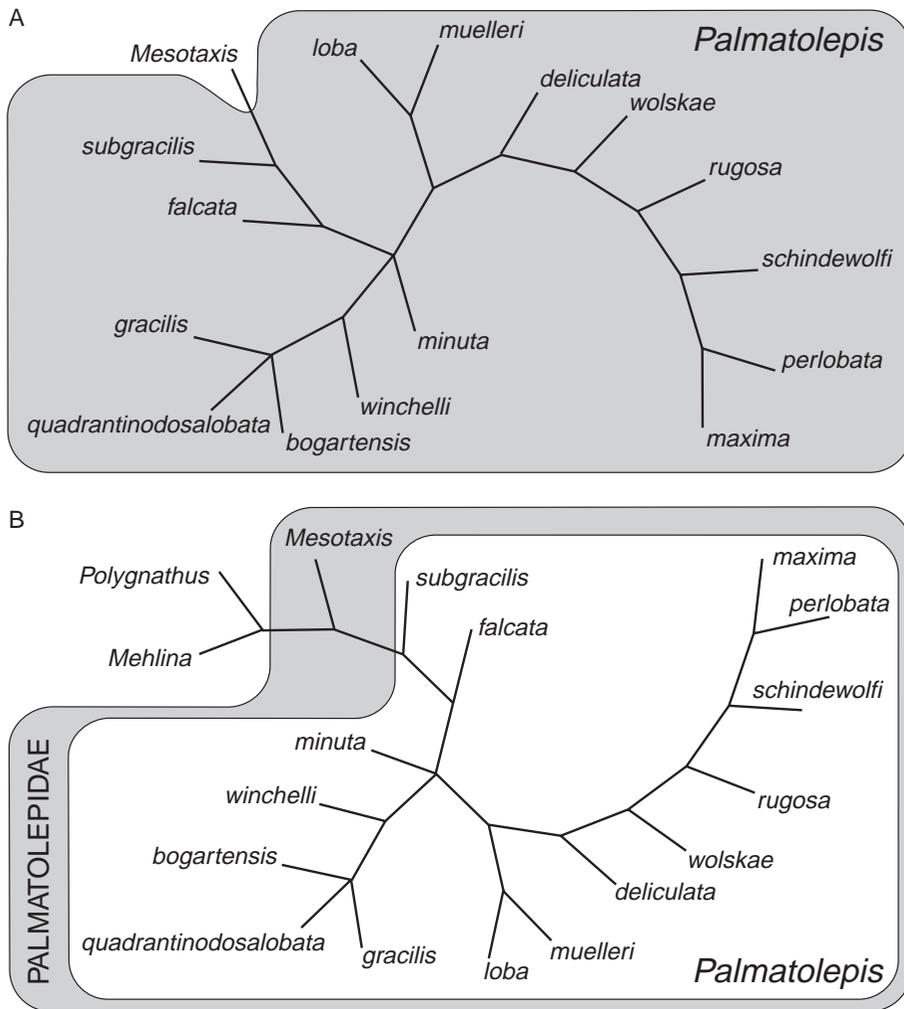
TEXT-FIG. 5. A, unrooted network for ingroup taxa only. B, unrooted network for ingroup and outgroup taxa.

Discussion

The most-parsimonious solution found when the Helms and Zeigler (1981) constraint tree is imposed is significantly longer than the shortest tree found in the absence of constraints (66 versus 56 steps, or over 17 per cent longer). However, in itself this is neither a criticism of the hypothesis of relationships derived from the unconstrained cladistic analysis, nor a criticism of the phylogeny established by Helms and Ziegler (1981). Resolving which tree is closer to the true tree depends largely upon the importance of stratigraphic data.

The importance of stratigraphic data depends largely upon the completeness of the fossil record, which itself depends upon sampling density. In the study of a hypothetical evolutionary lineage, Fortey and Jefferies (1982) determined that the likelihood of stratigraphic order correctly reflecting phylogenetic order increases in hand with sampling density. They concluded, therefore, that morphology alone is most effective in low sampling density/low completeness, and that stratigraphic data becomes an increasingly important corroborative test of relationships as sampling density/the quality of the fossil record increases.
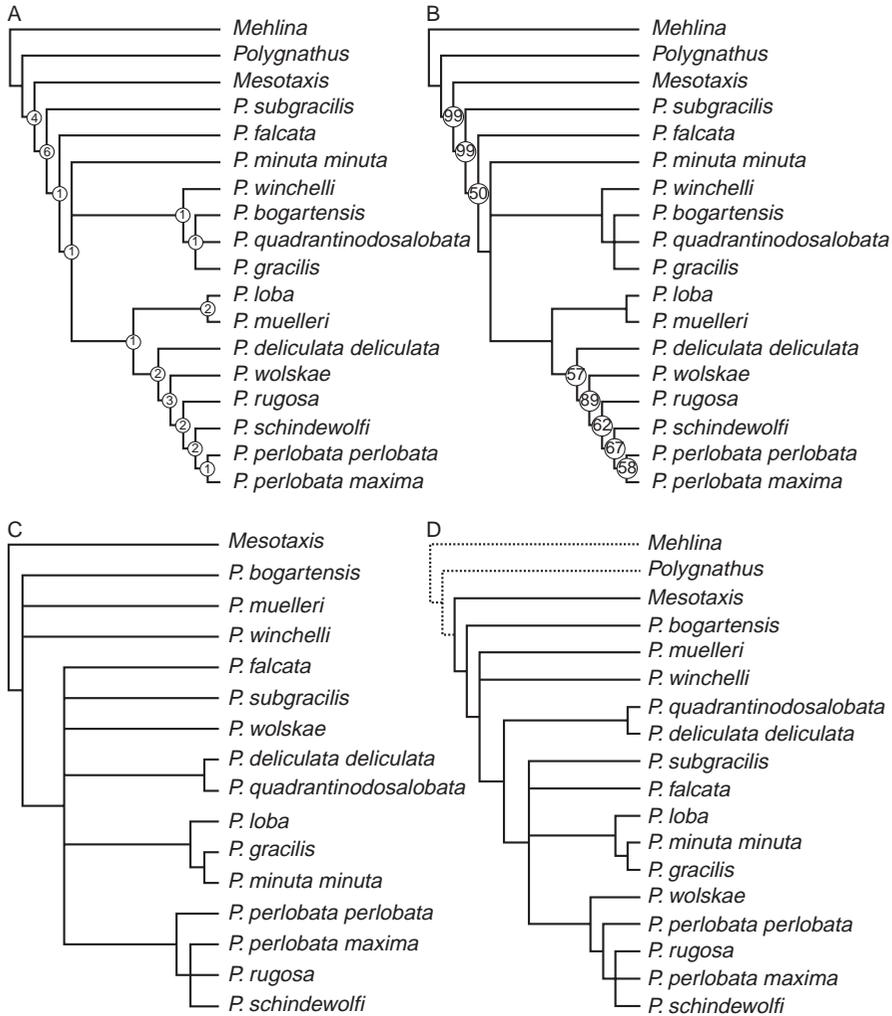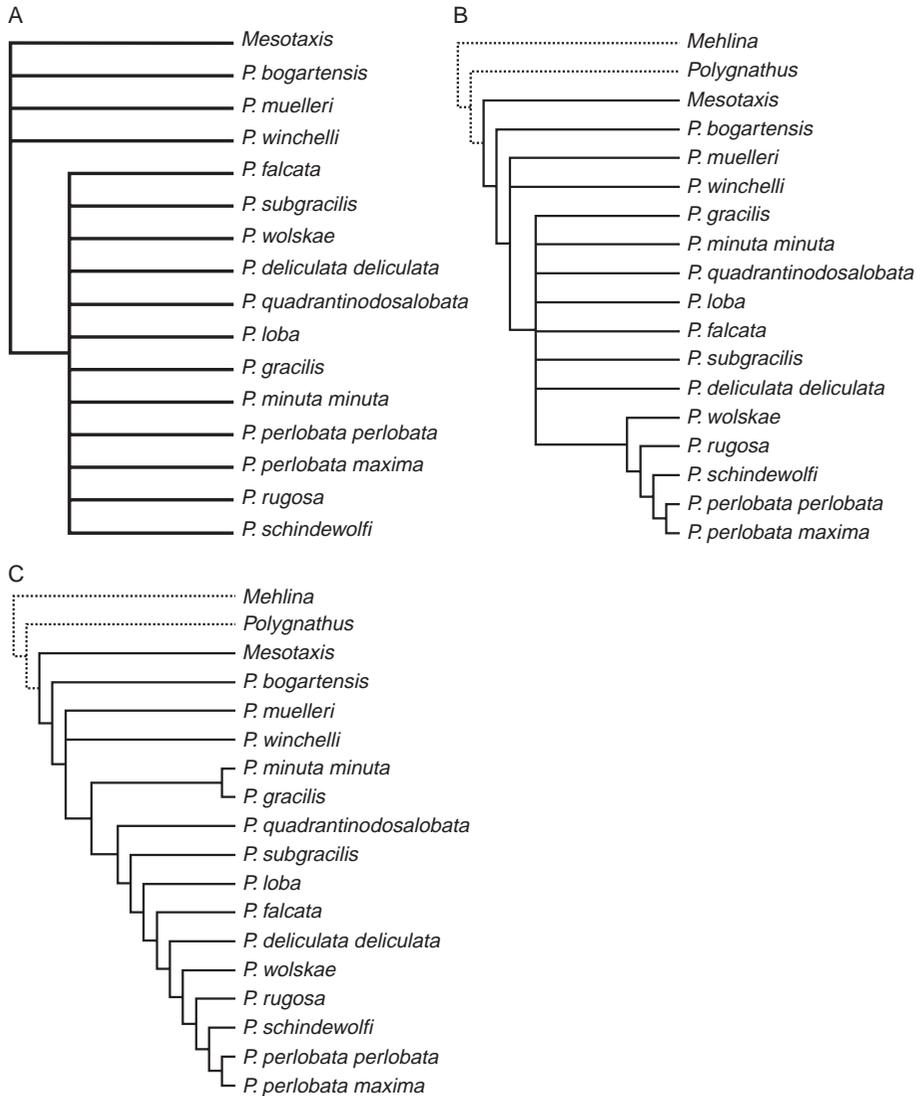
TEXT-FIG. 6. A–B, strict consensus tree of two equally most parsimonious trees. A, Bremer Support values. B, bootstrap values (50% majority rule). C, constraint tree summarising a hypothesis of relationships presented by Helms and Ziegler (1981) for taxa included in this analysis. D, single most-parsimonious solution when Helms and Ziegler (1981) constraint tree is enforced as a backbone constraint.
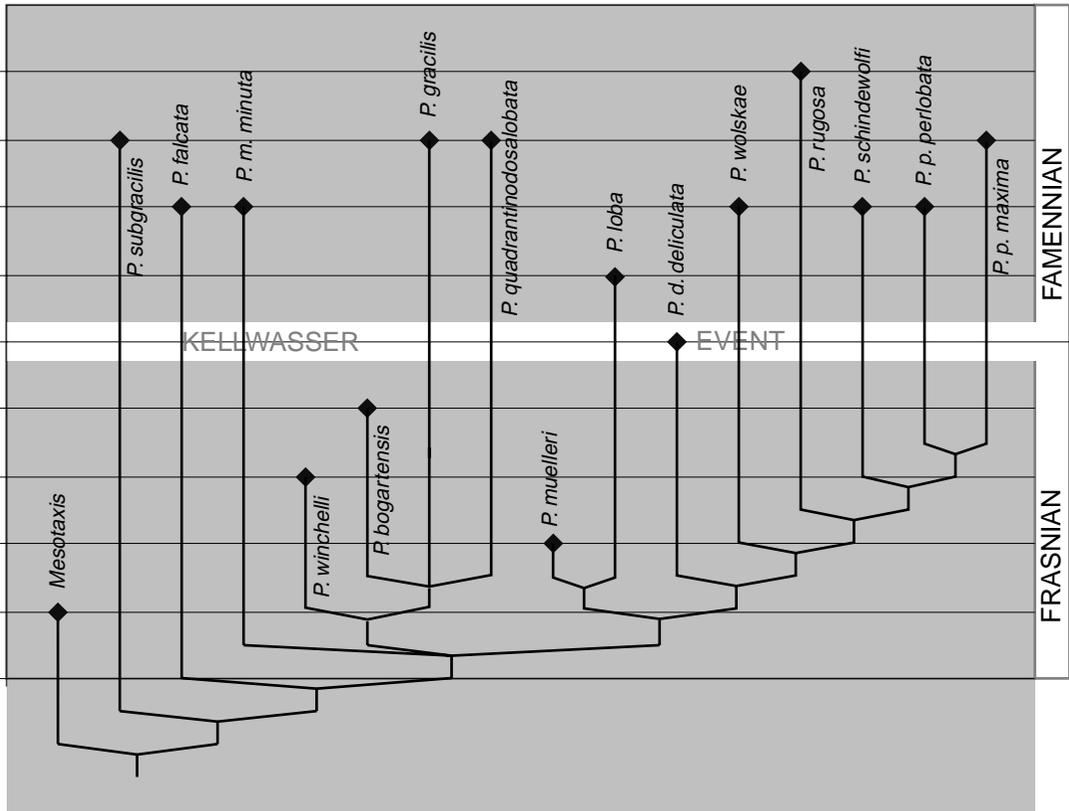
TEXT-FIG. 7. Correlation of rank age against the hypothesis of relationships presented in Text-figure 6A–B.

These conclusions have since been tested in simulation studies (Huelsenbeck and Wagner 1996) which suggest that phylogenetic hypotheses constructed using stratigraphic data are often as accurate or more accurate than estimates ignoring stratigraphic data, particularly when taxon sampling densities are high.

In this instance we know that taxon sampling density is low because only 16 palmatolepids are included in the analysis, whereas there are approximately 127 palmatolepid operational taxonomic units currently deemed taxonomically valid. The stratigraphic ranges of individual taxa are therefore likely to be of little use in constraining hypotheses of relationship. However, the importance of stratigraphic data depends also upon what kind of data are available, and what these data are to be used for. Masked behind the stratigraphic range of the individual taxa included in this analysis is a signal that becomes clear only when the stratigraphic ranges of all known palmatolepids are considered. During the 'Kellwasser', or Frasnian–Famennian extinction event, conodont diversity is believed to have crashed to such an extent that the group almost became extinct. Amongst the casualties were the palmatolepids that had flourished from their initial divergence in the mid-Givetian–early Frasnian, until immediately prior to the event. Only one palmatolepid species, *Palmatolepis triangularis*, is considered to have survived the event, but by the early Famennian, rapid post-event diversification led to unprecedented levels of diversity (Ziegler and Lane 1987; Aldridge 1988). The reality of this extinction event, corroborated by its effect upon other groups of conodonts as well as other fossil groups, provides an important test of the unconstrained tree (it does not provide a test of the constrained tree that incorporates these data *a priori*) as it suggests that all Famennian representatives of the Palmatolepidae share a common ancestor with, or in *P. triangularis*, and are thus more closely related to each other than to any other Givetian or Frasnian palmatolepid. The test

TEXT-FIG. 8. A, constraint tree summarising the relationships of taxa relative to the Frasnian–Famennian extinction event. B, strict consensus tree of 37 equally most-parsimonious solutions to the constraint tree figured in A. C, consensus of two equally most-parsimonious trees arising from two rounds of *a posteriori* reweighting of the dataset while the Frasnian–Famennian constraint tree figured in A is enforced.

requires that post-event taxa do not appear plesiomorphic relative to taxa that were in existence prior to the event; the unconstrained analysis fails the test because three of the most plesiomorphic members of the clade are Famennian (*Palmatolepis subgracilis*, *P. falcata*, *P. minuta minuta*) while many more derived taxa are restricted to the Frasnian (*Palmatolepis bogartensis*, *P. muelleri*, *P. winchelli*; Text-fig. 7). It is possible to determine the shortest tree compatible with the test by subjecting the dataset to parsimony analysis while enforcing a backbone constraint tree compatible with the hypothesis that all Famennian palmatolepids are more closely related to each other than to any earlier palmatolepids (Text-fig. 8A). The 37 equally most-parsimonious solutions are four steps longer than the shortest tree resulting from

unconstrained analysis (CIe = 0·6034; RI = 0·7745; 60 steps; Text-fig. 8B). Two rounds of *a posteriori* reweighting yielded two equally most-parsimonious trees (CIe = 0·6708; RI = 0·8314; 42·47143 steps; Text-fig. 8C); further rounds of reweighting had no effect upon tree topology or statistics. This result is also significantly shorter than the shortest tree(s) found while the Helms and Ziegler (1981) constraint tree was enforced, but even the Helms and Ziegler (1981) tree is preferable to the result of the unconstrained analysis as it does not violate the Kellwasser Event test.

Is the Kellwasser Event test fallible? The importance of this test rests with the validity of the hypothesis that all Famennian species of the genus *Palmatolepis* derived from *Palmatolepis triangularis* (or *Palmatolepis praetriangularis*), the only species to survive the extinction event. The result of the unconstrained analysis (Text-figs 6A–B, 7) could still be closer to the true tree if Famennian palmatolepids derived from more than one survivor and, thus, share a latest common ancestor that did not survive the Frasnian. In this way, species that first appear in the Famennian could appear cladistically primitive with respect to Frasnian taxa. Contrary to the popular view, records of three other Frasnian palmatolepids [*Palmatolepis hassi*, *P. winchelli* (*sensu* Klapper and Foster 1993) and *P. bogartensis*] persist into the Famennian Early *triangularis* Zone (e.g. Schülke 1995). Furthermore, palmatolepid biofacies are not represented amongst 'classic' Kellwasser Event sections due to a eustatic sea-level fall during which deep-water neritic palmatolepid-polygnathid biofacies are replaced by shallow-water polygnathid-icriodid biofacies (e.g. Girard and Feist 1997). Unfortunately, the multielement composition of *Palmatolepis triangularis* is unknown and so it is not possible to test cladistically the relationship of this taxon to exclusively Famennian palmatolepids.

Statistical and character support in the contentious part of the tree is insufficient (Text-fig. 6A–B) to reject outright the hypothesis of relationships supported by stratigraphic data. Nevertheless, the tree derived solely from morphological data is deemed preferable as it provides a basis for separating distinct sources of data. Thus, hypotheses of relationships can be used to test the completeness of the conodont fossil record without recourse to circular reasoning. Similarly, stratigraphic data can be used to test hypotheses of relationships and construct phylogenies. For this reason, the results of the morphology-only (unconstrained) analysis are used as the basis for examining character changes throughout the palmatolepid feeding apparatus. However, in recognition of the relatively poor statistical and character support in the contentious portion of the consensus tree (Text-fig. 6A–B), the differing implications for character evolution implied by the stratigraphically-constrained tree (Text-fig. 7) are also summarised below.

Homoplasy

As it is widely assumed that the fossil record of many micropalaeontological groups exhibits patterns of iterative evolution (e.g. Sweet 1988) and, thus, high levels of homoplasy either stated explicitly or implied, it is pertinent to consider the level of homoplasy inferred from the results of the cladistic analyses described above. In a classic study of the factors influencing tree statistics in cladistic analysis, Sanderson and Donoghue (1989) found that the standard measure of homoplasy, the consistency index (which is inversely proportional to homoplasy), is negatively correlated with the number of taxa, though not the number of characters, included in a cladistic analysis. From their dataset, Sanderson and Donoghue (1989) were able to resolve a predictive formula for the consistency index where

$$CI = 0 \cdot 90 - 0 \cdot 022 \text{ (number of taxa)} + 0 \cdot 000213 \text{ (number of taxa)}^2$$

and so for the cladistic analyses undertaken herein, the consistency index would be expected to approximate 0·573012. This is significantly less than the value for the morphology-only (unconstrained) most-parsimonious trees (0·6481), the most-parsimonious trees consistent with the Kellwasser Event backbone constraint (0·6034), and only slightly higher than the consistency index for the most-parsimonious trees consistent with the Helms and Ziegler (1981) backbone constraint tree (0·5469). Thus, the conodont fossil record exhibits no more, and possibly much less, homoplasy than that expected, based upon the number of taxa included in the analysis.

Character changes

As Dzik (1991*b*, p. 306) has noted, although the 'evolution of the palmatolepidid sp [P_1] elements has been extensively studied . . . the pattern of evolutionary transformations in the rest of the apparatus remains largely unknown'. The potential of numerical cladistics to resolve such patterns is unrivalled, not only because of its ability to cope with vast amounts of data in resolving relationships, but also in its ability to trace evolution of all these data *a posteriori*. Character change trees such as Text-figure 9B are invaluable in construction and/or testing of hypotheses. One such hypothesis contends that the conodont feeding apparatus was 'functionally integrated' (Aldridge *et al*. 1987 and many subsequent authors) and Dzik (1991*b*) has argued that the palmatolepid apparatus represents the very acme of sophistication. A prediction of such a functional-integration model would be coordinated character change, the recognition or rejection of which would represent an important advance not only for functional morphology but more practically, for character coding in future cladistic analyses where character independence should be an *a priori* assumption (e.g. Emerson and Hastings 1998).

Surprisingly, there appear to have been relatively few major changes in P_1 element morphology during palmatolepid evolution. Characters diagnostic of the genus *Palmatolepis* evolved progressively rather than coincident with the origin of the genus. In particular, although the P_1 elements of all species of *Palmatolepis* possess three processes, the palmatolepid lobe is resolved as the synapomorphy of a subclade of the genus, rather than a synapomorphy of the entire clade. The origin of the third, lateral process in the P_1 position represents a significant increase in platform surface area, concentrated in a rostral orientation at the same time that the caudad extent of the rostrally positioned S elements was being reduced.

Although less characteristic of the Palmatolepidae and the genus *Palmatolepis* itself, changes in the organisation of the S and M elements are perhaps more radical than the establishment of palmatolepid P_1 element morphology. The primitive condition in the outgroup comprises an array of bipennate elements in which the processes are arranged in a rostrad and caudad orientation relative to the cusp. Subsequent changes are first expressed in the apparatus of *Mesotaxis* where the S_1 element is strictly of modified digyrate morphology based on the disposition of processes relative to the cusps even though in outline it strongly resembles the bipennate S_1 elements of *Polygnathus* and *Mehlina*. Even the most plesiomorphic species of *Palmatolepis* included in this analysis exhibit a fundamental re-organisation of the S array in which the caudal process of the S_0 has been lost and at the same time, displacement of the lateral processes around the cusp of this element first appears. Through subsequent phylogeny, changes in element morphology sweep out from the axis to the S_4 and M elements. Concomitant with changes in the morphology of the S_0 element, processes on the S_1 element became more strongly lateral in their disposition relative to the cusp, and progressively more derived palmatolepids exhibit a shift from bipennate to digyrate S_2 elements and eventually, shortening of the caudal processes of bipennate S_3 and S_4 elements, and of the rostral processes of modified digyrate M elements.

The branch subtending all species of the genus *Palmatolepis* is interesting because it is supported by a proportionally high number of synapomorphies. There are a number of potential explanations for this: it could indicate that the *Palmatolepis* apparatus plan was established in one event, or that it was established gradually in a sequence of changes that are not detectable in this analysis because many of the putatively plesiomorphic members of the genus have not been included (because their apparatus composition is unknown). The first hypothesis is supported by evidence of gradual apparatus overhaul from the pattern of element remodelling abaxially from the S_0. However, it is possible that some of the character changes are correlated, such as loss of the caudal process on the S_0 element in *Palmatolepis*, requiring flanking elements with lateral rather than rostro-caudally disposed processes. It is worth noting that in all those taxa sharing the ozarkodinid bauplan (see Purnell and Donoghue 1997, 1998; Purnell *et al.* 2000) in which the S_0 lacks a caudal process, flanking S elements are of modified digyrate rather than bipennate morphology, and that this appears to be the plesiomorphic condition for ozarkodinids. If not a reflection of common ancestry, it is likely that these character changes are indeed correlated, presumably for functional reasons. Unfortunately, our understanding of how ozarkodinid S elements functioned is restricted to informed speculation and so the significance of these character changes remains equivocal. However, Purnell and Donoghue (1997) have suggested that the S_0 element was integral to the function of the apparatus, and they

speculated that it functioned in transferring food particles from the 'grasping' S elements to the shearing and crushing P elements. In this model, the caudal process of the S_0 could have provided leverage in rotating the element caudo-ventrally. It is possible that loss of a caudal process on the S_0 in *Palmatolepis* is linked to functional integration of the S_0 and adjacent S elements. The morphology of the S_1 elements remains reminiscent of polygnathaceans, where the orientation of the processes suggests that this element wrapped around the S_0 element allowing the S_0 free passage in rostral and caudal directions; thus, integration appears a likely hypothesis. Remodelling of the $S_{1,2}$ elements so that their processes were directed laterally rather than in rostral and caudal directions possibly obviated the need for the S_0 caudal process, or it is even possible that the modified digyrate elements in $S_{1,2}$ positions precluded an S_0 caudal process for functional and/or spatial reasons. It is also possible that loss of the S_0 caudal process is linked to wholesale rostro-caudal shortening of the ramiform array; however, given such a scenario we might expect progressive reduction of the S_0 caudal process rather than elimination in one step.

Patterns of character change are also important as they provide the ultimate test of hypotheses of homology (e.g. Patterson 1982; de Pinna 1991). For example, it has long been assumed that primary and secondary processes represent separate classes of morphological structures and this distinction has been exploited in systematics, even though distinction between the two can be entirely arbitrary. The results of this analysis would appear to contradict this practice. For instance, the rostral processes on the S_0 element constitute a symplesiomorphy of the genus *Palmatolepis* (absence of these processes in *Palmatolepis schindewolfi*, *P. perlobata perlobata* and *P. p. maxima* is a derived condition) and their homology is corroborated (i.e. it is a phylogenetically consistent hypothesis of homology) even though they are primitively secondary and secondarily primary. The current definition of a secondary process is 'a branch of a primary process' (Sweet 1981, p. W67); if primary and secondary processes can be homologous, as has been demonstrated in this analysis, we must revise our concepts of homology-recognition between element morphologies. Indeed, the implication of such a hypothesis of homology between a primary and a secondary process is that quite independently of the morphogenetic basis of element growth (*sensu* Donoghue 1998) the patterning of element development can be further reduced to a number of building blocks. In this instance, such a unit correlates with an individual process and the position of that process relative to the cusp is of little consequence. While this need not be the case in all instances, it is important that future attempts at resolving conodont interrelationships should bear this in mind.

Finally, it is pertinent to consider the differing implications for character evolution implied by constrained (Text-fig. 9A) *versus* unconstrained analysis (Text-fig. 9B). For putatively derived taxa to appear relatively plesiomorphic in unconstrained analysis obviously indicates that the taxa in question are most closely comparable to the outgroup. Some of the most significant differences in character change affect the origin and evolution of S_0 rostral processes which in constrained analysis evolve first as primary processes, only later switching to a secondary position. The result of constrained analysis also implies that lobe development on the P_1 element is a character uniting all species of *Palmatolepis*, rather than a specialisation of a derived sub-group of the genus. In summary, the main contrasting implications of the unconstrained analysis are that characters otherwise considered typically palmatolepid (cf. convention and the results of the constrained analysis) were acquired progressively rather than in a strictly correlated pattern.

IMPLICATIONS FOR CLASSIFICATION OF THE PALMATOLEPIDAE

Irrespective of which tree is accepted, the hypotheses of relationships presented (Text-fig. 10) have important implications for debate over the internal classification of the Palmatolepidae. The morphology-only tree (Text-fig. 10A) indicates that only one of the putative subclades (as currently conceived), the

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TEXT-FIG. 9. Character change trees. A, consensus tree resulting from parsimony analysis while enforcing Kellwasser Event backbone constraint tree. B, consensus tree based upon morphological data alone. Character changes have been optimised using ACCTRAN (accelerated transformation) in PAUP*4b4a. Solid blocks represent synapomorphies; forward arrowheads represent forward homoplasies; reversed arrowheads represent reverse homoplasies; italicised character changes are equivocal.
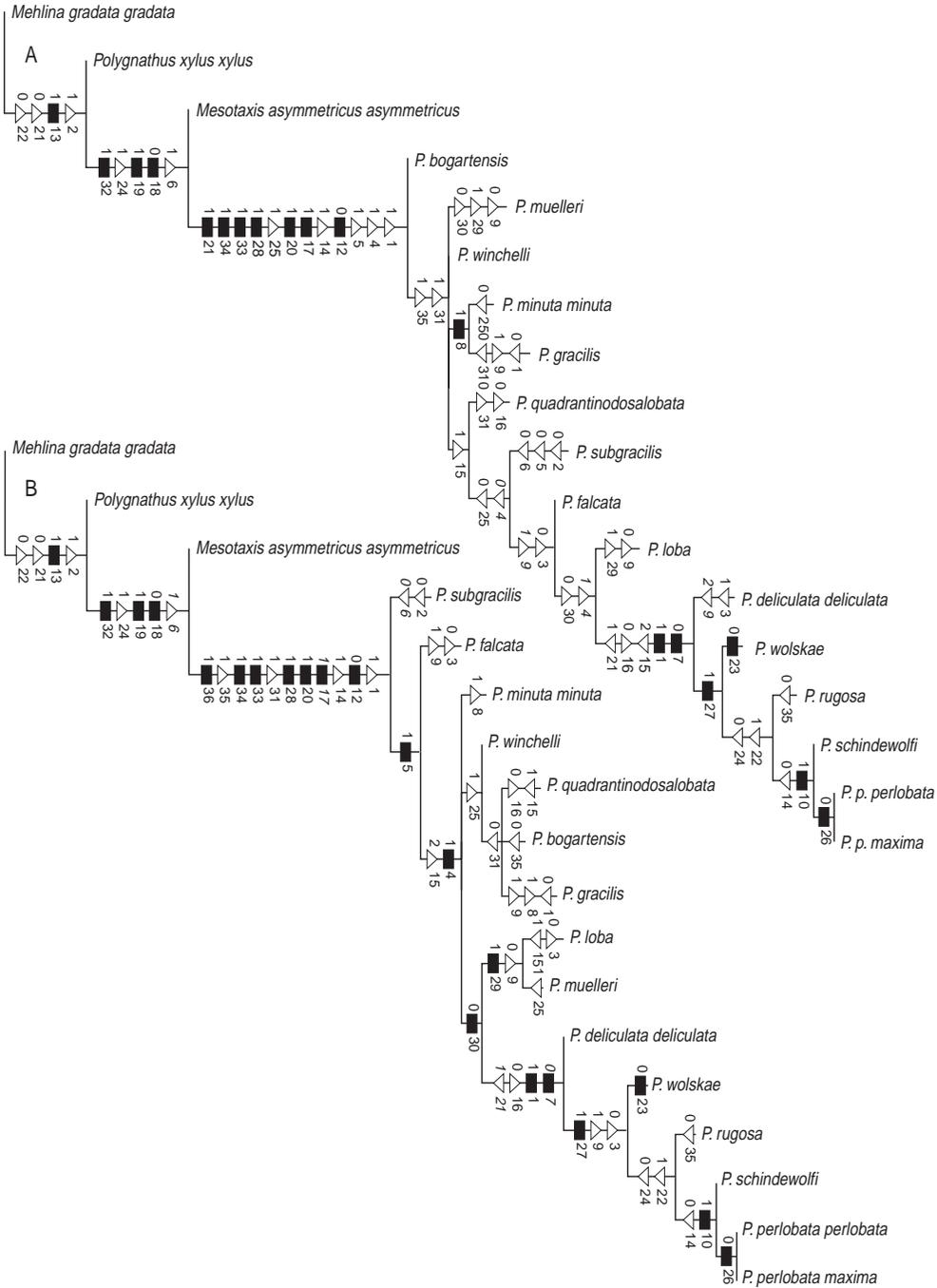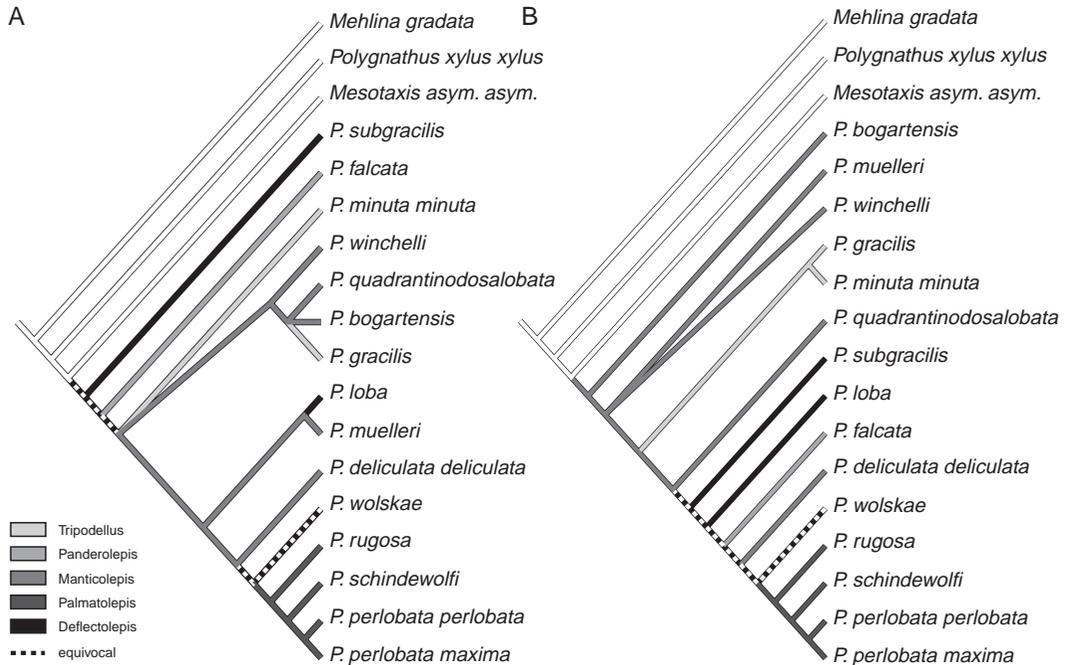
TEXT-FIG. 10. Distribution of subgeneric assignments relative to different hypotheses of relationships. A, consensus tree based upon morphological data alone. B, consensus tree arrived at while enforcing Kellwasser Event backbone constraint tree.

proposed subgenus *Palmatolepis*, constitutes a natural grouping. The remaining groups are either polyphyletic (*Tripodellus*, *Deflectolepis*), paraphyletic (*Manticolepis*), or else too few taxa are included for resolution. The tree derived from morphology plus the Kellwasser constraint reaches common conclusions except where *Tripodellus* is concerned (Text-fig. 10B). In this case, the subgenus *Tripodellus* constitutes a monophyletic clade when considered in the operational sense adopted herein, i.e. only those members of the more widely recognised clade that possess a P_2 element with three processes (the remainder of the group were retained under the subgenus *Deflectolepis* for operational purposes); *Tripodellus* in the sense of van den Boogaard and Kuhry (1979) is polyphyletic. It is therefore recommended that if any group need be recognised, in this instance, the *Tripodellus* concept should become more exclusive.

Whether or not paraphyletic subgenera should be recognised depends entirely upon the pre-disposition of the systematist undertaking revision. However, paraphyletic groups have no validity other than by convention and serve only to reinforce evolutionary scenarios and obscure relationships; they are characterised by the attributes that they do not possess rather than the characters that they do possess. Alternatively, restriction of recognised taxonomic groupings to monophyletic clades serves to aid in the communication of relationships and they are set by recognised synapomorphies rather than by convention. I have chosen, therefore, to recognise only monophyletic taxa by formal taxonomic names and I include a revised scheme of classification for the taxa included in this analysis, at the end of this contribution.

THE IMPORTANCE OF MULTIELEMENT TAXONOMY

'*gross morphology of single elements may not always be the best guide to relationship*'
Sweet (1988, p. 105)

The discovery of conodont elements of distinct morphology in natural association and the adoption of multielement taxonomy represents the greatest advance since the birth of conodontology. It provides a
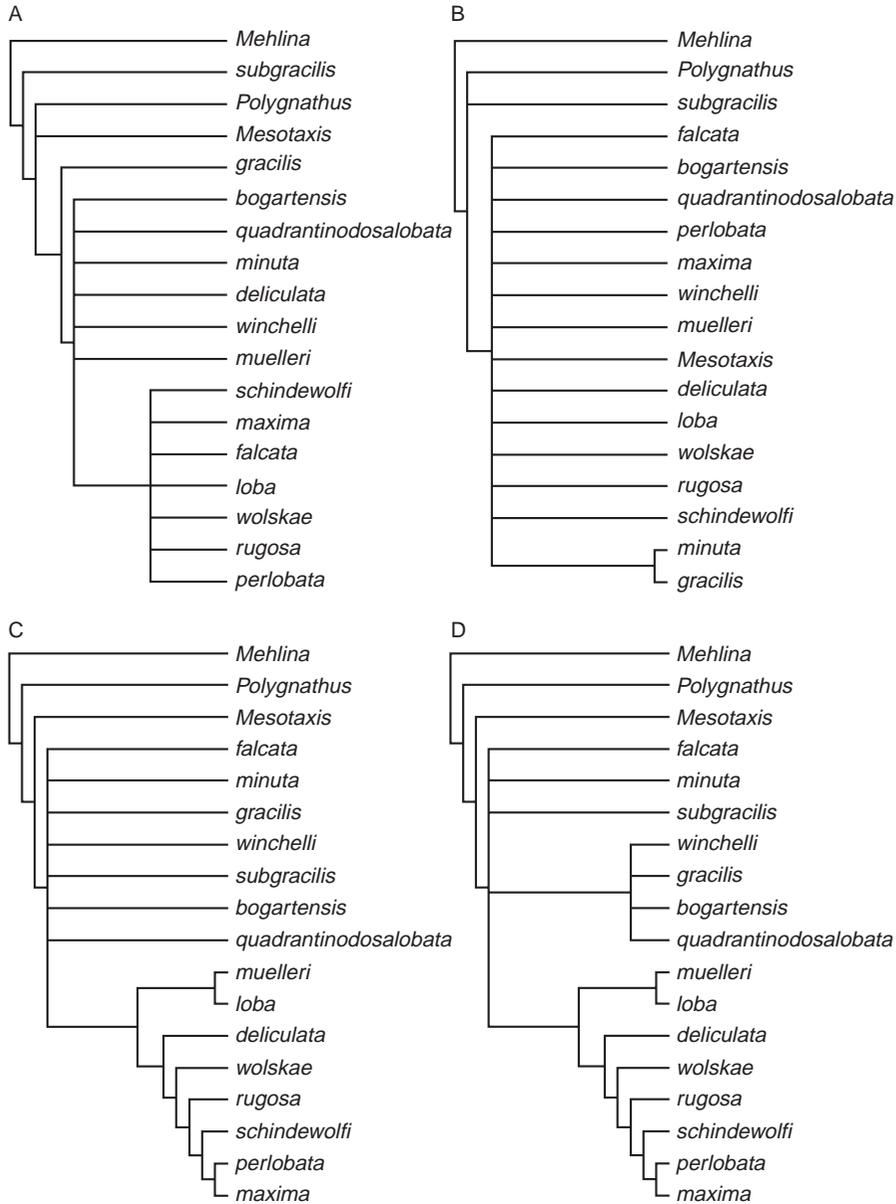
TEXT-FIG. 11. Strict consensus of trees arising from partitioned analysis of the dataset. A, when only data from P_1 elements are included. B, when only data from S elements are included. C, when only data from M elements are included. D, when data from P_1 and P_2 elements alone are combined.

basis from which to test hypotheses of relationships established on single elements, and the potential for a major (as yet unrealised) increase in the refinement of biostratigraphic schemes that are already very finely divided. Nevertheless, taxa are diagnosed almost exclusively by the characteristics of just one element position (the P_1) and it follows that characteristics of this element position should be of pre-eminent importance in taxonomy. This has been stated most explicitly by Klapper and Philip (1971, p. 439):

'Platform [P_1] elements evolved at higher rates than the more stable compound [P_2] elements and this fact is not altered by a multielement analysis. . . . A realistic taxonomy should, therefore, emphasise the evolution of the platform elements', and by Puchkov *et al.* (1982, p. 282): 'morphologic changes in the most rapidly evolving element of the apparatus should be expressed in a purposeful taxonomy that reflects the phenomenon of mosaic evolution in conodonts'. However, far from providing the basis for a total-evidence approach to conodont systematics, multielement taxonomy has served as an excuse for most conodont taxonomists to ignore all but the element occupying by the P_1 position, under the guise of adopting a biologically valid taxonomy. The character change trees which result from this analysis corroborate the observation of mosaic evolution amongst different element positions (Klapper and Philip 1971, 1972) but they also contradict the hypothesis that there is any general ordering of the rate of evolutionary changes from P to M to S elements, as originally proposed by Merrill *et al.* (1990). To determine the relative contribution of each of the positional groups a series of analyses were undertaken of partitions of the dataset, each partition relating to different element positions. In this instance, no constraint tree was enforced and so results should be compared to the consensus and preferred trees arising from unconstrained analysis of the entire dataset (Text-fig. 6A–B). Data from elements in P_1 positions provide very little resolution (Text-fig. 11A; 1 tree; CIe = 0·7143; RI = 0·8824; 7 steps); even those nodes which are resolved do not compare favourably with the results of the entire dataset, and suggest that the taxa previously recognised as members of the ingroup do not constitute a monophyletic clade with respect to the outgroup. This supports the *a priori* decision to exclude taxa that are not known in a total or even partial multielement sense. Data derived solely from elements in P_2 positions provide even less resolution (Text-fig. 11B; 3 trees; CIe = 1·0; RI = 1·0; 3 steps). Data from elements in M positions alone provide no resolution, while data from elements in S positions resolve more nodes than data from any others (Text-fig. 11C: 66 trees; CIe = 0·6774; RI = 0·8387; 33 steps, Text-fig. 11D: 23 trees; CIe = 0·7241; RI = 0·8683; 27·29048 steps), and the topology of relationships is common to those in the consensus tree of the entire dataset (Text-figs 6A–B, 7). This is not surprising as it reflects the dataset, over half of which is composed of characters that describe the attributes of S elements. What is surprising is that so many phylogenetically informative characters could be gleaned from elements occupying S positions, elements that have been deemed by some as having evolved so slowly that they are generally useful only in resolving relationships at generic or family level. Indeed, S elements appear more use in resolving relationships at the specific level within palmatolepid conodonts than P_1 elements. Although data from S elements provide greater resolution than characters based on P elements, many of the nodes are mutually exclusive, indicating that data from both positional-groups are imperative in resolving the relationships of conodonts. Thus, even when homoplasy is rife and independent analysis of individual element positions provides little or no phylogenetic resolution, global parsimony combining data from all element positions will always perform best.

CONCLUDING REMARKS

With the reclassification of conodonts as chordates (Aldridge *et al.* 1993; Donoghue *et al.* 2000), conodont systematics now occupies the extensive mid-ground between vertebrate palaeontology, which has championed the cause of phylogenetic systematics more than any other palaeontological discipline, and micropalaeontology, which is steeped in the tradition of phylogenetic inference through stratigraphy. It is appropriate, therefore, that conodonts should contribute to the debate over the relative importance of morphology and stratigraphy to the resolution of relationships. The results of the analyses presented herein find disagreement between morphological and stratigraphic data, and provide the basis for an ongoing study to examine the effects of taxonomic and stratigraphic sampling density upon the resolution of relationships. While many biostratigraphers may balk at accepting the morphology-based hypothesis of relationships and classification presented herein, they should accept that analyses excluding stratigraphic data provide one of the few (?only) tests of stratigraphic range data. Such hypotheses are not a replacement for phylogenies that use stratophenetics as a method of phylogenetic inference, but hypotheses based on morphology alone, combined with stratigraphic data *a posteriori*, will always provide superior phylogenies. This is because they make testable predictions (such as ghost ranges), and the data and arguments on which they are based are openly presented for scrutiny and criticism.

REVISED CLASSIFICATION

The Linnean rank classification below is based upon the consensus tree derived from unconstrained analysis (Text-figs 6A–B, 7) and follows the sequencing convention of Nelson (1972). The practice of using the suffix *sedis mutabilis* to indicate areas of ignorance in relation to relative branching follows Wiley (1979).

Family POLYGNATHIDAE Bassler, 1925
  Subfamily PALMATOLEPIDAE Sweet, 1988
    Mesotaxis asymmetrica asymmetrica (Bischoff and Ziegler, 1957)
    Palmatolepis subgracilis (Bischoff, 1956)
    Palmatolepis falcata (Helms, 1959)
    Palmatolepis minuta minuta Branson and Mehl, 1934 *sedis mutabilis*
    Unnamed taxon 1 *sedis mutabilis*
      Palmatolepis winchelli (Stauffer, 1938)
      Palmatolepis bogartensis (Stauffer, 1938) *sedis mutabilis*
      Palmatolepis gracilis Branson and Mehl, 1934 *sedis mutabilis*
      Palmatolepis quadrantinodosalobata Sannemann, 1955 *sedis mutabilis*
    Unnamed taxon 2 *sedis mutabilis*
      Unnamed taxon 3
        Palmatolepis muelleri Klapper and Foster, 1993
        Palmatolepis loba Helms, 1963
      Palmatolepis deliculata deliculata Branson and Mehl, 1934
      Subgenus *Palmatolepis* Müller, 1956*b*
      Palmatolepis wolskae Ovnatanova, 1969
      Palmatolepis rugosa Branson and Mehl, 1934
      Palmatolepis schindewolfi Müller, 1956*b*
      Palmatolepis perlobata perlobata Ulrich and Bassler, 1926
      Palmatolepis perlobata maxima Müller, 1956*b*

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